

## Ectoparasitic species of the genus *Trichodina* (Ciliophora: Peritrichida) parasitising British freshwater fish

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Key words: Protozoa, ciliate, *Trichodina*, fish parasites, UK

**Abstract.** Seven species of the genus *Trichodina* Ehrenberg, 1838 were identified during a sampling programme of twenty freshwater fish species from approximately sixty sites in Scotland, England and Wales. Species found include: *Trichodina acuta* Lom, 1961 from *Cyprinus carpio* L., *Carassius auratus* L., *Oncorhynchus mykiss* (Walbaum), *Salmo trutta* L. and *Phoxinus phoxinus* L.; *Trichodina domerguei* Wallengren, 1897 from *Gasterosteus aculeatus* L.; *Trichodina tenuidens* Faure-Fremiet, 1944 from *Gasterosteus aculeatus*; *Trichodina pediculus* Ehrenberg, 1838 from *Gasterosteus aculeatus*; *Trichodina modesta* Lom, 1970 from *Abramis brama* L.; *Trichodina nigra* Lom, 1960 from *Cyprinus carpio*, *Salmo trutta* and *Oncorhynchus mykiss*; and *Trichodina intermedia* Lom, 1960 from *Phoxinus phoxinus*. Morphological variation within and between host populations and host specificity of the *Trichodina* species recovered are described.

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The genus *Trichodina* Ehrenberg, 1838 is the largest within the family Trichodinidae Raabe, 1959. Over 100 species have been described from fish, most by means of Klein's silver impregnation and a further 69 species have been inadequately described (Lom and Dyková 1992). Despite this the *Trichodina* species found on British freshwater fish have received little attention, with only *Trichodina domerguei* Wallengren, 1897 and *T. tenuidens* Faure-Fremiet, 1944 previously recorded (Chubb 1970, Dartnall 1973).

Lom (1958) detailed the specific characteristics that have been used as the basis of trichodinid taxonomy. Measurements were taken from skeletal, nuclear and ciliary structures. The emphasis placed upon various characteristics has changed with time, to the extent that recent papers refer only to the structure of the adhesive disc.

Kazubski utilised Lom's (1958) criteria, significantly increasing our understanding of the silver stained adhesive disc as a taxonomic structure, firstly, with a study on the growth of skeletal elements in *T. pediculus* Ehrenberg, 1838 (Kazubski 1967), and secondly with a succession of papers investigating morphological variation of the adhesive disc (Kazubski and Migala 1968, Kazubski 1971, 1976, 1979, 1980, 1981, 1982a,b, 1991a,b,c, Kazubski and Piecka-Rapacz 1981). The growth of skeletal elements is important in determining the maturity of individual specimens. Trichodinids reproduce predominantly via asexual, binary fission. Thus, individuals with half the number of skeletal components are present in any population which must be excluded from taxonomic analyses.

Wellborn (1967) examined nearly 1,000 fish of 46 freshwater species from the southern United States

using Lom's scheme of uniform specific characteristics. He proposed the term "aperture" for the opening into the hollow central part of the denticle, and utilised two methods for the impregnation of formalin fixed material. Illustrations of the measurements used and a key to *Trichodina* species of North American freshwater fishes were also provided.

The most recent attempt to improve the criteria for description of the adhesive disc was by Van As and Basson (1989). They proposed, "a method to describe the shape of the denticles by constructing lines from the centre of the adhesive disc to the tip of the denticles, which provide fixed points of reference that can aid in an accurate description of the denticle elements". This method requires an enlarged photomicrograph or drawing, and has also been applied to specimens illustrated in the literature. The system proposed by Van As and Basson (1989) undoubtedly gives accurate descriptions of the specimens subjected to analysis, but it also focuses on comparisons of individuals rather than populations and for that reason has not been utilised in this study. However, the nomenclature used in their denticle descriptions is very useful, as no other standardised criteria exist in the literature.

Van As and Basson (1989) suggested that body diameter be excluded from descriptions due to its high degree of variability and deformation, and that the former term be used to represent the diameter of the adhesive disc plus border membrane. Using the term body diameter to represent adhesive disc diameter plus border membrane seems ambiguous and is already measured separately in Lom's criteria.

The objective of this study was to ascertain the *Trichodina* species present on British freshwater fish,

emphasising intra-specific morphological variability with reference to existing taxonomic problems within the genus.

## MATERIALS AND METHODS

Fish were sampled for trichodinids between October 1991 and September 1994 from approximately sixty sites, with one or more fish species sampled from each. Species sampled included: Atlantic salmon, *Salmo salar* L.; brown trout, *Salmo trutta* L.; rainbow trout, *Oncorhynchus mykiss* Walbaum; Arctic charr, *Salvelinus alpinus* L.; brook trout, *Salvelinus fontinalis* (Mitchill); whitefish, *Coregonus lavaretus* (L.); grayling, *Thymallus thymallus* L.; pike, *Esox lucius* L.; carp, *Cyprinus carpio* L.; goldfish, *Carassius auratus*; bream, *Abramis brama*; minnow, *Phoxinus phoxinus*; rudd, *Scardinius erythrophthalmus* L.; roach, *Rutilus rutilus* L.; dace, *Leuciscus leuciscus* (L.); stoneloach, *Noemacheilus barbatulus* (L.); eel, *Anguilla anguilla* L.; three-spined stickleback, *Gasterosteus aculeatus* L.; perch, *Perca fluviatilis* L.; and ruffe, *Gymnocephalus cernua* (L.) Where possible a minimum of ten fish per population were sampled from each site. The location and date of sampling are given in Tables 1-7 for infected fish populations.

Smears were processed using Klein's silver impregnation technique (Klein 1958). Where possible a minimum of forty specimens from each trichodinid population were photographed and measured.

The taxonomic criteria used during this study are essentially the same as those used in recent publications by other authors, and are illustrated in Lom and Dyková (1992). For morphometric measurements the range, mean, standard deviation followed by sample size are given, and for denticle number the mode is substituted for the mean.

## SURVEY OF SPECIES

### *Trichodina acuta* Lom, 1961

Seven populations of a skin trichodinid species were found during this study from *Salmo trutta*, *Oncorhynchus mykiss*, *Cyprinus carpio*, *Carassius auratus* and *Phoxinus phoxinus*, all consistent with Lom's (1961) original description of *Trichodina acuta*, (classified as *T. domerguei* f. *acuta*). Details of the seven populations, together with morphometric and meristic data are presented in Table 1. Individual specimens of trichodinids identified tentatively as *T. acuta*, were also obtained from *Gasterosteus aculeatus* (Airthrey Loch), *O. mykiss* (River Test) and *Scardinius erythrophthalmus* (Chorlton, Nr. Chester).

*T. acuta* has previously been recorded in Britain from *C. carpio* (Andrade - Salas 1991) obtained from a hatchery in the south of England. *T. acuta* is of medium size and adhesive disc diameter ranged from 45.3 to 64.0  $\mu\text{m}$  in the seven populations sampled, whilst denticle number ranged from 16-25. It is characterised by a small central circle, which remains free of silver. The denticle blades are broad 'sickle-like' structures, often coming to a point. The apophysis of the blade is



Fig. 1. Approximate localities of sampling sites, solid circles positive (*Trichodina*) and open circles negative.

unusually pronounced, as is the posterior projection of the central part. The denticle rays are straight or slightly curved, and terminate in either a rounded or pointed end. The rays are often angled backwards to the anterior of the denticle although this is variable. Specimens observed illustrated an adoral ciliary spiral of 360-380°. Photomicrographs of specimens from each population are illustrated in Fig. 2A-G. The individual cells illustrated do not necessarily represent "type" specimens for each population, but rather illustrate variation in denticle morphology within the species.

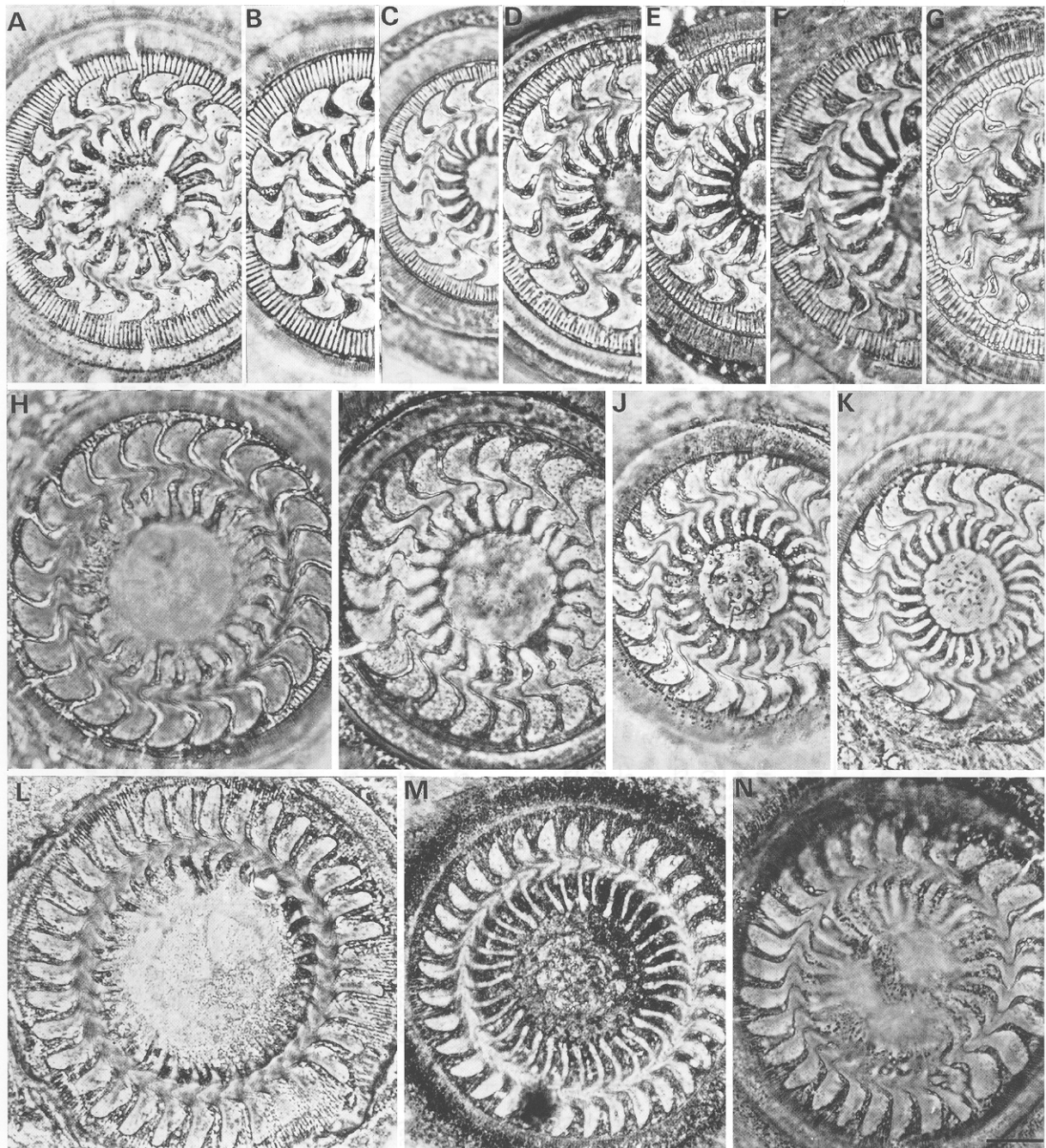
Morphological variation within each population is considerable, some specimens possess much broader denticles with a pronounced distal surface of the blade rather than the normal continuous curve of the anterior margin. Other variations of blade morphology include: reduced curvature of posterior margin or 'spatulate' appearance rather than the normal 'sickle' shape, a reduction in size relative to denticle span and a reduced appearance of the apophysis of the blade. No consistent marked variation in morphology could be differentiated between populations.

Specimens of *T. acuta* were found with a denticle form almost identical to that of *T. compacta* Van As et Basson, 1989, being more robust with a defined distal

**Table 1.** Morphometric and meristic data for *Trichodina acuta*

Author	Lom (1961)	This study (a)	This study (b)	This study (c)	This study (d)	This study (e)	This study (f)	This study (g)
Host	Various	<i>Salmo trutta</i>	<i>Cyprinus carpio</i>	<i>Phoxinus phoxinus</i>	<i>Oncorhynchus mykiss</i>	<i>Oncorhynchus mykiss</i>	<i>Carassius auratus</i>	<i>Oncorhynchus mykiss</i>
Localisation	Skin, gills	Skin	Skin	Skin	Skin	Skin	Skin	Skin
Locality	Bohemia	Airthrey Loch, Central Region 11/91	Norfolk 17/11/92	Castle Semple Water, Strathclyde 20/9/92*	Moffat, Dumfries 18/3/93	Loch Fad, Strathclyde 6/93	Pond, Institute of Aquaculture 4/4/94	River Devon, Dollar, Central Region, 14/8/94
A. d. diam.	42-53**	38.4-51.8 (44.7±3.6, 33) <sup>+</sup>	42.6-55.9 (50.0±4.7, 8)	46.4-64.0 (53.5±4.4, 25)	44.5-58.6 (51.0±3.8, 23)	39.9-53.6 (45.3±3.9, 17)	41.1-60.9 (52.3±4.7, 42)	39.7-52.4 (47.2±3.7, 26)
B. m. width	3.5-5	3.4-4.9 (4.0±0.3, 33)	3.7-5.1 (4.5±0.5, 8)	4.2-5.6 (4.8±0.4, 25)	3.9-4.9 (4.4±0.2, 23)	4.0-5.1 (4.6±0.3, 17)	4.4-5.3 (4.9±0.2, 42)	4.1-5.0 (4.4±0.5, 26)
D. r. diam.	23-32	21.8-31.0 (26.4±2.5, 33)	25.6-32.4 (28.8±2.5, 8)	21.0-29.3 (25.2±2.3, 25)	25.6-32.8 (29.4±2.0, 23)	22.1-32.7 (26.2±2.7, 17)	25.4-37.5 (31.1±3.0, 42)	22.6-31.6 (27.2±2.6, 26)
Dent. no.	18-21	17-22 (19, 33)	18-20 (19, 8)	18-21 (19, 25)	19-23 (20, 23)	17-20 (18, 17)	16-25 (21, 42)	17-20 (19, 26)
R. p./ d.	8	8-11 (9.4±1.0, 33)	8-11 (9.75±1.0, 8)	7-9 (8.5±0.7, 24)	8-10 (9.5±0.7, 22)	9-12 (10.0±1.0, 17)	8-12 (9.6±1.1, 42)	8-10 (9.2±0.5, 26)
D. length	10-11	7.2-9.7 (8.4±0.6, 33)	8.3-10.4 (9.3±0.3, 8)	6.4-8.6 (7.7±0.5, 25)	7.9-11.3 (9.3±0.8, 23)	8.0-9.7 (8.6±0.5, 17)	6.7-11.3 (8.8±1.0, 42)	7.7-9.6 (8.7±0.5, 26)
B. length	4.5-6	3.4-5.8 (4.8±0.5, 33)	4.3-6.3 (5.3±0.6, 8)	3.4-5.6 (4.9±0.4, 25)	4.6-7.9 (5.7±0.6, 23)	4.1-5.9 (4.9±0.5, 17)	4.3-6.7 (5.7±0.6, 42)	4.1-6.0 (5.1±0.5, 26)
R. length	4-7	4.9-6.8 (5.8±0.5, 33)	5.0-7.8 (6.3±0.9, 8)	4.9-6.7 (5.6±0.5, 25)	5.5-8.2 (6.7±0.7, 23)	5.6-7.2 (6.3±0.5, 17)	5.2-8.9 (7.1±0.9, 42)	4.6-7.2 (5.6±0.6, 26)
C. p. width	3-4	2.2-3.0 (2.6±0.2, 33)	2.5-3.6 (3.0±0.3, 8)	2.0-2.8 (2.4±0.2, 25)	2.4-3.4 (2.8±0.2, 23)	2.1-3.1 (2.6±0.3, 17)	2.3-3.8 (3.1±0.4, 42)	2.4-3.8 (2.8±0.4, 26)
C. c. diam.	9-12	6.7-11.8 (9.8±1.2, 25)	8.6-10.0 (9.4±0.8, 3)	4.3-10.9 (8.8±1.2, 25)	8.9-17.3 (11.2±1.9, 17)	7.3-11.4 (8.8±0.9, 16)	8.0-12.7 (10.2±1.4, 18)	7.6-11.5 (10.1±0.9, 26)
Dent.span	-	11.3-14.8 (13.1±1.0, 33)	12.9-16.2 (14.4±1.2, 8)	11.4-14.6 (12.7±0.9, 25)	12.9-19.1 (15.1±1.3, 23)	12.0-15.2 (13.6±0.9, 17)	11.7-18.4 (15.9±1.4, 42)	11.8-15.8 (13.6±1.1, 26)

\* kept at room temperature for two weeks; \*\*range of the mean for different populations and hosts; <sup>+</sup> in this and following tables, number of specimens measured



**Fig. 2.** **A** - *Trichodina acuta* from *Salmo trutta* (Airthrey Loch); **B** - *T. acuta* from *Cyprinus carpio* (Norfolk); **C** - *T. acuta* from *Phoxinus phoxinus* (Castle Semple Water); **D** - *T. acuta* from *Oncorhynchus mykiss* (Moffat); **E** - *T. acuta* from *O. mykiss* (Loch Fad); **F** - *T. acuta* from *Carassius auratus* (Institute of Aquaculture); **G** - *T. acuta* from *O. mykiss* (Dollar); **H,I** - *Trichodina domerguei* from *Gasterosteus aculeatus* (Airthrey Loch); **J,K** - *T. domerguei* from *G. aculeatus* (Ard Toe, marine); **L-N** - *Trichodina tenuidens* from *G. aculeatus* (Airthrey Loch). Scale bar = 10  $\mu$ m.

surface to the blade; the only discrepancy being in adhesive disc diameter and relative central circle diameter. The population described as *T. compacta* is said to be smaller than *T. acuta*. However, its mean

adhesive disc diameter is nearer to that given for the population with the smallest specimen size in this study, than the smallest population found here is to the largest. Both species were found together in populations from

Israel (Van As and Basson 1989) and the additional fact that a Philippino population (Duncan 1977) of *T. acuta* is described by Basson et al., 1983 as being intermediate in size and morphology between European forms (Kazubski and Migala 1968) and *T. compacta*, suggests that all these populations may represent different forms within *T. acuta*.

Lom (1961) reclassified *Diaptomus* trichodinid populations originally designated *T. domerguei* f. *latispina* Dogel, 1940 as *T. domerguei* f. *acuta*. The same species, again named as *T. domerguei* f. *latispina*, was described from the skin and rarely gills, of *C. carpio*, silver carp *Hypophthalmichthys molitrix*, grass carp *Ctenopharyngodon idella*, various tadpoles and on the surface of two copepod species in China (Chen Chih-Leu 1963). Basson and Van As (1991) have suggested that all copepod trichodinids belong to the same species, i. e. *T. diaptomi* Basson et Van As, 1991. South African specimens are compared to other authors data and one or two photomicrographs, including those of Lom (1961) and Chen Chih-Lieu (1963), both of whom originally described their specimens as synonyms of *T. acuta*. Basson and Van As (1991) state that all copepod populations include the presence of a central circle, a feature possessed by all fish populations of *T. acuta* described by Lom (1961). *T. diaptomi* is said to be smaller than *T. acuta*, however, specimens identified as *T. domerguei* f. *latispina* from copepods (Lom 1960) were smaller than populations of the same species found on fish; Chen Chih-Leu (1963) reported an increase in size when copepod specimens were transferred to fish and *vice versa*. Lastly, Van As and Basson state that “they have not yet encountered any specimens of trichodinids resembling *T. diaptomi* on fish hosts”; however, the specimens they re-identified so closely resembled those found on fish hosts that they were classified by Lom (1961) as *T. domerguei* f. *acuta*. This hypothesis based on comparisons of individual specimens from the literature overlooks the vast range of morphological variation present in species such as *T. acuta*.

#### ***Trichodina domerguei* (Wallengren, 1897)**

During this study *Trichodina domerguei* was recorded from *Gasterosteus aculeatus* from Airthrey Loch. A second population from *G. aculeatus* was identified from Ardtoe on the west coast of Scotland inhabiting water at a salinity of 33‰. Due to the reduced quality of stain produced with marine trichodinids, only a few good quality specimens were obtained from this population. Morphometric and meristic data for the two populations are given in Table 2.

*T. domerguei* has an adoral disc diameter of 39.8–68.3 µm (Airthrey Loch and Ardtoe) with broad,

rounded denticle blades and slightly curved, relatively short, broad rays, often with a well defined ray apophysis. An unusual feature of the denticle rays is that they are often broader at their distal ends than where they join the central part of the denticle. This species has a well defined central circle, interspersed with granules or vacuoles. The adoral cilia described a turn of approximately 390°. Photomicrographs of both populations are illustrated in Fig. 2 H-K.

*T. domerguei* has previously been recorded in Britain on *G. aculeatus* from Llyn Padarn (Chubb 1970) and from *Pungitius pungitius* in the River Roding, Essex (Dartnall 1973). There have been additional reports of *T. domerguei* from freshwater sticklebacks species by Lom and Stein (1966), and Grupcheva and Sedlacek (1993). It is similar to *T. jadratica* Raabe, 1958, *T. cottidarum* Lom, 1970 and *T. murmanica* Polyanski, 1955 (Lom 1970a, Lom and Dyková 1992). These species are euryhaline or marine trichodinids which may suggest that *T. domerguei* is of marine origin. This idea is supported by the high degree of host specificity (euryhaline sticklebacks) displayed in the freshwater environment and the comparatively large number of marine host species. The smaller dimensions of the marine specimens described in this study agree with the findings of Lom (1970a) who remarks on the small specimen size in marine populations.

#### ***Trichodina tenuidens* Faure-Fremiet, 1944**

A population of *Trichodina tenuidens* was found on the gills of *Gasterosteus aculeatus* from Airthrey Loch. This species is of medium size (a. d. diam. = 52.3–78.6 µm) with a relatively high number of denticles, which are finer and more elongated than in *T. domerguei*. The denticle blade has an almost straight or slightly curved posterior margin, and the blade itself is highly variable in form. The inner rays are longer than those of *T. domerguei*, but share the trait of widening towards their distal ends. The central part of the disc ranges from an argentophilic circular structure, to a few large granules. Photomicrographs are illustrated in Fig. 2L-N. The adoral cilia describe a turn of approximately 380–400°. Morphometric and meristic data for *T. tenuidens* (Airthrey Loch) are given in Table 3.

As in the case of *T. domerguei*, *T. tenuidens* is a euryhaline species. It was identified during this study from a marine population of *G. aculeatus* from Ardtoe on the west coast of Scotland, although insufficient numbers were available to enable morphometric comparison with freshwater specimens.

Previous British records include *G. aculeatus* from Llyn Padarn (Chubb 1970) and *Pungitius pungitius* in the River Roding, Essex (Dartnall 1973). Further records from *G. aculeatus* include those of Calenius (1980) and Grupcheva and Sedlacek (1993). The morphological variation of denticle form and

**Table 2.** Morphometric and meristic data for *Trichodina domerguei*

Author	Lom and Stein (1966)	This study	This study
Host	<i>Pungitius pungitius</i> and <i>Gasterosteus aculeatus</i>	<i>Gasterosteus aculeatus</i>	<i>Gasterosteus aculeatus</i>
Localisation	Skin, rarely gills	Skin, very rarely gills	Skin
Locality	Near Leningrad	Airthrey Loch, Central Region 2/5/92	Ardtoe, Highlands 11/8/94
A. d. diam.	43-61 (51)	51.6-68.3 (59.8±4.3, 24)	39.8-46.5 (43.7±2.5, 6)
B. m. width	3.5-5	4.0-5.6 (4.8±0.4, 24)	4.6-5.4 (4.8±0.3, 6)
D. r. diam.	28-33 (31)	27.8-40.8 (32.3±3.3, 24)	25.6-29.8 (27.9±1.5, 6)
Dent. no.	22-28 (24)	23-31 (24, 24)	23-27 (27, 6)
R. p / d.	9-10	8-11 (9.75±0.8, 6)	8-11 (9.2±1.2, 6)
D. length	11-12	7.8-9.6 (8.7±0.6, 24)	7.6-9.6 (8.2±0.7, 6)
B. length	3.5-7	5.0-9.3 (6.5±0.9, 24)	4.9-6.1 (5.7±0.5, 6)
R. length	4-5	4.2-5.8 (4.9±0.4, 24)	4.8-5.6 (5.0±0.3, 6)
C. p. width	3	2.3-3.1 (2.6±0.2, 24)	2.2-2.6 (2.4±0.1, 6)
C. c. diam.	-	15.1-26.8 (19.1±2.9, 23)	12.3-16.1 (14.5±1.3, 6)
Dent. span	-	11.9-15.6 (13.8±1.1, 24)	11.9-13.8 (13.2±0.7, 6)

**Table 3.** Morphometric and meristic data for *Trichodina tenuidens*

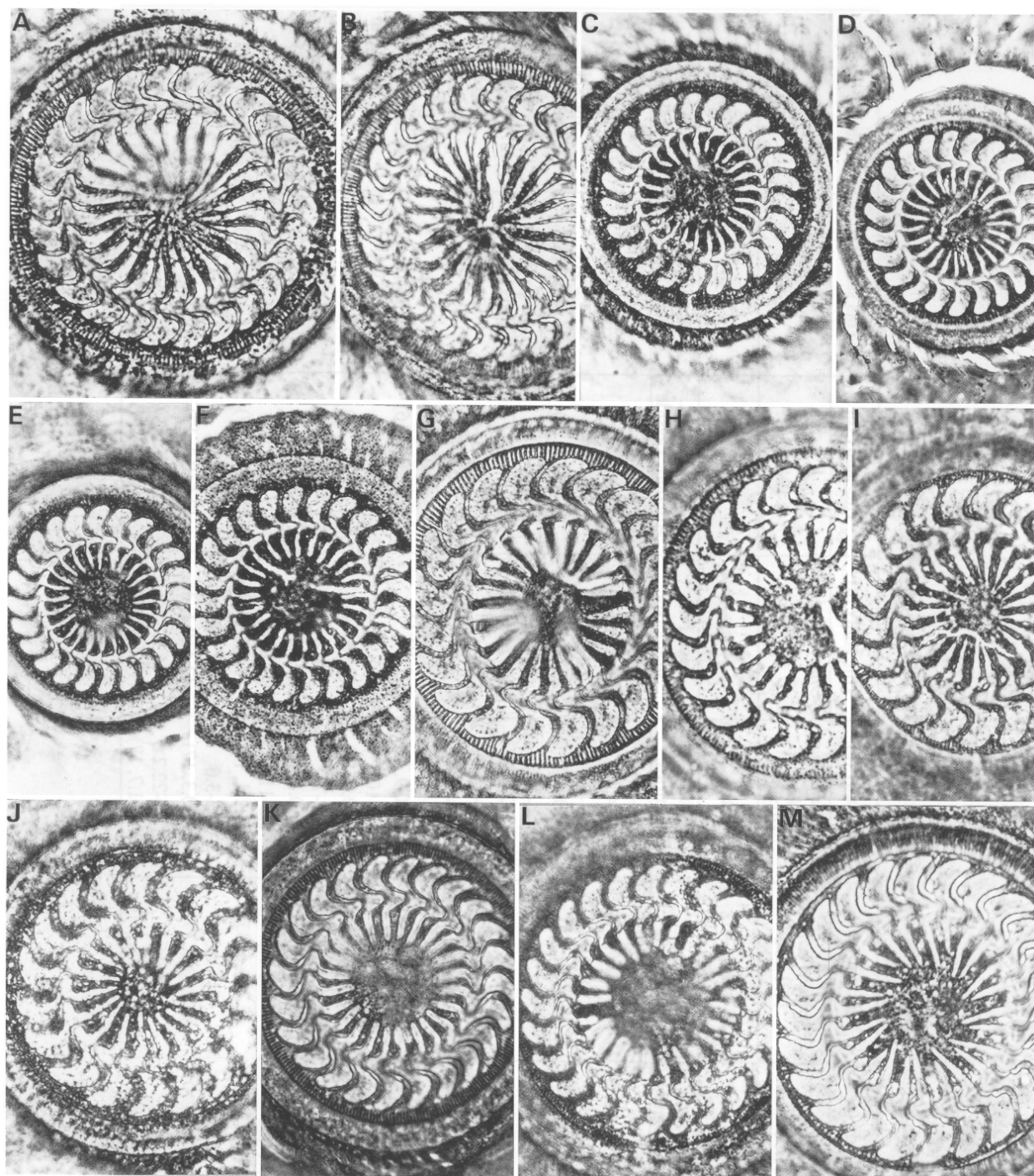
Author	Lom and Stein (1966)	This study
Host	<i>Gasterosteus aculeatus</i>	<i>Gasterosteus aculeatus</i>
Localisation	Gills, rarely skin	Gills, rarely skin
Locality	Lake Mamry, Poland	Airthrey Loch, Central Region 2/5/92
A. d. diam.	45-69	52.3-78.6 (70.8±6.3, 16)
B. m. width	4.5-5	4.1-5.8 (4.7±0.4, 16)
D. r. diam.	25-40 (31)	30.8-45.6 (40.7±3.9, 16)
Dent. no.	25-33 (28)	29-38 (37, 16)
R. p / d.	8-9	9-12 (9.5±0.1, 15)
D. length	7-9	6.4-8.2 (7.3±0.4, 16)
B. length	4.5-7	5.6-8.6 (7.2±0.9, 16)
R. length	5-7	6.1-9.8 (7.4±0.8, 16)
C. p. width	2-2.5	1.8-2.7 (2.3±0.2, 16)
Dent. span	-	14.2-19.4 (16.7±1.5, 16)

**Table 4.** Morphometric and meristic data for *Trichodina pediculus*.

Author	Kazubski (1991)	This study
Host	<i>Carassius carassius</i>	<i>Gasterosteus aculeatus</i> 1992-1993 (from weekly sampling of stickle back trichodinids over one year)
Localisation	-	skin
Locality	Kortowo, Poland	Airthrey Loch, Central Region
A. d. diam.	(54.96±4.52)	46.0-57.2 (50.1±3.6, 12)
B. m. width	(3.9)	3.4-5.0 (4.4±0.4, 12)
D. r. diam.	(35.70±2.83)	29.3-34.0 (32.0±1.6, 12)
Dent. no.	(28.29±1.54)	26-29 (27, 12)
R. p. / d.	-	6-8 (7.5±0.8, 9)
D. length	-	6.6-8.3 (7.5±0.6, 12)
B. length	-	4.9-6.2 (5.6±0.3, 12)
R. length	-	9.2-13.6 (11.6±1.3, 12)
C. p. width	-	1.3-2.5 (1.9±0.3, 12)
Dent. span	(19.12±2.38)	16.6-21.8 (18.9±1.6, 12)

**Table 5.** Morphometric and meristic data for *Trichodina nigra*.

Author	Kazubski and Migala (1968)	This study (a)	This study (b)	This study (c)	This study (d)	This study (e)	This study (f)	This study (g)
Host	<i>Cyprinus carpio</i> 20/4/64-27/10/65	<i>Salmo trutta</i> 11/91	<i>Cyprinus carpio</i> 17/11/92	<i>Oncorhynchus mykiss</i> 18/3/93	<i>Oncorhynchus mykiss</i> 6/93	<i>Salmo trutta</i> 19/8/93	<i>Salmo trutta</i> 23/8/93	<i>Oncorhynchus mykiss</i> 14/8/94
Localisation	Skin	Skin	Skin	Skin	Skin	Skin	Skin	Skin
Locality	Poland	Buckieburn, Central Region	Norfolk	Moffat, Dumfries	Loch Fad, Strathclyde	College Mill, R. Almond, Tayside	Almond Bank, R. Almond, Tayside	R. Devon, Dollar, Central Region
A. d. diam.	33.9-61.5 (47.2, 153)	47.2-70.6 (57.4±5.2, 22)	35.2-52.1 (43.1±4.5, 37)	42.4-57.2 (49.4±4.2, 17)	44.4-47.5 (45.7±1.6, 3)	36.5-47.7 (43.0±3.5, 17)	40.6-48.8 (44.6±2.3, 22)	41.2-53.6 (46.5±3.9, 22)
B. m. width	(5.0)	2.8-7.2 (4.8±0.8, 22)	3.8-5.9 (4.7±0.4, 37)	3.9-6.1 (5.0±0.5, 17)	4.8-5.3 (5.0±0.1, 3)	4.2-5.9 (5.0_0.4, 17)	4.2-5.4 (4.8±0.3, 22)	4.0-9.4 (5.0±0.5, 22)
D. r. diam.	22.6-34.0 (28.5, 153)	22.8-33.3 (28.4±2.2, 22)	20.5-31.8 (25.0±3.0, 37)	24.4-34.4 (29.3±2.7, 17)	24.8-27.4 (25.7±1.4, 3)	22±6-30.4 (26.1±2.2, 17)	24.7-31.3 (27.6±1.6, 22)	24.1-32.2 (27.9±2.3, 22)
Dent. no.	17-28 (22.5, 153)	16-21 (20, 22)	19-27 (22, 37)	20-24 (21, 17)	18	23-25 (25, 17)	23-26 (24, 22)	18-24 (22, 22)
R. p. / d.	9-11	9-11 (9.9±0.7, 22)	8-10 (9.4±0.5, 36)	8-12 (10.3±0.9, 16)	10-11	9-12 (10.3±0.9, 16)	9-12 (10.7±0.8, 22)	8-11 (9.6±0.9, 22)
D. length	-	8.3-10.6 (9.1±0.7, 22)	6.3-9.7 (7.8±0.7, 37)	7.9-10.2 (8.9±0.7, 17)	8.4-9.4 (8.9±0.4, 3)	5.8-7.8 (7.1±0.6, 17)	6.0-8.5 (7.5±0.6, 22)	7.0-9.8 (7.9±0.6, 22)
B. length	-	5.6-7.8 (7.1±0.5, 22)	4.9-6.7 (5.9±0.5, 37)	6.3-7.9 (7.2±0.1, 17)	6.8-7.4 (7.0±0.3, 3)	4.4-5.8 (5.3±0.4, 17)	4.8-5.9 (5.4±0.3, 22)	5.4-8.3 (6.9±0.6, 22)
R. length	-	6.1-8.6 (7.9±0.6, 22)	4.0-7.0 (5.3±0.6, 37)	6.5-11.1 (8.4±1.1, 17)	7.1-9.2 (8.0±1.0, 3)	4.8-7.2 (5.6±0.6, 17)	4.2-6.4 (5.4±0.5, 22)	6.0-9.3 (7.5±0.9, 22)
C. p. width	-	1.7-2.8 (2.2±0.3, 22)	1.7-2.8 (2.2±0.3, 37)	2.2-3.6 (2.7±0.3, 17)	2.1-2.6 (2.4±0.1, 3)	1.8-3.2 (2.5±0.3, 17)	2.1-3.6 (2.7±0.4, 22)	2.3-3.4 (2.9±0.3, 22)
Dent. span	11.1-17.5 (14.8, 153)	14.4-18.3 (17.2±1.1, 22)	11.6-16.0 (13.3±1.0, 37)	15.2-22.2 (18.4±1.7, 17)	16.9-17.5 (17.1±0.3, 3)	10.7-15.6 (13.4±1.1, 17)	11.5-14.6 (13.5±0.9, 22)	13.1-19.3 (17.0±1.5, 22)



**Fig. 3.** A,B - *Trichodina pediculus* from *Gasterosteus aculeatus* (Airthrey Loch); C-F - *Trichodina modesta* from *Abramis brama* (Yorkshire); G - *Trichodina nigra* from *Salmo trutta* (Buckieburn); H - *T. nigra* from *Cyprinus carpio* (Norfolk); I - *T. nigra* from *Oncorhynchus mykiss* (Moffat); J - *T. nigra* from *O. mykiss* (Loch Fad); K - *T. nigra* from *S. trutta* (College Mill); L - *T. nigra* from *S. trutta* (Almond Bank); M - *T. nigra* from *O. mykiss* (Dollar). Scale bar = 10  $\mu$ m.



**Table 6.** Morphometric and meristic data for *Trichodina modesta*

Author Host Localisation Locality	Lom (1970b) <i>Abramis brama</i> Gills River Tisza, Hungary	This study <i>Abramis brama</i> Gills Yorkshire 20/2/93
A. d. diam.	28-43(33)	31.3-42.6 (35.1±3.0, 21)
B. m. width	3-3.5	3.4-4.3 (3.9±0.3, 21)
D. r. diam.	15-20 (18)	18.5-23.9 (20.8±1.6, 21)
Dent. no.	22-25 (23)	22-26 (24, 21)
R. p. / d.	7-8	6-10 (8.3±0.9, 17)
D. length	3-3.5	4.5-5.9 (5.2±0.4, 21)
B. length	4-4.5	4.5-5.8 (5.1±0.4, 21)
R. length	3.5-4	3.8-5.1 (4.5±0.4, 21)
C. p. width	1.5	1.1-1.6 (1.3±0.1, 21)
Dent. span	-	9.3-12.1 (10.8±0.7, 21)

**Table 7.** Morphometric and meristic data for *Trichodina intermedia*

Author Host Localisation Locality	Lom (1961) <i>Phoxinus laevis</i> Gills, rarely skin Czechoslovakia	Our findings (a)* <i>Phoxinus phoxinus</i> Gills Allt Loin, Highlands, 25/5/92	Our findings (b) <i>Phoxinus phoxinus</i> (fry) Skin Castle Semple Water, Strathclyde, 1/10/92	Our findings (c) <i>Phoxinus phoxinus</i> Gills College Mill, R. Almond, Tayside, 3/8/93	Our findings (d) <i>Phoxinus phoxinus</i> Gills Lake Bala, Wales, 30/9/93
A. d. diam.	31-41 (34)	26.7-45.0 (36.0±4.7, 52)	27.5-40.2 (34.5±4.3, 11)	29.9-46.2 (37.6±4.6, 11)	29.2-42.1 (36.3±3.9, 18)
B. m. width	3	2.3-3.4 (2.8±0.3, 52)	1.8-3.0 (2.5±0.4, 11)	2.0-3.1 (2.7±0.3, 32)	2.3-3.3 (2.8±0.3, 18)
D. r. diam.	19-28 (22)	16.1-29.8 (22.9±3.5, 52)	16.6-28.8 (21.5±3.6, 11)	18.0-31.2 (24.2±3.5, 32)	19.3-27.1 (23.5±2.4, 18)
Dent. no.	27-36 (31)	25-37 (27, 52)	25-35 (30, 11)	26-34 (30, 32)	28-35 (31, 18)
R. p. / d.	6-7	6-10 (7.8±0.9, 44)	6.5-9 (7.3±1.0, 6)	5.5-7 (6.3±0.5, 19)	5.5-9 (7.1±1.0, 9)
D. length	5-6	3.0-5.7 (4.0±0.7, 52)	2.7-4.4 (3.6±0.6, 11)	2.7-5.2 (3.8±0.6, 32)	2.9-4.8 (3.6±0.5, 18)
B. length	4	4.0-6.7 (5.3±0.6, 52)	4.1-6.2 (5.0±0.8, 11)	4.3-7.7 (5.4±0.7, 32)	4.1-6.2 (5.2±0.6, 18)
R. length	3.3	2.5-5.7 (4.2±0.8, 52)	2.9-4.9 (4.0±0.7, 11)	3.4-6.0 (4.4±0.7, 32)	3.3-5.0 (4.1±0.5, 18)
C. p. width	1.5	0.8-1.8 (1.0±0.1, 52)	1.1-1.8 (1.4±0.2, 11)	0.9-2.7 (1.8±0.1, 32)	0.8-1.5 (1.2±0.2, 18)
Dent. span	-	8.2-16.3 (10.7±1.6, 52)	8.3-12.2 (10.2±1.4, 11)	8.8-14.1 (10.8±1.4, 32)	8.3-12.3 (10.5±1.2, 18)

\* Kept at room temperature (approximately 20° C) before sampling

**Table 8.** Morphometric and meristic data for recorded populations of *Trichodina intermedia* and *Paratrichodina phoxini*

Species Author	<i>Trichodina intermedia</i> Lom (1961)	<i>Trichodina intermedia</i> Stein (1984)	<i>Trichodina intermedia</i> This study	<i>Paratrichodina phoxini</i> Lom (1963)	<i>Paratrichodina phoxini</i> Stein (1984)
A. d. diam.	31-41 (34)	25.5-43.5	26.7-46.2 (36.3)	30-37 (33)	30-43
D. r. diam.	19-28 (22)	12-28	16.1-31.2 (23.3)	19-22 (21)	19-30
Dent. no.	27-36 (31)	22-36	25-37 (30.1)	30-35 (32)	30-39
Adoral spiral	310-340°	310-340°	280-340°	180-270°	180-270°

appearance of the central circle in *T. tenuidens* is said to be one of the greatest amongst trichodinid species (Lom and Stein 1966). Lom and Stein (1966) also comment on the presence of *T. tenuidens* and *T. domerguei* specimens which, if considered in isolation, cannot be distinguished as one species or the other. These 'intermediate' specimens were thought to represent the extremes in variation of either species. Having studied several thousand silver stained specimens of *T. domerguei* and *T. tenuidens* (this study, unpublished data), intermediate "morphometric" individuals were apparent but could still be identified by their denticle morphology. The high degree of host specificity exhibited by both species, especially *T. tenuidens*, and their presence in marine and freshwater environments, reinforces the close link between the two species.

#### ***Trichodina pediculus* Ehrenberg, 1838**

*Trichodina pediculus* is a widely distributed species occurring mainly on *Hydra*, but also on tadpoles and various species of fish (Kazubski 1991a,b,c). Small numbers of *T. pediculus* were found on the skin of *Gasterosteus aculeatus* (Fig. 3A,B) from Airthrey Loch; morphometric and meristic data are illustrated in Table 4. Denticle morphology is notable for the short, broad, curved blades almost forming a 'crook' at the apex of the anterior margin. In some specimens the anterior blade margin appears to form a continuous radius, in others a pronounced distal surface can be discerned parallel to the edge of the border membrane. The distinguishing features of *T. pediculus* are the denticle rays, which are extremely long and tapering. The centre of the adhesive disc appears granular, with no central circle visible. In view of the low numbers of *T. pediculus* found on sticklebacks in Airthrey Loch (N = 12) during a one year sampling programme (unpublished data), it may be that these findings represent accidental infections from a population parasitising *Hydra* or some fish species.

#### ***Trichodina modesta* Lom, 1970**

A single population of *Trichodina modesta* from the gills of *Abramis brama* in Yorkshire was found during this study. It is relatively small (a. d. diam = 31.1-42.6 µm) and the denticles have relatively delicate inner rays, straight or slightly curved posteriorly. The blades are elongated (Lom 1970b), and gently curved with a noticeable thickening of the posterior border. The denticle blades usually terminate with a rounded anterior margin, but sometimes form a flattened distal surface. The oral cilia express a turn of approximately 360-400°, similar to most other *Trichodina* species. Photo-micrographs, morphometric and meristic data are given in Fig. 3C-F and Table 6.

The population of *T. modesta* found in this study agrees closely with Lom's (1970b) nominate population

from *A. brama* in form and size. The description of *T. modesta* from *Blicca bjoerkna* collected during the spring (Arthur and Lom 1984), presents a smaller mean specimen size (mean a. d. diam = 27.0 µm). Due to the small number of observed populations, the extent of morphological variation in this species is unknown.

*T. modesta* bears some resemblance to summer forms of *T. mutabilis* Kazubski, 1968 (Grupcheva 1975, Lom et al. 1976, Albaladejo and Arthur 1989) and *T. rostrata* Kulemina, 1968 (Lom 1970b, Kashkovsky 1974, Grupcheva and Sedlacek 1993). However, both these species differ in denticle form and are considerably larger in size.

*T. spathulata* Kulemina, 1968 from *A. brama* fry is cited (Lom 1970b) as being significantly smaller than *T. modesta* with wider blades. However, Kashkovsky's (1974) photomicrograph and morphometric measurements for *T. spathulata* from *A. brama* (mean a. d. diam = 26 µm) do not appear to vary significantly from previous descriptions of *T. modesta*. The specimens of *T. modesta* found during this study illustrated greater variation in denticle blade form than has previously been reported; some specimens conforming to Lom's (1970b) original description, while others displayed slightly broader denticles. Considering that all the descriptions of *T. modesta* and *T. spathulata* are from closely related "bream" host species, the small discrepancy in form and size may suggest that the two species are synonymous. In this case the populations of *T. modesta* described so far, would revert to *T. spathulata*.

#### ***Trichodina nigra* Lom, 1960**

Seven populations of a *Trichodina* species were found on the skin of *Cyprinus carpio*, *Salmo trutta* and *Oncorhynchus mykiss* resembling *Trichodina nigra* as described in the literature, with an adoral ciliary spiral of 390-430°. Photomicrographs of specimens, and morphometric and meristic data from all the populations are illustrated in Fig. 3G-M and Table 6. Again, the individual cells illustrated do not necessarily represent "type" specimens for each population, but rather illustrate variation in denticle morphology within the species.

Populations (a) from *S. trutta*, (c), (d) and (g) from *O. mykiss* are very similar morphologically, and are characterised by massive denticles with broad curving blades, which display considerable inter- and intra-population variation. Some blades end in a sharp point, whilst others are more rounded; some specimens display a continuous curving anterior border and others a well defined distal surface. The denticle rays are generally longer than the blades and are angled straight down or to the posterior side of the denticle with a pronounced apophysis. They taper from a broad or very broad junction with the central part to a rounded tip.

Population (b) from *C. carpio* resembles the previous group in many ways, the exception being slightly more rounded points to the blades and slightly shorter denticle rays which are approximately equal in length to the blades. Some specimens of population (b) are identical with specimens from the previous group, except for slightly shorter rays.

Populations (e) and (f) from *S. trutta* have similar proportions to population (b), but have a higher mean denticle number. The denticle blades are slightly shorter, sometimes with a defined “elbow” in the lower anterior margin.

Thus, three basic morphological variants could be discerned in this study, the first from *S. trutta* and *O. mykiss* (a, c, d and g), the second from *C. carpio* (b) and the third from *S. trutta* (e and f). The effect of host species on morphology is unclear, with no obvious trend being apparent.

Population (a) from *S. trutta* (Buckieburn) is almost identical with some winter specimens of *T. nigra* as described by Kazubski and Migala (1968). The specimens in (a) are very large, but were sampled during late November when water temperature was very low. Some specimens in (a) bear a very close resemblance, although smaller, to specimens of *T. nigra* f. *cobitis* Lom, 1960 (later reclassified as *T. cobitis* Lom, 1970).

Population (b) from *C. carpio* (Norfolk) was readily identifiable with that of *T. nigra* described by Kazubski and Migala (1968), and only varied slightly in mean denticle span. Certain specimens from population (b) also bear some resemblance to specimens of *T. nigra* f. *kamchatika* Stein, 1967 described by Stein (1967); this species is considered a synonym of *T. strelkovi* Chan, 1960 by Lom (1970a).

Population (c) from *O. mykiss* (Moffat) consists of specimens agreeing with the descriptions of *T. nigra* by Kazubski and Migala (1968), although some specimens differ in blade form and more closely resemble *T. cobitis*.

Population (d) from *O. mykiss* (Loch Fad) consisted of only three specimens, which were very similar to some of Kazubski and Migala's winter specimens of *T. nigra*.

Populations (e) and (f) from *S. trutta* (College Mill and Almond Bank) were almost identical, and were most distinct from the normal form of *T. nigra* being smaller in diameter and possessing more angular denticle blades. Various specimens of populations (e) and (f) illustrated similar blade form to specimens of *T. nigra*, *T. nigra* f. *gobii* Lom, 1960 (later reclassified as *T. gobii* Lom, 1970) and *T. nigra* ssp. *lucioperca* Lom, 1970 (later reclassified as *T. lucioperca* Lom, 1970) described in the literature by Kazubski and Migala (1968) and Lom (1961, 1970b) respectively.

Population (g) from *O. mykiss* (Dollar) consisted of some ‘normal’ forms as described by Kazubski and

Migala (1968), but also had some specimens which displayed massive denticles. These specimens illustrated many of the typical *T. nigra* features, and were very similar to a specimen of this species illustrated by Albaladejo and Arthur (1989) from the Philippines.

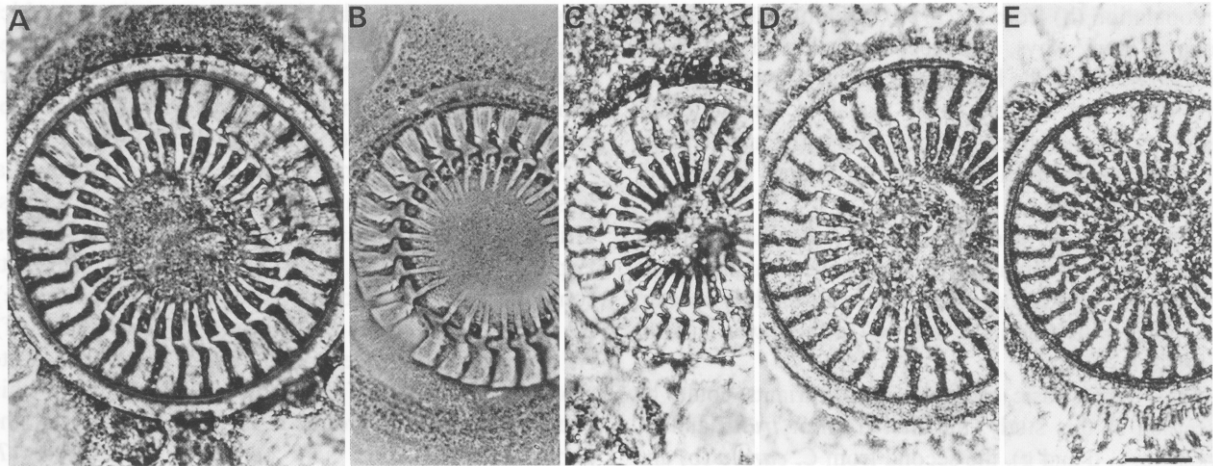
When all the specimens are considered together, at least one specimen in each population bears a close affinity to one specimen in each of the others. Population (b) appears to be intermediate in form, with some specimens resembling those in populations (a), (c), (d) and (g); and others those in populations (e) and (f). All the populations described in this study appear to represent a gradient of morphological variability within one closely related group. It is proposed that all the populations described here belong to the species *T. nigra*. The resemblance of specimens found in this study to several different species formerly classified as forms or subspecies of *T. nigra* underlines the reason why it remains one of the most difficult species to identify within the genus.

#### ***Trichodina intermedia* Lom, 1960**

Four populations of a species resembling *Trichodina intermedia* were found inhabiting the gills (also skin in fry) of *Phoxinus phoxinus* during this study. Specimens from the four populations described in Table 7 are characterised by an adhesive disc diameter of 26.7-46.2 µm and a denticle number of 25-37. The denticles appear to have rectangular blades which often widen towards a flattened distal surface. Most specimens display straight blades with parallel margins, but some illustrate a slight posterior curvature. The inner rays are slightly shorter than the blades and are stouter than in *Paratrachodina incisa* Lom, 1959, which was always found in mixed infections on *P. phoxinus*. The rays are straight or very slightly curved anteriorly, usually being angled straight down. The adoral ciliary spiral illustrates a turn of 280-340°.

Populations from (a) Allt Loin, (b) Castle Semple Water, (c) College Mill and (d) Lake Bala illustrate a high degree of similarity. Population (a) illustrates the greatest range in denticle number (25-37) which is probably due to the large sample size (N = 52). Population (b) has the smallest mean adhesive disc diameter, which may be due to the artificially high water temperature from which they were sampled.

The denticles vary considerably in size, with a denticle span ranging from 8.2-16.3 µm within the four populations. Denticle form is also variable, with some specimens illustrating broader blades with a high degree of curvature in population (a). Population (b) illustrates uniform denticle appearance, with the exception of one specimen with prominent notches in the anterior blade margins. A small number of specimens in population (c) have unusually curved blades, and population (d) displays typical denticle blade form. Photomicrographs



**Fig. 4.** A,B - *Trichodina intermedia* from *Phoxinus phoxinus* (Allt Loin); C - *T. intermedia* from *P. phoxinus* (Castle Sempole Water); D - *T. intermedia* from *P. phoxinus* (College Mill); E - *T. intermedia* from *P. phoxinus* (Lake Bala). Scale bar = 10  $\mu$ m.

of specimens found during this study are illustrated in Fig. 4A-E.

Only two reports of *T. intermedia* were found in the literature, Lom (1961) from *Phoxinus laevis* in Czechoslovakia and Stein (1979, 1984) from the same fish species in the USSR. The majority of specimens found during this study closely resembles the population described by Lom (1961), and are therefore identified as *T. intermedia*. As previously mentioned, this species was found in mixed populations with *P. incisa* in all cases. The mean adhesive disc diameter of the two species is considerably different, but the ranges overlap slightly. Some very small specimens of *T. intermedia* closely resemble *P. incisa*. They can only be differentiated in the context of a large number of photomicrographs of each species, enabling visual comparison. Blade form is usually different, with no apparent notch in most *T. intermedia* specimens. These small specimens of *T. intermedia* are also similar to specimens of *Paratrachodina corlissi* Lom et Halder, 1977 illustrated by Lom and Halder (1977). Cluster analysis was performed on the pooled data of *P. incisa* and *T. intermedia* using Systat 5.3 (1991). Cluster analysis detects natural groupings within a data set. This demonstrated that the highest probability was that two clusters existed within the data. When cross referenced with the original photomicrographs, the two clusters were found to contain the specimens visually determined as *T. intermedia* and *P. incisa*.

Two endozoic species of the genus *Paratrachodina* Lom, 1963 have been reported from *P. phoxinus*; these are *Paratrachodina alburni* Vojtek, 1957 and *P. phoxini* Lom, 1963, both reported by Lom and Halder (1976). Both these species are very similar to the populations of *T. intermedia* found during this study, but *P. phoxini* is almost identical in proportion and appearance. Table 8

illustrates measurements for the principal variables in recorded populations of *T. intermedia* and *P. phoxini*. Some specimens of *T. intermedia* found during this study illustrated a greater affinity to the photomicrographs of *P. phoxini* illustrated in Lom (1960), than those of *T. intermedia* shown in Lom (1961). The main difference between the two species is the smaller turn of the aboral cilia in *P. phoxini*.

*T. intermedia* through its morphology occupies a difficult position, apparently illustrating affinities with *Paratrachodina* species and displaying aboral cilia with a spiral smaller than the lower limits of *Trichodina*. Lom and Halder (1977) state that the upper limit of the adoral cilia in *Trichodinella* Šrámek-Hušek, 1963, *Tripartiella* Lom, 1959 and *Paratrachodina* is 290°, and the lower limit of *Trichodina* is 330°. Thus, *T. intermedia* with an adoral ciliary spiral of 280-340° (this study) straddles the divide.

Some other species of *Trichodina* have been found to have adoral ciliary spirals below 330° (Khan 1972, Grupcheva and Lom 1980) including *T. oviducti* Khan, 1972, *T. valkanovi* Grupcheva et Lom, 1980 and *T. jiroveci* Grupcheva et Lom, 1980. This latter species has typical *Trichodina* denticles, reminiscent of those seen in *T. nigra*.

Thus, the importance of the length of the adoral cilia as a generic characteristic appears to be less distinct than previously thought, and recently described species have been in effect classified on the basis of denticle morphology alone.

## CONCLUSIONS

Two *Trichodina* species, previously reported from the UK, *T. domerguei* and *T. tenuidens*, were redescribed. Five additional species, *T. acuta*, *T.*

*pediculus*, *T. modesta*, *T. nigra* and *T. intermedia*, are reported for the first time from British freshwater fish.

New host records include *Salmo trutta* and *Phoxinus phoxinus* for *T. acuta*, *Gasterosteus aculeatus* for *T. pediculus* and *S. trutta* for *T. nigra*.

All the *Trichodina* species described in this study have been previously recorded from continental Europe. Given the similarity in freshwater fish fauna and the relatively short period of separation between the UK and mainland Europe in evolutionary terms this is to be expected.

The host specificity displayed by *Trichodina* species found during this study agrees with reports by other authors. *T. acuta* and *T. nigra* illustrated low host specificity, whilst *T. domerguei*, *T. tenuidens*, *T.*

*modesta* and *T. intermedia* illustrated a high degree of host specificity.

Intraspecific morphological variation is considerable, with a greater degree of variation present in *T. acuta* than previously described. This variation in size and denticle morphology is probably the most important consideration in trichodinid taxonomy, the possibility remains that many populations are incorrectly classified as new species through under estimation of intraspecific morphological variability.

**Acknowledgements.** This work was carried out by W. Gaze during the tenure of a NERC funded studentship awarded to R. Wootten.

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Received 7 February 1997

Accepted 30 January 1998