Acta Protozool. (2005) 44: 19 - 32

ACTA
PROTOZOOLOGICA

Updating the Ciliate Genus *Chlamydodon* Ehrenberg, 1835, with Redescriptions of Three Species (Ciliophora: Cyrtophorida)

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Summary. The morphology and infraciliature of three marine cyrtophorid ciliates, *Chlamydodon obliquus* Kahl, 1931, *C. mnemosyne* Ehrenberg, 1835 and *C. triquetrus* (Müller, 1786), collected from coastal waters near Qingdao (Tsingtao), China, were investigated *in vivo* and using protargol impregnation. Based on the previous and current studies, the definition for the genus *Chlamydodon* is updated: chilodonellids with a cross-striated band around the periphery of the somatic field; rightmost kineties extending dorso-apically and bending to the left, making a conspicuous suture with left kineties; one preoral and two circumoral kineties obliquely arranged; equatorial fragment with loosely spaced kinetosomes; several to many terminal fragments. A revised diagnosis for the little known species *C. obliquus* is suggested: large-sized *Chlamydodon*, about 120-180 × 50-120 µm *in vivo*, body ellipsoid to triangular in outline; cross-striated band continuous, largest portion of which runs along cell margin, anterior region crossing onto dorsal surface; about 37 right, 4 postoral and 27 left kineties; 11-14 nematodesmal rods; about 7 terminal fragments on dorsal side; *ca*. 10 contractile vacuoles irregularly distributed; marine habitat. Improved diagnoses for *C. mnemosyne* and *C. triquetrus* are also supplied. Comparisons between congeners demonstrate that *C. exocellatus* Ozaki *et* Yagiu, 1941 and *C. kasymovi* Aliev, 1987 are synonyms of *C. obliquus* and *C. triquetrus*, respectively; *C. pedarius* Kaneda, 1953 and *C. apsheronica* Aliev, 1987, should be conspecific with the type species *C. mnemosyne*. Based on the data of morphology and infraciliature, an updated key to 5 *Chlamydodon* species is supplied.

Key words: *Chlamydodon*, Cyrtophorida, infraciliature, key to *Chlamydodon*, marine ciliate, morphology.

INTRODUCTION

Species of the cyrtophorid genus *Chlamydodon* are usually large and often occur in biofilm or in the periphyton of eutrophic biotopes (Sauerbrey 1928; Kahl 1931; Kiesselbach 1936; Borror 1963, 1972; Katter 1970; Hartwig 1973, 1980; Jones 1974; Hartwig and Parker 1977; Agamaliev 1978, 1983; Al-Rasheid 1996, 1997). One of the most recognizable features in this genus is the cross-striated band (CSB), which is located at the perimeter of the flattened cell and separates the dorsal and ventral sides of the cell. Using TEM and SEM methods, Kurth and Bardele (2001) gave a detailed observation of the type species *Chlamydodon mnemosyne*; they examined the CSB and other organelles such as the somatic cortex and oral structure. Morphogenetic processes in *C. mnemosyne* were also

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studied in detail by Fauré-Fremiet (1950) and Bardele and Kurth (2001).

Although the ultrastructural and morphogenetic characters of the genus *Chlamydodon* are well understood, there are many problems of species identification and separation in this genus. The confusion derived from that species have been distinguished by some live features (e.g. the body shape and size) and appearance of CSB, number of nematodesmal rods, and presence of a pigment spot (Kahl 1931, Ozaki and Yagiu 1941), many of which are likely variable or inconspicuous and thus cannot be used as diagnostic characters. Furthermore, only half of the 16 nominal species have been studied using silver impregnation methods (Fauré-Fremiet 1950; Kaneda 1960a; Borror 1963, 1972; Dragesco 1963, 1965, 1966; Katter 1970; Agamaliev 1978; Dragesco and Dragesco-Kernéis 1986; Aliev 1987; Alekperov and Asadullayeva 1997; Kurth and Bardele 2001). Several of these remain poorly described, which renders identification difficult.

Three morphotypes of *Chlamydodon* were isolated from coastal waters off Qingdao. Detailed investigations indicated that one is the species *Chlamydodon obliquus* and the other two are the well-known forms, *Chlamydodon mnemosyne* and *C. triquetrus.* Improved descriptions of these three species are here presented and their synonymy is discussed.

MATERIALS AND METHODS

Chlamydodon obliquus. One population was collected on 15 June 2002 from a rock pool of a tideland near Qingdao (Tsingtao, 36° 08' N; 120°43' E), China, which contained large amounts of seaweed. Temperature was 15°C, salinity was about 28‰, pH was about 7.3.

Chlamydodon mnemosyne. Three isolations were made (10 August 2002; 25 August 2002; 2 July 2003) from shrimp-farming ponds and from a rock pool near Qingdao. Temperature was 17-19°C, salinity was about 25-34‰, pH was about 7.3-7.6.

Chlamydodon triquetrus. Four isolations were made (12 March 2003; 10 April 2003; 10 May 2003; 17 May 2003) from an abalone-culture pond and from scallop-farming waters. Temperature was 13-16°C, salinity was about 26-31‰, pH was about 7.2-7.8.

Isolated specimens were maintained in Petri dishes with seawater (salinity *ca* 30‰) at 18°C. Some seaweeds and diatoms collected from original sites were supplied as food.

Living cells were observed with differential interference microscopy. The infraciliature was revealed by the protargol impregnation method according to Wilbert (1975). Living individuals were examined and measured at 1000× magnification; drawings of stained specimens were performed at 1250× with the aid of a camera lucida. Protargol impregnated voucher slides of three species are deposited in the Laboratory of Protozoology, OUC, China, with the following registration numbers: *Chlamydodon obliquus*, G02071501; *Chlamydodon mnemosyne*, G02081001; *Chlamydodon triquetrus*, G03041001. Terminology is mainly according to Corliss (1979).

RESULTS

To our knowledge, the definition of the genus *Chlamydodon* has not been revised following examination using modern methods. Therefore, we provide an improved diagnosis based on the data obtained.

Improved diagnosis for the genus *Chlamydodon*: Chilodonellids with a cross-striated band around the periphery of the somatic field; rightmost kineties extending apical-dorsally and bending to left, making a conspicuous suture with the left kineties; one preoral and two circumoral kineties obliquely arranged; equatorial fragment with loosely spaced kinetosomes; several to many terminal fragments.

Remarks: Considering the general infraciliature, *Chlamydodon* is similar to *Cyrtophoron* Deroux, 1974 in ciliary pattern (Deroux 1974, Aliev 1991). It differs from the latter, however, by possessing a CSB.

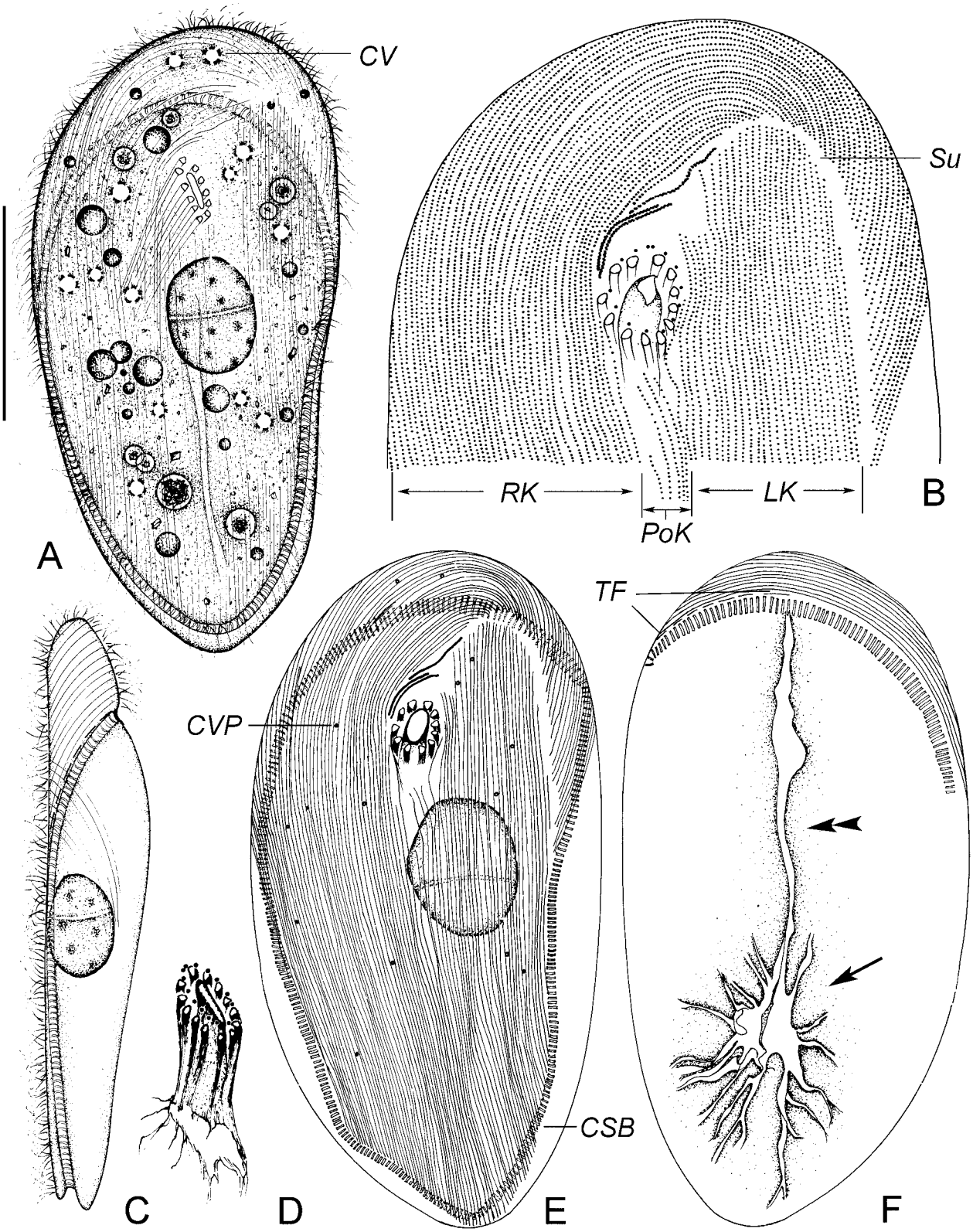
The CSB is a generic feature of another cyrtophorid taxon, *Coeloperix* Deroux in Gong and Song 2004, but *Chlamydodon* can be separated from *Coeloperix* by: (1) somatic kineties in three fields: right, postoral and left (*vs.* in two fields, preoral and postoral, in *Coeloperix*); (2) presence of anterior suture formed by right and left somatic kineties (*vs.* absent in *Coeloperix*); and (3) during morphogenesis, the oral kineties in the opisthe derive from postoral somatic kineties (*vs.* from leftmost ones in *Coeloperix*) (Deroux 1976, Gong and Song 2004).

Chlamydodon obliquus Kahl, 1931 (Figs 1, 2; Tables 1, 2)

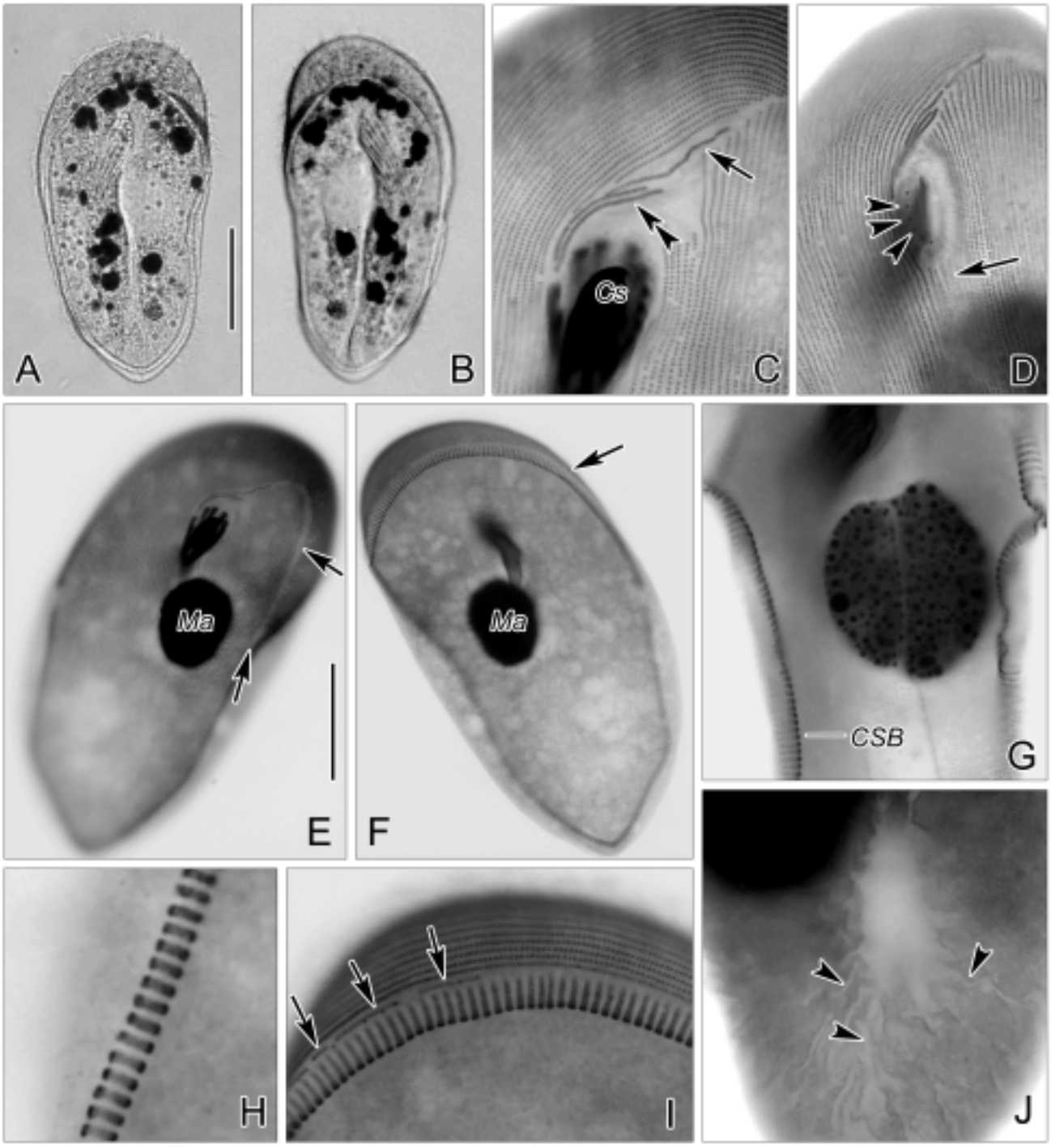
Syn**:** *Chlamydodon exocellatus* Ozaki *et* Yagiu, 1941

Improved diagnosis: About 120-180 × 50-120 μm *in vivo*, cell ellipsoid to triangular in outline; cross-striated band (CSB) continuous, anterior portion crossing to the dorsal surface, ~ 37 right, 4 postoral, and 27 left kineties; 11-14 nematodesmal rods; ~ 7 terminal fragments on dorsal side; ~5-15 irregularly distributed contractile vacuoles; macronucleus ~ 20-40 μm in diameter; marine habitat.

Description of Qingdao population: Size 160 × 90 μm *in vivo*, as calculated from some measurements of live specimens and values shown in Table 1, assuming a



Figs 1A-F. Morphology and infraciliature of *Chlamydodon obliquus* from life (A, C) and after protargol impregnation (B, D-F). **A** - ventral view of a typical individual; **B** - ventral view showing detailed infraciliature of anterior part; **C** - lateral view; **D** - cyrtos; **E, F** - ventral (E) and dorsal (F) views of infraciliature, arrow indicates the dorsal depression and double-arrowheads mark the long canal-like depression extending anteriorly. CSB - cross-striated band; CV - contractile vacuoles; CVP - contractile vacuole pores; LK - left kineties; PoK - postoral kineties; RK - right kineties; Su - suture; TF - terminal fragments. Scale bar 50 µm.



Figs 2A-J. Photomicrographs of *Chlamydodon obliquus* from life (A, B) and after protargol impregnation (C-J). **A, B** - ventral (A) and dorsal (B) views of a typical individual; **C** - detailed infraciliature of oral field, arrow indicates preoral kinety and double-arrowheads indicate circumoral kineties; **D** - focusing on basal body-like granules (arrowheads) and postoral kineties (arrow); **E** - ventral view of infraciliature, showing the anterior suture (arrows); **F** - dorsal view, focusing on the part of cross-striated band (arrow) that extends onto dorsal surface; **G** - macronucleus; **H** - a close-up of a section of cross-striated band; **I** - dorsal view, showing that terminal fragments (arrows) are variable in length; **J** - dorsal view of posterior portion of cell, to show the canal-like depressions. Cs - cytostome; CSB - cross-striated band; Ma - macronucleus. Scale bars 50 μm.

Table 1. Morphometric characteristics of *Chlamydodon mnemosyne* (first line), *C. triquetrus* (second line) and *C. obliquus* (third line). Data from protargol impregnated specimens. All measurements in µm. Abbreviations: Max - maximum, Mean - arithmetic mean, Min - minimum, n - number of individuals examined, SD - standard deviation.

Characters	Min	Max	Mean	SD	n
Body length	54.0	78.0	65.4	6.7	17
	69.0	96.0	84.6	8.5	19
	120.0	164.0	139.6	15.2	11
Body width	31.0	50.0	43.1	5.6	17
	26.0	45.0	36.7	3.9	19
	50.0	84.0	60.2	9.6	11
Total number of somatic kineties	29.0	35.0	31.4	1.4	17
	36.0	48.0	40.4	3.0	19
	66.0	72.0	69.2	2.0	11
Number of right kineties	14.0	18.0	15.3	1.1	17
	16.0	24.0	19.9	2.3	19
	34.0	40.0	37.1	1.7	11
Number of left kineties	11.0	13.0	12.1	0.6	17
	15.0	21.0	16.7	1.8	19
	26.0	29.0	27.7	1.2	11
Number of postoral kineties	4.0	4.0	4.0	0.0	17
	4.0	4.0	4.0	0.0	19
	3.0	5.0	4.0	0.8	11
Number of terminal fragments	2.0	4.0	2.5	1.0	16
	4.0	8.0	5.9	1.0	18
	6.0	10.0	7.0	1.3	11
Number of nematodesmal rods	8.0	11.0	9.4	0.7	16
	9.0	14.0	11.9	1.2	19
	11.0	14.0	12.8	1.0	9
Macronucleus length	22.0	30.0	25.2	2.2	17
	17.0	30.0	23.7	3.3	19
	24.0	36.0	29.5	4.3	11
Macronucleus width	10.0	22.0	13.8	3.5	17
	9.0	18.0	14.1	2.4	19
	24.0	36.0	29.5	4.3	11
Number of C-shaped structures in the whole CSB	80.0	110.0	104.0	-	4
	88.0	151.0	122.6	19.5	19
	255.0	298.0	275.2	17.1	9
Contractile vacuole pores, number	4.0	12.0	10.0	-	4
	3.0	15.0	7.2	3.5	18
	6.0	15.0	12.0	-	3

shrinkage of about 12% due to the preparation procedure. Ventral side flattened with a conspicuous canal-like depression, 3-4 µm in width, extending from postoral area to subcaudal region of cell (Figs 1A, 2A); dorsal side evenly humped, dorso-ventrally flattened, width: thickness ratio ~ 2:1 (Fig. 1C). From ventral view, cell outline reniform; anterior end evenly rounded and projects slightly to left (Figs 1A, 2A). Right ciliary rows cross to anterior region of dorsal surface. Cross-striated band 3-4 µm wide, continuous, with anterior portion lying across the dorsal surface and posterior portion running along cell margin (Figs 1A, C, F; 2B, F, I). Endoplasm with several to many granules (2-3 µm across) and 1-4 large food vacuoles (~ 10 µm in diameter); often containing ingested particles of seaweed. Cytostome oval, inconspicuous *in vivo*, positioned half way between mid-body and anterior end of cell. Cyrtos extends posteriorly and rightward. 5-15 contractile vacuoles, each 2-4 µm in diameter, irregularly distributed beneath ventral cortex (Fig. 1A); contractile vacuole pores recognizable after protargol impregnation (Fig. 1E). Cilia about 8 µm long *in vivo*. Movement by gliding on substratum or swimming. Feeds mainly on seaweed debris and microalgae.

Somatic kineties densely arranged, ~ 66-72. When viewed dorsoventrally, somatic kineties mostly confined to region bounded by cross-striated band. Somatic kineties are grouped: 3-5 postoral kineties (PoK) that terminate anteriorly below cytostome; 34-40 right kineties (RK)

Table 2. Morphometrical comparison between *Chlamydodon obliquus* and related species.

Character	*C. obliquus*	*C. minutus*	*C. roseus*	*C. exocellatus**
Body length in μm	120-180	50-60	80-100	215-230
Body width in μm	50-117	-	-	100-132
Number of somatic kineties (total)	66-72	30-32	54-58	-
Number of right kineties	34-40	14-15	c. 30	-
Number of postoral kineties	4 (3-5)	4	c. 6	-
Number of left kineties	26-29	12-13	c. 21	-
Number of nematodesmal rods	11-16	16-18	8-9	15-16
Pigment spot**	absent	present	present	absent
Number of contractile vacuoles	5-15	3-4	5-6	5
Data source	Original	Dragesco (1965)	Dragesco (1966)	Ozaki and Yagiu (1941)

- data not available; * misidentified; ** pigment spot: a conglomeration of tiny endoplasmic granules, usually positioned at the anterior-left of cell.

extend anteriorly beyond the level of cytostome and bend to left; 26-29 left kineties (LK) extend subapically and form a hook-like suture (Su) with the right kineties (Figs 1B, E; 2D, E; Table 1). Usually the outermost 10-18 rows of the right kineties extend onto dorsal surface; the innermost 2 are interrupted by oral kineties. ~ 7 terminal fragments, each composed of 7-16 basal bodies, arranged in a row adjacent to CBS (Figs 1F, 2I); equatorial fragment difficult to discern. CSB comprising ~ 280 C-shaped structures (Figs 1E, F; 2F arrows). Heteromerous macronucleus rounded to oval, ~ 30 μm in diameter/length after protargol, positioned in body center. Micronucleus not detected. Some canal-like depressions with one extending anteriorly always present in dorsal side of cell after protargol impregnation (Figs 1F, 2J).

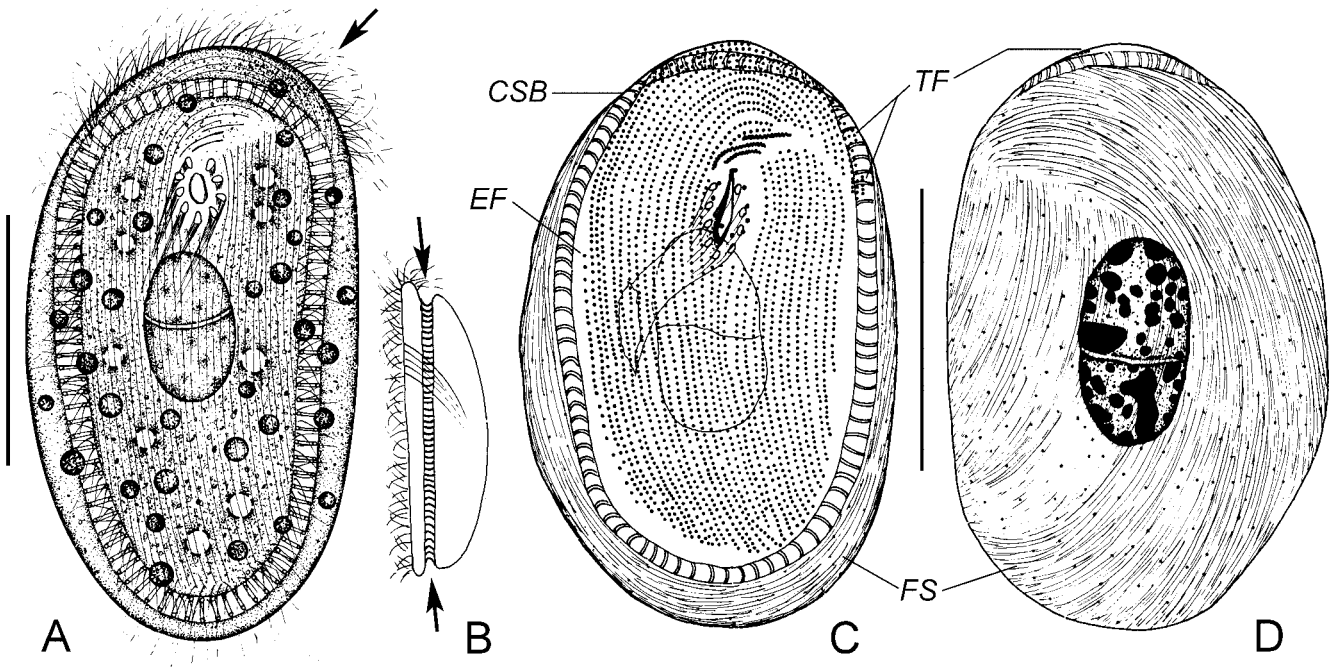
Three oral kineties typical of genus: the anterior preoral kinety overlap the two circumoral kineties, which are parallel and closely arranged; all three kineties obliquely oriented (Figs 1B, E; 2C). Cyrtos (Cy) relatively short (~ 30 μm in length), composed of ~ 13 nematodesmal rods; one circle of kinetosome-like dots always observed around cyrtos in protargol impregnated specimens (Figs 1B, D, 2D).

Remarks: *Chlamydodon obliquus* was originally described by Kahl (1931) with notes of characters observed *in vivo*. Subsequently, Chatton (1936) illustrated the lateral aspect of this species, showing the oblique appearance of its CBS. No redescriptions were published until Borror (1963) described an American population using the Chatton-Lwoff method (Figs 7H, I). Borror, however, did not report on the detailed structure of the somatic and oral kineties, the number and positions of the contractile vacuoles. Despite these, according to the original and the subsequent investigations, this species can be recognized by the combination of the following characters: (1) large size (130-180 μm in length); (2) continuous CSB; (3) ~10 contractile vacuoles; and (4) ~70 ciliary rows (Kahl 1931, Chatton 1936, Borror 1963).

Considering the size, general live appearance, number of kineties, continuous CBS positioned obliquely relative to the body axis when viewed from the side (Kahl 1931, Borror 1963), the Qingdao population resembles previous descriptions reasonably well except for having fewer nematodesmal rods (11-14 *vs.* 15-16) (Borror 1963). We suppose this difference is minor and hence establishment of a new species is not justified.

About 16 nominal species have been assigned to the genus *Chlamydodon*. With reference to the general morphology, the features of CSB, and the marine habitat, at least two species (*C. minutus* Dragesco, 1965 and *C. roseus* Dragesco, 1966) should be compared with *C. obliquus*: *C. minutus* can be distinguished from *C. obliquus* by its smaller size (50-60 *vs.* 120-180 μm in length), fewer somatic ciliary rows (30-32 *vs.* 66-72), and fewer contractile vacuoles (3-4 *vs.* 5-15) (Figs 7A, B; Table 2). Likewise, *C. roseus* differs from *C. obliquus* in its smaller body size (80-100 *vs.* 120-180 μm in length), presence of pigment spots in the anterior-left and posterior regions of the cell (*vs.* none in *C. obliquus*), and in having fewer somatic kineties (54-58 *vs.* 66-72) and nematodesmal rods (8-9 *vs.* 11-14) (Figs 7C, D; Table 2).

Alekperov and Asadullayeva (1997) misidentified a morphotype of *Chlamydodon obliquus* from the Caspian



Figs 3A-D. Morphology and infraciliature of *Chlamydodon mnemosyne* from life (A, B) and after protargol impregnation (C, D). **A** - ventral view of a typical individual, arrow indicates pigment spot located at the anterior-left of cell; **B** - lateral view showing the cross-striated band (arrows) around the perimeter of cell; **C, D** - ventral (C) and dorsal (D) views of infraciliature. CSB - cross-striated band; EF - equatorial fragment; FS - fine stripes; TF - terminal fragments. Scale bars 40 μm.

Sea (Russia) with only 38 somatic kineties (see Fig. 7E). The Russia form most resembles *C. rectus* Ozaki *et* Yagiu, 1941 in terms of numbers of kineties (*ca* 38 *vs. ca* 30) and nematodesmal rods (19 *vs*. 20-22), although it is somehow larger than the Japanese population of *C. rectus* (*vs*. 70-84 × 42-49 μm). Possibly, the Russia form represents a large-sized population of *C. rectus*.

Another nominal species, *Chlamydodon exocellatus* Ozaki *et* Yagiu, 1941, the infraciliature of which remains unknown, was isolated form Japanese coastal waters (Ozaki and Yagiu 1941). Besides the similarities in CSB, it also resembles *C. obliquus* in body shape, absence of pigment spots and numbers of contractile vacuoles and nematodesmal rods (Fig. 7G; Table 2). The only difference is its larger size (215-230 *vs.* 120-180 μm) which, however, could be variable among populations in different food conditions. Hence, we regard *C. exocellatus* as a junior synonym of *C. obliquus*.

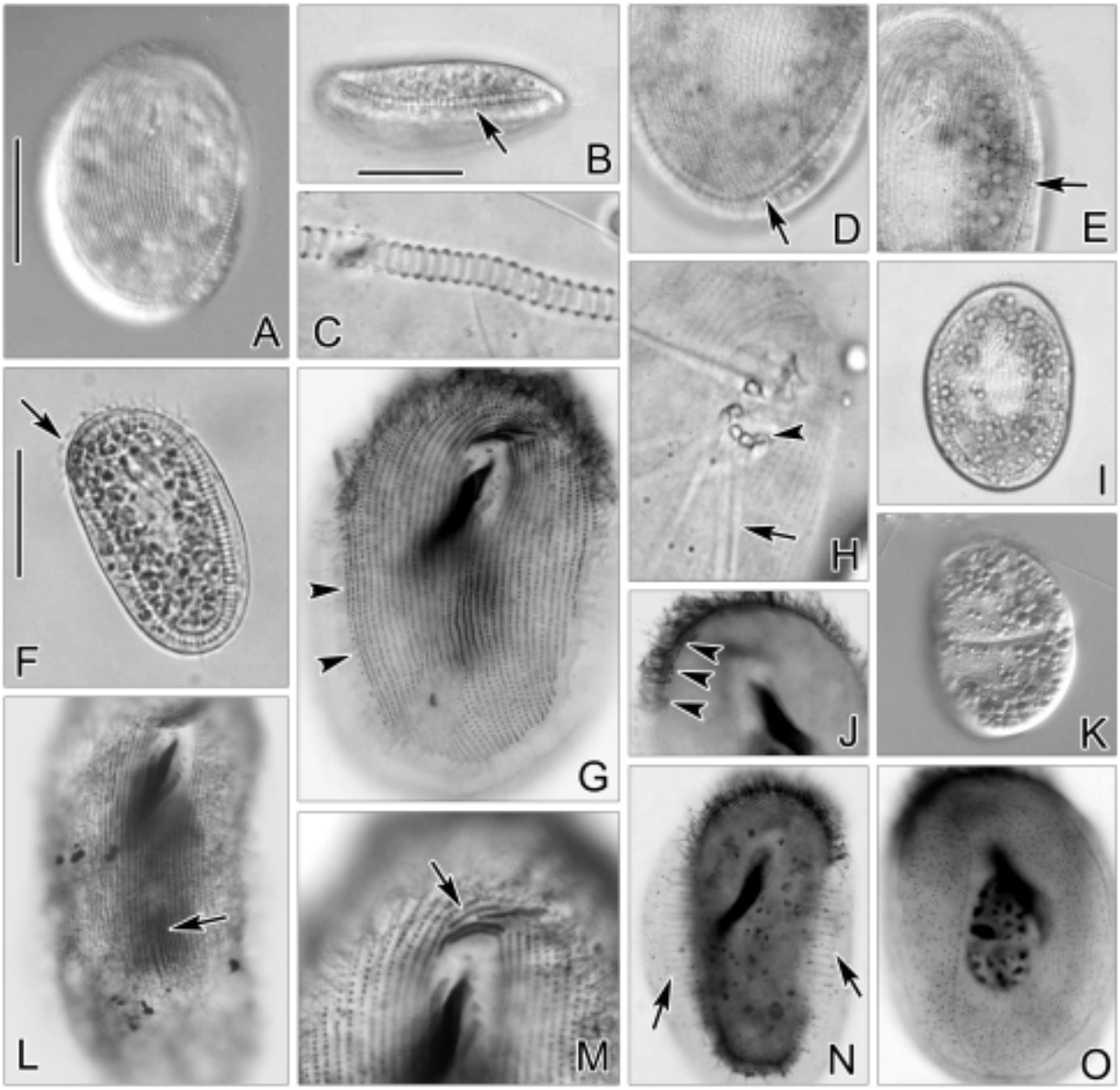
Chlamydodon mnemosyne Ehrenberg, 1835 (Figs 3, 4; Tables 1, 3)

Syn: *Chlamydodon pedarius* Kaneda, 1953
Chlamydodon apsheronica Aliev, 1987

Based on previous and the present studies, an improved diagnosis is suggested:

Improved diagnosis: Size 30-150 × 15-70 μm *in vivo*, body shape oval in outline; cross-striated band continuous around cell margin; 9-20 left, 11-18 right, and 3-4 postoral kineties; ~ 3 terminal fragments; 8-15 nematodesmal rods; macronucleus about 25 × 14 μm in size; marine habitat.

Description: Size usually 70 × 40 μm *in vivo*, as calculated from some measurements of live specimens and values shown in Table 1, assuming a shrinkage of about 7% due to the preparation procedure. From ventral view, cell oval in outline (Figs 3A; 4A, I). Ventral side flattened and dorsal side humped, dorsoventrally flattened, width: thickness ratio ~ 2:1 (Figs 3B, 4B). Both ends evenly rounded; left margin straight, right margin convex. Cross-striated band 2-3 μm wide, completely encircles cell perimeter (Figs 3A, B; 4B-F); a loop of the cross-striated band is positioned equatorially in the early stage of cell division (Fig. 4K). Cytoplasm colorless, with irregularly distributed food granules (3-4 μm across) and yellowish particles (~ 0.2 μm in diameter) which are densely located in the extreme anterior-left of cell to form the pigment spot; note that pigment spot inconspicuous and easily overlooked. Cytostome oval, ventrally located in anterior 1/5 of cell. Nematodesmal rods straight, each about 24 μm long and tipped with one tooth



Figs 4A-O. Photomicrographs of *Chlamydodon mnemosyne* from life (A-F, H, I, K) and after protargol impregnation (G, J, L-O). **A** - ventral view of a typical individual; **B** - lateral view, arrow indicates cross-striated band; **C** - part of cross-striated band at magnification; **D, E** - ventral views, focusing on sections of cross-striated band (arrows) in posterior (D) and anterior-left (E) portions of cell; **F** - dorsal view, arrow marks pigment spot; **G** - ventral view of infraciliature; arrowheads indicate the equatorial fragment; **H** - deformed cyrtos in a squeezed individual, showing the tooth (arrowhead) and rod (arrow); **I** - ventral view of a individual containing many food vacuoles; **J** - to note the terminal fragments (arrowheads) positioned at the anterior-left margin of dorsal surface; **K** - dorsal view of a individual in binary fission; **L** - to note the multiplying of basal bodies; **M** - anterior portion of infraciliature on ventral side, showing that the innermost right kinety (arrow) is interrupted by oral kineties; **N** - to show cross-striated band (arrows) encircling ciliated ventral surface; **O** - dorsal side showing fine stripes. Scale bars 40 µm.

(Fig. 2H). ~ 5-12 contractile vacuoles, irregularly distributed underneath ventral cortex (Fig. 3A). Cilia about 8 µm long *in vivo*. Feed on cyanobacteria and particles of seaweed.

Infraciliature as shown in Figs 3C, D, 4G, L-O. A total of 29-35 somatic kineties, 14-18 rows on right, 11-13 rows on left, and 4 postoral rows. In common with its congeners, three postoral kineties are involved in oral

Table 3. Comparison among populations of *Chlamydodon mnemosyne*, for which infraciliature is described.

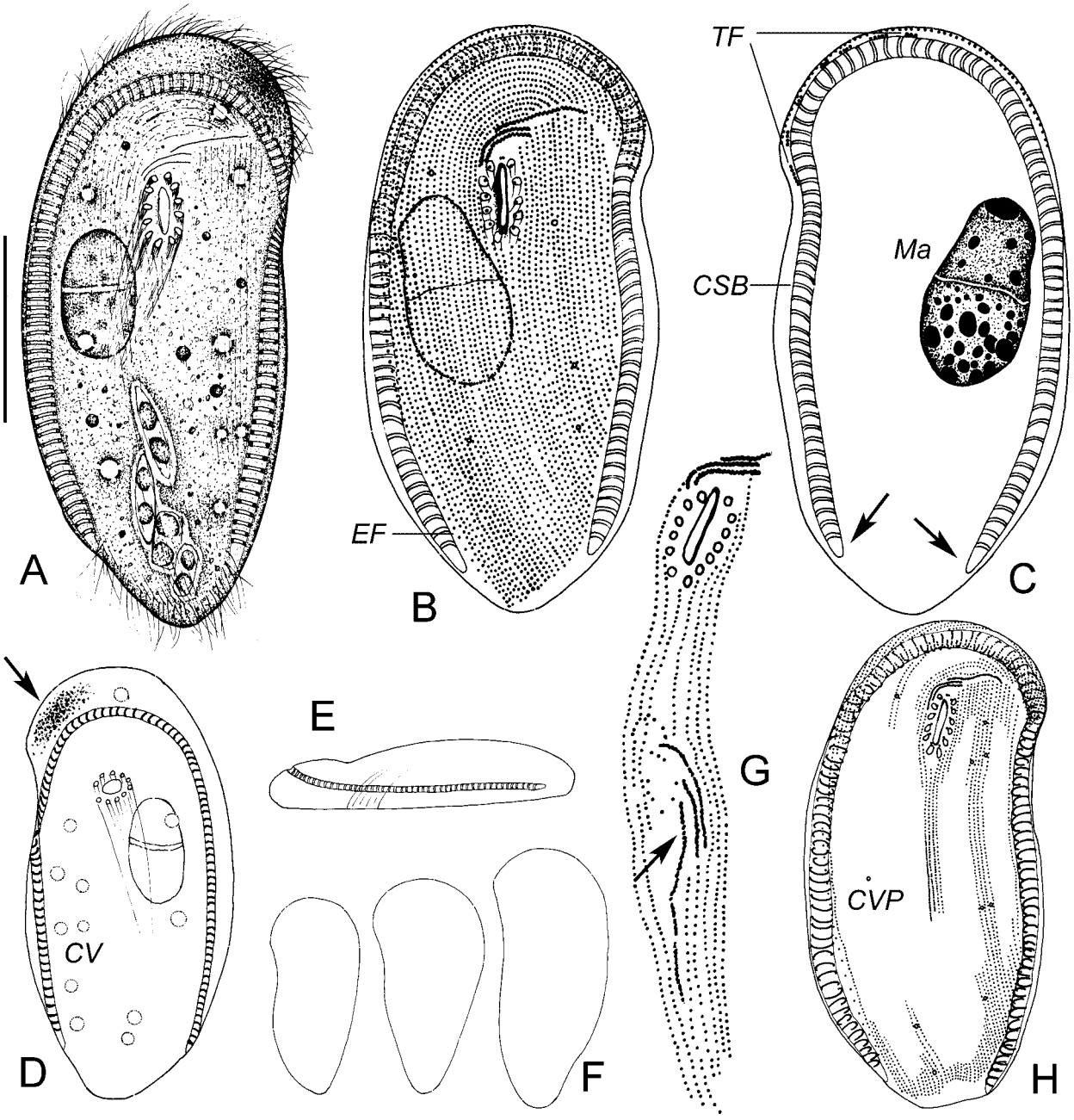
Character	*C. mnemosyne* Qingdao pop.	*C. mnemosyne* German pop.	*C. mnemosyne* African pop.	*C. mnemosyne* French pop.	*C. mnemosyne* Russian pop.	*C. pedarius** Japanese pop.	*C. apsheronica** Russian pop.
Body length in µm	50-100	40-100	30-150	50-110	60-110	110-138	60-70
Body width in µm	30-50	23-65	-	-	-	50-70	45-55
Number of right kineties	14-18	12-15	11-18	11-16	16	16-18	17
Number of postoral kineties	4	4	4	4	-	4	3
Number of left kineties	11-13	9-12	11-20	11-14	14	16-18	13
Number of somatic kineties (total)	29-35	25-31	26-40	26-34	36	35-40	30-35
Number of nematodesmal rods	8-11	9-13	10	-	10	11-13	*ca* 13
Number of contractile vacuoles	5-12	5-11	*ca* 5	*ca* 15	-	5-12	20-26
Data source	Original	Kurth and Bardele (2001); Bardele and Kurth (2001)	Dragesco and Dragesco-Kernéis (1986)	Fauré-Fremiet (1950)	Alekperov and Asadullayeva (1997)	Kaneda (1953, 1960a, b)	Aliev (1987)

* misidentified; - data not available.

Table 4. Comparison among populations of *Chlamydodon triquetrus.*

Character	*C. triquetrus* Qingdao pop.	*C. triquetrus* Brazilian pop.	*C. triquetrus* Russian pop.	*C. triquetrus* French pop.	*C. triquetrus* African pop.	*C. kasymovi* * Russian pop.
Body length in µm	60-100	70-100	120-140	50-90	50-140	220-260
Body width in µm	26-45	28-40	45-50	-	-	85-95
Number of somatic kineties (total)	36-48	40	48-50	38-40	30-50	40-45
Number of right kineties	16-24	-	26-28	20-21	-	c. 20
Number of postoral kineties	4	-	5	5	5	4
Number of left kineties	15-21	-	16-18	14-19	-	*ca* 19
Number of nematodesmal rods	9-14	15	13-15	14-16	*ca* 14	13-15
Data source	Original	Katter (1970)	Agamaliev (1978)	Dragesco (1963)	Dragesco and Dragesco-Kernéis (1986)	Aliev (1987)

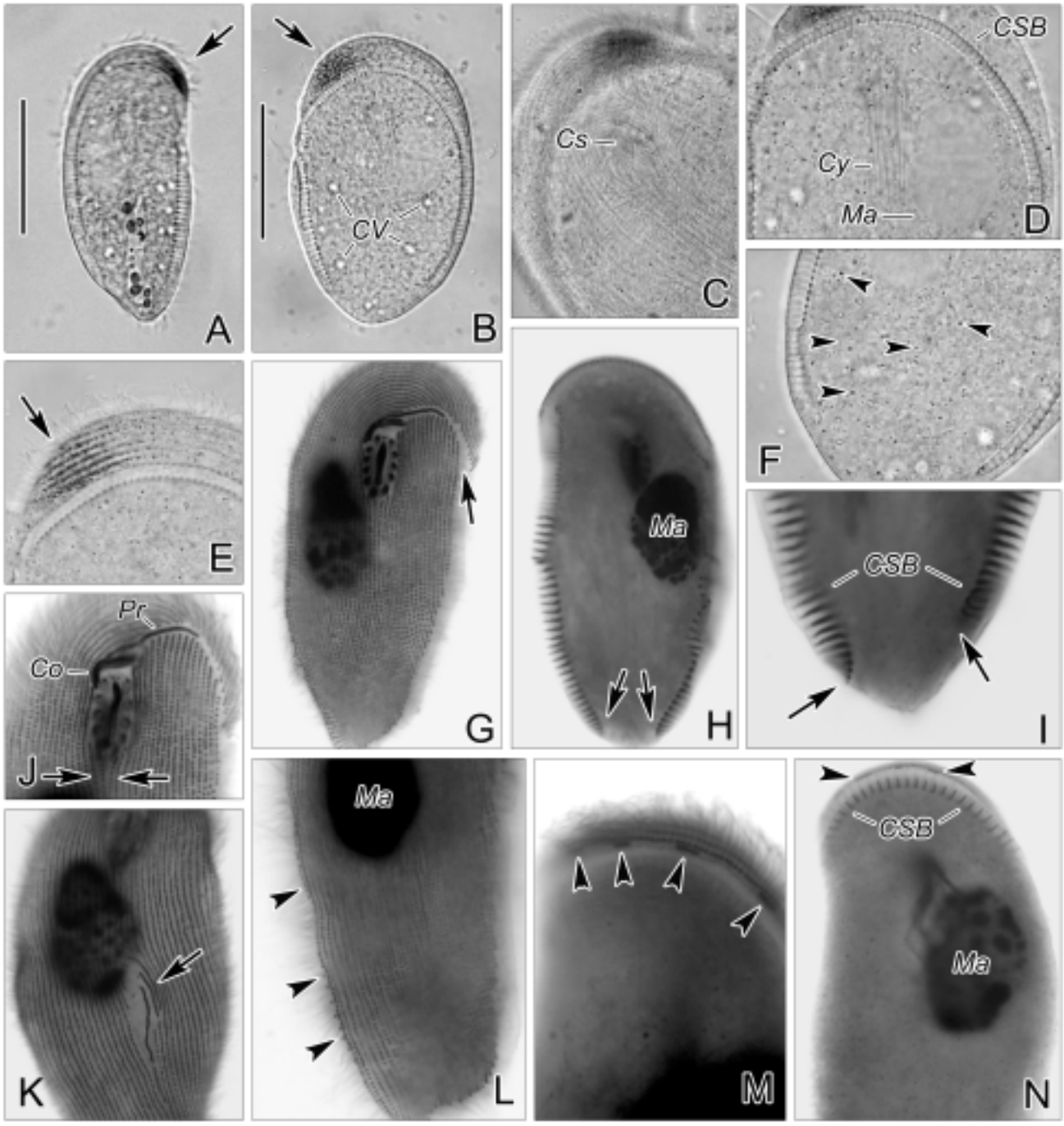
* misidentified; - data not available.



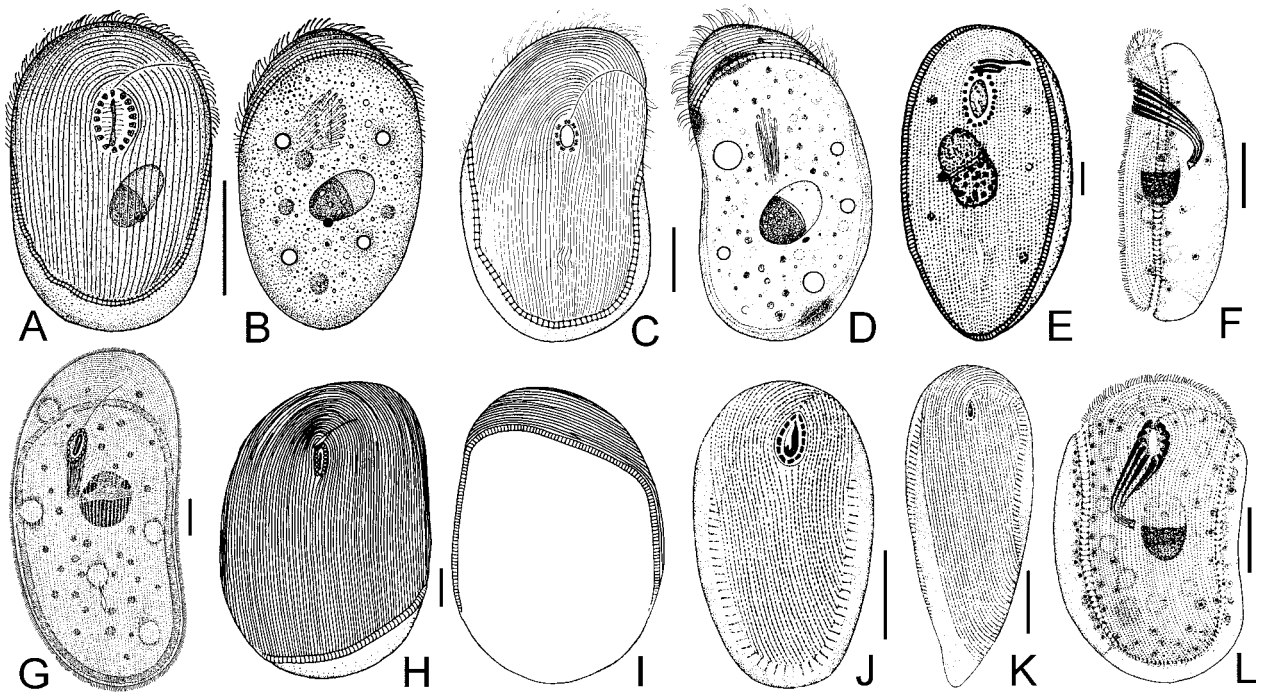
Figs 5A-H. Morphology and infraciliature of *Chlamydodon triquetrus* from life (A, D-F) and after protargol impregnation (B, C, G, H). **A** - ventral view of a typical individual; **B, C, H** - ventral (B, H) and dorsal (C) views of infraciliature, note that the cross-striated band is posteriorly discontinued (arrows); **D** - dorsal view showing pigment spot (arrow); **E** - lateral view; **F** - to show body shapes of different specimens; **G** - showing the multiplying of basal bodies (arrow) in the mid-body field of an individual at an early stage of morphogenesis. CSB - cross-striated band; CVP - contractile vacuole pores; EF - equatorial fragment; Ma - macronucleus; TF - terminal fragments. Scale bars 40 μm.

formation during morphogenesis (Fig. 4L). Anterior portion of the innermost row of right kineties interrupted by oral kineties (Fig. 4M). Equatorial fragment (EF, Fig. 3C; arrowheads in Fig. 4G) composed of about 25 loosely spaced basal bodies. Usually 3 terminal fragments (TF, Figs 3D, 4J), each comprising ~ 3 densely spaced basal bodies. Macronucleus ellipsoidal, heteromerous, ~ 25 × 14 μm after protargol impregnation. Micronucleus not detected.

Three oral kineties almost equal in length: two circumoral kineties (outer and inner) anterior of cytostome and one preoral kinety left of these. Cyrtos obliquely



Figs 6A-N. Photomicrographs of *Chlamydodon triquetrus* from life (A-F) and after protargol impregnation (G-N). **A** - ventral view of a slender specimens, arrows indicate pigment spot; **B** - dorsal view of a well-fed individual, arrow indicates pigment spot; **C** - anterior portion of ventral surface; **D** - focusing on anterior portion of dorsal surface; **E** - pigment spot at high magnification; **F** - showing numerous yellowish granules in endoplasm (arrowheads); **G** - ventral view of infraciliature; arrow indicates the anterior suture; **H, I** - dorsal view, arrows marks two ends of interrupted cross-striated band; **J** - oral field, arrows indicate postoral kineties; **K** - ventral view of a individual in morphogenesis, arrow marks the area where basal bodies of three kineties multiply; **L** - posterior portion of cell, arrowheads indicate sparsely-spaced basal bodies in equatorial fragment; **M, N** - dorsal view of anterior portions, arrowheads marks terminal fragments positioned near the margin of the ciliated field. Co - circumoral kineties; Cs - cytostome; CSB - cross-striated band; CV - contractile vacuole; Cy - cyrtos; Ma - macronucleus; Pr - preoral kinety. Scale bars 40 µm.



Figs 7A-L. Ventral (A, C, E, G, H, J-L), dorsal (B, D, I) and side (F) views of *Chlamydodon* species. **A, B** - *C. minutus* (from Dragesco 1965); **C**, **D** - *C. roseus* (from Dragesco 1966); **E** - *C. obliquus* sensu Alekperov and Asadullayeva, 1997; **F, L** - *C. pedarius* sensu Kaneda, 1953; **G** - *C. exocellatus* sensu Ozaki and Yagiu, 1941; **H, I** - *C. obliquus* (from Borror 1963); **J** - *C. apsheronica* sensu Aliev, 1987; **K** - *C. kasymovi* (from Aliev 1987). Scale bars 20 μm.

oriented, composed of 8-11 nematodesmal rods and associated fibrous membranes, extends posteriorly to about 40% of cell length (Fig. 3C).

Remarks: The type species *Chlamydodon mnemosyne* was originally described by Ehrenberg (1835) from the German Baltic Sea. The first description of its infraciliature was by Fauré-Fremiet (1950). Subsequent redescriptions based on live and silver impregnated cells indicate different populations possess overlapped/variable characters: cell size, numbers of somatic kineties, contractile vacuoles, and nematodesmal rods (Table 3, Dragesco 1960, Dragesco and Dragesco-Kernéis 1986, Alekperov and Asadullayeva 1997, Kurth and Bardele 2001). The Qingdao populations is most similar to those described by Fauré-Fremiet (1950) and Kurth and Bardele (2001) in terms of morphology and ciliature patterns (Table 3).

Chlamydodon pedarius Kaneda, 1953 isolated from Japanese coastal waters was later redescribed using living observations and silver impregnation (Kaneda 1953, 1960a, b). However, *C. pedarius* does not differ from *C. mnemosyne* in any of the main diagnostic features: cell size, configuration of CSB, numbers of somatic kineties, nematodesmal rods, and contractile vacuoles (Figs 7F, L; Table 3). Therefore, *C. pedarius* we regarded it as a junior synonym of *C. mnemosyne*.

Another nominal species *Chlamydodon apsheronica* Aliev, 1987, isolated from hypersaline water reservoirs, Russia (Aliev 1987), is similar to *C. mnemosyne* in cell size, configuration of the CSB, numbers of somatic kineties, and nematodesmal rods (Fig. 7J; Table 3). Considering that some ciliates may exhibit variable living features in waters with different salinities (Esteban and Finlay 2003), we suppose that the only difference of the number of contractile vacuoles (20-26 *vs.* 5-15) is not sufficient to circumscribe a new species, but rather represents a population variation. *Chlamydodon apsheronica* is therefore conspecific with, and a junior synonym of, *C. mnemosyne.*

Chlamydodon triquetrus (Müller, 1786) (Figs 5, 6; Tables 1, 4)

Syn: *Chlamydodon kasymovi* Aliev, 1987

Since there is no definition following examination using modern methods for *Chlamydodon triquetrus*,

we provide an improved diagnosis based on the data obtained.

Improved diagnosis: Yellowish *Chlamydodon*, size 50-140 × 25-60 μm *in vivo*, body elongate ellipsoid to triangle in outline; CSB posteriorly interrupted; one yellow pigment spot in anterior-left of cell; 14-21 left, 16-28 right, and 4-5 postoral kineties; ~ 6 terminal fragments; 9-16 nematodesmal rods; with 5-12 contractile vacuoles; macronucleus ~ 24 × 14 μm; marine habitat.

Description: Size 100 × 50 μm in vivo, as calculated from some measurements of live specimens and values shown in Table 1, assuming a shrinkage of about 15% due to the preparation procedure. Cell shape variable, usually ellipsoid to triangular in outline, with anterior protrusion to left. Anterior end evenly rounded, posteriorly tapering; left margin somewhat sigmoid, right margin convex (Figs 5A, D, F; 6A). Ventral side flattened, dorsal side humped, dorso-ventrally flattened, width: thickness ratio ~ 2:1 (Fig. 5E). Cross-striated band (3 μm wide) generally inverted U-shaped, i.e. encircles the cell perimeter but with a conspicuous gap in the subcaudal region (Figs 5A-D, H; 6A, B, D, F, H, I). Endoplasm colourless, with tiny yellow granules (0.2-0.3 μm across) that renders cell yellowish at lower magnifications (40×); granules irregularly distributed in most parts of the cell (Fig. 6F) except in anterior left region where they are relatively densely spaced forming an amorphous "pigment spot" (area ~ 14 × 7 μm; n = 30; Figs 5A, D, 6E); food vacuoles 4-10 μm across, usually filled with ingested diatoms. Cytostome oval, located at anterior 1/3 of ventral surface. Cyrtos composed of 9-14 nematodesmal rods. ~ 5-12 contractile vacuoles (CV), irregularly distributed underneath ventral cortex (Figs 5A, D; 6B); 3-15 contractile vacuole pores (CVP) recognizable after protargol impregnation (Figs 5B, H). Macronucleus oval, positioned slightly right of body centre. Cilia about 5 μm long *in vivo*. Gliding on substratum or swimming; when swimming, rotates around body axis. Feeds on seaweed debris and diatoms.

Infraciliature as shown in Figs 5B, C, 6J-N. In total 30-50 somatic kineties with 16-28, 14-21 and 4 rows in right, left and postoral fields, respectively (Table 1). Right kinety not interrupted by oral kineties. Three of the postoral kineties are involved in the formation of the oral structure during morphogenesis (Figs 5G, 6K). Left kineties progressively reduced at posterior ends. Equatorial fragment long (EF in Fig. 5B; arrowheads in Fig. 6L) composed of about 40 loosely spaced basal bodies. Usually 6 terminal fragments (TF) almost equal in length, each comprising ~ 5 basal bodies (Figs 5C; 6M, N). Macronucleus ellipsoidal, heteromerous, size ~24 × 14 μm after protargol impregnation. Micronucleus not detected.

Oral structure typical of genus: circumoral kineties (Co) almost equal in length, preoral kinety (Pr) relatively longer, extending leftwards to about mid-point of suture line. A circle of non-ciliated kinetosome always present with nematodesmal rods (Fig. 6J).

Remarks: The Qingdao population corresponds well with previous descriptions of *Chlamydodon triquetrus* in terms of living morphology (body size and shape, presence of yellowish pigment spot, posterior interruption in cross-striated band, number of contractile vacuoles, etc.) and features revealed by silver impregnation (number and pattern of somatic kineties, number of nematodesmal rods, etc.), thus the identification is undoubted (Dragesco 1963, Katter 1970, Hartwig 1973, Agamaliev 1978, Dragesco and Dragesco-Kerneis 1986; Table 4).

Chlamydodon kasymovi Aliev, 1987 is similar to *C. triquetrus* in every respect except it has a larger body size (220-260 *vs.* 50-140 μm; Aliev 1987) (Fig. 7K; Table 4). Considering that cell size may considerably vary between populations of *Chlamydodon* (e.g. *C. mnemosyne* and *C. obliquus*, this paper), we provisionally regard *C. kasymovi* as an extreme form of *C. triquetrus*.

Based on both morphology and infraciliature, a key to the species that have been defined by silver impregnation is supplied:

Key to *Chlamydodon* species whose infraciliature is known

1 CSB without interruption.....2
1' CSB posteriorly interrupted.....*C. triquetrus*
2 Sixteen to 18 nematodesmal rods.....*C. minutus*
2' Less than 16 nematodesmal rods.....3
3 More than 50 somatic kineties.....4
3' Less than 50 somatic kineties.....*C. mnemosyne*
4 More than 60 somatic kineties.....*C. obliquus*
4' Less than 60 somatic kineties.....*C. roseus*

Acknowledgements. This work was supported by "the National Science Foundation of China" (Project No. 40376045) and a Royal Society Joint Project Programme (No. Q822).

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Received on 28 April, 2004; revised version on 16th August, 2004; accepted on 10th September, 2004