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A Morphogenetic Description of *Thigmokeronopsis stoecki* Shao *et al*., 2008 (Ciliophora, Hypotricha) and a Comparison with Members of the Family Pseudokeronopsidae

Xumiao CHEN[1,2], Liqiong LI[1], Xiaozhong HU[2], Chen SHAO[3], Saleh A. AL-FARRAJ[4] and Khaled A. S. AL-RASHEID[4]

[1]School of Ocean, Yantai Academy, China Agricultural University, Yantai, China; [2]Laboratory of Protozoology, Institute of Evolution and Marine Biodiversity, Ocean University of China, Qingdao, China; [3]The Key Laboratory of Biomedical Information Engineering, Ministry of Education, School of Life Science and Technology, Xi'an Jiaotong University, Xi'an, China; [4]Zoology Department, King Saud University, Riyadh, Saudi Arabia

Abstract. The urostylid family Pseudokeronopsidae Borror and Wicklow, 1983 was considered to be a well-outlined taxon. Nevertheless, recent evidence, including morphological, ontogenetic, and molecular information, has consistently revealed the polyphyly of this family. In the present work, a new population of *Thigmokeronopsis stoecki* Shao *et al.*, 2008 was found and its binary divisional process was described for the first time. In addition, the morphogenetic features of *Thigmokeronopsis* species and all the other pseudokeronopsids, for which detailed ontogenetic data are available, were rechecked and compared. This reveals that: (1) the ontogenetic process of *T. stoecki* corresponds well with its congeners *T. jahodai* and *T. rubra* except for the macronuclear behavior; (2) *Apokeronopsis* and *Thigmokeronopsis* share a similar ontogenetic mode despite of the differences in the number and origin of their buccal cirri; (3) most pseudokeronopsids share the same pattern in the origins of their oral primordia and fronto-ventral-transverse cirral anlagen, except for *Pseudokeronopsis similis*, which may not be a valid member of the family Pseudokeronopsidae.

Key words: Hypotrichs, ontogenesis, Pseudokeronopsidae, *Thigmokeronopsis*.

INTRODUCTION

The ciliate group Hypotricha (s.l.) contains approximately 1,500 nominal species, all of which exhibit complicated processes of morphogenesis and physiological reorganization which are considered significant in determining the phylogenetic relationships among them (Foissner 1996, 2012; Berger 1999, 2006, 2008, 2011; Chen *et al*. 2010; Foissner *et al*. 2010; Küppers *et al*. 2011; Li *et al*. 2011; Shao *et al*. 2011; Xu *et al*. 2011; Choi and Shin 2012; Paiva *et al*. 2012). In addition, hypotrichs display highly diverse ontogenetic modes as well as diverse cortical structures and nuclear apparatus. This diversity is reflected in the division of

Address for correspondence: Liqiong Li, School of Ocean, Yantai Academy, China Agricultural University, Yantai 264670 China. Fax: +86 532 82032283; E-mail: lilyjone_new@163.com

hypotrichs into many phylogenetic subgroups (Foissner *et al*. 2004; Berger 2006; Foissner and Stoeck 2008, 2011; Chen *et al*. 2011; Miao *et al*. 2011).

Recent studies have assigned a range of new taxa (e.g. *Nothoholosticha*, *Apokeronopsis*, *Heterokeronopsis*) into the urostylid family Pseudokeronopsidae. Whilst this has served to reveal the polyphyly of the family, it has also led to confusion regarding the systematic relationships among pseudokeronopsids (Li *et al*. 2008; Shao *et al*. 2008a, b; Chen *et al*. 2011; Pan *et al*. 2013).

In the present work, we have observed the morphology and morphogenesis of a new isolate of *Thigmokeronopsis stoecki* Shao *et al*., 2008, and compared its developmental modes of cortical ciliature and macronuclei with those of all other pseudokeronopsids for which detailed morphogenetic data are available.

MATERIALS AND METHODS

Thigmokeronopsis stoecki was isolated from coastal waters used for aquaculture at Qingdao (Tsingtao), China (120°43′E; 36°08′N) on 25 May 2007. The water temperature was ca. 18°C, salinity ca. 30‰ and pH ca. 8.0. Water from the sampling site was maintained in Petri dishes at room temperature (ca. 23°C) for two weeks with rice grains as a food source to promote the growth of bacteria as food for the ciliates.

Cells were examined *in vivo* using bright field and differential interference contrast microscopy and were stained with protargol following the method of Wilbert (1975) in order to reveal the infraciliature. Counts and measurements of morphological characteristics on stained specimens were performed at a magnification of 1,250 ×. Drawings were made with the help of a camera lucida. Terminology mainly follows Berger (2006). New structures are shown in black and parental ones are shown by outline.

RESULTS

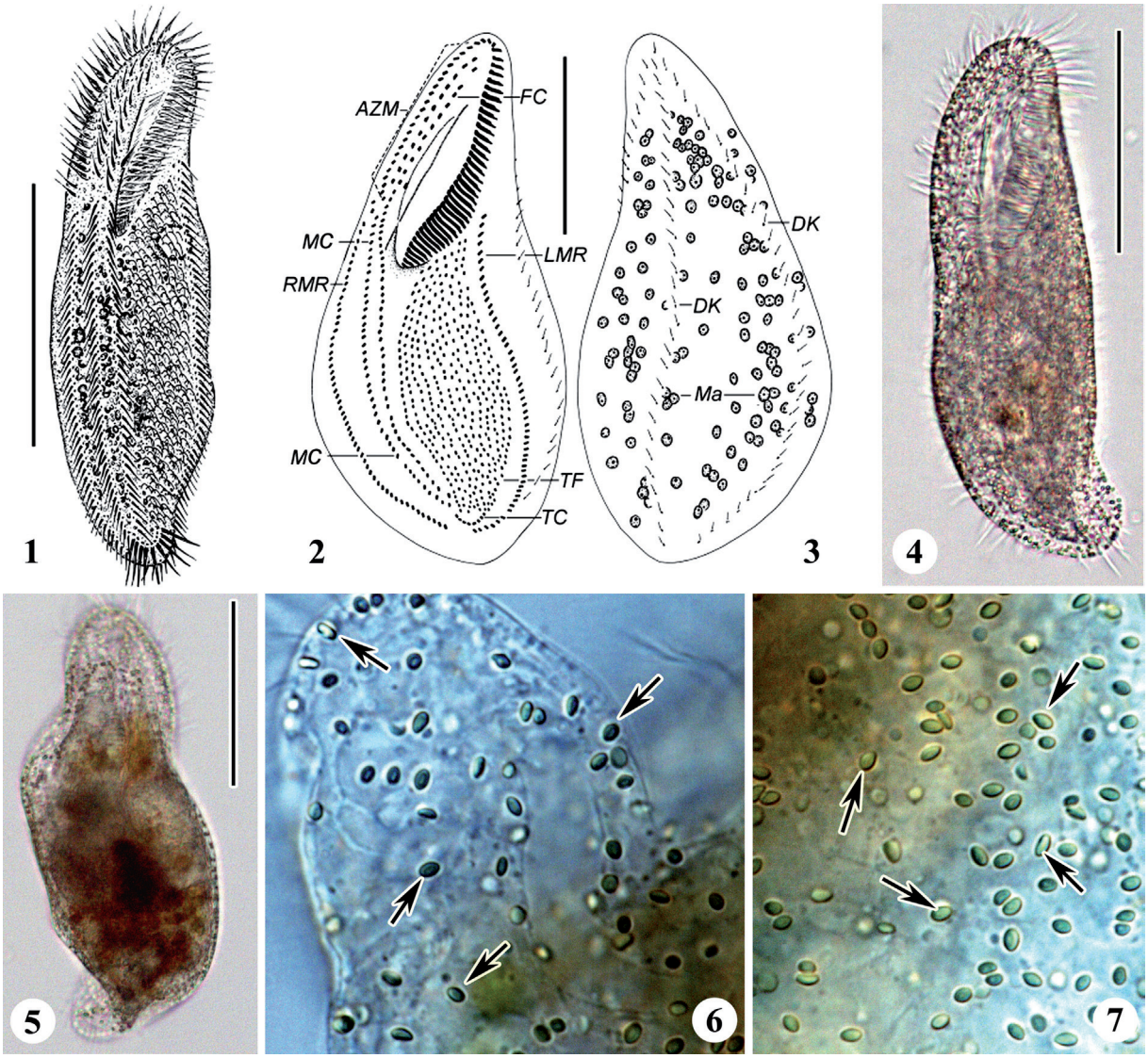
Morphology of *Thigmokeronopsis stoecki* based on present population (Figs 1–7, Table 1)

Body size *in vivo* about 140–230 × 70–80 μm; cell highly contractile and shape variable, generally elongated fusiform with anterior slightly narrow and rounded, and posterior tapered (Figs 1, 4, 5). Cell brownish to dark brown in color. Adoral zone about 40% of cell length. Pellicle flexible and thin, with brightly grass-green cortical granules (about 2 μm long, red blood cell-shaped) sparsely distributed beneath (Figs 6, 7). Cytoplasm colorless, filled with many tiny lipid droplets. More than 100 macronuclear nodules. Contractile vacuole positioned in anterior two-fifths on left side of cell.

Adoral zone composed of 70–83 membranelles, with its distal end curving strongly posteriad along the

Table 1. Morphometric characterization of *Thigmokeronopsis stoecki*. All data are based on protargol-impregnated specimens. Measurements in μm. CV – coefficient of variation in %, Max – maximum, Mean – arithmetic mean, Min – minimum, n – sample size, SD – standard deviation.

Character	Min	Max	Mean	SD	CV	n
Body length	216	290	252.20	21.58	8.56	25
Body width	96	134	113.72	8.64	7.60	25
Adoral zone length	88	110	102.52	5.05	4.93	25
Number of adoral membranelles	70	83	75.08	2.77	3.69	25
Number of buccal cirri	1	1	1.00	0	0	25
Number of frontal cirri	15	26	19.72	2.78	14.08	25
Number of frontoterminal cirri	2	2	2.00	0	0	25
Number of midventral pairs	32	40	35.04	2.30	6.56	25
Number of rows of thigmotactic cirri	11	15	12.64	1.19	9.38	25
Number of left marginal cirri	46	65	54.40	5.89	10.82	25
Number of right marginal cirri	47	55	50.52	2.28	4.50	25
Number of transverse cirri	5	8	6.92	0.76	10.97	25
Number of dorsal kineties	3	3	3.00	0	0	25
Number of macronuclear nodules	130	185	155.12	14.96	9.65	25



Figs 1–7. Morphology and photomicrographs of *Thigmokeronopsis stoecki* from life (1, 4–7) and after protargol impregnation (2, 3). **1** – ventral view of a representative individual (from Shao *et al.* 2008b); **2**, **3** – ventral and dorsal views of the infraciliature (from Shao *et al*. 2008b); **4** – ventral view of a typical individual; **5** – dorsal view, to show the distinct flexibility of the body; **6** – dorsal view of anterior portion, to show the transparent cytoplasm and sparsely distributed cortical granules (arrows); **7** – dorsal view, noting the arrangement of cortical granules (arrows). AZM – adoral zone of membranelles, DK – dorsal kineties, FC – frontal cirri, LMR – left marginal row, Ma – macronuclear nodules, MC – midventral complex, RMR – right marginal row, TC – transverse cirri, TF – thigmotactic field. Scale bars: 100 μm (in Figs 1, 4, 5) and 50 μm (in Figs 2, 3).

right cell margin and extending to about cytostome level. Fifteen to 26 frontal cirri, which are not clearly distinguished from the midventral cirri posteriorly, forming typical curved bicorona. Two frontoterminal, one buccal and five to eight transverse cirri. Midventral complex comprising a total of 32–40 pairs of cirri that are distinctly separated and thus are not arranged in a typical zig-zag pattern, terminating near the transverse cirri. Left and right marginal row with 46–65 and 47–55 cirri respectively, nearly confluent posteriorly. Thigmotactic field (TF) dominant, consisting of 11–15 densely arranged, longitudinal rows of cirri. Three complete dorsal kineties (Figs 2, 3).

Morphogenesis of *Thigmokeronopsis stoecki* (Figs 8–23)

Stomatogenesis and cirral streaks. Stomatogenesis commenced with the apokinetal appearance of the oral primordium, an anarchic field of basal bodies beneath the old undulating membranes (UMs) in the proter and a small elliptical field of basal bodies on the cell surface adjacent to the left row of the midventral cirri in the opisthe. Simultaneously, all the old oral apparatus and cirri remained apparently unchanged and were not involved in the formation of primordia (Figs 8, 16).

In the following stage, by further proliferation of basal bodies, both oral primordia gave rise to the new adoral membranelles in a posteriad direction. The anlagen for the new undulating membranes (UM-anlagen) were also generated to the right. In both dividers, the fronto-ventral-transverse cirral anlagen (FVT-anlagen) appeared on the cell surface as anarchic oblique streaks. At the same time, the old oral apparatus began to loose and be resorbed while the midventral complex remained unchanged, as did other old cirri (Figs 9, 17).

As shown in Fig. 10 the development of primordia in both dividers was remarkably simultaneous. As the further proliferation of the adoral membranelles proceeded, the UM-anlagen became longer and wider and gave rise to one cirrus anteriad, which would become the leftmost frontal cirrus. The FVT-anlagen organized into dozens of oblique streaks and each streak developed into several new cirri.

Soon after, the anterior ends of the two new adoral zones of membranelles (AZMs) started to arch to the right, although the two new UM-anlagen did not yet split. The FVT-anlagen differentiated clearly and each streak (except some of the last streaks) generated the first two strong cirri (forming the midventral pairs) and others that were fine and arranged closely (forming the thigmotactic cirri) (Figs 12, 18, 19).

Subsequently, new AZMs developed completely and the UM-anlagen split longitudinally to form the new paroral and endoral membranes. New cirri began migrating towards their final positions (Figs 13, 15, 21–23). Finally, streak n (the last FVT-anlagen) formed four cirri in each divider, of which the anterior two continued to migrate anteriad to become the frontoterminal cirri, while the posterior two would become the transverse cirri. Similarly, streak n-1 to n-6 gave two midventral and one transverse cirrus, and streak II (the first FVT-anlage) generated one frontal and one buccal cirrus. In addition, streak III to n-7 gave two midventral and several thin thigmotactic cirri. Before the separation of proter and opisthe, these fine cirri combined, migrated toward the left and located themselves between the midventral complex and the left marginal cirral row, that is, the thigmotactic field (Figs 13–15, 22, 23). The midventral cirri, however, formed two separate pseudorows instead of a typical zig-zag pattern.

Finally, the old oral apparatus and most of the cirri were resorbed and the daughters began to separate.

Marginal and dorsal structures. Shortly after the beginning of morphogenesis, the marginal cirral anlagen originated *de novo* both in the proter and the opisthe (Fig. 10). These anlagen then stretched and later gradually replaced the parental rows (Figs 12, 13, 15, 20).

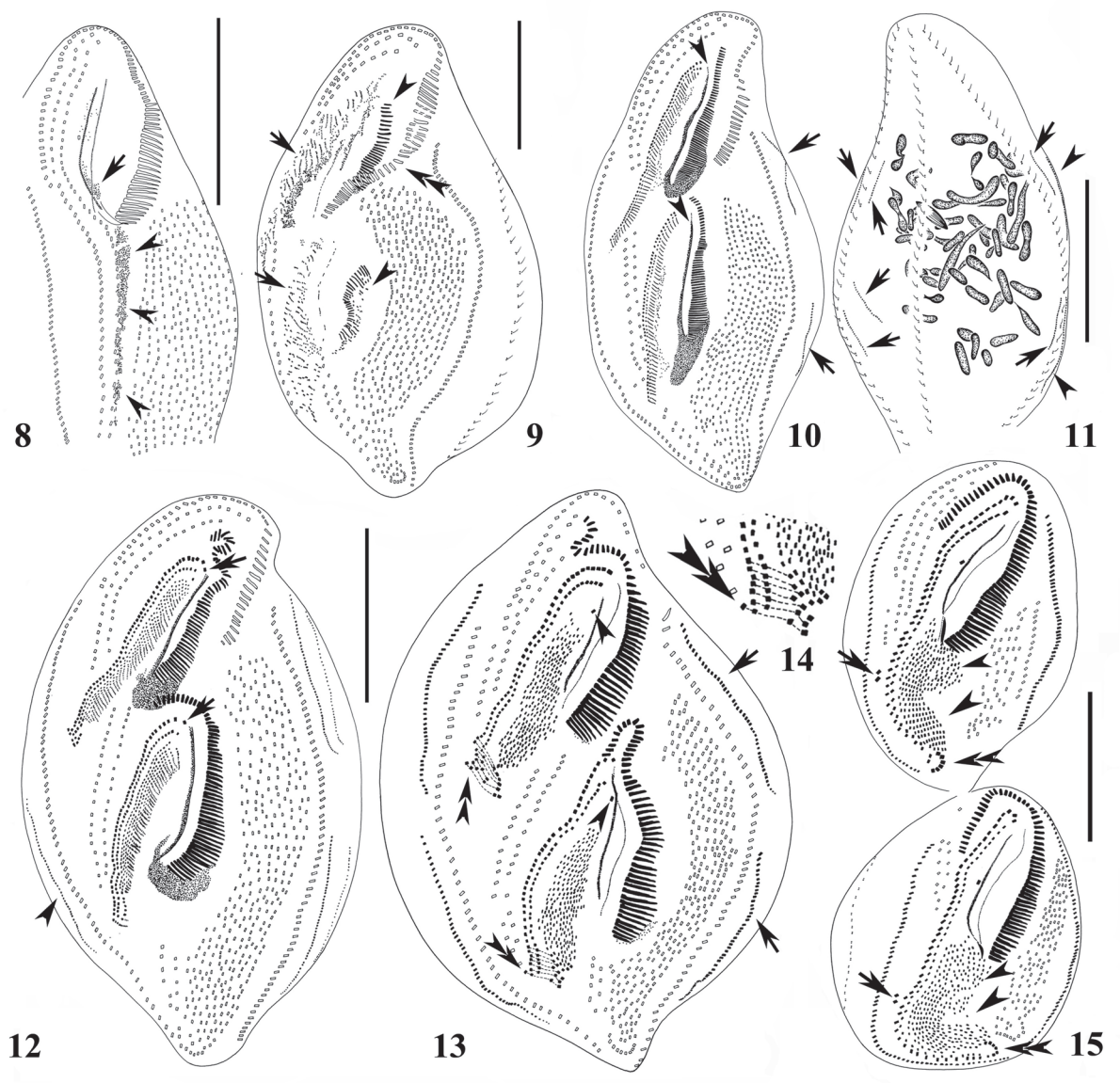
The anlagen of the new dorsal kineties also developed *de novo* (Fig. 11) through two anlagen close to the parental rows. The anlagen subsequently elongated by basal body proliferation until they were apparent through the whole cell length.

Division of nuclear apparatus. It was evident that the macronuclear nodules fused into numerous (with about 40 segments) masses (Fig. 11). In the middle to late stages, these masses began to elongate, divide into numerous oval macronuclear nodules, and then, distributed into the daughters. Division of the micronuclei was not observed.

DISCUSSION

Within this genus morphogenetic processes have been reported only for the type species *Thigmokeronopsis jahodai* and for *T. rubra* (Wicklow 1981, Hu *et al*. 2004). Our results show that *T. stoecki* exhibits almost the same process as its two congeners during the binary fission except for the macronuclear behavior. In *T. stoecki*, macronuclear nodules fuse into numerous masses and then divide; while in *T. rubra* they divide individually without obvious fusing. The process in *T. jahodai* is unknown.

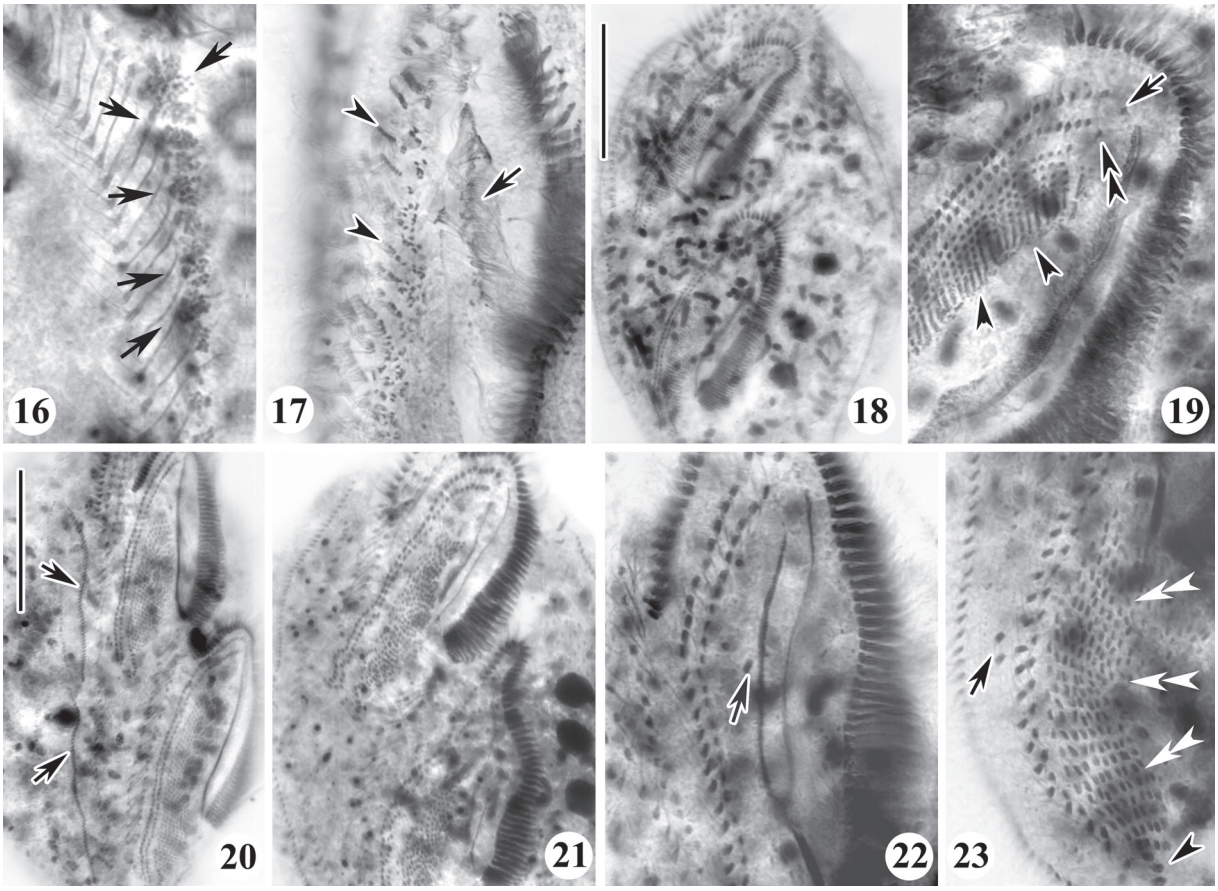
Apokeronopsis and *Thigmokeronopsis* share a similar ontogenetic mode: (1) the oral primordia originate *de novo* and the old adoral zone of membranelles and undulating membranes are replaced completely; (2) no old cirri join the formation of the cirral anlagen; (3) the anlagen of marginal rows and dorsal kineties develop *de novo*. The numerous macronuclear nodules fuse into many masses in *Apokeronopsis* as in *T. stoecki*. And *Apokeronopsis* species also have several buccal cirri



Figs 8–15. Infraciliature of *Thigmokeronopsis stoecki* during divisional process. **8 –** ventral view of an early divider, arrowheads and arrow show the oral primordium of the opisthe and proter respectively; **9 –** ventral view, double-arrowheads indicate the parental membranelles disaggregating, arrows indicating the fronto-ventral-transverse cirral anlagen and arrowheads marking the oral primordia for each of the dividers; **10**, **11 –** ventral and dorsal views of the same divider at mid-stage, in Fig. 10 arrows indicate the left marginal row anlagen and arrowheads mark the undulating membranes anlagen for each divider, in Fig. 11 arrows indicate the dorsal kineties anlagen and arrowheads mark the right marginal row anlagen; **12 –** ventral view, arrowhead indicates right marginal row anlage in the opisthe, and arrows mark the first frontal cirri generated from the undulating membrane anlagen; **13**, **14 –** ventral views of a late divider, arrows indicate the new left marginal rows, arrowheads mark the new buccal cirri, double-arrowheads show the frontoterminal cirri (Fig. 14 to show the details); **15 –** ventral view of a late stage divider about to separate, to show the formation of new frontoterminal cirri (arrows), the thigmotactic cirri (arrowheads) and the transverse cirri (double-arrowheads). Scale bars: 50 μm.

formed by single (*A. crassa* and *A. ovalis*) or multiple (*A. bergeri*) streaks of fronto-ventral-transverse cirral anlagen, whereas *Thigmokeronopsis* species have one or more buccal cirri all coming from single streak (Wicklow 1981, Petz 1995, Hu *et al*. 2004, Shao *et al*. 2007, Li *et al*. 2008, Shao *et al*. 2008a).

In the family Pseudokeronopsidae, most species share the same pattern in the development of their oral



Figs 16–23. Photomicrographs of *Thigmokeronopsis stoecki* during morphogenesis after protargol impregnation. **16 –** ventral view, arrows indicate the anarchic field of basal bodies; **17 –** ventral view of proter, arrow marks disorganized parental undulating membranes, and arrowheads indicate the fronto-ventral-transverse cirral anlagen; **18 –** ventral view of a mid-staged divider, noting the development of adoral zone of membranelles; **19 –** ventral view of proter, to show the newly formed first frontal cirrus (arrow), the buccal cirrus (double-arrowheads), and thigmotactic cirri (arrowheads); **20**, **21 –** ventral views, to show the newly formed right marginal rows (arrows in Fig. 20); **22**, **23 –** ventral views of the same divider, to show the new buccal cirrus (arrow in Fig. 22), frontoterminal cirri (arrow in Fig. 23), transverse cirri (arrowhead in Fig. 23) and the thigmotactic cirri (double-arrowheads in Fig. 23). Scale bars: 40 μm.

apparatus and fronto-ventral-transverse cirri, i.e. the opisthe's oral primordium occur apokinetally, the proter's oral primordium originate *de novo*, the old adoral zone of membranelles renew completely and the fronto-ventral-transverse cirral anlagen in both dividers form *de novo* (Mihailowitsch and Wilbert 1990, Hu and Song 2001, Berger 2004, Hu *et al*. 2004, Sun and Song 2005, Chen *et al*. 2011, Pan *et al*. 2013). More diversity, however, is evident in the origin of the anlagen of marginal cirral rows and dorsal kineties, thus, in *Apokeronopsis* and *Thigmokeronopsis*, they develop *de novo*; but in *Pseudokeronopsis*, *Uroleptopsis* and *Heterokeronopsis*, they develop intrakinetally. These differences in ontogenetic characteristics among pseudokeronopsids support the polyphyly of the family Pseudokeronopsidae that has been revealed by recent studies based on phylogenetic analyses (Chen *et al*. 2010, Foissner *et al*. 2010, Küppers *et al*. 2011, Li *et al*. 2011, Shao *et al*. 2011).

Pseudokeronopsis similis exhibits a unique ontogenetic pattern with differences in a number of the key characteristics shared by all the other pseudokeronopsids. Specifically, its old adoral zone of membranelles and old undulating membranes are partially renewed by dedifferentiation, and the opisthe's oral primordium is not related to the formation of the fronto-ventral-transverse cirral anlagen although some old midventral cirri contribute to it (Shi *et al*. 2007). This may suggest that *P. similis* does not belong to the genus *Pseudokeronopsis* or even the family Pseudokeronopsidae.

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