

Redescriptions of Two Marine Scuticociliates from China, with Notes on Stomatogenesis in *Parauronema longum* (Ciliophora, Scuticociliatida)

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Summary. The morphology and infraciliature of two marine scuticociliates, *Pleuronema puytoraci* Grolière and Detcheva, 1974, and *Parauronema longum* Song, 1995, collected from China, were investigated using live observation and protargol impregnation methods. Based on the data obtained for the China population, new information of the living morphology of *Pleuronema puytoraci* is documented and details of the complete infraciliature is available for the first time. The stomatogenesis of *Parauronema longum* is basically similar to that of its congeners and can be summarized as follows: membranelle 1, membranelle 2 and the scutica of the opisthe originate from the parental paroral membrane, whereas membranelle 3 of the opisthe develops from the parental scutica; the paroral membrane originates from the parental paroral membrane.

Key words: Scuticociliates, infraciliature, marine ciliates, morphogenesis, *Parauronema*, *Pleuronema*.

INTRODUCTION

Scuticociliate ciliates are ubiquitous in various habitats worldwide. Due to their small body size and great similarity in living morphology, the taxonomy of this group remains difficult and confused, notwithstanding the advances made in a number of recent investigations (Munday *et al.* 1997, Foissner *et al.* 2009, Bourland and

Struder-Kypke 2010, Fan *et al.* 2010, Harikrishnan *et al.* 2010, Lee and Kim 2010, Li *et al.* 2010, Long and Zufall 2010, Miao *et al.* 2010, Zhang *et al.* 2010, Fan *et al.* 2011a, Lobban *et al.* 2011). Many nominal species are inadequately investigated with regards to current taxonomic criteria, that is, they are poorly defined, lack the type material, are insufficiently described and/or morphogenetic and gene sequence data are absent (Grolière and Detcheva 1974, Wang *et al.* 2008a, Miao *et al.* 2009, Gao *et al.* 2010, Pan *et al.* 2010, Zhang *et al.* 2011).

During faunistic surveys of marine ciliates in coastal waters of China, two scuticociliates were isolated, namely *Parauronema longum* and *Pleuronema puytoraci*, giving the opportunity to investigate them us-

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ing modern methods for the first time. In this paper, we document the living morphology and infraciliature of both species and document the process of stomatogenesis for *Parauronema longum*.

MATERIALS AND METHODS

Pleuronema puytoraci was collected on 27 December 2010 from shrimp-culturing waters off the coast of Hong Kong (22°15'N, 114°15'E), southern China. The water temperature was about 18°C, pH 7.6 and salinity 16‰. *Parauronema longum* was collected on 12 March 2010 from coastal waters of the Yellow Sea at Qingdao (Tsingtao, 36°18'N, 120°43'E), northern China. The water temperature was 7.2°C, pH 7.4 and salinity 35‰. Both species were maintained in the laboratory as uniprotistan cultures (Shao *et al.* 2010).

Cells were observed *in vivo* using an oil immersion objective with bright field and Nomarski differential interference contrast microscopy. The protargol silver impregnation according to Wilbert (1975) was used to reveal the infraciliature. Measurements were performed at magnifications of 100–1250 \times . Drawings were carried out with the help of a camera lucida (Chen *et al.* 2010, Fan *et al.* 2011b). Systematics and terminology are mainly according to Lynn (2008) and Small and Lynn (1985).

RESULTS AND DISCUSSION

Parauronema longum Song, 1995

Although this species has been redescribed by Song and Wilbert (2000) since first report, it is necessary to redescribe it in terms of living observations as well as infraciliature based on the current isolation.

Morphology

Body 45–60 \times 20–30 μm *in vivo*, elongate oval to cylindrical, posterior end rounded, ventral side flat, dorsal side convex (Fig. 1A, D). Length of buccal field 40–50% of body (Fig. 1G). Pellicle slightly indented at bases of cilia (Fig. 1E). Extrusomes bar-shaped, ca. 2–3 μm long. Cytoplasm colourless to grayish, transparent, often filled with oil drop-like granules (Fig. 1E). Single ellipsoid to spherical macronucleus, ca. 15 \times 10 μm , located in mid-body with closely associated micronucleus. Crystals ca. 1–2 μm long, brick or dumbbell shaped, often concentrated in anterior and posterior ends of body (Fig. 1F). Contractile vacuole 5 μm in diameter, caudally located. Locomotion by moderately fast swimming, although stationary for rather long periods when feeding, or by slow crawling on substrate with occasional jumps.

Nineteen to 22 somatic kineties, somatic kinety 1 with ca. 32 basal bodies (Fig. 1B, C). Somatic cilia ca. 5–7 μm long. Caudal cilium about 10–15 μm long. Membranelle 1 (M1) long, consisting of 2 longitudinal rows of kinetids, each with 7–10 kinetosomes (Fig. 1H, J). Membranelle 2 (M2) well-separated from M1, composed of 3 rows of kinetosomes, each row containing about 6 kinetosomes (Fig. 1I). Membranelle 3 (M3) much shorter than M1 and M2, composed of 2 or 3 short, irregularly arranged rows of kinetosomes. Paroral membrane on right of buccal cavity, terminating anteriorly at level of mid-region of M2. Scutica Y-shaped comprising 4 pairs of kinetosomes (Fig. 1H).

Morphogenesis during binary fission

Morphogenesis in *Parauronema longum* commences with the proliferation and irregular rearrangement of kinetosomes in the scutica which form in 6–8 pairs. This structure is designated the primary field of the oral primordium (pF) because it appears first stage in stomatogenesis (Fig. 2B). Meanwhile, the zig-zag configuration of the paroral membrane (PM) begins to split longitudinally into two rows (Figs 1K–M, 2C), the outer (right) row of which serves as a new primordium which is designated the secondary field (sF). Later the number of kinetosomes in the primary field increases (Fig. 2D).

When the proliferation of basal bodies is complete the secondary field fragments into two parts, the anterior (sFa) and posterior (sFp) secondary field, each of which is 2-rowed (Fig. 2D). The proliferation of somatic kinetosomes can be recognized at this time with three basal bodies grouped together in the middle portion of each kinety and each monokinetid duplicating itself to form a pair (Fig. 2E).

A partial migration of the primary kinetosomal field then commences (Fig. 1N, O). Meanwhile, the posterior end of the sFa migrates to the anterior-right of the sFp (Figs 1N, 2E), following which the sFa gradually moves down (Fig. 2F). At this stage, somatic kinetosomal proliferation becomes more conspicuous with the basal bodies in groups of three in the mid-region of each kinety (Fig. 2F).

During the next stage, the pF is composed of two parts, the anterior one with three or four rows of basal bodies, whereas the posterior one comprises only three basal bodies (Figs 1P, 2G). While migrating posteriorly, the sFp becomes J-shaped with the posterior end curving to the right (Fig. 2E). Following a process of rearrangement the sF generates membranelles 1 and 2 for

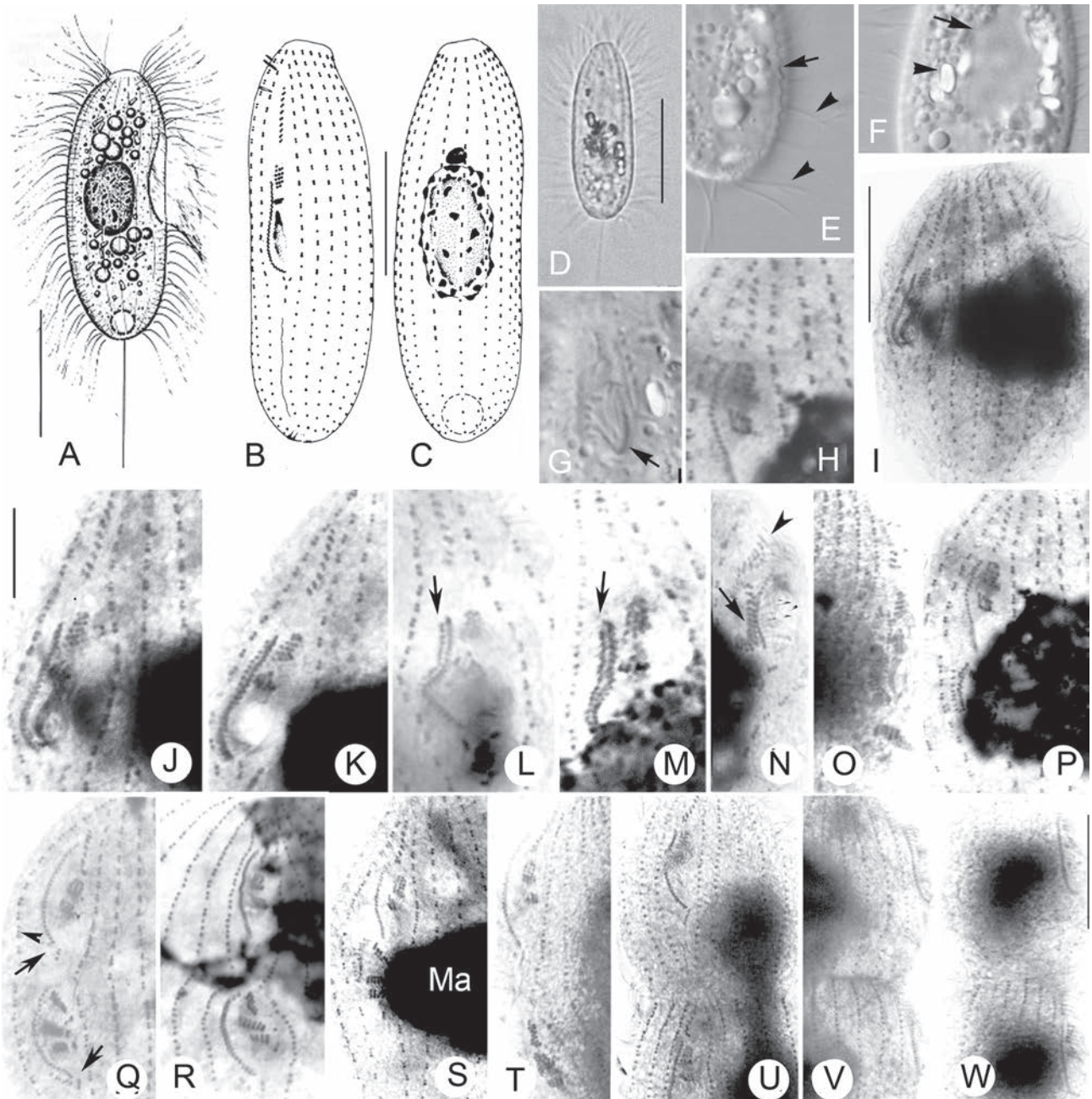


Fig. 1. *Parauronema longum* from life (A, D–G), after protargol impregnation (B, C, H–W), including stomatogenetic stages (K–W) (A–C from Song and Wilbert 2000). A, D – ventral view of a typical individual; B–C – ventral and dorsal views of the infraciliature; E – ventral view, arrow shows the notched pellicle, arrowheads mark the cilia; F – ventral view, arrow shows the macronucleus, arrowhead marks brick or dumb-bell shaped crystals; G – ventral view, arrow denotes the buccal field; H – ventral view of the posterior part of the oral apparatus; I – ventral view of infraciliature; J – buccal field of a non-dividing cell; K–M – initial morphogenetic stages, arrows show the splitting of the paroral membrane; N, O – early morphogenetic stage, to show the anterior (arrowhead) and the posterior part (arrow) of the secondary field; P–T – middle morphogenetic stages, arrows mark the paroral membranes each of which is hook-shaped at its posterior end, arrowhead shows the groups of 3-basal body within the somatic kinetosomes; U–W – late morphogenetic stages, to show the reconstruction of the oral apparatus in the proter and the opisthe. Ma – macronucleus. Scale bars: A, I = 30 μ m, B, C = 20 μ m, D = 35 μ m, J–W = 10 μ m.

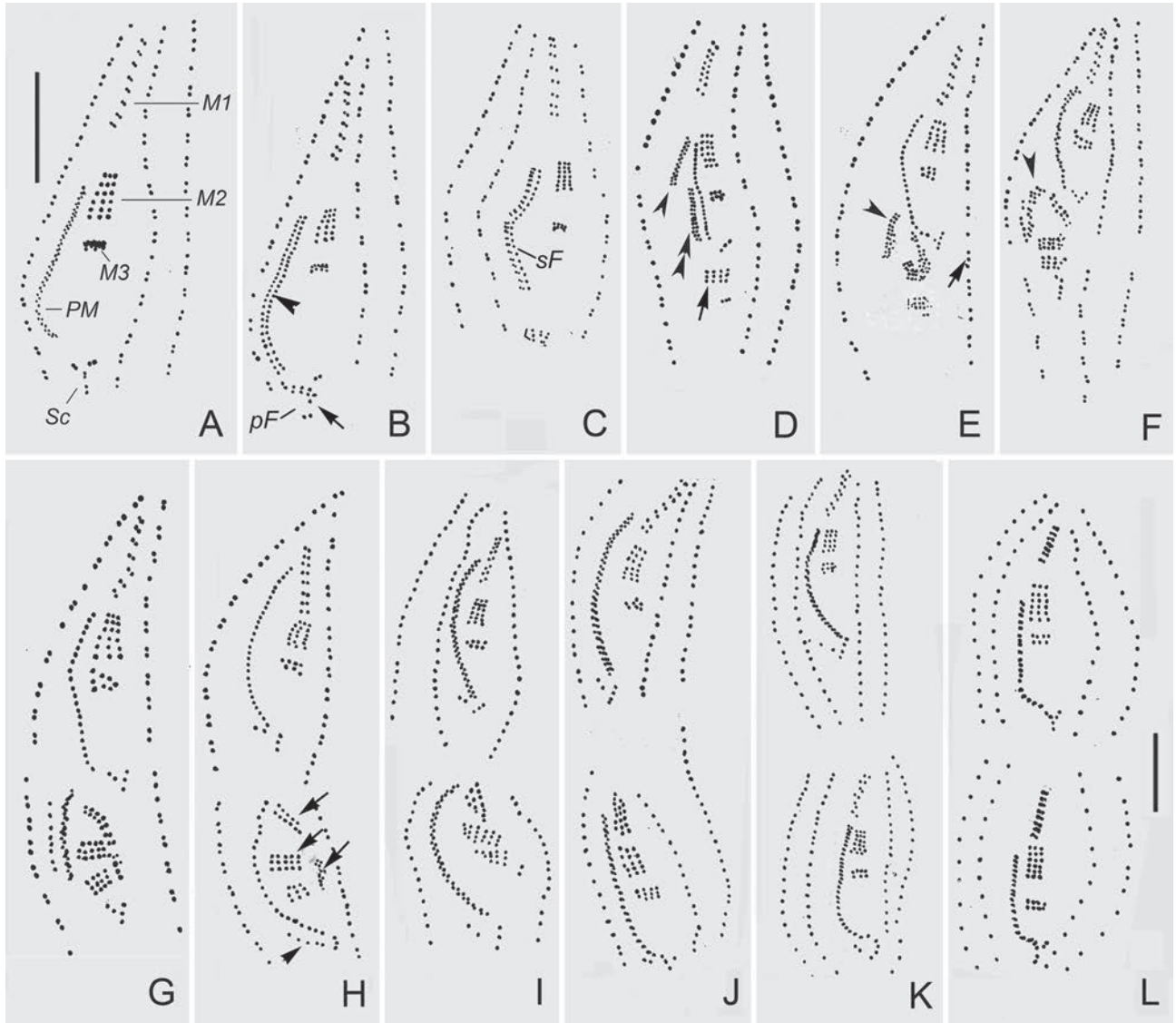


Fig. 2. Stomatogenetic stages in *Parauronema longum*. **A** – non-dividing stage; **B, C** – initial morphogenetic stages, showing the proliferation of kinetosomes in the scuticum forming the first oral primordium (arrow) and the splitting of the paroral membrane (arrowhead); **D** – fragmentation of the second oral primordium into anterior (arrowhead) and posterior (double-arrowhead) parts, arrow shows the first oral primordium; **E, F** – middle morphogenetic stages, arrowheads exhibit the anterior part of the second oral primordium, arrow shows the groups of 3 basal bodies groups within the somatic kineties; **G–I** – middle morphogenetic stages, to show the formation of the scuticum (arrowhead) and the three parts derived from the posterior part of the second oral primordium (arrows); **J–L** – final stages of stomatogenesis. M1–3 – membranelles 1–3, pF – the first oral primordium, sF – secondary field, PM – paroral membrane, Sc – scuticum. Scale bars: A, L = 5 μ m.

the opisthe (Fig. 2F, G), while the sFa develops into the paroral membrane, the posterior end of which is hook-shaped (Figs 1Q–T, 2H). By this stage little change has occurred in the primary field, the kinetosomes of which are positioned close to the anlagen of the membranelles.

Subsequent events take place simultaneously in the proter and opisthe (Fig. 1U). Several pairs of kineto-

somes appear at the posterior end of the proliferated remnants of the parent paroral membrane in both the proter and opisthe, which will eventually develop into the scuticum (Fig. 2I, J).

In the later stages, just before cytokinesis takes place the paroral membrane gradually migrates gradually closer to the membranelles (Fig. 2J, K, PM). Final-

Table 1. Morphometric characterization of *Pleuronema puytoraci* (upper row) and *Parauronema longum* (lower row). Data according to protargol-impregnated specimens. All measurements in μm .

Character	Minimum	Maximum	Mean	SD	CV	n
Body length	88	110	97.8	7.2	7.4	25
	52	65	59.1	4.3	7.3	25
Body width	64	82	71.4	4.9	6.9	25
	28	36	32.2	2.5	7.8	25
Length of buccal field	66	85	74.2	5.2	7.1	25
	25	30	27.5	2.0	7.3	25
Number of somatic kineties	28	29	28.3	0.5	1.8	25
	19	22	20.4	1.0	4.8	25
Number of preoral kineties	1	2	1.4	0.5	20.8	18
Number of basal bodies in somatic kinety 1	–	–	–	–	–	–
	32	35	33.0	1.0	2.8	25
Number of basal bodies in membranelle 1	–	–	–	–	–	–
	7	10	8.1	1.0	11.5	18
Number of macronuclei	1	1	1.0	0	0	25
	1	1	1.0	0	0	25

CV – coefficient of variation in %, n – number of specimens measured, SD – standard deviation – data not available.

ly, several kinetosomes are either reorganized or reabsorbed to complete the formation of the oral apparatus (Figs 1U, V, 2K, L).

The main process of the stomatogenesis can be summarized as follows: *in the proter* the parental membranelles remain unchanged, while the paroral membrane, with an experience of “regeneration”, forms the new paroral membrane and the scutica for the proter; *in the opisthe*, the primordia derive from the parental scutica and paroral membrane with the primordium from the parental paroral membrane generating M1 and M2 and the paroral membrane, whereas M3 is generated from the scutica.

Remarks

The population studied here corresponds well with the original description (Song 1995) and the redescription by Song and Wilbert (2000), hence the identity of this species is not in doubt. Compared with previous descriptions our population has a larger body length (45–60 μm vs. 30–55 μm) and the length of the buccal field relative to the body length is less (ca. 40–50% of cell length vs. 60%). We believe, however, that these dissimilarities are population-dependent.

Morphogenesis in the genus *Parauronema* has been studied in only one species: *P. virginianum* (Grolière

1974). The process of stomatogenesis in *Parauronema longum* corresponds well with that of its congener *P. virginianum* in that the PM, M1, M2, and scutica of the opisthe all derive from the parental PM whereas M3 originates from the proliferation of scutica (Grolière 1974). As revealed in previous and present work, the morphogenesis of *Parauronema*-species in binary fission confirmed that the developmental pattern of oral apparatus within congeners exhibit an extremely similar mode.

Hitherto, 11 genera have been investigated morphogenetically, and they show homologous/slightly different patterns in the formation of PM, M1-3 and scutica (Table 2). For the morphogenetic information is scarce and shows basically homologous characteristics, it cannot be used to generate and test evolutionary hypotheses. We hope the morphogenetic comparison in scuticociliates will contribute to the phylogenetic analysis in Scuticociliatia Small, 1967. More evidence is waited.

Pleuronema puytoraci Grolière and Detcheva, 1974

Hitherto this species was insufficiently described owing to an absence of a detailed description of its morphology *in vivo*. Hence, an improved diagnosis is presented based on data both from previous studies and on the present study which includes observations of the organism *in vivo*.

Table 2. Stomatogenetic subtypes of opisthe among 11 genera of Scuticociliatia.

Genera	Structure formed from the parental membrane	Structure formed from the parental scutica	Number of oral primordia	Stomatogenetic models	References
<i>Parauronema</i>	PM + M1 + M2 + Sc	M3	2	Scuticobuccokinetal	Grolière, 1974
<i>Uronema</i>	PM + M1 + M2 + Sc	M3	2	Scuticobuccokinetal	Foissner, 1972, Ma <i>et al.</i> , 2004
<i>Paranophrys</i>	PM + M1 + M2 + Sc	M3	2	Scuticobuccokinetal	Ma <i>et al.</i> , 2001
<i>Pseudo-cohnilembus</i>	PM + M1 + M2 + Sc	M3	2	Scuticobuccokinetal	Evans and Corliss, 1964 Ma <i>et al.</i> , 2003a
<i>Glauconema</i>	PM + M1 + M2 + Sc	M3	2	Scuticobuccokinetal	Ma <i>et al.</i> , 2006
<i>Philasterides</i>	PM + M1 + M2 + Sc	M3	2	Scuticobuccokinetal	Grolière, 1980
<i>Metanophrys</i>	PM + M1 + M2 + Sc	M3	2	Scuticobuccokinetal	Ma and Song, 2003
<i>Paralembus</i>	PM + Sc + M1 + M3 + M2 (partial)	M2 (partial)	2	Scuticobuccokinetal	Puytorac <i>et al.</i> , 1974
<i>Pleuronema</i>	PM + Sc + M1–3	–	1–2*	None Scuticobuccokinetal	Ma <i>et al.</i> , 2003b
<i>Cyclidium</i>	PM + Sc + M1 + M2–3 (partial)	M2–3 (partial) + Sc	1	Scuticobuccokinetal	Grolière, 1980
<i>Conhnilembus</i>	PM + Sc	M1 + M2 + M3	1	Scuticobuccokinetal	Didier and Detcheva, 1974

* The oral primordia of scuticociliates are derived either from the paroral membrane and a separate set of kinetosomes located posterior or solely from the paroral membrane.

PM – paroral membrane; Sc – scutica; M1–3 – membranelles 1–3.

Improved diagnosis

Size *in vivo* 70–120 × 45–70 µm, slender oval in outline; buccal field occupying 80% of body length; one contractile vacuole located slightly dorsally near posterior end; about 15 prolonged caudal cilia; one to three preoral kineties and 28 or 29 (usually 28) somatic kineties; length of membranelle 1, which comprises two longitudinal rows of basal bodies, about 20% that of the anterior part of membranelle 2 (M2a); anterior and posterior regions of M2a distinctly double-rowed but single-rowed in mid-portion; posterior end of M2a hooked-shaped; posterior part of membranelle 2 (M2b) V-shaped, distinctly separated from M2a; membranelle 3 three-rowed; length of paroral membrane about 75% of body length; one macronucleus; marine habitat.

Description of the Hong Kong population

Body shape and size relatively constant, *in vivo* 80–100 × 50–60 µm, slender oval in outline, widest at mid-body (Figs 3A, 4A). Ventral side almost flat, dorsal side convex (Figs 3C, 4D). Buccal field deep, about 80% of body length with conspicuous, sail-like undulating membrane (Fig. 4E). Pellicle rigid and slightly notched with extrusomes about 3 µm long, closely arranged beneath (Figs 3E, 4I). Cytoplasm colourless to slightly grayish, packed with many greasily shining globules

of varying size, food vacuoles which are usually large and filled with bacteria, and irregularly-shaped crystals about 6 × 3 µm (Figs 3A, 4B). One spherical macronucleus located in anterior 1/3 of cell, usually with many globular nucleoli. Single contractile vacuole about 10 µm in diameter, located slightly dorsally near posterior end of cell (Fig. 4A). Somatic cilia about 8 µm long (Fig. 4I); 15 prolonged caudal cilia on average, each about 30 µm in length (Fig. 4C).

Swims moderately fast while rotating about main body axis, sometimes drifting or lying motionless on debris for short periods (Fig. 3D).

Twenty eight to 29 somatic kineties, composed of paired basal bodies in anterior two-thirds of body and monokinetids in posterior third, extending almost entire length of the cell, terminating anteriorly at small glabrous apical plate (Fig. 3G, H). One to two preoral kineties to left of buccal field (Fig. 3B).

Oral apparatus typical for genus: M1 with one short and two longer rows of basal bodies; M2a mostly two-rowed but single rowed in mid-region, posterior end hooked-shaped; M2b V-shaped, distinctly separated from M2a; M3 three-rowed (Fig. 3B). Paroral membrane about 80% of cell length. Silverline system with a nearly-hexagonal honeycomb pattern (Fig. 3F).

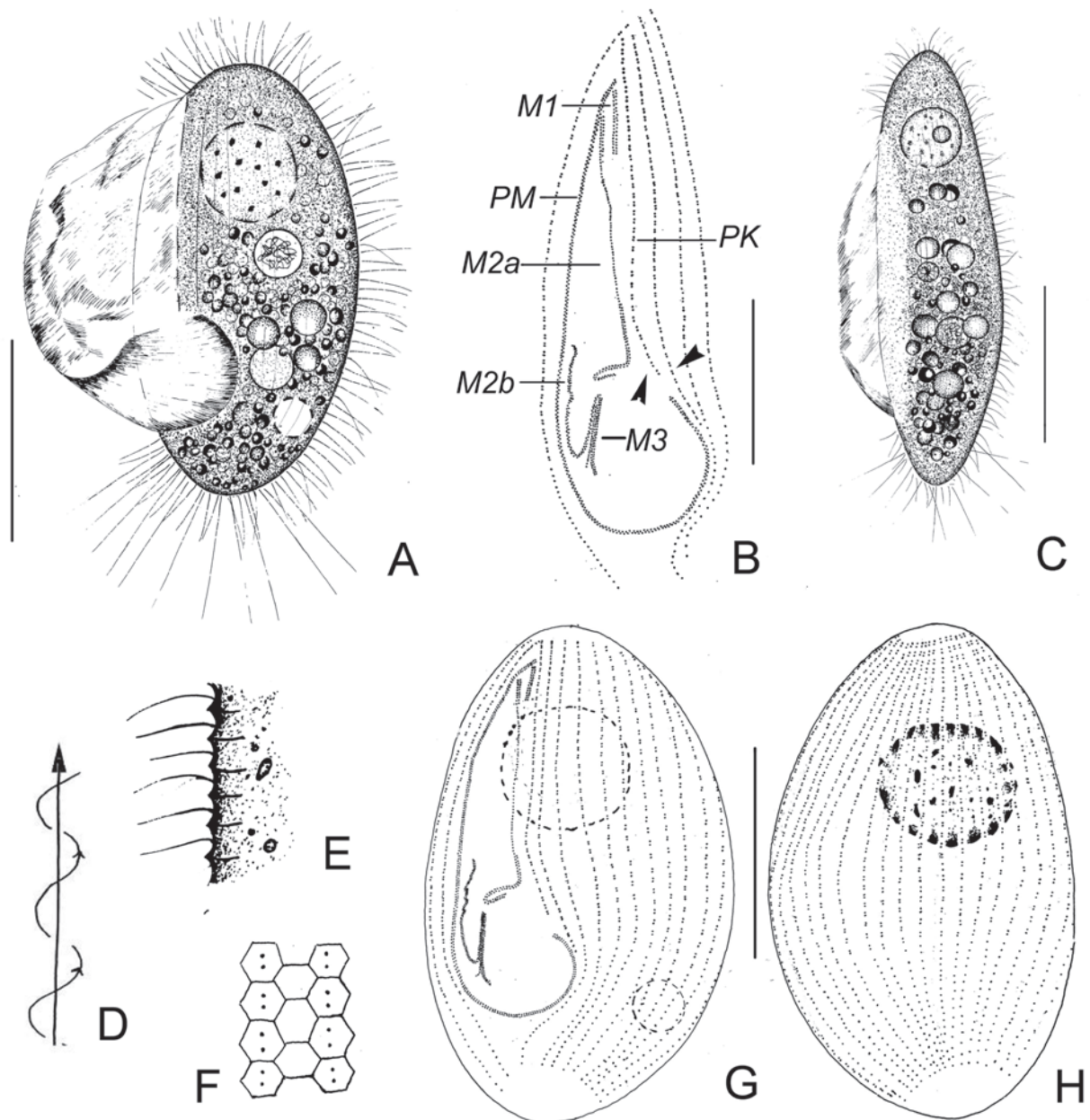


Fig. 3. *Pleuronema puytoraci* in vivo (A, C–E), after protargol (B, G, H) and silver nitrate impregnation (F). **A** – ventral view of a typical individual; **B** – oral apparatus, arrowheads mark the two preoral kineties; **C** – view from right side; **D** – swimming trace; **E** – detailed view of cortex to demonstrate the arrangement of extrusomes; **F** – part of the silverline system; **G**, **H** – ventral and dorsal views of the same specimen, showing the general infraciliature and nuclear apparatus. M1–3 – membranelles 1–3, M2a – the anterior part of membranelle 2, M2b – the posterior part of membranelle 2, PK – preoral kinety, PM – paroral membrane. Scale bars: A, C, G, H = 40 µm, B = 20 µm.

Comparison and remarks

Pleuronema comprises tens of nominal species, at least 20 of which have been studied using silver staining techniques (Dragesco 1968; Grolière and Detcheva 1974; Small and Lynn 1985; Dragesco and Dragesco-

Kernéis 1986; Agatha *et al.* 1993; Fernandez-Leborans and Novillo 1994; Song 2000; Wang *et al.* 2008a, b, 2009). *Pleuronema puytoraci* was originally reported by Grolière and Detcheva (1974) although they only documented the infraciliature, not the morphology

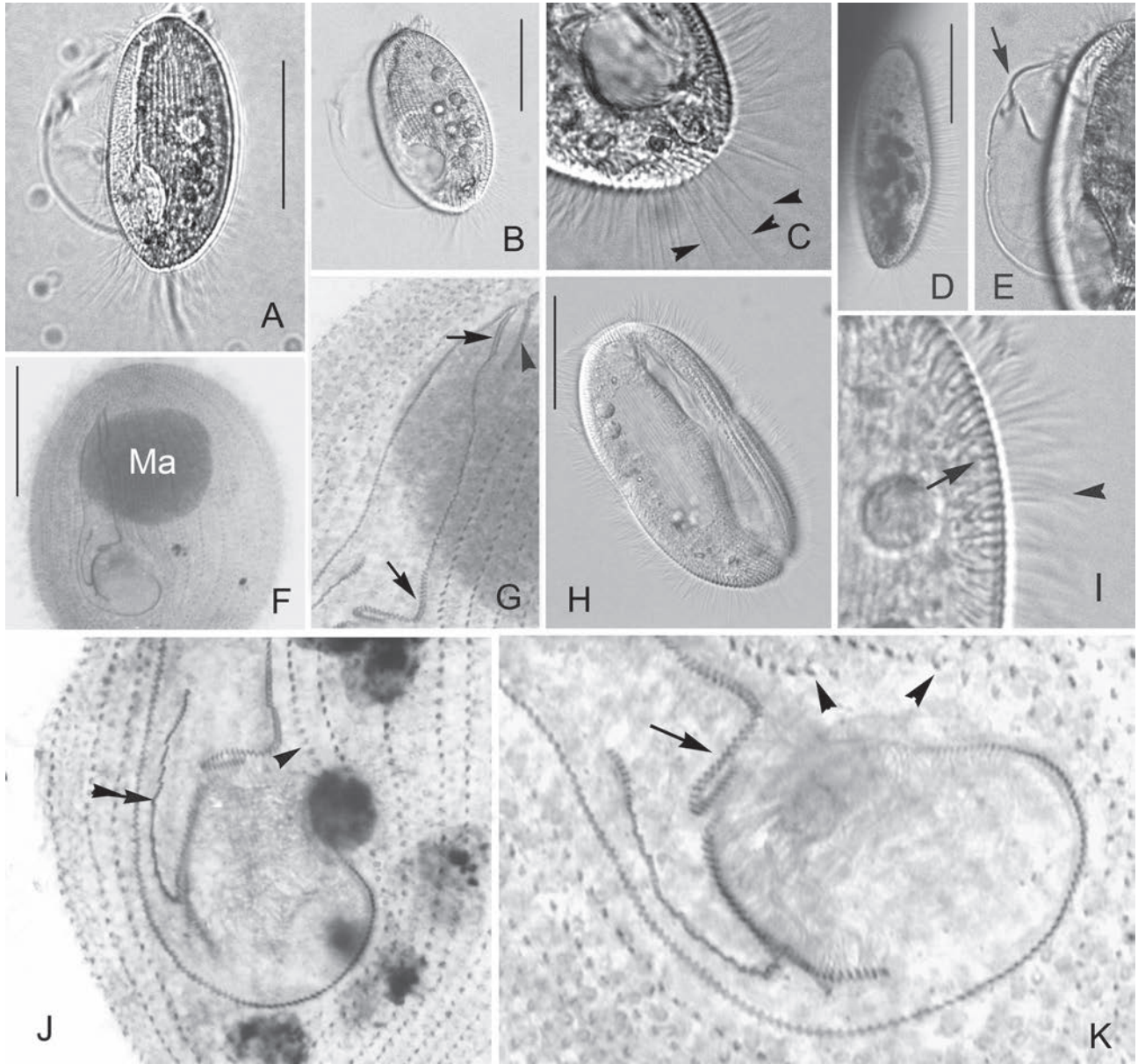


Fig. 4. Photomicrographs of *Pleuronema puytoraci* *in vivo* (A–E, H, I), after protargol impregnation (F, G, J, K). **A** – ventral view of a typical individual; **B** – ventral view of another individual with different shape; **C** – ventral view, arrowheads point to the prolonged caudal cilia; **D** – lateral view; **E** – ventral view, arrow marks the paroral membrane; **F** – ventral view, to show macronucleus; **G** – anterior part of oral apparatus, arrowhead points to membranelle 1, arrows refer to the dikinetids section of the anterior part of membranelle 2; **H** – individual in morphogenesis; **I** – ventral view, to show the extrusomes (arrow) and cilia (arrowhead); **J, K** – detailed view of the oral apparatus, arrow marks the hook-like structure, arrowheads show the preoral kineties; double-arrowhead shows the posterior part of membranelle 2. Ma – macronucleus. Scale bars: A, B, D, F, H = 50 μ m.

in vivo. The infraciliature of the Hong Kong population closely resembles that described by Grolière and Detcheva (1974) except for a minor difference in the number of preoral kineties (1–2 vs. 3).

Acknowledgements. This work was supported by the Natural Science of Foundation of China (project No. 31172041), the Fundamental Research Funds for the Central Universities to C. Shao, a joint grant from the Center of Biodiversity Research, King Saud University, Saudi Arabia. Many thanks to Prof. Weibo Song, who kindly read the draft and gave some helpful suggestions.

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Received on 8th June, 2011; revised on 30th September, 2011; accepted on 4th October, 2011