Zoogeography of Digenetic Trematodes from West African Marine Fishes[1]

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ABSTRACT: Of the 107 species of trematodes found in West African (Mauritania to Gabon) marine fishes, 100 are allocated to 64 genera in 24 families while seven are immature didymozoids. Many of these genera are located in most of the world's seas with the exception of the polar seas; only five are endemic to West Africa. The data for the 41 species known from West Africa and elsewhere, and those morphologically closest to the 55 endemic species, indicate that they are very widely distributed, particularly in the Western and North Atlantic, and Mediterranean. Historical and present-day events concerning physical and biological environmental factors and their effects on actual and potential hosts as well as on life cycle stages of the trematodes have resulted in the geographical distribution reported. The distribution of marine fishes has been emphasized to explain in part the trematode distribution.

Studies on the geographical distribution of digenetic trematodes of marine fishes in various seas have been presented by Manter (1955, 1963, 1967), Szidat (1961), and Lebedev (1969), but West African waters were not included as sufficient data were not available until more recently. The digenetic trematodes of West African marine fishes (mainly shore and shelf inhabitants) have been reported by Dollfus (1929, 1937a, b, 1946, 1951, 1960), Dollfus and Capron (1958), Thomas (1959, 1960), Nikolaeva (1965), Fischthal and Thomas (1968a, b, c, 1969, 1970a, b, 1971, 1972a, b, c), and Fischthal and Williams (1971).

According to Ekman (1953) the West African tropical marine fauna in general is poorer than any other tropical coastal fauna (Western Atlantic, Indo-West Pacific, Eastern Pacific) because of lower water temperatures, the considerably shallower layer of tropical water, the sandy sea floor which is unsuitable for coral reef formation, and the open coast which provides little or no shelter from the surf. He further noted that the region contains only an insignificant number of endemic genera, although endemic species are much more numerous and represent a fairly high percentage of the total number in several groups. Data on the oceanography of tropical West Africa (Gulf of Guinea from 5° S to 15° N) and warm temperate Mauritania have been presented by Ekman (1953), Buchanan (1958), Longhurst (1962), and Ingham (1970).

Zoogeographical Distribution

Of the 107 species of trematodes found in West African fishes, 100 are allocated to 64 genera in 24 families while seven are immature didymozoids of unknown generic status (Appendix I). A list of the host species and the trematodes found in each is given in Appendix II. The data on the geographical distribution of the genera (Table 1) indicate that many are located in most of the world's seas with the exception of the Arctic and Antarctic, and that only five (7.8%) are endemic to West Africa (Table 2). The latter figure is comparable to that for the North Atlantic (7.5%). The data for the species (Tables 1, 3) indicate that the 41 species elsewhere known and those morphologically closest to the 55 endemic species are very widely distributed, but with much larger numbers occurring in the Western Atlantic, North Atlantic, and Mediterranean, and mostly in tropical and warm temperate waters. Intermediate numbers occur in the tropical Eastern Pacific, Japanese region, and Red Sea.

Discussion

Explanations for the geographical distribution of the trematodes noted above relate in

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Table 1. Summary of geographical distribution of 58 genera[1] and 96 species of digenetic trematodes from West African marine fishes. Under No. spp. the first column of numbers indicates how many of 41 West African species are also known from the locality stated; the second column indicates how many species morphologically most like the 55 endemic species are known from the locality stated.

Locality	No. genera	No. spp.
N. Europe	21	9— 3
British Isles		8— 2
Belgium, Norway		3— 0
Baltic Sea		5— 1
Eastern N. Atlantic	15	11— 2
Europe		10— 2
Morocco		1— 0
Madeira Isl.		1— 0
Iceland		1— 0
Western N. Atlantic	38	20—11
Canada		2— 1
U. S.		14— 9
Bimini		7— 3
Bermuda		7— 2
Bahama		2— 0
Azores	3	2— 0
Eastern S. Atlantic	18	8— 2
South-West Africa		8— 2
Western S. Atlantic	17	6— 1
Brazil		3— 1
Argentina		3— 0
Mediterranean–Black Sea	31	17— 6
Mediterranean		17— 6
Black Sea		7— 3
Caribbean	35	19—10
Gulf of Mexico	42	20—17
Arctic	9	1— 1
Barents Sea		1— 1
N. Pacific	25	6— 8
Bering Sea		2— 0
Okhotsk Sea		3— 1
Alaska		1— 0
Canada		1— 1
U. S.		5— 6
Tropical E. Pacific	31	12—10
Mexico		8—10
Panama		6— 3
Ecuador		4— 1
Galápagos Isl.	11	4— 7
Central Pacific	31	3— 4
Hawaii		3— 4
Line Isl.		1— 0
Japan	39	13—21
Japan		9—16
Korea		0— 2
Yellow Sea		2— 0
E. China Sea		1— 3
Taiwan		1— 2
East Indies	31	5— 8
S. China Sea		4— 0
Philippines		3— 7
Mariana Isl.		1— 0
Celebes		2— 3
Borneo		0— 1
Indian Ocean	26	9— 7
India		4— 6
Ceylon		0— 1
Madagascar		1— 1
Gulf of Aden		5— 0
Red Sea	24	12— 4
New Zealand–Australia	30	8— 8
Australia		1— 3
Tasmania		1— 0
New Zealand		5— 0
New Caledonia		2— 2
Fiji Isl.		0— 3
Antarctic	4	0— 0

[1] Endemic genera excluded are: *Diplomonorcheides* Thomas, 1959; *Elopsium* Fischthal and Thomas, 1972; *Neochoanodera* Fischthal and Thomas, 1970; *Neolepocreadium* Thomas, 1960; *Pedunculotrema* Fischthal and Thomas, 1970. *Palaeorchis* Szidat, 1943, has only freshwater fishes from Japan and Europe as hosts.

great part to historical and present-day events concerning physical and biological environmental factors (geological occurrences, climates, temperatures, currents, salinity, bottom conditions, shore configurations, animal and plant populations, food chain, etc.) and their effects on actual and potential hosts as well as on stages in the life cycles of the trematodes. Migrations have been accomplished by adult fishes and mollusks and their pelagic larvae; mollusks probably have moved long distances via currents while attached to floating vegetation or debris.

Ekman (1953) noted that an immense Tethys Sea, already existing in the Lower Cambrian and continuing into the late Tertiary, included the Eastern Pacific, tropical Atlantic, Mediterranean, and Indo-West Pacific. The fauna of this sea was part of one major unit, the Tethys fauna, and was essentially tropical and more homogeneous than the present-day tropical–subtropical shelf fauna. This probably applied to the trematodes as well. Valentine (1967) noted that fluctuating climates act as a sort of diversity pump, enhancing species diversity during climatic deterioration and retaining some fraction of the new lineages during climatic improvement. He indicated that the Tethyan fauna was enriched by this process acting within the Tethys and also by recruitment of lineages from the extra-Tethyan provincial margins, especially during improving climatic phases. Trematodes probably were similarly affected.

During the course of geological time various barriers arose to divide the Tethys Sea into more or less separate seas. Other seas were also affected by the appearance or removal of

Table 2. Number of genera and per cent endemic of digenetic trematodes of marine fishes from various geographical regions.[1]

Locality	No. genera	% genera endemic
N. Atlantic	58	7.5
Tropical W. Atlantic	145	25
Mediterranean–Atlantic	69	23
Red Sea–Gulf of Aden	38	25
India	55	24
East Indies	84	31
Japan	168	32
New Zealand–Australia	76	17
Hawaii	169	40
Tropical E. Pacific	78	11
W. Africa	64	7.8

[1] Figures for Hawaii based on data by Yamaguti (1970); others, except W. Africa, from Lebedev (1969).

Table 3. Summary of geographical distribution in littoral provinces (Hedgpeth, 1957) of digenetic trematodes of West African marine fishes.

Province	No. of 41 spp. elsewhere known	No. of spp. morphologically closest to 55 endemic spp.
Arctic	3	2
Boreal	8	12
Antiboreal	4	1
Boreal–Antiboreal	6	1
Warm temperate	33	27
Tropic	32	36

barriers. Ruggieri (1967) noted that the separation of the Mediterranean from the Indian Ocean occurred during the Miocene, but Tortonese (1964) indicated the Pliocene. The former author further noted that towards the end of the Miocene the two straits connecting the Mediterranean with the Atlantic disappeared and the Mediterranean was transformed into a series of lagoons which either dried up or became gradually desalinified, thus decimating its marine fauna. During the Pliocene the Gibraltar straits formed and the Atlantic flowed anew into the Mediterranean, reestablishing truly marine conditions. Those elements of the Miocene fauna that had persisted in the Atlantic outside Gibraltar were reintroduced (with their trematodes) to the Mediterranean together with new species previously absent from the area; some of the latter may have been from West Africa. Ruggieri indicated that the Atlantic facing the Gibraltar straits probably was the true asylum for the Indo-Pacific relicts (with their trematodes) during the Miocene salinity crisis in the Mediterranean; some of these relicts along with other Mediterranean fishes may have migrated southward to West Africa during this time.

Ekman (1953), Briggs (1966, 1970), and Ruggieri (1967) reported that during the late Tertiary and early Quaternary there was a considerable change in the tropical nature of the North Atlantic and Mediterranean due primarily to the advent of colder climates. The northern fauna (with their trematodes) migrated southward when possible and simultaneously the tropical fauna disappeared in part. Much of the displaced Mediterranean fauna (with their trematodes) migrated to West Africa which still supports some of them. On the American side of the Atlantic (Florida, Georgia, neighboring states) colder climates of the Miocene also affected the tropical fauna but not as catastrophically as in the North and Eastern Atlantic and the Mediterranean. The major difference was that during the Pliocene and Quaternary the tropical climate and fauna reappeared on the American side, whereas only an insignificant part reappeared in tropical West Africa and especially the Mediterranean. Tortonese (1964) noted that the largest group comprising the present-day Mediterranean fish fauna (about 550 species) is Atlantic (boreal, West African, or amphi-Atlantic); other species are endemic (about 70 or 13%), cosmopolitan, or Indo-Pacific. In great part it is because of the historical events related above that significantly low percentages of endemic genera generally occur in the fauna of West Africa, the Mediterranean, and the North Atlantic, and also why many identical as well as closely related species of trematodes and other groups are found in these regions.

Ben-Tuvia (1966) indicated that at least 24 of about 800 species of fishes have migrated from the Red Sea to the Mediterranean since the opening of the Suez Canal in 1869, some as far west as Lampedusa near Sicily; no reliable records exist of a reverse migration although a few are found in the Suez Canal. Some 18 of the Red Sea species are now among the more common forms along the Mediterranean coast of Israel and nine are sufficiently abundant to be commercially exploited. Some of the trematodes from Red Sea fishes possibly have become established in closely related

Mediterranean fishes or in other fishes which feed on the same intermediate hosts. Wide-ranging Mediterranean fishes then may have moved into the Atlantic and to West Africa.

Briggs (1970) reported that during the Oligocene some boreal species (including fishes and their trematodes) north of the Bering Land Bridge moved out of the Arctic Basin to the North Atlantic. During the Miocene and again in the Pliocene the Bering Land Bridge disappeared, opening a seaway between the North Pacific and Arctic. The movement of species (including trematodes) was (and still is) predominantly northward from the Pacific to the Arctic Ocean to the North Atlantic. These events explain in great part Manter's (1963) observation that of 54 species of digenetic trematodes of marine fishes from the British Columbian region of Canada, 21 (40%) also occur in the North Atlantic. Briggs also noted that present-day species in the North Atlantic have broad latitudinal ranges. Some, with their trematodes, occur in West Africa.

Briggs (1967) observed that the Mid-Atlantic Barrier is a broad, deepwater expanse of ocean separating the West African tropics from those of the Western Atlantic. About 380 species of tropical shore fishes are found in the Eastern Atlantic and 900 species in the Western Atlantic, giving a total of 1,280. About 118 (9.2%) of this total are trans-Atlantic species, making the barrier about 91% effective. The migration has been and still is from west to east. The 118 trans-Atlantic species comprise 31% of the tropical West African shore fish fauna; many genera are also in common. Briggs noted further that West African invertebrate groups also show appreciable percentages of the species as being trans-Atlantic (6% of the prosobranch mollusks). These facts serve greatly to explain why such a large number of trematodes species from West African fishes are identical with or closely related to those in the tropical Western Atlantic and its neighboring warm temperate zones.

Briggs (1961, 1967) and Rosenblatt (1967) have discussed the New World Land Barrier. The former author noted that of the total number of shore fish species (about 1,000) that probably occur on both sides of Central America, only about 12 are identical (excluding 13 circumtropical and a few euryhaline species); this barrier is about 99% effective. Rosenblatt reported that the shore fish fauna of both sides of the Americas show great similarity at the family, subfamily, and generic levels, but not at the species level; however, there are a large number of pairs of sibling species. He further noted that a fair number of genera in the Western Atlantic are found also in the Indo-West Pacific. About 10 genera (2%) of the total for the Western Atlantic are common to and limited to the tropical Atlantic. The historical events relating to the continuous Tethys Sea and subsequent formation of the South and Central American land bridges during the Pliocene to separate the Atlantic and Pacific account in great part for the present-day distribution of fishes in this region. This also explains in part Manter's (1963) observation that of 226 species of digenetic trematodes from Caribbean fishes, about 18% also occur in the tropical Eastern Pacific. It also explains in part why many trematodes from West African fishes occur in the Eastern Pacific and Indo-West Pacific since, as noted above, about 31% of the West African shore fish species also occur in the tropical Western Atlantic and a fair number of genera from the latter locality also are found in the Indo-Pacific.

The Old World Land Barrier has been 98% effective in separating the shore fishes of the Indo-West Pacific from the Atlantic. Briggs (1967) indicated that the fish fauna of tropical Southeast Africa in the area between Mozambique and Algoa Bay numbers about 1,000 species and in tropical West Africa about 380, a total of 1,380. Migration has been from east to west around the Cape of Good Hope, involving only 31 species (8 to both sides of the Atlantic; 4 confined to West Africa; 3 to St. Helena Island; 16 circumtropical); however, many genera are in common. This distribution of fishes has to some extent affected the distribution of their trematodes.

Briggs (1961, 1964, 1967) noted that the East Pacific Barrier is a vast stretch of about 3,000 miles of deepwater lying between Polynesia and America. He reported 62 trans-

Pacific species of shore fishes (13 of which are circumtropical) out of a total of about 1,037 species for both regions (about 387 species assumed to be in the Line Islands lying at easternmost Polynesia in the Equatorial Countercurrent; about 650 species between southern Mexico and Peru); many common genera are in the two regions. This barrier is 94% effective. The successful migrations were recent or current invasions, and were almost exclusively from west to east via the countercurrent. Briggs (1967) related that 18 species of mollusks are trans-Pacific. Some of the trematodes probably moved across this barrier with their vertebrate and molluscan hosts.

Briggs (1960) reported that at least 107 species of marine fishes form homogeneous worldwide circumtropical species populations. Additional species are worldwide but form subspecific populations in parts of their range. Other species are nearly circumtropical but have not been found in the Eastern Pacific. A majority of the 107 fish species can be considered to be typical of the open seas (90 pelagic, 14 littoral, 3 benthic). In West Africa five of these 107 species were found infected with at least one species of trematode which occurs in the same host species elsewhere. The circumtropical (or nearly so) distribution of many genera and species of fishes has aided considerably the wide distribution of their trematodes; additionally, new and more localized hosts have been acquired by some.

Briggs (1967) summarized the information concerning tropical marine fishes and invertebrates as follows: "There is no doubt that the Indo-West Pacific Region has served as *the* evolutionary and distributional center for the entire marine tropics. Its fauna is almost unbelievably rich with, for example, more than 3,000 species of shore fishes. It seems clear that the unusually stable ecosystems and high level of competition provide the proper environment for the evolution of dominant species that can successfully invade the other regions. From the Indo-West Pacific, dominant species migrate eastward across the open ocean to America, westward around the Cape of Good Hope into the Atlantic, and northward through the Suez Canal into the Mediterranean. Successful reciprocal migrations are, at least, very rare and may be completely lacking. Furthermore, judging from the general indications of relationship among the four great tropical faunas, this process has been going on for many millions of years. Some of the dominant species are so successful that they have been able to establish and maintain circumtropical distributions (indicating more or less regular migrations across the East Pacific, Old World land, and mid-Atlantic barriers). The Western Atlantic tropics may be considered a secondary center of evolutionary radiation. Many species produced in this area have proved capable of migrating eastward to colonize the Eastern Atlantic region. However, species originating in the Eastern Atlantic are apparently incapable of successfully invading the western side. Again, the advantage seems to lie with the area that possesses the richer fauna and higher level of competition." The distributions exhibited by the digenetic trematodes of marine fishes from West Africa and from other regions are in agreement with Briggs' observations and conclusions.

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Appendix I

List of digenetic trematodes from West African marine fishes, and other localities from which known

Acanthocolpidae. *Stephanostomum africanum* Fischthal and Williams, 1971. *S. bicoronatum* (Stossich, 1883) Manter, 1940—also Mediterranean, Tyrrhenian, Adriatic, Black, Yellow, E. China Seas. *S. casum* (Linton, 1910) McFarlane, 1934—also Bermuda; Bahama; Caribbean; Gulf of Mexico; U. S. Atlantic; Mexican, Canadian Pacific; Galápagos; Philippines; New Caledonia; Red Sea. *S. coryphaenae* Manter, 1947—also Bimini; Caribbean; Gulf of Mexico. *S. ghanense* Fischthal and Thomas, 1968. *S. megacephalum* Manter, 1940—also Caribbean; Gulf of Mexico; Mexican, Panama, Ecuador Pacific; Red Sea. *S. sierraleonense* Fischthal and Williams, 1971. *S. trachinoti* Fischthal and Thomas, 1968. Azygiidae. *Otodistomum veliporum* (Creplin, 1837) Stafford, 1904—also Mediterranean, Black Seas; European, Moroccan, U. S., Canadian Atlantic; Iceland; British Isles; North, Baltic Seas; Argentina; New Zealand; Sea of Japan; Alaska; U. S., Mexican Pacific. Bucephalidae. *Bucephaloides ghanensis* Fischthal and Thomas, 1968. *B. gracilescens* (Rudolphi, 1819) Hopkins, 1954—also Mediterranean, Adriatic Seas; British Isles; South-West Africa; Barents Sea; Far Eastern Seas of Siberia. *B. ovatus* (Linton, 1900) Hopkins, 1954—also U. S. Atlantic; Panama Pacific. *Prosorhynchus aculeatus* Odhner, 1905, metacercaria—also Mediterranean, North, Baltic Seas; British Isles; Japan; Galápagos. *P. caudovatus* Manter, 1940—also Suez. *Rhipidocotyle ghanensis* Fischthal and Thomas, 1968. *R. senegalensis* Fischthal and Thomas, 1972. Cryptogonimidae.[1] *Paracryptogonimus ghanensis* Fischthal and Thomas, 1968. Didymozoidae. *Allonematobothrium ghanense* Fischthal and Thomas, 1968. Didymozoidae (*Monilicaecum*) larvae I Nikolaeva, 1965—also South-West Africa. Didymozoidae gen. sp. larvae V Nikolaeva, 1962—also Red Sea. Immature Didymozoid B Fischthal and Kuntz, 1964—also Philippines. Immature Didymozoid D Fischthal and Thomas, 1968. Immature Didymozoid E Fischthal and Thomas, 1968. Immature Didymozoid F Fischthal and Thomas, 1968. Immature Didymozoid G Fischthal and Thomas, 1968. Enenteridae. *Cadenatella brumpti* (Dollfus, 1946) Nahhas and Cable, 1964—also Bimini. *C. cadenati* (Dollfus, 1946) Nagaty, 1948. *Enenterum pimelepteri* Nagaty, 1942—also Red Sea. Fellodistomatidae. *Elopsium ghanense* Fischthal and Thomas, 1972. *Markevitschiella* sp. Fischthal and Thomas, 1968. *Monascus typicus* (Odhner, 1911) Looss, 1912—also Mediterranean, Adriatic, Black, Red Seas; Gulf of Aden; India. *Steringotrema divergens* (Rudolphi, 1809) Odhner, 1911—also Mediterranean, Tyrrhenian, Baltic Seas; British Isles. Gorgoderidae. *Nagmia africana* Fischthal and Thomas, 1972. *N. senegalensis* Fischthal and Thomas, 1972. Halipegidae. *Gonocercella trachinoti* (MacCallum, 1913) Yamaguti, 1954—also U. S. Atlantic; Gulf of Mexico. Haploporidae. *Megasolena hysterospina* (Manter, 1931) Overstreet, 1969—also U. S. Atlantic; Caribbean; Gulf of Mexico. Hemiuridae. *Adinosoma robusta* (Manter, 1934) Manter, 1947—also Gulf of Mexico. *Aponurus lagunculus* Looss, 1907—also Mediterranean, Tyrrhenian, Adriatic, Black Seas; South-West Africa; Gulf of Mexico; U. S., Mexican Pacific; Celebes; S. China Sea; Gulf of Aden; Red Sea. *Dinurus barbatus* (Cohn, 1903) Looss, 1907—also European Atlantic; Caribbean; Gulf of Mexico; Mexican, Panama Pacific. *D. breviductus* Looss, 1907—also

[1] *Siphodera ghanensis* described by Fischthal and Thomas (1968c) is from freshwater fishes from Ghana and Gabon, but the two other species in the genus, *S. vinaledwardsii* (Linton, 1901) Linton, 1910, and *S. cirrhiti* Yamaguti, 1970, are from marine fishes.

European, U. S. Atlantic; Caribbean; Gulf of Mexico; Argentina; Red Sea. *D. tornatus* (Rudolphi, 1819) Looss, 1907—also European, U. S. Atlantic; Azores; Caribbean; Gulf of Mexico; Gulf of Aden; Red Sea. *Ectenurus lepidus* Looss, 1907—also Mediterranean, Tyrrhenian, Adriatic, Black Seas; South-West Africa; Caribbean; Brazil; Hawaii; New Zealand; Gulf of Aden. *E. virgulus* Linton, 1910—also Bimini; Bermuda; Bahama; U. S. Atlantic; Caribbean; Gulf of Mexico; Argentina; Gulf of Aden; Red Sea. *Lecithaster africanus* Fischthal and Thomas, 1971. *L. ghanensis* Fischthal and Thomas, 1971. *Lecithochirium ghanense* Fischthal and Thomas, 1972. *L. microstomum* Chandler, 1935—also U. S. Atlantic; Caribbean; Gulf of Mexico; Brazil; Mexican, Panama Pacific; Galápagos; Taiwan; Madagascar. *Lecithocladium augustiovum* Yamaguti, 1953—also Philippines; Celebes; Red Sea. *L. excisum* (Rudolphi, 1819) Lühe, 1901—also Mediterranean, Adriatic, Black, Irish, North, Baltic Seas; European, U. S. Atlantic; South-West Africa; Gulf of Mexico; Japan; S. China Sea; New Zealand. *L. mecoderum* Fischthal and Thomas, 1971. *L. unibulbolabrum* Fischthal and Thomas, 1971. *Parahemiurus merus* (Linton, 1910) Woolcock, 1935—also South-West Africa; U. S. Atlantic; Bimini; Bermuda; Caribbean; Gulf of Mexico; Brazil; U. S., Ecuador Pacific; Bering, Okhotsk, S. China Seas; Japan. *Prosorchis ghanensis* Fischthal and Thomas, 1972. *Sterrhurus ghanensis* Fischthal and Thomas, 1972. *S. fusiformis* (Lühe, 1901) Looss, 1907—also Mediterranean, Adriatic Seas; British Isles; Azores; European, U. S. Atlantic; Bermuda; Caribbean; Gulf of Mexico; Ecuador Pacific; Japan. *S. musculus* Looss, 1907—also Mediterranean, Adriatic, Black Seas; Bimini; Bermuda; U. S. Atlantic; Caribbean; Gulf of Mexico; Japan. *Tubulovesicula lindbergi* (Layman, 1930) Yamaguti, 1934—also Madeira Isl.; Canadian, U. S., Panama Pacific; Bering, Okhotsk, S. China, Red Seas; Japan. Hirudinellidae. *Hirudinella ventricosa* (Pallas, 1774) Baird, 1853—also Bimini; Bermuda; Caribbean; Gulf of Mexico; Mexican, Panama, Ecuador Pacific; Galápagos; Hawaii; Line Isl.; Mariana Isl. Lepocreadiidae. *Aephnidiogenes africanus* Fischthal and Thomas, 1972. *A. senegalensis* Dollfus and Capron, 1958 also India. *Diploproctodaeum ghanense* (Fischthal and Thomas, 1970) Fischthal and Thomas, 1972. *D. haustrum* (MacCallum, 1918) LaRue, 1926—also Bimini; U. S. Atlantic; Caribbean; Hawaii. *Holorchis legendrei* Dollfus, 1946—also Mediterranean; European Atlantic. *Homalometron senegalense* Fischthal and Thomas, 1972. *Lepidapedon ghanense* Fischthal and Thomas, 1970. *Lepocreadioides cynoglossi* Fischthal and Thomas, 1970. *Lepocreadium ghanense* Fischthal and Thomas, 1970. *Neochoanodera ghanensis* Fischthal and Thomas, 1970. *Neolepocreadium caballeroi* Thomas, 1960. *Opechona bacillaris* (Molin, 1859) Looss, 1907—also Adriatic, Black, Baltic, Red Seas; European Atlantic; South-West Africa; British Isles India; New Zealand–Australia region. *O. ghanensis* Fischthal and Thomas, 1970. *O. pseudobacillaris* Fischthal and Thomas, 1970. *Pseudocreadium ghanense* Fischthal and Thomas, 1970. Monodhelminthidae. *Monodhelmis torpedinis* Dollfus, 1937. Monorchiidae. *Diplomonorcheides magnacetabulum* Thomas, 1959. *Lasiotocus accraensis* Fischthal and Thomas, 1969. *L. attenuatus* Fischthal and Thomas, 1969. *L. chaetodipteri* Thomas, 1959. *L. cynoglossi* Thomas, 1959. *L. ghanensis* Fischthal and Thomas, 1969. *L. synapturae* Fischthal and Thomas, 1969. *Palaeorchis senegalensis* Fischthal and Thomas, 1972. *Parahurleytrema trachinoti* (Thomas, 1959) Nahhas and Powell, 1965. *Proctotrema amphitruncatum* Fischthal and Thomas, 1969. *Proctotrematoides ophichthi* Fischthal and Thomas, 1969. Opecoelidae. *Coitocaecum cadenati* Dollfus, 1960. *Helicometra fasciata* (Rudolphi, 1819) Odhner, 1902—also Mediterranean, Black Seas; N. Atlantic; South-West Africa; Caribbean; Mexican Pacific; Japan; New Caledonia; Tasmania; Red Sea. *Pedunculotrema capecoastense* Fischthal and Thomas, 1970. *P. ghanense* Fischthal and Thomas, 1970. *Plagioporus gerridis* Fischthal and Thomas, 1970. *Podocotyle temensis* Fischthal and Thomas, 1970. *Podocotyloides chloroscombri* Fischthal and Thomas, 1970. *Poracanthium ghanense* Fischthal and Thomas, 1970. *Pseudopecoelus ghanensis* Fischthal and Thomas, 1970. *P. tortugae* von Wicklen, 1946—also Caribbean; Gulf of Mexico. *P. vulgaris* (Manter, 1934)

von Wicklen, 1946—also Gulf of Mexico; New Zealand. Opistholebetidae. *Pycnadena africana* Fischthal and Williams, 1971. *Pycnadenoides ghanensis* Fischthal and Thomas, 1968. *P. senegalensis* Fischthal and Thomas, 1972. Pelorohelminthidae. *Pelorohelmins ghanensis* Fischthal and Thomas, 1968. Pleorchiidae. *Pleorchis ghanensis* Fischthal and Thomas, 1968. Proctoecidae. *Mesolecitha ghanensis* Fischthal and Thomas, 1968. Ptychogonimidae. *Ptychogonimus megastomus* (Rudolphi, 1819) Lühe, 1900—also Mediterranean, Tyrrhenian, Adriatic Seas; British Isles; European Atlantic; North Sea; Bermuda; Caribbean; Japan; New Zealand. Sclerodistomatidae. *Sclerodistomum italicum* (Stossich, 1893) Looss, 1912—also Adriatic Sea. Syncoeliidae. *Syncoelium katuwo* Yamaguti, 1936 —also U. S. Pacific; Japan. Zoogonidae. *Diphtherostomum anisotremi* Nahhas and Cable, 1964—also Caribbean; Gulf of Mexico. *Zoogonus mirus* Looss, 1901—also Adriatic Sea; Gulf of Marseille.

Appendix II

Alphabetical list of host species with trematodes found in each[1]

Acanthocybium solandri (Cuv. and Val.), Scombridae
  Hirudinella ventricosa (G)
Acanthurus monroviae (Steind.), Acanthuridae
  Mesolecitha ghanensis (G)
  Prosorchis ghanensis (G)
Alutera punctata Cuv., Monacanthidae
  Diploproctodaeum haustrum (S)
Antennarius commersonii (Lac.), Antennariidae
  Immature Didymozoid E (S)
  Rhipidocotyle senegalensis (S)
Arius heudeloti Cuv. and Val., Ariidae
  Monodhelmis torpedinis (G)
Arius latiscutatus Günther
  Pelorohelmins ghanensis (G)
Arnoglossus imperialis (Raf.), Bothidae
  Lecithocladium excisum (S)
Bathygobius soporator (Cuv. and Val.), Gobiidae
  Helicometra fasciata (G)
Batrachoides liberiensis (Steind.), Batrachoididae
  Sterrhurus ghanensis (G)
Blennius sanguinolentus Pallas, Blenniidae
  Prosorhynchus aculeatus, metacercaria (S)
Brachydeuterus auritus (Cuv. and Val.), Pomadasyidae
  Didymozoidae (*Monilicaecum*) larvae I (G)
  Immature Didymozoid B (G)
  Immature Didymozoid E (G)
  Zoogonus mirus (G)
Caesiomorus glaucus (L.), Carangidae
  Lecithocladium excisum (G)
  Opechona ghanensis (G)
  Opechona pseudobacillaris (G)
Capros aper (L.), Caproidae
  Pycnadenoides senegalensis (S)
Caranx africanus Steind., Carangidae
  Ectenurus virgulus (G)
  Immature Didymozoid E (G)
Caranx crysos (Mitchill)
  Ectenurus virgulus (G)
Caranx hippos (L.)
  Parahemiurus merus (G)
  Poracanthium ghanense (G)
  Stephanostomum megacephalum (G)
Cephalacanthus volitans (L.), Dactylopteridae
  Lecithocladium unibulbolabrum (G) (S)
  Sterrhurus ghanensis (G)
  Sterrhurus musculus (G)
Chaetodipterus lippei Steind., Ephippidae
  Lasiotocus chaetodipteri (G)
  Megasolena hysterospina (SL)
  Neochoanodera ghanensis (G)
Chloroscombrus chrysurus (L.), Carangidae
  Ectenurus lepidus (G)
  Monascus typicus (G)
  Podocotyloides chloroscombri (G)
Clupisudis niloticus (Ehrenberg),[2] Osteoglossidae
  Sterrhurus musculus (G)
Corvina nigra Val., Sciaenidae
  Stephanostomum bicoronatum (S)
Coryphaena hippurus L., Coryphaenidae
  Dinurus barbatus (G)
  Dinurus breviductus (G) (S)
  Dinurus tornatus (G)
  Stephanostomum coryphaenae (G)
Cynoglossus canariensis Steind., Cynoglossidae

[1] Trematodes indicated by (C) are from Cameroon, (G) Ghana, (M) Mauritania, (S) Senegal, and (SL) Sierra Leone.

[2] Freshwater fish.

Diplomonorcheides magnacetabulum (G)
Cynoglossus goreensis Steind.
Diplomonorcheides magnacetabulum (G)
Immature Didymozoid E (G)
Lasiotocus cynoglossi (G)
Lepocreadioides ghanensis (G)
Parahemiurus merus (G)
Cynoglossus senegalensis (Kaup)
Diplomonorcheides magnacetabulum (G)
Immature Didymozoid E (G)
Lasiotocus cynoglossi (G) (SL)
Lepocreadioides ghanensis (SL)
Cynoscion macrognathus (Bleeker), Sciaenidae
Immature Didymozoid E (G)
Pleorchis ghanensis (G)
Pseudocreadium ghanense (G)
Pseudopecoelus ghanensis (G)
Cypselurus heterurus (Raf.), Exocoetidae
Immature Didymozoid F (G)
Cypselurus lutkeni Jordan and Evermann
Lecithaster ghanensis (G)
Decapterus rhonchus (Geoff.), Carangidae
Ectenurus lepidus (G)
Monascus typicus (G)
Dentex canariensis Steind., Sparidae
Sclerodistomum italicum (S)
Diagramma mediterraneum Guichenot, Pomadasyidae
Holorchis legendrei (S)
Drepane punctata (L.), Drepanidae
Pseudocreadium ghanense (G)
Pycnadenoides ghanensis (G)
Elops lacerta Cuv. and Val., Elopidae
Elopsium ghanense (G)
Engraulis encrasicholus (L.), Engraulidae
Parahemiurus merus (G)
Ephippion guttifer (Bennett), Tetraodontidae
Diploproctodaeum ghanense (G)
Epinephelus aeneus (Geoff.), Serranidae
Allonematobothrium ghanense (G)
Lepidapedon ghanense (G)
Sterrhurus musculus (G)
Epinephelus goreensis (Cuv. and Val.)
Podocotyle temensis (G)
Prosorhynchus caudovatus (G)
Ethmalosa dorsalis (Cuv. and Val.), Clupeidae
Parahemiurus merus (G)
Euthynnus alleteratus (Raf.), Scombridae
Immature Didymozoid B (G)
Lecithochirium microstomum (G)
Syncoelium katuwo (S)
Fodiator acutus (Val.), Exocoetidae
Neolepocreadium caballeroi (G)
Galeoides decadactylus (Bloch), Polynemidae
Ectenurus lepidus (G)
Lecithaster africanus (G)
Lecithochirium ghanense (G)
Lecithocladium excisum (G)
Lecithocladium mecoderum (G)
Poracanthium ghanense (G) (SL)
Stephanostomum sierraleonense (SL)
Sterrhurus musculus (G)
Galeorhinus mustelus (L.), Carcharhinidae
Ptychogonimus megastomus (M)
Gephyroberyx darwini (Johnson), Trachichthyidae
Adinosoma robusta (S)
Gerres melanopterus Bleeker, Liognathidae
Pedunculotrema ghanense (G)
Gerres nigri Günther
Plagioporus gerridis (G)
Glyphisodon saxatilis (L.), Pomacentridae
Helicometra fasciata (G)
Gymnothorax vicinus (Castelnau), Muraenidae
Sterrhurus fusiformis (G)
Hydrocyon brevis Günther,[2] Characidae
Tubulovesicula lindbergi (G)
Hyporhamphus calabaricus (Günther), Hemirhamphidae
Lecithaster ghanensis (G)
Ilisha melanota Derscheid, Clupeidae
Helicometra fasciata (G)
Lecithocladium excisum (G)
Kyphosus sectatrix (L.), Kyphosidae
Cadenatella brumpti (S)
Cadenatella cadenati (S)
Enenterum pimelepteri (S)
Labrax punctatus (Bloch), Serranidae
Acphnidiogenes senegalensis (S)
Labrisomus nuchipinnis (Quoy and Gaimard), Clinidae
Helicometra fasciata (G)
Lagocephalus laevigatus L., Tetraodontidae
Diploproctodaeum ghanense (G)
Immature Didymozoid D (G)
Lecithochirium ghanense (G)
Parahemiurus merus (G)
Larimus peli Bleeker, Sciaenidae
Helicometra fasciata (G)
Immature Didymozoid G (G)
Pseudopecoelus tortugae (G)

[2] Freshwater fish.

Lethrinus atlanticus Cuv. and Val., Lethrinidae
Lasiotocus accraensis (G)
Lobotes surinamensis (Bloch), Lobotidae
Bucephaloides ovatus (C)
Lophius sp., Lophiidae
Bucephaloides gracilescens (S)
Lutjanus guineensis Bleeker, Lutjanidae
Paracryptogonimus ghanensis (G)
Lutjanus maltzani (Steind.)
Prosorhynchus caudovatus (G)
Lutjanus modestus Bleeker
Helicometra fasciata (G)
Pycnadena africana (SL)
Stephanostomum casum (G)
Melanoglaea ventralis Barnard, Ateleopidae
Coitocaecum cadenati (S)
Mustelus canis (Mitchill), Carcharhinidae
Ptychogonimus megastomus (S)
Myxus curvidens (Val.), Mugilidae
Stephanostomum megacephalum (G)
Narcacion torpedo Klein, Torpedinidae
Monodhelmis torpedinis (M)
Ophichthus semicinctus (Richardson), Ophichthyidae
Proctotrematoides ophichthi (G)
Otolithus brachygnathus (Bleeker), Sciaenidae
Stephanostomum africanum (S)
Pagellus bogaraveo (Brünnich), Sparidae
Parahemiurus merus (S)
Pycnadenoides senegalensis (S)
Steringotrema divergens (S)
Pagrus ehrenbergi Cuv. and Val., Sparidae
Markevitschiella sp. (G)
Paraconger notialis Kantor, Congridae
Sterrhurus ghanensis (G)
Parakuhlia boulengeri Pellegrin, Kuhliidae
Holorchis legendrei (S)
Pentanemus quinquarius (L.), Polynemidae
Poracanthium ghanense (G)
Periophthalmus koelreuteri (Pallas), Gobiidae
Lecithaster ghanensis (G)
Phyllogramma regani Pellegrin, Muraenesocidae
Sterrhurus ghanensis (G)
Tubulovesicula lindbergi (G)
Pomadasys jubelini (Cuv. and Val.), Pomadasyidae
Aephnidiogenes senegalensis (G) (SL)
Diphtherostomum anisotremi (G)
Immature Didymozoid E (G)
Lasiotocus attenuatus (G)
Lasiotocus chaetodipteri (G)
Paracryptogonimus ghanensis (G)
Pedunculotrema capecoastense (G)
Pleorchis ghanensis (G)
Proctotrema amphitruncatum (G)
Pycnadenoides ghanensis (G)
Pomadasys suillus (Val.)
Palaeorchis senegalensis (S)
Psettodes belcheri Bennett, Psettodidae
Immature Didymozoid E (G)
Parahemiurus merus (G)
Rhipidocotyle ghanensis (G)
Sterrhurus ghanensis (G)
Pseudotolithus senegalensis (Günther), Sciaenidae
Stephanostomum africanum (SL)
Pseudupeneus cyclostomus (Lac.), Mullidae
Didymozoidae gen. sp. larvae V (G)
Pteroplatea micrura (Schneider), Trygonidae
Immature Didymozoid E (G)
Rhinobatus albomaculatus Norman, Rhinobatidae
Immature Didymozoid E (G)
Poracanthium ghanense (G)
Rhinoptera marginata (Geoff.), Myliobatidae
Nagmia africana (S)
Rupiscartes atlanticus (Val.), Blenniidae
Prosorhynchus aculeatus, metacercaria (S)
Sardinella cameronensis Regan, Clupeidae
Parahemiurus merus (G)
Sargus cervinus Val., Sparidae
Aephnidiogenes africanus (S)
Sciaena sp., Sciaenidae
Sterrhurus ghanensis (G)
Scomber colias Gmelin, Carangidae
Lecithocladium excisum (G)
Lepocreadium ghanense (G)
Opechona bacillaris (G)
Scomberomorus tritor (Cuv. and Val.), Scombridae
Bucephaloides ghanensis (G)
Didymozoidae (*Monilicaecum*) larvae I (G)
Immature Didymozoid E (G)
Lecithochirium ghanense (G)
Lecithocladium excisum (G)
Scorpaena scrofa L., Scorpaenidae
Helicometra fasciata (S)
Pseudopecoelus vulgaris (S)
Scorpaena senegalensis Steind.
Sterrhurus musculus (G)
Scyris alexandrinus (Geoff.), Carangidae
Immature Didymozoid E (G)

Selar crumenophthalmus (Bloch), Carangidae
Ectenurus virgulus (S)
Lecithochirium ghanense (S)
Monascus typicus (G) (S)
Parahemiurus merus (G)
Sterrhurus musculus (G)
Seriola dumerili (Risso), Carangidae
Sclerodistomum italicum (S)
Smaris melanurus Val., Maenidae
Holorchis legendrei (S)
Solea hexophthalma Bennett, Soleidae
Homalometron senegalense (S)
Sparisoma cretense (L.), Sparisomidae
Prosorhynchus aculeatus, metacercaria (S)
Syacium micrurum Ranzini, Bothidae
Sterrhurus ghanensis (G)
Synaptura lusitanica Capello, Soleidae
Lasiotocus cynoglossi (G)
Lasiotocus ghanensis (G)
Lasiotocus synapturae (G)
Temnodon saltator Val., Pomacentridae
Sclerodistomum italicum (S)
Tetraodon pustulus Murray, Tetraodontidae
Diploproctodaeum ghanense (G)
Torpedo narce Risso, Torpedinidae
Otodistomum veliporum (M)
Trachinocephalus myops (Schneider), Synodidae
Lecithochirium ghanense (G)
Sterrhurus ghanensis (G)
Trachinotus glaucus (L.), Carangidae
Aponurus lagunculus (G)
Ectenurus virgulus (G)
Lecithaster ghanensis (G)
Lecithochirium ghanense (G)
Lecithocladium augustiovum (G)
Neolepocreadium caballeroi (G)
Parahemiurus merus (G)
Stephanostomum trachinoti (G)
Sterrhurus ghanensis (G)
Trachinotus goreensis (Cuv. and Val.)
Gonocercella trachinoti (G)
Lecithochirium ghanense (G)
Lecithocladium augustiovum (G)
Neolepocreadium caballeroi (G)
Parahemiurus merus (G)
Parahurleytrema trachinoti (G)
Stephanostomum ghanense (G)
Trichiurus lepturus L., Trichiuridae
Lecithochirium ghanense (G)
Lecithochirium microstomum (G)
Pseudopecoelus tortugae (G)
Trygon marmorata (Steind.), Dasyatidae
Nagmia senegalensis (S)
Umbrina canariensis Val., Sciaenidae
Stephanostomum bicoronatum (S)
Umbrina cirrosa (L.)
Pycnadenoides ghanensis (G)
Umbrina ronchus Val.
Pleorchis ghanensis (S)
Pycnadenoides ghanensis (G)
Stephanostomum bicoronatum (S)
Umbrina steindachneri Cadenat
Stephanostomum bicoronatum (S)
Upeneus prayensis Cuv. and Val., Mullidae
Lecithocladium augustiovum (S)
Vomer setapinnis (Mitchill), Carangidae
Didymozoidae (*Monilicaecum*) larvae I (G)

Redescription of *Trichuris fossor* Hall, 1916 (Nematoda: Trichuridae) from the Northern Pocket Gopher, *Thomomys talpoides*[1]

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Trichuris fossor Hall, 1916, was described from the northern pocket gopher, *Thomomys talpoides* (syn. *fossor*), from Colorado on the basis of measurements of two males and one female specimen. Chandler (1945) briefly described *Trichuris fossor* from *Thomomys bottae* from California. During a survey of the parasites of *Thomomys talpoides* from

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