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淡水纤毛虫一新种沈氏齿蓬虫形态学研究及齿蓬虫属的回顾

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摘要: 管口亚纲(Cyrtophoria)纤毛虫既是水生生物膜和底栖微型生物群落的优势类群,也是水产动物常见的病原生物,其多样性长期被低估。本研究利用活体显微观察和蛋白银染色法对采自上海一淡水人工湖的沈氏齿蓬虫(*Odontochlamys shenae* sp. nov.)新种的活体特征及纤毛图式进行了详尽形态学研究。新种的主要特征包括:活体大小为60~80 μm \times 30~33 μm ,口区具12~15根咽杆,6~7列右侧体纤毛列,6~8列左侧体纤毛列,背端动基列片段由8~20个毛基粒组成,伸缩泡3个,大核1枚,淡水生。此外,对齿蓬虫属(*Odontochlamys*)进行了回顾,发现该属地理分布特征很可能呈中度限制性分布,并提供了该属的物种检索表。

关键词: 管口亚纲; 分类学; 原生动物; 纤毛图式

中图分类号: Q 959.11; S 941.42 **文献标志码:** A

管口亚纲(Cyrtophoria)纤毛虫是各类水体周丛和底栖微型生物群落的主要组分^[1]。该类群对细菌和藻类具有较强摄食能力,在生态系统的物质循环和能量流动中发挥重要作用^[2-4]。同时,因其包含鲤斜管虫(*Chilodonella piscicola*)、十六线斜管虫(*Chilodonella hexasticha*)等常见水产动物的寄生虫^[5-7],而在水产病害领域受到广泛关注。

形态上,管口亚纲纤毛虫因体纤毛大多集中于腹面且具有管状口器而较易辨识。但由于个体普遍微小、大多数种类体形相似、形态鉴别特征单一等原因,管口亚纲的研究在早期积累了大量分类学混乱^[8],如GONG等^[9]发现齿管虫属(*Chlamydodon*) 18个具名种中鸟脚齿管虫(*C. pedarius*)和阿歇齿管虫(*C. apsheronica*)应为摩涅齿管虫(*C. mnemosyne*)的同物异名,而卡氏齿管虫(*C. kasymovi*)是三角齿管虫(*C. triquetrus*)的同物异名。尽管部分类群[如齿管虫属、斜管虫属(*Chilodonella*)和偏体虫属(*Dysteria*)]已有较深入研究^[10-15],但多数已命名的管口亚纲纤毛虫因关键活体特征(如伸缩泡数量和位置等)和/或

纤毛图式信息的缺失,其分类混乱尚待厘清。近三十多年来,我国学者在海洋、淡水及土壤环境中报道了逾80种管口亚纲新种及罕见种^[8,16-23],发现我国管口类纤毛虫的物种多样性被严重低估。鉴于此,作者近期对长江口周边的淡水生境开展调查,采集到齿蓬虫属一种,经全面细致的形态学研究鉴定其为新种,命名为沈氏齿蓬虫(*Odontochlamys shenae* sp. nov.)。因齿蓬虫属(*Odontochlamys*)较为罕见,国内研究极少,本研究同时对该属进行了回顾,并给出了该属的种类检索表。

1 材料与方法

沈氏齿蓬虫新种于2018年8月31日采自上海海洋大学人工湖(30°53'8.99"N, 121°53'28.44"E),采样时水温25℃,盐度0。在实验室内参照宋微波等^[24]的研究方法,用微吸管进行虫体分离,在配有数码相机的微分干涉显微镜(Olympus BX53)下进行活体显微观察和拍照记录。同步利用WILBERT蛋白银法^[25]对虫体进行

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蛋白银染色以揭示纤毛图式特征,所用蛋白银药品参考 PAN 等^[10]的方法制作。名词术语参照 LYNN^[1]的研究。

2 结果

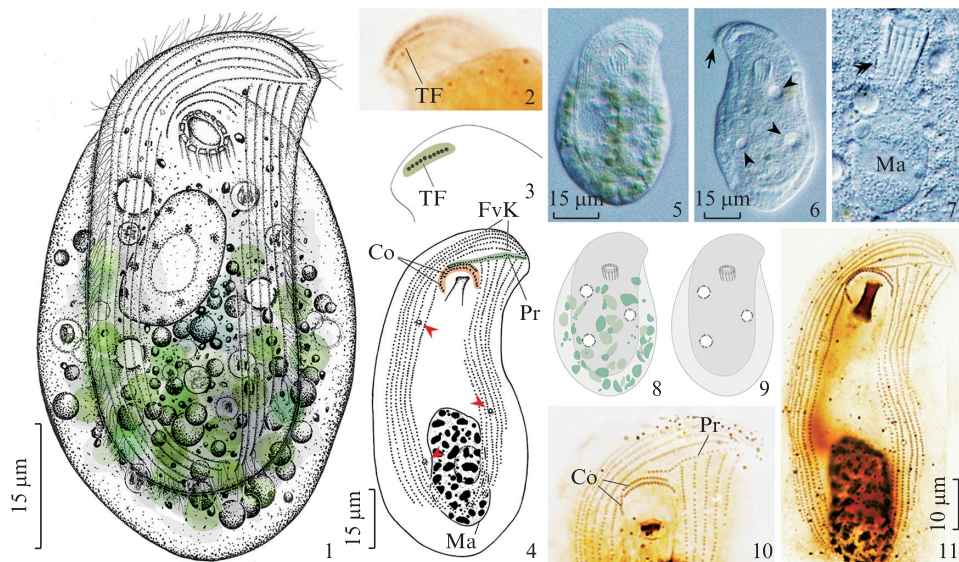
齿管虫目 Chlamyodontida Deroux, 1976

斜管虫科 Chilodonellidae Deroux, 1970

齿蓬虫属 *Odontochlamys* Certes, 1891

沈氏齿蓬虫新种 *Odontochlamys shenae* sp. nov. (图版和表 1)

鉴别特征:活体大小为 $60\sim 80\ \mu\text{m} \times 30\sim 33\ \mu\text{m}$;虫体呈椭圆形,左前部具突起;体纤毛列 12~14 列(右区 6~7 列,左区 6~8 列);背端动基列片段含 8~20 个毛基粒;大核 1 枚;伸缩泡 3 个;口区具 12~15 根咽杆;淡水生。



1, 5. 典型个体腹面观;2, 3. 示背端动基列片段的位置;4, 11. 正模标本的腹面观,示纤毛图式,短箭头示伸缩泡开口;6. 背面观,长箭头示背端动基列片段的纤毛,短箭头示伸缩泡;7. 示大核和胞口,双箭头示咽杆;8. 胞质内充满新鲜藻类食物的个体;9. 培养一段时间后,胞质不含藻类的个体;10. 示口纤毛器;Co. 围口动基列;FvK. 腹前体动基列;Ma. 大核;Pr. 口前动基列;TF. 背端动基列片段。1, 5. Ventral view of typical individual; 2, 3. Anterior end of dorsal side, teal-shaded area shows terminal fragment; 4, 11. Ventral view of the holotype, arrowheads point to contractile vacuole pores, orange-shaded area shows the circumoralkinetes and green-shaded area shows the preoralkinetes; 6. Dorsal view, arrow marks the cilia in the terminal fragment, arrowheads indicate the contractile vacuoles; 7. Details of cytoplasm, showing the macronucleus and cytostome, double-arrowheads indicate the nematodesmal rods; 8. An individual with algae in its cytoplasm on the first day of sampling; 9. An individual without algae in its cytoplasm after a period of the cultivation; 10. Details of oral ciliature; Co. Circumoralkinetes; FvK. Frontoventralkinetes; Ma. Macronucleus; Pr. Preoralkinetes; TF. Terminal fragment.

图版 沈氏齿蓬虫新种活体特征和纤毛图式

Plate Morphology and infraciliature of *Odontochlamys shenae* sp. nov. from life and after protargol impregnation

模式标本:一张含有正模(编号PHB2018083101-1)和一张含有副模(PHB2018083101-2)的蛋白银染色制片保存于中国海洋大学原生动物学实验室,正、副模均用黑色圆圈标记。

模式产地:上海海洋大学人工湖($30^{\circ}53'8.99''\text{N}$, $121^{\circ}53'28.44''\text{E}$)。

题献:该种题献给我国著名原生动物学家中国科学院水生生物研究所沈韞芬院士,以铭记她对我国原生动物学研究的巨大贡献。

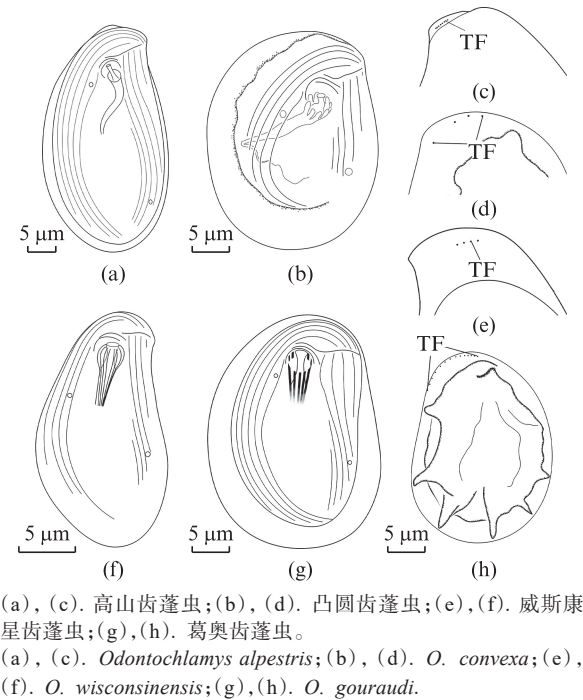
新种 Zoobank 注册号:urn:lsid:zoobank.org:act:C3F37043-1016-4512-A876-EA6BC2C140B7。

论文 Zoobank 注册号:urn:lsid:zoobank.org:pub:

89E75BF5-8AAF-4845-804C-17BCEB953F4E。

形态描述:活体大小为 $60\sim 80\ \mu\text{m} \times 30\sim 33\ \mu\text{m}$,蛋白银染色后大小为 $49\sim 77\ \mu\text{m} \times 21\sim 40\ \mu\text{m}$ 。虫体卵圆形,前后两端钝圆。右侧边缘向外凸起;左侧边缘弯曲呈“S”形,并在左前端呈鸟喙状凸起(图版-1、5、6)。背面宽于腹面,明显隆起,腹面平直。胞口位于虫体前 15% 处,直径 $4\sim 5\ \mu\text{m}$,胞咽由 12~15 根咽杆围绕(图版-1、6、7)。大核 1 枚,长卵圆形,中心异质,活体时大小约 $21\ \mu\text{m} \times 15\ \mu\text{m}$ (图版-7),蛋白银染色后大小为 $16\sim 30\ \mu\text{m} \times 8\sim 18\ \mu\text{m}$ (图版-11)。小核在活体和染色标本中均未观察到。伸缩泡 3 个,直径为 5~

8 μm , 其中2个位于右侧前后各1/3处, 另1个位于左后2/5处(图版-1、4、6)。新采到的虫体常因细胞内含多个未消化藻细胞呈蓝绿色(图版-1、5、8); 实验室培养2~3 d后, 胞质因藻类完全被消化, 呈灰色(图版-6、9)。该种的运动方式多为在基质上缓慢爬行。



(a), (c). 高山齿蓬虫; (b), (d). 凸圆齿蓬虫; (e), (f). 威斯康星齿蓬虫; (g), (h). 葛奥齿蓬虫。
(a), (c). *Odontochlamys alpestris*; (b), (d). *O. convexa*; (e), (f). *O. wisconsinensis*; (g), (h). *O. gouraudi*。
图1 齿蓬虫属已知种的形态特征示意图, 仿自各作者^[5, 27-28, 33]
Fig. 1 Morphology of *Odontochlamys* species redrawn from references^[5, 27-28, 33]

体纤毛长约5 μm 。纤毛图式如图版-2、3、4、10、11所示, 共12~14条体动基列, 其中右侧体动基列6~7列, 左侧6~8列(图版-4、11; 表1)。恒定5条腹前体动基列向虫体前方延伸并在前端向左

侧弯曲。最外侧6条左侧体动基列的前端起始于口前动基列下方, 其后端从右至左渐次缩短; 最内侧的2条左侧体动基列前端明显缩短, 分别起始于虫体前1/3处和2/5处, 并向后延伸至虫体亚尾端。赤道动基列片段未观察到。背端动基列片段位于虫体背面前端, 由8~20个毛基粒组成(图版-2、3)。

口纤毛器由2条等长的围口动基列和1条口前动基列组成: 内侧围口动基列起始于外侧围口动基列右1/4处; 口前动基列起始于围口动基列前方并向左延伸至虫体鸟喙状凸起处(图版-10)。

3 讨论

3.1 齿蓬虫属的回顾

齿蓬虫属曾长期被视为斜管虫属的同物异名, FOISSNER^[26]于1981年对该属的模式种葛奥齿蓬虫(*Odontochlamys gouraudi*)进行了形态学再研究, 认为齿蓬虫属背部隆起更高, 不应并入斜管虫属, 故将其重新激活, 同时给出了齿蓬虫属的新定义。然而该定义并不能清晰地将其与斜管虫属区分。此后, 随着更多齿蓬虫属物种的纤毛图式特征被揭示, FOISSNER^[27]、BLATTERER等^[28]和 FOISSNER等^[29]发现背端动基列片段位于虫体背面前端这一特征应是齿蓬虫属区别于斜管虫属的关键特征。PAN等^[17]利用核糖体小亚基基因首次对齿蓬虫属的系统地位进行了探讨, 发现其与斜管虫属的亲缘关系最密切, 但位于斜管虫属的外围。该结果与这2个属高度相似的形态特征相符, 也支持齿蓬虫属独立于斜管虫属。

表1 沈氏齿蓬虫新种蛋白银染色标本的形态特征统计
Tab. 1 Morphometric characteristics of *Odontochlamys shenae* sp. nov. from protargol-stained specimens

形态特征 Characters	最小值 Min	最大值 Max	平均值 Mean	标准差 SD	变异系数 CV/%	样本量 n
体长 Body length/ μm	49	77	64.00	6.48	10.1	19
体宽 Body width/ μm	21	40	30.90	5.07	16.4	19
大核长 Length of macronucleus/ μm	16	30	21.70	3.59	16.5	19
大核宽 Width of macronucleus/ μm	8	18	12.50	2.63	21.0	19
体动基列数目 Number of somatic kineties	12	14	12.80	0.62	4.8	18
右侧动基列数目 Number of right kineties	6	7	6.10	0.32	5.2	18
左侧动基列数目 Number of left kineties	6	8	6.70	0.67	10.0	18
腹前动基列数目 Number of frontoventral kineties	5	6	5.00	0	0	19
咽杆数目 Number of nematodesmal rods	5	5	5.00	0	0	19
背端动基列片段毛基粒数目 Number of basal bodies in terminal fragment	8	20	14.00	8.49	60.6	18

目前齿蓬虫属已报道物种可根据咽杆数量、背端动基列位置和毛基粒数量以及背部形态等性状分为4种,分别为高山齿蓬虫(*Odontochlamys alpestris* Foissner, 1981),凸圆齿蓬虫 [*O. convexa* (Kahl, 1931) Blatterer& Foissner, 1992],葛奥齿蓬虫(*O. gouraudi* Certes, 1891)和威斯康星齿蓬虫 [*O. wisconsinensis* (Kahl, 1931)Petz&Foissner, 1997],它们均栖息于苔藓及土壤等陆地生境(图1和表2)。此外,高山齿蓬虫和凸圆齿蓬虫在淡水生境中也曾被报道^[17, 27-29]。当前普遍认为纤毛虫原生动物的地理分布呈中度限制性分布模式^[29-30],即部分种类世界性分布,部分种类局域性分布。齿蓬虫属中,高山齿蓬虫在欧洲、非洲、亚洲及美洲岛屿等地均被发现^[17, 29],凸圆齿蓬虫和葛奥齿蓬虫见于西欧和中国^[26-27, 31-32],而威斯康星齿蓬虫在欧洲和南极洲被报道^[33],表明齿蓬虫属4个已知种很可能均为世界性分布。考虑该属物种的研究已有久远历史,但本研究报道的新种——沈氏齿蓬虫现在才被发现,其很有可能为局域性分布。因此,齿蓬虫属的生物地理分布特征很可能遵循中度限制性分布模式。

3.2 沈氏齿蓬虫新种与相似种的比较

与同属已知种相比,沈氏齿蓬虫新种在虫体大小和口区咽杆数量等形态特征方面均与威斯康星齿蓬虫极为相似(表2)。但新种具有更多的体动基列(12~14 vs. 10~11)、伸缩泡(3 vs. 2)和背端体动基列片段的毛基粒数目(8~20 vs. 3~5)^[33]。

与葛奥齿蓬虫相比,沈氏齿蓬虫新种体型更大(60~80 μm × 30~33 μm vs. 30~50 μm × 25~35 μm),体动基列(12~14 vs. 10~11)和伸缩泡数量(3 vs. 2)更多。此外葛奥齿蓬虫背部还具有放射状的隆起^[27]。

不同于高山齿蓬虫,沈氏齿蓬虫个体更大(60~80 μm × 30~33 μm vs. 30~60 μm × 20~35 μm),伸缩泡数量(3 vs. 2)、咽杆数量(12~14 vs. 6~8)和背端动基列片段毛基粒数(8~20 vs. 7~9)更多^[28],很容易区分。

而新种与凸圆齿蓬虫同样在体型大小(60~80 μm × 30~33 μm vs. 25~33 μm × 18~27 μm)和伸缩泡数量(3 vs. 2)有明显差异,此外背端动基列的毛基粒在凸圆齿蓬虫中排布稀疏,而在沈氏齿蓬虫中排列紧密^[28]。

综上所述,沈氏齿蓬虫与齿蓬虫属已知的4个种类在形态上均可清晰区分,应为新种。

表2 沈氏齿蓬虫新种与相似种的形态比较
Tab. 2 Morphometric comparison of *Odontochlamys shenae* sp. nov. and its congeners

特征 Characters	沈氏齿蓬虫 <i>O. shenae</i>	威斯康星齿蓬虫 <i>O. wisconsinensis</i>	葛奥齿蓬虫 <i>O. gouraudi</i>	高山齿蓬虫 <i>O. alpestris</i>	凸圆齿蓬虫 <i>O. convexa</i>
活体大小 Body size in vivo/μm	60~80 × 30~33	25~60 × 12~30	30~50 × 25~35	30~60 × 20~35	30~40 × 20~30
体动基列数量 Number of somatic kineties	12~14	10或11	11或12	11或12	11
右侧体动基列数量 Number of right kineties	6或7	4或5	5	5	5
左侧体动基列数量 Number of left kineties	6或8	6	6	6或7	6
背端动基列片段毛基粒数 Number of basal bodies in terminal fragment	8~20	3~5	11~15	7~9	4或5
咽杆数量 Number of nematodesmal rods	12~15	12~16	12~15	6~8	8或9
伸缩泡数量 Number of contractile vacuoles	3	2	2	2	2
背部形状 Shape of dorsal side	穹状隆起	穹状隆起	放射状隆起	穹状隆起	穹状隆起
数据来源 Data source	本研究	[33]	[27]	[28]	[5]

3.3 齿蓬虫属检索表

- 1 背端体动基列片段的毛基粒稀疏排布 … 2
- 背端体动基列片段的毛基粒紧密排布 … 3
- 2 背部穹状隆起, 不呈放射状 … 凸圆齿蓬虫 *O. convexa*
- 背部呈放射状隆起 … 葛奥齿蓬虫 *O. gouraudi*
- 3 具3个伸缩泡 … 沈氏齿蓬虫 *O. shenae*
- 具2个伸缩泡 … 4
- 4 具12~16根咽杆 … 威斯康星齿蓬虫 *O. wisconsinensis*
- 具6~8根咽杆 … 高山齿蓬虫 *O. alpestris*

作者声明本文无利益冲突。

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Morphological study of a new ciliate, *Odontochlamys shenae* sp. nov. (Alveolata: Ciliophora: Phyllopharyngea), with a review on the genus *Odontochlamys*

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Abstract: Cyrtophorian ciliates usually dominate the microbial community in aquatic biofilms and benthic habitats, and also are the common parasites of fish. However, recent studies indicate that their diversity is underestimated. The present study investigated the morphology and ciliature of *Odontochlamys shenae* sp. nov. collected from freshwater in Shanghai, China, using live observation and protargol staining. The new species was characterized by a combination of morphological features: cell size about 60–80 $\mu\text{m} \times 30\text{--}33 \mu\text{m}$ in vivo, 12–15 nematodesmal rods, 6 or 7 right and 6–8 left kineties, terminal fragment consisting of 8–20 basal bodies, three contractile vacuoles and freshwater habitat. Furthermore, we reviewed the genus *Odontochlamys* and its biogeography shows a moderate endemism model. In addition, a key for identifying *Odontochlamys* species were provided.

Key words: Cyrtophoria; infraciliature; protozoa; taxonomy