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Four first records of trichodinid (Ciliophora: Peritrichia) ectoparasites from cultured molluscs and fishes in China

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Abstract

Four species of *Trichodina* parasitizing the gills of cultured molluscs and fishes in China are described: *Trichodina pectenis* Stein, 1974 from the scallop *Mizuhopecten yessoensis*; *Trichodina jadranica* Raabe, 1958 from the fishes *Mugil cephalus* and *Anguilla bicolor bicolor*; *Trichodina acuta* Lom, 1961 and *Trichodina rostrata* Kulemina, 1968 from the fish *Acrossocheilus fasciatus*. The description of *T. pectenis* presented here first includes both live characters and morphometric data obtained from specimens impregnated using the wet silver nitrate and protargol methods. The other species were revealed by the dry silver nitrate method. Intensities of infestation and comparisons with related species and populations are provided for each of the four.

Key words: taxonomy, *Trichodina pectenis*, *Trichodina jadranica*, *Trichodina acuta*, *Trichodina rostrata*, trichodinid ciliates

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1 Introduction

Ciliates assigned to the genus *Trichodina* Ehrenberg, 1830 are parasites of a range of hosts, including fishes, molluscs, crustaceans, hydroids and amphibians (Raabe, 1959; Lom and Laird, 1969; Lom, 1970; Lom and Dykova, 1992; Xu et al., 1999a, b; Xu and Song, 2003, 2008; Xu, 2007). In recent years, trichodinid diseases of cultured marine fishes and molluscs have often been reported in China along with the development of the aquaculture industry. So far, no chemical or biological agents are really effective against these organisms without damaging their host animals. Thus, prompt identification and early treatment of trichodinids is crucial for the control of animal diseases. On the other hand, the diversity and distribution of trichodinids as well as the host-parasite relationship are still far from known. Compared to freshwater forms, marine trichodinids are still a poorly studied group (Lom and Dykova, 1992; Xu and Song, 2003).

During surveys of the parasites from culture molluscs and fishes on the coasts of the Yellow Sea and the East China Sea, four species of *Trichodina* were identified, and are described herein. This paper is one of a series of reports on the trichodinids of marine animals from the coastal areas off China, which aims to extend our knowledge of the diversity and distribution of these parasitic ciliates.

2 Materials and methods

Specimens of the host mollusc *Mizuhopecten yessoensis* were collected from the cultured cages on the coast of Dalian, China in November 2008. All the scallop specimens were maintained in laboratory for examination. The gills were removed and washed with sterilized seawater in a Petri dish. The ciliates were isolated with a micropipette and observed by light microscopy. With the exceptions of ciliate body shape, the ratio of body width to height and contractile vacuole position, the descriptions of the trichodinids from the scallops are based on examinations of specimens impregnated with the wet silver nitrate and protargol impregnation methods, as described in Foissner (1991).

Specimens of the host fishes *Anguilla bicolor bicolor* and *Mugil cephalus* were collected from the net cages in the estuary area of Fuzhou, China in May 2010. The water salinity was about 20.0 and the water temperature was about 18°C during sampling. Specimens of the host fish *Acrossocheilus fasciatus* were collected from a cultured pond with the water salinity of about 4.0 in Shanghai, China in May 2014. *Acrossocheilus fasciatus*, which has been tamed to adapt to the brackish environment, is formerly a freshwater fish. Wet smears of the skin and gills were prepared in the field using a dissecting microscope in order to detect the presence of trichodinids. The smeared slides were taken back to

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the laboratory for the dry silver nitrate method as described in Foissner (1991). For each host individual examined, the intensity of infestation was estimated qualitatively by assigning values ranging from + (light intensity of infestation) to +++ (heavy intensity of infestation) on one gill. Information concerning hosts collected and trichodinid infestations is provided in Table 1.

Table 1. List of hosts and ectoparasitic trichodinids examined from the Dalian and Fuzhou coasts, and the culture ponds of Shanghai, China

Host	Locality	n	n'	Parasitic trichodinids	Intensity of infestation
Mizuhopecten yessoensis	Dalian	5	5	*Trichodina pectenis*	++
Anguilla bicolor bicolor	Fuzhou	3	3	*Trichodina jadranica*	++
Mugil cephalus	Fuzhou	4	4	*Trichodina jadranica*	++
Acrossocheilus fasciatus	Shanghai	5	5	*Trichodina acuta*	+++
	Shanghai	5	5	*Trichodina rostrata*	++

Note: n represents number of hosts examined and n' number of hosts infested. Intensity of infestation: + represents light (fewer than ten individuals per each host), ++ moderate (ten to one hundred individuals), and +++ heavy (hundreds of individuals).

All measurements are in micrometres and follow the uniform specific characteristics proposed by Lom (1958). In each case, minimum and maximum values are given, followed in parentheses by the arithmetic mean and standard deviation. In the case of radial pins, the mode is given rather than the arithmetic mean. The span of the denticle was measured from the tip of the blade to the tip of the ray. The body diameter was measured as the adhesive disc plus the border membrane. The description of denticle elements follows the format recommended by Van As and Basson (1989).

The position of the micronucleus is given relative to the arch-shaped macronucleus, according to the format described by Lom (1958). In this system, the micronucleus is situated in one of three positions relative to the terminations of the arms of the macronucleus: (1) externally, near the right termination ($+y$); (2) externally, between the two terminations ($-y$); and (3) internally, near the right termination ($-y^1$).

3 Results

3.1 *Trichodina pectenis* Stein, 1974 (Fig. 1, Table 2)

Host and sites: *Mizuhopecten yessoensis*, gills.

Locality: Coast area off Dalian, China.

Voucher specimens: Four slides (ZZF-20081123-01, -02, -03, -04) with protargol and wet sliver nitrate impregnated specimens have been deposited in the Marine Biological Museum of the Chinese Academy of Sciences (MBMCAS) at Qingdao, China.

Description: Small-sized marine *Trichodina*. Body diameter ca. 35–45 μm *in vivo*, 31–42 μm in sliver-impregnated specimens. Body *in vivo* helmet-like, with body diameter/height ratio (1.2–1.6):1. Macronucleus horseshoe-shaped, with external diameter 28–30 μm. Micronucleus ellipsoidal, situated in $+y$ position. Single contractile vacuole near to oral cavity. Adoral ciliary spiral 380°–400°. Haplokinety consisting of two rows of kinetosomes, polykinety with three rows. Denticles small but fill most of adhesive disc, with denticle span 9–11 μm and length 4–6 μm (Figs 1e–g). Blade acute triangular in shape, sharply pointed in almost all specimens investigated. Distal blade surface slopes downward to apex, from which anterior blade surface cannot be clearly distinguished. Tangent point located at peak of distal blade. Posterior blade surface straight to slightly curved. Apophysis of blade indistinct, while posterior projection absent. Central part of ordinary appearance, with round point fitting

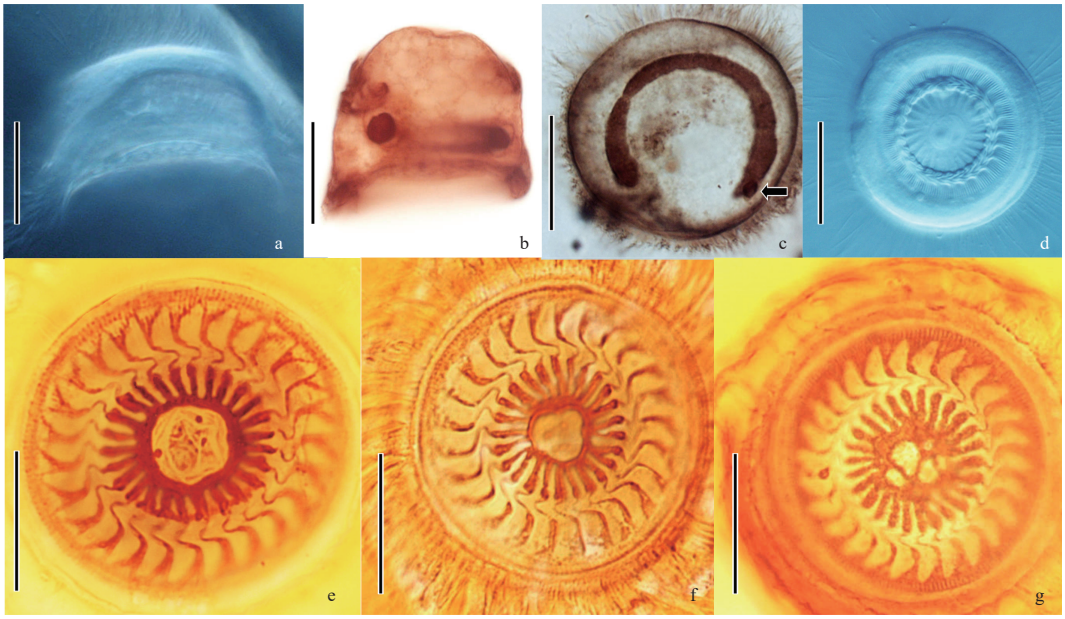

Fig. 1. *Trichodina pectenis* Stein, 1974 from the mollusc *Mizuhopecten yessoensis* on the coast of Dalian, China, from life (a, d) and after protargol (b, c) and wet silver nitrate impregnations (e–g). a and b. Body shape in lateral view; c. adoral view to show the macronucleus and micronucleus (arrow); and d–g. adhesive disc in aboral view. Scale bars: 20 μm.

Table 2. Morphometric (measurements in μm) data on populations of *Trichodina pectenis* Stein, 1974

	Source		
	This paper	Stien (1974)	Stien (1974)
Host	*Mizuhopecten yessoensis*	*Mizuhopecten yessoensis*	*Echinorachnius parma*
Locality	Dalian, China	Peter the great gulf, Russia	Peter the great gulf, Russia
Body diameter	31.0–42.0 (36.7±2.8)	–	–
Adhesive disc diameter	27.0–38.0 (33.0±2.9)	31.4–36.1	27.5
Border membrane width	1.0–4.5 (1.9±0.8)	2.6	–
Denticle ring diameter	16.0–22.0 (19.4±1.7)	17.6–24.1	15.9–21.9
Denticle number	22–28 (26.0±1.4)	22–31	22–30
Radial pins per denticle	7–9	–	–
Denticle span	9.0–11.0 (10.0±0.7)	7–9	–
Denticle length	4.0–6.0 (4.8±0.5)	3.9–6.5	3.9–6.0
Blade length	3.0–4.5 (4±0.5)	3.5–6.0	3.0–4.7
Central part width	2.0–3.0 (2.7±0.3)	–	–
Ray length	3.0–5.0 (4.2±0.6)	–	–
No. of central granules	normally 1 (n=19), rarely 2–5	1–3	1–3
Adoral ciliary spiral	ca. 380°–400°	–	–
No. of specimens measured	21	30	30

tightly into preceding denticle. Ray delicate and straight, tapers to sharp point. Ray apophysis distinct. Length of ray/blade ratio ca. 1.1:1. Central zone clear, with usually one, occasionally 2–5 globular granules recognizable both *in vivo* and in silver-impregnated specimens (Figs 1d–g).

3.2 *Trichodina jadranica Raabe, 1958 (Fig. 2, Table 3)*

Hosts and sites: *Mugil cephalus* and *Anguilla bicolor bicolor*, gills and skin.

Locality: Coast off Fuzhou, China.

Voucher specimens: Four slides (ZZF-20100528-01,-02, ZZF-20100531-01, -02) with dry sliver impregnated specimens have been deposited in the MBMCAS at Qingdao, China.

Description: The specimens from the skin and gills of *Mugil cephalus* and *Anguilla bicolor bicolor* match well in morphometry and denticle morphology. Morphometric data for the two populations from the two hosts are presented in Table 3. The description given below is based on all well impregnated specimens obtained from both the gills and skin. Medium-sized marine *Trichodina* with an average of cell diameter 46 μm from *Mugil cephalus* and 55 μm from *Anguilla bicolor bicolor*. Blade broad, sickle–shaped, filling most of space between *y*–axes, in certain specimens even extending beyond *y*–axes (Figs 2d, f). Distal blade surfaces difficult to separate from anterior blade surfaces, which distinctly slope downwards in most impregnated specimens. Posterior blade surfaces curved, the deepest point on

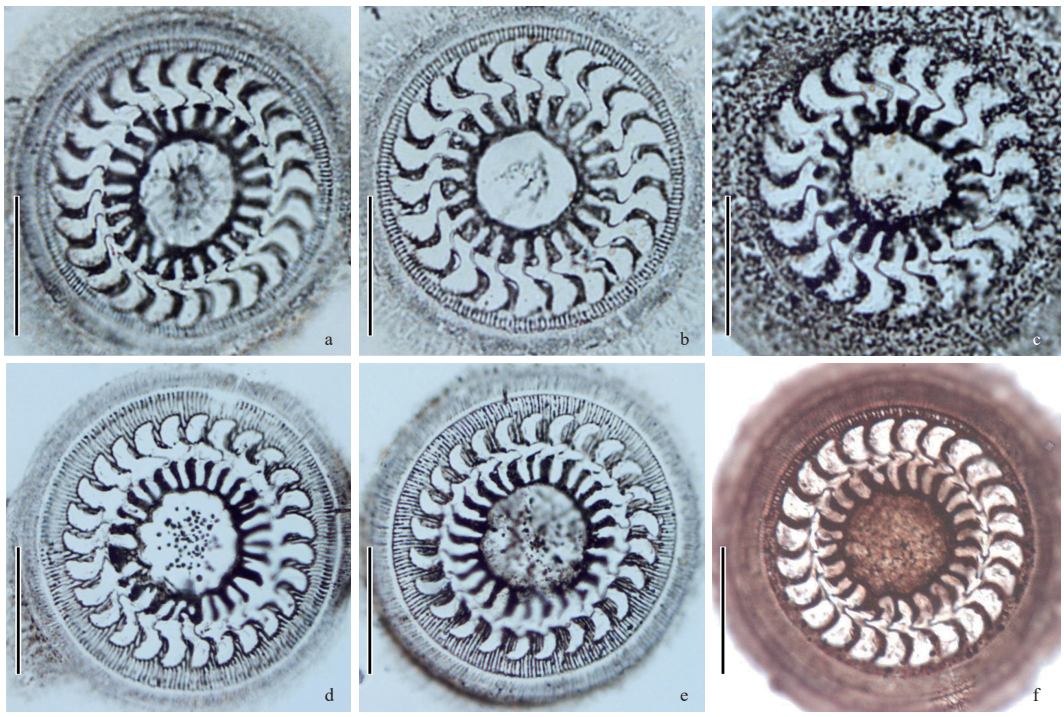

Fig. 2. *Trichodina jadranica* Raabe, 1958 from the fishes *Mugil cephalus* (a–c) and *Anguilla bicolor bicolor* (d–f) on the coast of Fuzhou, China, showing the adhesive discs impregnated with the dry silver nitrate method. Scale bars: 20 μm.

Table 3. Morphometric (measurements in μm) data on populations of *Trichodina jadranica* Raabe, 1958

	Source						
	This paper	This paper	Imai et al. (1991)	Imai et al. (1997)	Xu et al. (2001)	Xu (2007)	Raabe (1958)
Host	*Mugil cephalus*	*Anguilla bicolor bicolor*	*Anguilla japonica*	*Takifugu rubripes*	*Paralichthys olivaceus*	*Takifugu rubripes*	*Mullus barbatus*
Site	gills and skin	gills and skin	gilss	gills	skin	skin	gills
Locality	Shanghai, China	Fuzhou, China	Tsu, Japan	Nagasaki, Japan	Qingdao, China	Qingdao, China	Adriatic Sea
Body diameter	42.0–50.0 (45.8±3.0)	49.5–61.0 (54.7±3.7)	35.0–45.0 (38.9±7.4)	45–60 (51.3±5.4)	30–40 (35.2±2.8)	45–54 (49.7±3.1)	34–43
Adhesive disc diameter	34.0–44.0 (39.4±3.3)	43.0–55.0 (47.3±4.0)	30.0–35.0 (32.2±3.7)	29–44 (35)	24–34 (28.5±2.7)	38–47 (42.8±2.8)	28–38
Border membrane width	3.0–4.0 (3.5±0.5)	3.0–4.0 (3.3±0.4)	2.0–3.0 (2.6±0.5)	1.5–3	3–4 (3.3±0.4)	3–4 (3.5±0.5)	–
Denticle ring diameter	21.0–26.0 (24.0±1.4)	26.0–32.0 (29.4±1.8)	16.0–20.0 (17.8±2.1)	17–26 (22)	13–20 (16.2±1.7)	23–29 (27.4±1.8)	16–22
Denticle number	19.0–24.0 (20.9±1.5)	23–26 (24.7±0.8)	22–25 (23.3±0.7)	20–25 (23)	18–23 (20.1±1.2)	24–27 (25.7±1.0)	22–25
Radial pins per denticle	8–9	7–9, *n*=7	7–8	7–8	7–8	7–9	8
Denticle span	9.5.0–12.0 (10.6±0.8, *n*=9)	11.0–13.0 (11.4±0.7)	7.0–10.0 (8.0±2.4)	–	7.5–9 (7.9±0.4)	9–12.5 (10.1±1.0)	–
Denticle length	5.0–8.0 (6.1±1.2, *n*=9)	6.0–7.0 (6.3±0.3)	3.0–6.0 (4.5±1.0)	6–9	5–6.5 (6.0±0.4)	6–7 (6.5±0.5)	–
Blade length	3.0–4.0 (4.1±0.6, *n*=9)	4.0–5.0 (4.6±0.4)	3.0–4.0 (3.8±0.6)	2.5–6	3.5–4.5 (3.9±0.3)	4–6 (4.7±0.5)	3–4
Central part width	3.0–4.0 (3.4±0.4, *n*=9)	2.5–4.0 (3.3±0.5)	1.0–3.0 (1.7±0.8)	2–3	1.5–2.5 (2.1±0.2)	2–3 (2.4±0.4)	–
Ray length	2.5–4.0 (3.2±0.4, *n*=9)	3.0–4.0 (3.6±0.4)	2.5–4.0 (3.2±0.4)	2–4	1.5–2 (1.9±0.2)	2.5–3.5 (3.0±0.3)	2.5–3.0
Central circle diameter	9.0–15.0 (12.6±1.7, *n*=9)	13.0–20.0 (16.7±1.9)	–	–	9–14 (10.5±1.5)	14–19 (16.8±1.8)	–
Adoral ciliary spiral	–	380°–400°	–	–	380°–390°	about 390°	–
No. of specimens measured	10	10	10	30	20	12	?

same level as apex. Tangent point located at peak of distal blade, sharply pointed in almost all specimens investigated. Apophysis of blade distinct in most specimens examined, while prominent posterior projection at base of blade recognizable only in well impregnated specimens (Figs 2a, b and f). Central part robust, fitting tightly into preceding denticle and extending more than half way to near *y*–axis. Ray short, straight to slightly curved, with rounded to bluntly pointed end; length of ray to length of blade about 1:1.3. Ray apophysis distinct. Centre of adhesive disc contains a clear circle, which is 9–20 μm in diameter and studded with several dark granules 0.5–1.0 μm across.

3.3 *Trichodina acuta* Lom, 1961 (Figs 3a–c, Table 4)

Host and sites: *Acrossocheilus fasciatus*, gills and skin.

Locality: Fish culture pond in Shanghai, China.

Voucher specimens: Four slides (ZZF-20140506-01, -02, -03, -04) with dry sliver impregnated specimens have been deposited in the MBMCAS at Qingdao, China.

Description: The specimens from the gills and skin of the fish *Acrossocheilus fasciatus* match well in morphometry and denticle morphology. Thus, the description is based on all well impregnated specimens obtained from both the gills and skin. Medium-sized *Trichodina* with an average of cell diameter 61 μm (Table 4). Blade broad, sickle-shaped, filling most of space between *y*–axes, with sharp tangent point. Distal blade surface may be round, parallel to border membrane or sloping downwards to sharp apex, from which anterior blade surface cannot be clearly distinguished. Anterior blade surface, extending beyond *y*–axes (Figs 3a–c). Posterior blade surface curved, the deepest point on same level as apex. Apophysis and posterior projection of blade distinct in most specimens examined. Central part robust, fitting tightly into preceding denticle and extending more than half way to *y*–axis. Ray relatively long, straight or slightly curved, tapers to sharp point. Ray apophysis present. Length of ray/blade ratio ca. 1.2:1. Central zone clear, with one bright granule.

3.4 *Trichodina rostrata* Kulemina, 1968 (Figs 3d–f, Table 5)

Host and sites: *Acrossocheilus fasciatus*, gills and skin.

Locality: Culture pond of Shanghai, China.

Voucher specimens: Four slides (ZZF-20140506-01, -02, -03, -04) with dry sliver impregnated specimens have been deposited in the MBMCAS at Qingdao, China.

Description: The specimens from the gills and skin of *Acrossocheilus fasciatus* match well in morphometry and denticle shape. Thus, the description is based on all well impregnated specimens obtained from both the gills and skin. Medium-sized *Trichodina* with an average of cell diameter 50 μm (Table 5). Blade broad, beak-shaped, filling most of space between *y*–axes, with round to sharp tangent point. Distal blade surface may be round, parallel to border membrane or sloping downwards to sharp apex, from which anterior blade surface cannot be clearly distinguished. Anterior blade surface, extending beyond *y*–axes in most impregnated specimens (Figs 3d–f). Posterior blade surface curved, the deepest point on same level as apex. Apophysis of blade indistinct, while posterior projection absent. Central part robust, fitting tightly into preceding denticle and extending more than half way to *y*–axis. Ray straight, tapers to sharp point (on occasions, it slants forwards slightly; Figs 3d, e). Ray apophysis present. Length of ray/blade ratio ca. 1:1. Central zone clear, without bright granules.

4 Discussion

This is the first record of *Trichodina pectenis* reported and described since the original description by Stein (1974) from the

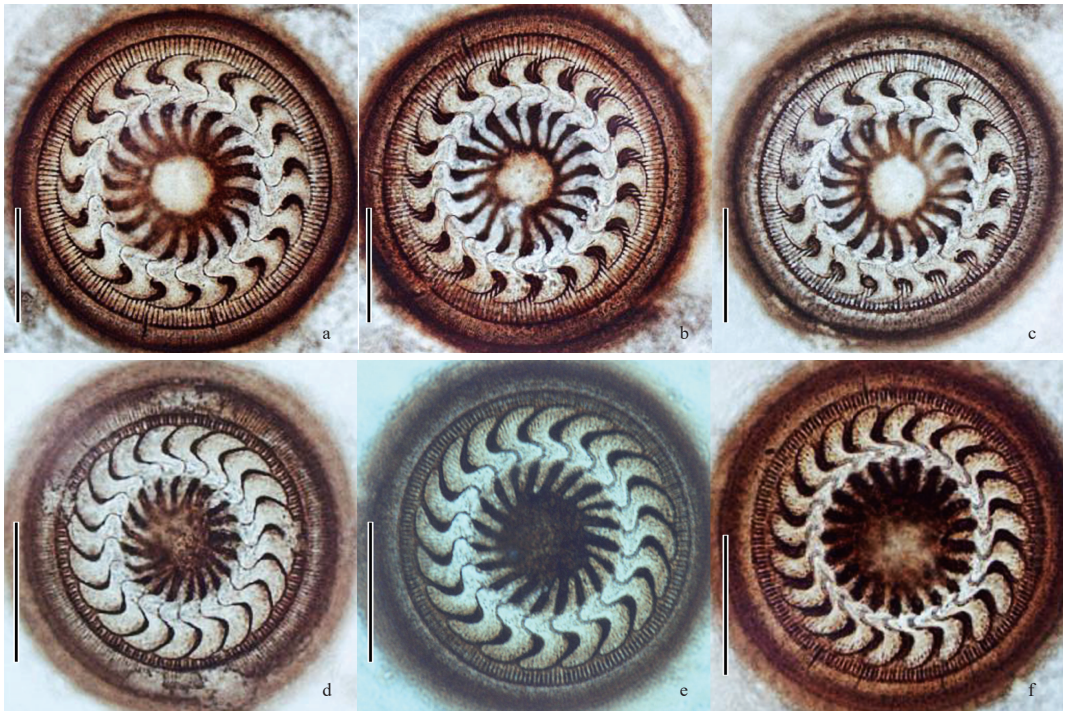

Fig. 3. *Trichodina acuta* Lom, 1961 (a–c) and *T. rostrata* Kulemina, 1968 (d–f) from the fish *Acrossocheilus fasciatus* in Shanghai, China, showing the adhesive discs impregnated with the dry silver nitrate method. Scale bars: 20 μm.

Table 4. Morphometric (measurements in μm) data on populations of *Trichodina acuta* Lom, 1961

	Source			
	This paper	Tao and Zhao (2006)	Lom (1961)	Lom (1961)
Host	*Acrossocheilus fasciatus*	*Aristichthys nobilis*	*Cyprinus carpio, Perca fluviatilis, Luciopera luciopera, L. delineatus, Rhodeus sericeus*	*Gobio holurus* (Syn.: *G. Gobio*)
Site	gills	gills	skin	skin
Locality	Shanghai, China	Chongqing, China	Bohemia, Czech Republic	Benesov, Czech Republic
Body diameter	46.0–68.0 (61.0±5.8)	60.0–70.0 (64.1±2.9)	50–86	84–110
Adhesive disc diameter	38.0–60.0 (52.3±6.0)	50.0–60.0 (56.2±3.2)	30–66	63–85
Border membrane width	4.0–5.0 (4.8±0.3)	4.0–5.0 (4.4±0.3)	3.5–5	3.5
Denticle ring diameter	22.0–35.0 (30.6±3.4)	28.0–37.0 (33.2±2.6)	18–40	42–57
Denticle number	16.0–20.0 (18.7±1.0)	21–25	15–23	25–30
Radial pins per denticle	8.0–10.0	9–10	9–11	10–11
Denticle span	10.0–17.0 (15.3±1.8)	15–18 (16.4±0.9)	10–11	14–15
Denticle length	6.0–12.5 (8.8±1.2)	8.5–10 (9.4±0.4)	–	–
Blade length	3.5–6.0 (4.9±0.6)	5.0–6.0 (5.5±0.4)	4–7	5.5–7
Central part width	2.5–5.0 (4.2±0.7)	3.0–4.0 (3.5±0.4)	3–4	3.3
Ray length	4.0–7.5 (6.2±0.9)	6.0–8.5 (7.4±0.6)	4.5–6	5
Central circle diameter	8.0–12.0 (10.7±1.3)	12–13	9–12	–
Adoral ciliary spiral	ca. 380°	>360°	380°–390°	380°–390°
No. of specimens measured	20	–	–	–

scallop *Mizuhopecten yessoensis* and the sea urchin *Echinorachnius parma* in Russia. The original description was based only on impregnated specimens. Some important morphological data, such as the body diameter and height, nucleus shape and position, adoral ciliary spiral value and contractile vacuole position were not provided. Our specimens which were isolated from the same host *M. yessoensis* correspond well with those described by Stein (1974) in the adhesive disc size, central granule number, and denticle shape and dimensions (Table 2). Thus, conspecificity is beyond reasonable doubt. We redescribed *T. pectenis* in

Table 5. Morphometric (measurements in μm) data on populations of *Trichodina rostrata* Kulemina, 1968

	Source		
	This paper	Kulemina (1968)	Liu and Zhao (2010)
Host	*Acrossocheilus fasciatus*	*Abramis brama, Rutilus rutilus*	*Silurus meridionalis*
Site	gills	skin	gills
Locality	Shanghai, China	Lake Seliger, Russia	Chongqing, China
Body diameter	47.0–53.0 (49.8±2.3)	49.5–84.7	53.0–56.0 (59.9±4.5)
Adhesive disc diameter	38.0–45.0 (41.3±2.8)	33.0–44.0	41.0–55.0 (47.0±4.5)
Border membrane width	3.5–5.0 (4.3±0.5)	–	6.0–7.0 (6.0±0.4)
Denticle ring diameter	22.0–28.0 (24.6±2.4)	–	24.0–34.0 (28.0±3.2)
Denticle number	20.0–22.0 (21.0±0.8)	23–25	22–25
Radial pins per denticle	8.0–9.0	9–11	–
Denticle span	11.5–14.5 (13.1±1.0)	–	12.0–15.0 (14.0±0.8)
Denticle length	6.5–8.5 (7.0±0.7)	–	6.0–8.0 (7.0±0.5)
Blade length	4.0–5.5 (4.9±0.4)	–	5.0–6.0 (5.0±0.4)
Central part width	2.5–4.0 (3.3±0.5)	–	2.0–4.0 (3.0±0.4)
Ray length	4.0–6.0 (4.9±0.6)	–	4.0–7.0 (5.0±0.7)
Adoral ciliary spiral	–	360°–390°	390°–400°
No. of specimens measured	8	–	12

detail based on both live and silver impregnated cells and supplemented the morphological data, which are lacking in the original description. *Trichodina pectenis* resembles, to some extent, *T. chlamydis* Xu, Song and Warren, 1999, a parasite of the marine scallop *Chlamys farreri*. However, the shape of the blades is distinctly different (triangular in *T. pectenis* vs. rectangular in *T. chlamydis*) (Figs 1g, 2a and b; Xu et al., 1999b). It is similar to *T. caecellae* Xu, Song and Warren, 2003 in the denticle shape and dimensions, but differs distinctly in the structure of the central zone (with 1–5 globular granules vs. absent).

Trichodina jadranica is a trichodinid parasite widely distributed on the gills and/or skin of various host fishes worldwide since Raabe (1958) established it based on specimens from the host fish *Mullus barbatus*. So far, most populations of *T. jadranica* were reported from marine fishes and only two from freshwater fishes (Arthur and Lom, 1984; Imai et al., 1991, 1997; Loubser et al., 1995; Xu et al., 2001; Xu, 2007). The morphological identification of *T. jadranica* is often difficult due to the population variability and the presence of misidentification. Xu (2007) made a thorough revision on *T. jadranica* and showed that the species is highly variable in body size, denticle dimensions, and the number of denticles. The present trichodinid specimens match well in the morphometry and denticle shape with the other Chinese and Japanese populations, though they are slightly larger than the type specimens reported by Raabe (1958) (Table 3). These are also the first host records for *T. jadranica* parasitizing *Mugil cephalus* and *Anguilla bicolor bicolor*. Both the host fish *Mugil cephalus* and *Anguilla bicolor bicolor* were collected from an estuary of Fuzhou, where the perennial salinity was 15–22. This is an intermediate environment among marine and fresh waters. Our study further supports the view of Xu (2007), who indicated that *T. jadranica* has the ability to live in marine, brackish and fresh environments.

Trichodina acuta and *T. rostrata* are typically freshwater fish parasites distributed worldwide. These trichodinids are easy to distinguish by their denticle shape and dimensions (Lom, 1961; Kulemina, 1968; Tao and Zhao, 2006; Liu and Zhao, 2010). Our specimens were detected from the freshwater fish *Acrossocheilus fasciatus*, a species has been tamed to adapt to brackish environment with the water salinity about 4. Thus, the fish *A. fasciatus* from the brackish water represents new host and locality records for these two trichodininids. It is reasonable to assume that the two trichodinids adapted the saline environment with their hosts because both trichodinids have never been detected from marine host animals.

To date, more than 260 *Trichodina* species have been reported, but at least one-third of trichodinids are still needed to be confirmed or redescribed using modern methods (Xu et al., 2001; Gong et al., 2005). The comparative analysis of the morphometry and denticle shape is the routine way to identify *Trichodina* species. Many *Trichodina* spp. show morphological similarity to closely related species, and some similar species even concomitantly occurred in the same host. Under such circumstances, morphological identification has its limitation. There is a pressing need for molecular methods, for example the DNA barcoding, to assist in the identification as well as the phylogenetic analysis of trichodinids (Zhan et al., 2009, 2013).

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