

# FOUR NEW SPECIES OF LORICATE CHOANOFLLAGELLATES FROM SOUTH BRITTANY, FRANCE

by

**B.S.C. Leadbeater**

Department of Plant Biology, University of Birmingham,  
Birmingham B15 2TT, England

## Résumé

Quatre nouvelles espèces de Choanoflagellés à logettes récoltées dans la Baie de Concarneau sont décrites. L'une, *Saepicula pulchra*, est l'holotype d'un nouveau genre. Toutes les espèces possèdent une logette composée de baguettes silicifiées disposées en forme de côtes. *Stephanoeca cauliculata* et *Parvicorbicula pedunculata* ont de longs pédoncules composés de plusieurs baguettes. *Saepicula pulchra* se distingue par une variante au niveau de la jonction entre les côtes longitudinales et les baguettes des côtes antérieures transversales.

## Introduction

Choanoflagellates are a well circumscribed group of colourless, protistan flagellates that are holozoic in nutrition feeding on bacteria, blue-green algae and other minute particles. Members of this group are easily recognised by the colourless protoplast with a single apical flagellum surrounded by a "collar" composed of fine tentacles. Loricata choanoflagellates (members of the family Acanthoecaceae (Norris, 1965) see also Leadbeater (1980) for description of terminology) live exclusively in marine and brackish water habitats and are distinguished from other choanoflagellate taxa by the presence of a basket-like lorica composed of siliceous costae. Each costa consists of linearly attached rod-shaped units known as costal strips (Leadbeater, 1972a, 1980). Loricata choanoflagellates are present in the nanoplankton and some species occur as epibionts attached to the surface of marine algae, bryozoans and other suitable objects. For a recent review of loricata choanoflagellates see Leadbeater (1980).

The four species described in this communication were found in the vicinity of Concarneau, South Brittany, during the summers of 1976 and 1977.

## Material and methods

Choanoflagellates were present in sea water samples collected from the coast around Concarneau, South Brittany, France, during the months of August and September 1976 and June-September 1977.

From each of the selected sites (rock pools and salt marshes) sea water samples were collected in 5 litre polythene containers and returned to Concarneau Marine Station where they were filtered through a 25µm mesh plankton net and then each sample was divided into two portions. One portion was processed immediately for whole mounts (see below) and the other was allowed to stand in a glass bowl at room temperature (20-23 °C) for 2-12 weeks.

For light and electron microscopy, cells were concentrated by filtering c. 1 litre of seawater through a millipore filter (pore size 3.0µm) and re-suspending the concentrated cells in the final 50ml of liquid. The cells were pelleted in a bench centrifuge, fixed with 2-3 drops of 1 percent osmium tetroxide in 0.1M cacodylate buffer at pH 7.0 and washed with three changes of distilled water. For light microscopy, a drop of the suspension of cells was dried on a glass slide. Slides were viewed and photographs of cells taken using a Reichert Zetopan microscope with phase-contrast accessories. For electron microscopy, cells were dried onto Formvar-coated copper grids and shadowcast with gold/palladium in Birmingham, England. Grids were viewed in a Philips EM300 electron microscope. For further details of these preparation techniques see Leadbeater (1978).

## OBSERVATIONS

### *SAEPICULA PULCHRA* sp. et gen. nov. (Plate I, 1-6)

*Saepicula* gen. nov. (L: saepicula, little fence)

#### Diagnosis

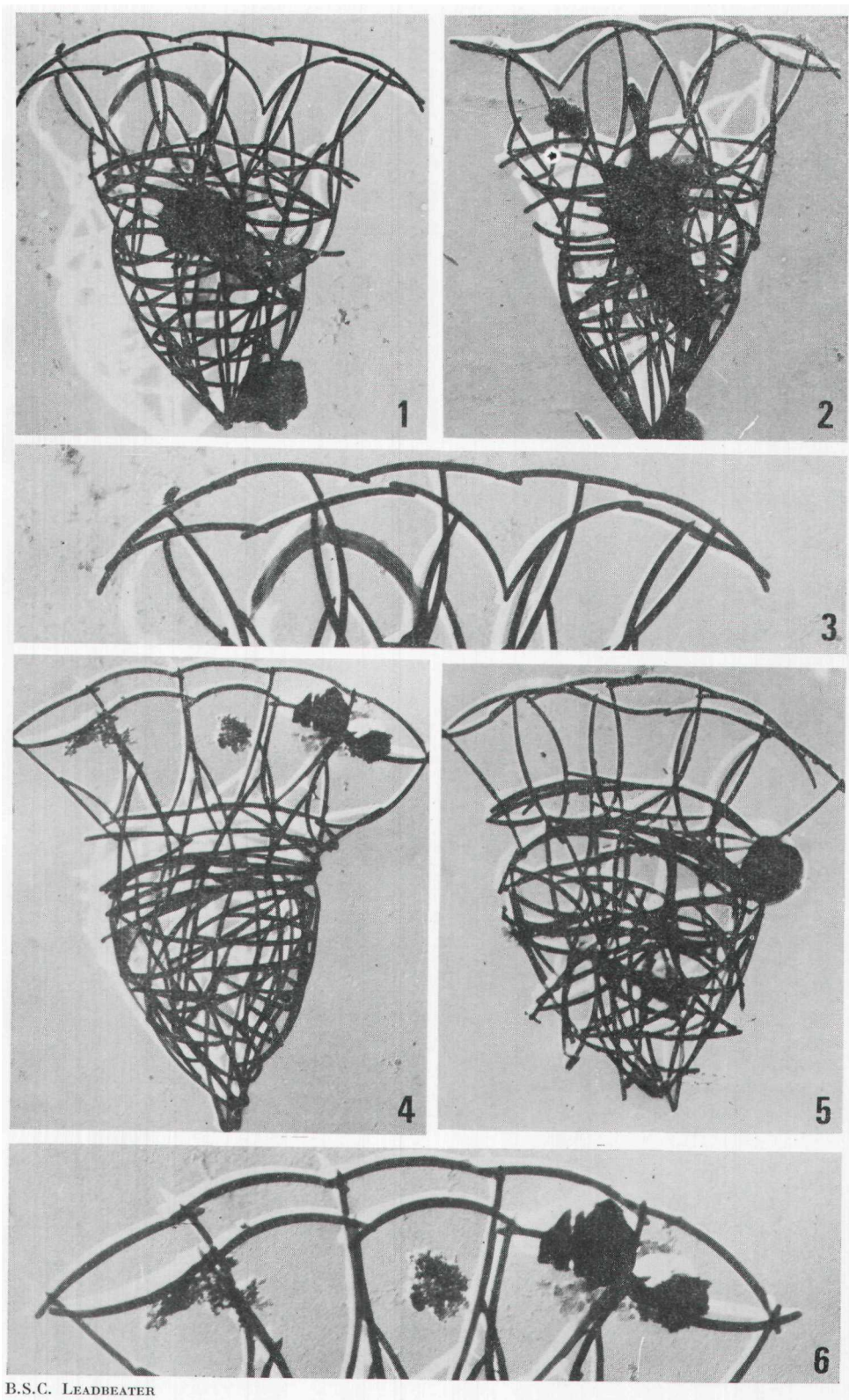
Cells solitary. Lorica consisting of two chambers delimited by a waist. Posterior chamber obconical with two series of costae located more or less regularly around chamber, one series almost parallel to the long axis of the cell and the second series almost perpendicular to the long axis. Anterior lorica chamber formed by a ring of equally spaced longitudinal costae surmounted by a single transverse costa.

*Saepicula pulchra* sp. nov. (L: pluchra, beautiful)

#### Diagnosis

Protoplast when dried 3-5µm long X 2-3µm wide, the flagellum 3-7µm long. Lorica 10-13µm long consisting of two chambers. Transverse costae of posterior chamber numerous, longitudinal costae numerous converging posteriorly to a blunt tip. Anterior chamber containing 10 divergent longitudinal costae each consisting of one costal strip. In most cells one end of a diagonally located strip attached to each longitudinal costal strip mid-way along its length. Anterior tips of longitudinal costae apiculate and attached to the anterior transverse costa at or between junctions of adjacent costal strips.

Type specimen shown in Fig. 4, found in a water sample collected from a seawater inlet at La Foret, near Concarneau, Sud Finistère,

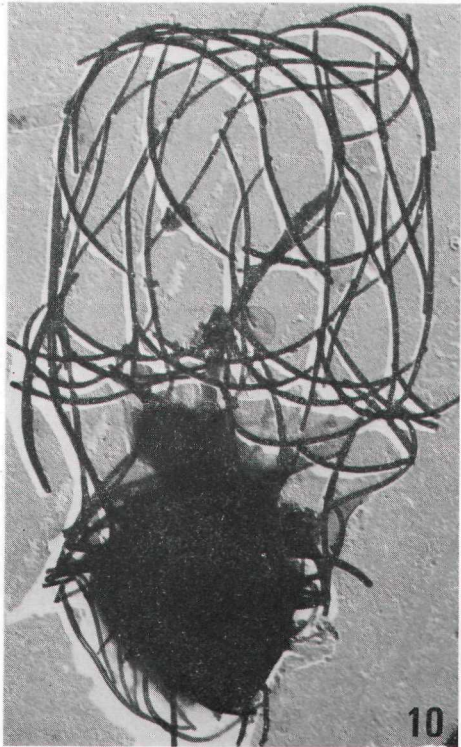
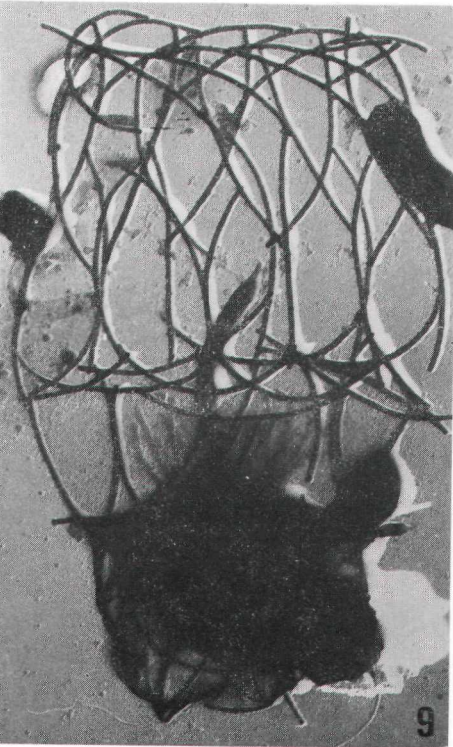
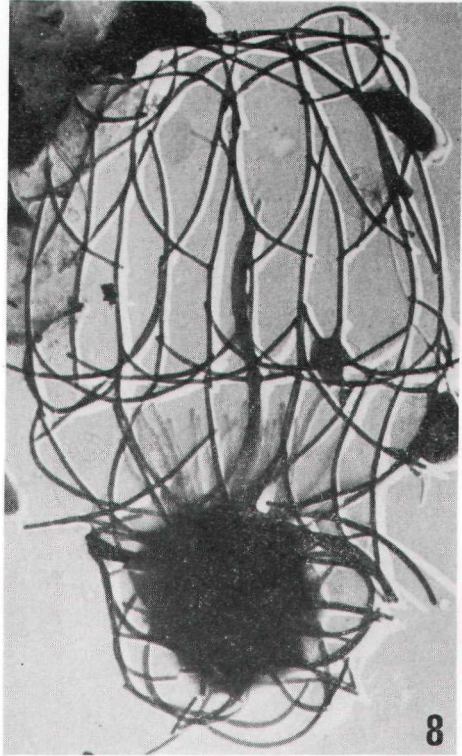
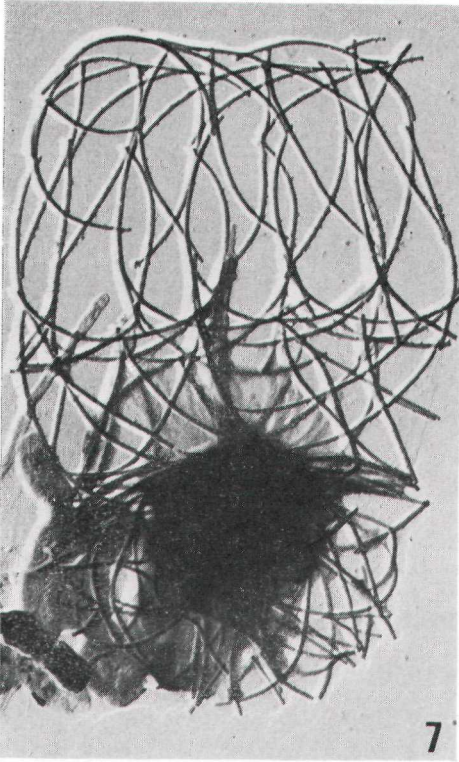


B.S.C. LEADBEATER

PLATE I

1-6. Shadowcast whole mounts of *Saepicula pulchra* gen. et sp. nov.  
 1-3: loricae with anterior tips of longitudinal costae forming T-joints with costal strips of anterior ring; 1, 2: x 6,000; 3: x 10,000 4-6: loricae with anterior tips of longitudinal costae attached to joints between adjacent strips of the anterior ring; 4,5: x 6,000; 6: x 10,000.



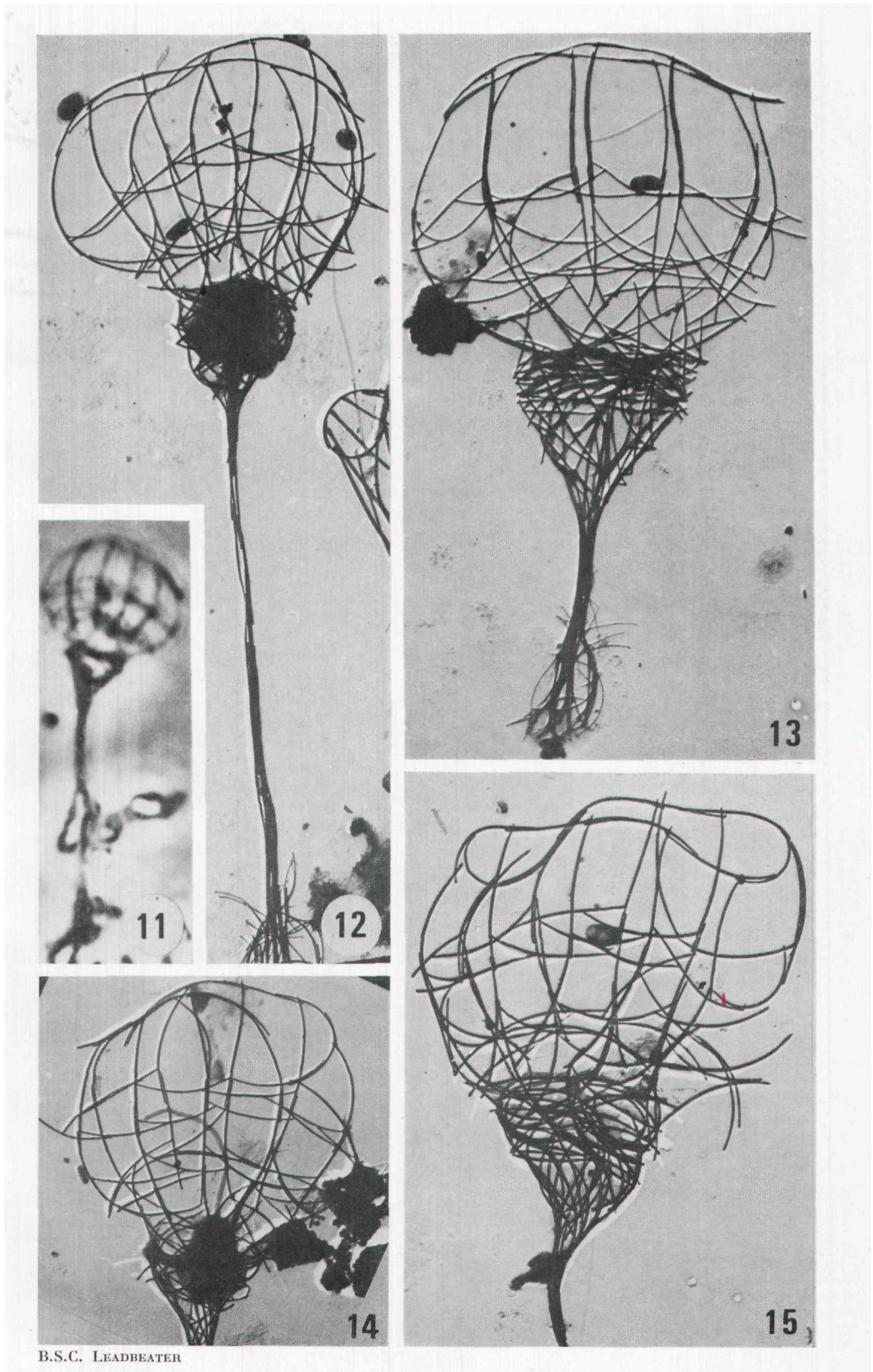


B.S.C. LEADBEATER

PLATE II

7-10: shadowcast whole mounts of *Stephanoeca pyxidoides* sp. nov. x 9,000.



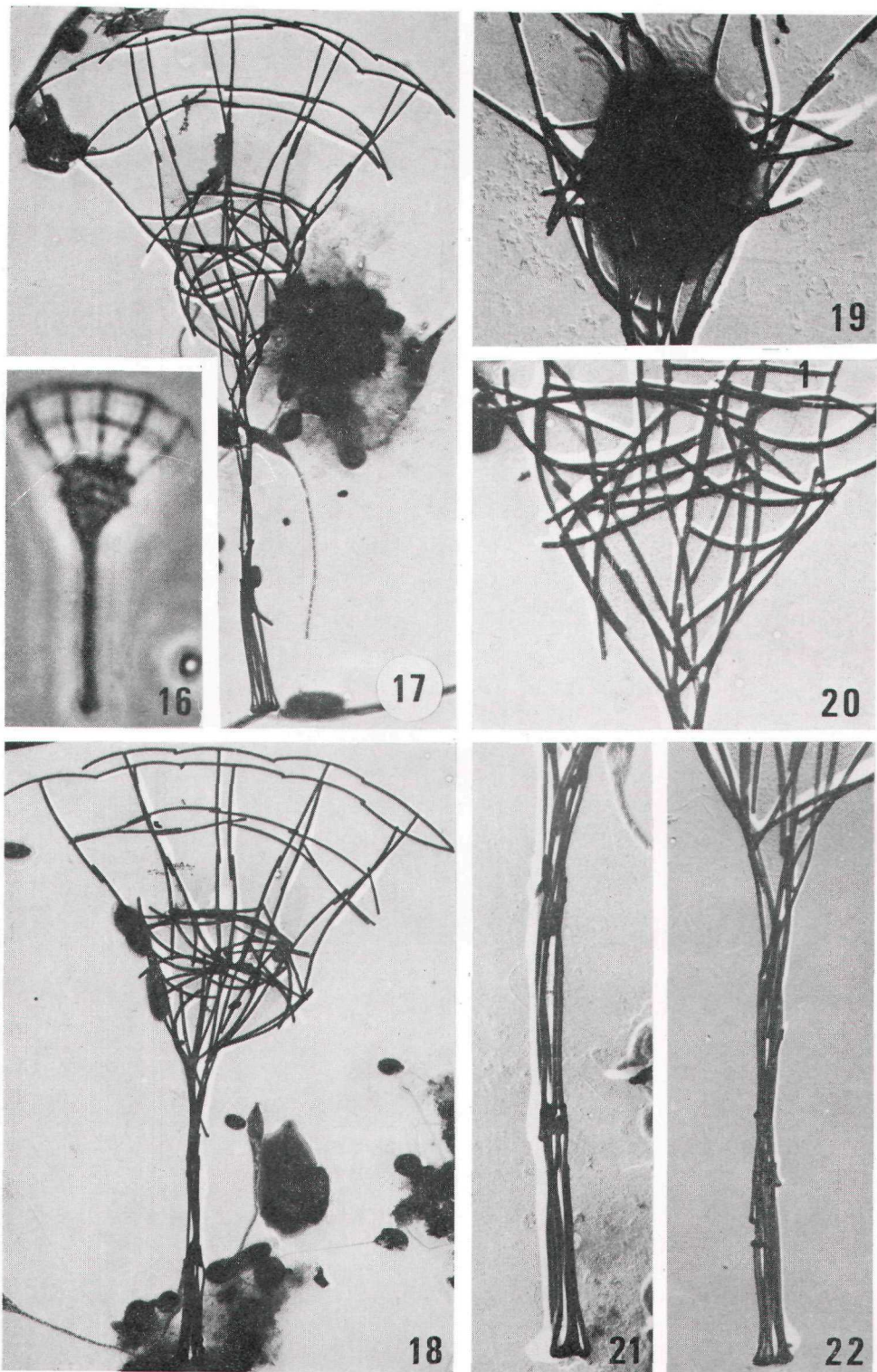


B.S.C. LEADBEATER

PLATE III

11: phase contrast light micrograph of *Stephanoeca cauliculata* sp. nov. x 2,000; 12-15: shadowcast whole mounts of *Stephanoeca cauliculata* sp. nov.; 12, 13: long and short stalked cells respectively x 4,000 and 5,000 respectively; 14: lorica chamber with protoplast x 4,000; 15: empty lorica showing arrangement of costae x 5,000.



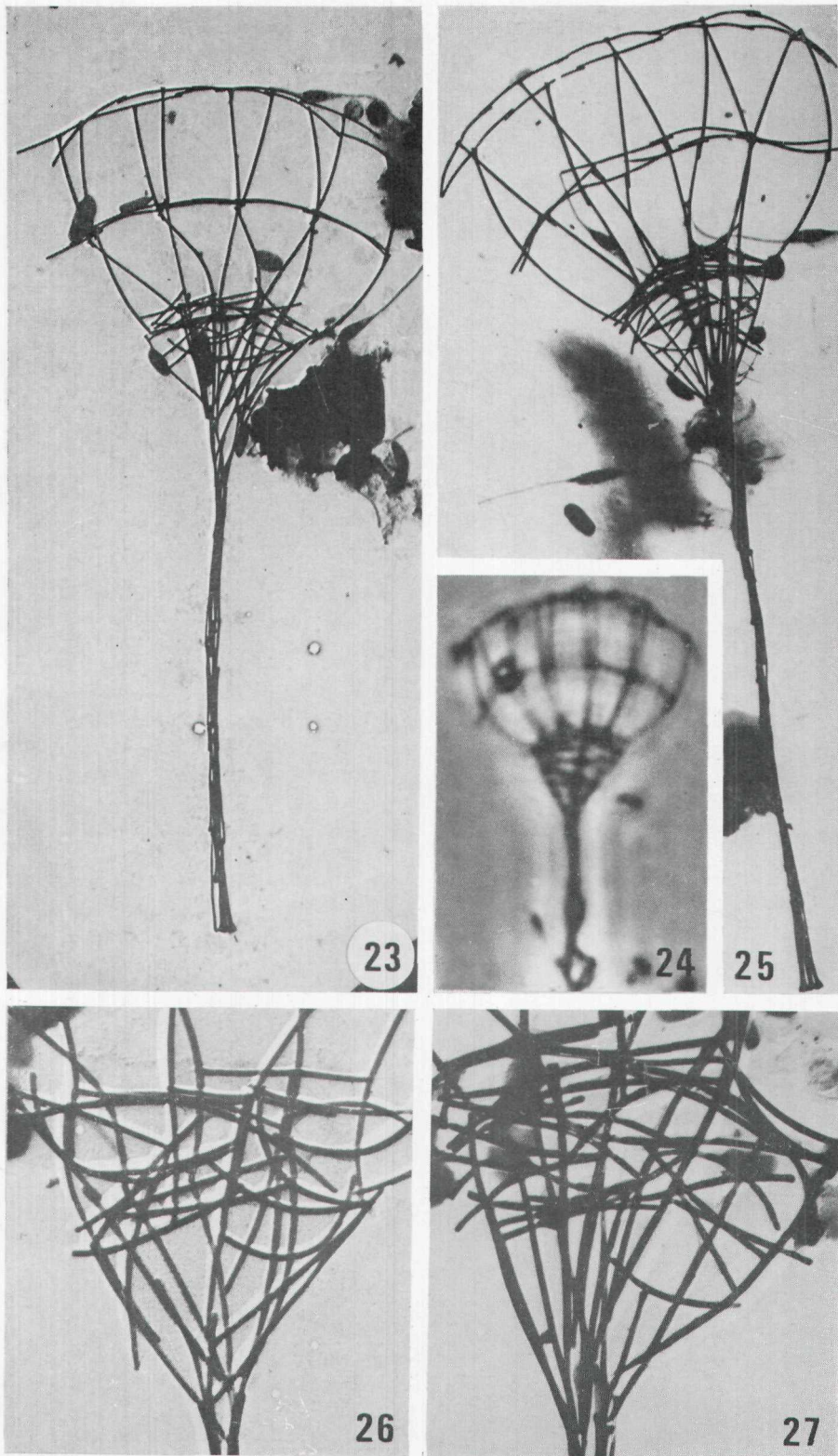


B.S.C. LEADBEATER

PLATE IV

16-22: *Parvicorbicula pedunculata* sp. nov. cells with 9 longitudinal costae in lorica chamber.

16: phase contrast light micrograph x 2,000; 17-22: shadowcast whole mounts; 17, 18: empty lorica x 4,000; 19: lorica with protoplast x 8,000; 20: posterior end of lorica chamber showing continuous longitudinal costae and band of transverse costae x 7,000; 21, 22: stalks composed of parallel arrays of linearly attached longitudinal strips x 7,500.



B.S.C. LEADBEATER

PLATE V

23-27. *Parvicorbicula pedunculata* sp. nov. Cells with 10 longitudinal costae in lorica chamber.

24: phase contrast light micrograph x 2,000; 23, 25-27: shadoweast whole mounts; 23, 25: empty loricae x 4,000; 28, 27: details of posterior end of lorica chamber showing continuous longitudinal costae and band of transverse costae x 7,500.



France on 5th. August 1976. Temperature at time of collection 18.0°C.

This species is easily recognised by the shape of the lorica and arrangement of costae (Plate I, 1, 2, 4, 5). Apart from minor variations in the numbers of costae, the most significant variation is the position at which the tips of the longitudinal costae join strips of the anterior ring. In *Saepicula pulchra* the attachment is either at the junction between adjacent costal strips of the transverse costa (Plate I, 4-6) or approximately mid-way between them (Plate I, 1,3). This variability is somewhat unexpected since in most loricate taxa the position of the joins between longitudinal costae and strips of a transverse costa is a consistent character and has therefore assumed taxonomic significance (Leadbeater, 1980).

Cells of *Acanthoecopsis unguiculata* Thomsen 1973, have certain features in common with those of *Saepicula pulchra*. In particular, the general shape of the lorica, the arrangement of the two series of costae in the posterior chamber and the longitudinal costae of the anterior chamber each with an apiculate tip. However, apart from the obvious absence of an anterior transverse costa in *Acanthoecopsis unguiculata* there are other differences. The loricae of most specimens of *A. unguiculata* (Gold, Pfister and Liguori, 1965; Thomsen, 1973, 1977; Thronsen, 1974; Manton, personal communication) contain more costae in both chambers and the terminal costal strips of the longitudinal costae of the anterior chamber are not attached to another strip midway along their length as in *Saepicula pulchra*.

Notwithstanding similarities between *Acanthoecopsis unguiculata* and *Saepicula pulchra* a new genus has been created for the latter. Recently the type species of *Acanthoecopsis*, *A. spiculifera* Norris, has been investigated by means of electron microscopy of shadowcast whole mounts (Leadbeater, 1979a) and as there is little similarity between this species and *Saepicula pulchra* it has not been possible to justify the inclusion of both in the same genus.

*Stephanoeca pyxidoides* sp. nov. (Plate I, 7-10) (Gr: πυξίς, casket)

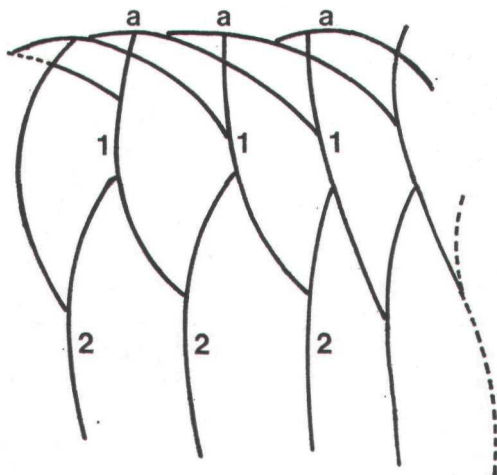
#### Diagnosis

Cells solitary, protoplast when dried c.3x3µm, the flagellum 3-5µm long. Lorica beaker-shaped, length 9-11µm comprising two chambers delimited by a waist near anterior end of protoplast. Posterior chamber 2-4µm long composed of two series of costae, one more or less parallel and the other more or less perpendicular to the long axis of the cell. Constriction at waist also marked by an apparently irregular transverse band of costal strips. Anterior chamber, 5-7µm long, 5-7µm wide at widest point, consisting of 10-12 longitudinal costae and two or occasionally three transverse costae. Anterior transverse costa delimiting the chamber composed of imbricated costal strips equal in number to longitudinal costae and each attached in a complex but regular manner to two successive longitudinal costae (details as in Text Fig. 1). Each longitudinal costa in wall of anterior chamber composed of three costal strips, the posterior and middle strips arranged linearly with a short overlap. The anterior



strip forms a T-join with a transverse strip of the anterior edge and receives in an intercalary position the proximal tip of the next transverse strip. Posteriorly it forms a T-join with the middle costal strip of the adjacent longitudinal costa. A transverse costa is located at the join between the middle and posterior costal strips of the longitudinal costa. A thin membrane lines the posterior chamber and extends to the level of the lower transverse costa of the anterior chamber.

Type specimen shown in Plate I, 7, found in a water sample collected from a seawater inlet at La Foret, near Concarneau, Sud-Finistère, France on 1st. August, 1976. Temperature of water at time of collection 18.5°C.



TEXT-FIG. 1

Drawing to illustrate the relationship between costal strips of the anterior costae (a) with the upper (1) and middle (2) costal strips of the longitudinal costae in *Stephanoeca pyxidoides* sp. nov.

The generic name *Stephanoeca* Ellis has been chosen for this species because of the resemblance of the lorica in morphology and structure to that of the type species *S. diplocostata* Ellis (Ellis, 1930; Leadbeater, 1972a, 1979b, c). In particular the shape of the two lorica chambers and position of the waist (Plate II, 7-10) is similar in both. The arrangement of costae forming the posterior chamber is common not only to *S. diplocostata* but also several other species of *Stephanoeca* e.g. *S. norrisii* Thomsen, 1973, and *S. urnula* Thomsen, 1979. The imbricated arrangement of strips in the anterior transverse costa with only one end of each strip attached to an adjacent strip of the transverse costa, the other being attached to the mid-point of a longitudinal costal strip (Plate II, 7-10 and Text-Fig. 1), is comparable to the organisation of strips in the anterior ring of *S. urnula*.

The distinctive feature of *S. pyxidoides* is the location of the anterior strip of each longitudinal costa (Text-Fig. 1). No other named species of *Stephanoeca* displays this organisation with such regularity. Some specimens of *S. urnula* do show similar although less

distinctive linkage between adjacent longitudinal costae (Thomsen, 1979, Fig. 6b) but in most cells the strips forming the longitudinal costae are arranged linearly.

*Stephanoeca cauliculata* sp. nov. (Plate III, 11-15) (L: caulis, stalk)

Diagnosis

Cells solitary, protoplast when dried  $5 \times 3 \mu\text{m}$ , the flagellum  $c.5 \mu\text{m}$  long. Lorica  $18-42 \mu\text{m}$  long consisting of two chambers and a long stalk. Two chambers delimited by a waist. Anterior chamber barrel-shaped,  $7-12 \mu\text{m}$  long, maximum width  $10-14 \mu\text{m}$ , composed of 9-11 longitudinal costae and three transverse costae. One transverse costa forms the anterior edge, another is located at the junction between the anterior and middle strips of the longitudinal costae and the posterior transverse costa usually consists of one or more ill-defined rings of costal strips located a short distance below the middle transverse costa. Posterior chamber  $3-6 \mu\text{m}$  long consisting of a wide band of more or less transverse costae and 15 or more longitudinal costae slightly spiralled at top of stalk. Stalk compound, up to  $30 \mu\text{m}$  in length and of uniform width throughout.

Type specimen shown in Plate III, 12, found in a water sample collected from a seawater inlet at La Forêt, near Concarneau, Sud Finistère, France, on June 28th. 1977.

In some respects *Stephanoeca cauliculata* is similar to *Pleurasiga cupula* Leadbeater, 1972b, although the latter species, which has so far only been recorded from Danish waters (Leadbeater, 1972b; Thomsen, 1973), was never observed with a stalk. *Pleurasiga diminutiva* Norris, 1965, is also similar in costal arrangement to both *P. cupula* and *Stephanoeca cauliculata* and Norris found some specimens with short stalks (up to  $6.5 \mu\text{m}$  long). Apart from the presence of a relatively massive stalk on *Stephanoeca cauliculata* (Plate III, 11-13), the significant differences between this species and *Pleurasiga diminutiva* are the greater number of longitudinal costae in the posterior chamber of *Stephanoeca cauliculata* (Plate III, 12-15). The middle transverse costa is nearer the anterior end of the lorica in *P. diminutiva* than in *Stephanoeca cauliculata*, although it must be emphasised that it is not entirely satisfactory to compare the arrangement of costae in photographs of whole mounts with that in drawings (Norris, 1965). There are also considerable similarities in costal arrangement between *Stephanoeca Campanula* Kent, 1880, as shown in the illustrations of Boucaud-Camou (1967, Pl. IV, Fig. 5) and *Stephanoeca cauliculata*. *Stephanoeca Campanula* also has a massive stalk but the anterior chamber apparently lacks intercalary transverse costae. Both *Pleurasiga diminutiva* and *Stephanoeca Campanula* require re-investigation with the aid of shadowcast whole mounts before the final taxonomic position of all these species can be decided.

The size and composition of the stalk of *Stephanoeca cauliculata* (Plate III, 12, 13) is of interest. The strips forming the stalk overlap each other in a less regular manner than in *Parvicorbicula pedunculata* and in this respect its construction is more like that of



*Acanthoecca spectabilis* and *Acanthoecopsis spiculifera* (Leadbeater, 1979a). Furthermore in common with these two species there is usually a cluster of unorientated strips at the base of the stalk (Plate III, 12, 13).

*Parvicorbicula pedunculata* sp. nov. (Plate IV, 16-27) (L: pedunculus, stalk)

#### Diagnosis

Cells solitary, protoplast when dried  $4 \times 3 \mu\text{m}$ , the flagellum  $4-6 \mu\text{m}$  long. Lorica  $20-26 \mu\text{m}$  long consisting of a chamber, interpretable as single, surmounting a relatively massive stalk. Chamber, conical,  $13-14 \mu\text{m}$  long, maximum width  $8-12 \mu\text{m}$ , composed of 9 or 10 longitudinal costae, each containing three costal strips, continuous to base of chamber where they unite in groups with the top of the stalk. Two transverse costae on anterior part of lorica both with same number of costal strips as there are longitudinal costae. Each component strip of anterior edge forming a T-join with the appropriate longitudinal costa and each component strip of the middle transverse costa exactly bridging the space between adjacent longitudinal costae. Arrangement of transverse costae at posterior end of chamber variable, usually consisting of two or three bands of somewhat ill-defined costae. Anterior band usually located at or above join between posterior and middle costal strips of each longitudinal costa. Stalk compound,  $6.5-10 \mu\text{m}$  long, of uniform width throughout and consisting of 4-6 parallel arrays of linearly attached longitudinal strips.

Type specimen shown in Plate IV, 17, found in a seawater sample collected from the sea outside Concarneau Marine Station, Concarneau, Sud-Finistère, France, on June 28th, 1977.

Amongst the specimens of *Parvicorbicula pedunculata* collected from Fiance, loricae of two distinct types were found though the differences do not justify taxonomic recognition. The majority of cells had loricae with nine longitudinal costae in the anterior chamber and the lower transverse costa of that chamber was positioned midway along the length of the anterior strip of each longitudinal costa (Plate IV, 16-18). However, a limited number of cells possessed loricae with ten longitudinal costae in the chamber and in these specimens the lower transverse costa was located at the joins between the anterior and middle costal strips of the longitudinal costae (Plate V, 23-25). Furthermore, loricae with nine longitudinal costae (Plate IV, 17, 18) usually had shorter stalks than those with ten (Plate V, 23, 25).

Features in common between *Parvicorbicula socialis* (Meunier) Deflandre 1960, the type species of *Parvicorbicula* Deflandre 1960 and *P. pedunculata* are mainly associated with the anterior end of the lorica. In particular in both species there is a similar distribution of transverse costae with T-joins between costal strips of the anterior ring and longitudinal costae. However, in most specimens of *P. pedunculata* the longitudinal costae are continuous throughout the chamber (Plate IV, 17-20) whereas in *P. socialis* at the posterior end of the chamber there is a reduction in the number of longitudinal costae as a result of their joining together in pairs, three's or four's (Manton, Sutherland and Leadbeater, 1976). Furthermore there is nothing

equivalent in *P. socialis* to the bands of transverse costae present in the loricae of *P. pedunculata* (Plate IV, 18, 20 ; Plate V, 23, 25-27).

No other species of *Parvicorbicula* has a massive stalk like that of *P. pedunculata*. Where a stalk is present e.g. *P. pedicellata* Leadbeater, 1973, *P. serrulata* Leadbeater in Manton, Sutherland and Leadbeater, 1975, and in some cells of *P. socialis* (Manton, Sutherland and Leadbeater, 1976) it consists either of a single costal strip as in *P. pedicellata* and *P. socialis* or a series of single strips attached end-to-end as in *P. serrulata*. The stalk of *P. pedunculata* also differs in construction from those of other species with massive stalks e.g. *Acanthoeca spectabilis* Ellis, 1930, and *Acanthoecopsis spiculifera* Norris, 1965 (Leadbeater and Morton, 1974; Leadbeater, 1979) and *Stephanoeca cauliculata* (Plate III, 11-15). In the latter species, strips forming the stalk are not grouped in regular bundles with the joins forming nodes as in *P. pedunculata* (Plate IV, 21, 22) and whereas in *Acanthoeca spectabilis*, *Acanthoecopsis spiculifera* and *Stephanoeca cauliculata* the base of the stalk is always associated with an irregular array of strips, the stalk of *P. pedunculata* terminates cleanly (Plate IV, 17, 21 ; Plate V, 23, 25).

At present *Parvicorbicula* is an ill-defined genus containing eight species which between them display a wide range of lorica construction. No doubt as more species are described the genus will be re-defined and some species will be transferred to other, probably newly created, taxa. Meanwhile *P. pedunculata* has been attributed to *Parvicorbicula* on account of similarities in lorica construction to *P. socialis*.

#### Discussion

The description of two new long-stalked species is of particular interest. Both were found in seawater that had been allowed to stand in glass troughs for twelve weeks. *Acanthoeca spectabilis* and *Acanthoecopsis spiculifera*, two other long-stalked species are also usually found in stagnant seawater or as epibionts on suitable surfaces in rock pools (Leadbeater and Morton, 1974; Gerchakov, Marszalek, Roth and Udey, 1976; Leadbeater, 1979a). Presumably the sedentary nature of these species explains their absence from nanoplankton samples collected from the open sea.

In pedicellate species such as *Stephanoeca diplocostata* which have a pedicel composed of two or three strips, the presence or absence of the pedicel can be directly related to whether or not the juvenile protoplast was attached to a surface at the time of lorica assembly (Leadbeater, 1979b). Free floating cells possess a pedicel, sedentary cells lack one and presumably the extra costal strips are incorporated into the posterior lorica chamber or appear as duplications elsewhere. However, in species with massive stalks e.g. *Parvicorbicula pedunculata*, *Stephanoeca cauliculata*, *Acanthoeca spectabilis* and *Acanthoecopsis spiculifera* it is rare to find a cell without a stalk although its length may vary considerably. Presumably, in these species, the length of the stalk is controlled by the number of costal strips produced by the juvenile protoplast prior to lorica assembly since



variations in stalk length **do** not appear to be compensated by variations in costal number and arrangement of the lorica chamber. Whether or not the conditions of growth exert a direct effect on the number of costal strips produced by the juvenile and ultimately on stalk length is not known.

### Acknowledgements

I am grateful to **Dr Y. Le Gal** for arranging accommodation at Concarneau Marine Station; Mlle Du Buit for collecting some of the seawater samples; Emeritus Professor **I. Manton** FRS and Dr Helge Thomsen (University of Copenhagen) for reading and discussing the manuscript. I also wish to thank Mr C.D.N. Costa (University of Birmingham) and Dr Marilyn Jones (Museum of Natural History, London) for assistance with matters related to nomenclature. Finally I am grateful to Mr. S. Price for technical assistance and **S.R.C.** and the University of Birmingham for financial assistance.

### Summary

Four new species of loricate choanoflagellates collected from the sea near Concarneau have been described. One, *Saepicula pulchra*, is the holotype of a new genus. All species possess a lorica composed of silicified costal strips which are arranged to form costae. *Stephanoeca cauliculata* and *Parvicorbicula pedunculata* have long stalks composed of many strips. *Saepicula pulchra* is unusual in that there is variation in the position of attachment between longitudinal costae and strips of the anterior transverse costa.

### REFERENCES

- BOUCAUD-CAMOU, E., 1967. — Les Choanoflagellés des côtes de la Manche. I. Systématique. *Bull. Soc. linn. Normandie*, Ser. 10, 7, pp. 191-209.
- DEFLANDRE, G., 1960. — Sur la présence de *Parvicorbicula* n.g. *socialis* (Meunier) dans le plancton de l'Antarctique (Terre Adélie). *Revue algol.*, N.S. 5, pp. 183-188.
- ELLIS, W.N.**, 1930. — Recent researches on the Choanoflagellata (Craspedomonadines) (freshwater and marine) with description of new genera and species. *Ann. Soc. roy. zool. Belgique*, 60, pp. 49-88.
- COLD, K., PFISTER, R.M. and LIGUORI, V.R., 1965. — Axenic cultivation and electron microscopy of two species of Choanoflagellida. *J. Protozool.*, 17, pp. 210-212.
- LEADBÈATER, B.S.C.**, 1972a. — Fine-structural observations on some marine choanoflagellates from the coast of Norway. *J. mar. biol. Ass. U.K.*, 52, pp. 67-79.
- LEADBÈATER, B.S.C.**, 1972b. — Ultra structural observations on some marine choanoflagellates from the coast of Denmark. *Br. phycol. J.*, 7, pp. 195-211.
- LEADBÈATER, B.S.C.**, 1973. — External morphology of some marine choanoflagellates from the coast of Yugoslavia. *Arch. Protistenk.*, 115, pp. 234-252.
- LEADBÈATER, H.S.C.**, 1978. — Other flagellates. *In*: Sournia, A. (ed.) *Phytoplankton Manual*, UNESCO, Paris, pp. 151-153.
- LEADBÈATER, B.S.C.**, 1979a. — Developmental and ultrastructural observations on two stalked marine choanoflagellates, *Acanthoecopsis spiculifera* Norris and *Acanthoeca spectabilis* Ellis. *Proc. R. Soc. London. B.*, 204, pp. 57-66.
- LEADBÈATER, B.S.C.**, 1979b. — Developmental studies on the loricate choanoflagellate *Stephanoeca diplocostata* Ellis. I. Ultrastructure of the non-dividing cell and costal strip production. *Protoplasma*, 98, pp. 241-262.
- LEADBÈATER, B.S.C.**, 1979c. — Developmental studies on the loricate choanoflagellate *Stephanoeca diplocostata* Ellis. II. Cell division and lorica assembly. *Protoplasma*, 98, pp. 311-328.

- LEADBEATER, B.S.C. 1980. — Ultrastructure and deposition of silicon in loricate choanoflagellates. In: Volcani, B.E., and Simpson, T.L. (ed.) *Silicon and siliceous structures in biological systems*. Springer-Verlag, New York, in press.
- LEADBEATER, B.S.C. and MORTON, C., 1974. — A light and electron microscope study of the choanoflagellates *Acanthoecca spectabilis* Ellis and *A. brevipoda* Ellis. *Arch. Microbiol.*, 95, pp. 279-292.
- MANTON, I., SUTHERLAND, J. and LEADBEATER, B.S.C. 1975. — Four new species of choanoflagellates from Arctic Canada. *Proc. R. Soc. London, B.*, 189, pp. 15-27.
- MANTON, I., SUTHERLAND, J. and LEADBEATER, B.S.C. 1976. — Further observations on the fine structure of marine collared flagellates (Choanoflagellata) from arctic Canada and West Greenland: species of *Paroicorbicula* and *Pleura-siga*. *Can. J. Bot.*, 54, pp. 1932-1955.
- NORRIS, R.E., 1965. — Neustonic marine Craspedomonadales (choanoflagellates) from Washington and California. *J. Protozool.*, 12, pp. 589-602.
- THOMSEN, H.A., 1973. — Studies on marine choanoflagellates. I. Silicified choanoflagellates of the Isefjord (Denmark). *Ophelia*, 12, pp. 1-26.
- THOMSEN, H.A., 1977. — Studies on marine choanoflagellates. III. An electron microscopical survey of the genus *Acanthoecopsis*. *Arch. Protistenk.*, 119, pp. 86-99.
- THOMSEN, H.A., 1979. — Electron microscopical observations on brackish water nanoplankton from the Tvärminne area, SW coast of Finland. *Acta Bot. Fennica*, 110, pp. 11-37.
- THRONDSSEN, J., 1974. — Planktonic choanoflagellates from North Atlantic waters. *Sarsia*, 56, pp. 95-122.