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Amphisiella annulata (Kahl, 1928) Borror, 1972 (Ciliophora: Hypotricha): Morphology, Notes on Morphogenesis, Review of Literature, and Neotypification

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Summary. The morphology and some morphogenetic details of the marine hypotrich *Amphisiella annulata* (Kahl, 1928) were investigated using live observation and protargol impregnation. The population from the Adriatic Sea matches almost perfectly the authoritative redescription by Kahl (1932). Characteristic features of *A. annulata* are (i) several ring-shaped structures (lithosomes?) 4-8 µm across scattered throughout the cytoplasm; (ii) the very narrowly spaced and rather wide cirri of the amphisiellid median cirral row; and (iii) the formation of an additional cirral anlage between the ordinary anlagen IV and V. This additional anlage produces only a transverse cirrus so that *A. annulata* has six transverse cirri. In addition, the oral primordium is formed from several roundish anlagen pits which originate left of the middle and rear portion of the amphisiellid median cirral row, resembling the situation in *A. marioni*, type of the genus. The literature on *A. annulata* is reviewed, showing that this conspicuous and thus easy to identify species has been recorded only about 11 times since its discovery before 75 years. The population from the Italian coast of the northern Adriatic Sea is designated as neotype because (i) no preparations are available of the original type population from saltwater in North Germany; (ii) synonymy with an older species was proposed in the revision by Hemberger (1982); and (iii) the descriptions available so far do not agree very well.

Key words: Adriatic Sea, cell division, Italy, marine ciliate, reorganization.

INTRODUCTION

The original description of *Holosticha annulata* is very brief (Kahl 1928b). Kahl (1932) reinvestigated this salt water hypotrich and provided more data and a much better illustration. The cirral pattern resembles that of *Amphisiella marioni*, type of *Amphisiella*. Consequently Kahl classified the present species in the subgenus *Holosticha (Amphisiella)*. The redescriptions by Borror (1963) and Aladro Lubel (1985) are based on live observations only and therfore did not increase the knowledge about this species significantly. Recently, Alekperov and Asadullayeva (1999) found *A. annulata* in the Caspian Sea. Their silver preparations basically confirmed Kahl's (1932) data.

In spring 2002, I found this hypotrichous ciliate in the northern Adriatic Sea. Live and protargol preparations showed that Kahl (1932) recognized the cirral pattern more or less perfectly. In addition, the present study revealed some interesting morphogenetic features in *Amphisiella annulata*.

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MATERIALS AND METHODS

Sampling and culture. *Amphisiella annulata* was found in a sample which I collected at the sandy beach of the northern Adriatic Sea ahead the campground Pra' delle Torri (45°34'N 12°49'E) near the Italian village of Duna Verde on 25.05.2002. The sample contained mainly seagrass run ashore and sand. It was transported to Salzburg (Austria) in a 1-litre bottle. In the laboratory raw cultures were established using Petri dishes 15 cm across filled with sea water from the sample site. Some squashed wheat grains were added to support microbial growth.

Morphological methods. Cells were studied in life using, inter alia, a high-power oil immersion objective and differential interference contrast optics. Live measurements were made at magnifications of 125-1250×. Although live values are more or less rough estimates, it is worth giving such data as specimens usually contract during fixation or shrink in preparations. The infraciliature was revealed with the protargol method according to protocol A in Foissner *et al.* (1999). Counts and measurements on prepared specimens were performed at a magnification of 1250×. Illustrations of live specimens are based on freehand sketches, while those of prepared cells were made with a camera lucida. Five neotype slides of protargol preparations are deposited in the Oberösterreichische Landesmuseum in Linz (LI), Austria (accession numbers 2003/146-150). The specimens illustrated and some used for morphometric analysis are marked.

The morphometric data shown in Table 1 are repeated in the description only as needed for clarity. All observations are from raw cultures, that is, not from clones. Consequently, it cannot be excluded that similar species are mixed, although this is very unlikely because specimens which deviate in at least one important character are excluded. Certainly, this can generate some bias in the data, if applied to uncritically. However, I usually excluded only such individuals which have, for example, a different nuclear structure (very likely often postconjugates), a distinctly deviating cirral pattern (very likely often injured, regenerating, or malformed specimens), or an unusually small size (very likely often degenerating or just divided specimens). The inclusion of such specimens would artificially increase variability.

Nomenclature and terminology. For authorship and date of scientific names, see Berger (2001). Terminology is basically according to Eigner and Foissner (1994) and Berger (1999). For the designation of the frontal-ventral-transverse cirri anlagen and cirri, the numbering system by Wallengren (1900) is used.

RESULTS AND DISCUSSION

Amphisiella annulata (Kahl, 1928) Borror, 1972 (Figs 1-23, Table 1)

1928 ***Holosticha annulata*** - Kahl, *Arch. Hydrobiol*., **19:** 212, Fig. 44f (Fig. 17; original description; no type material available).

1932 ***Amphisiella*** (***Holosticha***) ***annulata*** Kahl, 1928 - Kahl, *Tierwelt Dtl*., **25:** 590, Fig. 112 *1* (Fig. 18; authoritative redescription and revision; see nomenclature for correct name).

1933 ***Amphisiella annulata*** Kahl 1928 - Kahl, *Tierwelt N.- u. Ostsee*, **23:** 112, Fig. 17.21 (Fig. 19; guide to marine ciliates; see nomenclature for correct name).

1963 ***Holosticha annulata*** Kahl, 1928 - Borror, *Arch. Protistenk.*, **106:** 511, Fig. 118 (Fig. 20; redescription).

1972 ***Amphisiella annulata*** (Kahl, 1928) Kahl, 1932 - Borror, *J. Protozool*., **19:** 9 (combining author, see nomenclature; revision of hypotrichs).

1985 ***Amphisiella annulata*** (Kahl, 1928) - Aladro Lubel, *An. Inst. Biol. Univ. Méx*., **55:** 25, Lámina 12, Fig. 4 (Fig. 21; illustrated record).

1990 ***Amphisiella annulata*** (Kahl, 1928) - Aladro Lubel, Martínez Murillo and Mayén Estrada, Manual de Ciliados, p. 125, Figure on p. 125 (Fig. 22; review).

1992 ***Amphisiella annulata*** (Kahl, 1928) Kahl, 1930-5 - Carey, Marine Interstitial Ciliates, p. 179, Fig. 701 (guide; the illustration is a redrawing of Fig. 17).

1999 ***Amphisiella annulata*** (Kahl, 1928) - Alekperov and Asadullayeva, *Turkish J. Zool*., **23:** 219, Fig. 8 (Fig. 23; redescription).

Nomenclature. No derivation of the name is given in the original description. The species-group name *annulát·us*, *-a*, *-um* (Latin adjective [m, f, n]; ringed, having a small ring; Hentschel and Wagner 1996) obviously alludes to the ring-shaped structures in the cytoplasm. Kahl (1932, 1933) classified *Amphisiella* as subgenus of *Holosticha*. Thus, the correct name in his reviews is *Holosticha (Amphisiella) annulata* Kahl, 1928. This was obviously overlooked by Borror (1972) and Carey (1992), who assumed that Kahl (1932) has transferred it from the genus *Holosticha* to the genus *Amphisiella* (see list of synonyms). For the sake of simplicity I suggest to fix Borror (1972) as combining author, although he did not formally transfer it to *Amphisiella*.

Improved diagnosis. Body size about 130 × 33 µm in life. Body outline elongate elliptical to oval. Two macronuclear nodules. Cortical granules colourless, arranged mainly along dorsal kineties. Amphisiellid median cirral row extends sigmoidally from near right frontal cirrus to near transverse cirri, consists of about 44 narrowly spaced cirri which are conspicuously wide (4-5 µm!) in middle portion of row. On average 47 adoral membranelles and each 34 cirri in left and right marginal row. More or less invariably 1 buccal cirrus, 1 cirrus behind right frontal cirrus, 3 cirri left of anterior portion of median cirral row, 2 pretransverse ventral cirri, 6 transverse cirri, and 6-7 dorsal kineties. Oral primordium originates from several anlagen pits. Fourth transverse cirrus from left is formed from additional anlage which produces no other cirri.

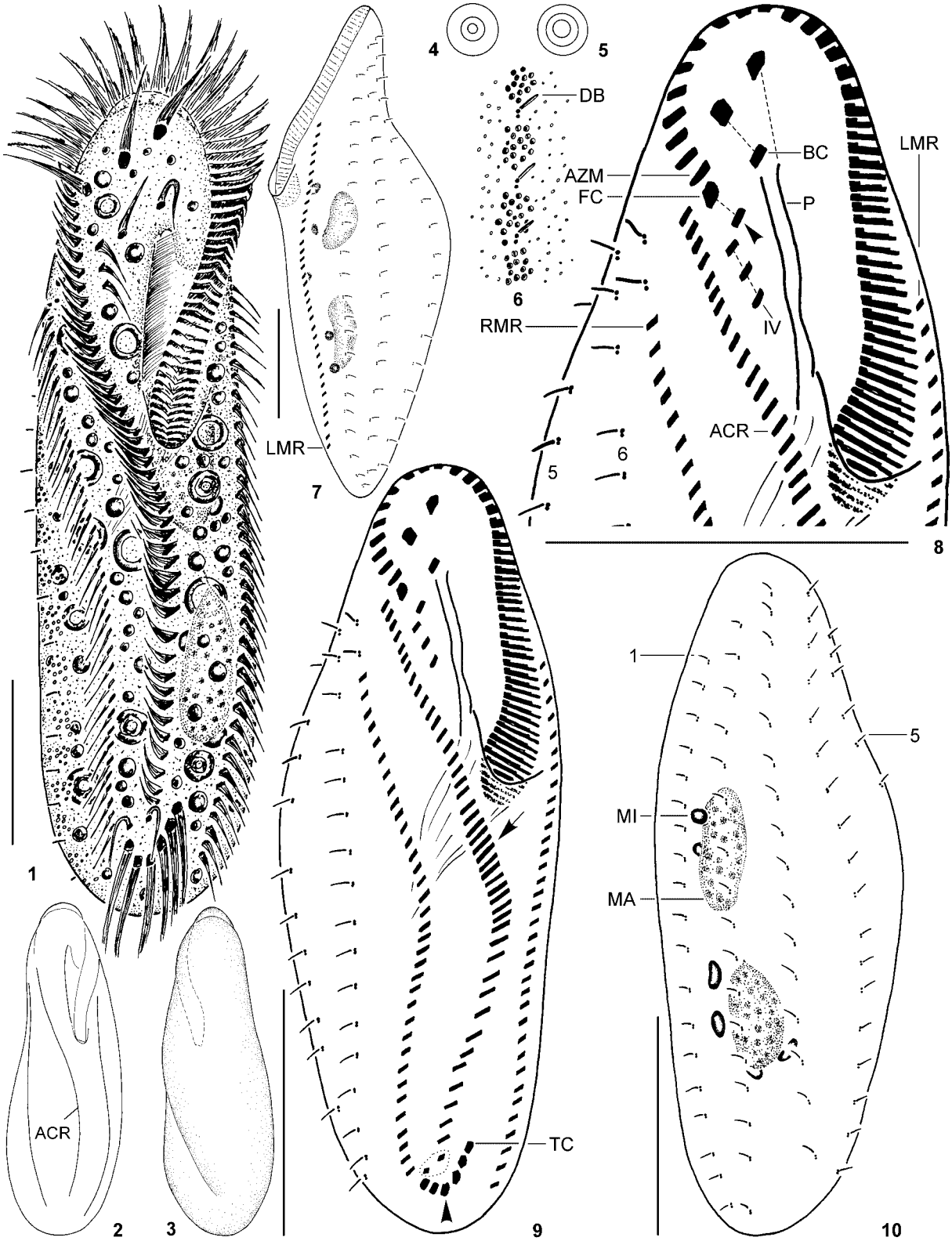
Table 1. Morphometric data on *Amphisiella annulata* [a].

Characteristics	x	M	SD	SE	CV	Min	Max	n
Body, length	96.4	97.0	12.3	2.3	12.8	68.0	121.0	30
Body, width	37.4	36.0	7.7	1.4	20.5	23.0	55.0	29
Body length : width, ratio	2.6	2.5	0.4	0.1	15.9	2.0	3.6	29
Adoral zone of membranelles, length [b]	40.6	40.0	5.1	0.9	12.5	26.0	50.0	29
Adoral zone, relative length (%)	42.3	42.9	4.0	0.7	9.4	33.3	49.5	29
Anterior body end to distal end of adoral zone, distance	11.3	11.5	3.5	0.7	31.0	4.0	19.0	28
Anterior body end to paroral, distance	11.3	12.0	3.1	0.6	27.3	5.0	17.0	28
Paroral, length	17.9	18.0	2.1	0.4	11.9	12.0	22.0	27
Anterior body end to buccal cirrus, distance	9.4	9.0	3.0	0.6	31.9	4.0	18.0	29
Anterior body end to cirrus III/2, distance	12.7	12.0	3.7	0.7	29.0	7.0	22.0	28
Anterior body end to anlagen IV cirri [c], distance	15.9	16.0	3.6	0.7	22.5	9.0	25.0	30
Anterior body end to amphisiellid median cirral row, distance	12.4	12.0	3.6	0.7	28.9	4.0	21.0	28
Anterior body end to left marginal row, distance	20.3	21.0	4.4	0.8	21.7	10.0	30.0	30
Posterior body end to left marginal row, distance	7.0	7.0	2.0	0.4	28.8	4.0	12.0	28
Anterior body end to right marginal row, distance	24.2	24.0	4.6	0.9	18.9	16.0	36.0	30
Posterior body end to right marginal row, distance	6.2	6.0	1.6	0.3	25.7	4.0	11.0	27
Rearmost transverse cirrus to rear body end, distance	4.5	4.0	1.6	0.3	35.4	2.0	8.0	30
Anterior macronuclear nodule, length	19.2	18.0	3.6	0.7	18.6	14.0	29.0	30
Anterior macronuclear nodule, width	6.9	7.0	1.2	0.2	17.0	4.0	9.0	30
Macronuclear nodules, distance in between	5.2	4.5	3.0	0.5	57.8	1.0	12.0	30
Posterior macronuclear nodule, length	18.1	18.0	3.1	0.6	17.2	13.0	27.0	30
Posterior macronuclear nodule, width	7.7	8.0	1.3	0.2	16.8	5.0	10.0	30
Anteriormost micronucleus, length	3.4	3.0	0.8	0.1	22.7	2.0	5.0	30
Anteriormost micronucleus, width	1.7	1.6	0.3	0.1	17.8	1.5	2.5	30
Macronuclear nodules, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	30
Micronuclei near anterior macronuclear nodule, number	2.6	2.5	1.0	0.2	39.2	1.0	5.0	30
Micronuclei near posterior macronuclear nodule, number	3.0	2.5	1.3	0.2	42.9	1.0	6.0	30
Micronuclei, total number	5.6	6.0	1.3	0.2	23.5	3.0	8.0	30
Adoral membranelles, number	47.2	48.0	5.9	1.1	12.4	31.0	57.0	28
Frontal cirri, number	3.0	3.0	0.2	0.0	6.0	3.0	4.0	30
Buccal cirri, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	30
Cirri behind right frontal cirrus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	30
Anlagen IV cirri [c], number	3.1	3.0	0.3	0.0	8.3	3.0	4.0	30
Amphisiellid median cirral row, number of cirri	44.5	45.0	5.7	1.2	12.9	25.0	54.0	24
Pretransverse ventral cirri, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	28
Transverse cirri, number	6.0	6.0	0.2	0.0	3.1	5.0	6.0	29
Left marginal cirri, number	34.6	34.0	3.5	0.6	10.0	25.0	41.0	29
Right marginal cirri, number	34.1	34.0	3.2	0.6	9.3	28.0	41.0	27
Dorsal kineties, number	6.4	6.0	0.6	0.1	9.2	6.0	8.0	23

[a] Measurements in µm. Data based on mounted and protargol-impregnated specimens (only specimens in which most characteristics were measurable, respectively, countable have been used). CV - coefficient of variation in %, M - median, Max - maximum, Min - minimum, n - number of specimens investigated, SD - standard deviation, SE - standard error of arithmetic mean, x - arithmetic mean. [b] Distance between anterior body end and proximal end of adoral zone of membranelles. [c] This is the short cirral row left of the anterior portion of the amphisiellid median cirral row.

Morphology (Figs 1-10, 17-23, Table 1). The improved diagnosis above is solely based on data from the Adriatic neotype population. However, it covers Kahl's data rather well. The ring-shaped structures (lithosomes?), although very conspicuous, have been omitted from the diagnosis because they can be absent (Kahl 1932; see below). The present chapter contains original observations and data from the populations studied by Kahl (1928b, 1932, 1933) and the other workers (Borror 1963, Aladro Lubel 1985, Aladro Lubel *et al.* 1990, Alekperov and Asadullayeva 1999). However, the data are kept separate.

Description of Adriatic population (Figs 1-10, Table 1): Size in life about 100-160 × 30-40 µm (I made only one live measurement, namely 160 × 40 µm; the range is derived from the morphometric data shown in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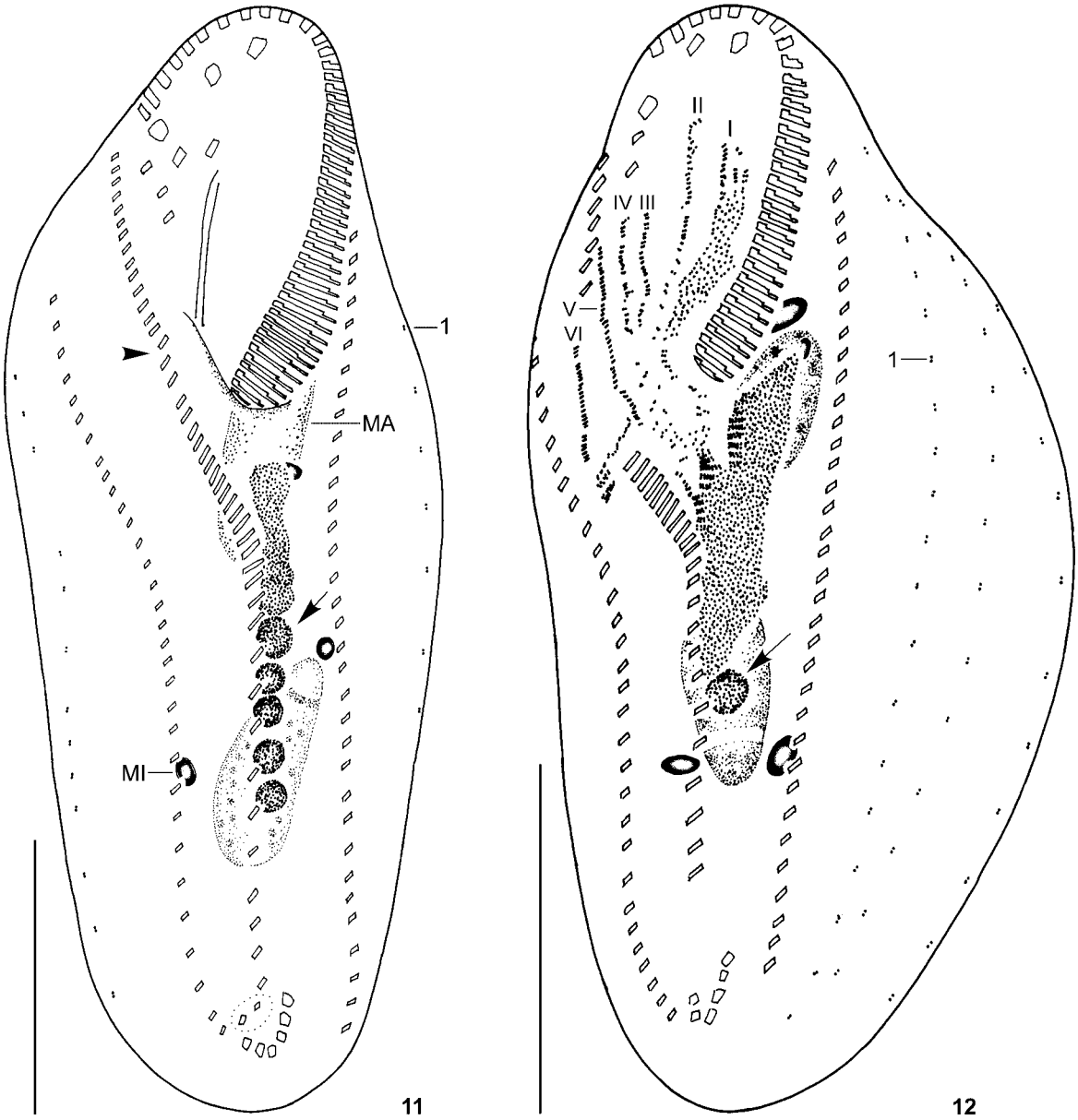
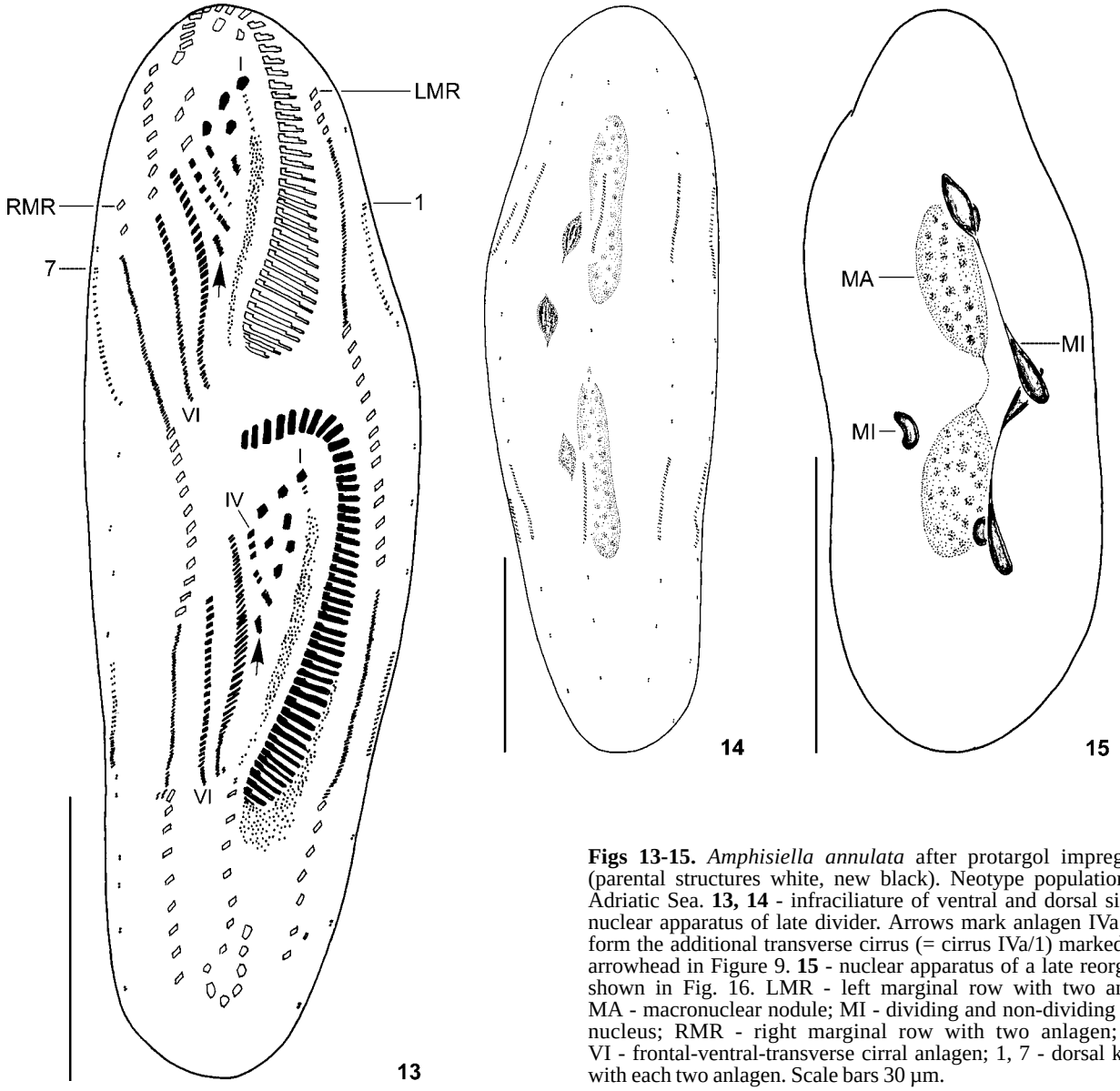


Figs 11, 12. *Amphisiella annulata* after protargol impregnation (parental structures white, new black). Neotype population from Adriatic Sea. **11** - infraciliature of ventral side and nuclear apparatus of early divider. Arrow marks an anlagen pit. Arrowhead denotes discontinuity in amphisiellid median cirral row (site where the 2 portions of the row join). Pretransverse ventral cirri encircled by dotted line; **12** - infraciliature of ventral side and nuclear apparatus of an early to middle reorganizer. Arrow marks an anlagen pit. I assume that this is a reorganizer because in dividers of such a stage the anlagen for both the proter and the opisthe would be recognizable. Note that the additional anlage IVa is not yet clearly recognizable. Area ahead transverse cirri not recognizable because covered by debris. MA - macronuclear nodule; MI - micronucleus; I-VI - cirral anlagen; 1 - dorsal kinety 1 (= leftmost kinety). Scale bars 30 µm.

Figs 1-10. *Amphisiella annulata* from life (1-6) and after protargol impregnation (7–10). Neotype population from Adriatic Sea. **1** - ventral view of a representative specimen. Note ring-shaped structures (hollow globules?); **2, 3** - body outline of posteriorly widened specimens in ventral and dorsal view showing, inter alia, marginal cirral rows, amphisiellid median cirral row, and a dorsal furrow; **4, 5** - ring-shaped structures (hollow globules?) about 4-8 µm across (fine structure not completely discerned); **6** - two size classes of cortical granules are present: (i) 0.8-1.0 µm sized, colourless globules which form patches between dorsal bristles; (ii) tiny (about 0.3-0.5 µm across) colourless globules scattered throughout cortex; **7** - infraciliature of left side. Note strong vaulting of dorsal side, that is, specimens almost not flattened dorsoventrally; **8-10** - infraciliature of ventral and dorsal side and nuclear apparatus of neotype specimen. Arrowhead in (8) denotes cirrus III/2, arrowhead in (9) marks the "additional" transverse cirrus IVa/1 (see Figs 13, 16). Note that the middle portion of the median cirral row is composed of rather wide and narrowly spaced cirri (arrow in 9). Pretransverse ventral cirri encircled by dotted line. Cirri which originate from same frontal-ventral-transverse cirral anlage are connected by broken lines (only shown for anlagen I-IV). ACR - amphisiellid median cirral row; AZM - distal end of adoral zone of membranelles; BC - buccal cirrus (= cirrus II/2); DB - dorsal bristle; FC - right frontal cirrus (= cirrus III/3); LMR - left marginal row; MA - macronuclear nodule; MI - micronucleus; P - paroral; RMR - right marginal row; TC - leftmost transverse cirrus (= cirrus II/1); IV - short row of three cirri left of anterior portion of median cirral row formed by anlage IV; 1, 5, 6 - dorsal kineties. Scale bars 30 µm.



Figs 13-15. *Amphisiella annulata* after protargol impregnation (parental structures white, new black). Neotype population from Adriatic Sea. **13, 14** - infraciliature of ventral and dorsal side and nuclear apparatus of late divider. Arrows mark anlagen IVa which form the additional transverse cirrus (= cirrus IVa/1) marked by an arrowhead in Figure 9. **15** - nuclear apparatus of a late reorganizer shown in Fig. 16. LMR - left marginal row with two anlagen; MA - macronuclear nodule; MI - dividing and non-dividing micronucleus; RMR - right marginal row with two anlagen; I, IV, VI - frontal-ventral-transverse cirral anlagen; 1, 7 - dorsal kineties with each two anlagen. Scale bars 30 µm.

Table 1 assuming a shrinkage of up to 30% due to the preparation procedure; Berger *et al.* 1983); body length : width ratio of live specimens ranging from 3-4 : 1; prepared specimens only 68-121 µm long, length : width ratio on average 2.6 : 1 (Table 1). Body outline elongate elliptical (Fig. 1) to slightly oval (Figs 2, 3), that is, posterior portion wider than anterior; both ends rounded. Body very flexible and often slightly twisted about main body axis, not distinctly contractile, rather resistant against cover glass pressure; ventral side flat, dorsal side often distinctly vaulted so that many specimens are arranged with dorsal or lateral surface above in protargol preparations (Fig. 7). Invariably two macronuclear nodules slightly left of midline; individual nodules ellipsoidal, in life up to about 28 × 12 µm, with many nucleoli of ordinary size; nodules usually connected by fine strand; length : width ratio of anterior nodule ranging from 1.8-4.8 : 1 (average 2.1 : 1), posterior nodule 1.4-3.4 : 1 (average 2.4 : 1; Table 1). Micronuclei ellipsoidal, arranged close to macronuclear nodules. No contractile vacuole recognizable. Two size-classes of colourless cortical granules; larger globules about 0.8-1.0 µm across, form distinct patches between individual bristles of a dorsal kinety; smaller granules about 0.3-0.5 µm across, more or less densely distributed in whole cortex (Figs 1, 6); stainability with methyl-green pyronin not checked; sometimes

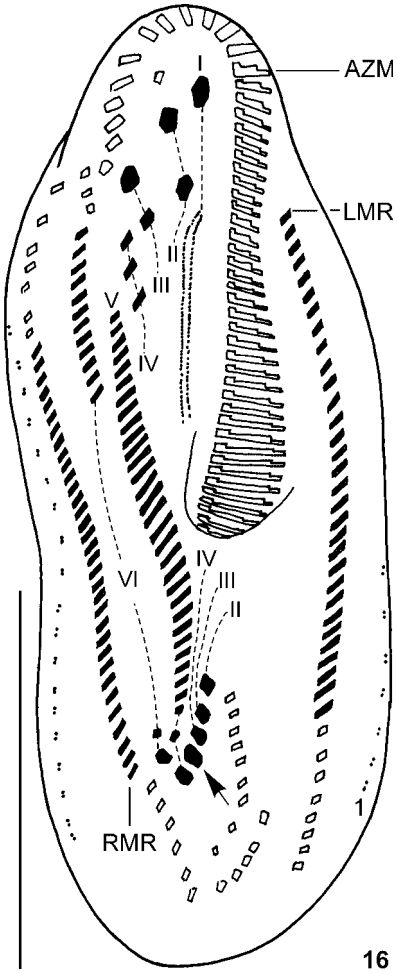


Fig. 16. *Amphisiella annulata* after protargol impregnation (old structures white, new black). Neotype population from Adriatic Sea. Infraciliature of ventral side of a late reorganizer (nuclear apparatus shown in Fig. 15). Cirri originating from same anlage connected by broken line. Arrow marks the additional transverse cirrus originating from the anlage IVa which is formed between anlagen IV and V (see Fig. 13). AZM - adoral zone of membranelles (possibly partially reorganized); LMR - anterior end of new left marginal row; I-VI - frontal-ventral-transverse cirral anlagen; RMR - posterior end of new right marginal row; 1 - dorsal kinety 1 (= leftmost kinety). Scale bar 30 µm.

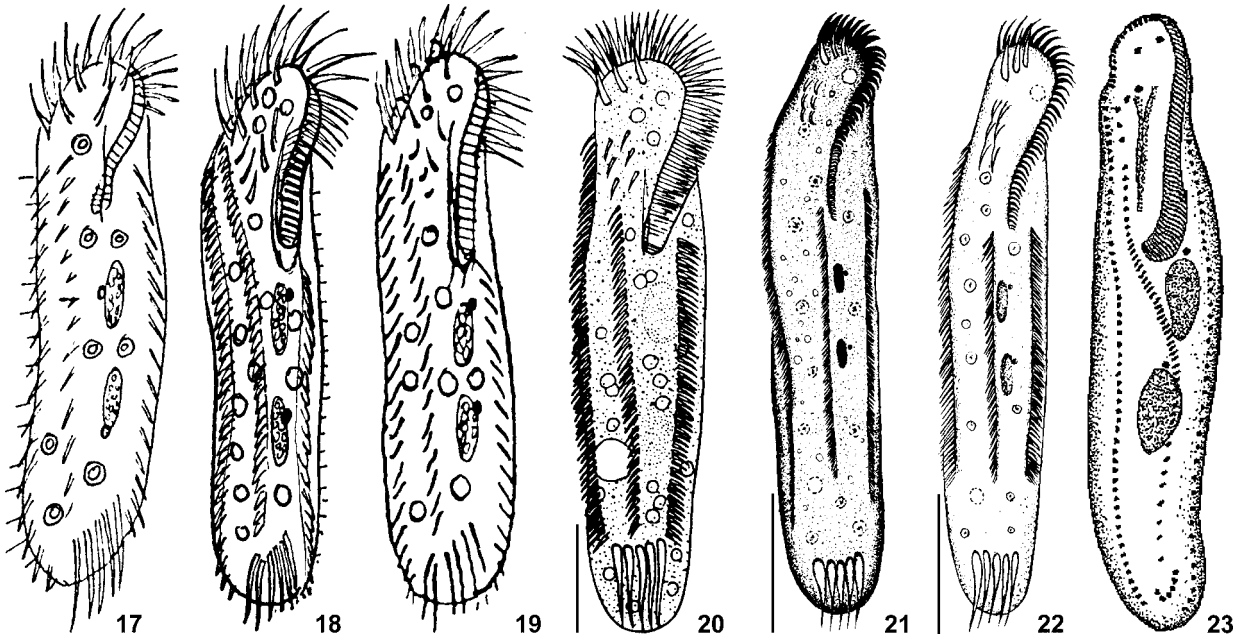
cortical granules impregnate with protargol. Cells appear steel-grey; cytoplasm colourless, contains many fatty-shining globules 2-5 µm across and several (up to about 20) fatty-shining, ring-shaped structures ("hollow" spheres; lithosomes?) about 4-8 µm in diameter (Figs 1, 4, 5); rings not clearly recognizable in protargol preparations. Movement fast gliding showing great flexibility.

Adoral zone occupies 42% of body length, composed of 47 membranelles on average, individual membranelles of ordinary fine structure (Figs 1-3, 7-9). Distal end of adoral zone extends on average to 12% of body length on right body margin, proximal portion usually slightly spoon-shaped widened. Buccal field inconspicuous, that is, narrow to ordinary wide. Buccal lip inconspicuous because it does not cover proximal portion of adoral zone distinctly. Undulating membranes more or less straight and in parallel; fine structure of membranes not clearly recognizable. Cytopharynx inconspicuous in life and protargol preparations.

Cirral pattern and number of cirri of usual variability (Figs 7-10, Table 1). Three distinctly enlarged frontal cirri in ordinary arrangement, that is, in oblique row along anterior body margin with right cirrus (= cirrus III/3) close behind distal end of adoral zone. Invariably one slightly enlarged buccal cirrus (= cirrus II/2) closely ahead anterior end of paroral, and one cirrus (= cirrus III/2; Fig. 8, arrowhead) left behind right frontal cirrus. A short row composed of three, occasionally of four cirri left of anterior portion of amphisiellid median cirral row; very rarely a second such row present. Amphisiellid median cirral row commences right of right frontal cirrus, extends slightly to distinctly sigmoidally close to transverse cirri, composed of 44 cirri on average (Figs 1, 8, 9, Table 1); median cirral row usually without distinct break although composed of two portions (see morphogenesis); cirri narrowly spaced, especially behind buccal vertex where they are also rather wide, that is, up to 4-5 µm! Invariably two pretransverse ventral cirri, one ahead right transverse cirrus, the other roughly in line with amphisiellid median cirral row. Usually six, rarely (1 out of 29 specimens) only five transverse cirri arranged in J-shaped, slightly subterminal row; cirri about 20 µm long in life and thus distinctly (right) to almost not (left) projecting beyond rear body end. Marginal cirri and cirri of amphisiellid median row only 8-10 µm long in life; marginal cirri relatively narrowly spaced. Left marginal row commences distinctly ahead level of buccal vertex, ends subterminally. Right marginal row begins on average at 25% of body length, often more or less distinctly sigmoidal, terminates near right transverse cirrus; usually two ciliated basal body pairs ahead right marginal row (Figs 7-10).

Dorsal cilia 2-3 µm long; about 2/3 of specimens with six and 1/3 with seven more or less bipolar kineties (Figs 7-10); rarely (1 out of 23 specimens analyzed morphometrically) eight kineties. Caudal cirri lacking.

Beside the very brief original description by Kahl (1928b, Fig. 17), four redescriptions are available, namely by Kahl (1932, 1933; Figs 18, 19), Borror (1963, Fig. 20), Aladro Lubel (1985; including a review by Aladro Lubel



Figs 17-23. *Amphisiella annulata* from life (17-19, from Kahl 1928b, 1932, 1933; 20, from Borror 1963; 21, from Aladro Lubel 1985; 22, from Aladro Lubel *et al.* 1990) and silver preparations (23, from Alekperov and Asadullayeva 1999). Ventral views showing, inter alia, basic cirral pattern, nuclear apparatus, and ring-shaped structures. Note that the cirral pattern illustrated by Kahl (1932) matches almost perfectly the pattern of the neotype (Fig. 9). Borror illustrated a large vacuole in the posterior body portion near the right body margin; it must not be misinterpreted as contractile vacuole because Borror did not mention such an organelle; interestingly enough, in Figures 21, 22 a somewhat smaller vacuole (inclusion?) is shown in a very similar position. Scale bars 30 µm for Figs 17-19, 23; individual sizes not indicated; see text for size ranges.

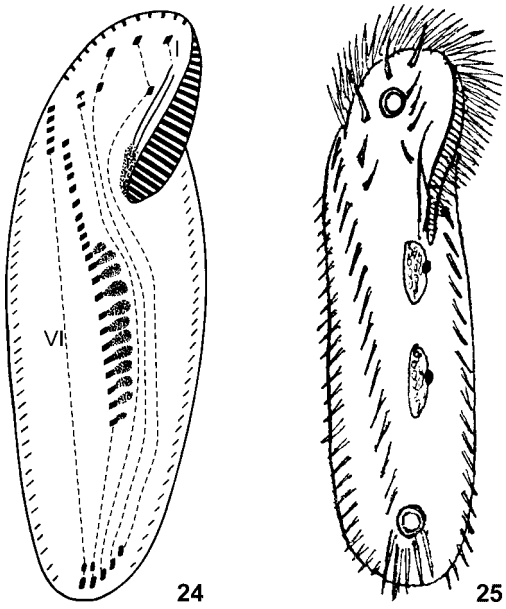
et al. 1990; Figs 21, 22), and Alekperov and Asadullayeva (1999; Fig. 23). To complete the picture of *A. annulata*, I provide the original data of these populations separately; see also corresponding illustrations for some features, for example, body outline, cirral pattern. For a detailed comparison of the populations, see below. The review by Carey (1992) is not considered further because it contains only a redrawing of Figure 17 and lacks original data.

Population described by Kahl (1928b; Fig. 17): body length 120-150 µm in life; five frontal cirri and five long transverse cirri; single ventral row; scattered ring-shaped "reserve bodies"; lively, metabolic, slightly contractile; two elongated macronuclear nodules.

Population described by Kahl (1932, 1933; Figs 18, 19): body length 150-200 µm in life; body slenderly ellipsoidal, soft, flexible, metabolic, slightly contractile, usually greyish granulated, with a variable number (zero to numerous, but never two, that is, never each one in anterior and posterior body portion) of ring-shaped (probably hollow-spherical) reserve bodies; ectoplasm colourless; two elongated macronuclear nodules, each with a single (?) micronucleus; 6-7 transverse cirri (specimen illustrated has 6 cirri) which project slightly beyond rear body end; frontal cirri likely as in *Oxytricha* (3 + 2 + 3; homologisation not quite correct, see last chapter); cirri of marginal rows and ventral row very short, wide, and narrowly spaced; for cirral pattern, see the excellent illustration (Fig. 18); posterior portion of adoral zone of membranelles longitudinally arranged.

Population described by Borror (1963; Fig. 20): body size 160×30-36 µm in life; body evenly rounded at ends, slightly flat ventrally. Two oval macronuclear nodules, each 18 µm long; cytoplasm with many spherical granules 4 µm across. Adoral zone of membranelles 55 µm long, composed of 60-65 membranelles. Nine frontal cirri, the anterior three larger; ventral row composed of about 40 narrowly spaced cirri; five transverse cirri 24 µm long, extending just beyond rear body end; about 50 left and 60 right marginal cirri, very closely set; six dorsal kineties.

Population described by Aladro Lubel (1985; Fig. 21): body size 123×21 µm; body outline elongated; two oval-shaped macronuclear nodules, each with a spherical micronucleus; contractile vacuole in posterior body third (side not mentioned and vacuole likely not illustrated);



Figs 24, 25. Marine *Amphisiella* species (24, from Wicklow 1982; 25, from Kahl 1932). **24** - *Amphisiella marioni* after protargol impregnation, infraciliature of ventral side of a very early divider, individual size not indicated (size range 75-125 µm in life?). Frontal-ventral-transverse cirri originating from same anlage connected by broken line. **25** - *Amphisiella milnei* from life, ventral view showing cirral pattern, nuclear apparatus, and each one ring-shaped structure in the anterior and posterior body portion, individual size not indicated (size range 100-140 µm in life). I, VI - frontal-ventral-transverse cirral anlagen I and VI.

several food vacuoles and cytoplasmic granules; adoral zone about 1/3 of body length; one left and one right marginal row and one ventral cirral row; cirri narrowly spaced in all rows; nine frontal cirri, three anteriormost larger; five transverse cirri which slightly protrude beyond rear body end.

Population described by Alekperov and Asadullayeva (1999; Fig. 23): body length 130-180 µm in life, 110-145 µm in silver preparations. Body elongated, strongly flattened dorsoventrally. Two macronuclear nodules, 2 micronuclei. Contractile vacuole near proximal end of adoral zone. Cytoplasm transparent, without inclusions. Adoral zone composed of 65-70 membranelles. Two frontal cirri near anterior end, 5 further frontal cirri at level of anterior portion of undulating membranes. Amphisiellid median cirral row composed of 48 cirri, extends from rear frontal cirri to near the 6 transverse cirri. 55 right and 40 left marginal cirri. Four dorsal kineties (3 bipolar, 1 shortened). Caudal cirri absent.

Notes on morphogenesis and reorganization. Only few dividers and reorganizers have been found. However, they allow to elucidate some highly interesting morphogenetic features (Figs 11-16). Some early and middle stages of division are lacking so that the origin of the frontal-ventral-transverse cirral anlagen remains basically unknown.

Cell division commences with the formation of some anlagen pits left of the third quarter of the median cirral row (Fig. 11). The pits are roundish and up to 5 µm deep. Very likely the cirri of the median cirral row beside the pits are not altered at this stage. Ahead the five pits of the divider shown is a large field of basal bodies which likely originated by the fusion of some further pits.

Figure 12 shows an early to middle reorganizer in which the anlagen I-VI are clearly recognizable. The additional anlage IVa, which produces the fourth transverse cirrus from left, is not yet clearly recognizable.

A middle to late divider shows the differentiation of the frontal-ventral-transverse cirri which originate from basically six anlagen (I-VI; Fig. 13). A curiosity is the formation of a small basal body field between anlagen IV and V (Fig. 13, arrows). This small basal body field only forms a transverse cirrus, namely the fourth from left. Consequently, the cirral anlagen produce the following structures: anlage I → undulating membranes (paroral, endoral) and left frontal cirrus (= cirrus I/1); anlage II → leftmost transverse cirrus (= cirrus II/1), buccal cirrus (= cirrus II/2), and middle frontal cirrus (= cirrus II/3); anlage III → second transverse cirrus from left (= cirrus III/1), cirrus left behind right frontal cirrus (= cirrus III/2), and right frontal cirrus (= cirrus III/3); anlage IV → third transverse cirrus from left (= cirrus IV/1) and three cirri left of anterior portion of amphisiellid median cirral row; anlage IVa (Fig. 13, arrows; see below, for explanation) → only fourth transverse cirrus from left (= cirrus IVa/1; Fig. 9, arrowhead; Fig. 16, arrow); anlage V → fifth transverse cirrus from left (= cirrus V/1), left pretransverse ventral cirrus (= cirrus V/2), and posterior portion (around 31 cirri) of amphisiellid median cirral row; anlage VI → sixth transverse cirrus from left (= cirrus VI/1), right pretransverse ventral cirrus (= cirrus VI/2), and anterior portion (about 13 cirri) of amphisiellid median cirral row. The parental adoral zone of membranelles remains obviously more or less unchanged whereas the parental undulating membranes are reorganized (Fig. 13).

A late reorganizer shows that the amphisiellid median cirral row of *A. annulata* is formed by cirri of the two rightmost anlagen (Fig. 16). Anlage V produces the posterior portion which commences slightly ahead the level of the buccal vertex in interphasic specimens. The front portion is formed by the anteriorly migrating cirri

(except the right pretransverse ventral cirrus and the right transverse cirrus) of anlage VI. This conspicuous migration enforces the homologisation of the anterior portion with the frontoterminal cirri of the oxytrichids and urostylids. In interphasic specimens the two portions form a continuous row (Fig. 9); only very rarely a discontinuity is recognizable (Fig. 11, arrowhead).

The development of the marginal rows and dorsal kineties does not show a peculiarity. Two primordia each occur within the parental cirral and bristle rows. No caudal cirri are formed (Figs 13, 14). The division of the nuclear apparatus proceeds in ordinary manner, that is, the two macronuclear nodules fuse to a single mass which subsequently divides. The micronuclei behave like those of other hypotrichs (Figs 11, 14).

The morphogenetic pattern of *A. annulata* largely agrees with that of *A. marioni* (Wicklow 1982). Of course there are also several agreements with many other hypotrichs, for example, that the left frontal cirrus originates from the undulating membrane anlage or that the buccal cirrus is the middle cirrus of anlage II. However, these are rather old symplesiomorphies and are therefore not considered further.

A very interesting morphogenetic feature of *A. annulata* is the formation of roundish anlagen pits left of the middle and posterior portion of the median cirral row (Fig. 11). Wicklow (1982) illustrated an early divider of *A. marioni* which shows several roundish patches of basal bodies, strongly resembling the pits of *A. annulata* (Fig. 24). However, Wicklow mentioned no details about this stage so that it is unknown whether these patches are invaginated or flat. Thus, reinvestigation of the morphogenesis of the type species is needed. In most hypotrichs the oral anlage develops on the cell surface (for review, see Foissner 1996). In euplotids, strombidiids, strobilidiids, and few non-euplotid hypotrichs, e.g., *Psilotricha succisa* (Foissner 1983), the anlage originates in a more or less distinct subsurface pouch (= hypoapokinetal stomatogenesis). In *Pseudoamphisiella lacazei* morphogenesis commences with the proliferation of loosely arranged basal bodies below the cortex and therefore parental cirri and fibres remain intact (Song *et al.* 1997). According to molecular data, the oligotrichs/choreotrichs and the euplotids are the next relatives of the remaining hypotrichs (e.g., Bernhard *et al.* 2001, Modeo *et al.* 2003). This indicates that the hypoapokinetal stomatogenesis is a plesiomorphy for the non-euplotid hypotrichs. Unfortunately, we do not know whether or not the roundish pits of *A. annulata* are homologous with the subsurface pouches of the groups mentioned above or with the subcortical formation of the anlagen field in *Pseudoamphisiella lacazei*. If they are not homologous then the anlagen pits can be interpreted as apomorphy of *Amphisiella*.

A further interesting morphogenetic feature of *A. annulata* is the formation of an additional cirral anlage between the ordinary anlagen IV and V. Since all anlagen of *A. annulata* - except this additional one - can be unequivocally homologized with the anlagen of *A. marioni*, I keep the ordinary numbering (I-VI) and designate the additional anlage, more or less arbitrarily, as anlage IVa. This anlage produces only a transverse cirrus so that *A. annulata* has six transverse cirri (Table 1). In contrast, *Amphisiella marioni* lacks such an additional anlage and therfore has the ordinary number of five transverse cirri (see Figs 45a-h in Wicklow 1982). *Amphisiella turanica*, described by Alekperov and Asadullayeva (1999), also has 6 transverse cirri indicating that it forms, like *A. annulata*, an additional anlage.

Occurrence and ecology. *Amphisiella annulata* is a salt water species. Kahl (1928b) discovered it in the Brennermoor, a saline (25‰), silt peat bog near the north German village Bad Oldesloe (Kahl 1928a). Later, he found it in the harbour of the German city of Kiel, Baltic Sea (Kahl 1932). Alekperov and Asadullayeva (1999) isolated their population from the periphyton of the South Apsheron coast of the Caspian Sea. I found *A. annulata* in the littoral of the northern Adriatic Sea at a water temperature of about 20°C (further details on the sample site, see materials and methods). It occurred together with *Uroleptopsis citrina*, *Pseudoamphisiella* sp., and some euplotids. In the cultures the abundance of *A. annulata* was rather low, while *U. citrina* grew very well.

Records from the Gulf of Mexico: rare in diatom detritus from the mouth of a saltmarsh near the Florida State University Marine Laboratory at Alligator Harbor, USA (Borror 1962, 1963); interstitial of Enmedio Island and Laguna de Mandinga, Veracruz, Mexico (Aladro Lubel 1985; Aladro Lubel *et al.* 1988, 1990).

Records not substantiated by morphological data: during summer and winter in the sublittoral (Stoller Grund, Großer Belt) of the Bay of Kiel, Baltic Sea (Bock 1952); Schlei, a polluted, brackish fjord in the western Baltic (Bock 1960, Jaeckel 1962); with a frequency of 2.7% at 21-22°C and 17-18‰ salinity at the Bulgarian coast of the Black Sea (Detcheva 1982, 1983); sediment of Loch Eil on the west coast of Scotland (Wyatt and Pearson 1982).

Amphisiella annulata feeds on small diatoms (Kahl 1932, Borror 1963; for review, see Fenchel 1968). In cultures, it ingests also wheat stark (own observations).

Comparison of *Amphisiella annulata* populations. The original description of *A. annulata* is very brief but contains most diagnostic features (Kahl 1928b). Accordingly, the present species has each five frontal and transverse cirri (Fig. 17). As concerns the frontal cirri, Kahl (1928b) very likely included only the three enlarged frontal cirri, the buccal cirrus, and cirrus III/2. The short row composed of three cirri left of the anterior portion of the median cirral row is less distinct than the other five "frontal cirri" and thus easily overlooked or misinterpreted as anterior end of the median cirral row. Somewhat more difficult is the interpretation of the five transverse cirri because this number was not mentioned by Kahl (1932) and Alekperov and Asadullayeva (1999) and occurred only very rarely in the Adriatic population (Table 1). The following possibilities exist: (i) Kahl (1928b) observed and illustrated a rare specimen which had indeed only five transverse cirri; (ii) Kahl (1928b) did not count correctly. On page 211, Kahl (1928b) wrote that he would like to investigate the species again, indicating that his observations are not very detailed and precise; (iii) the populations studied by Kahl (1928b) and Kahl (1932) are not conspecific. I prefer possibilities (i) and (ii) because it is unlikely that Kahl (1932) did not recognize his own species, inasmuch as it has a conspicuous feature, namely the large, ring-shaped structures. To avoid this permanent uncertainty it seems wise to designate a neotype (see last chapter).

My data match almost perfectly the redescription and illustrations by Kahl (1932, 1933) so that the identification is beyond reasonable doubt. Very likely all identifications listed in the synonymy and the occurrence and ecology section have been done after Kahl (1932), and not after the original description (Kahl 1928b). Consequently, the 1932 review was *de facto* the authoritative redescription. There are only few differences between Kahl's (1932) data and my observations which, however, can be explained: (i) body length is 150-200 µm against 100-160 µm. My sole live measurement, which I made some days before the fixation of the material, was 160 x 40 µm which fits into the range provided by Kahl. Obviously the Adriatic specimens became slightly smaller in cultures as indicated by the morphometric analysis (Table 1). Further, the specimens of Kahl's (1928b) population were also only 120-150 µm long. (ii) Kahl did not mention the cortical granules which are present in the population from the Adriatic Sea. However, the granules are colourless and rather small (0.3-1.0 µm) and thus easily overlooked especially with bright field illumination. Kahl (1932) wrote " ..., usually grey granulated and in between with numerous ring-shaped reserve bodies"; this indicates that the term grey granulated refers to the cytoplasm and not to a cortical granulation. Indeed, the specimens of my population were also steel-grey; however, I do not know whether this impression is mainly due to the cytoplasm or the colourless cortical granulation. (iii) The Adriatic population has two pretransverse ventral cirri which are neither mentioned nor illustrated by Kahl (1932, 1933). However, they are rather small and at least the left cirrus is almost not set off from the rear end of the median cirral row indicating that Kahl has not distinguished this small cirral group from the median cirral row. But more important than these few differences is the exact agreement in the remaining cirral pattern which is not very difficult to recognize in life. Kahl (1932) emphasized the short, wide, and narrowly spaced cirri in the marginal and median rows, a feature which is indeed very conspicuous (Figs 1, 9, 18).

The redescriptions by Borror (1963, Fig. 20) and Aladro Lubel (1985, Fig. 21) are less detailed than Kahl's (1932, Fig. 18) data. Especially the cirral patterns do not correspond very well with those described by Kahl (1932) and in the present paper (Fig. 9). The following differences are the most conspicuous ones: (i) the median cirral row is distinctly shortened against unshortened; (ii) only five transverse cirri present (Figs 20-22) against six (Fig. 18). Admittedly, five fits exactly the original description by Kahl (1928b), but as discussed above this is obviously not the ordinary number for *A. annulata*. (iii) Borror and Aladro Lubel did not mention the conspicuous ring-shaped structures, although some globules are illustrated which can be also interpreted as rings (Figs 20-22). They write about digestive vacuoles and cytoplasmic granules (Aladro Lubel 1985) and many endoplasmic spherical granules 4 µm in diameter (Borror 1963). The non-mention of these large, conspicuous ring-shaped structures indicates that they were not present in the American populations which is, however, not a proof for a misidentification because Kahl (1932) also mentioned that the rings, which could be lithosomes (for review, see Hausmann and Hülsmann 1996), can be absent. It is noticeable that the illustrations provided by Borror (1963; Fig. 20) on the one hand and by Aladro Lubel (1985, Fig. 21) and Aladro Lubel *et al.* (1990, Fig. 22) on the other hand are very similar, especially as concerns the anterior shortage of the

median cirral row, the five strong transverse cirri, and the six paired cirri ahead the median cirral row. The Caspian Sea population (Fig. 23) differs from the Adriatic population mainly by the lack of the ring-shaped structures (*vs*. present), in the higher number of adoral membranelles (65-70 *vs*. 31-57), the lack of pretransverse ventral cirri (*vs*. 2 such cirri present), and the lower number of dorsal kineties (4 *vs*. usually 6).

Generic classification and comparison with related species. The classification of the present species in the subgenus/genus *Amphisiella* by Kahl (1932), respectively, Borror (1972) seems correct because the cirral pattern matches very well that of *A. marioni*, type of the genus. Further, the morphogenesis proceeds largely identical in these two species (see above) also indicating that the assignment to *Amphisiella* - as defined recently by Voss (1992), Eigner and Foissner (1994), and Petz and Foissner (1996) - is correct.

More than 20 species have been originally described in *Amphisiella* and many species have been transferred to and excluded from this group (Berger 2001, Foissner *et al*. 2002). However, many of them are confined to terrestrial habitats. Thus, the comparison is restricted to similar marine congeners. According to Hemberger (1982), *Amphisiella marioni*, *A. annulata*, and *A. milnei* are junior synonyms of *A. capitata*. Indeed, synonymy of *A. capitata* and *A. marioni* could be possibly. However, this problem is beyond the scope of the present paper and therefore not considered further.

Amphisiella marioni, which is reliably redescribed by Wicklow (1982), has (i) only two cirri in the short row left of the anterior portion of the median cirral row (Fig. 24; against three in *A. annulata*, Figs 8, 9, 18); (ii) a shorter and distinctly interrupted median cirral row (terminates distinctly ahead transverse cirri *vs*. very near transverse cirri and usually continuous) which is composed of about 26-29 ordinary sized and spaced cirri (against 25-54, on average 44 rather wide cirri which are narrowly spaced); (iii) 4-5 transverse cirri (against usually 6). *Amphisiella marioni* and *A. annulata* agree, inter alia, in the marine habitat, the number of dorsal kineties (6, respectively, 6.4 on average), the arrangement of the undulating membranes (straight and in parallel), and the presence of invariably two pretransverse ventral cirri (termed accessory transverse cirri by Wicklow 1982) ahead the two rightmost transverse cirri. Further, morphogenesis obviously proceeds very similar (see above) so that a close relationship of these two species is very likely.

Amphisiella milnei (Kahl 1932; Fig. 25) has, inter alia, yellowish cortical granules (*vs*. colourless in *A. annulata*), five transverse cirri (*vs*. 6), possibly a different cirral pattern in the frontal area (cf. Fig. 25 with Fig. 18), and each one ring-shaped structure in the anterior and posterior body portion (rear one sometimes lacking *vs*. usually several rings scattered throughout cytoplasm). Further, the cirri of the marginal rows and the median row are of ordinary size and arrangement in *A. milnei* whereas they are rather wide and narrowly spaced in *A. annulata*.

Amphisiella turanica from the Caspian Sea is somewhat larger (170-210 µm long in life) than *A. annulata*, has 70-85 adoral membranelles, 4 dorsal kineties, and, most importantly, 4 macronuclear nodules (Alekperov and Asadullayeva 1999).

According to Kahl (1932), the frontal cirri of *A. annulata* are arranged "as in *Oxytricha* (3 + 2 + 3)". This is only correct for the first two parts (3 + 2), that is, the three enlarged frontal cirri (cirri I/1, II/3, III/3), the buccal cirrus (cirrus II/2), and cirrus III/2 which is behind the right frontal cirrus. The last three cirri of the (3 + 2 + 3) pattern are formed by the anlage IV in *A. annulata* whereas they are produced from two different anlagen in the 18-cirri oxytrichids, namely the anterior two cirri (cirri VI/3, VI/4 = frontoterminal cirri) from anlage VI and the rearmost cirrus from anlage IV (cirrus IV/3; for review on oxytrichids, see Berger 1999).

Kahl (1932, p. 582, 583) wrote that he had confused *A. annulata* with his *Holosticha setifera* earlier, likely because both species have large, ring-shaped structures. *Holosticha setifera*, which occurred like *A. annulata* in saltwater habitats near Bad Oldesloe (Germany), has a distinct midventral pattern, a single micronucleus between the two macronuclear nodules, and distinct caudal cirri (Kahl 1932, his Fig. 106 *9*) and therefore differs clearly from *A. annulata*. *Holosticha obliqua* sensu Kahl (1932, his Fig. 106 *26*) has also only one micronucleus between the two macronuclear nodules and five transverse cirri (against several micronuclei and six transverse cirri in *A. annulata*). Possibly, this illustration contains features of *H. setifera* and *A. annulata*, as supposed by Kahl (1932) himself.

In life, *Amphisiella annulata* is rather conspicuous mainly because of the wide and narrowly spaced cirri of the median cirral row. This feature and the conspicuous ring-shaped structures enable a very simple identification of this salt water species. Since the cell is rather

large and resistant against cover glass pressure, the cirral pattern can be studied very detailed even in life (own observations), as impressively demonstrated by Kahl more than 70 years ago!

Neotypification. No type or voucher slides are available from the *A. annulata* populations described by Kahl (1928b, 1932), Borror (1963), and Aladro Lubel (1985). Voucher slides of the Caspian Sea population studied by Alekperov and Asadullayeva (1999) are likely deposited in the Protistological Laboratory of the Institute of Zoology of the Academy of Sciences of Azerbaijan in Baku.

As mentioned above there are some discrepancies between the original description (Kahl 1928b) and the authoritative redescription by Kahl (1932). In addition, the redescriptions provided by Borror (1963) and Aladro Lubel (1985) do not fit very well the authoritative redescription and also not the original description. Further, Hemberger (1982) put *A. annulata* into the synonymy of *A. capitata*. Thus, it seems wise to define *A. annulata* objectively by the designation of a neotype (ICZN 1999, Foissner 2002). According to Article 75.3 of the ICZN (1999), the designation has to be accompanied by the publication of some particulars:

(i) the taxonomic status of the present species is somewhat unclear because the original description, the authoritative redescription, and two redescriptions do not agree in some important features (see above for details).

(ii) for a differentiation of *A. annulata* from related taxa, see above.

(iii) the neotype specimen (Figs 9, 10), respectively, neotype population from the Adriatic Sea is described in detail (see above); thus, recognition of the neotype designated is ensured.

(iv) it is generally known that no type material is available from species described by Kahl. Further, there is no indication that Borror (1963) or Aladro Lubel (1985) made permanent preparations of the present species. Alekperov and Asadullayeva (1999) did not designate a neotype.

(v) there is strong evidence that the neotype is consistent with *A. annulata* as originally described by Kahl (1928b). For a detailed comparison, see above. In addition, there is no reasonable doubt that the neotype population is conspecific with the population described by Kahl (1932). This 1932 revision, and certainly not the original description, was very likely used by most (all?) subsequent workers for the identification of *A. annulata*.

(vi) unfortunately, the neotype does not come from very near the original type locality (northern Adriatic Sea *vs*. saline waters in North Germany; distance about 1000 km). However, both sites are salt water habitats from the holarctic region, and many ciliates - especially marine ones, which live in a comparatively homogenous medium - are cosmopolitans (Patterson *et al.* 1989) so that this point should not be over-interpreted (for a thorough discussion of this problem, see Foissner *et al.* 2002, p. 44 and Foissner 2002). A detailed description of the new type locality, that is, the sample site of the neotype population, is given in the materials and methods section.

(vii) the slide containing the neotype specimen and four slides containing some further specimens (including those depicted in the present paper) of the neotype population are deposited in the Biologiezentrum des Oberösterreichischen Landesmuseums in Linz (LI), Austria.

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