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# A review of *Pseudo-nitzschia*, with special reference to the Skagerrak, North Atlantic, and adjacent waters

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ABSTRACT: The *Pseudo-nitzschia* flora of the Skagerrak, North Atlantic, and adjacent waters, comprising *P. pungens, P. multiseries, P. seriata, P. fraudulenta, P. heimii, P. delicatissima*, and *P. pseudodelicatissima*, has been examined. Except for *P. australis*, all *Pseudo-nitzschia* species shown to produce the toxin domoic acid are present in the area although an outbreak of amnesic shellfish poisoning has never been reported. For comparison of morphological and taxonomic characters, *Pseudo-nitzschia seriata* f. *obtusa, P. australis, P. subfraudulenta, P. subpacifica, P. lineola, P. inflatula*, and *P. cuspidata* have been included in this investigation. Fine details of band structure and poroid occlusions, previously ignored or unresolved, have proven to add to the morphological distinction between *P. pungens* and *P. multiseries, P. seriata* and *P. fraudulenta, P. seriata* and *P. australis*, and *P. delicatissima* and *P. pseudodelicatissima*. Additional information on the structure of the proximal mantle compared to that of the valve face has revealed similarities in most of the species but differences between *P. pungens* and *P. multiseries*. The species' seasonal and long-term distributional patterns during the sampling period (October 1978 through September 1993) in the Skagerrak area are outlined. The greatest abundances of *P. seriata*, a cold-water species most likely restricted to the northern hemisphere, occurred in the spring, and those of the presumably cosmopolitan diatoms *P. pungens, P. multiseries* and *P. pseudodelicatissima*, in the autumn. Whereas *P. multiseries* seems to have decreased in abundance in the 1990s, *P. pseudodelicatissima* has apparently increased.

## INTRODUCTION

*Pseudo-nitzschia* H. Peragallo in H. & M. Peragallo is present in inshore, offshore and oceanic plankton in all biogeographic zones (Hasle, 1972). Some diatomists follow Hustedt (1958) and classify *Pseudo-nitzschia* as a section of *Nitzschia* Hassall, whereas others give it the rank of genus as done by Peragallo & Peragallo (1900).

Recently, the genus has received much attention since several species have been implicated in outbreaks of domoic acid (DA) toxicity off the coasts of Canada and U.S.A. A bloom of *Pseudo-nitzschia multiseries* (Hasle) Hasle (as *Nitzschia pungens* f. *multiseries*) in Canadian coastal waters was shown to cause "amnesic shellfish poisoning" (ASP) in humans, through the consumption of DA-contaminated cultivated mussels (Bates et al., 1989). *Pseudo-nitzschia pseudodelicatissima* (Hasle) Hasle was regarded as the source of DA in shellfish and plankton in the Bay of Fundy, eastern Canada, in the autumn 1988, and cultures established from the area produced low concentrations of DA (Martin et al., 1990). *Pseudonitzschia australis* Frenguelli occurred in great abundance in

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Monterey Bay, California in the autumn of 1991. The occurrence was accompanied by mortalities of pelicans and cormorants, which had fed on DA-contaminated anchovies (Fritz et al., 1992). Cultures were established and *P. australis* was shown to be a DA producer (Garrison et al., 1992; Villac et al., 1993b). *Pseudo-nitzschia delicatissima* (P. T. Cleve) Heiden has been shown to produce small amounts of DA in cultures (Smith et al., 1991); recently, also *P. seriata* (P. T. Cleve) H. Peragallo has been found to produce DA in cultures (Lundholm et al., 1994). However, DA outbreaks in the field have not been traced back to either of these two species. These observations demonstrate the necessity of identification below the generic level or size-group ( *"Nitzschia seriata"* and *"Nitzschia delicatissima"* groups or complexes; Hasle, 1965a) in order to effectively monitor field distribution of dangerous species.

Records of *P. multiseries* in European coastal waters are scarce (Hasle, 1965a; Villac et al., 1993a). *Pseudo-nitzschia australis* is not known from North Atlantic waters (Hasle, 1972, Fig. 2 as *Nitzschia pseudoseriata*). Evidence exists for a wide distribution of *P. pseudodelicatissima, P. delicatissima* and *P. seriata* in North Atlantic waters (Hasle, 1965a; Hasle, 1972).

Cases of ASP have never been reported from European waters, neither had it been reported from Canadian and North Pacific waters until 1987 and 1991, respectively. The sudden outbursts of toxic blooms in other parts of the world stimulated a search for information on the distribution of *Pseudo-nitzschia* in European waters.

Access to a comprehensive collection of samples from the Skagerrak (Lange et al., 1992) gave an opportunity to examine seasonal and long-term distributions in an area influenced by water masses from the North Sea, the Norwegian Sea and the Baltic Sea. Because of better instrumentation and/or technique now available to us, information on the fine structure of *Pseudo-nitzschia* supplementary to that given by Hasle (1965a) could be obtained. Distinctive features of the genus and species are described, and the distribution of species recorded from the Skagerrak is given and compared with observations from Norwegian coastal waters.

## MATERIAL AND METHODS

The study material consisted of net hauls collected along a transect between southern Norway (58° 23′ N, 08°49′ E) and the northern part of Skagen, Jutland, Denmark (57° 42′ N, 09° 45′ E) (see Lange et al., 1992), from February 1979 through September 1993. Samples obtained prior to 1979 (May 1953, September 1966, scattered samples from May 1967 through June 1968, December 1976, October–December 1978) and from other sampling sites in the Skagerrak were also included. Samples from other parts of the world and unialgal cultures from the Trondheimsfjord, Norway (established by EES), Gulf of Mexico, the coasts of California and Washington, U.S.A. (by the courtesy of G. A. Fryxell, Texas A & M Univ.) were used for comparative, morphological studies. Additional material was examined for information on the distribution of *Pseudo-nitzschia* along the Norwegian coast, the Norwegian Sea and more southern European waters.

The distributional data represent mainly presence or absence. No effort was made, either by collection of samples or by preparation of diatom slides, to obtain quantitative data. High relative abundances of species were noted, however.

Material from the P. T. Cleve collections in Naturhistoriska Riksmuseet in Stockholm

(= S) and Friedrich-Hustedt-Arbeitsplatz für Diatomeenkunde in Bremerhaven (= BRM) has been used for lectotypification. The finder in use in the latter collection was made by Carl Zeiss and is no longer produced (Simonsen, 1987, p. 5).

Light microscope observations (LM) on uncleaned material in water mounts provided information on the shape of cells in girdle view and colony formation, but could be used only exceptionally for identification at the species level, especially when cells lay in girdle view. Phase contrast (Ph) with a Leitz Orthoplan or a Nikon Optiphot microscope, negative phase contrast (BM 100×) for especially weakly silicified structures, and differential interference contrast (DIC) with a Nikon Optiphot microscope, were used for examination of acid-cleaned material mounted in Hyrax, Naphrax, or more seldom, in Coumarone. In critical cases, e.g. to distinguish between the morphologically similar species, *P. pungens* (Grunow ex P. T. Cleve) Hasle and *P. multiseries,* and *P. pseudodelicatissima* and *P. delicatissima* (P. T. Cleve) Heiden, respectively, LM identification was checked by examination of acid-cleaned material with transmission electron microscopy (TEM = Jeol 100C, Jeol 100CX, JEM 1200EX). Scanning electron microscopy (SEM = JSM 6400) was used to elucidate certain morphological details although the SEM pictures are not included here.

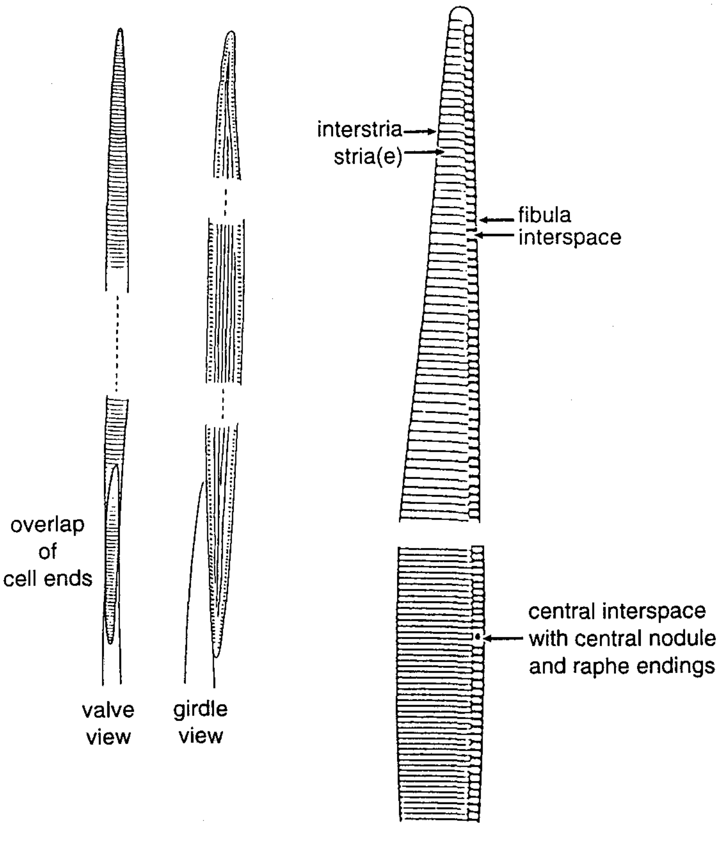

Fig. 1. Diagram showing terminology used in this paper

The terminology follows Anonymous (1975), Ross et al. (1979) and Mann (1978, 1981). Thus, the terms 'keel punctum', 'pseudonodulus', 'intercostal membrane' and 'costa', used by Hasle (1965a), are replaced by 'fibula', 'central nodule', 'stria' and 'interstria', respectively (Fig. 1). The space between two fibulae is called the interspace, and the space between the two central fibulae is called the central interspace. A central interspace consistently greater than the others indicates the presence of a central nodule and central raphe endings.

Argumentation for retaining *Pseudo-nitzschia* as a genus of its own, based on current information on fine structure, has been given by Hasle (1993, 1994). H. Peragallo originally used the spelling *Pseudo-Nitzschia*. The hyphen must be retained (ICBN Art. 60.9, Note 2) but not the capitalization of the second name (ICBN Art. 60.2) (Greuter et al., 1994). A proposal to proscribe hyphens in generic names has not been approved (P. C. Silva, personal communication), contrary to what was expected when the paper by Hasle (1993) was prepared.

Morphometric data are summarized in Tables 1 and 2, distributional data from the Skagerrak in Tables 3–8, and distributional data from the Norwegian coastal waters in Table 9. Two keys to species are presented, one based on observations with the light microscope, and the other on observations with the electron microscope. The keys show that fine structure alone is not sufficient to discriminate between all of the species observed, but needs to be supplemented with observations on valve outline (*P. seriata* and *P. multiseries*) and/or numerical data (*P. heimii* and *P. subpacifica*).

Table 1. Morphometric data for *Pseudo-nitzschia* spp.

| | Valve structure | | | | | Band structure |
|---|---|---|---|---|---|---|
| *Pseudo-nitzschia* | Apical axis (µm) | Transapical axis (µm) | Fibulae (in 10 µm) | Striae (in 10 µm) | Poroids (in 1 µm) | Striae (in 10 µm) |
| *pungens* | 74–142 | 2.9–4.5 | 9–15 | 9–15 | 3–4 | 15–19 |
| *multiseries* | 68–140 | 3.4–5.0 | 10–15 | 10–15 | 4–6 | 19–22 |
| *seriata* f. *seriata* | 91–160 | 5.5–8.0 | 14–18 | 14–18 | 7–8 | 21–24 |
| *seriata* f. *obtusa* | 61–100 | 4.5–5.5 | 15–20 | 15–20 | 7–8 | ND |
| *australis* | 75–144 | 6.5–8.0 | 13–16 | 13–16 | 4–5 | 19–20 |
| *fraudulenta* | 73–117 | 5–6 | 19–23 | 19–23 | 4–5 | 35–40 |
| *subfraudulenta* | 65–106 | 5–7 | 14–17 | 23–26 | 5–6 | ND |
| *heimii* | 50–78 | 5–6 | 14–18 | 26–28 | 7–8 | ~35 |
| *subpacifica* | 33–70 | 5–7 | 15–20 | 28–32 | 9–10 | 32–34 |
| *delicatissima* | 42–66 | 1.0–1.5 | 20–23 | ~40 | 10–12 | 48–52 |
| *pseudodelicatissima* | 77–108 | 1.3–2.0 | 18–24 | 32–44 | 4–5 | ~44 |

ND = no data

Table 2. Distinctive specific features of *Pseudo-nitzschia* spp.

| *Pseudo-nitzschia* | Valve symmetry (tt axis) |  | Central nodule | Fibulae & striae |  | Hymenate velum |  | Valve striae rows of poroids | Valvocop. striae height × width in nr. of poroids |
|---|---|---|---|---|---|---|---|---|---|
|  | iso | hetero |  | equal in nr. | unequal in nr. | simple | sectors |  |  |
| *seriata* |  | + |  | + |  | + |  | 3–4 | 4–6 × 2–3 |
| *multiseries* | + |  |  | + |  | + |  | 3–4 | 4–5 × 2–3 |
| *australis* | + |  |  | + |  | + |  | 2 | 3–5 × 3–4 |
| *pungens* | + |  |  | + |  | + |  | 2 | 1 × 1 |
| *fraudulenta* | + |  | + | + |  |  | + | 2–3 | 10 × 2 |
| *heimii* |  | + | + |  | + | + |  | 2 | 3–4 × 2 |
| *subpacifica* |  | + | + |  | + | + |  | 2 | 5–6 × 2 |
| *delicatissima* | + |  | + |  | + | + |  | 2 | 1 × 1 |
| *subfraudulenta* | + |  | + |  | + |  | + | 2 | ND |
| *pseudodelicatissima* | + |  | + |  | + |  | + | 1 | 4–6 × 2–3 |
| *cuspidata* | + |  | + |  | + |  | + | 1 | ND |
| *inflatula* | + |  | + |  | + |  | + | 1 | ND |
| *lineola* | + |  | + |  | + |  | + | 1–2 | ND |

ND = no data

### *Pseudo-nitzschia* H. Peragallo in H. & M. Peragallo, 1900, emend. Hasle, 1993

Lectotype: *Pseudo-nitzschia seriata* (P. T. Cleve) H. Peragallo in H. & M. Peragallo, chosen by Fryxell, Garza & Roelke, 1991, p. 241.

The generic characters as seen with LM are (i) strongly elongated cells in stepped colonies (formed by overlap of cell ends), (ii) asymmetry about the apical plane (in some species), (iii) a strongly eccentrical raphe system with central raphe endings commonly present, and (iv) two plate-like chloroplasts lying symmetrically about the median transapical plane. The cingulum (the portion of the girdle associated with a single valve) is composed of a varying number of perforated bands, mostly three, and an unknown number of unperforated bands; all of the bands are open. The bands taper gradually from the midregion of the cell towards both poles. At one pole a band is seen as two pointed ends and at the opposite pole as a loop. The bands break off easily at the loop and are therefore mostly present as halves in cleaned material.

Additional generic characters seen with EM are: (i) valve striae with one to several rows of poroids with vela close to valve exterior; (ii) interstriae level with the striae externally, and extending internally into the cell lumen; (iii) raphe not elevated above the general level of the valve; (iv) raphe canal walls without poroids; (v) striated bands (in most species the striae are groups of poroids), with an unperforated pars interior and a wide unperforated margin on the pars exterior, the size of the striae decreasing abvalvarly, and (vi) distal mantle (the one farthest away from the raphe; Mann, 1978) demarcated from valve face by a strip of non-perforated silica.

In contrast to the valve face striae, the band striae seem sunken towards the cell interior. The striae of the distal mantle are continuous with the valve face striae in structure and alignment. The proximal mantle (the one closest to the raphe; Mann, 1978) has, with a few exceptions, striae similar to those of valve face, which are aligned either with the fibulae or interspaces of the raphe, or with the valve face striae.

## RESULTS

The following *Pseudo-nitzschia* taxa were examined in detail: *P. pungens*, *P. multiseries*, *P. seriata* f. *seriata*, *P. fraudulenta* (P. T. Cleve) Hasle, and *P. heimii* Manguin of the "*seriata* complex" (transapical axis 3–4 µm or more) and *P. delicatissima*, and *P. pseudodelicatissima* of the "*delicatissima* complex" (transapical axis narrower than 3–4 µm). In addition, *Pseudo-nitzschia seriata* f. *obtusa* (Hasle) Hasle, *P. australis*, *P. subfraudulenta* (Hasle) Hasle, *P. subpacifica* (Hasle) Hasle, *P. lineola* (P. T. Cleve) Hasle, *P. inflatula* (Hasle) Hasle and *P. cuspidata* (Hasle) Hasle have been examined or referred to for comparison. Most of the species currently referred to *Pseudo-nitzschia* are thus dealt with.

The species differ: (1) in girdle view by (a) outline, (b) height of pervalvar axis, (c) shape and length of overlap of cell ends, and (2) in valve view by (a) valve outline, (b) size of transapical axis and (c) shape of valve ends. Other specific characters, not resolved with LM in all species, are (1) linear density of interstriae relative to fibulae, (2) presence of central raphe endings (= presence of central nodule, presence of larger central interspace), and (3) stria structure. The present investigation includes information on number and structure of bands, and structure of poroid occlusions as further specific distinctive features.

## KEY TO SPECIES

(based on light microscope observations)

| | | |
|---|---|---|
| 1a. | Transapical axis wider than 3 μm | 2 |
| 1b. | Transapical axis narrower than 3 μm | 9 |
| 2a. | Central larger interspace present | 3 |
| 2b. | Central larger interspace absent | 6 |
| 3a. | Outline of valve asymmetrical in the apical axis; one margin almost straight, the other curved | 4 |
| 3b. | Outline of valve symmetrical in the apical axis | 5 |
| 4a. | Fibulae and interstriae discernible with the light microscope | *P. heimii* |
| 4b. | Fibulae but not interstriae discernible with the light microscope | *P. subpacifica* |
| 5a. | Valve outline lanceolate; margins not parallel; fibulae and interstriae equal in number | *P. fraudulenta* |
| 5b. | Valve outline with parallel margins for the greater part of the valve length; fibulae and interstriae unequal in number | *P. subfraudulenta* |
| 6a. | Outline of valve asymmetrical in the apical axis; one margin almost straight, the other curved | *P. seriata* |
| 6b. | Outline of valve symmetrical in the apical axis | 7 |
| 7a. | Presence of poroids in the striae discernible with the light microscope | *P. pungens* |
| 7b. | Presence of poroids in the striae not discernible with the light microscope | 8 |
| 8a. | Transapical axis wider than 5 μm; valve apices rostrate; outline of smaller valves tends to be asymmetrical in the apical axis | *P. australis* |
| 8b. | Transapical axis narrower than 5 μm; valve outline lanceolate with pointed (not rostrate) apices | *P. multiseries* |
| 9a. | Cells in girdle view with truncate apices; in valve view with rounded apices; valve structure delicate, and central larger interspace barely visible with the light microscope | *P. delicatissima* |
| 9b. | Cells in girdle and valve view with pointed apices; fibulae and central larger interspace clearly visible with the light microscope | *P. pseudodelicatissima* |

## KEY TO SPECIES

(based on electron microscope observations)

| | | |
|---|---|---|
| 1a. | Poroids with simple hymens; central nodule present or absent | 2 |
| 1b. | Poroids with complex hymens; central nodule present | 8 |
| 2a. | Bands with striae composed of a single row of poroids | 3 |
| 2b. | Bands with striae composed of groups of poroids | 4 |
| 3a. | Fibulae and interstriae equal in number; central nodule absent | *P. pungens* |
| 3b. | Fibulae and interstriae unequal in number; central nodule present | *P. delicatissima* |
| 4a. | Fibulae and interstriae equal in number; central nodule absent | 5 |
| 4b. | Fibulae and interstriae unequal in number; central nodule present | 6 |
| 5a. | Valve striae with two rows of poroids | *P. australis* |
| 5b. | Valve striae with more than two rows of poroids | 7 |
| 6a. | Valve striae, in general, $\leq 28$ in 10 μm with $\leq 8$ poroids in 1 μm | *P. heimii* |
| 6b. | Valve striae, in general, $\geq 28$ in 10 μm with $> 8$ poroids in 1 μm | *P. subpacifica* |

7a. Outline of valve symmetrical in the apical axis, valve apices pointed . *P. multiseries*
7b. Outline of valve asymmetrical in the apical axis, valve apices rounded . . . *P. seriata*
8a. Fibulae and interstriae equal in number . . . . . . . . . . . . . . . . . . *P. fraudulenta*
8b. Fibulae and interstriae unequal in number . . . . . . . . . . . . . . . . . . . . . . . 9
9a. Valve striae with two rows of roundish poroids . . . . . . . . . . . . *P. subfraudulenta*
9b. Valve striae with one row of square poroids . . . . . . . . . . . *P. pseudodelicatissima*

## *Pseudo-nitzschia pungens* (Grunow ex P. T. Cleve) Hasle, 1993

(Figs 3–6, 30–37, Tables 1–3)

Basionym: *Nitzschia pungens* Grunow ex P. T. Cleve, 1897a.
Type locality: Yeddo Bay, Japan.
Lectotype: BRM W7/72a, Finder: 624.4; Hasle, 1995, Fig. 1.

Morphology (LM): The coarsely silicified cell is spindle-shaped to linear with sharply pointed ends and a deep pervalvar axis (i.e. wide in girdle view). The overlap of cell ends in colonies is ca one third of cell length. The cell is symmetrical with respect to the apical plane (transapical axis isopolar). The valve margins are curved, and the valve ends distinctly pointed (Fig. 3). The interstriae are visible in water mounts, in girdle as well as valve view. The numbers of fibulae and interstriae are equal; the interstriae are so coarsely silicified that fibulae and interstriae are not readily discriminated, especially in water mounts. A larger central interspace is missing. The valve face striae have two rows of large poroids resolved with LM in well silicified and properly preserved, cleaned and mounted specimens (acid-cleaned, Naphrax, Ph, Fig. 4). The bands have a ribbed appearance; the ribs are more widely spaced in the central, wide part of the bands than closer to the narrow ends (Figs 5, 6).

Morphology (EM): The two rows of poroids of the valve face striae are separated by a non-perforated space of about the same width as the diameter of the poroids. A single poroid or a single row of poroids are occasionally present between two regular rows (Figs 30, 31). The valve ends differ in structure, one end having fewer poroids per stria than the other (Figs 32, 33). The valves of a cell are arranged so that each cell has one well areolated and one poorly areolated valve end. The valve mantle is one poroid high (Fig. 31). The proximal mantle and the striae of the valve face differ in structure, the proximal mantle bearing pairs of or single poroids aligned to a fibula or an interspace, but seldom to the rows of poroids of the valve face striae (Figs 30, 31, 34).

We lack observations on whole cells. Three connected bands, representing the entire cingulum or part of it, have been photographed, however. Each band has one transverse row of large poroids (each poroid = one square or roundish opening seen with LM) (Fig. 35). The valvocopula is somewhat wider than the two other bands. The size of the poroids decreases abvalvarly (Fig. 35). The narrow pointed ends as well as the loop in the ligula area lack poroids (Fig. 36).

The vela of valve as well as band poroids are hymenate (Mann, 1981), regularly perforated by closely packed holes in a strict hexagonal array (Fig. 37).

Taxonomy: *Pseudo-nitzschia pungens* was the first to be discovered of the species now allocated to *Pseudo-nitzschia*. It appeared as a *nomen nudum* in the text to slide No. 307 of a Challenger sample of surface diatoms from Yeddo (= Tokyo) Bay, Japan (Cleve & Möller, 1882). The slide used here for lectotypification was made by Dr

Hustedt from a subsample of the same material received from the P.T. Cleve Collection in Stockholm. Cleve (1897a, p. 24, Pl. 2, Fig. 23) gave the first description and illustration of the species referring to the Cleve & Möller slide and to Grunow as the author. The correct author citation is therefore Grunow ex Cleve (ICBN Art. 46.4, Greuter et al., 1994).

When seen in girdle view, *P. pungens* may often have been confused with *P. seriata*, which is more frequently recorded in the literature. With LM, *P. pungens* can hardly be distinguished from *P. multiseries* in girdle view (e.g. Fig. 2 might illustrate *P. pungens* or *P. multiseries*). *Pseudo-nitzschia pungiformis* (Hasle) Hasle, has the same valve outline as *P. pungens* and *P. multiseries*, but has a central larger interspace with a central nodule and a more warm-water distribution; it has not been observed in the Skagerrak or other European waters (Hasle, 1972). As discussed below, *P. pungens* has a fairly unique

Table 3. Seasonal and interannual distribution pattern of *Pseudo-nitzschia pungens*

| | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sept | Oct | Nov | Dec |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1967 | | | | | ▨ | ▨ | | ▨ | | ▨ | | ▨ |
| 1968 | ▨ | | ▨ | ▨ | | ▨ | | | | | | |
| | | | | | | | | | | | | |
| | | | | | | | | | | | | |
| 1978 | | | | | | | | | | x | x | x |
| 1979 | | ▨ | ? | ▨ | ▨ | ▨ | | | ? | x | | ▨ |
| 1980 | | ▨ | ▨ | ▨ | ▨ | x | | x | x | x | x | ▨ |
| 1981 | | ▨ | ▨ | ▨ | ▨ | ▨ | | ▨ | x | x | x | x |
| 1982 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | | ▨ | x | x | | ▨ |
| 1983 | ▨ | ▨ | ▨ | ▨ | ▨ | | x | x | | x | x | ▨ |
| 1984 | x | ▨ | ▨ | ▨ | | | | | x | | ▨ | x |
| 1985 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | | ▨ | x | x | | x |
| 1986 | x | x | x | ▨ | ▨ | x | | x | x | ■ | | |
| 1988 | ▨ | x | ■ | ▨ | ▨ | ▨ | | ■ | | x | x | ▨ |
| 1989 | ▨ | x | ▨ | x | x | x | x | x | x | x | x | x |
| 1990 | x | ▨ | x | x | x | x | x | x | x | x | ▨ | x |
| 1991 | ? | ▨ | | ▨ | ▨ | x | x | ▨ | x | ■ | x | ■ |
| 1992 | x | ? | ▨ | ▨ | x | | x | x | x | ■ | x | |
| 1993 | x | x | x | ▨ | x | x | x | x | x | | | |

? identification questionable

x present

■ abundant

shaded areas = samples collected
clear areas = no collection

position within the *"Nitzschia seriata* complex", judging by the structure of the girdle and partly also by that of the proximal mantle.

Distribution: The records from the Skagerrak transect show a certain shift in seasonal distribution pattern as well as in relative abundance of *P. pungens* during the sampling period (Table 3). It was not recorded at all in 1967–1968, and from 1978 through 1985 it occurred mainly in the autumn. A change in the seasonal distribution pattern seems to have appeared since 1986. Although it still occurs in greatest abundances in the autumn, its occurrence has spread over most of the year.

### *Pseudo-nitzschia multiseries* (Hasle) Hasle, 1995

(Figs 2, 7–9, 38–44, Tables 1, 2, 4)

Basionym: *Nitzschia pungens* f. *multiseries* Hasle, 1974.
Synonym: *Pseudo-nitzschia pungens* f. *multiseries* (Hasle) Hasle, 1993.
Type locality: Drøbak, Oslofjord, Norway.
Holotype: IMBB (= Marine Botany, Department of Biology, Univ. of Oslo) no. 16, Hasle, 1995, Fig. 2.

Morphology (LM): The cell is spindle-shaped to linear in girdle view with sharply pointed ends (Fig. 2), lanceolate in valve view (Fig. 7), and with an overlap of ca one third of cell length in colonies (Fig. 2). Interstriae are discernible in water mounts in girdle as well as valve view. Fibulae and interstriae are present in the same number, the fibulae being more distinct than the interstriae in acid-cleaned mounted specimens (Fig. 7). A larger central interspace is missing. The stria structure is unresolvable with LM (Fig. 8, 100 DIC). The perforated bands seen in cleaned material of a clonal culture (TkA2, Galveston) are narrow and more delicate than those of *P. pungens* (cf. Figs 6 and 9).

Morphology (EM): The valve face striae have three to four separated, irregular rows of poroids (Fig. 38). Those located close to the interstriae are slightly larger than the others (Fig. 39). One of the two valve ends has more branched interstriae than the other (Figs 40, 41).

The mantle bears striae two to three poroids high. The proximal and distal valve mantles have the same structure, similar to that of the valve face, although often with fewer and more irregular poroid rows than those on valve face (Fig. 38). The fibulae are slightly displaced from the interstriae (Figs 40, 41), and the mantle striae are aligned with the raphe interspaces (Fig. 38).

Three categories of perforated bands, differing in the size of the striae, were found in unialgal cultures (Gulf of Mexico) as well as in the Skagerrak samples from 1968 dominated by *P. multiseries*. Whereas the valvocopula (Fig. 42) may have four to five poroids per stria in the pervalvar direction, the number decreases abvalvarly in the other bands, as well as towards the cell ends, to one or none (Figs 43, 44). Each of the square or rectangular "openings" seen with LM thus consists of several poroids. The unperforated margins of all categories of bands seem to have about the same width.

The poroids of the valve as well as of the bands have hymenate vela (Figs 39, 42–44).

Taxonomy: The distinctive morphological character of *P. multiseries* first realized was the "multiseriate" striae of the valve face with smaller poroids than in *P. pungens*. As shown here, these two diatoms differ also in the structure of the valve ends, the proximal valve mantle and the bands. Physiological and molecular genetic characters

Table 4. Seasonal and interannual distribution pattern of *Pseudo-nitzschia multiseries*

| | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sept | Oct | Nov | Dec |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1967 | | | | | ▨ | ▨ | | x | | x | | x |
| 1968 | ■ | | ■ | x | | ▨ | | | | | | |
| | | | | | | | | | | | | |
| 1978 | | | | | | | | | | ▨ | ? | ■ |
| 1979 | | x | x | ▨ | ▨ | ▨ | | | ? | ? | | x |
| 1980 | | ▨ | ▨ | ▨ | ▨ | ▨ | | ▨ | x | x | x | ▨ |
| 1981 | | ▨ | ▨ | ▨ | ▨ | ▨ | | ▨ | x | x | x | x |
| 1982 | ? | ▨ | ▨ | ▨ | ▨ | ▨ | | ▨ | ▨ | ▨ | | ? |
| 1983 | ? | ▨ | ▨ | ▨ | ▨ | | ▨ | ▨ | | ▨ | ▨ | ▨ |
| 1984 | x | ▨ | ▨ | ▨ | | | | | ▨ | | ▨ | ▨ |
| 1985 | x | ? | ▨ | ▨ | ▨ | ▨ | | x | x | ? | | ? |
| 1986 | ▨ | ? | ▨ | ▨ | ▨ | ▨ | | ? | ▨ | x | | |
| 1988 | ? | ▨ | x | ▨ | ▨ | ▨ | | x | | x | ▨ | ▨ |
| 1989 | ? | ▨ | ▨ | x | ▨ | ▨ | ▨ | x | x | x | ■ | x |
| 1990 | ? | ▨ | ▨ | ▨ | x | x | x | x | x | x | ▨ | ▨ |
| 1991 | ▨ | x | | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | x | ▨ | x |
| 1992 | x | ? | ▨ | ▨ | ▨ | | ▨ | ▨ | ▨ | ▨ | ▨ | |
| 1993 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | | | |

? identification questionable
x present
■ abundant

shaded areas = samples collected
clear areas = no collection

(Bates et al., 1993; Douglas et al., 1993; Manhart et al., 1995) corroborate with the morphology and support the raising of *P. pungens* f. *multiseries* to species level (Hasle, 1995).

A possible synonomy between *P. multiseries* and *Nitzschia pungens* var. *atlantica,* described by Cleve (1897a, p. 24, Pl. 2, Fig. 24) from Coruña Harbour, Spain, may be questioned. The variety differed from the nominate one by having more densely spaced striae. Type material of *N. pungens* var. *atlantica* has not been found, and the problem can thus not be solved.

Distribution: *Pseudo-nitzschia multiseries* was the predominant species of the genus in the 1967 and 1968 samples, especially in the winter of 1968; it was also seen in a sample from September 1966. This is in contrast to the poor representation in the early

1980s and in 1992 and 1993. The general trend in the seasonal distribution is its presence in autumn through winter (Table 4).

## *Pseudo-nitzschia seriata* (P.T. Cleve) H. Peragallo in H. & M. Peragallo, 1900

(Figs 10–14, 45–50, Tables 1, 2, 5)

### *Pseudo-nitzschia seriata* (P.T. Cleve) H. Peragallo f. *seriata*

Basionym: *Nitzschia seriata* P.T. Cleve, 1883.
Type locality: Tindingen, Greenland.
Lectotype: S405, Hasle, 1994, Fig. 3.

Morphology (LM): Cells in girdle view are linear to lanceolate, with pointed ends (Fig. 11). The overlap of cell ends in colonies is one third to a quarter of cell length (Figs 10, 11). The cell is asymmetrical with respect to the apical plane (transapical axis heteropolar). One valve margin is curved, and the other straight (Figs 10, 12), especially in the middle part of the valve. The valve ends are slightly prolonged with rounded poles (Fig. 12). The raphe may be located on the straight or curved margin (Figs 12, 14). The interstriae are discernible in water mounts in girdle (Fig. 11) as well as in valve view. Interstriae and fibulae are equal in number and indistinguishable in water mounts; in cleaned, mounted material the fibulae are more distinct than the interstriae (Figs 12–14). A central larger interspace is missing (Fig. 12).

The bands may be characterized as "striated" or "ribbed", having one row of rectangular openings (Figs 13, 14).

Morphology (TEM): The valve has three to four separated rows of poroids per stria (Fig. 46). The poroids close to the interstriae are larger than the others and more regular in appearance (Figs 46, 47). The interstriae of one valve end are slightly more branched than the other (Fig. 45).

The mantle is two to three poroids high, with striae similar to those on the valve face but two to three equally sized poroids wide (Figs 46, 47). The fibulae are mostly aligned with the interstriae, and the striae of the proximal mantle with the raphe interspaces (Fig. 47).

Three connected striated bands were repeatedly found, occasionally with a fourth non-perforated band attached (Fig. 48). The band striae, well developed on the valvocopula and the next band, have two rows of poroids, occasionally with a third poroid between them, compared to the three to four poroid rows on the valve. Near the centre of the cell the striae of the valvocopula have four to six poroids in the pervalvar direction (Figs 48, 49), gradually decreasing to two or one near the poles (Fig. 45). The striae of the second band are about half as high, and the third band has only one transverse row of poroids (Fig. 48). The unperforated part of the pars exterior has about the same width for all striated bands.

The poroids of the valve as well as of the bands have hymenate vela (Figs 47, 49).

Taxonomy: No holotype of *N. seriata* was found in the P.T. Cleve Collection. One of the slides labelled "Tindingen, Grönland" has been selected as a lectotype and a *P. seriata* specimen encircled.

In valve view *P. seriata* f. *seriata* differs conspicuously from *P. pungens* and *P. multiseries* by valve outline. This character is often obscured in EM examinations and the stria structure of *P. seriata* f. *seriata* can easily be confused with that of *P. multiseries*.

Attention has then to be paid to the pointed ends of *P. multiseries* compared with the rounded ends of *P. seriata* (cf. Figs 40, 41, and 45).

*Pseudo-nitzschia seriata* f. *obtusa* differs from the nominate form by more obtuse valve ends, shorter apical and transapical axes (Fig. 15), somewhat more closely spaced striae (Table 1), and the usual absence of poroids in the middle of the striae (Fig. 50). It should be noticed that f. *obtusa* was not recorded from the Skagerrak, but only from further north (Norwegian west coast from ca 63°N and northwards during the cold season) although it was once observed off Helsingør during winter, together with other "arctic" diatoms (Hasle, 1965a).

*Pseudo-nitzschia australis* (Synonym: *Nitzschia pseudoseriata* Hasle) may be the species most easily confused with *P. seriata*. Its identity as a separate species has been questioned by Rivera (1985) who claimed that *N. pseudoseriata* as well as *N. seriata* f.

Table 5. Seasonal and interannual distribution pattern of *Pseudo-nitzschia seriata*

| | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sept | Oct | Nov | Dec |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1967 | | | | | ▨ | ▨ | | ▨ | | x | | ▨ |
| 1968 | ▨ | | x | x | | ▨ | | | | | | |
| | | | | | | | | | | | | |
| 1978 | | | | | | | | | | ▨ | x | ▨ |
| 1979 | | x | x | x | ▨ | ▨ | | | x | ▨ | | ▨ |
| 1980 | | x | ■ | x | ▨ | ▨ | | ▨ | x | x | ▨ | ▨ |
| 1981 | | x | x | x | ▨ | ▨ | | ▨ | ▨ | ▨ | ▨ | x |
| 1982 | x | x | ■ | x | x | x | | ▨ | ▨ | x | | x |
| 1983 | ▨ | x | x | ■ | ■ | | ▨ | ▨ | | ▨ | x | ▨ |
| 1984 | x | x | ■ | ■ | | | | | ▨ | | ▨ | ▨ |
| 1985 | ■ | ■ | ■ | ■ | ■ | ▨ | | ▨ | ▨ | ▨ | | x |
| 1986 | x | x | x | x | x | x | | ▨ | ▨ | ▨ | | |
| 1988 | ▨ | x | x | ■ | x | ▨ | | ▨ | | ▨ | ▨ | ▨ |
| 1989 | x | x | x | x | x | x | x | ▨ | ▨ | x | ▨ | ▨ |
| 1990 | x | ▨ | ▨ | x | x | x | ▨ | ▨ | ▨ | x | ▨ | x |
| 1991 | x | x | | ▨ | ■ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
| 1992 | x | ▨ | x | ■ | x | | ▨ | ▨ | ▨ | ▨ | ▨ | |
| 1993 | x | x | x | x | ▨ | ▨ | ▨ | ▨ | ▨ | | | |

x present

■ abundant

shaded areas = samples collected
clear areas = no collection

*obtusa* were synonyms of *N. seriata*. *Pseudo-nitzschia australis* is on average larger and more coarsely structured than *P. seriata* (Table 1). Larger specimens of *P. australis* are symmetrical with respect to the apical plane, and the cell ends are somewhat rostrate (Fig. 16). These characters are less pronounced in smaller specimens. The branching of the interstriae of the two valve ends of *P. australis* (Figs 51, 52) follows the pattern seen in *P. seriata* f. *seriata* (Fig. 45). TEM studies of valve and band structure give further evidence for *P. australis* as a species of its own. The striae on valve face bear only two rows of hymenate poroids (Table 2) separated by a wide unperforated space, occasionally with a third poroid close to the raphe (Fig. 53). The mantle is one to two poroids high, and the mantle striae are two to three poroids wide (Figs 53, 54). The band striae differ from those on valve face by having more than two rows of poroids, and from the band striae of *P. seriata* f. *seriata* by shape and usually more rows of poroids (cf. Figs 48 and 55; Table 2). Three striated bands and one narrow unperforated band and hymenate vela have been observed in *P. australis* (Figs 55, 56), as in *P. seriata* f. *seriata*.

Distribution: *Pseudo-nitzschia seriata* is a typical winter-spring species in the Skagerrak area, although observed sporadically also in the autumn. It was scarce in the 1967/68 samples but occurred regularly during the whole sampling period 1979–93 (Table 5) with greatest relative abundances during the spring diatom peak.

### *Pseudo-nitzschia fraudulenta* (P. T. Cleve) Hasle, 1993

(Figs 17–19, 57–61, Tables 1, 2, 6)

Basionym: *Nitzschia fraudulenta* P. T. Cleve, 1897b.
Synonym: *Pseudo-Nitzschia seriata* var. *fraudulenta* (P. T. Cleve) H. Peragallo in H. & M. Peragallo, 1900.
Type locality: Plymouth Harbour.
Lectotype: S XV-21, Hasle, 1994, Fig. 4.

Morphology (LM): Cells in girdle view are linear to lanceolate, with pointed ends, and in valve view typically lanceolate, the valve margins being curved and gradually tapering towards pointed ends. The overlap of cell ends in colonies is one sixth to ca one eighth of cell length (Fig. 17). Fibulae and interstriae are approximately equal in numbers. Interstriae, but not fibulae, may be discerned in water mounts under optimal conditions. The fibulae, a larger central interspace and a central nodule are more distinct than the interstriae when acid-cleaned valves mounted in a medium of a high refractive index are examined (Fig. 18). The band structure is not resolved with LM (Fig. 19).

Morphology (TEM): The valve striae have two to three rows of closely packed square poroids that fill out almost the whole space between two interstriae (Figs 57, 58). One valve end has one or two oblique rows of poroids close to the apex, which are missing on the other end (Figs 59, 60). The mantle is one to two poroids high (Figs 57, 58). The fibulae are aligned with the valve face interstriae and, more irregularly, with the striae or the interstriae of the proximal mantle (Fig. 57). The central larger interspace spans three to four valve face striae (Fig. 57). The poroid velum consists of a central irregular unperforated part with branches towards the periphery. Between the branches are hymenate sectors (Fig. 58).

A culture from the Trondheimsfjord contained few striated and many vaguely or non-perforated bands (Fig. 19). The valvocopula bears rectangular striae with two rows of a varying number of irregularly shaped poroids, mostly ca 10 in the pervalvar direction

(Fig. 61), occasionally with a central third row of smaller poroids. The poroid occlusions are hexagonal hymenate and similar in size to the hymenate sectors of the valve poroids. A second, narrow, indistinctly structured, band might be present, and an unknown number of non-perforated bands.

Taxonomy: *Pseudo-nitzschia fraudulenta* as a species of its own and not a variety of *P. seriata* is justified by (i) the symmetrical valve outline, (ii) the larger central interspace with a central nodule, (iii) the more densely spaced fibulae and striae, (iv) the larger valve poroids with hymenate sectors, (v) the valvocopula striae, with smaller poroids and more densely spaced than in *P. seriata*, and (vi) the apparently single striated band and several unperforated bands.

*Pseudo-nitzschia subfraudulenta* is morphologically closely related to *P. fraudulenta* but has not been recorded from the Skagerrak with certainty, although it does occur further south, in the North Atlantic (off the Portuguese and the northwestern African coasts). *Pseudo-nitzschia subfraudulenta* differs from *P. fraudulenta* in valve outline, the margins being straight for a greater part of the valve length (Fig. 62). The interstriae are more densely spaced than in *P. fraudulenta*, and more numerous than the fibulae (Table 1). The central larger interspace has the width of five valve striae (Fig. 62). The mantle is

Table 6. Seasonal and interannual distribution pattern of *Pseudo-nitzschia fraudulenta*

| | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sept | Oct | Nov | Dec |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1980 | | ▨ | ▨ | ▨ | ▨ | ▨ | | ▨ | x | ▨ | ▨ | ▨ |
| 1981 | | ▨ | ▨ | ▨ | ▨ | ▨ | | ▨ | ▨ | x | ▨ | x |
| 1982 | ▨ | ▨ | x | ▨ | ▨ | x | | ▨ | ▨ | ▨ | | ▨ |
| 1983 | ▨ | ▨ | ▨ | ▨ | ▨ | | ▨ | ▨ | | ▨ | x | ▨ |
| 1984 | ▨ | ▨ | ▨ | ▨ | | | | | ▨ | | ▨ | ▨ |
| 1985 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | | ▨ | x | x | | ▨ |
| 1986 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | | ▨ | ▨ | ▨ | | |
| 1988 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | | x | | ▨ | ▨ | ▨ |
| 1989 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ■ | ? |
| 1990 | ? | x | ▨ | ▨ | x | ▨ | ▨ | x | ▨ | x | ▨ | ▨ |
| 1991 | ▨ | ▨ | | ▨ | ▨ | x | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
| 1992 | ▨ | x | ▨ | ▨ | ▨ | | ▨ | x | ▨ | ▨ | x | |
| 1993 | x | ▨ | ▨ | ▨ | ▨ | x | x | ▨ | ▨ | | | |

? identification questionable

x present

■ abundant

shaded areas = samples collected
clear areas = no collection

one to two poroids high, and the vela of valve face and mantle (Figs 63, 64) are structured as in *P. fraudulenta*.

Distribution: *Pseudo-nitzschia fraudulenta* was recorded sporadically during the sampling period 1980–93 and with one exception (November 1989) always in small concentrations (Table 6). Unlike *P. seriata* f. *seriata*, *P. pungens* and *P. multiseries*, it is most likely introduced from further south in the North Atlantic or from the Norwegian Sea.

### *Pseudo-nitzschia heimii* Manguin, 1957

(Figs 20, 65–69, Tables 1 and 2)

Synonym: *Nitzschia heimii* (Manguin) Hasle, 1965a.
Type locality: The coast of Adélie Land.
Type unknown.

Morphology (LM): The cells from the Skagerrak are asymmetrical (transapical axis heteropolar) in valve view with one valve margin almost straight, especially in the middle part, and the other convex. The valve ends are broadly rounded and not distinctly asymmetrical in shape (Fig. 20). The fibulae, along either the curved or the straight margin, and the central larger interspace are readily seen on cleaned valves mounted in a medium of high refractive index (Fig. 20). The interstriae are more closely spaced than the fibulae and less distinct, although discernible with LM (Fig. 20).

Morphology (TEM): Specimens examined from the Skagerrak have two rows of small poroids per valve stria separated by a wide unperforated space (Figs 65, 66, 69). The mantle is structured as the valve face and is three to four poroids high (Fig. 65). The striae of the proximal mantle are slightly displaced from those of the valve face (Figs 65, 68). The two central fibulae are widely spaced, the interspace corresponding to four or five valve face striae (Figs 65, 67).

The valvocopula has rectangular striae (Fig. 67), with two rows of three to four poroids in the pervalvar direction (Fig. 68). The valve as well as valvocopula vela are hymenate (Figs 66, 68).

Taxonomy: The Antarctic diatom Manguin (1957) described as *P. heimii* is larger (apical axis 104–117 µm, transapical axis 5.5–6.5 µm) and more coarsely structured (11–15 fibulae and 21–23 striae in 10 µm) than the specimens we have identified as *P. heimii* from the Skagerrak. A more delicately structured form of *P. heimii* has been recorded from the Subantarctic (40–50 °S) and in waters off Shetland, North Atlantic (Hasle, 1965a, 1972). Although it is somewhat longer and narrower than the Skagerrak specimens, we feel fairly confident that the diatoms from the Skagerrak and Shetland and, most likely also from the Subantarctic, belong to the same taxon.

Due to the asymmetry of the valve, *Pseudo-nitzschia heimii* may be confused with *P. seriata* f. *seriata* when seen in water mounts. However, examination of acid-cleaned material in a medium of high refractive index readily show the central larger interspace and the greater number of interstriae than fibulae. The distinction between *P. heimii* and *P. fraudulenta*, seen with the light microscope, depends on the difference in symmetry and the less distinct and more densely spaced fibulae of *P. fraudulenta*. The structure of the valve poroid occlusions is a further distinctive feature (cf Figs 58 and 66).

*Pseudo-nitzschia subpacifica* (Figs 21, 22), recorded from northwest African and Portuguese waters but not from the Skagerrak, has much of the same morphological characters as *P. heimii* including striated bands (Hasle, 1965a, Pl. 8, Fig. 4a), but is, on average, smaller (apical axis 33–70 µm), wider (transapical axis 5–7 µm) and more delicate in structure (15–20 fibulae and 28–32 striae in 10 µm).

Distribution: *Pseudo-nitzschia heimii* was recorded in 1983, 1985, 1986, 1989 and 1990 in small concentrations in the late autumn from the Skagerrak station closest to the Danish coast and the one in the middle of the transect. In October 1990 it was, however, the dominant *Pseudo-nitzschia* species in samples collected at Flødevigen Marine Research Station on the Norwegian south coast.

## *Pseudo-nitzschia delicatissima* (P. T. Cleve) Heiden in Heiden & Kolbe, 1928

(Figs 23–25, 70–75, Tables 1, 2, 7)

Basionym: *Nitzschia delicatissima* P. T. Cleve, 1897a.
Synonym: *Nitzschia actydrophila* Hasle, 1965a.
Type localities: Atlantic, 63° 10′ N, 0° 36′ E; Spitzbergen; Sweden.
Neotype locality: Helder, the Netherlands, 7th May 1897.
Neotype: S slide labelled "*Nitzschia delicatissima*, Helder 7/5-97", this paper, Fig. 23.

Morphology (LM): *Pseudo-nitzschia delicatissima* may be recognized in girdle view by the extremely short overlap (ca one-ninth of cell length) of the cells, which are slightly sigmoid, narrow, and truncate at their ends (Hasle, 1965a, Pl. 2, Fig. 10a). The cells are narrow and linear in girdle as well as valve view; in valve view they are slightly wider in the middle and taper towards rounded cell ends (Figs 23–25). The fibulae, and occasionally the central larger interspace, are visible on cleaned specimens mounted in a medium of a high refractive index (Fig. 25), whereas the interstriae and the band structure are not resolved with the light microscope (Ph, BM 100×).

Morphology (TEM): There are approximately two interstriae for each fibula and three striae for the central interspace (Figs 70–72). The striae have two rows of triangular to hexagonal poroids with hymenate vela (Figs 72, 73). The apparent variation in size and number of poroids present may be a result of degree of silicification. There is no noticeable difference in the structure of the two valve ends (Figs 70, 71). The mantle is one poroid high and bears one row of large poroids that may be split in two (Figs 73, 74). The striae of the proximal mantle are aligned either with valve face striae or possibly more often with the interstriae (Figs 73, 74).

Three structured and an unknown number of unstructured bands were observed inside a single cingulum (Fig. 75). The valvocopula has one row of rectangular poroids of about the same width as the valve striae but filled by hymenate vela (Figs 74, 75). The velum may be split into a few irregular portions (Fig. 75) giving the impression of striae with closely packed poroids. The next band has a silicified rib running along the band's length, separating the band into two halves, each ornamented with irregular poroids (Figs 74, 75). The third band in the abvalvar direction has small scattered poroids (Figs 74, 75).

Structural differences shown in Figs 73–75 may be due to stages in the morphogenesis of the girdle (incomplete in Fig. 73 but fully developed in Figs 74 and 75).

Taxonomy: Material from the localities Cleve referred to in the description of *P. delicatissima* has never been found. A slide in Naturhistoriska Riksmuseet, Sektionen för kryptogambotanik (the Swedish Museum of Natural History, Department of Botany), labelled "*Nitzschia delicatissima*, Helder 7/5-97" in Cleve's handwriting has therefore been suggested as the neotype (Hasle, 1976). A specimen on this slide (Fig. 23) is presented here for comparison with the Skagerrak specimens (Figs 24, 25). Cleve (1897a, p. 24, Pl. 2, Fig. 22) described and illustrated his species with a "central keel". The two valves of a single cell seldom separate, even during acid cleaning, and thus, when flattened on the slide, the specimens may easily be interpreted as having a central raphe.

*Pseudo-nitzschia delicatissima* seems to be the only one of the smaller *Pseudo-nitzschia* species (the "*delicatissima* complex") that has simple hymenate vela like the much larger *P. pungens, P. multiseries, P. seriata* and *P. heimii. Pseudo-nitzschia delicatissima* is also more similar to the coarsely structured *P. pungens* with regard to proximal mantle and valvocopula structure than to other delicate *Pseudo-nitzschia* species.

Table 7. Seasonal and interannual distribution pattern of *Pseudo-nitzschia delicatissima*

| | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sept | Oct | Nov | Dec |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1980 | | ▨ | ▨ | ▨ | ▨ | x | | ▨ | x | x | ▨ | ▨ |
| 1981 | | x | x | ▨ | ▨ | x | | ▨ | ▨ | ▨ | x | ■ |
| 1982 | ▨ | ▨ | ▨ | ▨ | ▨ | x | | ▨ | ▨ | x | | ▨ |
| 1983 | x | x | ▨ | x | ▨ | | x | ▨ | | x | x | x |
| 1984 | x | ■ | ▨ | ▨ | | | | | ▨ | | ▨ | ▨ |
| 1985 | ▨ | ▨ | ▨ | ▨ | x | ▨ | | ▨ | ▨ | ▨ | | x |
| 1986 | ■ | ▨ | ■ | ■ | x | x | | ▨ | ▨ | x | | |
| 1988 | ▨ | x | x | ▨ | ▨ | x | | ▨ | | x | ▨ | ▨ |
| 1989 | x | x | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
| 1990 | x | x | x | x | x | x | x | x | x | x | x | x |
| 1991 | ▨ | ▨ | | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | x |
| 1992 | x | ■ | x | ▨ | ▨ | | x | ▨ | x | ▨ | ▨ | |
| 1993 | ▨ | x | x | x | x | ▨ | ? | ▨ | ▨ | | | |

? identification questionable
x present
■ abundant

shaded areas = samples collected
clear areas = no collection

Distribution: *Pseudo-nitzschia delicatissima* is autochthonous to the area, although primarily a winter-spring form like *P. seriata*, with a somewhat erratic occurrence (Table 7). It occurred in mass concentrations in May 1953. In other material collected prior to 1980 it appeared in fair abundance in January 1964 (Drøbak, Oslofjord), September 1966, November and December 1978 (Flødevigen Marine Research Station, Norwegian south coast), and in December 1967 and March 1968 within the transect.

## *Pseudo-nitzschia pseudodelicatissima* (Hasle) Hasle, 1993

(Figs 26–29, 76–81, Tables 1, 2, 8)

Basionym: *Nitzschia pseudodelicatissima* Hasle, 1976.
Synonym: *Nitzschia delicatula* Hasle, 1965a, non *Nitzschia delicatula* Skvortzow, 1946.
Type locality: Denmark Strait.
Holotype: IMBB no. 23, this paper, Fig. 27.

Morphology (LM): The cells are linear to almost linear, tapering towards pointed ends in girdle as well as valve view (Figs 26, 27). The overlap of cells in chains is about one-eigth to one-ninth of cell length. The fibulae and a central larger interspace with a central nodule are readily seen on cleaned valves mounted in a medium of a high refractive index (Figs 28, 29). The interstriae of well silicified specimens may occasionally be resolved.

Morphology (TEM): There are approximately two striae per fibula. Each stria is composed of one row of large square poroids (Figs 76, 77). The valve ends are similar in

Table 8. Seasonal and interannual distribution pattern of *Pseudo-nitzschia pseudodelicatissima*

| | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sept | Oct | Nov | Dec |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1980 | | ▨ | ▨ | ▨ | ▨ | ▨ | | ▨ | x | x | ■ | ▨ |
| 1981 | | ▨ | ▨ | ▨ | ▨ | ▨ | | ▨ | ▨ | ▨ | ▨ | ▨ |
| 1982 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | | ▨ | ▨ | ▨ | | ▨ |
| 1983 | ▨ | ▨ | ▨ | ▨ | ▨ | | ▨ | ▨ | | x | ▨ | ▨ |
| 1984 | ▨ | ▨ | ▨ | ▨ | | | | | ▨ | | ▨ | ▨ |
| 1985 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | | ▨ | ▨ | x | | x |
| 1986 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | | ▨ | ▨ | ▨ | | |
| 1988 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | | x | | ▨ | ▨ | ▨ |
| 1989 | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ■ | ■ |
| 1990 | ? | ? | ? | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | x | ▨ | ▨ |
| 1991 | ▨ | ▨ | | ▨ | ▨ | ▨ | ▨ | ▨ | x | ■ | x | x |
| 1992 | x | x | ▨ | ▨ | ▨ | | ▨ | ■ | ■ | ■ | x | |
| 1993 | ▨ | ? | ▨ | ▨ | ▨ | ■ | x | ▨ | ▨ | | | |

? identification questionable
x present
■ abundant

shaded areas = samples collected
clear areas = no collection

structure (Figs 78, 79). The valve mantle is one large rectangular or roundish poroid high (Fig. 76). The proximal valve mantle poroids are usually aligned with the valve face striae (Fig. 77). The central interspace with the central nodule corresponds to four striae (Fig. 77). The vela of the valve face poroids consist of a central unperforated or hymenate part, surrounded by five to eight hymenate sectors (Fig. 76). The vela of the mantle poroids have basically the same pattern elongated in pervalvar direction and with more hymenate sectors (Fig. 76).

The cingulum has three striated bands, each stria having two to three rows of four to six poroids in the pervalvar direction. The valvocopula is slightly wider than the other bands (Figs 80, 81). A narrow unperforated band seems to form the edge of the cingulum (Fig. 81). The poroids of the band striae are shaped as the hymenate sectors of the valve vela (cf. Figs 76 and 81).

Taxonomy: *Pseudo-nitzschia pseudodelicatissima* and *P. delicatissima* both appear in North European inshore waters, sometimes in the same sample. Discriminating characters discernible with LM are pointed apices and linear valves in *P. pseudodelicatissima*, compared to rounded apices, short overlap of cell ends and a slight widening of the central part of *P. delicatissima*. TEM observations of valve striae, mantle and bands further clarify the distinction between the two species.

*Pseudo-nitzschia pseudodelicatissima* has also some resemblance to *P. lineola*, *P. inflatula* and *P. cuspidata*, the first two recorded from the northern part of the North Atlantic and the latter as far north as off the Portuguese coast. There are certain differences in valve outline of the species compared, and *P. lineola* (Hasle, 1965a, Pl. 13, Figs 11–14), *P. inflatula* (Hasle, 1965a, Pl. 13, Figs 7–10) and *P. cuspidata* (unpublished observations) all have more simply structured poroid vela than *P. pseudodelicatissima*.

Distribution: *Pseudo-nitzschia pseudodelicatissima* was abundant in a Skagerrak sample in December 1976 as well as in November 1980 (Table 8). The few records from the following years are from the autumn. Since 1989 it has increased in abundance (sometimes occurring in mass concentrations) and extended its occurrence from June–December.

## DISCUSSION

### Morphology

*Pseudo-nitzschia* species form a well-defined group, discriminated from other genera within the family Bacillariaceae Ehrenberg by a combination of morphological and ecological features.

The main reason put forward by Peragallo & Peragallo (1900) for transferring *Nitzschia seriata* and *N. fraudulenta* to the new genus *Pseudo-Nitzschia* seemed to be that fibulae ("keel puncta") are indistinct or not observed at all with light microscopy. The justification for the independent status of the genus obtained by SEM is the lack of prominent features that are characteristics of *Nitzschia* including the generitype *N. sigmoidea* (Nitzsch) W. Smith. These characteristics are a conopeum near the raphe, raphe central to moderately eccentric, raphe raised on a keel, bands with two or more transverse rows of isolated poroids, and raphe canal walls with poroids (Mann, 1986; Hasle, 1994).

The formation of stepped colonies is the prominent character by which *Pseudo-nitzschia* is recognized in fresh material. The cells of *Bacillaria* Gmelin (of the same family) slide along each other in colonies to form a linear array or to retract into a tabular array. When forming a linear array, the similarity to a stepped colony is striking. Although similar movements have to take place in *Pseudo-nitzschia* just after the cell division, the overlap of cell ends is fairly constant. Furthermore, the raphe system of *Bacillaria* is considerably more complicated in construction than that of *Pseudo-nitzschia* (Drum & Pankratz, 1965). The only other genus with stepped colonies beside *Pseudo-nitzschia* seems to be the taxonomically and morphologically isolated genus *Nanoneis* R. E. Norris (Norris, 1973).

The closest related genus is apparently *Fragilariopsis* which is also exclusively marine but forms ribbon-shaped non-motile colonies. *Fragilariopsis* also has a strongly eccentric raphe system not raised above the general level of the valve, and valve striae with 1–4, usually 2, rows of poroids with hymens. A central nodule and more striae than fibulae are present in a few *Fragilariopsis* spp. only, and the asymmetry found in some species is manifest in the heteropolar apical axis, rather than the transapical axis in *Pseudo-nitzschia* (Table 2). The *Fragilariopsis* bands observed so far have, with one exception viz. *F. oceanica* (P. T. Cleve) Hasle, no perforations or a single row of poroids only (Hasle, 1965b; Round et al., 1990; Medlin & Sims, 1993). The latter seems to be the common pattern in Bacillariaceae (Round et al., 1990; Lange-Bertalot & Krammer, 1993). Striated bands like those shown in *Pseudo-nitzschia* are, as far as we know, restricted to this genus and to *F. oceanica* (Hasle, 1965b, Pl. 2, Fig. 9).

All Bacillariaceae genera illustrated by Round et al. (1990) had hymenate poroid occlusions. Whether the hymens of these genera have the hexagonal array of *Fragilariopsis* and some *Pseudo-nitzschia* species (with simple hymenate velum in Table 2), is not evident from either their text or illustrations. Hexagonal array or regular scatter (pores scattered across the hymen in a somewhat disorderly fashion) are present in *Hantzschia* Grunow; *Nitzschia paeneperpetua* Mann has a centric array (the perforations are ordered with respect to the centre of the hymen), and in *N. sinuata* (W. Smith) Grunow delicate cribra are present, external to the hymens (Mann, 1981). The pore occlusions of *N. sinuata* (Mann, 1981, Fig. 8) are similar to those found in *Pseudo-nitzschia fraudulenta* and other species with hymenate velum divided into sectors by central, branched structures (Table 2). Unfortunately, we had no access to a scanning electron microscope with a resolution high enough to verify the nature and the level of the central structures.

In general, the *Pseudo-nitzschia* girdle consists of several open, usually three, striated bands and at least one unperforated band; all bands taper at the poles. Similar observations were made earlier by MacPhee et al. (1992, p. 306) who examined *P. multiseries* with SEM, except that they assumed the bands to "encircle the cell without a break".

Specific structures of the girdle support the status of *P. fraudulenta* (Fig. 61) as a separate species and not a variety of *P. seriata* (Figs 48, 49), of *P. australis* (Figs 55, 56) as distinct from *P. seriata*, and *P. pungens* (Fig. 35) and *P. multiseries* (Figs 42–44) as two taxa more remotely related than previously thought. The isolated position of *P. delicatissima* among the smaller species based on band and proximal mantle structure (Figs 73–75) is a further noteworthy observation.

*Pseudo-nitzschia pungens* (Figs 35, 37), *P. multiseries* (Figs 39, 42), *P. seriata* (Figs

47, 49), *P. australis* (Figs 53, 56), *P. heimii* (Figs 66, 68) and *P. delicatissima* (Figs 72, 74, 75) have band as well as valve poroids with simple hymenate vela (Table 2). *Pseudo-nitzschia fraudulenta* (Fig. 58), *P. subfraudulenta* (Fig. 64) and *P. pseudodelicatissima* (Fig. 76) form another group with valve poroid vela split into several hymenate sectors and bands with small angular hymenate poroids (Figs 61, 81). The vela of *P. cuspidata, P. inflatula* and *P. lineola* are, as far as we know, split like those of *P. pseudodelicatissima* but in fewer parts (Table 2).

Attempts to link the groups distinguished by velum structure with other morphological features showed that *P. pungens* and *P. delicatissima*, species that otherwise seem to be more remote than most species of the genus (Table 1), share as many characters as any two species in Table 2, viz. simple hymenate vela, bands with one row of poroids, proximal mantle non-striated (= 1–2 poroids), valves symmetrical along the apical axis, and valve striae with two rows of poroids.

*Pseudo-nitzschia subfraudulenta, P. pseudodelicatissima, P. cuspidata, P. inflatula* and *P. lineola*, with hymenate sectors, form a fairly homogeneous group, all having symmetrical valves, a central nodule, and more striae than fibulae. It should be noted, however, that *P. fraudulenta, P. granii* (Hasle) Hasle and *P. subcurvata* (Hasle) G. A. Fryxell also have this kind of poroid occlusions. But, *P. fraudulenta* has equal numbers of fibulae and striae per valve, and *P. granii* and *P. subcurvata* have no central nodule.

Presence/absence of a central nodule was used as a special character in the classification of *Nitzschia* section *Lanceolatae* Grunow (Lange-Bertalot, 1980), whereas Mann (1982) considered presence/absence of a central nodule as just one of the 30 characters that can be used. A certain taxonomic relationship based on presence/absence of a central nodule in combination with a kind of poroid vela and number of fibulae relative to number of valve striae, and in part also valve outline, is discernible in *Pseudo-nitzschia*. In *P. seriata, P. multiseries, P. australis* and *P. pungens* the absence of a central nodule corresponds well with simple hymenate vela and equal numbers of fibulae and valve striae per valve, and with the exception of *P. seriata*, with symmetrical valves (Table 2). In *P. heimii* and *P. subpacifica* with asymmetrical, and *P. delicatissima* with symmetrical valve, presence of a central nodule corresponds with simple hymenate vela, and more valve striae than fibulae (Table 2). *Pseudo-nitzschia turgidula* (Hustedt) Hasle will also belong to this group if the vela are shown to be simply hymenate (Hasle, 1965a, Table 3).

## Distribution

The most frequent occurrence of records and the greatest abundances of *P. pungens* in the Skagerrak over the entire sampling period extended from August to December. Since the late 1980s, *P. pungens* has been recorded during most of the year with greatest abundances in the autumn (Table 2), together with species of a more southern origin (see Lange et al., 1992). This pattern agrees well with the species' long-term distribution in the Oslofjord, and in the Trondheimsfjord as the northernmost locality (Table 9).

*Pseudo-nitzschia pungens* has a cosmopolitan distribution (Hasle, 1972), a statement supported by further investigations from Japan, Bay of Thailand, New Zealand, Atlantic and Pacific coasts of North and South America, and European waters (e.g. Takano & Kuroki, 1977; Rivera, 1985; Fryxell et al., 1990; Hargraves et al., 1993; Horner & Postel,

Table 9. Geographical distribution of *Pseudo-nitzschia* spp. in Norwegian coastal waters

| Site/Date | *P. pungens* | *P. multiseries* | *P. seriata* | *P. fraudulenta* | *P. pseudo-delicatissima* | *P. delicatissima* |
|---|---|---|---|---|---|---|
| **OSLOFJORD, ca 59° 40' N 10° 35' E** | | | | | | |
| Feb 1964 | | | | | | x |
| Apr 1966 | | | x | | | |
| Nov 1966 | | x | | | | |
| Mar 1967 | | | x | | | |
| Sept 1967 | | ■ | | | | |
| Oct 1967 | | x | | | | x |
| Mar 1968 | | x | | | | |
| Nov 1971 | | ■ | | | | x |
| Dec 1976 | x | x | | | ? | ■ |
| Dec 1980 | x | ? | | | | |
| Aug 1982 | x | ? | | | | |
| Nov 1982 | ■ | | x | | | |
| Dec 1982 | x | | | | | |
| Apr 1984 | | | x | | | |
| Feb 1985 | | | x | | | |
| Apr 1985 | | | x | | | |
| Dec 1985 | x | ? | | | | |
| Dec 1987 | x | | | | | |
| Jan 1988 | x | | x | | | |
| Mar 1988 | | | x | | | |
| Apr 1988 | | | x | | | x |
| May 1988 | | | x | | | x |
| Oct 1990 | x | | | | ? | ■ |
| Mar 1991 | | | x | | | |
| Oct 1991 | | | | | ■ | |
| Oct 1992 | | | | | ■ | |
| **TOPPSUND, RISØR ca 58° 45' N 09° 10' E** | | | | | | |
| Feb 1976 | | | | | | x* |
| Mar 1976 | | | ■ | | | |
| **RYFYLKEFJORD, ca 59° 20' N 05° 30' E** | | | | | | |
| May 1972 | | | | | | x |
| Oct 1972 | | | | | | x |
| Nov 1972 | | | | | | ■ |

Table 9 (continued)

| Site/Date | *P. pungens* | *P. multiseries* | *P. seriata* | *P. fraudulenta* | *P. pseudo-delicatissima* | *P. delicatissima* |
|---|---|---|---|---|---|---|
| **HARDANGERFJORD, ca 60° 15' N 06° E** | | | | | | |
| Feb 1972 | ? | | | | | |
| Apr 1972 | ? | | x | | | |
| Sept 1972 | | | | | x* | x* |
| **KORSFJORD, ca 60° 15' N 05° 30' E** | | | | | | |
| Oct 1974 | | | | | | x |
| Nov 1974 | | | | | | x |
| Mar 1975 | | | ■ | | | |
| Jun 1975 | | | x | | | |
| Mar 1976 | | | x | x | | |
| Apr 1978 | | | x* | | | |
| Sept 1978 | x | | | x | | ■ |
| Nov 1982 | | | x | | | x |
| May 1982 | x* | | | x | x* | |
| **ESPEGREND, ca 60° 20' N** | | | | | | |
| Mar 1976 | | | x | | | x* |
| Mar 1983 | | | | | | x |
| **BERGEN, ca 60° 21' N 05° 38' E** | | | | | | |
| Mar 1968 | | | x | | | |
| **AREA between 60° 40'- 60° 49' N and 04° 40'- 05° 04' E** | | | | | | |
| Mar 1981 | | | x | | | x |
| May 1981 | | | x | | | x |
| Mar 1982 | | | x | | | |
| **NORDFJORD, ca 61° 50' N 05° 30' E** | | | | | | |
| Mar 1966 | | | x | | | |
| Mar 1967 | | | x | | | |
| **MØRE, ca 63° N 06° E** | | | | | | |
| May 1929 | | | ■ | | | |
| Apr 1968 | | | x | x | | x |
| **KRISTIANSUND, ca 63° 15' N 07° 50' E** | | | | | | |
| Mar 1968 | | | x | | | ■ |
| Apr 1968 | | | x | | x* | x* |

Table 9 (continued)

| Site/Date | *P. pungens* | *P. multiseries* | *P. seriata* | *P. fraudulenta* | *P. pseudo-delicatissima* | *P. delicatissima* |
|---|---|---|---|---|---|---|
| **TRONDHEIMSFJORD, 63° 25' N 10° 20' E** | | | | | | |
| Mar 1964 | | | | | | x |
| Jun 1964 | | | x | x | | ■ |
| Mar 1970 | | | x | | x* | x* |
| Nov 1975 | x | | x | x | | x |
| Mar 1983 | | | x | | | x |
| Mar 1986 | | | x | | | x |
| Oct 1992 | ■ | | x | x | ■ | |
| Aug 1993 | | | | | ■ | |
| **AREA between 64° 40' N and 08° 50'-10° 05' E** | | | | | | |
| Apr 1968 | | | x* | x | x* | x* |
| **SALTFJORD, 67° 19' N 14° 22' E** | | | | | | |
| Jul 1992 | | | x | | | ■ |
| Aug 1992 | | | x* | x* | x* | x* |
| **TROMSØ, 69° 42' N 18° 59' E** | | | | | | |
| Aug 1975 | | | x | | | |
| Mar 1976 | | | x | | | |
| Jul 1992 | | | | | | ■ |

| | |
|---|---|
| ? | identification questionable |
| x | present |
| ■ | abundant |
| x* | TEM identification |

1993; Mackenzie et al., 1993; Villac et al., 1993b; Lange et al., 1994; personal observations). There are no records from polar waters.

Tables 3, 4 and 9 demonstrate a difference in the long-term distribution of *P. pungens* and *P. multiseries* but a similarity in seasonality. The number of records from the Oslofjord and the Skagerrak in the 1960s and 1970s (Tables 4, 9; Hasle, 1965a) gives evidence for *P. multiseries* as a species belonging to the area. It may have been recorded from the Skagerrak as early as 1912 by Cleve-Euler (1917, p. 13 as *Nitzschia pungens* var. *atlantica*) when it "abruptly occurred in rich quantities" in August.

We do not have an explanation for the lack of records from further north along the Norwegian coast and the sparse occurrence along the Skagerrak transect in 1991–1993. A similar drastic reduction of *P. multiseries* occurred in 1992 in the Cardigan River region, Atlantic Canada, and parasitism by a chytrid fungus was suggested as a possible cause (Smith, 1993).

Due to the necessity of electron microscopy for reliable identification of *P. multiseries*, information on its distribution is still scarce. Villac et al. (1993a) summarized the distribution area as Atlantic waters of North America, Europe and South America, and Pacific waters of North America and Northeast Asia. Our observations from European waters include records from The Sound (between Sweden and Denmark), Kiel Bay, Helgoland, with June 1992 as the most recent record, and the English Channel.

*Pseudo-nitzschia seriata* and *P. delicatissima* were recorded in phytoplankton investigations carried out in the Skagerrak around the turn of the century (e.g. Cleve, 1897a, 1900; Gran, 1915; Cleve-Euler, 1917), and in water samples collected every month from February 1957 through May 1958 at Drøbak, Oslofjord (Hasle & Smayda, 1960). The records of *P. seriata* and *P. delicatissima* in these investigations characterize *P. seriata* as a winter-spring form in the area while the seasonal distribution of *P. delicatissima* is more erratic.

The present study supports the former characterization of *P. seriata* as a winter-spring species (Table 5), not only in the Skagerrak area but also along the Norwegian west and north coasts (Table 9). Although the seasonal distribution pattern regarding the onset and time span of greatest abundances varied from year to year in the Skagerrak area, it occurred always during the coldest part of the year (between January and May; Lange et al., 1992, Table 3). This agrees with Hasle's (1972) characterization of *P. seriata* as a cold-water species, most likely restricted to the northern hemisphere, and with observations from northern European waters (English Channel as the southernmost locality) in the 1970s (pers. observations).

Our observations on the distribution of *P. delicatissima* (Table 7) also correspond well with those from the Skagerrak and the Oslofjord in the past; it may be found at all seasons but in greatest abundances during winter and spring. This seems to be the case also in the Oslofjord and further northwards along the Norwegian coast, if only records based on TEM are taken into consideration (Table 9). Since *P. delicatissima* is another species that often requires EM for reliable identification, its global distribution is poorly known. In addition to Norwegian waters it has been reported from Danish, northwest African and Californian waters (Hasle, 1965a; Villac et al., 1993b; Lundholm et al., 1994) and perhaps from Japan (Takano & Kuroki, 1977).

*Pseudo-nitzschia fraudulenta* (Table 6) and *P. heimii* are regular components of the plankton of the Norwegian Sea and the North Atlantic (Hasle, 1965a) and have most likely been advected into the Skagerrak area. It may be noted that *P. fraudulenta* was recorded as far north as 67 °N along the Norwegian coast (Table 9), and that in addition to the distribution reported by Hasle (1972) the species has been observed from Japan (Takano & Kuroki, 1977), from Chile (Rivera, 1985) and from Rhode Island, U.S.A. (Hargraves et al., 1993).

*Pseudo-nitzschia pseudodelicatissima* was observed in fair numbers in the autumn before the regular sampling program started (see above). The apparent increase in abundance as well as frequency of occurrence in the 1990s is considerable, however (Table 8). Massive blooms were reported from early July to mid-October 1992 in Scandinavian and western Baltic waters (Edler, 1993; Hansen & Horstmann, 1993; Lundholm & Skov, 1993), and high concentrations were seen even earlier in 1993 (Table

8, and K. Tangen, pers. comm.). We have observed *P. pseudodelicatissima* as far north as 67 °N along the Norwegian coast (Table 9). The known distribution may be summarized as: Atlantic waters of Europe and Africa (Denmark Strait to NW Africa), Canada and U. S. A. (Arctic to Gulf of Mexico), Pacific waters of British Columbia, California and Chile, and Japan (Hasle, 1965a; Takano & Kuroki, 1977; Martin et al., 1990; Villac et al., 1993b; Edler, 1993; Hansen & Horstmann, 1993; Lundholm & Skov, 1993; Taylor, 1993; Lange et al., 1994; Villareal et al., 1994).

In conclusion, the *Pseudo-nitzschia* species found to produce domoic acid are present (*P. australis* excepted) in the investigated area as well as in other North European waters, although ASP has never been reported.

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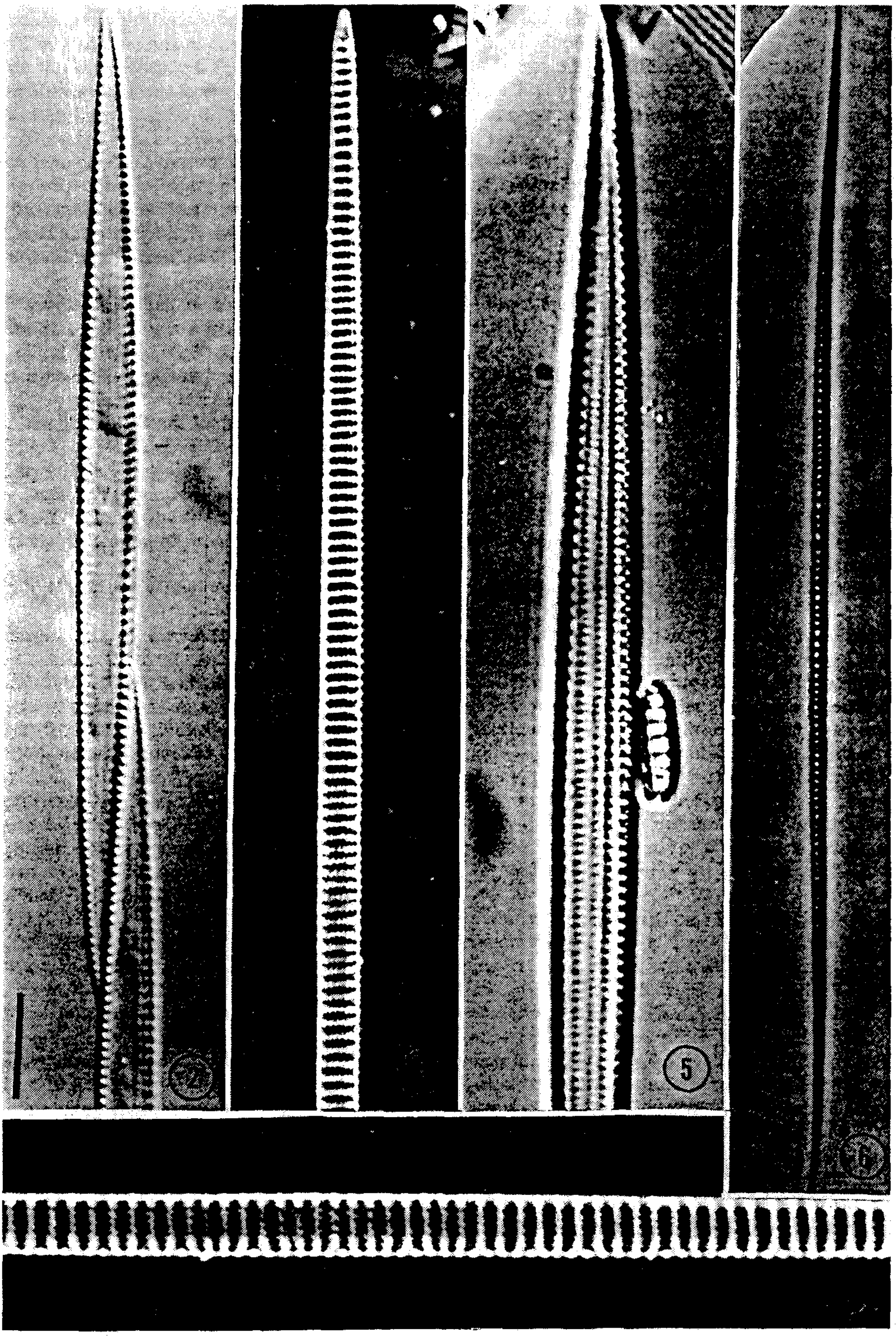
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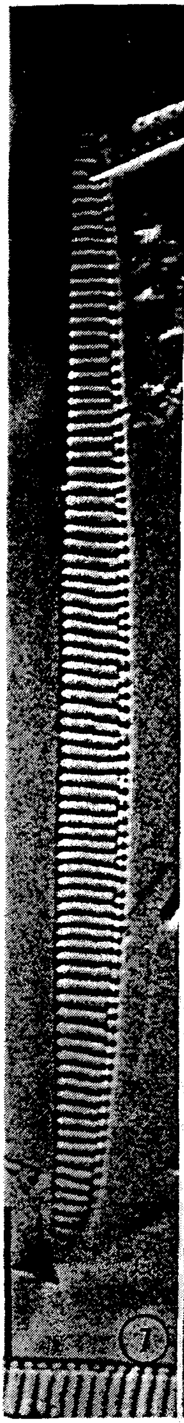
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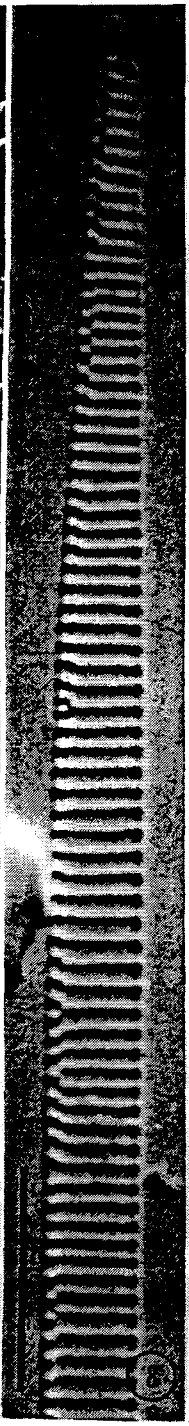
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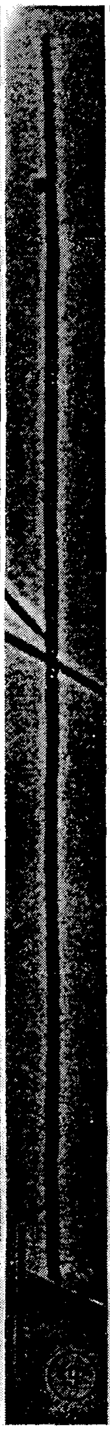
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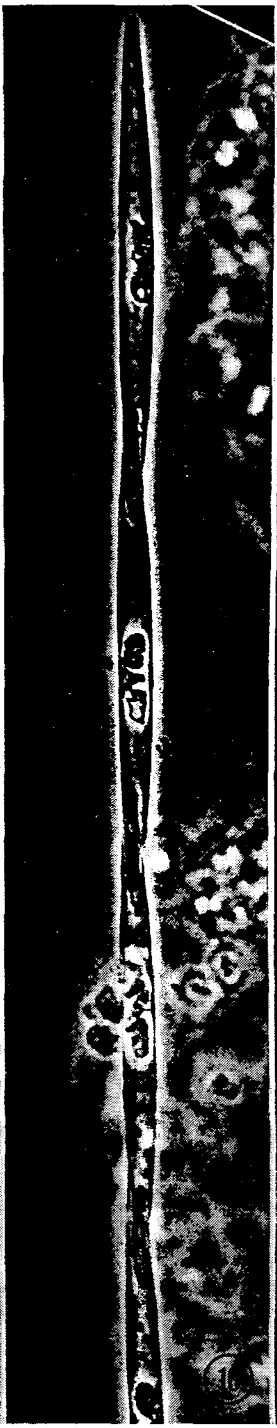
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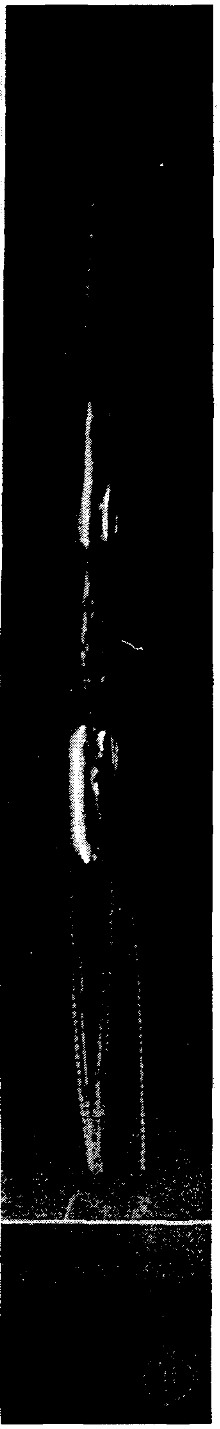
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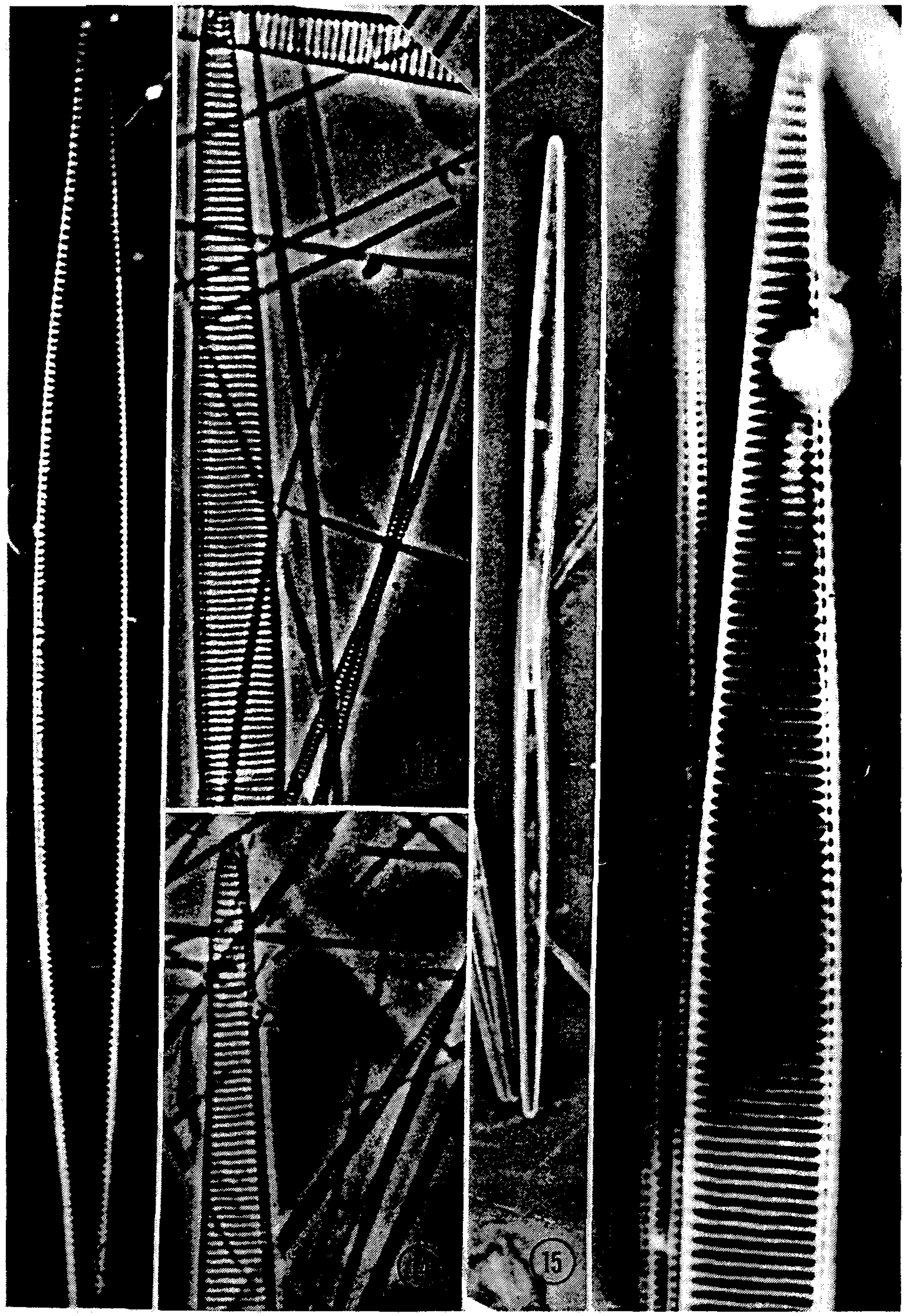
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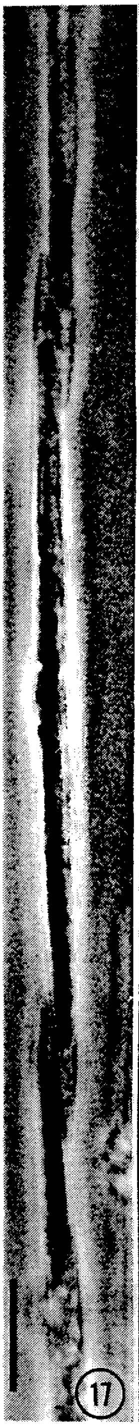
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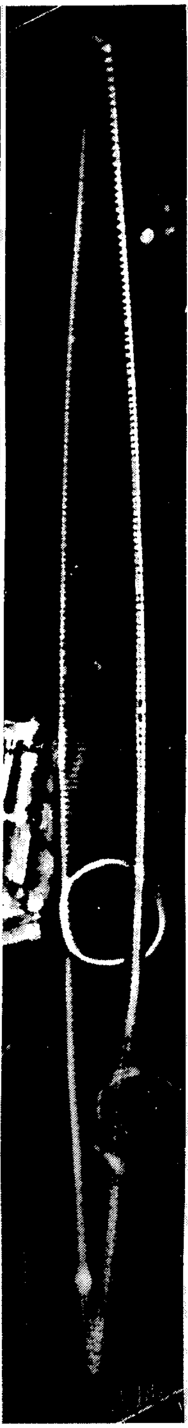

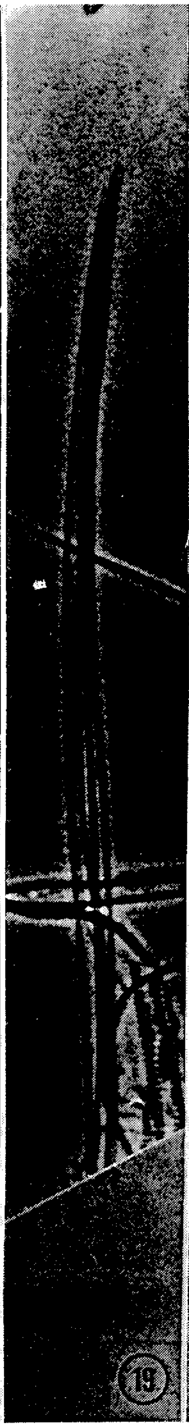
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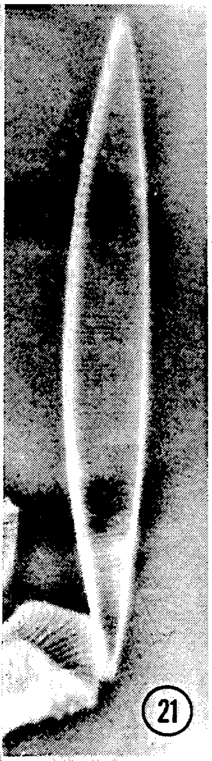
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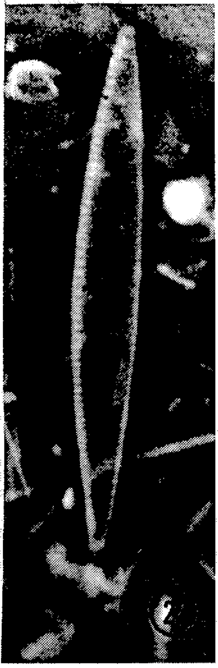
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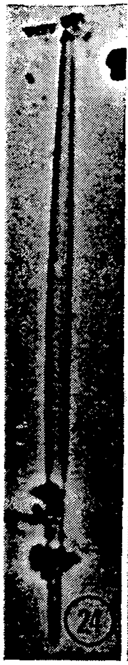
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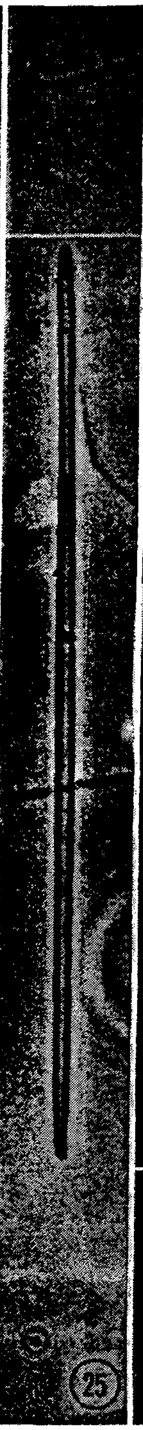
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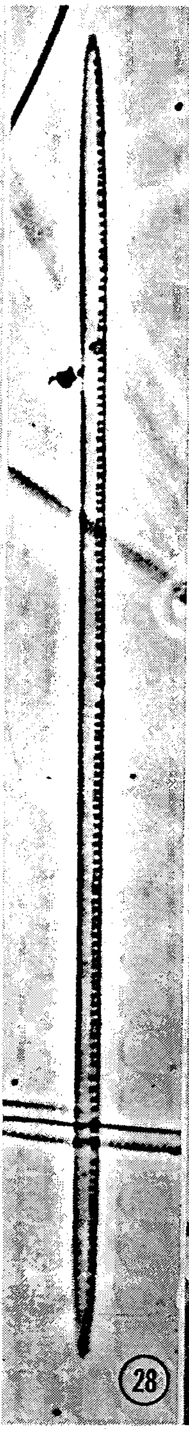
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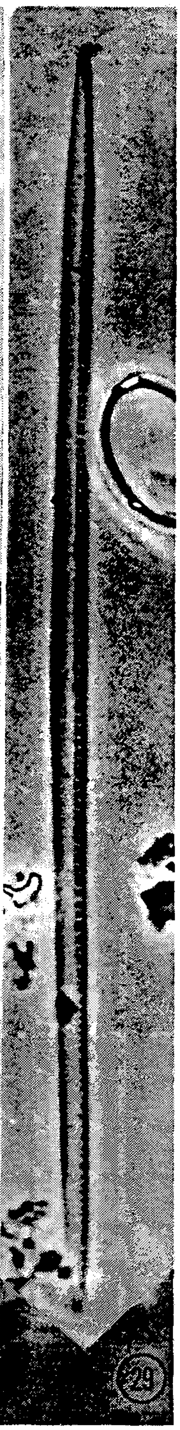
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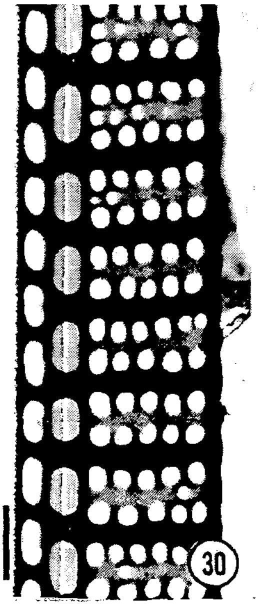

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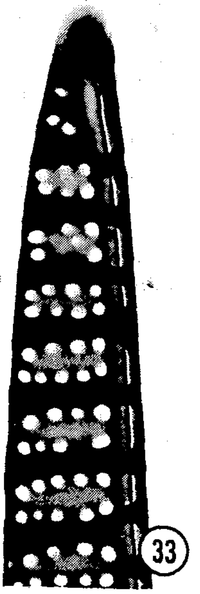

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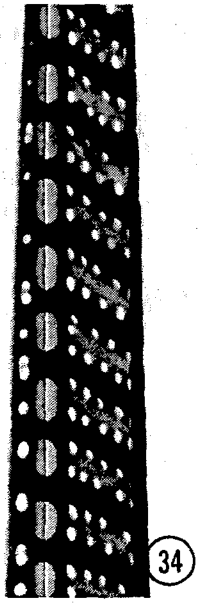

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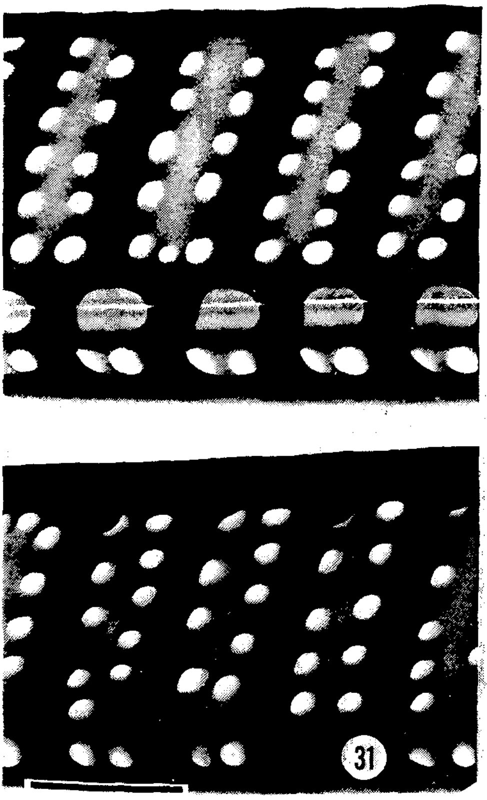

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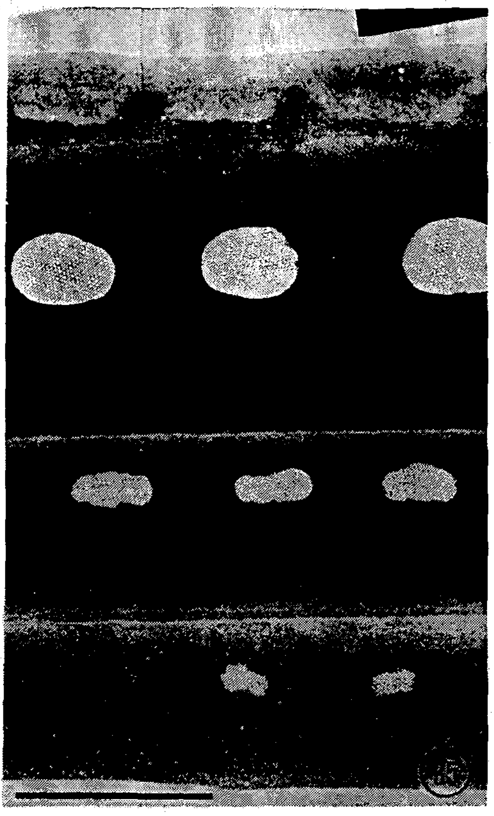

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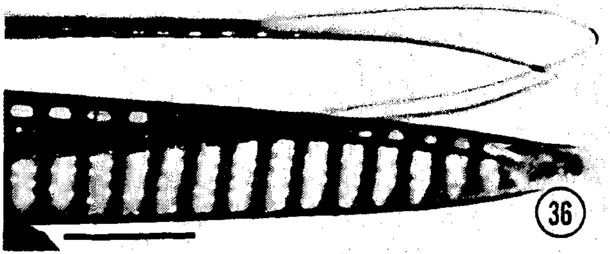
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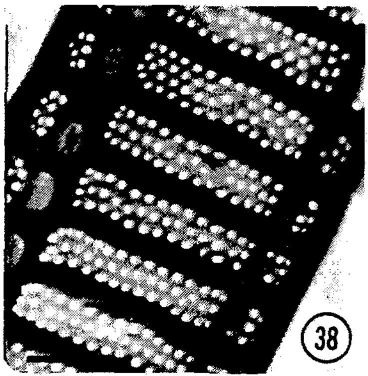
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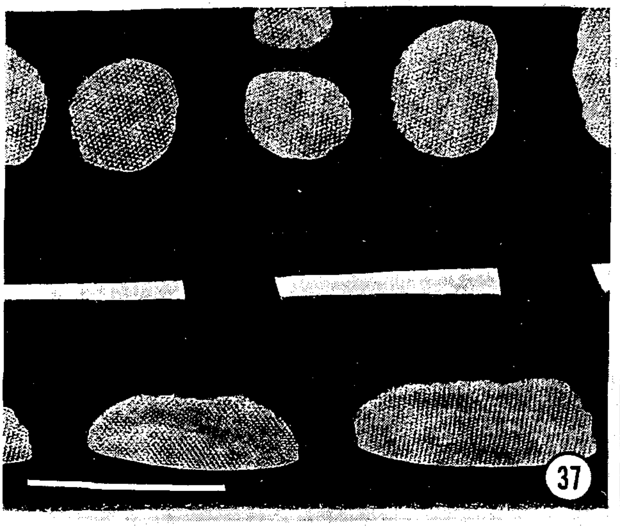
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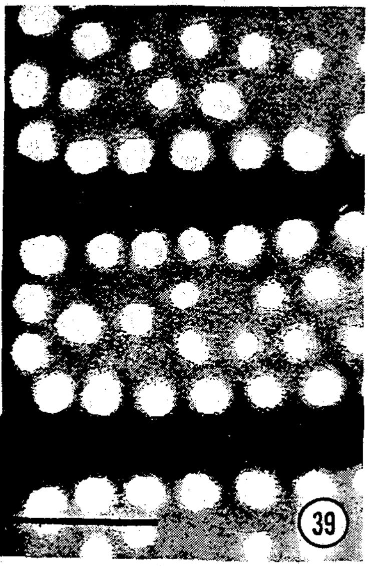
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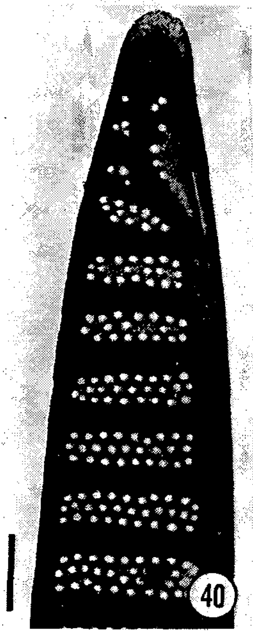
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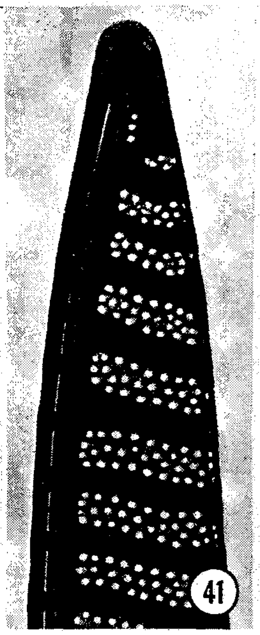
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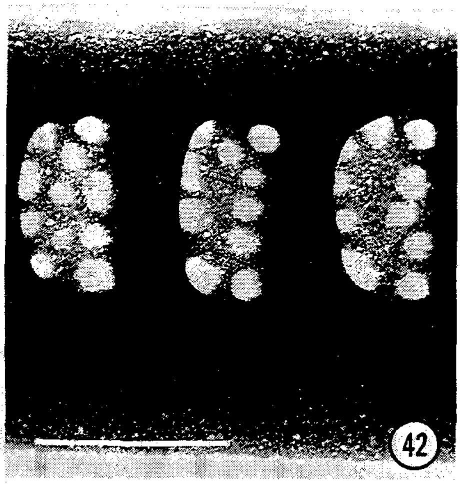
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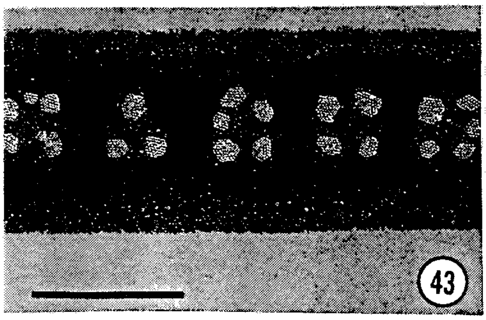
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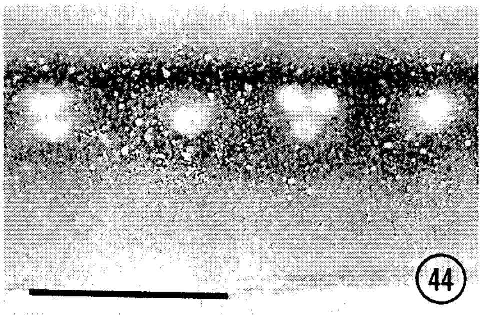
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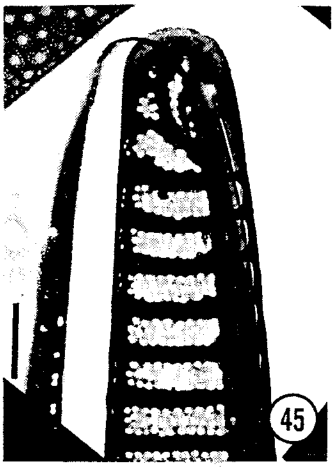
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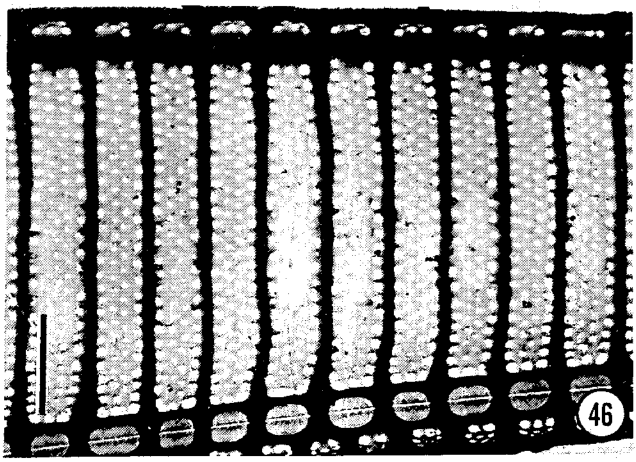
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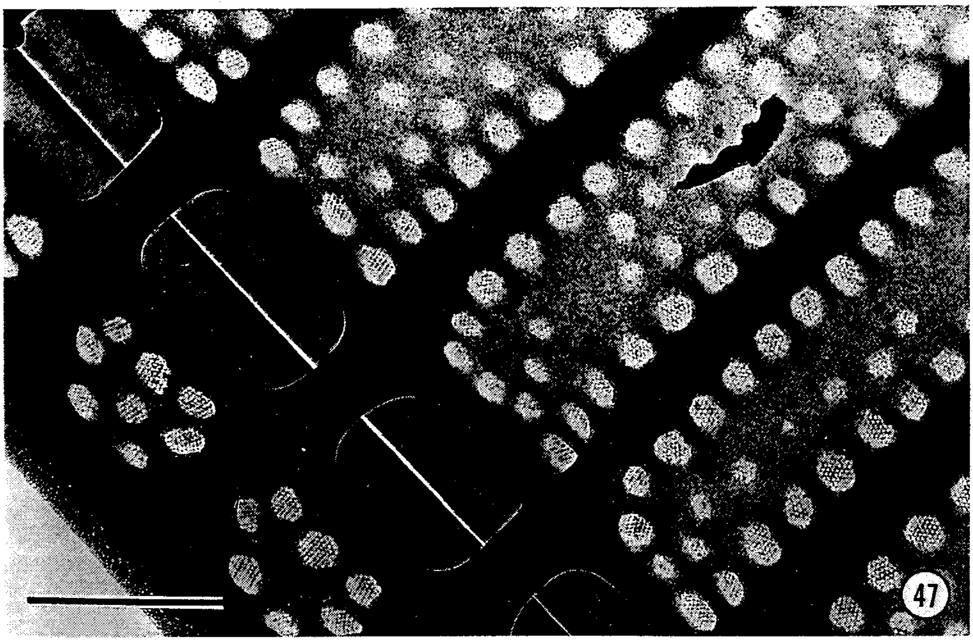
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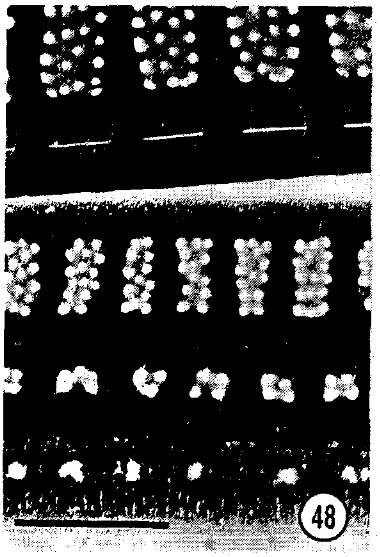
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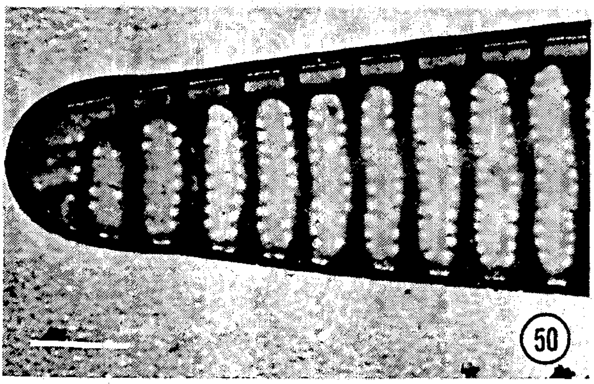
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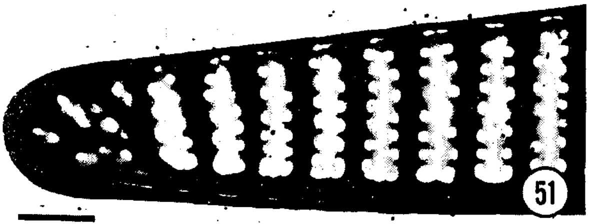
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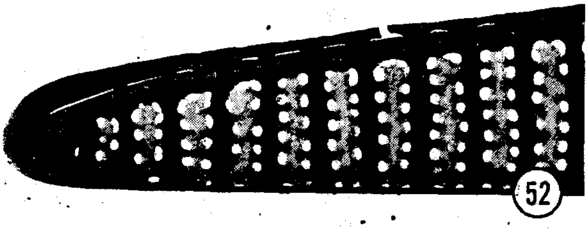
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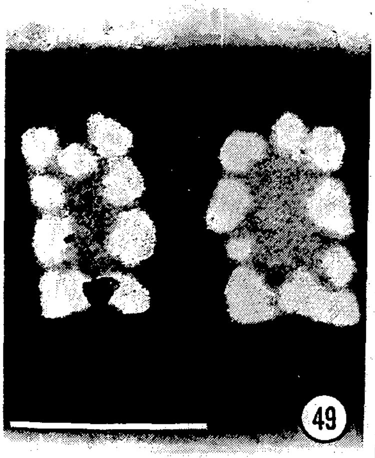
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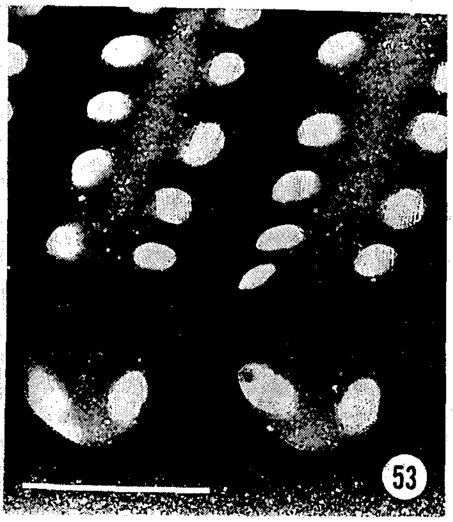
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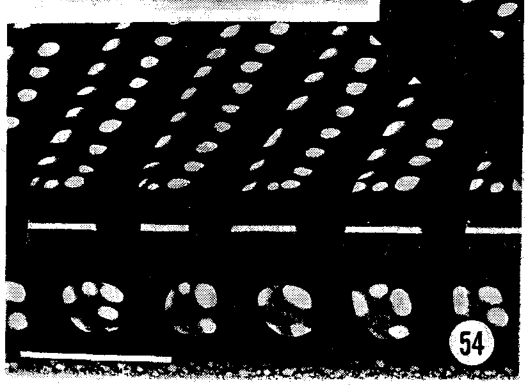
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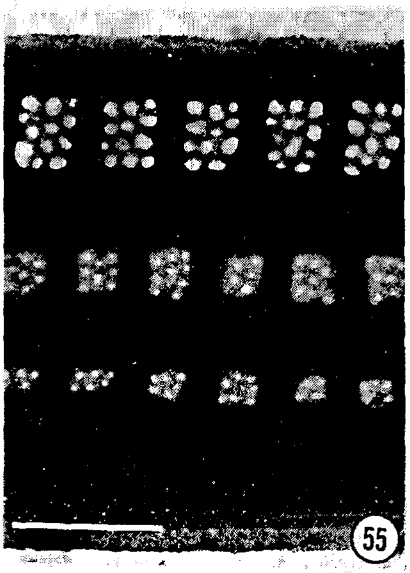
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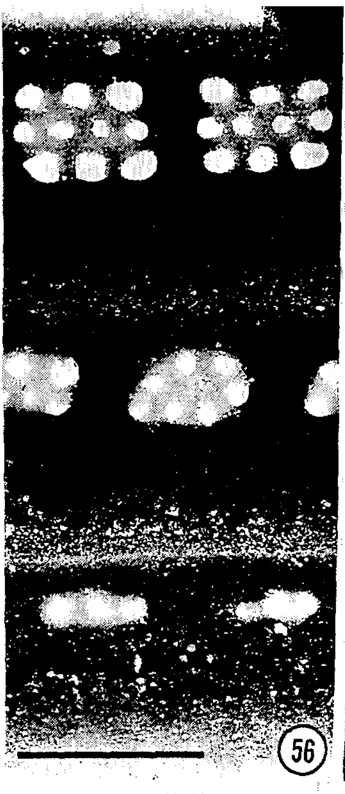
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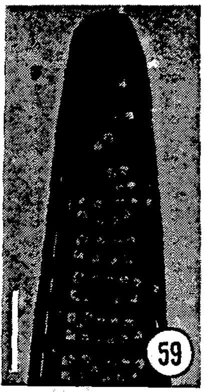
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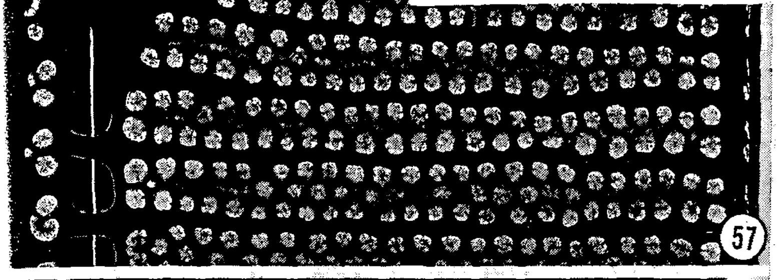
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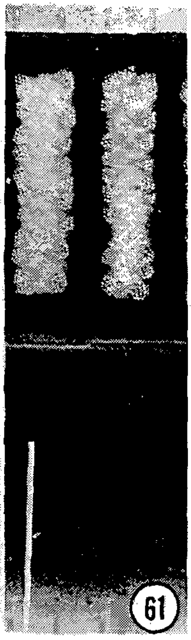
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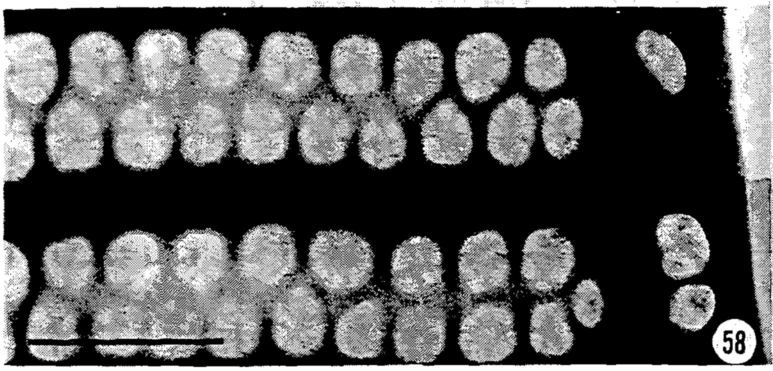
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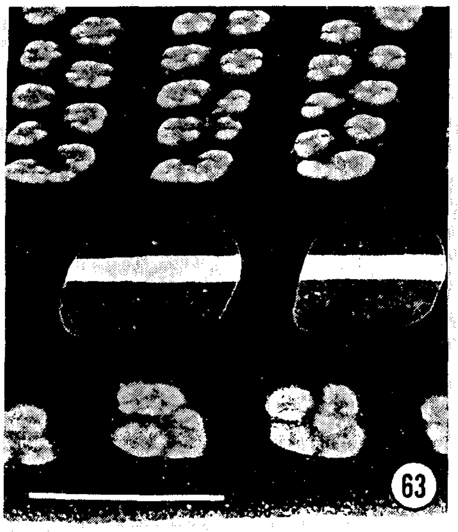
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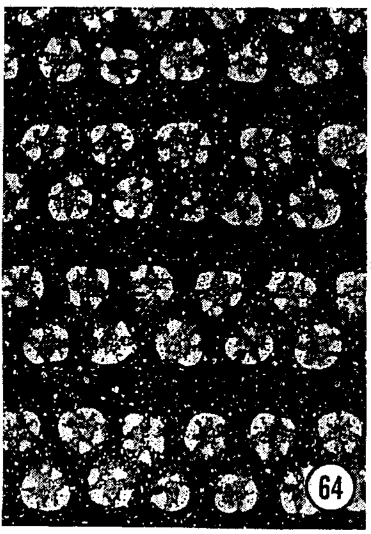
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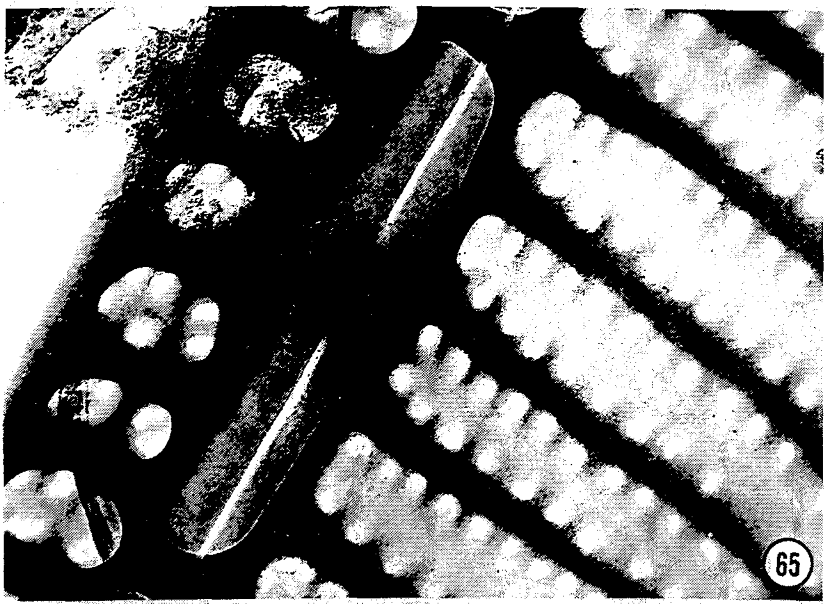
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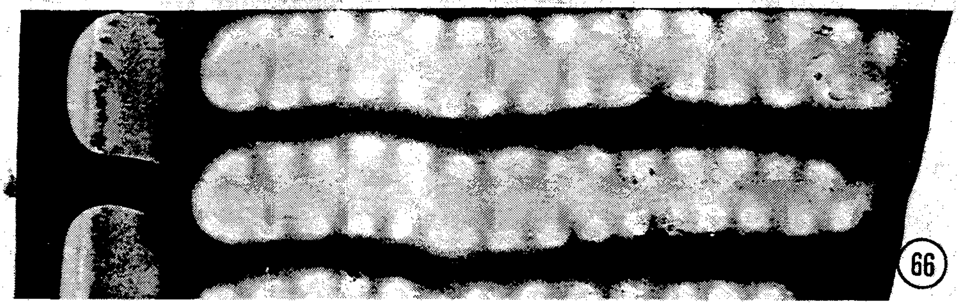
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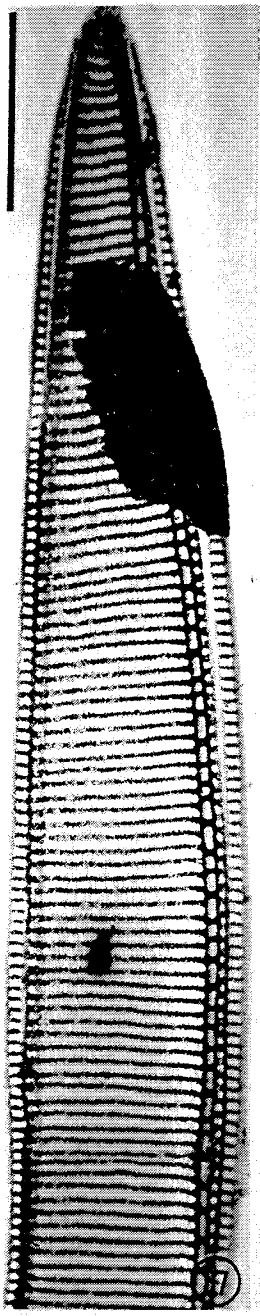

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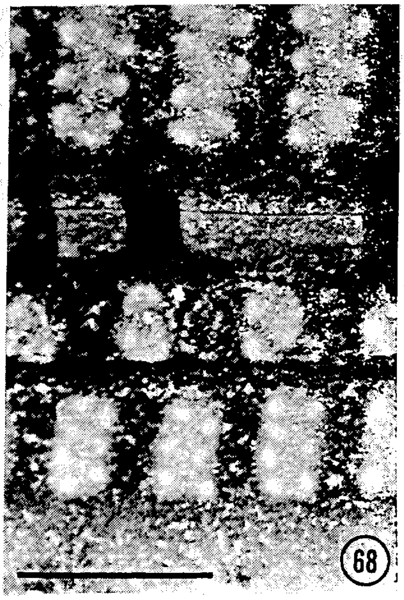

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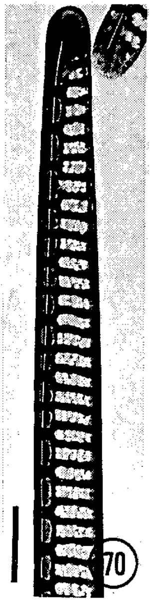

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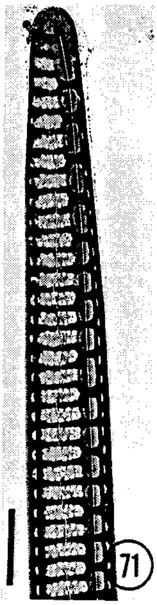

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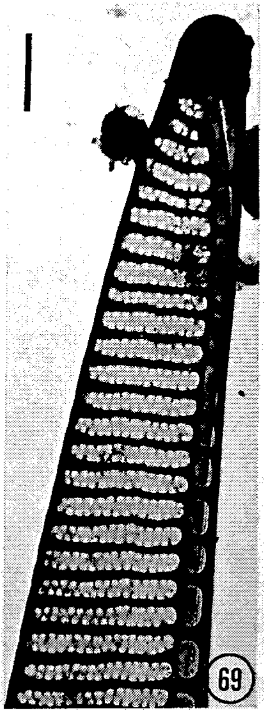

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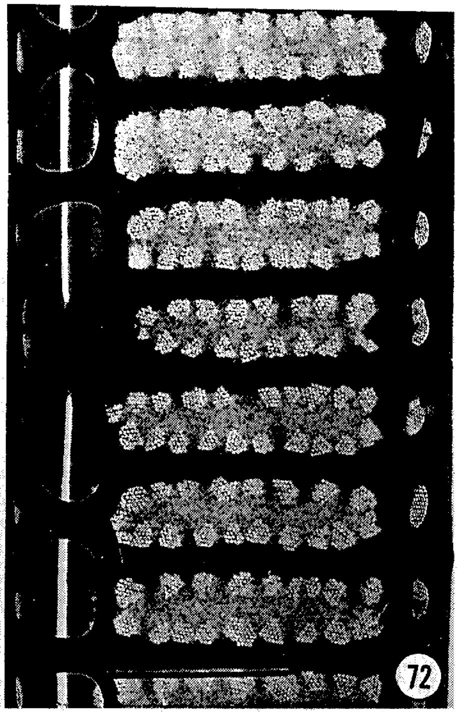

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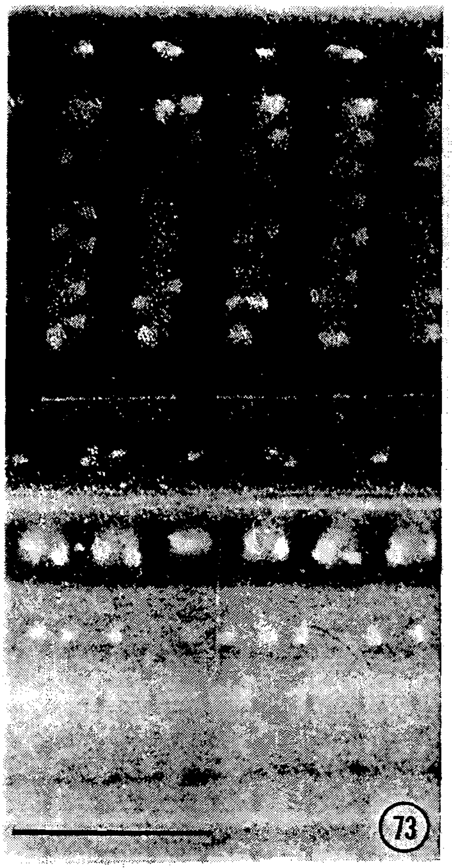
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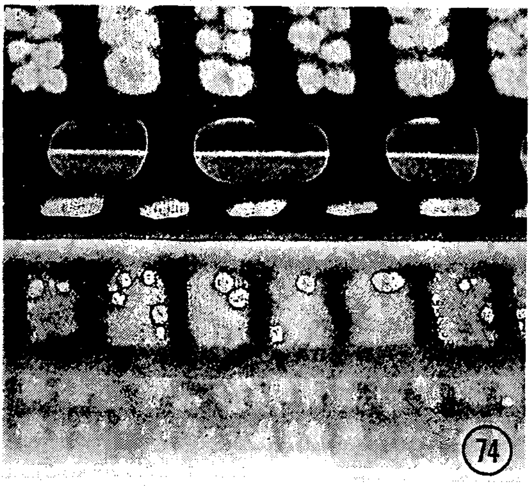
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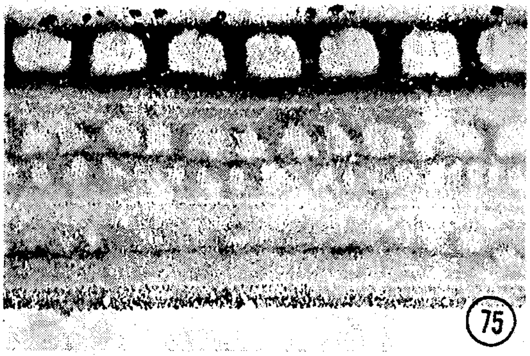
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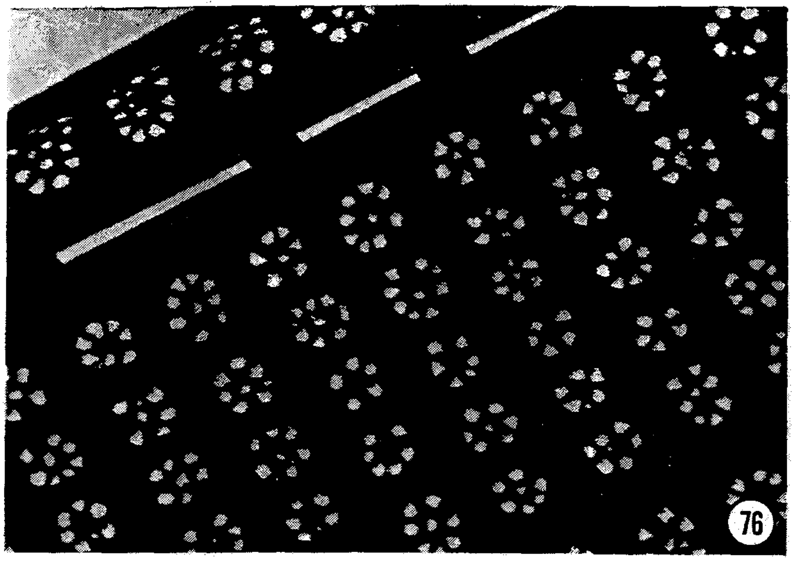
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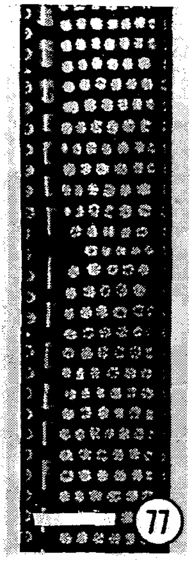
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Figs 2–6. LM. Fig. 2. *Pseudo-nitzschia multiseries*, Skagerrak, North Atlantic, 18th January 1968; part of chain in girdle view; note overlap and shape of cell ends and distinct interstriae. Figs 3, 4. *P. pungens*, Skagerrak, 12th September 1990; parts of valves in valve view, valve striae with two rows of poroids. Fig. 5. *P. pungens*, Dutch coastal waters; cell in girdle view, coarsely structured valves and bands. Fig. 6. *P. pungens*, clonal culture, Trondheimsfjord, Norway, 28th October 1992; half of a band. Scale bars = 10 μm, Figs 3, 5 and 6 the same magnification

Figs 7–11. LM. Figs 7–9. *Pseudo-nitzschia multiseries*. Figs 7, 8. Skagerrak, North Atlantic, 18th January 1968 and 7th December 1989, respectively; both valves in valve view; poroids are not resolved. Fig. 9. Clonal culture TKA2, Galveston, Gulf of Mexico; part of band. Figs 10, 11. *P. seriata* f. *seriata*, Oslofjord, Norway, 17th March 1976. Fig. 10. Chain in valve view, water mount; note overlap of cell ends and one straight and one curved valve margin. Fig. 11. Part of a chain in girdle view, water mount; note chloroplasts, overlap and shape of cell ends and indistinct interstriae. Scale bars = 10 μm

Figs 12–16. LM. Figs 12–14. *Pseudo-nitzschia seriata* f. *seriata*. Fig. 12. Møre, Norwegian west coast, 5th April 1968; valve in valve view showing fibulae (to the left) and faint interstriae. Figs 13, 14. Inner Oslofjord, Norway, 24th March 1976; parts of valves and bands, one band with the loop (closed end) intact. Fig. 15. *P. seriata* f. *obtusa*, Baffins Bay, Arctic Ocean, BM 33027; short chain in valve view, note obtuse shape of valve ends and one valve margin more curved than the other. Fig. 16. *P. australis*, Puerto Quequén, Argentina; part of valve in valve view and bands; note the prolonged valve end, the fibulae (to the right) and the interstriae. Scale bars = 10 μm; Figs 12–15 have the same magnification

Figs 17–22. LM. Figs 17–19. *Pseudo-nitzschia fraudulenta*. Figs 17, 19. Clonal culture, Trondheimsfjord, Norway, 28th October 1992. Fig. 17. Chain in girdle view, water mount; note overlap and shape of cell ends, interstriae are not resolved. Fig. 19. Bands. Fig. 18. Møre, Norwegian west coast, 5th April 1968; valve in valve view showing fibulae (to the right), central nodule in central larger interspace and faint interstriae. Fig. 20. *P. heimii*, Skagerrak, North Atlantic, 7th December 1989; valve in valve view; note one straight and one curved margin, fibulae (to the left), central larger interspace and faint interstriae. Figs 21, 22. *P. subpacifica*, off NW Africa, 1970; valves in valve view showing fibulae (to the left), central larger interspace (Fig. 22), and faint interstriae (Fig. 21). Scale bars = 10 μm; Figs 18–22 have the same magnification

Figs 23–29. LM. Figs 23–25. *Pseudo-nitzschia delicatissima*. Fig. 23. Helder, the Netherlands, 7th May 1897 (P. T. Cleve slide). Figs 24, 25. Skagerrak, North Atlantic, 7th December 1989 and 26th May 1953, respectively; all valves in valve view; note fibulae (Figs 23, 24 to the left, Fig. 25 to the right). Figs 26–29. *P. pseudodelicatissima*. Fig. 26. Outer Oslofjord, Norway, September 1991; part of a chain in girdle view, water mount; note overlap and shape of valve ends. Fig. 27. Holotype, Denmark Strait, 24th May 1898. Fig. 28. Outer Oslofjord, 18th September 1991; Fig. 29. Skagerrak, 7th December 1989; all valves in valve view showing fibulae (to the right) with central larger interspace. Scale bars = 10 μm; all figures except Fig. 26 have the same magnification

Figs 30–35. TEM. *Pseudo-nitzschia pungens*. Fig. 30. Skagerrak, North Atlantic, 30th August 1988; part of valve with raphe and proximal mantle with large single poroids. Figs 31–35. Clonal culture, Trondheimsfjord, Norway, 28th October 1992. Figs 31, 34. Parts of valves, tilt 40°; note the structure of the proximal mantle and the distal mantle (Fig. 31 at the bottom, with the strip of silica between valve face and distal mantle). Figs 32, 33. Two ends of one valve, note the difference in stria structure. Fig. 35. Part of girdle with three areolated bands, each with one row of hymenate poroids in the longitudinal direction. Scale bars: Figs 30–34 = 1 μm; Fig. 35 = 0.5 μm; Figs 30, 32–34 the same magnification

Figs 36–42. TEM. Figs 36, 37. *Pseudo-nitzschia pungens*. Fig. 36. Peruvian waters, 06°56′ S, 80°23′ W; valve end and two alternating bands, one showing the opening and the other the closed loop. Fig. 37. Helgoland, 30th June 1992; part of valve with raphe and proximal mantle, note the hexagonal hymenate vela. Figs 38–42. *P. multiseries*. Fig. 38. Drøbak, Oslofjord, Norway, 4th March 1959; part of valve with raphe, proximal and distal valve mantle, and strip of silica between valve face and distal mantle. Fig. 39. Clonal culture F445, Galveston, Gulf of Mexico, part of valve, showing hexagonal hymenate poroid vela. Figs 40–42. Skagerrak, 18th January 1968. Figs 40, 41. Two ends of one valve, note the difference in terminal interstriae. Fig. 42. Part of valvocopula with striae of small hymenate poroids. Scale bars: Fig. 36 = 5 μm; Figs 38, 40, 41 = 1 μm; Figs 37, 39, 42 = 0.5 μm

Figs 43–47. TEM. Figs 43, 44. *Pseudo-nitzschia multiseries*, clonal culture TKA2, Galveston, Gulf of Mexico; part of bands. Figs 45–47. *P. seriata* f. *seriata*. Fig. 45. Toppsund, Risør, Norwegian south coast, 29th February 1976; valve end and the narrow closed loop of a band. Fig. 46. Norwegian Sea, 17th April 1962; part of valve with raphe, proximal and distal mantle, and strip of silica between valve face and distal mantle. Fig. 47. Salten, Bodø, North Norway, 3rd August 1992; part of valve with raphe and proximal mantle, note hexagonal hymenate poroids. Scale bars: Figs 43, 44, 47 = 0.5 μm; Figs 45, 46 = 1 μm

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Figs 48–54. TEM. Figs 48, 49. *Pseudo-nitzschia seriata* f. *seriata*. Fig. 48. Toppsund, Risør, Norwegian south coast, 29th February 1976; part of girdle with three areolated and one narrow non-areolated band (at the bottom). Fig. 49. Salten, Bodø, North Norway, 3rd August 1992; valvocopula, striated with hexagonal hymenate poroids. Fig. 50. *P. seriata* f. *obtusa*, Kabelvåg, North Norway, 21st March 1962; valve end showing striae with two rows of poroids. Figs 51–54. *P. australis*. Figs 51, 52. Clonal culture MB-9, Monterey Bay, California; two ends of one valve, note the difference in terminal interstriae. Fig. 53. Clonal culture MB-9, Monterey Bay, California; part of valve with distal mantle and strip of silica at the bend between valve face and mantle, note hexagonal hymenate poroids, tilt 45°. Fig. 54. Cape Town, South Africa, 8th January 1993; part of valve with raphe and proximal mantle, tilt 55°. Scale bars: Figs 48, 50, 51, 54 = 1 μm; Figs 51 and 52 have the same magnification; Figs 49, 53 = 0.5 μm

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Figs 55–61. TEM. Figs 55, 56. *Pseudo-nitzschia australis*. Fig. 55. Cape Town, South Africa, 20th April 1967; part of girdle with three areolated and one narrow non-areolated band. Fig. 56. Clonal culture MB-9, Monterey Bay, California; part of girdle with three areolated bands, note hexagonal hymenate poroids. Figs 57–61. *P. fraudulenta*. Fig. 58. Flødevigen Marine Research Station, Norwegian south coast, 14th October 1990; part of valve with siliceous strip between valve face and distal mantle, note poroids with sectors of hymenate velum. Figs 57, 59–61. Clonal culture, Trondheimsfjord, 28th October 1992. Fig. 57. Part of valve showing raphe, central nodule, central larger interspace and proximal mantle, tilt 25°. Figs 59, 60. Two ends of the same valve, note difference in terminal interstriae. Fig. 61. Part of girdle with one wide, areolated and two non-areolated bands, note the angular hymenate vela which are different from those on the valve. Scale bars: Figs 55, 59 = 1 μm; Figs 55 and 57 have the same magnification; Figs 59 and 60 have the same magnification; Figs 56, 58, 61 = 0.5 μm

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Figs 62–66. TEM. Figs 62–64. *Pseudo-nitzschia subfraudulenta*, off Portugal, 41°50′ N, 08°54′ W, 23rd November 1985. Fig. 62. Part of valve showing the straight margins at the middle part and tapering valve end, the raphe with the central nodule and the central larger interspace. Fig. 63. Part of valve with raphe and proximal mantle. Fig. 64. Part of valve, note poroids with sectors of hymenate vela. Figs 65, 66. *P. heimii*, Flødevigen Marine Research Station, Norwegian south coast, 14th October 1990; parts of valves with raphe and proximal mantle, central nodule and central larger interspace (Fig. 65), note small hexagonal hymenate poroids (Fig. 66). Scale bars: Fig. 62 = 10 μm; Fig. 63 = 0.5 μm; Figs 63–66 have the same magnification

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Figs 67–72. TEM. Figs 67–69. *Pseudo-nitzschia heimii*. Figs 67, 68. Skagerrak, North Atlantic, 14th October 1991; part of a valve with valvocopula attached, raphe with central nodule along the curved margin (Fig. 67), proximal mantle and valvocopula striated as the valve (Fig. 68). Fig. 69. Flødevigen Marine Research Station, Norwegian south coast, 14th October 1990. Figs 70–72. *P. delicatissima*, Skagerrak, 26th May 1953. Figs 70, 71. Two ends of one valve, no difference in structure. Fig. 72. Part of valve with raphe, central nodule and larger interspace, mantle with single poroids, siliceous strip at the bend between valve face and distal mantle, valve striae with angular hymenate poroids. Scale bars: Fig. 67 = 5 μm; Figs 69–71 = 1 μm; Figs 68, 72 = 0.5 μm

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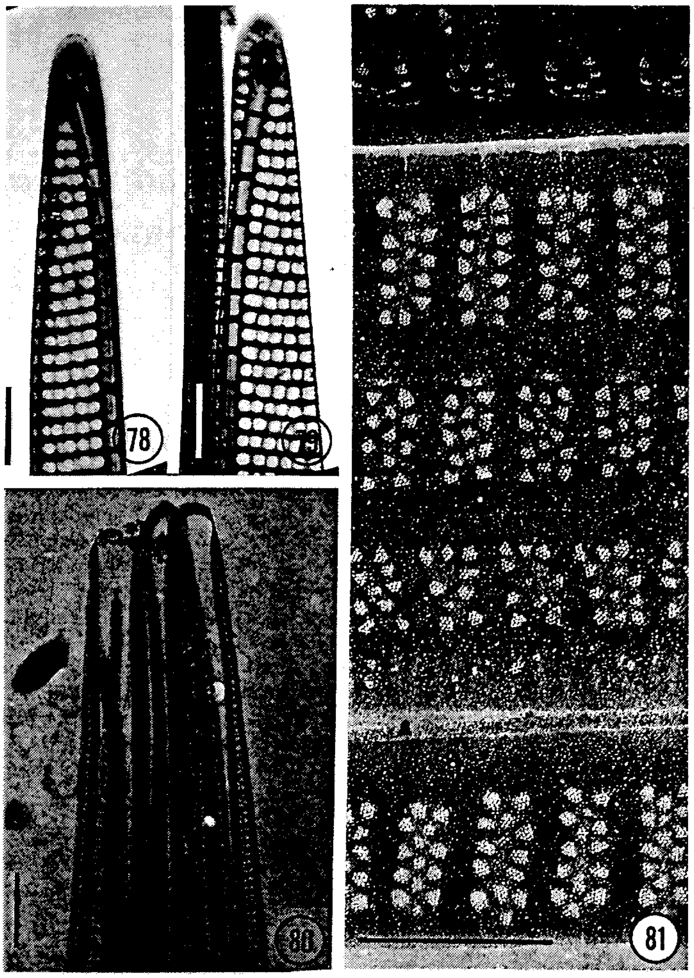
Figs 73–77. TEM. Figs 73–75. *Pseudo-nitzschia delicatissima*. Fig. 73. Toppsund, Risør, Norwegian south coast, 29th February 1976; part of valve and girdle showing two (?) areolated and two (?) non-areolated bands. Figs 74, 75. Skagerrak, 26th May 1953. Fig. 74. Part of valve with raphe and proximal mantle with 1–2 poroids per "stria", valvocopula with one row (in longitudinal direction) of large, square, single hymenate poroids, next band with two separated rows of more irregular poroids, at the bottom apparently an extremely narrow non-areolated band. Fig. 75. A similar girdle, but the poroids of the valvocopula are partly split. Figs 76, 77. *P. pseudodelicatissima*. Fig. 76. Kiel Bay, Baltic Sea, 9th September 1992; part of valve showing raphe, proximal mantle and hymenate vela divided into many sectors. Fig. 77. Skagerrak, North Atlantic, 7th December 1989; part of valve with proximal mantle, raphe, central nodule and central larger interspace. Scale bars: Fig. 73 = 0.5 μm; Figs 73–76 have the same magnification; Fig. 77 = 1 μm



Figs 78–81. TEM. *Pseudo-nitzschia pseudodelicatissima*. Figs 78, 79. Skagerrak, North Atlantic, 14th October 1991; two ends of one valve, no difference in structure. Fig. 80. Outer Oslofjord, 18th September 1991; part of girdle showing alternating open and closed poles (loops). Fig. 81. Skagerrak, 26th May 1953; part of girdle, epitheca at the top with epivalve, three wide, areolated bands and probably one, extremely narrow band, and valvocopula of hypotheca; note striae of angular hymenate poroids. Scale bars: Figs 78–80 = 1 μm; Fig. 81 = 0.5 μm