



New contributions to the marine hypotrichous ciliate, *Pseudokeronopsis qingdaoensis* Hu & Song, 2000 (Protozoa: Ciliophora: Stichotrichida)

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Abstract: A reinvestigation on the morphology and classification of *Pseudokeronopsis qingdaoensis* Hu & Song, 2000, a large and unique marine ciliate collected from the coastal water near Qingdao, China, was performed using living observation and silver impregnation methods. Based on previous and the current studies, a redescription and an updated diagnosis are supplied: marine *Pseudokeronopsis*; 150-300 x 40-70 µm *in vivo*; body colourless, flexible, and contractile. Bicrona comprising about 15 pairs of frontal cirri; 6-13 buccal and 2 (rarely 4) frontoterminal cirri; transverse row with 25-45 cirri extending to anterior 2/5 of cell; midventral complex consisting of two conspicuously separated rows with c. 40 pairs of cirri; distal end of adoral zone curved posteriorly to about cytostome level; constantly 3 dorsal kineties. Two kinds of cortical granules: one tiny and colourless; another one large and about 2 µm across, brownish to brown-reddish, blood-cell-shaped, distributed sparsely. Contractile vacuole positioned in anterior 1/3 of body. More than 100 macronuclear segments.

Résumé : Redescription du cilié marin *Pseudokeronopsis qingdaoensis* Hu & Song, 2000 (Protozoa: Ciliophora: Stichotrichida). Les observations faites sur le vivant et l'imprégnation argentique permettent une redescription et une nouvelle diagnose de *Pseudokeronopsis qingdaoensis* Hu & Song, 2000: *Pseudokeronopsis* marin, 150-300 x 40-70 µm *in vivo*, corps incolore, souple et contractile. Péristome assez important bordé à droite par une "bicrona" de 15 paires de cirres frontaux ; 6-13 cirres buccaux et 2 (rarement 4) cirres frontotermiaux. Infraciliature somatique: 25-45 cirres transversaux; deux rangées de cirres ventraux disposés par paires et en zig-zag comptant environ 40 éléments. 3 rangées de cils dorsaux. Deux types de granules ectoplasmiques: le premier incolore et minuscule, l'autre en petit nombre, rougeâtre à brunâtre, semblable à des globules sanguins, d'un diamètre d'environ 2 µm. Vacuole contractile à droite du cytostome; plus de 100 macronuclei.

Keywords: Ciliophora, Hypotrich, Redescription, *Pseudokeronopsis qingdaoensis*

Introduction

The hypotrichous genus *Pseudokeronopsis* is recognized by the ciliature of *Holosticha*-pattern but having the frontal

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cirri which form the so-called "bicrona", i.e. comprises two curved and parallel rows of frontal cirri continuous posteriorly with the developed midventral complex (= midventral rows in some previous reports; Borror & Wicklow, 1983; Wirnsberger, 1987; Berger 2003, 2004). Till now, almost all congeners of this genus were isolated from marine habitats and many of them exhibit beautiful colour deriving from the pigments beneath the pellicle (Morgan,

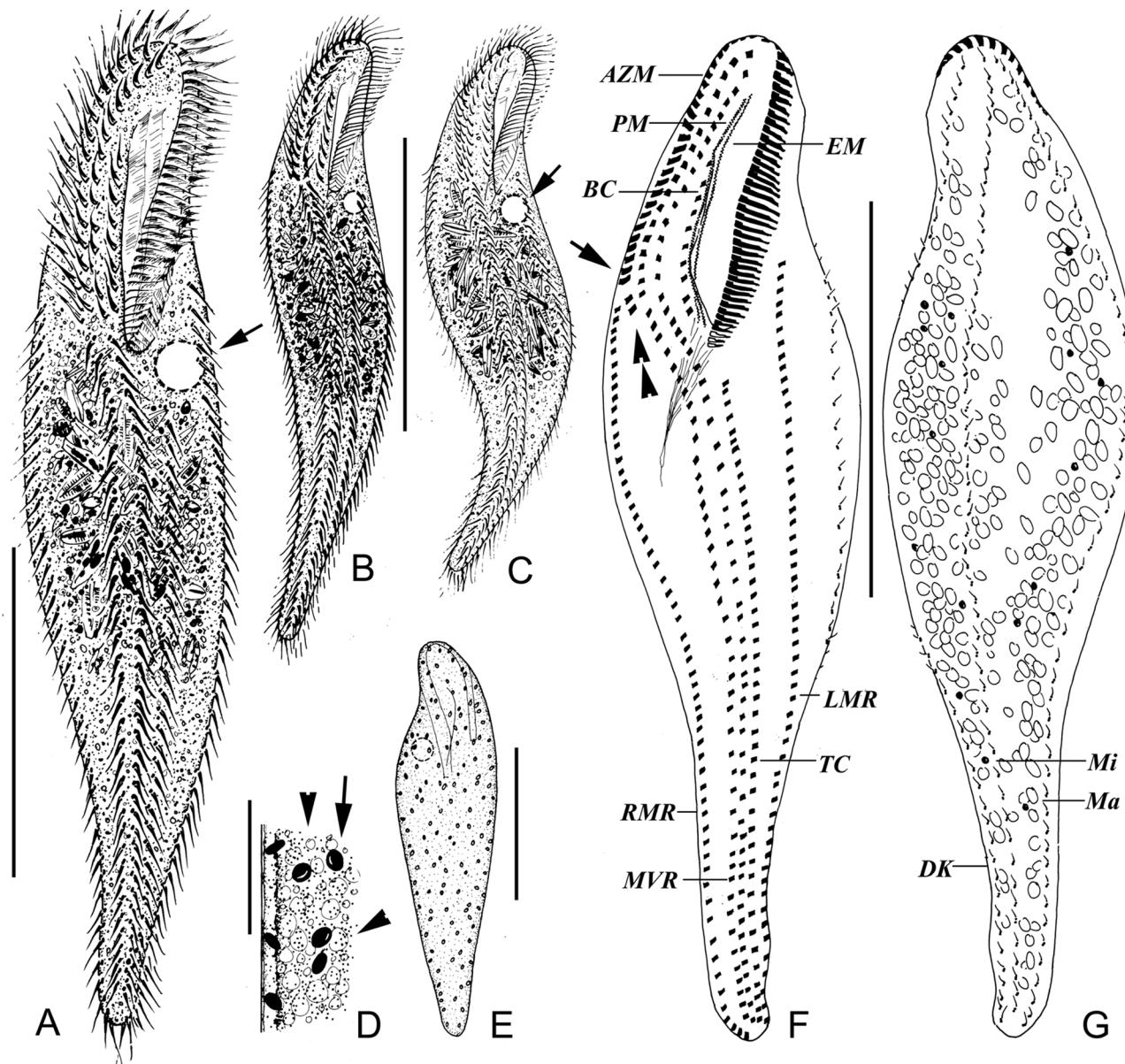


Figure 1. *Pseudokeronopsis qingdaoensis* from life (A-E) and after protargol impregnation (F, G). **A.** Ventral view of a typical individual; arrow marks the contractile vacuole. **B-C.** A slender and a slightly tortured specimen, to show the narrowed posterior portion, arrow in C indicates the contractile vacuole. **D.** Details of cortex, “blood-cell-shaped” pigments (arrow) and other tiny granules (or pigments, arrowheads). **E.** Dorsal view, distribution of the “blood-cell-shaped” pigments. **F.** Ventral view of infraciliature, arrow marks the distal end of the adoral zone of membranelles, double-arrowheads refer the frontoterminal cirri; note the par- and endoral membrane parallel and about equal in length. **G.** Dorsal view of the same specimen as F, macronucleus-nodules and the dorsal kineties. AZM: adoral zone of membranelles; BC: buccal cirrus; DK: dorsal kineties; EM: endoral membrane; LMR: left marginal row; Ma: macronuclei; Mi: micronuclei; MVR: midventral complex; PM: paroral membrane; RMR: right marginal row; TC: transverse cirri. Scale bars: 100 µm (A-C, E-G), 10 µm (D).

Figure 1. *Pseudokeronopsis qingdaoensis* (A-E) aspect général sur le vivant et (F, G) après imprégnation par le protargol. **A.** Face ventrale. **B-C.** Un individu svelte et légèrement tors pour mettre en évidence antérieur la partie rétrécie. La flèche (A, C) indique la vacuole contractile. **D.** Détail du cortex, pigments en forme de globules sanguins (flèche) et autres petits granules. **E.** Face dorsale, distribution des globules dans la cellule. **F.** Infraciliature ventrale, la flèche marque la fin de la zone des membranelles, la flèche double indique les cirres frontoterminal ; notez la longueur semblable et le parallélisme des membranes endorale (EM) et parorale (PM). **G.** Infraciliature dorsale et appareil nucléaire. AZM, zone de membranelles ; BC, cirres buccaux ; DK, cinéties dorsales ; EM, cinétique endorale ; LMR, cirres marginaux gauches ; Ma, macronoyaux ; Mi, micronoyaux ; MVR, cirres médicoventraux ; PM, cinétique parorale ; RMR, cirres marginaux droits ; TC, cirres transversaux. Echelle : 100 µm (Figs. A-C, E-G), 10 µm (Fig. D).

1926; Kahl, 1932; Rühmekorf, 1935; Borror, 1963; Agamaliev, 1972; Foissner 1984; Wirnsberger et al., 1987; Al-Rasheid, 1996; Song et al., 2002; Hu et al., 2003).

Pseudokeronopsis qingdaoensis is a unique form in this genus considering its infraciliature, and was originally found by Hu and Song in 1996 and described in a Chinese journal (Hu & Song, 2000), in which, however, some substantial features were failed to be observed or described. In summer of 2000, a new population was collected from the same area as for the holotype. Subsequent observations and morphological investigations have been carried out, which demonstrate some unreported features, e.g. the presence and position of the contractile vacuole, the second type of the cortical granules, variation of body shapes. Hence an updated redescription is supplied.

Table 1. *Pseudokeronopsis qingdaoensis* Morphometrical data of the holotype population (upper line, from Hu & Song, 2000) and the present population (lower line, in bold italics). Data based on protargol-impregnated specimens, in µm. Min, minimum; Max, maximum; Mean, arithmetic mean; SD, standard deviation; SE, standard error of mean; CV, coefficient of variation in %; n, number of measured cells.

Tableau 1. *Pseudokeronopsis qingdaoensis* Données morphométriques de la population holotype (ligne supérieure, d'après Hu & Song, 2000) et de la population de la présente étude (ligne inférieure, en italiques gras). Données sur des individus imprégnés de protargol, en µm. Min, minimum ; Max, maximum ; Mean, moyenne arithmétique ; SD, écart-type ; SE, erreur standard ; CV, coefficient de variation en % ; n, nombre de cellules mesurées.

Character	Min	Max	Mean	SD	SE	CV	n
Length of body	150	260	194.5	29.1	6.1	15.0	23
	158	196	178.9	11.5	3.1	6.4	14
Width of body	55	100	76.8	10.6	2.2	13.9	23
	68	98	78.5	8.0	2.1	10.1	14
Length of adoral zone of membranelles	63	83	75.6	6.4	1.3	8.5	23
	62	79	69.5	5.1	1.4	7.3	14
Number of membranelles	50	65	55.6	4.1	1.1	7.4	14
	46	60	52.5	4.5	1.4	8.5	10
Number of frontal cirri in bicorona*	21	35	26.6	3.75	0.86	14.1	19
	27	32	-	-	-	-	4
Number of buccal cirri	6	10	9.3	1.2	0.3	12.8	16
	8	13	9.4	1.9	0.7	20.2	7
Number of frontoterminal cirri	2	2	2	0	0	0	19
	2	4	2.3	0.8	0.3	33.1	7
Number of transverse cirri	27	45	34.3	5.1	1.2	14.9	19
	25	36	30.4	3.5	1.1	22.4	10
Number of left cirri in midventral complex	33	53	40.6	5.2	1.2	12.8	19
	41	59	-	-	-	-	5
Number of right cirri in midventral complex	33	56	40.8	6.0	1.4	14.8	19
	44	63	-	-	-	-	5
Number of cirri in left marginal row	38	70	53.2	8.5	1.9	15.9	19
	42	61	50.6	5.5	1.5	10.1	14
Number of cirri in right marginal row	43	74	49.3	12.7	2.9	25.7	19
	43	62	52.5	5.5	1.5	10.5	14
Number of dorsal kineties	3	3	3	0	0	0	16
	3	3	3	0	0	0	11

* Bicorona: anterior-most frontal cirri, which are positioned in two widely spaced rows, see also the text.

Materials and methods

The present population of *Pseudokeronopsis qingdaoensis* was collected in September 2000 from the littoral water near Qingdao, North China, which was used for mollusc-farming. The water salinity was ca 33, water temperature was about 28 °C.

Cells isolated were cultured in the laboratory with rice grains as food source for bacteria. Observations on live morphology were undertaken using both bright field and the Nomarski differential interference contrast microscopy. Protargol staining (Wilbert, 1975) was performed for revealing the infraciliature and nuclear apparatus.

Counts and measurements were made at a magnification of 1250x. Drawings were made with the help of a camera lucida. Terminology is mainly according to Berger (2004).

The voucher slides of protargol impregnated specimens

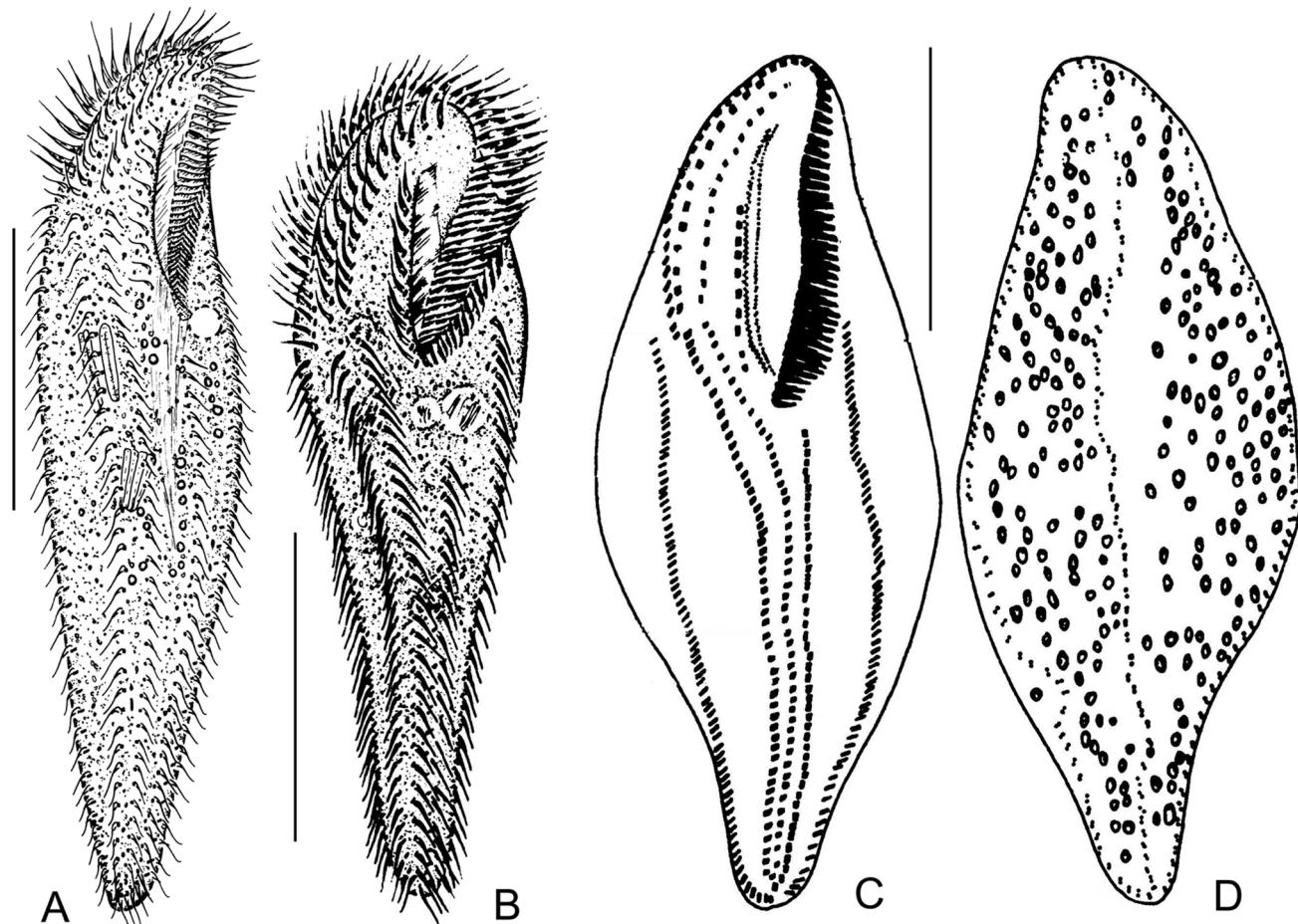
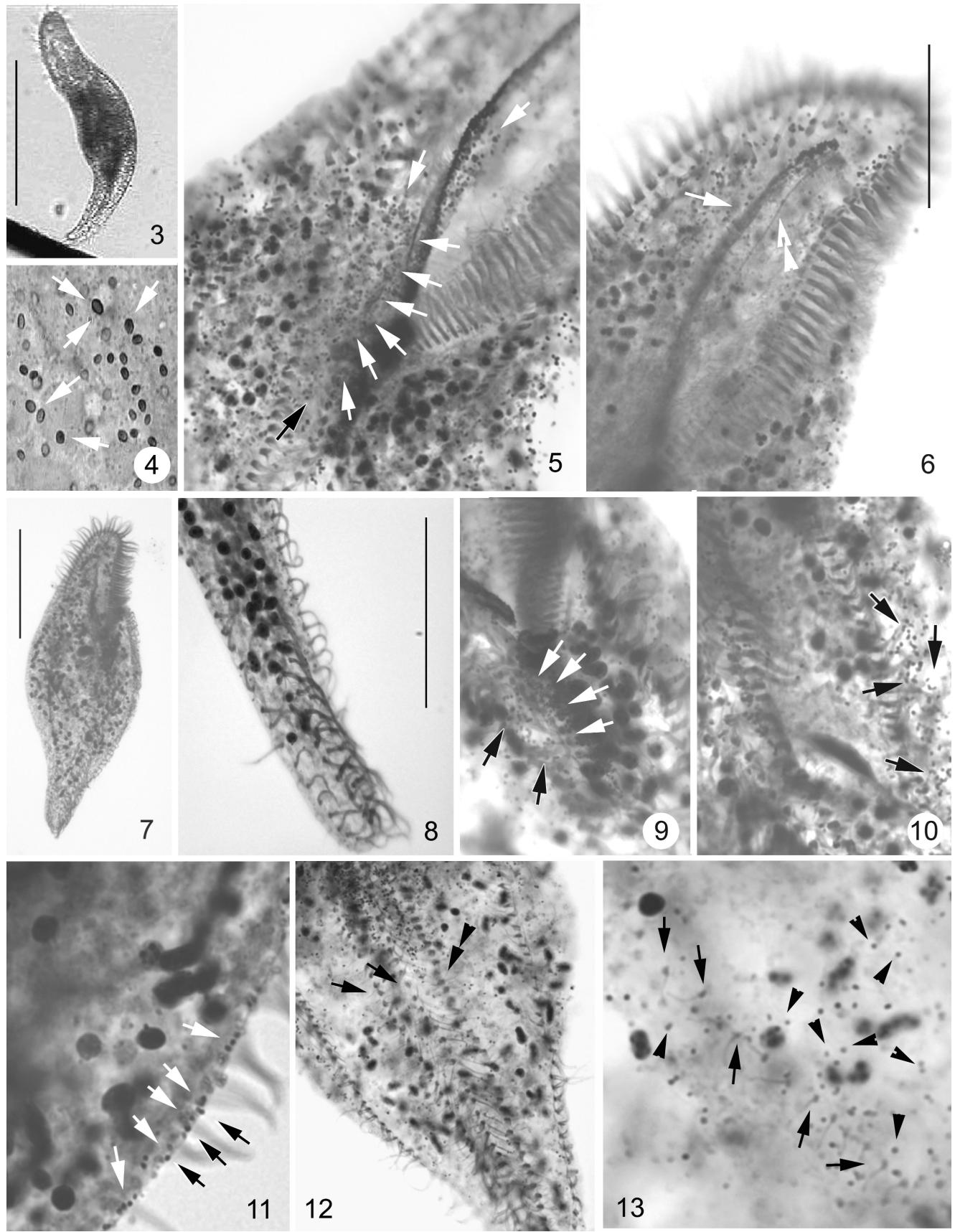


Figure 2. *Pseudokeronopsis qingdaoensis*. Populations reported previously, from life (A, B) and after impregnation (C, D). A. Slender form with both narrowed anterior and posterior cell ends (from Hu et al. 2003). B. Organism with broad anterior portion as depicted in original description (from Hu & Song, 2000). C-D. Ventral and dorsal view of the same specimen as described originally, infraciliature and nuclear apparatus (from Hu & Song 2000). Scale bars: 100 μm (A-B), 60 μm (C-D).

Fig. 2. *Pseudokeronopsis qingdaoensis*. A. Aspect général sur le vivant, morphotypes d'une souche décrite par Hu et al. 2003 et (B, C, D) de Hu & Song, 2000. B. Organisme à la partie antérieure large comme dans la description originale (d'après Hu & Song, 2000). C. Infraciliature ventrale. D. Infraciliature dorsale et appareil nucléaire. Echelle: 100 μm (Figs. A, B), 60 μm (Figs. C, D).

Figures 3-13. *Pseudokeronopsis qingdaoensis*. Photographs from life (3, 4) and after protargol impregnation (5-13). 3. Typical specimen *in vivo*, note the narrowed posterior part of the cell. 4. Dorsal view, “blood-cell-shaped” (arrows) and tiny, pigment-like cortical granules. 5. Buccal portion of ventral side, arrows mark the tiny pigment-like granules near the cytostome area. 6. Anterior portion, paroral (arrow) and endoral membrane (double-arrowheads). Note that many pigment-like granules are densely arranged along the paroral membrane. 7. Ventral view, general view of a contractive specimen after fixation. 8. Ventral view of the posterior body portion. 9-10. Ventral view of the central portion, arrows indicate the area where the tiny pigments (or granules) are closely packed. 11. Marginal area, arrows mark the tiny pigments (or granules). 12. Ventral view, to show the separated midventral cirri (arrows) and the transverse cirri (double-arrowheads). 13. Dorsal view, to show the dorsal cilia in kineties (arrows) and the pigments (or granules, arrowheads). Scale bars: 200 μm (Fig. 3), 20 μm (Fig. 6), 80 μm (Fig. 7), 40 μm (Fig. 8).

Figures 3-13. *Pseudokeronopsis qingdaoensi* (3, 4) morphologie générale *in vivo* et après fixation et (5-13) imprégnation par le protargol. 3. Individu typique, notez la région postérieure rétrécie. 4. Vue dorsale, granules des deux types (ceux en forme de globules sanguins sont marqués d'une flèche). 5. Vue ventrale de la partie buccale, les flèches marquent les petits granules. 6. Partie antérieure, membrane parorale (flèche) et endorale (flèche double), une bande de petits granules borde la membrane parorale. 7. Vue ventrale, aspect général d'un exemplaire contracté après fixation. 8. Vue ventrale, infraciliature postérieure. 9-10. Région ventrale. 11. Région latérale, les flèches marquent la position des petits granules. 12. Détail de l'infraciliature ventrale postérieure, cirres médiovenraux (flèches), cirres transversaux (flèche double). 13. Détail de l'infraciliature dorsale, cinétie dorsale (flèches), granules (pointes). Echelle: 200 μm (Fig. 3), 20 μm (Fig. 6), 80 μm (Fig. 7), 40 μm (Fig. 8).



are deposited in the Laboratory of Protozoology, OUC, China.

Results

Based on the new population and the previous descriptions, a revised diagnosis for *Pseudokeronopsis qingdaoensis* is suggested.

New diagnosis

Marine *Pseudokeronopsis*; 150-300 x 40-70 μm *in vivo*; body colourless, flexible, and contractile. Bicorona comprising about 15 pairs of frontal cirri; 6-13 buccal and 2-4 frontoterminal cirri; transverse row with 25-45 cirri extending to anterior 2/5 of cell; midventral complex consisting of two conspicuously separated rows with c. 40 pairs of cirri; distal end of adoral zone curved posteriorly to about cytostome level; constantly 3 dorsal kineties. Two kinds of cortical granules: one tiny and colorless; another one large and about 2 μm across, brownish to brown-reddish, blood-cell-shaped, distributed sparsely. Contractile vacuole positioned in anterior third of body. More than 100 macronuclear segments.

Morphological description of the new population (Table 1)

Body shape elongated, and the cell rather flexible and highly contractive. Specimens in newly-collected samples mostly about 250 μm long *in vivo* with ratio of length to width about 4-5:1 (Fig. 1A), whereas after days of culture, both size and shape would be variable: bigger cells (*ca* 300 μm) with long, tail-like caudal portion (Fig. 1B, C) could be about twice as long as smaller ones (*ca* 150 μm), in which the latter exhibit often short and narrowed posterior end (Fig. 1E). Different from the holotype specimens (Fig. 2B), widest mostly at about mid-body with anterior portion considerably narrowed. Cells dorsoventrally flattened about 1:2. Buccal field moderately narrow, about 1/3 of body length. Two types of cortical granules: type I pigment-like and tiny, about 0.2 μm across *in vivo* (Figs. 1D, arrows; 4, 10, 13), slightly ellipsoid after fixation (Fig. 11, arrows), colourless to greyish, which are sparsely and evenly arranged all over the dorsal side (Fig. 1D) but often densely and irregularly distributed on ventral side forming pattern of dark patches near buccal area or along cirral rows (Figs. 5, 10, arrows). Granules of type II “blood-cell-shaped” (like the erythrocyte of mammals), about 1:3 flattened and c. 2 μm across, reddish-brown to dark brown when observed under high magnifications, which are sparsely distributed and lower in number, non-grouped, hence never render cell any colour (Figs. 1D, 4, arrows).

Cytoplasm opaque and colourless, often dark grey or even black in central part of body due to the food vacuoles

and other granules (Fig. 3), often containing numerous light-reflecting globules (2-5 μm across). Contractile vacuole pulsating infrequently (more than 5 min. as observed in our population), positioned near left margin at about anterior 1/3 to 1/4 of cell length (Fig. 1A-C). Food vacuoles often full of diatoms (Fig. 1A). Over 100 macronuclear nodules (till more than 200 segments), oval to elongate in shape, scattered within cytoplasm and difficult to observe *in vivo* (Fig. 1G). Micronuclei (Mi) ovoid and large (about 3 μm long), several in number (Fig. 1G).

Locomotion slow, no particularities, that is, crawling without pause on debris or on bottom of Petri dish with conspicuous flexibility.

Infraciliature similar to that of holotype population (Hu & Song 2000). Distal end of adoral zone of membranelles (AZM) curving strongly posteriad along right margin and extending to about cytostome level (arrow in Fig. 1F). Bases of membranelles about 6-10 μm long. Paroral and endoral membranes (PM, EM) about equally long, lying parallel, of which the paroral is conspicuously thicker than the endoral (Figs. 1F, 6).

Most somatic cirri relatively fine, 10-15 μm long. Bicorona consisting of about 30 slightly enlarged frontal cirri, which are sometimes separated from the midventral complex with an inconspicuous gap. Frontoterminal cirri mostly two, near distal end of adoral zone and hence often difficult to recognize (Fig. 1F, double-arrowheads). One long row of buccal cirri (BC) close to paroral membrane (Fig. 1F). Midventral complex (MVR) terminating at posterior end of cell, cirri of each pair conspicuously separated from each other in most part (Figs. 1F; 12, arrows). Transverse cirri (TC) forming as an uncommonly long row, which is parallel to the midventral rows and extends anteriorly to about cytostome level (Figs. 1F; 12, double-arrowheads). Cirri in both marginal rows narrowly spaced; right marginal row (RMR) commences near distal end of adoral zone. Marginal rows clearly separated posteriorly (Fig. 1F).

Invariable 3 complete dorsal kineties, each comprising about 50 pairs of basal bodies; cilia about 2-3 μm long (Figs. 1G; 13, arrows).

Discussion

As known by now, many well-studied congeners in *Pseudokeronopsis* possess two types of cortical granules/pigments: one is large and highly specialized, i.e. “blood-cell-shaped”, which is invariably colourless and densely arranged throughout beneath both ventral and dorsal surface, while another is small (usually) and pigment-like, often with bright colour and grouped in rosette-pattern around ciliary structure (Hu & Song, 2000, 2001; Song et al., 2002, 2004; Hu et al., 2003). Contradicting these findings, *Pseudokeronopsis qingdaoensis* exhibits a unique

Table 2. *Pseudokeronopsis qingdaoensis* Morphological comparison with other well-described congeners.
Tableau 2. *Pseudokeronopsis qingdaoensis* Comparaison morphologique avec d'autres espèces du même genre.

Characters	<i>P. qingdaoensis</i>	Other <i>Pseudokeronopsis</i> species
Cortical granule type I (= pigments)	Colourless, extremely tiny (c. 0.2 µm)	Conspicuously larger (c. 0.5-1 µm), often coloured
Distribution of cortical granule type I	Sparsely distributed, never grouped	Grouped around cirri and dorsal cilia
Cortical granule type II (blood-cell type)	Brown-reddish, low in number	Always colorless, densely arranged
Appearance of the midventral complex	Two rows clearly separated (cirri not in zig-zag pattern)	Two rows parallel and closely arranged (cirri in zig-zag pattern)
Buccal cirrus	Long row with several cirri	Single one
Transverse cirrus row	Extremely long, extending	Short, subcaudally positioned to cytostome level
Anterior end of the adoral zone of membranelles (AZM)	Curved posteriorly to about 90% of AZM length	Slightly curved posteriad, about 20% of AZM length

and entirely different pattern, namely, the type II, the “blood-cell-shaped” one, is conspicuously low in number (hence only sparsely distributed) and has beautiful colour, whereas the type I is extremely tiny and colourless (Table 2).

Notably, the overall organization of the ciliature in *P. qingdaoensis* is mighty different from all other congeners (Table 2): 1) a higher number of buccal cirri (vs. one in congeners); 2) strongly bent distal end of adoral zone of membranelles, which extends posteriorly to about cytostome level; 3) cirri of midventral pairs considerably separated (vs. cirri arranged in conspicuous zig-zag pattern in other species); 4) an extremely long row of transverse cirri terminating anteriorly to about the level of cytostome (vs. short with less than 10 cirri) and 5) the brown-reddish “blood-cell-shaped” cortical granules (vs. colourless in other known forms of this genus) (Borror, 1972; Foissner, 1984; Wirnsberger et al., 1987; Al-Rasheid, 1996; Hu & Song, 2001; Song et al., 2002; Hu et al., 2003; Berger, 2004). However, the monophyly of these organisms (rather than being a convergent assemblage) could be assumed albeit there are so many morphological differences mentioned above and the developmental data in *P. qingdaoensis* remain unavailable. One reason is that most other well-known forms are likely sibling-species and hence exhibit great similarities among them (Table 2). The second reason for this conclusion is that it is reasonable to speculate that the pattern of the morphogenesis in this species should be the same as that known in other related urostylids, namely, the midventral complex originates from multiple cirral layout though the cirri might be not so typically arranged (Song et al., 1997).

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