

## Studies on the Morphology and Morphogenesis of *Allotricha curdsi* sp. n. (Ciliophora: Hypotrichida)

Xinlu SHI<sup>1</sup>, Alan WARREN<sup>2</sup> and Weibo SONG<sup>3</sup>

<sup>1</sup>Department of Biology, Shanghai Teachers University, Shanghai, China. Dept. of Biology, Harbin Normal University, Harbin, China; <sup>2</sup>Department of Zoology, The Natural History Museum, Cromwell Road, London, UK; <sup>3</sup>Laboratory of Protozoology, ARL, College of Fisheries, Ocean University of Qingdao, Qingdao, P.R. China

**Summary.** The morphology and morphogenesis of the freshwater hypotrichous ciliate *Allotricha curdsi* sp. n. was investigated using protargol silver impregnation. The new species is characterized thus: medium-sized, freshwater *Allotricha* 150-210x70-90 µm *in vivo*, ellipsoid with tapered posterior end; contractile vacuole in left half of midbody region; 2 macronuclei; one left and three right marginal cirral rows; 53-61 adoral membranelles; 9-10 frontal and 6-7 ventral cirri; usually with 4 complete dorsal kineties and 2 dorsomarginal kineties; cortical granules absent. The morphogenetic events reveal the following characteristics: (1) AZM in the opisthe arises from the new oral primordium while the proter retains the parental structure in its entirety; (2) 9-10 frontal, 6-7 ventral, and 5 transverse cirri are derived from 5 frontoventral transverse cirral anlagen, together with the undulating membrane anlage; (3) three new right marginal cirral rows derive from 3 separate anlagen, which originate in or near to the rightmost parental marginal row; all other parental cirri are resorbed just before cytokinesis; (4) the generation of the dorsal kineties is of "two-group-mode", 3 left primary dorsal and 2 dorsomarginal anlagen appear as two groups in both dividers and form all dorsal kineties (the 4th kinety is formed by the fragmentation of the 3rd anlage); (5) one caudal cirrus is formed at the posterior ends of the 1st, 2nd and 4th dorsal anlagen respectively.

**Key words:** *Allotricha curdsi* sp. n., freshwater ciliate, Hypotrichida, morphology and morphogenesis.

### INTRODUCTION

The genus *Allotricha* was established by Sterki (1878) for *A. mollis*, a flexible hypotrich with a typical *Oxytricha* cirral pattern but with more than 2 marginal cirral rows. Over the next 120 years the classification of this genus underwent a variety of changes including being reclassified as a subgenus of *Pleurotricha* (Bütschli, 1889) and being declared by Petz and Foissner

(1996) as *genus indeterminata* (for detailed discussion on the taxonomy of *Allotricha*, see Berger 1999). The genus was reactivated by Berger (1999) who defined it thus: adoral zone of membranelles formed like a question mark; undulating membranes in *Oxytricha* pattern, or rather straight and arranged almost side by side; frontoventral cirri in V-shaped pattern; post-oral ventral cirri in dense cluster behind buccal vertex; two pre-transverse ventral, and 5 transverse, cirri; two or more right, and one or more left, rows of marginal cirri; caudal cirri present; primordia V and VI of the proter originate from cirrus V/4 and V/3 respectively; no parental marginal rows retained after division; dorsal morphogenesis in *Oxytricha*-pattern.

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Address for correspondence: Alan Warren, Department of Zoology, The Natural History Museum, Cromwell Road, London, SW7 5BD, UK; Fax +44 (0)20 7942 5054; E-mail: a.warren@nhm.ac.uk

Song (2001) subsequently refined the diagnosis for *Allotricha* thus: flexible Oxytrichidae with frontoventral cirri in V-shaped pattern; 3 post-oral ventral cirri in dense cluster underneath (i.e. posterior to) buccal vertex, 2 pre-transverse ventral and 5 transverse cirri; 1 left and 2 or more right rows of marginal cirri; caudal cirri present; no parental marginal rows retained after division.

In August 1996, a freshwater *Allotricha*, collected from a eutrophic pond in northeast China, was brought into laboratory culture. A study of its morphology and morphogenetic processes during binary fission was carried out which revealed it to be a previously unknown taxon. We here provide detailed descriptions based primarily on protargol-impregnated specimens.

## MATERIALS AND METHODS

Samples were collected on 23 August 1996 from a small eutrophic pond in Mohe county in the northmost area of P. R. China (52° 55'N, 122° 12'E). The ciliates were cultured in Pringsheim solution, to which some rice grains were added as food source for bacteria. Ciliates were examined *in vivo* using bright field microscopy. The protargol sliver staining method according to Wilbert (1975) was used in order to reveal the infraciliature.

Measurements were performed at a magnification of x1500. Drawings were made with help of a camera lucida. To illustrate the changes during morphogenetic processes, parental cirri are depicted by contour whereas new ones are shaded black.

Terminology is mainly according to Corliss (1979), Hemberger (1982), Berger (1999) and Song and Warren (1999). Definitions of expressions, such as the primordium/a, anlage(n) and undulating membrane anlage are according to Song and Hu (1999).

## RESULTS

### *Allotricha curdsi* sp. n. (Figs 1a-c, 4, Table 1)

Diagnosis: freshwater *Allotricha* with broadly ellipsoid body shape, length:width ratio 2:1, tapering posteriorly. *In vivo* 150-210 x 70-90 µm. Dorsoventrally flattened, ratio of width to depth about 2:1. 9-10 frontal, 6-7 ventral, 5 transverse and 3 caudal cirri. 53-61 membranelles in adoral zone. One left and 3 right marginal cirral rows. Four dorsal and 2 dorsomarginal kineties. Two macro- and 2 micronuclei. Cortical granules absent.

Type locality: a small pond near a marsh in Mohe County (52° 55'N, 122° 12'E), Heilongjiang Province, P. R. China.

Type specimens: 1 holotype and 1 paratype slide of protargol impregnated specimens have been deposited in the Laboratory of Protozoology in Harbin Normal University, P.R. China. A second paratype slide is deposited in the Laboratory of Protozoology, College of Fisheries, Ocean University of Qingdao, P. R. China. A third paratype slide is deposited at the Natural History Museum, London, with registration number 2001:10:4:2.

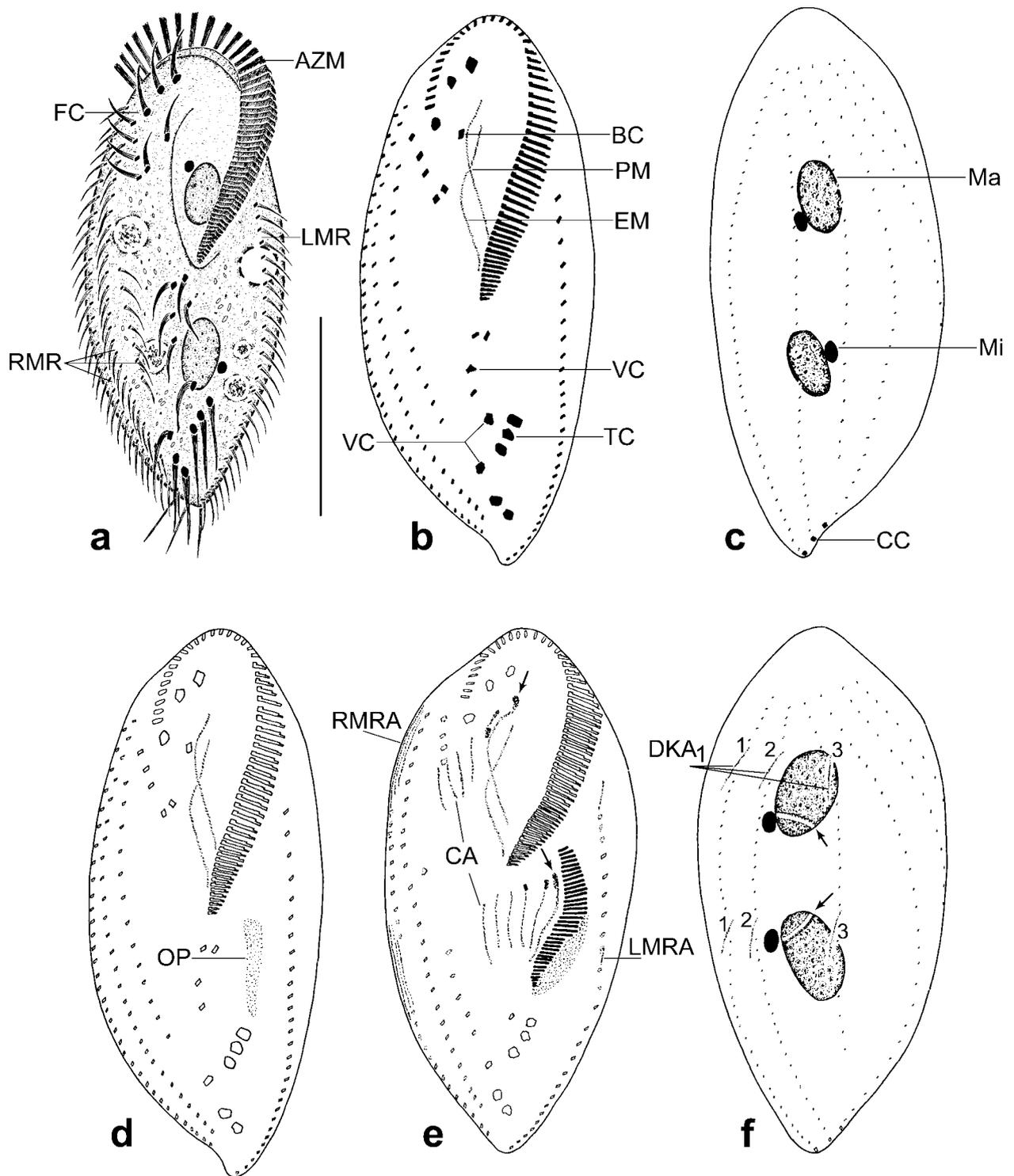
Dedication: named in honour of Professor Colin R. Curds who made many valuable contributions to the taxonomy of ciliates in general and of hypotrichs in particular.

### Morphology of *Allotricha curdsi* sp. n. (Figs 1a-c, 4, Table 1)

Body flexible, broadly ellipsoid in shape, tapering posteriorly (Fig. 1a), size *in vivo* 150-210 x 70-90 µm (150-200 x 50-70 µm after protargol impregnation), length to width ratio about 2:1; anterior end rounded, posterior more or less pointed; dorso-ventrally flattened, width to depth ratio about 2:1. Buccal field broadened due to extensive buccal lip. No cortical granules were observed. Cytoplasm colourless with numerous densely packed shining granules and food vacuoles containing flagellates and bacteria. Single contractile vacuole (CV) 12-15 µm in diameter, located near left margin at about mid-body of cell (Fig. 1a). Two widely separated macronuclei lying slightly left of main body axis, each 20-23 µm in diameter *in vivo* and with small spherical nucleoli (Figs 1a, c, 10). Two micronuclei about 5 µm in diameter, always adjacent to macronuclei. Locomotion typically like other oxytrichids.

Proximal end of adoral zone of membranelles (AZM) extends to about mid-body region (i.e. 50% body length), distal region markedly curved. AZM with on average 56 adoral membranelles, bases of largest membranelles about 11-12 µm wide. Most membranelles composed of four rows of kinetosomes (Figs 3b, 4); one short row (*ca* 1.2 µm long) of 3 kinetosomes; one intermediate row (*ca* 8.5 µm long) of 18-20 kinetosomes; two long rows of equal length (12-13 µm), each with 28-30 kinetosomes.

Cilia of frontal cirri about 20-22 µm long *in vivo*, although cilia of three anteriormost frontal cirri and buccal cirrus are noticeably longer. Buccal cirrus (II/2) lies close to right buccal wall at about level of anterior end of endoral membrane (Figs 1b, 4). Cirrus III/2 lies to left and slightly anterior to cirrus IV/3. Ventral cirri in three groups, 2 postoral, 2 pretransverse and 2 or 3 in region of posterior macronucleus (Figs 1b, 4). Five



**Figs 1a-f.** Non-dividing cell (a-c), early and early-mid stages of morphogenesis (d-f) in *Allotricha curdsi* sp. n.; **a** - ventral view *in vivo*; **b, c** - ventral (b) and dorsal (c) views showing infraciliature (after silver impregnation); **d-e** - ventral views showing early stages in morphogenesis (after protargol impregnation), arrows showing the anterior frontal cirrus forming at anterior end of each undulating membrane anlage; **f** - 1st group of dorsal view, showing development of dorsal kinety anlagen (1-3) and relative position of micronuclei to macronuclei during middle stage of morphogenesis; arrows mark replication bands. AZM - adoral zone of membranelles; BC - buccal cirrus; CA - cirral anlagen; CC - caudal cirri; DKA<sub>1</sub> - 1st group of dorsal kinety anlagen; EM - endoral membrane; FC - frontal cirri; LMR - left marginal row; LMRA - left marginal row anlagen; Ma - macronucleus; Mi - micronucleus; OP - oral primordium; PM - paroral membrane; RMR - right marginal row; RMRA - right marginal row anlagen; TC - transverse cirri; VC - ventral cirri. Scale bar - 80  $\mu$ m

**Table 1.** Morphometric data for *Allotricha curdsi* sp. n. All data are based on protargol impregnated specimens. Measurements in  $\mu\text{m}$ . Abbreviations: CV - coefficient of variation in %; Max - maximum; Min - minimum; n - number of cells measured; SD - standard deviation; SE - standard error of mean

Character	Min	Max	Mean	SD	CV	n
Length of body	150	200	172.9	16.5	9.6	20
Width of body	70	90	78.1	5.9	7.5	20
Length of adoral zone of membranelles*	60	100	74.8	10.8	14.4	20
No. of adoral membranelles	53	61	56	1.9	3.3	20
No. of frontal cirri**	9	10	9.2	0.4	4	20
No. of buccal cirri	1	1	1	0	0	20
No. of ventral cirri	6	7	6.3	0.57	9.1	20
No. of transverse cirri	5	5	5	0	0	20
No. of caudal cirri	3	3	3	0	0	20
No. of left marginal cirri	19	28	25.9	2.5	9.6	20
No. of cirri in right marginal row 1	26	36	31.9	2.7	8.5	20
No. of cirri in right marginal row 2	23	27	24	1.2	4.9	20
No. of cirri in right marginal row 3	3	15	7	2.8	40.7	20
No. of dorsal kineties***	6	6	6	0	0	20
No. of macronuclei	2	2	2	0	0	20
No. of micronuclei	2	2	2	0	0	20

\* total length from proximal to distal end; \*\*Including buccal cirrus (II/2);\*\*\*Including dorsomarginal kineties [not depicted in table]

transverse cirri separated into two groups of two and three (Figs 1a-b, 4). Cilia of transverse cirri 42-45  $\mu\text{m}$  long. Marginal cirri arranged in three right and one left marginal rows, those on the right being more conspicuously curved than that on the left. Rightmost marginal row beginning dorsally at anterior end of cell and terminating close to the two rightmost transverse cirri (Figs 1a, b). Left marginal row extending to posterior end of cell and not distinctly curved (Figs 1b, 4). Cilia of marginal cirri 20-23  $\mu\text{m}$  long. Three well-developed caudal cirri (CC) located at ends of dorsal kineties 1, 2 and 4 (DK<sub>1</sub>, DK<sub>2</sub> and DK<sub>4</sub> respectively) on right side of posterior end of cell (Figs 1a, c). Cilia of caudal cirri about 32  $\mu\text{m}$  long. Dorsal cilia 2-3  $\mu\text{m}$  long, not easily observed *in vivo* and arranged in 4 dorsal and 2 dorsomarginal rows.

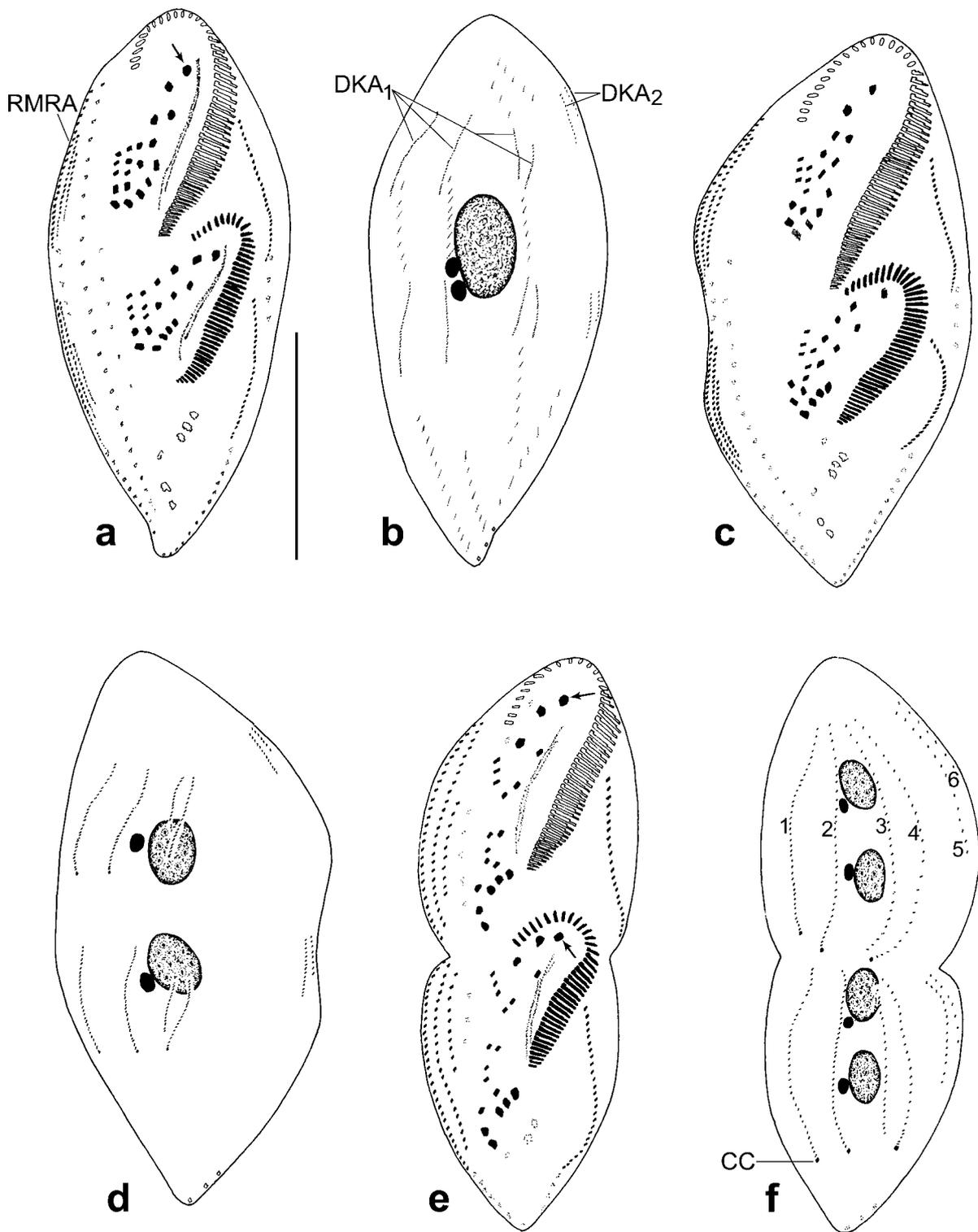
### Comparison with the related species

According to Berger (1999) there are two known species of *Allotricha*; *A. mollis* Sterki, 1878 and *A. antarctica* Berger, 1999. *A. curdsi* can be readily differentiated from *A. antarctica* by its body size (150-210  $\mu\text{m}$  vs. 90-125  $\mu\text{m}$  long for species of *A. antarctica* from wild), number of adoral membranelles (53-61 vs. 35), arrangement of transverse cirri (in two groups of 2 and 3 vs. in a hook-shaped row), arrangement of marginal cirral rows (3 right, 1 left vs. 2 right, 2 left),

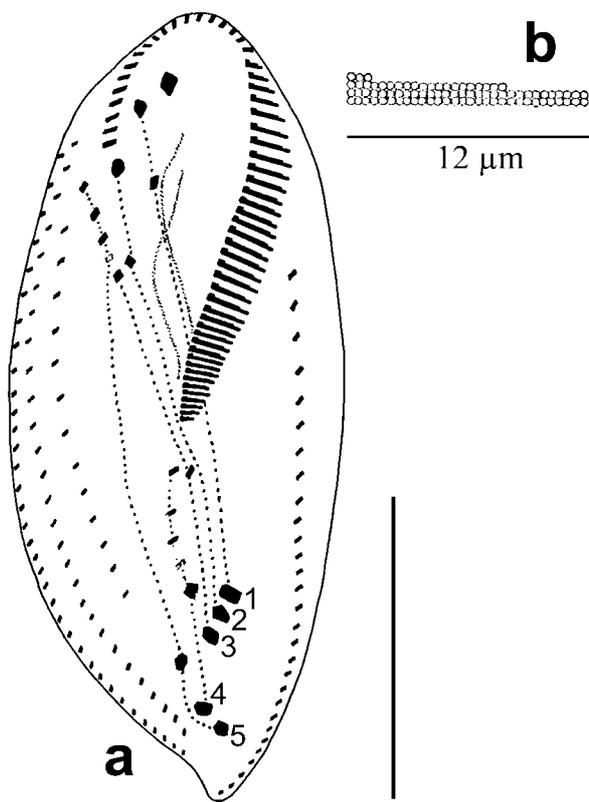
arrangement of undulating membranes (curved and intersecting vs. straight and parallel), cortical granules (absent vs. present), and habitat (freshwater vs. soil) (Petz and Foissner 1996, Berger 1999).

The new species bears a much stronger resemblance to *A. mollis* although it can be distinguished from the latter by the body shape (broad ellipsoid, length:width ratio 2:1, tapering posteriorly vs. elongate ellipsoid, length:width ratio ca 3:1, with rounded ends), length of AZM relative to the body length (about 50% vs. 35%), arrangement of transverse cirri (in two groups of 2 and 3 vs. in a single oblique row), and cortical granules (absent vs. present) (Berger 1999).

One other taxon with which *A. curdsi* could be confused is *Pleurotricha variabilis* Reuter, 1961, which Petz and Foissner (1996) considered a synonym of *Onychodromopsis flexilis*, but which Berger (1999) considers probably to be a member of the genus *Allotricha*. Both these taxa lack cortical granules, or at least they were not observed by Reuter (1961) in *P. variabilis*, and have similar patterns of infraciliature. However, *A. curdsi* differs from the latter species in terms of its body size and shape (150-210  $\mu\text{m}$  long; broadly ellipsoidal with tapering posterior; length:width ratio 2:1 vs. 200-220  $\mu\text{m}$  long; elongate ellipsoidal with rounded ends; length:width ratio 3:1); number of frontal cirri (9-10 vs. 8) and the length of AZM relative to the



**Figs 2a-f.** Middle and late stages of morphogenesis in *Allotricha curdsi*. **a, b** - ventral and dorsal views of the same individual. **a** - ventral view showing the cirral pattern during middle stage. Note the three new right marginal cirri anlagen which develop within or near the rightmost marginal cirral row. Arrow marks the first frontal cirrus which develops from the undulating membrane anlagen; **b** - dorsal view showing the single fused macronucleus; **c, d** - slightly later stage, ventral and dorsal views of same cell; **c** - ventral view, showing the frontal cirri starting to migrate and the well developed adoral zone of membranelles of the opisthe; **d** - dorsal view. Note the newly divided macronuclei and the two groups of dorsal kinety anlagen; **e, f** - late stage, ventral and dorsal views of the same cell; **e** - ventral view, showing the well-developed cirri and the new cirral patterns of the proter and the opisthe; **f** - dorsal view showing the six dorsal kinety anlagen in each divider. CC - caudal cirrus; DKA<sub>1</sub> - 1st group of dorsal kinety anlagen; DKA<sub>2</sub> - 2nd group of dorsal kinety anlagen. RMRA - right marginal row anlagen. Scale bar - 80 μm



**Figs 3a,b.** **a** - diagrammatic representation of *Allotricha curdsi*, ventral view, showing the origin of the transverse cirri; **b** - the standard structure of a membranelle with four rows of kinetosomes; one short row of 3 kinetosomes; an intermediate row of 18-20 kinetosomes; two long rows of 28-30 kinetosomes. Scale bars: **a** - 80  $\mu\text{m}$ ; **b** - 12  $\mu\text{m}$

body length (50% vs. 30-35%) (Reuter 1961, Berger 1999).

Considering the general appearance and size, especially the pattern of ciliature, comparison should be made with the well-known *Pleurotricha lanceolata*, which differs from the current species by lacking caudal cirri (vs. present) and in having a rigid (vs. flexible) cortex and a more slender body shape (Jeffries and Mellott 1968; Dragesco 1970, 1972; Martin-González *et al.* 1984; Berger 1999).

### Morphogenesis (Figs 1d-f, 2a-f, 5-14)

Morphogenesis during binary fission has been described for both previously described species of *Allotricha*, *A. mollis* and *A. antarctica* (Kramer 1988, Petz and Foissner 1996, Berger 1999). The morphogenetic processes in *A. curdsi* do not differ fundamentally from either of these.

The main events in the process of nuclear division in *A. curdsi* are similar to those of other oxytrichids, i.e. the macronuclei fuse into a single mass which splits twice, the last division being completed in the postdividers (Figs 1f, 2b, d, f, 6, 7, 10, 12, 14). Hence this process needs no further comment other than to note that the replication bands were observed at an earlier stage of morphogenesis than is normal for other oxytrichids (Fig. 1f, arrows).

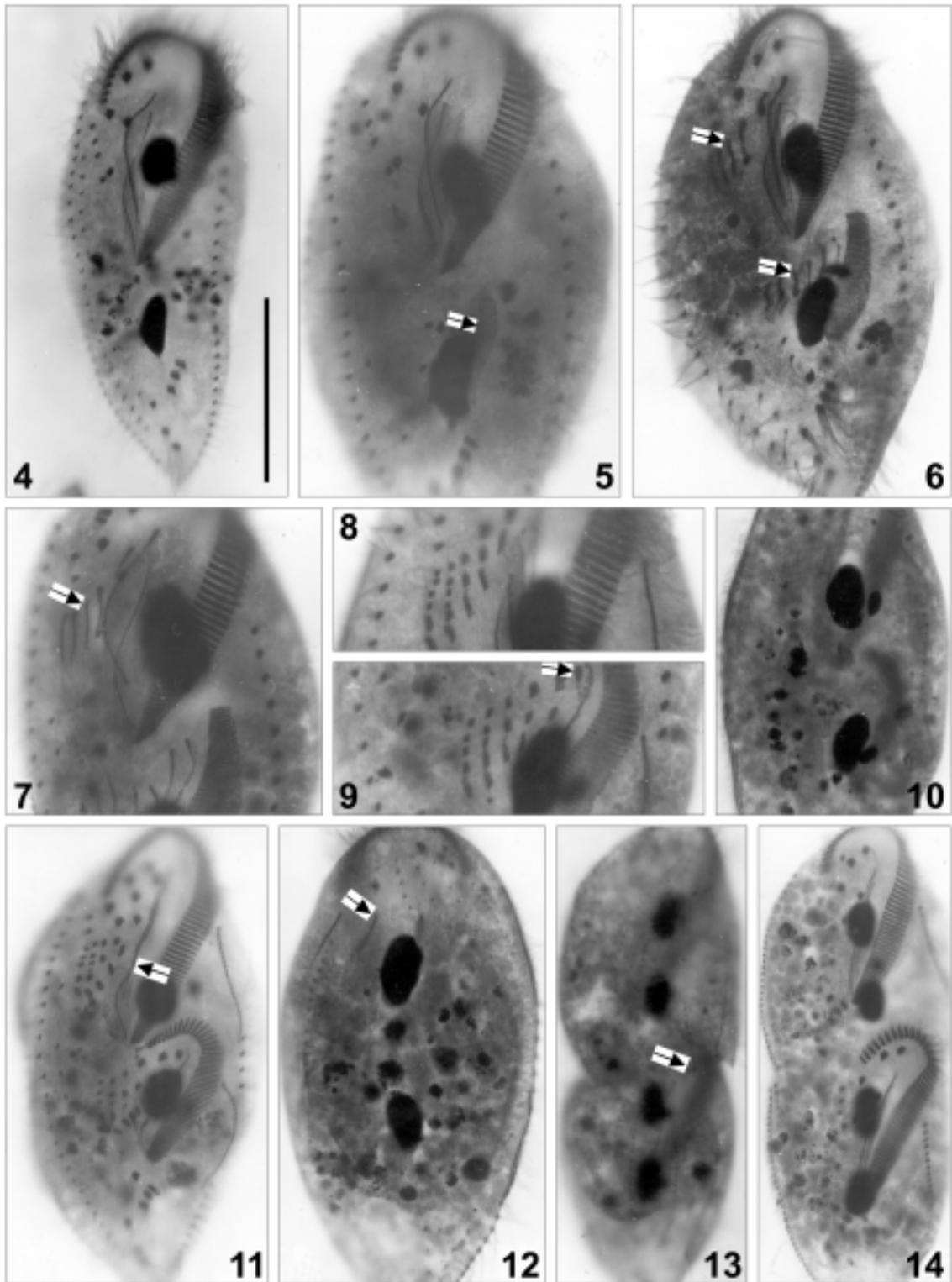
### Stomatogenesis

**In the opisthe.** Morphogenesis commences with the proliferation of loosely arranged basal bodies to form the oral primordium (OP), which occurs *de novo* between the left marginal row and the ventral cirri in the middle portion of the cell. During its formation the adjacent cirri seem to remain intact (Figs 1d, 5). It should be noted, however, that the very first stage in the division process was not observed. The basal bodies of the oral primordium increase in number as its anterior portion elongates to reach the level of the parental cytostome. The adoral membranelles begin to organize in a posteriad direction, while the primordium for the undulating membranes, i.e. the opisthe's undulating membrane-anlage, is generated to the right of the oral primordium as a long streak (Figs 1e arrows, 6).

During the later stages, the anterior end of the newly built adoral zone of membranelles bends to the right and the differentiation of membranelles is completed forming the new oral structure for the opisthe (Figs 2a, c, e, 7, 9, 11, 14). Meanwhile, the undulating membrane-anlage splits longitudinally to form two streaks from which the endoral and paroral membranes derive. Initially these streaks lie close together in parallel (Figs 2e, 14) but later they separate, arch to the left and intersect at around their mid-point (Fig. 3). At this stage, the leftmost frontal cirrus is generated from the anterior end of the undulating membrane-anlage (Figs 2a, c, e, arrows, 9).

**In the proter.** As in most other oxytrichids, the parental adoral zone of membranelles is retained completely intact during the morphogenetic process, so changes to the oral structure in the proter are confined to the paroral and endoral membranes. The first sign of the formation of the undulating membrane-primordium is the dedifferentiation of the anterior part in the old paroral membrane (Figs 1e, 2a, 7, 8). Slightly later, all basal bodies within both paroral and endoral membranes dedifferentiate giving rise to the undulating membrane-anlage (Figs 2c, 11, arrow).

In the subsequent stages, the basic development of the undulating membrane-anlage follows a similar pat-



**Figs 4-14.** Photomicrographs of *Allotricha curdsi* (after protargol impregnation); **4** - ventral view, showing the general infraciliature; **5-7** - ventral views of cell in early-middle stages of morphogenesis; arrow in Fig. 5 showing oral primordium, arrows in Figs 6-7 marking cirral anlagen in both dividers; **8, 9** - ventral view of cell in late-middle stage of morphogenesis; arrow marking the first cirrus from undulating membrane-anlage in the proter; **10** - showing the macro- and micronuclei; **11** - ventral view of cell in late stage in morphogenesis; arrow marks undulating membrane-anlage in the proter; **12** - dorsal view of cell in middle stage of morphogenesis; arrow marks one of the new dorsal kineties which develop *de novo*, separate from the parental structure; **13, 14** - dorsal (13) and ventral (14) views of the same individual in late stage of morphogenesis; arrow showing newly formed caudal cirrus. Scale bar - 80  $\mu$ m.

tern to that of the opisthe: one frontal cirrus is produced from the anterior end and, during late phases, the paroral and endoral membranes are regenerated (Figs 1e, 2a, c, e, 14).

#### Development of the somatic ciliature

The development of the somatic ciliature begins with the formation of the frontoventral transverse cirral anlagen. The ventral cirri appear to contribute to the formation of these anlagen. Thus, 5 thread-like anlagen are formed in both proter and opisthe, which lie to the right of the parental undulating membranes (Fig. 1e). Evidently some old frontal cirri join in the proliferation of basal bodies of these primordia (possibly the new anlagen arise directly from the parental structure).

Subsequently, these cirral anlagen will develop independently in both dividing parts. As in other oxytrichids, after segregation and migration of the cirri developed from the 5 anlagen, a total of 19–21 cirri are formed: 8–9 frontal, 6–7 ventral and 5 transverse (Figs 2a, c, e, 7, 8, 11, 14). Meanwhile the leftmost frontal cirrus is formed from the undulating membrane-anlage (Figs 2a, c).

Thus, the number and the origin of the frontoventral-transverse cirri formed during morphogenesis can be summarized as follows:

	UM-anlage	Cirral anlagen				
		I	II	III	IV	V
Number of cirri	1	3	3	3	5 or 6	5 or 6

i.e. for each daughter cell 9 or 10 frontal cirri originate from the undulating membrane-anlage (1) and cirral anlagen I (2), II (2), III (1), V (3 or 4); 6 or 7 ventral cirri derive from anlage III (1), IV (4 or 5) and V (1); each of these cirral anlagen contributes one transverse cirrus.

The formation of the new marginal rows in this species exhibits a “neokinetal” pattern (Eigner 1997), i.e. the new structures are built by newly generated basal bodies which are closely connected with disaggregating (or resorbed) old marginal cirri. The left marginal row anlagen develop within the old structures (Fig. 1e) while the three thread-like right marginal row anlagen appear within, or near, the rightmost old marginal row (Figs 1e, 10). At the same time the neighbouring parental cirri gradually disaggregate but were not seen to contribute to the development of these anlagen. The new marginal cirri develop and migrate posteriad to replace the old ones (Figs 2a, c, e, 11, 14).

New dorsal kineties are formed by two groups of primordia: one group develops intrakinetally within the parental structure which at first consists of only three streaks in both opisthe and proter (Figs 1f, 2). In middle and late dividers, the rightmost streak fragments in the posterior region, usually producing 2 new anlagen. Thus, 4 rows of long dorsal kineties are formed (Figs 2b, d, f). The second group of anlagen involved in the formation of the dorsomarginal kineties develops *de novo* to the right of the rightmost cirral row anlage. It later migrates to the dorsal side and develops into two short dorsal kineties (Figs 2b, d, f). It should be noted, however, that the initial stage of this process was not observed. During the morphogenetic process, one caudal cirrus is formed at the posterior ends of each of the 1st, 2nd, and 4th dorsal kineties (Figs 2d, f, 13, arrow).

#### Summary of morphogenesis

The most significant events in morphogenesis in *Allotricha curdsi* can be summarized as follows: (1) Three rows of new right marginal cirri derive from 3 separate anlagen, which originate within or near the rightmost marginal row. The newly-formed left marginal row is derived from the left marginal row anlage which develops within the old structure. (2) Five frontoventral-transverse cirral anlagen, together with undulating-membrane-anlage, develop into 9 frontal, 6–7 ventral and 5 transverse cirri, rather than the “8:5:5” pattern which is typical of other oxytrichids. (3) As in most other oxytrichids, the parental adoral zone of membranelles is completely retained by the proter. (4) Three left dorsal and one dorsomarginal anlagen are formed initially as two groups in both proter and opisthe and give rise to all dorsal kineties, the rest of the anlagenal streaks being formed following the fragmentation of these anlagen. (5) The caudal cirri derive from the posterior ends of the 1<sup>st</sup>, 2<sup>nd</sup> and 4<sup>th</sup> dorsal kineties; (6) Just before cytokinesis, the old undifferentiated cirri are resorbed.

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#### REFERENCES

Bütschli O. (1889) Protozoa III. Abtheilung: Infusoria und System der Radiolaria. In: Klassen und Ordnungen des Thier-Reichs,

- wissenschaftlich dargestellt in Wort und Bild, (Ed. H. G. Bronn) **1**: 1585-2035
- Berger H. (1999) Monograph of the Oxytrichidae (Ciliophora, Hypotrichia). **78**: Monographiae Biologicae, Kluwer, Dordrecht
- Corliss J. O. (1979) The Ciliated Protozoa: Characterization, Classification and Guide to the Literature. 2ed. Pergamon Press, Oxford
- Dragesco J. (1970) Ciliés libres du Cameroun. *Anals Fac. Sci. Univ. Féd. Cameroun (Numéro hors-série)*: 1-141
- Dragesco J. (1972) Ciliés libres de la cuvette tchadienne. *Anals Fac. Sci. Univ. Féd. Cameroun* **11**: 71-91
- Eigner (1997) Evolution of morphogenetic processes in the Orthoamphisiellidae n. fam., Oxytrichidae, and Parakahliellidae n. fam., and their depiction using a computer method (Ciliophora, Hypotrichida). *J. Euk. Microbiol.* **44**: 553-573
- Hemberger H. (1982) Revision der Ordnung Hypotrichida Stein (Ciliophora, Protozoa) an Hand von Protargolpräparaten und Morphogenesedarstellungen. Ph. D. Thesis, University of Bonn, Germany
- Jeffries W. B., Mellott J. L. (1968) New observations on the anatomy of *Pleurotricha lanceolata*. *J. Protozool.* **15**: 741-747
- Kramer M. (1988) Morphologische und enzymelektrophoretische Untersuchungen zur Taxonomie und Systematik der Gattung *Paraurostyla* (Oxytrichidae, Hypotrichida). Diplomarbeit Eberhard-Karls-Universität, Tübingen
- Martin-González A., Serrano S., Fernández-Galiano D. (1984) New aspects of the morphology of *Pleurotricha lanceolata* (Ciliophora, Hypotrichida): cirral and membranellar patterns and fibrillar systems. *J. Protozool.* **31**: 347-351
- Petz W., Foissner W. (1996) Morphology and morphogenesis of *Lantostyla edaphoni* Berger and Foissner and *Onychodromopsis flexilis* Stokes, two hypotrichs (Protozoa: Ciliophora) from Antarctic soils. *Acta Protozool.* **35**: 257-280
- Reuter J. (1961) Einige faunistische und ökologische Beobachtungen über Felsentümpel-Ziliaten. *Acta. Zool. Fennica* **99**: 1-42
- Song W. (2001) Morphology and morphogenesis of marine ciliate *Ponturostyla enigmatica* (Dragesco & Dragesco-Kernéis, 1986) Jankowski, 1989 (Ciliophora, Hypotrichida, Oxytrichidae). *Europ. J. Protistol.* **37**: 181-198
- Song W., Hu X. (1999) Divisional morphogenesis in the marine ciliate, *Hemigastrostyla enigmatica* (Dragesco & Dragesco-Kerneis, 1986) and redefinition of the genus *Hemigastrostyla* Song & Wilbert, 1997 (Protozoa, Ciliophora). *Hydrobiologia* **391**: 249-257
- Song W., Warren A. (1999) Observations on morphogenesis in a marine ciliate *Tachysoma ovata* (Protozoa: Ciliophora: Hypotrichida). *J. Mar. Biol. Ass., U.K.* **79**: 35-38
- Sterki V. (1878) Beiträge zur Morphologie der Oxytrichinen. *Z. wiss. Zool.* **31**: 29-58
- Wilbert N. (1975) Eine verbesserte Technik der Protargolimprägation für Ciliaten. *Mikrokosmos* **64**: 171-179

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