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The Diversity of Digeneans (Platyhelminthes: Cercomeria: Trematoda) in Vertebrates in Mexico

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ABSTRACT: The Digenea is one of the most common groups of helminths found in vertebrates. In Mexico, the inventory of the group began in the 1930s. After 70 yr of taxonomic research, 503 species in 312 genera have been reported in approximately 440 of the 4,697 species of vertebrates known to occur in the country. Of these 503 digenean species, 153 are endemic or at least have been recorded only within Mexican territory. Most of these species have been described as parasites of fishes, both freshwater and marine. The overall size of the fauna was estimated in 2 ways, based on available information. Between 5,300 and 8,000 species of digeneans in Mexican vertebrates is estimated, representing 8–10% of the world's digenean fauna; >77,000 digenean species are estimated worldwide. Digeneans, because of their prevalence and abundance in nature and their complex life cycles, are one of the most important groups of parasites to be considered in managing biodiversity, in conservation, and as indicators for ecosystem monitoring.

KEY WORDS: biodiversity, Platyhelminthes, Digenea, vertebrates, Mexico.

In Mexico, digeneans of wild vertebrates have been studied since the 1930s, following the pioneer work by Sokoloff and Caballero (1932) describing *Chiorchis fabaceus* (Diesing, 1838) Fischoeder, 1901, as a parasite of the manatee *Trichechus manatus latirostris* Hatt, 1934. Since then, the group has been studied more or less intensively by Mexican and foreign researchers, such as Caballero, Winter, Bravo-Hollis, Manter, Arai, and Lamothe-Argumedo (see Lamothe-Argumedo et al. [1997] and references therein). Over 25 authors have published nearly 300 articles describing, redescribing, or recording different species of digeneans parasitizing vertebrates collected within Mexico. Recently, Cribb (1998) analyzed the diversity of the Digenea of Australian animals, estimating the size of the fauna and describing the trends in the taxonomy of digeneans of different groups of vertebrates in that country. Here, I present an analysis of the digenean fauna of Mexican vertebrates to compare Australian and Mexican digenean faunas and provide information to allow a more accurate estimate of the size of the fauna on a worldwide basis. I also address the importance of the inclusion of parasites in biodiversity studies, using digeneans as an example. A database has been assembled during the last 3 yr with financial support from the National Commission for the Use and Conservation of Biodiversity. Currently, information is scattered among different kinds of bibliographical sources, and in many cases researchers have neglected to deposit specimens and their published accounts in the national depository of helminths in Mexico, the National Collection of Helminths. Therefore, we initiated a process to track all available published information, as well as data from different parasite collections, including the U.S. National Parasite Collection, the H. W. Manter Laboratory of Parasitology, and the British Museum of Natural History.

The task of describing new species of digeneans, as with many other groups of metazoan parasites, is important because the description of that portion of biodiversity is far from complete and parasites in general represent an important component of the biosphere. Brooks and Hoberg (2000) and Brooks et al. (2000) argued that parasites qualify under each of the criteria established by the Global Taxonomic Initiative (American Museum of Natural History, 1999) to be selected as part of any inventory activity; parasites are intrinsically important to humans and to ecosystems that humans want to preserve, they are geographically widespread, and they provide an opportunity for international networking of professionals for collaborative research and training.

In particular, digeneans are one of the most abundant groups of parasitic worms in the biosphere; the number of described species worldwide ranges from >5,000 (Hoberg, 1997b) to 18,000 (Gibson and Bray *in* Cribb, 1998). How-

Table 1. Digenean parasites of Mexican vertebrates.*

Vertebrate group	Hosts		Digeneans				
	Total no. of species in Mexico	No. of species studied (%)	No. of genera	No. of species	No. of species/host $\bar{x} \pm$ SD (range)	n	No. of new species (%)
Mammals	466	35 (7.5)	40	54	2 ± 1.8 (1–8)	32	13 (7.5)
Birds	1,060	48 (4.5)	41	73	2.6 ± 2.9 (1–13)	44	13 (17.8)
Reptiles	705	49 (6.9)	53	82	2.8 ± 2 (1–10)	49	27 (32.9)
Amphibians	295	16 (5.4)	18	37	4.7 ± 4.5 (1–17)	13	9 (24.3)
Fishes	2,171	292 (13.4)	164	257	2.9 ± 3.7 (1–30)	257	91 (35.4)
Totals	4,697	440 (9.4)	316	503	2.87 ± 3.36 (1–30)		153 (30.4)

* Five groups of vertebrates are considered, as in traditional classifications.

ever, there has been no precise count of digenean species. Some digeneans, because of their complex life cycles in relation to general patterns of host specificity, have been used as biological markers, providing information about the contemporary ecology of the hosts and the environments they live in (Kabata et al., 1988; Bartoli, 1989). In a broader sense, digeneans, along with other groups of helminths, can be used to infer patterns of historical ecology of the parasite communities and to track the history of host–parasite associations, thus providing more comprehensive information about ecosystems (Scott, 1988; Gardner and Campbell, 1992; Combes, 1996; Marcogliese and Cone, 1997).

Mexican Digeneans

General pattern of species richness

After 7 decades of taxonomic effort describing the digenean fauna of Mexican vertebrates, 503 species in 312 genera have been reported in approximately 300 articles. Digenean species whose larval and adult forms have been named and collected in different hosts were counted only once, based on the host group where the adult form was recorded. The 503 species of digeneans were reported in approximately 440 species of vertebrates (Table 1). Most of these articles consist of isolated reports of the presence of certain species of digeneans in a particular host species, and only a few studies dealing with the entire digenean fauna of a group of hosts or in a particular locality have been undertaken (see Scholz et al., 1995; Pérez-Ponce de León et al., 1999). Taxonomic surveys, checklists, or monographs where information is compiled are also very few (e.g., Pérez-Ponce de León, García-Prieto, Osorio-Sarabia, and León-Règagnon, 1996; Pérez-Ponce de León et al., 2000).

A striking feature of Mexican biological diversity is its vast species richness, a result of the country's location in both the Nearctic and Neotropical biogeographic realms, the diversity and heterogeneity of climates and habitats, and the complex topology of its territory. About 4,697 species of vertebrates have been described so far in Mexico (Table 1) (Flores-Villela and Gerez, 1994; Ramamoorthy et al., 1998), and the number is still rising slowly. After 70 yr of recording the digeneans of the vertebrate fauna in Mexico, fewer than 10% of the vertebrates have been studied. Host sampling effort has been mainly focused on marine and freshwater fishes, and no well-defined sampling program has been established. Records of digeneans range from a few specimens collected from single individual hosts in a particular locality to the collection of hundreds of specimens, either from 1 species of host along its distributional range or from different species of hosts at a single locality. Cribb (1998) demonstrated the sampling dilemma for digeneans, estimating that about 160,000 animals should be examined in Australia to collect most of the digeneans and suggesting that 30,000 days of collecting would be necessary for a parasitologist to accomplish that goal. Besides the sampling effort to dissect hosts and collect their digeneans, a similar time-consuming effort is necessary for processing (staining and mounting) and identifying the specimens and for publication of results.

The current database

Table 1 is a synthesis of current data on digeneans in Mexican vertebrates. Fishes are the largest group of vertebrates in Mexico, and from

Table 2. Comparison of the digenean faunas of vertebrates* of Australia and Mexico.

	Australia			Mexico		
Vertebrate group	No. of host species	No. of digenean species	No. of digenean genera	No. of host species	No. of digenean species	No. of digenean genera
Mammals	330	67	41	466	54	40
Birds	700	147	72	1,060	73	41
Reptiles	750	47	37	705	82	53
Amphibians	200	18	7	295	37	18
Fishes	3,300	289	160	2,171	257	164
Totals	5,576	566	306	4,697	503	316

* Five groups of vertebrates are considered, as in traditional classifications.

them the largest numbers of species and genera of digeneans (257 and 164, respectively) have been recorded. Traditionally, digenean systematists in Mexico have studied most intensively those parasites from fishes, especially marine fishes, and more than 50% of the digeneans described so far have been recorded from fishes (Table 1). This preponderance of fishes as hosts is not an artifact of sampling. The number of digenean species described from fishes in the world is several times larger than the number of species described for each of the other groups of vertebrates (Yamaguti, 1971). However, the percentages of digeneans with respect to the other groups of helminths in particular surveys demonstrate that digeneans are clearly the dominant component of the helminth communities of different kinds of hosts, sometimes sharing the largest species richness with the nematodes, at both host species or host community levels (e.g., see Pérez-Ponce de León, García-Prieto, Osorio-Sarabia, and León-Regagnón [1996] and Pérez-Ponce de León, León-Regagnón, and García-Vargas [1996], for chiropterans and fishes of continental waters respectively).

Using teleosts as a model, Cribb (1998) estimated the size of the digenean fauna in Australia, assuming a moderate average of 5 species of digeneans per fish species and 3 fish species per digenean. Emphasizing that the margin of error may be large and that the estimate should be treated with caution, he suggested that over 6,000 species of digeneans occur in Australian animals. Table 2 shows a comparative analysis of the digenean species richness in Australia and Mexico with respect to the number of hosts, using the same assumptions as Cribb (1998). Total numbers of hosts and parasites are similar. Although there are more fish species in Australia, the total number of vertebrates is approximately equal because in Mexico there are more bird, mammal, and amphibian species. Based on these data, I estimate that less than 10% of the digenean fauna of Mexico has been documented. The most conservative estimate of this percentage is that in Mexico only 440 (9.4%) of the 4,697 species of vertebrates have been surveyed for digeneans. From those 440 species of hosts, 503 digenean species were recorded, a ratio of a little more than 1 species of digenean per species of host analyzed. Under the assumption that the same rate of discovery of species is maintained and that all vertebrate species are sampled before they go extinct, with the minimum sample size necessary to maintain a digenean : host ratio of 1:1, then there should be more than 5,300 species. However, this is clearly an underestimate, because the data (Tables 1, 2) indicate that on average each vertebrate species harbors almost 3 species of digeneans (2.87), with a wide range between 1 and 30. Considering each group of vertebrates separately, digenean species richness per host species varies between 2 and 4.7, with amphibians showing the highest mean richness. Not all the vertebrates still to be studied will be parasitized by digeneans; there are species with restricted terrestrial habitats in combination with a feeding behavior that makes transmission of digeneans impossible. There is no way to estimate how many species of vertebrates have been surveyed but found to lack digenean parasites. However, if 60% of the vertebrates are infected by digeneans (considering this as a conservative estimate), and if the mean of 2.87 species of digeneans per host is maintained, then the estimated number of spe-

Table 3. Digenean species richness in Mexico per group of vertebrate* hosts. Only 3 to 5 species of hosts with the highest species richness are shown per group.

Hosts	Helminths		Reports	Localities	States†
	Genera	Species			
Mammalia					
Natalidae					
Natalus mexicanus Gray, 1838	7	7	3	3	3
Molossidae					
Tadarida brasiliensis (I. Geoffroy, 1824)	7	8	4	5	3
Didelphidae					
Philander opossum (Linnaeus, 1758)	5	6	3	5	3
Didelphis virginiana Kerr, 1792	4	5	3	8	3
Aves					
Anatidae					
Anas platyrhynchus (Linnaeus, 1758)	8	8	1	3	3
Ardeidae					
Casmerodius albus (Linnaeus, 1758)	8	13	8	4	3
Nycticorax nycticorax (Linnaeus, 1758)	8	9	5	7	4
Phalacrocoracidae					
Phalacrocorax olivaceus (Humboldt, 1801)	7	10	8	12	5
Reptilia					
Chelonidae					
Dermatemys mawii (Gray, 1847)	6	9	8	7	3
Chelonia mydas (Linnaeus, 1758)	7	7	4	3	3
Lepidochelys olivacea (Eschscholtz, 1829)	9	10	3	1	1
Amphibia					
Ranidae					
Rana montezumae (Baird, 1859)	6	17	11	3	2
Rana vaillanti Brocch, 1877	6	7	2	1	1
Bufonidae					
Bufo marinus Linnaeus, 1758	8	8	5	4	3
Pisces					
Characidae					
Astyanax fasciatus Cuvier, 1819	12	14	9	19	5
Cichlidae					
Petenia splendida Günther, 1862	13	19	13	17	5
Cichlasoma urophthalmus Günther, 1862	21	30	20	52	7
Cichlasoma geddesi (Regan, 1905)	16	18	3	4	2
Cichlasoma synspillum Hubbs, 1935	23	26	13	22	4

* Five groups of vertebrates are considered, as in traditional classifications.

† Number of states in Mexico where the host has been surveyed for helminths.

cies of digeneans in Mexican vertebrates rises to over 8,000. Therefore, estimated richness of this group of platyhelminths ranges from 5,000 to 8,000.

Patterns of species richness by group of vertebrates

Table 3 contains a list of the host species with the greatest species richness of digeneans in each group of vertebrates. Amphibians have the largest mean digenean richness, with 4.7 parasite species per amphibian species (Table 1). The greatest digenean richness, however, is exhibited by some freshwater fishes. For example, the cichlid fishes *Cichlasoma urophthalmus* Günther, 1862, and *Cichlasoma synspillum* (Hubbs, 1935) are parasitized by 30 and 26 digenean species, respectively. However, almost 50% of those species have been identified as larval stages (metacercariae), implying that these fishes are intermediate hosts for those digeneans whose life cycles are completed, in most cases, in fish-eating birds. More studies have been conducted on these cichlids, including more localities with-

in their distributional range (Table 3). Some attempts have been made to describe a general pattern of helminth parasite community richness in vertebrates using comprehensive data sets on gastrointestinal parasites from several species of hosts (Bush et al., 1990; Poulin, 1995, 1997). However, my database is not strictly comparable because it deals only with the digenean assemblage and not with the entire helminth community. For instance, Bush et al. (1990) found that birds possess a greater component community richness than do the other groups of vertebrates they analyzed (fishes, amphibians, reptiles, and mammals). My analysis shows that the richness of digeneans in birds is fourth greatest; however, comparison among data sets should be made with caution because only 4.5% of the bird species found in Mexico have been sampled for digeneans or even for helminths (Table 1).

Another general trend seen in Table 3 is that, regardless of the number of studies reported and the number of localities where each host has been sampled, aquatic organisms possess a larger digenean richness than do semiaquatic and terrestrial forms. A similar trend was found by Cribb (1998) for Australian digeneans. Studies of particular groups of hosts, e.g., amphibians, have demonstrated that this trend might be consistent within a group (Brandt, 1936; Prokopic and Krivanec, 1975; Brooks, 1976). The analyses of Bush et al. (1990) and Poulin (1995, 1997) provided more useful comparative information because species living in aquatic habitats tended to show higher parasite richness. Bush et al. (1990) found that when their data were examined by grouping major habitats within host taxa, terrestrial hosts consistently had fewer component species than did aquatic forms. Poulin (1995) demonstrated that by controlling for potential effects of host phylogeny, birds and mammals tended to show greater parasite richness relative to other vertebrates, but the difference was not statistically significant. The potential effect of host phylogeny was not removed in either Cribb's (1998) or my analysis, so that the hypothesized trends need to be tested in greater detail using the phylogenetic approach.

According to the general pattern of digenean life cycles, the more contact the host has with water, the greater the probability that the host will become infected with some digenetic trematode. Although this pattern may be very general, not all aquatic organisms or their habitats are comparable. The hypothesis that an increase in parasitism of a host group or species by digeneans can be directly related to an increase in water contact by that host group or species needs to be tested by partitioning the host habitats and behavioral ecology in detail. This approach will provide more robust estimates of the actual amount of time the host is in contact with water, either living in it or eating plants or animals living in it. The idea that parasites can actually serve as "Probes of Biodiversity" because of long-term historical association with geographic areas can probably be tested using the habitat partition/phylogeny scenario.

Patterns of geographical distribution

A striking feature of the digenean fauna of vertebrates in Mexico is the high percentage of endemism. Because the term *endemic* simply means occurring nowhere else, organisms can be endemic to a geographical location on a variety of spatial scales and at different taxonomic levels (Brown and Lomolino, 1998). Here, I consider endemic species those described in vertebrates within Mexican territory but not yet found elsewhere. However, I recognize that the limited number of reports may cause this estimate of endemism to be artifactual. Of 503 species, 153 (30%) were described as new species in Mexico and in most cases, with the information we have available, those species currently show a restricted distribution range. On the other hand, almost 70% of the digeneans in Mexican vertebrates also occur outside Mexico. Some species are considered endemics at a larger geographical scale, e.g., endemics of the Americas, endemics of the Neotropical biogeographical region, or endemics of Middle America. Some species have a cosmopolitan distribution, occurring in the same or different host species all over the world, such as the digeneans of marine turtles (Pérez-Ponce de León, García-Prieto, and León-Règagnon, 1996).

The complex topography, habitat diversity and heterogeneity, and geological history of the Mexican territory have led to an extraordinary richness of vertebrates (Ramamoorthy et al., 1998) and, consequently, of the digeneans that they harbor. The digenean fauna of Mexico is unique not only because of the large number of species known only from Mexico, but also because of their zoogeographical affinities. These affinities are the result of interrelated factors, in-

cluding the fact that the country encompasses the transition between the Nearctic and Neotropical biogeographical realms. As a result, its biota is a mixture of elements from both realms, plus an apparently endemic component. Biogeographers have described the exchange of organisms between the Nearctic and Neotropical regions following the breakup of Pangea, first through the Proto-Antilles, which served as a stepping-stone route for limited exchange of some terrestrial organisms (Brown and Lomolino, 1998), and more recently in geological time during the Pliocene (approximately 3.5 million yr ago), when a great biotic interchange took place once the archipelago finally fused to form the current Central American land bridge (Coney, 1982). This scenario of geological history seems to have influenced the distribution patterns of digeneans parasitizing terrestrial vertebrates. The distribution of digeneans of marine fishes, however, has been influenced by a different set of factors. Marine fishes are highly vagile, and their digenean fauna is shared with hosts of different parts of the world (e.g., the hemiurid *Opisthadena dimidia* Linton, 1910, has been found in kyphosid fishes off the eastern Pacific coast of Mexico, Hawaii, and Australia [León-Règagnon et al., 1996]). For marine fishes and their digenean fauna, the Central American land bridge acted as a geographical barrier determining the isolation that, in many cases, led to speciation events establishing the so-called geminate species (Jordan, 1908; for a review, see Brooks and McLennan [1991, 1993]).

Conclusions

Parasites may act as agents of population control because they cause acute or chronic diseases in hosts (Scott, 1988). The utility of having inventories of parasites as platforms for addressing ecological and evolutionary questions, managing biodiversity, and coping with emerging diseases has been recently discussed by Hoberg (1997a) and Brooks and Hoberg (2000). Recent information has suggested that pathogens are causing catastrophic mortalities and deformities in wild frog populations. In Australia, Panama, Costa Rica, and the U.S.A., a parasitic chytrid fungus, considered an emerging pathogen by Kaiser (1999), has been implicated in massive die-offs, and was considered the cause of declining in frog populations and species richness worldwide. A digenetic trematode has been implicated as the causal agent of abnormalities in tree frogs in the U.S.A. (Johnson et al., 1999). Researchers have found that severe limb abnormalities were induced at high frequencies in tree frogs exposed to the cercariae of the cathaemasid digenean *Ribeiroia* sp. Whether pathogens are the only, or even the main, cause of the decline of particular animal populations cannot be determined with the available evidence, but this possibility must be considered in future programs treating biodiversity and conservation management of wildlands.

Digenean species have been described since the last century. However, there is no reliable source of information concerning the number of species named so far. The data presented here provide a comparison of 2 countries (Australia and Mexico) where trematodology traditionally has been active pursued for nearly a century. Despite these relatively active investigations, it appears that less than 10% of the digenean species in those countries have been reported. If the biota of the planet is composed of 45,000 species of vertebrates (Systematics Agenda 2000, 1994) and we make the same conservative assumptions as for the Mexican fauna (60% of the vertebrates infected by digeneans and a mean of 2.87 digenean species per host species), then there are more than 77,000 digenean species worldwide. How many are so far described is unknown.

A complete inventory of a group of organisms is more than a list of names (Brook and Hoberg, 2000). Attached to the name itself should be as much information about the natural history of the organism as possible so that we understand the value of each species. Unless the possible consequences of extinction or translocation are understood, we will not be able to manage a particular ecosystem, such as a biosphere reserve, effectively. If we consider biodiversity in the wildlands as one of the most important factors for the development of nations, as important as urban landscapes and agrosystems (Janzen, 1993, 1997), then policymakers will be able to make decisions about conservation of natural resources and sustainable development on a scientific basis. Taxonomists are the scientists who are providing such a basis.

There are few digenean taxonomists, and they are mostly concentrated in the geographical areas with the lowest diversities of these organisms. If we are to inventory the world's dige-

neans, we must remove the so-called "taxonomical impediment." To do this, we need to establish more international collaborations, sharing information and experience, and establish training programs to encourage more students to pursue digenean taxonomy. Society needs to support these initiatives in the short term and to create more permanent positions for the long term. The more people involved in this task, the better chance we have to obtain critical information in a timely manner. If parasites are one of the main causes of ecosystem disturbances and ecological disasters (such as the worldwide population declines and abnormalities of amphibians, probably caused by digeneans and other pathogens), then society and biologists should realize that parasites are as important as free-living organisms for conservation and the sustainable use of biological resources.

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Helminth Parasites of Garter Snakes and Mud Turtles from Several Localities of the Mesa Central of Mexico

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ABSTRACT: Between 1996 and 1998, 212 specimens of aquatic snakes, the Mexican garter snake *Thamnophis eques* (77) and the black-bellied garter snake *Thamnophis melanogaster* (135), and 71 Mexican mud turtles *Kinosternon hirtipes* were collected in 7 localities along the Mesa Central of Mexico. We identified 22 species of helminths from these reptiles. Nematodes represented the most diverse group of helminths in these hosts, with 13 of the 22 species collected (59%). Next were digeneans with 5 species, cestodes with 2, and monogeneans and acanthocephalans with 1 each. In total, 17 new host and 48 new locality records were obtained. Ten of the 22 species infect reptiles accidentally since they frequently occur in sympatric species of freshwater fishes or amphibians, and 12 species are considered common members of the helminth parasite communities of these reptiles. Previous reports of all helminth species found are summarized, and biogeographical affinities of helminths are discussed.

KEY WORDS: helminths, nematodes, digeneans, acanthocephalans, monogeneans, taxonomy, reptiles, *Thamnophis melanogaster,* black-bellied garter snake, *Thamnophis eques,* Mexican garter snake, *Kinosternon hirtipes,* Mexican mud turtle, Mesa Central, Mexico.

Central Mexico is a region of complex geology and diverse surface configuration. Its major physiographic feature is the Mesa Central, one of the world's greatest tropical highlands (Miller and Smith, 1986). The Mesa Central was built up partly through accumulation of volcanoclastics produced by an episode of volcanism that began in the Miocene, reached its greatest intensity during the Pleistocene, and still continues today (West, 1964; Miller and Smith, 1986). Different groups of vertebrates, particularly fish and amphibians, have experienced a diversification as a result of repeated events of disruption of the former hydrographic system (the Lerma–Santiago drainage) by volcanic activity. In some cases, endemism reaches generic and familial levels. In particular, central Mexico supports a high reptile and amphibian species richness (Flores-Villela, 1993). During the last few years, we have surveyed the helminth fauna of fish, amphibians, and reptiles from several localities along the Mesa Central of Mexico in search of an independent source of information to explain the historical biogeography of the fauna inhabiting this part of the country (Pérez-Ponce de León, García-Prieto et al., 2000; Pérez-Ponce de León, León-Règagnon et al., 2000). Those surveys have been focused on the helminth communities at both local and regional geographical scales, considering endemic as well as introduced elements of the vertebrate fauna.

In Mexico, there are 20 species of garter snakes and 12 species of mud turtles (Ernst and Barbour, 1989; Rossman et al., 1996). According to Thatcher (1964), Jiménez and Caballero (1975), and Lamothe-Argumedo et al. (1997), 20 helminth species have been recorded, 12 of them as parasites of garter snakes (9 digeneans, 1 cestode, and 2 nematodes) and 8 as parasites of mud turtles (2 monogeneans, 2 digeneans, and 4 nematodes). Here, we present the results of a survey of the helminth fauna of the Mexican garter snake *Thamnophis eques* (Reuss, 1834), the black-bellied garter snake *Thamnophis melanogaster* (Peters, 1864), and the Mexican mud turtle *Kinosternon hirtipes* Wagler, 1830, in 7 localities of the Mesa Central of Mexico.

Materials and Methods

Two hundred twelve garter snakes and 71 Mexican mud turtles were caught in 7 localities of the Mesa Central of Mexico between 1996 and 1998: Ciénaga de Lerma (CLE, 19°11′08″N, 99°30′05″W) in Estado de México; Lago de Cuitzeo (LCU, 19°55′38″N, 101°08′27″W), Manantiales de Cointzio (MCO, 19°36′42″N, 101°15′29″W), Lago de Pátzcuaro (LPA,

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19°33′22″N, 101°40′59″W), Lago de Zirahuén (LZI, 19°26′37″N, 101°44′05″W), and Lago de Zacapu (LZA, 19°49′22″N, 101°46′40″W) in Michoacán State; and Lago de Chapala (LCH, 20°15′03″N, 103°10′22″W) in Jalisco State. Garter snakes were collected by hand or using a herpetological net, and mud turtles were collected with seine nets. Hosts were kept alive before parasitological analysis within 24 hr after capture. Hosts were killed with an overdose of sodium pentobarbital and examined using standard procedures. All organs were removed from the body, placed in saline (0.65%), and examined under a stereoscope. The body cavity, oral cavity, and subcutaneous tissue were also examined for helminths. Platyhelminths were relaxed with hot tap water and fixed under slight coverglass pressure using Bouin's fluid for 8 hr. Acanthocephalans were placed in distilled water at 4°C overnight, and fixed in 70% ethanol. Nematodes were fixed with Berland's fluid and transferred to 70% ethanol. Platyhelminths and acanthocephalans were stained with Mayer's paracarmine, Harris' hematoxylin, and Gomori's trichrome and mounted on permanent slides with Canada balsam. Nematodes were cleared with lactophenol. Voucher specimens were deposited in the Colección Nacional de Helmintos, Instituto de Biología, Universidad Nacional Autónomma de México (UNAM), México, D.F. (CNHE), and in the Harold W. Manter Laboratory of Parasitology, University of Nebraska–Lincoln (HWML), U.S.A. Hosts were identified following Rossman et al. (1996) and Ernst and Barbour (1989) and were deposited at the Colección Herpetológica del Museo de Zoología, Facultad de Ciencias, UNAM, and in the Colección Nacional de Anfibios y Reptiles (CNAR), Instituto de Biología, UNAM.

Results and Discussion

We identified 22 species of helminths as parasites of the 3 species of reptiles (Table 1). Nematodes represented the most diverse group of helminths, comprising 13 of the 22 species collected (59%). Digeneans comprised 5 species, cestodes 2, and monogeneans and acanthocephalans 1 each. The majority of the helminth species recorded herein represent adult worms (82%), and only 4 of the 22 are larval forms: the digenean *Diplostomum* (*Tylodelphys*) sp., the acanthocephalan *Polymorphus brevis* (Van Cleave, 1916) Travassos, 1926, and the nematodes *Contracaecum* sp. and *Eustrongylides* sp. We consider the presence of these larval forms in reptiles either as accidental infections, as in the case of *Diplostomum* (*Tylodelphys*) sp., or an alternative way to complete the life cycle using reptiles as paratenic hosts, as in the cases of the nematode *Contracaecum* sp. (Anderson, 1992) and the acanthocephalan *P. brevis,* or as intermediate hosts, as in the case of *Eustrongylides* sp.

The presence of all these larval stages in reptiles of the Mesa Central may be a result of their hosts preying on fish. Fish are the primary host group of these parasites and commonly harbor these larvae (Pérez-Ponce de León et al., 1996). The life cycles of these parasites are completed when a piscivorous bird feeds upon the intermediate or paratenic hosts.

The case of the digenean *Posthodiplostomum minimum* (McCallum, 1921) Dubois, 1936, is interesting because immature adult forms were found in the intestines of mud turtles. This species is predominantly a bird parasite; however, it might be able to infect other groups of vertebrates, such as mammals, reptiles, and amphibians, that include fish among their food items, resulting in extensive host-induced morphological variability (Pérez-Ponce de León, 1995).

Four helminth species deserve special attention because, although they were present as adults in reptiles, they seem to be found accidentally. According to previous records (Table 1), *Falcaustra mexicana* Chabaud and Golvan, 1957, and *Hedruris siredonis* Baird, 1858, seem to be primarily parasites of amphibians, mainly members of the neotenic salamander genus *Ambystoma*; however, the high prevalences and abundance of infection of *Hedruris siredonis* in the mud turtle from MCO might argue against this conclusion. Two species of helminths found in reptiles are typical parasites of fishes. We found only 1 specimen of *Spinitectus osorioi* Choudhury and Pérez-Ponce de León, 2001, in the intestine of the garter snake *T. melanogaster* in LPA. Members of the genus *Spinitectus* are parasites of marine and freshwater fishes, so the presence of this nematode with such low prevalence and abundance values must be interpreted as an accidental infection as a result of the snake eating fish. The Asian tapeworm *Bothriocephalus acheilognathi* Yamaguti, 1934, showed a prevalence of 1.6% and an abundance of 0.02 parasites/host analyzed in garter snakes from LPA and must also be considered an accidental infection because freshwater fishes are the primary hosts of this parasite (see Pérez-Ponce de León et al., 1996; Hoffman, 1999).

We established a total of 17 new host and 48 new locality records. Five of these species are recorded in Mexico for the first time: *Pneumatophilus variabilis* (Leidy, 1856) Odhner, 1910, *Proteocephalus variabilis* Brooks, 1978, *Dracunculus ophidensis* Brackett, 1938, *Rhabdias fuscovenosa* (Railliet, 1899) Goodey, 1924, and

Table 1. Helminth parasites of some garter snakes and mud turtles in Mexico.

Helminth	Infection site	Host(s)	Locality* (accession no.)	Prevalence (%)	Mean abundance	Previous records
Digenea						
Diplostomum (*Tylodelphys*) sp. (metacercariae)	Intestine	*Thamnophis eques*	CLE (3461)	2.3	0.04	
			LPA‖	9.1	0.3	
		Thamnophis melanogaster	LPA‖	3.2	0.03	
REMARKS: Adults of this species are parasites of fish-eating birds. The metacercarial stage of this parasite is frequently found in freshwater fishes (Pérez-Ponce de León et al., 1996). At CLE, León-Règagnon (1992) recorded *D.* (*T.*) *americana* (Dubois, 1936) Dubois, 1937 as a parasite of the duck *Podylimbus podiceps* Linnaeus, 1758; however, experimental infections are needed to demonstrate the correlation between larvae and adults.						
Ochetosoma brevicaecum	Mouth, esophagus	*T. eques*	CLE (3707, 15214‡)	51.2	7.3	Caballero (1941b)
			LPA (3440)§	18.2	0.7	
			LXO (3439)	ND	ND	
		T. melanogaster	CLE (3436, 3438, 3442)	53.8	8.3	Caballero (1941b), Bravo (1943)
			LCH (3434)§	5.5	1.9	
			LPA (3435, 15200‡)	56.4	12.0	
			LZA (3441)§	66.7	2.7	
			LXO			Bravo (1943)
		Thamnophis sp.	CLE			Parra (1983)
Pneumatophilus variabilis	Trachea, lungs, heart	*T. melanogaster*§	LPA (3462–3467, 15210–15213‡)§	40.3	0.7	
REMARKS: This is the first record of this digenean in Mexico, and LPA represents the southernmost locality of its distributional range.						
Posthodiplostomum minimum	Intestine	*Kinosternon hirtipes*	LPA (1739)	6.9	0.2	Pérez-Ponce de León (1995)
REMARKS: This record was previously published by Pérez-Ponce de León (1995), representing the first record of an adult (immature) parasitizing reptiles in Mexico. Adults of *P. minimum* have been recorded in several species of fish-eating birds from central Mexico (Lamothe-Argumedo et al., 1997; Guzmán and García-Prieto, 1999) and from southeastern Mexico (Aguirre-Macedo and García-Magaña, 1994). Metacercariae of *P. minimum* have been found in >35 freshwater fishes of Mexico (Pérez-Ponce de León et al., 1996).						
Telorchis corti	Intestine	*K. hirtipes*§	LCU (3811)§	3.8	0.1	
			LPA (3228–3230)§	26.7	0.2	
			LZA (3305)§	28.6	1.4	
			LZI (3306)§	33.3	2.6	
			MCO (3812)§	33.3	0.5	
		T. eques	CLE (3444, 15204 AA‡)	41.9	1.7	
			LCH‖§	6.7	11.1	
			LPA (3448)	54.4	30.9	
			LZA (3453)	33.3	19.7	
			CLE			Caballero (1941b)[1]
			LZU			Parra (1983)[2]
			TUL			Caballero (1941b)[3]

Table 1. Continued.

Helminth	Infection site	Host(s)	Locality* (accession no.)	Prevalence (%)	Mean abundance	Previous records
		T. melanogaster	CLE‖	53.8	9.6	
			LCH (15206‡)	11.1	0.2	
			LCU (3443, 15201‡)	42.1	2.4	
			LPA (3447, 15203‡)	79	32.3	
			LZA (3449)	100	10.0	
			LZI (3819)	100	10.0	
			CLE			Bravo (1943)[4]
			LTX			Bravo (1943)[2]
			LXO			Bravo (1943)[2]
		Apalone spinifera (Le Sueur, 1827) (spiny softshell turtle)	RIP, RSA, RSC			Iruegas et al. (1991)
		Chelydra serpentina (Linnaeus, 1758) (common snapping turtle)	RTE			Thatcher (1964)
		Claudius angustatus Cope, 1865 (narrow-bridged musk turtle)	RTE			Thatcher (1964)
		Kinosternon integrum Le Conte, 1824 (mud turtle)	IZM			Bravo (1944)
		Kinosternon leucostomum (Duméril and Bribon, 1851) (mud turtle)	RTE			Thatcher (1964)
		Kinosternon sp.	TEM			Ramos-Ramos (1995)
		Leptophis sp.	RTE			Thatcher (1964)
		Trachemys scripta (Schoepf, 1792)	RTE			Thatcher (1964)
Monogenea						
Polystomoidella oblonga	Urinary bladder	*K. hirtipes*	LCU (3204)§	26.9	3.3	
			LPA (3205)	6.9	0.2	Parra (1983)
			LZA (3206)§	28.6	2.8	
			LZI (3207)§	66.7	246.0	
			MCO (3810)§	16.7	0.8	
			EME, LXO			Lamothe-Argumedo (1972)
			LEM			Lamothe-Argumedo et al. (1997)
			VHE			Parra (1983)

REMARKS: Original records were made considering the following names: [4] *Telorchis diminutus* Stunkard, 1915; [2] *Telorchis thamnophidis* (Caballero, 1941) Bravo, 1943; [1] *Cercorchis kinosterni* Byrd, 1936; [3] *Cercorchis thamnophidis* Caballero, 1941.

Table 1. Continued.

Helminth	Infection site	Host(s)	Locality* (accession no.)	Prevalence (%)	Mean abundance	Previous records
		K. integrum	CAS			Caballero and Herrera (1947)
			CAC			Caballero (1940)
		K. leucostomum	LAV			Herrera (1951)
Cestoidea						
Bothriocephalus acheilognathi	Intestine	*Thamnophis melanogaster*§	LPA (3460†)	1.6	0.02	
REMARKS: This freshwater fish parasite is present at ≥30 localities throughout Mexico (Pérez-Ponce de León et al., 1996). The only record of *B. acheilognathi* in a nonfish host was in the salamander *Ambystoma dumerilii* (Dugès, 1879) (García et al., 1993).						
Proteocephalus variabilis	Intestine	*T. eques*§	CLE (3468, 3469†)§	4.6	0.9	
			LCH (3820)§	13.3	0.2	
			LPA (3474)§	54.5	0.3	
		T. melanogaster§	CLE (3821)	7.7	0.5	
			LCH (3477, 3478, 3480, 15207‡)	89.0	5.2	
			LCU (3470–3472)§	79.0	11.0	
			LPA (3473, 3476)	66.1	3.9	
			LZA (3900)§	33.3	0.7	
			LZI (3883)§	50.0	1.5	
REMARKS: This helminth has been found parasitizing *Nerodia* and *Thamnophis* in several localities of the eastern U.S.A. (Brooks, 1978). This is the first report of this cestode in Mexico.						
Acanthocephala						
Polymorphus brevis	Mesentery, body cavity	*K. hirtipes*§	LCU (3231)	26.9	0.7	
			LPA (3814)	6.9	0.1	
			LZA (3813)§	14.3	1.8	
		T. eques§	CLE (15215‡)§	2.3	0.02	
			LCH (3455, 15209‡)§	66.7	2.6	
				18.2	0.7	
			LPA‖	ND	ND	
			LXO (3459)§	ND	ND	
			LZA‖			
		T. melanogaster§	CLE‖	7.7	0.1	
			LCH‖	33.3	1.6	
			LCU (3456, 3457, 15216‡)	27.0	0.7	
			LPA (3458)	22.6	0.3	
			LZA (3454, 15208‡)	ND	ND	
REMARKS: Cystacanths of *P. brevis* have been recorded in several species of freshwater fishes of Mexico (Pérez-Ponce de León et al., 1996). The neotenic salamander *Ambystoma dumerilii* was found to be infected by *P. brevis* cystacanths (García et al., 1993). Adult forms of this acanthocephalan have been collected in the snowy egret *Egretta thula* Molina, 1782 and the black-crowned night heron *Nycticorax nycticorax* Linnaeus, 1758 at LPA (Lamothe-Argumedo et al., 1997).						

Table 1. Continued.

Helminth	Infection site	Host(s)	Locality* (accession no.)	Prevalence (%)	Mean abundance	Previous records
Nematoda						
Capillariinae gen. sp.	Intestine	*T. eques*	CLE‖	2.3	0.2	
REMARKS: We could not identify our specimens to genus and species level because no males were collected from the hosts. Only 1 species of capillarid nematode has been recorded in garter snakes in Mexico; it was described by Caballero and Cerecero (1943) as *Capillaria xochimilcensis* Caballero and Cerecero, 1943 from *T. melanogaster* at LXO. However we could not establish whether our specimens could be identified as the same species found at LXO.						
Contracaecum sp. (larvae)	Intestine	*T. eques*	LCH (3619, 3622)	100.0	12.7	
		T. melanogaster	LCH (3620)	88.9	10.6	
			LCU (3621)	7.9	0.2	
			LPA‖	1.6	0.03	
REMARKS: Larvae of *Contracaecum* sp. are frequently found in freshwater fishes in Mexico (Pérez-Ponce de León et al., 1996).						
Dracunculus ophidensis	Mesentery	*T. melanogaster*§	CLE (3639)§	7.7	0.5	
			LCH (3637)§	33.3	0.4	
			LCU (3640, 3641)§	10.5	0.1	
			LPA (3638, 15226–15234‡)§	40.3	0.8	
			LZA (15223‡)§	33.3	66.7	
			LZI§‖	50.0	2.0	
REMARKS: The distribution range of *D. ophidensis* extends from southern Canada to the southern U.S.A. (Baker, 1987). This is the first record of this species in Mexico.						
Eustrongylides sp. (larvae)	Mesentery, body cavity	*T. eques*	LPA (3628)	81.8	4.3	
		T. melanogaster	LCU (3627)	36.8	1.2	
			LPA (3626)	77.4	2.5	
			LZA‖	33.3	0.3	
REMARKS: Larvae of *Eustrongylides* sp. are also frequently found in freshwater fishes and frogs in 5 states of Mexico (Moravec et al., 1995; Caspeta, 1996; Jiménez, 1996; Pérez-Ponce de León et al., 1996). Adult worms have never been found in fish-eating birds in Mexico. Licthtenfels and Lavies (1976) established the presence of larvae of *Eustrongylides* sp. as the cause of mortality in individuals of the eastern garter snake *Thamnophis sirtalis* (Linnaeus, 1758).						
Falcaustra affinis	Intestine, stomach	*K. hirtipes*§	LPA (3759, 3760)§	3.4	2.1	
			MCO (3758, 15218‡)§	33.3	5.5	
		Unidentified turtle	UL			Caballero (1939b)
		Trachemys scripta	AXP			Moravec and Vargas-Vázquez (1998)
Falcaustra mexicana	Intestine	*Thamnophis eques*§	LPA (3623)	9.1	0.1	

Table 1. Continued.

Helminth	Infection site	Host(s)	Locality* (accession no.)	Prevalence (%)	Mean abundance	Previous records
REMARKS: *Spironoura cryptobranchi* (Walton, 1930) was recorded by Bravo and Caballero (1940) as a parasite of the ambystomid salamander *Rhyacosiredon altamirani* (Dugès, 1895). Based on this material, Chabaud and Golvan (1957) described *F. mexicana.* This transference was supported by Baker (1986, 1987). We studied specimens of *F. chabaudi* Dyer, 1973 deposited at CNHE as parasites of *Ambystoma dumerilii* and *Rana dunni* at LPA. They were not distinct morphologically from the species described by Chaubaud and Golvan (1957) as *F. mexicana.* Considering characters such as the size and shape of the pharynx, prebulb, and spicules, we propose that the specimens described as *F. chabaudi* by García et al. (1993) and Pulido-Flores (1994) be transferred to *F. mexicana.*						
Falcaustra wardi	Stomach	*K. hirtipes*§	LZA (3757)§	14.3	1.1	
REMARKS: Previous records of this species are restricted to turtles of Oklahoma, Ohio, and Ontario, Canada (Baker, 1987). This is the first record of this species in Mexico.						
Hedruris siredonis	Intestine, stomach	*K. hirtipes*§	LZA (3761)	14.3	1.0	
			MCO (3762, 15217‡, 15221‡)§	66.7	42.2	
REMARKS: Previous records of this species in Mexico were as parasites of ambystomatid salamanders in several localities of the Mesa Central (Caballero and Bravo, 1938; Dyer and Brandon, 1973; Dyer, 1984). This is the first time *H. siredonis* has been recorded in a turtle.						
Rhabdias fuscovenosa	Lungs	*T. eques*§	CLE (3629)§	7.0	0.2	
			LCH (3630)§	33.3	1.1	
			LZA§‖	100.0	3.3	
		T. melanogaster§	LCH (3479, 15220‡)	28.0	0.9	
			LCU (3631, 15219‡)§	15.5	0.1	
			LPA (3632)§	6.4	0.1	
			LZA (15224‡)	66.7	1.0	
REMARKS: This represents the first record of *R. fuscovenosa* in Mexico. Previously it was recorded parasitizing snakes in Europe, China, and northern North America (Baker, 1987).						
Serpinema trispinosum	Intestine, stomach	*K. hirtipes*	LCU (3748–3750)§	53.8	4.6	
			LPA (3751–3753)§	82.7	9.5	
			LZA (3754, 3755)§	71.4	57.0	
			MCO (3756)§	33.3	4.7	
		T. melanogaster§	LPA (3624)	1.6	0.02	
		Dermatemys mawii Gray, 1847 (Central American river turtle)	RCH			Caballero (1943)
		Trachemys scripta	AXP			Moravec and Vargas-Vázquez (1998)
REMARKS: Baker (1979) and Moravec and Vargas-Vázquez (1998) suggested that possibly *Serpinema parvus* (Caballero, 1939) Baker, 1979 is a junior synonym of *S. trispinosum.* The records of *S. parvus* by Caballero (1939a), Lamothe-Argumedo et al. (1997), and Dyer and Carr (1990) could then extend the distribution range of this species in Mexico. A similar situation occurs with *S. magnorugosus* (Caballero, 1939) Yeh, 1960. This species was described by Caballero (1939b) and was synonymized with *S. trispinosum* by Moravec and Vargas-Vázquez (1998); however, *S. magnorugosus* was considered valid by Baker (1987). The record from Caballero (1943) was recorded as *Camallanus scabrae* MacCallum, 1918, but this species was considered a synonym of *S. trispinosum* by Baker (1979) and later by Moravec and Vargas-Vázquez (1998).						

Table 1. Continued.

Helminth	Infection site	Host(s)	Locality* (accession no.)	Prevalence (%)	Mean abundance	Previous records
Spinitectus osorioi	Intestine	*Thamnophis melanogaster*§	LPA (3625)	1.6	0.02	
REMARKS: This species was recently described by Choudhury and Pérez-Ponce de León (2001) from 2 species of freshwater fishes in Lake Pátzcuaro. Species of *Spinitectus* are parasites of freshwater and marine fishes.						
Spiroxys contorta	Intestine, stomach	*K. hirtipes*§	LCU (3739–3741, 3744)§	42.3	1.1	
			LPA (3742, 3747)	48.3	4.0	
			LZA (3745)§	42.8	0.4	
			LZI (3743)§	33.3	5.6	
			MCO (3746)§	66.7	1.2	
		Chrysemis ornata	UL			Caballero (1939b)
		Trachemys scripta	AXP			Moravec and Vargas-Vázquez (1998)
REMARKS: This species was also found as a parasite of *Ambystoma dumerilii* by García et al. (1993) and of *Rana dunni* by Pulido-Flores (1994) at LPA.						
Spiroxys susanae	Cloaca, stomach	*Thamnophis eques*	CLE (3633–3636)	86.6	41.1	Caballero (1941a)
		T. melanogaster	CLE (3642–3644)	92.3	20.0	Caballero (1941a), Cid del Prado (1971)
REMARKS: This species seems to be endemic to CLE; it has not been found in garter snakes at any other locality.						

* ACA = Acámbaro, Guanajuato; AXP = Aguada Xpoc, Yucatán; CAC = Cacahuamilpa, Guerrero; CAS = Casasano, Morelos; CLE = Ciénaga de Lerma, Estado de México; EME = Estado de México (undetermined locality); IZM = Izúcar de Matamoros, Puebla; LAV = Laguna de Alvarado, Veracruz; LCH = Lago de Chapala, Jalisco; LCU = Lago de Cuitzeo, Michoacán; LEM = Laguna El Mortero, Durango; LEZ = Laguna Emiliano Zapata, Tabasco; UL = undetermined locality; LPA = Lago de Pátzcuaro, Michoacán; LTX = Lago de Texcoco, Estado de México; LXO = Lago de Xochimilco, Distrito Federal; LZA = Lago de Zacapu, Michoacán; LZI = Lago de Zirahuén, Michoacán; LZU = Lago de Zumpango, Estado de México; MCO = Manantiales de Cointzio, Michoacán; RCH = Río de Chilapa, Tabasco; RIP = Río Pesquería, Nuevo León; RSA = Río Salinas, Nuevo León; RSC = Río Santa Catarina, Nuevo León; RTE = Río Teapa, Tabasco; TAS = Tasquillo, Hidalgo; TEM = Temascal, Oaxaca; TUL = Tultepec, Estado de México; VHI = Villa Hidalgo, Nayarit.

‡ Specimens deposited at HWML. All others at CNHE.

§ First host or locality records.

‖ = Not deposited in museums.

Falcaustra wardi (Mackin, 1936) Teixeira de Freitas and Lent, 1941.

However, not considering accidental species (either larval or adult forms), the helminth community of these reptiles is structured basically of 12 species: the digeneans *Ochetosoma brevicaecum* (Caballero, 1941) Flores and Grocott, 1953, *Pneumatophilus variabilis,* and *Telorchis corti* Stunkard, 1915; the monogenean *Polystomoidella oblonga* (Wright, 1879) Price, 1939; the cestode *Proteocephalus variabilis*; and the nematodes *Dracunculus ophidensis, Rhabdias fuscovenosa, Falcaustra affinis* (Leidy, 1856), *Falcaustra wardi, Serpinema trispinosum* Leidy, 1852, *Spiroxys contorta* (Rudolphi, 1819) Schneider, 1866, and *Spiroxys susanae* Caballero, 1941. These species inhabit mostly the gastrointestinal tract (66.6%), with some species located in the urinary bladder, lungs, trachea, and mesentery. Considering only this parasite assemblage, we established 10 new host records, with 4 new records for *T. melanogaster,* 2 for *T. eques,* and 4 for *K. hirtipes.* In addition, 43 new locality records were established for them.

Thamnophis melanogaster showed the highest helminth species richness; 14 of the 22 species were found in this host, 13 of them in LPA, followed by *T. eques* and *K. hirtipes* with 11 and 9 species, respectively. The mud turtle was infected with 9 species in all 5 localities where it was found, and LPA was the locality with the highest species richness (7). *Thamnophis eques* harbored 11 species, with those collected from CLE exhibiting the highest richness (8).

In spite of the high species richness and the fact that many of these hosts occur together in most of the localities where we sampled, only a few helminth species were shared among them. Only 2 species, the digenean *Telorchis corti* and the acanthocephalan *Polymorphus brevis* (Table 1), infected all 3 species of hosts. Only the digenean *T. corti* was recovered from all species of hosts at the 7 localities sampled. The acanthocephalan *P. brevis* was found at 6 localities. Helminth parasites of the 2 species of garter snakes are very similar, as expected in closely related hosts. Nine species of helminths are shared between *T. melanogaster* and *T. eques.* However, 7 of them, as previously mentioned, are not characteristic parasites of reptiles. They were found as a result of an overlap of the feeding habits of the hosts, and the fact that they occur in sympatry with some freshwater fishes indicates that they were accidental infections. The species *Ochetosoma brevicaecum, Proteocephalus variabilis, Spiroxys susanae,* and *Rhabdias fuscovenosa* were found only in the 2 species of *Thamnophis.* However, some helminths were found only in 1 species of host, *Pneumatophilus variabilis* and *Dracunculus ophidiensis* in *Thamnophis melanogaster* and *Falcaustra affinis* Leidy, 1856, *Falcaustra wardi, Polystomoidella oblonga, Hedruris siredonis,* and *Spiroxys contorta* only in the mud turtle, *K. hirtipes.*

The taxonomic situation of the digenean *Telorchis corti* seems to be controversial. Here we attempt to clarify its taxonomic status. This species exhibits very high levels of intraspecific morphological variation, mainly in body size and vitellaria distribution (MacDonald and Brooks, 1989). Specimens that we collected from mud turtles were markedly larger than those recovered from snakes; however, specimens from both hosts possess an elongate body shape, an ovary located near the ventral sucker, and a bipartite seminal vesicle. These traits were used by MacDonald and Brooks (1989) to define the species *T. corti* within the context of the wide intraspecific variation, based on previous studies by Watertor (1967) using salamanders and turtles as experimental hosts.

In Mexico, 16 species of *Telorchis* have been recorded, 13 as parasites of freshwater turtles and 3 as parasites of garter snakes. The 3 species of *Telorchis* found in snakes are *Telorchis thamnophidis* (Caballero, 1941) Bravo, 1943, *Telorchis diminutus* Stunkard, 1915, and *Telorchis kinosterni* (Byrd, 1936) Yamaguti, 1958. Nasir (1974) proposed *T. thamnophidis* and *T. kinosterni* as junior synonyms of *T. diminutus,* based on descriptions and not on observation of type material. MacDonald and Brooks (1989) considered *T. diminutus* as a synonym of *T. corti.* We looked at specimens of the 3 original species (CNHE 1241, 1165, 994, 1424) and specimens of *T. corti* (HWML 20210, 20212, 20949, 20834), and we concur with the proposal of McDonald and Brooks. This means that *T. corti* is a parasite found in freshwater turtles as well as in garter snakes and salamanders, whose distributional range extends from southern Canada to Central America (MacDonald and Brooks, 1989).

Recently, *Telorchis attenuata* Goldberger, 1911 (=*T. attenuatus*), was recorded as a parasite of the red-eared slider *Trachemys scripta*

(Schoepf, 1792) in southeastern Mexico by Moravec and Vargas-Vázquez (1998). They proposed, with no justification, that *T. corti* is a junior synonym of *T. attenuata.* We examined specimens of *T. attenuata* (CNHE 2848) studied by Moravec and Vargas-Vázquez (1998) and determined that there are several differences between these species, mainly the ratio of the distance between the ovary and the testes and between the ovary and the ventral sucker. We agree that the specimens described by Moravec and Vargas-Vázquez (1998) are *T. attenuata.* Nevertheless, we do not agree with their assertion that *T. corti* should be considered a junior synonym of *T. attenuata.*

Biogeographical considerations

The influence of the Nearctic and Neotropical biogeographical zones on the composition of the helminth fauna of some amphibians and freshwater fishes occurring in Central Mexico has been addressed to a certain extent (Pérez-Ponce de León, García-Prieto et al., 2000; Pérez-Ponce de León, León-Règagnon et al., 2000; Choudhury and Pérez-Ponce de León, 2001). The helminth fauna of these hosts in that area of Mexico is composed of a larger number of Nearctic elements, which mainly structure the helminth parasite communities in aquatic vertebrates of the Mesa Central. Helminth parasite communities of aquatic reptiles seem to show the same tendency; almost 60% of the 12 species of helminths occurring in garter snakes and mud turtles as a result of historical association are Nearctic elements, and their presence in these reptiles in the Mesa Central of Mexico represents the southernmost North American distribution limit of each species. The Transverse Volcanic Axis forms the barrier of the distributional range for the Nearctic elements of the helminth fauna found in garter snakes and mud turtles. These species of helminths occur in closely related hosts in several localities in northern North America (U.S.A. and southern Canada). Here, the helminth fauna might reflect biogeographical and phylogenetic links of the hosts, whose distribution ranges extend between the Mesa Central (with the southernmost distribution limit in high elevation water bodies along the Transverse Volcanic Axis) and the northern part of Mexico. The other 5 species of helminths, representing 40% of the helminth fauna, include endemic elements (*Spiroxys susanae*), widespread elements (*Rhabdias fuscovenosa* and *Spiroxys contorta*), and 2 amphiregional species (*Ochetosoma brevicaecum* and *Serpinema trispinosum*), i.e., species whose distributional ranges extend from the Mesa Central of Mexico to the Canal Zone in Panama (*O. brevicaecum*) and from southern Canada to the lowlands of the Yucatán Peninsula and Cuba (*S. trispinosum*).

The present study provides an independent source of information, because it was done in a different host–parasite system, for describing patterns of diversity of the helminth fauna in water bodies of the Mesa Central of Mexico, where different groups of vertebrates have experienced diversification as a result of repeated events of disruption of the former hydrographic system (the Lerma-Santiago drainage) by volcanic activity (West, 1964). The history of the aquatic vertebrate fauna of this important transitional and biogeographical region seems to be more closely linked to the Nearctic elements. Parasitological evidence shows a well defined Nearctic influence as the key element to describe patterns of helminth community composition, with the addition of a few endemic elements originating through speciation events and diversification processes within that particular region, probably as a result of isolation of host and parasite populations due to the disruption of the former hydrographic system. Robust phylogenetic systematic hypotheses for particular hosts and parasite taxa in comprehensive parascript studies (Brooks and McLennan, 1993) are the necessary next step to describe more accurately the historical biogeography of this important region.

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Gastrointestinal Helminths of 51 Species of Anurans from Reserva Cuzco Amazónico, Peru

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ABSTRACT: Six hundred eighty-two anurans representing 51 species collected from the Reserva Cuzco Amazónico, Peru, were examined for helminths. One species of Trematoda (*Glypthelmins parva*), 1 species of Cestoda (*Cylindrotaenia americana*), 14 species of Nematoda (*Aplectana hylambatis, Batracholandros spectatus, Cosmocerca brasiliense, Cosmocerca parva, Cosmocerca podicipinus, Cosmocercella phyllomedusae, Ochoterenella vellardi, Oswaldocruzia lopesi, Physalopteroides venancioi, Rallietnema gubernaculatum, Schrankiana inconspicata, Schrankiana larvata, Schrankiana schranki,* and *Schrankianella brasili*) were found. Larvae representing Acuarioidae gen. sp., *Brevimulticaecum* sp., *Physaloptera* sp., *Porrocaecum* sp., *Ophidascaris* sp., and the Acanthocephala were also found. No host harbored more than 4 helminth species (larval forms included, $\bar{x} \pm$ SD): 1.4 ± 0.7 helminth species/infected anuran; 5.9 ± 13.6 helminths/infected anuran. *Cosmocerca brasiliense* had the greatest prevalence (162 of 682 anurans, 24%; mean intensity = 1.8); *Aplectana hylambatis* had the greatest mean intensity (13.4; prevalence, 33 of 682 anurans, 5%). No host species harbored more than 7 helminth species (larval forms included); 2.8 ± 1.6 helminth species/host species. *Cosmocerca brasiliense* was the most common helminth: 34 of 51 anuran species (67%). Twenty-nine new host records are reported.

KEY WORDS: Trematoda, Cestoda, Nematoda, Anura, Reserva Cuzco Amazónico, Peru.

Little information is available on the helminths of anurans of Peru. Freitas and Ibañez (1962) described *Thelandros spectatus* Freitas and Ibañez, 1962, from the Peru coast toad *Bufo limensis* Werner, 1901, but later (1965) reassigned their specimens to *Batracholandros spectatus* (Freitas and Ibañez, 1962) Freitas and Ibañez, 1965, and in that same article described *Raillietnema gubernaculatum* Freitas and Ibañez, 1962, and reported the presence of larvae of a species of *Physaloptera,* both from *Bufo limensis.* Naupay (1974) reported *Batracholandros spectatus* and *Rhabdias sphaerocephala* Goody, 1924, from the warty toad *Bufo spinulosus* Wiegmann, 1834. Ibañez and Cordova (1976) described *Falcaustra condorcanquii* Ibañez and Cordova, 1976, and *Hedruris moniezi* Ibañez and Córdova, 1976, from the Peru water frog *Telmatobius peruvianus* Wiegmann, 1835, and reported the presence of *H. moniezi* in an undetermined species of *Telmatobius.* Vaucher (1981) described *Mesopolystoma samiriensis* Vaucher, 1981, from the Manaus slender-legged treefrog *Osteocephalus taurinus* Steindachner, 1862. Jones (1987) reported *Cylindrotaenia americana* Jewell, 1916, from the montane robber frog *Eleutherodactylus lineatus* (Brocchi, 1879), and the cane toad *Bufo marinus* (Linnaeus, 1758). Gray (1993) described *Wetapolystoma almae* Gray, 1993, from the South American common toad *Bufo typhonius* (Linnaeus, 1758). Durette-Desset et al. (2000) described *Schulzia chiribita* Durette-Desset, Florindez, and Morales, 2000, from the Peru white-lipped frog *Leptodactylus rhodonotus* (Günther, 1868). Three additional helminth records were found in the U.S. National Parasite Collection: *Cylindrotaenia americana* (USNPC 84979), *Aplectana hylambatis* (Baylis, 1927) Travassos, 1931 (USNPC 84980), and *Oswaldocruzia subauricularis* (Rudolphi, 1819) Travassos, 1917 (USNPC 84981), from *Bufo typhonius.* Data on the helminths of anurans from Cuzco Amazónico, Peru, are included in the unpublished thesis of Chandler (1983). Here, we report helminths collected during the course of a trophic study of anurans from Cuzco Amazónico, Peru (Parmelee, 1998, 1999) and examine community structure within this sample of anurans.

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Materials and Methods

The 682 anurans representing 51 species used in this study were collected during a 10-yr biotic survey of the Reserva Cuzco Amazónico. Cuzco Amazónico is a privately maintained reserve of 10,000 ha on an alluvial plain, 200 m elevation, on the north bank of the Río Madre de Dios about 15 km ENE of Puerto Maldonado, Departamento Madre de Dios, Amazonian Peru (12°35′S, 69°05′W). Duellman and Koechlin (1991) described the reserve in detail, and Duellman and Salas (1991) provided an annotated checklist of the amphibans of the area. Collection data, dietary data, and accession numbers from the Museum of Herpetology, University of Kansas for the anurans used in this study have been previously published (Parmelee, 1999). Anurans were collected by hand, fixed in 10% buffered formalin within 6 hr of capture, and preserved in 70% ethanol. The body cavities were opened by a longitudinal incision from throat to vent and the alimentary canals (esophagus to cloaca) were slit longitudinally; stomach and intestinal contents were removed and examined with a dissecting microscope. Prey items were identified and recorded (Parmelee, 1999). Any helminths found in the alimentary canal or body cavity (lungs and bladders were not examined) were placed in vials of 70% ethanol for later identification, at which time each helminth was placed on a glass slide in a drop of undiluted glylcerol for study under a compound microscope. Nematodes were identified from these preparations; cestodes and trematodes were stained with hematoxylin and mounted in balsam for identification. Analyses of variance (ANOVAs) were used to compare anuran subpopulations. Scatter plots of prevalence (number of infected hosts divided by the number of hosts examined, expressed as a percentage) and abundance (number of helminths divided by number of hosts) were used to determine the most common helminth. Importance (an overall estimate of the influence of a species within a community) was calculated for helminth species: importance (I) = relative prevalence + relative abundance × 100.

Results

A total of 2,156 helminths was collected from 366 of the 682 anurans (54%) examined (Table 1). Of these, 1,829 were mature individuals of known anuran helminths and represented 1 species of Trematoda, *Glypthelmins parva* Travassos, 1924 (N = 10), 1 species of Cestoda, *Cylindrotaenia americana* (N = 31), 14 species of Nematoda, *Aplectana hylambatis* (N = 445), *Batracholandros spectatus* (N = 37), *Cosmocerca brasiliense* Travassos, 1925 (N = 285), *Cosmocerca parva* Travassos, 1925 (N = 127), *Cosmocerca podicipinus* Baker and Vaucher, 1984 (N = 193), *Cosmocercella phyllomedusae* Baker and Vaucher, 1983 (N = 109), *Ochoterenella vellardi* (Travassos, 1929) Esslinger, 1986 (N = 9), *Oswaldocruzia lopesi* Freitas and Lent, 1938 (N = 131), *Physalopteroides venancioi* (Lent, Freitas, and Proença, 1946) Sobolev, 1949 (N = 23), *Rallietnema gubernaculatum* Freitas and Ibañez, 1965 (N = 12), *Schrankiana inconspicata* Freitas, 1959 (N = 39), *Schrankiana larvata* (Vaz, 1933) Fahel, 1952 (N = 136), *Schrankiana schranki* (Travassos, 1925) Strand, 1942 (N = 221), and *Schrankianella brasili* (Travassos, 1927) Freitas, 1959 (N = 21). There were 327 larvae representing Acuarioidae gen. sp. (N = 18), *Brevimulticaecum* sp. (N = 33), *Ophidascaris* sp. (N = 1), *Physaloptera* sp. (N = 195), *Porrocaecum* sp. (N = 67), and the Acanthocephala (N = 13). Prevalences (number of hosts infected by a helminth species divided by the total number of hosts examined expressed as a percentage) of helminth infections by host species are presented in Table 1. Twenty-nine new host records are reported. Voucher specimens were deposted in the U.S. National Parasite Collection, Beltsville, Maryland (Table 2).

There were 22 helminth species represented in the sample. No host harbored more than 4 of the helminth species: 272 anurans (74%) harbored 1 species, 65 (18%) harbored 2 species, 23 (6%) harbored 3 species, and 6 (2%) harbored 4 species. There were 1.4 ± 0.7 ($\bar{x}$ ± SD) helminth species/infected anuran and 5.9 ± 13.6 helminth individuals/infected anuran. *Cosmocerca brasiliense* had the greatest prevalence (162 of 682 anurans, 24%; mean intensity = 1.8); *Aplectana hylambatis* had the greatest mean intensity (13.4; 33 of 682 anurans, 5%). No host species harbored more than 7 of the helminth species: 12 of 51 anuran species (24%) harbored 1 helminth species, 16 (31%) harbored 2 species, 10 (20%) harbored 3 species, 4 (8%) harbored 4 species, 4 (8%) harbored 5 species, 4 (8%) harbored 6 species, and 1 anuran species (2%) harbored 7 helminth species, all representing 2.8 ± 1.6 helminth species/host species. *Cosmocerca brasiliense* was the most common helminth species present in the supracommunity; it was found in 34 anuran species (67%).

The adult anurans of this study inhabited three general habitats (Table 1); there were 29 arboreal species, 20 terrestrial species, and 2 aquatic species (Parmelee, 1998, 1999). The arboreal species harbored 577 helminths (19.9 ± 23.1 helminth individuals/infected host; range, 1–73 helminth individuals) assigned to 15 species (2.6 ± 1.4 helminth species/host species). *Aplectana hylambatis, R. gubernaculatum, S. inconspicata,*

Table 1. Prevalence of helminth infections in 51 species of anurans from Reserva Cuzco Amazónico, Peru.

Host	N	Habitat	Mature helminths																Larval helminths					
			Glypthelmins parva	*Cylindrotaenia americana*	*Aplectana hylambatis*	*Batracholandros spectatus*	*Cosmocerca brasiliense*	*Cosmocerca parva*	*Cosmocerca podicipinus*	*Cosmocercella phyllomedusae*	*Ochoterenella vellardi*	*Oswaldocruzia lopesi*	*Physalopteroides venancioi*	*Raillietnema gubernaculatum*	*Schrankiana inconspicata*	*Schrankiana larvata*	*Schrankiana schrankai*	*Schrankianella brasili*	Acuarioidae gen. sp.	*Brevimulticaecum* sp.	*Ophidascaris* sp.	*Physaloptera* sp.	*Porrocaecum* sp.	Acanthocephalan cystacanth
Bufonidae																								
Bufo glaberrimus Günther, 1868 (Cundinamarca toad)	1	Terrestrial	—	—	—	—	—	100	—	—	—	100*	—	—	—	—	—	—	—	—	—	—	—	—
Bufo marinus (Linnaeus, 1758) (cane toad)	5	Terrestrial	—	60	20	—	20	20	—	—	—	—	—	—	—	—	—	—	—	—	—	20	—	—
Bufo typhonius (Linnaeus, 1758) (South American common toad)	27	Terrestrial	—	—	4	—	—	33	56	—	11	63*	—	—	—	—	—	—	—	—	—	33	—	4
Dendrobatidae																								
Colostethus marchesianus (Melin, 1941) (dull rocket frog)	28	Terrestrial	—	11*	—	—	—	—	68	—	—	—	—	—	—	—	—	—	—	—	—	4	—	—
Epipedobates femoralis (Boulenger, 1884) (brillant-thighed poison frog)	15	Terrestrial	—	—	—	—	—	—	60	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Epipedobates pictus (Tschudi, 1838) (spot-legged poison frog)	13	Terrestrial	—	—	—	—	—	85	—	—	—	15*	—	—	—	—	—	—	—	—	—	—	—	—
Hylidae																								
Hyla boans (Linnaeus, 1758) (rusty treefrog)	3	Arboreal	—	—	—	—	67	—	—	—	—	—	—	—	—	—	—	—	—	—	—	33	—	—
Hyla brevifrons Duellman and Crump, 1974 (Crump's treefrog)	2	Arboreal	—	—	—	—	100	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hyla calcarata Troschel, 1848 (Troschel's treefrog)	2	Arboreal	—	—	—	—	50	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hyla fasciata Günther, 1859 (Gunther's banded treefrog)	21	Arboreal	—	—	—	—	86	5	—	—	10	24*	—	—	—	—	—	—	—	5	—	14	—	—
Hyla granosa Boulenger, 1882 (Demerara Falls treefrog)	12	Arboreal	—	—	—	—	21	—	—	—	—	—	—	—	—	—	—	—	—	8	—	8	—	—

Table 1. Continued.

Host	N	Habitat	Mature helminths																Larval helminths					
			Glypthelmins parva	*Cylindrotaenia americana*	*Aplectana hylambatis*	*Batracholandros spectatus*	*Cosmocerca brasiliense*	*Cosmocerca parva*	*Cosmocerca padicipinus*	*Cosmocercella phyllomedusae*	*Ochoterenella vellardi*	*Oswaldocruzia lopesi*	*Physalopteroides venancioi*	*Raillietnema gubernaculatum*	*Schrankiana inconspicata*	*Schrankiana larvata*	*Schrankiana schrankai*	*Schrankianella brasili*	Acuarioidae gen. sp.	*Brevimulticaecum* sp.	*Ophidascaris* sp.	*Physaloptera* sp.	*Porrocaecum* sp.	Acanthocephalan cystacanth
Hyla koechlini Duellman and Trueb, 1989 (Koechlin's tree-frog)	8	Arboreal	—	—	—	—	100	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hyla leali Bokermann, 1964 (Leal's treefrog)	6	Arboreal	—	—	—	—	83	—	—	—	—	—	—	—	—	—	—	—	—	—	—	17	—	—
Hyla leucophyllata (Beireis, 1783) (Beireis' treefrog)	12	Arboreal	17*	—	—	—	58	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	—	—
Hyla marmorata (Laurenti, 1768) (marbled treefrog)	2	Arboreal	—	—	—	—	50	—	—	—	—	—	—	—	—	—	—	—	—	—	—	50	—	—
Hyla parviceps Boulenger, 1882 (Sarayacu treefrog)	25	Arboreal	—	—	—	—	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hyla rhodopepla Günther, 1859 (red-skirted treefrog)	23	Arboreal	—	—	—	—	17	—	—	—	—	—	—	—	—	—	—	—	9	—	—	—	—	—
Hyla schubarti Bokermann, 1963 (Schubart's Rondonia treefrog)	20	Arboreal	—	—	—	—	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Osteocephalus taurinus Steindachner, 1862 (Manaus slender-legged treefrog)	16	Arboreal	—	—	—	13*	50	—	—	—	6*	—	13*	—	—	—	—	—	—	—	—	13	—	—
Phrynohyas coriacea (Peters, 1867) (Surinam golden-eyed treefrog)	20	Arboreal	5*	—	—	—	65	—	—	—	—	10*	15*	—	—	—	—	—	—	30	—	15	—	—
Phrynohyas venulosa (Laurenti, 1768) (veined treefrog)	9	Arboreal	—	—	—	11*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	—	—
Phyllomedusa atelopoides Duellman, Cadle, and Cannatella, 1988 (toady leaf frog)	3	Terrestrial	—	—	—	—	66	33	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Phyllomedusa palliata Peters, 1872 (jaguar leaf frog)	5	Arboreal	—	—	—	—	20	—	—	80*	—	—	—	—	—	—	—	—	—	—	—	—	—	20

Table 1. Continued.

Host	N	Habitat	Mature helminths																Larval helminths					
			Glypthelmins parva	*Cylindrotaenia americana*	*Aplectana hylambatis*	*Batracholandros spectatus*	*Cosmocerca brasiliense*	*Cosmocerca parva*	*Cosmocerca podicipinus*	*Cosmocercella phyllomedusae*	*Ochoterenella vellardi*	*Oswaldocruzia lopesi*	*Physalopteroides venancioi*	*Raillietnema gubernaculatum*	*Schrankiana inconspicata*	*Schrankiana larvata*	*Schrankiana schrankai*	*Schrankianella brasili*	Acuarioidae gen. sp.	*Brevimulticaecum* sp.	*Ophidascaris* sp.	*Physaloptera* sp.	*Porrocaecum* sp.	Acanthocephalan cystacanth
Phyllomedusa tomopterna (Cope, 1868) (tiger-striped leaf frog)	7	Arboreal	—	—	—	—	57	—	—	14*	—	—	—	—	—	—	—	—	—	—	14	14	—	—
Phyllomedusa vaillanti Boulenger, 1882 (white-lined leaf frog)	7	Arboreal	—	—	—	—	29	—	—	29*	—	—	14*	—	—	—	—	—	—	—	—	—	—	—	—
Scarthyla ostinodactyla Duellman and de Sá, 1988 (Madre de Dios treefrog)	21	Arboreal	—	—	—	—	90	10	—	—	—	—	—	—	—	—	—	—	—	5	—	—	—	—
Scinax garbei (Miranda-Ribeiro, 1926) (Eirunepe snouted tree-frog)	12	Arboreal	—	—	—	—	50	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Scinax icterica Duellman and Wiens, 1993 (yellow snouted treefrog)	18	Arboreal	—	—	—	—	89	11	—	—	—	—	—	—	—	—	—	—	—	—	—	11	—	—
Scinax pedromedinai (Henle, 1991) (Henle's snouted treefrog)	25	Arboreal	8*	4	—	—	32	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4
Scinax ruba (Laurenti, 1768) (red snouted treefrog)	2	Arboreal	—	—	—	—	—	—	—	—	—	—	50*	—	—	—	—	—	—	—	—	50	—	—
Sphaenorhynchus lacteus (Daudin, 1802) (Orinoco lime treefrog)	14	Arboreal	—	—	—	—	43	—	—	—	—	—	—	—	—	—	—	—	—	7	—	—	—	—
Leptodactylidae																								
Adenomera andreae Müller, 1923 (lowland tropical bullfrog)	14	Terrestrial	—	—	—	—	14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Adenomera hylaedactyla (Cope, 1868) (Napo's tropical bullfrog)	20	Terrestrial	—	—	—	—	15	—	—	—	—	—	5*	—	—	—	—	—	—	—	—	—	—	—
Edalorhina perezi Jiménez de la Espada, 1870 (Perez's snouted frog)	28	Terrestrial	—	—	—	—	4	4	—	—	—	—	4*	—	—	—	—	—	4	—	—	7	—	—

Table 1. Continued.

Host	N	Habitat	Mature helminths																Larval helminths					
			Glypthelmins parva	*Cylindrotaenia americana*	*Aplectana hylambatis*	*Batracholandros spectatus*	*Cosmocerca brasiliense*	*Cosmocerca parva*	*Cosmocerca podicipinus*	*Cosmocercella phyllomedusae*	*Ochoterenella vellardi*	*Oswaldocruzia lopesi*	*Physalopteroides venancioi*	*Raillietnema gubernaculatum*	*Schrankiana inconspicata*	*Schrankiana larvata*	*Schrankiana schrankai*	*Schrankianella brasili*	Acuarioidae gen. sp.	*Brevimulticaecum* sp.	*Ophidascaris* sp.	*Physaloptera* sp.	*Porrocaecum* sp.	Acanthocephalan cystacanth
Eleutherodactylus cruralis (Boulenger, 1902) (La Paz robber frog)	5	Arboreal	—	—	—	—	20	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20	—	—
Eleutherodactylus fenestratus (Steindachner, 1864) (Río Mamore robber frog)	29	Arboreal	—	—	—	—	14	21	—	—	—	10*	3*	—	—	—	—	—	—	—	—	24	—	—
Eleutherodactylus imitatrix Duellman, 1978 (imitator robber frog)	11	Arboreal	—	—	—	—	—	—	18	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Eleutherodactylus peruvianus (Melin, 1941) (Peru robber frog)	21	Arboreal	—	—	—	—	19	14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Eleutherodactylus toftae Duellman, 1978 (Pachitea robber frog)	30	Arboreal	—	—	—	—	3	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Leptodactylus bolivianus Boulenger, 1898 (Bolivian white-lipped frog)	14	Terrestrial	—	—	64	—	13	—	—	—	—	50	14	—	—	—	—	—	—	13	—	64	—	—
Leptodactylus leptodactyloides (Andersson, 1945) (no common name)	14	Terrestrial	—	—	29	—	—	21	29	—	—	—	—	—	—	—	—	—	—	—	—	43	—	—
Leptodactylus mystaceus (Spix, 1824) (basin white-lipped frog)	12	Terrestrial	—	—	—	—	—	23	—	—	—	—	17*	—	—	17*	58*	—	—	—	—	42	—	—
Leptodactylus pentadactylus (Laurenti, 1768) (South American bullfrog)	6	Terrestrial	—	—	33	—	17	—	—	—	—	—	—	—	—	17	—	17	—	17	—	17	—	—
Leptodactylus petersii (Steindachner, 1864) (Peter's frog)	24	Terrestrial	—	—	—	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Leptodactylus rhodonotus (Günther, 1868) (Peru white-lipped frog)	22	Terrestrial	—	—	50	—	—	—	—	—	—	—	—	—	23*	—	—	—	—	—	—	14	—	—
Lithodytes lineatus (Schneider, 1799) (gold-striped frog)	2	Terrestrial	—	—	100	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	50	—	—

Table 1. Continued.

Host	N	Habitat	Mature helminths																Larval helminths					
			Glypthelmins parva	*Cylindrotaenia americana*	*Aplectana hylambatis*	*Batracholandros spectatus*	*Cosmocerca brasiliense*	*Cosmocerca parva*	*Cosmocerca podicipinus*	*Cosmocercella phyllomedusae*	*Ochoterenella vellardi*	*Oswaldocruzia lopesi*	*Physaloptéroides venancioi*	*Raillietnema gubernaculatum*	*Schrankiana inconspicata*	*Schrankiana larvata*	*Schrankiana schrankai*	*Schrankianella brasili*	Acuarioidae gen. sp.	*Brevimulticaecum* sp.	*Ophidascaris* sp.	*Physaloptera* sp.	*Porrocaecum* sp.	Acanthocephalan cystacanth
Microhylidae																								
Ctenophryne geayi (Mocquard, 1904) (brown egg frog)	2	Terrestrial	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	50	—	—
Elachistocleis ovalis (Schneider, 1799) (common oval frog)	11	Terrestrial	—	—	27	—	—	9	—	—	—	—	—	18*	—	—	—	—	—	—	—	—	—	—
Hamptophryne boliviana (Parker, 1927) (Bolivian bleating frog)	25	Terrestrial	—	—	—	—	—	32	—	—	—	4*	—	—	—	—	—	—	—	—	—	47	—	—
Pipidae																								
Pipa pipa (Linnaeus, 1758) (Surinam toad)	6	Aquatic	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	83	—
Pseudidae																								
Pseudis paradoxa (Linnaeus, 1758) (swimming frog)	2	Aquatic	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	100	—	—

* New host record.

Table 2. U.S. National Parasite Collection (USNPC) accession numbers for helminths collected from anuran hosts in Reserva Cuzco Amazónico, Peru.

Host	Helminth, USNPC number
Adenomera andreae	*Cosmocerca brasiliense,* 89572
Adenomera hylaedactyla	*Cosocerca brasiliense,* 89573; *Physalopoteroides venancioi,* 89574
Bufo glaberrimus	*Cosmocerca parva,* 89486; *Oswaldocruzia lopesi,* 89487
Bufo marinus	*Cylindrotaenia americana,* 89488; *Aplectana hylambatis,* 89489; *Cosmocerca brasiliense,* 89490; *Cosmocerca parva,* 89491; *Physaloptera* sp. (larvae), 89492
Bufo typhonius	*Aplectana hylambatis,* 89493; *Cosmocerca parva,* 89494; *Cosmocerca podicipinus,* 89495; *Ochoterenella vellardi,* 89496; *Oswaldocruzia lopesi,* 89497; *Physaloptera* sp. (larvae), 89498; acanthocephalan cystacanths, 89499
Colostethus marchesianus	*Cylindrotaenia americana,* 89500; *Cosmocerca podicipinus,* 89501; *Physaloptera* sp. (larvae), 89502
Ctenophryne geayi	*Physaloptera* sp. (larvae), 89619
Edalorhina perezi	*Cosmocerca brasiliense,* 89575; *Cosmocerca parva,* 89576; *Physalopteroides venancioi,* 89577; acuarioid larvae, 89578; *Physaloptera* sp. (larvae), 89579
Elachistocleis ovalis	*Aplectana hylambatis,* 89620; *Cosmocerca parva,* 89621; *Raillietnema gubernaculatum,* 89622
Eleutherodactylus cruralis	*Cosmocerca brasiliense,* 89580; *Physaloptera* sp. (larvae), 89581
Eleutherodactylus fenestratus	*Cosmocerca brasiliense,* 89582; *Cosmocerca parva,* 89583; *Oswaldocruzia lopesi,* 89584; *Physalopteroides venancioi,* 89585; *Physaloptera* sp. (larvae), 89586
Eleutherodactylus imitatrix	*Cosmocerca podicipinus,* 89587
Eleutherodactylus peruvianus	*Cosmocerca brasiliense,* 89588; *Cosmocerca parva,* 89589
Eleutherodactylus toftae	*Cosmocerca brasiliense,* 89590; *Cosmocerca parva,* 89591
Epipedobates femoralis	*Cosmocerca podicipinus,* 89503
Epidedobates pictus	*Cosmocerca parva,* 89504; *Oswaldocruzia lopesi,* 89505
Hamptophryne boliviana	*Cosmocerca parva,* 89623; *Oswaldocruzia lopesi,* 89624; *Physaloptera* sp. (larvae), 89625
Hyla boans	*Cosmocerca brasiliense,* 89506; *Physaloptera* sp. (larvae), 89507
Hyla brevifrons	*Cosmocerca brasiliense,* 89508
Hyla calcarata	*Cosmocerca brasiliense,* 89509
Hyla fasciata	*Cosmocerca brasiliense,* 89510; *Cosmocerca parva,* 89511; *Ochoterenella vellardi,* 89512; *Oswaldocruzia lopesi,* 89513; *Brevimulticaecum* sp. (larvae), 89514; *Physaloptera* sp. (larvae), 89515
Hyla granosa	*Cosmocerca brasiliense,* 89516; *Brevimulticaecum* sp. (larvae), 89517; *Physaloptera* sp. (larvae), 89518
Hyla koechlini	*Cosmocerca brasiliense,* 89519
Hyla leali	*Cosmocerca brasiliense,* 89520; *Physaloptera* sp. (larvae), 89521
Hyla leucophyllata	*Glypthelmins parva,* 89522; *Cosmocerca brasiliense,* 89523; *Physaloptera* sp. (larvae), 89524
Hyla marmorata	*Cosmocerca brasiliense,* 89525; *Physaloptera* sp. (larvae), 89526
Hyla parviceps	*Cosmocerca brasiliense,* 89527
Hyla rhodopepla	*Cosmocerca brasiliense,* 89528; acuarioid larvae, 89529
Hyla schubarti	*Cosmocerca brasiliense,* 89530
Leptodactylus bolivianus	*Aplectana hylambatis,* 89592; *Cosmocerca brasiliense,* 89593; *Oswaldocruzia lopesi,* 89594; *Physalopteroides venancioi,* 89595; *Brevimulticaecum* sp. (larvae), 89596; *Physaloptera* sp. (larvae), 89597
Leptodactylus leptodactyloides	*Aplectana hylambatis,* 89598; *Cosmocerca parva,* 89599; *Cosmocerca podicipinus,* 89600; *Physaloptera* sp. (larvae), 89601
Leptodactylus mystaceus	*Cosmocerca parva,* 89602; *Physalopteroides venancioi,* 89603; *Schrankiana larvata,* 89604; *Schrankiana schranki,* 89605; *Physaloptera* sp. (larvae), 89606
Leptodactylus pentadactylus	*Aplectana hylambatis,* 89607; *Cosmocerca brasiliense,* 89608; *Schrankiana larvata,* 89609; *Schrankianella brasili,* 89610; *Brevimulticaecum* sp. (larvae), 89611; *Physaloptera* sp. (larvae), 89612
Leptodactylus petersii	*Cosmocerca brasiliense,* 89613
Leptodactylus rhodonotus	*Aplectana hylambatis,* 89614; *Schrankiana inconspicata,* 89615; *Physaloptera* sp. (larvae), 89616
Lithodytes lineatus	*Aplectana hylambatis,* 89617; *Physaloptera* sp. (larvae), 89618
Osteocephalus taurinus	*Batracholandros spectatus,* 89531; *Cosmocerca brasiliense,* 89532; *Ochoterenella vellardi,* 89533; *Physalopteroides venancioi,* 89534; *Physaloptera* sp. (larvae), 89535

Table 2. Continued.

Host	Helminth, USNPC number
Phrynohyas coriacea	*Glypthelmins parva,* 89536; *Cosmocerca brasiliense,* 89537; *Oswaldocruzia lopesi,* 89538; *Physalopteroides venancioi,* 89539; *Brevimulticaecum* sp. (larvae), 89540; *Physaloptera* sp. (larvae), 89541
Phrynohyas venulosa	*Batracholandros spectatus,* 89542; *Physaloptera* sp. (larvae), 89543
Phyllomedusa atelopoides	*Cosmocerca brasiliense,* 89544; *Cosmocerca parva,* 89545
Phyllomedusa palliata	*Cosmocerca brasiliense,* 89546; *Cosmocercella phyllomedusae,* 89547; acanthocephalan cystacanth, 89548
Phyllomedusa tomopterna	*Cosmocerca brasiliense,* 89549; *Cosmocercella phyllomedusae,* 89550; *Ophioascaris* sp. (larvae), 89551; *Physaloptera* sp. (larvae), 89552
Phyllomedusa vaillanti	*Cosmocerca brasiliense,* 89553; *Cosmocercella phyllomedusae,* 89554; *Physalopteroides venancioi,* 89555
Pipa pipa	*Porrocaecum* sp. (larvae), 89626
Pseudis paradoxa	*Physaloptera* sp. (larvae), 89627
Scarthyla ostinodactyla	*Cosmocerca brasiliense,* 89556; *Cosmocerca parva,* 89557; *Brevimulticaecum* sp. (larvae), 89558
Scinax garbei	*Cosmocerca brasiliense,* 89559; *Cosmocerca parva,* 89560
Scinax icterica	*Cosmocerca brasiliense,* 89561; *Cosmocerca parva,* 89562; *Physaloptera* sp. (larvae), 89563
Scinax pedromedinai	*Cylindrotaenia americana,* 89564; *Glypthelmins parva,* 89565; *Cosmocerca brasiliense,* 89566; acanthocephalan cystacanth, 89567
Scinax ruber	*Physaloptera* sp. (larvae), 89569
Sphaenororhynchus lacteus	*Cosmocerca brasiliense,* 89570; *Brevimulticaecum* sp. (larvae), 89571

S. larvata, S. schrankai, S. brasili, and larvae of *Porrocaecum* sp. were not found in the aboreal group. The terrestrial species harbored 1,493 helminths (74.7 ± 101.9 helminth individuals/infected host) assigned to 17 species (3.2 ± 1.9 helminth species/host species). *Glypthelmins parva, B. spectatus, C. phyllomedusae,* and larvae of *Ophidascaris* sp. and *Porrocaecum* sp. were not found in the terrestrial group. The aquatic species harbored 91 larvae assigned to 2 species (1 helminth species/host species). When all helminth species were included, there was no significant difference in number of helminth species harbored between arboreal and terrestrial host species (ANOVA, $F = 1.7$, df = 1, 47, $P > 0.05$); but there was significant difference in the number of individual helminths harbored between arboreal and terrestrial host species (ANOVA, $F = 7.8$, df = 1, 47, $P < 0.01$). A similar pattern was present when species represented by larvae only are excluded from testing (ANOVA, $F = 3.3$, $P > 0.05$; $F = 7.59$, $P < 0.01$, respectively). Aquatic host species were not included in statistical tests because of low helminth species numbers.

Discussion

All of the helminths encountered in this study have been reported in other South American anurans. *Glypthelmins parva* has been reported from the Criolla frog *Leptodactylus ocellatus* (Linnaeus, 1758) from Brazil and Uruguay (Travassos, 1924; Freitas, 1941). *Hyla leucophyllata, P. coriacea,* and *S. pedromedinai* represent new host records, which brings the host list to 4 species of frogs from 2 families, Hylidae and Leptodactylidae. Peru is a new locality record.

The life history of *G. parva* has apparently not been studied, but the type species, *Glypthelmins quieta* (Stafford, 1900) Stafford, 1905 has been examined and found to have cercariae that when released from the snail host swim to the surface and remain infective for about 72 hr. Cercariae penetrate the skin of frogs and encyst beneath the epidermis; encysted metacercariae are introduced into the gut of the frog host when the frog ingests its own cast skin after molting (Smyth and Smyth, 1980). It is interesting to note that, in this study, only arboreal anuran species harbored *G. parva.*

Cylindrotaenia americana is a common Western Hemisphere cestode species known to infect anurans of the families Bufonidae, Ranidae, Hylidae, and Leptodactylidae (Jones, 1987). Its presence in *C. marchesianus* adds a fifth family, Dendrobatidae, to this list. *Cylindrotaenia americana* has also been reported from ambystomid

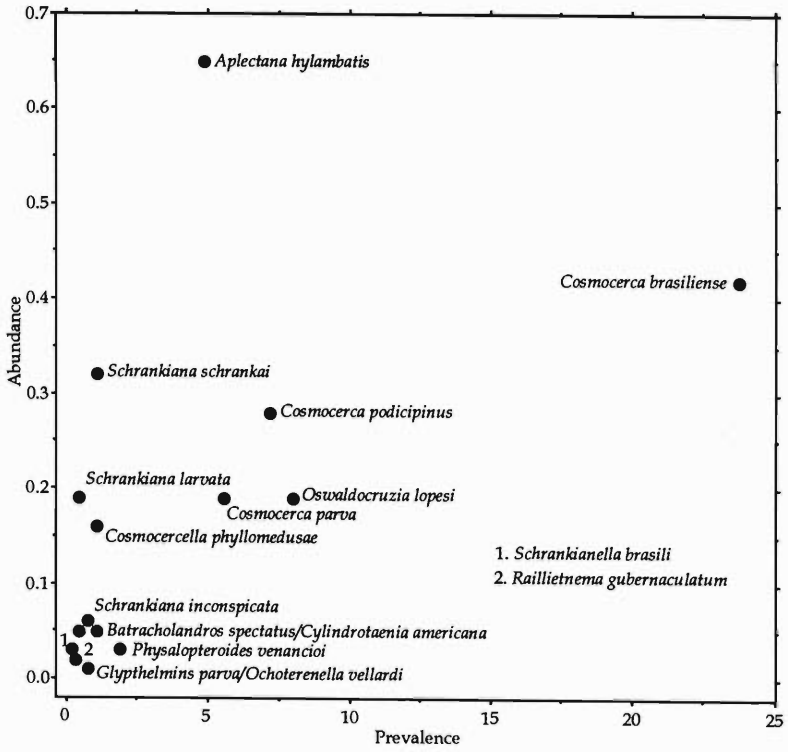

Figure 1. Scatterplot of prevalence and abundance for adult helminths from 51 species of anurans from Reserva Cuzco Amazónico, Peru.

and plethodontid salamanders (Dunbar and Moore, 1979; McAllister and Upton, 1987) and from a scincid lizard (Brooks, 1972). We have found 32 articles in which 47 hosts of *C. americana* were reported. Dyer (1986) suggested that although Neotropical species of *Cylindrotaenia* are morphologically indistinguishable from the Nearctic species, they are probably not conspecific. Jones (1987) recognized *Cylindrotaenia idahoensis* (Waitz and Mehra, 1961) Jones, 1987, a parasite of plethodontid salamanders, as distinct from *C. americana* and indicated the need to re-examine material from other plelthodontid salamanders to determine whether the material is indeed *C. americana.* Joyeux (1924) concluded that *C. americana* has a direct life cycle. Both arboreal and terrestrial species of this study harbored *C. americana.*

Aplectana hylambitis, C. brasiliense, and *C. parva* are common South American anuran parasites. Baker (1987) provided host lists for these 3 species; we know of no reports of additional hosts. Baker (1987) also provided a host list for *O. vellardi,* to which *O. taurinus* is added (this study) as a new host record. Peru is a new locality record.

The remaining nematodes were previously known to infect a single family. *Batracholandros spectatus* was known only from *B. limensis* and *B. trifolium* from Peru (Freitas and Ibañez, 1962; Naupay, 1974). *Osteocephalus taurinus* and *P. venulosa* represent new host records; thus, 2 anuran families have now been reported as hosts, Bufonidae and Hylidae (terrestrial and arboral hosts, respectively). *Physalopteroides venancioi* has been reported only from the Cururu toad *Bufo paracnemis* Lutz, 1925, from Uruguay (Lent et al., 1946). *Osteocephalus taurinus, P. coriacea, P. vaillanti, S. ruba, A. hylaedactyla, E. perezi, E. fenestratus,* and *L. mystaceus* are new host records; 3 families are now known as hosts: Bufonidae, Hylidae, and Leptodactylidae (terrestrial and arboral hosts). *Raillietnema gubernaculatum* has been reported from *B. limensis* from Peru and *B. ictericus* from Brazil (Gomes, 1964; Freitas and Ibañez, 1965).

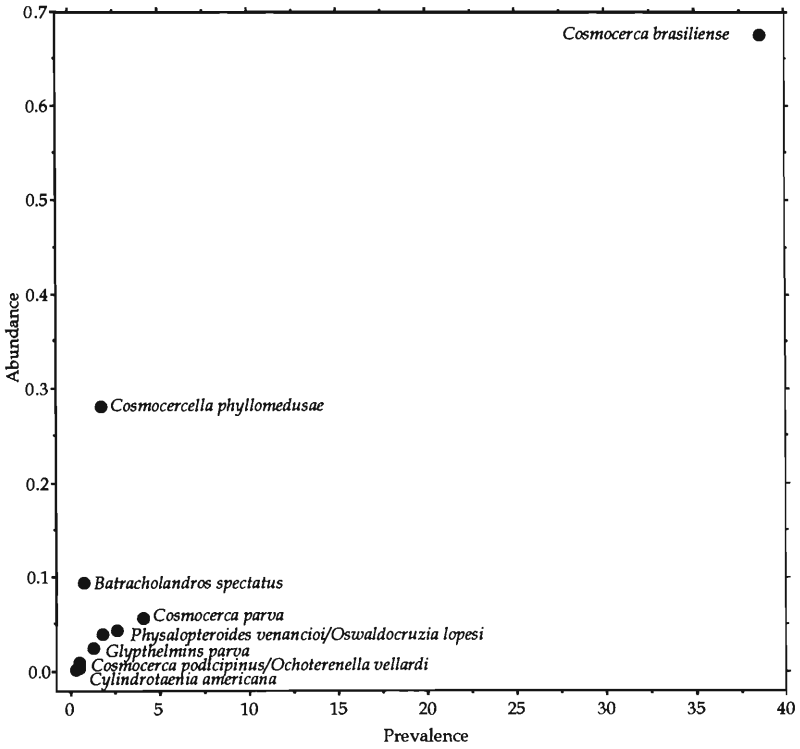

Figure 2. Scatterplot of prevalence and abundance for adult helminths harbored by species of arboreal anurans from Reserva Cuzco Amazónico, Peru.

Elachistocles ovalis is a new host record; Bufonidae and Microhylidae are the host families (terrestrial hosts).

Cosmocercella phyllomedusae was previously known from the orange-legged leaf frog *Phyllomedusa hypocondrialis* (Daudin, 1802), from Paraguay (Baker and Vaucher, 1983). *Phyllomedusa palliata, P. tomopterna,* and *P. vaillanti* represent new host records; 4 species of 1 family (all arboreal) are now known as hosts. Peru is a new locality record.

Oswaldocruzia lopesi, S. inconspiculata, S. larvata, S. schrankai, and *S. brasili* have been reported previously only from species of the family Leptodactylidae. *Oswaldocruzia lopesi* was known only from *L. ocellatus* from Brazil and Uruguay (Freitas and Lent, 1938; Freitas, 1956). *Bufo glaberrimus, B. typhonius, E. pictus, H. fasciata, P. coriacea, E. fenestratus,* and *H. boliviana* are new host records for *O. lopesi*; 4 families are now known to serve as hosts: Bufonidae, Hylidae, Leptodactylidae, and Microhylidae (arboreal and terrestrial hosts). *Schrankiana inconspiculata* has been reported from the labyrinth frog *Leptodactylus labyrinthicus* (Spix, 1824) and *L. pentadactylus* from Brazil (Freitas, 1959); *L. rhodonotus* represents a new host record. *Schrankiana larvata* has been reported from the rufous frog *Leptodactylus fuscus* (Schneider, 1799), *L. labyrinthicus,* and *L. pentadactylus* from Brazil (Vaz, 1933; Freitas, 1959); *L. mystaceus* repesents a new host record. *Schrankiana schranki* was known only from *L. pentadactylus* from Brazil and Ecuador (Travassos, 1925; Dyer and Altig, 1977); *L. mystaceus* repesents a new host record. *Schrankianella brasili* has been reported only from *L. pentadactylus* and *L. labyrinthicus* from Brazil (Travassos, 1927; Fahel, 1952). Peru is a new locality record.

Of the 2,156 helminths found in this study, 1,829 (85%) were individuals of species that reach maturity in anurans and were assigned to 14 species of nematodes distributed among 5 superfamiles: Cosmocercoidea, Filarioidea, Physalopteroidea, Oxyuroidea, and Trichostrongylo-

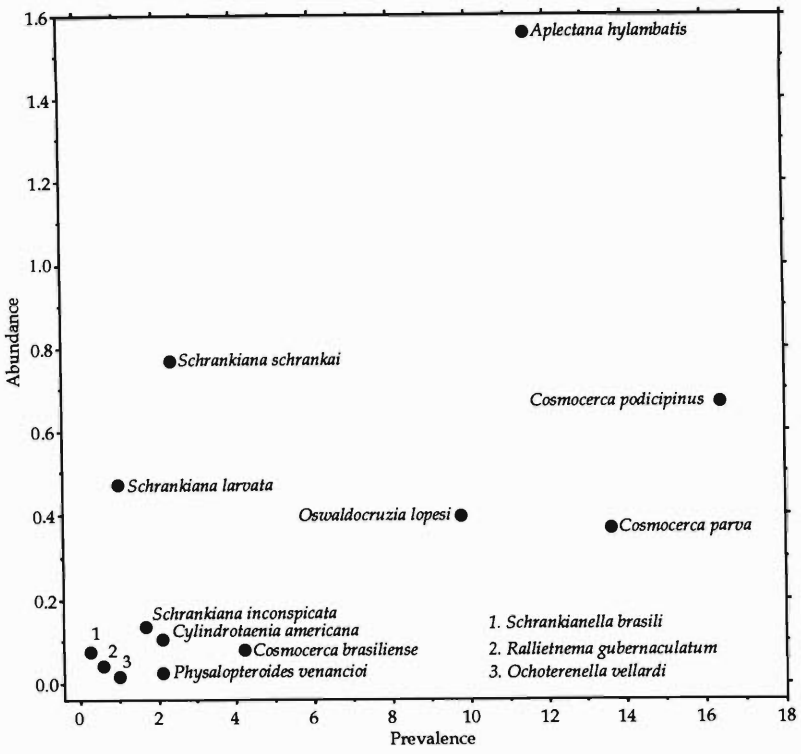

Figure 3. Scatterplot of prevalence and abundance for adult helminths harbored by species of terrestrial anurans from Reserva Cuzco Amazónico, Peru.

idea. Members of the Oxyuroidea are strictly monoxenous, and eggs dispersed into the environment can become a continual source for oral infection (Anderson, 2000). In this study, 1 oxyuroid species, *B. spectatus,* was harbored by arboreal host species. Two families of the Cosmocercoidea were present: Cosmocercidae and Atractidae. Cosmocercids produce eggs that larvate in utero or develop into first stage larvae in the environment and when hatched molt twice to form the infective larvae; the final host becomes infected either orally or by skin penetration (Anderson, 2000). The eggs of atractids develop into third stage larvae in utero and are autoinfective. In this study, no atractids were found in aboreal host species and the cosmocercid *C. phyllomedusae* was absent from terrestrial host species. Physalopteroids require an insect intermediate host, filarioids are all transmitted by haematophagous arthropods, and trichostrongyloid infections may occur by skin penetration or ingestion of third-stage larvae (Anderson, 2000). Both arboreal and terrestrial host species harbored members of these three superfamilies.

The 327 (15%) remaining helminths were larvae of species that do not reach maturity in anurans. All of these species require invertebrate intermediate hosts (Anderson, 2000); thus, the presence of these larvae in insectivorous host species was anticipated. The lack of adult acanthocephalans in this sample is in agreement with the results of studies of North American anurans but is in contrast with studies of European anurans in which helminth communities regularly include adult Acanthocephala (McAlpine, 1996). Anurans may serve as transport hosts for encysted larvae of *Brevimulticaecum* sp., *Ophaidascris* sp., *Porrocaecum* sp., species of the family Acuariidae, and acanthocephalan cystacanths (Anderson, 2000). Species of *Physaloptera* are parasites of mammals and reptiles, and do not complete their life cycles in amphibians (Goldberg et al., 1993). In this sample, there were no encysted physalopterids.

Bush et al. (1997) presented a hierarchy of parasite community terms, including infracommunity (helminths in a single host), component community (helminths of a host species), and supracommunity (helminths in sympatric hosts). Figure 1 is a scatterplot of prevalence and abundance, which can be used to categorize important helminth species within a supracommunity. Because the species represented by larvae only do not reach maturity in frogs or toads, we have excluded them from Figure 1. Because this plot gives equal weight to prevalence and abundance, the most important species of the supracommunity appear in the upper right quadrant of the graph, and less important species appear in the lower left quadrant. Helminth species appearing in the upper left quadrant occur in high numbers but in few hosts. The most important helminth in the supracommunity of anuran hosts from the Reserva Cuzco Amazónico was *C. brasiliense* (I = 50), followed by *A. hylambatis* (I = 32) and *S. schrankai* (I = 13).

However, when host species are separated into habitat groups and a second method of analysis of host–helminth interaction (see Brandt [1936] for habitat categories) is applied, a different conclusion is reached. For arboreal host species (Fig. 2), *C. brasiliense* was again the most common helminth (I = 129), but *A. hylambatis* was absent (I = 0). For terrestrial host species (Fig. 3), *A. hylambatis* was most important (I = 50), but *C. brasiliense* was of minor importance (I = 8). Too little is known about the life cycles of these 2 species of nematodes to speculate on this difference, but the reported modes of infection, oral infection by *Aplectana* spp. and skin penetration by *Cosmocerca* spp. (see Anderson, 2000), may play an important role.

A third method of examining host–helminth interaction is family helminth lists. Seven anuran families were represented in this study (Table 3). *Batracholandros spectatus, O. lopesi,* and *R. gubernaculatum* have previously been reported from the Bufonidae (Lent et al., 1946; Freitas and Ibañez, 1962, 1965). Thus, all of the helminths found in this study, with the exception of the atractids *S. inconspicata, S. larvata, S. schrankai,* and *S. brasili* and the cosmocercid *C. phyllomedusae,* are known to infect at least 2 anuran families. The atractids are autoinfective (Anderson, 2000). Petter (1966) suggested that tortoises become infected by atractids only after attaining sexual maturity and thought that hel-

Table 3. Presence of helminth species by anuran family found in Reserva Cuzco Amazónico, Peru.

Anuran family	Helminths																
	Glypthelmins parva	*Cylindrotaenia americana*	*Aplectana hylambatis*	*Batracholandros spectatus*	*Cosmocerca brasiliense*	*Cosmocerca parva*	*Cosmocerca podicipinus*	*Cosmocercella phyllomedusae*	*Ochoterenella vellardi*	*Oswaldocruzia lopesi*	*Physaloptera venancioi*	*Raillietnema gubernaculatum*	*Schrankiana inconspicata*	*Schrankiana larvata*	*Schrankiana schrankai*	*Schrankianella brasili*
Bufonidae	—	X	X	—	X	X	X	—	X	X	—	—	—	—	—	—
Dendrobatidae	—	X	—	—	—	X	X	—	—	X	—	—	—	—	—	—
Hylidae	X	X	—	X	X	X	—	X	X	X	X	—	—	—	—	X
Leptodactylidae	—	—	X	—	X	X	X	—	—	X	X	—	X	X	X	X
Microhylidae	—	—	X	—	—	X	—	—	—	X	—	X	—	—	—	—
Pipidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pseudidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

minth transmission occurred during mating. Some unknown aspect of leptodactylid behavior may be important to infection by atractids. The life cycle of *C. phyllomedusae* has apparently not been studied; the mode of tranmission to species of *Phyllomedusa* is not known. The presence of too few individuals (<10) in 20 (39%) of the anuran genera examined here precludes analysis of genera helminth lists. The best measure of the infection plasticity of a helminth species may be its host list.

Aho (1990) compiled distributional patterns for anurans in general and reported the mean (±SE) total number of helminth species per host species as 3.54 ± 0.24 (range, 0–9). When helminth species represented by larvae only were excluded from our analyses, the number of helminth species harbored per host species was 1.96 ± 0.17 (range, 0–5). The reason that our overall value is about half of that reported by Aho is at present unknown, but it may be related to regional (tropical vs. temperate or tropical vs. worldwide) helminth distributional patterns (with the exception of *C. americana,* all helminths in this study are known only from the Neotropical biogeographical realm), the small number of individuals examined in some species (39% of the host samples contained fewer than 10 individuals), or our inability to examine lungs and bladders of these anurans, where we would have expected to find several species of extraintestinal helminths (Chandler, 1983).

The data presented here suggest that Peruvian anurans are infected by helminth generalists, i.e., helminths not restricted to a single host species; all helminths examined in this study are now known to infect at least 2 host species. The supracommunity was composed of 16 species of anuran helminths, with some helminths more important to arboreal host species and some more important to terrestrial species. In each host species, the composite helminth community was depauperate.

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Endohelminths of White Croaker (*Genyonemus lineatus*) from Los Angeles Harbor, Southern California, U.S.A.

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ABSTRACT: We examined 243 white croakers *Genyonemus lineatus* (Ayres, 1855) from Los Angeles Harbor for endohelminths in 1997 and 1998. Twelve helminth taxa were found: 1 Acanthocephala, 2 Cestoidea, 5 Digenea, and 4 Nematoda. Cestodes (tetraphyllidean plerocercoids and *Lacistorhynchus dollfusi* Beveridge and Sakanari, 1987) dominated the helminth assemblage of croakers. A nematode, *Anisakis* sp., and an acanthocephalan, *Corynosoma* sp., were also common in this host. Observed differences in the seasonal prevalence of *Anisakis* sp., *Corynosoma* sp., *L. dollfusi,* and tetraphyllideans may reflect seasonal fluctuations in invertebrate host availability to croaker. Age and gender differences in parasite intensity occurred for the dominant cestodes, i.e., tetraphyllideans. Female croakers and croakers that were 2 yr old were more likely to be infected with the plerocercoids of tetraphyllidean cestodes.

KEY WORDS: endohelminths, white croaker, Pisces, *Genyonemus lineatus,* Acanthocephala, Cestoidea, Digenea, Los Angeles Harbor, California, U.S.A.

White croaker *Genyonemus lineatus* (Ayres, 1855) is a popular sportfish in southern and central California. It has been the subject of many studies, including aspects of croaker life history (Love et al., 1984), bioaccumulation of toxicants in croaker tissues (Castle and Woods, 1972), and histopathological changes in croakers inhabiting polluted waters (Stehr et al., 1997). White croaker also serves as an indicator species in pollution-monitoring studies of Los Angeles Harbor that are conducted by the City of Los Angeles' Hyperion Treatment Plant ("Hyperion") (Huang, 1998).

One aspect of white croaker biology that has received little attention is the composition of its endohelminth fauna. Helminths previously reported from white croaker include *Lacistorhynchus dollfusi* Beveridge and Sakanari, 1987, *Stephanostomum californicum* Manter and Van Cleave, 1951, and *Anisakis* sp. (Love and Moser, 1983). However, previous studies on parasites of croaker did not quantify parasitism or follow parasitism in this host species over time. Here, we report on the endohelminths infecting white croaker from Los Angeles Harbor off southern California and examine the effect of season, host age, and sex on parasitism in croakers.

Materials and Methods

Two hundred forty-three white croaker from Los Angeles Harbor (33°43′N, 118°17′W) were examined for helminths. The fish were obtained from otter trawls of 2 research vessels, the *Vantuna* (owned and operated by Occidental College in Eagle Rock, California) and the *Marine Surveyor* (owned by the City of Los Angeles and operated by the Environmental Monitoring Division at Hyperion). Fish were sampled seasonally from these trawls in August 1997 (summer), November 1997 (fall), February 1998 (winter), and May 1998 (spring). Bottom trawls for fish in the harbor ranged in depth from 9 to 20 m.

Fish removed from trawls were kept on ice and transported to the laboratory within 5 hr of capture. Based on dissections of nonfrozen fish after this time period, fish harbored live, mobile parasites. Fish were measured and weighed, and their otoliths were removed for age determination prior to preservation of fish tissue. Otoliths of each fish were sectioned using the techniques of Love et al. (1984), and visible growth annuli were counted.

The quick-freezing technique of Bush and Holmes (1986) was used to preserve whole small fish and the internal organs of large fish. Fish were later thawed and necropsied. Fish organs examined for helminths included the heart, liver, gallbladder, spleen, and the entire gastrointestinal tract. Parasites found were sorted into major taxonomic groups, cleaned, counted, and fixed. Digeneans, cestodes, and acanthocephalans were fixed in alcohol–formalin–acetic acid (AFA), stained with Semichon's acetocarmine, and mounted in Canada balsam. Nematodes were fixed in 70% glycerin alcohol, cleared, and examined as temporary mounts in glycerin.

Prevalence, intensity, and mean abundance (as defined by Bush et al., 1997) were calculated. Chi-square analyses (2 × 2 contingency table analyses) were performed to determine whether the prevalence of each helminth was independent of season. Because parasite intensity data were not normally distributed, differences in mean intensities were analyzed using nonparametric tests. Mean parasite intensities were com-

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Table 1. Prevalence, mean intensity, mean abundance, and location of helminths infecting 243 white croaker from Los Angeles Harbor, 1997 to 1998.

Taxon	Prevalence (no. infected) (%)	Intensity ($\bar{x}$ ± SE)	Abundance ($\bar{x}$ ± SE)	Location in host*
Digenea				
Manteriella sp.	2 (1)	6.5 ± 5.5	0.1 ± 0.1	P, I
Stephanostomum spp.†	30 (12)	2.7 ± 0.4	0.3 ± 0.1	P, I
Aponurus sp.	4 (2)	4.3 ± 1.3	0.1 ± 0.1	S, I
Lecithochirium sp.	2 (1)	1.0 ± 0.0	0.1 ± 0.1	I
Zoogonoides sp.	4 (2)	3.0 ± 1.2	0.1 ± 0.0	I
Cestoidea				
Lacistorhynchus dollfusi	115 (47)	16.9 ± 1.8	8.0 ± 15.7	M, P, I
Tetraphyllidean plerocercoids	179 (74)	29.4 ± 2.8	21.6 ± 2.2	S, P, I
Nematoda				
Anisakis sp.	125 (52)	—	—	L, M, S, P, I
Spirocamallanus sp.	22 (9)	1.3 ± 0.1	0.1 ± 0.03	S, PC, I
Juvenile nematode A	8 (3)	2.5 ± 1.2	0.1 ± 0.05	S, I
Juvenile nematode B	3 (1)	3.7 ± 0.9	0.05 ± 0.03	S, I
Acanthocephala				
Corynosoma sp.	100 (41)	3.2 ± 0.3	1.3 ± 0.2	M

* L = liver; M = mesentery; S = stomach; P = pyloric ceca; I = intestine.
† 2 species: *S. californicum* and *S. tristephanum.*

pared for the 4 seasons sampled and for 3 age (yr) classes of hosts (0+, 1+, and 2+) using the Kruskal–Wallis test. The 2+ age class was produced by pooling 2+ and 3+ age classes, because few 3+ fish were caught. The average length of fish in each of the 3 age classes was 80.9 mm (range, 41–174 mm) for 0+ croakers, 148.6 mm (107–269 mm) for 1+ croakers, and 213.5 mm (125–285 mm) for 2+ croakers. The effect of croaker sex on parasite intensity and prevalence of the more common helminths was evaluated using the Z normal approximation to the Mann–Whitney test and the chi-square test, respectively. A significance level of $P \leq 0.05$ was used for all statistical tests performed.

Voucher specimens of the following helminths found in white croaker were deposited in the Harold W. Manter Laboratory of Parasitology (HWML), University of Nebraska–Lincoln: *Anisakis* sp. (HWML 15049), *Corynosoma* sp. (HWML 15047), *Lacistorhynchus dollfusi* (HWML 15048), *Manteriella* sp. (HWML 15045), *Spirocamallanus* sp. (HWML 15050), *Stephanostomum californicum* (HWML 15044), *Stephanostomum tristephanum* McFarlane, 1936 (HWML 15043), and tetraphyllidean plerocercoids (HWML 15046).

Results

Twelve helminth taxa were found infecting white croaker from Los Angeles Harbor (Table 1). Two cestodes dominated the parasite infracommunities of these fish: tetraphyllidean plerocercoids (family Onchobothriidae) and plerocercoids of *Lacistorhynchus dollfusi* (order Trypanorhyncha). Juvenile *Anisakis* sp. and *Corynosoma* sp. were also common in croaker. Parasites found less frequently in white croaker included *Spirocamallanus* sp. and *Stephanostomum* spp. Two species of *Stephanostomum, S. californicum* and *S. tristephanum,* dominated the digenean infracommunity of croaker. An important taxonomic feature used to distinguish these 2 species is the number and rows of circumoral spines, 2 rows in *S. californicum* and 3 rows in *S. tristephanum* (Manter and Van Cleave, 1951). The number of rows of circumoral spines was not visible in all specimens examined because of missing spines, possibly lost during freezing of the host. Genera of Digenea that were rare in these croaker were *Aponurus, Lecithochirium, Manteriella,* and *Zoogonoides.* These 4 genera represented <1% of the total parasites found infecting white croaker.

Prevalence of infection of white croaker with the major helminth taxa varied significantly over the 4 seasons in which the study was conducted (*Anisakis* sp., $\chi^2 = 15.24$, 3 df; *Corynosoma* sp., $\chi^2 = 54.88$, 3 df; *L. dollfusi,* $\chi^2 = 54.01$, 3 df; tetraphyllidean plerocercoids, $\chi^2 = 19.53$, 3 df). Both tetraphyllidean plerocercoids and juveniles

Table 2. Seasonal mean (±SE) intensity and prevalence of helminths infecting white croaker from Los Angeles Harbor, 1997 to 1998.

	1997				1998			
	Summer		Fall		Winter		Spring	
Taxon	Intensity	Prevalence	Intensity	Prevalence	Intensity	Prevalence	Intensity	Prevalence
Anisakis sp.*	—	33	—	53	—	57	—	66
Corynosoma sp.	3.4 ± 1.2	15	3.7 ± 1.8	25	3.3 ± 0.3	72	3.0 ± 0.4	56
Lacistorhynchus dollfusi†	13.2 ± 3.9	26	7.0 ± 2.6	25	8.6 ± 1.3	56	26.3 ± 3.3	82
Tetraphyllidean plerocercoids†	24.8 ± 4.9	65	12.8 ± 3.2	65	19.9 ± 5.0	69	49.1 ± 5.6	95

* Only presence/absence of *Anisakis* sp. was recorded.

† Seasonal mean intensities are significantly different, $P \leq 0.05$.

of *Anisakis* sp. were recruited year-round in white croaker. Over 60% of the croakers sampled were infected with the plerocercoid stage of tetraphyllideans each season (Table 2). Except for the summer of 1997, *Anisakis* sp. infected >50% of white croaker examined. The greatest differences in seasonal prevalence were seen for *Corynosoma* sp. and *L. dollfusi,* with the highest number of hosts infected in winter and spring 1998.

Seasonal mean intensities were compared for *Corynosoma* sp., *L. dollfusi,* and tetraphyllidean plerocercoids but not for *Anisakis* sp. Although anisakine nematodes were present in over half of the fish sampled, only those juveniles infecting the liver, mesentery, stomach, pyloric ceca, and intestine were counted. Presence/absence of *Anisakis* in host muscle was noted, but nematodes were not quantified from this location. Mean intensities of both *L. dollfusi* and tetraphyllidean plerocercoids varied significantly over the 4 seasons, with the highest mean number of parasites seen in the spring and summer. However, no significant differences were found between the seasonal mean intensities for *Corynosoma* sp. (Table 2).

The effect of host age (Fig. 1) and sex on helminth infection was evaluated for 3 major parasite taxa of white croaker. Both of these factors influenced infection with tetraphyllidean

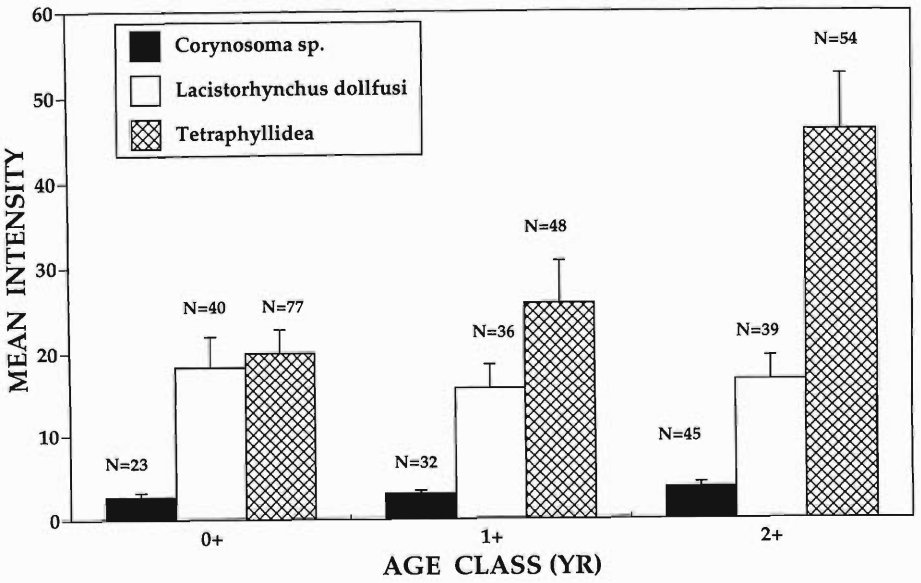

Figure 1. Mean intensity ± SE of 3 endohelminth taxa infecting 3 age classes of white croaker. *N* = number of fish infected with each helminth species.

cestodes but not infection with *Corynosoma* sp. or plerocercoids of *L. dollfusi.*

Age 2+ croakers harbored more tetraphyllidean plerocercoids than did 0+ and 1+ hosts. All 2+ hosts were large enough to be sexually mature, and for most of these (91) the sex could be determined: 37 females ($\bar{x} \pm$ SE) (length = 177 ± 9.2 mm; weight = 103.7 ± 10.0 g) and 54 males (length = 176.3 ± 6.9 mm; weight = 85.8 ± 7.9 g). Most of these fish (>75%) were infected with *Corynosoma* sp. and tetraphyllidean cestodes. The highest prevalence of tetraphyllidean cestodes was seen in female hosts: 92% were infected compared with 80% for male hosts. No sex-related differences in prevalence were seen for tetraphyllidean cestodes, *Corynosoma* sp., or *L. dollfusi.* Only the mean intensities of tetraphyllidean cestodes in female (48.7) and male (29.5) croaker were significantly different ($Z = -2.063$, $P = 0.039$).

Discussion

Genyonemus lineatus is a common fish in the nearshore zone off southern California. It is very abundant in deteriorated habitats such as Los Angeles Harbor. This harbor receives about 15.9 million gallons of secondary treated wastewater per day from the Terminal Island Treatment Plant (McGeorge, 1997). The harbor is part of the Los Angeles–Long Beach Harbor complex and is an important nursery area for many fish, including croakers (Cross and Allen, 1993).

Ware (1979) studied the food habits of 484 white croaker from various localities in Los Angeles Harbor; this fish is opportunistic and omnivorous and consumes a variety of invertebrate species. Over 100 invertebrate taxa comprised the diet of croakers. The more common food items reported from the stomach of croakers were polychaetes (planktonic larvae and adults), free-living nematodes, and calanoid copepods. This diverse assemblage of invertebrates consumed by croakers has resulted in a rich parasite fauna, as illustrated by the 12 endohelminth taxa reported in the present study.

The state of maturity of the helminths found in white croaker indicated that this species functioned as a definitive host for *Aponurus* sp., *Lecithochirium* sp., *Manteriella* sp., *Zoogonoides* sp., *Stephanostomum californicum,* S. *tristephanum,* and *Spirocamallanus* sp. The acanthocephalan *Corynosoma* sp., the nematode *Spirocamallanus* sp., and all digeneans except for *S. californicum* represent new host records for white croaker. *Anisakis* sp., *Corynosoma* sp., *Lacistorhynchus dollfusi,* and tetraphyllidean cestodes were represented only by juvenile stages. Both *Anisakis* sp. and *Corynosoma* sp. use marine mammals as definitive hosts, and a final host for these parasites in Los Angeles Harbor is the California sea lion, *Zalophus californianus* (Lesson, 1828). California sea lions were reported by Frey (1971) to prey on white croaker. *Anisakis* sp. juveniles were previously reported from white croaker by Dailey et al. (1981), and this nematode uses croaker as either a paratenic or second intermediate host. White croaker is a known second intermediate host for *L. dollfusi* (Sakanari and Moser, 1989) and also functions as a second intermediate host for the tetraphyllideans. Infective plerocercoids of this cestode group were common in croaker. Adult stages of *L. dollfusi* and tetraphyllideans occur in elasmobranchs.

Abundance of the more common endohelminths of croaker changed over time. Seasonal changes in parasite numbers in fish hosts are well documented (Chubb, 1982; Aho and Kennedy, 1984). Some of the most important factors that can account for changes in parasite numbers are environmental temperature, host diet and behavior, and distribution of intermediate hosts (Williams and Jones, 1994). Host diet and intermediate host distribution influenced prevalence of helminths in croakers from Los Angeles Harbor.

Ware (1979) reported that white croakers switch diet as they grow, consuming zooplankton when young and epibenthic and benthic infaunal invertebrates when older. Planktonic species can be quite common in croaker diets. Copepods are a frequent component of the diet of both young and old croakers. Copepods function as first intermediate hosts of *L. dollfusi* and tetraphyllidean plerocercoids. The availability of copepods to croaker throughout the study produced a predominance of cestodes in this host.

In Los Angeles Harbor, the composition of invertebrate assemblages can vary both seasonally and across years (Deets and Roney, 1997). Molluscs are a typical intermediate host for digenetic trematodes. Molluscs were reported in lower numbers from the harbor in both 1997 and 1998 (Deets and Roney, 1999). Consequently, digeneans were less common than the other helminth groups parasitizing this host.

Anisakine nematodes and *Corynosoma* sp. were frequently found infecting white croaker. *Anisakis* can be transmitted to fish via intermediate hosts such as krill or shrimp (Smith and Wootten, 1978). Amphipods are first intermediate hosts of *Corynosoma* sp. *Crangon nigromaculata* (the black spotted bay shrimp) is a very common epibenthic invertebrate in the harbor. In 1997, this species dominated the invertebrate trawls conducted by Hyperion (Deets and Roney, 1999). The presence of *C. nigromaculata* in the stomach of croakers could account for the high prevalence of *Anisakis* in this host. *Corynosoma* sp. occurred in croakers throughout the study. Amphipods were previously reported to be more common in the stomachs of 1+ and 2+ croakers (Ware, 1979). No such trend was seen in our study, i.e., no correlation between host age and *Corynosoma* sp. intensity was seen.

It is not uncommon to find that host factors such as age and sex can significantly influence parasite intensity (Williams and Jones, 1994). Intensity of tetraphyllidean plerocercoids in croakers was correlated with both age and sex; older hosts and female hosts harbored more parasites. Older croakers may feed longer, consuming greater quantities of the intermediate host for these cestodes.

Many reasons have been proposed for differences in parasite numbers in female and male hosts, e.g., hormonal differences, different feeding habits, and variation in intermediate host abundance (Williams and Jones, 1994). Female croakers in southern California are generally more robust and feed more during their peak spawning season (January through March) as compared with males (Love et al., 1984). Approximately 40% of the fish for which sex was determined were collected in February 1998, a peak spawning month for southern California croaker populations. Although female croakers were comparable in length to male croakers, females weighed more than males on average, suggesting that females fed more often and consequently were exposed more frequently to the intermediate host of the tetraphyllideans.

Juvenile parasites dominated the helminth infracommunity of croaker from Los Angeles Harbor. Up to 75% of fish examined contained plerocercoids of *L. dollfusi* and Tetraphyllidea. Juvenile anisakine nematodes and acanthocephalans were also frequently found in this host. Digeneans, although diverse in croaker (6 species infected this host), were less common. Seasonal distribution of helminths in croakers was related to fluctuations in the composition and size of invertebrate host populations during the time that this study was conducted. Both age and sex affected populations of the most prevalent helminths in croaker, tetraphyllidean cestodes. Older croakers and female croakers were more likely to be infected with cestodes than were younger and male fish.

Helminth infection in white croaker may also be influenced by pollution in Los Angeles Harbor. The harbor's sediments contain a variety of contaminants (e.g., PCBs and DDT), and croakers associating with the bottom are exposed to them (Shoja-Chaghervand, 1997; Huang, 1998). Future studies on endohelminth parasitism in white croaker will focus on sampling croakers from multiple sites within and outside Los Angeles Harbor and from less polluted sites farther from the harbor in an attempt to evaluate the effect of pollution on parasitism in white croaker.

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Obituary Notice

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Larval Helminths Parasitizing Freshwater Fishes from the Atlantic Coast of Nicaragua

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ABSTRACT: During a survey of the parasitic helminths of 8 fish species from the South Atlantic Autonomous Region, Nicaragua, 23 helminth species were collected. Sixteen of them were digenean species in metacercarial stage: *Apharyngostrigea* sp., *Ascocotyle* (*Ascocotyle*) *tenuicollis, Ascocotyle* (*Phagicola*) *mollienisicola, Ascocotyle* (*Phagicola*) *diminuta, Ascocotyle* (*Phagicola*) *nana, Cladocystis trifolium, Clinostomum complanatum, Clinostomum* sp., Cryptogonimidae gen. sp., *Diplostomum compactum,* Heterophyidae gen. sp., *Oligogonotylus manteri, Posthodiplostomum minimum,* Proterodiplostomidae gen. sp., *Stunkardiella minima,* and *Uvulifer* sp.; 1 was a cestode larva: Proteocephalidea gen. sp.; and 6 were larval nematodes: *Brevimulticaecum* sp., *Contracaecum* sp. type II, *Eustrongylides* sp., *Falcaustra* sp., *Serpinema trispinosum,* and *Spiroxys* sp. With the exception of *O. manteri,* this is the first reported occurrence of these helminth species in Nicaragua. The larval helminth fauna in freshwater fishes from Nicaragua closely resembles that of freshwater fishes from southeastern Mexico.

KEY WORDS: metacercariae, cestodes, nematodes, helminth larvae, freshwater fishes, Autonomous Region of the South Atlantic, Nicaragua.

It is well known that the helminth fauna of freshwater fishes from tropical America is highly diverse. This has been shown in a number of studies on the helminths of a relatively large number of fish species from South America and Mexico (Thatcher, 1991; Moravec, Huffman, and Swin, 1995; Moravec, Vivas-Rodríguez, et al., 1995; Scholz et al., 1995a, b, 1996; Pérez-Ponce de León et al., 1996; Salgado-Maldonado et al., 1997). In Central America, there are almost no data on helminths. The only study on the parasites of freshwater fishes in Nicaragua was carried out by Watson (1976), who reported 9 species of adult digeneans, 7 of which were new to science. He also reported the presence of 2 species in metacercarial stage, *Neochasmus ackerti* Watson, 1976, and *Allomacroderoides lepisostei* Watson, 1976, the adult forms of which were also found in the fish.

During a brief visit (9–14 March, 1999) to Nicaragua by 4 of the authors (M.L.A.-M., T.S., V.M.V.-M., and G.A.-T.), freshwater fishes from the South Atlantic Autonomous Region were examined. A survey of the larval stages found in freshwater fish is presented herein.

Materials and Methods

Using hook and line and throw nets, 8 freshwater fish species were collected from the South Atlantic Autonomous Region on the Atlantic coast of Nicaragua (Fig. 1). Table 1 shows the collection localities and fish species recovered in the present study.

The collected fish were transported live to the laboratory of the Bluefields Indian and Caribbean University (BICU), where external and internal parasitological examinations were carried out immediately thereafter (MAFF/ADAS, 1986). All helminths were studied in fresh preparations and counted in situ. Digeneans and cestodes were fixed in hot 4% formalin, stained with hydrochloric carmine, and mounted in Canada balsam. Digenean metacercariae were also fixed with glycerin–ammonium picrate mixture, following the methodology outlined by Scholz and Aguirre-Macedo (2000). Nematodes were fixed with hot 4% formalin in saline solution and cleared in a series of glycerin–water solutions (1:20, 1:10, 1:5, and 1:2). Morphological descriptions were made only for those helminths recorded for the first time in Central America (which includes Nicaragua and southeastern Mex-

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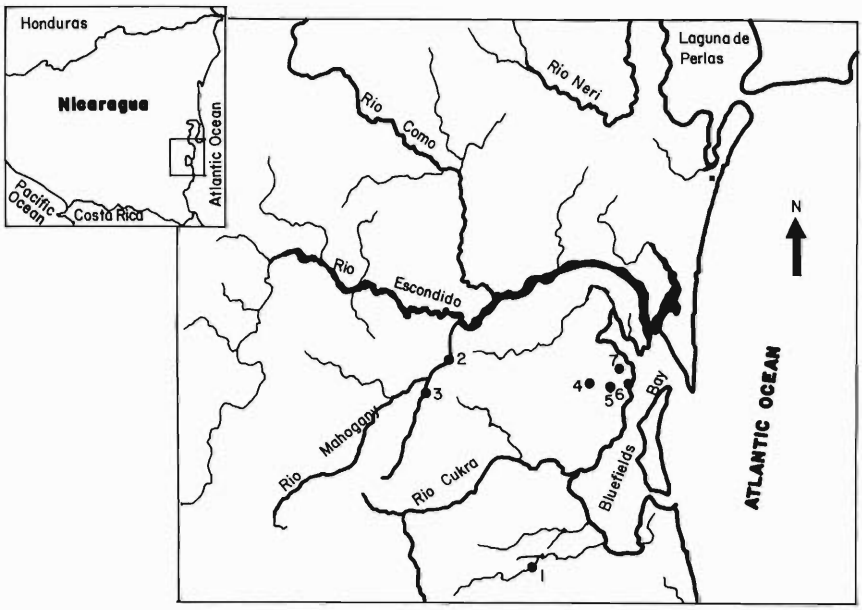


Figure 1. Map showing sites sampled. 1 = Torsuani River; 2 = Mahogany River; 3 = Caño Negro; 4 = Walpatara; 5 = Loonku Creek; 6 = Caño Marañón; 7 = Puente Chino.

Table 1. Number of freshwater fish examined for larval helminths at various localities in Nicaragua.

Fish species	Collection location (Geographical positioning)*						
	Caño Marañon stream	Caño Negro stream	Loonku Creek	Mahogany River	Puente Chino stream	Torsuani River	Walpatara bridge
Characidae							
Astyanax fasciatus (Cuvier, 1819), tetra	—	—	2	1	—	4	1
Cichlidae							
Amphilophus alfari (Meek, 1907), pastel cichlid	—	—	1	—	2	—	—
Archocentrus nigrofasciatus (Günther, 1869), convict cichlid	—	—	2	—	1	—	—
Cichlasoma maculicauda (Regan, 1805), blackbelt cichlid	7	—	1	—	1	3	—
Cichlasoma managuense (Günther, 1867), jaguar cichlid	—	4	—	7	2	—	—
Herotilapia multispinosa (Günther, 1867), butterfly cichlid	—	—	3	2	3	—	—
Pimelodidae							
Rhamdia nicaraguensis (Günther, 1864)	—	—	1	—	3	—	—
Poeciliidae							
Poecilia velifera (Regan, 1814), Yucatan molly	3	—	—	—	—	2	—

* Caño Marañon: 12°00′01″N, 83°46′39″W; Caño Negro: 12°00′55″N, 84°01′10″W; Loonku Creek: 11°59′05″N, 83°46′48″W; Mahogany River: 12°03′22″N, 83°59′07″W; Puente Chino: 12°00′30″N, 83°46′13″W; Torsuani River: 11°47′06″N, 83°52′38″W; Walpatara: 12°00′14″N, 83°45′58″W.

ico). In these descriptions, all measurements are given in micrometers, unless otherwise stated. All illustrations were made using a camera lucida. The numbers of hosts infected and examined for each helminth species, followed by intensity range, are given in parentheses for each host species and locality.

Reference specimens were deposited in the Colección Nacional de Helmintos (CNHE), México D.F., Mexico; the United States National Parasite Collection (USNPC), Beltsville, Maryland, U.S.A.; and the Parasitology Laboratory, CINVESTAV (CHCM) Mérida, Mexico.

Results

A total of 23 helminth species in larval stage were recovered from the 8 species of freshwater fishes reported in Table 1. Table 2 is the list of these helminth species: 16 digenean species, 1 cestode, and 6 nematodes. To date, 3 species in Table 2 have not been described for Mesoamerica (tropical Mexico to Nicaragua: Vidal-Martínez and Kennedy, 2000): *Ascocotyle (Phagicola) mollienisicola, Clinostomum* sp, and Cryptogonimidae gen. sp. Taxonomic descriptions of these larvae and those of Heterophyidae gen. sp. are provided here, and all the taxonomic summary information for these species has been included in Table 2.

Ascocotyle (Phagicola) mollienisicola Sogandares-Bernal and Bridgman, 1960 (Figs. 2, 3)

DESCRIPTION: Cyst spherical, double walled, with thick external and thin, hyaline internal walls. Excysted metacercariae pyriform, 444 long and 276 wide, tapered to anterior end, covered with tegumental spines to three-quarters of body length. Eyespots dispersed at prepharyngeal level. Oral sucker subterminal, 35 wide, preoral lobe absent, lacking oral spines, posterior muscular appendage short. Ventral sucker widely oval, almost equatorial, larger than oral sucker, 40 long and 48 wide. Sucker ratio 1:1.37. Prepharynx narrow, 76 long; pharynx muscular, 33 long and 29 wide; esophagus very short or absent depending upon contraction of body. Ceca extending post acetabulum, widening posteriorly, curved at ovarian level, and filled with discoid bodies. Testes symmetrical, 66–68 long and 74–89 wide, near posterior extremity, separated by excretory bladder. Ovary postacetabular, 32 long and 60 wide. Gonotyl conspicuous, anterosinistral to acetabulum, with 15–17 refractile bodies. Excretory bladder X-shaped, with anterior arms reaching to intestinal ceca.

REMARKS: The metacercariae correspond to *A. (P.) mollienisicola* based on their morphology, in particular the absence of circumoral spines, and infection site. This species was described by Sogandares-Bernal and Bridgman (1960) in the poeciliid *Mollienisia* (=*Poecilia*) *latipinna* from Florida, U.S.A. as the type species of a new genus, *Pseudascocotyle*. Sogandares-Bernal and Lumsden (1963), however, suppressed this genus and placed the species among members of *Phagicola* Faust, 1920. Stein (1968) found metacercariae of *A. (P.) mollienisicola* in the liver, spleen, and musculature of *M. latipinna* from Florida.

Adults recovered from experimentally infected chicks (accession nos. CNHE-4156; USNPC-90846; CHCM-374) in the present study corresponded to those obtained by Sogandares-Bernal and Lumsden (1963) from an experimentally infected hamster. This is the first record of this parasite from Mesoamerica.

Cryptogonimidae gen. sp. (Fig. 4)

DESCRIPTION: Body elongate, 1,090 long and 406 wide, covered entirely with fine tegumental spines that decrease in size posteriorly. Oral sucker subterminal, 134 long and 139 wide. Ventral sucker at posterior third of body, smaller than oral sucker, 100 long and 88 wide. Sucker ratio 1.45:1. Prepharynx short and wide, 29 long; pharynx strongly muscular, 88 long and 96 wide; esophagus very short and wide. Cecal bifurcation slightly pre-equatorial; ceca long and wide, reaching to posterior end of body. Genital primordium postacetabular, transversely wide, 26 long and 102 wide. Excretory bladder voluminous, V-shaped, with branches reaching to mouth opening and filling most of body width.

REMARKS: The metacercariae encountered possessed a voluminous, V-shaped excretory bladder extending anteriorly to the oral sucker, a small ventral sucker with a small opening, entirely spined tegument, and large intestinal ceca reaching posteriorly to the body extremity. All these features suggest that the larvae belong to the family Cryptogonimidae. However, more specific identification is not possible without adults. Predatory fish may be definitive hosts (Yamaguti, 1971).

Table 2. Larval helminths collected from Nicaraguan freshwater fishes.

Parasite species (no. specimens studied)	Hosts (no. infected/no. examined)	Intensity	Site of infection	Locality*	Accession nos. (CNHE/USNPC/CHCM)
Digenea					
Apharyngostrigea sp. (3)	*Herotilapia multispinosa* (2/2)	4–6	Liver, mesentery	PC	4152/—/370
Ascocotyle (*A.*) *tenuicollis* Price, 1932 (3)	*Astyanax fasciatus* (2/4)	1	Heart	TR	4153/—/—
	Cichlasoma maculicauda (1/3)	2	Heart	TR	
	Poecilia velifera (1/3)	29	Heart	TR	
Ascocotyle (*Phagicola*) *mollienisicola* Sogandares-Bernal and Bridgman, 1960 (13)	*P. velifera* (2/3)	33–570	Gills, gonads, liver, mesentery, muscles	CM	4154/90845/365
Ascocotyle (*P.*) *diminuta* (Stunkard and Haviland, 1924) (5)	*P. velifera* (3/3)	19–214	Gills	CM	4157/—/366
Ascocotyle (*P.*) *nana* Ransom, 1920 (1)	*C. maculicauda* (1/3)	2	Kidney	TR	4158/—/—
Cladocystis trifolium (Braun, 1901) (2)	*Cichlasoma managuense* (2/7)	3–5	Gills	MR	
Clinostomum complanatum (Rudolphi, 1814) (3)	*C. managuense* (1/7)	1	Gills, pectoral fins	MR, CN	
Clinostomum sp. (2)	*C. managuense* (1/7)	1	Body cavity	MR, CN	—/—/1371
Cryptogonimidae gen. sp. (1)	*P. velifera* (1/3)	2	Base of gills, liver	CM	—/—/1367
Diplostomum (*A.*) *compactum* (Lutz, 1928) (2)	*Amphilophus alfari* (1/3)	2	Eye (humor body)	LC	4159/90847/373
Heterophyidae gen. sp. (="*Haplorchoides*" sp. of Sholz and Vargas-Vázquez, 1998) (5)	*A. alfari* (1/1)	24	Base of gills, Intestinal wall, Mesentery, pectoral fin, scales	LC	4160/—/—
	C. managuense (2/7)	3–10		MR	
	H. multispinosa (1/4)	1		LC	
Oligogonotylus manteri Watson, 1976 (1)	*C. maculicauda* (1/7)	1	Gills	CM	
Posthodiplostomum minimum (MacCallum, 1921) (1)	*C. maculicauda* (1/3)	10	Muscles, base of gills, eyes (periorbital space), mesentery, swimbladder	TR	
	C. managuense (5/7)	1–3		MR	
	C. managuense (3/4)	1–3		CN	
	Archocentrus nigrofasciatus (3/3)	2–10		LC	
	H. multispinosa (3/3)	1–2		PC	
	P. velifera (2/3)	1–12		CM	4161/90848/369
Proterodiplostomidae gen. sp.	*Astyanax fasciatus* (1/4)	4	Gills, swimbladder	TR	—/—/368
	Rhamdia nicaraguensis (2/3)	2–12		PC	
	H. multispinosa (1/4)	1		LC	
		1			
Stunkardiella minima (Stunkard, 1938) (1)	*C. maculicauda* (1/7)	1	Pectoral fins	CM	
Uvulifer sp.	*Amphilophus alfari* (2/2)	3–8	Eyes (periorbital space), fins, gills, muscles	PC	
	Archocentrus nigrofasciatus (1/3)	1		PC	
	Astyanax fasciatus (4/4)	2–58		TR	

Table 2. Continued.

Parasite species (no. specimens studied)	Hosts (no. infected/no. examined)	Intensity	Site of infection	Locality*	Accession nos. (CNHE/USNPC/CHCM)
	C. maculicauda (2/3)	3–34		TR	
	C. maculicauda (2/7)	2–3		CM	
	C. maculicauda (1/1)	1		LC	
	C. managuense (7/7)	2–36		MR	
	C. managuense (4/4)	8–328		CN	
	H. multispinosa (1/1)	12		MR	
	H. multispinosa (3/4)	8–10		LC	
Cestoda					
Proteocephalidea gen. sp. (3)	*A. fasciatus* (1/4)	1	Mesentery, wall of stomach and intestine	TR	—/—/372
	C. managuense (2/7)	1		MR	
	H. multispinosa (1/1)	1		MR	
Nematoda					
Brevimulticaecum sp. (2)	*A. fasciatus* (1/4)	1	Muscles	TR	4147/—/—
	C. maculicauda (1/3)	1		TR	
	Rhamdia guatemalensis (1/1)	1		LC	
Contracaecum Type 2 of Moravec et al. (1995a)	*Amphilophus alfari* (1/3)	1	Gonads, liver, mesentery	TR	4145/—/—
	Archocentrus nigrofasciatus (1/3)	1		LC	
	Astyanax fasciatus (1/4)	1		TR	
	C. maculicauda (1/1)	1		LC	
	C. managuense (5/7)	1–115		MR	
	C. managuense (4/4)	6–38		CN	
	H. multispinosa (2/4)	1–6		LC	
	P. velifera (1/2)	1		TR	
Eustrongylides sp. (2?)	*C. managuense* (1/4)	2	Muscles	MR	4149/—/—
Falcaustra sp. (1)	*Amphilophus alfari* (2/2)	4 to >100	Intestinal wall, liver, mesentery	PC	4146/—/—
	Archocentrus nigrofasciatus (1/1)	>100		LC	
	A. nigrofasciatus (1/2)	>100		PC	
	C. maculicauda (2/3)	9 to >100		TR	
	H. multispinosa (2/3)	>100		MR	
	H. multispinosa (1/2)	>100		LC	
	H. multispinosa (3/3)	>100		PC	
Serpinema trispinosum sp. (1)	*Amphilophus alfari* (1/2)	1	Rectum	PC	4144/—/—
	C. managuense (1/2)	1		PC	
	H. multispinosa (1/3)	1		PC	
Spiroxys sp. (1)	*A. alfari* (1/2)	4	Liver, mesentery	PC	
	Astyanax fasciatus (1/1)	1		PC	4148/—/—
	C. maculicauda (1/1)	26		LC	

Table 2. Continued.

Parasite species (no. specimens studied)	Hosts (no. infected/no. examined)	Intensity	Site of infection	Locality*	Accession nos. (CNHE/USNPC/CHCM)
	C. managuense (4/4)	35–444		CN	
	C. managuense (5/7)	1–243		MR	
	C. managuense (2/2)	2–5		PC	
	H. multispinosa (2/4)	3–4		LC	

* CM = Caño Marañon; CN = Caño Negro; LC = Loonku Creek; MR = Mahogany River; PC = Puente Chino; TR = Torsuani River.

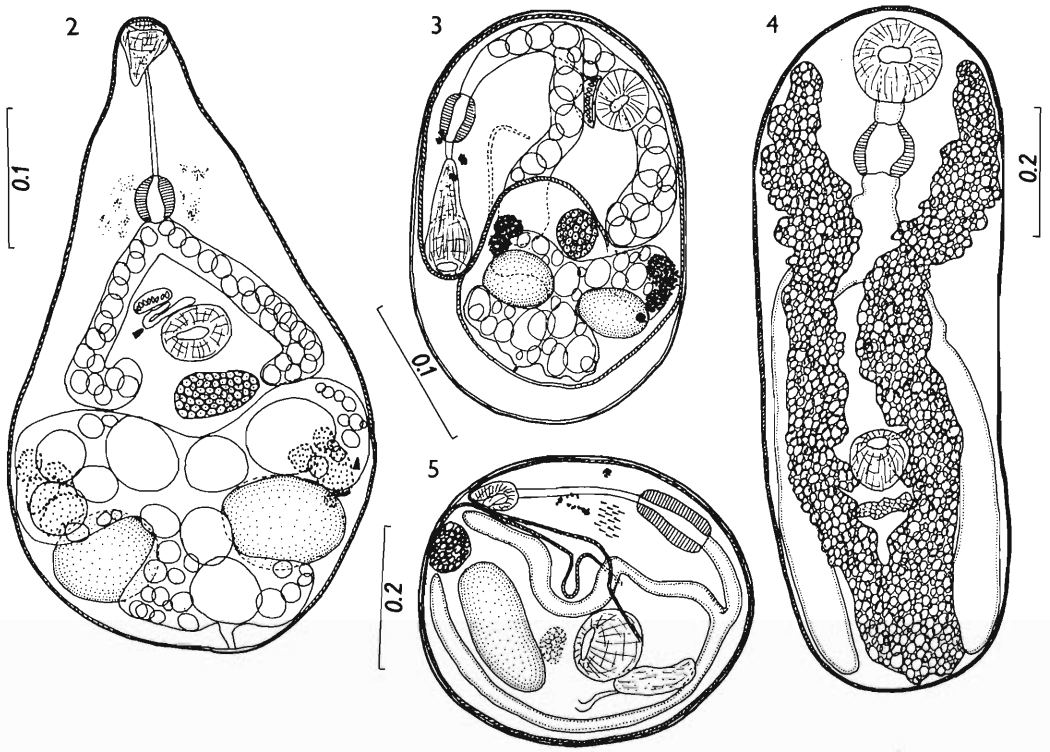
Heterophyidae gen. sp. (="*Haplorchoides*" sp. of Scholz and Vargas-Vázquez, 1998) (Fig. 5)

DESCRIPTION: Cyst almost spherical, transparent, thin walled, 500 long and 426 wide, containing folded metacercaria. Excysted metacercaria elongate, tapering to both ends. Body entirely covered with simple, long tegumental spines. Two pairs of eye spots at prepharyngeal level. Oral sucker subterminal, spherical, 71 wide. Ventral sucker spherical, postequatorial, larger than oral sucker, 98 long and 107 wide, with fine spines surrounding sucker opening. Sucker ratio 1:1.44. Prepharynx very long (176), narrow; pharynx large, bell-shaped, 115 long and 59 wide; esophagus shorter than prepharynx, 112 long. Intestinal ceca narrow and long, reaching near posterior extremity. Testis single, oval, intercecal, 202 long and 88 wide. Ovary oval, diagonal, between ventral sucker and testis. Excretory bladder sacciform, elongate, filled with numerous dark granules. Excretory pore subterminal.

REMARKS: The metacercariae correspond to those found in cichlid fishes from the Hondo River in southeastern Mexico and designated as *Haplorchoides* sp. by Scholz and Vargas-Vázquez (1998). However, they differ from members of this genus in that they lack a reduced ventral sucker possessing lobes armed with sclerites and hooklets (Yamaguti, 1971; Scholz et al., 1991).

Clinostomum sp. (Fig. 6)

DESCRIPTION (measurements in mm): Metacercariae very large, elongated 39 long and 11 wide, covered by fine, thin cyst wall, and break easily when touched. Body dorsoventrally flattened, divided into segments by slight constriction at acetabular level. Forebody 6 long and 6 wide, hind body 33 long. Oral sucker subterminal, widely oval, 0.65 long and 0.90 wide, surrounded by a collar-like fold. Ventral sucker situated at level of body constriction, larger than oral sucker, 3.5 long and 3.5 wide. Sucker ratio 1:3.88. Prepharynx absent; esophagus swollen without forming typical pharynx. Intestinal ceca very long, wide, reaching to posterior extremity. Testes X-shaped, lobate, in tandem, one near another, close to posterior end of body. Ovary intertesticular; uterus ascending anteriorly near



Figures 2–5. Helminth species new to Mesoamerica. 2, 3. *Ascocotyle* (*Phagicola*) *mollienisicola* (2 = excysted; 3 = encysted) from the mesenteries of *Poecilia velifera*, Bluefields. 4. Cryptogonimidae gen. sp. Metacercaria from the base of gills of *P. velifera*, Bluefields. 5. Heterophyidae gen. sp. Metacercaria from the fins of *Cichlasoma managuense*, Mahogany River. Scale bars are in millimeters.

ventral sucker. Excretory bladder Y-shaped, with anterior branches reaching almost to acetabular level. Excretory pore terminal.

REMARKS: Metacercariae found in the body cavity of *Cichlasoma managuense* differed from those occurring in tissues of the same fish and identified as *Clinostomum complanatum* by their extremely large size, location of the genitalia, and shape of the testis. This helminth species likely belongs to another species of *Clinostomum*, but species identification requires adults and comparison of adults with other congeners. In addition, the taxonomy of the genus is ill defined, making revision of this group necessary.

Discussion

Even though this study was based on examination of a relatively small number of fish from a limited area on the Atlantic Coast of Nicaragua, the results show a striking similarity between the larval helminth fauna of fish in Nicaragua and the known helminth fauna of southeastern Mexico. All the helminth species in this study, with the exception of *Ascocotyle* (*Phagicola*) *mollienisicola* and *Brevimulticaecum* sp., have been found recently in freshwater fishes from cenotes (sinkholes), rivers, and lakes in tropical regions of Mexico (Aguirre-Macedo and García-Magaña, 1994, 1996; Moravec, Vivas-Rodríguez, et al., 1995; Scholz et al., 1995a, b, 1996, 1997; Salgado-Maldonado et al., 1997; Moravec, 1998; Scholz and Vargas-Vázquez, 1998; Vidal-Martínez et al., 2000).

As in Mexico, the metacercariae were the principal component of the larval helminth fauna in Nicaragua (16 of 23 species found). Most of these species have piscivorous birds as definitive hosts, which may be responsible for the wide dispersion of these parasites into different parts of the Americas along migratory pathways (Tallman et al., 1985; Bourne, 1989; Kennedy, 1998). A small number of species, such as *Oligogonotylus manteri, Stunkardiella minima,* and the metacercariae of the family Proterodiplos-

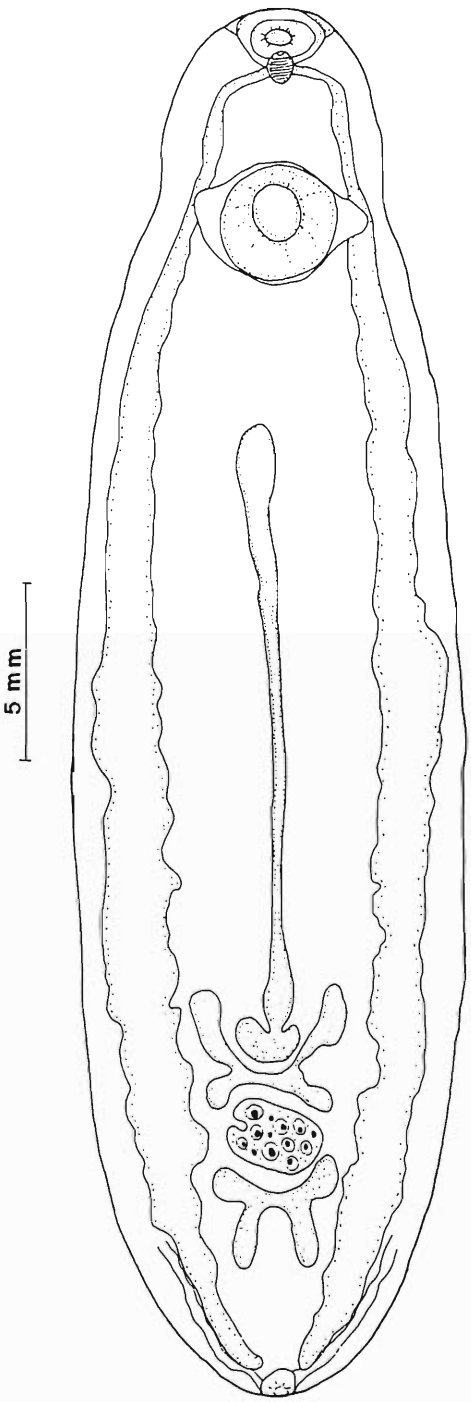


Figure 6. ***Clinostomum*** **sp. Metacercaria from body cavity of** ***Cichlasoma managuense*****, Mahogany River. Scale bar = 5 mm.**

tomidae, have aquatic definitive hosts (reptiles or predatory fish), and their distribution range seems to be restricted to southeastern Mexico and Central America. Unfortunately, the sample size of the fish species obtained in Nicaragua was too small to make meaningful prevalence or abundance comparisons with data from Mexico, such as those of Salgado-Maldonado et al. (1997).

Most of the nematodes found reach maturity in reptiles, with the exception of *Contracaecum* and *Eustrongylides* larvae, which have piscivorous birds as definitive hosts. The most abundant species found were *Falcaustra* sp. and *Spiroxys* sp., which probably mature in freshwater turtles (Moravec, 1998), since these were very abundant in the localities studied (personal observation).

For all but 1 of the species listed in this survey, this is the first reported occurrence of these helminths in Nicaragua and Central America. The exception is *O. manteri,* first described by Watson (1976) as adults in cichlid fishes from Lake Nicaragua. Nevertheless, most of the species encountered have been reported previously in the Americas, either as adults or larval stages (Travassos et al., 1969; Thatcher, 1991; Moravec, Vivas-Rodríguez, et al., 1995; Scholz et al., 1995a, b, 1997; Salgado-Maldonado et al., 1997; Moravec, 1998; Scholz and Vargas-Vázquez, 1998; Hoffman, 1999; Vidal-Martínez et al., 2000). New host records are reported for the following helminth species: *Diplostomum* (*Austrodiplostomum*) *compactum,* Heterophyidae gen. sp., *Uvulifer* sp., *Contracaecum* Type 2, *Falcaustra* sp., *Serpinema trispinosum*, and *Spiroxys* sp. reported for the first time from the fish species *Amphilophus alfari*; *Ascocotyle* (*Ascocotyle*) *tenuicollis, Ascocotyle* (*Phagicola*) *nana, Oligogonotylus manteri, Posthodiplostomum minimum, Stunkardiella minima, Uvulifer* sp., *Brevimulticaecum* sp., *Contracaecum* Type 2, *Falcaustra* sp., and *Spiroxys* sp. from the fish species *Cichlasoma maculicauda*; and *Apharyngostrigea* sp., Heterophyidae gen. sp., *Posthodiplostomum minimum,* Proterodiplostomidae gen. sp., *Uvulifer* sp., Proteocephalidea gen. sp., *Contracaecum* Type 2, *Falcaustra* sp., *Serpinema trispinosum* sp., and *Spiroxys* sp. from the fish species *Herotilapia multispinosa.*

Our study is the first since Watson's (1976) study and the only one of its kind providing data on freshwater fish helminths from Central Amer-

ica in the last 20 yr. However, much more data on the parasites of freshwater fish in this region are needed to better understand the migration patterns and phylogeny of freshwater fishes and their parasites during their migration from South to Central and North America (Vidal-Martínez and Kennedy, 2000). Some species, such as *D. (A.) compactum,* those of the *Ascocotyle* complex (i.e., *A. (P.) diminuta, A. (P.) mollienisicola, A. (P.) nana,* and *A. (A.) tenuicollis*), and nematodes of the genera *Brevimulticaecum, Falcaustra,* and *Spiroxys,* have a wide distribution range in the Americas, from the U.S.A. to Argentina. Still others, such as *P. minimum, C. complanatum,* and nematodes of the genera *Eustrongylides* and *Contracaecum,* extend to other continents. Only a small number of species, mainly those with aquatic definitive hosts (*C. trifolium, O. manteri, S. minima, S. trispinosum,* and metacercariae of the family Proterodiplostomidae), seem to be restricted to southeastern Mexico and Central America.

These results suggest that both the Atlantic coast of Nicaragua and southeastern Mexico exhibit a close similarity in their freshwater fish helminth fauna, in particular for cichlid fishes. This similarity may be associated with bird migrations; most (13 of 23) of the helminth species found in this study have piscivorous birds as definitive hosts, and these birds may have showered a "propagule rain" across Central America. However, similarity among the helminths with aquatic definitive hosts suggests that reptiles and fish likely also have an important role in helminth species dispersion between Nicaragua and southeastern Mexico, although on a more restricted geographical scale. To understand how extensive a role aquatic hosts play in the dispersion of helminths, many more studies are needed on the freshwater fish helminth fauna in this region, northern South America (most South American data are from Brazil and Argentina), Panama, and Costa Rica.

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Advice to Authors—Writing and Using Scientific Names

All scientific names (parasites, hosts, etc.) comprising the binomen of the genus and species epithets must be written out in full (accompanied by the taxonomic authorities and years), the first time that they are used in the text of the paper. Thereafter, the genus name can be abbreviated to the first letter, unless it is the first word of a sentence, when it must always be written out in full. The name of a species must always consist of the generic and specific epithets; the specific epithet must not be used alone. In listing species of the same genus, the genus portion of the name of **each species** must be written out in full the first time that it is used [Example: write "*Langeronia macrocirra* Caballero and Bravo-Hollis, 1949, *Langeronia provitellaria* Sacks, 1952, and *Langeronia burseyi* Dailey and Goldberg, 2000," NOT "*Langeronia macrocirra* Caballero and Bravo-Hollis, 1949, *L. provitellaria* Sacks, 1952, and *L. burseyi* Dailey and Goldberg, 2000"]. Species and genus names are always nouns; they must not be used as adjectives (e.g., write "cercariae of *S. mansoni*," NOT "*Schistosoma mansoni* cercariae"). When used as an adjective, the scientific name should be romanized (e.g., schistosome cercariae, hymenolepid cestodes).

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Three New Species of *Acanthobothrium* (Cestoda: Tetraphyllidea) from the Ocellated Electric Ray, *Diplobatis ommata,* in the Gulf of California, Mexico

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ABSTRACT: Examination of the spiral intestines of 12 female specimens of the ocellated electric ray *Diplobatis ommata* from 4 sites in the Gulf of California, Mexico, in 1996 resulted in the discovery of 3 new species of *Acanthobothrium*: *A. dollyae* sp. n., *A. maryanskii* sp. n., and *A. royi* sp. n.. *Acanthobothrium dollyae* and *A. royi* are <15 mm in total length, possess <50 proglottids, <80 testes, and a symmetrical ovary, and thus are Category 1 species. *Acanthobothrium maryanskii* is a Category 5 species; it is >15 mm in total length, possesses >50 proglottids and <80 testes, and has a symmetrical ovary. *Acanthobothrium royi* differs from *A. dollyae* in the arrangement of its testes and in its possession of a shorter scolex. *Acanthobothrium dollyae* and *A. royi* differ from the 4 other Category 1 species known from the eastern Pacific Ocean in total length, proglottid number, cirrus sac size, testis number, extent of vas deferens, and hook shape. Both new species differ from the 6 other Category 1 species known from the western Atlantic Ocean in proglottid number, cirrus sac size, ovary size, genital pore position, and hook shape. *Acanthobothrium maryanskii* differs from all 6 of the Category 5 species known from the eastern Pacific Ocean and all 5 of the Category 5 species known from the western Atlantic Ocean in hook shape and in its possession of mature proglottids that are wider than long rather than longer than wide. This brings the number of species of *Acanthobothrium* reported from rays in the order Torpediformes to 12. It brings the number of species of *Acanthobothrium* reported from the eastern Pacific Ocean to 37 and the total number of *Acanthobothrium* species reported from elasmobranchs in the Gulf of California to 7. This is the first report of tapeworms from a member of the ray genus *Diplobatis*.

KEY WORDS: Cestoda, Tetraphyllidea, elasmobranchs, ocellated electric ray, *Diplobatis ommata, Acanthobothrium,* taxonomy, Gulf of California, Mexico.

In the most recent revision of the electric ray genus *Diplobatis* Bigelow and Schroeder, 1948, Fechhelm and McEachran (1984) recognized only 2 valid species: *Diplobatis ommata* (Jordan and Gilbert, 1890) from the eastern Pacific Ocean and *Diplobatis pictus* Palmer, 1950, with 3 subspecies, all from the western Atlantic Ocean. Neither species of electric ray has previously been examined for tapeworms. Collections conducted as part of a survey of the metazoan parasites of elasmobranchs in the Gulf of California, Mexico, provided an opportunity to examine the tapeworms of the ocellated electric ray *D. ommata* and thus the genus *Diplobatis* for the first time. The 3 new species of *Acanthobothrium* discovered parasitizing this host species are described below.

Materials and Methods

Twelve female *D. ommata* were collected from 4 localities in the Gulf of California as follows: 2 specimens from Bahía de Los Angeles, 2 specimens from Isla San Esteban, 5 specimens from Loreto, and 3 specimens from Punta Arena near La Paz. All individuals were collected in 1996 using hand spears. The spiral intestine of each electric ray was removed, opened with a longitudinal incision along the primary mesenteric vessel, and examined for tapeworms in the field or fixed in 4% formalin buffered in seawater. Worms removed in the field were preserved in 4% buffered formalin. All worms were transferred to 70% ethanol for storage.

Specimens prepared for light microscopy were hydrated in a graded ethanol series, stained in Delafield's hematoxylin, dehydrated in a graded ethanol series, cleared in methyl salicylate, and mounted on glass slides in Canada balsam. Material of 2 species was prepared for examination with scanning electron microscopy (SEM). These specimens were hydrated in a graded ethanol series, postfixed in 1% osmium tetroxide overnight, dehydrated in a graded ethanol series, transferred to hexamethyldisilazane (Ted Pella, Inc., Redding, California) for approximately 15 min and, following removal of the bulk of the hexamethyldisilazane, were allowed to air dry. Dried specimens were mounted on aluminum stubs with carbon tape and grounded with carbon paint before being sputter coated with approximately 100 Å of gold/palladium. SEM was performed using a LEO/Zeiss DSM 982® Gemini Field Emission Scanning Electron Microscope.

Illustrations were prepared with the aid of a Zeiss drawing tube. Measurements are given in micrometers unless otherwise specified. The range of each measurement is given in the text; the mean and standard deviation, number of observations (when >1 structure

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per worm was measured), and number of worms measured are given in Table 1. Hook measurements are presented following the formula of Euzet (1959); hook terminology follows Caira (1985). The measurements taken for lateral and medial hooks, respectively, consisted of hook base length (A, A′) as the distance from the anterior extremity of the hook base to the anteriormost point of the curve connecting the axial and abaxial prongs, axial prong length (B, B′) as the distance from the anteriormost point of the curve connecting the axial and abaxial prongs to the posterior extremity of the axial prong, abaxial prong length (C, C′) as the distance from the anteriormost point of the curve connecting the axial and abaxial prongs to the posterior extremity of the abaxial prong, and total hook length (D, D′) as the distance from the anterior extremity of the hook base to the posterior extremity of the axial prong. Total length of the scolex was measured from the anterior margin of the apical sucker of the bothridium to the posterior margin of the cephalic peduncle. Following Caira et al. (1999), total number of testes, number of testes in the postvaginal testicular field, and number of testes in the primary field (i.e., all areas of the proglottid other than the postvaginal region) are presented.

Museum abbreviations used are CNHE (Colección Nacional de Helmintos, Instituto de Biología, Universidad Nacional Autonóma de México, México, DF, Mexico), LRP (Lawrence R. Penner Parasitology Collection, Department of Ecology & Evolutionary Biology, University of Connecticut, Storrs, Connecticut, U.S.A.), and USNPC (U.S. National Parasite Collection, Beltsville, Maryland, U.S.A.).

The strategy of Ghoshroy and Caira (in press) was used to facilitate comparison of the new species with the more than 120 described species in this genus. Thus, general comparisons were made between each new species and all other congeneric species, and more detailed comparisons were made between the new species and the 57 species of *Acanthobothrium* previously reported from the eastern Pacific or western Atlantic oceans, as summarized by Ghoshroy and Caira (in press, tables I, II). Following Ghoshroy and Caira (in press), the new species were each categorized for their possession of 1 of 2 states of each of the following 4 characters: total length (≤15 mm vs. >15 mm), number of proglottids (≤50 vs. >50), number of testes (≤80 vs. >80), and ovary symmetry (poral and aporal lobes symmetrical or asymmetrical). Each species was explicitly compared with species that received the same coding and thus the same category designation in these 2 tables. In addition, each species was explicitly distinguished from species from other regions of the world to which it is similar in the following conspicuous and easily assessed morphological features: total length, number of proglottids, and number of testes per proglottid. The measurement ranges for these features that were similar enough to justify explicit comparisons are provided for each species. If the new species is not explicitly compared with another species, then the 2 species differ in at least 1 of these 3 characters.

Results

Acanthobothrium dollyae sp. n. (Figs. 1–3, 12–14)

Description

Based on 5 whole worms, 6 scolices attached to partial strobilae, and 4 strobilae lacking scolices. Worms euapolytic, 2.9–3.8 mm long, maximum width at scolex; 33–48 proglottids/worm. Scolex 830–1,150 long by 660–1,070 wide, consisting of cephalic peduncle and 4 muscular acetabula in form of bothridia. Bothridia free anteriorly and posteriorly, 790–1,150 long by 264–520 wide; each with 3 loculi and specialized anterior region in form of muscular pad; muscular pad 63–110 long by 168–260 wide, with rounded posterolateral margins, bearing single apical sucker and 1 pair of hooks; apical sucker 44–98 long by 56–125 wide, with thickened anterior rim; anterior loculus 392–690 long, middle loculus 121–180 long, posterior loculus 110–200 long; ratio of loculus lengths (anterior : middle : posterior) 2.4–5.8:1–1.5:1–2.5; maximum width of scolex usually at level of posterior margin of anterior loculus. Velum present between medial margins of adjacent bothridia at level of septum between middle and posterior loculus. Hooks bipronged, hollow; internal channels of axial and abaxial prongs continuous, smooth; anterior portion of axial prongs of medial and lateral hooks with conspicuous tubercle on proximal surface; medial and lateral hooks approximately equal in size; axial prongs of medial and lateral hooks slightly longer than abaxial prongs.

Lateral hook formula:

$$\frac{65\text{–}110,\ 161\text{–}292,\ 160\text{–}290}{226\text{–}380}$$

Medial hook formula:

$$\frac{48\text{–}110,\ 177\text{–}306,\ 162\text{–}308}{230\text{–}384}$$

Bases of medial and lateral hooks approximately equal in length, coming into contact along medial axis of bothridium (Fig. 2). Bases and anterior portions of both prongs of medial and lateral hooks embedded in musculature of scolex. Cephalic peduncle 161–550 long by 128–250 wide.

Scolex, velum, and distal bothridial surfaces covered with short filiform microtriches only. Proximal bothridial surfaces and cephalic peduncle covered with densely arranged blade-like spiniform microtriches interspersed with long filiform microtriches. Surfaces of strobila covered with long filiform microtriches only.

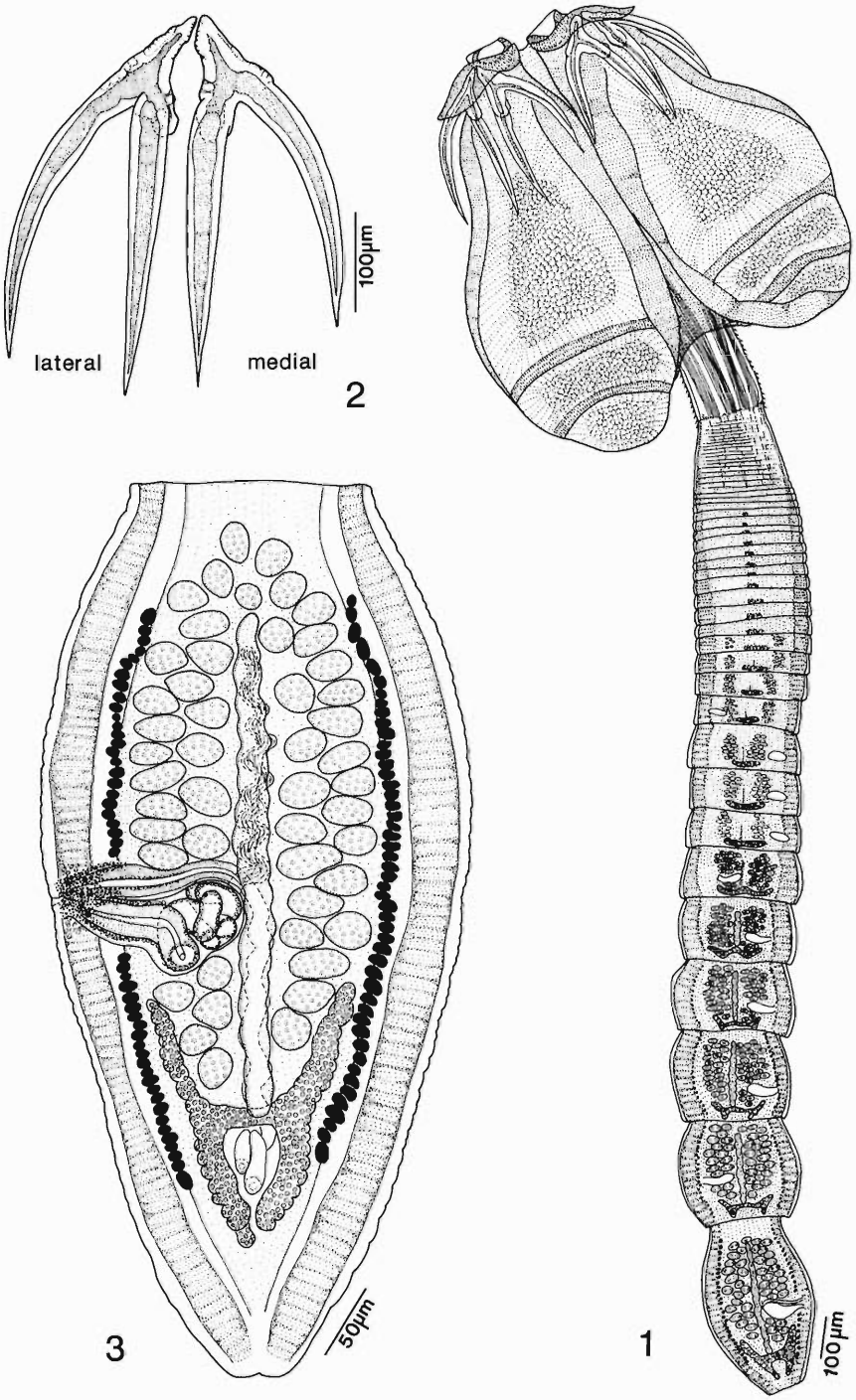
Proglottids acraspedote. Immature proglottids 33–47, wider than long, becoming longer than wide with maturity. Mature proglottids 1 or 2, longer than wide, 270–630 long by 248–310 wide.

Table 1. Morphological characters of the new species of *Acanthobothrium*.*

Character	*A. dollyae* sp. n.	*A. maryanskii* sp. n.	*A. royi* sp. n.
Total length (mm)	3.5 ± 0.3; 5	>29.0; 1	4.5 ± 0.8; 2
Maximum width (μm)	789.5 ± 108.6; 10	763.3 ± 414; 3	364.8 ± 19.8; 4
No. segments	42.0 ± 6.5; 4	>262.0; 1	22.5 ± 24.9; 2
Scolex length (μm)	969.0 ± 106.4; 11	1,787.5 ± 17.7; 2	624.0 ± 118.9; 4
Scolex width (μm)	780.5 ± 107.3; 11	575.0 ± 63.7; 2	364.8 ± 19.8; 4
Bothridium length (μm)	926.6 ± 95.8; 39; 11	541.7 ± 21.1; 7; 2	390.2 ± 38.9; 11; 4
Bothridium width (μm)	377.5 ± 60.5; 36; 10	266.3 ± 44.1; 7; 2	181.6 ± 9.5; 12; 4
Muscular pad length (μm)	82.9 ± 18.5; 6; 3	42.5 ± 0; 2; 1	78.8 ± 6; 4; 1
Muscular pad width (μm)	203.7 ± 26.6; 6; 3	102.3 ± 34.6; 3; 2	125.9 ± 18.5; 9; 4
Apical sucker length (μm)	66.5 ± 14.2; 14; 8	33.8 ± 1.8; 2; 1	41.8 ± 5.0; 3; 2
Apical sucker width (μm)	79.3 ± 17.4; 13; 8	46.0 ± 6.2; 4; 2	46.0 ± 2.9; 5; 2
Anterior loculus length (A) (μm)	512.3 ± 86.3; 30; 11	280.0 ± 32.7; 6; 2	170.7 ± 17.5; 10; 4
Middle loculus length (M) (μm)	164.9 ± 13.6; 30; 11	106.3 ± 22.4; 6; 2	71.2 ± 14.8; 10; 4
Posterior loculus length (P) (μm)	153.7 ± 22.3; 30; 11	119.9 ± 14.6; 6; 2	94.8 ± 13.9; 10; 4
Loculus ratio (A:M:P)	3.4 : 1.1 : 1.1 ± 0.8 : 0.1 : 0.3; 30; 11	2.9 : 1.1 : 1.1 ± 0.6 : 0.2 : 0.2; 6; 2	2.6 : 1.1 : 1.4 ± 0.5 : 0.3 : 0.3; 9; 4
Hook measurements (μm)			
Lateral A	79.0 ± 13.5; 14; 8	60.0 ± 9.0; 3; 2	45.8 ± 4.4; 13; 4
Lateral B	22.3 ± 44.1; 17; 9	51.7 ± 1.4; 3; 2	105.0 ± 12.4; 13; 4
Lateral C	203.3 ± 46; 16; 8	46.3 ± 1.8; 2	93.9 ± 8.2; 13; 4
Lateral D	292.5 ± 57.8; 16; 8	81.7 ± 21.8; 3; 2	139.4 ± 12.7; 13; 4
Medial A′	66.7 ± 17.2; 18; 10	40.6 ± 10.5; 4; 2	40.8 ± 5.2; 15; 4
Medial B′	223.8 ± 35.4; 20; 10	54.2 ± 8.0; 3; 2	105.2 ± 13.2; 13; 4
Medial C′	198.3 ± 44.2; 20; 10	35.0 ± 2.5; 3; 2	99.1 ± 8.0; 16; 4
Medial D′	290.1 ± 47.9; 18; 10	75.0 ± 5; 3; 2	142.5 ± 13.95; 15; 4
Cephalic peduncle length (μm)	297.1 ± 106.4; 10	1,192.0 ± 124.5; 2	304.6 ± 77.6; 4
Cephalic peduncle width (μm)	170.5 ± 35.3; 10	320.0 ± 56.6; 2	136.1 ± 17.2; 4
No. immature segments	41.5 ± 6.2; 4	241.5 ± 29; 2	20.5 ± 4.9; 2
No. mature segments	1.4 ± 0.5; 5	24 ± 0; 1	2.0 ± 0; 2
Mature segment length (μm)	422.9 ± 132.6; 7; 4	492.5 ± 33.0; 4; 1	705.0 ± 139.6; 4; 2
Mature segment width (μm)	276.0 ± 19.4; 7; 4	1,147.5 ± 34.0; 4; 1	133.8 ± 17.0; 4; 2
No. gravid segments	0	19.0 ± 0; 1	0
Genital pore position (% from posterior)	46.7 ± 3.1; 7; 5	46.5 ± 4.7; 13; 5	54.1 ± 3.9; 4; 2
No. testes	46.5 ± 3.3; 15; 7	51.5 ± 5.2; 15; 6	33.3 ± 3.1; 3; 2
No. testes in primary field	41.8 ± 3.3; 16; 7	46.2 ± 5.1; 16; 6	27.3 ± 3.1; 3; 2
No. testes in postvaginal field	4.3 ± 0.9; 16; 7	5.9 ± 0.7; 15; 6	6.0 ± 0; 3; 2
Testes length (μm)	23.1 ± 4.1; 21; 5	33.5 ± 6.2; 36; 5	26.0 ± 3.1; 12; 2
Testes width (μm)	31.7 ± 5.3; 17; 5	58.9 ± 8.2; 36; 5	30.0 ± 5.8; 12; 2
Cirrus sac length (μm)	47.1 ± 6.3; 7; 5	78.0 ± 31.1; 13; 5	71.2 ± 6.6; 4; 2
Cirrus sac width (μm)	156.3 ± 112.5; 7; 5	256.7 ± 33; 12; 5	89.4 ± 14.2; 4; 2
Ovary width (μm)	154.6 ± 31.2; 7; 5	389.1 ± 79.1; 15; 5	92.5 ± 10.6; 2
Ovary length (poral arm) (μm)	139.1 ± 38.1; 7; 5	137.5 ± 67.7; 13; 5	284.4 ± 53.6; 4; 2
Ovary length (aporal arm) (μm)	146.1 ± 41.8; 7; 5	146.5 ± 58.8; 14; 5	290.0 ± 71.4; 4; 2

* Mean ± SD; no. measurements taken; no. worms measured.

Gravid proglottids lacking. Genital pores lateral, irregularly alternating, opening well anterior to ovarian isthmus, 44–53% of proglottid length from posterior of proglottid. Testes 42–55 in total number, 35–50 in primary field, 3–5 in postvaginal field, generally arranged in 4 columns in primary field and 1 or 2 columns in postvaginal field, extending from ovarian isthmus to near anterior margin of proglottid, 1 layer deep; individual testes 18–30 long by 26–43 wide. Vas deferens minimal, slightly coiled, extending from anteriomedian margin of cirrus sac along median line of proglottid approximately to anterior fifth of proglottid. Cirrus sac pyriform, bent slightly anteriorly, 36–56 long by 106–441 wide, containing coiled cirrus; cirrus with minute microtriches. Vagina thick walled, slightly sinuous, extending from ootype along median line of proglottid to anterior margin of cirrus sac, then laterally along anterior margin of cirrus sac, not crossing cirrus sac, opening into common



Figures 1–3. ***Acanthobothrium dollyae*** **sp. n. 1. Whole worm. 2. Hooks. 3. Terminal mature proglottid.**

genital atrium anterior to cirrus; vaginal sphincter absent; proximal extremity of vagina slightly expanded to form seminal receptacle. Ovary H-shaped in dorsoventral view, tetralobed in cross section, with lobulated margins, located at posterior end of proglottid, 130–220 wide; ovarian arms approximately symmetrical, both not reaching posterior margin of cirrus sac; poral arm 94–208 long, aporal arm 110–226 long. Mehlis' gland inconspicuous. Vitellarium consisting of 2 lateral bands; each band consisting of 2 columns of follicles, extending from slightly posterior to anterior margin of primary testicular field to slightly posterior to ovarian isthmus, interrupted by cirrus sac and vagina on poral side, not interrupted by ovary. Uterus sacciform, extending anteriorly from ootype along median line of proglottid to slightly posterior to anterior margin of primary testicular field. Uterine pore not seen. Eggs not observed. Excretory ducts lateral.

Taxonomic summary

TYPE HOST: Ocellated electric ray *Diplobatis ommata* (Jordan and Gilbert, 1890).

SITE OF INFECTION: Spiral intestine.

TYPE LOCALITY: Bahía de Los Angeles (28°55′N, 113°32′W), Gulf of California, Mexico.

ADDITIONAL LOCALITIES: Isla San Esteban (28°42′N, 112°36′W), Punta Arena (24°04′N, 109°50′W), Gulf of California, Mexico.

HOLOTYPE: CNHE 4169.

PARATYPES: CNHE 4170; LRP 2097–2101; USNPC 90837–90839.

ETYMOLOGY: This species is named in honor of the mother of one of the authors (A.N.B.).

Remarks

Acanthobothrium dollyae, based on the criteria of Ghoshroy and Caira (in press), is a Category 1 species; it is <15 mm in total length and possesses <50 proglottids, <80 testes, and a symmetrical ovary. It can be distinguished from the 4 Category 1 species reported previously from the eastern Pacific Ocean (Ghoshroy and Caira, in press, table II) as follows. It possesses a much smaller cirrus sac than *Acanthobothrium monksi* Marques, Brooks, and Barriga, 1997 (approx. ⅛ rather than approx. ⅓ the length of the proglottid), and it has more proglottids and more testes than *Acanthobothrium nicoyaense* Brooks and McCorquodale, 1995 (33–48 vs. 13–17 and 42–45 vs. 14–32, respectively). The hooks of *Acanthobothrium atahualpai* Marques, Brooks, and Barriga, 1997, differ conspicuously in shape from those of *A. dollyae* in that the abaxial prongs of the medial and lateral hooks of *A. atahualpai* are reflexed away from the axis of the bothridium proximally and towards the axis of the bothridium distally so that they are S-shaped, whereas both prongs of the medial and lateral hooks of *A. dollyae* are essentially straight. *Acanthobothrium atahualpai* also possesses fewer proglottids than does *A. dollyae* (≤17 vs. 41–48). *Acanthobothrium dollyae* can be distinguished from *Acanthobothrium minusculus* Marques, Brooks, and Barriga, 1997, by its greater total length (2.9–3.8 vs. 1–2 mm) and possession of more proglottids (33–48 vs. 11) and more testes (42–55 vs. 6–10).

Acanthobothrium dollyae differs from the 6 Category 1 species reported previously from the western Atlantic Ocean (Ghoshroy and Caira, in press, table III) as follows. In *A. dollyae,* the ovary extends only ¼–⅓ the length of the proglottid, whereas it extends at least ½ the length of the proglottid in *Acanthobothrium lineatum* Campbell, 1969. In *A. dollyae,* the cirrus sac is only approximately ⅛ the length of the proglottid, whereas it extends ¼–⅓ the length of the proglottid in *A. lineatum. Acanthobothrium lineatum* also possesses fewer proglottids than *A. dollyae* (6–19 vs. 33–48). Based on the redescription of *Acanthobothrium paulum* Linton, 1890, by Campbell (1969), *A. dollyae* is smaller than *A. paulum* (2.9–3.8 vs. 3–16 mm in total length) but has a larger scolex (830–1,150 vs. 380–930). *Acanthobothrium dollyae* is distinguished from *Acanthobothrium fogeli* Goldstein, 1964, in that its genital pore opens approximately midlevel in the proglottid rather than at the posterior end of the proglottid. In addition, the internal channels of the axial and abaxial prongs of the hooks of *A. dollyae* are continuous but they are discontinuous in *A. fogeli. Acanthobothrium dollyae* differs from *Acanthobothrium himanturi* Brooks, 1977, by its possession of more proglottids (33–48 vs. 17–26) and in the arrangement of the testes in 4 columns anterior to the cirrus sac in *A. dollyae* but in only 2 columns in *A. himanturi.* In addition, in *A. himanturi* the genital pore is in the anterior half of the proglottid, whereas it is approximately midlevel in the proglottid of *A. dollyae. Acanthobothrium lintoni* Goldstein, Henson, and Schlicht, 1969, possesses a cirrus sac that is more globose than that of *A. dollyae.* The testes in *A. lintoni* are

arranged in 2 irregular columns anterior to the cirrus sac but in 4 columns in *A. dollyae*. *Acanthobothrium marplatensis* Ivanov and Campbell, 1998, differs from *A. dollyae* in that the abaxial prongs of its lateral and medial hooks are conspicuously shorter than the axial prongs, rather than approximately equal in length. In addition, *A. marplatensis* has fewer proglottids than *A. dollyae* (18–30 vs. 33–48), and the lateral breaks in the distribution of the spiniform microtriches of the peduncle of *A. marplatensis* reported by Ivanov and Campbell (1998) are not present in *A. dollyae,* which exhibits spiniform microtriches on all surfaces of the cephalic peduncle.

Acanthobothrium dollyae can be distinguished from all species of *Acanthobothrium* from other regions of the world in that it is >2 but <5 mm in total length and possesses >30 and <50 proglottids and >40 and <60 testes.

Acanthobothrium maryanskii sp. n. (Figs. 4–7)

Description

Based on 2 incomplete worms with scolices and 5 strobilar fragments. Worms euapolytic, >29 mm long; maximum width 425–1,220 at level of terminal proglottids; 221–>262 proglottids per worm. Scolex 1,770–1,800 long by 430–620 wide, consisting of cephalic peduncle and 4 muscular acetabula in form of bothridia. Bothridia free anteriorly and posteriorly, 504–568 long by 180–310 wide; each with 3 loculi and specialized anterior region in form of muscular pad; muscular pad 42.5 long by 72–140 wide, with inconspicuous posterior margins, bearing single apical sucker and 1 pair of hooks; apical sucker 33–35 long by 40–54 wide, anterior margin not conspicuously thickened; anterior loculus 232–320 long, middle loculus 75–136 long, posterior loculus 103–144 long; ratio of loculus lengths (anterior : middle : posterior) 2.2–3.9:1–1.4:1–1.4; maximum width of scolex at midlevel of anterior loculus. Velum present between medial margins of adjacent bothridia at level of septum between middle and posterior loculus. Hooks bipronged, hollow; internal channels of axial and abaxial prongs continuous, smooth; axial prongs lacking tubercles; medial hook slightly larger than lateral hook; axial prong of medial hook conspicuously wider than abaxial prong of medial hook and axial prong of lateral hook; axial prongs of medial and lateral hooks conspicuously longer than abaxial prongs. Lateral hook formula:

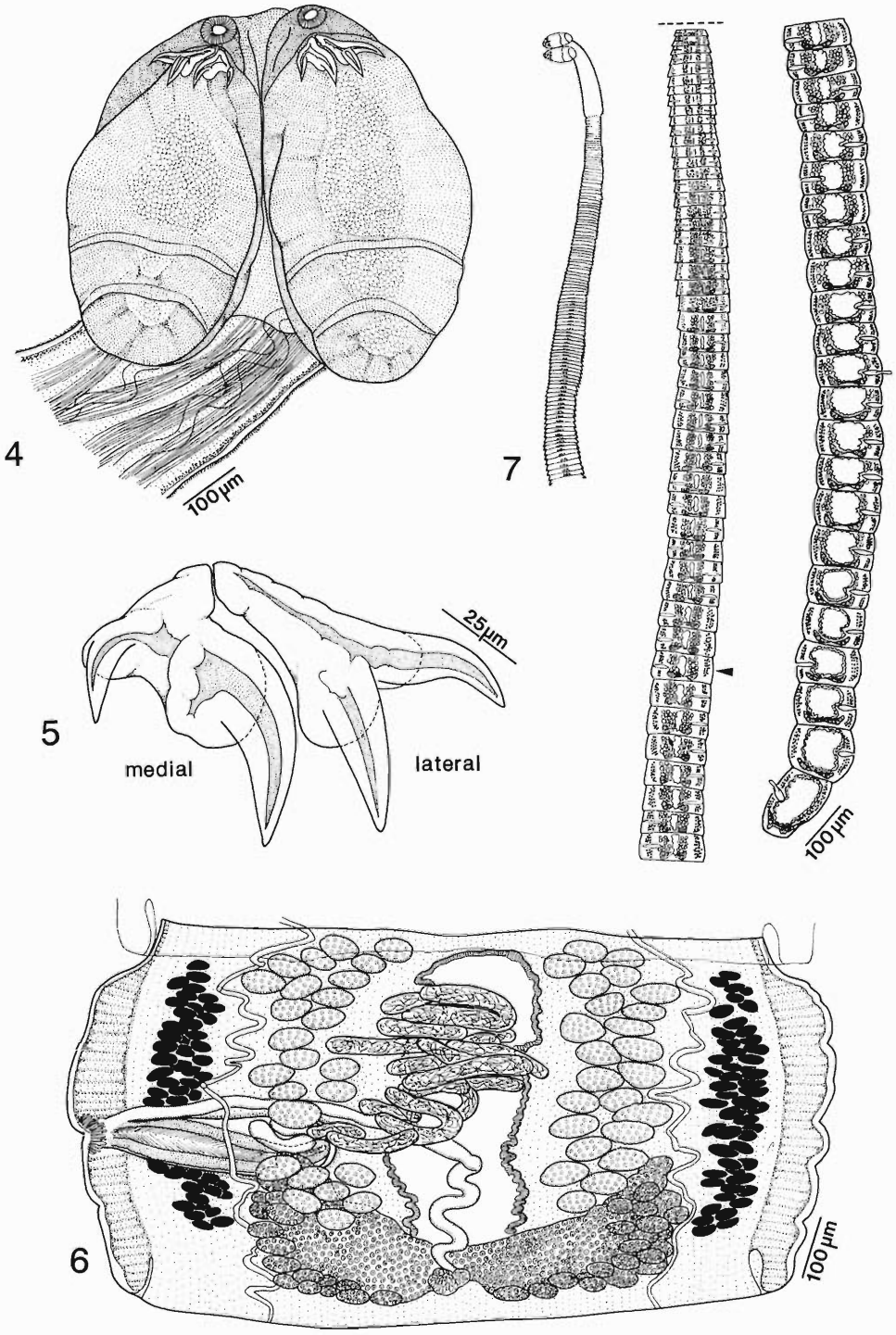
$$\frac{50\text{–}68,\ 50\text{–}53,\ 45\text{–}48}{58\text{–}100}$$

Medial hook formula:

$$\frac{30\text{–}55,\ 45\text{–}60,\ 33\text{–}38}{70\text{–}80}$$

Base of lateral hook longer than base of medial hook, coming into contact along medial axis of bothridium (Fig. 5). Bases and anterior portions of both prongs of medial and lateral hooks embedded in musculature of scolex. Cephalic peduncle extensive, 1,104–1,280 long by 280–360 wide, covered with spiniform microtriches. Microtriche pattern of remaining regions of scolex and strobila not determined.

Proglottids craspedote. Immature proglottids 221–262, wider than long, becoming longer than wide when gravid. Mature proglottids 30, wider than long, 450–530 long by 1,100–1,180 wide. Gravid proglottids 19 in number. Genital pores lateral, irregularly alternating, 37.5–53.5% of proglottid length from posterior end of proglottid. Testes 41–59 in total number; 35–53 in primary field, 5–8 in postvaginal field, generally arranged in 4–6 irregular columns in primary field and 2 or 3 irregular columns in postvaginal field, extending from slightly posterior to ovarian isthmus to anterior margin of proglottid, 1 layer deep; individual testes 23–45 long by 45–85 wide. Vas deferens extensive, conspicuously coiled, extending from anteromedial margin of cirrus sac along median line of proglottid to near anterior margin of proglottid. Cirrus sac elongate, straight, 32–113 long by 216–304 wide, containing coiled cirrus; cirrus densely covered with slender microtriches. Vagina thin walled, sinuous, extending from ootype along median line of proglottid to anterior margin of cirrus sac, then laterally along anterior margin of cirrus sac, not crossing cirrus sac, opening into common genital atrium anterior to cirrus; vaginal sphincter absent; seminal receptacle not seen. Ovary weakly H-shaped in dorsoventral view, shape in cross section not determined, with lobulated margins, located at posterior end of proglottid, 303–576 wide; ovarian arms symmetrical, extending approximately to level of genital pore; poral arm 50–275 long, aporal arm 68–238 long. Mehlis' gland inconspicuous. Vitellarium consisting of 2 lateral bands; each band consisting of multiple follicles not arranged conspicuously in columns, extend-



Figures 4–7. ***Acanthobothrium maryanskii*** **sp. n. 4. Scolex. 5. Hooks. 6. Mature proglottid. 7. Whole worm. Arrow indicates location of proglottid drawn in Fig. 6. Note: Because no complete worm was found, in order to provide an indication of the form of a full worm; this figure is a composite of the anterior portion of 1 worm and the posterior portion of another; the dashed line indicates the break between worm fragments.**

ing from slightly posterior to anterior margin of proglottid approximately to midlevel of ovary, interrupted by cirrus sac and vagina on poral side, not interrupted by ovary. Uterus sacciform, extending anteriorly from ootype along median line of proglottid to anterior margin of proglottid. Uterine pore not seen. Eggs round, filaments apparently lacking. Excretory ducts lateral.

Taxonomic summary

TYPE HOST: Ocellated electric ray *Diplobatis ommata* (Jordan and Gilbert, 1890).

SITE OF INFECTION: Spiral intestine.

TYPE LOCALITY: Loreto (26°01′N, 111°21′W), Gulf of California, Mexico.

ADDITIONAL LOCALITY: Punta Arena (24°04′N, 109°50′W), Gulf of California, Mexico.

HOLOTYPE: CNHE 4171.

PARATYPES: CNHE 4172; LRP 2012, 2013; USNPC 90840, 90841.

ETYMOLOGY: This species is named in honor of Fred Maryanski, in recognition of his dedicated and expert service to the University of Connecticut.

Remarks

Acanthobothrium maryanskii is >15 mm in total length and has >50 proglottids, <80 testes, and a symmetrical ovary. Based on the criteria of Ghoshroy and Caira (in press), it is a Category 5 species. It is distinguished from all 6 Category 5 species reported previously from the eastern Pacific Ocean (Ghoshroy and Caira, in press, table II) in having mature proglottids wider than long rather than longer than wide. *Acanthobothrium maryanskii* differs from *Acanthobothrium franus* Marques, Centritto, and Stuart, 1997, in hook shape. Whereas the new species possesses robust, short, asymmetrical hooks in which the axial prong of the medial hook is longer and wider than the abaxial prong of the medial hook, *A. franus* possesses hooks with slender, elongate prongs symmetrical within and between pairs. *Acanthobothrium maryanskii* differs from *Acanthobothrium inbiorium* Marques, Centritto, and Stuart, 1997, and *Acanthobothrium psammobati* Carvajal and Goldstein, 1969, in that the hooks of both of those species are symmetrical within and between pairs. *Acanthobothrium maryanskii* differs from *Acanthobothrium goldsteini* Appy and Dailey, 1973, in that the latter species lacks the inflated scolex seen in the former species, and the hooks of *A. goldsteini* are less robust than those of *A. maryanskii*. *Acanthobothrium maryanskii* differs from *Acanthobothrium rhinobati* Alexander, 1953, and *Acanthobothrium hispidum* Riser, 1955, in having more proglottids (221–262+ vs. 50, and up to 200, respectively).

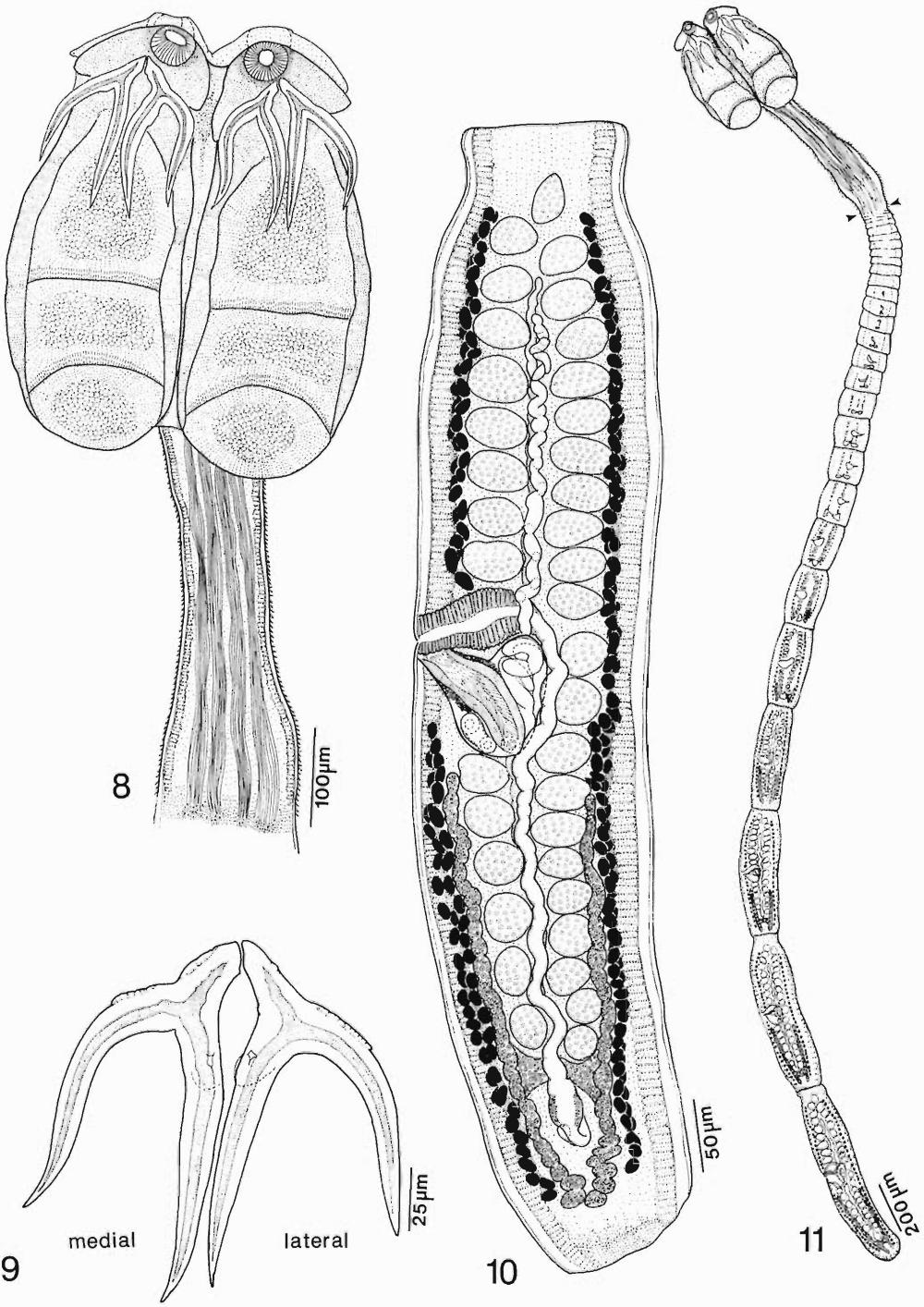
Acanthobothrium maryanskii differs from all 5 of the Category 5 species reported previously from the western Atlantic Ocean (Ghoshroy and Caira, in press, table III) in having mature proglottids wider than long rather than longer than wide. In addition, whereas *A. maryanskii* possesses an ovary that is only minimally H-shaped in dorsoventral view and medial hooks in which the axial prong is conspicuously wider than the abaxial prong, this is not the case for *A. paulum, A. lintoni, Acanthobothrium amazonensis* Mayes, Brooks, and Thorson, 1978, *Acanthobothrium regoi* Brooks, Mayes, and Thorson, 1981, and *Acanthobothrium quinonesi* Mayes, Brooks, and Thorson, 1978, which possess ovaries that are conspicuously H-shaped in dorsoventral view and medial hooks in which the axial and abaxial prongs are approximately equal in width. In addition, *A. maryanskii* possesses a greater number of proglottids than do *A. amazonensis, A. quinonesi,* and *A. regoi* (221–262 vs. 75–100, 55–75, and 87–120, respectively). *Acanthobothrium maryanskii* also has more proglottids than do both *A. paulum* and *A. lintoni* (≤238 vs. 22–50 and 5–60, respectively).

Acanthobothrium maryanskii can be distinguished from all but the following species of *Acanthobothrium* from other regions of the world in that it is >25 mm but <50 mm in total length, possesses >200 proglottids, and has >40 but <60 testes. It differs from *Acanthobothrium pintanensis* Wang, 1984, and *Acanthobothrium zschokkei* Baer, 1948, by medial hooks in which the axial prong is conspicuously wider than the abaxial, prong rather than medial hooks in which both prongs are of approximately equal width. *Acanthobothrium maryanskii* further differs from *A. pintanensis* in its central bothridial loculi that are oval rather than dumbbell shaped and further differs from *A. zschokkei* in its mature proglottids, which are wider than long rather than longer than wide.

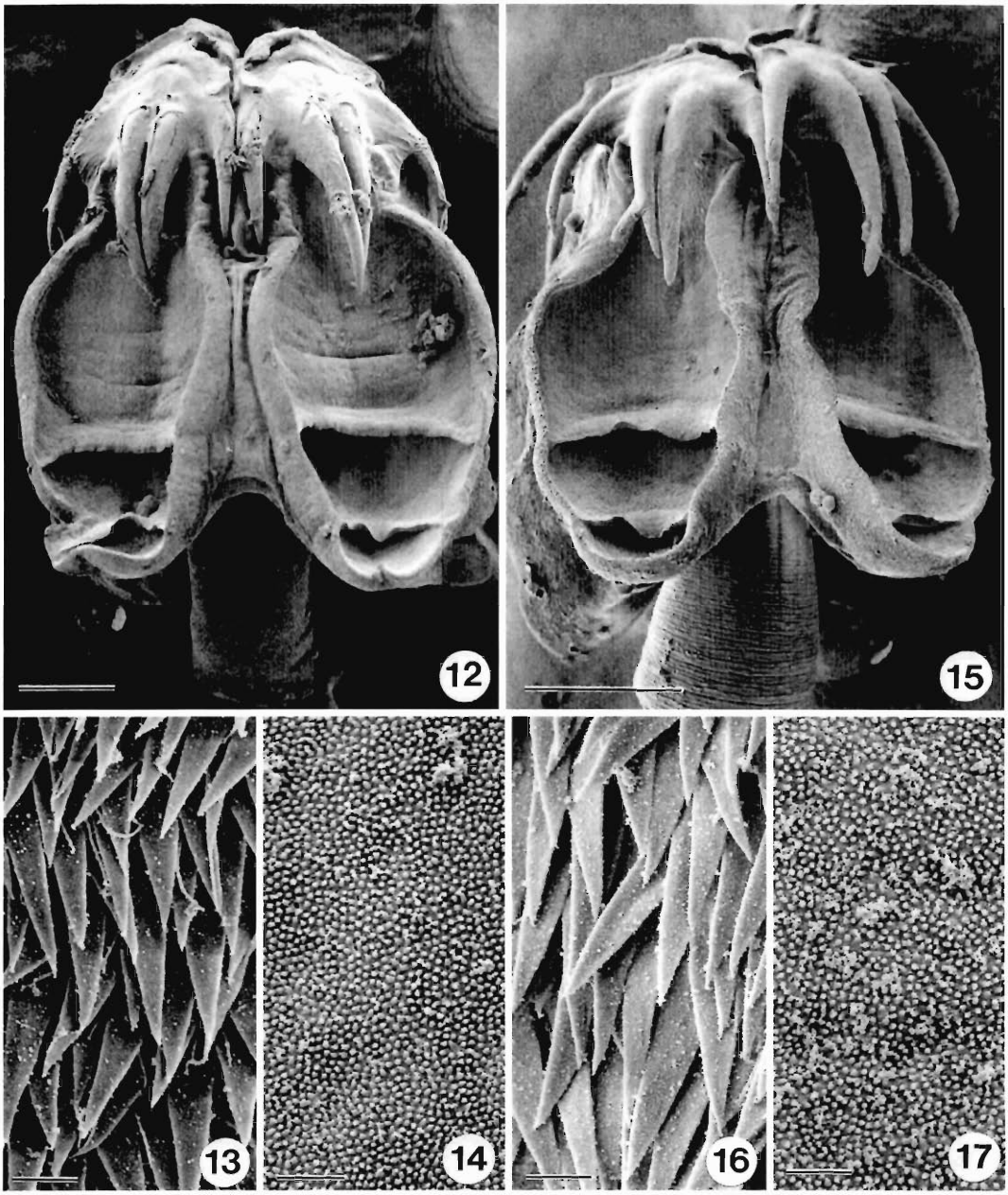
Acanthobothrium royi sp. n. (Figs. 8–11, 15–17)

Description

Based on 2 whole worms and 2 scolices with



Figures 8–11. ***Acanthobothrium royi*** **sp. n. 8. Scolex. 9. Hooks. 10. Terminal mature proglottid. 11. Whole worm. Arrows indicate location of break in the actual specimen.**



Figures 12–17. Scanning electron micrographs of scolices. 12–14. *Acanthobothrium dollyae* sp. n. 12. Scolex. Bar = 100 μm. 13. Enlarged view of proximal bothridial surface. Bar = 1 μm. 14. Enlarged view of distal bothridial surface. Bar = 1 μm. 15–17. *Acanthobothrium royi* sp. n. 15. Scolex. Bar = 100 μm. 16. Enlarged view of proximal bothridial surface. Bar = 1 μm. 17. Enlarged view of distal bothridial surface. Bar = 1 μm.

partial strobilae. Worms euapolytic, 3.9–5.0 mm long; maximum width 336–380 at level of scolex; 19–26 proglottids per worm. Scolex 512–770 long by 336–380 wide, consisting of cephalic peduncle and 4 muscular acetabula in form of bothridia. Bothridia free anteriorly and posteriorly, 328–450 long by 160–195 wide; each with 3 loculi and specialized anterior re-

gion in form of muscular pad; muscular pad 75–88 long by 106–163 wide, with rounded posterolateral margins, bearing single apical sucker and 1 pair of hooks; apical sucker 38–48 long by 43–50 wide, anterior margin conspicuously thickened; anterior loculus 138–200 long, middle loculus 55–100 long, posterior loculus 75–113 long; ratio of loculus lengths (anterior : middle : posterior) 1.6–3.2:1–1.7:1–1.8; maximum width of scolex usually at posterior margin of anterior loculus. Velum present between medial margins of adjacent bothridia at midlevel of posterior loculus. Hooks bipronged, hollow, internal channels of axial and abaxial prongs continuous, smooth; anterior portion of axial prongs of medial and lateral hooks with inconspicuous tubercle on proximal surface; hooks approximately equal in size; axial prongs of medial and lateral hooks longer than abaxial prongs.

Lateral hook formula:

$$\frac{38\text{–}50,\ 88\text{–}123,\ 83\text{–}108}{123\text{–}165}$$

Medial hook formula:

$$\frac{30\text{–}50,\ 78\text{–}123,\ 88\text{–}113}{113\text{–}163}$$

Bases of medial and lateral hooks approximately equal in length, coming into contact along medial axis of bothridium (Fig. 9). Bases and anterior part of both prongs of medial and lateral hooks embedded in musculature of scolex. Cephalic peduncle 256–420 long by 120–152 wide, covered with spiniform microtriches.

Scolex, velum, and distal bothridial surfaces covered with short filiform microtriches only. Proximal bothridial surfaces and cephalic peduncle covered with densely arranged blade-like spiniform microtriches; filiform microtriches not visible in these regions. Strobilar surfaces covered with long filiform microtriches only.

Proglottids acraspedote. Immature proglottids 17–24, wider than long, becoming longer than wide with maturity. Mature proglottids 2, longer than wide, 590–900 long by 120–155 wide. No gravid proglottids seen. Genital pores lateral, irregularly alternating, opening anterior to ovarian isthmus, 50–59% of proglottid length from posterior end of proglottid. Testes 30–36 in total number; 24–30 in primary field, 6 in postvaginal field, generally arranged in 2 columns in primary field and 1 column in postvaginal field; extending from ovarian isthmus to near anterior margin of proglottid, 1 layer deep; individual testes 23–30 long by 23–40 wide. Vas deferens minimal, slightly coiled, extending from anteromedian margin of cirrus sac along median line of proglottid into anterior fifth of proglottid. Cirrus sac pyriform, bent anteriorly, 63–78 long by 78–110 wide, containing coiled cirrus; cirrus densely covered with slender microtriches. Vagina thick walled, weakly sinuous, extending anteriorly from slightly posterior to ovarian bridge along median line of proglottid to anterior margin of cirrus sac, then laterally along anterior margin of but not crossing cirrus sac, opening into common genital atrium anterior to cirrus; vaginal sphincter absent; base of vagina expanded to form seminal receptacle. Ovary H-shaped in dorsoventral view, tetralobed in cross section, with lobulated margins, located at posterior end of proglottid, 85–100 wide; ovarian arms symmetrical, not reaching posterior margin of cirrus sac; poral arm 205–320 long; aporal arm 195–345 long. Mehlis' gland inconspicuous. Vitellarium consisting of 2 lateral bands; each band consisting of 2 columns of follicles. Vitelline follicles extending from slightly posterior to anterior margin of testicular field to near posterior margin of ovary, interrupted by cirrus sac and vagina on poral side, not interrupted by ovary. Uterus sacciform, extending anteriorly from ootype along median line of proglottid to slightly posterior to anterior margin of vitelline follicles. Uterine pore not seen. Eggs not seen. Excretory ducts lateral.

Taxonomic summary

TYPE HOST: Ocellated electric ray *Diplobatis ommata* (Jordan and Gilbert, 1890).

SITE OF INFECTION: Spiral intestine.

TYPE LOCALITY: Punta Arena (24°04′N, 109°50′W), Gulf of California, Mexico.

ADDITIONAL LOCALITY: Loreto (26°01′N, 111°21′W), Gulf of California, Mexico.

HOLOTYPE: CNHE 4173.

PARATYPES: CNHE 4174; LRP 2104; USNPC 90842.

ETYMOLOGY: This species is named in honor of the father of one of the authors (A.N.B.).

Remarks

Acanthobothrium royi is <15 mm in total length, possesses <50 proglottids and <80 testes, and generally exhibits a symmetrical ovary. Based on the criteria of Ghoshroy and Caira (in press), it is a Category 1 species. However, be-

cause the ovary was slightly asymmetrical in a few proglottids, comparisons with Category 2 species are also made. *Acanthobothrium royi* can be distinguished from the 4 Category 1 species reported previously from the eastern Pacific Ocean (Ghoshroy and Caira, in press, table II) as follows. *Acanthobothrium royi* has a much smaller cirrus sac than *A. monksi* (1/6 proglottid length vs. 1/3–1/2 proglottid length), a genital pore that is more posterior than that of *A. nicoyaense,* and more testes than *A. nicoyaense* (30–36 vs. 12–22). *Acanthobothrium royi* differs from *A. atahualpai* in that the vas deferens of the latter species fills the anterior portion of the mature proglottid, whereas in *A. royi* the vas deferens is minimal, even in what otherwise appear to be fully mature proglottids. The S-shaped abaxial prongs of the medial and lateral hooks of *A. atahualpai* also serve to distinguish this species from *A. royi,* which possesses straight abaxial prongs on both its medial and lateral hooks. *Acanthobothrium minusculus* possesses fewer testes than *A. royi* (6–10 vs. 30–36). *Acanthobothrium royi* differs from *A. dollyae* in its possession of testes arranged in 2 rather than 4 columns anterior to the cirrus sac and in having a shorter scolex (512–770 vs. 830–1,150).

Acanthobothrium royi is distinguished from 13 of the 14 Category 2 species reported previously from the eastern Pacific Ocean (Ghoshroy and Caira, in press, table II) in that the aporal lobe of the ovary does not reach the level of the posterior margin of the cirrus sac. The 13 species that possess a poral lobe that extends at least to the cirrus sac are *Acanthobothrium bullardi* Ghoshroy and Caira, in press; *Acanthobothrium dasi* Ghoshroy and Caira, in press; *Acanthobothrium rajivi* Ghoshroy and Caira, in press; *Acanthobothrium cimari* Marques, Brooks, and Monks, 1995; *Acanthobothrium costarricense* Marques, Brooks, and Monks, 1995; *Acanthobothrium puntarenasense* Marques, Brooks, and Monks, 1995; *Acanthobothrium vargasi* Marques, Brooks, and Monks, 1995; *Acanthobothrium unilateralis* Alexander, 1953; *Acanthobothrium coquimbensis* Carvajal and Jeges, 1980; *Acanthobothrium annapinkiensis* Carvajal and Goldstein, 1971; *Acanthobothrium brachyacanthum* Riser, 1955; *Acanthobothrium olseni* Dailey and Mudry, 1968; and *Acanthobothrium campbelli* Marques, Brooks, and Monks, 1955. *Acanthobothrium royi* can be distinguished from *Acanthobothrium batailloni* Euzet, 1955, in that it is a much smaller worm (3.9–5 vs. 15–20 mm in total length) and it possesses testes arranged in 2 rather than ≥4 columns anterior to the cirrus sac.

Acanthobothrium royi differs from the 6 Category 1 species reported previously from the western Atlantic Ocean (Ghoshroy and Caira, in press, table III) as follows. It possesses more proglottids (19–26 vs. 6–19), and its cirrus sac is smaller in proportion to the length of the proglottid (1/6–1/7 vs. 1/2–1/3) than in *A. lineatum. Acanthobothrium paulum* differs from *A. royi* in its possession of a cirrus sac that is straight rather than curved anteriorly, and testes that are arranged in 4 irregular columns anterior to the cirrus sac rather than 2 columns. *Acanthobothrium royi* differs from *A. fogeli* by a genital pore that opens slightly anterior to the midpoint of the proglottid, rather than at the posterior extremity. In addition, whereas the axial and abaxial prongs of the hooks of *A. fogeli* possess channels that are discontinuous, the channels of these prongs are continuous in the hooks of *A. royi.* The aporal arm of the ovary of *A. royi* does not reach the level of the cirrus sac, but extends slightly anterior to the posterior margin of the cirrus sac in *A. himanturi.* In addition, *A. himanturi* possesses a genital pore more anterior than that of *A. royi.* The bothridia of *A. royi* are conspicuously rounded posteriorly, whereas those of *A. lintoni* are conspicuously pointed. In addition the cirrus sac of *A. lintoni* is ovoid, whereas that of *A. royi* is curved anteriorly. *Acanthobothrium marplatensis* differs from *A. royi* in that the abaxial prongs of the lateral and medial hooks are conspicuously shorter than the axial prongs, whereas *A. royi* possesses lateral and medial hooks in which the abaxial prongs are only slightly shorter than the axial prongs. In addition, the lateral breaks in the spiniform microtriches of the peduncle of *A. marplatensis* reported by Ivanov and Campbell (1998) are not present in *A. royi,* which exhibits spiniform microtriches throughout all surfaces of the cephalic peduncle.

Acanthobothrium royi differs from 4 of the 5 Category 2 species reported from the western Atlantic Ocean in that the aporal lobe of the ovary does not extend to the level of the posterior margin of the cirrus sac. The 4 species that possess an aporal lobe that extends at least to the cirrus sac are *Acanthobothrium woodsholei* Baer, 1948; *Acanthobothrium brevissime* Linton, 1908; *Acanthobothrium tasajerasi* Brooks, 1977; and *Acanthobothrium urotrygoni* Brooks

and Mayes, 1980. *Acanthobothrium royi* can further be distinguished from *A. woodsholei* in its possession of 2 rather than ≥4 columns of testes anterior to the cirrus sac. *Acanthobothrium royi* can further be distinguished from *A. brevissime* as redescribed by Campbell (1969) in having a wider scolex (336–386 vs. 183–300) and longer posterior loculus (75–113 vs. 25–79). In addition, *A. royi* lacks the extensive genital atrium seen in *A. tasajerasi,* and whereas the cirrus sac of *A. royi* is bent anteriorly, that of *A. urotrygoni* is bent posteriorly. *Acanthobothrium royi* differs from *Acanthobothrium zapterycum* Ostrowski de Nunez, 1971, the other species reported from the western Atlantic Ocean in which the ovary does not extend to the cirrus sac, in its possession of a genital atrium that is approximately at midlevel in the proglottid rather than conspicuously anterior. In addition, whereas the cirrus sac of *A. royi* is bent anteriorly, that of *A. zapterycum* is bent posteriorly.

Acanthobothrium royi can be distinguished from all species of *Acanthobothrium* from other regions of the world in that it is >2 but <10 mm in total length and has >15 but <30 proglottids and >30 but <40 testes. *Acanthobothrium royi* is easily distinguished from *Acanthobothrium mujibi* Bilquees, 1980, in its possession of 2 regular rather than 4 irregular columns of testes anterior to the cirrus sac, and in its genital pores located slightly anterior to equatorial rather than in the posterior fifth of the proglottid.

Discussion

In their comprehensive treatments of the genus *Acanthobothrium,* both Goldstein (1967) and Williams (1969) suggested that there is a substantial degree of host specificity between species of *Acanthobothrium* and their elasmobranch hosts. Thus, it is not surprising that this first investigation of *Acanthobothrium* from the ocellated electric ray *Diplobatis ommata* has resulted in the discovery of new species. Species of *Acanthobothrium* have been reported from other species of torpediniform rays, including 4 species of electric rays in 2 genera in the family Narcinidae and 2 species of *Torpedo* in the family Torpedinidae. Among the members of the family Narcinidae distributed in the coastal waters of North and South America, Brooks and Mayes (1978) described *Acanthobothrium electricolum* Brooks and Mayes, 1978, from the Brazilian electric ray *Narcine brasiliensis* (Olfers, 1831) in the Caribbean Sea, and Goldstein et al. (1969) described *A. lintoni* from *N. brasiliensis* in the Gulf of Mexico. Marques, Centritto, and Stewart (1997) described *A. inbiorium* and *A. franus* from the giant electric ray *Narcine entemedor* Jordan and Starks, 1895, from the west coast of Costa Rica, and Riser (1955) described *A. hispidum* from *N. entemedor* (as "*Tetranarce californica*") from Monterey Bay, California, U.S.A. Records also exist for species of Narcinidae distributed in other regions of the world. Subhapradha (1955) described *Acanthobothrium indicum* from *Narcine braunii* off the Madras coast of India. Yamaguti (1952) described *A. gracile* from the electric numbray *Narke japonica* (Temminck and Schlegel, 1850) in Tokusima, Japan. The localities of record for both species of *Acanthobothrium* described from members of the Torpedinidae are unclear. Baer (1948) described *A. zschokkei* from the common torpedo ray *Torpedo ocellata* presumably somewhere off Europe, and Zschokke (1889) described *A. filicolle* (Zschokke, 1889) from the common crampfish *Torpedo marmorata* Risso, 1810, also possibly off Europe. At present, affinities and/or trends in morphology are difficult to detect among the species of *Acanthobothrium* reported from torpediniform rays. However, 8 of the 12 species of *Acanthobothrium* hosted by the 6 species of torpediniform rays examined to date are relatively large worms (>15 mm in total length).

As discussed by Ghoshroy and Caira (in press), it is not unusual for a single species of ray to host multiple species of *Acanthobothrium.* Thus, the existence of 3 species of *Acanthobothrium* in *D. ommata* is consistent with existing knowledge of the genus. The *Acanthobothrium* fauna of *D. ommata* is not as diverse as it appears to be in some host species. For example, the longtail stingray *Dasyatis longus* (Garman, 1880) has been reported to host a total of 8 species of *Acanthobothrium* (Marques et al., 1995; Monks et al. 1996; Marques, Brooks, and Barriga, 1997). However, other species of elasmobranchs have been reported to host only a single species of *Acanthobothrium.* For example, 5 species of freshwater stingrays in the genus *Potamotrygon* Garman, 1877, have each been reported to host only a single species of *Acanthobothrium* (Ghoshroy and Caira, in press).

The 3 species of *Acanthobothrium* described here from *D. ommata,* in combination with the 4

species described from the whiptail stingray *Dasyatis brevis* Garman, 1880, by Ghoshroy and Caira (in press), brings the total number of *Acanthobothrium* species reported from the Gulf of California to 7. Presently, all 7 of these species are known only from the Gulf of California. However, because neither of these host species has been examined for *Acanthobothrium* in other regions of their geographic distributions, these data are insufficient to suggest that these 7 species comprise a fauna unique to the Gulf of California.

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Neotropical Monogenoidea. 38. Revision of *Rhabdosynochus* Mizelle and Blatz, 1941 (Polyonchoinea: Dactylogyridea: Diplectanidae), with Descriptions of Two New Species from Brazil

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ABSTRACT: We emended the generic diagnosis of *Rhabdosynochus* Mizelle and Blatz, 1941, and described *Rhabdosynochus hargisi* sp. n. and *Rhabdosynochus hudsoni* sp. n. from cultured common snook *Centropomus undecimalis* from Itamaracá, Pernambuco, Brazil. Members of *Rhabdosynochus* lack peduncular or haptoral adhesive plaques and possess a scaled tegument on the posterior trunk and peduncle; the lateral plaques (=placodiscs) in *R. hargisi* are not considered homologs of the ventral and dorsal squamodiscs or lamellodiscs present in most other diplectanids. Illustrations and measurements of the sclerotized components of the haptor of the newly designated lectotype and paralectotypes of *Rhabdosynochus rhabdosynochus* Mizelle and Blatz, 1941, are provided. An undescribed species of *Rhabdosynochus* occurs on *Centropomus ensiferus* and *C. undecimalis* in Puerto Rico.

KEY WORDS: Monogenoidea, Diplectanidae, *Rhabdosynochus, Rhabdosynochus rhabdosynochus, Rhabdosynochus hargisi* sp. n., *Rhabdosynochus hudsoni* sp. n., Perciformes, Centropomidae, *Centropomus undecimalis,* Brazil, Puerto Rico.

The monotypic *Rhabdosynochus* was proposed by Mizelle and Blatz (1941) for their new species, *Rhabdosynochus rhabdosynochus,* from the gills of the common snook *Centropomus undecimalis* (Bloch, 1792), Centropomidae, in the Myakka River, East Sarasota, Florida. Hargis (1955) provided an emended generic diagnosis and placed the genus in the Diplectanidae, based on specimens thought to represent the type species from *C. undecimalis* in Tampa Bay, Florida; his complete redescription of *R. rhabdosynochus* based on his specimens has served for the identification of the type species by subsequent workers (Yamaguti, 1963; Oliver, 1987; Bunkley-Williams and Williams, 1994, 1995). During 1995, we collected 2 species of *Rhabdosynochus* from the gills of cultured *C. undecimalis* in eastern Brazil. Specimens of 1 of these species were identical with those reported by Hargis (1955). Based on examination of the type specimens of *R. rhabdosynochus* deposited in the U.S. National Parasite Collection (USNPC) and in the University of Nebraska State Museum (HWML), Hargis' (1955) specimens clearly represent an undescribed species. Here, *Rhabdosynochus* is revised, the anchors, hook, and copulatory complex of *R. rhabdosynochus* are illustrated, and the 2 new species are described. An undescribed species of *Rhabdosynochus* (synonym of *R. rhabdosynochus* of Bunkley-Williams and Williams, 1994, 1995) is reported from Puerto Rico.

Materials and Methods

Hosts were obtained from culture facilities (earthen ponds) on the island of Itamaracá, State of Pernambuco, Brazil (7°41′S, 34°53′W), during 1995. Standard lengths of infected hosts ranged from 15.5 cm to 31.6 cm (total length, 16.8–37.1 cm). Diplectanids were removed from the gills of hosts with a 1:4,000 formalin solution and fixed and stored in 4% formalin; vials containing the helminths were then shipped to Idaho State University. Methods of staining, mounting, and illustration of diplectanids were those described by Kritsky et al. (1986). Measurements (in micrometers) were made with a filar micrometer according to procedures of Mizelle and Klucka (1953). Average measurements are followed by ranges and number of specimens measured (*n*) in parentheses. Unstained flattened specimens mounted in Gray and Wess' medium were used to obtain measurements of the haptoral sclerites; all other measurements were obtained from unflattened specimens stained in Gomori's trichrome and mounted in Canada balsam. The dimension of the pyriform germarium was the greatest width, and measurement of the copulatory complex was the straight-line distance

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between the parallel lines on Figures 1, 8, and 20. Numbering of hook pairs follows Mizelle (1936; see Mizelle and Price, 1963). Type specimens were deposited in the Instituto Nacional de Pesquisas da Amazônia, Manaus, State of Amazonas, Brazil (INPA); the Instituto Oswaldo Cruz, Rio de Janeiro, State of Rio de Janeiro, Brazil (IOC); the USNPC, Beltsville, Maryland; the HWML, Lincoln, Nebraska; and the Meguro Parasitological Museum, Meguro-ku, Tokyo, Japan (MPM), as indicated in the respective descriptions. The following museum specimens were examined: lectotype, 3 paralectotypes, *R. rhabdosynochus* (USNPC 89848, 36822, HWML 21551); 9 voucher specimens, *R. rhabdosynochus* of Hargis (1955) (synonym *Rhabdosynochus hargisi* sp. n.) (USNPC 49347); 3 voucher specimens, *R. rhabdosynochus* of Dyer (unpublished) (synonym *R. hargisi*) (USNPC 82667); 2 voucher specimens, *R. rhabdosynochus* of Bunkley-Williams and Williams (1995) (synonym of an undescribed species of *Rhabdosynochus*) (USNPC 84684, 84685); holotype, numerous paratypes, *Murraytrematoides ditrematis* Yamaguti, 1958 (MPM 22563); holotype, numerous paratypes, *Geneticoenteron lateolabracis* Yamaguti, 1958 (MPM 22562); holotype, 9 paratypes, *Murraytrematoides kuhliae* Yamaguti, 1968 (USNPC 63655); and type, *Diplectanum bychowskyi* Nagibina, 1976 (Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia [ZIRAS] 5116). Host names follow those in the Food and Agriculture Organization of the United Nations Fish Base (http://www.fao.org/waicent/faoinfo/fishery/fishbase/fishbase.htm).

Results

Order Dactylogyridea Bychowsky, 1937
Suborder Dactylogyrinea Bychowsky, 1937
Diplectanidae Monticelli, 1903
Rhabdosynochus Mizelle and Blatz, 1941

EMENDED DIAGNOSIS: Body fusiform to subtriangular, flattened dorsoventrally, comprising cephalic region, trunk, peduncle, haptor; haptoral or peduncular adhesive plaques absent. Tegument scaled on all surfaces of posterior trunk, peduncle; scales plate-like, lightly sclerotized, directed anteriorly. Two terminal, 2 bilateral cephalic lobes; 3 bilateral pairs of head organs; cephalic glands unicellular, lateral or posterolateral to pharynx. Two pairs of eyes; eye granules ovate, small. Mouth subterminal, ventral to pharynx; single pharyngeal bulb muscular, glandular; esophagus short to absent; 2 intestinal ceca terminating blindly posterior to gonads, lacking diverticula. Genital pore midventral, posterior to copulatory complex. Gonads tandem. Testis postgermarial; vas deferens looping left intestinal cecum (in *R. hargisi* sp. n.); seminal vesicle a dilation of vas deferens; 1 prostatic reservoir. Copulatory complex comprising nonarticulated male copulatory organ, accessory piece; male copulatory organ tubular, coiled, with clockwise ring or rings (see Kritsky et al., 1985). Accessory piece comprising several sclerotized subunits; 1 subunit grooved, serving as guide for male copulatory organ. Germarium pyriform, looping right intestinal cecum dorsoventrally; seminal receptacle pregermarial; vaginal aperture ventral, near common genital pore; vitellaria throughout trunk, peduncle, absent in regions of other reproductive organs. Haptor bilaterally lobed, armed with dorsal, ventral anchor/bar complexes, 7 pairs of similar hooks; each hook lying near tip of small haptoral peduncle; hook distribution ancyrocephaline (Mizelle, 1936; see Mizelle and Price, 1963). Haptoral bars closely associated; ventral bar with longitudinal groove; paired dorsal bars with expanded medial end. Hook thumb protruding, slightly depressed; shank nondilated. Parasites of gills of Centropomidae (marine, freshwater, brackish water) (Perciformes).

TYPE SPECIES: *Rhabdosynochus rhabdosynochus* Mizelle and Blatz, 1941 (type specimens present in USNPC).

OTHER SPECIES: *Rhabdosynochus hargisi* sp. n., *Rhabdosynochus hudsoni* sp. n., *Rhabdosynochus* sp. (synonym *R. rhabdosynochus* of Bunkley-Williams and Williams, 1995).

REMARKS: The original diagnosis of *Rhabdosynochus* by Mizelle and Blatz (1941) only included features associated with the haptoral armament, gut, eyes, vagina, and copulatory complex (2 bars fused in their midportons, dissimilar anchors, 14 hooks, gut bifurcated with nonconfluent ceca, 4 eyes, vagina absent, and copulatory complex comprised of a basally articulated male copulatory organ and accessory piece). These authors placed the genus in the Tetraonchinae Monticelli, 1903, which at that time included species currently ensconced in the Ancyrocephalinae Bychowsky, 1937, and the Tetraonchidae Monticelli, 1903. Mizelle and Blatz's (1941) assignment of *Rhabdosynochus* to the Tetraonchinae was apparently based in part on their erroneous observations that a single dorsal bar and an intercecal germarium occurred in the type species. Hargis (1955) emended the generic diagnosis and transferred the genus to the Diplectanidae, in part because paired dorsal bars were present and the germarium looped the right intestinal cecum in his specimens.

Hargis (1955) apparently assumed that the lat-

eral plaques (frills) in his specimens were homologous to the ventral and dorsal adhesive discs of most other Diplectanidae. He considered the presence of lateral plaques a diagnostic feature of *Rhabdosynochus,* which along with the assumed homology further supported his transfer of the genus to the Diplectanidae. Unfortunately, Hargis' (1955) identification of his specimens as *R. rhabdosynochus* was erroneous, and his specimens represent an undescribed species, which is the only member of the genus with lateral plaques or frills on the peduncle. Based on the absence of dorsal and ventral adhesive discs in putative outgroups (Kritsky and Boeger, 1989; Boeger and Kritsky, 1993) and in all other species of *Rhabdosynochus,* the genus apparently diverged comparatively early in the evolutionary history of the Diplectanidae. Because the frills differ in morphology and position from the adhesive discs of most other diplectanids, they are likely not homologous to squamodiscs or lamellodiscs but probably are a secondarily derived trait within *Rhabdosynochus.* Nonetheless, we consider that the transfer of *Rhabdosynochus* to the Diplectanidae is defensible based on the general position and morphology of the haptoral sclerites and reproductive organs.

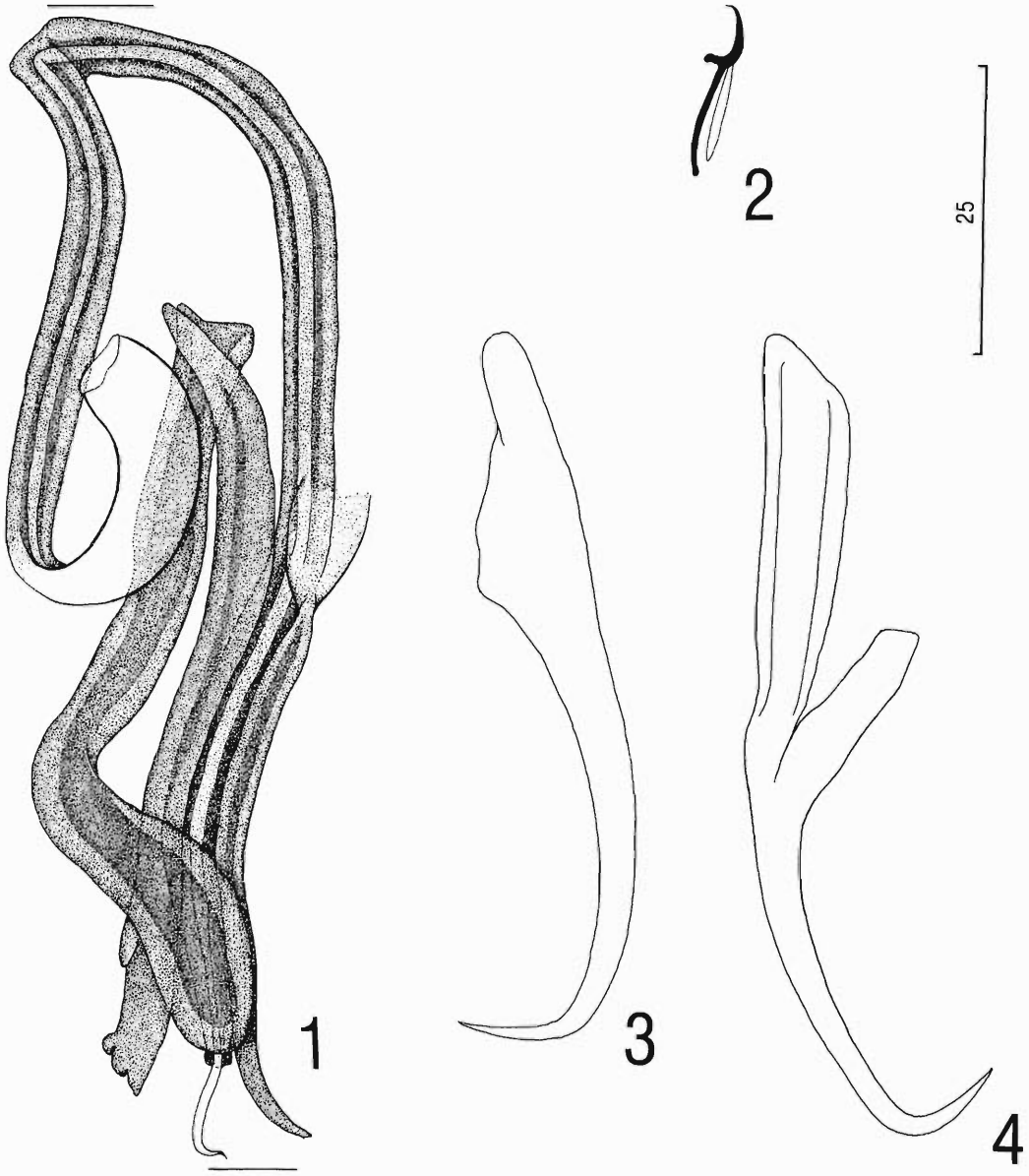
Characters defining *Rhabdosynochus* include the combined presence of 1) anteriorly directed plate-like tegumental scales on the trunk and peduncle, 2) 2 pairs of eyes comprised of small ovate granules, 3) intestinal ceca terminating blindly in the peduncle, 4) genital pore midventral, posterior to the copulatory complex, 5) tandem gonads (testis postgermarial, germarium looping right intestinal cecum), 6) male copulatory organ a coil with clockwise ring(s), 7) accessory piece comprising several sclerotized subunits, 1 subunit serving as a guide for the male copulatory organ, 8) vaginal aperture ventral, near common genital pore, 9) haptor bilobed, armed with paired dorsal bars, ventral bar, dorsal and ventral anchor pairs, and 14 hooks with ancyrocephaline distribution, 10) ventral bar in close proximity with the dorsal bars, with longitudinal groove, 11) hook shank nondilated, and 12) absence of haptoral (peduncular) adhesive plaques. Of these features, the general morphology of the copulatory complex and tegumental scales apparently serve as synapomorphies for the genus. Known species of *Rhabdosynochus* are restricted to members of the Centropomidae (Perciformes) in the Gulf of Mexico and southwestern Atlantic Ocean.

In addition to *Rhabdosynochus,* 3 other diplectanid genera, *Murraytrema* Price, 1937, *Murraytrematoides* Yamaguti, 1958, and *Lobotrema* Tripathi, 1959, lack adhesive plaques on the haptor or peduncle. *Rhabdosynochus* is most similar to *Murraytrematoides* in the general morphology and distribution of the haptoral sclerites and of the internal organ systems. It differs from *Murraytrematoides* in possessing a scaled tegument (tegument smooth in species of *Murraytrematoides*) and a coiled male copulatory organ (copulatory organ a comparatively straight, poorly sclerotized tube in species of *Murraytrematoides*). *Rhabdosynochus* differs from *Lobotrema* and *Murraytrema* in the position and number of haptoral bars (2 bars in species of *Lobotrema*; 3 widely separated bars in species of *Murraytrema*) (Oliver, 1987).

Rhabdosynochus rhabdosynochus Mizelle and Blatz, 1941 (Figs. 1–4)

MEASUREMENTS (original measurements by Mizelle and Blatz [1941] are in brackets following respective values from the present study): Body 402 (329–474; $n = 2$) [452 (290–622)] long, 129 (118–140; $n = 2$) [120 (94–152)] wide at midlength; haptor 94 (87–101; $n = 2$) [69 (54–94)] long, 207 (204–210; $n = 2$) [228 (169–259)] wide; ventral anchor 72 (69–74; $n = 3$) [72 (67–76)] long, base 18–19 ($n = 1$) [21 (17–24)] wide; dorsal anchor 64 (62–68; $n = 3$) [64 (57–67)] long, base 11–12 ($n = 1$) [13 (10–15)] wide; dorsal bar 92 (88–95; $n = 2$) [200 (145–229)] long; hook 13–14 ($n = 2$) [8–11] long; copulatory complex 105–106 ($n = 1$) long. Mizelle and Blatz (1941) did not observe 2 dorsal bars; their measurement of the dorsal bar corresponds to the distance between the lateral terminations of each dorsal bar in the haptor. The poor condition of available type specimens prevented measurement of soft body parts and the ventral bar, but Mizelle and Blatz (1941) reported a pharyngeal diameter of 31 (24–36).

PREVIOUS RECORDS: Gills of common snook *C. undecimalis* (Centropomidae) from Myakka River State Park, East Sarasota, Florida (type host and locality) (Mizelle and Blatz, 1941); South Jetty, Port Aransas, Texas (species identification unconfirmed) (Seamster and Monaco, 1956).



Figures 1–4. ***Rhabdosynochus rhabdosynochus*** **Mizelle and Blatz, 1941. 1. Copulatory complex (ventral) (parallel lines indicate dimension measured). 2. Hook. 3. Dorsal anchor. 4. Ventral anchor. All figures are drawn to the 25-μm scale.**

SPECIMENS STUDIED: Lectotype, USNPC 89848; 3 paralectotypes, USNPC 36822, HWML 21551.

REMARKS: We were able to locate only 4 of 10 cotypes used by Mizelle and Blatz (1941) for their original description of *R. rhabdosynochus.* All cotypes were highly cleared and mounted in glycerine jelly, and bubbles had developed around the specimens. The condition of the types prevented determination of internal organ features. One of these 4 specimens (USNPC 89848) is designated herein as the lectotype for the species. The following observations of these specimens were made: 1) bilateral peduncular

frills are absent, 2) tegumental scales are absent or few and may extend anteriorly to the level of the germarium, 3) the accessory piece comprises 4 subunits, 1 of which is grooved and serves as a guide for the male copulatory organ, 4) the basal opening of the male copulatory organ is directed anteriorly, 5) the male copulatory organ is in the form of a coil with 1½ rings, and 6) the vagina (if present) is nonsclerotized. This species requires redescription to include details of the internal organ systems.

With the possible exception of the record reported by Seamster and Monaco (1956), all geographic and host records of *R. rhabdosynochus* published subsequent to the original description clearly represent misidentifications (Hargis, 1955; Bunkley-Williams and Williams, 1994, 1995). We were not successful in locating the specimens used by Seamster and Monaco (1956) for their note on the distribution of *R. rhabdosynochus*; this record requires verification.

Rhabdosynochus hargisi sp. n. (Figs. 5–12)

DESCRIPTION (respective measurements reported by Hargis [1955] follow those of present specimens in brackets): Body 395 (262–533; n = 33) [503] long, subtriangular; 84 (59–119; n = 41) wide at level of germarium. Tegumental scales with rounded to slightly tapered (acute) anterior margins, extending anteriorly to level of germarium. Cephalic margin broad; cephalic lobes poorly developed; cephalic glands at level of pharynx. Posterior pair of eyes larger, closer together than anterior pair; accessory granules usually absent. Pharynx subspherical, 23 (16–32; n = 44) [27] in diameter; esophagus short; intestinal ceca diverging in peduncle. Peduncle broad, concave ventrally, with delicate bilateral membranous frills; haptor 189 (140–229; n = 42) [237] wide, 70 (57–98; n = 38) [49] long, with pair of bilateral tegumental scales directed toward body midline on anterior haptoral margin. Ventral anchor 41 (36–47; n=42) [47] long, with elongate roots, curved shaft, recurved point; deep root flattened; point extending to level of tip of superficial root; anchor base 14 (12–16; n = 4) [4] wide. Dorsal anchor 37 (35–43; n = 47) [28] long, with triangular base, nearly straight shaft, recurved point extending past tip of superficial root; anchor base 8 (6–10; n = 9) [3] wide. Ventral bar 134 (113–159; n = 30) [163] long, narrow, with delicate tapered ends; paired dorsal bar 58 (51–64; n = 40) [63] long, medially spatulate. Hook 12–13 (n = 25) [16] long, with elongate slightly depressed thumb, delicate point, uniform shank; filamentous hooklet (FH) loop nearly shank length. Copulatory complex 53 (48–59; n = 43) [54] long. Male copulatory organ a loose coil of about ½ ring, frequently appearing inverted U-shaped; base to right of body midline, elongate ovate, with delicate basal margin, basal opening directed posteriorly. Accessory piece comprising 3 subunits: 1 variably flabellate; 1 rod shaped; 1 grooved, serving as guide for male copulatory organ. Testis 27 (18–36; n = 21) [26] wide, subtriangular; seminal vesicle delicate, fusiform, to left of midline; prostatic reservoir elongate, inverted U-shaped. Germarium 22 (14–29; n = 28) wide; oviduct, ootype not observed; vagina funnel shaped, opening into small seminal receptacle lying to left of body midline; vitellaria dense.

TYPE HOST: Common snook (cultivated) *Centropomus undecimalis* (Bloch, 1792) (Centropomidae).

TYPE LOCALITY: Earthen ponds, Itamaracá, State of Pernambuco, Brazil (7°41′S; 34°53′W).

SYNONYMS: *Rhabdosynochus rhabdosynochus* of Hargis (1955) and of Dyer (unpublished).

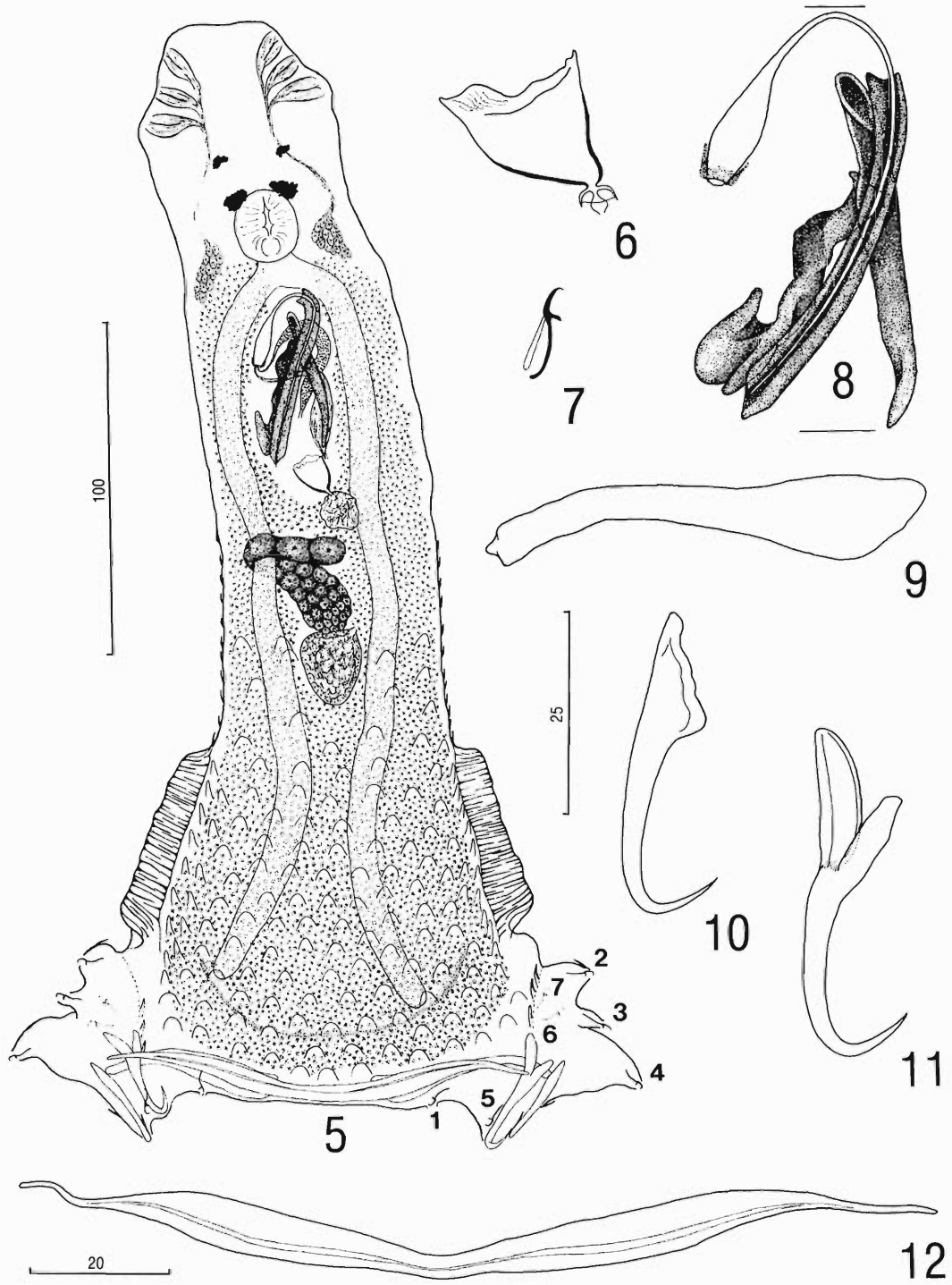
PREVIOUS RECORDS: *Centropomus undecimalis* from the Añasco River, Puerto Rico (Dyer, unpublished); Tampa Bay, Florida (Hargis, 1955).

INFECTION SITE: Gills.

DEPOSITED SPECIMENS: Holotype, INPA 383; 59 paratypes, INPA 384a–y, IOC 34298a–d, USNPC 89784, HWML 15373, MPM 19758.

ETYMOLOGY: This species is named in honor of Dr. William J. Hargis, Jr., Professor Emeritus, Virginia Institute of Marine Science, Gloucester Point, Virginia, in recognition of his important contributions to the systematics of the Monogenoidea. Dr. Hargis provided the first complete diagnosis of *Rhabdosynochus,* which has served for 45 yr for identification of the genus.

REMARKS: This species was first identified and reported as *R. rhabdosynochus* by Hargis (1955) from *C. undecimalis* in Florida. Comparison of our specimens and those of Hargis (1955) and Dyer (unpublished) with the type specimens of *R. rhabdosynochus* indicates that the specimens under consideration herein represent a new species (cf. Figs. 1–4 with Figs. 5–12). *Rhabdosynochus hargisi* differs from *R.*



Figures 5–12. ***Rhabdosynochus hargisi*** **sp. n. 5. Whole mount (composite, ventral) showing position of hook pairs 1–7. 6. Vagina. 7. Hook. 8. Copulatory complex (ventral) (parallel lines indicate dimension measured). 9. Left dorsal bar. 10. Dorsal anchor. 11. Ventral anchor. 12. Ventral bar. All drawings are to the 25-μm scale, except Figures 5 and 12 (100-μm and 20-μm scales, respectively).**

rhabdosynochus by possessing bilateral membranous frills on the peduncle, a coiled male copulatory organ comprised of <1 ring, a sclerotized vagina, and smaller anchors. *Rhabdosynochus hargisi* differs from its congeners in having a subtriangular body with a concave ventral surface of the peduncle and a comparatively longer ventral bar and in the morphology of the copulatory complex. *Rhabdosynochus hargisi* lacks a blade on the distal shaft of the dorsal anchor.

We could not determine the course of the vas deferens in the specimens of *R. hargisi* from Brazil, but 1 of Hargis' (1955) voucher specimens of this species clearly shows the vas deferens looping the left intestinal cecum. This configuration of the vas deferens is apparently symplesiomorphic for the Diplectanidae; the feature occurs in other members of the family and in the putative outgroups Dactylogyridae Bychowsky, 1933, and Pseudomurraytrematidae Kritsky, Mizelle, and Bilqees, 1978 (Boeger and Kritsky, 1993). In diplectanids, we have observed the vas deferens looping the left intestinal cecum in *Diplectanum piscinarius* Kritsky and Thatcher, 1984 (unpublished). Kritsky et al. (2000) reported a looping vas deferens in *Protolamellodiscus senilobatus* Kritsky, Jiménez-Ruiz, and Sey, 2000; Bychowsky and Nagibina (1977) showed a looping vas deferens in *Murraytrema pricei* Bychowsky and Nagibina, 1977 (synonym *Murraytrema bychowskyi* Oliver, 1987) and *Allomurraytrema sciaenae* Bychowsky and Nagibina, 1977 (synonym *Lobotrema sciaenae* (Bychowsky and Nagibina, 1977) Oliver, 1987), and Yamaguti (1958, 1968) reported the feature in *Murraytrematoides ditrematis* Yamaguti, 1958, and *Murraytrematoides kuhliae* Yamaguti, 1968, respectively.

Rhabdosynochus hudsoni sp. n. (Figs. 13–20)

DESCRIPTION: Body 317 (229–413; n = 14) long, fusiform, with parallel lateral margins; 71 (51–93; n = 15) wide at level of germarium. Tegumental scales flattened, with rounded to slightly tapered (pointed) anterior margins, extending anteriorly to level of posterior margin of testis. Cephalic margin broad; cephalic lobes moderately developed; cephalic glands at level of pharynx. Posterior pair of eyes larger and closer together than members of anterior pair; accessory granules usually absent or few in cephalic area. Pharynx subspherical to ovate, 19 (15–24; n = 14) in greatest width; esophagus short to nonexistent. Peduncle broad; haptor 105 (95–120; n = 16) wide, 56 (50–61; n = 15) long, with 2 pairs of bilateral tegumental scales directed toward body midline: 1 pair of scales on anterior haptoral margin, 1 pair on posterior haptoral margin. Ventral anchor 39 (33–46; n = 12) long, with elongate roots, evenly curved shaft, recurved point; deep root bulbous, fusiform; point extending slightly past level of tip of superficial root; anchor base 16 (14–19; n = 3) wide. Dorsal anchor 37 (32–43; n = 12) long, with triangular base, straight shaft, superficial bulbous blade arising from inner surface of distal shaft, straight recurved point extending past tip of superficial root; anchor base 10 (9–11; n = 2) wide. Ventral bar 64 (57–69; n = 15) long, with tapered ends; paired dorsal bar 34 (30–39; n = 12) long, with spatulate medial end, posteromedial flap. Hook 13 (12–14; n = 8) long, with elongate, slightly depressed thumb, delicate point, uniform shank; FH loop nearly shank length. Copulatory complex 41 (37–44; n = 14) long. Male copulatory organ a loose coil of about 1 ring; base with delicate sclerotized basal margin, subterminal posterior flap; basal opening directed sinistrally. Accessory piece comprising 3 subunits: 1 variably flabellate, 1 pyriform, apparently continuous, with grooved guide for male copulatory organ; 1 rod shaped, with distal point. Testis 23 (18–27; n = 12) in diameter, subspherical; vas deferens not observed; seminal vesicle delicate, fusiform, to left of midline; prostatic reservoir not observed. Germarium 16 (11–25; n = 13) wide; oviduct, ootype not observed; vagina lightly sclerotized, bulb shaped, opening into small seminal receptacle near midline; vitellaria dense.

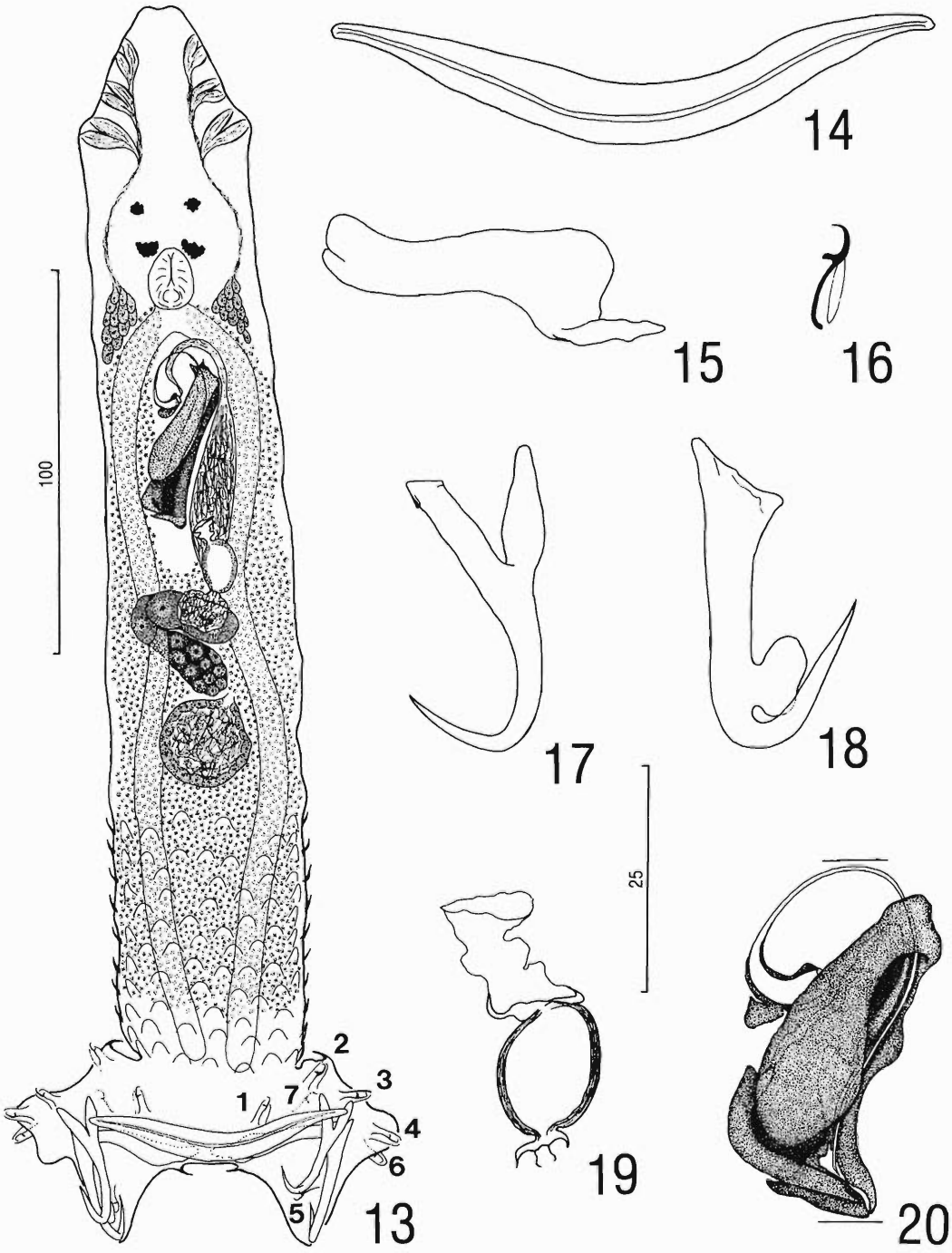
TYPE HOST: Common snook (cultivated) *Centropomus undecimalis* (Bloch, 1792) (Centropomidae).

TYPE LOCALITY: Earthen ponds, Itamaracá, Pernambuco, Brazil (7°41′S; 34°53′W).

INFECTION SITE: Gills.

DEPOSITED SPECIMENS: Holotype, INPA 381; 25 paratypes, INPA 382a–g, IOC 34297a–d, USNPC 89783, HWML 15374, MPM 19759.

ETYMOLOGY: This species is named in honor of Mr. James R. Hudson, Jr., President and CEO of Research Genetics, Inc., Huntsville, Alabama. Mr. Hudson is a strong supporter of scientific endeavors at local colleges through the estab-



Figures 13–20. ***Rhabdosynochus hudsoni*** **sp. n. 13. Whole mount (composite, ventral) showing position of hook pairs 1–7. 14. Ventral bar. 15. Dorsal bar. 16. Hook. 17. Ventral anchor. 18. Dorsal anchor. 19. Vagina. 20. Copulatory complex (ventral) (parallel lines indicate dimension measured). All drawings are to the 25-μm scale, except Figure 13 (100-μm scale).**

lishment of scholarships and funding of research grants at these institutions. He also provides strong educational incentives for his employees.

REMARKS: *Rhabdosynochus hudsoni* sp. n. differs from all other congeneric species in possessing a superficial blade-like projection on the distal shaft of the dorsal anchor. Blades on the dorsal anchor shafts in species of Diplectanidae are uncommon but have been reported in *Heteroplectanum nenuoides* Rakotofiringa, Oliver, and Lambert, 1987, and *Heteroplectanum parastomatei* Rakotofiringa, Oliver, and Lambert, 1987 (see Rakotofiringa et al., 1987). Anchor blades have also been reported in a few species of Dactylogyridae, i.e., species of *Pterocleidus* Mueller, 1937, and some species of *Dactylogyrus* Diesing, 1850, among others, where they have apparently developed independently within their respective genera.

Rhabdosynochus sp.

SYNONYM: *Rhabdosynochus rhabdosynochus* of Bunkley-Williams and Williams (1994, 1995).

HOSTS: Common snook *Centropomus undecimalis*; swordspine snook *Centropomus ensiferus* Poey, 1860 (both Centropomidae).

LOCALITIES: Mayagüez, mouth of the Guanajibo River, Puerto Rico (*C. ensiferus*); Caria Coya Zones, western Puerto Rico (*C. undecimalis*).

INFECTION SITE: Gills.

SPECIMENS STUDIED: Two voucher specimens (USNPC 84684, 84685) deposited by Bunkley-Williams and Williams (1995).

REMARKS: Although the drawings presented by Bunkley-Williams and Williams (1994, 1995) suggest that *R. hargisi* occurs on *C. undecimalis* and *C. ensiferus* in Puerto Rico, the validity of these records is unclear. Bunkley-Williams and Williams (1994, 1995) stated that their drawings of *R. rhabdosynochus* (=*R. hargisi*) were obtained from the literature rather than from their specimens, and the 2 reference specimens deposited in the USNPC from their 1995 study are of this undescribed *Rhabdosynochus* species. Unless additional specimens from their collection become available, we consider their records from Puerto Rico to reflect only the undescribed species.

The 2 available specimens of *Rhabdosynochus* sp. are insufficient for description and illustration. The species is differentiated from its congeners primarily by the morphology of the male copulatory organ (a thickened coiled tube with <1 ring) and the accessory piece. The species is further differentiated from *R. hargisi* and *R. hudsoni* by lacking bilateral frills on the peduncle (present in *R. hargisi*) and a blade on the dorsal anchor (present in *R. hudsoni*). It differs from *R. rhabdosynochus* in having smaller and morphologically different haptoral and copulatory sclerites.

Key to Species of *Rhabdosynochus*

1. Peduncle lacking bilateral membranous frills ... 2
   Peduncle with bilateral pair of membranous frills ..... *R. hargisi* sp. n.
2. Accessory piece of copulatory complex comprising 3 subunits; superficial bulbous blade arising from inner surface of distal shaft of dorsal anchor ..... *R. hudsoni* sp. n.
   Accessory piece of copulatory complex comprising 4 subunits; blade on inner surface of dorsal anchor shaft absent ..... *R. rhabdosynochus* Mizelle and Blatz, 1941

Discussion

Oliver (1987) proposed the Rhabdosynochinae for *R. rhabdosynochus* of Hargis (1955) (synonym *R. hargisi* sp. n., nec *R. rhabdosynochus* Mizelle and Blatz, 1941), and based the subfamily primarily on the presence of bilateral placodiscs (=lateral plaques of Hargis, 1955) on the margins of the peduncle. Our discovery of *R. hargisi* and *R. hudsoni,* both clear congeners of *R. rhabdosynochus,* revealed that placodiscs, occurring only in *R. hargisi,* are unlikely to be homologs of the squamodiscs and lamellodiscs of most other diplectanid species. *Rhabdosynochus hargisi* is apparently a derived member of the genus, where the membranous frills represent secondarily derived traits that are autapomorphic for the species and thus cannot be used to define the Rhabdosynochinae. The terms "placodisc" and "lateral plaques" are misnomers, because these structures are not disc shaped, as the terms suggest, but rather comprise a delicate membranous frill on each side of the peduncle.

In addition to *Rhabdosynochus* spp., species of 3 other diplectanid genera (*Murraytrema, Lobotrema,* and *Murraytrematoides,* all Murraytrematoidinae Oliver, 1982) lack squamodiscs or lamellodiscs. These genera likely have basal origins within the Diplectanidae, because squamodiscs and lamellodiscs are absent in putative

outgroups, Dactylogyridae and Pseudomurraytrematidae (see Boeger and Kritsky, 1993).

Several characters differentiate the Rhabdosynochinae and Murraytrematoidinae, and it is unlikely that these subfamilies are synonyms. In *Rhabdosynochus* spp., the tegument possesses plate-like tegumental scales on the posterior portion of the body, but scales are apparently absent in species of Murraytrematoidinae. Absence of tegumental scales has been verified in *Murraytrematoides bychowskyi* (synonym *Diplectanum bychowskyi*), *M. ditrematis, M. kuhliae,* and *M. lateolabracis* (synonym *Geneticoenteron lateolabracis*). In species of Murraytrematinae, the male copulatory organ is a comparatively straight tube lacking an accessory piece, whereas a complex accessory piece associated with a coiled (clockwise) male copulatory organ occurs in all species of *Rhabdosynochus.*

Acknowledgments

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Dactylogyridae of Cichlid Fishes from Nicaragua, Central America, with Descriptions of *Gussevia herotilapiae* sp. n. and Three New Species of *Sciadicleithrum* (Monogenea: Ancyrocephalinae)

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ABSTRACT: *Gussevia herotilapiae* sp. n., *Sciadicleithrum maculicaudae* sp. n., *Sciadicleithrum nicaraguense* sp. n., and *Sciadicleithrum bicuense* sp. n. are described from *Herotilapia multispinosa, Cichlasoma maculicauda, Amphilophus alfari,* and *Archocentrus nigrofasciatus* (Pisces: Cichlidae), respectively, from the Atlantic coast of Nicaragua. *Sciadicleithrum mexicanum* and *Sciadicleithrum meekii,* originally described in Mexico, are recorded for the first time in Nicaragua. The morphology of these species of *Sciadicleithrum* is similar to that of their congeners in southeastern Mexico, and it is suggested that both cichlids and their monogeneans speciated in Central America and subsequently dispersed to southeastern Mexico. *Gussevia,* originally described from South American cichlids, is recorded for the first time in Central America.

KEY WORDS: Monogenea, Dactylogyridae, new species, taxonomy, *Gussevia, Sciadicleithrum,* fishes, Cichlidae, Nicaragua, Central America.

Monogeneans of the genera *Sciadicleithrum* Kritsky, Thatcher, and Boeger, 1989 and *Gussevia* Kohn and Paperna, 1964, are gill parasites of neotropical cichlid fishes. In South America, 9 species of *Sciadicleithrum* and 13 species of *Gussevia* have been described from 8 species of cichlids (Kritsky et al., 1986, 1989). In southeastern Mexico, by contrast, 36 species of cichlids have been examined for monogeneans, but only 4 species of *Sciadicleithrum* and no *Gussevia* have been reported (Kritsky et al., 1994; Mendoza-Franco et al., 1997, 2000; Vidal-Martínez et al., 2000). However, there is a complete absence of data on the monogeneans of cichlid fishes in Central America.

During studies of the helminth fauna of fishes from Nicaragua, 5 species of *Sciadicleithrum* and 1 species of *Gussevia* were found parasitizing the native cichlids of the genera *Amphilophus* Agassiz, 1859, *Archocentrus* Gill and Bransford, 1877, *Cichlasoma* Swainson, 1839, and *Herotilapia* Pellegrin, 1904, most of the helminths being new to science. In this paper, the new monogenean species are described, and new geographical and host records for previously described *Sciadicleithrum* species from southeastern Mexico are presented. Current information on the Dactylogyridae (Monogenea: Ancyrocephalinae) of cichlid fishes from Nicaragua is expanded with this description of *Gussevia herotilapiae* sp. n. and 3 new species of *Sciadicleithrum.*

Materials and Methods

Five cichlid species (pastel cichlid *Amphilophus alfari* (Meek, 1907); blackbelt cichlid *Cichlasoma maculicauda* (Regan, 1905); jaguar cichlid *Cichlasoma managuense* (Günther, 1867); convict cichlid *Archocentrus nigrofasciatus* Günther, 1869; and butterfly cichlid *Herotilapia multispinosa* (Günther, 1867)) were collected with line, hook, and thrownets from 6 localities in the Autonomous Region of the South Atlantic (Región Autónoma del Atlántico Sur-R.A.A.S) on the Atlantic coast of Nicaragua (see Aguirre-Macedo et al., 2001, fig. 1). The geographical references for, and species collected from, each locality are as follows: 1. Torsuani River, 11°47′06″N; 83°52′38″W (3 *C. maculicauda*); 2. Mahogany River, 12°03′22″N; 83°59′07″W (7 *C. managuense,* 2 *H. multispinosa*); 3. surroundings of Bluefields City, Caño Negro Stream, 12°00′55″N; 84°01′10″W (4 *C. managuense*); 4. Loonku Creek, 11°59′05″N; 83°46′48″W (1 *A. alfari,* 1 *C. maculicauda,* 2 *A. nigrofasciatus,* 3 *H. multispinosa*); 5. Caño Marañón Stream, 12°00′10″N; 83°46′39″W (7 *C. maculicauda*); and 6. Puente Chino, 12°00′30″N; 83°46′13″W (2 *A. alfari,* 1 *C. maculicauda,* 2 *C. managuense,* 1 *A. nigrofasciatus,* 3 *H. multispinosa*).

The fish were transported alive to the laboratory and dissected by standard parasitological procedures (Man-

[3] Corresponding author.

ual of Veterinary Parasitological Laboratory Techniques, 1986). Monogeneans were isolated from the gills and fixed with a glycerin–ammonium picrate mixture (GAP) to observe their hard parts. After evaluation, the specimens fixed with GAP were remounted in Canada balsam (Ergens, 1969).

Some of the parasites were fixed in a hot 4% formaldehyde solution, stained with Gomori's trichrome, and mounted in Canada balsam for study of their internal organ morphology. Sampling dates are provided for each species. All measurements are in micrometers (μm); the mean is followed by the range and the number (n) of morphological structures measured in parentheses. Measurements of the tube and the accessory piece of the male copulatory organ represent straight-line measurements between extreme ends. Numbering of hook pairs follows that recommended by Mizelle (1936). Direction of the coil of the tube of the male copulatory organ (counterclockwise vs. clockwise) follows the procedure proposed by Kritsky et al. (1985).

Drawings were made with the aid of an Olympus drawing tube. The number of infected fishes of the total examined is followed by the number of worms collected in parentheses.

Specimens were deposited in the National Helminthological Collection of Mexico (CNHE), Institute of Biology, National Autonomous University of Mexico, Mexico; the United States National Parasite Collection (USNPC), Beltsville, Maryland, U.S.A.; the Institute of Parasitology (IPCAS), Academy of Sciences of the Czech Republic, Branišovská, České Budějovice, Czech Republic; and the Laboratory of Parasitology of the Centre of Investigation and Advanced Studies of the National Polytechnic Institute (CINVESTAV-IPN) (CHCM), Mérida, Yucatán, Mexico.

Results

Gussevia herotilapiae sp. n. (Figs. 1–7)

Description

Body 515 (424–638; n = 5) long, fusiform; greatest width 101 (92–133; n = 5). Four cephalic lobes moderately developed. Eyes 4; posterior pair larger than anterior; eye granules variable in size, elongate ovate. Pharynx spherical, 26 (21–29; n = 12) in diameter; esophagus short. Peduncle broad; haptor trapezoidal, 72 (62–85; n = 3) wide. Posterior haptoral lobe reduced. Ventral anchor 21 (18–24; n = 12) long, with short deep root, well-developed superficial root, curved shaft, point; base width 8 (6–10; n = 12). Dorsal anchor 62 (59–64; n = 12) long, lacking deep root, having well-developed superficial root, straight shaft, curved point; base width 15 (12–20; n = 12). Ventral bar 21 (18–23; n = 5) long, straight, with 2 holes, slightly enlarged ends; dorsal bar 23 (18–25; n = 5) long, robust, with large anteromedial projection, slightly enlarged ends. Hook pairs 1 and 7–10 (10–11; n = 4) long, with upright thumb, delicate point, shank varying in diameter along length; domus $^{9}/_{10}$ shank length; hook pairs 2–4 and 6–13 (12–14; n = 7) long, with upright thumb, delicate point, shank varying in diameter along length; domus $^{9}/_{10}$ shank length; hook pair 5–13 (n = 3) long, without thumb, slender shank; domus $^{9}/_{10}$ shank length. Gonads subovate. Testis 80 (72–95; n = 4) long, 29 (25–38; n = 4) wide, elongate ovate; seminal vesicle elongate, fusiform. Male copulatory organ a coil of about 1½ counterclockwise ring; base of copulatory organ with sclerotized margin; copulatory organ 29 (25–32; n = 5) long, proximal ring diameter 6 (5–7; n = 2). Accessory piece 13 (12–16; n = 5) long, comprising delicate sheath enclosing distal portion of copulatory organ. Germarium 61 (53–75; n = 3) long, 25 (23–28; n = 3) wide; oviduct, ootype, uterus not observed; nonsclerotized vaginal aperture dextral; seminal receptacle midventral, inconspicuous; vitellaria dense throughout trunk, except in region of reproductive organs.

Taxonomic summary

TYPE HOST: *Herotilapia multispinosa* (Günther, 1867) (butterfly cichlid).

SITE: Gills.

TYPE LOCALITY: Mahogany River, Nicaragua (12°03′22″N, 83°59′07″W) (1 fish infected of 1 examined, with 13 specimens) (13 March 1999).

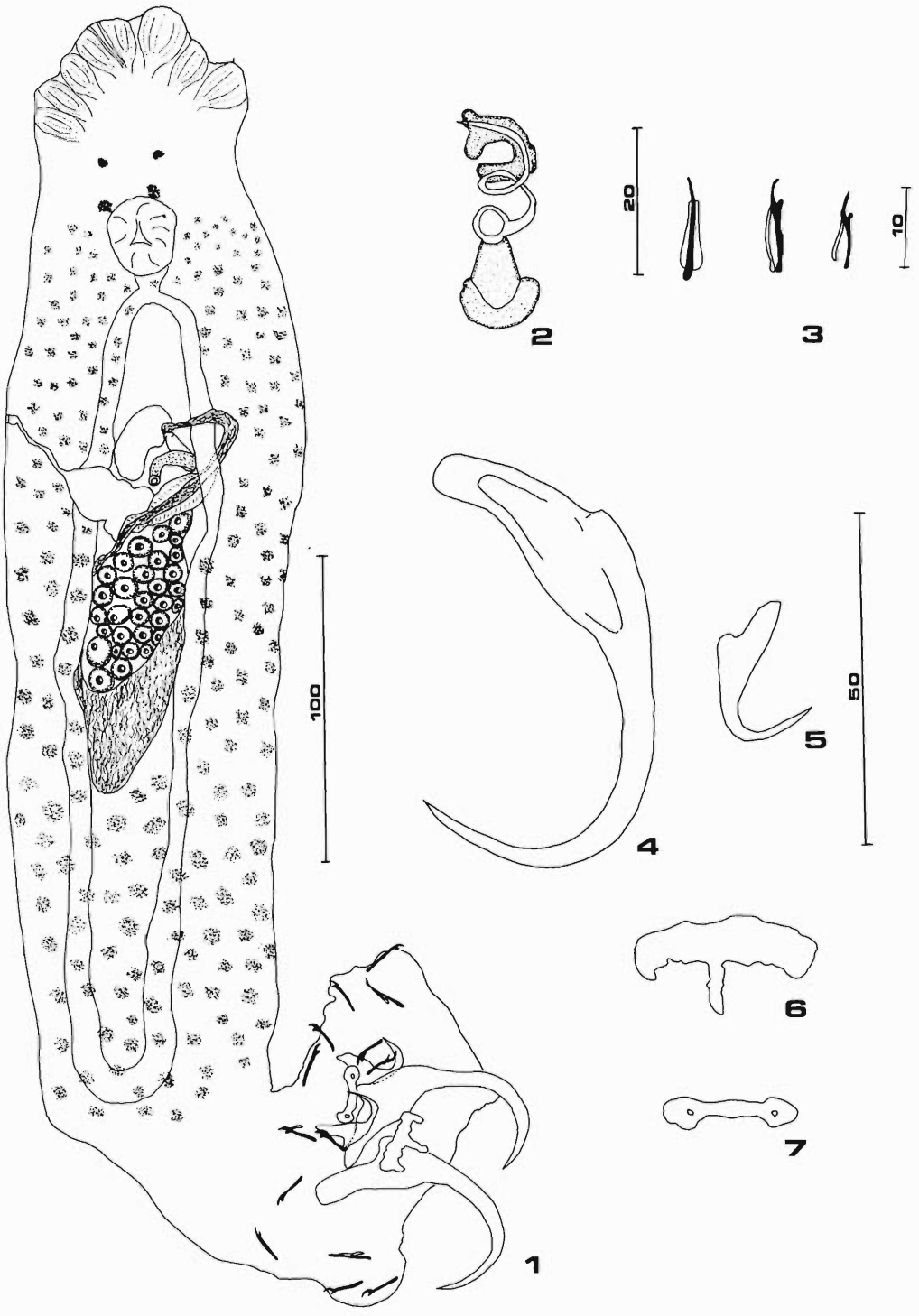
SPECIMENS STUDIED: Five specimens fixed with GAP.

DEPOSITION OF SPECIMENS: Holotype in CNHE (no. 4165). Paratype in CNHE (no. 4166) (2), USNPC (no. 90879) (1), IPCAS (no. M-362) (1).

ETYMOLOGY: The species name refers to the genus of the type host.

Remarks

This species was assigned to *Gussevia* because the fifth pair of hooks lack a thumb and have a reduced base, the umbelliform membranes in the dorsal and ventral bars are absent, and the ventral anchors are modified (see Kritsky et al., 1989 for a full set of the characteristics of *Gussevia*). *Gussevia herotilapiae* differs from its congeners by having very large dorsal anchors and a dorsal bar with a large anteromedial projection (see Kritsky et al., 1986). This species is the only representative of this genus in cichlid fishes from Nicaragua. Therefore, its



Figures 1–7. ***Gussevia herotilapiae*** **sp. n. 1. Ventral view of holotype. 2. Copulatory complex. 3. Hook pairs 5, 2, and 1, respectively. 4. Dorsal anchor. 5. Ventral anchor. 6. Dorsal bar. 7. Ventral bar. Figures 4–7 are drawn to the same scale (50 μm).**

finding represents the first record of a member of this genus in Central America.

Sciadicleithrum maculicaudae sp. n. (Figs. 8–15)

Description

Body 538 (332–745; n = 2) long, fusiform; maximum width 98 (78–118; n = 2) near midlength. Mouth ventral to pharynx; cephalic lobes inconspicuous. Eyes 4; posterior pair with conspicuous lens, larger than those of anterior pair; eye granules variable in size, elongate ovate. Pharynx spherical, 25 (18–30; n = 2) in diameter; esophagus moderately long. Peduncle broad; haptor subovate, 98 (75–122; n = 2) wide. Ventral anchor 29 (29–30; n = 4) long, with short deep root, tapering superficial root, curved shaft, point with longitudinal lateral grooves; base width 14 (12–18; n = 4). Dorsal anchor 33 (32–35; n = 4) long, short deep root, having elongate superficial root, bent shaft, point with longitudinal lateral grooves; base width 15 (10–18; n = 4). Ventral bar 34 (34–35; n = 2) long, slender, yoke-shaped, with enlarged ends; dorsal bar 31 (30–33; n = 2) long, broad V-shaped rod, slightly expanded medially, with enlarged ends. Hooks similar; each 15 (15–16; n = 3), with upright thumb, delicate point, shank varying in diameter along length; domus ¾ shank length. Gonads overlapping. Testis 59 (n = 1) long, 39 wide, elongate ovate; seminal vesicle fusiform, with medial constriction; prostatic reservoir clavate. Male copulatory organ roughly C-shaped; clockwise oriented, 42 (41–43; n = 2) long. Accessory piece 49 (44–55; n = 2) long, comprising incomplete sheath supporting distal part of copulatory organ, articulated to its base. Germarium irregular; oviduct, ootype, uterus not observed; cup-shaped sclerotized vaginal aperture sinistral, with thick nonsclerotized tube leading to midventral seminal receptacle. Vitellaria dense throughout trunk, except in region of reproductive organs.

Taxonomic summary

TYPE HOST: *Cichlasoma maculicauda* (Regan, 1905) (blackbelt cichlid).

SITE: Gills.

TYPE LOCALITY: Caño Marañón stream, Nicaragua (12°00′10″N; 83°46′39″) (1/7, 3) (9–10 March 1999).

SPECIMENS EXAMINED: Two specimens fixed with GAP.

DEPOSITION OF SPECIMENS: Holotype in CNHE (no. 4164).

ETYMOLOGY: This species is named after its type host.

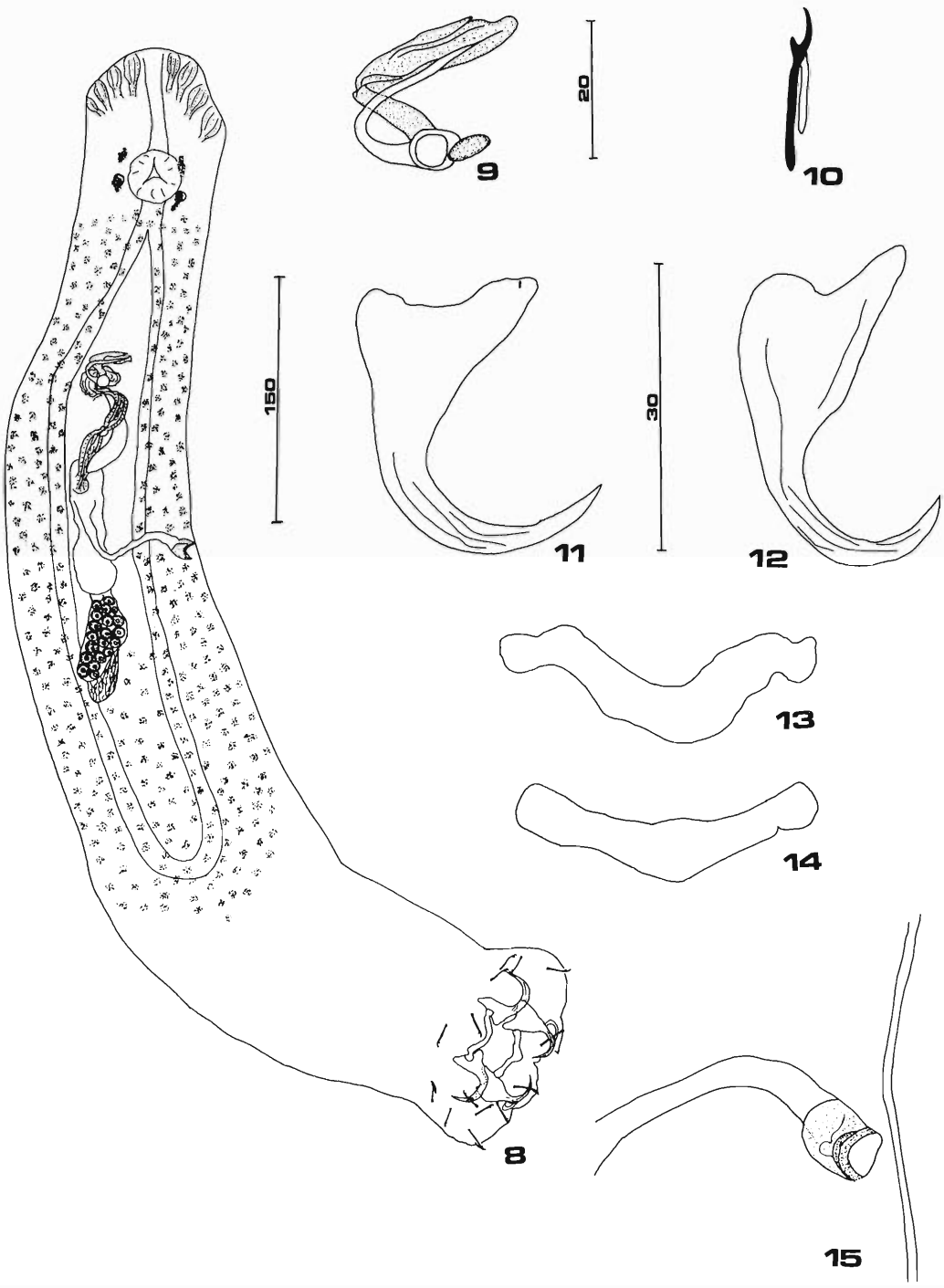
Remarks

Sciadicleithrum maculicaudae sp. n. resembles the Mexican species of *Sciadicleithrum* (*S. bravohollisae, S. mexicanum, S. meekii,* and *S. splendidae*) in having longitudinal lateral grooves on the shafts and points of the ventral and dorsal anchors, and the accessory piece comprising a delicate sheath enclosing the male copulatory organ. *Sciadicleithrum maculicaudae* differs from its congeners in that it has an incomplete accessory piece covering the distal portion of the male copulatory organ and a sclerotized, cup-shaped vaginal aperture. This species differs from *S. nicaraguense* by having a larger total body size, an C-shaped male copulatory organ, a larger surface of this organ covered by the accessory piece, and a ventral bar without ragged edges.

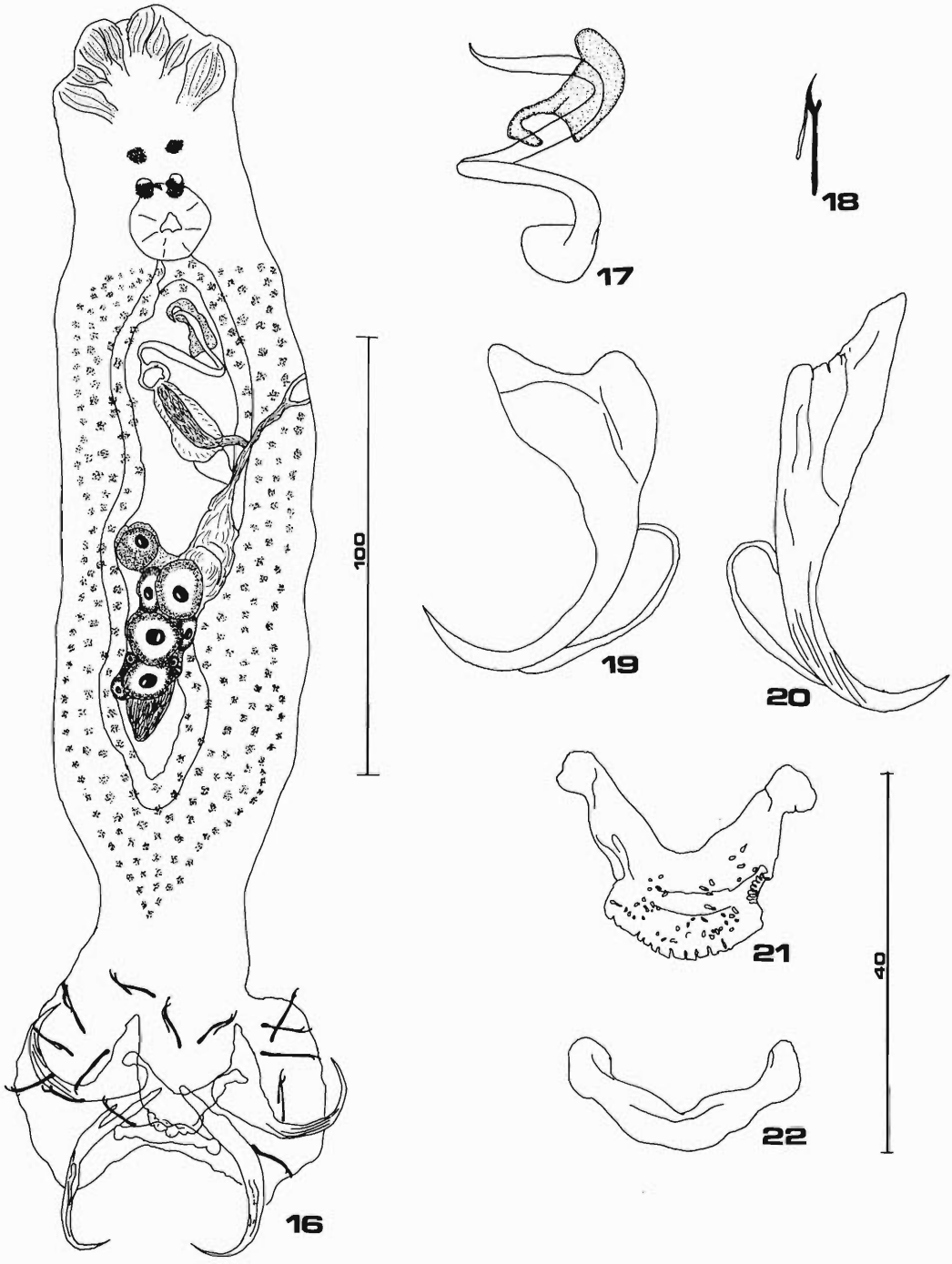
Sciadicleithrum nicaraguense sp. n. (Figs. 16–22)

Description

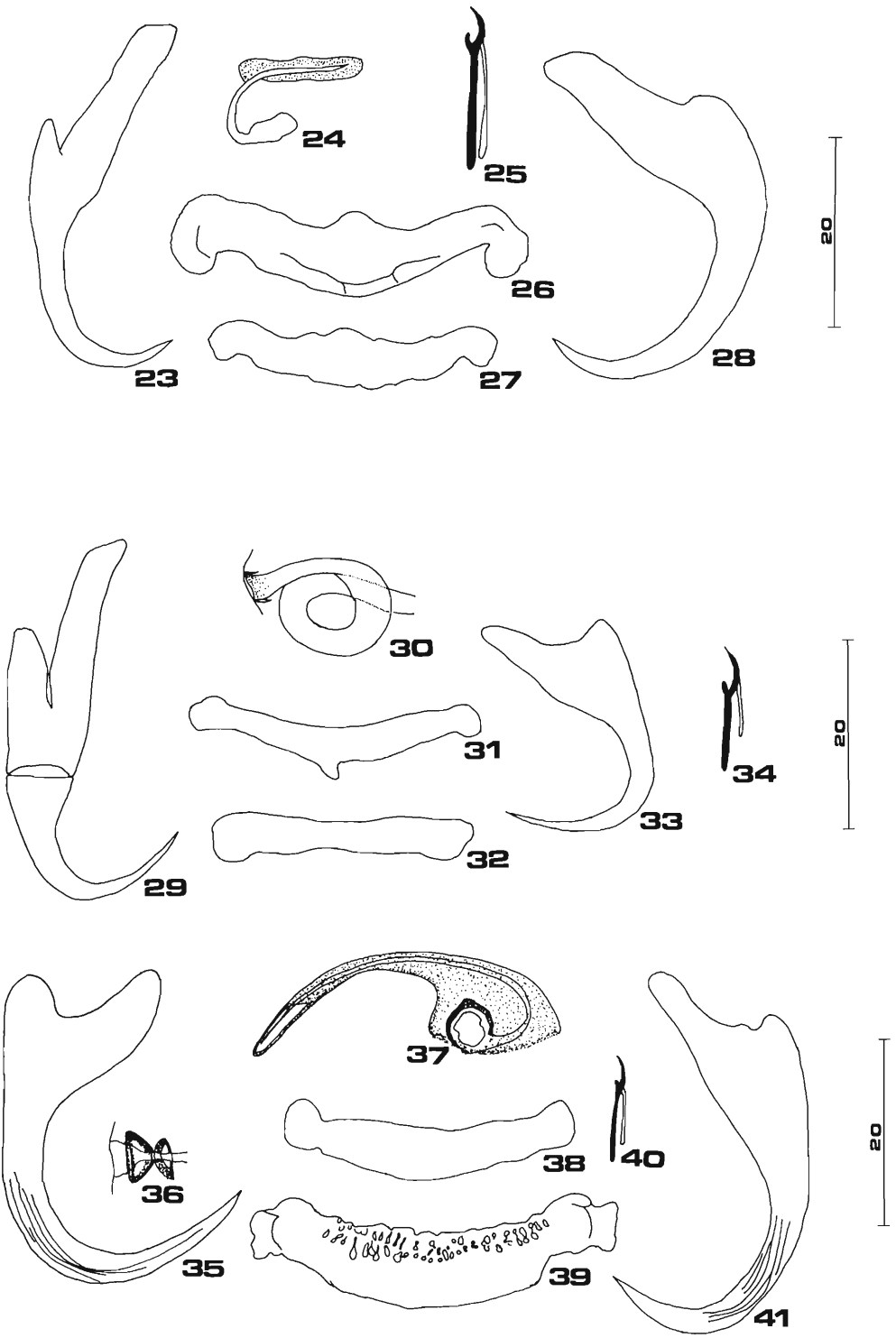
Body 294 (269–320; n = 4) long, fusiform; greatest width 69 (58–85; n = 4) near midlength. Mouth ventral to pharynx, cephalic lobes moderately developed; eyes 4; posterior pair with conspicuous lens, larger than those of anterior pair; interocular zone of the posterior pair with few eye (pigment) granules; eye granules variable in size, elongate ovate. Pharynx spherical, 17 (16–19; n = 2) in diameter; esophagus short. Peduncle broad; haptor subhexagonal, 72 (62–85; n = 3) wide. Ventral anchor 34 (26–39; n = 18) long, with short deep root, tapering superficial root, curved shaft, point with longitudinal lateral grooves; base width 16 (12–18; n = 18). Dorsal anchor 43 (40–46; n = 17) long, lacking deep root, having elongate superficial root, bent shaft, point with longitudinal lateral grooves; base width 12 (8–15; n = 16). Ventral bar 29 (26–32; n = 8) long, yoke-shaped, expanded medially with ragged edge, enlarged ends; dorsal bar 26 (24–30; n = 8) long, U-shaped, with umbelliform membranes, small medial constriction, and enlarged ends. Hooks similar; each 14 (12–15; n = 29) long, with upright thumb, delicate point, shank varying in diameter along length; domus ¾ shank length. Gonads overlap-



Figures 8–15. *Sciadicleithrum maculicaudae* **sp. n. 8. Ventral view of holotype. 9. Copulatory complex. 10. Hook. These 2 figures are drawn to the same scale (20 μm). 11. Ventral anchor. 12. Dorsal anchor. 13. Ventral bar. 14. Dorsal bar. 15. Vagina. Figures 11–15 are drawn to the same scale (30 μm).**



Figures 16–22. ***Sciadicleithrum nicaraguense*** **sp. n. 16. Ventral view of holotype. 17. Copulatory complex. 18. Hook. 19. Ventral anchor. 20. Dorsal anchor. 21. Ventral bar. 22. Dorsal bar. Figures 17–22 are drawn to the same scale (40 μm).**



Figures 23–28. *Sciadicleithrum bicuense* **sp. n. 23. Ventral anchor. 24. Copulatory complex. 25. Hook. 26. Ventral bar. 27. Dorsal bar. 28. Dorsal anchor. Figures 23–28 were drawn to the same scale (20 μm), excepting Figure 25 (10 μm).**

ping. Testis 40 long (n = 2), 22–25 wide, elongate ovate; seminal vesicle elongate, fusiform, with thick wall; prostatic reservoir saccate. Coil of male copulatory organ comprising about 1 counterclockwise ring; base of copulatory organ with sclerotized margin; copulatory organ length 54 (43–62; n = 9). Accessory piece 16 (12–20; n = 9) long, comprising delicate sheath enclosing distal portion of copulatory organ. Germarium 29 (25–33; n = 2) long, 20 (12–29; n = 2) wide, with irregular margin; oviduct, ootype, uterus not observed; nonsclerotized bell-shaped vaginal aperture sinistral; seminal receptacle midventral, small; vitellaria dense throughout trunk except in region of reproductive organs.

Taxonomic summary

TYPE HOST: *Amphilophus alfari* (Meek, 1907) (pastel cichlid).

SITE: Gills.

TYPE LOCALITY: Loonku Creek, Nicaragua (11°59′05″N; 83°46′48″W) (1/1; 34) (11 March 1999).

SPECIMENS STUDIED: Five specimens in GAP and 5 stained with Gomori's trichrome.

DEPOSITION OF SPECIMENS: Holotype in CNHE (no. 4162). Paratypes in USNPC (no. 90880) (1), IPCAS (no. M-363) (1), and CHCM (no. 378) (3).

ETYMOLOGY: This species is named after the country in which it was found.

Remarks

Sciadicleithrum nicaraguense sp. n. closely resembles the Mexican species of *Sciadicleithrum* (*S. bravohollisae, S. mexicanum, S. meekii,* and *S. splendidae*) (see Kritsky et al., 1994 Mendoza-Franco et al., 1997) in having longitudinal lateral grooves on the shafts and points of the ventral and dorsal anchors and the accessory piece comprising a delicate sheath enclosing the distal portion of the male copulatory organ. *Sciadicleithrum nicaraguense* differs from its congeners by having a small accessory piece enclosing only the distal portion of the male copulatory organ; a nonsclerotized, bell-shaped vagina; and a yoke-shaped ventral bar with ragged edges.

Sciadicleithrum bicuense sp. n. (Figs. 23–28)

Description

Body 382 (338–434; n = 3) long, fusiform; greatest width 59 (40–70; n = 3) near midlength. Mouth ventral to pharynx; cephalic lobes moderately developed; 4 eyes. Pharynx spherical, 24 (21–27; n = 5) in diameter; esophagus moderately long. Peduncle broad; haptor trapezoidal, 125 (112–137; n = 3) wide. Ventral anchor 33 (32–35; n = 6) long, with small deep root, elongate superficial root, straight shaft, curved point; base width 15 (12–18; n = 4). Dorsal anchor 36 (35–37; n = 6) long, with short deep root, elongate superficial root, bent shaft, point; base width 16 (15–18; n = 4). Ventral bar 37 (34–40; n = 3) long, yoke-shaped, with enlarged ends, small anteromedial expansion; dorsal bar 30 (n = 3) long, straight, with umbelliform membranes, enlarged ends. Hooks similar; each 16 (15–18; n = 22) long, with upright thumb, delicate point, shank varying in diameter along length; domus $^{7}/_{10}$ shank length. Gonads slightly overlapping. Testis, seminal vesicle, prostatic reservoir not observed. Male copulatory organ roughly C-shaped; clockwise oriented, 19 (19–20; n = 2) long. Accessory piece 16 (n = 1) long, comprising a delicate sheath enclosing distal part of copulatory organ. Germarium, oviduct, ootype, uterus not observed; cup-shaped nonsclerotized vaginal aperture dextral, vagina a fine tube leading to midventral seminal receptacle. Vitellaria dense throughout trunk except in region of reproductive organs.

Taxonomic summary

TYPE HOST: *Archocentrus nigrofasciatus* Günther, 1869 (convict cichlid).

SITE: Gills.

TYPE LOCALITY: Loonku Creek, Nicaragua

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Figures 29–34. ***Sciadicleithrum meekii*** **Mendoza-Franco, Scholz, and Vidal-Martínez, 1997. 29. Dorsal anchor. 30. Vagina. 31. Ventral bar. 32. Dorsal bar. 33. Ventral anchor. 34. Hook.**

Figures 35–41. ***Sciadicleithrum mexicanum*** **Kritsky, Vidal-Martínez, and Rodríguez-Canul, 1994. 35. Ventral anchor. 36. Vagina. 37. Copulatory complex. 38. Dorsal bar. 39. Ventral bar. 40. Hook. 41. Dorsal anchor.**

(11°59′05″N; 83°46′48″W) (1/2, 7) (14 March 1999).

SPECIMENS STUDIED: Three specimens fixed with GAP.

DEPOSITION OF SPECIMENS: Holotype in CNHE (no. 4163). Paratype in CHCM (no. 37).

ETYMOLOGY: This species is named in honor of the Bluefields Indian and Caribbean University (BICU), Bluefields, Nicaragua, which provided support for collecting fish.

Remarks

Sciadicleithrum bicuense sp. n. resembles the South American species of *Sciadicleithrum* in lacking longitudinal lateral grooves on the shafts and points of the ventral and dorsal anchors (see Kritsky et al., 1989). However, the accessory piece, comprising a delicate sheath enclosing the male copulatory organ, is similar to that found in Mexican species of *Sciadicleithrum. Sciadicleithrum bicuense* differs from its congeners in possessing a very small copulatory organ (19–20 long), a ventral bar with an anteromedial expansion, and a sclerotized, cup-shaped vagina.

Sciadicleithrum meekii Mendoza-Franco, Scholz, and Vidal-Martínez, 1997 (Figs. 29–34)

Description

MEASUREMENTS: Haptor subtrapezoidal 84 (66–107; n = 6) wide. Pharynx 19 (13–22; n = 6) in diameter. Ventral anchor 27 (25–33; n = 12) long; base width 15 (13–17; n = 10). Dorsal anchor 36 (30–39; n = 11) long; base width 8 (8–11; n = 12). Ventral bar 33 (30–37; n = 6) long; dorsal bar 32 (30–36; n = 5) long. Hooks similar in size and shape 15 (13–18; n = 20) long. Male copulatory organ 79 (71–94; n = 3) long. Accessory piece 15 (12–18) long.

Taxonomic summary

HOST: *Archocentrus nigrofasciatus* Günther, 1869 (convict cichlid).

SITE: Gills.

LOCALITY: Loonku Creek, Nicaragua (11°59′05″N; 83°46′48″) (2/2; 4–6) (14 March 1999).

SPECIMENS STUDIED: Six specimens fixed with GAP.

DEPOSITION OF SPECIMENS: CHCM (no. 375).

Remarks

The morphology and measurements of the specimens found in *A. nigrofasciatus* correspond well to those of *S. meekii* as described by Mendoza-Franco et al. (1997, 2000), especially with respect to the shape of the dorsal anchors and the presence of a tubular vagina forming 1 ring. The present finding represents a new host record for this parasite and its first record in Central America.

Sciadicleithrum mexicanum Kritsky, Vidal-Martínez, and Rodríguez-Canul, 1994 (Figs. 35–41)

Description

MEASUREMENTS: Haptor 95 (82–109; n = 11) wide. Pharynx spherical 22 (21–24; n = 11). Ventral anchor 32 (29–35; n = 22) long; base width 14 (12–16; n = 22). Dorsal anchor 35 (32–39; n = 22) long; base width 14 (11–18; n = 22). Ventral bar 33 (29–39; n = 11) long; dorsal bar 31 (29–33; n = 11) long. Hooks of the same shape and size 15 (14–16; n = 15) long. Male copulatory organ 49 (41–57; n = 11) long. Accessory piece 41 (30–49; n = 10) long.

Taxonomic summary

HOSTS: *Cichlasoma managuense* (Günther, 1869) (jaguar cichlid), *Cichlasoma maculicauda* (Regan, 1905) (blackbelt cichlid).

SITE: Gills.

LOCALITIES: *Cichlasoma managuense*: Caño Negro (4/4, 14–53) (12–13 March 1999), Puente Chino (1/3, 1) (11 March 1999); Rio Mahogany (6/6, 2–69) (13 March 1999); for *C. maculicauda*: Torsuani (1/3, 2) (7–10 March 1999); Caño Marañon (3/7, 1–5) (9–10 March 1999).

SPECIMENS STUDIED: Eleven specimens fixed with GAP.

DEPOSITION OF SPECIMENS: CHCM (nos. 376, 317).

Remarks

The morphology and measurements of the specimens found in *C. maculicauda* and *C. managuense* correspond well to the original description of *S. mexicanum* by Kritsky et al. (1994). However, they reported a larger size of the accessory piece in specimens from southeastern Mexico. All these data suggest that *S. mexicanum,* a species infecting a wide spectrum of cichlids (Mendoza-Franco et al., 2000), shows a high

intraspecific variability. This variation should be taken into account when comparing the specimens from different geographical areas. *Cichlasoma maculicauda* represents a new host for *S. mexicanum,* and this is the first time it has been recorded in Nicaragua. *Sciadicleithrum bravohollisae* was the most widely distributed monogenean species in cichlids in this study, and it has been reported from 8 species of *Cichlasoma* and *Petenia* Günther, 1862, in Mexico, Guatemala, and Nicaragua (Kritsky et al., 1994; Mendoza-Franco et al., 2000; Vidal-Martínez et al., 2000; present study).

Discussion

The results reported in this paper demonstrate that *Sciadicleithrum* species composition and morphology differ between South America, and Central America and southeastern Mexico. The fact that none of the South American *Sciadicleithrum* species was found in Nicaragua during this study (see Kritsky et al., 1986, 1989, 1994; Mendoza-Franco et al., 1997) supports this observation. Additionally, the results show that, although 3 of the species found are new to science, they exhibit morphology similar to that of *Sciadicleithrum* taxa from southeastern Mexico but not to those from South America. The presence of *S. mexicanum* and *S. meekii,* 2 species previously recorded in southeastern Mexico, provides further support for considering the monogenean fauna of cichlids from Nicaragua to be closely related to those of southeastern Mexico.

In Mexico, 36 cichlid species have been examined for monogeneans, with only 4 species of *Sciadicleithrum* (*S. bravohollisae, S. meekii, S. mexicanum,* and *S. splendidae*) having been identified (Kritsky et al., 1994; Mendoza-Franco et al., 1997, 2000; Vidal-Martínez et al., 2000). In contrast, 8 cichlid species in South America have been examined for monogeneans, resulting in the recording of 9 species of *Sciadicleithrum* and 13 species of *Gussevia* (Kritsky et al., 1986, 1989). These patterns may be explained by a host speciation in Central America and Mexico that has outpaced that of their parasites. It is even possible that the cichlid speciation rate has been so rapid that these hosts are not morphologically and/or physiologically different for monogeneans. As a result, host switching increased as these parasites were able to survive in different host species from the same family.

The presence of *Sciadicleithrum* and *Gussevia* in Central America suggests an ancestral relationship between Central and South American cichlids. These hosts likely brought ancestral members of both these monogenean genera from South America when they migrated into Central America. This pattern fits into the allopatric speciation model II (Brooks and McLennan, 1991), which states that new helminth species will be produced when both hosts and their parasites are genetically isolated from the ancestral gene pool. This coincides with previous research that shows that cichlids came from South America into Central America at the end of the Tertiary (Bussing, 1976; Conkel, 1993), where they became isolated from the ancestral gene pool in South America. Therefore, it is possible that these ancestral cichlids carried ancestral *Sciadicleithrum* and *Gussevia* with them when dispersing into Central America, where they subsequently speciated.

Acknowledgments

We are especially indebted to Gregory Arjona-Torres (CINVESTAV-IPN Mérida Unit) for his assistance in field and laboratory work. Thanks are also due Petr Posel, Rene Cassells, Svetlana Dumailo, and Eduardo Siu, all from the Bluefields Indian and Caribbean University (BICU), Bluefields, Nicaragua, for allowing us to use their facilities during both field and laboratory work, and to Dr. Delane Kritsky (Idaho State University) for suggestions on an earlier version of this paper.

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On *Ancyrocephalus etropli* Gussev, 1963, from *Etroplus suratensis* (Perciformes: Cichlidae) in India, with Proposal of *Sclerocleidoides* gen. n. (Monogenoidea: Dactylogyridae: Ancyrocephalinae)

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ABSTRACT: The monotypic genus *Sclerocleidoides* gen. n. (Monogenoidea: Dactylogyridae) is proposed, and *Ancyrocephalus etropli* Gussev, 1963, is redescribed and transferred to *Sclerocleidoides* as its type species. Presence of a dextral vaginal sclerite apparently is a synapomorphy for the genus. The finding of *S. etropli* on *Etroplus suratensis* from Chilka Lake, Balugaon, Orissa, India, represents the first geographic record of this species in India.

KEY WORDS: Monogenoidea, Dactylogyridae, *Sclerocleidoides* gen. n., *Sclerocleidoides etropli* comb. n., *Ancyrocephalua etropli, Etroplus suratensis,* green chromide, Perciformes, Cichlidae, India.

Ancyrocephalus etropli Gussev, 1963, was described from the gill filaments of the green chromide *Etroplus suratensis* (Bloch, 1790) and the orange chromide *Etroplus maculatus* (Bloch, 1795) (Perciformes: Cichlidae) from the vicinity of Colombo, Ceylon (Sri Lanka) by Gussev (1963). Although the monogenoideans *Onchiodiscus pterodiscoides* Kulkarni, 1969, and *Enterogyrus globodiscus* (Kulkarni, 1969) Gussev and Fernando, 1973, have subsequently been reported from *E. suratensis* in India (Kulkarni, 1969), *A. etropli* has not been recorded since its original description. During a survey of Monogenoidea of Asian cichlids, we collected numerous specimens of *A. etropli* from the gills of *E. suratensis* from a brackish-water lake near the Indian coast on the Sea of Bengal. In the present study, *Sclerocleidoides* gen. n. (Dactylogyridae: Ancyrocephalinae) is proposed for *A. etropli,* and the species is redescribed.

Materials and Methods

Specimens of *E. suratensis* were collected by seine on 2 February 1998 from the brackish water of Chilka Lake, Balugaon, Orissa, India. Gill baskets were removed from the hosts, immediately placed on ice to narcotize the helminths, and subsequently preserved in 5% formalin and shipped to Idaho State University. Methods of staining, mounting, and illustration of dactylogyrids were those described by Kritsky et al. (1986). Measurements (in micrometers) were made with a calibrated filar micrometer according to procedures of Mizelle and Klucka (1953); average measurements are followed by ranges and number of specimens measured (*n*) in parentheses. Unstained flattened specimens mounted in Hoyer's medium were used to obtain measurements of haptoral sclerites (except the ventral and dorsal bars); all other measurements including those of the haptoral bars were obtained from unflattened specimens stained in Gomori's trichrome and mounted in Canada balsam. Numbering of hook pairs follows Mizelle (1936; see Mizelle and Price, 1963). Voucher specimens used in the present study were deposited in the U.S. National Parasite Collection (USNPC), Beltsville, Maryland, and in the helminthological collection of the University of Nebraska State Museum (HWML), Lincoln, Nebraska, U.S.A. as indicated in the redescription. Some voucher specimens not used in the present study were deposited in the Helminthological Section of the Zoological Survey of India, Calcutta, India. Host names follow those in the FAO Fish Base (http://www.fao.org/waicent/faoinfo/fishery/fishbase/fishbase.htm).

Results

Order Dactylogyridea Bychowsky, 1937
Suborder Dactylogyrinea Bychowsky, 1937
Dactylogyridae Bychowsky, 1933
Sclerocleidoides gen. n.

DIAGNOSIS: Body fusiform, slightly flattened dorsoventrally, comprising cephalic region, trunk, peduncle, haptor. Tegument smooth. Two terminal, 2 bilateral cephalic lobes; 3 bilateral pairs of head organs; cephalic glands unicellular, posterolateral to pharynx. Two pairs of eyes; eye granules ovate, small. Mouth subterminal, ventral to pharynx; single pharyngeal bulb muscular, glandular; esophagus short to absent; 2 intestinal ceca confluent posterior to gonads, lacking diverticula. Genital pore midventral. Gonads

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overlapping, intercecal. Testis posterodorsal to germarium; vas deferens looping left intestinal cecum; seminal vesicle a dilation of vas deferens; prostatic reservoir(s) not observed. Copulatory complex comprising articulated male copulatory organ, accessory piece; male copulatory organ tubular, coiled with counterclockwise ring(s) (Kritsky et al., 1985). Accessory piece comprising articulation piece within rings of male copulatory organ, distal guide. Germarium pyriform; seminal receptacle pregermarial; tubular vagina lightly sclerotized; vaginal pore midventral, pregermarial near body midlength; dextral vaginal sclerite. Vitellaria throughout trunk except absent in regions of other reproductive organs. Haptor subhexagonal, armed with dorsal, ventral anchor/bar complexes, 7 pairs of similar hooks with ancyrocephaline distribution (Mizelle, 1936; see Mizelle and Price, 1963). Haptoral bars rod-shaped. Hook thumb erect, acute; shank comprised of 2 subunits, proximal subunit dilated. Parasites of gills of Asian Cichlidae (Perciformes).

TYPE SPECIES: *Sclerocleidoides etropli* (Gussev, 1963) comb. n.

ETYMOLOGY: The generic name is from Greek (*sklēros* ["hard, hardened"] + *kleidos* ["a key or clavicle"]) and refers to the presence of the dextral vaginal sclerite.

Sclerocleidoides etropli (Gussev, 1963) comb. n. (Figs. 1–10)

DESCRIPTION: Body 198 (154–233; n = 28) long, fusiform; greatest width 53 (41–64; n = 26) in posterior trunk. Cephalic margin broad; cephalic lobes well developed. Members of anterior pair of eyes small, frequently absent, slightly farther apart than those of posterior pair; posterior eyes with conspicuous anterior lenses; accessory granules usually absent, uncommon in cephalic, anterior trunk regions. Pharynx spherical, 14 (12–17; n = 24) in diameter. Peduncle broad; haptor subhexagonal, 73 (56–87; n = 25) wide, 49 (39–54; n = 28) long. Anchors similar; each with short roots, evenly curved shaft, slightly recurved point extending to level of tip of superficial anchor root; ventral anchor 31 (29–33; n = 8) long, base 11–12 (n = 2) wide; dorsal anchor 29 (25–31; n = 8) long, base 9–10 (n = 1) wide. Ventral bar 26 (23–28; n = 20) long, yoke shaped, with truncate ends directed posteriorly; dorsal bar 24 (21–26; n = 17) long, straight, with ends enlarged posteriorly. Hook with delicate point; hook pairs 1 and 5—12 (11–13; n = 8); pairs 2, 3 and 6—15 (14–16; n = 7); pair 4—17 (16–18; n = 5); pair 7—18 (17–20; n = 6) long; filamentous hook (FH) loop extending proximally to union of shank subunits. Male copulatory organ with 4 or 5 rings, base with lightly sclerotized margin; coil diameter 14 (12–18; n = 18). Accessory piece comprising twisted articulation process, sheath enclosing end of shaft of male copulatory organ. Testis 34 (28–45; n = 8) long, 22 (18–25; n = 7) wide, ovate; seminal vesicle small. Germarium pyriform, 31 (25–38; n = 9) long, 18 (14–22; n = 10) wide; oviduct elongate; ootype, uterus not observed; vaginal sclerite 23 (19–26; n = 9) long, Y shaped, distal arms forming claw; vagina with funnel-shaped vestibule, coiled tube with 4 rings; vaginal tube slightly expanded at attachment to small seminal receptacle.

TYPE HOST: Green chromide, *Etroplus suratensis* (Bloch, 1790) (Cichlidae: Perciformes).

TYPE LOCALITY: Vicinity of Colombo, Sri Lanka (Ceylon).

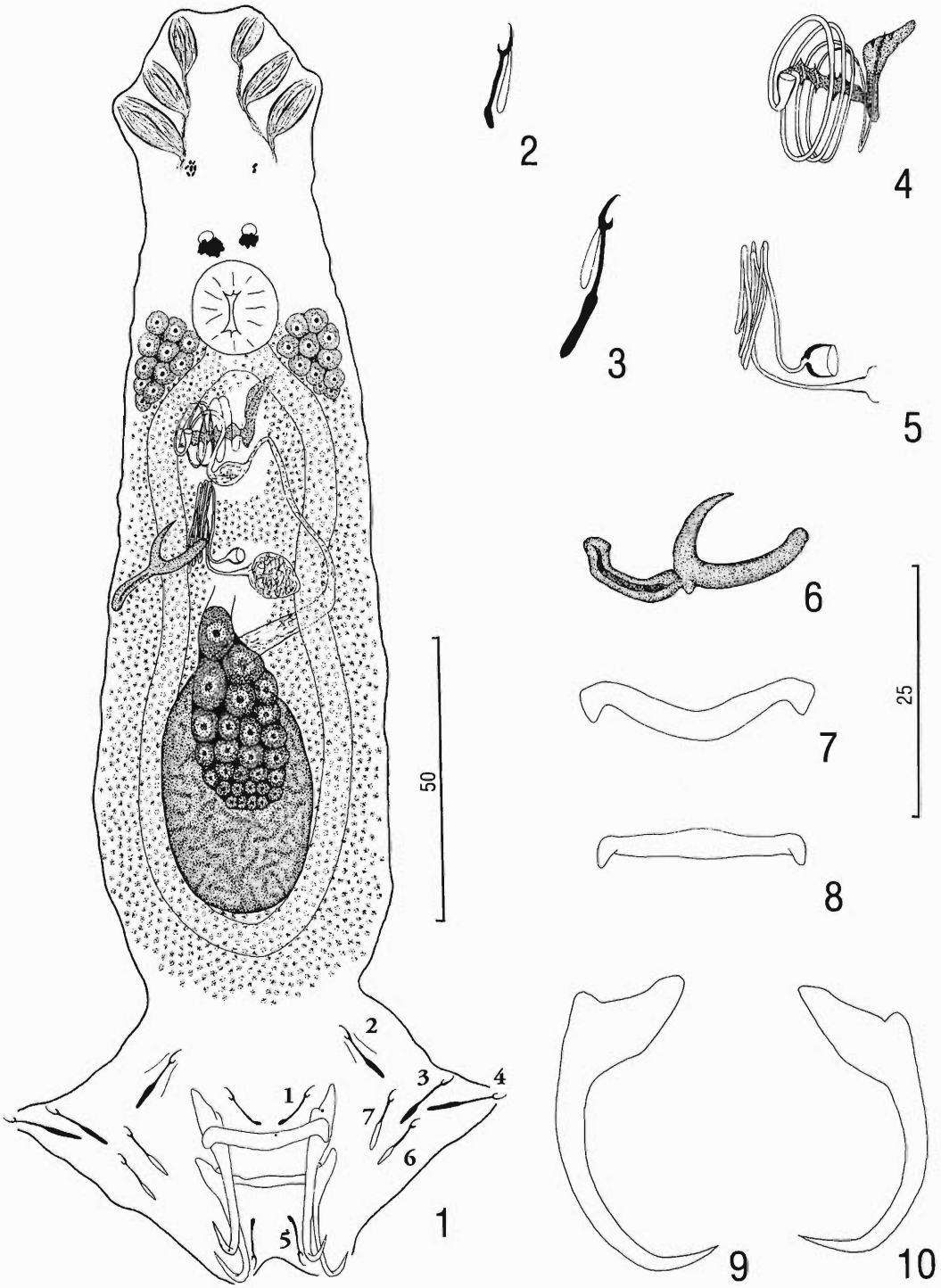
OTHER RECORDS: Orange chromide, *Etroplus maculatus* (Bloch, 1795), vicinity of Colombo, Sri Lanka (Ceylon) (Gussev, 1963); *E. suratensis,* Balugaon, Chilka Lake, Orissa, India (85°27′E; 19°47′N) (2 February 1998) (*nobis*).

INFECTION SITE: Gills.

DEPOSITED SPECIMENS: Thirty-eight voucher specimens, USNPC 90093, HWML 15477.

Remarks and Discussion

Sclerocleidoides gen. n. is monotypic. The genus is defined by species with the combined presence of 1) a dextral vaginal sclerite, 2) a ventral vaginal pore, 3) 4 eyes (anterior pair frequently absent) comprised of small ovate granules, 4) intestinal ceca confluent posterior to gonads, 5) intercecal, overlapping gonads (testis dorsoposterior to germarium), 6) articulated accessory piece and male copulatory organ, 7) coiled male copulatory organ with counterclockwise rings, and 8) haptor armed with ventral and dorsal anchor/bar complexes, 14 hooks (7 pairs) with ancyrocephaline distribution; hook shank comprised of 2 subunits (proximal subunit dilated). Of these features, the presence of a dextral vaginal sclerite apparently serves as a synapomorphy for the genus. Two other dactylogyrid genera, *Urocleidoides* Mizelle and Price, 1964 (sensu Kritsky et al., 1986), and *Gonocleithrum* Kritsky and Thatcher, 1983, contain



Figures 1–10. ***Sclerocleidoides etropli*** **(Gussev, 1963) comb. n. 1. Whole mount (composite, ventral view). 2. Hook pair 2 (typical of pairs 2, 5). 3. Hook pair 4 (typical of pairs 2–4, 6, 7). 4. Copulatory complex (ventral view). 5. Vagina. 6. Vaginal sclerite. 7. Ventral bar. 8. Dorsal bar. 9. Ventral anchor. 10. Dorsal anchor. All figures are drawn to the 25-μm scale, except Figure 1 (50-μm scale).**

members with sclerites in the trunk that apparently function during copulation. *Sclerocleidoides* differs from *Urocleidoides* by having a dextral vaginal sclerite (sinistral in *Urocleidoides*) and having a ventral vaginal pore (lateral in *Urocleidoides*) (see Kritsky et al., 1986). The new genus is differentiated from *Gonocleithrum* in that the sclerites in the trunk (gonadal bar of Kritsky and Thatcher, 1983) of *Gonocleithrum* species are ventral and form pouch-like structures on the ventral surface of the body (see Kritsky and Thatcher, 1983). Based on comparative position and morphology of the body sclerites in species of *Urocleidoides, Gonocleithrum,* and *Sclerocleidoides,* it is unlikely that these structure are homologs; each apparently developed independently within the respective genera.

Including *S. etropli,* 4 species of Dactylogyridae have been described from *Etroplus* species occurring on the Indian subcontinent. Gussev (1963) proposed *Ceylonotrema* for his new species, *C. colombensis,* from the gills of *E. suratensis* from Ceylon (Sri Lanka). Kulkarni (1969) described 2 new species, *Onchiodiscus pterodiscoides* Kulkarni, 1969, and *Haplocleidus globodiscus* Kulkarni, 1969, from this host in India and proposed *Onchiodiscus* Kulkarni, 1969. Gussev and Fernando (1973) transferred *H. globodiscus* to *Enterogyrus* as *E. globodiscus* (Kulkarni, 1969) Gussev and Fernando, 1973. In addition, *O. pterodiscoides* may be a junior synonym of *C. colombensis* Gussev, 1963, in which case *Onchiodiscus* is a junior synonym of *Ceylonotrema.* The only character used by Kulkarni (1969) that distinguishes *Onchiodiscus* from *Ceylonotrema* is the presence of an "onchium" on the anteroventral surface of the haptor. However, the onchium in *O. pterodiscoides* may represent the enlarged pair of hooks (pair 1) described by Gussev (1963) in *C. colombensis.* Kulkarni (1969) observed only 4 pairs of hooks in *O. pterodiscoides,* 5 pairs if the onchium represents pair 1, suggesting that he missed 2 or 3 hook pairs (hook pair numbers uncertain, based on his drawing of the haptor of *O. pterodiscoides*). Unfortunately, type specimens of *O. pterodiscoides* were not available to confirm the potential synonymy of these species.

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Heteronchocotyle gymnurae sp. n. (Monogenea: Hexabothriidae), a Gill Parasite of *Gymnura altavela* (Elasmobranchii: Gymnuridae) from the Mediterranean Sea

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ABSTRACT: *Heteronchocotyle gymnurae* sp. n. is decribed from the gills of the spiny butterfly ray *Gymnura altavela* in the Gulf of Gabès, Tunisia. The new species is compared with the 2 species of *Heteronchocotyle* already known and with other hexabothriids possessing an asymmetrical haptor. The diagnosis of the genus *Heteronchocotyle* Boeger and Kritsky, 1989, is emended by adding the course of the vagina, which opens into the transverse vitelloducts near the median plane, the unarmed cirrus, which is not dilated distally, and the presence of a prostatic gland. This report is the first record of specimens of the genus *Heteronchocotyle* from Myliobatiformes.

KEY WORDS: *Heteronchocotyle gymnurae* sp. n., Monogenea, Hexabothriidae, gills, parasite, *Gymnura altavela*, spiny butterfly ray, Elasmobranchii, Mediterranean Sea, Tunisia.

From 1995 to 1998, we collected helminth parasites inhabiting elasmobranchs from the Tunisian coast. The southeastern coast of Tunisia is known to possess many species of tropical ichthyofauna, including the spiny butterfly ray *Gymnura altavela* (Linnaeus, 1758). Among the helminths collected from *G. altavela* were specimens of a new species of *Heteronchocotyle* (Hexabothriidae), which is described herein.

Materials and Methods

Specimens of *G. altavela* caught by local fishermen were examined shortly after death. Gills were removed, placed in separate petri dishes containing seawater, and examined for parasites with a stereomicroscope with incident light. Monogeneans were detached from the gills and transferred to a dish containing seawater. Some living parasites were partially compressed beneath a coverslip and studied with a light microscope. Others were fixed between the slide and coverslip with buffered neutral buffered formalin or 75% ethanol and stored in 75% ethanol. Specimens were stained with Semichon's acetic carmine, dehydrated, cleared with clove oil, and mounted in Canada balsam. Measurements, given in micrometers, were made with a drawing tube and are expressed as the mean and standard deviation, followed by the range in parentheses.

Members of Hexabothriidae possess a haptor consisting of 1 posterior haptoral appendix with 2 muscular unarmed suckers and a cotylophore plate with 6 suckers, each armed with a semicircular sclerite. Generally, the appendix possesses a pair of small hamuli between the suckers. Sucker sclerites were measured as indicated in Figure 1. The cotylophore suckers were numbered as indicated in Figure 2.

The classification of Hexabothriidae follows that proposed by Euzet and Maillard (1974) and revised by Boeger and Kritsky (1989).

Results

Heteronchocotyle Brooks, 1934

EMENDED DIAGNOSIS: Monogenea. Hexabothriidae. Haptor asymmetrical, reflexed dorsally, longitudinal axis forming an angle = 45° with the sagittal midline of the body on the side of haptorial appendix. Haptor with 6 suckers, armed with sclerites. Sucker sclerites very dissimilar in shape and size. Haptoral appendix lateral. Hamuli present. Distal cirrus ovate or not, proximal cirrus elongate, tubular with thick muscular wall. Pars prostatica absent or present. Vas deferens convoluted, looping before entering posterior end of prostatic region. Ovary dextral, coiled, J-shaped. Two vaginal openings ventrolaterally. Vaginal ducts parallel, opening into transverse vitelloducts near median plane of body. Oviduct dilated, forming receptaculum seminis. Ootype smooth. Eggs fusiform, united in chain, with 2 polar filaments.

TYPE SPECIES, HOST, AND LOCALITY: *Heteronchocotyle hypoprioni* Brooks, 1934, from the Atlantic lemon shark *Negaprion brevirostris* (Poey, 1868), Florida, U.S.A.

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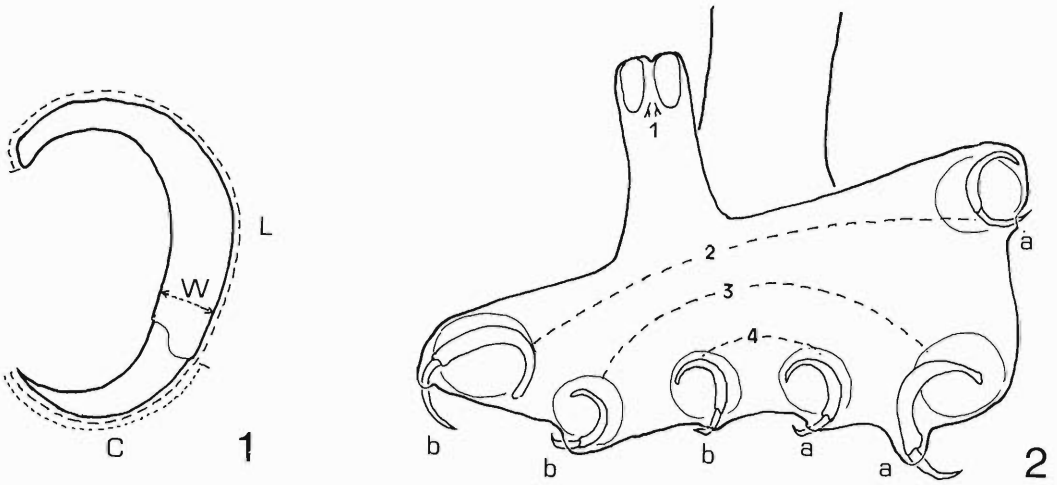


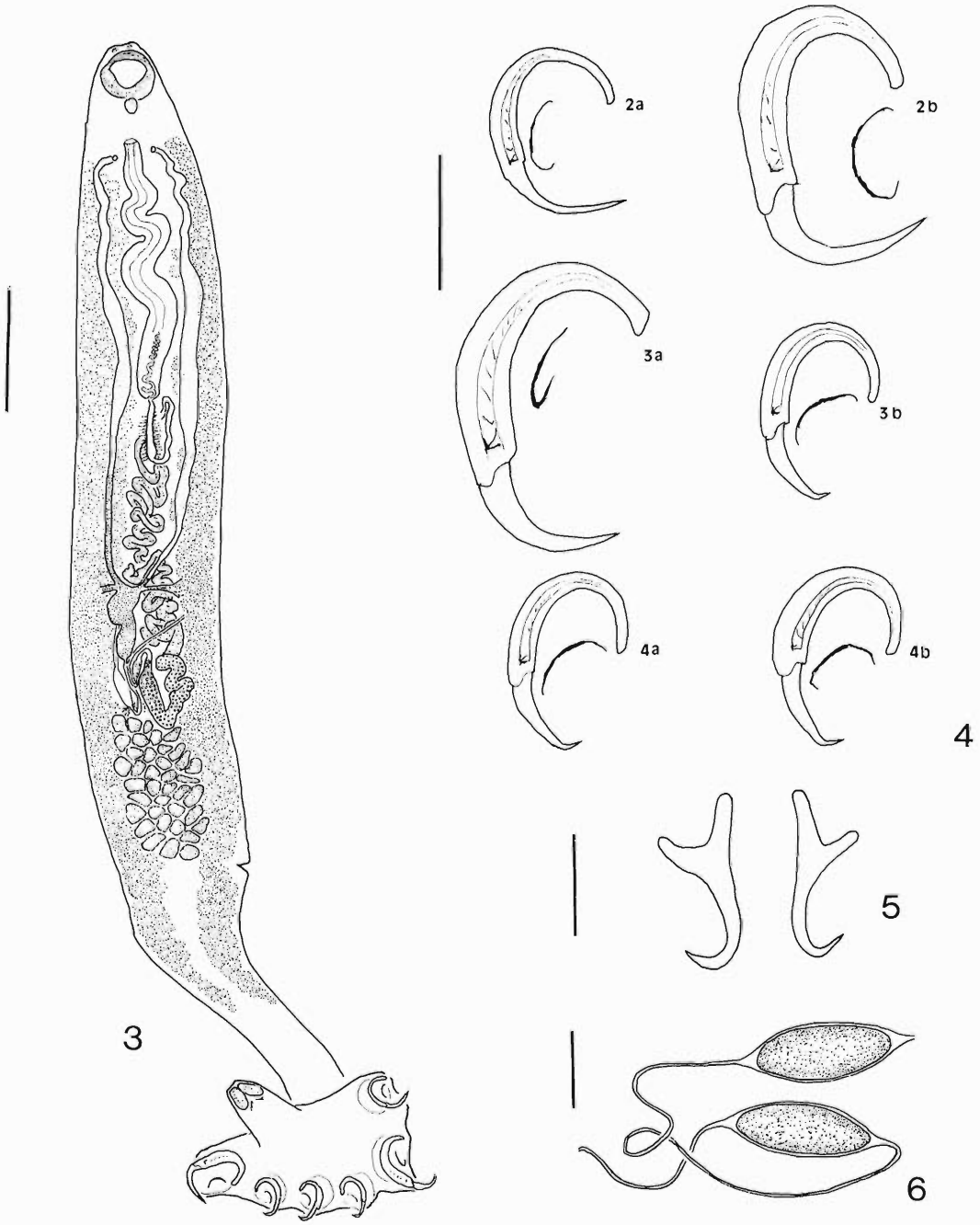
Figures 1, 2. 1. Schematic representation of morphometric measurements of haptoral sucker sclerites. L = total length, W = width, C = claw length. 2. Numbering system used for sucker and sucker sclerite pairs symmetry (after Euzet and Maillard, 1974).

OTHER SPECIES: *Heteronchocotyle leucas* Hargis, 1955, from the bull shark *Carcharhinus leucas* (Valenciennes, 1841).

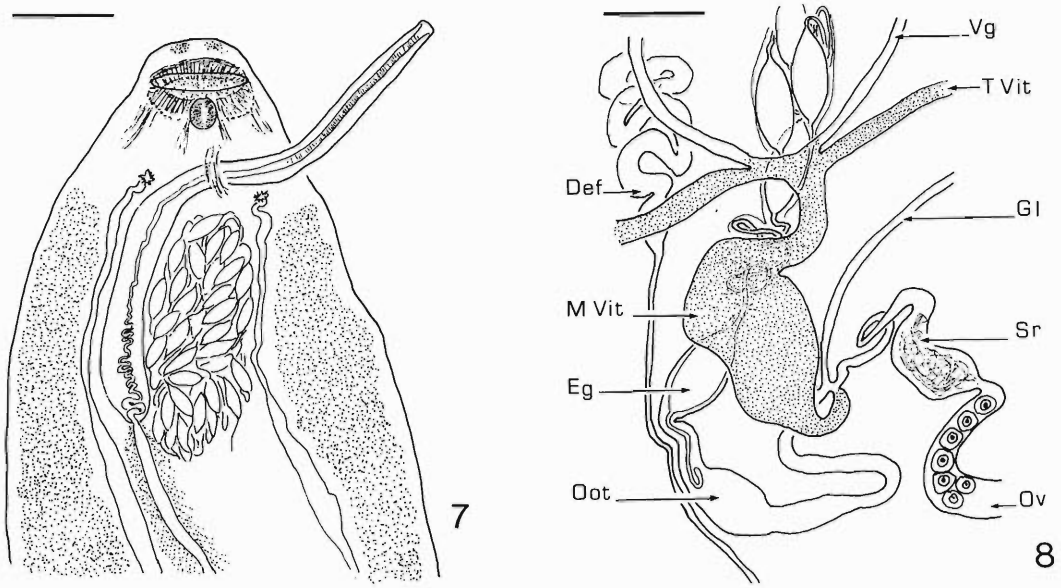
Heteronchocotyle gymnurae sp. n. (Figs. 3–8)

Description

Measurements based on 11 flattened adult specimens. Body elongate, sides nearly parallel, 4,510 ± 540 (4,100–5,250) long including haptor, 809 ± 174 (700–1,200) wide at level of ovary, narrowed posteriorly before haptor (Fig. 3). Cotylophore triangular, 1,200 ± 154 (1,000–1,500) long by 597 ± 76 (500–700) wide, with 6 armed suckers, 5 on posterior edge. Sucker sclerites robust (Fig. 4). Sucker sclerite 2a, L = 421.0 ± 26.1 (380–455), W = 30.1 ± 2.6 (25–32), C = 133 ± 8.1 (110–145); sucker sclerite 2b, L = 610 ± 22 (582–645), W = 43.8 ± 3.7 (35–45), C = 203 ± 11.3 (180–225); sucker sclerite 3a, L = 604 ± 31.7 (550–655), W = 52.9 ± 3.8 (50–60), C = 184 ± 15.8 (155–215); sucker sclerite 3b, L = 372 ± 24.8 (345–420), W = 31.6 ± 2.4 (30–36), C = 105 ± 7.2 (95–120); sucker sclerite 4a, L = 388 ± 21.9 (365–430),W = 32.9 ± 2.6 (30–38), C = 108 ± 7.1 (100–120); sucker sclerite 4b, L = 380 ± 16.4 (350–405), W = 32.3 ± 2.6 (30–38), C = 104 ± 6.8 (95–115). Sucker sclerites 2a and 2b differ from other pairs of sucker sclerites by claw bent at its base. Sucker rim decorated with rounded papillae. Sucker aperture with semicircular sclerotized structure. Structure 123–127 long, except for 2b (153). Haptoral appendix lateral, 252 ± 42.9 (200–350) long by 177 ± 46.1 (120–250) wide, with unarmed muscular suckers (1a and 1b), each 118 ± 10.2 (105–140) long, 59.3 ± 8.2 (40–60) wide. Two hamuli between suckers. Hamuli 42.2 ± 3.5 (40–47) long, with subequal guard and shaft (Fig. 5). Oral sucker anterior, 253 ± 18.7 (240–300) long, 190 ± 29.4 (150–250) wide, studded with small round papillae. Pair of apical glandular openings. Pharynx subspherical, 56.7 ± 4.6 (50–62) long, 60.4 ± 4.1 (50–65) wide. Two lateral intestinal crura, each with lateral diverticula, crura confluent posteriorly. Testes 37 ± 6 (31–44) in number, postequatorial, between intestinal crura. Vas deferens very sinuous, preovarian, along midline, forming seminal vesicle. Vas deferens narrowed, looping before pars prostatica. Pars prostatica 323 ± 61.8 (240–350) long. Cirrus bulb 1,120 ± 125 (1,000–1,400) long, 59.5 ± 7.2 (50–65) wide. Cirrus unarmed, not dilated distally, protrusible (Fig. 7). Ovary (germarium) dextral, J-shaped tubular, coiled, pre-equatorial. Oviduct emerging from posterior extremity of ovary, dilated to form receptaculum seminis. Vitelline follicles lateral, surrounding intestinal ceca, extending from level of genital pore to narrowed posterior part of body. No follicles in haptor. Transverse vitelloducts joining at midline to



Figures 3–6. ***Heteronchocotyle gymnurae*** **sp. n. 3. Whole specimen, dorsal view; scale bar = 500 μm. 4. Sucker sclerites of pairs 2, 3, and 4; scale bar = 100 μm. 5. Hamuli; scale bar = 25 μm. 6. Two eggs in chain; scale bar = 20 μm.**



Figures 7, 8. ***Heteronchocotyle gymnurae*** **sp. n. 7. Anterior part of body, dorsal view. Cirrus evaginated. Scale bar = 100 μm. 8.** ***Heteronchocotyle gymnurae*** **sp. n. Genital complex; scale bar = 100 μm. Eg = egg, Def = vas deferens, GI = genito-intestinal duct, M Vit = median vitelloduct, Oot = ootype, Ov = ovary, Sr = seminal receptacle, T Vit = transverse vitelloduct, Vg = vagina.**

form median vitelline reservoir. Two vaginae opening ventrolaterally slightly posterior to genital pore, each entering transverse vitelline commissure near median plane (Fig. 8). Uterus ventral, in midline. Eggs fusiform, with polar filaments united in chain. Eggs in utero 108 ± 4.6 (95–110) long by 39.5 ± 0.6 (35–40) wide (Fig. 6).

Taxonomic summary

TYPE HOST: *Gymnura altavela* (Linnaeus, 1758) (Gymnuridae).

INFECTION SITE: Gills, between gill filaments.

TYPE LOCALITY: Bizerte (37°30′N; 9°50′E), Tunisia.

OTHER LOCALITY: Zarzis (33°15′N; 11°10′E), Tunisia.

PREVALENCE: Eight of 12 hosts infected.

SPECIMENS DEPOSITED: Holotype, Muséum National d'Histoire Naturelle (Paris), MNHM 837 HF Tk228; 2 paratypes, Muséum National d'Histoire Naturelle (Paris), MNHN 837, HF Tk227, and Tk229; 2 paratypes deposited at The Natural History Museum (London), BNHM 2000.3.17.1–2; 2 paratypes deposited in the U.S. National Parasite Collection Beltsville, Maryland, U.S.A., USNPC MT30-16H and MT30-16I.

ETYMOLOGY: The species is named after the host.

Remarks and Discussion

On the basis of its haptoral morphology, we have placed this species in *Heteronchocotyle*. *Heteronchocotyle gymnurae* sp. n. differs from both previously described species, *H. hypoprioni* Brooks, 1934, and *H. leucas* Hargis, 1955, in the morphology and size of sucker sclerite pairs 2–4 (Fig. 9).

Heteronchocotyle gymnurae is the first species of *Heteronchocotyle* reported to parasitize a member of the order Myliobatiformes. Previous records include *H. hypoprioni* from *Negaprion brevirostris* and *H. leucas* from *Carcharhinus leucas,* both parasites of Carcharhinidae.

This new species, with the distal part of cirrus not ovate and having the prostatic region of cirrus, does not fit the diagnosis of *Heteronchocotyle* as proposed by Boeger and Kritsky (1989). These differences are not sufficient to distinguish a new genus, requiring that we emend the diagnosis to accommodate this new

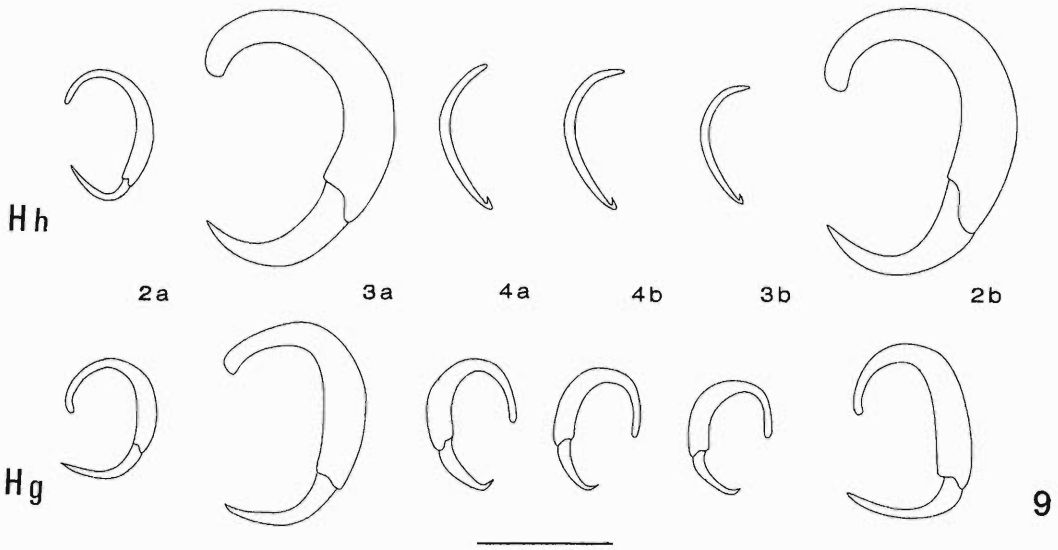


Figure 9. Comparison at the same scale of haptoral sucker sclerites from *Heteronchocotyle hypoprioni* Brooks, 1934, and *Heteronchocotyle gymnurae* sp. n. Scale bar = 200 μm.

species. Because of this, the position of *Heteronchocotyle* in the cladogram of Boeger and Kritsky (1989) should be reconsidered and revised if necessary. Before this can be done, however, some questions regarding the anatomy of the genus need to be clarified. For example, there is ambiguity in the definition of the seminal receptacle. Brooks (1934) defined the seminal receptacle in *Heteronchocotyle* as an enlargement of the oviduct. Boeger and Kritsky (1989), on the other hand, defined the seminal receptacle as a blind sac opening into the oviduct. Under this definition, the seminal receptacle does not exist in *H. gymnurae.* We believe that various terms must be used to differentiate structures for sperm storage. Also, the illustration of the haptor given by Boeger and Kritsky (1989) for *Heteronchocotyle* (fig. 3, p. 426) is not exact. The haptorial appendix is shown as median posterior, whereas it is in fact lateral (Euzet and Maillard, 1976).

In order to make taxonomic placements simpler, some large groups can be subdivided into smaller groups. This subdivision need not be based on evolutionary relationships because it serves merely as an aid for taxonomists. The family Hexabothriidae can be subdivided into 2 groups on the basis of haptor morphology. Parasites belonging in genera of the first group possess suckers that are symmetrically arranged. Parasites belonging in genera of the second group, *Heteronchocotyle* Brooks, 1934; *Rhinobatonchocotyle* Doran, 1953; *Neonchocotyle* Ktari and Maillard, 1972; *Pristonchocotyle* Watson and Thorson, 1976; *Paraheteronchocotyle* Mayes, Brooks, and Thorson, 1981; *Callorynchocotyle* Suriano and Incorvaia, 1982, possess suckers that are asymmetrically arranged.

Four of the genera in the second group, *Heteronchocotyle, Rhinobatonchocotyle, Paraheteronchocotyle,* and *Pristonchocotyle,* contain species that are characterized by a dorsal reflexed haptor that is asymmetrical, a cotylophore plate that is elongated almost perpendicularly to the body proper, and 5 suckers more or less aligned on the posterior edge. *Rhinobatonchocotyle* and *Pristonchocotyle* differ from *Heteronchocotyle* in that their species are characterized by the possession of vaginae that are X-shaped rather than parallel or V-shaped and sucker sclerites of nearly equal size rather than very different in size. The course of the vaginae of *Paraheteronchocotyle* is unknown, but the genus was distinguished from *Heteronchocotyle* by Mayes et al. (1981) on the basis of absence of hamuli and the size of the sucker sclerites.

As pointed out by Euzet and Maillard (1967), in all hexabothriids with asymmetrical haptors, "right" and "left" individuals are known. Of the 11 specimens of *H. gymnurae,* 8 are right

and 3 are left. These morphologies depend on the placement, anterior or posterior, of the parasite on the gill filament. This phenomenon is comparable to that reported by Llewellyn (1956) in *Gastrocotyle trachuri* Van Beneden and Hesse, 1863, from *Trachurus trachurus* (Linnaeus, 1758); by Euzet and Lopez-Roman (1973) in *Axine belones* Abildgaard, 1794, from *Belone acus* (Linnaeus, 1758); and by Euzet and Wahl (1970) in *Rhinecotyle crepitacula* Euzet and Trilles, 1960, from *Sphyraena piscatorum* Cadenat, 1964.

Parasites of *G. altavela* appear to indicate an alteration of benthic and pelagic lifestyles. In the nasal fossae, we collected an individual of Monocotylidae (Neifar *et al.*, unpublished) that is normally present in benthic Rajiformes, whereas other species of *Heteronchocotyle* have been reported from members of the Carchariniformes, which are pelagic. It is possible that this difference is related to the ecology of *G. altavela.*

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Advice to Authors — Citing Taxonomic Authorities and Dates

All scientific names, either the genus name standing alone or the binomen consisting of the genus and species names, must be accompanied by the taxonomic authority(ies) and date(s) the first time that they are used in the text of the paper. The Editors encourage but do not require authors to cite taxonomic authorities (either with or without the date) in the Title and/or Abstract. Once the taxonomic authorities have been cited, they do not need to be repeated subsequently. In papers containing long lists of parasites and/or hosts, the taxonomic authors and years can be cited in a table and not repeated in the text, as long as reference to the table is made early in the paper. When discussing unidentified species of a genus (e.g., *Langeronia* sp. or *Langeronia* spp.), it is not necessary to provide the taxonomic author and year of the genus. However, if discussing the genus by itself, the taxonomic author and year must be provided (e.g., "The taxonomic statuses of the genera *Langeronia* Caballero and Bravo-Hollis, 1949, and *Loxogenes* Stafford, 1904, have been the subject of much controversy."). Taxonomic authorities must not be included in the Literature Cited section of the paper unless they are presented as a text reference [Example: "Caballero and Bravo-Hollis (1949) erected the genus *Langeronia* for a new species, *Langeronia macrocirra,* from the northern leopard frog, *Rana pipiens* Schreber, 1782, in Mexico." In this example, the authors presented the taxonomic authorities of the genus *Langeronia* and the species *Langeronia macrocirra* as a text citation, which was included in the Literature Cited, and they do not need to present them again following each scientific name; Schreber (1782), however, should not be included in the Literature Cited.]

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Cyathostomum montgomeryi and Its Place in the Cyathostominae (Nematoda: Strongylidae)

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ABSTRACT: *Cyathostomum montgomeryi* (Boulenger, 1920) K'ung, 1964, a common parasite of zebras, has not been redescribed since its original description. It is still almost unknown outside of Africa. This species was placed in different tribes (Murshidiinea or Cyathostominea) by recent workers. As part of an international effort to clarify the classification of the Cyathostominae of horses, we studied 210 specimens from Burchell's zebra *Equus burchelli antiquorum* Smith, 1841, from the Kruger National Park (Republic of South Africa) and Etosha National Park (Namibia) and made measurements of 15 males and 15 females. Specimens that we measured were larger than those described by Boulenger. *Cyathostomum montgomeryi* has 2 *corona radiata* or leaf crowns surrounding the mouth. The internal leaf crown (ILC) is inserted near the middle of the buccal capsule. The external leaf crown (ELC) has fewer elements than the ILC. The bases of the ILC elements are inserted in a curved line on the wall of the buccal capsule, and those of the ELC elements are recessed from the tips of the elements of the ILC on which they rest. All of these characters are shared with the other species of the genus *Cyathostomum*. The extrachitinous supports are similar to those of *Cyathostomum catinatum*. The distal ends of the spicules are identical to others in the Cyathostominea but differ from those in the Murshidiinea. The bursa is typical for *Cyathostomum*. Thus, we retain this species in the Cyathostominea.

KEY WORDS: nematode systematics, *Cyathostomum montgomeryi*, Strongylidae, zebras, nematode morphology, *Equus burchelli*, South Africa, Namibia.

The Cyathostominea or "small strongyles" of equids can cause considerable morbidity and mortality in horses (Herd, 1990). Research activity on these nematodes is currently high because 1) larval cyathostominosis, a syndrome in which large numbers of larvae emerge from the walls of the large colon and cecum and cause severe colitis that may result in death, is increasingly recognized (Mair, 1994; van Loon et al., 1995); 2) resistance to anthelmintics in the Cyathostominea has been reported widely (Gawor, 1995; Herd and Coles, 1995; Ihler, 1995); and 3) prospects for biological control using nematode-trapping fungi appear to be promising (Bird and Herd, 1995; Larsen et al., 1996).

Most species of Cyathostominea are widely distributed and are parasites of all species of equids. However, several of them show specificity to 1 host or are distributed in limited areas. For this reason, some species, including *Cyathostomum montgomeryi* (Boulenger, 1920) K'ung, 1964, are studied much less than those that have considerable economic significance. Participants in an international workshop in Sun City, South Africa (Lichtenfels et al., 1998), recognized 51 valid species of Cyathostominea and indicated problems in the identification and/or the classification of some of them. The redescription and classification of *C. montgomeryi* was one of the tasks identified by the workshop. This common parasite of zebras has not been redescribed since its original description. It was reported in African zebras by several researchers (Scialdo-Krecek, 1983; Krecek, Malan, et al., 1987; Krecek, Reinecke, and Malan, 1987), in donkeys (Eysker and Pandey, 1987, 1989; Matthee et al., 2000), and in horses and mules (Monnig, 1928) (Fig. 1). It is still almost unknown outside of Africa. This species was placed in the group Montgomeryi by Ihle (1922), in the genus *Cylicotoichus* by Cram (1924), and moved to the tribe Murshidiinea by Hartwich (1986). However, K'ung (1964) and Lichtenfels (1975) placed it in the genus *Cyathostomum* and the tribe Cyathostominea. The objective of the pre-

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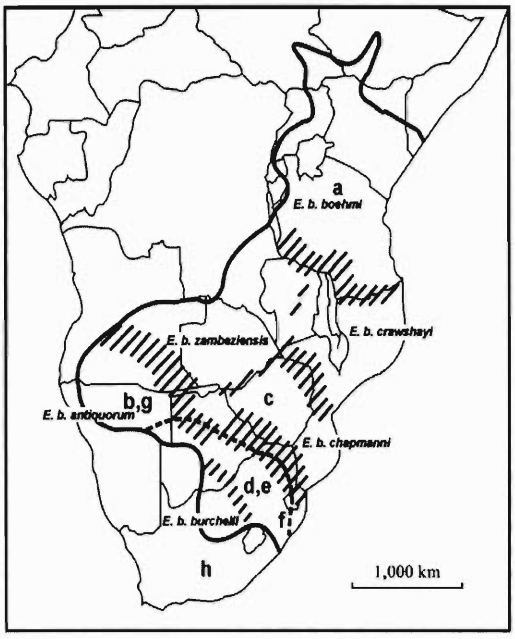
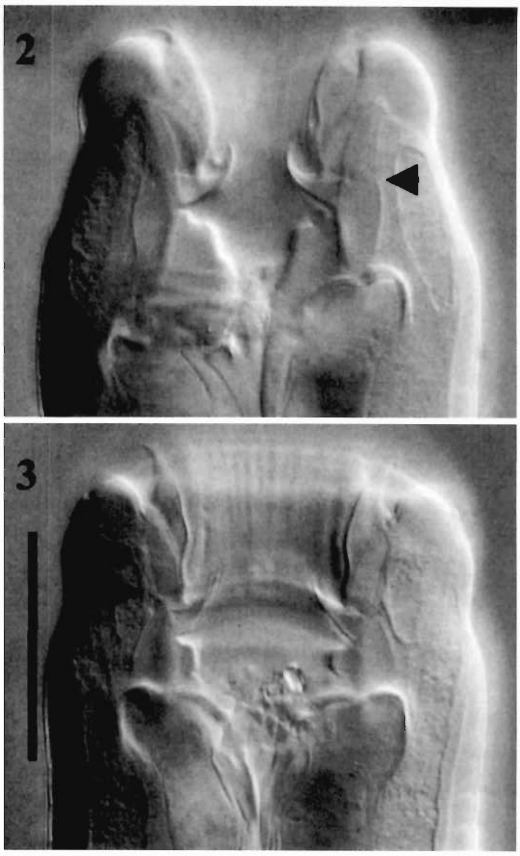


Figure 1. Distribution map of 6 subspecies of Burchell's zebras (*Equus burchelli* sspp.) in southern Africa. The solid line is the original distribution of these 6 subspecies. The dashed line marks the present southern boundary of the species range, and the hatched areas represent regions where subspecies are presumed to intergrade (modified from Ansell [1971] and Smithers [1983]). Studies that reported *Cyathostomum montgomeryi* in Burchell's zebra and other equids are also included. a = Boulenger, 1920; b = Krecek, Reinecke, and Malan, 1987; c = Eysker and Pandey, 1987, 1989 (donkeys); d = Matthee et al., 2000 (donkeys); e = Monnig, 1928 (horses and mules); f = Scialdo-Krecek, 1983; Krecek, Malan, et al., 1987; g = Krecek, Reinecke, and Malan, 1987 (Hartmann's mountain zebra, *Equus zebra hartmannae* Matschie, 1898); h = Krecek et al., 1994 (Cape mountain zebra, *Equus zebra zebra* Linnaeus, 1758).



Figures 2, 3. *Cyathostomum montgomeryi,* photomicrographs. Scale bar = 100 μm (arrowheads at junction of buccal capsule wall and extrachitinous support). 2. Buccal capsule, lateral view. 3. Buccal capsule, ventral view.

sent study was to provide an improved description of *C. montgomeryi* and determine its place in the Cyathostominae.

Materials and Methods

We have studied 210 specimens from Burchell's zebra *Equus burchelli antiquorum* Smith, 1841, from the Kruger National Park (Republic of South Africa) and Etosha National Park (Namibia) collected by R. C. Krecek and made measurements of 15 males and 15 females. Two specimens of each sex have been accessioned in the U.S. National Parasite Collection (USNPC), Agricultural Research Service, U.S. Department of Agriculture, Beltsville, Maryland 20705, as 78991. Nematodes were fixed in 4% formalin and studied in temporary mounts, cleared in 80% phenol in glycerol, with the aid of interference-contrast light microscopy. Photomicrographs were obtained with a 35-mm camera mounted on an Olympus Vanox® research microscope at magnifications ranging from ×100 to ×400, with Kodak T-Max® negative film.

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Figures 4–7. *Cyathostomum montgomeryi,* photomicrographs. Scale bars = 100 μm. 4. Esophageal region, ventral view. 5. Male tail, lateral view. 6. Genital cone of male, lateral view, showing gubernaculum. 7. Female tail, lateral view, showing vulva, anus, and ovejector (v = vestibule, s = sphincter, i = infundibulum; lower arrow at vulva, upper arrows at ends of infundibulum).

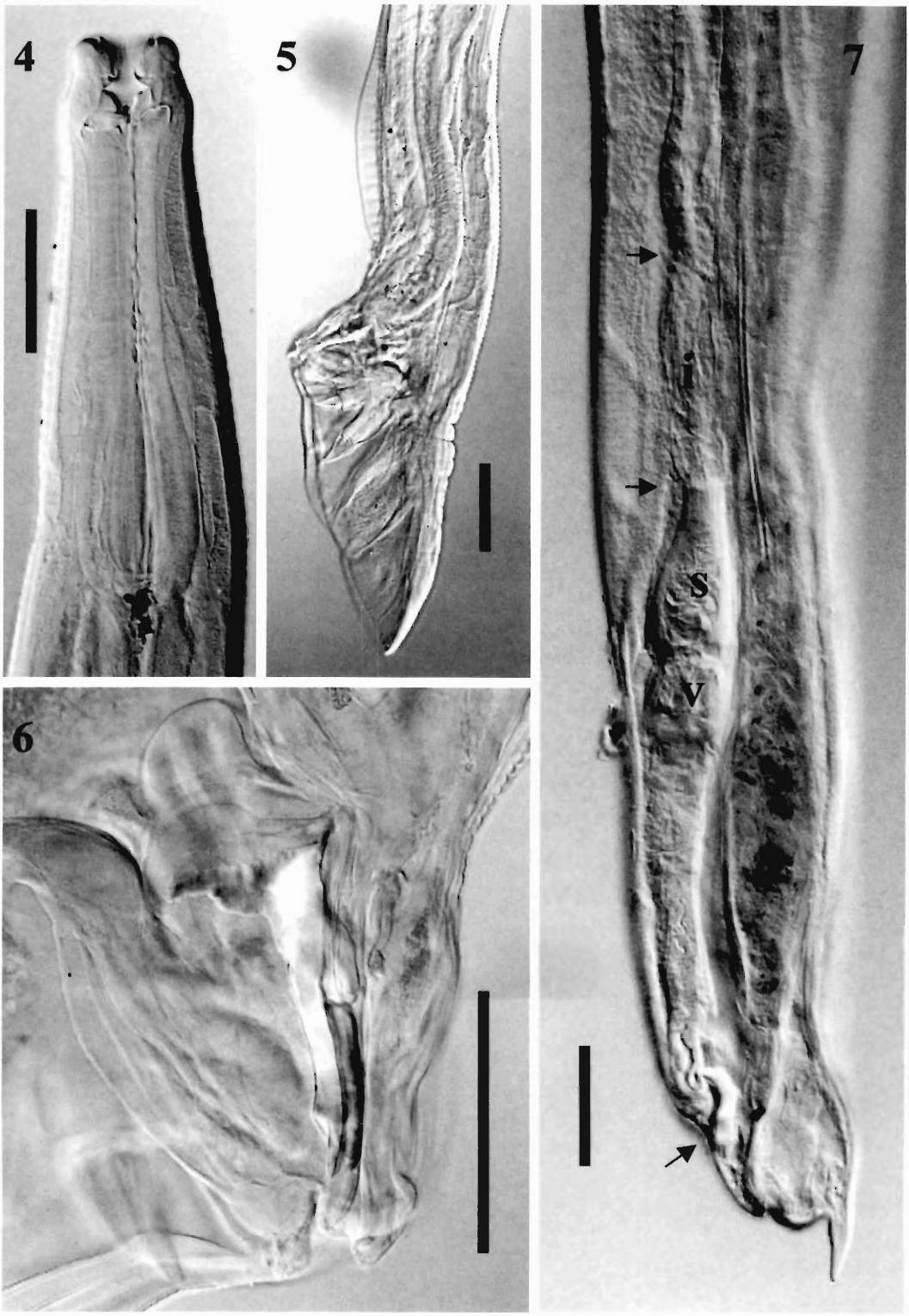

Table 1. Morphometrics (in micrometers unless otherwise indicated); range (with mean in parentheses) of males and females of *Cyathostomum montgomeryi*, compared with data by Boulenger (1920).

Morphological characters	Present study	Boulenger (1920)
Males (n = 15)		
		4.3–6
Body length (mm)	6.05–7.28 (6.62)	280
Body width	258–315 (288)	
Buccal capsule depth	33–44 (38)	22–32
Nerve ring*	138–229 (200)	
Cervical papillae* (n = 3)	300–328 (312)	240
Excretory pore*	256–321 (287)	240
Esophagus length	300–370 (335)	330
Spicule length (n = 3)	540–642 (580)	
Gubernaculum length	114–166 (148)	
Dorsal ray length	261–400 (324)	250
Females (n = 15)		
Body length (mm)	6.62–8.68 (7.46)	4.5–6.5
Body width	284–442 (349)	280
Buccal capsule depth	34–47 (42)	22–32
Nerve ring*	187–240 (212)	
Cervical papillae* (n = 2)	307–328 (318)	240
Excretory pore*	240–334 (285)	240
Esophagus length	353–454 (390)	330
Vagina length	204–408 (295)	
Vulva-to-tip-of-tail length	180–252 (214)	130
Tail length	66–120 (97)	60

* Measured from the anterior end.

Results

Cyathostomum montgomeryi (Boulenger, 1920) K'ung, 1964 (Figs. 2–7; measurements in Table 1)

Redescription

GENERAL: Cyathostominae. Mouth collar of medium height, not distinctly separated from body. Amphids short, projected slightly above mouth collar surface. Submedian papillae of medium length, reaching upper edge of external leaf crown (ELC), papilla tip demarcated by notch. ELC consisting of 18 slender pointed leaves, considerably longer than wide. Internal leaf crown (ILC) consisting of 36 similar leaves at ½ of buccal capsule depth. Base of ILC located more deeply laterally than dorsoventrally. Buccal capsule, as noted by Boulenger, characterized by peculiar bilateral symmetry, dorsal and ventral walls considerably longer than lateral walls; absence of radial symmetry making optical section of head in lateral view (Fig. 2) different from ventral view (Fig. 3). Buccal cavity depth and width nearly equal in lateral view, but dorsoventrally, buccal capsule nearly twice as wide as deep. Walls of buccal capsule thick, oval in profile. Extrachitinous support located above walls, continuous, and attached to them. Support more developed on dorsal and ventral sides of buccal capsule; reaching to ½–⅔ of height of walls of buccal capsule. (This and the dorsoventrally elongated mouth create the apparent bilateral symmetry.) Internal cuticular lining of buccal cavity inflated behind base of ILC. Dorsal gutter absent. Esophageal funnel poorly developed, 3 esophageal teeth small, triangular. Esophagus moderately wide, enlarged in proximal part. Comparatively long cervical papillae and excretory pore situated almost at same level posterior to nerve ring.

MALES: Dorsal lobe of bursa slightly longer and not visibly separated from lateral lobes (Fig. 5). Bursal rays typical for Cyathostominea. Additional branches may be situated on dorsal ray. Appendages of genital cone consisting of pair of hardly distinguishable oval protrusions. Dermal collar also poorly developed on ventral surface of genital cone. Genital cone short (Figs. 5, 6). Gubernaculum with well-developed handle and ventral notches in its middle part (Fig. 6). Distal ends of spicules hook-like.

FEMALES: Tail straight; nearly equal in length to vulva-to-anus distance. Vagina long, vestibule short, paired sphincters and infundibula elongate; latter slightly longer than former (Fig. 7).

Parasitic larvae were not available and are therefore not described.

Taxonomic summary

TYPE HOST: "Zebra."

TYPE LOCALITY: Nairobi, Kenya, Africa.

TYPE SPECIMENS: Efforts to locate type specimens were unsuccessful.

SPECIMENS STUDIED: 210 specimens from Burchell's zebra *Equus burchelli antiquorum* from Kruger National Park, Republic of South Africa, and Etosha National Park, Namibia.

SPECIMENS DEPOSITED: 2 males and 2 females, USNPC 78991.

Discussion

Boulenger (1920) described this species from zebras fairly adequately, although the specimens we measured from the same host species were slightly larger than those he described (Table 1).

We were unable to locate the types of *C. montgomeryi.* Boulenger noted that "In the structure of its mouth capsule this form differs from all other known species of *Cylicostomum* with the exception of *Cylicostomum falciferum* (Cobbold, 1882)," a parasite of the elephant now placed in the genus *Murshidia* Lane, 1914. In the latter species, however, the bilateral symmetry extends to the elements of the leaf crown; this is not the case in *C. montgomeryi,* where these structures are radially arranged. Hartwich (1986) transferred this species to Murshidiinea on the basis of the posterior insertion of the ILC on the wall of the buccal capsule. However, this species has 2 corona radiata instead of the single 1 present in most of the Murshidiinea. The genus *Quilonia,* which is in the Murshidiinea, has 2 corona radiata but is quite different from *C. montgomeryi.* The copulatory bursa of *C. montgomeryi* also is typical for *Cyathostomum.* The existence of an extrachitinous support in this species is demonstrated in this study for the first time. The extrachitinous support is the same as in other Cyathostominea but differs from those in the Murshidiinea. Therefore, we place *C. montgomeryi* in the genus *Cyathostomum,* tribe Cyathostominea, following K'ung (1964) and Lichtenfels (1975), because 1) the extrachitinous support is attached to the anterior edge of the buccal capsule wall and forms an extension of it, 2) the ELC has fewer elements than the ILC, and 3) the ILC is inserted near the middle of the buccal capsule in a curved line, typical of other species of *Cyathostomum,* but not at its bottom as shown in text-figure 6 of Boulenger (1920).

This species can be separated from other species of the genus by its appearance of bilateral symmetry of the buccal capsule walls and extrachitinous support. In contrast to *Cyathostomum catinatum* Looss, 1900, and *Cyathostomum alveatum* Looss, 1900, the base of the ILC of *C. montgomeryi* is situated deeper in the buccal capsule laterally than dorsally and ventrally. The tail of the female, unlike *C. catinatum* and *Cyathostomum pateratum* (Yorke and Macfie, 1919) K'ung, 1964, is straight.

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New Book Available

An Atlas of Metazoan Parasites in Animal Tissues. By C. H. Gardiner and S. L. Boynton. 1999. Armed Forces Institute of Pathology, Washington, DC. 63 pp. ISBN 1-881041-49-2. 8¼ × 10¾″ soft cover. Available from the American Registry of Pathology Bookstore, Room G-134, Armed Forces Institute of Pathology, 14th Street and Alaska Avenue, Washington, DC 20306-6000. Cost is US$35.00 per copy plus shipping and handling. The atlas is a companion to the recently published *An Atlas of Protozoan Parasites in Animal Tissues* and can be purchased online from the American Registry of Pathology Bookstore Web site www.afip.org/ or toll-free phone 1-888-838-1297 (U.S. only). **Abstract**: "This atlas illustrates metazoan parasites in animal tissues. To facilitate identification, it provides a brief description of parasites, hosts, transmission, and pathogenesis of the most important metazoans. Also included are 270 color photographs of metazoans and associated lesions, recorded using optimal conditions for identification."

Pathology of Infectious Diseases. Volume 1: Helminthiases. Editor: Wayne M. Meyers. 2000. Coeditors: Ronald C. Neafie, Aileen M. Marty, and Douglas J. Wear. Armed Forces Institute of Pathology, Washington, DC. 562 pp. ISBN 1-881041-65-4. 8½ × 11″ hard cover. Available from the American Registry of Pathology, Room G-134, Armed Forces Institute of Pathology, 14th Street and Alaska Avenue, Washington, DC 20306-6000. Cost is US$145.00 per copy plus shipping and handling, and purchase can be made online from the American Registry of Pathology Bookstore Web site www.afip.org/ or toll-free phone 1-888-838-1297 (U.S. only). **Abstract**: "Drawing on the greatest repository of human pathologic material in the world, [the] authors . . . discuss the more common, as well as the unique, rare, and unusual helminths that infect human beings. With over 500 pages of text and more than 1300 figures and . . . photographs, . . . the book provides . . . comprehensive descriptions and illustrations of the morphology and life cycles of helminths, and the history, clinical features, histopathology, diagnosis, and treatment of helminthic infections. The book has many new features not found in similar texts, including tables of morphologic features and geographic locations, and a specially designed index to guide readers to a correct identification of helminths and pathologic changes they cause."

Comp. Parasitol.
68(1), 2001 pp. 103–107

Neoechinorhynchus didelphis sp. n. (Acanthocephala: Neoechinorhynchidae) from the Redfin Pickerel, *Esox americanus*, in Georgia, U.S.A.

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ABSTRACT: *Neoechinorhynchus didelphis* sp. n. (Neoechinorhynchidae) is described from the intestine of the redfin pickerel *Esox americanus* Gmelin, 1789, in the Ogeechee–Little Ogeechee River System, Georgia, U.S.A. The new species is separated from all members of the genus *Neoechinorhynchus* Hamann, 1892, *in* Stiles and Hassall, 1905, on the basis of characters of the uterine bell, size of proboscis hooks, the neck girdle, proboscis receptacle, uterine complex, and vaginal retractor ligaments.

KEY WORDS: Acanthocephala, *Neoechinorhynchus didelphis* sp. n., Neoechinorhynchidae, Pisces, *Esox americanus*, redfin pickerel, Georgia, U.S.A.

A new species of the acanthocephalan genus *Neoechinorhynchus* Hamann, 1892, *in* Stiles and Hassall, 1905, was found in Georgia, U.S.A. It is herein described from the redfin pickerel *Esox americanus* Gmelin, 1789, and distinguished from other species of the genus.

Materials and Methods

Fish were collected in 3 sites along the Ogeechee River System, Georgia, in 1990. All sites were moderately deep (up to 3 m) and acid (pH 4.5–6.9) blackwater streams flowing through cypress–red maple–water oak associations. Two of the 3 sites, Mill Creek at U.S. Highway 280, 8 km east of Pembroke, Bryan County (32°8′23″N; 81°27′30″W), and Baker Swamp at Georgia State Route 196, 6 km northwest of Midway, Liberty County (31°49′24″N; 81°28′16″W), were associated with the major river system. The third site (where most of the acanthocephalans were collected, Little Ogeechee River, 11 km southwest of Savannah, Chatham County [32°00′00″N; 81°15′00″W]) is a tributary of the major river. Acanthocephalans were collected from *E. americanus* during March, 1990. The collecting sites dried completely after June 1990. Five male and 21 female worms were available.

Specimens were fixed in 5% formalin, stained in Grenacher's borax carmine, cleared in clove oil, and mounted in Permount®. Measurements are in micrometers unless otherwise stated. The range is followed by mean values (in parentheses). Width measurements refer to maximum width. Body (=trunk) length does not include neck, proboscis, or male bursa. "Eggs" refers to mature eggs. Figures were drawn with the aid of photoprojection. Specimens were deposited at the United States National Parasite Collection (USNPC), Beltsville, Maryland.

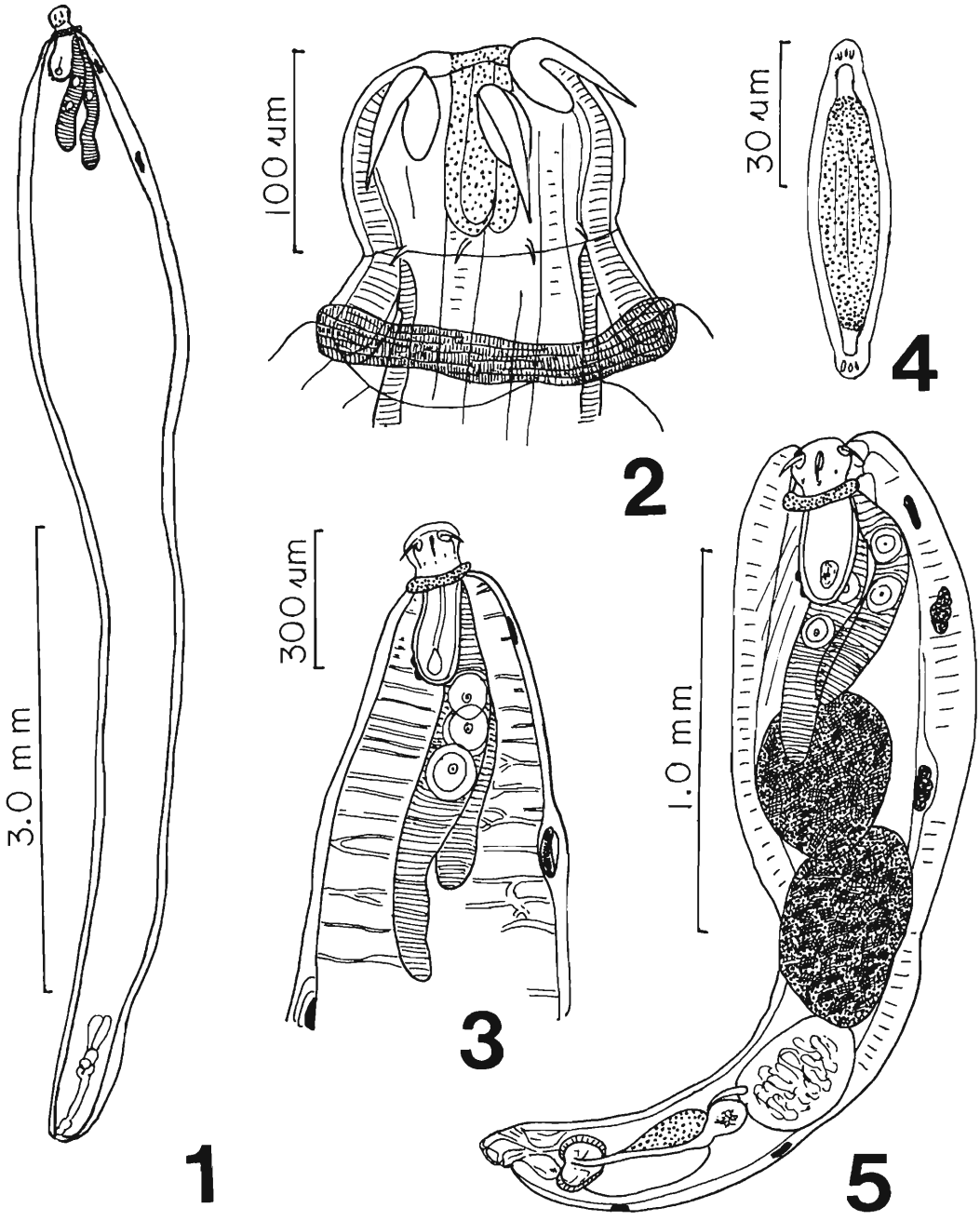
Results

Neoechinorhynchus Hamann, 1892, *in* Stiles and Hassall, 1905 *Neoechinorhynchus didelphis* sp. n. (Figs. 1–10)

Description

GENERAL: Neoechinorhynchidae, Neoechinorhynchinae, with characters of the genus *Neoechinorhynchus*. Trunk cylindrical, markedly enlarged anteriorly, and gradually tapering into a longer slender posterior region; with 5 or 6 dorsal and 1 ventral giant nuclei (Figs. 1, 5, 10). Proboscis subglobular, wider than long, with prominent apical structure. Large hooks in anterior circle alternating at 2 levels; hooks in anterior level slightly shorter than hooks in posterior level; all with prominent spoon-like roots. Proboscis hooks in posterior 2 circles very small, not rooted, widely separated from anterior circle hooks, and placed nearly at level of distal tips of anterior hooks. Neck bordered posteriorly with prominent thick girdle (Figs. 1–3, 5). Proboscis receptacle about 3 times as long as proboscis and with 2 distinct ventral muscular expansions and cephalic ganglion (brain) near posterior end of receptacle (Figs. 1–3, 5). Lemnisci broad, subequal, considerably longer than proboscis receptacle, overlapping anterior testis in males (Fig. 5), with 2 large giant nuclei each (Figs. 1, 3, 5, 10). Gonopore terminal in male, subterminal in female.

MALES (based on 3 specimens): Trunk 2.03–2.22 (2.14) mm long by 0.42–0.60 (0.49) mm



Figures 1–5. *Neoechinorhynchus didelphis* **sp. n. 1. Allotype female; eggs not shown. 2. Proboscis, neck, and girdle of allotype female; note apical organ and insertion of receptacle. 3. Anterior end of a paratype female, showing size relationship between the proboscis, the receptacle, and the double nucleated subequal lemnisci; note the 2 muscular extensions of the proboscis receptacle. 4. A mature egg. 5. Holotype male.**

wide. Proboscis 92–100 (95) long by 107–130 (116) wide. Proboscis hooks in anterior circle 55–68 (60) long, in middle circle 16–25 (21) long, in posterior circle 14–22 (19) long. Neck 13–37 (25) long by 103–120 (110) wide. Girdle 20–35 (27) long by 105–180 (135) wide. Proboscis receptacle 175–280 (217) long by 75–135 (103) wide. Longer lemniscus 634–728 (666) long by 82–166 (110) wide, shorter lemniscus 520–562 (548) long by 70–114 (86) wide. Testes large, equatorial, slightly overlapping. Anterior testis 333–500 (409) long by 250–322 (277) wide; posterior testis 300–520 (409) long by 242–312 (275) wide. Cement gland 275–458 (362) long by 132–250 (204) wide. Cement reservoir 83–150 (126) long by 73–125 (102) wide. Saefftigen's pouch 212–322 (278) long by 62–104 (80) wide. Common sperm duct 212–270 (237) long by 73–83 (77) wide.

FEMALES (based on 10 gravid specimens): Trunk 2.91–7.13 (4.13) mm long by 0.42–0.98 (0.62) mm wide. Proboscis 90–112 (102) long by 112–142 (130) wide. Proboscis hooks in anterior circle 57–75 (66) long, in middle circle 17–27 (22) long, in posterior circle 14–25 (19) long. Neck 10–30 (16) long by 90–135 (114) wide. Girdle 28–55 long by 137–175 (151) wide. Proboscis receptacle 200–325 (279) long by 90–125 (102) wide. Longer lemniscus 572–1100 (716) long by 75–156 (97) wide; shorter lemniscus 425–1,020 (646) long by 75–135 (92) wide. Reproductive system 385–832 (559) long (Fig. 6), with 2 uterine bells (Figs. 6, 7, 9), vaginal retractor ligaments (Figs. 6, 8) near subterminal gonopore, and composite uterine complex between uterus and uterine bell (Figs. 6, 7). Uterine bells of same individual independently contractile (Fig. 7). Mature eggs fusiform, with polar prolongation of fertilization membrane, 52–68 (58) long and 10–17 (13) wide (Fig. 4); prolongation more pronounced in more mature eggs, showing some sculpturing at both ends.

Taxonomic summary

TYPE HOST: *Esox americanus* Gmelin, 1789 (redfin pickerel).

SITE OF INFECTION: Intestine.

TYPE LOCALITY: Little Ogeechee River, 11 km southwest of Savannah, Chatham County (32°00′00″N; 81°15′00″W), Georgia, U.S.A.

ETYMOLOGY: The new species is named for the 2 uterine bells of the female reproductive system.

SPECIMENS DEPOSITED: USNPC 89003 (holotype male and allotype female on 1 slide); USNPC 89004 (paratype females).

Remarks and Discussion

The new species is distinguished from all other species of the genus *Neoechinorhynchus* by having 2 functional uterine bells at the distal end of the uterus. Uterine bells of the same female were observed to be equally (Figs. 6, 9) or unequally (Fig. 7) extended. In the latter case, 1 uterine bell is usually fully extended and the other almost completely retracted, with ripe eggs observed in both. The female reproductive system is further distinguished by the highly complex selector apparatus between the uterus and uterine bells (Fig. 6), as well as dorsal and ventral vaginal ligament strands connected to the body wall anteriorly (Fig. 6). The ventral strand is much better developed than the dorsal strand and appears to accentuate the near subterminal position of the gonopore when retracted (Fig. 8). The anteriorly swollen trunk contains 5 or 6 dorsal and 1 ventral giant hypodermic nuclei that appear in different stages of development (Fig. 10). All stages, however, were similar to those described in other neoechinorhynchid worms undergoing reproductive activities (Amin and Vignieri, 1986a, b; Amin and Gunset, 1992). Unusual characteristic features of *N. didelphis* include the neck girdle and the 2 muscular extensions of the proboscis re-

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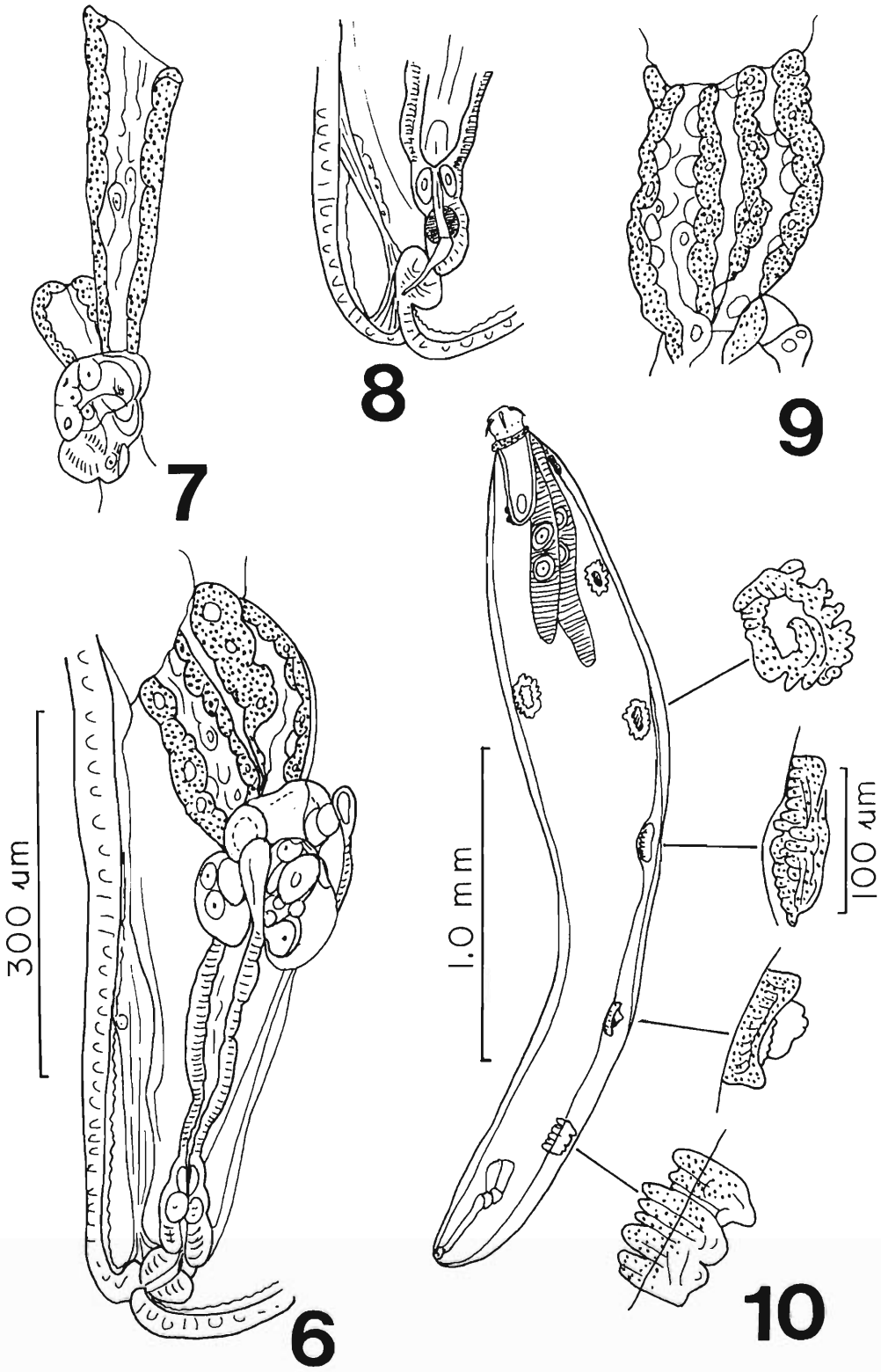
Figures 6–10. ***Neoechinorhynchus didelphis*** **sp. n. 6. The reproductive system of a paratype female; note the composite uterine complex, double uterine bells, and the strong ventral vaginal retractor ligament (left). (Measurement bar also applies to Figs. 7–9.) 7. Simultaneous extension and contraction of uterine bells in a paratype female. 8. Extreme contraction of the vaginal retractor ligament, affecting the position of the vagina of a paratype female. 9. A clear perspective of the double uterine bells of a paratype female. 10. A reproductively active paratype female, showing various developmental stages of giant hypodermic nuclei; the 3 posterior nuclei are in profile. Eggs not shown in all figures.**



ceptacle (Figs. 2, 3, 5). The latter are dissimilar to the pouches characteristic of the genus *Fessisentis* Van Cleave, 1931, and are considered to be of some taxonomic significance. The very large proboscis hooks in the anterior circle, distanced from the very small hooks in the posterior 2 circles, represent an additional characteristic feature of the new species.

In addition to the unique double uterine bells of *N. didelphis,* the combination of other unusual characters is not found in any other species of *Neoechinorhynchus.* These characters include the shape of the trunk, the proboscis armature, the neck girdle, the proboscis receptacle muscular extensions, the uterine complex, and the vaginal ligament retractors. For example, a few species of *Neoechinorhynchus* have somewhat similar proboscis armature to that of *N. didelphis* (but without extreme variation in hook size), but they have none of the other characters listed above. These species include *Neoechinorhynchus chrysemydis* Cable and Hopp, 1954; *Neoechinorhynchus oreini* Fotedar, 1968; *Neoechinorhynchus paraguayensis* Machado, 1959; *Neoechinorhynchus prolixoides* Bullock, 1963; and *Neoechinorhynchus pungitius* Dechtiar, 1971. Even this limited similarity is compromised by differences in the shape of the proboscis and hook roots.

Acknowledgment

I am grateful to Timothy Foard, Athens, Georgia, for providing the collection data and the specimens described herein.

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Amin, O. M., and M. Gunset. 1992. The pattern of giant nuclei in *Neoechinorhynchus rutili* (Acanthocephala: Neoechinorhynchidae). Transactions of the American Microscopical Society 111:65–69.

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New Book Available

Diagnosing Plant Diseases Caused by Nematodes. By Malcome C. Shurtleff and Charles W. Averre III. 2000. The American Phytopathological Society Press, St. Paul, Minnesota. 187 pp. ISBN 0-89054-254-6. 8¾ X 11¼ hard cover. Cost is US$79.00 per copy plus shipping and handling. Available from the APS Press, 3340 Pilot Knob Road, St. Paul, MN 55121-2097 or toll-free phone 1-800-328-7560 (U.S. only) or on-line at www.scisoc.org. **Abstract**: "This book focuses on the diagnosis of plant diseases caused by parasitic nematodes commonly encountered by specialists in agronomy, forestry, and horticulture. It is written for plant professionals, including farm advisors (county agents), plant scientists, diagnosticians, students of nematology and plant disease diagnosis, agribusiness personnel, agricultural inspectors, consultants, and others who diagnose diseases caused by plant-parasitic nematodes in the field, in clinics, and in laboratories. Readers should have considerable training in botanical and related sciences and experience in growing plants. This book should serve as a useful reference in diagnosing nematode-induced diseases and identifying these minute roundworms at least to the level of genus and, in two important genera (*Heterodera* and *Meloidogyne*), to the species and subspecies levels."

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68(1), 2001 pp. 108–111

Neoechinorhynchus iraqensis sp. n. (Acanthocephala: Neoechinorhynchidae) from the Freshwater Mullet, *Liza abu* (Heckel), in Iraq

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ABSTRACT: *Neoechinorhynchus iraqensis* sp. n. (Neoechinorhynchidae) is described from the freshwater mullet *Liza abu* (Heckel, 1843) in the Euphrates River, Iraq. The previous reports of *Neoechinorhynchus agilis* (Rudolphi, 1819) Van Cleave, 1916, from *L. abu* as well as from 4 other freshwater fishes in Iraq may refer to the new species. The new species is distinguished from all other species of the genus *Neoechinorhynchus* by a combination of characters including lemniscal size, inner lining of the body wall, shape of proboscis and neck, and size of proboscis hooks and testes. It is specifically separated from *N. agilis* by differences in size and shape of trunk, lemnisci, proboscis, proboscis hooks, and testes.

KEY WORDS: Acanthocephala, *Neoechinorhynchus iraqensis* sp. n., Neoechinorhynchidae, mullet, *Liza abu*, Mugilidae, Iraq.

The new species described herein probably was first reported in Iraq as *Neoechinorhynchus agilis* (Rudolphi, 1819) Van Cleave, 1916, from *Liza abu* (Heckel, 1843) in the Shatt al-Arab River at Basrah, southern Iraq, by Habash and Daoud (1979). The following year, Al-Hadithi et al. (1980) reported on the seasonality of the same species from mugilid fishes of the same waters. About 25 papers have been published since then, reporting the distribution of the same species as *N. agilis* from *L. abu* in many Iraqi waters associated with the Euphrates and Tigris rivers, as well as in fish farms throughout most Iraqi provinces (Ali et al., 1989; Mhaisen, 1993). The same acanthocephalan species has also been reported as *N. agilis* from 4 species of cyprinid fishes in Iraq as follows: *Alburnus caeruleus* Heckel, 1843, in Tharthar Lake, central Iraq, by Al-Saadi (1986); *Aspius vorax* Heckel, 1843, in Al-Qadissiya Dam Lake by Al-Alusi (1989); *Barbus luteus* (Heckel, 1843) in Mehaijeran River, south of Basrah, southern Iraq, by Khamees (1983); and *Barbus xanthopterus* in Bahr Al-Najaf Depression, mid-Euphrates region, by Al-Awadi (1997).

The new species of *Neoechinorhynchus* is probably a freshwater species that is morphologically distinct from the marine *N. agilis*. The description reported herein distinguishes between the 2 species and provides a basis for the revision of all ecological and host/geographical distributional records in Iraq published since 1979.

Materials and Methods

The primary host of the new species, *L. abu*, is a relatively small fish that may reach 26 cm in total length. It is well established in the Euphrates and Tigris river basins and is abundant in waters of northern central and southern Iraq. It mainly inhabits freshwaters but also enters estuaries at the southern reaches of its distribution in Iraq. It is well represented in fish markets despite its small size, which reduces its economic value. The mullet is also found in the Syrian Euphrates River basin (Beckman, 1962).

Fish were collected in the Euphrates River at the town of Al-Faluja (33°21′22″N; 43°46′58″E) in Al-Anbar Province, west of Baghdad. Weekly collections were made between October 1998 and September 1999. Fish were brought to the laboratory alive in plastic containers, measured, weighed, sexed, and examined for parasites. Acanthocephalans were collected in 0.9% saline solution or tap water and later fixed in 70% ethanol after eversion of the proboscis. Worms from a representative sample were stained in Mayer's acid carmine, dehydrated in ascending concentrations of ethanol, cleared in graduated concentrations of terpineol in 100% ethanol, and whole-mounted in Canada balsam. Measurements are in micrometers unless otherwise stated. The range is followed by mean values (in parentheses). Width measurements refer to maximum width. Body (=trunk) length does not include neck, proboscis, or male bursa. Eggs refer to fully developed ripe eggs measured in situ through the body wall of females. Specimens were deposited in the United States National Parasite Collection (USNPC), Beltsville, Maryland, U.S.A.

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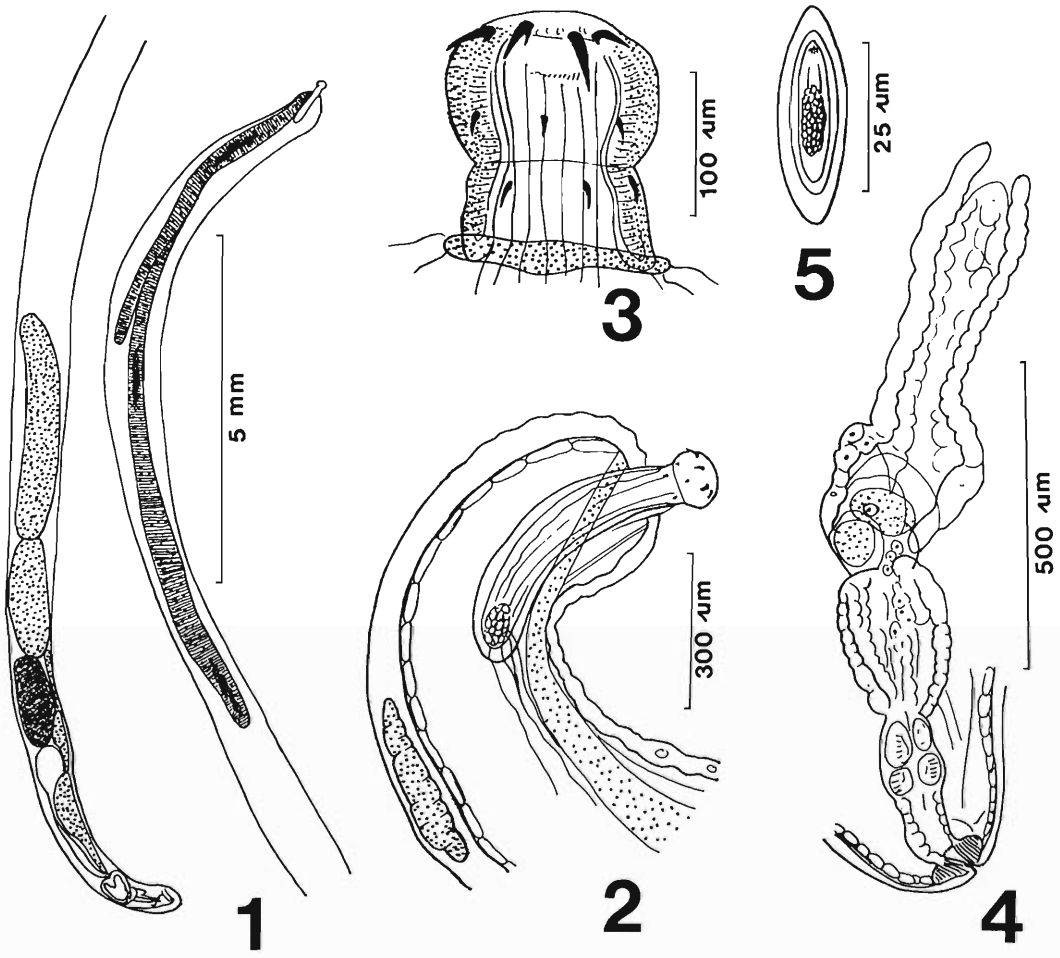

Figures 1–5. ***Neoechinorhynchus iraqensis*** **sp. n. from** ***Liza abu*****. 1. Holotype male, Saefftigen's pouch masked by common sperm duct. 2. Anterior end of allotype female, showing typical curvature of trunk, proboscis, proboscis receptacle, and anterior dorsal hypodermal nucleus. 3. Proboscis, neck, and girdle of allotype female. 4. Reproductive system of a paratype female. 5. Egg from the body cavity of a paratype female.**

Results

Neoechinorhynchus iraqensis sp. n. (Figs. 1–5)

Description

GENERAL: Neoechinorhynchidae, Neoechinorhynchinae with characters of the genus. Long slender worms (Fig. 1), with shared structures distinctly larger in females than in males. Trunk cylindrical, curved ventrad, particularly anteriorly, and normally with 4 dorsal and 1 ventral giant hypodermal nuclei. Innermost surface of body wall with prominent elongate beady lining (Figs. 2, 4). Proboscis bulbous anteriorly where first 2 circles of hooks are found. Posterior part of proboscis supporting third circle of hooks narrowest anteriorly but gradually and slightly expanding posteriorly into neck. Proboscis hooks in anterior circle alternating at 2 levels; hooks in anterior level smaller than hooks in posterior level (Fig. 3). Hooks in posterior circle slightly longer than hooks in middle circle. Cuticular thickening forming girdle at base of neck (Fig. 3). Proboscis receptacle single-walled, 4–5 times as long as proboscis, with cephalic ganglion (brain) at its base (Fig. 2). Lemnisci large, markedly unequal; larger lemniscus, with 3 giant nuclei (proximal, middle, and distal), more than twice size of smaller lemniscus, which has only

1 proximal giant nucleus. Hypodermal and lemniscal giant nuclei elongate, multilobulate (Figs. 1, 2).

MALES (based on 7 specimens with sperm): Trunk 15.1–27.0 (20.6) mm long by 0.57–0.80 (0.71) mm wide. Proboscis 100–130 (112) long by 88–120 (101) wide. Neck 30–67 (48) long by 80–125 (98) wide at base. Anterior bulbous part of proboscis 80–110 (90) long by 88–120 (101) wide. Posterior part of proboscis, following constriction, and neck 55–87 (70) long by 80–125 (98) wide. Larger proboscis hooks in anterior circle 30–37 (33) long; smaller hooks in same circle 22–30 (26) long. Hooks in middle and posterior circles 12–15 (14) and 15–18 (17) long, respectively. Proboscis receptacle 364–614 (475) long by 114–146 (128) wide. Smaller lemniscus 1.82–4.60 (2.95) mm long by 0.09–0.17 (0.13) mm wide. Larger lemniscus 4.26–8.42 (6.77) mm long by 0.15–0.31 (0.25) mm wide. Reproductive system in posterior third of trunk (Fig. 1). Testes oblong and contiguous; anterior testis 1.59–4.99 (3.03) mm long by 0.37–0.57 (0.47) mm wide, about twice as long as posterior testis 0.94–3.12 (1.74) mm long by 0.35–0.66 (0.52) mm wide. Syncytial cement gland 0.76–1.98 (1.28) mm long by 0.33–0.62 (0.47) mm wide. Cement reservoir 395–624 (531) long by 260–416 (341) wide. Common sperm duct 0.83–1.32 (1.06) mm long by 0.17–0.44 (0.32) mm wide. Saefftigen's pouch masked by common sperm duct. Bursa 624–998 (766) long by 364–915 (556) wide.

FEMALES (based on 11 gravid specimens): Trunk 27.0–73.8 (53.8) mm long by 0.54–1.27 (0.88) mm wide. Proboscis 100–132 (110) long by 107–137 (121) wide. Neck 30–55 (39) long by 102–135 (120) at base. Anterior bulbous part of proboscis 62–100 (79) long by 105–137 (117) wide. Posterior part of proboscis, following constriction, and neck 55–87 (68) long by 102–135 (122) wide. Larger proboscis hooks in anterior circle 27–42 (34) long; smaller hooks in same circle 22–32 (27). Hooks in middle and posterior circles 12–20 (16) and 15–22 (19) long, respectively. Proboscis receptacle 364–624 (511) long by 114–177 (148) wide. Smaller lemniscus 2.39–4.68 (3.25) mm long by 0.09–0.21 (0.13) mm wide. Larger lemniscus 5.41–10.4 (7.84) mm long by 0.19–0.36 (0.30) mm wide. Reproductive system 0.96–1.40 (1.22) mm long. Uterine bell about as long as vagina and uterus. Uterus with composite uterine complex between uterus and uterine bell (Fig. 4). Gonopore subterminal. Ripe eggs fusiform, with concentric membranes and no polar prolongation of fertilization membrane, 32–40 (36) long by 10–14 (12) wide (Fig. 5).

Taxonomic summary

TYPE HOST: Freshwater mullet (Arabic name: Khishni) *Liza abu* (Heckel, 1843) (=*Mugil abu* Heckel, 1843; *Mugil hishni* Hora and Misra, 1943) (Mugilidae).

SITE OF INFECTION: Intestine.

TYPE LOCALITY: Euphrates River at the town of Al-Faluja (33°21′22″N; 43°46′58″E) in Anbar Province, west of Baghdad, Iraq.

SPECIMENS DEPOSITED: USNPC 89469 (holotype male); 89470 (allotype female); 89471 (paratypes).

ETYMOLOGY: The new species is named for the country of Iraq where it is found.

Remarks and Discussion

Neoechinorhynchus iraqensis is distinguished from all other species of the genus *Neoechinorhynchus* by the sharp difference in the sizes of its lemnisci and the following combination of characters: long slender trunk with beady structure of inner body wall lining; proboscis bulbous anteriorly; posterior part of proboscis continuous with neck. The proboscis hooks in the first circle are in 2 levels, and the hooks in the anterior level are smaller than the hooks in the posterior level; the hooks in the third circle are larger than the hooks in the second circle; the anterior testis is much larger than the posterior testis. The lemniscal pattern of *N. iraqensis* is similar to that of *Neoechinorhynchus australis* Van Cleave, 1931. In the latter species, however, specimens are much smaller (males 3.4–7.3 mm long), the proboscis is rounded and considerably larger (146–230 × 117–170); the proboscis hooks in the anterior circle are of equal length and much larger (80–88 μm long); the longer lemniscus reaches the posterior testis; and the testes are equal in size. The lemniscal pattern of *N. iraqensis* is also similar to that of *Neoechinorhynchus proxilus* Van Cleave and Timmons, 1952. In the latter species, however, specimens are smaller (males 5–12 mm long, females 7–16 mm long); the proboscis is cylindrical; the hooks in the first circle are equal in size; the larger lemniscus is binucleate; the anterior testis is smaller than the posterior testis; and the latter is about

equal in size to the cement gland. Other species of the genus *Neoechinorhynchus* with unequal lemnisci similarly differ from *N. iraqensis* primarily by the sizes of their trunk, proboscis, proboscis hooks, and testes and by the shape of the proboscis; the lemnisci are usually more similar in size.

The brief initial report of *N. agilis* in Iraq by Habash and Daoud (1979), which set the precedent for all subsequent Iraqi literature on this acanthocephalan species, included an incomplete and barely informative text description of worms (sex?) that were 6.00–24.00 mm long, which was inconsistent with the authors' own illustration. For example, their text refers to 75–123-long anterior proboscis hooks, a size similar to anterior hooks of *N. agilis*. However, this cannot be true according to their figure 1. The anterior portion of their worm (their fig. 1) is identical to that of *N. iraqensis* and not *N. agilis* in size (calculated from the figure) and shape of the proboscis (bulbous anteriorly with constriction between the second and third circles of hooks), proboscis hooks, neck, and girdle, as well as the beady lining of the body wall. Hooks in the anterior circle appear to be in 2 levels as in *N. iraqensis*. The above comparisons as well as the similarities in host and geographical distribution of the *N. agilis* of Habash and Daoud (1979) and other Iraqi observers and our *N. iraqensis* further support their conspecificity.

Neoechinorhynchus agilis differs from our *N. iraqensis* specimens by having a smaller body (7.00 mm long) tapering toward both ends; lemnisci equal, reaching to the anterior testis; a cylindrical proboscis without anterior enlargement or constriction; proboscis hooks in the anterior circle equal in size and much larger (84–140 long); testes that are equal in size and in the middle of trunk; and the body wall with 6 dorsal and 2 ventral hypodermal giant nuclei. All Iraqi records and specimens of "*N. agilis*" from inland freshwater fishes must be re-examined in order to establish their true identities. Regrettably, the Arabic papers quoted herein made no reference to the deposit of type or voucher specimens, and none could be located for examination. In the absence of such voucher specimens, new parasite materials must be collected and examined from the same hosts and localities. The presence of the type and primary host species, *L. abu,* in the Syrian Euphrates basin suggests the possible presence of *N. iraqensis* there. Five other species of the genus *Neoechinorhynchus* have been reported to be present in freshwater fishes of Iraq, i.e., *N. australis* Van Cleave, 1931; *Neoechinorhynchus cristatus* Lynch, 1936; *Neoechinorhynchus dimorphospinus* Amin and Sey, 1996; *Neoechinorhynchus macronucleatus* Machado, 1954; and *Neoechinorhynchus rutili* (Müller, 1780) Stiles and Hassall, 1905 (Mhaisen, unpublished data).

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Transmission of *Diphyllobothrium dendriticum* (Nitzsch) from Calanoid Copepods to Arctic Charr, *Salvelinus alpinus* (Linnaeus)

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ABSTRACT: Copepod hosts for freshwater North American species of *Diphyllobothrium* are presently unknown. First intermediate hosts previously reported were based on the assumption that European host species are also hosts in North America. Our primary objective was to identify North American calanoids that could be used in the laboratory to transmit *Diphyllobothrium dendriticum* to fish and could also act as hosts for the parasite in natural lakes. A second objective was to establish an infection protocol that allowed high rates of prevalence and mean intensity of infection to be obtained with the use of these copepods and Arctic charr *Salvelinus alpinus*. Our experiments indicated that *Diaptomus* (*Aglaodiaptomus*) *leptopus* and *Diaptomus* (*Leptodiaptomus*) *minutus* readily became infected by coracidia of *D. dendriticum* (prevalence 14.9–60.8%). It is likely that *D.* (*L.*) *minutus* is a natural host for *D. dendriticum* because it co-occurs in lakes with infected Arctic charr. Both copepods successfully transmitted *D. dendriticum* to Arctic charr (prevalences were 72.3% and 52.6%). The rate of parasite establishment was lower (7.7%) in fish given 10–20 procercoids than it was for a dose range of 6–12 procercoids (29.3%). These data suggest that if infection intensity greater than 10 plerocercoids is desired, it may be more effective to repeatedly expose fish to fewer parasites rather than use a single higher dose.

KEY WORDS: cestode, *Diphyllobothrium dendriticum, Diaptomus,* life cycle, experimental infection, salmonid, Arctic lakes, North America, Arctic charr, *Salvelinus alpinus.*

The North American freshwater copepod hosts of species of *Diphyllobothrium* (*Diphyllobothrium dendriticum* (Nitzsch, 1824), *Diphyllobothrium ditremum* (Creplin, 1825), and *Diphyllobothrium latum* (Linnaeus, 1758)) are presently unknown. First intermediate hosts previously reported were based on the assumption that copepod hosts in Europe were also hosts in North America. Accordingly, North American hosts for *D. latum* were considered to be *Diaptomus* (*Skistodiaptomus*) *oregonensis* Lilljeborg, 1889, *Diaptomus* (*Leptodiaptomus*) *sicilis* S. A. Forbes, 1882, and *Diaptomus* (*Leptodiaptomus*) *siciloides* Lilljeborg, 1889, by Vergeer (1936) and *Diaptomus* (*Eudiaptomus*) *gracilis* Sars, 1862, and *Cyclops scutifer* Sars, 1863, by Rausch and Hilliard (1970). Hosts for *D. dendriticum* were believed to be *D.* (*S.*) *oregonensis* by Thomas (1946) and *C. scutifer* by Bérubé and Curtis (1986). Although more than 1 copepod species can probably successfully host *D. dendriticum* in a given lake, if a lake with *Diphyllobothrium* contains only a single copepod species, that species can be regarded as a host. One clear example of this is found in Char Lake, in Arctic Canada, where *Limnocalanus macrurus* Sars, 1863, is the only copepod species known to be present (Rigler et al., 1974; Curtis, 1982).

Laboratory experiments on the life cycle of *Diphyllobothrium* generally use copepods that are easily maintained and readily infected with the parasite (Sharp et al., 1990; Rahkonen and Valtonen, 1997). In North America, the culture of most species mentioned above is problematic because the species are often difficult to collect in remote field locations and then to maintain under laboratory conditions. It is therefore expedient to use copepods that are readily available from the field and are easily cultured in the laboratory.

Consequently, this study had 2 goals, the first being to identify calanoid copepods that could be used in the laboratory to transmit *D. dendriticum* to fish and that may also act as natural hosts for the parasite. Second, we attempted to establish a protocol for obtaining high rates of prevalence and mean intensity of infection for copepods and fish.

Materials and Methods

Plerocercoids of *D. dendriticum* used for these experiments originated from Arctic charr *Salvelinus alpinus* (Linnaeus, 1758) collected in Lake Lille Rosta (69°00′N; 19°37′E), Norway. The plerocercoids were dissected from wild Arctic charr and administered by gavage to Fraser River strain Arctic charr maintained

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in our fish culture facility. Re-established plerocercoids 110 days postinfection (PI) were removed from infected fish and were fed by gavage to a 22-day-old female golden hamster *Mesocricetus auratus* (Waterhouse, 1839). The hamster was provided with a commercial diet and water *ad lib.* Feces were collected by placing the hamster in a wire-bottomed cage during the normal diurnal dark cycle. Cestode eggs were separated from fecal debris with 6 brass screens (consecutive mesh sizes 425, 150, 83, 75, 53, 38 μm). Egg incubation took place under 24-hr standard laboratory fluorescent light at 20 ± 1°C in 1-liter glass jars filled with aerated dechlorinated water. After 7 d, the jars were covered with aluminum foil and incubation continued for another 13–19 d.

Cestode eggs were placed in 1.5-liter glass jars with copepods under standard laboratory fluorescent light. The light stimulated the embryos to hatch, and because emerging coracidia are negatively geotactic, they rose through the water, where they were consumed by the copepods. The remaining eggs and coracidia were removed after approximately 48 hr to prevent further infections. Thus, procercoids were all approximately the same age and developmental stage. Throughout the experiment, copepods were kept in a 10:14 hr light: dark cycle at 20 ± 1°C and fed biweekly rations of brine shrimp flakes crushed through a 53-μm mesh and laboratory cultured *Chlorella* sp. and *Scenedesmus acutus* Meyen, 1828.

For the first experiment, *Diaptomus* (*Aglaodiaptomus*) *leptopus* S. A. Forbes, 1882, were collected from a temporary pond in the McGill University Morgan Arboretum, and a subsample was screened for natural infections prior to exposure. Live copepods infected with 13–17-d PI procercoids were placed in a drop of dechlorinated water inside a Torpac® gelatin capsule (size 5, capacity 0.13 ml; Fairfield, New Jersey, U.S.A.). The gelatin capsule was pushed into the stomach of Arctic charr that had been lightly anesthetized with Benzocaine. Each of 48 fish was given a single capsule containing 6 to 12 procercoids. Gelatin capsules containing only water were given to 64 control fish. After administration of gelatin capsules, individual fish were monitored to ensure that there was no regurgitation. Arctic charr ranged in size and weight from 108 to 191 mm and 15.7 to 71.2 g, respectively, at the beginning of the experiment. After approximately 12 wk, fish were killed and examined for plerocercoids. Plerocercoids were removed, and the site where they were found was recorded.

In a second experiment, *Diaptomus* (*Leptodiaptomus*) *minutus* Lilljeborg, 1889, were collected in Lac St. Louis, Ste. Anne-de-Bellevue, Québec, and a subsample was screened for infections prior to use. Copepods harboring procercoids 14–17 d PI were killed in carbonated water and placed with a drop of dechlorinated water in a gelatin capsule. We had earlier verified that procercoids from dead copepods would successfully infect fish. Each of 40 Arctic charr was given a single capsule containing 10 to 20 procercoids. Monitoring of individual fish indicated that there was no regurgitation of capsules. Gelatin capsules containing only water were given to 42 control fish. Arctic charr ranged in size and weight from 115 to 186 mm and 15.5 to 57.8 g, respectively, at the beginning of the experiment. After approximately 12 wk, the fish were killed, and the parasites were removed as in the first experiment.

Table 1. Infection status for 5 samples of *Diaptomus* (*Aglaodiaptomus*) *leptopus* exposed to coracidia of *Diphyllobothrium dendriticum*.

Sample no.	No. counted	No. infected	% Infection
1	195	29	14.9
2	234	69	29.5
3	146	31	21.2
4	237	64	27.0
5	360	132	36.7
Total	1,172	325	27.7

Prevalences and mean intensities of *D. dendriticum* infections were calculated for Arctic charr and for *D.* (*L.*) *minutus*. Prevalence was calculated for *D.* (*A.*) *leptopus*. One-way analysis of variance (ANOVA) was used to test for differences by the GLM procedure of the SAS package (SAS Institute, Inc., 1999). The level of statistical significance was set at $P < 0.05$.

Specimens have been deposited in the collection of the Canadian Museum of Nature (CMN) with the catalog numbers CMNPA 2000-0029 to CMNPA 2000-0030 (*D. dendriticum*) and CMNC 2000-0051 to CMNC 2000-0052 (*D.* (*A.*) *leptopus* and *D.* (*L.*) *minutus*).

Results

Diaptomus (*A.*) *leptopus* became readily infected with *D. dendriticum* in the first experiment, and prevalence ranged from 14.9 to 36.7% (Table 1). Three fish died before the end of the experiment, and all were eliminated from further analysis. Of the 47 Arctic charr that were exposed to procercoids of *D. dendriticum* in this experiment, 34 became infected (72.3%). Infected fish harbored 1 to 10 plerocercoids with a mean intensity of 4.0.

In total, 468 procercoids in *D.* (*A.*) *leptopus* were administered to fish, and 137 (29.3%) plerocercoids established and were recovered. Most plerocercoids (79.6%) were encysted. Cysts were recovered primarily from the pyloric ceca, esophagus, and stomach but were also found in the liver, intestine, and visceral fat. Plerocercoids found free (20.4%) were mainly located on the pyloric ceca but were also found on the surface of the viscera, in the visceral fat, and on the liver.

Results from the second experiment indicated that *D.* (*L.*) *minutus* was also readily infected by *D. dendriticum,* with prevalence ranging from

Table 2. Infection status for 9 samples of *Diaptomus* (*Leptodiaptomus*) *minutus* exposed to coracidia of *Diphyllobothrium dendriticum*. Developed parasites were distinguished by the presence of a cercomer and/or an invagination.

Sample no.	No. examined	No. infected	No. with undeveloped procercoids	No. with 1 developed procercoid	No. with 2 developed procercoids	% Infected
1	56	29	1	25	3	51.8
2	149	76	5	58	13	51.0
3	158	90	1	63	25	57.0
4	171	81	1	71	9	47.4
5	130	61	0	57	4	46.9
6	82	36	0	33	3	43.9
7	180	49	0	49	0	27.2
8	199	105	0	90	14	52.8
9	214	130	0	102	26	60.8
Total	1,339	657	8	548	97	49.0

27.2 to 60.8% (Table 2). Individual *D.* (*L.*) *minutus* harbored 1 to 4 developed procercoids, with a mean intensity of 1.2 procercoids. After 20–25 d PI, only 8 copepods harbored procercoids that were undeveloped (lacking a cercomer and/or an invagination, indicative that the parasite was not infective [Kuperman, 1973]). Four fish died before the end of the experiment, and these were eliminated from further analysis. Of the 38 Arctic charr exposed to *D. dendriticum,* 20 became infected (52.6% prevalence). Infected fish harbored 1 to 5 plerocercoids, and the mean intensity was 2.8.

In this second experiment, 717 procercoids in *D.* (*L.*) *minutus* were administered to fish, and 55 (7.7%) became established as plerocercoids. Most (81.8%) plerocercoids were encysted. Cysts were recovered primarily from the pyloric ceca but were also found on the stomach, liver, and viscera. Plerocercoids that were free (18.2%) were mainly found on the pyloric ceca, but they were also found in the visceral fat and on the surfaces of the stomach and viscera.

Discussion

This study has shown for the first time that *D.* (*A.*) *leptopus* and *D.* (*L.*) *minutus* are suitable hosts for *D. dendriticum.* The use of *D.* (*A.*) *leptopus* is notable because it is a species inhabiting temporary ponds that are unlikely to have *Diphyllobothrium* populations and where copepods may be easily sampled for laboratory work. This species has no previous record of presence in lakes with *Diphyllobothrium.* Although diaptomid copepods are reportedly difficult to rear in the laboratory (Guttowa, 1961; Sharp, 1990), *D.* (*A.*) *leptopus* was maintained under controlled conditions for several months and readily reproduced.

Diaptomus (*L.*) *minutus* also became infected with *D. dendriticum.* It is almost certainly a natural host because it has been reported in North American lakes containing the parasite (Curtis, 1982; Bérubé and Curtis, 1986; Due and Curtis, 1995). The cultures of *D.* (*L.*) *minutus* were relatively easy to maintain, although reproduction was limited. Developed procercoids of *D. dendriticum* were maintained in *D.* (*L.*) *minutus* for 43 d PI, but the majority of infected copepods suffered mortality between 35 and 43 d PI. This demonstrates that *D.* (*L.*) *minutus* is a host that can remain alive and harbor infections throughout the time periods necessary for experimental research.

Prevalence in Arctic charr was 72.3% with *D.* (*A.*) *leptopus* and 52.6% with *D.* (*L.*) *minutus.* When 10 to 20 procercoids in *D.* (*L.*) *minutus* were administered to fish, only 7.7% of parasites became established, and there was no case in which all parasites successfully established infections in individual fish. In contrast, the parasite establishment rate was 29.3% for doses of 6 to 12 procercoids in *D.* (*A.*) *leptopus.* In 4 cases, individual Arctic charr were given 10 procercoids, and all parasites established and were recovered at the end of the experiment. This is the first documentation of complete *D. dendriticum* establishment under experimental conditions and provides further support for the suitability of the transmission method. Kuhlow (1953) transmitted *D. dendriticum* to fish using copepods, but he did not use calanoid copepods

in the experiments, nor was he able to achieve 100% establishment of parasites in the individual fish (although he was able to infect 100% of the exposed fish). Unless there is a difference in procercoid infectivity between copepod species, our data suggest that if levels of infection intensity greater than 10 plerocercoids are desired, it may be more effective to repeatedly expose fish to fewer parasites rather than use a single higher dose.

In our study, most of the parasites were encysted and were located among the pyloric ceca. Additional sites included other visceral organs and the visceral fat. These sites are consistent with reports from field studies, which indicate that plerocercoids of *D. dendriticum* are often encysted and are recovered from the visceral organs, particularly the liver, stomach, and pyloric ceca, of Arctic charr (Henricson, 1977; Curtis, 1984).

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Helminth Community Structure and Pattern in Merriam's Kangaroo Rats, *Dipodomys merriami* Mearns, from the Chihuahuan Desert of New Mexico, U.S.A.

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ABSTRACT: Helminth community structure and pattern were examined in the Merriam's kangaroo rat *Dipodomys merriami* from burned and unburned plots in the northern Chihuahuan Desert of New Mexico. From 53 adult kangaroo rats, 7 helminth species were found, of which 2 species commonly occurred (*Mastophorus dipodomis*, 72%; *Pterygodermatites dipodomis*, 68%). The remaining species occurred infrequently (≤13% prevalence). Prevalence and rank abundance values of *M. dipodomis* and *P. dipodomis* were similar between burned and unburned plots and host sex, respectively. Kangaroo rats averaged 1.8 ± 0.1 species and 10.5 ± 3.9 individuals. Both Jaccard's index and the percentage similarity index indicated that component communities were dissimilar between burned and unburned plots. However, these differences resulted from the occurrence of rare species. Our results suggest that the helminth component community is depauperate and is dominated by 2 heteroxenic species that occupy different microhabitats within the host.

KEY WORDS: Chihuahuan Desert, community ecology, component communities, *Dipodomys merriami*, helminths, Merriam's kangaroo rat, New Mexico, prescribed fire, U.S.A.

Rainfall and fire are 2 environmental factors that can play an important role in shaping parasite communities. Helminth communities in hosts inhabiting xeric environments often differ in species richness and diversity from those found in mesic habitats (Mollhagan, 1978; Waid et al., 1985; Stubblefield et al., 1987), suggesting that arid environments decrease the transmission potential of certain helminths. Those helminth species that have complex life cycles, requiring threshold densities of both intermediate and definitive hosts for completing their life cycles, may be at a disadvantage in regions where environmental conditions limit host densities. Dobson (1989) hypothesized that extreme environmental conditions may favor monoxenic species, which are not dependent upon intermediate hosts. If true, helminth communities in desert environments should be dominated by direct life cycle species. Prescribed fire has been shown to alter densities of ectoparasites (Jacobson and Hurst, 1979; Scifres et al., 1988; Cully, 1999) and protostrongylids (Seip and Bunnell, 1985), presumably by killing infective stages of these parasites. There is some evidence that helminth communities in the white-footed mouse *Peromyscus leucopus* (Rafinesque, 1818) Osgood, 1909, were altered by combinations of herbicide and prescribed burn treatments (Boren et al., 1993). However, the effect of prescribed fire on helminth community structure and pattern in many rodent species remains unknown.

To examine further the impact of extreme environmental conditions on parasite communities, we evaluated the helminth community in Merriam's kangaroo rats *Dipodomys merriami* Mearns, 1890, from an arid region of the U.S.A. Our specific objectives were to (1) determine the helminth fauna of Merriam's kangaroo rats from the Chihuahuan Desert of southern New Mexico, (2) examine the structure and pattern of helminth communities in kangaroo rats from burned and unburned plots, and (3) relate these findings to host–parasite–habitat interactions.

Materials and Methods

The study was conducted in the northern Chihuahuan Desert on the McGregor Missile Range of Fort Bliss Military Reservation in Otero County, New Mexico, U.S.A. (32°27′N; 105°50′W; Fig. 1). The region is arid to semiarid (8–25 cm annual rainfall) and is dominated by the creosote bush *Larrea tridentata* (De

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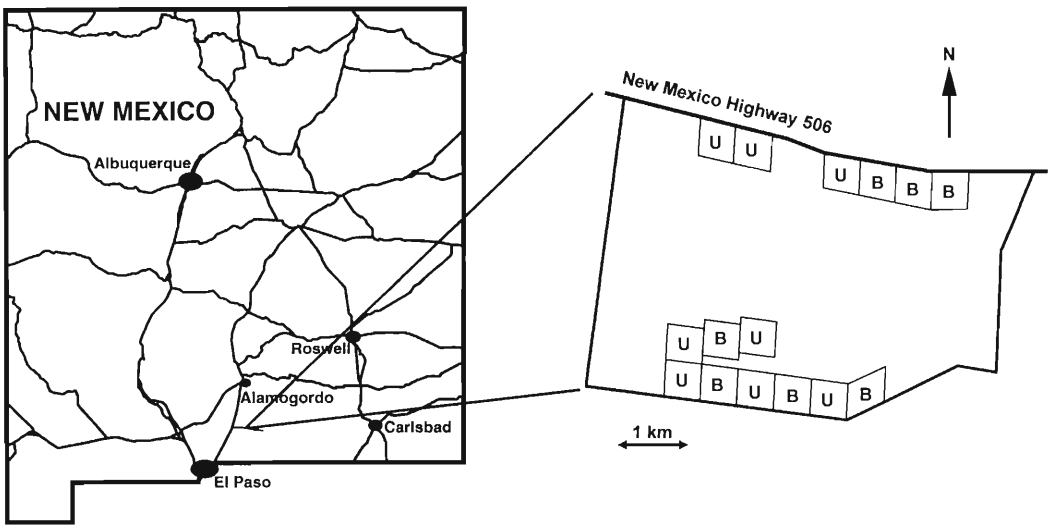

Figure 1. Location of the study area and arrangement of burned (B) and unburned (U) study plots on Fort Bliss Military Reservation, Otero County, New Mexico.

Candolle) Coville and tarbush *Flourensia cernua* De Candolle plant association.

Twenty 25-ha plots (500 × 500 m) were selected during January 1995 for a study examining the effects of fire on small mammal and vegetation communities (Monasmith, 1997). Plots were paired and randomly assigned a treatment (treatment = burned, control = unburned). Treatment plots were burned during 13–15 June 1995 with strip headfires. Permanent 100 × 100-m trapping grids (90 × 90 m actual, plus 5 m boundary strip; 100 traps per grid; 1 trap every 10 × 10 m) were constructed at the center of each plot with Sherman live-traps. Kangaroo rats were captured from 7 burned and 8 unburned plots (Fig. 1) during 10–21 August 1996, weighed to the nearest 1.0 g with a Pesola spring balance, and sexed. Adult kangaroo rats were those individuals >30 g (Reynolds, 1960; Zeng and Brown, 1987). Kangaroo rats were killed by thoracic compression. Viscera from each kangaroo rat was placed in an individually labeled plastic bag and quick-frozen within 5 min of host death with a mixture of ethyl alcohol and dry ice (approximately −70°C), which preserved helminths within their microhabitats (Bush and Holmes, 1986). Frozen viscera were stored in freezers at −10°C until necropsy. Kangaroo rats were collected in accordance with established guidelines and protocols of New Mexico Department of Game and Fish Scientific Permit 2870.

Helminths were collected, preserved, and counted according to methods described in Fedynich (1993). Helminths were identified following the taxonomic keys of Tiner (1948), Read and Millemann (1953), Lichtenfels (1970), and Kruidenier and Peebles (1958). Representative specimens of helminth species were deposited in the U.S. National Parasite Collection, Beltsville, Maryland 20705, U.S.A. (USNPC accession numbers 088939–088941).

The terms prevalence, mean intensity, abundance, and mean abundance follow the definitions of Bush et al. (1997). Common helminth species were arbitrarily defined as those with ≥50% prevalence; intermediate species were those with ≥10<50% prevalence; all other species were considered rare. Infracommunity refers to all infrapopulations of parasite species that occur within a single host; component community refers to all infrapopulations of parasites occurring within a particular subset of a host species (Bush et al., 1997). The term microhabitat, in relation to helminths, refers to anatomical localities within the host.

Frequency data were analyzed with log-linear models (CATMOD®; SAS Institute, Inc., 1990) to determine if the prevalence of the common helminth species varied by the main effects of habitat treatment (burn, control) and host sex (male, female). Jaccard's coefficient of similarity index (J_i) (Krebs, 1989) was used to measure the similarity of shared species between host populations by treatments. The percentage similarity index (PS_i) (Pielou, 1975) was used to measure similarity of helminth communities between treatments on the basis of the relative proportion of helminth individuals contributed by each helminth species. The numerical dominance index (DI) of Leong and Holmes (1981) was used to rank helminth species by the number of individuals that each species contributed to the total number of helminth individuals by treatment.

The frequency distribution pattern of abundance for the common species was tested for normality (PROC UNIVARIATE NORMAL®; SAS Institute, Inc., 1990). Because overdispersion occurred, abundance values were rank transformed (PROC RANK®; SAS Institute, Inc., 1990) prior to further statistical analyses. Rank-transformed abundance values were examined for the main effects of treatment and sex with analysis of variance (ANOVA; SAS Institute, Inc., 1990) for each common helminth species and with multivariate analysis of variance (MANOVA; SAS Institute, Inc., 1990)

Table 1. Descriptive statistics for helminths collected from 53 adult Merriam's kangaroo rats in Otero County, New Mexico.

Helminth species	Prevalence No. infected (%)	Intensity $\bar{x} \pm SE$	Intensity Range	Abundance $\bar{x} \pm SE$	Abundance Total
Cestoda					
Catenotaenia sp. (SI)*	4 (8)	1.3 ± 0.3	1–2	0.1 ± <0.1	5
Cysticerci (L, SI)	1 (2)	184.0	184	3.5 ± 3.5	184
Nematoda					
Filaria sp. (H-LU)	1 (2)	1.0	1	<0.1 ± <0.1	1
Gongylonema dipodomysis Kruidenier and Peebles, 1958 (USNPC 088941)† (S)	1 (2)	1.0	1	<0.1 ± <0.1	1
Mastophorus dipodomis Read and Millemann, 1953 (USNPC 088939) (S)	38 (72)	2.7 ± 0.4	1–14	1.9 ± 0.3	101
Pterygodermatites dipodomis (Tiner, 1948) Quentin, 1973 (USNPC 088942) (SI)	36 (68)	3.7 ± 0.5	1–11	2.5 ± 0.4	134
Heteromoxyuris deserti (Read and Millemann, 1953) Quentin, 1973 (USNPC 088940) (C)	7 (13)	12.9 ± 7.0	1–51	1.7 ± 1.1	90

* C = cecum; H-LU = heart-lung; L = liver; S = stomach; SI = small intestine.
† Tentative identification based on a single female specimen.

for the collective common species. Descriptive statistics are presented as a mean ± 1 SE.

Results

We collected 60 kangaroo rats, of which 53 were adults. The low juvenile sample precluded any meaningful comparisons to assess host age effects; consequently, juveniles were excluded. Twenty-seven (14 males and 13 females) kangaroo rats were trapped on burned plots and 26 (14 males and 12 females) on unburned plots. Nine were recaptured from Monasmith's (1997) study; all were retrapped on the same plots where they were originally captured.

Seven helminth species (2 cestodes and 5 nematodes) were found in 49 (92%) kangaroo rats (Table 1). Five species were found in kangaroo rats from burned plots and 6 species were recovered on the unburned plots (Table 2). Of the 53 kangaroo rats examined, 4, 18, 23, and 8 were infected with 0, 1, 2, and 3 helminth species (Fig. 2). Number of helminth species averaged 1.8 ± 0.1 (range: 1–3), and number of helminth individuals averaged 10.5 ± 3.9 (range: 1–189); neither varied between burned and unburned plots ($P > 0.48$ and $P > 0.36$, respectively) or between males and females ($P > 0.91$ and $P > 0.68$, respectively).

No differences in prevalence were found between burned and unburned plots for each of the 2 common nematodes, *Mastophorus dipodomis* ($P = 0.11$) and *Pterygodermatities dipodomis* ($P = 0.43$). Additionally, no difference in rank abundance was found between burned and unburned plots of these species individually ($P > 0.19$ and $P > 0.68$, respectively) or collectively (MANOVA: $P > 0.43$). There were no differ-

Table 2. Dominance index (DI) values for helminths collected from 53 adult Merriam's kangaroo rats on burned and unburned plots in Otero County, New Mexico.

Burned (n = 27)		Unburned (n = 26)	
Helminth species	DI	Helminth species	DI
Pterygodermatites dipodomis	39.3	Cysticerci	54.4
Heteromoxyuris deserti	30.3	*Pterygodermatites dipodomis*	18.9
Mastophorus dipodomis	28.1	*Mastophorus dipodomis*	15.1
Catenotaenia sp.	1.7	*Heteromoxyuris deserti*	10.7
Gongylonema dipodomysis	0.6	*Catenotaenia* sp.	0.6
		Filaria sp.	0.3

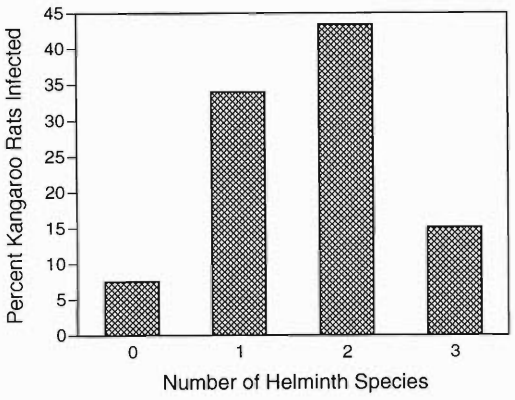

Figure 2. Distribution of helminth species found in 53 adult Merriam's kangaroo rats collected on Fort Bliss Military Reservation, Otero County, New Mexico, during 10–21 August 1996.

ences in prevalence by host sex for *M. dipodomis* ($P = 0.24$) or *P. dipodomis* ($P = 0.56$) between burned and unburned plots. Host sex did not influence rank abundance for these species individually ($P > 0.58$ and $P > 0.35$, respectively) or collectively (MANOVA: $P > 0.45$).

Both J_i (0.57) and PS_i (45%) indicated that communities were dissimilar between burned and unburned plots. The low commonality of species (as suggested in the J_i value) resulted from 3 rare species, 2 of which were found as single infections on the unburned plots, and 1 of which was found in a single kangaroo rat on a burned plot. Additionally, inclusion of cysticerci substantially influenced PS_i. With these metacestodes removed, PS_i was 92%, indicating minor differences in overall community composition between burned and unburned plots.

Three species, *P. dipodomis, Heteromoxyuris deserti,* and *M. dipodomis,* dominated on the burned plots, accounting for 98% of the helminth individuals (Table 2). Only cysticerci dominated numerically on the unburned plots, accounting for 54% of all helminth individuals (Table 2). This was the result of 1 cysticerci-infected host. With this host individual removed, *P. dipodomis, M. dipodomis,* and *H. deserti* dominated.

Discussion

Helminth communities in arid regions are thought to be species poor and lack diversity, reflecting the decreased transmission potential of parasites within these environments (Dobson, 1989). In our study, 34% of the kangaroo rats contained only 1 helminth species (i.e., no helminth infracommunity), infracommunities were small (2–3 species, 2–55 worms, excluding cysticerci), and the component community consisted of 7 species, in which 2 species dominated (*P. dipodomis* and *M. dipodomis*). Patrick (1994) found a similar pattern in a study that spanned 5 summers in central New Mexico. Many of these characteristics are found in isolationist communities, in which few species regularly co-occur and a larger group rarely occurs (i.e., core and satellite species, respectively, of Bush and Holmes [1986]). These infrequently occurring species tend to represent the more random elements of the helminth community, contribute relatively little, and tend to obscure overall community patterns (Stock and Holmes, 1987).

Whether monoxenic or heteroxenic species are favored under arid conditions is less certain. Gray et al. (1978) suggested that evapotranspiration rates in semiarid environments may result in very low transmission potentials for direct life cycle species because infective stages are directly exposed to adverse environmental conditions. Alternatively, Dobson (1989) believed that in desert environments where host populations are typically low, monoxenic parasite species would dominate. We found that heteroxenic species dominated at the component community level, in both number of species and number of individuals. Patrick (1994) also found heteroxenic species dominated in desert habitats and believed that this was likely the result of relatively high intermediate and definitive host populations within his study area.

Rodenberg and Pence (1978) suggested that community composition within a host species may be influenced by other closely related sympatric host species. During 1995 and 1996, Monasmith (1997) captured 15 rodent species on the study area, representing 766 individuals; the 4 most common species were the Merriam's kangaroo rat (57%), silky pocket mouse *Perognathus flavus* Baird, 1855 (21%), desert pocket mouse *Chaetodipus pencillatus* (Woodhouse, 1852) Hoffmeister and Lee, 1967 (13%), and plains pocket mouse *Perognathus flavescens* Merriam, 1889 (5%). We could not find any published account of the helminth species that were found in our study occurring in these species of pocket mice. However, ongoing research

conducted at the Sevilleta National Wildlife Refuge in central New Mexico by Duszynski et al. (personal communication; Long Term Ecological Research data) indicates that *P. dipodomis* and *H. deserti* occur infrequently in silky and plains pocket mice. This suggests the possibility of some overlap in helminth species within the host community that may aid in the persistence of at least these 2 helminth species.

Prescription burns appeared to influence community patterns. However, after the rare species were accounted for, communities were similar between burned and unburned plots. Also, prevalence and abundance of the 2 common helminth species were not influenced by prescribed burns. Movements by kangaroo rats between burned and unburned plots could mask the effects of burning. However, all recaptured kangaroo rats during Monasmith's (1997) 2-yr study and the 9 we recaptured from his study were trapped on the same plots where they were originally captured and tagged. Rather, foraging behavior may have played an important role. Kangaroo rats typically forage in open areas where low or nonexistent fuel loads exclude fire needed to kill infective stages of helminths. Constraints of this study prevented an assessment of the role of fire over extended time intervals and the impact of repetitive burning. Consequently, firm conclusions can not be made about the role of fire on this helminth community until long-term assessments are conducted.

Acknowledgments

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2001 MEETING SCHEDULE OF THE HELMINTHOLOGICAL SOCIETY OF WASHINGTON

10 January 2001	Nematology Laboratory, Beltsville Agricultural Research Service, USDA, Beltsville, Maryland (Contact Person: Lynn Carta, 301-504-8787).
14 March 2001	Naval Medical Research Center, 503 Robert Grant Avenue, Silver Spring, Maryland (Walter Reed Forest Glen Annex Bldg. 503) (Contact Person: Eileen Franke-Villasante, 301-319-7667).
5 May 2001	Joint Meeting with the New Jersey Society for Parasitology at the New Bolton Center, University of Pennsylvania, Kennett Square, Pennsylvania (Contact Person: Jay Ferrell, 215-898-8561).
October 2001	Date and location to be announced
November 2001	Date and location to be announced

Comp. Parasitol.
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Species of *Eimeria* (Apicomplexa: Eimeriidae) from the Southern Red-Backed Vole, *Clethrionomys gapperi*, in Northwestern Wyoming, U.S.A.

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ABSTRACT: During the summers of 1997 and 1998, 95 southern red-backed voles (*Clethrionomys gapperi*) from northwestern Wyoming were examined for coccidia by necropsy or collection of feces from live-caught individuals. Because vole specimens caught in 1997 were frozen, eimerian oocysts did not sporulate, but morphology of unsporulated oocysts suggests that 3 species, *Eimeria clethrionomyis, Eimeria marconii,* and *Eimeria pileata* might be present. In 1998, sporulated oocysts of *E. clethrionomyis* (prevalence = 11%) were observed. Oocysts of *E. clethrionomyis* were similar to the original description of this species from southern red-backed voles in Pennsylvania, U.S.A. This is only the second report identifying eimerians from this host species in North America and is the first from the western U.S.A.

KEY WORDS: Apicomplexa, *Eimeria,* southern red-backed vole, *Clethrionomys gapperi,* Wyoming, U.S.A.

Few studies have been conducted on the occurrence of species of *Eimeria* (Schneider, 1875) (Apicomplexa: Eimeriidae) in wild rodents in the genus *Clethrionomys* (Tilesius, 1850). In the only North American report, Straneva and Kelley (1979) named and described 4 species from southern red-backed voles *Clethrionomys gapperi* Vigors, 1830, in Pennsylvania: *Eimeria clethrionomyis, Eimeria gallatii, Eimeria marconii,* and *Eimeria pileata.* In Europe, Levine and Ivens (1990) recognized *Eimeria cernae* Levine and Ivens, 1965, and *Eimeria rysavyi* Levine and Ivens, 1965, from bank voles *Clethrionomys glareolus* Schreber, 1780, in Czechoslovakia, and Arnastauskiene (1977) described *Eimeria schiwicki* from northern red-backed voles *Clethrionomys rutilus* Pallas, 1779, in Russia.

In 1990 and 1991 after the 1988 fires in northwestern Wyoming, U.S.A., Stanton et al. (1991) and Spildie (1994) surveyed a variety of habitats to determine small mammal distributions in Grand Teton National Park (GTNP) and the Rockefeller Parkway between GTNP and Yellowstone National Park, and they began investigating the responses of small mammals to fire by monitoring rodent community dynamics in areas burned in 1988 and in unburned areas. In 1997 and 1998, the burned and unburned study sites along the Rockefeller Parkway were revisited and sampled following the identical protocol developed previously (Seville et al., 1998). During the course of this later study, we examined animals found dead in traps (trap mortalities) in 1997 and 1998 and fecal samples from live-trapped southern red-backed voles in 1998 to survey for coccidia species in southern red-backed voles.

Here we report results of this investigation and, because there is only 1 previous report of eimerians from this host in North America, include descriptions of sporulated oocysts of *E. clethrionomyis* and unsporulated oocysts that appear to be *E. marconii* and *E. pileata.* We also compare these with the original descriptions by Straneva and Kelley (1979).

Materials and Methods

In 1997 and 1998, southern red-backed voles were live-trapped on Huckleberry Mountain (43°53′N, 110°30′W, elevation 2,250 m) along the John D. Rockefeller Jr. Parkway between Yellowstone and GTNP. Scientific research permits were obtained from GTNP and Wyoming Game and Fish Department. Four 1-hectare trapping grids (100 traps/grid) established by Spildie (1994) and Stanton et al. (1991) were re-established: 2 in areas burned in 1988 and 2 in adjacent unburned forest. One pair of grids (burned and adjacent unburned) was located on a west-facing slope, and the other on an east-facing slope. Each trapping session consisted of 4 consecutive days each in June, July, and August. Sherman live-traps (8 × 9 × 23 cm) were set at 1800 h and checked the following day by 0600 h. Traps remained closed during the day. Traps were baited with peanut butter and rolled oats and provided with polyfill fiber bedding insulation to reduce mortality. In 1997 and 1998, trap mortalities were collected for later necropsy in the laboratory, and in 1998,

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feces were collected from some live-trapped southern red-backed voles and examined for coccidia.

In 1997 and 1998, necropsies were performed on all trap mortalities. Intestines were removed and opened lengthwise, and the contents were transferred into petri plates. Intestinal contents and feces collected from live-trapped southern red-backed voles were stored in 2% aqueous (w/v) potassium dichromate ($K_2Cr_2O_7$) solution at room temperature (25°C) for a minimum of 10 d to allow oocyst sporulation for species identification (Hammond, 1973). Oocysts were isolated by direct flotation in saturated sugar solution (specific gravity = 1.2) and identified on the basis of standard morphologic features (Hammond, 1973). All measurements are reported in micrometers (μm). The description presented here of *E. clethrionomyis* adheres to the guidelines proposed by Duszynski and Wilber (1997) for species of *Eimeria*. Representative photomicrographs of sporulated oocysts were accessioned to the United States National Parasite Collection (USNPC), Beltsville, Maryland.

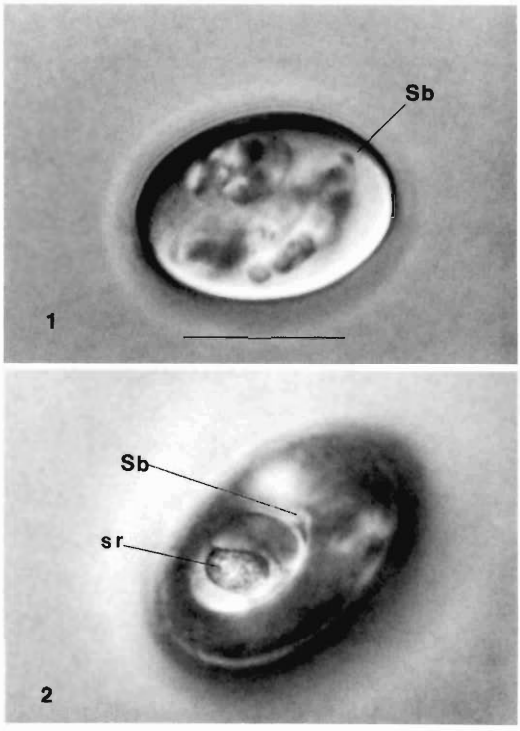
Because trap mortalities were frozen in 1997, oocysts did not sporulate. Therefore, we noted the oocyst wall characteristics and measured dimensions (length × width) of unsporulated oocysts, compared these with the eimerian species descriptions of Straneva and Kelley (1979), and tentatively identified the oocysts we observed to genus and species.

Results

In 1997, 42 southern red-backed vole trap mortalities were collected and necropsied, and their intestinal contents were examined for the presence of coccidia. Of these, 8 animals (19%) were shedding coccidia. Probably because of freezing of 1997 trap mortalities, the recovered oocysts did not sporulate. However, on the basis of wall characteristics and length/width measurements of the unsporulated oocysts and previously reported sporulated oocyst dimensions, we tentatively identified 3 species of *Eimeria*: *E. clethrionomyis, E. marconii, and E. pileata.*

In 1998, both trap mortalities and feces collected in the field from live-trapped animals were examined for *Eimeria* species. Overall, 6 of 53 (11%) southern red-backed voles were positive for *Eimeria.* Four (18%) trap mortalities (n = 22) were positive for *Eimeria* species, and 2 fecal samples from live-trapped animals (n = 31) were positive. In 1998, the only *Eimeria* species observed was *E. clethrionomyis.* In 1998, infected animals never harbored more than a single species. Over the 2 yr, few red-backed voles were captured and examined from unburned study sites, so we were unable to compare burned and unburned forests.

Below we present descriptions of sporulated oocysts of *E. clethrionomyis* and unsporulated oocysts tentatively identified as *E. marconii* and *E. pileata* and compare these with the original descriptions of Straneva and Kelley (1979).



Figures 1, 2. Sporulated oocysts of *Eimeria clethrionomyis* collected from southern red-backed voles *Clethrionomys gapperi* in the Greater Yellowstone Area of northwestern Wyoming. 1. Slightly flattened ends of oocyst present and sporocyst with Stieda body (Sb). 2. Sporocyst with Sb and compact sporocyst residuum (sr). Scale bar = 10 μm.

Eimeria clethrionomyis Straneva and Kelley, 1979 (Figs. 1, 2)

Description of Wyoming specimens

Oocyst wall about 1.1 μm thick, consisting of 2 layers: outer clear to yellow, smooth; inner clear, smooth; oocyst residuum and micropyle absent; sporulated oocysts (n = 55) ovoid to ellipsoid, often with 1 end flattened, mean length by width 18.9 × 14.5 (range 16.2–21.1 × 12.9–17.0); usually 1–2 polar granules present with fused, bilobed appearance. Sporocysts (n = 56) elongate, ovoid, uniform wall with mean length by width 9.6 × 6.3 (8.0–11.1 × 3.4–8.0); Stieda body distinct, dark at pointed end of sporocyst, substieda body absent; sporocyst residuum con-

sisting of spheroid granules dispersed throughout sporocyst and/or a mass of compact granules; sporozoites positioned lengthwise in sporocyst, partly curled around each other. Unsporulated oocysts (n=110) ellipsoid, typically with 1 end flattened, measuring 18.8 × 15.4 (16.1–21.7 × 10.5–17.7).

Taxonomic summary

TYPE HOST: *Clethrionomys gapperi* (Vigors, 1830), southern red-backed vole.

TYPE LOCALITY: North America: U.S.A.: Brush Valley, Indiana County, Pennsylvania.

PREVALENCE: In Pennsylvania, 20% (3 of 15) of hosts examined were infected. In northwestern Wyoming in 1998, 11% (6 of 53) of animals were positive. In 1997, 14% (6 of 42) of animals examined were possibly infected with this species, although only unsporulated oocysts were recovered.

SITE OF INFECTION: Unknown, oocysts recovered from feces in Pennsylvania and oocysts collected from fecal samples and intestinal contents at necropsy in northwestern Wyoming.

MATERIAL DEPOSITED: None deposited from Pennsylvania. Photomicrographs of the sporulated oocyst from red-backed voles in northwestern Wyoming deposited in the USNPC No. 90586.

Remarks

The description of *E. clethrionomyis* from southern red-backed voles in northwestern Wyoming is similar to the description provided by Straneva and Kelley (1979) for the same species collected in Pennsylvania. Oocyst size is virtually identical from the 2 host populations: 18.9 × 14.5 (16.2–21.1 × 12.9–17) in northwestern Wyoming compared with 18.8 × 14.9 (16.5–21.5 × 14.0–16.5) in Pennsylvania. Thirty-six of 55 (65%) of the oocysts we observed were ovoid–ellipsoid with flattened ends. The remaining oocysts (35%) lacked flattened ends. All of the oocysts in the original description were ellipsoid with 1 or both ends flattened. Sporocysts measured 10.6 × 6.1 (9.5–12.0 × 5.5–7.0) compared with 9.6 × 6.3 (8.0–11.1 × 3.4–8.0) for the Pennsylvania specimens. Rarely, our sporocysts had a compact granular residuum not dispersed throughout the sporocyst as compared with the dispersed spheroid granules we observed in most specimens and described originally. In all other aspects of morphology we examined, the oocysts from northwestern Wyoming were identical to the specimens described from Pennsylvania.

In addition, in 1997, we recovered unsporulated oocysts of what appeared to be 2 other coccidian species that we tentatively identified as *E. marconii* and *E. pileata.* Unsporulated oocysts believed to be *E. marconii* (n=106) were ellipsoid, did not possess a micropyle, and measured 13.3 × 11.1 (10.5–15.7 × 9.2–13.3). The oocyst wall was comprised of a single layer that was smooth and yellow and measured ~1.0 thick. Straneva and Kelley (1979) reported sporulated oocysts of *E. marconii* were ellipsoid, did not possess a micropyle, and measured 13.0 × 10.6 (10.5–15.0 × 9.5–12.0). The oocysts also had a smooth, yellow, single-layered wall. We observed this type of oocyst in 3 of 42 animals examined.

Unsporulated oocysts believed to be *E. pileata* (n = 6) were spherical, did not possess a micropyle, and measured 21.9 × 18.9 (20.25–28.25 × 17.0–22.5). The oocyst wall was ~1.0 thick and comprised of 2 layers with the outer rough, pitted/striated, and clear to yellow and the inner layer yellow in color. Straneva and Kelley (1979) reported that sporulated oocysts of *E. pileata* were subspherical to spherical, did not possess a micropyle, and measured 25.2 × 22.5 (20.5–29.5 × 19.5–25.5). They also noted that the oocyst wall was rough, pitted, striated, and composed of two layers: outer layer yellow/yellow brown and inner layer clear/yellow in color. We observed this type of oocyst in 3 of 42 (7%) of the animals examined.

Discussion

Species of *Eimeria* previously documented from the southern red-backed vole in North America include *E. clethrionomyis, E. gallatii, E. marconii,* and *E. pileata* (Straneva and Kelley, 1979). We found 1 species, *E. clethrionomyis,* present in both years of this study and evidence suggesting that *E. marconii* and *E. pileata* may be present in northwestern Wyoming in southern red-backed voles. The finding of *E. clethrionomyis* in northwestern Wyoming is a new geographic record for this parasite from the southern red-backed vole, with the only previous report from Pennsylvania (Straneva and Kelley, 1979). Recovery of unsporulated oocysts that are likely *E. marconii* and *E. pileata* suggests

that these species are also present in the western U.S.A.

Acknowledgments

We thank Dave Spildie, United States Forest Service Aldo Leopold Wilderness Research Station, Dr. Willard Robinson, Casper College, and the many students from Casper College and the University of Wyoming who helped in the field and laboratory studies. This study was supported in part with funds provided by the University of Wyoming/Casper Center and grants from the University of Wyoming National Park Service Research Center and the University of Wyoming NSF/EPSCoR Community College Research Support Program.

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Diagnostic Parasitology Course

The "Diagnostic Parasitology Course" is being offered July 30–August 10, 2001 at the Uniformed Services University of the Health Sciences, Bethesda, Maryland 20814-4799. This course will consist of a series of lectures and hands-on laboratory sessions covering the diagnosis of parasitic infections of humans. In addition to the examination of specimens, participants will be able to practice various methods used in the diagnosis of intestinal, blood, and tissue parasitic infections. Parasitic diseases encountered throughout the world will be included. Slide presentations and videotapes will be available for study. The course will be held at the University's campus, utilizing up-to-date lecture rooms and laboratory facilities. Microscopes will be available on a loan basis and laboratory supplies will be provided. Certain reference specimens will also be available for personal use.

The registration fee for the 2-week course is US$1,200 (This does not include lodging and meals). Enrollment is limited, so those interested should register as soon as possible. Previous laboratory experience is recommended.

For further information contact Dr. John H. Cross at phone (301) 295-3139 (e-mail: jcross@usuhs.mil) or Ms. Ellen Goldman at phone (301) 295-3129 (e-mail: egoldman@usuhs.mil).

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Excystation and Infectivity of *Echinostoma caproni* Metacercariae After Prolonged Storage

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ABSTRACT: This study examined excystation and infectivity of *Echinostoma caproni* Richard, 1964, metacercariae stored in Locke's solution 1:1 at 4°C for up to 12 mo or maintained in *Biomphalaria glabrata* (Say, 1816) snails for 3 mo. Comparisons were made with fresh encysted metacercariae obtained from *B. glabrata* within 14 d postinfection. Excystation was scored as the number of excysted metacercariae obtained after cyst treatment for 1 hr at 41 ± 1°C in an Earle's alkaline solution with trypsin-bile salts. The percentage excystation in trials with fresh cysts was 98.3% compared with 51.5% for cysts stored in Locke's solution for 5 mo. Cysts stored for 8 or 12 mo did not excyst. The percentage of worm recovery in mice fed fresh cysts was 66% compared with 13.5% in mice fed cysts stored for 5 mo. The percentage of worm recovery in mice fed cysts that had been maintained in *B. glabrata* for 3 mo was 75%. Some experiments were done with mice fed excysted metacercariae. The percentage of worm recovery in mice fed excysted metacercariae from fresh cysts was 44% compared with 13% in mice fed excysted metacercariae from cysts stored in Locke's solution for 5 mo. Implications of these findings for the maintenance of encysted metacercariae of *E. caproni* in the laboratory are discussed.

KEY WORDS: trematodes, *Echinostoma caproni*, mice, metacercariae, encystation, excystation, infectivity, worm recovery, cyst storage.

Echinostoma caproni Richard, 1964, is an intestinal trematode useful for various studies on the biology of echinostomes; it is maintained in our laboratory by cycling it through the planorbid snail *Biomphalaria glabrata* (Say, 1816) and ICR mice (*Mus musculus* Linnaeus, 1758) (Fried and Huffman, 1996). Fried and Emili (1988) compared excystation rates of metacercarial cysts of *E. caproni* and *Echinostoma trivolvis* (Cort, 1914) Kanev, 1985. They found that the metacercariae of *E. caproni* excysted more rapidly than those of *E. trivolvis*. Because we supply about 12 researchers a year with metacercarial cysts of *E. caproni*, it is important to know how long these cysts remain viable after removal from snail hosts. The purpose of this study was to extend the work of Fried and Emili (1988) and to provide more information on excystation and infectivity of metacercarial cysts after prolonged storage. We also examined the effects of cyst storage on infectivity in mice, which was not done by Fried and Emili (1988). Light microscope observations of the metacercariae during excystation have been provided by Ursone and Fried (1995).

Materials and Methods

Metacercarial cysts of *E. caproni* were removed from the kidney–pericardial region of experimentally infected *B. glabrata* snails. Cysts were removed from the snails 1–14 d postinfection and were considered fresh if used within 2 wk after removal. Cysts were maintained (usually 1,000 to 1,500 cysts/20 ml of solution) at 4°C in half strength Locke's solution (see Ursone and Fried [1995] for the formulation of the Locke's solution) for up to 1 yr after removal from snails. Chemical excystation was done in an Earle's (1943) medium containing trypsin-bile salts at pH 7.8–8.0. All chemicals were purchased from Sigma (St. Louis, Missouri, U.S.A.). The medium contained the following chemicals, added in order: 100 ml of Earle's balanced salt solution (Sigma catalog number E-6132; 1×), 0.5 g trypsin (1:250 from porcine pancreas; catalog number T-4799), 0.5 g bile salts (50% sodium cholate, 50% sodium deoxycholate, catalog number B-8756), and 5.0 ml of 7.5% sodium bicarbonate (catalog number S-8761). The solution was filtered and either refrigerated at 4°C for up to 2 wk or frozen at −20°C before use. Frozen medium was thawed at 42°C and filtered again before use. There was no difference in the rate or percentage of excystation in either the fresh, frozen, or refrigerated medium. The use of bile salts and trypsin from other sources may produce different results from those reported herein. For each trial, 25 cysts were placed in 2 ml of medium in a 3-cm plastic petri dish and maintained at 41 ± 1°C for 1 hr. Upon removal from the incubator, encysted and excysted metacercariae were removed from the medium and rinsed several times in Locke's solution, and the number of excysted metacercariae was counted under the dissecting microscope. Only organisms completely free of all cyst walls were scored as excysted. See Ursone and Fried (1995, fig. 7) for a photograph of this stage.

Five groups of mice with $n = 4$ to 8 per group were

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Table 1. Chemical excystation trials for encysted *Echinostoma caproni* metacercariae of various ages.*

No. months of cyst storage	No. trials	Total no. excysted	% Excysted
0.5	12	295/300	98.3
1.0	6	143/150	95.3
3.0	7	156/175	89.1
5.0	8	105/200	51.5
7.0	5	3/125	0.6
8.0	8	0/200	0.0
12.0	8	0/200	0.0

* n = 25 encysted metacercariae per trial.

Table 2. Infectivity of mice fed with either 25 encysted *Echinostoma caproni* or 25 excysted metacercariae.

Group*	No. mice used	Total no. worms recovered	% Worm recovery
A	8	132/200	66.0
B	4	44/100	44.0
C	8	27/200	13.5
D	4	13/100	13.0
E	4	75/100	75.0

* Group A = fresh encysted metacercariae; B = chemically excysted metacercariae from fresh cysts; C = encysted metacercariae stored in Locke's solution 1:1 at 4°C for 5 mo; D = chemically excysted metacercariae from cysts stored in Locke's solution 1:1 at 4°C for 5 mo; E = encysted metacercariae removed from snails at 3 mo postinfection.

inoculated via stomach tube, each mouse with 25 cysts or excysted metacercariae, to determine the effects of cyst aging on subsequent worm recovery. At 14 d postinfection, all mice were killed with light ether anesthetization and cervical dislocation, and the small intestine was examined from the pylorus to the ileocecal valve. The number of worms per mouse was counted, and the total number of worms recovered per group was recorded.

Results

Table 1 shows the results of chemical excystation trials for cysts of various ages. Excystation approached 100% in trials with fresh cysts and decreased to 51.5% in trials with 5-mo-old stored cysts. The percentage excystation declined rapidly when cysts stored for more than 5 mo were used. In trials that used cysts stored for 7 mo, only 0.6% excysted metacercariae were recovered. In all trials beyond this point (cysts stored for 8 or 12 mo in Locke's solution 1:1 at 4°C), none of the encysted metacercariae excysted.

Table 2 summarizes the infectivity trials with fresh and stored metacercariae. In mice fed fresh cysts, 66% (132/200) of the organisms were recovered. Mice fed 5-mo-old cysts showed a 13.5% (27/200) recovery of adult worms. Mice infected with 3-mo-old in vivo cysts had the highest worm recovery of 75% (75/100). Mice inoculated with fresh excysted metacercariae had a 44% worm recovery, and mice fed excysted metacercariae from cysts stored for 5 mo had a 13% worm recovery.

Fresh cysts and those stored for less than 5 mo appeared similar by light microscopy and showed the oral sucker and acetabulum, the double-layered cyst wall, collar spines, and calcareous corpuscles (Fig. 1). However, most cysts stored beyond 5 mo no longer showed these structures and were characterized by granular inclusions, indefinitely layered cyst walls, and the absence of suckers, collar spines, or excretory concretions (Fig. 2). Although most cysts stored for less than 5 mo were transparent and spherical, others contained brown pigment and were ovoidal, subspherical, or misshapen. Some cysts were surrounded by numerous hemocytes, whereas others showed few or no hemocytes. Regardless of hemocytic infiltration, shape of cysts, or presence of pigment, cysts stored for less than 5 mo were capable of excystation.

Discussion

The findings suggest that chemical excystation by the procedure described herein is very successful (about 90% excystation within 1 hr) with fresh cysts or those stored for up to 3 mo at 4°C in Locke's solution 1:1. This is important information for those using the excysted metacercariae of this species for various studies on morphology, histochemistry, and biochemistry of echinostomes as described in Fried (1994). Cysts stored for 5 mo will produce about 50% excystation, which may be suitable for some studies. We now routinely discard cysts after 5 mo of storage because their potential for excystation is reduced. Likewise, the ability to infect mice with either encysted or excysted metacercariae is markedly reduced after 5 mo of storage as seen in Groups C and D mice (Table 2). Fresh cysts and excysted metacercariae from fresh cysts are quite infective to mice, leading to worm recoveries of 66 and 44%, respectively.

The finding of the use of excysted metacercariae to infect mice via the oral route is new.

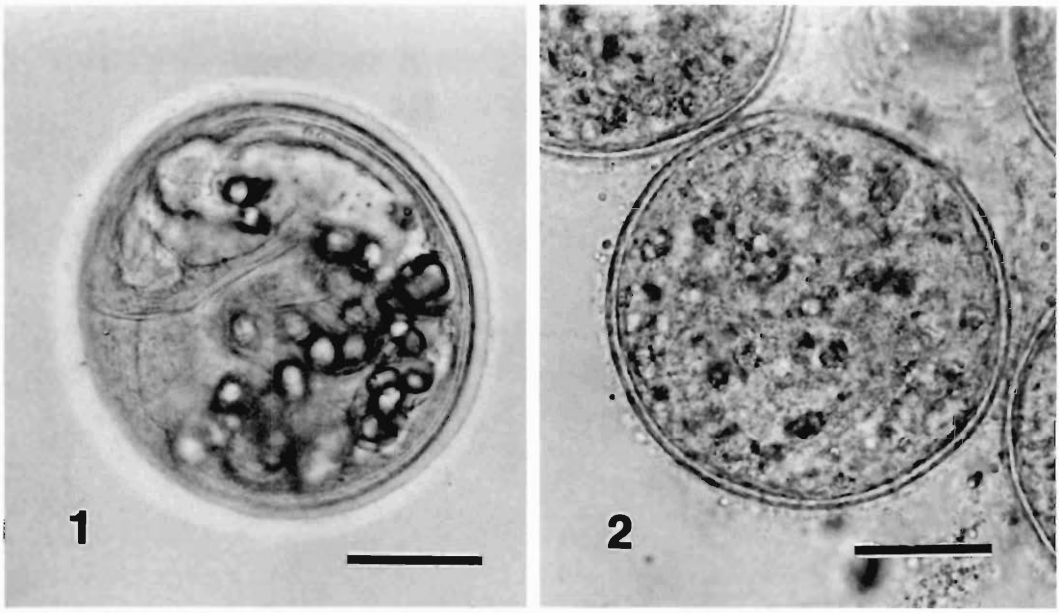

Figure 1. A representative fresh cyst showing distinct cyst layers, an intact organism within the cyst, and excretory concretions. Not all characteristics of the fresh cyst mentioned in the text are visible in this micrograph. Scale bar = 50 μm.

Figure 2. A representative nonviable cyst stored beyond 5 mo in Locke's solution. Granular inclusions are apparent within the cyst. There is no appearance of an organism within the cyst. Not all characteristics of a nonviable cyst mentioned in the text are visible in this micrograph. Scale bar = 50 μm.

Excysted metacercariae have been implanted only into the intestine of mice (Chien et al., 1993). This is the first study that reports the use of excysted metacercariae intubated into the mouse stomach to infect these hosts. Apparently, the acidity in the stomach is not lethal to excysted metacercariae for the length of time that they remain in the stomach. Presumably, the excysted metacercariae pass out of the stomach in a reasonable time (the exact time is unknown) to establish in the jejunum–ileum region of the mouse. Some detrimental effects of using fresh excysted metacercariae compared with fresh encysted metacercariae are based on 44% worm recovery for the former and 66% for the latter.

The finding of 75% worm recovery in the mice with cysts maintained in vivo for 3 mo postinfection was surprising. In fact, these cysts showed remarkably little hemocytic infiltration, indicating that they were not yet in the process of being rejected by the snail. Thus, maintenance of cysts of this species in the snail for at least up to 3 mo is an option for cyst storage, in addition to the usual procedure of storing the cysts in Locke's solution 1:1 at 4°C.

Fried and Emili (1988) obtained almost 100% excystation in metacercariae of *E. caproni* stored for 5.5 mo. Beyond that time, the percentage of excystation dropped markedly in that study (see Fried and Emili [1988, fig. 9]). In the present study, only 51.5% of the metacercariae stored for 5 mo excysted. We are not certain how to account for the discrepancies in the 2 studies. The Fried and Emili (1988) study used cysts dissected from the M-line strain of *B. glabrata* at 1–28 days post-cercarial encystment. In the present study, we used cysts obtained from the NMRI strain of *B. glabrata* at 1–14 days post-cercarial encystment. Perhaps these minor differences in cyst procurement account in part for the discrepancies seen in the 2 studies.

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Research Note

Parasitic Helminths of Five Species of Owls from Florida, U.S.A.

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ABSTRACT: Five species of owls collected in Florida, U.S.A., between 1971 and 1992 were examined for parasitic helminths. In all, 29 helminth species (10 trematodes, 1 cestode, 16 nematodes, and 2 acanthocephalans) were recovered from the barred owl *Strix varia,* great horned owl *Bubo virginianus,* eastern screech-owl *Otus asio,* barn owl *Tyto alba,* and burrowing owl *Athene cunicularia.* The great horned owl harbored the most species per infected host ($\bar{x}$ = 6.2), whereas the burrowing owl harbored the least ($\bar{x}$ = 1.3). Sixteen helminth species were considered generalists in raptors and 8 as bird generalists. Euryphagic host species such as the barred and great horned owls harbored more helminth species than more specialized feeders such as the eastern screech-owl and barn owl. Helminths were not implicated as the cause of death of any of the hosts examined.

KEY WORDS: owls, *Strix varia, Bubo virginianus, Otus asio, Tyto alba, Athene cunicularia,* Aves, helminths, parasites, trematodes, cestodes, nematodes, acanthocephalans, Florida, U.S.A.

Perhaps because of the protected status of owls under federal law, very little information is available on the parasites of owls in North America. Early studies on raptor helminths resulted in information on the taxonomy of specific groups of helminths. Only a few authors have listed the overall prevalences and intensities of helminths in owls: Ramalingam and Samuel (1978) for great horned and snowy owls in Alberta, Canada; Hoberg et al. (1989) for spotted owls in Oregon, U.S.A.; and Taft et al. (1993) for 8 species of owls in Minnesota and Wisconsin, U.S.A.

Since 1971, large numbers of dead or dying raptors have been submitted to the Department of Pathobiology, College of Veterinary Medicine at the University of Florida, Gainesville, Florida, U.S.A., for determinations of cause of death. Earlier papers reported on helminths of hawks and falcons (Kinsella et al., 1995), ospreys (Kinsella et al., 1996), and bald eagles (Kinsella et al., 1998). In this paper, we report on the helminths of 5 species of owls.

Eighty birds obtained from 17 counties in Florida between 1971 and 1992 were examined at necropsy. Helminths were not implicated as the cause of death in any of the owls; however, collisions with vehicles, collisions with wires, predation, poisoning, and gunshot wounds were. Most birds were found dead, but a small number of birds were found alive with injuries too severe to be treated, and these were euthanized. Carcasses were frozen within 4 hr of collection or death, transported to the laboratory, and later thawed and examined at necropsy. Techniques for recovering, fixing, staining, and examining helminths followed Kinsella and Forrester (1972). Hosts were not examined for subcutaneous helminths or *Trichinella.* Because of the disparity in dates and localities of collection of the hosts, no statistical analysis was attempted. Terminology used follows Bush et al. (1997). The term "core species" was defined by Bush and Holmes (1986) as those species with both high prevalences and high intensities of infection. Voucher specimens of helminths were deposited in the Harold W. Manter Collection, University of Nebraska, Lincoln, Nebraska, U.S.A. (accession numbers 37045–37062).

Twenty-nine species of helminths (10 trematodes, 1 cestode, 16 nematodes, and 2 acanthocephalans) were collected. Prevalences and intensities of helminth infections from the barred owl *Strix varia* Barton, 1799, the great horned owl *Bubo virginianus* (Gmelin, 1788), the eastern screech-owl *Otus asio* (Linnaeus, 1758), the barn owl *Tyto alba* (Scopoli, 1769), and the burrowing owl *Athene cunicularia* (Molina, 1782) are listed in Table 1. The number of helminth species per infected host varied from 1 to 10 ($\bar{x}$ = 2.8). No worms were present in 16 birds. The great horned owl harbored the most species, with a mean of 6.2 species per infected bird

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(range 3–10), whereas the burrowing owl averaged only 1.3 species (range 1–2). The other owls were intermediate between these extremes.

Twenty-eight new host records were found (Table 1), and 5 nematodes (*Capillaria tenuissima, Capillaria dispar, Dispharynx affinis, Synhimantus laticeps,* and *Excisa excisiformis*) were recorded for the first time from North America. With the exceptions of *Tetrameres strigiphila,* which was reported from a barred owl in Florida by Pence et al. (1975), and *Centrorhynchus kuntzi* and *Centrorhynchus spinosus,* both of which were reported from great horned owls in Florida by Nickol (1983), all the helminths found were new records for Florida for these hosts. The trematode *Neodiplostomum americanum* was the only species of helminth found in all 5 owl species; 1 nematode (*Porrocaecum depressum*) was found in 3 owl species; and 1 trematode (*Neodiplostomum reflexum*), 1 nematode (*E. excisiformis*), and 1 acanthocephalan (*C. spinosus*) occurred in 3 owl species. *Strigea elegans, N. americanum, N. reflexum, C. tenuissima,* and *C. spinosus* were considered core species in the great horned owl, and *N. americanum, C. tenuissima,* and *C. spinosus* were considered core species in the barred owl. No core species could be identified in the other owls.

No helminth in this paper could be considered a host specialist. In previous papers (Kinsella et al., 1995, 1996), we divided host generalists into raptor generalists, reported from hawks and owls but not other birds, and true generalists, reported from other orders of birds, including waterfowl and passerines. We consider 16 helminth species in owls to be raptor generalists and 8 to be true generalists in birds (Table 1). The remaining helminths not identified to species were excluded because their host relationships were unknown. These numbers are remarkably similar to the helminths of 6 hawks and falcons in Florida (Kinsella et al., 1995), which had 16 raptor generalists and 9 bird generalists. Raptor generalists found in both Falconiformes (hawks and falcons) and Strigiformes (owls) in Florida included *N. americanum, C. falconis, P. depressum,* and *C. kuntzi.*

Helminth species considered as bird generalists included *Stomylotrema vicarium,* which has been reported from white ibis (Bush and Forrester, 1976) and sandhill cranes (Forrester et al., 1975) in Florida, *Dispharynx nasuta,* which is more characteristic of galliforms and passeriforms (Rickard, 1985), and *Tetrameres microspinosa,* normally a parasite of pelicans and herons (Mollhagen, 1976). Although *Chandleronema longigutturata* was described originally from the raccoon in Texas by Chandler (1942), it has been recorded from bald eagles (Kinsella et al., 1998) and little blue herons (Sepulveda et al., 1996) in Florida and is considered here to be a bird generalist.

As in the falconiforms, cestode infections were quite rare in Florida owls, limited to 2 eastern screech-owls infected with *Choanotaenia speotytonis.* In surveys of 714 Florida rodents of 5 species, Kinsella (1974, 1988, 1991) found no larval stages of *Paruterina* spp., the common cestode genus in owls in other areas of North America (Freeman, 1959; Ramalingam and Samuel, 1978).

Although the falconiforms and strigiforms are not considered closely related, they have similar ecological niches and food habits, dividing the habitat not spatially but temporally (Bosakowski and Smith, 1992). Apparently as a consequence, their helminth faunas are quite similar, and there is a good number of sibling species (e.g., *Neodiplostomum attenuatum* (von Linstow, 1906) and *Neodiplostomum reflexum*; *Strigea falconis* Szidat, 1928, and *Strigea elegans*; *Synhimantus hamatus* (von Linstow, 1877) and *Synhimantus laticeps*; Porrocaecum angusticolle (Molin, 1860) and *Porrocaecum depressum*; and *Centrorhynchus kuntzi* and *Centrorhynchus spinosus*), the first of each pair being found primarily in falconiforms and the second in strigiforms, with occasional crossover (Kinsella et al., 1995; this paper). It seems likely that these pairs may each have a common ancestor that evolved with the host groups.

Within each group of raptors, Bosakowski and Smith (1992) found that body size was correlated with prey classes. The larger great horned and barred owls had a greater variety of prey items, which included mammals, birds, fish, and amphibians, whereas the small eastern screech-owl consumed the largest percentage of invertebrates. This difference may explain the greater species richness in the great horned owl (6.2) and barred owl (3.1) compared with the eastern screech-owl (1.3), as well as the presence of species like *D. nasuta,* with arthropod intermediate hosts, in the eastern screech-owl. Taft et al. (1993) found a similar pattern of species richness in the great horned and barred owls in Min-

Table 1. Prevalences and intensities of helminth infections in 5 species of owls in Florida, U.S.A.

Helminth	Site*	Prevalence/intensity†				
		Barred owl (n = 23)	Great horned owl (n = 11)	Eastern screech-owl (n = 32)	Barn owl (n = 9)	Burrowing owl (n = 5)
Trematoda						
Neodiplostomum americanum Chandler and Rausch, 1947‡	SI	12(52)/25(1–62)	8(73)/395(2–2,353)	1(3)/5(5)§	3(33)/4(3–7)§	1(20)/1(1)§
Neodiplostomum reflexum Chandler and Rausch, 1947‡	SI	7(30)/31(1–83)	4(36)/889(5–3,533)	1(3)/17(17)	—	—
Strigea elegans Chandler and Rausch, 1947‡	SI	1(4)/2(2)	8(73)/20(2–108)	—	—	—
Stomylotrema vicarium Braun, 1900‖	SI	—	6(55)/9(2–21)§	—	—	—
Brachylaima mcintoshi Harkema, 1939‡	SI	4(17)/3(1–5)	1(9)/5(5)§	—	—	—
Brachylecithum rarum (Travassos, 1917)‖	L	2(9)/9(5–12)§	—	—	—	—
Prosthogonimus ovatus (Rudolphi, 1803)‖	LI	—	—	—	—	1(20)/1(1)§
Plagiorchis sp.	SI	—	—	1(3)/4(4)§	—	—
Maritrema sp.	SI	—	—	—	—	1(20)/3(3)§
Microphallus sp.	SI	—	—	—	—	1(20)/1(1)§
Cestoda						
Choanotaenia speotytonis Rausch, 1948‡	SI	—	—	2(6)/15(14–16)§	—	—
Nematoda						
Capillaria tenuissima (Rudolphi, 1803)‡	CE	9(39)/7(2–12)§	8(73)/10(1–23)§	—	—	—
Capillaria falconis (Rudolphi, 1819)‡	SI	2(9)/2(2)§	3(27)/8(4–14)	—	—	—
Capillaria dispar (Dujardin, 1845)‡	E	1(4)/2(2)§	—	—	—	—
Capillaria sp.	SI	—	—	4(13)/1(1)	—	—
Dispharynx affinis (Seurat, 1916)‡	P	—	—	—	3(33)/4(1–5)	—
Dispharynx nasuta (Rudolphi, 1819)‖	P	—	—	3(9)/19(7–41)§	—	—
Synhimantus laticeps (Rudolphi, 1819)‡	P	—	2(18)/2(1–2)§	—	—	—
Chandleronema longigutturata (Chandler, 1942)‖	P	6(26)/3(1–5)§	1(9)/1(1)§	—	—	—
Excisa excisiformis (Yamaguti, 1935)‡	P	1(4)/2(2)§	2(18)/5(2–7)§	4(13)/4(1–6)§	—	—
Tetrameres strigiphila Pence, Mollhagen, and Forrester, 1975‡	P	1(4)/40(40)	—	—	—	—
Tetrameres microspinosa Vigueras, 1935‖	P	4(17)/3(1–8)§	—	—	—	—
Porrocaecum depressum (Zeder, 1800)‡	SI	1(4)/4(4)	5(45)/7(1–18)	—	1(11)/1(1)	—
Subulura forcipata Rudolphi, 1819‖	CE	—	—	—	—	1(20)/1(1)§
Subulura reclinata (Rudolphi, 1819)‖	CL	—	—	1(3)/2(2)§	—	—
Lemdana wernaati Bartlett and Anderson, 1987‡	BC	—	1(9)/1(1)	—	—	—
Strongyloides sp.	SI	1(4)/3(3)§	—	2(6)/3(1–4)§	—	—
Larval spirurids	P	—	1(9)/4(4)	4(13)/1(1)	1(11)/1(1)	—

Table 1. Continued.

Helminth	Site*	Prevalence/intensity†				
		Barred owl (n = 23)	Great horned owl (n = 11)	Eastern screech-owl (n = 32)	Barn owl (n = 9)	Burrowing owl (n = 5)
Acanthocephala						
Centrorhynchus spinosus (Kaiser, 1893)‡	SI	18(78)/13(1–41)	9(82)/65(1–340)	7(22)/5(1–14)§	—	—
Centrorhynchus kuntzi Schmidt and Neiland, 1966‡	SI	—	3(27)/1(1–2)	—	—	—

* BC = body cavity, CE = ceca, CL = cloaca, E = esophagus, L = liver, LI = large intestine, P = proventriculus, SI = small intestine.
† Number of owls infected (% infected)/mean (range) number of worms per host individual.
‡ Raptor generalist.
§ New host record.
‖ Host generalist.

nesota and Wisconsin, U.S.A., but it is difficult to make a direct comparison because most of their parasites were identified only to genus. Ramalingam and Samuel (1978) reported 14 species of helminths from 69 great horned owls in Alberta, Canada, but only 3 of their 14 species were found in Florida birds (*S. elegans, C. falconis,* and *P. depressum*). Four of the core species in Florida birds (*N. americanum, N. reflexum, C. tenuissima,* and *C. spinosus*) were absent in Alberta birds. Obviously, more data are needed on owl helminths before we fully understand their host distribution and community structure.

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Research Note

Records of *Eimeria* spp. and Their Patterns of Excretion in Captive North African Gazelles

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ABSTRACT: The species of *Eimeria* occurring in 3 species of captive gazelles (*Gazella dama mhorr, Gazella cuvieri,* and *Gazella dorcas neglecta*) were identified. This is the first report of *Eimeria pallida, Eimeria elegans,* and *Eimeria gazella* in these hosts and also the first report of *E. elegans* and *E. gazella* in Spain. Feces were collected from each of 9 young gazelles for periods of 3–7 mo to determine their oocyst shedding profile. Most oocysts appeared at 20–25 d, peaked, and decreased to undetectable levels between 40 and 115 d. *Eimeria gazella* delayed its excretion, which continued at low levels throughout the observation stage. No clinical signs of infection were observed in the gazelles during the study.

KEY WORDS: gazelle, *Gazella dama mhorr, Gazella cuvieri, Gazella dorcas neglecta,* Coccidia, coccidio-

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sis, *Eimeria pallida, Eimeria elegans, Eimeria gazella,* oocyst, excretion pattern, Spain.

Coccidia of the genus *Eimeria* Schneider, 1875, are obligatory protozoan parasites commonly detected in most animals (Soulsby, 1987). Although ruminants of all ages can be infected, younger ones are more susceptible to coccidiosis (Catchpole et al., 1993; Taylor and Catchpole, 1994). Coccidiosis is common in sheep and goats in Spain (Hidalgo and Cordero, 1987; De la Fuente and Alunda, 1992; Cordero et al., 1994), and the presence of these parasites has also been recorded in wild ruminants (Gómez-Bautista et al., 1996). Both domestic and wild ruminants usually have multispecies coccidial infections, and most of the species can be clearly differentiated by the morphological characteristics of the sporulated oocyst (Pellérdy, 1974; Catchpole et al., 1975; Cordero and Hidalgo, 1996).

Seven species of *Eimeria* have been reported in members of the genus *Gazella* Blainville, 1816 (Levine and Ivens, 1986; Hussein and Mohammed, 1992; Mohammed and Hussein, 1992), all of them described in the mountain gazelle (*Gazella gazella* Pallas, 1766), the goitered gazelle (*Gazella subgutturosa* Gueldenstaedt, 1780), or Dorcas gazelle (*Gazella dorcas* Linnaeus, 1758). Also, some parasite species more commonly associated with sheep or goats have been detected in gazelles (Pellérdy, 1974).

The main objective of this study was to identify the eimerians occurring in 3 species of African gazelles kept in captivity in Almería (southeastern Spain). The secondary aim was to determine the age of appearance of these parasites in feces and to describe their pattern of oocyst shedding.

In the Parque de Rescate de la Fauna Sahariana (Estación Experimental de Zonas Aridas, Consejo Superior de Investigaciones Científicas, Almería, Spain), 3 species of endangered Antilopinae (the Mohor gazelle *Gazella dama mhorr* Bennett, 1932, Cuvier's gazelle *Gazella cuvieri* Ogilby, 1840, and the Dorcas gazelle *Gazella dorcas neglecta* Lavauden, 1926) originating from the western Sahara have been kept in captivity since 1971. Approximately 270 gazelles are distributed in reproductive herds of 5 to 12 individuals (1 male plus females and young) in enclosures of 400 to 1,500 m^2. The adult males are kept in individual 20- to 80-m^2 pens.

Table 1. Gazelles included in the evaluation of pattern of oocyst excretion.

Gazelle*	Sex	Herd	Age at first sampling (days)	Age at last sampling (days)
Gc1	F	8	22	212
Gc2	M	8	6	198
Gc3	F	8	25	89
Gc4	M	7	25	184
Nd1	M	3	8	234
Nd2	F	3	2	226
Nd3	F	3	8	187
Gd1	F	1	2	90
Gd2	M	1	3	182

* Gc = *Gazella cuvieri*; Nd = *Gazella dama mhorr*; Gd = *Gazella dorcas neglecta.*

From October to December 1997, fecal samples from 18 animals less than 3 mo old, including members of each species of gazelle, were individually collected by observing animals defecate and immediately collecting the feces from the ground. After the discovery of *Eimeria* spp. oocyst shedding, fecal samples were pooled for identification. They were mixed with an aqueous 2.5% (w/v) potassium dichromate solution, strained through cheesecloth to remove coarse matter, placed in thin layers in Petri dishes, and allowed to sporulate both at 27°C and at room temperature (20 ± 2°C). Samples were examined periodically to determine sporulation times. Oocysts were observed at ×400 and ×1,000 magnifications and measured with an ocular micrometer. Species were identified on the basis of their morphological and morphometric characteristics (Pellérdy, 1974; Mohammed and Hussein, 1992). When possible, 100 sporulated oocysts from each species were measured. All measurements are in micrometers (μm) (means followed by the range in brackets).

The study of the pattern of excretion of coccidial oocysts was carried out from March to October 1998. Both sexes of these 3 species of gazelles were included in this survey. Distribution of host species, sex, and duration of the study in each animal are summarized in Table 1. Feces were collected from each of 9 gazelles for 6 to 7 mo except for 2 animals (Gc3 and Gd1) that were studied for only 3 mo. Sampling was carried out twice a week during the first 4 mo and then at 7 d intervals until the end of the study. All fecal specimens were taken from the

ground immediately after defecation. Feces were analyzed by the McMaster modified method recommended by the British Ministry of Agriculture, Fisheries, and Food (1977). Results are presented as the number of oocysts per gram of feces (o.p.g.).

Careful examination of the sporulated oocysts showed 3 species of *Eimeria*: *Eimeria pallida* Christensen, 1938, *Eimeria gazella* Svanbaev, 1979, and *Eimeria elegans* Yakimoff, Gousseff, and Rastegaieff, 1932.

The oocyst excretion patterns were different in each species of *Eimeria* (Fig. 1). *Eimeria pallida* was found in feces from all animals between 20 and 80 d of age. The number of oocysts ranged from 0 to 8,256 o.p.g. Over time, the rate of elimination of this parasite decreased to 0. The 3 species of gazelle followed this pattern of excretion, although 1 individual of *G. dama mhorr* showed a second peak of excretion around the sixth month of age, probably caused by reinfection.

Oocysts of *E. gazella* were shed by all animals, but this shedding followed different patterns. Most animals reached higher excretion values (ranging from 0 to 51,900 o.p.g.) between 40 and 60 d old. However, in a few *G. dorcas* and *G. cuvieri,* this peak of excretion was delayed until around 150 d old. Later, all of them showed a low but constant rate of shedding throughout the study.

Only *G. cuvieri* and *G. dorcas* excreted *E. elegans.* The shedding continued for only a few days. Most *G. cuvieri* showed this excretion between 55 and 115 d old. The studied *G. dorcas* shed this parasite earlier (around d 55), although 1 individual showed a low, new excretion rate between 150 and 175 d old. Four gazelles (3 *G. dama mhorr* and 1 *G. cuvieri*) did not excrete *E. elegans* during the observation period. Despite the presence of these parasites, there were no clinical signs of infection throughout the study.

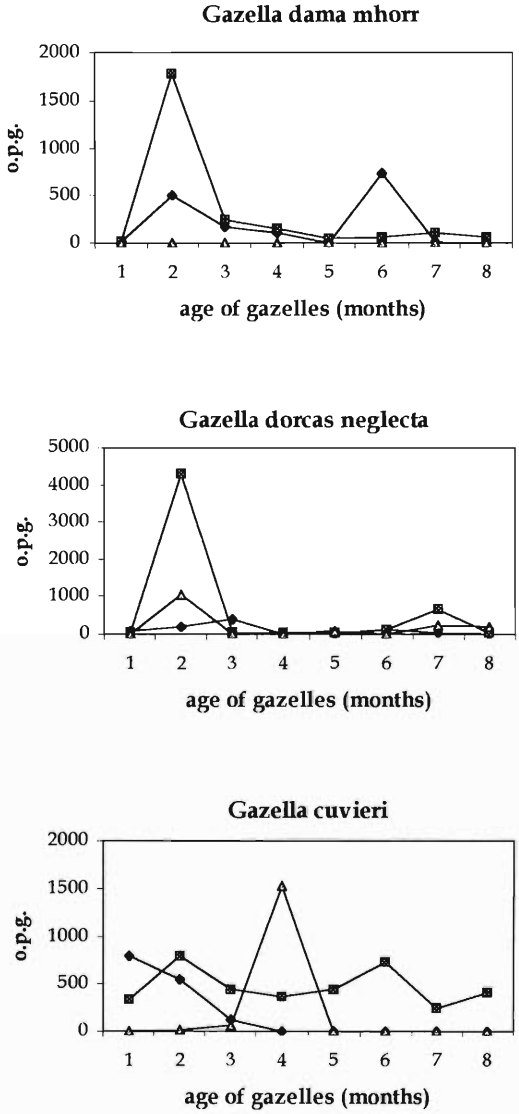

Figure 1. Oocyst excretion profile, expressed as oocysts per gram of feces (o.p.g.), of *Eimeria pallida* (solid diamonds), *Eimeria gazella* (hatched squares), and *Eimeria elegans* (open triangles) in gazelles.

Little information about coccidial infections in gazelles is available, and the few references mostly describe oocysts from species of gazelles different from the ones kept in the Parque de Rescate de la Fauna Sahariana. Seven species of *Eimeria* described from the genus *Gazella* have recently been reviewed (Hussein and Mohammed, 1992; Mohammed and Hussein, 1992). These studies included *G. subgutturosa, G. gazella,* and *G. dorcas,* but this is the first reference of Coccidia in *G. dama mhorr* and *G. cuvieri.*

With the use of their morphometric and morphologic characteristics and their sporulation time, the oocysts found in this study were identified as *E. elegans, E. gazella,* and *E. pallida.* This is the first report of *E. pallida* in the genus *Gazella.* It is also the first record of both *E. elegans* and *E. gazella* in hosts other than *G. sub-*

gutturosa and in Spain. In this respect, the African origin of the gazelles kept in Almería should be considered when the origin of the infection by *E. gazella* and *E. elegans* is investigated. The absence of oocysts of *E. elegans* in some animals (Gc1, Nd1, Nd2, and Nd3) seems to be because of the random selection of particular animals rather than the species of animals. Although domestic flocks of sheep graze near the park, this source should be cautiously considered to explain the presence of *E. pallida* in the feces of these animals because entrance to the park is restricted and careful management and control measures are observed by all the staff of the park. In conclusion, the possibility of the presence of these parasites in the gazelles housed in the Parque de Rescate de la Fauna Sahariana since before their arrival in Almería should be considered as the more feasible origin of the infection.

There were differences in the pattern of excretion of the oocysts, although these differences were not related to the number of species of *Eimeria* found in each animal. Shedding of *E. pallida* started around 20 d and continued until approximately 80 d. But when this wave of elimination declined, most animals no longer shed the parasite. A similar sequence, but one which occurred later, was found in *E. elegans.* Animals also showed a short peak of excretion but later than that described for *E. pallida* (between 55 and 115 d). A different pattern occurred with *E. gazella.* Its excretion began and peaked in coincidence with that of *E. pallida,* but all animals continued to shed low quantities of coccidia throughout the observation period, probably because of reinfection.

The observed pattern of excretion corresponded to the main characteristics described for coccidiosis in domestic animals (Taylor and Catchpole, 1994). On the one hand, most animals will probably become infected during the first few months of life. These early infections with subsequent low levels of challenge infections could actually stimulate protective immune responses in the host, which become protected against heavy subsequent challenge (Catchpole et al., 1993). Alternatively, although individuals that reach adulthood are highly resistant to these parasites, they may continue hosting small numbers throughout their lives (Taylor, 1995).

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Research Note

Gastrointestinal Helminths of Gekkonid Lizards (Sauria: Gekkonidae) from the Philippine Islands and Thailand

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ABSTRACT: The gastrointestinal tracts of 4 species of gekkonid lizards from the Philippine Islands, *Cosymbotus platyurus, Gehyra mutilata, Hemidactylus frenatus,* and *Lepidodactylus aureolineatus,* and 4 species of gekkonid lizards from Thailand, *Cosymbotus platyurus, Hemidactylus frenatus, Hemidactylus garnotii,* and *Hemiphyllodactylus typus* were examined for helminths. One species of cestode, *Oochoristica javaensis,* and 2 species of nematodes, *Skrjabinelazia machidai* and *Spauligodon hemidactylus,* were found in Philippine lizards. One species of trematode, *Postorchigenes ovatus,* 1 species of cestode, *Oochoristica javaensis,* and 2 species of nematodes, *Parapharyngodon maplestoni* and *Spauligodon hemidactylus,* were found in lizards from Thailand. Three new host records and 5 new locality records are reported. The occurrence of *Skrjabinodon dossae,* a nematode parasite of lizards of Madagascar, is invalidated for the Philippine Islands.

KEY WORDS: lizard, Gekkonidae, *Cosymbotus platyurus, Gehyra mutilata, Hemidactylus frenatus, Hemidactylus garnotii, Hemiphyllodactylus typus, Lepidodactylus aureolineatus,* Trematoda, Cestoda, Nematoda, Philippines, Thailand.

Thirty-one species of gecko are known from the Philippines (Alcala, 1986) and 39 from Thailand (Chan-Ard et al., 1999). Reports of helminths exist for 4 species of Philippine geckos: the flat-bodied house gecko *Cosymbotus platyurus* (Schneider, 1792), the tokay gecko *Gekko gecko* (Linnaeus, 1758), the house gecko *Hemidactylus frenatus* Duméril and Bibron, 1836, and the Indo-Pacific gecko *Hemidactylus garnotii* (Duméril and Bibron, 1836) (Tubangui, 1928, 1933; Fischthal and Kuntz, 1964, 1967; Schmidt and Kuntz, 1972), and reports of helminths exist for *H. frenatus* from Thailand (Bursey and Goldberg, 1996; Amin et al., 1998). A list of trematodes from Philippine vertebrates will be found in Tubangui (1933); a list of nematodes from Philippine reptiles will be found in Schmidt and Kuntz (1972). The purpose of this note is to provide additional helminth data for *C. platyurus* from the Philippines and *H. frenatus* from the Philippines and Thailand and first reports of helminths from the stump-toed gecko *Gehyra mutilata* Wiegmann, 1835, and the yellow-lined smooth-scaled gecko *Lepidodactylus aureolineatus* Taylor, 1915, from the Philippines and *C. platyurus, H. garnotii,* and the tree gecko *Hemiphyllodactylus typus* Bleeker, 1860, from Thailand.

With the exception of *L. aureolineatus,* which is endemic to the Philippines (Alcala, 1986), the geckos examined in this study have wide geographical distribution. *Cosymbotus platyurus* ranges from India through southeast Asia and the East-Indian Archipelago to the Philippines. *Gehyra mutilata* occurs from southeast Asia through southern China and the Philippines. *Hemidactylus frenatus* is known from Africa, Asia, Australia, Polynesia, Mexico, and parts of Central America. *Hemidactylus garnotii* is found from northeastern India and southern China through southeastern Asia, Indonesia, the Philippines, and Oceania. *Hemiphyllodactylus typus* ranges from Sri Lanka, Thailand, Indonesia, and the Philippines east through Oceania (Alcala, 1986; Welch, 1994; Chan-Ard et al., 1999).

Forty-one geckos from the Philippine Islands and 106 from Thailand were examined. Collection data by locality are presented in Table 1. Geckos were collected by hand and decapitated. The body cavities were opened, and the digestive tracts were searched for helminths with a

[3] Corresponding author.

Table 1. Localities, collection dates, and numbers (*N*) of geckos examined from the Philippine Islands and Thailand, and prevalences (P), mean intensities (I) ± 1 SD, and ranges of helminths by hosts.

Location and host	*N*	Trematoda	Cestoda	Nematoda		
		Postorchigenes ovatus (P, I ± 1 SD, range)	*Oochoristica javaensis* (P, I ± 1 SD, range)	*Parapharyngodon maplestoni* (P, I ± 1 SD, range)	*Skrjabinelazia machidai* (P, I ± 1 SD, range)	*Spauligodon hemidactylus* (P, I ± 1 SD, range)
Philippine Islands, September–October 1990						
Camiguin (09°11′N; 124°42′E)						
Gehrya mutilata	1	—	—	—	—	—
Lepidodactylus aureolineatus	12	—	—	—	8*, 1, —	—
Luzon (16°00′N; 121°00′E)						
Cosymbotus platyurus	7	—	—	—	—	57, 8.8 ± 6.4, 4–18
Gehyra mutilata	2	—	—	—	—	—
Hemidactylus frenatus	17	—	6, 1, —	—	—	53, 5.0 ± 5.1, 1–17
Negros (09°30′N; 122°40′E)						
Gehrya mutilata	3	—	—	—	—	33*, 2, —
Thailand, October 1988						
Bangkok (13°45′N; 100°35′E)						
Cosymbotus platyurus	2	—	—	—	—	—
Hemidactylus frenatus	9	11, 14, —	—	22, 1.5 ± 0.7, 1–2	—	11, 3, —
Doi Inthanon (18°34′N; 98°30′E)						
Cosymbotus platyurus	6	—	—	—	—	20, 1, —
Hemidactylus frenatus	10	20, 6.0 ± 7.1, 1–11	—	—	—	40, 2.3 ± 1.9, 1–5
Hemidactylus garnotii	8	—	—	—	—	38, 5.3 ± 2.9, 2–7
Hemiphyllodactylus typus	14	—	—	—	—	7*, 2, —
Doi Suthep (18°50′N; 98°58′E)						
Cosymbotus platyurus	5	—	—	—	—	40, 2.5 ± 0.7, 2–3
Hemidactylus frenatus	14	—	—	—	—	36, 1.6 ± 0.9, 1–3
Hemidactylus garnotii	1	—	—	—	—	—
Hat Yai (07°01′N; 100°27′E)						
Cosymbotus platurus	9	—	—	—	—	33, 1.3 ± 0.6, 1–2
Hemidactylus frenatus	14	29, 11.6 ± 9.9, 4–26	—	14, 2.0 ± 1.4, 1–3	—	43, 3.0 ± 2.4, 1–7
Thaleban National Park (06°33′N; 100°00′E)						
Cosymbotus platyurus	1	—	—	—	—	100, 5, —
Hemidactylus frenatus	13	8, 1, —	8, 1, —	—	—	46, 7.0 ± 10.0, 2–27

* New host record.

dissecting microscope. Helminths were removed and placed in 10% formalin. Selected trematodes and cestodes were dehydrated, cleared, stained in hematoxylin, mounted in balsam, and identified under a compound microscope. Nematodes were placed on glass slides in a drop of glycerol, allowed to clear, and identified with a compound microscope.

One species of Trematoda, *Postorchigenes ovatus* Tubangui, 1928; 1 species of Cestoda, *Oochoristica javaensis* Kennedy, Killick, and Beverly-Burton, 1982; and 3 species of Nematoda, *Parapharyngodon maplestoni* Chatterji, 1933, *Skrjabinelazia machidai* Hasegawa, 1984, and *Spauligodon hemidactylus* Bursey and Goldberg, 1996, were found. Localities, collection dates, and numbers of geckos examined and prevalences, mean intensities ± 1 SD, and ranges of helminths by host are presented in Table 1. Gravid individuals were present for each helminth species found in this study.

Trematodes and cestodes, as whole mounts on slides and nematodes in vials of 70% ethanol, were deposited in the United States National Parasite Collection, USNPC, Beltsville, Maryland, U.S.A. Philippines: from *C. platyurus*: *S. hemidactylus* 90224; from *G. mutilata*: *S. hemidactylus* 90225; from *H. frenatus*: *O. javaensis* 90222; from *L. aureolineatus*: *S. machidai* 90223. Thailand: from *C. platyurus*: *S. hemidactylus* 89716; from *H. frenatus*: *P. ovatus* 89710, *O. javaensis* 89713, *P. maplestoni* 89714, *S. hemidactylus* 89717; from *H. garnotii: S. hemidactylus* 89721; from *H. typus: S. hemidactylus* 89722.

Postorchigenes ovatus was originally described from *H. frenatus* collected on Luzon, Philippines, by Tubangui (1928) and was subsequently reported from the same host species collected on the same island by Fischthal and Kuntz (1964, 1967). Thailand is a new locality record.

Oochoristica javaensis was first described from *G. mutilata, C. platyurus,* and *H. frenatus* from Java, Indonesia, by Kennedy et al. (1982). It has been reported from *G. mutilata* and the oceanic gecko *Gehyra oceanica* (Lesson, 1830) from Guam (Goldberg et al., 1998). The Philippine Islands and Thailand are new locality records.

Parapharyngodon maplestoni was originally described from the variable agama *Calotes versicolor* (Daudin, 1802) collected in Burma by Chatterji (1933). It has subsequently been reported from 2 agamid lizards, the Borneo bloodsucker *Bronchocela cristatella* (Kuhl, 1820) from Borneo and *C. versicolor,* as well as the Indian leaf-toed gecko *Hemidactylus flaviviridis* Ruppell, 1835, and *H. frenatus* of India. It also occurs in an anguid lizard (no common name) *Ophisaurus apodus* (Pallas, 1775) from Russia and a scincid lizard (no common name) *Sphenomorphus emigrans* (Lidth de Jeude, 1895) from Indonesia (Baker, 1987). Thailand is a new locality record.

Skrjabinelazia machidai was first described from Schlegel's Japanese gecko *Gekko japonicus* Duméril and Bibron, 1836, from Okinawa (Hasegawa, 1984) and has been reported from the mourning gecko *Lepidodactylus lugubris* (Duméril and Bibron, 1836) from Hawaii (Goldberg and Bursey, 1997). *Lepidodactylus aureolineatus* represents a new host record; *S. machidai* is the first helminth to be recorded for this lizard. The Philippine Islands represent a new locality record.

Spauligodon hemidactylus was originally described from *H. frenatus* from American Samoa by Bursey and Goldberg (1996), who also reported it in the same host from Fiji, Guam, Hawaii, Marshall Islands, Palau, Samoa, Solomon Islands, Society islands, and Vanuatu, as well as in this sample of *H. frenatus* from the Philippine Islands and Thailand. Schmidt and Kuntz (1972) reported *C. platyurus, H. frenatus,* and *H. garnotii* from the Philippine Islands to harbor *Skrjabinodon dossae* (Caballero, 1968) Schmidt and Kuntz, 1972 (USNPC 63242, 63243, and 63244, respectively). *Skrjabinodon dossae* was originally described from geckos of Madagascar (Caballero, 1968). In our examination of the voucher specimens (the males have caudal alae, characteristic of the genus *Spauligodon* but absent in males of the genus *Skrjabinodon* [see Petter and Quentin (1976)]), we found them to be indistinguishable from the paratypes of *S. hemidactylus* (USNPC 83572), which caused us to assign these specimens to *S. hemidactylus.* Our reassignment of the specimens collected by Schmidt and Kuntz (1972) invalidates the occurrence of *S. dossae* in the Philippine Islands. The host list of *S. hemidactylus* now contains 5 lizard species, *C. platyurus, G. mutilata, H. frenatus, H. garnotii,* and *H. typus.*

Knowledge of transmission and development of the helminth species found in this study is

limited and is based primarily on knowledge of related species. As oxyurids, species of *Parapharyngodon* and *Spauligodon* are monoxenous, and eggs dispersed into an environment with favorable conditions of humidity and temperature can become a continued source of eggs for oral infection (Anderson, 2000). It would not be suprising to find that most Philippine and Thailand lizard species harbor *P. maplestoni* and *S. hemidactylus.* Chabaud et al. (1988) claimed that females of *Skrjabinelazia galliardi* Chabaud, 1973, of Brazil produce 2 types of eggs: young females have thin-shelled eggs containing third-stage larvae thought to be autoinfective; older females have pigmented, thicker shelled eggs containing third-stage larvae thought to require an insect intermediate host. Digenetic trematodes are generally considered to require a mollusc intermediate host, and cyclophyllidean cestodes have arthropod intermediate hosts (Smyth, 1994). Thus infection by *S. machidai, P. ovatus,* and *O. javaensis* may be diet related.

Further studies of lizard species from the Philippine Islands and Thailand will be necessary before the diversity of helminths infecting these hosts and the structure of the helminth community can be known.

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IN MEMORIAM
W. HENRY LEIGH 1912–1997

W. Henry Leigh, longtime member of the Helminthological Society of Washington, died 2 July 1997 in Bradenton, Florida. Henry was 85 years old. He attended Wheaton College in Illinois for the bachelor's degree and received the M.A and Ph. D. (1938) degrees from the University of Illinois, where Harley Van Cleave was his major advisor. His dissertation work dealt with the life cycle of the digenetic trematode, *Glypthelmins quieta.* He discovered a new mode of infection of the final host, in this case the frog, by ingestion of its shed skin containing the metacercarial stage.

Henry served as an Aviation Physiologist during World War II and later taught Biology at Chicago City College. In 1949 he joined the faculty of the University of Miami in Coral Gables, Florida. He quickly rose through the academic ranks to full professor in 1954 and became Chairman of the Department of Biology in 1957. During those years the Biology Department was housed in the never quite finished Anastasia Hotel building. The hotel had failed following the 1926 hurricane and collapse of the real estate market in south Florida. Although spacious, it was never designed for laboratory use; nonetheless, undergraduate and graduate programs flourished.

Henry's research centered on trematode life cycles. He described a new species of bird schistosome with a marine dermatitis-producing cercaria and worked out its life cycle. Several life cycles of species of *Macroderoides* and of heterophyid trematodes were elucidated while he chaired the Biology Department, mentored graduate students, taught the general Parasitology course every year, and did research in his "spare time".

For those of us who had the good fortune to take it, Henry's Experimental Parasitology course was the best thing that ever happened in our graduate training. Henry had the students read from a list of papers from the primary literature that included true classics. Then these papers were discussed and evaluated by the class. Each week the students infected laboratory hosts with parasites or harvested parasites from animals previously infected. Techniques were learned: staining and whole mounting flatworms, making blood smears, embedding and sectioning infected tissues, electrophoresis, and egg counting methods. Principles were tested, such as the crowding effect of *Hymenolepis,* and the host eosinophil response to *Trichinella.* The students learned to maintain protozoan and helminth parasites in the laboratory. For each species a formal written report was required that was carefully critiqued and evaluated by Dr. Leigh. What a wonderful learning experience!

Henry collaborated with Dr. J. Walter Beck at the University of Miami Medical School for the award of an N.I.H. Parasitology Training Grant used to support graduate students and to support travel and training of biology graduate students and medical students in Costa Rica. Henry was so impressed with Costa Rica when he visited that he sought to establish a tropical biology research facility there. At his behest, the University of Miami invited several institutions to a meeting in early 1963 to form a consortium of universities for that purpose. Thus was born the Organization for Tropical Studies (OTS) with the University of Miami as a charter member and Henry as Treasurer. The La Selva property was soon purchased and the OTS station at La Selva has trained tropical biologists ever since.

Henry saw the Biology Department move into a new modern building in 1967 and he stepped down as department chair in 1970. He continued his teaching and research until he retired in 1977. He was proud of the growth and development of programs in the Biology Department, of his involvement with OTS, of his graduate students, and of his family. What a fine legacy.

Ralph P. Eckerlin
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*Theodor von Brand	1975	A. Morgan Golden	1989
*May Belle Chitwood	1975	Thomas K. Sawyer	1989
*Carlton M. Herman	1975	*J. Allen Scott	1990
Lloyd E. Rozeboom	1975	Judith H. Shaw	1990
*Albert L. Taylor	1975	Milford N. Lunde	1991
David R. Lincicome	1976	*Everett L. Schiller	1991
Margaret A. Stirewalt	1976	Harley G. Sheffield	1991
*Willard H. Wright	1976	Louis S. Diamond	1994
*Benjamin Schwartz	1976	Mary Hanson Pritchard	1994
*Mildred A. Doss	1977	John S. Mackiewicz	2000

*Deceased.

CONTENTS

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