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Trichodinids (Ciliophora: Trichodinidae) from Native and Exotic Australian Freshwater Fishes

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Summary. There are very few data on trichodinids of freshwater fishes in Australia. 2003 fishes were surveyed across Eastern Australia to investigate the diversity of trichodinids present, to determine which species have been introduced with exotic fishes and to determine the extent to which these species have crossed into native fish populations. Twenty-one putative trichodinid species were recovered from the 33 fish species examined. *Trichodina heterodentata*, *T. mutabilis* and *T. reticulata* were the exotic species recovered regularly; a single specimen matched a fourth exotic species, *T. acuta*. All four exotic species are redescribed from Australian material. *Trichodina heterodentata* was recorded from 17 species of fishes, 15 of which were new host records; this species is identified as one of emerging importance in fish parasitology and a list of its known hosts is presented. Two new native species are also described based on silver stained specimens: *T. cribbi* sp. n. from *Hypseleotris galii*, *H. klunzingeri*, and *Hypseleotris* sp. 5; and *T. bassonae* sp. n. from *Selenotoca multifasciata*. *Trichodina cribbi* is characterised by a large circular central inclusion and approximately 28 denticles, which have a blade length slightly greater than the ray length. *Trichodina bassonae* is characterised by a small, round, central inclusion and approximately 25 denticles, which have straight, non tapering rays that are in line with the leading edge of the denticle blade. It is estimated that the Australian trichodinid fauna may include up to 150 as yet undescribed species and represents a major source of unexplored biodiversity.

Key words: Australian, endemic, exotic, richness, *Trichodina bassonae* sp. n., *Trichodina cribbi* sp. n., trichodinids.

INTRODUCTION

Data on trichodinids of Australian freshwater fishes are sparse and fragmentary. No individual species have been described from either native or exotic freshwater fishes in Australia. Lom and Dyková (1992) recorded an unspecified *Trichodina* species from the gills of *Gambusia holbrooki* at Armidale, New South Wales. Langdon (1989) listed *Trichodina* spp. as "parasitic on native and introduced fishes" but provided no data on which *Trichodina* species infected which host species, nor any data on shared *Trichodina* species. Rowland and Ingram (1991) discussed the ectoparasitic diseases of Murray cod (*Maccullochella peeli*), golden perch (*Macquaria ambigua*) and silver perch (*Bidyanus bidyanus*). Although they identified *Chilodonella hexasticha*, *Ichthyophthirius multifilis* and *Ichthyobodo necator* specifically, *Trichodina* spp. (and *Tetrahymena* spp.) were regarded as a single group. These authors recognised that "the identity and

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number of species of *Trichodina* on freshwater fishes in Australia are not known".

The aims of this study were: to identify which trichodinid species occur on Australian populations of exotic freshwater fishes; to investigate the diversity of the Australian trichodinid fauna; and to quantify the degree to which trichodinid species have been exchanged between native and exotic fishes. The null hypothesis that no exchange of trichodinid species between native and exotic fish species has occurred was tested using survey data and comparisons with known trichodinid records on Australia's exotic fishes in their original ranges.

MATERIALS AND METHODS

Collection and dissection protocol

Trichodinid ciliates were collected on an opportunistic basis during a survey for other parasites that encompassed 58 sites throughout Victoria, New South Wales, the Australian Capital Territory and Queensland. In addition, a dedicated survey was conducted at 15 sites in Queensland to obtain accurate data on prevalence, host and microhabitat specificity. Site abbreviations are as follows: **ALR** - Albert River; Queensland (Qld); **ATH** - Atherton, Qld; **BCF** - Crayfish Farm, Beenleigh Qld; **BMP** - Lake Burley-Griffin at Black Mountain Peninsula, Australian Capital Territory (ACT); **BOC** - Boorolong Creek, New South Wales (NSW); **BRB** - Billabong at Bangarang Road, Echuca, Victoria (Vic); **BRF** - Brisbane River at Fernvale, Qld; **CBL** - Condamine River below Leslie Dam, Qld; **CRH** - Condamine River Headwaters, Qld; **CRW** - Condamine River at Warwick, Qld; **EBK** - Lake Burley-Griffin at East Basin Kingston, ACT; **EGC** - England Creek, Qld; **ENC** - Enoggerra Creek, Qld; **ERS** - Edward River at Steven's Weir, Deniliquin, NSW; **GBL** - Gum Bend Lake, Condobolin, NSW; **KB216** - Kalinga Park Creek, Qld; **LGN** - Lake Ginninderra, ACT; **MNC** - Monsildale Creek, Qld; **MOC** - Moody's Creek, north Qld; **NFC** - Narranderra Fisheries Centre, NSW; **NPR** - North Pine River, Qld; **OVR** - Ovens River, Vic; **RGR** - Moggill Creek at Rafting Ground Road, Qld; **SRW** - Shoalhaven River at Warri Bridge, NSW; **WCC** - West Court Creek, north Qld; **WKN** - Walkamin Research Station, north Qld; **WVN** - Lake Wivenhoe, Qld.

Fishes were collected by cast-netting, dip-netting, electrofishing and line fishing, and were separated into species-specific plastic bags on site. In the laboratory, fishes were maintained in aerated 20 l tanks with water from the collection site. Dissections were made within three days to minimise the effect of collection stress on trichodinid prevalence.

Fish were killed by pithing the brain, then identified, measured (caudal fork length) and sexed (if possible), and immediately dissected in freshwater. Each fin and gill was removed and placed in a separate Petri dish in aged water and the skin scraped into another dish of aged water. Each dish was then examined under dissecting microscope for the presence of trichodinids; any present were pipetted onto a clean or albuminised glass slide (depending on staining regimen) and allowed to air dry.

Morphometrics

Stained preparations were made using two silver salt staining protocols: Foissner's modification of Klein's dry silver nitrate technique (Foissner 1991), and Basson's version of Lom's dry silver nitrate technique (Lom 1958). Measurements presented here follow the protocols of Lom (1958). Three denticles were measured from each specimen and the means for denticle measurements are therefore based on 3n denticles. Measurements were made using a system similar to that described by Roff and Hopcroft (1986), with a digitising tablet and a drawing tube attached to a compound microscope. All measurements are given in micrometres. Type material was lodged in the Queensland Museum.

Drawing and photography techniques

Representatives of each putative species from each host species were photographed using a 35 mm camera attached to a DIC compound microscope. These photographs were the basis for the drawings of each trichodinid species. Drawings were made by enlarging the photographs by 200% on a photocopier, overlaying the resulting image with architectural film and tracing the morphological features. The ink drawings were then scanned and the resulting files edited in Adobe Photoshop© 5.0.

RESULTS

A total of 2003 fishes was dissected, representing 33 host species and 58 sites across Queensland, New South Wales, Victoria and the Australian Capital Territory. From these, 21 putative species of trichodinids were recovered, 6 of which are discussed here. Three exotic trichodinid species were recovered: *Trichodina heterodentata*, *T. mutabilis* and *T. reticulata*. A single specimen matching a fourth exotic species, *T. acuta*, was also recovered. These four species of exotic trichodinids are redescribed here to confirm their identity and to provide data on their distribution among hosts in Australia. In addition, two new species of *Trichodina* are described from native fish species: *T. cribbi* sp. n. and *T. bassonae* sp. n. The remaining 15 trichodinid morphotypes are not described here.

Descriptions

Trichodinidae Raabe, 1963
Trichodina Ehrenberg, 1838

***Trichodina heterodentata* Duncan, 1977 (Fig. 1)**

Hosts: [Host (number of infected hosts examined)] Ambassidae: *Ambassis agassizi* (4); Apogonidae: *Glossamia aprion gilii* (1); Cichlidae: *Oreochromis mossambicus* (1); Cyprinidae: *Cyprinus carpio* (2); Eleotridae: *Hypseleotris compressa* (2); *Hypseleotris*

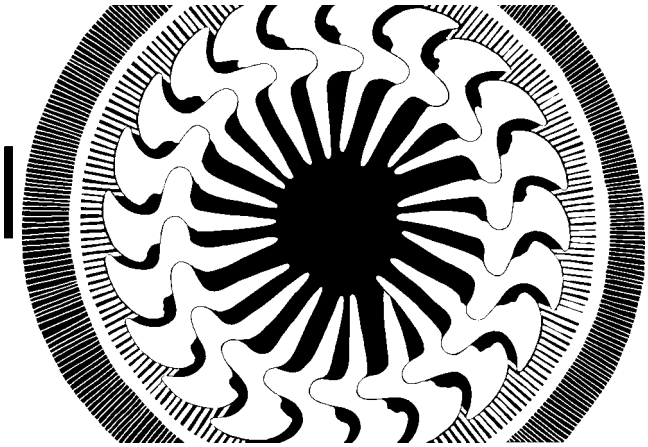

Fig. 1. *Trichodina heterodentata* Duncan, 1977 from the skin of *Ambassis agassizi.* Scale bar 10 µm.

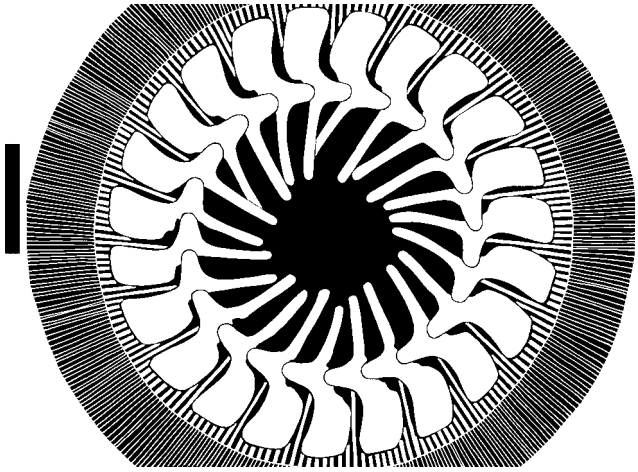

Fig. 2. *Trichodina mutabilis* Kazubski *et* Migala, 1968 from the skin of *Cyprinus carpio.* Scale bar 10 µm.

galii (2); *Hypseleotris klunzingeri* (9); *Philypnodon grandiceps* (1); Galaxiidae: *Galaxias maculatus* (2); *Galaxias olidus* (1); Gerreidae: *Gerres* sp. (1); Percichthyidae: *Macquaria ambigua* (2); Poeciliidae: *Gambusia holbrooki* (5); *Poecilia reticulata* (6); *Xiphophorus helleri* (1); *Xiphophorus maculatus* (6); Pseudomugilidae: *Pseudomugil signifer* (1).

Localities: KB216, WKN, BRB, NPR, NFC, BCF, EBK, WVN, GBL, MNC, BOC, SRW.

Microhabitat: Skin, fins, occasionally gills.

Description: Description based on 18 specimens: [Host species, Autopsy number (number of specimens)] *A. agassizi*, AD334 (3); *C. carpio*, T141 (1); *G. holbrooki*, AD309 (1); *G. aprion gilii*, AD311 (1); *H. compressa*, NPR5 (1); *H. galii*, T137 (1), BCF5 (1), BCF6 (1); *H. klunzingeri*, T130 (1); *O. mossambicus*, NPR12 (1); *P. signifer*, AD252 (1); *X. helleri*, KB20/10/97_8 (1); *X. maculatus*, AD307, AD310, KB20/10/97_1 (1) KB20/10/97_3 (1). Medium to large disc-shaped cell; adhesive disc 56.9 (41.2-89.2) in diameter; denticle ring 31.2 (24.7-37.4) in diameter. Denticles 23 (21-26); denticle span 17.2 (12.5-23.9). Denticle with strongly curved blade ending in a sharp point, blade 5.2 (4-7.4) long, 5.6 (4-8.3) wide. Central part elongate, tip rounded, 3 (2.3-4.6) long, 4.4 (3.1-6.4) wide. Projection of central part not visible. Ray tapering evenly from central part to pointed tip, 7.9 (5.5-11.2) long, 1.9 (1.1-3) wide at widest point. Central disc without inclusions of any kind. Radial pins prominent, 11 (10-13) pins per denticle. Nuclear apparatus not observed.

Taxonomic remarks: *Trichodina heterodentata* is a distinctive species characterised by the robust, strongly sickle-shaped denticle blades with pointed ends, the evenly tapering rays with pointed tips, the absence of any central inclusions and the prominence of the radial pins. It was originally described from cultured cichlids, *Oreochromis mossambicus* from the Philippines, but has subsequently been recorded from a large number of fish species (see Table 1). Morphometric data for the present material fall within the ranges for *T. heterodentata* presented in the original description by Duncan (1977) and subsequent redescriptions by Van As and Basson (1989), Kruger *et al.* (1993) and Basson and Van As (1994). Van As and Basson (1989) and Basson and Van As (1994) noted a degree of morphological variability in isolates of *T. heterodentata*; a similar degree of variability was evident in the present material, especially with respect to the ray length and the degree of curve in the distal blade edge. The distinctiveness of the denticle shape, however, made identification of this species relatively easy.

Trichodina mutabilis Kazubski *et* Migala, 1968 (Fig. 2)

Hosts: Cyprinidae: *Cyprinus carpio* (3); Poeciliidae: *Gambusia holbrooki* (1)

Localities: BCF.

Microhabitat: Fins, gills.

Description: Description based on seven individuals: *C. carpio* BCF12/1/98_1 (4), BCF12/1/98_6 (1);

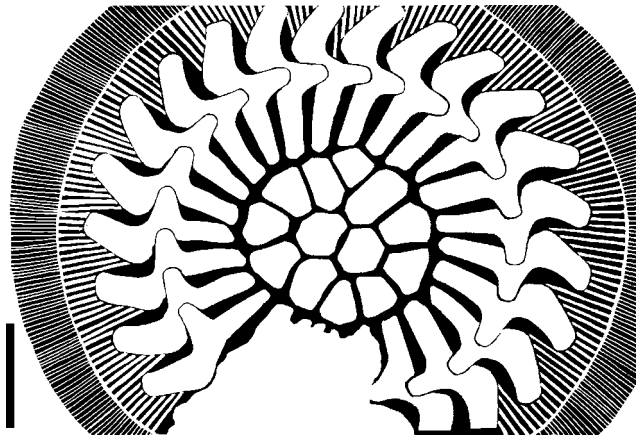

Fig. 3. *Trichodina reticulata* Hirschmann *et* Partsch, 1955 from the skin of *Carassius auratus*. Scale bar 10 µm.

G. holbrooki BCF12/1/98_8 (2). Medium to large disc-shaped cell; adhesive disc 45.9 (40.5-55.7) in diameter, denticle ring 27.6 (24-37.5) in diameter. Denticles 24 (22-26); denticle span 15.4 (11.5-19). Denticle blade oblong, largely parallel to radial of disc, with squared distal end, blade 5.6 (4.6-7) long, 4 (3.4-5.3) wide. Central part narrow, with oblong to rounded overlapping end; 1.9 (1.3-2.4) long, 3.5 (2.7-4.5). Projection of central part not visible. Ray narrow with no taper, tip blunt to square; 7.3 (5.4-9) long, 1.4 (1-2) wide. Central disc without inclusions of any kind. Radial pins 11 (9-13) per denticle. Nuclear apparatus not observed.

Taxonomic remarks: Our material falls within the ranges for this species in the description by Kazubski and Migala (1968) and a subsequent redescription by and Basson and Van As (1994).

Trichodina reticulata Hirschmann *et* Partsch, 1955 (Fig. 3)

Hosts: Cyprinidae: *Carassius auratus* (2), *Cyprinus carpio* (1).

Localities: SRW, GBL, NFC.

Microhabitat: Skin, fins.

Description: Description based on five individuals from *C. auratus* G372. Medium to large disc-shaped cell; adhesive disc 48.6 (40.9-54.2) in diameter, denticle ring 30.4 (26-34.3) in diameter. Denticles 24 (23-25); denticle span 13.8 (11.8-14.9). Denticle blade curved on inside margin but roughly angular on outside margin, with squared distal end, 5.6 (4.8-6.7) long, 4 (3.4-4.6) wide. Central part oblong, with oblong to rounded overlapping end; 2.5 (2.2-2.9) long, 3.7 (3.3-4.3) wide. Projection of central part not visible. Ray with little taper, tip blunt to square; 5.2 (4.2-5.8) long, 1.9 (1.7-2.1) wide at widest point. Central disc with 12 (10-14) icosahedral inclusions (mean diameter 4 (2.5-6.3)); inclusions give impression of a single large inclusion with reticulated markings. Radial pins prominent 10 (9-11) per denticle. Nuclear apparatus not observed.

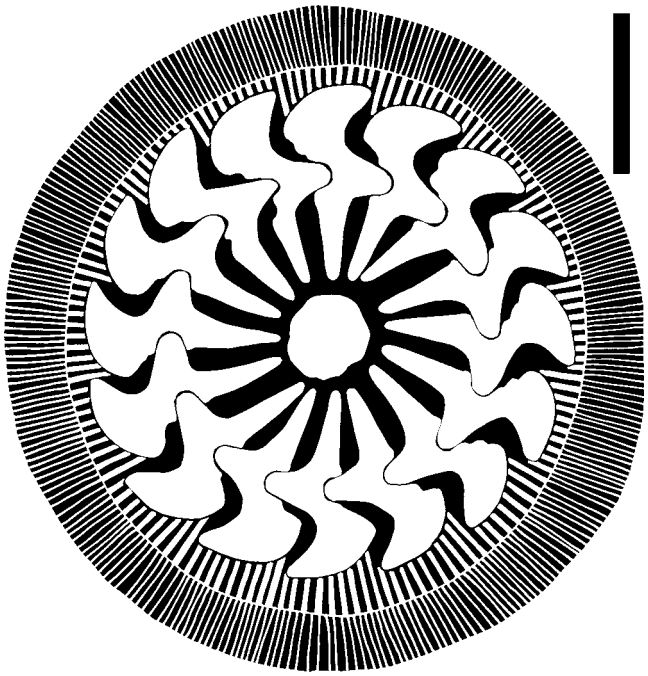

Fig. 4. *Trichodina cf. acuta* Lom, 1961 from the skin of *Poecilia reticulata*. Scale bar 10 µm.

Taxonomic remarks: *Trichodina reticulata* is a highly distinctive species well-known as a pathogen of *Carassius* spp. and other cyprinids in aquaculture and aquaria. The central inclusions are unlike those of almost any other *Trichodina* species, while the angular outer edge to the blade, prominent radial pins and large cell size only serve to confirm the diagnosis. Our material is indistinguishable from the redescription in Basson *et al*. (1983) as well as photographs of this species in Lom (1961), Wellborn (1967) and Van As and Basson (1987). Basson and Van As (1994) observed that this species is primarily a parasite of *Carassius* species and that it has been widely distributed around the world with goldfish, *C. auratus*, and crucian carp, *C. carassius* and is now present in the former USSR, Eastern Europe, Iran, North Korea, Japan, China, Indonesia, Israel and the USA. Neither *C. auratus* nor *Cyprinus carpio* is a new host record for this parasite (see Lom and Dyková 1992).

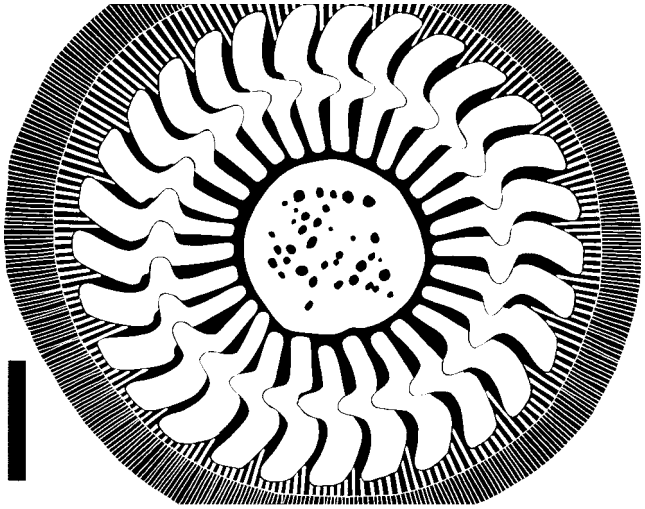

Fig. 5. *Trichodina cribbi* sp. n., from the skin of *Hypseleotris klunzingeri*. Scale bar 10 µm.

Trichodina cf. acuta Lom, 1961 (Fig. 4)

Hosts: Poeciliidae: *Poecilia reticulata* (1)
Localities: WKN.
Microhabitat: Skin

Description: Description based on the single specimen from T144. Medium disc-shaped cell; adhesive disc 33.8 in diameter; denticle ring 20.7 in diameter. Denticles 16; denticle span 12.4 (12.1-12.8). Denticle with curved blade ending in a sharp point, blade 4 (3.9-4.1) long, 4.5 (4.1-4.6) wide. Central part slightly elongate, tip rounded, 2.4 (2.3-2.6) long, 3.8 (3.6-4) wide. Projection of central part not visible. Ray tapering evenly from central part to pointed tip, 5.3 (4.8-5.7) long, 1.8 wide at widest point. Central disc with single, roughly circular inclusion 5.1 in diameter. 10 (9-11) radial pins per denticle. Nuclear apparatus not observed.

Taxonomic remarks: *Trichodina cf. acuta* is a problematic specimen. It is certainly very similar to figures of *T. acuta* from a number of sources (Lom 1961; Kulemina 1968; Basson *et al*. 1983; Van As and Basson 1989; Basson and Van As 1993, 1994), more so in fact than *T. compacta*, which was only discriminated from *T. acuta* by Van As and Basson (1989). One significant difference concerns the number of denticles. Our specimen has 16 denticles, which is two fewer than the smallest number seen in any of the figures mentioned above and three fewer than the mean in the original description of Lom (1961). The absolute range given in Lom (1961), however, is from 15-23, a range which incorporates our specimen. The central disc of our specimen is also rather small at 5.1, slightly more than half the diameter of the disc measured in Van As and Basson (1989). It may be worth noting, though, that the specimens in that paper were the largest and had the highest number of denticles of any description we are aware of (20-23). Apparently the species shows considerable morphological variability. The characteristics of this specimen are sufficient to assign tentatively this specimen to *T. acuta*, but the examination of more specimens is essential to confirm the diagnosis.

Trichodina cribbi sp. n. (Fig. 5)

Type host: Eleotridae: *Hypseleotris klunzingeri* (3)
Other hosts: Eleotridae: *Hypseleotris galii* (1), *Hypseleotris* sp. 5 (1)
Type locality: Black Mountain Peninsula, Lake Burley Griffin, Canberra, Australia
Localities: BCF, EC, NFC, ERS, CRW, GBL.
Microhabitat: Gills
Etymology: This species is named after Australian parasitologist Thomas H. Cribb.

Description: Description based on 12 specimenss from *H. klunzingeri*: T121 (1), T126 (5), T136 (6). G464586-G464590 Medium to large disc-shaped cell; adhesive disc 51.7 (45.6-59.2) in diameter, denticle ring 28.2 (23.7-31.9) in diameter. Denticles 29 (25-31); denticle span 13.7 (11.6-15.5). Denticle blade curved on inside margin but roughly angular on outside margin, with bluntly-squared distal end, 6.3 (5.1-7.7) long, 3.3 (2.4-4.3) wide. Central part oblong, with slightly-tapered, rounded overlapping end; 2.0 (1.4-2.7) long, 2.9 (2.3-3.5) wide. Projection of central part not visible. Ray with little taper, sometimes curved anteriorly, tip blunt to rounded; 4.6 (3.5-6) long, 1.2 (0.9-1.9) wide at widest point. Central disc with 1 large, roughly circular inclusion (mean diameter 14.3 (10.6-17.4)); sometimes with darker argentophilic spots towards its centre. Radial pins indistinct, 10 (9-11) per denticle. Nuclear apparatus and adoral spiral not observed.

Taxonomic remarks: This species is somewhat similar to the population of *T. jadranica* Raabe, 1958 as described by Lom and Dyková (1992), but differs in having blunter denticle blades, thicker denticle rays and in having twice the diameter of the adhesive disc. In morphology, the denticles are very similar to *T. porocephalusi* Asmat, 2001, a species also described from eleotrid fishes. There are several important differences, however. The mean disc width of our material (51.7) is greater than the maximum reported for *T. porocephalusi* (50.5). We also recorded a mean

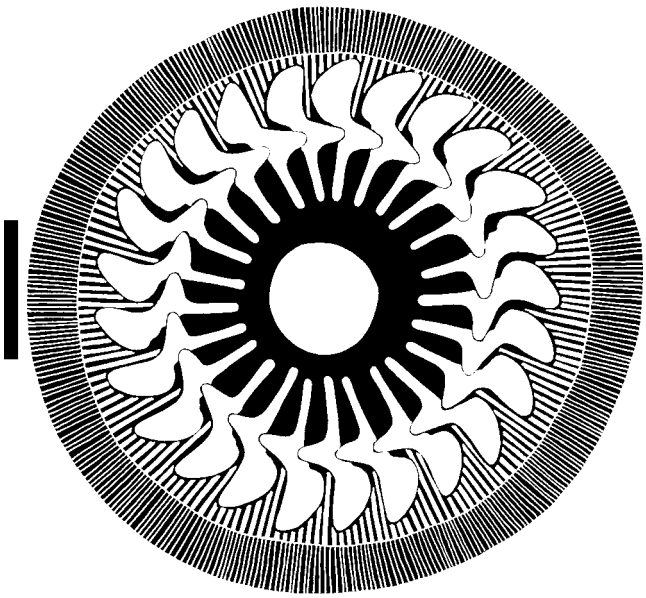

Fig. 6. *Trichodina bassonae* sp. n., from the fins of *Selenotoca multifasciata*. Scale bar 10 µm.

denticle number (29) five greater than that of Asmat's material (Asmat 2001). Finally, our mean number of pins per denticle (10) is greater than the maximum number in *T. porocephalusi* (9). These differences serve to unequivocally separate the species, though the similarity of morphology and hosts suggests a close relationship.

***Trichodina bassonae* sp. n. (Fig. 6)**

Type host: Scatophagidae: *Selenotoca multifasciata* (1)

Type locality: Albert River, South-East Queensland, Australia.

Microhabitat: Fins, particularly the anal fin.

Etymology: This species is named after South African parasitologist Linda Basson, whose contribution to the taxonomy and systematics of trichodinids has been extensive.

Description: Description based on 12 specimens from T143. G464591-G464593. Small to medium-sized disc-shaped cell; adhesive disc 33.3 (30.2-37.9) in diameter, denticle ring 22.9 (19.7-26.4) in diameter. Denticles 24 (23-26); denticle span 9.8 (8.7-10.8). Denticle blade straight on leading edge, roughly rounded on trailing margin, with bluntly-pointed distal end, 3.9 (3.4-4.4) long, 2.9 (2.5-3.6) wide. Central part oblong, with slightly-tapered, rounded overlapping end; 1.4 (1.0-1.8) long, 2.8 (2.2-3.5) wide. Projection of central part not visible. Denticle ray with no taper, tip blunt to rounded; 3.5 (3.0-4.4) long, 1.0 (0.5-1.4) wide at widest point. Central disc with 1 small to medium, roughly circular inclusion of mean diameter 9.0 (5.9-11.3). Radial pins 10 (9-11) per denticle. Nuclear apparatus and adoral spiral not observed.

Taxonomic remarks: This material is characterised by a unique configuration of having a denticle blade with a straight leading edge and a ray which is not tapered. This conformation, in combination with the circular central inclusion, is not similar to any published trichodinid species.

DISCUSSION

Exotic trichodinids

Of the 21 putative trichodinid species recovered, four have probably been introduced with exotic fishes. *Trichodina mutabilis* has almost certainly been introduced along with carp, *Cyprinus carpio*. Since its original description by Kazubski and Migala (1968), it has become a well-known and characterised parasite of carp as well as a number of other cyprinid species (Basson *et al*. 1983). In addition to carp, it also infected the unrelated exotic mosquitofish, *Gambusia holbrooki*, at the sole site from which it was recovered in this study, a crayfish farm near Beenleigh, Queensland. *Trichodina mutabilis* may not be widespread in Australia, however, despite the extensive distribution of carp in inland drainages. It was not recovered from any carp or mosquitofish (combined sample size N > 400) collected in inland areas and, as such, appears to be restricted to the Albert River carp population (the ultimate source of the crayfish farm fish). We have collected additional parasitological evidence that suggests that this population has a distinct and separate origin to that of the inland, Boolarra strain of carp; carp at the crayfish farm harbour a dactylogyrid monogenean species (*Dactylogyrus cf arcuatus*) and a bomolochid copepod which are not found on inland carp, which only harbour *Dactylogyrus anchoratus* (Dove and Ernst 1998).

Trichodina reticulata appears to have been introduced with its type host, the ornamental goldfish *Carassius auratus*. In the survey, it was restricted to the two cyprinid fish species: carp, *Cyprinus carpio*, and goldfish, *Carassius auratus*. Based on these data it may be premature, however, to conclude that this species is restricted to these two host species. Kazubski (1982a, 1988), for example, has documented infections of this parasite on tadpoles of the frog *Rana temporaria*

Table 1. Hosts of *Trichodina heterodentata* Duncan, 1977.

Family	Host species	Locality	Reference
Anura: Ranidae	*Kassina senegalensis*	experimental	Kruger *et al.* 1993
Anura: Ranidae	*Rana fuscigula*	experimental	Kruger *et al.* 1993
Anura: Xenopidae	*Xenopus laevis*	South Africa	Kruger *et al*. 1993
Ambassidae	*Ambassis agassizi*	Australia	Present study
Apogonidae	*Glossamia aprion gilii*	Australia	Present study
Balitoridae	*Crossostoma lacustre*	Taiwan	Basson and Van As 1994
Characidae	*Hydrocynus forskali*	Egypt	Al-Rasheid *et al*. 2000
Characidae	*Micralestes actuidens*	South Africa	Van As and Basson 1989
Cichlidae	*Chetia flaviventris*	South Africa	Van As and Basson 1989
Cichlidae	*Oreochromis aureus*	Israel	Van As and Basson 1989
Cichlidae	*Oreochromis aureus* × *niloticus*	Israel	Van As and Basson 1989
Cichlidae	*Oreochromis mossambicus*	Philippines	Duncan 1977
		South Africa	Van As and Basson 1989
		Venezuela	Van As and Basson 1989
		Taiwan	Van As and Basson 1989
		Australia	Present study
Cichlidae	*Pseudocrenilabrus philander*	South Africa	Van As and Basson 1989
Cichlidae	*Sarotherodon galilaeus*	Israel	Van As and Basson 1989
Cichlidae	*Tilapia rendalli swierstrae*	South Africa	Van As and Basson 1989
Cichlidae	*Tilapia spearmanii*	South Africa	Van As and Basson 1989
Cichlidae	*Tilapia zillii*	Philippines	Duncan 1977
		Israel	Van As and Basson 1989
Cobitidae	*Misgurnus anguillicaudatus*	Taiwan	Basson and Van As 1994
Cyprinidae	*Acanthobrama* sp.	Israel	Van As and Basson 1989
Cyprinidae	*Aristichthys nobilis*	Taiwan	Albaladejo and Arthur 1989
Cyprinidae	*Barbus eutaenia*	South Africa	Van As and Basson 1989
Cyprinidae	*Barbus marequensis*	South Africa	Van As and Basson 1989
Cyprinidae	*Barbus paludinosus*	South Africa	Van As and Basson 1989
Cyprinidae	*Barbus trimaculatus*	South Africa	Van As and Basson 1989
Cyprinidae	*Candida barbata*	Taiwan	Basson and Van As 1994
Cyprinidae	*Carassius auratus*	Israel	Van As and Basson 1989
Cyprinidae	*Ctenopharyngodon idella*	Israel	Van As and Basson 1989
		Taiwan	Albaladejo and Arthur 1989
Cyprinidae	*Cyprinus carpio*	South Africa	Van As and Basson 1989
		Israel	Van As and Basson 1989
		Indonesia	Albaladejo and Arthur 1989
		Australia	Present study
Cyprinidae	*Hypopthalmichthys molitrix*	Taiwan	Basson and Van As 1994
Cyprinidae	*Labeo cylindricus*	South Africa	Van As and Basson 1989
Cyprinidae	*Neobola brevianalis*	South Africa	Van As and Basson 1989
Cyprinidae	*Sarcocheilichthys nigripinnis*	Taiwan	Basson and Van As 1994
Eleotridae	*Hypseleotris compressa*	Australia	Present study
Eleotridae	*Hypseleotris galii*	Australia	Present study
Eleotridae	*Hypseleotris klunzingeri*	Australia	Present study
Eleotridae	*Philypnodon grandiceps*	Australia	Present study
Galaxiidae	*Galaxias maculatus*	Australia	Present study
Galaxiidae	*Galaxias olidus*	Australia	Present study
Gerreidae	*Gerres* sp.	Australia	Present study
Gobiidae	*Glossogobius giurus*	South Africa	Van As and Basson 1989
Gobiidae	*Rhinogobius brunneus*	Taiwan	Basson and Van As 1994
Mormyridae	*Marcusenius macrolepidotus*	South Africa	Van As and Basson 1989
Mormyridae	*Petrocephalus catostoma*	South Africa	Van As and Basson 1992
Percichthyidae	*Macquaria ambigua*	Australia	Present study
Poeciliidae	*Aplocheilichthys johnstonii*	South Africa	Van As and Basson 1989
Poeciliidae	*Gambusia affinis*	Taiwan	Basson and Van As 1994
Poeciliidae	*Gambusia holbrooki*	Australia	Present study
Poeciliidae	*Poecilia reticulata*	Australia	Present study
Poeciliidae	*Xiphophorus helleri*	Australia	Present study
Poeciliidae	*Xiphophorus maculatus*	Australia	Present study
Pseudomugilidae	*Pseudomugil signifer*	Australia	Present study
Synodontidae	*Synodontis zambezensis*	South Africa	Van As and Basson 1989

in Poland. The frog species which are commonly sympatric with carp and goldfish in Australia include *Limnodynastes tasmaniensis, L. fletcheri, L. interioris, Litoria peroni, L. leseuri* and *Crinia parinsignifera* (pers. obs.) and a number of other species. Tadpoles were not examined during the survey, but it is conceivable that *T. reticulata* may be using these hosts also. Further, the two sites from which infected fishes were collected, the Shoalhaven River and Gum Bend Lake, are separated by more than 500 km and the Great Dividing Range, which suggests that the parasite is widespread or, at least, occurs at multiple foci. The importance of *T. reticulata* may have been underestimated in this study.

The presence of *Trichodina acuta* in Australia, although equivocal because it is based on a single specimen, is a pattern consistent with published records of successful trichodinid invasions of alien systems. Kulemina (1968) recorded *T. acuta* from redfin, *Perca fluviatilis*, in Poland, whereas Basson *et al.* (1983) recorded the species from fry of *Tilapia* sp. and Basson Van As (1993) recorded it from cage-cultured rainbow trout, *Oncorhynchus mykiss*, in Qua-Qua, South Africa. Australia has populations of all three of these host species, and therefore any one of them is the potential source for this parasite in Australia. The Barron River drainage, however, harbours only one, *Tilapia* sp. (in this case *T. mariae*) as well as the closely-related cichlid *Oreochromis mossambicus*, seemingly identifying the source host species. Interestingly, however, *T. acuta* was not recovered from any of the *T. mariae* or *O. mossambicus* examined in this study. Until more specimens can be examined, *T. acuta* will remain an enigma in Australia.

Undoubtedly the most significant exotic trichodinid recovered in terms of host range and zoogeography was *Trichodina heterodentata*. The origin of Australian populations of *T. heterodentata* is unclear. The simplest explanation is that because it was originally described from cultured cichlids, *Oreochromis mossambicus*, in the Philippines by Duncan (1977), it has been imported to Australia with that species, which is now widespread along coastal drainages of Queensland (Mather and Arthington 1991). However, some specimens were collected from sites more than 1000 km away and on the other side of the Great Dividing Range from the nearest wild *O. mossambicus* population. This suggests either that the pattern of spread of this species in Australia is somewhat more complex or that *T. heterodentata* is, in fact, a species native to Australia, giving it a Gondwanan distribution. Assuming it is introduced, then a likely culprit in the dissemination of *T. heterodentata* in Australian waterways is the mosquitofish, *Gambusia holbrooki*. This species has spread to become perhaps the most widely-distributed freshwater fish in Australia (Merrick and Schmida 1984) and, unlike any other fish in the study, has a range which incorporates the entire known range of *T. heterodentata*. Mosquitofish may well have acted as a vector for spreading this parasite to the hosts and localities observed in the present study. The possibility that *T. heterodentata* is a native Australian species cannot, however, be excluded.

Native trichodinids

The native fishes of Australia harbour a species-rich fauna of native trichodinids, with at least 17 species of undescribed trichodinids detected from 33 species of native fishes examined from all three survey sources. From the sampling regimes employed, it was apparent that these species vary greatly in zoogeography, microhabitat-specificity and host-specificity and should not be regarded as a single homogenous assemblage. Undoubtedly, a number of cryptic species lie within the 17 native "species" discriminated in this study, also.

The richness of trichodinids recovered during the study can be used to estimate the biodiversity of Australian trichodinids, using the technique of Cribb *et al.* (1994). Native fishes for which more than 9 specimens were examined had a mean trichodinid richness of 2.4 species. Cribb *et al.* (1994) considered that 9 specimens was sufficient to conservatively estimate the parasite richness on a host. Given the host range of *T. heterodentata*, this can be assumed to represent 1.4 native trichodinids, plus *T. heterodentata*. Given the low sampling effort for most species (the most heavily-sampled species, *Hypseleotris klunzingeri*, harboured 5 trichodinid species, the most of any fish species) it seems reasonable to round this figure up to 2 trichodinid species per fish species. The average number of host species per native trichodinid species was also 2.4. Using the following formula, the species-richness of the Australian trichodinid fauna can be calculated.

$$R = \frac{h \times ph}{hp}$$

where R is the richness of the fauna, h is the number of host species, ph is the number of parasite species per host species and hp is the number of host species per parasite species. In this case:

$$R = \frac{180 \times 2}{2.4}$$

$$R = 150$$

In other words, it may be expected that the Australian native freshwater fish fauna will harbour about 150 species of trichodinids. This number approaches the total number of trichodinid species described from all host families to date!

Flux of trichodinids

We have shown that there have been host-switching events whereby parasites have crossed from native fishes to exotic and *vice versa*. In this study there were three records of host-switches involving trichodinids; *Trichodina* sp. J was recorded from *Gambusia holbrooki* at the crayfish farm near Beenleigh, Queensland; *Trichodina* sp. P was recorded from *Cyprinus carpio* from the same site; and *Trichodina heterodentata* was recorded from 11 native species and 6 exotic species at 13 different sites in Eastern Australia. The first record is somewhat intriguing in that *Trichodina* sp. J was not recorded from any other host at the crayfish farm near Beenleigh, however it's only other focus of infection, the Albert River, is the water source for the farm and the two water bodies may be considered to be freely interacting (Ben Brookman, pers. comm.). The second record is not surprising and supports the hypothesis proposed in the section above, that *Trichodina* sp. P is one of the species most likely to undergo host-switching, in this case to the exotic fish, *C. carpio*. It is the third case of host-switching, however, that provides the most informative data on parasite flux between native and exotic hosts.

Trichodina heterodentata was the most widespread and least host-specific trichodinid recovered. The fact that it is an exotic parasite makes this fact all the more remarkable. We contend that *T. heterodentata* is a parasite of emerging importance in studies of parasites of freshwater fishes, especially those which include species introductions. The fact that it was described as late as 1977 (Duncan 1977) demonstrates the lack of attention paid to the taxonomy of this group in the earlier 20th century. However, enough data have now been collected to indicate that *T. heterodentata* may be as important as any of the other, more prominent parasite species often associated with fish introductions: *Argulus* spp. (Branchiura), *Myxobolus cerebralis* (Myxozoa), *Bothriocephalus acheilognathi* (Cestoda), *Camallanus cotti* (Nematoda) and *Lernaea* spp. (Copepoda).

Van As and Basson (1989) discussed the biology of *T. heterodentata* in some detail. They contended that, although described from the Philippines, the parasite is almost certainly native to Eastern South Africa. They based their contention on the fact that they collected *T. heterodentata* from sites in the Limpopo River system which have never been exposed to exotic fish introductions, and that the host from which Duncan (1977) described the species, *Oreochromis mossambicus*, is native to that area. This contradicts the theory of Kazubski (1982b) that their material was not representative of *T. heterodentata* sensu Duncan (1977). Van As and Basson (1989) also recorded a number of new host records for *T. heterodentata*. A revised host list for this species is given in Table 1. The presence of this species on at least 50 host species including fishes from at least 16 diverse families and the tadpoles of three frog species indicates that it is a truly adaptable species.

The results of this study highlight the importance of taxonomy for studies of exotic animal phenomena. It is convenient to suggest that parasites are introduced with exotic fishes and that they are therefore directly responsible for declines in native fishes. That may be so in some cases, but it is far from a safe assumption. This study has clearly demonstrated that Australia has a unique and species-rich native trichodinid fauna, perhaps as many as 150 spp. and that species have crossed from native to exotic hosts and *vice versa*. These complex patterns of species richness and flux require a more rigorous approach to taxonomy than that which has been employed in the past.

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