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CLASS SILICOFLAGELLATA
LEMMERMANN, 1901

By ØJVIND MOESTRUP and CHARLES J. O'KELLY

The Silicoflagellata (known in botanical literature as the Dictyochophyceae Silva, 1982) comprises three small (c. 30 extant species) but distinctive groups of free-living protists sometimes counted among the "chrysomonads" ("chrysophytes"): the silicoflagellates *sensu stricto,* the pedinellids, and the rhizochromulinids. These organisms, according to recent research, form a clade that is most closely related to pelagomonads and diatoms (Saunders et al., 1995). In some classifications (Cavalier-Smith 1993, Saunders et al., 1995) silicoflagellates, pedinellids, and pelagomonads are each afforded class status.

Silicoflagellata are small to medium size unicellular protists (range 5-50, exceptionally to 500 μm), usually occurring either as flagellates or as axopodial amoebae. As in most other members of the heterokont/stramenopile clade, the youngest (anterior or only) flagellum on swimming cells bears tripartite tubular hairs. The defining characteristic is the presence of cytoplasmic microtubules that arise from differentiated pads (presumed nucleating sites) on the nuclear envelope (Fig. 4). These microtubules extend into the axopodia, although they may be present even when axopodia are not expressed. The axopodial microtubules are either not united into axonemes or they form axonemes consisting of three microtubules; this feature distinguishes Silicoflagellata from the actinophryid amoebae, in which the axopodial axonemes contain numerous, highly organized microtubules.

No root microtubules are associated with the kinetid in flagellate cells, a feature that links Silicoflagellata with pelagomonads and separates them from other heterokont/stramenopile taxa. Also lacking is the "transitional helix" typically found distal to the transition zone between kinetosomes and flagella in other heterokonts, but two rings (or a helix of two gyres) may be present proximal to the transition zone. This feature also links Silicoflagellata and pelagomonads.

Most species of Silicoflagellata are photosynthetic, containing chloroplasts with thylakoid membranes in stacks of three and the "chrysomonad" pigments (chlorophylls *a* and *c*, fucoxanthin), but a few pedinellids are known that lack chloroplasts.

Silicoflagellates *sensu stricto* form complex siliceous external skeletons, which fossilize well. From these palynomorphs, a silicoflagellate fossil record including several form genera and extending back to the Cretaceous is known. Other Silicoflagellata are naked or have a covering of organic scales. For these taxa, no fossil record is known.

Silicoflagellata are common in marine planktonic and benthic habitats. Blooms are usually benign, but a few have been associated with fish kills although toxins have not been identified. Some species of pedinellids are known from fresh water.

Species of Silicoflagellata may have complex asexual life histories including several different trophic stages and cysts, but sexual reproduction has yet to be observed. Accounts of the

structure, reproduction and diversity of Silicoflagellata have been given by Moestrup and Thomsen (1990), Moestrup (1995) and O'Kelly and Wujek (1995).

Key to the Orders

1. Siliceous exoskeleton present..... ..... Order **Dictyochales**
1'. Siliceous exoskeleton absent, cells radially symmetrical, axopodial microtubules in groups of three..... **Pedinellales**
1''. Siliceous exoskeleton absent, cells bilaterally or not symmetrical, no fixed number of axopodial microtubules ..... **Rhizochromulinida**

ORDER DICTYOCHALES HAECKEL, 1894
(Silicoflagellata Borgert 1890)

by ØJVIND MOESTRUP

The silicoflagellates *sensu stricto* are very common and important members of the marine plankton in many seas. When occurring in bloom conditions, they may cause mortality of fish, due to mechanical irritation of the fish gills by the spines of the skeleton (Fig. 1A) (Erardle Denn and Ryckaert, 1990). Numerous fossil representatives are known from the Cretaceous onwards, peaking with more than a hundred species and varieties in the Miocene (Tappan, 1980), but the number of extant species is probably limited to three (Moestrup and Thomsen, 1990). These are readily identified as silicoflagellates because of the characteristic siliceous skeleton that surrounds the cell as a lateral bowl (Figs. 2A,B). Naked stages can be confused with raphidophytes but differ in the presence of only one long flagellum (Fig. 1B) (van Valkenburg and Norris 1970; Moestrup and Thomsen 1990). Classification of the silicoflagellates is blessed with many names. Apparently the oldest class name is Silicoflagellata Lemmermann 1901 and the oldest order name Silicoflagellata Borgert 1890, p. 231. Borgert coined the term silicoflagellates.

The extant species are classified into a single family, for which the oldest name appears to be Dictyochida Borgert, 1891, p. 661 (=Dictyochaceae in the botanical nomenclature, Dictyochidae in the zoological nomenclature). They belong to a single genus *Dictyocha.*

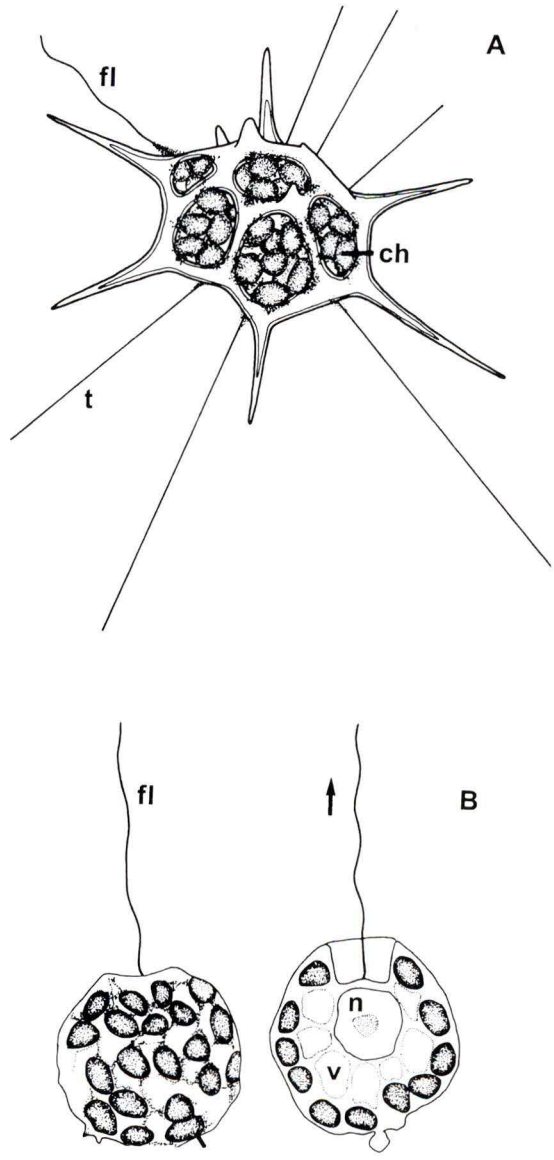

Fig. 1. *Dictyocha (=Distephanus) speculum.* A. Skeleton-bearing stage; B. Naked stage. ch, chloroplast; fl, long flagellum; n, nucleus; t, tentacle; v, vacuole. Arrow indicates direction of swimming. Not to scale. (From Moestrup and Thomsen, 1990)

Key characters

1. Only a single (hairy) flagellum is present, but a second, barren, basal body is located within the cell. Cells of the skeleton-lacking stage have two flagella, a long hairy flagellum and a very short stubby one. The flagella insert in an apical pit (Fig. 1B). The hairy flagellum

and a very short stubby one. The flagella insert in an apical pit (Fig. 1B). The hairy flagellum membrane extends into a wing-like structure supported by a cross-banded paraxonemal rod, as in the order Pedinellales. Microtubular flagellar roots are unknown and a distinct rhizoplast has not been identified (Moestrup and Thomsen, 1990).

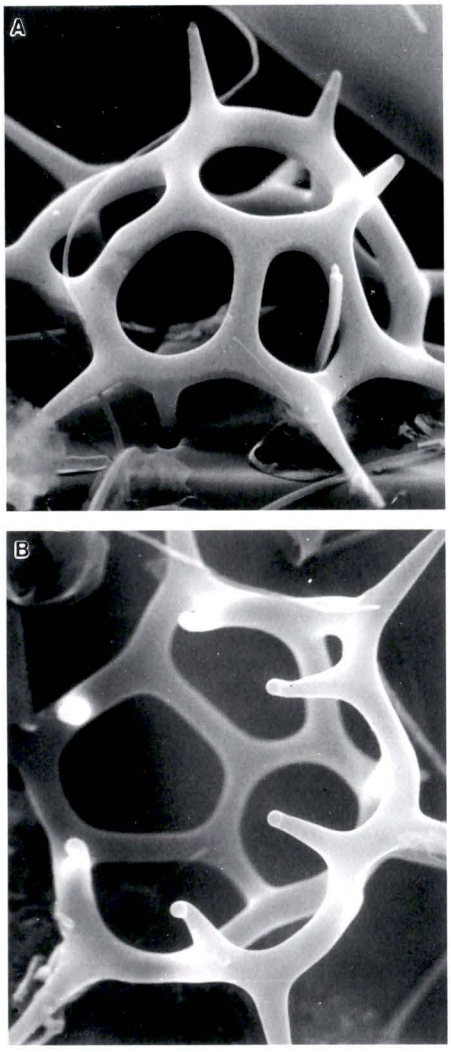

Fig. 2. *Dictyocha speculum*. Scanning electron micrographs of the siliceous skeleton, in B showing the cavity that houses the living cell. x3600. (From Moestrup and Thomsen, 1990).

2. Many chloroplasts, located peripherally (Fig. 1), each containing a single embedded pyrenoid.
3. Numerous Golgi bodies located as an anterior collar around the centrally located nucleus.
4. No cell wall, but cell surrounded by external silicified skeleton (Figs 1A, 2A, B) or naked (Fig. 1 B) (see below).
5. No eyespot or ejectile organelles.
6. The naked stage of the life cycle with an extensive layer of vacuoles between the outer layer of chloroplasts and the central part (Fig. 1B) which comprises the nucleus and the Golgi apparatus.
7. The skeleton-bearing stage with an internal canal system surrounding the central nucleus and Golgi apparatus-containing region. The canal system is connected by radial canals to the exterior.
8. Tentacles (Fig. 1A) supported by variable number of microtubules that extend from the nuclear envelope. Tentacles apparently emerging from any part of the cell.

9. The life cycle not yet fully understood, but comprising at least three main stages: the typical skeletonbearing stage, the naked stage, and a multinucleate stage which may reach 500 μm in diameter (Moestrup and Thomsen, 1990; Henriksen et al., 1993). All stages are present in marine plankton. A multinucleate, amoeboid stage has been seen in culture.
10. Classification based mainly on morphology of the siliceous skeleton. This can be highly variable (see e.g. Boney, 1973; van Valkenburg and Norris, 1970) and in large populations, specimens which cannot be referred to species level may occur.

Genus ***Dictyocha,*** Ehrenberg, 1837

The extant species may all be referred to this genus. Only three species are well known. They have been classified into three different genera, but this appears to be unwarranted. For distribution of the species in the seas in relation to temperature and salinity, see Henriksen et al. (1993).

Dictyocha speculum Ehrenberg, 1837. The skeleton comprises two well-separated rings, interconnected by six bars. The outer ring hexagonal, the inner almost circular Six spines extend in a radial direction from the outer ring, two opposite spines usually slightly longer than the others. The cell is located in a cavity formed by the rings. The diameter of the outer ring is c. 20 μm and in Danish material the distance between the tips of the longest spines was 37.5-56 μm (Moestrup and Thomsen, 1990). The naked stage is more or less spherical,

15-20 μm in diameter, occasionally smaller (to 10 μm in culture), the front end slightly flattened with a distinct pit. Flagellum 20-30 μm long. Cells contain 30-50 chloroplasts. The multinucleate stage with numerous. organelles; of all types, more or less spherical, 45-500 μm in diameter. Widely distributed in cold and temperate seas, at temperatures up to 18-20°C (Henriksen et al., 1993).

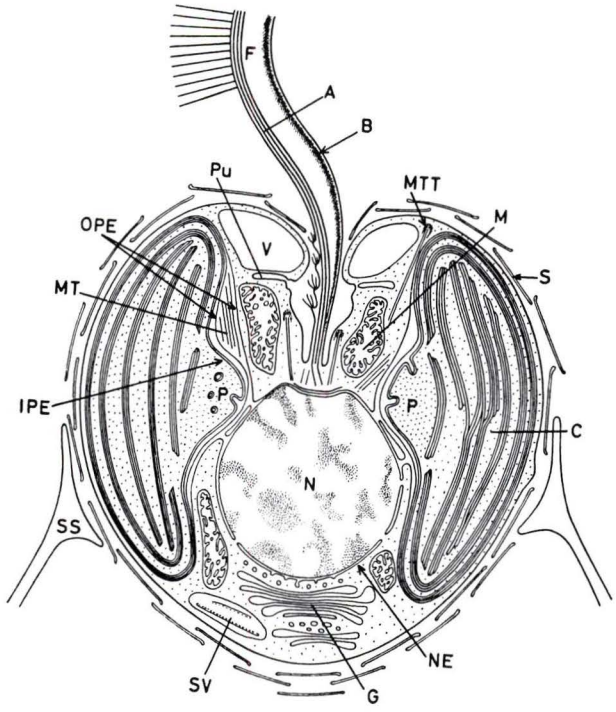

Fig. 3. *Apedinella radians (=A. spinifera).* A, axoneme of flagellum; B, paraxonemal rod supporting the flagellar wing; C, chloroplast; F, flagellum; G, Golgi body; IPE, OPE, chloroplast envelope; MT, immature flagellar hairs, MTT, microtubules; N, nucleus; NE, nuclear envelope; Pu, pusule-like cavity; S, plate scales; SS, spine scales; V, vacuole. Not to scale. (From Throndsen, 1971).

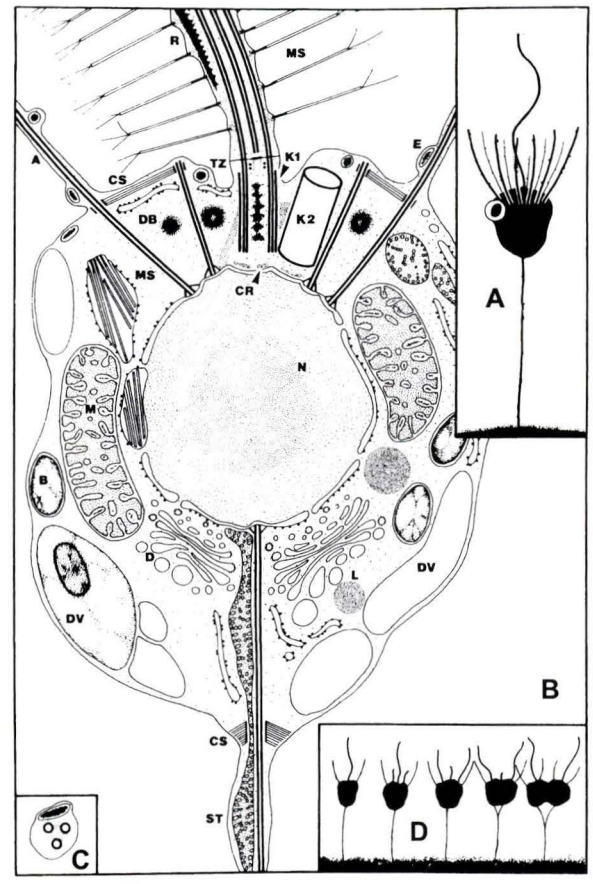

Fig. 4. *Pteridomonas danica.* A. Cell with food vacuole. B, Details of cell structure. C. Tentacle with triplet of microtubules. D. Cell division. Abbreviations in Fig. 4B: A, tentacle; B, endosymbiotic bacteria; CR, dense material on the nuclear envelope; CS, cytoskeletal elements; D, Golgi body; DB, dense bodies; DV, digestion vesicles; E, extrusomes; KI, K2, basal bodies; L, lipid; M, mitochondrion; MS, tripartite flagellar hairs; N, nucleus; R, paraxonemal rod; TZ, flagellar transition zone; ST, stalk. Fig. 4A=18,000x. (After Patterson and Fenchel, 1985).

ORDER PEDINELLALES

Zimmermann, Moestrup and Hällfors 1984

By ØJVIND MOESTRUP

The pedinellid flagellates comprise more or less spherical cells with a single anterior (hairy) flagellum. The flagellum beats in a planar sine wave and bears a more or less well-developed wing supported internally by a paraxonernal rod (Figs. 3,4). Tentacles emanate from the cell surface, supported by triplets of microtubules attached proximally to the nuclear envelope

(Figs. 4A-C). Cells with three or six chloroplasts and auto- or mixotrophic(*Pedinella*) or without chloroplasts and heterotrophic. Some species free swimming, often with a trailing stalk, others attached. The body in some species clad in a cover of organic scales (Fig. 3), some of which may be spine-shaped. In fresh water and marine plankton. Synonym: order Ciliophryida Febre-Chevalier 1985.

With a single family Actinomonadidae Kent, 1880.

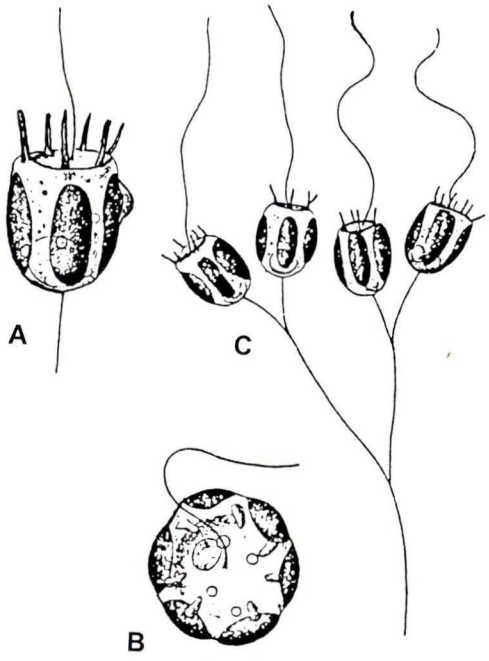

Fig. 5. *Pedinella hexacostata,* a colony- forming, mixotrophic pedinellid. A,B=2000x. C: x1000. (From Conrad, 1926).

Key characters

1. One emergent flagellum, but a second, barren, basal body is present in the cell (Fig. 4B). Flagellum with more or less distinct wing, supported by paraxial rod (Figs. 3,4). Two rows of tripartite flagellar hairs. Small ring-shaped flagellar scales found in two genera. No microtubular or striated flagellar roots are known.
2. Three or six lateral chloroplasts in one tier, or without chloroplasts. Pyrenoids present or absent.
3. No eyespot.
4. With stalk of very variable length. Cells free swimming (trailing stalk) or attached.
5. Contractile vacuoles in freshwater species.
6. Cell body covered with organic scales in some genera.
7. Ejectile organelles unknown.
8. Division by fission.
9. Organic cysts known, sexuality unknown.
10. Species are distinguished by cell size and shape, etc. As these are often highly variable characters, species taxonomy is unsatisfactory and awaits alternative characters. A few species are recognized by the morphology of the scales.

Key to the genera

1. Cells with three or six chloroplasts..... 2
1′. Cells without chloroplasts..... 4

2. Cells attached by means of a stalk, pyrenoids absent ..... ***Pedinella***
2′. Cells with trailing stalk or stalkless, pyrenoids present..... 3

3. Cells with long to very long trailing stalk..... ***Pseudopedinella***
3′. Cells with six posteriorly-directed spines, held together in swimming cells..... ***Apedinella***

4. Cells with long or very long trailing stalk..... ***Actinomonas***
4′. Cells attached with shorter or longer stalk 5

5. With very short stalk, hardly visible in the light microscope, flagellum in a figure-of-eight, numerous tentacles from all sides..... ***Ciliophrys***
5′. With long stalk ..... ***Pteridomonas***

Genus ***Pedinella*** Vysotskii, 1888

Cells with an anterior ring of c. 12 tentacles surrounding the flagellum. Cells naked. Six chloroplasts without pyrenoids. Contractile vacuoles anteriorly. With posterior stalk. Cells mixotrophic, mainly ingesting bacteria, which are caught near the ring of tentacles. Uptake process unknown, but the tentacles contain

small vacuoles with dense contents that may be involved. One species.

Pedinella hexacostata Vysotskii (Fig. 5). Cells apple-shaped, 7-8 μm long (range 6-11 μm) and 9-10 (8-11) μm wide. Flagellum 17-28 μm long. Cells contain numerous contractile vacuoles. In fresh water and inland saline waters. Rarely sighted, the most recent detailed description by Swale (1969).

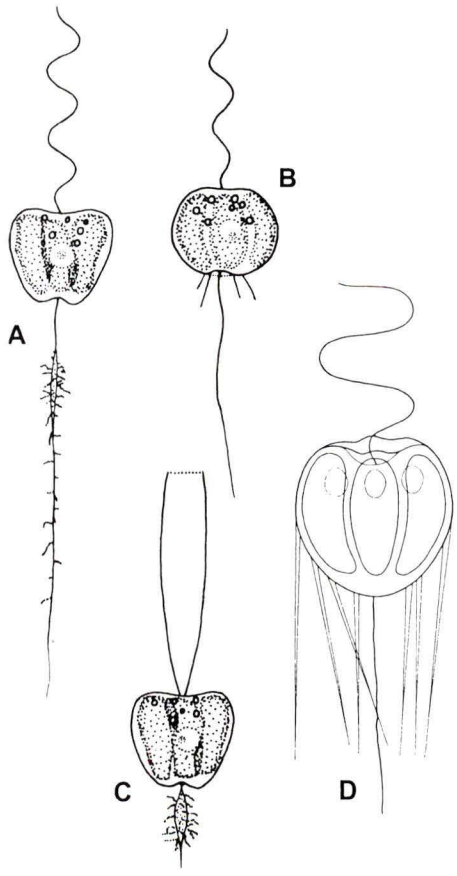

Fig. 6. Autotrophic pedinellids. A-C, *Pseudopedinella elastica,* with naked cells. D, *Apedinella radians,* with spines. A-C=1200x, (From Zimmermann et al., 1984) D=2700x. (From Throndsen, 1969)

Genus ***Pseudopedinella,*** N. Carter, 1937

As *Pedinella,* but cells free-swimming with trailing stalk that may reach over 100 μm in length. Three or six chloroplasts, each with a pyrenoid. Ultrastructural descriptions by Zimmermann et al. (1984) and Thomsen (1988). Common in freshwater and marine plankton. Half a dozen species but taxonomy very uncertain due to variability.

Pseudopedinella elastica Skuja (Fig. 6A-C). Cells 9-15 μm in diameter. With six chloroplasts in a tier along the cell periphery. Trailing stalk up to c. 140 μm long. Widely distributed in brackish and marine plankton.

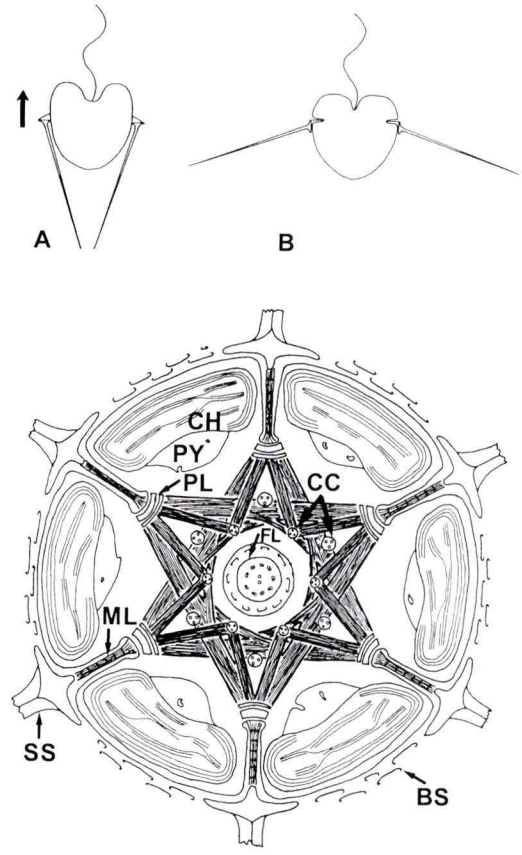

Fig. 7. *Apedinella radians.* A,B. Movement of scales. C. Transverse section of the cell near the base of the flagellum, showing the very complex system of fibers that interconnects the bases of the six spines and serve in motility. BS, flat body scales; CC, triplets of microtubules; CH, chloroplast; FL, flagellum; ML microligament; PL, plaque; PY, pyrenoid; SS, spine scales. Not to scale. (From Koutoulis et al., 1988)

Genus ***Apedinella*** Throndsen, 1971

Cells free-swimming, without or very rarely with a trailing stalk. Tentacles rarely present externally, but triplets of microtubules present in the cell. Some tentacles associate with the spines but are not usually visible in the light microscope. Cell covered with plate scales and 6 spine scales. The latter insert laterally and are directed backwards during swimming. They may serve as brakes by being swung to a position

perpendicular to the direction of swimming. Movement of spines mediated by a complex system of fibers in the cell (Koutoulis et al., 1988). Six chloroplasts, each with a pyrenoid. One species.

Apedinella radians (Throndsen) Campbell (Figs. 3,6D,7). Cells 7-10 μm in diameter. Flagellum 1-2 x cell length. Very common in marine plankton and widely distributed.

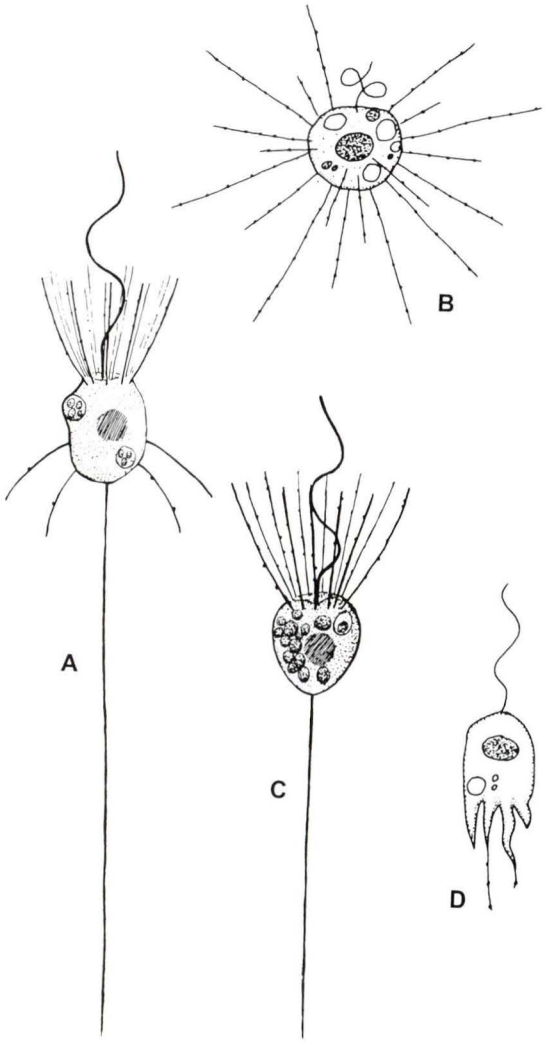

Fig. 8. Heterotrophic pedinellids. A. *Actinomonas mirabilis*. B,D, *Ciliophrys infusionum*, in B a sessile cell, in D a swimming cell. C. *Pteridomonas danica*. A,C:=3000x, (From Larsen and Patterson, 1990) B, D=1000x, (After Preisig et al., 1991)

Genus ***Actinomonas*** Kent, 1880

Cells colorless, with tentacles emanating from the cell in all directions but particularly numerous at the front end. Tentacles of the front end interconnected by complex system of fibers (Larsen, 1985). With well-developed flagellar wing supported by paraxonemal rod. Heterotrophic. Very common in marine plankton. One well-described species.

Actinomonas mirabillis Kent, 1880 (Fig. 8A). Cells 4-8 μm in diameter. With trailing stalk up to c. 120 μm long. Sometimes more than one trailing stalk present. With annular scales on the flagellum. Ultrastructural study by Larsen (1985, as *Actinomonas pusilla*). *Parapedinella reticulata* S. M. Pedersen and Thomsen somewhat resembles *Actinomonas*. It has numerous tentacles emanating from the cell surface but the cell, which is 7-15 μm in diameter, is covered with plate-like organic scales (Pedersen et al. 1986). Annular scales are present on the flagellar surface. Known from Australia and Denmark.

Genus ***Pteridomonas*** Penard, 1890

Cells very similar to *Actinomonas*, but tentacles are mainly confined to an anterior ring around the flagellum, and the cells are usually attached to a substratum. They also differ in the presence of a very reduced flagellar wing and paraxonemal rod and in the presence of 2 ring-like structures below the transverse septum of the flagellar transition region (Patterson and Fenchel 1985). Such rings are also present in *Apedinella* but not in any other pedinellid. Heterotrophic, feeding on bacteria and on other protists. Three species in marine, freshwater, and brackish environments.

Pteridomonas danica Patterson and Fenchel (Figs. 4A-D,8C). Cells 3.5-5.5 μm in diameter. Attached with a narrow contractile stalk of variable length, mostly 15-25 long. With c. 12 tentacles around the flagellum base. Cells may detach from the substrate and swim freely, often with the tentacles resorbed and occasionally with the stalk resorbed. Cells caught in debris may deform and move by amoeboid locomotions (Patterson and Fenchel 1985). Common but often confused with *Actinomonas*.

Genus ***Ciliophrys*** Cienkowsky, 1875

Colorless cells occurring in 2 different stages. Sessile (feeding) cells with granular 'tentacles over the entire cell surface. Flagellum inactive or moving very slowly in a figure-of-eight posture. Attached to a substrate with a very short stalk. The cell may change within a few minutes to a swimming condition, in which the tentacles are more or less retracted and the flagellum moves in a typical pedinellid fashion. The cell feeds on bacteria or very small protists which are caught on the tentacles, transported, to the cell body and ingested. Ultrastructural work by Davidson (1982), see also Larsen and Patterson (1990). Two very similar species, one marine, the other from fresh water.

Ciflophrys infusionum Cienkowsky, 1875 (Fig. 8B, D). Cells 5.5-11 μm in diameter with tentacles extending another 10-15 μm. Very widely distributed, attached to detritus or other objects.

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