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Mobiline peritrich riders on Australian calanoid copepods

John D. Green[1] & Russell J. Shiel[2]
[1]*Centre for Biodiversity and Ecology Research, Department of Biological Sciences, University of Waikato, Private Bag 3105, Hamilton, New Zealand*
[2]*CRCFE, The Murray-Darling Freshwater Research Centre P.O. Box 921, Albury, NSW 2640, Australia*
E-mail: j.green@waikato.ac.nz

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Abstract

Calanoid copepods from billabongs near Wodonga, Victoria, Australia were found to be infested with a disc-shaped mobiline peritrich ciliate belonging to the genus *Trichodina*. Biometrical data, including mean body diameter (43.6 μm), mean adhesive disc diameter (35.9 μm), mean denticle ring diameter (20.1 μm), modal denticle number (17), modal number of radial pins per denticle (9), and denticle shape and dimensions, indicate that the species is *T. diaptomi* Basson & Van As (1991). This is the first record of *T. diaptomi* from Australasia. Adults of *Boeckella fluvialis* and *B. minuta* were infected, but adult *Calamoecia lucasi* were not. Levels of infestation were higher on *B. fluvialis* (67.5% of females, 54.5% of males) than *B. minuta* (47.4% of females, 33.3% of males). Mean numbers of *Trichodina* per adult *B. fluvialis* were 7.68 (range 0–78) for females and 4.06 (range 0–43) for males, and differed significantly between sexes. Although calanoid copepods were present in the plankton from January to early December 1991, *Trichodina* infestations occurred during October and November only, peaking during late November just before the copepods disappeared from the plankton. Whether the infestation was a cause of the copepod decline, developed because the copepods were rendered susceptible to infection by some other cause, or was determined by physical and/or chemical environmental factors is unknown.

Introduction

Small attached organisms (epibionts or epizoites) often are observed on the external surfaces of planktonic copepods and cladocerans. Some epibionts are larger forms such as rotifers (e.g., Morris, 1913; Ahlstrom, 1940; Shiel & Koste, 1985), but the most frequently observed are sessile peritrich ciliophorans, particularly of the genera *Zoothamnium*, *Epistylis*, *Vorticella* and *Trichodina* (e.g., Herman & Mihursky, 1964; Turner et al., 1979; Kankaala & Eloranta, 1987; Xu & Burns, 1991; Basson & Van As, 1991). Infestations of suctorians (e.g., *Tokophrya* spp. (Evans et al., 1981)) and euglenoid flagellates (e.g., *Colacium vesiculosum* (Willey et al., 1990)) are also known. Although such epizoites have been regarded as harmless commensals, various studies have shown that some may be detrimental to their hosts by competing for food, hampering and increasing the costs of locomotion, and increasing the risks of predation (e.g. Kankaala & Eloranta, 1987; Willey et al., 1990; Xu & Burns, 1991). Such effects may be particularly marked when the host is starving (Xu & Burns, 1991). There have been no specific records of epizoic ciliates from zooplankton in Australia, although Shiel & Koste (1985), in a report on epizoic rotifers on *Daphnia* and *Pseudomoina*, noted the presence of epizoic protozoans.

During surveys of plankton in billabongs of the River Murray, we encountered a non-stalked, mobiline peritrich ciliate of the genus *Trichodina* moving freely over the surfaces of calanoid copepods. Trichodinids are a diverse group of ecto- and endoparasitic forms, mostly of fish, amphibians and molluscs (Lom, 1958), and characterised by a sucker-like disc that enables them to adhere to host surfaces (Van As &

Basson, 1990). The disc is supported by an intracellular skeletal ring of interlinking denticles, the number, shape and dimensions of which are used in trichodinid taxonomy (e.g., Lom, 1958; Van As & Basson, 1989). There have been a small number of reports of trichodinids on the external surfaces of calanoid copepods and, although these occurrences are from a wide geographical range, including Europe, China and South Africa, they are all of the one species, *Trichodina diaptomi* Basson & Van As (1991) (Mobilina: Trichodinidae).

The present record is the first of an epizoic peritrich on calanoid copepods in Australasian freshwaters, and only the second record of a trichodinid on calanoids from the Southern Hemisphere. Our purpose here is to provide a first description of this Australian trichodinid, to review its taxonomic identity and to make preliminary comments on its ecology, based on sampling of plankton in Ryan's 2 billabong, Victoria and laboratory observations of live animals *in situ* on calanoid hosts from this site.

Methods

Live calanoid copepods (*Boeckella fluvialis*, *B. minuta* and *Calamoecia lucasi*) were collected on 25 and 26 November, 1991 from Ryan's 2 Billabong, Wodonga (36° 06′ 51″ S, 146° 58′ 12″ E) and returned to the laboratory (<20 min. travel time) at ambient temperature (ca. 20° C). They were transferred to petri dishes and examined under a Zeiss SV-8 dark-field stereo microscope. After narcotisation with ca. 1% procaine hydrochloride (5–10 min.), adult male and female *Boeckella fluvialis* bearing *Trichodina* were removed by pasteur pipette to cavity microslides in a drop of billabong water. They were then examined using an Olympus BH-2 microscope (Nomarski optics), and VHS video and 35 mm micrographs of both host and ciliates taken. Infested calanoids for electron microscopy were dehydrated through an alcohol series to 100% ethanol, critical point dried (Polaron CPD), sputter coated (CS minicoater) and examined using a Philips SEM505 electron microscope. In order to determine the % incidence of ciliates, adults of all three copepod species and juvenile instars (not identified to species) were randomly selected with a pasteur pipette (this procedure did not dislodge the ciliates from the copepods) and individually mounted on slides in a drop of lactic acid. This caused the ciliates to detach and slowed their movements. Counts were made of the number of ciliates per copepod.

Additional material was collected from Ryan's 2 Billabong on 5 December 1995 and preserved in 10% formalin. Specimens were extracted, smeared on slides, air dried, and silver stained using Klein's dry method (Curds, 1982), and mounted in euparal. Details of the adhesive disc were examined at ×400–1000 magnification. Images were grabbed onto a computer using a Sony DXC-107AP video camera and a Targa+ frame grabber (Truevision Inc.), and printed via a Sony CVP G-700 videoprinter. The standard taxonomic characteristics proposed by Lom (1958) were measured on the grabbed images using the image analysis program ImagePro Plus (Media Cybernetics, 1993). All these measurements were in micrometres. Minimum and maximum values are given, followed in parentheses by the mean, standard deviation and number of specimens examined. The denticles were traced from laser prints of the captured frames, and their shape described, following the guidelines of Van As & Basson (1989, 1992).

The seasonal occurrence of *Trichodina* in the plankton was determined using plankton samples from Ryan's 2 billabong, taken originally for routine monitoring purposes, in the Murray–Darling Freshwater Research Centre's microfaunal sample collection. A relatively complete set of seasonal samples, taken monthly in winter and approximately weekly in other seasons, was available from 1991. The samples were qualitative and obtained by towing cone net of 30 cm mouth diameter and 35 μm mesh from the shore. Unfortunately no suitable quantitative samples were available. The relative abundance of calanoid copepodites was determined as the numerical percentage of total zooplankton from a count of 300 randomly selected zooplankters in an aliquot taken from the well-stirred sample. The abundance of *Trichodina* relative to adult calanoid copepodites was assessed from a second aliquot from the sample. Counts of *Trichodina* and adult calanoids were made until 200 adults had been counted or, if there were fewer than this in the sample, until the entire sample had been counted.

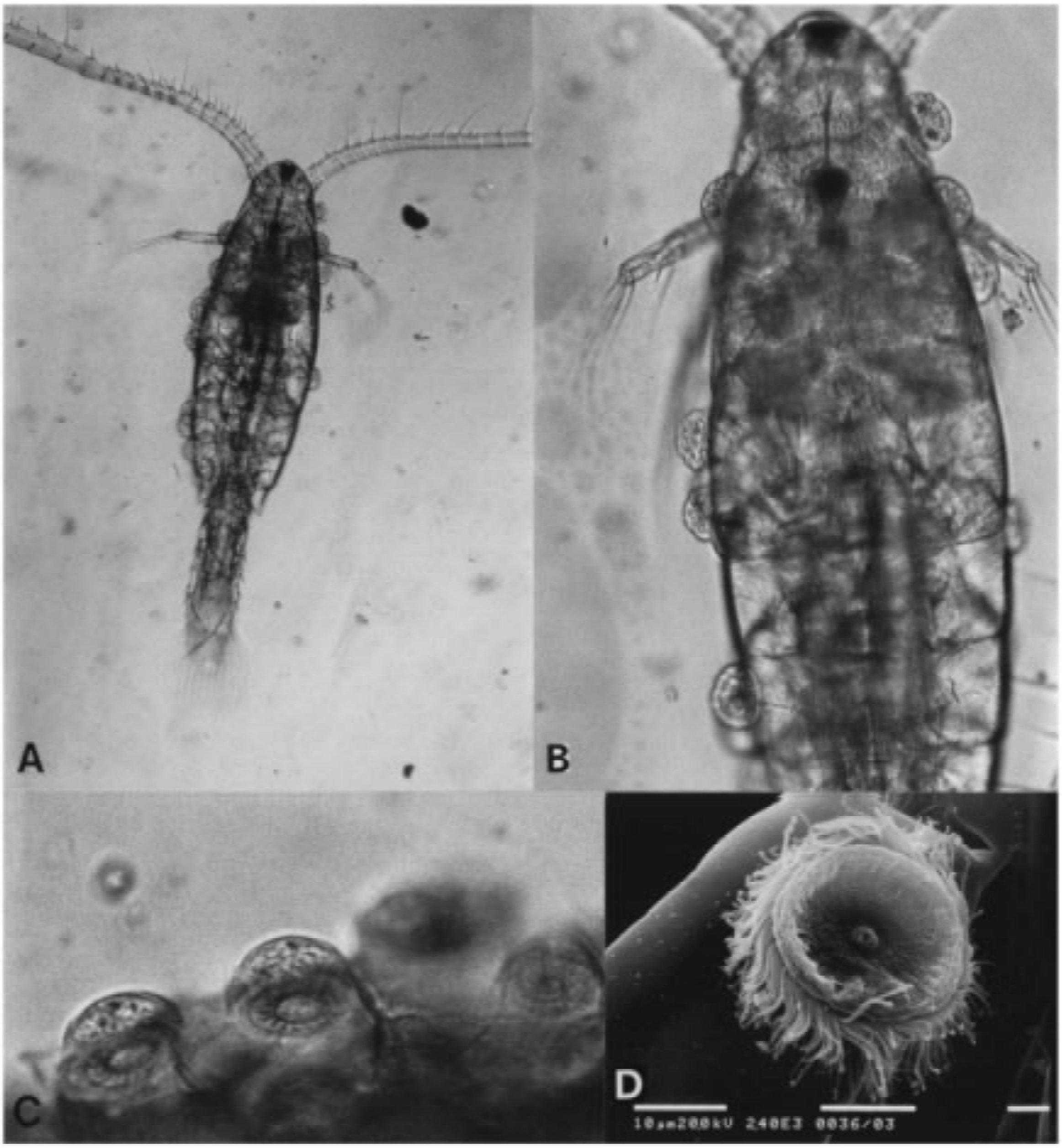

Figure 1. Photomicrographs of *Trichodina* from Ryan's 2 billabong. (A) *Boeckella fluvialis* infested with *Trichodina*; (B), (C) Detail of live specimens on *B. fluvialis*; (D) Scanning electron micrograph of *Trichodina* on *Boeckella fluvialis*. In life the adoral surface is convex (see B and C).

Results and discussion

Taxonomic description

(Figures 1–5)

Host and locality: Boeckella fluvialis Henry, 1922 and *Boeckella minuta* Sars, 1896 from Ryan's 2 billabong (36° 06′ 51″ S, 146° 58′ 12″ E) 10 km east of Wodonga, NE Victoria, Australia.

Site: Prosome of both calanoid species.

Biometrical data are given in Table 1.

Table 1. Comparison of the biometrical data of the trichodinids described in this study with those of *Trichodina diaptomi* from South Africa. Values given are ranges, followed by the mean, standard deviation and number of observations in parentheses, except in instances marked [†] where the values in parentheses are mode and number of observations. All values are in micrometres. [‡] * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

Locality	South Africa	Ryan's 2 Billabong	t-test[‡]
Host	*Metadiaptomus meridianus*	*Boeckella fluvialis*	
Reference	Basson & Van As 1991	This study	
Body diam.	33.8–48.7 (41.5±4.4, 27)	35.3–49.6 (43.6 ± 3.2, 50)	$t = 2.187$, *
A.d.diam.	27.9–39.9 (33.8 ± 3.5, 27)	30.2–42.6 (35.9 ± 2.8, 50)	$t = 2.873$, **
B.m.width	2.6–5.4 (4.0 ± 0.7, 27)	1.8–4.8 (3.6 ± 0.7, 50)	$t = 2.393$, *
D.r.diam.	14.8–22.6 (19.6 ± 2.3, 27)	14.7–39.1 (20.1 ± 3.5, 50)	$t = 0.205$, ns
D.no.[†]	15–20 (18, 27)	15–19 (17, 49)	
R.p.d.[†]	7–11 (9, 27)	5–9 (9, 43)	
D.l.	4.8–7.7 (6.2 ± 0.8, 27)	4.4–7.6 (6.2 ± 0.7, 50)	$t = 0$, ns
B.l.	2.9–6.9 (3.8 ± 0.7, 27)	3.4–5.7 (4.4 ± 0.4, 50)	$t = 4.106$, ***
R.l.	2.8–6.1 (4.4 ± 0.8, 27)	3.8–6.4 (4.9 ± 0.7, 50)	$t = 2.844$, **
C.p.w.	1.4–2.7 (2.0 ± 0.4, 27)	1.2–2.9 (2.0 ± 0.3, 50)	$t = 0$, ns
Ma. shape	C-shaped	C-shaped	
Ma.e.d.	32.3–50.2 (38.3 ± 5.1, 20)	29.1–42.0 (35.1 ± 3.1, 24)	$t = 2.454$, *
Ma.th.	4.1–10.2 (6.4 ± 1.3, 20)	6.8–13.4 (10.4 ± 1.4, 24)	$t = 9.745$, ***
Ma.x.	7.6–19.1 (12.6 ± 3.2, 20)	5.2–18.3 (11.8 ± 3.2, 24)	$t = 0.826$, ns

Abbreviations: A.d. – adhesive disc, B.l. – blade length, B.m. – border membrane, C.p.w. – central part width, diam. – diameter, D.l. – denticle length, D.no. – denticle number, D.r. – denticle ring, e.d. – external diameter, Ma. – macronucleus, R.l. – ray length, R.p.d – number of radial pins per denticle, th. – thickness, x. – length of sector between terminations of the macronucleus.

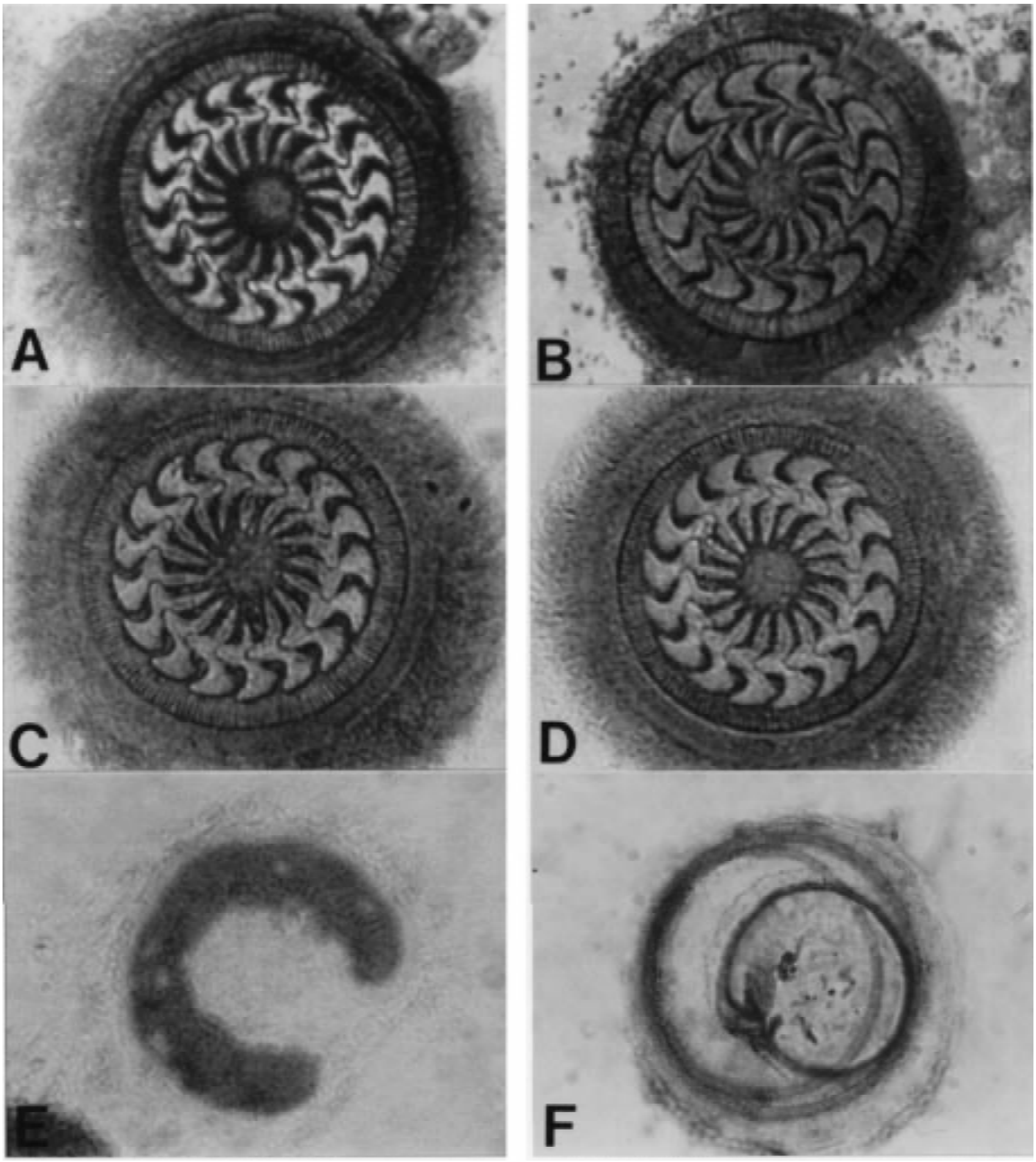

Figure 2. Morphological features of *Trichodina* from Ryan’s 2 billabong. (A), (B), (C), (D). Examples of silver impregnated adhesive discs; (E). macronucleus; (F). adoral ciliary groove. Dimensions are given in Table 1. (A–E), videoprints; (F), 35 mm micrograph.

Description: Medium-sized trichodinid with flattened saucer-shaped body (Figure 1). Central circle not as well defined in some specimens as in others, impregnates variably and appears elevated (Figure 2). Blade broadly sickle-shaped. The distal surface is slightly curved and a little higher than the tangent point, which is sharply curved. Anterior blade surface slopes smoothly away from the distal surface and the apex is rounded. Apex usually extends to or slightly beyond the y+1 axis, although in some cases, it does not quite reach this axis. Blade is variable in its development, although usually prominent. Posterior blade surface usually forming a smooth semi-lunar curve, interrupted in a few cases by a central bump. Deepest point of ventral curve lies opposite the apex. Blade connection thin. Central part tapers to a sharply rounded point, extends more than half way to the y-1 axis, and only loosely connected to the next denticle. Section above x axis triangular, but that below tends to be more parallel to the axis, at least in the posterior half. No indentation in the lower central part. Connection to ray delicate, and the ray is thin and with a sharply rounded proximal point. Ray is straight and is bent towards the y+1 axis, usually extending half way to this line, but in some cases reaching or extending beyond it. Ratio of section of denticle above x axis to that below is slightly less than one (0.81–0.95). Shape of the denticles differs slightly between specimens, and between different denticles within the one specimen (Figure 3): distal blade surface sometimes less smoothly curved (e.g., D in Figure 3), tangent point more rounded in some, blade apophysis slightly variable in development, central bump on posterior blade surface not always present, ray thickness slightly variable, in some being thicker medially and thinning proximally and in others there is a small bump midway along its length (e.g., H in Figure 3). Nuclear apparatus consists of a C-shaped macronucleus (Figure 2E). Micronucleus was not observed. The adoral zone of cilia was observed in only a few cases, and turned ca. 400° (Figure 2F)

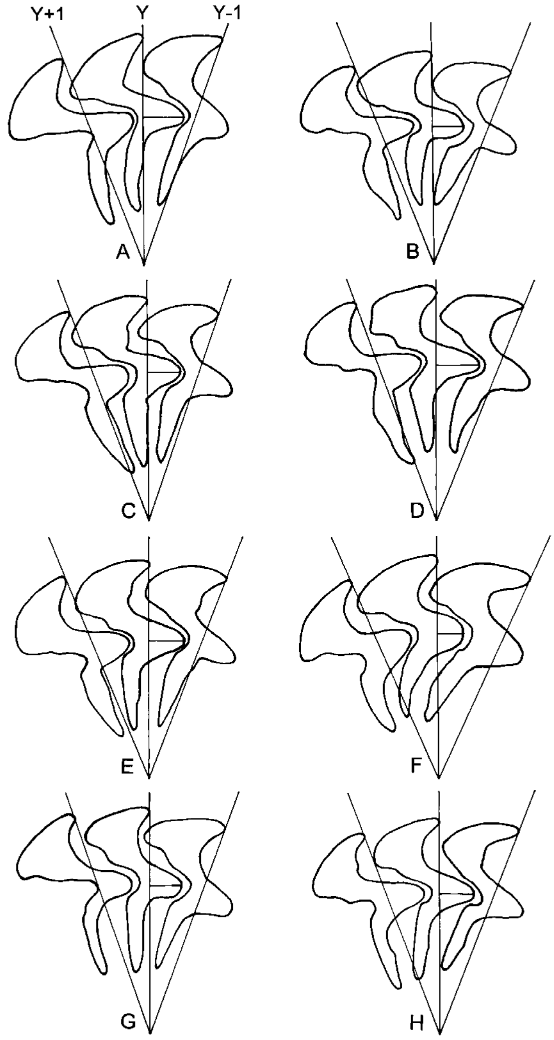

Figure 3. Diagrams of denticles of *Trichodina* from *Boeckella fluvialis* in Ryan's 2 billabong, N.E. Victoria, Australia, showing intraspecific variation in morphology.

Taxonomic identity

Trichodinids have previously been reported from a number of calanoid copepod species, over a wide geographical range (*Trichodina domerguei* f. *megamicronucleata* on *Diaptomus* sp. from USSR, Dogiel, 1940; *T. domerguei* var. *diaptomi* on *Diaptomus vulgaris* from Czechoslovakia, Sramek-Husek, 1953; *T. domerguei* f. *latispina* on *D. vulgaris, D. castor* and *Eudiaptomus gracilis* from Czechoslovakia, Lom, 1960; *T. domerguei* f. *latispina* on *Sinodiaptomus sarsi* and *Neodiaptomus handeli* from China, Chen, 1963; *T. domerguei* subsp. *megamicronucleata* on *Diaptomus* sp. and *Eudiaptomus zachariasi* from Poland, Migala & Grygierek, 1972; *T. diaptomi* on *Metadiaptomus meridianus* from South Africa, Basson & Van As, 1991). Basson & Van As (1991) reviewed these records and concluded that they all represented the same widely distributed trichodinid. They named this *Trichodina diaptomi* and provided a full description, based on the South African material.

In general, the Australian specimens correspond closely to the description of *T. diaptomi* given by Basson & Van As (1991). The characteristics of the *Trichodina* from Ryan's 2 billabong are compared with those of *T. diaptomi* in Figure 4 and Table 1. The denticle shape is very similar to that in the various populations of *T. diaptomi*, and is perhaps most similar to those from Czechoslovakia and China (Figure 4E, F). The various biometrical dimensions (Table 1) are also

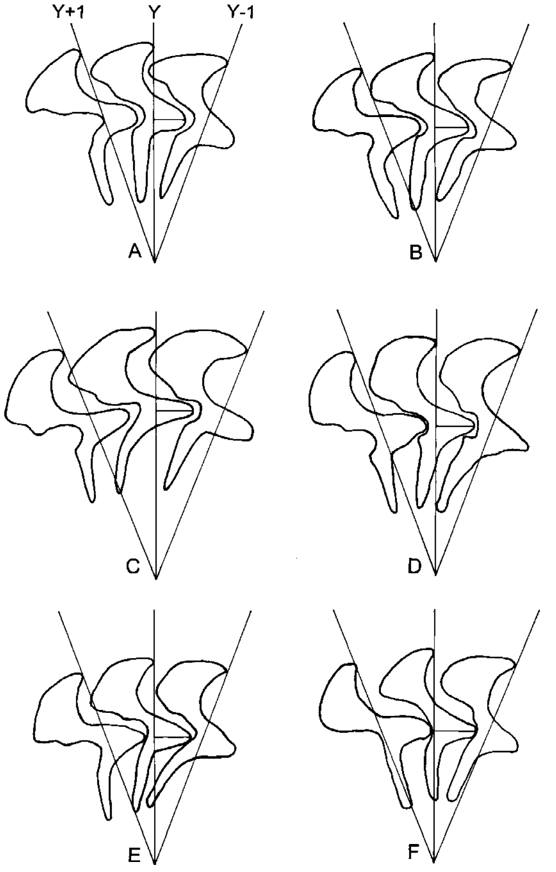

Figure 4. Comparison of denticles of *Trichodina* from calanoid copepods in Ryan's 2 billabong, N.E. Victoria, Australia, with denticles of *T. diaptomi* from various countries. (A), (B). From Ryan's 2 billabong, host *Boeckella fluvialis*; (C) From South Africa, host *Metadiaptomus meridianus* (Basson & Van As, 1991); (D) From Poland, host *Eudiaptomus zachariasi* (Migala & Grygierek, 1972); (E) From Czechoslovakia, host *Diaptomus vulgaris* (Lom, 1960); F. From China, host *Sinodiaptomus sarsi* (Chen, 1963). (C)–(E) from Basson & Van As (1991).

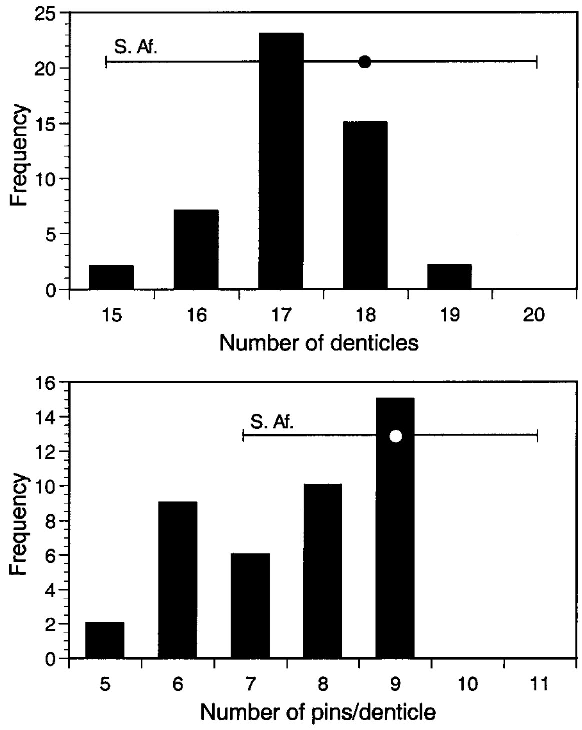

Figure 5. Frequency distributions of counts of denticle number (upper) and number of radial pins per denticle (lower) in specimens of *Trichodina* collected from Ryan's 2 billabong, N.E. Victoria, Australia. The modal values and ranges for South African *T. diaptomi* (Basson & Van As, 1991) are also shown.

very similar to those of *T. diaptomi,* although there are some small, and occasionally statistically significant, differences. For example, the mean body and adhesive disc diameters, and blade and ray lengths are larger in the Ryan's 2 population. Denticle number and number of radial pins per denticle are regarded as being particularly important taxonomically and relatively invariable within a species, varying by only ±3–4 denticles and ±2–4 radial pins per denticle (Lom, 1958). The modal number of denticles was 17 for the Ryan's 2 population, cf. 18 in the South Africa population of *T. diaptomi* (Figure 5) and the ranges of values overlap. The modal value of pins per denticle is 9 in both populations, although the ranges differ slightly, being 5–9 for the Ryan's 2 population cf. 7–11 for South African *T. diaptomi* (Figure 5).

Overall, though, the differences between the features of the Ryan's 2 population and those of *T. diaptomi* are minor. We conclude, therefore, that the Ryan's 2 population belongs to *T. diaptomi*, with the morphological differences between it and the South African population providing some evidence of ecotypic/geographical variation.

Ecology

Calanoid copepods were present year round in Ryan's 2 billabong during 1991, but were a major component of the zooplankton only from May to early November. Their percentage abundance declined sharply in early October and, apart from a brief resurgence in late October, remained very low for the remainder of the year (Figure 6). *Trichodina* were recorded in the 1991 plankton samples from October and November (late spring) only, following the main period of copepod abundance. There was an initial peak in infestation in early October, a decline during the brief copepod resurgence in late October and then two successive larger peaks in late November. *Boeckella fluvialis* was the dominant calanoid present during October and November, with *B. minuta* and *Calamoecia lucasi* present in low numbers. *Trichodina* has been recorded in Ryan's 2 billabong on 30 November 1992 and 5 December 1995 also, on *B. fluvialis* in both instances.

Mean infestations, as determined from the plankton counts, peaked at slightly less than one *Trichodina* per adult copepod, but the observations on living copepods showed that the incidence of infection was very variable between different individuals and between calanoid species and developmental stages (Figure 7, Table 2), and that some individuals were very heavily infested. Incidences of *Trichodina* were higher on *B. fluvialis* than *B. minuta* and none were ever found on *C. lucasi*, the smallest species. In both *B. fluvialis* and *B. minuta*, levels of infection were higher on females than on males (Table 3). Too few individuals of *B. minuta* were observed for reliable infection statistics to be calculated and statistical tests to be carried out. In *B. fluvialis*, however, the counts of *Trichodina* on females and males ranged from 0 to 78 and 0 to 43, respectively, and mean numbers of ciliates on males (7.68) and females (4.06) were significantly different (Table 3). Similarly, Xu & Burns (1991) found that levels of *Epistylis* infestation were higher on females than males of *Boeckella triarticulata*. They suggested that these differences may have been due to differences in swimming behaviour, exoskeleton characteristics or secretion of chemicals between the sexes. We were not able to positively identify immature copepodites to species, but from their size they probably belonged to *B. fluvialis*. *Trichodina* occurred on CV and CIV, but not on CIII, CII, CI or nauplii. One explanation is that *Trichodina* may occur only on copepodites above a certain size, about that of *B. fluvialis* CIV, and this could also account for the absence of *Trichodina* from *C. lucasi*, the adults of which are of similar size to the CIII of *B. fluvialis*. Alternatively, the absence of *Trichodina* from young copepodites may be because infection rates were low in these stages as a result of them having higher moulting rates than CIV and CV, although such a mechanism would not explain the absence of *Trichodina* from *Calamoecia lucasi* adults.

Observations of living *Trichodina* (Figure 1) showed that most specimens were rotating, and that the majority remained in one position with only a few moving about over the host's surface. None were observed to detach from the host and swim freely in the water. Lom (1960) made similar observations. Trichodinids can have deleterious effects on their hosts, and in fish cause the disease trichodiniasis (e.g., Rowland & Ingram, 1991). There is no information in the literature on whether *T. diaptomi* has equivalent deleterious effects on its copepod hosts, although other epizoic ciliates are known to have detrimental effects on their hosts. *Epistylis* produces lesions on copepod exoskeletons, and loss of body fluids and bacterial infections at these sites have been put forward as possible causes of declines of *Acartia tonsa* populations (Turner et al., 1979). We examined at ×400 magnification, the surfaces of copepods that had been infected, to determine whether there was any abrasion or other damage to the exoskeleton caused by the adhesive discs of *Trichodina*, but no such damage was observed. The presence of *Trichodina*, even when at very

Table 2. The incidence of infection by *Trichodina* on calanoid copepods from Ryan's 2 billabong. Combined data from 25 and 26 November 1991

Copepod species & development stage	% infected with *Trichodina*	Total number of specimens examined
Boeckella fluvialis ♀	67.5	157
Boeckella fluvialis ♂	54.5	132
Boeckella minuta ♀	47.4	19
Boeckella minuta ♂	33.3	3
Calamoecia lucasi ♀	0	10
Calamoecia lucasi ♂	0	5
Copepodite V	11.1	54
Copepodite IV	12.5	8
Copepodite III	0	8
Copepodite II	0	4
Copepodite I	0	4
Nauplius	0	6

Table 3. Comparison of mean counts of *Trichodina* on female and male *Boeckella fluvialis* from Ryan's 2 billabong, using the combined data of 25 & 26 November 1991. The *t*-test of means was made after log-transformation of the data, in order to equalise variances

Count per copepod	*Boeckella fluvialis* Female	*Boeckella fluvialis* Male
Mean	7.68	4.06
Range	0–78	0–43
SD	14.15	7.48
n	82	80

t-test $t = 1.986$, $p = 0.049$

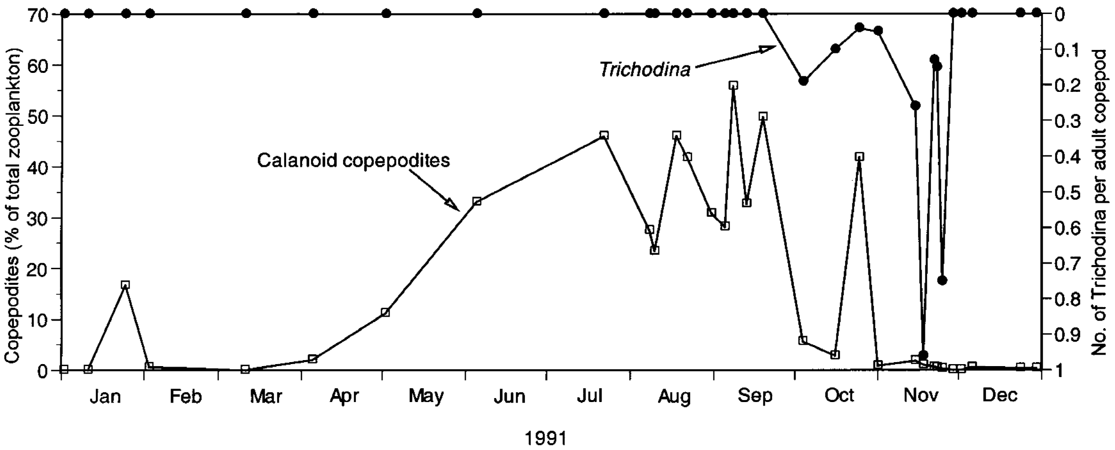

Figure 6. Seasonality of *Trichodina* and their calanoid copepod hosts in Ryan's 2 billabong, N.E. Victoria, Australia, during 1991.

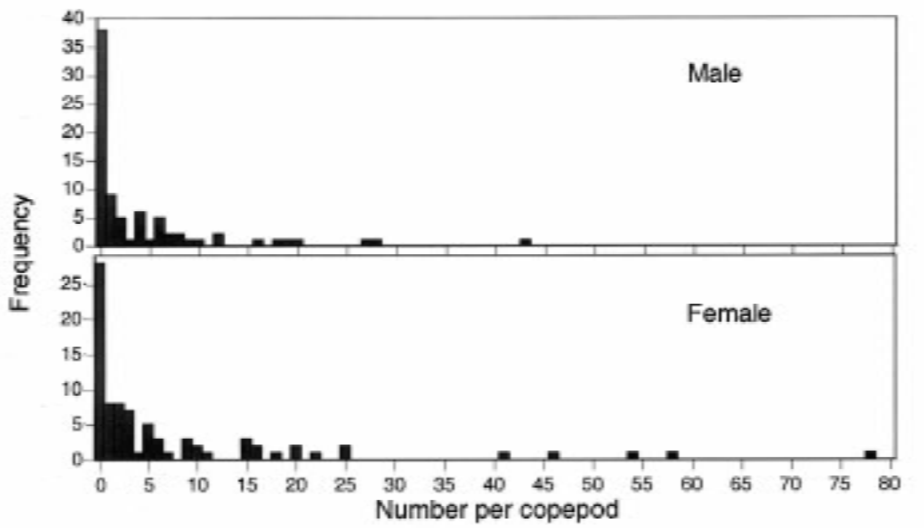

Figure 7. Frequency distributions of counts of *Trichodina* on male and female *Boeckella fluvialis* from Ryan's 2 billabong, N.E. Victoria, Australia, from observations of live specimens.

high densities, did not appear to affect either feeding or swimming movements of the copepods. However, over the longer term, epibionts may have cumulative effects on the reproduction and survival of their hosts by hampering locomotion, competing for food and increasing host susceptibility to predation (Willey et al., 1990). Thus, *Acartia tonsa*, when burdened with *Zoothamnium*, sinks more quickly (Herman & Mihursky, 1964) and this finding led Xu & Burns (1991) to suggest that, in starved *Boeckella triarticulata*, the energetic burden to locomotion imposed by infections of *Epistylis daphniae* may have been the cause of shorter survival in carriers than non-carriers. Kankaala & Eloranta (1987) reported that *Vorticella* epizoic on *Daphnia longispina* competes for food with its host, and Willey et al. (1990) found that infestations of *Colacium vesiculosum* increase the susceptibility of *Daphnia*, *Ceriodaphnia* and cyclopoid copepods to predatory fish by influencing visibility and escape efficiency of the hosts. Whether *Trichodina* has effects of these sorts on *B. fluvialis* was not determined by our study and requires further investigation. The data on occurrence of *Trichodina* in Ryan's 2 billabong show that levels of infestation were high when the copepod population was declining as a proportion of the total zooplankton, perhaps indicating that the infestation contributed to the decline of the copepod population by one of the mechanisms mentioned above. Alternatively, it may be that *Trichodina* was able to establish only when the copepod population was declining for other reasons (e.g., poor nutrition, senescence etc), or that its seasonality may be determined entirely by physical and/or chemical environmental factors and bear no relationship to the condition of the copepod population. A detailed year-long study, using quantitative samples as opposed to the qualitative ones used here, is required to test these hypotheses.

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