

Fine Structure of *Cosmocolpoda naschbergeri* (Ciliophora, Colpodida)

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Summary: In both the light and scanning electron microscope, *Cosmocolpoda naschbergeri* FOISSNER, 1993 looks rather dissimilar to other members of the order Colpodida due to its unique cortical ornamentation, viz. 1–2 μm high, equidistantly spaced crests which extend between the somatic ciliary rows. A transmission electron microscope study was thus put forward to substantiate the colpodid affinity suggested by some light microscopic observations and to establish whether the peculiar ornamentation is associated with special ultrastructural characteristics. The cortical ultrastructure and the fibrillar associates of the somatic dikinetids of *C. naschbergeri* are very similar to those described from members of the order Colpodida, especially to those known from small *Colpoda* species, viz. *C. steinii* and *C. maupasi*. However, extrusomes (mucocysts, trichocysts) are absent and the epiplasmic layer, which is continuous with the cortical crests, is thicker than in other small colpodids and might help to stabilize the cortical ornamentation. No other special differentiations were found in the crests which contain mitochondria and a tubular cistern of the granular endoplasmic reticulum. It is concluded that *C. naschbergeri* is closely related to the genus *Colpoda*. The ornamentation of its cortex is apparently a young evolutionary acquisition.

Key Words: Central America; Colpoda; Colpodea; Cortical ornamentation; Costa Rica; Ultrastructure.

Introduction

Cosmocolpoda naschbergeri FOISSNER, 1993 inhabits sandy, saline soils on the Caribbean Sea coast of Costa Rica, Central America. It is unique in having conspicuous cortical crests forming a ladder-like pattern between the ciliary rows. However, its somatic and oral infraciliature is very similar to that known from small members of the genus *Colpoda*, e.g. *C. maupasi*. The genus was thus assigned to the family Colpodidae (FOISSNER 1993). The present study was undertaken to confirm the colpodid nature of *C. naschbergeri* and to establish whether the cortical ornamentation is associated with special ultrastructural characteristics.

Material and Methods

Raw material from the type population was used for all investigations. Cells were processed for scanning and transmission electron microscopy as described in FOISSNER (1993) and FOISSNER & FOISSNER (1985).

Results

Light and Scanning Electron Microscopy

A detailed light and scanning electron-microscopic description of *Cosmocolpoda naschbergeri* has been pu-

published by FOISSNER (1993). Thus, we repeat only the important characteristics and refer for details to Figs. 1–8. This small (in vivo 40–70 x 30–60 µm), bacteria feeding ciliate has a roughly triangular (trophonts) to ovoid (theronts) shape, a single macronucleus and micronucleus near the centre of the cell, and a contractile vacuole in the posterior end (Fig. 1). The somatic ciliary rows course slightly to distinctly spirally and are composed of paired basal bodies; the anterior basal body of the dikinetids is nonciliated, with the exception of the condensed anteriormost 2–4 dikinetids in the right lateral kineties (Fig. 8). The cortex is deeply furrowed by the somatic kineties and ornamented ladder-like by conspicuous crests which extend between the somatic ciliary rows (Figs. 1, 5, 8). The crests are regularly spaced and 1–2 µm high, and thus easily recognizable even in live cells (Figs. 3, 4). The small oral apparatus is near the ventral anterior end and composed of two distinct ciliary fields (Figs. 1, 3, 8). The left field is narrow-rectangular and consists of 5–8 short, equidistantly spaced ciliary rows. The right field is triangular and composed of about 7 curved kineties with slightly disordered basal bodies and a row of dikinetids on the dorsal margin (Figs. 6, 8). The silverline meshes are narrow-rectangular and the horizontal lines extend in the cortical crests (Figs. 2, 7).

Transmission Electron Microscopy

Membrane systems and cortical ornamentation: A typical cell membrane covers the entire organism (Figs. 9, 24). It is subtended by flat alveoli on all surfaces with the exception of ciliary shafts and pits (Fig. 19), excretory pore (Fig. 13), cytopharynx, parasomal sacs (Fig. 19), and between the bases of the oral basal bodies (Fig. 14). The alveoli are unit-membrane-bound sacs which lie above the epiplasm and extend between the cortical ridges. The alveolar junctions are thus in the furrows of the cortical crests and are filled with electron-dense material resembling that of the epiplasmic matrix (Figs. 9, 11, 12). The epiplasm is a single, homogeneously electron-dense layer, 40–60 nm (\bar{x} = 45, n = 8) in thickness, which underlies the cell membrane or alveoli of all cortical structures with the exception of the cytostome, parasomal sacs, and the bottom of the excretory pore (Figs. 9–13, 15, 19, 21).

The cortex is distinctly ridged between the somatic kineties (Fig. 24). The cortical crests, which extend between and at right angles to the ciliary rows, are rectangular to triangular in transverse section and contain a tubular cistern of the granular endoplasmic reticulum and mitochondria at those sites where no basal body associated microtubules extend (Figs. 9, 11, 12). Often the

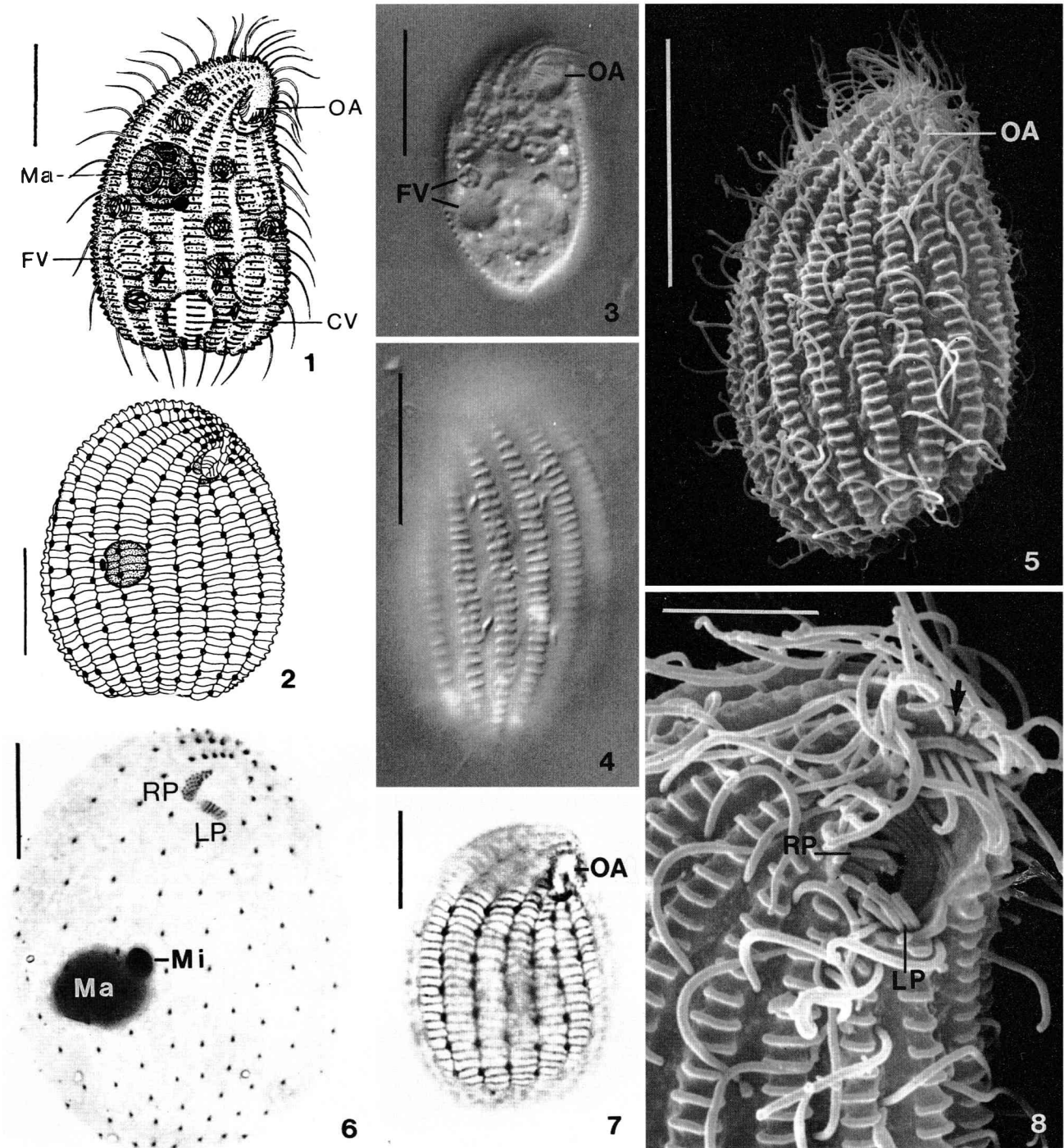
space between the walls of the crest is entirely or almost entirely occupied by the thick epiplasm (Fig. 9).

Somatic kinetids: The somatic dikinetids possess the typical colpodid ultrastructure as described, e.g. by AESCHT et al. (1991), FOISSNER (1993) and LYNN (1976b). The microtubular ribbons associated with the dikinetids consist of 5–8 microtubules each, except for the postciliary ribbon of the anterior basal body, which is made of a single microtubule only. The LK fibre, which is formed by the posterior transverse microtubular ribbons, is comparatively inconspicuous, i.e. consists of two to three ribbons with about five microtubules each lying side by side in the interkinetal ridges close beneath the epiplasm (Figs. 10, 12, 15–22). Nematodesmal microtubules are associated with the proximal ends of the anterior right lateral dikinetids and may contribute to the pharyngeal apparatus (Fig. 14).

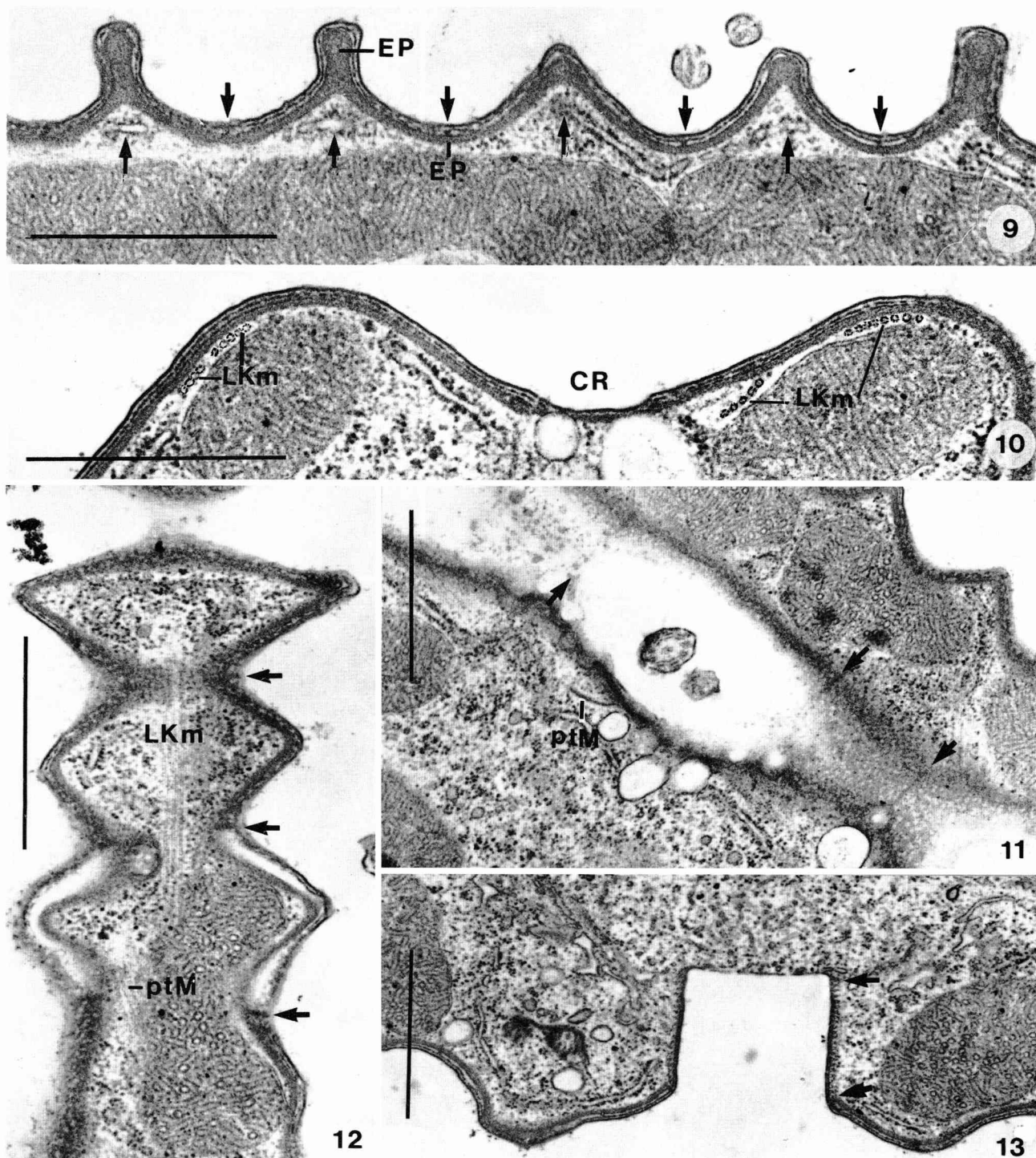
Oral structures: The oral apparatus was not studied in detail. However, some sections indicate that the fine structure of the oral ciliary fields is very similar to that known from, e.g. *Colpoda maupasi* (LYNN 1976b) and *C. variabilis* (HOFMANN-MÜNZ 1991). Nematodesmal microtubules originate at the proximal end of the oral basal bodies and form the pharyngeal fibres (Fig. 14).

Internal organization: The macronucleus of *C. naschbergeri* is quite similar to that of *Colpoda steinii* (FOISSNER 1993; FRENKEL 1980; LYNN 1976a), i.e. it contains many small chromatin bodies and one to four large, spherical endosomes composed of an aggregate of nucleoli (Figs. 1, 24). The nucleoli are of variable shape and apparently composed of many small, heavily staining granules, possibly ribosomes (Fig. 27); small peripheral nucleoli are sometimes found. The ellipsoid micronucleus is of the chromosomal type (RAIKOV 1982) and its heavily stained chromatin has a lattice-like appearance (Fig. 25). Both macro- and micronucleus have their own nuclear membranes which are perforated by nuclear pores (Fig. 25). The contractile vacuole is very similar to that of *Colpoda maupasi* (LYNN 1976b), i.e. the excretory pore canal has a diameter of about 900 nm and a depth of about 1000 nm and is surrounded by approximately 22 pore microtubules (Fig. 13).

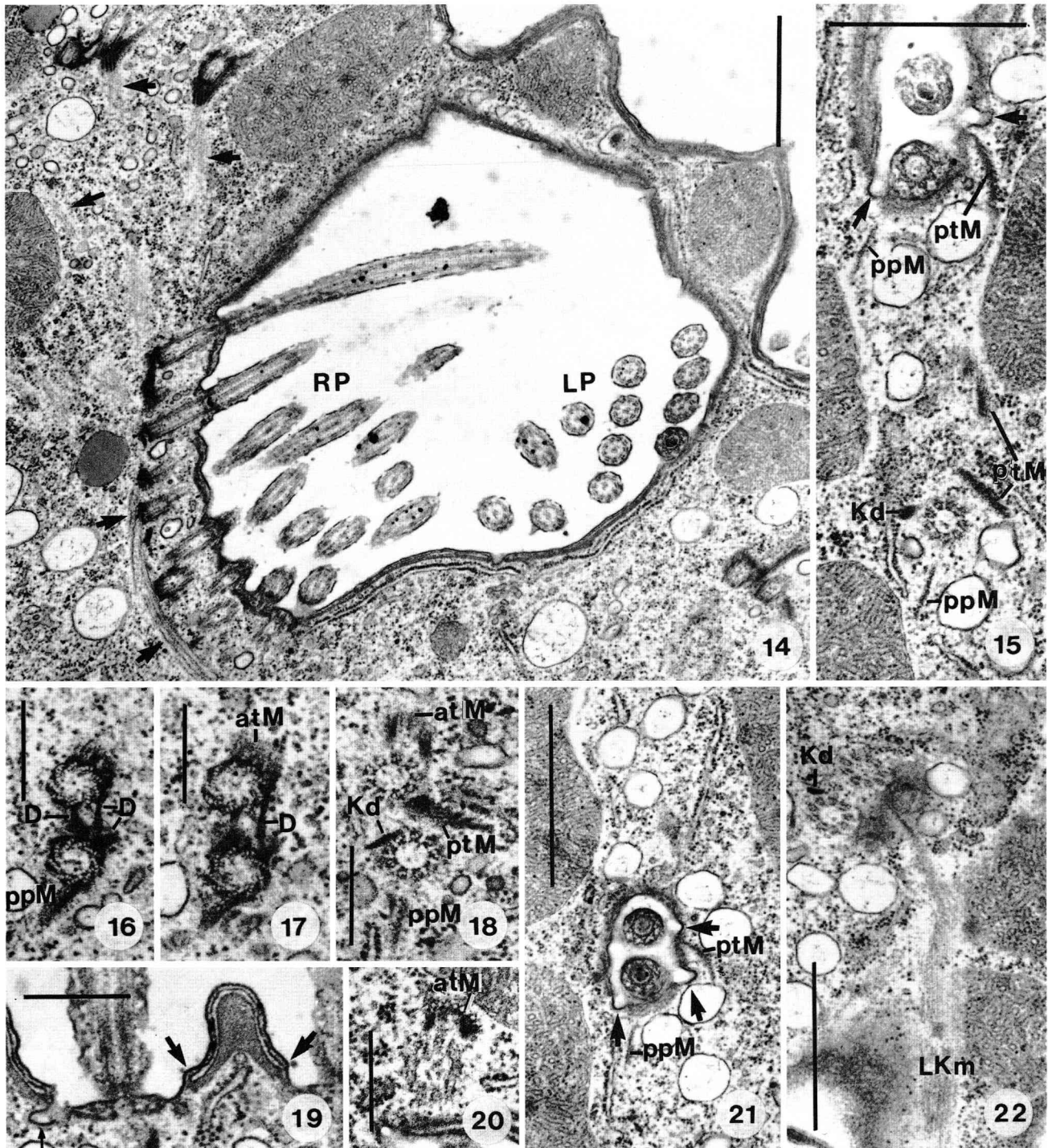
The cytoplasm contains small and large food vacuoles with bacteria and bacterial remnants (Fig. 24), many small (0.5–1 µm) and medium-sized (1–3 µm) vacuoles with fluffy content (Figs. 15, 21) or small crystals (Fig. 23), many rather distinct dictyosomes (Fig. 26) and granular endoplasmic reticulum (Figs. 9, 10), mitochondria up to 3 µm long with tubular cristae (Figs. 12, 13, 24), and some liposomes. The crystal-containing vacuoles are concentrated in the vicinity of the contractile vacuole and have a rather dense content. The crystals are dumb-bell shaped and only 400–600 nm in size (Fig. 23), and thus hardly recognizable in the light microscope (FOISSNER 1993).



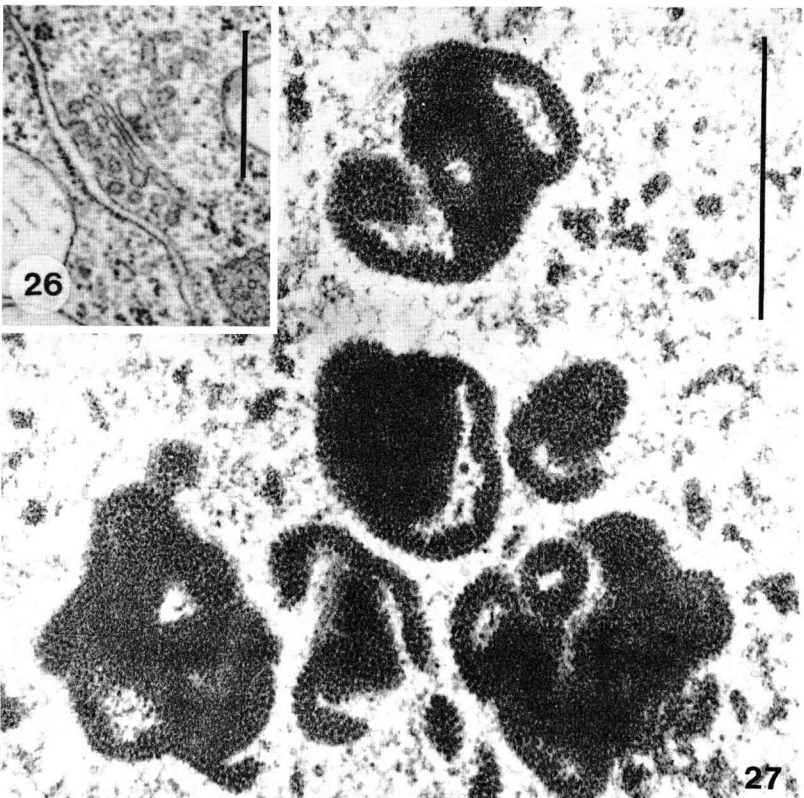
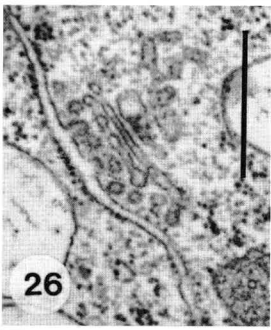
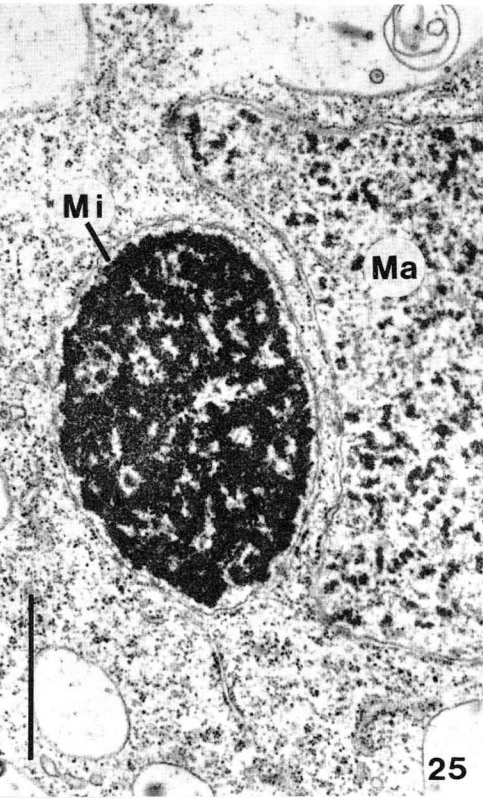
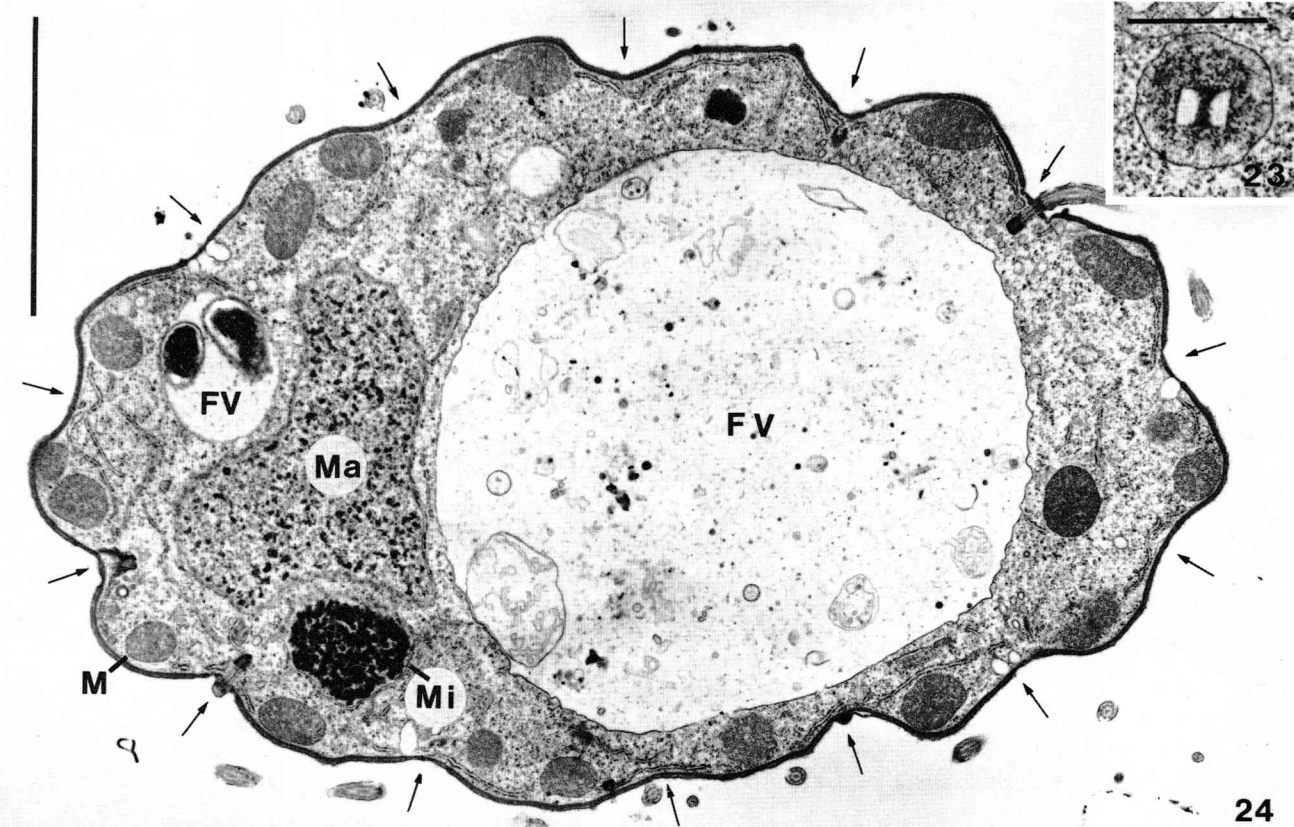
Figs. 1–8. General morphology of *Cosmocolpoda naschbergeri* from life (Figs. 1, 3, 4), after wet (CHATTON-LWOFF) silver nitrate impregnation (Figs. 2, 7), silver carbonate impregnation (Fig. 6), and in the scanning electron microscope (Figs. 5, 8). All figures from FOISSNER (1993). – 1, 3, 5. Right lateral views showing triangular body shape and cortical ornamentation. – 2, 7. Silverline system and infraciliature of right side. – 4. Cortical crests of the left side. – 6. Somatic and oral infraciliature of ventral side. – 8. Anterior ventral side at higher magnification showing conspicuous cortical ornamentation and paired cilia (arrow). CV = contractile vacuole, FV = food vacuoles, LP = left oral polykinetid (ciliary field), Ma = macronucleus, Mi = micronucleus, OA = oral apparatus, RP = right oral polykinetid (ciliary field). Bars 20 μm except in Fig. 8, where it indicates 5 μm .



Figs. 9–13. Cortical fine structure (TEM micrographs) of *Cosmocolpoda naschbergeri*. – 9. Longitudinal section showing cortical crests transversely sectioned. Thick arrows mark alveolar junctions in the furrows between the crests; thin arrows mark cisterns of the granular endoplasmic reticulum in the proximal portion of the crests. – 10. Transverse section showing two LKm fibres which are formed by the transverse microtubule ribbons originating from the posterior basal bodies of the dikinetids. – 11, 12. Grazing sections showing alveolar junctions (arrows) and posterior transverse microtubule ribbons (ptM) which form the LKm fibre. – 13. Longitudinal section of the excretory pore of the contractile vacuole, which is surrounded by about 22 microtubules (arrows). CR = ciliary row, EP = epiplasm, LKm = left kinetodesmal fibre, ptM = posterior transverse microtubular ribbons. Bars 1 μ m.



Figs. 14–22. TEM micrographs of the oral apparatus and somatic dikinetids of *Cosmocolpoda naschbergeri*. – 14. Oblique section through the vestibulum. Arrows mark nematodesmal microtubule bundles originating from the basal bodies of the right oral polykinetid and from the anteriormost somatic dikinetids of the right side. – 15–18, 20–22. Transverse sections of somatic dikinetids. Arrows mark parasomal sacs. – 19. Longitudinal section showing a parasomal sac (thin arrow) and an alveolus (thick arrows) extending over a cortical crest. atM = transverse microtubules of anterior basal body, D = desmoses, Kd = kinetodesmal fibre, LKm = left kinetodesmal fibre, LP = left oral polykinetid (ciliary field), ppM = postciliary microtubules of posterior basal body, ptM = transverse microtubules of posterior basal body, RP = right oral polykinetid (ciliary field). Bars 1 μm (Figs. 14, 15, 21, 22), 400 nm (Figs. 16–20).



Extrusomes (mucocysts or trichocysts) were found neither in the light microscope (FOISSNER 1993) nor in the electron microscope. Likewise, no structure is recognizable which could form the conspicuous silverlines (Figs. 2, 7).

Discussion

FOISSNER (1993) suggested that *C. naschbergeri* belongs to the family Colpodidae and probably evolved from a *Colpoda maupasi* – like ancestor. This is indicated not only by its somatic and oral infraciliature (FOISSNER 1993) but also by the outcome of this study. The somatic dikinetids and the cortical membrane systems of *C. naschbergeri* undoubtedly match the colpodid pattern as described by FOISSNER (1993) and SMALL & LYNN (1981). The LK_m fibre is formed, as in *Colpoda maupasi* and *C. steinii* (LYNN 1976 a, b), by a monolayer of microtubules, whereas it is composed of oblique microtubule stacks in the larger members of the genus, e. g. in *C. cucullus* (LYNN 1976c). Somatic nematodesmal bundles are restricted to a few anterior right lateral dikinetids in *C. naschbergeri* (Fig. 14) and *Colpoda maupasi* (LYNN 1976b), whereas all kinetids bear such microtubules in the large *C. magna* (LYNN 1976d). Furthermore, a cortical ornamentation of more or less pronounced tooth-like processes is found in some small colpodids (*Colpoda elliotti*, *C. aspera*, *C. ecaudata*, *Maryna* sp.), but never in the large species of the order (FOISSNER 1993 and unpubl. material).

Although being very conspicuous in the light and scanning electron microscope, the cortical crests of *C. naschbergeri* lack microtubular or fibrillar differentiations. However, it is reasonable to assume that the thick epiplasmic layer, which is continuous with the cortical crests, at least helps to stabilize the cortical ornamentation. As regards the thickness of the epiplasm, *C. naschbergeri* resembles the medium-sized and large members of the family, e.g. *Colpoda cucullus* (LYNN 1976c) and *Bresslaia insidiatrix* (LYNN 1979).

The absence of extrusomes in *C. naschbergeri*, indicated already by the light microscopic investigations (FOISSNER 1993), is remarkable because such structures are present and often very conspicuous in all other well investigated species of the family (FOISSNER 1993). LYNN (1978) claims that extrusomes are also lacking in

Colpoda steinii and *C. maupasi* which has, however, been disproved by recent data (FOISSNER 1993).

It was originally hoped that this study would shed some light on the nature of the silverlines of the colpodid ciliates, because their location, viz. in the peak of the cortical crests (FOISSNER 1993), is clearly recognizable in *C. naschbergeri* in the light microscope. However, no special structures were found at these sites with the electron microscope, but it is apparent that they are not identical with the alveolar junctions, as was widely assumed (for review see FOISSNER 1981), because these are between the cortical crests (Figs. 9, 11, 12).

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Figs. 23–27. TEM micrographs of the internal organization of *Cosmocolpoda naschbergeri*. – 23. Small vacuoles containing a crystal are mainly found in the vicinity of the contractile vacuole. Bar 1 µm. – 24. Transverse section in the posterior body portion. Arrows mark ciliary rows which extend in deep furrows. Bar 5 µm. – 25. Nuclear apparatus. Bar 1 µm. – 26. A dictyosome. Bar 500 nm. – 27. Section through a nucleolus of the macronucleus. Bar 1 µm. FV = food vacuoles, Ma = macronucleus, Mi = micronucleus.

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