THE LARGER ANIMAL PARASITES OF THE

FRESH-WATER FISHES OF MAINE

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PART ONE

PART TWO

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I. INTRODUCTION

Animals which obtain their livelihood at the expense of other animals, usually without killing the latter, are known as parasites. During recent years the general public has taken more notice of and concern in the parasites, particularly those occurring externally, free or encysted upon or under the skin, or internally, in the flesh, and in the body cavity, of the more important fresh-water fish of the State. As a result many inquiring letters are received by the Department of Inland Fisheries and Game from anglers and other interested individuals who have caught or observed parasitized fish. Since a great majority of these queries involve a relatively small number of fairly widespread parasites, an investigation has been made in an attempt to determine the parasites present, their distribution, their effects upon the fish involved, and to present these findings in a manner understandable to the interested general public.

The questions asked by anglers and camp owners who encounter such infected fish are usually : 1) What is a parasite? 2) What are the animals that are parasitic on native fresh-water fish? 3) How is the fish affected and how do these hosts affect the parasite? 4) What, if anything, can be done about fish parasites?

A parasite is an animal which obtains its livelihood at the expense of another, usually larger, animal of a different species. Or, in a more restricted sense, the parasite lives upon or within and at the expense of the host. The living animal harboring the parasite is known as the host, which in the following discussion is generally a fish. The term parasite was first used to designate those persons who fed regularly and gratuitously at the tables of the rich and influential in ancient Greece and who courted these favors through fawning and flattery. The condition, then, has always been regarded as an infamous one.

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Contrary to the popular belief, parasitism is very common. There are, in fact, strong indications that there may be more organisms living as parasites than there are living a free and independent, non-parasitic existence. Under conditions in nature there is rarely a single individual fish, among all the numerous species, from the smallest minnows to the choicest game fishes, which does not harbor at least one or more species of parasites somewhere in its body. Often the parasites are confined to the internal organs and hence are usually not noticed when the fish is cleaned. But some of the parasites take up their abode in other places in or on the body of the host. At times they form in the skin and even in the flesh conspicuous cysts or nodules, which render the fish unsightly ; as a result it is often discarded as unfit for human consumption. No organ or tissue is immune from attack. While all kinds of fish harbor parasites, they are found in some more frequently than in others, depending sometimes upon the age of the fish, the season in which they are taken, and the type of lake or stream in which the fish are found.

There is a notion prevalent in certain quarters that a limited amount of dirt and vermin is wholesome rather than harmful. This is erroneous, nor is there any truth in the idea that a few parasites do their host no real harm, but that a considerable number must be present in order to become really injurious.

The title of this paper has been chosen because it indicates we are concerned primarily with the parasites of fish ; those of other animals are considered only in so far as they are secondarily involved in the life cycle of the parasites attacking the first group of hosts ; further, because the title indicates that only the larger animals attacking the fresh-water fishes of the State are considered. It does not treat the smaller, one-celled animals (Protozoa) , except incidentally, and the other kinds of living organisms which may be parasitic upon fish, namely, the bacteria, the fungi, and the viruses.

Two groups of people were kept in mind in the preparation of this report. An attempt has been made to make the subject matter of interest to the fishermen, camp owners and other interested laymen without involving them with more than the minimum of technical terminology. Likewise it is hoped that it will be useful to students and teachers of biology, and of value to parasitologists. Since it is impossible to talk about parasites and the phenomena involved in parasitism without employing

some scientific terminology, an attempt has been made to define such terms as they are used. Both the common and scientific names (when available) of all animals referred to have been included in order to facilitate comparison and additional study on fish parasites if desired. To some, the sequence in which the different topics are discussed will appear not to be in logical order. In defense of the sequence the critic should bear in mind that it was the interest of the general reader, rather than the scientist, which influenced their order of arrangement.

The introductory portion of this paper has been designed especially for reading by sportsmen, who should be cautioned at this point that the subject of parasites is complicated, and the language employed in dealing with parasites is technical. Technical terms are used by the parasitologist in referring to precise conditions, just as do the carpenter, printer, automotive mechanic, and every other occupation, terms which must be understood when discussing a particular profession. For example, it is doubtful if few other than ardent fishermen know the meaning of such terms as Warden's Worry, Mickey Finn, hellgrammite, etc.

Until recently a relatively small number of scientists studied parasites and their effects upon living animals ; those scientists found it easiest to adopt a highly specialized language for communicating their ideas to each other. That language made their work accurate and precise, regardless of whether they spoke French, English, or German. But for all its wonderful accuracy, the language is a barrier to the person looking for a few facts about the parasites encountered in the fish he catches. But the barrier of the technical terminology, though difficult to understand, can be hurdled by the reader who will bend his mind to it. The task can be likened to that of learning some of the principles of the functioning of an automobile ; it is not easy, but the average person can, *if he will,* achieve such a goal. A knowledge of fish parasites is useful to the serious sportsman because it vastly deepens his understanding and appreciation of the fishes he tries so hard to catch. To smooth the reader's pathway, there is included a Glossary, page 83. There the reader will find an explanation of those terms that might prove troublesome ; if he will use the glossary faithfully as he proceeds through the generalized

portion of this paper, he should gain a reasonable understanding of its offering to him.

Similarly it is essential that scientific names be used when referring to any particular organism, whether it belongs to the animal or plant kingdom. As early as the time of Aristotle (384-322 B.C.) the necessity for this was realized and varied schemes were proposed. But the plan first proposed by Linnaeus in 1758, although undergoing numerous necessary changes, is the one that is followed today throughout the world.

While common or vernacular names are useful and have been applied to many animals, they leave much to be desired. Their chief shortcoming is that a half-dozen or more such names might be given the same animal. Not only do the names employed for fish vary among the different groups (sport fishermen, commercial fishermen, fish-culturists, and scientific workers), but purely local names are often applied to the same species of fish in different, or even closely situated, geographical regions. While "smallmouth bass" is the approved common name of *Micropterus dolomieu,* in certain quarters it is known as black bass, smallmouth, Oswego bass, bronzeback, rock bass, redeye bass. To escape these pitfalls, and in the interest of uniformity, the scientific name, with or without the generally accepted common name, is always used in technical works to indicate the exact species of animal in question.

A scientific name consists of two parts : the capitalized generic or genus name *(Salmo)* and the uncapitalized trivial name *(trutta).* The two used in combination *(Salmo trutta)* comprise the scientific or species name of the brown trout. The surname of the author, the person who first published the species name together with a description of the animal to which it was applied, with or without the date, often follows the species name. For example, *Salmo trutta* Linnaeus, 1758. When a species is transferred from the original genus to another the name of the author of the trivial name is retained in parentheses. For example, *Lepomis gibbosus* (Linnaeus, 1758) .

Various higher systematic categories have been established for the inclusion of related species, genera, etc. Not only does this indicate relationship but it serves as a convenient label for the identification of such groups. The basic units in this system

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are the following, in which the bass tapeworm, *Proteocephalus ambloplitis,* serves as an illustration :

Phylum	Platyhelminthes
Class	Cestoda
Order	Proteocephala
Family	Proteocephalidae
Genus	Proteocephalus
Trivial	ambloplitis
Species	Proteocephalus ambloplitis

Although this paper contains numerous results of original observations, the literature on fish parasites has been drawn up-on freely. But since the material is generalized, no attempt has been made to give detailed references for each source of information or to refer by title to all the literature consulted. The inclusion of each individual reference citation would detract from readability. Those who desire such references will find most of them listed at the end under References.

II. MATERIALS

The study consisted of two distinct parts, the field and the laboratory phases. Field work consisted of obtaining and examining the fish, recovering and preserving the parasites encountered, and the taking of other pertinent data. Laboratory work involved the staining and mounting of the parasites on slides, after which they were studied microscopically. A detailed discussion of these aspects of the problem is included under, VIII, Methods Employed.

Collection of Hosts.—During the summer and early fall of 1952 a study was made of the parasites of fresh-water fishes of the State as one of the projects under the direction of the Fishery Research and Management Division of the Department of Inland Fisheries and Game. During this period 478 fish, belonging to 25 different species, were examined for parasites. Each fish was weighed, scale samples taken, total and fork length measurements were made, and the sex was recorded. Fish came from some 30 different locations, chiefly lakes and the larger ponds. Of the total involved, 292 were game fish, 105 were pan fish, and 81 were rough fish. The fish were obtained by several methods : by angling, by gill and fyke netting, and by seining. Of the 292 classified as game fish, 85 or nearly one-third were taken by anglers and were kindly made available by them or through co-operating camp owners at whose camps the fishermen were staying. In such cases an external examination for parasites was made, the usual data were obtained, and the viscera taken, accompanied by an inspection for cysts in the abdominal cavity, after which the carcass was returned to the successful angler.

Table 1 presents the summary of the field operations in terms of number of species and number of individuals of fishes examined for parasites. The scientific and common names employed for the fish are the same as those appearing in Everhart's 1950. "Fishes of Maine" (Dept. Inland Fisheries and Game, Augusta) . These are in agreement with, 1948. "A list of common and scientific names of the better known fishes of the United States and Canada." Spec. Publ. No. 1, Ann Arbor, as amended (1952. Trans. Amer. Fisheries Soc., 81: 324-327; 1953. 82: 326-

328) , except that due to its historic colloquial use the common name of LANDLOCKED SALMON has been retained for *Salmo salar.* In the amended list LAKE ATLANTIC SALMON has been proposed for the landlocked form.

Table I. Summary of field operations in terms of number of species and number of individuals of fishes examined.

	Name of Fish	Number Examined
1.	Alewife : *Pomolobus pseudoharengus*	2
2.	Landlocked salmon : *Salmo salar*	74
3.	Brown trout : *Salmo trutta*	14
4.	Lake trout : *Cristivomer namaycush*	46
5.	Eastern brook trout : *Salvelinus fontinalis*	38
6.	Lake whitefish : *Coregonus clupeaformis*	15
7.	American smelt : *Osmerus mordax*	5
8.	White sucker : *Catostomus commersoni*	25
9.	Longnose sucker : *Catostomus catostomus*	12
10.	Golden shiner : *Notemigonus crysoleucas*	12
11.	Fallfish : *Semotilus corporalis*	5
12.	Common shiner : *Notropis cornutus*	*10*
13.	Blacknose dace : *Rhinichthys atratulus*	1
14.	Brown bullhead : *Ameiurus nebulosus*	17
15.	Chain pickerel : *Esox niger*	35
16.	American eel : *Anguilla rostrata*	2
17.	Banded killifish : *Fundulus diaphanus*	2
18.	Burbot : *Lota iota*	3
19.	Threespine stickleback : *Gasterosteus aculeatus*	2
20.	White perch : *Morone americana*	39
21.	Yellow perch : *Perca flavescens*	25
22.	Smallmouth bass : *Micropterus dolomieu*	76
23.	Largemouth bass : *Micro pterus salmoides*	9
24.	Yellowbelly sunfish : *Lepomis auritus*	6
25.	Pumpkinseed : *Lepomis gibbosus*	3
	Total number of examinations	478

The lack of balance among the numbers of different species examined does not necessarily reflect their relative abundance **in**

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the State. Due to their importance, game fish, particularly the trouts and the salmons, when available, received first priority in the order of examination. However, the non-game species were examined when time permitted, as they were available. On the other hand the numbers of examinations of some species were regrettably low.

To these 478 examinations are added the results of four un-published reports dealing with fish parasites, each done as a problem in parasitology by graduate students of the Department of Zoology, University of Maine. These include that of Keith A. Havey, who during the summer of 1951 examined 66 smallmouth black bass and eight landlocked salmon from Long Pond, Mount Desert; Robert S. Rupp, who during the fall of the same year examined 22 eastern brook trout from Sunkhaze Stream, near Old Town ; John E. Watson, who during the summer of 1952 examined 70 smallmouth black bass from Big Lake, near Prince-ton ; and Carll N. Fenderson, who during the summer and early fall of 1952 examined 63 fish, belonging to six species, from Branch Lake, near Ellsworth. Augmenting this were more than 200 hosts contributed by fishermen, wardens, and camp owners during the past seven years because the fish were parasitized. Thus the combined examinations, upon which qualitative data are available, total nearly a thousand fish.

III. BIOLOGY OF PARASITES

1. How parasites are acquired.—Before a parasitic relationship can be established it is necessary that the parasite not only make but maintain contact with an appropriate host. Contact is generally made in one of two ways, either passively or actively on the part of the parasite. Roughly speaking, the terms passive and active host contact are identified with internal and external parasites respectively.

Passive entrance to the host occurs when the parasites are taken in along with the food. In the case of passive entry the parasites cannot, of course, influence their entry into the host. They must wait until the host itself takes them in. More species of parasites enter their hosts through the mouth than any other way. Acanthocephala or thorny-headed worms, digenetic trematodes or flukes, cestodes or tapeworms and nematodes or round worms gain entrance in this way. When this occurs the parasites are usually in an advanced larval stage. In this case sexual maturity is usually reached in the alimentary canal of the host. If, however, the fish is not the final host but is one of the necessary intermediate hosts or if it is the proper final host, but the larval parasites have not yet reached the stage to be infective to the next host, they usually migrate through the gut wall and undergo further development outside the alimentary tract but still within the host. Active migration involving the penetration of tissues occurs most frequently among digenetic trematodes and cestodes.

When they first begin to take food, the fry of most fishes start to accumulate a parasitic population. Regardless of the feeding habits of the adult, almost without exception fresh-water fishes feed on crustacea and other small organisms for a while after hatching. Since some crustacea serve as the normal hosts for certain larval worms, the young fish feeding upon them are particularly open to invasion by these larval parasites. The young of fishes not infrequently have parasitic populations unlike those of the older ones of the same species and these dissimilarities may be traced directly to differences in food habits at different ages.

Active contact with the host by the parasite, on the other hand, is generally the result of the parasite's own activities. The parasite actively seeks out or lies in wait among the vegetation for the host and, as the latter passes by, it quickly makes contact and attaches. Copepods, leeches, monogenetic trematodes and those larvae of digenetic trematodes attacking fish infest their hosts in this way.

In order that attachment may be maintained, once contact has been made, various structural modifications are present among the various members of this group. The mouth parts of parasitic copepods are adapted for piercing the skin of the host, leeches have two well developed suckers, monogenetic trematodes have a large disc, usually provided with hooks, at the posterior end of the body, and the cercariae of digenetic trematodes have penetration glands, enabling them to enter the tissues of the fish.

But regardless of the method of establishing contact, the food habits of a fish and many of the conditions under which it lives influence the nature and the number of the parasites which it will carry. So definitely are the habits of the fish correlated with its parasites that it has been stated as a generalization, that the parasites present reflect clearly the manner of life led by the host. Or, stated slightly differently, the parasitic population of an animal is primarily a function of its habits.

Weedy bays with mud bottoms, generally speaking, yield a high degree of parasites among fishes because the conditions here are favorable for the necessary intermediate hosts. It is here that one finds snails, used in the life cycle of digenetic trematodes, copepods and other crustacea, which serve as intermediate hosts and food for young fishes, and this is where certain species of the larger fish come to feed. Migratory movements and random wanderings of fishes tend to prevent the establishment of absolute limits of such areas of parasitic distribution, but it is known that these areas exist in a number of cases. The entire life cycle of any particular parasite is intimately tied up with and conditioned by food chains and the feeding habits of its hosts, and it follows that an analysis of the species of parasites harbored by an animal mirrors the habits of that particular animal.

2. *Effect upon the host.*—*While* few investigations have been undertaken in an attempt to measure the effects of parasites up-

on fish, there remains no doubt that all kinds of parasites, whether occurring singly or in great numbers, whether larvae or adults, have a harmful effect upon the host. This would seem to be true, even in the absence of obvious symptoms. Even a single parasite withdraws from its host enough food for its own sustenance. While this amount may be small, and the actual harm done the host may not be visible by available measuring methods, it is nevertheless a loss, and it weakens the fish's vitality by just that much. The simple fact that a sufficient number of parasites can weaken or even kill a fish is enough proof that each one does its share toward that end and is therefore harmful. It should be borne in mind that the parasite's existence is ideally a compromise between the host and the parasite, the parasite extracting its daily toll while not sufficiently injuring the host to cause its death. The amount of injury is only a question of degree and the host would be better off without it, even if only a single parasite were present. But there are ample cases involving obvious injury, that are of even greater importance than the mere loss of host sustenance. The parasites may consume the body tissues or body fluids of the fish, or produce substances which are poisons and act as irritants. They may inflict serious body wounds, subject to secondary infection, or cause mechanical injury by pressure or obstruction and biological injury by impairing the normal functioning of certain organs. They may bring about changes in both the metabolism and the behavior of the host. While some of these harmful effects are difficult to demonstrate, enough evidence is available for others so that there is no question as to the harm done by parasites Regardless of the kind or degree, some injury to the host is always there.

For the purpose of discussing the harm done by parasites, they will be considered in two groups, those attacking as larvae and those that attack fish as adults. Of these groups the adults are less damaging to the host and although usually present, they generally pass unnoticed by the angler.

The chief damage caused by adult external parasites, such as fish-lice, leeches and monogenetic trematodes, is that they may extract large quantities of blood and sometimes cause mechanical injury to the tissues at the point of attachment, which may result in frayed fins and in secondary infestations by fungi and bacteria. Under natural conditions, however, these seldom occur in great numbers and they do comparatively little harm. But when

abundant, as is likely to be the case under crowded conditions in hatchery pools, the fish are greatly weakened and may eventually succumb in large numbers. Atkins reported that an epidemic of a monogenetic trematode, *Gyrodactylus elegans,* on lake trout occurred at the Craig Brook hatchery during the late summer of 1896, reducing the number of young fish from 39,000 to 10,000.

In addition to interfering with the normal growth of the host as a result of utilizing its food materials, certain of those forms reaching maturity in the intestine, which include the Acantho-cephala, digenetic trematodes, cestodes and nematodes, may affect the host in other and even more serious ways. The most serious damage done by members of this group can be charged to certain of the thorny-headed worms. These worms hang free in the lu-men or hollow of the intestine and caeca, being anchored to the lining of these organs by numerous hooks covering the proboscis or beak. These hooks may cause serious damage in the area where they are embedded. And it is not unusual to find adult worms that have worked their way through the wall of the di-gestive tract and lie free in the body cavity. In some cases, after reaching the body cavity, they even burrow through the body wall and can be seen from the outside.

In the case of some of the tapeworms the scolex may be so deeply buried in the intestinal lining that a prominent pit can be seen, marking the point of attachment. The caeca of some species of fish may be so solidly packed with certain species of parasites that it seems impossible that the fat absorption function of the caeca is not interfered with.

In addition to serving as hosts for adult parasites, fishes very commonly harbor advanced larval forms of worms which reach sexual maturity in other fishes, birds, or even mammals. It is these larval forms, usually encysted, of Acanthocephala, di-genetic trematodes, tapeworms and nematodes, that are the more damaging and likely to come to the attention of the angler. If not evident from the outer surface, they are observed encysted on the viscera, the walls of the body cavity, or in the flesh of the fish. When the larvae are discovered, the host is often adjudged unfit for human food and is discarded. It is unfortunate that many fish are thrown away because of a few unsightly, minor abnormalities, usually due to worm cysts, which actually do not affect the edible qualities of the fish. The larval forms are more

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damaging because, among other reasons, they are more intimately a part of the host. As indicated above they are usually encysted *within* the host, while those adult parasites occurring on the outer body surface as well as those of the intestinal canal are on the outside, so to speak. Although not often thought of in this way, the inner surface of the alimentary tract, which is a tube with openings at both ends, is *without* the body.

In addition to causing more damage, larval forms are observed much more frequently than sexually mature adults. As pointed out earlier, those parasites which occur internally as adults gain entrance to the final host with its food. They are not able to influence their own fate but must wait until passively transferred with the food. Since many larval forms never make this vital transfer to the final host, great numbers of larvae must be produced to compensate for the loss resulting from the failure to make this contact. In a balanced condition in nature, only a limited number of any one species survives in order to replace the loss resulting from death of the adults. Since the number of parasites apparently remains relatively constant, each individual theoretically produces, on the average, only one adult to succeed it.

Perhaps the most common larval form encountered externally is the "yellow grub" or metacercaria of the digenetic trematode *(Clinostomum marginatum)** (Pl. VI) . They occur most frequently in the region of the gills and gill-covers, and less commonly under the skin and in the muscles. The cyst wall, consisting of two membranes formed by the host in an attempt to wall off the parasite, is fibrous and sometimes so thin that the larval worm escapes when the fish is handled. Cysts are yellowish in color and are easily distinguished from "black spot" by their color and greater size. There is no evidence that "yellow grub" kills fish, despite the economic loss as a result of the larval cysts. While the parasite is perfectly harmless to man, the fish, being made unattractive for human consumption, is often discarded. Cooking, of course, would completely destroy it. Likewise, "black spot" (Pl. I) appears to be disfiguring rather than harmful to the fish host. The only possible objection to eating infected fish

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* The detailed life cycle of this species and of *Pro teocephalus ambloplitis,* mentioned on P. 17, are given in Part Two under Trematoda and Cestoda respectively. Since a knowledge of these life cycles is essential to an understanding of the present discussion, it is suggested that the reader refer to the life cycles first.

is an emotional one, as adequate cooking certainly destroys this parasite as it does all others. If, however, there is a fear of eating cooked worms, infected fish should be skinned and practically all cysts will thus be removed.

PLATE I. Chain pickerel infested with "black spot" (metacercariae of fluke), probably *Crassiphiala bulboglossa:* A, host showing general distribution of metacercariae; B, enlargement of mid-body region showing same. (Photographs by Arthur G. Rogers.)

During this investigation, as in others elsewhere, a large variety of various other metacercariae were found encysted in and upon the liver, heart, kidneys, intestine, and the body cavity.

Even though the life cycles of those that are known are similar (involving snail, fish, bird or mammal) they are more detrimental to fish since they infect vital organs. Fish may sometimes carry large numbers of these larvae apparently without harmful effect, yet in other cases heavy losses have been found among fish whose livers were infected with encysted metacercariae. These losses are fairly common among white perch and are thought to be associated with other factors. Heavy losses are usually observed during the spawning season in lakes having large areas of shallow water. The low water level and the very warm days which elevate the temperature of such waters to a point that is dangerous for fish life, the presence of the larval worms, and the spawning season, when the fish are normally weakened, probably combine to result in the high mortality. Even if the harm done by the parasites alone is not sufficient to cause death, there remains no doubt that the mortality is increased due to their presence.

A one-celled animal, Ichthyophthirius *multifilis* and commonly known as "ich," while usually identified with warm-water species, has been observed to kill landlocked salmon and eastern brook trout fingerlings while yet in the hatchery runways. The disease caused by this protozoan is characterized by small, greyish-white swellings on the outer body and fins.

While the glochidia or larval stage of fresh-water mussels (Pl. IV, Fig. D) ordinarily are of little parasitological concern, cases of their presence resulting in serious damage to the host fish are on record. Murphy (1942), working in California, reported that heavy infestations (600 to 1,200 glochidia per fish) interfered with the circulation of blood in the gills, causing a high mortality among rainbow trout (Salmo gairdneri) fingerlings. Deaths among rainbow fingerlings infested with less than 400 glochidia were usually the result of secondary infestations by fungi or bacteria.

The plerocercoid larva of the bass tapeworm, *Proteocephalus* ambloplitis (Pl. II) , does considerable damage to mature bass in Maine as in other parts of the country. As an adult it is the largest of the cestodes found in bass and it is the only tapeworm known to pass two developmental stages in the same species of fish. Once the fish has taken a copepod infected with the procercoid larva, the latter bores through the intestinal wall and migrates into the mesenteries, spleen, liver, or reproductive

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organs and encysts there. They are very common in the reproductive organs and many fish are rendered sterile by their presence. In this case neither the host nor the parasite is able to accomplish its primary mission of reproduction to insure the survival of its respective species. Near the larval worms the eggs of the fish undergo degeneration and fibrous and bloody areas are frequent in infected ovaries. Doubtless these organs are high in nutritional elements which are favorable for development of the parasite. When encystment involves the mesenteries, inflammation, bloody areas and fibrous adhesions result, the organs being so matted together that they must be literally pulled apart when opening the fish. In the case of heavy infections it is hardly possible that they would pass unnoticed when cleaning the fish, and an experienced individual can recognize such cases by feeling the host prior to opening it. The ventral region has a solid, turgid texture rather than the soft resilience characteristic of normal fish.

As mentioned in the latter portion dealing with the life cycle of this species, the presence of the larval worms in the large bass means that both the host and the parasite suffer. The worms never will reach sexual maturity because it is impossible for another fish to eat the infected host, due to the large size of the latter, and on the other hand as a result of the worms, the host is often rendered sterile.

The salmonid nematode, *Philonema agubernaculum* (Pl. III), is another species of worm which has a very serious effect upon its hosts, the landlocked salmon and the eastern brook trout. This worm, like the bass tapeworm, is found in both the immature and the mature stage in the same fish host. In the larger fish worms cause adhesions of the viscera. These adhesions may not only bind the organs together but also attach the mass of viscera to the body wall. This condition may become so severe that an experienced individual can recognize such heavily infected fish by the feel. When these adhesions are broken and the organs separated, many worms of both sexes in different stages of development are freed. Apparently this is what happens during

PLATE **II.** Smallmouth bass infected with plerocercoids of the tapeworm *Proteocephalus ambloplitis :* A, host fish with body wall removed so as to show the characteristic matted condition of the stomach and intestine; B, enlargement showing adhesions of the stomach and the intestinal region, and two plerocercoids; C, enlargement showing plerocercoids. (Photographs by Arthur G. Rogers.)
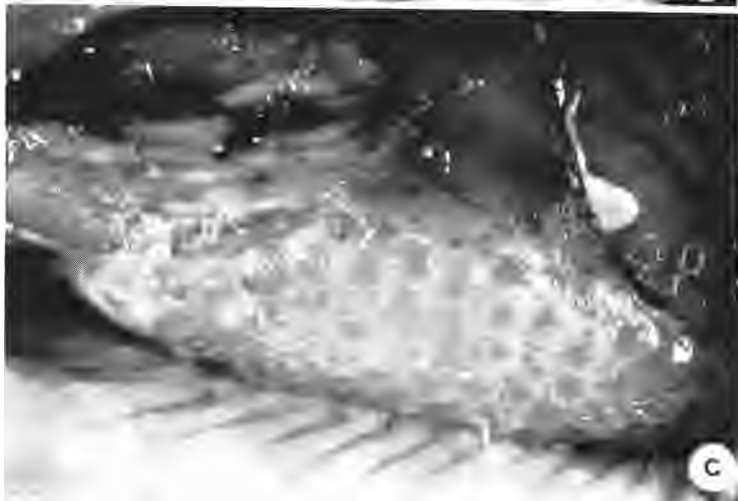
stripping, when a mass of worms is often forced out with the eggs or sperm. In such cases the organs are so strongly adhered together that neither normal spawning nor stripping is possible, in which case the host is actually egg-bound. In such cases pathological changes, particularly of the gonads, are apparent. The wall of the ovary is greatly thickened and firmly attached to the other viscera. The wall loses its normal transparency, becoming nearly opaque. While fully-sized eggs are present, they are abnormally colored, brittle and hard. Also there are membranes of eggs, presumably from the preceding season, the egg proper having been resorbed in the meantime.

Usually, however, as Van Cleave and Mueller (1934: 176) have aptly stated :

> The adjustment between the parasite and its host is so delicately balanced that epidemics of injurious parasites under conditions in nature rarely have a lasting influence upon the host species. Wholesale destruction of the host spells ultimate destruction of its dependent parasites. Consequently an epidemic is followed by a period of relative freedom from the species which caused the high mortality in its host. Thus the balance of nature is maintained and the well adapted parasite never causes the extermination of its host species nor does nature permit the host to become wholly free from parasites.

3. *Transmission of parasites to man as a result of eating infected fish.—Recently* there has been widespread unfavorable publicity among uninformed quarters concerning the possible transmission of parasites to man through eating fish infected with certain larval forms. This is particularly unfortunate for the sporting interests of the state since it is nothing more than a surmise, lacking even in circumstantial evidence. While the worm in question, known under the vernacular name as the

PLATE III. Eastern brook trout infected with the nematode worm *Philonema agubernaculum:* A, host fish opened so as to show the characteristic matted condition of the internal abdominal region; B, body walls spread farther apart, showing same; C, enlargement of ovarian region showing abundance of nematodes *(Philonema agubernaculum)* and an encysted tapeworm plerocercoid (the tag-shaped structure to the right). (Photographs by Frances Fling.)

"broad" tapeworm and scientifically as *Dibothriocephalus latus*,* does occur in certain parts of North America (Manitoba, Michigan, Minnesota, and recently reported from Florida) , and under certain conditions infections with the adult may be acquired by man, evidence that the larvae occur among native fish is fortunately lacking. This is the only species of larval worm in North American fish that is known to include man among its normal adult hosts. In North America the plerocercoids of this worm, as determined by rearing tests of the actual larvae, occur unencysted in the body wall muscles of only four species of fish, namely; the walleye *(Stizostedion vitreum),* the sauger *(Stizostedion canadense),* the pike *(Esox lucius),* and the yellow perch *(Perca flavescens).* Rearing tests consist of feeding the plerocercoids to uninfected hosts and recovering the adult worms.

Similar larvae were found *encysted* on the viscera and body wall of landlocked salmon and eastern brook trout (Pl. III, Fig. C). But the nature of the host and the encystment location preclude them from being larvae of the "broad" tapeworm. However, in the absence of rearing tests, which specialists find necessary to differentiate these closely related plerocercoids, the exact identity of the species involved remains undetermined. It may be taken as certain, however, that any plerocercoid that is enclosed in a cyst is not that of *Dibothriocephalus latus.* There is, however, much confusion about both the larvae and the adults of the species of *Dibothriocephalus,* the adults being found in both fish-eating birds and mammals. Attempts to infect man with *Diphyllobothrium cordiceps,* a close relative of the "broad" tapeworm, occurring in a member of the cutthroat trout series *(Salmo lewisi)*** in Yellowstone National Park, which is similar to if not identical with that found in native landlocked salmon and eastern brook trout, were unsuccessful. Woodbury on one

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* The names employed for the parasites are those which seem to be in general current usage. In view of the fact that authorities on tapeworms are divided as to the status of the generic name *Dibothriocephalus* Lühe, 1899, I have followed Wardle and McLeod without any commitment as to the possible validity of the generic name *Diphyllobothrium* Cobbold, 1858 for the forms involved. Consequently, in the discussion concerning the plerocercoids found in salmonids they are treated under the name *Dibothriocephalus.* When reference is made to other publications in which the author employed the name *Diphyllobothrium,* it is understood to be the same or similar form to which I apply *Dibothriocephalus.*

** According to R. R. Miller (1950. Occas. Papers Mus. Zool. Univ. Michigan, No. 529, 42 pp.), this species is presently referable to *Salmo clarki lewisi* (Girard).

occasion swallowed eight living plerocercoids and in a second experimental test, a year later, he took six larvae. But fecal examinations for eggs followed by an antihelminthic (carbon tetrachloride) failed to show any evidence of worm development in both experiments. Known hosts for the adult of this species are the American white pelican *(Pelecanus erythrorhynchus)* and the California sea gull *(Larus californicus).*

The larvae of worms, including any plerocercoids of *Dibothriocephalus latus,* would be killed by cooking and/or adequate freezing and the infected fish is perfectly safe for human consumption. The failure of most Americans to appreciate the virtues of raw fish serves to prevent the spread of this or any other parasite from fish to man. If one has qualms at the thought of swallowing cooked worms, he should be reminded that raw oysters are highly prized articles of food by many people. But the case is hardly a parallel one, because along with the uncooked oyster has gone the entire alimentary canal with its contents and any of the parasites it happens to be carrying, to say nothing of the possible typhoid germs, if the shellfish in question happens to come from fattening grounds that the sewage of the city reaches before it is rendered innocuous by the cleansing waters of the sea.

4. *Control measures.—The* control of the various parasites of fish in nature is an exceedingly complex problem, and much more information on its various aspects is necessary before any success can even be hoped for. While the prospects for progress are dim, any approach is dependent upon a thorough knowledge of every phase of each parasite's life cycle and also its relationship with all the hosts in which it can live. Once this information is available, it is sometimes possible to achieve limited control by attacking the weakest link in the life cycle of certain parasites.

In reality the control of parasites among animals generally means that they must be eliminated through the use of chemicals or some other means during some phase of their life cycle, or, if not destroyed, they must be prevented from making contact with the host. Either of these methods would spell destruction of the parasites. Man, once he has learned how he acquires parasites, can try to prevent these contacts or at least avoid them as much as possible. He can, moreover, extend this protection to his domesticated animals. Yet, despite the fact that the public is

repeatedly informed that raw, or inadequately cooked or cured pork is dangerous and the Bureau of Animal Industry of the U. S Department of Agriculture, through its meat inspection service, has a requirement that no ready-to-eat article of food entering into interstate commerce* shall contain any muscle tissue of pork, unless that meat has been refrigerated, or heated, or otherwise treated in a manner that will insure the destruction of trichina worm larvae, approximately one in every six Americans is infected with the trichina worm *(Trichinella spiralis).*

But when fish are involved, over which man has practically no control so far as the parasite making contact with the host is concerned, the methods he uses for himself and the domesticated animals are not possible of application. It is to be remembered that the acquisition of internal parasites by fish is directly related to their feeding habits, which, if they are going to escape these parasites, in reality means that they would be denied food. Obviously this is as impossible as it is impracticable. When the method to be employed would involve the elimination of an intermediate host not used as food by the fish in question, while such a step might appear theoretically desirable, one must always proceed with caution. Not only is such a method seldom capable of execution, but more serious consequences might result through disturbing the normal balance in nature. For example, in the case of the yellow grub *(Clinostomum marginatum)* it could be eliminated through destroying the snails involved and/or the wholesale killing of fish-eating birds, such as cormorants, herons, loons, kingfishers and pelicans.

Obviously control measures that depend upon the extermination of any group of animals are indefensible from the point of view of conservation, and wholly impossible of application. The birds are protected under the Migratory Birds Treaty and killing them is illegal. But even if it were legal, control by destroying them would be extremely difficult in practice and would meet with considerable opposition from the public. And snails play such an

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* In this connection it should be pointed out that one-third or more of such products are not subject to Federal inspection since they are sold within the state in which they are produced. Such products, sold within the state in which they are prepared, are subject to no inspection, or are inspected by city, county or state authorities, a procedure which is frequently inadequate, owing to the lack of trained personnel and the failure of public health authorities to insist that such meats sold within the state be subject to the same standards as similar products crossing state lines.

important role in the food chains of many aquatic organisms that the removal of this one form of life, even were it possible, would upset the entire balance of the body of water involved. All possible consequences should be weighed and the greatest caution exercised before meddling with the "Balance of Nature." It is obvious that complete or nearly complete extermination of the host over a large area would be necessary for any real control effectiveness and this with any animal is a task not to be taken lightly.

The most ambitious and only concerted attempt with which the author is familiar at the control of a parasite of fish in nature was begun in Canada about ten years ago by R. B. Miller and his co-workers. The parasite involved is a tapeworm, known scientifically as *Triaenophorus crassus,* the third larval stage of which is found in various members of the whitefish group, particularly *Leucichthys tullibee,* and other species. In 1944, several years after the U. S. Food and Drug Administration began (about 1932) to refuse to allow heavily infected fish to be imported into the United States, the Dominion Government established a commission to make an investigation of the *Triaenophorus* situation and to make recommendations on the solution of the problem.

The life cycle of this species, with one principal exception, parallels that of the bass tapeworm *(Proteocephalus ambloplitis)* described later on. And as in that species, it is the larval stage which causes concern. Briefly the life cycle is this. The adult worm lives in the intestine of the northern pike *(Esox lucius)*; here it reaches maturity, releases its eggs and dies. The embryos pass into the water where they soon hatch from the shell enclosing them. The errant hair-covered larva which emerges, called a coracidium, must be eaten by a certain species of copepod *(Cyclops bicuspidatus)* to survive and develop. In the body cavity of this crustacean the parasite develops into a procercoid. Infected *Cyclops,* when eaten by ciscoes, carry the parasites to these fish, where they develop into plerocercoids enclosed in a cyst. The cycle is completed when the pike swallows a fish containing cysts. It is these cysts in the ciscoes, while harmless to man, that are objectionable in appearance and, when numerous, render the infected fish unmarketable.

According to Miller (1952), the following four approaches are theoretically possible : reduction or elimination of 1) the

pike, the final host, 2) of the coracidia, the errant, first larval stage, 3) of *Cyclops,* the host for the procercoids, and 4) of ciscoes, the principal host for the plerocercoids. Research has proceeded along all these lines except the possible reduction or elimination of *Cyclops,* the first intermediate host. The possibility of successful attack through effective reduction in the numbers of this host was considered too remote for further consideration. Reduction of the final host, the northern pike, has proved too expensive and inefficient to be practical. Killing the coracidia was unsuccessfully attempted by treating the lake with an acid and it was found that they were too resistant to allow economical control with electricity. The reduction of ciscoes, while showing some promise in one lake, appears to be limited in application and only temporarily effective.

As Miller aptly stated, after discussing the detail control research and problems encountered during the past ten years, in the abstract of his 1952 paper : "It has become obvious that control, if it ever comes, will be only after a period of long and patient research on the life-history of the parasite, its relationship to the environment and its host and the interrelationships of the various hosts."

However, despite the fact that the prospects of control in nature are dim, so were the prospects approximately 50 years ago for the control of malaria and yellow fever. Yet today the number of deaths resulting from malaria naturally acquired in the United States is less than ten a year, as compared with nearly 5,000 annually 20 years ago. This remarkable accomplishment is attributable to something more than compiling a list of those infected and counting the tombstones of the victims. Instead, it involved the discovery of additional species of mosquitoes transmitting malaria, studies of their breeding habits and their relative importance in the transmission of the disease from man to man, further studies on the cycle of the malaria in man and in the mosquito, studies of the phenomena of immunity in malaria, field studies on control of malaria, scientific screening and clinical tests of antimalarial drugs, and the development of a wide range of insecticides which were highly efficient against the larval and adult mosquitoes involved. So we may also hope for greater success in the control of fish parasites, after exhaustive studies of the various problems involved have been completed.

IV. REMARKS AND RECOMMENDATIONS

Surveys to determine the prevalence of parasites among fish in different areas are difficult if not impossible to compare with one another because of differences in the thoroughness of the examinations of the hosts and the determinations of the species encountered, differences in the species of hosts and the number of each species involved, differences in the habitats from which the hosts were taken, differences in the season during which the hosts were examined, and finally, but of no less importance, because of the differences in the competence of the surveyors. In the same area, and even among individuals of the same species of fish, results have differed several fold due to inequalities of sampling or other factors for which there is no readily apparent explanation.

As indicated in the Introduction nearly one-half of the individuals of our 25 host species belonged to three species of salmonids and one species of bass (see Table I). They came from approximately 30 locations, chiefly lakes and larger ponds, some of which are connected, while others are a part of a different flowage. All the fish were not taken at random ; in fact, some were selected for autopsy because they were known to harbor parasites. This applies particularly to the landlocked salmon and the eastern brook trout examined at the Oquossoc and the Raymond hatcheries during the stripping season. Consequently a quantitative computation of the incidence of parasitism would be misleading. Since there are some 2,500 such lakes and ponds, each with its tributaries, and 66 species of fish reported for the state, and since there are all the possible variables listed above, what would be the value of determining the percentage of parasitism obtained and comparing the figures with those of other studies, few of which included any salmonids among their hosts?

Under conditions in nature control measures for the elimination or even the reduction of parasitism have never proven practicable. However, in hatcheries and rearing pools, where the young are kept under controlled conditions, programs for the extermination of dangerous parasites may be inaugurated with expectations of reasonable success. Pools and tanks may be treated chemically to destroy pests, and fishes may be subjected

to periodic dips like those administered to domesticated animals for the removal of external parasites. The food supply may often be controlled to eliminate sources of infection by internal parasites. These various methods, which are applicable under controlled hatchery and rearing pool conditions, are discussed in detail by Davis (1946, 1953) and Allison and it seems unnecessary to include them here.

In the planting program every precaution should be taken to prevent the spread of parasites into uninfected or only lightly infected waters through the introduction of diseased fish. Particularly is this true when the bass tapeworm *(Proteocephalus ambloplitis)* and the salmonid nematode *(Philonema agubernaculum) ,* both of which have been found to have a limited distribution within the State, are involved. The first species, unlike the "yellow grub," "black-spot," and certain other species spread by fish-eating birds, owes its introduction into new waters for all practical purposes only through the planting of fish infected with either the larvae and/or adult worms. It is possible, of course, to spread the worm through the introduction of the crustacean host, but this is highly unlikely in nature. It is a safe assumption that the bass tapeworm originally entered the State along with the introduction of the fish host, either with the initial planting in 1869 or subsequently. Since this species of worm is among the most harmful parasites and since its host, already popular with non-resident fishermen offers prospects of gaining in popularity among native anglers, a significant number of fish should be carefully examined for the presence of the larvae before they are taken from the hatchery to insure against the introduction of additional parasitized fish into the waters of the State. Issuance of stocking permits might be made contingent upon certification that such commercial stock is free of the larval stage of this worm. Adult fish likewise should not be transferred from infected to parasite-free waters.

While the presence of *Philonema agubernaculum* is equally harmful to the landlocked salmon and the eastern brook trout, the two species of hosts found harboring it in this investigation, it is of even greater concern than the bass tapeworm due to the importance of the hosts to the State. But, since the life cycle is unknown, the only sure recommendation that can be made at present is that care should be taken to prevent the introduction of fish harboring this dangerous worm into parasite-free waters.

Because of its dual importance it is recommended that attention be directed towards an elaboration of the life cycle of the worm. Not until this has been accomplished will it be possible to determine whether other control measures are feasible.

A better understanding of the diseases of fish, particularly those caused by animal parasites, is essential to a complete fish management program. The study of these organisms is an important phase of any management program and therefore should be continued.

V. ACKNOWLEDGMENTS

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PART TWO

VI. GROUPS INVOLVED, LIFE CYCLES AND SPECIES ENCOUNTERED

During the life of an animal, whether it be parasitic or non-parasitic, developmental stages follow one another in a series from the *egg* to the sexually mature adult, and these successive stages are known as the life cycle of that particular animal. The life cycle of the common house fly, for example, begins with the fertilized *egg,* which hatches into a maggot, and this transforms into a third stage, the pupa, from which the adult eventually emerges. Life cycles of parasitic animals may be either direct or indirect. In the former type only one kind of host is involved. The parasite lives and reproduces upon (or within) this host, the young remaining upon the same or another host of the same or closely related species.

The indirect life cycle involves two or more hosts ; they harbor different successive stages of the parasite. The animal in which the parasite reaches sexual maturity is known as the final host and the host in which the larval stage is spent, as the intermediate host. If two intermediate hosts are involved they are known as the first and the second intermediate hosts respectively. At the time of transfer to the final host the larval forms are usually enclosed in a cyst, which is one or more membranes or walls surrounding the young parasitic worm.

The life cycles of different kinds of animals vary greatly, and it is necessary that particular names be given to the different stages occurring among them. While the term larva is a broad term that may be applied generally to any young animal between the time it has left the *egg* and has not yet assumed the structural characters of the adult, it is necessary that more precise names be given to the different larval stages. The unhatched larva, while yet in the egg shell, is commonly termed an embryo.

In order that a clearer understanding may be obtained of the different life cycle plans and certain of the various factors involved in the cycles of some of the parasites with which we are concerned, it seems desirable that we begin with the simplest and proceed to the highly complicated, indirect life cycle. The one is direct and involves only a single host while the other is indirect and at least three hosts are required for the completion of the cycle. The first is the simplest of all the life cycles of parasitic

animals and probably represents one of the earliest methods by which animals became parasitic. Consequently, the group having the simplest life cycle will be treated first and the one having a complicated cycle will appear last. Thus, the arrangement of the different groups in this work depends upon complexity of the cycle rather than upon their relative importance as parasites or their taxonomic position in the animal kingdom.

1. COPEPODA

The fish louse *(Salmincola edwardsi* Pl. IV, Fig. A) of the eastern brook trout and related species from other fish (Pl. IV, Figs. B, C) belong to the Copepoda of the class Crustacea. The crustaceans are a large group, composed chiefly of non-parasitic forms, including the familiar and closely related lobster, crayfish, sowbug, and the amphipods (Pl. V, No. 1). Copepods are aquatic and can be readily distinguished from the other external parasites of fish by the rigid body, which is not contractile but maintains a fixed shape. The sexes are separate, fertilization is accomplished by sperm packets known as spermatophores, and the eggs are usually carried in paired sacs attached to the posterior end of the female. In the case of the parasitic species, free-living larval stages may be present or absent. When there are no free larval stages, comparable developmental stages are passed in the *egg* before hatching occurs. In neither case, hcwever, is an intermediate host involved.

As an example of a simple, direct life cycle of a parasitic copepod known to most Maine anglers, that of *Salmincola edwardsi* will be used. Upon hatching from the egg, which is carried by the parent female, the copepod attaches itself at once to the same host fish, or, in some cases, within not more than a few hours at the most, to another brook trout with which it has been successful in making contact. No host other than the one species of fish is involved in the life cycle of this form, and therefore the cycle is termed direct.

While a few of the Crustacea, particularly some of the copepods, are important as external parasites of fish, they are of even greater importance in two other widely different respects. One of these is also harmful, but in an indirect way ; the other is in a very useful way.

As will be shown later, certain species of copepods and amphipods, none of which are parasitic, are used as intermediate hosts in the life cycle of certain worms. In this way the worms
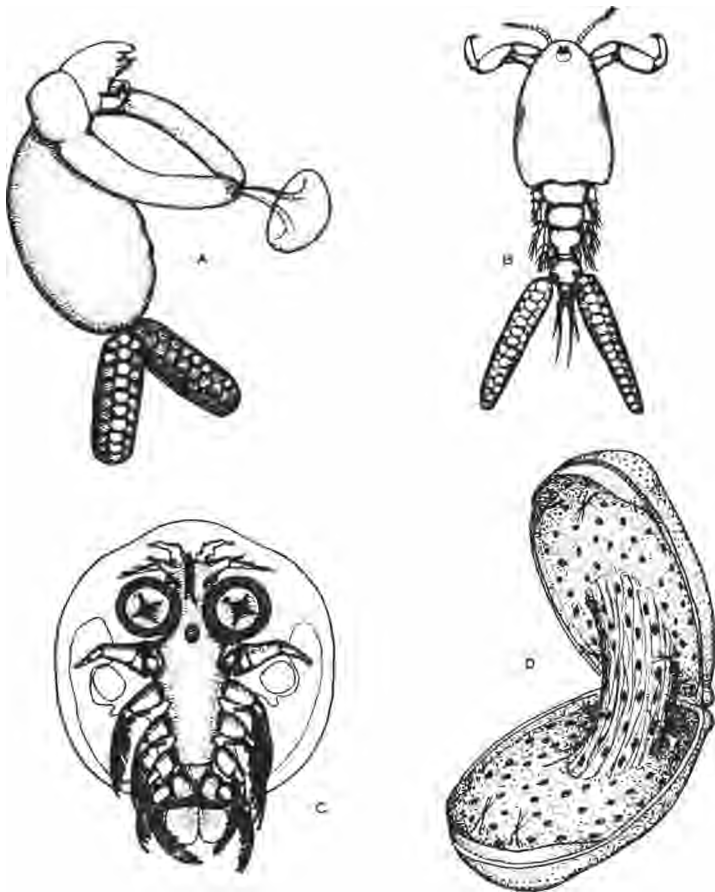
PLATE IV. Drawings of parasites other than worms: A, lateral view of *Salmincola edwardsi,* found only on the eastern brook trout; B, dorsal view of *Ergasilus* sp., infesting various species; C, ventral view of *Argulus catostomi,* found on the white sucker; D, antero-lateral view of a hookless glochidium (larva) of mussel. A, B and C are copepods. (All enlarged and original.)

are able to complete a stage in their development, which would be impossible if the particular crustacean were unavailable. As a result they are considered harmful, although in an indirect way. On the other hand they are of utmost importance since they serve as a link between the inorganic constituents of the water and the food supply of the animals which inhabit it, especially fish. All young fish feed for a time upon copepods, and some, such as herring, sardines and smelts, continue to feed upon them throughout life. Were they unavailable in nature, the young fish

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could not survive the critical period following emergence from the egg.
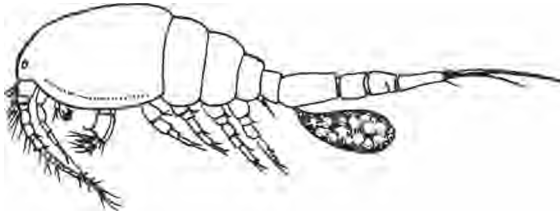
FIG. 1. Side view of copepod *(Cyclops* sp.), used as the first intermediate host by certain tapeworms and important as food for young fish.

Suborder ARGULOIDA
Family ARGULIDAE

Argulus catostomi Dana and Herrick, 1837

HOST.—White sucker *(Catostomus commersoni);* externally.

Argulus canadensis Wilson, 1916

HOST.—Lake trout *(Cristivomer namaycush);* externally.

Suborder CYCLOPOIDA
Family ERGASILIDAE
Ergasilus sp.*

HOSTS.—Golden shiner *(Notemigonus crysoleucas),* three-spine stickleback *(Gasterosteus aculeatus),* white perch *(Morone americana),* smallmouth bass *(Micropterus dolomieu),* yellowbelly sunfish *(Lepomis auritus),* pumpkinseed *(Lepomis gibbosus);* on gills and fins.

Suborder LERNAEOPODOIDA
Family LERNAEOPODIDAE
Salmincola edwardsi (Olsson, 1869)

HOST.—Eastern brook trout *(Salvelinus fontinalis);* on gills and fins. This species is common and when occurring in abundance, may do considerable damage. The following numbers were taken from each of three eastern brook trout found dead and submitted for examination : 25, 35 and 69.

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* Whenever the genus name followed by sp. (abbreviation for species) appears, it means that it was not possible to identify all or some of the available material to species. This may have been due to one or several reasons or a combination thereof : too few adult specimens, adult material in poor condition or immature worms. When the trivial name (the second of the two words forming the species or scientific name of an animal) is preceded by "?", it means that the material belonging to the genus involved was identified only provisionally to species.

2. PELECYPODA (GLOCHIDIA)

Another parasite requiring only one host, although having a more complicated life cycle than that of the fish louse, is the larva of the familiar fresh-water mussels. These larvae are known as glochidia (Pl. IV, Fig. D) and may occur in such numbers as to be harmful to the host fish. The glochidia undergo part of their development in the gills of the female mussels, and when sufficiently advanced are expelled in great numbers and fall to the bottom. Since they are very light in weight the slightest disturbance of the water throws up a cloud of them. The turmoil caused by the fins of passing fishes creates a tempest of glochidia that brings them into contact with their host. Most of the larvae are drawn in by the respiratory action of the fish and distributed over the gills and other parts of the body. Upon making contact with the appropriate host the larvae attach by closing their two valves on host tissue, marking the beginning of the parasitic phase. If they succeed in grasping a favorable fish, they cling firmly and are overgrown by the host's tissues, which form a protective cyst within about a day. The time they remain on the fish is governed largely by the water temperature and varies from 10 days to a month or longer in summer. If attachment takes place late in the fall, they remain attached until the following spring. While encysted they undergo development in the direction of the adult form but do not increase in size. At the completion of this stage the cyst is ruptured, freeing the tiny young mussel, which begins growth on the bottom. Only the larvae are parasitic, the corresponding adults are free-living.

HOSTS.—White sucker *(Catostomus commersoni),* chain pickerel *(Esox niger),* pumpkinseed *(Lepomis gibbosus);* attached to the gills and the fins.

3. HIRUDINEA

The leeches attacking fresh-water fish are distinguished by their relatively large size, their extreme contractibility and the presence at each end of the body of a sucker, which they attach alternately when moving over the surface of the host, humping the body in a characteristic manner as they progress. The suckers are usually disc-shaped and distinct from the body, with a proboscis which is capable of distention and retraction opening within the anterior one. They may or may not have pigmented

eyes on the oral region, and often there are pigmented flecks on the posterior sucker. The alimentary tract is complete and possesses numerous out-pocketings for the storage of reserve food. Each animal is monoecious, that is to say both sexes are possessed by the same individual, but sperms are transferred to another individual by means of sperm packets as in the copepods. Eggs are deposited in cocoons, which are usually attached to foreign objects.

After the young, which resemble the adult, hatch, they remain in wait to attack an unsuspecting host which chances to come close enough for the worm to make contact. There are neither larval stages nor an intermediate host. After attaching and feeding for a time they usually leave the host, returning when more food is needed. This is not a permanent association of parasite with its host and therefore is usually known as temporary parasitism.

Order RHYNCHOBDELLAE
Family GLOSSIPHONIIDAE
Actinobdella triannulata Moore, 1924

HOST.—White sucker *(Catostomus commersoni);* attached to the gills, fins and oral cavity.

This species, the description of which was based upon specimens from Lake Nipigon in Ontario, was taken only from the above host. Specimens taken in New Hampshire and several localities in Canada, and contributed to the author for identification, were likewise all taken from the white sucker.

Family PISCICOLIDAE
Piscicola milneri (Verrill, 1874)

HOST.—Landlocked salmon *(Salmo salar);* attached externally.

Piscicolaria reducta Meyer, 1940

HOST.—Golden shiner *(Notemigonus crysoleucas);* attached to fins.

4. ACANTHOCEPHALA

The thorny-headed worms found in fishes are elongate and flattened and become distended and plumply cylindrical when placed in water or in a killing solution. The sexes are separate

and the anterior region of the body is provided with a specialized attachment organ known as the proboscis. The proboscis is capable of eversion and retraction within the front end of the body. When everted, its surface bears numerous recurved hooks which grapple into the host tissue and thereby provide secure attachment for the worm. These parasites have no trace of a digestive system, and the digested food of the host is absorbed directly through the body surface of the worm. Normally, acanthocephalans live as adults in the lumen of the digestive tract only, but occasionally adult worms bore through the wall of the digestive tract and come to lie in the body cavity, or undergo encystment in the viscera. The proboscis with its recurved hooks causes damage to the intestinal wall of the host ; ulcer-like lesions and conspicuous areas of laceration and inflammation sometimes result. Acanthocephala have been reported as among the most injurious parasites of fishes because of the apparent injury to the host tissues. The members of this group are the most thoroughly adjusted to the parasitic habit of all the parasitic worms. The dependent state has been so firmly impressed on all acanthocephalans that there is no time in the life cycle when the individual leads a free life, even for a brief interval.

Few of the life cycles of the Acanthocephala of fishes are known. But, in so far as known, every species utilizes at least two hosts, one of which is a vertebrate or back-boned animal, in the digestive tract of which sexual maturity is reached, and the other is an arthropod, which shelters the larval forms. Eggs produced by the mature female leave the body of the vertebrate host along with the feces. Each *egg* contains an acanthor, as the first larval stage is known, which is wholly incapable of breaking its confining shells and never hatches unless it is swallowed by some suitable species of arthropod. Some species of crustacean or insect acts as the first intermediate host in every life cycle which has been determined. In the simplest conditions, the larva inside the body of the arthropod host is liberated in the digestive tract of a fish which swallows the infected arthropod. Consequently, there is no period when the acanthocephalan leads a free existence.

After several years of investigation by DeGiusti the life cycle of *Leptorhynchoides thecatus,* a widespread parasite of fresh-water fish in this country, was established. However, nearly

30 years earlier Van Cleave reported finding the immature stage of this parasite as a natural infection in what proved to be the intermediate host.
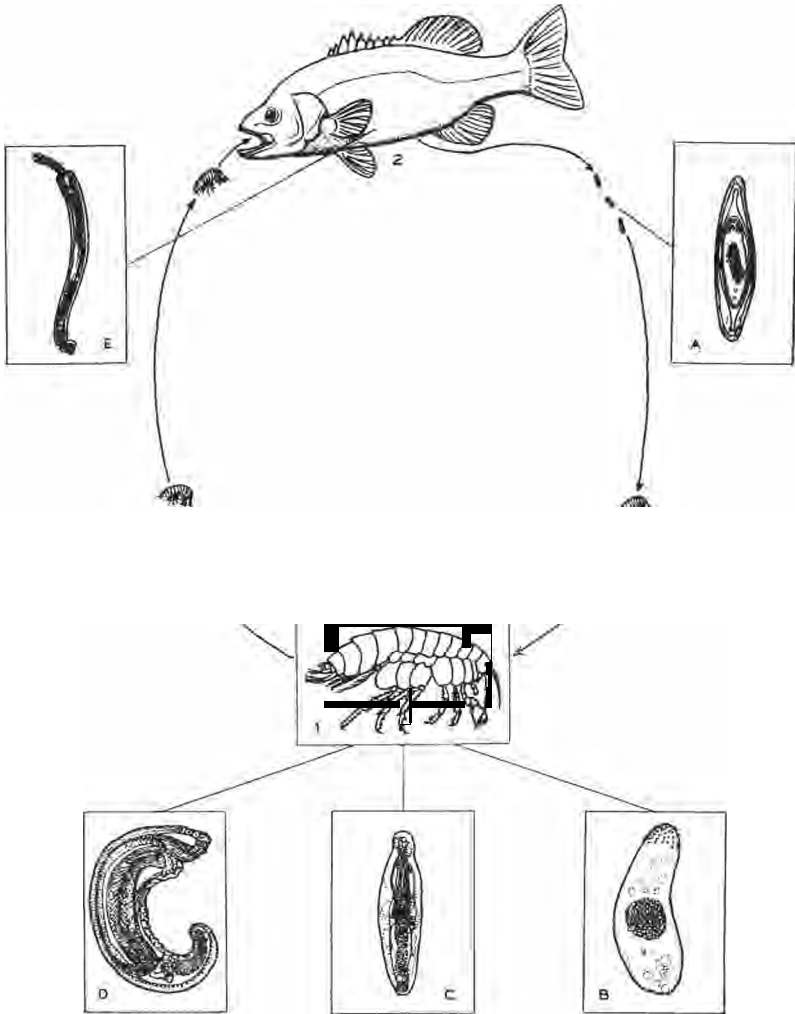

PLATE V. Life cycle of thorny-headed worm *(Leptorhynchoides the-catus)* : A, *egg* containing larva (acanthor), after escaping from adult female worm in fish's intestine and before being eaten by amphipod (number 1); B, acanthor, after escaping from the embryonic membranes within the digestive tract of amphipod; C, acanthella within body cavity of amphipod; D, cystacanth, later stage within body cavity of amphipod; E, adult worm within intestine of smallmouth bass (number 2). Numbers 1 and 2 indicate intermediate and final hosts respectively. Enlarged. (Modified from DeGiusti, 1949; 1, 2 and E original.)

Leptorhynchoides thecatus is able to utilize a great variety of fish as final hosts, but the basses are the most commonly infected. Since they harbor greater numbers of worms and show a higher incidence of infection, they are regarded as the normal hosts of this species. The adult worm lives in the intestine, especially the pyloric caeca, of the appropriate host. The eggs, containing the developing larvae (Pl. V, Fig. A), escape from the female worm and are passed into the water with the fish's droppings. Typically the acanthor is surrounded by a series of membranes or shells. When the egg is taken as food by the amphipod *(Hydella azteca)* (Pl. V, No. 1) the *egg* shells are weakened by the action of the digestive juices in the fore-intestine of the crustacean. The escape of the larva from the egg is apparently the result of the combined action of the digestive juices of the host and the movements of the larva.

The recently liberated acanthor (Pl. V, Fig. B) is elongate, with rounded ends, and the anterior region is provided with several rows of stout, backward-directed spines. The larva, free in the intestine of the host, is actively motile. After a short period within the intestine of the amphipod, the acanthor makes its way through the host's gut wall and encysts on its outer surface. Having completed penetration, the acanthor ceases motility and enters the acanthella (Pl. V, Fig. C), as this second larval stage is known.

Some two weeks after the egg was originally consumed by the amphipod, a period during which growth in size and conspicuous internal changes takes place, the acanthella is freed from its previous attachment to the outer surface of the intestine. After becoming detached and as it lies within the body of the host, the rudiments of the structures of the adult worm make their appearance.

About two weeks later, or a month after being taken by the intermediate host, these rudimentary structures, characteristic of the acanthella, have developed into structures distinctive of the adult worm. The proboscis and its hooks have become functional and the earlier, unformed organs have become differentiated into the respective organs of the adult (Pl. V, Fig. D). With the appearance of these features of the mature worm, the individual is recognizable as an immature acanthocephalan to which the term cystacanth is applied. Here it remains, undergoing no further

development, until the infected amphipod is consumed by a suitable fish host (Pl. V, No. 2) in whose intestine further growth and development into the sexually mature adult occur.

After the infective cystacanth is released from the surrounding amphipod tissue, as a result of the fish host's digestive juices, it usually enters the pyloric caeca and attaches to the caecal wall (Pl. V, Fig. E). Some two months later the female produces eggs, marking the completion of that life cycle, and the cycle of the next generation is begun anew.

Should the amphipod bearing acanthellas or cystacanths be eaten by a host incapable of bringing them to maturity, they become secondarily encysted and are then known as juveniles. Since the parasite neither undergoes further development nor increases in numbers, such a host, when entering into the cycle, **is** known as a paratenic host. If the paratenic host is eaten by the proper final host, the worms attain sexual maturity.

Order PALAEACANTHOCEPHALA
Family RHADINORHYNCHIDAE
Leptorhynchoides thecatus (Linton, 1891)

HOSTS.—Smallmouth bass *(Micropterus dolomieu),* **pumpkinseed *(Lepomis gibbosus),*** yellowbelly sunfish *(Lepomis auritus),* landlocked salmon *(Salmo salar),* eastern brook trout *(Salvelinus fontinalis),* yellow perch *(Perca flavescens),* brown bullhead *(Ameiurus nebulosus),* largemouth bass *(Micropterus salmoides),* chain pickerel *(Esox niger),* white perch *(Morone americana).*

Family **ECHINORHYNCHIDAE**
Pomphorhynchus bulbocolli Linkins, 1919

HOSTS.—White sucker *(Catostomus commersoni),* brown bullhead *(Ameiurus nebulosus),* yellow perch *(Perca flavescens),* pumpkinseed *(Lepomis gibbosus).*

Family POLYMORPHIDAE
Corynosoma hardweni* Van Cleave, 1953

HOST.—Cystacanths removed from visceral cysts of American smelt *(Osmerus mordax),* the second intermediate host. Since the original material *was* submitted to Van Cleave, the cystacanths have been taken in several instances from the same

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* These were kindly identified by the late Dr. Harley J. Van Cleave, and reported by Van Cleave (1953).

species of fish. Final hosts reported for these larval acantho-cephalans are the grey seal *(Halichoerus grypus)* and the ringed seal *(Phoca hispida).*

Order NEOACANTHOCEPHALA

Family **NEOECHINORHYNCHIDAE**

Neoechinorhynchus cylindratus (Van Cleave, 1913)

HOSTS.—White sucker *(Catostomus commersoni),* eastern brook trout *(Salvelinus fontinalis),* common shiner *(Notropis cornutus),* white perch *(Morone americana).*

The life cycle, as determined by Helen Ward, involves three hosts. Eggs escape with the feces of the final host and are eaten **by** an ostracod crustacean *(Physocypria pustulosa** [$=$ *Cypria (Physocypria) globula]),* the first intermediate host. The in-fected ostracods are eaten by bluegills *(Lepomis macrochirus* [$=$ *L. pallidus])* after which encystment of the larvae occurs **in** the host's liver. When infected bluegills are taken by the final host, the parasite reaches sexual maturity in the intestine.

Neoechinorhynchus saginatus" Van Cleave and Bangham, 1949

HOST.—Fallfish *(Semotilus corporalis).*

Octospinifera macilentus Van Cleave, 1919

HOST.—White sucker *(Catostomus commersoni).*

5. **TREMATODA**

The flukes or Trematoda are small parasitic worms which **live** upon or within bodies of various vertebrates, and are known as ecto- and endoparasites respectively. The trematodes of fish **are** almost always monoecious, that is to say one animal contains a set of both male and female reproductive organs ; the body is usually somewhat flattened. In all trematodes there are digestive organs, consisting of a mouth connecting with a tubular portion, which usually divides into two lateral branches, known as crura. One or two suckers for attachment are commonly present, though **in** some flukes living as ectoparasites, grappling hooks and spines are developed for fixation.

The trematodes are divided into three orders but only two of these are of concern here. These are the orders Monogenea and

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** Kindly identified by the late Dr. Harley *J.* Van Cleave.

Digenea. The monogenetic trematodes are typically ectoparasitic upon aquatic vertebrates and they have direct life cycles. Most species occur upon the body surface and the gills of fishes, and when present in large numbers they sometimes cause pathological conditions, especially to fishes kept in captivity or in hatcheries. Although most species are oviparous, that is the adult worm produces eggs, certain representatives, species of the genus *Gyrodactylus,* are viviparous and the young before emerging may contain a daughter in which there is a daughter, and within that in turn a larva of a fourth generation. Under such a set of conditions the young at birth are almost immediately ready to reproduce another generation. Because of this special adaptation to rapid reproduction, outbreaks of epidemic proportions are especially likely to accompany the crowded conditions of fishes under cultural management. The case of the outbreak of *Gyrodactylus elegans* among lake trout at the Craig Brook hatchery, referred to previously, can be cited as a striking example. From such sources gyrodactylid worms may be spread when infested fishes are planted in native waters previously free of these parasites. However, the development within this group is direct, whether reproduction is oviparous or viviparous. The changes undergone by the larvae as they develop into adults are of a simple type and the transformation occurs upon the host harboring the parent worm or upon a similar host with which the young has been successful in making contact. No intermediate host is involved, as in the case of the Digenea.

The other order of trematodes, the Digenea, are, as adults, endoparasites of all groups of vertebrates and no host-organ is immune. In their life cycles, which are always indirect and complicated, two, or more (usually three) hosts, which harbor different but successive stages in the cycle, are involved. The forms occurring in fishes fall into two distinct biological groups : 1) those which reach sexual maturity in the body of the fish ; and 2) those which remain immature in the fish and become adults only when introduced into some other fish-eating animal. This final host of the larval trematodes found in fish is usually a bird or a mammal, though in some instances larvae in the body of fish may represent developmental stages in the life cycle of species which reach sexual maturity in fishes that feed upon their own kind.

The variations in the number and the different groups of hosts involved and the wide variation in details and even in the

patterns make it undesirable to attempt to present broad generalizations concerning the life cycles of the digenetic trematodes. The single common feature in the cycle is that with very few exceptions the first intermediate host is a mollusk, usually a snail, but in a few cases a small bivalve. Yet even here, the manner in which the first larval stage of the parasite gains entrance into the snail, and the number of larval stages passed in this first host, differ among the various species of worms.

As LaRue (1951: 341) recently stated,

Each species seems to play the game of parasitic life within the broad rules laid down by, and for, its family [of digenetic trematodes] ; but it appears to have developed within this code its own special rules and regulations, its own deviations from what we poor humans assume to be normal and regular for the family.

For the above reasons and because of the widespread interest concerning it, the so-called "yellow grub" *(Clinostomum marginatum)* will be used to illustrate a digenetic life cycle.

The trematode eggs upon reaching the water, after being voided by the final host, give rise to cilia-covered larvae. This first larval stage or miracidium (Pl. VI, Fig. A) , the term used to designate the first larval stage in the life cycle of a digenetic trematode, must find and enter a suitable snail within a matter of hours or it will die. Not only are these miracidia host-specific, only certain species of the genus *Helisoma* being the "right" host, but the snail host must not be more than two or three months old. When the miracidia come near a suitable snail they make a dash for it, attach themselves to the soft head region and by the secretion of certain glands they bore or digest their way into the internal tissues, usually the digestive gland or liver. Once having migrated to the organ or tissue suitable for its development the miracidium enters upon the second phase of its existence, during which it reproduces extensively, thus compensating for the enormous mortality suffered by other miracidia which were less fortunate in encountering a suitable snail host. Here the miracidium degenerates into a hollow sac-like body representing the second larval stage, and is known as the sporocyst (Pl. VI, Fig. B). The sporocyst is an immobile simple sac-like structure, absorbing nourishment and excreting waste products through its body wall, and devoting its energies to the production of the next genera-

tion, the body cavity serving as a brood chamber. This next generation, which is more complicated structurally, is known as the redia (Pl. VI, Fig. C) . These, too, are hollow forms but possess a pharynx, primitive gut and an excretory system. They are capable of a limited amount of movement, and apparently feed actively upon the tissues of the host. Within these rediae there develop daughter rediae, distinguishable from their mothers, which escape through a birth pore and further contribute to the increase in production. Next the daughter rediae produce still a different type of larva known as cercariae (Pl. VI, Fig. D) , which resemble the adult worm much closer than they do the second generation of redia in which they were produced. A mature cercaria has a pharynx, a pair of intestinal crura, a more complicated excretory system, several rows of heavy cephalic spines, a pair of eye spots, a penetration organ consisting of four pairs of glands (enabling it to penetrate the tissues of the next host) , and a body provided with two suckers and a forked tail.

When these cercariae reach a certain stage of development they emerge from the redia and undergo further development within the snail, after which they escape into the water. The cercariae are short lived and are infective for only a comparatively few hours. After leaving the snail they suspend themselves for a short time in the water with the anterior end hanging downward (Pl. VI, Fig. E) , then slowly sink to the bottom. Upon striking the bottom they are stimulated to activity and resume their former position by lashing the tail. If a cercaria accidentally makes contact with the second intermediate host, a fish of almost any species, it immediately attaches itself by means of the anterior spines, casting off its tail. The contents of the penetration glands are secreted, breaking down the tissues of the host, and the cercaria quickly bores its way inside. It soon comes to rest on the gill filaments, gill cover, base of the fins or in the flesh elsewhere in the body. In the fish it forms the familiar yellowish-white, abscess-like cyst, while undergoing further development, and loses such larval characteristics as the eye-spots and cephalic spines. This is the encysted stage, known as the metacercaria (Pl. VI, Fig. F) , and infected fish are said to be "grubby."

When one of these infected fish, in which the larva has undergone sufficient development, is eaten by a double-crested cormorant (Pl. VI, No. 3) , several species of heron and certain other fish-eating birds, the worm escapes from the cyst in the stomach

of the bird as a result of its digestive juices and, crawling up the gullet, becomes located in the buccal cavity, where it reaches sexual maturity (Pl. VI, Fig. G) , thus completing the cycle. Apparently most of the eggs reach the water when the infected bird dips its bill into the water, but some are swallowed and passed with the bird's droppings.

An examination of the above life cycle shows that there are eight distinct stages in the development of the worm and that three hosts belonging to as many different animal groups, are required. These distinct stages are : 1) egg, 2) miracidium, 3) sporocyst, 4) mother redia, 5) daughter redia, 6) cercaria, 7) encysted metacercaria, and 8) the sexually mature adult. A portion, or all, of stages two, three, four, five, and six are spent in an appropriate snail ; stage seven uses a fish ; and number eight or the adult occurs in the buccal cavity of a fish-eating bird. Not only is each of these stages in the series structurally distinct, but other important differences among them should be explained in order that the problems and adaptations involved may be better understood. As might be suspected, the hazards encountered by the worms in the perilous journey from one suitable host to another, result in an enormous mortality. They may die as a result of being unsuccessful in making connections with the next appropriate host, or, in the case of the miracidium and the cercaria, before they have entered and after they have left the snail respectively, a considerable number must fall prey to small aquatic animals of various kinds as food. In addition to the large numbers of *eggs* produced to compensate for this great loss of larval forms, multiplication occurs in the sporocyst, mother redia and daughter redia, each resulting in the number of the next successive stage being increased many, many fold. Cort and co-workers (1950: 160), while working on certain phases of the life cycle of this species, reported finding an average of 2,025 rediae in eleven snails examined. In two snails redial counts of 4,002 and 4,072

PLATE **VI.** Life cycle of yellow grub *(Clinostomum marginatum):* A, ciliated larva in water, after hatching from the egg and before entering the digestive gland of snail (number 1) ; B, sporocyst containing rediae within snail; C, redia with daughter rediae; D, cercaria produced by daughter redia within snail. E, same, having escaped from the snail into the water; F, cercaria encysted (metacercaria) in flesh of fish (number 2) ; G, adult worm in pharynx and esophagus of double-crested cormorant (number 3). Numbers 1, 2, and 3 indicate first, second and third or final hosts respectively. Enlarged. (Modified from Hunter and Hunter, 1935; 2, 3, and G original.)
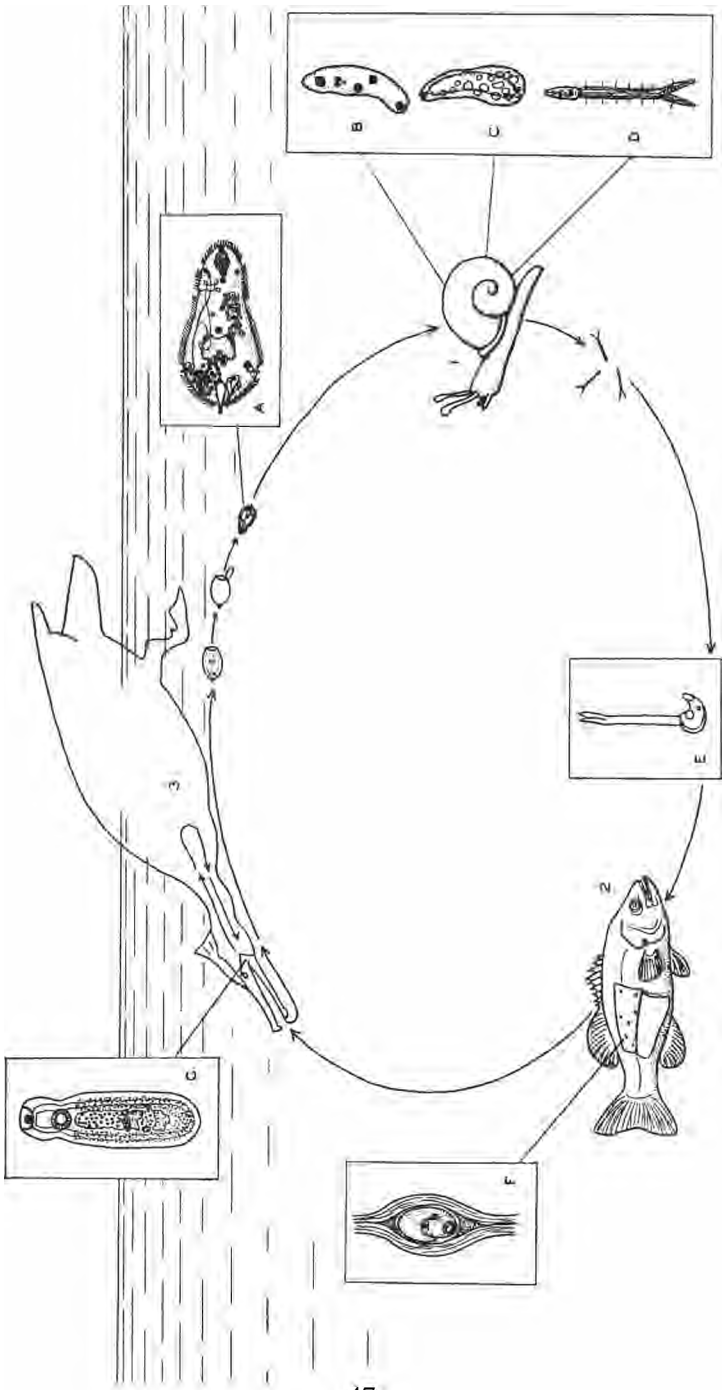
were obtained. It was estimated that a single infected snail might contain as many as half a million cercarial larvae at one time (2,000 rediae each containing 250 cercarial larvae) and during the course of an infection several millions of cercariae would be produced ! During a six-hour period 8,576 cercariae, by actual count, were recently observed emerging from a single snail by Edney (1950: 186) . While it is unknown how long this rate of cercarial production is maintained, the author's evidence suggests production will continue during the life of the snail, which is estimated to be four to five years. As indicated above, only young snails, three months or under, are capable of being infected by the miracidia.

It is only when one encounters "grubby" fish, caused by the metacercariae, that the parasite comes to his attention. It is unknown how long the metacercariae must be on the fish before they are infective to a fish-eating bird, but cysts will remain for more than a year if for some reason the fish is not taken by a bird.

While some anglers are of the opinion that "grubby" fish are taken only during the summer, suggesting they leave the host fish during the winter, Fischthal, working in Wisconsin has shown that this is not actually the case. Of 30 fish infected with a total of 324 metacercaria, it was found that they had lost only 14 or 4.3 per cent in the course of six months over-wintering. If the infected fish is not eaten, as is the case with many a large fish, it is likely that the cysts automatically burst eventually, shedding the immature worms to their destruction. For mature cysts near the surface are so easily ruptured that often worms burst forth upon mere handling of the host.

Another fairly common condition with an entirely different appearance, but caused by worms with similar life cycle, is known as "black spot" (Pl. I, Figs. A, B) . Actually, however, the black spot is a concentration of black pigment caused by the presence of the metacercaria in the skin of the fish. Black spot in different species of fish is caused by different species of digenetic trematodes, and studies have shown that species of at least two groups are involved. Most "black spot" infestations studied have been found to belong to the family Strigeidae, and more than one species of worm is incriminated. The "black spot" of the yellow perch, the creek chub *(Semotilus atromaculatus),*

and probably of the chain pickerel is caused by *Crassiphiala bulboglossa.* This condition in smallmouth bass, the largemouth bass and the pumpkinseed is caused by *Uvulifer ambloplites,* while the "black spot" of the eastern brook trout has been shown to be caused by the larvae of *Apo phallus imperator* of the family Heterophyidae.

Although the "black spot"-causing parasites are not the same for the different species of fish, they do have similar life cycles. The cycle parallels closely that of the "yellow grub" *(Clinostomum marginatum),* although different hosts, both intermediate and final, are usually involved. The adult worm lives in the intestine of a fish-eating bird. There it lays numerous eggs which escape into the water with the host's droppings. These eggs contain miracidia which must be swallowed by or burrow into certain species of snails before they can develop further. Once in the snail, like the previous species, the larvae undergo a complicated development and after a month or two an enormous number of cercariae escape. Those few cercariae that succeed in contacting the right species of fish burrow into the skin or flesh. Each larva then surrounds itself with a thin wall and the fish, in turn, surrounds this with black cells and the black spot results. When the infected fish is eaten by the correct species of bird the wall is digested away, the young parasite escapes into the intestine and continues its development to the adult egg-laying stage. After a few weeks it commences to produce eggs and the cycle is begun anew. Occasionally a fish swims into a swarm of emerging cercariae and the simultaneous penetration of great numbers of the larvae, results in the surface looking as if it has been heavily sprinkled with large grains of pepper.

Each of these parasites, it is to be noted, has three essential hosts through which it must pass : bird to snail to fish and back again to bird. It is unable to short-circuit this cycle and pass, for example, from bird to fish or from fish to fish. Moreover, in order for the cycle to be completed, the correct species of snail, or fish, and of bird is required by the particular larval stage of the parasite. In the cycle of each parasite there are two free-living stages : the miracidium (free in the water or not escaping until after the egg has been eaten by an appropriate snail) and the cercarial stage. The free life is very limited and short and the parasite must pass on to the next host without delay. In view of the enormous mortality encountered by the miracidia and the

cercariae, it is rather remarkable that the species manages to survive. The large numbers of eggs produced by the adult worm and the great increase in the number of individuals within the snail compensate for this tremendous loss. But even with the very prolific birth rate, the parasite would die out if the correct host were not available at the critical moment.

Order MONOGENEA

Suborder MONOPISTHOCOTYLEA

Family GYRODACTYLIDAE

Gyrodactylus medius Kathariner, 1894

HOST.—Eastern brook trout *(Salvelinus fontinalis);* on fins.

Family DACTYLOGYRIDAE

Actinocleidus bursatus (Mueller, 1936)

HOST.—Smallmouth bass *(Micropterus dolomieu);* in the mouth.

Suborder POLYOPISTHOCOTYLEA

Family OCTOCOTYLIDAE

Octomacrum lanceatum Mueller, 1934

HOST.—White sucker *(Catostomus commersoni);* on the gills.

Order DIGENEA

Family GORGODERIDAE

Phyllodistomum staffordi Pearse, 1924

HOST.—Brown bullhead *(Ameiurus nebulosus);* in urinary bladder.

Family PLAGIORCHIIDAE

Macroderoides spiniferus Pearse, 1924

HOST.—Chain pickerel *(Es ox niger);* in intestine.

Macroderoides flavus Van Cleave and Mueller, 1932

HOST.—Chain pickerel *(Esox niger);* in intestine.

Alloglossidium geminus (Mueller, 1930)

HOST.—Brown bullhead *(Ameiurus nebulosus);* in intestine.

Family ALLOCREADIIDAE

Crepidostomum farionis (Muller, 1784)

HOSTS.—Eastern brook trout *(Salvelinus fontinalis),* land-locked salmon *(Salmo salar);* in digestive tract. The life cycle of this species, as determined by Crawford, involves three hosts. The first intermediate host is a fingernail clam *(Pisidium* sp.), larval development taking place in the gills ; the metacercariae encyst in the abdomen of mayfly nymphs *(Ephemera* sp.) . Adults occur in various salmonids.

Crepidostomum cornutum (Osborn, 1903)

HOSTS.—Golden shiner *(Notemigonus crysoleucas),* white perch *(Morone americana);* in digestive tract. **The metacercariae occur in** crayfish (second intermediate host) , first intermediate host fingernail clam *(Sphaerium).*

Crepidostomum cooperi Hopkins, 1931

HOSTS.—Yellowbelly sunfish *(Lepomis auritus);* in digestive tract. Hopkins has shown that the life cycle is similar to that of *Crepidostomum farionis,* **but different** hosts are involved. While he found the first intermediate host to be a fingernail clam, it belonged to a different genus *(Musculium transversum);* and the second intermediate host was a mayfly, but of a different genus *(Hexagenia limbata).* Centrarchids or members of the sunfish family, are the usual final hosts.

Creptotrema funduli Mueller, 1934

HOST.—Banded killifish *(Fundulus diaphanus);* in intestine.

Bunodera luciopercae (Muller, 1776)

HOST.—Largemouth bass *(Micropterus salmoides);* in intestine.

Allocreadium lobatum Wallin, 1909

HOST.—Common shiner *(Notropis cornutus);* in intestine.

Family LISSORCHIIDAE

Triganodistomum attenatum Mueller and Van Cleave, 1932

HOST.—Longnose sucker *(Catostomus catostomus);* in intestine.

Family CLINOSTOMIDAE

Clinostomum marginatum (Rudolph, 1819)

HOSTS (for the metacercariae).—Brown bullhead *(Ameiurus nebulosus),* chain pickerel *(Esox niger),* banded killifish *(Fundulus diaphanus),* yellow perch *(Perca fiavescens),* smallmouth bass *(Micropterus dolomieu).* The yellowish cysts occur most frequently in the region of the gills and operculum, and occasionally under the skin particularly at the base of the dorsal fin. Adults of this species were taken from the pharynx and mouth of double-crested cormorant *(Phalocrocorax auritus).* The complete life cycle is given above.

Family AZYGIIDAE

Azygia longa (Leidy, 1851)

HOSTS.—Landlocked salmon *(Salmo salar),* chain pickerel *(Esox niger),* burbot *(Lota iota);* in esophagus, stomach and intestine. Sillman has shown experimentally when eggs were fed the snail *Amnicola limnosa,* the usual intramolluscan stages were passed and cercariae emerged 42 days after infection. Cercariae fed to grass pickerel *(Esox vermiculatus)* developed directly into egg-bearing adults 20 to 30 days later.

Azygia angusticauda (Stafford, 1904)

HOSTS.—Chain pickerel *(Esox niger),* yellow perch *(Perca fiavescens),* smallmouth bass *(Micropterus dolomieu),* pumpkinseed *(Lepomis gibbosus);* in esophagus, stomach and intestine.

In addition to the above species of digenetic trematodes, numerous unidentified metacercarial cysts were found. These encysted forms were found on the outer surface, resulting in "black spot," and through the viscera. The following species of fish were found infested with "black spot": the eastern brook trout *(Salvelinus fontinalis),* presumably caused by the metacercariae of the heterophyid, *Apophyllus imperator;* the yellow perch *(Perca fiavescens),* the fallfish *(Semotilus corporalis),* and the chain pickerel *(Esox niger),* probably in all these caused by the metacercariae of the strigeid, *Crassiphiala bulboglossa;* and the smallmouth bass *(Micropterus dolomieu),* the largemouth bass *(Micropterus salmoides)* and the pumpkinseed *(Lepomis gibbosus),* presumably in all the result of the metacercariae of another species of Strigeidae, *Uvulifer amblopites.*

The host list for the various encysted trematodes found scattered throughout the body, would include almost every species of fish examined. However, some types of cysts and larval worms were usually found to be localized and limited to certain hosts. These were not studied in detail, either in the living condition or after they were stained and mounted, nor were feeding experiments conducted in an attempt to obtain the adults of the larval forms. The latter procedure is desirable and is essential to an understanding of the life cycle.

6. CESTODA

The tapeworms, or Cestoda, are a group of wholly parasitic animals belonging to the phylum of flatworms. As adults tapeworms are usually long, flat and ribbon-like, occurring in the intestine and caeca of vertebrates. A single, mature specimen has a very small head or scolex at one end, which is buried in the intestinal lining of the host and serves to anchor the worm and prevent it from being swept out by the muscular action of the intestine. To aid in this function, the scolex is provided with suckers and often with small hooks. Attachment is the only function of the scolex ; no food enters through it, and, indeed, there is no mouth or digestive canal in any part of the worm. Food is absorbed through the body surface from the contents of the host's intestine. The rest of the animal, known as the body, consists of a series of similar segments, joined together in a chain, each segment containing a set of male and female reproductive organs. Some tapeworms lack this division into segments, while certain of the most primitive forms have but a single complement of reproductive organs. Consequently the most primitive cestodes resemble the trematodes, from which, however, they are readily distinguishable in that they have no trace of digestive organs.

One of the most remarkable things about tapeworms is their life cycle, which, with very few known exceptions, always involves two and often three hosts. The larval tapeworms of beef and pork, which infect man if consumed with raw or insufficiently cooked meat, are of the two-host type ; a number of the tapeworms of fishes are of the three-host type. One of the latter group, *Proteocephalus ambloplitis,* important to the angler, who knows it as the bass tapeworm, will be taken to illustrate this type of life cycle.

The eggs of this species escape from the egg-filled segments after they have matured, separated from the rest of the tapeworm, and been passed by the fish host. The eggs are relatively short-lived and if not taken by the next host within 36-48 hours, start to break down. Typically the hexacanth (Pl. VII, Fig. B), as the first larval stage is known, is surrounded by an outer clear membrane which gives the egg its typical dumbbell-shape (Pl. VII, Fig. A). This outer membrane is thought to be attractive for the first intermediate host, a crustacean, which has been observed to consume it and discard the inner hexacanth. Infections occur, however, when the hexacanth is accidentally taken with the membrane by suitable species of copepods (Pl. VII and No. 1) and certain amphipods (Pl. V, No. 1).

Once in the intestine of the crustacean the hexacanth, probably through the action of its three pairs of hooks, migrates into the body cavity. Here is develops into the procercoid (Pl. VII, Fig. C) , the next larval stage. A mature procercoid is worm-like in shape, with the region of the scolex formation about twice as thick as the remainder of the larva. The scolex region is invaginated and the small suckers can be seen in the early stage of formation.

When the crustacean containing properly developed procercoids is taken by appropriate species of fish fry (basses, perches and others) the larva escapes from the cyst in the stomach, as a result of the digestive juices, and passes through the gut wall into the body space of the host fish. Here further development, involving chiefly an increase in size and further development of the scolex, continues, resulting in the next larval stage, the plerocercoid (Pl. VII, Figs. D, E) .

This larval stage encysts in the liver, spleen, body lining, and the reproductive organs. It is not unusual to find the organs matted together in an indistinguishable tangle. The reproductive

PLATE VII. Life cycle of bass tapeworm (Proteocephalus *amblo-plitis*); A, dumbbell-shaped egg containing six-hooked (hexacanth) larva, after escaping from adult worm and before being eaten by copepod (number 1) ; B, hexacanth larva, after escaping from the outer hyaline, dumbbell-shaped membrane, within digestive tract of copepod; C, procercoid larva within body cavity of copepod; D, encysted plerocercoid larva within body cavity of fish (number 2) ; E, later stage of same; F, adult worm within intestine of smallmouth bass (number 3). Numbers 1, 2 and 3 indicate first, second and third or final hosts respectively. Enlarged. (Modified from Hunter and Hunter, 1929; 1, D and E original.)
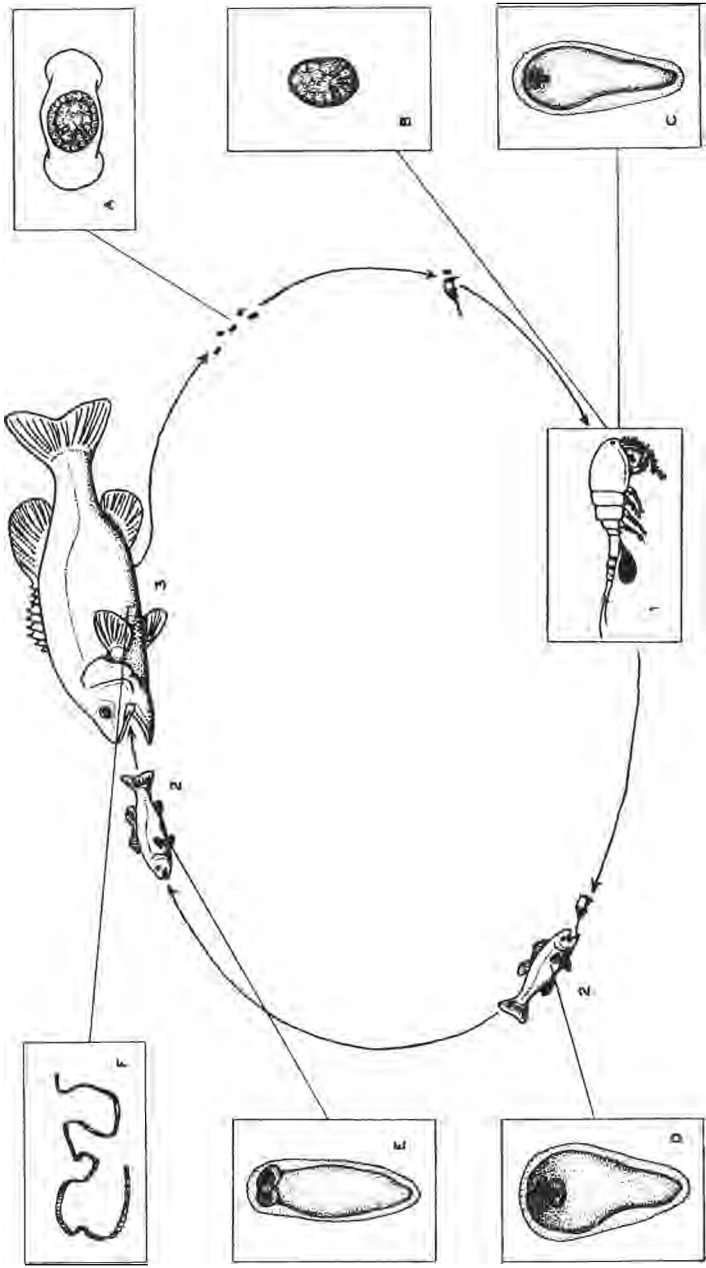
organs may be so heavily infected that spawning is not possible. Unless the host fish, with the plerocercoids in the proper stage of development, is taken as food by an appropriate larger fish, the worm never develops to sexual maturity. But when the infected host is taken by a larger bass, the larva escapes from the cyst in the stomach, as a result of the action of the digestive juices, and develops into a sexually mature adult (Pl. VII, Fig. F) in the intestine of the bass.

It is to be noted that this is an entirely different type of parasitism from that displayed by the forms considered earlier. In the previous forms involving intermediate hosts, these hosts have always belonged to a group entirely different from that serving as the final host. For example in the acanthocephalan, the intermediate host was an amphipod and the fish served only as the final host ; in both of the trematodes considered the successive intermediate hosts were snails and fish while the final hosts were fish-eating birds. Here, however, the same species of fish may serve both as the second intermediate and the final host. Moreover, it is not unusual to find both these respective stages of the worm, that is the larval plerocercoids and adults, in the same individual bass, the former being encysted in the liver, spleen, body lining and the reproductive organs, while the adults are found only in the intestine.

The reader might logically ask, how does it happen that a single species and even the same fish may serve as both the second intermediate and the final host for the one species of worm? An explanation of this not only involves an understanding of the above life cycle of the worm but, in addition, a knowledge of the change in feeding habits of the host fish. As has been indicated above, all fish fry feed largely upon small crustaceans, particularly copepods and water fleas (Cladocera) during their early stages of development. Murphy (1949) , working in California with the largemouth bass, which is similar to the smallmouth in feeding habits, has shown that fingerlings feed largely on planktonic crustaceans until they reach a length of approximately 11/4 inches ; insects predominate in the diet of those between $1\frac{1}{2}$ and about 3 inches ; and fish are almost the exclusive food of bass after that. Smallmouths are believed to prefer crayfish, when available, to fish. It is during this period that the young bass obtain by eating copepods the procercoids, which migrate and develop into plerocercoids in the body cavity. When the small

infected bass, after the worm larvae have undergone sufficient development, are taken as food by older bass, the worm reaches sexual maturity in the second fish. This is the normal life cycle. It serves to explain the presence of the larval plerocercoids in the smaller fish and the adult worms in the larger bass. But a further explanation is necessary to account for the larger bass being infected with the larval worms. This can be accomplished in either of two ways, both of which are considered abnormal. In the one case the young bass with the mature plerocercoids escape being eaten by a larger bass as food, the worms never developing beyond the larval stage in the body cavity. Obviously many of the infected, sexually mature bass, which escaped being eaten when in the proper food-size, later become too large to be taken as food by another fish. On the other hand, a larger, fish-eating bass may take among its food a young bass which only recently has eaten a copepod infected with the mature procercoids. In this case the procercoids develop into plerocercoids in the second fish rather than the first, since they had not yet reached the infective stage in the first fish because insufficient time had been spent in that host. When both larval and adult worms occur in a large bass, it means that the adult worms have undergone the normal cycle, while the larval plerocercoids have arrived at their destination through either of the abnormal routes.

This tapeworm relies for its entry into the intermediate hosts, not upon the activity of the larval phases, as in the case of the trematodes, but upon the fact that these hosts normally eat one another. All the larval phases here, unlike those of the trematodes described, are parasitic.

Order PROTEOCEPHALA

Family PROTEOCEPHALIDAE

Corallobothrium parvum Larsh, 1941

HOST.—Brown bullhead *(Ameiurus nebulosus);* in intestine. The life cycle has been worked out experimentally by Larsh, who found that a copepod *(Cyclops prasinus)* will ingest the eggs of *Corallobothrium parvum,* and that procercoid larvae develop within the copepods' bodies in eight days after the eggs are eaten. His further experiments showed that when infected copepods were eaten by small tropical fish *(Glaridichthys talcatus),* the larvae develop into plerocercoids in the body cavity of the fish in

about three days. In nature, of course, some minnow probably takes the place of the tropical fish used in the experiment. The brown bullhead, then, becomes infected by eating the fish with the plerocercoids. It is not known whether the second intermediate host is a necessary one in the cycle or merely a storage place for the larval form of the worms until they can be taken by the final host.

Essex (1927) has shown that catfishes may become infected with *Corallobothrium* fimbriatum either by feeding on copepods bearing the plerocercoids or by feeding on minnows which have become infected by eating copepods bearing the larvae. Thus in the case of this species the life cycle may involve either a single larval host, a copepod, or two larval hosts, one of which is a fish serving the final host as food. The same condition may obtain for Corallobothrium parvum.

Proteocephalus ambloplitis (Leidy, 1887)

HOST.—Smallmouth bass (Micropterus dolomieu); in intestine. The larval plerocercoids occurred encysted in the mesenteries and viscera of the smallmouth bass, the largemouth bass *(Micropterus* salmoides) and the yellow perch (Perca flavescens). The encysted larvae of this or a closely related species were also found in the white perch (Morone americana) and the pumpkinseed (Lepomis gibbosus). Life cycle given above.

Proteocephalus nematosoma (Leidy, 1890)

HOST.—Chain pickerel (Esox niger); in intestine.

Proteocephalus pusillus Ward, 1910

HOST.—Eastern brook trout (Salvelinus fontinalis); alimentary tract. The type material serving as a basis for the description was taken by Ward (1910) from the intestine and the esophagus of Salmo salar (= Salmo sebago) at Sebago Lake, while engaged in an investigation of the lake for the U. S. Bureau of Fisheries, during the summer of 1907. Later LaRue (1914) took it in lake trout (Cristivomer namaycush), Lake Temagami, Ontario.

Proteocephalus pinguis LaRue, 1911

HOST.—Chain pickerel (Esox niger); alimentary tract. The material serving for the description of this species, like the preceding, was taken by Ward (1910) during the investigation referred to above.

Proteocephalus pearsei LaRue, 1919

HOST.—Smallmouth bass *(Micropterus dolomieu);* in intestine. The intermediate host of this species, as demonstrated by Bangham (1925), involves either of two species of copepods *(Epischura lacustris* or *Cyclops* sp.). Unlike the cycle of *Proteocephalus ambloplitis,* which requires two intermediate hosts, only the crustacean host is necessary in this species.

Proteocephalus wickliffi Hunter and Bangham, 1933

HOST.—Lake whitefish *(Coregonus clupeaformis);* in intestine.

Proteocephalus parallacticus MacLulich, 1943

HOST.—Lake trout *(Cristivomer namaycush) ;* pyloric caeca and intestine. Life cycle unknown. However, once worked out, it will probably be found to parallel that of other proteocephalids : involving a copepod, with or without a smaller fish as a second intermediate host before being taken by the final host.

Proteocephalus sp.

HOST.—American smelt *(Osmerus mordax);* in intestine.

Order CARYOPHYLLIDEA

Family CARYOPHYLLAEIDAE

Glaridacris catostomi Cooper, 1920

HOST.—White sucker *(Catostomus commersoni);* in intestine. According to Van Cleave and Mueller (1934) , suckers become infected through eating aquatic worms (Tubificidae) carrying the larval form of the worm.

Order PSEUDOPHYLLIDEA

Family DIBOTHRIOCEPHALIDAE

Ligula intestinalis (Linnaeus, 1758)

HOSTS for the post-plerocercoid larvae.—Longnose sucker *(Catostomus catostomus),* American smelt *(Osmerus mordax),* common shiner *(Notropis cornutus),* lake chub *(Couesius plumbeus);* free in the body cavity. Infected fish are often distinguishable because cf their greatly distended bellies, which, in some cases, are so crowded with worms that the body wall bursts with handling. Plehn reported that the weight of the plerocer-

FIG. 2. Opened body cavity of longnose sucker infected with the post-plerocercoid larvae of the tapeworm *Ligula intestinalis.* (Photograph by Charles T. Snell.)

coids may equal that of the host fish. Generally speaking, the size attained by the worms in the fish is directly correlated with the size of the host and the number of worms present. Five was the greatest number taken from a fish in this survey, but as many as 15 worms have been reported in the literature. Adult worms were taken from the intestine of American mergansers *(Mergus merganser americanus).*

Schistocephalus solidus (Muller, 1776)

HOST for the plero3ercoid larvae.—Eastern brook trout *(Salvelinus fontinalis);* in the stomach. While the normal location for the plerocercoids is in the body cavity of the fish host, their presence in the stomach is not especially surprising. The hosts in which the worms occurred in the stomach, being piscivorous, only shortly prior to examination had eaten an infected fish in which the larval worms were in the normal location. Adults were taken from the intestine of American mergansers *(Mergus merganser americanus).* The procercoids of this species, like those of the closely allied *Ligula intestinalis,* are found in certain species of copepods. In this country Thomas (1947) has shown experimentally that the copepod, *Cyclops leucharti* may serve as the first intermediate host.

60

Family BOTHRIOCEPHALIDAE

Bothriocephalus rarus Thomas, 1937

HOST.—Banded killifish *(Fundulus diaphanus);* in intestine. Of the two killifish examined, one contained four worms, which with some hesitation are assigned to this species. Since *Bothriocephalus rarus* has, so far as I am aware, never been reported from fish, its presence seems worthy of comment. Thomas, in his report on the life cycle of this species, gave the newt *(Triturus viridescens)* as the final host. And he called attention to the fact that the tapeworm was unusual in being the second adult pseudophyllidean known from Amphibia and the only one thus far described for the genus *Bothriocephalus* that does not necessarily have a second intermediate host.

Thomas (1937) has shown that the final host becomes infected either by feeding on copepods *(Cyclops* spp.) bearing the plerocercoids or by feeding on larval newts which have become infected by eating the copepods bearing the larval worms.

Bothriocephalus cuspidatus Cooper, 1917

HOST.—Burbot *(Lota lota);* in intestine. According to the observations of Essex (1928) , the larvae of *Bothriocephalus cuspidatus* develop in the bodies of several species of copepods belonging to the genus *Cyclops.* After about ten days in the body of the copepod host, the larvae are fully developed and are recognizable as the procercoid stage, which in this case are capable of becoming established in the digestive tract of a suitable host. While it is possible that the final host may acquire the infection through eating a smaller fish, which earlier had ingested a *Cyclops* sp. with the procercoid larva, the second intermediate host is thought unnecessary.

Family AMPHICOTYLIDAE

Eubothrium salvelini (Schrank, 1790)

HOSTS.—Landlocked salmon *(Salmo salar)* and eastern brook trout *(Salvelinus fontinalis);* pyloric caeca and intestine. This species, which is comparatively common in both the salmon and the brook trout, apparently, is herein reported for the first time from the landlocked form of *Salmo salar.* In view of the abundance of available material, some of which came from the same locality, it appears that Ward's (1910: 1184 & 1185) record
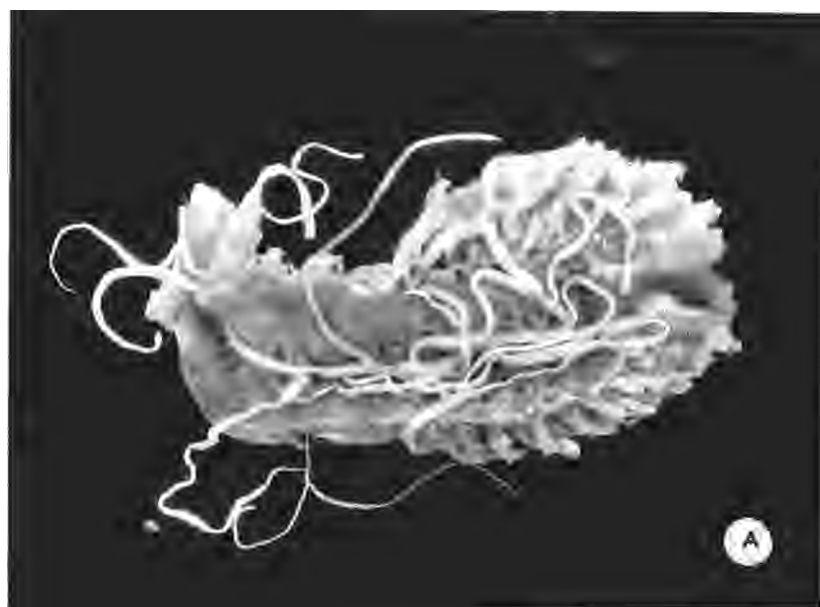
of the presence of *Eubothrium* *crassum (* = *Abothrium crassum)*
in landlocked *Salmo* *salar (* = landlocked *Salmo sebago),* from
Sebago lake is in error. But *Eubothrium* *crassum* has been re-
ported by Ekbaum from the anadromous form of *Salmo salar* in
the Miramichi River of nearby New Brunswick, and it is entirely
possible that this species is present locally in the same form of
the salmon. It may be that such proof is lacking only because the
anadromous form of the host has not been examined from Maine
waters.

Despite its abundance in salmonids in this country and in
Canada, nothing is known of the developmental stages of *Euboth-*
rium *salvelini* in either habitat. Ward examined "Sebago smelt"
(presumably *Osmerus* *mordax*), as a possible host for the plero-
cercoid larvae, with negative results.

Plerocercoids of **Dibothriocephalus** sp.

In two species of salmonids taken from certain waters, the
landlocked salmon *(Salmo salar)* and the eastern brook trout
(Salvelinus fontinalis), pseudophyllidean dibothriocephalid lar-
vae (plerocercoids) were found to be fairly common. There is,
however, nothing peculiar in their presence in Maine ; they are
also recorded in most comparable studies in North America in-
volving various species of Salmonidae fishes (Ward [1910] in
Maine ; Bangham [1951], Leidy, Linton [1891], and Woodbury in
Wyoming ; Haderlie, and Hobmaier in California ; Shaw in Ore-
gon; Fasten in Washington ; Wardle [1932, 1932a] in British
Columbia and the Hudson Bay region ; Choquette, and Richard-
son in Quebec ; MacLulich in Ontario ; Babero in Alaska ; and by
others) .

The larvae are contained in raised, yellow-colored cysts, at-
tached to the lining of the body wall or the outer surface of the
viscera, particularly the stomach. In shape the cysts vary from
ovoid to long, thin and spindle-shaped. They vary in size ; the
ovoids in millimeters from approximately 2 0 to 10.0 in diameter,
while the elongated forms ranged in length from 5.0 to 15.0 by 0.6
to 1.0 wide. The larvae varied correspondingly in size, depend-

PLATE VIII. Two typical cases of tapeworm infections: A, opened
stomach of lake trout infected with *Proteocephalus* *parallacticus;* B, opened
stomach (including a portion of the esophagus) of landlocked salmon in-
fected with *Eubothrium salvelini.* The anterior portion of the worm is
usually deep in the caecum, the body protruding in loops hanging from the
caeca into the cavity or crossing over into other caeca in a tangled mass.
(Photographs by J. Franklin Witter.)

ing upon the shape and the size of the cyst from which they came. The body is flattened in the plane of the bothria or so-called sucking grooves, the posterior end rounded or possessing a short spherical appendage, the cercomer. Anteriorly the larva is sub-triangular, occasionally elongated, or it may be invaginated ; depending upon different degrees of development. No internal organization is apparent.

There remains much uncertainty as to the specific identity of these plerocercoid larvae as well as that of the worms in the adult stage. Leidy, who first observed immature forms from *Salvelinus fontinalis* taken in Wyoming, described them under the name *Dibothriocephalus* cordiceps (*Dibothrium* cordiceps) and subsequent earlier workers referred to them under that name. But more recent workers have become more cautious in their determination, merely referring to them as larvae of the dibothriocephalid type. Upon two points, however, there is general agreement : 1) in the absence of the adults obtained from rearing tests, specific identification of the larvae is not possible, and 2) they are not the plerocercoids of *Dibothriocephalus* latus. But the identification, based upon anatomical characters, of adults including those resulting from rearing tests, is difficult if not impossible. Qualified investigators working at the Arctic Health Research Center, Anchorage, Alaska, after recovering the adult worms from several experimentally infected mammals and gulls *(Larus glaucescens)* which were fed the plerocercoids obtained from rainbow trout *(Salmo gairdneri),* made no commitment as to the species of *Diphyllobothrium* involved in their reports. Rausch (1951: 932) stated, "Speciation on the basis of morphological characters of tapeworms of the genus *Diphyllobothrium* is impossible for the Alaskan forms." Earlier Stunkard (1949: 623) commented :

Species now included in the genus *[Diphyllobothrium]* constitute a heterogeneous collection, from a variety of hosts and bionomic areas, but the morphological diversity is so distributed among the species and so many different combinations of characters exist that arrangement of the species into related groups must await further information.

7. NEMATODA

The Nematoda are commonly known as round worms. The members of this class have an elongate, cylindrical or spindle

shape, and lack segmentation. An elastic, hyaline covering clothes the external surface and this may be entirely smooth, marked with very fine transverse annulations, or set with knobs, spines or ornaments of various sizes and forms. As in the Acanthocephala the sexes are separate, and the female is usually somewhat larger than the male. The male usually possesses a spirally coiled tail adapted to encircling the body of the female during copulation, while the female usually possesses a straight, tapered tail. In each sex there is a complete alimentary tract, marked anteriorly by the mouth and at the other end by the anus.

Nematodes may be either oviparous or viviparous. Egglaying is more common, but the live-bearing habit is highly developed among some of the tissue-parasites of some groups. hi the latter worms the uterus becomes greatly inflated and fills the whole body of the female worm. Within swarm myriads of minute, wriggling larvae. Frequently in these worms the entire alimentary canal, and even the uterus, disappears in the adult stage so that the worm is merely a sac of living larvae.

The class Nematoda is very large and comprises both parasitic and non-parasitic forms. Parasitic nematodes, which occur widely throughout all groups of animals, show a great variety in their life cycles. The pattern varies from the simple type with direct transmission to that in which intermediate hosts are employed. The diversity in life cycles indicates that the parasitic nematodes are not such a closely unified group as either the trematodes or the cestodes. Structural considerations bear this out, as does the fact that the nematodes have not as yet become so thoroughly adapted to the parasitic habit as have the flatworms. The flatworms show marked specializations as a result of the parasitic habit, for instance, the lack of all trace of the alimentary canal in cestodes, and the interpolation of multiple reproductive stages into the life cycle of trematodes to compensate for the hazards of the parasitic mode of life.

The nematodes, with the possible exception of one group, show no such wide departure from the structural plan of their non-parasitic relatives and do not have larval reproductive life cycles. Thus, from a single nematode egg a single adult develops, as in the case of the Acanthocephala ; whereas from a single trematode egg, and from the egg of some cestodes, the number of possible adults is increased by the thousands. The development of nematodes in its simplest form is direct, not marked by the

variety of larval forms as occurs in trematodes and tapeworms. In general the newly hatched nematode resembles the adult in form with the exception of the reproductive system and secondary sexual characters.

Order TRICHUROIDEA*

Family **TRICHURIDAE**

?Hepaticola bakeri Mueller and Van Cleave, 1932

HOST.—Eastern brook trout *(Salvelinus .fontinalis);* in intestine.

Order DIOCTOPHYMOIDEA

Family DIOCTOPHYMATIDAE

Eustrongylides sp., immature

HOST.—White sucker *(Catostomus commersoni);* encysted on body wall and viscera.

Order ASCARIDOIDEA

Family ASCARIDIDAE

Porrocaecum ?decipiens (Krabbe, 1878)

HOST.—American smelt *(Osmerus mordax);* in the flesh. This worm is common in the anidromous form. In 1947 larvae of this form sent Dr. G. Dikma. ι, Bureau of Animal Industry, USDA, were identified by J. T. Li eker of that laboratory as *Porrocaecum* sp. The next spring additional worms were sent Prof. D. M. Scott, who at that time was attempting to determine its life cycle while at the nearby Atlantic Biological Station, St. Andrews, N. B. In reply to my recent letter of inquiry as to the trivial identity of the nematode material sent him, he wrote (26 October 1953), "The worms you sent me were similar in all respects to other larval *Porrocaecum* that I have seen from fishes and there is little doubt that all these larvae are cospecific. . . . I was successful in infecting seals with larval worms from smelt and the adult worms were clearly *Porrocaecum decipiens.* I have not found any other species of *Porrocaecum* either in the flesh of fishes or in cormorants, seals, or porpoises that I have examined."

What are here called orders are sometimes regarded as superfamilies; and when they are raised to ordinal rank, the ending *oidea* is often altered to *ida* or *ata.*

Scott found experimentally the life cycle to be the following: adult worms present in the stomach of a seal, the harbor seal *(Phoca vitulina)* and the grey seal *(Halichoerus grypus)* being involved as final hosts, lay eggs which are passed by the seal and hatch in the sea; the young larvae are probably eaten by an invertebrate animal, such as a shrimp, which is eaten by a fish. The worms in the fish, the second intermediate host, are incapable of reproduction but when the infected fish is eaten by a seal, the worms mature and complete the cycle.

Raphidascaris sp.

HOSTS.—Chain pickerel *(Esox niger)* and eastern brook trout *(Salvelinus fontinalis);* in intestine.

Contracaecum sp., immature

HOST.—Alewife *(Pomolobus pseudoharengus);* in intestine.

Order SPIRUROIDEA

Family SPIRURIDAE

Spinitectus gracilis Ward and Magath, 1916

HOST.—White perch *(Morone americana);* in intestine. Mayfly nymphs of the genera *Hexagenia, Heptagenia* and *Streptonoura* were observed by Gustafson (1939) to ingest the eggs. Adult worms were recovered from green sunfish three days after being experimentally infected with eleven-day old larvae.

Spinitectus carolini Holl, 1928

HOSTS.—Pumpkinseed *(Lepomis gibbosus)* and yellowbelly sunfish *(Lepomis auritus);* in intestine.

Spinitectus sp.

HOST.—White perch *(Morone americana);* in intestine.

Metabronema sp., immature

HOST.—White perch *(Morone americana);* in intestine.

Family THELAZIIDAE

Rhabdochona ?cascadilla Wigdor, 1918

HOST.—Common shiner *(Notropis cornutus);* in intestine. Gustafson (1942) reported immature stages in nature in mayfly nymphs *(Hexagenia).*

Order DRACUNCULOIDEA
Family ?PHILOMETRIDAE

Philonema agubernaculum Simon and Simon, 1936

HOSTS.—Landlocked salmon *(Salmo salar)* and eastern brook trout *(Salvelinus fontinalis);* free in body cavity or encysted between the mesenteries or beneath the peritoneal lining of the cavity. Life cycle unknown. While these worms were encountered during the course of the summer investigation, special attention was given them during the fall. At the Oquossoc and at the Raymond hatchery stations during the 1952 stripping season a total of 18 fish, 12 salmon and six brook trout, were examined. This worm, which was present in all the fish examined at this time, occurs in the body cavity of the host, both as immature and adult individuals, and in the latter stage it may be either living or dead. As pointed out earlier under the discussion of the *Effect of Parasites upon their Host,* its presence results in the formation of multiple mesenteric and peritoneal adhesions, which bind the visceral organs into a compact mass. This may be so severe, especially in large females, that sterility results. The cysts, which are imbedded amongst the adhesions and beneath the mesenteric lining, are easily recognizable from those of other species of worms. They are whitish in color, flat and thin, and the worm is visible through it. When worms are removed to physiological solution or water, they move slowly and soon burst. They are so delicate that difficulty is experienced in preserving specimens entire and perfect. If gravid females are included, a coil of the uterus commonly protrudes through the body wall and almost immediately the liquid is teeming with thousands of eggs and/or larvae, the uterus having burst. It is possible that it is the same species of Nematoda Ward found in the body cavity of landlocked salmon examined from Sebago Lake, and listed simply as "Nematode B".

Order CAMALLANOIDEA
Family CAMALLANIDAE

Camallanus truncatus (Rudolphi, 1914)

HOSTS.—Smallmouth bass *(Micropterus dolomieu)* and white perch *(Morone americana);* in intestine.

Camallanus ?locustris Zoega, 1776

HOST.—Landlocked salmon *(Salmo salar);* in intestine.

Family CUCULLANIDAE

Dichelyne cotylophora (Ward and Magath, 1916)
HOST.—Yellow perch *(Perca fiavescens);* in intestine.

Cucullanus sp.

HOST.—White perch *(Morone americana);* in intestine.

8.   KEY, BASED UPON EXTERNAL CHARACTERS, TO THE ADULTS OF THE DIFFERENT GROUPS FOUND PARASITIZING FRESH-WATER FISHES IN MAINE

1.   Animal covered with hard shell, body shape not change-able ; found externally on gills, fins or elsewhere ...   2

Animal not enclosed within hard shell, contractile, worm-like ; found externally or internally   3

2.   Animal with appendages (Pl. IV, Figs. A, B, C)   .
Copepods (P. 33)

Animal without appendages ; hinged shells, clam-like (Pl. IV, Fig. D) .... Glochidia* (P. 36)

3.   Animal segmented ; found externally or internally .. .   4

Animal unsegmented ; adults usually found in intestine   5

4.   Animal usually rounded ; strong suckers at both ends of body ; highly contractile ; found externally ....
Leeches (P. 36)

Adult animal long, flat, ribbon-like ; sluggish ; found only in intestine (Pls. VII, Fig. F; Fig. 2; VIII, Figs. A, B) .... Tapeworms (P. 53)

5.   Animal flattened, adult usually found in intestine (Pl. VI, Fig. G) .... Flukes (P. 42)

Animal not flattened, rounded in cross-section   6

6.   Animal with hook-covered, eversible and retractile pro-boscis; adult in intestine (Pl. V, Fig. E) ....
Thorny-headed worms (P. 37)

Animal without proboscis ; adult in intestine, larva also here, in body cavity, or elsewhere (Pl. III, Fig. C)
Round worms (P. 64)

_____

* This is the larval form of fresh-water clams.

VII. LITERATURE ON FISH PARASITES

The parasites of the fresh-water fishes of Maine are very imperfectly known. Apparently the first record from the State was by Smith (1874) , who reported a copepod, *Lernaeopoda fontinalis,* parasitic on brook trout taken at Norway. Wilson (1915; 1916), after re-examining the specimens studied by Smith, identified them as *Salmincola edwardsi,* the same scientific name by which this common eastern brook trout parasite is presently known. Another lot of copepods, taken from a blueback trout at Rangeley Lakes by Prof. L. A. Lee of Bowdoin College, Wilson described as *Salmincola oquossa.* Linton (1901; 1940) reported three forms, based upon worms sent him from a salmon taken at Bucksport, from pickerel at Orono ; and a smallmouth bass from a pond near Portland. In 1901, Atkins, in a paper entitled, "The Study of Fish Diseases," based upon his observations at the Craig Brook hatchery and presented at the thirtieth annual meeting of the American Fisheries Society, reported the fluke *Gyrodactylus elegans* from young lake trout. Except for their historical interest, these reports are otherwise of little importance.

Ward (1910) , who made a personal examination of seven landlocked salmon and numerous other fish (including American smelt, American eel, yellow perch, and chain pickerel) from Sebago Lake, was the first to give any serious, first-hand attention to the subject of fish parasites within the state. In 1926, Manter, while studying the parasites of marine fishes at Mount Desert Island Biological Laboratory, included a list of the parasites taken from American eel, banded killifish, and American smelt, all of which host species are included in the present report. Cooper (1941: 121) reported, the smallmouth bass in certain lakes of the Androscoggin River drainage were heavily infected with the bass tapeworm [presumably *Proteocephalus ambloplitis] ;* and (1942: 93) , yellow perch were commonly infected with "grubs" [presumably the metacercariae of *Clinostomum marginatum].* No further data are available in the literature except for the short note by de Roth (1953) . This last report is based upon an examination of 175 fish, belonging to nine species, from Pushaw Pond, near Orono, and was done during the summer of 1947 while he was a graduate student of the Department of Zoology, University of Maine. These last three reports, it is to be noted, were based upon personal examinations, rather than

specimens taken incidentally and contributed by others, as in the case of those of Smith, Wilson, and Linton. Hunter (1942), working in Connecticut, has published the only other such report from New England.* Therefore the value of more information in this field is self-evident, especially in New England, and particularly in Maine.

Elsewhere in this country, particularly within the last 50 years, numerous studies dealing with the parasites of fresh-water fishes have been made. But the first of these were limited almost entirely to the description of new forms and for the most part were devoted to restricted groups, such as a family, an order or, in a few cases, a class. These intensive studies have been undertaken principally by Ward, his students and grand-students. Ward (1912) inaugurated a new era for the general student of parasitology in that a critical analysis of the literature and a comprehensive survey of all the parasites known to infect fresh-water fish of this country were presented for the first time. Among his students who have made noteworthy contributions toward a better understanding of this subject are Beaver, A. R. Cooper, Cort, Essex, Faust, Guberlet, Hopkins, George Hunter, LaRue, Manter, Mueller, Thomas, and Van Cleave.

Others, several of whom are Ward's second generation students, who have been actively engaged in the study of the parasites of the fresh-water fishes of this country are Allison, Bangham, Davis, Fischthal, Haderlie, Wanda Hunter, Meyer, Mizelle, Pearse, Snieszko, Venard and Woodhead. Most of these studies, however, like those of the previous workers, have been limited to life cycle studies or to particular groups of parasites rather than approaching the problem in its larger, more involved aspects. The foregoing list is admittedly incomplete. There are others who have made substantial contributions to the field of parasitism among fresh-water fish. But the list is encouraging, since a critical examination of it indicates that during recent years several capable young workers have been attracted to cope with one or more of the many problems involved. The most comprehensive treatise dealing with this subject, treating the ecological aspects of fish parasites and their relations to the host, is that of Mueller (1932) , Mueller and Van Cleave (1932) , and Van Cleave

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* On the eve of publication Sinderman's (1953) report entitled, "Parasites of fishes of north central Massachusetts," came to my attention.

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and Mueller (1932, 1934) , entitled "The Parasites of Oneida Lake Fishes."

In this connection it might be pointed out that the most work has been done in those states which for years have been among the most active in the various phases of fishery and wild-life research. California, Illinois, Michigan, New York, Ohio and Wisconsin are notable examples.

VIII. METHODS EMPLOYED

1. Examination of Hosts.—The search for parasites is not an easy one. Many fish parasites are small and easily escape notice. A complete examination is not accomplished within a few minutes, but may take hours when a heavy infection is encountered. A binocular dissecting microscope, magnifying approximately ten times, is essential if anything other than macroscopic specimens are to be recovered.

The external examination, covering the head, eyes, fins and outer surface, was preferably made under water in an appropriately sized container. Next the gill opercula were cut away and the gill arches cut at each end so they could be removed individually. In this way copepods and the larger monogenetic trematodes were recovered. The gills of 11 togue were frozen according to Mizelle's (1938) method, but no worms were recovered upon thawing and examination. In the absence of refrigeration, when working away from the laboratory, additional gills were not frozen.

The intestine and other viscera were examined next. The abdominal cavity was opened by a small incision in the mid-ventral line. Blunt-ended scissors were inserted and the incision extended anteriorly and posteriorly, passing lateral to the anus. In making the cut care was taken to have the blunt end of the scissors slide along the inner ventral abdominal wall, so as not to injure the viscera. The abdominal cavity and mesenteries were inspected for cysts and free parasites. The viscera were removed and each organ—esophagus, stomach and pyloric caeca, intestine, liver, heart, swim bladder, kidneys, urinary bladder, gonads and gonoducts—severed and placed. in a separate dish of physiological saline or water. The physiological solution, although highly desirable, was not always available when working in the field. The different regions of the alimentary canal, including the caeca, were opened with the blunt-ended scissors, as were some of the other organs, or tissues of the latter were teased apart with dissecting needles. The parasites, which usually freed themselves from the mucus by their own active movements, were transferred by spatula or pipette (in the case of the smaller forms) to separate dishes containing physiological solution.

When the author was pressed for time or dealing with a large number of fish, the intestine, having first been opened as described above, was placed together with its contents in physiological solution or water and shaken for a minute or so in an appropriately sized bottle. The contents were then allowed to settle for approximately one-half minute, after which the upper, clearer portion of the liquid was poured off. This process was repeated once or twice, with the decanted liquid being replaced each time by fresh solution. The parasites, which were heavier than the organic debris, settled to the bottom and were concentrated in the remaining liquid. They were removed individually from the solution, only a small portion of which was examined at a time in a Syracuse- or petri dish. With the exception of 29 specimens, all fish were examined within a few hours after being taken. In this way, which is really the only satisfactory method, the parasitic worms were found alive when removed from the body of the host. As a result, the activity of the worms, aided by the sharp color contrast of them against the host tissue, decreased the likelihood of their escaping notice.

The search for larval trematodes and cestodes, after both the external and the internal examinations were completed, was done in the following manner. The fish was held in one hand with the forefinger and thumb placed inside the opercular flap so that the host would not slip ; a thin horizontal slice was then removed from the base of the skull to the tail fin and vertical incisions were made on either side to divide the musculature into slices less than one-half inch thick, which were then carefully inspected.

2. *Killing and Preserving.*—Worms were thoroughly washed and freed of mucus prior to killing and preserving. Trematodes and cestodes were transferred to Bouin's (Picro-formol-acetic) fluid or A-F-A (Alcohol-formol-acetic) fluid, heated until bubbles appear (but not boiling) for killing and fixation. The worms expand and die instantly upon contacting the hot fluid. This method not only results in a considerable time saving but is an improvement over pressure flattening methods in that all specimens become uniformly expanded, and hence are properly comparable. Any further flattening and straightening that may be needed is done later during the mounting process. Specimens were left in Bouin's or A-F-A for some 24 hours, after

which they were washed in several changes of 70 per cent alcohol until most of the yellow color, in the case of the former solution, was removed. This entire process could usually be done in the preserving vial, and the liquids decanted or drawn off with a pipette.

Acanthocephala were left in tap water until the proboscis was extruded, after which they were placed in A-F-A solution. Nematodes were dropped into hot 70 per cent alcohol to which a few drops of glacial acetic acid had been added. This causes them to straighten out instantly and die in an extended position, thus avoiding the curled and distorted specimens obtained when using ordinary methods. Since heat causes some of the smaller, more delicate species to shrivel, they were fixed in cold A-F-A fluid.

Parasitic leeches, which are even more difficult to kill in an extended and straightened condition, were handled in the following, somewhat time-consuming, manner. Specimens were placed in a water-filled petri dish to which a small pinch (some half-dozen flakes) of tobacco was added. Usually the tobacco was added only once and they were left overnight before being killed the next morning. Carbonated water or water that has been boiled previously so as to be oxygen-free serves to expedite the process. In either case, however, specimens should remain in the nicotine solution until they cease responding to stimuli. The worms are then straightened on a slide wrapped with toilet paper, in a petri dish with just enough water to moisten the paper so it does not adhere to the specimen and at the same time not so much water as to float the animal. Hot 70 per cent alcohol is then added slowly until specimens are covered.

Copepods, after being freed of mucus, were killed in cold 70 per cent alcohol.

3. *Staining and Mounting.—Some* of the trematodes and cestodes were stained in Delafield's hematoxylin, but Mayer's HC1 carmine (modified) was used for most of them. Not only is this more rapid in its action, but the results obtained are as satisfactory as when the more generally used Delafield's is employed. Acanthocephala were stained with Mayer's HC1 carmine and counterstained with fast green. The fast green is especially recommended to bring out the proboscis hooks. Prior to the initial staining acanthocephalans were placed in a 0.5 per cent

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solution of trisodium phosphate. This serves to soften the specimens, thus resulting in a more uniform staining than when the usual puncturing methods are employed. Likewise, as does puncturing of the body wall, it generally prevents the all too common difficulty of "vacuum opacity." Copepods and glochidia were mounted unstained and leeches and nematodes were neither stained nor mounted.

For permanent mounts, clarite, piccolyte, balsam or any of the usual media soluble in benzene, xylene or toluene are satisfactory. But in the transfer from the preparation dish to the slide direct exposure of the surfaces of the specimen to the air must be avoided or the mounts will turn opaque. Thin slivers of glass slide or cover glass, suited to the thickness of the specimen, should be used to support the cover glass, keeping it from tilting to one side. As the mounting medium retracts from the edges of the cover glass while in the drying oven, it should be replaced with new mounting medium so that the entire area between the slide and the cover glass is filled. Excess medium may be removed from the surface of the slide and cover glass by scraping with a safety razor blade. After the slide and cover glass have been wiped with a clean cloth moistened with xylene to remove the powdered mounting medium, the mount is ready for study.

It is clear from the foregoing that the problem is not solvable as a simple field project. In a survey of this sort, the field study and collecting mark but the beginning, for prolonged and exacting procedures of technical preparations are required before the specimens are ready for microscopical study. Even then, final identification and recognition of the species rest upon close microscopical observation and minute comparison. Both phases are time-consuming and can be extremely tedious. Until a given habitat has been thoroughly surveyed and exact specific identifications of the parasites have been made, there are relatively few species of parasites which may be recognized with certainty in the field. Unexpected and wholly unknown species are so often encountered that field identifications closer than to genus are rarely reliable and militate against the recognition and differentiation of unknown forms.

IX. REFERENCES

Allison, L. N.   1950.   Common diseases of fish in Michigan. Michigan Dept. Conserv., Misc. Publ. No. 5, 27 pp.

Atkins, C. G.   1901.   The study of fish diseases. Trans. Amer. Fish. Soc., 1901, pp. 82-89.

Babero, B. B.   1953.   Studies on the helminth fauna of Alaska: XII, The experimental infection of Alaskan gulls *(Larus glaucescens* Naumann) with *Diphyllobothrium* sp. Jour. Washington Acad. Sci. 43: 166-168.

Bangham, R. V.   1925.   A study of the cestode parasites of the black bass in Ohio, with special reference to their life history and distribution. Ohio Jour. Sci. 25: 255-270.

Bangham, R. V.   1951.   Parasites of fish in the upper Snake River drainage and in Yellowstone Lake, Wyoming. Zoologica. 36: 213-217.

Choquette, L. P. E.   1948.   Parasites of freshwater fish IV. Internal helminths parasitic in speckled trout *(Salvelinus fontinalis* (Mitchill)) in rivers and lakes of the Laurentide Park, Quebec, Canada.   Canad. Jour. Res. 26: 204-211.

Cooper, G. P.   1939.   A biological survey of thirty-one lakes and ponds of the upper Saco River and Sebago Lake drainage systems in Maine. Maine Dept. Inland Fish. Game, Augusta, Fish Survey Rept., No. 2, 147 pp.

Cooper, G. P.   1941.   A biological survey of lakes and ponds of the Androscoggin and Kennebec River drainage systems in Maine. Maine Dept. Inland Fish. Game, Augusta, Fish Survey Rept., No. 4, 238 pp.

Cooper, G. P.   1942.   A biological survey of lakes and ponds of the central coastal area of Maine. Maine Dept. Inland Fish. Game, Augusta, Fish Survey Rept., No. 5, 184 pp.

Cort, W. W., D. J. Ameel and Anne Van der Woude. 1950. Germinal material in the rediae of *Clinostomum marginatum* (Rudolphi). Jour. Parasitol. 36: 157-163.

Crawford, W. W.   1943.   Colorado trematode studies. I. A further contribution to the life history of *Crepidostomum farionis* (Muller). Jour. Parasitol. 29: 379-384.

Davis, H. S.   1946.   Care and diseases of trout. U. S. Dept. Interior, Fish and Wildlife Serv., Research Rept. No. 12, 98 pp.

Davis, H. S.   1953.   Culture and diseases of game fishes. x + 332 pp. Univ. California Press, Berkeley.

DeGiusti, D. L.   1949.   The life cycle of *Leptorhynchoides thecatus* (Linton), an acanthocephalan of fish. Jour. Parasitol. 35: 437-460.

Edney, J. M.   1950.   Productivity in *Clinostomum marginatum* (Trematoda : Clinostomatidae).   Trans. Amer. Micr. Soc. 69: 186-188.

Ekbaum, E. K.   1933.   A study of the cestode genus *Eubothrium* of Nybelin in Canadian fishes. Contrib. Canad. Biol. Fish. 8 (33) : 89-98.

Essex, H. E.   1927.   The structure and development of *Corallobothrium.* Illinois Biol. Monog. 11 (3) : 1-74.

Essex, H. E.   1928.   On the life-history of *Bothriocephalus cuspidatus* Cooper, 1917.   Trans. Amer. Micr. Soc. 47: 348-355.

Fasten, Nathan.   1922.   The tapeworm infection in Washington trout and its related biological problems. Amer. Natur. 56: 439-447.

Fischthal, J. H.   1949.   The over-wintering of black grubs and yellow grubs in fish. Jour. Parasitol. 35: 191-192.

Gustafson, P. V.   1939.   Life cycle studies on *Spinitectus gracilis* and *Rhabdochona* sp. (Nematoda : Thelaziidae). Jour. Parasitol. 25 (Suppl.) : 12-13.

Gustafson, P. V.   1942.   A peculiar larval development of *Rhabdochona* spp. (Nematoda : Spiruroidea).   Jour. Parasitol. 28 (Suppl.) : 30.

Haderlie, E. C.   1953.   Parasites of the fresh-water fishes of northern California. Univ. California Publ. Zool., 57 (5) : 303-440.

Hobmaier, M.   1938.   *Diphyllobothrium* larvae in trout of California waters. California and West. Med. 49: 111.

Hopkins, S. H.   1934   The papillose Allocreadiidae.   Illinois Biol. Monog. 13 (2) : 1-80.

Hunter, G. W. III.   1942.   Studies on the parasites of fresh-water fishes of Connecticut. Connecticut State Geol. Nat. Hist. Survey, Bull. No. 63, pp. 228-288.

Hunter, G. W. III and Wanda S. Hunter. 1929. Further experimental studies on the bass tapeworm, *Proteocephalus ambloplitis* (Leidy). *In* Biological survey of the Erie-Niagara system, Suppl. 18th Ann. Rept. 1928, New York State Conserv. Dept., Albany, pp. 198-207.

Hunter, G. W. III and Wanda S. Hunter. 1935. Further studies on fish and bird parasites. *In* Biological survey Mohawk-Hudson watershed, Suppl. 24th Ann. Rept. 1934, New York State Conserv. Dept., Albany, pp. 267-283.

LaRue, G. R. 1914. A revision of the cestode family Proteocephalidae. Illinois Biol. Monog. 1 (1 & 2) : 1-350.

LaRue, G. R. 1951. Host-parasite relations among the digenetic trematodes. Jour. Parasitol. 37: 333-342.

Larsh, J. E., Jr. 1941. *Corallobothrium parvum* n. sp., a cestode from the common bullhead, *Ameiurus nebulosus* Le-Sueur. Jour. Parasitol. 27: 221-228.

Leidy, Joseph. 1871. Notice of some worms, *Dibothrium cordiceps, Hirudo, Gordius.* Proc. Acad. Nat. Sci. Philadelphia. 23: 305-307.

Linton, Edwin. 1891. On two species of larval dibothria from the Yellowstone National Park. Bull. U. S. Fish Comm. 9: 65-79.

Linton, Edwin. 1901. Parasites of fishes of the Woods Hole region. U. S. Fish Comm. Bull. for 1899, pp. 405-492.

Linton, Edwin. 1940. Trematodes from fishes mainly from the Woods Hole region Massachusetts. Proc. U. S. Natl. Mus. 88: 1-172.

MacLulich, D. A. 1943. Parasites of trout in Algonquin Provincial Park, Ontario. Canad. Jour. Res. 21: 405-412.

Manter, H. W. 1926. Some North American fish trematodes. Illinois Biol. Monog. 10(2) : 1-138.

Meyer, M. C. 1940. A revision of the leeches (Piscicolidae) living on fresh-water fishes of North America. Trans. Amer. Micr. Soc., 59: 354-376.

Meyer, M. C. 1946. Further notes on the leeches (Piscicolidae) living on fresh-water fishes of North America. Trans. Amer. Micr. Soc. 65: 237-249.

Miller, M. J. 1940. Black spot in fishes. Canad. Jour. Comp. Med. 4: 303-305.

Miller, R. B. 1952. A review of the *Triaenophorus* problem in Canadian lakes. Fisheries Res. Board Canada. Bull. No. 95, 42 pp.

Mizelle, J. D. 1938. Comparative studies on trernatodes (Gyrodactyloidea) from the gills of North American fresh-water fishes. Illinois Biol. Monog. 17(1) : 1-81.

Mueller, J. F. 1934. Parasites of Oneida Lake fishes. IV. Additional notes on parasites of Oneida Lake fishes, including descriptions of new species. Roosevelt Wild Life Ann. 3: 335-373.

Mueller, J. F. and H. J. Van Cleave. 1932. Parasites of Oneida Lake fishes. II. Descriptions of new species and some general taxonomic considerations, especially concerning the trematode family Heterophyidae. Roosevelt Wild Life Ann. 3: 79-137.

Murphy, G. I. 1942. Relationship of the fresh-water mussel to trout in the Truckee River. California Fish Game. 28: 89-137.

Murphy, G. I. 1949. The food of young largemouth black bass *(Micropterus salmoides)* in Clear Lake, California. California Fish Game. 35: 159-163.

Plehn, Marianne. 1924. Praktikum der Fischkrankheiten. viii + 179 pp. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Rausch, Robert. 1951. Biotic interrelationships of helminth parasitism. Public Health Repts. 66 (29) : 928-934.

Richardson, L. R. 1937. Observations on the parasites of the speckled trout in Lake Edward, Quebec. Trans. Amer. Fish. Soc., 1936, pp. 343-356.

deRoth, G. C. 1953. Some parasites from Maine fresh-water fishes. Trans. Amer. Micr. Soc., 72: 49-50.

Scott, D. M. 1950. A preliminary report on the cod-worm investigation. Prog. Repts. Atlantic Coast Stations, Fish. Res. Board Canada, No. 48, pp. 10-11.

Shaw, J. N. 1947. Some parasites of Oregon wild life. Oregon Agr. Expt. Sta. Tech. Bull. No. 11, 16 pp.

Sillman, E. I. 1953. The life history of *Azygia longa* (Leidy, 1851) (Trematoda : Azygiidae) . Jour. Parasitol. 39 (No. 4, Sect. 2) : 15.

Sinderman, C. J. 1953. Parasites of fishes of north central Massachusetts, 1950, Div. Fish. Game, Boston, 28 pp.

Smith, S. I. 1874. The crustacean parasites of the fresh-water fishes of the United States. Rept. U. S. Comm. Fish Fisheries 1872-1873, pp. 661-665.

Stunkard, H. W. 1949. *Diphyllobothrium stemmacephalum* Cobbold, 1858, and *D. latum* (Linn., 1758 . Jour. Parasitol. 35: 613-624.

Thomas, L. J. 1937. Environmental relations and life history of the tapeworm *Bothriocephalus rarus* Thomas. Jour. Parasitol. 23: 133-152.

Thomas, L. J. 1947. Notes on the life cycle of *Schistocephalus* sp., a tapeworm from gulls. Jour. Parasitol. 33 Suppl. : 10.

Van Cleave, H. J. 1953. A preliminary analysis of the acanthocephalan genus *Corynosoma* in Mammals in North America. Jour. Parasitol. 39: 1-13.

Van Cleave, H. J. and J. F. Mueller. 1932. Parasites of the Oneida Lake fishes. I. Descriptions of new genera and new species. Roosevelt Wild Life Ann. 3: 1-71.

Van Cleave, H. J. and J. F. Mueller. 1934. Parasites of Oneida Lake fishes. III. A biological and ecological survey of the worm parasites. Roosevelt Wild Life Ann. 3: 161-334.

Ward, Helen L. 1940. Studies on the life history of *Neoechinorhynchus cylin,dratus* (Van Cleave, 1913 (Acanthocephala). Trans. Amer. Micr. Soc. 59: 327-347.

Ward, H. B. 1910. Internal parasites of the Sebago salmon. Bull. U. S. Bur. Fish. 28: 1151 1194.

Ward, H. W. 1912. The distribulion and frequence of animal parasites and parasitic diseas in North American fresh-water fish. Trans. Amer. Fish Soc., 1911, pp. 207-244.

Wardle, R. A. 1932. The Cestad of Canadian fishes I. The Pacific Coast Region. Contrib. Canadian Biol. Fish. 7(15) : 220-243.

Wardle, R. A. 1932a. The Cestoda of Canadian fishes II. The Hudson Bay Drainage system. Contrib. Canad. Biol. Fish. 7(27) :377-403.

Wardle, R. A. 1935. Fish-tapeworm. Biol. Board Canada Bull., No. 45, 25 pp.

Wardle, R. A. and J. A. McLeod. 1952. The zoology of tape-
    worms. xxiv + 780 pp. Univ. Minnesota Press, Minne-
    apolis.

Wilson, C. B. 1915. North American parasitic copepods be-
    longing to the Lernaeopodidae, with a revision of the entire
    family. Proc. U. S. Natl. Mus. 47 (2063) : 565-755.

Wilson, C. B. 1916. Copepod parasites of fresh-water fishes
    and their economic relations to mussel glochidia. Bull. U. S.
    Bur. Fisheries 34 (824) : 331-374.

Wilson, C. B. 1944. Parasitic copepods in the United States
    National Museum. Proc. U. S. Natl. Mus. 94(3177) : 529-
    582.

Woodbury, L. A. 1935. Infectivity of the plerocercoids of
    Diphyllobothrium cordiceps (Leidy) for man. Jour. Para-
    sitol. 21: 315-316.

X. GLOSSARY

In the preparation of the glossary an attempt has been made to explain the strictly scientific terms used in the text in a manner understandable to the layman, without sacrificing the meaning given them by parasitologists generally. Some of these terms, the use of which is unavoidable, will doubtless be encountered by the reader for the first time. Some unfamiliar terms are defined with the help of other technical terms, perhaps equally unfamiliar. This, too, is unavoidable and the solution lies in following up the terms until a clear understanding has been attained. To assist in the process of understanding, reference is made to contrasting terms and to illustrations. Since names are frequently used as adjectives, the adjectival form is also given (Adj.) .

Acanthella. The second larval form in the life cycle of an acanthocephalan. Occurs in the body cavity of the crustacean host ; rudiments of the structures of the adult worm have made their appearance. (Plate V, Fig. C.) See *Acanthor* and *Cystacanth.*

Acanthor. The first larval form in the life cycle of an acanthocephalan. It is elongate, with rounded ends, and the anterior region is provided with several rows of backward-directed spines. (Plate V, Fig. B.) See *Acanthella.*

Adult. The final stage in the life cycle of an animal, at which time it has reached sexual maturity. See *Larva.*

Alimentary canal. The gut ; a tube concerned with the digestion and absorption of food. In trematodes it has only one opening, the mouth. In the other parasitic animals involved (copepods, glochidia, leeches, roundworms) it has two openings: a mouth, through which food is taken, and an anus, from which waste materials are excreted.

Anadromous. Fishes that leave the sea and ascend streams to spawn.

Anterior. In front, towards the head. See *Posterior.*

Antihelminthic. Drugs used to free the host of worms.

Bacterium (Pl. Bacteria) . A large group of small one-celled plant organisms, without green coloring matter. Adj. Bacterial.

Bothrium (Pl. Bothria). A groove found on the scolex of certain tapeworms, used for attachment.

Buccal cavity. Pertaining to the mouth.

Caecum (Pl. Caeca). A blind out-pocketing of the intestine. Adj. Caecal.

Cephalic. Pertaining to the head.

Cercaria (Pl. Cercariae). The fourth larval form of a digenetic trematode ; produced by the redia in the snail host. It leaves the snail and swims for a time, by the aid of its tail, in the water. Adj. Cercarial. (Plate VI, Figs. D and E.)

Cercomer. An oval or club-shaped structure with three pairs of hooks, attached to the narrow end of the procercoid stage of certain larval tapeworms.

Cilium (Pl. Cilia). A minute, hair-shaped, moveable structure. Adj. Ciliated. (Plate VI, Fig. A.)

Class. A division of a phylum and including orders.

Coelom. A body cavity, enclosed by mesothelium, of an animal. Adj. Coelomic.

Coracidium (Pl. Coracidia). The first larval form in the life cycle of pseudophyllidean tapeworms ; covered by hair-like structures used in swimming. Adj. Coracidial.

Crus (Pl. Crura). The branched digestive system of digenetic trematodes.

Cyst. The membrane or membranes surrounding the larval form of a worm. (Plate VII, Figs. C, D and E.)

Cystacanth. The third larval form in the life cycle of an acanthocephalan. It is infective to the final host and already possesses structural characters of the adult worm. (Plate V, Fig. D.) See *Acanthella.*

Digenea. Trematodes which utilize different hosts and undergo different kinds of reproduction in their life cycle. Adj. Digenetic. See *Monogenea.*

Dioecious. An animal having either male or female gonads, but not both, in the same individual. See *Monoecious.*

Dorsal. Pertaining to the upper surface or back. See *Ventral.*

Ectoparasite. A parasite which lives upon the fins, scales or other outside surface of the fish host. Adj. Ectoparasitic. (Plate IV, Figs. A, B, C and D.) See *Endoparasite.*

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Embryo.   The larva before it escapes from the egg. (Plate V, Fig A.) See *Larva.*

Encyst.   To surround a larval form by a cyst wall.

Endo parasite.   A parasite which lives within the body of the host. Adj. Endoparasitic. (Plate III, Fig. C; VIII, Figs. A and B.) See *Ectoparasite.*

Errant.   Wandering, not stationary.

Family.   A division of an order and including genera.

Final host.   An animal harboring the adult (sexually mature) stage of the parasite. (Plates V, No. 2; VI, No. 3; VII, No. 3.) See *Intermediate host.*

Fungus (Pl. Fungi). A low form of plant life, without green coloring matter.

Genus (Pl. Genera). A division of a family and including species. Adj. Generic.

Glochidium (Pl. Glochidia). The larval form in the life cycle of a freshwater clam, found on fish. Adj. Glochidial. (Plate IV, Fig. D.)

Gonad.   An organ which produces egg cells or sperm cells.

Gravid.   An adjective applied to the female reproductive system with eggs.

Haptor.   Adhesive organ of monogenetic trematodes, located posteriorly.

Hexacanth.   The six-hooked embryo of cestodes, while yet in the egg shell. (Plate VII, Fig. A.)

Host.   An animal that harbors a parasite ; may be either intermediate or final.

Host specificity.   The ability of a parasite to thrive in a host. Every parasite has at least one species of host, and sometimes several, in which it finds conditions at an optimum. Adj. Host specific.

Infection.   The presence of a parasite within a host. (Plates III, Fig. C; VIII, Figs. A and B.) See *Infestation.*

Infestation.   The presence of a parasite externally upon a host. (Plate VI, Figs. A, B, C and D.) See *Infection.*

Intermediate host.   An animal harboring the larval or immature stages of a parasite. For those parasites requiring more than one intermediate host for their development before

reaching the final host, these hosts are then designated in order "first intermediate" and "second intermediate." (Plates I; II; V, No. 1; VI, Nos. 1 and 2; VII, Nos. 1 and 2.) See *Final host* and *Paratenic host.*

Juvenile. A fully developed and infective acanthocephalan larva, which has re-encysted in a paratenic host.

Larva. The young animal between the time it leaves the egg and before it has assumed the structural characters of the adult. Adj. Larval. See *Embryo* and *Adult.*

Life cycle. The various stages through which an animal passes from the fertilization of the egg to the death of the organism. (Plates V, VI and VII.)

Lumen. The cavity of the alimentary canal.

Mesentery. A sheet of tissue attaching the alimentary canal and other internal organs to the body wall. Adj. Mesenteric.

Metabolism. The sum of the chemical changes in a living animal. Adj. Metabolic.

Metacercaria. The fifth larval form in the life cycle of a digenetic trematode ; an encysted cercaria which has lost its tail and has become more adult-like. Adj. Metacercarial. (Plate VI, No. 2, Fig. F.)

Miracidium (Pl. Miracidia). The first larval form in the life cycle of a digenetic trematode. It is ciliated and usually errant (Plate VI, Fig. A.) Adj. Miracidial.

Monoecious. An animal having both male and female gonads in the same individual. See *Dioecious.*

Monogenea. Trematodes utilizing only one host and undergoing only one kind of reproduction in their life cycle. Adj. Monogenetic. See *Digenea.*

Operculum (Pl. Opercula). The gill covering of a fish.

Order. A division of a class and including families.

Organ. An assemblage of tissues cooperating in the performance of some particular function. See *Tissue.*

Oviparous. Laying *eggs* in which the embryos have as yet developed little, if at all. See *Viviparous.*

Parasite. An animal which obtains its livelihood at the expense of another, usually larger, animal of a different species. Adj. Parasitic.

Paratenic host. A host inserted between the last intermediate host and the final host. The parasite undergoes no development in this host, so that the completion of the life cycle of the worm is contingent upon this paratenic host being eaten by the normal final host. See *Intermediate host.*

Pathology. The science dealing with the nature of disease, through the study of its causes, its processes, and its effects, together with the associated changes of structure and function. Adj. Pathological.

Pharynx. A region of the alimentary canal between the mouth cavity and the esophagus. Adj. Pharyngeal.

Phylum (Pl. Phyla) . The largest division employed in the classification of the animal kingdom. About 22 phyla are recognized at the present time. Each phylum includes one or more classes.

Physiological saline. A solution of salts in water prepared so that the concentration of the salts in the solution is equal to that in the tissues of the animals to be kept in the solution, thus permitting the animals to survive for a longer time than if they were held in pure water.

Plankton. Organisms that float more or less passively in the water, such as Cladocera, copepods, many protozoans, and other small animals. Adj. Planktonic.

Plerocercoid. The third larval form in the life cycle of certain tapeworms. (Plate VII, Figs. D and E.) See *Procercoid.*

Posterior. Behind, away from the head. See *Anterior.*

Proboscis. A beak-like process at the anterior end of an animal. (Plate V, Fig. E.)

Procercoid. The second larval form in the life cycle of certain tapeworms. (Plate VII, Fig. C.) See *Plerocercoid.*

Protozoa. A phylum including the small, one-celled animals. Adj. Protozoan.

Pylorus. The opening from the stomach into the intestine. Adj. Pyloric.

Rearing tests. The feeding of larval forms to uninfected hosts and the recovery of the adult worms.

Redia (Pl. Rediae). The third larval form in the life cycle of a digenetic trematode ; produced by the sporocyst in the snail. (Plate VI, Fig. C.) Adj. Redial.

Scolex.   Part of a tapeworm provided with hooks and/or suck-
　　ers, by which the parasite attaches to gut wall of the host.

Segment.   A unit of the tapeworm's body. Adj. Segmental.

Species.   The smallest unit commonly used in classification ; a
　　taxonomic concept which includes closely allied individuals.
　　Adj. Specific. The species or scientific name of an animal
　　consists of two parts : a capitalized generic or genus name
　　and an uncapitalized trivial name. Example *Salmo salar.*

Spermatophore.   A packet of sperm.

Sporocyst.   The second larval form in the life cycle of a di-
　　genetic trematode ; develops from the miracidium and pro-
　　duces rediae in the snail. (Plate VI, Fig. B.)

Sterile.   Incapable of sexual reproduction.

Tissue.   A mass of similarly specialized cells. See *Organ.*

Trivial.   The uncapitalized, second name which together with
　　the generic name forms the species name of an animal.

Ventral.   The side normally directed downwards, the belly. See
　　Dorsal.

Virus.   A group of disease-producing organisms smaller than
　　bacteria, none being visible with the ordinary microscope.

Viscera.   The soft organs contained in the coelom. Adj. Visceral.

Viviparous.   Having young born alive after a period of em-
　　bryonic development within the parent animal. See *Ovi-
　　parous.*

X. INDEX

Numbers in bold-face indicate that a figure occurs on that page. Words in italics are names of genera or species.

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