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Pseudomaryna australiensis nov. gen., nov. spec. and *Colpoda brasiliensis* nov. spec., two new colpodids (Ciliophora, Colpodea) with a mineral envelope

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Pseudomaryna australiensis **and** ***Colpoda brasiliensis*** **were discovered in floodplain soils from Australia and Brazil and studied in vivo and in silver preparations. They have a common feature, viz., a sheath of clay (mineral) particles embedded in a slimy matrix. Such sheaths, which evolved convergently in various ciliates, are termed "mineral envelopes" and make cells appear like inorganic soil particles, possibly protecting them from predators. The new genus** ***Pseudomaryna*** **belongs to the family Colpodidae and is characterized by the preoral suture which extends for the whole body length right of the oral opening due to the widely projecting left side ciliary rows.** ***Maryna antarctica*** **Foissner, 1993 has the same ciliary pattern and is thus transferred to the new genus:** ***Pseudomaryna antarctica*** **(Foissner, 1993) nov. comb. Both,** ***P. australiensis*** **and** ***P. antarctica*** **are small (length 25–60 µm), reniform soil ciliates differing in the macronuclear structure (with vs. without central nucleolus), the mineral envelope (present vs. absent), and details of the somatic and oral ciliary pattern.** ***Colpoda brasiliensis*** **is also a small ciliate (about 33 × 18 µm), differing from the congeners by the mineral envelope and a combination of ordinary features, viz., the location and structure of the macronucleus and the preoral ciliary pattern. Probably, it is related to the** ***Colpoda steinii*** **group.**

Key words: Amazon River floodplain; Australia; Brazil; Colpodea; Murray River floodplain; ***Pseudomaryna antarctica*** **nov. comb.**

Introduction

Colpodids are among the best known ciliate groups due to the detailed monograph by Foissner (1993a), who recognized about 170 species in 55 genera. Since then, 11 new genera and 26 new species were described, raising the total number of already described colpodids to nearly 200 species (for a brief review, see Foissner et al. 2002). Two further new species and a new genus are described in the present paper. Twenty-eight species are a considerable gain in 10 years, showing that colpodid diversity is far from being exhausted, which is emphasized by about 15 unpublished, new species in my notebooks.

The two species described in the present paper highlight several features rarely used in colpodid alpha-taxonomy, viz., the location and structure of the macronucleus and preoral suture, and the arrangement of the preoral ciliary rows. Further, the mineral envelope is introduced as a new feature for colpodids in general. It is likely, that additional species can be discriminated by a broad application of these characteristics, provided they are supported by very accurate and detailed investigations.

Materials and methods

Pseudomaryna australiensis was discovered in soil from the Murray River floodplain in Australia. The sample was collected by Mag. Hubert Blatterer in

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August 1997 and investigated by me in November 1998. *Colpoda brasiliensis* was discovered in soil from a small island in the Amazon River near the town of Manaus, Brazil. The sample was collected in November 1996 and investigated in September 1997. See type location and occurrence sections for details on sites and soils.

The samples were air-dried for about a month and stored in plastic bags. For investigation, they were slightly over-saturated (~120%) with distilled water to obtain a "non-flooded Petri dish" culture, as described in Foissner et al. (2002). Pure culture trials failed. Thus, material as obtained with the non-flooded Petri dish method was used for all investigations. Living cells were studied using a microscope equipped with a high-power oil immersion objective and differential interference contrast. Silver impregnation and methyl green-pyronin staining were performed as described in Foissner (1991).

Counts and measurements on silvered specimens were performed at a magnification of ×1000. *In vivo* measurements were conducted at magnifications of ×100–1000. Drawings of live specimens were based on free-hand sketches and micrographs, those of impregnated cells were made with a camera lucida.

Terminology is according to Corliss (1979) and Foissner (1993a).

Results

Genus *Pseudomaryna* nov. gen.

Diagnosis: Small, bacteriophagous Colpodidae with oral opening near mid-body and preorally widely projecting left side ciliary rows, producing a spatulate (preoral) suture, that is, a bare stripe extending from anterior to posterior body end right of oral opening. Vestibulum of ordinary size, conical, pharyngeal fibres directed posteriorly. Left wall of vestibulum overhangs right. Right oral polykinetid composed of few, slightly disordered kineties.

Type species: *Pseudomaryna australiensis* nov. spec.

Etymology: Composite of the Greek adjective *pseudo* (false) and the generic name *Maryna*. Feminine gender.

Description of *Pseudomaryna australiensis* nov. spec. (Figs 1–41, 58; Table 1)

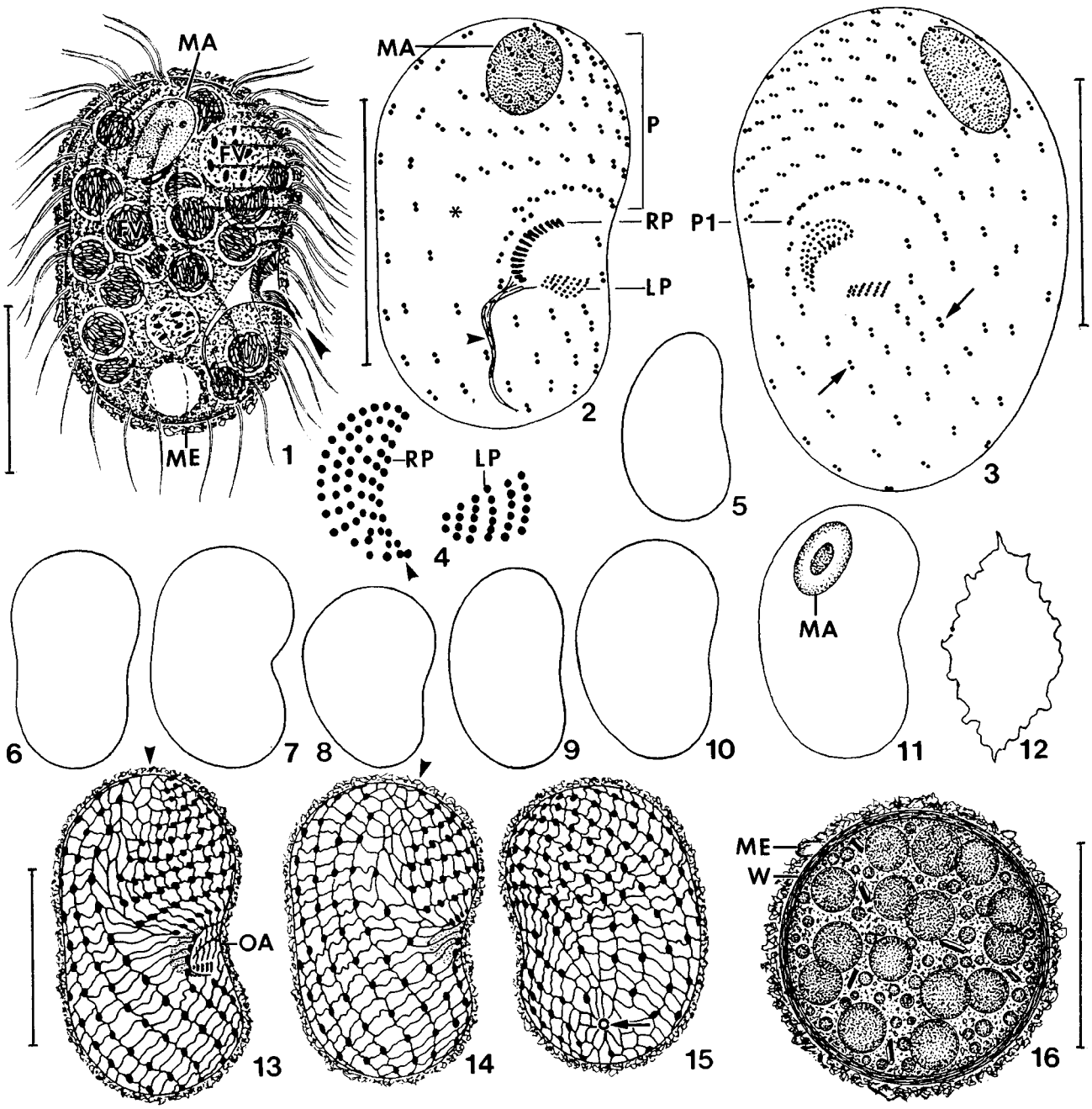
Diagnosis: Size about 45 × 30 µm *in vivo*. Body reniform and closely covered with a thin mineral envelope. Macronucleus near dorsal anterior body end, with single central nucleolus. On average 17 ciliary rows, first preoral kinety conspicuously convex because distinctly shortened posteriorly. Left oral polykinetid cuneate, composed of an average of 6 ciliary rows. Resting cyst globular and smooth, covered with the mineral envelope of the trophic cell.

Type location: Soil from Murray River floodplain near the town of Albury, waterside of Ryans road, Australia, 37° S 147° E.

Type specimens: 1 holotype slide each with silver nitrate (Chatton-Lwoff method) and protargol-impregnated specimens and 4 paratype slides have been deposited in the Biology Centre of the Museum of Upper Austria, Linz (LI), Austria. Relevant specimens are marked by black ink circles on the cover glass.

Etymology: Named after the country in which discovered.

Description: Size 35–60 × 20–35 µm, usually near 45 × 30 µm, slightly flattened laterally, no diagonal (postoral) groove (Table 1). Specimens often highly refractive, that is, opaque and dark at low magnification (≤ ×100) due to the mineral envelope and many compact food vacuoles. Shape basically reniform due to a more or less distinct indentation near mid-body, that is, in oral area; in detail, however, highly variable, viz., ellipsoidal (when oral bay indistinct), *Metopus*-like (when broader preorally than postorally), *Colpoda maupasi*-like (when narrower preorally than postorally), or indistinctly dumb-bell-like; rarely fusiform with very irregular mineral envelope (Figs 1, 2, 5–15, 18–20, 29–33, 37, 38). Macronucleus in anterior body half, usually even in anterior dorsal third of cell, a curious location found in only a few other colpodids, viz., *Dragescozoon terricola*, *Kreyella minuta*, and *Orthokreyella schiffmanni* (Foissner 1993a; Foissner et al. 2002); hyaline and thus difficult to recognize even with interference contrast optics, except for the more compact central nucleolus (Figs 1, 2, 3, 11, 39), another rare feature present only in *Colpoda steinii*, *C. formisanoi*, *Dragescozoon terricola*, *Pseudokreyella terricola*, *P. australis*, and *Microdiaphanosoma terricola* (Foissner 1993a; Foissner et al. 2002). Micronucleus not found. Contractile vacuole in rear body end, with single excretory pore in pole centre (Figs 1, 15, 22). Cortex flexible, specific cortical granules (mucocysts) not recognizable, covered by a 1–2 µm thick, brownish "mineral envelope" appearing as a bright, rough layer separated from pellicle by a distance of about 0.5 µm in living and prepared



Figs 1–16. *Pseudomaryna australiensis* from life (1, 5–12, 16) and after protargol (2, 3), silver carbonate (4), and Chatton-Lwoff silver nitrate (13–15) impregnation. **1:** Right side view of a representative specimen packed with food vacuoles containing bacterial rods. Note the mineral envelope and the oral entrance (arrowhead). **2:** Ventrolateral view of ciliary pattern. Note pharyngeal fibres (arrowhead) and the large, bare area (asterisk) right of the oral opening. **3:** Ciliary pattern of ventral side. Note the almost semicircular first preoral kinety (P1) and the four postoral kineties (arrows). **4:** Oral ciliary fields. The right field has a row of dikinetids proximally (arrowhead). **5–12:** Shape variants with macronucleus shown in figure 11. **12:** A fusiform specimen with irregular outline. **13–15:** Ventrolateral, right lateral, and left lateral view of ciliary and silverline pattern. Arrowheads mark broad preoral suture with irregularly-meshed silverline pattern. Arrow in figure 15 denotes the excretory pore of the contractile vacuole. **16:** The resting cyst is globular and has a smooth wall covered by the mineral envelope of the trophic cell. LP – left oral polykinetid, MA – macronucleus, ME – mineral envelope, OA – oral apparatus, P – preoral kineties, P1 – preoral kinety 1, RP – right oral polykinetid, W – cyst wall. Scale bars 20 µm.

cells and with an opening over the oral area (Fig. 1). Mineral envelope compact, composed of 1–2 µm-sized, irregular mineral particles embedded in a slimy matrix to which environmental debris and bacteria adhere and which stains pink with methyl green-pyronin; mineral inclusions similar to clay particles common in the environment and to minute, cytoplasmic crystals conspicuously sparkling under interference contrast optics, quite similar to those shown by Foissner et al. (2002) in micrograph 421y of *Maryna namibiensis*. Cytoplasm colourless, in most cells packed with 4–10 µm-sized food vacuoles containing tightly packed bacterial rods or their loosely dispersed indigestible remnants (Figs 1, 18–22). Swims rapidly by rotation about main body axis; never rests.

Cilia about 8 µm long *in vivo*, paired, except for barren anterior basal body of dikinetids in rear third; no elongated caudal cilia; arranged in an average of 17 rows more densely ciliated anteriorly than posteriorly, especially on left side of cell. Ciliary rows in *Colpoda* pattern modified by the genus-specific, spatulate preoral suture, which is not above but right of oral opening and thus ex-

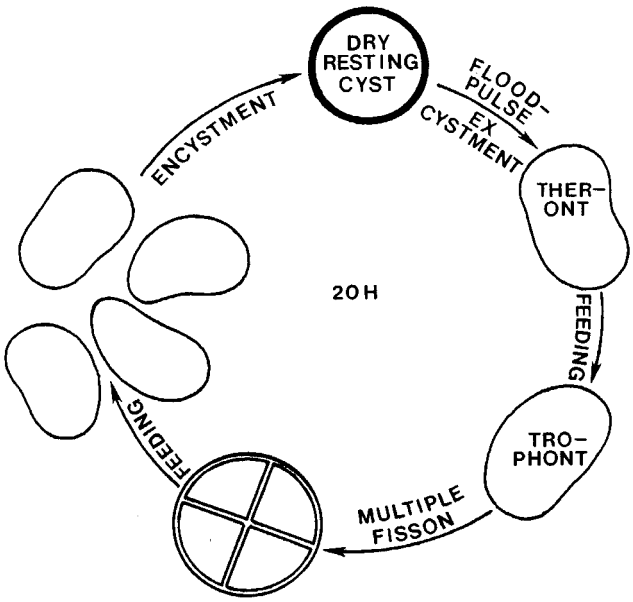


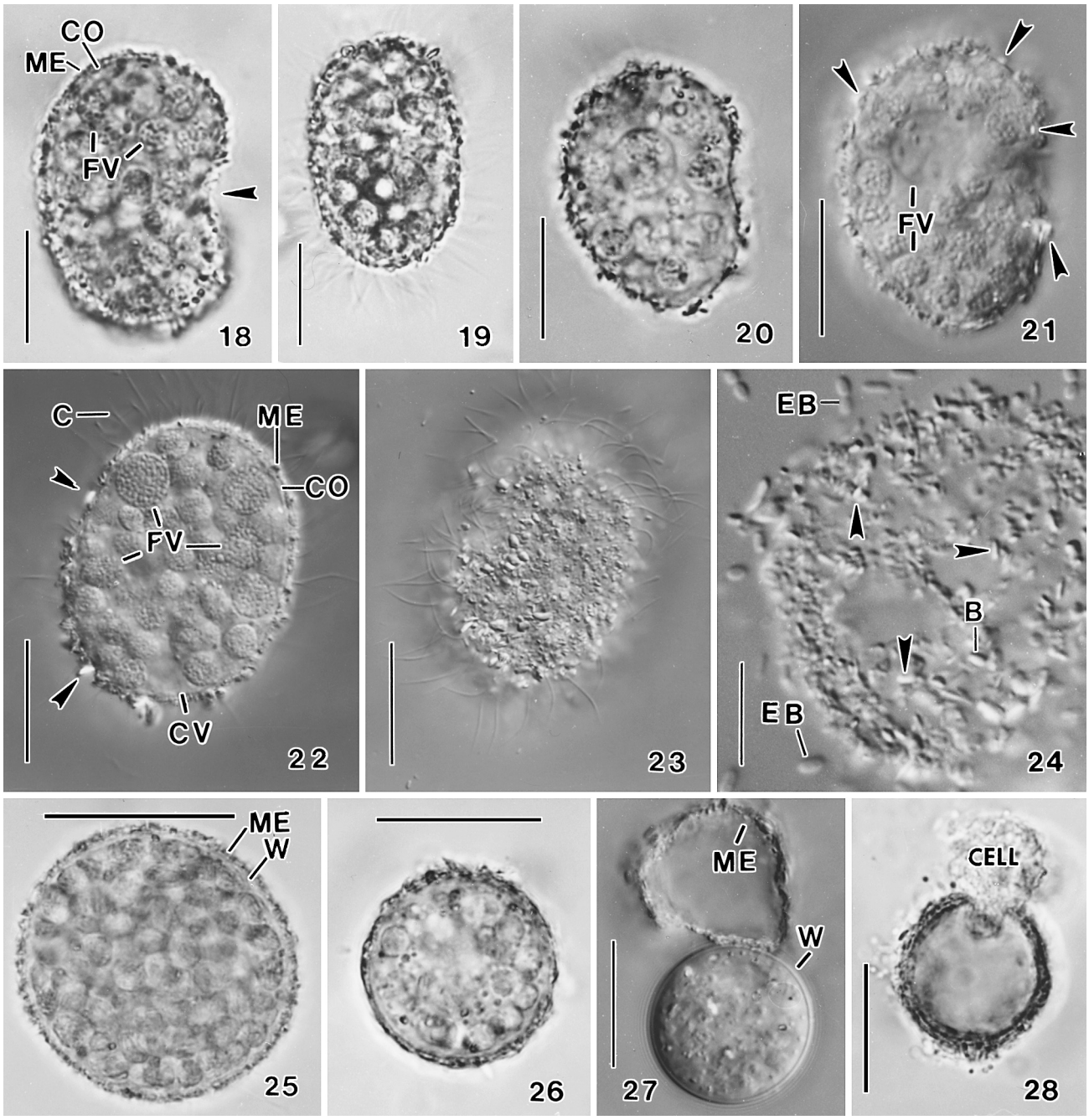
Fig. 17. Proposed life cycle of *Pseudomaryna australiensis*. For explanation, see section on "cysts and life cycle". Note that some details are doubtful, viz., whether every fission product forms a resting cyst after growth, or can undergo another round of division before resting encystment.

Table 1. Morphometric data on *Pseudomaryna australiensis*.

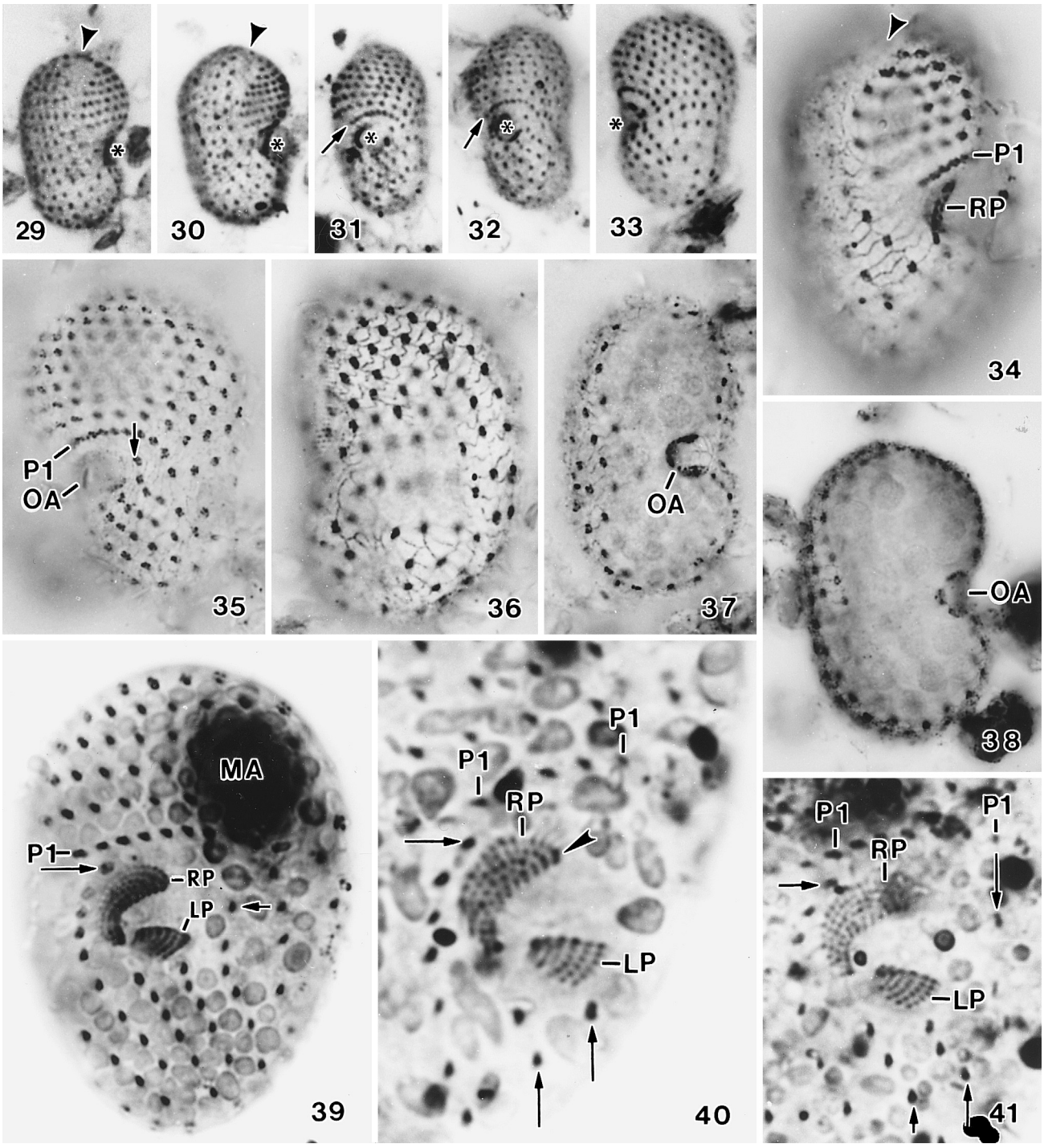
Characteristics[1]	Method[2]	x̄	M	SD	SE	CV	Min	Max	n
Body, length	CHL	40.8	41	3.3	0.7	8.1	36	47	21
Body, width in lateral view	CHL	26.5	27	2.8	0.6	10.5	22	32	21
Body, width in ventral or dorsal view	CHL	20.1	20	1.8	0.4	8.9	17	24	21
Anterior body end to macronucleus, distance	P	5.3	5	3.5	0.8	66.9	1	17	21
Anterior body end to summit of first preoral kinety, distance	CHL	16.6	17	1.9	0.4	11.7	13	20	21
Anterior end to posterior margin of left oral polykinetid, distance	CHL	25.1	25	2.0	0.4	7.9	22	28	21
Macronucleus, length	P	9.3	10	1.7	0.4	18.1	6	13	21
Macronucleus, width	P	6.0	6	0.7	0.2	11.8	5	7	21
Right oral polykinetid, length	P	5.4	5	0.6	0.2	11.1	5	7	20
Left oral polykinetid, length	P	4.0	4	0.4	0.1	9.7	3	5	21
Left oral polykinetid, width	P	2.8	3	–	–	–	2	3	21
Left oral polykinetid, number of ciliary rows	P	6.1	6	–	–	–	6	7	21
Somatic ciliary rows, total number	CHL	16.9	17	1.1	0.3	6.7	15	19	21
Postoral ciliary rows, number	CHL	4.0	4	0	0	0	4	4	21
Kinetids in first row right of suture, number	CHL	11.0	12	1.7	0.4	15.8	8	13	21
Kinetids in first preoral kinety, number	CHL	11.8	12	1.1	0.3	9.5	10	14	21
Kinetids in fourth preoral kinety, number	CHL	20.1	20	2.5	0.6	12.5	17	25	21
Resting cysts, diameter without mineral envelope	IV	26.3	27	2.4	0.6	9.3	22	30	18

[1] Data based on randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, x̄ – arithmetic mean.

[2] CHL – silver nitrate impregnation after Chatton-Lwoff, as described in Foissner (1991), IV – *in vivo*, P – protargol impregnation, protocol A in Foissner (1991).



Figs 18–28. *Pseudomaryna australiensis*, trophic cells (18–24) and resting cysts (25–28) from life. **18, 19:** Right side and dorsal view of a specimen packed with food vacuoles. The oral bay (arrowhead) produces the reniform shape of the organism, which is slightly flattened laterally (19). The rough surface is produced by the mineral envelope. **20, 21:** Right lateral view of a *Metopus*-shaped specimen in the bright field and interference contrast microscope, where some of the mineral particles of the envelope are highly refractive (arrowheads). **22–24:** Optical section (22) and surface views (23, 24) of a specimen with many food vacuoles containing tightly packed bacteria. The rough surface is caused by the mineral envelope, that is, a 1–2 µm thick, slimy coat containing organic debris, bacteria, and 1–2 µm-sized mineral particles, some being highly refractive in the interference contrast microscope (arrowheads). **25, 26:** Resting cysts showing the thin (1–2 µm), but compact mineral envelope. **27**: Resting cyst separated from its mineral envelope by slight cover glass pressure. **28:** When squashed, the cyst content (cell) flows out, leaving behind the strongly refractive cyst wall and mineral envelope. B – bacteria in mineral envelope, C – cilia, CO – ciliate cortex, CV – contractile vacuole, EB – environmental bacteria, FV – food vacuoles, ME – mineral envelope, W – cyst wall. Scale bars 20 µm.



Figs 29–41. *Pseudomaryna australiensis*, body shape and ciliary and silverline pattern after silver nitrate (29–38) and silver carbonate (39–41) impregnation. Length of specimens 36–47 µm. **29–33:** Right lateral (29, 30), ventral (31, 32), and left lateral (33) overviews. Arrows mark preoral kinety 1; arrowheads denote spatulate preoral suture; asterisks mark oral apparatus. **34–36:** Ventrolateral, ventral, and left lateral views showing, inter alia, the preoral suture (arrowhead) and the beginning of the leftmost postoral kinety (arrow). **37, 38:** Optical sections showing body shape and location of oral apparatus. **39–41:** Ventral overview and details of oral ciliary pattern. Arrows mark the four postoral kineties. Arrowhead in figure 40 denotes row of dikinetids at proximal margin of right ciliary field. LP – left oral polykinetid, MA – macronucleus, OA – oral apparatus, P1 – preoral kinety 1, RP – right oral polykinetid.

tends, as spatula-handle, to posterior body end between right side and postoral kineties (Figs 1–3, 13–15, 22, 23, 30–39; Table 1). Right side ciliary rows indistinctly sigmoidal, first two to three rows slightly shortened anteriorly producing, together with the gradually shortened left side preoral rows, a roundish, bare anterior pole area, that is, the spatula of the preoral suture. Preoral ciliary rows conspicuous because numerous and distinctly convex, extend transversely over ventral side and spiral posteriorly on left and dorsal side of cell; first preoral kinety above oral opening especially distinct because very densely ciliated and almost semicircular, that is, shortened postorally. Invariably four postoral ciliary rows, leftmost and rightmost row extend to upper mouth margin almost touching first preoral kinety, oral area thus surrounded by a key-hole shaped kinety pattern.

Oral apparatus in flat indentation slightly underneath mid-body, posterior margin of left ciliary field 62% distant from anterior body end on average (Figs 1–3, 13, 14, 18, 29–35, 37–39; Table 1). Vestibulum broadly conical and small, that is, about 6 µm wide and deep, a bundle of pharyngeal fibres originates at proximal end and extends to rear body end. Left oral polykinetid cuneate, composed of an average of six slightly convex rows becoming longer distally; cilia only about 3 µm long and thus not forming a beard as in *Colpoda steinii*. Right oral polykinetid crescentic, composed of four slightly disordered kineties and a row of about 10 dikinetids proximally (Figs 1–4, 39–41; Table 1).

Silverline pattern colpodid throughout, irregularly meshed only in bare regions, that is, in preoral suture and around excretory pore of contractile vacuole. A tree-shaped silverline pattern extends in left vestibular wall (Figs 13–15, 34–37).

Occurrence: As yet found only at type location, where it was abundant already one day after rewetting. The site, which is used as a cattle pasture, is flooded for months in wet years. The sample was a mixture of almost black, humic top soil, many fine roots, and *Myriophyllum and Valisneria* litter; it had pH 5.2 (in water) and contained more than 100 ciliate species, of which many were undescribed.

Cysts and life cycle: Unfortunately, pure culture trials failed. Thus, all observations and the proposed life cycle (Fig. 17) are from specimens as obtained with the non-flooded Petri dish culture, which was air-dried and rewetted three times to simulate the flood-pulses typical for the habitat. Accordingly, the life cycle could be not elucidated in full detail, for instance, whether every fission product forms a resting cyst after some growth, or can undergo another round of division before resting encystment.

Pseudomaryna australiensis divides exclusively in thin-walled reproductive cysts with up to four offspring, and produces thick-walled resting cysts, as common in small colpodids (Foissner 1993a). Both cyst types retain the brownish mineral envelope of the trophic cell, but cyst and envelope can be separated by mild cover glass pressure (Fig. 27). Resting cysts globular and 26 µm across on average, wall colourless, smooth, and about 1 µm thick; cytoplasm with some 2–3 µm-sized crystals and many opaque globules 1–5 µm across (Figs 16, 17, 25–28; Table 1).

Pseudomaryna australiensis becomes abundant already 20–30 h after rewetting the sample and encysts after one or two days, even if the sample is undisturbed. The same has been observed in some marynid colpodids from temporary pools (for a review, see Foissner 1993a, p. 337). This indicates that *P. australiensis* has a marynid life cycle and is an r-selected organism, as are colpodids in general (Foissner 1993a), adapted to the floodplain environment in that it quickly excysts and reproduces when the flood comes, and encysts when other organisms and potential predators become abundant; the mineral envelope may be an additional shelter (see discussion).

Colpoda brasiliensis nov. spec. (Figs 42–57; Table 2)

Diagnosis: Size about 33 × 18 µm *in vivo*. Body covered with a mineral envelope and *Colpoda maupasi*-shaped, that is, reniform with anterior half narrower than posterior. Macronucleus usually in posterior dorsal quadrant of cell, ellipsoidal, with single central nucleolus. On average 12 ciliary rows, distance between first and second row right of oral opening distinctly widened anteriorly; number of preoral kineties thus higher at left than right side. Oral apparatus in second quarter of cell, left polykinetid composed of about 5 kineties becoming slightly longer distally.

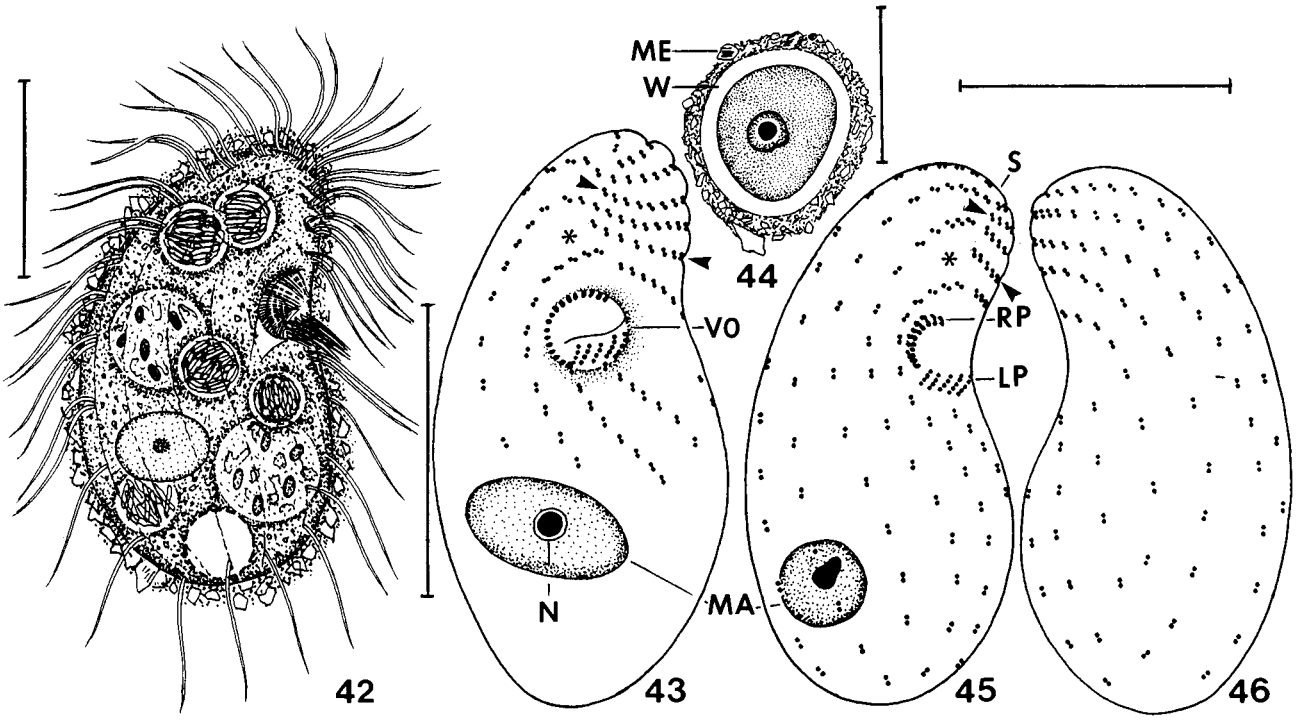
Type location: Clayic top soil from a small island in the Amazon River near Manaus, Brazil, 04° S 60° W.

Type specimens: 1 holotype and 1 paratype slide with protargol-impregnated trophic and cystic specimens have been deposited in the Biology Centre of the Museum of Upper Austria in Linz (LI), Austria. Relevant specimens are marked by black ink circles on the cover glass.

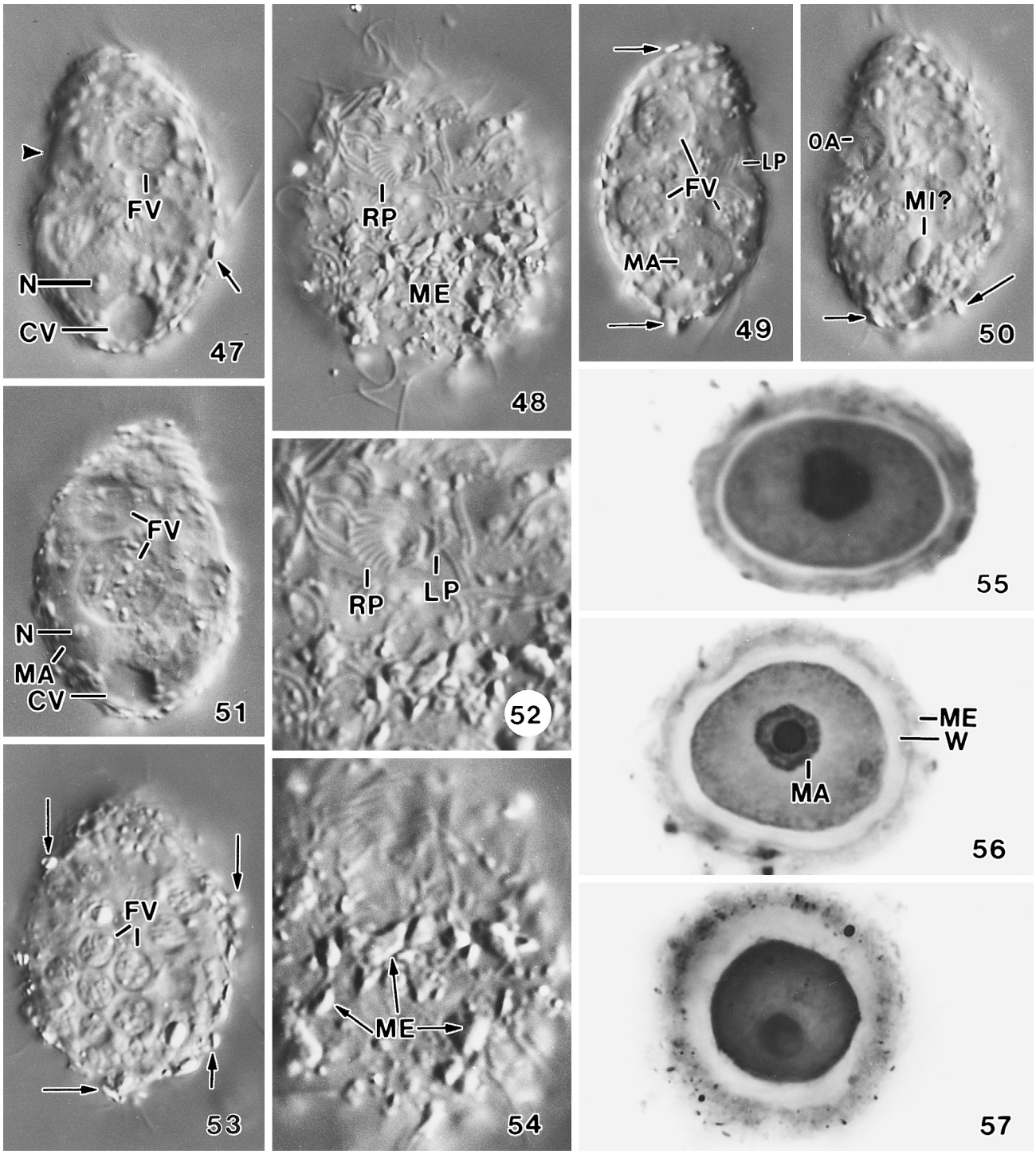
Etymology: Named after the country in which discovered.

Description: When I first saw this species, it was rather abundant but misidentified as a "small, dirty variety of *C. maupasi*". Two weeks later, when I recognized it as a distinct species, it was already rare. Thus, the morphometric data are incomplete. Further, the protargol preparations are of only mediocre quality because the mineral envelope impregnates rather intensely and hides the ciliary pattern. Thus, the description should be refined by observations on other populations.

Size 30–40 × 15–25 µm *in vivo*, usually about 33 × 18 µm. Invariably *Colpoda maupasi*-shaped, that is, reniform with flat oral indentation above mid-body and narrowed anterior half; no diagonal (postoral) groove (Figs 42, 45, 47, 49; Table 2). Macronucleus in rear half of cell, usually in posterior dorsal quadrant, about 7 × 5 µm and very hyaline *in vivo*, except for the small central nucleolus, which stains red with methyl green-pyronin and impregnates rather intensely with protargol; micronucleus not unequivocally identified, probably attached to macronucleus and ellipsoidal (Figs 42, 43, 45, 47, 49–51; Table 2). Contractile vacuole in centre of rear body end. Cortex flexible, special cortical granules (extrusomes) recognizable neither *in vivo* nor with methyl green-pyronin stain. Mineral envelope 1–3 µm thick, composed of clay particles up to 3 µm in sized embedded in a slimy matrix to which environmental organic debris and bacteria may adhere; stains bluish with methyl green-pyronin and provides cells with a rough, dirty surface (Figs 42, 47–54). Cytoplasm colourless, usually packed with food vacuoles 5–10 µm across and with many minute crystals conspicuously sparkling under interference contrast optics, as in many other small colpodids and marynids (Foissner et al. 2002).



Figs 42–46. *Colpoda brasiliensis* from life (42) and after protargol impregnation (43–46). **42:** Right side view of a representative, *C. maupasi*-shaped specimen. Note the rough surface caused by the mineral envelope. **43, 45, 46:** Ciliary pattern of ventral side and of right and left side of holotype specimen. Note the circular vestibular opening (VO) and the two specific features of the ciliary pattern, viz., the increased distance between the anterior portion of the two first right side kineties (asterisks) and the intercalated left side kineties (arrowheads). This pattern is different from that of *C. maupasi*, which resembles *C. brasiliensis* in the shape of the body and the oral ciliary fields (Figs 61–66). **44:** Resting cyst covered by the mineral envelope of the trophic cell. LP – left oral polykinetid, MA – macronucleus, ME – mineral envelope, N – central nucleolus of the macronucleus, RP – right oral polykinetid, S – preoral suture, VO – vestibular opening, W – cyst wall. Scale bars 15 µm.



Figs 47–57. *Colpoda brasiliensis*, trophic cells (length 30–40 µm) *in vivo* (47–54) and resting cysts after protargol impregnation (55–57). Arrows mark mineral particles of the mineral envelope. **47, 49, 50, 51, 53:** Right (49, 51, 53) and left (47, 50) side views of slightly squeezed (by cover glass) specimens showing the main organelles. Arrowhead in figure 47 denotes oral bay. **48, 52, 54:** Ventral surface views of a strongly flattened (by cover glass pressure) specimen to show the oral structures and the mineral envelope. **55–57:** Resting cysts, 17–37 × 13–26 µm. CV – contractile vacuole, FV – food vacuoles, LP – left oral polykinetid, MA – macronucleus, ME – mineral envelope, MI? – supposed micronucleus, N – nucleolus, OA – oral apparatus, RP – right oral polykinetid, W – cyst wall.

Feeds on bacteria, whose compact spores become distinct in late food vacuoles (Figs 42, 47, 49, 53). Crawls clumsily on soil particles, but may also rapidly glide on microscope slide.

Cilia about 10 µm long *in vivo*, paired, except in rear body portion, where only the dikinetid's posterior basal body is ciliated; no elongated caudal cilia; arranged in an average of 12 rows, more densely ciliated anteriorly than posteriorly. Ciliary rows in typical *Colpoda* pattern with, however, some specializations; abut preorally, except for three postoral kineties, forming narrow suture extending from anterior pole to summit of oral opening (Figs 43, 45, 46; Table 2). Right side ciliary rows slightly sigmoidal, distance between first and second row right of oral opening conspicuously widened anteriorly. Left side ciliary rows rather distinctly sigmoidal, more narrowly spaced than right side rows along preoral suture, producing a special pattern in that an additional row is intercalated between each two right side rows. Invariably three postoral kineties, leftmost kinety slightly shortened anteriorly.

Oral apparatus small and thus inconspicuous, in flat indentation of second quarter of cell, posterior margin of left ciliary field on average 43% distant from anterior body end (Figs 42, 43, 45, 47, 49; Table 2). Vestibulum conical, about 6 µm wide and deep, vestibular opening and oral ciliary fields form conspicuous, circular pattern (Fig. 43); pharyngeal fibres not impregnated. Left oral polykinetid indistinctly cuneate, composed of an average of five slightly convex rows becoming slightly longer distally, cilia of proximal rows about 3 µm long, those of distal rows 5 µm, do not form a distinct beard as in *Colpoda steinii*. Right oral polykinetid semicircular, probably composed of three or four rows of cilia projecting about 5 µm from vestibular margin (Figs 42, 45, 48, 49, 52).

Cysts: Resting cysts observed only in protargol slides, globular to broadly ellipsoidal, about 24 × 22 µm on average (Table 2). Wall up to 2.5 µm thick

Table 2. Morphometric data on *Colpoda brasiliensis*.

Characteristics[1]	x̄	M	SD	SE	CV	Min	Max	n
Body, length	29.4	28.5	3.4	1.1	11.5	26	37	10
Body, width in lateral view	16.5	15.5	3.0	1.0	18.4	13	22	10
Anterior body end to macronucleus, distance	17.4	17.0	2.8	0.9	15.8	14	22	10
Anterior body end to right polykinetid, distance	7.8	8.0	0.7	0.2	8.6	7	9	9
Anterior body end to posterior margin of left oral polykinetid, distance	12.7	13.0	–	–	–	12	13	9
Macronucleus, length	6.3	6.0	1.1	0.3	16.8	5	8	10
Macronucleus, width	4.4	4.0	0.5	0.2	11.7	4	5	10
Right oral polykinetid, length	4.3	4.0	–	–	–	4	5	4
Left oral polykinetid, length	3.2	3.0	–	–	–	3	4	5
Left oral polykinetid, width	1.9	2.0	–	–	–	1	2	5
Left oral polykinetid, number of ciliary rows	4.8	5.0	–	–	–	4	5	5
Somatic ciliary rows, total number	12.2	12.0	–	–	–	12	13	5
Postoral ciliary rows, number	3.0	3.0	0.0	0.0	0.0	3	3	6
Kinetids in first ciliary row right of oral opening, number	12.5	12.0	1.7	0.9	13.9	11	15	4
Resting cysts, total length[2]	24.3	21.0	7.6	1.7	31.1	17	37	21
Resting cysts, total width[2]	21.6	20.0	8.0	1.7	37.0	13	36	21
Resting cysts, length of cell	15.1	13.0	3.2	0.7	21.0	11	22	21
Resting cysts, width of cell	13.1	13.0	4.1	0.9	31.0	7	22	21
Resting cysts, macronucleus length	5.3	5.0	0.9	0.2	17.4	4	7	21
Resting cysts, macronucleus width	4.9	5.0	0.6	0.1	13.1	4	6	21

[1]Data based on mounted, protargol-impregnated (protocol A in Foissner 1991), and randomly selected specimens from a non-flooded Petri dish culture. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, x̄ – arithmetic mean.
[2]With wall and mineral envelope.

and not impregnated, covered by the brownish-impregnated mineral envelope of the trophic cell, providing cysts with a rough, irregular surface. Central nucleolus of macronucleus distinct (Figs 44, 55–57).

Occurrence and ecology: As yet found only at type location, where it was moderately abundant one week after rewetting the sample, which had pH 5.1 (in water) and was a mixture of clayic soil, fine roots, and leaf litter from the top 1 cm. The site represents one of the typical small islands found in the Amazon River and is flooded annually.

Discussion

Pseudomaryna as a new genus

The generic diagnosis of *Pseudomaryna* has been written to conform with the monograph of Foissner (1993a), the last reviser of the group. At first glance, *Pseudomaryna* appears as a member of the Marynidae because both the trophic cells and the resting cysts have a kind of tectinic case ("mineral envelope"), as is typical for many species of this family (for a review, see Foissner 1993a). Further, the life cycle of *P. australiensis* is likely more similar to that of common marynids than to colpodids (Fig. 17), and the preoral suture and ciliary pattern of the marynid genus *Ilsiella* basically matches that of *P. australiensis* (Foissner 1993a). However, the main features of the marynids, viz., the posteriorly located oral opening and the anteriorly directed pharyngeal fibres are not found in *P. australiensis*, which has the oral opening at or slightly underneath mid-body and the pharyngeal fibres directed posteriorly (Figs 1, 2, 18), as have all "good" members of the family Colpodidae (Foissner 1993a). Thus, *Pseudomaryna* most likely evolved the marynid features convergently and belongs to the family Colpodidae, as defined by Foissner (1993a). This is emphasized by *Colpoda brasiliensis*, a typical *Colpoda* species, except for the mineral envelope, which is similar to the tectinic case of the Marynidae.

Pseudomaryna differs from the colpodid genera described in Foissner (1993a, b, c) and Foissner et al. (2002) mainly by the ciliary pattern: the left side preoral kineties extend to the right side of the cell causing the preoral suture to become located to the right of the oral opening and to continue into the postoral body region. Thus, a broad, unciliated stripe extends whole body length to the right of the oral apparatus (Fig. 58), while the preoral suture is narrower and extends between the anterior end of the body and the oral opening in *Colpoda* and most marynids (Figs 59, 60).

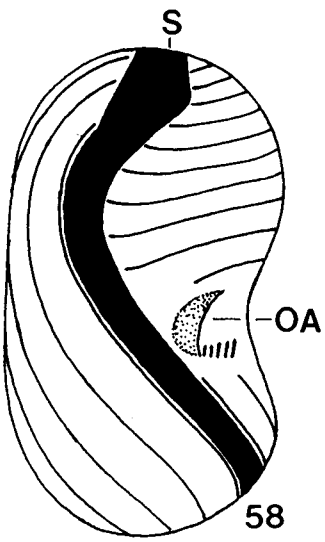
Maryna antarctica Foissner, 1993a has a very similar mouth location and somatic ciliary pattern as *P. australiensis*, and is thus transferred to the new genus: *Pseudomaryna antarctica* (Foissner, 1993) nov. comb. Unfortunately, the transfer is not entirely certain because the direction of the pharyngeal fibres is not recognizable in the slides of *M. antarctica*.

Pseudomaryna australiensis and *Colpoda brasiliensis* as new species

Colpodids with a mineral envelope have not been described previously (Foissner 1993a; Foissner et al. 2002). Thus, *P. australiensis* and *C. brasiliensis* are very distinct species, easy to recognize even without silver impregnation and interference contrast optics (Figs 18, 20, 47, 49). They differ from each other, *inter alia*, by body shape (*Colpoda cucullus*-like vs. *Colpoda maupasi*-like), the location of the macronucleus (in anterior vs. posterior body end), and the somatic ciliary pattern (Figs 2, 3, 43, 45).

Pseudomaryna australiensis differs from *Maryna antarctica* Foissner, 1993a, combined with *Pseudomaryna* above, by body size (35–60 × 20–35 µm vs. 25–35 × 20–25 µm), the structure of the macronucleus (with vs. without central nucleolus), the mineral envelope (present vs. absent), the number (about 17 vs. 11) and arrangement of the ciliary rows (first preoral kinety conspicuous vs. inconspicuous; second and third preoral kinety in parallel vs. V-like spread anteriorly), and the structure of the left oral polykinetid (composed of an average of 6 vs. 8 rows becoming longer vs. shorter distally). These constitute quite a number of differences, suggesting that further species exist. Of course, *P. australiensis* resembles several small *Colpoda* species, especially small-sized specimens of the *Colpoda cucullus* group, which have a similar body shape as the specimen of *P. australiensis* shown in figure 18. However, all *Colpoda* spp. lack a mineral envelope and have a different ciliary pattern (Figs 60–66 and Foissner 1993a).

Colpoda brasiliensis highly resembles small specimens of *Colpoda maupasi*, one of the most frequent soil ciliates (Foissner 1993a; Foissner et al.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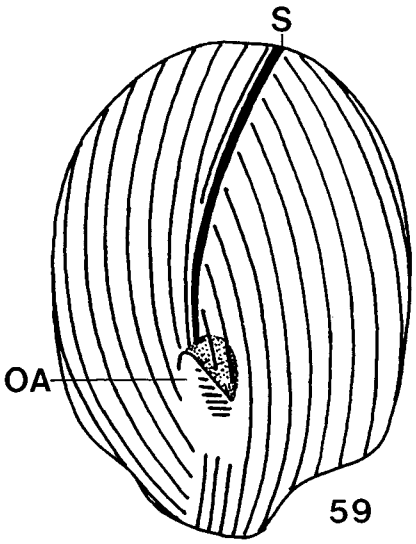
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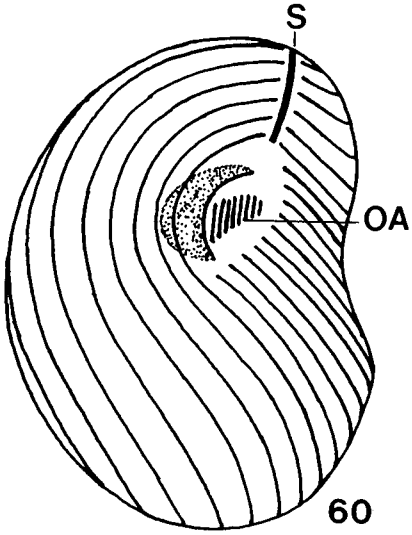
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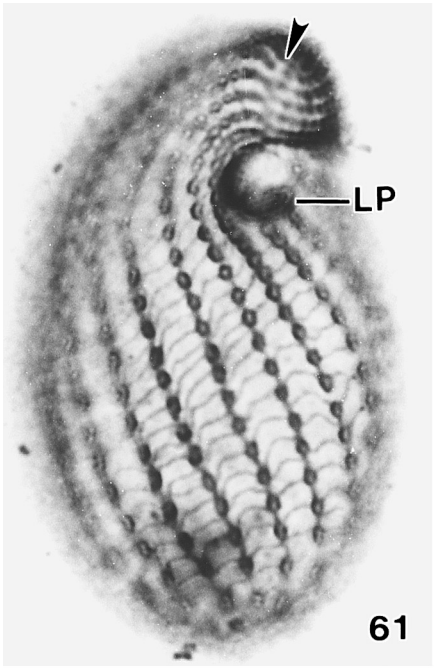
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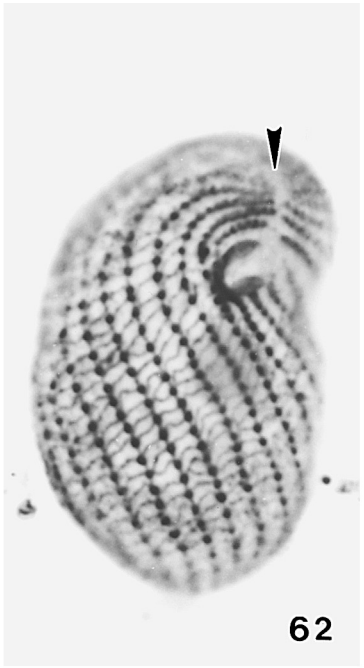
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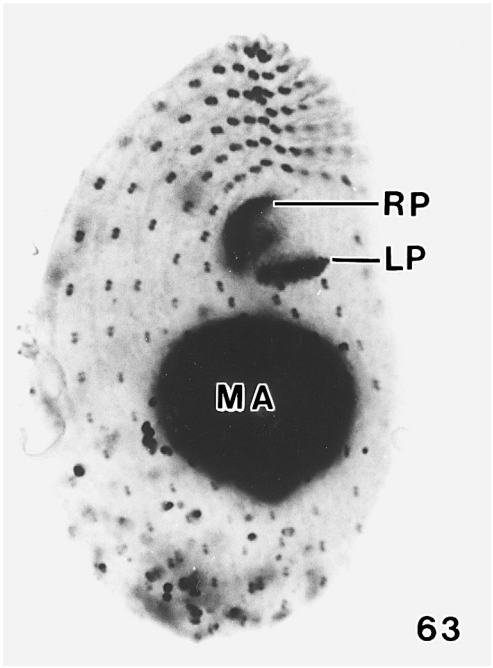
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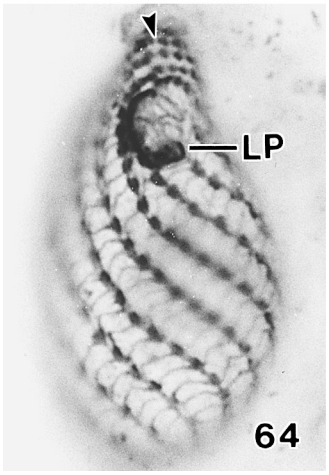
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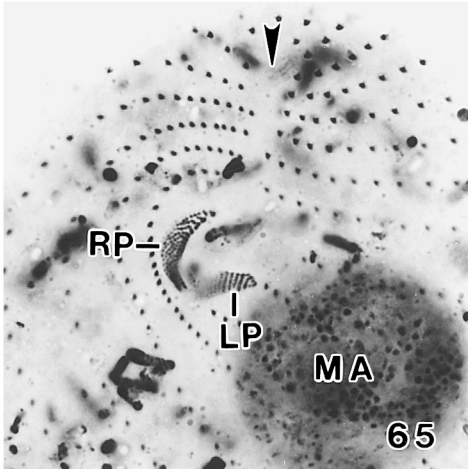
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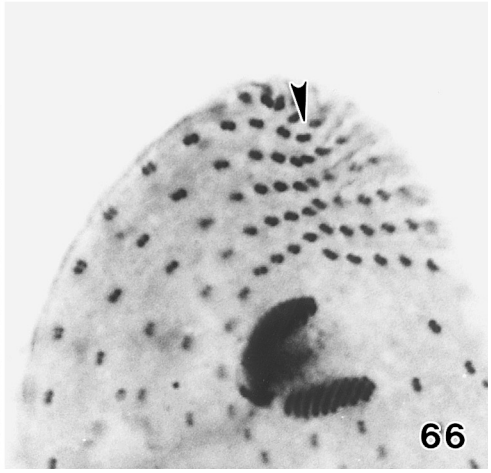
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2002), but is easily distinguished from that species by the mineral envelope (present vs. absent), the structure of the macronucleus (with vs. without central nucleolus), the arrangement of the preoral ciliary rows (cp. Figs 43, 45, 61–66), and the number of somatic ciliary rows (about 12 vs. 15–40, usually 20–30; Figs 61–66 and Foissner 1993a) and kineties comprising the left oral polykinetid (about 5 vs. 9–10). Several populations of *C. steinii*, *C. formisanoi*, and *Dragescozoon terricola* also resemble *C. brasiliensis*, especially in body size and shape, the location and structure of the macronucleus, and the preoral ciliary pattern. However, all *C. steinii* populations have a highly characteristic, spoon-shaped, comparatively large left oral polykinetid, conspicuously different from the rectangular or slightly cuneate, minute polykinetid of *C. brasiliensis*; all *C. formisanoi* populations have an acute posterior body end, distinctly different from the broadly rounded end of *C. brasiliensis*; and *Dragescozoon terricola* has the macronucleus in the anterior body end and a somewhat different preoral ciliary pattern. Of course, all these species, described in detail in Foissner (1993a) and Foissner et al. (2002), lack a mineral envelope. On the other hand, they have conspicuous similarities suggesting a common ancestor and resurrecting the genus *Paracolpoda* Lynn, 1978. Probably, *C. brasiliensis* is more closely related to the *Colpoda steinii* group than to the *C. maupasi* group, with which it shares mainly body shape.

The mineral envelope, a distinct type of sheath in ciliates, and its proposed protective function

The mineral envelope of *Pseudomaryna australiensis* and *Colpoda brasiliensis* appears as a rather inconspicuous structure and as a simple forerunner of the slimy case inhabited by many ciliates, including several colpodids (for reviews, see Corliss 1979 and Foissner 1993a). Mineral envelopes are known also from other ciliates, for instance, the peritrichs *Geleiella vagans* Stiller, 1939 and *Zoothamnium kentii* Grenfell, as redescribed by Foissner et al. (1992); the cyrtophorid *Atopochilodon arenifer* Kahl, 1933; the oligotrich *Strobilidium minimum* Gruber, as redescribed in Kahl (1932); and the karyorelictid *Ciliofaurea arenicola* Dragesco, 1960. Obviously, mineral envelopes evolved independently several times. This is why I do not lump together *P. australiensis* and *C. brasiliensis* in a separate genus. Likewise, the feature is probably useful only for defining species, not genera, because enveloped species are frequently very similar to their ordinary congeners in most other characteristics, as shown by *Colpoda brasiliensis* and *Geleiella vagans*, which Dingfelder (1962) and, later, also Stiller (1971) and Foissner (1977) transferred to *Astylozoon*.

Generally, however, mineral envelopes are much rarer than slimy cases or compact loricas. It is likely, that mineral envelopes are not simple progenitors of slimy cases because case-building ciliates are never covered by mineral particles, not even during case construction, although later often some mineral particles adhere to the slimy case surface. Accordingly, the mineral particles of the envelope of *Pseudomaryna*, *Colpoda*, and other ciliates are most likely actively searched for and attached to the body surface by a slimy substance.

Stiller (1939) and Dingfelder (1962) already suggested a protective function for the mineral envelopes and slimy cases because they occur rather frequently in ciliates living in ephemeral, often turbid puddles. Both, *P. australiensis* and *C. brasiliensis* occur in very fine-grained floodplain soils.

Figs 58–60. Comparison of the ciliary pattern of *Pseudomaryna*, *Maryna*, and *Colpoda* (based on Foissner 1993a). The most conspicuous difference concerns the preoral suture (S, in black), which extends from the anterior body end to the summit of the oral opening in *Maryna* (59) and *Colpoda* (60), while right of the oral opening and whole body length in *Pseudomaryna* (58). OA – oral apparatus, S – preoral suture.

Figs 61–66. Ciliary pattern of *Colpoda maupasi* populations from Venezuela (61), various sites of Namibia (62, 63, 65, 66), and Costa Rica (64) after Chatton-Lwoff silver nitrate (61, 62, 64) and silver carbonate (63, 65, 66) impregnation. The ciliary pattern of *C. maupasi* is obviously very similar in populations globally (see Foissner 1993a for further figures), but slightly different from that of *C. brasiliensis*, although both species largely agree in the shape of the body and oral ciliary fields (cp. Figs 42, 43, 45, 46). The ciliary rows are narrowly spaced at both sides of the preoral suture in *C. maupasi*, while the right side rows are wider spaced than the left side rows in *C. brasiliensis*. This causes a different preoral ciliary pattern: a ciliary row each at the right and left side abuts in *C. maupasi*, while an additional row is intercalated in *C. brasiliensis* (Figs 43, 45; arrowheads). LP – left oral polykinetid, MA – macronucleus, RP – right oral polykinetid.

When looking at these ciliates in a drop of floodplain water, they appear like soil particles. Thus, I suggest that the envelope greatly decreases the probability of being recognized by predators as a latent food source. This applies also to the resting cysts, which take over the envelope of the trophic cell (Figs 16, 25–28, 44, 55–57). Alternatively, the envelope could protect the inhabitants from being injured by swirling mineral particles, which often have sharp edges.

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