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Morphology and Notes on Morphogenesis during Cell Division of *Deviata polycirrata* n. sp. and of *Deviata bacilliformis* (Gelei, 1954) Eigner, 1995 (Ciliophora: Kahliellidae) from Argentina

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ABSTRACT. Described herein are the morphology and certain morphogenetic stages of a new freshwater ciliate species, *Deviata polycirrata* n. sp., and of *Deviata bacilliformis* recorded in the soil of a dried temporary pond from Argentina. Ciliates were studied alive and after silver impregnation with Protargol. *Deviata polycirrata* n. sp. measures 130–180 × 45–70 µm in vivo. The species possesses 8–9 long cirral rows on the right and 9–13 on the left of the oral zone, and 3 dorsal rows of dikinetids. The adoral zone is composed of 39–48 membranelles. There are four macronuclear nodules and usually two micronuclei. A single contractile vacuole is located equatorially on the left body margin. This new species mainly differs from its congeners in having a higher number of cirral rows, the three long dorsal rows of dikinetids (vs. usually one to two dorsal rows of dikinetids), and a higher number of adoral membranelles. The other species reported here, *D. bacilliformis*, is recorded for the first time in Argentina. Unlike previous observations on this species, on the dorsal surface there are cirral rows that are preceded by cilia (combined cirral rows), and stomatogenesis begins with the proliferation of non-ciliferous basal bodies some distance posterior to the buccal vertex.

Key Words. Buenos Aires Province, freshwater, kahliellid species, soil, Stichotrichida.

THE family Kahliellidae was erected by Tuffrau (1979) for those genera that lack transverse cirri, have frontoventral somatic rows arranged longitudinally, have more or less distinctive marginal rows, and well developed frontal cirri. Tuffrau (1979) recognized 12 genera within the Kahliellidae but several of them are now placed within different families (Lynn 2008). Eigner (1995) redefined the kahliellids on the basis of morphological and ontogenetic data as having more than one longitudinal cirral row on the right side of the body and neokinetal anlagen developing during morphogenesis. Eigner (1995) created two new genera, *Deviata* and *Neogeneia*, and recognized a total of nine genera and species within the family. In a subsequent paper, Eigner (1997) transferred *Deviata* to the Oxytrichidae and considered the Kahliellidae as a junior synonym of this family. On the contrary, the family Kahliellidae is maintained by Lynn (2008) for organisms with ventral cirral files that may be preserved through a variable number of cell divisions before being resorbed and replaced through additional new (= neokinetal) anlagen. Since Eigner (1995), two new *Deviata* species were discovered: *Deviata estevesi* (Paiva and Silva-Neto 2005) and *Deviata rositae* (Küppers, Lopretto, and Claps 2007), although their division morphogenesis has not been investigated. A recently published paper by Siqueira-Castro, Paiva, and Silva-Neto (2009) proposes the transference of *D. estevesi* to the genus *Parastrongylidium* Fleury and Fryd-Ver-savel, 1984, as well as the description of a new *Deviata* species.

The aim of the present study is to describe the morphology and some morphogenetic stages during the cell division of a new *Deviata* species and of an Argentinian population of *Deviata bacilliformis* (Gelei, 1954) Eigner, 1995, both by means of live observation and Protargol staining.

MATERIALS AND METHODS

Water samples were taken during February 2004 from a temporary pond located near the Provincial Route 63, close to Dolores city in the Buenos Aires Province, Argentina (36°18'55"S, 57°32'12"W) (Fig. 1). The following physical and chemical variables were measured with a multiparameter sensor (Horiba U21,

Kyoto, Japan): water temperature, electrical conductivity, dissolved-oxygen concentration, total dissolved solids, and pH. *Deviata bacilliformis* was isolated from rewetted soil samples from the dried bed of a temporary pond located near the city of Poblet, Buenos Aires Province, collected during the summers of 2004 and 2005 (see Küppers et al. 2007 for the detailed description of the sampling site and sample treatment). Ciliates were grown in the laboratory in raw cultures that were made by adding table water and a wheat grain to the water sample and by resuspending the soil samples in Petri dishes. Observations on living cells were performed under a stereomicroscope and a bright-field microscope. Ciliates were picked from the cultures with micropipettes and fixed in Bouin's solution for treatment by the Protargol technique according to Wilbert (1975). Living and silver-impregnated cells were observed and measured under a bright-field microscope with a calibrated ocular micrometer at final magnifications of 125X, 425X, and 1,250X. The drawings of the organisms in vivo are freehand sketches, and Fig. 2 was rendered by scratching an ink-painted high-impact paper. Details of the silver-impregnated organisms were traced with the aid of a drawing tube under a bright-field microscope at a final magnification of 1,000X. Photographs were also taken by bright-field microscopy. The terminology used is according to Lynn (2008) and Eigner (1995). The cirral rows on the right of the adoral membranelles in the interphase organisms are numbered from left to right (i.e. R1, R2, etc.), while the cirral rows on the left of the adoral zone are num-

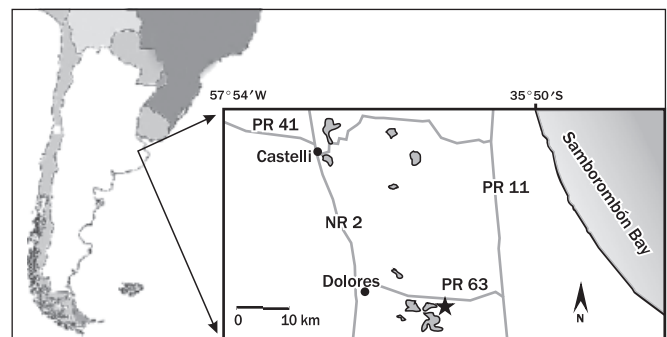


Fig. 1. Type locality of *Deviata polycirrata* n. sp. near Dolores city in the Buenos Aires Province, Argentina (star). NR, National route; PR, Provincial route.

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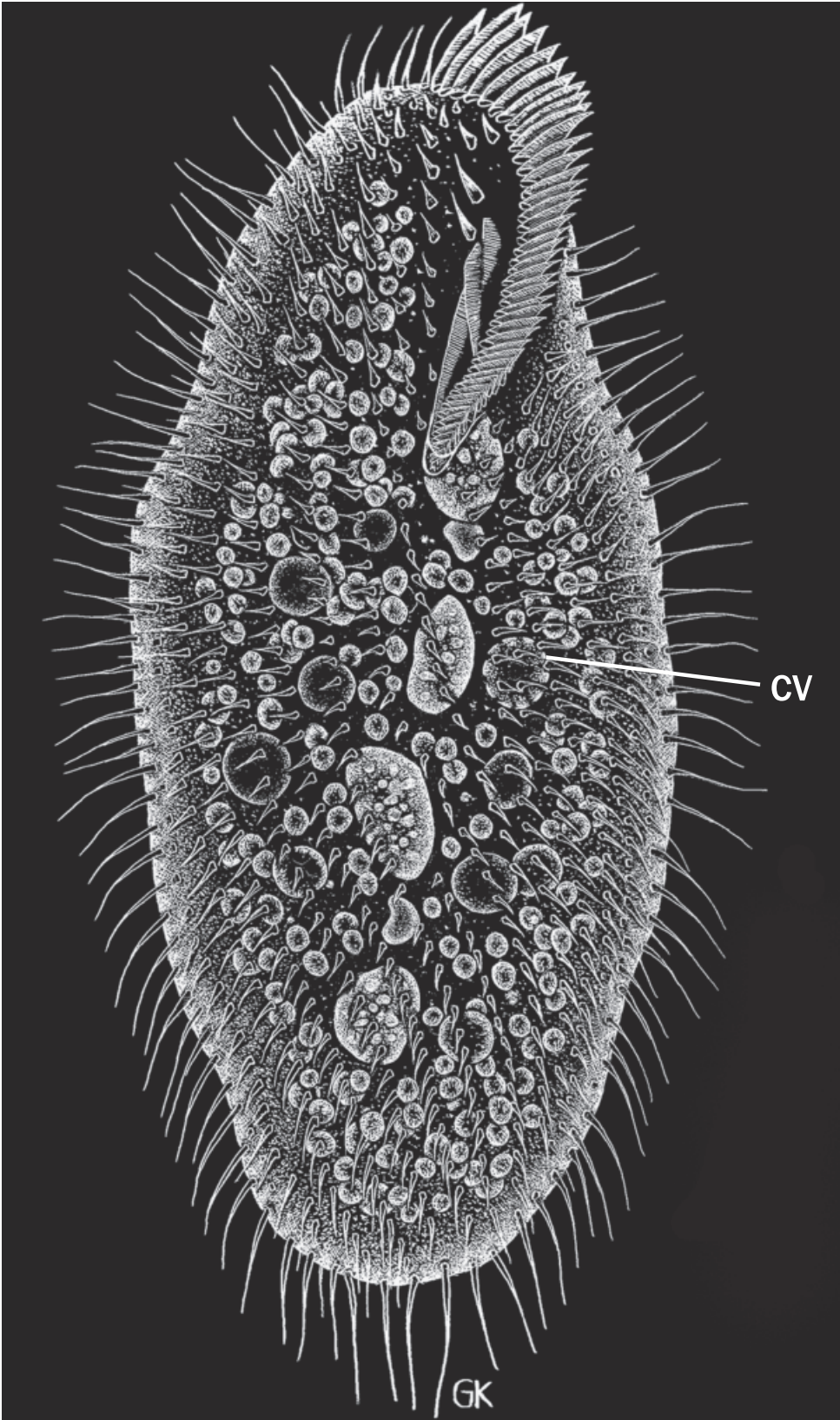


Fig. 2. Morphology of *Deviata polycirra* n. sp. in vivo. CV, contractile vacuole.

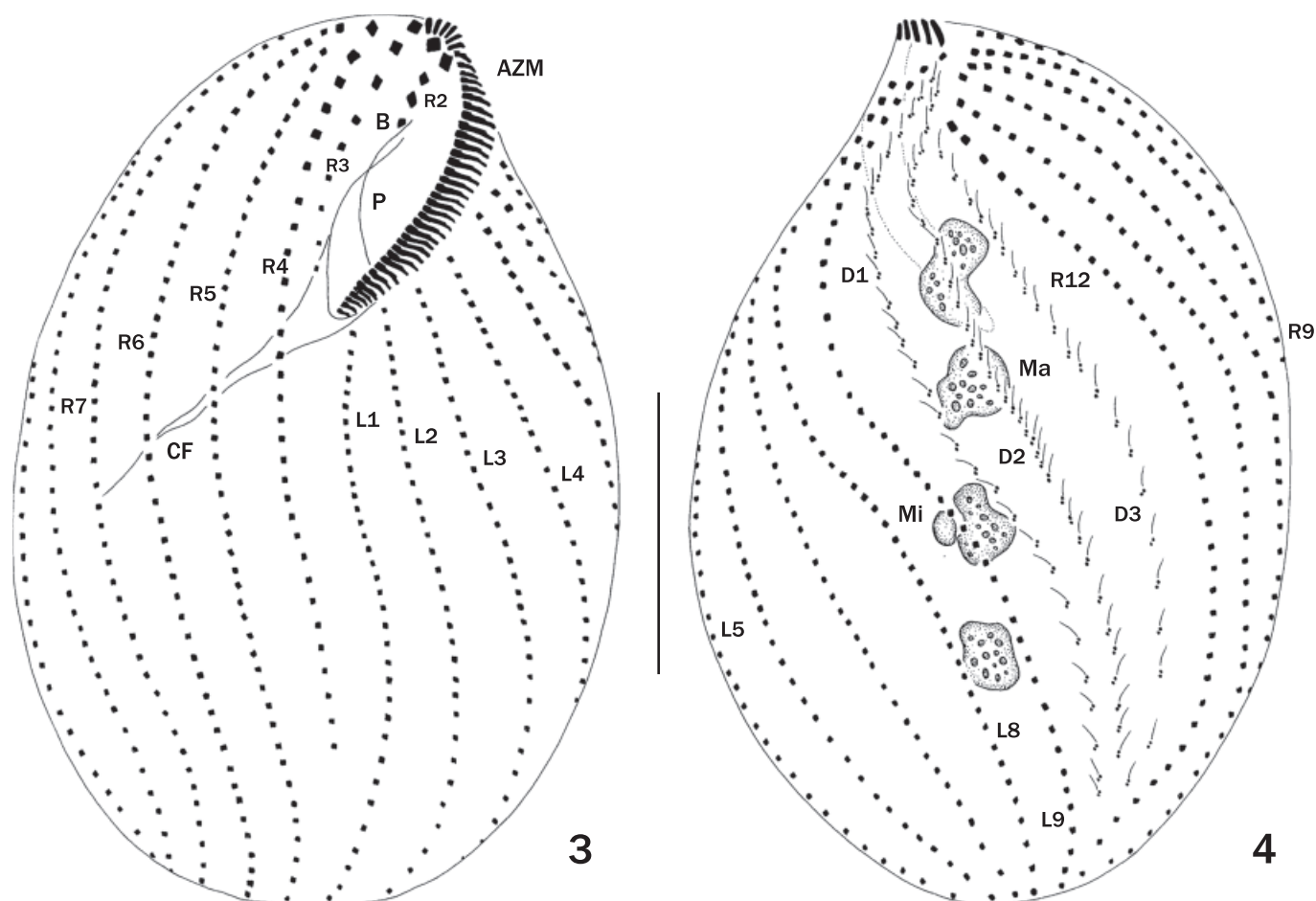


Fig. 3, 4. Morphology of *Deviata polycirrata* n. sp. after Protargol impregnation. 3. Ventral view. 4. Dorsal view. AZM, adoral zone of membranelles; B, buccal cirrus; CF, cytopharyngeal fibers; D1–D3, dorsal kineties one to three; L1–L9, left rows of cirri one to nine; Ma, macronuclear nodule; Mi, micronucleus; P, paroral membrane; R1–R12, right rows of cirri 1–12. Scale bar = 50 μ m.

bered from right to left (i.e. L1, L2, etc.) following Paiva and Silva-Neto (2005). Anlagen are indicated with Roman numerals. Voucher slides of *Deviata polycirrata* n. sp. (accession numbers MLP63 and USNM1135042) and of *D. bacilliformis* (MLP64) were deposited in the Colección de Invertebrados of the Museo de La Plata, Argentina, and the Smithsonian Institution, Washington, USA.

RESULTS

Description of *Deviata polycirrata* n. sp. (Table 1 and Fig. 2–4, 9, 14–19). The body size in vivo is length 130–180 μ m and width 45–70 μ m. The body shape is variable; sometimes elliptical and slender, with both ends being rounded, but sometimes globular with the anterior end being pointed and flattened and the posterior rounded. The body is very flexible. The cytoplasm is colorless but appears dark gray at low magnification (<10X) because of the presence of densely packed refractive globules ~ 10 μ m in width and ingested wheat starch from the cultures. Cortical granules are absent. The contractile vacuole is equatorial and on the left margin of the body and lacks collecting canals (Fig. 2). At times a defecation vacuole was observed at the posterior end. There are always four macronuclear nodules, with the two anterior and two posterior connected by a thin strand, sometimes faintly stained. The macronuclear nodules are variable in shape and usually are bilobed or ellipsoid. There are usually two

micronuclei, each one often located between a pair of macronuclear nodules. The adoral zone of membranelles represents 30% of total body length (calculated on the average values measured on silver-impregnated cells). This adoral zone is composed of 39–48 membranelles of four basal-body rows each. Paroral and endoral membranes consist of dikinetids and the former is shorter at its proximal end and slightly curved. In several specimens these membranes intersected optically due to a preparation artifact, because the cells became very inflated after the treatment with Protargol (Fig. 14–19). The buccal cavity is small and flattened, with cytopharyngeal fibers extending posteriorly from the cytostome. In the buccal field there are three strong frontal cirri and one buccal cirrus next to the paroral membrane. Behind the middle frontal cirrus there are two cirri aligned with the buccal cirrus (R2). Behind the rightmost frontal cirrus there is a row of 6–11 cirri (R3) that extends up to the buccal vertex. There are 17–21 long rows of cirri (i.e. rows that extend beyond the buccal vertex), of which 8–9 are located on the right of the adoral zone of membranelles (R4–R12) and 9–13 on the left of it (L1–L13) (Fig. 3, 4). The first long cirral row from the right (R4), usually shorter than the others, terminates at the posterior third of the body, without reaching the posterior end. Sometimes this row is barely shorter posteriorly; and in 10 individuals from a total of 57 organisms observed, it reached the posterior end of the body. The other long cirral rows from the right terminate at the posterior end of body. The row R5 is slightly shorter anteriorly than its neighboring

Table 1. Mophometric data on *Deviata polycirrata* n. sp.

Character	$\bar{X}$	<i>M</i>	Min.	Max.	SD	<i>n</i>
Body length in vivo	152	150	130	180	16.8	10
Body width in vivo	61.5	65	45	70	10	10
Body length	181.2	172.5	155	220	20.9	20
Body width	130.2	127.5	100	180	21.2	20
AZM, length	54.7	55	50	70	5.2	20
Cytopharyngeal fibers, length	48.8	49.8	41.5	53.9	5.2	5
Macronuclear nodules, number	4	4	4	4	0	20
Macronuclear nodules, length	14.3	14.5	7.5	23.2	3.7	20
Macronuclear nodules, width	8.5	8.3	5.8	12.4	1.2	20
Distance between macronuclear nodules	23.7	21.6	14.9	37.3	6.6	20
Micronuclei, number	1.7	2	1	2	0.4	20
Micronuclei, length	5.4	5.8	4.1	6.6	0.6	20
Micronuclei, width	4.3	4.1	3.3	5	0.5	20
Adoral membranelles, number	43.3	43	39	48	2.2	20
Frontal cirri, number	3	3	3	3	0	20
Buccal cirri, number	1	1	1	1	0	20
Cirri behind middle frontal cirrus, number	2	2	2	2	0	20
Cirri behind rightmost frontal cirrus, number	8.9	9	6	11	1.1	20
Long cirral rows, total number	19	19	17	21	1.3	20
Right long cirral rows, number	8.4	8	8	9	0.5	20
Left long cirral rows, number	10.6	11	9	13	1.3	20
Cirri in R4, number	34.1	34.5	30	38	2.5	10
Cirri in R5, number	47.6	47	43	52	2.9	10
Cirri in R6, number	55.9	55.5	51	63	4	10
Cirri in R7, number	58	54.5	52	85	9.8	10
Cirri in R8, number	55.9	55	52	62	3.3	10
Cirri in R9, number	54.3	54	49	60	3.1	10
Cirri in R10, number	47.9	48	43	52	2.5	10
Cirri in R11, number	42.8	42.5	37	48	3.1	10
Cirri in R12, number	40.3	41	38	42	2.1	3
Cirri in L1, number	35.2	35.5	34	37	1.1	10
Cirri in L2, number	37.2	38	32	40	2.7	10
Cirri in L3, number	36.8	37	32	40	2.1	10
Cirri in L4, number	37.6	38.5	32	43	3.7	10
Cirri in L5, number	37.1	36.5	34	41	2.5	10
Cirri in L6, number	37.7	37	33	44	3.4	10
Cirri in L7, number	40.8	40	36	46	3.3	10
Cirri in L8, number	42.7	42	39	47	2.4	10
Cirri in L9, number	42.3	43	37	47	3.2	10
Cirri in L10, number	42.4	41.5	41	46	1.8	10
Cirri in L11, number	40.4	39	36	45	3.5	7
Cirri in L12, number	42	42	42	42	0	2
Cirri in L13, number	45	45	45	45	0	1
Dorsal kineties, number	3	3	3	3	0	20
Dorsal bristles, length	2.1	2.1	1.7	2.5	0.3	10
Dikinetids in D1, number	28.2	28	22	32	3	10
Dikinetids in D2, number	33.5	34	30	36	2.4	10
Dikinetids in D3, number	22.5	22.5	20	25	1.6	10

Measurements are in micrometers and unless indicated, taken on Protargol stained specimens.

AZM, adoral zone of membranelles; D1–D3, dorsal rows of dikinetids 1–3; L1–L13, long rows of cirri on the left of the adoral zone of membranelles; M, median; max., maximum value; min., minimum value; *n*, number of observations; R4–R12, long rows of cirri on the right of the adoral zone of membranelles; SD, standard deviation; $\bar{X}$, arithmetic mean.

rows. The long cirral rows from the left abut anteriorly on the adoral zone of membranelles and extend up to the posterior end of the body. The anterior cirri from each row possess nine, six, or four basal bodies; while the subsequent cirri are composed only of four or two basal bodies. The rows of cirri are spiraled and those that are located laterally commence ventrally at the anterior end, and terminate dorsally at the posterior end. There are three long dorsal rows of dikinetids (D1–D3) that are bounded by the long rows of cirri on the dorsal surface and extend between the anterior and posterior ends of the dorsalized cirral rows (Fig. 4). The dorsal kinety D1 is slightly longer in the anterior portion. The dikinetids of dorsal kinety D2 are densely packed within the row and are therefore more numerous than those in the other two dorsal rows;

D2 also sometimes extends further posteriorly. The dorsal kinety D3 is one to two basal body pairs shorter anteriorly than the other two rows of bristles. According to Eigner (1995), retained parental cirral rows in the interphase organism have widely spaced cirri and half the cirri of a neighboring row. These retained parental rows seem to be absent in the species described here, as well as caudal cirri (see notes on morphogenesis below).

Some variability in the cirral pattern was observed. In one specimen, R4 is very short and does not surpass the buccal vertex, while R5 reaches the posterior end of the body (Fig. 19). Another specimen possessed a short row of five narrowly spaced cirri between R3 and R4. In still another specimen this extra row presented 13 cirri, R4 ended subequatorially, and there was another

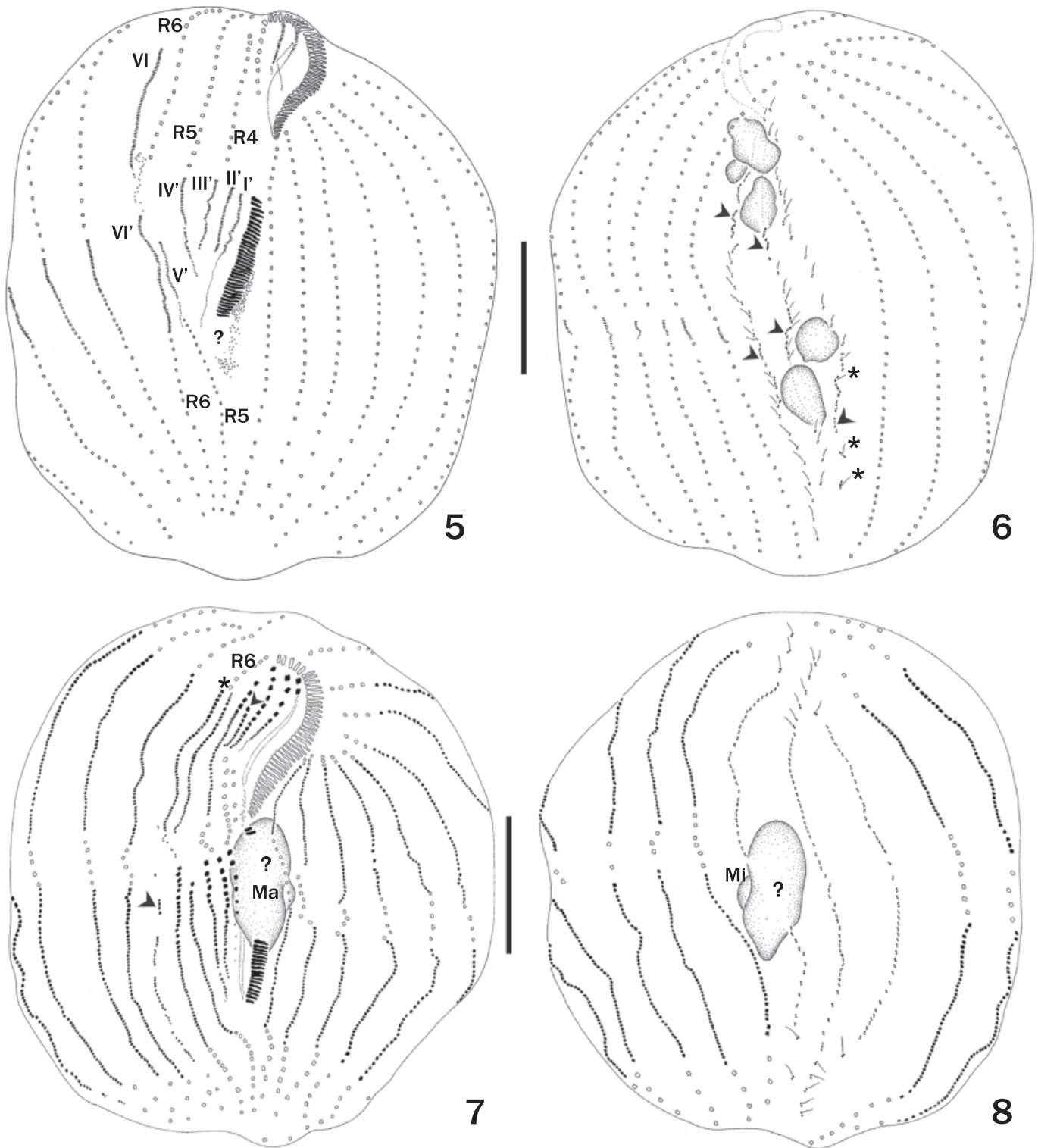


Fig. 5–8. Morphogenesis during cell division of *Deviata polycirrata* n. sp. after Protargol impregnation. **5.** Middle divider in ventral view. **6.** Middle divider in dorsal view. Primordia of dorsal kineties (arrowheads). Parental dikinetids among new proliferating basal bodies (*). **7.** Late divider in ventral view. Additional rows of cirri (arrowheads). Connection of anterior fragment of parental R6 with the new row generated by anlage VI of the proter (*). **8.** Late divider in dorsal view. Dark stained zones (?). Ma, fused macronuclear nodules; Mi, micronucleus; R4–R6, parental rows four to six; VI, anlage six of the proter; I'–VI', anlagen one to six of the opisthe. Scale bars = 50 μm .

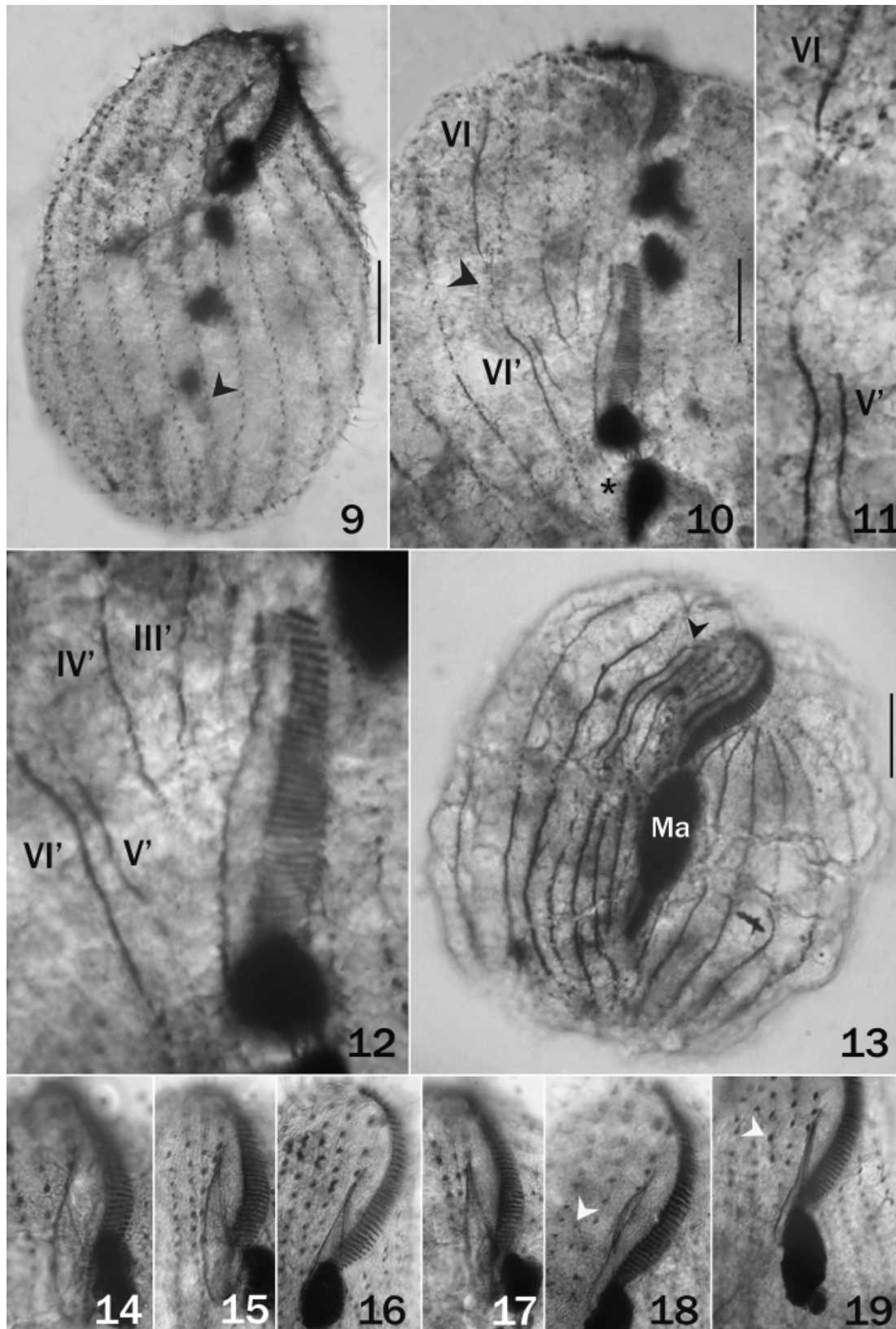


Fig. 9–19. Micrographs of *Deviatia polycirrata* n. sp. in interphase (9, 14–19) and during morphogenesis (10–13) after Protargol impregnation. **9.** Interphase organism in ventral view. Cirral row that ends subequatorially (arrowhead). **10.** Middle divider in ventral view. Field of basal bodies (arrowhead). Posterior fragment of parental row R5 (*). **11.** Magnification of field of basal bodies between anlagen VI and VI'. **12.** Magnification of the right side of oral primordium of the opisthe. **13.** Late divider. Connection of anterior fragment of parental R6 with the new row generated by anlage VI of the proter (arrowhead). **14–19.** Disposition of undulating membranes. Arrowheads point to additional cirri (18, 19). Ma, fused macronuclear nodules. Scale bars = 50 μ m.

Table 2. Morphometric data on *Deviata bacilliformis*.

Character	$\bar{X}$	M	Min.	Max.	SD	n
Body length in vivo	105.7	105	65	154	28.5	10
Body width in vivo	44.8	42	35	70	10	10
Body length	111	112	98	133	12.9	15
Body width	56.5	56	42	70	8	15
AZM, length	24	24.5	21	28	2.2	15
Adoral membranelles, number	21	21	19	24	1.5	15
Cytopharyngeal fibers, length	37.2	39.2	28	42	5.4	5
Macronuclear nodules, number	2	2	2	2	0	15
Macronuclear nodules, length	20.2	19.6	14.7	30.1	5	15
Macronuclear nodules, width	7.2	7.7	5.6	8.4	1	15
Micronuclei, number	2.7	2	2	4	0.7	15
Micronucleus, length	2.5	2.4	2.1	3.1	0.3	15
Micronucleus, width	2.3	2.1	2.1	2.8	0.3	15
Frontal cirri, number	3	3	3	3	0	15
Cirri behind rightmost frontal cirrus, number	1	1	1	1	0	15
Buccal cirri, number	1	1	1	1	0	15
Long rows of cirri, total number	11	11	9	13	1	15
Right long rows of cirri, number	5.5	6	4	6	0.6	15
Left long rows of cirri, number	5.1	5	4	7	0.7	15
Cirri in R4, number	4	4	3	5	0.6	15
Cirri in R5, number	10.6	10.5	9	13	1.3	10
Cirri in R6, number	27.8	27	24	33	2.6	10
Cirri in R7, number	23.4	23	16	32	4.1	10
Cirri in R8 number	22.3	21.5	16	32	4.1	10
Cirri in R9, number	17.5	17.5	15	21	2	10
Cirri in L1, number	21.1	20.5	18	25	2.5	10
Cirri in L2, number	18.8	19	14	24	3	10
Cirri in L3, number	18.4	17	16	23	2.5	10
Cirri in L4, number	18.4	18	15	24	3.1	10
Cirri in L5, number	19.7	19	16	25	2.9	10
Cirri in L6, number	21	21	21	21	0	1
Cirri in L7, number	19	19	19	19	0	1
Dorsal kineties, number	1	1	1	1	0	15
Dikinetids in dorsal row, number	15.4	15.5	12	17	1.4	10

See abbreviations in Table 1.

extra short row of nine cirri posterior to the buccal vertex. In one further specimen, R3 surpassed the buccal vertex, while R4 ended at the center of the body.

Notes on morphogenesis of cell division in *Deviata polycirrata* n. sp. (Fig. 5–8, 10–13). A few well silver-impregnated middle and late dividers were observed. Unfortunately, no early dividers were found. In the middle divider (Fig. 5–6, 10–12), the adoral zone of membranelles of the opisthe is almost completely differentiated, although some basal bodies at its posterior end are still not forming membranelles. The anlagen I'–IV' of the opisthe are lengthened and very likely developed from the oral primordium. The parental right row R6 has split earlier and formed a long primary primordium anteriad, which developed parallel to and on the right side of the anterior fragment of parental row R6. This long primary primordium split into anterior and posterior secondary primordia, becoming the Anlage VI of the proter and Anlage VI' of the opisthe. An irregular field of basal bodies remains between both these anlagen (Fig. 5, 11). Anlage VI' of the opisthe lengthens posteriad by kinetosomal proliferation within its length. Anlage V' of the opisthe apparently developed from the field of basal bodies (disaggregated cirri) between the Anlagen VI and VI', migrated posteriad, and is about to connect to parental row R5. At this stage, the anterior fragment of parental row R6 remains unchanged. The undulating membranes (UM) of the proter are in the process of dedifferentiation. The leftmost frontal cirrus differentiates from the distal end of the UM primordium and Anlage II from disaggregating cirri of parental row R2. Anlage III of the proter is still not generated. In the right paren-

tal rows of cirri R7–R10 anlagen are developing at an equatorial location within the rows. The left parental rows of cirri remain unchanged. Dorsal kinety anlagen are also developing within the rows at two levels in parental kineties D1 and D2, but only at the posterior part of parental dorsal kinety D3. Parental dikinetids remain among the new basal bodies. The macronuclear nodules are still not fused.

In the late divider (Fig. 7, 8, 13) there are supernumerary rows and the new cirri are segregated. The new row generated by Anlage VI of the proter is about to connect with an anterior fragment of row R6 (Fig. 7, 13). Apparently, the proters Anlage V developed within the anterior parental fragment of row R6. Anlage IV of the proter could have developed within the parental row R5 posteriad. There is an extra row between Anlagen III and IV, possibly resulting from a complex neokinetal anlagen development. The UM of the proter are reorganizing and have arisen from a longitudinal split of Anlage I. The leftmost frontal cirrus differentiated from the distal end of the UM primordium and the cirri of Anlagen II and III are already segregated. The new cirri from anlagen I' to VI' of the opisthe are also segregated and only a few widely spaced parental cirri remain posteriorly. There is an extra row on the right of Anlage VI', which seems to be resorbing and could also be the result of a neokinetal anlage. The adoral zone of the opisthe is completely differentiated and Anlage I' split longitudinally to form both UM. In the remaining right and left long rows of cirri (i.e. R7–R9, L1–L11) two anlagen developed within parental rows of cirri, one anteriorly and another posteriorly, from which almost all new cirri are segregated. The dorsal kineties are

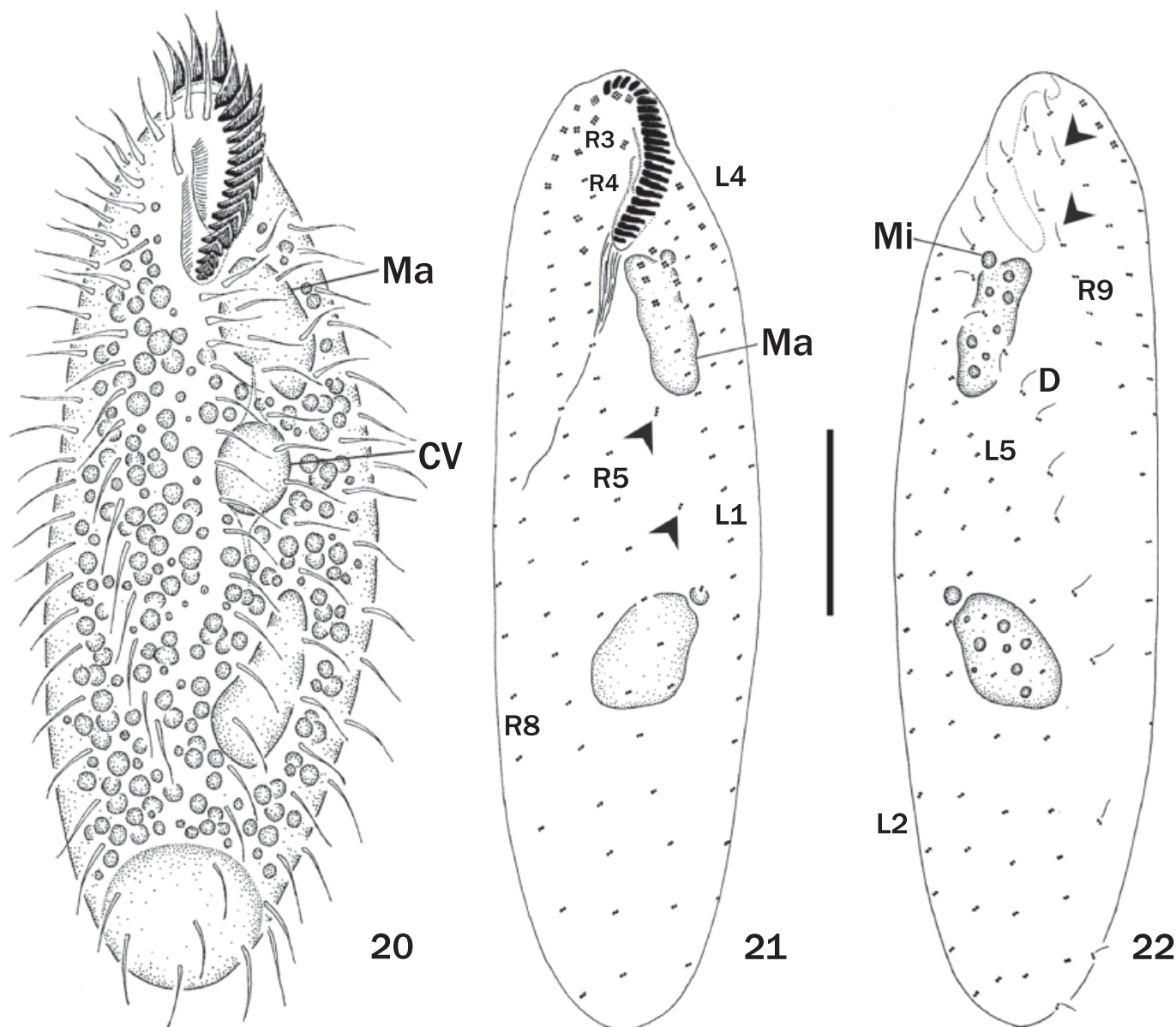


Fig. 20–22. Morphology of *Deviata bacilliformis* from Argentina. 20. Ventral view in vivo. 21. Ventral view after Protargol impregnation. Barren basal bodies (arrowheads). 22. Dorsal view after Protargol impregnation. Combined cirral rows (arrowheads). CV, contractile vacuole; D, dorsal kinety; Ma, macronuclear nodule; Mi, micronucleus; L1–L5, left rows of cirri one to five; R3–R9, right rows of cirri three to nine. Scale bar = 20 μ m.

lengthened by development within the rows. Dorsomarginal kineties and caudal cirri are not formed. Extra rows of cirri are later resorbed because parental cirral rows are absent in the interphase organisms. Macronuclear nodules appear condensed in a single unified structure, and the micronucleus is dividing.

Description of an Argentinian population of *Deviata bacilliformis* (Gelei, 1954) Eigner, 1995 (Table 2 and Fig. 20–27).

The body size in vivo is of length 65–154 μ m and width 35–70 μ m. The body shape is variable; sometimes it is vermiform, other times it is slightly pyriform and wider, round in cross section but dorsoventrally flattened anteriorly. The cytoplasm is grayish-blackish at low magnification ($<10\times$) due to inclusions. Cortical granules are absent. The contractile vacuole is located on the left in midbody and have anterior and posterior collecting canals (Fig. 20). The macronucleus is composed of two nodules that are variable in shape. Some specimens have two ellipsoidal or reniform

nodules, while in other specimens the anterior-most nodule is bilobed. There are two to four spherical or ellipsoidal micronuclei. The adoral zone is composed of 19–24 membranelles and represents approximately 22% of the total body length (calculated on the average values measured on silver-impregnated cells). In the frontal field, there are nine cirri, which are termed R1–R4. The R1 has one cirrus—the leftmost frontal cirrus; R2 has two cirri—the middle frontal cirrus and the buccal cirrus; R3 has also two cirri—the rightmost frontal cirrus and one cirrus behind it; R4 begins on the right of the cirrus behind the rightmost frontal cirrus and is composed of three to five cirri (Fig. 21). The anterior-most frontal cirri have nine basal bodies each, while the cirrus behind the rightmost frontal cirrus is composed of six basal bodies. There are 9–13 long rows of cirri. Five (4–6) of these rows are located on the right of the adoral zone of membranelles, while 5 (4–7) are on the left of it. The first row that extends past the buccal vertex is

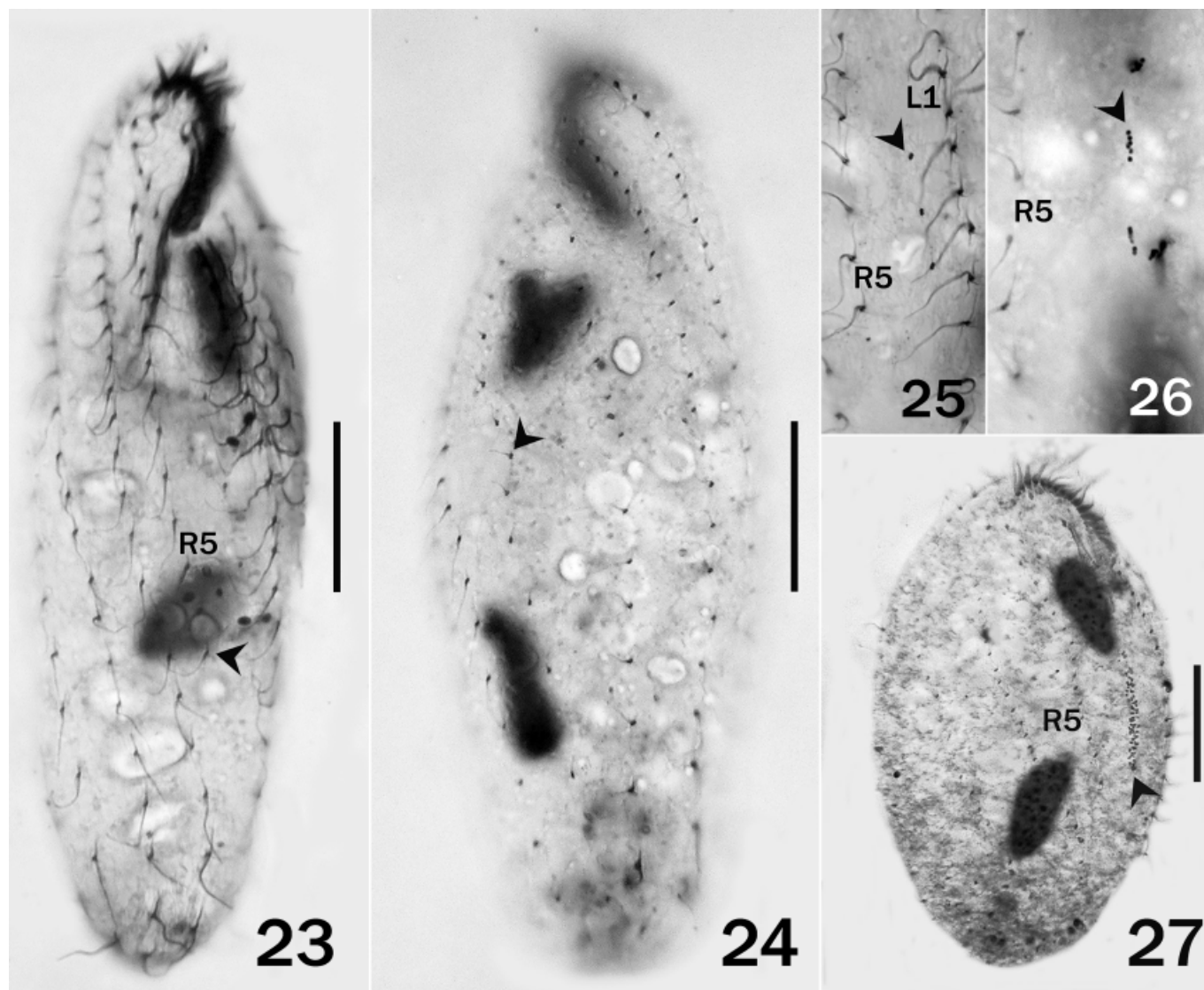


Fig. 23–27. Micrographs of *Deviata bacilliformis* in interphase (23, 24) and during stomatogenesis (25–27) after Protargol impregnation. 23. Ventral view. Long row that ends subequatorially (arrowhead). 24. Dorsal view. Dorsal kinety (arrowhead). 25, 26. Magnification of proliferating barren basal bodies between R5 and L1 (arrowheads). 27. Anarchic field of basal bodies of the oral primordium (arrowhead). L1, left long row one; R5, right long row five. Scale bars = 20 µm.

R5, which begins nearly at the same level as the last cirrus of R4 and extends just posterior to the equator of the cell. The anterior-most cirri of long rows are composed mainly of four basal bodies each, while the cirri behind them have only two basal bodies each, and are consequently more delicate. There are combined cirral rows on the dorsal surface: the two rows on the right of the dorsal kinety are preceded by two pairs of dikinetids with the anterior basal body bearing a cilium (Fig. 22). The single dorsal row of dikinetids extends from the anterior to the posterior of the body, and is parallel to the last left row of cirri, which is generally L5 (Fig. 22).

A few specimens were observed in the first stages of stomatogenesis (Fig. 25–27). One to three pairs of non-ciliferous basal bodies proliferated between the row of cirri that ends subequatorially (R5) and the first left long row of cirri (L1). These cirri apparently were formed *de novo* and later a longitudinally elongated anarchic field develops between R5 and L1. The contribu-

tion of the posterior cirri of the adjacent right row R5 to this oral primordium was not observed.

Deviata bacilliformis was isolated from soil samples from a dried temporary pond collected in January 2004 and rewetted in December 2006, and from samples collected and rewetted in January 2005.

DISCUSSION

The new kahliellid species, *D. polycirrata* n. sp., was placed within the genus *Deviata* on the basis of the following significant features: it usually presents a long ventral row of cirri that terminates subequatorially, typical parental cirral rows are absent; and the mode of replication of some right ventral rows of cirri, which develop multiple anlagen within the row during division morphogenesis (Eigner 1995). It is worth mentioning that *D. polycirrata*

n. sp. resembles *Parastrongylidium* because there are numerous spiraled rows of cirri, but in *Parastrongylidium* most of these rows replicate by means of anlagen generated within the parental rows (Aesch and Foissner 1992; Fleury and Fryd-Versavel 1984).

Comparison of *Deviata polycirrata* n. sp. with congeners. At the moment, there are four species described within the genus *Deviata*. These species can be distinguished by the number and disposition of dorsal rows of dikinetids and/or the number of macronuclear nodules (Berger and Foissner 1987). *Deviata polycirrata* n. sp. differs from the type species, *Deviata abbrevescens* Eigner, 1995, mainly in the number of dorsal kineties (3 vs. 2), the number of cirral rows (17–21 vs. 7–8), and the number of adoral membranelles (39–48 vs. 19–26, respectively; Eigner 1995). Compared with *D. bacilliformis*, this newly isolated species not only possesses a higher number of dorsal kineties (3 vs. 1), more cirral rows (17–21 vs. 9–10), and more adoral membranelles (39–48 vs. 18–21, respectively), but also its contractile vacuoles are different because there are collecting canals only in *D. bacilliformis* (Berger and Foissner 1987; Eigner 1995; Gelei 1954). Moreover, the species described by Fleury and Fryd-Versavel (1984) as *D. bacilliformis* (formerly *Kahliella bacilliformis*) has 3 dorsal kineties, but unlike *D. polycirrata* n. sp. there are 7–10 long rows of cirri. As was suggested by Eigner (1995), the isolate of Fleury and Fryd-Versavel (1984) is possibly a different species. In contrast to *D. polycirrata* n. sp., the type population of *D. estevesi* has 2 dorsal kineties, 10 rows of cirri, 28–33 adoral membranelles, and the contractile vacuole is also located in mid body, away from the margins. Siqueira-Castro et al. (2009) transferred *D. estevesi* to the genus *Parastrongylidium* after studying its morphogenesis. The new kahliellid described here differs from *D. rositae* in the number of macronuclear nodules (4 vs. 7–14), the number of dorsal kineties (3 vs. 2), the number of rows of cirri (17–21 vs. 6), and the number of adoral membranelles (39–48 vs. 14–18, respectively) (Küppers et al. 2007). Finally, like *D. polycirrata* n. sp., *D. brasiliensis* Siqueira-Castro, Paiva & Silva Neto, 2009 usually has 4 macronuclear nodules, but these species differ in the number of long rows of cirri (17–21 vs. 7–11), the number of dorsal kineties (3 vs. 2), and the number of adoral membranelles (39–48 vs. 18–31, respectively).

Within the genus *Kahliella* Corliss, 1960 there are some species with four macronuclear nodules that should also be compared with the new isolate reported here. *Kahliella spirostoma* Alekperov, 1988 was found among putrefying vegetation from a freshwater reservoir in Azerbaijan (Alekperov 1988) and, like *D. polycirrata* n. sp., has a high number of adoral membranelles (45–50 vs. 39–48) and three dorsal rows of bristles, but the latter differ in the number of long rows of cirri (3 rows on the right of the adoral zone of membranelles (AZM), 2 rows on the left of it vs. 8–9 on the right of the AZM and 9–13 on the left of it). Another species with four macronuclear nodules is *Kahliella quadrinucleata* Dragesco, 2003; but relative to that species, the new isolate described here presents also a higher number of long rows of cirri (17–21 vs. 10–12), of dorsal kineties (3 vs. 2), and more adoral membranelles (on average 43 vs. 22). Unlike the species described in the genus *Deviata*, in both *K. spirostoma* and *K. quadrinucleata*, the first right long row of cirri on the ventral side terminates at the posterior end of the body, as can be seen from the illustrations in Alekperov (1988) and in Dragesco (2003). In *Deviata* this row ends equatorially, and this characteristic is considered diagnostic for the genus (Eigner 1995). Further morphological and ontogenetic studies on *K. spirostoma* and *K. quadrinucleata* are needed to determine whether these species should be transferred to the genus *Deviata*.

Notes on morphogenesis during cell division of *Deviata polycirrata* n. sp. We observed some well silver-impregnated morphogenetic stages that should be compared with the morpho-

genesis of *D. abbrevescens* studied by Eigner (1995), and with that of *D. brasiliensis* studied by Siqueira-Castro et al. (2009). In the new isolate, Anlagen VI for the proter and for the opisthe (VI') seem to develop from a split long primary primordium. Anlage V' of the opisthe is generated in the field of basal bodies (disaggregated cirri) between the fragmented long primary primordium (Anlagen VI and VI') and later deviates to and develops within the posterior fragment of parental row R5, as occurs in *D. abbrevescens* and possibly in *D. brasiliensis*. On the contrary, the rows R4 and R5 of the proter seem to be generated in a different way in the three species. In *D. polycirrata* n. sp., Anlagen IV and V of the proter possibly develop from R5 and R6, respectively; while in *D. abbrevescens* Anlage IV originates in R4 (14 in Eigner 1995) and further extends into R5 (15), with Anlage V originating from the anterior region of R6 (16). In *D. brasiliensis*, Anlagen IV and V are formed in the anterior regions of R4 and R5, respectively. In addition, in the present new species some morphogenetic events occur at a different time compared with *D. abbrevescens*. For instance, at the same time the long primary primordium splits and the Anlage V' is connected to the posterior parental fragment of row R5, Anlagen IV and V of the proter are still not generated. A comparison of Eigner's Fig. 12 would indicate that these phenomena occur at the same time in *D. abbrevescens*. In the late divider, when Anlage VI of the proter is about to connect with the old parental anterior fragment of row R6 in *D. polycirrata* n. sp., there are extra rows between Anlagen III and IV of the proter and also an extra row on the right of Anlage VI' of the opisthe. As has been stated by Eigner (1995), these extra rows could result from the complex neokinetical anlagen development and are later resorbed, because extra rows are absent in the interphase organism. The field of barren basal bodies between Anlagen VI of the proter and Anlage VI' of the opisthe was not mentioned by either Eigner (1995), or Siqueira-Castro et al. (2009). These basal bodies persisted in the late divider as well.

The presence of extra rows of cirri in four interphase specimens from the present study is not considered as retention of parental cirri, because these were densely packed within the rows and the rows did not have half the cirri of a neighboring row, as was suggested by Eigner (1995) to recognize a retained parental row in interphase. These specimens could also be interpreted as postdividers with parental or neokinetically generated rows still unresorbed completely.

Further studies are needed to make a complete description of the morphogenesis during cell division of *D. polycirrata* n. sp., although the observations on the few dividers found support the placement of the new isolate within the genus *Deviata*. As stated in preceding paragraphs, *D. polycirrata* n. sp. typically differs from all its congeners by having three dorsal rows of dikinetids, a higher number of cirral rows, and a higher number of adoral membranelles. Unfortunately, gene sequence data were not surveyed at the time of preparing the slides in 2004. Nowadays, these data are increasingly being considered necessary for the accurate description of new species of protists, especially in those forms that are not as rich in morphological features (Lynn and Simpson 2009). Nevertheless, morphological traits make this new isolate clearly different from the other species within the genus *Deviata* and diagnosis of the ciliate as a new species is warranted.

Subclass Stichotrichia Small & Lynn

Family Kahliellidae Tuffrau

Deviata polycirrata n. sp.

Diagnosis. Body size in vivo, 130–180 × 45–70 µm, with 8–9 long cirral rows on the right of the adoral zone membranelles and 9–13 on the left of the latter, plus 3 long dorsal rows of dikinetids. Adoral zone with 39–48 membranelles. With four macronuclear

nodules and one to two micronuclei. Single contractile vacuole located on the left body margin.

Etymology. The term *polycirrata* is a composite from the Greek *poly-* (many), and the Latin *cirratus* (cirrated, curly-haired), and refers to the presence of numerous rows of cirri.

Type locality. Near Dolores city, Buenos Aires Province, Argentina, near the Provincial Route No. 63 (36°18'55"S, 57°32'12"W).

Type habitat. Temporary pond covered by the floating macrophytes *Lemna* sp., *Spirodella* sp., and *Limnobioum spongiae*. The new isolate was found under the following physical-chemical conditions, which were measured at the sampling site: pH 7; electrical conductivity, 242 µS/cm; water temperature, 15.5 °C; total dissolved solids, 0.16 g/l; depth, 40–55 cm.

Type material. One Protargol-stained hapantotype slide is deposited in the Colección de Invertebrados from Museo de La Plata, Buenos Aires Province, Argentina (accession number MLP 63), and a paratype slide is registered in the Ciliate Type Slide Collection of the Smithsonian Institution, Washington, USA (accession number USNM1135042).

Deviata bacilliformis was discovered in Hungary (Gelei 1954) and later recorded by other authors in Israel (Berger and Foissner 1987). Fleury and Fryd-Versavel (1984) found it in France, although it was possibly misidentified (Eigner 1995). In Africa, Dragesco (2003) recorded *D. bacilliformis* in moss samples from Rwanda, and Foissner, Agatha, and Berger (2002) found this species in terrestrial habitats from Namibia. For Argentina and the rest of South America, it represents a new finding. The morphological characters of *D. bacilliformis* in this study differ from the observations of Berger and Foissner (1987) in the number of rows of cirri (9–11 or occasionally 13 vs. 10–11), the number of macronuclear nodules (invariably 2 vs. 2–4), and in the presence of combined cirral rows on the dorsal surface. The most constant trait in the Argentinian population, comparable to the European isolates, is the pattern of cirri in the frontal field. In contrast, the African population of *D. bacilliformis* described by Dragesco (2003) presents three to five macronuclear nodules, and as seen from the illustrations (fig. 33–37 in Dragesco 2003), there are two cirri behind the rightmost frontal cirrus (vs. one cirrus in the present study and in Berger and Foissner 1987), and the short row of cirri in the frontal field is lacking (R4 with three to five cirri in the present study; row five with three to six cirri in Berger and Foissner 1987).

The formation of the oral primordium during the morphogenesis in *D. bacilliformis* begins apparently de novo, from the barren basal bodies between R5 and L1. These basal bodies proliferate and an anarchic longitudinal field develops between R5 and L1. In *D. abbrevescens* stomatogenesis begins with the proliferation of basal bodies by disaggregation of the fifth and sixth posterior cirri of the row that ends at the center of the ventral surface (I4 sensu Eigner 1995), eventually forming two conspicuous fields that later fuse. Then the posteriormost cirri of I4 contribute to the formation of triangle-shaped primordium that differentiates the membranelles. Whether posteriormost cirri of R5 contribute to the formation of the oral primordium in *D. bacilliformis* could not be determined because individuals in later stages of stomatogenesis were not found. The presence of non-ciliferous basal bodies between the right row that ends at the subequatorial region of the cell and the first left row of cirri was also observed in *D. rositae*, although specimens in subsequent morphogenesis stages were also not found by Küppers et al. (2007). Siqueira-Castro et al. (2009) also reported similar structures in one specimen of *D. brasiliensis*, but with no apparent relationship to the formation of the oral primordium. It is worth mentioning that stomatogenesis is apokinetal in *Parastrogylidium martini* Fleury and Fryd-Versavel, 1984 and

Aescht and Foissner (1992) stated that the morphogenesis of *Parastrogylidium oswaldi* Aescht and Foissner, 1992 occurs as in *P. martini*. Further ontogenetic studies of species within the genus *Deviata* are necessary to ascertain the stomatogenetic mode, with the phylogenetic consequences that these would imply, and also to clarify the complex neokinetal anlage development in some ventral cirral rows.

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