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A new approach to the taxonomy

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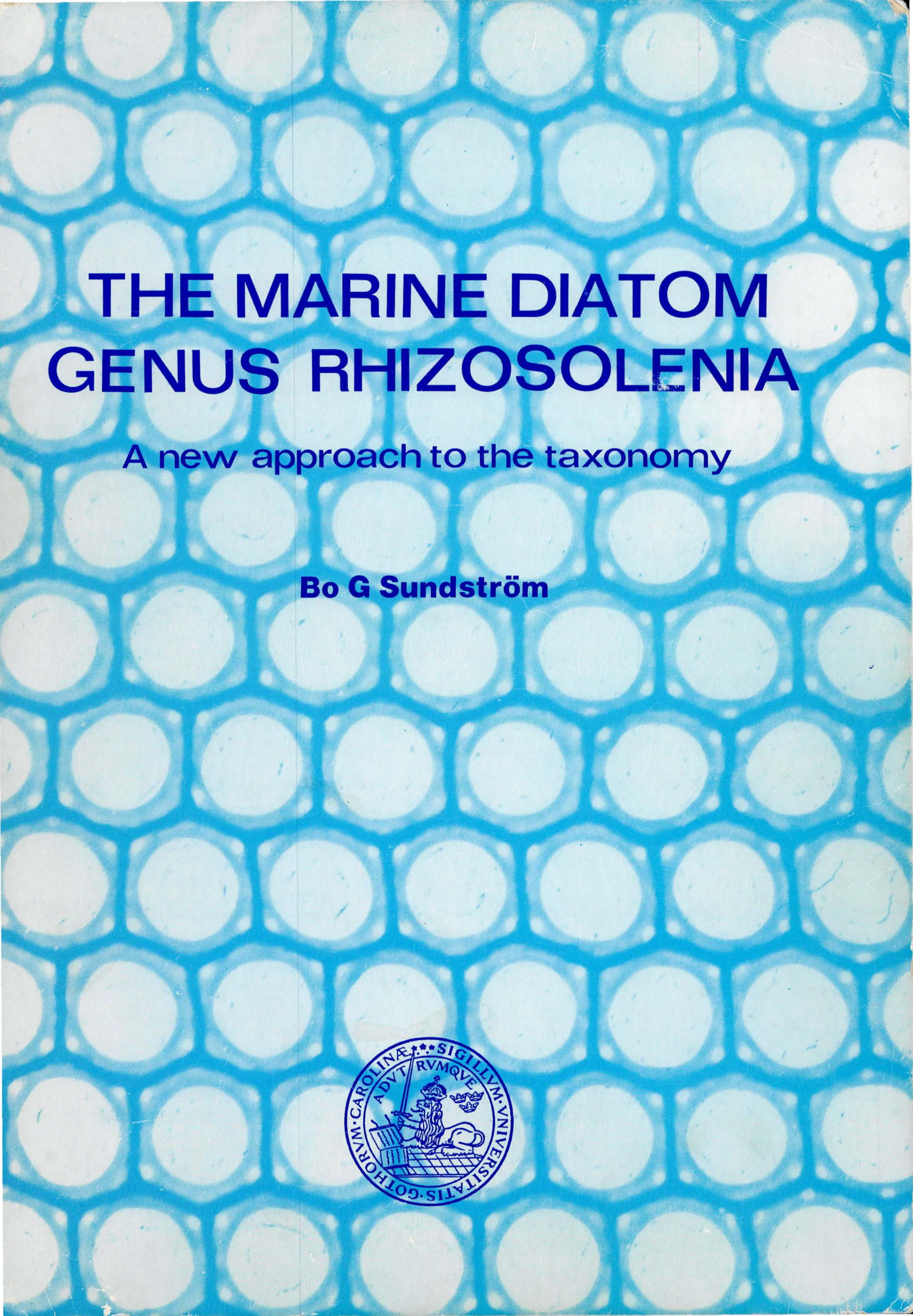

THE MARINE DIATOM GENUS RHIZOSOLENIA

A new approach to the taxonomy

Bo G Sundström

SIGILLVM·VNIVERSITATIS·GOTHORVM·CAROLINÆ

ADVTRVMQVE

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Title and subtitle

THE MARINE DIATOM GENUS RHIZOSOLENIA
A new approach to the taxonomy

Abstract

The silica wall in 35 species of the marine planktonic diatom genus *Rhizosolenia* Brightwell has been examined with light and electron microscopy. The genus *Rhizosolenia* is revised and an emended circumscription comprising 24 species is proposed. Five new species (*Rh. acicularis, Rh. borealis, Rh. ostenfeldii, Rh. fallax, Rh. decipiens*) and four new infraspecific taxa (*Rh. polydactyla* f. *squamosa, Rh. castracanei* var. *neglecta, Rh. antennata* f. *semispina, Rh. sima* f. *silicea*) are described. *Rh. calcar-avis* Schultze has been transferred to the new genus *Pseudosolenia,* and *Rh. alata* Brightw. to the new genus *Proboscia.* Several traditional *Rhizosolenia* species are regarded as belonging to other genera but pending further research are retained in the genus.

The taxonomy of the species recognized in *Rhizosolenia, Pseudosolenia* and *Proboscia*, and the circumscription of the family Rhizosoleniaceae are discussed. The use of the concepts of species, variety and form in diatom taxonomy is discussed. A key is provided. All taxa are illustrated.

Key words: Diatoms; *Bacillariophyceae;* phytoplankton; marine; taxonomy; *Rhizosolenia; Pdseudosolenia; Proboscia;* revision; monograph.

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CONTENS

INTRODUCTION

The diatom genus *Rhizosolenia* Brightwell is one of the most important genera of marine phytoplankton and sometimes dominates the phytoplankton biomass in highly productive areas of the ocean.

Of tradition *Rhizosolenia* comprises an inhomogeneous group of centric planktonic diatoms having in common the tubular cell shape and the valve terminated by a single process or process-like structure. Simonsen (1974) expressed the opinion that a modern revision of *Rhizosolenia* was badly needed: "...not only of the several species belonging to this genus, but also very likely a total revision of the present species concept within this genus."

This monograph is an attempt to sort out the taxonomy of *Rhizosolenia* . To accomplish this I have found it necessary to emend the circumscription of the genus itself as well as that of many of the commonly accepted species. Moreover, it has been necessary to leave many of the traditional species in a taxonomical vacuum since neither time nor money have allowed of a complete treatment of all species described under the name of *Rhizosolenia.* It is my hope that I shall be able to continue research on them in the future.

EARLIER TREATMENTS

The name *Rhizosolenia* was introduced by Ehrenberg (1843). His concept of the genus was, however, soon replaced by Brightwell's (1858), whose genus definition was, after a proposal by Hendey (1937), conserved with *Rhizosolenia styliformis* Brightwell as the type (International Code of Botanical Nomenclature, 1952). The reasons for this were reviewed by Hendey (1937, 1964).

Brightwell's description of *Rhizosolenia* reads: "Rhizosolenia. Filamentous, frustules subcylindrical, greatly elongated, silicious, marked by transverse lines, extremities calyptriform, pointed with a bristle." The definition was evidently based on morphological traits common to the four species he described (*Rh. styliformis, Rh. imbricata, Rh. setigera* and *Rh. alata*).

Brightwell's circumscription of the genus was adopted by his contemporaries, and new *Rhizosolenia* species were soon added to through the works of Schultze (1858), Norman (in Pritchard 1861), Greville (1865), Smith (1872), Cleve (1881), Castracane (1886), Hensen (1887) and H. Peragallo (1888) and also came to include species that did not accord with Brightwell's description in that they lacked "pointed calyptriform extremities".

H. Peragallo (1892) treated 32 *Rhizosolenia* taxa (he himself being the author of 13 of them) in his classical monograph. Karsten (1905a, 1905b, 1907) added 14 new species in his reports on phytoplankton collected during the "Deutschen Tiefsee-Expedition 1898-1899". Substantial contributions to the list of *Rhizosolenia* taxa were also made by the Scandinavians Cleve, Ostenfeld and Gran, who between them named about 20 taxa in papers published between 1880 and 1910.

Hustedt (1930) treated only 23 marine and 4 fresh-water taxa in his monumental diatom Flora, since many of the earlier described "species" had by that time been regarded as conspecific; on a global scale probably not more than c. 35 species were accepted. Approximately a dozen marine taxa have since been added, and Van Landingham (1978) listed about 50 marine species in his catalogue.

The traditional classification of *Rhizosolenia* is mainly based on the shape of the valve and on the shape, number and arrangement of the girdle segments (H. Peragallo 1892, Pavillard 1925, Hustedt 1930). When the electron microscope became a tool in diatom research attempts were made, by especially Okuno (1952, 1954, 1957, 1959, 1960, 1966, 1968), to make use of the fine structure of the frustule in the classification of *Rhizosolenia.* Okuno, however, misidentified many of the taxa he treated and his papers are taxonomically misleading. Hasle (1975) made the first modern contribution of real value to the taxonomy of *Rhizosolenia* by examining the type material of the genus type *Rh. styliformis,* and of *Rh. imbricata,* and in comparing the morphology of many species within Rhizosoleniaceae by electron microscopy. Hasle's paper has provided the necessary basis for a modern approach in dealing with the confused taxonomy of *Rhizosolenia.*

MATERIAL

This investigation is mainly based on examinations of preserved net samples and permanent slides. The samples were collected by myself or were placed att my disposal by P. Boonruang and W. Janekarn, Phuket; G. R. Hasle, Oslo; H. A. von Stosch, Marburg; V. Zernova, Moscow; M. Estrada, Barcelona; G. Fryxell, Texas; G. Hallegraeff, Hobart; E. Sakshaug, Trondheim; L. Edler and T. Wallin, Lund.

Discovery Expedition samples are kept at the Institute of Oceanographic Sciences, Wormley, England.

Type slides and referens material were provided by; British Museum (BM), Muséum d'Histoire Naturelle (PC), Laboratoire de Botanique (TALE), Universitetets Botaniske Museum (C) and Naturhistoriska Riksmuseet (S).

A large number of samples and slides have been examined in the long process of building up the floristic and taxonomic insight necessary for this investigation.

The samples and slides most important to this investigation are listed below and are indicated in the text by the corresponding number, i.e. **(000).**

Samples examined with electron microscopy (T=TEM, S=SEM).

Samples are kept at the Department of Marine Ecology, University of Lund, unless otherwise indicated. Most of the Thai samples are subsamples of material kept at the Phuket Marine Biological Center (P.M.B.C.).

Samples from the collection of G. R. Hasle (IMBB) are indicated by IMBB and the filing number.

001	T	Swedish Arctic Expedition, Ymer-80, 78°45' N, 00°01' E, 23.8 1980.
002	T,S	Skagerrak, Torungen-Hirtshals, 15.6 1981, IMBB 2111.
003	T	Kattegat, 57°33' N, 11°31.5' E, 16.10 1975.
004	T,S	Laholm Bay, 56°34' N, 12°40' E, 18.8 1983.
005	T	Öresund (the Sound), 56°19'N, 12°30' E, 9.9 1975.
006	T,S	Öresund (the Sound), 56°07' N, 12°35' E, 15.3 1975.
007	T	Öresund (the Sound), 2.8 1977.
008	T	Villefranche (near Nice), 6.3 1975.

009	T	Adriatic Sea, March 1982.
010	T	Sea of Marmara, 19.2 1970, IMBB 900.
011	T,S	Atlor VII, 19°00' N, 17°00' W, Nov. 1975.
012	T	Ghana.
013	T	Cape Town I, 34°21.8' S, 18°24.8' E, 12.9 1961, IMBB 1310.
014	T	Cape Town III, 33°11' S, 17°52.5' E, 24.4 1967, IMBB 1312.
015	T	67-A-10, St.11, 23°13.6' N, 97°25.8' W, 12.11 1967, IMBB 914.
016	T	Bahia de Campeche (Gulf of Mexico).
017	T	SCOR WG 15, St.018, 19°21' N, 73°47' W - 19°33' N, 73°56' W, 29.5 1970, IMBB 283.
018	T	SCOR WG 15, St.002, 18°28' N, 81°22' W - 18°12' N, 81°24' W, 5.5 1970, IMBB 267.
019	T	SCOR WG 15, St.003, 16°21' N, 78°45' W - 16°23'N, 78°42' W, 6.5 1970, IMBB 268.
020	T	Apalachee Bay, Florida, 8.12 1970, IMBB 951.
021	T	Tampa, Florida, 27°42' N, 82°37' W, 10.12 1970, IMBB 955.
022	T	Caribbean Sea, 08°58' N, 56°00' W, 16.9 1964, IMBB 969.
023	T,S	Brasil, 23°40' S, 46°12' W, IMBB 1856.
024	T	Brasil, 24°05' S, 46°20' W, IMBB 1855.
025	T	Brasil, Cananeia, 25° S, 48° W, 1.2 1967, IMBB 1315.
026	T	Convergenzia St.2, 40°49.2' S, 53°43.6' W, IMBB 1321.
027	T,S	Discovery Exped., St.440, 30°19.5' S, 32°48' E, 21.9 1930.
028	T,S	Discovery Exped., St.427, 36°37.5' S, 28°52' E, 7.9 1930.
029	T,S	Discovery Exped., St.721, 53°58.5' S, 61°59.1' W, 13.11 1930.
030	S	Discovery Exped., St.334, 55°43' S, 36°51' W, 4.2 1930.
031	T,S	Discovery Exped., St.387, 56°50' S, 66°39' W, 16.4 1930.
032	T,S	Vulcan 7 Exped., St.142, 61° S, 55° W, 7.3 1981.
033	T	R/V Kurchakov, Antarctic, St.909.
034	T	Antarktisexped. 78/79, 45°08' S, 10°36' E, 19.12 1978, IMBB 1804.
035	T	"Brategg" Exped., St.1, 52°50' S, 90°00' W, 13.12 1947, IMBB 1.
036	T	"Brategg" Exped., St.8, 60°26' S, 90°00' W, 16.12 1947, IMBB 8.
037	T	"Brategg" Exped., St.16, 61°59' S, 100°03' W, 22.12 1947, IMBB 15.
038	T,S	"Brategg" Exped., St.29, 57°31' S, 150°00' W, 20.1 1948, IMBB 28.
039	T,S	"Brategg" Exped., St.32, 54°32' S, 150°00' W, 21.1 1948, IMBB 31.
040	T	"Brategg" Exped., St.44, 68°13' S, 120°16' W, 31.1 1948, IMBB 43.
041	T,S	"Brategg" Exped., St.47, 70°01' S, 98°50' W, 6.2 1948, IMBB 46.
042	T	"Brategg" Exped., St.54, 69°12' S, 94°06' W, 18.2 1948, IMBB 53.

Material from Phuket Marine Biological Center (P.M.B.C.), Thailand.

-Ko Phuket (Phuket Island) area:

043	T	Ao Sapam, 13.3 1980.
044	T,S	Ko Hung, 11.4 1980.
045	T,S	Ao Sapam, 9.3 1981.
046	T	P.M.B.C. pier, 19.3 1981.
047	T	P.M.B.C. pier, 28.4 1981.
048	T	P.M.B.C. pier, 14.5 1981.
049	T	P.M.B.C. pier, 19.5 1981.
050	T	P.M.B.C. pier, 27.5 1981.
051	T	Ao Pang Nga, St.1, 29.5 1981.
052	T	P.M.B.C., St.S, 4.6 1981.

053	T	P.M.B.C., St.S, 18.6 1981.
054	T,S	P.M.B.C. pier, 22.6 1981.
055	T	P.M.B.C., St.S, 9.7 1981.
056	T	P.M.B.C. pier, 13.7 1981.
057	T	P.M.B.C. pier, 15.7 1981.
058	T	P.M.B.C. pier, 20.7 1981.
059	T	P.M.B.C., St.S, 24.7 1981.
060	T	Ao Pang Nga, St.1, 27.7 1981.
061	T	Ao Pang Nga, St.A, 28.7 1981.
062	T	Ao Pang Nga, St.T1, 25.8 1981.
063	T	Ao Pang Nga, St.5, 26.8 1981.
064	T	P.M.B.C., St.S, 23.11 1981.
065	T	Ao Pang Nga, St.B, 24.11 1981.
066	T	Ao Pang Nga, St.2, 25.11 1981.
067	T	Ao Pang Nga, St.3, 25.11 1981.
068	T,S	Ao Pang Nga, St.B, 25.11 1981.
069	T,S	St.12, 5.4 1983.

-Cruise to Satun (west coast of Thailand):

070	T,S	St.36/2, 07°00' N, 99°30' E, 12.1 1983.
071	T,S	St.40/1, 06°45' N, 99°30' E, 13.1 1983.
072	T,S	St.42/2, 06°45' N, 99°45' E, 14.1 1983.
073	T,S	St.16/1, 08°00' N, 98°00' E, 25.1 1983.
074	T,S	St.13/1, 08°15' N, 98°00' E, 26.1 1983.
075	T,S	St.4/1, 09°15' N, 98°45' E, 5.2 1983.

076	T,S	Gulf of Thailand, 13°04' N, 100°48' E, 5.6 1981.

077	T	Off Cap St André, Madagascar, 28.9 1967, IMBB 441.
078	T	Mozambique Channel, off Comoro Isls, 28.9 1967, IMBB 443.
079	T	"Anton Bruun", N.E. Bay of Bengal, IMBB 1419.
080	T	"Anton Bruun", Andaman Sea, IMBB 1418.
081	T	Cruise SP 5/81, 36°30' S, 151° E, IMBB 2072.
082	T	Port Hacking, Sidney, 7.9 1981, IMBB 2074.
083	T,S	Australia, 20°28' S, 116°21' E, 4.12 1982.
084	T	Eltanin Cruise 28, St.9, 43°13' S, 173°51' E, March 1967, IMBB 96.
085	T	Eltanin Cruise 28, St.35, 43°15' S, 83°54' W, IMBB 106.
086	T	Eltanin Cruise 30, St.9, 05°51' S, 167°31.4' E, 21.8 1967, IMBB 112.
087	T	Eltanin Cruise 30, St.24, 19°29' N, 164°02' W, 4.9 1967, IMBB 122.
088	T	Ecuador, coll. Jimenez (No.7), IMBB 1467.
089	T	West of Galapagos, IMBB 1769.

090	T,S	SCOR WG 15, St.008, 03°09' S, 84°42' W - 03°12' S, 84°54' W, 12.5 1970, IMBB 273.
091	T,S	South America No.2, 4° S, 87°28' W, IMBB 183.
092	T	Monterey Bay, California, 16.8 1967, IMBB 228.
093	T	Bering Sea, Komandor Trench, R/V "Vityaz", St.1587, 26.6 1952.
094	T	Bering Sea, 59°10' N, 171°49' E, 21.9 1950.
095	T	Schicatan (Kuril Isls), St.7497, 18.6 1976.

096	T	Villefranche, printemps.

Selected slides and samples examined by light microscopy (LM).

Slides from British Museum (BM):
-Tempère & Peragallo 1889 (1st edition), Diatomées;
100 BM 14205, T. & P. No.43, Bengale.
101 BM 14336, T. & P. No.84, Cotê Ecuatoriel d'Africue.
102 BM 14360, T. & P. No.103, Yokohama (Exped. de la Vega).
103 BM 14400, T. & P. No.147, Villefranche.
104 BM 14401, T. & P. No.148, Villefranche.
105 BM 14402, T. & P. No.148, Villefranche.
- Tempère & Peragallo 1907 (2nd edition), Diatomées du Monde entier;
106 Saxton coll. No.68826, T. & P. No.477, Cap de Bonne-Esperance.
107 Saxton coll. No.69268, T. & P. No.917, Ajaccio, Corse.
- Tempère & Peragallo, Diatomées de France;
108 BM 15175, Deby coll., *Rh. Temperei, Rh. Castracanei,* Villefranche.
-

109 BM 1225, Ascidia, Hull, Norman I. 58, Greville coll.
110 BM 1948, Ascidians, Shark Bay, Australia, Greville coll.
111 BM 31053, Arafura Sea - Kittons, Comber coll.
112 BM 31056, Arafura Sea, surface, Comber coll.
113 BM 31057, " "
114 BM 31058, " "
115 BM 31059, " "
116 BM 31060, " "
117 BM 31062, " "
118 BM 31063, " "
119 BM 31066, Antarctic, surface, Comber coll.
120 BM 31067, Antarctic, surface, Comber coll.
121 BM 31963, S. Shetland Ils, Antarctic, surface, Comber coll.
122 BM 32080, Hongkong, surface, Comber coll.
123 BM 32534, Atlantic plankton, Comber coll.
124 BM 66885, Hull, Stomach of Ascidia, Nov.56, Ralfs coll.
125 BM 21352, Hull, Stomach of Ascidia, Apr.57, Roper coll.

126 Adams coll., F 1082, Atlantic Ocean, 23° N, 39.14° W.
127 Adams coll., No.1869, Surface of Arafura Sea.
128 Adams coll., J 4817, Arafura Sea, Challenger Exped.

Slides from Muséum d'Histoire Naturelle (PC):
-Tempère & Peragallo 1907 (2nd edition), Diatomées du Monde entier;
129 T. & P. No.477, Cap de Bonne-Esperance (Afrique).
130 T. & P. No.792, Arachon - Gironde.
131 T. & P. No.793, Banyuls (France), pelagique.
132 T. & P. No.917, Ajaccio - Corse (France).
133 Manguin coll., Terre Adélie, No.11.
134 Manguin coll., Terre Adélie, No.16.

Slides from Laboratoire de Botanique (TALE):
-Tempère & Peragallo 1889, Diatomées;
135 T. & P. No.147, (H.P. 91), Villefranche, (pelagique).

-Tempère & Peragallo 1907 (2nd edition), Diatomées du Monde entier;
136 T. & P. No.477, Cap de Bonne Esperance.
-Herb. H. Peragallo, Diatomaceae;
137 No.276, "*Rhizosolenia Temperei* H.P. et *Robusta*, Villefranche".
138 No.280, "*Rhizosolenia Temperei, -Castracanei,* Villefranche".
139 No.1631, "*Rhizosolenia Bergonii* H.P., Marseille, 13/1/02".
140 No.1632, "*Rhizosolenia Bergonii,* Marseille, 13/1/02".

Slide from Universitetets Botaniske Museum (C):
141 Siam No.10 (type of *Rhizosolenia clevei* Ostenfeld), Ostenfeld coll.

Slides from Naturhistoriska Riksmuseet (S):
-Cleve and Möller (1887-1892) collection;
142 No.10, Northern Atlantic.
143 No.65, Bohuslän, Lysekil, Sweden.
144 No.118, Atlantic Ocean between Iceland and Greenland.
145 No.125, Antarctic Ocean, Challenger Exp.
146 No.145, Diatoms from Java.
147 No.146, Diatoms from Java.
148 No.286, St. Vincent, Austr.
149 No.287, Island of Sheppey, coll. by Mr Shrubsole.
150 No.308, Sea of Behring.
151 No.319, Cape Wankarema, Vega Exp.

Selected samples from the collection of G.R. Hasle (IMBB):
152 IMBB No.12, "Brategg" Exped., St.12, 63°17' S, 90°00' W. 18.12 1947.
153 IMBB No.17, "Brategg" Exped., St.17, 62°02' S, 119°37' W. 30.12 1947.
154 IMBB No.37, "Brategg" Exped., St.38, 62°01' S, 120°00' W. 28.1 1948.
155 IMBB No.56, "Brategg" Exped., St.57, 66°04' S, 69°56' W. 22.2 1948.
156 IMBB No.126, Eltanin Cruise 30, St.31, 30°08' N, 146°50' W, 11.9 1967.
157 IMBB No.1422, 26°12.2' N, 95°05.5' W, 6.10 1975.

Selected samples from the Swedish Arctic Expedition; Ymer-80:
158 St. MPP 38, 79°19' N, 43°53' E, 3.8 1980.
159 St. FP 4, 82°21' N, 24°12' E, 15.8 1980.
160 St. FP 6, 80°00' N, 17°33' E, 18.8 1980.
161 St. FP 21, 80°47' N, 05°08' E, 5.9 1980.
162 St. FP 25, 81°06' N, 22°17' E, 11.9 1980.
163 St. FP 32, 82°20' N, 45°56' E, 17.9 1980.
164 St. FP 36, 78°49' N, 29°25' E, 20.9 1980.

Selected samples from Swedish coastal waters:

-Transect: Göteborg - Fredrikshavn;
165 Ser. 349, 11.12 1975.
166 Ser. 389, 18.2 1976.
166 Ser. 389, 18.2 1976.
168 Ser. 487, 9.6 1976.
169 Ser. 557, 18.11 1976.
170 Ser. 746, 6.12 1976.

-Öresund (the Sound);
171 11.1 1977.
172 1.3 1977.
173 5.4 1977.
174 31.5 1977.
175 7.7 1977.
176 2.8 1977.
177 5.9 1977.
178 2.10 1977.
179 31.10 1977.
180 7.12 1977.
181 10.1 1978.

Selected samples from Thailand:
-Cruise to Satun (west coast of Thailand);
182 St. 29/1, 07°30' N, 99°00' E, 9.1 1983.
183 St. 11/1, 08°30' N, 98°00' E, 27.1 1983.
184 St. 7/1, 09°00' N, 98°00' E, 30.1 1983.
185 St. 5/1, 09°15' N, 98°00' E, 1.2 1983.
186 St. 3/1, 09°30' N, 98°00' E, 1.2 1983.
187 St. 1/1, 09°45' N, 98°15' E, 2.2 1983.
188 St. 2/1, 09°30' N, 9745' E, 4.2 1983.

METHODS

Material examined by transmission electron microscopy (TEM) and scanning electron microscopy (SEM) was rinsed and centrifuged in distilled water at least five times. Cells to be examined with TEM or SEM were first identified by light microscopy (LM) then transferred by micro-pipette to formvar-coated grids for TEM or to round coverslips for SEM and were finally dried in air at moderate temperatures. The final stage of the drying process was monitored by LM and the position of the specimen(s) to be examined was noted.

The instruments used for TEM micrographs were: the JEOL 100 C at the Electron Microscopical Unit, University of Oslo and the ZEISS EM 10 at the Electron Microscopical Laboratory, Zoological Institution, University of Lund, where also the Nanolab 2000 instrument used for SEM micrographs is placed. A variety of light microscopes were used for the LM micrographs.

Data on qualitative and quantitative variables in the descriptions are based on my own observations. Where other sources have been cited this is indicated in the text.

Terminology for the siliceous components of the frustule in *Rhizosolenia*, *Pseudosolenia* and *Proboscia*.

The terminology in Ross et al. (1979) has been used where applicable.

The following terms are new or have been used in a sense differing from that in Ross et al. (1979).

PROCESS: The projection terminating the valve in *Rhizosolenia* and *Pseudosolenia.* It consists of an internal canal or lumen opening at the tip and communicating with the cell interior by a labiate structure, and a wall that is homogeneously silicified and usually diminishing in thickness towards the tip. (Figs 1a-b).

LABIATE STRUCTURE: The internal, more or less complex, structure through which the canal or lumen of the process communicates with the cell interior. (Figs 194, 253, 254).
Note: A "labiate process" sensu Ross et al. (1979) comprises both the external process and the internal labiate structure.

CONTIGUOUS AREA: The part of the valve contiguous with the sister-cell valve when the cells are linked together. The contiguous area usually differs somewhat from other parts of the valve in structure and degree of silicification and is usually delimited by low marginal ridges laterally (see Hasle 1975). (Fig. 1a).

CLASPERS: The pair of membranous structures usually continuous with the marginal ridges and clasping the otaria of the sister-cell valve when the valves are linked together (Fig. 1a). In *Proboscia* the term is used for the structures clasping the distal end of the proboscis in linked valves (Fig. 263).

PROBOSCIS (-ES): In *Proboscia.* The elongated distal part of the valve, often distinct from the rest of the valve but sometimes not clearly delimited proximally. The tip is truncate, with the distal surface usually surrounded by a marginal ring of short spinulae (Fig. 263). A longitudinal slit in the wall is usually found immediately below the tip. In *P. alata* the proboscis is circular in cross-section but the shape varies between species (unpubl. data). The fine structure of the proboscis wall does not differ much from that of the rest of the valve. In two linked valves the distal part of the proboscis fits into a groove on the adjacent valve (Fig. 263), the longitudinal slit below the tip then always being positioned in the narrow gap between the claspers covering the groove.

VALVOCOPULA: A segment adjacent to the valve and with the whole of the advalvar margin contiguous with usually most of the valve margin. (Figs 1a-b).

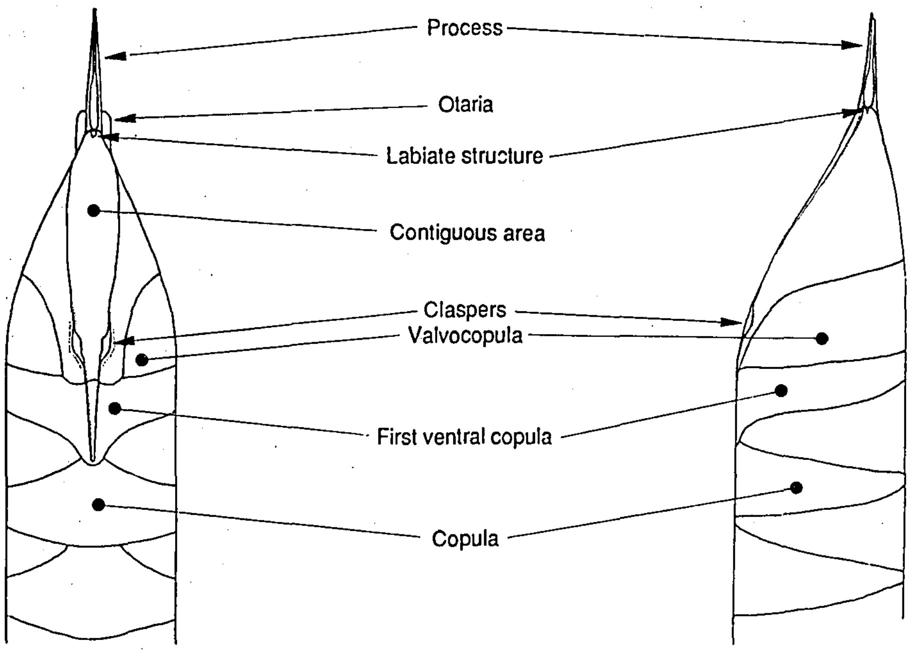


Fig. 1a. Theca in ventral view

Fig. 1b. Theca in lateral view

Fig. 1. Diagram to illustrate terminology.

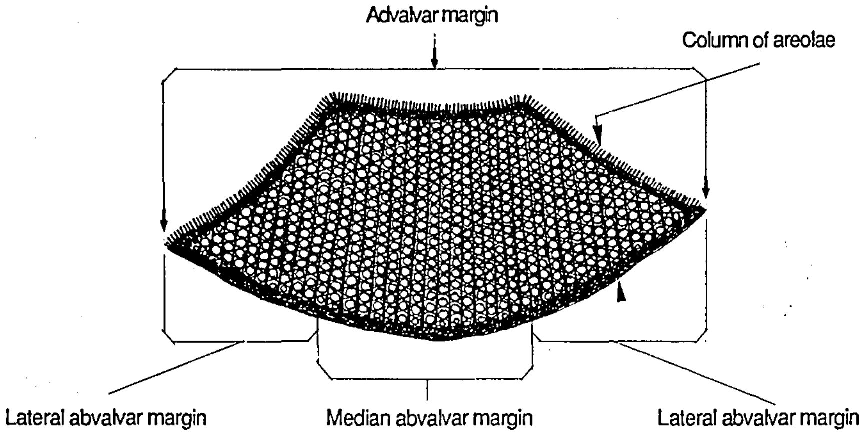


Fig. 2. Copula.

FIRST VENTRAL COPULA: In section *Rhizosolenia*. A girdle segment with the median advalvar margin contiguous with the median ventral part of the valve margin, and with the lateral advalvar margins contiguous with the valvocopula(-e). Usually accommodating the impression of the distal part of the sister-cell process, and usually differing in size and shape from the other copulae. (Fig. 1a)

FIRST COPULA: In section *Imbricatae* : A girdle segment homologous with the first ventral copula in sect. *Rhizosolenia*. Differing in shape from other copulae and towards one side usually accommodating the impression of the distal part of the sister-cell process. (Figs 36b, 222).

GIRDLE SEGMENT: A single element of the girdle (Ross et al. 1979).
Note: I discourage the use of the terms "open band", "half band", "segmented band" (von Stosch 1975) when describing the girdle in *Rhizosolenia, Pseudosolenia* and *Proboscia.*

The axes and planes of symmetry in species of *Rhizosolenia, Pseudosolenia* and *Proboscia* with bilaterally symmetrical valves.

The PERVALVAR AXIS runs up the middle of the straight or curved cylinder that makes up the greater part of the cell.

The APICAL PLANE of a theca divides the valve and the rest of the theca into two equal parts and coincides with the pervalvar axis.

An APICAL AXIS lies within the apical plane and is perpendicular to the pervalvar axis.

The TRANSAPICAL PLANE is perpendicular to the apical plane and coincides with the pervalvar axis.

A TRANSAPICAL AXIS lies within the transapical plane and is perpendicular to the pervalvar axis.

Note that in cells that are circular in cross-section the apical and transapical planes of the one theca often do not coincide with the respective planes of the other theca. In cells that are laterally compressed (elliptical in cross-section) the planes always coincide. In thecae lacking a bilateral symmetry only the pervalvar axis is definable.

In most *Rhizosolenia* species the valve is bilaterally symmetrical. It is usually subconical with the ventral side, accommodating the contiguous area, more or less sharply inclined to the pervalvar axis. The dorsal side of the valve is usually almost parallel to the pervalvar axis and is usually much shorter than the ventral side.

The terms "in ventral view, in dorsal view, in lateral view" are used in the figure texts to denote which side of a valve or a theca is facing the viewer. The term "in dorsiventral view" is used when it has not been possible to tell which of the ventral or dorsal sides is the closest to the focal plane.

Biogeographical terms

The terms Northern Cold-water Region, Circumglobal Warm-water Region and Southern Cold-water Region are defined in Zeitschel (1982). The terms boreal, temperate, subtropical, tropical, austral and Antarctic are used in a general sense and do not denote exactly delimited regions or areas.

A practical key to the Rhizosoleniae.

1. Girdle composed of two columns of segments........2
\- Girdle composed of more than two columns of segments........21

2. Segment columns bilaterally arranged........32
\- Segment columns not bilaterally arranged........3

3. Valve terminated by one process........4
\- Valve terminated by two processes........*Rh. antennata* f. *antennata*

4. Otaria and claspers present........5
\- Otaria and claspers lacking........19

5. Otaria pointed........6
\- Otaria not pointed........9

6. Otaria extending along basal part of process........7
\- Otaria completely confined to the valve proper........*Rh. acicularis*

7. In Antarctic waters........8
\- In boreal waters........*Rh. hebetata* f. *semispina*

8. Otaria and claspers prominent. Cell diameter usually > 100 µm........*Rh. crassa*
\- Otaria and claspers comparatively small. Cell diameter < 45 µm........*Rh. antennata f. semispina*

9. Otaria extending along basal part of process........10
\- Otaria ending either at the base of the process or slightly above
or slightly below or completely confined to the valve proper........14

10. In Antarctic waters........11
\- Not in Antarctic waters........13

11. Basal part of process bulbous........*Rh. sima* f. *sima*
\- Basal part of process not bulbous........12

12. Distal margin of otaria concave........*Rh. crassa*
\- Margin of otaria rounded........*Rh. polydactyla* f. *polydactyla*

13. In boreal waters........*Rh. borealis*
\- In tropical to subtropical waters. (Host to *Richelia intracellularis*)........*Rh. clevei* var. *communis*

14. Otaria ending either at the base of the process or slightly above or slightly below........15
\- Otaria completely confined to the valve proper........18

15. Areolae of copulae visible using a X25 objective........*Rh. castracanei* var. *neglecta*
\- Areolae of copulae not visible using a X25 objective........16

16. In the North Atlantic........*Rh. styliformis*
\- In tropical to subtropical waters........17

17. Cell diameter 80-230 µm........*Rh. formosa*
\- Cell diameter 13-58 µm........*Rh. sp.* (see *Rh. formosa*)

18. Cells curved. (In Antarctic waters)..*Rh. curvata*
\- Cells straight. (Areolae of copulae visible using a X25 objective)..............*Rh. catracanei* var. *neglecta*

19. In Antarctic waters...*Rh. sima* f. *silicea*
\- Not in Antarctic waters...20

20. In boreal waters...*Rh. hebetata* f. *hebetata*
\- In tropical to temperate waters. (Process claw-like)...............................*Pseudosolenia calcar-avis*

21. Otaria and claspers present...22
\- Otaria and claspers lacking.. 27

22. Otaria extending along basal part of process..23
\- Otaria completely confined to the valve proper...26

23. In Antarctic waters...24
\- In tropical to subtropical waters.. 25

24. Distal margin of otaria concave...*Rh. crassa*
\- Margin of otaria rounded..*Rh. polydactyla* f. *squamosa*

25. Host to *Richelia intracellularis*..*Rh. clevei* var. *clevei*
\- Not host to *R. intracellularis.* (Otaria narrow)...*Rh. hyalina*

26. Areolae of copulae visible using a X25 objective........................*Rh. castracanei* var. *castracanei*
\- Areolae of copulae not visible using a X25 objective..*Rh. debyana*

27. Valve bilaterally symmetrical...28
\- Valve not bilaterally symmetrical..30

28. In Antarctic waters...*Rh. polydactyla* f. *squamosa*
\- In tropical to temperate waters.. 29

29. Tip of process funnel-shaped...*Rh. bergonii*
\- Tip of process not funnel-shaped..*Rh. acuminata*

30. In Antarctic waters. (Valve conical)..*Rh. simplex*
\- In tropical to temperate waters.. 31

31. Process claw-like..*Pseudosolenia calcar-avis*
\- Process not claw-like. (Cells very large)...*Rh. temperei*

32. Striae on each copula converging on line running up the middle of the copula...........................33
\- Striae almost parallel to pervalvar axis in medial area of copula.. 35

33. Pervalvar axis at least 10 times as long as apical axis.. 34
\- Pervalvar axis less than 10 times as long as apical axis..*Rh. chunii*

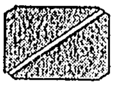
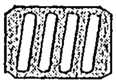
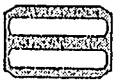
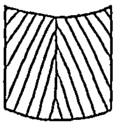
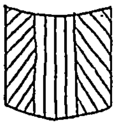
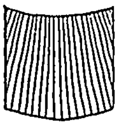
34. Cells laterally compressed. Process triangular in outline...*Rh. striata*
\- Cells circular to slightly elliptical in cross-section. Process swollen basally................ .*Rh. imbricata*

35. Striae almost parallel to pervalvar axis in medial area of copula, on each side gradually diverging..36
- Two to six parallel striae running up middle of copula, other striae at oblique angles to those in the middle........................*Rh. fallax*

36. Process swollen basally..37
- Process not swollen basally........................*Rh. decipiens*

37. Pervalvar axis at least 10 times as long as apical axis........................*Rh. ostenfeldii*
- Pervalvar axis usually less than 10 times as long as apical axis................*Rh. sp.* (see *Rh. chunii*)

See also Table 1.

	Velum structure			Striation		
						
Rh. imbricata	+			+		
Rh. striata	+			+		
Rh. ostenfeldii		+				+
Rh. fallax		+			+	
Rh. decipiens			+			+
Rh. chunii		+		+		
Rh. sp.		+				+

Tabel 1. Velum structure and striation in *Rhizosolenia* sect. *Imbricatae.*

DESCRIPTION OF SPECIES.

1. Section Rhizosolenia

Species with the girdle segments arranged in two dorsiventral columns, or in several columns.

RHIZOSOLENIA STYLIFORMIS Brightwell (Figs 5, 47-56)

Brightwell 1858, p. 94, pl. 5, figs 5, 5a-e.

Synonyms: *Rhizosolenia styliformis* (Brightw.) var. *longispina* Hustedt 1914,
pl. 316, figs 5-7, 12.
Rh. styliformis (Brightwell) forma *latissima* "Brightwell"
in H. Peragallo 1892, p. 111. (Nom. inval.)

Non: *Rhizosolenia styliformis* Brightwell sensu H. Peragallo 1892, pl. 4, figs 1-3, (= *Rh. borealis*).
Rh. styliformis Brightw. sensu H. & M. Peragallo 1897-1908, pl. 124, fig. 1, (= *Rh. borealis*).
Rh. styliformis sensu Schmidt in Ostenfeld and Schmidt 1901, fig. 2, (= *Rh. clevei* var. *communis*).
Rh. styliformis Btw., var. *latissima* Btw. sensu Ostenfeld 1902, p. 231, (= *Rh. spp.*).
Rh. styliformis var. *latissima* Btw. sensu Schröder 1906, figs 6a-b, (= *Rh. formosa* ?).
Rh. styliformis Brightw. var. sensu Van Heurck 1909, fig. 65, (= *Rh. polydactyla*).
Rh. styliformis var. *polydactyla* Castr. sensu Van Heurck 1909, figs 66, 67, 70, 71, 74, 75, (= *Rh. sima*).
Rh. styliformis Brightw. sensu Okamura 1911, p. 5, (= *Rh. spp.*).
Rh. styliformis Btw. var. *latissima* Btw. sensu Okamura 1911, p. 5, (= *Rh. spp.*).
Rh. styliformis Brightw. sensu Hustedt 1914, pl. 316, figs 1-4, 8-11, (= *Rh. borealis*).
Rh. styliformis Brightw. sensu Mangin 1915, fig. 53, (= *Rh. sp.*).
Rh. styliformis Brightw. sensu Heiden and Kolbe 1928, p. 516, (= *Rh. polydactyla*).
Rh. styliformis Brightw. f. *bidens* (Karsten) Heiden sensu Heiden and Kolbe 1928, p. 517, (= *Rh. antennata* ?).
Rh. styliformis Brightwell sensu Hustedt 1930, fig. 333, (= *Rh. borealis*).
Rh. styliformis Brightwell sensu Hendey 1937, pl. 11, figs 15-17, (= *Rh. polydactyla*).
Rh. styliformis Brightwell sensu Cupp 1943, fig. 48-A, (fig. 48Aa = *Rh. borealis*; fig. 48Ab = *Rh. clevei* var. *communis*).
Rh. styliformis Brightw. sensu Frenguelli 1943, pl. 3, fig. 10, (= *Rh. crassa* ?).
Rh. styliformis var. *longispina* Hust. sensu Frenguelli 1943, pl.3, fig. 11, (= *Rh. sp.*).
Rh. styliformis var. *oceanica* Wimpenny 1946, (= *Rh. spp.*).
Rh. styliformis var. *semispina* (Hensen) Karsten sensu Wimpenny 1946, (= *Rh. spp.*).
Rh. styliformis Brightwell sensu Subrahmanyan 1946, fig. 125, (= *Rh. sp.*).

Rh. styliformis Brightwell var. *longispina* Hustedt sensu Subrahmanyan 1946, figs 126-129, (= *Rh. spp.*).
Rh. styliformis Brightwell var. *latissima* Brightwell sensu Subrahmanyan 1946, figs 130-132, 143, (= *Rh. castracanei* var. *neglecta* ?).
Rh. styliformis Brightwell var. *longispina* sensu Okuno 1952a, figs 1-1', (= *Rh. antennata* f. *semispina*).
Rh. styliformis Brightwell var. *longispina* sensu Okuno 1952c, pl. 2, figs 1-1", (= *Rh. sp.*).
Rh. styliformis Brightwell var. *latissima* Brightwell sensu Okuno 1952c, pl.2, figs 2-2", (= *Rh. sp.*).
Rh. styliformis Brightwell var. *latissima* Brightwell sensu Okuno 1957, pl. 2, figs 2a-d, (= *Rh. spp.* ?).
Rh. styliformis Brightwell var. *latissima* Brightwell sensu Okuno 1959, text-fig. 2b, (= *Rh. formosa* ?).
Rh. styliformis fa. *bidens* (Karst.) Frenguelli in Frenguelli and Orlando 1958, p.136, pl. 7, fig. 5, (= *Rh. antennata*).
Rh. styliformis var. *latissima* Brightw. sensu Frenguelli and Orlando 1958, pl. 7, fig. 6, (= *Rh. sp.*).
Rh. styliformis var. *longispina* Hust. sensu Frenguelli and Orlando 1958, pl. 7, fig. 4, (= *Rh. sp.*).
Rh. styliformis Brightwell sensu Müller Melchers 1959, fig. 18, (= *Rh. sp.*).
Rh. styliformis Bright. var. *latissima* Bright. sensu Manguin 1960, figs 71-75, (= *Rh. polydactyla*).
Rh. styliformis fa. *bidens* (Karst.) sensu Frenguelli 1960, pl. 1, fig.7, (= *Rh. antennata*).
Rh. styliformis Brightwell sensu Hendey 1964, pl. 2, fig. 1, (= *Rh. borealis* ?).
Rh. styliformis Brightwell, 1858 var. *styliformis* sensu Sournia 1968, (= *Rh. spp.* ?).
Rh. styliformis var. *longispina* Hustedt sensu Sournia 1968, pl. 2, fig. 9, (= *Rh. clevei* var. *communis*).
Rh. styliformis Brightw. sensu Navarro 1981, figs 49-51, (= *Rh. clevei* var. *communis*).

Selected figures: Hustedt 1914, pl. 316, figs 5-7, 12; Hustedt 1930, fig. 334; Hasle 1975, figs 1-3.

Material examined: TEM: 002.
SEM: 002.
LM: 109, 124, 144.

Original material:

Hasle's (1975) observations on the BM slide No.66885 **(124)** are confirmed.

The BM slide No.1225 **(109)** comprises part of the material Brightwell referred to when describing *Rhizosolenia styliformis.* The slide includes intact frustules.

Observations: Diameter 57-90 µm. Copulae wing-shaped, arranged in two dorsiventral columns. Otaria arising near valve apex, ending at process base, width c. 1.5 µm, distal margin perpendicular or slightly oblique to process wall, angle between distal margin and outer margin usually slightly rounded. Copular areolae forming quincuncial pattern, columns parallel to pervalvar axis, 21 areolae to 10 µm within a column, 20 columns to 10 µm.

Note that Fig. 53 of the BM slide No.1225 shows part of a dessicated frustule with comparatively short and overlapping segments as those illustrated in fig. 5e in Brightwell (1858).

Lectotype: BM slide No.66885 (124), c.f. Hasle 1975.

LM OBSERVATIONS

Cells long, cylindrical, usually circular in cross-section. Diameter 23-90 µm. Usually solitary or in pairs.

Valve: Conoidal, bilaterally symmetyrical. Lateral profiles straight to weakly convex. Ventral part up to twice as long as dorsal part. Marginal ridges of contiguous area usually distinct along whole ventral side. Claspers distinctly visible at X250. (Figs 5, 47).

Process: Usually 30-50 µm long, seldom intact in preserved material (Figs 47-52), tapering from base into narrow distal tube. Tip pointed with opening on dorsal side, ventral side of process wall slightly extended; process, however, usually broken off below tip. Internal canal widest basally, connected with cell interior by labiate structure.

Otaria: Continuous with marginal ridges of contiguous area, arising below valve apex, usually ending where process begins, but sometimes ending below process base and sometimes extending a short distance along basal part of process (Figs 47-49, 51). Width usually c. 1.5 µm (range 1.0-2.5 µm). Outer margin straight to weakly convex, sometimes curving slightly upwards. Distal margin weakly convex, normal or slightly oblique to long axis of process (Figs 47, 49). Angle between outer and distal margins obtuse (usually somewhat rounded) (Fig. 48).

Valvocopula: One segment contiguous with most of valve margin.

Copulae: In two dorsiventral columns. First two ventral copulae usually differing in shape from other copulae: First ventral copula accommodating distal part of impression of sister-cell process, often with a medial tongue-like protrusion on abvalvar margin; second ventral copula with corresponding concavity on advalvar margin. Other copulae variable in size and shape, trapezoid to wing-shaped with fairly long median margins and longer lateral margins (Figs 50, 51, 53).

Auxospores: None observed.

SEM OBSERVATIONS

Areolae of valve and copulae loculate, velum external, foramen internal. Wall segments between areolae entire.

TEM OBSERVATIONS

All observations made on cells from sample No.002.

Valve: Areolae in columns converging at apex; 27-28 areolae to 10 µm within a column, 27-32 columns to 10 µm.

Areolae of valve: Subrectangular to ellipsoid in outline. Foramen large. Velum perforated by 1-6 round marginal pores, number of pores varying with size of areola (Fig. 56).

Copulae: Marginal zone with advalvar edge fringed, abvalvar edge entire. Areolae in columns parallel to pervalvar axis. Areolar pattern quincuncial. 20-21 areolae to 10 µm within a column, 19-22 columns to 10 µm.

Areolae of copulae: Subhexagonal to subrectangular in outline. Wall segments between areolae within a column usually longer than wall segments between areolae in adjacent columns (Fig. 55). Foramen circular to elliptical, varying in size. Velum perforated by six round marginal pores, one in each of the two angles made by the wall segments between columns, one opposite each of these four wall segments near the other four angles (Figs 54, 55).

DISTRIBUTION

Rhizosolenia styliformis is common in northern parts of the North Atlantic but its biogeographical limits are uncertain.

NOTE

According to my preliminary observations there is in tropical waters at least one undescribed taxon that closely resembles *Rh. styliformis.* (See also *Rh. formosa*).

DISCUSSION

Rhizosolenia styliformis was described by Brightwell (1858) from North Sea material. It has since been reported in the literature from virtually all parts of the world ocean but is probably the species that is oftenest confused with other *Rhizosolenia* taxa and the majority of alleged records can safely be disregarded as misidentifications.

Since undescribed taxa of uncertain status are involved I have only partially been able to sort out the confused taxonomy of *Rh. styliformis.* The list of erroneous records is too long to discuss in detail, but since the only records that are sufficiently well documented are from the North Atlantic (Brightwell 1858, Hustedt 1930, Wimpenny 1946, Robinson and Waller 1966, Robinson and Colburn 1970, Hasle 1975), it seems advisable to start again from scratch and tentatively regard *Rh. styliformis* as a North Atlantic species. More research is clearly needed before the range of variation and the geographical delimitation can be determined.

It should, furthermore, be noted that the copular areolae of *Rh. styliformis, Rh. acicularis* and *Rh. curvata* are indistinguishable in size, shape and velum structure, perhaps pointing to a close relation between these species.

It was pointed out by Sournia (1968) that the name "*Rh. styliformis* var. *latissima* " originates from H. Peragallo (1892), who included the name *Rh. styliformis* forma *latissima* "Brightwell" as a synonym of *Rh. polydactyla* on very dubious grounds. The name derives from the text ("portion of the broadest frustule yet found") to fig. 5e in Brightwell (1858) which simply illustrates part of a dessicated, not particularly broad, frustule with the dorsal and ventral copulae overlapping (cf. Fig. 53). The name was unfortunately adopted by Ostenfeld (1902), and he and many subsequent authors have used it for various large Rhizosoleniae with two columns of segments. The species that H. Peragallo (1892) called "*Rh.* (*styliformis* var.) *polydactyla* " (and gave the alternative name *Rh. styliformis* forma *latissima*) in the text, and called *Rh. polydactyla* Castr. in the figure text, is perhaps identical with his own species *Rh. formosa* which he had only seen in the dessicated state (H. Peragallo 1892, H. & M. Peragallo 1897-1908).

Hasle (1975) studied part of the material Brightwell referred to in his description of *Rh. styliformis.* The otaria in her fig. 1 differ slightly from the otaria I saw on frustules on the BM slide No.1225 **(109)**. On this slide the distal margin of the otaria is almost perpendicular to the pervalvar axis, whereas in Hasle's fig. 1 it is oblique. The discrepancy is, however, probably of minor significance since I observed a range of variation that included both shapes in a North Sea population (sample No. 002). Furthermore, Wimpenny (1946) observed that both the position of the otaria relative to the process base and the angle between the distal and outer margins of the otaria varied, which agrees with my pooled observations on *Rh. styliformis.*

Hasle (1975) presented a micrograph (fig. 6) of "part of a band" of *Rh. styliformis* in which the shape of the areolae differs slightly from that I usually observed in copulae (Fig. 55). However, Fig. 54 shows a part of a copula with less typical areolae reminiscent of those in Hasle (1975).

RHIZOSOLENIA CURVATA Zacharias (Figs 57-63)

Zacharias 1905, p. 120, text-fig.

Synonym: *Rhizosolenia curva* Karsten 1905a, pp. 97, 164, pl. 11, figs 2, 2a, 2b.

Selected figures: Müller Melchers 1959, pl. 4, fig. 17; Sournia et al. 1979, fig. 20.

Material examined: TEM: 31, 36.
SEM: 31.
LM: 30, 34, 39, 119, 152.

Type material not studied.

Lectotype: Zacharias 1905, p. 120, text-fig.

LM OBSERVATIONS

Cells long, slightly curved (Fig. 57), circular in cross-section. Usually solitary in preserved material. Diameter 30-95 µm. (See also under Discussion).

Valve: Acute conoidal, bilaterally symmetrical. Ventral part longer than dorsal part. Marginal ridges of contiguous area usually distinct. Claspers comparatively small. (Figs 59-61).

Process: Tapering from base, seldom intact. Internal canal widest basally, connected with cell interior by fairly small labiate structure. (Fig. 58).

Otaria: Comparatively small, continuous with marginal ridges, arising on distal part of valve, ending below valve apex. Distal margin almost normal to pervalvar axis, outer margin straight. Angle between margins obtuse (rounded). (Figs 58, 59, 61).

Valvocopula: One segment contiguous with most of valve margin. (Fig. 61).

Copulae: In two dorsiventral columns. First ventral copula accomodating impression of distal part of sister-cell process, abvalvar margin with a median tongue-like protrusion. Other copulae rhomboidal to trapezoid in outline, varying also in size. (Fig. 60).

Auxospores: None observed.

SEM OBSERVATIONS

Areolae loculate, velum external, foramen internal. Outer silicious layer continuous on each copula, perforated by round pores in the same pattern as seen with TEM. Wall segments between areolae apparently entire.

TEM OBSERVATIONS

Valve: No observations.

Copulae: Marginal zone with advalvar edge fringed and abvalvar edge entire. Areolae forming a quincuncial pattern with areolar columns parallel to pervalvar axis. 20 areolae to 10 µm within a column, 20 columns to 10 µm.

Areolae of copulae: Subhexagonal to subrectangular in outline. Wall segments between areolae within a column usually longer than wall segments between areolae in adjacent columns (Fig. 62). Foramen circular to broadly ellipsoid, varying in size. Velum perforated by six round marginal pores, one in each of the two angles made by the wall segmets between columns, one opposite each of these four wall segments near the other four angles (Fig. 63).

DISTRIBUTION

I observed *Rh. curvata* in samples from near the Antarctic Convergence. According to Hasle (1969) it can be regarded as endemic to the "Subantarctic Zone".

DISCUSSION

It was not felt necessary to look for type material since *Rhizosolenia curvata* is well delimited (long curved cells of a unique appearance; limited geographical distribution) and since the cell in the text figure in Zacharias (1905) corresponds in habit with all specimens I have seen. Moreover, no disagreement regarding its identity was found in the literature (Karsten 1905b, Hart 1937, Hendey 1937, Müller Melchers 1959, Manguin 1960, Sournia et al.1979, and others).

Zacharias (1905) described the process ("Spitzchen") of *Rh. curvata* as being flanked by otaria ("flügelartigen Leistchen"), which does not correspond with my observations since in all cells I saw the otaria ended well below the base of the process. The position of the otaria relative to the process may thus vary considerably more than my observations would suggest. It is, however, possible that Zacharias overlooked the diagnostic importance of the precise position of the otaria, which seems more probable from my observations and from fig. 17 in Müller Melchers (1959) and fig. 20 in Sournia et al. (1979), which show the otaria to be confined to the valve proper.

I found no auxospores in the material I examined. Hart (1937) assumed that "auxospores" arose terminally from "the broken end" of the frustule. He apparently never observed complete auxospores or initial cells and his fig. 6, pl. 14, allegedly depicting an "auxospore", could equally well represent a broken cell with the contents extruded. Only lateral auxospores have been documented in other species of *Rhizosolenia* (within the circumscription of the genus proposed here) and it seems unlikely that *Rh. curvata* should differ in this respect. The unambiguous documentation of auxospore formation in *Rh. curvata* thus remains to be presented.

The fine structure of copulae in *Rh. curvata* is indistinguishable from that in *Rh. styliformis* and *Rh. acicularis,* possibly indicating a close relation between these species.

Hart (1937) recorded a diameter range of 20-135 µm for *Rh. curvata,* which is wider than the one I observed.

According to Karsten (1905b, p. 164) the name *Rh. curvata* was published before the name *Rh. curva* (Karsten 1905a).

RHIZOSOLENIA ACICULARIS sp. nov. (Figs 6, 64-69)

Diagnosis: Cellula longa, cylindrica, in sectione transversa circularis. Valva acute conoides, lateribus subrectis. Otaria parva, paulum infra apicem valvae surgentia, sub basi processus terminata, apice cava, dorso subrecta aliquantulum convergentia. Velum areolae copulae sex poris marginalibus parietibus adjunctis oppositis pertusum.

Material examined: TEM: 88, 90.
SEM: 88.
LM: 28, 73, 75.

Type material: SCOR WG 15, St.008, 12.5 1970, 03°09' S, 84°42' W,- 03°12' S, 84°54'W. IMBB No.273, **(090)**.

Holotype: Slide labelled *Rhizosolenia acicularis* Sundström, SCOR WG, St. 008, 12.5 1970, 03°09' S, 84°42' W,- 03°12' S, 84°54'W. (BM).
Isotypes will be placed in the Hustedt collection, Bremerhaven (BRM); the Smithsonian Institution, Washington D.C. (US); the Institute of Oceanology, Moscow (IOAS).

LM OBSERVATIONS

Cells long cylindrical, circular in cross-section. Diameter 13-40 µm. Usually solitary.

Valve: Acutely conoidal, bilaterally symmetrical, lateral profiles almost straight. Ventral part longer than dorsal part, strap-shaped proximally. Contiguous area distinct, narrow. Claspers fairly small. (Figs 6, 64).

Process: Up to 55 µm long, seldom intact (Figs 64, 65), tapering from base into long narrow tube. Internal canal widest basally, communicating with cell interior through fairly large labiate structure.

Otaria: Narrow, continuous with marginal ridges of contiguous area, arising well below valve apex, ending below process base. Outer margin nearly straight, roughly parallel to pervalvar axis. Distal margin concave. Angle between outer and distal margins acute (pointed). (Fig. 66).

Valvocopula: One segment contiguous with most of valve margin (Fig. 6).

Copulae: In two dorsiventral columns. First ventral copula accommodating impression of distal part of sister-cell process, with a medial narrow tongue-like protrusion on abvalvar margin and a corresponding deep concavity on advalvar margin of second ventral copula. Other copulae rhomboidal, median margins short, lateral margins long.

Auxospores: None observed.

SEM OBSERVATIONS

Areolae of copulae loculate, foramen internal, velum external. Wall segments between areolae entire.

TEM OBSERVATIONS

Valve: No observations.

Copulae: Marginal zone with advalvar edge fringed, abvalvar edge entire. Areolae in columns parallel to pervalvar axis, pattern quincuncial. 20-21 areolae to 10 µm within a column, 20-21 columns to 10 µm.

Areolae of copulae: Subhexagonal to subrectangular in outline. Wall segments between areolae within a column usually longer than wall segments between areolae in adjacent columns (see Figs 68, 69). Foramen circular to elliptical, variable in size. Velum perforated by six round marginal pores; one in each of the two angles made by the wall segments between columns, one opposite each of these four wall segments near the other four angles. (Fig. 69).

DISTRIBUTION

Rhizosolenia acicularis was only found in a few samples and the geographical delimitation could not be determined. I did not find it in material collected outside the Circumglobal Warm-water Region.

DISCUSSION

Rhizosolenia acicularis is perhaps closely related to *Rh. styliformis,* the shape and the structure of the copular areolae being the same in both species. However, *Rh. acicularis* varied little in habit in the material I investigated and the shape and position of the otaria was characteristic in all cells. Since, furthermore, *Rh. acicularis* may be restricted to warm waters and *Rh. styliformis* is possibly restricted to the North Atlantic it seems best to treat them as separate species. (See also under *Rh. styliformis*).

RHIZOSOLENIA POLYDACTYLA Castracane (Figs 7-9, 70-79)

Castracane 1886, p. 71, pl. 71, fig. 2.

Rhizosolenia polydactyla Castracane **f. polydactyla**

Synonym: *Rhizosolenia styliformis* var. *oceanica* Wimpenny; Wimpenny 1946, pro parte, text-fig. 1e.

Non: *Rh.* (*styliformis* var.) *polydactyla* Castr. sensu H. Peragallo 1892, p.111, pl. 4, fig. 7. (Nom. inval.). (= *Rh. formosa* ?, see *Rh. styliformis*).
Rh. styliformis Brightw. var. *polydactyla* Castr. sensu Van Heurck 1909, pl. 4, figs 67, 70, 71, 74, 75. (= *Rh. sima*).
Rh. polydactyla Castr. sensu Mangin 1915, fig. 52. (= *Rh. sima*).
Rh. styliformis var. *polydactyla* (Castr.) Per. sensu Frenguelli and Orlando 1958, figs 19a-b. (= *Rh. sima*).
Rh. styliformis var. *polydactyla* (Castracane) H. Peragallo sensu Sournia 1968, p.70. (= *Rh. spp.*).

Misidentifications: *Rh. styliformis* Brightw. var. in Van Heurck 1909, pl. 4, fig. 65.
Rh. styliformis Brightwell in Hendey 1937, pl. 11, figs 15, 16, 17.
(?) *Rh. styliformis* Brightwell var. *longispina* Hustedt in Okuno 1952a, pl. 2, fig. 1.
Rh. styliformis Bright. var. *latissima* Bright. in Manguin 1960, pl. 5, fig. 71, pl. 6, figs 72-75.

Material examined: TEM: 31, 37, 38, 39.
SEM: 31, 38.
LM: 30, 36, 119, 133, 134, 152, 153, 154.

Type material:
The BM slide No.31066 **(119)** is probably part of a collection made in the Antarctic during the Challenger Expedition (P. Sims, BM, pers. comm.). There are at least 7 incomplete frustules that all conform to the original description of *Rh. polydactyla* in essential details. Six of these frustules are from cells which before dessication would have had diameters of between 22 and 32 µm and one is from a cell with an original diameter of c. 63 µm. Morphological characters conform with those described under LM observations.

Neotype: BM slide No. 31066 **(119).**

LM OBSERVATIONS

Cells long, cylindrical, circular in cross-section. Usually solitary. Diameter 15-105 µm.

Valve: Conoidal, bilaterally symmetrical. Lateral profiles straight to convex. Ventral part longer than dorsal part. Ventral median margin usually shallowly retuse. Contiguous area usually distinct only towards proximal part of ventral valve surface. Ridges continuing as prominent claspers over impression of sister-cell otaria. (Figs 8, 9, 71, 74).

Process: 18-34 µm long, usually intact. Widest basally, narrowing slightly over first half of its length, tapering distally. Tip resembling the point of an hypodermic needle (Fig. 77). Internal canal widest near base, connected with cell interior by a fairly large labiate structure.

Otaria: Arising at valve apex and extending to about half the length of thicker basal part of process. Outer margin straight to slightly convex. Distal margin approximately perpendicular to long axis of process. Angle between outer and distal margins obtuse (rounded) (Fig. 77).

Valvocopula: One segment contiguous with most of valve margin (Figs 7-9).

Copulae: In two dorsiventral columns. First ventral copula accommodating distal part of impression of sister-cell process, abvalvar margin usually more sharply curved than abvalvar margins of other copulae (Fig. 6). Size and shape of copulae varying considerably in cells of different diameters, larger cells usually having comparatively short segments with long lateral margins. Wing-shaped to trapezoid in outline (Figs 7-9, 70).

Auxospores: None observed.

SEM OBSERVATIONS

Areolae of copulae loculate, foramen internal, velum external. Wall segments between areolae apparently entire.

TEM OBSERVATIONS

Valve: Areolae in columns converging at apex. 26-28 areolae to 10 µm within a column, 24-25 columns to 10 µm.

Areolae of valve: Rounded rectangular in outline (Fig. 79). Foramen sometimes less distinct. Velum perforated by marginal pores, usually roundish. Number of pores varying with size of areola, usually four or less.

Copulae: Marginal zone fairly broad, advalvar edge fringed, abvalvar edge entire. Areolae in columns usually parallel to pervalvar axis. Pattern quincuncial. 20-23 areolae to 10 µm within a column, 20-25 columns to 10 µm.

Areolae of copulae: Hexagonal in outline. Foramen circular to broadly elliptical (Fig. 78). Velum perforated by usually six roundish pores in the angles, six interjacent pores often also present (Fig. 76).

Rhizosolenia polydactyla Castracane **f. squamosa** f. nov.

Diagnosis: Otariis deficientibus, cingulo e 2n (n = 2, 3, 4, ...) columnis segmentorum formato a f. polydactyla diversa.

Misidentification: *Rhizosolenia styliformis* var. *latissima* Brightw. in Frenguelli and Orlando 1958, p. 137, pl. 7, fig. 6.

Type material: Discovery Expedition, St. 387, 56°50' S, 66°39' W. **(031).**

Holotype: Slide labelled *Rh. polydactyla* f. *squamosa* Sundström. Discovery Expedition, St. 387, 56°50' S, 66°39' W, 16.4 1930. (BM).
Isotypes will be placed in the Hustedt Collection, Bremerhaven (BRM); the Smithsonian Institution, Washington, D.C. (US); the Institute of Oceanology, Moscow (IOAS).

Material examined: Type material **(031)** only.

The type material is dominated by *Rh. polydactyla* f. *polydactyla.* Cells with one f. *polydactyla* theca and one f. *squamosa* theca are common, and numerous intermediate forms are present. Typical f. *squamosa* cells are few. In heterothecate frustules the epitheca always more closely resembles that of f. *polydactyla*, the hypotheca that of f. *squamosa* (Figs 71, 72). Morphological details described below.

LM OBSERVATIONS

Cells cylindrical, circular in cross-section. Usually with a fairly short girdle when fully developed. Diameter 56-105 µm. Unable to form chains.

Valve: Acutely conoidal, bilaterally symmetrical, projecting ventrally to form a narrow tongue (Fig. 7). Lateral profiles weakly convex to weakly concave (Figs 8, 9, 73). Distal part of valve usually with irregular ridges, more coarsely silicified than proximal parts (Figs 73, 75). Contiguous area and claspers lacking in characteristic specimens (Fig. 9).

Process: 20-35 µm long, usually intact, tapering. Tip somewhat blunter than in f. *polydactyla* (Figs 73, 75). Internal canal connected with cell interior by a labiate structure. Process wall smooth in typical specimens, but rough surface of distal part of valve often extending as far as basal part of process (Figs 9, 75).

Otaria: Lacking in characteristic specimens (Figs 9, 72, 73, 75).

Valvocopula: One segment contiguous with most of valve margin (Fig. 9).

Copulae: 2n (n= 2, 3, 4, ...) columns of segments, somewhat variable in size and shape but usually rhomboidal with short median margins and long lateral margins (Figs 8, 9).

SEM OBSERVATIONS

Areolae as in *Rh. polydactyla* f. *polydactyla.*

TEM OBSERVATIONS

Valve: Areolae in columns converging at apex. Fine structure as in f. *polydactyla.*

Copulae: 22-23 areolae to 10 µm within a column, 22-24 columns to 10 µm.

Areolae of copulae: No differences in the fine structure of f. *polydactyla* and f. *squamosa* were found.

DISTRIBUTION

Rhizosolenia polydactyla is apparently restricted to the Southern Cold-water Region and to water masses of such origin.

DISCUSSION

Castracane (1886) gave only a sketchy description of *Rhizosolenia polydactyla* : "This frustule is peculiar on account of the shortness and multiplicity of its rings. The terminal mucro is strong and very acute, even more so than indicated in the figure. The specific name of this Antarctic form is intended to be indicative of the remarkable character of its rings." The Latin diagnosis provides no essential additional information. It can thus be deducted from the description that the illustration in Castracane (1886, pl. 24, fig. 2) is not exact. This is also indicated by the uneven girdle segments in the figure giving the girdle the appearance of being dessicated.

All cells of *Rh. polydactyla* f. *polydactyla* in the material fit in with the original description in having strong acute processes. Many cells, especially larger ones, had short girdle segments, agreeing with the other characteristic stressed by Castracane. The shape of the girdle segments varies, however, and cannot be used as a diagnostic character.

Castracane did not designate a type for *Rh. polydactyla,* nor did he state an exact locality for the original collection. However, the origin of the material on the type slide **(119)** supports the view that *Rh. polydactyla* f. *polydactyla* as described here is *Rh. polydactyla* sensu orig. Castracane's (1886) original figure is too inexact to serve as lectotype.

The interpretation suggested by Van Heurck (1909) was not supported by any other comment than: "Nous représentons une série de formes qui peuvent toutes se rapporter au *R. polydactyla* Castr." His fig. 70, pl. 4 shows a cell which cannot be characterized as having a "strong and acute process" and in this does not correspond with the original description of *Rh. polydactyla* . Mangin (1915) adopted Van Heurck's interpretation and also included *Rh. styliformis* "f. *latissima* Brightw." and *Rh. styliformis* var. *lata* Lemmermann as synonyms of "*Rh. polydactyla* ". However, the illustrations in both Van Heurck (1909) and Mangin (1915) evidently represent *Rh. sima,* which was also described from the Antarctic by Castracane (1886) (see also under *Rh. sima*). The *Rh. polydactyla* cell in fig. 2, pl. 24 in Castracane (1886) had a diameter of either 60 or 38 µm, depending on whether the illustration represents an intact or a dessicated specimen, and assuming that the scale is correct. Both these diameters fall well inside the range I have observed for *Rh. polydactyla* f. *polydactyla* while the diameter of *Rh. sima* almost always is smaller.

It is probable that Van Heurk's and Mangin's misidentifications have also confused the interpretation of other species, especially since "*Rh. styliformis* f. *latissima* " was included as a synonym of *Rh. polydactyla* by Mangin (a suggestion originally put forward by H. Peragallo in 1892). Thus, Hendey (1937) reported the presence of "*Rh. polydactyla* " in the Mediterranean, in the tropical waters off "Somaliland" and in the Antarctic. Sournia (1968) recorded "*Rh. styliformis* var. *polydactyla* (Castracane) H. Peragallo" from the Indian Ocean and moreover regarded *Rh. formosa* H. Peragallo as conspecific.

I have not seen *Rh. polydactyla* in samples from outside the Southern Cold-water Region and records from other regions are best attributed to misidentifications. It is also probable that in samples from the Antarctic *Rh. polydactyla* have sometimes been misidentified as *Rh. styliformis,* e.g. Hendey 1937, Crosby and Wood 1957, Hasle 1969, Sournia et al.1979.

Rh. polydactyla f. *squamosa* could be regarded as an "exogenous resting spore" of *Rh. polydactyla,* but has here been accorded the rank of forma for reasons given under General discussion.

It is evident from the type material **(031)** that the transformation from f. *polydactyla* to f. *squamosa* takes place during cell division, and that either two typical f. *squamosa* valves or two identical valves morphologically intermediate between f. *polydactyla* and f. *squamosa* can be formed. A cell with a f. *squamosa* valve at one end and a f. *polydactyla* or an intermediate valve at the other end gives rise to one *Rh. polydactyla* f. *squamosa* cell and one sister cell with heteromorphic valves, since the hypotheca apparently always more closely resembles f. *squamosa* morphologically.

Rh. polydactyla and *Rh. sima* seem to differ from other dimorphic diatoms (i.e. those forming "resting spores") in that the transformation from the commonly seen "vegetative" form to the "resting" form can take place through intermediate stages. It is not possible to deduce from the material I have examined whether *Rh. polydactyla* f. *squamosa* can continue to divide to form new f. *squamosa* cells, nor is it known whether f. *squamosa* can revert to f. *polydactyla* (c.f. *Rh. hebetata*).

It is an interesting fact that the girdle segmentation is obligately distichous in *Rh. polydactyla* f. *polydactyla* and obligately polystichous (squamose) in f. *squamosa,* and shows that the genetic material of a species can allow for both types.

The morphological similarities between *Rh. polydactyla* f. *squamosa* and *Rh. bergonii* are striking and warrant placing the latter in sect. *Rhizosolenia* in the classification suggested. (See also under *Rh. borealis, Rh. bergonii* and General discussion).

RHIZOSOLENIA BOREALIS sp. nov (Figs 10, 11, 80-87).

Diagnosis: Rh. styliformi Brightwell affinis, imprimis otariis ab ea diversa ad apicem valvae surgentibus, juxta partem basalem processus extensis. Margo exterior et margo apicalis otarii angulum totundatum inter se formantes. Species non ut Rh. polydactyla Castracane dimorpha. E regionibus borealibus modo cognita.

Synonym: *Rhizosolenia styliformis* var. *oceanica* Wimpenny, pro parte. Wimpenny 1946, text-fig. 1d (non 1e).

Misidentifications: *Rhizosolenia styliformis* in: Peragallo 1892, pl.4 (17), figs 2, 3; Meunier 1910, pl. 2, fig 18, (? 19); Hustedt 1914, pl. 316, figs 2, 3, 4, 8, 9, 11; Hustedt 1930, fig. 333; Cupp 1943, fig. 48A-a; Hendey 1964, pl. 2, figs 1b, (?1c).

Selected figures: Robinson and Waller 1966, text-fig. 1; Hasle 1975, figs 8-20.

Material examined:	TEM: 1, 92, 93.
	SEM: 93.
	LM: 94, 142, 144, 150, 160, 161, 162.

Type material: Swedish Arctic Expedition, Ymer-80, 78°45' N, 00°01' E, 23.8 1980. **(001).**

Holotype: Slide labelled *Rhizosolenia borealis* Sundström, Ymer-80, 78°45' N, 00°01' E, 23.8 1980. (BM).
Isotypes will be placed in the Hustedt Collection, Bremerhaven (BRM); the Smithsonian Institution, Washington D.C. (US); the Institute of Oceanology, Moscow (IOAS).

LM OBSERVATIONS

Cells long, cylindrical, circular in cross-section. Usually solitary or in pairs. Diameter 13-65 µm. (See also under Discussion).

Valve: Conoidal, bilaterally symmetrical. Ventral part longer than dorsal part. Contiguous area distinct at least towards proximal part of ventral valve surface. Prominent claspers over impression of sister-cell otaria (Figs 10, 11, 81).

Process: 15-28 µm long, usually intact. Widest basally, narrowing only slightly in first half, tapering distally. Tip resembling the point of a hypodermic needle, with opening on dorsal side (Fig. 82). Internal canal widest near base, communicating with cell interior by fairly large labiate structure (Fig. 84).

Otaria: Arising at valve apex, extending to about half the length of thicker basal part of process. Outer margin slightly convex. Distal margin almost perpendicular to long axis of process. Angle between outer and distal margins obtuse (rounded) (Figs 10, 11, 80-82).

Valvocopula: One segment contiguous with most of valve margin (Figs 10, 80).

Copulae: In two dorsiventral columns. First ventral copula accommodating impression of distal part of sister-cell process; sometimes with a slight protrusion midway along abvalvar margin. Other copulae variable in outline, usually with fairly short median margins. Length:width ratio varies, outline being rhomboidal to wing-shaped (Figs 10, 11, 80).

Auxospores: In a sample from the Bering Sea **(093)** an initial cell with a diameter of 62 µm was seen laterally attached to a mother cell with a diameter of 22 µm.

SEM OBSERVATIONS

Areolae loculate, velum external, foramen internal. Wall segments between areolae apparently entire.

TEM OBSERVATIONS

Valve: Areolae in columns converging at apex. 22-24 areolae to 10 µm within a column, 28-30 columns to 10 µm.

Areolae of valve: Rounded rectangular in outline. Foramen roundish. Velum usually perforated by 1-4 round to somewhat oblong pores (Fig. 83).

Copulae: Marginal zone fairly broad, advalvar edge fringed, abvalvar edge entire (Figs 85, 86). Areolar columns usually parallel to pervalvar axis. Areolar pattern quincuncial. 15-17 areolae to 10 µm within a column, 17-19 columns to 10 µm.

Areolae of copulae: Hexagonal in outline. Foramen circular to broadly elliptical. Velum perforated by usually six circular to kidney-shaped pores in the angles (Figs 85-87).

DISTRIBUTION

Restricted to the Northern Cold-water Region and to water masses of such origin.

DISCUSSION

In his description of *Rh. styliformis* var. *oceanica*, Wimpenny (1946) referred to collections from the North Atlantic Ocean, the Bering Sea, the Arafura Sea and the Antarctic Ocean. I studied the BM slide

No.31057 **(113)** from which Wimpenny recorded his variety, but found no *Rh. borealis.* It does, however, include a few cells of *Rh. clevei* var. *communis* that are reminiscent of *Rh. borealis.* I have not seen the Antarctic samples from the Discovery Expedition that Wimpenny used, but what he called *Rh. styliformis* var. *oceanica* in Antarctic material (Wimpenny 1946, 1966) is evidently *Rh. polydactyla.* Wimpenny's taxon was thus based on discordant elements.

Rh. borealis and *Rh. polydactyla* f. *polydactyla* resemble each other closely, but *Rh. borealis* is restricted to the Northern Cold-water Region and *Rh. polydactyla* to the Southern Cold-water Region and no cells of either species were found in samples from the Circumglobal Warm-water Region. They are thus well separated geographically. The fact that only *Rh. polydactyla* is dimorphic and that its areolae are smaller lends further support to that it is genetically different from *Rh. borealis,* and I can see no reason to include them in a single species.

Hasle (1975) pointed to a close structural similarity between "*Rh. styliformis* Brightw. var. *styliformis*" and "*Rh. styliformis* var. *oceanica* Wimpenny" in material from the North Atlantic and North Pacific, and pointed out that it was difficult to distinguish the fine structures of valves and segments of the two taxa. However, the fine structure of the areolae common to them, with the velum perforated by marginal pores, is seen in many *Rhizosolenia* species and is not in itself a useful character for lumping or splitting taxa (cf. *Rh. acicularis, Rh. castracanei, Rh. curvata, Rh. polydactyla, Rh. styliformis, Rh. formosa*). Since, furthermore, *Rh. borealis* and *Rh. styliformis* are readily distinguished in areas of common distribution, and since no intermediate forms were seen in the material and none are reported in the literature consulted it can not be justified to include *Rh. borealis* and *Rh. styliformis* in one species.

Wimpenny (1946) reported that mother cells of *Rh. styliformis* var. *oceanica* (*Rh. borealis*) with a diameter of 24 µm gave rise to auxospores with diameters of 44 and 76 µm. Robinson and Waller (1965) reported that the diameter could increase from 26 to 64 µm through auxosporulation, and Robinson and Colburn (1970) reported an increase from 28 to 82 µm. The one attached initial cell I observed (diameter 62 µm) had arisen from a mother cell with a diameter of 22 µm. It thus appears that mother cells within a diameter range of 22-28 µm can give rise to initial cells ranging from 44 to 82 µm in diameter.

In their fig.2 Robinson and Colburn (1970) recorded a diameter range for *Rh. styliformis* var. *oceanica* of approximately 15-87 µm, which is wider than the range in the material I have studied.

Meunier (1910) observed (once ?) "endocyctes" in cells that can only be interpretated as being *Rh.*

borealis (Meunier 1910, pl. 28, fig. 18). The "endocystes" resemble the endogenous resting spores (also known as *Pyxilla baltica* Grun.) often recorded from *Rh. setigera* Brightwell. However, no other records of this type of cell inclusion were found in the literature consulted (although Meunier's observation is often quoted), nor did I find any endogenous resting spores in any of the *Rhizosolenia* taxa treated here. (*Rh. setigera* is not included in my proposed circumscription of the genus). Meunier's observation must thus be queried.

RHIZOSOLENIA FORMOSA H. Peragallo (Figs 12, 13, 88-93, 96-99)

H. Peragallo 1888, p. 91, pl. 6, fig. 43.

Synonyms: ? *Rh. styliformis* (Brightwell) forma *latissima* "Brightwell" in H. Peragallo
1892, p. 112. (Nom. inval.).
? *Rhizosolenia annulata* Karsten 1907, p. 378, pl. 41, figs 4a, 4b.

Non: *Rh. styliformis* Btw., var. *latissima* Btw. sensu Ostenfeld 1902, p. 231, (= *Rh. spp.*).
Rh. styliformis Btw. var. *latissima* Btw. sensu Okamura 1911, p. 5, (= *Rh. spp.*, cf. Misidentifications).
Rh. styliformis var. *latissima* Brightwell sensu Hustedt 1930, p. 586, (= *Rh. spp.*, cf. Misidentifications).
Rh. styliformis Brightwell var. *latissima* Brightwell sensu Subrahmanyan 1946, figs 130-132, 143, (= *Rh. castracanei* var. *neglecta* ?).
Rh. styliformis Brightwell var. *latissima* Brightwell sensu Okuno 1952c, pl. 2, figs 2-2", (= *Rh. sp.*).
Rh. styliformis Brightwell var. *latissima* Brightwell sensu Okuno 1957, p. 106, (= *Rh. spp.* ?, cf. Misidentifications).
Rh. styliformis var. *latissima* Brightw. sensu Frenguelli and Orlando 1958, pl. 7, fig. 6, (= *Rh. sp.*).
Rh. styliformis Bright. var. *latissima* Bright. sensu Manguin 1960, figs 71-75, (= *Rh. polydactyla*).

Misidentifications: ? *Rh. styliformis* var. *latissima* in Schröder 1906, p. 345, figs 6a, b.
Rh. styliformis var. *latissima* in Okamura 1911, pl. 10, figs 23b-e.
Rh. styliformis var. *latissima* in Hustedt 1930, figs 335a, b.
Rh. styliformis var. *latissima* in Allen and Cupp 1935, p. 130, figs 40, 40a.
? *Rh. styliformis* var. *latissima* in Okuno 1957, pl. 2, figs 2b, 2c.
Rh. styliformis var. *latissima* in Okuno 1959, p. 62, pl. 1, figs 3, 4.

Selected figures: Pavillard 1925, p. 33, figs 51a, b.

Material examined: TEM: 18, 22, 23, 45, 46, 69, 74, 78, 96.
SEM: 74.
LM: 49, 50, 57, 62, 64, 68, 70, 73, 75, 182-188.

Material examined by H. Peragallo:
On the TALE slide Tempère & Peragallo No.147 **(135)** is one dessicated cell of *Rh. formosa* (Figs 90, 91). The cell was evidently used for fig. 3, pl. 123 in H. & M. Peragallo (1897-1908) since the broken valve in the figure conforms almost exactly with that in my Fig. 90.

Neotype: Specimen on TALE slide labelled Diatomées, Villefranche (pelagique), No.147, Collection J. Tempère, H. Peragallo, Paris. (See above).

LM OBSERVATIONS

Cells large, cylindrical, circular in cross-section. Diameter 80-230 µm. Solitary or in pairs.

Valve: Bilaterally symmetrical. Apex conoidal, shallow. Ventral part much longer than dorsal part, medially extended into tongue accommodating impression of sister-cell process (Fig. 92). Contiguous area distinct along proximal part of ventral valve surface. Claspers fairly prominent. (Figs 12, 13, 88, 89).

Process: 17-30 µm long, usually intact. Tapering from base, distally resembling the point of a hypodermic needle (Fig. 93). Internal canal widest near base, communicating with cell interior by labiate structure.

Otaria: Arising below valve apex, usually ending where process begins (Figs 12, 93), but sometimes ending slightly below process base and sometimes ending a short distance along basal part of process. Outer margin straight to weakly convex. Distal margin weakly concave to weakly convex, at an oblique angle to long axis of process. Angle between outer and distal margins obtuse, usually rounded.

Valvocopula: One large segment contiguous with most of valve margin (Figs 12, 13, 88, 89).

Copulae: Usually in two dorsiventral columns (Figs 12, 88, 89). First ventral copula usually accommodating distal part of sister-cell process (Fig. 12). Other copulae wing-shaped, median margins short, lateral margins extremely long (Figs 12, 88, 91).

Auxospores: None observed.

SEM OBSERVATIONS

Areolae of valve and copulae loculate, velum external, foramen internal. Wall segments between areolae entire.

TEM OBSERVATIONS

Valve: Areolae in columns converging at apex. 22-25 to 10 µm within a column, 18-24 columns to 10 µm.

Areolae of valve: Rounded rectangular in outline. Foramen large, ellipsoid (Fig. 99). Velum perforated by four round pores in the angles.

Copulae: Marginal zone fairly broad (Fig. 98), advalvar edge entire or fringed, abvalvar edge entire. Areolar columns usually parallel to pervalvar axis. Areolar pattern quincuncial. 18-19 areolae to 10 µm within a column, 20-22 columns to 10 µm.

Areolae of copulae: Usually hexagonal in outline. Foramen fairly large, usually circular. Velum perforated by usually 6 round pores in the angles (Figs 96-98).

DISTRIBUTION

Rhizosolenia formosa is probably circumglobal within the Warm-water Region. It was present in the waters surrounding Ko Phuket, Thailand throughout the year, but seldom in abundance.

NOTE

I often found *Rhizosolenia* cells (diameter 13-58 µm) reminiscent of *Rh. styliformis* (Figs 14, 94, 95) together with *Rh. formosa* in the Thai material. The areolar patterns and structures of both valve and copulae (Figs 100, 101) were indistinguishable from these of *Rh. formosa*, but differed from those in *Rh. styliformis* (Figs 54, 56).

It is interesting to note that the three large species *Rh. castracanei, Rh. debyana* and *Rh. formosa* occurred together in samples from both Villefranche (France) and Thailand.

DISCUSSION

The TALE slide Tempère & Peragallo No.147 **(135)** incudes *Rh. formosa* according to H. Peragallo's personal card index (J. Eymé, TALE, pers. comm.). The single specimen on the slide is evidently the one used for illustrating *Rh. formosa* in H. & M. Peragallo (1897-1908). Since the original material could not be found and since the original illustration does not show essential diagnostic characters, it seems best to let the specimen on this slide serve as neotype for *Rh. formosa.* All *Rh. formosa* cells I have observed conform in essential details with the neotype.

Under the light microscope *Rh. formosa* is distinguished on the shape of the girdle segments and on the usually large size. In TEM the shape and structure of the copular areolae were characteristic and invariable.

Pavillard (1925) suggested that *Rh. formosa* could be a large form of *Rh. styliformis.* This I cannot agree with since the areolae differ distinctly in shape. Confusions between *Rh. formosa* and *Rh. polydactyla* (e.g. Pavillard 1925, Hustedt 1930, Sournia 1968) can probably mainly be accorded misconceptions concerning the latter. (See also under *Rh. styliformis* and *Rh. polydactyla*).

The invalid names *Rh. styliformis* forma *latissima* (H. Peragallo 1892) and *Rh. styliformis* var. *latissima* (Ostenfeld 1902) have greatly contributed to the taxonomical confusion in *Rh. styliformis, Rh. polydactyla* and *Rh. formosa.* Thus Ostenfeld (1902) included the name *Rh. polydactyla* as a synonym of *Rh. styliformis* var. *latissima,* Pavillard (1925) included the names *Rh. styliformis* var. *latissima* and *Rh. polydactyla* as possible synonyms of *Rh. formosa*, Hustedt (1930) included the names *Rh. formosa* and *Rh. polydactyla* as synonyms of *Rh. styliformis* var. *latissima* and Sournia (1968) included all three names as synonyms of *Rh. styliformis* var. *polydactyla.* I have found that *Rh. styliformis, Rh. polydactyla* and *Rh. formosa* are all good species with no transitions. Furthermore, it is probable that the dessicated frustule of *Rh. styliformis* in my Fig. 53 was used for fig. 5e in Brightwell (1858) which is the figure that H. Peragallo (1892) referred to when introducing the "latissima" concept into *Rhizosolenia* taxonomy.

The description and illustrations of *Rh. annulata* in Karsten (1907) fit *Rh. formosa* well when the doubtful statement that the lumen of the process is not connected with the cell interior and the strange interpretation of the copulae near the valve are disregarded. Furthermore, Karsten recorded *Rh. annulata* but not *Rh. formosa* from the tropical parts of the Indian Ocean, where the latter is fairly common according to my observations, and it seems safe to regard them as conspecific.

It is conceivable that *Rh. sp.* (Figs 12, 94, 95, 100, 101) is a variety of *Rh. formosa* (corresponding to the var. *communis* of *Rh. clevei* ?) but further research is necessary.

RHIZOSOLENIA CASTRACANEI H. Peragallo (Figs 15-17, 102-111)

H. Peragallo 1888, p. 91, pl. 6, fig. 42.

Rhizosolenia castracanei H. Peragallo var. **castracanei**

Synonyms: *Rhizosolenia squamosa* Karsten 1907, p. 382, pl. 52, figs 3, 3a, (non Pantocsek 1892). Nom. illegit.
Rhizosolenia magna Stüwe 1909, p. 276, pl. 1, figs 3, 4.
Rhizosolenia squamifera Sournia 1968, p. 79, pl. 3, fig. 21.

Non: *Rh. Castracanei* Peragallo var. *rhomboidea* Subrahmanyan 1946, p. 123, figs 153, 154, 156-160. (= *Rh. clevei* var. *clevei*).
Rh. castracanei sensu Okuno 1968, p. 81, figs 4, 7, 11h, 16. (= *Pseudosolenia calcar-avis*).
Rh. castracanei sensu Hasle 1975, p. 107, figs 27-33, 40. (= *Rh. debyana*).

Selected figures: H. & M. Peragallo 1897-1908, pl. 123, fig. 9; Pavillard 1925, fig. 55; Hustedt 1930, fig 351.

Material examined:
TEM: 9, 18, 19, 80, 87, 91.
SEM: 74.
LM: 8, 73, 74, 90, 103, 108, 131, 135, 137, 138, 182, 183, 188.

Observations on type material:

The BM slide No.15175 **(108)** probably includes part of the collection H. Peragallo referred to in his original description (P. Sims, BM, pers. comm.). The *Rh. castracanei* frustules on the slide correspond with H. Peragallo's (1888, 1892) descriptions and figures in having 10-12 areolae to 10 µm on the girdle segments and a bilobed ventral valve margin. It is also probable that the TALE "Herb. H. Peragallo" slide No.276 **(137)** includes part of the same collection.

Lectotype: BM slide No.15175; Deby coll., *Rh. Temperei, Rh. Castracanei,* Villefranche.

LM OBSERVATIONS

Cells large, cylindrical, circular in cross-section. Diameter 108-250 µm. Length usually between 1 and 1.5 mm.

Valve: Bilaterally symmetrical. Apex conoidal, shallow. Ventral part strap-shaped, about 5 times as long as dorsal part (Figs 15a, c). Ventral margin bilobed (Fig. 108). Contiguous area distinct along strap-shaped part. Prominent claspers over impression of sister-cell otaria (Fig. 108). Areolae much smaller than on copulae, in columns convergin at apex.

Process: Prominent but comparatively short (25-35 μm), usually not intact. Widest at the base, tapering towards the tip (Figs 15a-c, 16). Internal canal connected with cell interior by fairly large labiate structure.

Otaria: Continuous with marginal ridges of contiguous area, wholly confined to valve proper. Outer margin straight to weakly concave. Distal margin straight to weakly convex, at an oblique angle to long axis of process. Angle between outer and distal margins usually obtuse (Fig. 15a).

Valvocopulae: Two large segments contiguous with most of valve margin. (Figs 15a-c). Areolation as in copulae.

Copulae: 2n (n = 2, 3,...., 8) columns of segments. First ventral copula accommodating impression of distal part of sister-cell process (Figs 15a, 108). Other copulae very variable in size and shape, usually with short median and long lateral margins (Figs 15a-c, 16, 102 -104); latitudinal extension varying between 42 and 205 μm and longitudinal extension between 15 and 45 μm (segments close to the valve disregarded). Areolation readily discernable in water mounts using a X25 objective (Fig. 103). 9-12 areolae to 10 μm within a column, 9-12 columns to 10 μm. Pattern quincuncial.
Note: The number of segment columns often differs in the two halves of the cell. One complete frustule was seen with one cingulum made up of 4 segment columns and the other of 14. I also found a few cells in which the number of segment columns varied within a cingulum (Fig. 16).

Auxospores: None observed.

SEM OBSERVATIONS

Areolae of valve and copulae loculate, foramen internal, velum external. Wall segments between areolae entire (Fig. 109). Outer layer of siliceous wall continuous on each segment and perforated in a manner corresponding to the pore pattern of the vela (Fig. 109). (Cf. TEM observations).

A fairly large labiate structure with the labia directly attached to the inner surface under the process was seen inside a few valves.
Note: The valves are almost indistinguishable from those of *Rh. debyana* in the same size range, whereas the girdle segments are readily distinguished by the larger areolae.

TEM OBSERVATIONS

Valve: Fine structure differing from that of copulae (Fig. 110). Circa 24 areolae to 10 μm within a column, c. 18 columns to 10 μm.

Areolae of valve: Foramen roundish, velum perforated by round or oblong pores not regularly arranged (cf. *Rh. debyana*).

Copulae: Marginal zone fairly broad, advalvar edge fringed, abvalvar edge entire.

Areolae of copulae: Outline hexagonal, foramen circular to ellipsoid, velum perforated by oblong to kidney-shaped pores in the angles (Figs 110, 111).

Rhizosolenia castracanei H. Peragallo var. **neglecta** var. nov.

Diagnosis: Differt a var. castracanei columnis duabus segmentorum cingularium.

Type material: Discovery Expedition St. 427, 36°37.5' S, 28°52' E, 7.9 1930. **(028).**

Holotype: Slide labelled *Rhizosolenia castracanei* (H. Peragallo) var. *neglecta* Sundström, Discovery Exped. St. 427, 36°37.5' S, 28°52' E, 7.9 1930. (BM).

Isotypes will be placed in the Hustedt Collection, Bremerhaven (BRM); the Smithsonian Institution, Washington D.C. (US); the Institute of Oceanology, Moscow (IOAS).

Misidentification: ? *Rh. styliformis* Brightwell var. *latissima* Brightwell in Subrahmanyan 1946, figs 130-132, 143.

Material examined: TEM: 28, 78, 81.
SEM: 28..
LM: 73, 74, 91, 184.

LM OBSERVATIONS

Cells long, cylindrical, circular in cross-section. Differing from var. *castracanei* in having only two segment columns (dorsiventrally arranged) and one valvocopula. Diameter 14-127 µm.

Valve: Conoidal, bilaterally symmetrical, ventral part longer than dorsal part. Ventral valve margin bilobed to trapezoid in outline. Contiguous area usually distinct along most of ventral part of valve (Figs 17, 107). Areolae in columns converging at apex, much smaller than in copulae.

Note: The shape of the valve is on the whole related to cell diameter, with valves of larger cells resembling those of var. *castracanei* and valves of narrow cells reminiscent of *Rh. styliformis* valves.

Process: Length of process and size of labiate structure vary somewhat.

Otaria: As in var. *castracanei* but usually smaller and sometimes (especially in narrow cells) extending to the base of the process. (Figs 106, 107).

Valvocopula: One segment contiguous with most of valve margin.

Copulae: First ventral copula accommodating impression of distal part of sister-cell process, abvalvar margin sometimes protruded. Other copulae rhomboidal to wing-shaped, shape varying with cell diameter. Areolation as in var. *castracanei.* 10-13 areolae to 10 µm within a column, 10-13 columns to 10 µm.

Auxospores: None observed.

TEM OBSERVATIONS

Structural details as in *Rh. castracanei* var. *castracanei.*

NOTE

The diameter ranges of *Rhizosolenia castracanei* var. *castracanei* and *Rh. castracanei* var. *neglecta* overlap between 108 and 127 µm (Fig. 3). A few cells with the one cingulum made up of 2 segment columns and the other of 4 were observed within this diameter range. Cell diameter in var. *neglecta* usually varied between 20 and 65 µm and the diameter in var. *castracanei* usually between 120 and 200 µm. Cells in the intermediate diameter range were rare.

DISTRIBUTION

Rhizosolenia castracanei var. *castracanei* has a circumglobal distribution within the Warm-water Region. The biogeographical limits of var. *neglecta* cannot be determined from the few samples in which I found it, but the distribution seems to resemble that of var. *castracanei.*

DISCUSSION

The size of the copular areolae is a distinguishing character in *Rh. castracanei.* Since the diameter of a cell with only 2 columns of segments can overlap with that of cells with 4, 6 and 14 columns it can be argued that it is superfluous to divide the species into infraspecific taxa. *Rh. castracanei* var. *neglecta* cells were, however, in general much narrower than var. *castracanei* cells and only a few cells of each variety were observed within the diameter range common to the two. The possibility that two genetically different form-series exist can therefore not be excluded on the basis of my observations. Since, moreover, *Rh. castracanei* cells with only two segment columns have apparently not been reported previously and may have ecological significance, it seems justifiable to accord them taxonomic

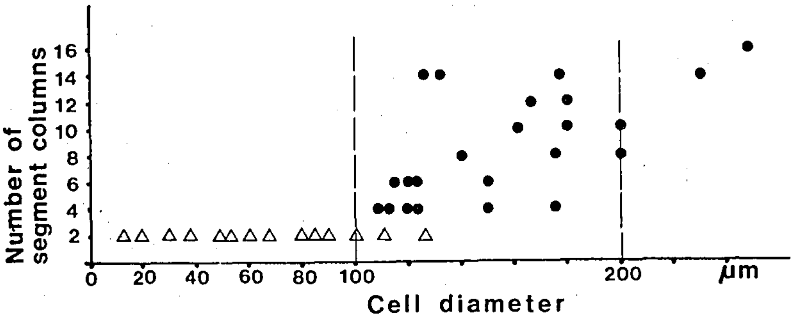


Fig. 3. Diameter of selected cells of *Rh. castracanei* var. *castracanei* (•) and var. *neglecta* (△).

status. Further research is needed before the relation between the two varieties can be conclusively determined. The rank of *varietas* is not entirely satisfactory but is currently the most acceptable (see General discussion).

Karsten (1907) described his *Rh. squamosa* from the Indian Ocean as a species with a diameter range of 220-264 µm and with 9 areolae to 10 µm in the girdle segments. He characterized *Rh. castracanei* as having a diameter range of 168-182 µm and 9 areolae to 10 µm (Karsten 1905b). In his descriptions the main distinction between the two lies in the shape of the copulae. It is evident from the material I have studied that the segmentation of the girdle, and hence the shape of the segments, can vary considerably from cell to cell in any population of *Rh. castracanei* and it seems quite safe to regard *Rh. squamosa* Karsten as conspecific with *Rh. castracanei* sensu orig.

Sournia (1968) noted that the name *Rh. squamosa* Karsten was illegitimate and introduced the name *Rh. squamifera* to replace it. He also suggested that *Rh. magna* Stüwe was conspecific with *Rh. castracanei*, an interpretation I fully agree with.

Subrahmanyan (1946) characterized the "intercallary bands" of *"Rh. styliformis* var. *latissima* " as having "12 punctae in 10 µm". His observations and figures correspond with my observations on large cells of *Rh. castracanei* var. *neglecta* and probably refer to this taxon. The name *Rh. castracanei* var. *rhomboidea* Subrahmanyan (1946) is synonymous with *Rh. clevei*, as pointed out by Sournia (1968). It should be stressed, however, that Subrahmanyan's misidentification has probably led to many misconceptions regarding both *Rh. castracanei* and *Rh. clevei* (cf. Sundström, 1984).

On the evidence of the texts and figures, descriptions of the fine structure of frustular elements of "*Rh. castracanei* " in Okuno (1968) were based on observations on a large frustule of *Pseudosolenia calcar-avis*, and those in Hasle (1975) on observations of *Rh. debyana* frustules.

It is an intriguing fact that with both LM and EM large valves of *Rh. castracanei* closely resemble valves of *Rh. debyana* whereas they clearly differ in fine structure of the copulae. It is also noteworthy that the size of the copular areolae is the main character for distinguishing *Rh. castracanei* var. *neglecta* from *Rh. formosa.* This could indicate that the genus *Rhizosolenia* is taxonomically more complicated than the species circumscriptions used here suggest.

RHIZOSOLENIA ANTENNATA (Ehrenberg) Brown (Figs 20, 114-116, 119, 120)

Brown 1920, p. 233, fig.8

Rhizosolenia antennata (Ehrenberg) Brown f. **antennata**

Basionym: *Dicladia antennata* Ehrenberg 1844, p. 23.

Synonyms: *Rhizosolenia bidens* Karsten 1905a pro parte, p. 98, pl. 9, fig. 13, (non figs 13a, 13b).
Rh. hebetata (Bail.) Gran f. *bidens* Heiden in Heiden and Kolbe 1928, p. 519, figs 158-161.
Rh. styliformis fa. *bidens* (Karst.) Frenguelli in Frenguelli and Orlando 1958, p. 136, pl. 7, fig. 5.

Non: *Rh. bergonii* Peragallo f. *bidens* (Karsten) Gaarder 1951, p. 25, fig. 11a, (nomen, non planta).

Selected figures: Van Heurck 1909, pl. 4, fig. 64; Heiden and Kolbe 1928, figs 158-160; Okuno 1952c, pl. 2, fig. 3; Frenguelli and Orlando 1958, pl. 7, fig. 5; Frenguelli 1960, pl. 1, fig. 7.

Material examined: TEM: 38.
SEM: 38.
LM: 36, 37, 119, 153.

Type material not found.

Lectotype: Drawing of *Dicladia antennata* on Ehrenberg's "Zeichenblatt" No.1920 (BHU).

LM OBSERVATIONS

Cells long, cylindrical, circular in cross-section. Diameter 18-45 µm. Solitary.

Valve: Conoidal with two apical processes (Figs 115, 119). Bilaterally symmetrical, lacking contiguous area and claspers. Valve margin in a plane perpendicular to pervalvar axis.

Processes: Two; symmetrically placed at valve apex, sometimes almost parallel but usually diverging at an acute angle, straight or curving slightly inwards, tapering from base, usually equal in length (30-80 µm) when intact. Internal canal widest near base, narrowing towards tip (Fig. 115), connected with cell interior by a labiate structure usually discernible at X200.

Otaria: Lacking.

Copulae: Rhomboidal, with short median and long lateral margins, varying only slightly in shape. In two columns, parallel to pervalvar axis but with no fixed orientation relative to plane of symmetry of valve.

Auxospores: None observed.

SEM OBSERVATIONS

Areolae loculate, foramen internal, velum external.

TEM OBSERVATIONS

Areolae and marginal zones of valve and copulae as in *Rh. antennata* f. *semispina* (Fig. 120). 23-26 areolae to 10 µm within a column, 24-26 columns to 10 µm on copulae.

NOTE

Rhizosolenia antennata f. *antennata* was found in material comprising five slides and samples. About 35 % of the *Rh. antennata* valves in the "Brategg" Exped. St. 29 sample (038) were f. *antennata*. Three heterovalvate cells were observed comprising a f. *antennata* valve at the one end and a f. *semispina* valve at the other. The diameter of two of these cells was c. 40 µm and of the third 23 µm. The hypotheca bore the f. *antennata* valve in all three cells. In the sample the valves of f. *antennata* ranged in diameter from 18 to 45 µm and f. *semispina* valves from 8 to 40 µm.

Rhizosolenia antennata (Ehrenberg) Brown f. **semispina** f. nov.

Diagnosis: Imprimis valva processu unico munita a f. antennata diversa. Rh. hebetatae Bailey f. semispinae (Hensen) Gran satis similis, areolis paulo majoribus et antarctica solum distributione ab ea diversa.

Type material: "Brategg" Exped. St. 29, 57°31' S, 150°00' W, 20.1 1948, (IMBB 28).

Holotype: Slide labelled *Rh. antennata* f. *semispina* Sundström, "Brategg" Exped. St. 29, 57°31' S, 150°00' W, 20.1 1948. (BM).
Isotypes will be placed in the Hustedt Collection, Bremerhaven (BRM); the Smithsonian Institution, Washington D.C. (US); the Institute of Oceanology, Moscow (IOAS).

Misidentifications: *Rh. styliformis* Brightwell var. *longispina* Hustedt in Okuno 1952a, p. 47, pl. 1, figs 1, 1'.
Commonly referred to as *Rh. hebetata* f. *semispina.*

Selected figures: Okuno 1952a, pl. 1, figs 1, 1'; Okuno 1954, pl.2, figs 1, 1'; Hasle 1975, figs 23a, 23b.

Material examined: TEM: 30-33, 36-39.
SEM: 30, 38.
LM: 35, 40, 41, 119, 133, 145, 152-154.

The type material **(038)** contains both forms of *Rh. antennata.*

LM OBSERVATIONS

Cells long, cylindrical, circular in cross-section. Solitary or in pairs. Diameter 6.5 - 42 µm.

Valve: Acutely conoidal, bilaterally symmetrical. Ventral part much longer than dorsal part. Marginal ridges of contiguous area usually readily discernible towards proximal part of valve, claspers clearly seen in permanent mounts, even in thin specimens, using a X100 objective.

Process: Comparatively long (Figs 20, 114), usually not intact in preserved material, widest basally, tapering into long narrow tube. Length of intact process indicated by length of impression of sister-cell process (Fig. 20). Basal lumen connected with cell interior by a labiate structure usually discernible at high magnification (X400).

Otaria: Extending at least 3 µm along basal part of process (Fig. 20), continuous with marginal ridges of contiguous area in large cells, usually wholly confined to basal part of process in narrow cells (cf. Fig. 19). Outer margin straight to slightly convex, almost parallel to long axis of process. Distal margin concave. Angle between outer and distal margins forming a point.

Valvocopula: One segment contiguous with most of valve margin (Fig. 20).

Copulae: In two dorsiventral columns. First ventral copula accommodating impression of sister-cell process, abvalvar margin extended into a tongue medially (Fig. 116). Other copulae rhomboidal with short median and long lateral margins, fairly uniform in shape, variable in size. (Fig. 20).

SEM OBSERVATIONS

Areolae loculate, foramen internal, velum external.

TEM OBSERVATIONS

Valve: Areolae in columns converging at apex, resembling those on copulae but less uniform in size and outline, usually with two slits in vela close to margin and one slit closer to apex.

Copulae: Marginal zone fairly broad, advalvar edge fringed, abvalvar edge entire. Areolae in columns parallel to pervalvar axis. Areolar pattern quincuncial. 23-26 areolae to 10 µm within a column, 24-26 columns to 10 µm.

Areolae of copulae: Rounded-rectangular in outline, foramen ellipsoidal to circular, velum perforated by two slit-like oblong pores orient parallel to areola column (Fig. 120).

NOTE

The original drawing of *Dicladia antennata* is on Ehrenberg's "Zeichenblatt" No.1920 (the Ehrenberg Collection, BHU). The "Zeichenblatt" shows fragments, spicules and shells of organisms collected in (or from ?) "Pancake Ice off the Barrier, Laht. 78.10. S, Longit.162 W." The drawing of *D. antennata* differs from the figure in Ehrenberg (1854) in not showing the valve fragment as having a defined proximal margin, and in showing the processes as being straight rather than both slightly curved in the same direction, as they are in Ehernberg's (1854) pl. 35, fig XII/9.

DISTRIBUTION

Rhizosolenia antennata was found only in material from the Southern Cold-water Region.

DISCUSSION

Figure XII/9, pl. 35 in Ehrenberg (1854) is somewhat misleading in showing the processes as being both slightly curved in the same direction, not straight as in the original drawing ("Zeichenblatt" No.1920). I am in no doubt that Brown (1920) was right in transferring *Dicladia antennata* to *Rhizosolenia* regarding it conspecific with *Rh. bidens* Karsten. *Rh. antennata* f. *antennata* is unique among the Rhizosoleniae in that the valve is always terminated by two processes. The shape and orientation of the processes are characteristic and are well shown in the original drawing which cannot be interpreted as depicting any other known diatom.

The dimorphism displayed by *Rh. antennata* was first documented by Heiden and Kolbe (1928). Hustedt (1958) regarded "bidens" variants as anomalies. Valves with two processes are in fact found in many *Rhizosolenia* species, but except in *Rh. antennata* are of isolated occurrence. *Rh. antennata* f. *antennata* was abundant in some of the Antarctic samples I saw and cannot be regarded as an abnormal variant.

Since Karsten (1905a) had observed bidentate valves on initial cells of "*Rh. alata*" he regarded *Rh. bidens* (syn. *Rh. antennata*) and *Rh. alata* as being related. It is, however, quite safe to regard figs 13a and 13b, pl. 9 in Karsten (1905a) as illustrations of abnormal initial cells of a *Proboscia sp.* (*Rh. alata* sensu Karsten). I myself have also observed a few such cells.

Rhizosolenia antennata f. *semispina* and *Rh. hebetata* f. *semispina* are almost indistinguishable with both LM and EM, but *Rh. antennata* is restricted to the Southern Cold-water Region and is presumably well separated geographically from *Rh. hebetata* since I found no cells of either species in samples from the Circumglobal Warm-water Region. Since, furthermore, *Rh. antennata* has never been recorded from boreal waters and since the few existing records of *Rh. hebetata* f. *hebetata* from austral waters can fairly safely be disregarded as misidentifications I see no reason to regard the species as conspecific. (See also discussion under *Rh. hebetata*).

RHIZOSOLENIA HEBETATA Bailey (Figs 18a-b, 19, 112, 113, 117, 118)

Bailey 1856, pl. 1, figs 18, 19.

Rhizosolenia hebetata Bailey f. **hebetata**

Synonym: *Rhizosolenia hebetata* f. *hiemalis* Gran (nom. illeg.), Gran 1904, p. 524.

Non: *Rh. hebetata* Bailey sensu H. Peragallo 1892, pl. 5, fig. 10. (= *Rh. sima* f. *silicea* ?).
Rh. hebetata Bail. f. *hiemalis* Gran sensu Karsten 1907, pl. 17, fig. 4a.
(= *Proboscia sp.*).
Rh. hebetata f. *hiemalis* sensu Crosby and Wood 1958, pl. 39, fig. 73A. (= *Rh. sp.*).

Selected figures: Meunier 1910, pl. 28, fig. 14; Hustedt 1920, pl. 319, fig. 16;
Cupp 1943, fig. 50-A; Okuno 1957, pl. 1, figs 2a, 2b; Hustedt 1930, fig. 337;
Seaton 1970, figs 1, 2; Drebes 1974, fig. 41b.

Material examined: TEM: 93.
LM: 94, 150, 151.

Neotype: Cleve and Möller (1887-1892) collection (S); Slide No. 308, Sea of Behring. **(150).**

LM OBSERVATIONS

Cells long, cylindrical, circular in cross-section (Fig. 112). Diameter 15-44 µm. Solitary or in pairs.

Valve: Acutely conical with valve margin in a plane slightly oblique to pervalvar axis. Fairly heavily silicified, especially towards apex. Contiguous area and claspers lacking (Figs 18a-b, 113).

Process: Heavily silicified, 15-25 µm long. Tapering slightly from base, tip rounded (Fig. 113). Internal lumen wide in basal part, tapering into a narrow canal opening at tip, connected with cell interior by a labiate structure usually visible at high magnification (X400) but smaller than in f. *semispina* cells of corresponding diameter.

Otaria: Lacking.

Valvocopula: One segment contiguous with most of valve margin.

Copulae: In two columns. Rhomboidal with short median margins, resembling those of f. *semispina* (Figs 18a-b).

SEM OBSERVATIONS. None made.

TEM OBSERVATIONS

Areolae of copulae: Velum perforated by one slit parallel to pervalvar axis observed in one specimen but not photographed.

DISTRIBUTION

Rhizosolenia hebetata f. *hebetata* was only found in material from the Northern Cold-water Region.

Rhizosolenia hebetata f. semispina (Hensen) Gran

Gran 1904, p. 524, pl. 17. (Not seen). Gran 1905, p. 55, fig. 67b.

Basionym: *Rhizosolenia semispina* Hensen 1887, p. 84, pl. 5, fig. 39.

Synonyms: *Rhizosolenia hebetata* Bailey "*semispina*"-phase Hendey 1937, p. 315, (pro parte).
Rh. styliformis var. *semispina* (Hensen) Karsten Wimpenny 1946, p. 277, (pro parte).
Rh. hebetata Gran f. *decora* Takano 1972, p. 171.
Rh. hebetata f. *heterothrix* Meunier 1910, pl. 30, fig. 50. (= *Rh. hebetata* with one f. *hebetata* valve and one f. *semispina* valve).

Non: *Rh. semispina* Hensen sensu Pavillard 1925, figs 48A-B, 49. (= *Rh. clevei* var. *communis* ?).
Rh. hebetata (Bail.) Gran f. *semispina* (Hensen) Gran sensu Allen and Cupp 1933, figs 42, 42a. (= *Rh. clevei* var. *communis* ?).
Rh. styliformis var. *semispina* (Hensen) Karsten sensu Wimpenny 1946, text-figs 1f, 1g, 1i. (= *Rh. spp.*).
Rh. hebetata (Bailey) Gran var. *semispina* (Hensen) Gran sensu Subrahmanyan 1946, figs 133, 136. (= *Rh. clevei* var. *communis* ?).
Rh. hebetata f. *semispina* (Hensen) Gran sensu Eskinazi and Sato 1963, pl. 2, figs 7-9. (= *Rh. clevei* var. *communis* ?).
Rh. hebetata (Bail.) Gran f. *semispina* (Hensen) Gran sensu Margalef 1969, fig. 4K. (= *Rh. clevei* var. *communis* ?).
Rh. hebetata f. *semispina* (Hensen) Gran sensu Pankow 1976, pl. 8, fig. 6. (= *Rh. setigera* Brightw. ?).
Rh. hebetata f. *semispina* (Hensen) Gran sensu Navarro 1981, figs 39, 40. (= *Rh. clevei* var. *communis*).

Selected figures: Okuno 1957, pl. 1, figs 3a, 3b; Takano 1972, figs 1a-c; Hasle 1975, figs 21, 22, 24-26.

Material examined: TEM: 2, 6, 92, 93, 95.
SEM: 6.
LM: 158-167, 169-173, 179-181.

Neotype: Slide labelled Ymer 80, FP 32; Neotype Rh. heb. f. semisp.; Department of Marine Ecology, University of Lund.

LM OBSERVATIONS

Cells long, cylindrical, circular in cross-section (Fig. 19). Diameter 4.5 - 25 µm. Solitary or in pairs.

Valve: Acutely conoidal, bilaterally symmetrical. Ventral part much longer than dorsal part. Marginal ridges of contiguous area usually discernible towards proximal part of valve, claspers clearly seen in permanent mounts, even in thin specimens using a X100 lens. (Figs 19, 117).

Process: Comparatively long (Fig. 117), usually not intact in preserved material, widest basally, tapering into narrow tube. Length of intact process indicated by length of impression of sister-cell process (Fig. 19). Basal lumen connected with cell interior by a labiate structure usually discernible at high magnification (X400).

Otaria: Extending at least 3 µm along basal part of process, continuous with marginal ridges of contiguous area in large specimens, usually wholly confined to basal part of process in narrow specimens (Figs 19, 117). Outer margin straight to weakly convex, almost parallel to long axis of process. Distal margin concave. Angle between outer and distal margins acute forming a point (Fig. 117). In narrow specimens the otaria are often inconspicuous but their presence can always be confirmed by the outline of the contiguous area.

Valvocopula: One segment contiguous with most of valve margin (Fig. 19).

Copulae: In two dorsiventral columns. First ventral copula accommodating impression of distal part of sister-cell process, abvalvar margin extended into a tongue medially (cf. Fig. 116). Other copulae rhomboidal with short median margins, fairly uniform in shape, variable in size. (Fig. 19).

Auxospores: None observed.

SEM OBSERVATIONS

Areolae loculate, velum external, foramen internal. Wall segments between areolae apparently entire.

TEM OBSERVATIONS

Valve: Areolae in columns converging at apex, resembling those on copulae but less uniform in size and outline, usually with two slits in vela close to margin and one slit closer to apex.

Copulae: Marginal zone fairly broad, advalvar edge fringed, abvalvar edge entire. Areolae in columns parallel to pervalvar axis. Areolar pattern quincuncial. 28-30 areolae to 10 µm within a column, 30-32 columns to 10 µm.

Areolae of copulae: Rounded-rectangular in outline, foramen ellipsoidal to circular, velum perforated by two slit-like, oblong pores oriented parallel to areola column (Fig. 118).

DISTRIBUTION

Rhizosolenia hebetata f. *semispina* is apparently restricted to the Northern Cold-water Region.
Note: *Rh. hebetata* f. *semispina* is almost indistinguishable from *Rh. antennata* f. *semispina* of the Southern Cold-water Region. Neither species was seen in material from the Circumglobal Warm-water Region.

DISCUSSION

I have not found type material for either of the two forms of *Rh. hebetata.* The commonly accepted circumscription of *Rh. hebetata* as a dimorphic species derives from Gran (1904), (see Gran 1905). His two forms conform with the sketchy original descriptions and I find no reason to doubt that Gran's interpretation is correct.

Rhizosolenia hebetata f. *semispina* has often been recorded in samples from all parts of the ocean and the distribution is generally regarded as global. Many of the alleged records of *Rh. hebetata* f. *semispina* are, however, misidentifications. I have found no *Rh. hebetata* in samples from the tropics, and I can only regard it as a most unlikely component of the phytoplankton there. The taxon most commonly mistaken for *Rh. hebetata* f. *semispina* is undoubtedly *Rh. clevei* var. *communis,* since *Rh. hebetata* f. *semispina* has often been recorded as host for *Richelia intracellularis* in warm waters. The two taxa resemble each other superficially, but while *Rh. clevei* is apparently always host for the cyanobacterium (Sundström 1984) I found no evidence of *Rh. hebetata* as host. It is also probable that narrow cells of the *Rh. styliformis* -complex and narrow cells of *Pseudosolenia calcar-avis* have sometimes been mistaken for *Rh. hebetata* f. *semispina* in warm parts of the ocean.

The dimorphism displayed by *Rh. hebetata* is well documented from the Northern Hemisphere (Gran 1905, Meunier 1910, Ramsfjell 1959, Seaton 1970, Drebes 1974). *Rh. hebetata* f. *hebetata* has also been reported from the Southern Hemisphere (as f. *hiemalis*) by H. Peragallo (1892), Karsten (1907), Crosby and Wood (1958) and Seaton (1970). There is, however, an important distinction between the records from the two hemispheres, there being no records of heterovalvate cells from the Southern Hemisphere. Since, furthermore, both *Rh. sima* and *Rh. polydactyla* have forms that superficially resemble *Rh. hebetata* f. *hebetata*, it is conceivable that they have sometimes been mistaken for the better-documented *Rh. hebetata* f. *hebetata*. The illustration of "*Rh. hebetata*" in H. Peragallo (1892) is probably of *Rh. sima* f. *silicea*, judging from the general appearance of the valve. The alleged record in Karsten (1907) from "Kratersee St. Paul" (St. 164) was probably based on a misidentification of *Proboscia sp.*, since on valves of *Rh. hebetata* f. *hebetata* there is no structure for holding them together in the manner shown in his pl. 17, fig. 4b. Valves of *Proboscia*, however, are usually furnished with claspers that enable sister valves to stick together. In addition, *Rh. hebetata* f. *hiemalis* was not mentioned in Schrimper's species list from the same station (Karsten 1907), but *Rh. alata* (= *Proboscia sp.*) was recorded as dominant.

Crosby and Wood (1958) reported "*Rh. hiemalis*" from the Southern Hemisphere, but it is not clear from the illustration what taxon they had found. Seaton (1970) relied on second-hand information when he stated that *Rh. hebetata* f. *hiemalis* was to be found in the Southern Hemisphere. There were no *Rh. hebetata* in the Antarctic material I examined.

Rh. hebetata f. *semispina* and *Rh. antennata* f. *semispina* are almost indistinguishable with both LM and EM and are commonly treated as belonging to the same species (i.e. *Rh. hebetata)* in the literature. However, since *Rh. antennata* and *Rh. hebetata* are so widely separated geographically and have forms that are so dissimilar in gross morphology, I find it hard to regard the two populations as belonging to the same species. Nor can I see how a gene flow would be possible between *Rh. hebetata* and *Rh. antennata* if there are no occurrences in the Circumglobal Warm-water Region.

The name *Rh. styliformis* var. *semispina* sensu Wimpenny (1946) can be regarded as a "nomen confusum", since on the evidence of the figures and description it apparently refers to a combination of at least three taxa. *Rh. styliformis* var. *semispina* sensu Robinson and Waller (1966) probably also comprises more than one taxon, since the diameter range they give (12-68 µm) does not agree with my observations on *Rh. hebetata* f. *semispina* nor with those of Ramsfjell (1959), Seaton (1970) or Drebes (1974). The name *Rh. hebetata* f. *decora* introduced by Takano (1972) is unnecessary, since one of the distinguishing characters of *Rh. hebetata* f. *semispina* is the presence of otaria, and is indicated in the original illustration (Hensen 1887, pl. 5, fig. 39) by the shape of the contiguous area ("Narbe"). The drawing of the valve as a whole, however, is inexact. Takano (1972) presented no illustration of his "wingless" form, and no conclusion can be drawn as to its identity. The drawing of of the "barked" specimen in Takano's fig. 2b probably depicts a valve of *Rh. setigera* (sensu lato) since it would be physically impossible to "strip" a *Rh. hebetata* f. *semispina* valve in the way he suggested.

Seaton (1970) observed one dividing *Rh. hebetata* f. *hebetata* cell giving rise to daughter valves of the f. *semispina* type. On the evidence of my Fig. 112, and fig. 337b in Hustedt (1930), it also appears that *Rh. hebetata* f. *hebetata* can divide to give rise to new individuals of the f. *hebetata* type. Seaton, furthermore, observed that mother cells of c. 4.7 µm in diameter could give rise to three kinds of initial cells through auxosporulation: (a) large *Rh. hebetata* f. *semispina* cells; (b) large *Rh. hebetata* f. *hebetata* cells; (c) large cells with a f. *semispina* valve at one end and a f. *hebetata* valve at the other. The initial cells ranged in diameter from 19 to 27 µm. Auxospore formation in *Rh. hebetata* f. *semispina* has also been described by Ramsfjell (1959) and Drebes (1974) on material from the Norwegian Sea and the North Sea. Apparently *Rh. hebetata* f. *semispina* cells cannot produce f. *hebetata* cells other than by auxosporulation (cf. *Rh. polydactyla* and *Rh. sima*).

The "lateral pore" that Okuno (1957, text-fig. 1A) allegedly observed in the wall segments between areolae was never present in frustules I examined. Okuno's observation should be queried.

Owing to lack of original material and of adequate original illustrations neotypes are designated for *Rh. hebetata* f. *hebetata* and *Rh. hebetata* f. *semispina.*

RHIZOSOLENIA CLEVEI Ostenfeld (Figs 21-23, 121-127)

Ostenfeld 1902, p. 229, fig. 6.

Rhizosolenia clevei Ostenfeld var. **clevei**

Sundström 1984, p. 348, figs 1, 4-9.

Synonyms: ? *Rhizosolenia similis* Karsten 1907, p. 383, pl.41, fig. 9.
Rh. Castracanei Peragallo var. *rhomboidea* Subrahmanyan 1946, p. 123, figs 153, 154, 156-160.

Misidentifications: *Rh. temperei* sensu Okuno 1952b, pl. 2, figs 3-3'''.
Rh. acuminata sensu Okuno 1957, pl. 1, figs 1a-c; 1968, figs 1, 10d, 11j, 12.

Selected figures: Hustedt 1933, pl. 384, fig. 2; Sournia 1968, pl. 10, fig. 68; Sundström 1984, figs 1, 4-9.

Material examined: TEM: 45, 46, 48, 76, 77, 83.
SEM: 83.
LM: 62, 111, 112, 128, 141, 187.

Lectotype: Slide labelled Siam No.10; Universitetets Botaniske Museum, Copenhagen (C). (Cf. Sundström 1984).

LM OBSERVATIONS

Cells large, cylindrical, circular in cross-section (Fig. 121). Solitary or in pairs. Diameter 80-250 µm.

Valve: Conoidal, bilaterally symmetrical. Ventral part about twice as long as dorsal part. Contiguous area and claspers distinct (Fig. 21).

Process: Tapering from base, seldom intact in preserved material. Impression of sister-cell process indicating length of intact process (Fig. 21). Internal canal opening at tip, connected with cell interior by labiate structure.

Otaria: Continuous with marginal ridges of contiguous area, arising at valve apex, extending along basal part of process, ending roughly 5 µm beyond process base. Distal margin straight to weakly convex, at an oblique angle to process. Outer margin roughly parallel to long axis of process, straight to weakly convex. Angle between between distal and outer margins obtuse (rounded) (Fig. 21).

Valvocuopula: One large segment contiguous with most of valve margin.

Copulae: 2n (n = 4, 5, 6, 7, 8) segment columns. Number of columns not always the same on hypotheca and epitheca. First ventral copula accommodating impression of distal part of sister-cell process, differing in size and shape from other copulae (Fig. 21). Other copulae rhomboidal, median margins short, lateral margins long, fairly uniform in shape (Figs 21, 122). Areolar pattern quincuncial, visible with a X100 objective.

Auxospores: None observed.

Endophyte: All intact cells I examined were host for the cyanobacterium *Richelia intracellularis* Schmidt (Figs 121, 122).

SEM OBSERVATIONS

Areolae loculate, velum external, foramen internal. Wall segments between areolae entire.

TEM OBSERVATIONS

Valve: Areolae resembling those on copulae but usually smaller and less uniform in outline; in columns converging at apex.

Copulae: Marginal zone with advalvar edge fringed (Fig. 125), abvalvar edge entire. Areolar columns usually parallel to pervalvar axis. 18-23 areolae to 10 µm within a column, 16-22 columns to 10 µm.

Areolae of copulae: Sub-rectangular in outline. Foramen fairly large, circular to elliptical. Velum perforated by a median row of oblong pores, long axes of pores parallel to areolar column. Number of pores 3-8, varying with width of areola but usually 4-6. (fig. 125).

DISTRIBUTION

The distribution of *Rhizosolenia clevei* var. *clevei* is poorly known. I found it only in material from the Indian Ocean, the Gulf of Thailand and the Arafura Sea.

Rhizosolenia clevei Ostenfeld var. **communis** Sundström

Sundström 1984, p. 348, figs 2, 3, 10-15.

Misidentifications: Commonly misidentified as *Rh. styliformis* and *Rh. hebetata* f. *semispina* (cf. Sundström 1984).

Material examined: TEM: 17-19, 22, 44, 45, 62, 67, 76, 78, 80, 81, 83, 86-88.
SEM: 45, 83.
LM: 11, 15, 43, 49, 64, 68, 74, 79, 111-113, 115, 117, 127, 141, 156, 157, 182.

Holotype: Slide labelled Siam No.10; Universitetets Botaniske Museum, Copenhagen (C).
(Cf. Sundström 1984).

LM OBSERVATIONS

Cells long, cylindrical, circular in cross-section (Figs 22, 23, 124). Solitary or in pairs. Diameter 7-55 µm.

Valve: Conoidal, bilaterally symmetrical. Ventral part longer than dorsal part. Contiguous area and claspers usually readily discernable. (Figs 22, 23).

Process: Tapering from base, seldom intact in preserved material, impression of sister-cell process indicating length of intact process (Figs 22, 23, 124). Internal canal opening at tip, connected with cell interior by labiate structure.

Otaria: Usually continuous with marginal ridges of contiguous area, arising at valve apex, extending along basal part of process, ending roughly 4 µm beyond process base. Shape as in var. *clevei.* (Figs 22, 23, 124).
Note: The otaria are usually inconspicuous in narrow specimens and therefore easily overlooked. Their presence can, however, always be deduced from the outline of the contiguous area.

Valvocopula: One segment contiguous with most of valve margin.

Copulae: In two dorsiventral columns. First ventral copula differing in shape from other copulae, accommodating impression of distal part of sister-cell process (Figs 22, 23, 124). Other copulae variable in size and shape, median margins usually short, lateral margins usually long.

Auxospores: None observed.

Endophyte: All intact cells examined were host for the cyanobacterium *Richelia intracellularis* (Fig. 123).

SEM OBSERVATIONS

Areolae loculate, velum external, foramen internal. Wall segments between areolae entire.

TEM OBSERVATIONS

Areolar pattern and fine structure of areolae as in *Rh. clevei* var. *clevei.* Number of velum pores on copulae, however, ranging from 2-9. 19-25 areolae to 10 µm within a column, 14-22 columns to 10 µm on copulae. (figs 126, 127).

DISTRIBUTION

Rhizosolenia clevei var. *communis* is probably restricted to the Circumglobal Warm-water Region and apparently more widespread than var. *clevei.*

Rh. clevei was present throughout the year expect in June and July in the waters surrounding Ko Phuket, Thailand. *Rh. clevei* var. *clevei* did, however, seem to appear and reappear more sporadically than *Rh. clevei* var. *communis.*

DISCUSSION

Sundström (1984) showed that, in the description of *Richelia intracellularis,* Schmidt (in Ostenfeld and Schmidt 1901) misidentified the host as *Rh. styliformis.* In addition *R. intracellularis* is reported in the literature as being associated with many other planktonic diatoms in subtropical and tropical parts of the ocean. In Sundström (1984) it is argued that the species is probably only associated with *Rhizosolenia clevei,* and that most other records can be discarded as misidentifications of either the host or the cyanobacterium. The presence of *R. intracellularis* thus appears to be a good diagnostic character for *Rh. clevei.*

There seems to be a discontinuity in cell diameter and type of girdle segmentation between the two varieties of *Rh. clevei,* indicating that they belong to two different form-series and meriting the rank proposed in Sundström (1984). More research is needed before the relation between the two varieties can be determined conclusively.

RHIZOSOLENIA DEBYANA H. Peragallo (Figs 24a-b, 25, 128-138)

H. Peragallo 1892, p. 111, pl. 2, figs 7, 7a.

Synonym: ? *Rhizosolenia Karsteni* Hustedt 1920, pl. 318, figs 9, 9a, 9b.

Misidentification: *Rh. castracanei* H. Peragallo in Hasle 1975, p. 107, figs 27-33, 40.

Selected figures: Hasle 1975, figs 27-33, 40.

Material examined: TEM: 18, 19, 22, 23, 73-75, 78, 87, 96.
SEM: 23, 74.
LM: 12, 101, 123, 126, 182-186, 188.

Type material not located.

Lectotype: Fig. 7, pl. 3 in H. Peragallo 1892.

LM OBSERVATIONS

Cells large, cylindrical, circular in cross-section (Fig. 24a). Diameter 180-310 µm. Length usually between 0.7 and 1.5 mm. Solitary.

Valve: Bilaterally symmetrical. Apex conoidal, shallow. Ventral part of valve strap-shaped, 5-7 times as long as dorsal part. Ventral margin bilobed (Fig. 133). Contiguous area distinct towards end of strap-shaped part of valve (Fig. 24a, 25). Prominent claspers over impression of sister-cell otaria. Areolar pattern somewhat finer than on copulae, columns converging at apex.

Process: Prominent but comparatively short, usually not intact. Widest at base, tapering towards tip. Internal canal connected with cell interior by a fairly large labiate structure.

Otaria: Wholly confined to valve proper. Outer margin straight to weakly concave. Distal margin roughly straight, at an oblique angle to long axis of process. Angle between outer and distal margins obtuse. (Figs 24a-b, 25).

Valvocopulae: Two large segments contiguous with most of valve margin (Figs 24a-b, 25).

Copulae: 2n (n = 5, 6, 7, 8, 9) columns of segments. First ventral copula accommodating impression of distal part of sister-cell process. Other copulae variable in size and shape (Figs 128-130, 134), lateral margins usually weakly sigmoid and longer than median margins.

SEM OBSERVATIONS

Areolae of both valve and copulae loculate, velum external, foramen internal. Wall segments between areolae entire. Labiate structure fairly large as in figs 32a, 32b and 33 in Hasle (1975). See also *Rh. castracanei.*

TEM OBSERVATIONS

Valve: Areolae in columns converging at apex, 20-26 to 10 µm within a column, 20-32 columns to 10 µm.

Areolae of valve: Velum perforated by 1-3 circular to oblong pores either in a row as on copulae or irregularly placed. Foramen roundish.

Copulae: Marginal zone fairly broad, advalvar edge fringed, abvalvar edge entire. Areolae in columns usually parallel to pervalvar axis, in quincuncial pattern. 19-22 areolae to 10 µm within a column, 16-24 columns to 10 µm. (Figs 135, 138).

Areolae of copulae: Subrectangular to subhexagonal in outline. Foramen ellipsoid to circular, varying in diameter. Velum perforated by 2-5 (usually 3) circular to oblong pores in a median row (Figs 131, 132, 136-138).

DISTRIBUTION

H. Peragallo's original material was from an unspecified locality in the North Atlantic Ocean. My own few records suggest a circumglobal distribution within the Warm-water Region. Off the west coast of Thailand *Rh. debyana* was found in conjunction with upwelling but was never seen in the inshore samples.

DISCUSSION

No type material of *Rhizosolenia debyana* could be located, but the specimens I examined agreed with the original illustrations in shape of valve and valvocopulae, in the shape of the girdle segments and in size. According to H. Peragallo (1892) *Rh. debyana* is distinguished from *Rh. castracanei* on larger girdle segments with a much finer punctation. The smaller areolae of the copulae is indeed the main character distinguishing *Rh. debyana* from *Rh. castracanei* var. *castracanei* in LM, but the girdle segments of both vary much more in size and shape than the original descriptions would suggest.

It seems that *Rh. debyana* has largely been overlooked or else confused with other species. Ostenfeld (1902) regarded it as being "allied to *Rh. clevei*" and Hustedt (1930) placed it among

"Zweifelhafte Formen" (doubtful forms). The illustrations of *Rh. Karsteni* in Hustedt (1920) suggest that it is conspecific with *Rh. debyana. Rh. Karsteni* was not included by Hustedt (1930) in his monumental diatom flora. On the evidence of text and figures *Rh. debyana* was misidentified as *Rh. castracanei* in Hasle (1975).

Valves of *Rh. debyana* and *Rh. castracanei* that are of the same size are indistinguishable with LM, SEM and TEM. On the other hand the fine structure of the copulae in no way suggest that the two species are closely related.

It is curious that the minimum diameter of *Rh. debyana* seems to be as large as 180 µm. In all other species of *Rhizosolenia* I examined it was much less than this.

RHIZOSOLENIA CRASSA Schimper (Figs 26, 27, 139-143)

Schimper in Karsten 1905a, p. 99, pl. 11, figs 6, 6a, 6b.

Misidentifications: ? *Rhizosolenia annulata* Karsten in Hendey 1937, p. 311.
? *Rhizosolenia styliformis* in Frenguelli 1943, pl. 3, fig 10.

Selected figures: Hustedt 1920, pl. 318, figs 6-8.

Material examined: TEM: 29.
SEM: 29.

Type material not examined.

Neotype: Fig. 6, pl. 318 in Hustedt 1920.

LM OBSERVATIONS

Cells large, cylindrical, circular in cross-section (Figs 26, 139). Fairly heavily silicified. Solitary or in pairs. Diameter 100-165 µm. (See also under Discussion).

Valve: Conoidal, bilaterally symmetrical. Ventral part about twice as long as dorsal part (Fig. 143). Marginal ridges of contiguous area distinct over whole length of valve, continuous with otaria (Figs 26, 142). Prominent claspers over impression of sister-cell otaria (Fig. 142).

Process: Robust, about 50 µm long when intact, usually broken. Internal canal widest basally, connected with cell interior by labiate structure (Figs 140, 141).

Otaria: Prominent, characteristic in shape (Figs 26, 141), bordering both valve apex and basal part of process. Outer margin slightly convex, slightly upcurved. Distal margin concave, oblique to long axis of process (Fig 141). Angle between outer and distal margins obtuse, sometimes forming a point.

Valvocopula: One large segment contiguous with most of valve margin (Figs 142, 143).

Copulae: Cells with 2 and 4 columns of segments observed. Cells with one of the cingula composed of 2 columns and the other of 4 columns were common in the sample (Fig. 26). Two segment columns were observed in cells of all sizes, four columns in cells ranging from 115-140 µm in diameter. First ventral copula accommodating impression of sister-cell process; sometimes with slight protrusion on its abvalvar margin (Fig. 142). Other copulae variable in outline, usually having short median margins amd long lateral margins.

Auxospores: None observed.

SEM OBSERVATIONS

Areolae of copulae loculate, velum external, foramen internal.

TEM OBSERVATIONS

Valve: Details hard to discern. Areolae finer than on copulae, apparently with one slit in velum and lacking foramen. 27 areolae to 10 µm within a column and 29 columns to 10 µm counted on a single valve.

Copulae: Marginal zone fairly broad, advalvar edge fringed, abvalvar edge entire. Areolae in columns usually parallel to pervalvar axis. Pattern quincuncial. 22-24 areolae to 10 µm within a column, 22-24 columns to 10 µm.

Areolae of copulae: Rounded hexagonal in outline. Foramen ellipsoid to circular, varying in diameter. Velum perforated by two oblong to circular pores, long axes parallel to areolar column.

No TEM pictures worth reproducing were obtained because of the degree of silicification. Instead a drawing was made from TEM negatives (Fig. 27).

DISTRIBUTION

Rhizosolenia crassa is apparently confined to the Southern Cold-water Region. Few reliable records exist.

DISCUSSION

From the general wording of the original description it can be assumed that it was written by Karsten. Unfortunately, the description and figures are not sufficiently detailed to be of diagnostic value. The specimens I found in the Discovery Expedition, St. 721 sample **(029)** corresponded in all essential details with Hustedt's (1920) illustrations of *Rh. crassa* from one of the original samples. I have therefore regarded them as representative and chosen his fig. 6, pl. 318 as neotype. The cells I examined varied in diameter between 100 and 165 µm as compared with the diameter range of 140-250 µm given in Karsten (1905a) which, however, should be queried since the cells in his figs 6 and 6a have diameters of 100 µm and 96 µm respectively, and since Hustedt's figs 6-8 show cells with diameters of 115 and 150 µm, assuming the scales are correct.

It is evident from the sample that *Rh. crassa* can have either 2 or 4 columns of segments in cells of the size range I observed. Both Karsten (1905a) and Hustedt (1920), furthermore, presented drawings of specimens with at least 6 columns of segments.

Rh. crassa completely dominated the sample I examined and no other species of *Rhizosolenia* were found. According to Hendey (1937) "*Rh. annulata* " was the only *Rhizosolenia* in the sample. However, it is probable that he used the name erroneously since Karsten (1907) described *Rh. annulata* from material collected in the tropical part of the Indian Ocean. It is also likely that Hendey had an erroneous concept of *Rh. crassa* since he recorded this species in samples from both subtropical and Antarctic waters. I examined two of these samples **(027, 030)** and found no *Rh. crassa.*

In Frenguelli (1943) is a detailed drawing of a "*Rhizosolenia styliformis* " valve (pl. 3, fig. 10; no scale given). It is probable that the drawing is of a *Rh. crassa* valve since the otaria correspond in outline only with those in this species. If this is so it would imply that *Rh. crassa* can have a minimum diameter much less than that I found since the valve in the drawing is distinctly acuter than the valves I have observed.

RHIZOSOLENIA SIMA Castracane (Figs 28, 29, 144-154)

Castracane 1886, p. 71, pl. 24, fig. 11.

Rhizosolenia sima Castracane f. **sima**

Non: ? *Rhizosolenia sima* n. sp., var. nov. sensu Castracane 1886, p. 71, pl. 29, fig. 9, (= *Rh. sp.*).

Misidentifications: *Rh. styliformis* Brightw. var. *polydactyla* Castr. in Van Heurck 1909, p. 28, pl. 4, figs 67, 70, 74, 75.
Rh. styliformis var. *polydactyla* (Castr.) Per. in Frenguelli and Orlando 1958, p. 137, fig. 19.
Rh. polydactyla Castr. in Mangin 1915, p. 73, fig. 52.

Selected figures: Van Heurck 1909, pl. 4, fig. 70; Mangin 1915, fig. 52.

Material examined: TEM: 40, 41, 42.
SEM: 41.
LM: 32, 121, 155.

Neotype: BM slide No. 31963; S. Shetland Ils, Antarctic, surface, Comber coll. **(121).**

LM OBSERVATIONS

Cells long, straight or slightly curved, circular in cross-section (Figs 28, 144, 145). Usually solitary or in pairs. Diameter 12-39 µm.

Valve: Conoidal, shallow, bilaterally symmetrical. Ventral part longer than dorsal part. Contiguous area distinct only near beginning of impression of sister-cell process. Claspers prominent. (Figs 28, 148, 149).

Process: Basal bart bulbous, thick-walled, narrowing abruptly into a fairly long, narrow, thin-walled distal tube (Fig. 147). In valves that are not attached to the sister-valve the tube has usually broken off near the base (Figs 146, 149). Process lumen characteristically spindle-shaped basally (Fig. 145), connected with cell interior by a labiate structure clearly discernible using a X40 objective.

Otaria: Comparatively large, arising on valve apex, extending along basal part of process. Characteristic in outline. Outer margin straight, roughly parallel to long axis of process. Distal margin weakly convex to weakly concave, oblique to long axis of process. Angle between outer and distal margins obtuse, rounded (Figs 145, 146, 149).

Valvocopula: One segment contiguous with most of valve margin (Fig. 28).

Copulae: In two dorsiventral columns. First ventral copula accommodating extremely narrow impression of distal part of sister-cell process (Figs 28, 147). Other copulae wing-shaped (Figs 28, 146) with short median margins and long lateral margins.

Auxospores: None observed.

SEM OBSERVATIONS

Areolae loculate, velum external, foramen internal.

TEM OBSERVATIONS

Valve: No observations.

Copulae: Marginal zone broad, advalvar edge usually fringed (a papillous advalvar marginal zone observed in one specimen, Fig. 154), abvalvar edge entire. Areolae in columns usually parallel to pervalvar axis. Pattern quincuncial (Fig. 154). 31-36 areolae to 10 µm within a column, 28-34 columns to 10 µm.

Areolae of copulae: The following description of foramen and velum is tentative since the copulae had partially dissolved: Foramen large. Velum perforated by two parallel oblong pores. Pores oriented parallel with to normal to areolar column, no clear pattern of orientation. (Fig. 152).

Rhizosolenia sima Castracane f. **silicea** f. nov.

Diagnosis: Cellula in sectione transversa circularis. Frustulum plerumque satis crasse silificatum. Valva subconica, processu robusto, membrana partis apicalis et processus plerumque cristas longitudinalis irregulares praebente. Cingulum e duabus columnis segmentorum formatum. Otaria nulla.

Misidentifications: ? *Rh. hebetata* Bailey in H. Peragallo 1892, p. 114, pl. 5, fig. 10.
Rh. styliformis Brightw. var. *polydactyla* Castr. in Van Heurck 1909, p. 28, pl. 4, figs 66, 67, 71, 74, 75.
Rh. polydactyla Castr. in Mangin 1915, p. 73, figs 52b, 52f.

Selected figures: Van Heurck 1909, pl. 4, fig. 71; Mangin 1915, fig. 52.

Material examined:	TEM: 42.
	SEM: 41.
	LM: 40.

Type material: "Brategg" Expedition, St. 54, 69°12' S, 94°06' W, 18.2 1948. **(042).**

Holotype: Slide labelled *Rhizosolenia sima* f. *silicea* Sundström, "Brategg" Exped. St. 54, 69°12' S, 94°06' W, 18.2 1948. (BM).
Isotypes will be placed in the Hustedt Collection, Bremerhaven (BRM); the Smithsonian Institution, Washington D.C. (US); the Institute of Oceanology, Moscow (IOAS).

LM OBSERVATIONS

Cells long, usually heavily silicified, cylindrical, circular in cross-section (Figs 150, 151). Diameter 18-40 µm.

Valve: Conical, margin in plane roughly normal to pervalvar axis (Fig. 29). Heavily silicified, especially towards apex. Contiguous area and claspers lacking.

Process: Robust, varying in length. Wall heavily silicified, usually with uneven longitudal ridges (Figs 29, 151). Internal canal comparatively narrow (Fig. 150), apparently opening at tip, widest basally, connected with the cell interior by a small labiate structure.

Otaria: Lacking.

Valvocopula: One segment contiguous with most of valve margin.

Copulae: In two columns. Variable in shape, usually with long lateral and short median margins. Sutures usually broad, distinct. (Fig. 29).

SEM OBSERVATIONS

Areolae loculate, velum external, foramen internal.

TEM OBSERVATIONS

Part of one copula was examined. Areolae arranged in a quincuncial pattern, areolar columns parallel to pervalvar axis, 30 areolae to 10 µm within a column, 28 columns to 10 µm. Velum perforated by two comparatively wide oblong pores, long axes almost perpendicular to areolar column (Fig. 153). Foramen large roundish.

DISTRIBUTION

Rhizosolenia sima was present in four of the "Brategg" samples I examined. Of these, samples No. 040, 041 and 042 had been collected at "ice-stations" according to Hasle (1969) and sample No. 155 is from a station similar to the other three in hydrographic characters (cf. Hasle 1969, figs 18, 26). Records are too few to determine the biogeographical limits of *Rh. sima* but it is probably restricted to the Southern Cold-water Region and ice-associated.

DISCUSSION

Rhizosolenia sima f. *sima* is distinguished on the bulbous basal part of the process, and the cells are often curved. These characteristics were stressed by Castracane (1886) in his description, but he evidently overlooked the extremely thin tube terminating the intact process.

Castracane did not designate type material for *Rh. sima.* It is, however, quite safe to assume that *Rh. sima* f. *sima* as described above is *Rh. sima* sensu orig., since only this species has the characters stated in Castracane (1886). It is, furthermore, probably significant that the original collection was made "ad glacies impervios" (near impassable ice) since *Rh. sima* apparently is associated to ice.

I have not found any records of *Rh. sima* in the literature apart from the original description, but according to the lable on the BM slide No.31963 **(121)** it was identified by Comber from the South Shetland Islands. Since Comber was familiar with the Challenger material it seems safe to assume that the identification was correct. The slide will serve as neotype until *Rh. sima* can be typified with material from the Challenger Expedition. The original illustration is too poorly drawn to serve as lectotype.

Rh. sima presumably soon became confused with *Rh. polydactyla.* Neither *Rh. styliformis* var. *polydactyla* sensu Van Heurck (1909) nor *Rh. polydactyla* sensu Mangin (1915) correspond with Castracane's description of *Rh. polydactyla.* They do, however, fit his description of *Rh. sima.* (See also Discussion under *Rh. polydactyla*).

Rh. sima f. *silicea* can be regarded as a "resting spore" of *Rh. sima,* but for reasond discussed under General discussion is here treated as a form.

I have only seen fully developed *Rh. sima* f. *silicea* cells and cells with a f. *sima* valve at one end and a f. *silicea* valve at the other end. Mangin (1915) evidently observed intermediate stages, and it is therefore conceivable that *Rh. sima* f. *silicea* can develope from *Rh. sima* f. *sima* in a manner similar to that seen in *Rh. polydactyla.*

The "endospore" illustrated in fig. 72 in Van Heurck (1909) is undoubtedly *Rh. sima* f. *silicea*. However, neither my observations nor those made by Mangin (1915) can confirm that a endogeneous developement of f. *silicea* can take place and Van Heurck's observation is therefore queried.

RHIZOSOLENIA TEMPEREI H. Peragallo (Figs 30, 155-163)

H. Peragallo 1888, p. 91, pl. 5, fig. 40.

Synonym: *Rhizosolenia Temperei* var. *acuminata* f. *inequalis* Schröder 1900, p. 25, pl. 1, fig. 6.

Non: *Rh. Temperei* sensu Okuno 1952b, pl. 2, figs 3-3'". (= *Rh. clevei* var. *clevei*).

Selected figures: H. & M. Peragallo 1897-1908, pl. 123, figs 5, 6; Karsten 1905b, pl. 30, fig. 15.

Material examined: TEM: 8, 96.
LM: 108, 131, 135, 137-140.

Type material: The TALE "Herb. H. Peragallo" slide No.276 **(137)** and the BM slide No.15157 **(108)** include part of the material H. Peragallo referred to in his description of *Rh. temperei.*
Observations: The frustules on the slides are dessicated, but the living cells would have ranged in diameter from c. 128 to c. 278 µm. Morphological details as described below under LM observations.

Lectotype: TALE slide labelled Herb. H. Peragallo, No.276, *Rh. Temperei* H.P. et *Robusta*, Villefranche. **(137)**.

LM OBSERVATIONS

Cells large, cylindrical, circular in cross-section (Figs 155, 165). Solitary or in pairs held together by girdle of mother cell. Diameter 125-278 µm. (See also under Discussion).

Valve: Asymmetrical, shallow, apex conoidal. Ventral part much longer than dorsal part, protruding medially into asymmetrical tongue (Fig. 30). Valve contour sigmoid (Figs 30, 155). Distal part of valve abruptly narrowed (Fig. 156). Contiguous area and claspers lacking. Areolae in columns converging at apex, 16-18 areolae to 10 µm within a column.

Process: 10-30 µm long, tapering from base. Wall fairly thin. Internal lumen wide basally, narrowing into canal opening at tip. Tip truncated at right angles to long axis, sometimes rounded. Basal lumen connected with cell interior by small labiate structure. (Fig. 156).

Otaria: Lacking.

Valvocopulae: One large or two smaller segments contiguous with most of valve margin. Easily mistaken for part of valve (Fig. 157).

Copulae: Variable in size and shape (Figs 157, 158), usually with short median and long lateral margins. 2n (n = 8, 9,......, 20) segment columns, roughly parallel to pervalvar axis.

Auxospore: None observed.

SEM OBSERVATIONS. None made.

TEM OBSERVATIONS

Valve: Areolae thick-walled, not loculate, smaller than on copulae. Velum perforated by usually two roundish pores.

Copulae: Marginal zone fairly broad, advalvar edge fringed, abvalvar edge entire (Fig. 159). Areolae in columns usually parallel to symmetry axis of copula, pattern quincuncial (Fig. 159). 20-21 areolae to 10 µm within a column, 22-23 columns to 10 µm.

Areolae of copulae: Subrectangular in outline. Walls beween areolar columns wavy in outline, varying in thickness (Figs 161, 162). Foramen circular to broadly elliptical. Velum perforated by four roundish pores in the angles of the areola (Figs 160-163).

NOTE

The Tempère and Peragallo (1st edition) slide No.84 includes *Rh. temperei* according to H. & M. Peragallo (1897-1908) and the Tempère and Peragallo (1889) catalogue also mentions an undescribed variety on the slide: "*Rh. Temperei* var. *gracilior*". The BM slide No.1433 **(101)** (T. & P. No. 84) includes dessicated valves probably of *Rh. acuminata* (Fig. 164), but contains no frustules or valves resembling *Rh. temperei* on the type slide **(137)** or in other material I examined.

DISTRIBUTION

I identified *Rh. temperei* with certainty in material from the Mediterranean only. Karsten (1905b) reported it from the tropical Atlantic.

DISCUSSION

H. Peragallo reported a diameter range of 200- 500 µm for *Rh. temperei* which does not correspond with the range (128-278 µm) I observed on his slides. On the other hand, the width (i.e. half the circumference) of dessicated frustules on the slides ranged from 210-437 µm, and it seems likely that the "diameter" range given by H. Peragallo is better interpretated as pertaining to width of dessicated frustules than to cell diameter.

The diameter range of 232-336 µm reported by Karsten (1905b) should also be queried since his fig. 15 illustrates a frustule with a diameter of c. 196 µm (assuming the scale is correct). Moreover, his statement that the girdle segments have "ca. 50-60 Punkte auf 10 µm" is curious since such a fine pattern would hardly be resolved in a light microscope. It thus seems as if Karsten confused magnifications in his observations on *Rh. temperei.*

In the material I examined *Rh. temperei* was invariable in habit and differed from *Rh. acuminata* in the shape of the valve, in usually being larger and in having only four pores in each velum. (See also *Rh. acuminata*).

The name *Rh. Temperei* var. *acuminata* f. *inequalis,* proposed by Schröder (1900) for frustules in which the shapes of the girdle segments differ between the two halves, is unnecessary since this is a common phenomenon in many *Rhizosolenia* species.

RHIZOSOLENIA ACUMINATA (H. Peragallo) H. Peragallo

(Figs 31a-c, 165-176)

H. Peragallo in H. & M. Peragallo (1897-1908), p. 463, pl. 123, figs 7, 8.

Basionym: *Rhizosolenia temperei* var. *acuminata* H. Peragallo 1892, p. 110, pl. 3, fig. 4.

Synonyms: ? *Rh. simplex* G.K. var. *major* Karsten 1907, p. 376, pl. 41, figs 1a-b.
? *Rh. acuminata* (Perag.) f. *debilis* Gran 1905, p. 50, fig. 58.
? *Rh. obtusa* Hensen 1887, pl. 5, fig. 41, (nom. dubium).

Non: *Rh. acuminata* sensu Okuno: 1957, pl.1, figs 1a-c; 1968, figs 1, 10d, 11j, 12.
(= *Rh. clevei* var. *clevei*).

Material examined: TEM: 12, 33, 45, 73, 74, 76, 86, 87.
SEM: 23.
LM: 16, 19, 22, 28, 46, 62, 64, 78, 88, 90, 101, 103-106, 128, 139, 140.

Material examined by H. Peragallo:

The TALE slides "Herb. H. Peragallo" Nos 1631, 1632 **(139, 140)** include intact frustules of *Rh. acuminata* that almost perfectly match figs 7, 8, pl. 123 in H. & M. Peragallo (1897-1908).

Observations: Diameter range 132-144 µm. Circa 20 areolae to 10 µm within a column, 20-23 columns to 10 µm on copulae. The slide No.1631 **(139)** has been marked with a circle (by H. Peragallo ?) inside which is one *Rh. acuminata* frustule and one *Rh. temperei* frustule (Fig. 165). The left-hand one (in Fig. 165) will serve as neotype of *Rhizosolenia acuminata.*

Neotype: See above.

LM OBSERVATIONS

Cells long, cylindrical, circular in cross-section (Fig. 165). Solitary or in pairs held together by girdle of mother cell. Diameter 50-190 µm. (See also under Discussion).

Valve: Bilaterally symmetrical, acutely conoidal. Ventral part much longer than dorsal part, protruding medially into narrow tongue accommodating faint impression of sister-cell process (Figs 31a, 31c, 166, 170). Valve contour almost straight in dorsiventral view. Distal part of valve usually slightly narrowed (Fig. 168). Claspers lacking. Areolae in columns converging at apex.

Process: 10-40 µm long, usually fairly short (broken off ?), tapering from base. Wall fairly thin. Internal lumen wide basally, narrowing into canal opening at tip. Tip truncated at right angles to the long axis, sometimes rounded. Basal lumen connected with cell interior by small labiate structure. (Figs 31b, 167, 168).

Otaria: Lacking.

Valvocopula: One large segment contiguous with most of valve margin. Easily mistaken for part of valve (Fig. 31a, 31c). Valvocopula and valve together forming oblique cone.

Copulae: Variable in size and shape (Figs 31a, 31c, 166), usually rhomboidal with median margins extremely short and lateral margins long. 2n (n = 4, 5, ..., 11) segment columns, roughly parallel to pervalvar axis.

Auxospore: None observed.

SEM OBSERVATIONS

Areolae usually loculate, foramen internal, velum external. (Fig. 169).

TEM OBSERVATIONS

Valve: Areolae resembling thick-walled areolae on copulae but usually smaller and with fewer perforations in velum.

Copulae: Marginal zone fairly broad, advalvar edge fringed, abvalvar edge entire (Figs 169, 171, 174). Areolae in columns usually parallel to axis of symmetry of copula. Pattern quincuncial. 18-22 areolae to 10 µm within a column, 22-25 columns to 10 µm.

Areolae of copulae: Subrectangular to ellipsoid in outline, wall segments between areolae varying in thickness. Transition from thin-walled to thick-walled areolae continuous, even within single frustulae (Figs 173, 174). Walls between areolar columns usually characteristically wavy in outline, becoming less so with increasing thickness (Figs 171-176). Foramen usually large, lacking in thick-walled areolae (Fig. 176). Velum perforated by usually six circular to oblong pores, three along each lateral margin (Figs 172, 174, 175).

DISTRIBUTION

Rhizosolenia acuminata probably has a circumglobal distribution within the Warm-water Region. It was absent from the waters surrounding Ko Phuket, Thailand only during the south-west monsoon.

DISCUSSION

Rhizosolenia acuminata is distinguished from *Rh. temperei* on the bilaterally symmetrical valve and the conical shape of the valve plus valvocopula. No forms intermediate between *Rh. temperei* and *Rh. acuminata* were found. Moreover, in the two samples in which I examined *Rh. temperei* with TEM the areolar structure differed from that in *Rh. acuminata* in that the vela of the copular areolae were perforated by only four pores.

H. Peragallo (1892) first regarded *Rh. acuminata* as a variety of *Rh. temperei* but had in H. & M. Peragallo (1897-1908) accorded it specific status. Pavillard (1916) reported having found forms intermediate between the two and regarded them as conspecific, but later (1925) treated them as separate species. Hustedt (1930) also questioned the status of *Rh. acuminata.* He discussed whether the shape of the valve could be dependant on cell diameter, the broader forms of "*Rh. acuminata*" perhaps having shallower valves corresponding to the shape in *Rh. temperi.* However, in the material I examined there was considerable overlapping in the diameter of the two species, whereas the characteristic shape of their respective valves remained invariable.

The distinction between *Rh. acuminata* and *Rh bergonii* lies mainly in the shape of the process, the funnel-shaped opening at the process tip being characteristic of *Rh. bergonii* (lacking in *Rh. acuminata*). Moreover, the process and the distal part of the valve are usually more heavily silicified in *Rh. bergonii.* Note, however, that no difference in the fine structure of the copulae of the two species could be observed.

On the evidence of general appearance and areolar structure it is clear that *Rh. temperei, Rh. acuminata* and *Rh. bergonii* are closely related, but they seem to be well separated on apparently invariable characters.

The description and figures of *Rh. simplex* var. *major* in Karsten (1907) fit *Rh. acuminata* well. Since Karsten did not record *Rh. acuminata* in his comprehensive material from the Indian Ocean (where it is quite common) it seems fairly safe to assume that his variety is in fact *Rh. acuminata.*

Gran (1905) and Gaarder (1951) recorded cells of "*Rh. acuminata* f. *debilis* " and "*Rh. acuminata* " respectively from northern parts of the North Atlantic with much smaller diameters than those I have observed. Their descriptions and figures fit *Rh. acuminata* better than *Rh. bergonii* (the alternative possibility), suggesting that the variation in size in *Rh. acuminata* is greater than I have found evidence of.

Gaarder's (1951) suggestion that the "*Rh. acuminata* " cells she had seen were in fact *Rh. obtusa* Hensen is probably correct and finds support in Hensen's (1887) species lists for the area in which he found *Rh. obtusa.* The plankton association there apparently included species that, like *Rh. acuminata,* have their main area of distribution in warm waters. However, the name *Rh. obtusa* has been used for at least three other taxa (Gran 1905, Hustedt 1930, Sournia 1968) and since, furthermore, Hensen's material has presumably been lost and his description and illustrations are insufficient, *Rh. obtusa* is best treated as a dubious name. On the evidence of the text and figures *Rh. acuminata* sensu Okuno (1957, 1968) is *Rh. clevei* var. *clevei.*

The neotype was designated because the material H. Peragallo used when describing *Rh. acuminata* (1892) could not be found. The original illustration of *Rh. acuminata* (1892, pl. 3, fig. 4) is too inexact to be usable as lectotype.

RHIZOSOLENIA BERGONII H. Peragallo (Figs 32, 33, 177-189)

H. Peragallo 1892, p.110, pl. 2, fig. 5.

Synonyms: *Rhizosolenia amputata* Ostenfeld 1902, p. 227, fig. 4.
? *Rhizosolenia stricta* Karsten 1905b, p. 162, pl. 29, figs 11, 11a-b.
Rhizosolenia bergonii Peragallo f. *bidens* (Karsten) Gaarder 1951, p. 25, fig. 11a.
(Nomen, non planta).

Selected figures: Cupp 1943, fig. 43.
Process: Ostenfeld 1902, fig. 4c; Hustedt 1920, pl. 318, fig. 3; Hustedt 1930, fig. 372b.

Material examined:
TEM: 23, 27, 28, 44-46, 48, 49, 52, 53, 61, 62, 65, 67, 69, 73-76, 78-81, 85, 86, 88, 89.
SEM: 23, 73, 75, 76.
LM: 8, 16, 24, 43, 47, 50, 51, 54, 57, 59, 60, 63, 64, 68, 83, 90, 91, 110-112, 117, 128, 135, 140, 141, 182-188.

Material examined by H. Peragallo:
The TALE slide "Herb. H. Peragallo" No.1632 **(140)** includes *Rh. bergonii* according to Peragallo's personal card index (TALE).
Observations: There is at least one frustule fitting the original description of *Rh. bergonii.* Diameter c. 45 µm. Morphological details as described below under LM observations.

Neotype: TALE slide labelled Herb. H. Peragallo, Marseille, No.1632. **(140).**

LM OBSERVATIONS

Cells long, cylindrical, circular in cross-section (Fig. 182). Diameter 9-115 µm. Usually solitary.

Valve: Acutely conoidal, bilaterally symmetrical. Ventral part much longer than dorsal part, protruding medially into narrow tongue accommodating impression of sister-cell process (Figs 32, 33, 178). Distal part of valve narrowed, usually more heavily silicified than rest of valve with areolation usually distinct in permanent mounts using a X40 lens (Figs 177, 181). Areolae in columns converging at apex. Claspers lacking.

Process: 10-20 µm long, usually intact. Wall usually fairly thick. Basal lumen spindle-shaped, abruptly narrowing into canal with funnel-shaped opening at tip. Tip appearing cleft under the light microscope. Basal lumen connected with cell interior by small labiate structure. (Figs 177, 181).

Otaria: Lacking.

Valvocopula: One large segment contiguous with most of valve margin, easily mistaken for part of valve. Valvocopula and valve together forming oblique cone. (Figs 32, 33).

Copulae: Very variable in size and shape, rhomboidal to trapezoid in outline. 2n (n = 2, 3, 4, 5, 6) segment columns. Narrow cells always with rhomboidal segments in 4 columns (Fig. 33).

Auxospore: None observed. (See under Discussion).

SEM OBSERVATIONS

Valvar areolae lacked internal constriction on the only valve on which they were examined (Fig. 179). Areolae of copulae usually loculate, foramen internal, velum external.

Opening at process tip funnel-shaped, with irregularly toothed margin. Impression of sister-cell process usually seen as slight depression on the tongue-like protrusion of the valve margin (Fig.178).

TEM OBSERVATIONS

Valve: Areolae resembling thick-walled areolae on copulae but usually smaller and with fewer perforations in velum.

Copulae: Marginal zone fairly broad, advalvar edge fringed, abvalvar edge entire (Fig. 180). Areolae in columns parallel to pervalvar axis. Pattern quincuncial. 19-24 areolae to 10 µm within a column, 21-26 columns to 10 µm.

Areolae of copulae: Subrectangular to ellipsoid in outline, wall segments between areolae varying in thickness. Transition from thin-walled to thick-walled areolae continuous in material examined. Walls between areolar columns usually characteristically wavy in outline, becoming less so with increasing thickness (Figs 183-189). Foramen large, circular to broadly elliptical (Figs 183-186), usually lacking in thick-walled areolae (Figs 187, 188). Velum perforated by usually six circular to oblong pores three along each lateral margin (Figs 183-189).

NOTE

On the slide I have designated as lectotype for *Rh. clevei* (Sundström 1984) are also cells that fit Ostenfeld's (1902) description of *Rh. amputata.* The slide was probably made from part of the only sample from which Ostenfeld (1902) recorded *Rh. amputata.* The frustules on the slide do not differ from those of *Rh. bergonii* in the rest of the material I have examined.

DISTRIBUTION

Rhizosolenia bergonii is circumglobal within the Warm-water Region. It was present throughout the year in the waters surrounding Ko Phuket, Thailand and was most abundant during the north-east monsson.

DISCUSSION

H. Peragallo (1892) at first contemplated regarding *Rh. bergonii* as a variety of *Rh. temperei,* but accorded it specific status on the grounds of its having girdle segments with long median margins and a robust process with a small interior cavity which he did not find in *Rh. temperei.* He also pointed to differences in size and in girdle segmentation.

The circumscription of *Rh. bergonii* I propose is mainly based on a charcter not mentioned in the original description, viz. the funnel-shaped opening at the tip of the process, which H. Peragallo had probably overlooked. His descriptions and illustrations of processes were, moreover, not accurate (cf. Pavillard 1925). The "small interior cavity" of the process can be seen in most *Rh. bergonii* cells but was less conspicuous in some weakly silicified cells and is thus not a reliable character. The shape of the girdle segments is too variable to be of diagnostic value (cf. Gaarder 1951). A long and narrow valve apex is, however, charcteristic of *Rh. bergonii* and is seen in H. Peragallo's figures. *Rh. bergonii* varies considerably in diameter and in areolar structure, but I found no discontinuities neither in the diameter range nor in the thickness of areolar walls.

Ostenfeld (1902) described the process of his *Rh. amputata* as "transversely cut off, with an excavation at the apex and a cavity in the lower part". He did not connect his species with *Rh. bergonii* although he was acquainted with Peragallo's *Rhizosolenia* monograph. Pavillard (1925) found cells that accorded with the description of *Rh amputata* in material from the western Mediterranean, and assumed that they were *Rh. bergonii.* It is clear from the type slide that the characteristic funnel -shaped opening at the process tip was also present in cells examined by H. Peragallo. With this in mind it is safe to regard *Rh. amputata* Ostenfeld and *Rh. bergonii* as conspecific. Ostenfeld's figures are more detailed than H. Peragallo's and better show the characteristic shape of the *Rh. bergonii* process, though they do not accurately depict the outline of the valve margin (cf. Figs 32, 33).

Rhizosolenia stricta Karsten has the same type of process as *Rh. bergonii* (Karsten 1905b, pl. 29, fig. 11b). It has only been reported by Karsten and is probably best regarded as conspecific with *Rh. bergonii,* as was also pointed out by Gaarder (1951). However, Karsten described his species as having two columns of girdle segments which does not agree with my observations on *Rh. bergonii,* since even the narrowest cells I observed had four segment columns. Karsten's description of *Rh. stricta* should be queried. Gaarder's (1951) fig. 11 of "*Rh. bergonii* f. *bidens* " undoubtedly depicts abnormal valves (cf. *Rh. antennata*).

Areolar patterns and structures are the same in *Rh. bergonii* and *Rh. acuminata* the main distinction between them lying in the shape of the process. *Rh. bergonii,* furthermore, is usually smaller, the distal part of the valve usually narrower, the valve apex more heavily silicified and the distribution probably wider than that of *Rh. acuminata.* There can, however, be no doubt that the two species are very closely related. Since I have seen no transition forms, and none have been reported in the literature, it seems best to treat the species as separate, a view also held by Gaarder (1951).

Rh. bergonii closely resembles *Rh. polydactyla* f. *squamosa* in gross morphology, which warrants incorporating *Rh. bergonii* in sect. *Rhizosolenia* in the classification of *Rhizosolenia* I put forward. It is possible that these observations could be used as guidelines for sorting out evolutionary problems in *Rhizosolenia.* However, I have not found any evidence pointing to which form of *Rh. polydactyla* should be regarded as the more primitive and refrain from speculation.

I found no auxospores in the material I examined. According to Cupp (1943) the auxospore is lateral.

The original illustration of *Rh. bergonii* is too inexact to serve as lectotype.

RHIZOSOLENIA HYALINA Ostenfeld (Figs 34, 190-194)

Ostenfeld in Ostenfeld and Schmidt 1901, p. 160, fig. 11.

Synonym: *Rhizosolenia pellucida* Cleve 1901, p. 56, pl. 8, fig. 4.

Selected figures: Hustedt 1920, pl. 319, figs 11-13; Gaarder 1951, p. 26, fig. 13;
Sournia 1968, pl. 3, figs 19a-b.

Material examined:
TEM: 16, 20, 44, 46, 47, 49, 50, 55, 57, 58, 68, 72, 75, 79.
SEM: 43, 44.
LM: 23, 24, 27, 28, 51-53, 59, 61, 63, 65, 69, 80, 81, 83,122, 182-186, 188.

Type material not examined.

Lectotype: Fig. 11, p. 160 in Ostenfeld and Schmidt 1901.

LM OBSERVATIONS

Cells long, cylindrical, circular in cross-section (Figs 190, 192). Diameter 9-60 µm. Chain-forming, usually solitary in preserved material.

Valve: Conoidal, bilaterally symmetrical. Ventral part much longer than dorsal part (Fig. 34). Contiguous area clearly visible only near margin where impression of sister-cell process starts (Figs 34, 191). Claspers easily discernible. Valve outline with characteristic undulation (Figs 34, 192).

Process: Up to 40 µm long, usually not intact. Bilaterally symmetrical, slightly bent near end of otaria, then tapering (Figs 34, 191, 192). Internal canal opening at tip, connected with cell interior by labiate structure (Fig. 191).

Otaria: Narrow, extending along process for c. 4-6 µm (Figs 34, 192).

Valvocopula: One segment contiguous with most of valve margin (Fig. 34).

Copulae: First ventral copula accommodating impression of distal part of sister-cell process, extended into tongue on abvalvar side (Fig. 34). Other copulae rhomboidal (Fig. 34), somewhat variable in size. Usually weakly silicified, scarcely discernible in water mounts. Areolation not visible with LM. 2n (n = 2, 3, ..., 8) segment columns. No cells with only two segment columns were found.

SEM OBSERVATIONS

Otaria were seen to originate close to valve apex. Areolae of valve and copulae with velum external, foramen apparently lacking.

TEM OBSERVATIONS

Valve: Areolae in columns converging at apex, fine structure resembling that of copulae.

Copulae: Marginal zone fairly broad, advalvar edge fringed, abvalvar edge entire. Areolae arranged in columns usually parallel to pervalvar axis. Pattern quincuncial. 31-36 areolae to 10 µm within a column, 27-32 columns to 10 µm.

Areolae of coplae: Circular to rounded-rectangular in outline, apparently without internal constriction. Velum perforated by two, less often one or three, parallel oblong pores parallel to or perpendicular to areolar columns, different orientations apparently at random within a column (Fig. 193).

DISTRIBUTION

Rhizosolenia hyalina probably has a circumglobal distribution within the Warm-water Region. It was present throughout the year in the waters surrounding Ko Phuket, Thailand and was most abundant during the SW monsoon. I did not find many records of *Rh. hyalina* in the literature and it has probably been overlooked by many investigators.

DISCUSSION

Rhizosolenia hyalina was clearly and concisely described by Ostenfeld (Ostenfeld and Schmidt 1901) and his fig. 11 nicely shows the outline characteristic of this species. I did not look for type material of *Rh. hyalina* since Ostenfeld's description conforms with all cells I observed and since *Rh. hyalina* varies little in habit.

Only a few floristic works include *Rh. hyalina* (i.e. Hustedt 1920, Gaarder 1951, Sournia 1968). It was perhaps also included within Allen and Cupp's (1935) circumscription of *Rh. clevei* which it can resemble superficially. However, *Rh. clevei* apparently always contains the endophyte *Richelia intracellularis* (Sundström 1984) which I never observed in association with *Rh. hyalina.*

In general morphology *Rh. hyalina* agrees with the generic type and I have therefore placed it in sect. *Rhizosolenia* in the classification I put forward although the structure of the areolae differs somewhat from that in most other sect. *Rhizosolenia* species.

According to Sournia (1968) Ostenfeld had his paper published before Cleve (1901), who described the species under the name of *Rh. pellucida.*

RHIZOSOLENIA SIMPLEX Karsten (Figs 35, 195-199)

Karsten 1905a, p. 95, pl. 10, figs 1, 1a, 1b, 1c.

Synonym: ? *Rhizosolenia torpedo* Karsten 1905a, p. 95, pl. 10, figs 2, 2a.

Non: *Rhizosolenia simplex* var. *major* Karsten 1907, p. 376, pl. 41, fig. 1. (= *Rh. acuminata* ?).

Selected figures: Hustedt 1920, pl. 321, fig. 1; Sournia et al. 1979, p. 191, fig. 16.

Material examined: TEM: 34, 35, 38, 39.
SEM: 31, 38.
LM: 36, 37, 133.

Type material not found.

Lectotype: Figure 1c, pl. 10 in Karsten 1905a.

LM OBSERVATIONS

Cells long, circular in cross-section (Figs 35, 195). Diameter 5-48 µm. Usually weakly silicified. Solitary.

Valve: Conical, valve margin in a plane normal to or almost normal to pervalvar axis (Fig. 35). Valve and process together often forming a continuous cone (Figs 34, 195, 196). Contiguous area and claspers lacking.

Process: Roughly 15-20 long. Often conical; sometimes cylindrical over most of its length then narrowing abruptly and terminating in a short narrow tube (Fig. 34), intermediate shapes fairly common. Internal canal widest close to base, connected with cell interior by a small labiate structure.

Otaria: Lacking.

Valvocopula: One segment, contiguous with more than half valve margin.

Copulae: Not readily distinguishable. Usually rhomboidal; median margins short, lateral margins long. 2n (n = 2, 3, 4) segment columns usually parallel to pervalvar axis.

SEM OBSERVATIONS

Areolae poroid to loculate, velum external.

TEM OBSERVATIONS

Valve: Areolae in columns converging at apex. 24-28 areolae to 10 µm within a column, 29-32 columns to 10 µm.

Areolae of valve: Elliptical in outline, apparently lacking internal constriction (foramen). Velum perforated by one oblong pore parallel to areola column (Fig. 199).

Copulae: Marginal zone fairly broad, advalvar edge fringed, abvalvar edge entire. Areolae in columns generally parallel to pervalvar axis. Pattern quincuncial (Fig. 198). 30-33 areolae to 10 µm within a column, 36-39 columns to 10 µm.

Areolae of copulae: Circular to broadly elliptical in outline, sometimes with an internal foramen. Velum perforated by two parallel oblong pores oriented parallel to areola column (Fig. 198).

DISTRIBUTION

Rhizosolenia simplex was only seen in samples from the Southern Cold-water Region. According to Hasle (1969) it probably has its main distribution in the "Subantarctic Zone".

NOTE

In Ehrenberg's "Zeichenblatt" No.1920 (cf. *Rh. antennata*) is a drawing of a valve of "*Rhizosolenia Lingua* ". It is evident from the shape of the valve and the process that the drawing is of a *Rh. simplex* valve. To my knowledge Ehrenberg never published the name, but if a published description exists the name *Rh. lingua* would have priority over *Rh. simplex.*

DISCUSSION

The specimens examined conform with the original description and with the illustration in Hustedt (1920). Figure 16 in Sournia et al. (1979) fits in with my conception of *Rh. simplex* but I did not find cells with only two columns of segments, as in their fig. 24. The structure of the velum in *Rh. simplex* does not vary and the species also seems to vary little in general appearance.

Rh. simplex was not found outside the Southern Cold-water Region and was always associated with species I considere characteristic of that region. Heiden and Kolbe (1928) and Hendey (1937) did, however, recorded "*Rh. simplex* " from well within the subtropics and in association with species characteristic of warm waters. I examined two samples from which Hendey recorded "*Rh. simplex* " (Discovery Expedition, St. 427 and St. 440) and found that neither of them contained *Rh. simplex.* It is conceivable that some of the smaller cells of *Rh. bergonii,* present in both samples, could at first sight be confused with *Rh. simplex.* The record in Heiden and Kolbe (1928) from 24°56' S, 01°14' W should also be queried since *Rh. bergonii* (syn. *Rh. amputata*) was also apparently a member of the plankton association.

Rh. simplex var. *major* Karsten (1907) should probably be regarded as a synonym of *Rh. acuminata* (see under *Rh. acuminata*).

The description and figures of the dubious species *Rh. torpedo* Karsten (1905a) indicate that it falls within the range of variability observed for *Rh. simplex.* Moreover it does not seem to have been identified with certainty by anyone but Karsten.

The areola structure of *Rh. simplex* closely resembles that of *Rh. hyalina* , which probably indicates a close phylogenetic relation and warrants placing also the former in sect. *Rhizosolenia* in the classification I propose.

2. Sect. Imbricatae

Cells with two lateral columns of girdle segments.

RHIZOSOLENIA IMBRICATA Brightwell (Figs 200-208)

Brightwell 1858, p. 94, pl. 5, fig. 6.

Synonyms: *Rhizosolenia shrubsolei* Cleve 1881, p. 26.
Rhizosolenia imbricata var. *shrubsolei* (Cleve) Schröder 1906, p. 346.
Rhizosolenia imbricata Bright., var. *Shrubsolei* (Cl.) Schröder, fo. *tenuissima* Manguin 1960, p. 269, pl. 5, fig. 69.
? *Rhizosolenia atlantica* H. Peragallo 1892, p. 114, pl. 5, figs 4, 5.

Non: *Rh. imbricata* Brightw. sensu Hustedt 1914, pl. 315, figs 11-15; 1930, p. 580, figs 331a-c (331d ?). (= *Rh. striata*).
Rh. imbricata var. *imbricata* sensu Sournia 1968, p. 69, pl. 10, fig. 65. (= *Rh. striata*).
"*Rh. shrubsolei* ?" sensu Hasle 1975, figs 37a, 37b, 38. (= *Rh. fallax*).

Material examined: TEM: 2, 3, 9, 12-14, 16, 20, 24, 25, 27, 28, 44-47, 49, 50, 53, 54, 60, 68, 70-72, 75, 77, 80-82, 88, 90.
SEM: 2, 9, 28, 44, 68, 70, 71, 75.
LM: 48, 59, 83, 102, 103, 106, 107, 109, 112, 113, 117, 122, 125, 128-132, 136, 139, 140, 149, 165, 170, 180, 183, 184, 187.

Observations on type material:
The BM slide No.1225 **(109)** includes part of the material Brightwell referred to in his description of *Rh. imbricata* (D. Williams, BM, pers. comm.). On it are complete frustules of *Rh. imbricata* (Fig. 200), with the apical axis ranging from 14 to19 µm and with 12-15 striae to 10 µm on the copulae.

The BM slide No.21352 **(125)**, which also forms part of the original material (cf. Hasle 1975), includes mainly detached segments. One almost complete but dessicated frustule I observed would have had an original diameter (apical axis) of c. 8 µm. The copulae on the slide have the pattern of striae characteristic of the species (see below), and 11-15 striae (columns of areolae) to 10 µm. The largest segment seen was from a cell with an estimated diameter of c. 14 µm. The shape of the otaria could not be discerned on any valve on the slide. Slide No.287 in the Cleve-Möller Collection (S) **(149)** includes part of the material Cleve (1881) referred to when naming the species *Rh. shrubsolei.* On it are frustules of "*Rh. shrubsolei*". They are apparently slightly elliptical in cross-section since most cells lie with the transapical axis roughly perpendicular to the slide. The length of the apical axis varies between 6 and 12 µm. All copulae examined had the pattern of striae characteristic of *Rh. imbricata* (see below), and 14-18 striae to 10 µm. The shape of the otaria was not discernible. The shape of the process (Fig. 201) and the orientation of the girdle segments match the description of *Rh. imbricata* below.

Lectotype: BM slide No.1225. **(109)**.

LM OBSERVATIONS

Cells long, cylindrical, circular to slightly elliptical in cross-section (Figs 200-203). Length of apical axis 2.5 - 57 µm. Transapical axis : apical axis = 0.82 - 1.00. Solitary or in pairs.

Valve: Obliquely conoidal, bilaterally symmetrical (Fig. 207). Ventral part much longer than dorsal part. Shape of valve varying with cell diameter, narrow cells having a more acute apical angle than broad cells (Figs 201, 202). Contiguous area large (Fig. 207), becoming unproportionally smaller with decreasing cell diameter. Marginal ridges well developed, claspers discernible even in very thin specimens using a X40 lens and phase contrast equipment. Surface outside contiguous area almost at right angles to former in large specimens, becoming increasingly rounded with decreasing cell diameter (Figs 205, 207).

Process: 8-18 µm long, usually not intact in preserved material. Dorsiventrally compressed in large specimens, but decreasingly so with decrease in cell diameter. Swollen basally then narrowing abruptly into distal tube (Figs 201, 202, 205). When intact distal tube much longer than basal part (Figs 201, 205). Wall of almost even thickness (apart from otaria), outline of lumen thus resembling outer surface (Fig. 201).

Otaria: Comparatively small, extending along swollen basal part of process (Fig. 205), in large specimens sometimes arising slightly below (< 1 µm) process base.

Valvocopula: One segment contiguous with most of valve margin.

Copulae: In two lateral columns. Scale-like to trapezoid in outline, median margins longer than lateral margins in large cells only (Figs 204, 208). First copula accommodating impression of distal part of sister-cell process towards one side. A pattern of striae (10-18 to 10 µm) clearly discernible on copulae on permanent slides in phase contrast at X400 (Figs 203, 204). Pattern becoming progressively coarser in larger specimens. Striae at an oblique angle to transapical plane converging along a line running up middle of copula (Figs 204, 206, 208).

Auxospores: Newly formed auxospores and initial cells were seen in one sample from the Skagerrak (002). Initial cells with diameters of 23 - 25.5 µm were seen attached to mother cells ranging from 5.5 to 9 µm in diameter. The orientation and shape of the auxospores and initial cells match that in figs 37b, c, d and 38 in Drebes (1974).

SEM OBSERVATIONS

Intact process tip oblique, internal canal opening on oblique dorsal side. Outer margin of otaria weakly convex, almost parallel. Distal margin concave, forming an oblique angle with long axis of process. Angle between outer and distal margins obtuse, usually forming a fine point. (Fig. 207). The labiate structure (just discernible inside a few valves) appeared as a narrow slit running across a low dome-shaped elevation with a circular base, at varying angles with the transapical plane.

Areolae of copulae loculate with large internal foramen, velum external. Wall segments between areolae entire.

TEM OBSERVATIONS

Valve: Areolae in columns converging at apex, fine structure resembling that of copulae although modified near apex.

Copulae: Marginal zone fairly broad, advalvar edge entire or irregularly toothed, abvalvar edge entire. (Figs 206, 208). 23-32 areolae to 10 µm within a column (stria), 10-18 columns to 10 µm.

Areolae of copulae: Rounded rectangular to diamond-shaped in outline. Wall segments between areolae unevenly silicified. Foramina only slightly smaller in diameter than areolae, outline even, corners rounded. Velum perforated by a narrow slit, usually along longest diagonal (Fig. 206).

NOTE

Under the light microscope the otaria usually appeared to be rounded in profile but were in EM usually seen to be pointed. Presumably the light microscope does not resolve the extremely fine point (Fig. 206) at the angle between the outer and distal margins of the otarium.

DISTRIBUTION

Rhizosolenia imbricata is widely distributed and is apparently adapted to a wide range of temperatures, but it was not found in samples from the polar regions.

DISCUSSION

According to Hasle (1975) the "cell diameter" on the three BM slides Nos 64, 21350 and 21352 ranged from "10 µm and less" to 25 µm. Moreover, she reported "about 10 ribs in 10 µm", whereas I counted 11-15 striae (columns of areolae) to 10 µm on copulae on the BM slide No.21352 **(125)**, but the discrepancy is of little significance in view of the extent of the total variation I have observed.

The diameter of many cells on the Cleve and Möller slide **(149)** of *Rh. shrubsolei* Cleve I examined falls inside the diameter range for *Rh. imbricata* on the original slides of this species and since the number of striae to 10 µm on copulae on slides No. **125** and **149** overlaps I see no reason to regard *Rh. imbricata* and *Rh. shrubsolei* as separate taxa. Note that *Rh. imbricata* cells within a diameter range of 5.5 - 9 µm could give rise to initial cells with diameters of 23 - 25.5 µm. Furthermore, it is of no little significance that the original localities for *Rh. imbricata* Brightw. and *Rh. shrubsolei* Cleve lie only c. 250 km apart on the North Sea coast of England.

The diameter range of *Rh. imbricata* varies in different parts of the ocean, in the North Sea ranging from c. 5 to c. 30 µm and in samples from the Indian Ocean from 2.5 to 57 µm. A continuum could be observed in the pooled observations but the whole range was never seen in a single sample. Auxospores were not seen in samples from tropical waters. It is probable, however, that mother cells giving rise to initial cells at the upper end of the range are wider than the widest mother cells from the

Skagerrak sample **(002)**. Whether size range is genetically determined or whether it is influenced by external variables cannot, however, be decided on the basis of the material I have examined.

As pointed out by Hasle (1975) it seems to be common practice to call narrow cells of *Rh. imbricata* either *Rh. shrubsolei* or *Rh. imbricata* var. *shrubsolei.* It is also evident that the name *Rh. imbricata* has commonly been used for *Rh. striata,* following Hustedt (1914, 1930) who considered the names synonymous. (See also discussions on other species of sect. *Imbricatae*).

Rh. atlantica H. Peragallo is probably a synonym of *Rh. imbricata* but is better regarded as a nomen dubium since the species was not described in sufficient detail.

RHIZOSOLENIA STRIATA Greville (Figs 36a-c, 209-217)

Greville 1865, p. 234, pl. 3, fig. 4.

Synonyms: *Rhizosolenia imbricata* var. *striata* Grunow in Van Heurck 1882, pl. 79, figs 3, 7.
? *Rhizosolenia inaequalis* Castracane 1886, p. 71, pl. 24, fig. 15.

Misidentifications: *Rh. imbricata* Brightw. in: Hustedt 1914, pl.315, figs 11-15; Hustedt 1930, p. 580, figs 331a-c (? 331d).
Rh. imbricata Brightw. var. *imbricata* in Sournia 1968, p. 69, pl.10, fig. 65.

Material examined: TEM: 45, 59, 70.
SEM: 43, 44, 46, 62, 70, 74.
LM: 49, 50, 76, 110, 112-114, 116, 118, 148, 183.

Observations on type material:
The British Museum slide No.1948 **(110)** forms part of the type material of *Rh. striata.* Greville's description is somewhat confusing, but since only one species on the slide (Figs 209, 210) corresponds to his illustration of *Rh. striata* there can be no doubt about its identity. There are only incomplete frustules of *Rh. striata,* and the following data mainly refer to detached valves and segments: Apical axis 17-49 µm (broad diameter). Transapical axis : apical axis = 0.64 - 0.75. Number of columns of areolae (striae) to 10 µm on copulae 7-11. Morphological details conform with those described below under LM observations.

Lectotype: BM slide No.1948. **(110)**.

LM OBSERVATIONS

Cells long, cylindrical, elliptical in cross-section (Fig. 36a, 36b). Length of apical axis (broad diameter) 11-110 μm. Transapical axis : apical axis = 0.64 - 0.78.

Valve: Shallow, obliquely conoidal, bilaterally symmetrical (Figs 36a, 36b, 209). Ventral part much longer than dorsal part. Contiguous area extremely large and bounded by prominent marginal ridges (Figs 36a, 209). Claspers well-developed. Surface outside ridges almost perpendicular to surface of contiguous area (Fig. 36a).

Process: 10-18 μm long, usually intact. Strongly compressed dorsiventrally (Figs 36a, 36b, 212), broad at base, almost triangular in outline with lateral edges usually weakly concave (Figs 36a, 209, 211). Wall almost of even thickness (apart from otaria), outline of lumen thus corresponding to outer surface in outline (Fig. 211).

Otaria: Comparatively small, extending along lower part of process. Distal margin weakly concave, at an oblique angle to long axis of process. Angle between distal and outer margins obtuse (rounded). (Figs 36a, 209).

Valvocopula: One segment contiguous with most of valve margin (Fig. 36a, 36b).

Copulae: In two lateral columns (Fig. 36a, 36b). Trapezoid, usually with long median and shorter lateral margins (Figs 36a-c, 215). First copula accommodating impression of distal part of sister-cell process towards one side. Areolar columns (striae) forming distinct coarse pattern visible in water mounts. Striae at an oblique angle to transapical plane, converging along a line running up middle of copula (Figs 36c, 215).

SEM OBSERVATIONS

Process tip like the point of a hypodermic needle, opening on oblique dorsal side. Valvar areolae in columns converging at apex. Areolae of copulae loculate, foramen internal, velum external. Wall segments between areolae entire. (Figs 215, 216).

Inside one valve a labiate structure was observed as along narrow slit running across the convex internal wall below the process and parallel to the base of the isosceles triangle making up the process. (Fig. 217).

TEM OBSERVATIONS

Copulae: Marginal zone with advalvar edge entire or irregularly toothed, abvalvar edge entire (Fig. 213). 12-19 areolae to 10 µm within a column (stria), 6-12 columns to 10 µm.

Areolae of copulae: In outline resembling a parallelogram with rounded corners. Wall segments between areolae unevenly silicified. Foramen large. Velum perforated by a narrow slit usually along longest diagonal (Fig. 214).

NOTE

In lateral view large *Rh. imbricata* cells are almost indistinguishable from large *Rh. striata* cells, but the distinction is clear in cells where the apical axis is directed towards the observer (cf. Figs 200, 212 and 202, 211).

DISTRIBUTION

Rhizosolenia striata is probably restricted to warm waters. I did not find it in samples collected outside the South-East Asian -- Australian area.

DISCUSSION

Single copulae of *Rh. striata* and of large cells of *Rh. imbricata* are indistinguishable with TEM. Cells of *Rh. striata* can, however, always be distinguished from those of the latter with LM since they are distinctly elliptical in cross-section and have a broad-based triangular process. No intermediate forms were seen and the species were often found together in the Thai material.

Grunow (in Van Heurck 1882) was apparently the first to regard *Rh. striata* as a variety of *Rh. imbricata.* Ostenfeld (1902) and Hustedt (1914, 1930) regarded them as conspecific. Ostenfeld gave no reason for this circumscription; while Hustedt (1930) stated that not the slightest specific ("spezifischen") difference was to be found between *Rh. striata, Rh. imbricata* and *Rh. shrubsolei.* According to him there was a continuum in regard to size and coarseness of the structure (of the frustular elements). Although it is evident that *Rh. striata* is closely related to *Rh. imbricata* the diagnostic characters for *Rh. striata* (triangular process, distinctly elliptical in cross-section) do not match corresponding details in *Rh. imbricata* in material I have examined. Since, futhermore, in the alleged continuity from *Rh. striata* through *Rh. imbricata* to *Rh. shrubsolei,* Hustedt (1930) overlooked these characteristics, I can see no reason to accept his circumscription.

It is important to bear in mind that the name *Rh. imbricata* has commonly been used for *Rh. striata* (e.g. Hustedt 1930) and that the names *Rh. imbricata* var. *shrubsolei* and *Rh. shrubsolei* have been just as often used for *Rh. imbricata.* It is significative of this practice that Hustedt (1930) stated that in European waters "die Art" (i.e. *Rh. imbricata*) was only to be found in the Mediterranean Sea, overlooking the fact that Brightwell (1858) described the species from material collected in the North Sea.

It is obvious that the description of *Rh. inaequalis* Castracane was based on dessicated or otherwise distorted cells. The species was described as being "oval" in cross-section thus probably being conspecific with *Rh. striata* rather than with *Rh. imbricata* (c.f. H. Peragallo 1892).

RHIZOSOLENIA OSTENFELDII sp. nov. (Figs 37a-c, 218-226)

Diagnosis: Cellula longa, cylindrica, in sectione transversa circularis, 32-56 µm diam. Valva humilis. Processus 11-15 µm longus, basi tumidus. Otaria per partem basalem processus extensa, parva. Segmenta cingularia duas columnas laterales formantia. Areolae copularum columnas subparallelas formantes. Velum poris oblongis parallelis, plerumque 3-5 per medium seriatis pertusum.

Holotype: Slide labelled *Rhizosolenia ostenfeldii* Sundström. Cruise to Satun, St. 40/1, 06°45' N, 99°30' E, 13.1 1983. (BM).
Isotypes will be placed in the Hustedt Collection, Bremerhaven (BRM); the Smithsonian Institution, Washington D.C. (US); the Institute of Oceanology, Moscow (IOAS).

Material examined:		
	TEM:	16, 43, 45, 50, 63, 64, 66, 70, 71.
	SEM:	45, 70, 71, 75.
	LM:	28, 46, 62, 69, 72, 73, 76, 112, 182, 183, 187.

LM OBSERVATIONS

Cells long, cylindrical in cross-section (Figs 37a, 220, 221). Diameter 32-56 µm. Solitary or in pairs.

Valve: Shallow, obliquely conoidal, bilaterally symmetrical, ventral part longer than dorsal part (Figs 37a, 218). Contiguous area broad, delimited by marginal ridges continuous with otaria.

Process: 11-15 µm long, usually intact. Swollen basally, slightly compressed dorsiventrally, distal part tubular (Figs 37a, 218, 221). Internal canal opening at tip, basally connected with cell interior by a labiate structure.

Otaria: Extending along basal part of process. Outer margins weakly convex, almost parallel. Distal margin straight to weakly concave, forming oblique angle with long axis of process. (Figs 37a, 218).

Valvocopula: One segment contiguous with most of valve margin.

Copulae: In two lateral columns, wing-shaped (Figs 37a, 37b, 218) with short median and long lateral margins. First copula accommodating impression of distal part of sister-cell process towards one side (Figs 37a, 222). Striae in medial area almost parallel to pervalvar axis, on each side of medial area slightly diverging, discernible at a magnification of X400. (Figs 219, 222, 223).

SEM OBSERVATIONS

A labiate structure was observed inside one valve; a narrow slit transversed the greater part of what appeared to be a low dome-shaped structure under the process base. The resolving power of the microscope used was, however, not sufficient to produce a clear image and the description may thus need to be adjusted.

The contiguous area of the valve is flattened and is delimited by low marginal ridges. Outside the marginal ridges the valve wall slopes fairly abruptly. Areolae of copulae and valve loculate, foramen internal, velum external. Wall segments between areolae entire.

TEM OBSERVATIONS

Valve: Fine structure similar to that on copulae. Areolae in columns converging at apex.

Copulae: Marginal zone comparatively broad, edges entire (Figs 222, 224). Areolae in columns (striae) almost parallel to pervalvar axis. A few bifurcations of interstriae usually seen near abvalvar margin of central area (Figs 37c, 223). 30-34 areolae to 10 µm within a column, 21-25 columns to 10 µm.

Areolae of copulae: Loculate, rectangular in outline. Wall segments between areolae unevenly silicified (Fig. 226). Foramen large, rounded-rectangular to ellipsoid (Figs 225, 226). Velum perforated by median row of ellipsoid pores with long axes usually parallel to areolar column. 1-7 pores (usually 3-5) depending on width of areola (Figs 225, 226).

DISTRIBUTION

Rhizosolenia ostenfeldii is apparently a warm-water species and may be more widely distributed than my records suggest. In the Thai material it was commonest in samples taken during the north-east monsoon.

DISCUSSION

Rhizosolenia ostenfeldii can be distinguished on the shape of the copulae and the almost parallel striae, and these characters were invariable in all cells observed. The fine structure of the copular areolae is, however, of a type also seen in other species of sect. *Imbricatae* (cf. *Rh. fallax*, *Rh. chunii*).

It was not until at a rather late stage in my investigation that I became aware that *Rh. ostenfeldii* was a separate species and had thus probably overlooked it or confused it with *Rh. imbricata* during the earlier stages. Additional research is needed before the range of variation and the geographical limits of *Rh. ostenfeldii* can be finally determined.

RHIZOSOLENIA FALLAX sp. nov. (Figs 38a-b, 40, 227-233)

Diagnosis: Cellula longa, cylindrica, in sectione transversa circularis vel subelliptica, juxta axem apicalem 3-23 µm diam. Processus circter 10 µm longus, basi tumidus. Otaria per partem basalem extensa, parva, apice cava. Segmenta duas columnas laterales formantia. Columnae areolares mediae cum plano transapicali subparallelae, laterales divergentes. Velum poris oblongis parallelis, plerumque 3-5 per medium seriatis pertusum.

Type material: Skagerrak, Torungen-Hirtshals, 15.6 1981, IMBB 2111, **(002)**.

Holotype: Slide labelled *Rhizosolenia fallax* Sundström. Torungen-Hirtshals, 15.6 1981. (BM).
Isotypes will be placed in the Hustedt Collection, Bremerhaven (BRM); the Smithsonian Institution, Washington D.C. (US); the Institute of Oceanology, Moscow (IOAS).

Selected figures: Hasle 1975, figs 37a, 37b, 38.

Material examined: TEM: 2, 9, 63, 68, 74, 75, 78, 81, 87, 89, 91.
SEM: 2, 68, 74.
LM: 28, 67, 73, 77, 80, 84, 86, 88.

The type material **(002)** contains *Rh. fallax* and *Rh. imbricata* in about equal numbers. *Rh. fallax* ranges in diameter from 5 to 10 µm, whereas the range for *Rh. imbricata* is 5-28 µm. The two species are alike in habit but are distinguishable in LM at X400 (phase contrast, permanent mount) on the pattern of striae.

LM OBSERVATIONS

Cells long, cylindrical, circular to slightly elliptical in cross-section (Figs 38a, 231). Diameter (apical axis) 3-23 µm. Solitary or in pairs.

Valve: Obliquely conoidal, bilaterally symmetrical (Fig. 38a). Ventral part much longer than dorsal part. Contiguous area fairly large (Figs 38a, 230, 231). Marginal ridges usually distinct, claspers discernible even in thin specimens using a X40 lens and phase contrast equipment.

Process: 8-12 µm long, usually not intact in preserved material. Swollen basally then narrowing abruptly into distal tube. When intact distal tube usually much longer than basal part (Figs 227, 230). Wall of almost even thickness (apart from otaria), outline of lumen thus corresponding to outer surface in outline (Figs 38a, 227).

Otaria: Comparatively small, extending along swollen basal part of process (Figs 38a, 230).

Valvocopula: One segment contiguous with most of valve margin (Fig. 38a).

Copulae: In two lateral columns, scale-like, median margins usually shorter than lateral margins (Figs 38b, 228). First copula accommodating impression of sister-cell process towards one side. A pattern of striae easily discrenible on copulae in permanent mounts in phase contrast with a X100 lens (Fig. 228). Two to six parallel striae running up middle of copula, other striae at oblique angles to those in middle (Fig. 38b).

Auxospores: None observed.

SEM OBSERVATIONS

Otaria: Outer margin weakly convex, almost parallel to long axis of process. Distal margin concave, forming oblique angle with long axis of process. Angle between outer and distal margins forming a point. (Figs 230, 231).

Intact process tip oblique, internal canal opening on oblique dorsal side (Fig. 233).

Areolae of valve in columns converging at apex. Areolae of copulae loculate, velum external, foramen internal. Wall segments between areolae entire.

TEM OBSERVATIONS

Labiate structure: Barely discernible but probably of the same type as in *Rh. imbricata.*

Areolae of valve: Becomming progressively smaller towards valve apex. Velum structure as in copulae.

Copulae: Marginal zone fairly broad, advalvar edge entire or irregularly toothed, abvalvar edge entire (Fig. 229). 33-41 areolae to 10 µm within a column, 17-25 columns (striae) to 10 µm.

Areolae of copulae: Rectangular in outline. Wall segments between areolae unevenly silicified. Foramen only slightly smaller than areola, outline even, corners rounded. Velum perforated by a median row of oblong pores with long axes usually parallel to areolar column. 2-8 pores (usually 3-5) depending on width of areola. (Fig. 229).

DISTRIBUTION

The distribution is apparently circumglobal in temperate to tropical waters.

DISCUSSION

Hasle (1975) was apparently the first to present micrographs of *Rh. fallax* (as "*Rhizosolenia shrubsolei* ?"), and she also suggested that it could be a separate species. *Rh. fallax* is usually indistinguishable from *Rh. imbricata* in the same size range in water mounts in lower magnifications, but can be distinguished on the striation in permanent mounts using phase contrast. WithTEM and SEM the two species are seen to differ clearly in velum structure. The velum structure found in *Rh. fallax* is also characteristic of *Rh. ostenfeldii* (Fig. 225) and *Rh. chunii* (Fig. 244), but since these species differ from *Rh. fallax* in other characters they can hardly be confused with it. *Rh. fallax* and *Rh. decipiens* are sometimes hard to tell apart with LM, the striation on the copulae being similar, but can usually be distinguished on the shape of the process. (See also *Rh. decipiens*).

Rhizosolenia fallax and *Rh. imbricata* not only resemble each other in habit, they were also often found in the same samples from temperate to tropical waters, and it is tempting to take this as an indication that they may be more closely related than the differences in fine structure would suggest. However, no forms intermediate between *Rh. fallax* and *Rh. imbricata* were seen, which warrants distinguishing the two at specific level.

RHIZOSOLENIA DECIPIENS sp. nov.

(Figs 39a-b, 234-240)

Diagnosis: Cellula longa, cylindrica, in sectione transversa plerumque circularis, 3.5 - 20 µm diam. Processus 9-14 µm longus, a basi attenuatus. Otaria per partem basalem processus extensa, angusta, apice cava. Cingula duas columnas laterales formantia. Columnae areolares copularum mediae cum plano transapicali subparallelae, laterales paulum divergentes. Velum duobus poris late oblongis pertusum cum columna areolari angulos rectos formantibus.

Type material: Atlor VII, 19°00' N, 17°00' W, Nov. 1975. **(011)**.

Holotype: Slide labelled *Rhizosolenia decipiens* Sundström, Atlor VII, 19°00' N, 17°00' W, Nov. 1975. (BM).

Isotypes will be placed in the Hustedt Collection, Bremerhaven (BRM); the Smithsonian Institution, Washington D.C. (US); the Institute of Oceanology, Moscow (IOAS).

Material examined:	TEM: 11, 28, 46, 69, 73, 75, 81, 88.
	SEM: 75.

Rhizosolenia decipiens was the only species of sect. *Imbricatae* I found in the type material.

LM OBSERVATIONS

Cells long, cylindrical, usually circular in cross-section (Figs 39a, 234, 235). Diameter 3.5 - 20 µm. Solitary or in pairs.

Valve: Obliquely conoidal, bilaterally symmetrical (Fig. 39a). Ventral part much longer than dorsal part. Contiguous area fairly narrow. Marginal ridges and claspers usually discernible in permanent mounts using a X40 lens and phase contrast equipment.

Note: The impression of the distal part of the sister-cell process barely reached beyond the valve in the cells I examined.

Process: 9-14 µm long, usually intact. Basal part conical, gradually narrowing into distal tube of roughly equal length (Figs 39a, 239). Wall almost even in thickness (apart from otaria), outline of lumen thus corresponding to outer surface (Fig. 39a).

Otaria: Narrow, extending along basal (conical) part of process (Figs 39a, 239).

Valvocopula: One segment contiguous with most of valve margin (fig. 39a).

Copulae: In two lateral columns, scale-like, median margins shorter than lateral margins (Fig. 39b). First copula usually accommodating impression of extreme distal part of sister-cell process towards one side (Fig. 39b). A pattern of fine striae discernible on copulae on permanent slides at X400 using phase contrast (Fig. 236). Several (>5) parallel striae running up middle of copula, others gradually diverging (Fig. 39b).

Auxospores: None observed.

SEM OBSERVATIONS

Areolae of copulae loculate, velum external, foramen internal (Fig. 237). Wall segments between areolae entire.

TEM OBSERVATIONS

Labiate structure: Not discerned.

Valve: Areolae in columns converging at apex (Fig. 239).

Areolae of valve: Becoming progressively smaller towards apex. Velum structure as in copulae.

Otaria: Narrow, arising at or slightly above process base, extending along basal part of process. Outer margin weakly convex, almost parallel to long axis of process. Distal margin concave, forming an oblique angle with long axis of process (Fig. 239).

Copulae: Marginal zone fairly broad, advalvar edge irregularly toothed, abvalvar edge entire. 25-30 areolae to 10 µm within a column, 22-30 columns (striae) to 10 µm.

Areolae of copulae: Rectangular to quadratic in outline. Wall segments between areolae usually evenly silicified. Foramen only slightly smaller than areola, outline even, corners rounded. Velum perforated by two wide oblong pores at right angles to areola column (Fig. 238).

DISTRIBUTION

My few records of *Rh. decipiens* suggest a circumglobal distribution within the Warm-water Region.

DISCUSSION

With TEM *Rhizosolenia decipiens* can be distinguished from other species in section *Imbricatae* on the velum structure. Under the light microscope it closely resembles *Rh. fallax* but can usually be distinguished on the shape of the process.

RHIZOSOLENIA CHUNII Karsten (Figs 241-244)

Karsten 1905a, p. 99, pl. 11, figs 5, 5a, 5b.

Synonym: ? *Rhizosolenia murrayana* Castracane 1886, p. 72, pl. 24, fig. 12.

Selected figures: Manguin 1960, figs 58a, 60, 322a; Sournia et al. 1979, fig. 17.

My observations on *Rh. chunii* are incomplete and need to be followed up before the taxonomy can be sorted out. I hope to treat this species in more detail in a future article when I have examined more material.

OBSERVATIONS AND COMMENTS

Rhizosolenia chunii was described by Karsten from material collected in the Antarctic. Manguin (1960) presented micrographs of *Rh. chunii,* and his observations fit well those in Karsten (1905a). I identified *Rh. chunii* with certainty in many of the "Brategg" Exped. samples and it seems to be common in Antarctic waters, as can also be deduced from Hasle (1969).

Rhizosolenia chunii was fairly invariable in the Antarctic material I examined and was distinguished on the short pervalvar axis (Figs 241, 242), the contiguous area at an angle almost perpendicular to the pervalvar axis (Fig. 242) and on the short boomerang-shaped girdle segments (Fig. 242). With TEM the structure of the areolae was similar to that in *Rh. ostenfeldii* and *Rh. fallax* (Fig. 244), whereas the arrangement of the striae was similar to that in *Rh. imbricata* (Fig. 243).

In samples from Sidney **(082)** and Chile (IMBB No.186, 08°30' S, 79°35' W) were cells reminiscent of *Rh. chunii* in gross morphology and of *Rh. ostenfeldii* in the structure and arrangement of the areolae (Figs 245, 246). These observations need to be followed up before *Rh. chunii* can be conclusively circumscribed. Furthermore, it is conceivable that *Rh. chunii* is conspecific with *Rh. murrayana,* described by Castracane (1886) from the Antarctic, since the shape and arrangement of girdle segments appears to be the same for both (compare fig. 12, pl. 24 in Castracane 1886 with fig. 5b, pl. 11 in Karsten 1905a).

PSEUDOSOLENIA gen. nov.

Diagnosis: Pseudosolenia gen. nov. Bacillariophycearum. Cellula longa, cylindrica. Valva irregulariter subconica, processu curvo, attenuato, compresso terminata. Processus labiatus internus convolutus. Impressio cellulae sororiae in valvam modo facta. Linea hyalina quasi suturalis margini advalvari copulae appropinquata; ipse margo hyalinus, integer. Velum areolae copulae fissura perforatum angulum rectum cum columna areolari formante.

Typus: *Rhizosolenia calcar-avis* Schultze.

Pseudosolenia calcar-avis comb. nov. (Figs 40-46, 247-257)

Basionym: *Rhizosolenia calcar-avis* Schultze 1858, p. 339, pl. 13, figs 5-10.

Synonyms: *Rhizosolenia cochlea* Brun 1891, p. 43, pl. 19, fig. 9.
Rh. calcar avis Schultze, var. *cochlea* (Brun) Ostenfeld 1902, p. 228, fig. 5.
Rh. calcaravis f. *lata* Schröder 1911, p. 632.
Rh. calcaravis f. *gracilis* Schröder 1911, p. 632.

Non: ? *Rh. calcar avis* sensu Karsten 1907.

Misidentification: *Rh. castracanei* in Okuno 1968, p. 81, figs 4, 7, 11h, 16.

Material examined:
TEM: 9, 15, 17, 18, 21, 24, 26-28, 43-45, 47-66, 68, 73, 83, 84, 86-89.
SEM: 9, 68, 74.
LM: 8, 46, 67, 80, 81, 90, 101, 103, 104, 106, 107, 110, 111-113, 115, 122, 127-129, 131, 132, 136, 139, 140, 146-148, 182-188.

Type material not studied.

Neototype: Fig. 5, pl. 2 in Schultze 1859. (Schultze 1858 not seen).

LM OBSERVATIONS

Cells long, cylindrical, circular in cross-section (Figs 40, 41, 247-249). Diameter 4.5 -190 µm. Usually solitary.

Valve: Subconical, lacking plane of symmetry. Contiguous area roughly sigmoid, narrow, distincter in wide valves (Figs 42-46). In narrow cells the valve margin is in a plane roughly at right angles to the pervalvar axis; in wide cells a slight protrusion where the impression of the sister-cell process ends (Figs 42, 252).

Process: 28-52 µm long, usually intact. Clawlike, narrowly elliptical in cross-section, tapering from base. Basal lumen gradually narrowing into a canal opening at tip. Process wall thickest midway along the process, when seen in broad view. Lumen connected with cell interior by a labiate structure, in large cells visible as an uneven projection below the process base (Fig. 251).

Otaria: Lacking.

Valvocopulae: One or more; advalvar margin contiguous with valve margin (Figs 40, 41).

Copulae: Variable in size and shape. Rhomboidal to wing-shaped (Figs 40, 41), median margins shorter to much shorter than lateral margins. A seamlike structure usually apparent near advalvar margin (Figs 40, 41, 250, 257). 2n (1, 2, 3,.....,8) columns of segments usually parallel to pervalvar axis. Number of columns often differing in the two halves of a frustule, epicingulum then usually having two columns more than hypocingulum. Hypocingulae with more columns than corresponding epicingulae were also observed. Areolation usually discernible in permanent mounts using a X100 lens.

Auxospores: None observed.

SEM OBSERVATIONS

Areolae: Poroid, without internal constriction. Velum external. Wall segments betweeen areolae entire, thick.

Contiguous area: A shallow, tapering, sigmoid depression beginning at base of process and ending near valve margin (Fig. 252).

Labiate structure: Differs from those in other taxa studied for this monograph in being convoluted (Figs 253, 254). Similar labiate structures ("curved labiate processes") are found in Coscinodiscineae (Fryxell and Hasle 1972). Semina and Bekjlemishev (1981) preferred the name "cornuportula" for this type of structure.

TEM OBSERVATIONS

Valve: Areolae in columns converging at apex. Fine structure resembling that of copulae, modified close to apex.

Copulae: Marginal zone fairly broad, hyaline, without regular markings and with entire edges (Fig. 257). Areolar columns roughly parallel to pervalvar axis. 28-31 areolae to 10 µm within a column. Pattern quincuncial.

Areolae of copulae: Poroid, rounded rectangular to ellipsoid in outline. Velum perforated by an oblong pore at right angles to areolar column. Areolar columns usually interrupted close to advalvar margin by a narrow irregular seamlike hyaline structure. (Figs 256, 257).

NOTE

Cell diameter was compared with number of segment columns for cells in one sample **(044)** (Fig. 4). The range of variation in both diameter and number of segment columns was wider than is usually seen in a single sample. The total diameter range in the sample was 16-170 µm and the number of segment columns varied between 2 and 14. Number of columns was, on the whole, related to cell diameter but considerable overlapping occurred. Cells with a diameter of c. 82 µm were, for example, observed with 4, 6, 8 or 10 segment columns.

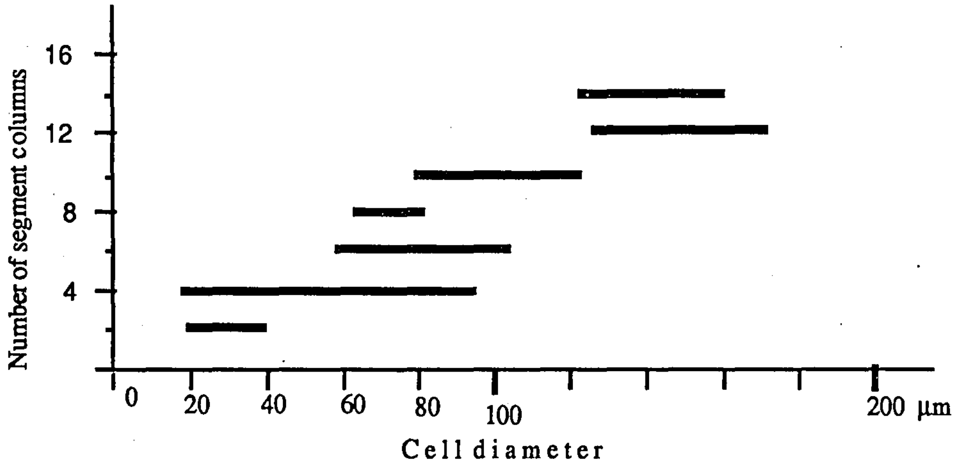


Fig. 4. Variation in cell diameter in *Pseudosolenia calcar-avis* cells with different numbers of segment columns; in one sample from Ko Phuket, Thailand.

DISTRIBUTION

Circumglobal. Common in both oceanic and near-shore samples from warm waters. Occurring seasonally in temperate waters. Found throughout the year in the waters surrounding Ko Phuket, Thailand.

DISCUSSION

The genus *Pseudosolenia* is distinguished from *Rhizosolenia* by the coiled labiate structure, the asymmetrical valve, the characteristic impression of the sister-cell valve and process on the valve and the hyaline "seam" near the advalvar margin of the copulae. From a conservative standpoint it can be argued that it is superfluous to create a new genus for *P. calcar-avis* since it closely resembles the Rhizosoleniae in general shape and in the shape of the valve. However, I considere it inapropriate to retain in the genus *Rhizosolenia* a species with a labiate structure clearly more complex and quite different from those found in the generic type and in other typical Rhizosoleniae. It is, furthermore, inadequate to use the general shape of the valve as a criterium for lumping taxa, as is illustrated by the taxonomical histories of genera such as *Thalassiosira, Coscinodiscus, Biddulphia* and others.

It was not felt necessary to look for type material, since the diagnostic characters were constant in the material I examined and since my observations correspond with the original descriptions of *Rh. calcar-avis* and *Rh. cochlea* in all essential details. Note, however, that *P. calcar-avis* varies considerably in size, girdle segmentation and habit.

According to Brun (1891) *Rh. cochlea* is characterized by a curved flattened process. My observations show that this distinction also holds good for *P. calcar-avis* cells where the diameter is smaller than in his *Rh. cochlea.* In tropical waters the "cochlear" valve type (Figs 41-43, 249) is common in cells at the upper extreme of the diameter range, but it is seldom encountered in temperate waters where the cell diameter seldom approaches the maximum.

H. Peragallo (1892) treated *Rh. cochlea* and *Rh. calcar-avis* as separate species but pointed out that they were related. Ostenfeld (1902) regarded *Rh. cochlea* as a variety of *Rh. calcar-avis* "corresponding to the var. *indica* of *R. alata* ". Karsten (1907) insisted that they should be regarded as separate species. However, the observations on which he founded his opinion were of doubtful accuracy. Moreover, he probably confused *P. calcar-avis* with a *Proboscia* species, since the irregular areolar pattern he stated as being characteristic of "*Rh. calcar-avis* " is in fact typical of *Proboscia*, nor have I seen it reported elsewhere for *Rh. calcar-avis.*

I have not been able to ascertain on what grounds the two taxa have been separated by other workers. It seems probable that three variable features in *P. calcar-avis* have influenced this treatment. First, wide cells tend to develop valves with a less regular appearance (the "cochlear" type) than narrow cells. Secondly, wide cells usually have more than two columns of segments, and this in combination with the general appearance has probably tempted workers to regard such cells as taxonomically deviating.

Thirdly, the contiguous area is usually only distinct on wide valves, which may also have been regarded as a diagnostic character by some workers.

From Kustenko's (1981) results it can be deduced that the diameter range in *P. calcar-avis* in samples taken many months apart in the Black Sea may differ considerably (25-49 µm in March 1980 as compared with 5-29 µm in August 1981). It is important to bear this in mind when samples well separated in time or space are compared.

PROBOSCIA gen. nov.

Diagnosis: Proboscia gen. nov. Bacillariophycearum. Cellula longa, cylindrica. Valva irregulariter subconica, in proboscidem attenuata, processu nullo. Auxospora terminalis. Pori interloculares plerumque praesentes. Genus marinum, plancticum, per universum globum distributum.

Typus: *Rhizosolenia alata* Brightwell.

The genus *Proboscia* comprises species with valves terminating in a proboscis. The presence of a proboscis and the lack of a process distinguishes *Proboscia* from *Rhizosolenia* and other solenoid diatoms.

Proboscia comprises the generic type *P. alata* and an undetermined number of species commonly referred to in the literature as *Rhizosolenia alata, Rh. arafurensis, Rh. indica, Rh. inermis, Rh. truncata,* etc. More research is needed before any species in *Proboscia* can be satisfactorily circumscribed.

Proboscia alata (Brightwell) Sundström comb. nov. (Figs 258-266)

Basionym: *Rhizosolenia alata* Brightwell 1858, p. 95, pl. 5, figs 8, 8a.

Synonyms: *Rhizosolenia gracillima* Cleve in Cleve and Möller 1878 (S), text on slide No.65.
Rhizosolenia (*alata* var. ?) *gracillima* Cleve 1881, p. 26, pl. 6, fig. 78.
Rhizosolenia alata var. *gracillima* (Cleve) Grunow in Van Heurck 1880-1881, pl. 79, fig. 10.
Rhizosolenia alata f. *genuina* (Brightw.) Gran 1905, p. 56. (Nom. illeg.).

Non: Most descriptions and records of *Rh. alata* and intraspecific taxa are probably referrable to other *Proboscia* species than *P. alata.*

Selected figures: Drebes 1974, figs 39c-d; Hasle 1975, figs 56, 58, 60.

Material examined:
TEM: 2-5, 7.
SEM: 4.
LM: 109, 143, 165-170, 174-181.

Type material: According to D. Williams (BM) (pers. comm.) the BM slide No. 1225 (109) forms part of the material Brightwell (1858) referred to in his description of *Rhizosolenia alata*. The slide will serve as lectotype.

Observations: The slide holds frustules of only one *Proboscia* species (Figs 258, 259). The areolar pattern is not discernible with a X100 lens, neither on valves nor segments, probably because of the size of the areolae; interlocular pores are probably present as indicated by "dots" irregularly distributed over the copulae. Cell diameter 8.5 - 11.5 µm. Morphological details conform with those described below under LM observations.

The Cleve and Möller Collection (S) slide No.65 (143) includes frustules of *Proboscia alata* ("*Rhizosolenia gracillima* ") differing from the frustules on the type slide only in the smaller diameters (3.0 - 5.5 µm).

LM OBSERVATIONS

Cells long, cylindrical, circular in cross-section (Figs 258, 259). Diameter 2.5 - 13 µm. Usually solitary.

Valve: Conoidal, tapering into proboscis, lacking a plane of symmetry. Contiguous area developed into distinct groove proximally, in linked valves accommodating distal part of sister-cell proboscis. (Figs 258, 259, 263).

Proboscis: Circular in cross-section, tip truncate (Figs 263, 264). Short longitudinal slit just below tip.

Valvocopula: One segment contiguous with most of valve margin.

Copulae: In two columns. Rhomboidal in outline, median margins short, lateral margins long. (Fig. 262).

Auxospore: Terminal (Fig. 260). Diameter of mother cell 3 - 4.5 µm; diameter of initial cell 10 - 12.5 µm. Primary valve of initial cell lacking proximal groove (Fig. 261). Girdle segments in two columns.

SEM OBSERVATIONS

Valve: The groove accommodating the distal part of the sister-cell process is covered by two claspers of unequal size (Fig. 263). The distal surface of the truncated proboscis is surrounded by a ring of spinulae (Fig. 263).

Copulae: Areolae loculate, passage pores present, velum external, foramen internal. Areolar pattern quincuncial, orientation varying in different parts of the copula (Fig. 262). Interlocular pores irregularly distributed, each surrounded by six areolae (Figs 263, 265).

TEM OBSERVATIONS

Valve: Areolae in columns converging at apex. Areolae near margin resembling those on copulae, foramina and passage pores becoming fewer towards apex where they are entirely lacking (Fig. 264).

Copulae: Marginal zone fairly broad, advalvar and abvalvar edges entire. 45-50 areolae to 10 µm.

Areolae of copulae: Foramen circular, velum perforated by one central pore (Fig. 266). Passage pores present except between areolae and interlocular pores. Outer and inner silicious layers connected by triangular columellae, one in the middle of each areolar triad (Fig. 266).

Interlocular pores: Thick-walled pores scattered between areolae. Resembling six-pointed star in outline, penetrated by central canal. (Figs 265, 266).

Initial cell: Fine structure of copulae as in mother-cell copulae.

NOTE

Proboscia taxa are common in all parts of the oceans, from the poles to the tropics. The genus varies most in the tropics where it ranges in diameter from c. 3 µm to at least 100 µm and where even cells with a similar diameter can vary considerbly in habit. My observations suggest that in material from the tropics the copular areolae are either fairly large with vela perforated by three to at least 12 pores (Fig. 267), or of the same type as in *P. alata.* I observed no frustules in which both types occurred, and there seems to be a discontinuity between them.

DISTRIBUTION

Proboscia alata was identified conclusively in material from European coastal waters but it probably also occurs off the east coast of North America on the evidence of references in the text to figs 56, 58 and 60 in Hasle (1975). The biogeographical limits cannot be determined without further research.

DISCUSSION

It has long been recognized that "*Rh. alata* " and its relatives differ from *Rhizosolenia* in several characters. Hasle (1975) pointed out that *Rh. alata* was unique in certain morphological details. She discussed the possibility of establishing a new genus with *Rh. alata* as the generic type, but considered this premature in view of the lack of information on other *Rhizosolenia* taxa.

The new genus *Proboscia* is distinguished on the presence of a proboscis. The interlocular pores and the columellae are also characteristic. There is no reason for retaining *P. alata* and its relatives in *Rhizosolenia* since they, furthermore, all lack the process characteristic of this genus.

It is necessary to approach the study of the genus *Proboscia* from a new angle since most taxa in the "*Rh. alata* " group are poorly defined and have often been confused. I have chosen to treat only the generic type here, since it would not have been possible to clear up the prevaling confusion within the scope of this study. My preliminary observations (unpubl.) have convinced me that *Proboscia* comprises at least four good species, but the variation must be studied in greater detail before the species can be circumscribed.

Since "*Rh. alata* " has been reported from virtually every part of the ocean, and the epithet has been used for probably all taxa to be included in the genus *Proboscia* I have found it necessary to start again from scratch in circumscribing *P. alata*, although I am aware that the delimitations must be tentative pending further data. Thus until otherwise shown *Proboscia alata* should be regarded as invariable in valve morphology, areolar structure and girdle segmentation, and as having a fairly limited diameter range and a limited geographical distribution.

It should be noted that another *Proboscia* taxon is also present in temperate European waters. It is commonly referred to as *Rh. indica* or *Rh. alata* f. *indica* in the literature (e.g. Robinson 1957, Drebes 1974) and can usually be distinguished from *P. alata* on the larger size (cf. Robinson 1957, p. 206). The figures 52, 54, 55 and 59 in Hasle (1975) are probably of this taxon, which also differs from *P. alata* in the larger areolae and the velum perforated by more than one pore. Hasle's figs 49, 50 and 57 are of two other *Proboscia* taxa, mainly distinguished on the bilaterally symmetrical valves.

The primary valve of initial cells of *Proboscia* differs from other valves in lacking the characteristic groove. The names *Rh. arafurensis* Castr. and *Rh. arafurensis* Wood probably refer to specimens with such valves.

OBSERVATIONS AND COMMENTS ON TAXA NOT INCLUDED

The following taxa differ considerably from the *Rhizosolenia* species treated earlier and can, in my opinion, not be regarded as fitting in the genus. They are heterogeneous in morphology and more research is needed before their taxonomic position can be determined.

Rhizosolenia fragilissima Bergon (1903) differs from the true Rhizosoleniae in the low valve, absence of otaria, the sister-cell process accommodated in a pocket on the valve (Fig. 268) and the girdle composed of single-layered segments regularly perforated by small rectangular pores (Fig. 269) - see also Hasle (1975). (Figs 268, 269).

Rhizosolenia phuketensis Sundström (1980) is closely related to *Rh. fragilissima* but differs in having curved cells and the process and the pocket nearer the valve margin (Fig. 270) - see also Sundström (1980). (Figs 270, 271).
Note: *Rh. phuketensis* is more widespread than I first assumed (Sundström 1980). It is usually associated with *Rh. stolterfothii* and its distribution is probably similar. I have recently found it also in samples from the North Sea and the Skagerrak (unpubl. observ.).

Rhizosolenia delicatula Cleve (1900) has a flat valve face surrounded by a valve mantle. A fairly long narrow process is situated at the margin of the valve face and a sheath-like depression for the sister-cell process is seen near it on a tongue-like protrusion of the valve margin. The depression is partly covered by two claspers (Fig. 272). The girdle segments are single-layered and regularly perforated by small rectangular pores (Fig. 273). (Figs 272, 273).
Note: Figure 63 in Hasle (1975), allegedly of *Rh. delicatula*, probably shows a valve of *Rh. phuketensis.*

Rhizosolenia stolterfothii H. Peragallo (1888) has a flat weakly silicified valve face and a sloping mantle similar in structure but more heavily silicified (Fig. 274). A process flanked by structures comparable to the otaria of the true Rhizosoleniae is located at the margin of the valve face (Fig. 274). A shallow depression for the sister-cell process is also evident in Fig. 274. The girdle segments are single-layered and regularly perforated by small rectangular pores (Fig. 275) - see also Hasle (1975). (Figs 274, 275).

Rhizosolenia cylindrus Cleve (1897) has a conoidal valve terminated by a long tubular process with a cleft-shape opening at the tip (cf. Fig. 280). The species is essentially solitary, but (newly formed ?) sister cells are often found in pairs. In such cell-pairs the processes bridge the gap between them (cf.Fig. 279). A small V-shaped depression of the tip of the sister-cell process can be seen on the valve fragment in Fig. 277. The girdle segments are single-layered and regularly perforated by small rectangular pores (Fig. 278). (Figs 276-278).

Rhizosolenia antarctica Karsten (1905a) differs from the previous species mainly in the less pointed valve (Fig. 279). Hasle (1969) regarded them as conspecific. (Figs 279-281).

Rhizosolenia tubiformis Hasle (1975) has a flattened valve face with an eccentrically located, small, dome-shaped, hollow process with a small pore at the top (Figs 284, 285). It can be assumed that a corresponding depression is also present. The girdle segments are single-layered and regularly perforated by small rectangular pores (Fig. 283). As pointed out by Hasle (1975) the shape and arrangement of the girdle segments resembles that in *Rh. cylindrus.* (Figs 282-285).

The main distinction between the above taxa and the true Rhizosoleniae lies in the structure of the silicious wall of the girdle elements. In true Rhizosoleniae the structure is characteristically complex, whereas in the others the segments are built up by a single layer regularly perforated by small rectangular pores. This wall structure is also found in *Guinardia* H. Peragallo (cf. Hasle 1975) and in *Lauderiopsis* Ostenfeld (Fig. 291), but not in true Rhizosoleniae.

Rhizosolenia robusta Norman (in Pritchard 1861) resembles a true *Rhizosolenia* in having the wall structure of the girdle segments similar (see Hasle 1975, figs 44, 45) and in the calyptriform valve. However, the apex of the valve differs entirely from that in Rhizosoleniae sensu stricto in that it ends in a cup-shaped structure from the bottom of which projects a tubular process (Fig. 289). The internal labiate structure (Fig. 290) also appeared (a clear view could not be obtained) to differ from the types found in true Rhizosoleniae in comprising a short stemlike basal part and an expanded quadrangular distal surface diagonally transversed by a narrow slit flanked by low labia. (Figs 289,290).

Rhizosolenia setigera Brightwell (1858), *Rh. pungens* Cleve-Euler (1937), *Rh. crassispina* Schröder (1906) and other morphologically similar taxa make up a poorly understood complex. The common denominator is a conical valve terminated by a long needle-like process. In all frustules with such valves that I have observed the pattern of the girdle segments was much finer (Figs 286-288) than seen in *Rhizosolenia* sensu stricto. Poroid areolae with the velum perforated by an oblong slitlike pore were seen in a few cases, but loculate areolae were never observed. The members of this complex also differs from the true Rhizosoleniae in lacking otaria and in the impression of the sister-cell process which runs across more than one girdle segment. The decisive motive for my reluctance to regard them as true Rhizosoleniae lies, however, in the endogeneous resting spores of *Rh. setigera.* Since, furthermore, these are produced in pairs and are entirely different from the mother cell (Brightwell 1858, Drebes 1974, Hargraves 1976) no good reason remain to regard *Rh. setigera* and its relatives as fitting the genus. (Figs 286-288).

Fresh-water Rhizosoleniae: *Rh. longiseta* Zacharias (1893), *Rh. eriensis* H.L. Smith (1872), *Rh. minima* Levander (1904) et.c. were not closely examined for this thesis. It is, however, fairly obvious from the literature that they do not fit the genus: According to Okuno (1957) the "intercalary bands" of *Rh. longiseta* are perforated by longitudal rows of subrectangular holes; c. 60-65 rows to 10 µm and c. 40-45 holes to 10 µm within a row. Bourelly (1968) observed that *Attheya zachariasi* Brun, apart from each valve having two setae, structurally resembled *Rh. longiseta* and *Rh. eriensis.* Furthermore, endogeneous resting spores quite different from the vegetative cells have been reported from both *Rh. eriensis* and *Rh. longiseta* (Hustedt 1930, Bourelly 1968).

GENERAL DISCUSSION

1. Taxonomy

The four species *Rh. styliformis, Rh. imbricata, Rh. alata* and *Rh. setigera* described by Brightwell (1858) formed the basis for his circumscription of *Rhizosolenia.* With the generitype *Rh. styliformis* serving as a standard of reference it is clear that *Rh. imbricata* should be accommodated in the genus, since it too has the type of claspers and otaria unique for the genus *Rhizosolenia. Rh. alata* and *Rh. setigera,* on the other hand, differ from *Rh. styliformis* in several characters, and neither of them can be regarded as closely related to it (see Discussions under *Proboscia alata* and under Observations and comments on taxa not included). Since Brightwell's definition of *Rhizosolenia* was thus based on discordant elements I propose the following emended diagnosis:

> Rhizosolenia.
> Cells cylindrical, straight or slightly curved, circular to elliptical in cross-section, pervalvar axis usually much longer than apical axis. Valves conical to subconical, otaria and claspers usually present, apex characteristically terminated by one process (two in *Rh. antennata* f. *antennata*). Internal canal (or lumen) of process opening at tip and communicating with cell interior by a labiate structure. Labiate structure usually comprising simple labia arising directly from the inner surface below the base of the process; in section *Imbricatae* appearing as a low dome-shaped structure perforated by a slit. Girdle segments in longitudinal columns parallel or roughly parallel to pervalvar axis. Areolae of copulae in a quincuncial arrangement, usually loculate, but internal foramen sometimes lacking. Vela of copulae perforated by pores or by one or more slits. Recent, planktonic, marine.

Thus circumscribed *Rhizosolenia* forms a fairly homogeneous group of solenoid diatoms characterized by conoidal valves terminated by a process, the presence of otaria and claspers and copulae perforated by areolae (as opposed to pores). The four species *Rh. temperei, Rh. acuminata, Rh. bergonii* and *Rh. simplex* entirely lack otaria and claspers but should, nevertheless, be retained in the genus. The first three are evidently closely related and form a distinct group with no immediately obvious affinity to species with otaria and claspers. However, the relationship becomes clear when the dimorphism displayed in *Rh. polydactyla* is taken into account. Thus *Rh. polydactyla* f. *polydactyla* has the typical morphology of *Rhizosolenia* while *Rh. polydactyla* f. *squamosa* lack otaria and claspers and closely resembles *Rh. bergonii* in the shape of the valve and in girdle segmentation. *Rh. simplex* has an areolar structure resembling to that in *Rh. hyalina,* which indicates a closer affinity to the true Rhizosoleniae rather than to the superficially similar *Rh. setigera.*

Earlier subdivisions of *Rhizosolenia* (H. Peragallo 1892, Karsten 1905a, Gran 1905, Pavillard 1925, Hendey 1964) all include species that cannot be accommodated in the genus, and it serves no purpose to discuss them in detail. It can be noted, however, that much emphasis has been placed on valve shape and on the arrangement of girdle elements, and that most of the true *Rhizosolenia* species fall within the sections *Rhizosolenia (Genuinae)*, *Squamosae* and *Imbricatae* in Pavillard's (1925) commonly adopted classification.

The *Rhizosolenia* species treated in this monograph can be subdivided into two natural sections: sect. *Rhizosolenia*, and sect. *Imbricatae* typified by *Rh. imbricata*. The main distinction between the two sections lies in the arrangement of the girdle segments, which is bilateral in sect. *Imbricatae* and dorsiventral or in several columns in sect. *Rhizosolenia*. In addition, the labiate structure is probably always low and dome-shaped in sect. *Imbricatae* as opposed to the distinct labia in sect. *Rhizosolenia*. There are also common traits in the fine structure of the girdle elements in the sect. *Imbricatae* species that set them apart from all the species within sect. *Rhizosolenia*, eg. unevenly silicified walls between areolae, advalvar marginal zone of copulae not fringed. A further subdivision of sect. *Rhizosolenia* could perhaps also be argued for on the grounds that *Rh. temperei*, *Rh. acuminata* and *Rh. bergonii* form a fairly distinct group and that *Rh. hyalina* and *Rh. simplex* differ slightly from other species in the fine structure of the areolae. However, a further subdivision seems at present to serve no practical purpose. The traditional sect. *Squamosae* (girdle composed of more than two segment columns) is entirely artificial, since the number of segment columns is mainly a function of cell diameter, and varies widely even within single species.

The new genus *Proboscia* resembles *Rhizosolenia* in the solenoid shape of the cell, but there are a number of characters that clearly set it apart from the latter, the terminal position of the auxospore, the presence of interlocular pores and the lack of a process being particularly obvious. The genus is, furthermore, well defined on the characteristic proboscis which, however, can vary greatly in length and shape between taxa (unpubl. observ.). Hasle (1975) considered the possibility that "*Rh. alata* " could have affinities with the freshwater Rhizosoleniae and possibly with *Rh. bergonii* but my observations do not support this.

It is perhaps arguable that the new genus *Pseudosolenia* is unnecessary in view of its close resemblance to *Rhizosolenia* in general appearance and in the fine structure of the girdle segments. However, in my opinion the complex convoluted labiate structure ("cornuportula") seen in *P. calcar-avis* differs sufficiently from the types of labiate structures found in *Rhizosolenia* to suggest a different line of evolution for *Pseudosolenia* . It is curious that otherwise "cornuportulae" are apparently only found within the suborder Coscinodiscineae (sensu Simonsen 1974). This may be of phylogenetic interest.

The species treated under "Observations and comments on taxa not included" must await further research on other genera within Rhizosoleniaceae before they can be transferred.

2. Circumscription of Rhizosoleniaceae.

Many opinions have, in the course of time, been expressed as to the circumscription of the family Rhizosoleniaceae, e.g. De Toni (1890), H. Peragallo (1892), Hustedt (1930) and others. More recently Hasle (1975) have suggested that *Rhizosolenia, Guinardia, Dactyliosolen* Castrac. and *Streptotheca* Shrubs. comprise this family. Simonsen (1979) placed *Streptotheca* in the family Lithodesmiaceae.

My circumscription of *Rhizosolenia* comprises species that differ considerably from those in *Guinardia, Dactyliosolen* and *Streptotheca.* A reclassification is necessary, with the erection of new families. Thus, if the presence of otaria and claspers in combination with the complex anatomy of the copular areolae are diagnostic there is no close affinity between *Rhizosolenia* and any of the other genera. A new circumscription of Rhizosoleniaceae should include, apart from *Rhizosolenia,* the genus *Pseudosolenia,* which differs from *Rhizosolenia* in only a few characters and which is similar in valve shape and girdle anatomy. *Proboscia* could possibly be included in the family in view of the similar anatomy of the copular areolae. Moreover, the claspers of *Proboscia* could be homologous to those of *Rhizosolenia.* On the other hand, *Proboscia* species apparently form terminal auxospores as compared with the lateral auxospores that have been observed in some *Rhizosolenia* species. It is unlikely that *Rhizosolenia* species form terminal auxospores which are more firmly attached to the mother cell and would thus almost certainly have been documented if they occur.

Rhizosolenia robusta could, under a new generic name, also perhaps be included in Rhizosoleniaceae on the similar anatomy of the copular areolae and the similar shape of the valve. *Rh. setigera* (sensu lato), on the grounds of the general cell shape and the occasional presence of poroid areolae (as opposed to pores), might be retained in the family (under a new generic name) although paired endogenous resting spores such as are found in *Rh. setigera* presumably do not occur in *Rhizosolenia.*

The two closely related species *Rh. fragilissima* and *Rh. phuketensis* resemble *Dactyliosolen blavyanus* (H. Perag.) Hasle (see Hasle 1975) in the shape of the girdle segments and in valve morphology, and are probably more closely related to this genus than to any other. On the other hand, labiate structures are present in *Dactyliosolen* but apparently not in *Rh. fragilissima* and *Rh. phuketensis.*

The taxonomic position of *Rh. stolterfothii, Rh. delicatula, Rh. cylindrus, Rh. antarctica* and *Rh. tubiformis* is uncertain, but they resemble *Guinardia flaccida* (Castr.) H. Perag. most closely in the shape and structure of the girdle segments (see Hasle 1975).

The fresh-water Rhizosoleniae are probably not even remotely related to *Rhizosolenia,* the "process" in these species being better regarded as a seta.

3. Species, varieties and forms.

Since little is known about the genetics of diatoms, and crossing experiments are currently not possible, our knowledge of evolutionary patterns in diatoms is slight. Gallagher (1982), for example, has shown that the genetic differences between morphologically indistinguishable populations of *Skeletonema costatum* (Grev.) Cleve may be as great as between "terrestial organisms". Moreover, since many diatoms are dimorphic or polymorphic it is clear that the gene pool of a single species can also allow of variation in morphological expression.

As in all "practical" taxonomy discontinuity in morphological traits is the basis for distinguishing taxa, but distribution patterns and environmental demands should also be taken into account.

The taxonomy of diatoms is almost wholly based on structural features of the silica wall. The electron microscope has revealed a wealth of hitherto unknown morphological characters and has become an indispensable tool in diatom research. For instance, the traditional circumscription of *Rhizosolenia* provides a good example of how a single character, the presence of a solitary process on a valve, has led to the grouping together of species which electron microscopic studies have shown to differ widely in other morphological features.

The intraspecific ranks of variety and form are commonly used in diatom taxonomy, but since there is no general agreement on their application they have become a source of confusion. An example of this is to be found in the traditional *Rhizosolenia* taxonomy where infraspecific taxa of *"Rh. alata"* have usually been accorded the rank of form, whereas those of *Rh. styliformis* have been treated as varieties. Moreover, there is a tradition in diatom taxonomy to give formal names to morphological variants that evidently do not differ genetically. For example, in *Bellerochea malleus* (Brightw.) Van Heurck three forms are recognized (f. *biangulata*, f. *malleus* and f. *tetragona*) and are distinguished on the number of angles in the cell, but according to von Stosch (1977) all three can be produced from a single clone, and recently Syvertsen and Hasle (1983) decribed a variant of *Eucampia zodiacus* Ehrenb. (f. *cylindrocornis*) that sometimes appears in chains together with the normal cells. In *Rhizosolenia*, the dimorphism displayed by *Rh. hebetata* and by *Rh. antennata* provide further examples of the formal recognition of morphotypes (Gran 1905, Heiden and Kolbe 1928, present monograph).

Although the practice of according intraspecific morphological variants formal recognition is disputable from the viewpoint of modern plant taxonomy, it is of definite advantage in phytoplankton research. As pointed out by Taylor (1976), a formal name once established in the floristic literature will also appear in non-taxonomic studies as a label for a category. If not formally named, a variant will probably not be recorded by ecologists and potentially valuable environmental data will thus be lost. For instance, information on "resting spores" and "cysts" is seldom given in ecological studies of phytoplankton communities.

Having accepted that the ranks of variety and form are commonly recognized and currently indispensable in diatom taxonomy it remains to apply the terms with as little ambiguity as possible. However, very few attempts have so far been made to set standards for the use of the ranks and those that have been made are not in accordance.

Variety:

Hustedt (1930) regarded varieties as end-points of form-series and considered it unnecessary to give names to intermediate stages. Taylor (1976), working with dinoflagellates, used the concept in rather the same way but argued that also a "nominate variety", based on the original specimen (or figure) and perhaps not representing an end-point, should be recognized. Hendey (1964) used the term varietas "to describe variants that more probably have arisen as a result of accumulation of a series of minute differences." According to him such variants would be achieved by an "evolutionary process involving the passage of time." He furthermore regarded varieties as "much less real than forms" in diatoms, and was of the opinion that if a complete series of intermediates was available linking two "possible varieties" the establishment of varietal taxa was not justified.

I have used the rank variety in subdividing *Rh. castracanei* and *Rh. clevei.* Each species comprises two fairly distinct groups that differ in girdle segmentation and in size range but that are indistinguishable in the fine structure of the silica wall. Intermediates occur within *Rh. castracanei* and possibly also within *Rh. clevei*, but my observations indicate that they are rare. To what degree the varieties differ genetically cannot be determined from the present data, but it is logical to assume that they belong to different gene pools since the vast majority of individuals within each variety fall inside well-defined size ranges in nature, and are therefore probably adapted in different ways to the environment. The rank of variety, in the sense I have used it thus indicates a morphologically stable form-series probably with the occurrence of minor gene exchange with a second equally distinct and morphologically stable form-series. The appearance of varieties in nature can be regarded as a step towards speciation.

On the basis of the morphology of the "vegetative" cells the species *Rh. hebetata* and *Rh. borealis* could perhaps be treated as varieties of *Rh. antennata* and *Rh. polydactyla* respectively. However, I prefer to treat them as separate species, since in each pair the distribution is disjunct and since other stages in their life cycles differ markedly. On the other hand, Fryxell et al. (1981) treated the two disjunct populations of *Thalassiosira antarctica* Comber as varieties even though their resting spores differ considerably. The taxonomic treatment of such populations is largely a matter of personal opinion.

Form:

Hendey (1964) used the term to describe: (a) "Units that possess undoubted resemblances of pattern or type of valve face, yet have totally different geometrical outlines, i.e. morphological variants that could not possibly have evolved by the gradual accumulation of minute differences. Examples of forms in this sense are found in *Triceratium favus* Ehrenb., and *Biddulphia antediluviana* (Ehren.) Van Heurck." He also used the term to describe variants: (b) "...when, as in *Rhizosolenia hebetata*, two or more morphological expressions arise,...". "A form in this sense may be said to be the result of genetic instability and may arise suddenly and equally suddenly revert to type. A form is not the result of slow evolutionary change." Taylor (1976) used the term to denote phenotypic variants ("ecophenes") among which the plasticity could be related to external environmental influences. He proposed that life-cycle variants should be dealt with informally as "phases" or "stages".

I have used the rank of form to denote the life-cycle variants of the dimorphic species *Rh. antennata*, *Rh. hebetata, Rh. polydactyla* and *Rh. sima* , but admit that the treatment is not entirely satisfactory since at least the forms in *Rh. polydactyla* and *Rh. sima* could equally well be regarded as "resting spores" and be treated informally. However, the forms in these species can apparently divide several times before the final stage is reached, and the term resting spore, in its strict application (Ross et al. 1979), can only be used for the final stage. Hoban et al. (1980), on the other hand, chose not to give formal recognition to life-cycle variants in *Odontella litigosa* (Van Heurck) Hoban, another species showing a gradual change from the vegetative stage to the "resting" stage.

Rh. hebetata f. *semispina* is the common or vegetative form of *Rh. hebetata,* f. *hebetata* being less common, and more heavily silicified. From the morphology of the silica wall f. *hebetata* could be considered a "resting spore" of f. *semispina,* but both f. *semispina* and f. *hebetata* (syn. f. *hiemalis*) have numerous chromatophores (Gran 1905), which is not characteristic of "resting spores". Since, moreover, *Rh. hebetata* f. *hebetata* can apparently only be formed through auxosporulation, and can evidently divide to produce daughter cells of the f. *hebetata* type, "resting spore" is hardly the proper term for it. However, it should be noted that typical resting spores of *Leptocylindrus danicus* Cleve are apparently formed from auxospores only (Davis et al. 1980) and that "exogenous resting spores" in *Eucampia balaustium* Castracane can divide to form new "spores" (Syvertsen and Hasle 1983).

Rh. antennata f. *semispina* is the common or vegetative form of *Rh. antennata.* Forma *antennata* is less common but can apparently develop directly from f. *semispina* by mitotic cell division without forming intermediate valve types. Forma *antennata* is not more heavily silicified than f. *semispina* except for having two processes on each valve. It is indistinguishable from f. *semispina* in the fine structure of the silica wall and can hardly be considered a "resting spore" in the strict sense of the term. The cell content was poorly fixed in the material containing *Rh. antennata* , and it was not possible to see if there were any differences in number of chromatophores in the two forms.

Whether life-cycle variants should be treated informally or accorded taxonomic recognition is largely a matter of personal choice. This is reflected in the literature, especially as regards some taxa in the genera *Eucampia, Odontella* and *Rhizosolenia* (Van Heurck 1909, Heiden and Kolbe 1928, Hendey 1937, Hendey 1964, Drebes 1974, Hoban et al. 1980, Syvertsen and Hasle 1983). It is highly desirable from the ecologist's point of view that life-cycle variants are reported in studies involving diatoms, since their presence is presumably related to environmental factors. Although it is not common practice to formally recognize pure phenotypes I find this unavoidable in diatom taxonomy. The use of informal categories such as "phase", "stage" or morph would be preferable, but must await international agreement among diatom taxonomists.

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Plate 1

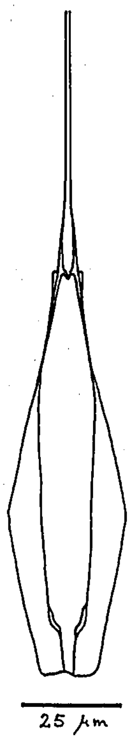
Fig. 5. **_Rh. styliformis._** Valve in ventral view.

Fig. 6. **_Rh. acicularis._** Valve and valvocopula in ventral view.

Fig. 7. **_Rh. polydactyla_ f. _polydactyla._** Theca in lateral view.

Fig. 8. **_Rh. polydactyla._** Cell in ventral view. Left, theca characteristic of f. *polydactyla;* right, theca intermediate between f. *polydactyla* and f. *squamosa.*

Fig. 9. **_Rh. polydactyla._** Cell in ventral view. Left, theca intermediate between f. *polydactyla* and f. *squamosa;* right, theca characteristic of f. *squamosa.*



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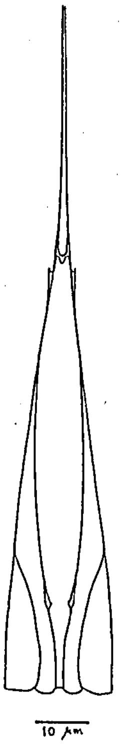

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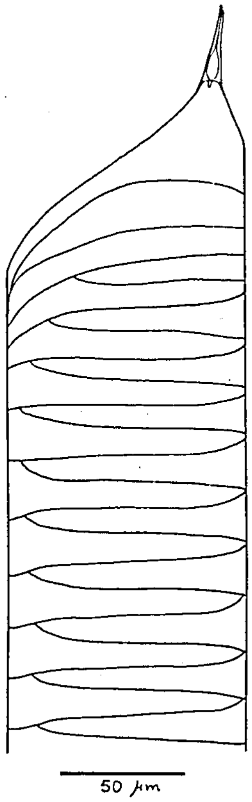

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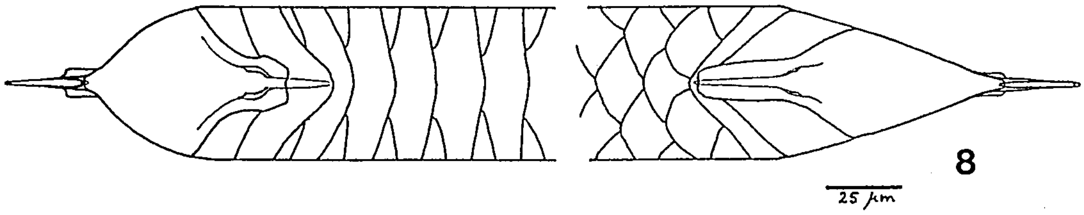

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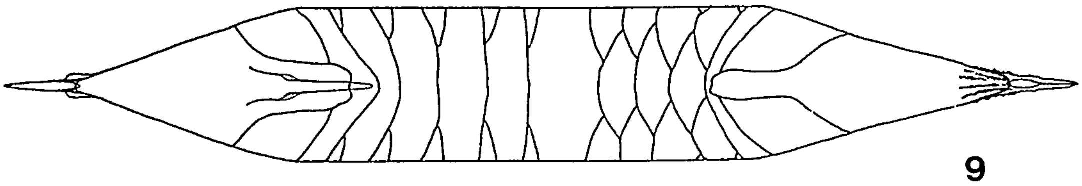

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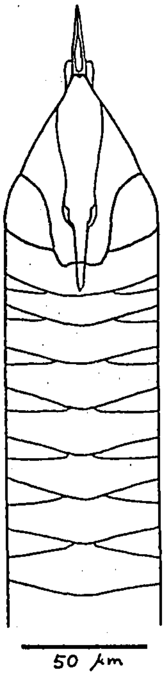
Plate 2

Fig. 10. ***Rh. borealis.*** Theca in ventral view.
Fig. 11. ***Rh. borealis.*** Theca in ventral view.
Fig. 12. ***Rh. formosa.*** Theca in ventral view.
Fig. 13. ***Rh. formosa.*** Theca in oblique lateral view. Note difference in segmentation in distal and proximal parts.
Fig. 14. ***Rh. sp.*** Theca in ventral view.



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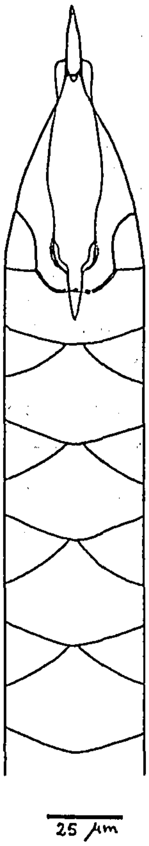

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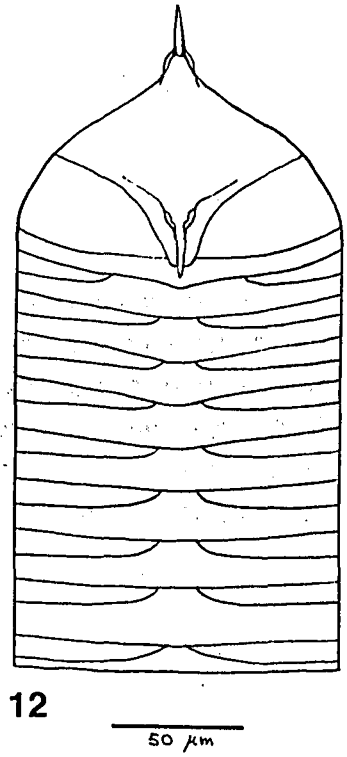

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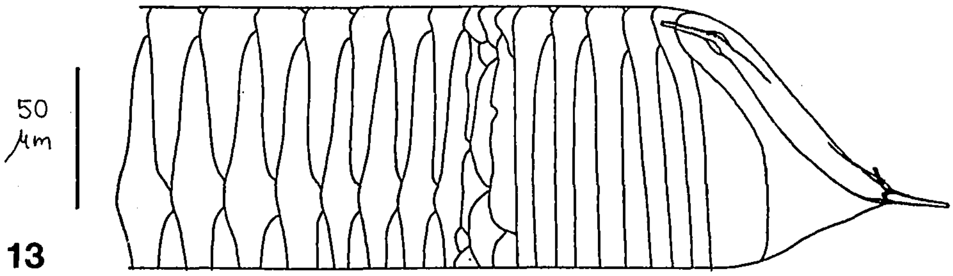

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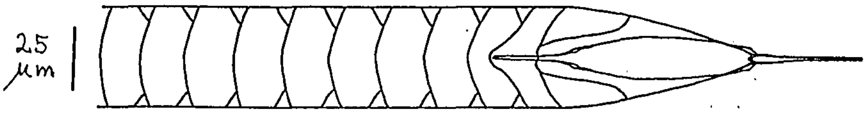

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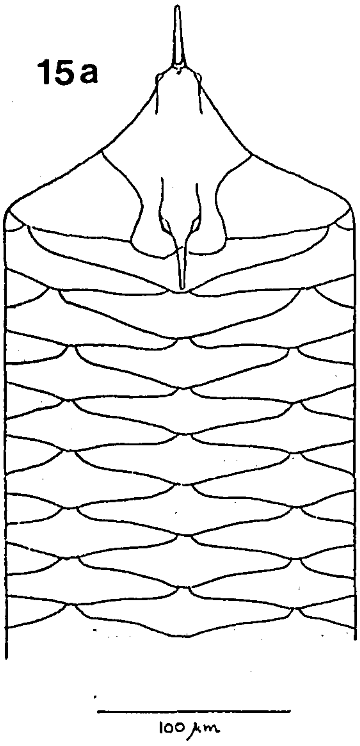
Plate 3

Fig. 15 a. ***Rh. castracanei* var. *castracanei.*** Theca in ventral view.
Fig. 15 b. ***Rh. castracanei* var. *castracanei.*** Theca in dorsal view.
Fig. 15 c. ***Rh. castracanei* var. *castracanei.*** Theca in oblique lateral view.
Fig. 16. ***Rh. castracanei* var. *castracanei.*** Theca in oblique lateral view. Note difference in segmentation in distal and proximal parts.
Fig. 17 ***Rh. castracanei* var. *neglecta.*** Theca in ventral view.

15a



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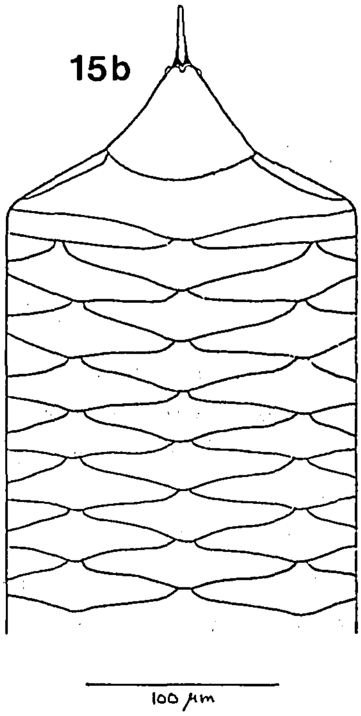

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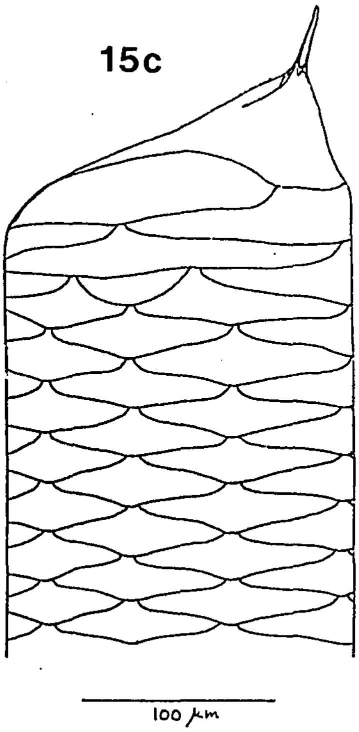

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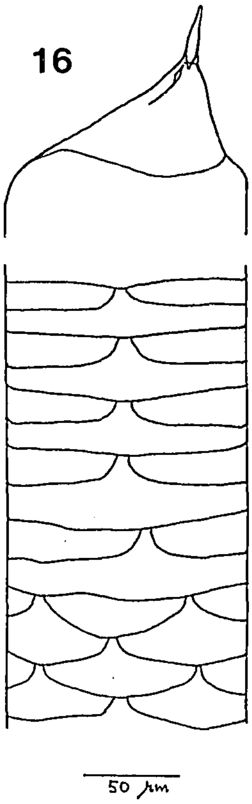

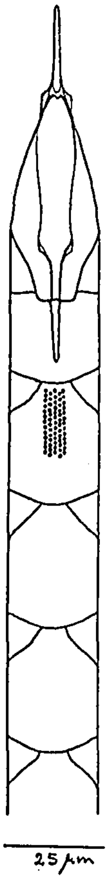

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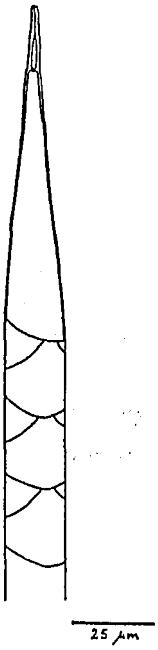
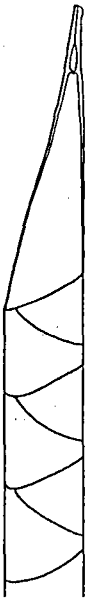
Plate 4

Fig. 18 a. ***Rh. hebetata* f. *hebetata.*** Distal part of theca.
Fig. 18 b. ***Rh. hebetata* f. *hebetata.*** Distal part of theca.
Fig. 19. ***Rh. hebetata* f. *semispina.*** Distal part of theca in ventral view.
Fig. 20. ***Rh. antennata* f. *semispina.*** Distal part of theca in ventral view.
Fig. 21. ***Rh. clevei* var. *clevei.*** Theca in ventral view.
Fig. 22. ***Rh. clevei* var. *communis.*** Theca in ventral view.
Fig. 23. ***Rh. clevei* var. *communis.*** Distal part of theca in ventral view.

18a



18b



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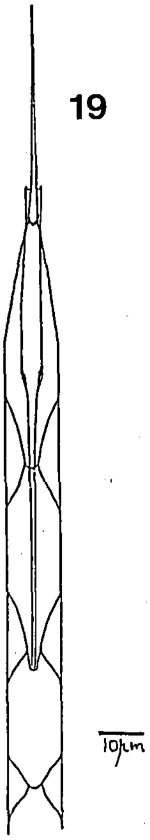

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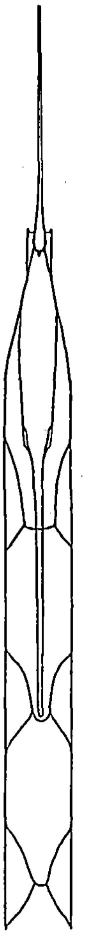

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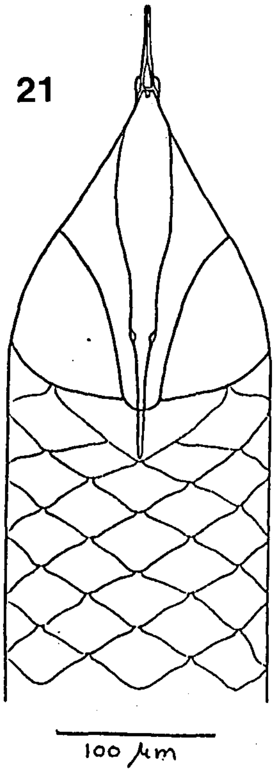

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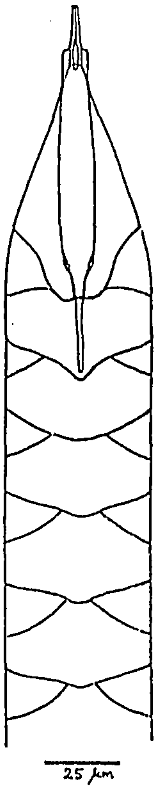

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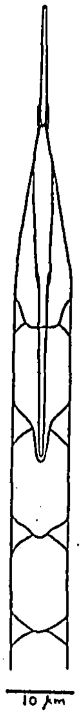
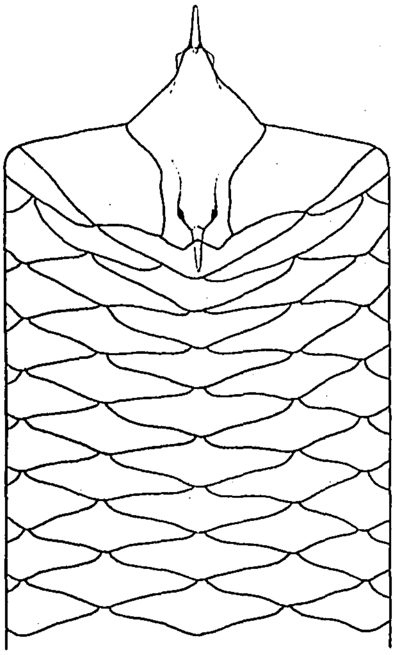


Plate 5

Fig. 24 a. **Rh. debyana.** Theca in ventral view.
Fig. 24 b. **Rh. debyana.** Distal part of theca in dorsal view.
Fig. 25. **Rh. debyana.** Valve, valvocopulae, first ventral copula and two large lateral copulae as seen in the direction of the pervalvar axis.
Fig. 26. **Rh. crassa.** Cell. Note difference in segmentation in hypotheca and epitheca.
Fig. 27. **Rh. crassa.** Copular areolae. Drawing of made from TEM negatives.



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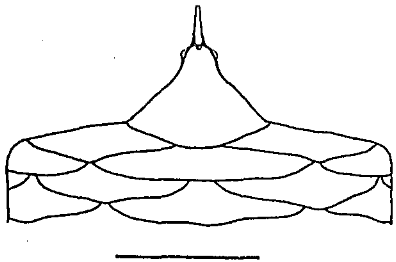

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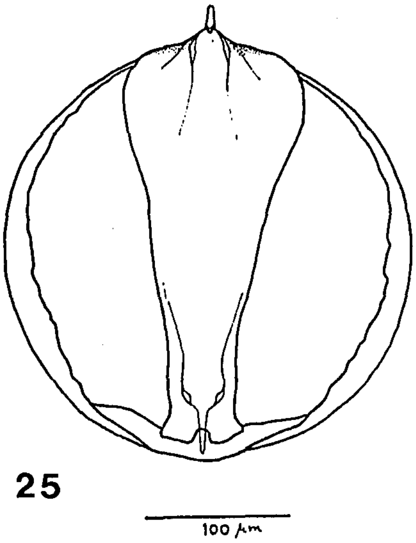

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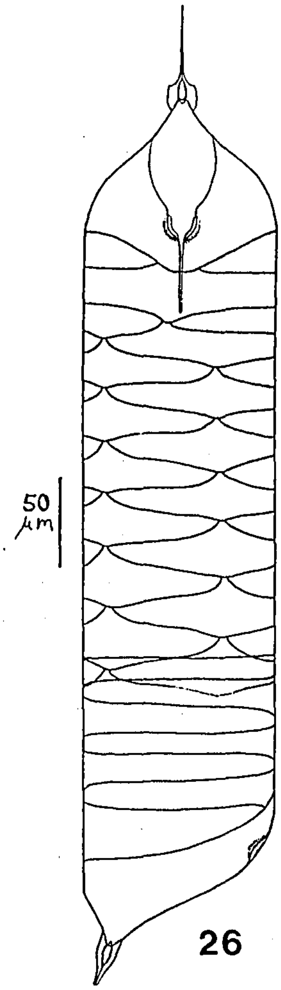

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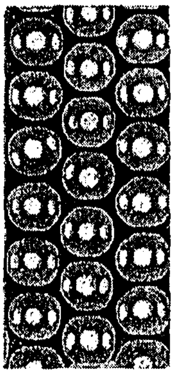

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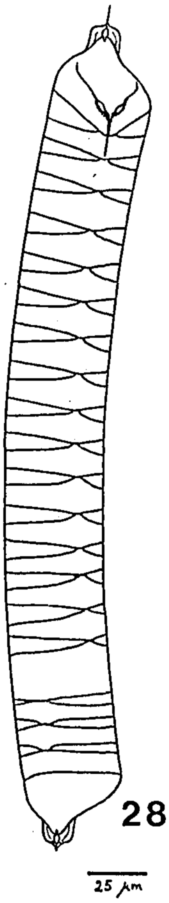
Plate 6

Fig. 28. ***Rh. sima* f. *sima.*** Curved cell.
Fig. 29. ***Rh. sima* f. *silicea.*** Distal part of theca.
Fig. 30. ***Rh. temperei.*** Distal part of theca. Note asymmetrical valve.
Fig. 31 a. ***Rh. acuminata.*** Theca in ventral view.
Fig. 31 b. ***Rh. acuminata.*** Process.
Fig. 31 c. ***Rh. acuminata.*** Theca in dorsal view.
Fig. 32. ***Rh. bergonii.*** Theca in ventral view.
Fig. 33. ***Rh. bergonii.*** Theca in ventral view.



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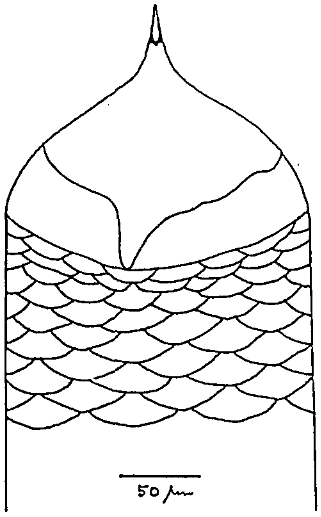

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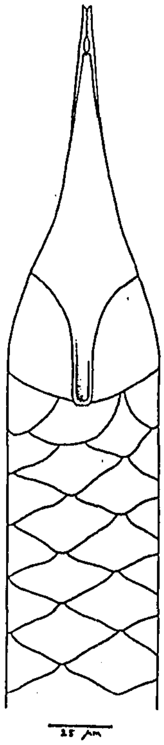

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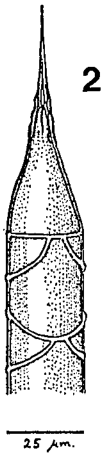

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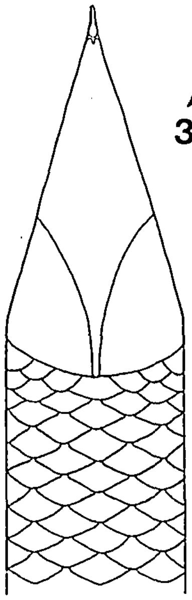

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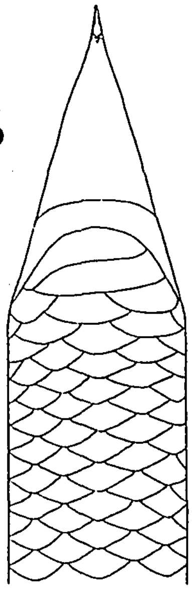

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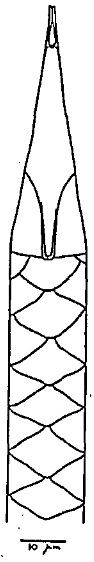


33

Plate 7

Fig. 34. ***Rh. hyalina.*** Distal part of two thecae, in ventral view (above) and lateral view (below).

Fig. 35. ***Rh. simplex.*** Cell with valves of different shape.

Fig. 36 a. ***Rh. striata.*** Theca in lateral view.

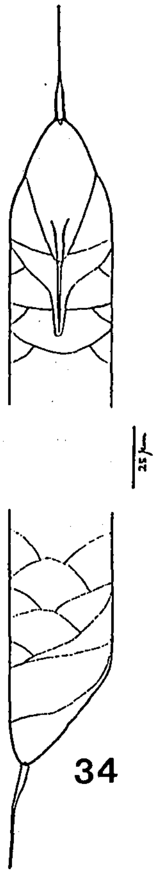
Fig. 36 b. ***Rh. striata.*** Theca in ventral view.

Fig. 36 c. ***Rh. striata.*** Copula showing orientation of striae.

Fig. 37 a. ***Rh. ostenfeldii.*** Theca in ventral view.

Fig. 37 b. ***Rh. ostenfeldii.*** Girdle segment opened up.

Fig. 37 c. ***Rh. ostenfeldii.*** Middle part of copula showing orientation of striae.



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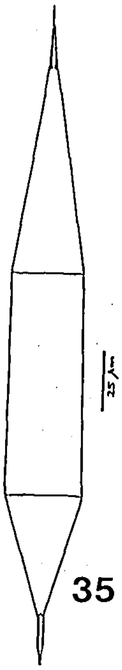

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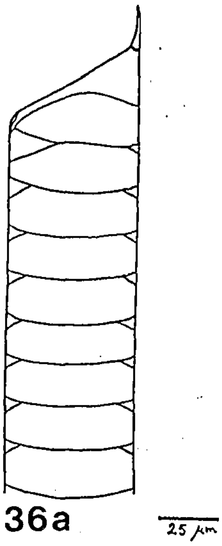

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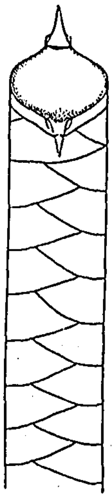

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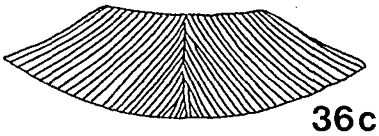

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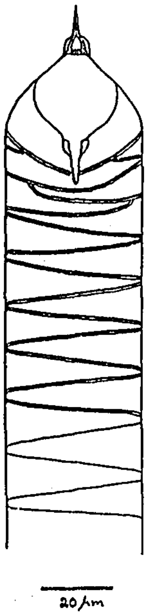

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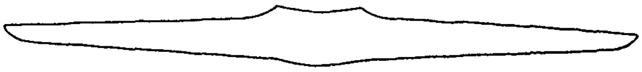

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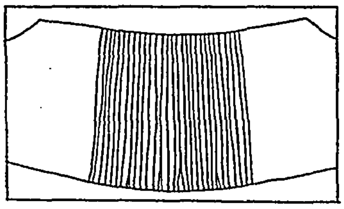
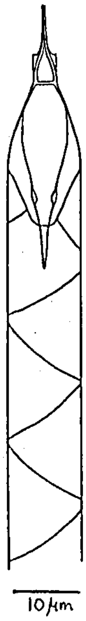


37c

Plate 8

Fig. 38 a. ***Rh. fallax.*** Distal part of theca in ventral view.
Fig. 38 b. ***Rh. fallax.*** Girdle segment opened up, showing orientation of striae.
Fig. 39 a. ***Rh. decipiens.*** Distal part of theca in ventral view.
Fig. 39 b. ***Rh. decipiens.*** Girdle segment opened up, showing orientation of striae.
Fig. 40. ***Pseudosolenia calcar-avis.*** Distal part of hypotheca and epitheca.
Fig. 41. ***P. calcar-avis.*** Theca.
Figs 42-46. ***P. calcar-avis.*** Valves. Note variation in shape.



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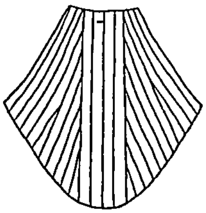

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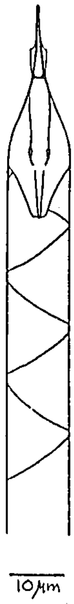

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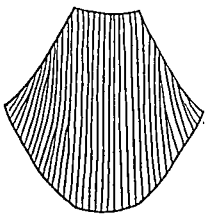

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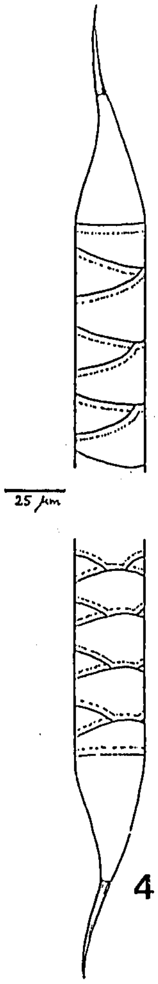

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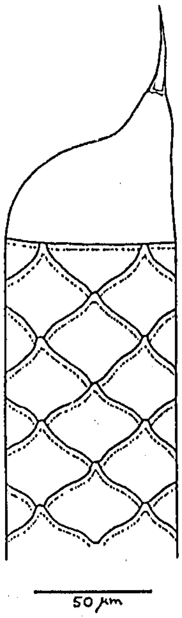

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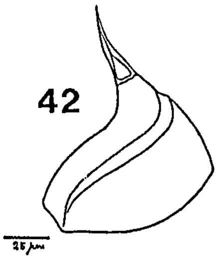

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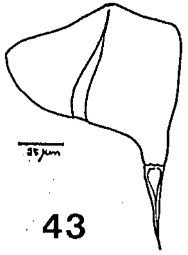

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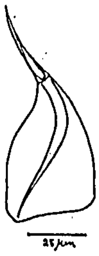

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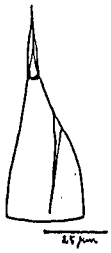

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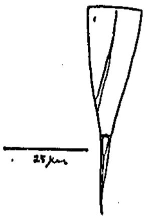


46

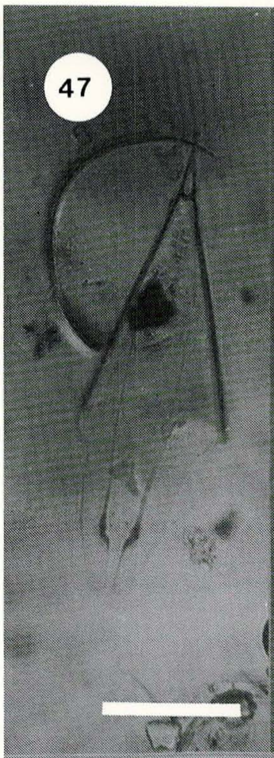
Plate 9

RHIZOSOLENIA STYLIFORMIS

LM: Figs 47-53. TEM: Figs 54-56.

Fig. 47.	(124).	Valve in ventral view. Note position of otaria.
Fig. 48.	(124).	Part of valve in dorsal view. Note position of otaria.
Fig. 49.	(144)	Valve with valvocopula in dorsal view. Note long process.
Fig. 50.	(109).	Part of cell in lateral view.
Fig. 51.	(002).	Part of cell in dorsal view.
Fig. 52.	(002).	Part of cell in lateral view. Note shape of process.
Fig. 53.	(109).	Part of dessicated cell. Note overlapping dorsal and ventral copulae.
Fig. 54.	(002).	Part of copula. Note outline of areolae and size of foramina. Cf. fig. 55.
Fig. 55.	(002).	Part of copula. Note outline of areolae, size of foramina and positions of velum pores. Cf. fig. 54.
Fig. 56.	(002).	Part of valve.

Scales: Fig. 50 = 100 µm. Figs 47, 51-53 = 50 µm. Figs 48, 49 = 25 µm.
Figs 54-56 = 1 µm.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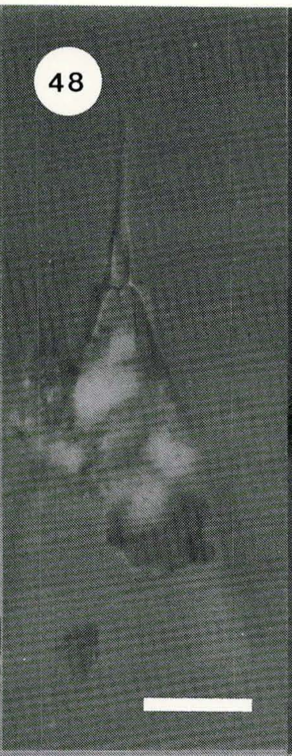
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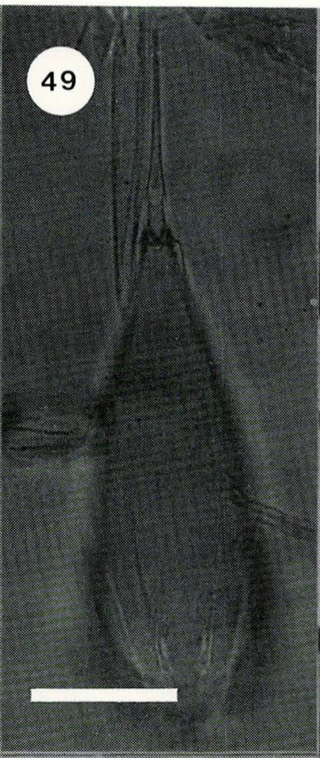
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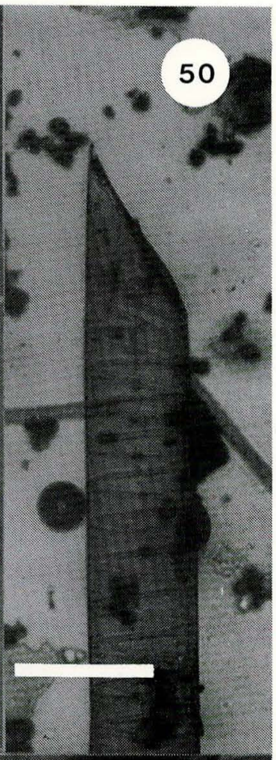
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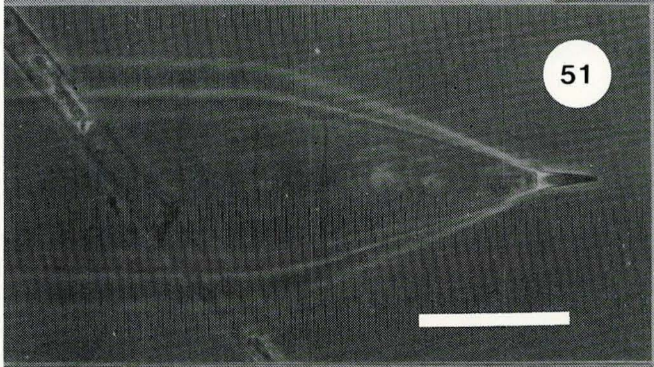
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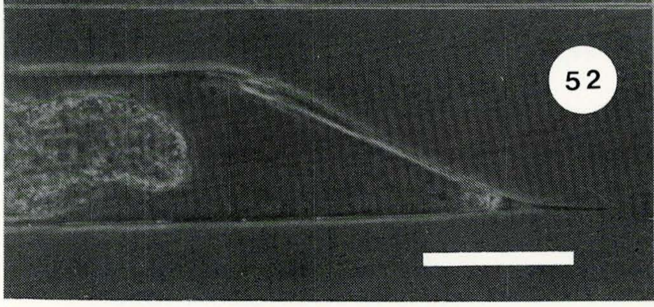
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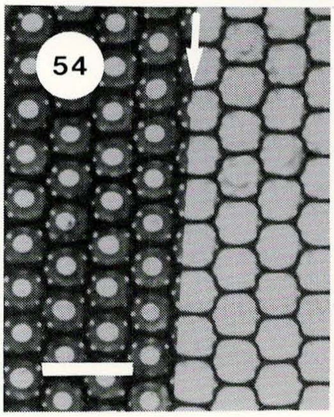
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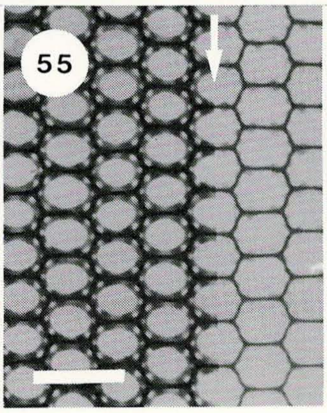
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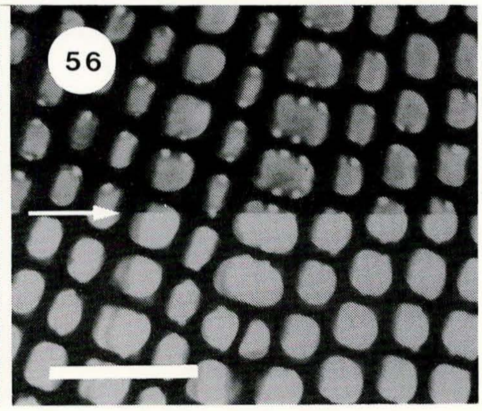

56

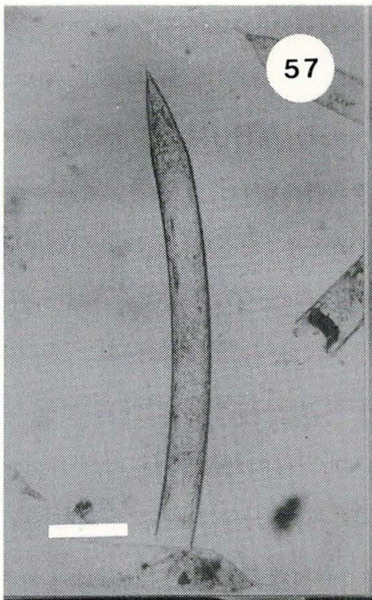
Plate 10

RHIZOSOLENIA CURVATA

LM: Figs 57-59. SEM: Figs 60, 61. TEM: Figs 62, 63.

Fig. 57.	(031).	Part of cell in dorsiventral view.
Fig. 58.		Detail of fig. 57. Note shape and position of otaria.
Fig. 59.	(031).	Valve in ventral view. Note shape and position of otaria.
Fig. 60.	(031).	Part of frustule in ventral view.
Fig. 61.	(031).	Distal part of frustule in ventral view showing valve, valvocopula and part of first ventral copula.
Fig. 62.	(036).	Parts of two copulae. Note long transverse wall segments and short lateral wall segments between areolae.
Fig. 63.	(031).	Part of copula. Note positions of velum pores.

Scales: Fig. 57 = 100 µm. Figs 58, 59 = 25 µm. Figs 62, 63 = 1 µm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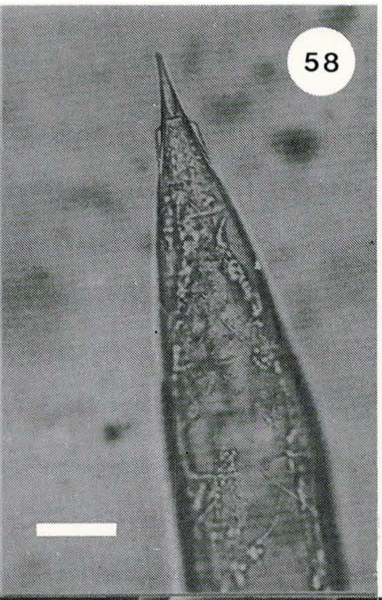
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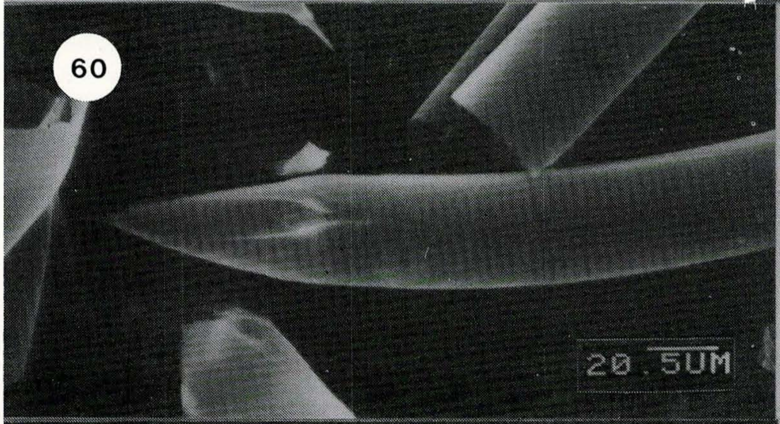
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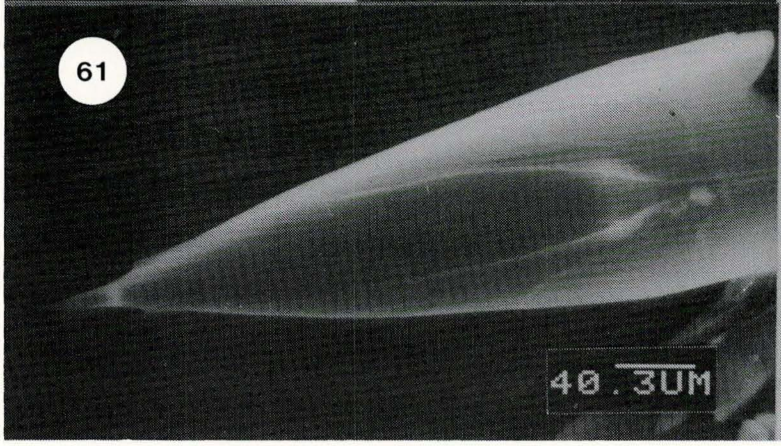
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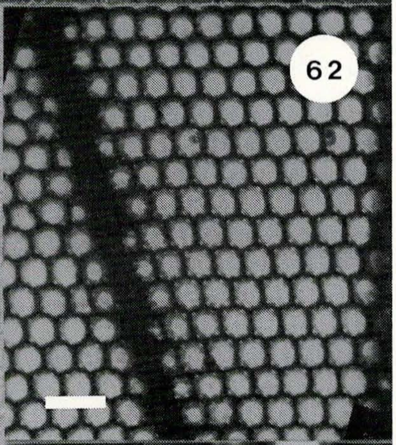
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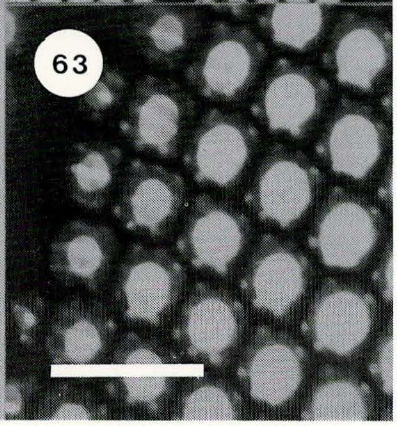

63

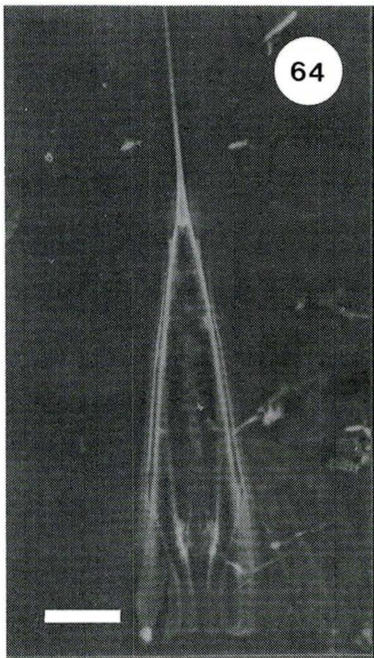
Plate 11

RHIZOSOLENIA ACICULARIS

LM: Fig. 64. SEM: Fig. 65. TEM: Figs 66-69.

Fig. 64.	(090).	Valve and valvocopula in ventral view. Note length of process and position of otaria.
Fig. 65.	(090).	Valve in dorsal view. Note position of otaria.
Fig. 66.	(088).	Part of valve. Note outline of otaria.
Fig. 67.	(090).	Part of first ventral copula. Note impression of sister-cell process.
Fig. 68.		Detail of fig. 67. Note long transverse wall segments between areolae within a colmn.
Fig. 69.	(088).	Part of copula. Note positions of velum pores. Arrowheads indicate direction of pervalvar axis.

Scales: Fig. 64 = 10 µm. Figs 66, 67 = 5 µm. Figs 68, 69 = 1µm.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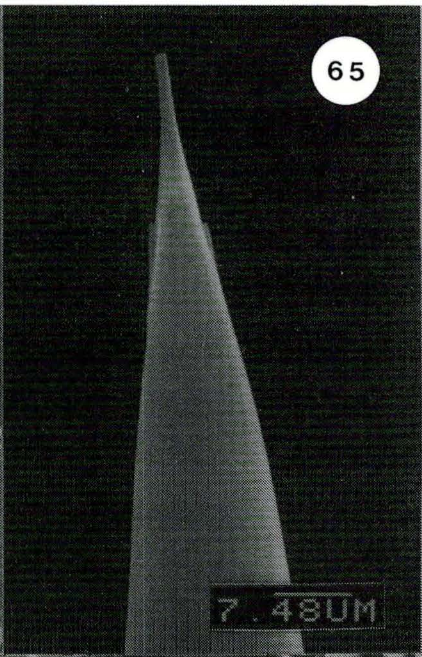
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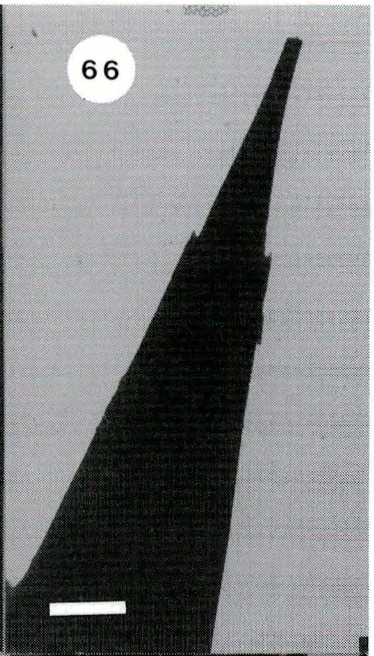
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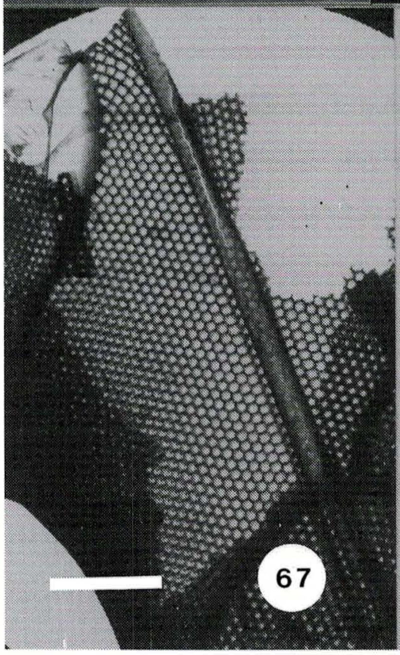
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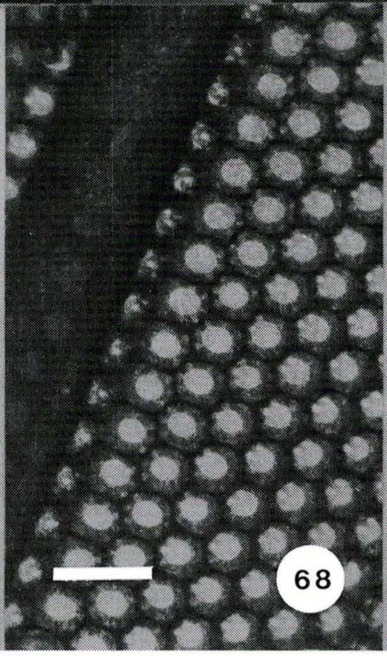
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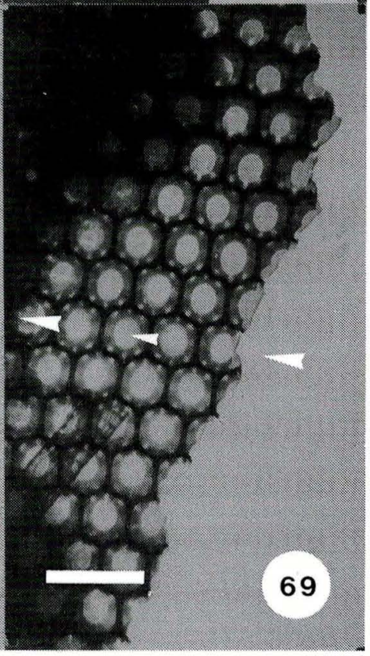

69

Plate 12

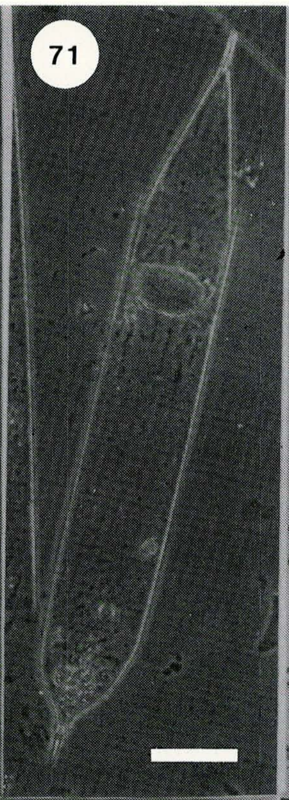
RHIZOSOLENIA POLYDACTYLA

LM: Figs 70-73. SEM: Figs 74, 75. TEM: Figs 76-79.

Fig. 70.	(031).	*Rh. polydactyla* f. *polydactyla*. Broad cells in lateral view. Note short girdle segments.
Fig. 71.	(031).	Heterothecate cell.
Fig. 72.	(031).	Newly divided cell. Upper valve intermediate between f. *polydactyla* and f. *squamosa*. Lower valves characteristic of f. *squamosa*.
Fig. 73.	(031).	f. *squamosa*. Note silica ridges on valve apex.
Fig. 74.	(031).	f. *polydactyla*. Valve apex in dorsal view. Note claspers of sister cell clasping otaria (arrowhead).
Fig. 75.	(031).	f. *squamosa*. Upper part of valve. Note unevenly silicified valve apex and process base.
Fig. 76.	(037).	f. *polydactyla*. Part of copula. Note velum pores.
Fig. 77.	(037).	f. *polydactyla*. Process with otaria. Note process tip and shape of otaria.
Fig. 78.	(031).	f. *squamosa*. Parts of copulae. Note variation in size of areolae.
Fig. 79.	(038).	f. *polydactyla*. Part of valve.

Scales: Figs 70-72 = 50 µm. Fig. 73 = 25 µm. Fig. 77 = 5 µm.
Figs 76, 78, 79 = 1 µm.

70



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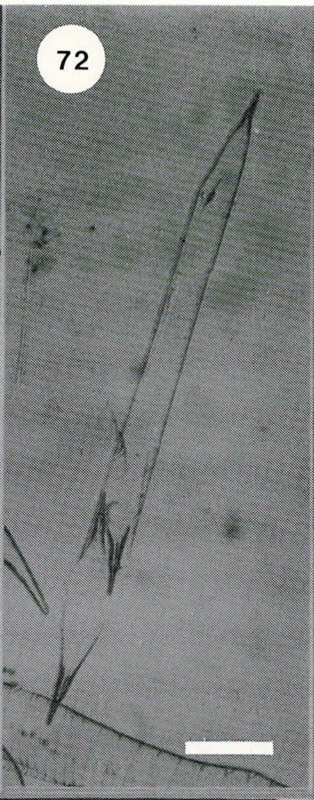

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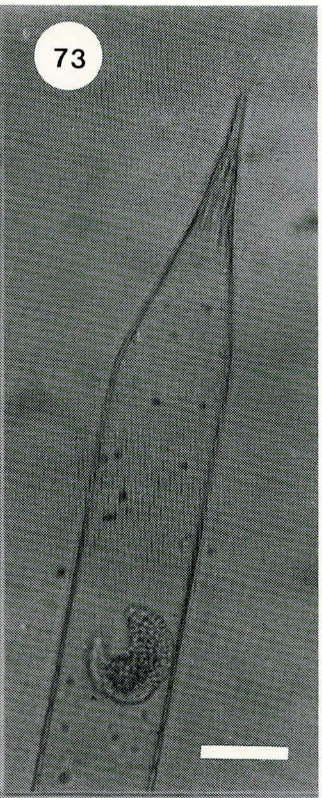

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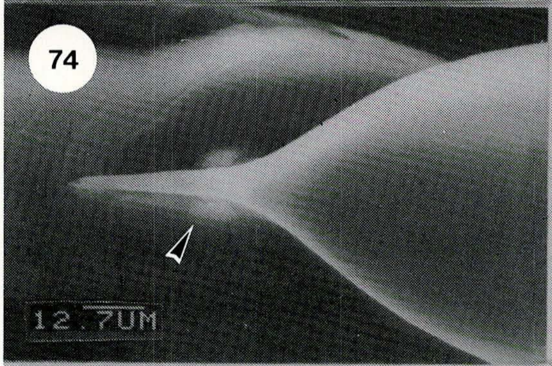

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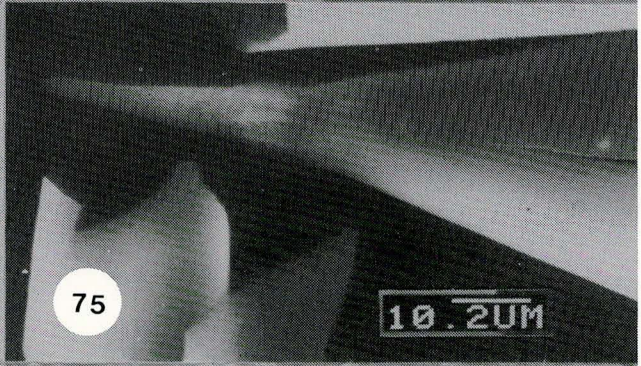

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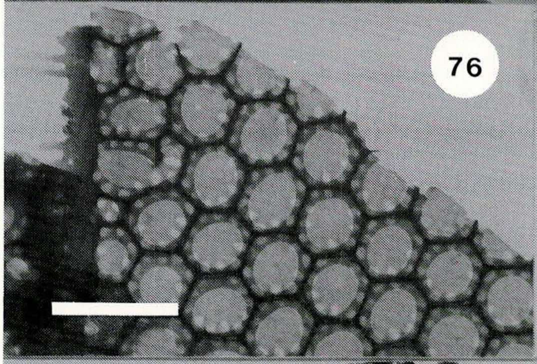

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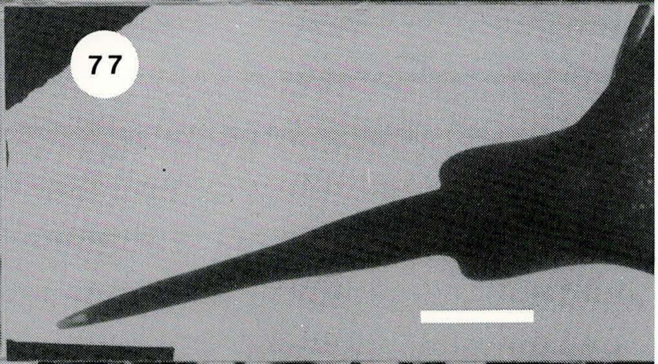

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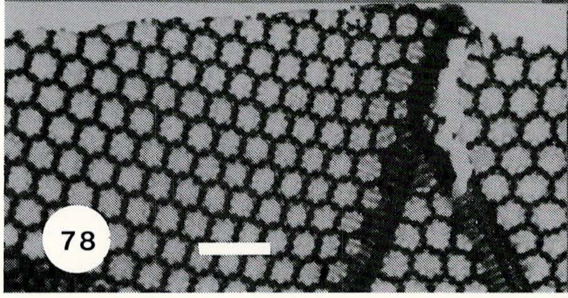

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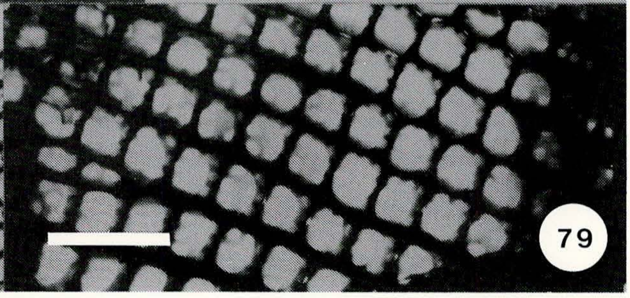


79

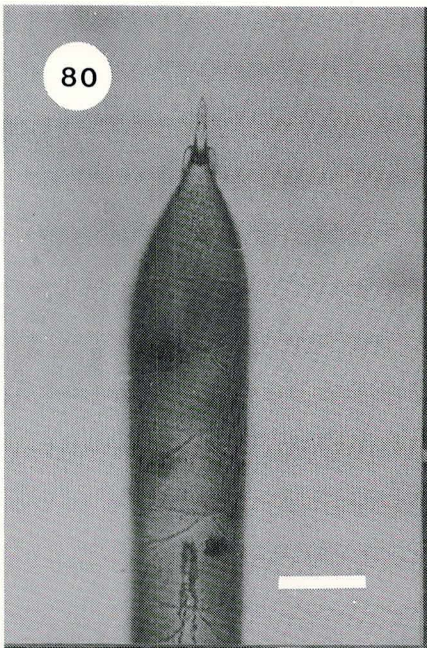
Plate 13

RHIZOSOLENIA BOREALIS

LM: Figs 80-82. TEM: Figs 83-87.

Fig. 80.	(142).	Part of cell in dorsal view.
Fig. 81.	(001).	Valve in ventral view.
Fig. 82.	(001).	Process and otaria. Note process tip and shape of otaria.
Fig. 83.	(001).	Part of valve.
Fig. 84.	(001).	Labiate structure in surface view.
Fig. 85.	(001).	Parts of three copulae. Note fringed edge of advalvar margin and variation in size of foramina.
Fig. 86.	(093).	Part of copula. Note edge of abvalvar margin.
Fig. 87.	(093).	Part of copula. Note hexagonal outline of areolae and position of velum pores.

Scales: Fig. 80 = 25 µm. Fig. 81. = 10 µm. Fig. 82 = 5 µm. Figs 85, 86 = 2 µm.
Figs 83, 84, 87 = 1 µm.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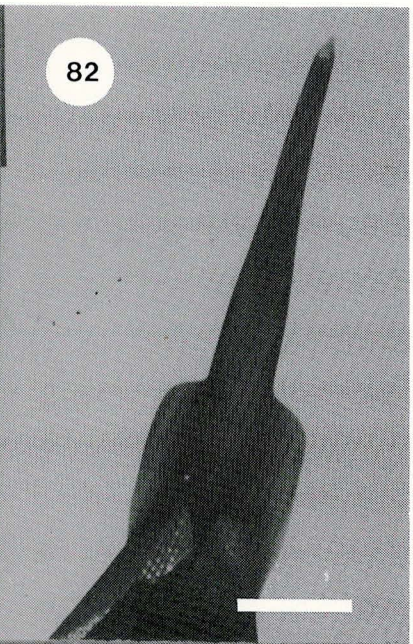
81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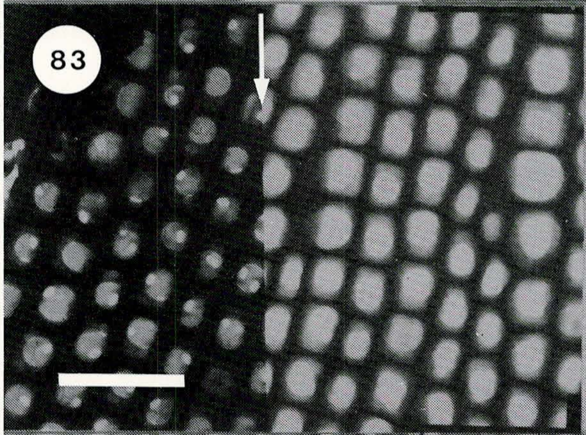
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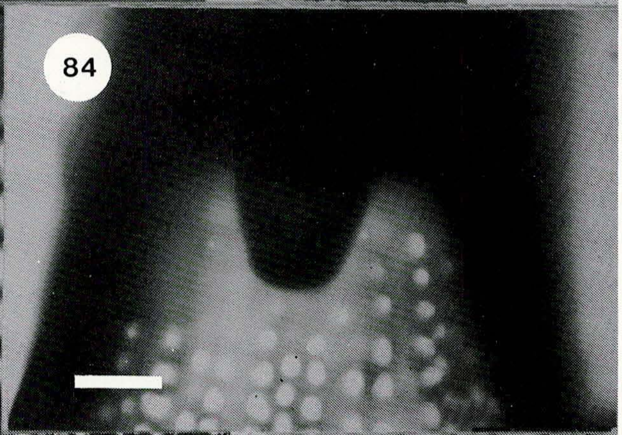
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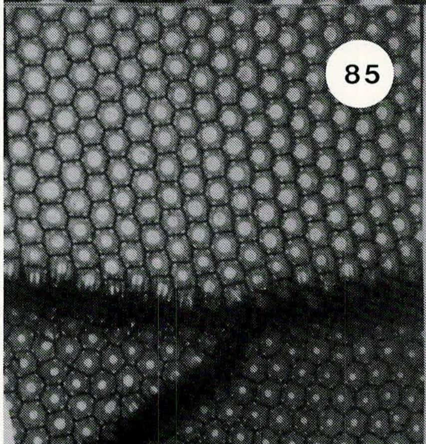
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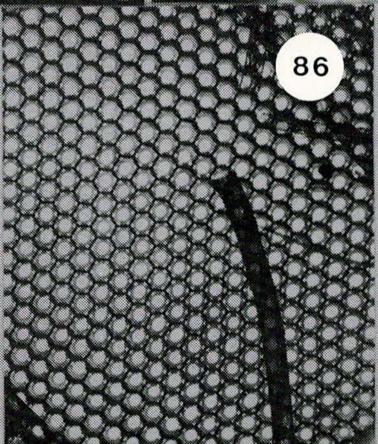
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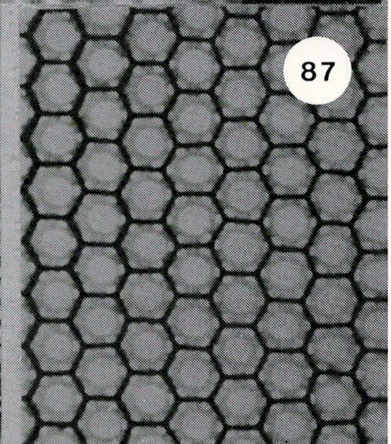

87

Plate 14

RHIZOSOLENIA FORMOSA (Figs 88-93)

Rhizosolenia sp. (Figs 94, 95)

LM: Figs 88-91, 94. SEM: Figs 92, 93, 95.

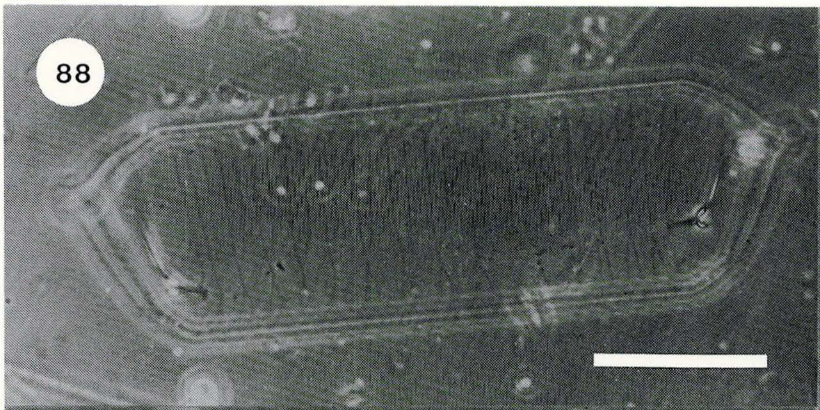
Rhizosolenia formosa.

Fig. 88.	(188).	Oblique ventral view of cell. Note shape of girdle segments.
Fig. 89.		Same cell as in fig. 88. Dorsal side in focus.
Fig. 90.	(135).	Dessicated frustule. Note shape of broken valve (arrowheads).
Fig. 91.		Part of the frustule in fig. 90.
Fig. 92.	(074).	Proximal protruding part of ventral side of valve. Note claspers.
Fig. 93.	(074).	Distal part of broken valve. Note shape of process and shape and position of otaria.

Rhizosolenia sp.

Fig. 94.	(057).	Part of cell.
Fig. 95.	(068).	Distal part of cell. Note shape and position of otaria.

Scales: Figs 88-90, 94 = 100 µm. Fig. 91 = 50 µm.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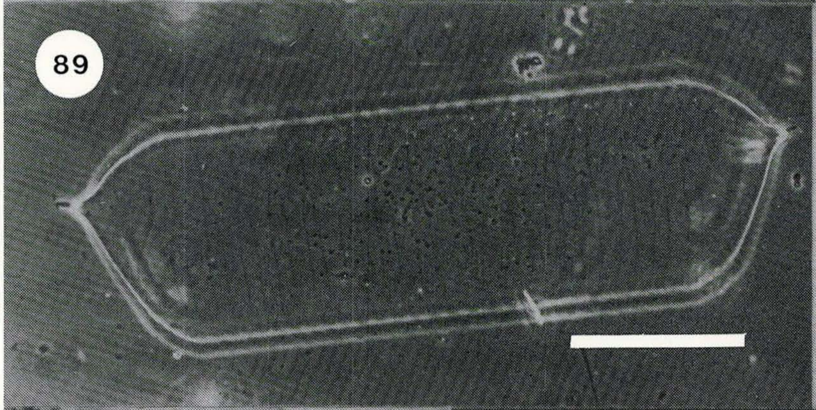
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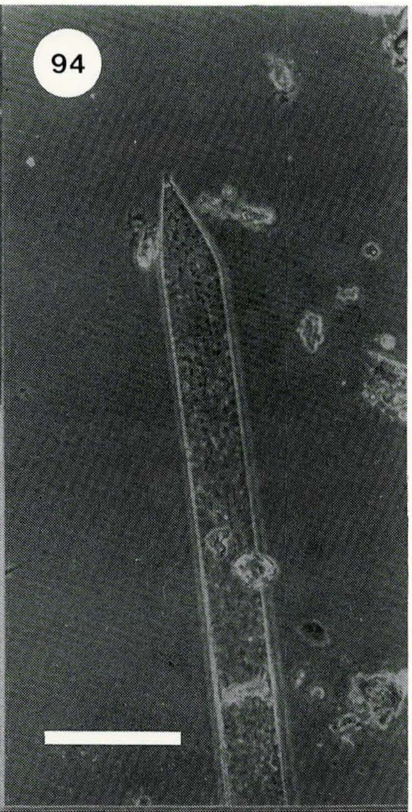
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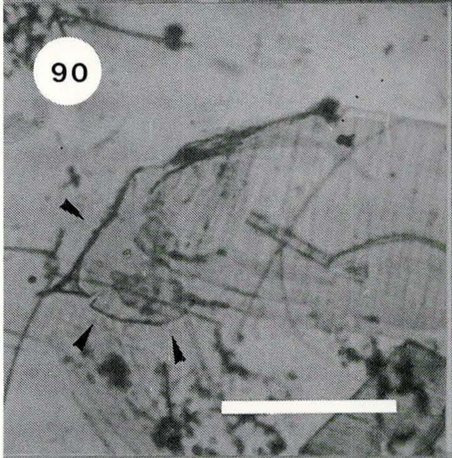
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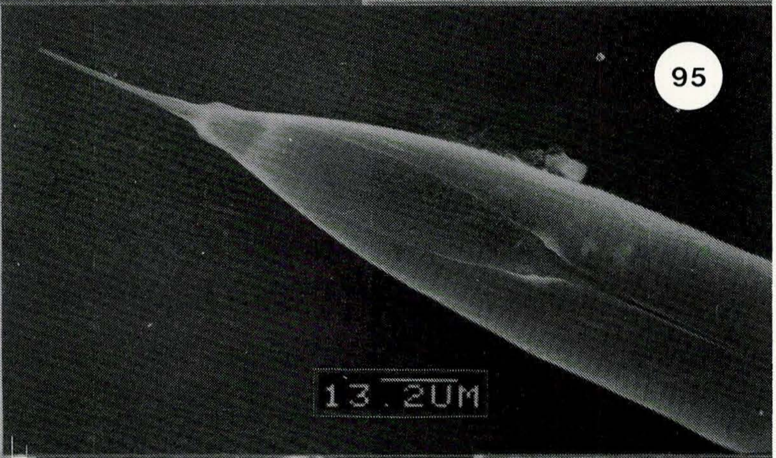
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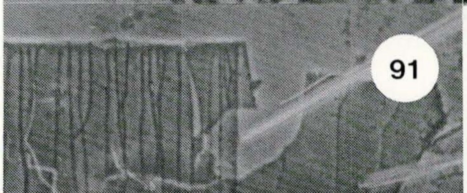

91


92


93

Plate 15

RHIZOSOLENIA FORMOSA (Figs 96-99)

Rhizosolenia sp. (Figs 100, 101)

TEM: Figs 96-101.

Rhizosolenia formosa.

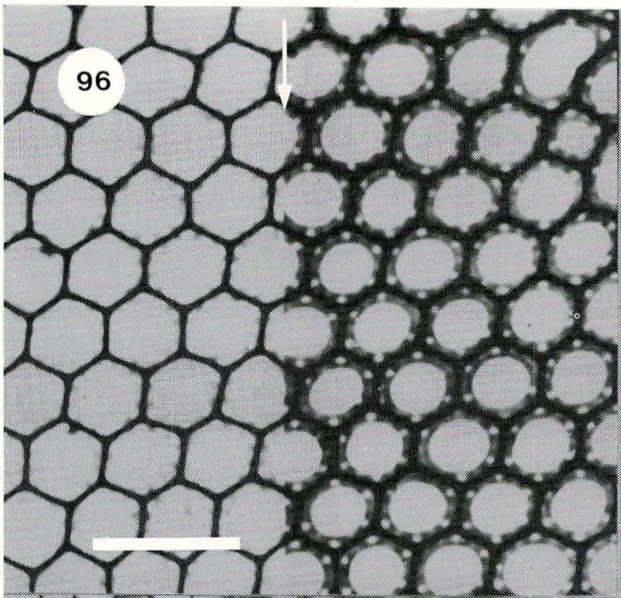
Fig. 96.	(096).	Part of copula. Note shape of areolae and position of velum pores.
Fig. 97.	(023).	Part of copula.
Fig. 98.	(069).	Parts of two copulae.
Fig. 99.	(023).	Part of valve.

Rhizosolenia sp.

Fig. 100.	(075).	Part of copula. Cf. figs 96-98.
Fig. 101.	(075).	Part of valve. Cf. fig. 99.

Different exposures on each side of arrow.

Scales: Fig. 101 = 2 µm. Figs 96-100 = 1 µm.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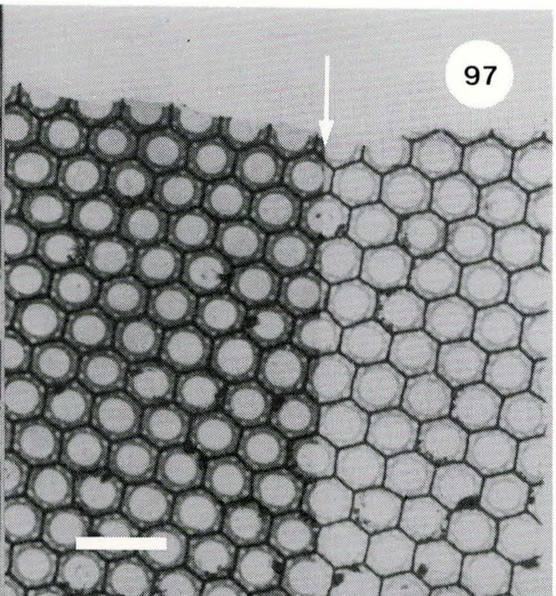
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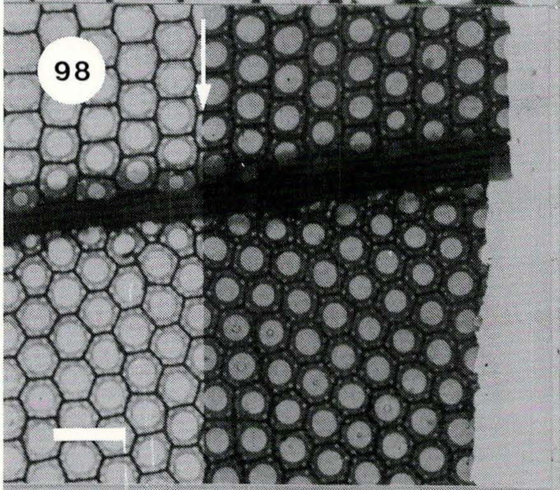
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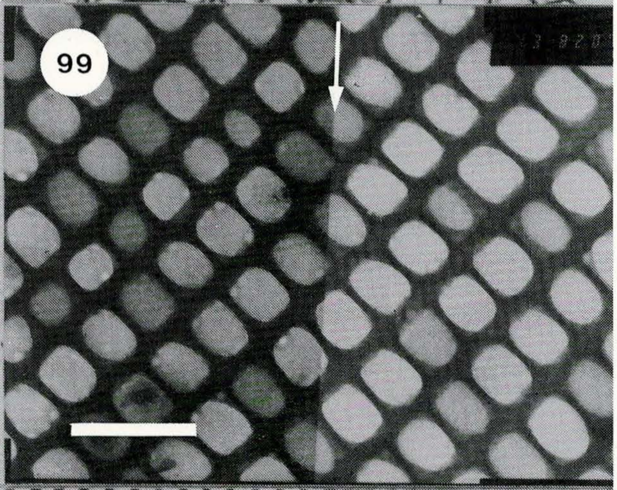
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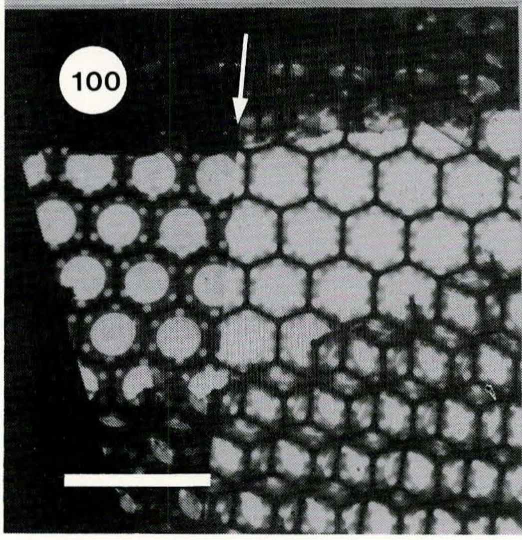
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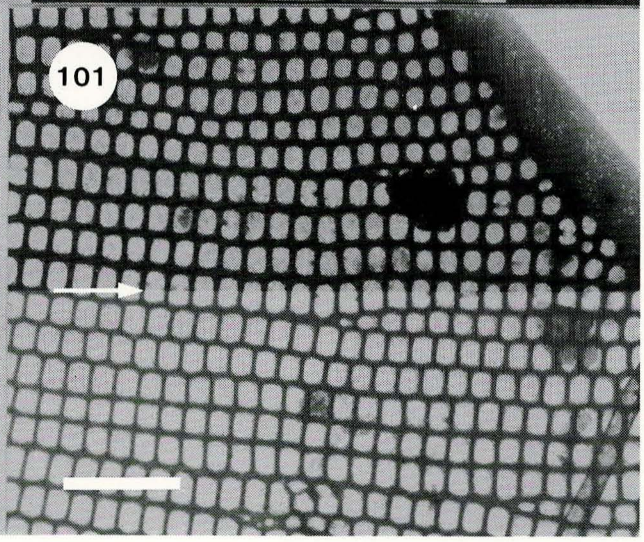
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Plate 16

RHIZOSOLENIA CASTRACANEI

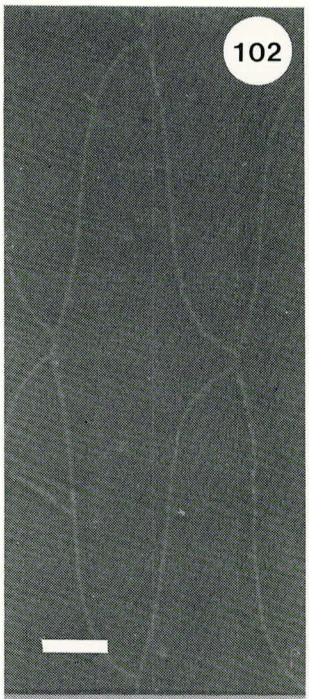
LM: Figs 102-104, 106. SEM: 105, 107-109. TEM: 110, 111.

Figs 102-104.	(091).	*Rh. castracanei* var. *castracanei.* Copulae from three cells. Note areolar pattern and variation in outline.
Fig. 105.	(028).	var. *neglecta.* Part of frustule. Note size of areolae.
Fig. 106.	(078).	var. *neglecta.* Distal part of cell in dorsiventral view. Note shape and position of otaria.
Fig. 107.	(028).	var. *neglecta.* Ventral view of distal part of frustule. Note shape and position of otaria.

Rh. castracanei var. *castracanei.*

Fig. 108.	(074).	Proximal part of valve. Note bilobed median margin.
Fig. 109.	(074).	Fragments of two copulae: above, inner surface; below, outer surface. Note wall segments (entire) between areolae at broken edge of upper fragment. Note also that the silicious layer (below) penetrated by the velum pores is continuous.
Fig. 110.	(087).	Parts of valve and valvocopula. Note difference in areolar size and structure in valve (upper part of figure) and valvocopula.
Fig. 111.	(080).	Parts of copulae. Note edge of abvalvar margin of upper copula (entire) and fringed edge of advalvar margin of lower copula.

Scales: Fig. 106 = 25 µm. Figs 102-104 = 10 µm. Fig. 110 = 5 µm.
Fig. 111 = 2 µm.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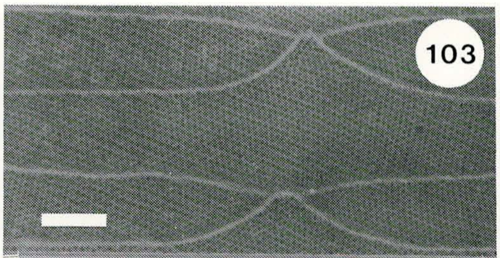
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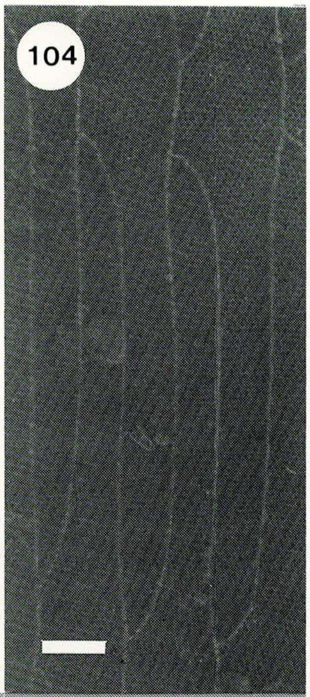
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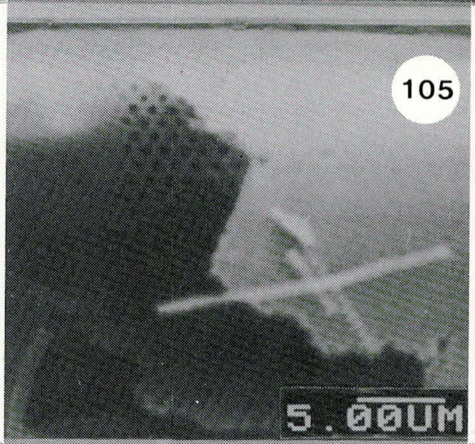
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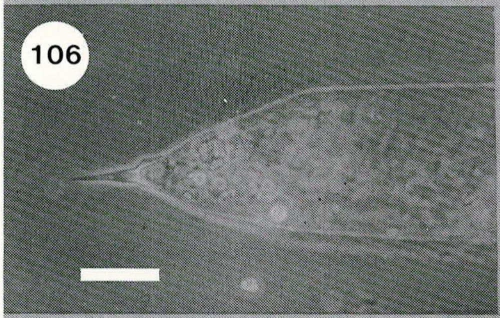
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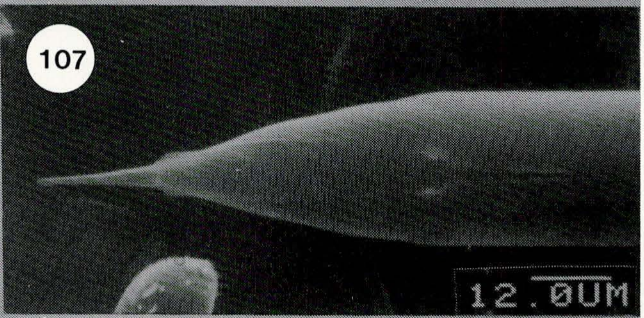
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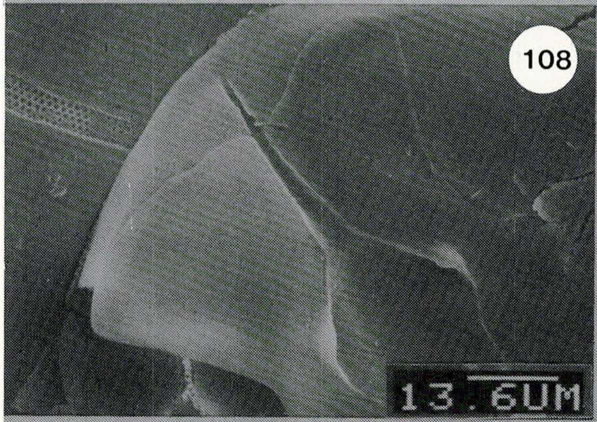
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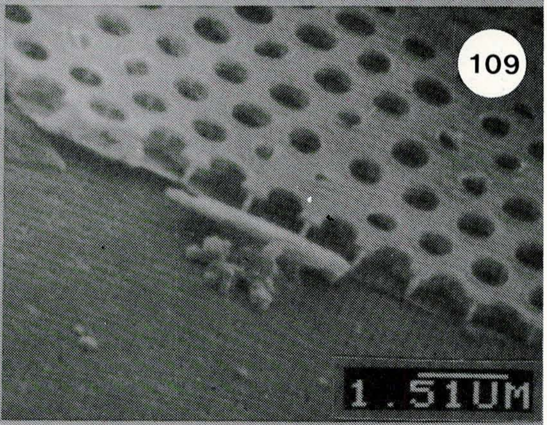
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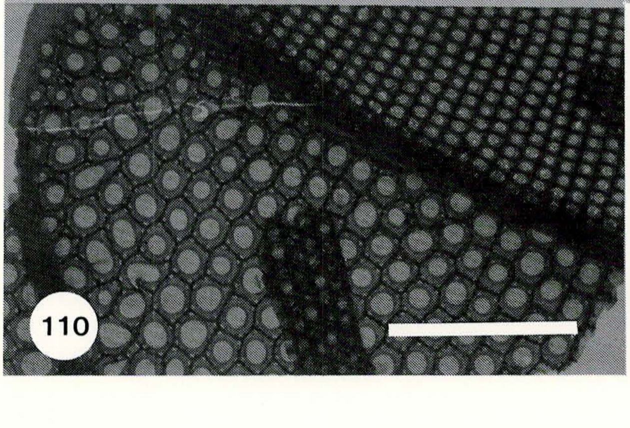
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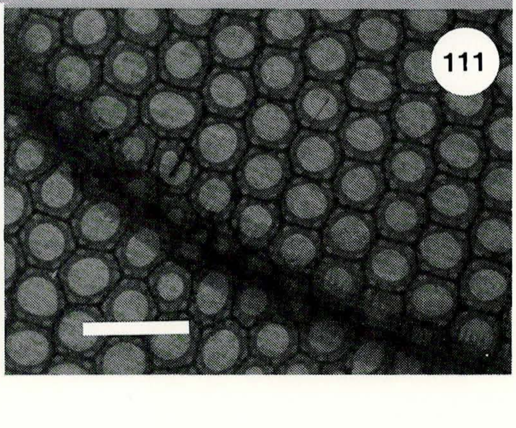
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Plate 17

RHIZOSOLENIA HEBETATA (Figs 112, 113, 117, 118)

RHIZOSOLENIA ANTENNATA (Figs 114-116, 119, 120)

LM: Figs 112-115. SEM: Figs 117, 119. TEM: Figs 116, 118, 120.

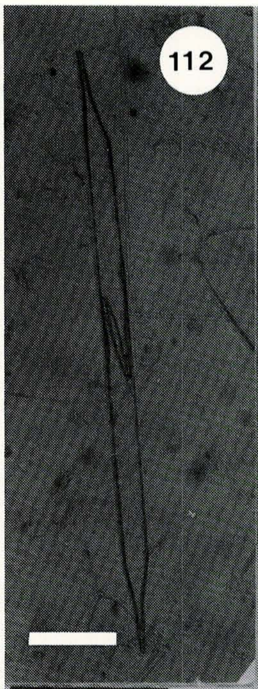
Fig. 112. (094). *Rh. hebetata* f. *hebetata*. A pair of daughter cells held together by the girdle of the mother cell.
Fig. 113. Detail of fig. 112. Note shape of process.

Fig. 114. (038). *Rh. antennata* f. *semispina*. Distal part of cell. Note shape and position of otaria.
Fig. 115. (038). *Rh. antennata* f. *antennata*. Valve.
Fig. 116. (033). *Rh. antennata* f. *semispina*. First ventral copula. Note impression of sister-cell process and protruding abvalvar margin.

Fig. 117. (006). *Rh. hebetata* f. *semispina*. Valve in ventral view. Note small pointed otaria.
Fig. 118. (006). *Rh. hebetata* f. *semispina*. Part of copula. Note velum pores.

Fig. 119. (038). *Rh. antennata* f. *antennata*. Distal part of cell.
Fig. 120. (038). *Rh. antennata* f. *antennata*. Part of copula. Note velum pores.

Scales: Figs 122, 114 = 25 µm. Figs 113, 115-117 = 10 µm. Figs 118, 120 = 1 µm.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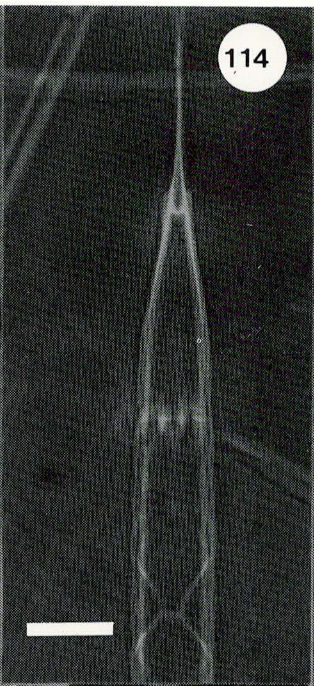
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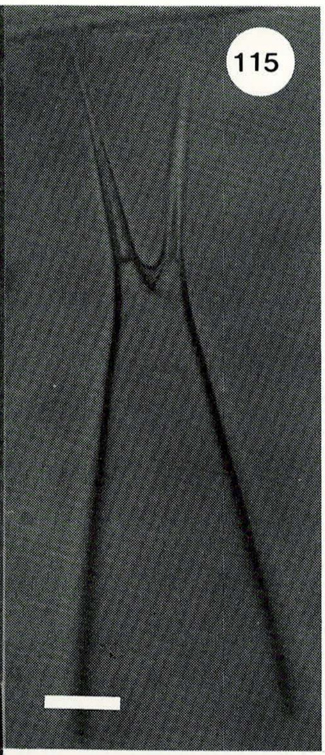
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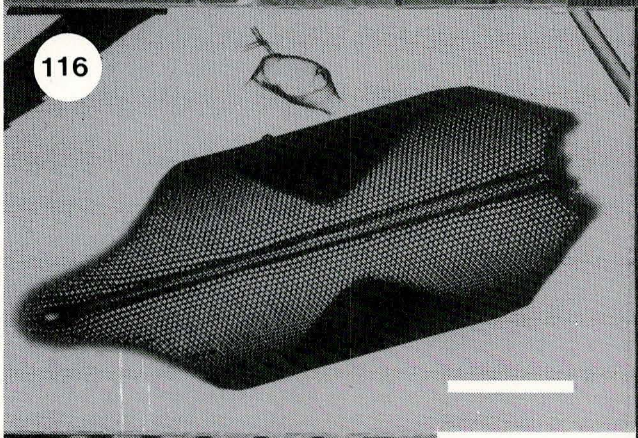
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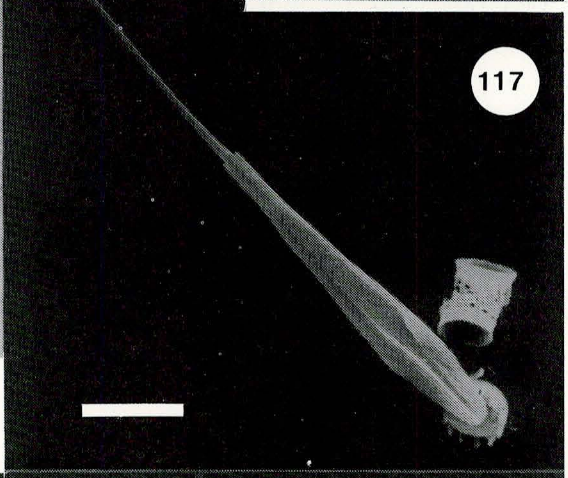
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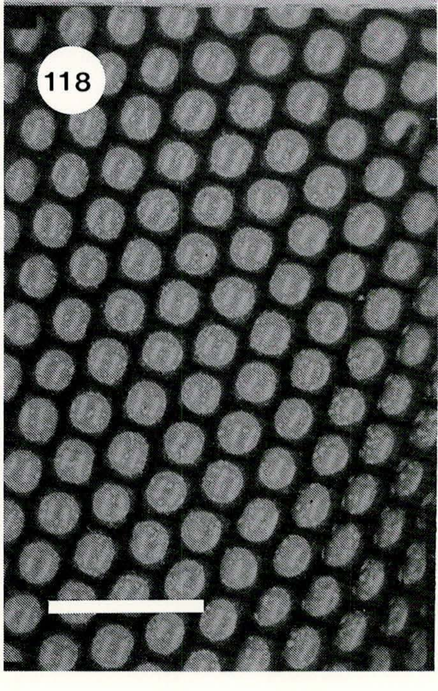
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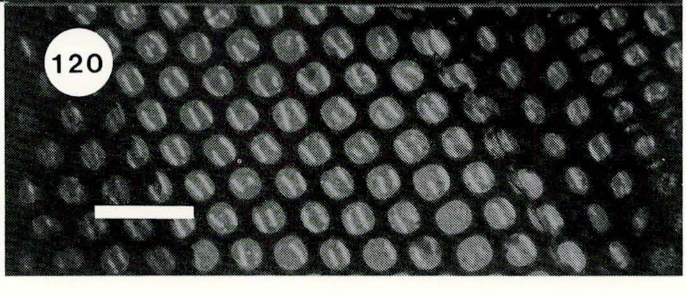
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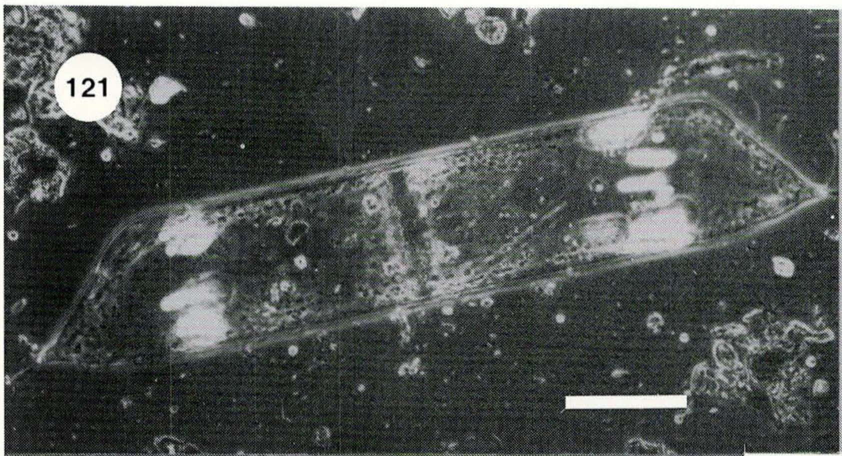
Plate 18

RHIZOSOLENIA CLEVEI

LM: Figs 121-123. SEM: Fig. 124. TEM: Figs 125-127.

Fig. 121. (Ko Phuket, 19.2 1980). *Rh. clevei* var. *clevei.* Cell with *Richelia intracellularis* filaments at both ends.
Fig. 122. (046) var. *clevei.* Part of cell with *Richelia intracellularis* filaments. Note shape of girdle segments.
Fig. 123. (Caribbean Sea, 17.2 1973). var. *communis.* Part of cell with *Richelia intracellularis* filaments.
Fig. 124. (083). var. *communis.* Parts of two cells. Compare length of processs with impression of sister-cell process in upper cell. Note shape and position of otaria.
Fig. 125. (077). var. *clevei.* Part of copula. Note variation in arolar size and fringed advalvar edge of adjacent copula.
Fig. 126. (081). var. *communis.* Part of copula. Note variation in areolar size.
Fig. 127. (022). var. *communis.* Part of copula. Note edge of abvalvar margin (entire).

Scales: Fig. 121 = 100 µm. Figs 122, 123 = 25 µm. Figs 125-127 = 1 µm.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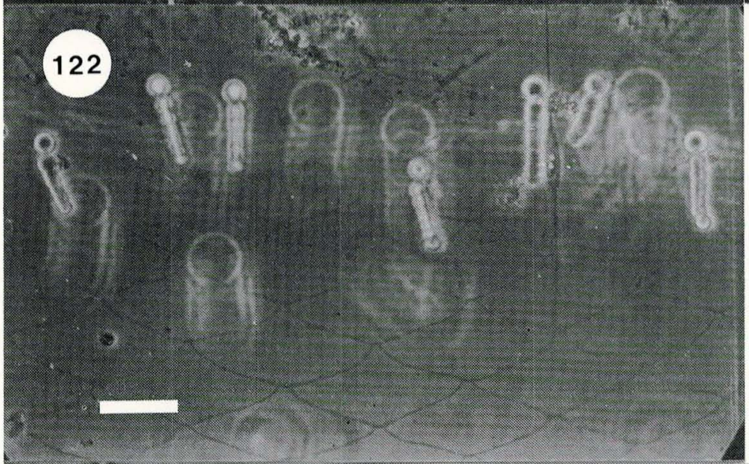
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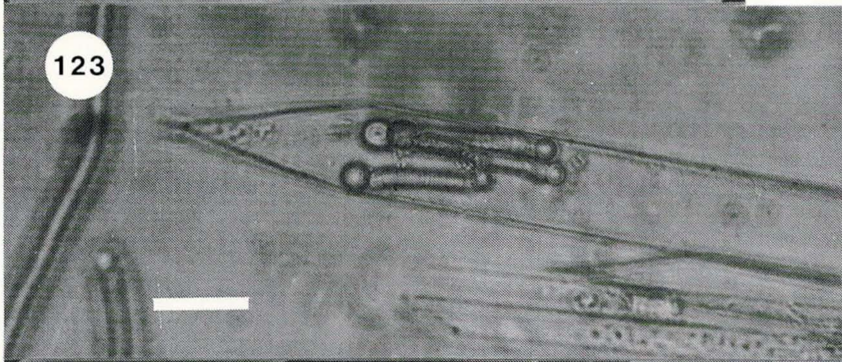
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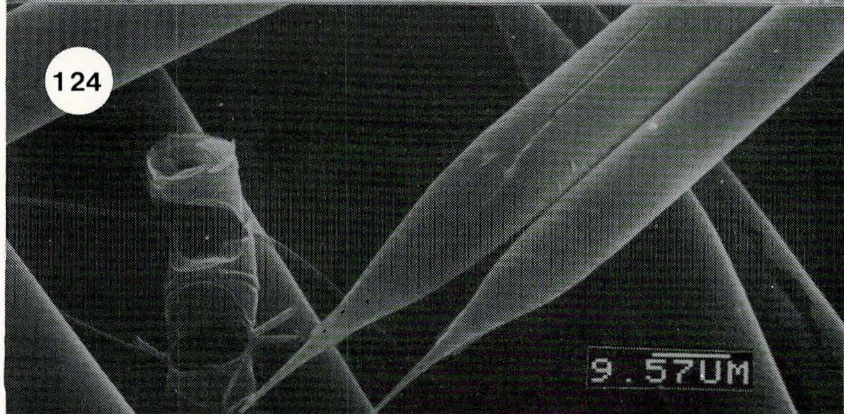
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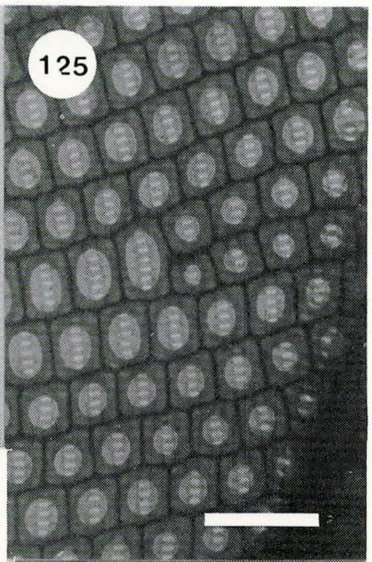
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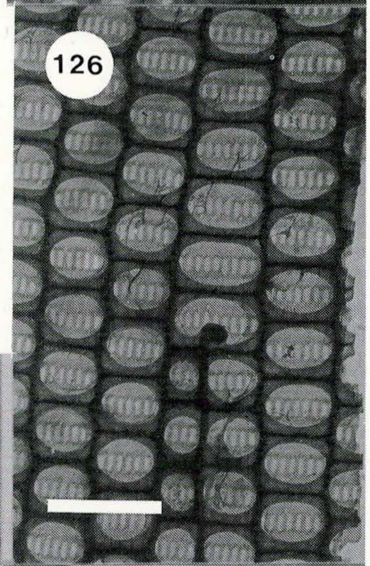
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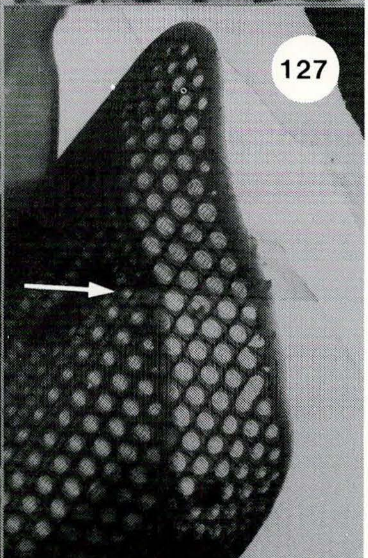
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Plate 19

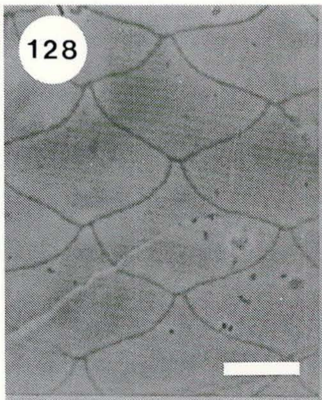
RHIZOSOLENIA DEBYANA

LM: Figs 128-130, 134. SEM: Figs 133, 135. TEM: Figs 131, 132, 136-138.

Figs 128-130. (073). Copulae from three cells. Note variation in size and outline.

Fig. 131.	(075).	Part of copula. Note outline of areolae and size of foramina.
Fig. 132.	(023).	Part of copula. Note outline of areolae and size of foramina.
Fig. 133.	(074).	Valve showing inner surface. Note strap-shaped ventral part and bilobed median ventral margin.
Fig. 134.	(073).	Copula.
Fig. 135.	(023).	Part of valvocopula (left) and valve (right). Note fringed edge of of advalvar margin of valvocopula.
Fig. 136.	(023).	Areola. Note pores in velum.
Fig. 137.	(023).	Part of copula. Note outline of areolae and size of foramina.
Fig. 138.	(075).	Part of valvocopula (left) and valve (right).

Scales: Figs 128-130, 134 = 25 µm. Fig. 138 = 2 µm. Figs 131, 132 = 1 µm.
Fig. 137 = 0.5 µm. Fig. 136 = 0.2 µm.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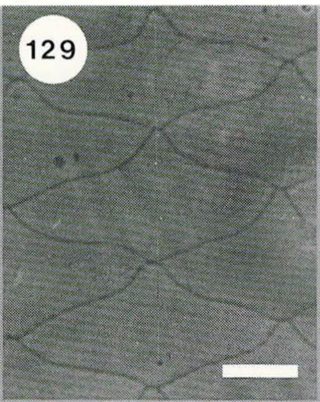
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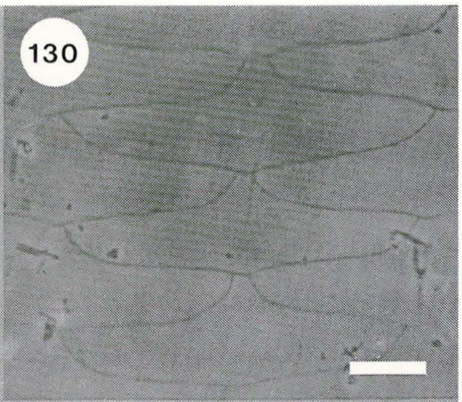
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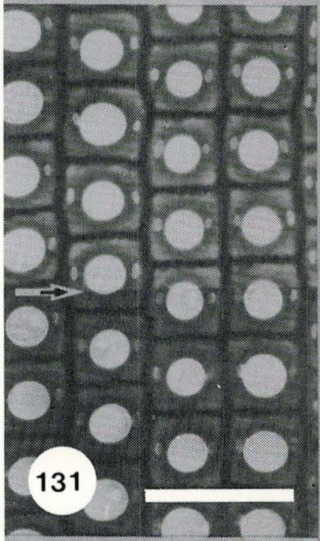
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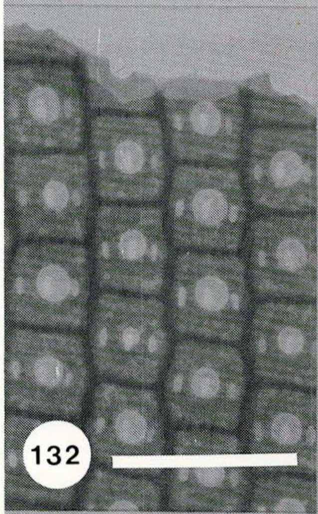
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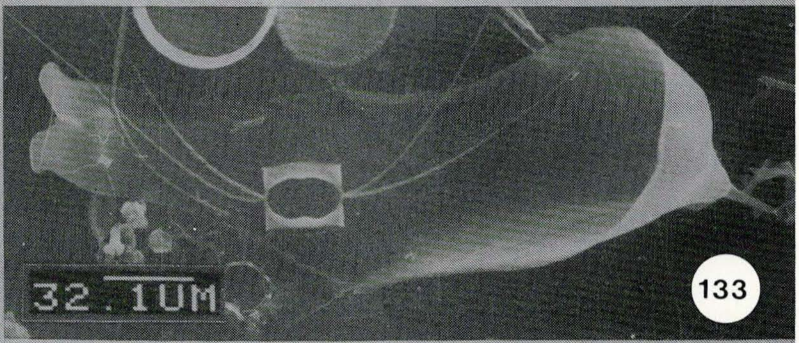
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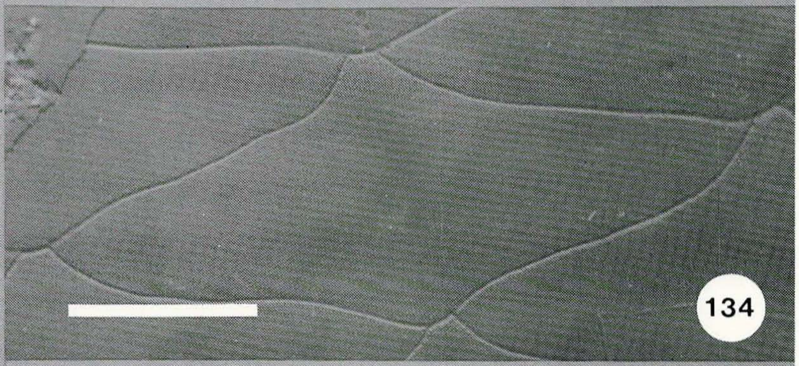
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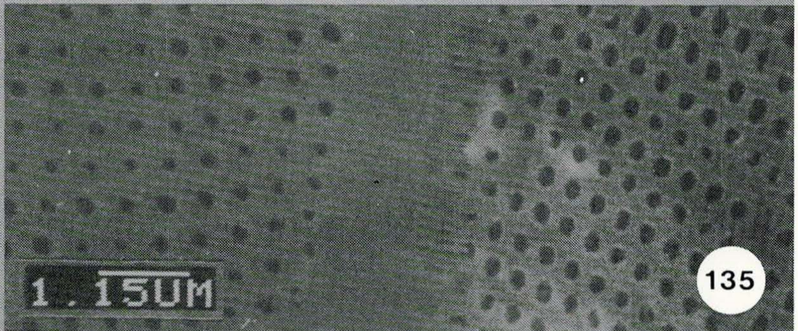
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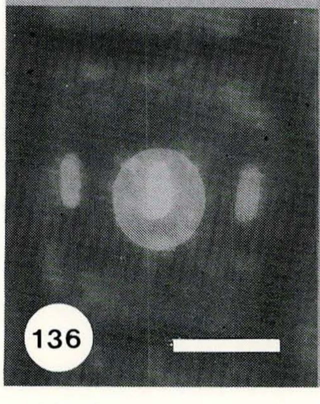
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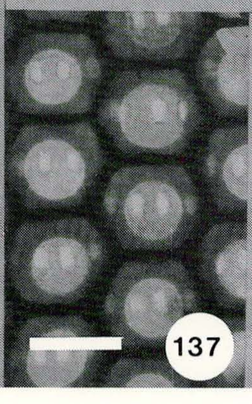
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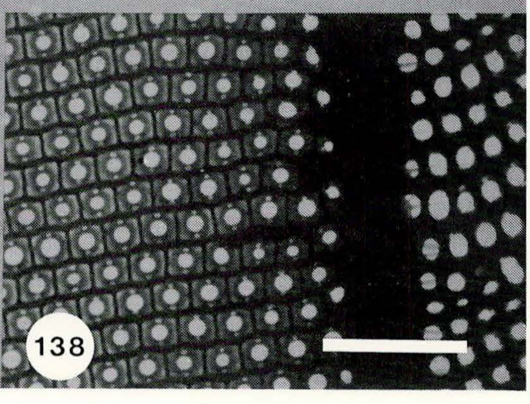

138

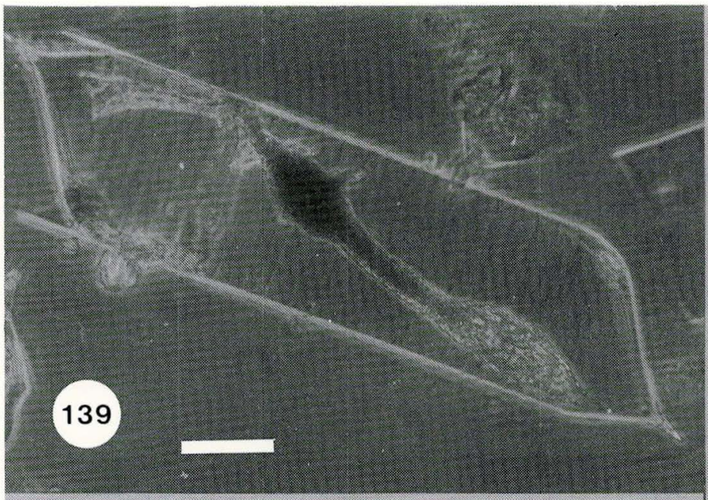
Plate 20

RHIZOSOLENIA CRASSA

LM: Figs 139-141. SEM: Figs 142, 143.

Fig. 139. (029). Cell in lateral view. Note shape of girdle segments.
Fig. 140. (029). Part of cell in lateral view. Note shape of process.
Fig. 141. (029). Part of cell in dorsiventral view. Note shape of otaria.
Fig. 142. (029). Part of cell in oblique ventral view. Note shape of contiguous area and claspers. Note also length of impression of sister-cell process.
Fig. 143. (029). Part of cell in lateral view.

Scales: Fig. 139 = 50 µm. Figs 140, 141 = 25 µm.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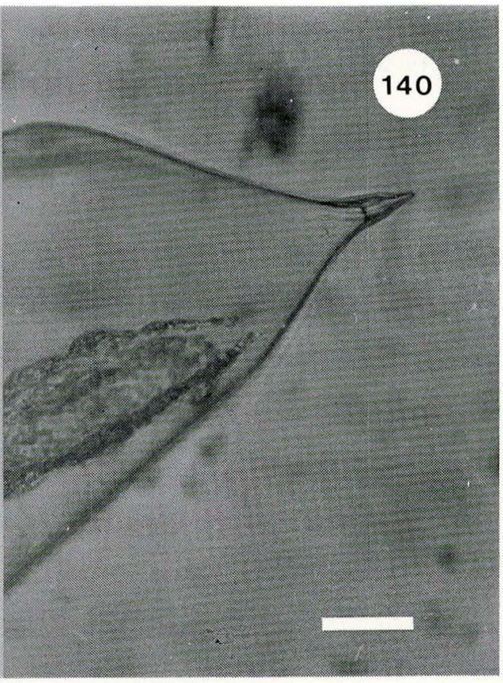
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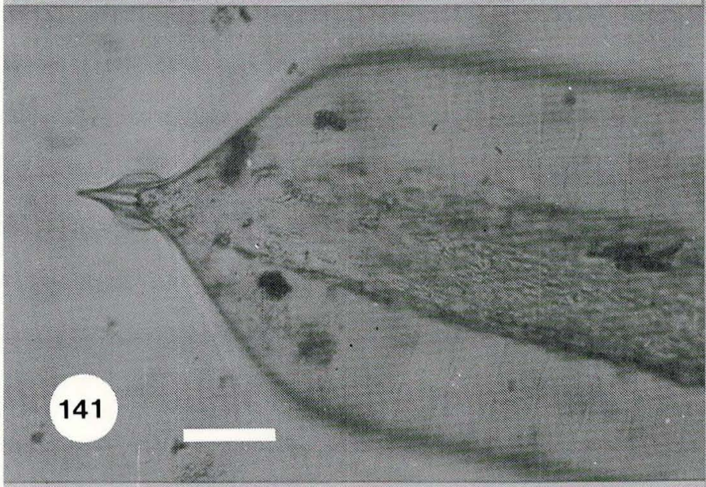
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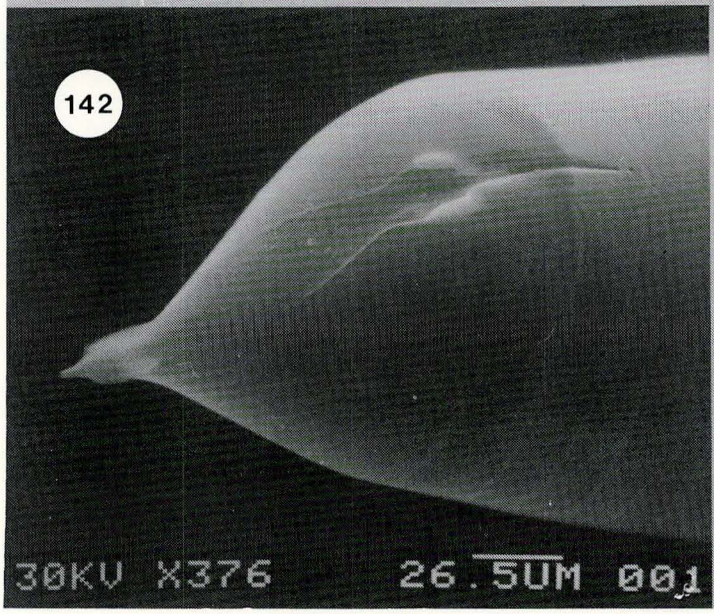
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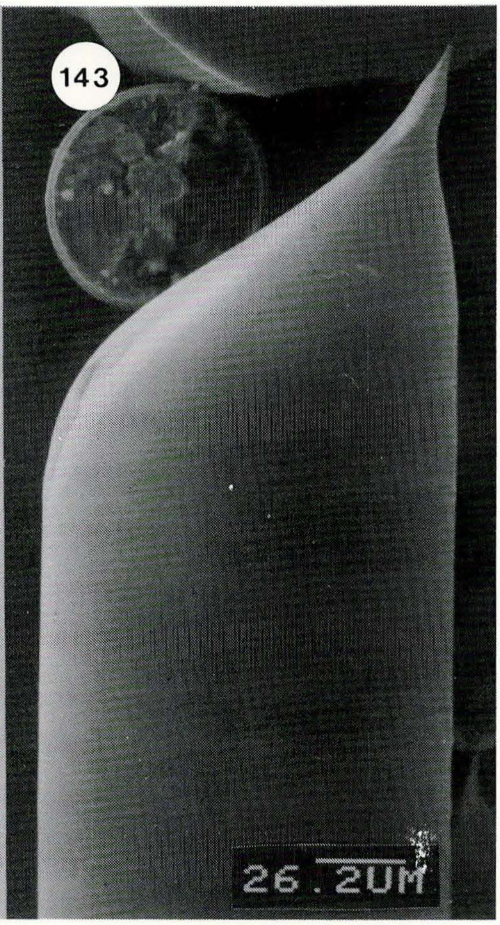

143

Plate 21

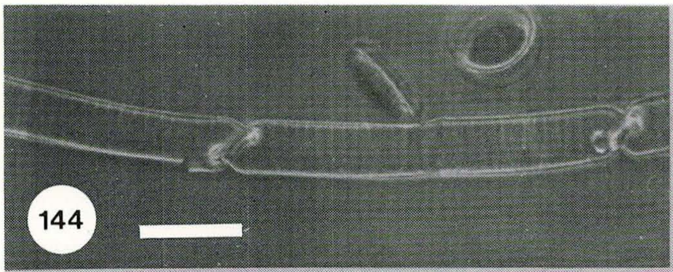
RHIZOSOLENIA SIMA

LM: Figs 144-146, 150, 151. SEM: Figs 147-149. TEM: Figs 152-154.

Fig. 144. (121). *Rh. sima* f. *sima*. Note slightly curved cells.
Fig. 145. (S. Shetland Islands, BM No.31962). f. *sima*. Note shape of process.
Fig. 146. (041). f. *sima*. Note shape of girdle segments and process.
Fig. 147. (041). f. *sima*. Parts of cells in dorsiventral view. Note length of intact process of valve to the left (tip indicated by arrowhead). Note claspers over otaria.
Fig. 148. (041). f. *sima*. Part of cell in lateral view. Note bulbous basal part of process.
Fig. 149. (041). f. *sima*. Part of cell in dorsal view. Note girdle segments and shape of otaria.
Fig. 150. (042). f. *silicea*. Part of cell. Note shape of process.
Fig. 151. (042). f. *silicea*. Intact frustule. Note heavily silicified distal part of valves.
Fig. 152. (042). f. *sima*. Part of copula (probably partially dissolved). Arrowheads indicate direction of pervalvar axis.

Fig. 153. (042). f. *silicea*. Part of copula (probably partially dissolved). Different exposures left and right.
Fig. 154. (041). f. *sima*. Part of copula. (Papillous margin not characteristic).

Scales: Fig. 144 = 50 μm. Figs 145, 146, 150, 151 = 25 μm. Fig. 154 = 2 μm.
Figs 152, 153 = 0.5 μm.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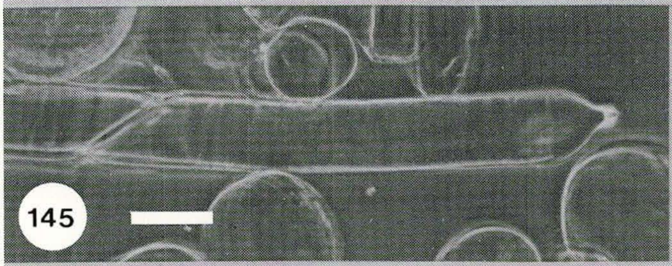
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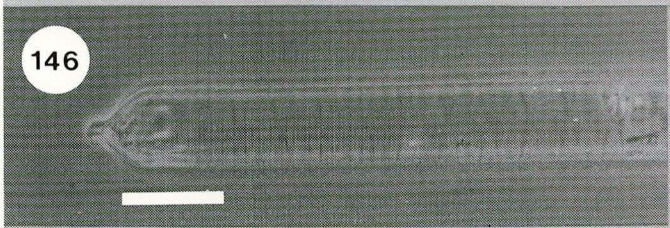
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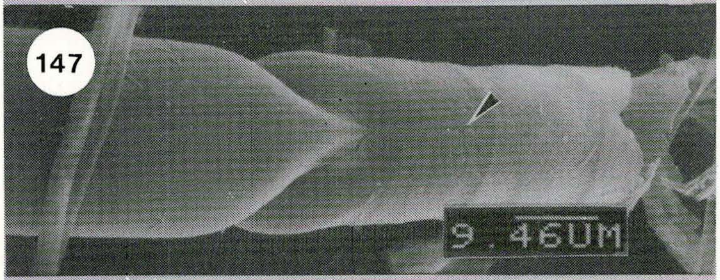
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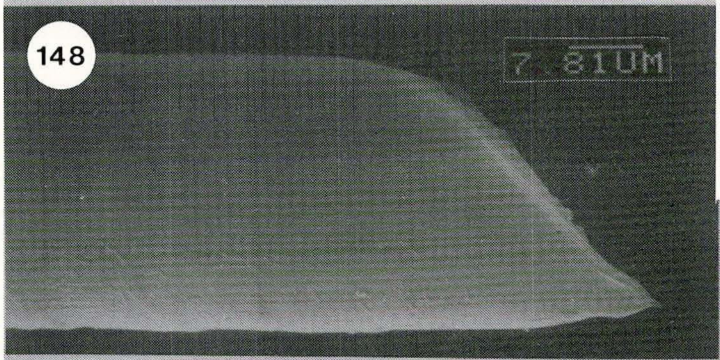
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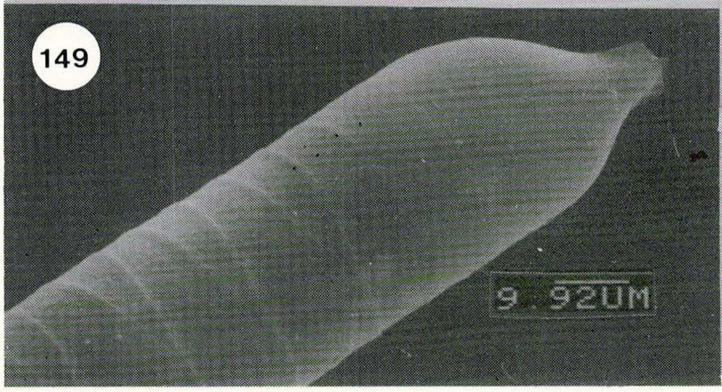
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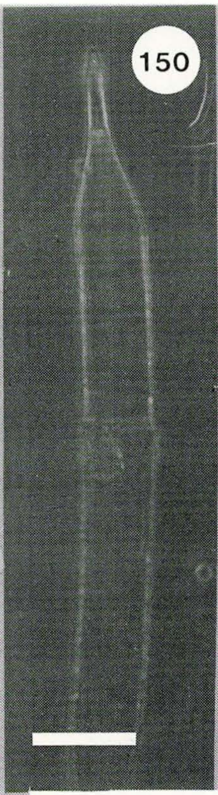
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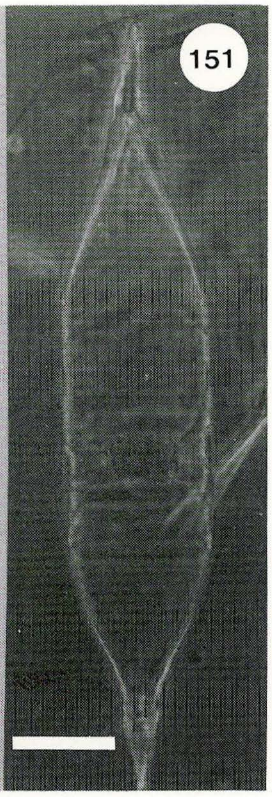
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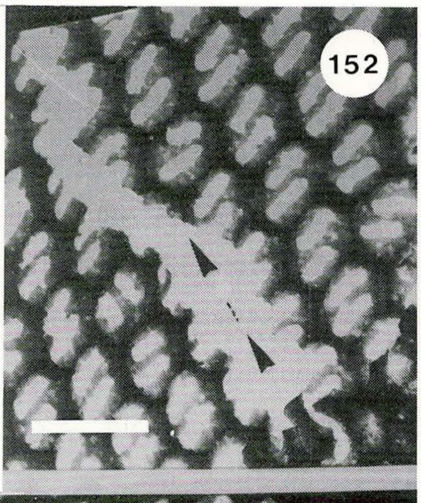
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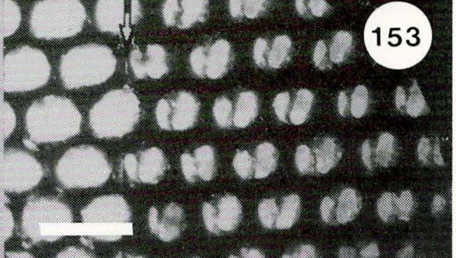
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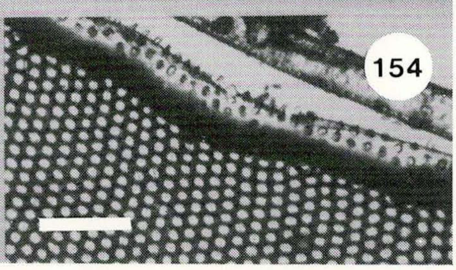
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Plate 22

RHIZOSOLENIA TEMPEREI (Figs 155-163)

"*Rh. temperei* var. *gracilior*" (Fig. 164)

LM: Figs 155-158, 164. TEM: 159-163.

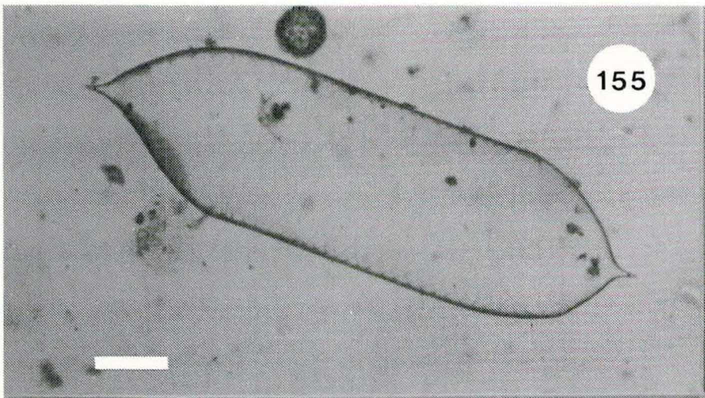
Fig. 155. (139). Complete frustule. Note sigmoid outline of valves.
Fig. 156. (108). Valve apex.
Fig. 157. (104). Fragments of valve, valvocopula and girdle. Note asymmetrical tongue-like extension of valve margin (arrowheads).
Fig. 158. (108). Girdle segments.
Fig. 159. (008). Parts of incompletely silicified girdle segments (pleurae).
Fig. 160. (008). Part of copula. Note four pores in each velum, and small foramina.

Figs 161, 162. (096). Parts of two copulae in the same frustule. Note differences in thickness of wall segments between areolae.

Fig. 163. (096). Part of copula. Note large foramina. Cf. fig. 160.

Fig. 164. (101) "*Rh. temperei* var *gracilior*". Dessicated valve.

Scales: Fig. 155 = 100 µm. Figs 157, 164 = 50 µm. Figs 156, 158 = 10 µm.
Fig. 159 = 5 µm. Figs 160-163 = 1 µm.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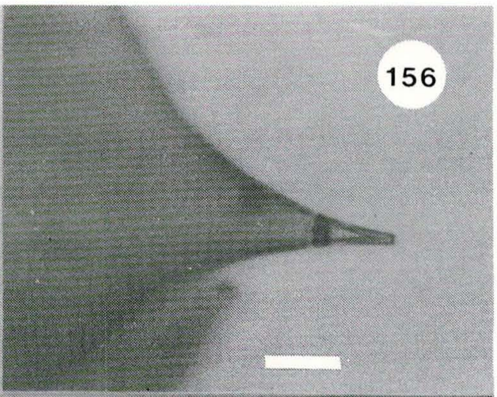
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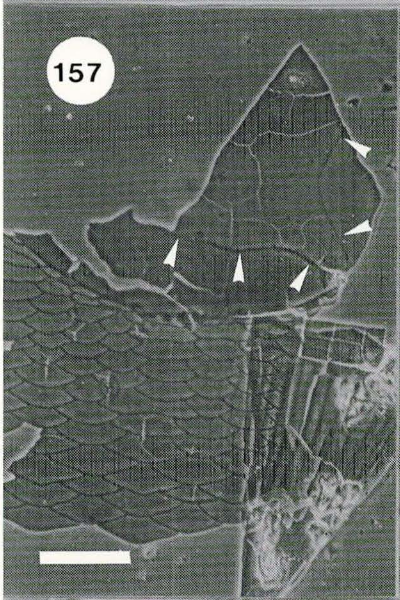
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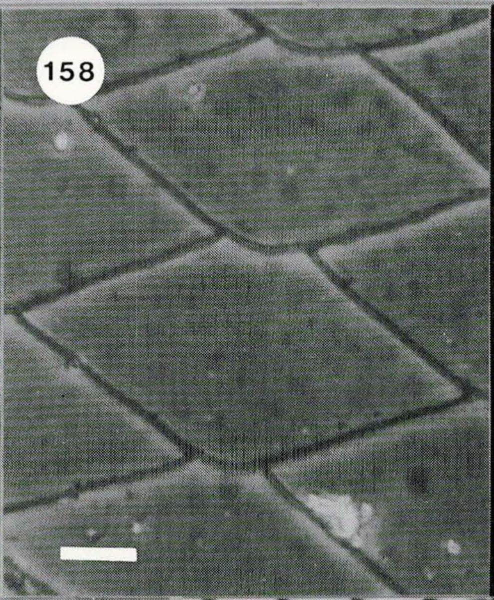
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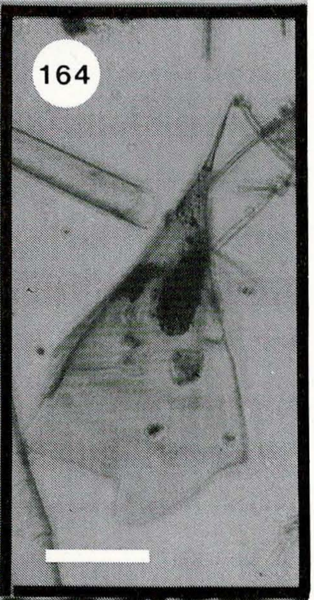
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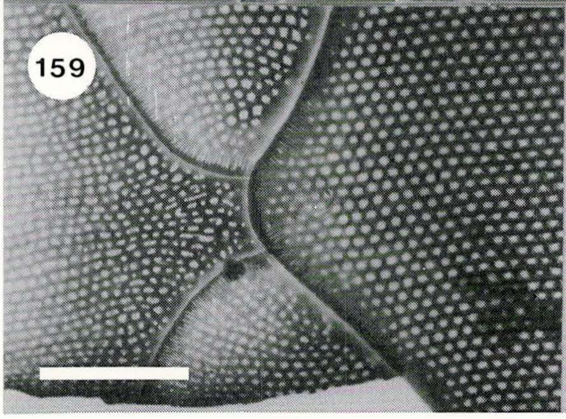
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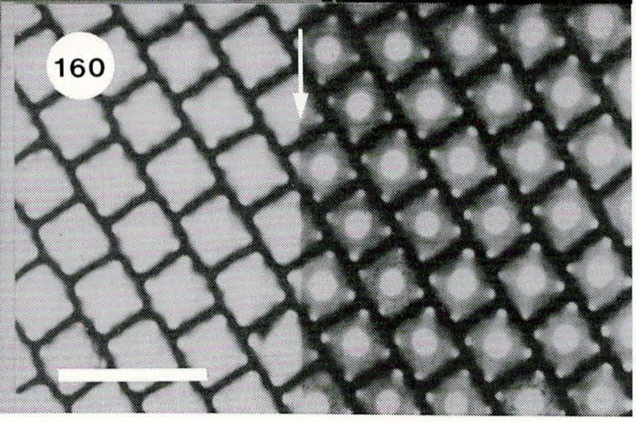
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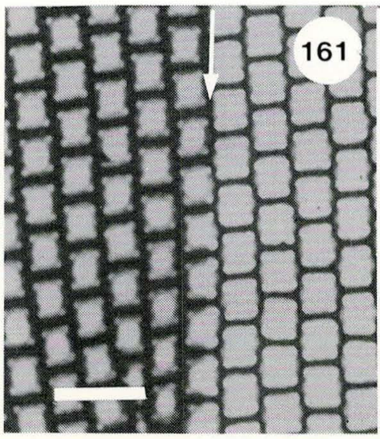
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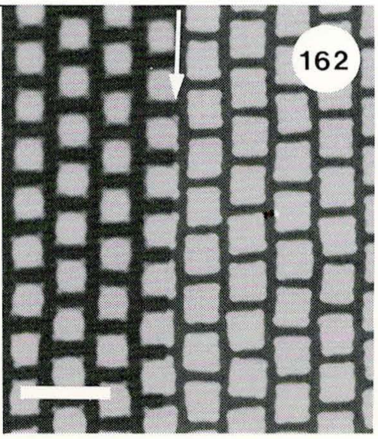
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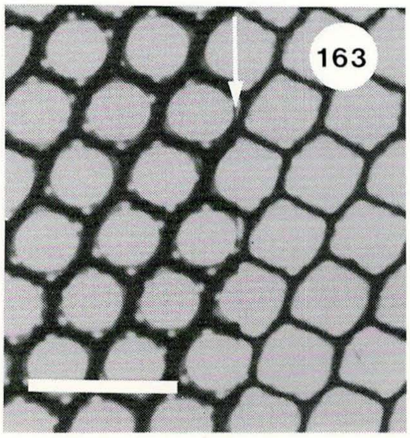

163

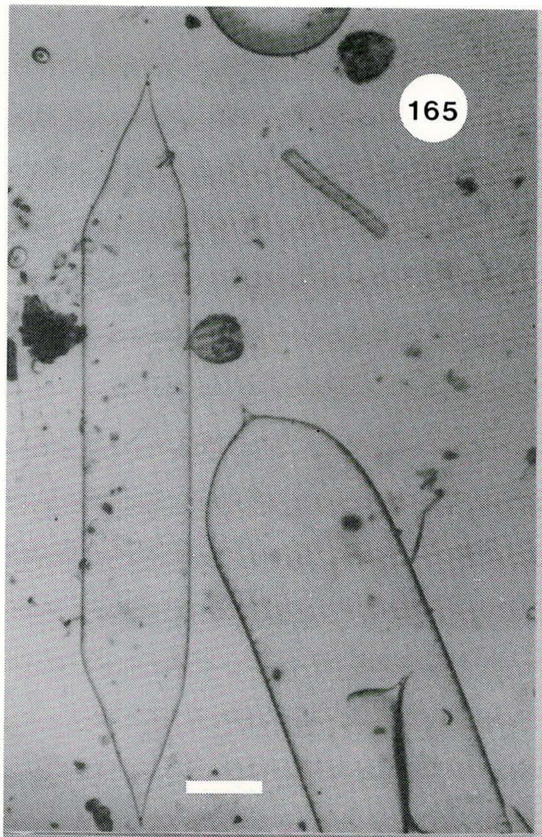
Plate 23

RHIZOSOLENIA ACUMINATA

LM: Figs 165-168. SEM: Fig. 169. TEM: Fig. 170.

Fig. 165.	(139).	Cells of *Rh. acuminata* (left) and *Rh. temperei* (right). Note difference in valve shape.
Fig. 166.	(073).	Part of cell.
Fig. 167.	(073).	Distal part of valve. Note length of process.
Fig. 168.	(073).	Distal part of valve. Note length of process.
Fig. 169.	(023).	Parts of copulae. Note foramina.
Fig. 170.	(023).	Parts of valve, valvocopula and copulae. Note tongue-like extension of valve (arrowheads).

Scales: Figs 165, 166 = 100 µm. Figs 167, 168 = 25 µm. Fig. 170 = 10 µm.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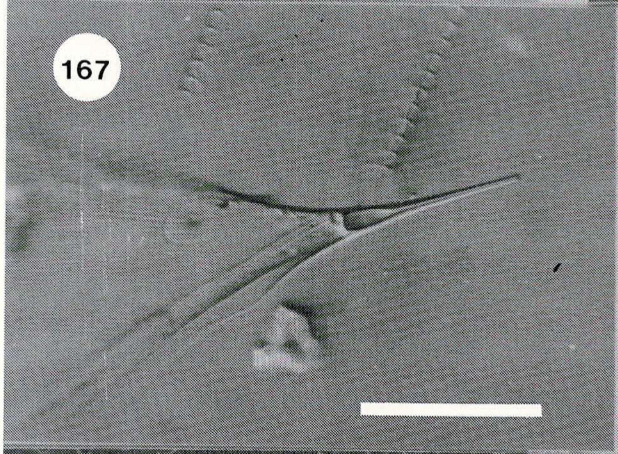
166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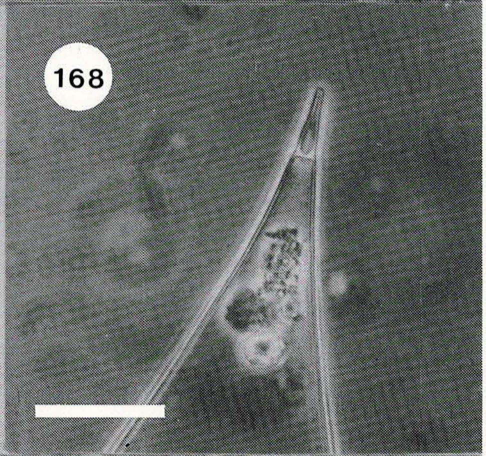
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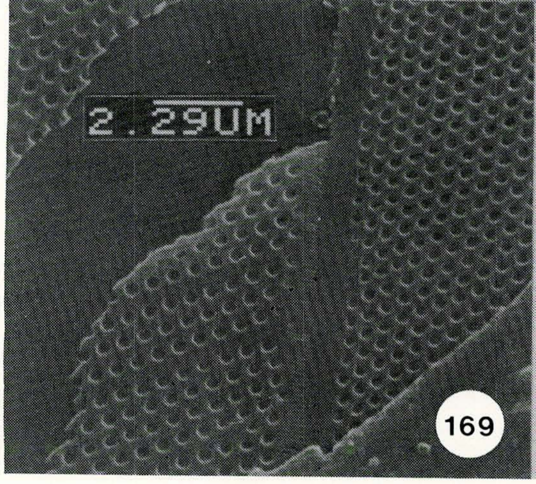

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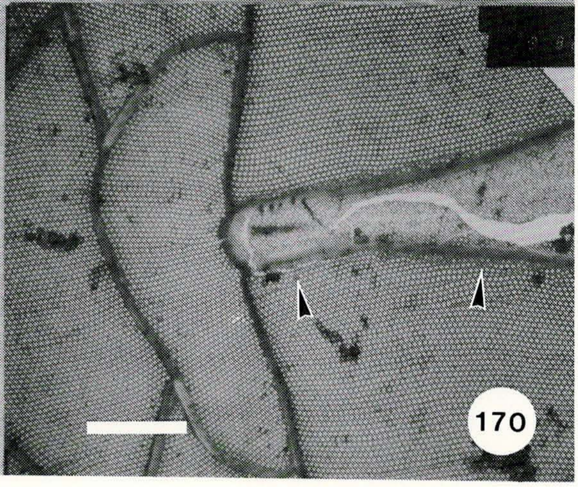
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Plate 24

RHIZOSOLENIA ACUMINATA

TEM: Figs 171-176.

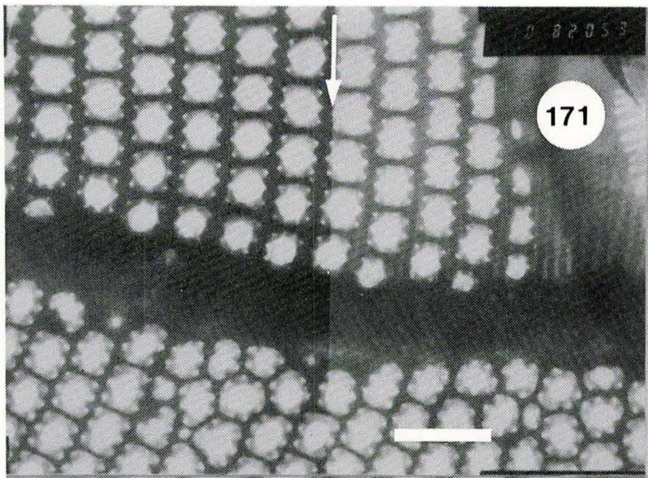
Fig. 171. (023). Parts of copulae. Note difference in thickness of wall segments between areolae in upper and lower copula. Note fringed edge of advalvar margin.
Fig. 172. (023). Part of copula. Note shape and position of velum pores.

Figs 173, 174. (074). Parts of copulae belonging to the same frustule. Note zigzagged wall segments between areolar columns and different degree of silicification.

Fig. 175. (023). Part of copula. Note thick wall segments between areolae.
Fig. 176. (023). Part of copula. Note absence of foramina.

Different exposures on each side of arrow.

Scales: Figs 171, 173-176 = 1 µm. Fig. 172 = 0.2 µm.



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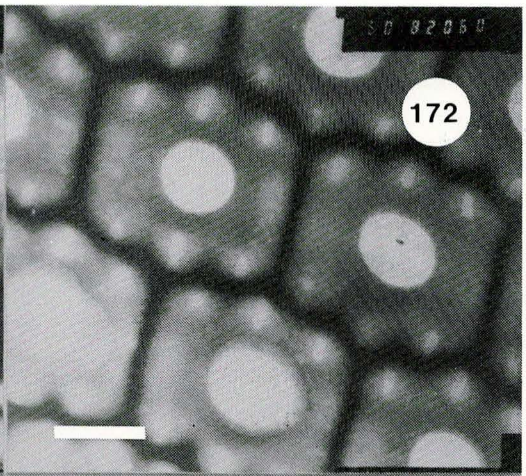

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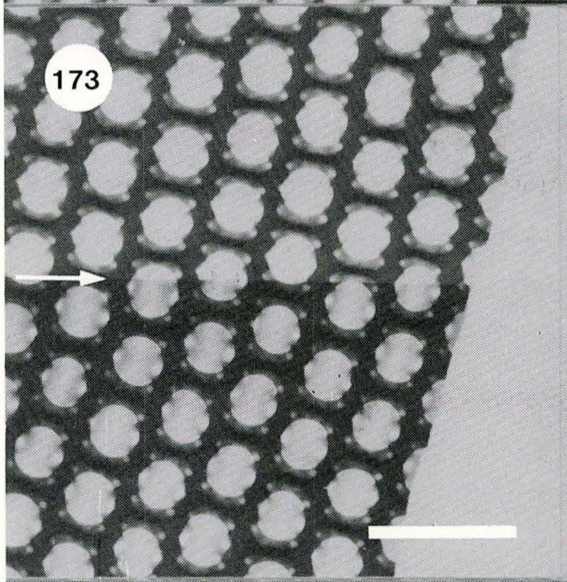

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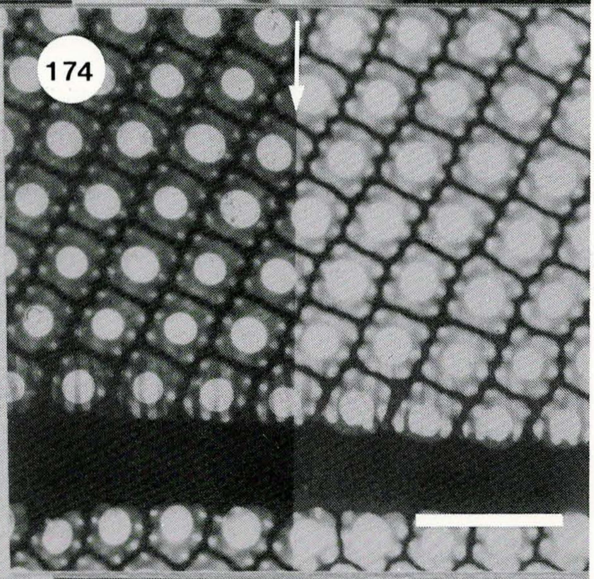

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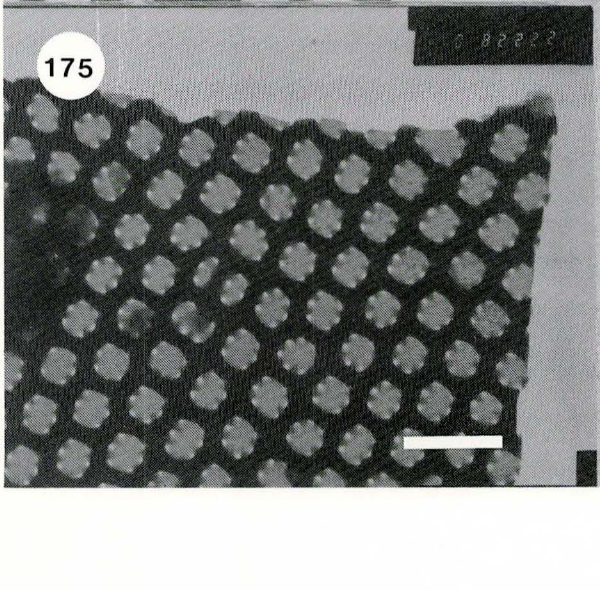

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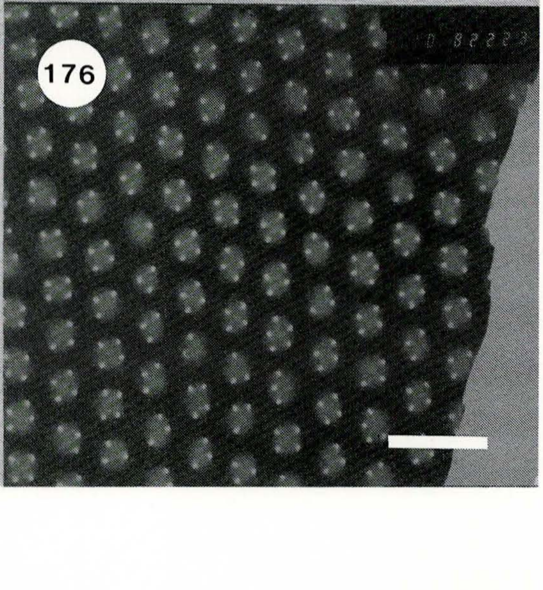


176

Plate 25

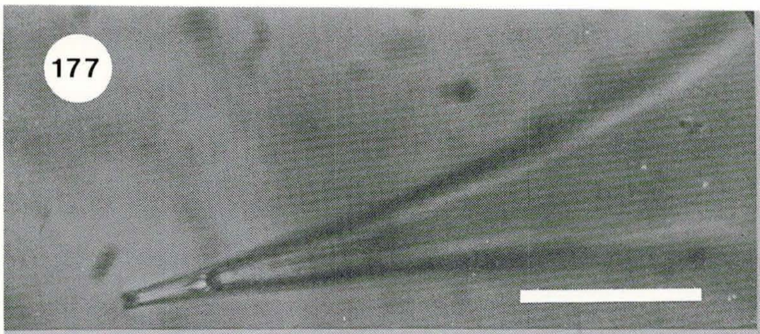
RHIZOSOLENIA BERGONII

LM: Figs 177, 181, 182. SEM: Figs 178, 179. TEM: Fig. 180.

Fig. 177. (135). Distal part of valve. Note shape of process.
Fig. 178. (073). Part of cell in ventral view. Note tip of process and impression of sister-cell process on valve.
Fig. 179. (023). Part of dessicated valve. Note that the areolae lack foramina.
Fig. 180. (088). Part of copula. Note fringed edge of advalvar margin and edge of abvalvar margin (entire).
Fig. 181. (075). Parts of dessicated cells. Note heavily silicified valves and shape of process.
Fig. 182. (046). Part of cell. Note outline of valve.

Scales. Figs 177, 181, 182 = 25 µm. Fig. 180 = 1 µm.

177



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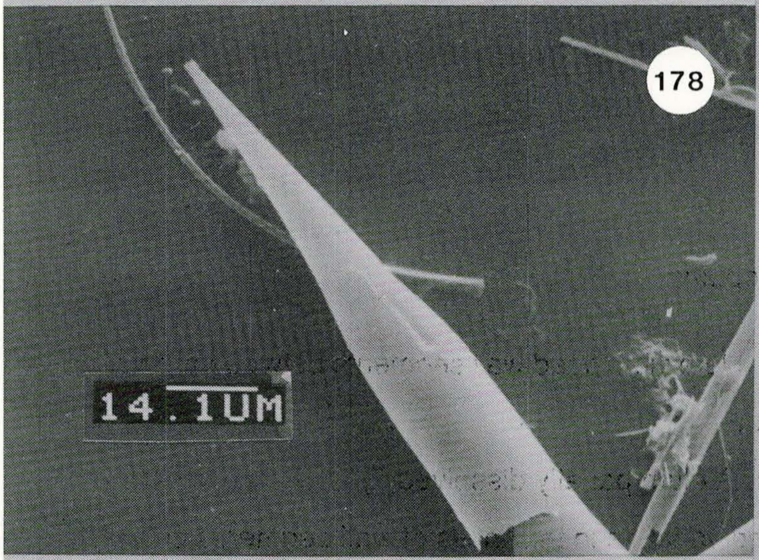

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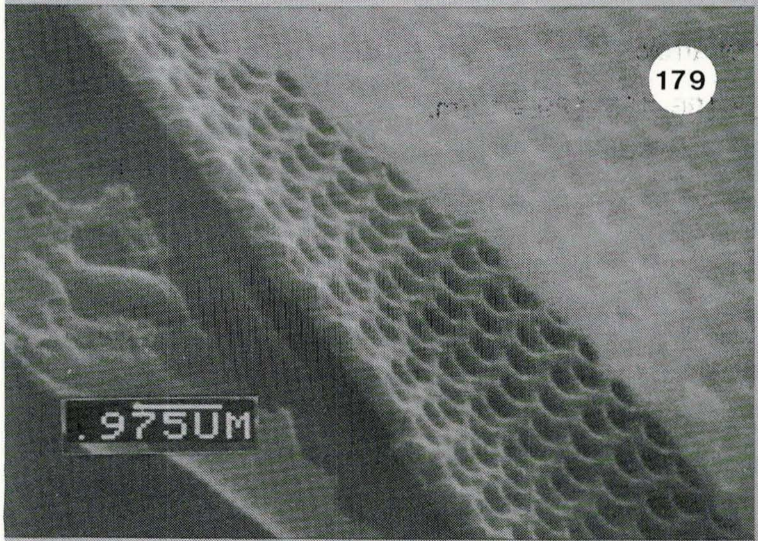

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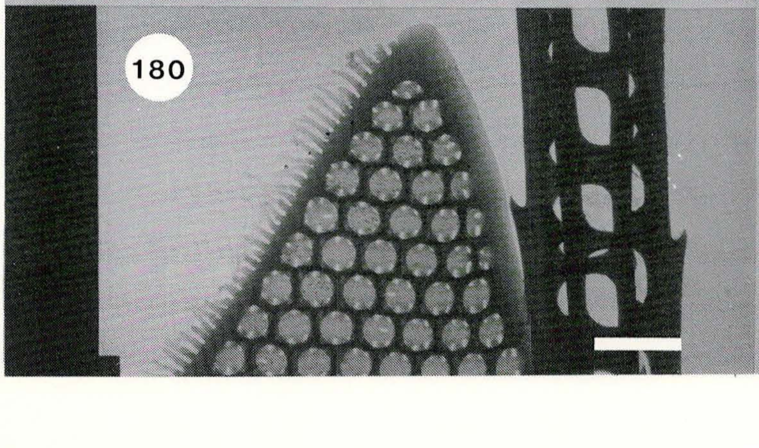

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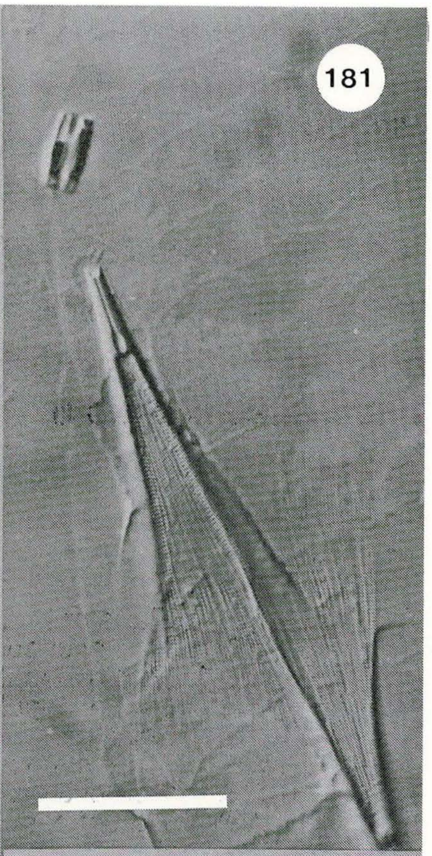

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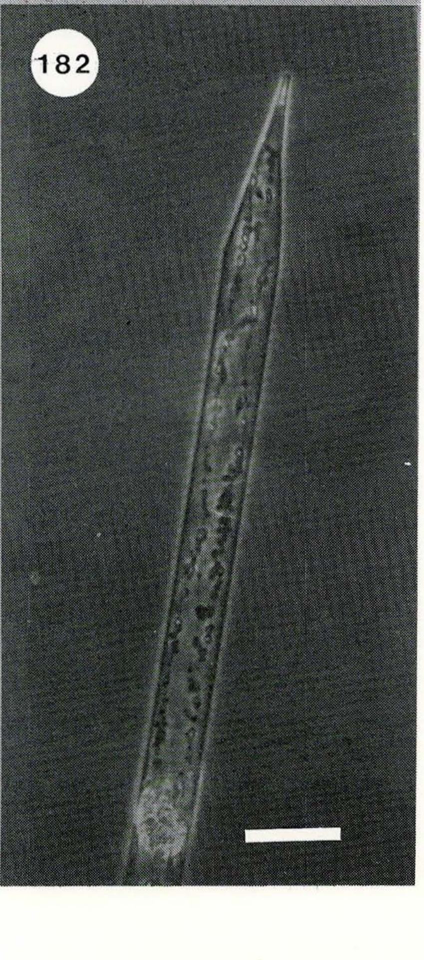


Plate 26

RHIZOSOLENIA BERGONII

TEM: Figs 183-189.

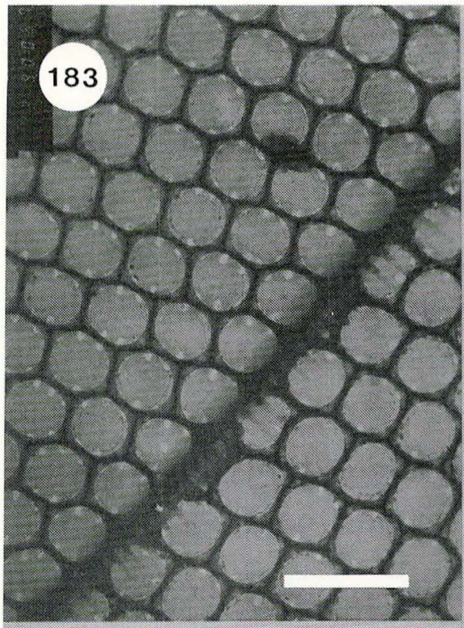
Fig. 183.	(081).	Parts of two copulae.
Fig. 184.	(073).	Part of copula.
Fig. 185.	(078).	Part of copula.
Fig. 186.	(074).	Part of copula. Note zigzagged wall segments between areolar columns.
Fig. 187.	(076).	Parts of copulae.
Fig. 188.	(067).	Part of copula.
Fig. 189.	(089).	Part of copula. (Velum parially dissolved ?).

Note positions of velum pores and variation in thickness of wall segments between areolae. Cf. plate 24.

Different exposures on each side of arrow.

Scales. Fig. 187 = 2 µm. Figs 183-186, 188, 189 = 1 µm.

183



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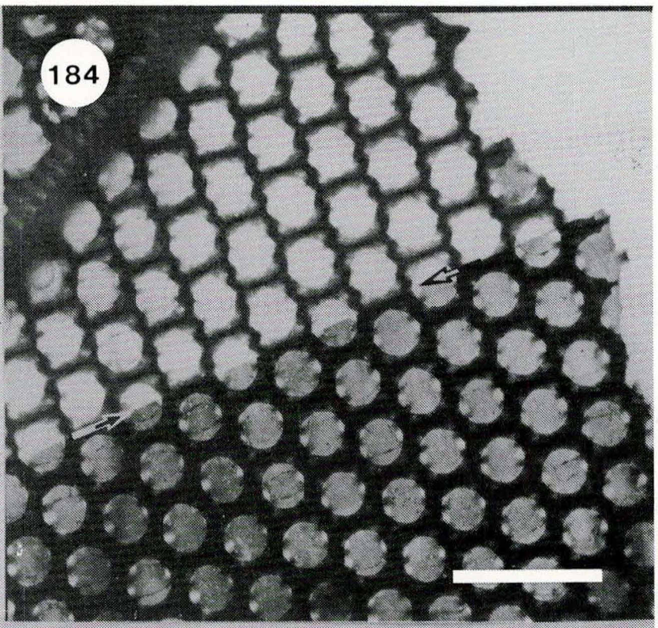

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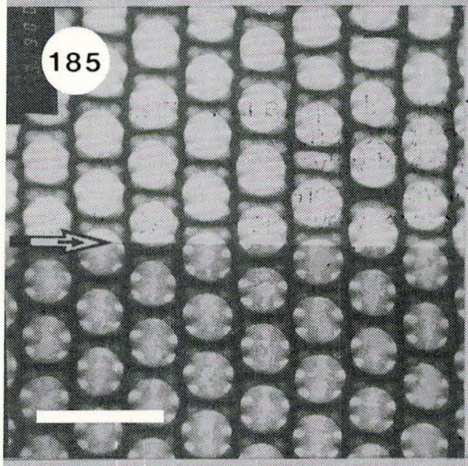

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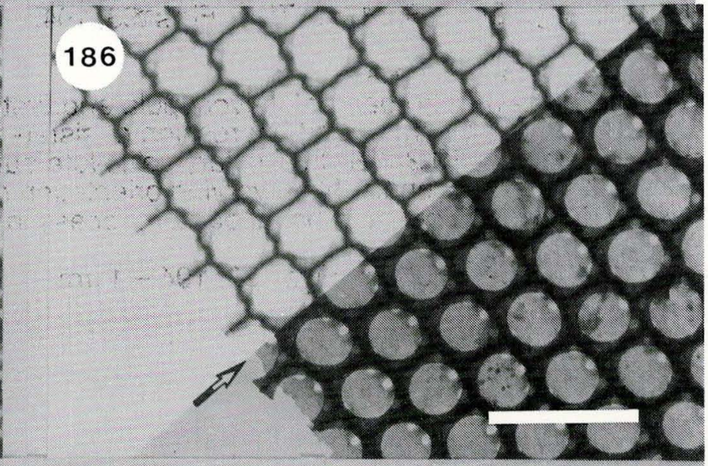

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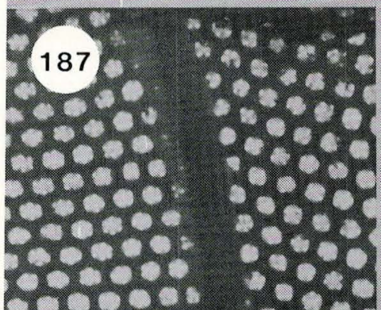

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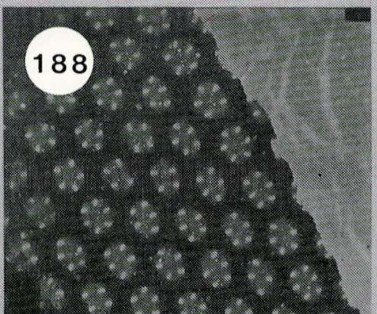

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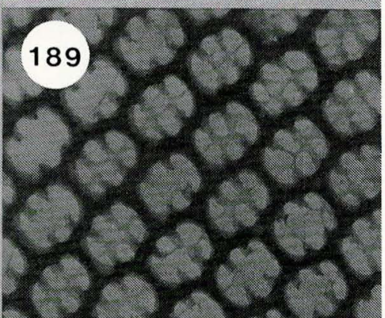


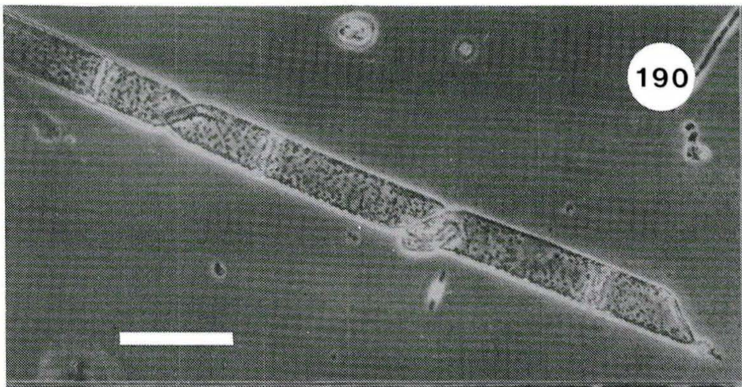
Plate 27

RHIZOSOLENIA HYALINA

LM: Figs 190, 192. SEM: Fig. 191. TEM: Figs 193, 194.

Fig. 190. (043). Chain of cells.
Fig. 191. (044). Valve and parts of valvocopula and first ventral copula in ventral view. Note otaria and impression of sister-cell process.
Fig. 192. (Ko Phuket, 19.2 1980). Solitary cell. Note outline of valve.
Fig. 193. (072). Part of copula. Note varying orientation of velum pores.
Fig. 194. (075). Valve apex and basal part of process in lateral view. Note labiate structure.

Scales: Figs 190, 192 = 50 µm. Figs 193, 194 = 1 µm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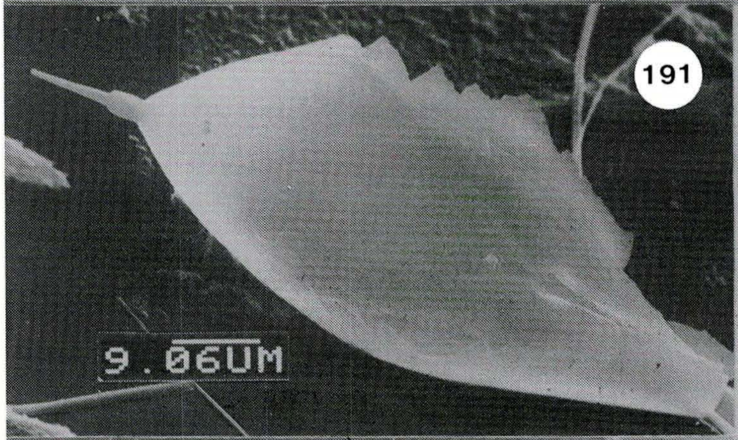
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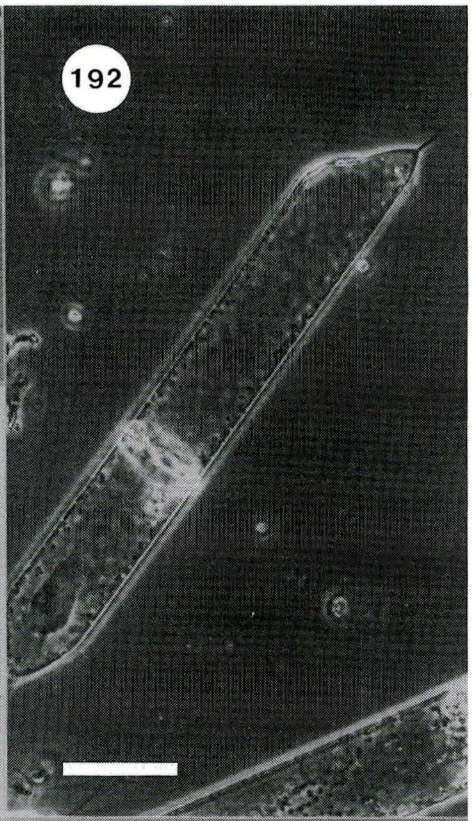
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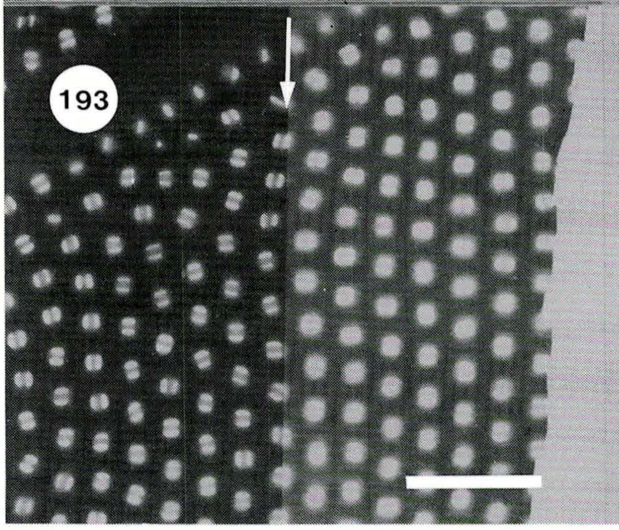
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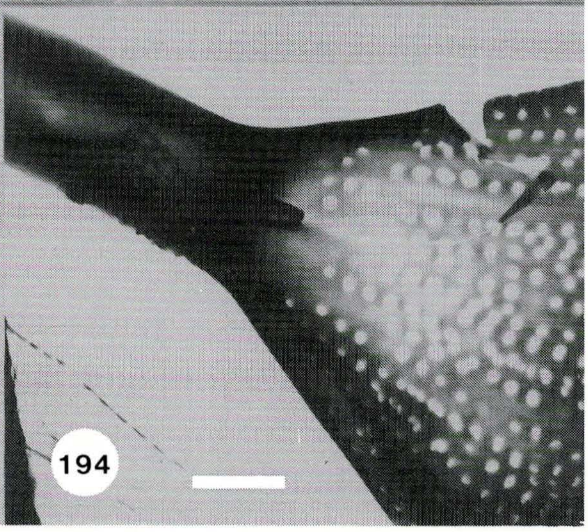

194

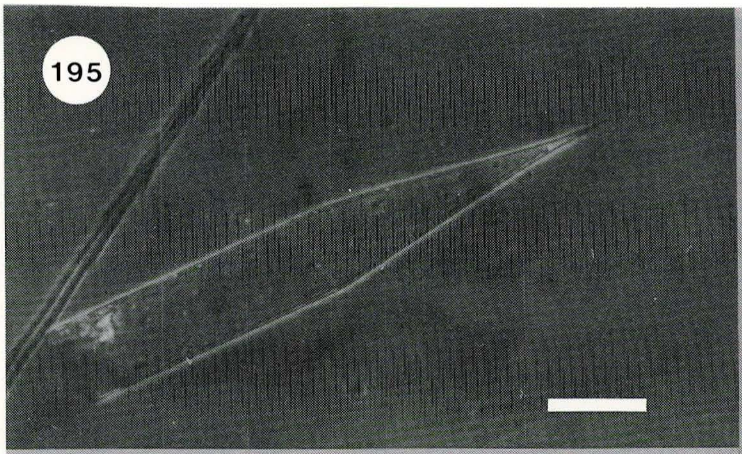
Plate 28

RHIZOSOLENIA SIMPLEX

LM: Figs 195, 196. SEM: Fig. 197. TEM: 198, 199.

Fig. 195. (038). Part of cell. Note continuous outline of valve and process.
Fig. 196. (038). Incompletely developed cell detached from sister cell.
Fig. 197. (038). Dessicated cell. Note copulae.
Fig. 198. (038). Parts of copulae. Note parallel orientation of velum pores.
Fig. 199. (038). Part of valve (above) and copula (below). Note one velum pore in areolae of valve.

Scales: Figs 195, 196 = 25 µm. Fig. 198 = 2 µm. Fig. 199 = 1 µm.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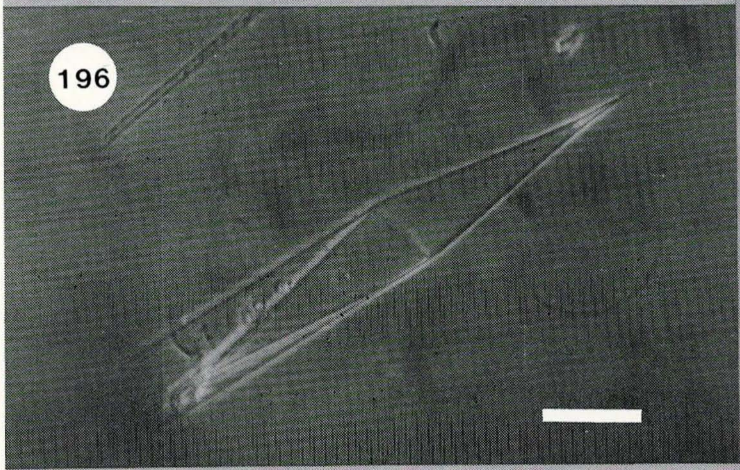
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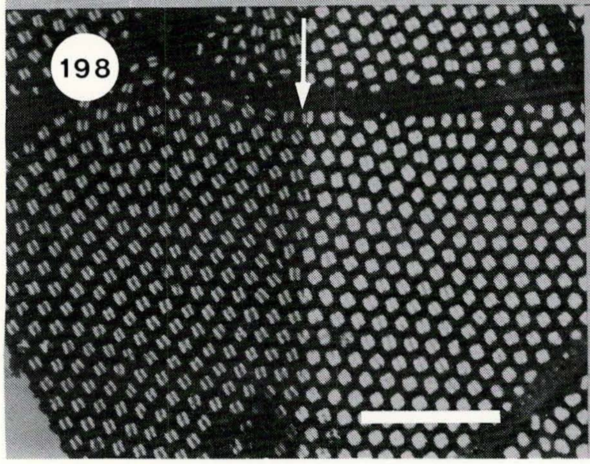
197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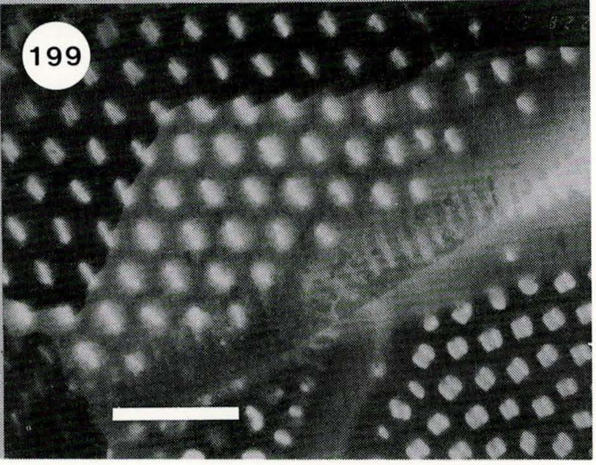

199

Plate 29

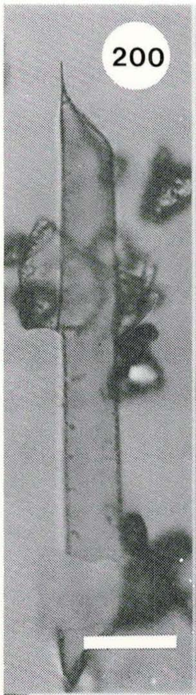
RHIZOSOLENIA IMBRICATA

LM: Figs 200-204. SEM: Figs 207, 208. TEM: Figs 205, 206.

Fig. 200. (109). Part of cell in lateral view.
Fig. 201. (149). Parts of two cells, upper cell in dorsiventral view. Note swollen basal part of valve.
Fig. 202. (071). Part of cell in dorsiventral view. Note orientation of girdle segments.
Fig. 203. (002). Part of girdle in oblique ventral view. Note orientation of striae.
Fig. 204. (075). Middle part of girdle in lateral view. Note orientation of striae and different orientation of girdle segments above and below.
Fig. 205. (081). Distal part of cell in dorsiventral view. Note shape of process and otaria.
Fig. 206. (002). Part of copula. Note diagonal slit in velum.
Fig. 207. (075). Distal part of cell in ventral view. Note large contiguous area and impression of sister-cell process.
Fig. 208. (Transect Göteborg-Fredrikshavn, 9.10 1975). Internal view of copula.

Scales: Figs 200, 202 = 25 µm. Figs 201, 203-206 = 10 µm. Fig. 208 = 5 µm.
Fig. 206 = 2 µm.

200



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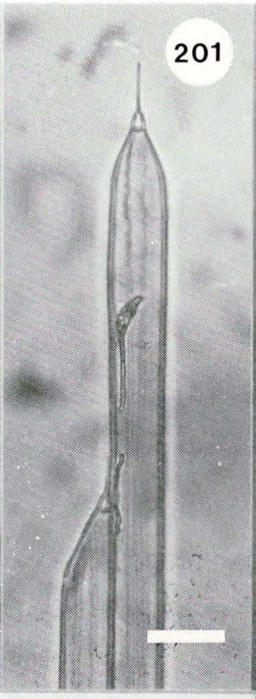

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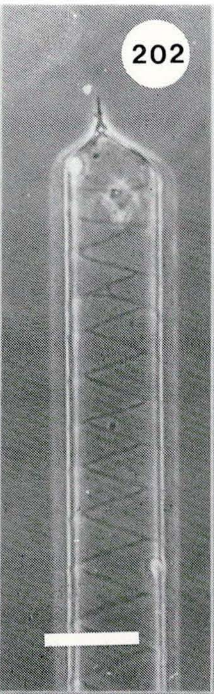

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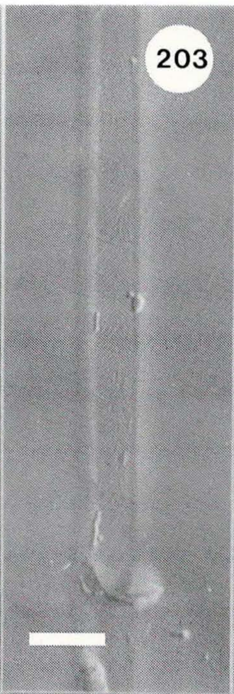

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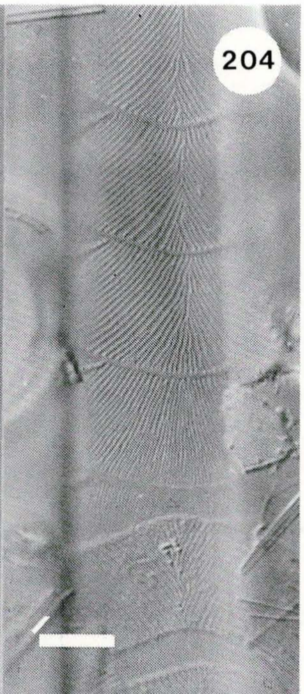

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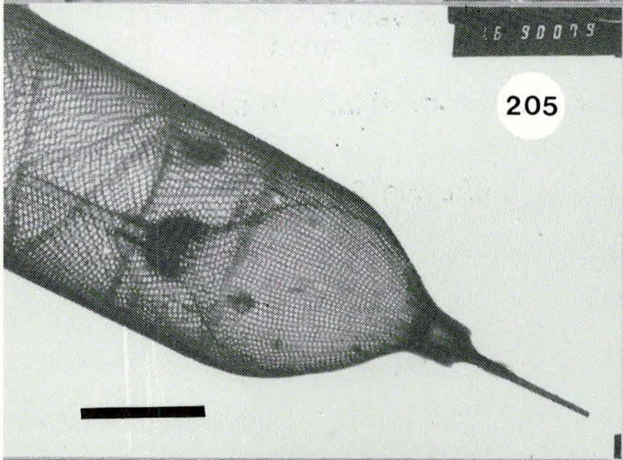

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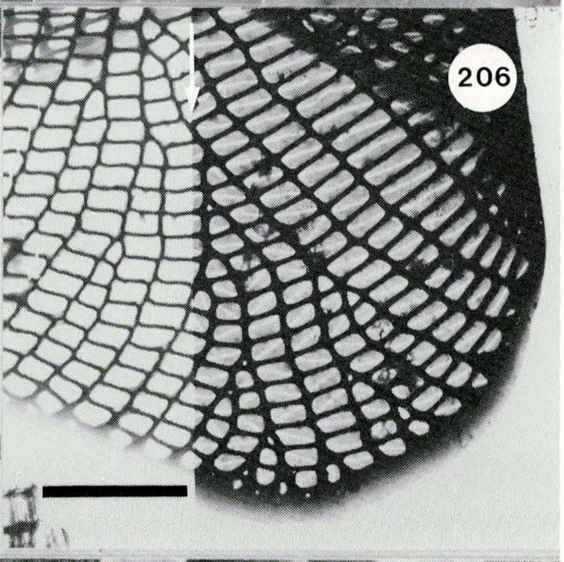

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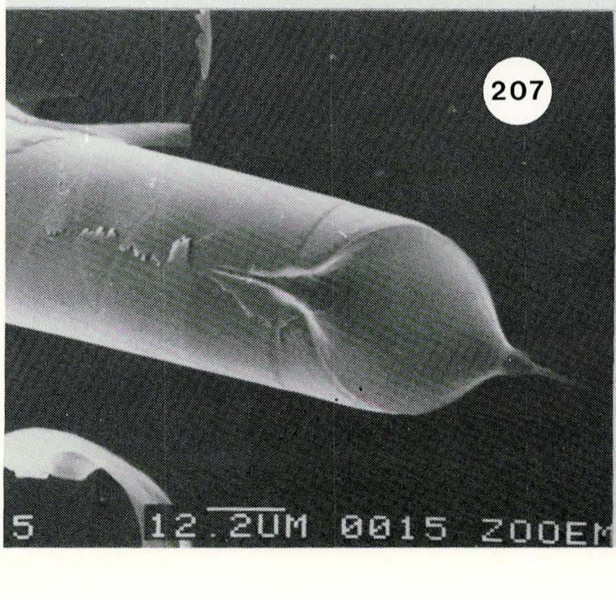

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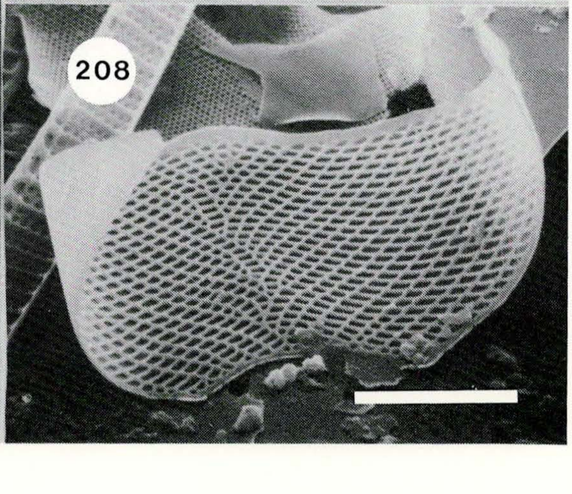


Plate 30

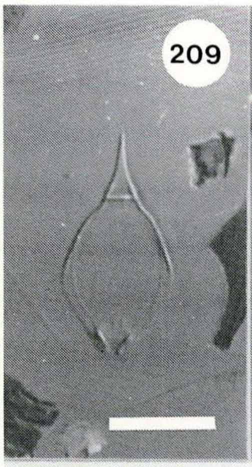
RHIZOSOLENIA STRIATA

LM: Figs 209-212. SEM: Figs 215, 216. TEM: 213, 214.

Fig. 209.	(110).	Valve in dorsiventral view. Note shape of process.
Fig. 210.	(210).	Part of girdle in lateral view. Note orientation of striae.
Fig. 211.	(046).	Distal part of cell in dorsal view. Note shape of process.
Fig. 212.	(070).	Distal part of cell in lateral view. Note shape of process.
Fig. 213.	(045).	Part of copula. Note irregularly toothed edge of advalvar margin.
Fig. 214.		Detail of fig. 213. Note diagonal slit in velum.
Fig. 215.	(074).	Inner surface of copulae. Note orientation of striae.
Fig. 216.	(070).	Broken edge of copula.
Fig. 217.	(070).	Inner surface of valve apex. Note slit of labiate structure between arrowheads.

Scales: Figs 209, 210 = 24 µm. Figs 211, 212 = 10 µm. Fig. 213 = 5 µm.
Fig. 214 = 2 µm.

209



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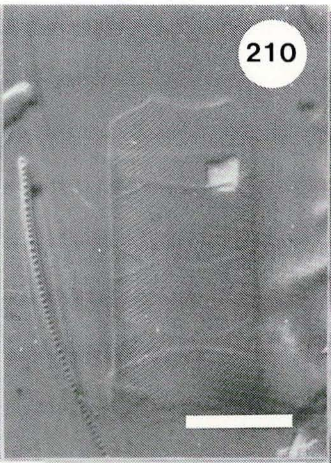

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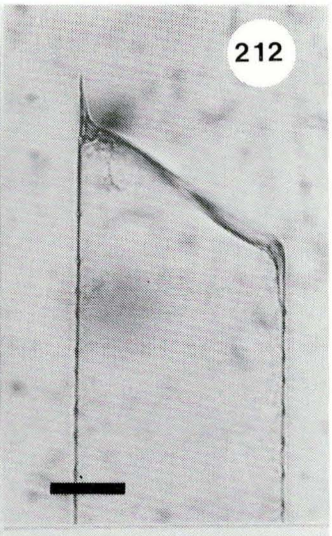

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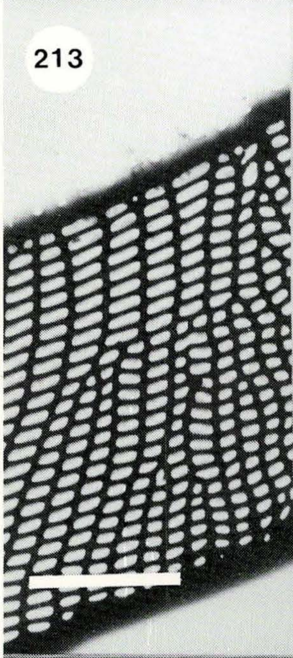

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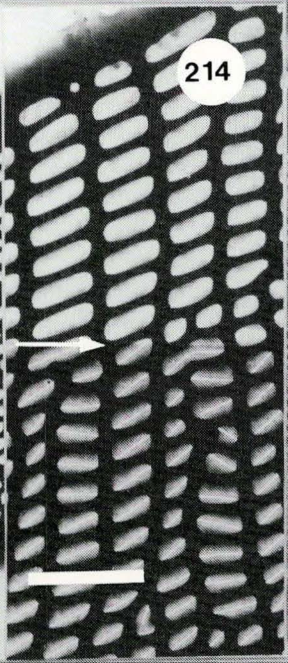

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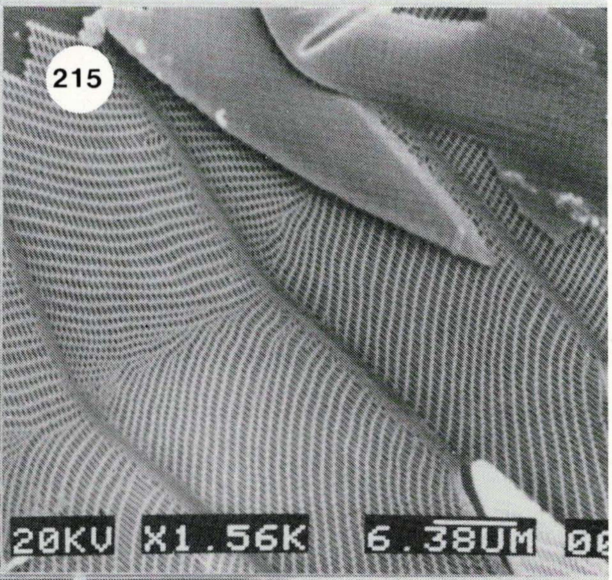

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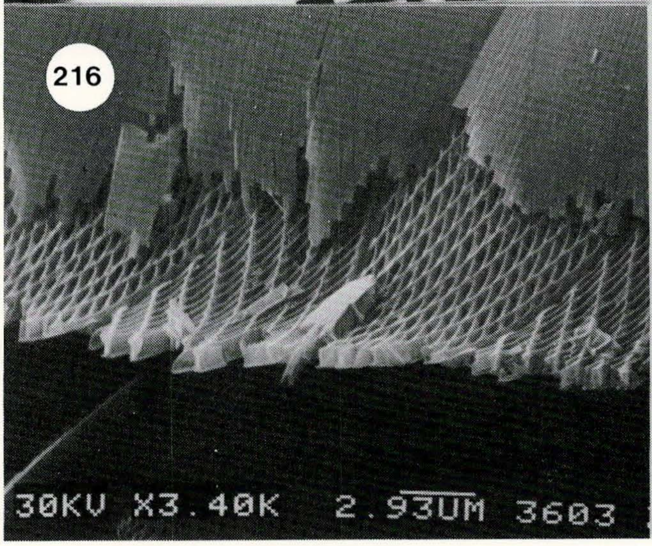

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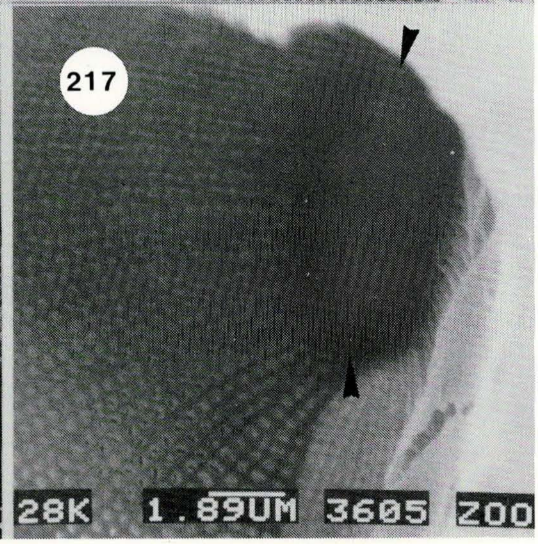


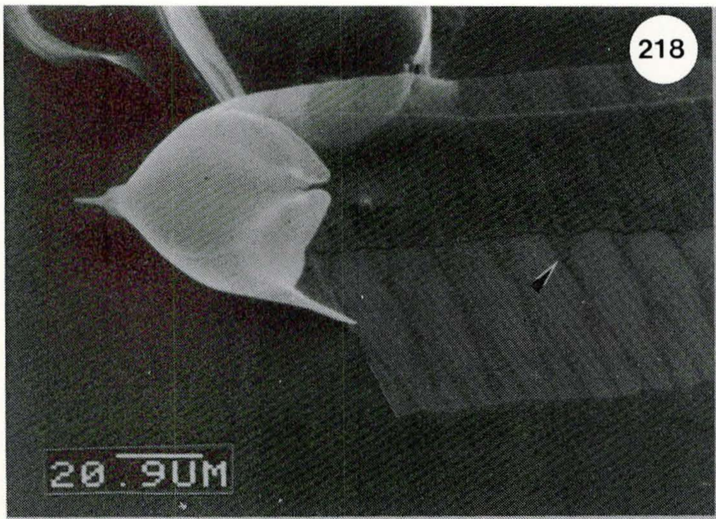
Plate 31

RHIZOSOLENIA OSTENFELDII

LM: Figs 220, 221. SEM: Figs 218, 219. TEM: Figs 222-226.

Fig. 218. (075). Part of dessicated cell. Note shape of otaria, contiguous area and copulae.
Fig. 219. Detail of cell in fig. 218 (arrowheads). Inner surface of copula. Note striation.
Fig. 220. (071). Part of cells in dorsiventral view. Note orientation of girdle segments.
Fig. 221. (070). Part of cell in dorsiventral view.
Fig. 222. (070). Part of valve, valvocopula and copulae. Note orientation of striae.
Fig. 223. (070). Parts of copulae.
Fig. 224. (045). Parts of copulae.
Fig. 225. Detail of fig. 224. Note velum pores.
Fig. 226. (043). Part of copula. Note unevenly silicified wall segments between areolae (below).

Scales: Figs 220, 221 = 25 µm. Fig. 222 = 10 µm. Fig. 223 = 5 µm. Fig. 224 = 2 µm. Fig. 225 = 1 µm. Fig. 226 = 0.5 µm.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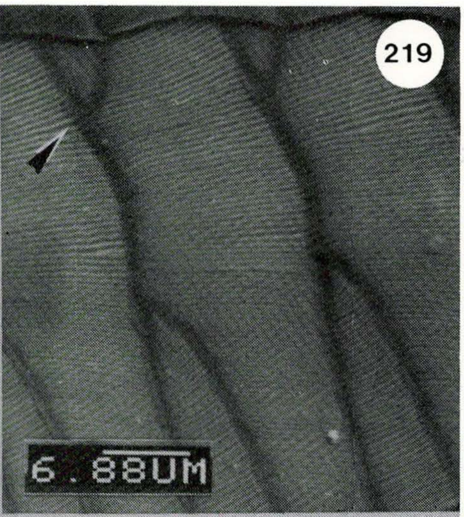
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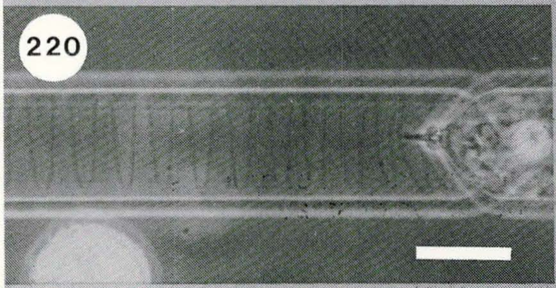
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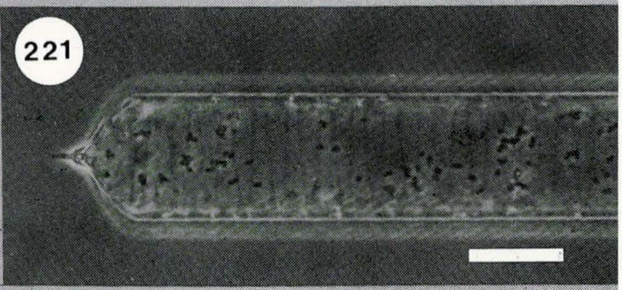
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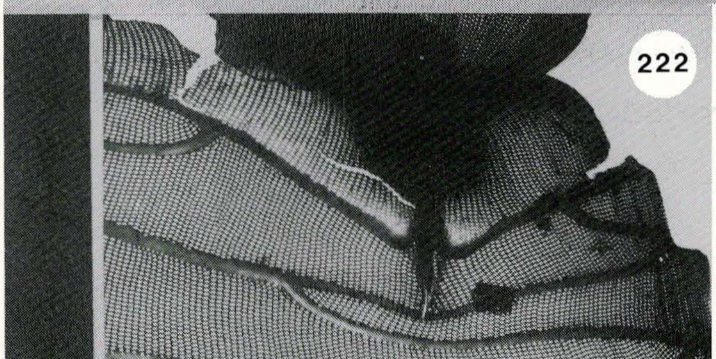
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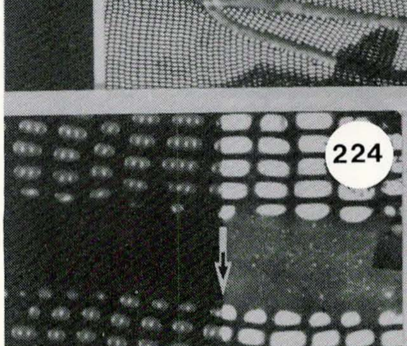
223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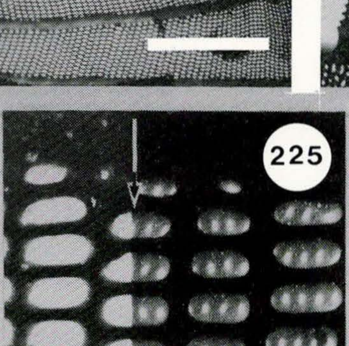
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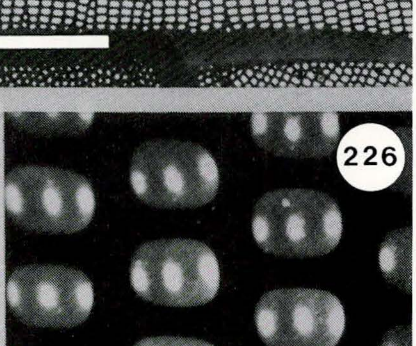
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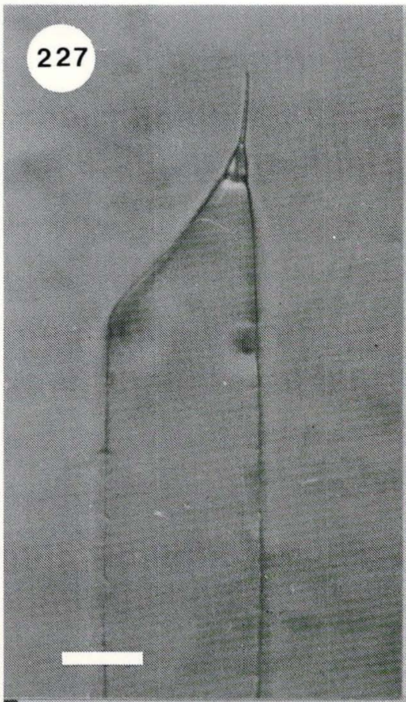
Plate 32

RHIZOSOLENIA FALLAX

LM: Figs 227, 228. SEM: Figs 230-233. TEM: Fig. 229.

Fig. 227. (087). Part of cell in lateral view. Note swollen basal part of process.
Fig. 228. (002). Part of girdle in lateral view. Note orientation of striae.
Fig. 229. (088). Part of copula. Note velum pores.
Fig. 230. (074). Part of cell in ventral view.
Fig. 231. (068). Part of cell in ventral view. Note shape of otaria.
Fig. 232. Detail of fig. 231. Note velum pores.
Fig. 233. (002). Distal part of valve in lateral view. Note shape of process tip.

Scales: Figs 227, 228, 231 = 10 µm. Figs 229, 232 = 1 µm.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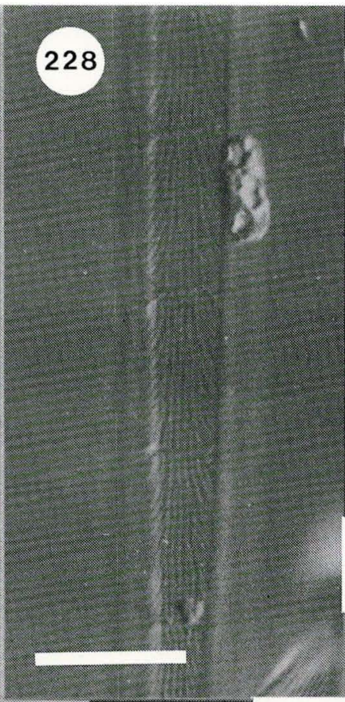
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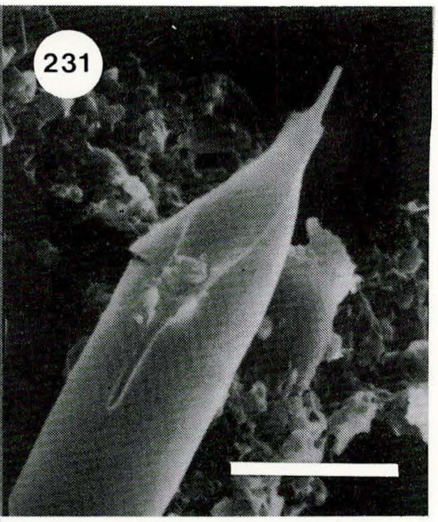
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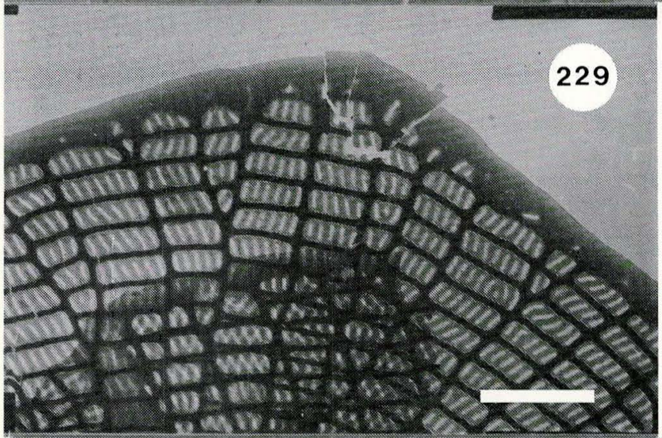
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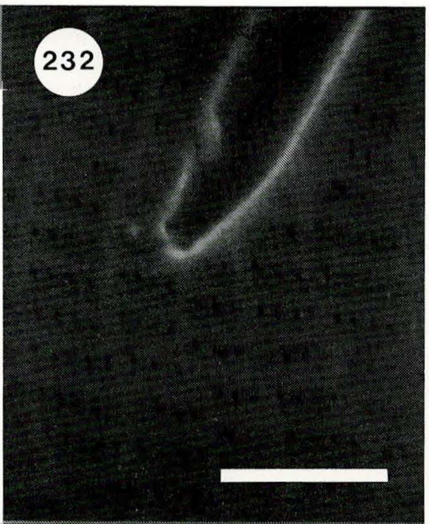
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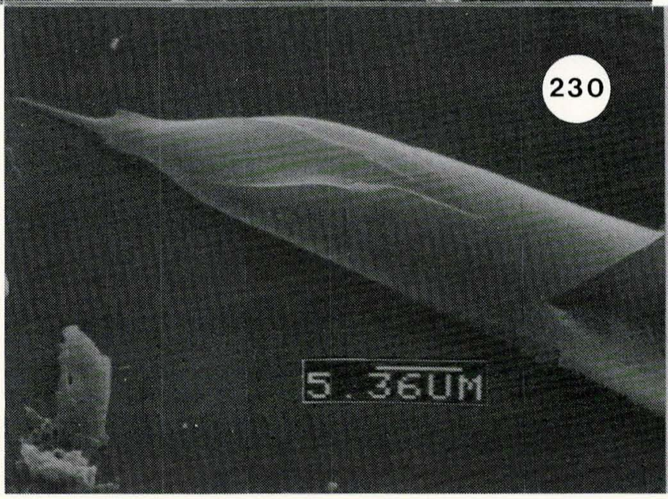
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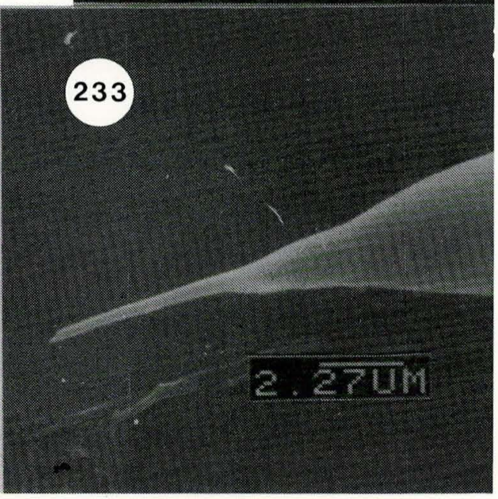
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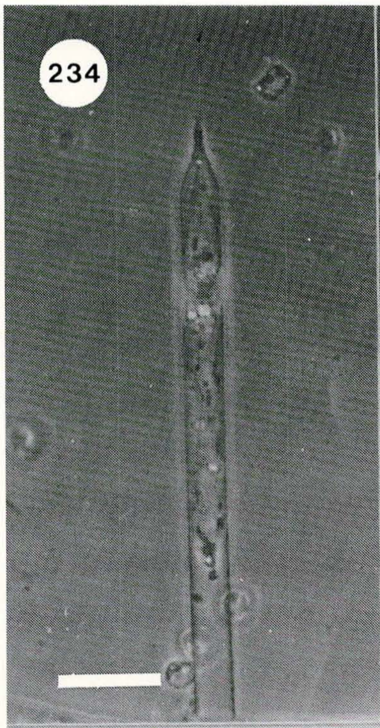
Plate 33

RHIZOSOLENIA DECIPIENS

LM: Figs 234-236. SEM: Fig. 237. TEM: Figs 238-240.

Fig. 234. (011). Part of cell in dorsiventral view. Note shape of process.
Fig. 235. (075). Part of cell in dorsiventral view. Note shape of process.
Fig. 236. Part of cell in fig. 235. Note striation.
Fig. 237. (075). Part of broken girdle. Note foramina and velum pores.
Fig. 238. (081). Part of copula. Note velum pores.
Fig. 239. (046). Distal part of valve in dorsiventral view. Note shape of process and otaria.
Fig. 240. (081). Part of girdle in lateral view, overlapping girdle segments. Note orientation of striae.

Scales: Fig. 234 = 25 µm. Figs 235, 236 = 10 µm. Fig. 240 = 5 µm.
Fig. 239 = 2 µm. Fig. 238 = 1 µm.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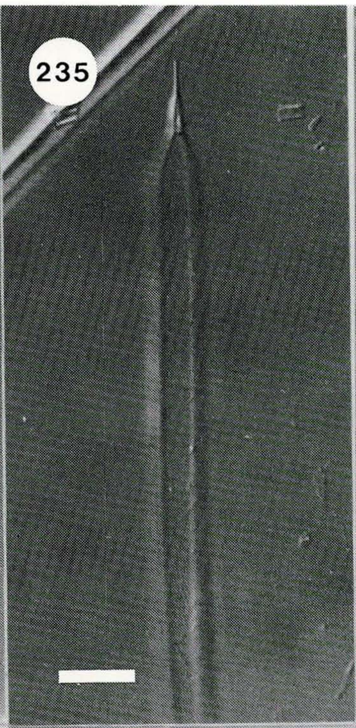
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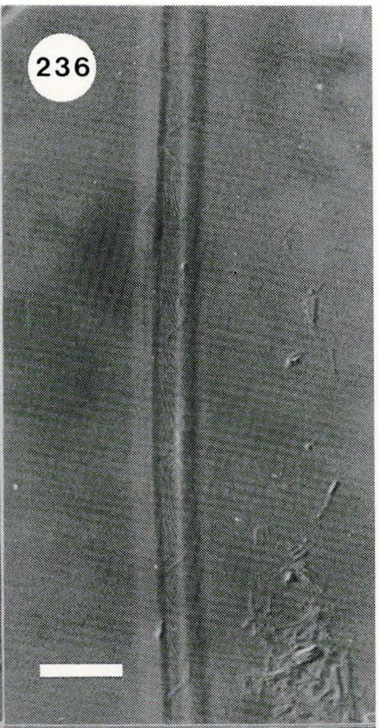
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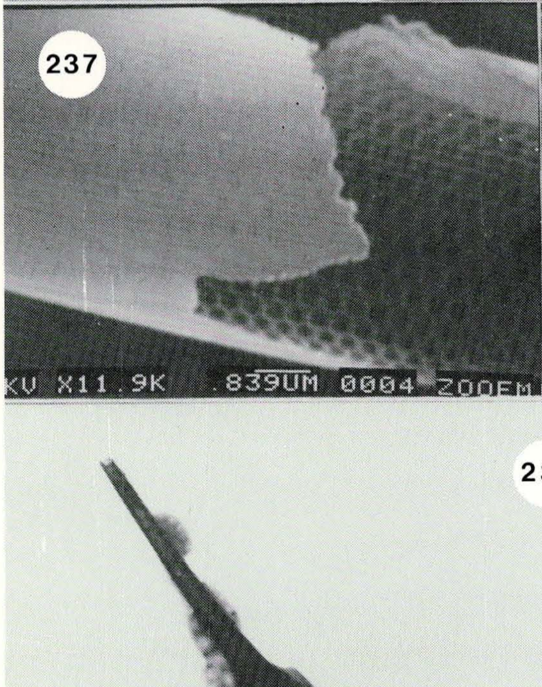
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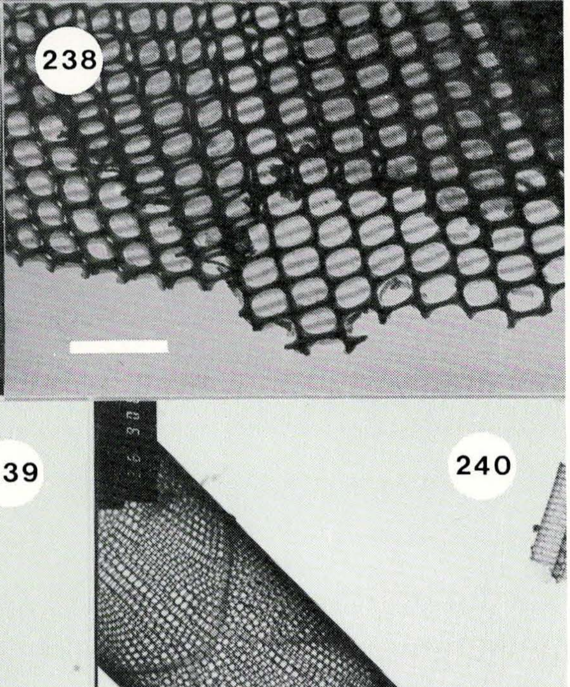

238


239


240

Plate 34

RHIZOSOLENIA CHUNII (Figs 241-244)

Rhizosolenia sp. (Figs 245, 246)

LM: Figs 241, 242. TEM: Figs 243-246.

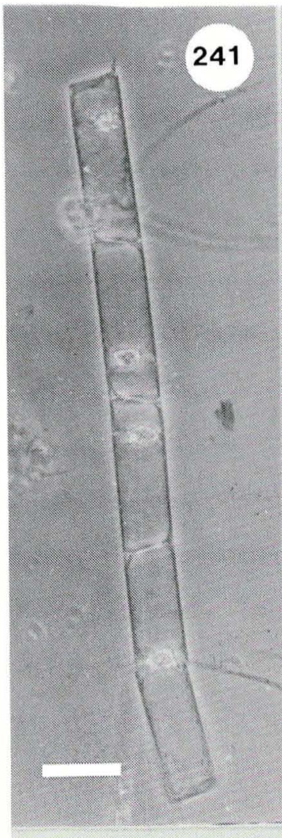
Rhizosolenia chunii.

Fig. 241. (038). Chain of cells in lateral view. Note valve face at an angle almost perpendicular to pervalvar axis.
Fig. 242. (134). Chain of cells in lateral view. Note shape of girle segments.
Fig. 243. (039). Part of frustule in lateral view. Note shape of process, and orientation of striae in proximal copula.
Fig. 244. (039). Part of copula. Note velum pores.

Rhizosolenia sp.

Fig. 245. (082). Parts of copulae. Note orientation of striae.
Fig. 246. Detail of fig. 245. Note velum pores.

Scales: Figs 241-243 = 25 µm. Fig. 245 = 5 µm. Figs 244, 246 = 1 µm.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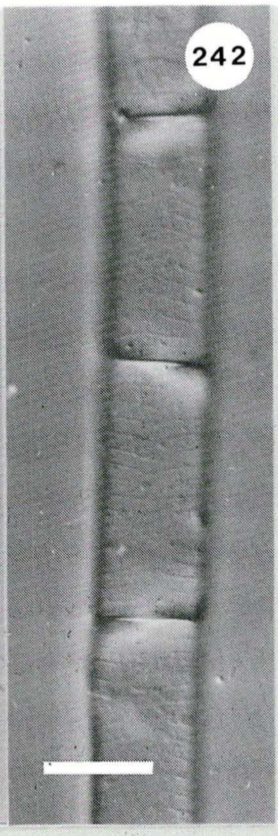
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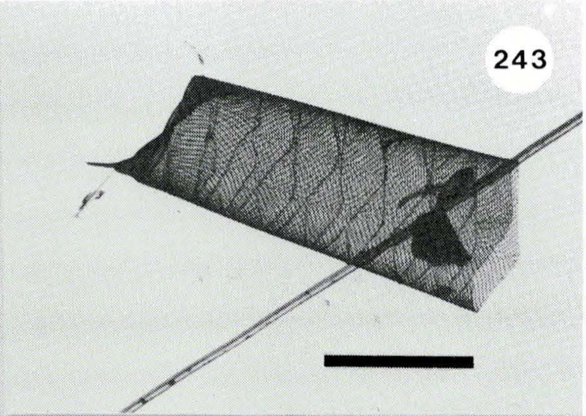
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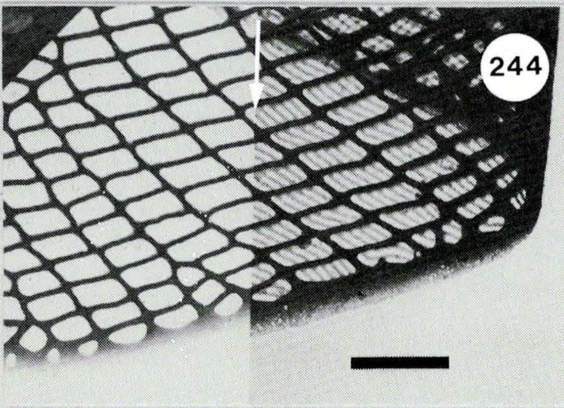
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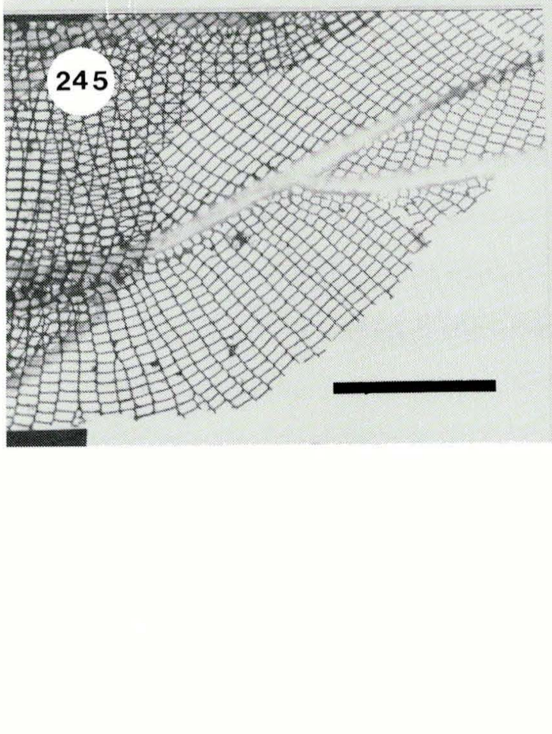
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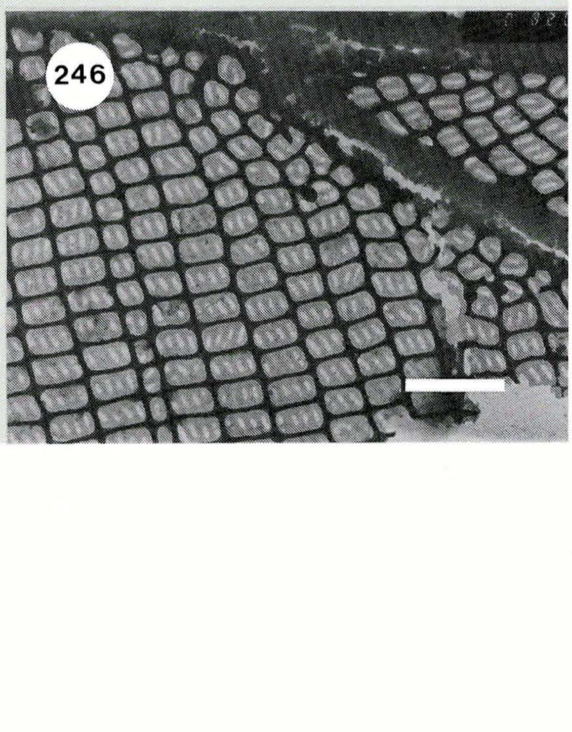
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Plate 35

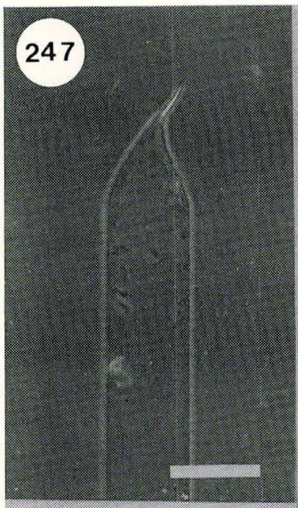
PSEUDOSOLENIA CALCAR-AVIS

LM: Figs 247- 251. SEM: Figs 252-255. TEM: Figs 256, 257.

Figs 247-249. (044). Distal part of cells. Note variation in valve shape.
Fig. 250. (009). Part of girdle. Note seam-like structure near advalvar margin of copulae (arrowheads).
Fig. 251. (009). Distal part of valve. Process in broad view.
Fig. 252. (068). Valve. Note sigmoid impression of sister-cell valve and process.
Fig. 253, 254. (074). Convoluted labiate structure from different angles.
Fig. 255. (074). Inner surface of valve. Note impression of sister-cell valve and process.
Fig. 256. (087). Part of copula. Note velum structure. Different exposures on each side of arrows.
Fig. 257. (044). Part of copula. Note seam-like structure (arrowheads) and edges of marginal zone (entire).

Scales: Figs 247-249 = 100 µm. Figs 250, 251 = 50 µm. Fig. 257 = 5 µm. Fig. 256 = 1 µm.

247



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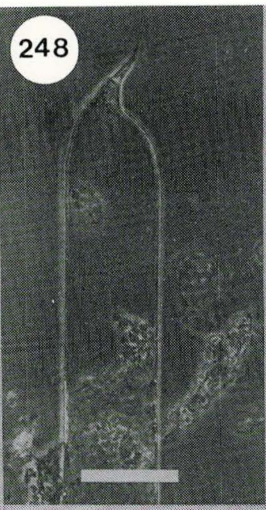

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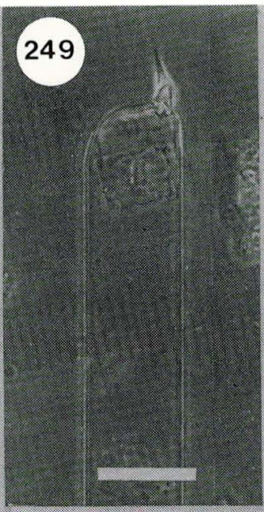

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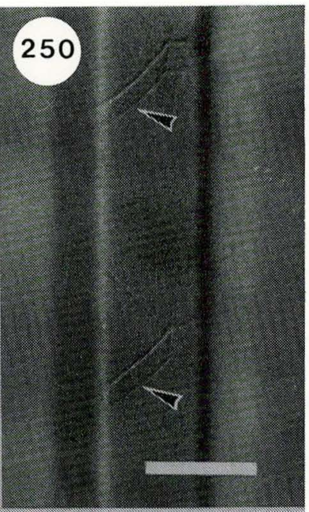

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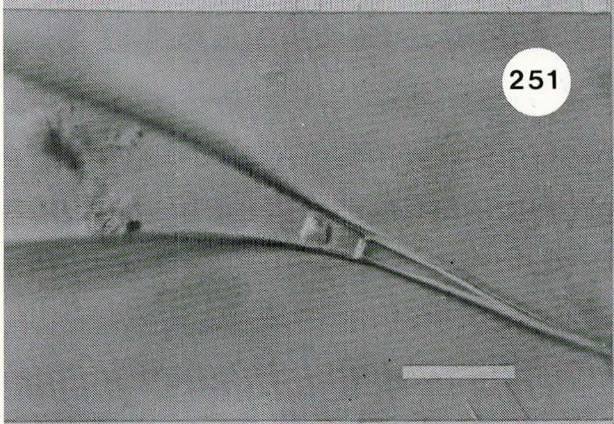

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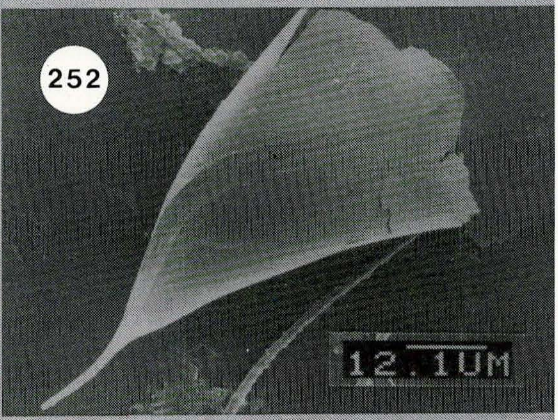

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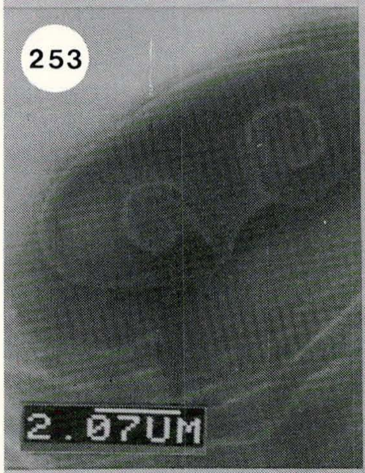

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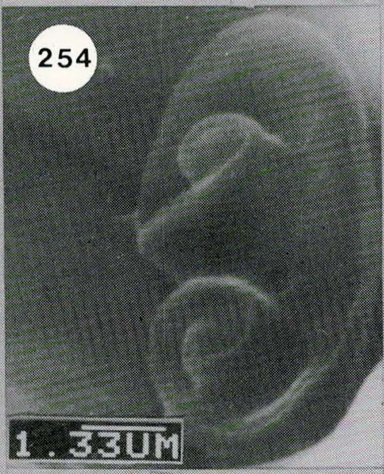

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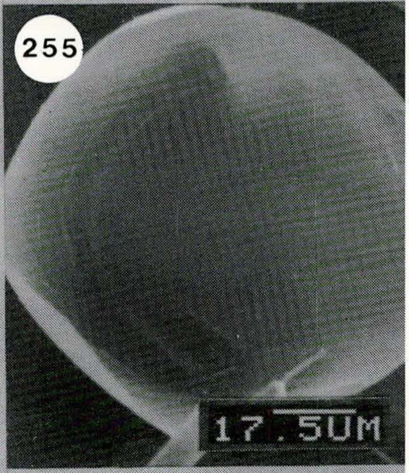

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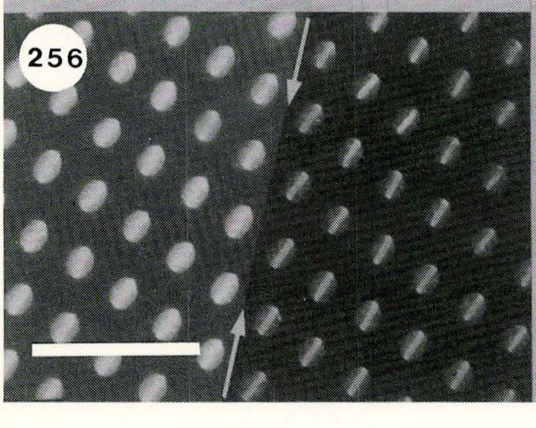

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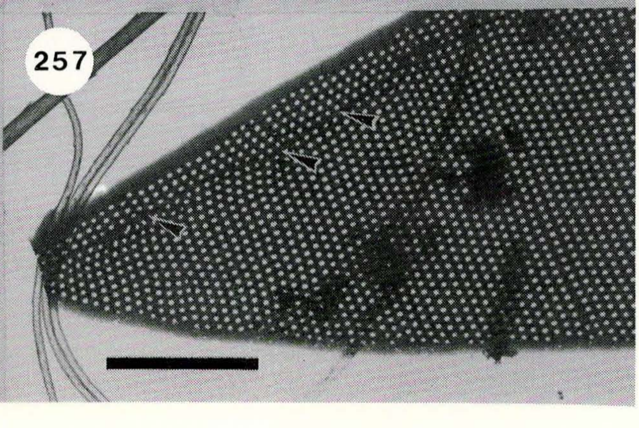


Plate 36

PROBOSCIA ALATA (Figs 258-266)

Proboscia spp. (Fig. 267)

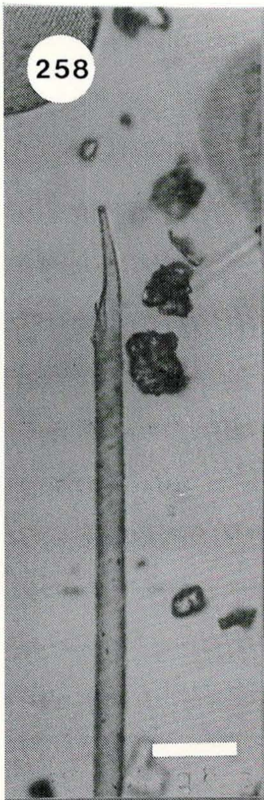
LM: Figs 258-261. SEM: Figs 262, 263. TEM: Figs 264-267.

Figs 258, 259. (109). Part of two cells showing valves viewed from different angles.
Fig. 260. (Laholm Bay, Sweden). Terminal initial cell.
Fig. 261. (004). Detached theca of initial cell. Note smooth surface of valve.
Fig. 262. (Transect Göteborg-Fredrikshavn). Copula. Note irregularly distributed interlocular pores.
Fig. 263. (Transect Göteborg-Fredrikshavn). Valve. Note unequal claspers (arrowhead).
Fig. 264. (007). Valve.
Fig. 265. (Transect Göteborg-Fredrikshavn). Part of copula. Note interlocular pores, each surrounded by six areolae.
Fig. 266. (007). Part of copula. Note velum pore, and triangular columellae in the middle of each areolar triad.

Proboscia spp.

Fig. 267. (088). Parts of copulae of two (one ?) *Proboscia* species. Note varying areolar size and varying number of velum pores.

Scales: Figs 258-261 = 25 µm. Fig. 263 = 10 µm. Figs 262, 264 = 5 µm.
Figs 265, 267 = 1 µm. Fig. 266 = 0.5 µm.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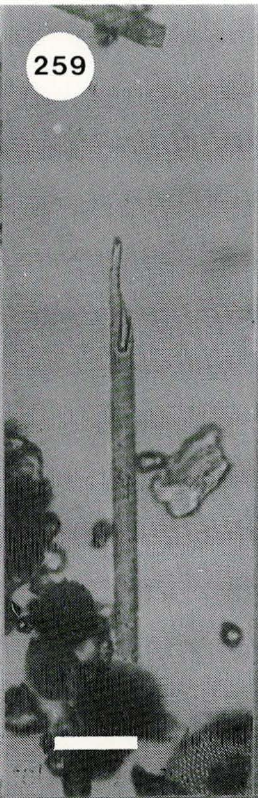
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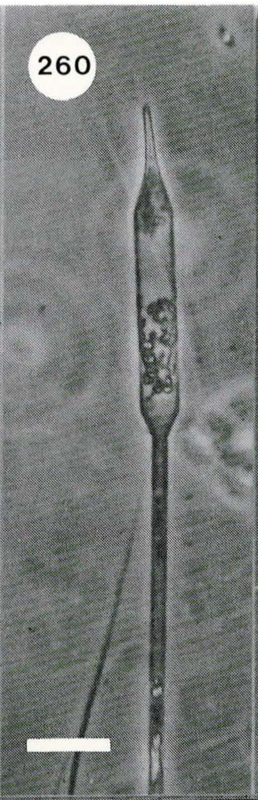
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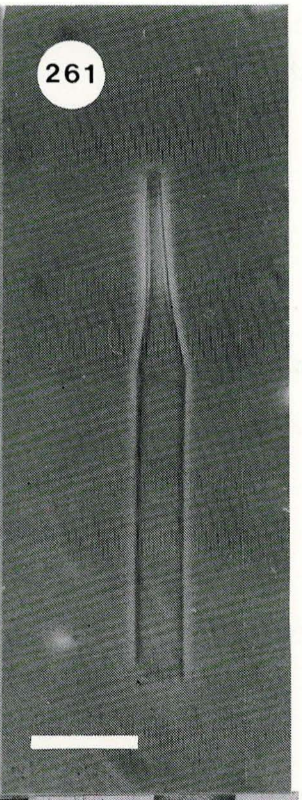
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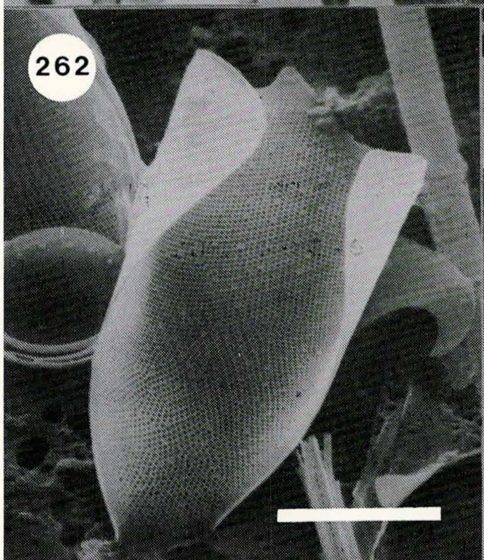
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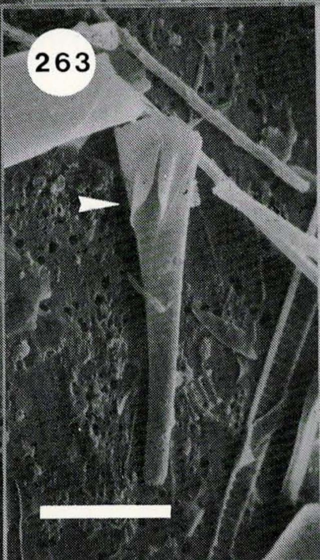
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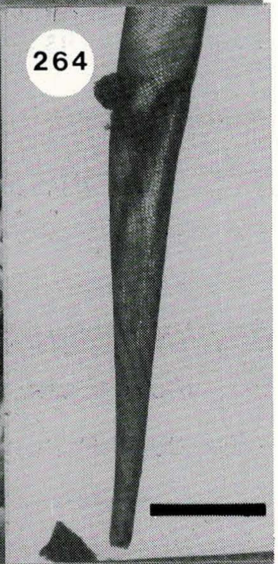
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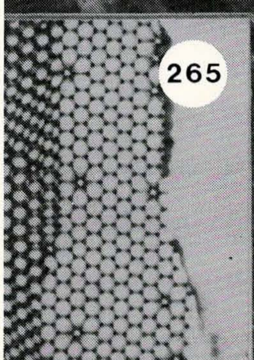
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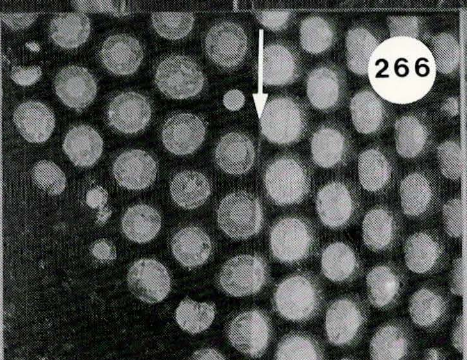
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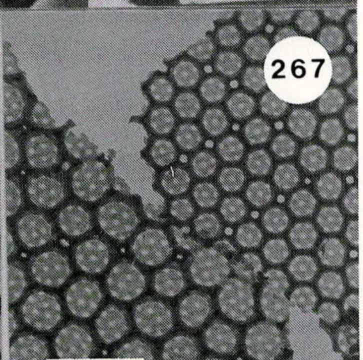
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Plate 37

Rhizosolenia fragilissima	(Figs 268, 269)
Rhizosolenia phuketensis	(Figs 270, 271)
Rhizosolenia delicatula	(Figs 272, 273)

SEM: Figs 268, 270. TEM: Figs 269, 271-273.

Rh. fragilissima

Fig. 268. (004). Valve in oblique view. Note process to the left and pocket-like invagination to the right.
Fig. 269. (081). Distal part of dessicated frustule.

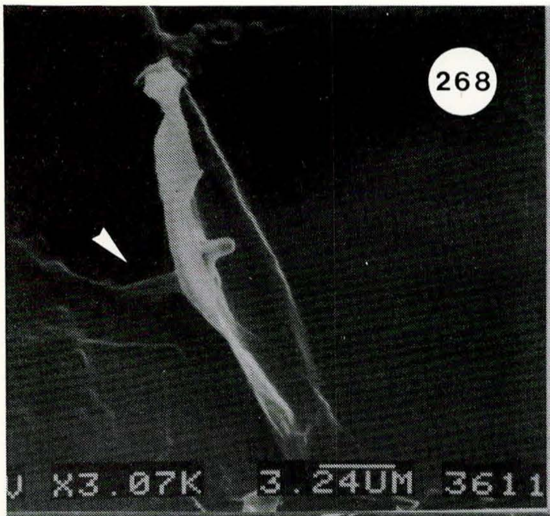
Rh. phuketensis

Fig. 270. (070). Part of dessicated frustule. Note eccentric position of process and pocket-like invagination.
Fig. 271. (Ko Phuket, 6.11 1980). Parts of copulae. Note pore pattern.

Rh. delicatula

Fig. 272. (004). Dessicated valve partly covered by girdle segment. Note process (arrowheads) and depression for sister-cell process.
Fig. 273. (004). Parts of copulae. Note pore pattern.

Scales: Figs 269, 271 = 5 µm. Figs 272, 273 = 2 µm.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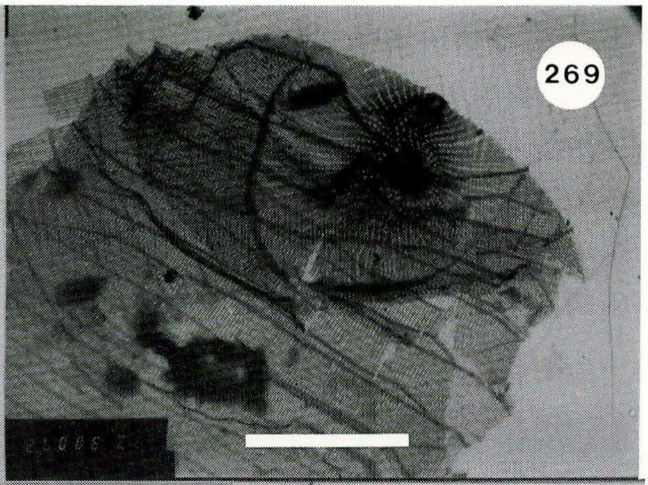
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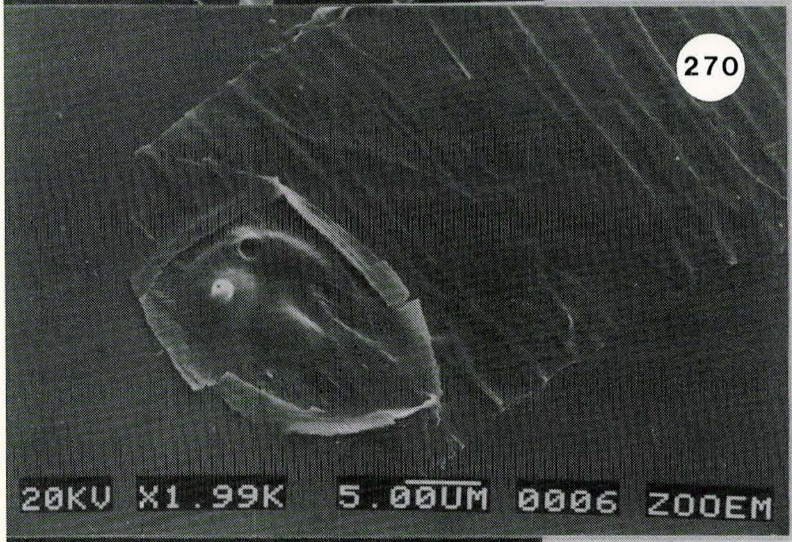
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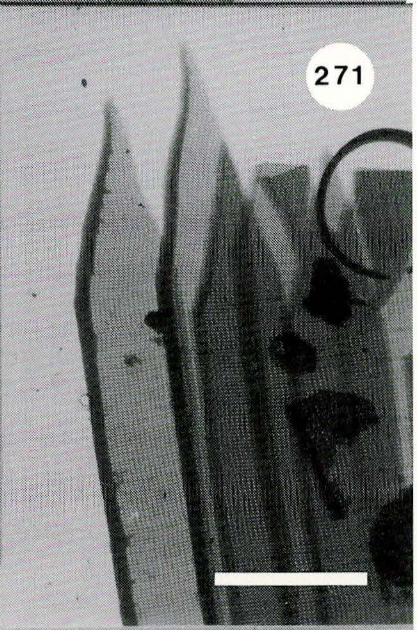
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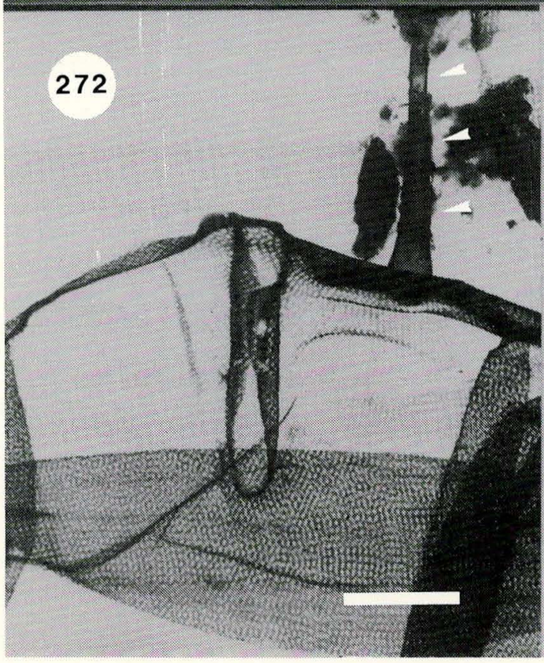
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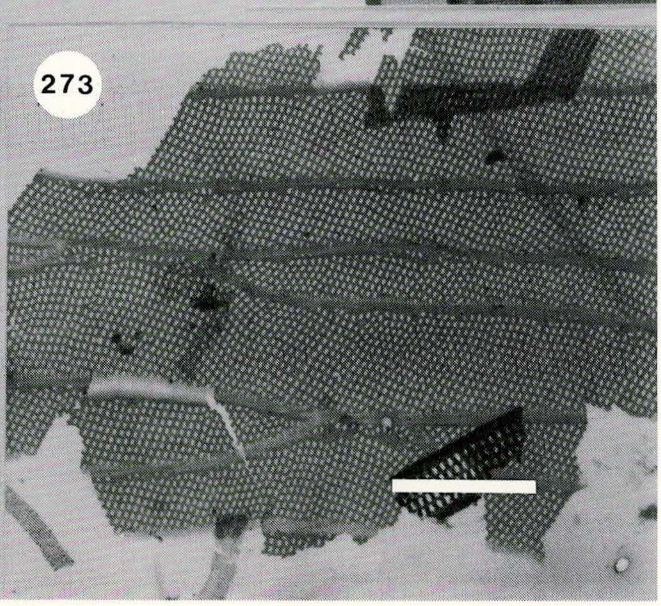
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Plate 38

Rhizosolenia stolterfothii	(Figs 274, 275)
Rhizosolenia cylindrus	(Figs 276-278)
Rhizosolenia antarctica	(Figs 279-281)

LM: Figs 276, 279. TEM: Figs 274, 275, 277, 278, 280, 281.

Rh. stolterfothii

Fig. 274. (Ko Phuket, 6.11 1980). Valve (partly covered by copula of other species). Note difference in silicification of valve face and mantle. Note also depression for sister-cell process (arrowhead).
Fig. 275. (081). Parts of copulae. Note pore pattern.

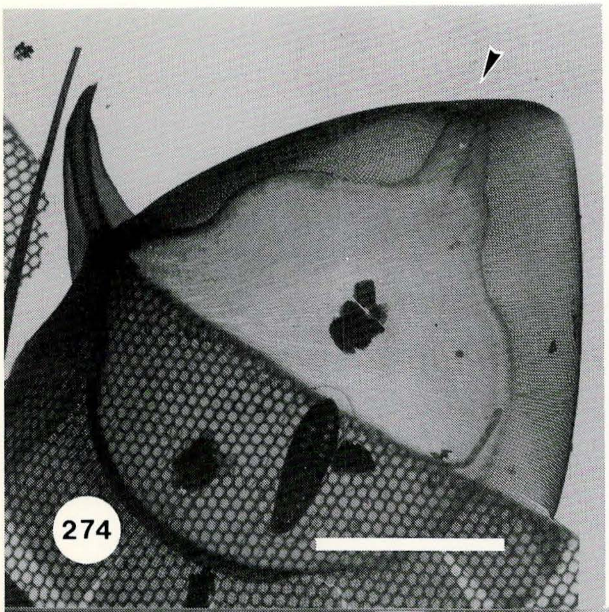
Rh. cylindrus

Fig. 276. (Ko Phuket, 19.2 1980). Distal part of cell. Note outline of valve.
Fig. 277. (019). Valve fragment. Note V-shaped depression for distal part of sister-cell process.
Fig. 278. (081). Parts of copulae. Note pore pattern.

Rh. antarctica

Fig. 279. (038). Cells held together by girdle of mother cell.
Fig. 280. (039). Process (arrowheads).
Fig. 281. (039). Parts of copulae (overlapping in lower part of figure).

Scales: Figs 276, 279 = 25 µm. Fig. 274 = 10 µm. Fig. 277 = 5 µm.
Figs 275, 278, 280 = 2 µm. Fig. 281 = 1 µm.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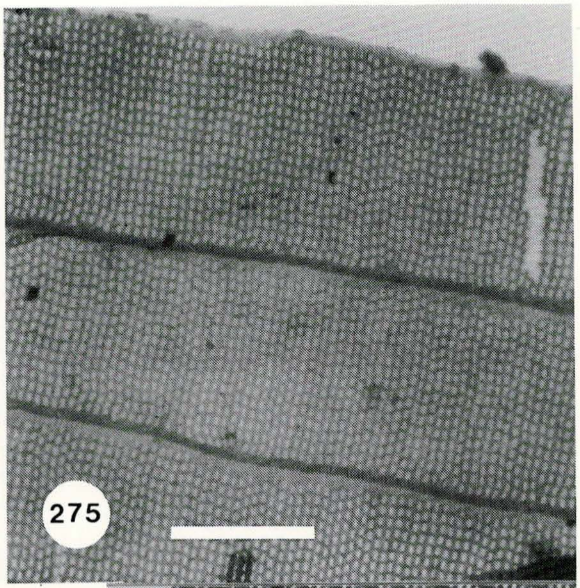
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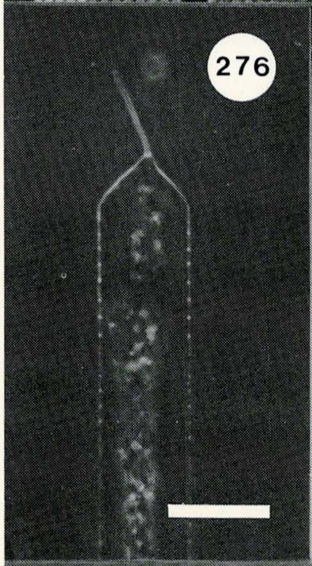
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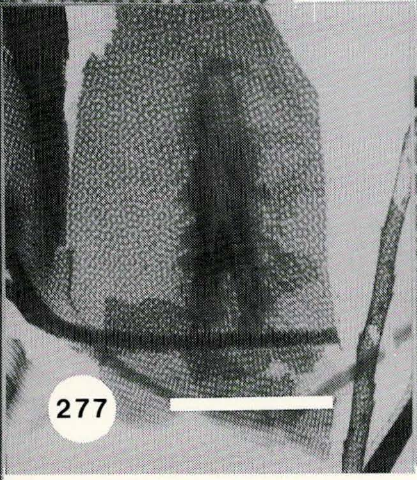
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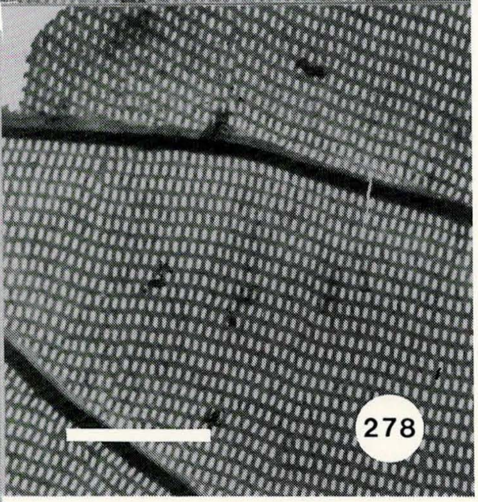
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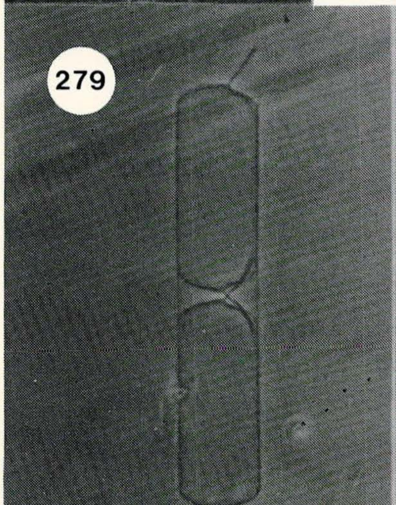
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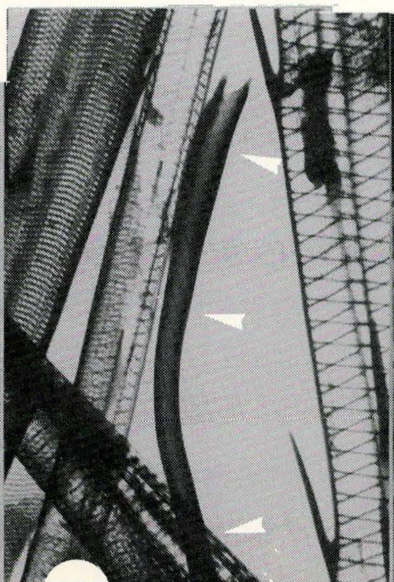
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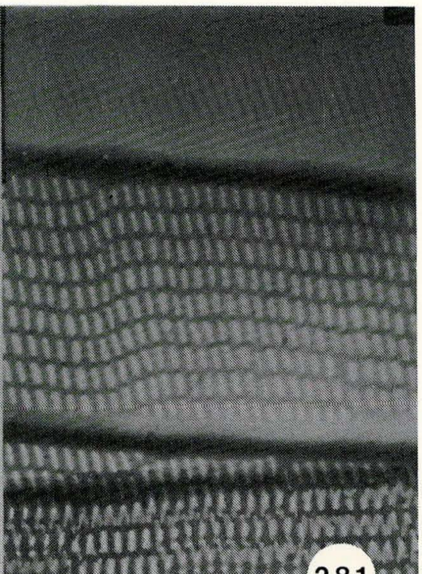
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Plate 39

Rhizosolenia tubiformis	(Figs 282-285)
Rhizosolenia setigera (sensu lato)	(Figs 286, 287)
Rhizosolenia pungens	(Fig. 288)
Rhizosolenia robusta	(Figs 289, 290)
Lauderiopsis costata	(Fig. 291)

LM: Fig. 282. SEM: Fig. 289. TEM: Figs 283-288, 290, 291.

Rh. tubiformis

Fig. 282. (038). Complete cell.
Fig. 283. (038). Partly overlapping girdle segments. Note pore pattern.
Fig. 284. (038). Part of dessicated frustule. Note small dome-shaped process.
Fig. 285. (038). Process. Note small pore.

Rh. setigera (sensu lato)

Fig. 286. (Ko Phuket, 6.11 1980). Parts of girdle segments
Fig. 287. (Ko Phuket, 6.11 1980). Parts of girdle segments. Note pore pattern.

Rh. pungens

Fig. 288. (005). Part of girdle segment (partially dissolved). Note pore pattern.

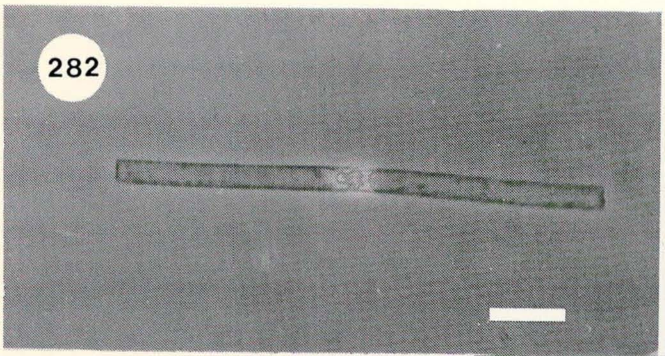
Rh. robusta

Fig. 289. (023). Valve apex. Note process protruding from cup-shaped structure.
Fig. 290. (016). Valve apex. Note homogeneous silicification of cup-shaped structure and part of internal labiate structure.

Lauderiopsis costata

Fig. 291. (Ko Phuket). Below; part of valve. Above; part of valvocopula, note pore pattern.

Scales: Figs 282, 286 = 10 µm. Fig. 284 = 5 µm. Figs 287, 288, 290, 291 = 2 µm.
Fig. 283 = 1 µm. Fig. 285 = 0.5 µm.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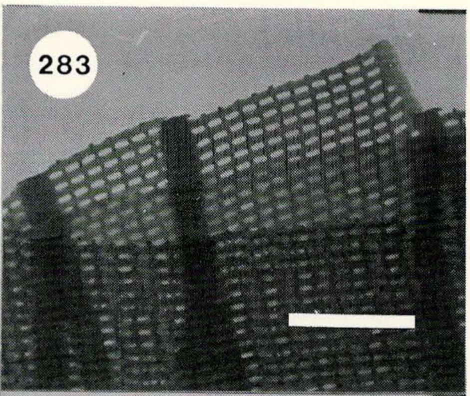
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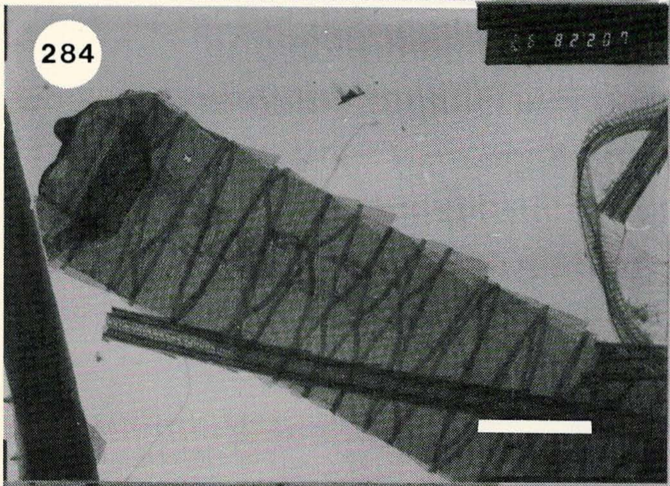
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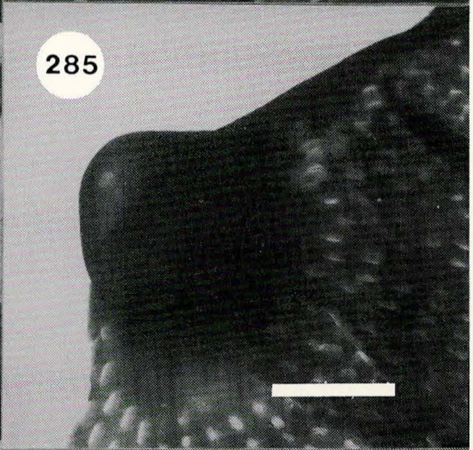
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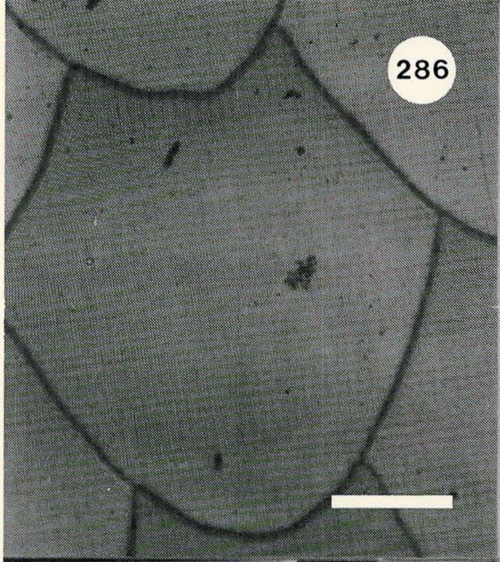
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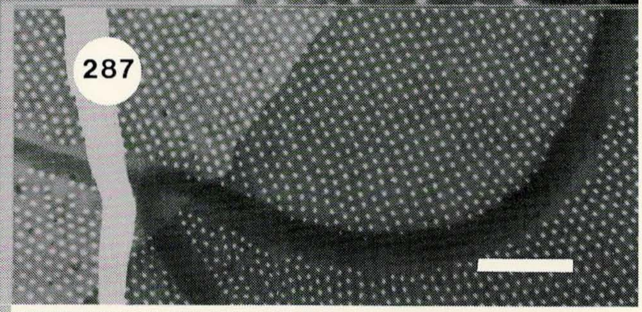
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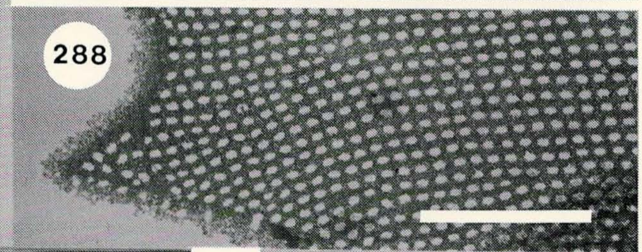
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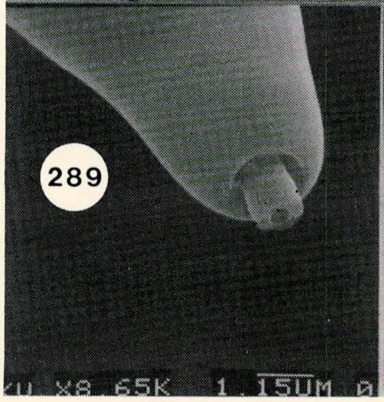
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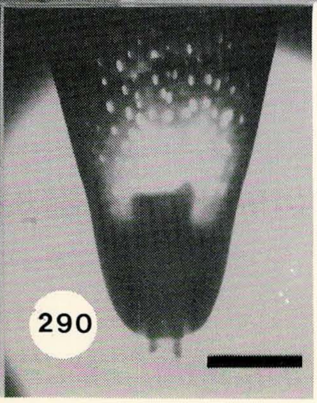
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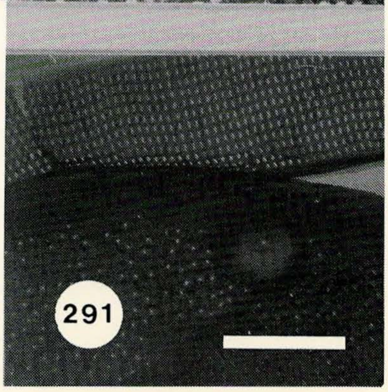
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