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Trichodina diaptomi (Ciliophora: Peritrichia) from Two Calanoid Copepods from Botswana and South Africa, with Notes on its Life History

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Abstract. Members of the genus *Trichodina* are mostly found on fish, but have also been recorded from a variety of other aquatic organisms, including calanoid copepods. So far, it appears that all the trichodinid populations collected from calanoids in various parts of the world are the same species, i.e. *Trichodina diaptomi* Šrámek-Hušek, 1953. This paper reports on a new record of *T. diaptomi* from *Metadiaptomus meridianus* in a large reservoir in South Africa, as well as on a new host species, *Metadiaptomus transvaalensis*, and the first record of *T. diaptomi* from pools in an ephemeral river in north-eastern Botswana, therefore adding a new country to the distribution of this species. We used the history of the discovery of *T. diaptomi* in different parts of the world and came to the conclusion that it is a cosmopolitan species, exclusively associated with copepods of the order Calanoida. Based on existing information, *T. diaptomi* does not appear to have a reservoir host. Against this background, we provide a discussion on the possibility that, although no dormant stage has been recorded for any trichodinid, it may be possible that *T. diaptomi* possesses some form of diapause and that this might be related to that of calanoid copepods.

Key words: Ephemeral habitat, *Metadiaptomus meridianus, Metadiaptomus transvaalensis*, trichodinid, survival strategies

INTRODUCTION

Members of the genus *Trichodina* Ehrenberg 1830 of the order Mobilida are epibionts or ectoparasites represented by more than 200 species (Silva-Briano *et al.* 2011). Most species are associated with freshwater fish, but a number have been described from amphibians, a coelenterate, molluscs, sponges, tunicates, hydrozoans and marine piscean hosts (Basson and Van As 2006). On a number of occasions trichodinids have been found associated with different species of freshwater planktonic copepods in the former Soviet Union (Dogiel 1940), the former Czechoslovakia (Šrámek-Hušek 1953, Lom 1960a), China (Chen 1963), Poland (Migala and Grygierek 1972), South Africa (Basson and Van As 1991), Australia (Green and Shiel 2000), India (Asmat 2004), Brazil (Da Silva *et al.* 2009) and Mexico (Silva-Briano *et al.* 2011).

Copepods form critical components of the world's aquatic ecosystems and are cornerstones in aquatic food webs. These secondary producers consume microorganisms and serve as primary prey for early life-history stages of many economically important fish, amongst others (Bron *et al.* 2011). Dormancy is one of the life-history characters of freshwater zooplankton that is affected by environmental factors. The term dormancy encompasses both diapauses and quiescence

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and in the order Calanoida the typical dormant stages are diapausing eggs that differ from subitaneous eggs in the structure of the envelope (Gyllström and Hansson 2004). The trichodinid association with Copepoda of the order Calanoida makes for an interesting story and opens up many questions concerning trichodinid life history.

The present record is the first of a mobiline trichodinid on calanoid copepods in Botswana, as well as the first record of *Metadiaptomus transvaalensis* Methuen, 1910 as host species. The aim of this study is to confirm that trichodinids collected from calanoid copepods in the Nata River in north-eastern Botswana are in fact *T. diaptomi* Šrámek-Hušek, 1953, and to record a new host species for this ciliophoran. A discussion on the life-history stages of trichodinids is provided, following their discovery on copepods that are capable of forming dormant stages in this seasonal and highly unpredictable river.

A second record of *T. diaptomi* from *M. meridianus* (Douwe, 1912) in the Free State, South Africa, is also provided. Morphometric data of both populations are provided.

MATERIALS AND METHODS

During a long-term qualitative survey aimed at determining the diversity and distribution of zooplankton of the rivers, lakes and wetlands of northern Botswana, zooplankton was sampled from a variety of habitats using a plankton net of 50 µm mesh size. Samples collected from the Nata River (Fig. 1A) (S 20°12.290' E 026°11.302') on 15 and 16 August 2012 (latewinter) contained the calanoid copepod *Metadiaptomus transvaalensis*. On 20 and 21 November 2012 (late spring) plankton was collected during a fish and plankton survey at Rustfontein Dam in the Free State Province, South Africa that contained *M. meridianus*. These copepod species were infested with a mobiline trichodinid of the genus *Trichodina*. Live observations were made in a temporary field laboratory using both a Nikon Eclipse E100 and a Nikon SMZ800 light microscope and micrographs taken using a Nikon DS-Fi1 camera attached to both the compound and dissecting microscopes. Thereafter, infested calanoids were placed on slides and air-dried. In the laboratory in Bloemfontein, air-dried smears were impregnated with silver nitrate using a modified version of Klein's technique, proposed by Lom (1958) and described by Wellborn (1967), in order to study details of the adhesive disc using a Zeiss Axiophot compound microscope and photos taken with a Zeiss AxioCam ICc 5 camera. All measurements were made using Zen 2012 SP2 Software, are presented in micrometres and follow the uniform specific characteristic system described by Lom (1958). Denticle descriptions are based on the method provided by Van As and Basson (1989). Minimum and maximum values are given, followed in parentheses by the arithmetic mean, standard deviation and number of specimens measured. In the case of the number of denticles and number of radial pins, the mode is provided instead of the arithmetic mean. Body diameter is measured as the adhesive disc plus border membrane.

Physical water quality parameters, i.e. temperature, pH, dissolved oxygen concentration, conductivity, total dissolved solids (TDS) and salinity were measured on site using a Hanna HI 9828 Multiparameter.

COLLECTION LOCALITIES

Nata River, Botswana (Fig. 1A)

The Nata River is a sandy-bedded seasonal river which originates in the Zimbabwe Plateau just beyond the eastern margin of the Kalahari Desert and ends in the low lying depression comprising the Makgadikgadi Pans in north-eastern Botswana. It has a mean annual flow of 279 million m^3. The climate in the Nata River region is semi-arid, with low, unpredictable rainfall and high evaporation rates. Flow is erratic and during some years it flows for an extended period, while it may not flow at all for several years during periods of drought (Hitchcock and Nangati 2000, Hitchcock 2003). Peak flow in the Nata River is between January and March (Hitchcock 1995) and when the river begins to dry, water is retained in the riverbed in a number of large pools (Friederich and Gould 1986).

Rustfontein Dam, South Africa (Fig. 1B)

Rustfontein Dam is fed by the Upper Modder River that is a tributary of the Orange-Vaal River System, drains an area of 7960 km^2 and has a mean annual runoff of 184 million m^3 (Koning and Roos 1999, Koning *et al.* 2000).

RESULTS

Trichodina species – Nata population (Figs 2A–D, 4A, B)

Host and locality: *Metadiaptomus transvaalensis*, Nata River (S 20°12.290' E 026°11.302'), Nata, Botswana.

Site: Carapace (Figs 3A–E).

Reference material: Slides 2012/08/16-48 and 2012/08/16-79 in the collection of the Aquatic Ecology Laboratory, Department of Zoology and Entomology, University of the Free State, Bloemfontein, South Africa.

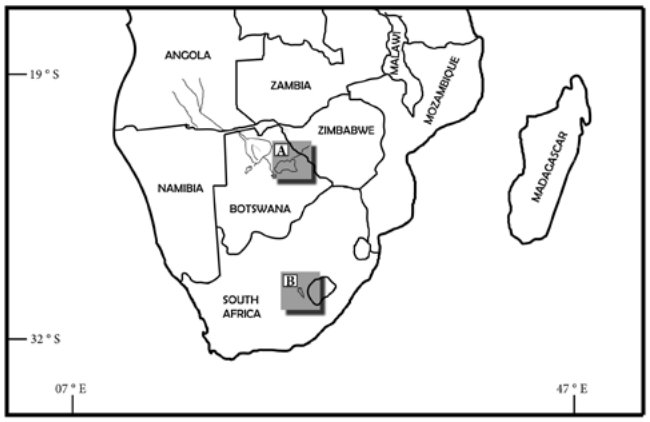


Fig. 1. Map of southern Africa indicating the two localities where *Trichodina diaptomi* Šrámek-Hušek, 1953 was collected: from the carapace of *Metadiaptomus transvaalensis* Nata River in Botswana (A) and *M. meridianus* in the Rustfontein Dam in South Africa (B).

Description: Medium-sized trichodinid with flattened, disc-shaped body. Body dimensions are presented in Table 1. Centre of adhesive disc shows a clear circle. Denticles are tightly packed with small spaces between them.

Nuclear apparatus consists of a large C-shaped macronucleus, very constant in shape. In some specimens (just more than 50% of measured specimens) small oval micronucleus visible in +y position, sometimes lying in clear indentation of macronucleus (see Table 1).

Denticle description: Blade strongly developed, filling large part of area between y-axes. Distal surface slightly rounded, higher than tangent point. Posterior margin forming semi-lunar curve with deepest point at same level as apex. Apex pointed, almost touching y+1 axis in some specimens, while extending slightly beyond y+1 axis in others (Figs 4A, B). Blade apophysis prominent in all denticles. Section connecting blade and central part relatively delicate. Central part robust, tapering to a sharply rounded point in some specimens, but more rounded in others. Central part not loosely connected to previous denticle. Central part extends more than halfway to y-axis. Section above x-axis triangular, whilst section below x-axis parallel for half the distance, then slanting away towards ray. In some denticles central part shows slight indentation corresponding to ray apophysis. Apophysis of ray strongly developed in most denticles. Central part connecting ray strongly developed. Ray strongly developed, of same thickness throughout length with a rounded point in some denticles and sharper in others. Rays parallel to y-axes in some specimens, while slightly curved towards y+1 axis in some denticles. Rays almost touching central circle in most denticles. Ratio of section below and above x-axis just less than 1 (0.8–0.9). Central circle's border (periphery) well defined, but does not always impregnate in same way in all specimens. Central circle mostly only slightly granular in appearance with uneven wavy border in some.

Trichodina species – Rustfontein population (Figs 2E, F)

Host and locality: *Metadiaptomus meridianus*, Rustfontein Dam (S 29°16.246' E 026°36.366'), Free State Province, South Africa.

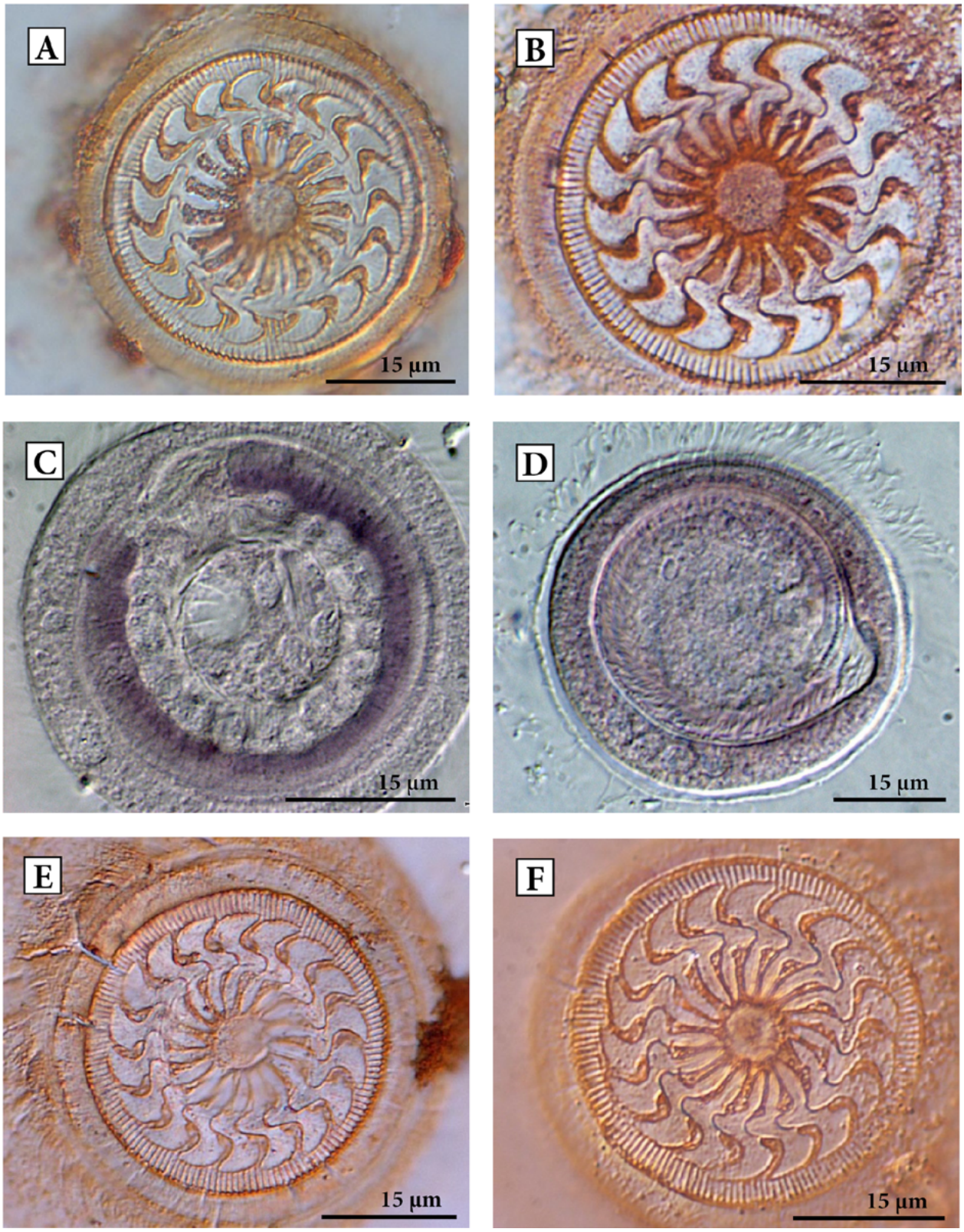
Site: Carapace.

Reference material: Slides 2012/11/30-16 and 2012/11/30-17 in the collection of the Aquatic Ecology Laboratory, Department of Zoology and Entomology, University of the Free State, Bloemfontein, South Africa.

Description: Measurements for this population are included in Table 1.

Denticle description: Similar to previous population.

Remarks: These two trichodinid populations without doubt both belong to the same species, i.e. *T. diaptomi*. The *T. diaptomi* population from Rustfontein Dam is very similar in overall body dimensions to the population described by Basson and Van As (1991) from Bloemfontein. Both these populations were not only collected from the same host, i.e. *M. meridianus*, but also during the warmer months, i.e. late spring and early summer months (from Rustfontein Dam and Bloemfontein respectively). This could explain the similarities in the dimensions of these two populations. *Trichodina diaptomi* from the Nata River (Botswana), collected at much lower water temperatures during late winter (see Table 2) as well as from a new host record (*M. transvaalensis*), shows overall body dimensions that are larger than those from *M. meridianus*. The occurrence of larger winter specimens corresponds with findings of other authors such as Kazubski and Migala (1967, 1968) and therefore the larger Nata River population is most likely due to the fact that these specimens were collected in the winter when the water temperature was an average of 17.5°C, compared to a temperature of 23.2°C measured at Rustfontein during late spring (see Table 2). The population of *T. diaptomi* from Australia from *B. fluvialis* as presented by Green



Figs 2 A–F. Micrographs of silver impregnated adhesive discs (**A**, **B**, **E** and **F**) and haematoxylin stained specimens (**C** and **D**), showing the nuclear apparatus (**C**) and adoral spiral (**D**) of *Trichodina diaptomi* Šrámek-Hušek, 1953 from the Nata River (**A–D**) and Rustfontein Dam (**E** and **F**).

Table 1. Biometrical data (in µm) of different populations of *Trichodina diaptomi* Šrámek-Hušek, 1953.

Trichodinid Species	*T. diaptomi*	*T. diaptomi*	Not *T. diaptomi*, probably *T. acuta*	*T. diaptomi*	*T. diaptomi*	*T. diaptomi*	*T. diaptomi*
Host	*Metadiaptomus meridianus*	*Boeckella fluvialis*	*Tetraodon cutcutia*	*Notodiaptomus deitersi*	*M. albuquerquensis*	*M. transvaalensis*	*Metadiaptomus meridianus*
Locality	South Africa	Australia	India	Brazil	Mexico	Botswana	South Africa
Reference	Basson and Van As (1991)	Green and Shiel (2000)	Asmat (2004)	Da Silva *et al.* (2009)	Silva-Briano *et al.* (2011)	Present study	Present study
Body Diam	33.8–48.7 (41.5)	35.3-49.6 (43.6)	40.8–55.5 (50.1)	(38.3 ±4.2)	38.1–44.6 (40.4)	40.3–53.7 (45.9 ± 2.9)	37.1–45.9 (41.3 ± 2.2)
Adh disc diam	27.9–39.9 (33.8)	30.2–42.6 (35.9)	32.6–46.6 (41.4)	(31.5 ± 3.1)	29.3–39.8 (34.5)	31.9–43.5 (36.9 ± 2.5)	28.3–38.8 (33.1 ± 2.3)
B.m.w.	2.6–5.4 (4.0)	1.8–4.8 (3.6)	3.6–5.1 (4.3)	–	2.6–3.8 (3.0)	3.5–4.9 (4.3 ± 0.3)	3.4–5.1 (4.1 ± 0.4)
Dent ring diam	14.8–22.6 (19.6)	14.7–39.1 (20.1)	18.3–26.5 (23.4)	–	18.1–22.8 (19.8)	16.3–24.6 (21.1 ± 1.9)	15.0–20.2 (18.1 ± 1.4)
C.c.d.	4.4–7.9 (5.9)	–	7.1–9.2 (8.0)	–		5.2–9 (6.8 ± 0.9)	3.7–6.3 (5.0 ± 0.6)
Dent number	15–20 (18)	15–19 (17)	18–25 (–)	18–20 (19)	20–24 (22)	17–21 (18)	16–22 (18)
Rad p/dent	7–11 (9)	5–9 (9)	7–10 (–)	8–10 (–)	8–11 (9)	8–10 (9)	8–11 (10)
Dent length	4.8–7.7 (6.2)	4.4–7.6 (6.2)	5.6–8.2 (6.4)	–	5.7–6.9 (6.3)	5.2–7.4 (6.3 ± 0.6)	4.1–7.2 (5.5 ± 0.6)
Blade length	2.9–6.9 (3.8)	3.4–5.7 (4.4)	3.1–4.6 (3.9)	–		3.2–4.8 (4.2 ± 0.4)	2.7–4.7 (3.5 ± 0.4)
C.p.w.	1.4–2.7 (2.0)	1.2–2.9 (2.0)	2.0–3.6 (3.2)	–		1.9–3.1 (2.4 ± 0.3)	1.6–2.7 (2.2 ± 0.3)
Ray length	2.8–6.1 (4.4)	3.8–6.4 (4.9)	3.1–5.2 (4.1)	–	4.8–6.2 (5.72)	3.4–6.7 (5.0 ± 0.6)	3.5–6.0 (4.6 ± 0.6)
Denticle span	–	–	9.3–12.7 (11.3)	–		9.8–12.9 (11.4 ± 0.8)	9.2–12.5 (10.4 ± 0.8)
Ma – shape	C	C	–	C	C	C	C
Ma – ext diam	32.3–50.2 (38.3)	29.1–42.0 (35.1)	–	–		26.5–39.2 (30.6 ± 3.3)	25.7–38.7 (32.7 ± 3.4)
Ma – thickness	4.1–10.2 (6.4)	6.8–13.4 (10.4)	–	–		3.6–6.2 (4.8 ± 0.8)	3.5–7.3 (5.0 ± 1.0)
Ma – x value	7.6–19.1 (12.6)	5.2–18.3 (11.8)	–	–		5.8–14.4 (9.0 ± 2.5)	8.6–19.0 (12.2 ± 2.3)
Mi – shape	oval	–	–	–		oval	oval
Mi – length	4.5–7.6 (5.8)	–	–	–		2.3–5.6 (3.6 ± 1.0)	2.4–7.3 (4.1 ± 1.3)
Mi – width	1.7–3.8 (2.8)	–	–	–		1.1–2.1 (1.5 ± 0.3)	0.8–2.6 (1.9 ± 0.4)
Mi – y position	+y	–	–	–		+y	+y
Mi– y value	7.0–26.8 (16.0)	–	–	–		0.9–17.8 (10.4 ± 4.5)	3.1–18.5 (9.5 ± 3.7)
Adoral spiral	400°	ca. 400°	390°	–		390–440°	395–410°
n1	27	50	20	10–20		30	34
n2	20	24	–	–		27	33
n3	9	–	–	–		12	24

Adh – adhesive, B.m.w. – Border membrane width, C.c.d. – Central circle diameter, C.p.w. – central part width, dent – denticle, Diam – diameter, ext – external, Ma – macronucleus, Mi – micronucleus, n1 – number of silver impregnated specimens measured, n2 – number of haematoxylin stained specimens measured for macronucleus, n3 – number of haematoxylin stained specimens measured for micronucleus, Rad p/dent – Radial pins per denticle.

Table 2. Physical water quality parameters measured in the Nata River and Rustfontein Dam during collection of infested metadiaptomids in August and November 2012, respectively.

Location	Nata River	Rustfontein Dam
Date and time	14/08/2012 at 10:45; 15/08/2012 at 12:50; 16/08/2012 at 09:12	20/11/2012 at 11:04
Temperature (°C)	15.37–19.19 (17.51)	23.32
pH	8.39–8.62 (8.54)	8.40
Dissolved oxygen concentration (%)	113.2–126.8 (119.72)	110.9
Conductivity (µS/cm)	1295–1374 (1334)	284
Total dissolved solids (TDS) (ppm)	647–687 (667)	142
Salinity	0.65–0.69 (0.67)	0.13

and Shiel (2000) also concurs with that from *M. transvaalensis* in overall body dimensions. Some small differences were found in the mean body and adhesive disc diameters between the two South African populations and the Australian population, also collected during spring, with the latter being slightly larger. These differences could be due to the fact that the trichodinids were found on a completely different host species. Furthermore, the Australian population was collected and then kept at an ambient temperature of 20°C that was lower than the water temperature the South African populations were collected at. The latter is most likely a more plausible explanation. The only population that does not agree with the dimensions of *T. diaptomi* is the population provided by Asmat (2004). This author described a trichodinid he identified as *T. diaptomi* from two fish species. This trichodinid very likely represents *Trichodina acuta* Lom 1961, not *T. diaptomi* as the latter species has never before been reported from fish. Furthermore, the much larger body dimensions (see Table 1) fall well within the range of the well-known fish trichodinid *T. acuta*.

Water quality

Several standard physical water quality parameters such as temperature, pH, dissolved oxygen concentration, conductivity, TDS and salinity were measures for both localities (see Table 2). While *T. diaptomi* is considered to be a freshwater species, this study clearly shows the wide tolerance it has for various water parameters, specifically conductivity, TDS and salinity as it was found in water with low values for these three parameters (284µS/cm, 142 ppm and 0.13 respectively at Rustfontein Dam) to values averaging 1334 µS/cm, 667 ppm and 0.67 respectively in the Nata River. In no other study to date has any reference been made to the water quality parameters and therefore no indication has been made of the ability of this trichodinid species to occur and survive an array of environmental conditions.

DISCUSSION

The characteristics and measurements of both the Nata and Rustfontein populations are practically identical to the population described from the Free State, South Africa, by Basson and Van As (1991), although the Nata population is slightly larger as discussed above. There is no doubt that this is the same species, i.e. *Trichodina diaptomi.* As mentioned previously, a trichodinid has been reported from several calanoid hosts in various locations worldwide. A comparison of the characteristics and measurements of all the previously documented populations (some summarised in Basson and Van As 1991 and the rest in Table 1) from calanoids indicates that these are all the same species, i.e. *Trichodina diaptomi*. It is interesting that this species, associated with members of the order Calanoida, is so widely distributed all over the world. This raises questions on its host specificity and method of dispersion that requires a revisit to previous reports on its discovery from different parts of the world.

Dogiel (1940) first described a trichodinid from the body surface of a *Diaptomus* species in the former Soviet Union (USSR), which he named *Trichodina domerguei* f. *megamicronucleata* and reported that the population of trichodinids he collected from a goldfish was the same species (Lom 1960a, Basson and Van As 1991, Green and Shiel 2000).

Initially trichodinids were not stained with silver nitrate and many species were mistakenly considered to be the same. Some trichodinid species were identified as different forms and/or subspecies of *Trichodina domerguei*, some of which displayed similar characteristics (such as the central circle) to that of the calanoid trichodinid, hence the name given to the latter by Dogiel (1940).

The next report was that of Šrámek-Hušek (1953) who described a new form, i.e. *Trichodina domerguei* var. *diaptomi* Šrámek-Hušek, 1953 from *Diaptomus vulgaris* from the former Czechoslovakia (Lom 1960a, Basson and Van As 1991, Green and Shiel 2000). Up until this point no photomicrographs had been presented, making it difficult for later authors to know exactly what Dogiel (1940) and Šrámek-Hušek (1953) were dealing with.

In 1960, Lom (1960a) included photomicrographs of silver impregnated adhesive discs of a trichodinid he collected from *Diaptomus vulgaris*, *Diaptomus castor* and *Eudiaptomus gracilis*, also from the former Czechoslovakia (Basson and Van As 1991, Green and Shiel 2000). Lom (1960a) concluded that the trichodinids from goldfish and those from calanoids were two different species based on dimensions and transmission experiments. He split Dogiel's (1940) material into two groups and suggested that the trichodinids from goldfish are representatives of *Trichodina reticulata* Hirschmann and Partsch, 1955 and that those from calanoids be assigned to *Trichodina domerguei* f. *latispina* Dogiel, 1940.

The next report of a calanoid trichodinid originated from mainland China when Chen (1963) reported it from various fish and tadpole species, as well as the calanoids *Sinodiaptomus sarsi* and *Neodiaptomus handeli*. He followed Lom (1960a) in also identifying it as *T. domerguei* f. *latispina*, as well as conducting cross-infestation experiments. Chen (1963) reportedly succeeded in transferring this trichodinid from calanoids to different carp species, but did not manage to transfer known fish trichodinids (*T. reticulata*, *T. nobilis* Chen, 1963 and *T. nigra* Lom, 1961) to the copepods (Basson and Van As 1991).

In 1964 trichodinids of calanoids were placed into a separate subspecies for the first time by Haider (1964) in his comprehensive monograph on trichodinids when he named them *T. domerguei* subsp. *megamicronucleata* Dogiel, 1940. He also synonymised *T. domerguei* f. *diaptomi* with *T. domerguei* f. *megamicronucleata* (Basson and Van As 1991). Almost a decade later *T. domerguei* subsp. *megamicronucleata* was found on an unidentified *Diaptomus* species and *Eudiaptomus zachariasi* from Poland by Migala and Grygierek (1972).

Finally, 19 years later, Basson and Van As (1991) provided a full taxonomic description of this ciliophoran based on material collected from *Metadiaptomus meridianus* in Bloemfontein, South Africa. Basson and Van As (1991) reviewed all the previous records and concluded that they all represented the same widely distributed trichodinid and named it *Trichodina diaptomi*. Similar to Lom (1960a) they concluded that fish do not provide a suitable substrate for *T. diaptomi* to establish a viable population.

During plankton surveys in 1991, 1992 and 1995 in billabongs of the Murray River, Australia, Green and Shiel (2000) collected calanoid trichodinids that they identified as *Trichodina diaptomi* as described by Basson and Van As (1991), as it corresponded closely with the description provided by these and earlier authors. Three calanoid species were collected, namely *Boeckella fluvialis*, *Boeckella minuta* and *Calamoecia lucasi*. Trichodinids, however, were only present on the former two and only on adults and copepodites of a certain size. Green and Shiel (2000) suggested that one explanation might be that these trichodinids only occur on copepods and copepodites of large species. This would also explain their absence from *Calamoecia lucasi*, the adults of which are smaller in size than the infested copepodites of the two larger species.

The next report of *T. diaptomi* is worthy of note as Asmat (2004) claims to have collected *T. diaptomi* from the gills of two freshwater fishes, *Tetraodon cutcutia* and *Gagata cenia*, from West Bengal, India in 1996.

This was followed by collections of *T. diaptomi* from a South American calanoid *Notodiaptomus deitersi* in 2006 and 2007 in Brazil (Da Silva *et al.* 2009).

The most recent report on *T. diaptomi* was published in 2011 by Silva-Briano *et al.* (2011) after they collected it from *Mastigodiaptomus albuquerquensis* and *Mastigodiaptomus montezumae* in the north-central region of Mexico.

We believe all the trichodinid populations so far described from calanoids represent the same species, namely *T. diaptomi*, with the exception of that of Chen (1963). His description of *T. domerguei* f. *latispina* from fish, calanoids and tadpoles most likely represents more than one trichodinid species. He did not employ silver impregnation, making it impossible to come to a conclusion concerning the trichodinids from fish and tadpoles. However, since his population measurements

show such a wide range and the lower range falls well within that for *T. diaptomi*, we suspect that he probably did encounter this species on calanoid copepods. The upper range, however, coincides with the ranges of various trichodinids found on fish. It could be that he had a mixed population of *T. diaptomi* as well as fish trichodinids, but mistakenly took it to be a single species. Workers such as Lom (1960a) and Basson and Van As (1991) could not succeed in forming viable populations of *T. diaptomi* on any fish species; therefore the trichodinids Chen (1963) observed from calanoids were in all probability *T. diaptomi*, while those from fish and tadpoles were not.

The other doubtful record of *T. diaptomi* is that of Asmat (2004) in which he described a trichodinid he identified as *T. diaptomi* from two fish species. His morphometric dimensions are far above that of the other *T. diaptomi* populations, but fall well within the range of *Trichodina acuta* that is a well-known trichodinid of fish and also possesses a central circle. He makes no reference to ever finding trichodinids from a calanoid. Furthermore, he provided a micrograph of the alleged *T. diaptomi*, which shows clear similarities with the cosmopolitan *T. acuta*.

Presently the known worldwide distribution of *T. diaptomi*, associated with calanoids, includes the former Soviet Union (Dogiel 1940), the former Czechoslovakia (Šrámek-Hušek 1953, Lom 1960a), China (Chen 1963), Poland (Migala and Grygierek 1972), South Africa (Basson and Van As 1991, present study), Australia (Green and Shiel 2000), Brazil (Da Silva *et al.* 2009), Mexico (Silva-Briano *et al.* 2011) and Botswana (present study). Some authors (Da Silva *et al.* 2009, Silva-Briano *et al.* 2011) express their uncertainty as to the origin of the occurrence of *T. diaptomi* in specific parts of the world and whether it was introduced or occurs there naturally.

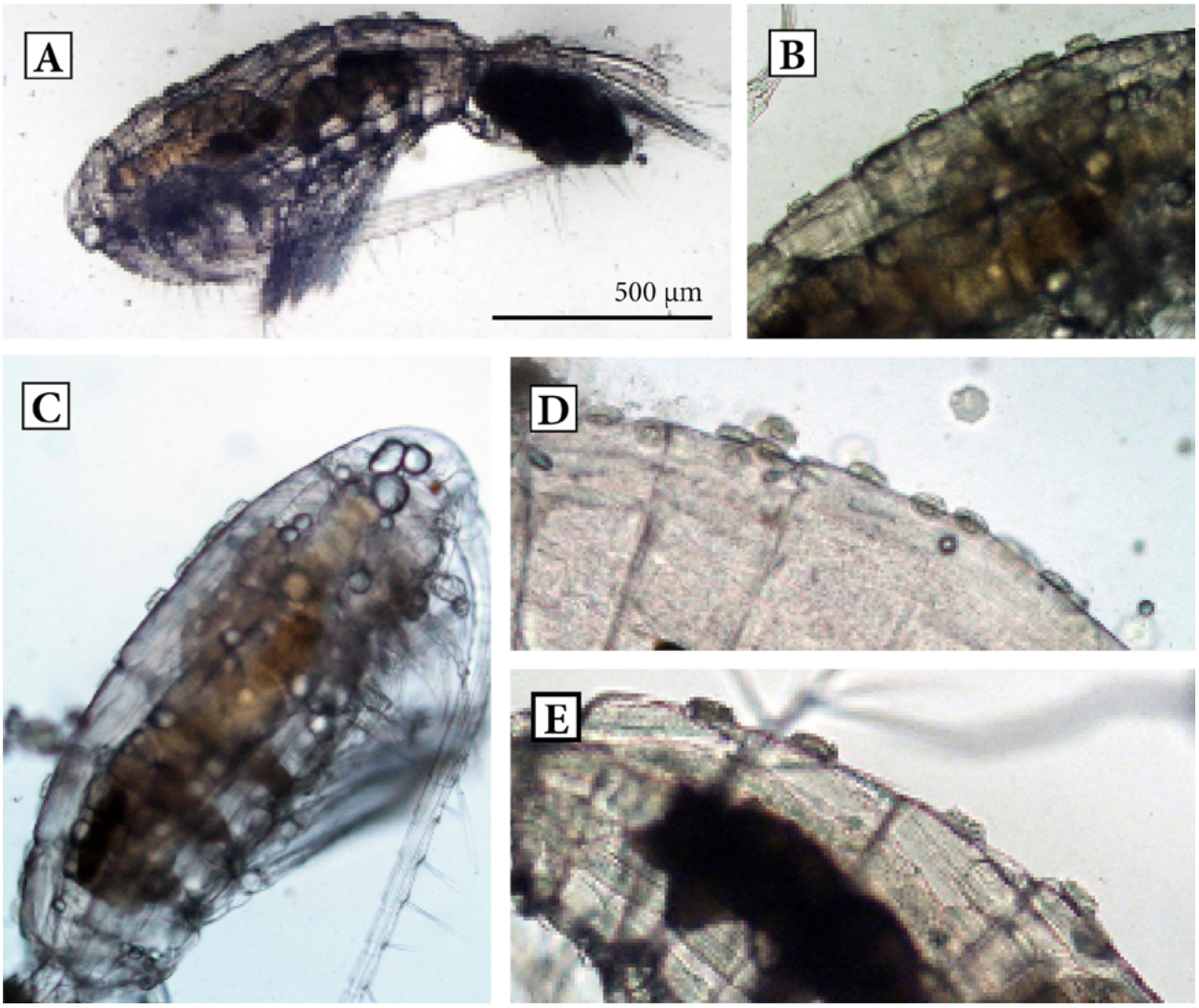
We believe *T. diaptomi* to be a cosmopolitan species naturally associated with calanoid hosts exclusively. The present study was a joint survey of zooplankton and fish parasites and despite the sampling of all trichodinids from fish from the same pools in the Nata River, *T. diaptomi* was never collected from any fish species. We believe fish are not reservoir hosts for these ciliophorans, which raises the important question on how these trichodinids survive when populations of calanoids decline or temporarily disappear from a water body in response to harsh environmental conditions caused by abiotic or biotic factors.

Green and Shiel (2000) observed that *T. diaptomi* only occurred during October and November, despite the calanoids being present year round, but did not provide potential reasons for the absence of trichodinids during the rest of the year. If *T. diaptomi* does not have a reservoir host and cannot form viable infestations on fish, the question involuntarily arises as to where they go for the other 10 months of the year? The answer to this question has never been addressed by any workers, as most merely recorded and described the trichodinid they encountered on calanoids. We believe that in order to provide a feasible hypothesis for this, one will have to have a look at the hosts in this particular case, especially since *T. diaptomi* was reported for the first time from a habitat that was rapidly drying up, in a system where this is a natural and regular occurrence.

Zooplankton was only sampled on one occasion in November from Rustfontein Dam, so it was not possible to observe whether the trichodinid population fluctuated or even disappeared at times. However, Green and Shiel (2000) sampled plankton year round in 1991, and they observed that despite the fact that calanoids were present from January to early December, they only harboured trichodinids in October and November (spring). Interestingly, these calanoids formed a major component of the zooplankton from May (late autumn) to early November, with a sharp percentage abundance decline in early October and a brief recovery in late October. Their percentage abundance then remained low for the rest of the year. Simultaneously, the trichodinid infestations peaked in early October, declined during the copepod resurgence and peaked again when the copepod abundance declined in late November. Green and Shiel (2000) suggested that this may either indicate that the infestation contributed to the copepod decline or that the trichodinids were able to establish when the copepod population was declining for other reasons such as poor nutrition or environmental factors.

While seasonality was not investigated during the present study, trichodinids were common on their hosts during mid-winter (July) in Botswana, as well as in early summer in South Africa, both in Rusfontein Dam (the present study) and Bloemfontein (Basson and Van As 1991). The occurrence of *T. diaptomi* during mid-winter in Botswana differs with the findings of Green and Shiel (2000) who found trichodinids only in October and November (summer) in their study.

Although sampling in the Nata River took place in August only, we do know that it is an ephemeral river that dries up annually. Since peak flow in this system takes place between January and March, the last pools in which we sampled would have dried up before the

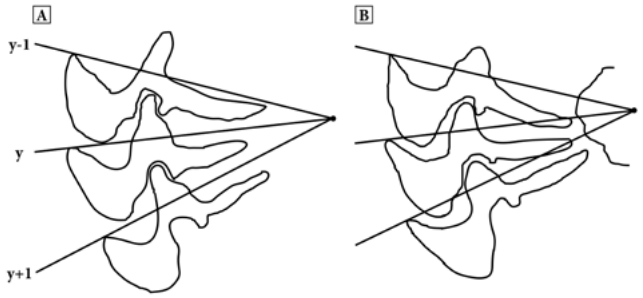


Figs 3 A–E. Micrographs of *Metadiaptomus transvaalensis* with *Trichodina diaptomi* Šrámek-Hušek, 1953 on the carapace collected from the Nata River, Botswana in August 2012. Whole specimen of *M. transvaalenis* with several trichodinids visible on dorsal surface of body (A), *M. transvaalensis* with several trichodinids visible on dorsal surface opposite locomotory appendages of copepod (C) and close-up views of dorsal carapace of *M. transvaalensis* with trichodinids clearly visible on surface of copepod (B, D, E) with two detached trichodinids visible in D.

next flood, which, for the organisms of such aquatic environments, is a catastrophic event.

Natural zooplankton population densities and dynamics fluctuate seasonally and annually in response to their abiotic environment, including catastrophic events such as drying, as well as to biotic factors. Adaptive responses to these factors can be expressed as morphological, behavioural or life history changes. Of the latter responses, dormancy is one of the most evident and may be viewed as an escape in time, which may range from days to hundreds of years (Dahms 1995).

In temporary habitats that dry seasonally, such as the Nata River, the advantage of dormancy is quite obvious, but it is also extremely important in large permanent water bodies (Gyllström and Hansson 2004), such as Rustfontein Dam and most probably also the billabongs of the River Murray in Australia. This is because environmental variables in permanent water bodies also fluctuate temporarily. The question arising from the drying event in the Nata River is this: zooplankton, such as calanoids, possess a life-history adaptation, which most probably evolved a long time ago, but what



Figs 4 A and B. Diagrammatic drawings of the denticles of two different specimens of *Trichodina diaptomi* Šrámek-Hušek, 1953 from the carapace of *Metadiaptomus transvaalensis* from the Nata River, Botswana to illustrate variation in denticle shape.

do the trichodinids do to survive such an event? According to Mueller (1938) and Lom (1960b) no cyst or dormant stage is known for the genus *Trichodina*, and none has ever been recorded by any worker. Against the background of the narrative of *T. diaptomi*, it appears that not only does this cosmopolitan trichodinid successfully occur on hosts that are not available year round, but it also appears to be able to somehow survive catastrophic events such as the complete desiccation of their aquatic habitat and consequent disappearance of their hosts, sometimes for extended periods. We would therefore like to postulate that some form of dormant stage probably exists for *T. diaptomi* and that, in the case of this trichodinid species specifically, it may be linked to the diapause of the calanoids.

FOOTNOTES

[1] According to Articles 45.6.4 and 50.3.1 of the ICZN (1999) the correct taxon author of this species should be *Trichodina diaptomi* Šrámek-Hušek, 1953 and not *T. diaptomi* Basson and Van As, 1991.

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