Morphology and infraciliature of two new species of marine oligotrich ciliates (Ciliophora: Oligotrichida) from China

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Abstract
Two new marine oligotrich ciliates, Parallelostrombidium paralatum nov. sp. and Strombidium montagnesi nov. sp., were isolated from the littoral area of Qingdao (Tsingtao), China. The morphology and infraciliature of each was studied using live observation and protargol impregnation. Based on the Qingdao population, the diagnosis for P. paralatum is given: marine Parallelostrombidium, in vivo about 70 × 60 μm; dorsoventrally flattened ca 2:3; cell ellipsoidal in outline with conspicuous apical protrusion; on average 27 anterior and 17 ventral membranelles; two posteriorly directed thigmotactic membranelles; macronucleus broadly ellipsoidal; extrusomes ca 10 μm long, arranged along equatorial area; girdle and ventral kineties with 71–99 and 32–42 dikinetids, respectively. Strombidium montagnesi nov. sp. is characterized thus: small marine Strombidium ~30 × 20 μm in vivo with truncated conical cell shape and conspicuous equatorial ridge; hemitheca covering the posterior one-quarter to one-third of the cell; dorsoventrally flattened ca 2:3; about 21 anterior membranelles and six ventral membranelles; girdle kinety located in posterior one-quarter to one-third of the cell and has 25–27 dikinetids, while ventral kinety has 6–12 dikinetids; extrusomes ca 5 μm long, arranged along girdle kinety; single ellipsoidal macronucleus centrally positioned.

Keywords: Marine ciliate, Oligotrichida, Parallelostrombidium paralatum nov. sp., Strombidium montagnesi nov. sp.

Introduction
Oligotrichs play an important role in marine planktonic microbial food webs because they serve as an important link between smaller unicellular organisms and those of higher trophic levels (Pierce and Turner 1992). Since the beginning of the 19th century, about 200 aloricate oligotrichs have been reported. Unfortunately, many descriptions were based only on live specimens or on material fixed using classical methods (Busch 1921, 1930; Fauré-Fremiet 1924; Kahl 1932), leaving doubt about the validity of these species. Thus, modern techniques, in which cells are investigated in life as well as following silver
impregnation, are regarded as essential for adequate species description (Song and Bradbury 1998; Song et al. 2000; Agatha 2003a, 2003b, 2004a, 2004b; Modeo et al. 2003; Agatha et al. 2004; Xu et al. 2005; Xu and Song 2006).

The genus *Parallelostrombidium* was recently established by Agatha (2004a), and is characterized thus: “ventral kinety follows posterior portion of dextrally spiraled girdle kinety; thus, both with same orientation”. Only two species are included in this genus: *P. rhyticollare* (Corliss and Snyder, 1986) Agatha, 2004 and *P. siculum* (Montagnes and Taylor, 1994) Agatha, 2004.

During surveys of the ciliate fauna in the coastal regions near Qingdao, China, two oligotrich ciliates were collected. After comparison with known congener, they are believed to be new species of *Parallelostrombidium* and *Strombidium*, respectively: *Parallelostrombidium paralatum* nov. sp. and *Strombidium montagnesi* nov. sp.

**Materials and methods**

**Sample collection**

*Parallelostrombidium paralatum* was collected from shrimp-culturing waters in Jiaozhou Bay off Qingdao (Tsingtao, 36°08’N, 120°43’E), China on 21 April 2004, the salinity of which was ~30psu, the pH ~7.8 and the temperature ~16°C. Glass slides fixed in a slide frame served as artificial substrates and were immersed in the water until biofilm was formed (~15 days). The slides were retrieved and transferred to Petri dishes with marine water from the sampling site.

*Strombidium montagnesi* was collected by 20 μm mesh plankton nets on 13 April 2004 from coastal waters near Qingdao. The salinity was ~33psu, pH ~7.0 and the water temperature ~16°C.

**Morphological investigations**

The behaviour of the organisms was studied in the Petri dishes under a dissecting microscope. The morphology was investigated under a compound microscope equipped with a high-power oil immersion objective as well as differential interference contrast optics. The infraciliature was revealed by protargol impregnation (Wilbert 1975). Counts, drawings (with the help of a camera lucida) and measurements were performed at a magnification of 1250 ×.

Terminology is mainly according to Agatha et al. (2005).

**Results and discussion**

*Parallelostrombidium paralatum* nov. sp.

(Figures 1, 2; Table I)

**Diagnosis**

Marine *Parallelostrombidium*, *in vivo* about 70 × 60 μm; dorsoventrally flattened ca 2:3; cell ellipsoidal in outline with conspicuous apical protrusion; on average 27 anterior and 17 ventral membranelles; two posteriorly directed thigmotactic membranelles; macronucleus broadly ellipsoidal; extrusomes *ca* 10 μm long, arranged along equatorial area; girdle and ventral kineties with 71–99 and 32–42 dikinetids, respectively.
Etymology

The specific epithet refers to the superficial similarity in body shape between this species and *Strombidium latum*.

Type location

Shrimp-culturing waters in Jiaozhou Bay off Qingdao (Tsingtao, 36°08′N, 120°43′E), China.

Figure 1. *Parallelostrombidium paralatum* nov. sp. from life (A, B, E–G) and after protargol impregnation (C, D, H–J). (A) Ventral view of a typical individual; (B) lateral view, arrowheads show the two thigmotactic membranelles; (C) pattern of somatic ciliature; (D) details of the anterior membranelles; (E) pattern of locomotion; (F) to show the creeping state, note the cell attached to the substrate with its two thigmotactic membranelles; (G) extrusomes; (H, I) ventral (H) and dorsal (I) views showing ciliary pattern; (J) ventral view of a middle divider, to show the newly built oral primordium and new thigmotactic membranelles (arrowheads); basal bodies proliferate within the girdle and ventral kinety (arrows). AM, anterior membranelles; AP, apical protrusion; E, endoral membrane; GK, girdle kinety; Ma, macronucleus; Pe, pellicle; TM, thigmotactic membranelles; VK, ventral kinety; VM, ventral membranelles. Scale bars: 30 μm (A, B, H, I); 5 μm (G); 40 μm (J).
One holotype slide (registration number 2005:8:24:1) of protargol-impregnated specimens is deposited in the collection of the Natural History Museum, London, UK and two paratypes are deposited in the Laboratory of Protozoology, Ocean University of China (registration numbers 04:04:21:01 and 04:04:21:02).

**Slide deposition**

Figure 2. Photomicrographs of *Parallelostrombidium paralatum* nov. sp. from life (A–E) and after protargol impregnation (F–J). (A) Ventral view of a representative specimen, arrow marks the apical protrusion; (B) ventral view of the anterior region of the cell, to show the apical protrusion and the ventral membranelles; (C) ventral view of the posterior region of the cell, arrows mark the oral primordium of the opisthe; (D) lateral view, to show the apical protrusion and the ingested algae; (E) extrusomes after cell bursts; (F) early divider in left ventral view, arrowheads indicate the oral primordium; (G) dorsal view, arrows mark the girdle kinety; (H) to show the macronucleus and the nucleoli; (I) ventral view, to show the two thigmotactic membranelles (arrowheads), girdle kinety (arrows) and the ventral kinety (double-arrowheads); (J) early divider in left ventral view, arrowhead marks the oral primordium. Scale bars: 35 μm (A, D); 5 μm (E).
Table I. Morphometric data for *Parallelostrombidium paralatum* and *Strombidium montagnesi* (data based on protargol-impregnated specimens).

| Character                        | Minimum | Maximum | Median | Mean | SD  | n  |
|----------------------------------|---------|---------|--------|------|-----|----|
| Cell length (μm)                 | *P. paralatum* | 51     | 72     | 64   | 63  | 6.39 | 15  |
|                                  | *S. montagnesi* | 22     | 26     | 24   | 25  | 1.76 | 12  |
| Cell width (μm)                  | *P. paralatum* | 48     | 60     | 52   | 54  | 3.44 | 16  |
|                                  | *S. montagnesi* | 14     | 17     | 16   | 15  | 1.10 | 12  |
| Apex to cytostome (distance)a (μm) | *P. paralatum* | 22     | 32     | 26   | 27  | 3.09 | 16  |
|                                  | *S. montagnesi* | 6      | 10     | 6    | 7   | 1.98 | 12  |
| Girdle kinety to distal end (distance) (μm) | *P. paralatum* | –     | –      | –    | –   | –   | –   |
|                                  | *S. montagnesi* | 6      | 9      | 6    | 6   | 1.54 | 12  |
| No. of anterior membranellesb     | *P. paralatum* | 26     | 30     | 27   | 28  | 1.33 | 14  |
|                                  | *S. montagnesi* | 21     | 23     | 21   | 22  | 0.80 | 15  |
| No. of thigmotactic membranelles | *P. paralatum* | 2      | 2      | 2    | 2   | 0.00 | 15  |
|                                  | *S. montagnesi* | –     | –      | –    | –   | –   | –   |
| No. of ventral membranelles      | *P. paralatum* | 15     | 19     | 17   | 17  | 1.25 | 15  |
|                                  | *S. montagnesi* | 6      | 7      | 6    | 6   | 0.40 | 15  |
| No. of dikinetids in girdle kinety | *P. paralatum* | 71     | 99     | 83   | 84  | 9.11 | 13  |
|                                  | *S. montagnesi* | 25     | 27     | 26   | 26  | 0.76 | 12  |
| No. of dikinetids in ventral kinety | *P. paralatum* | 32     | 42     | 38   | 38  | 3.14 | 14  |
|                                  | *S. montagnesi* | 6      | 12     | 9    | 9   | 1.00 | 12  |
| Length of macronucleus (μm)      | *P. paralatum* | 20     | 37     | 27   | 28  | 5.56 | 15  |
|                                  | *S. montagnesi* | 9      | 14     | 10   | 10  | 1.20 | 12  |
| Width of macronucleus (μm)       | *P. paralatum* | 16     | 28     | 22   | 23  | 4.45 | 15  |
|                                  | *S. montagnesi* | 6      | 13     | 9    | 9   | 2.15 | 21  |

*a* Measured from the anteriormost point to the posterior end of the ventral membranelles; *b* including the two thigmotactic membranelles.

**Description**

Size *in vivo* 55–80 × 50–65 μm, usually 70 × 60 μm. Cell ellipsoidal in shape with bluntly rounded posterior end; when viewed from ventral side, usually broadest in the equatorial area (Figures 1A, 2A). Slightly flattened dorsoventrally ca 2:3 (Figures 1B, 2D). Collar region domed to form a conspicuous apical protrusion ~6 μm high (Figure 2A, arrow), which may disappear or be undetectable after protargol impregnation. Buccal cavity relatively deep, extending obliquely towards right side of cell and terminating about one-third of the way down the cell (Figures 1A, 2A).

Cell extremely fragile, highly sensitive to presence of cover-slip and easily bursts. Pellicle delicate with thin and transparent hemitheca that covers posterior half of cell (Figure 1A), but no polygonal cortical platelets recognizable either *in vivo* or in silvered specimens. Cytoplasm colourless to greyish, containing many ingested algae (including diatoms) which often render cells opaque or dark when observed at lower magnifications (Figure 2A). Extrusomes prominent and acicular-shaped, ca 10 μm long, evenly arranged in a single row at about the level of the hemitheca margin, but not in bundles (Figures 1A, 2E). Neither contractile vacuole nor cytopyge were detected. Single macronucleus broadly ellipsoidal in shape and centrally located, containing several large nucleoli each ~5 μm across (Figures 1I, 2H); no micronucleus detected.

Locomotion with two patterns: moderately fast and irregular when swimming (Figure 1E), or very fast when crawling on debris, using its two thigmotactic membranelles for attachment with ventral side facing down (Figure 1F).

Somatic ciliature as shown in Figures 1 and 2, consisting of one girdle kinety and one ventral kinety. Girdle kinety originates in mid-ventral region (to the left of the ventral
kinety) and extends transversely across right ventral and dorsal sides, curves obliquely across left ventral side of cell and terminates at mid-caudal area (Figures 1C, H, I, 2G, I). On average there are 84 (71–99) widely spaced dikinetids. Within each dikinetid, the left basal body bears a short cilium about 2 μm long while the right is subtended by a conspicuous argentophilic fibre (Figure 2G, I, arrows). Ventral kinety, which is composed of about 38 (32–42) densely arranged dikinetids, extends anteriad from posterior pole, parallel to the distal end of the girdle kinety and terminates at equatorial level (Figures 1C, H, I, 2I, double-arrowheads). Each dikinetid has a cilium (about 2 μm in length) associated with the anterior basal body. Girdle kinety and ventral kinety thus both with same orientation. No extra kinety detected.

Oral apparatus occupies anterior end of cell, consisting of a short endoral membrane on inner wall of buccal lip and a membranellar zone (Figures 1H, I, 2I). Adoral zone of membranelles bipartite with an anterior portion of about 28 (26–30) membranelles and a ventral portion of about 17 (15–19) membranelles, all of which are composed of three kinety rows (Figure 1D). Cilia of most anterior membranelles ca 20 μm in length, stretching anteriorly when swimming (Figure 1A). Bases of anterior membranelles about 11–12 μm long. Anterior membranelles distinctly separated from ventral ones by the two thigmotactic membranelles, the bases of which are about 15 μm long (Figures 1H, 2I, arrowheads). Cilia of two thigmotactic membranelles about 30–35 μm long and always directed posteriorly like two tails (Figure 1A, B, arrowheads). Bases of ventral membranelles about 7–8 μm in length, distinctly shorter than those of the thigmotactic membranelles. Endoral membrane extending to centre of protrusion, probably composed of monokinety (Figure 1H). Pharyngeal fibres not detected.

**Stomatogenesis**

Several stages in division were found which permit the reconstruction of the main stomatogenetic processes. Stomatogenesis commences with the apokinetically development of cuneate, longitudinally orientated basal bodies in a shallow depression underneath the ventral membranelles and to the left of the anterior end of the girdle kinety (Figure 2C, arrows; J, arrowhead). While the oral primordium elongates posteriorly, membranelles differentiate from anterior to posterior (Figure 2F, arrowhead) and the endoral membrane originates de novo. At the same time, new basal bodies are generated by intrakinety proliferation (Figure 1J, arrows). Simultaneously, the membranelles become ciliated. When the final number of membranelles is formed, the oral primordium moves to the left ventral side of cell. The oral primordium positions to the left of the anterior end of the girdle and ventral kinety and above the left portion of the girdle kinety (Figure 1J).

**Comparison with related species**

To date, approximately 12 species of oligotrich ciliates with thigmotactic membranelles inhabiting marine biotopes have been reported: *Ome gastrombidium elegans* (Florentin, 1901) Agatha, 2004; *Spirostrombidium urceolare* (Stein, 1867) Lei et al., 1999; *Spirostrombidium cinctum* (Kahl, 1932) Petz et al., 1995; *Strombidium paracalkinsi* (Lei et al., 1999) Agatha, 2004; *Strombidium calkinsi* Fauré-Fremiet, 1932; *Strombidium clavellinae* von Buddenbrook, 1922; *Strombidium sauerbreyae sensu* Fauré-Fremiet, 1950; *Strombidium fourneleti* Dragesco, 1960, *Strombidium faurei* Dragesco, 1960, *Strombidium latum sensu* Kahl, 1932, *Strombidium latum sensu* Fauré-Fremiet, 1950, and *Parallelostrombidium paralatum* (von Buddenbrook
1922; Fauré-Fremiet 1932, 1950; Kahl 1932; Dragesco 1960; Lei et al. 1999; Song et al.
2000; Xu and Song 2006; present study). The infraciliature of each of the first four species
listed have recently been revealed (Lei et al. 1999; Song et al. 2000; Xu and Song 2006).
Based on those data they belong to genera other than Parallelostrombidium and so can easily
be distinguished from P. paralatum. Although the infraciliature of Strombidium calkinsi Fauré-
Fremiet, 1932 still remains unknown, it can easily be separated from P. paralatum by the
position of the thigmotactic membranelles (dorsal versus ventral).
Fauré-Fremiet (1950) described two forms under the name Strombidium sauerbreyae, despite
the fact that their morphology is quite different from that of the original (Sauerbrey 1928).
Considering the general morphology (namely cell size and shape, presence of the two thigmotactic
membranelles, locomotion pattern etc.), S. sauerbreyae sensu Fauré-Fremiet, 1950 bears a strong
resemblance to Parallelostrombidium paralatum, but it can be differentiated from the latter by (1)
arrangement of extrusomes (sparsely arranged in the ventral side versus evenly arranged at about
the level of hemitheca margin), and (2) much lower number of anterior membranelles (ca 17
versus 26–30) and ventral membranelles (ca 15 versus 15–19) (Fauré-Fremiet 1950).
Strombidium latum sensu Fauré-Fremiet, 1950 also has thigmotactic membranelles. However, it
can be separated from Parallelostrombidium paralatum by its much larger cell
size (110–170 µm versus 55–80 µm), different distribution of extrusomes (surrounding the
cell versus arranging along the equatorial area) and much larger oral cavity (about two-
thirds of cell length versus about one-third of cell length) (Fauré-Fremiet 1950).
Strombidium latum sensu Kahl, 1932 has two to three thigmotactic membranelles, which
should also be compared with Parallelostrombidium paralatum. The former can be separated
from the latter by its much larger cell size (100–140 µm versus 55–80 µm), and different
arrangement of extrusomes (surrounding the cell margin versus arranging along the
equatorial area) (Kahl 1932).
Strombidium fourneleti Dragesco, 1960 is similar in size to Parallelostrombidium paralatum
and also has two thigmotactic membranelles. However, it can be distinguished from the
latter by the cell shape (globular versus ellipsoidal), the fine adoral membranelles (versus
prominent and well-developed), the presence of polygonal cortical platelets (versus absent),
the sparsely distributed extrusomes (versus densely arranged), and the total number of
anterior and ventral membranelles (~24 versus 41–49) (Dragesco 1960).
Strombidium clavellinae von Buddenbrock, 1922 is also very similar to Parallelostrombidium
paralatum in terms of its general appearance (von Buddenbrock 1922). It differs from the
latter, however, in having four thigmotactic membranelles (versus two), and fewer
membranelles (total of anterior and ventral membranelles 32–35 versus 41–49).
Considering the size and presence of two thigmotactic membranelles, Strombidium faurei
Dragesco, 1960 should also be compared with Parallelostrombidium paralatum. The former
differs from the latter in terms of cell shape (ovoid versus ellipsoidal and dorsoventrally
flattened), total number of anterior and ventral membranelles (~27 versus 41–49) and the
arrangement of extrusomes (sparsely distributed on the somatic area versus densely
arranged along the equatorial area) (Dragesco 1960).

Ontogenetic comparison

Only early dividers were found in Parallelostrombidium paralatum, so comparisons between
Parallelostrombidium and its congeneres were based on stomatogenesis information.
The position of the oral primordium of Parallelostrombidium is very similar to that of
Novistrombidium, i.e. oral primordium originates above the left portion of the girdle kinety
(Agatha 2003a).
Parallelostrombidium differs from Strombidium in the location of the oral primordium (anterior versus posterior portion of the girdle kinety) (Song and Wang 1996; Agatha 2003a).

Similar to Laboea and Spirotontonia, the parental oral ciliature of Parallelostrombidium does not reveal any signs of reorganization. However, the position of the oral primordium of the latter is different from that of the former (oral primordium originates anterior to the left ventral portion of the girdle kinety versus oral primordium develops posterior to the left portion of the girdle kinety) (Agatha et al. 2004).

**Strombidium montagnesi** nov. sp.
(Figures 3, 4; Table I)

**Diagnosis**

Small marine Strombidium $\sim30 \times 20\mu m$ *in vivo* with truncated conical cell shape and conspicuous equatorial ridge; hemitheca covering the posterior one-quarter to one-third of

Figure 3. *Strombidium montagnesi* nov. sp. from life (A–D) and after protargol impregnation (E–I). (A) Ventral view of a typical individual, arrows indicate the ridge along equatorial region; (B) extrusomes; (C) ventral view, to show different cell shape; (D) right side view to show the dorsoventrally flattened cell shape, arrows mark the ridge along subequatorial region; (E) ventral view of an early divider, arrow marks the oral primordium; (F) pattern of somatic ciliature; (G, H) ventral and dorsal views showing ciliary pattern; (I) ventral view of an early divider. AM, anterior membranelles; AP, apical protrusion; EM, new endoral membrane; GK, girdle kinety; Ma, macronucleus; VK, ventral kinety; VM, ventral membranelles. Scale bars: 15 $\mu m$ (A, G, H); 3 $\mu m$ (B).
Figure 4. Photomicrographs of *Strombidium montagnesi* nov. sp. from life (A–E) and after protargol impregnation (F–J). (A) Ventral view of a representative specimen, arrows indicate the ridge along equatorial region; (B) lateral view, arrows mark the ridge along subequatorial region; (C) to show the cilia of the ventral kinety (arrows); (D) arrows mark the edge of the transparent hemitheca; (E) to show different cell shape, the flame-shaped anterior membranelles when cell is at rest, and the densely arranged extrusomes; (F) ventral view, to show the oral primordium (arrowhead) and the girdle kinety (arrows); (G) to show the macronucleus and the nucleoli; (H) dorsal view, arrows indicate the girdle kinety; (I) to show the oral primordium; (J) to show the ventral kinety (arrowheads). Scale bars: 15 μm (A, B, E); 10 μm (F); 20 μm (G, J).
the cell; dorsoventrally flattened ca 2:3; about 21 anterior membranelles and six ventral membranelles; girdle kinety located in posterior one-quarter to one-third of the cell and has 25–27 dikinetids, while ventral kinety has 6–12 dikinetids; extrusomes ca 5 μm long, arranged along girdle kinety; single ellipsoidal macronucleus centrally positioned.

Dedication

We dedicate this new species to Dr David J. S. Montagnes, University of Liverpool, UK, for his great contribution to the taxonomy and ecology of planktonic ciliates.

Type location

Coastal waters near Qingdao (Tsingtao, 36°08′N, 120°43′E), China.

Slide deposition

One holotype slide of protargol-impregnated specimens is deposited in the Natural History Museum, London, UK (registration number 2005:8:24:2). Two paratypes (registration numbers 2004:04:13:01 and 2004:04:13:02) of protargol-prepared specimens are deposited in the collection of the Laboratory of Protozoology, Ocean University of China.

Description

Size 25–30 × 15–20 μm in vivo, usually 30 × 20 μm. Cell shape usually elongated cordate or obconical, anterior end slightly domed with hyaline apical protrusion, ~3 μm high, at right side of peristome when observed in vivo (Figures 3A, C, 4A, E); posterior end of cell usually broadly rounded but truncated in some individuals (Figures 3C, 4E). Cell dorsoventrally flattened, width: thickness ratio about 3:2 (Figures 3D, 4B). Buccal cavity relatively shallow, extending obliquely to right side of cell (Figure 3A, C).

Cytoplasm colourless, contains lipid droplets 1–2 μm across and food vacuoles 1–4 μm across containing remnants of green algae and bacteria (Figures 3A, C, 4A, E). Pellicle delicate with transparent hemitheca, which covers the posterior one-quarter to one-third of the cell, but no polygonal platelets observed (Figures 3A, C, 4E). Girdle kinety lying below equatorial region and on upper margin of the hemitheca (Figure 4D, arrows), where there is a conspicuous ridge around the subequatorial region (Figure 4A–C, arrows). Extrusomes prominent, 5 μm long, closely spaced (but not in bundles) anterior to margin of hemitheca (Figures 3A, C, 4E). Outer ends of extrusomes located along the ridge (Figures 3A, D, 4A, B, arrows). Cilia of ventral kinety about 4 μm long, conspicuous in vivo (Figure 4C, arrows). Contractile vacuole not observed. Single macronucleus ~10 μm in diameter, round in shape and centrally located, contains some small nucleoli ~1 μm across and several larger nucleoli ~3 μm across (Figures 3G, H, 4G). Micronucleus not observed.

Cell swims slowly and continuously with smooth turns, while rotating about main cell axis. When under cover-slip, cilia of anterior membranelles sometimes densely pack together forming a flame shape when cell rests (Figure 4E).

Somatic ciliature as shown in Figures 3 and 4, arranged in a girdle and ventral kinety. Girdle kinety sub-equatorial, namely on average ~70–75% of the way down the cell, completely closed, composed of ~26 (25–27) horizontally orientated dikinetids (Figures 3F, G, H, 4H, arrows). Ventral kinety extends down right-ventral side of cell, under posterior
pole and terminates on left dorsal side, composed of \( \sim 9 \) (6–12) dikinetids (Figures 3F–H, 4J, arrowheads).

Oral apparatus typical of genus, occupies anterior end of cell. Adoral zone of membranelles surrounds apical protrusion, divided into an anterior portion with 21–23 membranelles and a ventral portion with six to seven membranelles (Figure 3G, H). Anterior membranelles continuous with ventral ones, each composed of three equally long basal body rows. Ventral membranelles invaginate ventrally to the right side of the cell. Cilia of anterior membranelles \( \sim 15 \mu m \) in length, projecting anteriorly when swimming. Endoral membrane on inner wall of buccal lip on right side of oral cavity, rarely recognizable in protargol-impregnated specimens, probably composed of monokinetids. Pharyngeal fibres not observed.

Stomatogenesis

In our specimens, the oral primordium originates on the left ventral side immediately posterior to the ventral membranelles. The very early stage of stomatogenesis shows only a few disordered basal bodies, which do not appear to be formed in contact with parental structure, i.e. the oral primordium develops apokinetally (Figures 3E, arrow, 4F, arrowhead). The basal bodies then align almost instantly into membranelles and move deeper into the cell while the oral primordium becomes orientated longitudinally and curves. The oral primordium is always positioned anterior to the girdle kinety until its differentiation into the adoral membranelles is complete (Figures 3I, 4I).

Comparison with similar species

With respect to its small size, dorsoventrally flattened body shape (width: thickness 3:2–3:1) and the sub-equatorially located girdle kinety (positioned in posterior one-quarter to one-third of the cell), *Strombidium montagnesi* can be easily separated from most other congeners. Comparison should be made with two morphologically similar species. Considering the ciliary pattern, *Strombidium constrictum* (Meunier, 1910) Wulff, 1919 is similar to *S. montagnesi*. The former, however, can be separated from the latter by: (1) shape of macronucleus (V-shaped versus globular); (2) the number of anterior (11–16 versus 21–23) and ventral (8–14 versus 6–7) membranelles; and (3) presence of monokinetids in ventral kinety (versus dikinetids) (Lynn et al. 1988).

*Strombidium coronatum* can be separated from *S. montagnesi* by its cell shape (posterior end sharply pointed versus posterior end usually broadly rounded but truncated in some individuals) and much larger cell size (ca. 100 \( \mu m \) versus 25–30 \( \mu m \)) (Leegaard 1915).

Ontogenetic comparison

The process of stomatogenesis differs from that in the improved diagnosis of the genus *Strombidium* supplied by Agatha (2004b): “Girdle kinety horizontal. Ventral kinety longitudinal, occasionally reduced or lacking. Oral primordium develops at or below level of girdle kinety”. These differences might indicate that the ontogenetic patterns in *Strombidium* are more diverse than hitherto realized. Gene sequence analysis has revealed a paraphyly of *Strombidium* and a considerably larger genetic variation among oligotrichs than among stichotrichs (Snoeyenbos-West et al. 2002; Modeo et al. 2003). Further investigations of strombidiid morphology and ontogenesis may well lead to a split of the
genus *Strombidium* reflecting the situation in the phylogenetic trees inferred from gene sequence analyses (Agatha et al. 2005).

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