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European Journal of Protistology 53 (2016) 61–95

European Journal of PROTISTOLOGY

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High cryptic soil ciliate (Ciliophora, Hypotrichida) diversity in Australia

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Received 24 August 2015; received in revised form 6 October 2015; accepted 11 October 2015
Available online 19 October 2015

Abstract

The diversity and distribution of soil ciliates from Australia is poorly known. Thus, we studied eight taxa, using the non-flooded Petri dish culture method, live observation, silver impregnation, detailed morphometrics, ontogenesis, and reinvestigation of type slides. At first glance, the Australian taxa looked very similar to described species, however, detailed investigations resulted in the identification of six cryptic species: *Afroamphisiella multinucleata minima* nov. subspec., *Cladotricha similis* nov. spec., *Erimophrya similis* nov. spec., *Heterogonostomum salinarum* nov. gen., nov. spec., *Pseudohemisincirra arabica australiensis* nov. subspec., and *Pattersoniella* (*Pattersoniellides*) *australiensis* nov. subgen., nov. spec. This new subgenus is unique among all described hypotrichs in having reduced some anterior paroral dikinetids the fibrillar associates of which are, however, still present. Only two of the eight taxa are possibly cosmopolitans: *Apourosomoida halophila* Foissner et al., 2002 and *Urosoma karinae* Foissner, 1987. This supports the moderate endemicity model, i.e., that a third of protists have a restricted distribution (Foissner, Chao and Katz 2008).

Keywords: Biogeography; Cryptic species; Endemicity; Ontogenesis; Saline habitats

Introduction

Very few studies have been made on Australian soil ciliates. The most comprehensive investigations were performed by Blatterer and Foissner (1988) and Foissner (1988). In 21 samples, they identified 139 species of which 23 species and 12 genera were undescribed; 39 of the 139 species were hypotrichs, and Kumar and Foissner (2015) added *Australocirrus shii*. The situation is also poor for testate amoebae while flagellates have been studied well (Lee, 2015). Thus, we invented a research project on Australian soil ciliates, which was granted by the Austrian Science Fund.

It is well known that misidentifications occur easily when European guides are used for the identification of organisms from other biogeographic realms. Thus, we tested eight Australian taxa, that looked – at first glance – rather similar to described species from other regions of the world. The outcome were one new genus, a new subgenus, four new species, and two new subspecies all described in the present paper! Only two cosmopolitans remained.

Still, there is some debate whether or not most or all microscopic organisms have cosmopolitan or restricted distribution. Fortunately, two recent paper collections on a great variety of small organisms showed endemics in most groups (Foissner, 2008; Fontaneto, 2011). The reasons for restricted distribution of certain genera and species are difficult to research but time, distance, and habitat are very likely of great importance, as in plants and animals (Foissner 2008, 2011).

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http://dx.doi.org/10.1016/j.ejop.2015.10.001
0932-4739/

Material and Methods

Ciliates were reactivated from resting cysts in air-dried soil samples from Australia, collected and studied between 1985 and 1990, using the non-flooded Petri dish method. For details on samples, see the individual species descriptions. Briefly, the non-flooded Petri dish method involved placing 50–500 g litter and soil in a Petri dish and saturating, but not flooding it, with distilled water. Such a culture was analysed for ciliates by inspecting about 2 ml of the run-off on days 2, 7, 14, 21, and 28. For a detailed description, see Foissner et al. (2002).

Live observation and protargol impregnation were performed according to Foissner (1991, 2014). Counts and measurements on silver-impregnated specimens were conducted at a magnification of 1000×. In vivo measurements were performed at magnifications of 40–1000×. Illustrations of live specimens were based on free-hand sketches, while those of impregnated cells were made with a drawing device. Classification is according to Berger (1999, 2008, 2011) and Foissner et al. (2002, 2008b). Terminology is according to Berger (1999, 2008, 2011) and Wallengren (1900).

Results and Discussion

Afroamphisiella Foissner et al., 2002

Improved diagnosis: Non-dorsomarginalian hypotrichs with one or several cirri left of frontoventral cirral row, which is involved in oral primordium formation. Adoral zone of membranelles bipartite or continuous. Transverse cirri, postperistomial cirri, and caudal cirri lacking. Two to three dorsal kineties.

Remarks: Foissner et al. (2002) and Berger (2011) classified *Afroamphisiella* provisionally into the Amphisiellidae whose main feature is the amphisiellid median cirral row, i.e., a long frontoventral cirral row originating from at least two anlagen. Here, we show that the long frontoventral cirral row of *Afroamphisiella multinucleata*, type of the genus, is produced by a single anlage. Thus, we change the diagnosis from "amphisiellid median cirral row" to "frontoventral cirral row" and remove the genus from the Amphisiellidae.

Afroamphisiella multinucleata Foissner et al., 2002

Improved diagnosis (averages from four populations; Table 1). Size in vivo about 85 μm × 25 μm or 60 μm × 20 μm; elongate rectangular. On average 12–16 macronuclear nodules and two to three micronuclei. Cortical granules in rather dense rows, globular to ellipsoid, yellowish to colourless, about 0.3–1 μm in size. On average 12–16 cirri in frontoventral row, three frontal cirri, one to two cirri posterior of right frontal cirrus, and one buccal cirrus. Left marginal row composed of 16 or 10 cirri, right of 23 or 14. Adoral zone occupies about 32–34% of body length, composed of 16–18 membranelles on average. Two dorsal kineties.

Afroamphisiella multinucleata multinucleata Foissner et al., 2002 nov. stat.

Diagnosis (averages are from the three populations mentioned in Table 1): Size about 85 μm × 25 μm in vivo. Left marginal row slightly shortened posteriorly (≤10% of body length) and composed of 16 cirri, right of 23.

Afroamphisiella multinucleata minima nov. subspec. (Figs 1A–G, 2A–F, 3A–I; Tables 1 and 2)

Diagnosis: Size about 60 μm × 20 μm in vivo. Left marginal row distinctly shortened posteriorly (16% of body length) and composed of 10 cirri, right of 14.

Type locality: Highly saline soil and root carpet from a grass-covered hill in the Meningie salt lake, Adelaide, Australia, 35°41′S 139°20′E.

Material deposited: One holotype and five paratype slides with protargol-impregnated specimens have been deposited in the Biologiezentrum of the Oberösterreichische Landesmuseum in Linz (LI), reg. no. 2015, 811, 813–817. Relevant specimens have been marked with black ink circles on the coverslip.

Etymology: The species group name "*minima*" refers to the small body size compared with the nominotypical subspecies.

Observations: The new subspecies differs from *Afroamphisiella multinucleata multinucleata* mainly by the features mentioned in the diagnosis. Thus, the description is restricted to the detailed morphometrics (Table 2) and figures (1a–E, 3A–E) as well as to a few details: (i) Size in vivo about 60 μm × 20 μm while only 47 μm × 16 μm in the protargol preparations. Very likely, this big difference is partially caused by insufficient fixation due to the high salinity of the sample; (ii) cortical granules colourless and 0.3 μm across (Fig. 1B); (iii) on average 13 frontoventral cirri including 1 (2 in 6 out of 126 specimens analysed) cirrus posterior of third frontal cirrus (Figs 1A, D, 3A, B, D).

Ontogenesis: The ontogenesis begins with the formation of an oral primordium by the posteriormost cirri of the long frontoventral row (Fig. 3F). Early and mid-dividers show the formation of only four frontoventral cirral anlagen each in proter and opisthe (Figs 1F, 2A, 3G). Anlagen I–III of the opisthe originate from the oral primordium whereas anlagen I and II of the proter originate from the undulating membranes and the buccal cirrus, respectively. Anlage III of the proter originates either *de novo* or from the cirrus posterior to the third frontal cirrus (Fig. 1F). Anlage IV of proter and opisthe

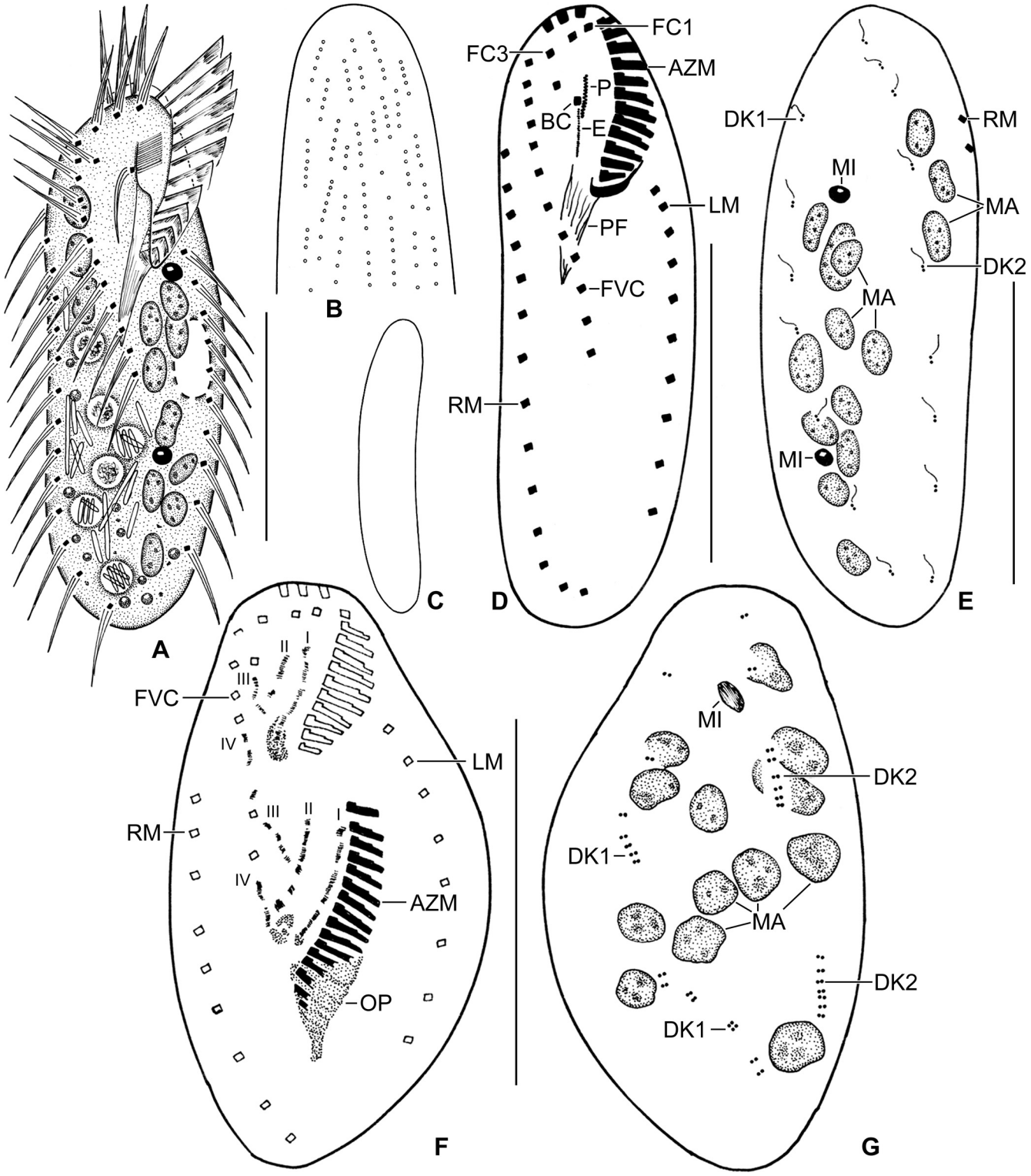

Fig. 1. A–G. *Afroamphisiella multinucleata minima* nov. subspec. from life (A–C) and after protargol impregnation (D–G). **A**: Ventral view of a representative specimen, length 60 μm. **B**: Cortical granulation. **C**: Right lateral view. **D**: Ventral view of holotype specimen, showing the infraciliature. **E**: Dorsal view of a paratype specimen, showing the infraciliature and nuclear apparatus. **F, G**: Ventral and dorsal view of an early divider, showing the formation of four frontoventral cirral anlagen and within row anlagen formation in the dorsal kineties. AZM – adoral zone of membranelles, BC – buccal cirrus, DK1,2 – dorsal kineties, E – endoral membrane, FC1,3 – frontal cirri, FVC – frontoventral cirral row, LM – left marginal cirral row, MA – macronuclear nodules, MI – micronuclei, OP – oral primordium, P – paroral membrane, PF – pharyngeal fibres, RM – right marginal cirral row. Roman numerals denote cirral anlagen. Scale bars 25 μm.

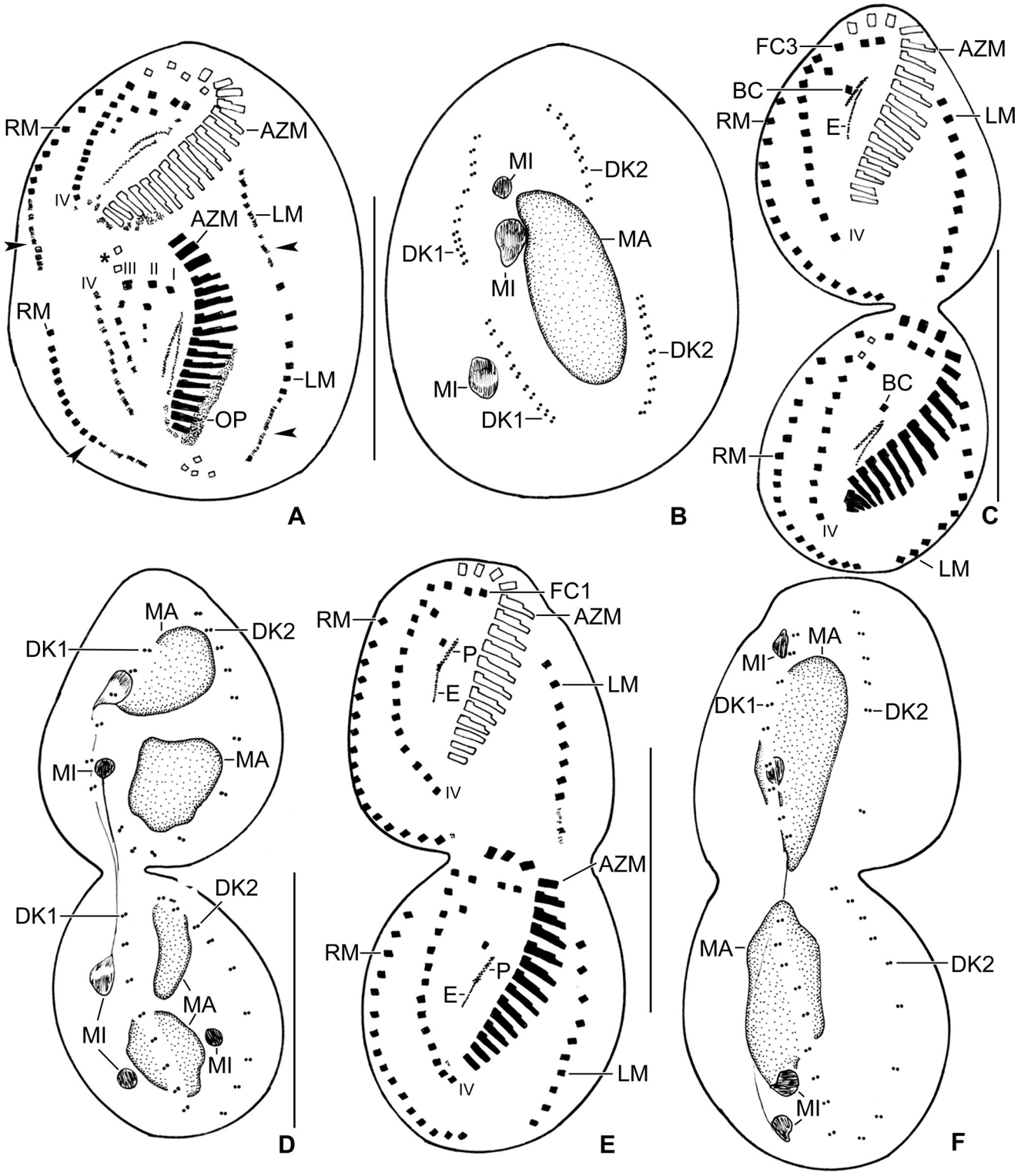

Fig. 2. A–F. *Afroamphisiella multinucleata minima* nov. subspec. after protargol impregnation. Parental cirri that did not form anlagen shown by contour. **A, B**: Ventral and dorsal view of a mid-divider with fused macronuclear nodules. It shows four frontoventral cirral anlagen (Roman numerals), two anlagen each (arrowheads) for the marginal cirri of proter and opisthe, and the formation of the dorsal kineties. Asterisk marks two parental cirri from the long frontoventral row. **C–F**: Ventral and dorsal view of late dividers. The frontoventral cirri migrate to their specific sites and most parental cirri have been resorbed. AZM – adoral zone of membranelles, BC – buccal cirrus, DK1,2 – dorsal kineties, E – endoral membrane, FC1,3 – frontal cirri, LM – left marginal cirral row, MA – macronuclear nodules, MI – micronuclei, OP – oral primordium, P – paroral membrane, RM – right marginal cirral row. Roman numerals denote cirral anlagen. Scale bars 20 μm.

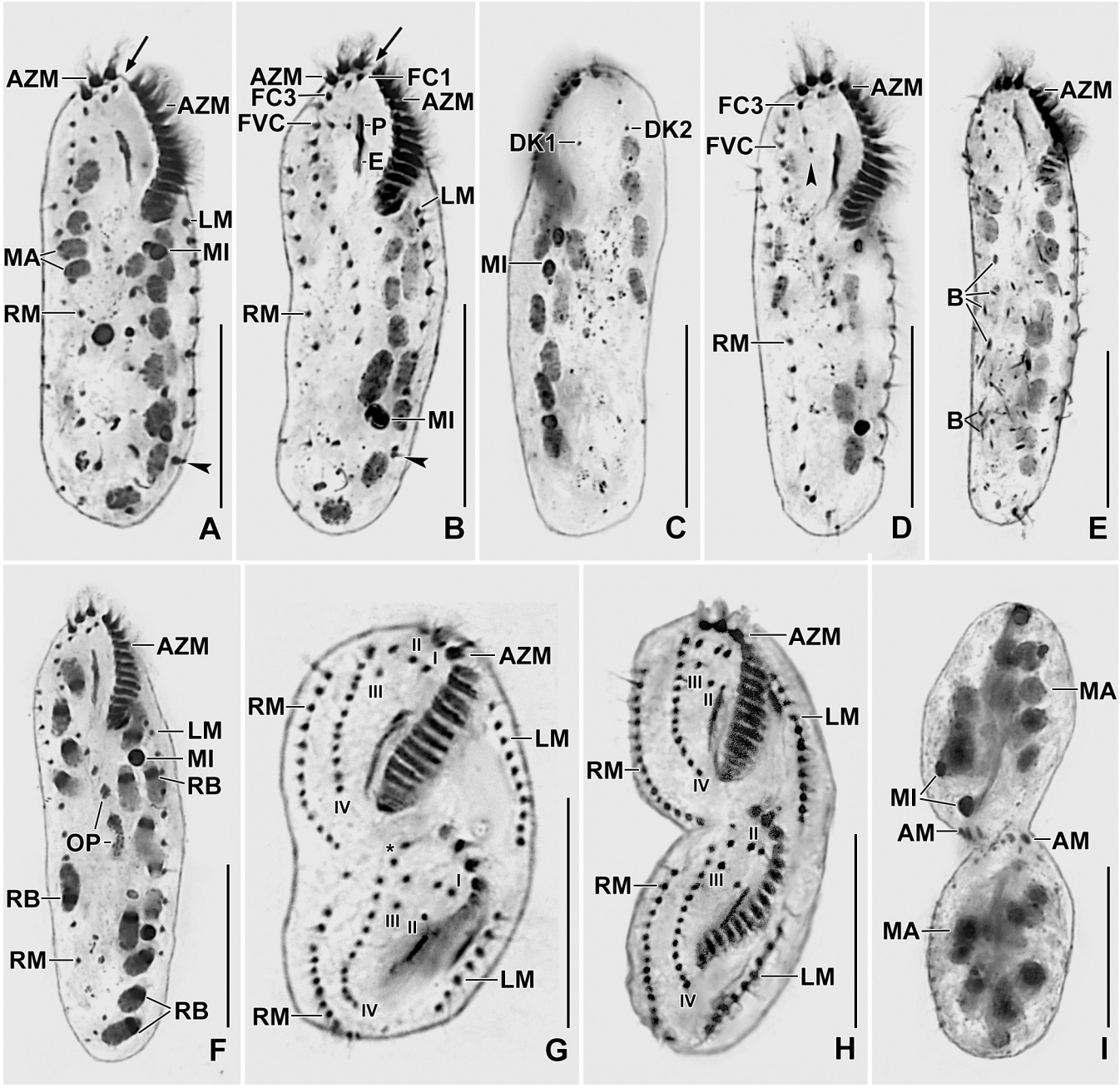

Fig. 3. A–I. *Afroamphisiella multinucleata minima* nov. subspec. after protargol impregnation. **A, B**: Ventral view of ordinary specimens, showing the infraciliature and nuclear apparatus. Arrowheads point to the posteriorly shortened left marginal cirral row, very likely an important feature of this subspecies. The arrows mark an increased distance between the frontal and ventral adoral membranelles, an important feature present in all populations investigated. **C**: Dorsal view, showing dorsal kineties and nuclear apparatus. **D**: A rare specimen with two cirri posterior to the third frontal cirrus (arrowhead). **E**: A specimen possibly showing bacteria in the posterior region. **F**: An early divider, showing the formation of the oral primordium from the last cirri of the frontoventral row and the replication band in the macronuclear nodules. **G, H**: Late dividers, showing the migration of the frontoventral cirri to their specific sites. Parental cirri that did not form anlagen have been resorbed except of two between the anlagen in the long frontoventral row (asterisk). The gap between frontal and ventral adoral membranelles has not yet formed, indicating that it is a comparatively young feature. **I**: A conjugant, showing the fusion of the oral area. This is a late stage as indicated by the scattered globular macronuclear nodules and some micronuclei. AM – adoral membranelles, AZM – adoral zone of membranelles, B – bacteria, DK1,2 – dorsal kineties, E – endoral membrane, FC1,3 – frontal cirri, FVC – frontoventral cirral row, LM – left marginal cirral row, MA – macronuclear nodules, MI – micronuclei, OP – oral primordium, P – paroral membrane, RB – replication band, RM – right marginal cirral row. Roman numerals denote cirral anlagen. Scale bars 20 μm.

Table 1. Comparison of main morphometrics of *Afroamphisiella multinucleata* populations from Australia (present study), Korea (Choi and Shin, 2012), Namibia (Foissner et al., 2002), and the USA (Borror and Evans, 1979). Main distinguishing features bold.

Characteristics[a]	Australia	Korea	Namibia	USA
Body, length (in vivo)	**60**	**80**	**85**	–
Body, width (in vivo)	**20**	**25**	**23**	–
Number of specimens investigated in vivo	2	?	Some	–
Body, length	**47.2** (36–57)	**80.3** (65–94)	**71.5** (59–84)	**53.0**
Body, width	**16.5** (14–20)	**25.0** (17–31)	**24.0** (18–29)	**15.0**
Body length:width, ratio	2.9 (2.4–3.9)	3.2 (2.8–4.2)	3.0 (2.5–3.7)	3.5
Anterior body end to proximal end of adoral zone, % of body length	33.8 (26.3–41.3)	33.9[b]	30.9[b]	32.1[b]
Adoral membranelles, number	16.0 (15–18)	18.0 (16–20)	17.5 (16–19)	18.0
Macronuclear nodules, number	12.0 (6–17)	15.5 (11–20)	18.4 (14–29)	14.0
Right marginal row, number of cirri	**14.1** (12–17)	**24.2** (21–30)	**20.9** (13–34)	**25.0**
Left marginal row, number of cirri	**9.7** (8–13)	**15.6** (10–19)	**16.6** (11–22)	**17.0**
Posterior end to left marginal row, % of body length	**16.1** (8.7–22.6)	**5.5**[c]	**9.7**[c]	**2.7**[c]
Cirri posterior of right frontal cirrus, number	1.0[d]	2.7 (1–4)	1.3 (1–3)	2.0
Anterior body end to rear end of frontoventral cirral row, % of body length	57.4 (50.9–63.9)	–	55.4[b]	62.3[b]
Frontoventral row, number of cirri	11.8 (10–14)	16.9 (14–21)	14.4 (11–22)	17.0
Number of specimens investigated (protargol)	21	17–20	29	1
Protargol method	Foissner (1991)	Wilbert (1975)	Foissner (1991)	–

[a] Data based, if not stated otherwise, on protargol-impregnated specimens. Measurements in μm; minimum and maximum in parentheses; first value arithmetic mean.
[b] Calculated from arithmetic mean.
[c] According to the related illustrations.
[d] Two cirri in six out of 126 specimens analysed.

originates within the frontoventral cirral row, at two levels separated by some parental cirri (Figs 1F, 2A, 3G). Some proximal membranelles of the parental adoral zone perform reorganisation in mid-dividers (Fig. 2A). In late dividers, the specific cirral pattern is well recognisable (Figs 2C, E, 3G, H). The dorsal kineties are formed by within row proliferation of basal bodies (Figs 1G, 2B, D, F). The macronuclear nodules fuse to a single mass in mid-dividers; the micronuclei undergo typical mitotic division (Fig. 2B, D, F).

Occurrence and ecology: As yet found only at type locality.

Species and generic comparison: Compared to the nominotypical subspecies, the subspecies *minima* is considerably smaller and has much less marginal cirri, indicating that the body size differences are real, i.e., not only caused by poor fixation (Table 1). This is confirmed by the descriptions of Choi and Shin (2012) and Borror and Evans (1979). A further, possibly important difference concerns the cortical granules which are colourless and about 0.3 μm across in *minima*, while yellowish and 1 μm × 0.5 μm or 0.5 μm across in the nominotypical subspecies, respectively (Choi and Shin, 2012; Foissner et al., 2002). These data are at variance because slight colour differences are common in various populations (Foissner, 2016) and the size of the granules is quite similar in the Australian and Korean populations, while considerably different to the Namibian population.

As explained in the remarks to the genus, *Afroamphisiella* does not fit into the Amphisiellidae. Possibly, *Afroamphisiella* belongs to the Orthoamphisiellidae Eigner, 1997 because the morphostatic cirral pattern is quite similar. However, *Orthoamphisiella stramenticola* Eigner and Foissner, 1991, type of the genus, has a rather different ontogenesis so that *Afroamphisiella* is better placed incertae sedis in the non-dorsomarginalian hypotrichs.

Apourosomoida halophila Foissner et al., 2002 (Fig. 4A–D; Table 3)

Remarks: The Australian population is highly similar in morphology, morphometry, and ontogenesis to the Namibian type population (Fig. 4A–D; Table 3). Some minor differences are: (i) Size in vivo about 85 μm × 20 μm, while only 58 μm × 20 μm (vs. 71 μm × 21 μm in the type) in the protargol preparations. Very likely, this considerable difference between in vivo and protargol size is partially caused by insufficient fixation due to the high salinity of the sample because the in vivo size is about 70–100 μm × 20 μm; (ii) The adoral zone of membranelles occupies about 31% (vs. 26% in the type) of body length in the protargol preparations; part of this difference is possibly caused by the strong shrinkage mentioned above; (iii) The paroral membrane extends on average 8.7% (vs. 6.1%; calculated from arithmetic mean) of body length and begins about 7 μm posterior to the anterior body end, i.e., at level of buccal cirrus.

Material deposited: Four voucher slides with protargol-impregnated specimens have been deposited in the Biologiezentrum of the Oberösterreichische Landesmuseum

Table 2. Morphometric data on *Afroamphisiella multinucleata minima* nov. subspec.

Characteristics[a]	Mean	M	SD	SE	CV	Min	Max	n
Body, length	47.2	47.0	5.5	1.2	11.7	36.0	57.0	21
Body, width	16.5	16.0	2.0	0.4	12.1	14.0	20.0	21
Body length:width, ratio	2.9	2.9	0.3	0.1	10.4	2.4	3.9	21
Anterior body end to proximal end of adoral zone, distance	15.9	16.0	1.4	0.3	8.8	14.0	19.0	21
Body length:length of adoral zone, ratio	3.0	3.0	0.3	0.1	10.0	2.4	3.8	21
Anterior body end to proximal end of adoral zone, % of body length	33.8	33.3	3.4	0.7	10.1	26.3	41.3	21
Adoral membranelles, total number	16.0	16.0	0.8	0.2	5.0	15.0	18.0	21
Ventral adoral membranelles, number	13.0	13.0	0.8	0.2	6.2	12.0	15.0	21
Frontal adoral membranelles, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Adoral membranelles, width of longest base	3.8	4.0	–	–	–	3.0	4.0	17
Anterior body end to paroral membrane, distance	5.7	6.0	0.7	0.2	12.5	4.0	7.0	21
Anterior body end to anteriormost macronuclear nodule, distance	9.7	9.0	2.2	0.5	22.3	7.0	14.0	21
Posterior body end to posteriormost macronuclear nodule, distance	4.8	4.0	2.1	0.5	45.0	2.0	9.0	21
Macronuclear figure, length	33.2	36.0	5.1	1.1	15.4	21.0	41.0	21
Anteriormost macronuclear nodule, length	4.3	4.0	1.2	0.3	27.4	3.0	7.0	21
Anteriormost macronuclear nodule, width	2.6	3.0	0.6	0.1	20.8	2.0	4.0	21
Macronuclear nodules, number	12.0	13.0	3.5	0.8	29.4	6.0	17.0	21
Macronuclear nodules right of midline, number	3.3	3.0	1.0	0.2	30.5	2.0	5.0	21
Anterior body end to anteriormost micronucleus, distance	16.0	16.0	2.8	0.7	17.8	7.0	21.0	19
Anteriormost micronucleus, length	2.3	2.0	–	–	–	2.0	3.0	21
Anteriormost micronucleus, width	1.8	2.0	–	–	–	1.0	2.5	21
Micronuclei, number	2.2	2.0	0.5	0.1	23.4	1.0	3.0	21
Anterior body end to right marginal cirral row, distance	11.4	12.0	1.3	0.3	11.6	9.0	13.0	21
Posterior body end to right marginal cirral row, distance	1.5	1.0	0.7	0.1	44.6	1.0	3.0	21
Posterior body end to right marginal cirral row, % of body length	3.2	2.5	1.4	0.3	43.6	1.8	7.5	21
Right marginal row, number of cirri	14.1	14.0	1.3	0.3	9.2	12.0	17.0	21
Anterior body end to left marginal cirral row, distance	15.2	15.0	1.6	0.3	10.4	13.0	19.0	21
Posterior body end to left marginal cirral row, distance	7.7	8.0	2.1	0.5	27.8	4.0	12.0	21
Posterior body end to left marginal cirral row, % of body length	16.1	16.3	3.7	0.8	23.2	8.7	22.6	21
Left marginal row, number of cirri	9.7	10.0	1.1	0.2	11.0	8.0	13.0	21
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Anterior body end to buccal cirrus, distance	7.8	8.0	1.5	0.3	18.7	6.0	11.0	19
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Cirri posterior to right frontal cirrus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Anterior body end to rear end of frontoventral cirral row, distance	27.0	27.0	2.8	0.6	10.4	22.0	31.0	21
Anterior body end to rear end of frontoventral row, % of body length	57.4	57.4	3.1	0.7	5.4	50.9	63.9	21
Frontoventral row, number of cirri	11.8	12.0	0.8	0.2	6.9	10.0	14.0	21
Dorsal kineties, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Anterior body end to dorsal kinety 1, distance	9.3	9.0	1.0	0.2	11.3	7.0	11.0	19
Dorsal kinety 1, number of bristles	6.9	7.0	0.9	0.2	13.1	6.0	9.0	19
Anterior body end to dorsal kinety 2, distance	4.6	5.0	0.8	0.2	16.4	3.0	6.0	19
Dorsal kinety 2, number of bristles	7.9	8.0	0.7	0.2	8.3	7.0	9.0	19

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

in Linz (LI), reg. no. 2015, 824–827. Relevant specimens have been marked with black ink circles on the coverslip.

Occurrence and ecology: As yet found in the highly saline sandy soil from the Unjab river bed, northern Namib Desert, 20°10′S 13°10′E (Foissner et al., 2002) and in the highly saline soil and root carpet from a grass-covered hill in the Meningie salt lake, Adelaide, Australia, 35°41′S 139°20′E. Feeds mainly on bacteria and zooflagellates, very likely prefers high salinities.

Cladotricha similis nov. spec. (Figs 5A–J, 6A–E; Table 4)

Diagnosis: Size in vivo about 110 μm × 15 μm; pisciform to elongate ellipsoid and more or less narrowed posteriorly and sigmoid. Multimacronucleate, three micronuclei. Cortical granules colourless, mainly around dorsal kinetids and cirral bases, slightly ellipsoid, about 0.7 μm in size. Two buccal cirri anterior to paroral membrane; ventral cirral row

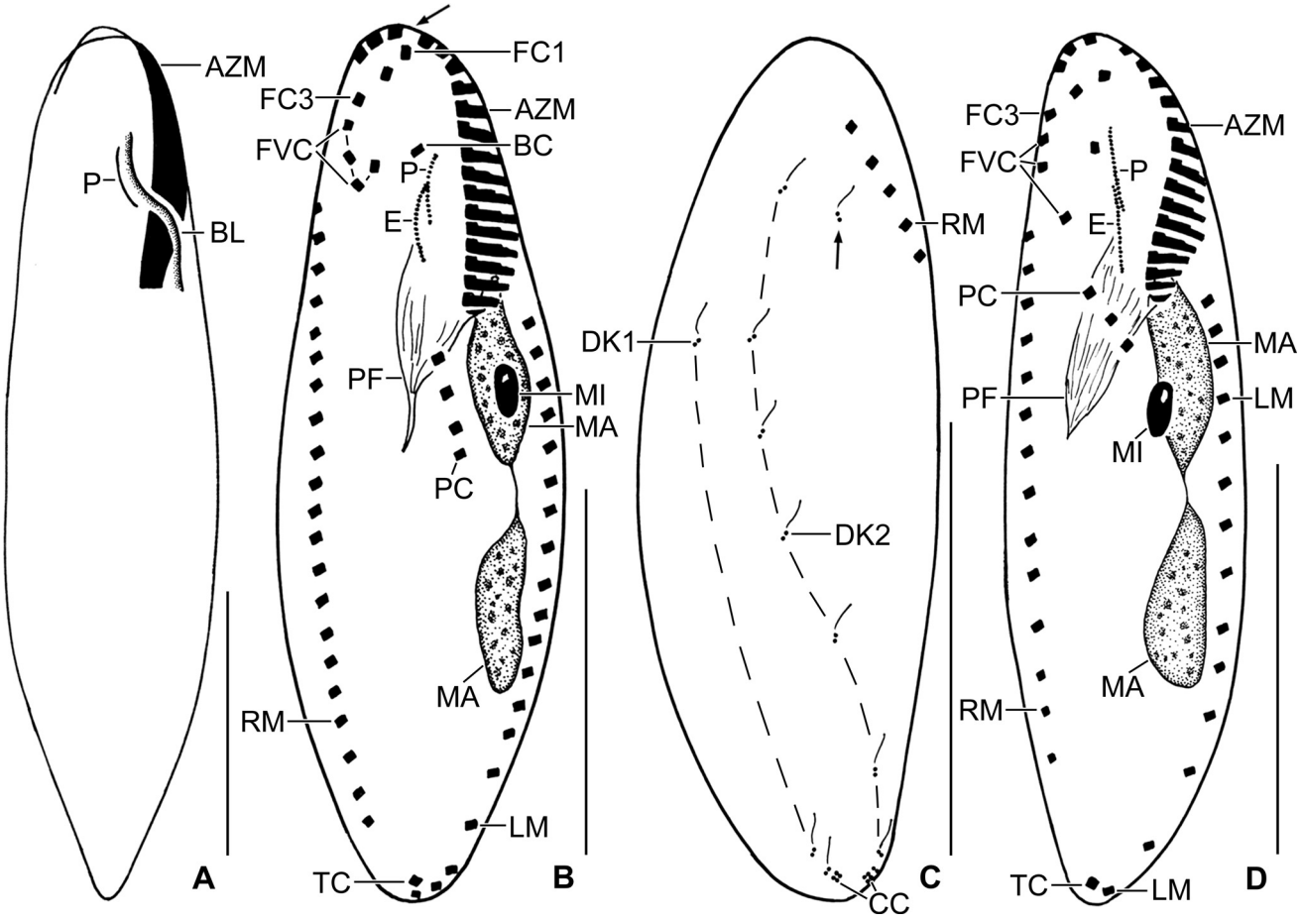

Fig. 4. A–D. *Apourosomoida halophila*, Australian specimens from life (A) and after protargol impregnation (B–D). **A**: Body outline and details of oral area. **B**: Ventral view of an ordinary specimen, showing the infraciliature and the nuclear apparatus. Arrow marks the discontinuity in the adoral zone of membranelles. **C**: Dorsal view, showing the two dorsal kineties (broken lines). Arrow points to the dislocated bristle of dorsal kinety 2. **D**: A specimen with reduced number of frontoventral, postoral and marginal cirri. Note the rather long paroral membrane. AZM – adoral zone of membranelles, BC – buccal cirrus, BL – buccal lip, CC – caudal cirri, DK1,2 – dorsal kineties, E – endoral membrane, FC1,3 – frontal cirri, FVC – frontoventral cirri, LM – left marginal cirral row, MA – macronuclear nodules, MI – micronuclei, P – paroral membrane, PC – postoral cirral row, PF – pharyngeal fibres, RM – right marginal cirral row, TC – transverse cirrus. Scale bars 25 μm.

5 strongly shortened, composed of an average of six cirri. Adoral zone occupies about 36% of body length, on average composed of 22 membranelles. Buccal cavity minute; paroral membrane usually composed of three kinetids.

Type locality: Highly saline soil and root carpet from a grass-covered hill in the Meningie salt lake, Adelaide, Australia, 35°41′S 139°20′E.

Material deposited: One holotype and four paratype slides with protargol-impregnated specimens have been deposited in the Biologiezentrum of the Oberösterreichische Landesmuseum in Linz (LI), reg. no. 2015, 808–812. Relevant specimens have been marked with black ink circles on the coverslip.

Etymology: The Latin adjective *similis* (similar) refers to the similarity with *Cladotricha edaphoni*.

Description: *Cladotricha similis* is moderately variable, most variation coefficients being smaller than 15%, except of distances and nuclear apparatus.

Size in vivo 100–130 μm × 15–20 μm, usually about 110 μm × 15 μm, strongly shrunken (up to 40%) in protargol preparations due to insufficient fixation at high salinity, as indicated by the high difference in length:width ratio is 7:1 in vivo while 3.3:1 in protargol preparations (Table 4). Body shape rather variable, i.e., very elongate pisciform and more or less narrowed posteriorly and sigmoid to elongate ellipsoid in vivo (Fig. 5A, B); in protargol preparations usually elongate ellipsoid, possibly due to insufficient fixation; slightly flattened dorsoventrally (Figs 5A–C, E, F, 6A, B, D; Table 4). Macronuclear nodules scattered throughout cell, globular to ellipsoid, contain some globular nucleoli of ordinary size. On average three globular to ellipsoid micronuclei scattered in cytoplasm or attached to macronuclear nodules, on average 2.0 μm × 1.7 μm in protargol preparations (Figs 5A, G, 6A, B; Table 4). Contractile vacuole in mid-body at left cell margin, with short collecting canals rarely recognisable (Fig. 5B). Cortex flexible, contains

Table 3. Morphometric data on an Australian population of *Apourosomoida halophila*.

Characteristics[a]	Mean	M	SD	SE	CV	Min	Max	n
Body, length	57.5	58.0	8.5	1.8	14.8	46.0	70.0	23
Body, width	19.5	20.0	2.8	0.6	14.2	15.0	25.0	23
Body length:width, ratio	3.0	2.9	0.5	0.1	15.9	2.3	4.4	23
Anterior body end to proximal end of adoral zone, distance	17.8	17.0	2.2	0.5	12.5	14.0	21.0	23
Body length:length of adoral zone, ratio	3.3	3.3	0.4	0.1	11.2	2.7	3.9	23
Anterior body end to proximal end of adoral zone, % of body length	31.2	30.6	3.5	0.7	11.1	25.8	37.0	23
Adoral membranelles, total number	17.9	17.0	1.6	0.4	9.0	16.0	22.0	21
Frontal adoral membranelles, number	3.1	3.0	–	–	–	3.0	4.0	21
Ventral adoral membranelles, number	14.8	14.0	1.6	0.3	10.6	13.0	19.0	21
Adoral membranelles, width of longest base	4.1	4.0	–	–	–	4.0	5.0	17
Anterior body end to paroral membrane, distance	6.8	6.0	1.4	0.3	21.1	5.0	9.0	21
Paroral membrane, length	5.0	5.0	0.9	0.2	18.3	3.0	6.5	19
Paroral membrane, % of body length	8.7	8.7	1.3	0.3	15.1	5.4	10.9	19
Anterior body end to endoral membrane, distance	9.6	10.0	1.5	0.3	15.7	7.0	12.0	21
Endoral membrane, length	6.5	7.0	0.8	0.2	11.9	5.0	8.0	13
Anterior body end to anterior macronuclear nodule, distance	17.3	17.0	2.7	0.6	15.4	13.0	22.0	21
Posterior body end to posterior macronuclear nodule, distance	12.0	13.0	2.3	0.5	19.4	8.0	16.0	21
Macronuclear figure, length	27.6	28.0	5.7	1.2	20.7	18.0	38.0	21
Macronuclear nodules, distance in between	2.9	3.0	1.8	0.4	61.9	1.0	8.0	21
Anterior macronuclear nodule, length	13.3	14.0	2.7	0.6	20.2	9.0	18.0	21
Anterior macronuclear nodule, width	4.1	4.0	0.9	0.2	20.6	3.0	5.0	21
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Anteriormost micronucleus, length	3.4	3.5	0.7	0.2	20.5	2.0	4.0	13
Anteriormost micronucleus, width	1.8	2.0	–	–	–	1.5	2.0	13
Micronuclei, number	1.5	1.0	0.7	0.2	42.9	1.0	3.0	13
Anterior body end to right marginal row, distance	5.4	5.0	0.7	0.1	12.4	4.0	7.0	21
Posterior body end to right marginal row, distance	5.5	5.0	2.1	0.5	28.6	2.0	10.0	21
Right marginal row, number of cirri	20.8	21.0	3.2	0.7	15.3	15.0	29.0	21
Anterior body end to left marginal row, distance	17.6	17.0	2.4	0.5	13.7	14.0	22.0	21
Left marginal row, number of cirri	16.9	16.0	2.5	0.5	14.8	12.0	21.0	21
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Anterior body end to buccal cirrus, distance	7.3	7.0	1.3	0.3	18.0	5.0	9.0	21
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Anterior body end to last frontoventral cirrus, distance	10.8	11.0	1.5	0.3	13.8	7.0	13.0	21
Frontoventral cirri, number	3.9	4.0	0.6	0.1	16.0	2.0	5.0	21
Anterior body end to first cirrus of postoral row, distance	18.6	18.0	2.4	0.5	12.9	15.0	23.0	21
Anterior body end to last cirrus of postoral row, distance	25.9	25.0	4.5	1.0	17.4	19.0	34.0	21
Postoral row, number of cirri	4.4	4.0	1.5	0.3	33.9	2.0	7.0	21
Transverse cirri, number	1.1	1.0	–	–	–	1.0	2.0	21
Dorsal kineties, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	17
Dorsal kinety 1, number of bristles	2.6	2.0	0.8	0.2	29.7	2.0	4.0	17
Dorsal kinety 2, number of bristles	6.9	7.0	1.2	0.3	16.9	4.0	8.0	17
Dorsal kinety 3, number of bristles	2.1	2.0	0.6	0.2	28.3	1.0	3.0	17
Dorsal kinety 2 + 3, number of bristles	9.0	9.0	1.3	0.3	14.2	6.0	11.0	17
Caudal cirri, number	2.0	2.0	0.4	0.1	18.8	1.0	3.0	21

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

colourless, slightly ellipsoid granules about 0.7 μm in size, mainly around dorsal kinetids and cirral bases (Fig. 5D). Cytoplasm colourless, some crystals 2–4 μm long in posterior half. Usually studded with slightly ellipsoid food vacuoles containing bacteria and their spores (Fig. 5A).

Cirri arranged in *Cladotricha* pattern described by Berger (2011), i.e., in five frontoventral rows or anlagen with all cirri composed of four cilia (basal bodies) except for first (eight basal bodies) and second (four to six basal bodies) frontal cirrus and some posterior marginal cirri composed of only two cilia (Figs 5A, E, 6A–C). See Table 4 for the

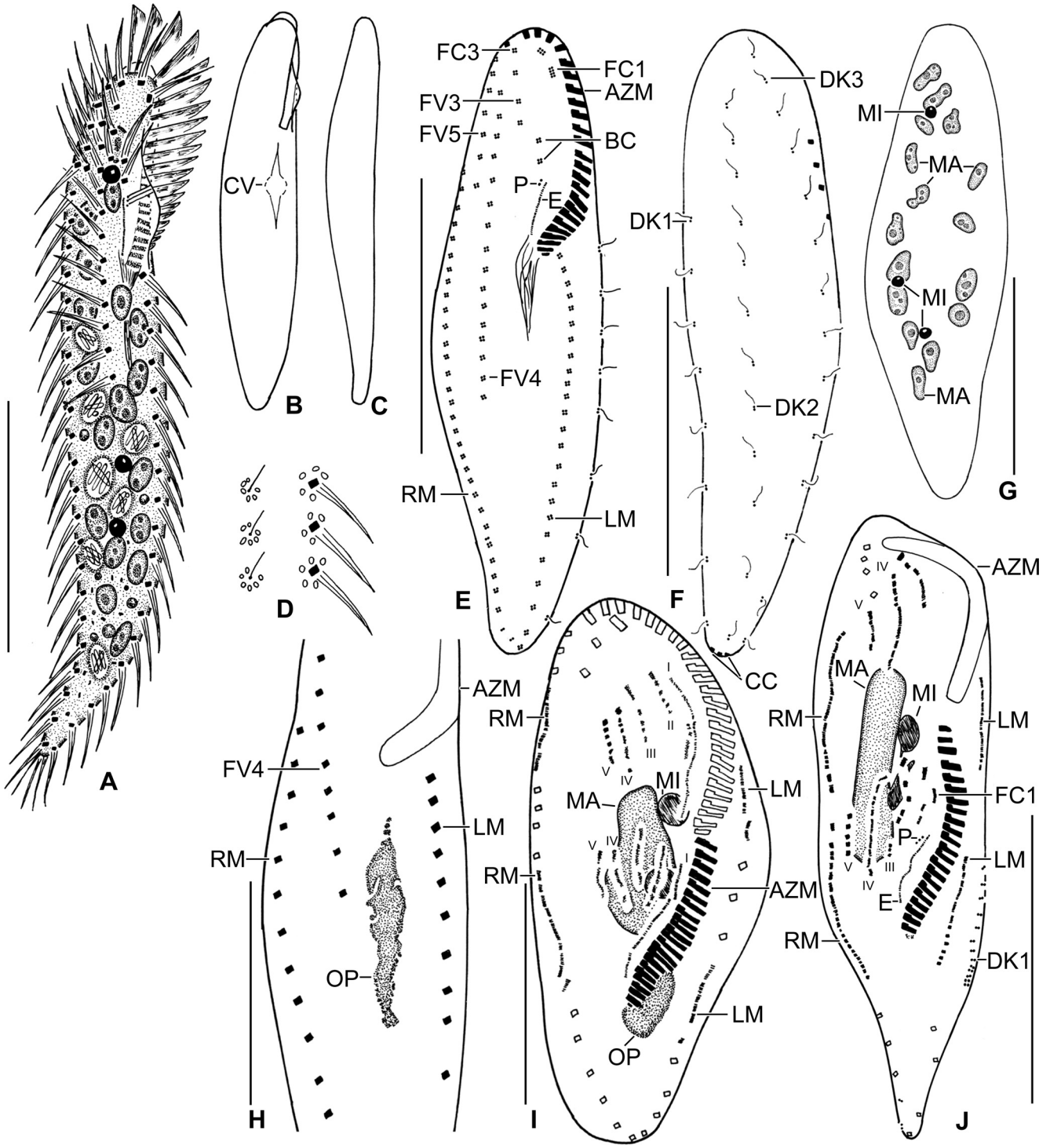

Fig. 5. A–J. *Cladotricha similis* nov. spec. from life (A–D) and after protargol impregnation (D–J). **A**: Ventral view of a representative specimen, length 110 μm. **B, C**: Ventral and right lateral view of a blunt specimen. **D**: Cortical granules. **E**: Ventral view of holotype specimen, showing the infraciliature. **F, G**: Dorsal and ventral view of paratype specimens, showing the infraciliature and the nuclear apparatus. **H**: The oral primordium develops left of frontoventral cirral row 4. **I, J**: Ventral and dorsal view of a middle and of a late divider. The macronuclear nodules fused to a single mass. Cirri originate from five frontoventral anlagen. AZM – adoral zone of membranelles, BC – buccal cirri, CC – caudal cirri, CV – contractile vacuole, DK1–3 – dorsal kineties, E – endoral membrane, FC1,3 – frontal cirri, FV3–5 – frontoventral rows, LM – left marginal cirral row, MA – macronuclear nodules, MI – micronuclei, OP – oral primordium, P – paroral membrane, RM – right marginal cirral row, I–V – cirral anlagen. Scale bars 20 μm (H, I), 30 μm (E–G, J), and 40 μm (A).

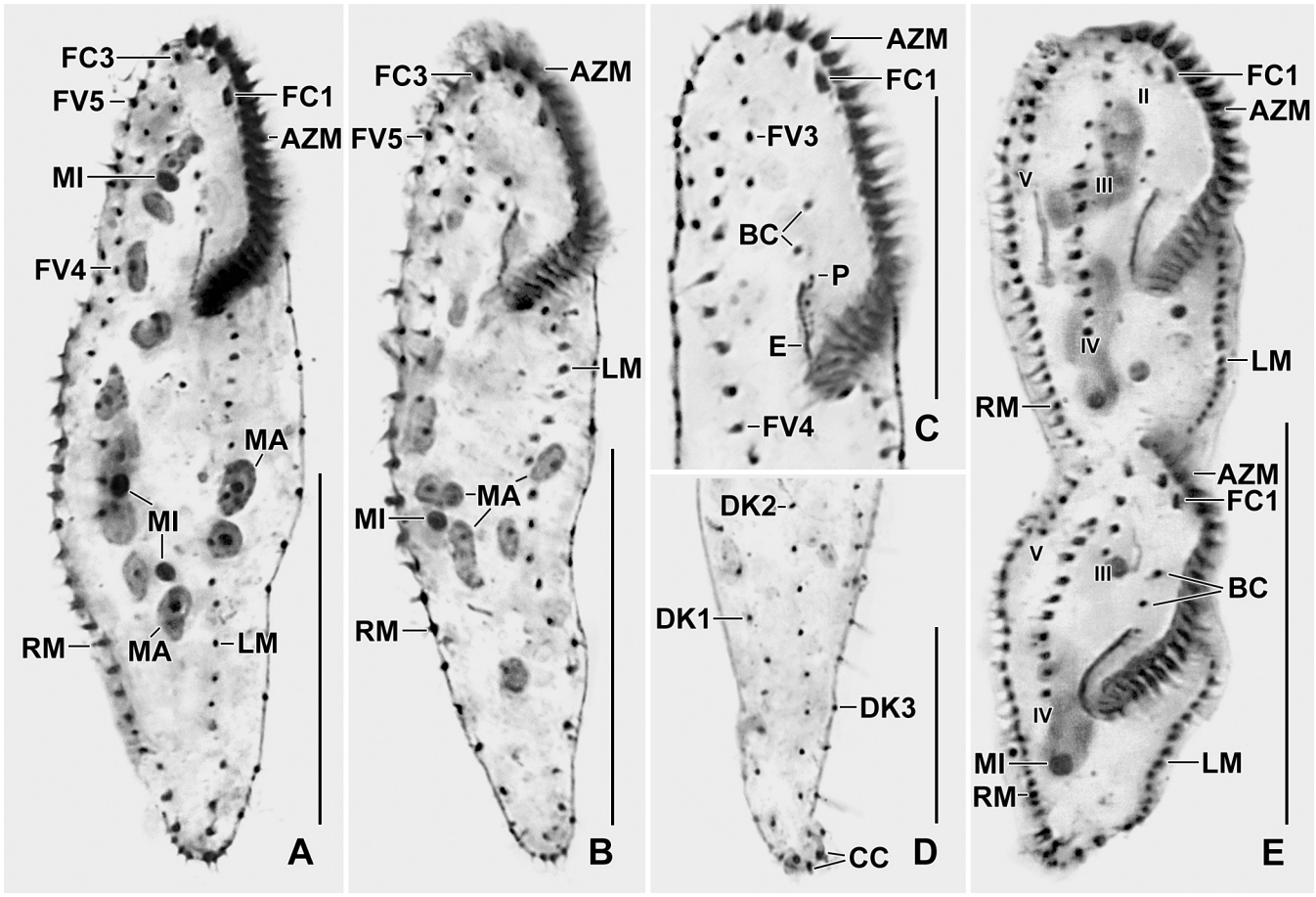

Fig. 6. A–E. *Cladotricha similis* nov. spec. after protargol impregnation. **A, B**: Ventral view of ordinary specimens, showing infraciliature and nuclear apparatus. **C**: Oral area of a paratype specimen, showing the two buccal cirri, a main feature of this species. **D**: Posterior region, showing three dorsal kineties and caudal cirri. **E**: A late divider, showing five frontoventral cirral anlagen each in proter and opisthe. AZM – adoral zone of membranelles, BC – buccal cirri, CC – caudal cirri, DK1–3 – dorsal kineties, E – endoral membrane, FC1,3 – frontal cirri, FV3–5 – frontoventral cirral rows, LM – left marginal cirral row, MA – macronuclear nodules, MI – micronuclei, P – paroral membrane, RM – right marginal cirral row, II–V – cirral anlagen. Scale bars 20 μm (C, D) and 30 μm (A, B, E).

number of cirri comprising the individual frontoventral rows. Right marginal row commences subapically and extends to posterior body end, composed of about 24 cirri, left row of about 20 cirri.

Dorsal bristles 2.5–3 μm long in vivo and in protargol preparations, arranged in three rows each associated with a caudal cirrus. Row 1 commences at level of buccal vertex, row 2 subapically, and row 3 near anterior body end; all rows end slightly subterminally (Figs 5F, 6D; Table 4).

Oral apparatus in *Gonostomum* pattern (Berger, 1999), i.e., adoral zone extends straight along anterior and left body margin before bending abruptly into cell at about 36% of body length, on average composed of 22 ordinary membranelles with up to 10 μm long cilia, bases of largest membranelles about 4 μm wide in vivo and in protargol preparations (Figs 5A, E, 6A–C; Table 4). Buccal cavity short, narrow and hyaline; buccal lip convex and thus covering proximal half of adoral zone. Paroral membrane at base of buccal lip, begins at level of endoral membrane, composed of one to four, on average of three kinetids; endoral membrane slightly curved and about 6 μm long. Pharyngeal fibres of ordinary length and structure, extend vertically backwards (Figs 5A, E, 6A–C; Table 4).

Notes on ontogenesis: We found only a few stages similar to those reported by Berger (2011) and Foissner (2016). The oral primordium originates *de novo* left to the posterior cirri of frontoventral row 4 (Fig. 5H). Middle and late dividers show the formation of five frontoventral cirral anlagen each in proter and opisthe, the absence of transverse cirri, and the presence of caudal cirri one each produced at posterior end of dorsal kineties (Figs 5I, J, 6E).

Occurrence and ecology: As yet found only at type locality, i.e., in highly saline soil from the Meningie salt lake, Adelaide, Australia.

Species comparison: The genus *Cladotricha* contains three multinucleate species, namely, *C. edaphoni* Wilbert, 1995; *C. australis* Blatterer and Foissner, 1988; and *C.*

Table 4. Morphometric data on *Cladotricha similis* nov. spec.

Characteristics[a]	Mean	M	SD	SE	CV	Min	Max	n
Body, length	65.3	65.0	5.1	1.0	7.7	56.0	76.0	25
Body, width	20.3	20.0	2.4	0.5	11.6	16.0	25.0	25
Body length:width, ratio	3.3	3.2	0.4	0.1	11.3	2.7	4.3	25
Anterior body end to proximal end of adoral zone, distance	23.3	24.0	1.9	0.4	8.2	18.0	26.0	25
Anterior body end to proximal end of adoral zone, % of body length	35.8	35.7	3.2	0.6	8.9	30.5	43.1	25
Adoral membranelles, number	22.0	22.0	1.2	0.3	5.6	20.0	25.0	21
Adoral membranelles, width of longest base	3.9	4.0	–	–	–	3.0	4.0	15
Anterior body end to paroral membrane, distance	15.1	15.0	1.6	0.4	10.7	12.0	17.0	21
Paroral membrane, number of kinetids	2.8	3.0	0.8	0.2	27.8	1.0	4.0	21
Anterior body end to endoral membrane, distance	15.3	15.0	1.7	0.4	10.8	12.0	18.0	21
Endoral membrane, length	6.4	6.0	0.9	0.2	14.4	5.0	9.0	21
Anterior body end to anteriormost macronuclear nodule, distance	7.8	7.0	1.6	0.4	21.1	5.0	11.0	21
Posterior body end to posteriormost macronuclear nodule, distance	11.9	12.0	2.8	0.6	23.6	5.0	17.0	21
Macronuclear figure, length	45.3	45.0	4.1	0.9	9.1	40.0	52.0	21
Anteriormost macronuclear nodule, length	3.8	4.0	1.0	0.2	27.1	2.0	6.0	21
Anteriormost macronuclear nodule, width	2.6	2.0	0.7	0.2	26.3	2.0	4.0	21
Macronuclear nodules, number	18.3	17.0	2.8	0.6	15.2	15.0	25.0	21
Anterior body end to anteriormost micronucleus, distance	14.3	15.0	1.5	0.4	10.7	11.0	17.0	19
Anteriormost micronucleus, length	2.0	2.0	0.3	0.1	14.4	1.5	3.0	19
Anteriormost micronucleus, width	1.7	1.5	0.4	0.1	22.2	1.5	3.0	19
Micronuclei, number	2.8	3.0	0.8	0.2	26.9	2.0	4.0	19
Anterior body end to right marginal row, distance	11.8	12.0	1.6	0.3	13.4	10.0	15.0	21
Right marginal row, number of cirri	24.1	24.0	3.5	0.8	14.5	19.0	35.0	21
Anterior body end to left marginal row, distance	22.7	23.0	1.8	0.4	7.9	18.0	25.0	21
Left marginal row, number of cirri	19.6	19.0	3.3	0.7	16.7	15.0	28.0	21
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Anterior body end to buccal cirrus, distance	11.3	11.0	1.4	0.3	12.3	9.0	14.0	21
Buccal cirri, number	2.0	2.0	–	–	–	1.0	2.0	19
Frontoventral row 1, number of cirri	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Frontoventral row 2, number of cirri	3.0	3.0	–	–	–	2.0	3.0	21
Anterior body end to end of frontoventral row 3, distance	10.4	11.0	1.5	0.3	14.1	8.0	13.0	21
Frontoventral row 3, number of cirri	4.2	4.0	0.6	0.1	14.4	3.0	5.0	21
Anterior body end to end of frontoventral row 4, distance	34.8	35.0	4.0	0.9	11.5	27.0	41.0	21
Frontoventral row 4, number of cirri	12.4	12.0	1.9	0.4	15.0	10.0	16.0	21
Anterior body end to end of frontoventral row 5, distance	11.4	11.0	1.9	0.4	16.7	9.0	17.0	21
Frontoventral row 5, number of cirri	5.7	5.0	0.9	0.2	16.1	5.0	8.0	21
Dorsal kineties, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Anterior body end to dorsal kinety 1, distance	17.6	19.0	2.5	0.7	14.0	13.0	20.0	11
Dorsal kinety 1, number of bristles	10.6	11.0	1.4	0.4	13.5	8.0	12.0	11
Anterior body end to dorsal kinety 2, distance	7.6	7.0	1.8	0.5	23.2	6.0	12.0	11
Dorsal kinety 2, number of bristles	13.3	13.0	1.3	0.4	9.6	11.0	15.0	11
Anterior body end to dorsal kinety 3, distance	3.9	4.0	1.0	0.3	26.7	2.0	5.0	11
Dorsal kinety 3, number of bristles	15.6	16.0	1.4	0.4	8.8	13.0	18.0	11
Caudal cirri, number	3.1	3.0	–	–	–	3.0	4.0	15

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

halophila Wilbert, 1995. The new species resembles *C. edaphoni* (for a recent description, see Foissner, 2016) in body shape and ciliature but differs by the number of buccal cirri (2 vs. 1) and the presence (vs. absence) of cortical granules. *Cladotricha australis* and *C. halophila* can be separated from *C. similis* by the much higher number of cirri in frontoventral row five (18 and 28 vs. 6).

Erimophrya similis nov. spec. (Figs 7A–J, 8A–J; Table 5)

Diagnosis: Size in vivo about 95 μm × 30 μm; elongate obovate. Nuclear apparatus composed of two ellipsoid, narrowly spaced macronuclear nodules and two micronuclei. On average 15 fronto-ventral-transverse cirri, buccal cirrus

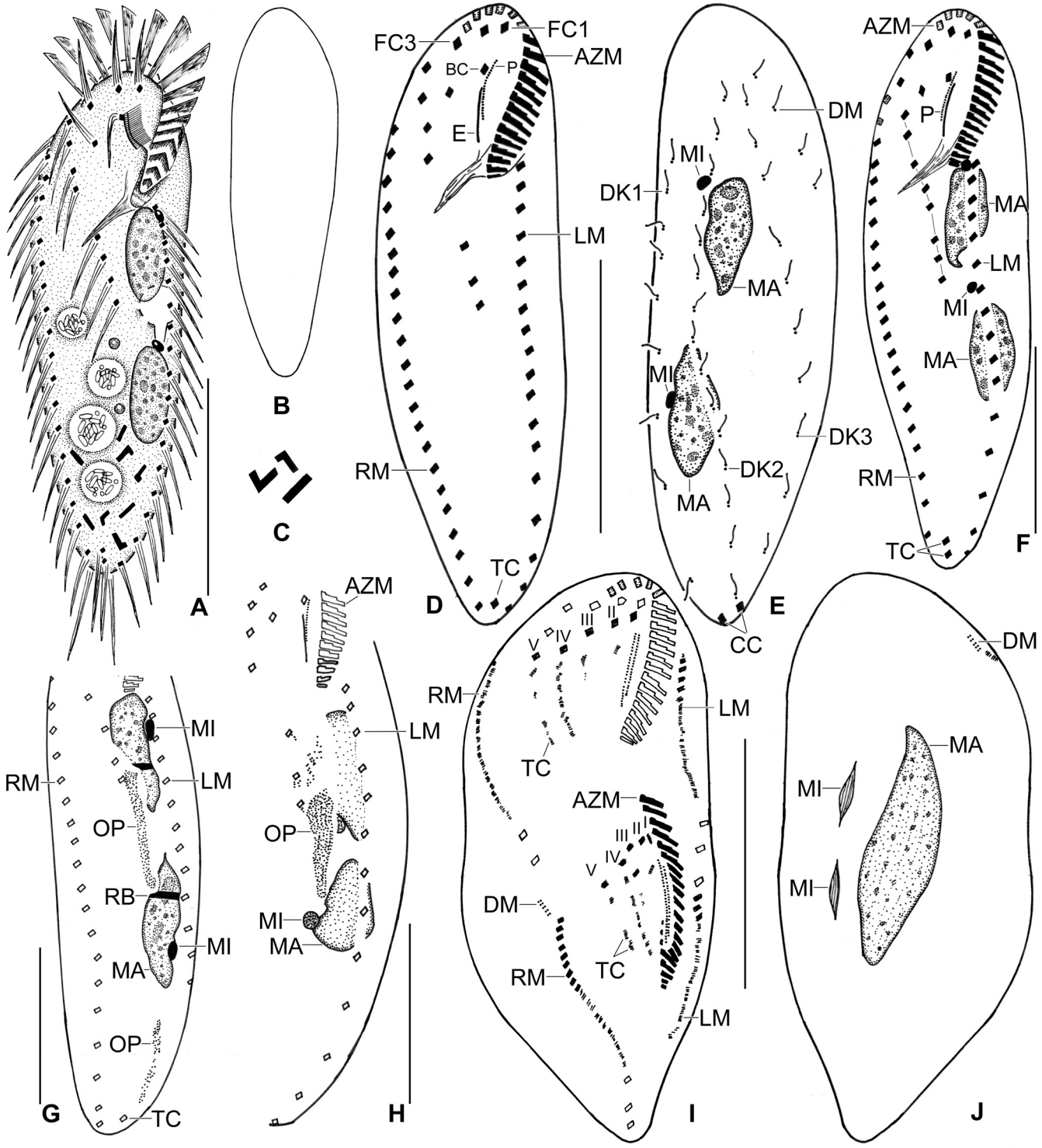

Fig. 7. A–J. *Erimophrya similis* nov. spec. from life (A–C) and after protargol impregnation (D–J). **A**: Ventral view of a representative specimen, length 95 μm. **B**: Dorsal view of another specimen. **C**: Cytoplasmic crystals. **D, E**: Ventral and dorsal view of holotype specimen, showing infraciliature and nuclear apparatus. **F**: A specimen with increased frontoventral and postoral cirri, those originating from anlage IV connected by a broken line. **G, H**: The oral primordium develops from anarchic fields of basal bodies left of the postoral cirri and the anterior transverse cirrus. **I, J**: Ventral and dorsal view of a mid-divider with macronuclear nodules fused to a lenticular mass. Cirri originate from five fronto-ventral-transverse anlagen; a dorsomarginal kinety originates close to the anterior end of the right marginal cirral row. AZM – adoral zone of membranelles, BC – buccal cirrus, CC – caudal cirri, DK1–3 – dorsal kineties, DM – dorsomarginal kinety, E – endoral membrane, FC1,3 – frontal cirri, LM – left marginal cirral row, MA – macronuclear nodules, MI – micronuclei, OP – oral primordium, P – paroral membrane, RB – replication band, RM – right marginal cirral row, TC – transverse cirri. Roman numerals denote cirral anlagen. Scale bars 30 μm (F–H) and 40 μm (A, D, E, I, J).

Table 5. Morphometric data on *Erimophrya similis* nov. spec.

Characteristics[a]	Mean	M	SD	SE	CV	Min	Max	n
Body, length	83.9	85.0	7.4	1.4	8.9	70.0	99.0	29
Body, width	25.0	25.0	3.0	0.6	12.1	18.0	31.0	29
Body length:width, ratio	3.4	3.3	0.4	0.1	12.5	2.8	5.0	29
Anterior body end to proximal end of adoral zone, distance	22.4	22.0	1.9	0.4	8.6	19.0	27.0	29
Anterior body end to proximal end of adoral zone, % of body length	26.9	27.3	2.7	0.5	10.2	22.2	32.9	29
Anterior body end to distal end of adoral zone, % of body length	5.1	4.9	1.4	0.3	27.1	3.1	9.1	19
DE-value[b]	0.2	0.2	0.0	0.0	25.0	0.1	0.3	19
Adoral membranelles, number	18.4	19.0	1.4	0.3	7.6	15.0	20.0	21
Adoral membranelles, width of longest base	4.9	5.0	0.4	0.1	7.4	4.0	5.5	21
Anterior body end to paroral membrane, distance	8.5	8.0	1.4	0.3	16.4	6.0	12.0	21
Paroral membrane, length	7.8	8.0	1.4	0.3	17.7	5.0	10.0	21
Anterior body end to endoral membrane, distance	10.4	11.0	1.3	0.3	12.4	8.0	13.0	21
Anterior body end to anterior macronuclear nodule, distance	22.8	22.0	2.9	0.6	12.7	18.0	27.0	21
Macronuclear nodules, distance in between	7.7	7.0	2.2	0.5	29.3	5.0	11.0	21
Macronuclear figure, length	40.1	38.0	4.2	0.9	10.4	34.0	47.0	21
Anterior macronuclear nodule, length	15.7	16.0	2.4	0.5	15.0	10.0	20.0	21
Anterior macronuclear nodule, width	7.1	7.0	0.9	0.2	12.7	6.0	9.0	21
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Anterior body end to anterior micronucleus, distance	23.7	24.0	3.4	0.8	14.3	17.0	29.0	19
Anteriormost micronucleus, length	2.4	2.5	0.5	0.1	20.9	1.5	3.5	19
Anteriormost micronucleus, width	1.5	1.5	–	–	–	1.0	2.0	19
Micronuclei, number	2.1	2.0	0.4	0.1	19.7	1.0	3.0	19
Anterior body end to right marginal row, distance	14.6	14.0	2.4	0.5	16.1	11.0	19.0	21
Posterior body end to right marginal row, distance	3.5	3.0	1.0	0.2	29.2	2.0	6.0	21
Right marginal row, number of cirri	19.7	19.0	1.6	0.3	7.9	17.0	23.0	21
Anterior body end to left marginal row, distance	22.1	22.0	1.9	0.4	8.4	18.0	26.0	21
Posterior body end to left marginal row, distance	2.1	2.0	1.1	0.2	52.1	1.0	5.0	21
Left marginal row, number of cirri	16.3	17.0	1.5	0.3	8.9	14.0	18.0	21
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Anterior body end to buccal cirrus, distance	8.6	9.0	1.2	0.3	14.0	6.0	11.0	21
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Frontoventral cirri, number	5.0	5.0	0.3	0.1	6.3	4.0	6.0	21
Anterior body end to posteriormost postoral cirrus, distance	39.2	38.0	4.9	1.1	12.6	30.0	52.0	21
Postoral cirri, number	3.8	4.0	0.9	0.2	23.6	3.0	6.0	21
Transverse cirri, number	1.8	2.0	0.5	0.1	30.6	1.0	3.0	21
Dorsal kineties, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	21
Anterior body end to dorsal kinety 1, distance	21.1	21.0	2.7	0.6	13.0	16.0	28.0	21
Dorsal kinety 1, number of bristles	8.3	8.0	0.8	0.2	9.5	7.0	9.0	21
Anterior body end to dorsal kinety 2, distance	13.1	13.0	2.5	0.5	18.8	9.0	18.0	21
Dorsal kinety 2, number of bristles	12.5	12.0	1.3	0.3	10.6	10.0	15.0	21
Anterior body end to dorsal kinety 3, distance	11.2	11.0	2.2	0.5	19.7	8.0	16.0	21
Dorsal kinety 3, number of bristles	10.0	10.0	1.0	0.2	10.3	8.0	12.0	21
Anterior body end to dorsal kinety 4, distance	9.1	9.0	1.7	0.4	18.7	7.0	13.0	21
Dorsal kinety 4, number of bristles	4.3	4.0	0.7	0.1	15.2	3.0	6.0	21
Caudal cirri, number	2.1	2.0	0.3	0.1	14.4	2.0	3.0	21

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

[b] *Distal end* of adoral zone (Berger, 2006).

near anterior end of paroral membrane. Left marginal row on average composed of 16 cirri, right row of 20. Adoral zone occupies about 27% of body length, on average composed of 18 membranelles. Four dorsal kineties. Usually two caudal cirri slightly right of body's midline. Ontogenesis in *Erimophrya* pattern.

Type locality: Non-saline soil from the surroundings of the town of Darwin, Australia, 12°26′S 130°50′E.

Material deposited: One holotype and five paratype slides with protargol-impregnated specimens have been deposited in the Biologiezentrum of the Oberösterreichische Landesmuseum in Linz (LI), reg. no. 2015, 791–796. Relevant

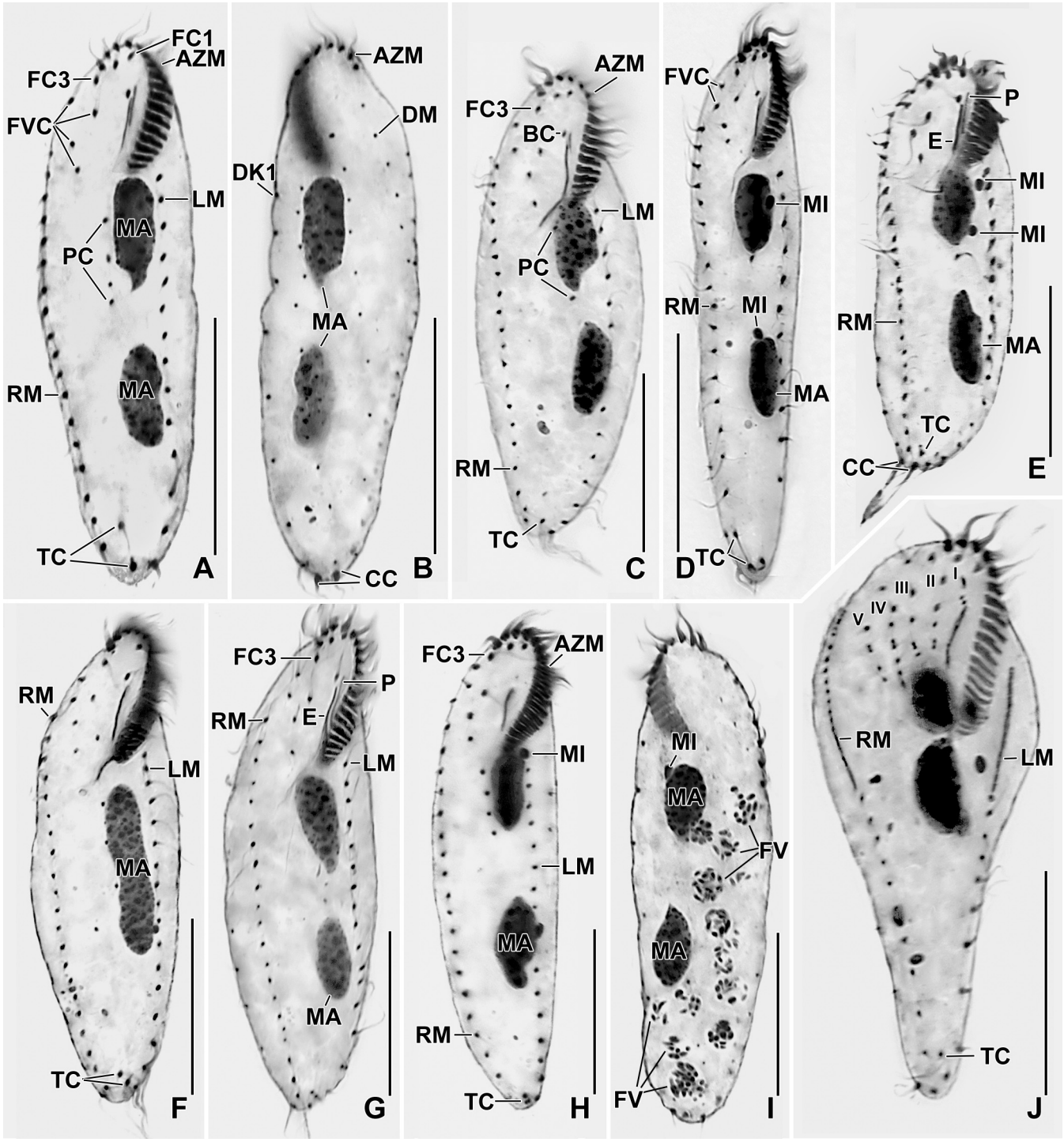

Fig. 8. A–J. *Erimophrya similis* nov. spec. after protargol impregnation. **A, B**: Ventral and dorsal view of an ordinary specimen, showing infraciliature and nuclear apparatus. **C, G**: Ventral view of elongate ellipsoid specimens. **D, E**: A very slender specimen (length:width ratio 5:1) and a rectangular specimen. **F**: A specimen with not separated macronuclear nodules. **H**: A specimen without buccal cirrus. **I**: A specimen studded with food vacuoles containing bacterial spores. **J**: A reorganiser, showing five fronto-ventral-transverse cirral anlagen. AZM – adoral zone of membranelles, BC – buccal cirrus, CC – caudal cirri, DK1 – dorsal kinety 1, DM – dorsomarginal kinety, E – endoral membrane, FC1,3 – frontal cirri, FV – food vacuoles, FVC – frontoventral cirri, LM – left marginal cirral row, MA – macronuclear nodules, MI – micronuclei, P – paroral membrane, PC – postoral cirri, RM – right marginal cirral row, TC – transverse cirri. Roman numerals denote cirral anlagen. Scale bars 30 μm (C, E–J) and 40 μm (A, B, D).

specimens have been marked with black ink circles on the coverslip.

Etymology: The Latin adjective *similis* (similar) refers to the similarity with *Erimophrya glatzeli*.

Description: *Erimophrya similis* is rather variable, even in important features, e.g., the distance between the macronuclear nodules (CV ~ 29%), the number of postoral cirri (CV ~ 24%), and the number of transverse cirri (CV ~ 31%).

Size in vivo 70–100 μm × 20–40 μm, usually about 95 μm × 30 μm, as calculated from some in vivo measurements and the morphometric data in Table 5 adding 15% preparation shrinkage (Foissner, 2014); length:width ratio rather variable, that is, 2.5–5.0:1, on average 3.3:1 both in vivo and in protargol preparations (Table 5). Body in vivo elongate obovate, rarely elongate ellipsoid, obovate shape usually insufficiently preserved in protargol preparations (Figs 7A, B, D, E, 8A–I; Table 5). Macronuclear nodules in middle body third left of midline, broadly ellipsoid to elongate ellipsoid, on average rather close together and sometimes connected by a fine strand (7 out of 30 specimens analysed), very rarely (in 2 out of 100 specimens) a single, oblong nodule (Fig. 8E); contain many globular nucleoli of ordinary size. On average two globular to broadly ellipsoid micronuclei, one attached to each macronuclear nodule in variable position (Figs 7A, E, 8A–I; Table 5). Contractile vacuole in mid-body at left cell margin, with lacunar collecting canals (Fig. 7A). Cortex flexible, specific cortical granules absent. Cytoplasm colourless, with few to many crystals 2–5 μm long and usually concentrated in posterior third (Fig. 7A, C). Food vacuoles scattered throughout body, in vivo up to 10 μm across, contain bacterial spores (Figs 7A, 8I). Swims and creeps moderately fast.

Cirral pattern and number of cirri of usual variability, except for the varying number of postoral and transverse cirri (Figs 7A, D, F, 8A, C, G, H; Table 5). On average 15 fronto-ventral-transverse cirri. Three frontal cirri in vivo about 12 μm long, right cirrus posterior of distal end of adoral zone, middle cirrus anterior of buccal cirrus, left cirrus anterior of distal end of paroral membrane. Buccal cirrus right of anterior end of paroral membrane. Five frontoventral cirri, four form an oblique row, cirrus (III/2) usually slightly posterior to level of buccal cirrus. Four widely spaced (when compared with *Urosomoida* spp.) postoral cirri about 12 μm long in vivo, form a row distinctly posterior of buccal vertex. Usually two transverse cirri between last cirri of marginal rows, that is, in midline near posterior body end, about 15 μm long in vivo and thus distinctly projecting from body proper. Marginal cirri in two non-confluent rows, end slightly subterminally, about 12 μm long in vivo; left row composed of an average of 16 cirri, right of 20, intracirral distances gradually increase from anterior to posterior (Figs 7A, D, F, 8A, C, G, H; Table 5).

Dorsal bristles 2.5–3 μm long in vivo and in protargol preparations, arranged in four rows (Figs 7E, 8B, E; Table 5). Rows 1–3 almost bipolar, bristle distance gradually increases from anterior to posterior; row 4 dorsomarginal, extends to second quarter of cell, composed of three to six bristles. Two caudal cirri at right posterior margin of cell, rather stiff, about 17 μm long in vivo.

Adoral zone occupies about 27% of body length, on average composed of 18 ordinary membranelles with up to 12 μm long cilia, bases of largest membranelles on average 5 μm wide in vivo and in protargol preparations (Figs 7A, D, F, 8A, C–H; Table 5). Buccal cavity flat and moderately wide; buccal lip angularly projecting and thus prominent partially covering proximal third of adoral zone, bears paroral membrane. Undulating membranes slightly curved and side by side, paroral begins about 2 μm in front of endoral at level of buccal cirrus. Pharyngeal fibres of ordinary length and structure, extend obliquely backwards (Figs 7A, 8A, C, D, E, G; Table 5).

Notes on ontogenesis: The oral primordium originates close to the anterior transverse cirrus and the postoral cirri (Fig. 7G, H). A late divider and a reorganiser show the formation of five fronto-ventral-transverse cirral anlagen and a dorsomarginal kinety close to the anterior end of the right marginal row (Figs 7I, J, 8J).

Occurrence and ecology: As yet found only at type locality, i.e., in non-saline soil with pH 6.7 from the sea-side of the town of Darwin, Australia.

Species comparison: The new species resembles *E. glatzeli* Foissner et al., 2002 in body shape but differs by the number of frontoventral (5 vs. 4), postoral (4 vs. invariably 2) and transverse cirri (2 vs. 1) as well as by the distance between the macronuclear nodules (7.7 μm vs. 14 μm); further it is smaller and stouter (84 μm × 25 μm, 3.4:1 vs. 103 μm × 22 μm, 4.8:1). *Erimophrya similis* can be separated from *E. arenicola* Foissner et al., 2002 by the number of postoral cirri (4 vs. invariably 1) and the number of dorsal kineties (4 vs. 3). *Erimophrya similis* differs from *E. monostyla* Foissner et al., 2008b mainly by the number of postoral cirri (4 vs. invariably 1) and the higher number of bristles in the dorsal kineties. *Erimophrya sylvatica* Foissner et al., 2005 can be distinguished from *E. similis* by the more slender body (7.1:1 vs. 3.4:1), the number of postoral cirri (invariably 2 vs. 4), and the number of dorsal kineties (3 vs. 4). *Erimophrya similis* differs from *E. quadrinucleata* Foissner et al., 2005 by the number of macronuclear nodules (2 vs. 4).

Heterogonostomum nov. gen.

Diagnosis: Gonostomatidae with a reduced number of pretransverse and transverse cirri. One right and one left marginal cirral row. Fronto-ventral-transverse cirri originate from only five anlagen because anlage IV is absent; anlagen II, III, V and VI of proter and opisthe originate from primary primordia. Three dorsal kineties each associated with a caudal cirrus.

Etymology: The genus name is a composite of the Greek adjective *heteros* (different, deviating) and the genus group name *Gonostomum*.

Type species: *Heterogonostomum salinarum* nov. spec.

Species included: *Heterogonostomum salinarum* nov. spec.

Heterogonostomum salinarum nov. spec. (Figs 9A–I, 10A–C; Table 6)

Diagnosis: Size about 55 μm × 20 μm in protargol preparations; elongate ellipsoid. Nuclear apparatus on average composed of four macronuclear nodules in two pairs; two micronuclei. Cortical granules loosely spaced, about 0.5 μm × 0.3 μm in size. On average 13 fronto-ventral-transverse cirri including three frontal, one buccal, two frontoterminal, three frontoventral, two pretransverse and two transverse cirri. Left marginal row on average composed of 15 cirri, right of 25. Adoral zone extends about 42% of body length, on average composed of 24 membranelles. Buccal cavity small; paroral membrane usually composed of seven kinetids.

Type locality: Highly saline soil and root carpet from a grass-covered hill in the Meningie salt lake, Adelaide, Australia, 35°41′S 139°20′E.

Material deposited: One holotype and three paratype slides with protargol-impregnated specimens have been deposited in the Biologiezentrum of the Oberösterreichische Landesmuseum in Linz (LI), reg. no. 2015, 828–831. Relevant specimens have been marked with black ink circles on the coverslip.

Etymology: *Salinarum* (living in saline environments) is a noun in plural genetive and thus does not change the gender when combined with another genus.

Description: Unfortunately, we misidentified this species in vivo as a described *Gonostomum*, and thus we did not study it in detail. Accordingly, all data are from protargol-impregnated specimens. *Heterogonostomum salinarum* is moderately variable, most variation coefficients being smaller than 15%, except of half of distances and the nuclear apparatus.

Size 45–67 μm × 16–24 μm, usually about 55 μm × 20 μm, strong shrinkage (up to 40%) is likely because of the high salinity which makes fixation difficult (Fig. 9C–G; Table 6). Body usually elongate ellipsoid (Fig. 9A, C–G). Number and arrangement of macronuclear nodules highly variable; usually four macronuclear nodules forming a pair each anterior and posterior of mid-body; individual nodules globular to ellipsoid or irregular, contain some globular nucleoli of ordinary size (Fig. 9C–F; Table 6). On average two globular to ellipsoid micronuclei scattered in cytoplasm or attached to macronuclear nodules, about 2.7 μm × 1.9 μm in size (Fig. 9C–F; Table 6). Cortical granules about 0.5 μm × 0.3 μm in size, loosely arranged, impregnated sometimes with the protargol method used (Fig. 9A, B). Cytoplasm with some lipid droplets and food vacuoles containing flagellates, bacteria and their spores.

Cirral pattern and number surprisingly constant, i.e., three frontal cirri in gonostomatid pattern. Left frontal cirrus distinctly subapical, usually slightly increased in size; buccal cirrus slightly anterior of paroral membrane; five frontoventral cirri including two frontoterminal cirri near anterior end of right marginal row; two tiny pretransverse cirri and two transverse cirri (Fig. 9F; Table 6). Right marginal row commences subapically and extends to near posterior body end, composed of an average of 25 cirri; left row of about 15 cirri (Fig. 9F; Table 6).

Dorsal bristles 2.5–4 μm long, arranged in three rows each associated with a caudal cirrus. Row 1 commences at level of buccal vertex, row 2 subapically, and row 3 begins near anterior body end; all rows end subterminally (Fig. 9G; Table 6).

Oral apparatus in *Gonostomum* pattern (Berger, 1999), i.e., adoral zone flat and following anterior and left body margin before bending abruptly into cell at about 42% of body length, on average composed of 24 ordinary membranelles, bases of largest membranelles about 3.5 μm wide (Fig. 9F; Table 6). Buccal cavity of ordinary size, inconspicuous. Paroral membrane begins slightly anterior of endoral membrane, composed of five to nine, on average of seven kinetids; endoral membrane slightly curved and about 7 μm long. Pharyngeal fibres of ordinary length and structure, impregnate rarely, extend obliquely backwards (Fig. 9F; Table 6).

Notes on ontogenesis: The oral primordium originates *de novo* posterior to the buccal vertex (Fig. 9H). Early and mid-dividers show the formation of primary primordia and of only five frontal-ventral-transverse cirral anlagen each in proter and opisthe (Figs 9I, 10A, B). Pretransverse and transverse cirri originate from the posterior portion of the two rightmost anlagen indicating that anlage IV is lacking (Fig. 10B). Late dividers show the formation of three dorsal kineties and the presence of caudal cirri one each produced at the posterior end of the kineties (Fig. 10C). The macronuclear nodules fuse to a single mass in mid-dividers; the micronuclei undergo typical mitotic division (Fig. 10A, B).

Occurrence and ecology: As yet found only at type locality, i.e., in highly saline soil from a salt lake in Australia.

Generic and species comparison: The family Gonostomatidae Small and Lynn, 1985 includes seven genera: *Gonostomum* Sterki, 1878; *Paragonostomum* Foissner et al., 2002; *Wallackia* Foissner, 1976; *Cladotricha* Gaievskaïa, 1925; *Neowallackia* Berger, 2011; *Paracladotricha* Shao et al., 2014a; and *Cotterillia* Foissner and Stoeck, 2011. With the exception of *Gonostomum*, all genera lack transverse cirri and thus can be easily separated from the new genus. *Heterogonostomum* differs from *Gonostomum* by the number of fronto-ventral-transverse cirral anlagen (5 vs. 6).

Heterogonostomum salinarum highly resembles *Gonostomum albicarpathicum* Vd'ačný and Tirjaková, 2006 in body shape and nuclear apparatus but differs by the strongly reduced number of frontoventral cirri (9 vs. 16) and by the higher number of cirri in the right marginal row (25 vs. 16).

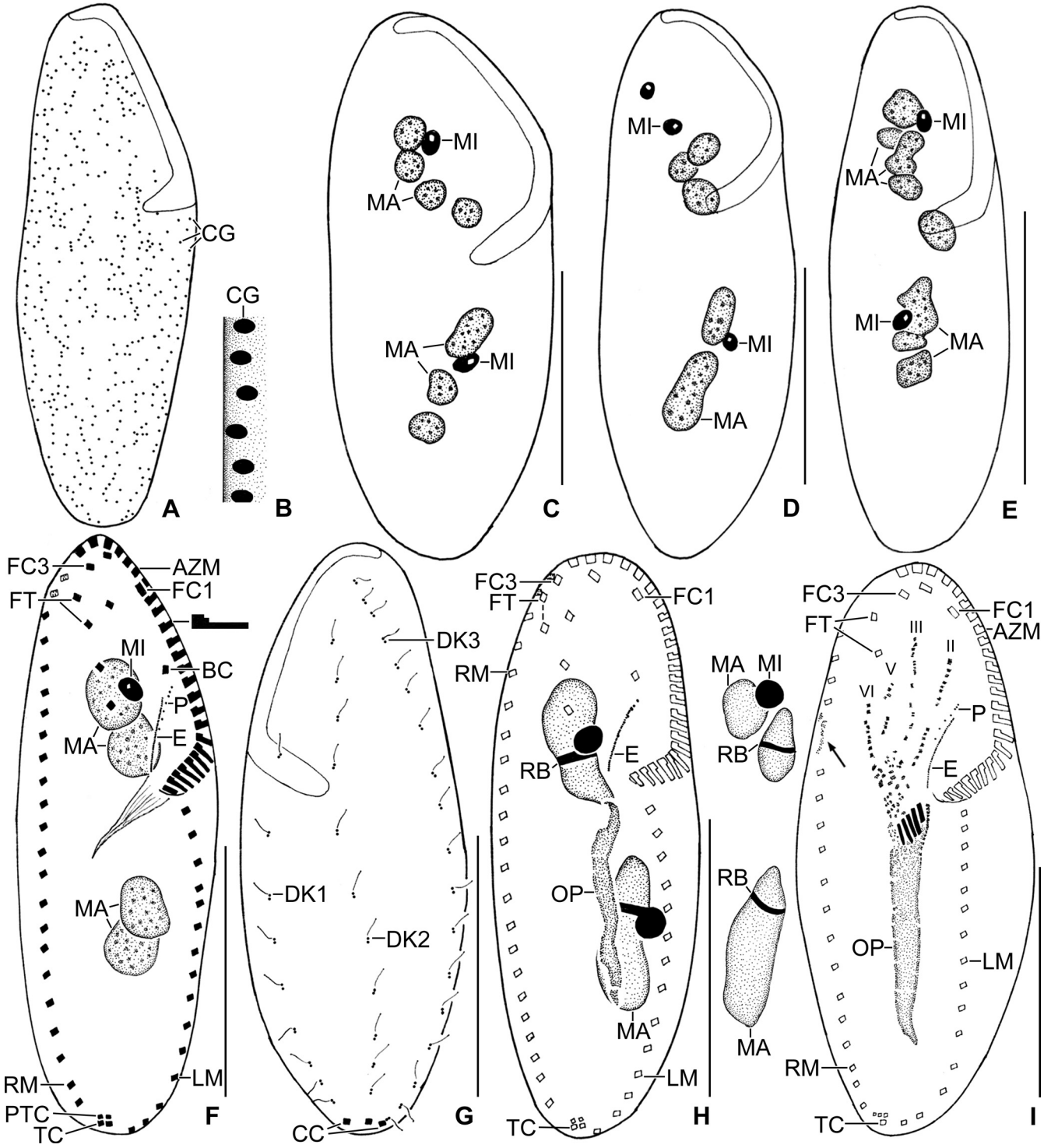

Fig. 9. A–I. *Heterogonostomum salinarum* nov. gen., nov. spec., ventral (A, C–F, H, I) and dorsal (G) views after protargol impregnation. **A**: Cortical granulation. **B**: The cortical granules are slightly ellipsoid and about 0.5 μm × 0.3 μm in size. **C–E**: Variability of body outline and nuclear apparatus. **F**: Ventral view of holotype specimen, showing the infraciliature and nuclear apparatus. **G**: Dorsal view of a paratype specimen, showing the three dorsal kineties each associated with a caudal cirrus. **H**: The oral primordium develops *de novo* posterior to the buccal vertex. **I**: Ventral view of an early divider, showing four cirral anlagen formed by primary primordia (Roman numerals). The arrow marks an anlage in the right marginal cirral row of the proter. The macronuclear nodules show the replication band. AZM – adoral zone of membranelles, BC – buccal cirrus, CC – caudal cirri, CG – cortical granules, DK1–3 – dorsal kineties, E – endoral membrane, FC1,3 – frontal cirri, FT – frontoterminal cirri, LM – left marginal cirral row, MA – macronuclear nodules, MI – micronuclei, OP – oral primordium, P – paroral membrane, PTC – pretransverse cirri, RB – replication band, RM – right marginal cirral row, TC – transverse cirri, II, III, V, VI – cirral anlagen. Scale bars 25 μm.

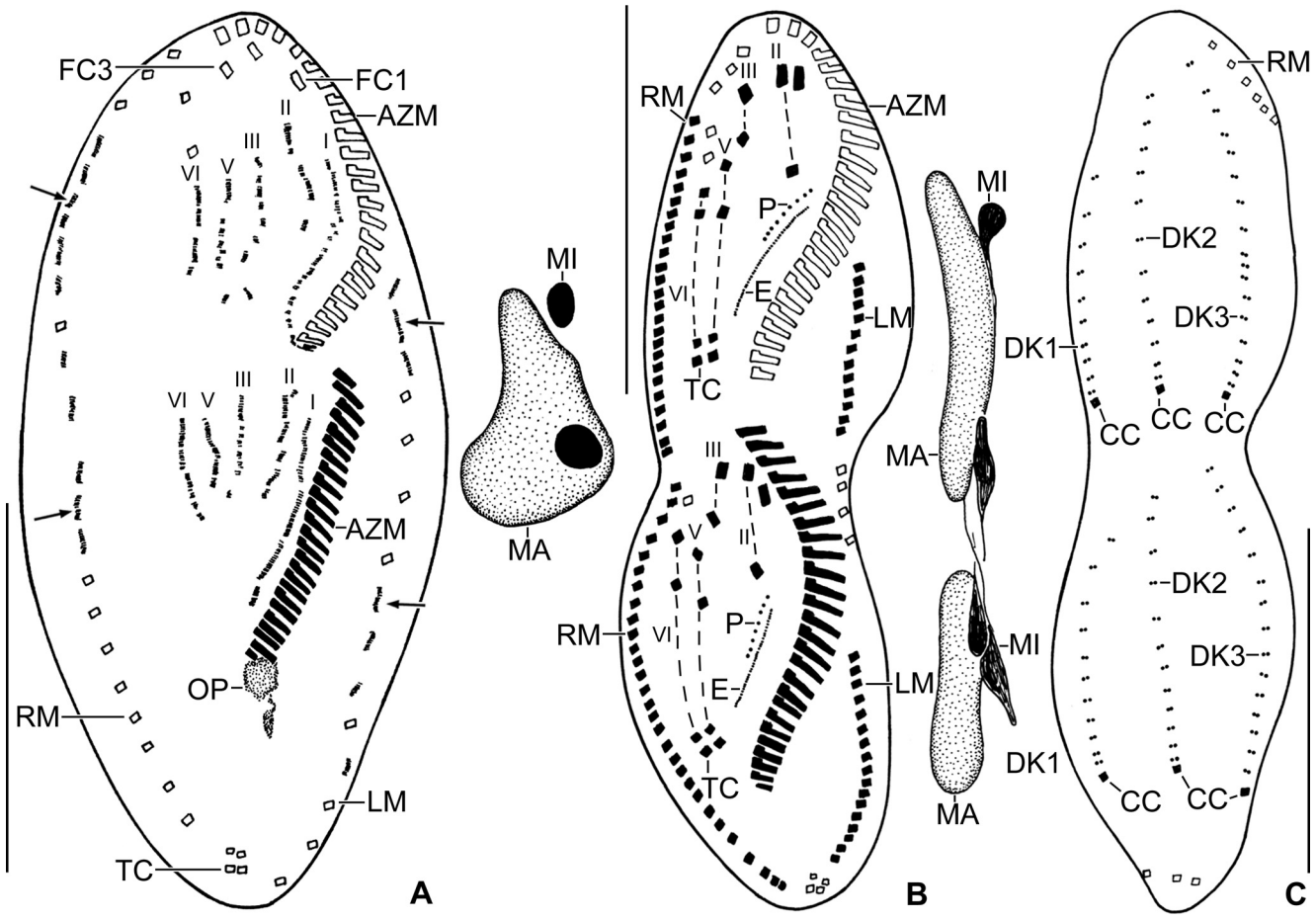

Fig. 10. A–C. *Heterogonostomum salinarum* nov. gen., nov. spec. after protargol impregnation. Parental cirri that did not form anlagen shown by contour. **A**: Ventral view of a mid-divider with fused macronuclear nodules. It shows five frontoventral cirral anlagen (Roman numerals) and two anlagen each (arrows) for the new marginal cirri of proter and opisthe. **B**: Ventral view of a late divider, showing the migration of cirri (connecting lines) to their specific sites. The macronucleus undergoes the first division. Parental cirri which were not involved in primordia formation get resorbed. **C**: Dorsal view of a late divider, showing the formation of three dorsal kineties each associated with a caudal cirrus in proter and opisthe. AZM – adoral zone of membranelles, CC – caudal cirri, DK1–3 – dorsal kineties, E – endoral membrane, FC1,3 – frontal cirri, LM – left marginal cirral row, MA – macronuclear nodules or mass, MI – micronuclei, OP – oral primordium, P – paroral membrane, RM – right marginal cirral row, TC – transverse cirri, I–III, V, VI – cirral anlagen. Scale bars 25 μm.

Table 6. Morphometric data on *Heterogonostomum salinarum* nov. gen., nov. spec.

Characteristics[a]	Mean	M	SD	SE	CV	Min	Max	n
Body, length	55.7	55.0	5.1	1.1	9.2	45.0	67.0	23
Body, width	20.3	20.0	2.7	0.6	13.4	16.0	24.0	23
Body length:width, ratio	2.8	2.7	0.4	0.1	14.9	2.2	3.9	23
Anterior body end to proximal end of adoral zone, distance	23.4	23.0	1.8	0.4	7.6	20.0	27.0	23
Body length:length of adoral zone, ratio	2.4	2.4	0.2	0.0	7.6	2.1	2.8	23
Anterior body end to proximal end of adoral zone, % of body length	42.0	42.1	3.0	0.6	7.1	35.8	47.9	23
Adoral membranelles, total number	24.3	25.0	1.4	0.3	5.8	22.0	27.0	21
Adoral membranelles, width of longest base	3.4	3.5	–	–	–	3.0	4.0	17
Anterior body end to paroral membrane, distance	13.5	13.0	1.6	0.4	12.1	11.0	17.0	21
Paroral membrane, length	4.7	4.5	0.7	0.2	14.3	4.0	7.0	19
Paroral membrane, number of kinetids	6.8	7.0	1.3	0.3	19.8	5.0	9.0	21
Anterior body end to endoral membrane, distance	14.6	15.0	1.4	0.3	9.4	12.0	17.0	21
Endoral membrane, length	7.5	7.0	0.7	0.1	9.1	6.0	9.0	21
Anterior body end to anteriormost macronuclear nodule, distance	11.2	11.0	2.3	0.5	20.9	6.0	16.0	21

Table 6. (*Continued*)

Characteristics[a]	Mean	M	SD	SE	CV	Min	Max	n
Posterior body end to posteriormost macronuclear nodule, distance	13.5	14.0	2.5	0.5	18.4	8.0	17.0	21
Macronuclear figure, length	30.9	31.0	3.1	0.7	9.9	25.0	35.0	21
Macronuclear nodule pairs, distance in between	6.6	7.0	3.5	0.8	52.4	2.0	14.0	21
Anteriormost macronuclear nodule, length	7.2	7.0	1.3	0.3	17.4	5.0	10.0	21
Anteriormost macronuclear nodule, width	4.2	4.0	0.8	0.2	18.3	3.0	6.0	21
Macronuclear nodules, number	4.3	4.0	1.1	0.2	25.7	2.0	8.0	21
Anteriormost micronucleus, length	2.7	2.5	–	–	–	2.0	3.5	21
Anteriormost micronucleus, width	1.9	2.0	–	–	–	1.0	2.5	21
Micronuclei, number	2.0	2.0	0.4	0.1	19.7	1.0	3.0	21
Anterior body end to right marginal row, distance	3.0	3.0	0.8	0.2	27.3	2.0	4.0	21
Posterior body end to right marginal row, distance	3.3	3.0	1.2	0.3	37.5	1.0	5.0	15
Right marginal row, number of cirri	25.1	25.0	1.9	0.4	7.8	22.0	29.0	21
Anterior body end to left marginal row, distance	24.1	24.0	1.9	0.4	8.0	22.0	28.0	21
Posterior body end to left marginal row, distance	0.9	1.0	0.6	0.1	60.3	0.0	2.0	15
Left marginal row, number of cirri	15.0	15.0	1.3	0.3	8.8	11.0	17.0	21
Anterior body end to first frontal cirrus, distance	4.7	5.0	0.7	0.2	14.3	3.0	6.0	19
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Anterior body end to buccal cirrus, distance	12.0	12.0	1.4	0.3	11.7	9.0	15.0	21
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Anterior body end to last frontoventral cirrus, distance	16.0	16.0	1.9	0.4	11.6	13.0	21.0	21
Frontoventral cirri, number	3.0	3.0	–	–	–	3.0	4.0	21
Anterior body end to first frontoterminal cirrus, distance	5.2	5.0	0.8	0.2	15.5	4.0	7.0	19
Frontoterminal cirri, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Pretransverse cirri, number	2.0	2.0	0.4	0.1	19.7	1.0	3.0	21
Posterior body end to transverse cirri, distance	1.6	1.0	1.0	0.2	60.5	0.5	4.0	15
Transverse cirri, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Dorsal kineties, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
Anterior body end to dorsal kinety 1, distance	19.3	20.0	2.4	0.6	12.2	15.0	23.0	15
Dorsal kinety 1, number of bristles	11.0	11.0	1.1	0.3	10.3	9.0	13.0	15
Anterior body end to dorsal kinety 2, distance	9.4	9.0	2.1	0.5	22.2	7.0	14.0	15
Dorsal kinety 2, number of bristles	13.2	13.0	1.1	0.3	8.2	12.0	15.0	15
Anterior body end to dorsal kinety 3, distance	3.8	4.0	1.1	0.3	30.5	2.0	6.0	15
Dorsal kinety 3, number of bristles	16.9	17.0	1.2	0.3	7.0	15.0	19.0	15
Caudal cirri, number	2.7	3.0	–	–	–	2.0	3.0	15

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

Pattersoniella Foissner, 1987a

Improved diagnosis: Rigid oxytrichids with three frontal and one buccal cirrus or with distinctly increased fronto-ventral cirri forming a bicorona. Two pretransverse and more than five transverse cirri. One right and one left row of marginal cirri. Undulating membranes in *Australocirrus* pattern; paroral membrane complete or some basal bodies reduced anteriorly while their fibrillar associates still present. Number of fronto-ventral-transverse cirral streaks distinctly increased (7–11 vs. 6 in "typical" oxytrichids). More than six dorsal kineties due to multiple fragmentation of dorsal kinety 3 and two dorsomarginal rows; some parental kinetids retained after division. Caudal cirri present.

Pattersoniella (*Pattersoniella*) Foissner, 1987a nov. stat.

Diagnosis: *Pattersoniella* with an increased number of fronto-ventral cirri forming a bicorona. Paroral membrane complete.

Type species: Pattersoniella (Pattersoniella) vitiphila Foissner, 1987a.

Pattersoniella (Pattersoniellides) nov. subgen.

Diagnosis: *Pattersoniella* with three frontal and one buccal cirrus arranged in *Oxytricha* pattern. Paroral basal bodies reduced anteriorly while their fibrillary associates still present.

Type species: *Pattersoniella* (*Pattersoniellides*) *australiensis* nov. spec.

Etymology: Composite of the generic name *Pattersoniella* and the Greek suffix *ides* (similar), meaning similar to *Pattersoniella*. Masculine gender.

Pattersoniella (*Pattersoniellides*) *australiensis* nov. spec. (Figs 11A–H, 12A–F, 13A–F, 14A–C, 15A–C; Table 7)

Diagnosis: Size in vivo about 200 μm × 90 μm; ellipsoid to elongate ellipsoid. Nuclear apparatus on average composed of eight broadly ellipsoid, narrowly spaced macronuclear nodules, forming a row in midline of body; seven micronuclei. Several contractile vacuoles along left body margin. On average 21 fronto-ventral-transverse cirri. Left marginal row on average composed of 27 cirri, right of 28. Adoral zone occupies about 45% of body length, on average composed of 49 membranelles. Eight to twelve dorsal kineties; usually three narrowly spaced, inconspicuous caudal cirri in body's midline. Resting cyst with wrinkled surface and fused macronuclear nodules. Ontogenesis in *Pattersoniella* pattern.

Type locality: Litter and soil from the rain forest in the centre of Green Island near to the town of Cairns, Australia, 16°45′32″S 145°58′26″E.

Material deposited: One holotype and five paratype slides with protargol-impregnated specimens have been deposited in the Biologiezentrum of the Oberösterreichische Landesmuseum in Linz (LI), reg. no. 2015, 797–802. Relevant specimens have been marked with black ink circles on the coverslip.

Etymology: The species group name *australiensis* refers to the country the species was discovered, i.e., Australia.

Description: Most important features of *P.* (*Pattersoniellides*) *australiensis* have an ordinary variability (CV ≤15%; Table 7), including the number of fronto-ventral-transverse cirri (Table 7). Of those having higher coefficients of variation, the number of postoral cirri (CV ∼ 26%) should be mentioned.

Size in vivo 170–230 μm × 60–115 μm, usually about 200 μm × 90 μm, as calculated from some in vivo measurements and the morphometric data in Table 7 adding 15% preparation shrinkage (Foissner, 2014); length:width ratio on average 2.2:1 in protargol preparations. Body ellipsoid to elongate ellipsoid, both ends broadly rounded; dorsoventrally flattened about 2:1 (Figs 11A, C, G, H, 12A–C; Table 7). Nuclear apparatus in or slightly left of body's midline, on average composed of eight macronuclear nodules and seven micronuclei (Figs 11A, H, 12A–C; Table 7). Macronuclear nodules globular to broadly ellipsoid, one after the other, producing a straight or slightly curved row on average 114 μm long in protargol preparations; contain many granular nucleoli. Micronuclei attached to or near to macronuclear nodules, globular to broadly ellipsoid, on average 3.0 μm × 2.4 μm in protargol preparations. Some contractile vacuoles near left cell margin, connected by canals during diastole, each functioning independently (Fig. 11D). Cortex rigid, specific cortical granules absent. Cytoplasm colourless, with rather many ordinary crystals 1–7 μm in size (Fig. 11A, B). Food vacuoles scattered throughout body, in vivo up to 40 μm across, contain ciliates (*Colpoda* sp. and *Vorticella* sp.) and flagellates (Figs 11A, 12E). Swims and creeps rather rapidly.

Cirral pattern and number of cirri of usual variability, except for the more varying number of postoral cirri (Figs 11A, G, 12A, B; Table 7). On average 21 fronto-ventral-transverse cirri. Three enlarged frontal cirri, in vivo about 28 μm long, right cirrus left of distal adoral membranelle, middle cirrus anterior of buccal cirrus, left cirrus anterior of distal end of undulating membranes. Invariably one slightly thickened buccal cirrus about 9 μm posterior of distal end of paroral membrane in protargol preparations (further measurements also from preparations). On average six frontoventral cirri, four arranged in a hook-like pattern as in typical oxytrichids, posterior two cirri usually slightly anterior of proximal end of undulating membranes. On average three postoral cirri, last cirrus slightly posterior of mid-body, i.e., about 106 μm distant from anterior end. Two slightly obliquely arranged pretransverse cirri, anterior cirrus on average 46 μm distant from posterior body end. On average six transverse cirri arranged in a hooked pattern, about 30 μm long in vivo, distinctly subterminal and thus projecting only slightly from body proper. Marginal cirri in vivo about 23 μm long their length gradually decreases posteriorly, arranged in two almost confluent rows extending to posterior body margin,; left row composed of 27 cirri on average, right of 28 (Figs 11A, G, 12A, B; Table 7).

On average 10 dorsal kineties with bristles 3–5 μm long in protargol preparations (Figs 11H, 12C, E; Table 7): kineties 1 and 2 bipolar; 3–8 slightly to distinctly shortened anteriorly; 9 and 10 slightly shortened anteriorly and posteriorly; parental dorsal kineties partially retained (Fig. 12C). Three narrowly spaced caudal cirri at posterior margin of cell, indistinctly separate from marginal rows.

Adoral zone very conspicuous because extending over 45% of body length, commences far subapically on right margin of cell (about 14% of body length, DE-value 0.3), on average composed of 49 ordinary membranelles with up to 20 μm long cilia, bases of largest membranelles on average 20 μm wide in vivo and 15 μm in protargol preparations (Figs 11A, G, 12A, B; Table 7). Buccal cavity large and deep, wall supported by thick fibres originating from paroral kinetids (Figs 11E, G, 12A, B, D). Buccal lip narrow, covers proximal membranelles. Undulating membranes in or slightly right of body's midline, moderately curved, intersect optically between first and last third, cilia about 12 μm long in protargol preparations (Figs 11A, E, G, 12A, B, D). Basal bodies of paroral membrane reduced in anterior region while associated fibres still present; endoral membrane commences left of paroral and extends to buccal vertex. Pharyngeal fibres

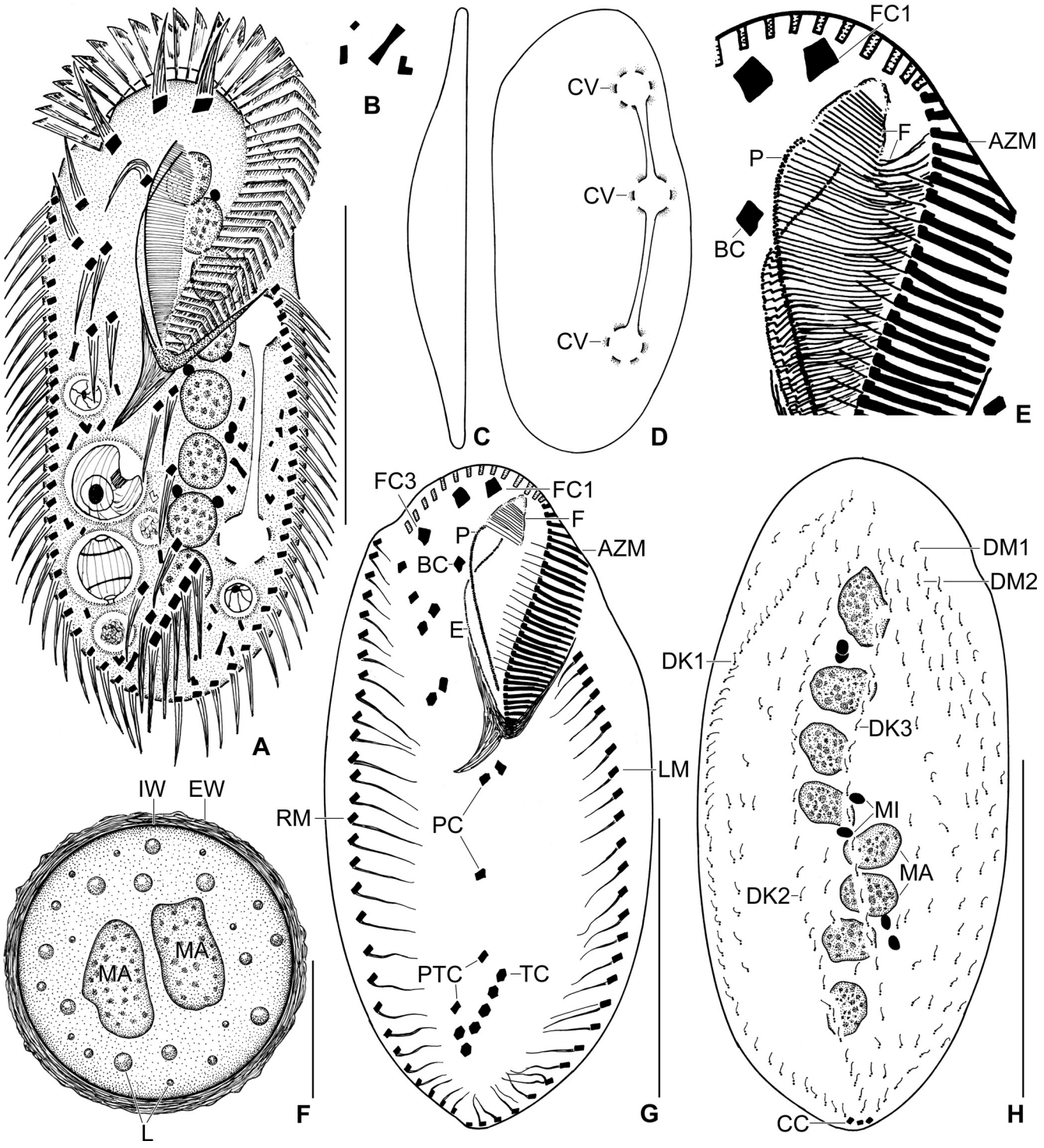

Fig. 11. A–H. *Pattersoniella (Pattersoniellides) australiensis* nov. subgen., nov. spec. from life (A–D, F) and after protargol impregnation (E, G, H). **A**: Ventral view of a representative specimen, length 200 μm. **B**: Cytoplasmic crystals. **C, D**: Right lateral and ventral view of a specimen with three contractile vacuoles. **E**: Oral apparatus, detail from (G). The buccal wall fibres lack paroral basal bodies anteriorly. **F**: Resting cyst in optical section. The eight macronuclear nodules fuse to two masses. **G, H**: Ventral view of holotype and dorsal view of a paratype specimen, showing the infraciliature and the nuclear apparatus. AZM – adoral zone of membranelles, BC – buccal cirrus, CC – caudal cirri, CV – contractile vacuoles, DK1–3 – dorsal kineties, DM1,2 – dorsomarginal kineties, E – endoral membrane, EW – external cyst wall, F – buccal wall fibres, FC1, 3 – frontal cirri, IW – internal cyst wall, L – lipid droplets, LM – left marginal cirral row, MA – macronuclear nodules, MI – micronuclei, P – paroral membrane, PC – postoral cirri, PTC – pretransverse cirri, RM – right marginal cirral row, TC – transverse cirri. Scale bars 25 μm (F), 80 μm (G, H) and 100 μm (A).

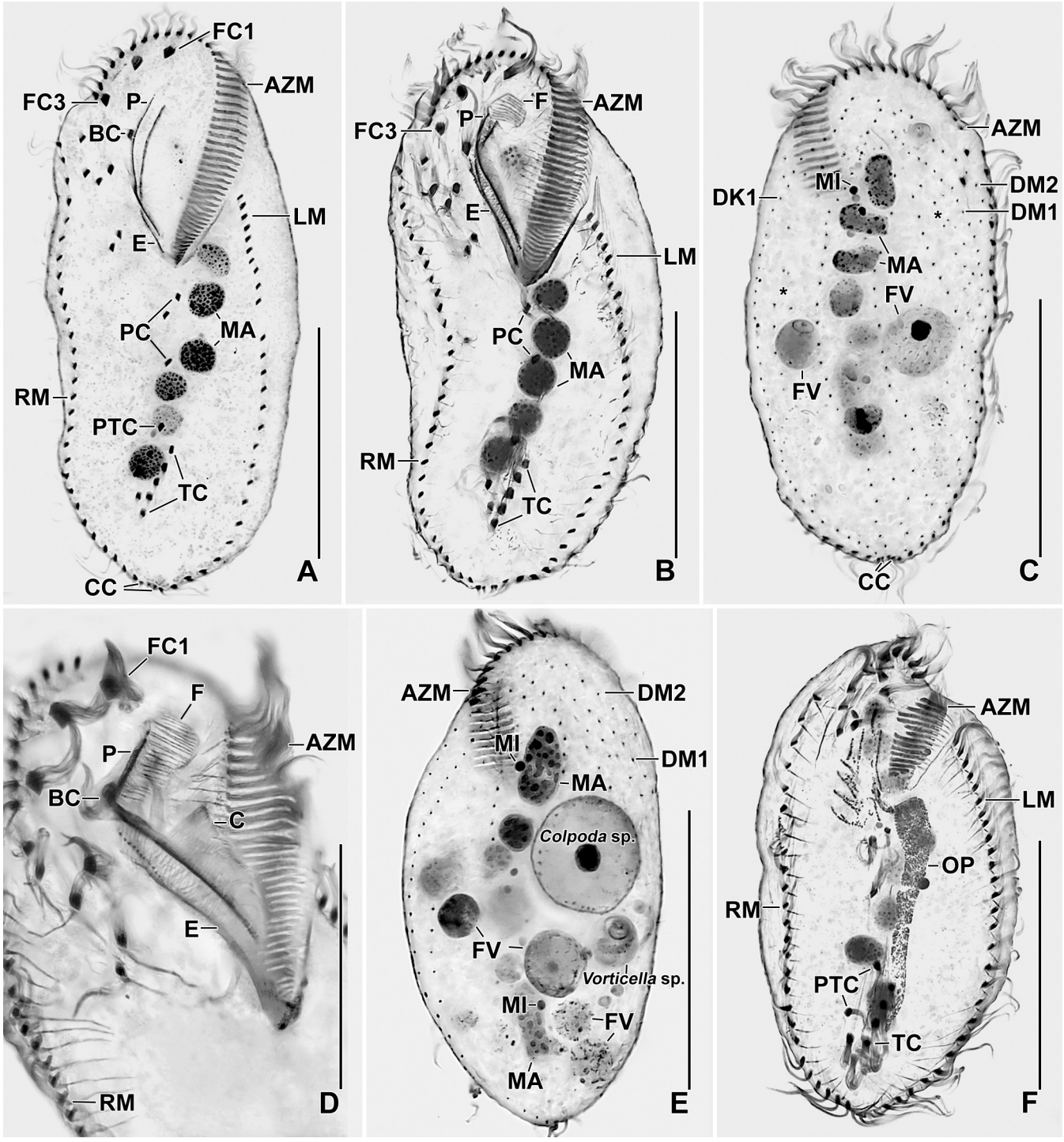

Fig. 12. A–F. *Pattersoniella (Pattersoniellides) australiensis* nov. subgen., nov. spec. after protargol impregnation. **A–C**: Ventral and dorsal view of ordinary specimens, showing infraciliature and nuclear apparatus. The asterisks mark areas with parental dorsal bristles. **D**: Oral area, showing buccal wall fibres anterior of the paroral membrane whose cilia are about 12 μm long in protargol preparations. **E**: A specimen studded with food vacuoles containing ciliates and flagellates. **F**: A reorganiser, showing the huge oral primordium and seven fronto-ventral-transverse cirral anlagen. AZM – adoral zone of membranelles, BC – buccal cirrus, C – paroral cilia, CC – caudal cirri, DK1 – dorsal kinety 1, DM1,2 – dorsomarginal kineties, E – endoral membrane, F – buccal wall fibres, FC1,3 – frontal cirri, FV – food vacuoles, LM – left marginal cirral row, MA – macronuclear nodules, MI – micronuclei, OP – oral primordium, P – paroral membrane, PC – postoral cirri, PTC – pretransverse cirri, RM – right marginal cirral row, TC – transverse cirri. Scale bars 50 μm (D) and 80 μm (A–C, E, F).

Table 7. Morphometric data on *Pattersoniella* (*Pattersoniellides*) *australiensis* nov. subgen., nov. spec.

Characteristics[a]	Mean	M	SD	SE	CV	Min	Max	n
Body, length	174.8	175.0	11.9	2.2	6.8	152.0	198.0	29
Body, width	79.3	78.0	8.5	1.6	10.7	62.0	98.0	29
Body length:width, ratio	2.2	2.2	0.2	0.0	9.0	1.9	2.7	29
Body width:length, percentage	45.4	45.7	4.2	0.8	9.2	37.1	53.8	29
Anterior body end to proximal end of adoral zone, distance	78.2	75.0	7.9	1.5	10.1	60.0	99.0	29
Anterior body end to distal end of adoral zone, distance	24.7	25.0	3.8	0.7	15.6	15.0	32.0	29
Body length:length of adoral zone of membranelles, ratio	2.2	2.3	0.2	0.0	9.5	1.8	2.7	29
Anterior body end to proximal end of adoral zone, % of body length	44.8	44.3	4.1	0.8	9.1	37.5	54.4	29
Anterior body end to distal end of adoral zone, % of body length	14.2	14.0	2.7	0.5	18.7	8.2	19.4	29
DE-value (see text)	0.3	0.3	0.1	0.0	19.3	0.2	0.5	29
Adoral membranelles, number	48.5	48.0	4.4	1.0	9.0	42.0	59.0	19
Adoral membranelles, width of longest base	15.4	15.0	2.1	0.5	13.8	12.0	20.0	19
Gap between adoral zone of membranelles and paroral membrane	18.6	18.0	3.6	0.7	19.2	12.0	26.0	27
Anterior body end to paroral membrane, distance	20.3	20.0	2.4	0.5	11.7	16.0	24.0	19
Cilia of paroral membrane, length	12.0	12.0	1.6	0.3	13.5	10.0	15.0	23
Anterior body end to endoral membrane, distance	22.8	24.0	2.6	0.6	11.4	17.0	26.0	19
Anterior body end to anteriormost macronuclear nodule, distance	30.1	30.0	3.1	0.7	10.2	22.0	35.0	19
Macronuclear figure, length	114.4	114.0	9.6	2.2	8.4	97.0	130.0	19
Anteriormost macronuclear nodule, length	17.5	17.0	2.5	0.6	14.2	14.0	23.0	19
Anteriormost macronuclear nodule, width	12.7	13.0	2.5	0.6	19.5	9.0	17.0	19
Macronuclear nodules, number	8.1	8.0	0.7	0.1	8.1	6.0	10.0	29
Anterior body end to anteriormost micronucleus, distance	44.4	45.0	9.0	2.1	20.3	25.0	64.0	19
Anteriormost micronucleus, length	3.0	3.0	0.4	0.1	12.4	2.5	4.0	19
Anteriormost micronucleus, width	2.4	2.5	–	–	–	2.0	3.0	19
Micronuclei, number	7.1	7.0	1.5	0.3	20.9	5.0	11.0	19
Anterior body end to right marginal cirral row, distance	33.8	35.0	6.1	1.4	18.1	20.0	41.0	19
Posterior body end to right marginal cirral row, distance	3.2	3.0	1.3	0.3	41.2	1.0	6.0	19
Right marginal row, number of cirri	28.3	29.0	1.8	0.4	6.4	25.0	33.0	19
Anterior body end to left marginal cirral row, distance	53.4	54.0	8.2	1.9	15.3	37.0	74.0	19
Left marginal row, number of cirri	27.2	27.0	1.9	0.4	7.0	23.0	31.0	19
Gap between last cirri of marginal rows	5.6	5.0	1.6	0.4	29.1	3.0	8.0	19
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	29
Anterior body end to buccal cirrus, distance	28.6	28.0	2.8	0.6	9.7	25.0	35.0	19
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	29
Anterior body end to posteriormost frontoventral cirrus, distance	68.2	67.0	5.8	1.3	8.6	60.0	85.0	19
Frontoventral cirri, number	6.2	6.0	0.5	0.1	8.7	6.0	8.0	29
Anterior body end to posteriormost postoral cirrus, distance	106.0	106.0	9.6	2.2	9.1	88.0	122.0	19
Postoral cirri, number	3.4	3.0	0.9	0.2	25.9	2.0	5.0	27
Posterior body end to anterior pretransverse cirrus, distance	46.2	45.0	5.0	1.2	10.9	40.0	61.0	19
Posterior body end to rear pretransverse cirrus, distance	31.5	31.0	5.3	1.2	16.9	24.0	48.0	19
Pretransverse cirri, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	29
Posterior body end to rear transverse cirrus, distance	18.5	18.0	4.0	0.9	21.6	12.0	30.0	21
Transverse cirri, number	6.4	6.0	–	–	–	6.0	7.0	29
Dorsal kineties, number	9.6	10.0	1.3	0.3	13.7	8.0	12.0	17
Anterior body end to dorsal kinety 1, distance	11.5	11.0	2.1	0.5	17.9	8.0	15.0	17
Dorsal kinety 1, number of bristles	46.3	47.0	5.5	1.3	12.0	38.0	57.0	17
Anterior body end to dorsal kinety 2, distance	13.5	12.0	3.0	0.7	22.0	10.0	20.0	17
Dorsal kinety 2, number of bristles	32.1	32.0	3.2	0.8	9.8	26.0	38.0	17
Dorsomarginal row 1, number of bristles	18.9	19.0	3.4	0.8	17.8	13.0	24.0	17
Dorsomarginal row 2, number of bristles	11.3	11.0	2.0	0.5	17.6	8.0	15.0	17
Caudal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	19

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

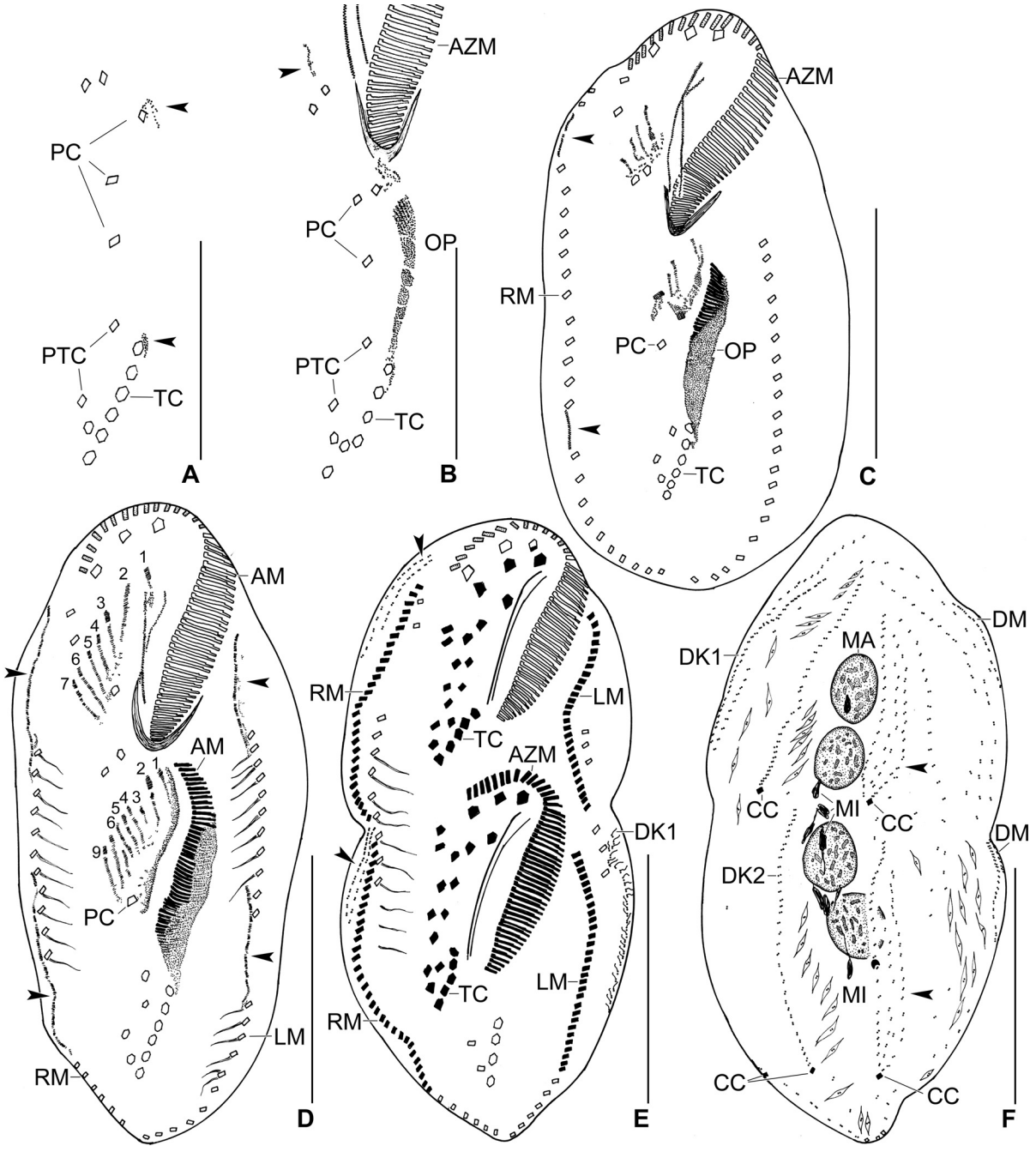

Fig. 13. A–F. *Pattersoniella (Pattersoniellides) australiensis* nov. subgen., nov. spec., ventral (A–E) and dorsal (F) view of dividers after protargol impregnation; parental structures shown by contour, newly formed structures shaded black. **A, B**: Early dividers, showing the oral primordium close to the postoral and transverse cirri. Arrowhead marks a cirral anlage. **C**: The oral primordium and the anterior postoral cirri differentiate cirral streaks for the opisthe. The buccal and two parental frontoventral cirri disaggregate to produce cirral streaks for the proter. Arrowheads mark anlagen in the right marginal cirral rows. **D**: Seven to nine cirral streaks are produced in each daughter cell; arrowheads point to the anlagen for the marginal cirri. **E**: The fronto-ventral-transverse cirri migrate to their specific sites and dorsomarginal kineties (arrowheads) develope close to the right marginal row. **F**: Dorsal kinety 3 splits into three or four fragments, the rightmost (arrowheads) producing a caudal cirrus each in proter and opisthe. The macronucleus completes the second division. AM – adoral membranelles, AZM – adoral zone of membranelles, CC – caudal cirri, DK1,2 – dorsal kineties, DM – dorsomarginal kineties, LM – left marginal cirral row, MA – macronuclear nodules, MI – micronuclei, OP – oral primordium, PC – postoral cirri, PTC – pretransverse cirri, RM – right marginal cirral row, TC – transverse cirri. Numerals denote cirral anlagen. Scale bars 50 μm (D) and 80 μm (A–C, E, F).

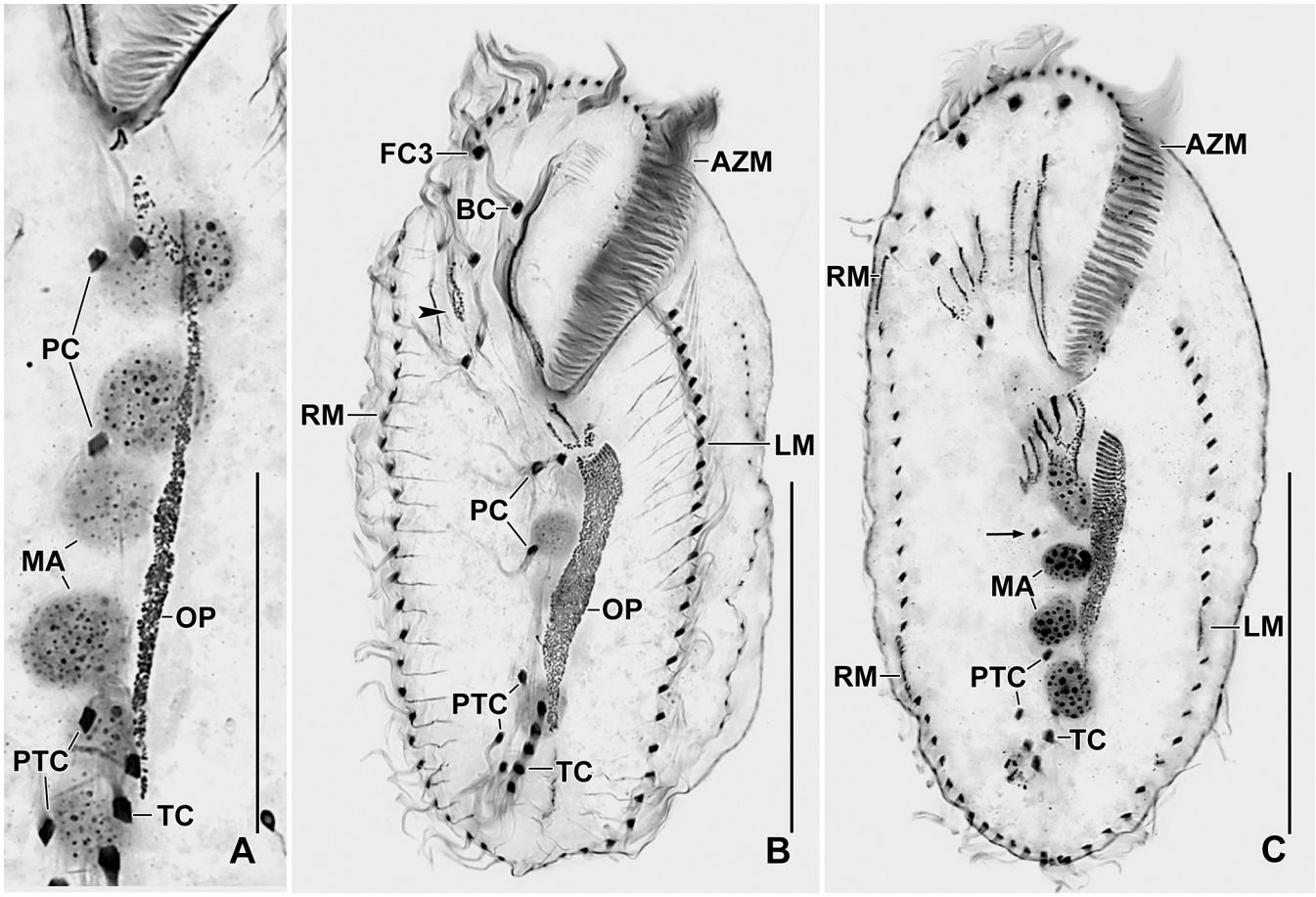

Fig. 14. A–C. *Pattersoniella (Pattersoniellides) australiensis* nov. subgen., nov. spec., ventral view of early dividers after protargol impregnation. **A**: The oral primordium forms close to the postoral and transverse cirri. **B**: The anterior end of the OP differentiates into cirral streaks and a parental frontoventral cirrus begins to disaggregate (arrowhead). **C**: The buccal and two parental frontoventral cirri disaggregate to form cirral streaks for the proter; two of the three (arrow) postoral cirri transform to cirral anlagen for the opisthe; three anlagen for marginal cirri develop in proter and opisthe. AZM – adoral zone of membranelles, BC – buccal cirrus, FC3 – frontal cirrus 3, LM – left marginal cirral row, MA – macronuclear nodules, OP – oral primordium, PC – postoral cirri, PTC – pretransverse cirri, RM – right marginal cirral row, TC – transverse cirri. Scale bars 50 μm (A) and 80 μm (B, C).

short, extend obliquely backwards (Figs 11E, G, 12A, B, D; Table 7).

Resting cyst: Cysts about 55 μm across in vivo (Fig. 11F). Cyst wall wrinkled and about 3 μm thick, without mucous layer. Cytoplasm finely granulated and with some lipid droplets 1–3 μm across, central area with two macronuclear nodules.

Notes on ontogenesis: The ontogenesis is highly similar to that of *Pattersoniella vitiphila* and, therefore, described only briefly but shown by many figures. The oral primordium originates close to the anteriormost transverse cirrus and the postoral cirri (Figs 13A–C, 14A–C). As typical for stylonychine oxytrichids, the three frontal cirri, the migratory cirri (VI/3 and VI/4), and cirrus V/3 are not involved in primordia formation (Figs 13A–E, 14A–C, 15A, B). Seven to nine anlagen streaks are formed each in proter and opisthe (Figs 13D, E, 15A, B). The dorsal ontogenesis is also the same as in *Pattersoniella vitiphila*, i.e., shows multiple fragmentation of dorsal kinety 3 and invariably two dorsomarginal kineties (Figs 13F, 15C).

Occurrence and ecology: As yet found only at type locality. Very likely a litter species, as indicated by the big size.

Justification of the new subgenus: The molecular analyses of Bernhardt et al. (2001) and Kim et al. (2014) confirmed the original classification of *Pattersoniella* in the family Oxytrichidae (Foissner, 1987a). The present species is a "good" *Pattersoniella* with respect to the increased number of transverse cirri, the dorsal infraciliature, the multinodular nuclear apparatus, and the ontogenesis. In contrast, the frontal ciliature is as in typical oxytrichids. Indeed, this species is on the way to become a typical stylonychid, as shown by the unique paroral membrane, i.e., the lacking basal bodies for the anterior wall fibres. Possibly, the two macronuclear nodules of the resting cyst, a frequent pattern in typical oxytrichids, support this hypothesis because the nodules of *P. vitiphila* fuse to a single mass (Berger, 1999).

Generic comparison: *Pattersoniella* (*Pattersoniellides*) shows similarities with the following genera: *Pattersoniella* (*Pattersoniella*), *Territricha*, *Apoterritricha*, and *Afrophrya*. *Pattersoniellides* can be separated from *Pattersoniella*

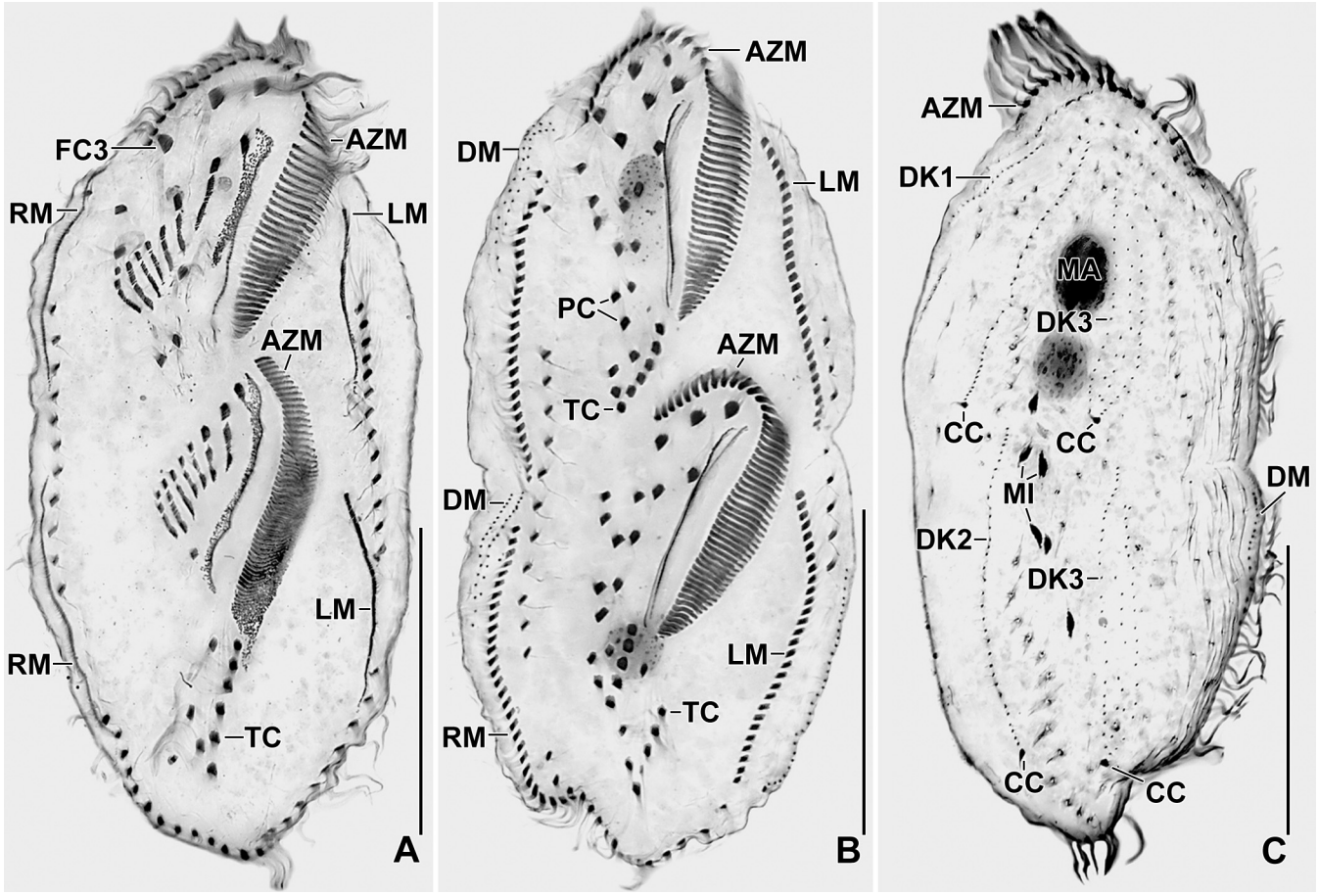

Fig. 15. A–C. *Pattersoniella (Pattersoniellides) australiensis* nov. subgen., nov. spec., ventral (A, B) and dorsal (C) view of dividers after protargol impregnation. **A**: Mid-divider, showing the formation of cirral streaks in proter and opisthe and the primordia for the marginal cirri. **B**: Late divider, showing cirral and oral patterning and the origin of dorsomarginal kineties close to the right marginal row. **C**: Late divider, showing the multiple split of dorsal kinety 3 and the origin of caudal cirri at end of kineties 1 and 2 and at the end of the right fragment of kinety 3. AZM – adoral zone of membranelles, CC – caudal cirri, DK1–3 – dorsal kineties, DM – dorsomarginal kineties, FC3 – frontal cirrus 3, LM – left marginal cirral row, MA – macronuclear nodule, MI – micronuclei, PC – postoral cirri, RM – right marginal cirral row, TC – transverse cirri. Scale bars 80 μm.

(*Pattersoniella*) Foissner, 1987a by the frontal ciliature (oxytrichid vs. bicorona). *Territricha* Berger and Foissner, 1988 and *Apoterritricha* Kim et al., 2014 can be distinguished from the new subgenus *Pattersoniellides* in having a flexible (vs. rigid) body and more than two (vs. invariably two) dorsomarginal kineties. The genus *Afrophrya* Foissner and Stoeck, 2006 differs mainly in having midventral rows (vs. *Oxytricha* pattern) and the undulating membranes in *Cyrtohymena* (vs. *Australocirrus*) pattern.

Pseudohemisincirra arabica Foissner et al., 2008b

Improved diagnosis: Size in vivo about 85 μm × 15 μm; narrowly oblong. On average 15 macronuclear nodules and two micronuclei in a series left of body's midline. Cortical granules colourless to yellowish, form clusters around bases of cirri and dorsal kinetids, about 0.5–1 μm across. On average seven frontoventral cirri arranged in a more or less continuous row (?), two frontoterminal cirri, and two transverse cirri. Left marginal row on average composed of 18 cirri, right of 17. Three or four dorsal kineties. Adoral zone occupies about 24% of body length, composed of an average of 15 membranelles.

Remarks: Foissner et al. (2008b) mentioned a short row of frontoventral cirri in *P. arabica*. Here, we show that the frontoventral cirri of most Australian specimens have a rather distinct midventral pattern, indicating an urostylid or an oxytrichid relationship. Thus, we reinvestigated the type slides of *P. arabica*, where a midventral pattern is hardly recognisable (Fig. 17D–F). Accordingly, ontogenetic and molecular data are required for the final classification of the genus.

Pseudohemisincirra arabica arabica Foissner et al., 2008b nov. stat. (Fig. 17D–F)

Diagnosis: Three dorsal kineties with about two dikinetids in kinety 3.

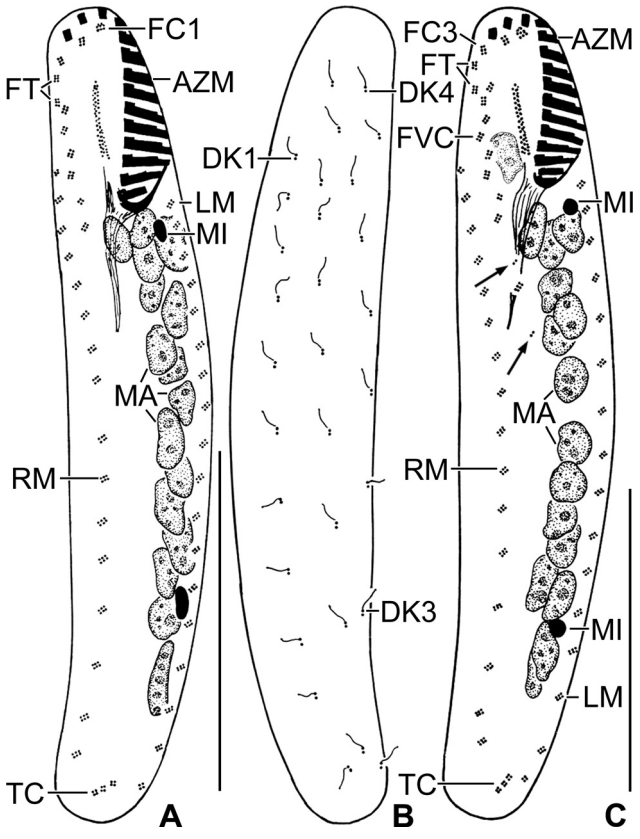

Fig. 16. A–C. *Pseudohemisincirra arabica australiensis* nov. subspec. after protargol impregnation. **A, B**: Ventral and dorsal view of holotype specimen, showing infraciliature and nuclear apparatus. **C**: A specimen with distinctly paired and increased number of frontoventral cirri; arrows mark posteriormost cirri with only two kinetids. AZM – adoral zone of membranelles, DK1,3,4 – dorsal kineties, FC1,3 – frontal cirri, FT – frontoterminal cirri, FVC – frontoventral cirral row, LM – left marginal cirral row, MA – macronuclear nodules, MI – micronuclei, RM – right marginal cirral row, TC – transverse cirri. Scale bars 30 μm.

Pseudohemisincirra arabica australiensis nov. subspec. (Figs 16A–C, 17A–C; Table 8)

Diagnosis: Four dorsal kineties with about two dikinetids in kinety 4.

Type locality: Semi-desert soil from margin of Lake Amadeus near to the town of Alice Springs, Australia, 24°48′S 130°54′E.

Material deposited: One holotype and five paratype slides with protargol-impregnated specimens have been deposited in the Biologiezentrum of the Oberösterreichische Landesmuseum in Linz (LI), reg. no. 2015, 818–823. Relevant specimens have been marked with black ink circles on the coverslip.

Etymology: The species group name *australiensis* refers to the country the subspecies was discovered, i.e., Australia.

Observations: The new subspecies differs from *Pseudohemisincirra arabica arabica* mainly by the feature mentioned in the diagnosis. Thus, we do not provide an ordinary description but focus on some further differences, namely: (i) size in vivo about 85 μm × 20 μm (vs. 90 μm × 15 μm) while only 68 μm × 14 μm (vs. 87 μm × 15 μm) in the protargol preparations; this difference is very likely caused by insufficient fixation due to the high salinity of the sample; (ii) the cirri are slightly larger, e.g., marginal cirri composed of six (vs. four) basal bodies; (iii) on average 16 (vs. 14) fronto-ventral-transverse cirri including 8 (vs. 7) frontoventral and 3 (vs. 2) transverse cirri; and (iv) left marginal row composed of 17 (vs. 19), right of 16 (vs. 18) cirri.

Occurrence and ecology: As yet found only at type locality.

Species comparison: As mentioned in the diagnosis, *Pseudohemisincirra arabica australiensis* differs from *P. arabica arabica* mainly by the increased number of dorsal

Table 8. Morphometric data on *Pseudohemisincirra arabica australiensis* nov. subspec.

Characteristics[a]	Mean	M	SD	SE	CV	Min	Max	n
Body, length	67.6	65.0	7.2	1.6	10.6	58.0	83.0	19
Body, width	14.4	14.0	1.4	0.3	9.6	13.0	17.0	19
Body length:width, ratio	4.7	4.8	0.4	0.1	8.9	3.9	5.5	19
Anterior body end to proximal end of adoral zone, distance	16.9	17.0	1.5	0.3	8.8	14.0	20.0	19
Anterior body end to proximal end of adoral zone, % of body length	25.1	25.0	1.8	0.4	7.4	21.1	28.8	19
Anterior body end to distal end of adoral zone, distance	3.0	3.0	0.6	0.1	19.2	2.0	4.0	19
DE-value[b]	0.2	0.2	–	–	–	0.1	0.2	19
Adoral membranelles, number	14.8	15.0	0.7	0.2	4.6	13.0	16.0	19
Adoral membranelles, width of longest base	4.6	5.0	–	–	–	4.0	5.0	19
Anterior body end to paroral membrane, distance	6.8	7.0	0.9	0.2	12.7	5.0	8.0	15
Anterior body end to anteriormost macronuclear nodule, distance	15.1	15.0	3.2	0.8	21.3	10.0	20.0	15
Posterior body end to rearmost macronuclear nodule, distance	12.0	11.0	3.0	0.8	24.6	7.0	18.0	15
Macronuclear figure, length	42.3	40.0	7.4	1.9	17.6	30.0	58.0	15
Anterior macronuclear nodule, length	5.2	5.0	0.8	0.2	14.9	4.0	7.0	15
Anterior macronuclear nodule, width	3.4	3.0	–	–	–	3.0	4.0	15
Macronuclear nodules, number	14.6	15.0	1.5	0.4	10.0	12.0	16.0	15
Anteriormost micronucleus, length	1.9	2.0	0.4	0.1	19.2	1.5	3.0	15
Anteriormost micronucleus, width	1.4	1.5	–	–	–	1.0	1.5	15

Table 8. (*Continued*)

Characteristics[a]	Mean	M	SD	SE	CV	Min	Max	n
Micronuclei, number	2.0	2.0	0.8	0.2	37.8	1.0	4.0	15
Anterior body end to right marginal row, distance	13.8	14.0	1.9	0.5	14.0	9.0	16.0	15
Posterior body end to right marginal row, distance	3.9	4.0	1.4	0.4	36.4	1.0	6.0	15
Right marginal row, number of cirri	16.5	16.0	1.8	0.5	11.0	13.0	20.0	15
Anterior body end to left marginal row, distance	17.1	17.0	1.5	0.4	8.7	14.0	19.0	15
Posterior body end to left marginal row, distance	4.3	4.0	1.5	0.4	34.8	2.0	7.0	15
Left marginal row, number of cirri	16.9	17.0	2.5	0.6	14.7	11.0	22.0	15
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	15
Anterior body end to posteriormost frontoventral cirrus, distance	22.8	21.0	5.3	1.4	23.2	16.0	34.0	15
Frontoventral cirri, number	7.8	7.0	1.9	0.5	24.8	5.0	12.0	15
Anterior body end to rearmost frontoterminal cirrus, distance	7.9	8.0	1.1	0.3	14.3	5.0	10.0	15
Frontoterminal cirri, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	15
Posterior body end to posteriormost transverse cirrus, distance	1.8	2.0	0.7	0.2	37.3	1.0	3.0	13
Transverse cirri, number	2.7	3.0	0.6	0.2	21.7	1.0	3.0	15
Dorsal kineties, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	15
Anterior body end to dorsal kinety 1, distance	10.5	12.0	3.1	0.9	29.4	5.0	14.0	13
Dorsal kinety 1, number of bristles	9.9	10.0	0.9	0.2	8.7	9.0	11.0	13
Anterior body end to dorsal kinety 2, distance	14.7	14.0	4.6	1.3	31.5	8.0	24.0	13
Dorsal kinety 2, number of bristles	7.1	7.0	1.0	0.3	13.5	6.0	9.0	13
Anterior body end to dorsal kinety 3, distance	7.3	7.0	1.8	0.5	24.0	5.0	12.0	13
Dorsal kinety 3, number of bristles	8.5	8.0	0.8	0.2	9.2	7.0	10.0	13
Anterior body end to dorsal kinety 4, distance	6.7	7.0	1.8	0.5	26.2	3.0	10.0	13
Dorsal kinety 4, number of bristles	2.1	2.0	–	–	–	2.0	3.0	13

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

[b] *Distal end* of adoral zone (Berger, 2006).

kineties (4 vs. 3); minor differences occur in the number of transverse cirri (3 vs. 2) and in the number of cirri in the left marginal row (17 vs. 19). The live appearance and the ventral ciliature are highly similar to that of *P. arabica arabica* but a midventral cirral pattern is more pronounced in *P. arabica australiensis*.

Pseudohemisincirra arabica australiensis differs from *Hemisincirra gellerti* (Foissner, 1982) Foissner in Berger, 2001 and *H. gellerti verrucosa* Foissner and Schade, 2000 in Foissner (2000) by the lack (vs. presence) of a buccal cirrus.

Pseudohemisincirra Foissner et al., 2008b differs from the *Periholosticha* Hemberger, 1985 by the round (vs. acute) body end, the presence (vs. absence) of transverse cirri, and absence (vs. presence) of caudal cirri.

Urosoma karinae Foissner, 1987b (Figs 18A–J, 19A–C; Table 9)

Improved diagnosis (includes the Austrian and Australian populations and the Chinese *Urosoma karinae sinense*; averages from all populations): Size in vivo about 130 μm × 30 μm or 215 μm × 60 μm; elongate ellipsoid to very narrowly ellipsoid. Two ellipsoid to elongate ellipsoid macronuclear nodules, usually two micronuclei. Cortical granules colourless, arranged in loose rows, about 0.5 μm across. Sixteen to 17 or 18 fronto-ventral-transverse cirri, buccal cirrus near anterior end of endoral membrane. Left marginal row composed of 29 or 35 cirri, right of 30 or 38. Adoral zone occupies 22% or 27% of body length, composed of an average of 24 or 36 membranelles. Paroral membrane short, posterior half along anterior portion of endoral. Four dorsal kineties with 11 or 22 dikinetids in kinety 1. Usually three caudal cirri slightly right of body's midline.

Material deposited: Five voucher slides with protargol-impregnated specimens have been deposited in the Biologiezentrum of the Oberösterreichische Landesmuseum in Linz (LI), reg. no. 2015, 803–807. Relevant specimens have been marked with black ink circles on the coverslip.

Description: Most important features of the Australian population of *Urosoma karinae karinae* have an ordinary variability (CV ≤ 15%; Table 9). Of those having higher coefficients, the distance between the macronuclear nodules (CV ~ 36%) and the number of postoral cirri (CV ~ 24%) should be mentioned.

Size in vivo 95–150 μm × 20–30 μm, usually about 120 μm × 25 μm, as calculated from some in vivo measurements and the morphometric data in Table 9 adding 15% preparation shrinkage (Foissner, 2014); length:width ratio moderately variable, that is, 4.0–6.0:1, on average 5.1:1 both in vivo and in protargol preparations. Body thus elongate ellipsoid to very elongate ellipsoid, both ends rounded; dorsoventrally flattened about 2:1 (Fig. 18A–C, F–H; Table 9). Two macronuclear nodules in middle body third left

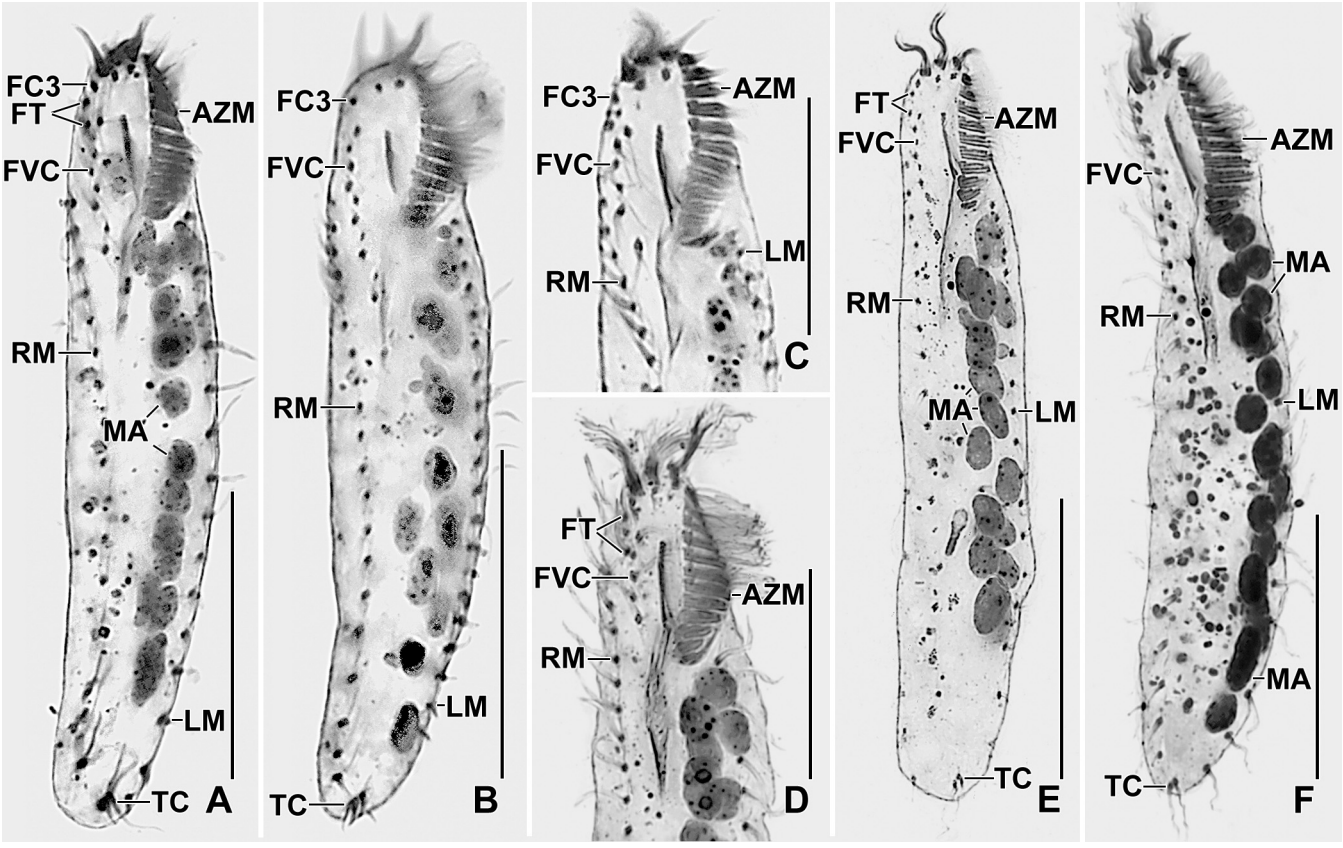

Fig. 17. A–F. Ventral views of *Pseudohemisincirra arabica australiensis* nov. subspec. (A–C) and *P. arabica arabica* (D–F) after protargol impregnation. **A–C**: Infraciliature and nuclear apparatus of representative specimens. Note the rather distinct midventral pattern in the frontoventral row. **D–F**: Holotype (E, from Foissner et al., 2008b) and two paratype specimens (originals) of *P. arabica arabica* where a midventral pattern is hardly recognisable. AZM – adoral zone of membranelles, FC3 – frontal cirrus 3, FT – frontoterminal cirri, FVC – frontoventral cirral row, LM – left marginal cirral row, MA – macronuclear nodules, RM – right marginal cirral row, TC – transverse cirri. Scale bars 20 μm (C, D) and 30 μm (A, B, E, F).

of midline, ellipsoid to elongate ellipsoid, narrowly to widely spaced (CV ~ 36%); in three out of 100 specimens only a single, oblong nodule; contain many granular nucleoli and 1–3 rhombic protein(?) crystals 4–8 μm × 2–4 μm in vivo and in protargol preparations (Figs 18A, F, H–J, 19B, C; Table 9). On average three globular to ellipsoid micronuclei, one attached to each macronuclear nodule in variable position, on average 2.3 μm × 2.0 μm in protargol preparations (Fig. 18A, F, H–J; Table 9). Contractile vacuole in mid-body at left cell margin (Fig. 18A). Cortex highly flexible, contains inconspicuous, colourless, 0.5 μm-sized granules in loose rows (Figs 18E, 19A). Cytoplasm colourless, with few to many crystals 2–4 μm long and usually concentrated in posterior third (Figs 18A, D, 19B). Food vacuoles in vivo up to 5 μm across, contain granular, brownish material or colourless granules, possibly bacterial spores (Figs 18A, 19B). Swims and creeps rapidly.

Cirral pattern and number of cirri of usual variability, except for the highly variable number (1–3) of postoral cirri (Fig. 18A, F, H–J; Table 9). On average 16 fronto-ventral-transverse cirri. Three frontal cirri, right cirrus posterior of distal end of adoral zone, middle cirrus anterior of buccal cirrus, left cirrus anterior of distal end of paroral membrane. Buccal cirrus right of anterior end of endoral membrane, about 14 μm posterior from anterior body end in protargol preparations. Four frontoventral cirri, three form an oblique row with cirrus (III/2) usually slightly anterior to and close to cirrus (VI/4), as typical for *Urosoma*. Usually three postoral cirri forming a straight, rarely a slightly curved row slightly posterior of buccal vertex. Usually four transverse cirri between last cirri of marginal rows, about 20 μm long in vivo and thus distinctly projecting from body proper. Usually only one (the posterior) pretransverse cirrus close to transverse cirri; in seven out of 100 specimens two pretransverse cirri in ordinary position. Marginal cirri in two non-confluent rows, about 15 μm long in vivo; left row slightly longer than right, extends to or near to body midline, composed of an average of 27 cirri, right row terminates about 6 μm anterior from posterior body end, composed of an average of 31 cirri (Fig. 18A, F, H–J; Table 9).

Dorsal bristles 2.5–3 μm long in vivo and in protargol preparations, arranged in four rows (Fig. 18G; Table 9). Rows 1–3 almost bipolar, composed of an average of 11, 14, and 10 bristles, respectively; row 4 extends to or into second quarter

Table 9. Morphometric data on Australian population of *Urosoma karinae*.

Characteristics[a]	Mean	M	SD	SE	CV	Min	Max	n
Body, length	103.2	103.0	11.2	2.1	10.8	82.0	127.0	29
Body, width	20.2	20.0	2.2	0.4	10.8	17.0	25.0	29
Body length:width, ratio	5.1	5.2	0.4	0.1	8.7	4.0	5.9	29
Anterior body end to proximal end of adoral zone, distance	25.7	26.0	1.8	0.3	6.9	22.0	29.0	29
Anterior body end to proximal end of adoral zone, % of body length	25.1	24.3	2.3	0.4	9.3	21.3	30.5	29
Anterior body end to distal end of adoral zone, distance	4.0	4.0	0.8	0.2	20.4	3.0	6.0	21
DE-value[b]	0.1	0.1	–	–	–	0.1	0.2	21
Adoral membranelles, number	25.5	26.0	1.5	0.3	5.8	23.0	29.0	21
Adoral membranelles, width of longest base	5.0	5.0	0.4	0.1	8.9	4.0	6.0	21
Anterior body end to paroral membrane, distance	12.0	12.0	1.4	0.3	11.5	10.0	15.0	21
Paroral membrane, length	4.2	4.0	0.8	0.2	19.3	3.0	5.0	13
Anterior body end to anterior macronuclear nodule, distance	26.8	27.0	3.2	0.7	12.0	21.0	32.0	21
Posterior body end to posterior macronuclear nodule, distance	32.2	32.0	4.7	1.0	14.7	25.0	43.0	21
Macronuclear nodules, distance in between	11.2	12.0	4.0	0.9	35.5	5.0	18.0	21
Macronuclear figure, length	44.0	46.0	6.5	1.4	14.7	33.0	53.0	21
Anterior macronuclear nodule, length	16.4	15.0	3.3	0.7	19.9	12.0	24.0	21
Anterior macronuclear nodule, width	6.0	6.0	0.9	0.2	15.8	4.0	8.0	21
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	21
Anterior body end to anterior micronucleus, distance	29.0	29.0	5.4	1.2	18.7	22.0	47.0	21
Anteriormost micronucleus, length	2.3	2.0	–	–	–	2.0	3.0	21
Anteriormost micronucleus, width	2.0	2.0	–	–	–	1.5	2.0	21
Micronuclei, number	2.9	3.0	0.6	0.1	21.5	2.0	4.0	21
Anterior body end to right marginal row, distance	6.0	6.0	1.2	0.3	19.7	5.0	10.0	21
Posterior body end to right marginal row, distance	6.1	6.0	1.6	0.3	25.9	3.0	10.0	21
Right marginal row, number of cirri	31.3	30.0	3.0	0.7	9.6	28.0	39.0	21
Anterior body end to left marginal row, distance	24.8	25.0	1.9	0.4	7.7	21.0	28.0	21
Left marginal row, number of cirri	27.3	27.0	2.8	0.6	10.4	23.0	34.0	21
Frontal cirri, number	3.0	3.0	0.0	0.0	0.0	3.0	3.0	21
Anterior body end to buccal cirrus, distance	13.6	13.0	1.3	0.3	9.9	11.0	17.0	19
Buccal cirrus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	21
Anterior body end to cirrus III/2, distance	11.5	12.0	1.2	0.3	10.8	10.0	14.0	21
Anterior body end to cirrus IV/4, distance	13.0	13.0	1.7	0.4	12.7	10.0	16.0	21
Anterior body end to posteriormost frontoventral cirrus, distance	22.8	23.0	2.8	0.6	12.3	18.0	28.0	21
Frontoventral cirri, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	21
Anterior body end to anteriormost postoral cirrus, distance	29.1	29.0	3.0	0.7	10.4	23.0	35.0	21
Anterior body end to posteriormost postoral cirrus, distance	39.3	40.0	5.6	1.2	14.3	27.0	48.0	21
Postoral cirri, number	2.7	3.0	0.6	0.1	24.4	1.0	3.0	23
Pretransverse cirri, number	1.2	1.0	–	–	–	1.0	2.0	29
Posterior body end to posteriormost transverse cirrus, distance	2.9	3.0	0.7	0.1	22.9	2.0	4.0	21
Transverse cirri, number	3.9	4.0	0.4	0.1	10.5	3.0	5.0	29
Dorsal kineties, number	4.0	4.0	0.0	0.0	0.0	4.0	4.0	21
Anterior body end to dorsal kinety 1, distance	20.3	21.0	2.9	0.6	14.3	16.0	25.0	21
Dorsal kinety 1, number of bristles	10.8	10.0	1.6	0.3	14.7	9.0	14.0	21
Anterior body end to dorsal kinety 2, distance	14.0	14.0	3.0	0.7	21.8	6.0	21.0	21
Dorsal kinety 2, number of bristles	13.6	13.0	1.3	0.3	9.4	12.0	16.0	21
Anterior body end to dorsal kinety 3, distance	11.2	11.0	1.9	0.4	16.9	7.0	16.0	21
Dorsal kinety 3, number of bristles	10.4	10.0	1.6	0.3	15.3	8.0	15.0	21
Anterior body end to dorsal kinety 4, distance	5.8	6.0	1.4	0.3	23.9	4.0	9.0	21
Anterior body end to end of dorsal kinety 4, distance	36.4	36.0	4.5	1.0	12.5	29.0	45.0	19
Dorsal kinety 4, number of bristles	6.7	7.0	1.1	0.3	17.1	5.0	9.0	21
Caudal cirri, number	2.9	3.0	0.4	0.1	15.0	2.0	4.0	21

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

[b] *Distal end* of adoral zone (Berger, 2006).

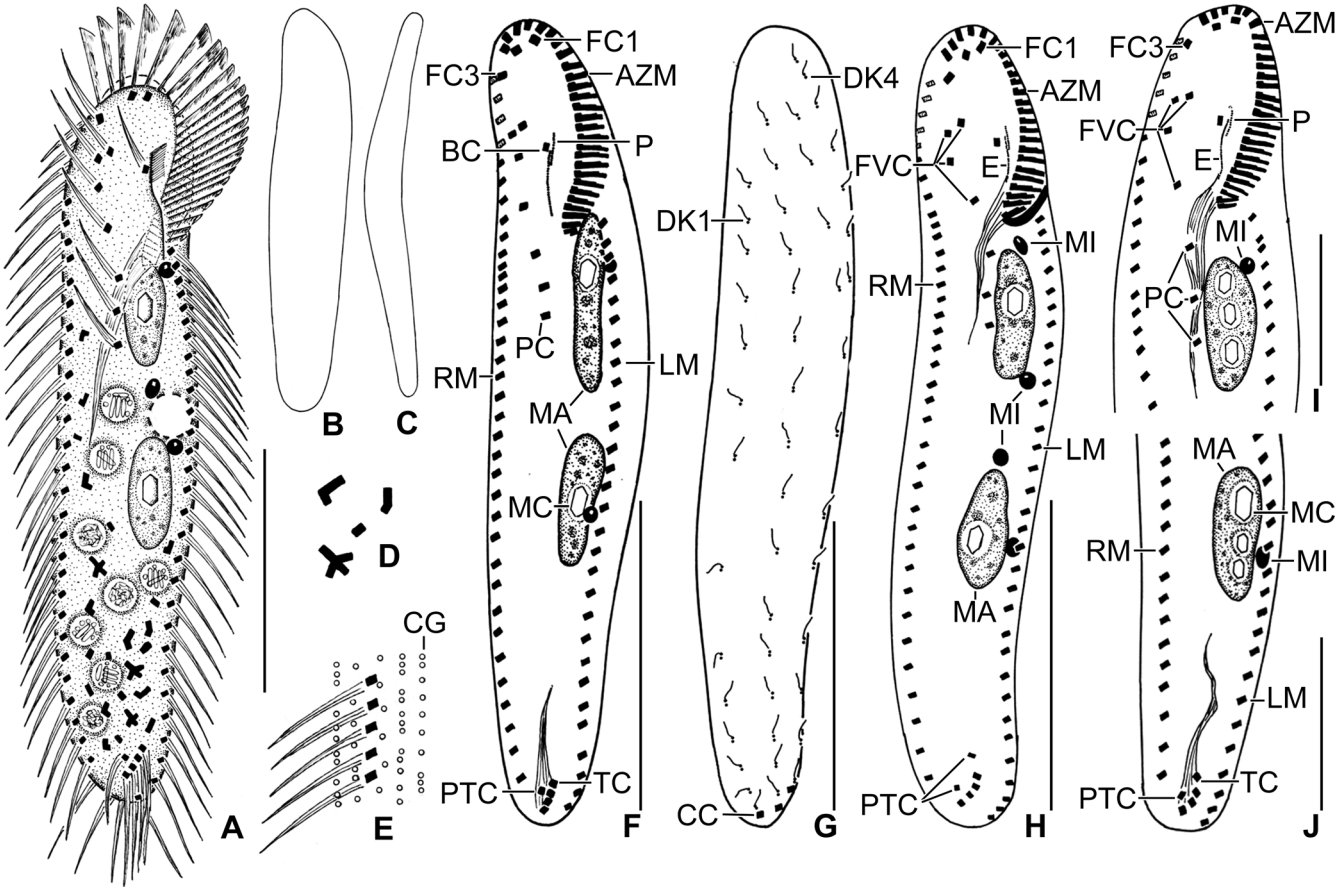

Fig. 18. A–J. *Urosoma karinae karinae*, Australian specimens from life (A–E) and after protargol impregnation (F–J). **A**: Ventral view of a representative specimen, length 120 μm. **B, C**: Dorsal and right lateral view of same specimen. **D**: Cytoplasmic crystals. **E**: Cortical granulation. **F, G**: Ventral and dorsal view of main voucher specimens, showing the infraciliature and the nuclear apparatus. **H**: A specimen with two pretransverse cirri. **I**: Anterior region, showing the arrangement of frontal and ventral cirri and rhombic crystals in the macronuclear nodule. **J**: Posterior region, showing the arrangement of marginal and transverse cirri. AZM – adoral zone of membranelles, BC – buccal cirrus, CC – caudal cirri, CG – cortical granules, DK1,4 – dorsal kineties, E – endoral membrane, FC1,3 – frontal cirri, FVC – frontoventral cirri, LM – left marginal cirral row, MA – macronuclear nodules, MC – macronuclear crystals, MI – micronuclei, P – paroral membrane, PC – postoral cirri, PTC – pretransverse cirri, RM – right marginal cirral row, TC – transverse cirri. Scale bars 20 μm (I, J) and 40 μm (A, F–H).

of cell, composed of five to nine bristles. Usually three caudal cirri at right posterior margin of cell.

Adoral zone occupies about 25% of body length, on average composed of 26 ordinary membranelles with up to 12 μm long cilia, bases of largest membranelles on average 5 μm long in vivo and in protargol preparations (Fig. 18A, F, H, I; Table 9). Buccal cavity flat and narrow, almost completely covered by the angularly projecting buccal lip, bears short paroral membrane about 12 μm posterior from anterior body end; anterior half of paroral surpassing endoral by about 2 μm, posterior half side by side with endoral; endoral membrane slightly curved, commences right of paroral at level of buccal cirrus. Pharyngeal fibres of ordinary length and structure, extend longitudinally backwards (Fig. 18A; Table 9).

Occurrence and ecology: Type population found in the upper soil layer of an alpine pasture, pH 7.5, in Salzburg, Austria (Foissner, 1987b). In Australia it occurred in a slightly saline soil (pH 6.4 in water) from a mangrove forest in the surroundings of the town of Cairns, Australia, 16°55′32″S 145°46′31″E. The Chinese subspecies was discovered in the upper soil layer of the Sangke Grass Land, pH 8.0, Gansu Province, China, 35°06′N 102°25′E. Further records, see Foissner et al. (2002).

Species comparison: Only three *Urosoma* species have a rounded posterior body end, namely, *Urosoma salmastra* (Dragesco and Dragesco-Kernéis, 1986) Berger, 1999; *Urosoma karinae* Foissner, 1987b; and *Urosoma gigantea* (Horváth, 1933) Berger, 1999. The Australian specimens of *Urosoma karinae* are very similar to the Austrian type population, except for a more slender body (5.1:1 vs. 3.3:1) in the protargol preparations and the number of adoral membranelles (26 vs. 22).

Shao et al. (2014b) split *Urosoma karinae* into two subspecies, viz., *Urosoma karinae sinense* and *Urosoma karinae karinae* mainly based on a distinctly increased number of dorsal bristles in a Chinese grassland population. *Urosoma karinae karinae* is highly similar to *Urosoma salmastra*. Berger (1999) mentioned two differences viz., the arrangement of

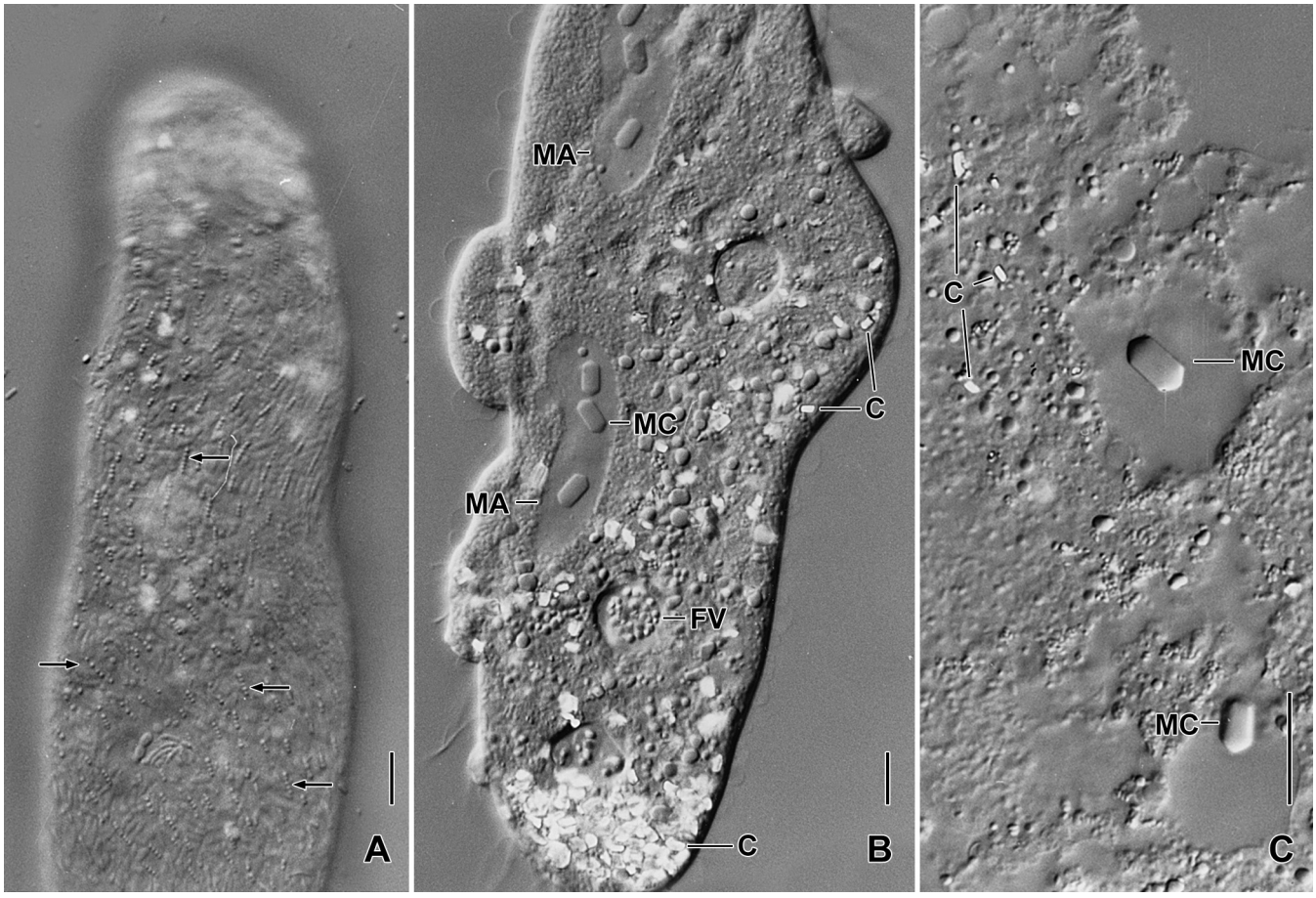

Fig. 19. A–C. *Urosoma karinae karinae*, Australian specimens from life. **A**: The cortical granules are in loose rows and minute (~0.5 μm, arrows). **B**: A squeezed specimen, showing macronuclear crystals and cytoplasmic crystals accumulated in the posterior region. **C**: Macronuclear crystals. C – cytoplasmic crystals, FV – food vacuole, MA – macronuclear nodules, MC – macronuclear crystals. Scale bars 10 μm (A, B) and 15 μm (C).

the undulating membranes (paroral and endoral of equal length and in parallel vs. paroral short and distinctly ahead of the ordinarily sized endoral) and the presence vs. supposed absence of cortical granules; however, Dragesco and Dragesco-Kernéis (1986) very likely did not look for this feature. The Australian population of *Urosoma karinae karinae* differs from the African *Urosoma salmastra* in having a more slender body (5.1:1 vs. 3.5:1), the arrangement of the undulating membranes (part of paroral posterior of endoral vs. distinctly ahead), and by the presence (vs. absence) of rhombic crystals in the macronuclear nodules; however, the last character is probably caused by the slightly saline habitat (mangrove forest). Shao et al. (2014b) redescribed *Urosoma salmastra* from a mangrove forest in China; however, the undulating membrane pattern does not match that described by Dragesco and Dragesco-Kernéis (1986) but is highly similar to that of *Urosoma karinae karinae*. Thus, we did not include these data in the improved diagnosis of *U. karinae*.

Urosoma gigantea can be distinguished from *Urosoma karinae karinae* by the large size (170–230 μm vs. 95–150 μm), the number of adoral membranelles (47 vs. 26), and by the location of cirrus III/2 (between cirrus VI/3 and VI/4 vs. slightly anterior of cirrus VI/4).

Improved diagnosis of *Urosoma karinae karinae* Foissner, 1987b (averages are from the Austrian and Australian population): Size about 130 μm × 30 μm in vivo. Left marginal row composed of 29, right of 30 cirri. Adoral zone occupies 22% of body length, composed of 24 membranelles. Dorsal kineties 1–4 with about 11, 14, 10, and 7 bristles, respectively.

Improved diagnosis of *Urosoma karinae sinense* Shao et al., 2014b: Size about 215 μm × 60 μm in vivo. Left marginal row on average composed of 35, right of 38 cirri. Adoral zone occupies about 27% of body length, composed of an average of 36 membranelles. Dorsal kineties 1–4 with about 22, 22, 21, and 10 bristles, respectively.

Acknowledgements

Financial support was provided by the Austrian Science Fund (FWF Project P26325_B16). The technical assistance of Michael Gruber M.Sc., Robert Schörghofer, and

Andreas Zankl is greatly acknowledged. We thank Dr. J. P. O'Donoghue (University of Adelaide, Australia) for help with sampling in Australia. We also thank Prof. Mann Kyoon Shin (Department of Biological Science, University of Ulsan, Korea) for providing information on the Korean population of *Afroamphisiella multinucleata*.

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