

## Morphological and molecular information of a new species of *Geleia* (Ciliophora, Karyorelictea), with redescription of two *Kentrophoros* species from China

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### Abstract

The morphology and infraciliature of three karyorelictean ciliates, *Geleia sinica* spec. nov. and two poorly known *Kentrophoros* species, *K. flavus* and *K. gracilis*, isolated from the intertidal zone of a beach at Qingdao, China, were investigated. *Geleia sinica* spec. nov. is distinguished from its congeners by the following combination of characters: body medium-sized and slender-cylindrical; with a conspicuous prebuccal fossa; 28–34 somatic kineties; about 40 short adoral polykineties; intrabuccal kinety composed of 25–34 dikinetids; paroral kineties composed of closely spaced dikinetids. The comparison with similar congeners clearly supports the validity of this new species based on morphological and small subunit (SSU) rRNA gene sequence data. In light of these new data the “well-known” morphotype, *Geleia simplex* (Fauré-Fremiet, 1951), is redefined. Two *Kentrophoros* species are redescribed and improved diagnoses are supplied. *Kentrophoros flavus* Raikov and Kovaleva, 1968 is mainly characterized by having about 33 macronuclei and 12 micronuclei forming a row that extends along the cell meridian, and 12–19 ciliary rows on the right side of the cell. *Kentrophoros gracilis* Raikov, 1963 is characterized by having about 14 macronuclei, 13 micronuclei and 10–13 kineties on the right side of the cell.

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**Keywords:** Karyorelictea; Marine ciliate; New species; SSU rRNA; Taxonomy

### Introduction

The class Karyorelictea Corliss, 1974 is widely believed to represent the nature of the ancestral ciliate lineage (Lynn 2008). Karyorelicteans are characterized by their elongated, vermiform, often flattened body and numerous

non-dividing macronuclei that arise from the division of a micronucleus and are often clustered around a micronucleus (Lynn 2008). Karyorelicteans are common in marine interstitial environments (Alekperov et al. 2007; Al-Rasheid 1996, 1997, 1998, 2001; Al-Rasheid and Foissner 1999; Dragesco 1960). Hitherto, 17 genera and about 130 morphospecies of karyorelicteans have been reported (Carey 1992; Foissner 1996, 1997a, 1997b; Foissner and Al-Rasheid 1999a, 1999b; Foissner and Dragesco 1996a, 1996b; Lynn 2008; Mazei et al. 2009). Molecular data for karyorelicteans,

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however, are limited and gene sequences are available for only 26 morphotypes (Andreoli et al. 2009; Gao et al. 2010).

In the present study, one new species of *Geleia* and two poorly known *Kentrophoros* species, isolated from the intertidal zone of a sandy beach at Qingdao, China, are described or redescribed based on their living morphology and infraciliature which, in each case, was revealed for the first time following silver impregnation. The small subunit (SSU) rRNA gene was also sequenced for the new species of *Geleia*. The implications of our findings for the definitions of the order Protoheterotrichida Nouzarède, 1977 and the family Geleidae Kahl, 1933 are briefly discussed.

## Material and Methods

Ciliates were isolated from the intertidal zone of the No. 1 Beach at Qingdao (36°06'N; 120°32'E), China. Sampling was mainly according to Fan et al. (2010). Briefly, a 15 cm-deep hole was dug in the sand into which seawater gradually seeped. The sample comprised a mixture of seawater and sand from the bottom of the hole.

*Geleia sinica* spec. nov. was collected on 29 April 2009, when the water temperature was 11 °C and salinity 32%. *Kentrophoros flavus* was collected on 23 November 2006, water temperature 15 °C, salinity 26%. Two populations of *K. gracilis* were collected, one on 26 November 2006 (pop I) the other on 18 September 2009 (pop II); the salinity was about 25% on both occasions, water temperature about 15 °C and 20 °C respectively. Cells were isolated using the method described by Fauré-Fremiet (1951), i.e. in order to stabilize the cells, a 12% (w/v) MgCl<sub>2</sub> solution was added to the sample to give a final concentration of 2.5% MgCl<sub>2</sub>. Cells were then picked up with a capillary pipette. Living cells were studied by bright field and differential interference microscopy (100× to 1000× magnifications). The infraciliature was revealed by the protargol impregnation method (Wilbert 1975) using the following fixative: 10 ml saturated, aqueous mercuric chloride and 3 ml Bouin's solution, mixed just before use. Counts and measurements of stained specimens were performed at a magnification of 1250×. Drawings were made with the help of a camera lucida. Terminology is mainly according to Dragesco (1999) and Foissner (1998).

Since some structures found in certain karyorelicteans are not commonly known, the following terms are briefly explained:

**Adoral polykineties (Ap).** An oral ciliary field located on the left side of the buccal field, consisting of numerous, densely arranged fragment-like rows.

**Fossa (=“dimple” after Dragesco 1999).** A cavity or depression located subapically on the ventral surface, anterior of the buccal field.

**Intrabuccal kinety (Ibk).** A single-rowed structure, located on the right side of the buccal field.

**Paroral kineties (Pk).** An oral ciliary field located on the right side of the buccal cavity consisting of numerous rows of di- or polykinetids.

**Preoral kinety (Prek).** A fragment-like, single-rowed ciliary structure consisting of dikinetids, located on the right side of the fossa and within the preoral suture.

DNA extraction and polymerase chain reaction (PCR) amplification were performed according to Shen et al. (2010). In brief, cells were isolated and repeatedly washed using sterilized seawater. DNA was extracted using an REExtract-N-Amp Tissue PCR Kit (Sigma, St. Louis, MO, USA) according to the manufacturer's protocol, with the slight modification that only 1/10 of the volume suggested for each reagent solution was used (Gong et al. 2009). DNA samples were stored at –20 °C. Amplification of the SSU rDNA using the universal eukaryotic primers EukA (5'-AACCTGGTTGATCCTGCCAGT-3') and EukB (5'-TGATCCTTCTGCAGGTTACCTAC-3') (Medlin et al. 1988) failed. However, the SSU-ITS2 region was successfully amplified using the primers EukA and Rev3 (5'-GCATAGTTCACCATCTTTTCG-3'). Direct sequencing of PCR products was performed on an ABI-PRISM 3730 Automated DNA Sequencer (Applied Biosystems Inc., Foster City, CA), using the original PCR primers and four additional primers (+B: 5'-GGTAAAAAGCTCGTAGT-3'; +C: 5'-GTATGGTCGCAAGDCTGAACTTA-3'; RevD: 5'-TCAGGCTCCYTCTCCGGAAY-3').

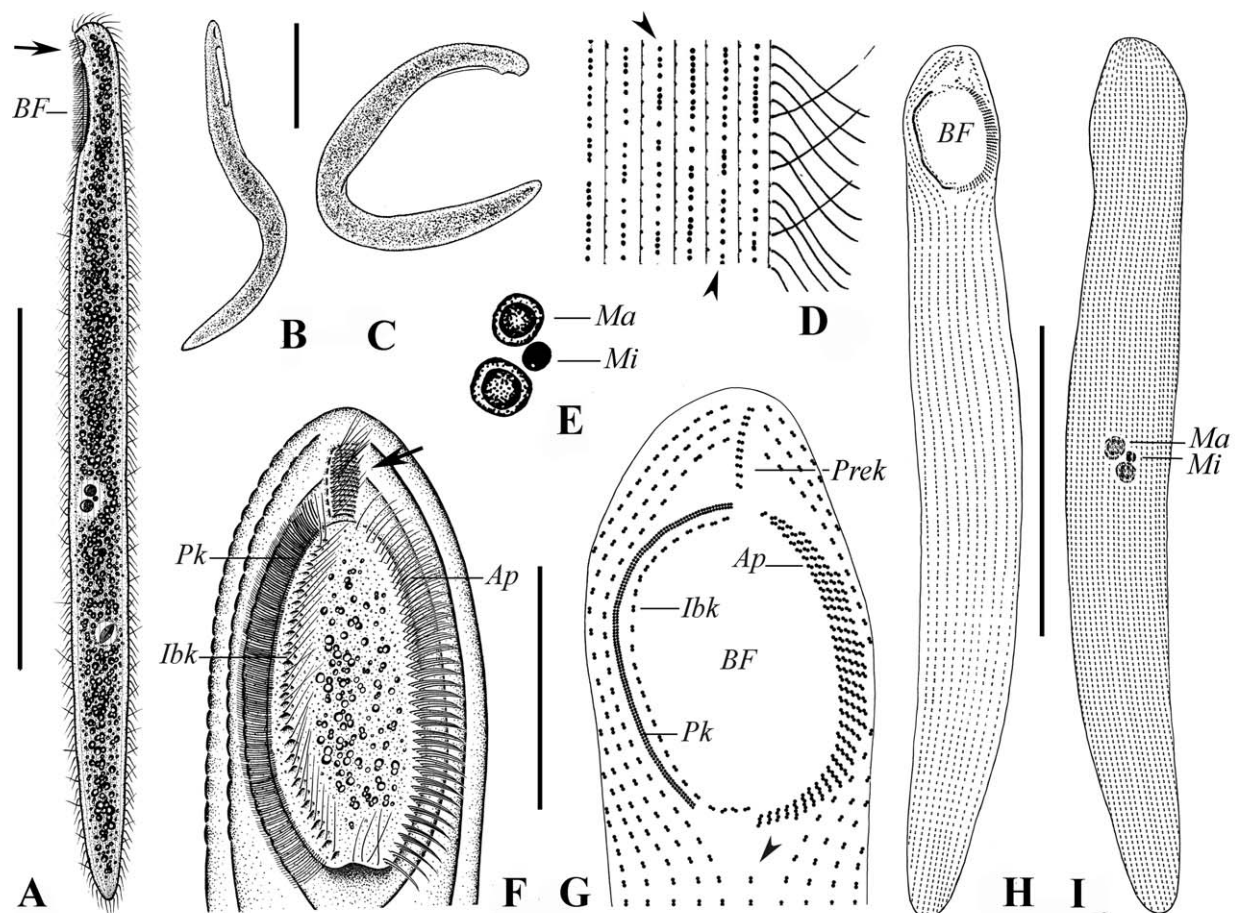
## Results and Discussion

### Genus *Geleia* Foissner, 1998

The genus *Geleia* was first established by Kahl (1933) who failed to designate a type species. Consequently Foissner (1998) declared *Geleia* a nomen nudum and re-established it as a new genus, designating *G. fossata* Kahl, 1933 as the type species. Based on the redescrptions by Dragesco (1999), Dragesco and Dragesco-Kernéis (1986), Nouzarède (1977) and the present work, an improved diagnosis is here supplied.

**Improved diagnosis of *Geleia*:** Geleidae with cylindrical body shape; cells completely ciliated with longitudinal rows consisting of dikinetids; buccal field located subapically; preoral kinety present; typical geleiid oral structure with dominant conspicuous adoral polykineties that comprise numerous long rows of kineties.

**Remarks:** Based on the findings of Nouzarède (1977) and Dragesco (1999), Foissner (1998) described geleiids as being “completely ciliated and with oral monokinetids forming a right and left oral ciliary field”. Furthermore he considered these ‘paracytostomal’ monokinetids to be the most important autapomorphy of the geleiids (Foissner 1998). Lynn (2008) likewise considered the monokinetid nature of the oral ciliature to be the defining character of the order Protoheterotrichida, which was established by Nouzarède (1977) for the family Geleidae. According to Dragesco



**Fig. 1.** A–I. *Geleia sinica* spec. nov. from life (A–D, F) and after protargol impregnation (E, G–I). A. Left lateral view of typical individual, noting buccal field. Arrow marks the fossa between apical beak and buccal field. B, C. Different body shapes. D. Detail of mid-region of cell to show the distribution of cortical granules (arrowheads) between ciliary rows. E. Macronuclei and micronucleus. F, G. Fine structure of anterior body end to show the buccal field and fossa (arrow in F). Note the preoral kinety, paroral kineties, intrabuccal kinety, adoral polykineties and postoral kinety (arrowhead in G). H, I. Ventral (H) and dorsal (I) view of the holotype specimen, showing infraciliature and nuclear apparatus. Ap, adoral polykineties; BF, buccal field; Ib, intrabuccal kinety; Ma, macronuclei; Mi, micronucleus; Pk, paroral kineties; Prek, preoral kinety. Scale bars = 150  $\mu$ m (A); 100  $\mu$ m (B, C, H, I); 25  $\mu$ m (F, G).

(1999), however, the infraciliature of the left and right oral fields is not composed exclusively of monokinetids in any of the four geleiid genera, namely *Avelia* Nouzarède, 1977, *Geleia* Foissner, 1998, *Gellertia* Dragesco, 1999 and *Parduczia* Dragesco, 1999. This observation is supported by the present work which reveals that, in *Geleia sinica*, the adoral polykineties (Ap), intrabuccal kinety (Ibk) and paroral kineties (Pk) are all composed of dikinetids (see below). These findings suggest that the validity both of the order Protoheterotrichida and the family Geleiididae need to be reinvestigated, ideally using a combination of morphological, morphogenetic and molecular data.

To date, 12 nominal species have been assigned to the genus *Geleia* (Dragesco 1999). Of these, only five have been investigated following silver impregnation (*G. decolor*, *G. fossata*, *G. major*, *G. simplex* and *G. swedmarki*) and can thus be confirmed unambiguously as valid members of the genus *Geleia* (Dragesco 1999). The generic assignment of

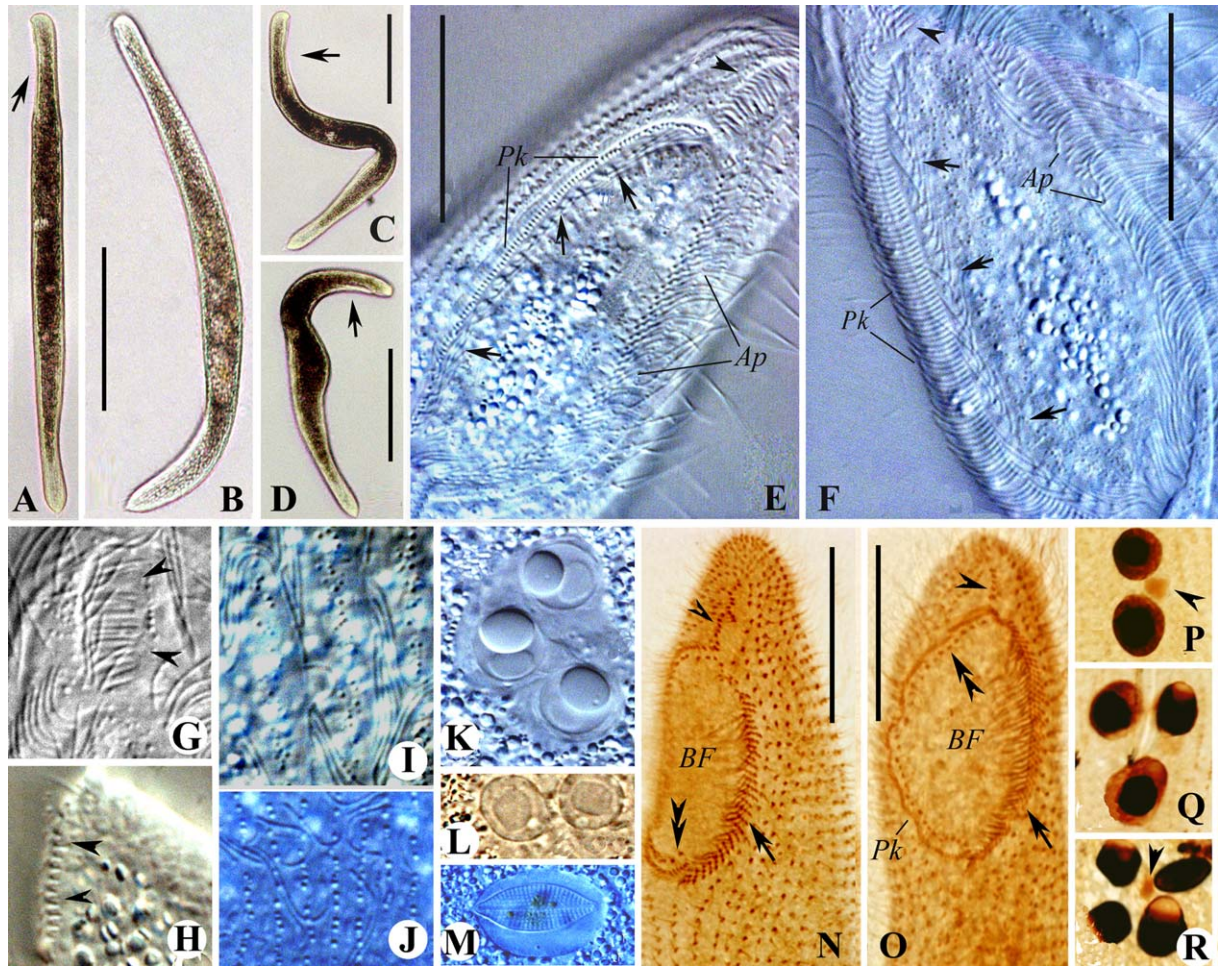
the other seven species remains uncertain pending further investigation. Gene sequence data for only four species are currently available, namely *Geleia* sp., *G. simplex*, *G. fossata*, and *G. swedmarki* (Andreoli et al. 2009; Gao et al. 2010).

### *Geleia sinica* spec. nov. (Figs 1A–I, 2A–R, Table 1)

Syn. *Geleia simplex* variété II (Roscoff) of Dragesco (1999) ? (= *Geleia swedmarki* sensu Dragesco 1963) (Table 3).

**Diagnosis:** Body about 250–500  $\mu$ m  $\times$  20–35  $\mu$ m in vivo, cylindrical in shape; fossa conspicuous; 2–4 macronuclei; cortical granules colorless; 28–34 somatic kineties; 30–50 short adoral polykineties; intrabuccal kinety comprising 25–34 dikinetids; preoral kinety with 7–16 dikinetids; paroral kinety with closely spaced dikinetids.





**Fig. 2.** A–R. Photomicrographs of *Geleia sinica* spec. nov. from life (A–M) and after protargol impregnation (N–R). A. Left lateral view of typical individual, arrow shows buccal field. B–D. Variation in body shape; arrows in C and D mark the buccal field. E, F. Fine structures of anterior portion to mark buccal field, paroral kineties, and adoral polykineties. Arrows indicate intrabuccal kinety, while arrowhead shows the fossa between apical beak and buccal region. G, H. Frontal and lateral view of anterior end of body to mark the fossa (arrowheads). I, J. Detail of cell showing the distribution of cortical granules between the ciliary rows. K, L, P–R. Macronuclei and micronucleus (arrowhead in P and R). M. Food vacuole containing diatom. N, O. Infraciliature of anterior portion, showing the buccal field and its associated ciliature. Arrow shows adoral polykineties; arrowhead marks the preoral kinety within the fossa near its right side, double arrowheads indicate intrabuccal kinety. Ap, adoral polykineties; BF, buccal field; Pk, paroral kineties. Scale bars = 150  $\mu$ m (A–D); 25  $\mu$ m (E, F, N, O).

**Deposition of slides:** The protargol slide containing the holotype specimen (Fig. 1H, I) is deposited in the Natural History Museum, London, UK, with registration number (NHMUK 2010.9.20.1); one paratype slide is deposited in the Laboratory of Protozoology, OUC, China (No. XY09042901).

**Etymology:** The species name *sinica* reflects the fact that the type material was found in China.

**Type locality:** The intertidal zone of the No. 1 Beach at Qingdao (36°06'N; 120°32'E), China.

**Gene sequence data:** The SSU rDNA sequence of *Geleia sinica* spec. nov. was deposited in GenBank with accession number JF437558. The length and G + C content of the SSU rRNA gene are 1549 bp and 50.55% respectively. The available SSU rDNA sequences of four species in the genus *Geleia*, namely *G. simplex*, *G. swedmarki*, *G. fossata* and

*Geleia* sp., differ in 13, 15, 25, 32 nucleotides from our new isolate, *G. sinica* spec. nov. respectively (Fig. 3).

**Description:** Cell size in vivo mostly about 400  $\mu$ m  $\times$  30  $\mu$ m; body vermiform and cylindrical, anterior and posterior ends both slightly narrowed (Figs 1A–C, 2A–D); flexible and slightly contractile (Fig. 1B, C). Small beak positioned near anterior end. Fossa located between apical beak and buccal field; several transversely oriented grooves within fossa (Figs 1A, F, 2E–G). Buccal field about 40–60  $\mu$ m long (Figs 1A, F, 2A, C, D). Somatic cilia about 10  $\mu$ m long in vivo. Cytoplasm packed with inclusions, about 1–5  $\mu$ m in diameter, that render the cell grayish to slightly dark-brownish at lower magnifications while at higher magnifications the cell is almost opaque (Fig. 2A–D). Cortical granules colorless, about 0.5  $\mu$ m in diameter, distributed along ciliary rows (Figs 1D, 2I, J).

**Table 1.** Morphometric data from *Geleia sinica* spec. nov. (first line), and Qingdao populations of *Kentrophoros flavus* (second line) and *K. gracilis* (pop I, third line; pop II, fourth line).

Characters	Min	Max	Mean	SD	CV	n
Body length	110	352	239.5	58.5	24.4	20
	182	465	286.2	70.2	24.5	18
	185	451	308.9	81.7	26.5	19
	201	630	498.6	143	28.7	7
Body width	24	45	30.9	6.0	19.6	20
	48	81	66.3	8.8	13.2	18
	20	51	34.1	7.9	23.2	19
	31	40	37.4	3.8	10.2	7
Somatic kineties, number	28	34	30.2	1.5	5.1	20
	14	19	16.8	1.3	7.5	18
	10	12	10.8	0.6	5.4	16
	10	13	–	–	–	4
Macronuclei, number	2	4	2.2	0.6	25.2	17
	21	49	33.3	7.2	21.1	17
	10	20	13.9	2.7	19.3	16
	15	25	–	–	–	3
Micronuclei, number	1	1	1.0	0	0	18
	9	17	12.2	2.6	21.1	17
	9	18	12.6	2.8	22.4	15
	21	–	–	–	–	1
Dikinetids in the longest adoral polykineties, number	4	7	5.5	1.0	17.6	16
	–	–	–	–	–	–
	–	–	–	–	–	–
	–	–	–	–	–	–
Dikinetids in intrabuccal kinety, number	25	34	29.4	2.8	9.7	11
	–	–	–	–	–	–
	–	–	–	–	–	–
	–	–	–	–	–	–

All data are based on protargol-impregnated specimens. Measurements in  $\mu\text{m}$ . Abbreviations: CV, coefficient of variation in %; Max, maximum; Mean, median; Min, minimum; n, number of specimens investigated; SD, standard deviation of the mean; –, data not available.

Contractile vacuole absent. Locomotion by sluggish gliding along bottom of Petri dish.

Infraciliature as shown in Figs 1G–I, 2N, O. One preoral kinety comprising 7–16 dikinetids located within the fossa near its right side, and within preoral suture (Figs 1G, 2N, O). Somatic kineties composed of 28–34 rows of dikinetids and extended entire length of body; one postoral kinety extending to posterior end of cell (Figs 1G, H, 2O). Oral structures comprising three parts: adoral polykineties which form a ciliary field on left side of oral cavity composed of 30–50 rows of dikinetids, the longest row consisting of up to seven dikinetids (Figs 1G, 2N, O); intrabuccal kinety on right side of buccal field, composed of 25–34 sparsely spaced dikinetids (Figs 1G, 2N, O); paroral kineties, which form a ciliary field on right side of buccal field parallel to intrabuccal kinety, composed of numerous rows of closely spaced dikinetids (Figs 1G, 2O).

Usually two macronuclei, but three in two specimens and four in one specimen, out of 17 examined; one micronucleus (Figs 1E, I, 2K, L, P–R).

**Comparison with related species:** Although there are 12 nominal species of *Geleia*, data on the infraciliature are avail-

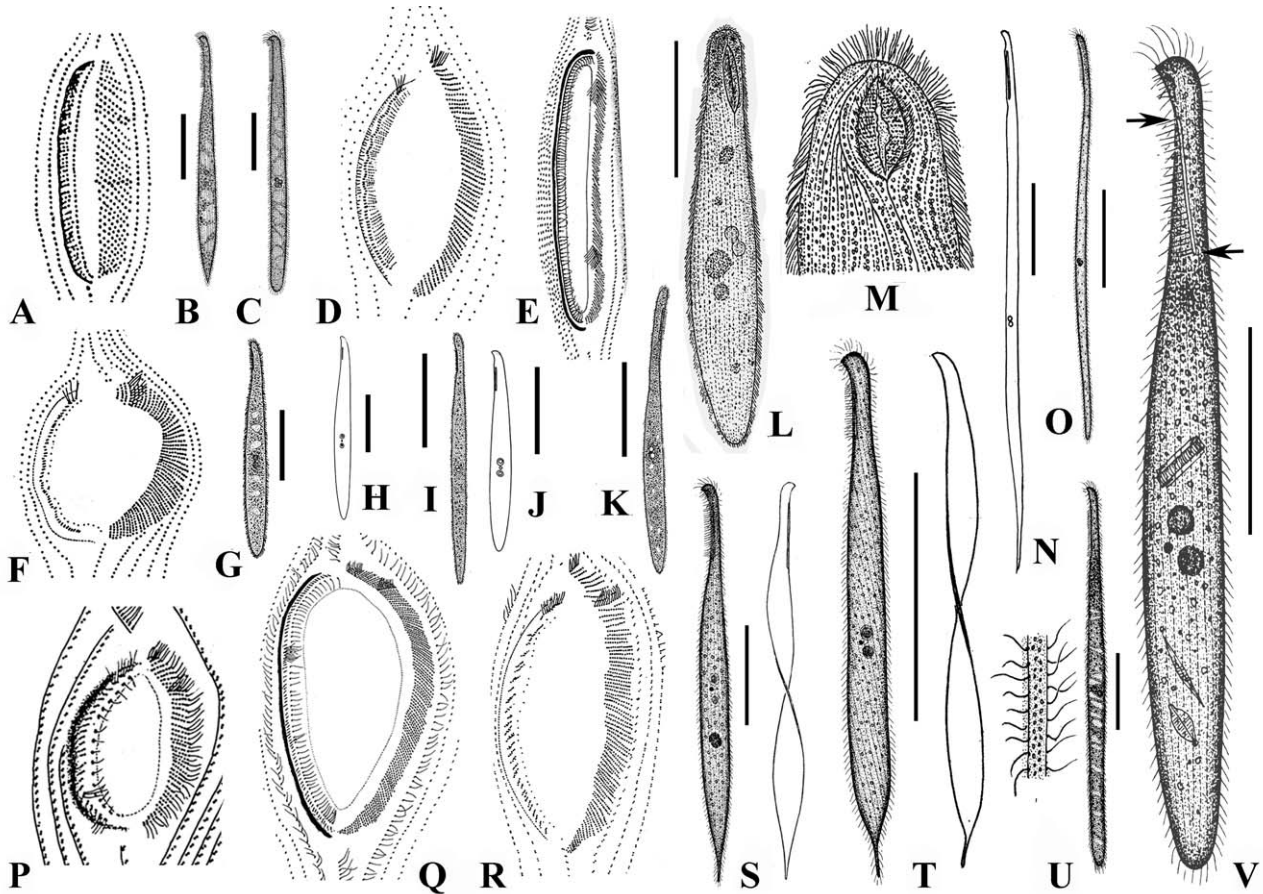
able for only five of these (Fig. 4A–V, Table 2) (Carey 1992; Dragesco 1963, 1999; Dragesco and Dragesco-Kernéis 1986; Fauré-Fremiet 1951; Foissner 1996, 1997a, 1997b; Foissner and Al-Rasheid 1999a, 1999b; Foissner and Dragesco 1996a, 1996b).

*Geleia fossata* (Kahl, 1933) Foissner, 1998 closely resembles *G. sinica* regarding the general morphology, including the size of the preoral fossa, the small beak and the slightly pointed tail (Fig. 4B). However, *G. fossata* differs from the latter by having more dikinetids in the longest adoral polykineties (12 vs. 4–7) and in the longest paroral kineties (2–4 vs. 1) (Fig. 4A, Table 2; Dragesco 1999).

*Geleia decolor* (Kahl, 1933) Foissner, 1998 can be recognized by having considerably more somatic kineties (40–48 vs. 28–34) and adoral polykineties (58–95 vs. about 40) than *G. sinica* (Fig. 4J, R, Table 2; Dragesco 1999).

*Geleia major* (Dragesco, 1954) Foissner, 1998 is larger with a body length of 400–1300  $\mu\text{m}$  in vivo (vs. 250–500  $\mu\text{m}$ ) and has significantly more somatic kineties (48–70 vs. 28–34) and adoral polykineties (80–140 vs. about 40) than *G. sinica* (Fig. 4E, I, K, Q, Table 2; Dragesco 1999).



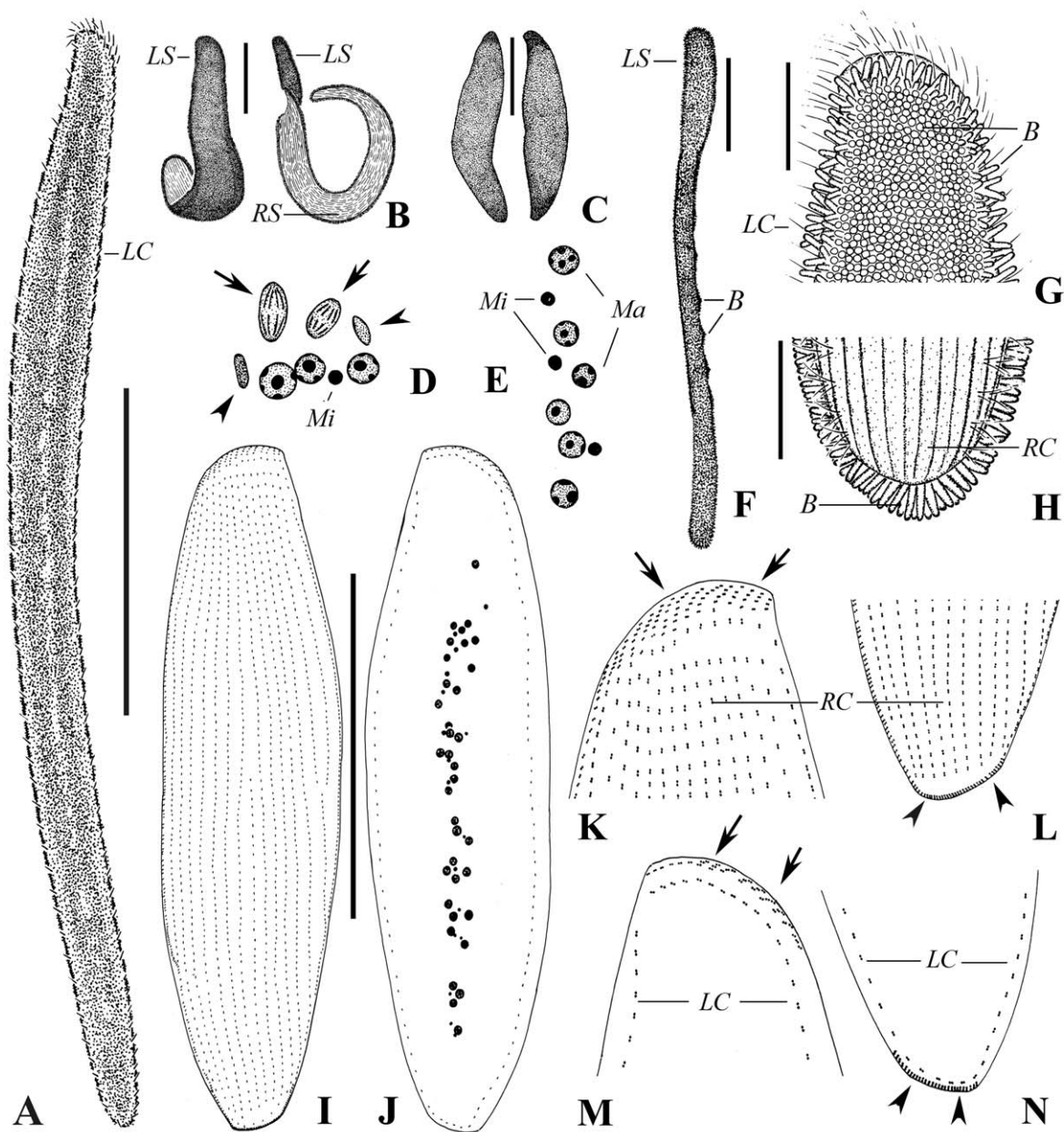


**Fig. 3.** A–V. Morphology and some buccal infraciliature of nominal species of *Geleia*. A, B. *Geleia fossata* (Fig. A from Nouzarède 1977; Fig. B from Dragesco 1960). C, D. *Geleia swedmarki* (from Dragesco and Dragesco-Kernéis 1986). E, K. *Geleia major* variété II of Dragesco (1999) (from Dragesco 1999). F, H. *Geleia simplex* (from Dragesco and Dragesco-Kernéis 1986). G, P. *Geleia simplex* variété II of Dragesco (1999) (from Dragesco 1963). I, Q. *Geleia major* variété I sensu Dragesco, 1999 (from Dragesco 1999). J, R. *Geleia decolor* (from Dragesco and Dragesco-Kernéis 1986). L, M. *Geleia nigriceps* (from Raikov 1962). N. *Geleia luci* (from Dragesco 1960). O. *Geleia tenuis* (from Dragesco 1960). S. *Geleia acuta* (from Dragesco 1960). T. *Geleia hyalina* (from Dragesco 1960). U. *Geleia vacuolata* (from Dragesco 1960); inset: to show the cortical granules between the ciliary rows. V. *Geleia oblique* (from Dragesco 1960); arrows in V mark the position of the oblique buccal field. Scale bars = 100  $\mu\text{m}$  (B, C, G, H, J, L, N, O, S–V); 200  $\mu\text{m}$  (I, K).

*Geleia simplex* (Fauré-Fremiet, 1951) Foissner, 1998 was originally reported with only a simple illustration and no detailed information about the buccal field (Fauré-Fremiet 1951). The infraciliature was first described by Dragesco and Dragesco-Kernéis (1986). Dragesco (1999) subsequently revised this species and assigned *Geleia swedmarki* sensu Dragesco (1963) to *G. simplex*. However, these two isolates differ from each other regarding the structure of the buccal apparatus: variété I of Dragesco (1999) has considerably more adoral polykineties (58–68 vs. 36–50 in variété II), the longest of which contain up to 14 basal bodies (vs. maximum eight in variété II). Hence, they might not be conspecific, although this conclusion needs to be confirmed, for example using molecular methods. Assuming *G. simplex* variété I of Dragesco (1999) is conspecific with the original description (Fauré-Fremiet 1951), *G. simplex* can be diagnosed as follows: body slender and colorless, in vivo 260–400  $\mu\text{m}$ , with about 60 adoral polykineties

and 38–48 somatic kineties. By contrast, *G. simplex* variété II of Dragesco (1999) is very likely a misidentification and is probably identical with *G. sinica*, despite having slightly more (32–46 vs. 28–34) somatic kineties (Fig. 4G, P, Table 2; Dragesco 1999). *Geleia simplex* can thus be separated from *G. sinica* by having more adoral polykineties (58–68 vs. 30–50) and more somatic kineties (38–48 vs. 28–34) than the latter (Fig. 4F, H, Tables 2 and 3; Dragesco 1999; Dragesco and Dragesco-Kernéis 1986; Fauré-Fremiet 1951).

*Geleia swedmarki* (Dragesco, 1954) Foissner, 1998 was re-defined by Dragesco and Dragesco-Kernéis (1986) following an investigation of the infraciliature in protargol-impregnated specimens. It can be clearly separated from *G. sinica* by its body length in vivo (500–800  $\mu\text{m}$  vs. 250–450  $\mu\text{m}$  in *G. sinica*), the number of somatic kineties (40–46 vs. 28–34) and the number of dikinetids in the longest adoral polykineties (10–11 vs. 4–7) (Fig. 4C, D, Table 2). Dragesco



**Fig. 4.** A–N. *Kentrophoros flavus* from life (A–C, F–H) and after protargol impregnation (D, E, I–N). **A.** View of typical individual. Note the left ciliary rows. **B.** Contorted individuals. **C.** Contracted cells. **D, E.** Macronuclei and micronuclei, arrows in D indicate the macronuclear primordia while arrowheads mark micronuclear mitosis. **F.** Partial lateral view, to show flattened cell and epibiotic bacteria surpassing the body margin. **G, H.** Anterior end of left side (G) and posterior end of right side (H), showing the epibiotic bacteria, and left and right ciliary rows. **I, J.** Right (I) and left (J) view showing the infraciliature and nuclear apparatus. **K–N.** Anterior and posterior body end in right and left lateral view to show right and left ciliary rows. Arrows mark the obliquely oriented anteriormost dikinetids, arrowheads indicate distinctly condensed dikinetids. B, bacteria; LC, left ciliary row; LS, left side; Ma, macronuclei; Mi, micronuclei; RC, right ciliary rows; RS, right side. Scale bars = 130  $\mu\text{m}$  (A, I, J); 100  $\mu\text{m}$  (B, C); 60  $\mu\text{m}$  (F); 20  $\mu\text{m}$  (G, H).

(1963) described a new isolate under the name of *G. swedmarki* which he subsequently renamed *G. simplex* variété II (Dragesco 1999), although this isolate differs conspicuously from *G. simplex* variété I (see above).

Among the seven congeners whose infraciliature remains unknown, *G. vacuolata* (Dragesco, 1960) Foissner, 1998 resembles *G. sinica* most closely with respect to the general

body shape (Fig. 4U, Table 4). Nevertheless, it can be separated from the latter by its larger body size in vivo (400–700 vs. 250–500  $\mu\text{m}$ ) and in having a terminally located contractile vacuole (vs. contractile vacuole absent in *G. sinica*) (Dragesco 1960).

*Geleia sinica* can be clearly distinguished from *G. nigriceps* (Kahl, 1933) Foissner, 1998 by its slender body shape



**Table 2.** Comparison of *Geleia sinica* spec. nov. with those congeners for which the infraciliature is described.

Character <sup>a</sup>	<i>Geleia sinica</i> spec. nov.	" <i>G. simplex</i> variété II" <sup>b</sup>	<i>G. simplex</i>	<i>G. decolor</i>	<i>G. major</i> variété I	<i>G. major</i> variété II	<i>G. fossata</i>	<i>G. swedmarki</i>
Body, length in vivo	250–500	150–460	260–400	600	400–900	600–1300	300–700	500–800
SK, number	28–34	32–46	38–48	40–48	48–62	60–70	–	40–46
Ap. number	ca. 40	36–50	58–68	58–95	80–140	80–130	ca. 34 <sup>c</sup>	30–78
Dikinetids in the longest Ap. number	4–7	up to 8	up to 14	8–16	7–18	7–14	12 <sup>c</sup>	10–11
Data source	Present work	Dragesco (1963, 1999)	Dragesco and Dragesco-Kernéis (1986)	Dragesco (1999)	Dragesco (1999)	Dragesco (1999)	Dragesco (1999)	Dragesco and Dragesco-Kernéis (1986)

Abbreviations: Ap, adoral polykineties; SK, somatic kineties; –, data not available.

<sup>a</sup>Measurements in  $\mu\text{m}$ .<sup>b</sup>Very likely a misidentification, could be a population of *Geleia sinica* spec. nov. (see text).<sup>c</sup>Counted from Fig. 86 in Dragesco (1999).**Table 3.** List of synonyms of *Geleia simplex*, *G. swedmarki* and *G. sinica* spec. nov.

Basionym or misidentified	Current name
<i>Geleia simplex</i> (Fauré-Fremiet, 1951)	<i>Geleia simplex</i>
<i>G. simplex</i> sensu Dragesco and Dragesco-Kernéis (1986)	<i>G. simplex</i>
<i>G. simplex</i> variété I sensu Dragesco (1999)	<i>G. simplex</i>
<i>G. swedmarki</i> (Dragesco, 1954)	<i>G. swedmarki</i>
<i>G. swedmarki</i> sensu Dragesco and Dragesco-Kernéis (1986)	<i>G. swedmarki</i>
<i>G. swedmarki</i> sensu Dragesco (1963) <sup>a</sup>	<i>G. sinica</i> ?
<i>G. simplex</i> variété II sensu Dragesco (1999) <sup>a</sup>	<i>G. sinica</i> ?

<sup>a</sup>New supposed synonym suggested in the present work.

with length:width ratio 12–18:1 (vs. body short and plump with length:width ratio ca. 5:1), the position of the buccal field (sub-apical vs. almost apical) and the presence (vs. absence) of a fossa (Fig. 4L, M, Table 4; Raikov 1962).

*Geleia luci* (Dragesco, 1960) Foissner, 1998 and *G. tenuis* (Dragesco, 1954) Foissner, 1998 differ from *G. sinica* by the body shape which, in the former two species, is extremely thin with a length:width ratio of about 25:1 (vs. about 15:1) and with a conspicuously pointed (vs. slightly narrowed) caudal tail (Fig. 4N, O, Table 4; Dragesco 1960).

Both *Geleia acuta* (Dragesco, 1960) Foissner, 1998 and *G. hyalina* (Dragesco, 1960) Foissner, 1998 have an extremely flattened body with a conspicuously pointed tail (vs. cylindrical body, tail not conspicuously pointed) and hence can be clearly separated from *G. sinica* (Fig. 4S, T, Table 4; Dragesco 1960).

*Geleia obliqua* (Dragesco, 1960) Foissner, 1998 differs from *G. sinica* by its obliquely oriented (vs. longitudinally oriented) buccal field (Fig. 4V, arrows; Dragesco 1960).

## Genus *Kentrophoros* Sauerbrey, 1928

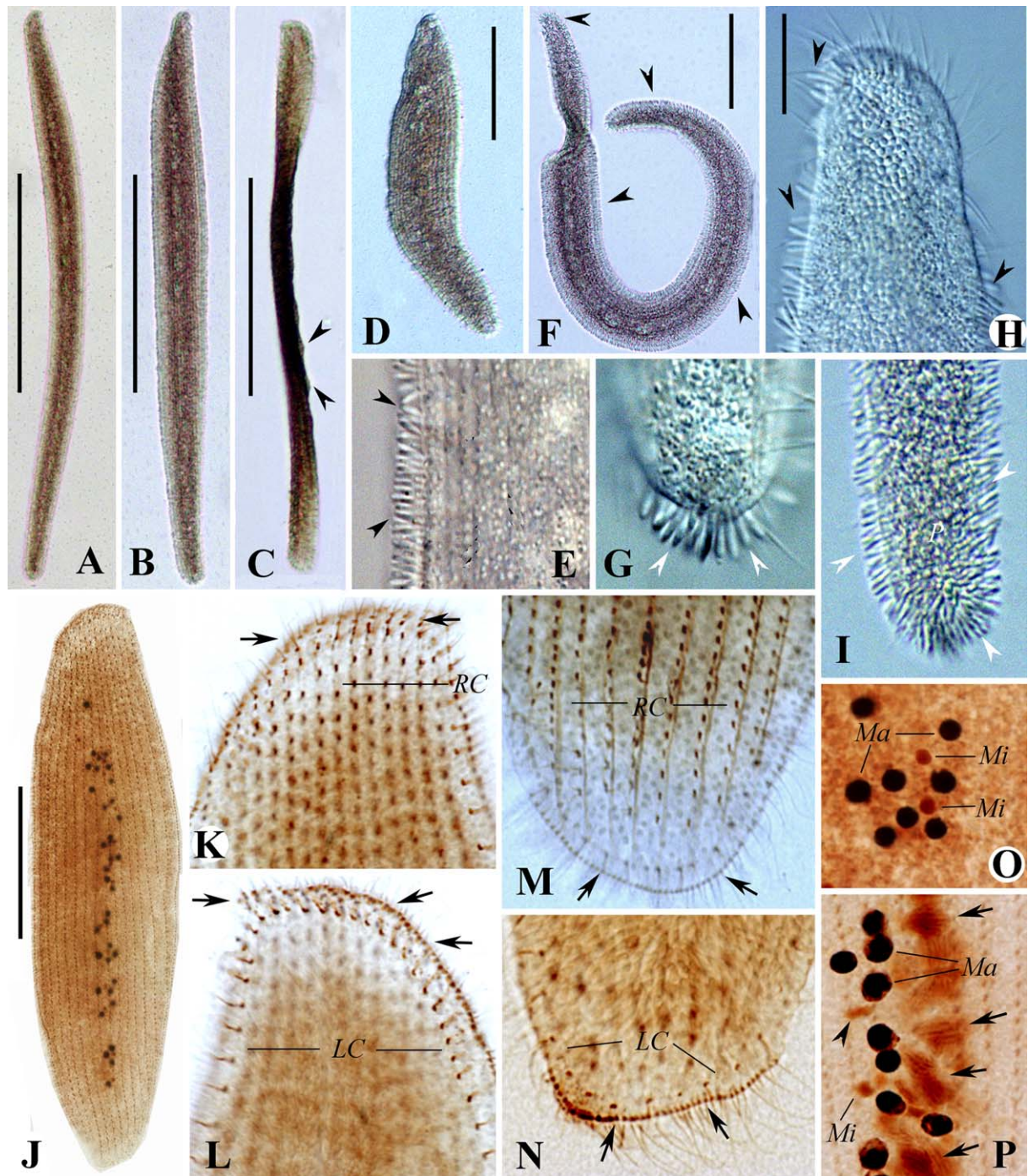
### *Kentrophoros flavus* Raikov and Kovaleva, 1968 (Figs 5A–N, 6A–P, Table 1)

Although originally called *K. flavum* (Raikov and Kovaleva 1968), the species name was emended by Foissner (1995) to *K. flavus*. Since Raikov and Kovaleva (1968) failed to give either morphometric data or details of the infraciliature, an improved diagnosis based on previous observations and on new data is supplied here.

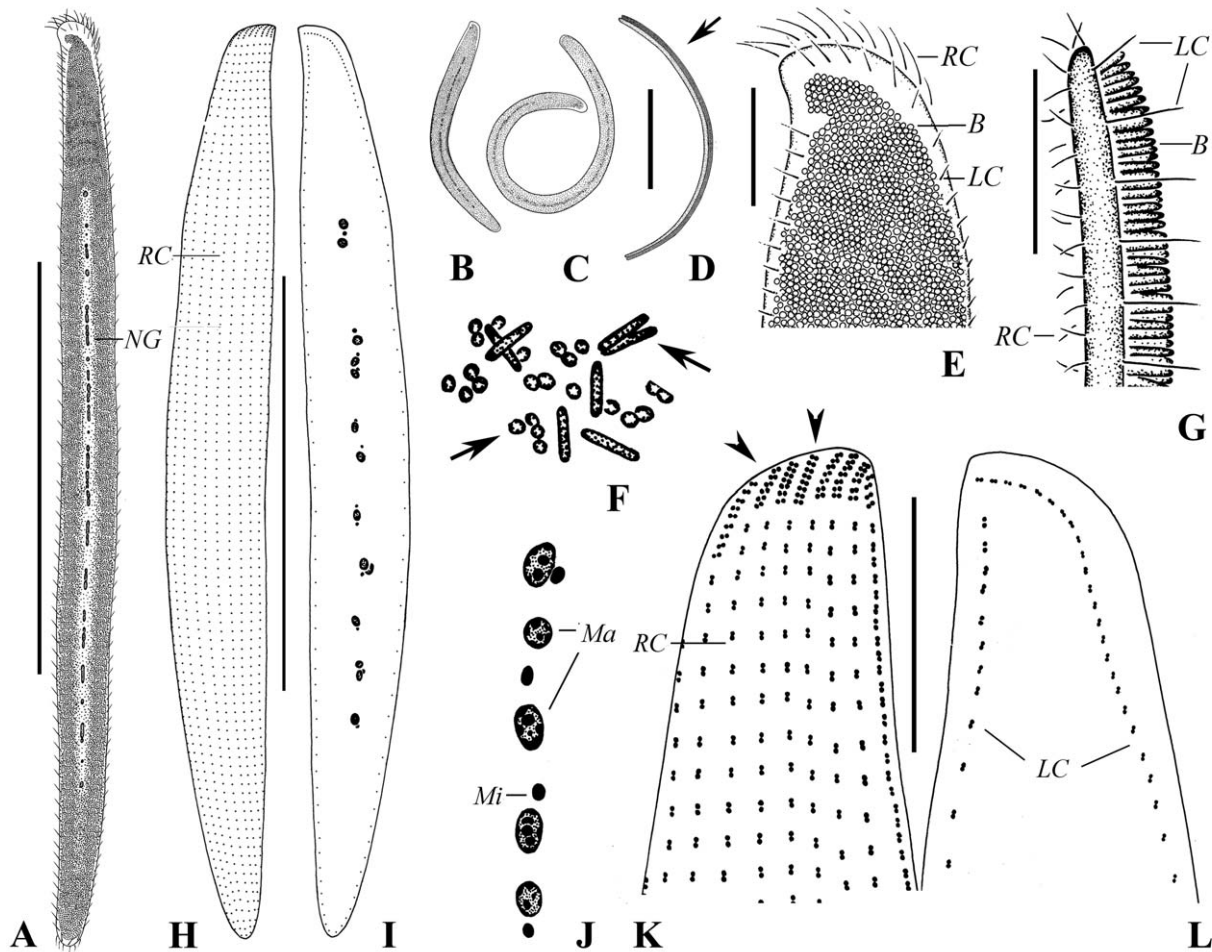
**Improved diagnosis:** Highly flattened *Kentrophoros* about 250–600  $\mu\text{m} \times 30$ –60  $\mu\text{m}$  in vivo; 9–49 macronuclei and 3–17 micronuclei arranged in a long irregular row; about 12–19 somatic kineties on right side of cell; densely packed epibiontic bacteria covering left side of cell.

**Description of Qingdao population:** Cell size in vivo mostly about 300–500  $\mu\text{m} \times 40$ –50  $\mu\text{m}$ , cell moderately contractile and flexible, highly flattened and ribbon-like; body length:width ratio about 8–14:1 when fully





**Fig. 5.** A–P. Photomicrographs of *Kentrophoros flavus* from life (A–I) and after protargol impregnation (J–P). A, B. Different individuals to show typical body shapes. C. Partial lateral view, indicating flattened cell and epibiontic bacteria projecting beyond body margin (arrowheads). D. Contracted specimen. E. Marginal mid-body region of right side, marking epibiontic bacteria (arrowheads). F. Contorted individual indicating flexible body and epibiontic bacteria covering the entire left side (arrowheads). G–I. Posterior region of right side (G), and anterior (H) and posterior (I) regions of left side; arrowheads show the epibiontic bacteria. J. Infraciliature of right side. K, L. Infraciliature of right (K) and left (L) side of anterior body end; arrows indicate the obliquely oriented anteriormost dikinetids. M, N. Right (M) and left (N) lateral view of posterior end; arrows mark the distinctly condensed dikinetids. O, P. Macronuclei and micronuclei; arrows in P show the macronuclear primordia, arrowhead indicates micronuclear mitosis. LC, left ciliary row; Ma, macronuclei; Mi, micronuclei; RC, right ciliary rows. Scale bars = 150  $\mu\text{m}$  (A, B, C); 80  $\mu\text{m}$  (D, J); 50  $\mu\text{m}$  (F); 20  $\mu\text{m}$  (H).



**Fig. 6.** A–L. *Kentrophoros gracilis* from life (A–G) and after protargol impregnation (H–L). A. Typical individual, showing the nuclear apparatus forming a longitudinal row along the cell median. B, C. Shape variants. D. Lateral view, arrow shows bacterial layer. E, G. Anterior body portion marking left and right ciliary rows and epibiontic bacteria. F. Arrows indicate rod-like bacteria several of which are shown in top view. H, I. Right (H) and left (I) lateral view of the same cell, showing the infraciliature and nuclear apparatus. J. Macronuclei and micronuclei. K, L. Right (K) and left (L) lateral view of anterior body portion of the same specimen to show the infraciliature. Arrowheads mark the obliquely oriented anteriormost dikinetids. B, bacteria; LC, left ciliary row; Ma, macronuclei; Mi, micronuclei; NG, nuclear group; RC, right ciliary rows. Scale bars = 250  $\mu\text{m}$  (A); 150  $\mu\text{m}$  (D, H, I); 25  $\mu\text{m}$  (E, G, K, L).

extended although only about 5:1 in contracted specimens (Figs 5A–C, 6A, B, D). Anterior and posterior portions slightly narrowed (Figs 5A, 6A, B, H, I). Body opaque due to the dense lawn of epibiontic bacteria (about  $4\text{ }\mu\text{m} \times 1\text{ }\mu\text{m}$ ), completely covering left side of cell and extending beyond body margins (Figs 5F, G, H, 6C, E–I). Cytoplasm colorless, rather transparent. Elongated, vacuole-like, longitudinal strand extending almost entire length of body along cell meridian marking the position of the nuclear apparatus (Figs 5A, 6A, B). Neither food vacuoles nor contractile vacuoles observed. Locomotion by gliding on bottom of Petri dish, usually attaching to substrate when disturbed.

Fourteen to 19 longitudinal somatic kineties on right side composed of dikinetids throughout (Figs 5I, 6J). Dikinetidal axes parallel to main body axis, except for obliquely oriented and more closely spaced dikinetids at anterior end

(Figs 5K, M, 6K, L). Marginal dikinetids at posterior end of cell densely arranged (Figs 5L, N, 6M, N). Single kinety on left side, curving around cell margin almost forming a circle (Figs 5J, M, N, 6L, N). Somatic cilia about  $7\text{ }\mu\text{m}$  long in vivo.

Nuclear apparatus forming a longitudinally oriented strand along cell meridian, composed of 21–49 macronuclei, each about  $2\text{--}4\text{ }\mu\text{m}$  in diameter, and 9–17 micronuclei (Figs 5D, E, J, 6J, O, P). Nuclei mostly globular or ellipsoidal but unusual nuclear shapes were found in one out of 18 specimens, which were probably micronuclei undergoing mitosis (Figs 5D, 6P) and macronuclear primordia (Figs 5D, 6P; Raikov 1994).

**Remarks and comparison:** According to Foissner (1995), *Kentrophoros* is characterized by having a flattened or tubular body shape, condensed dikinetids in the anterior region of the right side of the cell and symbiotic sulphur bacteria



**Table 4.** Comparison between *Geleia sinica* and seven nominal species assigned to the genus *Geleia* for which no information about the infraciliature is available.

Character <sup>a</sup>	<i>Geleia sinica</i> spec. nov.	<i>G. nigriceps</i>	<i>G. obliqua</i>	<i>G. tenuis</i>	<i>G. acuta</i>	<i>G. luci</i>	<i>G. hyaline</i>	<i>G. vacuolata</i>
Body, length in vivo	250–500	250–400	400–500	ca. 550	ca. 400	ca. 650	ca. 200	400–700
Body shape	Slim and cylindrical	Plump and cylindrical	Laterally flattened	Very slim	Extremely flattened	Very slim	Extremely flattened	Cylindrical
Length:width ratio	12–18:1	ca. 5:1 <sup>b</sup>	ca. 9:1 <sup>b</sup>	ca. 22:1 <sup>b</sup>	ca. 11:1 <sup>b</sup>	ca. 30:1 <sup>b</sup>	ca. 10:1 <sup>b</sup>	ca. 20:1 <sup>b</sup>
Body color (due to food?)	Slightly brownish	–	Brown	Colorless	Brown	Colorless	Colorless	Colorless
Data source	Present work	Raikov (1962)	Dragesco (1999)	Dragesco (1960)	Dragesco (1960)	Dragesco (1960)	Dragesco (1960)	Dragesco (1960)

–, data not available.

<sup>a</sup>Measurements in  $\mu\text{m}$ .<sup>b</sup>Data from relevant figure.

covering the left side of the cell. To date, 15 species have been reported (Dragesco, 1954, 1960; Fauré-Fremiet 1950, 1951; Foissner 1995; Kovaleva 1966; Raikov 1962, 1963; Raikov and Kovaleva 1968; Sauerbrey 1928; Wright 1982), of which only one, *K. fistulosus* (Fauré-Fremiet, 1950), has been investigated using silver impregnation methods and scanning electron microscopy (Foissner 1995).

*Kentrophoros flavus* was discovered by Raikov and Kovaleva (1968). The Qingdao population resembles the original population rather well in terms of its general morphology in vivo. The main differences are the numbers of macronuclei and micronuclei (21–49 and 9–17 vs. 9–28 and 3–14 in the original population) and ciliary rows on right side (14–19 vs. 12 in the original population). Additionally, *K. flavus* was originally described as “incontractile”, whereas the cells of the Qingdao population are moderately contractile. However, we believe these features to be population-dependent and given their strong similarity in other respects, we conclude that the two populations are conspecific.

Considering their general morphological features (e.g. body shape and size), two congeners are similar to *Kentrophoros flavus*, namely *K. gracilis* Raikov, 1963 (see below) and *K. grandis* (Dragesco, 1954) Foissner, 1995, both of which have a flattened, ribbon-like body shape and both lack a pointed posterior end and a slender neck. According to the new data presented here, *K. flavus* differs from *K. gracilis* by having conspicuously more macronuclei (on average 33 vs. 14) and right somatic kineties (on average 17 vs. 11) (Table 1; Raikov 1963).

*Kentrophoros grandis* is also an insufficiently described species that resembles *K. flavus* in body shape and multiple macronuclei. The two can be separated, however, by the arrangement of the nuclear nodules which form a longitudinal row along the cell meridian in *K. flavus* whereas in *K. grandis* they are arranged in four distinct groups (Dragesco, 1954, 1960).

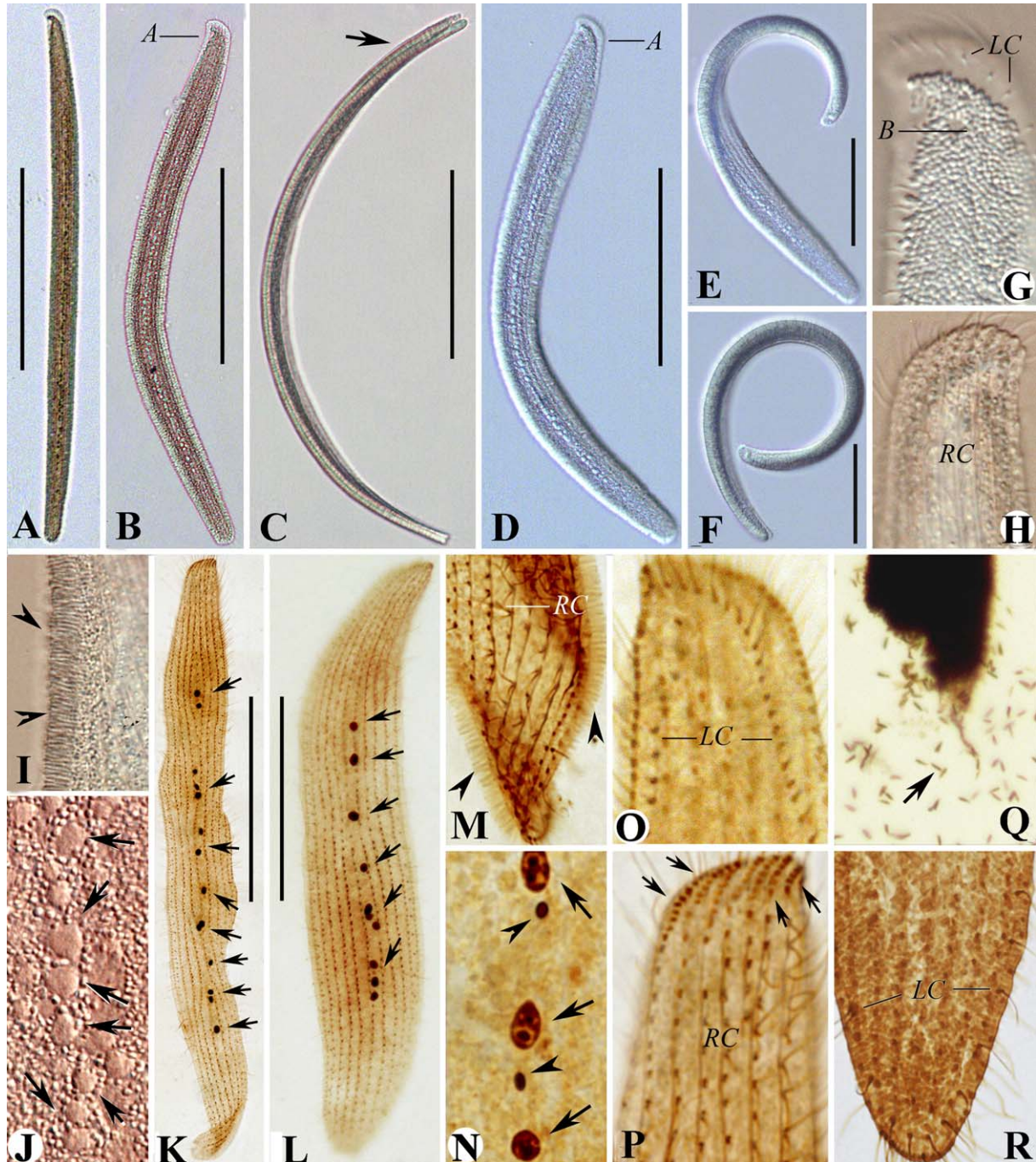
The small subunit rRNA gene sequence of the Chinese population of *Kentrophoros flavus* is deposited in GenBank with accession number FJ467505 (Gao et al. 2010).

#### ***Kentrophoros gracilis* Raikov, 1963 (Figs 7A–L, 8A–R, Table 1)**

Although originally called *Kentrophoros gracile* (Raikov 1963), the species name was emended by Foissner (1995) to *K. gracilis*. Since this organism has been only superficially described (Raikov 1963) and neither infraciliature nor detailed morphometric data are available, an improved diagnosis and a redescription based on the original and two Qingdao populations are supplied here.

**Improved diagnosis:** Size rather variable, about 150–600  $\mu\text{m} \times 25$ –70  $\mu\text{m}$  in vivo; body flattened and ribbon-like; 7–25 macronuclei and 4–21 micronuclei arranged in a line along the cell meridian; 10–13 ciliary rows on right side of cell; densely arranged epibiontic bacteria covering left side of cell except for anterior end.





**Fig. 7.** A–R. Photomicrographs of *Kentrophoros gracilis* from life (A–J) and after protargol impregnation (K–R). A. Typical individual. B, D–F. Shape variants. C. Lateral view, showing bacterial layer (arrow). G, H. Anterior portion of left (G) and right (H) side, marking epibiontic bacteria and ciliary rows. I. Detail of body margin showing epibiontic bacteria (arrowheads). J. Macronuclei (arrows). K, L. Views of right side, noting the macronuclei (arrows). M. Middle region to show right ciliary rows and bacteria (arrowheads). N. Macronuclei (arrows) and micronuclei (arrowheads). O, P. Ciliary rows on anterior portions of left (O) and right (P) side. Arrows indicate the obliquely oriented anteriormost dikinetids of right side. Q. Rod-like bacteria (arrow). R. Posterior portion of left side to show the left ciliary row. A, anterior end; B, bacteria; LC, left ciliary row; RC, right ciliary rows. Scale bars = 150  $\mu\text{m}$  (A–F); 100  $\mu\text{m}$  (K, L).

**Redescription:** Cell size mostly about 150–600  $\mu\text{m} \times 25\text{--}70 \mu\text{m}$  in vivo; body flattened and ribbon-like (Figs 7A, D, G, 8A–D, M). Cell flexible but not contractile (Figs 7B, C, 8D–F). Anterior part slightly curved

and forming a short rostrum with both ends broadly rounded (Figs 7A, E, 8A, B, D, G).

Cell often slightly yellow-brownish at low magnifications, colorless or grayish at high magnifications. Left side of cell

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- Fauré-Fremiet, E., 1951. The marine sand-dwelling ciliates of Cape Cod. *Biol. Bull. Mar. Biol. Lab. Woods Hole* 100, 59–70.
- Foissner, W., 1995. Kentrophoros (Ciliophora, Karyorelictea) has oral vestiges: a reinvestigation of *K. fistulosus* (Fauré-Fremiet, 1950) using protargol impregnation. *Arch. Protistenk.* 146, 165–179.
- Foissner, W., 1996. Updating the trachelocercids (Ciliophora Karyorelictea). II. *Prototrachelocerca* nov. gen. (Prototrachelocercidae nov. fam.), with a redescription of *P. fasciolata* (Sauerbrey, 1928) nov. comb. and *P. caudata* (Dragesco & Raikov, 1966) nov. comb. *Eur. J. Protistol.* 32, 336–355.
- Foissner, W., 1997a. Updating the trachelocercids (Ciliophora, Karyorelictea). IV. Transfer of *Trachelocerca entzi* Kahl, 1927 to the Gymnostomatea as a new genus, *Trachelotractus* gen. n. (Helicoprordontidae). *Acta Protozool.* 36, 63–74.
- Foissner, W., 1997b. Updating the trachelocercids (Ciliophora, Karyorelictea). V. Redescription of *Kovalevaia sulcata* (Kovaleva, 1966) gen. n., comb. n. and *Trachelocerca incaudata* Kahl, 1933. *Acta Protozool.* 36, 197–219.
- Foissner, W., 1998. The karyorelictids (Protozoa: Ciliophora), a unique and enigmatic assemblage of marine, interstitial ciliates: a review emphasizing ciliary patterns and evolution. In: Coombs, G.H., Vickerman, K., Sleight, M.A., Warren, A. (Eds.), *Evolutionary Relationships Among Protozoa*. Chapman & Hall, London, pp. 305–325.
- Foissner, W., Al-Rasheid, K.A.S., 1999a. Updating the trachelocercids (Ciliophora, Karyorelictea). VI. A detailed description of *Sultanophrys arabica* nov. gen., nov. spec. (Sultanophryidae nov. fam.). *Eur. J. Protistol.* 35, 146–160.
- Foissner, W., Al-Rasheid, K.A.S., 1999b. Ontogenesis in a trachelocercid ciliate (Ciliophora, Karyorelictea), *Sultanophrys arabica*, with an account of evolution at the base of the ciliate tree. *Acta Protozool.* 38, 273–290.
- Foissner, W., Dragesco, J., 1996a. Updating the trachelocercids (Ciliophora, Karyorelictea). I. A detailed description of the infraciliature of *Trachelolophos gigas* n. g., n. sp. and *T. filum* (Dragesco and Dragesco-Kernéis, 1986) n. comb. *J. Eukaryot. Microbiol.* 43, 12–25.
- Foissner, W., Dragesco, J., 1996b. Updating the trachelocercids (Ciliophora, Karyorelictea). III. Redefinition of the genera *Trachelocerca* Ehrenberg and *Tracheloraphis* Dragesco, and evolution in trachelocercid ciliates. *Arch. Protistenk.* 147, 43–91.
- Gao, S., Strüder-Kypke, M.C., Al-Rasheid, K.A.S., Lin, X., Song, W., 2010. Molecular phylogeny of three ambiguous ciliate genera: *Kentrophoros*, *Trachelolophos* and *Trachelotractus* (Alveolata, Ciliophora). *Zool. Scr.* 39, 305–313.
- Gong, J., Stoeck, T., Yi, Z., Miao, M., Zhang, Q., Roberts, D., Warren, A., Song, W., 2009. SSU rRNA phylogenies support that the class Nassophorea is not monophyletic, and its two subgroups synhymeniids and microthoracids are closely related to the class Phyllopharyngea (phylum Ciliophora). *J. Eukaryot. Microbiol.* 56, 339–347.
- Kahl, A., 1933. Ciliata libera et ectocommensalia. *Tierwelt N.- u. Ostsee* 23 (Teil II, C<sub>3</sub>), 29–146.
- Kovaleva, V.G., 1966. Infusoria of the mesopsammon in sand bays of the Black Sea. *Zool. Zh.* 45, 1600–1611.
- Lynn, D.H., 2008. *The Ciliated Protozoa: Characterization, Classification and Guide to the Literature*, 3rd ed. Springer, Dordrecht.
- Mazei, Y., Gao, S., Warren, A., Li, L., Li, J., Song, W., Esaulov, A., 2009. A reinvestigation of the marine ciliate *Trachelocerca ditis* (Wright, 1982) Foissner and Dragesco, 1996 (Ciliophora, Karyorelictea) from the Yellow Sea and an assessment of its phylogenetic position inferred from the small subunit rRNA gene sequence. *Acta Protozool.* 48, 213–221.
- Medlin, L., Elwood, H.L., Stickel, S., Sogin, M.L., 1988. The characterization of enzymatically amplified eukaryotic 16S-like rRNA-coding regions. *Gene* 71, 491–499.
- Nouzarède, M., 1977. Cytologie fonctionnelle et morphologie expérimentale de quelques protozoaires ciliés mésopsammiques géants de la famille des Geleidae (Kahl). *Bull. Stat. Biol. Archon, N.S.* 28 (Suppl., year 1976), Vol I, IX+315 pp. and Vol II, plates.
- Raikov, I.B., 1962. Les ciliés mésopsammiques du littoral de la Mer Blanche (U.R.S.S.) avec une description de quelques espèces nouvelles ou peu connues. *Cah. Biol. Mar.* 3, 325–361.
- Raikov, I.B., 1963. Ciliates of the mesopsammon of the Ussuri Gulf (Japan Sea). *Zool. Zh.* 42, 1753–1767 (in Russian).
- Raikov, I.B., 1994. The nuclear apparatus of some primitive ciliates, the karyorelictids: structure and divisional reorganization. *Boll. Zool.* 61, 19–28.
- Raikov, I.B., Kovaleva, V.G., 1968. Complements to the fauna of psammobiotic ciliates of the Japan Sea (Posjet Gulf). *Acta Protozool.* 6, 309–333.
- Sauerbrey, E., 1928. Beobachtungen über einige neue oder wenig bekannte marine Ciliaten. *Arch. Protistenk.* 62, 355–407.
- Shen, Z., Huang, J., Lin, X., Yi, Z., Li, J., Song, W., 2010. Morphological and molecular characterization of *Aspidisca hongkongensis* spec. nov. (Ciliophora, Euplotida) from the South China Sea. *Eur. J. Protistol.* 46, 204–211.
- Wilbert, N., 1975. Eine verbesserte Technik der Protargolimprägung für Ciliaten. *Mikrokosmos* 64, 171–179.
- Wright, J.M., 1982. Some sand-dwelling ciliates of South Wales. *Cah. Biol. Mar.* 23, 275–285.