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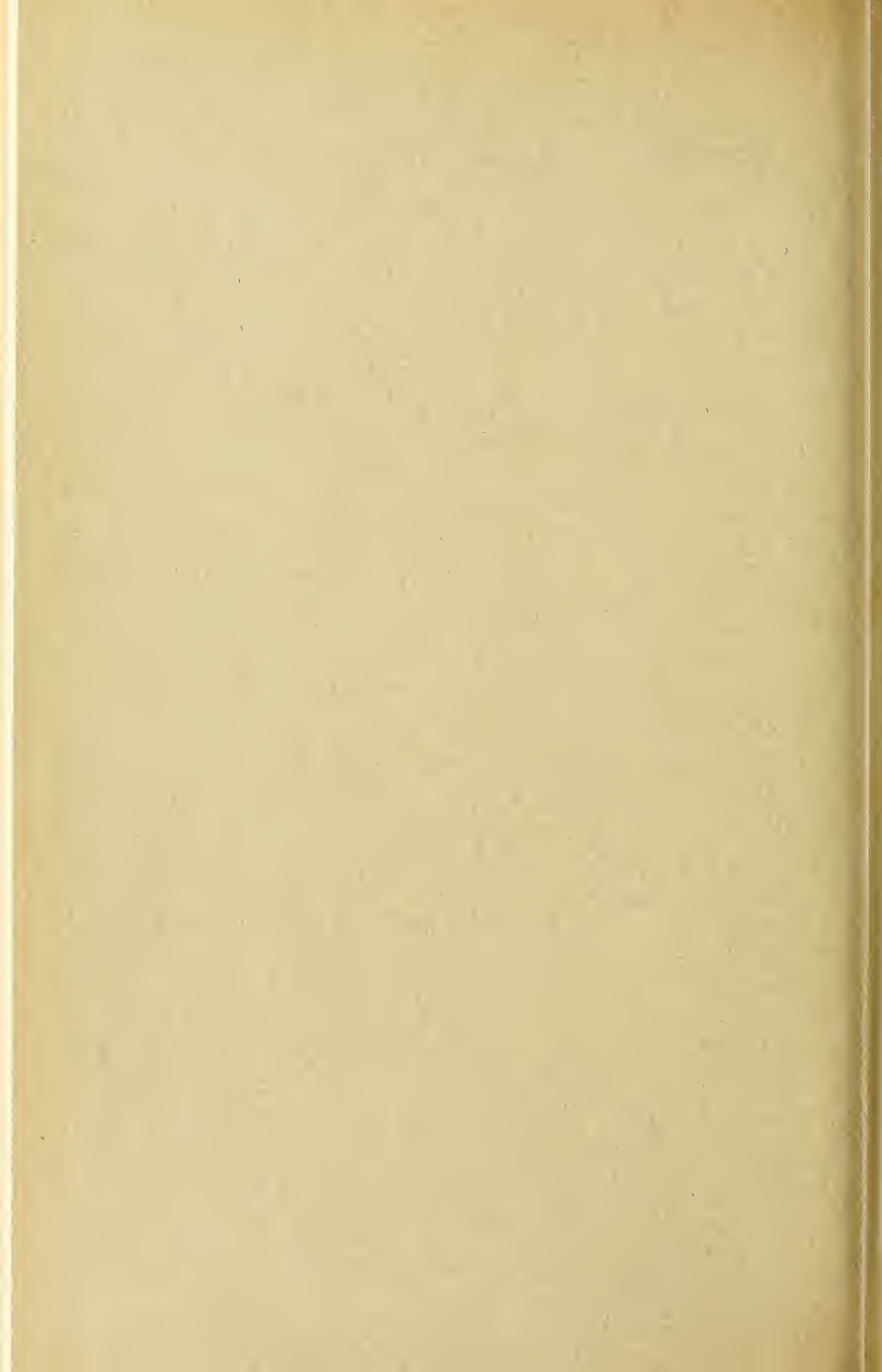
MAURICE C. HALL

Chief, Zoological Division, Bureau of Animal Industry, U. S. Department of Agriculture



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CITY OF WASHINGTON
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ARTHROPODS AS INTERMEDIATE HOSTS OF HELMINTHS

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INTRODUCTION

The phylum Arthropoda contains numerous forms which serve as intermediate hosts of many parasitic worms, including nematodes, acanthocephalids, flukes, and tapeworms. This fact follows naturally from the fact that the arthropods are an exceedingly large group of animals, including the ubiquitous insects and the numerous and widely distributed crustaceans. It also follows from the fact that these arthropods constitute the food supply, wholly or in part, for so many higher animals, especially for such forms as fish, many amphibians, some reptiles, numerous birds, and some mammals. To a lesser extent it follows from the fact that in feeding on various plants the higher animals are certain to swallow the arthropods habitually present on or in these plants. It follows from the fact that many insects feed on or breed in manure and consequently are exposed to infection from the eggs or larvae of worms parasitic in the hosts responsible for the manure. Last, but not least, the importance of arthropods as intermediate hosts of parasitic worms follows from the fact that large numbers of arthropods, especially the innumerable biting insects, whether transient or permanent ectoparasites, feed on blood and so serve as intermediate hosts of worms which have larval stages living in the blood of vertebrates.

The worm parasites may be classified from one point of view as monoxenous or heteroxenous. The monoxenous worms have life histories in which the worms pass from one host animal to a similar host animal without the intervention of an intermediate host. The heteroxenous worms have life histories in which in most cases the worms pass from mature stages in one host animal to larval stages in a host animal of a different sort, the intermediate host, and then return to a host animal of the first sort or a more or less closely related species and develop in this animal to maturity. In some instances two intermediate hosts are utilized in sequence for larval stages.

Of the four worm groups named, the cestodes are almost exclusively heteroxenous. We have the rare exception of *Hymenolepis nana* of the rat, which develops as an adult in the small intestine of the rat, produces eggs which pass out in the feces and by contamination of the rat's food infects the rat with the larval stage of the tapeworm, a small cysticercoid which develops in an intestinal villus of the rat, and which then returns to the lumen of the intestine to become an adult worm, the rat serving as both the primary and the intermediate host for the worm. Even in this case it has been claimed that rat fleas may act as intermediate hosts, but this has not yet been confirmed. This may be one of those cases in which a parasite can use an intermediate host or do without it. We seem to have similar cases in such parasites as the common gape-worm of poultry which can utilize the earthworm as an intermediate host or can infect chickens directly, and the blackhead organism which can use the cecum worm as an intermediate host or can infect turkeys directly. In the great majority of cases, the tapeworm is adult in an animal which eats the intermediate host animal and thereby becomes infested with the adult worm as the larval worm from the intermediate host comes to maturity in the primary host. In some of the bothriocephalids, in cases in which the life histories are well known, the eggs of the adult tapeworms present in the primary host, a higher vertebrate, hatch on entering water, infect such small animals as the copepods, and develop in the body cavity of these first intermediate hosts to an early larval stage, the proceroid. When such infested entomostracans are eaten by such intermediate hosts as fish, the proceroid undergoes further development and becomes a plerocercoid in the flesh of the fish. When infested fish are eaten by a suitable higher vertebrate, such as a human being or dog, the plerocercoid develops to the adult tapeworm in the small intestine of this host.

Among the flukes we have one large group, the Monogenea, which are usually ectoparasitic, mostly on fish, but sometimes endoparasitic, as in the respiratory tract of turtles or the urinary bladder of amphibians, and these flukes are monoxenous, developing without an intermediate host; another large group, the Digenea, are regularly endoparasitic and are heteroxenous. The digenetic flukes occurring in vertebrates produce eggs which pass out in the feces or urine and hatch after entering water. Usually the newly hatched worm (miracidium) attacks a mollusk host and develops in this host to the stage known as a cercaria. It may now be eaten by its primary host, or may escape and encyst in water or on vegetation and be swallowed by its primary host, developing in either case to an adult worm, or it may

enter a second intermediate host, an aquatic arthropod or a small fish, and encyst in this host. When such a second intermediate host is eaten by a primary host, the fluke develops to maturity in the new host.

Among the nematodes we have several groups which are usually monoxenous, although some of the ascarids, belonging to a superfamily, the *Ascaroidea*, which is ordinarily monoxenous, may be heteroxenous, as in the case of a seal ascarid having a larval stage encysted in fish. One large and important group, the *Filariata*, composed of two superfamilies, the *Filarioidea* and the *Spiruroidea*, is a heteroxenous group with larvae developing in blood-sucking arthropods or in arthropods which feed in some stage of development on the feces of the primary host or on food contaminated with these feces.

Among the acanthocephalids we know of the occurrence of intermediate hosts, but for the most part we must assume that this is the rule, as very few life histories are known in this group. In the known cases the worm eggs passing from the primary host infect secondary hosts, develop to a larva and infect primary hosts when these eat infected secondary hosts, or else re-encyst in another intermediate host and infect the primary host when it eats the second intermediate host.

The lists of heteroxenous worms and their arthropod hosts, given in this paper, are the most complete of those published and the omissions are probably few. The lists for certain groups have been compiled from time to time, some of the more important and more recent being those of Joyeux (1920), Ransom (1921), Van Zwaluwenburg (1928), Seurat (1916, 1919), MacGregor (1917), and Henninger (1928), and, of course, the indispensable catalogues of Stiles and Hassall, but no previous paper has attempted to cover all the arthropod hosts of the parasitic worms of vertebrates. On the basis of the lists given here this paper includes a consideration of the general facts and of the broad principles which may be derived from a correlation of these facts. While it will serve as a reference for the trained scientist in the groups involved, its principal value will be as a reference and guide to the younger worker and student and to the man who works in places remote from adequate library facilities and the specialized literature on arthropods or parasitic worms. The subject of the paper excludes from consideration the worms which have arthropods as primary hosts, and the arthropods which are intermediate hosts for Protozoa or animal parasites other than the worm

groups occurring as parasites in vertebrates. The intermediate arthropod hosts are listed here as completely as possible; the primary host list is frequently abbreviated to only representatives of groups.

In the lists arranged on a basis of parasite groups the names of hosts are given as they are found in the literature, regardless of spelling, synonymy, recognizable status, or validity. This is to enable the reader to trace the records if desired. In the final lists, arranged on a basis of intermediate host groups, the parasites are listed under the valid names of their arthropod hosts as far as possible. Synonyms of host names are indicated as synonyms, but names which cannot be recognized as valid or synonyms are retained. The insect host names have been checked by Dr. E. A. Chapin and the late Dr. H. G. Dyar of the Federal Bureau of Entomology through the courtesy of Mr. Harold Morrison, Chief of the Division of Taxonomy, and the crustacean host names have been checked by Dr. Waldo Schmitt of the U. S. National Museum, and I wish to acknowledge my indebtedness to these workers for their assistance.

ARTHROPODS AS INTERMEDIATE HOSTS OF CESTODES

The known number of arthropods acting as intermediate hosts for tapeworms is so small that this subject can be covered rather comprehensively. At the same time, one must generalize here as elsewhere rather carefully, since we know the life histories of only about 1 per cent of the known tapeworms. In addition to arthropods, the intermediate hosts of tapeworms include mammals, birds, reptiles, amphibia, fish, mollusks, annelids, and other animals. In all probability many worms now known only as having one intermediate host will be found to require two successive intermediate hosts. The following list will show the tapeworms, their primary hosts, and their intermediate hosts, for such tapeworms as have arthropods as intermediate hosts.

ANOPLOCEPHALIDAE

It is still true that the life histories of the anoplocephaline tapeworms are unknown. The larval cestode which has been reported from *Aphodius obscurus* and tentatively referred to *Cittotaenia marmotae* has not been definitely coupled with that worm by the test of successful feeding experiments, and the record is of value primarily as a possible clue to solving the unknown life histories in this group.

Arthropod Hosts of Cestodes

Family	Cestode	Primary host	Group	Secondary host	Group
ANOPLOCEPHALIDAE ..	<i>? Ciittotaenia marmotae</i> ..	Arctomys marmota	Rodent	<i>Aphodius obscurus</i>	Coleoptera
		Dog	Carnivores	<i>Trichodectes latus</i>	Mallophaga
		Cat			
HYMENOLEPIDIDAE	<i>Dipylidium caninum</i>	Man	Primate	<i>Ctenocephalus canis</i> .. <i>Ctenocephalus felis</i> .. <i>Pulex irritans</i>	Siphonaptera
	<i>Hymenolepis diminuta</i> ..	Rat	Rodents	<i>Asopia farinalis</i>	Dermaptera
		Mouse			
		Man	Primate	<i>Tinea granella</i>	Lepidoptera
				<i>Pyralis farinalis</i>	
				<i>Aglossa dimidiata</i>	Dermaptera
				<i>Paralipsa gularis</i>	
				<i>Anisolabis amulipes</i>	Dermaptera
				<i>Akis spinosa</i>	
				<i>Scaurus striatus</i>	Coleoptera
				<i>Tenebrio molitor</i>	
				<i>Tribolium ferrugineum</i>	Siphonaptera
				<i>Ceratophyllus fasciatus</i>	
		<i>Leptopsylla musculi</i>	Siphonaptera		
		<i>Xenopsylla cheopis</i> ..			
		<i>Ctenocephalus canis</i>	Myriapoda		
		<i>Pulex irritans</i>			
		<i>Fontaria virginiana</i> ..	Myriapoda		
		<i>Julus</i> sp.			
		Rat	Rodents	<i>? Ceratophyllus fascia-</i> <i>tus.</i>	Siphonaptera
		Mouse			
	<i>Hymenolepis nana</i>	Man	Primate	<i>? Xenopsylla cheopis</i> ..	Siphonaptera
				<i>Tenebrio molitor</i>	
					Coleoptera

Arthropod Hosts of Cestodes.—Continued

Family	Cestode	Primary host	Group	Secondary host	Group
HYMENOLEPIDIDAE	<i>Hymenolepis arvicolae</i> . . .	<i>Arvicola campestris</i> . . .	Rodent	<i>Tenebrio molitor</i>	Coleoptera
	<i>Hymenolepis microstoma</i> .	Mouse	Rodent	<i>Tenebrio molitor</i> <i>Anisolabis annulipes</i> <i>Ceratophyllus fasciatus</i>	Coleoptera Dermoptera Siphonaptera
	<i>Weinlandia uncinata</i>	<i>Crocidura aranea</i> <i>Crocidura leucodon</i>	Insectivores	<i>Silpha laevigata</i>	Coleoptera
	<i>Hymenolepis carioca</i>	Chicken	Galliformes	<i>Stomoxys calcitrans</i> <i>Aphodius granarius</i>	Diptera Coleoptera
	<i>Hymenolepis anatina</i>	<i>Anas</i> spp. Swan <i>Dafila acuta</i>	Anseriformes	<i>Eucandona hungarica</i> <i>Cypris incongruus</i> <i>Cypris ovata</i> <i>Cypris compressa</i> <i>Eucypris crassa</i> <i>Cypris ophthalmica</i> <i>Cyclops vernalis</i> <i>Diaptomus alnandi</i> <i>Diaptomus spinosus</i>	Ostracoda Copepoda
	<i>Hymenolepis brachycephala</i> .	<i>Pavonella pugnax</i> <i>Totanus pugnax</i> <i>Tringa</i> sp.	Charadriiformes	<i>Cyclops fimbriatus</i> <i>Cyclops crassicornis</i>	Copepoda

Arthropod Hosts of Cestodes.—Continued

Family	Cestode	Primary host	Group	Secondary host	Group
HYMENOLEPIDIDAE . . .	<i>Hymenolepis collaris</i> . . .	<i>Anas</i> spp. <i>Anser</i> spp. <i>Aythya fuligula</i> <i>Dafila acuta</i>	Anseriformes	<i>Gammarus pulxer</i> <i>Diaptomus coeruleus</i> <i>Cyclops vireidis</i> <i>Cyclops agilis</i> <i>Cyclops lucidulus</i> <i>Cyclops serrulatus</i> <i>Cyclops vernalis</i> ? <i>Potamobius astacus</i>	Amphipoda Copepoda
	<i>Hymenolepis gracilis</i> . . .	Duck Goose Wild water fowl Green pigeon	Anseriformes Columbiformes	<i>Caudona rostrata</i> <i>Caudona neglecta tuberculata</i> . <i>Dolerocypris fasciata</i> <i>Cypris compressa</i> <i>Cypris ophthalmica</i> <i>Cypris chierca</i> <i>Cypris virens</i> <i>Diaptomus coeruleus</i> <i>Diaptomus spinosus</i> <i>Cyclops vireidis</i>	Ostracoda Copepoda
	<i>Hymenolepis tenuirostris</i> .	Duck Goose <i>Merganser</i> spp. <i>Aythya</i> spp.	Anseriformes	<i>Cyclops agilis</i> <i>Cyclops pulchellus</i> <i>Cyclops serrulatus</i> <i>Cyclops bicuspidatus</i> <i>Diaptomus coeruleus</i> <i>Gammarus pulxer</i> <i>Astacus fluviatilis</i>	Copepoda Amphipoda Decapoda

Arthropod Hosts of *Cestodes*.—Continued

Family	Cestode	Primary host	Group	Secondary host	Group
HYMENOLEPIDIDAE	<i>Hymenolepis coronula</i> . . .	Duck	Anseriformes	<i>Cypris ozum</i>	Ostracoda
		Wild duck		<i>Cypris compressa</i>	
				<i>Cypris ophithalmica</i>	
	<i>Hymenolepis liophthallos</i> . . .	Duck	<i>Cypris cinerea</i>	Ostracoda	
			<i>Cylocypris lacris</i>		
		Wild water fowl	<i>Cylocypris glohosa</i>	Ostracoda	
			<i>Eucypris virens</i>		
	<i>Hymenolepis setigera</i> . . .	Wild water fowl	<i>Candona candida</i>	Ostracoda	
			<i>Cylocypris glohosa</i>		
		Wild water fowl	<i>Cypris cinerea</i>	Ostracoda	
<i>Cypris agilis</i>					
Wild water fowl		<i>Cypris cinerea</i>	Ostracoda		
		<i>Cylocypris glohosa</i>			
Wild water fowl		<i>Cyclops agilis</i>	Copepoda		
		<i>Cyclops serrulatus</i>			
Wild water fowl		<i>Cyclops agilis</i>	Copepoda		
		<i>Cyclops viridis</i>			
Wild water fowl	<i>Cyclops serrulatus</i>	Copepoda			
	<i>Diaptomus coeruleus</i>				
Wild water fowl	<i>Cyclops brevicaudatus</i>	Copepoda			
	<i>Cyclops strenuus</i>				
Wild water fowl	<i>Diaptomus coeruleus</i>	Copepoda			
	<i>Diaptomus coeruleus</i>				

Arthropod Hosts of Cestodes.—Continued

Family	Cestode	Primary host	Group	Secondary host	Group
HYMENOLEPIDIDAE ...	<i>Hymenolepis serpentulus</i> .	Duck Crow Magpie	Anseriformes Passeriformes	<i>Geotrupes sylvaticus</i> ...	Coleoptera
	<i>Drepanidotaenia lamco- lata</i> .	Goose Duck Wild water fowl.	Anseriformes	<i>Diaptomus spinosus</i> ... <i>Cyclops serratus</i> ...	Copepoda
	<i>Dicranotaenia dubia</i> ...	?	?	<i>Diaptomus alluaudi</i> ...	Copepoda
	<i>Choanotaenia infundi- bulum</i> .	Chicken	Galliformes	<i>Musca domestica</i> ... <i>Geotrupes sylvaticus</i> ...	Diptera Coleoptera
	<i>Aphorobasis dujardini</i> .. (= <i>Cysticercus integrus</i> ?)	<i>Sturnus</i> spp. <i>Turdus</i> spp.	Passeriformes	<i>Gammarus pulex</i> ...	Amphipoda
	<i>Echinocotyle rosseteri</i> ..	Duck	Anseriformes	<i>Cypris cinerea</i> ... <i>Cypris ophthalmica</i> ... <i>Cycocypris globosa</i> ...	Ostracoda
	<i>Echinocotyle linstoevi</i> ...	?	?	<i>Diaptomus asiaticus</i> ... <i>Diaptomus spinosus</i> ...	Copepoda
	<i>Echinocotyle polyacantha</i> ..?	?	?	<i>Diaptomus asiaticus</i> ...	Copepoda
	<i>Echinocotyle mrazeki</i> ...	<i>Pyromelana franciscana</i> .	Passeriformes	<i>Gammarus pulex</i> ... <i>Boeckella brazilensis</i> ..	Amphipoda Copepoda

Arthropod Hosts of *Cestodes*.—Continued

Family	Cestode	Primary host	Group	Secondary host	Group
HYMENOLEPIDIDAE	<i>Fimbriaria fasciolaris</i> ..	Duck	Anseriformes	<i>Diaptomus vulgaris</i> ... <i>Cyclops</i> sp.	Copepoda
		Goose			
		Wild water fowl			
		? Chicken	Galliformes		
DAVAINIDAE	<i>Davainea tetragona</i>	Chicken	Galliformes	<i>Musca domestica</i>	Diptera
		Turkey			
		Guinea fowl			
		Chicken			
		Turkey	Galliformes	<i>Musca domestica</i>	Diptera
Guinea fowl					
<i>Phasianus colchicus</i>					
AMABILIDAE	<i>Tatria acanthorhyncha</i> ..	Chicken	Ralliformes	<i>Agrion puella</i>	Odonata
		Turkey			
		Guinea fowl			
PROTOCEPHALIDAE	<i>Proteocephalus agonis</i> ..	<i>Colymbus</i> spp.	Fish	<i>Leptodora kindtii</i> ... <i>Bythotrephes longi-</i> <i>manus</i> .	Cladocera
		<i>Alosa finta</i>			
		<i>Aspius</i> spp.	Fish	<i>Cyclops scutellatus</i> ... <i>Cyclops breviceaudatus</i> . <i>Cyclops agilis</i>	Copepoda
		<i>Leuciscus</i> spp.			
		<i>Lota vulgaris</i>			
		<i>Idtus melanotus</i>			
		<i>Abramis brama</i>			
		<i>Alburnus lucidus</i> ... <i>Coregonus fera</i>			

Arthropod Hosts of Cestodes.—Continued

Family	Cestode	Primary host	Group	Secondary host	Group	
PROTOCEPHALIDAE . .	<i>Protocephalus filicollis</i> . .	<i>Gasterosteus aculeatus</i> . .	Fish	<i>Cyclops varius</i>	Copepoda	
	<i>Protocephalus longicollis</i> .	<i>Coregonus albula</i>	Fish	<i>Cyclops strenuus</i> <i>Cyclops serrulatus</i>	Copepoda	
	<i>Protocephalus percae</i> . .	<i>Gasterosteus aculeatus</i> . .	Fish	<i>Cyclops strenuus</i> <i>Cyclops serrulatus</i> <i>Cyclops oithonoides</i>	Copepoda	
	<i>Protocephalus ambloplitis</i> .	<i>Ambloplites rupestris</i> } <i>Micropterus dolomieu</i> . . }	Fish	<i>Cyclops leuckartii</i> <i>Cyclops prasinus</i> <i>Cyclops albidus</i> <i>Hyalella knickerbockeri</i> .	Copepoda Amphipoda	
	<i>Ichthyotania</i> sp. Fuhrmann, 1926.	?	?	<i>Cyclops strenuus</i>	Copepoda	
	<i>Corallobothrium giganteum</i> .	<i>Ameiurus melas</i> <i>Leptops olivarius</i> <i>Ictalurus punctatus</i>	Fish	<i>Cyclops serrulatus</i> <i>Cyclops prasinus</i>	Copepoda	
	<i>Corallobothrium fimbriatum</i> .	<i>Ameiurus melas</i> <i>Leptops olivarius</i> <i>Ictalurus punctatus</i>	Fish	<i>Cyclops serrulatus</i> <i>Cyclops bicuspidatus</i>	Copepoda	
	DIPHYLLOBOTHRIDAE.	<i>Schistocephalus solidus</i> . .	Duck Wild water fowl	Anseriformes	<i>Cyclops serrulatus</i> <i>Cyclops bicuspidatus</i>	Copepoda

Arthropod Hosts of Cestodes.—Continued

Family	Cestode	Primary host	Group	Secondary host	Group	
DIPHYLLOBOTHRIDAÆ.	<i>Diphyllobothrium mansoni</i> .	Dog	Carnivores	<i>Cyclops leuckartii</i>	Copepoda	
		Cat				
	<i>Diphyllobothrium latum</i> .	Dog	Carnivores	Carnivores	<i>Diaptomus oregonensis</i> <i>Diaptomus gracilis</i> ... <i>Diaptomus graciloides</i>	Copepoda
		Cat				
		Fox				
		Wild carnivores				
	Man	Primate				
	<i>Bothriocephalus cuspidatus</i> .	<i>Stizostedion vitreum</i> .	Fish	Fish	<i>Cyclops prasinus</i> ... <i>Cyclops serrulatus</i> ... <i>Cyclops leuckartii</i> ... <i>Cyclops bicuspidatus</i> . <i>Cyclops brevispinosus</i> .	Copepoda
		<i>Hiodon tergisus</i>				
		<i>Percina caprodes</i>				
<i>Abothrium crassum</i>	<i>Salmo</i> spp.	Fish	Fish	<i>Cyclops strenuus</i> ... <i>Cyclops serrulatus</i> ...	Copepoda	
	<i>Coregonus</i> spp.					
	<i>Thymallus thymallus</i> .					
<i>Abothrium infundibuliformis</i> .	<i>Trutta lacustris</i>	Fish	Fish	<i>Cyclops strenuus</i> ... <i>Cyclops serrulatus</i>	Copepoda	
	<i>Salmo</i> spp.					
<i>Triaenophorus nodulosus</i> .	<i>Coregonus</i> spp.	Fish	Fish	<i>Cyclops strenuus</i> ... <i>Cyclops fimbriatus</i> ...	Copepoda	
	<i>Trutta</i> spp.					
	<i>Thymallus thymallus</i> .					
	<i>Esox lucius</i>					

Arthropod Hosts of Cestodes.—Continued

Family	Cestode	Primary host	Group	Secondary host	Group
RHYNCHOBOTHRIDAE.	<i>Rhynchobothrius ruficollis</i> .	<i>Mustelus vulgaris</i>	Fish	Marine decapods	Decapoda
UNCERTAIN	Proceroid (?) of Gallio, 1923.	?	?	<i>Agrion</i> sp.	Odonata
	Cysticeroid of Dampf, 1910.	?	?	<i>Mesopsylla eucta</i>	Siphonaptera
	Cysticeroid of Mrazek, 1896; 13.	?	?	<i>Diaptomus</i> sp.	Copepoda
	Cysticeroid of Mrazek, 1896; 14.	?	?	<i>Gammarus pulex</i>	Amphipoda
	Cysticeroid of Rossiter, 1890.	?	?	<i>Cypris cinerea</i>	Ostracoda
	Cysticeroid of Rossiter, 1893.	?	?	<i>Cyclops agilis</i>	Copepoda
	<i>Cysticerus bifurcus</i>	?	?	<i>Gammarus pulex</i>	Amphipoda
	<i>Cysticerus gruberi</i>	?	?	<i>Cyclops brevicaulatus</i> , <i>Cyclops agilis</i>	Copepoda
				<i>Cyclops strenuus</i>	Copepoda
	<i>Cysticerus hamanni</i>	?	?	<i>Gammarus pulex</i>	Amphipoda
	<i>Cysticerus taeniaepachy-</i> <i>acanthiae</i> .	?	?	<i>Gammarus pulex</i>	Amphipoda
	<i>Cysticerus quadricurva-</i> <i>tus</i> .	?	?	<i>Cyclops agilis</i>	Copepoda

Arthropod Hosts of Cestodes.—Continued

Family	Cestode	Primary host	Group	Secondary host	Group
UNCERTAIN	<i>Cysticercus</i> sp. of Luehe, 1910.	?	?	<i>Gammarus pulex</i>	Amphipoda
	<i>Cysticercus</i> sp. of Luehe, 1910.	?	?	<i>Cyclops serrulatus</i>	Copepoda
	<i>Cysticercus</i> sp. of Luehe, 1910.	?	?	Ostracod	Ostracoda
	<i>Cysticercus</i> sp. of Mrasek, 1910.	?	?	<i>Gammarus pulex</i>	Amphipoda
	<i>Cercocystis dendrocerus</i> .	?	?	<i>Diaptomus</i> sp.	Copepoda
	<i>Onchoscolex decipiens</i> ..	?	?	<i>Tenebrio molitor</i>	Coleoptera
	<i>Plerocercus africanus</i> ..	?	?	<i>Diaptomus africanus</i>	Copepoda
	<i>Taenia</i> sp. Daday, 1900; 167.	?	?	<i>Cypris elongata</i>	Ostracoda
	<i>Taenia</i> sp. Daday, 1900; 168.	?	?	<i>Gammarus pulex</i>	Amphipoda
	<i>Taenia zichyi</i>	?	?	<i>Diaptomus asiaticus</i>	Copepoda

HYMENOLEPIDIDAE

The hymenolepid tapeworms are predominantly parasitic in birds, the above list of species with known life histories including 22 species in birds and only 6 in mammals. An inspection of the intermediate hosts for hymenolepids in mammals shows that they include members of the Coleoptera, the Siphonaptera, the Mallophaga, Lepidoptera, Dermaptera and the Myriapoda, of which the Coleoptera seem at this time to be somewhat the more important. In the case of one tapeworm, *Hymenolepis diminuta*, members of all the groups named, with the exception of the Mallophaga, can function as intermediate hosts, but such a wide range of intermediate hosts is rather unusual.

In no case does the intermediate host appear to depend primarily for its function as host on a rôle as food for the primary host, but rather on the chance of being swallowed accidentally as a contaminating element in food, or occasionally on the fact that such primary hosts as dogs will root out and swallow the fleas which are annoying them. Of the 3 species of hymenolepids infesting man, all are particularly likely to occur in children, largely because children are less careful in their food habits and in matters of personal cleanliness, and are more disposed to be intimate with such tapeworm hosts as dogs and cats.

When we consider the hymenolepid tapeworms of birds, the case is somewhat clearer as to the predominance of certain arthropod groups as intermediate hosts and the reason for this predominance. The Entomostraca, especially the Copepoda, are very decidedly the predominant group of intermediate hosts known at present for hymenolepids in birds. The birds in these cases with entomostracan hosts are practically all members of the Anseriformes and the rôle of intermediate host in these cases is clearly also that of food for the primary host. The exceptional cases, such as that of the green pigeon as a host for *Hymenolepis gracilis*, or the chicken as a host for *Fimbriaria fasciolaris*, must be explained as probably due to accidental swallowing of an intermediate host. One can say from the available facts that the intermediate host of a hymenolepid in anseriform birds should be sought among the Entomostraca and that the chance of entomostracans being the intermediate hosts is very great. The one case of a malacostracan, *Potamobius astacus*, as a host of a hymenolepid, *Hymenolepis collaris*, occurring in anseriform birds is regarded by Railliet as doubtful, and in general the larger Crustacea are not yet incriminated as intermediate hosts of avian tapeworms.

As regards hymenolepid tapeworms occurring in the Galliformes, the intermediate hosts shift naturally to the insects, the Coleoptera and Diptera standing close together in importance at this time. The reports to date indicate that at least two tapeworms, *Hymenolcpis carioca* and *Choanotaenia infundibulum*, can utilize members of both of these insect groups as intermediate hosts, and that the beetle host of *C. infundibulum* will also serve as a host of *H. serpentulus*, the latter usually a parasite of passeriform birds. The rôle of these insects as intermediate hosts of tapeworms of galliform and passeriform birds follows from their rôle as food for these birds and from the fact that the beetles feed on excrement and the stable flies breed in straw which is readily contaminated with excrement. Aside from arthropods, the intermediate hosts of hymenolepids include such forms as earthworms and leeches.

Stafford (1927) reports in a preliminary note that a number of American amphibious insects serve as intermediate hosts for various flukes and for hymenolepid tapeworms. The record of these tapeworms in more definite form has not yet come to the attention of the present writer.

DAVAINIIDAE

The known life histories of tapeworms of the Davainiidae cover forms parasitic in birds and incriminate flies as intermediate hosts, the common house fly being reported as the host for *Davainea tetragona* and *D. cesticillus*. The possible rôle of ants and grasshoppers as intermediate hosts for *D. friedberggeri* is noted in the literature but has only the value of a surmise and has not been included in the list of hosts. Diptera would appear to be especially promising among the arthropods as intermediate hosts of davainid tapeworms, but these worms also utilize such intermediate hosts as snails and slugs, aside from arthropods, and the total number of known life histories does not warrant much generalization.

AMABILIIDAE

The only known life history for a tapeworm belonging in the *Amabiliidae* is that for *Tatria acanthorhyncha*, and this involves the Odonata or dragonflies as intermediate hosts. The only genera other than *Tatria* assigned to this family by Ransom are *Amabilia* and *Schistotaenia*, but until we have more information as to life histories we cannot assume that the Odonata have special importance as intermediate hosts in this family. In the one known life history, the dragon-

fly evidently plays the rôle of host for the tapeworm and food for the ralliform bird host.

PROTEOCEPHALIDAE

So far as final hosts and intermediate hosts are known, the copepods are outstandingly important as intermediate hosts of proteocephalid tapeworms in fish, the Cladocera serving as hosts in only one case. Apparently these tapeworms form a proceroid in the entomostracan host, and this develops to a second larval stage in small fish or other suitable hosts, and then to an adult when this second intermediate host is eaten by a suitable primary host.

DIPHYLLOBOTHRIDAE

In the Diphyllobothriidae we have tapeworms in which the life history sometimes, though apparently not always, involves two intermediate hosts. For the known cases, the first intermediate host is always an entomostracan and the second intermediate host is a fish. The known entomostracan hosts are copepods. Since the rôle of intermediate host played by entomostracans in these life cycles is evidently based on the rôle of Entomostraca as fish food, it is obvious that the Entomostraca would be first choice as intermediate hosts of diphyllobothrids in a search for the first host, and the copepods would be first choice among the Entomostraca.

RHYNCHOBOTHRIDAE

The life history is known for only one species of rhynchobothrid tapeworm, and in this case decapod crustaceans serve as intermediate hosts. Additional data are needed before one could safely generalize in regard to the intermediate hosts of tapeworms of the family Rhynchobothriidae.

ARTHROPODS AS INTERMEDIATE HOSTS OF TREMATODES

The following list will serve as a basis on which to draw some conclusions as to the rôle of arthropods as intermediate hosts of trematodes. In assigning flukes to various families, the writer has followed various authorities as there is considerable disagreement in regard to the taxonomy of fluke groups, and the arrangement used will not meet with anything like unanimous approval. It is only intended to serve as a tentative basis for a discussion within the scope of this paper.

Arthropod Hosts of Trematodes

Family	Trematode	Primary host	Group	Secondary host	Group		
PLAGIORCHIDAE	<i>Plagiorchis amciurensis</i> .	<i>Ameiurus natalis</i>	Fish	Crayfish	Decapoda		
				Dragon fly	Odonata		
	<i>Plagiorchis maculosus</i> ...		<i>Cypselus apus</i>	Passeriformes ...	<i>Drusus trifidus</i>	Trichoptera	
			<i>Caprimulgus europaeus</i>		Perlid larva	Plecoptera	
			<i>Hirundo riparia</i>				
			<i>Hirundo arbica</i>				
		<i>Hirundo rustica</i>					
	<i>Lissorchis fairporti</i>	<i>Ictiobus cyprinella</i>	Fish	<i>Cheironomus lobiferus</i> }	Diptera		
		<i>Ictiobus bubalus</i>		<i>Tonyopus decoloratus</i> }			
	<i>Pneumonocees variegatus</i> .	Frogs	Amphibians	<i>Calopteryx virgo</i>	Odonata		
		Toads					
	<i>Pneumonocees simili-</i>	Frogs	Amphibians	<i>Calopteryx virgo</i>	Odonata		
<i>genus.</i>							
<i>Ophistholytpe endolobum.</i>		Frogs	Amphibians	<i>Phryganica grandis</i> ...	Trichoptera		
		Salamanders		<i>Anabolia nervosa</i> ...			
				<i>Limnophilus rhombicus</i>			
				<i>Limnophilus griseus</i> ..			
				<i>Limnophilus lunatus</i> ..			
				<i>Limnophilus flavicornis</i>			
		? <i>Chlocon dipterum</i> ..	Ephemera				
		? <i>Ephemerella vulgata</i>		Plecoptera			
		<i>Gommanus puler</i>			Amphipoda		

Arthropod Hosts of Trematodes.—Continued

Family	Trematode	Primary host	Group	Secondary host	Group
PLAGIORCHIDAE	<i>Haplometra cylindracea</i> .	Frogs	Amphibians	<i>Ilybius fuliginosus</i>	Coleoptera
	<i>Prosthogonimus</i> sp. Kotlan & Chandler.	Chicken	Galliformes	<i>Tetragoncuria</i> spp.	Odonata
	<i>Prosthogonimus intercalandus</i> .	Water fowl	Anseriformes	<i>Libellula quadrimaculata</i> .	Odonata
	<i>Prosthogonimus pellucidus</i> .	Chicken	Galliformes	<i>Libellula quadrimaculata</i> .	Odonata
LECITHODENDRIIDAE ..	<i>Lecithodendrium lagenæ</i> .	Bats	Cheiropterans	Perfid larva	Plecoptera
	<i>Lecithodendrium chilostomum</i> .	Bats	Cheiropterans	Ephemeroïd larva	Ephemeroïda
PLEUROGENES MEDIANUS ...	<i>Pleurogenes medians</i> ...	Frogs	Cheiropterans	<i>Chironomus plumosus</i>	Diptera
	<i>Pleurogenes claviger</i>	Toads	Cheiropterans	? <i>Anopheles maculipennis</i> .	
PROTOCUS COIFUSUS	<i>Pleurogenes claviger</i>	Frogs	Amphibians	<i>Phryganca grandis</i> ..	Trichoptera
	<i>Protocus coifus</i>	Toads	Amphibians	<i>Phryganca</i> sp.	Coleoptera
COLEOPTERA	<i>Prosthenops</i>	Frogs	Amphibians	Water beetles	Odonata
	<i>Prosthenops</i>	Toads	Amphibians	<i>Agrion</i> sp.	Coleoptera
COLEOPTERA	<i>Prosthenops</i>	Frogs	Amphibians	Water beetles	Coleoptera
	<i>Prosthenops</i>	Toads	Amphibians	<i>Asclina</i> sp.	Odonata
ODONATA	<i>Prosthenops</i>	Frogs	Amphibians	<i>Cordulia</i> sp.	Odonata
	<i>Prosthenops</i>	Toads	Amphibians		

Arthropod Hosts of Trematodes.—Continued

Family	Trematode	Primary host	Group	Secondary host	Group
LECTHODENDRIIDAE	<i>Eumegacetes</i> sp.	?	?	Amphibious insects	Insecta
OPTISTHORCHIIDAE	<i>Plagioporus</i> sp.	?	?	Amphibious insects	Insecta
ALLOCREADIIDAE	<i>Allocreadium commune</i> ..	<i>Catostomus catostomus</i> <i>Fundulus diaphanus</i> <i>menona</i> . <i>Notropis cornutus</i>	Fish	<i>Blasturus cupidus</i>	Ephemera
	<i>Allocreadium isoporum</i> ..	<i>Cyprinus carpio</i>		<i>Ephemera vulgata</i>	Ephemera
		<i>Barbus barbatus</i>		<i>Anabolia nervosa</i>	Trichoptera
		<i>Rutilus rutilus</i>		<i>Chaetopteryx villosa</i> . }	
		<i>Leuciscus cephalus</i>			
		<i>Phoxinus phoxinus</i>	Fish		
		<i>Tinca tinca</i>			
		<i>Abramis brama</i>			
		<i>Cobitis taenia</i>			
		<i>Esox lucius</i>			
	<i>Astacotrema cirrigerum</i> ..	? Swallow	Bird	<i>Astacus fluviatilis</i>	Decapoda
				Crayfish	
	<i>Crepidostomum cornutum</i> .	Black bass		<i>Cambarus</i> spp.	Decapoda
		Rock bass		<i>Hexagenia</i> sp.	
		Channel cat			Ephemera
		Perch	Fish		
		Sunfish			
		Darter			

Arthropod Hosts of Trematodes.—Continued

Family	Trematode	Primary host	Group	Secondary host	Group	
ALLOCREADIDAE	<i>Acrolichanus petalosa</i> ..	<i>Acipenser rubicundus</i> ...	Fish	Crayfish	Decapoda	
	? <i>Sphaerostoma globi- porum</i> .	<i>Cyprinus erythrophthal-</i> <i>mus</i> .	Fish	<i>Anopheles maculipen-</i> <i>nis</i> .	Diptera	
GORGODERIDAE	<i>Stephanophiala farionis</i> ..	<i>Trutta fario</i>	Fish	<i>Hexagenia</i> spp.	Ephemera	
		<i>Trutta trutta</i>				
		<i>Epitomynis salvelinus</i>				
		<i>Thymallus thymallus</i> .				
		<i>Coregonus oxyrrhyn-</i> <i>chus</i> .				
		<i>Salvelinus fontinalis</i> ..				
		<i>Perca flavescens</i>				
		<i>Eupomotis gibbosus</i> ..				
		<i>Boleosoma nigrum</i>				
		<i>Eithcostoma torvae</i>				
		<i>Stizostedion vitreum</i> ..				
		<i>Salmo mykiss levisii</i> ..				
GORGODERIDAE	<i>Gorgoderia pagenstecheri</i> .	<i>Necturus maculatus</i>	Amphibians	<i>Agrion</i> sp.	Odonata	
		Frogs	Amphibians			
		<i>Gorgoderia varsoviensis</i> ..	Amphibians			<i>Epitheca</i> sp.
		Frogs	Amphibians			
GORGODERIDAE	<i>Gorgoderia cynoides</i> ...	Frogs	Amphibians	<i>Agrion</i> sp.	Odonata	
		<i>Gorgoderia vitelliloba</i> ...	Frogs	Amphibians	<i>Epitheca</i> sp.	Odonata
			Frogs	Amphibians	"Raubinsekten"	Insecta

Arthropod Hosts of Trematodes.—Continued

Family	Trematode	Primary host	Group	Secondary host	Group
GORGONERIDAE	<i>Microphallus opacus</i>	<i>Amia calva</i> <i>Ictalurus punctatus</i> <i>Percia flavescens</i>	Fish	<i>Cambarus propinquus</i>	Decapoda
HALIPEGIDAE	<i>Halipegus ovocaudatus</i>	Frogs	Amphibians	<i>Calopteryx virgo</i>	Odonata
TROGLOTREMATIDAE	<i>Paragonimus westermani</i>	Man ? Dog ? Cat ? Swine	Primate Carnivores Ungulate	<i>Geothelphusa obtusipes</i> <i>Geothelphusa dchaanii</i> . <i>Sesarma dchaanii</i> <i>Eriochelir japonicus</i> <i>Pseudothelphusa iturbei</i> ? <i>Cambaroides similis</i> . ? <i>Astacus japonicus</i>	Decapoda
HEMIURIDAE	<i>Hemiuroides appendiculatus</i>	<i>Percia fluviatilis</i> <i>Coregonus oxyrrhynchus</i> . <i>Lampetra fluviatilis</i> <i>Lota lota</i> <i>Esox lucius</i> <i>Salmo fario</i> <i>Clupea finia</i> <i>Caspialosa kessleri</i> <i>Osmerus mordax</i>	Fish	<i>Acartia clausa</i>	Copepoda

Arthropod Hosts of Trematodes.—Continued

Family	Trematode	Primary host	Group	Secondary host	Group
HEMURIIDAE	<i>Derogoches varicus</i>	<i>Coregonus oxyrrhynchus</i> .	Fish	<i>Acartia</i> sp.	Copepoda
		<i>Thymallus thymallus</i> ..			
		<i>Gadus callarias</i>			
		<i>Urophycis tenuis</i>			
		<i>Anarrhichas lupus</i>			
		<i>Hippoglossus hippoglossus</i> .			
		<i>Salmo salar</i>			
		<i>Coryphaena equisetis</i> ..			
		<i>Coryphaena hippuris</i> ..			
		<i>Gadus aeglefinus</i>			
<i>Cottus scorpius</i>					
<i>Phobos ventralis</i>					
<i>Hemirhamphus americanus</i> .					
<i>Leptocephalus conger</i> ..					
<i>Limanda ferruginea</i>					
<i>Microgadus tomcod</i>					
<i>Micropogon undulatus</i> ..					
BRACHYCOELIIDAE	<i>Brachycoelium retusum</i> ..	<i>Rana esculenta</i>	Amphibians	<i>Phryganea grandis</i>	Trichoptera
		<i>Rana halscina</i>			
UNCERTAIN	<i>Macroorchis spinulosus</i> ..	Dog	Carnivores	<i>Potamon dehaanii</i>	Decapoda
		Cat			
		Small animals	Rodents		

DICROCOELIIDAE

Themisto libellula

Fish

Amphipoda

Arthropod Hosts of Trematodes.—Continued

Family	Trematode	Primary host	Group	Secondary host	Group
UNCERTAIN	<i>Stephanolecithus parvus</i> .	Dog	Carnivore	? <i>Potamon obtusifpes</i> .. ? <i>Potamon dehaanii</i> ... ? <i>Potamon sinensis</i> ... ? <i>Sesarma dehaanii</i> ... ? <i>Eriocheir japonicus</i> ..	Decapoda
	<i>Distomum kalapai</i>	Dog	Carnivores	Crabs	Decapoda
		Cat			
	<i>Distomum agamos</i>	?	?	<i>Gammarus pulex</i>	Amphipoda
	<i>Distomum gammari</i> Rentsch.	?	?	<i>Gammarus ornatus</i>	Amphipoda
	<i>Distomum gammari</i> Linstow.	?	?	<i>Gammarus pulex</i>	Amphipoda
	<i>Distomum pulicis</i>	?	?	<i>Gammarus pulex</i>	Amphipoda
	<i>Distomum limnophilii</i> ...	?	?	<i>Limnophilus (?) rhombicus</i>	Trichoptera
	<i>Distomum phryganeae</i> ...	?	?	<i>Phryganea grandis</i>	Trichoptera
	<i>Distomum mystacidis</i> ..	?	?	<i>Mystacides nigra</i>	Neuroptera
	<i>Distomum notidobiac</i> ...	?	?	<i>Sialis lutaria</i>	Neuroptera
	<i>Distomum reinhardi</i>	?	?	<i>Notidobia ciliaris</i>	Trichoptera
	<i>Distomum sialisidis</i>	?	?	<i>Astacus leptodactylus</i> ...	Decapoda
		?	?	<i>Sialis lutaria</i>	Neuroptera

Arthropod Hosts of Trematodes:—Continued

Family	Trematode	Primary host	Group	Secondary host	Group	
UNCERTAIN	<i>Distomum</i> sp. Herrick..	?	?	<i>Cyclops tenuicornis</i>	Copepoda	
	<i>Distomum</i> of Cooper, 1883.	?	?	Crayfish	Decapoda	
	<i>Distomum</i> sp. of Villot..	?	?	<i>Agrion</i> sp.	Odonata	
	<i>Distomum</i> of Linstow, 1892.	?	?	Crayfish	Decapoda	
	<i>Agamodistomum apodis</i> .?	?	?	<i>Apus</i> sp.	Branchio- poda	
	<i>Agamodistomum anophe-</i> <i>lis</i> .	?	?	<i>Anopheles maculipennis</i> ..	Diptera	
	<i>Agamodistomum siutoni</i> .?	?	?	<i>Anopheles funestus</i> var. <i>listoni</i> . <i>Anopheles culifacies</i> ..	Diptera	
	<i>Agamodistomum marti-</i> <i>ranoi</i> .	?	?	<i>Anopheles claviger</i>	Diptera	
	Cercaria of Soparkar, 1918.	?	?	<i>Anopheles rossi</i>	Diptera	
	Cercaria of Stephens & Christophers, 1902.	?	?	<i>Anopheles rossi</i>	Diptera	
	Cercaria of Joyeux, 1918.	?	?	<i>Anopheles fuliginosus</i> ..		
			?		<i>Culex hortensis</i>	Diptera

Arthropod Hosts of Trematodes.—Continued

Family	Trematode	Primary host	Group	Secondary host	Group
UNCERTAIN	<i>Cercaria prima</i>	?	?	<i>Corethra</i> sp. <i>Ilybius</i> sp. Dragon fly	Diptera Coleoptera Odonata
	<i>Cercaria secunda</i> ...	?	?	<i>Corethra</i> sp. Ephemerid	Diptera Ephemerida
	Fluke	?	?	<i>Rhyacophila nubila</i>	Trichoptera
	Fluke	?	?	<i>Nymphula nymphaeata</i> ..	Lepidoptera

An analysis of the records given shows the following:

PLAGIORCHIIDAE

In the Plagiorchiidae we have a group of flukes which have a wide range of intermediate hosts, including the insect groups Odonata, Diptera, Trichoptera, Plecoptera, Ephemera, and Coleoptera, and the crustacean groups, Decapoda and Amphipoda. This range of intermediate hosts is associated with the range of primary hosts, which include fish, amphibians, and birds. Considered on the basis of primary hosts, the plagiorchids in birds utilize Odonata as intermediate hosts, those in fish use the Diptera, Odonata, Trichoptera, Plecoptera and Decapoda; while those in frogs use the Odonata, Trichoptera, Coleoptera, Ephemera, Plecoptera, and Amphipoda. The Trichoptera and the Odonata appear to be the most important intermediate hosts.

LECITHODENDRIIDAE

In the Lecithodendriidae the insects serve as intermediate hosts and they include the Plecoptera, Ephemera, Coleoptera, Diptera, Trichoptera, Odonata and "amphibious insects." The frog flukes of this family use Odonata and Coleoptera as intermediate hosts; the bat flukes use Plecoptera, Ephemera, Diptera, and Trichoptera. Here also the insects have the double rôle of intermediate host for the fluke and of food for the primary host.

OPISTHORCHIIDAE

In the Opisthorchiidae, insects, specified by Stafford (1927), as amphibious insects, are the only reported hosts. Since this is a large family with a wide range of hosts, little of a general nature could be concluded from the foregoing.

ALLOCREADIIDAE

In the Allocreadiidae, parasitic for the most part in fish, the intermediate hosts include Ephemera, Trichoptera, Diptera, and Decapoda, the more important being the Ephemera and the Decapoda. The intermediate hosts probably serve as such by virtue of their rôle as food for fish. The record for *Astacotrema cirrigerum* of a bird as primary host is found in a footnote reference based apparently on correspondence and lacks evidence or detail.

GORGODERIDAE

In the Gorgoderidae, commonly parasitic in frogs, the intermediate hosts known at present are mostly Odonata, the rôle of intermediate host here being combined with the rôle of food for frogs. One of the Decapoda, a crayfish, is the host for a gorgoderid parasitic in fish.

HALIPEGIDAE

In the Halipegidae, the only reported life history involves the Odonata as intermediate hosts, the primary hosts here being frogs.

TROGLOTREMATIDAE

In the Troglotrematidae the only known life history, that of the human lung fluke, involves several species of decapods, crabs being known hosts and crayfish probable hosts.

HEMIURIDAE

In the Hemiuridae, which are fish parasites, all known intermediate hosts are crustaceans, those for two flukes being copepods and those for one fluke being decapods.

DICROCOELIIDAE

The one dicrocoelid with a known life history utilizes an amphipod as an intermediate host, the primary hosts being fish.

BRACHYCOELIIDAE

The one brachycoelid with a known life history has a trichopteran as an intermediate host, the primary hosts being amphibians.

FAMILY UNCERTAIN

The three flukes of uncertain relationship for which we know primary as well as secondary hosts, and not merely secondary hosts for larval stages, all have carnivores as primary hosts and crabs as secondary hosts.

ARTHROPODS AS INTERMEDIATE HOSTS OF
NEMATODES

In listing the nematodes having intermediate stages in arthropods, no attention has been paid to nematodes listed only as nematodes without reference to whether the nematodes were mature or immature. Nematodes occurring consistently as larvae in insects may be the

larvae of worms which will develop to maturity on reaching a suitable host, although larval nematodes specified as such with no further discussion may be the larvae of such worms as the mermithids which will develop to maturity as free-living forms. In this paper the mermithids and gordians are not considered, as they are not regarded as true parasites of vertebrates in the scope of treatment of that subject as limited here. The gordians may parasitize immature frogs in the course of development of the worms, but this topic is disregarded here owing to a lack of space for its consideration.

All records which are merely surmises to the effect that a certain arthropod is the intermediate host of some nematode are likewise disregarded. Such surmises have their value in directing exploratory research, but for the purpose of analyzing existing records to obtain valid data they are worthless. There is sufficient uncertainty in connection with a number of existing records to introduce certain elements of possible error as it is.

The following list covers the important cases of arthropod hosts for nematodes. The worms involved fall in the Filariata or Filariida and most of them fall in the superfamilies Spiruroidea and Filarioidea, two closely related superfamilies which are markedly heteroxenous and hence in sharp contrast with most of the other nematode groups which are usually monoxenous. In the exceptional cases in which members of other superfamilies utilize intermediate hosts, the hosts are never arthropods so far as the writer is aware, but are such forms as fish or earthworms.

SPIRURIDAE

As intermediate hosts of nematodes of the Spiruridae, which is made up predominantly of mammalian parasites and to a lesser extent of bird parasites, the Coleoptera are of outstanding importance. In this family the common mode of transmission of the larval worm to the primary host is by means of the ingestion of the secondary host, either as a deliberate act of eating or because of the more or less accidental presence of the secondary host in the food of the primary host. In general, dogs, sheep, cattle and horses cannot be called insectivorous animals, but the presence of beetles in their customary food seems to be sufficiently common to enable various spirurid parasites of these animals to maintain themselves with the aid of these beetle hosts. It is evident that some of the spirurids utilizing beetle hosts may have alternative life histories which are more complicated than the mere infection of the beetle host by means of infective worm eggs and the infection of the primary host as a result of swallowing infected beetles. Thus Seurat has shown that *Physocephalus*

Arthropod Hosts of Nematodes

Family	Nematode	Primary host	Group	Secondary host	Group
SPIRURIDAE	<i>Spirura gastrophila</i>	Dog	Carnivores	<i>Blatta orientalis</i>	Orthoptera
		Cat			
		Fox			
		Mongoose			
	Hedgehog	Insectivore	Akis goryi	Akis sp.	Coleoptera
	Mole	Insectivore	Onthophagus sp.	Scarabaeus sacer	Coleoptera
	Dog	Carnivore	Cetonia aurata	Cetonia aurata	Coleoptera
Dog	Carnivore	Akis goryi	Akis goryi	Orthoptera	
					Copris hispanis
					Geotrupes douci
					Gymnopleurus sturmi ..
Mole	Insectivore	Scarabaeus sacer	Scarabaeus sacer	Coleoptera	
					Canthon sp.
Horse	Ungulates	Sarcophaga melanura ..	Sarcophaga melanura ..	Diptera	
					Ass
					Mule

Arthropod Hosts of Nematodes.—Continued

Family	Nematode	Primary host	Group	Secondary host	Group
SPIRURIDAE	<i>Habronema megastoma</i>	Horse	Ungulates	<i>Musca domestica</i> <i>Musca fergusoni</i> <i>Musca humilis</i> <i>Musca lusoria</i> <i>Musca terrae-reginae</i> <i>Musca ventrosa</i> <i>Musca vetustissima</i> <i>Pseudopyrellia</i> sp.	Diptera
		Ass			
		Mule			
	<i>Habronema muscae</i>	Horse	Ungulates	<i>Musca domestica</i> <i>Musca fergusoni</i> <i>Musca humilis</i> <i>Musca lusoria</i> <i>Musca terrae-reginae</i> <i>Musca ventrosa</i> <i>Musca vetustissima</i> <i>Sarcophaga misera</i> <i>Pseudopyrellia</i> sp.	Diptera
		Ass			
		Mule			
	<i>Habronema</i> spp.	Horse	Ungulates	<i>Anastellorhina augur</i> <i>Musca bezzi</i>	Diptera
		Ass			
		Mule			
	<i>Protospirura muris</i>	Mouse	Rodents	<i>Tenebrio molitor</i> (?) <i>Xenopsylla cheopis</i>	Coleoptera Siphonoptera
		Rat			
		<i>Apodemus sylvaticus</i>			

Arthropod Hosts of Nematodes.—Continued

Family	Nematode	Primary host	Group	Secondary host	Group	
SPIRURIDAE	<i>Protospirura gracilis</i> . . .	Cat	Carnivore	<i>Aphodius fimetarius</i>	Coleoptera	
	<i>Protospirura columbiana</i> .	<i>Rattus norvegicus</i>	Rodent	<i>Blattella germanica</i>	Orthoptera	
	<i>Hartertia gallinarum</i> . . .	Chicken	Galliformes	<i>Hodotermes pretoriensis</i> .	Isoptera	
	<i>Arduenna strongylina</i> . . .	Swine	Ungulates	<i>Aphodius rufus</i>	Coleoptera	
		Cow		<i>Aphodius castaneus</i> . . .		
		<i>Physocephalus sexalatus</i> .	Swine	Ungulates	<i>Geotrupes douci</i>	Coleoptera
		<i>Sus cristatus</i>	<i>Geotrupes stercorarius</i> .			
					(?) <i>Geotrupes stercorosus</i> .	
					<i>Onthophagus bedeli</i>	
					<i>Onthophagus hecate</i> . . .	
				<i>Onthophagus nebulosus</i> .		
				<i>Scarabaeus sacer</i>		
				<i>Scarabaeus variolosus</i> .		
<i>Gongylonema neoplasticum</i> .		Rat	Rodents	<i>Blatta orientalis</i>	Orthoptera	
		Mouse		<i>Blattella germanica</i> . . .		
				<i>Periplaneta americana</i> .		
				<i>Tenebrio molitor</i>	Coleoptera	

Arthropod Hosts of Nematodes.—Continued

Family	Nematode	Primary host	Group	Secondary host	Group	
SPIRURIDAE	<i>Gongylonema mucronatum.</i>	<i>Erinaceus algirus</i>	Insectivore	<i>Atenichus sacer</i>	Coleoptera	
						<i>Onitis irroratus</i>
						<i>Onthophagus bedeli</i> ..
						<i>Geotrupes donci</i>
	<i>Gongylonema pulchrum.</i>	Swine	Ungulate	<i>Gymnopleurus sturmi.</i> <i>Blatella germanica</i>	Orthoptera	
	<i>Gongylonema brevispiculum.</i>	Jerboa	Rodent	(?) <i>Aphodius haemorrhoidalis.</i> <i>Caccobius schreberi</i> ..	Coleoptera	
	<i>Gongylonema</i> sp.,	?	?	<i>Blaps strauschi</i>	Coleoptera	
THELAZIIDAE	<i>Oxyspirura mansonii</i>	Chicken	Galliformes	<i>Blaps</i> sp.	Coleoptera	
	<i>Oxyspirura parvorum</i> ..	Chicken	Galliformes	<i>Tenebrio obscurus</i>	Coleoptera	
ACUARIDAE	<i>Echinuria uncinata</i>	<i>Anas boschas</i>	Anseriformes	<i>Blatta orientalis</i>	Orthoptera	
						<i>Anas penelope</i>
						<i>Anas rubripes</i>
						<i>Anser cinereus domesticus.</i>
						<i>Cygnus olor domesticus</i> <i>Nettion carolinense</i> ..
		Chicken	Galliformes	<i>Periplaneta americana.</i>	Orthoptera	
				<i>Pycnoscelus surinamensis.</i>	Orthoptera	
				<i>Pycnoscelus surinamensis.</i>	Orthoptera	
				<i>Daphnia pulex</i>	Cladocera	

Arthropod Hosts of Nematodes.—Continued

Family	Nematode	Primary host	Group	Secondary host	Group
ACUARIIDAE	<i>Dispharynx spiralis</i>	Chicken	Galliformes	<i>Forcellio lacris</i>	Isopoda
		<i>Bonasa umbellus</i>			
		<i>Phasianus gallus</i>			
		Pea fowl			
		<i>Quiscalus quiscula</i>			
		Pigeon			
		<i>Passeriformes</i>			
		<i>Columbiformes</i>			
		<i>Reptile</i>			
		<i>Coleoptera</i>			
PHYSALOPTERIDAE	<i>Physaloptera abbreviata</i>	<i>Lacerta ocellata</i>	Reptile	<i>Ateuchus</i> sp.	Coleoptera
		<i>Anas boschas fera</i>			
		<i>Anas boschas domestica</i>			
		<i>Cygnus melanocoryphus</i>			
		<i>Fulica atra</i>			
		<i>Mergus merganser</i>			
		<i>Nyroca ferina</i>			
		<i>Podiceps fluviatilis</i>			
		Chicken			
		Turkey			
Pigeon					
TETRAMERIDAE	<i>Tetrameres fississima</i>	<i>Anas boschas domestica</i>	Anseriformes	<i>Daphnia pulex</i>	Cladocera
		<i>Cygnus melanocoryphus</i>			
		<i>Fulica atra</i>			
		<i>Mergus merganser</i>			
		<i>Nyroca ferina</i>			
		<i>Podiceps fluviatilis</i>			
		Chicken			
		Turkey			
		Pigeon			
		<i>Gammarus pulex</i>			
CUCULLANIDAE	<i>Cucullanus elegans</i>	<i>Esox lucius</i>	Galliformes	<i>Cyclops quadricornis</i>	Copepoda
		<i>Gadus lota</i>			
		<i>Perca fluviatilis</i>			
		<i>Anguilla vulgaris</i>			
		<i>Aspius rapax</i>			
		<i>Silurus glanis</i>			
		<i>Fish</i>			
		<i>Columbiformes</i>			
		<i>Isopoda</i>			
		<i>Asellus aquaticus</i>			

Arthropod Hosts of Nematodes.—Continued

Family	Nematode	Primary host	Group	Secondary host	Group
CAMALLANIDAE	<i>Camallanus lacustris</i>	<i>Perca fluviatilis</i>	Fish		Copepoda
		<i>Lucioperca sandra</i>			
		<i>Acerina cernua</i>			
		<i>Aspro zingel</i>			
		<i>Leuciscus rutilus</i>			
		<i>Aspius rapax</i>			
		<i>Barbus fluviatilis</i>			
		<i>Tinca vulgaris</i>			
		<i>Esox lucius</i>			
		<i>Lota vulgaris</i>			
		<i>Salmo salar</i>			
		<i>Trutta trutta</i>			
		<i>Salvelinus fontinalis</i>			
		<i>Coregonus oxyrrhynchus</i>			
<i>Osmerus eperlanus</i>					
<i>Silurus glanis</i>					
<i>Anguilla vulgaris</i>					
HEDERURIDAE	<i>Camallanus microcephalus</i>	<i>Emys lutaria</i>	Reptile	? <i>Cyclops</i> sp.	Copepoda
		<i>Amblystoma mexicana</i>			
		<i>Triton taeniatus</i>			
		<i>Bufo calamita</i>			
		<i>Lissotriton punctatus</i>			
HEDERURIDAE	<i>Hederuris androphora</i>	<i>Asellus aquaticus</i>	Amphibians		Isopoda
		<i>Emys guttata</i>			

Arthropod Hosts of Nematodes:—Continued

Family	Nematode	Primary host	Group	Secondary host	Group
HEDRURIDAE	<i>Hedruris orestiae</i>	<i>Orestias muelleri</i> <i>Orestias albus</i>	Fish	(?) <i>Allorchestes</i> sp....	Amphipoda
FILARIIDAE	<i>Filaria maris</i>	<i>Mustela martes</i> <i>Mustela foina</i> <i>Putorius putorius</i> <i>Hystrix cristata</i>	Carnivores Rodent	(?) <i>Ixodes ricinus</i>	Arachnida
	<i>Filaria ozzardi</i>	Man	Primate	<i>Aedes aegypti</i> <i>Anopheles albimanus</i> <i>Anopheles albitarsis</i> <i>Anopheles maculipennis</i> <i>Anopheles tarsinaculatus</i> <i>Culex quinquefasciatus</i>	Diptera
	<i>Filaria cypseli</i>	<i>Cypselus affinis</i>	Passeriformes	Bird louse	Mallophaga
	<i>Filaria mitchelli</i>	<i>Heloderma suspectum</i>	Reptile	? Tick	Arachnida
	<i>Filaria</i> sp. of Fuelleborn, 1909.	?	?	<i>Anopheles maculipennis</i> .	Diptera
	<i>Filaria</i> sp. of Castellani and Chalmers, 1913.	?	?	<i>Mansonioides unifornis</i> .	Diptera
	<i>Filaria</i> sp. of Med. Rept., Lagos, Nigeria, 1918 (<i>Loa</i> ?).	?	?	<i>Chrysops silaceus</i>	Diptera

Arthropod Hosts of Nematodes.—Continued

Family	Nematode	Primary host	Group	Secondary host	Group
FILARIIDAE	<i>Wuchereria bancrofti</i> ..	Man	Primate	<i>Aedes aegypti</i> <i>Aedes (Finlaya) togoi</i> . <i>Aedes gracilis</i> <i>Aedes perplexus</i> <i>Aedes pseudoscutel-</i> <i>laris</i> . <i>Aedes scutellaris</i> <i>Aedes variegatus</i> <i>Anopheles albimanus</i> . <i>Anopheles annulipes</i> .. <i>Anopheles argyrotar-</i> <i>sus</i> . <i>Anopheles barbrostris</i> . <i>Anopheles costalis</i> ... <i>Anopheles rossi</i> <i>Anopheles sinensis</i> ... <i>Anopheles sinensis</i> <i>vanus</i> . <i>Scutomyia albolineata</i> . <i>Taeniorrhynchus an-</i> <i>nulipes</i> . <i>Taeniorrhynchus do-</i> <i>mesticus</i> . <i>Culex gelidus</i>	Diptera

Arthropod Hosts of Nematodes.—Continued

Family	Nematode	Primary host	Group	Secondary host	Group
FILARIDAE	<i>Wuchereria bancrofti</i> .. (continued)	Man	Primate	<i>Culex fatigans</i> <i>Culex fuscocephalus</i> .. <i>Culex microannulatus</i> .. <i>Culex ciliaris</i> <i>Culex pipiens</i> <i>Culex procar</i> <i>Culex tenuis</i> <i>Culex sitiens</i> <i>Culex quinquefasciatus</i> <i>Culex vigilax</i> <i>Panoptiles africanus</i> . <i>Howardia albolineata</i> . <i>Mansonia pseudotitillans</i> . <i>Mansonioides annulipes</i> . <i>Mansonioides pseudotitillans</i> . <i>Mansonioides unifornis</i> . <i>Stegomyia fasciata</i> ..	Diptera

Arthropod Hosts of Nematodes.—Continued

Family	Nematode	Primary host	Group	Secondary host	Group
FILARIDAE	<i>Dirofilaria immitis</i>	Dog	Carnivore	<i>Aedes aegypti</i>	Diptera
				<i>Aedes punctatus</i>	
<i>Aedes vagans</i>					
<i>Aedes vexans</i>					
<i>Anopheles algeriensis</i> ..					
<i>Anopheles bifurcatus</i> ..					
<i>Anopheles maculipennis</i> ..					
<i>Anopheles palestinus</i> ..					
<i>Anopheles sinensis</i> ...					
<i>Anopheles superpictus</i> ..					
<i>Culex malariae</i>					
<i>Culex penicillaris</i>					
<i>Culex pipiens</i>					
<i>Culex quinquefasciatus</i> ..					
<i>Culex fatigans</i>					
<i>Myzorchynchus pseudopictus</i> ..					
<i>Myzomyia superpicla</i> ..	Siphonaptera				
<i>Ctenocephalus canis</i> ...					
<i>Ctenocephalus felis</i> ...					
<i>Rhipicephalus sanguineus</i> ..	Arachnida				
<i>Dirofilaria repens</i>	Dog	Carnivore	<i>Aedes aegypti</i>	Diptera	
			<i>Aedes fasciatus</i>		
			<i>Anopheles maculipennis</i> ..		

Arthropod Hosts of Nematodes.—Continued

Family	Nematode	Primary host	Group	Secondary host	Group
FILARIIDAE	<i>Oncoercera volkulus</i>	Man	Primate	<i>Simulium damnosum</i>	Diptera
	<i>Oncocerca caecutiens</i>	Man	Primate	(?) <i>Culex</i> sp. (?) <i>Simulids</i>	Diptera
	<i>Loa loa</i>	Man	Primate	<i>Chrysops centurionis</i> <i>Chrysops dimidiatus</i> <i>Chrysops longicornis</i> <i>Chrysops silaceus</i> <i>Haematopota cordigera</i> <i>Hippocentrum trimaculatum</i>	Diptera
	<i>Setaria labiatio-papillosa</i>	Cattle	Ungulate	(?) <i>Stomoxys calcitrans</i>	Diptera
	<i>Dipetalonema reconditum</i>	Dog	Carnivore	<i>Haematopinus piliferus</i>	Anopleura
				<i>Culex fatigans</i> <i>Culex quinquefasciatus</i>	Diptera
				<i>Ctenocephalus canis</i> <i>Ctenocephalus felis</i> <i>Pulex irritans</i>	Siphonaptera
				? <i>Rhipicephalus siculus</i> ? <i>Rhipicephalus sanguineus</i>	Arachnida

Arthropod Hosts of Nematodes.—Continued

Family	Nematode	Primary host	Group	Secondary host	Group
FILARIIDAE	<i>Dipetalonema persiansi</i> ..	Man	Primate	<i>Aedes aegypti</i>	Diptera
				<i>Aedes suguens</i>	
				<i>Culex pipiens</i>	
				<i>Anopheles costalis</i> ...	
				<i>Anopheles maculipennis</i> .	
				<i>Chrysoconops fuscopematus</i> .	
				<i>Culicoides austeni</i>	
				<i>Culicoides grahamsi</i> ...	
				<i>Mansonioides uniformis</i> .	
				<i>Panophiles</i> sp.	
				(?) <i>Chrysops centuri-</i>	Siphonaptera
				<i>onis</i> .	
				<i>Pulex irritans</i>	
				<i>Ornithodoros moubata</i> .	Arachnida
				<i>Argas</i> sp.	
	<i>Dipetalonema grassii</i> ...	Dog	Carnivore	<i>Rhipicephalus sanguineus</i> .	Arachnida

Arthropod Hosts of Nematodes.—Continued

Family	Nematode	Primary host	Group	Secondary host	Group
DRACUNCULIDAE	<i>Dracunculus medinensis</i> .	Man Dog Leopard Horse Cattle Sheep Goat <i>Gazella bennetti</i>	Primate Carnivores Ungulates	<i>Cyclops coronatus</i> <i>Cyclops leuckartii</i> <i>Cyclops quadricornis</i> .. <i>Cyclops viridis</i> <i>Cyclops prasinus</i> <i>Cyclops bicuspidatus</i> .. <i>Cyclops strenuus</i>	Copepoda
	<i>Dracunculus</i> sp. ?	Indian cobra	Reptile	<i>Cyclops</i> sp.	Copepoda
	<i>Dracunculus globocephalus</i> .	<i>Chelydra serpentina</i>	Reptile	<i>Cyclops bicuspidatus</i>	Copepoda
	<i>Philometra sanguineus</i> ..	<i>Carassius vulgaris</i> <i>Abramis vimba</i> <i>Galaxias scriba</i> <i>Leuciscus rutilus</i> <i>Osmerus eberlani</i> <i>Coltus gobio</i>	Fish	<i>Cyclops</i> sp. <i>Diaptomus</i> sp.	Copepoda
UNCERTAIN	<i>Agamospirura muscarum</i> ?	?	?	<i>Musca terrae-reginae</i>	Diptera
	<i>Agamofilaria tabanicola</i> ..?	?	?	<i>Tabanus circumdatus</i>	Diptera
	<i>Spiroptera ephemeridarum</i> .	?	?	<i>Ephemerella vulgata</i> <i>Oligoneuria rheana</i>	Ephemera

Arthropod Hosts of Nematodes.—Continued

Family	Nematode	Primary host	Group	Secondary host	Group
UNCERTAIN	<i>Cystopsis acipenseris</i> ...	<i>Acipenser huso</i> <i>Acipenser ruthenus</i> ... }	Fish	<i>Eusimulium reptans</i>	Diptera
	<i>Agamonematodum blaps-mortisagae</i> .	?	?	<i>Blaps mortisaga</i>	Coleoptera
	<i>Agamonema</i> sp. Johnston, 1913.	?	?	<i>Ceratophyllus fasciatus</i> } <i>Xenopsylla cheopis</i> .. }	Siphonaptera
	Larval nema of Cobb, 1922.	?	?	<i>Aphodius fmetarius</i>	Coleoptera
	Larval nema of Cram, 1924.	?	?	<i>Pinotus carolinus</i>	Coleoptera
	Larval nema of Johnston & Bancroft, 1920.	?	?	<i>Fannia</i> sp.	Diptera

seaxalatus, a spirurid parasite not uncommon in the stomachs of swine and peccaries, will develop to an infective third-stage larva in its beetle host, and when these beetles are fed to some unusual host, such as rodents, birds, or even cold-blooded animals, the larval worm will re-encyst as a third-stage larva in the unusual host; but if the infected unusual host is fed to a suitable primary host, the larva will continue its development to maturity. How extensive this device is we do not know, but it may prove to be a common means of transmitting the spirurid worms of rapacious birds, as Cram has suggested, the spirurids of these birds producing eggs which infect some arthropod host, such as a beetle, the beetle being eaten by a small mammal, bird, amphibian or reptile, which is infected in turn with the third-stage larva, and the bird of prey eating these animals and becoming infested with the adult worms. The investigation of these life histories is a thing on which the mammalogist, the ornithologist, the herpetologist, the entomologist and the parasitologist might collaborate to great advantage, and the results might show some very interesting and surprising biological interrelationships.

As intermediate hosts of spirurids, the Orthoptera are also of some importance. The arthropods in question are all cockroaches, and they are probably of special importance as intermediate hosts for parasites of such rodents as rats and mice. These rodents seem to eat cockroaches with dependable certainty, and the association of rats, mice and roaches in the household provides a suitable and, so to speak, natural combination of factors for the benefit of these spirurids. On the other hand, the development of spirurid parasites of sheep, cattle and horses in cockroaches must be regarded as a case in which the roach merely serves as a host for a worm which cannot depend on such a host for its transmission, but which is capable of developing in that host as a case of accidental parasitism. In this connection it may be noted that roaches will serve as intermediate hosts for so many worms in this way that these insects make excellent experiment animals for carrying out life-history experiments in the laboratory. The plentiful supply of these insects in winter, a thing so unfortunate from some points of view, is a fortunate thing for the parasitologist who obtains interesting worms in winter at a time when other insects are scarce, and wishes to carry out feeding experiments on some insect.

The Diptera appear as intermediate hosts of spirurids with 14 species serving as hosts for 3 known species of spirurids, all species of the genus *Habronema* and all parasitic in horses and other members of the Equidae. This association obviously depends in part on the importance of the manure of horses and other Equidae as a breeding

place for Diptera. The transmission of the worm from the fly to the horse appears to present several complications. It was surmised by Ransom that horses might swallow flies which had fallen in drinking troughs or were benumbed in feed troughs on cold mornings. Subsequent work has indicated that the worms may escape from the proboscis of flies as they feed on the moist lips of horses, and presumably these worms may get to the stomach and develop to adult worms. However, if the fly feeds on the conjunctiva of the eye the larval worms may escape to the eye, remaining there as larvae and causing a habronemic conjunctivitis. If the fly feeds on a wound, the worms may escape and remain in the wound as larvae, causing "summer sores" or cutaneous habronemiasis. Finally, the worms may be found as larvae in the lungs, causing pulmonary habronemiasis, but the precise method of infection here remains to be ascertained. These cases illustrate the fact that there are numerous deviations from the cut-and-dried rule that intermediate hosts either transmit worms by being eaten by the primary host, or else transmit the worms by biting the primary host.

One member of the Siphonaptera occurs as a somewhat doubtful host of a rat spirurid, *Protospirura muris*, but the case for this should be developed by feeding experiments.

The one bird nematode of the family Spiruridae having a known life history is *Hartertia gallinarum*, and this worm utilizes a termite as its intermediate host, the host here serving as food for chickens which devour them with great eagerness.

THELAZIIDAE

In the Thelaziidae, we have a member of the Orthoptera, the roach *Pycnoscelis surinamensis*, serving as the intermediate host of the chicken eyeworm, *Oxyspirura mansoni*, and also for the somewhat dubious species, *O. parvovum*, distinguished from *O. mansoni* only by the smaller size of the egg. This life history was worked out by Fielding in Australia and somewhat later, but independently, by Sanders in Florida in the United States. At present the eyeworm, *O. mansoni*, appears to be confined in the United States to Florida, so far as our records show, but the intermediate host now has a much wider range in this country and unless measures are taken to stamp out the worm in Florida we can confidently expect it to spread beyond the confines of that state. The movements of the infected primary and secondary hosts by the swift methods of modern transportation over wide areas can hardly fail to ensure this result. [Since the above was written, the eyeworm has been found outside of Florida in this country.]

ACUARIIDAE

In the Acuariidae, we are dealing with bird parasites. Of the two worm species involved, one is a parasite of water birds, Anseriformes, and it is not surprising to find that this worm, *Echinuria uncinata*, uses Cladocera as its intermediate hosts, the one known intermediate host being *Daphnia pulex*. The other worm is a parasite of land birds, Galliformes and Columbiformes, and utilizes an isopod, *Porcellio laevis*. [Cram has since found grasshoppers to be intermediate hosts for Acuariidae of terrestrial birds.]

TETRAMERIDAE

In the Tetrameridae we are again dealing with bird parasites, and here again the intermediate hosts are Entomostraca, a cladoceran, *Daphnia pulex*, and an amphipod, *Gammarus pulex*. The one worm for which we know the life history, *Tetrameres fissispina*, is usually and normally a parasite of water birds, Anseriformes, and its occurrence in land birds must be regarded as following from the accidental swallowing of the infected entomostracans while drinking, whereas in water birds we are dealing with a dependable arrangement, from the standpoint of the parasite, based on Entomostraca in the double rôle of food for the primary host and of secondary host for the worm. [Cram has recently found grasshoppers serving as intermediate host of tetramerids of terrestrial birds.]

CUCULLANIDAE

For the one cucullanid with a known life history, a fish nematode, copepods and aquatic isopods serve as intermediate hosts, the hosts also serving as food for fish.

CAMALLANIDAE

For the two camallanids with known life histories, one a fish nematode and one a turtle nematode, copepods are hosts for both and dragonflies also serve as hosts for one. These hosts are also food for the primary hosts.

HEDRURIDAE

Of two species of hedrurids, parasitic in reptiles, amphibians and fish, one uses aquatic isopods and one amphipods as intermediate hosts.

The foregoing families are regarded by many parasitologists as part of the superfamily Spiruroidea, and in this superfamily the life history is usually one in which the transfer of the larval nematode to the primary host is accomplished when this host swallows the sec-

ondary host, either as food or accidentally, such apparent exceptions as in the case of *Habronema* being the unusual thing. We now take up a group of worms which all fall in the family Filariidae, regarded by those who recognize the superfamily Spiruroidea as described above, as being part of the superfamily Filarioidea, the two superfamilies being grouped on their affinities as the Filariata.

FILARIIDAE

In the Filariidae the customary mode of transmission of the worm is by the bite of the secondary host, this host becoming infected when it bites an infested primary host and in turn infecting a primary host by biting it after an interval in which the worm develops to the infective stage in the secondary host. It is to be expected, then, that the biting Diptera will show up prominently in this list of intermediate hosts, and we find a long list of such hosts recorded as transmitting numerous species of filarid worms. Here we have a number of important worm parasites of man and dogs, including such filarids as *Wuchereria bancrofti* and *Loa loa* of man, and the heart worm, *Dirofilaria immitis*, a serious pest of dogs in the hunting field. Mosquitoes take first place in this group of Diptera, many species transmitting *W. bancrofti* and *D. immitis*, while the tabanids, especially *Chrysops* spp., function for *Loa loa*.

The Siphonaptera, Mallophaga, Anopleura, and Arachnida are all charged with the transmission of filarid worms.

DRACUNCULIDAE

In the peculiar genus *Dracunculus*, including the guinea worm of man, *D. medinensis*, the worms usually infest superficial body parts of the primary host, and when these come in contact with water, the worms release large numbers of embryos, some of which are swallowed by copepods. The larval worms develop in these hosts to the infective stage and when these hosts are swallowed by suitable primary hosts the worms develop to maturity.

ARTHROPODS AS INTERMEDIATE HOSTS OF ACANTHOCEPHALIDS

The acanthocephalids quite generally utilize at least one intermediate host, and sometimes two such hosts, the second one a fish, amphibian, or bird in some cases, in their life history. These first intermediate hosts are sometimes snails or leeches, but in most of the reported cases the first intermediate host is an arthropod. The following list shows the reported hosts for the species having known life histories:

Arthropod Hosts of Acanthocephalids

Family	Acanthocephalid	Primary host	Group	Secondary host	Group
NEOECHINORHYNCHI- DAE.	<i>Neoechinorhynchus rutili</i> .	<p><i>Abramis björkna</i></p> <p><i>Abramis brama</i></p> <p><i>Alburnus alburnus</i></p> <p><i>Acerina cernua</i></p> <p><i>Anguilla anguilla</i></p> <p><i>Barbus barbuis</i></p> <p><i>Carassius carassius</i></p> <p><i>Chondrostoma nasus</i></p> <p><i>Cobitis taenia</i></p> <p><i>Cyprinus carpio</i></p> <p><i>Esox lucius</i></p> <p><i>Gasterosteus aculeatus</i></p> <p><i>Gasterosteus pungitius</i></p> <p><i>Gobio gobio</i></p> <p><i>Leuciscus leuciscus</i></p> <p><i>Leuciscus idus</i></p> <p><i>Leuciscus erythrophthalmus</i>.</p> <p><i>Leuciscus phoxiniscus</i></p> <p><i>Leuciscus rutilus</i></p> <p><i>Lota lota</i></p> <p><i>Perca fluviatilis</i></p> <p><i>Salmo fario</i></p> <p><i>Tinca tinca</i></p> <p><i>Emys orbicularis</i></p> <p><i>Rana esculenta</i></p>	Fish	<p><i>Sialis niger</i></p> <p><i>Sialis lutaria</i></p>	Neuroptera

Arthropod Hosts of Acanthocephalids.—Continued

Family	Acanthocephalid	Primary host	Group	Secondary host	Group
MONILIFORMIDAE	<i>Moniliformis moniliformis</i> .	Rat	Rodents	<i>Blaps gigas</i> <i>Blaps mucronata</i>	Coleoptera
		Mouse			
		<i>Mus fuscirostris</i>			
		<i>Cricetus frumentarius</i>			
		<i>Microtus arvalis</i>		<i>Periplaneta americana</i>	Orthoptera
		<i>Myoxus quercinus</i>		<i>Blatta orientalis</i>	
		<i>Arvicola arvalis</i>			
		<i>Mustela putorius</i>	Carnivore		
		Man	Primate		
		<i>Falco cinereus</i>	Accipitriformes		
ECHINORHYNCHIDAE .	<i>Pomphorhynchus laevis</i> ..	<i>Abramis blicca</i>	Fish	<i>Gammarus pulex</i>	Amphipoda
		<i>Abramis brama</i>			
		<i>Abramis vimba</i>			
		<i>Acerina vulgaris</i>			
		<i>Acipenser huso</i>			
		<i>Anguilla vulgaris</i>			
		<i>Belone acis</i>			
		<i>Cobitis barbata</i>			
		<i>Coregonus wartmannii</i>			
		<i>Cottus</i> spp.			
		<i>Cyprinus idbarus</i>			
		<i>Esox lucius</i>			
		<i>Salmo</i> spp.			
Many other fish.					

Arthropod Hosts of Acanthocephalids.—Continued

Family	Acanthocephalid	Primary host	Group	Secondary host	Group
ECHINORHYNCHIDAE	<i>Acanthocephalus lucii</i> ...	<i>Abramis brama</i> <i>Acerina cernua</i> <i>Anguilla anguilla</i> <i>Barbus barbus</i> <i>Coregonus</i> spp. <i>Cottus gobio</i> <i>Cyprinus carpio</i> <i>Esox lucius</i> <i>Gasterosteus aculeatus</i> <i>Gobio gobio</i> Many other fish.....	Fish	<i>Asellus aquaticus</i>	Isopoda
	<i>Echinorhynchus ranae</i> ...	<i>Rana temporaria</i> <i>Rana esculenta</i> <i>Bombinator igneus</i> ... <i>Bufo vulgaris</i> <i>Bufo viridis</i> <i>Salamandra atra</i> <i>Triton</i> spp.	Amphibians	<i>Pontoporeia hoyi</i> <i>Asellus aquaticus</i>	Amphipoda Isopoda
	<i>Echinorhynchus thecatus</i> .	<i>Roccus americanus</i> ... <i>Catostomus commersonii</i> <i>Micropterus dolomieu</i> <i>Micropterus salmoides</i> <i>Ambloplites rupestris</i> . <i>Percina caprodes</i> <i>Percia flavescens</i> <i>Esox lucius</i> <i>Esox reticulatus</i> <i>Anguilla rostrata</i> <i>Ameiurus nebulosus</i> .. <i>Stizostedion vitreum</i> ...	Fish	<i>Hyalella knickerbockeri</i> .	Amphipoda

An inspection of the tables indicates, first of all, that we have but limited knowledge of the life histories of acanthocephalids in any one family, and that it will not be possible to generalize to any great extent on such limited data. What may be said is as follows:

NEOECHINORHYNCHIDAE

In the Neoechinorhynchidae we know the life history of one acanthocephalid, a parasite occurring in a large number of fish and in some reptiles and amphibians, and the known intermediate hosts are species of *Sialis*, one an unrecognized species, in the Neuroptera, other hosts being leeches and snails.

GIGANTORHYNCHIDAE

In the Gigantorhynchidae we again have only one known life history. In this case the echinorhynch occurs as an adult in mammals of various groups, including primates, carnivores, and insectivores, and has a species of *Blaps*, a coleopteron, as an intermediate host.

OLIGACANTHORHYNCHIDAE

In the Oligacanthorhynchidae we again have one acanthocephalid with a known life history, the well-known thorn-headed worm of swine, occurring in such animals as swine, carnivores, and man and other primates. This worm has a number of species of scarabaeid beetles as its intermediate hosts.

CORYNOSOMIDAE

In the Corynosomidae we have one known life history, that of an acanthocephalid of water fowl, Anseriformes, using crustaceans, amphipods and crayfish, as intermediate hosts.

MONILIFORMIDAE

In the Moniliformidae we have a parasite with a wide range of primary hosts, from man, carnivores and rodents to rapacious birds, and having as its intermediate hosts two species of Coleoptera and two of Orthoptera.

ECHINORHYNCHIDAE

In the Echinorhynchidae we have three acanthocephalids parasitic in fish of numerous species, two of them with an amphipod as an intermediate host and one with an aquatic isopod as an intermediate host; and one acanthocephalid parasitic in various amphibians and with an amphipod as its intermediate host.

By way of summary it may be noted that of three acanthocephalids parasitic in mammals, all develop in insects, all with Coleoptera and one with Orthoptera also as intermediate hosts; the one acanthocephalid habitually parasitic in water birds uses crustaceans as intermediate hosts; and that of five acanthocephalids parasitic in fish and amphibians, four use crustaceans as intermediate hosts, these being amphipods in two cases, isopods in one case, and both amphipods and isopods in one case. In the case of one acanthocephalid in fish, the Neuroptera serve as hosts. Insects are apparently of major importance for acanthocephalids of mammals and crustaceans for acanthocephalids of fish.

In the foregoing lists of parasites arranged by orders and families, the names given for the arthropod hosts are those under which they are reported in the literature and no attempt is made in these lists to eliminate synonyms for the reason already given that it is easier to trace these references in the literature under the names quoted. In the following lists arranged on the basis of intermediate hosts, synonyms are cross-referenced to the names accepted by the authorities already mentioned in the first part of the paper.

ARTHROPOD HOSTS OF HELMINTHS, ARRANGED BY HOST GROUPS

INSECTA

ANOPLERA

Haematopinus piliferus. See *Linognathus piliferus*.
Linognathus piliferus
Dipetalonema reconditum

DERMAPTERA

Anisolabis annulipes
Hymenolepis diminuta
Hymenolepis microstoma

EPHEMERIDA

Blasturus cupidus. See *Leptophlebia cupida*.
Clocon dipterum
 ? *Opisthioglyphe endoloba*
Ephemera danica
Stephanophiala farionis
Ephemera vulgata
Allocreadium isoporum
Opisthioglyphe endoloba
Spiroptera ephemeridarum

Ephemerid

Lecithodendrium lagena
Cercaria secunda
Hexagenia sp.
Crepidostomum cornutum
Stephanophiala farionis
Leptophlebia cupida
Allocreadium commune
Oligoneuria rhenana
Spiroptera ephemeridarum

COLEOPTERA

Ablattaria laevigata
Weinlandia uncinata
Akis goryi
Spirura gastrophila
Spirocercia sanguinolenta
Akis spinosa
Hymenolepis diminuta
Aphodius castaneus. See *Aphodius rufus castaneus*.
Aphodius coloradensis
Gongylonema scutatum

- Aphodius distinctus*
Gongylonema scutatatum
Aphodius femoralis
Gongylonema scutatatum
Aphodius finetarius
Protospirura gracilis
Gongylonema scutatatum
 Larval nema of Cobb, 1922
Aphodius granarius
Hymenolepis carioca
Gongylonema scutatatum
Aphodius haemorrhoidalis
 ? *Gongylonema pulchrum*
Aphodius obscurus
 ? *Cittotaenia marmotae*
Aphodius rubeolus
Gongylonema scutatatum
Aphodius rufus
Arduenna strongylina
Aphodius rufus castaneus
Arduenna strongylina
Aphodius sp.
Gongylonema scutatatum
Aphodius vittatus
Gongylonema scutatatum
Ateuchus sacer. See *Scarabaeus sacer*.
Ateuchus sp.
Physaloptera abbreviata
Blaps appendiculata
Gongylonema scutatatum
Blaps emondi
Gongylonema scutatatum
Blaps gigas
Moniliformis moniliformis
Blaps mortisaga
Agamonematodum blapis-mortisagae
Blaps mucronata
Moniliformis moniliformis
Blaps spp.
Spirura gastrophila
Gongylonema scutatatum
Gongylonema brevispiculum
Gigantorhynchus spirula
Blaps strauchi
Spirura gastrophila
Gongylonema scutatatum
Gongylonema brevispiculum
Caccobius schreberi
 ? *Gongylonema pulchrum*
Canthon sp.
Spirocerca sanguinolenta
Cetonia aurata
Spirura talpac
Macracanthorhynchus hirudinaceus
Chironitis irroratus
Gongylonema mucronatum
Copris hispanus
Spirocerca sanguinolenta
Diloboderus abderus
Macracanthorhynchus hirudinaceus
Geotrupes douei. See *Geotrupes* (*Stereopyge*) *douei*.
Geotrupes (*Stereopyge*) *douei*
Spirocerca sanguinolenta
 ? *Physocephalus sexualatus*
Gongylonema mucronatum
Geotrupes (*Anoplotrupes*) *stercorosus*
Choanotaenia infundibulum
Hymenolepis serpentulus
 ? *Physocephalus sexualatus*
Geotrupes stercorarius
Physalocephalus sexualatus
Geotrupes stercorosus. See *Geotrupes* (*Anoplotrupes*) *stercorosus*.
Geotrupes sylvaticus
Choanotaenia infundibulum
Hymenolepis serpentulus
Gymnopleurus mopsus
Gongylonema mucronatum
Gymnopleurus sturmi
Spirocerca sanguinolenta
Gongylonema mucronatum
Ilybius fuliginosus
Haplometra cylindracea
Ilybius sp.
Cercaria prima
Melolontha melolontha
Macracanthorhynchus hirudinaceus
Melolontha vulgaris. See *Melolontha melolontha*.
Onticellus fulvus
Gongylonema scutatatum
Onitis irroratus. See *Chironitis irroratus*.
Onthophagus bedeli
Physocephalus sexualatus
Gongylonema mucronatum

Onthophagus hecate
Arduenna strongylina
Physocephalus sexalatus
Gongylonema scutatum
Onthophagus nebulosus
Physocephalus sexalatus
Onthophagus pennsylvanicus
Gongylonema scutatum
Onthophagus sp.
Spirura gastrophila
Onthophagus taurus
 ? *Gongylonema scutatum*
Phyllophaga arcuata
Macracanthorhynchus hirudinaceus
Phyllophaga fervens. See *Phyllophaga fusca*.
Phyllophaga fusca
Macracanthorhynchus hirudinaceus
Phyllophaga rugosa
Macracanthorhynchus hirudinaceus
Phyllophaga vehemens
Macracanthorhynchus hirudinaceus
Pinotus carolinus
 Larval nema of Cram, 1924
Scarabaeus sacer
Spirura gastrophila
Spirocerca sanguinolenta
Physocephalus sexalatus
Gongylonema mucronatum
Scarabaeus variolosus
Spirocerca sanguinolenta
Physocephalus sexalatus
Scaurus striatus
Hymenolepis diminuta
Silpha laevigata. See *Ablattaria laevigata*.
Strategus julianus
Macracanthorhynchus hirudinaceus
Tenebrio molitor
Hymenolepis arvicolae
 ? *Hymenolepis nana*
Hymenolepis diminuta
Hymenolepis microstoma
Onchoscolex decipiens
Protospirura muris
Gongylonema neoplasticum
Tenebrio obscurus
Gongylonema sp.
Tribolium ferrugineum
Hymenolepis diminuta

"Water beetles"
Pleurogenes medians
Pleurogenes claviger
Pleurogenes confusus
Xyloryctes satyrus
Macracanthorhynchus hirudinaceus

DIPTERA

Aedes aegypti
Filaria ozzardi
Wuchereria bancrofti
Dirofilaria immitis
Dirofilaria repens
Dipetalonema perstans
Aedes albolineata
Wuchereria bancrofti
Aedes albopictus
Wuchereria bancrofti
Aedes caspius
Dirofilaria immitis
Aedes fasciatus. See *Aedes aegypti*.
Aedes (Finlaya) *togoi*
Wuchereria bancrofti
Aedes gracilis. See *Bironella gracilis*
 and *Anopheles gracilis*.
Aedes perplexus
Wuchereria bancrofti
Aedes pseudoscutellaris. See *Aedes variegatus*.
Aedes punctatus. See *Aedes caspius*.
Aedes scutellaris. See *Aedes albopictus*.
Aedes sugens. See *Aedes vittatus*.
Aedes vagans
Dirofilaria immitis
Aedes variegatus
Wuchereria bancrofti
Aedes vexans
Dirofilaria immitis
Aedes vigilax
Wuchereria bancrofti
Aedes vittatus
Dipetalonema perstans
Anastellorhina augur
Habronema sp.
Anopheles albimanus
Filaria ozzardi
Wuchereria bancrofti
Anopheles albitarsis
Filaria ozzardi

- Anopheles algeriensis*
Dirofilaria immitis
Anopheles annulipes
Wuchereria bancrofti
Anopheles argyritarsis
Wuchereria bancrofti
Anopheles barbirostris
Wuchereria bancrofti
Anopheles bifurcatus
Dirofilaria immitis
Agamodistomum martiranoi
Anopheles claviger. See *Anopheles bifurcatus*.
Anopheles costalis. See *Anopheles gambiae*.
Anopheles culifaciens
Agamodistomum sintoni
Anopheles fuliginosus
Cercaria of Stephens & Christophers, 1902
Anopheles funestus listoni. See *Anopheles listonii*.
Anopheles gambiae
Wuchereria bancrofti
Dipetalonema perstans
Anopheles gracilis
? *Wuchereria bancrofti*
Anopheles hyrcanus pseudopictus
Dirofilaria immitis
Anopheles hyrcanus sinensis
Wuchereria bancrofti
Dirofilaria immitis
Anopheles listonii
Agamodistomum sintoni
Anopheles maculipennis
Lecithodendrium lagena
Agamodistomum anophelis
Filaria ozzardi
Filaria sp. Fuelleborn, 1909
Dirofilaria immitis
Dirofilaria repens
Dipetalonema perstans
Anopheles palestinus. See *Anopheles superpictus*.
Anopheles rossi. See *Anopheles subpictus*.
Anopheles sinensis. See *Anopheles hyrcanus sinensis*.
Anopheles sinensis peditaeniatus
Wuchereria bancrofti
- Anopheles sinensis pseudopictus*
Dirofilaria immitis
Anopheles sinensis vanus. See *Anopheles barbirostris*.
Anopheles subpictus
Cercaria of Soparkar, 1918
Cercaria of Stephens & Christophers, 1902
Wuchereria bancrofti
Anopheles superpictus
Wuchereria bancrofti
Dirofilaria immitis
Anopheles tarsimaculatus
Filaria ozzardi
Bironella gracilis
? *Wuchereria bancrofti*
Chironomus libiferus
Lissorthis fairporti
Chironomus plumosus
Lecithodendrium lagena
Chrysoconops fuscopennatus. See *Mansonia fuscopennatus*.
Chrysops centurionis
Loa loa
? *Dipetalonema perstans*
Chrysops dimidiatus
Loa loa
Chrysops longicornis
Loa loa
Chrysops silaceus
Filaria sp. of Med. Rept., Lagos, Nigeria, 1918
Loa loa
Corethra sp.
Cercaria *prima*
Cercaria *secunda*
Culex ciliaris. (May be *Aedes cinereus*, fide Dyar.)
Wuchereria bancrofti
Culex fatigans. See *Culex quinquefasciatus*.
Culex fuscocephalus
Wuchereria bancrofti
Culex gelidus
Wuchereria bancrofti
Culex hortensis
Cercaria of Joyeux, 1918
Culex malariae. See *Aedes vexans*.
Culex microannulatus. See *Culex sitiens*.

- Culex penicillaris*. See *Aedes caspius*.
Culex pipiens
Wuchereria bancrofti
Dirofilaria immitis
Dipetalonema perstans
Culex procax. See *Aedes vigilax*.
Culex quinquefasciatus
Filaria ozzardi
Wuchereria bancrofti
Dirofilaria immitis
Dipetalonema reconditum
Culex sitiens
Wuchereria bancrofti
Culex sp.
? *Onchocerca caecutiens*
Culex tenuatus. See *Aedes aegypti*.
Culex vigilax. See *Aedes vigilax*.
Culicoides austeni
Dipetalonema perstans
Culicoides grahami
Dipetalonema perstans
Eusimulium reptans
Cystopsis acipenseris
Fannia sp.
Larval nema of Johnston & Bancroft, 1920
Haematopota cordigera
Loa loa
Hippocentrum trimaculatum
Loa loa
Howardina albolineata. See *Aedes albolineata*.
Lyperosia exigua
Habronema microstoma
Mansonia africana
Wuchereria bancrofti
Mansonia annulipes
Wuchereria bancrofti
Mansonia fuscopennatus
Dipetalonema perstans
Mansonia pseudotitillans
Wuchereria bancrofti
Mansonia sp.
Dipetalonema perstans
Mansonia uniformis
Filaria sp. Castellani & Chalmers, 1913
Wuchereria bancrofti
Dipetalonema perstans
- Mansonioides annulipes*. See *Mansonia annulipes*.
Mansonioides pseudotitillans. See *Mansonia pseudotitillans*.
Mansonioides uniformis. See *Mansonia uniformis*.
Musca bezzi
Habronema spp.
Musca domestica
Choanotaenia infundibulum
Davainea tetragona
Davainea cesticillus
Habronema microstoma
Habronema megastoma
Habronema muscae
Musca fergusonii
Habronema megastoma
Habronema muscae
Musca humilis
Habronema microstoma
Habronema muscae
Musca lusoria
Habronema megastoma
Habronema muscae
Musca terrae-reginae
Habronema megastoma
Habronema muscae
Agamospirura muscarum
Musca ventrosa
Habronema megastoma
Habronema muscae
Musca vetustissima
Habronema megastoma
Habronema muscae
Myzomyia superpicta. See *Anopheles superpictus*.
Myzorhynchus pseudopictus. See *Anopheles hyrcanus pseudopictus*.
Panoplites africanus. See *Mansonia africanus*.
Panoplites sp.
Dipetalonema perstans
Pseudopyrellia sp.
Habronema megastoma
Habronema muscae
Sarcophaga melanura
Habronema microstoma
Sarcophaga misera
Habronema muscae

- Scutomyia albolineata*. See *Aedes albolineata*.
- Simulids
Oncocerca caecutiens
Simulium damnosum
Oncocerca volvulus
- Stegomyia fasciata*. See *Aedes aegypti*.
- Stomoxys calcitrans*
Hymenolepis carioca
Habronema microstoma
? *Habronema muscae*
? *Setaria labiato-papillosa*
- Tabanus circumdatu*
Agamofilaria tabanicola
- Taeniorhynchus annulipes*. See *Mansonias annulipes*.
- Taeniorhynchus domesticus*. Probably
Culex pipiens, q. v.
Wuchereria bancrofti
- Tanypus decoloratus*
Lissorchis fairporti
- ISOPTERA
- Hodotermes pretoriensis*. See *Macrohodotermes mossambicus transvaalensis*.
- Macrohodotermes mossambicus transvaalensis*
Hartertia gallinarum
- LEPIDOPTERA
- Aglossa dimidiata*
Hymenolepis diminuta
- Aphornia gularis*
Hymenolepis diminuta
- Asopia farinalis*
Hymenolepis diminuta
- Nymphula nymphaeata*
Fluke
- Paralipsa gularis*. See *Aphornia gularis*.
- Pyralis farinalis*. See *Asopia farinalis*.
- Tinea granella*
Hymenolepis diminuta
- MALLOPHAGA
- "Bird louse"
? *Filaria cypseli*
Trichodectes latus
Dipylidium caninum
- NEUROPTERA
- Mystacides nigra*
Distomum mystacidis
- Sialis lutaria*. See *Sialis flavilatera*.
- Sialis flavilatera*
Distomum notidobiae
Distomum sialidis
Neoechinorhynchus rutili
- Sialis niger*
Neoechinorhynchus rutili
- ODONATA
- Aeschna* sp.
Prostotocus confusus
- Agrion puella*. See *Cocnagrion puella*.
- Agrion* spp.
Gorgodera pagenstecheri
Gorgodera varsoviensis
Pleurogenes medians
Distomum sp. of Villot
Procercoid of Galli-Valerio, 1923
Camallanus lacustris
- Agrion virgo*
Pneumonoeces variegatus
Pneumonoeces similigenus
Halipegus ovocaudatus
- Calopteryx virgo*. See *Agrion virgo*.
- Coenagrion puella*
Tatria acanthorhyncha.
- Cordulia* sp.
Prostotocus confusus
- "Dragonfly"
Plagiorchis ameiurensis
Cercaria prima
- Epitheca* sp.
Gorgodera pagenstecheri
Gorgodera varsoviensis
Gorgodera cygnoides
- Libellula quadrimaculata*
Prosthogonimus intercalandus
Prosthogonimus pellucidus
- Tetragoneuria* sp.
Prosthogonimus sp. of Kotlan and Chandler

PLECOPTERA

- Perla bicaudata*
Opisthioglyphe endolobum
 "Perlid larva"
Plagiorchis maculosus
Lecithodendrium lagena

ORTHOPTERA

- Blatta orientalis*
Spirura gastrophila
 ? *Spirocerca sanguinolenta*
Gongylonema neoplasticum
Gongylonema sp.
Moniliformis moniliformis
Blattella germanica
Protospirura columbiana
Gongylonema neoplasticum
Gongylonema scutatum
Gongylonema pulchrum
Periplaneta americana
Gongylonema neoplasticum
Gongylonema orientale
Gongylonema sp.
Moniliformis moniliformis
Periplaneta australasiae
Gongylonema orientale
Pycnoscelus surinamensis
Oxyspirura mansonii
Oxyspirura parvovum

SIPHONAPTERA

- Ceratophyllus fasciatus*
Hymenolepis diminuta
 ? *Hymenolepis nana*
Hymenolepis microstoma
Agamonema sp. Johnston, 1913
Ctenocephalus canis
Dipylidium caninum
Hymenolepis diminuta
Dirofilaria immitis
Dipetalonema reconditum
Ctenocephalus felis
Dipylidium caninum
Dirofilaria immitis
Dipetalonema reconditum
Leptopsylla musculi
Hymenolepis diminuta

Mesopsylla eucta

- Cysticeroid* of Dampf, 1910
Pulex irritans
Dipylidium caninum
Hymenolepis diminuta
Dipetalonema reconditum
Dipetalonema perstans
Xenopsylla cheopis
Hymenolepis diminuta
 ? *Hymenolepis nana*
 ? *Protospirura muris*
Agamonema sp. Johnston, 1913

TRICHOPTERA

- Anabolia nervosa*
Allocreadium isoporum
Opisthioglyphe endolobum
Chaetopteryx villosa
Allocreadium isoporum
Drusus trifidus
Plagiorchis maculosus
Limnophilus flavicornis
Opisthioglyphe endolobum
Limnophilus griseus
Opisthioglyphe endolobum
Limnophilus lunatus
Opisthioglyphe endolobum
Limnophilus rhombicus
Opisthioglyphe endolobum
Distomum limnophili
Notidobia ciliaris
Distomum notidobiae
Phryganea grandis
Opisthioglyphe endolobum
Lecithodendrium cheilostomum
Brachycoelium retusum
Distomum phryganeae
Phryganea sp.
Lecithodendrium cheilostomum
Rhyacophila nubila
 Fluke

UNPLACED

- "Amphibious insects"
Plagioporus sp.
Eumegacetes sp.
 "Raubinsekten"
Gorgodera vitelliloba

ARACHNIDA

ACARINA

<i>Argas</i> sp.	<i>Rhipicephalus sanguineus</i>
<i>Dipetalonema perstans</i>	<i>Dipetalonema reconditum</i>
<i>Ixodes ricinus</i>	<i>Dipetalonema grassii</i>
? <i>Filaria martis</i>	<i>Dirofilaria immitis</i>
<i>Ornithodoros moubata</i>	<i>Rhipicephalus siculus</i>
<i>Dipetalonema perstans</i>	? <i>Dipetalonema reconditum</i>
	"Tick"
	? <i>Filaria mitchelli</i>

MYRIAPODA

<i>Fontaria virginiensis</i>	<i>Julus guttulatus</i>
<i>Hymenolepis diminuta</i>	Nematode larva
<i>Glomeris limbata</i>	<i>Julus</i> sp.
Cestode larva	<i>Hymenolepis diminuta</i>

CRUSTACEA

AMPHIPODA

<i>Allorchestes</i> sp.	<i>Hyallela knickerbockeri</i> . See <i>Hyallela azteca</i> .
? <i>Hedruris orestiae</i>	<i>Pontoporeia hoyi</i>
<i>Gammarus locusta</i>	<i>Echinorhynchus ranae</i>
<i>Distomum gammarum</i> Rentsch	<i>Themisto libellula</i>
<i>Polymorphus boschadisi</i>	<i>Sinistroporus simplex</i>
<i>Gammarus ornatus</i> . See <i>Gammarus locusta</i> .	BRANCHIOPODA
<i>Gammarus pulex</i>	<i>Apus</i> sp.
<i>Opisthoglyphe endolobum</i>	<i>Agamodistomum apodis</i>
<i>Distomum agamos</i>	CLADOCERA
<i>Distomum gammarum</i> Linstow	<i>Bythotrephes longimanus</i>
<i>Distomum pulicis</i>	<i>Proteoccephalus agonis</i>
<i>Hymenolepis collaris</i>	<i>Daphnia pulex</i>
<i>Hymenolepis tenuirostris</i>	<i>Echinuria uncinata</i>
<i>Aploparaksis dujardini</i>	<i>Tetrameres fissispina</i>
<i>Echinocotyle mrazeki</i>	<i>Leptodora kindtii</i>
<i>Cysticercoides</i> sp. Mrazek, 1896	<i>Proteoccephalus agonis</i>
<i>Cysticercus bifurcus</i>	COPEPODA
<i>Cysticercus hamanni</i>	<i>Acartia clausa</i>
<i>Cysticercus taeniae-pachyacanthae</i>	<i>Hemiusurus appendiculatus</i>
<i>Cysticercus</i> sp. Luehe, 1910	<i>Acartia</i> sp.
<i>Cysticercus</i> sp. Mrazek, 1890	<i>Derogenes varius</i>
<i>Taenia</i> sp. Daday, 1900; 168	<i>Boeckella braziliensis</i> . See <i>Pseudo-boeckella braziliensis</i> .
<i>Tetrameres fissispina</i>	<i>Cyclops agilis</i> . See <i>Cyclops serrulatus</i> .
<i>Polymorphus boschadisi</i>	<i>Cyclops albidus</i>
<i>Pomphorhynchus laevis</i>	<i>Proteoccephalus ambloplitis</i>
<i>Hyallela azteca</i>	
<i>Echinorhynchus thecatus</i>	
<i>Proteoccephalus ambloplitis</i>	

- Cyclops bicuspidatus*
Hymenolepis tenuirostris
Drepanidotaenia lanceolata
Schistocephalus solidus
Bothriocephalus cuspidatus
Corallobothrium fimbriatum
Dracunculus globocephalus
Cyclops brevicaudata. See *Cyclops strenuus*.
Cyclops brevispinosus
Bothriocephalus cuspidatus
Diphyllobothrium latum
Cyclops coronatus. See *Cyclops fuscus*.
Cyclops crassicornis
Hymenolepis brachycephala
Cyclops fimbriatus. See *Platycyclops fimbriatus*.
Cyclops fuscus
Dracunculus medinensis
Cyclops leuckarti
Proteocephalus ambloplitis
Bothriocephalus cuspidatus
Diphyllobothrium mansoni
Dracunculus medinensis
Cyclops lucidulus
Hymenolepis collaris
Cyclops oithonoides. See *Mesocyclops oithonoides*.
Cyclops prasinus
Proteocephalus ambloplitis
Corallobothrium giganteum
Bothriocephalus cuspidatus
Dracunculus medinensis
Cyclops pulchellus. See *Cyclops bicuspidatus*.
Cyclops quadricornis
Cucullanus elegans
Dracunculus medinensis
Cyclops robustus
Diphyllobothrium latum
Cyclops serratus. See *Cyclops bicuspidatus*.
Cyclops serrulatus
Hymenolepis collaris
Hymenolepis tenuirostris
Hymenolepis fasciculata
Hymenolepis microsoma
Proteocephalus torulosus
Proteocephalus longicollis
Proteocephalus percae
- Corallobothrium giganteum*
Corallobothrium fimbriatum
Bothriocephalus cuspidatus
Schistocephalus solidus
Abothrium infundibuliformis
Abothrium crassum
Cysticercoid of Rossiter, 1893
Cysticercus quadricurvatus
Cysticercus gruberi
Cysticercus sp. Luehe, 1910
Cyclops sp.
Fimbriaria fasciolaris
Camallanus lacustris
Camallanus microcephalus
Dracunculus sp.
Philometra sanguineum
Cyclops strenuus
Proteocephalus torulosus
Proteocephalus longicollis
Proteocephalus percae
Ichthyotaenia sp. Fuhrmann, 1926
Hymenolepis setigera
Diphyllobothrium latum
Abothrium crassum
Abothrium infundibuliformis
Triaenophorus nodulosus
Cysticercus gruberi
Dracunculus medinensis
Cyclops tenuicornis. Probably *Cyclops albidus* q. v.
Distomum sp. Herrick
Cyclops varius. See *Cyclops serrulatus*.
Cyclops vernalis
Hymenolepis anatina
Hymenolepis collaris
Cyclops viridis
Hymenolepis collaris
Hymenolepis gracilis
Hymenolepis fasciculatus
Dracunculus medinensis
Diaptomus africanus
Plerocercus africanus
Diaptomus alluaudi
Hymenolepis anatina
Dicranotaenia dubia
Diaptomus asiaticus
Echinocotyle linstowi
Echinocotyle polyacantha
Taenia zichi

- Diaptomus castor*
Proteocephalus torulosus
Diaptomus coeruleus
Hymenolepis collaris
Hymenolepis gracilis
Hymenolepis tenuirostris
Hymenolepis fasciculatus
Hymenolepis setigera
Diaptomus gracilis
Diphyllobothrium latum
Diaptomus graciloides
Diphyllobothrium latum
Diaptomus oregonensis
Diphyllobothrium latum
Diaptomus sp.
Cysticercoides sp. Mrazek, 1898
Cercocystis dendrocercus
Philometra sanguineum
Diaptomus spinosus
Hymenolepis anatina
Hymenolepis gracilis
Drepanidotacnia lanceolata
Echinocotyle linstowi
Diaptomus vulgaris
Fimbriaria fasciolaris
Leptocyclops agilis. See *Cyclops ser-
rulatus*.
Mesocyclops oithonoides
Proteocephalus percae
Platycyclops fimbriatus
Hymenolepis brachycephala
Trienophorus nodulosus
Pseudoboeckella braziliensis
Echinocotyle mrazeki
- OSTRACODA
- Candona candida*
Hymenolepis coronula
Candona neglecta tuberculata
Hymenolepis gracilis
Candona rostrata
Hymenolepis gracilis
Cyclocypris globosa
Hymenolepis gracilis
Hymenolepis coronula
Hymenolepis liophallos
Hymenolepis venusta
Echinocotyle rosseteri
Cysticercoides sp. Rossiter, 1890
- Cyclocypris laevis*
Hymenolepis coronula
Cyclocypris ovum
Hymenolepis coronula
Cypria ophthalmica
Hymenolepis anatina.
Hymenolepis gracilis
Hymenolepis coronula
Echinocotyle rosseteri
" *Cypris agilis* "
- Hymenolepis venusta*
Cypris cinerea. See *Cyclocypris glo-
bosa*.
Cypris compressa. See *Cypria ophthal-
mica*.
Cypris elongata
Taenia sp. Daday, 1900
Cypris incongruens. See *Heterocypris*
incongruens.
Cypris ophthalmica. See *Cypria oph-
thalmica*
Cypris ovata. See *Cypris pubera*.
Cypris ovum. See *Cyclocypris ovum*.
Cypris pubera
Hymenolepis anatina.
Cypris virens. See *Eucypris virens*.
Cypris viriens. See *Eucypris virens*.
Dolerocypris fasciata
Hymenolepis gracilis
Eucandona hungarica
Hymenolepis anatina
Eucypris crassa
Hymenolepis anatina
Eucypris virens
Hymenolepis collaris
Hymenolepis coronula
Hymenolepis gracilis
Heterocypris incongruens
Hymenolepis anatina
" *Ostracod* "
- Cysticercus* sp. Luehe, 1910
- DECAPODA
- Astacus astacus*
Astacotrema cirrigerum
Hymenolepis collaris
Hymenolepis tenuirostris
Polymorphus boschadis

- Astacus fluviatilis*. See *Astacus astacus*.
Astacus japonicus. See *Cambaroides japonicus*.
Astacus leptodactylus
Distomum reinhardi
Cambaroides japonicus
Paragonimus westermani
Cambaroides similis
 ? *Paragonimus westermani*
Cambarus propinquus
Microphallus opacus
Cambarus spp.
Crepidostomum cornutum
Cerataspis monstrosa
Dinurus tornatus
 "Crabs"
Distomum kalapāi
 "Crayfish"
Astacotrema cirrigerum
Acrolichanus petalosa
Plagiorchis ancuvrensis
Distoma of Cooper, 1883
Distomum of Linton, 1892
Eriocheir japonicus
Paragonimus westermani
Stephanolecithus parvus
Geothelphusa dehaani. See *Potamon*
 (*Geothelphusa*) *dehaani*.
Geothelphusa obtusipes. See *Potamon*
 (*Geothelphusa*) *obtusipes*.
 "Marine decapods"
Rhynchobothrius ruficollis
Potamobius astacus. See *Astacus astacus*.
Parathelphusa (*Parathelphusa*) *sinensis*
Stephanolecithus parvus
Potamon dehaanii. See *Potamon*
 (*Geothelphusa*) *dehaani*.
Potamon obtusipes. See *Potamon*
 (*Geothelphusa*) *obtusipes*.
Potamon sinensis. See *Parathelphusa*
 (*Parathelphusa*) *sinensis*.
Potamon (*Geothelphusa*) *dehaani*
Paragonimus westermani
Macroorchis spinulosus
Stephanolecithus parvus
Potamon (*Geothelphusa*) *obtusipes*
Paragonimus westermani
Stephanolecithus parvus
Pseudothelphusa iturbei
Paragonimus westermani
Sesarma dehaanii
Paragonimus westermani
Stephanolecithus parvus

ISOPODA

- Asellus aquaticus*
Camallanus elegans
Hedruris androphora
Acanthocephalus lucii
Echinorhynchus ranae
Porcellio lacvis
Dispharynx spiralis

GENERAL DISCUSSION

On the basis of the foregoing lists, the arthropod hosts are arranged below in their approximate order of relative importance for each order of parasites, with a résumé of the numbers of host and parasite species involved.

As intermediate hosts for tapeworms with primary hosts living in water or feeding on arthropods which live in water, the Copepoda are of outstanding importance, the next most important group being the Ostracoda. The Amphipoda, Decapoda, and Cladocera are much less extensively involved as intermediate hosts for tapeworms so far as is known at the present time.

Cestoda

Intermediate host group	No. of host spp. involved	No. of parasite spp. with known hosts for adults	No. of parasite spp. reported as larvae without known hosts for adults
CRUSTACEA:			
Copepoda	27	29	8
Ostracoda	15	6	3
Amphipoda	1	5	7
Decapoda	2	3	0
Cladocera	2	1	0
INSECTA:			
Coleoptera	8	9	1
Siphonaptera	7	4	1
Diptera	2	4	0
Lepidoptera	4	1	0
Odonata	2	1	1
Dermaptera	1	2	0
Mallophaga	1	1	0
MYRIAPODA	2	1	0

As intermediate hosts for tapeworms of land animals, the Coleoptera are distinctly the most important group, other insect groups being of much less importance so far as we know.

Trematoda

Intermediate host group	No. of host spp. involved	No. of parasite spp. with known hosts for adults	No. of parasite spp. reported as larvae without known hosts for adults
CRUSTACEA:			
Decapoda	15	8	4
Amphipoda	3	1	4
Copepoda	3	2	1
Branchiopoda	1	0	1
INSECTA:			
Diptera	11	2	8
Trichoptera	11	2	4
Odonata	8	6	2
Ephemera	5	5	1
Coleoptera	3	3	1
Unplaced insects	2	4	0
Neuroptera	2	0	3
Plecoptera	2	1	0
Lepidoptera	1	0	1

Among the Crustacea, the Decapoda are of outstanding importance as hosts for flukes, some of these flukes occurring in land mammals which eat raw crabs or crayfish.

Among the Insecta, the apparent importance of the Diptera and Trichoptera is not well established. These groups rate high in number of species serving as hosts, but as the flukes reported from them are mostly larval forms of which the adults are not known and which may later prove to represent no more known species than are already known and recorded here from these hosts, or only a few more, these groups cannot be rated at the present time as any more important than the Odonata or Ephemera as hosts for flukes.

Nematoda

Intermediate host group	No. of host spp. involved	No. of parasite spp. with known hosts for adults	No. of parasite spp. reported as larvae without known hosts for adults
CRUSTACEA :			
Copepoda	8	7	0
Amphipoda	2	2	0
Isopoda	2	2	0
Cladocera	1	1	0
INSECTA :			
Diptera	67	17	4
Coleoptera	39	10	3
Orthoptera	5	5	0
Siphonaptera	5	4	1
Ephemera	2	0	1
Anopleura	1	1	0
Isoptera	1	1	0
Mallophaga	1	1	0
Odonata	1	1	0
ARACHNIDA	6	6	0

Among the Crustacea, the Copepoda are the important group as carriers of parasitic nematodes. Among the Insecta the Diptera are of striking importance, no less than 67 of the Diptera being reported as carriers for a total of 17 nematode species, this fact being the result largely of the rôle of the mosquitoes as carriers of filarids. The Coleoptera take first rank as carriers of spirurids. Of lesser importance are the Orthoptera and Siphonaptera, and the other groups of insects show but few host species and these accused of carrying but one nematode parasite. The Arachnida as a whole have been accused of carrying 6 nematodes, and but 6 arachnids are incriminated. The arachnids have not been reported as carriers of any parasitic worms other than nematodes.

Acanthocephala

Intermediate host group	No. of host spp. involved	No. of parasite spp. with known hosts for adults	No. of parasite spp. reported as larvae without known hosts for adults
CRUSTACEA:			
Amphipoda	4	4	0
Isopoda	1	2	0
Decapoda	1	1	0
INSECTA:			
Coleoptera	11	3	0
Neuroptera	2	1	0
Orthoptera	2	1	0

Among the Crustacea, the Amphipoda are of special significance as hosts for acanthocephalids of aquatic animals, so far as the life histories of such worms are known. The only other crustaceans involved are Isopoda and Decapoda.

Among the Insecta, the Coleoptera are of major importance as carriers of acanthocephalids with known life histories. The only other insects involved are Neuroptera and Orthoptera.

If we take the outstanding groups of intermediate hosts for each order of parasites, we have the following:

For Cestoda: Copepoda and Ostracoda; Coleoptera.

For Trematoda: Decapoda; Diptera, Trichoptera, Odonata, and Ephemera.

For Nematoda: Copepoda; Diptera and Coleoptera.

For Acanthocephala: Amphipoda; Coleoptera.

Among the insects, the importance of the Coleoptera is indicated by the fact that this group is of decided significance for Cestoda, Nematoda, and Acanthocephala. The Diptera are important as carriers of Trematoda and Nematoda. The Trichoptera, Odonata, and Ephemera only figure as outstandingly important for Trematoda.

Among the crustaceans, the Copepoda are the major group as hosts for both Cestoda and Nematoda. The Ostracoda are only known to be important as hosts for Cestoda, the Decapoda as hosts for Trematoda, and the Amphipoda as hosts for Acanthocephala.

The following table is inserted to give a rapid check on the known occurrence in the different arthropod hosts of parasites of the groups involved in this paper. If an arthropod group is known to contain intermediate hosts for the worm groups involved, an X is placed under the worm group and opposite the host group. If there are no such hosts known, an O is placed in the corresponding position.

LIST SHOWING RECORDS (X) OR LACK OF RECORDS (O) OF
PARASITE GROUPS IN HOST GROUPS

Arthropod group	Cestoda	Trematoda	Nematoda	Acanthocephala
Amphipoda	X	X	X	X
Branchiopoda	O	X	O	O
Cladocera	X	O	X	O
Copepoda	X	X	X	O
Decapoda	X	X	O	X
Isopoda	O	O	X	X
Ostracoda	X	O	O	O
Anopleura	O	O	X	O
Coleoptera	X	X	X	X
Dermaptera	X	O	O	O
Diptera	X	X	X	O
Ephemera	O	X	X	O
Isoptera	O	O	X	O
Lepidoptera	X	X	O	O
Mallophaga	X	O	X	O
Neuroptera	O	X	O	X
Odonata	X	X	X	O
Orthoptera	O	O	X	X
Plecoptera	O	X	O	O
Siphonaptera	X	O	X	O
Trichoptera	O	X	O	O
Insecta; unplaced	O	X	O	O
Myriapoda	X	O	O	O
Arachnida	O	O	X	O

It is of interest to note that of the 24 arthropod groups listed above, the number of groups used as hosts by cestodes, trematodes, and nematodes is the same or almost the same, namely, 13 by cestodes and trematodes and 14 by nematodes; only 6 are used by acanthocephalids.

From the foregoing something may be indicated as to the range of parasites on the part of the various intermediate host groups, as follows:

Hosts for 4 worm groups: Amphipoda and Coleoptera.

Hosts for Cestoda, Trematoda and Nematoda: Copepoda; Diptera and Odonata.

Hosts for Cestoda, Trematoda and Acanthocephala: Decapoda.

Hosts for Cestoda and Trematoda: Lepidoptera.

Hosts for Cestoda and Nematoda: Cladocera; Mallophaga and Siphonaptera.

Hosts for Trematoda and Nematoda: Ephemera.

Hosts for Trematoda and Acanthocephala: Neuroptera.

Hosts for Nematoda and Acanthocephala: Isopoda; Orthoptera.

Hosts for Cestoda only: Ostracoda; Dermaptera; Myriapoda.

Hosts for Trematoda only: Branchiopoda; Plecoptera, Trichoptera, and unplaced insects.

Hosts for Nematoda only: Anopleura and Isoptera; Arachnida.

No group is yet reported as a host group for Acanthocephala only.

Taking the major host groups, the Crustacea, Insecta, Myriapoda, and Arachnida, as a whole and the four worm groups as a whole, we may make the following summary:

There are 48 species in the Cestoda which have arthropods as intermediate hosts and for which we know the primary hosts; there are 22 larval forms in addition for which the primary hosts are not known.

There are 37 species in the Trematoda which have arthropods as intermediate hosts and for which we know the primary hosts; there are 27 larval forms in addition for which the primary hosts are not known.

There are 49 species in the Nematoda which have arthropods as intermediate hosts and for which we know the primary hosts; there are 12 larval forms in addition for which the primary hosts are unknown.

There are 9 species in the Acanthocephala which have arthropods as intermediate hosts and for which we know the primary hosts.

There are altogether 143 species of worms parasitic in vertebrates which have arthropods as intermediate hosts and for which the primary hosts are known; there are 61 larval forms in addition for which the primary host is unknown.

In the Crustacea there are 49 species which serve as intermediate hosts for Cestoda, 22 for Trematoda, 12 for Nematoda, and none for Acanthocephala.

In the Insecta there are 25 species which serve as intermediate hosts for Cestoda, 46 for Trematoda, 122 for Nematoda, and 15 for Acanthocephala.

In the Myriapoda there are 2 species which serve as intermediate hosts for Cestoda, and none for Trematoda, Nematoda, or Acanthocephala so far as we know at present.

In the Arachnida there are 6 species which serve as intermediate hosts for Nematoda, and none for Cestoda, Trematoda, or Acanthocephala so far as we know at present.

The Insecta are far in the lead as regards number of species known to serve as intermediate hosts for parasitic worms, as there are 186 species of insects, 77 species of crustaceans, 6 species of arachnids, and only 2 species of myriapods included in these lists of intermediate hosts. The total number of arthropod species listed here as intermediate hosts for the worm groups involved is 271.

CONCLUSION

It should be reiterated that one must not draw too sweeping conclusions in regard to the importance of host groups or in regard to

several other things at this time. For one thing, the lists given here are such as could be compiled in the time at the writer's disposal and while reasonably comprehensive must necessarily be incomplete. For another thing, our total knowledge in regard to the life histories of heteroxenous helminths is very slight. As already stated, we know the life histories of approximately 1 per cent of the known tapeworms, and this status is sufficiently representative of conditions for all heteroxenous worm groups to need no detailed statement in regard to the other groups. There may be important intermediate host groups of which no member has yet been incriminated. We know about 143 life histories involving arthropods; there are certainly hundreds, perhaps thousands, of such life histories still to be ascertained.

Admitting all of these defects in our data, we are nevertheless justified in saying that the lists presented here will be of value in affording the student a clue as to the probabilities in beginning a search for the intermediate host of a heteroxenous worm parasite, or in considering the probable identity of a larval worm found in an arthropod. This will fulfill one of the purposes of this paper—to aid the student. The young students of to-day will include among their ranks the competent scientists of to-morrow.

Another purpose of this paper is to point out the opportunities for cooperation among scientists in adding to our knowledge of the life histories of parasitic worms. Zwaluwenberg, an entomologist, has said recently: "The interrelationships of insects and nematodes is a subject of which most entomologists seem to have little adequate conception." Some months ago, in discussing the scope of this paper with Dr. L. O. Howard, the writer told him that he expected to call attention to the fact that our knowledge of these life histories had come almost entirely from the parasitologists, and that the workers on insects and crustaceans had aided very little in the process. Dr. Howard, characteristically, suggested that this be done very diplomatically. It is the writer's intention to do this diplomatically. It is primarily the business of the parasitologist to ascertain the life histories of the parasites with which he deals. It would not be in order to ask the specialist on insects or crustaceans to ascertain the life histories of the larval worms which he finds in these insects and crustaceans, nor would it add greatly to our knowledge to have persons unfamiliar with parasitic worms publish findings in an unfamiliar field.

Nevertheless, there is an opportunity for cooperation between the workers on parasitic helminths and the workers on their arthropod hosts, and little advantage has been taken of this fact in the past.

My friend, Dr. Wm. A. Riley, has called my attention to Stein's pioneer contributions; conceding the point, Stein's good example has not been followed by most entomologists. The competent worker in either field should be primarily a zoologist, and as such able to see the possibilities for cooperation with other zoologists in connection with incidental findings which come to his attention. The larval helminth in an arthropod is an animal which concerns the helminthologist in one direction and the "arthropodologist" in another. A sound consideration of the worm calls for a sound consideration of its host, and *vice versa*. Prophylactic measures directed against heteroxenous worms call for control measures for intermediate hosts, and if this host is an arthropod the helminthologist must draw on the knowledge of the man who knows about arthropods.

One of the promising developments in this connection is the fact that whereas the entomologist in the past has devoted his attention to the outside of the insects with only casual attention to the internal anatomy, there is now a tendency to devote more attention to the internal structures. In examining the interior of the insects, the entomologist is certain to find larval worms in some of them. In such cases he would be rendering a service if he would do one of the following things:

If the entomologist is well trained in zoology, and has the time, facilities, and inclination to carry out an adequate investigation of these worms, he can proceed with feeding experiments and ascertain the life history. Lacking the training, time, facilities, or inclination to do such work, he can turn the material over to a parasitologist for investigation, or call attention in his publications to his findings in order that they may serve as a guide to the parasitologist who is working along this line.

Some of the hosts given in this paper are not well established, but are included for completeness. In establishing a life history for a parasitic worm, one may be guided with profit by the remarks of Stiles in 1896 in connection with the life histories of bird tapeworms:

The known or supposed life history has been based upon four different methods of work, *i. e.*:

1. Experimental infection of the fowls by feeding to them known larval stages found in invertebrates, and thus raising the adult stage.
2. Experimental infection of invertebrates by feeding to them the eggs of tapeworms found in birds, and thus raising the larval stage.
3. Comparison of the hooks upon the heads of adult tapeworms of birds with the hooks of larvae found in invertebrates, and thus associating the young and the old stages.
4. Wild speculations as to the intermediate hosts, based upon negative results and totally devoid of any scientific foundation.

Of these four methods of work the first two give positive proof of the life history when the experiments are successful; the third gives a probability to the statements, but not a proof; the less said about the fourth method the better.

In this later epoch it is advisable to establish a life history by both of the first methods, not ignoring the third, if adequate evidence is desired. Raising *Diphyllobothrium latum* in dogs by feeding plerocercoids from fish did not show that a copepod was the first host; failure to infect fish with the tapeworm eggs necessitated further search and so led to the discovery of the copepod host. Another thing deserves emphasis: Finding that one arthropod is an intermediate host does not settle the problem of a life history of a worm. The worm may have a score of intermediate hosts, and the most important one may not be an arthropod.

ADDENDUM

Since the foregoing was written the following records have come to hand and are given here without discussion:

LIST BY PARASITES

(Crust. = Crustacea)

CESTODA

CESTODARIA

- Amphilina foliacea*—*Corophium curvispinum*; Crust.; Amphipoda
Dikerogammarus haemobaphes; Crust.; Amphipoda
Gammarus platycheir; Crust.; Amphipoda
Metamysis strauchi; Crust.; Mysidacea

DIPHYLLOBOTHRIDAE

- Diphyllobothrium ranarum*—*Cyclops fuscus*; Crust.; Copepoda
Diphyllobothrium decipiens—*Cyclops* sp.; Crust.; Copepoda
Diphyllobothrium erinacei—*Cyclops* sp.; Crust.; Copepoda
Diphyllobothrium mansoni—*Cyclops* sp.; Crust.; Copepoda
Cyclops strenuus; Crust.; Copepoda

PROTEOCEPHALIDAE

- Proteocephalus ambloplitis*—*Hyaella azteca*; Crust.; Amphipoda
Cyclops serrulatus; Crust.; Copepoda
Cyclops viridis; Crust.; Copepoda
Proteocephalus pinguis—*Cyclops serrulatus*; Crust.; Copepoda
Cyclops viridis; Crust.; Copepoda
Ophiotaenia testudo—*Cyclops* sp.; Crust.; Copepoda

CESTODA (*Continued*)

HYMENOLEPIDIDAE

- Hymenolepis collaris*—*Cypris* sp., Crust.; Ostracoda
Hymenolepis anatina—*Cypris* sp.; Crust.; Ostracoda
Hymenolepis coronula—*Cypris* sp.; Crust.; Ostracoda
Hymenolepis carioca—*Choeridium histeroides*; Insecta; Coleoptera
 Hister (Carcinops) 14-striatus; Insecta; Coleoptera
 Anisotarsus agilis; Insecta; Coleoptera
 ? *Choanotaenia infundibulum*—*Cratacanthus dubius*; Insecta; Coleoptera *

DAVAINIIDAE

- Railletina cesticillus*—*Anisotarsus agilis*; Insecta; Coleoptera
 Anisotarsus terminatus; Insecta; Coleoptera
 Choeridium histeroides; Insecta; Coleoptera
 Aphodius granarius; Insecta; Coleoptera *
 Selenophorus ovalis; Insecta; Coleoptera *
 Selenophorus pedicularis; Insecta; Coleoptera
 Triplectrus rusticus; Insecta; Coleoptera *

TREMATODA

PLAGIORCHIIDAE

- Plagiorchis maculosus*—*Chironomus plumosus*; Insecta; Diptera
 Chironomus sp.; Insecta; Diptera

HETEROPHYIDAE

- Microphallus minus*—*Macrobrachium nipponensis*; Crust.; Decapoda

TROGLOTREMATIDAE

- Paragonimus westermani*—*Cambaroides dauuricus*; Crust.; Decapoda
 Eriocheir sinensis; Crust.; Decapoda

FAMILY UNCERTAIN

- Distome of Eckstein—*Culex pipiens*; Insecta; Diptera
 Metacercaria of Joyeux, 1928—*Anopheles maculipennis*; Insecta; Diptera
 Cercaria X.I of Harper, 1929—*Gammarus pulex*; Crust.; Amphipoda
 Orchestia littorea; Crust.; Amphipoda
 Chironomus plumosus; Insecta; Diptera
 Culex pipiens; Insecta; Diptera
 Tipula maxima; Insecta; Diptera
 Pedicia rivosa; Insecta; Diptera
 Dysticus marginalis; Insecta; Coleoptera
 Sialis lutarius; Insecta; Diptera
 Halesus sp.; Insecta; Trichoptera
 Limnophilus centralis; Insecta; Trichoptera
 Limnophilus rhombicus; Insecta; Trichoptera
 Plectrocnemia conspersa; Insecta; Trichoptera
 Rhyacophila dorsalis; Insecta; Trichoptera

* Unpublished work by M. F. Jones.

NEMATODA

SPIRURIDAE

- Gongylonema ingluvicola*—*Copris minutus*; Insecta; Coleoptera *
Phanaeus carnifex—Insecta; Coleoptera *
Physocephalus sexalatus—*Canthon laevis*; Insecta; Coleoptera
Gymnopleurus simatus; Insecta; Coleoptera
Phanaeus carnifex; Insecta; Coleoptera
 Larval spirurid (?)—*Camptodea* sp.; Insecta; Thysanura

PHYSALOPTERIDAE

- Proleptus scillicola*—*Carcinus maenas*; Crust.; Decapoda
Eupagurus bernhardus; Crust.; Decapoda

ACUARIIDAE

- Cheilospirura hamulosa*—*Melanoplus femurrubrum*; Insecta; Orthoptera *
Cheilospirura spinosa—*Melanoplus femurrubrum*; Insecta; Orthoptera
Acuaria anthuris—*Melanoplus femurrubrum*; Insecta; Orthoptera *
 Crickets; Insecta; Orthoptera *

TETRAMERIDAE

- Tetrameres americana*—*Melanoplus differentialis*; Insecta; Orthoptera
Melanoplus femurrubrum; Insecta; Orthoptera *

FILARIIDAE

- Wuchereria bancrofti*—*Aedes albopictus*; Insecta; Diptera
Aedes chemulpoensis; Insecta; Diptera
Aedes galloisi; Insecta; Diptera
Aedes subpictus; Insecta; Diptera
Armigeres obturbans; Insecta; Diptera
Culex annulus; Insecta; Diptera
Culex bitaeniorhynchus karatsuensis; Insecta; Diptera
Culex japonicus; Insecta; Diptera
Culex pipiens pallens; Insecta; Diptera
Culex tipuliformis; Insecta; Diptera
Culex tripunctatus; Insecta; Diptera
Culex tritaeniorhynchus; Insecta; Diptera
Culex whitmorei; Insecta; Diptera

DRACUNCULIDAE

- Philometra nodulosa*—*Cyclops brevispinosus*; Crust.; Copepoda

FAMILY UNCERTAIN

- Cystopsis accipenseris*—*Dikerogammarus haemobaphes*; Crust.; Amphipoda
Gammarus platycheir; Crust.; Amphipoda
Cyclopsinema mordens—*Pachycyclops signatus*; Crust.; Copepoda

* Unpublished work of E. B. Cram.

LIST BY HOSTS

(Cest. = Cestoda; Trem. = Trematoda; Nem. = Nematoda)

CRUSTACEA

AMPHIPODA

- Corophium curvispinum*—*Amphilina foliacea*; Cest.; Cestodaria
Dikergammarus haemobaphes—*Amphilina foliacea*; Cest.; Cestodaria
Cystopsis accipenseris; Nem.; Family?
Gammarus platycheir—*Amphilina foliacea*; Cest.; Cestodaria.
Cystopsis accipenseris; Nem.; Family?
Hyalella azteca—*Proteocephalus ambloplitis*; Cest.; Proteocephalidae

COPEPODA

- Cyclops brevispinosus*—*Philometra nodulosa*; Nem.; Dracunculidae
Cyclops fuscus—*Diphyllobothrium ranarum*; Cest.; Diphyllobothriidae
Cyclops serrulatus—*Proteocephalus pinguis*; Cest.; Proteocephalidae
Proteocephalus ambloplitis; Cest.; Proteocephalidae
Cyclops sp.—*Diphyllobothrium decipiens*; Cest.; Diphyllobothriidae
Diphyllobothrium erinacci; Cest.; Diphyllobothriidae
Ophiotaenia testudo; Cest.; Proteocephalidae
Cyclops strenuus—*Diphyllobothrium mansoni*; Cest.; Diphyllobothriidae
Cyclops viridis—*Proteocephalus pinguis*; Cest.; Proteocephalidae
Proteocephalus ambloplitis; Cest.; Proteocephalidae
Macrocylops signatus—*Cyclopsinema mordens*; Nem.; Family?
Pachycylops signatus—See *Macrocylops signatus*

DECAPODA

- Cambaroides dauuricus*—*Paragonimus westermanni*; Trem.; Troglotrematidae
Carcinides (Carcinus) maenas—*Proleptus scillicola*; Nem.; Physalopteridae
Carcinus maenas—See *Carcinides (Carcinus) maenas*
Eriocheir sinensis—*Paragonimus westermanni*; Trem.; Troglotrematidae
Eupagurus bernhardus—See *Pagurus bernhardus*.
Macrobrachium nipponensis—*Microphallus minus*; Trem.; Heterophyidae
Pagurus bernhardus—*Proleptus scillicola*; Nem.; Physalopteridae

MYSIDACEA

- Metamysis trauchi*—*Amphilina foliacea*; Cest.; Cestodaria

OSTRACODA

- Cypris* sp.—*Hymenolepis anatina*; Cest.; Hymenolepididae
Hymenolepis collaris; Cest.; Hymenolepididae
Hymenolepis coronula; Cest.; Hymenolepididae

INSECTA

COLEOPTERA

- Anisotarsus agilis*—*Raillietina cesticillus*; Cest.; Davainiidae
Hymenolepis carioca; Cest.; Hymenolepididae
Anisotarsus terminatus—*Raillietina cesticillus*; Cest.; Davainiidae
Aphodius granarius—*Raillietina cesticillus*; Cest.; Davainiidae
Canthon laevis—*Physocephalus sexualatus*; Nem.; Spiruridae
Choeridium histeroides—*Raillietina cesticillus*; Cest.; Davainiidae
Hymenolepis carioca; Cest.; Hymenolepididae
Copris minutus—*Gongylonema ingluvicola*; Nem.; Spiruridae
Cratacanthus dubius?—*Choanotaenia infundibulum*; Cest.; Hymenolepididae
Dysticus marginalis—*Cercaria* X.1 of Harper, 1929; Trem.; Family?
Gymnopleurus sinuatus—See *Gymnopleurus sinuatus*
Gymnopleurus sinuatus—*Spirocerca sanguinolenta*; Nem.; Spiruridae
Hister (Carcinops) 14-striatus—*Hymenolepis carioca*; Cest.; Hymenolepididae
Phanaeus carnifex—See *Phanaeus vindex*
Phanaeus vindex—*Gongylonema ingluvicola*; Nem.; Spiruridae
Physocephalus sexualatus; Nem.; Spiruridae
Selenophorus ovalis—*Raillietina cesticillus*; Cest.; Davainiidae
Selenophorus pedicularis—*Raillietina cesticillus*; Cest.; Davainiidae
Triplectrus rusticus—*Raillietina cesticillus*; Cest.; Davainiidae

NEUROPTERA

- Sialis lutarius*—See *Sialis flavilatera*
Sialis flavilatera—*Cercaria* X.1 of Harper, 1929; Trem.; Family?

TRICHOPTERA

- Halesus* sp.—*Cercaria* X.1 of Harper, 1929; Trem.; Family?
Limnophilus centralis—*Cercaria* X.1 of Harper, 1929; Trem.; Family?
Limnophilus rhombicus—*Cercaria* X.1 of Harper, 1929; Trem.; Family?
Plectrocnemia conspersa—*Cercaria* X.1 of Harper, 1929; Trem.; Family?
Rhyacophila dorsalis—*Cercaria* X.1 of Harper, 1929; Trem.; Family?

DIPTERA

- Aedes albolateralis*—*Wuchereria bancrofti*; Nem.; Filariidae
Aedes chemulpoensis—*Wuchereria bancrofti*; Nem.; Filariidae
Aedes galloisi—*Wuchereria bancrofti*—Nem.; Filariidae
Anopheles maculipennis—*Metacercaria* of Joyeux, 1928; Trem.; Family?
Anopheles rossi—See *Anopheles subpictus*
Anopheles subpictus—*Wuchereria bancrofti*; Nem.; Filariidae
Armigeres obturbans—See *Desvoidya obturbans*
Chironomus plumosus—*Plagiorchis maculosus*; Trem.; Plagiorchiidae
Cercaria X.1 of Harper, 1929; Trem.; Family?
Chironomus sp.—*Plagiorchis maculosus*; Trem.; Plagiorchiidae
Culex annulus—See *Culex tritaeniorhynchus*

INSECTA (*Continued*)DIPTERA (*Continued*)

- Culex bitaeniorhynchus karatsucensis*—*Wuchereria bancrofti*; Nem.; Filariidae
Culex japonicus—*Wuchereria bancrofti*; Nem.; Filariidae
Culex pipiens—Distome of Eckstein; Trem.; Family?
 Cercaria X.1 of Harper, 1929; Trem.; Family?
 Wuchereria bancrofti; Nem.; Filariidae
Culex pipiens pallens—See *Culex pipiens*
Culex tipuliformis—*Wuchereria bancrofti*; Nem.; Filariidae
Culex tripunctatus—*Wuchereria bancrofti*; Nem.; Filariidae
Culex tritaeniorhynchus—*Wuchereria bancrofti*; Nem.; Filariidae
Culex whitmorei—*Wuchereria bancrofti*; Nem.; Filariidae
Desvoidya obturbans—*Wuchereria bancrofti*; Nem.; Filariidae
Tipula maxima—Cercaria X.1 of Harper, 1929; Trem.; Family?
Pedicia rivosa—Cercaria X.1 of Harper, 1929; Trem.; Family?

THYSANURA

- Campodea* sp.—Larval spirurid (?); Nem.; Spiruridae?

ORTHOPTERA

- Cricket—*Acuaria anthuris*; Nem.; Acuariidae
Melanoplus differentialis—*Tetrameres americana*; Nem.; Tetrameridae
Melanoplus femurrubrum—*Tetrameres americana*; Nem.; Tetrameridae
 Cheilospirura hamulosa; Nem.; Acuariidae
 Cheilospirura spinosa; Nem.; Acuariidae
 Acuaria anthuris; Nem.; Acuariidae