

## Taxonomic Assessment of Three North American Trichodinids by Re-evaluating the Taxon Validity of *Trichodina heterodentata* Duncan, 1977 (Peritrichia)

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**Abstract.** *Trichodina heterodentata* was first described from fish breeding farms in the Philippines by Bryan Duncan in 1977 as ectoparasites of imported cichlids, more specifically the southern African *Oreochromis mossambicus* (Peters, 1852) from the Limpopo River System. This trichodinid has subsequently been described from almost every continent, bar North America. Being a cosmopolitan species, with a preference for cichlid hosts, it has unambiguous morphological features, but with distinct variances between and within populations. After reviewing previous descriptions of North American trichodinids, analysing the morphological data (both generally published information along with the original type material from the Smithsonian Museum, Washington, U.S.A.) and investigating the distribution patterns of the southern African introduced *O. mossambicus* throughout the North American water systems, three of the four studied trichodinids (*T. hypsilepis* Wellborn, 1967, *T. salmincola* Wellborn, 1967 and *T. vallata* Wellborn, 1967) are proposed to represent the same species as *T. heterodentata*. According to nomenclature rules *T. hypsilepis* henceforth represents the valid taxon (synonyms: *T. salmincola*, *T. vallata* and *T. heterodentata*). This not only questions the validity of several trichodinid species, but also indicates the probability of an African alien introduction into North America.

**Keywords:** *Trichodina hypsilepis*, *T. heterodentata*, *Oreochromis mossambicus*.

### INTRODUCTION

Members of the family Trichodinidae Raabe, 1959 are all protozoan, ciliophoran mobile ecto- and endosymbionts, using the tissue of their hosts as a substrate to hover across or to temporarily attach to. Trichodinids are usually associated with freshwater, estuarine or marine teleost fishes, but have also been described from amphibians (Fulton 1923; Lom 1958; Kazubski

1988; Kruger *et al.* 1991, 1993, 1995; Dias *et al.* 2009), aquatic and terrestrial invertebrates (Basson and van As 1991, 1992; Kazubski 1991), found in the urinary tract of chondrichthyans (van As and Basson 1996) and recently in the reproductive tracts of waterfowl (Carnaccini *et al.* 2016). Members of the family Trichodinidae are highly cosmopolitan with more than 300 species described, representing 11 genera (Basson and van As 1989, van As and Basson 1993, Hu 2011), with the genus *Trichodina* Ehrenberg, 1830, having the largest number of species. According to Lom (1958) representatives within the family Trichodinidae are primarily identified on morphological differences in the reach

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of their adoral spiral and structure of the aboral denticle ring of the adhesive disc.

One of the species from the genus *Trichodina* with a cosmopolitan distribution and commonly encountered from a variety of freshwater fish hosts is *T. heterodontata* Duncan, 1977 (Pádua *et al.* 2012, Valladão *et al.* 2016) showing a distinct preference for cichlids (Basson and van As 2006). *Trichodina heterodontata* was initially described by Duncan (1977) from the Philippines from three fish species, with the holotype population described from *Oreochromis mossambicus* (Peters, 1852), a native fish from southern Africa. The Mozambique tilapia is probably one of the most widely distributed aquaculture fishes, to such a degree that it has been declared an invasive species in certain parts of the world (Wilson *et al.* 2019).

*Trichodina heterodontata* is credited in having a large range of biometric variation in its denticle structure, hence Duncan's (1977) comments and reason for naming this species. Using the large variation in adhesive disc morphometrics, all *T. heterodontata* populations described from various hosts were clumped into three overarching groupings in the present study.

Even though trichodinids have been described from the United States of America by Fulton (1923), Mueller (1937), Hirshfield (1949), Uzmann and Stickney (1954) and Wellborn (1967), there have basically been no recent records.

An important contribution was made by Wellborn (1967) when he described eight new and ten known species from freshwater teleost hosts from the South-eastern U.S. Of these new species, *T. hypsilepis* Wellborn, 1967, *T. salmincola* Wellborn, 1967, *T. vallata* Wellborn, 1967 and *T. funduli* Wellborn, 1967 shared similar denticle morphology and biometrics as those of the cosmopolitan *T. heterodontata*. Both Wellborn (1967) and Duncan (1977) used the morphological characteristics proposed by Lom (1958) in their descriptions, although not all the new species were described using silver impregnated specimens.

The present paper investigates the validity of four trichodinid species of Wellborn (*T. hypsilepis*, *T. salmincola*, *T. vallata* and *T. funduli*), comparing these relatively unknown species with the well-stud-

ied *T. heterodontata* by incorporating alpha-taxonomy from historical data and examining museum type material. Comments are also provided on the introduction of *T. heterodontata* from the southern African continent into North America by tracing the distribution history of the cichlid fish *O. mossambicus* and the validity of certain North American trichodinid species.

## MATERIAL AND METHODS

Photomicrographs used in this study for the re-measurements of biometric data were based on the original museum type material (holo- and paratypes) housed in the Protozoan and Helminth collections of the Smithsonian Institute in Washington, USA. The type material for *T. heterodontata* was collected by Duncan (1977) from three populations of freshwater teleost hosts (USNM No. 24485, USNM 24486 and USNM No. 24487) in the Philippines. Wellborn's (1967) type material was used for *Trichodina hypsilepis* (USNM No. 61651 & 61652) and *T. funduli* (1357367 & 1357368) from Alabama, *T. salmincola* (USNM 1357379 & 1357380) from North Carolina and *T. vallata* (USNM 1357384) from Georgia. The above-mentioned material was collected from various species of freshwater fish hosts (see Wellborn 1967).

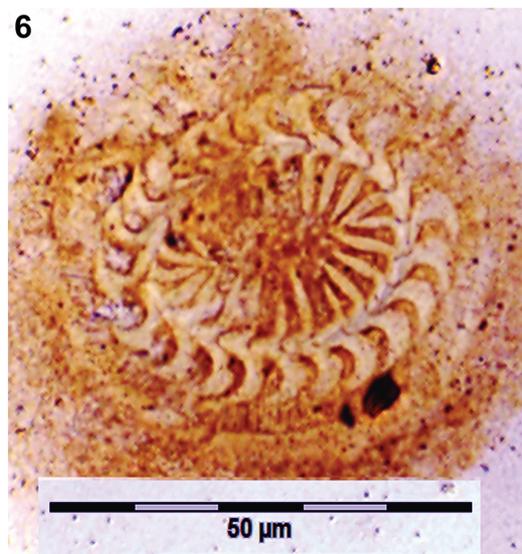
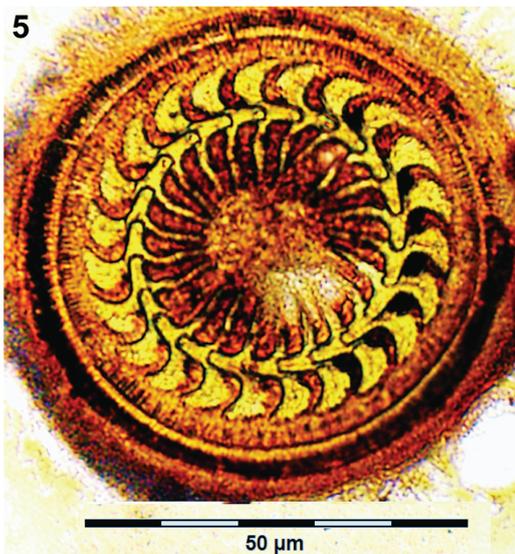
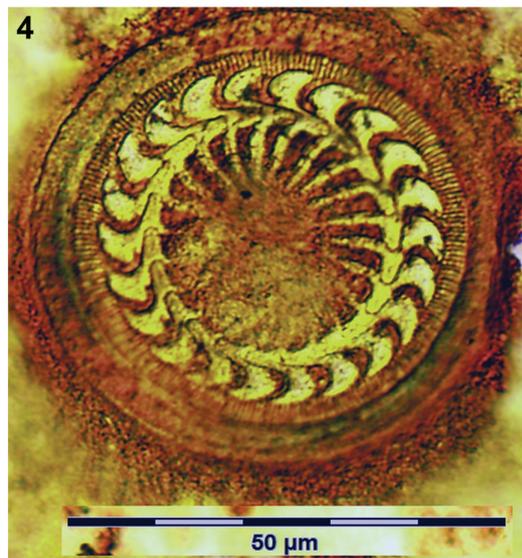
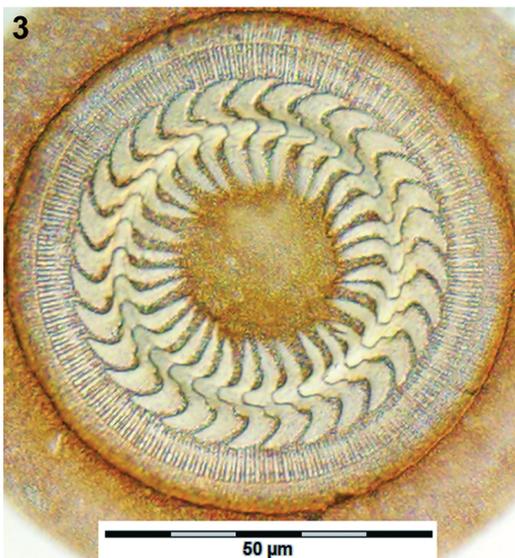
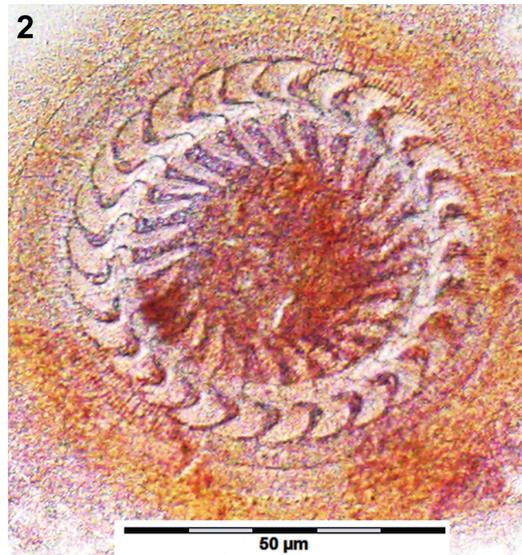
The type material for these five species was impregnated with silver nitrate by the original authors using Klein's (1926) method, as recommended by Lom (1958). All these morphometric measurements follow the proposed uniform characteristics system suggested by Lom (1958) and are given in micrometres ( $\mu\text{m}$ ). Minimum and maximum values, followed by the arithmetic mean and standard deviation, are provided where possible. For two characteristics; number of denticles and number of radial pins per denticle, the mode, rather than the arithmetic mean, is provided. Denticle descriptions for all species from the Smithsonian micrographs were done according to the methods proposed by van As and Basson (1989), except for *T. funduli*, since the type material destined to such a degree that denticle details could not be determined.

## RESULTS

Morphometric measurements of the type material from the Smithsonian of Duncan's (1977) original *T. heterodontata* populations (Figs 1–3) and Wellborn's original descriptions for *T. hypsilepis*, *T. salmincola*, *T. vallata* and *T. funduli* (Figs 4–6) are provided in Tables 1 and 2.



**Figs 1–6.** Micrographs of representative specimens from the paratype material of Duncan's (1977) *Trichodina heterodontata* Duncan, 1977 (Figs 1–3) and Wellborn's (1967) (Figs 4–6) collections at the Smithsonian Institute, **1** – Population A from *Oreochromis mossambicus* (Peters, 1885) hosts, **2** – Population B from *Coptodon zillii* (Gervais, 1884), **3** – Population C from *Trichopodus trichopterus* (Pallas, 1770), **4** – *Trichodina hypsilepis* Wellborn, 1967 from *Notropis hypsilepis* Suttkus & Raney, 1955, **5** – *T. salmincola* Wellborn, 1967 from *Oncorhynchus mykiss* (Walbaum, 1792) and **6** – *T. vallata* Wellborn, 1967 from *Ictalurus punctatus* (Rafinesque, 1818). Scale bars: 50  $\mu\text{m}$ .



**Table 1.** Comparison of Duncan's (1977) original *Trichodina heterodentata* Duncan, 1977 measurements with remeasured data obtained from his paratype specimens in the Smithsonian museum, with biometric data from two populations of *T. hypsilepis* Wellborn, 1967 (ADD – adhesive disc diameter, BD – body diameter, BMW – border membrane width, CL – collection locality, DBL – denticle blade length, DCPW – denticle central part width, DL – denticle length (= denticle width), DRD – denticle ring diameter, DRL – denticle ray length, DS – denticle span, HS – host species, LoH – location on host, n – population size, nD – number of denticles, nRP/D – number of radial pins per denticle) (all measurements in µm) (\* pertains to the mode, rather than the mean) (\*\* individuals measured for number of denticles) (° host taxonomy in original article: *Tilapia mossambica*) (°°° host taxonomy in original article: *Tilapia zillii*) (°°°° host taxonomy in original article: *Trichogaster trichopterus*).

CL	<i>Trichodina heterodentata</i>									
	Duncan (1977)					Wellborn (1967)				
	Philippines A		Philippines B		Philippines C	Alabama, USA		Smithsonian 2017 measurements of Wellborn's paratype material		
LoH	Skin & Fins	Smithsonian 2017 re-measurements of Duncan's paratype material	Skin, Fins & Gills	Smithsonian 2017 re-measurements of Duncan's paratype material	Skin	Smithsonian 2017 re-measurements of Duncan's paratype material	Skin & Fins	Smithsonian 2017 measurements of Wellborn's paratype material		
HS	<i>Oreochromis mossambicus</i> °		<i>Coptodon zillii</i> °°, <i>O. mossambicus</i>		<i>Trichopodus trichopterus</i> °°°		<i>Notropis hypsilepis</i>			
BD	71–106 (85)	69.0–84.7 (76.1)	58–108 (80)	68.8–85.6 (75.0±4.6)	70–122 (93)	66.1–85.8 (74.7±7.5)	63–80 (70)	52.4–60.2 (56.3)		
ADD	47–63 (56)	57.9–74.6 (66.4)	47–63 (57)	58.4–74.0 (64.4±4.5)	54–81 (67)	57.8–79.5 (66.1±7.2)	46–57 (52)	45.7–49.9 (47.3)		
DRD	26–37 (32)	34.5–47.5 (41.8)	26–37 (36)	35.5–48.6 (41.5±3.5)	30–52 (41)	34.6–49.8 (41.3±5.1)	27–35 (32)	26.5–30.6 (29.3)		
DL	8	6.8–8.1 (7.6)	7.5–11 (9.2)	6.7–9.7 (8.2±0.8)	6.3	6.9–9.6 (7.8±0.9)	–	5.4–6.4 (5.8)		
DBL	4.1	6.0–7.1 (6.6)	4.7–7.1 (5.7)	5.8–7.8 (6.5±0.6)	5.5	5.5–6.5 (5.9±0.4)	5–6 (5.3)	4.7–5.5 (5.1)		
DRL	6.9	6.2–10.1 (7.7)	6.9–10.3 (8.1)	7.2–9.6 (8.7±0.7)	8.2	6.4–8.9 (7.5±0.9)	7–9 (8)	6.5–8.7 (7.4)		
DCPW	3.4	2.2–3.4 (2.7)	1.4–3.4 (2.6)	2.2–3.5 (2.8±0.4)	4.1	1.8–4.4 (2.8±0.6)	2–3 (2.6)	2.0–2.4 (2.2)		
DS	–	15.5–20.0 (16.8)	–	14.8–19.0 (17.5±1.4)	–	14.5–18.9 (16.5±1.6)	11–13 (12)	14.3–16.4 (15.1)		
BMW	2.7	3.4–5.3 (4.3)	3.4–5.5 (4.7)	3.9–7.4 (5.4±0.9)	4.1	2.6–5.4 (4.4±0.9)	4.0–4.5 (4.3)	4.1–5.4 (4.8)		
nD	20–27 (23*)	24–29 (28)	29–31 (26*)	23–30 (26±1.6)	18–31 (27*)	22–31 (28*±2.2)	21–24 (23*)	22–25 (22*)		
nRP/D	11	11–13 (13*)	6–14 (10*)	10–13 (11*±1.1)	11	7–14 (12*±1.6)	10	9–10 (9*)		
n	52	6	25 (100**)	14	59	13	20	4		

**Table 2.** Comparison of Wellborn's (1967) original *Trichodina salmincola* Wellborn, 1967, *T. vallata* Wellborn, 1967 and *T. funduli* Wellborn, 1967 measurements (ADD – adhesive disc diameter, BD – body diameter, BMW – border membrane width, CL – collection locality, DBL – denticle blade length, DCPW – denticle central part width, DL – denticle length (= denticle width), DRD – denticle ring diameter, DRL – denticle ray length, DS – denticle span, HS – host species, LoH – location on host, n – population size, nD – number of denticles, nRP/D – number of radial pins per denticle) (\* pertains to the mode, rather than the mean) (all measurements in µm) (°host taxonomy in original article: *Salmo gairdneri*).

CL	<i>Trichodina salmincola</i>			<i>Trichodina vallata</i>			<i>Trichodina funduli</i>		
	North Carolina	Georgia	Alabama	Wellborn (1967)	Smithsonian 2017				
	Skin & Fins <i>Onchorhynchus mykiss</i> °	Skin, Fins & Gills <i>Ictalurus punctatus</i>	Skin & Fins <i>Fundulus nottii</i>	Smithsonian 2017 paratype material					
BD	61–85	58.1–72.1 (65.2)	52–80 (61)	68.7	68.7	70–104 (90)	68.7	68.7	68.7
ADD	40–59 (51)	49.5–58.4 (54.7)	31–49 (44)	58.8	58.8	54–65 (60)	58.8	58.8	58.8
DRD	29–39 (33)	32.0–38.1 (34.2)	24–29 (27)	30.5	30.5	33–41 (37)	30.5	30.5	36.6
DL	10–12 (11)	6.3–9.8 (7.3)	9–11 (10)	6.5	6.5	11–13 (12)	6.5	6.5	6.3
DBL	5–6 (5.8)	3.7–6.7 (5.7)	9–11 (10)	5.1	5.1	5–7 (6)	5.1	5.1	5.9
DRL	8–10 (8.5)	5.3–9.9 (7.5)	6.5–7.5 (7)	6.7	6.7	7–10 (9)	6.7	6.7	6.2
DCPW	2.0	1.5–2.2 (1.8)	1.5–2.0	2.7	2.7	2.0–3.0 (2.2)	2.7	2.7	2.6
DS	–	12.8–18.4 (15.3)	–	15.3	15.3	–	15.3	15.3	14.9
BMW	2–4 (3)	2.9–6.5 (4.6)	3–5 (4)	4.7	4.7	3–5 (4)	4.7	4.7	4.2
nD	21–26 (24*)	23–26 (24*)	20–23 (22–23*)	22	22	23–27 (26*)	22	22	27
nRP/D	12	8–11 (11*)	10	7	7	10	7	7	9
n	20	6	20	1	1	20	1	1	1

Morphological descriptions from the Smithsonian type material follows:

*Trichodina heterodentata* Duncan, 1977 (Figs 1–3, 7a–c) (Table 1)

Hosts: *Oreochromis mossambicus* (Peters, 1852), Mozambique tilapia (population A), *Coptodon zillii* (Gervais, 1848), redbelly tilapia (population B) and *Trichopodus trichopterus* (Pallas, 1770) (previously *Trichogaster trichopterus*), three spot gurami (Population C).

Location on host: Gills, body and fins.

Locality: Populations A, B and C from the Freshwater Aquaculture Centre, Central Luzon State University, Muñoz, Nueva Ecija, Philippines.

Specimens: Holotype slide USNM No. 24485 (Population A), Paratype slide USNM No. 24486 (Population B) and Paratype slide USNM No. 24487 (Population C) (Smithsonian).

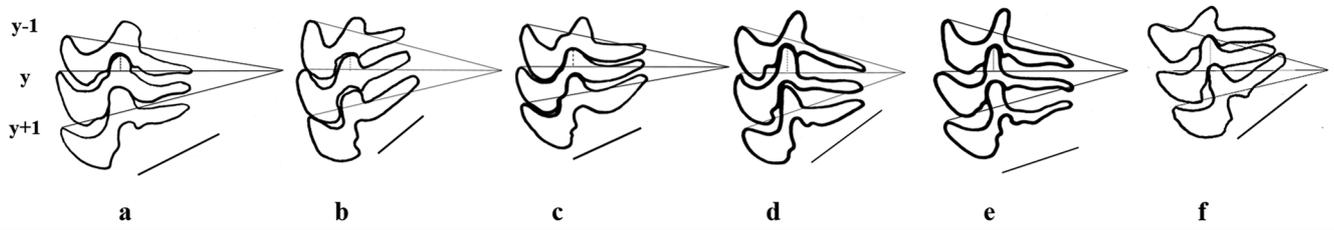
Description: Remeasured type material results and Duncan's (1977) original morphometric data are provided in Table 1.

Population A (Fig. 7a): Blade strongly developed, sickle-shaped, filling most of area between y axes. Distal blade margin mostly smooth, sloping gradually with posterior part of distal margin parallel to border membrane and anterior part at angle to border membrane. Tangent point relatively narrow, situated slightly proximal to distal blade margin. Anterior blade margin mostly smoothly rounded, extending slightly past y+1 axis in most cases. Blade apophysis present and prominent. Posterior blade surface shallow V- to L-shaped in majority of denticles, with deepest point on same level as blade apex. No posterior projection present/observed. Slight posterior projection present, fitting into corresponding notch distal to central part of following denticle. Blade connection very strongly developed, thicker or as thick as central part width. Central part robust, with notched proximal and distal edges, broad base narrowing slightly posteriorly, fitting tightly into preceding denticle and extending halfway towards y axes. Central part distal to x axis in shape of slender triangle, while part proximal to x axis shaped into broad rectangle. Indentation in lower central part is present and directed towards apophysis of ray in most denticles. Ray connection strongly developed, almost of same thickness as base of ray. Anterior ray apophysis present, delicate and directed anteriorly. Rays robust and basically same thickness for most of ray length. Rays taper slightly at tips producing narrower but rounder tips. Rays directed predominantly in posterior direc-

tion, some touching or even crossing y-1 axis. Ratio of denticle above and below x axis is 0.78 (0.8–1.0).

Population B (Fig. 7b): Blade robust, almost U-shaped, filling most of area between y axes. Distal blade margin slightly rounded, mostly smooth, sloping gradually with larger posterior part of distal margin parallel to border membrane and smaller anterior margin at angle to border membrane. Tangent point relatively narrow, situated slightly proximal to distal blade margin. Anterior blade margin mostly smoothly rounded, extending slightly past y axes in all cases. Blade apophysis present and prominent. Posterior blade surface deep U-shape, with deepest point almost halfway to y+1 axis, and deepest point slightly proximal to blade apex. No posterior projection present / observed. Blade connection broad but thinner than central part width. Central part robust with smooth proximal and distal edges, broad and squat, extending almost halfway to y axes. Central part distal to x axis triangular with sloping edge, while part proximal to x axis shaped into broad shape, basically rectangular. No indentation in lower central part. Ray connection strongly developed, of same thickness as ray base. Anterior ray apophysis present, delicate and directed anteriorly. Rays robust and of same thickness for whole ray length, ending in strongly blunt rounded tips. Rays all directed prominently in posterior direction, all clearly crossing y axes. Ratio of denticle above and below x axis 0.81 (0.78–0.86).

Population C (Fig. 7c): Blade robust and angular, open C-shaped, filling up large but not most part of area between y axes. Small part of posterior distal blade margin parallel to border margin, with largest part of distal blade margin sloping strongly away from border membrane. Tangent point narrow, situated proximal to distal blade margin. Anterior blade margin smooth but angular and narrow, extending well past y axes in all cases. Blade apophysis present and strongly developed, in most cases proximal edge of anterior blade margin with two prominent notches. Posterior blade surface L-shaped, with deepest point well proximal to blade apex. Posterior projection present and prominent, forming strong step-like notch into which following denticle fits with prominent corresponding notch distal to central part. Blade connection well developed, but thinner than central part width. Central part robust with smooth proximal and distal edges, fitting tightly into preceding denticle and extending more than halfway to y axes. Shape range from almost slender to broad with base as wide as rest of central part. Central part distal to x axis similar to proximal part. No indentation in



**Figs 7a–f.** Comparisons of denticles redrawn from micrographs taken of **a** – *Trichodina heterodontata* Duncan, 1977, Population A, **b** – *T. heterodontata* Duncan, 1977, Population B, **c** – *T. heterodontata* Duncan, 1977, Population C, **d** – *T. hypsilepis* Wellborn, 1967, **e** – *T. salmincola* Wellborn, 1967 and **f** – *T. vallata* Wellborn, 1967 paratypes housed at the Smithsonian Museum, USA.

lower central part. Ray connection strongly developed, but slightly narrower than base of ray. Ray apophysis present, delicate and directed anteriorly. Rays robust, prominently widening directly after ray connection and then gradually tapering to narrow, rounded tips. Rays lightly curved, though directed mostly towards centre of adhesive disc, some rays directed slightly in posterior direction, touching and barely crossing  $y-1$  axis. Ratio of denticle above and below  $x$  axis 0.85 (0.79–0.92).

Remarks: The denticle structure of both populations A and B is very similar in all criteria, differing only marginally, for instance the absence of the indentation in the lower central part (population B), where it is present and directed towards the apophyses of the rays in population A. Another difference is that all the rays of population B clearly cross the  $y$  axis, whereas some rays touch while others cross the  $y$  axis in population A. These differences still fall well within the variation demonstrated by all other records for *T. heterodontata*. However, population C shows prominent characteristics in denticle shape that has not been reported from any other populations. The anterior blade margin is clearly angular and narrow, extending well past the  $y$  axis in all cases, the blade apophysis is strongly developed and in most cases the proximal edge of the anterior blade margin has two uniquely prominent notches never observed for this species. Furthermore, the deepest point of the posterior blade surface lies well proximal to the blade apex. Finally, another distinct feature is the prominent posterior projection forming strong step-like notches into which the following denticle fits with conspicuous corresponding notches distal to the central part (Fig. 7c).

*Trichodina hypsilepis* Wellborn, 1967 (Figs 4 and 7d) (Table 1)

Host: *Notropis hypsilepis* Suttkus and Raney, 1955, highscale shiner.

Location on host: Body and fins.

Locality: Halawakee Creek, Chambers County, Alabama and the Chattahoochee River, Chambers County, Alabama, USA.

Type-specimens: Holotype USNM Helm. Coll. No. 64651 and one paratype slide and USNM Helm. Coll. No. 61652 (Smithsonian).

Description: Remeasured type material results and Wellborn's (1967) original morphometric data are provided in Table 1.

Blade strongly developed, semi-circular, filling most of area between  $y$  axes. Distal blade margin smoothly rounded, not parallel to border membrane, but gradually angling proximally towards anterior margin. Tangent point narrow, situated almost at same level as distal blade margin. Anterior blade margin mostly smoothly rounded, extending to and sometimes slightly past  $y+1$  axis. Blade apophysis present and prominent. Posterior blade surface performs smooth semi-lunar curve, C-shaped, with deepest point at same level as blade apex. Clear notch in proximal blade margin anterior to apophysis. Posterior projection not visible. Blade connection narrow. Central part well developed, but slender and elongated, fitting tightly into preceding denticle and extending most of the way towards  $y$  axes. Central part distal to  $x$  axis in shape of elongated slender triangle, while part proximal to  $x$  axis slender, almost rectangular. Clear indentation in lower central part present, accommodating apophysis of preceding ray. Ray connection well developed to delicate, only slightly thinner than base of ray. Anterior ray apophysis present and prominent, directed anteriorly. Rays straight, strongly developed, but slender, of equal thickness for whole length of ray. Rays taper slightly to small rounded tips. Most rays directed straight towards centre of disc, with a few directed only slightly in anterior direction. Ratio of denticle above and below  $x$  axis is 0.7.

*Trichodina salmincola* Wellborn, 1967 (Figs 5 and 7e) (Table 2)

Host: *Oncorhynchus mykiss* (Walbaum, 1792), rainbow trout.

Location on host: Fins and body.

Locality: Haywood county, North Carolina.

Type-specimens: Holotype USNM Helm. Coll. No. 61657 and one paratype USNM Helm. Coll. No. 61658.

Description: Remeasured type material results and Wellborn's (1967) original morphometric data are provided in Table 2.

Blade strongly developed, semi-circular, filling most of area between y axes. Distal blade margin not parallel to border membrane, gradually sloping proximally towards anterior margin. Tangent point small, situated proximally to distal blade margin. Anterior blade margin smoothly rounded towards apex, with rounded apex not reaching y+1 axis in some blades, but touching or extending slightly past y axes. Blade apophysis present and prominent. Posterior blade surface performs smooth shallow to L-shaped curve, with deepest point either at same level or somewhat proximal to blade apex. Posterior projection not visible. Clear notch in proximal blade margin anterior to apophysis. Blade connection narrow. Central part well developed, elongated, fitting tightly into preceding denticle, extending all the way and touching y-1 axis, curving slightly proximally. Central part distal to x axis slightly larger and in shape of elongated slender triangle, in contrast to part proximal to x axis shaped into very slender rectangle. Indentation in lower central part not visible. Ray connection delicate, slightly thinner than base of ray. Anterior ray apophysis present and prominent, directed distally in some and slightly anteriorly in others. Majority of rays straight, some minimally curved. Majority directed straight towards centre of disc with a few directed only slightly in anterior direction. Rays very slender and delicate, of equal thickness for whole length of ray, then tapering slightly to small bluntly rounded tips. Ratio of denticle above and below x axis is 0.79 (0.74 to 0.84).

*Trichodina vallata* Wellborn, 1967 (Figs 6 and 7f) (Table 2)

Host: *Ictalurus punctatus* (Rafinesque, 1818), channel catfish.

Location on host: Fins, body and gills.

Locality: National Fish Hatchery, Whitfield County, Georgia.

Type-specimens: Holotype in USNM Helm. Coll. No. 61662.

Description: Remeasured type material results and Wellborn's (1967) original morphometric data are provided in Table 2.

Blade strongly developed, sickle-shaped, filling most of area between y axes. Distal blade margin not parallel to border membrane, gradually sloping proximally towards anterior margin. Tangent point small, situated proximally to distal blade margin. Anterior blade margin rounded towards apex, with rounded apex not reaching y+1 axis in some blades, but touching or extending slightly past y axes in others. Blade apophysis present and prominent. Posterior blade surface performs smooth shallow curve, slight C- to L-shaped, with deepest point at same level of blade apex. Clear notch in proximal blade margin anterior to apophysis. Posterior projection not clearly visible. Blade connection broad. Central part well developed, robust and squat, fitting tightly into preceding denticle and extending all the way to and even touching y axes. Central part distal to x axis slightly smaller and in shape of elongated slender triangle, in contrast to part proximal to x axis shaped into very slender rectangle. Distal edge slopes gradually in anterior direction, while proximal edge of central part has edge straighter in anterior direction. Indentation in lower central part small and inconspicuous. Ray connection strong, only slightly thinner than base of ray. Anterior ray apophysis present and prominent, directed in anterior-distal direction. Rays robust, becoming slightly thicker directly after connection, tapering towards bluntly rounded tips. Rays vary from directed sharply anteriorly to sharply posteriorly, crossing y axes in both directions. Ratio of denticle above and below x axis is 0.80 (0.79 to 0.82).

*Trichodina funduli* Wellborn, 1967 (Table 2)

Host: *Fundulus notti* (Agassiz, 1854), starhead topminnow.

Location on host: Body and fins

Locality: Swift Creek, Autauga County, Alabama.

Type-specimens: Holotype USNM Helm. Coll. No. 61645 and paratype USNM Helm. Coll. No. 61646.

Description: Remeasured type material results and Wellborn's (1967) original morphometric data are provided in Table 2.

The silver nitrate impregnation of Wellborn's (1967) original holotype and paratype material was of such quality that denticle structures could not successfully be drawn for descriptive purposes.

Remarks: The denticle structures of *T. hypsilepis*, *T. salmincola* and *T. vallata* exhibit remarkably similar

**Table 3.** Biometrical data (in  $\mu\text{m}$ ) of published populations of *Trichodina heterodontata* Duncan, 1977 (ADD – Adhesive disc diameter, BD – Body diameter, BMW – Border membrane width, CL – Collection locality, DBL – Denticle blade length, DCPW – Denticle central part width, DL – Denticle length (=denticle width), DRD – Denticle ring diameter, DRL – Denticle ray length, DS – Denticle span, HS – Host species, LoH – Location on host, n – population size, nD – Number of denticles, nRP/D – Number of radial pins per denticle) (\*pertains to the mode, rather than the mean) (\*pertains to the data as is in publication, but probably an error).

	Basson, van As & Paperma (1983)	van As & Basson (1989)	Bondad-Reantaso & Arthur (1989)	Philippines	Basson & van As (1994)	Asmat (2004)	Tao <i>et al.</i> (2008)	Valladao <i>et al.</i> (2016)
CL	South Africa	Israel	Gills – rarely	Taiwan	India	China		Brazil
LoH	Skin, Fins & Gills	Skin & Fins	Gills	Skin, Fins & Gills	Gills	–		Skin
HS								
				<i>C. barbata</i> , <i>C. auratus</i> , <i>C. carpio</i> , <i>H. molitrix</i> , <i>S. nigripinnis</i> , <i>F. lacustris</i> , <i>M. anguillicaudatus</i> , <i>G. affinis</i> , <i>Tilapia</i> sp., <i>R. brunnus</i>				
	<i>P. philander</i>	<i>Tilapia</i> fry	<i>O. niloticus</i>		<i>A. testudineus</i> , <i>P. gelius</i>	<i>C. auratus</i>	<i>O. mossambicus</i>	
BD	47.5–69.1 (55.3±3.8)	48.1–67.3 (59.3±4.7)	39.2–53.0 (47.1±3.8)	49.0–61.0 (53.9±3.2)	46.1–61.2 (54.6±3.3)	37.0–62.5 (49.8±3.2)	38.4–59.2 (50.5±4.1)	
ADD	39.5–59.8 (46.9±4.1)	39.6–56.7 (49.9±4.5)	32.8–45.0 (39.4±3.9)	40.0–52.0 (44.4±3.5)	41.8–52.0 (45.6±2.8)	28.0–51.0 (42.6±2.3)	31.3–50.3 (42.3±4.0)	
DRD	23.2–37.8 (29.3±2.9)	23.9–35.6 (30.3±3.4)	19.2–28.4 (24.3±2.5)	24.5–32.5 (27.9±2.6)	26.0–33.6 (30.4±1.7)	23.0–37.0 (28.5±2.1)	12.2–32.4 (25.4±3.1)	
DL	5.1–8.6 (6.6±0.8)	5.2–8.9 (7.5±1.1)	4.8–8.8 (7.0±1.0)	6.0–9.0 (7.4±0.7)	7.6–9.2 (8.3±0.6)	6.4–9.0 (7.4±0.8)	5.6–9.7 (6.9±0.6)	
DBL	3.4–5.5 (4.3±0.4)	3.7–5.6 (4.8±0.5)	4.0–5.6 (4.6±0.5)	4.0–5.5 (4.8±0.3)	4.1–7.1 (5.3±0.6)	4.5–5.5 (5.1±0.3)	2.9–5.2 (4.2±0.4)	
DRL	4.6–8.1 (6.3±0.9)	5.5–8.9 (7.4±1.0)	4.0–6.4 (5.6±1.2)	5.5–7.0 (6.4±0.4)	5.9–8.2 (6.9±0.7)	5.0–6.5 (6.1±0.7)	(3.1–8.1) (6.1±1.0)	
DCPW	1.6–3.3 (2.7±0.3)	1.8–3.5 (2.9±0.4)	1.6–2.4 (2.1±0.3)	2.0–3.0 (2.3±0.3)	2.0–3.1 (2.8±0.4)	2.0–2.5 (2.2±0.3)	1.4–3.2 (2.3±0.4)	
DS	–	–	10.4–13.6 (12.6±0.9)	12.0–16.0 (13.8±0.8)	13.7–17.9 (15±1.0)	11.0–15.0 (13.2±1.2)	7.8–15.5 (12.5±1.4)	
BMW	3.2–6.4 (4.2±0.6)	2.9–6.1 (4.8±0.7)	3.1–4.8 (2.9* ±6.3)	4.0–5.0 (4.8±0.3)	3.1–5.6 (4.5±0.6)	3.0–5.0 (4.2±0.5)	3.2–5.2 (4.2±4.0)	
nD	22–29 (25)*	22–25 (22)*	21–25 (22.3±1.1)	21–24 (22 & 23)*	21–26 (23.1±1.2)	22–29 (25±0.8)	11–27 (23.7±2.2)	
nRP/D	9–13 (10)*	10–12 (11)*	10–13	8–10 (10)*	9–13 (10.8±1.2)	10–12 (11)	7–16 (11.3±1.9)	
n	51	20	31	20	40	25	114	

**Table 4.** List of all morphologically recorded/described *Trichodina hypsilipsis* Welborn, 1967, included are the teleost hosts, locality (country) of record/description and authors.

Host/s	Locality	Author
<i>T. vallata</i>	United States of America	Davies (1947)
<i>T. vallata</i>	United States of America	Wellborn (1967)
<i>T. salmincola</i>	United States of America	Wellborn (1967)
<i>T. heterodontata</i>	Philippines	Duncan (1977)
<i>T. heterodontata</i>	South Africa	Basson <i>et al.</i> (1983)
<i>T. heterodontata</i>	Taiwan	van As & Basson (1986)
<i>T. heterodontata</i>	Philippines	Natividad <i>et al.</i> (1986)
<i>T. heterodontata</i>	Philippines	Albaladejo & Arthur (1989)
<i>T. heterodontata</i>	Philippines	Albaladejo & Arthur (1989)
<i>T. heterodontata</i>	Philippines	Albaladejo & Arthur (1989)
<i>T. heterodontata</i>	Israel	van As & Basson (1989)
<i>T. heterodontata</i>	Venezuela	van As & Basson (1989)
<i>T. heterodontata</i>	Philippines	Bondad-Reantaso & Arthur (1989)
<i>T. heterodontata</i>	Namibia	van As & Basson (1992)
<i>T. heterodontata</i>	Taiwan	Basson & van As (1994)
<i>T. heterodontata</i>	Egypt	Al-Rasheid <i>et al.</i> (2000)
<i>T. heterodontata</i>	Indonesia	Dana <i>et al.</i> (2002)
<i>T. heterodontata</i>	Indonesia	Dana <i>et al.</i> (2002)
<i>T. heterodontata</i>	Indonesia	Dana <i>et al.</i> (2002)
<i>T. heterodontata</i>	India	Asmat (2004)
<i>T. heterodontata</i>	Australia	Dove & O'Donoghue (2005)
<i>T. heterodontata</i>	China	Tao <i>et al.</i> (2008)
<i>T. heterodontata</i>	Brazil	Martins <i>et al.</i> (2010)
<i>T. heterodontata</i>	China	Qi <i>et al.</i> (2011)
<i>T. heterodontata</i>	Peru	Miranda <i>et al.</i> (2012)
<i>T. heterodontata</i>	Brazil	Pádua <i>et al.</i> (2012)
<i>T. heterodontata</i>	Turkey	Öztürk & Çam (2013)
<i>T. heterodontata</i>	Brazil	Valladão <i>et al.</i> (2013)
<i>T. heterodontata</i>	Brazil	Pádua <i>et al.</i> (2014)
<i>Ictalurus punctatus</i>		
<i>Ictalurus punctatus</i>		
<i>Oncorhynchus mykiss</i>		
<i>Oreochromis mossambicus</i> (Population A), <i>Coptodon zilli</i> (Population B)		
<i>Pseudocrenilabrus philander</i>		
<i>O. mossambicus</i>		
<i>O. niloticus</i>		
<i>Hypophthalmichthys nobilis</i> (previously <i>Aristichthys nobilis</i> )		
<i>Ctenopharyngodon idella</i>		
<i>Cyprinus carpio</i>		
<i>Tilapia</i> sp. fry		
<i>O. mossambicus</i>		
<i>O. niloticus</i>		
<i>Marcusenius macrolepidotus</i> , <i>Petrocephalus catostoma</i> , <i>P. philander</i>		
<i>Candida barbata</i> , <i>Cyprinus auratus</i> , <i>C. carpio</i> , <i>Hypophthalmichthys molitrix</i> , <i>Sarcocheilichthys nigripinnis</i> , <i>Formosania lacustre</i> , <i>Misgurnus anguillicaudatus</i> , <i>Gambusia affinis</i> , <i>Tilapia</i> sp., <i>Rhinogobius brunneus</i>		
<i>Hydrocynus forskalli</i>		
<i>Oxyeleotris marmorata</i>		
<i>C. carpio</i>		
<i>Clarias gariepinus</i>		
<i>Anabas testudineus</i> , <i>Puntius gelius</i>		
<i>C. barbata</i> , <i>Glossamia aprion gillii</i> , <i>O. mossambicus</i> , <i>C. carpio</i> , <i>Hypseleotris compressa</i> , <i>H. galli</i> , <i>H. klunzingeri</i> , <i>Philymodon grandiceps</i> , <i>Galaxias maculatus</i> , <i>G. olidus</i> , <i>Gerres</i> sp.		
<i>C. auratus</i>		
<i>Ictalurus punctatus</i>		
<i>C. carpio</i>		
<i>Arapaima gigas</i>		
<i>Piaractus mesopotamicus</i>		
<i>Neogobius fluviatilis</i> , <i>Pomatoschistus marmoratus</i> , <i>Proterorhinus marmoratus</i>		
<i>Prochilodus lineatus</i>		
<i>Pseudoplatystoma reticulatum</i>		

<i>T. heterodontata</i>	<i>Osphronemus goramy</i>	Java	Nurrochmah & Riwidharso (2016)
<i>T. heterodontata</i>	<i>O. niloticus</i>	Brazil	Valladão <i>et al.</i> (2016)
<i>T. heterodontata</i>	<i>O. niloticus</i> x <i>O. mossambicus</i>	Thailand	Worananthakij & Maneepitaksanti (2014)
<i>T. heterodontata</i>	<i>Osphronemus goramy</i>	Java	Rokhmani <i>et al.</i> (2017)
<i>T. heterodontata</i>	<i>Sciaenochromis fryeri</i> , <i>Poecilia sphenops</i>	Turkey	Çelik & Korun (2018)
<i>T. heterodontata</i>	<i>Osteochilus vittatus</i> (previously <i>Osteochilus hasselti</i> )	Java	Riwidharso <i>et al.</i> (2019)
<i>T. heterodontata</i>	<i>O. niloticus</i>	Brazil	Rodrigues <i>et al.</i> (2019)
<i>T. heterodontata</i>	<i>Tachysurus fulvifracco</i>	China	Wang <i>et al.</i> (2019)

traits with minor differences. For both *T. hypsilepis* and *T. salmincola* the blade connections are narrow, but broad for *T. vallata*. The central part extends most of the way towards the y axis for *T. hypsilepis*, whereas in the case of both *T. salmincola* and *T. vallata* the central part extends all the way to and touches the y axis. The ray connection is strongly developed for *T. hypsilepis* and *T. vallata*, but delicate in *T. salmincola*. The rays differ for all three species where the rays are strongly developed, but slender (*T. hypsilepis*), very slender and delicate (*T. salmincola*) and robust becoming slightly thicker towards the ray connection (*T. vallata*).

## DISCUSSION

*Trichodina heterodontata* characteristically shows a range of variation in both denticle morphology and morphometrics worldwide (Tables 1 and 3). The body diameter of this species is just such an example; there is variation across, and even within populations of *T. heterodontata* described from a large number of teleost species. However, in some cases this large variation in body diameter can be misleading, mainly due to the measuring differences between the two historic schools of trichodinid research, where most of the earlier authors used Dogiel's 1940 method of measuring the span of the whole soft body for body diameter (Lom 1958), compared to the current accepted method by most workers of measuring the adhesive disc plus the border membrane (Basson *et al.* 1983). Duncan (1977) and many other authors, did not state exactly how the body diameter was measured, therefore it was decided to disregard this measurement, but rather use the adhesive disc diameter for comparative size groupings of the populations under discussion. Adhesive disc diameter variation makes it possible to clump this species into three overarching groups. Group I, observed from teleost hosts from Thailand (Worananthakij and Maneepitaksanti 2014), Taiwan (Basson and van As 1994) and the Philippines (Duncan 1977) comprises the "largest" described populations with a mean adhesive disc diameter larger than 61 µm. Members of group II ("middle sized"), are between 51 and 60 µm recorded exclusively from teleost hosts from Indonesia (Albaladejo and Arthur 1989, Dana *et al.* 2002, Nurrochmah and Riwidharso 2016), Australia (Dove and O'Donoghue 2005) and Venezuela (Basson and van As 1989). Group III ("smallest") includes those populations with a mean

diameter of between 35 and 50  $\mu\text{m}$  from South America (Martins *et al.* 2010; Pádua *et al.* 2012; Miranda *et al.* 2012; Valladão *et al.* 2013, 2016), Africa (Basson *et al.* 1983, van As and Basson 1992, Al-Rasheid *et al.* 2000), the Middle East (van As and Basson 1989, Öztürk and Çam 2013), the Far East (Albaladejo and Arthur 1989, Basson and van As 1994, Asmat 2004, Tao *et al.* 2008) and the Philippines (Bondad-Reantoso and Arthur 1989). This last group boasts with the majority of records and includes all reported populations from amphibian tadpole hosts (Kruger *et al.* 1993, Dias *et al.* 2009, Pala *et al.* 2018).

Re-examining Duncan's (1977) material, it is clear that two of his populations; A and B (both from cichlid hosts) have the typical and recognised *T. heterodontata* morphometrics (Table 1, Figs 1 and 2 respectively), but with a larger body diameter than any other recorded in the literature (Table 3). His third population, C (Fig. 3) deviates from the previously mentioned populations and all other published records of *T. heterodontata* (Table 3) as this population: (i) is extremely homogeneous, which is not an attribute of this species, (ii) the denticle and body measurements fall into the top range of Group I, while most of the measured population consists of immature individuals and (iii) the denticle morphology is atypical for *T. heterodontata*, as per the denticle description method of van As and Basson (1989). We suspect that this species is not *T. heterodontata*, but will refrain from elaborating on this in the present paper.

Amongst the mobiline species described by Wellborn (1967), four of these (*T. hypsilepis*, *T. salmincola*, *T. vallata* and *T. funduli*) appeared to be remarkably similar in denticle shape, form and size. For this reason, photomicrographs from the original type material was acquired from the Smithsonian Museum (Washington, D.C.) and re-examined by using both Lom's (1958) and the van As and Basson (1989) denticle description methods. Due to de-staining of the silver nitrate impregnation over time, no feasible material could be measured for *T. funduli*, making acceptable taxonomic inferences about this species impossible.

After comparing the denticle morphology and morphometrics of *T. hypsilepis*, *T. salmincola*, *T. vallata* and *T. heterodontata* we conclude that these all belong to the same taxon. The International code of Zoological nomenclature (Ride *et al.* 1985) states in Article 23, that the Principle of Priorities (using the oldest available name for a valid taxon) must always be applied. This implies that the lesser known *T. hypsilepis* be the valid taxon with *T. salmincola*, *T. vallata* along with the

cosmopolitan and widely studied *T. heterodontata* from all teleost hosts as synonyms.

The species originally described as *T. heterodontata* showed a clear preference for cichlid hosts, with strong evidence that this trichodinid originates from Africa. If this assumption is correct, the next question to be asked is how, and through what mechanism an African trichodinid got into the North American river systems? The translocation of *O. mossambicus* (endemic to the eastern part of southern African) due to aquaculture ventures worldwide is significant.

*Oreochromis mossambicus* was initially exported from Africa to the East. The first stock, according to Guerrero (1994) was brought to Java by East African traders in 1938, from there they were exported into most of Pacific Asia and eventually to the Philippines, through Thailand during the 1950s and 60s (De Silva *et al.* 2004). At the same time 60 Mozambique tilapias were sent from Singapore to Hawaii in 1954, and the progeny of these fish were then sent to the public aquarium in New York, where in turn, the offspring of those were sent to Alabama (Rogers 1961, Smith-Vaniz 1968), Arizona (Hoover and St. Amant 1970, Minckley 1973) and California (St. Amant 1966) for aquaculture purposes or sport fishing. At this time many tilapias escaped into the natural water systems during loading and harvesting or through containment failures, resulting in the first reported Mozambique tilapia in the Alabaman River System in 1965, which is the same river system in which *T. hypsilepis*, was first described in 1967. This distribution and introduction of *O. mossambicus* across the East into the southern states of North America supports the present theory that *T. hypsilepis* and *T. heterodontata* indeed represent the same species.

To confuse matters more, Kazubski (1986) described a species, *T. equatorialis* Kazubski, 1986, based on a population from unidentified cichlids from Kenya. With this publication Kazubski (1986) suggested that *T. hypsilepis* (syn. *T. heterodontata*) described from South Africa and Israel by Basson *et al.* (1983) be designated as a synonym of *T. equatorialis* and furthermore that *T. hypsilepis* does not occur in Africa. This species cannot be equated to *T. hypsilepis*, as it was quite large (with body diameter of 72 to 84  $\mu\text{m}$  and adhesive disc diameter 45–52  $\mu\text{m}$ ), much larger than any other *T. hypsilepis* recorded from Africa and Israel and that the denticle shape provided by the diagrammatic illustration does not resemble any *T. hypsilepis* population worldwide. These large dimensions and characteristic denticle shape most probably resembles another cichlid

trichodinid from Africa; *T. magna* van As and Basson, 1983 (van As and Basson 1989). Due to the absence of any silver impregnated micrographs as per Lom (1958), the validity of this taxon and its relationship to *T. magna* can unfortunately not be validated. However, this species shows no relationship to *T. hypsilepis*, and nullifies Kazubski's (1986) claim that *T. hypsilepis* (syn. *T. heterodentata*) from Africa and Israel is a synonym of *T. equatorialis*, as also concluded by Bondad-Reantoso and Arthur (1989).

The trichodinid taxon known up to now as *T. heterodentata* has not only been described from fish hosts, but also from anuran tadpoles, although all amphibian host observations have been restricted to the Southern Hemisphere. The anuran trichodinids seem to paint a completely different picture; which will be addressed in de Jager *et al.* (2019) focussing on morphometric and molecular results.

To avoid more confusion in the already bewildering world of mobiline taxonomy, Table 4 is included with all the recorded valid populations that will henceforth be known as synonyms of *Trichodina hypsilepis* Wellborn, 1967. There are several reports of *T. heterodentata* from various countries which have not been included in Table 4, due to the fact that either no taxonomic description (just a record) or quality micrographs were included (Pádua *et al.* 2014; Dar *et al.* 2016; Tanry *et al.* 2016; Utami and Rokhmani 2016; Santos *et al.* 2017; Rokhmani *et al.* 2018, 2019; Enyidi and Uwanna 2019; Maneepitaksanti *et al.* 2019).

This case study illustrates that the weight of almost 200 years of diligent morphological techniques cannot be ignored, especially when it comes to investigating historical data and making taxonomic inferences from it. It also illustrates that morphology cannot stand alone as the pinnacle of taxonomy, because without the understanding of parasite-host interactions and knowledge of host distribution history those inferences would be mere sweeping statements.

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