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# *Mesopedinella arctica* gen. et sp. nov. (Pedinellales, Dictyochophyceae) I: fine structure of a new marine phytoflagellate from Arctic Canada*

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A new marine phytoflagellate is described by means of light and electron microscopy. Clonal cultures were established from sea water samples collected in June 1989 in the vicinity of Igloolik Island, northern Foxe Basin, Northwest Territories, Canada. It was observed again when visiting Igloolik Island in June 1992. Cells are radially symmetrical, 6–8 μm long and 7–10 μm wide, with a single projecting flagellum inserted in an apical depression. The flagellum bears two rows of tripartite flagellar hairs but lacks flagellar scales. A trailing stalk is present at the posterior end of some cells but appears to be missing in others. The cell body is covered by flat oval scales with a slightly thickened marginal rim. Body scales are composed of fibres forming a fine but irregular network. Cells possess six parietal chloroplasts without pyrenoids. The cytoskeleton consists of microtubular triads originating on the surface of the nuclear envelope. Triads were not observed to emanate into tentacles. Anteriorly the triads are interconnected, forming a double ring-like network around the flagellar pit. The cysts have a three-layered not silicified wall. The flagellate studied here is closely related to phototrophic genera of the order Pedinellales (Dictyochophyceae) but possesses a number of distinct ultrastructural features. It is described as *Mesopedinella arctica* gen. et sp. nov.

## INTRODUCTION

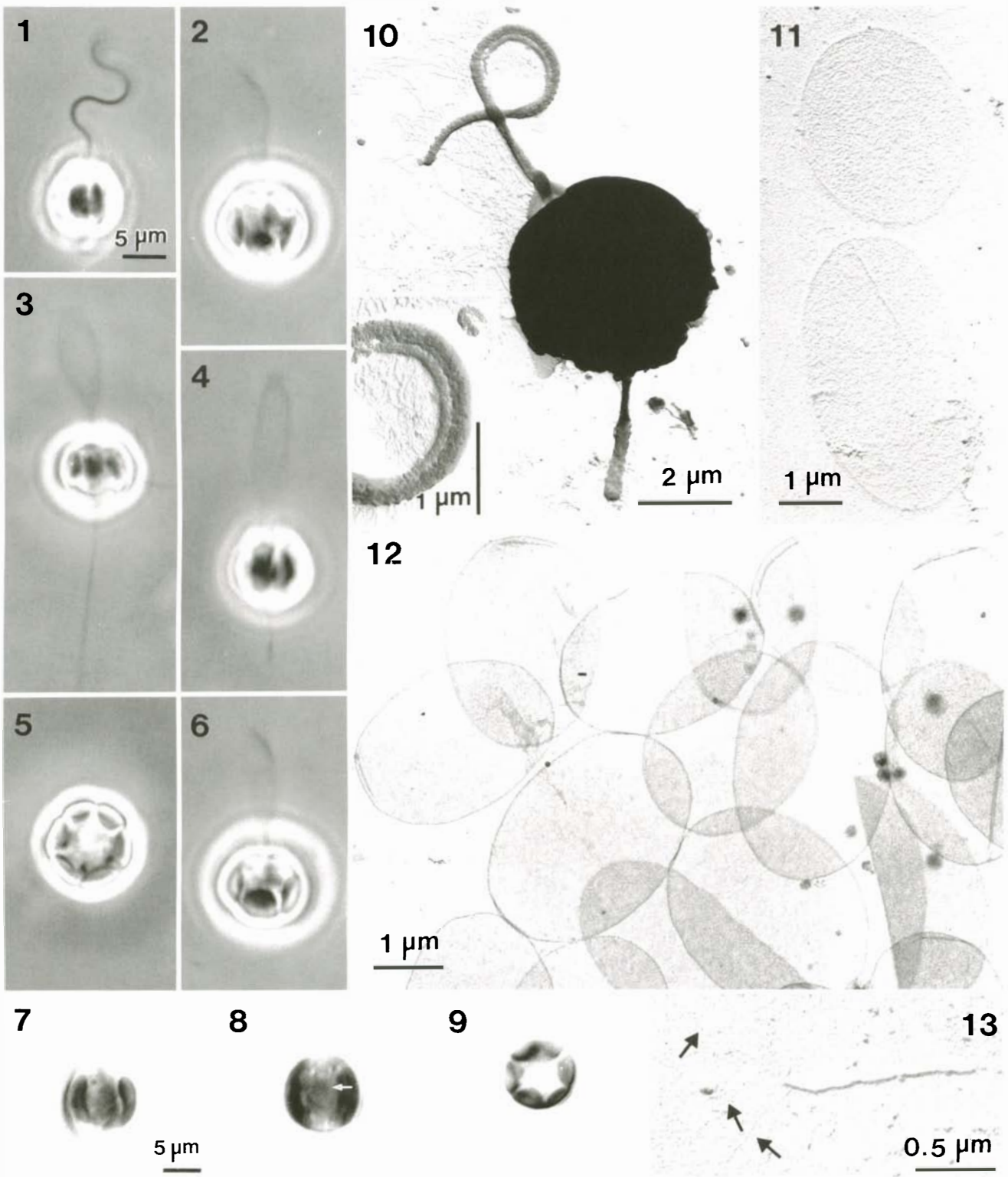
The pedinellids are unique in comprising both phototrophic (*Apedinella* Throndsen, *Pseudopedinella* Carter), mixotrophic (*Pedinella* Wyssotzki) and phagotrophic (*Actinomonas* Kent, *Ciliophrys* Cienkowski, *Parapedinella* Pedersen et Thomsen, *Pteridomonas* Penard) genera. As with other heterokonts they possess (1) tripartite tubular flagella hairs, (2) a transitional plate in the flagellar transition region, and (3) mitochondria with tubular cristae and have been placed by some authors in the Heterokontophyta (e.g. Moestrup 1992; van den Hoek *et al.* 1995). The following seven morphological characters are considered important for the circumscription of pedinellids: (1) three interconnected microtubules, referred to as triads, associated proximally with the nucleus and distally terminating at the plasmalemma or extending into tentacles; (2) basal bodies at a slight angle to each other and attached directly to the surface of the nuclear envelope (sometimes in a depression) and embedded in amorphous material; (3) a long apical flagellum inserted in a pit, the second flagellum reduced to a basal body; (4) the long flagellum extended into a lateral wing supported by a paraxonemal rod (reduced in *Pteridomonas*); (5) cells radially symmetrical with a large central nucleus and a posteriorly located Golgi apparatus; (6) often with a posterior trailing stalk in connection with a more or less complex system of vacuoles; and (7) no microtubular flagellar roots.

The pedinellids have had a controversial systematic history. Based on chloroplast features the phototrophic genera have generally been considered to be chrysophytes and included in the Chromulinales Pascher (Bourrelly 1957, 1968) or Ochromonadales Bourrelly (Christensen 1980), whereas phagotrophic taxa were classified in the order Actinophryida (class Heliozoa, Levine *et al.* 1980). Zimmermann *et al.* (1984) proposed the order Pedinellales (with one family Pedinellaceae) to reflect the close relationship among pedinellids with and without chloroplasts. Kristiansen (1990) established the class Pedinellophyceae (nomen nudum) based on ideas of Hibberd (1976) who had long argued for separating the pedinellids from the main chrysophyte line due to a different cell organization compared to the *Ochromonas* type.

Moestrup (1995) has given the latest and probably most satisfactory treatment for the classification of pedinellids. He suggests that Pedinellales be included in the class Dictyochophyceae Silva together with Rhizochromulinales O'Kelly et Wujek and Dictyochales Haeckel (silicoflagellates). The latter two orders also possess microtubules which may extend into tentacles, basal bodies attached to the nuclear envelope, a dense ring-like structure at the level of the transitional plate, a ring-like structure below the transitional plate of the flagellar transition region (although this structure has not been observed in all pedinellids) and no trace of microtubular flagellar roots.

The new phytoflagellate described here was discovered in a 6-month-old culture originally collected in northern Foxe Basin (Arctic Canada) in June 1989. It disappeared before being successfully isolated into a clonal culture. Almost a year later it bloomed in the same crude culture, which in the meantime had been transferred several times to fresh media. The flagellate displays some characters typical for pedinellids but

* This paper is dedicated to the memory of Dr Naja Vørs (1960–1994)—her approach to science and organisation was a true inspiration.




**Figs 1–13.** *Mesopedinella arctica* sp. nov.
**Figs 1–6.** Light micrographs of live cells (phase contrast optics).
**Fig. 1.** Slow sinusoidal beating of the single emergent flagellum.
**Fig. 2.** Rapidly beating flagellum obscuring the sinusoidal motion.
**Figs 3–4.** Cells with long and short trailing stalk, respectively.
**Fig. 5.** Optical transverse section showing six parietal chloroplasts.
**Fig. 6.** Oblique apical view.
**Figs 7–9.** Live cells seen in Nomarski interference contrast. Note large central nucleus in Fig. 8 (arrow).
**Fig. 10.** Shadowcast whole mount of cell with trailing stalk. The insert shows high magnification of the wing-like projection and paraxonemal flagellar rod.

also possesses a number of unique features incompatible with described phototrophic genera. To accommodate this organism within the pedinellids, the new genus *Mesopedinella* is proposed.

## MATERIALS AND METHODS

Cells of *Mesopedinella arctica* were collected in the vicinity of Igloolik Island (69°20′N, 81°45′W) northern Foxe Basin, Arctic Canada. Salinity and temperature was *c.* 34‰ and −1.5°C, respectively. For further information on sampling area, see Daugbjerg & Moestrup (1992).

### Cultures

A clonal culture was established by micropipetting from enriched cultures. It is maintained at the Department of Phycology, University of Copenhagen in modified Erdschreiber medium (30‰ salinity) (Throndsen 1978) at 4°C, a photon flux density of 13 μmol $m^{-2}$ $s^{-1}$, and a 16 : 8 h L : D cycle.

### Light and electron microscopy

Live cells were observed using an Olympus BH-2 microscope with phase contrast and Nomarski interference optics. Whole mounts for electron microscopy were shadowcast with chromium following Moestrup & Thomsen (1980) or stained for 30 min in 2% uranyl acetate followed by a 30-s wash in distilled water.

For sectioning, cells were fixed for 1 h at 4°C in 2% glutaraldehyde in 0.1 M cacodylate buffer (pH 7.7) containing 0.2 M sucrose. They were rinsed for 10 min in 0.1 M sucrose followed by a rinse in pure (0.1 M cacodylate) buffer. The cells were postfixed for 30 min in 1% osmium tetroxide in 0.1 M cacodylate buffer, rinsed in buffer for 10 min and dehydrated in an ethanol series (15 min in 15, 30, 50, 70, and 96% ethanol at 4°C and twice in 100% ethanol at room temperature). Following dehydration, cells were treated for 2×5 min in propylene oxide and left refrigerated overnight in a 1 : 1 mixture of propylene oxide and Spurr's resin. The embedding medium was then replaced with fresh Spurr's resin at room temperature and transferred 5 h later to an embedding dish for polymerisation at 70°C overnight.

Sections were stained for 30 min in 2% uranyl acetate, rinsed, and stained for 20 min in Reynold's lead citrate. The material was examined in a JEOL-100SX electron microscope at the Department of Phycology, University of Copenhagen.

## RESULTS

### *Mesopedinella* Daugbjerg gen. nov.

DIAGNOSIS: Cellulae solitariae, libere natantes, radialiter symmetricae, flagellum cum duabus seriebus pilorum tripartitorum armatum

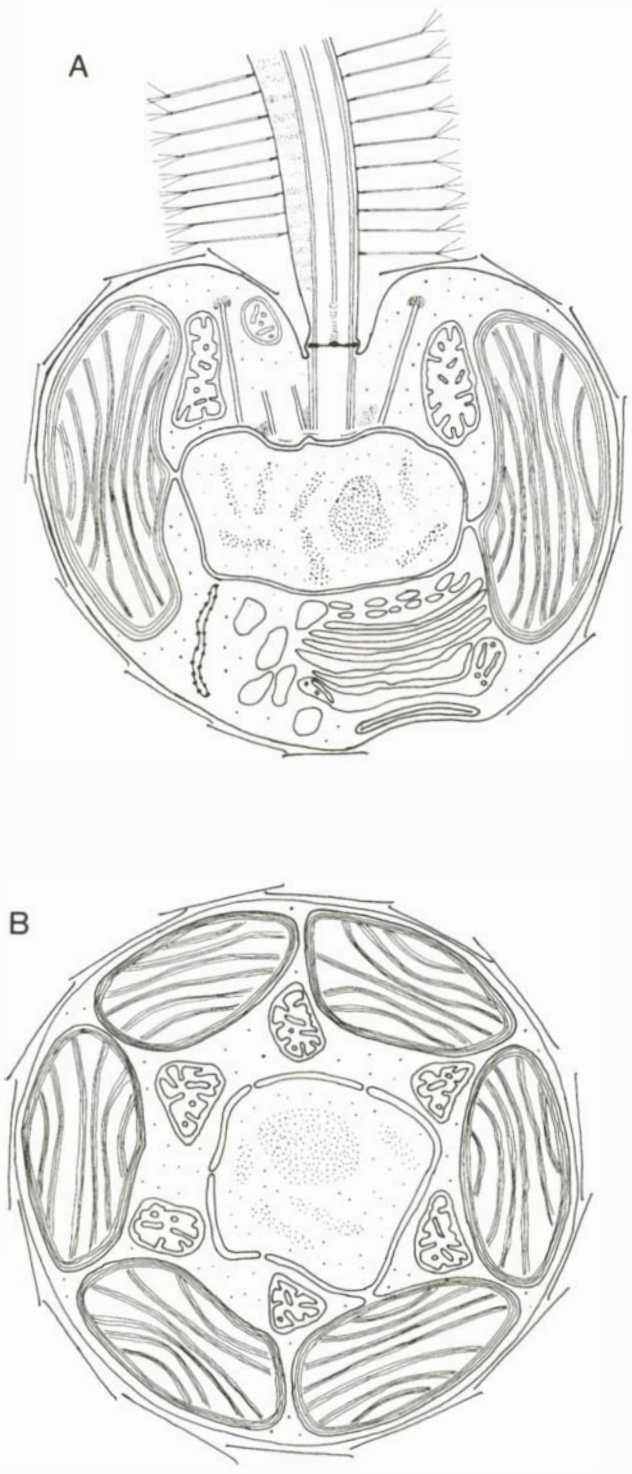



**Fig. 14.** Schematic drawing of *Mesopedinella arctica.* A, longitudinal section; B, transverse section through the middle part of the cell (for simplicity only the outer membrane of one chloroplast is shown to be continuous with the outer nuclear envelope). Not to scale.

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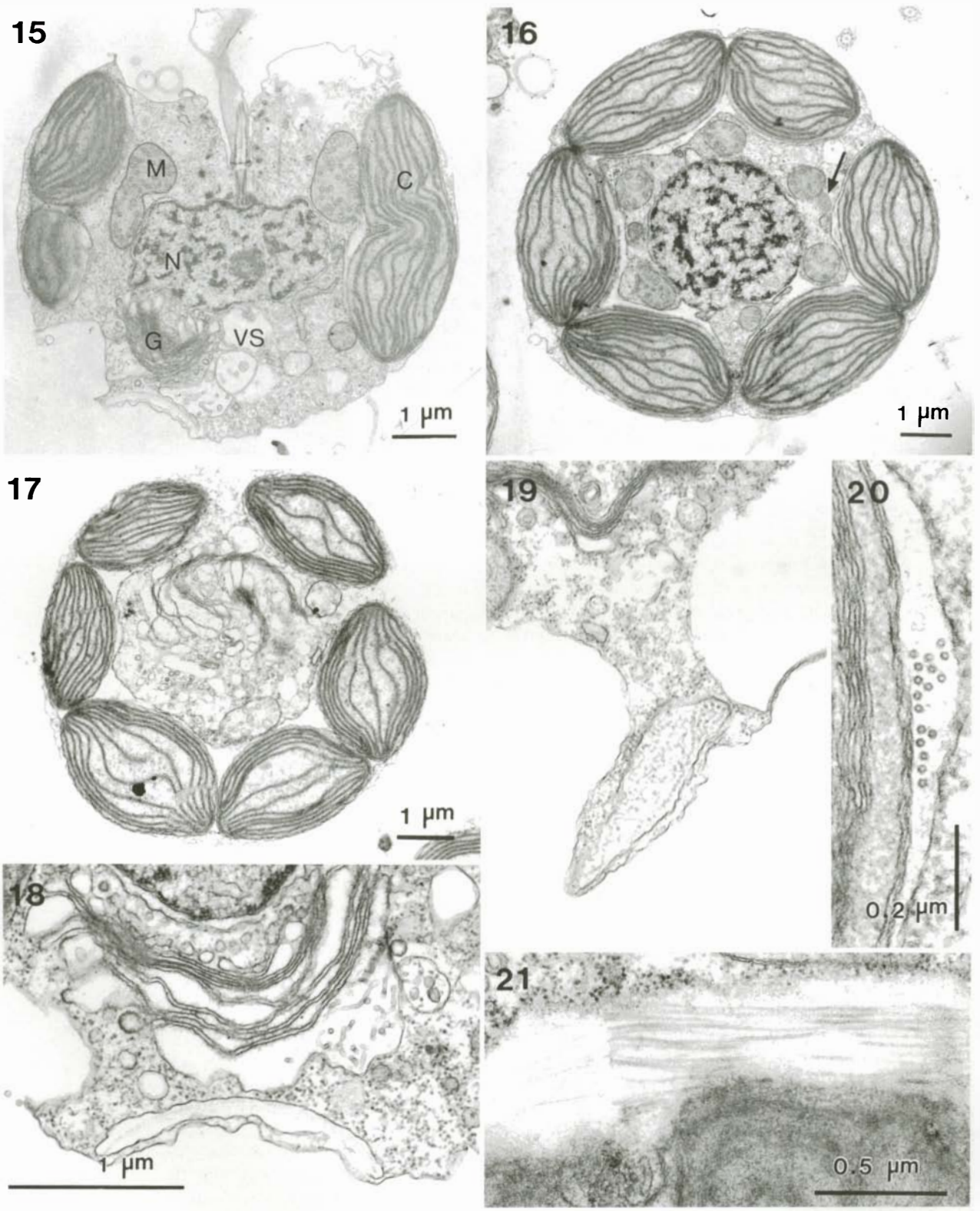
**Figs 11, 12.** Flat oval body scales. Note irregular (interwoven) arrangement of fibres (Fig. 11 shadowcast whole mount; Fig. 12 whole mount stained with uranyl acetate). Note slightly thickened marginal rim.
**Fig. 13.** Tripartite tubular flagellar hair with three thin terminal filaments (arrows).




**Figs 15–21.** Transmission electron micrographs of *Mesopedinella arctica.*

**Fig. 15.** Longitudinal section. The flagellum protrudes from an apical pit and the proximal part of the basal body is attached to the surface of the nuclear envelope. Central nucleus (N), parietal chloroplasts (C), posterior Golgi body (G) next to vacuolar system (VS), and mitochondria with tubular cristae (M) are labelled.

**Figs 16, 17.** Transverse sections through middle (Fig. 16) and lower part (Fig. 17) of the cell showing general organization of organelles. Mitochondrial profiles are present close to adjacent chloroplasts. Microbodies often occur in proximity to mitochondrial profiles (arrow). Note also chloroplast girdle lamella.

**Fig. 18.** Longitudinal section through Golgi body. The underlying vacuole contains a scale, presumably to be released across the plasma membrane. The concavity at the posterior end of the cell is probably caused by a body scale just released to the cell exterior.

hastili paraxonemali fultum habentes, squamis planis ovalibus tectae. Chloroplasta parietalia sine pyrenoidibus. Discus transitionalis in medio inspissatus sine annulis superioribus vel inferioribus. Triades microtubulares e superficie nuclei radiantes. Saepe pedunculus tractus ad finem posteriorem cellulae. Sine tentaculis et squamis flagellaribus.

Cells solitary, free swimming, radially symmetrical, with an apically inserted flagellum possessing two rows of tripartite hairs and a paraxonemal rod. Cell body covered by flat oval scales. Parietal chloroplasts without pyrenoids. Transitional plate with a central thickening, no rings above or under this structure. Microtubular triads emanate from the nuclear surface. Usually a trailing stalk at the posterior end of the cell. Without tentacles and flagellar scales.

TYPE SPECIES: *Mesopedinella arctica.*

### *Mesopedinella arctica* Daugbjerg sp. nov.

DIAGNOSIS: Cellulae maliformes, 6–8 μm longae, 7–10 μm latae. Sex chloroplasta aurea parietalia. Flagellum longitudine cellulae 2–3plo longius. Pendunculus tractus longitudine aliquantum variat. Squamae monomorphae 3.3 μm longae, 2.1 μm latae, cum margine parum incrassato et basi reticulo fibrarum tenuum et irregularium.

Cells apple-shaped, 6–8 μm long and 7–10 μm wide. Six golden-brown parietal chloroplasts. Flagellum 2–3 times the cell length. The smooth trailing stalk varies considerably in length. Body scales with a slightly thickened marginal rim, one type only. The base with a network of fine but irregular fibres. Scales *c.* 3.3 μm long and 2.1 μm wide.

HOLOTYPE: Fig. 14A.

TYPE LOCALITY: Hooper Inlet (69°20′N, 81°45′W), northern Foxe Basin, Northwest Territories, Canada.

### Light microscopy

CELL MORPHOLOGY: Live cells of *Mesopedinella arctica* are shown in Figs 1–9. Cells are radially symmetrical (Figs 6, 9), but the posterior end may appear irregular in outline (Fig. 4). Cells are typically wider than long. The sinusoidal beating flagellum (Fig. 1) is 2–3 times longer than the cell. The six golden-brown chloroplasts are the most distinct organelles. They are evenly positioned and form a tight layer at the periphery of the cell (Figs 6–8). A large nucleus is positioned in the centre of the cell. At the antapical end of the cell a trailing stalk, highly variable in length, is often observed (Figs 3, 4). It is unbranched and without knots or swellings. Other cells apparently lack the trailing stalk (Figs 1, 2). Tentacles were not observed.

CELL MOVEMENT: Cells swim with a rotation about their longitudinal axis. They were never observed to attach to any object. Their swimming behaviour is very similar to that described for *Pseudopedinella elastica* Skuja (Zimmermann *et al.* 1984).

### Electron microscopy

WHOLE MOUNTS: The cell body is completely covered by layers of a single type of flat oval scale with a slightly thickened marginal rim (Figs 11, 12). The base of the scales comprises fibres which form a fine irregular network (Fig. 11), similar to that of *Apedinella radians* (Lohmann) Campbell (Throndsen 1971). The scales vary in size, 2.3–4.3 μm in length (mean 3.3 μm; SD ± 0.4) and 1.7–2.6 μm in width (mean 2.1 μm; SD ± 0.2) (n = 50). The flagellum has a wing-like structure with a paraxonemal rod (Fig. 10) and bears tripartite flagellar hairs (Figs 10, 13). No flagellar scales were observed.

GENERAL ULTRASTRUCTURE: The general organisation of cell organelles is illustrated in Figs 14–19.

CHLOROPLASTS: In transverse sections (Figs 16, 17) the chloroplasts are seen to be positioned adjacent to the plasmalemma, surrounding the other organelles. In longitudinal section the length of each chloroplast is almost equal to the cell length. The outer chloroplast membrane is continuous with the outer nuclear membrane (Fig. 16). The thylakoids are arranged in stacks of three (Fig. 20) to form lamellae. Most sections show eight to nine lamellae surrounded by the girdle lamella (Figs 14–17), as typical for heterokont algae. Pyrenoids are lacking.

NUCLEUS, MITOCHONDRIA, GOLGI APPARATUS, AND MICROBODIES: The nucleus is relatively large and located in the central part of the cell (Figs 14–16). Tubular tripartite flagellar hairs are frequently seen in the chloroplast endoplasmic reticulum which is continuous with the perinuclear space (Figs 20, 21). In transverse sections six profiles of mitochondria are visible between the nucleus and the chloroplasts (Figs 14B, 16). Judging from numerous transverse and longitudinal sections it seems likely that the mitochondria form a single reticulum similar to that observed in *Apedinella radians* (Koutoulis *et al.* 1988) and suggested for *Pseudopedinella tricostata* (Rouchijajnen) Thomsen (Thomsen 1988). The mitochondria have tubular cristae with inclusions as observed in *Apedinella radians* (Throndsen 1971), *Ciliophrys infusionum* Cienkowski (Davidson 1982, as *C. marina*), *Pseudopedinella elastica* (Zimmermann *et al.* 1984). These inclusions are seen as electron-dense material in Figs 15 and 16. Microbodies occur adjacent to the mitochondria (Fig. 16).

The Golgi apparatus consists of a single dictyosome located eccentrically below the nucleus (Figs 14B, 15, 17). It contains six to eight somewhat swollen cisternae. Although scales have never been identified convincingly in any of the cisternae, scale vacuoles containing mature scales were always observed in proximity of the trans-Golgi reticulum. The scales are probably released across the plasmalemma in the posterior end of the cell and only after their exterior deployment are relocated to cover the whole cell (Fig. 18). The indentation seen to the left of the scale vacuole in Fig. 18 probably results from a scale being released prior to fixation for thin sectioning. Such

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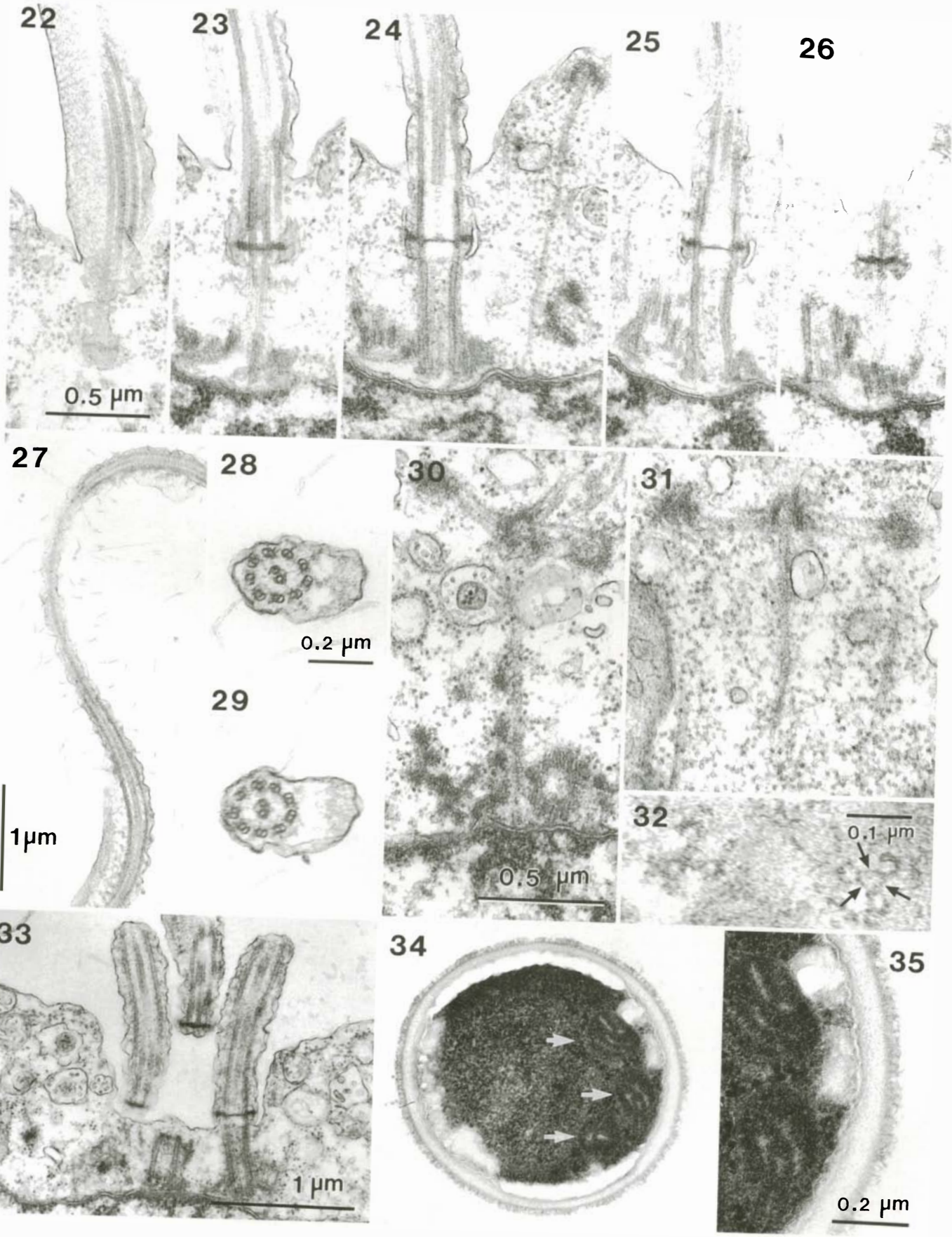
**Fig. 19.** Posterior end of cell, presumably showing parts of trailing stalk.
**Fig. 20.** Section through chloroplast endoplasmic reticulum with tubular flagellar hairs. Thylakoids are in groups of three, the typical arrangement in heterokonts.
**Fig. 21.** Section showing tripartite flagellar hairs in chloroplast endoplasmic reticulum.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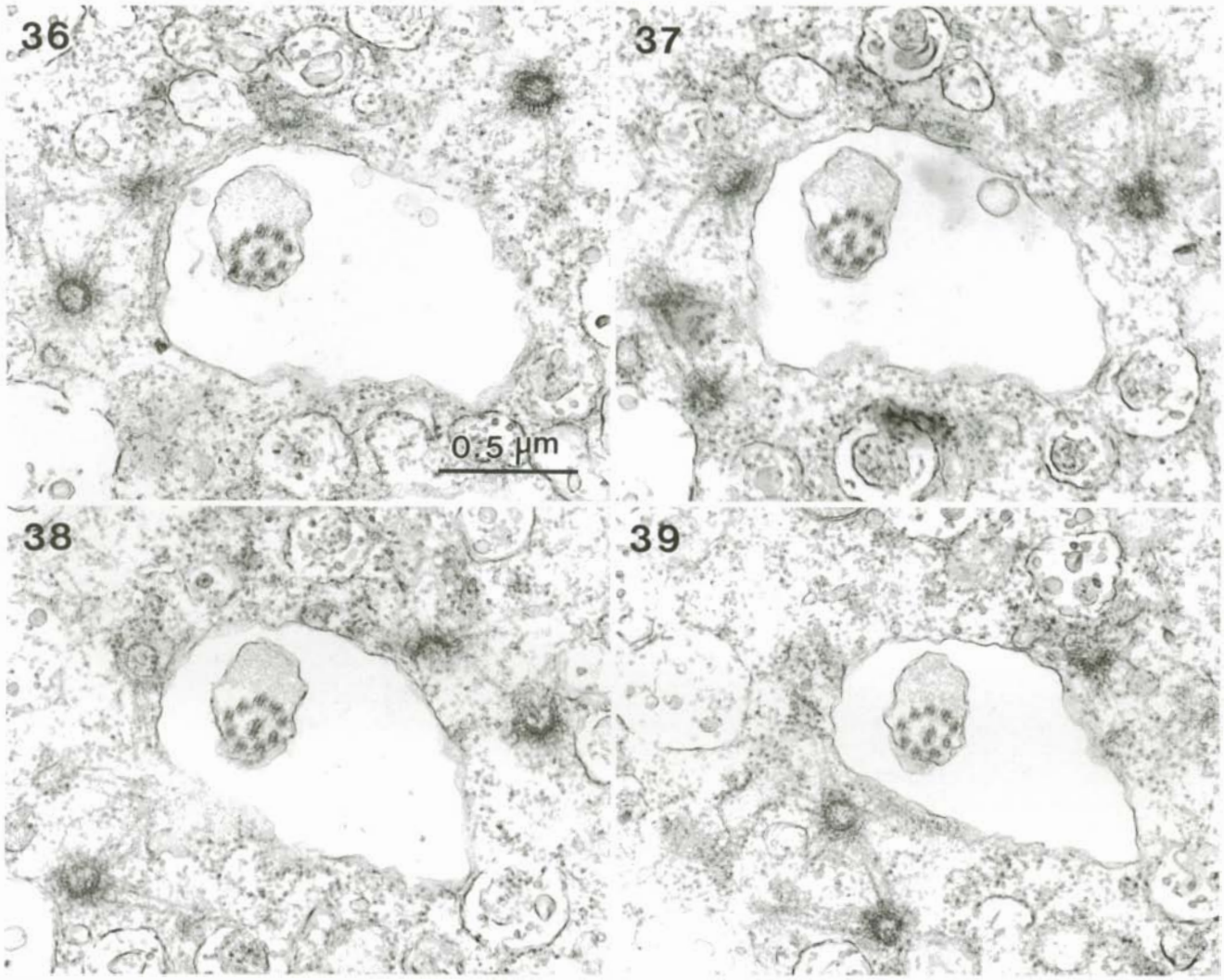


**Figs 36–39.** Four transverse serial sections of cytoskeleton in *Mesopedinella arctica.* Interconnected triads form two circles around the flagellar pit.

invaginations may perhaps explain the irregular contour of the posterior end often noticed in the light microscope. Cisternae towards the maturing side of the Golgi apparatus are frequently seen to contain elongated tubular structures (Fig. 18). Vacuoles comprising these or similar structures are also scattered throughout the cytoplasm (Figs 24, 33). Similar vacuoles were observed in *Pseudopedinella elastica* (Zimmermann *et al.* 1984).

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**Figs 22–35.** Transmission electron micrographs of *Mesopedinella arctica.*

**Figs 22–26.** Five longitudinal sections from a series through the flagellar bases.

**Fig. 22.** Cross-banding of paraxonemal rod visible.

**Fig. 23.** Ring-like structure surrounding the transitional plate is visible at this level of the flagellar transition region.

**Fig. 24.** The two central microtubules terminate some distance above the transitional plate. A centrally constricted structure is visible between the transitional plate and the central pair. Amorphous electron-dense material is present at the proximal end of both basal bodies. Microtubules are in close association with nuclear envelope proximally and capped distally.

**Figs 25, 26.** Basal bodies insert at a slight angle to each other.

**Fig. 27.** Longitudinal section of flagellum showing two rows of tripartite flagellar hairs and rotation of the central pair of microtubules.

**Figs 28, 29.** Two consecutive transverse serial sections of a flagellum showing wing-like extension and paraxonemal rod. Note also two opposite rows of tripartite flagellar hairs.

**Figs 30, 31.** Two sections showing triads interconnected anteriorly. Triad in Fig. 30 clearly terminates on the nuclear envelope.

**Fig. 32.** Cross-section of triads. Individual microtubules are interconnected by thin filaments (arrows).

**Fig. 33.** Longitudinal section through a tri-flagellate cell indicating duplication of basal bodies and development of new flagella. Only the long flagellum of the mother cell bears a paraxonemal rod.

**Fig. 34.** Section through cyst. Three chloroplasts can be discerned (arrows).

**Fig. 35.** Higher magnification of cyst wall, showing three wall layers.

**Table 1.** A comparison of phototrophic genera of pedinellids. − = character absent; + = character present; −/+ = character present or absent

| Species | Length (μm) | Width (μm) | Chloroplast (number) | Pyrenoid (−/+) | No. of scale types | Trailing stalk (−/+) | Anterior tentacles | Vacuolar system associated with trailing stalk |
|---|---|---|---|---|---|---|---|---|
| *Apedinella radians* | 6–9.5 | 7–10.5 | 6 | + | 2 | −/+ | + | − |
| *Pedinella hexacostata* | 7–8 | 9–10 | 6 | − | − | + | + | − |
| *Pseudopedinella elastica* | 9–15 | 10–14 | 6 | + | − | + | + | + |
| *Pseudopedinella pyriformis* | 8–10 | 9–12 | 6 | + | − | + | − | + |
| *Pseudopedinella tricostata* | 5.5–7 | 6–8 | 3 | + | − | + | − | + |
| *Mesopedinella arctica* | 6–8 | 7–10 | 6 | − | 1 | −/+ | − | − |

| | Mode of nutrition | Habitat | Salinity (‰ S) | Temperature (°C) | Reference |
|---|---|---|---|---|---|
| *A. radians* | Phototrophic | Marine | 6–34 | 17–20 | Throndsen (1971); Koutoulis *et al.* (1988); Edler *et al.* (1984) |
| *Pe. hexacostata* | Mixotrophic | Freshwater saline lake, marine[2] | 10, 30[2] | 20 | Swale (1969) |
| *Ps. elastica* | Phototrophic | Brackish | 2–6 | 10–15 | Zimmerman *et al.* (1984); Edler *et al.* (1984) |
| *Ps. pyriformis* | Phototrophic | Marine | 10, 20[1] | 7 | Ostroff & van Valkenburg (1978); Edler *et al.* (1984) |
| *Ps. tricostata* | Phototrophic | Marine, ice | 6, 18–23 | −0.6 | Thomsen (1988); Edler *et al.* (1984) |
| *M. arctica* | Phototrophic | Marine, ice | 34 | −1.5 | Present study |

[1] Moestrup, unpublished.
[2] T. Christensen, personal communication.

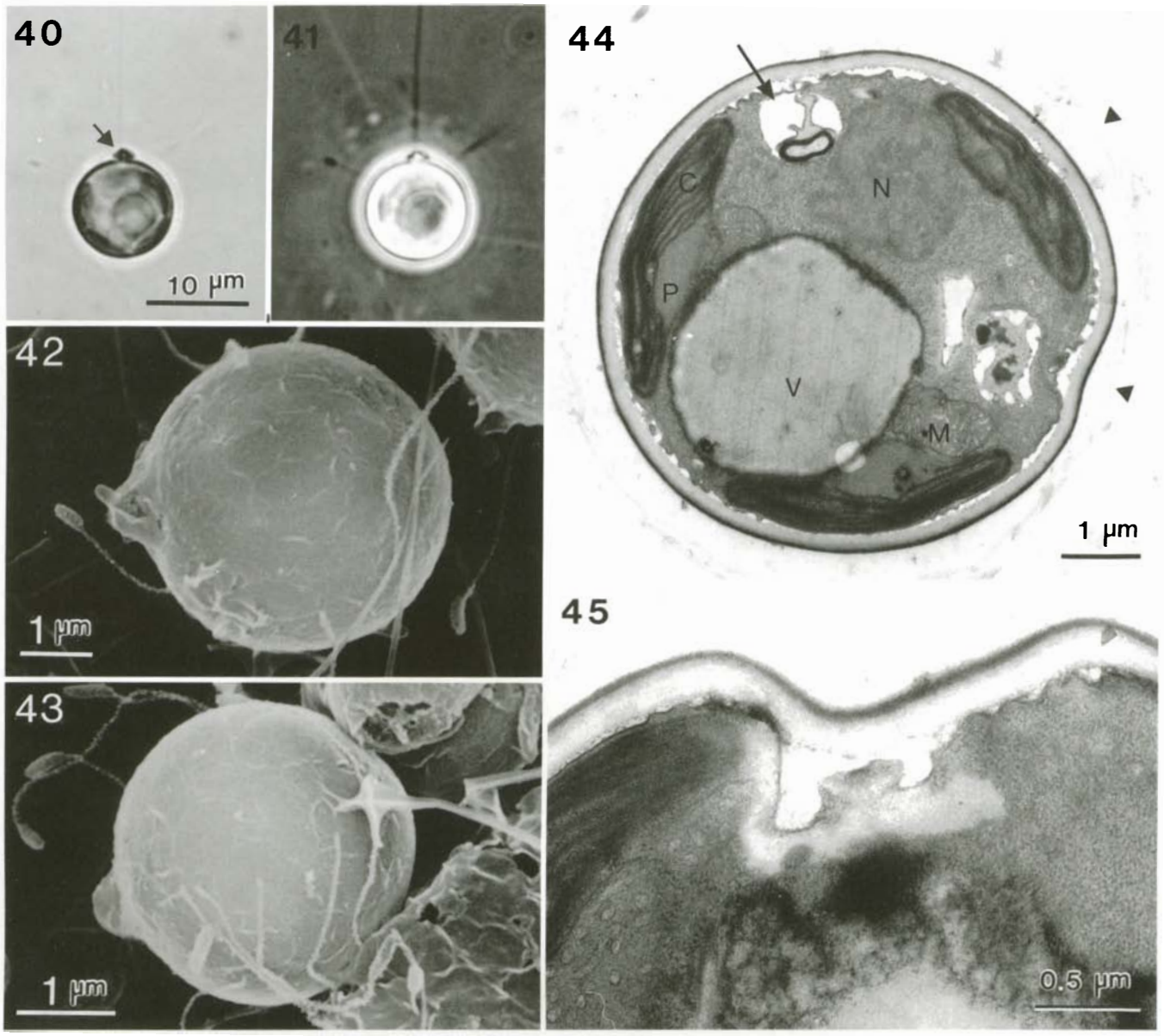
FLAGELLUM AND ASSOCIATED STRUCTURES: The basal bodies are inserted at a slight angle (*c.* 10°). The mature ('non-functioning') basal body, which lacks a flagellum, is approximately ⅔ the length of the immature ('functioning') basal body. The proximal ends of the basal bodies are closely associated with the outer nuclear membrane and presumably attached to this by the amorphous electron-dense material visible in Figs 23–26 and 33. However, the proximal ends of the basal bodies and the nuclear envelope are separated by thin crescent-shaped structures (Figs 25, 26). Similar structures were found in *Pteridomonas danica* Patterson et Fenchel (Patterson & Fenchel 1985) and in *Actinomonas mirabilis* Kent (Larsen 1985, as *A. pusilla*). The transitional plate is located a short distance above the level of flagellar attachment to the cell body (Figs 23–26, 33). It is characterised by a central thickening (Fig. 25). A thin fibre links the proximal end of the central microtubular pair with the thickening of the transitional plate (Fig. 24). A much more conspicuous fibre is visible in *Apedinella radians* (Koutoulis *et al.* 1988; Moestrup, unpublished observations). No additional structures are evident in the region of the transitional plate. The axoneme is supported by the conventional 9 + 2 microtubules (Figs 28, 29). A paraxonemal rod lies adjacent to the axoneme, forming the dense wing-like extension (Figs 22, 27–29). Two rows of tripartite tubular flagellar hairs are arranged on almost opposite sides of the flagellum (Figs 27–29), the distance between two adjacent flagellar hairs in a row being *c.* 200 nm (Fig. 27).

The tri-flagellate cell shown in Fig. 33 is indicative of duplication of basal bodies as well as development of two new flagella. The newly formed flagella are located on each side of the long flagellum and the paraxonemal rod characteristic of the protruding flagellum in pedinellids is not visible in this section or has not yet been formed. Detailed studies of flagellar development in *Pseudopedinella elastica,* however, showed that the two newly formed flagella both contained a paraxonemal rod (Heimann *et al.* 1989).

CYTOSKELETON: Compared to *Apedinella radians* (Koutoulis *et al.* 1988; Koutoulis & Wetherbee 1993a, 1993b, 1993c), the cytoskeletal system of *Mesopedinella arctica* is very simple. It consists of triads of microtubules interconnected at the apical end to form a double ring-like network (Figs 36–39). The inner ring consists of probably six and the outer ring of probably 12 microtubular triads, similar to the cytoskeleton in *Actinomonas mirabilis* (Larsen 1985), *Pteridomonas danica* (Patterson & Fenchel 1985) and probably *Pseudopedinella tricostata* (Thomsen 1988). The individual triads are associated proximally with the nuclear envelope and terminate close to the plasma membrane, but they never extend into tentacles (Figs 24, 30, 31).

VACUOLE SYSTEM AND TRAILING STALK: A trailing stalk connected to a well-developed posterior vacuole system and supported by microtubules is lacking. The vacuole system is more like that of *Pedinella hexacostata* with many vacuoles of different sizes. A detailed account of the ultrastructure of the trailing stalk cannot be presented as only few sectioned cells were observed to possess this structure. However, Fig. 19 shows part of a trailing stalk containing high numbers of small bleb-like structures, similar to the trailing stalk of *Actinomonas* (Larsen 1985), *Pteridomonas* (Patterson & Fenchel 1985), and *Pseudopedinella* (Zimmermann *et al.* 1984).

CYST STAGE: The cyst of *Mesopedinella arctica* has been observed only in thin sectioned material (Fig. 34). The cyst wall (Fig. 35) seems to consist of three layers. The darkly staining outermost layer is irregular and fibrous, measuring *c.* 50 nm. The middle layer is *c.* 90 nm thick, and the thin innermost layer measures *c.* 15 nm. The cytoplasm appears electron dense and uniform and only three small chloroplasts are visible in Fig. 34. The diameter of the cyst is *c.* 2 μm, approximately one quarter of the diameter of the flagellate stage. The factor(s) inducing encystment and excystment in *Mesopedinella* is not known.




**Figs 40–45.** Cysts of *Apedinella radians.* Micrographs courtesy of Gert Hansen.
**Figs 40, 41.** Light micrographs of cyst photographed with Nomarski interference contrast (Fig. 40) and phase contrast (Fig. 41). A distinct plug (arrow), a thickened wall, chloroplasts, and a large vacuole are visible. Note also the characteristic spine scales.
**Figs 42, 43.** Scanning electron microscopy showing the three-dimensional shape of the cyst. Flat oval body scales cover the cell entirely (Fig. 42) and a single spine scale is seen in Fig. 43. The cyst plug is also visible.
**Fig. 44.** Oblique section through cyst plug (arrow). The cyst has a three-layered wall surrounded by body scales (arrowheads). Note also chloroplasts (C) with bulging pyrenoids (P), nucleus (N), vacuole (V) and mitochondria (M).
**Fig. 45.** Higher magnification of cyst plug.

## DISCUSSION

When viewed with light microscopy, cells of *Pseudopedinella elastica, Pseudopedinella pyriformis* Carter, and *Mesopedinella arctica* can be difficult to distinguish. They are similar in shape and cell dimensions and each possesses six parietal chloroplasts. Though *P. elastica* is slightly bigger, species of *Pseudopedinella* vary considerably in width and length (cf. table 1 in Zimmermann *et al.* 1984). Cell size alone is not justified as a diagnostic character in species identification. In species of *Pseudopedinella* the trailing stalk is variable in length and is sometimes branched with swellings. When present in *Mesopedinella* it is always unbranched without small knobs and it varies markedly in length. When *Pseudopedinella* hits an object or is fixed in e.g. Lugol's iodine the trailing stalk retracts and appears as a dense posterior appendage. Retraction of the stalk was not seen in *Mesopedinella.* This difference and the tentacles sometimes present in species of *Pseudopedinella* may be used as reliable characters in separating the species in the light microscope. Under the electron microscope several distinct features become apparent. The plasmalemma of *Mesopedinella* is covered by scales whereas

cells of *Pseudopedinella* are naked. The cell bodies of *Apedinella radians* (Throndsen 1971; Koutoulis *et al.* 1988) and *Parapedinella reticulata* Pedersen et Thomsen (Pedersen *et al.* 1986) are also covered by scales (two types in *Apedinella,* one in *Parapedinella*). Except for the large spine scales of *Apedinella,* the body scales of the three pedinellids are structurally alike. They are similar in size, flat, elliptical, and with an irregular fibrillar (interwoven) network. In *Parapedinella* the body scales have two morphologically different sides whereas in *Apedinella* and *Mesopedinella* both scale sides are identical. The flat oval scales in *Apedinella* and *Mesopedinella* are practically identical.

Minute annular scales cover the flagellum of the heterotrophic pedinellids *Actinomonas* (Larsen 1985), *Parapedinella* (Pederson *et al.* 1986), and *Pteridomonas* (Preisig *et al.* 1991). Flagellar scales are not known from chloroplast-bearing pedinellids, and it is doubtful that flagellar scales will prove to be characteristic of the order Pedinellales as suggested by Pedersen *et al.* (1986).

*Mesopedinella arctica* has several other distinct features when compared to other phototrophic pedinellids (Table 1). As in *Pedinella hexacostata,* the chloroplasts of *M. arctica* lack pyrenoids whereas each chloroplast in *Pseudopedinella* spp. and *Apedinella radians* contains a prominent pyrenoid (Swale 1969; Throndsen 1971; Ostroff & van Valkenburg 1978; Zimmermann *et al.* 1984; Thomsen 1988).

The posterior vacuole system in *Mesopedinella* and *Pedinella* is not as well developed as in *Pseudopedinella* spp., the heterotrophic pedinellids or in *Apedinella* which probably represents an intermediate stage. In *Mesopedinella* and *Pedinella* the vacuolar system is not encircled by the Golgi apparatus and does not indicate an area of particular activity.

*Pedinella hexacostata* is known from both fresh and saline waters and is often attached to particles (Swale 1969). In the Danish Wadden Sea *P. hexacostata* grew in 30‰ salinity, attached to *Vaucheria* spp. (T. Christensen, personal communication). Apparently, populations of *P. hexacostata* have adapted to differences in salinity from brackish to highly saline waters indicating the existence of ecotypes. *Pedinella hexacostata* is mixotrophic and identified by the numerous tentacles arranged around the anterior pit and the presence of several contractile vacuoles. *Mesopedinella arctica* does not possess tentacles or contractile vacuoles and has never been observed attached.

The cyst morphology of *Mesopedinella arctica* is very similar to that of *Pseudopedinella tricostata* (Thomsen 1988). Pronounced size differences between cysts and flagellate stages were not reported in the latter whereas in *Mesopedinella* the diameter of the cysts were ⅓ to ¼ the diameter of the monad. Cyst stages of *Apedinella radians* have also been observed by Hibberd (1986) and by Moestrup (unpublished observations) though not illustrated. A culture of *Apedinella radians* (presumably clonal) was obtained from a dilution series ($10^{-5}$) based on a water sample from Kattegat near Sealand, Denmark, 3 April 1989. The culture, isolated by Gert Hansen, was later observed to form many cysts possessing a plug, a thickened wall and spine scales (Figs 40, 41). The plug was also visible with SEM as were the two types of body scales (flat oval scales and spine scales—Figs 42, 43). The ultrastructure of the cyst is illustrated in Figs 44 and 45. This is the first record of a pedinellid cyst with a plug superficially resembling the siliceous endogenous cyst (statospore) of the Chrysophyceae and Synurophyceae. Though the plug of the *Apedinella* cyst and the chrysophyte statospore is strikingly similar, the cyst wall in pedinellids is apparently unsilicified. Thus, the presence of a plug is not considered a phylogenetic argument for a close relationship between pedinellids and the Chrysophyceae and Synurophyceae but probably represents a homoplasy in these groups. A cyst plug was not observed in the cysts of *Pseudopedinella tricostata* (Thomsen 1988). Studies of cyst development in pedinellids are needed.

The morphological differences observed by light and electron microscopy reveal *Mesopedinella* as a distinct genus with a well-defined taxonomic position within the Pedinellales. This is also supported by a cladistic analysis (Daugbjerg 1996). *Mesopedinella arctica* is the first phototrophic pedinellid recorded in polar marine waters while the colourless *Actinomonas mirabilis* was seen in Disko Bay, West Greenland (Thomsen 1981) and *Actinomonas mirabilis/Pteridomonas danica* in northern Foxe Basin (Daugbjerg & Vørs 1993; Vørs 1993). Preliminary experiments have shown that *Mesopedinella arctica* is stenothermic and can not survive in temperatures above 8–10°C. It is therefore probably restricted to cold water (cryophilic).

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