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Acanthocephala of Cichlids (Pisces) in Lake Malawi, Africa, with a Description of *Acanthogyrus (Acanthosentis) malawiensis* sp. n. (Quadrigyridae) from *Labeo cylindricus* Peters, 1852 (Cyprinidae)

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ABSTRACT: Two species of acanthocephalans are reported from fishes collected during the summer of 1996 in the southeast arm of Lake Malawi (Lake Nyasa), East Africa. The common *Acanthogyrus (Acanthosentis) tilapiae* (Baylis, 1948) had infected 18 cichlid and 1 bagrid host species (all new host records) netted by divers wearing scuba gear around Harbor Island or caught by hook and line in deep water. The specimens of this parasite were some of the smallest ever reported for that species. Two males of a new species, *Acanthogyrus (Acanthosentis) malawiensis*, are described from 2 male *Labeo cylindricus* (Cyprinidae). This is the fifth species of this genus and subgenus described in Africa. It is distinguished from the other 4 African and 33 mostly Asian species in that the proboscis hooks of the middle circle are longer than those of the anterior circle. The new species further differs from the other African species in proboscis and hook size, posterior hook root, trunk spination, and lemniscal form. Observations on host and geographical distribution, prevalence, and developmental stages of *A. (A.) tilapiae* are also reported.

KEY WORDS: Acanthocephala, *Acanthogyrus (Acanthosentis) malawiensis* sp. n., *Acanthogyrus (Acanthosentis) tilapiae*, cichlids, *Labeo cylindricus*, Lake Malawi, Lake Nyasa.

The acanthocephalan family Quadrigyridae Van Cleave, 1920 (Order Gyraacanthocephala Van Cleave, 1936) includes 2 subfamilies, Quadrigyridae Van Cleave, 1920, with 2 genera, and Pallisentinae Van Cleave, 1928, with 6 genera, including the genus *Acanthogyrus* Thapar, 1927 (= *Acanthosentis* Varma and Datta, 1929; *Hemigyris* Achmerov and Dombrowskaja-Achmerova, 1941). In synonymizing *Acanthosentis* with *Acanthogyrus*, the former taxon was reduced to a subgenus of the latter (Golvan, 1959). The 2 subgenera were distinguished based on the number of hooks on the proboscis, being 18 in *Acanthosentis* (3 circles of 6 hooks each) and 24 in *Acanthogyrus* (3 circles of 8 hooks each). This arrangement was accepted by systematists, including Amin (1985), but Golvan (1994) decided to elevate *Acanthosentis* back to generic status, without justification. The latter decision is not accepted and the subgeneric classification is herein retained.

Only 5 of the 38 known species of the subgenus *Acanthosentis* (including the new species) are found in Africa. Thirty-one of the remaining 33 species are Asian, found mostly in the Indian subcontinent and China. Of the African species,

Acanthogyrus (Acanthosentis) tilapiae (Baylis, 1948) is an endemic and widely distributed species of Oriental affinities (Khalil, 1971b). The other African species appear to be of more restricted distributions and include *Acanthogyrus (Acanthosentis) maroccanus* (Dollfus, 1951) from Morocco, *Acanthogyrus (Acanthosentis) nigeriensis* Dollfus and Golvan, 1956, from the Niger River, *Acanthogyrus (Acanthosentis) papilio* Troncy and Vassiliades, 1974, from West Africa, and the new species, *Acanthogyrus (Acanthosentis) malawiensis*, from Lake Malawi.

In this paper, the new species is described and distinguished from other species of the subgenus, and some host–parasite relationships of *A. (A.) tilapiae* are reported.

Materials and Methods

Cichlid and cyprinid fishes were collected, usually late in the afternoon, by netting by divers wearing scuba gear in the southeast arm of Lake Malawi, mostly at or near Harbor Island during July and August 1996. Bagrid and clariid fishes were caught by hook and line in the deeper water offshore in the southeast arm of the lake. Fish were held alive overnight in buckets and examined the following day. All acanthocephalans were alive when removed from the fish small intestine and placed in Lake Malawi water to evert the proboscis. Worms were then fixed in alcohol-formalin-acetic acid fixative and eventually transferred to 70% ethanol.

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Not all fishes examined had acanthocephalans. Preserved fishes were deposited as voucher specimens in the Pennsylvania State University Fish Museum (PSUFM).

Worms were stained in Mayer's acid carmine, dehydrated in ascending concentrations of ethanol, cleared in graded terpineol-100% ethanol, and mounted in Canada balsam. Measurements are in micrometers unless otherwise stated. Width measurements refer to maximum width. Body (=trunk) length does not include neck, proboscis, or male bursa. Specimens are deposited in the U.S. National Parasite Collection (USNPC), Beltsville, Maryland.

Results

Sixty-four fishes (primarily cichlids) of 28 species were examined for parasites. Twenty-eight fishes of 19 species were infected with 95 (44 males, 51 females) *A. (A.) tilapiae*. A single *Bagrus meridionalis* (Bagridae) contained 1 male *A. (A.) tilapiae*. Most worms were sexually mature adults that were quite small in size (Table 1). Two male *Labeo cylindricus* Peters, 1852, were infected with a new species of *Acanthogyryrus* (*Acanthosentis*), which is described below. Fish species (and numbers) that were examined for acanthocephalan infections, along with prevalence and measurement data, are included in Table 1.

Acanthogyryrus (Acanthosentis) malawiensis

sp. n.
(Figs. 1-9)

The description of this species is based on the only 2 male specimens available; females are unknown.

Description

Quadrigyridae, Pallisentinae, with characters of the genus *Acanthogyryrus* and the subgenus *Acanthosentis*. Males small, spindle-shaped, with gradual, almost equal tapering toward both ends, with some ventral curvature (Fig. 1). Trunk 4.545-6.363 mm long by 1.273-1.333 mm wide at middle. Transverse anastomoses connect main dorsal and ventral lacunar canals. Giant subcuticular nuclei very few; 1 ventral and 1 or 2 dorsal, and complex vessel-shaped in profile or amoeboid-star-shaped in face view. Many spheroid, rib, or double-walled sensory papillae, 12-23 in diameter, randomly distributed mostly in the middle region of the trunk (about 40) and bursa (about 5) (Fig. 7). Rose-thorn-shaped cuticular spines with a shaft and robust, complex fan-shaped rayed or ribbed subcuticular plate an-

teriorly (Figs. 3-6). Spines in 32-38 circles; anteriorly 23-26 complete circles. Anterior circles with 30-46 spines that increase to 40-55, then decrease in number posteriorly as they become less closely spaced. Next, circles of spines become progressively more incomplete laterally where only dorsal and ventral spines remain in posteriormost circles near posterior end of trunk. Anterior spines somewhat larger, 20-25 long, with root, than posterior spines. Dorsal and ventral spines symmetrical, with no numerical differentiation anteriorly, but more ventral than dorsal spines retained as spine circles become incomplete posteriorly (Figs. 1, 2). Proboscis small, cylindrical, straight-sided, about as long as wide, 98-112 long by 98-112 wide, with a remarkable apical organ, abruptly widening posteriorly into a broadening neck (Fig. 8). Proboscis hooks slender; hooks in middle circle longer (42-45 long) than those of anterior circle (31-36), with posteriormost hooks only slightly shorter (28-36) than anterior hooks. Hook roots simple, directed posteriorly, and markedly shorter than blades. Roots of posteriormost hooks with short anterior manubria (Fig. 8). Proboscis receptacle 381-419 long by 114-140 wide, with cerebral ganglion at its base (Fig. 2). Lemnisci subequal, about twice as long as proboscis receptacle, with successive constrictions, and gradually tapering posteriorly (Fig. 2). Longer lemniscus 660-775 long by 102-140 wide; shorter lemniscus 546-648 long by 102-140 wide. Reproductive system in posterior half of trunk (Fig. 1). Testes broad, pear-shaped, greatly overlapping. Anterior testis 533-762 long by 571-787 wide; posterior testis 406-889 long by 470-737 wide. Cement gland 444-999 long by 343-533 wide, with at least 4 giant nuclei. Sperm sac 190-316 long by 190-305 wide. Saeftigen's pouch 432-698 long by 165 wide. Bursa 851 long by 508 wide.

Taxonomic Summary

TYPE HOST: *Labeo cylindricus* Peters, 1852 (Cyprinidae).

SITE OF INFECTION: Small intestine.

TYPE LOCALITY: Southeast arm of Lake Malawi at Harbor Island, Nankumba Peninsula, Mangochi District, Malawi, Africa (14°04'07.21"S, 34°55'49.94"E).

DATE COLLECTED: 31 July 1996.

SPECIMENS DEPOSITED: USNPC No. 88013 (holotype male); No. 88014 (paratype male).

HOST SPECIMENS DEPOSITED: PSUFM No. 3243.

ETYMOLOGY: The new species is named for the country of the type locality.

Remarks

Of the 38 species of the subgenus *Acanthosentis* known from freshwater fishes, 5 are found in Africa (including *A. (A.) malawiensis* sp. n.) and 31 in Asia (India and China). The new species is distinguished from all other species of the subgenus by having the proboscis hooks of the middle circle longer than those in the anterior circle, instead of the opposite. In addition, the large number of sensory papillae found on the trunk and bursa of *A. (A.) malawiensis* sp. n. has not been reported in any of the other species. It is unlikely that they may have been overlooked in other species.

The new species is further distinguished from the other African species based on host and geographical distribution and distinct anatomical differences. *Acanthogyrus (Acanthosentis) maroccanus* was described from *Barbus setivimensis* in Morocco by Dollfus (1951). It has a considerably longer proboscis, 184 long by 107 wide, that does not broaden posteriorly and lacks an apparent apical organ. Its proboscis hooks are larger, 62, 62, 48 from the anterior, and all have simple roots, none of which have anterior manubria. The trunk has 10–12 giant nuclei and only 12–18 circles of spines spread over the interior quarter of the trunk, with the posterior circles having 2–4 spines each. The lemnisci have no constrictions and the testes appear to be oblong. All measurements are calculated from Dollfus' (1951) figure 60. *Acanthogyrus (Acanthosentis) nigeriensis* was described from *Labeo coubie* in the Niger River, Mali, by Dollfus and Golvan (1956). It is a larger species than ours. Males are 12–15 mm long by 2.0–2.4 mm wide; the proboscis is 150 long by 200 wide, and the proboscis receptacle is 700 long by 200 wide. The proboscis hooks are situated in successive circles and measure 70 (2 hooks), 55–65 (4 hooks), 40 (6 hooks), and 40 (6 hooks) from the anterior. Each possesses an apical granular structure set in a heavy muscular wall. Cuticular spines are 30 long, covering the whole length of the trunk in 70 circles. *Acanthogyrus (Acanthosentis) papilo* was described from *Periophthalmus papilo* in Senegal by Troncy and Vassiliades (1974). Specimens of that species are very small

(less than 2 mm). The anterior proboscis hooks are 35–40 long and are widely separated from the smaller hooks of the middle and posterior circles, which are 8–11 long. The lemnisci have no constrictions. The trunk is totally covered with 1–2 long spines in up to approximately 30 unequally spaced circles. *Acanthogyrus (Acanthosentis) tilapiae* is an endemic species that was originally described from *Oreochromis (Tilapia) lidole* from an unknown locality in Lake Malawi (Lake Nyasa), Tanzania, by Baylis (1948) and has since been reported from a large number of fish species, mostly of the genus *Tilapia*, in many African countries, including Malawi (Khalil, 1971a; Amin, 1978). The reports by Baylis (1948) and Amin (1978) described smaller males (1.2–3.5 mm long by 0.4–1.1 mm wide), with a smaller proboscis (90 long by 64 wide), larger anterior proboscis hooks (45–48), and considerably smaller hooks in the middle circle (12–22 long) and posterior circle (10–13 long) compared to the new species. The lemnisci are without constrictions. The trunk possesses 28–38 circles of small (10 long) cuticular spines distributed throughout and 2–4 dorsal and 4–6 ventral giant nuclei. The middle trunk of about half of the 79 *A. (A.) tilapiae* specimens examined by Amin (1978) had shallow sensory pits with an eversible knoblike center (Amin, 1978, figs. 15, 17). There was usually 1 such pit observed in each of these specimens. Similar pits were observed in a few specimens of our *A. (A.) tilapiae* from Lake Malawi.

The shape of the giant subcuticular nuclei of *A. (A.) malawiensis* was similar to that observed in mature *A. (A.) tilapiae* (Amin, 1978) and is considered indicative of an active reproductive state of the worms, as has been demonstrated in other sexually mature acanthocephalans (Amin and Vignieri, 1986a, b; Amin and Gunset, 1992).

Acanthogyrus (Acanthosentis) tilapiae (Baylis, 1948)

This acanthocephalan is endemic in Africa and has been reported in at least 10 species of the cichlid genus *Tilapia* in Tanzania (Baylis, 1948), Congo (Prudhoe, 1951; Golvan, 1957), Madagascar (Golvan, 1965), Uganda (Khalil and Thurston, 1973), Chad (Troncy, 1974), Nigeria (Shotton, 1974), Egypt (Amin, 1978), and unidentified locations (Marchand and Mattei, 1976; Marchand, 1984). These host species are *T. aurea*, *T. galilaea*, *T. heudelotti*, *T. lidole*, *T. leu-*

Table 1. Fishes examined for prevalence and size of *Acanthogyryus (Acanthosentis) tilapiae* collected in the southeast arm of Lake Malawi during July and August 1996.

Host species (USNPC No.)	Local- ity ¹⁸	Prevalence (%) ¹⁷	No. worms		Male length × width (n)			Female length × width (n)						
			MM	FF	Immature	With sperm	With ovarian balls only	With ovarian balls & eggs	With mostly eggs					
<i>Cichlidae</i>														
<i>Aristochromis christyi</i> Trewavas, 1935	H	1/2 (50)	1	3	—	2.121 × 576 (1)	3.030 × 818 (1)	2.121 × 636 (1)	2.424 × 848 (1)					
<i>Coptidochromis cf. thinos</i> (Regan, 1922) (USNPC 88016)	H	1/1 (100)	1	4	—	1.515 × 454 (1)	2.424–2.545 × 606 (3)	—	2.545 × 727 (1)					
<i>Ctenopharynx (Otopharynx)</i> <i>pictus</i> (Trewavas, 1935)	K	1/1 (100)	2	1	—	1.363–1.424 × 515–545 (2)	—	—	1.818 × 727 (1)					
<i>Dimidochromis kiviinge</i> (Ahl, 1926)	H	0/1 (0)	—	—	—	—	—	—	—					
<i>Genyochromis mento</i> Trewavas, 1935 (USNPC 88017)	H	1/2 (50)	1	1	—	—	—	—	1.909 × 606 (1)					
<i>Labretropheus fullerborni</i> Ahl, 1926 (USNPC 88018)	H	3/3 (100)	1	6	—	1.121 × 364 (1)	788–1,606 × 303–606 (6)	—	—					
<i>Labidochromis vellitans</i> Trewavas, 1935	H	0/3 (0)	—	—	—	—	—	—	—					
<i>Lichnochromis acuticeps</i> Trewavas, 1935 (USNPC 88019)	H	1/1 (100)	1	—	—	970 × 364 (1)	—	—	—					
<i>Melanochromis auratus</i> (Boulenger, 1897)	H	1/3 (33)	2	1	—	1.363–2,030 × 424–818 (2)	—	—	2.303 × 970 (1)					
<i>Melanochromis cf. melanapertus</i> Trewavas, 1935	H	0/1 (0)	—	—	—	—	—	—	—					
<i>Melanochromis heterochromis</i> Trewavas, 1935 (USNPC 88020)	H	4/5 (80)	13	8	—	727–1,969 × 242 × 606 (13)	788–2,424 × 333–697 (5)	—	1.212–2,272 × 515–727 (3)					
<i>Metriacolina zebra</i> BB (Boulenger, 1899) (USNPC 88027)	H	2/5 (40)	5	4	—	818–909 × 212–242 (3)	1,303–1,386 × 424–576 (3)	—	2.424 × 970 (1)					
<i>Metriacolina zebra</i> "redtop"	K	0/1 (0)	—	—	—	—	—	—	—					
<i>Oreochromis</i> sp. (USNPC 88021)	H	1/1 (100)	1	—	—	1,666 × 666 (1)	—	—	—					
<i>Petratilapia genalutca</i> Marsh, 1983 (USNPC 88022)	H	1/1 (100)	10	7	—	697–879 × 303–364 (2)	909–1,666 × 364–666 (8)	3.030 × 757 (1)	1.666–3,030 × 818–1,151 (3)					

Table 1. Continued.

Host species (USNPC No.)	Local- ity*	Prevalence (%)†	No. worms		Male length × width (n)			Female length × width (n)		
			MM	FF	Immature	With sperm	With ovarian balls only	With ovarian balls & eggs	With mostly eggs	
<i>Placidochromis johnstoni</i> "gold"‡ (Günther, 1894) (USNPC 88023)	K	1/1 (100)	1	—	—	1,363 × 545 (1)	—	—	—	—
<i>Placidochromis johnstoni</i>	S	0/1 (0)	—	—	—	—	—	—	—	—
<i>Protomelas annectens</i> (Regan, 1922) (USNPC 88024)	S	1/3 (33)	1	—	—	1,151 × 364 (1)	—	—	—	—
<i>Protomelas cf. taeniolatus</i> (Trewavas, 1935)	K	0/1 (0)	—	—	—	—	—	—	—	—
<i>Pseudotropheus elongatus</i> "aggressive" Fryer, 1956 (USNPC 88025)	H	1/1 (100)	2	4	—	970–1,030 × 394 (2)	1,060–1,454 × 454–606 (4)	—	—	—
<i>Pseudotropheus tropheops</i> "broadmouth" (Regan, 1922)	H	0/1 (0)	—	—	—	—	—	—	—	—
<i>Pseudotropheus tropheops</i> "orange chest" (USNPC 88026)	H	2/2 (100)	—	4	—	—	1,069–2,272 × 606–848 (3)	—	—	1,606 × 576 (1)
<i>Stigmatochromis woodi</i> (Regan, 1922) (USNPC 88028)	H	3/3 (100)	1	1	—	1,969 × 666 (1)	Not observed	—	—	—
<i>Taeniolethrinops praeorbitalis</i> (Regan, 1922)	S	0/2 (0)	—	—	—	—	—	—	—	—
<i>Trematochromis placodon</i> (Regan, 1922) (USNPC 88029)	S	1/2 (50)	1	6	—	1,363 × 454 (1)	—	1,151–1,515 × 424–515 (2)	1,242–1,727 × 636–879 (4)	—
<i>Tyannochromis macrostoma</i> (Regan, 1922) (USNPC 88030)	H	1/2 (50)	—	1	—	—	2,363 × 1,030 (1)	—	—	—
<i>Tyannochromis macrostoma</i>	K	0/1 (0)	—	—	—	—	—	—	—	—
<i>Tyannochromis nigriventer</i> Eccles, 1989	H	0/1 (0)	—	—	—	—	—	—	—	—
Bagridae										
<i>Bagerus meridionalis</i> Günther, 1893 (USNPC 88015)	D	1/1 (100)	1	—	—	1,666 × 606 (1)	—	—	—	—

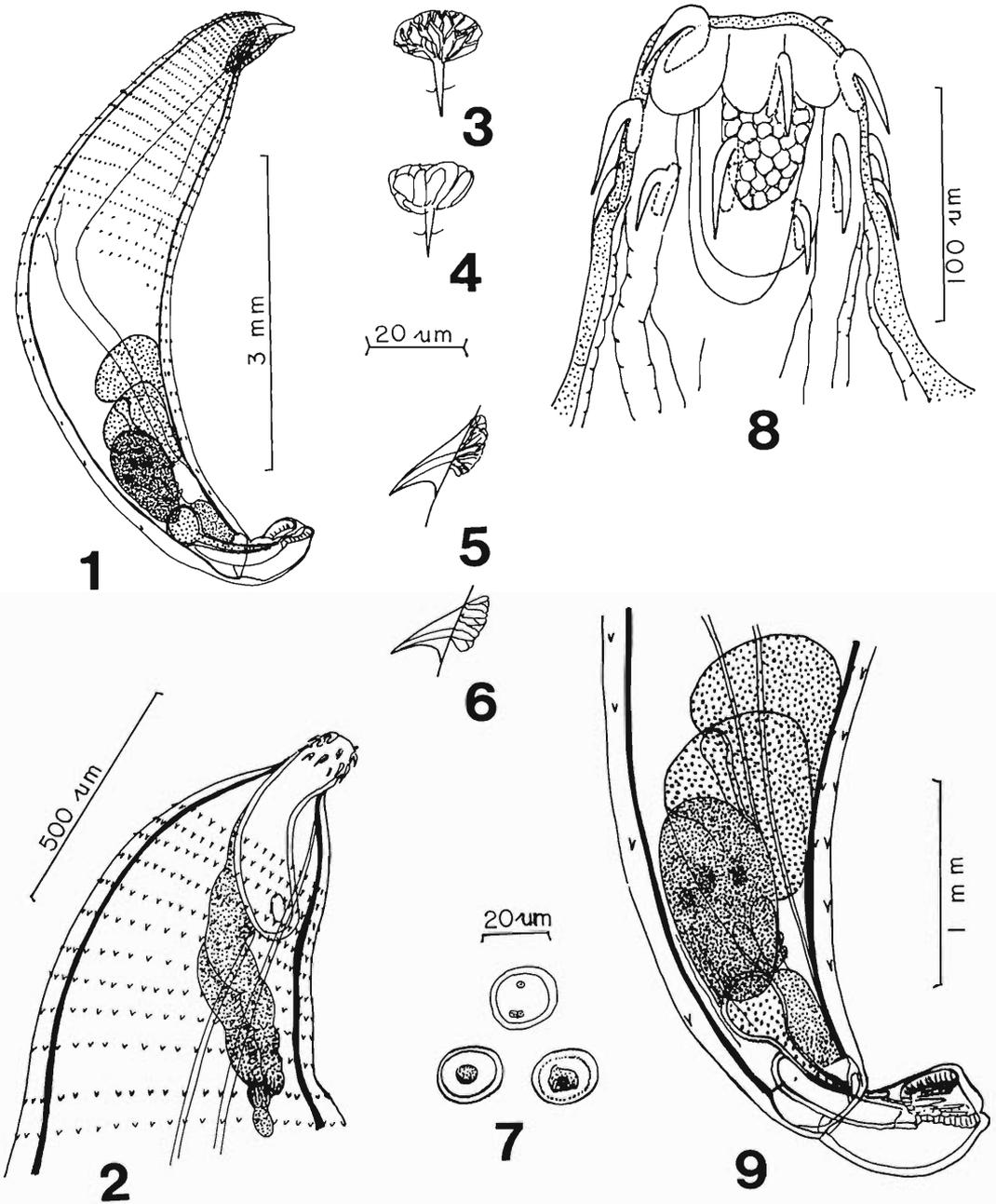
Table 1. Continued.

Host species (USNPC No.)	Local- ity*	Prevalence (%)†	No. worms		Male length × width (n)		Female length × width (n)		
			MM	FF	Immature	With sperm	With ovarian balls only	With ovarian balls & eggs	With mostly eggs
Clariidae									
<i>Bathyclarias nyasensis</i> (Worthington, 1933)	D	0/1 (0)	—	—	—	—	—	—	—
<i>Clarias mossambicus</i> Peters, 1852	D	0/1 (0)	—	—	—	—	—	—	—
Cyprinidae									
<i>Labeo cylindricus</i> Peters, 1852	H	0/4 (0)	—	—	—	—	—	—	—
<i>Labeo cylindricus</i>	K	0/1 (0)	—	—	—	—	—	—	—
Mastacembelidae									
<i>Mastacembelus shiranus</i> Günther, 1896	M	0/4 (0)	—	—	—	—	—	—	—
Totals and size range		28/64	44	51	697–909 × 212–364 (5)	727–2,121 × 242–818 (39)	788–3,030 × 303–1,030 (30)	1,151–3,030 × 424–757 (4)	1,212–3,030 × 515–1,151 (17)

* H = Harbor Island; D = deep water of southeast arm; K = Kanchedzda Island; M = Marsh near Massasa Village; S = Songwe Hill site.

† No. infected/No. examined (%).

‡ Names in quotes are aquarium trade color morphs.



Figures 1-9. *Acanthogyrus (Acanthosentis) malawiensis* sp. n., holotype male. 1. Whole specimen. 2. Anterior end. 3-6. Face and lateral views of trunk spines. 7. Sensory papillae. 8. Proboscis. 9. The reproductive system. Sensory papillae and lacunar vessels are not shown in Figs. 1, 2, and 9.

costicta, *T. melanopleura*, *T. multiradiata*, *T. nilotica*, *T. tanganicae*, and *T. zilli*. Fish hosts of *A. (A.) tilapiae* belonging to other genera are few and include *Potamogale velox* (possibly an

accidental host) and *Tetraodon fohaka* in Chad (Troncy 1970, 1974) and 2 cichlids, *Haplochromis squamipinnus* and *Haplochromis* sp. in Uganda (Khalil and Thurston, 1973). The re-

ported records of *A. (A.) tilapiae* from the 18 cichlid and 1 bagrid species collected in south-eastern Lake Malawi (Table 1) represent new host records. Khalil and Thurston (1973) also reported *A. (A.) tilapiae* from unidentified cichlids in Lake Malawi, Lake Tanganyika, and various lakes in The Congo.

Morphologically, our specimens from Lake Malawi were similar to those collected from *T. nilotica* and *T. zilli* in Egypt during June 1975 (Amin, 1978), except our specimens were markedly smaller, even though the 2 populations were comparable in their developmental and reproductive states (Table 1). Specimens from Egypt were 1.20–3.40 mm (mean, 1.99) long (males) and 1.20–5.00 mm (mean, 3.22) long (females) and 50% of females ($n = 52$) had only ovarian balls in their body cavity, thus indicating a young summer population. Most males from Lake Malawi (39 of 44) were mature with sperm, and most females (30 of 51) were also in the ovarian ball stage (Table 1). A few Lake Malawi specimens had 1 sensory papilla each, and the trunk spines of some younger worms were so underdeveloped as to be barely visible.

Shotter (1974) reported *A. (A.) tilapiae* from *T. zilli* in a northern Nigeria stream and lake throughout the year with peak densities and greatest declines during winter (November–February, dry season) and summer (June and July), respectively. If this pattern is similar to that in Lake Malawi, the prevalence and abundance and perhaps the degree of sexual maturity of the Malawi worms (Table 1) would be expected to be higher during the winter.

SPECIMENS DEPOSITED: USNPC No. 88015-88030.

HOST SPECIMENS DEPOSITED: PSUFM Nos. 3243–3253.

Acknowledgments

We would like to thank Matthew Arnegard for netting the fishes, Dr. Jay R. Stauffer, Pennsylvania State University, for permission to work at his research camp at Lake Malawi, and the Government of Malawi for enabling us to collect the fishes under Dr. Stauffer's permit through the University of Malawi.

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An Atlas of Protozoan Parasites in Animal Tissues (Second Edition). By C. H. Gardiner, R. Fayer, and J. P. Dubey. 1998. Armed Forces Institute of Pathology, 84 pp. ISBN 1-881041-48-4. 8¼" × 10¾" softcover. Available from the American Registry of Pathology, Room G-134, Armed Forces Institute of Pathology, Washington DC 20306-6000. Cost is US\$35.00 per copy plus shipping and handling cost of US\$4.00 within the continental United States or US\$8.75 outside of the continental United States. "Abstract: This atlas illustrates protozoan parasites in animal tissues. To facilitate identification, it provides a brief description of parasites, hosts, transmission, and pathogenesis of the most important protozoans and simplified life-cycle drawings. Also included are 257 color photographs of protozoans and associated lesions, recorded using optimal conditions, and 36 color photomicrographs of fungi that are commonly confused with protozoans."

Atlas of Ultrastructure of the Infective Juveniles of the Soybean Cyst Nematode, *Heterodera glycines*. By Burton Y. Endo. 1998. U.S. Department of Agriculture, Agriculture Handbook No. 711, 224 pp. 8½" × 11" softcover. While supplies last, single copies of this publication may be obtained at no cost from the Nematology Laboratory, USDA-Agricultural Research Service, 10300 Baltimore Avenue, Building 011A, Room 165B, Beltsville, MD 20705-2350. Copies may then be purchased from the National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22161, phone (703) 605-6000. ISBN and prices not available at this printing. "Abstract: This atlas . . . shows the transition from preparasitic to parasitic juveniles and their relation to host tissues The electron micrographs are grouped into subunits to emphasize various features of the nematode and host-parasite interactions. Illustrations also include changes in nematode anatomy related to . . . nematode development and early host responses. This handbook is a comprehensive compilation of previously published electron micrographs, combined with new data. [It] is an educational tool for those interested in nematode morphology and a reference for researchers interested in applying physiological studies to functional units of the nematode."