CHOANOFLAGELLATES IN THE ANTARCTIC OCEAN, WITH SPECIAL REFERENCE TO *PARVICORBICULA SOCIALIS* (MEUNIER) DEFLANDRE

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Abstract: Distribution and morphology of choanoflagellates, collared heterotrophic flagellates bearing an extracellular siliceous lorica, were reviewed.

Eleven species were reported from the Antarctic Ocean. Three of the eleven species were originally described from the Antarctic and are known to be endemic to the Antarctic. The other eight were found in various oceanic areas. Choanoflagellates had been found in both ice and water, which suggested their wide and abundant distribution in the Antarctic. Ecological significance of the choanoflagellate, *Parvicorbicula socialis* (MEUNIER) DEFLANDRE, most common species in the Antarctic, was stressed as the food of the Antarctic krill, *Euphausia superba* DANA.

Morphological variation of the lorica structure of *P. socialis,* caused by water temperature, was discussed on specimens collected in various oceanic areas from polar to equatorial.

1. Outline of Choanoflagellates

The choanoflagellates are a well defined group of colorless protozoa characterized by a single flagellum surrounded by a ring of tentacles (collar) at the anterior end of the protoplast (Figs. la, b). The systematic position of choanoflagellates is under subkingdom Protozoa, phylum Sarcomastigophora, class Zoomastigophora, order Choanoflagellida (LEVINE *et al.*, 1980). The order Choanoflagellida is divided into three families according to the existence and the structure of an investment (NORRIS, 1965); cells in Codonosigidae are naked (Figs. 1a, b), protoplasts within Salpingoecidae are surrounded by an investment of organic matter, and protoplasts in Acanthoecidae are suspended within loricae, built up from interconnected rod-shaped or flattened silicified bars known as costae (Figs. 1c, d). Each costa is composed of linearly attached subunits known as costal strips (LEADBEATER, 1972; MANTON *et al.*, 1975) (Fig. 2). Many of the marine species belong to the family Acanthoecidae (MANTON *et al.*, 1976). All certainly attested members of the choanoflagellates appear to be heterotrophic, engulfing bacteria and detritus (LEADBEATER and MANTON, 1974; LEADBEATER and MORTON, 1974). The site of ingestion is the body surface just outside the ring of tentacles. Ingestion is performed by means of pseudopodia, which may be developed from the base of the tentacle ring (LEADBEATER and MORTON, 1974).

Forms of choanoflagellates, at least their protoplasts, are so small that they have only become prominent in the literature since electron microscopes were applied in the studies of small plankton (LEADBEATER, 1972). During the last ten years, however,

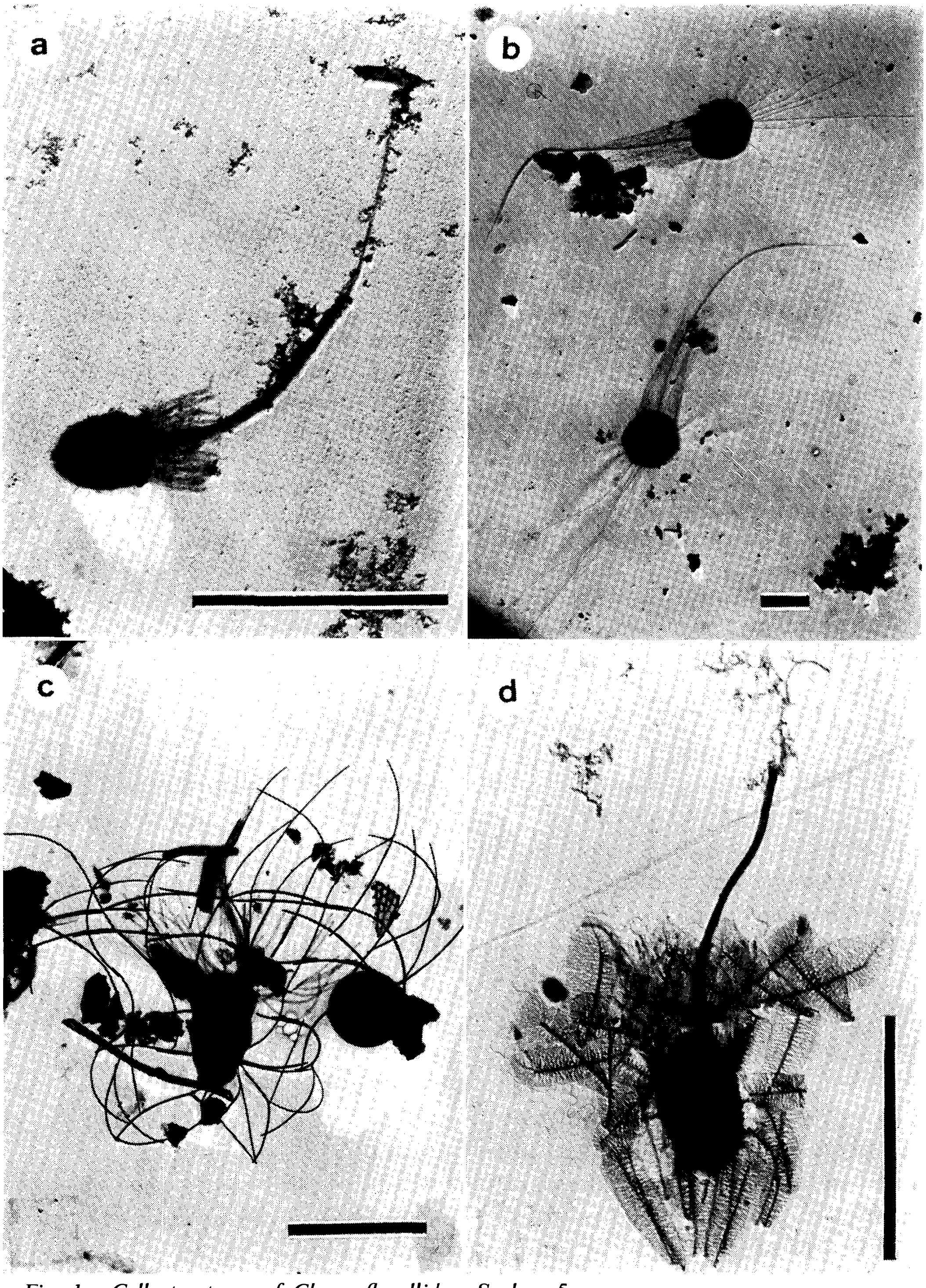

Fig. 1. Cell structures of Choanoflagellida. Scales: 5 μm.

a and b: Cells of Codonosigidae (Monosiga *spp.*) *with a flagellum surrounded by a rhizopodial collar. Cells shown in Fig. 1b are carrying also long posterior tentacles.*

c and d: Cells of Acanthoecidae (Acanthocorbis apoda (*LEADBEATER*) *HARA and TAKAHASHI in c and* Syndetophyllum pulchellum (*LEADBEATER*) *THOMSEN and MOESTRUP in d*). *A Codonosigidae-like protoplast is invested in the silicified lorica.*

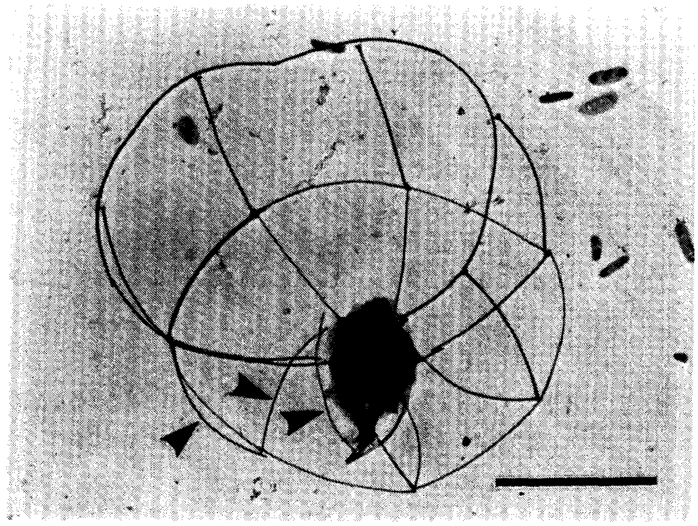

Fig. 2. A lorica structure of Pleurasiga minima *THRONDSEN (Acanthoecidae). The lorica comprises two transverse costae and seven longitudinal costae. Each costa is composed of rod-shaped costal strips (arrowheads indicating three costal strips constituting a longitudinal costa). Scale: 5 μm*

there have been numerous studies on the taxonomy of choanoflagellate species in the sea, especially concerning members of Acanthoecidae, in which the protoplast is surrounded by a basket-like lorica composed of siliceous costae.

The sea water samples taken from all latitudes have been studied, *e.g.* arctic waters (MANTON *et al.*, 1981), subarctic waters (BOOTH *et al.*, 1982), northern temperate waters (HARA, 1984; HARA and TAKAHASHI, 1984; LEADBEATER, 1980; MANTON *et al.*, 1980; TAKAHASHI, 1981a), tropical and subtropical waters (THOMSEN, 1978; THOMSEN and BOONRUANG, 1983; MANTON and BREMER, 1981), southern temperate waters (MOESTRUP, 1979; MANTON *et al.*, 1980), and antarctic waters (BUCK, 1981; TAKAHASHI, 1981b; TANOUE and HARA, 1984). The Acanthoecidae comprises for the moment about 75 species. The range of the environment in which the Acanthoecidae are able to live is known to vary from −2.4°C (antarctic water in BUCK, 1981) to 28°C (coast of Thailand in THOMSEN and BOONRUANG, 1983) in water temperature and from 3 g/kg (coast of Finland in THOMSEN, 1979) to 40 g/kg (Red Sea in THOMSEN, 1978) in salinity. From a qualitative point of view, they form one of the most prominent groups of marine nanoplankton (HARA, 1984; LEADBEATER and MANTON, 1974; MOESTRUP, 1979; THOMSEN, 1979; THOMSEN and BOONRUANG, 1983).

Although intensive studies have been carried out on the taxonomy of Acanthoecidae, there have been fewer investigations on their qualitative contribution to nanoplanktonic communities in the marine ecosystem, despite the fact that they dominate the colorless nanoplankton in arctic neritic waters (MANTON *et al.*, 1975), subarctic oceanic waters (BOOTH *et al.*, 1982), and temperate neritic waters (HARA, 1984). Species of Acanthoecidae may be among the most common and the most abundant members of nanoplankters distributed in the surface sea waters of the world.

2. Acanthoecidae in the Antarctic Ocean

A species of loricate choanoflagellates (Acanthoecidae) was reported by DEFLANDRE (1960) to be rather abundant in Adélie Land, and it was described as a new combination *Parvicorbicula socialis* (MEUNIER) DEFLANDRE. Eleven species of Acanthoecidae, including *P. socialis*, have been recorded in samples obtained from the Weddell Sea (BUCK, 1981) and from Lützow-Holm Bay (TAKAHASHI, 1981b). Moreover, the presence of many undescribed species of Acanthoecidae in the antarctic waters has been pointed out by TAKAHASHI (1981b). The present authors also found *P. socialis* in a pack-ice area of the Antarctic Ocean (65°50.6′S, 155°16.1′E) during the cruise of the T/S UMITAKA MARU of Tokyo University of Fisheries in 1980–1981 (BIOMASS Cruise) (Table 1).

Table 1. Species of Acanthoeciade recorded in nanoplankton investigations in Terre Adélie (DEFLANDRE, 1960), Weddell Sea (BUCK, 1981), Lützow-Holm Bay (TAKAHASHI, 1981b) and 65°50.6′S, 155°16.1′E (present study).

	Terre Adélie	Weddell Sea	Lützow-Holm Bay	65°50.6′S, 155°16.1′E
Bicosta antennigera		+	+	
B. spinifera		+	+	
Calliacantha multispina		+		
C. natans			+	
C. simplex		+		
Crinolina aperta		+	+	
Diaphanoeca multiannulata		+	+	
*D. pedicellata**		+		
Parvicorbicula ongulensis			+	
P. socialis	+	+	+	+
Saepicula leadbeateri			+	

* A micrograph illustrated under the name of *Acanthoecopsis spiculifera* in BUCK (1981).

The Antarctic Ocean is the type locality of three of the eleven species mentioned above, *viz. Diaphanoeca multiannulata* BUCK, *Parvicorbicula ongulensis* TAKAHASHI, and *Saepicula leadbeateri* TAKAHASHI. These three species are at present collected from the Antarctic Ocean only. The other eight species have been reported from various parts of the world (THOMSEN, 1976, 1978, 1979; MANTON and OATES, 1979; MANTON *et al.*, 1980).

The Antarctic Ocean is characterized by ice, in which choanoflagellates can live. Indeed nine of the eleven species recorded in the Antarctic Ocean were known as ice-dwelling choanoflagellates (BUCK, 1981; TAKAHASHI, 1981b). Only one of the nine ice-dwelling species was restricted to the ice-habitat. The other eight species were found in both water and ice. Only two species of the antarctic choanoflagellates were known to be distributed in the water column only. Many species of Acanthoecidae can live in ice as well as in water column. Further investigations are expected to elucidate whether or not there are any other ice-dwelling species of Acanthoecidae in a narrow sense.

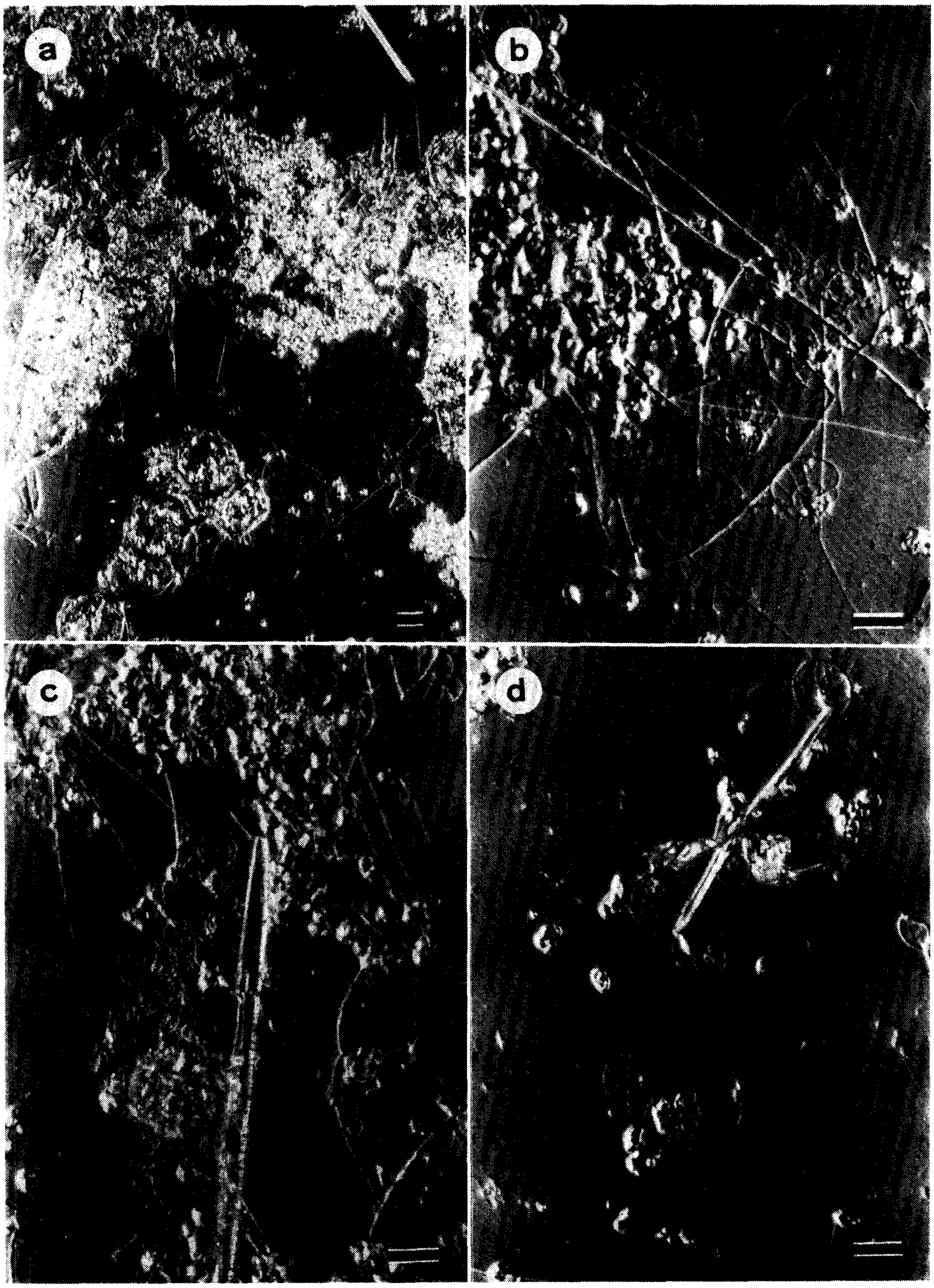

Fig. 3. A net plankton community at the edge of pack-ice area, 65°50.6'S, 155°16.1'E, in the Antarctic Ocean (NOMARSKY interference). Scales: 10 μm.
a: A low magnification image indicating clustae of large centric diatoms.
b, c and d: High magnification image revealing abundant population of Parvicorbicula socialis (*MEUNIER*) *DEFLANDRE*.

The choanoflagellate population in the Antarctic Ocean remains unclear, since only a little quantitative data are available on the antarctic nanoplankton. However, a subdominant population of choanoflagellates in the sea ice as well as in the sea water in Lützow-Holm Bay was revealed by TAKAHASHI (1981b). Our observation on a net sample (Norpac net, XX13), collected in the pack-ice area of the Antarctic Ocean, at 65°50.6′S, 155°16.1′E, also indicated that the proportion of choanoflagellate cells to diatom cells is very high (Fig. 3). Choanoflagellates may be among the most abundant nanoplankters in the Antarctic Ocean.

3. *Parvicorbicula socialis* (MEUNIER) DEFLANDRE

P. socialis is one of the most popular species in Acanthoecidae (MANTON *et al.*, 1976). The form of the lorica of this species is shown in Fig. 4. The lorica is composed of a conical lorica chamber, without anterior spine, with or without posterior spine (MANTON *et al.*, 1976). The lorica chamber comprises 10 longitudinal costae and 2 transverse costae.

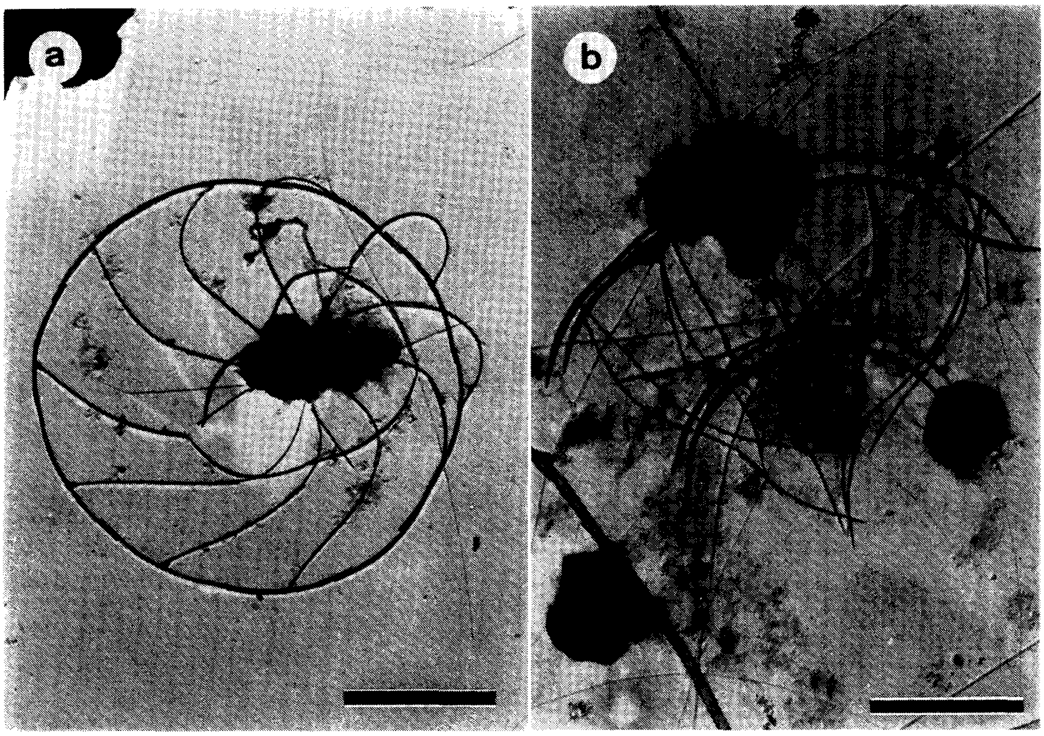

Fig. 4. A lorica structure of Parvicorbicula socialis *(MEUNIER) DEFLANDRE. The lorica comprises two transverse and ten longitudinal costae which are composed of costal strips. a: Upper oblique view. b: Side view. Scales: 5 μm.*

3.1. Distribution of P. socialis in the Antarctic Ocean

BUCK (1981) suggested that *P. socialis* was the most widely distributed species in the Weddell Sea. The habitat of this species in the Weddell Sea was diverse (*e.g.*, water column, ice floe pond and ice floe itself). Its known distribution in the Antarctic Ocean is shown in Fig. 5 (DEFLANDRE, 1960; BUCK, 1981; TAKAHASHI, 1981b). Although only

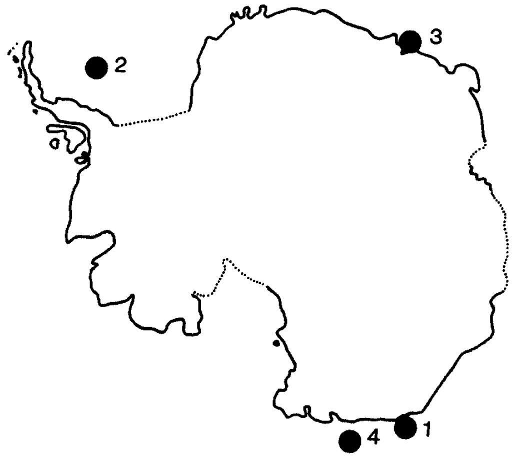

Fig. 5. A map showing the known distribution of Parvicorbicula socialis *(*MEUNIER*)* DEFLANDRE *in the Antarctic Ocean. (1, Terre Adélie in* DEFLANDRE*, 1960; 2, Weddell Sea in* BUCK*, 1981; 3, Lützow-Holm Bay in* TAKAHASHI*, 1981b; 4, 65°50.6'S, 155°16.1'E in the present study).*

four reports are available to estimate the distribution of this species in the Antarctic Ocean, the investigated fields in these reports were scattered around the pack-ice area in the Antarctic Ocean. The extensive distribution of *P. socialis* in the pack-ice area of the Antarctic Ocean is suggested.

At present, quantitative information on the mass of this species in the Antarctic Ocean is very poor. However, DEFLANDRE (1960) reported a rather great community of *P. socialis* in Adélie Land. Almost all the choanoflagellate organisms in the net sample (Norpac net; 65°50.6'S, 155°16.1'E) collected and examined by the present authors were cells of *P. socialis* (Fig. 3). This species may be the most abundant among the choanoflagellates, at least in Adélie Land and the vicinity.

3.2. Ecological importance of P. socialis in the Antarctic Ocean

Although large-scale distribution of many choanoflagellates in the Antarctic Ocean has been suggested, little investigation has been made on their ecological contribution to the antarctic ecosystem. On the other hand, as the krill, *Euphausia superba* DANA, is the key species in the antarctic ecosystem, it is extremely important to clarify the food of the krill, to elucidate the food web and the energy flow in the ecosystem. The electron micrographs of the fecal pellets of *E. superba* kept in running sea water on board (TANOUE and HARA, 1984) (Fig. 6) and the light micrographs of the net sample of plankton in this sea water (Fig. 3) revealed that the fecal pellets of the krill included many costal strips of *P. socialis* together with numerous fractions of the frustules of diatoms. The krill, *E. superba*, has been thought to be strongly herviborous (KAWAMURA, 1981). However, the numerous costal strips of *P. socialis* found in the fecal pellets of the krill indicate that the krill is an omnivore feeding on zooplankton (*e.g. P. socialis*) in addition to phytoplankton (*e.g.* diatoms). Moreover, as choanoflagellates are known to be bacteriophagous, the existence of a food-chain bacteria *via* choanoflagellates to the krill and then to other animals of higher levels is suggested in the Antarctic Ocean.

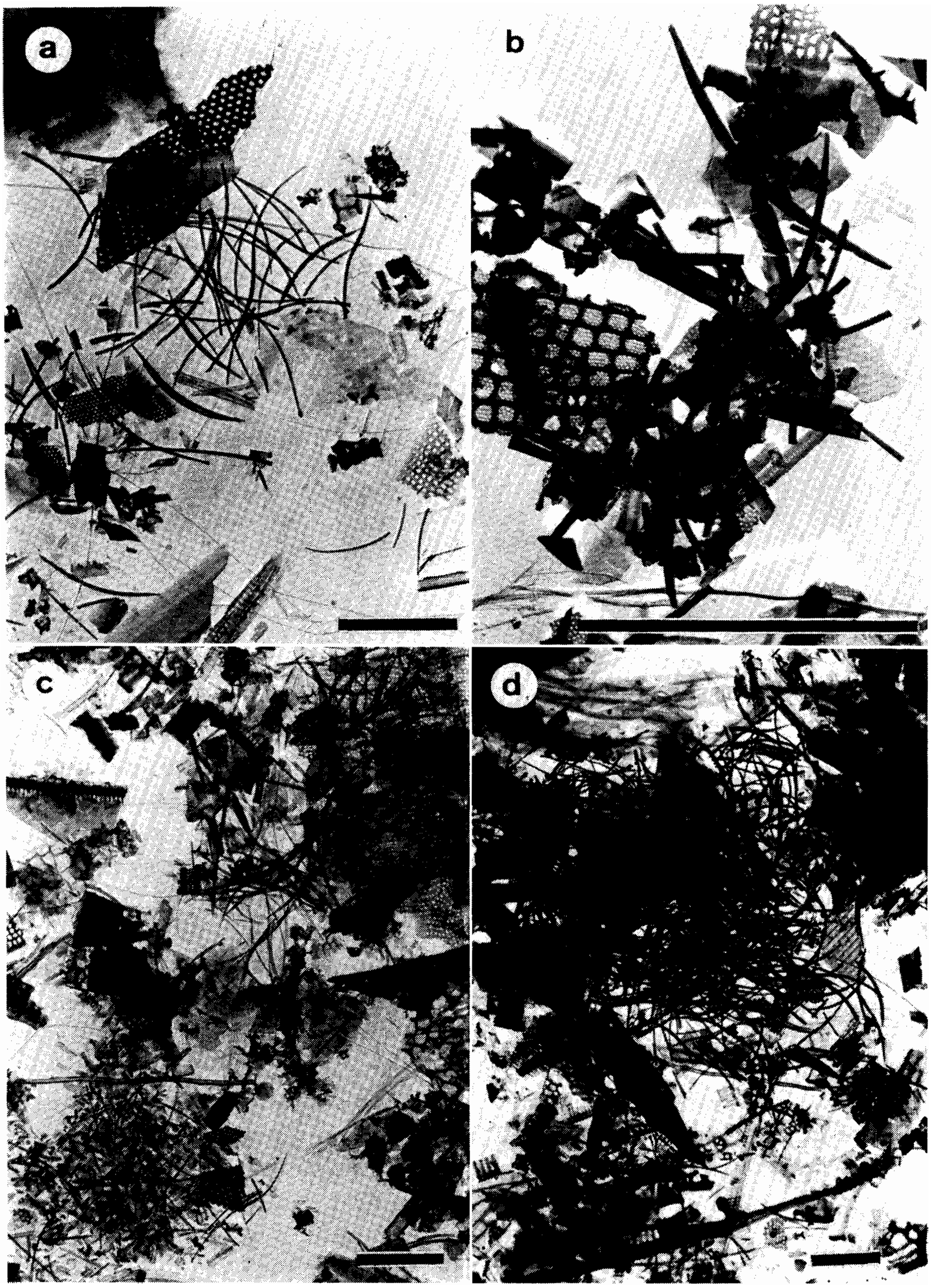

Fig. 6. Electron micrographs of fecal pellets of Euphausia superba *DANA, revealing numerous costal strips forming the lorica of Acanthoecidae* (Parvicorbicula socialis) *besides fractions of diatom frustules (a and b). Very often the costal strips are gathered in dense clusters (c and d). Scales: 5 μm.*

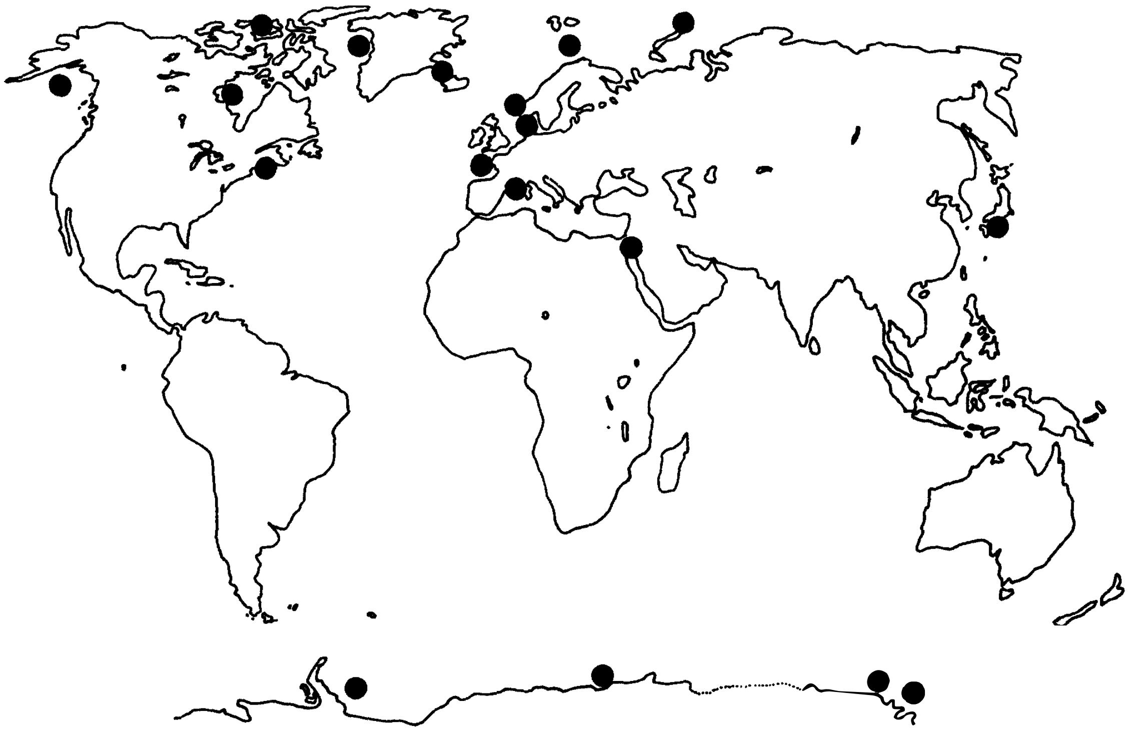

Fig. 7. A map showing the known distribution of Parvicorbicula socialis (*MEUNIER*) *DEFLANDRE in the world.*

3.3. Taxonomy of P. socialis

Individuals of *P. socialis* were collected from various parts of the world (Fig. 7), including tropical waters as well as the two polar seas (MANTON *et al.*, 1976; THOMSEN, 1978; BUCK, 1981; TAKAHASHI, 1981b; BOOTH *et al.*, 1982; HARA, 1984). The apparent absence of this species in the Southern Hemisphere (Fig. 7) may be due to fewer investigations there. Indeed, this species has been widely found in the Antarctic Ocean. The water temperature at which *P. socialis* can live varies from −2.4°C (BUCK, 1981 in the Antarctic Ocean) to 25°C (THOMSEN, 1978 in the Red Sea). This species must be able to tolerate the extremes in the range.

The conical lorica of *P. socialis* is composed of 10 longitudinal costae converging posteriorly, and two transverse costae. The anterior transverse costa is made up of ten costal strips, each with an anterior end of longitudinal costa attached to the middle part of the transverse costal strips forming "T-junction" (Fig. 4). These general features of the lorica structure are fairly constant among the cells noted in the previous reports from various parts of the world. For instance, in a very large number of specimens from the Antarctic Ocean, the number of longitudinal costae between the two transverse costae and the number of costal strips forming the anterior transverse costa were invariably ten. Changes, however, occurred in the way of reducing the number of longitudinal costae behind the posterior transverse costa. The final number near the pointed tip was no more than 3 (Fig. 8a), 4 (Fig. 8b) or 5 (Figs. 8c, d). This variation of lorica structure at the posterior part of the lorica has also been reported in cells collected from the arctic Canada (MANTON *et al.*, 1976).

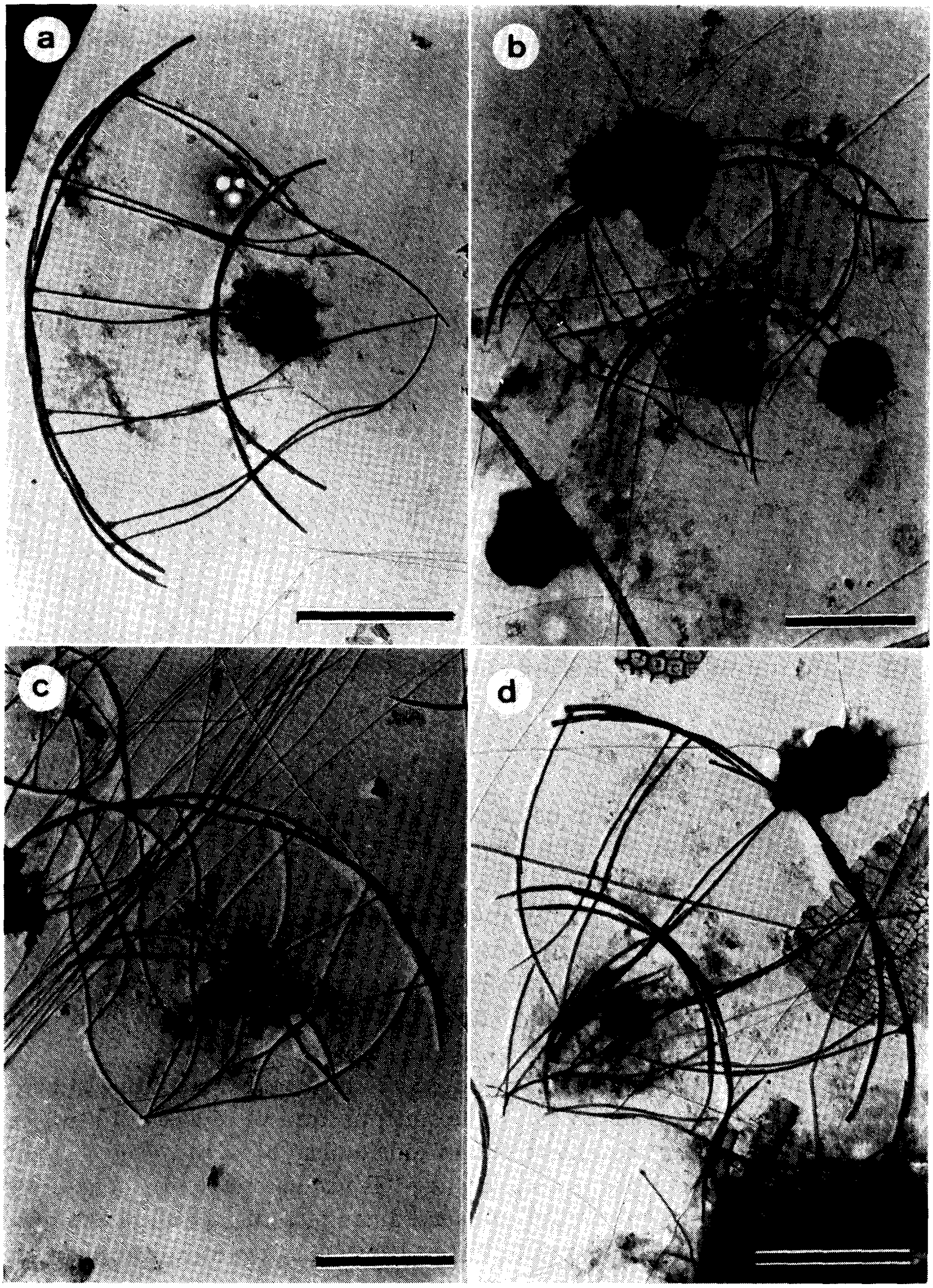

Fig. 8. Various lorica structures of Parvicorbicula socialis *(MEUNIER) DEFLANDRE. Ten longitudinal costae reducing in number posteriorly to three (a), four (b) or five (c and d). Each longitudinal costa comprises three costal strips. Scales: 5 μm.*

MANTON *et al.* (1976) reported other differences in lorica structure among the cells of *P. socialis*; costal strips (thinner in the summer type than in the large winter type) and the length of the posterior spine (absent or shorter in the summer type than

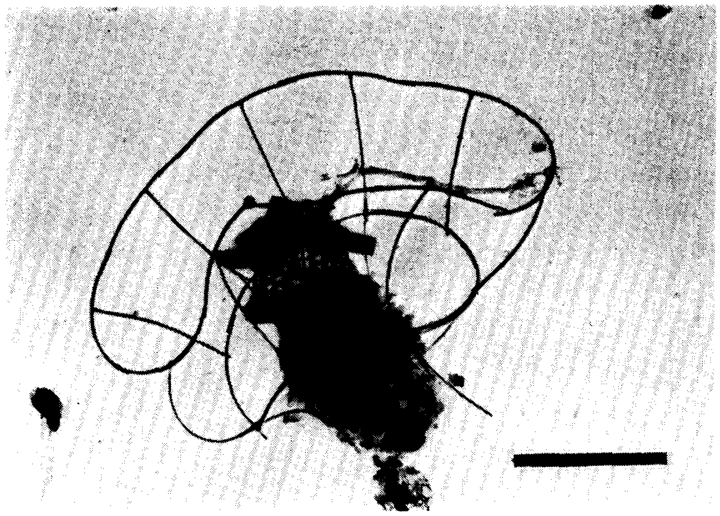

Fig. 9. A lorica of Parvicorbicula socialis *(MEUNIER) DEFLANDRE living in the coastal water of the Shioya Coast (Kobe, Japan) (HARA, 1984). The longitudinal costa comprises two costal strips. Scale: 5 μm.*

in the large winter type). They regarded these variations of lorica structure as seasonal differences. On the other hand, the costal arrangement behind the posterior transverse costa sometimes has a considerable variation among specimens reported from different parts of the world. The longitudinal costa was composed of only two costal strips in the cells collected from Denmark (THOMSEN, 1973) and Japan (HARA, 1984) (Fig. 9), and in these cells, behind the posterior transverse costa, the longitudinal costa was composed of only one costal strip. On the contrary, the longitudinal costa consisted of three costal strips in the cells collected from the Arctic and Antarctic

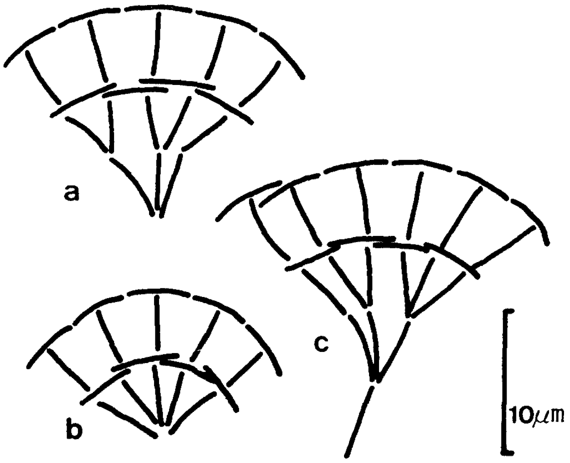

Fig. 10. Parvicorbicula socialis *(MEUNIER) DEFLANDRE. Only the costal strips lying uppermost are drawn.*

a: A lorica collected from the Antarctic Ocean.

b: A lorica found in the Shioya Coast (Seto Inland Sea, Kobe, Japan).

c: A lorica of the spring form obtained from the arctic Canada (after MANTON et al., 1976).

Oceans (MANTON *et al*., 1976) (Fig. 8), and the longitudinal costa behind the posterior transverse costa was composed of two costal strips.

These variations of the lorica structure are shown schematically in Fig. 10. The invariability of the lorica structure at the anterior part and the variability of the lorica structure at the posterior part, which was seasonal difference in the arctic Canadian population (MANTON *et al*., 1976), reflect the difference of lorica structure in various parts of the world. This can be regarded as an example of the variation depending on different water temperature in a single species (longitudinal costa with two costal strips in the warmer type and three in the colder type; without posterior spine in the warmer type and shorter or longer in the colder type).

4. Concluding Remarks

Taxonomical and faunistic studies of choanoflagellates in the Antarctic Ocean can be expected to develop still more, not only because of the many unidentified species in the Antarctic Ocean as indicated by TAKAHASHI (1981b). A variation of lorica structure in *P. socialis* will presumably reflect changes in some environmental factor, as well as the mode of life and morphogenetic processes. It can be expected that the choanoflagellates in the Antarctic Ocean will play an important role in the food web, especially as the linkage between bacteria and the krill, *E. superba*. Quantitative evaluation of this flow in the Antarctic Ocean is anticipated.

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