TREMATODES OF NORTH AMERICA is intended as an identification manual and a concise source of information on larval stages, life cycles, anatomy, host relationships, and habitats of trematodes. The book should be useful to parasitologists, students of parasitology, and wildlife managers.

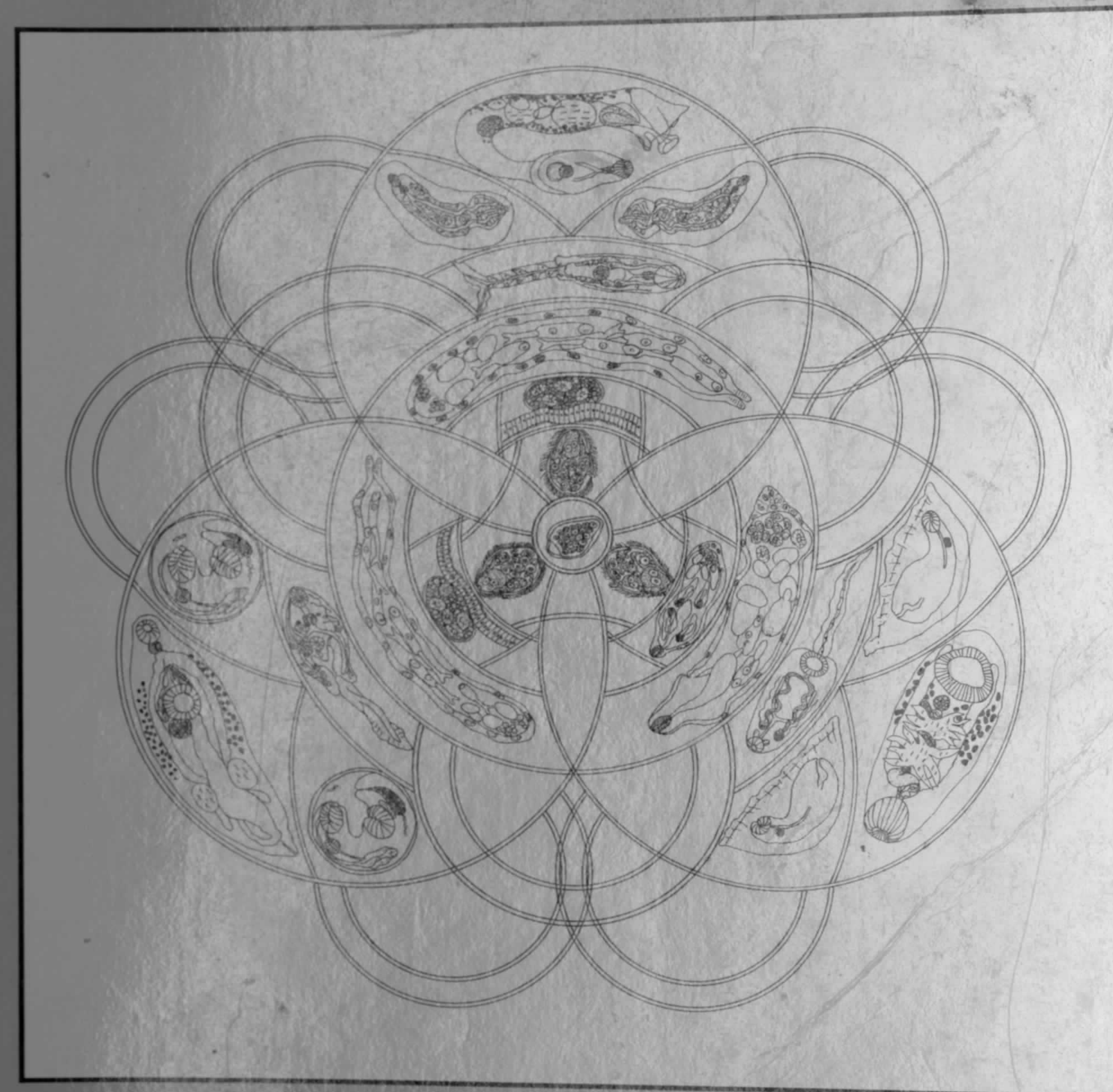
Keys have been written to make use of the most easily observed anatomical features. Keys to families and genera of adult trematodes are provided, as well as a key to the more common groups of cercariae. Published keys to species are also cited. Numerous illustrations assist with identification.

Dr. Stewart C. Schell is Professor and Chairman of Zoology Emeritus, University of Idaho.

ISBN 0-89301-095-2

TREMATODES of North America

North of Mexico



Stewart C. Schell

ISBN 0-89301-095-2
Library of Congress Catalog Number 83-51527

Published by the University Press of Idaho
A Division of the Idaho Research Foundation, Inc.
Box 3368, University Station, Moscow, Idaho 83843

PREFACE

This revised edition is meant to be of use as an identification manual and easy source of concise information on larval stages and life cycles of trematodes for undergraduate and graduate students in parasitology and for the professional parasitologist, pathologist, veterinarian, or medical technician. The coverage is restricted to the genera and higher categories known to occur in North America north of Mexico. Parasites of shore fishes and other shore fauna are included, but the parasites of deep sea animals are largely excluded.

The keys are designed to facilitate identification and not to show phylogenetic relationship. A key for the identification of families is provided for each of the three subclasses of trematodes. Keys to the genera of adult trematodes follow under the individual family headings. A key is also included for the more common types of cercariae. In writing keys, every effort was made to use the most easily-observed anatomical features; however, there are cases in which this procedure could not be followed. The key to the families of digenetic trematodes was exceptionally difficult to write. The author is not pleased with some parts of it. Although the superfamilies of the monogenetic trematodes are included in the key, this plan was not followed for the digenetic trematodes because their diagnoses are based primarily on the characters of the larval stages. Host relationship, habitat of the parasites, and the numerous line drawings will also aid identification.

The classification of the subclasses Monogenea and Aspidogastrea seems to be well established at this time, but that of the Digenea is still in a state of change, due primarily to inadequate knowledge of life cycles. There are numerous families in which no life cycles are known. This is especially true of those that parasitize marine vertebrates.

The author is responsible for the line drawings, many of which were prepared after examination of type specimens or reliably identified specimens. The type species is illustrated when this is known to occur in North America. Under Literature Cited I have included only those papers that pertain to life cycle studies and published keys to species.

The author is indebted to J.R. Lichtenfels and his predecessor, the late W.W. Becklund for the loan of numerous type specimens from the National Parasite Collection. I am grateful to R.M. Cable, M.H. Pritchard, and the late H.W. Manter for advice and the loan of reprints. J.C. Pearson was especially helpful with the family Heterophyidae and H.L. Ching with the family Gymnophallidae. Finally I want to express my appreciation to the many parasitologists who loaned specimens from which I prepared drawings or who sent reprints or copies of reprints for my use. Without their cooperation the book would be far less satisfactory.

Moscow, Idaho Stewart C. Schell

CONTENTS

THE ADULT TREMATODE

The trematodes represent a class in the phylum Platyhelminthes (flatworms) which are characterized as having the body usually flattened dorso-ventrally and have the internal organs embedded in parenchyma tissue which arises from mesoderm and resembles the mesenchyme of embryos. They also have an osmoregulatory or excretory system composed of flame cells, tubules, ducts, and one or two vesicles. Most platyhelminths are hermaphroditic. The phylum contains the classes Turbellaria or ciliated free-living flatworms, the Cestoidea or tapeworms and the Trematoda or flukes. The class Trematoda contains subclasses Monogenea, Aspidogastrea, and Digenea.

All species of trematodes are parasitic. There are approximately 200 families, 1800 genera, and more than 8000 described species. Sizes range from a fraction of a millimeter to about 12 meters. Body shape varies greatly as the illustrations on the following pages reveal. Adult trematodes in the three subclasses are quite different in their anatomy. Those in the subclass Monogenea (Fig. 1) are recognized most readily by the structure of the holdfast organs which are located at the anterior and posterior ends of the body. The prohaptor at the anterior end may contain a single oral sucker, a pair of small buccal suckers, one or more pseudosuckers, a pair of bothria, paired head lappets, or it can be glandular with gland ducts and their pores distributed along the anterior margin or grouped to form compact head organs. The opisthaptor at the posterior end of the body may be in the form of a muscular disc, with or without septa and loculi (alveoli); anchors and hooks might also be present on this type of opisthaptor. In some monogeneans, the opisthaptor is membranous and contains anchors and hooks. The opisthaptor of a few species contains muscular suckers, with or without curved sclerites or it may contain clamps. In some species, the clamps are mounted directly on the sides of the body instead of on a distinct opisthaptor. Clamps are bivalved structures, consisting of two membranous flops which have a supporting frame work of sclerites which vary in size, shape, number and arrangement. Clamps thus provide features which aid in identification of families and genera. In some monogenetic trematodes, the larval opisthaptor persists and after some increase in size becomes the opisthaptor of the adult, on which the larval marginal hooks are retained. In a few species, the opisthaptor of the adult is a new one on which the tiny larval haptor is retained.

Most trematodes in the subclass Aspidogastrea (Fig. 2) have a large ventral adhesive disc which contains septa and rows of alveoli or in the family Stichocotylidae a linear series of muscular suckers along the ventral body surface. In the family Rugogastridae about three-fourths of the ventral surface of the body contains transverse ridges and grooves (rugae).

In the subclass Digenea (Fig. 3) a muscular oral and a ventral sucker are the usual holdfast organs, however, some digenetic flukes are without suckers (e.g. Cyclocoelidae and Bivesiculidae). The spiny retractile proboscides in the family Rhopaliidae and the spiny collar in the Echinostomatidae also serve as organs for attachment to host tissues.

In other anatomical features, the trematodes in the three subclasses display some similarity. The digestive system consists of a mouth, pharynx, esophagus, and one or two intestinal ceca. In some trematodes the pharynx and/or esophagus is absent. Intestinal ceca may be long or short and might have side branches (diverticula) as in many monogenetic trematodes and in digenetic trematodes in the families Campulidae, Fasciolidae, and Pronocephalidae. A single cecum is present in most species of aspidogastreans, some digeneans (e.g. Haplosplanchnidae, Monascidae and Bucephalidae), and in some monogeneans (e.g. Udonellidae and Tetraonchidae). The mouth is located at or near the anterior end of the body in all trematodes, except those in the family Bucephalidae in which it is on the midventral body surface. In most species, the ceca end blindly but in some they are fused posteriorly to form a cyclocoel as in several families of the monogeneans and in the digeneans of the family Cyclocoelidae. Cecal variations are common in the family Opecoelidae in which ceca can end blindly, fuse to form a cyclocoel, open through separate ani posteriorly, fuse to open through a single anus, or fuse with the excretory vesicle to form a uroproct or cloaca which then opens through a cloacal pore.

Most trematodes are hermaphroditic (monoecious), but those in the family Schistosomatidae and some species in the family Didymozoidae are dioecious (gonochoristic) with a distinct sexual dimorphism. The female reproductive system is composed of an ovary, oviduct, ootype, Mehlis' gland, uterus, vitelline glands, seminal receptacle, and Laurer's canal. In some monogenetic trematodes (Polyopisthocotylea), a genito-intestinal canal joins the right cecum with the oviduct. This canal is thought to be homologous to Laurer's canal in the digenetic trematodes. The monogenetic flukes may have one, two, or no vaginae with pores that may be ventral, marginal, or in a few species, dorsal and located in the anterior third of the body. Laurer's canal functions as a vagina in those digenetic trematodes that cross inseminate. It can also receive excess reproductive products as in the hemiuroid flukes where vitelline material has been found in it. In some species, Laurer's canal contains a dilated area that serves as a seminal receptacle. Copulation may occur by way of the genital pore, thus introducing sperm into the uterus for eventual storage in a uterine seminal receptacle.

The terminus of the uterus in most families of digenetic trematodes is modified to form a muscular metraterm of more rarely a spiny terminal organ as in some species in the family Monorchiidae. Both of the above organs function in the release of eggs. Vitelline glands can be follicular, tubular or compact. The glands consist of clusters of multiplying vitelline cells which secrete shell material and some lipid. Some vitelline cells surround the zygote within the egg.

The male reproductive system consists of one to many testes, vasa efferentia, vas deferens, prostate gland and vesicle, ejaculatory duct, cirrus, and cirrus sac. Most species of digenetic trematodes have two testes; a few have one testis. Many species of monogeneans have multiple testes. The seminal vesicle can be internal, inside the cirrus sac, or external, outside the cirrus sac. In some species both external and internal sacs are present. If the cirrus sac is absent, the seminal vesicle is said to be "free in the parenchyma." The cirrus, which is frequently spinous and usually eversible in many species, is the male copulatory organ. It is enclosed within the cirrus sac with the prostate gland and prostatic vesicle. The functions for the latter are unknown.

The reproductive system opens to the exterior through one or two (male and female) genital pores which can be located in almost any part of the body, depending upon the species. Genital pores are usually ventral and median but in some species they

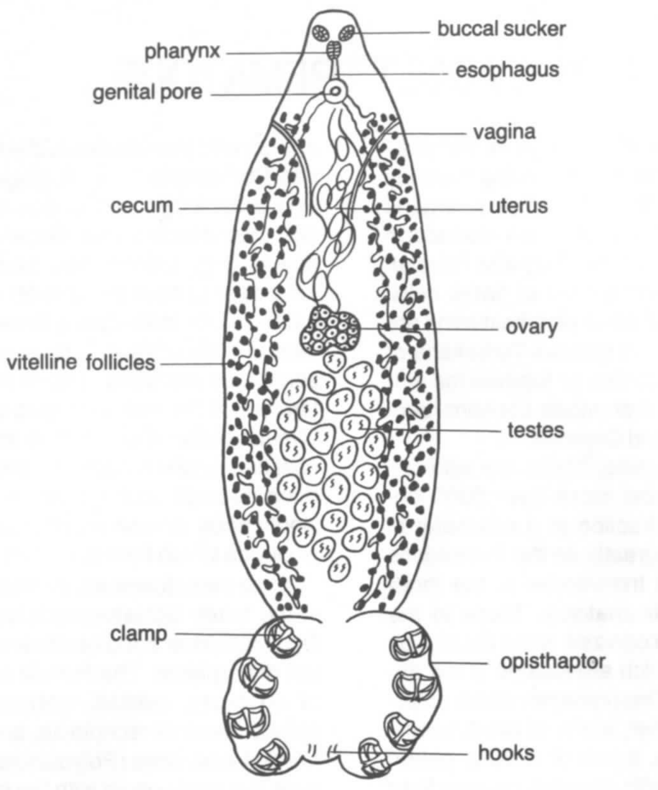


Fig. 1. Generalized monogenetic trematode.

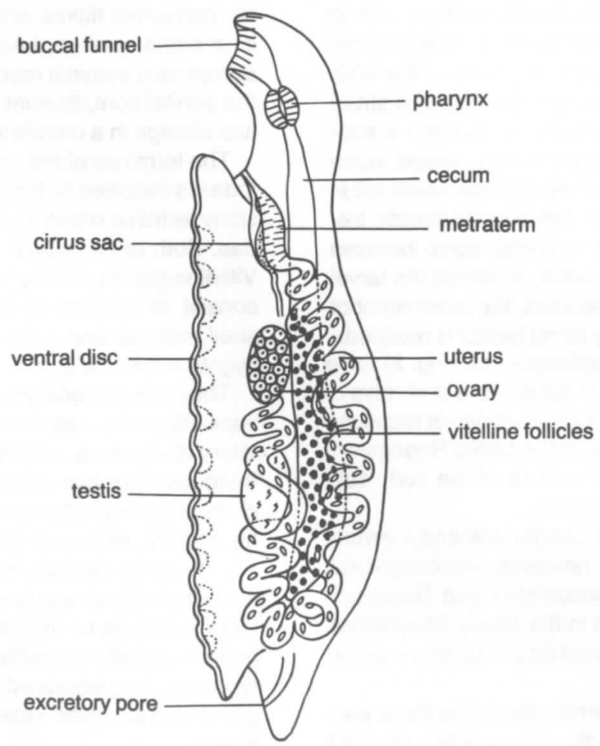


Fig. 2. Generalized aspidogastrean trematode.

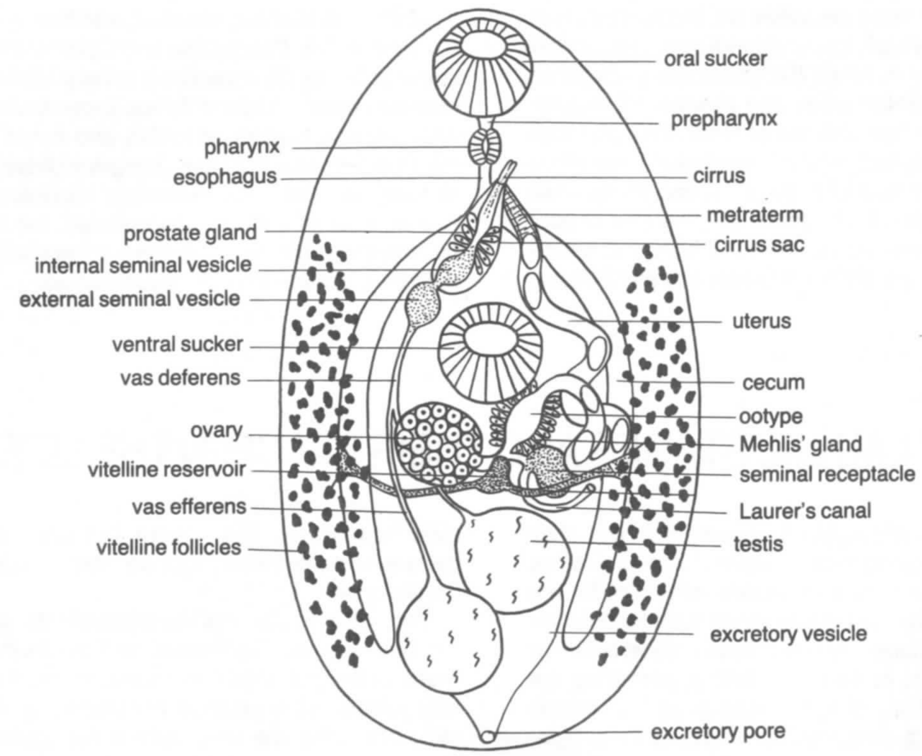


Fig. 3. Generalized digenetic trematode.

are lateral, submedian, or even dorsal. Species in the families Hemiuridae, Deropristiidae, Cryptogonimidae, Haploporidae, Heterophyidae, Strigeidae, Acanthocolpidae, *et al* have the terminal portions of the male and female systems fused to form the hermaphroditic duct (= genital sinus). In the families Hemiuridae and Haploporidae, this duct is enclosed in a sinus- or hermaphroditic sac. Most species in the superfamily Strigeoidea have the hermaphroditic duct within a genital cone that opens into a copulatory bursa at the posterior end of the body.

In the families Heterophyidae and Cryptogonimidae the ventral sucker and the genital pore are in some instances withdrawn into a ventrogenital sac which might also contain one or more fleshy gonotyls. In some heterophyids a genital sac is present, a cavity containing the genital pore and the gonotyl if the latter is present. Many species in the family Microphallidae *et al* have a genital atrium, a ventral chamber that receives the openings from the male and female reproductive ducts and opens on the body surface through a genital pore. In some species, the genital atrium contains papillae, pockets (alveoli), and spines.

The osmoregulatory system is composed of a bilateral system of flame cells, tubules, collecting ducts, and one or two vesicles. The system opens to the exterior through a pore which is located at the posterior end of the body in the digeneans and aspidogastreans. In the monogeneans, there are two vesicles and two lateral pores near the anterior end of the body.

The nervous system consists of a group of ganglia located in the anterior part of the body and joined to paired longitudinal trunks that extend anterior and posterior from the ganglia.

Numerous transverse commissures join the longitudinal trunks, forming a network. In some species, pigmented eyespots are present, as in digeneans in the families Lepocreadiidae, Deropristiidae, and Crytogonimidae, as well as in numerous species of monogenetic trematodes.

THE HABITAT OF ADULT TREMATODES

Most species of monogenetic trematodes are ectoparasites on the skin and gills of fishes, however, a few species inhabit the urinary tract of fish, amphibians, and reptiles. Species in the family Udonellidae parasitize parasitic copepods on marine fishes.

The aspidogastrean trematodes almost all exist as endoparasites of gastropod or lamellibranch molluscs, fishes, and turtles. Some have been reported from the body surface of molluscs. Those in the family Stichocotylidae inhabit the gall bladder and bile duct of rays, and *Taeniocotyle elegans* has a similar habitat in chimaeras. The single species in the family Rugogastridae was collected from the rectal glands of chimaeras.

Most species of digenetic trematodes inhabit the lumen of various parts of the digestive tract of vertebrates. Some of the more unusual habitats for these parasites are the bursa of Fabricius of birds (Gymnophallidae, Leucochloridiidae, Leucochloridiomorphidae); the coelom of fishes (Didymozoidae, Azygiidae, Gorgoderidae); the Eustachian tubes and pharynx of amphibians (Hemiuridae); the conjunctival sac of birds (Philophthalmidae); ovaries of fishes (Cephaloporidae); oviduct of birds (Prosthogonimidae); pancreatic duct of birds (Dicrocoeliidae); nasal cavities of marine mammals (Nasitrematidae); the skin of birds (Collyriclidae); beneath the scales of fishes (Transversotrematidae); the kidneys and ureters of birds (Renicolidae and Eucotylidae); the gall bladder, bile duct, and liver of birds and mammals (Dicrocoeliidae, Fasciolidae and Opisthorchiidae); the branchial cavity of fishes (Syncoelidae); urinary bladder of fishes (Gorgoderidae); swim bladder of fishes (Isoparorchiidae and Tetrasteridae); urinary bladder of turtles and fishes (Pronocephalidae); the blood vessels of fishes (Sanguinicolidae), of reptiles (Spirorchiidae), of birds and mammals (Schistosomatidae); trachea and air sacs of birds (Cyclocoelidae); the lungs of amphibians (Haematoloechidae), of reptiles (Heronimidae and Ochetosomatidae), of mammals (Paragonimidae).

THE EARLY LARVAL STAGES AND THEIR PLACE IN THE LIFE CYCLE

The trematode egg is ectolecithal, composed of an egg shell or capsule which envelopes the zygote and a cluster of vitelline cells which surround the zygote and provide nutriment for the developing embryo. Egg size and shape varies with the different species (Fig. 4). Most eggs are ovoid and have an operculum or lid at one end which opens at time of hatching, permitting the embryo to escape. The shells of some eggs have filamentous prolongations at one or both ends, thus forming unipolar or bipolar filaments. The filaments probably serve to anchor the eggs after oviposition, preventing them from being swept away by water currents.

Eggs that contain a fully developed embryo are said to be embryonated. The embryo or hatching stage in the three subclasses differ in their anatomy and in the names applied to them. The hatching stage of the monogenetic trematodes is an *onchomiracidium* (Fig. 5). They are ciliated in almost all species, with the cilia arranged in patches or tufts on the body surface. A typical onchomiracidium has two pairs of pigmented eyespots, a pharynx, one or two intestinal ceca and an excretory system with flame cells and tubules. Anchors and hooks are attached at the posterior end of the body, sometimes on a distinct opisthaptor. After hatching the onchomiracidium attaches to the same or a different host and, after undergoing some anatomical changes and growth, develops to the adult stage. Some larval structures such as eyespots, hooks, anchors, and the digestive system are retained by the adult. If suckers or clamps are destined to be present on the opisthaptor these develop one pair at a time, the most posterior pairs developing first. In some species, the life cycle of the parasite is closely synchronized with the life cycle of the host, as in the family Polystomatidae. Seasonal changes are known to have considerable influence on the production of eggs and the developing larvae of monogenetic trematodes.

The hatching stage of the aspidogastrean trematodes is a *cotylocidium* (Fig. 6) which is almost always nonciliated, has a muscular sucker near the posterior end and a buccal funnel and mouth at the anterior end of the body. Internal anatomy resembles that of the onchomiracidium. Once the cotylocidium hatches and attaches to a suitable host, it undergoes gradual development to the adult stage. This involves the development of a new and somewhat elaborate adhesive disc which extends over most of the ventral surface of the body and may contain several rows of alveoli (loculi) and septa or sometimes conical papillae as in the family Aspidogasteridae, transverse rugae as in the family Rugogastridae or a linear series of muscular suckers as in the family Stichocotylidae. Organs of reproduction also develop. Only one host is used for completion of most of these life cycles; however, in the genera *Lobatostoma* and *Rugogaster* there is some possibility that an intermediate host is involved in the life cycle.

The hatching stage of the digenetic trematodes is a *miracidium* (Fig. 7) which is ciliated and motile in all species except those in the superfamilies Hemiuroidea, Azygioidea and Didymozooidea which produce nonciliated spinous, and nonmotile miracidia. Cilia are mounted on flat epidermal cells which in most species are distributed uniformly over the body surface, however, in the families Bucephalidae and Leucochloridiomorhidae the cilia are arranged in clusters or mounted on paddle-like bars that protrude from the body. The number and arrangement of the epidermal cells, expressed as an epidermal cell formula, is of use in classification and provides evidence of phylogenetic relationship of families and superfamilies. It is assumed that closely related species produce miracidia that are similar in their anatomy. Criteria for determining relationship are number of pairs of flame cells, number and arrangement of germinal cells, presence or absence of penetration glands and of course the epidermal cell formula.

The miracidia of many species have a terebratorium, containing sensory papillae and pores of gland ducts, located at the anterior tip of the body. Internal structures consist of germinal cells, penetration glands, apical gland (hatching gland), subepidermal cells, flame cells, excretory tubules, central nerve ganglion (brain) and in some species pigmented eyespots. The germinal cells multiply and produce embryos for the succeeding generation of larvae. The penetration glands are thought to secrete enzymes that aid penetration of a mollusc which is always the first intermediate host for digenetic trematodes. The flame cells are joined to tubules that open through pores at the sides of the body and function in maintaining a satisfactory osmotic relationship in the body.

The life cycles of the digenetic trematodes involve a series of multiplying larval stages in the host mollusc. After hatching, the miracidium either penetrates a mollusc or the embryonated eggs are eaten by the mollusc and then the hatching occurs in the intestine of the host. After entering the mollusc, the miracidium usually metamorphoses to a sporocyst (Fig. 8) through loss of ciliated epidermal cells, resorption of glands and multiplication of germinal cells. The flame cells and tubules are retained as the early excretory system of the sporocyst which is barely more than a mass of proliferating germinal cells enclosed in a delicate limiting membrane. The germinal cells eventually give rise to a second generation of larvae which might be either rediae or daughter sporocysts depending upon the species. Daughter

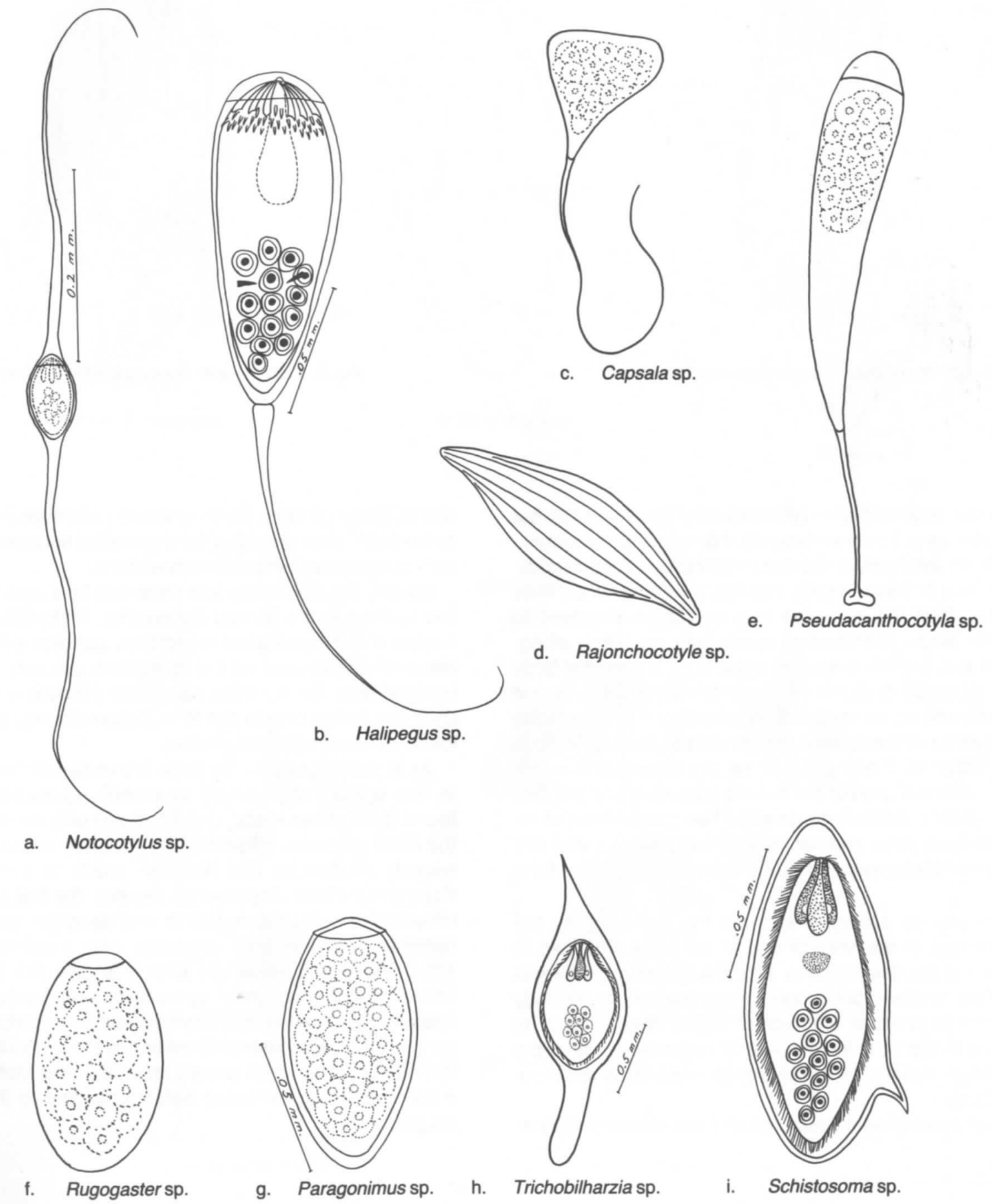


Fig. 4. Trematode eggs.

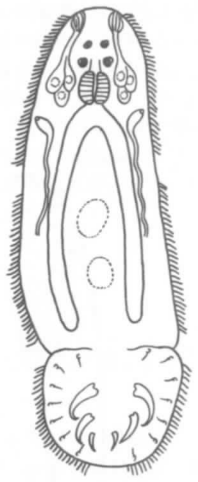


Fig. 5. Onchomiracidium of monogenetic trematode.

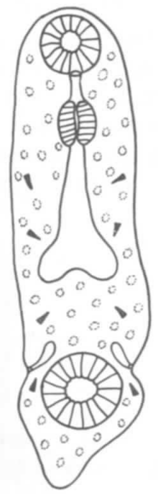


Fig. 6. Cotylocidium of aspidogastrean trematode.

sporocysts can be branched or unbranched (Figs. 9 and 10), but in either case they produce embryos that develop into cercariae. The branched sporocysts of species in the family Leucochloridiidae contain one or more brightly colored, pulsating brood sacs (Fig. 9) into which the cercariae migrate for development to metacercarial stage. Unbranched sporocysts are either elongate or ovoid and, like the branched ones, have a syncytial body wall, a central cavity or lumen which contains the embryos and germinal cells and an osmoregulatory (excretory) system in the body wall. Larvae of the succeeding generation escape through a terminal birthpore. If two generations of sporocysts are produced, the first is designated the mother sporocyst and the second the daughter sporocyst generation. Two generations of rediae are likewise mother and daughter rediae (Figs. 11 and 12). Granddaughter sporocysts and rediae have been reported for a few species.

The redia can be distinguished from the sporocyst by the muscular pharynx at the anterior end of the body. Attached to the pharynx is a sac-like intestine. Like the sporocyst, the redia also has a body wall and body cavity. Germinal cells in the body cavity multiply to produce embryos of future larval stages. In most rediae a birthpore is located laterally somewhere near the pharynx. The germinal cells eventually give rise to daughter rediae or cercariae.

The type of development described above involves multiplication of germinal cells, some of which pass from one generation to the next, thus providing for a germinal lineage which begins with the germinal cells in the miracidium.

Usually the first rediae are produced by a sporocyst but in a few species in the genera *Stichorchis, Philophthalmus, Cyclocoelum* and *Parorchis* the miracidium contains a tiny mother redia which is released as the miracidium contacts the first intermediate host. Such rediae can either produce a generation of daughter rediae or give rise to cercariae directly, the routine followed depends upon the species.

As in all living organisms there are variations from the normal. In one species of digenetic trematode, sporocysts have been found to be of two kinds. One produces only miracidia whereas the other produces miracidia and daughter sporocysts simultaneously (Mohandas and Nadakal, 1970). In another species, three generations of sporocysts develop, the first producing only miracidia, the second miracidia and daughter sporocysts concurrently and the third produces only cercariae (Premvati, 1955). Several species are known to give rise to sporocysts which produce daughter sporocysts and cercariae simultaneously, the daughter sporocysts eventually producing only cercariae. Both sporocysts and rediae are therefore capable of producing cercariae which usually leave the host mollusc and lead a brief free-living existence before changing to the next larval stage.

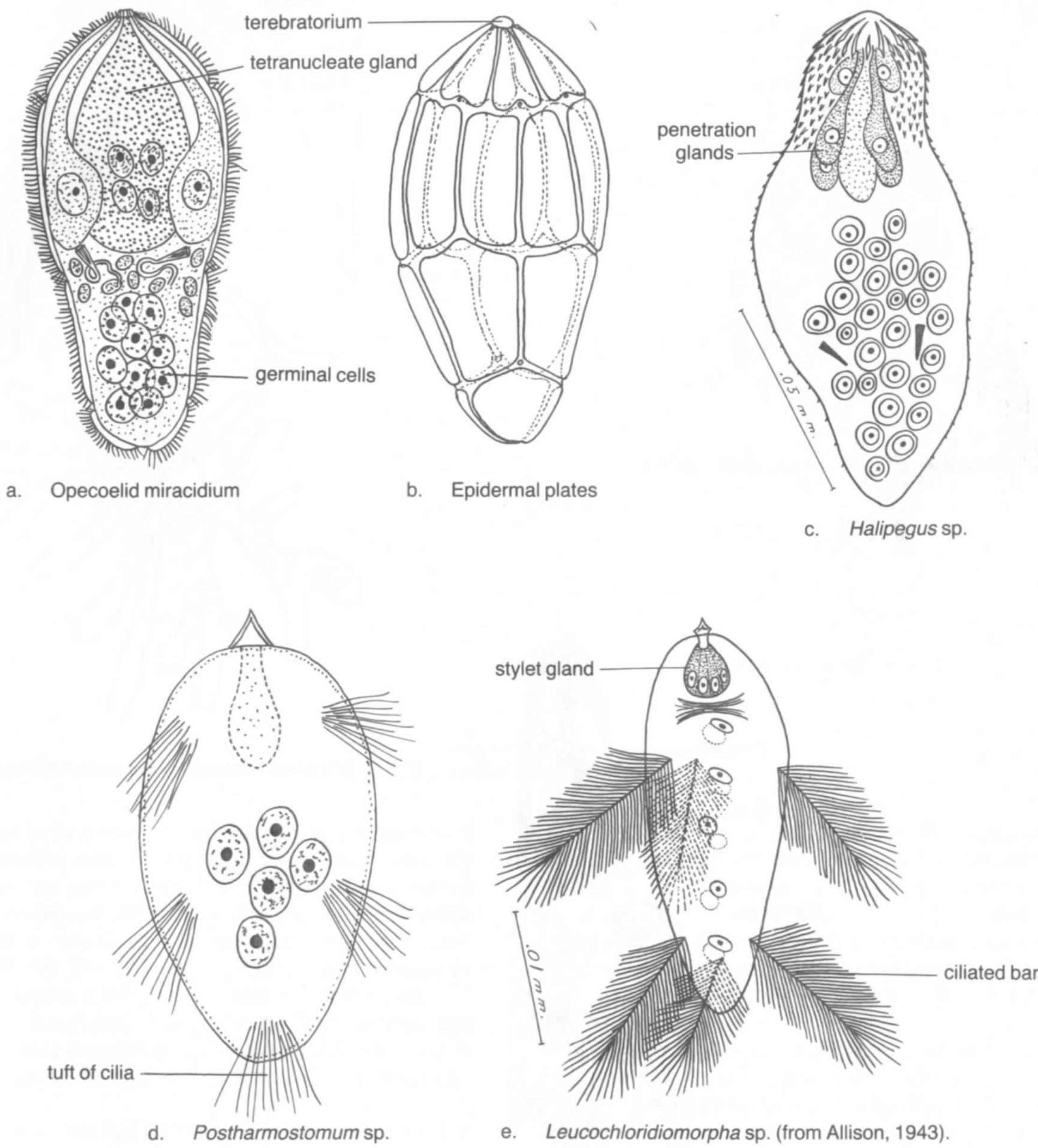


Fig. 7. Miracidia of digenetic trematodes.

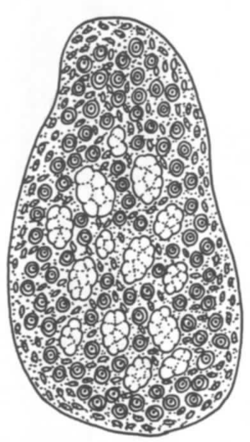


Fig. 8. Mother sporocyst of opecoelid trematode.

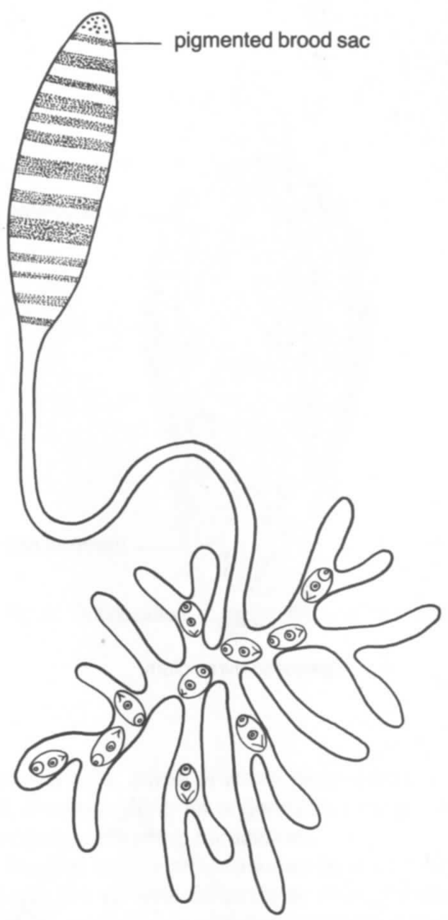


Fig. 9. Branched sporocyst of leucochloridiid trematode.

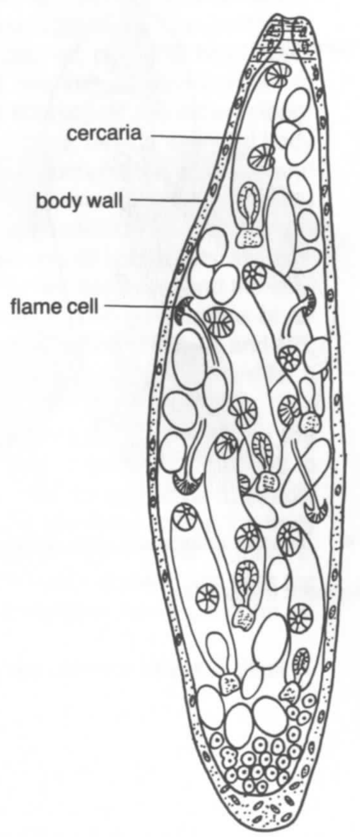


Fig. 10. Daughter sporocyst of opecoelid trematode.

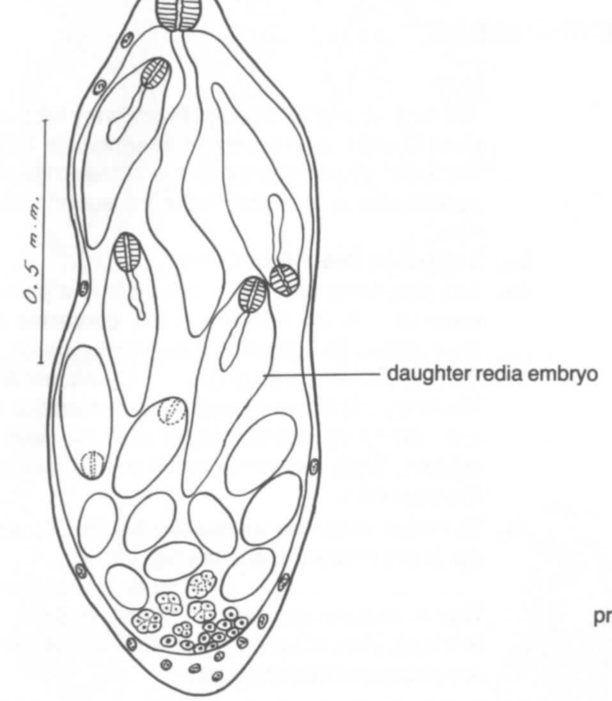


Fig. 11. Mother redia.

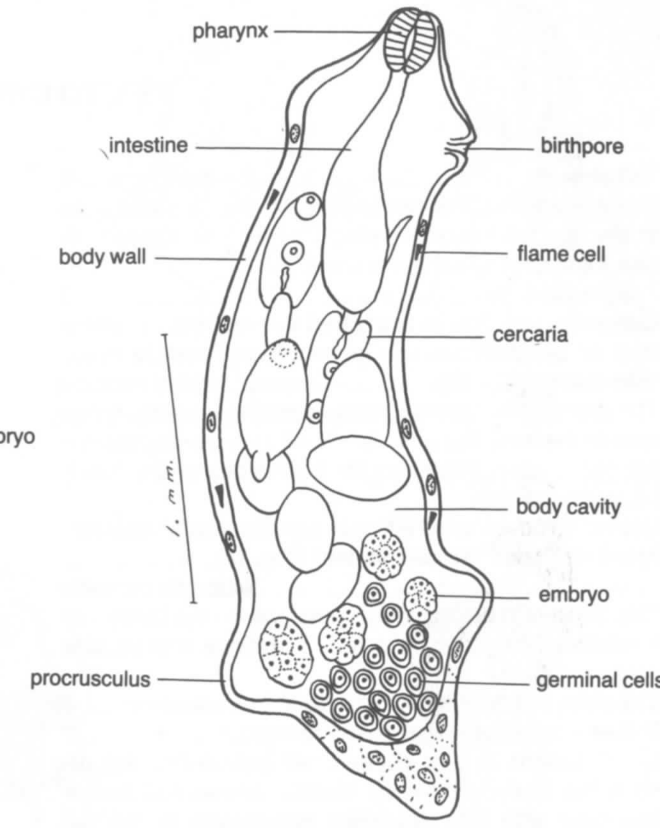


Fig. 12. Daughter redia.

THE CERCARIA

Most cercariae have a so-called tail which in many species is conical (leptocercous) and as long as or longer than the body and may be provided with finfolds, finlets, finger-like processes or setae which can be in clusters or singly along the tail. In some cercariae the tail is very short (microcercous) or absent (acercous or cercariaeum). The tail is used for locomotion. Tailless or microcercous cercariae are limited to creeping movements.

In the families Azygiidae, Bivesiculidae, Gorgoderidae and Hemiuridae the tail is enormous, enveloping the entire body of the cercaria. These are the cystocercous and cystophorous cercariae.

Considerable attention has been given to the anatomy of the excretory system in cercariae. Comparative anatomy of this system is of use in determining phylogenetic relationship. The excretory vesicle can be cellular or syncytial, or it can be thin-walled and membranous. When cellular, the cells are applied to the inner surface of a thin, membranous sac. Later these cells tend to slough off leaving the membranous sac or vesicle. Shape of the vesicle varies in different groups and is also of use in determining phylogenetic relationship. The system can be either mesostomate, with the main collecting ducts extending only to the midbody region where they join the anterior and posterior tubules, or it can be stenostomate with the main ducts extending into the anterior part of the body where they turn sharply posteriad before joining the tubules (Fig. 38). The number and arrangement of the flame cells is expressed as a flame cell formula which for some plagiorchioid trematodes is $2\ [(3+3+3) + (3+3+3)] = 36$. In this formula the "2" represents the two sides of the body and in each side there are six groups of three flame cells with three groups anterior and three groups posterior, all totaling 36 cells. Other internal organs consist of penetration glands, the secretions of which tend to be cytolytic and of use during entrance into the host. Their ducts lead forward and empty through pores at the anterior end of the body. The cercariae of some blood flukes have glands of two kinds, each secreting a different substance.

Cystogenous glands are present in those cercariae that secrete their own cyst membrane material. The cystogenous glands of the cercariae in several families in the order Echinostomida are specifically referred to as bâtonnet cells (Stäbchenkorper). Their cytoplasm is filled with rod-like bodies or bâtonnets which are rolled up scrolls of cyst membrane material which unroll to produce the proteinaceous inner layer for the cyst membrane. This type of gland is usually present in cercariae that encyst rapidly on vegetation or other external substrates.

Pigmented or nonpigmented eyespots are present in the forebody of some cercariae, usually close to the nerve ganglia. A spear-like stylet is present in several groups of cercariae. It is used to penetrate the tissues of the second intermediate host.

Many species of cercariae have been described and illustrated in published works on trematodes. When this is done, the generic name *Cercaria* is used for all species. The term cercaria can thus be used jointly as a common name for larvae and as a generic name. The accompanying key to cercariae includes the most common types or at least those that can be accurately assigned to families.

KEY TO CERCARIAE

1a. Tail absent. .... Cercariaeum 2
These are the tailless cercariae, produced by trematodes in the families Leuchloridiidae, Zoogonidae, Cyclocoelidae, Lissorchiidae and Mesocoelidae.

1b. Tail present. 3

2a. Cercariae develop in branched sporocysts in terrestrial or amphibious snails; excretory vesicle small thin-walled (Fig. 13). .... Leucochloridiid cercaria
The sporocysts of some of these contain pigmented brood sacs in the tentacles of snails. The cercariae migrate into the brood sacs. Produced by trematodes in the family Leucochloridiidae.

2b. Cercariae develop in rediae in aquatic snails; excretory vesicle has thick cellular wall (Fig. 14). ....Mutabile cercaria
This cercaria is produced by trematodes in the family Lissorchiidae. They encyst in an invertebrate intermediate host.

3a. Tail short or knoblike. . Microcercous cercariae 4

3b. Tail as long as or longer than the body. 7

4a. Stylet absent in oral sucker; tail indistinctly set off from the body; excretory vesicle thin-walled (membranous) with two pronglike extensions in the tail (Fig. 15). .... Obscuromicrocercous cercaria
These cercariae develop in branched sporocysts in terrestrial snails. Produced by species in the family Brachylaimidae.

4b. Stylet present; tail distinctly set off from body; excretory vesicle with cellular wall. 5

5a. Tail cupshaped; contains unicellular adhesive glands; cercariae develop in sporocysts (Fig. 16). .... Cotylomicrocercous(= Cotylocercous) cercaria
These cercariae develop in snails and encyst in fishes or in arthropods. The tail functions as an adhesive organ. These cercariae are produced by trematodes in the family Opecoelidae and by some species in the family Dicrocoeliidae.

5b. Tail knoblike, unicellular glands absent; develop in a redia in prosobranch snails. 6

6a. Tail knoblike and densely spinous, body also spinous (Fig. 17). .... Chaetomicrocercous cercaria
This type of cercaria is produced by trematodes in the families Nanophyetidae, Paragonimidae and some species in the family Lissorchiidae.

6b. Tail more triangular with a ventral groove or sulcus; body and tail nonspinous (Fig. 18). ....Sulcatomicrocercous cercaria
They are produced by trematodes in the family Troglotrematidae.

7a. Tail unusually large, base of tail with a cavity which envelopes body of cercaria. ....Macrocercous cercariae 8

7b. Tail not unusually large or if large, body not enveloped by tail, body entirely anterior to tail. 10

8a. Tail bulbous and cystlike, contains body of cercaria and long delivery tube; develop in a redia in snails (Fig. 19). .... Cystophorous cercaria
The body is ejected through the delivery tube after the cercaria is eaten by the second intermediate host. They are produced by trematodes in the families Hemiuridae and possibly some other families in the superfamily Hemiuroidea.

8b. Tail not as described above. 9

9a. Tail very long and thick, tapering to a point, cavity in base of tail, no delivery tube; cercariae develop in sporocysts in lamellibranch molluscs of the family Sphaeridae (Figs. 20, 21). ...... Cystocercous cercaria
The body of this cercaria contains penetration glands, cellular excretory vesicle, stylet and two well developed suckers. They are produced by trematodes in the family Gorgoderidae.

9b. Tail thick with two paddlelike furcae; develop in a redia in prosobranch snails (Fig. 22) .... Furcocystocercous cercaria
These cercariae are eaten by fishes which serve as definitive host. They are produced by trematodes in the families Azygiidae and Bivesiculidae.

10a. Tail forked but not unusually large .... Furcocercous cercariae 11

10b. Tail not forked, tapering to a point (Leptocercous). 17

11a. Tail stem almost nonexistent, furcae long, contractile; mouth on midventral surface or body and opening into saclike single cecum; rhynchus or sucker at anterior end of body (Fig. 23) .... Bucephaloid or Gasterostome cercaria
These cercariae develop in branched sporocysts in lamellibranch molluscs and encyst in fishes. They are produced by trematodes in the family Bucephalidae.

11b. Tail stem at least as long as furcae; mouth at anterior end of body and enveloped by an oral sucker or by an anterior organ; two intestinal ceca usually present. 12

12a. Body with dorso-median finfold. .... Lophocercous cercariae 13

12b. Body without dorso-median finfold. 14

13a. Pigmented eyespots present; ventral sucker vestigial or absent; some flame cells in base of tail; pharynx absent but esophagus enlarged in restricted area; develop in a redia. (Fig. 26). .... Clinostomoid cercaria
These cercariae are produced by trematodes in the family Clinostomidae. They encyst in fishes and amphibians, eventually developing into large precocial metacercariae that are eaten by piscivorous birds. Adults then develop rapidly in the mouth and esophagus of birds.

13b. Pigmented eyespots absent; ventral sucker absent or vestigial; no flame cells in tail stem; pharynx absent and no thickening of esophagus; develop in a sporocyst (Fig. 24). .... Lophocercous-apharyngeate cercaria
These cercariae are produced by trematodes in the family Sanguinicolidae, the blood flukes of fishes. They penetrate the skin and mucous membranes of fishes directly.

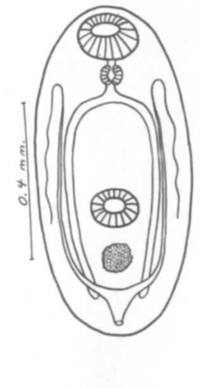


Fig. 13. Leucochloridiid cercariaeum.

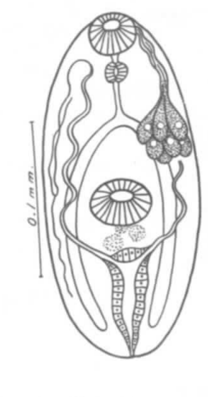


Fig. 14. Mutabile cercariaeum.

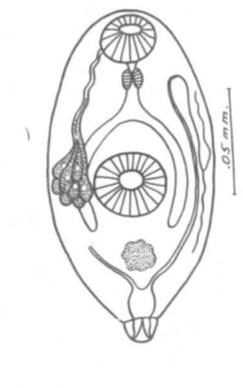


Fig. 15. Obscuromicrocercous cercaria.

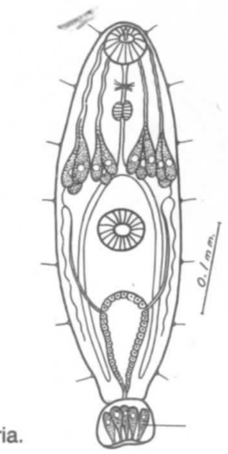


Fig. 16. Cotylomicrocercous cercaria.

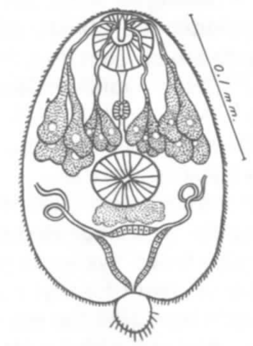


Fig. 17. Chaetomicrocercous cercaria.

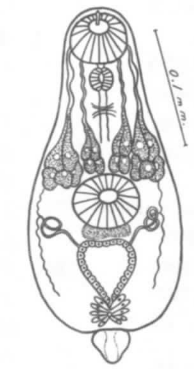


Fig. 18. Sulcatomicrocercous cercaria.

Fig. 19. Cystophorous cercaria.

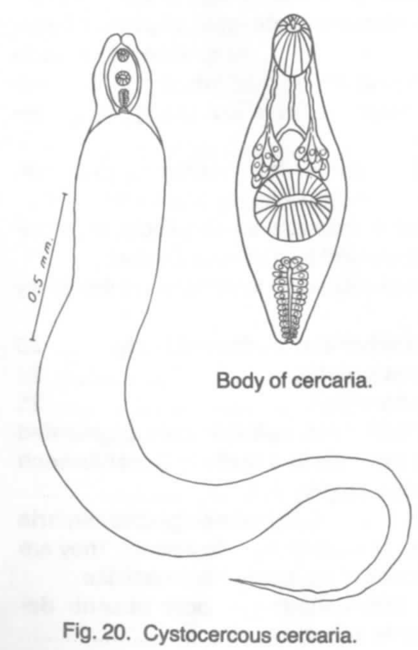


Fig. 20. Cystocercous cercaria.

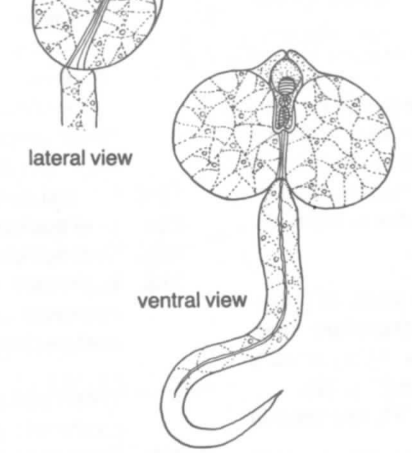


Fig. 21. Cystocercous

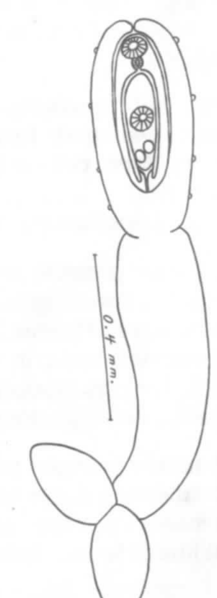


Fig. 22. Furcocystocercous cercaria.

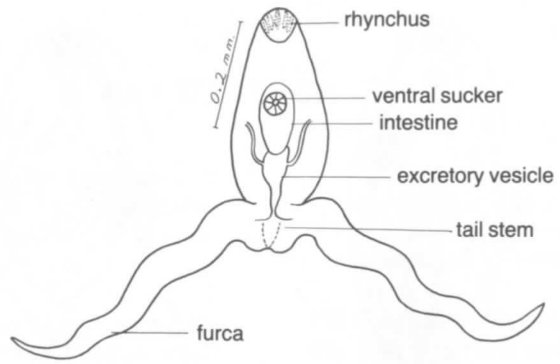


Fig. 23. Bucephaloid cercaria.

14a. Pharynx absent; pigmented eyespots usually present; penetration glands large, of two kinds; tail stem distinctly longer than furcae (Fig. 25). .... Brevifurcate-apharyngeate cercaria

These are produced by trematodes in the families Spirorchiidae and Schistosomatidae, the blood flukes of reptiles, birds and mammals. They penetrate the skin and mucous membranes of the host directly.

14b. Pharynx present; pigmented eyespots seldom present; penetration glands all of one kind; tail stem only slightly longer than furcae or shorter than furcae. 15

15a. Cercariae very small; excretory vesicle large and U-shaped; ceca short; develop in sporocysts in marine lamellibranchs or prosobranch molluscs. (Fig. 27). ... . Dichotoma cercaria ....

These cercariae are produced by trematodes in the families Gymnophallidae and Leucochloridiomorphidae. In some species the tail regresses before the cercaria leaves the sporocyst, causing it to resemble a metacercaria. Metacercariae are frequently found in molluscs, encysted or not encysted.

15b. Cercariae not unusually small; excretory vesicle small, not U-shaped; furcae about as long as tail stem; some flame cells in tail stem; develop in sporocysts in snails. .... Longifurcate-pharyngeate cercaria 16

16a. Ventral sucker present; one pair of longitudinal collecting ducts connected to excretory vesicle, excretory pores at sides of furcae (Fig. 28) .. Strigea cercaria

These cercariae develop in sporocysts in aquatic pulmonate snails. They are produced by trematodes in the families Strigeidae and Diplostomidae.

16b. Ventral sucker vestigial or absent; two pairs of longitudinal collecting ducts connected to excretory vesicle, the median pair fuse in midline of body; excretory pores at tips of furcae, finfolds on furcae (Fig. 29). .... Vivax cercaria

These cercariae develop in sporocysts in prosobranch snails. They are produced by trematodes of the family Cyathocotylidae.

17a. Tail contains paired lateral fingerlike processes and one terminal process; intestine is a single cecum; body contains many cystogenous glands (bâtonnet cells); pigmented eyespots are present (Fig. 30). .... Haplosplanchnid cercaria

These cercariae develop in sporocysts in marine snails and encyst on vegetation. It is assumed to be the cercaria of trematodes of the family Haplosplanchnidae.

17b. Tail without fingerlike processes; two intestinal ceca present; pigmented eyespots present or absent. 18

18a. Ventral sucker absent; pigmented eyespots present; adhesive organs at posterior end of body; excretory system of the stenostomate type with the main ducts united across the anterior part of the body; many cystogenous glands present (Fig. 31) .... Monostome cercaria

These cercariae develop in a redia and encyst within hemispherical cyst membranes on aquatic vegetation. They are produced by trematodes in the families Notocotylidae, Nudacotylidae and Pronocephalidae.

18b. Oral and ventral suckers present. 19

19a. Ventral sucker large, at posterior end of body; excretory system of the stenostomate type; pigmented eyespots present (Fig. 32). .... Amphistome cercaria

These cercariae encyst on aquatic vegetation in hemispherical cyst membranes. There are two types of amphistome cercariae:

1. Diplocotylea: Oral sucker has diverticula; main collecting ducts are not connected by a transverse duct.
2. Pigmentata: Oral sucker without diverticula; main collecting ducts connected by a transverse duct.

These cercariae are produced by trematodes of the family Paramphistomidae.

19b. Ventral sucker on midventral surface of body. 20

20a. Oral sucker contains a stylet. 21

20b. Oral sucker without a stylet. 25

21a. Excretory vesicle has thick cellular wall; pigmented eyespots present; develop in a redia in lamellibranch and gastropod molluscs (Fig. 33)................................. .... Ophthalmoxiphidiocercaria

These cercariae encyst in larval aquatic insects. They are produced by trematodes of the family Allocreadiidae.

21b. Excretory vesicle thin-walled; eyespots absent; develop in sporocysts in aquatic snails........................... .... Xiphidiocercariae 22

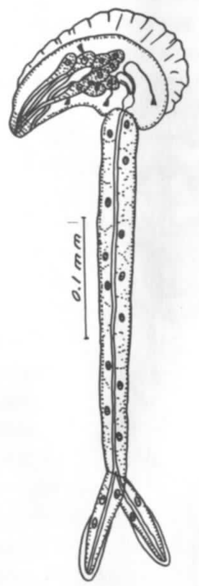


Fig. 24. Lophocercous-apharyngeate cercaria.

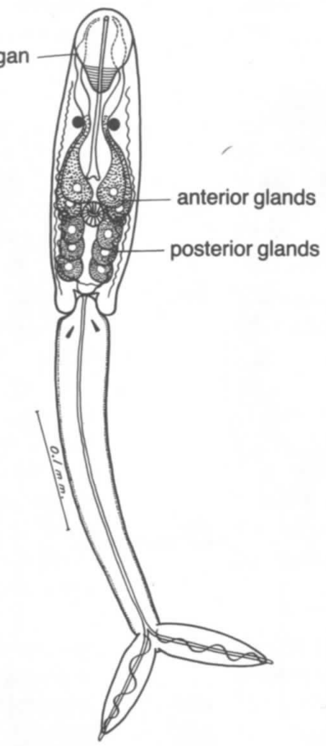


Fig. 25. Brevifurcate-apharyngeate cercaria.

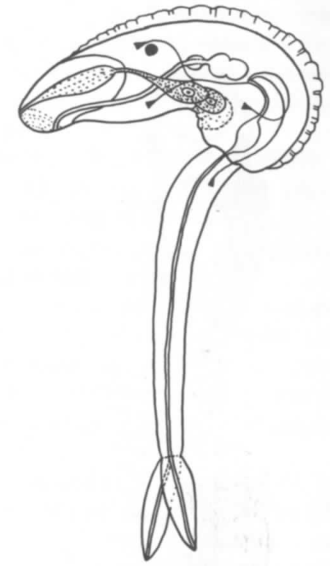


Fig. 26. Brevifurcate-pharyngeate (clinostomoid) cercaria.

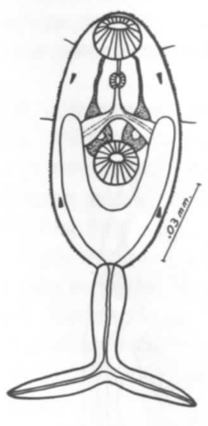


Fig. 27. Dichotoma cercaria.

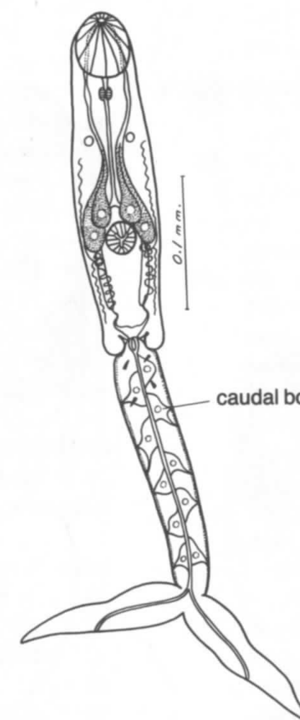


Fig. 28. Longifurcate-pharyngeate (strigea) cercaria.

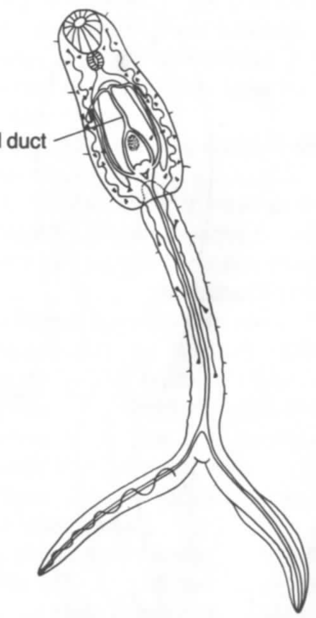


Fig. 29. Vivax cercaria.

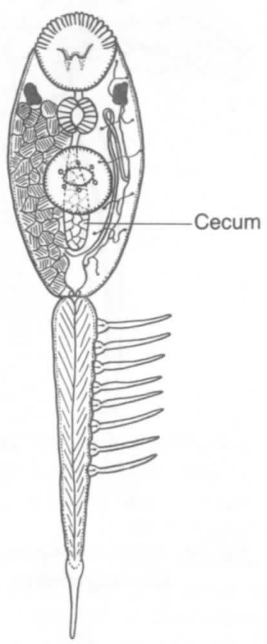


Fig. 30. Haplosplanchnid cercaria (from Cable, 1954).

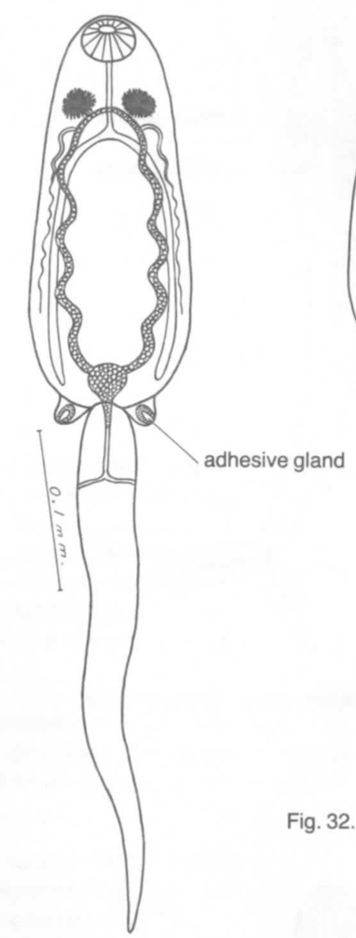


Fig. 31. Monostome cercaria.

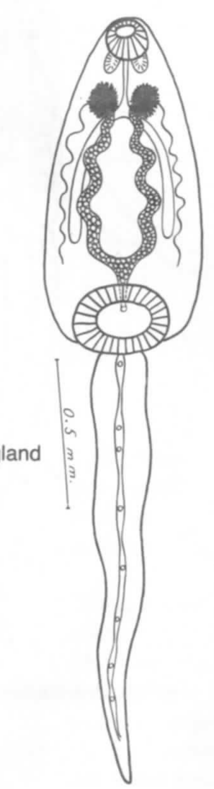


Fig. 32. Amphistome cercaria.

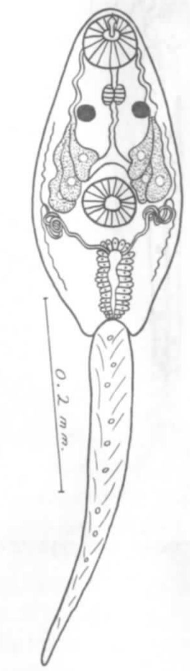


Fig. 33. Ophthalmoxiphidio cercaria.

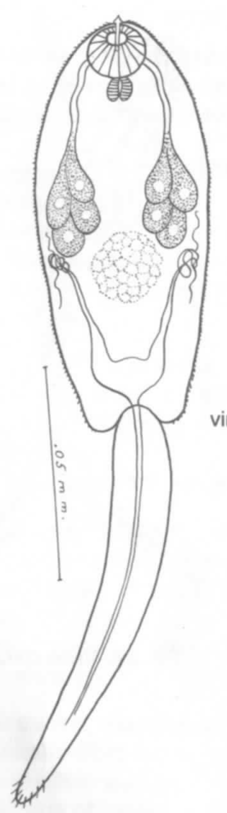


Fig. 36. Ubiquita cercaria.

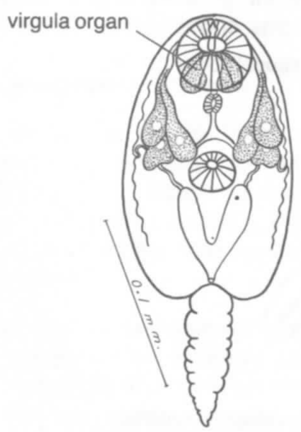


Fig. 35. Virgulate cercaria.

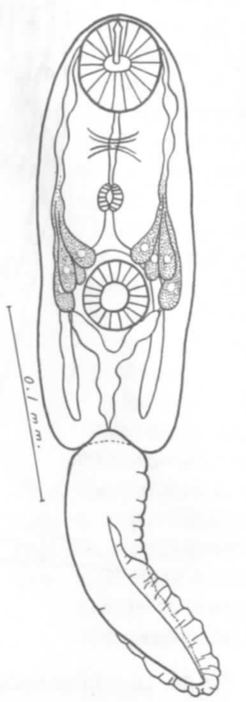


Fig. 34. Ornatae cercaria.

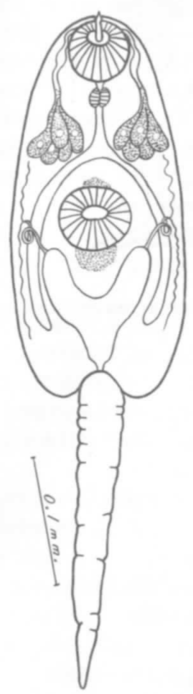


Fig. 37. Armatae cercaria.

22a. Tail has dorso-ventral finfolds; ventral sucker smaller than oral sucker (Fig. 34). .... Ornatae cercaria
These cercariae are produced by trematodes in the families Macroderoididae and Haematoloechidae.

22b. Tail without finfolds. 23

23a. Bilobed or pyriform virgula organ located in region of oral sucker; tail shorter than body; ventral sucker smaller than oral sucker (Fig. 35) ....Virgulate cercaria
The virgula organ contains mucoid secretions which are of use to the cercaria. They develop in sporocysts in prosobranch snails and are produced by trematodes in the families Lecithodendriidae, Allassogonoporidae and Pleurogenidae. Hall (1960) published a key to species of virgulate cercariae.

23b. Virgula organ absent; tail about same length as body. 24

24a. Ventral sucker vestigial or absent; ceca absent; cercaria usually very small; develop in sporocysts in prosobranch snails; (Fig. 36). .... Ubiquita cercaria
These cercariae encyst in aquatic arthropods and are produced by trematodes in the family Microphallidae. (See remarks under family diagnosis)

24b. Ventral sucker present and at least as large as oral sucker (Fig. 37). .... Armatae cercaria
Trematodes in the families Plagiorchiidae, Telorchiidae, Auridistomidae, Ochetosomatidae and Cephalogonimidae produce this kind of cercaria.

25a. Oral sucker surrounded by a spiny collar; stenostomate excretory system; develop in a redia. 26

25b. Spiny collar absent; excretory system of the mesostomate type or some modification of that type. 27

26a. Tail narrower than body (Fig. 38). .... Echinostome cercaria
These cercariae encyst in molluscs and other invertebrates. They are produced by trematodes in the family Echinostomatidae.

26b. Tail much wider and three to five times as long as body. (Fig. 39). .... Magnacauda cercaria
These are like the Echinostome cercariae except for the unusually large tail. They are eaten by fishes in which they encyst. Trematodes in the families Echinostomatidae and some Psilostomidae produce this type of cercaria. Nasir and Scorza (1968) published a key to species of these cercariae.

27a. Cercariae emerge from snails in clusters with tails intertwined; body like that of echinostome cercaria except for absence of spiny collar (Fig. 40). .... Zygocercous cercaria
These cercariae encyst in fishes. They are thought to be produced by some species in the families Psilostomidae and Echinostomatidae.

27b. Cercariae emerge singly; tails not intertwined; body not echinostome-like. 28

28a. Tail has long lateral setae or finlets (Figs. 41,42) .. 29

28b. Tail without setae or finlets but may have finfolds. 31

29a. Tail with long lateral finlets; excretory vesicle large and U-shaped; eyespots absent; cercariae develop in sporocysts in marine lamellibranch molluscs (Fig. 41). .... Nonoculate trichocercous cercaria (= Fellodistomid cercaria)
The finlets are really clusters of long setae enclosed in a membrane. These cercariae encyst in invertebrates and are thought to be produced by some trematodes in the family Fellodistomidae.

29b. Tail has lateral setae, singly or in clusters (Figs. 42,43); excretory vesicle not U-shaped; pigmented eyespots present; develop in a redia 30

30a. Tail much longer than body; setae in lateral clusters; excretory vesicle thin-walled (Fig. 42). .... Oculate trichocercous cercaria (= Lepocreadiid cercaria)
These cercariae develop in rediae in marine prosobranch snails and penetrate a variety of marine invertebrates. They are produced by some species in the family Lepocreadiidae.

30b. Tail about as long as body; single setae on tail and body; excretory vesicle has cellular wall (Fig. 43). .... Homalometronine cercaria (= Anallocreadine cercaria)

31a. Tail has dorso-ventral and sometimes lateral finfolds; eyespots present; develop in a redia in snails. 32

31b. Tail without finfolds; eyespots absent. 34

32a. Tail has dorso-ventral finfolds; excretory vesicle large, with thick cellular (syncytial) wall; ventral sucker vestigial; excretory pores at sides of basal portion of tail. .... Pleurolophocercous cercaria (= Opisthorchioid)
If lateral finfolds are also present the cercaria is parapleurolophocercous (Fig. 44). Both types develop in a redia in prosobranch snails and encyst in fishes. Species in the families Cryptogonimidae and Opisthorchiidae produce pleurolophocercous cercariae. Both types have been reported for the family Heterophyidae.

32b. Excretory vesicle Y-shaped and thin-walled; ventral sucker always well developed 33

33a. Ventral finfold small, lateral finfolds wide and supported by filaments; main collecting ducts of excretory vesicle short and without numerous lateral branches (Fig. 45). .... Megaperid cercaria

33b. Tail with dorsal and ventral finfolds and short lateral finfolds or finlets; main collecting ducts of excretory vesicle extend to anterior end of body and have many lateral branches (Fig. 46). ..... Rhodometopa cercaria
This cercaria is assumed to be one type produced by some species in the family Renicolidae. Flame cells are in groups of five or six. These cercariae develop in large yellow sporocysts in prosobranch snails.

34a. Tip of tail contains adhesive glands; no excretory duct in base of tail (Fig. 47). ...... Megalurous cercaria
Trematodes in the family Philophthalmidae produce this type of cercaria.

34b. Tip of tail without adhesive glands; excretory duct extends into base of tail; excretory pores on margin of tail (Fig. 48). .... Gymnocephalous cercaria
This cercaria is produced by species in the family Fasciolidae and possibly some species in the family Renicolidae.

Fig. 38. Echinostome cercaria.

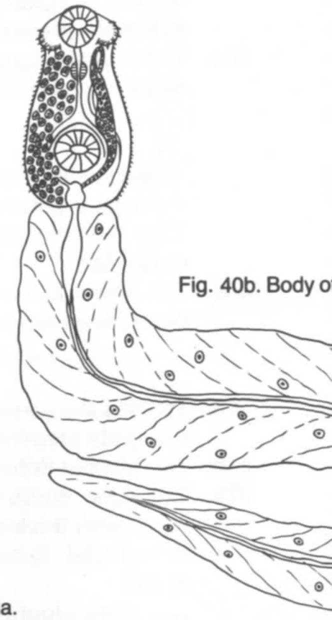



Fig. 39. Magnacauda cercaria.

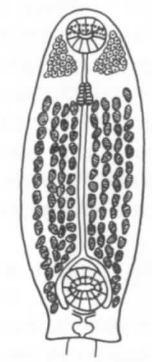


Fig. 40b. Body of zygocercous cercaria.

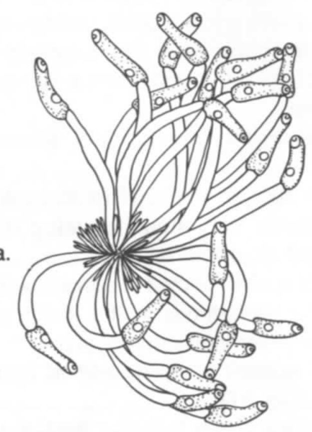


Fig. 40a. Zygocercous cercariae

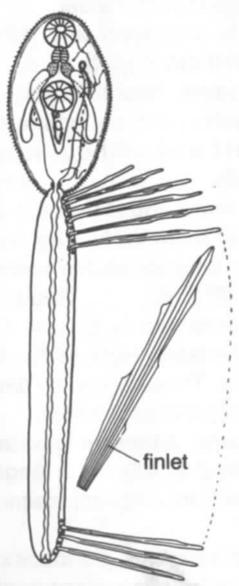


Fig. 41. Nonoculate trichocercous cercaria (from Cable, 1954).

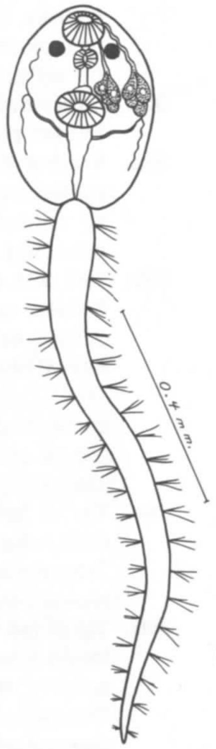


Fig. 42. Oculate trichocercous cercaria.

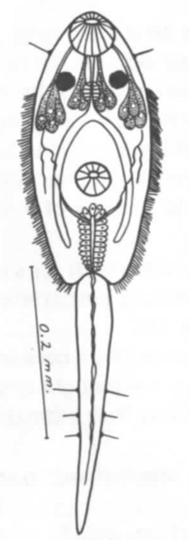


Fig. 43. Homalometronine cercaria.

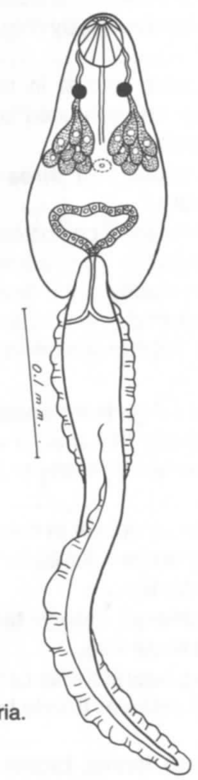


Fig. 44. Parapleurolophocercous cercaria.

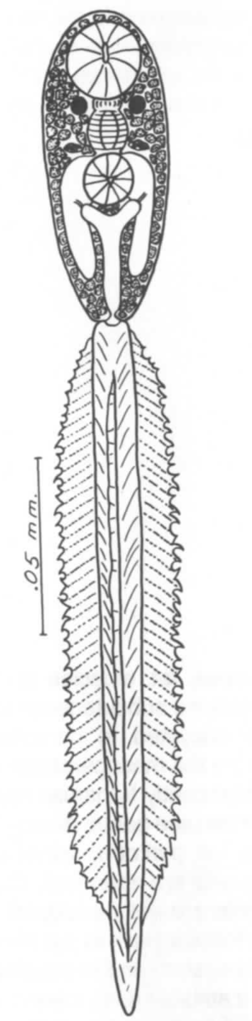


Fig. 45. Megaperid cercaria (from Cable, 1954).

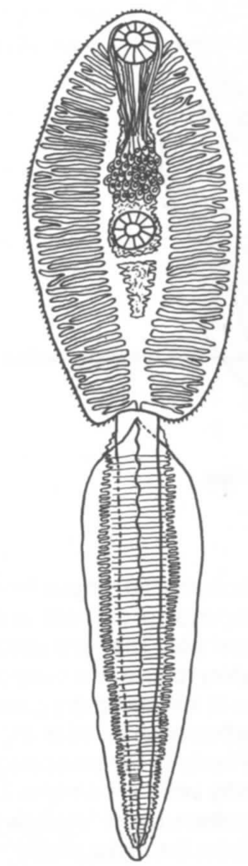


Fig. 46. Rhodometopa cercaria (from Rothschild, 1936).

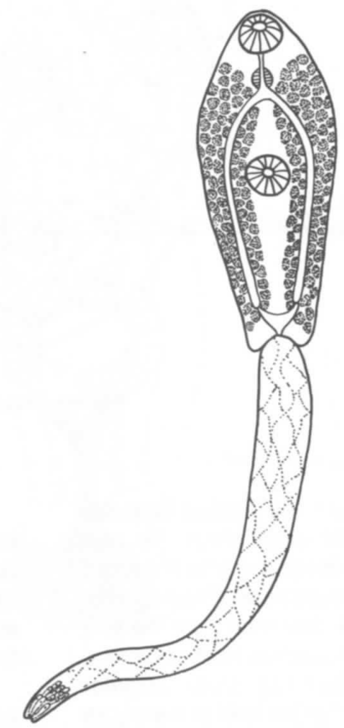


Fig. 47. Megalura cercaria.

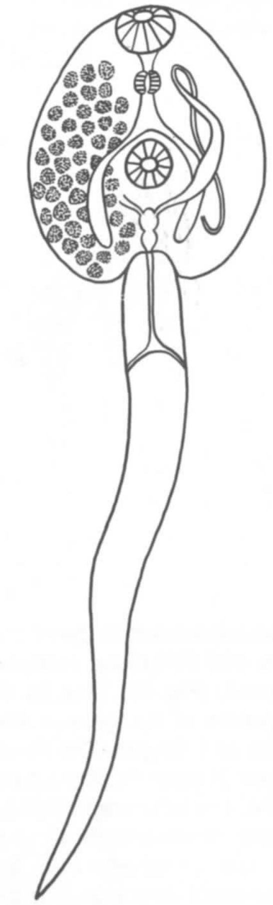


Fig. 48. Gymnocephalous cercaria.

THE MESOCERCARIA

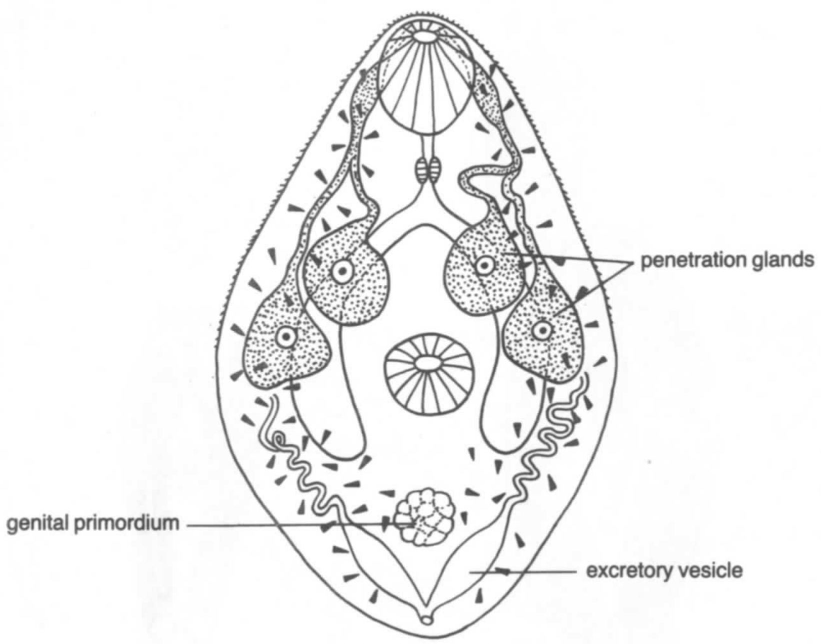


Fig. 49. Mesocercaria.

Some species of strigeoid trematodes in the families Diplostomidae and Strigeidae produce an extra larval stage, the mesocercaria (Fig. 49). Thus far this stage is known to be produced by species in the genera *Alaria, Procyotrema, Pharyngostomoides* and *Strigea.* The mesocercaria develops from the strigea type of cercaria after it penetrates a suitable host, such as a tadpole. The latter might then be eaten by a frog, snake, alligator or mammal which might serve as the definitive host or merely as a paratenic or collector host. In the latter, the mesocercariae accumulate but do not develop further unless the paratenic host is eaten by some animal in which the metacercaria can develop.

There have been reports of mesocercariae in the retina, lungs and skin of human beings. Such infections are probably the result of eating raw or insufficiently cooked flesh of frogs, alligators or mammals such as raccoon or opossum. Contamination of hands when cleaning animals might result in accidental ingestion of these larvae.

Mesocercariae inhabit lymph spaces, fat, muscles and connective tissue of the host. In mammals the subcutaneous fat is a common site. They are usually not encysted. In the opossum, laboratory mouse and possibly in cats the mesocercariae accumulate in the mammary glands and recently transmammary infection has been found to occur in mice (see genus *Alaria*).

The body of the mesocercaria is flat, pyriform, spinous. The excretory vesicle is small but flame cells are abundant. The oral and ventral suckers, pharynx and ceca are well developed. They differ from the metacercaria which follows them in the life cycle in having a less extensive excretory system and in the size and shape of the body. When eaten by a suitable host, the mesocercaria changes to either a diplostomulum or a tetracotyle type of metacercaria, the type depending upon the species involved. Johnson (1970) published a key to species of mesocercariae.

THE METACERCARIA

Except for a few species of strigeoid trematodes in which a mesocercaria is produced, the metacercaria is the larval stage between the cercaria and the adult. Cercariae of many species penetrate a second intermediate host and then encyst; however, some penetrate a lost but do not encyst (e.g. *Lepocreadium* and *Halipegus* spp.) Some species do not enter a second host but encyst on aquatic vegetation or on the shells of molluscs or the body surface of invertebrates. Regardless of procedure, the cercaria must eventually undergo anatomical and physiological changes to become an infective metacercaria.

Before encystment the tail of the cercaria detaches, only the body is involved in development of a metacercaria. Cyst membrane material is secreted by cystogenous glands in the cercaria. If the encysted metacercaria is in a second intermediate host, there is sometimes a host cellular response resulting in the formation of a capsule of connective tissue around the cyst membrane. Cysts are usually spherical or ovoid but exceptions are those in the families Notocotylidae and Paramphistomidae which are hemispherical (Fig. 50d) and some in the family Philophthalmidae are flask shaped. (Fig. 50c).

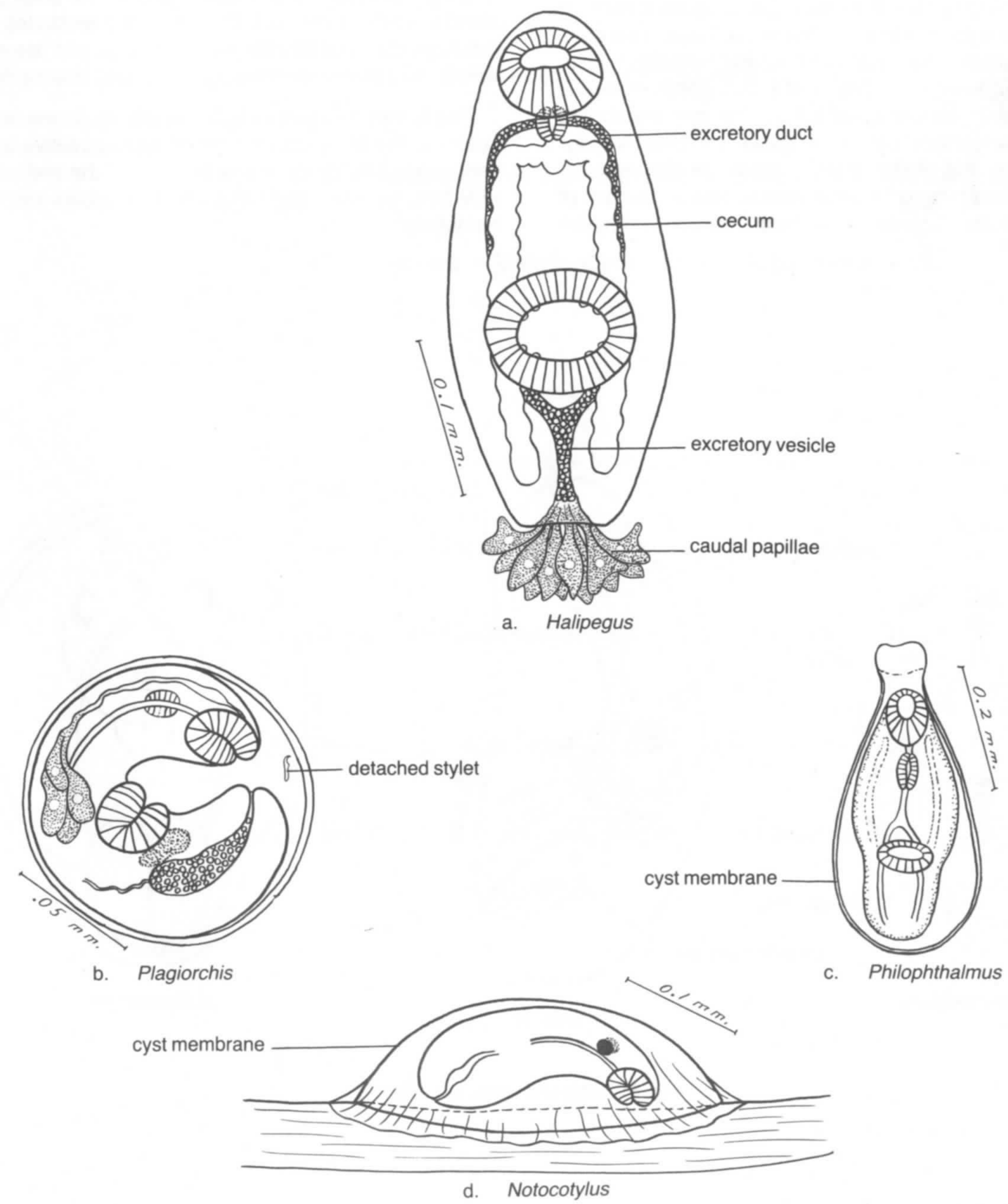


Fig. 50. Metacercariae.

The metacercaria differs from the cercaria in being larger and it frequently contains the primordia of the ovary, testes, vitellaria and cirrus sac. Glands of the cercaria are resorbed during development. When fully developed, the metacercaria is infective for the definitive host.

Metacercariae in the families Strigeidae and Diplostomidae have been studied intensively and numerous species described. Their common and generic names are identical. Three are of common occurrence in North America. The "tetracotyle", genus *Tetracotyle* (Fig. 51c), encysts in snails, leeches and fishes. The cyst membrane is thick and transparent, and fits snugly around the metacercaria, muscular pseudosuckers (cotylae) are located on each side of the oral sucker. The adults are intestinal parasites of birds, especially ducks. The "diplostomulum", genus *Diplostomulum* (Fig. 51a), inhabits the eyes, central nervous system and sometimes the coelom of fishes and amphibians, usually not encysted but the host might produce a capsule of connective tissue around them. Cotylae are located on each side of the oral sucker. The adults are intestinal parasites of piscivorous birds and mammals. The "neascus", genus *Neascus* (Fig. 51b), encysts in the viscera of fishes. The cyst membrane is thin and much larger than the metacercaria. The body is divided into distinct fore- and hindbody and contains an elaborate excretory system consisting of a large vesicle and a network of anastomosing tubules. Cotylae are absent. The adults develop in the intestine of piscivorous birds.

There are species of digenetic trematodes in which the life cycle has become shortened or abbreviated. Progenesis, or the attainment of sexual maturity by a metacercaria in a second intermediate host is one example of this. Elimination of the second intermediate host is another way of shortening a cycle. This can occur in several ways. In some species in the families Microphallidae and Plagiorchiidae the cercariae exhibit some anatomial degeneration in that they are weakly developed, nonmotile and tailless. They encyst and develop to metacercariae not only in the same mollusc but sometimes in the sporocyst in which they were produced, thus eliminating the need for a second intermediate host. In the families Schistosomatidae, Sanguinicolidae and Spirorchiidae the cercariae penetrate the tegument and mucous membranes of the definitive host, then gradually develop as schistosomules to the adult stage in the blood vessels of the host. Cercariae of trematodes in the families Azygiidae and Bivesiculidae are large and are eaten by the definitive host, thus eliminating the second intermediate host.

The table on page 21 illustrates the sequence of stages produced in the life cycle of several representative species. The brief reviews of life cycles in the body of the text will reveal the wide host selection and variation in life cycles among digenetic trematode.

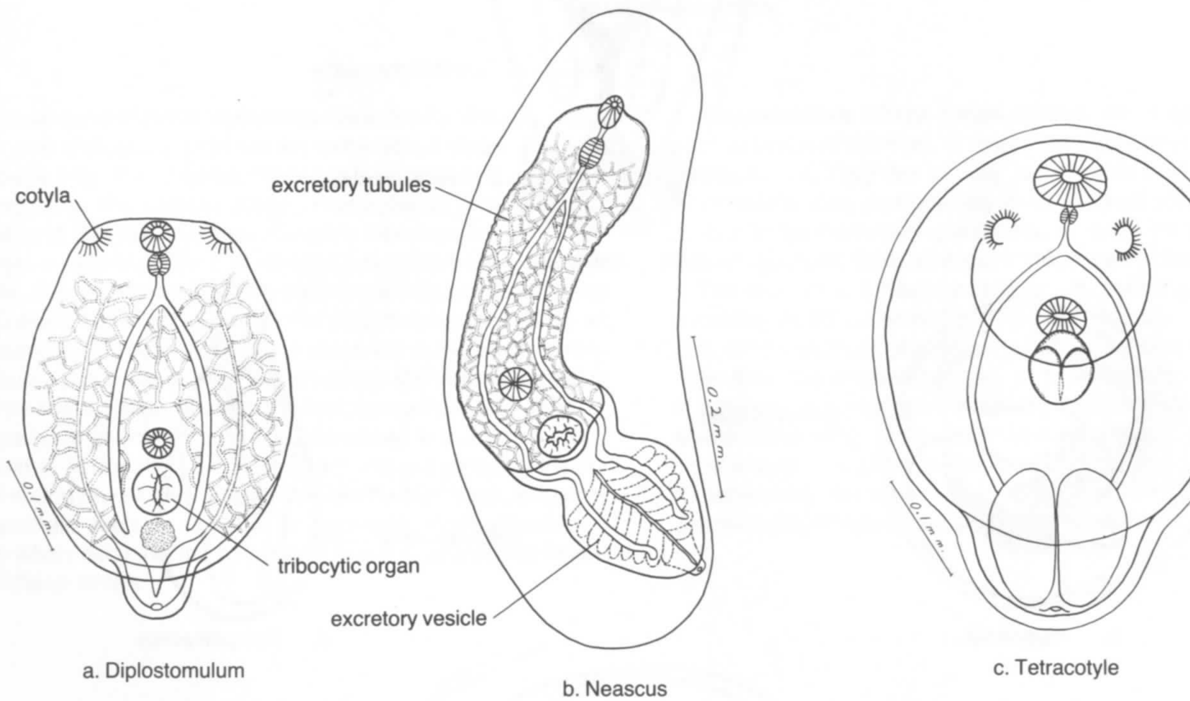
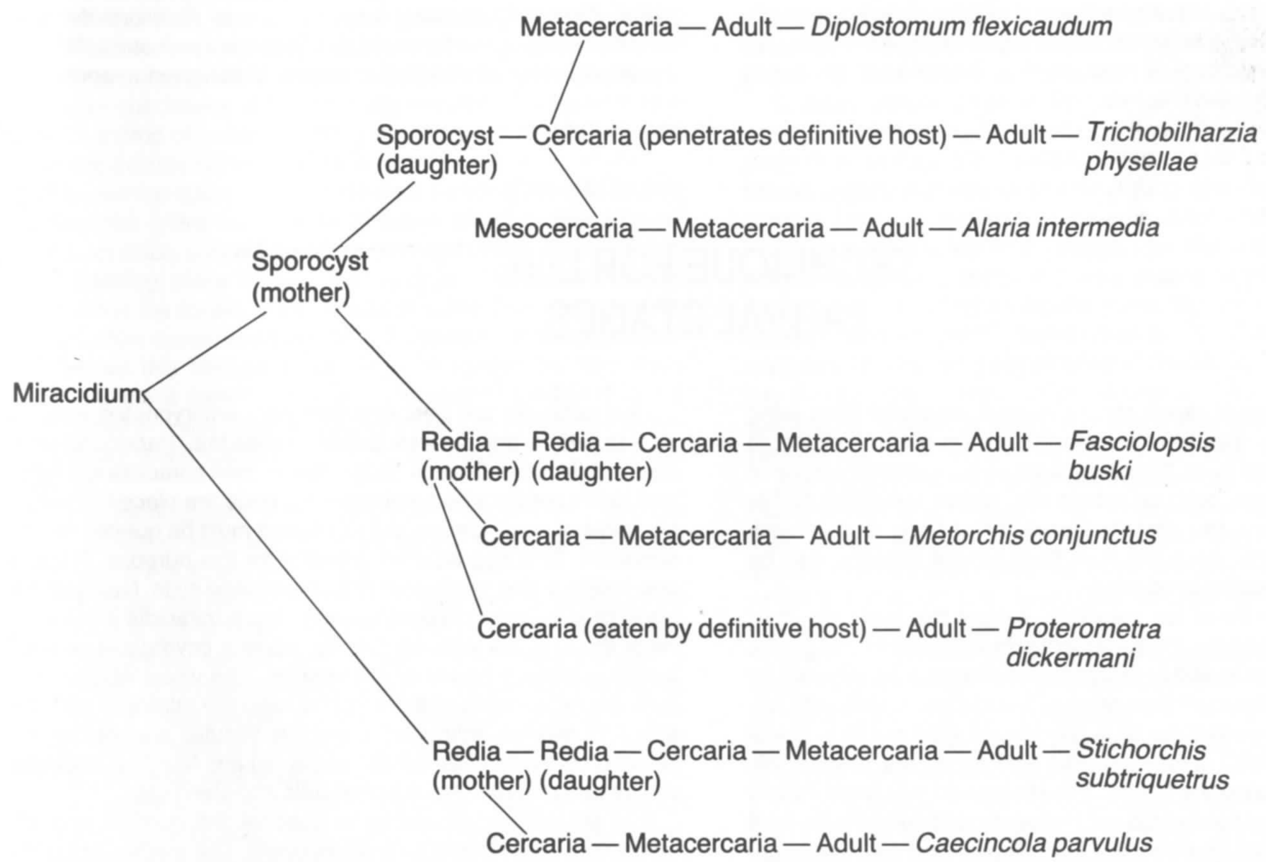


Fig. 51. Strigeoid metacercariae.

REPRESENTATIVE LIFE CYCLES OF DIGENETIC TREMATODES



PROGENESIS

Progenesis, or the development to sexual maturity in an invertebrate which might normally serve only as second intermediate host, is being found to occur in more and more species. To date, 14 families of digenetic trematodes are known to contain one or more progenetic species. In the families Allocreadiidae, Opecoelidae, Microphallidae, Dicrocoeliidae, Orchipedidae and Lecithodendriidae aquatic arthropods such as insects, amphipods and crayfishes are used as second intermediate host and one or more species in each of the above families have been reported as being progenetic in them.

Several species in the family Macroderoididae are progenetic in leeches, shrimp and crayfishes. Some species in the families Lissorchiidae, Paramphistomidae, Plagiorchiidae, Hemiuridae and Azygiidae can develop to sexual maturity in aquatic snails. One species in the family Brachylaimidae has been reported as being progenetic in terrestrial snails and another in the family Fellodistomidae can attain sexual maturity in marine lamellibranch molluscs. At least 15 species are known to be progenetic in molluscs.

Some progenetic adults are encysted in the coelom or in certain internal organs of the host. The cyst membrane or capsule is the result of a host cellular response. Release of eggs by such progenetic forms must await the death and disintegration of the host. There is some indication that progenesis is influenced by temperature, the incidence increasing with temperature. The development of progenetic forms is one way of shortening the life cycle in some species.

Some progenetic forms are also neotenic in that they retain one or more larval features such as pigmented eyespots and/or stylet. *Pseudallocreadium neotenicum* and *P. alloneotenicum* which develop in the larvae of diving beetles and caddisflies respectively serve as classical examples of this phenomenon.

TECHNIQUE FOR LIVE LARVAL STAGES

The anatomy of larval stages is best observed from living specimens. As digenetic trematodes always use a mollusc as first intermediate host, the latter serve as an excellent source of live larval stages, such as sporocysts, rediae, cercariae and in some instances the metacercariae. Gastropod and lamellibranch molluscs, collected from their natural habitats, can be kept alive in aerated pond water.

To examine them for parasites, extract the body of larger snails by grasping the muscular foot with forceps and pull gently. The smaller snails and lamellibranch molluscs are examined by first crushing the shell then remove the pieces of shell with forceps. Place the soft parts on a microscope slide in a drop of water or dilute NaCl solution (0.1%) and shred the tissues with needles to expose the larvae. The rediae and cercariae usually float free but the sporocysts are frequently embedded in the host tissues and must be dissected free. Rediae and sporocysts are nonmotile and can be observed more clearly when slightly flattened under a coverglass. Dyes such as neutral red or Nile blue sulphate can be used as 0.01 to 0.1 percent aqueous solutions to stain the germinal cells and nuclei. A drop of the dye solution is placed at the edge of the coverglass and allowed to run under slowly.

Naturally emerged cercariae can be obtained by placing live molluscs in dishes, vials or small jars of water for several hours or overnight. Stain and anaesthetize live cercariae by adding enough dilute neutral red or Nile blue sulphate to color the water. Cercariae become stained and relaxed in 10 to 15 minutes. Slight flattening under a coverglass helps bring flame cells, gland cells and excretory tubules into view.

Live miracidia are best obtained from embryonated eggs of trematodes in the families Echinostomatidae, Paramphistomidae, Schistosomatidae or Strigeidae as their miracidia are large and hatch readily when embryonated eggs are placed in water. Miracidia of most species are motile and must be quieted for observation. Thin egg albumin is useful for this purpose. Place a one-half inch ring of albumin on a microscope slide. Next place a small drop of water containing one or more miracidia in the center of the ring, stir with a toothpick, apply a coverglass and examine under low power of microscope. The viscid albumin will slow the movements of the cilia and keep the miracidia alive for about 15 minutes although the first five minutes are best for observation of flame cells. Dilute neutral red and Nile blue sulphate can be used to color the germinal cells and gland cells.

It is sometimes necessary to observe the number and arrangement of epidermal cells on miracidia. The method of Lynch (1934) is useful for this purpose. Squirt live miracidia from a medicine dropper into hot (65 to 70 C.) 0.5 percent aqueous solution of silver nitrate. Allow specimens to settle to the bottom of the container then carefully draw off the supernatant fluid with a small medicine dropper. Wash specimens in several changes of distilled water by alternate settling and drawing off the supernatant fluid as described above. Next place the dish in bright sunlight for 3 to 10 minutes. Wash one more time in water then clear in glycerine and mount in glycerine or glycerine jelly. Specimens can be left in glycerine for storage if desired. The margins of the epidermal cells become blackened and stand out clearly so that their arrangement and numbers can be observed (Fig. 7b.).

COLLECTION AND PRESERVATION OF ADULT TREMATODES

Vertebrate animals harbor most of the adult trematodes, whereas the larval stages are found mostly in molluscs, annelid worms and arthropods. The techniques employed for collection of the more delicate monogenetic trematodes differ from those used for collection of digenetic trematodes. Most species of monogenetic trematodes occur on the skin and gills of fishes. Only a few species have been found in the urinary tract of fishes or in the mouth, nasal cavities or urinary bladder of fishes, amphibians and reptiles (turtles). The small, delicate specimens in the families Dactylogyridae, Gyrodactylidae and Diplectanidae are best studied alive. Remove infested gills and pieces of skin and place them in fresh- or seawater, depending upon the habitat of the host. Separate and examine the gill filaments for live worms. Dislodge specimens with dissecting needles and transfer to a slide in a drop of water and apply a coverglass. Slight flattening will bring the internal organs into clearer view.

If preserved specimens are desired, freezing the gills or skin or even the entire fish for 6 to 24 hours will kill worms in a relaxed condition and will also loosen mucus that clings to them. After freezing, place tissues in a vial or jar of water for thawing, then shake the container for several minutes. Pour the liquid into a dish, allow specimens to settle and decant supernatant material. Repeat this several times. Remove specimens from sediment and place them in formalin acetic alcohol solution (F.A.A.). Later rinse in water, clear in glycerine and mount in glycerine jelly. Usually these specimens are not satisfactory for permanent mounts.

Small monogenetic trematodes from marine fishes are first killed in boiling seawater, flattened slightly under a coverglass and fixed in F.A.A. solution.

The larger and more muscular monogenetic trematodes from the skin and gills of fishes or from the urinary bladder of amphibians and reptiles can be removed with forceps. It is sometimes necessary to refrigerate these specimens overnight to loosen their hold on host tissues. For preservation, place specimens on a microscope slide in a drop of water, apply coverglass, then kill and preserve by adding several drops of F.A.A. solution at edge of coverglass and draw it through by placing piece of absorbent paper at opposite edge. After about 10 minutes transfer specimens to dish containing F.A.A. solution and leave them in this for at least one hour, then transfer to 70% ethyl alcohol for storage.

Formalin acetic alcohol solution (F.A.A.)

Ethyl alcohol (95%)	50 pts.
Commercial formalin (37%)	10 pts.
Glacial acetic acid	2 pts.
Distilled water	40 pts.

If live fish cannot be brought to the laboratory, small monogenetic trematodes can be preseved with some success outdoors by first relaxing them in 0.4% solution of chloretone (trichlortertiary butyl alcohol). The solvent for the chloretone can be fresh- or seawater depending upon the habitat of the host. First place gills, skin or fins of fishes in vials containing the chloretone solution for 30 to 45 minutes with intermittent shaking. Next add two parts of F.A.A. solution to one part of chloretone solution, shake container to mix then set aside for at least 15 minutes. Specimens can remain in this mixture indefinitely but for examination shake the material again, pour it into a dish, remove pieces of tissue, decant supernatant fluid then examine sediment for parasites. Pipette worms into 70% alcohol for storage.

Sexually mature digenetic trematodes inhabit the internal organs of vertebrates. First remove the individual organs and place them in separate dishes of water or saline solution. Open tubular organs with scissors or dissecting needles. Cut or shred other organs with scissors or needles. After soaking for a few minutes, grasp tissues with forceps and shake them to loosen parasites. Examine lining of hollow organs to which parasites might cling. Pull attached worms loose. Scrape lining of hollow organs with a scalpel to loosen small worms. If mucus is abundant, loosen it by using salt solution (1.0% NaCl) in place of water. Finally remove organs from dishes and decant and wash specimens repeatedly until supernatant fluid is clear. Examine sediment for worms, removing them with pipette or forceps.

The uterus of some trematodes contains so many eggs as to interfere with observation of other internal organs. Place live specimens in water for about 15 minutes before preservation for release of some eggs. Isolated specimens are ready for preservation in F.A.A. solution, fixing them as described for the larger monogenetic trematodes.

Small delicate trematodes deteriorate quickly in water but remain in good condition in saline solution (0.8-0.9%). These can be pipetted into 5% formalin brought to a boil and removed from the heat source before adding the specimens. It is usually undesirable to flatten these specimens.

Keeping Records: Host parasite records can be kept on 3 x 5 inch or larger index cards. A card is used for each host examined and each host is given a number which is recorded on the card and also on the label in the vial with the specimens. In addition to the number, the card should contain the scientific name of the host, locality in which it was collected, list of parasitized organs and number of parasites in each organ. When parasites are later identified their genus and species names are added to the card. The label in each vial should contain the host number and name of organ infected.

PROGENESIS

Progenesis, or the development to sexual maturity in an invertebrate which might normally serve only as second intermediate host, is being found to occur in more and more species. To date, 14 families of digenetic trematodes are known to contain one or more progenetic species. In the families Allocreadiidae, Opecoelidae, Microphallidae, Dicrocoeliidae, Orchipedidae and Lecithodendriidae aquatic arthropods such as insects, amphipods and crayfishes are used as second intermediate host and one or more species in each of the above families have been reported as being progenetic in them.

Several species in the family Macroderoididae are progenetic in leeches, shrimp and crayfishes. Some species in the families Lissorchiidae, Paramphistomidae, Plagiorchiidae, Hemiuridae and Azygiidae can develop to sexual maturity in aquatic snails. One species in the family Brachylaimidae has been reported as being progenetic in terrestrial snails and another in the family Fellodistomidae can attain sexual maturity in marine lamellibranch molluscs. At least 15 species are known to be progenetic in molluscs.

Some progenetic adults are encysted in the coelom or in certain internal organs of the host. The cyst membrane or capsule is the result of a host cellular response. Release of eggs by such progenetic forms must await the death and disintegration of the host. There is some indication that progenesis is influenced by temperature, the incidence increasing with temperature. The development of progenetic forms is one way of shortening the life cycle in some species.

Some progenetic forms are also neotenic in that they retain one or more larval features such as pigmented eyespots and/or stylet. *Pseudallocreadium neotenicum* and *P. alloneotenicum* which develop in the larvae of diving beetles and caddisflies respectively serve as classical examples of this phenomenon.

TECHNIQUE FOR LIVE LARVAL STAGES

The anatomy of larval stages is best observed from living specimens. As digenetic trematodes always use a mollusc as first intermediate host, the latter serve as an excellent source of live larval stages, such as sporocysts, rediae, cercariae and in some instances the metacercariae. Gastropod and lamellibranch molluscs, collected from their natural habitats, can be kept alive in aerated pond water.

To examine them for parasites, extract the body of larger snails by grasping the muscular foot with forceps and pull gently. The smaller snails and lamellibranch molluscs are examined by first crushing the shell then remove the pieces of shell with forceps. Place the soft parts on a microscope slide in a drop of water or dilute NaCl solution (0.1%) and shred the tissues with needles to expose the larvae. The rediae and cercariae usually float free but the sporocysts are frequently embedded in the host tissues and must be dissected free. Rediae and sporocysts are nonmotile and can be observed more clearly when slightly flattened under a coverglass. Dyes such as neutral red or Nile blue sulphate can be used as 0.01 to 0.1 percent aqueous solutions to stain the germinal cells and nuclei. A drop of the dye solution is placed at the edge of the coverglass and allowed to run under slowly.

Naturally emerged cercariae can be obtained by placing live molluscs in dishes, vials or small jars of water for several hours or overnight. Stain and anaesthetize live cercariae by adding enough dilute neutral red or Nile blue sulphate to color the water. Cercariae become stained and relaxed in 10 to 15 minutes. Slight flattening under a coverglass helps bring flame cells, gland cells and excretory tubules into view.

Live miracidia are best obtained from embryonated eggs of trematodes in the families Echinostomatidae, Paramphistomidae, Schistosomatidae or Strigeidae as their miracidia are large and hatch readily when embryonated eggs are placed in water. Miracidia of most species are motile and must be quieted for observation. Thin egg albumin is useful for this purpose. Place a one-half inch ring of albumin on a microscope slide. Next place a small drop of water containing one or more miracidia in the center of the ring, stir with a toothpick, apply a coverglass and examine under low power of microscope. The viscid albumin will slow the movements of the cilia and keep the miracidia alive for about 15 minutes although the first five minutes are best for observation of flame cells. Dilute neutral red and Nile blue sulphate can be used to color the germinal cells and gland cells.

It is sometimes necessary to observe the number and arrangement of epidermal cells on miracidia. The method of Lynch (1934) is useful for this purpose. Squirt live miracidia from a medicine dropper into hot (65 to 70 C.) 0.5 percent aqueous solution of silver nitrate. Allow specimens to settle to the bottom of the container then carefully draw off the supernatant fluid with a small medicine dropper. Wash specimens in several changes of distilled water by alternate settling and drawing off the supernatant fluid as described above. Next place the dish in bright sunlight for 3 to 10 minutes. Wash one more time in water then clear in glycerine and mount in glycerine or glycerine jelly. Specimens can be left in glycerine for storage if desired. The margins of the epidermal cells become blackened and stand out clearly so that their arrangement and numbers can be observed (Fig. 7b.).

COLLECTION AND PRESERVATION OF ADULT TREMATODES

Vertebrate animals harbor most of the adult trematodes, whereas the larval stages are found mostly in molluscs, annelid worms and arthropods. The techniques employed for collection of the more delicate monogenetic trematodes differ from those used for collection of digenetic trematodes. Most species of monogenetic trematodes occur on the skin and gills of fishes. Only a few species have been found in the urinary tract of fishes or in the mouth, nasal cavities or urinary bladder of fishes, amphibians and reptiles (turtles). The small, delicate specimens in the families Dactylogyridae, Gyrodactylidae and Diplectanidae are best studied alive. Remove infested gills and pieces of skin and place them in fresh- or seawater, depending upon the habitat of the host. Separate and examine the gill filaments for live worms. Dislodge specimens with dissecting needles and transfer to a slide in a drop of water and apply a coverglass. Slight flattening will bring the internal organs into clearer view.

If preserved specimens are desired, freezing the gills or skin or even the entire fish for 6 to 24 hours will kill worms in a relaxed condition and will also loosen mucus that clings to them. After freezing, place tissues in a vial or jar of water for thawing, then shake the container for several minutes. Pour the liquid into a dish, allow specimens to settle and decant supernatant material. Repeat this several times. Remove specimens from sediment and place them in formalin acetic alcohol solution (F.A.A.). Later rinse in water, clear in glycerine and mount in glycerine jelly. Usually these specimens are not satisfactory for permanent mounts.

Small monogenetic trematodes from marine fishes are first killed in boiling seawater, flattened slightly under a coverglass and fixed in F.A.A. solution.

The larger and more muscular monogenetic trematodes from the skin and gills of fishes or from the urinary bladder of amphibians and reptiles can be removed with forceps. It is sometimes necessary to refrigerate these specimens overnight to loosen their hold on host tissues. For preservation, place specimens on a microscope slide in a drop of water, apply coverglass, then kill and preserve by adding several drops of F.A.A. solution at edge of coverglass and draw it through by placing piece of absorbent paper at opposite edge. After about 10 minutes transfer specimens to dish containing F.A.A. solution and leave them in this for at least one hour, then transfer to 70% ethyl alcohol for storage.

Formalin acetic alcohol solution (F.A.A.)

Ethyl alcohol (95%)	50 pts.
Commercial formalin (37%)	10 pts.
Glacial acetic acid	2 pts.
Distilled water	40 pts.

If live fish cannot be brought to the laboratory, small monogenetic trematodes can be preseved with some success outdoors by first relaxing them in 0.4% solution of chloretone (trichlortertiary butyl alcohol). The solvent for the chloretone can be fresh- or seawater depending upon the habitat of the host. First place gills, skin or fins of fishes in vials containing the chloretone solution for 30 to 45 minutes with intermittent shaking. Next add two parts of F.A.A. solution to one part of chloretone solution, shake container to mix then set aside for at least 15 minutes. Specimens can remain in this mixture indefinitely but for examination shake the material again, pour it into a dish, remove pieces of tissue, decant supernatant fluid then examine sediment for parasites. Pipette worms into 70% alcohol for storage.

Sexually mature digenetic trematodes inhabit the internal organs of vertebrates. First remove the individual organs and place them in separate dishes of water or saline solution. Open tubular organs with scissors or dissecting needles. Cut or shred other organs with scissors or needles. After soaking for a few minutes, grasp tissues with forceps and shake them to loosen parasites. Examine lining of hollow organs to which parasites might cling. Pull attached worms loose. Scrape lining of hollow organs with a scalpel to loosen small worms. If mucus is abundant, loosen it by using salt solution (1.0% NaCl) in place of water. Finally remove organs from dishes and decant and wash specimens repeatedly until supernatant fluid is clear. Examine sediment for worms, removing them with pipette or forceps.

The uterus of some trematodes contains so many eggs as to interfere with observation of other internal organs. Place live specimens in water for about 15 minutes before preservation for release of some eggs. Isolated specimens are ready for preservation in F.A.A. solution, fixing them as described for the larger monogenetic trematodes.

Small delicate trematodes deteriorate quickly in water but remain in good condition in saline solution (0.8-0.9%). These can be pipetted into 5% formalin brought to a boil and removed from the heat source before adding the specimens. It is usually undesirable to flatten these specimens.

Keeping Records: Host parasite records can be kept on 3 x 5 inch or larger index cards. A card is used for each host examined and each host is given a number which is recorded on the card and also on the label in the vial with the specimens. In addition to the number, the card should contain the scientific name of the host, locality in which it was collected, list of parasitized organs and number of parasites in each organ. When parasites are later identified their genus and species names are added to the card. The label in each vial should contain the host number and name of organ infected.

PREPARATION OF STAINED WHOLE MOUNTS

Although many staining techniques are known for whole mounts, only two of the most reliable are presented here.

Ehrlich's Hematoxylin Stain

Formula: Powdered hematoxylin .... 2 gm.
Ethyl alcohol (100%) .... 100 ml.
Glycerol .... 100 ml.
Glacial acetic acid .... 10 ml.
Distilled water .... 100 ml.
Aluminum potassium sulphate .... 10 gm.

First dissolve the hematoxylin in the alcohol, then add the glycerol and the acetic acid. Next dissolve the alum in warm distilled water, then slowly pour the alum solution into the hematoxylin solution with stirring. This is a stock solution that should ripen for about one month. For use, dilute one part of ripened stock solution with three to four parts of 35% alcohol. Staining procedure: Transfer specimens from 70% alcohol to 35% alcohol for 10 to 15 minutes then place them in diluted staining solution for 15 to 20 minutes. Remove excess stain by soaking specimens in 70% alcohol to which one or two drops of strong hydrochloric acid have been added. Allow specimens to remain in this until parenchyma cells are free of stain and internal organs such as testes, ovary and vitelline glands become pink. Now transfer specimens to 70% alcohol to which a few crystals of sodium bicarbonate have been added. This alkaline solution will cause internal organs to become dark blue. After one-half hour, transfer specimens to 95% alcohol (30 min.) and then to 100% alcohol (30 min.). Finally clear in toluene or xylene (10 to 15 min.), then place specimens on slide, add one or two drops of resinous mounting medium such as gum damar or a synthetic resin and apply coverglass.

Gower's Acetic Carmine Stain

Formula: Add 10 gm. of powdered carmine to 100 ml. of 45% acetic acid. Dissolve carmine by heating acid until it starts to boil. Allow solution to cool, then filter through coarse filter paper. Save filter paper containing residue and spread it out to dry. Store dried residue in vial or small jar until needed.

Preparation of Staining Solution:

Dried acidified carmine residue .... 1 gm.
Aluminum ammonium sulphate .... 10 gm
Distilled water .... 200 ml.

Dissolve the alum in warm distilled water then add the powdered carmine. When cool, filter into a glass-stoppered bottle, add a crystal of thymol for preservation. Store in refrigerator.

Staining procedure: Transfer preserved specimens from 70% alcohol to distilled water for 10 to 15 minutes, then place them in staining solution for about 8 hours or overnight, the time depending upon the size of the specimens. Next pour off the staining solution and save it for later use. Rinse specimens in two changes of distilled water. Dehydrate through 35% and then 70% alcohol (15 min. each). Remove excess stain in 70% alcohol to which 2 or 3 drops of strong hydrochloric acid have been added. Continue destaining until the parenchyma cells are free of stain and internal organs are light pink. Replace the acid alcohol with 70% alcohol to which a few crystals of sodium bicarbonate have been added. After 30 to 60 minutes place specimens in 95% alcohol (30 min.) then 100% alcohol (30 min.). Finally clear in toluene or xylene (10 to 15 min.), then mount in resinous mounting medium.

Labeling the Microscope Slide

The slide label, pasted at one end of the slide, should contain the genus and species name of the parasite, the habitat of the parasite, the name of the host, the locality in which the host was collected, date of collection and the host number as recorded on the record card. Use waterproof ink for recording this information. In some cases two labels might be needed.

Class Trematoda Rudolphi, 1808

Key to Subclasses

1a. **Endoparasites of all groups of vertebrates and some invertebrates; holdfast organs in form of oral and ventral suckers; life cycle indirect, involving two or more hosts; reproduction by larval stages in a mollusc; larva in egg is a miracidium. ...Subclass Digenea ...p. 78**

1b. **Ectoparasites or occasionally endoparasites; holdfast organs not in form of oral and ventral suckers; life cycle usually direct, involving one host in most cases; no reproduction by larval stages; 2**

2a. **Adults usually endoparasites of fishes, turtles or gastropod or lamellibranch molluscs; holdfast organ in the form of a large ventral disc containing septa and loculi, conical papillae, transverse rugae or a linear series of ventral suckers; buccal funnel at anterior end of body; larva in egg is a cotylocidium. .... Subclass Aspidogastrea .... p. 73**

2b. **Usually ectoparasites of fishes, occasionally endoparasites of frogs and turtles; holdfast organs in the form of a prohaptor containing small buccal suckers, an oral sucker, head organs, preoral suckers or marginal gland ducts from cephalic glands; opisthaptor at posterior end of body may contain an assortment of clamps, suckers, anchors and hooks; larva in egg is an onchomiracidium. .... Subclass Monogenea .... p. 32**

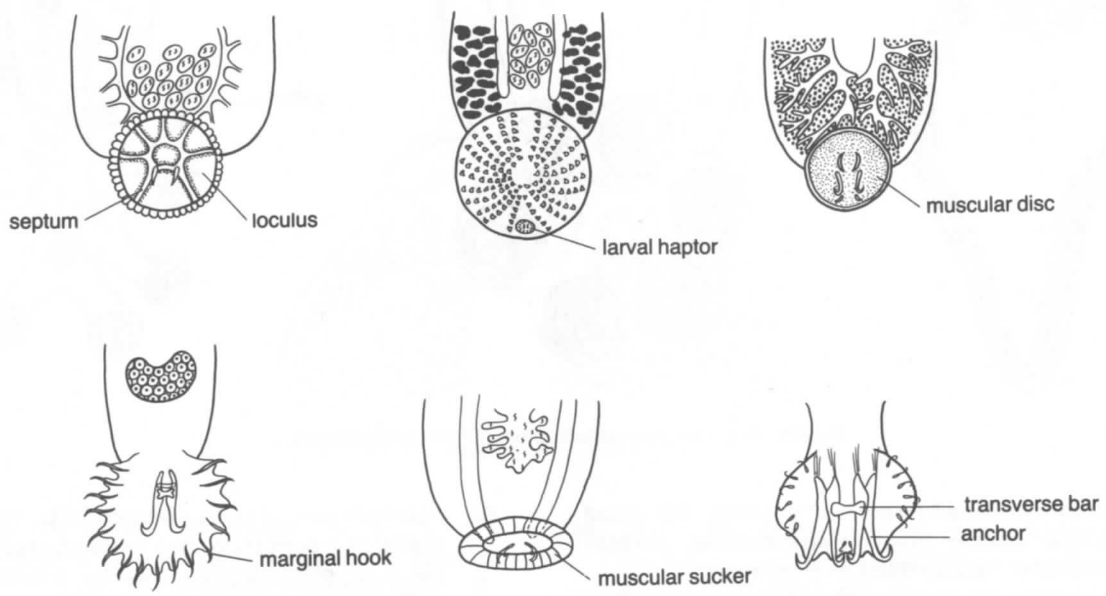


Fig. 52. Representative opisthaptors of Monopisthocotylea.

Subclass Monogenea Carus, 1863

Key to Suborders, Superfamilies and Families

1a. **Opisthaptor a muscular disc, with or without loculi; a muscular sucker or membranous and having one or two pairs of anchors, transverse bars and marginal hooks; genito-intestinal canal absent (Fig. 52). ....Suborder Monopisthocotylea 2**

1b. **Opisthaptor composed of one or more pairs of suckers or clamps; genito-intestinal canal present (Fig. 53). .... Suborder Polyopisthocotylea 13**

2a. **Opisthaptor membranous, usually with one or two pairs of anchors and one to three transverse bars; prohaptor contains marginal head organs or lappets. 3**

2b. **Opisthaptor in form of a muscular disc or a single sucker, with or without anchors but if anchors are present they are not supported by transverse bars; prohaptor may contain a pair of preoral suckers, many marginal gland ducts or head organs. 7**

3a. **Intestine a single cecum. 4**

3b. **Intestine composed of two ceca. 5**

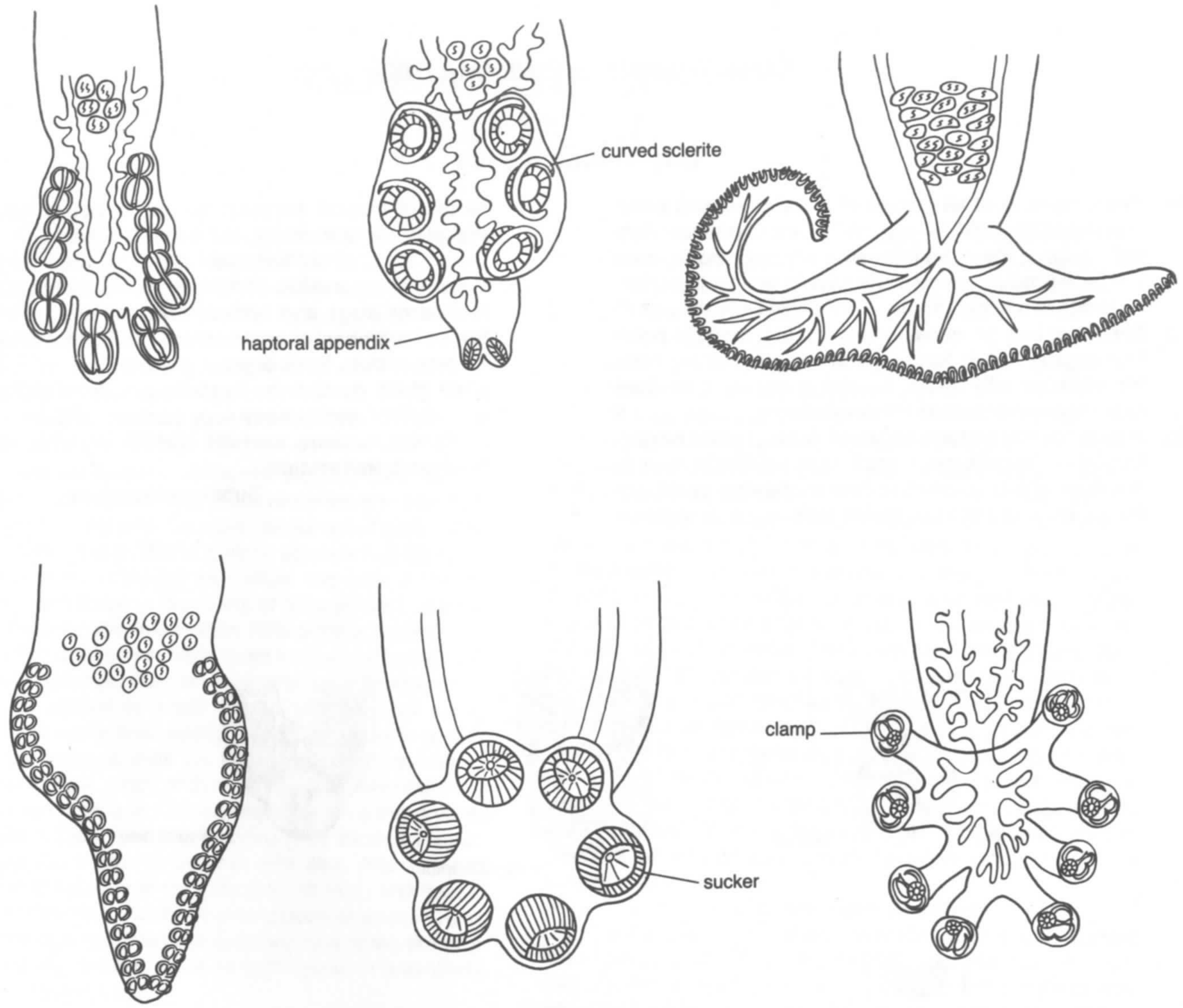


Fig. 53. Representative opisthaptors of Polyopisthocotylea.

4a. **Opisthaptor contains two pairs of anchors with broad bases and a butterfly-shaped transverse bar; parasitic on the gills of salmonid fishes (Fig. 104) ....Superfamily Tetraonchoidea .... Family Tetraonchidae .... p. 41**

4b. **Opisthaptor contains one pair of anchors; two V-shaped transverse bars and many radiating tubular structures; parasite of marine fishes .... Superfamily Dactylogyroidea (in part) .... Family Bothitrematidae .... p. 40**

5a. **Viviparous (embryo in uterine pouch); vitelline glands absent or weakly developed; opisthaptor with scalloped margin and 16 marginal hooks, one pair of anchors and one or two transverse bars. .... Superfamily Gyrodactyloidea .... Family Gyrodactylidae .... p. 32**

5b. **Oviparous; vitelline glands well developed; opisthaptor with 14 to 16 marginal hooks, one or two pairs of anchors and one to three transverse bars .... Superfamily Dactylogyroidea 6**

6a. **Posterior part of body covered with recurved spines; transverse bars long; two pairs of anchors; squamodiscs or plaques may also be present (Figs. 100-103). .... Family Diplectanidae .... p. 41**

6b. **Body without recurved spines, squamodiscs or plaques; opisthaptor contains one or two pairs of anchors; transverse bars short; marginal hooks present .... Family Dactylogyridae .... p. 32**

7a. **Opisthaptor a flat disc with many radiating rows of spines; small larval haptor with hooks also present; anchors absent; parasitic on skin and gills of elasmobranchs. (Figs. 136, 137). ....Superfamily Acanthocotyloidea .... Family Acanthocotylidae .... p. 50**

7b. **Opisthaptor not as described above. 8**

8a. **Opisthaptor a concave muscular disc without anchors or hooks; intestine a single cecum; prohaptor composed of one pair of head organs; hyperparasitic on marine parasitic copepods (Fig. 138). .... Superfamily Udonelloidea ... Family Udonellidae .... p. 51**

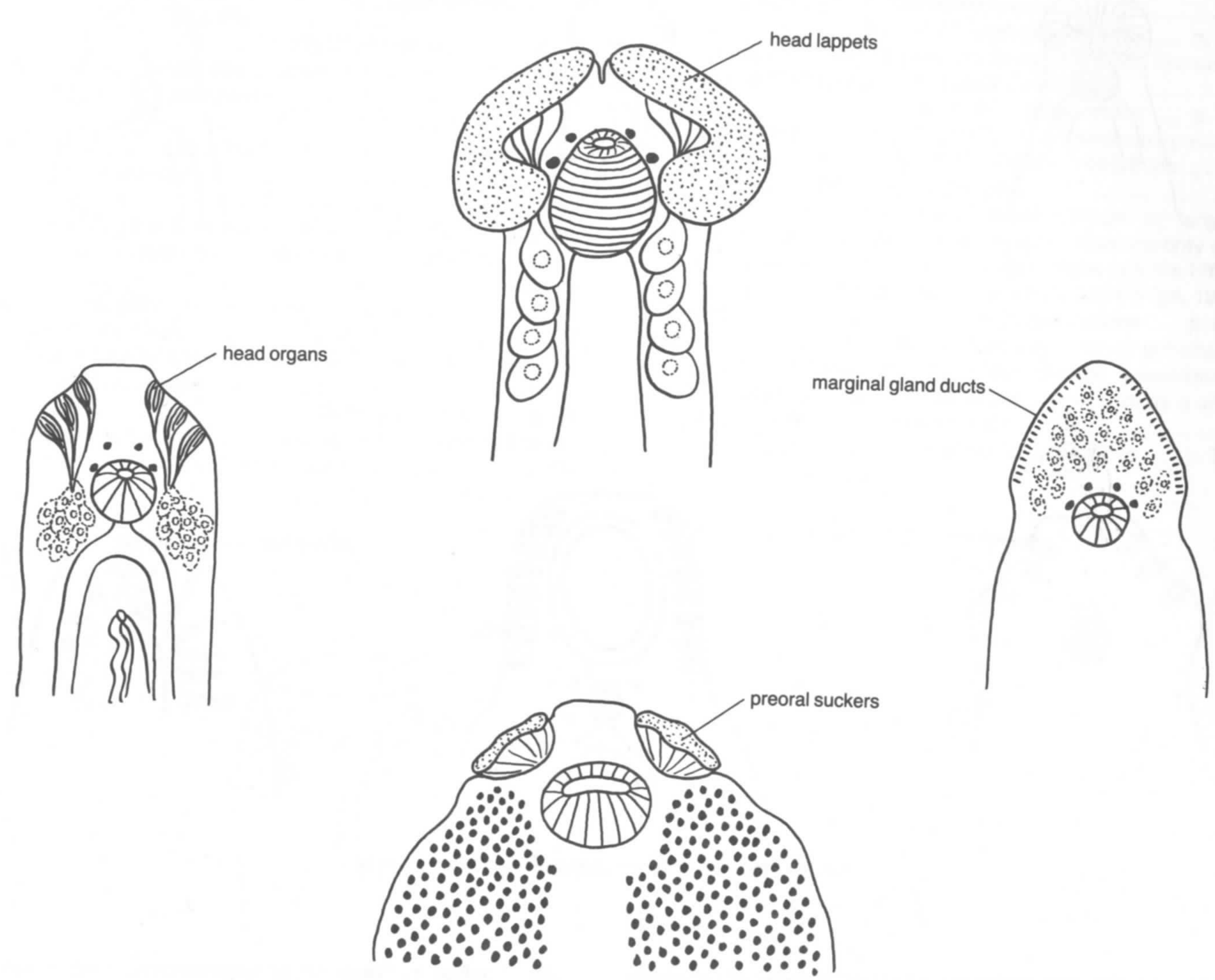


Fig. 54. Prohaptors of Monopisthocotylea.

8b. **Opisthaptor and habitat not as described above; intestine composed of two ceca; parasitic on marine fishes. .... Superfamily Capsaloidea 9**

9a. **Opisthaptor an oval muscular cup or two muscular flaps; anchors and hooks absent; prohaptor in form of two buccal suckers (Figs. 133, 134). .... Family Microbothriidae .... p. 50**

9b. **Opisthaptor not as described above; one or more pairs of anchors present; buccal suckers absent. 10**

10a. **Opisthaptor composed of a muscular sucker with one pair of anchors; prohaptor in form of two preoral suckers, an oral sucker or head organs. .... Family Loimoidae .... p. 49**

10b. **Opisthaptor discoid, with or without septa and loculi. 11**

11a. **Opisthaptor with two or three pairs of anchors; septa and loculi present or absent; prohaptor composed of two preoral lobes, suckers, pseudosuckers or glandular areas. .... Family Capsalidae .... p. 43**

11b. **Opisthaptor with one pair of anchors and 14 marginal hooks; septa and loculi present. 12**

12a. **Opisthaptor septate with 10-12 marginal and one central loculus; prohaptor contains numerous marginal gland ducts; two pairs of eyespots present; parasitic on gills of suck fish of the family Echeneidae (Fig. 129). .... Family Dionchidae .... p. 46**

12b. **Opisthaptor septate with *more* or *less* than 10 marginal loculi, submarginal loculi also sometimes present; marginal hooks usually present; prohaptor composed of a single sucker, preoral flap, head organs or diffuse marginal gland ducts; parasitic on skin and gills or in nasal cavities of marine fishes (Fig. 55). .... Family Monocotylidae .... p. 46**

13a. **Opisthaptor contains either two or six muscular suckers; prohaptor either a single oral sucker or a pair of ventral bothria. .... Superfamily Polystomatoidea 14**

13b. **Opisthaptor contains eight or more clamps; prohaptor a pair of small buccal suckers or a weakly developed oral sucker. 17**

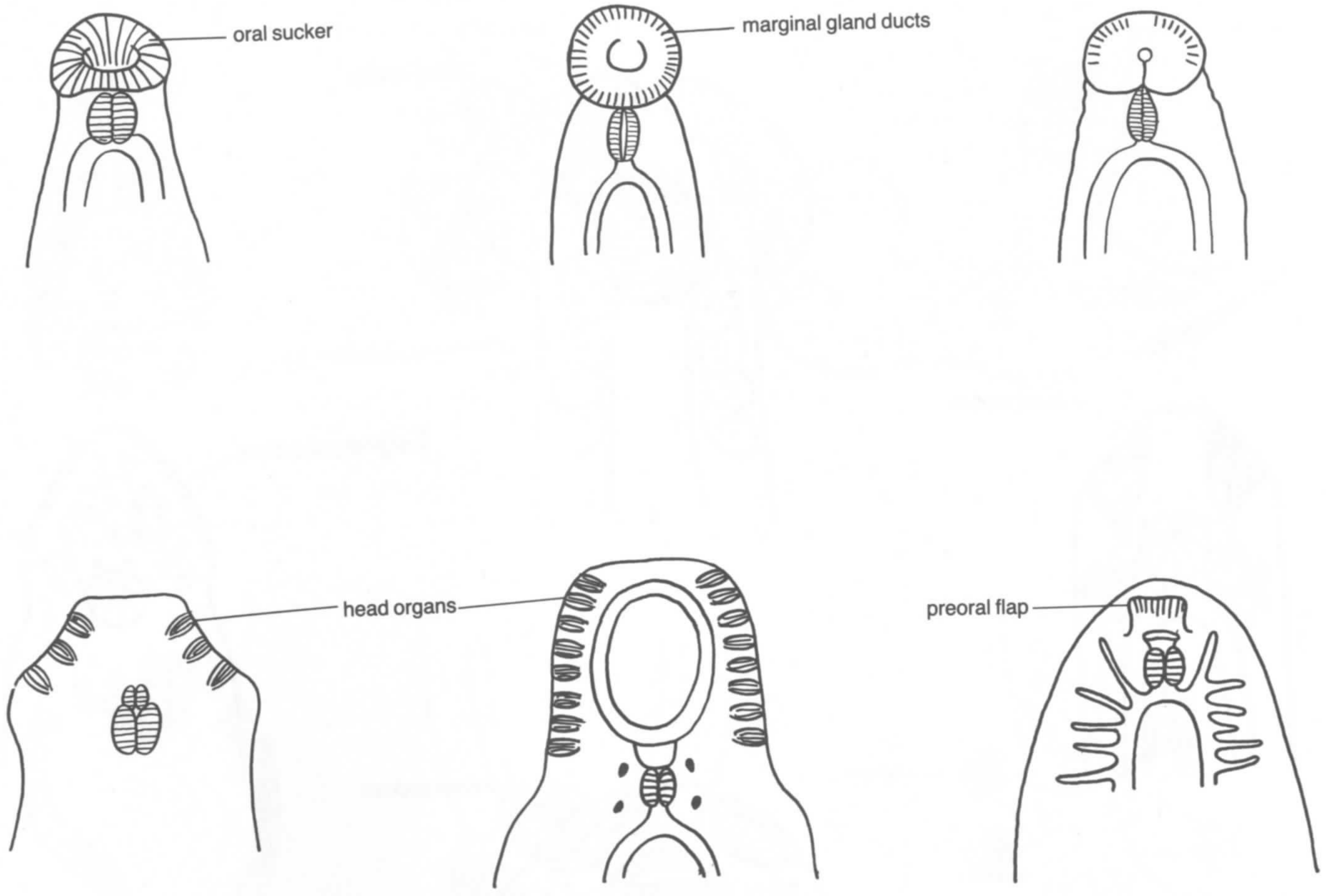


Fig. 55. Representative prohaptors of family Monocotylidae.

14a. Opisthaptor contains six muscular suckers, each with a curved sclerite; haptoral appendix also present. ...15
14b. Opisthaptor with six suckers but curved sclerites and haptoral appendix absent. 16
15a. Prohaptor an oral sucker; haptoral appendix contains one pair of small suckers and one pair of small anchors (Fig. 53b.). ....Family Hexabothriidae....p. 54
15b. Prohaptor a pair of ventral bothria; haptoral appendix contains three pairs of large anchors but no suckers (Fig. 152). .... Family Diclybothriidae .... p. 54
16a. Opisthaptor contains six muscular suckers (Fig. 53e). .... Family Polystomatidae .... p. 52
16b. Opisthaptor contains two muscular suckers (Fig. 153). .... Family Sphyranuridae .... p. 56
17a. Opisthaptor contains four pairs of clamps (muscular suckers also present in Hexostomatidae). 18
17b. Opisthaptor contains more than four pairs of clamps. .... Superfamily Microcotyloidea 24
18a. Clamps symmetrical, composed of three U-shaped sclerites; body divided into wide anterior and narrow posterior regions; oral sucker weakly developed; uterus arranged in several longitudinal folds; parasitic on gills of chimaeras (Holocephali). (Fig. 155). .... Superfamily Chimaericoloidea .... Family Chimaericolidae .... p. 57
18b. Clamps symmetrical or asymmetrical, one quadrant of clamp may contain a muscular and/or a spinous or denticulate pad; muscular suckers might also be present with clamps; wall of clamp may contain riblike sclerites. .... Superfamily Diclidophoroidea 19
19a. Opisthaptor indistinctly set off from body; clamps weakly developed, each composed of three X-shaped sclerites embedded in a muscular sucker (Fig. 180). .... Family Hexostomatidae .... p. 64
19b. Clamps well developed; muscular suckers absent. 20
20a. Clamps guitar-, firetong- or oblong-shaped; buccal cavity large, terminal, cupshaped; two buccal suckers open into buccal cavity (Fig. 56). .... Family Macrovalvitrematidae .... p. 63
20b. Clamps not as described above; buccal cavity small, opens ventrally. 21
21a. One quadrant of each clamp provided with a denticulate, muscular or spinous pad; clamps pedunculate. 22
21b. Clamps without pads of any kind. 23
22a. Clamps symmetrical in structure, one quadrant contains a denticulate (toothed) pad; ribs absent (Fig. 57). .... Family Dactylocotylidae .... p. 62

22b. Clamps asymmetrical in structure, one quadrant provided with a muscular sucker and/or spinous pad; ribs present (Fig. 58). .... Family Diclidophoridae .... p. 57
23a. Clamps contain two U-shaped sclerites; clamps may be pedunculate or sessile (Fig. 59). .... Family Mazocraeidae .... p. 59
23b. Clamps contain a median sclerite (spring) and curved lateral sclerites and spurs; clamps always sessile (Fig. 60). .... Family Discocotylidae .... p. 59
24a. Opisthaptor truncate or fishtail-shaped; clamps arranged in two end-to-end rows across opisthaptor. 25
24b. Opisthaptor wedge-shaped or clamps mounted directly on sides of body. 27
25a. Opisthaptor truncate: rows of clamps separated by anchors; ovary U- or J-shaped. .... Family Axinidae .... p. 66
25b. Opisthaptor fishtail-shaped; rows of clamps not separated by anchors; anchors absent. 26
26a. Clamps all of same kind, longer than wide, asymmetrical in structure (Fig. 207). .... Family Allopyragraphoridae .... p. 72
26b. Clamps of two types, microcotylid and firetong-shaped; symmetrical in structure (Fig. 61). .... Family Pyragraphoridae .... p. 72
27a. Clamps all of microcotylid type, no accessory sclerites, no ribs (Fig. 62). ..p. Family Microcotylidae ..p. 64
27b. Clamps not of microcotylid type. 28
28a. Opisthaptor asymmetrical, more clamps or larger clamps on one side than on the other (clamps only on one side in genus *Leuresthicola*); median sclerite bifid or trifid at tips; ovary has inverted U-shape (Figs. 197, 198) .... Family Heteraxinidae .... p. 66
28b. Clamps usually contain ribs and accessory sclerites; median sclerite usually wide; clamps sometimes mounted directly on sides of body instead of on a distinct opisthaptor; ovary folded (Fig. 63). .... Family Gastrocotylidae .... p. 70

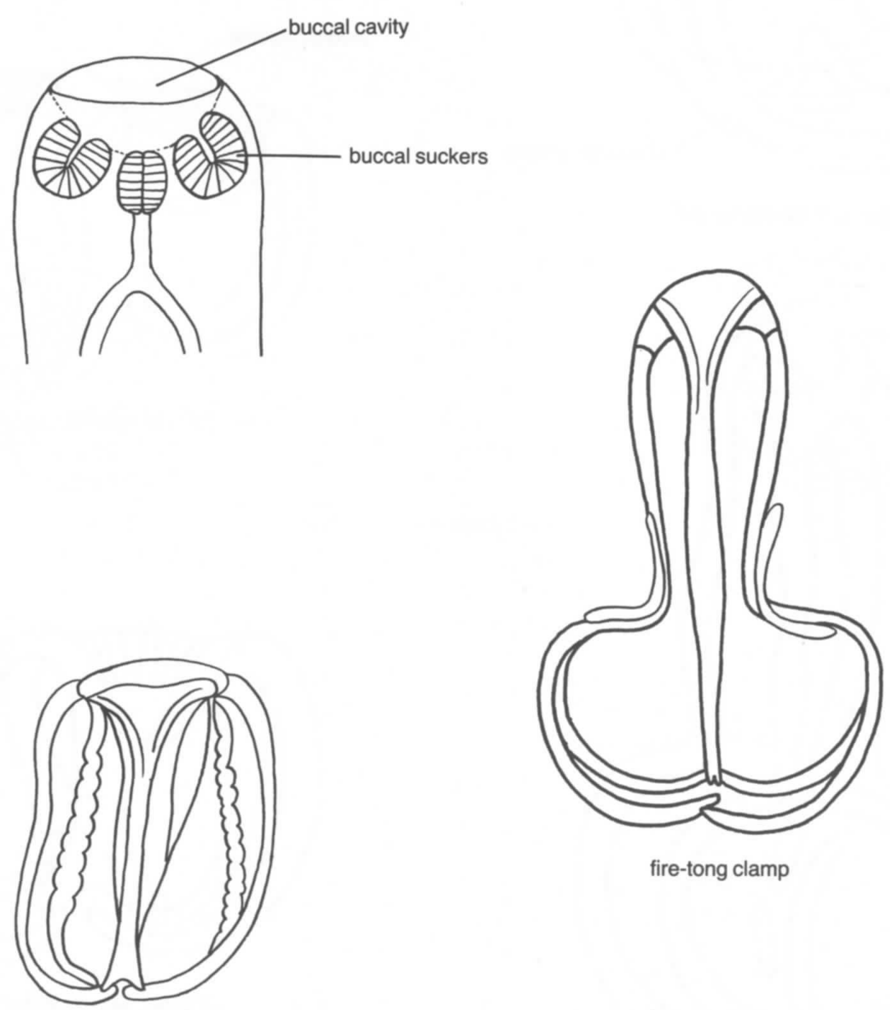


Fig. 56. Family Macrovalvitrematidae.

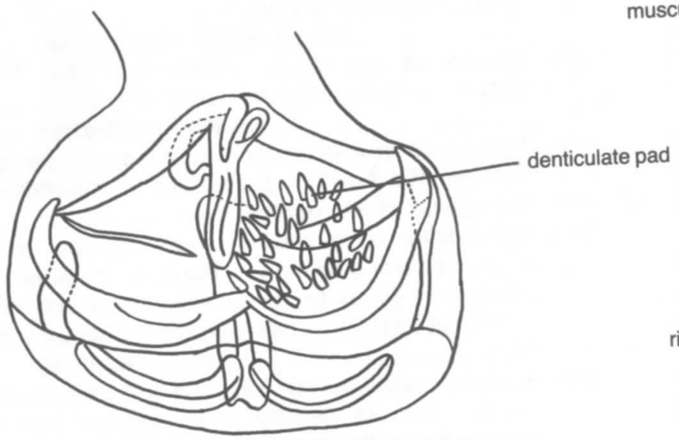


Fig. 57. Clamp of Dactylocotylidae.

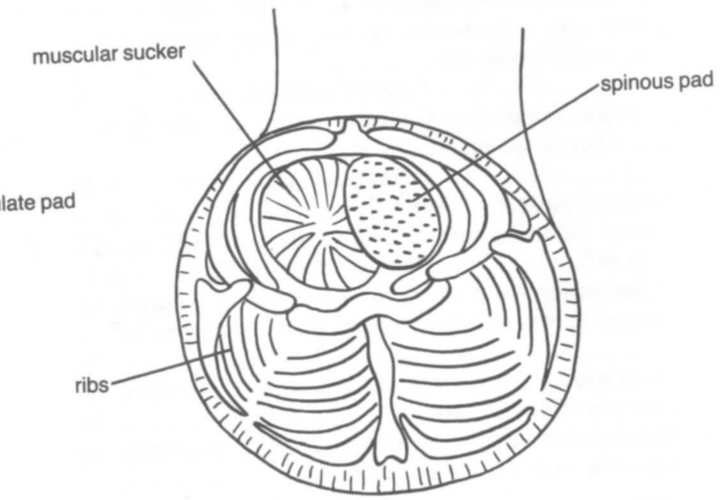


Fig. 58. Clamps of Diclidophoridae.

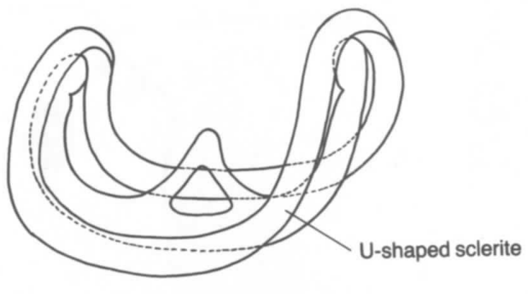


Fig. 59. Clamp of Mazocraeidae.

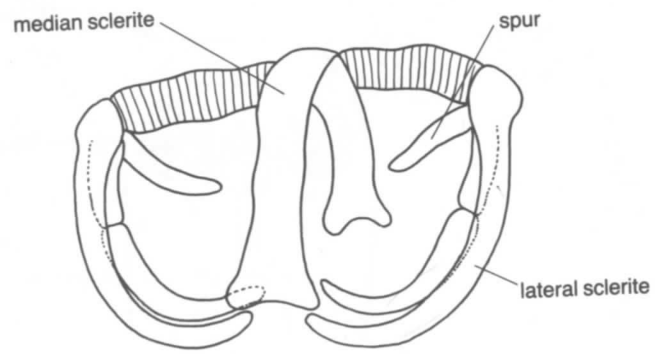


Fig. 60. Clamp of Discocotylidae.

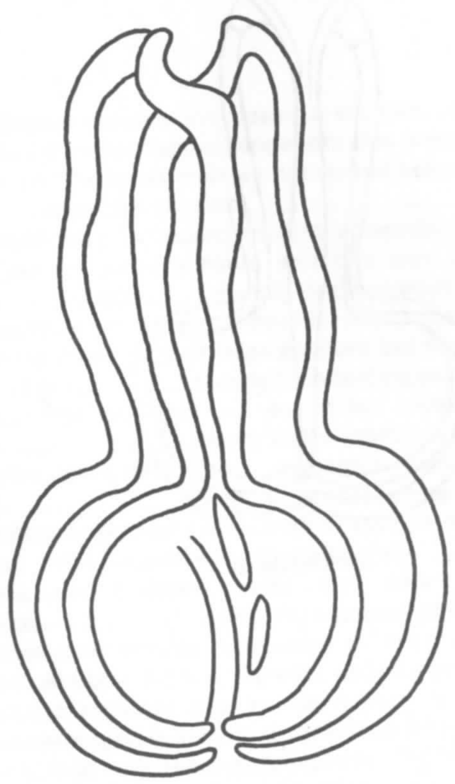


Fig. 61. Clamp of Pyragraphoridae.

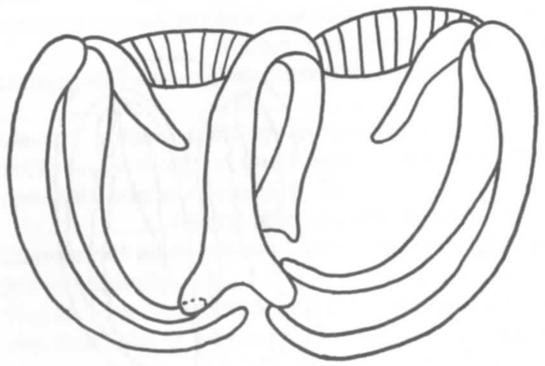


Fig. 62. Microcotylid clamp.

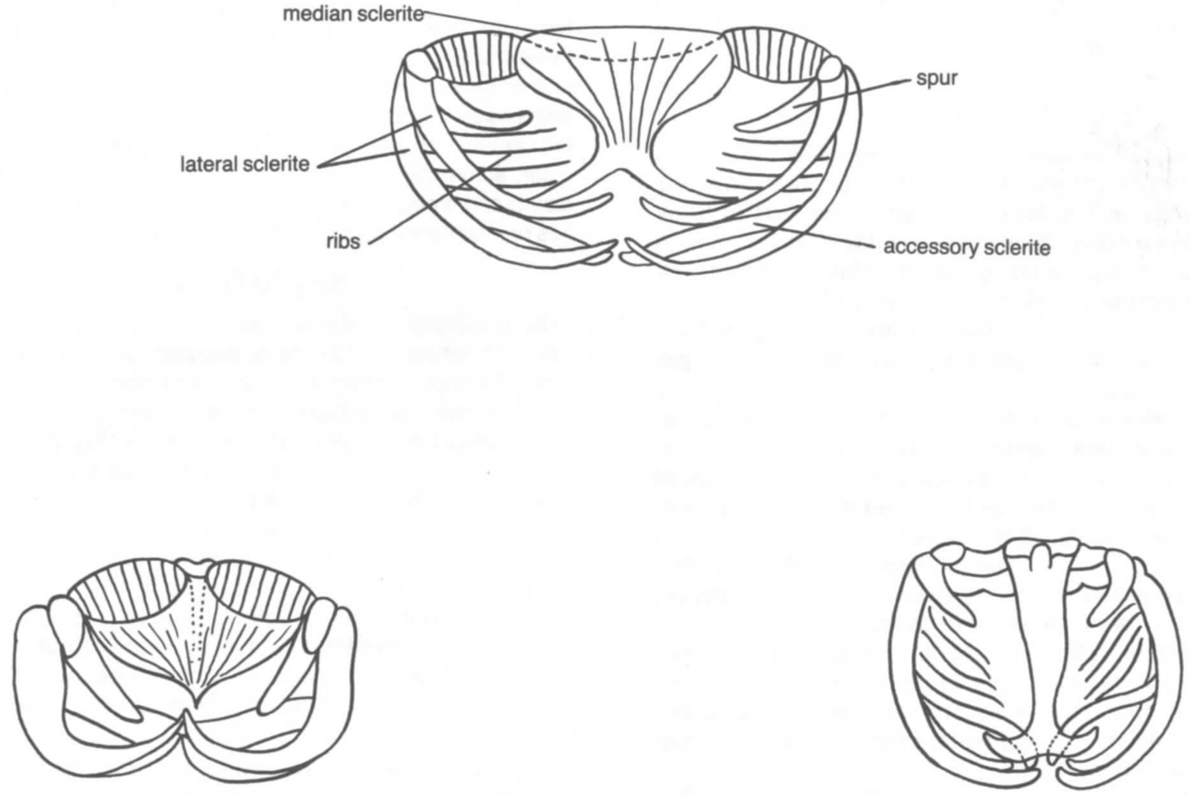


Fig. 63. Gastrocotylid Clamps.

Suborder Monopisthocotylea Odhner, 1912

Opisthaptor a single disc or membranous, containing anchors, hooks or occasionally loculi and septa; prohaptor with head organs, lappets, pseudosuckers or a single sucker; genito-intestinal canal usually absent.

Superfamily Gyrodactyloidea Johnston and Tiegs, 1922
Family Gyrodactylidae Cobbold, 1864

Viviparous; body minute (1 mm or less); opisthaptor membranous, margins sometimes scalloped; one pair anchors; two or three transverse bars, 16 marginal hooks; prohaptor contains one pair head organs; eyespots absent; testis single; ovary pre- or post-testicular; pharynx divided into two zones; vitelline follicles absent or weakly developed; parasitic on skin and gills of fishes and amphibians.

Key to Genera

1a. **Opisthaptor contains two lateral winglike bars and a large ventral bar with a shield; anchors slender, base of anchor with a dense cap; posterior part of body contains a spiny, transverse pedunculate bar; hooks arranged in a posterior group of 10 hooks and two lateral groups of three hooks each (Fig. 65). .... Genus *Swingleus* Rogers, 1969**

1b. **Opisthaptor not as described above; body without pedunculate bar. 2**

2a. **Three pairs of accessory bars in addition to dorsal and ventral bars; hooks arranged in two anterolateral groups of four hooks each and one posterior group of eight hooks; ventral bar has elongate posterior process; parasite of mullet (Fig. 66). .... Genus *Polyclithrum* Rogers, 1967**

2b. **Accessory bars absent; hooks not grouped as above; ventral bar without posterior process. 3**

3a. **Opisthaptor indistinctly set off from body margins not scalloped; anchors have broad roots; deep and superficial roots about equal; transverse bars absent but thin delicate plates replace them; parasitic on marine fishes (Fig. 67). .... Genus *Archigyrodactylus* Mizelle and Kritsky, 1967**

3b. **Opisthaptor distinctly set off from body, margins scalloped; anchors with well developed superficial root but weakly developed deep root; dorsal and ventral bars well developed (Fig. 68). .... Genus *Gyrodactylus* Nordmann, 1832**

Key to North American species in Mizelle and Kritsky (1967).

Life cycle: *G. elegans*- Adults viviparous, producing embryos *in utero*. The first embryo may in turn produce another and still another within that one. This kind of reproduction is regarded as serial polyembryony. After the embryo forms an opisthaptor with anchors and hooks, it is released. Newly released larvae are nonciliated and closely resemble the parent worm. They first attach to the skin and gills of the same host but might later transfer to a different host when contact is made (Katheriner, 1904).

Superfamily Dactylogyroidea Yamaguti 1963
Family Dactylogyridae Bychowsky, 1963

Oviparous; body small (1 mm or less), delicate; pigmented eyespots present; opisthaptor membranous, containing one or two pairs of anchors or anchors absent, 16 hooks; one, two or three transverse bars or bars absent; prohaptor provided with one or more pairs of head organs or rarely with head lappets; testis usually single; vas deferens may or may not loop around left cecum; cirrus supported by accessory piece; ovary pretesticular, sometimes looping around right cecum; vitelline follicles distributed along ceca; parasitic on skin and gills, in nasal cavities or in urinary tract of freshwater and marine fishes.

Key to Genera

1a. **Opisthaptor without anchors. 2**

1b. **Opisthaptor with one or two pairs of anchors. 4**

2a. **Prohaptor has gland ducts and pores confined to one or more pairs head organs; parasitic in urinary bladder or mesonephric ducts of fishes (Fig. 70). .... Genus *Acolpenteron* Fischthal and Allison, 1940**

Life cycle: *A. catostomi*- Eggs pass in urine of host. Onchomiracidia with four tufts of cilia, two pairs of eyespots, pharynx and 14 hooks develop and hatch in six to nine days following oviposition (Fischthal and Allison, 1940).

2b. **Prohaptor with or without lappets; pores of gland ducts distributed along anterior margin of prohaptor; opisthaptor discoid or cupshaped; vas deferens loops around left cecum; ovary loops around right cecum. 3**

3a. **Lappets present on prohaptor, contain gland ducts and pores; opisthaptor discoid; cephalic glands confined to anterior third of body (Figs. 71, 72. .... Genus *Anonchohaptor* Mueller, 1938**

3b. **Lappets absent; opisthaptor cupshaped with distinct muscular rim; cephalic glands distributed along sides of anterior half of body (Fig. 73). .... Genus *Icelanonchohaptor* Leiby, Kritsky and Peterson, 1972**

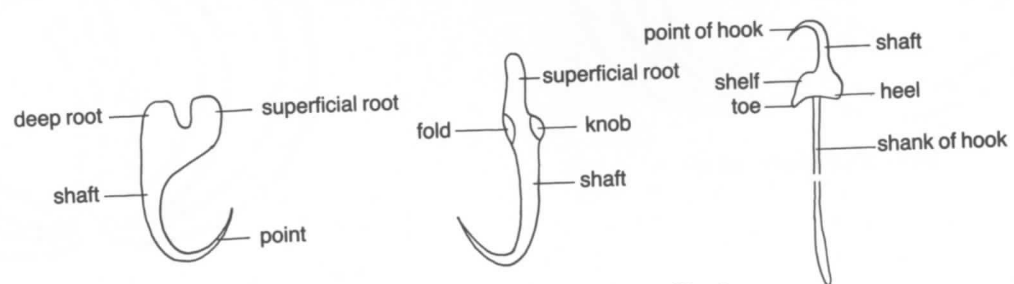


Fig. 64. Terminology for gyrodactylid anchors and hooks

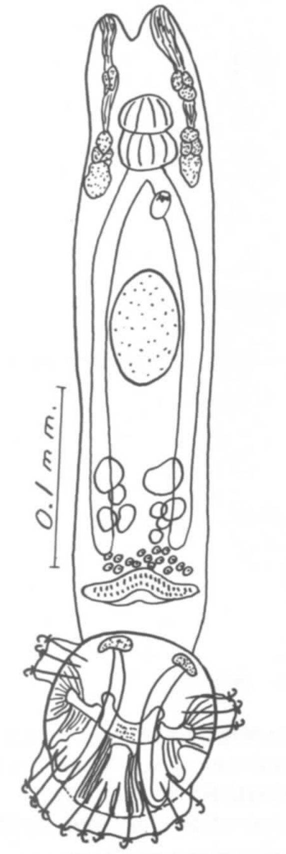


Fig. 65a. *Swingleus polyclithroides* (from Rogers, 1969).

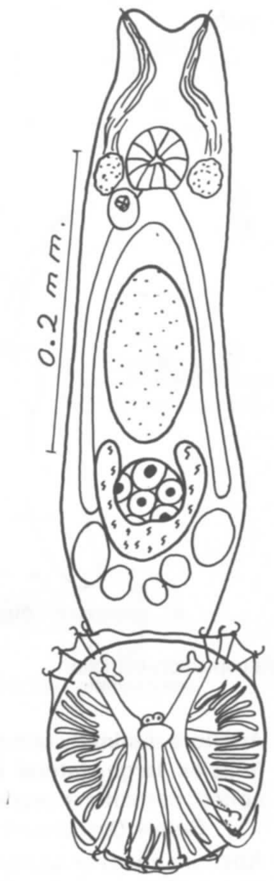


Fig. 66a. *Polyclithrum mugilini* (from Rogers, 1967).

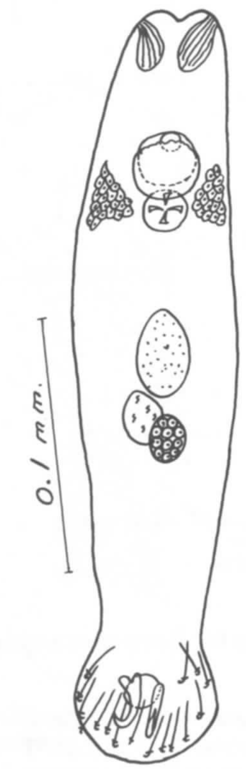


Fig. 67a. *Archigyrodactylus archigyrodactylus* (from Mizelle and Kritsky, 1967).

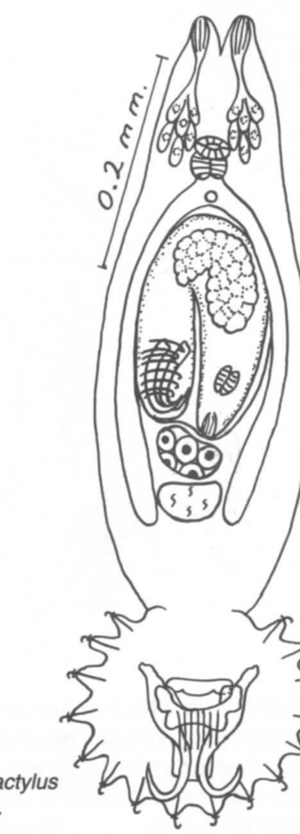


Fig. 68. *Gyrodactylus rhinichthius.*

Fig. 65b. Lateral wing bar.

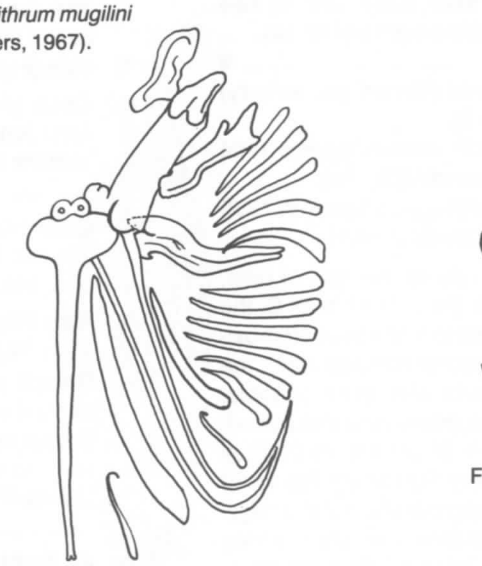


Fig. 66b. Dorsal, ventral and accessory bars.

Fig. 67b. Anchors and plate.

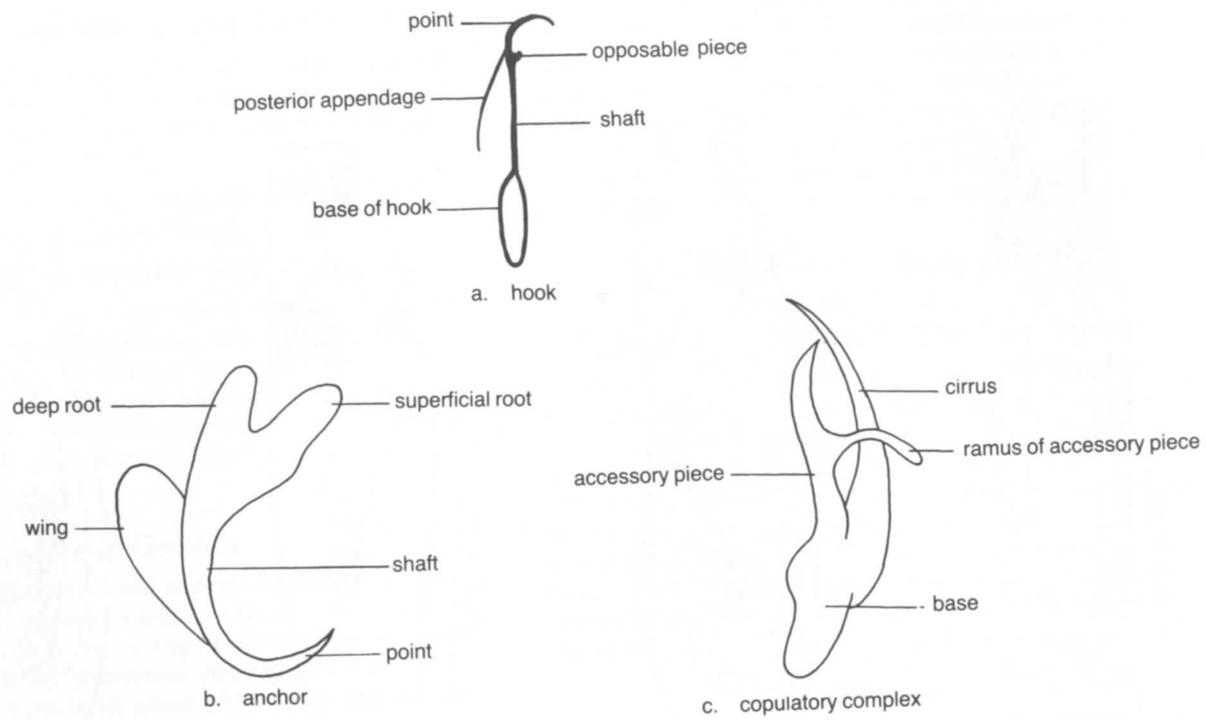


Fig. 69. Dactylogyrid armature and male copulatory complex.

4a. **Opisthaptor with one pair of anchors.** 5
4b. **Opisthaptor with two pairs of anchors.** 7
5a. **Opisthaptor indistinctly set off from body; transverse bars absent; parasitic in nasal cavities of freshwater fishes (Fig. 74).** .... **Genus** *Aplodiscus* **Rogers, 1967**
5b. **Opisthaptor distinctly set off from body; one or two transverse bars present; parastic on gills of fishes.** 6
6a. **Tips of anchors doubly recurved (turned posteriorly) and provided with wings (Fig. 75).** .... **Genus** *Pellucidhaptor* **Price and Mizelle, 1964**
6b. **Tips of anchors not doubly recurved (Fig. 76).** .... **Genus** *Dactylogyrus* **Diesing, 1850**
Key to species in Mizelle and McDougal (1970).

Lifecycle: *D. vastator*- Adults are parasitic on the gills of carp, *Cyprinus carpio* in Europe and the Near East. At 24 to 28 C. the onchomiracidia develop and hatch in two to three days after oviposition. The host fish is thought to become infected when the onchomiracidia are swept into the mouth with water currents. After attachment to the gills, the parasite grows to sexual maturity in four or five days at 28 to 29 C. or in 20 days at 15 C. They cause some injury to the gills. Only very small carp (up to 60 mm) seem to be infected. The rate of reproduction of the parasite decreases during the fall and winter and increases in spring and summer. They overwinter as adults or as dormant eggs. Many generations are produced annually. The entire cycle requires 11 to 13 days at 24 to 28 C. (Wunder, 1926 and 1929; Kulwiec, 1929; Izumova, 1956; Paperna, 1963).

7a. **Opisthaptor without transverse bars (Fig. 77).** .... **Genus** *Amphibdella* **Chatin, 1874**
7b. **Opisthaptor with one to three transverse bars.** 8
8a. **Opisthaptor with one transverse bar.** 9
8b. **Opisthaptor with two or three transverse bars.** 12
9a. **Prohaptor with one pair of head organs.** 10
9b. **Prohaptor with three pairs of head organs.** 11
10a. **Anchors distinctly unequal in size and shape; vitelline follicles large, lateral in position; cirrus short, not coiled; parasitic in marine teleost fishes (Fig. 78).** .... **Genus** *Diplectanotrema* **Johnston and Tiegs, 1922**
10b. **Anchors equal or nearly equal in size and shape; vitelline follicles small and distributed across most of body; cirrus long, coiled; parasitic in freshwater teleosts (Fig. 79).** .... **Genus** *Leptocleidus* **Mueller, 1936**
11a. **Ceca fused posteriorly to form cyclocoel; vas deferens loops around left cecum; ovary oval; parasitic in marine teleosts (Fig. 80).** .... **Genus** *Protancyrocephaloides* **Burns, 1978**
11b. **Ceca not fused posteriorly; vas deferens not looped around left cecum; ovary elongate, folded on itself (Fig. 81).** .... **Genus** *Amphibdelloides* **Price, 1937**
12a. **Opisthaptor with three transverse bars.** 13
12b. **Opisthaptor with two transverse bars.** 14
13a. **Dorsal anchors supported by two articulated bars, ventral anchors supported by one slender ventral bar; dorsal anchors larger than ventral anchors; vas deferens loops around left cecum; parasitic on marine fishes (Fig. 82).** .... **Genus** *Hargitrema* **Tripathi, 1959**
13b. **All three transverse bars separated (nonarticulated); vas deferens forms a loop but not around cecum; anchors nearly equal; ventral anchors articulate with median (ventral) bar, dorsal anchors articulate individually with lateral (dorsal) bars; parasitic on catostomid fishes (Fig. 83).** .... **Genus** *Pseudomurraytrema* **Bychowsky, 1957**
14a. **Base of anchors dilated and flattened, covering much of ventral surface of opisthaptor.** 15
14b. **Base of anchors not greatly dilated.** 16

(Continued)

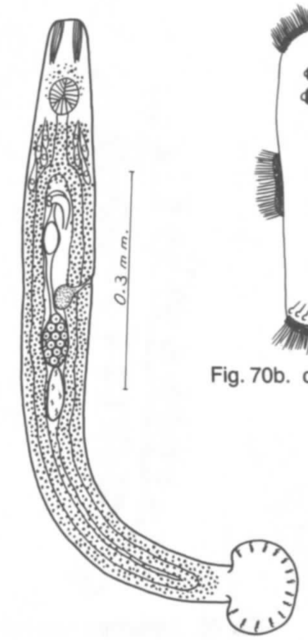


Fig. 70a. *Acolpenteron ureteroecetes.*

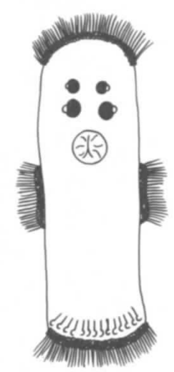


Fig. 70b. onchomiracidium.

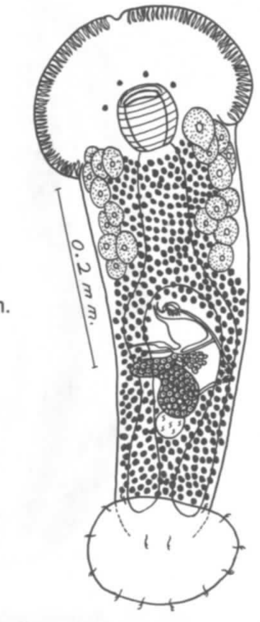


Fig. 72. *Anonchohaptor muelleri.* (from Kritsky *et al*, 1972).

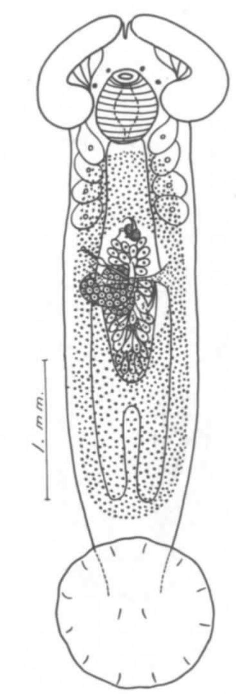


Fig. 71. *Anonchohaptor anomalum.*

Fig. 73. *Icelanonchohaptor icelanonchohaptor.* (from Leiby *et al* 1972).

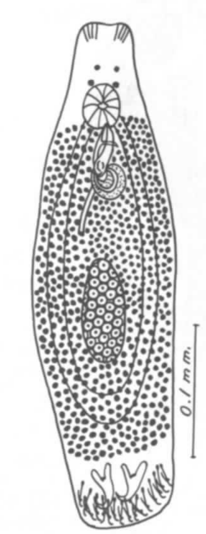


Fig. 74a. *Aplodiscus nasalis.* (from Rogers, 1967).

Fig. 74b. Anchor.

Fig. 75. *Pellucidhaptor pellucidhaptor.* (from Price and Mizelle, 1964).

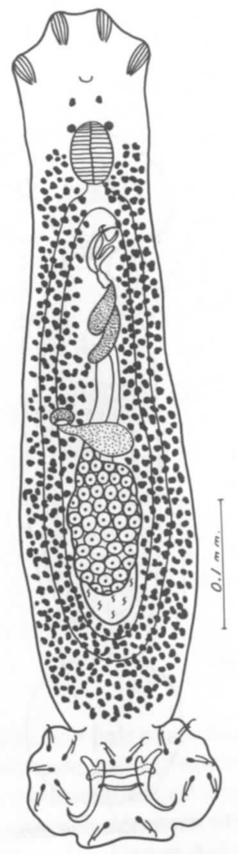


Fig. 76. *Dactylogyrus banghami.*

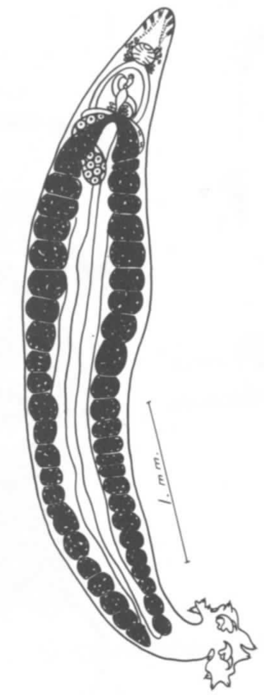


Fig. 77. *Amphibdella flavolineata.* (from Price, 1937).

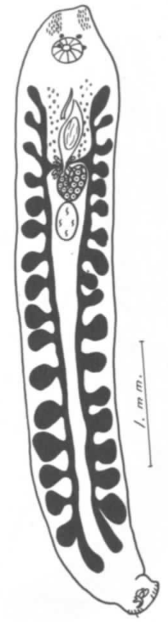


Fig. 78. *Diplectanotrema balistes.* (from Price, 1937).

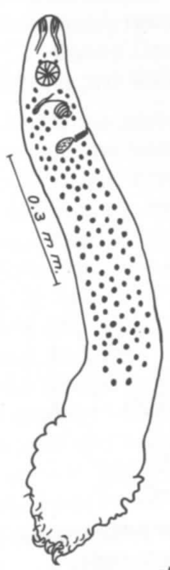


Fig. 79a. *Leptocleidus megalonchus.* (from Sullivan et al, 1978).

Fig. 79b. anchors

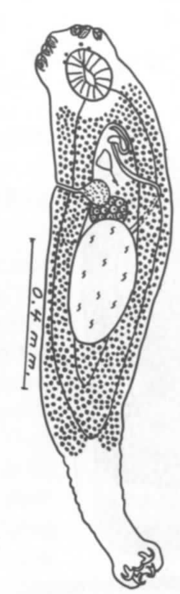


Fig. 80a. *Protancyrocephaloides liopsettae.* (from Burns, 1978).

Fig. 80b. anchor

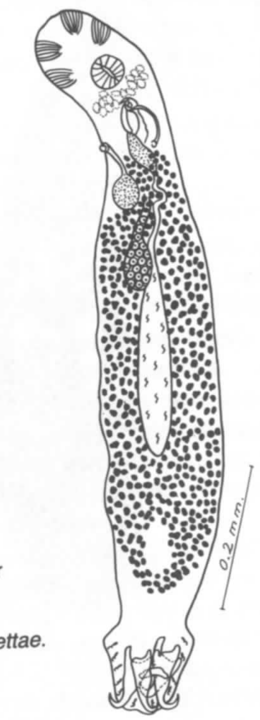


Fig. 81. *Amphibdelloides narcine.*

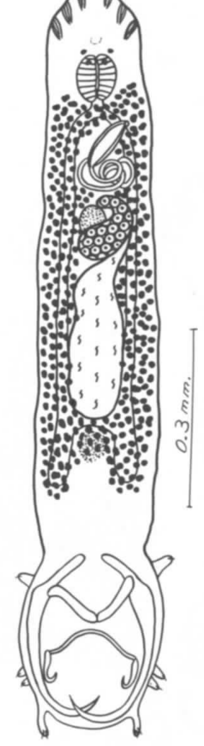


Fig. 82. *Hargitrema bagre.*

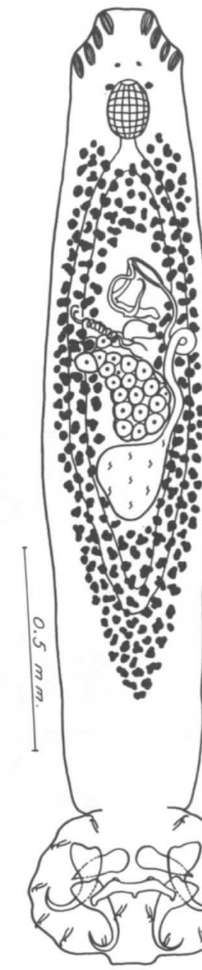


Fig. 83. *Pseudomurraytrema copulatum.*

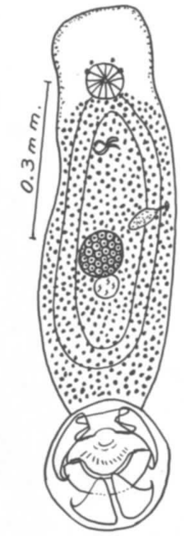


Fig. 84. *Anchoradiscoides serpentinus.* (from Rogers, 1967).

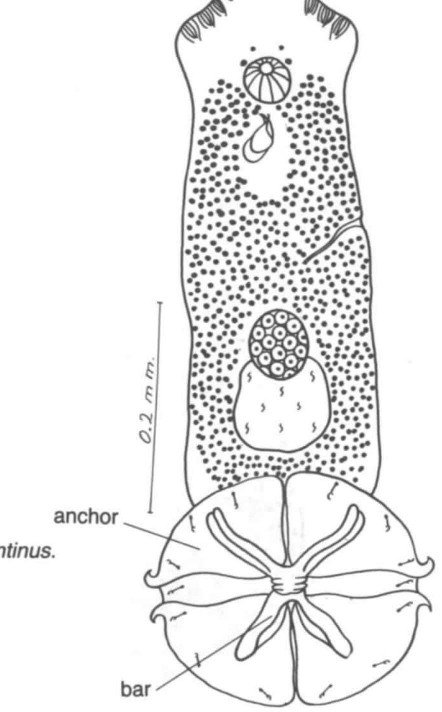


Fig. 85. *Anchoradiscus anchoradiscus*

15a. **Anchors similar in size and shape, bases greatly dilated and covering most of ventral surface of opisthaptor (Fig. 85). .... Genus *Anchoradiscus* Mizelle, 1941**

15b. **Anchors dissimilar in size and shape, bases dilated but covering only about one-third of ventral surface of opisthaptor (Fig. 84). .... Genus *Anchoradiscoides* Rogers, 1967**

16a. **Opisthaptor at least twice as wide as body; bars long, dissimilar; two pairs of dissimilar anchors, ventral anchors have deep and superficial roots, dorsal anchors are without deep and superficial roots (Fig. 86) .... Genus *Macrohaptor* Allison, 1967**

16b. **Opisthaptor about as wide as body; transverse bars usually shorter than anchors. 17**

17a. **Transverse bars fused; anchors similar in size and shape; vaginal pore on left margin of body (Fig. 87). .... Genus *Syncleithrium* Price, 1967**

17b. **Transverse bars not fused. 18**

18a. **Transverse bars V-shaped, articulated with each other and with base of anchors; vagina and vaginal pore sinistral (Fig. 88). .... Genus *Actinocleidus* Mueller, 1937**

18b. **Transverse bars separated (nonarticulated). 19**

19a. **Anchors similar in size and shape. 20**

19b. **Anchors dissimilar in size and/or shape. 23**

20a. **Vas deferens passes median to left cecum. 21**

20b. **Vas deferens loops around left cecum. 22**

21a. **Intestinal ceca fused to form cyclocoel (Fig. 89). .... Genus *Cleidodiscus* Mueller, 1934**

21b. **Intestinal ceca end blindly (Fig. 90). .... Genus *Ancyrocephalus* Creplin, 1839**

22a. **Ovary loops around right cecum; testis and ovary overlap; cirrus U-shaped, accessory piece complex; parasite of blue sucker (Fig. 91) .... Genus *Myzotrema* Rogers, 1967**

22b. **Ovary does not loop around right cecum; cirrus not U-shaped; accessory piece simple; testis posterior to ovary; not parasites of suckers. 23**

23a. **Vagina and vaginal pore sinistral; cirrus enveloped by spiral sheath; parasite of freshwater fishes (Percidae) (Fig. 92). .... Genus *Aethycteron* Suriano and Beverley-Burton, 1982**

23b. **Vagina and vaginal pore dextral; cirrus without spiral sheath; parasite of marine fishes (Mugilidae) (Fig. 93). .... Genus *Haliotrema* Johnston and Tiegs, 1922**

(Continued)

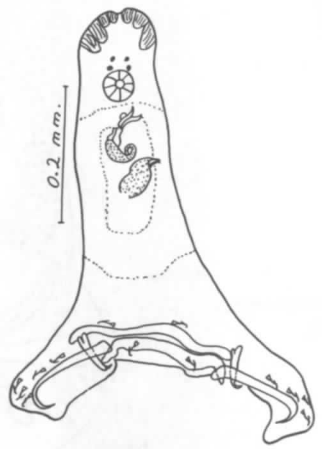


Fig. 86. *Macrohaptor hopkinsi.* (from Allison, 1967).

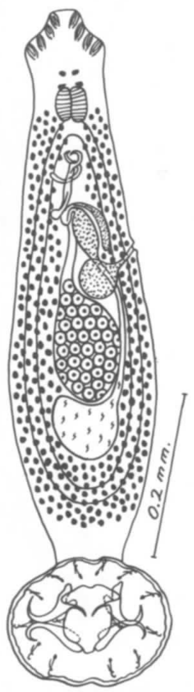


Fig. 87. *Syncleithrium fusiformis.*

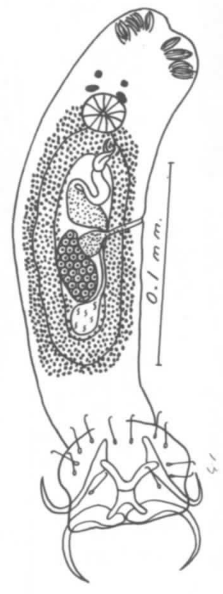


Fig. 88. *Actinocleidus oculatus.*

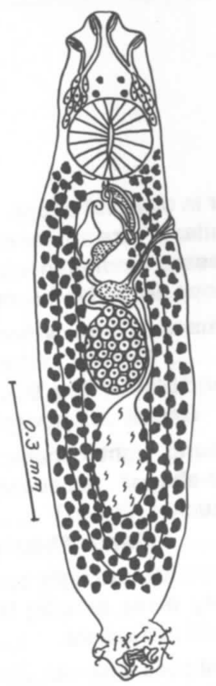


Fig. 89. *Cleidodiscus capax.*

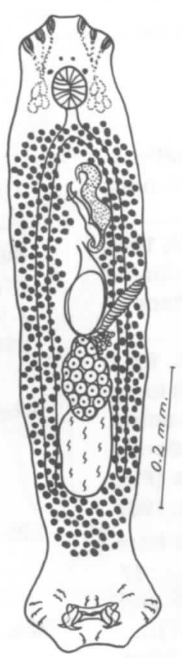


Fig. 90. *Ancyrocephalus lactophrys.*

Fig. 91. *Myzotrema cyclepti.* (from Rogers, 1967).

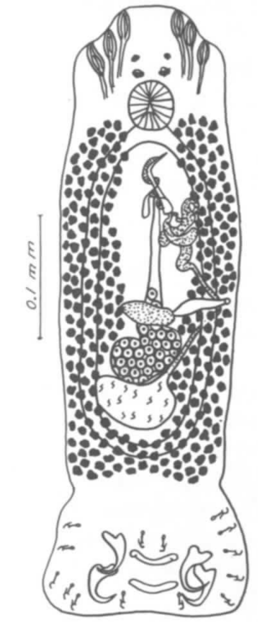


Fig. 92a. *Aethycteron moorei*

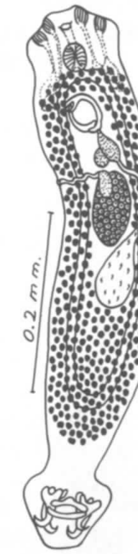


Fig. 93. *Haliotrema mugilinus.*

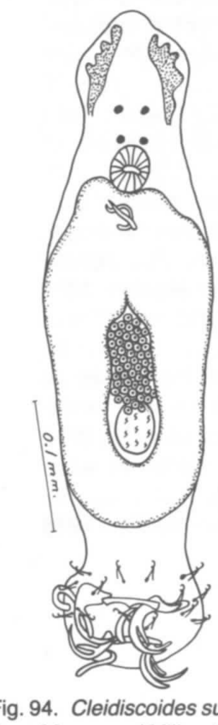


Fig. 94. *Cleidiscoides sulcata.* (from Mayes and Miller, 1973).

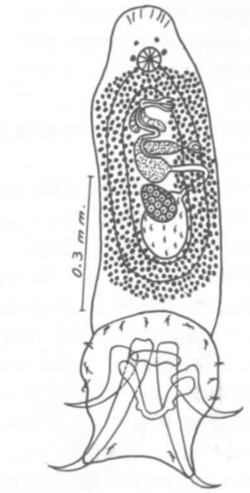


Fig. 95. *Lyrodiscus muricatus.* (from Rogers, 1967).

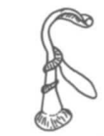


Fig. 92b. cirrus with spiral sheath


Fig. 96. *Aristocleidus hastatus.* (from Mueller, 1936).


Fig. 98b. opisthaptor, lateral view.


Fig. 97. *Haplocleidus dispar.* (from Mueller, 1936).

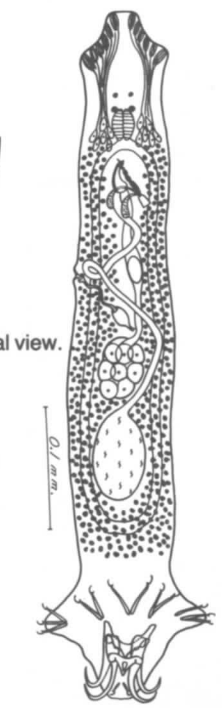


Fig. 98a. *Onchocleidus ferox.*

24a. **Anchors deeply cleft at tip and provided with wings; bars dissimilar in shape; accessory piece of male genitalia sickle-shaped (Fig. 94). .... Genus *Cleidodiscoides* Mayes and Miller, 1973**

24b. **Anchors not cleft at tip, wings absent. 25**

25a. **Opisthaptor lyre-shaped due to projection of tips of long anchors from sides of opisthaptor; dorsal bar U-shaped; dorsal anchors smaller than ventral anchors; vas deferens loops around left cecum; vaginal pore ventral to left cecum (Fig. 95). .... Genus *Lyrodiscus* Rogers, 1967**

25b. **Opisthaptor not lyre-shaped; anchors and bars not as described above. 26**

26a. **Anchors similar in size but not in shape; roots of dorsal anchors cleft, their tips bent at 45 degree angle; roots of ventral anchors not cleft, their tips curved (Fig. 96). .... Genus *Aristocleidus* Mueller, 1936**

26b. **Anchors similar in shape, might or might not differ in size; roots of anchors not cleft. 27**

27a. **Dorsal anchors twice as large as ventral anchors; hooks not unusually large, their tips weakly developed (Fig. 97). .... Genus *Haplocleidus* Mueller, 1937**

27b. **Dorsal and ventral anchors nearly equal in size; hooks large with thick shanks (Fig. 98). .... Genus *Onchocleidus* Mueller, 1936**

Family Bothitrematidae Bychowsky, 1957

Body small (less than 2 mm), delicate, contains two pairs of eyespots; prohaptor contains four pairs of cupshaped head organs; opisthaptor discoid with one pair of anchors, two V-shaped bars and a circle of radially oriented tubular structures; intestine a single cecum; one testis; ovary pretesticular; vitelline follicles fill lateral areas of body; produce one egg at a time; parasitic on gills of marine fishes.

The family is monotypic, containing only *Bothitrema bothi* (Fig. 99).

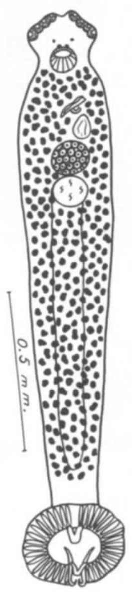


Fig. 99a. *Bothitrema bothi.*

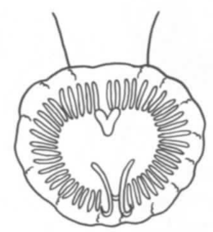


Fig. 99b. opisthaptor

Family Diplectanidae Bychowsky, 1957

Body small (less than 1 mm), posterior part contains recurved spines, squamodiscs or adhesive plaques; prohaptor provided with three pairs of head organs; opisthaptor has two pairs of anchors and two or three transverse bars; testis single; ovary pretesticular, sometimes looped around cecum; vitelline follicles abundant, in lateral areas of body; intestine composed of one or two ceca; parasitic on gills of marine and freshwater fishes.

Key to Genera

1a. **Posterior part of body constricted to form peduncle which is clothed in recurved spines; opisthaptor wider than body (rectangular), contains three transverse bars, two pairs of similar anchors and groups of recurved spines: on gills of marine fishes (Fig. 100). . ... Genus *Rhamnocercus* Monaco, Wood and Mizelle, 1954**

1b. **Posterior part of body wide, containing either squamodiscs or lateral adhesive plaques. 2**

2a. **Lateral adhesive plaques and recurved spines on posterior part of body; opisthaptor with three transverse bars; ovary loops around left cecum; on gills of marine fishes (Fig. 101). .... Genus *Rhabdosynochus* Mizelle and Blatz, 1941**

2b. **Posterior part of body contains dorsal and ventral squamodiscs. 3**

3a. **Intestine composed of two ceca; opisthaptor contains three separate transverse bars (Fig. 102). .... Genus *Diplectanum* Diesing, 1858**

Key to species in Tripathi (1957).

3b. **Intestine a single cecum; opisthaptor contains two fused bars (Fig. 103). .... Genus *Neodiplectanum* Mizelle and Blatz, 1941**

Superfamily Tetraonchoidea Yamaguti, 1963
Family Tetraonchidae Bychowsky, 1957

Body small (about 2 mm), delicate; prohaptor without lobes, contains one or more pairs of weakly developed head organs; opisthaptor membranous, distinct, contains two pairs of similar anchors, 16 hooks, a butterfly-shaped ventral bar, dorsal bar absent or vestigial; pharynx present; intestine a single cecum; one testis; ovary pretesticular; parasitic on gills of trout, pike, and grayling.

The family contains only the genus *Tetraonchus* Diesing, 1858 of which three species have been reported in North America. (Fig. 104).

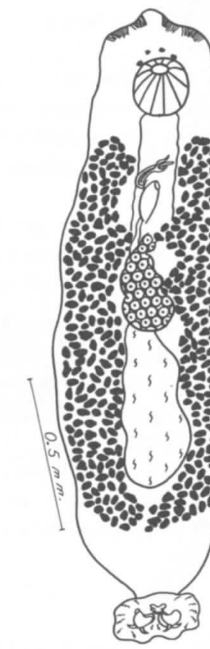


Fig. 104a. *Tetraonchus alaskensis.*

Fig. 104b. opisthaptor

Fig. 100. *Rhamnocercus rhamnocercus*.

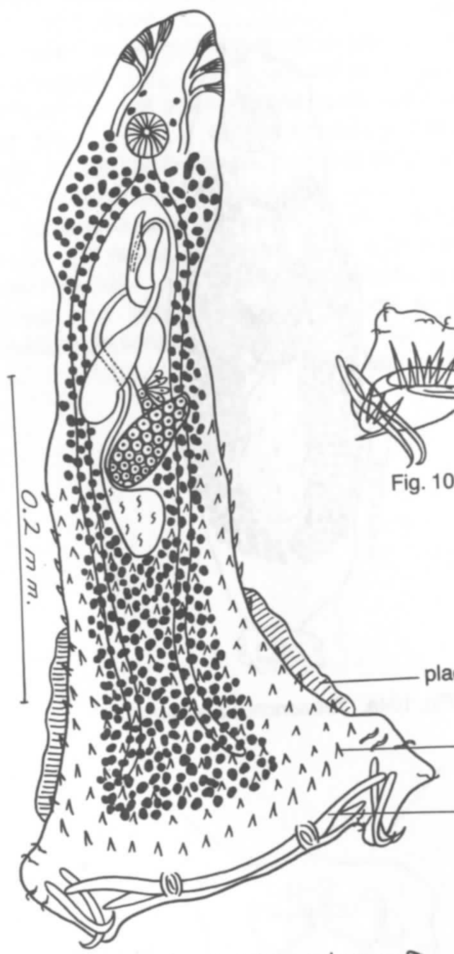


Fig. 101. *Rhabdosynochus rhabdosynochus*. (from Hargis, 1955).

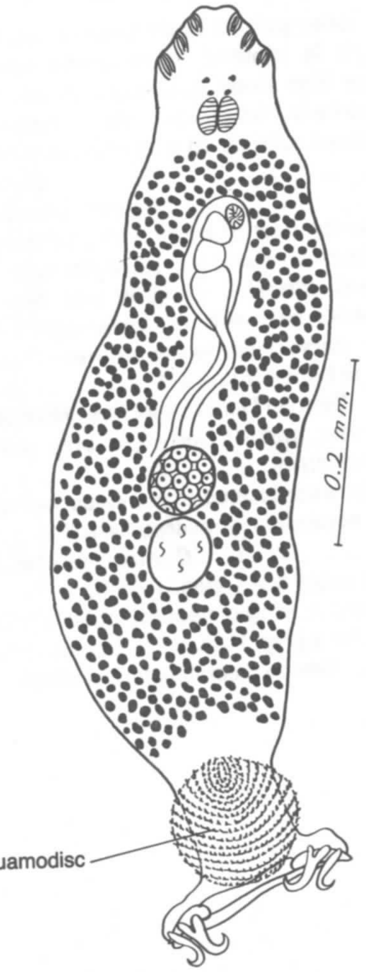


Fig. 102. *Diplectanum americanum*

Fig. 103. *Neodiplectanum wenningeri*, fused transverse bars.

Superfamily Capsaloidea Price, 1936
Family Capsalidae Baird, 1853

Body large, broad, flat, usually spinous; eyespots present or absent; pharynx present; intestinal ceca usually branched; prohaptor composed of two preoral suckers, bothria or pseudosuckers; opisthaptor a muscular disc, with or without septa and containing two or three pairs of anchors; one, two, or multiple testes; ovary pretesticular; vagina present or absent; male and female genital pores open separately into genital atrium; vitelline follicles abundant, fill most of area around other organs; parasitic on skin, gills or in nostrils and mouth of marine fishes. Price (1939a.) published a taxonomic revision of the family.

Key to Genera

1a. More than two testes present. 2
1b. One or two testes present. 5
2a. Opisthaptor without septa; prohaptor contains two earlike preoral bothria; four testes present; parasitic on gills of sturgeon (Fig. 105). .... **Genus *Nitschia* Baer, 1826**
2b. Opisthaptor with septa; prohaptor contains two preoral suckers; testes multiple. 3
3a. Pharynx constricted in the middle; testes either intercecal or both inter-and extracecal (Fig. 106). .... **Genus *Capsala* Bosc, 1811**
3b. Pharynx globose, not constricted; testes always intercecal. 4
4a. Posterior septa of opisthaptor bifid at the tips; anchors have clawlike tip; marginal spines of body crownshaped (Fig. 107). .... **Genus *Capsaloides* Price, 1938**
4b. Posterior septa of opisthaptor not bifid at the tips; anchors not clawlike; marginal spines of body bifid or serrate at tip (Fig. 108). .... **Genus *Tristoma* Cuvier, 1817**
5a. One testis; opisthaptor small, at end of a ventral peduncle, contains one pair of large and one pair of small anchors; lateral margins of body folded ventrally; preoral suckers surrounded by scalloped membrane (Fig. 109). ..... **Genus *Encotyllabe* Diesing, 1850**
5b. Two testes; opisthaptor discoid, sessile; anchors about equal in size; no scallops around preoral suckers; lateral margins of body not folded ventrally. 6
6a. Opisthaptor septate with seven marginal loculi and three pairs of anchors (Fig. 111). .... **Genus *Megalocotyle* Folda, 1929**
6b. Opisthaptor without septa and loculi. 7
7a. Prohaptor composed of two preoral suckers. 8
7b. Prohaptor composed of a single preoral lobe containing glands, suckers, sucking grooves or pseudosuckers. 9
8a. Vagina long, pore on left body margin; parasitic on skin of elasmobranchs (Fig. 110). .... **Genus *Benedeniella* Johnston, 1929**
8b. Vagina absent parasitic on marine teleost fishes (Fig. 113). .... **Genus *Neobenedenia* Yamaguti, 1963**

Life cycle: *N. melleni*- Adults inhabit the gills, nasal cavities, cornea and conjunctiva of many genera and species of marine fishes. Eggs are pyramidal with one long filament. A ciliated onchomiracidium develops and hatches in five to eight days. The larval opisthaptor remains folded until the parasite attaches to the host. At this time the cilia are shed (Jahn and Kuhn, 1932).

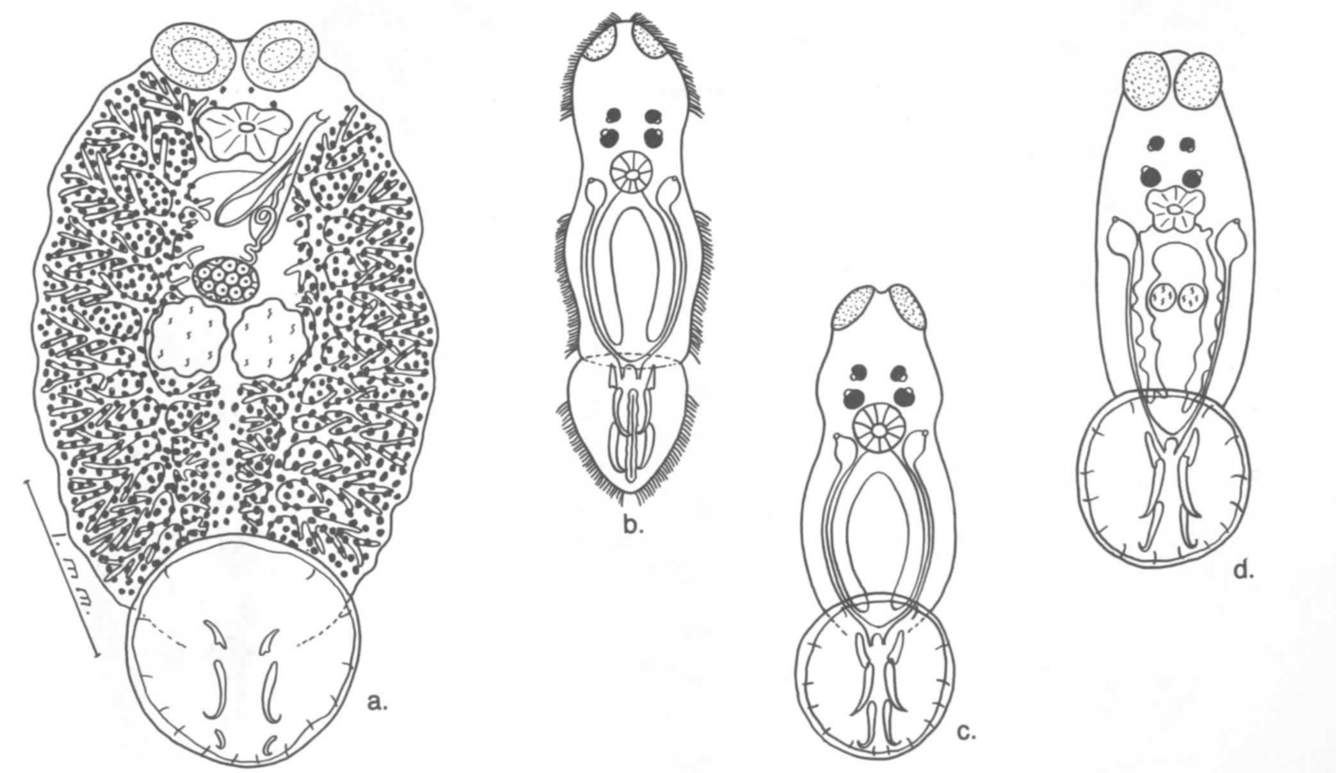


Fig. 113. *Neobenedenia melleni*.
a. adult b. onchomiracidium c. and d. developmental stages (from Jahn and Kuhn, 1932)

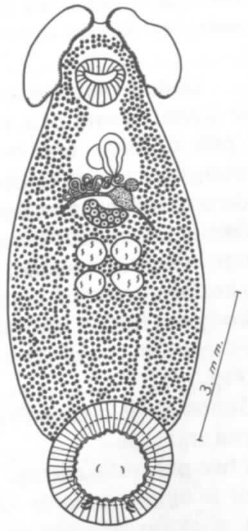


Fig. 105. *Nitschia quadritestis.*

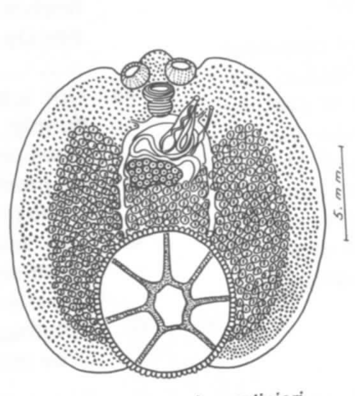


Fig. 106. *Capsala martinieri.*

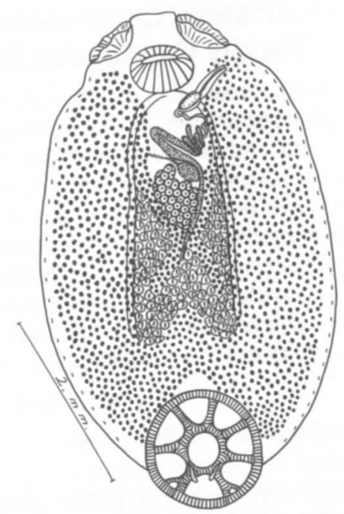


Fig. 107a. *Capsaloides cornuta.*

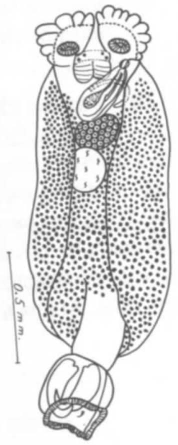


Fig. 109. *Encotyllabe lintoni.*

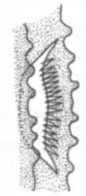


Fig. 107b. marginal spines

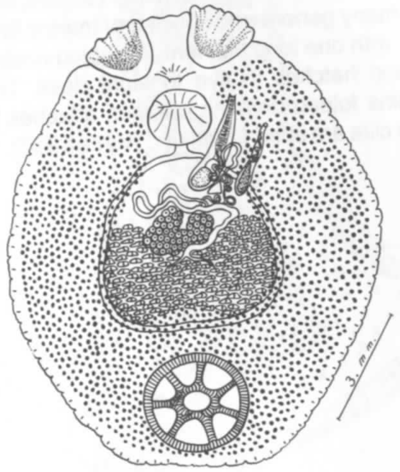


Fig. 108a. *Tristoma coccineum.*

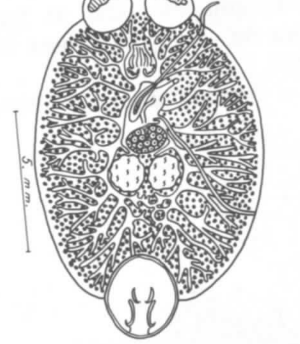


Fig. 110. *Benedeniella posterocolpa.* (from Hargis, 1955).

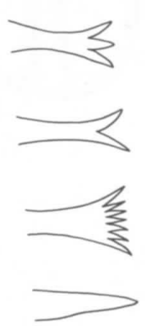


Fig. 108b. marginal spines

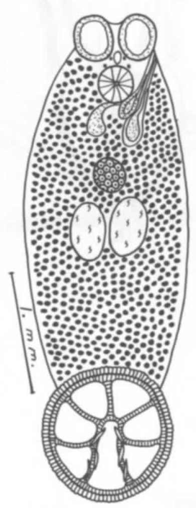


Fig. 111. *Megalocotyle marginata.*

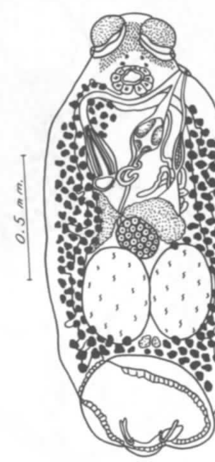


Fig. 112. *Pseudobenedenia noblei.* (from Menzies, 1946)

9a. Prohaptor a single preoral lobe containing one pair of suckers; opisthaptor aseptate with marginal scallops; vagina long, pore marginal, sinistral (Fig. 112). .... **Genus *Pseudobenedenia* Johnston, 1931**

9b. Prohaptor and opisthaptor not as described above. **10**

10a. Prohaptor contains sucking grooves or pseudosuckers; opisthaptor with two pairs of anchors; ceca branched at posterior ends, not fused; no vitelline follicles between ovary and testes (Fig. 114). .... **Genus *Pseudentobdella* Yamaguti, 1963**

10b. Prohaptor with one pair of glandular masses on single preoral lobe; opisthaptor with three pairs of anchors; ceca branched and fused posteriorly; some vitelline follicles between ovary and testes (Fig. 115). .... **Genus *Entobdella* Blainville in Lamarck, 1818**

Life cycle: *E. soleae*- Adults inhabit the skin on the ventral surface of the common sole, *Solea solea.* Eggs are cemented to sand grains by a sticky stalk. Onchomiracidia (Fig. 116) develop and hatch and attach to the skin on the dorsal surface of fish as this is the only part of the host exposed when they lie partially buried in sand. After some development the parasites move to the ventral body surface where they mature (Kearn, 1963).

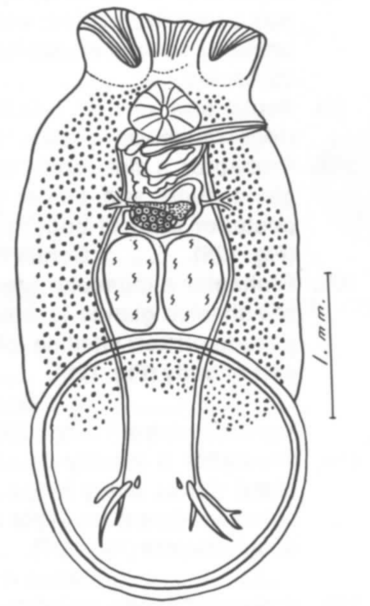


Fig. 114. *Pseudentobdella pacifica.* (from Guberlet, 1936)

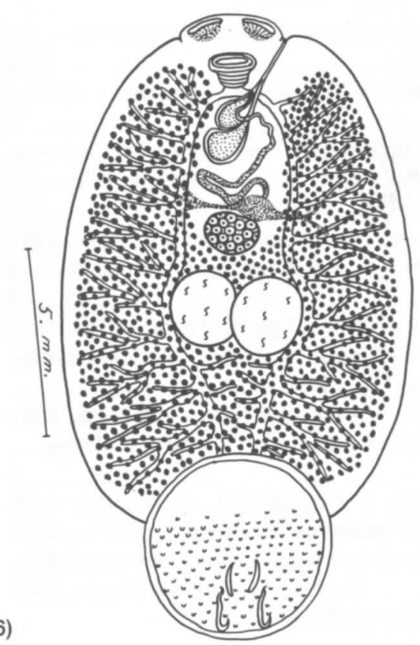
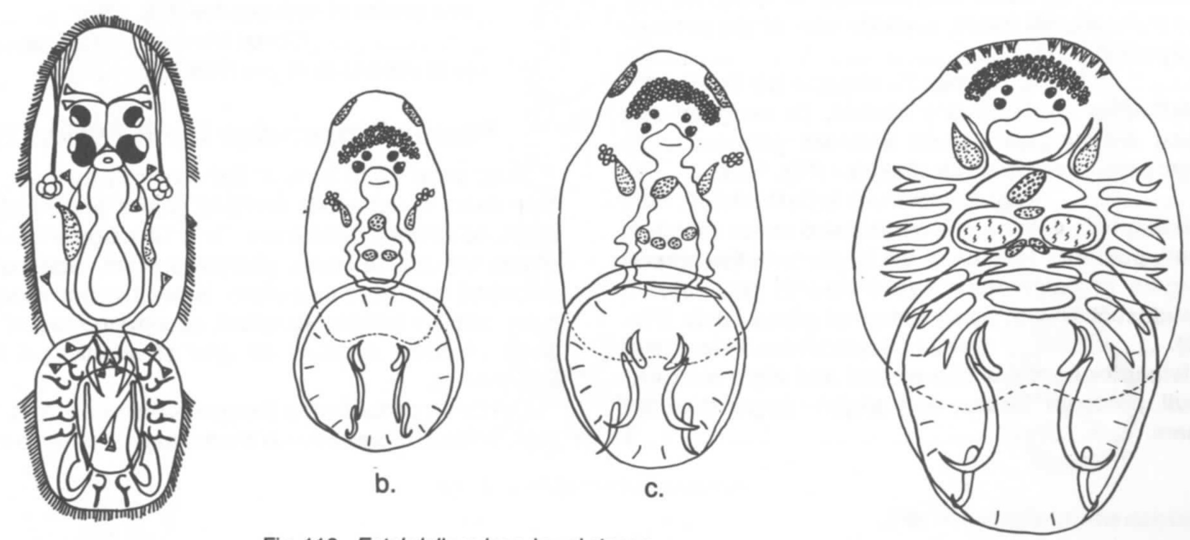


Fig. 115. *Entobdella hippoglossi.*



a. b. c. d.

Fig. 116. *Entobdella soleae*, larval stages.
a. onchomiracidium b., c., d. developmental stages (from Kearn, 1963)

Family Monocotylidae Taschenberg, 1879

Body variable in shape, flat; eyespots present or absent; pharynx present; intestinal ceca branched or unbranched, fused or not posteriorly; prohaptor in form of an oral sucker with or without head organs, or a single lobe containing gland ducts and pores, a preoral flap sometimes present; opisthaptor discoid, septate, anchors present or absent; marginal, submarginal and central loculi present, marginal papillae sometimes present; dorsum of opisthaptor may contain muscular papillae or small muscular holdfast organs; usually one testis present; ovary pretesticular, usually elongate and looped around right cecum; vitelline follicles distributed around ceca; eggs usually with unipolar filament; parasitic in nostrils or on skin and gills of marine fishes. Price (1938b.) and Young (1967) published taxonomic revisions of the family.

Key to Genera

1a. **Opisthaptor contains more than nine loculi; two vaginae.** 2

1b. **Opisthaptor contains nine loculi or less; one vagina.** 6

2a. **Anchors absent; opisthaptor has one central, 14 marginal and five submarginal loculi; parasitic in the nasal cavities of rays (Fig. 117).** .... **Genus** *Empruthotrema* **Johnston and Tiegs, 1922**

2b. **Anchors present; opisthaptor not as described above.** 3

3a. **Prohaptor contains marginal gland ducts; opisthaptor contains many small loculi; parasitic in nasal cavities of elasmobranchs (Fig. 118).** .... **Genus** *Cathariotrema* **Johnston and Tiegs, 1922**

3b. **Prohaptor and opisthaptor not as described above.** 4

4a. **Prohaptor contains a preoral flap; opisthaptor with one central and 10 marginal loculi; muscular papillae on dorsal surface of opisthaptor; anchors small (Fig. 121).** .... **Genus** *Papillocotyle* **Young, 1967**
Key to species in Young (1967).

4b. **Prohaptor with head organs; opisthaptor not as described above.** 5

5a. **Opisthaptor contains one central, 13 marginal and four submarginal loculi; anchors very large; parasite of rays (Fig. 119).** .... **Genus** *Thaumatocotyle* **Scott, 1904**

5b. **Opisthaptor contains one central, 18 marginal and seven submarginal loculi; anchors not unusually large; parasitic in nostrils of skates (Fig. 120).** .... **Genus** *Merizocotyle* **Cerfontaine, 1894**

6a. **Opisthaptor contains one central and seven marginal loculi, posterior loculus much larger than the others; margins of opisthaptor has festoons; prohaptor a pseudosucker with many marginal gland ducts (Fig. 122).** .... **Genus** *Dasybatotrema* **Price, 1936**

6b. **Opisthaptor contains one central and eight marginal loculi, posterior loculus only slightly larger than the others.** 7

7a. **Lateral margins of posterior part of body has bilateral cuticular bars; opisthaptor with transverse rows of recurved spines on dorsal surface; parasite of guitarfish (Fig. 123).** .... **Genus** *Spinuris* **Doran, 1953**

7b. **Body without cuticular bars; Opisthaptor without recurved spines.** 8

8a. **Prohaptor with a distinct preoral flap; opisthaptor contains one central and eight submarginal loculi plus numerous marginal ridges; anchors absent; ceca profusely branched; parasitic in skin of rays (Fig. 124)** .... **Genus** *Dendromonocotyle* **Hargis, 1955**
Key to species in Young (1967) and in Olson and Jeffries (1983)

8b. **Prohaptor without preoral flap; opisthaptor without marginal ridges; anchors present, ceca unbranched.** 9

9a. **Septa and rim of opisthaptor surmounted by a sinuous sclerotized ridge; dorsal surface of opisthaptor contains several muscular holdfast organs in a transverse row.** 10

9b. **Septa and rim of opisthaptor without sclerotized ridge; muscular holdfast organs absent.** 11

10a. **Prohaptor a flat reniform disc with many marginal gland ducts and pores; vitelline follicles absent in posterior third of body; parasitic on gills of sawfish (Fig. 125).** .... **Genus** *Neoheterocotyle* **Hargis, 1955**

10b. **Prohaptor a muscular preoral lobe with three groups of adhesive glands located dorsal and lateral to oral pseudosucker; vitelline follicles extend into posterior part of body (Fig. 126).** .... **Genus** *Heterocotyle* **Scott, 1904**
Key to species in Young (1967).

11a. **Prohaptor a weakly-developed oral sucker without gland ducts; ovary loops around right cecum; ridge sclerites absent on septa and papillae absent on rim of opisthaptor (Fig. 127).** .... **Genus** *Anoplocotyloides* **Young, 1967**

11b. **Prohaptor a large membranous pseudosucker with bilateral rows of 10 small head organs; ovary does not loop around cecum; septa and marginal ridge of opisthaptor has tetrapartite ridge sclerites; marginal papillae on rim of opisthaptor (Fig. 128).** .... **Genus** *Monocotyle* **Taschenberg, 1878**
Key to species in Young (1967).

Family Dionchidae Bychowsky, 1959

Body small (2 to 3 mm), flat; eyespots present; prohaptor composed of numerous cephalic glands and marginal gland ducts; opisthaptor discoid with 10 to 12 marginal loculi, one pair of anchors and 14 hooks; pharynx present; intestinal ceca unbranched and fused posteriorly; testes tandem; ovary pretesticular; vitelline follicles abundant, occupying most of lateral regions of body; parasitic on gills of suckfish of the family Echeneidae.

The family contains only the genus *Dionchus* Goto, 1899 (Fig. 129), which is represented in North America by three species.

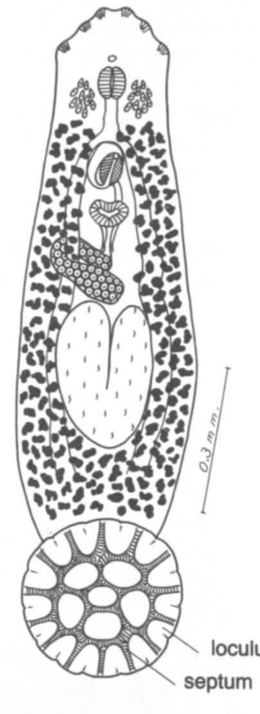


Fig. 117. *Empruthotrema raiae.*

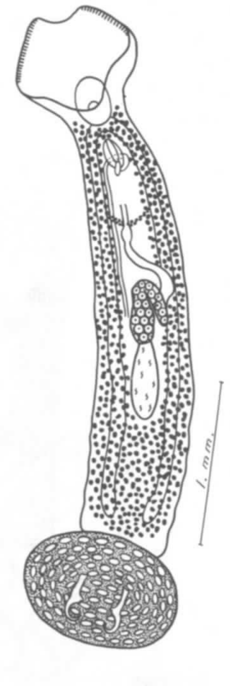


Fig. 118. *Cathariotrema selachii.*

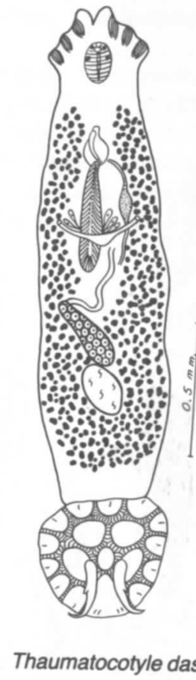


Fig. 119. *Thaumatocotyle dasybatis.*

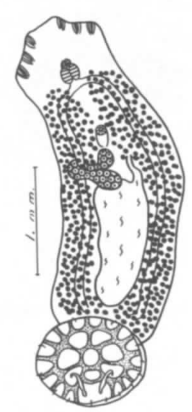


Fig. 120. *Merizocotyle pugetensis.*

Fig. 121a. *Papillocotyle floridana.*

Fig. 121b. opisthaptor, dorsal view

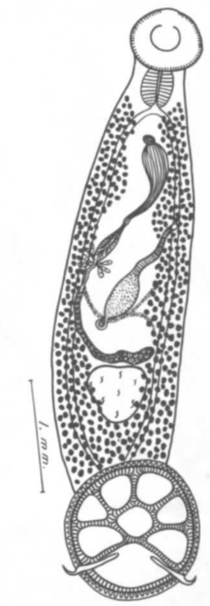


Fig. 122. *Dasybatotrema dasybatis.*

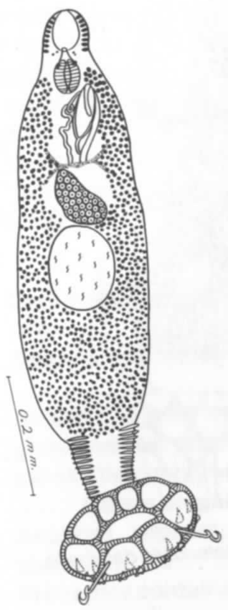


Fig. 123. *Spinuris lophosoma.*

Fig. 124a. *Dendromonocotyle octodiscus.*

Fig. 125a. *Neoheterocotyle inpristi.*

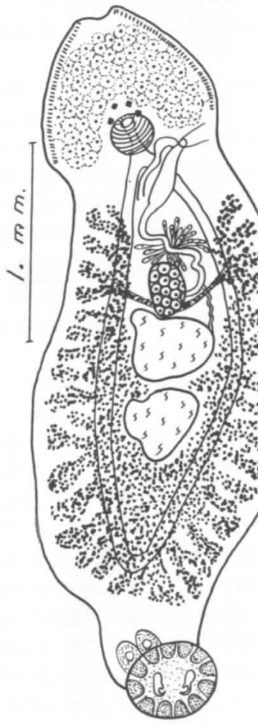


Fig. 129. *Dionchus rachycentris.*

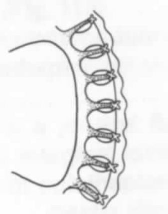


Fig. 124b. Marginal ridges.

Fig. 125b. Opisthaptor, lateral view.

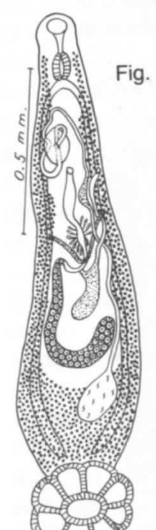


Fig. 126. *Heterocotyle minima.*

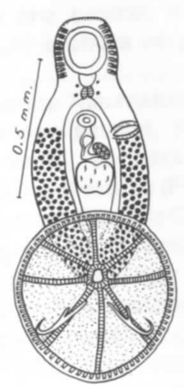
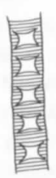


Fig. 128a. *Monocotyle pricei.*

c. egg



b. septal ridge

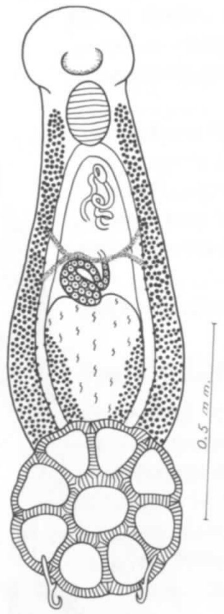


Fig. 127. *Anoplocotyloides papillata.*

Family Loimoidae Bychowsky, 1957

Body small (2 to 4 mm); pharynx present; ceca unbranched; prohaptor contains two or more preoral suckers or one pair head organs; opisthaptor a large muscular sucker with one pair of anchors, margin of sucker with muscular papillae in one genus; one or two testes; ovary pretesticular, variable in shape; vagina single, pore ventral; vitelline follicles abundant along ceca; parasitic on gills of elasmobranchs.

Key to Genera

1a. Prohaptor contains head organs and cephalic glands; sucker on opisthaptor with 12 to 14 marginal papillae; ovary elongate and looped around right cecum; two testes. (Fig. 130). .... Genus *Loimopapillosum* Hargis, 1955

1b. Prohaptor contains preoral suckers; opisthaptor without marginal papillae; ovary not looped around cecum; one testis. 2

2a. Testis large, lobed; prohaptor contains five or six preoral suckers; body broad and flat (Fig. 131). .... Genus *Loimosina* Manter, 1944

2b. Testis small, elongate; prohaptor contains one or two pairs preoral suckers; body elongate, narrow (Fig. 132). .... Genus *Loimos* MacCallum, 1917

Fig. 131b. prohaptor

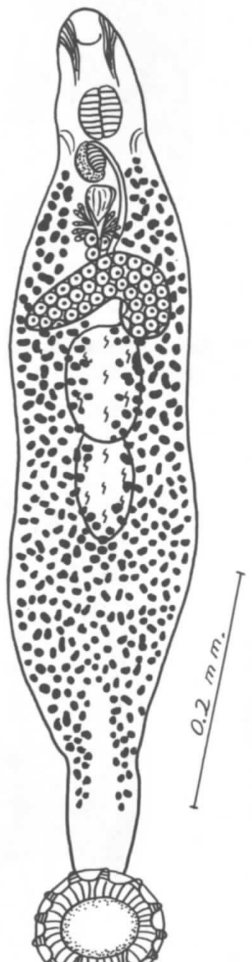


Fig. 130. *Loimopapillosum dasybatis.*

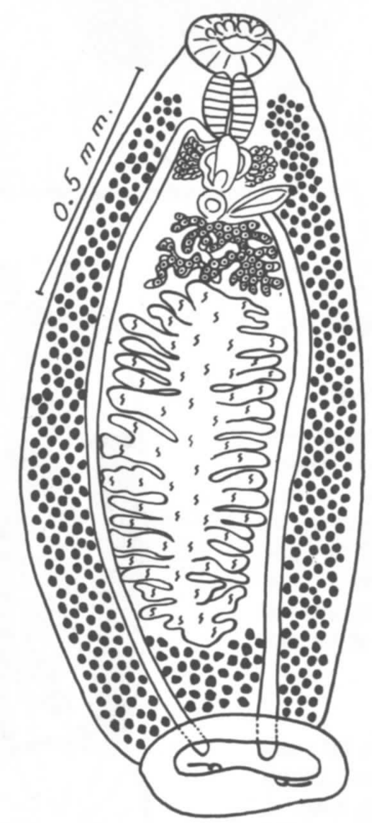


Fig. 131a. *Loimosina wilsoni.* (from Manter, 1944)

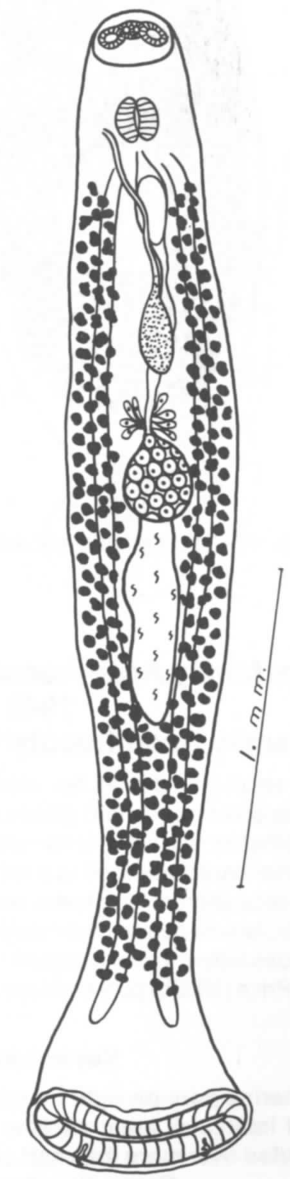


Fig. 132. *Loimos salpingoides.*

Family Microbothriidae Price 1936

Body small (2 to 3 mm), flat; prohaptor in form of a pseudosucker containing gland ducts or two small buccal suckers; opisthaptor without anchors or hooks, in the form of a muscular cup or two muscular flaps (?); testes one, two or multiple; ovary pretesticular; vagina single or double; parasitic in nostrils or on skin of elasmobranchs. Price (1938b) published a taxonomic revision of the family.

Key to Genera

1a. **One testis; opisthaptor an oval muscular cup; buccal suckers very small (Fig. 133). .... Genus *Microbothrium* Olsson, 1869**

1b. **Two or multiple testes. 2**

2a. **Testes two, opposite; opisthaptor in form of two muscular flaps; pharynx without lobelike papillae (Fig. 134). .... Genus *Dermophthirius* MacCallum, 1926**

2b. **Testes multiple, intercecal; opisthaptor a small circular cup; pharynx with lobelike papillae (Fig. 135). .... Genus *Neodermophthirius* Price, 1963**

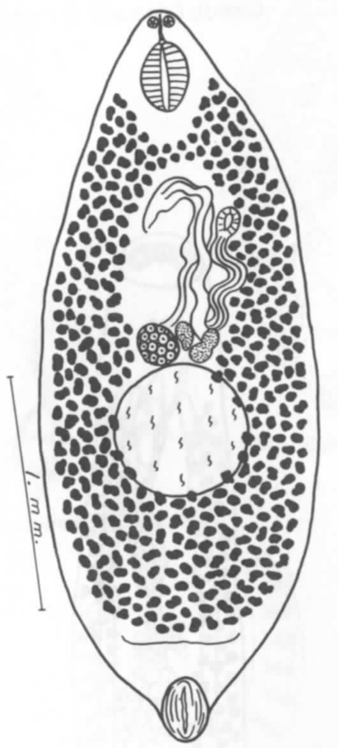


Fig. 133. *Microbothrium apiculatum.*

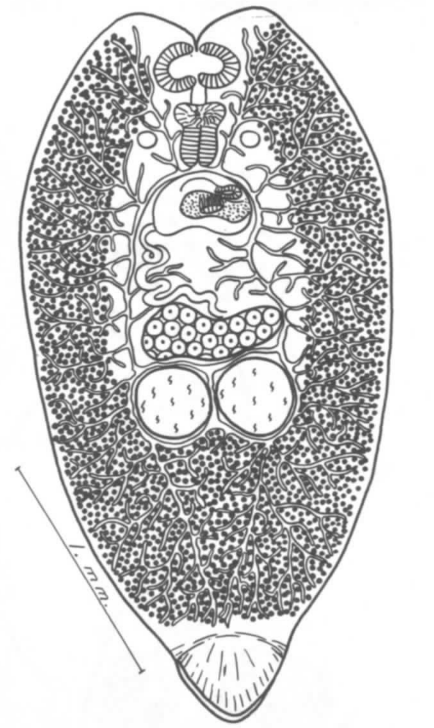


Fig. 134. *Dermophthirius carcharini.*

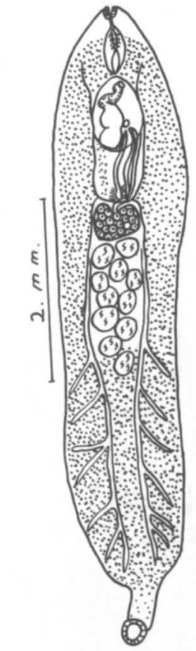


Fig. 135. *Neodermophthirius harkemai.* (from Price, 1963)

Superfamily Acanthocotyloidea Sproston, 1948
Family Acanthocotylidae Price, 1936

Body small (1 to 3 mm), flat, sides parallel; eyespots absent; prohaptor contains cephalic glands and one pair of preoral suckers; opisthaptor discoid with numerous radiating rows of spines, small larval haptor attached to adult haptor; pharynx present; intestinal ceca unbranched; testes multiple, intercecal; ovary pretesticular; female genital pore marginal; male pore median; vitelline follicles lateral to ceca; parasitic on skin and gills of rays and skates. Price (1938b) published a taxonomic revision of the family.

Key to Genera

1a. **Uterine pore on right margin of body; testes fill most of intercecal area; vitelline follicles abundant, distributed over more than half of body length (Fig. 136). ... . Genus *Pseudacanthocotyla* Yamaguti, 1963**

1b. **Uterine pore on left margin of body; testes not abundant, restricted to posterior part of body; vitelline follicles confined to posterior third of body (Fig. 137). ... . Genus *Allacanthocotyla* Yamaguti, 1963**

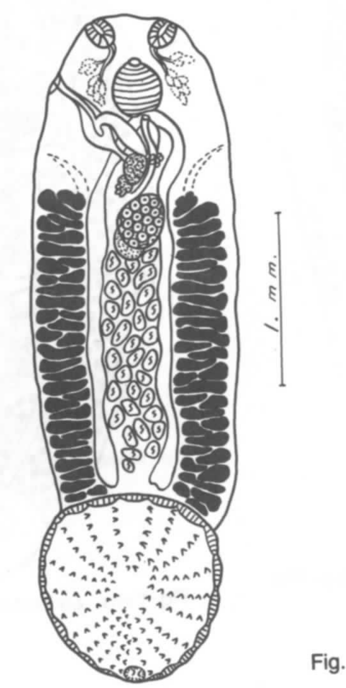


Fig. 136. *Pseudacanthocotyla williamsi.*

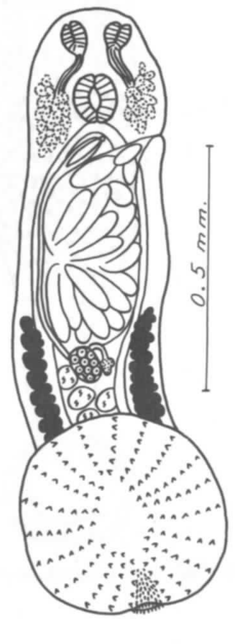


Fig. 137. *Allacanthocotyla pugetensis.*

Superfamily Udonelloidea Yamaguti, 1963
Family Udonellidae Taschenberg, 1879

Body small (about 2mm) cylindrical; prohaptor contains one pair of head organs; opisthaptor in form of a concave muscular disc without anchors or hooks; intestine a single cecum; pharynx large; one testis; ovary pretesticular; vitelline glands large, along sides of body; uterus contains one egg at a time; eggs have unipolar stalk for attachment to host; parasites of parasitic copepods on marine fishes. Price (1938b) published a taxonomic revision of the family.

This family is represented in North America by only the genus *Udonella* Johnston, 1835 (Fig. 138). Post-hatching development was studied by Ivanov (1952) and prehatching development by Schell (1972).

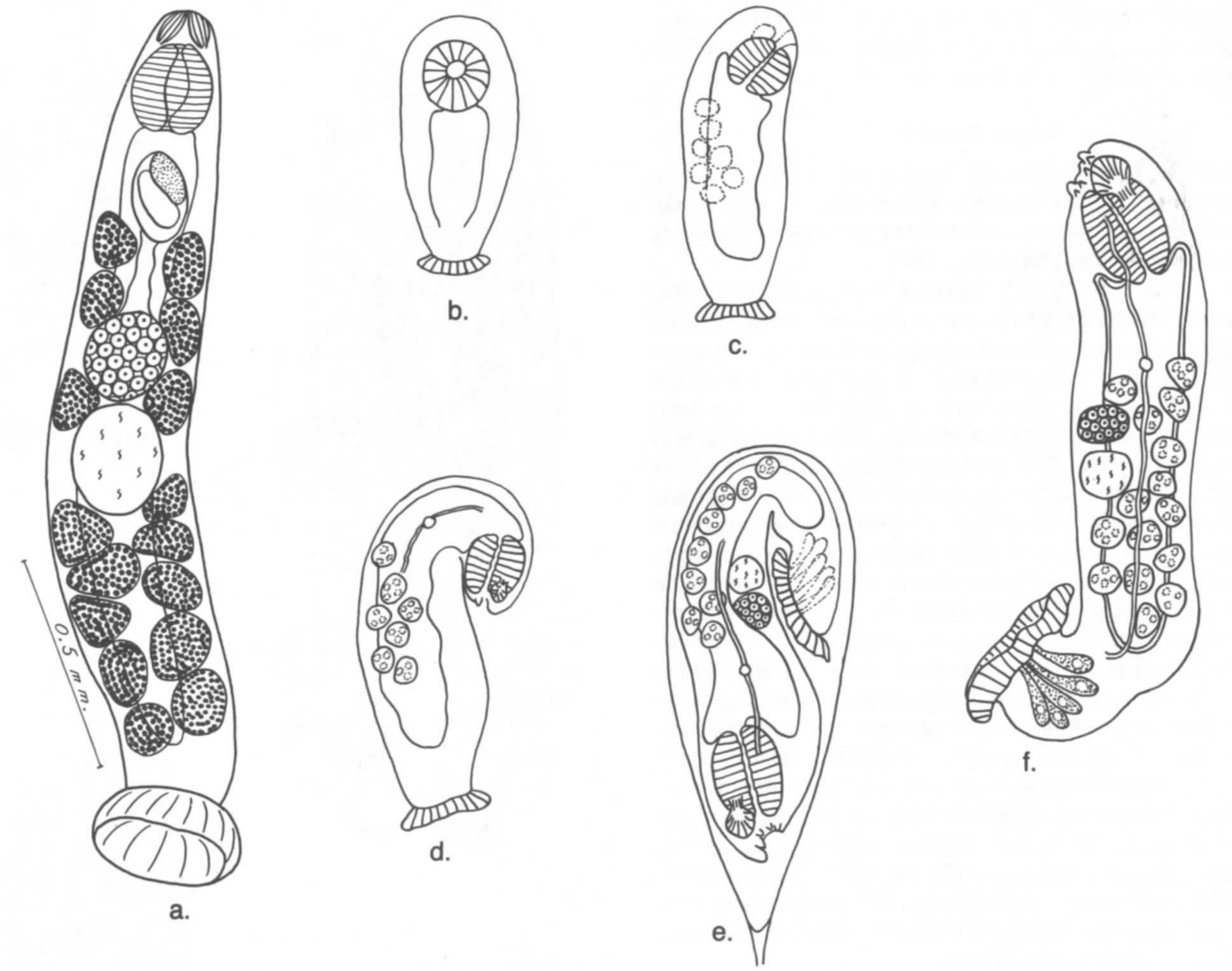


Fig. 138. *Udonella caligorum.*
a. adult b. to e. prehatching development
f. hatched larva (from Schell, 1972)

Suborder Polyopisthocotylea Odhner, 1912

Opisthaptor contains two or more muscular suckers and/or clamps; anchors sometimes present; prohaptor contains single oral sucker or pair of small buccal suckers; genito-intestinal canal usually present.

Superfamily Polystomatoidea Price, 1936
Family Polystomatidae Gamble, 1896

Body flat, muscular; eyespots absent; pharynx present; intestinal ceca branched or unbranched, not fused posteriorly; prohaptor a muscular sucker; opisthaptor contains six suckers plus one or more pairs of anchors and hooks; one, two or multiple testes; ovary pretesticular; vitelline follicles occupy most of area around ceca and gonads; parasitic in urinary bladder, nasal cavities, mouth, pharynx or esophagus of amphibians and reptiles. Price (1939b) published a taxonomic revision of the family.

Key to Genera

1a. Testes multiple; intestinal ceca branched, the branches anastomosing; opisthaptor contains six suckers and one pair of anchors; parasitic in urinary bladder of amphibians (Fig. 139). .... **Genus *Polystoma* Zeder, 1800**

Life cycle: *P. integerrimum* - Adults in the urinary bladder start laying eggs in the spring when the frogs lay their eggs. Parasite eggs pass in the frog urine. A ciliated onchomiracidium develops and hatches in 20 to 50 days, the time determined by the temperature of the water. Onchomiracidia attach to the external gills of small tadpoles where they feed and develop to mature adults in 20 to 25 days. These adults lay eggs until the external gills are resorbed when they die. Onchomiracidia from these eggs hatch and attach to internal gills of older tadpoles. Some later eggs from adults in the urinary bladder also produce onchomiracidia that attach to internal gills, but when the tadpoles metamorphose to frogs the developing parasites migrate via the digestive tract to the cloaca and then to the urinary bladder where they develop slowly to sexually mature adults. Adults of the gill generation differ from those of the bladder generation in having a rudimentary cirrus, no vaginae, no uterus, no genito-intestinal canal, smaller ovary, only one testis, rudimentary vitellaria, sperm without heads and fewer ova. Like their host, the bladder parasites are dormant during the winter. Complete development of this generation requires three years (Zeller, 1872, 1876; Gallien, 1932, 1933; Bychowsky, 1957). Paul (1938) studied the life cycle of *P. nearcticum*, a parasite in the urinary bladder of the tree frogs, *Hyla versicolor* and *H. cinerea*.

1b. One or two testes present. **2**
2a. One testis; parasitic in urinary bladder of turtles. **3**
2b. Two testes; in urinary bladder of amphibians. **5**
3a. Opisthaptor without anchors (Fig. 140). .... **Genus *Neopolystoma* Price, 1939**
3b. Opisthaptor contains one or two pairs of anchors. . **4**
4a. Opisthaptor contains one pair of anchors (Fig. 141). .. .. **Genus *Polystomoidella* Price, 1939**
4b. Opisthaptor contains two pairs anchors, one pair larger than the other (Fig. 144). .... **Genus *Polystomoides* Ward, 1917**

Life cycle: *P. oris*- Adults parasitize the oral cavity of the turtle, *Chrysemys picta*. Operculate eggs without polar filaments are produced year around and are released at the rate of two or three every 24 hours. Development and hatching of the onchomiracidium requires 28 days (Fig. 145). At least one year is required for development to sexual maturity in the turtle (Paul, 1938).

5a. Opisthaptor has one pair of anchors; testes in middle of body (Fig. 142). .... **Genus *Neodiplorchis* Yamaguti, 1963**
5b. Opisthaptor without anchors; testes in anterior third of body (Fig. 143). .... **Genus *Pseudodiplorchis* Yamaguti, 1963**

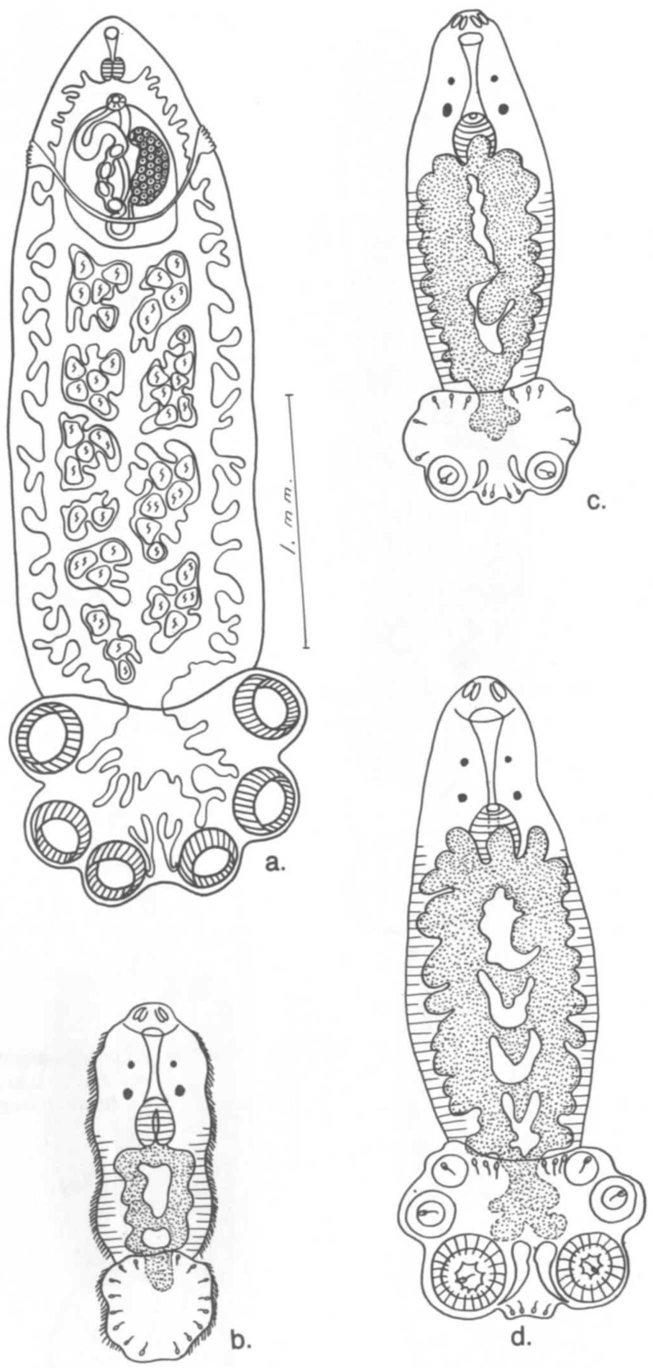


Fig. 139. *Polystoma integerrimum*.
a. adult b. onchomiracidium
c. and d. developmental stages (from Zeller, 1872).

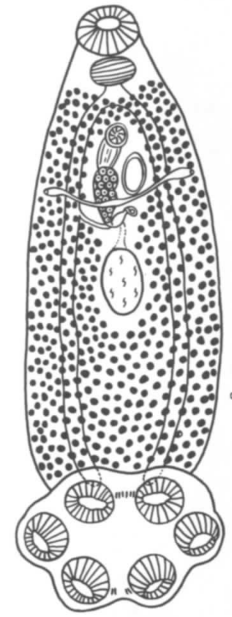


Fig. 140. *Neopolystoma* sp.

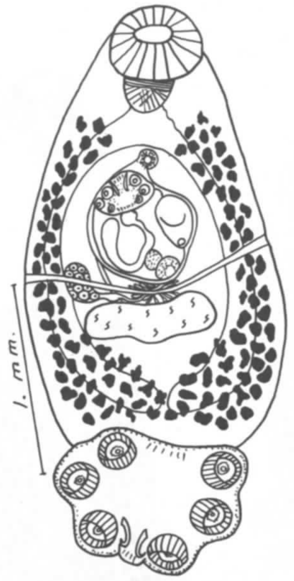


Fig. 141. *Polystomoidella* sp.

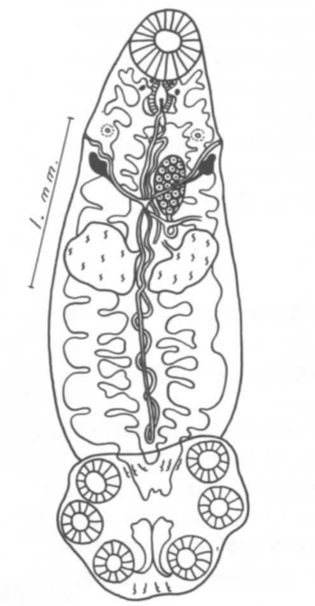


Fig. 142. *Neodiplorchis scaphiopi*. (from Rodgers, 1941)

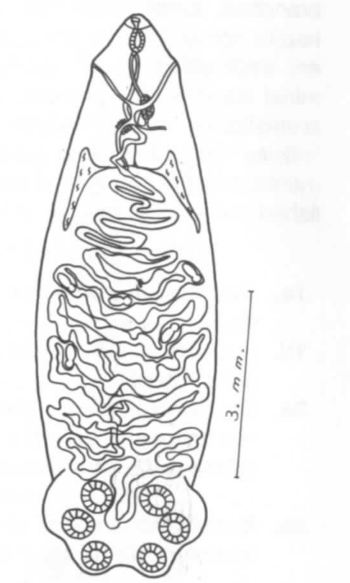


Fig. 143. *Pseudodiplorchis americanus*. (from Rodgers and Kuntz, 1940)

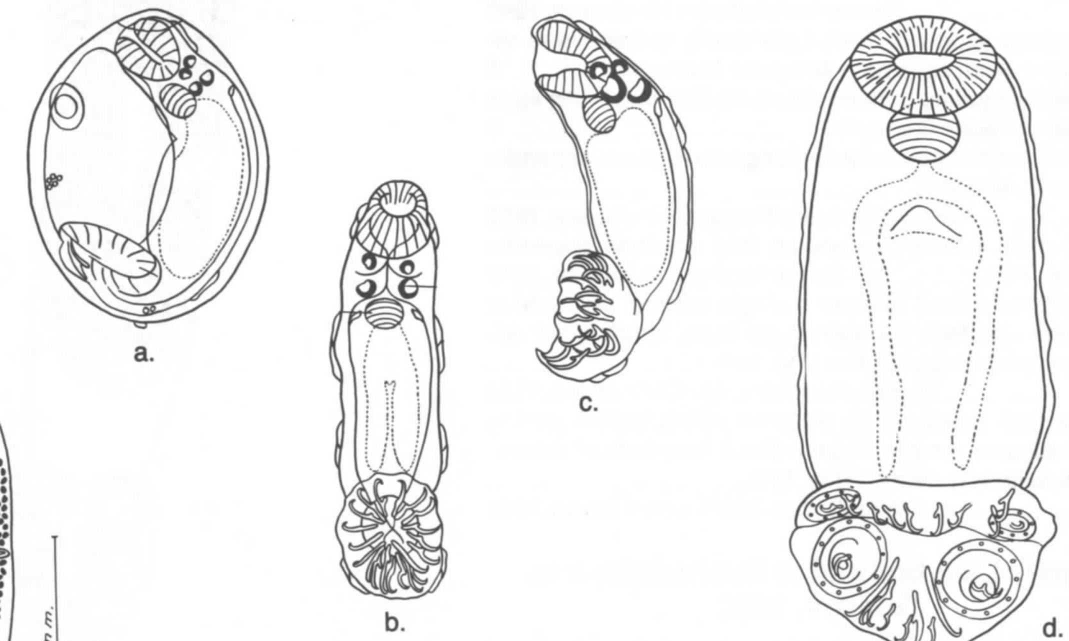


Fig. 145. *Polystomoides oris*.
a. to d. developmental stages (from Paul, 1938)

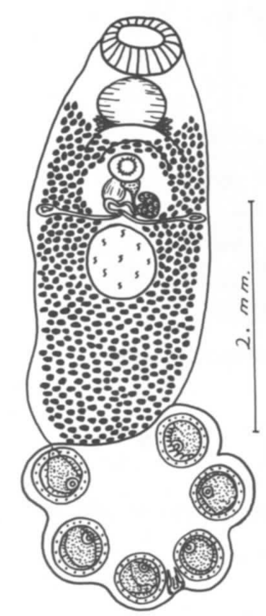


Fig. 144. *Polystomoides coronatum*. (from Price, 1939)

Family Hexabothriidae Price, 1942

Body flat, very contractile; pharynx present; intestinal ceca branched, fused posteriorly and extending into opisthaptor; haptor contains oral sucker; opisthaptor provided with six suckers, each with a curved sclerite; haptoral appendix with two terminal suckers also present; testes multiple, intercecal; ovary pretesticular; two vaginae present, pores ventro-lateral; vitelline follicles distributed along ceca; eggs with or without polar filaments; parasitic on gills of elasmobranchs. Price (1942) published a taxonomic revision of the family.

Key to Genera

1a. Suckers and sclerites of opisthaptor not of uniform size. 2

1b. Suckers and sclerites of opisthaptor of uniform size or nearly so. 4

2a. Oral sucker surrounded by a membranous collar; cirrus large and spiny; vaginae fused before joining vitelline duct; parasites of stingrays (Fig. 146). .... **Genus *Dasyonchocotyle* Hargis, 1955**

2b. Membranous collar absent around oral sucker; vaginae separate for their full length; parasites of sharks. 3

3a. Cirrus small and nonspinous (Fig. 147). .... **Genus *Heteronchocotyle* Brooks, 1934**

3b. Cirrus large, bulbous, spiny; eggs have monopolar filament (Fig. 148). .... **Genus *Hexabothrium* Nordmann, 1840**

4a. Vaginae separate, open individually to transverse vitelline duct; eggs have two polar filaments. 5

4b. Vaginae united before joining vitelline reservoir; eggs without polar filaments. 6

5a. Vitelline follicles not extending into haptoral appendix (no illustration). .... **Genus *Erpocotyle* Beneden and Hesse, 1863**

5b. Vitelline follicles extending into haptoral appendix (Fig. 149). .... **Genus *Neoerpocotyle* Price, 1942**

6a. Vaginae united to form a single median duct which joins vitelline reservoir; eggs have longitudinal ridges; parasites of skates (Fig. 150). .... **Genus *Rajonchocotyle* Cerfontaine, 1899**

6b. Vaginae fused at two different points before joining vitelline reservoir; eggs without longitudinal ridges; parasite of guitarfish (Fig. 151). .... **Genus *Rhinobatonchocotyle* Doran, 1953**

Family Diclybothriidae Bychowsky and Gussev, 1950

Body elongate, cylindrical; intestinal ceca branched and fused posteriorly; prohaptor with two small buccal suckers (bothria) opening into buccal cavity; opisthaptor contains three pairs of suckers, each with a curved sclerite, short haptoral appendix present, bearing three pairs of anchors but no suckers; testes multiple; ovary elongate, folded pretesticular; vaginae united, pores sublateral; vitelline follicles distributed along ceca; eggs without filaments; parasitic on gills of acipenserid fishes (Acipenser and Polyodon).

Only the genus *Diclybothrium* Leuckart, 1835 is known to occur in North America (Fig. 152). The genus contains two species.

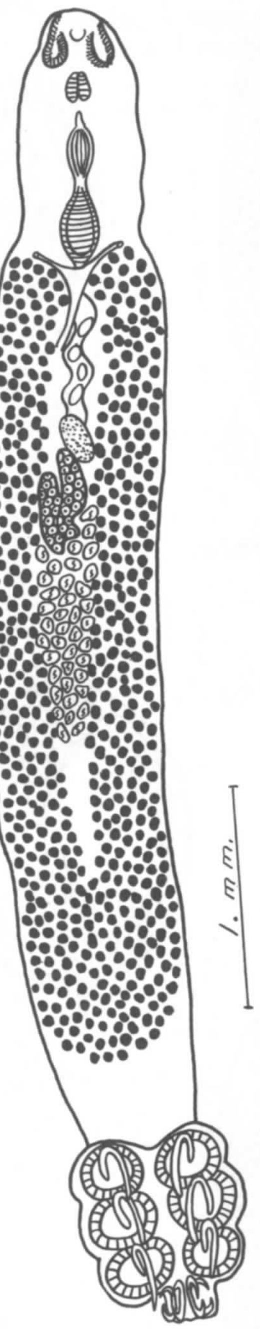


Fig. 152. *Diclybothrium hamulatum.*

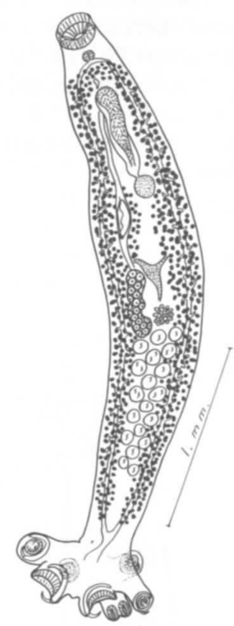


Fig. 146. *Dasyonchocotyle spiniphallus.*

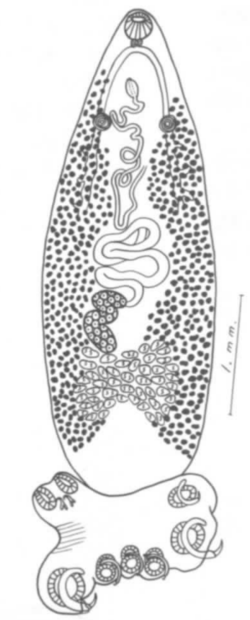


Fig. 147. *Heteronchocotyle hypoprioni.*

Fig. 148b. Cirrus, lateral view.

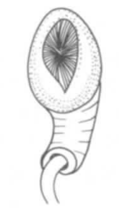


Fig. 148c. Cirrus, ventral view.

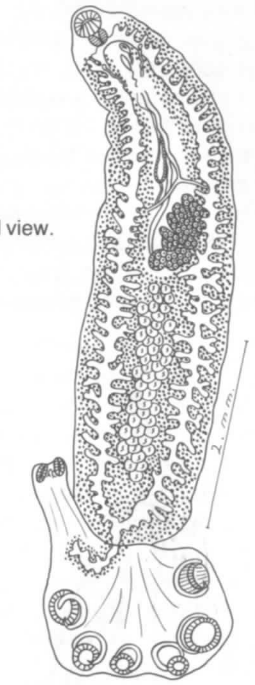


Fig. 148a. *Hexabothrium canicula.* (from Sproston, 1946).

Fig. 149a. *Neoerpocotyle ginglymostomae.*

Fig. 149b. Vaginae.

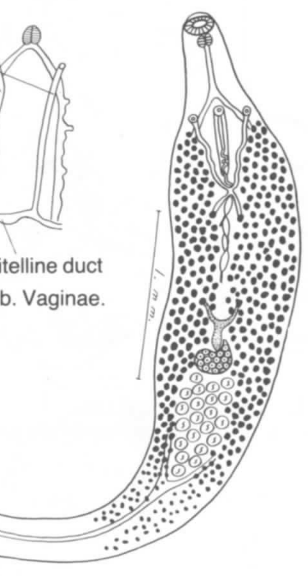


Fig. 150a. *Rajonchocotyle wehri.* (from Price, 1942)

Fig. 151b. Vaginae.

Fig. 150b. Vaginae.

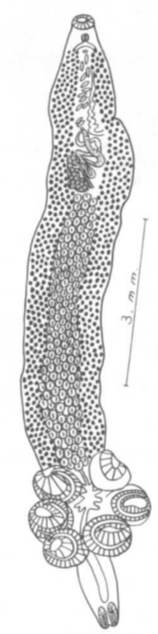


Fig. 151a. *Rhinobatonchocotyle cyclovaginatus.*

Family Sphyranuridae Poche, 1926

Body small (about 2mm), cylindrical; eyespots absent; pharynx present; intestinal ceca without branches, fused posteriorly to form cyclocoel; prohaptor in form of an oral sucker; opisthaptor bilobed and contains two large suckers, one pair of anchors and 14 marginal hooks; testes multiple; ovary pretesticular; two vaginae present; vitelline follicles distributed along ceca lateral to testes; parasitic on gills and skin of caudate amphibians.

The family contains only the genus *Sphyranura* Wright, 1879 (Fig. 153). Four species have been reported from North America as parasites of waterdogs, *Necturus maculosus* and the Oklahoma salamander, *Eurycea tynerensis*.

Life cycle: *S. oligorchis* - Adults inhabit the gills of *Necturus maculosus*. An onchomiracidium develops and hatches in 28 to 32 days following oviposition. The newly hatched larva (Fig. 154) has a bilobed opisthaptor which contains one pair of anchors, 16 hooks and two developing suckers. Larvae creep inchworm fashion in search of a host. They apparently attach to the gills first, then move to the skin as very young larvae are not found on the skin. Testes first appear on days 12 to 15 and the ovary on days 15 to 19 following attachment. The entire cycle is completed in less than two months (Alvey, 1936).

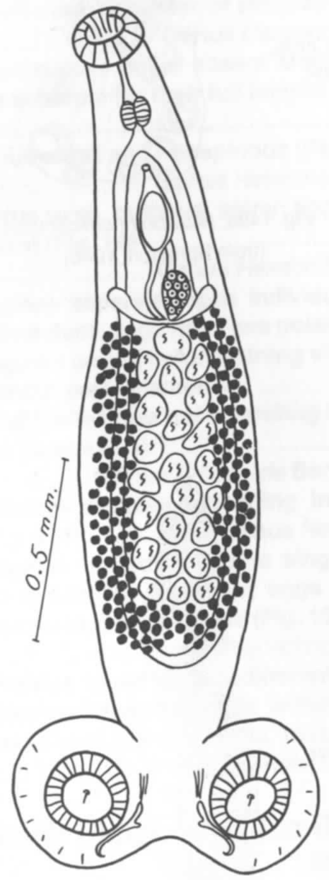


Fig. 153. *Sphyranura osleri.*

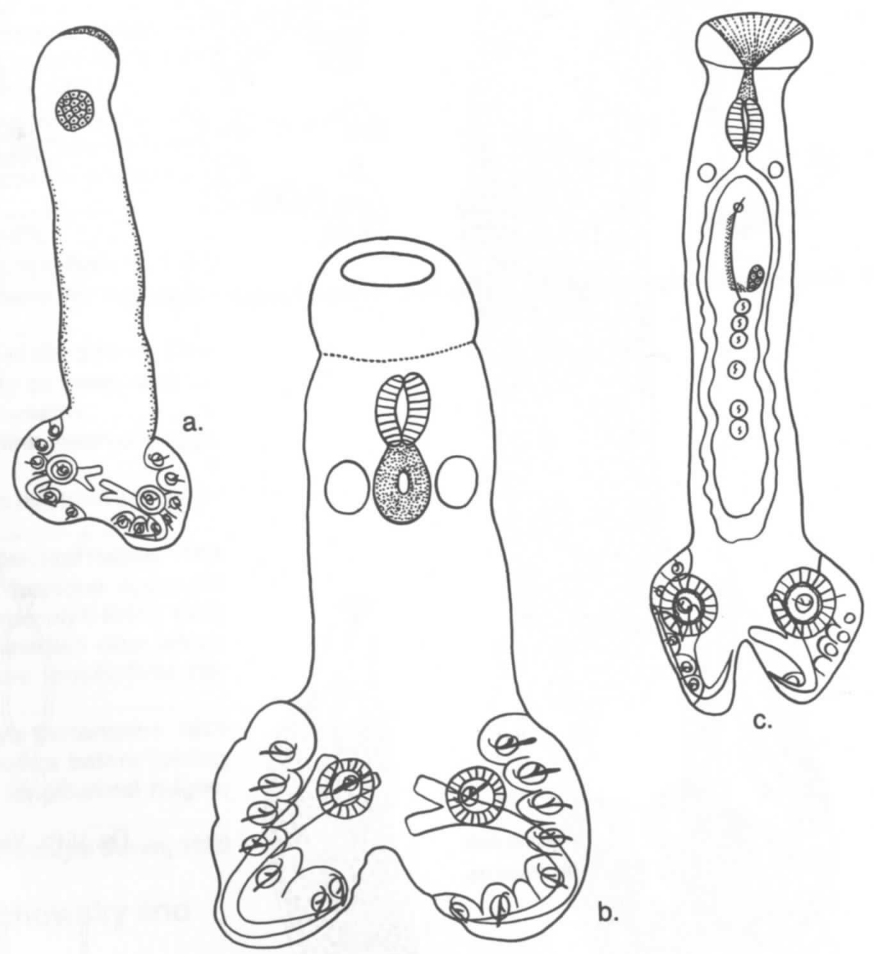


Fig. 154. *Sphyranura oligorchis.*
a. to c. developmental stages (from Alvey, 1936)

Superfamily Chimaericoloidea Brinkmann, 1952
Family Chimaericolidae Brinkmann, 1952

Body long, divided into wide anterior part and narrower posterior part; prohaptor a weakly developed oral sucker; ceca branched in wide part of body but not in narrow part, extend into opisthaptor which is distinct and contains four pairs of pedunculate clamps, each composed of three U-shaped sclerites; wide part of body contains reproductive organs; testes multiple; ovary lobed, pretesticular; genital pore median, in anterior fourth of body; vitelline follicles around ceca in wide part of body; vagina double, pores ventrolateral; uterus composed of many longitudinal folds; eggs have polar filaments; parasitic on gills of Holocephali.

The genus *Chimaericola* Brinkmann, 1942 is represented in North America by *C. leptogaster,* a parasite of the ratfish, *Hydrolagus colliei* (Fig. 155).

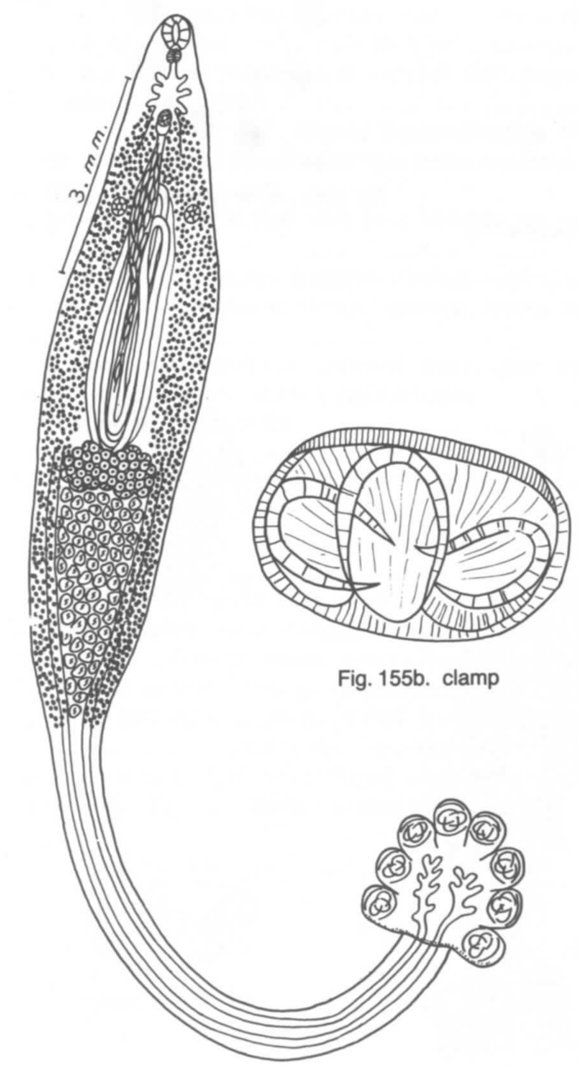


Fig. 155b. clamp

Fig. 155a. *Chimaericola leptogaster.*

Superfamily Diclidophoroidea Price, 1936
Family Diclidophoridae Cerfontaine, 1895

Body elongate, flat; eyespots absent; intestinal ceca branched, fused or not fused posteriorly, sometimes extend into opisthaptor; prohaptor composed of two small buccal suckers; opisthaptor contains eight pedunculate asymmetrical clamps, some with a muscular, spinous and/or adhesive pad or a sucker in the inner quadrant, wall of clamp may have riblike sclerites; testes multiple; ovary usually pretesticular; vitelline follicles distributed along ceca; eggs have bipolar filaments; parasitic on gills of marine fishes. Price (1943a) published a taxonomic revision of the family.

Key to Genera

1a. Opisthaptor has three pairs of large pedunculate clamps and a haptoral appendix with one pair of small clamps; clamps have a sucker on the inner quadrant plus rib sclerites in the wall; ovary has inverted U-shape; vagina absent; parasite of marine perch (Fig. 156). .... Genus *Pedocotyle* MacCallum, 1913

1b. Haptoral appendix absent. 2

2a. Posterior third of body narrow and without vitelline follicles; ovary N-shaped; clamps without adhesive pad or sucker; parasite of flounder and sea trout (Fig. 157). .... Genus *Neoheterobothrium* Price, 1943

2b. Posterior part of body as wide as rest of body and contains vitelline follicles. 3

3a. Testes distributed anterior and posterior to ovary; clamps contain a muscular and a spinous pad (Fig. 158). .... Genus *Echinopelma* Raecke, 1945

3b. Testes all posterior to ovary. 4

4a. Clamps contain a sucker and ribs (Fig. 160). .... Genus *Choricotyle* Beneden and Hesse, 1863

4b. Clamps without a sucker and ribs. 5

5a. Clamps uniform in size; ovary N-shaped (Fig. 159). .... Genus *Diclidophora* Kroyer, 1838

Life cycle: *Diclidophora* sp. - Eggs are produced at the rate of one every 13 minutes. The onchomiracidium develops and hatches in about 32 days at 12.5 C. They attach to gills and gradually produce clamps. Sexual maturity is attained in 135 days following hatching. Several species of sea perch serve as host under natural conditions but experimental infections were established in redtail, silver and walleye sea perch (Hanson, 1973).

5b. Clamps unequal in size, the size decreasing posteriorly, last pair the smallest and on terminal lappet; ovary elongate, folded back on itself (Fig. 161). .... Genus *Absonifibula* Lawler and Overstreet, 1976

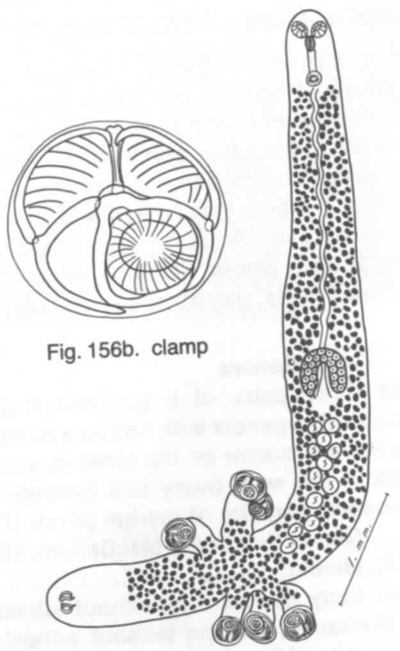


Fig. 156b. clamp

Fig. 156a. *Pedocotyle morone.*

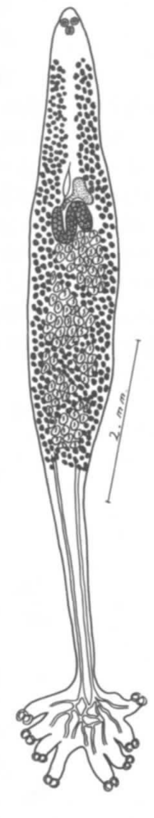


Fig. 157a. *Neoheterobothrium pugetensis.*

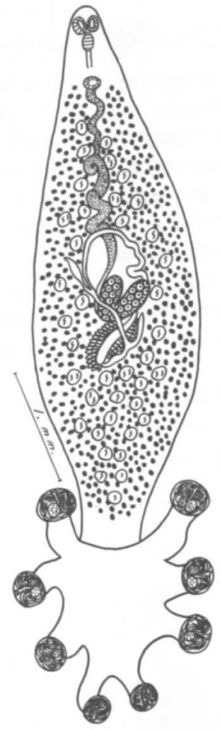


Fig. 158a. *Echinopelma bermudae.*

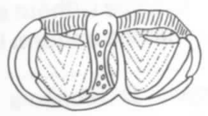


Fig. 157b. clamp

Fig. 158b. clamp

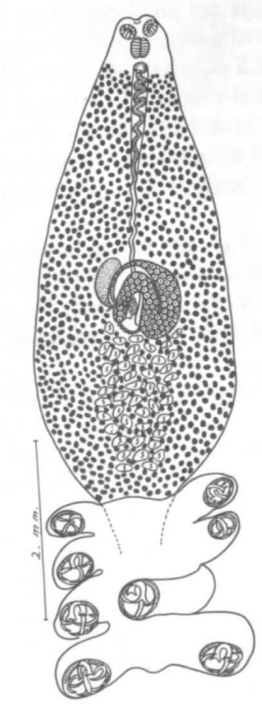


Fig. 159a. *Diclidophora maccallumi*

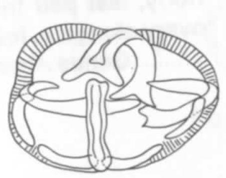


Fig. 159b. clamp

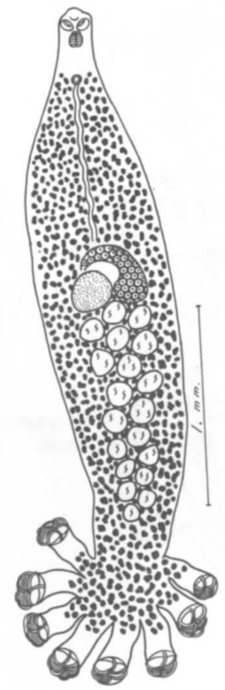


Fig. 160a. *Choricotyle prionoti*

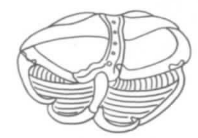


Fig. 160b. clamp

Family Mazocraeidae Price, 1936

Body small, flat; intestinal ceca branched; prohaptor composed of two small buccal suckers; opisthaptor symmetrical or asymmetrical, distinctly set off from body or clamps mounted directly on sides of body; clamps sessile or pedunculate, sclerites U-shaped; one or more pairs of anchors on terminal lappet; single or multiple testes; ovary long, usually folded, pretesticular or opposite to testis; vitelline follicles abundant, filling most of body around gonads; parasitic on gills of herring and mackerel. Price (1961b) published a taxonomic revision of the family.

Key to Genera

1a. Clamps mounted on sides of body, extending forward as far as anterior end of testis and ovary; parasite of herring. 2

1b. Clamps restricted to a distinct opisthaptor. 3

2a. Testis single and opposite to ovary; clamps small, extending forward to anterior end of ovary (Fig. 162). .... Genus *Mazocraeoides* Price, 1936

2b. Testis posterior to ovary; clamps large, extending forward at least to level of testis (Fig. 163). .... Genus *Pseudomazocraeoides* Price, 1961

3a. Opisthaptor asymmetrical with four large clamps on right side and one very small one on left side; parasite of mackerel (Fig. 164). .... Genus *Grubea* Diesing, 1856 (Note: Left-handed opisthaptor has been reported by Wagner (1975).

3b. Opisthaptor symmetrical with four clamps on each side. 4

4a. Terminus of opisthaptor a single lobe containing one or two pairs of anchors; clamps sessile; testes multiple. 5

4b. Terminus of opisthaptor bilobed, each lobe containing one anchor; clamps pedunculate; testis single; parasite of menhaden. 6

5a. Clamps of uniform size; ovary elongate, folded; hooks of genital coronet in two longitudinal rows; testes large, transverse; parasite of scombrid fishes (Fig. 165). .... Genus *Kuhnia* Sproston, 1945

5b. Clamps of anterior pair distinctly larger than the others; ovary oval; hooks of genital coronet in a transverse arc; testes small; parasite of gizzard shad (Fig. 166). .... Genus *Pseudanthocotyloides* Price, 1958

6a. Clamps of anterior two pairs distinctly larger than posterior two pairs; testis large and deeply lobed (Fig. 167). .... Genus *Neoclupeocotyle* Price, 1961

6b. All clamps of uniform size; testis large only slightly lobed (Fig. 168). ..... Genus *Clupeocotyle* Hargis, 1955

Family Discocotylidae Price, 1936

Body flat, elongate; intestinal ceca branched; prohaptor composed of two small suckers opening into buccal cavity; opisthaptor indistinctly set off from body, containing four pairs of discocotylid clamps; testes multiple or one large testis (in *Octomacrum*); ovary either pre- or post-testicular; vagina either single or double, pores lateral, single pore lateral or median; vitelline follicles along ceca; eggs with or without polar filaments; parasitic on gills of freshwater and marine fishes. Price (1943b) published a taxonomic revision of the family.

Key to Genera

1a. Testis single, large, lobed; clamps of posterior pair smaller than the others; on gills of freshwater fishes (Fig. 169). .... Genus *Octomacrum* Mueller, 1934

1b. Testes multiple. 2

2a. Ovary posttesticular; clamps with accessory sclerites. 3

2b. Ovary pretesticular; clamps without accessory sclerites. 4

3a. Anterior part of body permanently oriented at right angles to remainder of body; ceca fused in opisthaptor; two vaginae with bilateral pores; parasitic on gills of leatherjacket (Fig. 170). .... Genus *Vallisia* Parona and Perrugia, 1890

3b. Body straight; ceca not fused in opisthaptor; vagina single, pore lateral; parasitic on gills of lookdown (Fig. 171). .... Genus *Pseudomazocraes* Caballero and Bravo-Hollis, 1955

4a. Clamps of anterior pair much larger than the others; end of opisthaptor with three pairs of dissimilar anchors (Fig. 172). .... Genus *Anthocotyle* Beneden and Hesse, 1863.

4b. Clamps all of uniform size or posterior pair slightly smaller than the others. 5

5a. Opisthaptor deeply lobed posteriorly with four equal clamps in each lobe; vagina single, pore dorso-median; parasite of marine fishes (Fig. 173). .... Genus *Bicotylophora* Price, 1936

5b. Opisthaptor not lobed, somewhat oval or rectangular; vagina single or double. 6

6a. Vagina double, Y-shaped, pores lateral; genital atrium unarmed; clamps of uniform size; parasitic on gills of salmonid fishes (Fig. 174). .... Genus *Discocotyle* Diesing, 1850

6b. Vagina single, pore ventrolateral; genital atrium armed; clamps of posterior pair distinctly smaller than the others; parasitic on gills of carpsucker (Fig. 175). .... Genus *Neodiscocotyle* Dechtiar, 1967

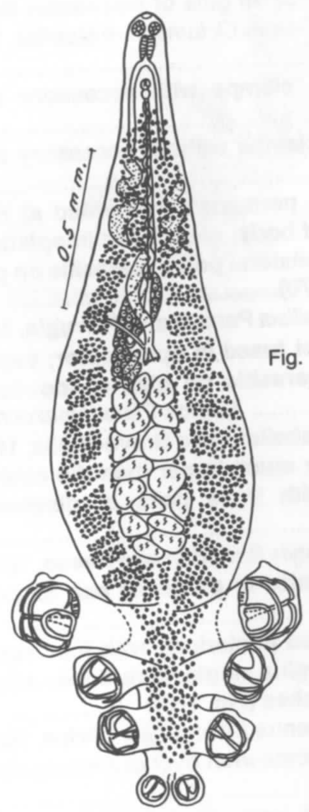


Fig. 161a. *Absonifibula bychowskyi.* (from Lawler and Overstreet, 1976)

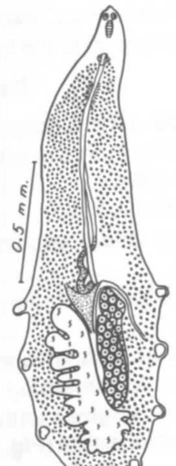


Fig. 162a. *Mazocraeoides georgei*

Fig. 162b. genital atrium

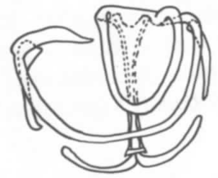


Fig. 161b. clamp

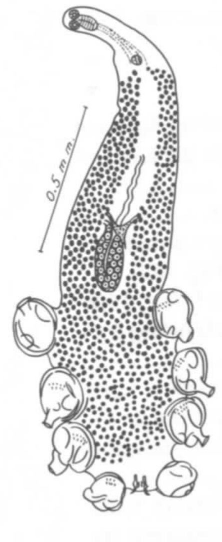


Fig. 163. *Pseudomazocraeoides megalocotyle.*

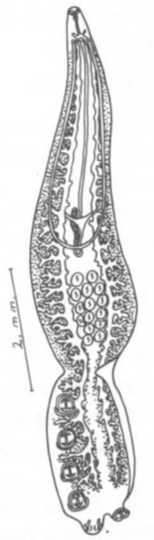


Fig. 164a. *Grubea cochlear.*

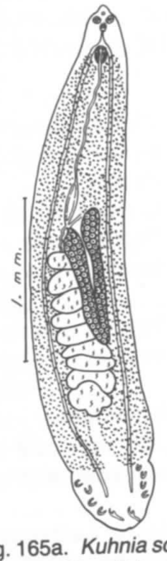


Fig. 165a. *Kuhnia scombri.* (from Price, 1961).

Fig. 164b. clamp

Fig. 165b. genital coronet

Fig. 165c. clamp

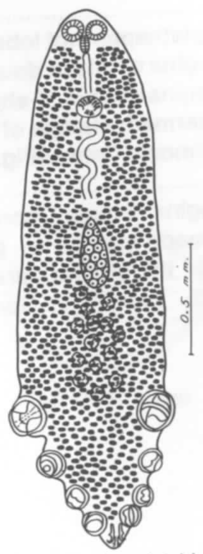


Fig. 166. *Pseudanthocotyloides banghami.*

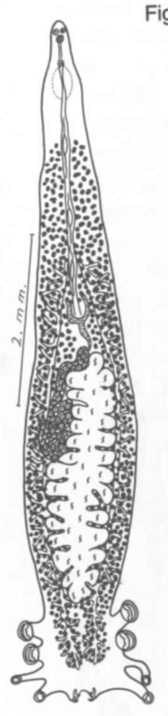


Fig. 167a. *Neoclupeocotyle megaconfibula.*

Fig. 167b. clamp

Fig. 168b. clamp

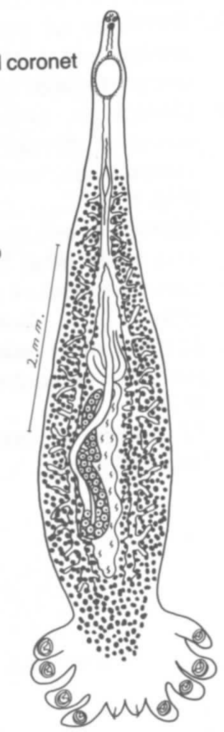


Fig. 168a. *Clupeocotyle brevoortia.*

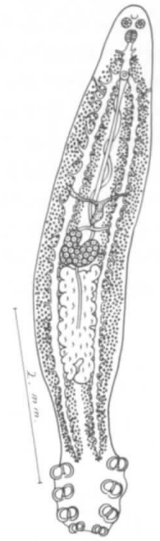


Fig. 169. *Octomacrum lanceatum.*

Fig. 170a. *Vallisia oligoplites.*

Fig. 170b. clamp

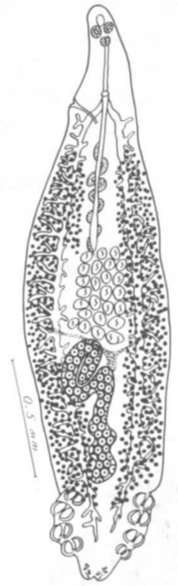


Fig. 171a. *Pseudomazocraes selene.*

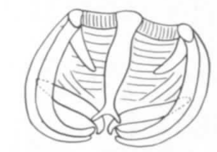


Fig. 171b. clamp

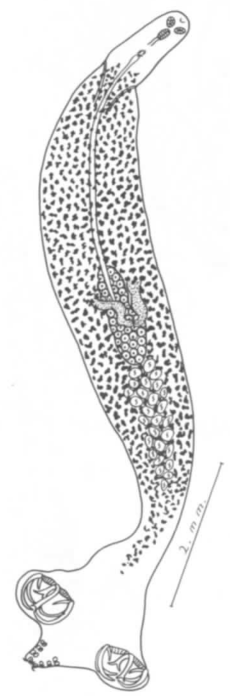


Fig. 172a. *Anthocotyle americanus.*

Fig. 172b. clamp

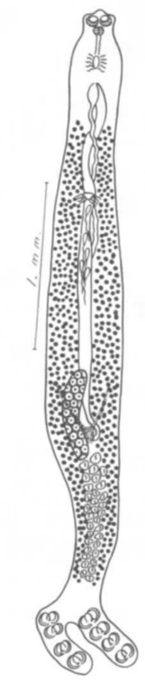


Fig. 173. *Bicotylophora trachinoti.*

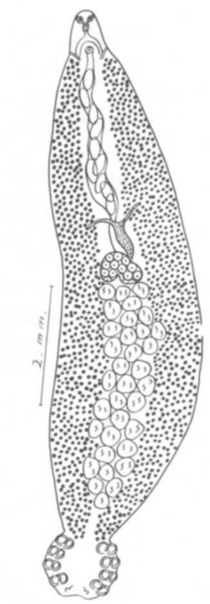


Fig. 174. *Discocotyle salmonis.*

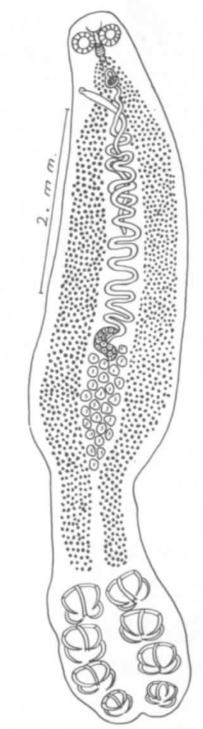


Fig. 175. *Neodiscocotyle carpioditis.*

Family Dactylocotylidae Brinkmann, 1942

Body flat, gradually widening toward posterior end; intestinal ceca branched, fused posteriorly; prohaptor composed of two buccal suckers that open into buccal cavity; opisthaptor contains four pairs pedunculate clamps, each with a denticulate patch in one quadrant; haptoral appendix absent; testes multiple, pre- and postovarian (only postovarian in North American forms); ovary N-shaped; vitelline follicles abundant, extend into opisthaptor; eggs with bipolar filaments; parasitic on gills of marine fishes.

The genus *Dactylocotyle* Beneden and Hesse, 1863 has been reported from North America (Fig. 176).

Life cycle: *D. denticulata* - Adults parasitize the gills of pollock, *Pollachius virens*. Eggs are laid in clusters of 100 to 200 with their filaments intertwined. Onchomiracidia develop in 18 to 19 days at 14° C. After hatching, they attach to the gills of the host fish, lose the cilia and start to produce clamps. Experimental infections were followed for 38 days, through the first and second larval stages. Second stage larvae were produced in 5 to 13 days after hatching. Later larval stages were obtained from natural infections. Clamps develop in pairs, starting with the posterior pair. As clamps develop, the larval hooks are gradually shed. Development to sexual maturity requires about six months (Frankland, 1955).

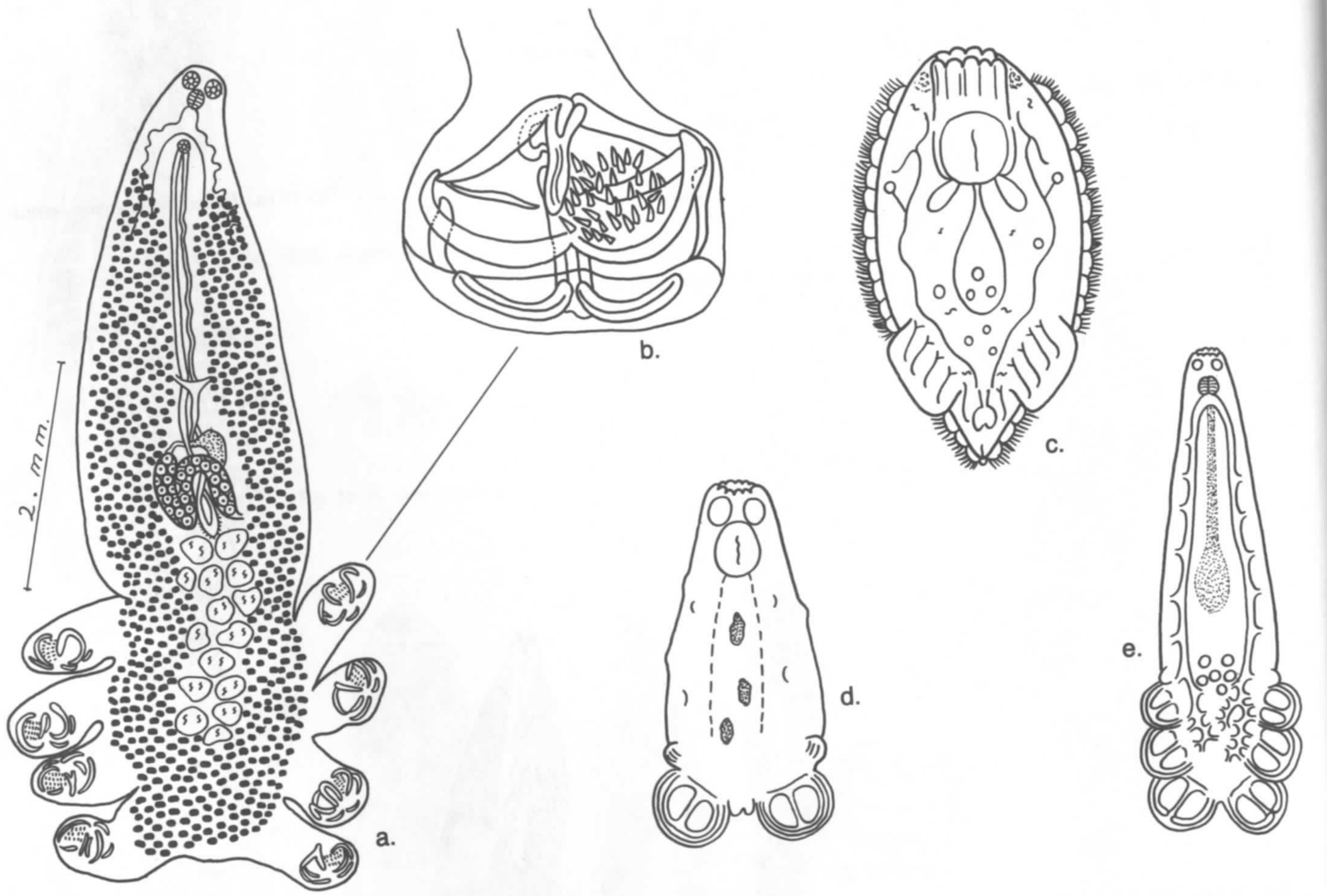


Fig. 176. *Dactylocotyle denticulata*.
a. adult b. clamp c. onchomiracidium
d. and e. development stages (from Frankland, 1955).

Family Macrovalvitrematidae Yamaguti, 1963

Body small (1 to 2mm), cylindrical; ceca branched united posteriorly within opisthaptor; prohaptor has large cupshaped buccal cavity with a pair of small buccal suckers opening into it; opisthaptor contains eight guitar- or firetong-shaped or oblong clamps; testis single or testes multiple; ovary pretesticular; vaginae present, pores lateral; vitelline follicles distributed along ceca; on gills of marine fishes.

Key to Genera

1a. Testis single; bilateral placodes on anterior third of body; clamps of two kinds, posterior pair oblong, the others firetong-shaped; parasite of marine perch (Fig. 177). .... Genus *Hargisia* Yamaguti, 1963

1b. Testes multiple; body without placodes; all clamps similar in size and shape. 2

2a. Clamps guitar-shaped; parasite of croakers (Fig. 178). .... Genus *Macrovalvitrematoides* Yamaguti, 1963

2b. Clamps oblong with serrated margins; parasite of pigfish (Fig. 179). .... Genus *Pseudotagia* Yamaguti, 1963

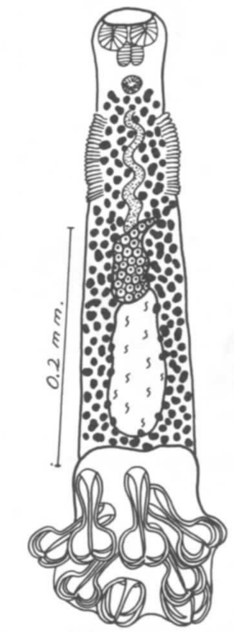


Fig. 177a. *Hargisia bairdiella*

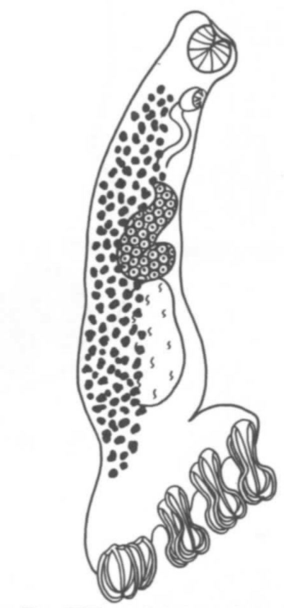


Fig. 177b. adult, lateral view

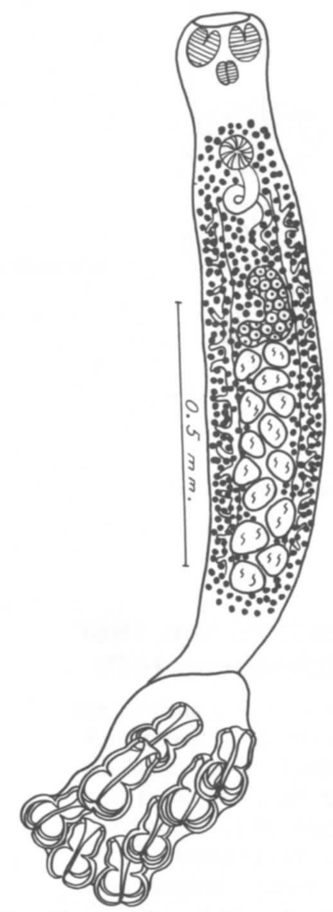


Fig. 178a. *Macrovalvitrematoides micropogoni.*

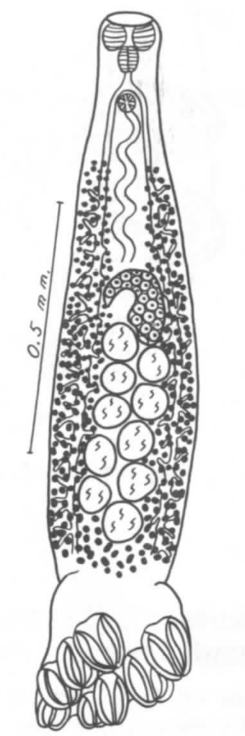


Fig. 179a. *Pseudotagia cupida.*

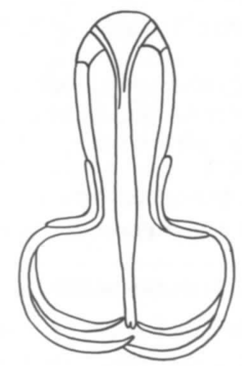


Fig. 177c. fire-tong clamp

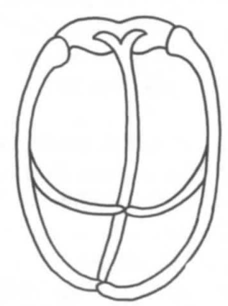


Fig. 177d. oblong clamp

Fig. 178b. clamp

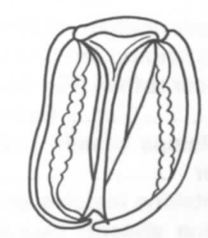


Fig. 179b. clamp

Family Hexostomatidae Price, 1936

Body flat; eyespots absent; prohaptor contains a pair of small buccal suckers; opisthaptor indistinctly set off from body, contains four pairs of sessile clamps, each consisting of three vestigial sclerites embedded in a large sucker; one or two pairs of anchors between posterior clamps; testes multiple; ovary inverted U-shape, pretesticular; vaginal pore dorsomedian; eggs have bipolar filaments; parasitic on gills of marine fishes. Price (1961a) published a taxonomic revision of the family.

Key to Genera

1a. Clamps arranged along lateral and posterior margins of opisthaptor, clamps of posterior pair slightly smaller than the others (Fig. 180). ....Genus *Neohexostoma* Price, 1961

1b. Clamps arranged along posterior margin of opisthaptor, clamps of posterior pair much smaller than the others (Fig. 181). .... Genus *Hexostoma* Rafinesque, 1815

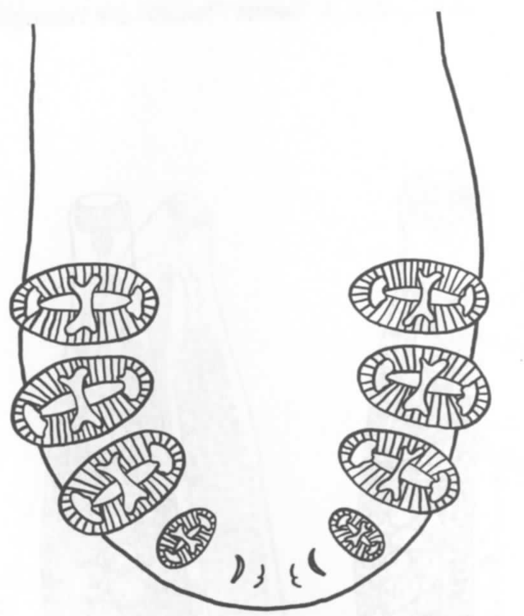


Fig. 180. *Neohexostoma* sp., opisthaptor

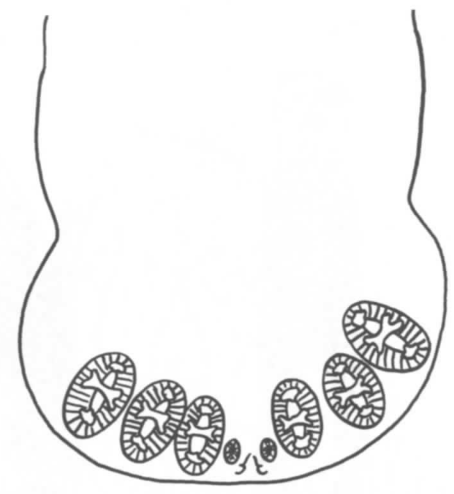


Fig. 181. *Hexostoma* sp., opisthaptor

Superfamily Microcotyloidea Unnithan, 1957
Family Microcotylidae Taschenberg, 1879

Body flat, large (4 to 12mm); intestinal ceca branched, not fused posteriorly; prohaptor composed of two small buccal suckers which open into buccal cavity; opisthaptor symmetrical, distinct or not; clamps numerous and of the microcotylid type; anchors absent; testes multiple; ovary pretesticular, folded or C-shaped; vagina usually present, pore lateral or dorsal; vitelline follicles around ceca; eggs with one or two polar filaments; parasitic on gills of freshwater and marine fishes.

Key to Genera

1a. Pedunculate clamps mounted on sides of body, extending forward to level of ovary; body margins appear ruffled (Fig. 182). .... Genus *Prosomicrocotyla* Yamaguti, 1958

1b. Clamps sessile and mounted on a distinct opisthaptor 2

2a. Vitelline follicles absent in posterior fifth of body; vagina absent; buccal suckers spinous; parasitic on gills of mullet (Fig. 183) .... Genus *Metamicrocotyla* Yamaguti, 1953

2b. Vitelline follicles extend into posterior part of body; one or two vaginae present; buccal suckers nonspinous. 3

3a. Two vaginae present, pores lateral and recessed; genital atrium domeshaped and ribbed; ejaculatory duct long, thick and muscular (Fig. 184). .... Genus *Bivagina* Yamaguti, 1963

3b. One vagina present; genital atrium and ejaculatory duct not as described above. 4

4a. Vaginal pore on right margin of body; parasite of gray snapper (Fig. 185) .... Genus *Microcotyloides* Fujii, 1944

4b. Vaginal pore on dorso-median body surface. 5

5a. Genital atrium unarmed; clamps in double rows along sides of opisthaptor (Fig. 187). .... Genus *Aspinatrium* Yamaguti, 1963

5b. Genital atrium armed with spiny coronet; clamps in single rows (Fig. 186). .... Genus *Microcotyle* Beneden and Hesse, 1863

Life cycle: *M. spinicirrus* - Adults inhabit the gills of freshwater drum, *Aplodinotus grunniens*. The onchomiracidium (Fig. 188) develops in 5 to 11 days following oviposition. They have three bands of cilia, pigmented eyespots, pharynx, six pairs of hooks, two pairs anchors and three pairs of flame cells. They attach to the gills of a suitable host fish then shed the cilia and start to produce clamps which develop from clamp primordia at the anterior end of the series. The larval hooks and anchors are eventually lost (Remley, 1942).

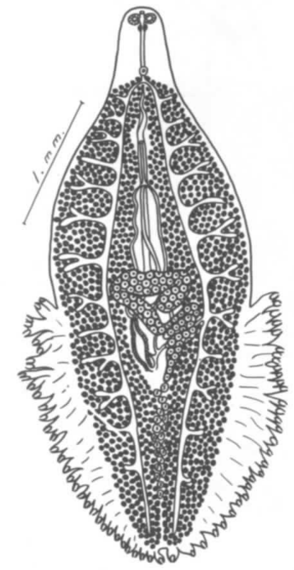


Fig. 182. *Prosomicrocotyla chiri.*

Fig. 183a. *Metamicrocotyla* macracantha

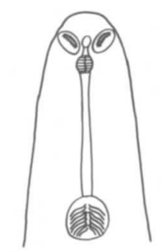


Fig. 183b. genital armature

Fig. 184b. vaginae

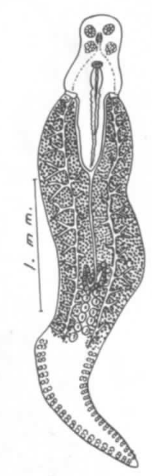


Fig. 184a. *Bivagina punctipinnis.*

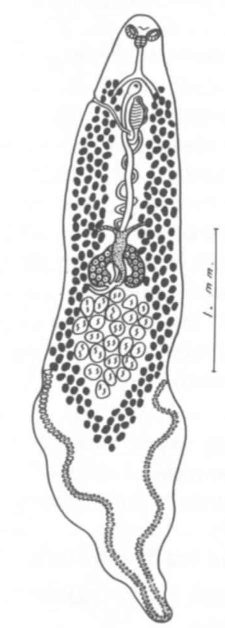


Fig. 185. *Microcotyloides incisa.*

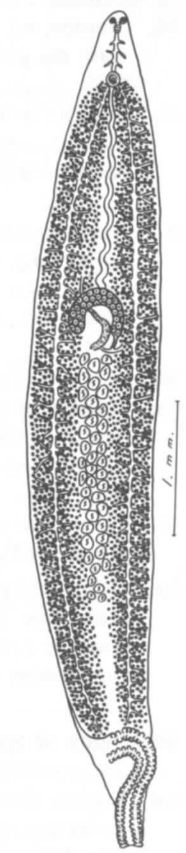


Fig. 186. *Microcotyle pseudomugilis.*

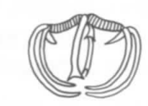


Fig. 187b. Microcotylid clamp.

Fig. 187a. *Aspinatrium pogoniae.*

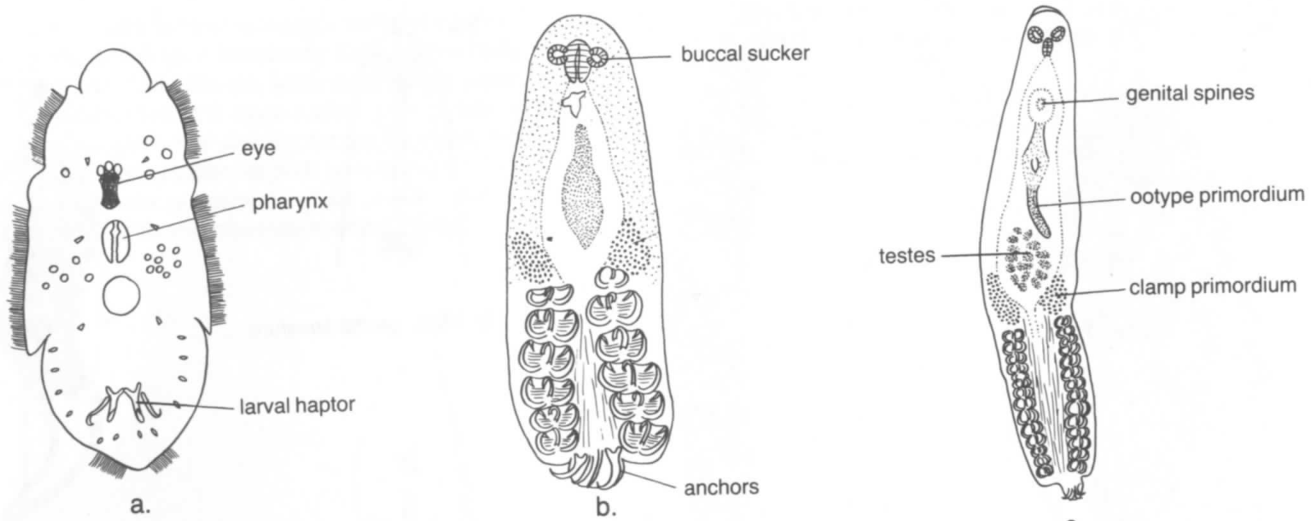


Fig. 188 *Microcotyle spinicirrus*, larvae.
a. onchomiracidium b. and c. developmental stages.

Family Axinidae Unnithan, 1957

Body flat, narrow anteriorly and gradually widened posteriorly; intestinal ceca branched; prohaptor composed of two small buccal suckers; opisthaptor truncate, clamps arranged in two end-to-end rows, the rows separated by anchors; testes multiple; ovary pretesticular, U or J-shaped, the ends directed forward; vitelline follicles distributed around ceca; eggs have bipolar filaments; parasitic on gills of marine fishes. Price (1962a) published a taxonomic revision of the family.

Key to Genera

1a. Genital atrium armed, the spines arranged in two lateral and one transverse row plus a spinous genital coronet (Fig. 189). .... Genus *Axine* Abildgaard, 1794

1b. Genital atrium unarmed. 2

2a. Body broadly triangular; cirrus spinous; vaginal pore dorso-lateral and has horn-like spines; parasites of houndfish (Fig. 190). .... Genus *Chlamydaxine* Unnithan, 1957

2b. Body elongate, only slightly wider posteriorly; lateral sclerites of clamp segmented; parasites of hound-and needlefish. 3

3a. Cirrus spinous; vaginal pore dorso-median, spinous; clamps rectangular (Fig. 191). .... Genus *Axinoides* Yamaguti, 1938

3b. Cirrus nonspinous; vaginal pore dorsal and sublateral, armed with horn-like spines; clamps transversely oval (Fig. 192). .... Genus *Nudaciraxine* Price, 1962

Family Heteraxinidae Price, 1962

Body triangular or elongate; prohaptor composed of two small buccal suckers; opisthaptor triangular, asymmetrical, clamps more abundant or larger on one side or arranged in a single row across posterior end of opisthaptor; median sclerite of clamp bifid or trifid at tip; testes multiple; ovary pretesticular, U-, C- or M-shaped; vagina present or absent; eggs have one or two polar filaments; parasites of freshwater and marine fishes. Price (1962b) published a taxonomic review of the family.

Key to Genera

1a. Clamps on only one side of opisthaptor or in a single row across posterior end; tips of median sclerite bifid. 2

1b. Clamps on both sides of opisthaptor. 3

2a. Clamps on only one side of opisthaptor; vagina absent; on gills of grunnion; ovary U- or C-shaped (Fig. 193). .... Genus *Leuresthicola* Price, 1962

2b. Clamps in a single row across posterior end of opisthaptor; vagina present; ovary M-shaped; on gills of barracuda (Fig. 194). .... Genus *Pseudochauhanea* Yamaguti, 1965

3a. Opisthaptor contains large and small clamps, the larger are asymmetrical, having the outer sclerite larger than the inner; smaller clamps are symmetrical with trifid median sclerite; parasite or jackfish (Fig. 195). .... Genus *Cemocotyle* Sproston, 1946

3b. All clamps symmetrical, can be of one or two sizes....4

4a. Clamps of uniform size on both sides of opisthaptor; genital atrium has two anterior and two posterior spinous pockets; parasites of weakfish and seatrout (Fig. 196). .... Genus *Cynoscionicola* Price, 1962

4b. Clamps of one side of opisthaptor much larger than those of other side. 5

5a. Sides of opisthaptor of nearly equal length; clamps fewer and larger on one side; genital atrium has two rows of spines attached to anterior wall; parasite of freshwater drumfish (Fig. 197). .... Genus *Lintaxine* Sproston, 1946

5b. Sides of opisthaptor of unequal length, clamps fewer and usually smaller on one side. 6

6a. Vagina absent; eggs few; genital atrium has two antero-lateral spiny pockets; parasite of spat and margate (Fig. 198). .... Genus *Heteraxinoides* Yamaguti, 1963

6b. Vagina present; eggs abundant; genital atrium armed with concentric rows of spines, no pockets; parasite of amberjack (Fig. 199). .... Genus *Allencotyla* Price, 1962

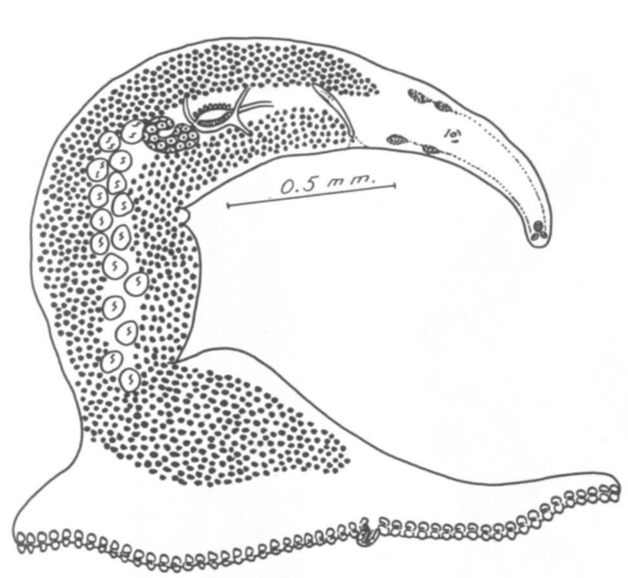


Fig. 189a. *Axine hyporamphi*.

Fig. 189b. genital atrium

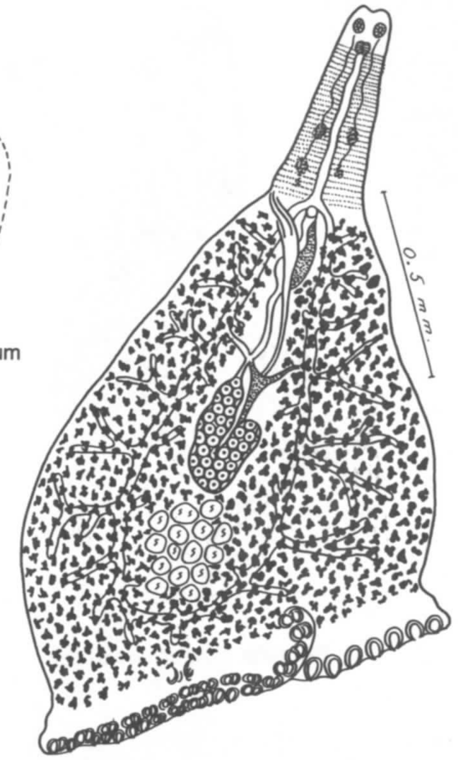


Fig. 190a. *Chlamydaxine truncata*.

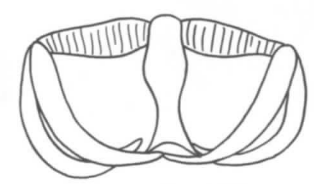


Fig. 190b. clamp

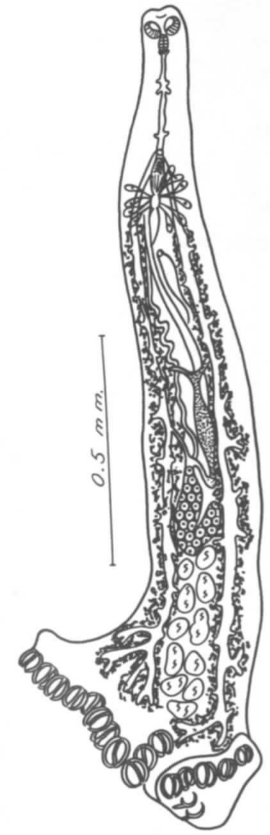


Fig. 191a. *Axinoides raphidoma*.

Fig. 191b. clamp

Fig. 192b. clamp

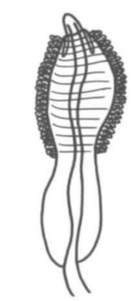


Fig. 192c. cirrus

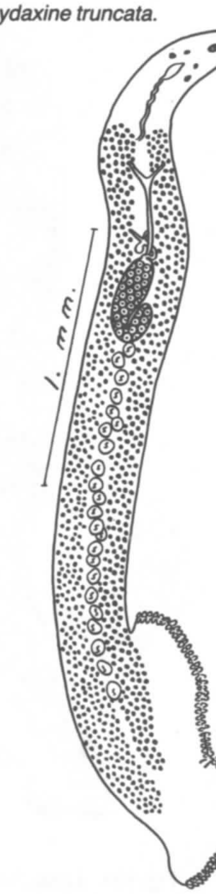


Fig. 192a. *Nudaciraxine gracilis*.

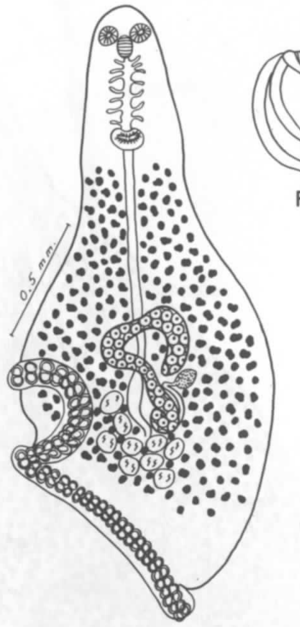


Fig. 193a. *Leuresthicola olsoni.*

Fig. 193b. clamp

Fig. 194b. clamp

Fig. 194a. *Pseudochauhanea argentea.*

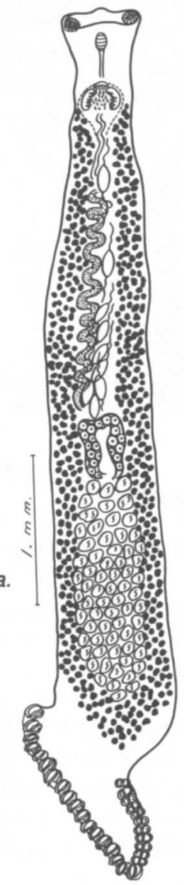


Fig. 195a. *Cemocotyle carangis.*

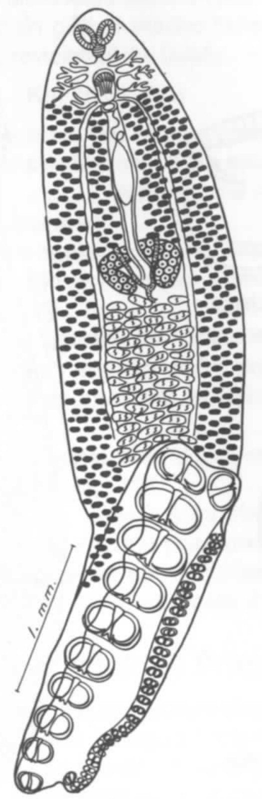


Fig. 197. *Lintaxine cokeri.*

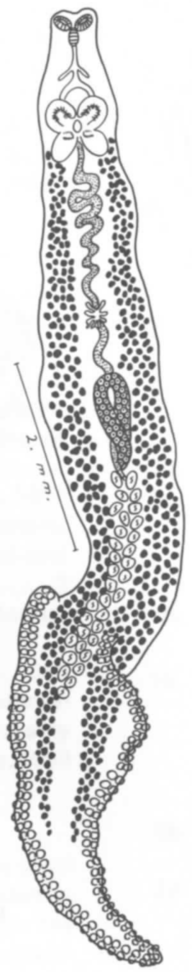


Fig. 196. *Cynoscionicola heteracantha.*

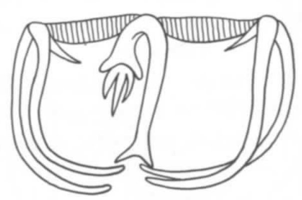


Fig. 195c. small clamp

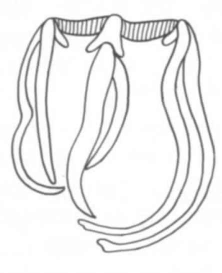


Fig. 195b. large clamp

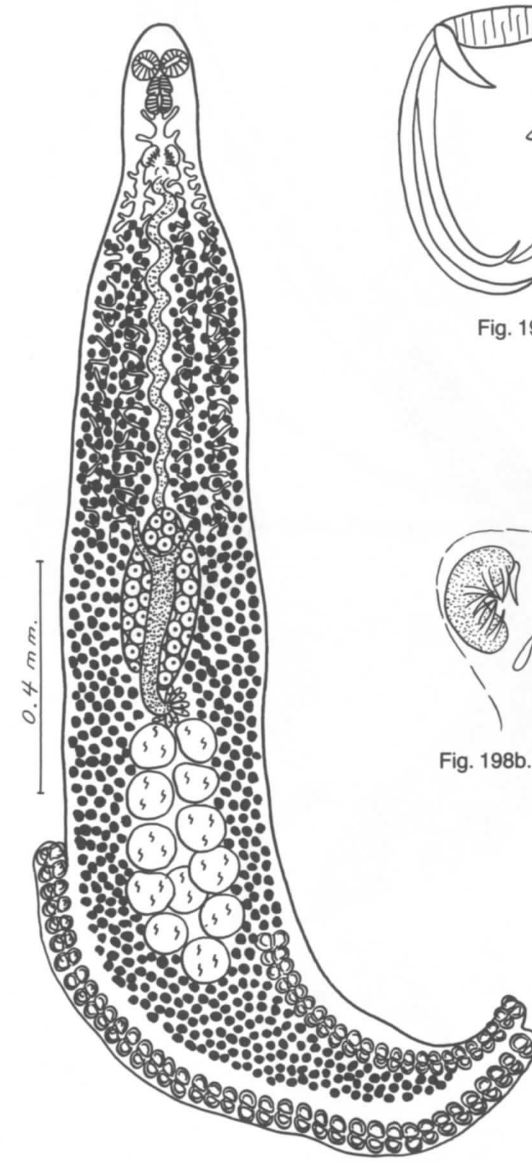


Fig. 198a. *Heteraxinoides xanthophilis.*

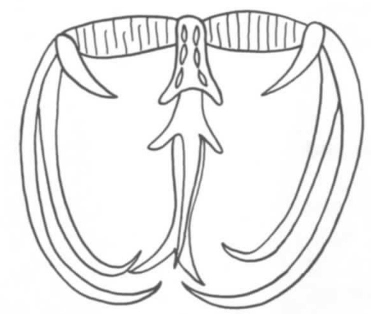


Fig. 199b. clamp

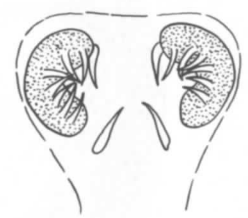


Fig. 198b. genital atrium

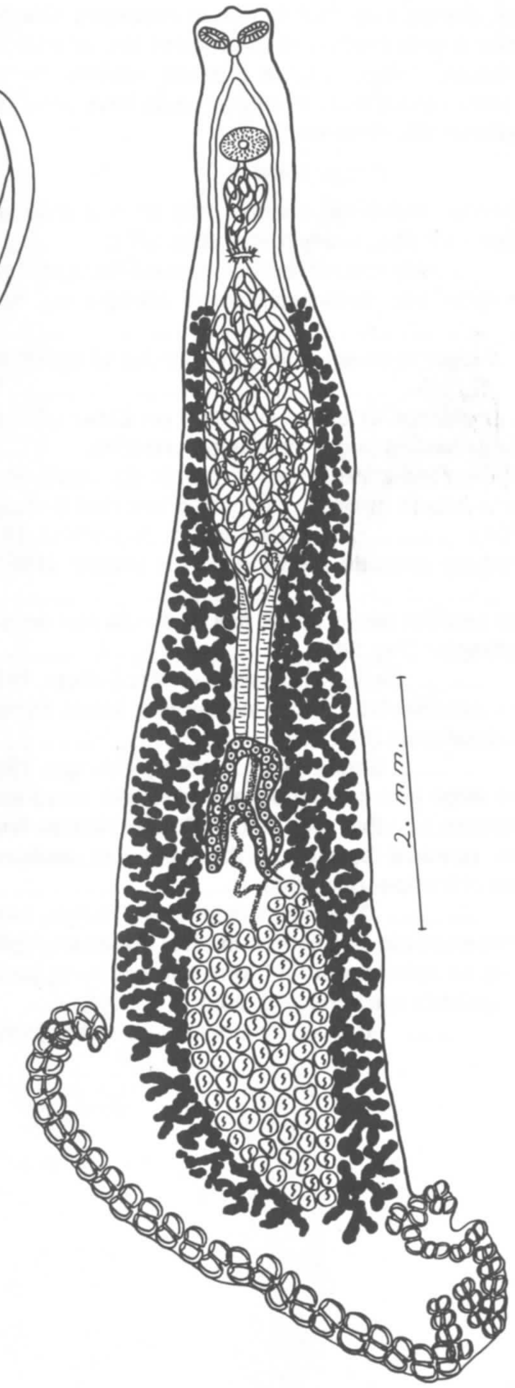


Fig. 199a. *Allencotyla mcintoshi.*

Family Gastrocotylidae Price, 1943

Body variable in shape; intestinal ceca branched, fused or not fused posteriorly; prohaptor composed of two buccal suckers; opisthaptor symmetrical or asymmetrical; clamps pedunculate or sessile, confined to a distinct opisthaptor or distributed along body margins, clamps may contain ribs or accessory sclerites and sometimes a wide median sclerite; testes two or multiple; ovary pretesticular, folded; vagina present; vitelline follicles along ceca; uterus preovarian, intercecal; eggs have polar filaments; parasitic on gills of marine fishes.

Key to Genera

1a. Opisthaptor unilateral; clamps only on one side and provided with ribs; ovary folded (Fig. 200). .... Genus *Pseudaxine* Parona and Perugia, 1890

1b. Opisthaptor not unilateral, some clamps on both sides. 2

2a. Rows of clamps of equal length on sides of opisthaptor. 3

2b. Rows of clamps of unequal length on sides of opisthaptor or having larger clamps on one side. 5

3a. Opisthaptor indistinctly set off from body, confined to posterior fourth of body; ovary has inverted U-shape (Fig. 201). .... Genus *Gotocotyla* Ishii, 1936

3b. Opisthaptor extends far forward on ventral side of body. 4

4a. Clamps sessile; testes large, few, in single row dorsal to opisthaptor (Fig. 202). .... Genus *Thoracocotyle* MacCallum, 1913

4b. Clamps pedunculate; testes numerous, small, in two longitudinal rows (Fig. 203). .... Genus *Neothoracocotyle* Hargis, 1956

5a. Clamps large and sessile on one side and small and pedunculate on other side of opisthaptor; testes two, tandem; terminal lappet with three pairs of anchors; parasite of bumper (Fig. 204). .... Genus *Amphipolycotyle* Hargis, 1957

5b. All clamps sessile and similar in size; testes multiple; terminus of opisthaptor with one pair anchors; parasite of Spanish mackerel (Fig. 205). .... Genus *Scomberocotyle* Hargis, 1956

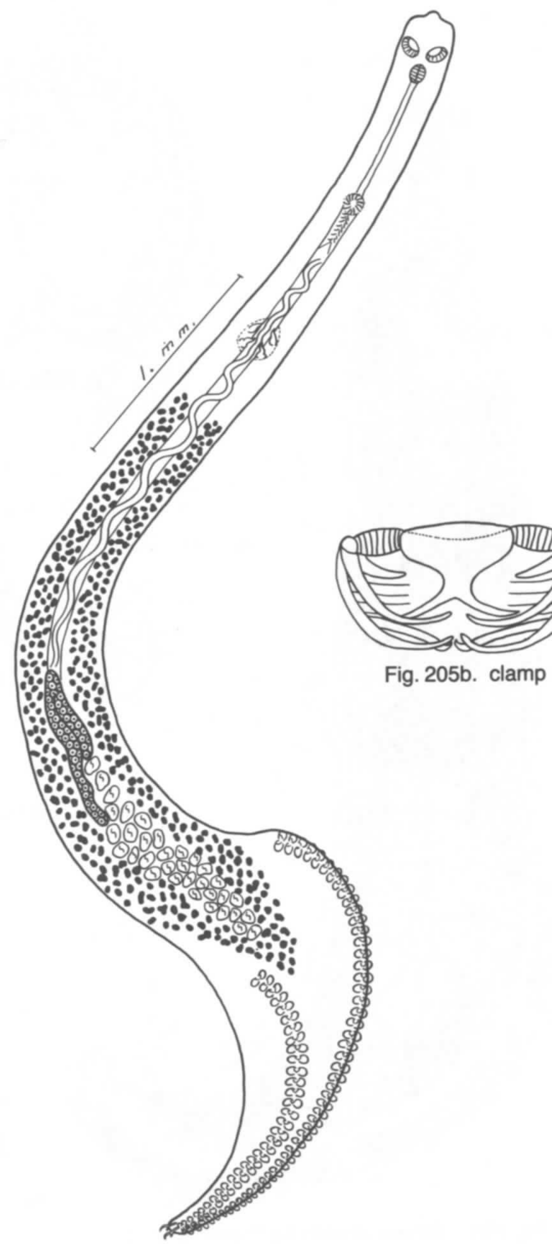


Fig. 205b. clamp

Fig. 205a. *Scomberocotyle scomberomori.*

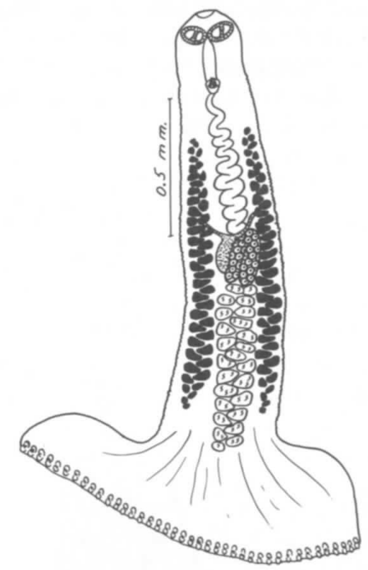


Fig. 200a. *Pseudaxine mexicana.*

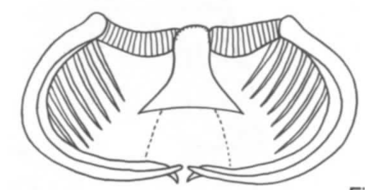


Fig. 200b. clamp

Fig. 201a. *Gotocotyla acanthophallus.*

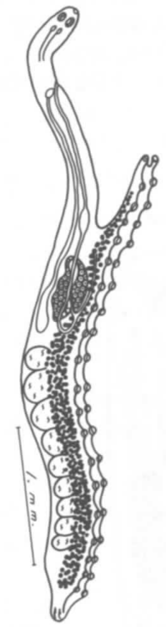


Fig. 202a. *Thoracocotyle crocea.* (from MacCallum, 1913)

Fig. 202b. clamp

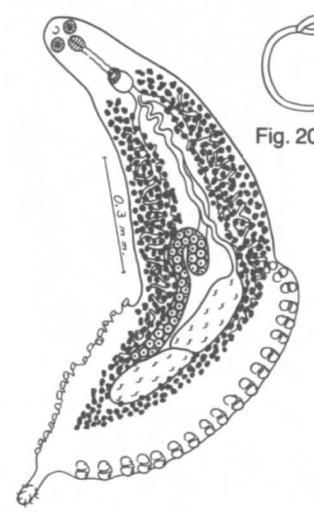


Fig. 204a. *Amphipolycotyle chloroscombrus.*

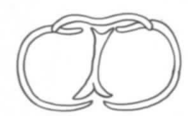


Fig. 204b. large clamp

Fig. 201b. clamp

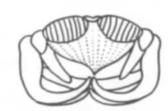


Fig. 204c. small clamp

Fig. 203b. clamp

Fig. 203a. *Neothoracocotyle coryphenae.* (from Yamaguti, 1938)

Family Pyragraphoridae Yamaguti, 1963

Body small, cylindrical; intestinal ceca branched, not united posteriorly; prohaptor with two buccal suckers; opisthaptor fishtail shaped; clamps of two types, microcotylid and firetong shaped; testes multiple; ovary pretesticular, elongate; eggs have polar filaments; parasitic on gills of marine fishes.

The family is monotypic, containing only the genus *Pyragraphorus* Sproston, 1946. *P. pyragraphorus* is a parasite of pompano, *Trachinotus carolinus* on the Atlantic coast. (Fig. 206).

Family Allopyragraphoridae Yamaguti, 1963

Body small, flat; intestinal ceca branched and fused within opisthaptor; prohaptor with two buccal suckers; opisthaptor fishtail shaped; clamps asymmetrical in structure and longer than wide; testes multiple; ovary elongate, sinuous, pretesticular; vitelline follicles distributed around ceca; eggs have polar filaments; parasites of marine fishes.

The family contains only the genus *Allopyragraphorus* Yamaguti, 1963. Two species have been reported from North America. (Fig. 207).

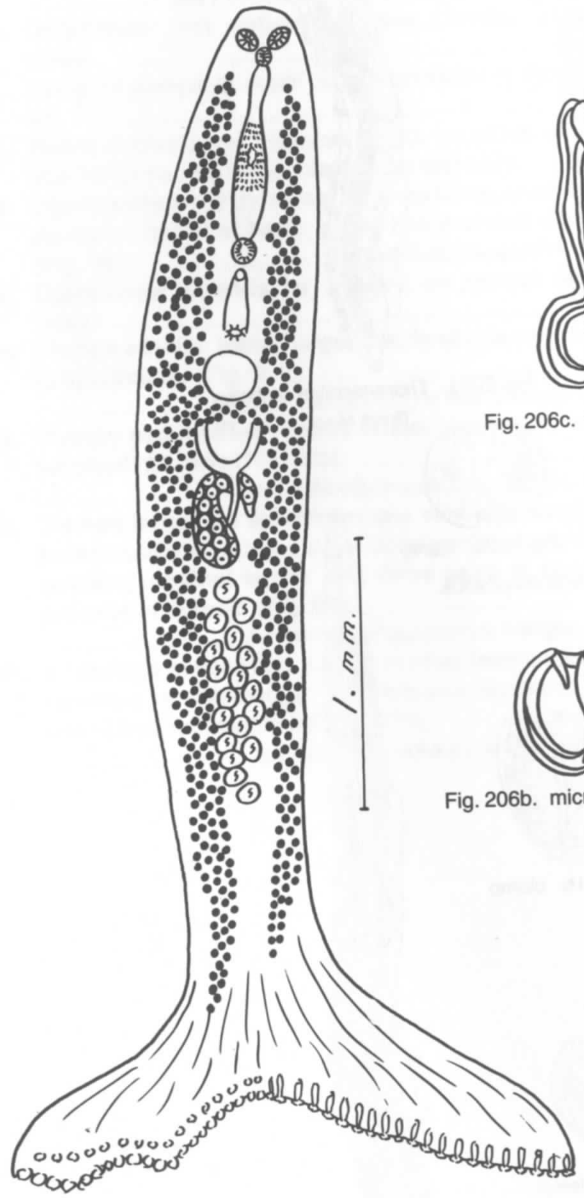


Fig. 206a. *Pyragraphorus pyragraphorus.*

Fig. 206c. fire-tong clamp

Fig. 206b. microcotylid clamp

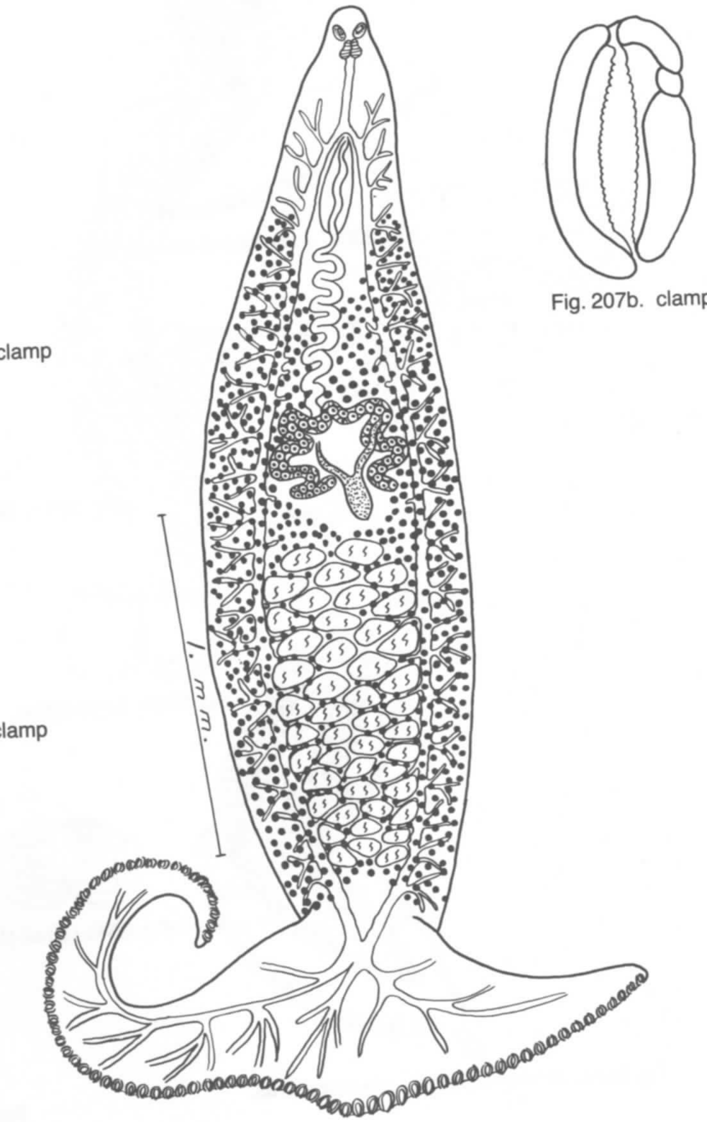


Fig. 207a. *Allopyragraphorus hippos.*

Fig. 207b. clamp

Subclass Aspidogastrea Faust and Tang, 1936

Key to Families

1a. Holdfast organ in form of a large ventral adhesive disc containing septa and loculi (alveoli) or sometimes conical papillae; adults are endoparasites of molluscs, fishes and turtles. (Figs. 208-211). .... Family Aspidogasteridae .... p. 73

1b. Ventral part of body without septa, loculi or papillae. .2

2a. Adults 12 to 16 mm long; ventral surface flattened and contains numerous transverse ridges or rugae; two intestinal ceca; multiple testes; parasitic in rectal glands of Holocephali (Fig. 215). .... Family Rugogastridae .... p. 76

2b. Body very large, up to 115 mm long; ventral surface contains linear series of muscular suckers; one intestinal cecum; two testes; parasitic in gallbladder and bile duct of elasmobranch (Fig. 214). .... Family Stichocotylidae .... p. 76

Family Aspidogasteridae Poche, 1907

Body composed of a ventral adhesive disc and a dorsal hump; the disc contains one or more rows of loculi (alveoli) separated by septa and serves as an organ for attachment; the hump contains the organs for reproduction; oral sucker usually absent; pharynx present; intestine a single cecum; one or two testes; cirrus sac present or absent; ovary pretesticular; genital pore ventral, anterior to adhesive disc; vitellaria follicular or tubular; uterus long; eggs operculate; excretory vesicle V-shaped, arms extending to level of pharynx, pore near posterior end of body; parasitic in molluscs, fishes and turtles.

Key to Genera

1a. Body long (up to 25 mm); adhesive disc with one longitudinal row of transverse loculi (100±); one testis; parasitic in gall bladder of Holocephali (Fig. 208). .... Genus *Taeniocotyle* Stunkard, 1962

1b. Adhesive disc with three or four longitudinal rows of loculi. 2

2a. Adhesive disc with three longitudinal rows of loculi, the median loculi wider than the lateral ones. 3

2b. Adhesive disc with four longitudinal rows of loculi; papillae may also be present. 4

3a. One testis; vitelline glands follicular; parasitic in turtles and freshwater lamellibranch molluscs (Fig.209). .... Genus *Cotylaspis* Leidy, 1857

Key to species in Skrjabin (1964).

Adults have been reported adhering to the outer surface of the kidneys and the inner gill lamellae of unionid clams of the genus *Anodonta.* They have also been found in the intestine of turtles.

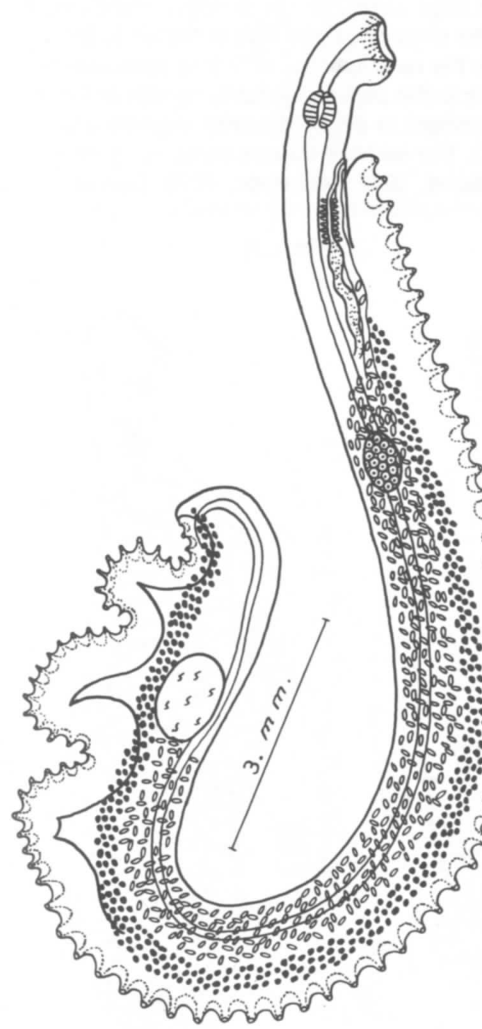


Fig. 208. *Taeniocotyle elegans,* lateral view.

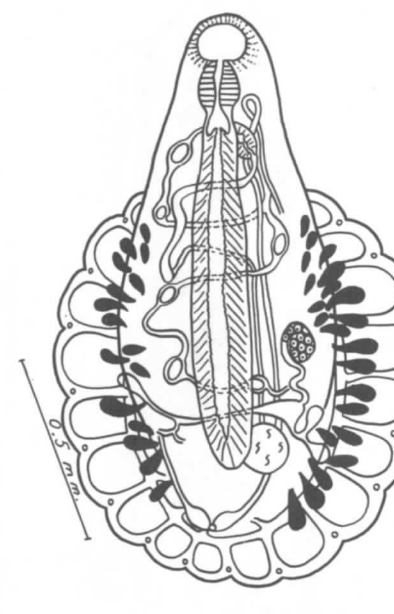


Fig. 209a. *Cotylaspis insignis,* dorsal view

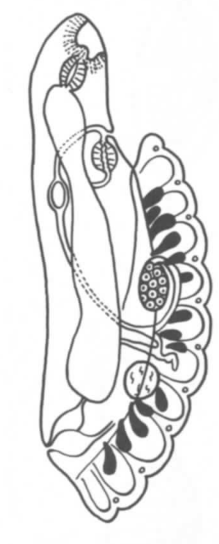


Fig. 209b. lateral view

3b. Two testes; vitelline glands tubular, asymmetrical; parasitic in the intestine of fishes and also in freshwater snails and mussels (Fig. 210). .... Genus *Cotylogasteroides* Monticelli, 1892

Life cycle: *C. occidentalis*- The cotylocidium of this species has two bands of cilia arranged in eight anterior and four posterior patches. After hatching, they enter the host molluscs via water currents and some are also eaten. Molluscs involved are the freshwater mussel, *Lampsilis luteola* and the freshwater prosobranch snails of the genus *Goniobasis*. The parasite is known to undergo its entire development in *Goniobasis*. Natural infections also occur in the freshwater drum, *Aplodinotus grunnions*. Drum were infected by feeding parasites from *Goniobasis*, indicating that natural infections in drum might be the result of eating infected molluscs (Nickerson, 1902; Kelly, 1926; Dickerman, 1948; Wootton, 1966a).

Frederickson (1980) found that this species develops in the freshwater mussel, *Ligumia nasuta* which apparently ingests embryonated eggs of the parasite. Young developing forms inhabit the mouth and esophagus of the mussel, later moving to the intestine where they mature. Alveoli of the ventral disc arise gradually, the entire disc developing within the posterior sucker of the cotylocidium.

4a. Median area of adhesive disc with numerous conical papillae; cirrus sac absent; parasitic in the intestine of freshwater fishes and turtles, developing forms have been found in the pericardial cavity and kidneys of freshwater mussels (Fig. 211). .... Genus *Lophotaspis* Looss, 1901

4b. Adhesive disc without conical papillae; cirrus sac present. 5

5a. Oral lobes around mouth; median septum of ventral disc vestigial; intestinal parasite of marine fishes (Fig. 212). .... Genus *Lobatostoma* Eckmann, 1932

Life cycle: *L. manteri*- Adults inhabit the intestine of the pompano, *Trachinotus blochi*. Eggs, which are embryonated when laid, are eaten by the marine snails, *Cerithium moniliferum* and *Peristernia australiensis*. The cotylocidia hatch in the stomach of the snail then migrate to the digestive gland where they change to the preadult stage which has the full number of alveoli on the ventral disc. Fish become infected by eating infected snails (Rohde, 1973).

5b. Oral lobes absent; median septum on ventral disc well developed; intestinal parasites of freshwater fishes and in the kidneys and pericardial cavity of gastropod and lamellibranch molluscs (Fig. 213). .... Genus *Aspidogaster* Baer, 1827

Life cycle: *A. conchicola*- Operculate eggs in the uterus of the parasite contain cotylocidia which hatch when eggs get into water. They then enter freshwater mussels of the genera *Anodonta*, *Unio* and *Gonidea*, and also the gastropods of the genus *Viviparus*, entering via water currents. As development progresses, the large ventral sucker enlarges and slowly metamorphoses to the alveolar ventral disc of the adult. Developing forms remain in the renal cavities until they approach maturity when they move to the pericardial cavity by way of the nephridiopore. Development to sexual maturity requires about three months at 18 C. The parasite causes some injury to the renal epithelium (Williams, 1942; Michelson, 1970; Bakker and Davids, 1973).

(Continued)

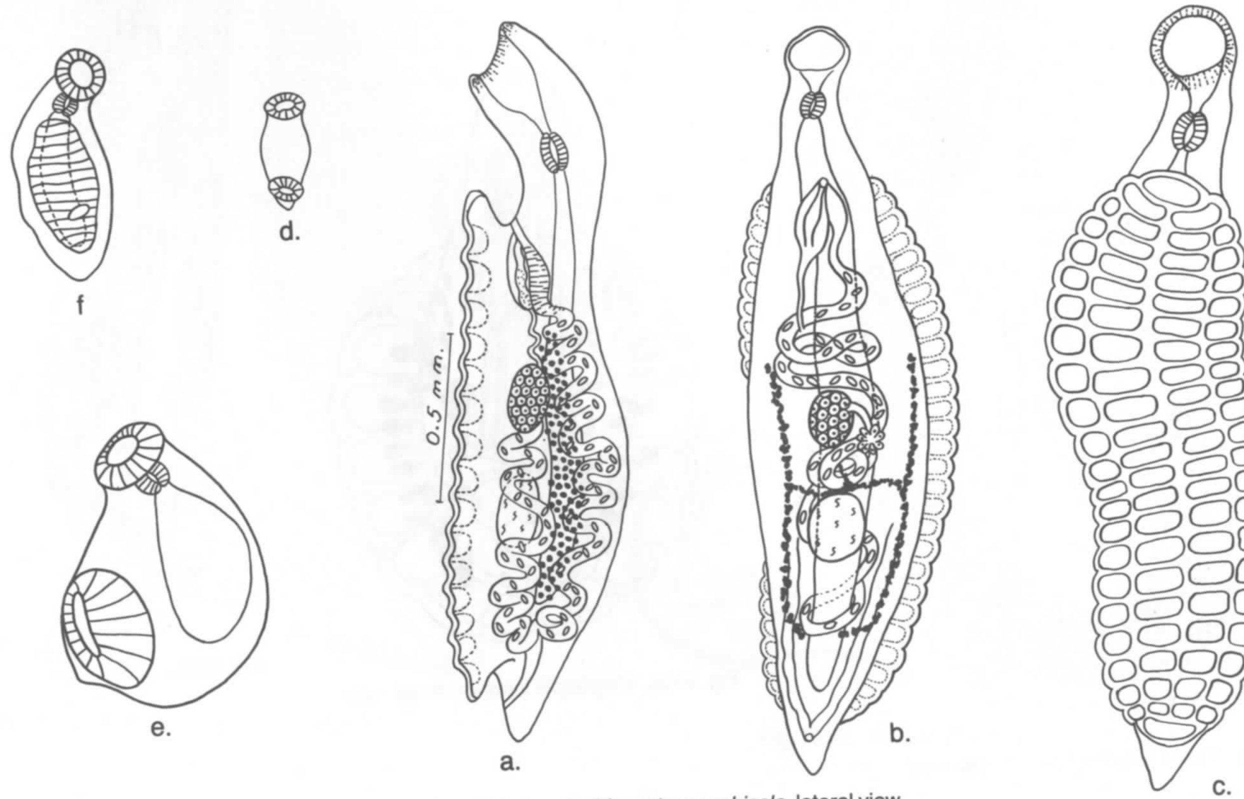


Fig. 213. a. *Aspidogaster conchicola*, lateral view
b. dorsal view
c. ventral view
d. to f. developmental stages

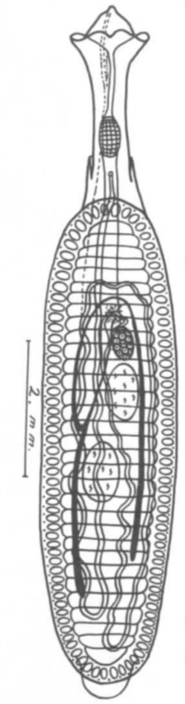


Fig. 210a. *Cotylogasteroides occidentalis*, ventral view

Fig. 210b. lateral view

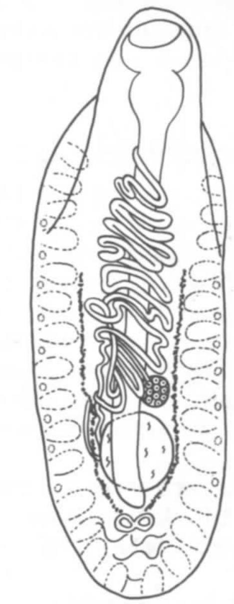


Fig. 211a. *Lophotaspis inferiora*, dorsal view

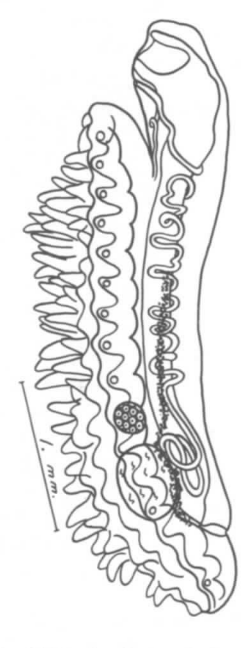


Fig. 211b. *Lophotaspis inferiora*, lateral view

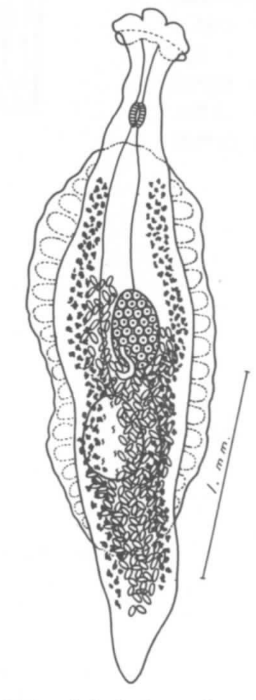


Fig. 212a. *Lobatostoma ringens*, dorsal view

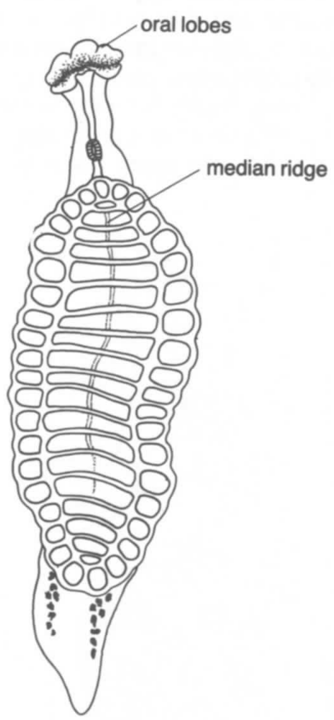


Fig. 212b. ventral view

Huehner and Etges (1977) studied the life cycle of *A. conchicola* in gastropods, paying special attention to the development of the alveolated ventral disc. This disc develops within the margins of the posterior sucker of the cotylocidium. Order of development of alveoli is from anterior to posterior end of disc. Longitudinal septa appeared only after 11 or 12 alveoli had formed, the medial septum appearing first, followed by the two lateral ones. Gastropods involved were *Viviparus malleatus* and *Goniobasis livescens*.

Family Stichocotylidae Faust and Tang, 1936

Body very long (up to 115 mm); oral sucker absent; one intestinal cecum; holdfast organ in the form of a linear series of 20 to 30 ventral suckers distributed along most of length of body; two testes in anterior third of body; cirrus sac small; ovary pretesticular; genital pore anterior to first sucker; uterus very long with many transverse folds; vitellaria composed of a slender median tube flanked by follicles; excretory system composed of two sinuous ducts which extend from posterior end of body to level of pharynx; parasitic in bile duct and gall bladder of elasmobranchs (rays).

The family contains one genus and species, *Stichocotyle nephropis* (Fig. 214). Larval stages have been found encysted in the wall of the rectum of lobsters in Europe and North America.

Family Rugogastridae Schell, 1973

Body large (up to 16 mm); ventral surface contains 25 or more transverse ridges (rugae); buccal funnel present; oral and ventral suckers absent; intestine composed of two blind ceca; testes multiple, arranged in two longitudinal rows in dorsal part of body; two large vasa efferentia present, usually filled with sperm and opening into short vas deferens; cirrus sac present; ovary pretesticular, usually dextral; vitelline follicles dorsolateral to testes and ceca; uterus long, ventral to testes; eggs oval, operculate; parasitic in lumen of rectal glands of Holocephali *(Hydrolagus)*.

The family contains one genus and species, *Rugogaster hydrolagi* (Fig. 215). Adults fit tightly in the lumen of the rectal glands with their anterior end protruding into the lumen of the rectum. The transverse rugae serve to anchor them (Schell 1973a).

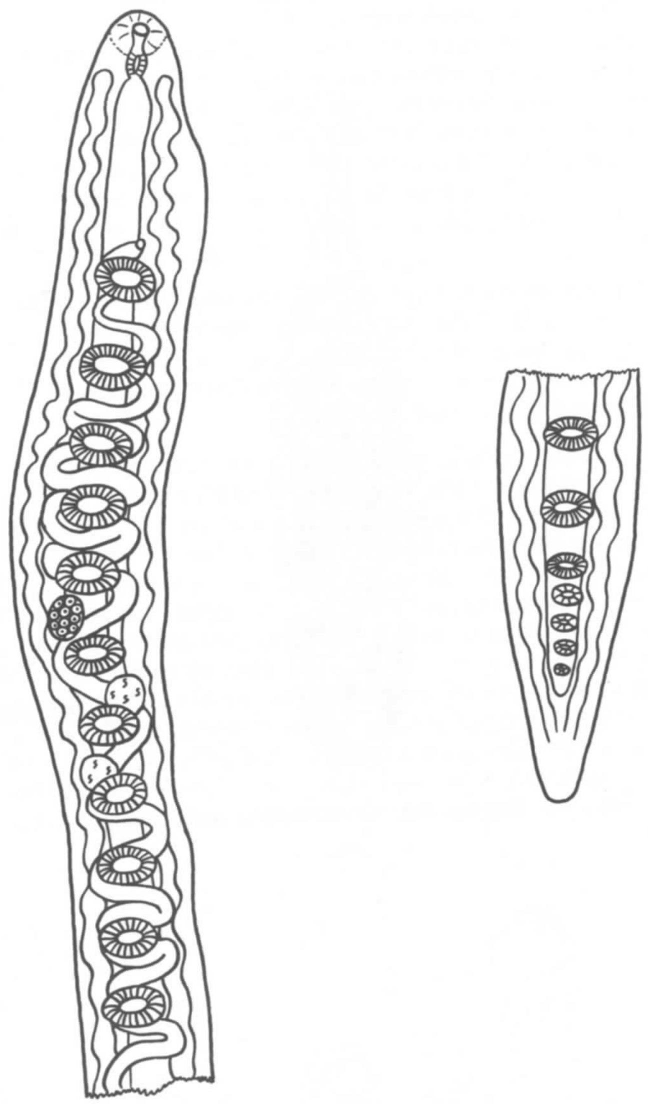


Fig. 214. *Stichocotyle nephropis.*

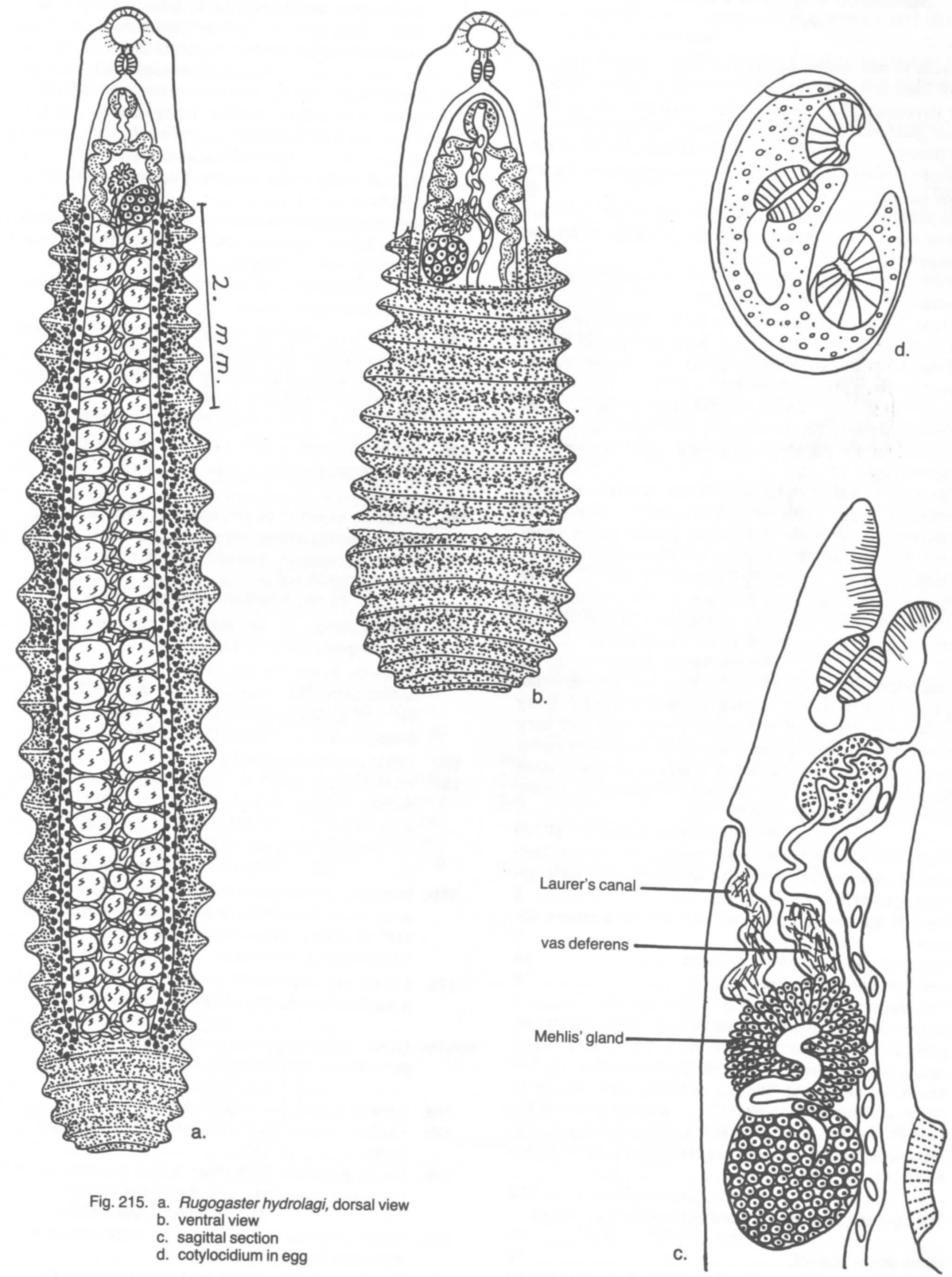


Fig. 215. a. *Rugogaster hydrolagi*, dorsal view
b. ventral view
c. sagittal section
d. cotylocidium in egg

Subclass Digenea Carus, 1863

Key to Families

1a. Mouth in midventral surface of body, opens into sac-like intestine; anterior end of body contains sucker or rhynchus (Fig. 345); genital pore and cirrus sac near posterior end of body; parasitic in digestive tract of fishes. .... Family Bucephalidae .... p. 126
1b. Mouth at anterior end of body, usually surrounded by oral sucker. 2
2a. Parasitic in blood vessels of vertebrates; pharynx absent; testes usually multiple; either hermaphroditic or dioecious. 3
2b. Not in blood vessels of host; pharynx usually present; testes one or two, rarely multiple. 5
3a. Sexes separate (dioecious); in blood vessels of birds and mammals; genital pore in anterior third of body; males have gynaecophoric canal; ceca fused posteriorly to form common cecum. .... Family Schistosomatidae .... p. 99
3b. Hermaphroditic (monoecious); in blood vessels of poikilothermic vertebrates; genital pore in posterior third of body. 4
4a. Parasitic in blood vessels of fishes; suckers absent; intestine X- or H- shaped due to presence of anterior intestinal ceca; male and female genital pores separate, opening on dorsal surface of posterior third of body. .... Family Sanguinicolidae .... p. 105
4b. Parasitic in heart and arteries of turtles; suckers usually present; intestine composed of one or two ceca; genital pore on ventral surface of body. .... Family Spirorchiidae .... p. 107
5a. Embedded in muscles, skin, mucous membranes, connective tissue or visceral organs of fishes; body either very long and threadlike or anterior part very narrow and posterior part very thick; hermaphroditic or gonochoristic (dioecious); testes, ovary and vitellaria tubular; ovary and vitellaria posterior to testes; genital pore close to mouth. .... Family Didymozoidae .... p. 139
5b. Body and habitat not as described above; always hermaphroditic; usually parasitic in lumen of some internal organ of host. 6
6a. Ventral sucker or both oral and ventral suckers absent. 7
6b. Oral and ventral suckers present. 18
7a. Oral and ventral suckers absent. 8
7b. Oral sucker present, ventral sucker absent. 9
8a. Intestinal ceca fused posteriorly to form cyclocoel; gonads near posterior end of body; parasitic in respiratory tract of birds.......Family Cyclocoelidae....p. 160
8b. Intestinal ceca end blindly; gonads near middle of body; one testis; two excretory vesicles present, extend forward to level of pharynx and esophagus; pigmented eyespots usually present; parasitic in digestive tract of marine fishes. .... Family Bivesiculidae .... p. 130
9a. Triangular, nonspinous head collar usually present. 10
9b. Head collar absent. 11
10a. Parasitic in urinary tract of birds; testes opposite in middle third of body; pharynx present (genus *Eucotyle*) .... Family Eucotylidae (in part) .... p. 203
10b. Parasitic in urinary tract of turtles and marine fishes; testes near posterior end of body; pharynx absent; main ducts of excretory system extend far forward and fuse (multiple testes in genus *Diaschistorchis*). .... Family Pronocephalidae .... p. 169
11a. Parasitic in urinary tract of birds; testes tandem or oblique, in middle third of body; ovary lobed; ceca fused posteriorly to form cyclocoel (genus *Tanaisia*). .... Family Eucotylidae (in part) .... p. 203
11b. Habitat other than urinary tract of birds; ceca not fused. 12
12a. Adults encysted in skin of birds; body nonspinous; ovary lobed in anterior half of body; testes opposite in posterior half of body.......Family Collyriclidae....p. 214
12b. Not encysted in skin of birds and anatomy not as described above. 13
13a. Parasitic in respiratory tract of turtles; testes and vitellaria tubular, both extend through about two-thirds of body length; excretory pore dorsal to pharynx; genital pore ventral to pharynx. .... Family Heronimidae .... p. 166
13b. Not in respiratory tract of turtles; testes and vitellaria not tubular; excretory pore at posterior end of body. 14
14a. Parasitic in lungs of amphibians; body spinous; pharynx present; uterus very long, contains many eggs; testes oblique or opposite (some species of the genus *Haematoloechus*). .... Family Haematoloechidae (in part) .... p. 175
14b. Not in lungs of amphibians; pharynx absent but esophageal bulb might be present. 15
15a. Parasitic in marine mammals; body flat, broad, oval; testes opposite, near posterior end of body; cirrus sac and genital pore at posterior end of body; ovary deeply lobed. .. Family Opisthotrematidae .... p. 171
15b. Not in marine mammals. 16
16a. Intestinal parasites of turtles; testes lobed, tandem, in middle of body; ovary posterior to testes; esophageal bulb might be present (in *Hexangitrema*); oral sucker has angular projections (in *Dictyangium*). .... Family Microscaphidiidae .... p. 171
16b. Intestinal parasites of birds and mammals; eggs have long polar filaments; testes opposite, near posterior end of body; uterus has many transverse folds, entirely anterior to gonads. 17
17a. Cirrus sac and genital pore in anterior third of body; parasitic in intestine of birds and mammals. .... Family Notocotylidae .... p. 166
17b. Cirrus sac and genital pore in posterior third of body; parasitic in intestine of mammals. .... Family Nudacotylidae .... p. 167
18a. Ventral sucker at or near posterior end of body. ... 19
18b. Ventral sucker near midbody or anterior to middle of body. 21
19a. Ovary posterior to testes; testes tandem or oblique; intestinal parasites of all classes of vertebrates. .... Family Paramphistomidae .... p. 162
19b. Ovary anterior to testes; testes opposite; parasitic in digestive tract of marine fishes. 20
20a. Muscular ring between oral sucker and pharynx; ventral sucker enveloped by body fold; uterus entirely anterior to testes..... Family Opistholebetidae .... p. 232

20b. Muscular ring absent; ventral sucker not enveloped by body fold; uterus extends posterior to testes. .... Family Cephaloporidae .... p. 183
21a. Bulbous or foliaceous tribocytic organ posterior to ventral sucker, sometimes overlapping it; body usually divided into distinct fore- and hindbody; copulatory bursa and genital pore at posterior end of body; organs of reproduction confined to hindbody. 22
21b. Tribocytic organ absent; body not subdivided as described above; copulatory bursa absent. 25
22a. Cirrus sac present, located near posterior end of body; body very small; fore- and hindbodies not distinct; tribocytic organ bulbous (Fig. 256); intestinal parasites of birds and mammals. .... Family Cyathocotylidae .... p. 95
22b. Cirrus sac absent; fore- and hindbodies distinct; tribocytic organ either bulbous or foliaceous. 23
23a. Forebody cupshaped; tribocytic organ foliaceous (Fig. 232); intestinal parasites of birds and mammals. .... Family Strigeidae .... p. 86
23b. Forebody flat or spoonshaped; tribocytic organ bulbous (Fig. 247); intestinal parasites of reptiles, birds and mammals. 24
24a. Hindbody contains thick-walled paraprostate organ surrounded by gland cells (Fig. 216); parasitic in reptiles (alligators). .... Family Proterodiplostomidae .... p. 98
24b. Paraprostate organ absent; parasitic in birds and mammals. (Fig. 217). Family Diplostomidae .... p. 90
25a. Genital pore and cirrus sac in posterior third of body or at posterior tip of body, some distance from ventral sucker. 26
25b. Genital pore in anterior half or middle third of body, usually anterior to ventral sucker or at least close to ventral sucker, sometimes immediately posterior to ventral sucker. 32
26a. Parasitic in mouth and esophagus of aquatic birds; anterior end can be retracted into collar-like body fold; ventral sucker much larger than oral sucker; ovary between testes; genital pore in posterior third of body. .... Family Clinostomidae .... p. 110
26b. Anatomy and habitat not as described above. .... 27.
27a. Genital pore and cirrus sac at posterior end of body, posterior to gonads. 28
27b. Genital pore and cirrus sac in posterior third of body, ventral to gonads or ventral to ceca, not at posterior end. 29
28a. Ovary anterior to testes; uterus confined to hindbody; both suckers close to anterior end of body. .... Family Urotrematidae .... p. 117
28b. Ovary between testes; uterus extends into forebody; suckers large, ventral sucker in middle of body; usually parasitic in birds. .... Family Leucochloridiidae .... p. 114
29a. Testes tandem and some distance from posterior end of body; ovary between testes; body elongate, fusiform or spatulate. 30
29b. Testes oblique or opposite and close to posterior end of body; ovary anterior to testes or opposite to anterior testis; body small, oval or pyriform. 31
30a. Seminal vesicle bipartite, enclosed in cirrus sac; genital pore ventral to left cecum; vitelline follicles confluent anterior to gonads; parasitic in intestine of reptiles (alligators) (Fig. 302). .... Family Harmotrematidae .... p. 114
30b. Seminal vesicle unipartite and either inside or outside of cirrus sac; cirrus sac sometimes absent; genital pore usually median; vitelline follicles lateral to ceca; parasitic in bursa Fabricius of birds or lower intestine of mammals. .... Family Brachylaimidae .... p. 111
31a. Ovary opposite testes; testes oblique; parasitic in intestine of mammals (rabbits). .... Family Hasstilesiidae .... p. 117
31b. Ovary anterior to testes; testes opposite or oblique, at posterior end of body; parasitic in cloaca or bursa of Fabricius of birds or in intestine or salivary glands of mammals ..Family Leucochloridiomorphidae....p. 116
32a. Genital pore on right or left margin of body. 33
32b. Genital pore median or submedian. 38
33a. Testes tandem; seminal vesicle bipartite; body spinous; parasitic in the intestine of fishes. .... Family Lissorchiidae .... p. 207
33b. Testes opposite or nearly opposite. 34

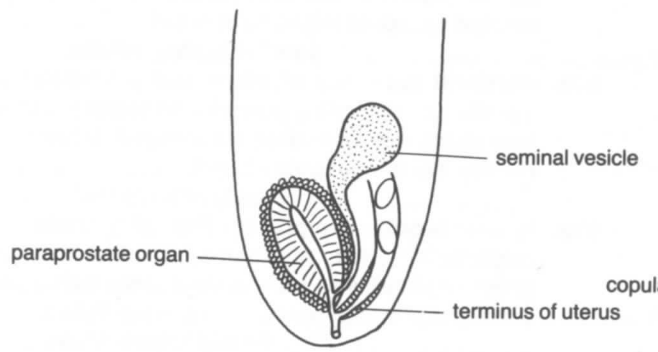


Fig. 216. Proterodiplostomidae

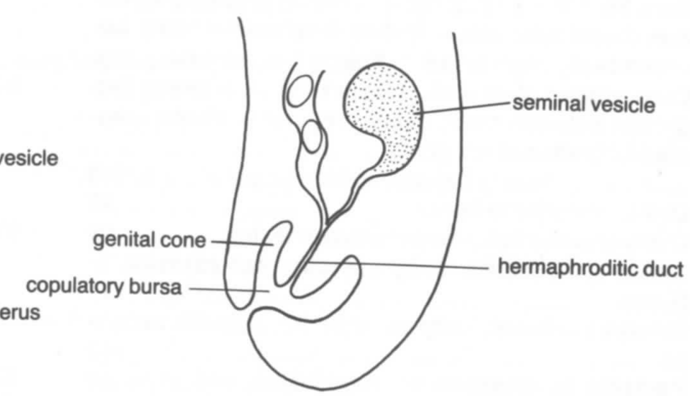


Fig. 217. Diplostomidae

34a. Cirrus sac absent; seminal vesicle free in parenchyma; body spinous; testes in hindbody; parasitic in bats and rodents. .... Family Allassogonoporidae .... p. 197

34b. Cirrus sac present; seminal vesicle in cirrus sac; parasitic in birds or fishes. 35

35a. Testes opposite, in forebody; ovary close to pharynx; suckers large; genital pore at level of pharynx; parasitic in large intestine and cloaca of birds. .... Family Stomylotrematidae .... p. 198

35b. Testes opposite, in hindbody; genital pore posterior to pharynx. 36

36a. Vitellaria in the form of one or two compact masses; body spinous; seminal vesicle bipartite, enclosed in cirrus sac; ovary usually posterior to testes; parasitic in intestine of marine fishes. .... Family Zoogonidae .... p. 204

36b. Vitellaria follicular, in lateral regions of body; ovary anterior to testes or between testes. 37

37a. Body nonspinous; vitellaria confined to forebody parasitic in cloaca or bursa Fabricius of birds. .... Family Laterotrematidae .... p. 198

37b. Body spinous; vitellaria in both fore- and hindbody; parasitic in intestine of marine fishes. .... Steganodermatidae .... p. 204

38a. Testes multiple (5 or more). 39

38b. Testes one or two. 43

39a. Body cylindrical, elongate; cirrus sac absent; testes 15 to 20; ventral sucker pedunculate; ceca fused posteriorly to form cyclocoel; ovary posterior to testes; parasitic in pharynx of marine fishes. .... Family Syncoeliidae .... p. 137

39b. Body flat; ventral sucker sessile; ceca end blindly; ovary anterior to testes. 40

40a. Cirrus sac absent; uterus entirely anterior to testes; body nonspinous; parasitic in respiratory tract of birds. .... Family Orchipedidae .... p. 159

40b. Cirrus sac present; parasitic in digestive tract of marine fishes. 41

41a. Body nonspinous; testes 9 to 10; uterus anterior to ovary; eggs have unipolar filament (Genus *Helicometrina*). .... Family Opecoelidae (in part) .... p. 226

41b. Body spinous; eyespots in young adults; eggs without polar filaments. 42

42a. Ceca have pair of anterior diverticula plus shorter lateral diverticula; testes in two longitudinal rows between ceca; ovary lobed. ....Family Pleorchiidae 224

42b. Ceca without diverticula; testes 10 to 12 in one or two groups between ceca; ovary irregular in shape (genera *Multitestis* and *Rhagorchis*). .... Family Lepocreadiidae (in part) .... p. 219

43a. Ovary posterior to testes. 44

43b. Ovary anterior to testes or between testes. 49

44a. Cirrus sac present; body spinous; not parasitic in fishes. 45

44b. Cirrus sac absent; body nonspinous; parasitic in fishes. 46

45a. Parasitic in intestine of amphibians and reptiles; testes lateral to ventral sucker; ceca short, extend only to level of ovary. ....Family Mesocoeliidae .... p. 180

45b. Parasitic in liver, bile duct, gall bladder or pancreatic duct of reptiles, birds and mammals; testes opposite, oblique or tandem, usually posterior to ventral sucker; ceca long, extend well beyond ovary. .... Family Dicrocoeliidae .... p. 199

46a. Body long, cylindrical; ventral sucker pedunculate; ceca fused with excretory vesicle to form uroproct; seminal vesicle long and convoluted; hermaphroditic duct usually present; parasitic in intestine of marine fishes. .... Family Accacoeliidae .... p. 139

46b. Body cylindrical or flat but ventral sucker not pedunculate; ceca not fused with excretory vesicle; not intestinal parasites. .... 47.

47a. Body cylindrical; sensory papillae on forebody; hermaphroditic duct absent; excretory ducts not fused dorsal to pharynx; ejaculatory duct long, convoluted, inside ejaculatory pouch; parasitic in stomach of marine fishes. .... Family Lampritrematidae .... p. 137

47b. Forebody not papillated; ejaculatory duct short and not in a pouch; hermaphroditic duct present, enclosed in sinus sac or genital cone. 48

48a. Vitellaria tubular, branched, forming a network in hindbody; seminal vesicle and pars prostatica long, convoluted, free in parenchyma; main excretory ducts not united dorsal to pharynx; parasitic in stomach of marine fishes. .... Family Sclerodistomidae .... p. 137

48b. Vitellaria, compact or follicular, not forming a network if tubular; body sometimes divided into soma and ecsoma (Fig. 218); Main excretory ducts usually united dorsal to pharynx; parasitic in stomach of marine fishes or in Eustachian tubes, pharynx or esophagus of amphibians. .... Family Hemiuridae .... p. 130

49a. Testes tandem; ovary between testes; body long (about 18 mm), cylindrical; ventral sucker enveloped by body fold; hermaphroditic duct absent; parasitic in stomach of marine fishes. .... Family Bathycotylidae .... p. 137

49b. Ovary anterior to testes; body not long and cylindrical; not parasitic in stomach of fishes. 50

50a. Ventrogenital or genital sac present (Fig. 219, 220); cirrus sac absent; hermaphroditic duct (genital sinus) present, opens into sac. 51

50b. Ventrogenital or genital sac absent; cirrus sac present or absent. 52

51a. Intestinal parasites of fishes; uterus extends posterior to testes; main excretory ducts extend forward as far as pharynx; intestinal ceca usually long; pigmented eyespots might be present. .... Family Cryptogonimidae .... p. 243

51b. Intestinal parasites of birds and mammals; uterus usually not extending posterior to testes; main excretory ducts not extending far forward; intestinal ceca usually short; eyespots absent. .... Family Heterophyidae .... p. 237

52a. Hermaphroditic sac present (Fig. 221), enclosing hermaphroditic duct, metraterm, seminal vesicle and prostate gland; external seminal vesicle also present; usually one testis; parasitic in marine fishes. .... Family Haploporidae .... p. 154

52b. Anatomy not as described above. 53

53a. Uterus entirely anterior to testes. 54

53b. Uterus extends posterior to testes, between testes, or uterus opposite to ovary. 75

54a. Intestinal ceca have anterior and/or lateral diverticula. 55

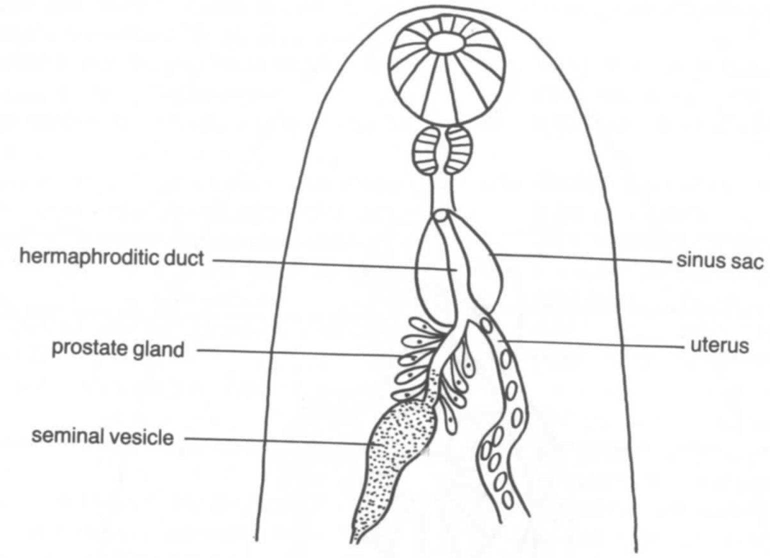


Fig. 218a. Hemiuridae, terminal reproductive organs.

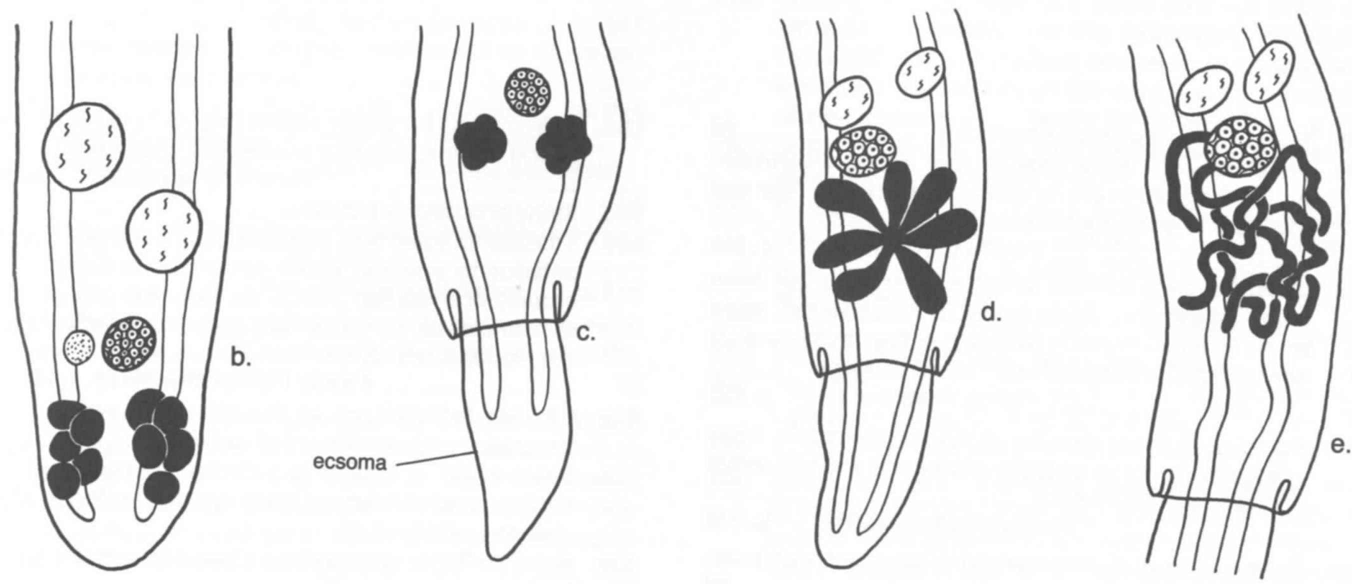


Fig. 218b. Hemiuridae, ecsoma and vitellaria b. to e. vitelline glands

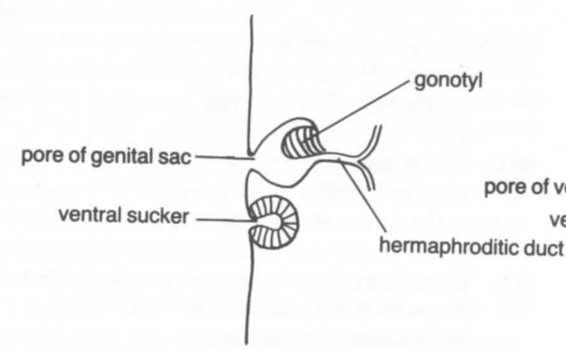


Fig. 219 Genital sac, sagittal section

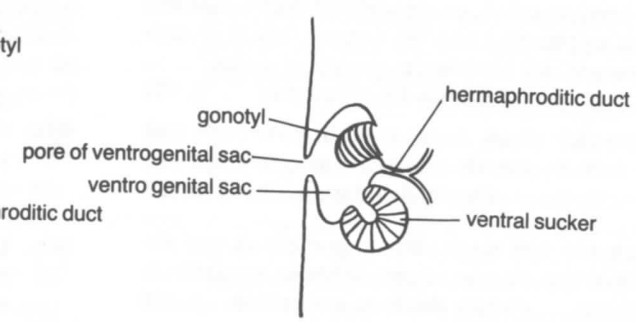


Fig. 220. Ventro genital sac, sagittal section

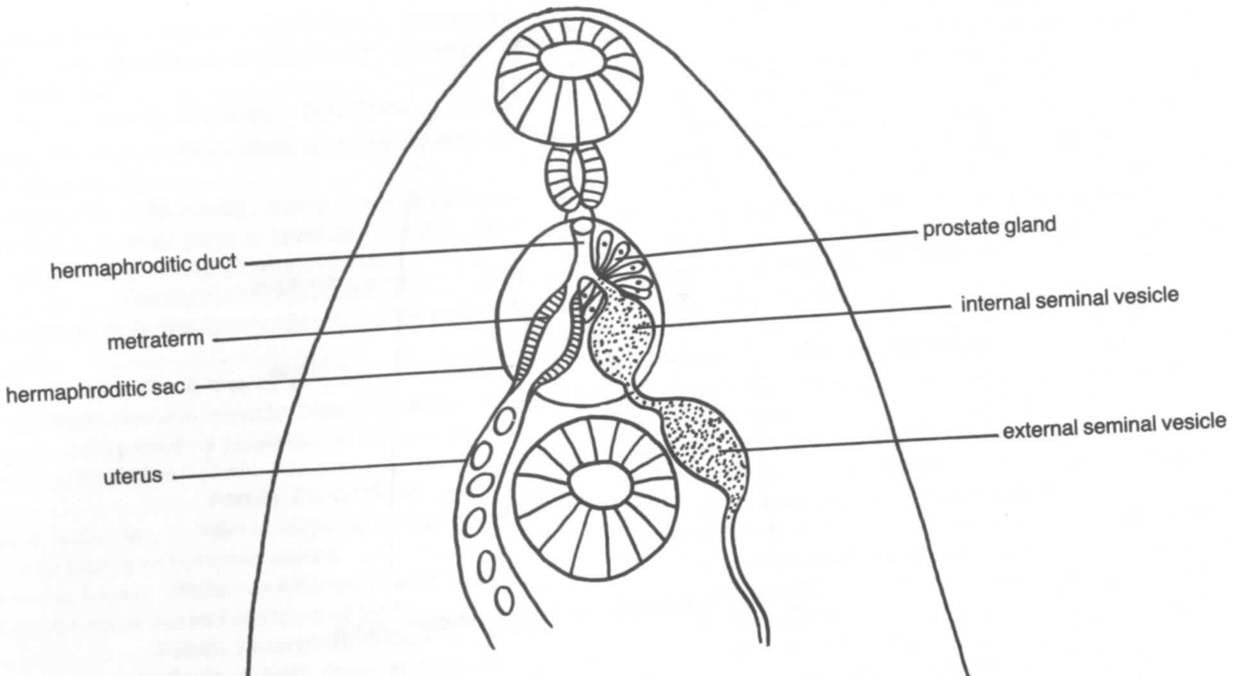


Fig. 221. Haploporidae, terminal reproductive organs.

54b. Intestinal ceca without diverticula. 56

55a. Intestinal ceca have anterior and lateral diverticula; eggs triangular in cross section; parasitic in liver and bile duct of marine mammals. .... Family Campulidae .... p. 248

55b. Intestinal ceca without anterior diverticula but have many lateral diverticula (none in *Fasciolopsis*); eggs round in cross section; parasitic in liver and bile duct of herbivorous mammals and human beings. .... Family Fasciolidae .... p. 158

56a. Parasitic in nasal cavities of marine mammals; eggs triangular in cross section; cirrus sac absent; ovary and testes deeply lobed. .... Family Nasitrematidae .... p. 248

56b. Not parasitic in marine mammals; eggs not triangular; cirrus sac present or absent. 57

57a. Oral sucker has one pair of ventro-lateral muscular papillae; parasitic in the intestine of turtles. 58

57b. Oral sucker without muscular papillae. 59

58a. Excretory vesicle small, ducts without diverticula and ward as far as pharynx and have many lateral diverticula; uterus entirely anterior to ovary and testes. .... Family Rhytidodidae .... p. 182

58b. Excretory vesicle small, ducks without diverticula and not long; uterus extends posterior to ovary but not posterior to testes..... Family Auridistomidae p.182

59a. One cecum and one testis; cirrus and cirrus sac absent; seminal vesicle free in parenchyma; parasitic in marine fishes. ....Family Haplosplanchnidae....p. 156

59b. Two ceca and two testes; cirrus sac usually present. 60

60a. Retractile spiny proboscides (Fig. 433) on each side of oral sucker; parasitic in intestine of opossum. .... Family Rhopaliidae .... p. 153

60b. Spiny proboscides absent. 61

61a. Vitelline follicles few, arranged in a U-shaped pattern anterior to gonads; some genera have spiny collar around oral sucker (*Parorchis, Echinostephilla*); parasitic in cloaca, bursa of Fabricius or beneath nictitating membrane of birds. .... Family Philophthalmidae .... p. 151

61b. Vitelline follicles not as described above; primarily parasitic in digestive tract of vertebrates. 62

62a. Spiny collar or one or two circles of large spines at anterior end of body or body densely spinous especially on anterior half. 63

62b. Spiny collar or large spines absent in anterior part of body. 65

63a. Spiny collar present; testes tandem; vitelline follicles abundant; hermaphroditic duct absent; parasitic in intestine of birds and mammals. .... Family Echinostomatidae .... p. 142

63b. Spiny collar absent but one or two rows of large spines around oral sucker (no circumoral spines in genus *Tormopsolus*); intestinal parasites of fishes and reptiles. 64

64a. Cirrus sac present; seminal vesicle inside cirrus sac; hermaphroditic duct present; not enclosed in a sac; oral sucker terminal or not; gonotyl absent. .... Family Acanthocolpidae .... p. 247

64b. Cirrus sac absent; seminal vesicle free in parenchyma, sometimes coiled; oral sucker large, terminal; gonotyl present in some genera; pre- and postacetabular pits usually present. .... Family Acanthostomidae .... p. 246

65a. Testes opposite and anterior to ventral sucker; anterior margin of pharynx scalloped; ceca open through separate ani; parasitic in intestine of trunkfishes. .... Family Megaperidae .... p. 157

65b. Testes posterior to ventral sucker; pharynx not scalloped. 66

66a. Parasitic in kidneys of aquatic birds; body rounded anteriorly, tapered posteriorly; testes opposite; ventral sucker small or vestigial; gonads and vitellaria near posterior end of body; uterus fills most of body anterior to gonads. .... Family Renicolidae .... p. 202

66b. Body not as described above; not parasitic in urinary tract; ventral sucker well developed. 67

67a. Cirrus sac absent; seminal vesicle and prostate gland free in parenchyma. 68

67b. Cirrus sac present; seminal vesicle and prostate gland in cirrus sac. 70

68a. Parasitic in intestine of fishes; hermaphroditic duct usually present; testes usually tandem, rarely opposite and some distance from posterior end of body. ... . Family Homalometridae .... p. 222

68b. Parasitic in liver, gall bladder or bile duct of reptiles, birds and mammals; hermaphroditic duct absent; testes and ovary close to posterior end of body. .. 69

69a. Testes opposite; ovary between or slightly posterior to testes; body broadly oval and flat. .... Family Pachytrematidae .... p. 247

69b. Testes tandem or oblique, oval lobed or dendritic; ovary anterior to testes. .... Family Opisthorchiidae .... p. 235

70a. Parasitic in intestine of fishes and amphibians. 71

70b. Parasitic in intestine of reptiles, birds and mammals. 74

71a. Body densely spinous; eyespots present in young adults; parasitic in marine fishes. .... Family Lepocreadiidae .... p. 219

71b. Body nonspinous; eyespots usually absent; parasitic in freshwater and marine fishes, rarely in amphibians. 72

72a. Body plump, muscular; excretory vesicle Y-shaped, the main ducts long and sometimes fused dorsal to the pharynx; ceca long, end blindly; suckers well developed; parasitic in digestive tract of freshwater fishes or in coelom of marine cartilaginous fishes (elasmobranchs and chimaeras). .... Family Azygiidae .... p. 129

72b. Body not very muscular or plump; excretory vesicle tubular, the main ducts small; ceca variable in length; usually parasitic in fishes, rarely in amphibians. .. 73

73a. Primarily parasitic in marine fishes; muscular papillae absent on oral sucker but might be present on ventral sucker; ceca may end blindly, open through one or two ani, fuse with excretory vesicle to form uroproct or fuse with each other to form cyclocoel. .... Family Opecoelidae (in part) .... p. 226

73b. Primarily parasitic in freshwater fishes, rarely in amphibians or progenetic in aquatic arthropods; muscular papillae on oral sucker; ceca end blindly. .... Family Allocreadiidae (in part) .... p. 215

74a. Anatomy resembling that of echinostomatids except spiny collar is absent; body contains subcutaneous network of excretory canals; testes round or ovoid; parasitic in intestine of reptiles, birds and mammals. .... Family Psilostomidae .... p. 148

74b. Body without subcutaneous network of excretory canals; testes usually lobed and tandem; usually parasitic in birds, rarely in mammals. .... Family Cathaemasiidae .... p. 153

75a. Genital pore immediately posterior to ventral sucker; testes opposite. 76

75b. Genital pore anterior or lateral to ventral sucker. .. 78

76a. Parasitic in the lungs of mammals; testes opposite and lobed; cirrus sac absent; ovary lobed and anterior to right testis; uterus opposite to ovary; excretory vesicle tubular, long, extends to pharynx. .... Family Paragonimidae .... p. 213

76b. Not parasitic in lungs; testes and ovary ovoid; cirrus sac present; uterus extends between testes; excretory vesicle Y-, V- or sac-shaped. 77

77a. Parasitic in intestine or frontal sinuses of mammals; testes opposite, near posterior end of body; excretory vesicle Y- or V-shaped. .... Family Troglotrematidae .... p. 212

77b. Parasitic in the intestine of carnivorous mammals; testes opposite, some distance from posterior end of body; excretory vesicle saccular. .... Family Nanophyetidae .... p. 214

78a. Metraterm in the form of a spiny terminal organ enclosed in a metraterm sac (Fig. 222); spiny genital atrium might also be present; one testis in most genera but testes opposite when two are present; parasitic in marine fishes. .... Family Monorchiidae .... p. 209

78b. Metraterm not as described above; metraterm sac absent; two testes usually present. 79

79a. Primarily parasites of bats; ceca short; testes opposite; vitelline follicles confined to anterior half of body; body oval or pyriform; uterus fills most of posterior region of body. .... Family Lecithodendriidae .... p. 193

79b. Parasitic in vertebrates other than bats. 80

80a. Excretory vesicle large, U-, Y- or V-shaped, the arms extending forward to level of pharynx. 81

80b. Excretory vesicle not as described above. 85

81a. Excretory vesicle Y-shaped, arms of Y united dorsal to oral sucker; intestinal ceca and arms of excretory vesicle have diverticula anteriorly; testes opposite; uterus mostly posterior to testes; parasitic in intestine of turtles. .... Family Pachypsolidae .... p. 182

81b. Arms of excretory vesicle not united anteriorly; ceca and arms without diverticula; not parasitic in turtles. 82

82a. Cirrus and cirrus sac absent; seminal vesicle free in parenchyma; vitellaria in one or two compact clusters of follicles; parasitic in intestine, bursa of Fabricius or gall bladder of birds. .... Family Gymnophallidae .... p. 124

82b. Cirrus and cirrus sac present; seminal vesicle bipartite and inside of cirrus sac; vitelline follicles not in compact clusters; parasitic in fishes. 83

83a. Esophagus has pair of lateral pouches; genital pore lateral to ventral sucker; ovary between testes or nearly so; excretory vesicle V-shaped. .... Family Botulisaccidae .... p. 126

83b. Esophagus without lateral pouches; genital pore anterior to ventral sucker; ovary anterior to testes. .. 84

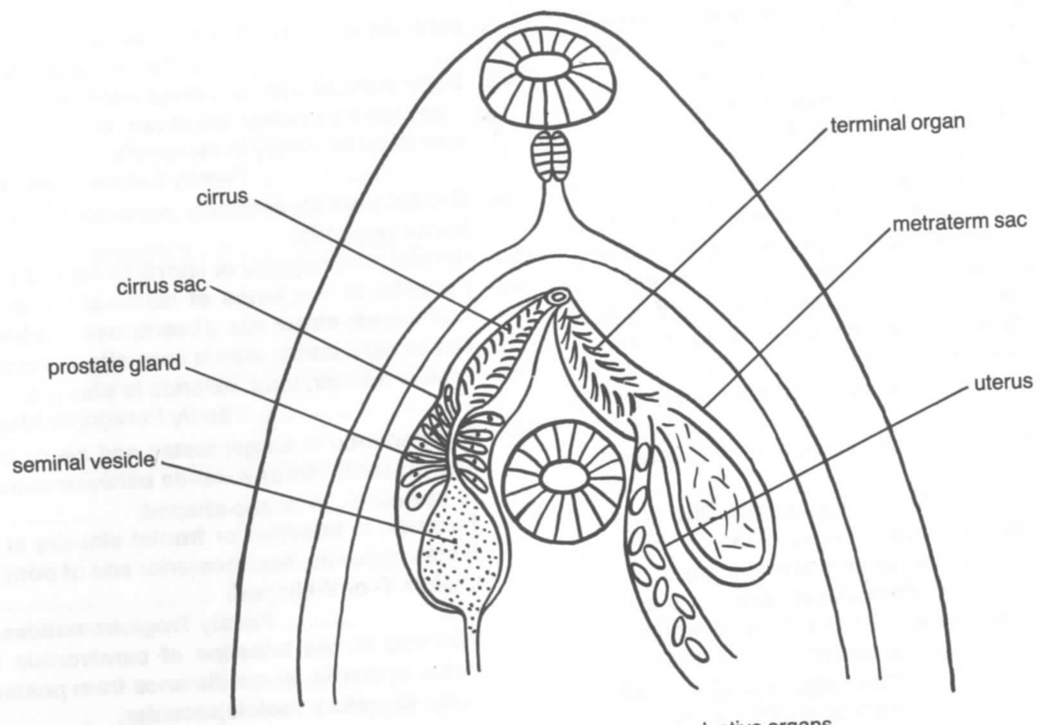


Fig. 222. Monorchiidae, terminal reproductive organs.

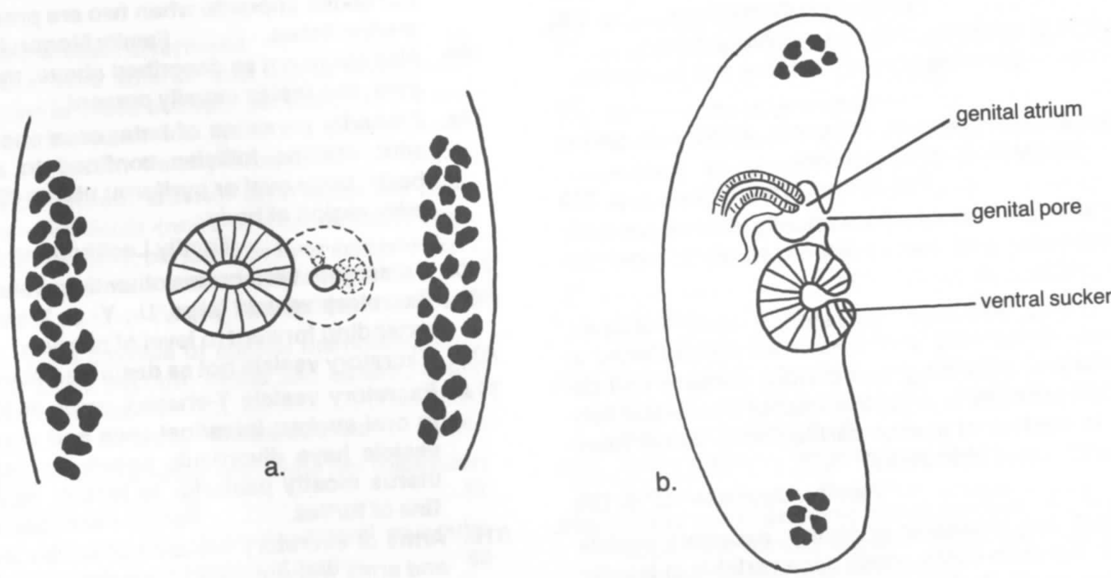


Fig. 223. Genital atrium, a. ventral view b. cross section

84a. Body filiform, cylindrical; one intestinal cecum present and fused with excretory vesicle to form uroproct; testes tandem... Family Monascidae .... p. 123

84b. Body oval or elongate, flat; two ceca present, end blindly; testes usually opposite but might be tandem or oblique; excretory vesicle Y- or V-shaped. .... Family Fellodistomidae .... p. 118

85a. Genital atrium and genital pore lateral to ventral sucker; genital atrium may be spinous or contain pockets; ceca short and divergent; testes opposite (Fig. 223). .... Family Microphallidae .... p. 188

85b. Genital atrium absent or weakly developed; genital pore anterior to ventral sucker; ceca usually long. 86

86a. Parasitic in urinary bladder of fishes and amphibians or in coelom of elasmobranchs; cirrus sac absent; vitellaria compact or dendritic; pharynx absent in some genera. .... Family Gorgoderidae .... p. 232

86b. Not in urinary tract; pharynx always present; cirrus sac present; vitelline glands follicular. 87

87a. Genital pore close to oral sucker or ventral to pharynx. 88

87b. Genital pore anterior to ventral sucker and usually close to it, median or submedian. 90

88a. Genital pore antero-dorsal to oral sucker; cirrus sac long, entirely confined to forebody; excretory vesicle Y-shaped with lateral diverticula; parasitic in the intestine of amphibians and reptiles. .... Family Cephalogonimidae .... p. 180

88b. Genital pore ventral to pharynx or lateral to oral sucker; not parasitic in the intestine. 89

89a. Parasitic in lungs of amphibians; vitelline follicles in distinct clusters along sides of the body; uterus very long, composed of many folds; body translucent; testes opposite or oblique; ventral sucker sometimes vestigial or absent (see couplet 14). .... Family Haematoloechidae (in part) .... p. 175

89b. Parasitic in cloaca, oviducts, bursa of Fabricius or liver of mammals; testes opposite; ovary lobed; vitelline follicles confined to lateral regions of middle third of body. .... Family Prosthogonimidae .... p. 186

90a. Body densely spinous; large circumoral spines present in some genera; pigmented eyespots present in young adults; hermaphroditic duct present; seminal vesicle bipartite; parasitic in intestine of fishes. .... Family Deropristiidae .... p. 224

90b. Body spinous or nonspinous but never densely spinous; circumoral spines absent; hermaphroditic duct absent; seminal vesicle not bipartite. 91

91a. One or both testes close to posterior end of body; testes tandem; excretory vesicle Y-shaped, stem of Y long, arms of vesicle encircle ventral sucker; genital pore median, submedian or dorsal and lateral; parasitic in intestine of amphibians and reptiles. .... Family Telorchiidae .... p. 187

91b. Anatomy not as described above. 92

92a. Body nonspinous; muscular papillae usually present on oral sucker; excretory vesicle tubular; parasitic in intestine of fishes and amphibians. .... Family Allocreadiidae (in part) .... p. 215

92b. Body spinous; muscular papillae absent. 93

93a. Parasitic in mouth; lungs or esophagus of snakes; uterus has prominent longitudinal ascending and descending folds; genital pore median or submedian; stem of excretory vesicle long, arms encircle ventral sucker. .... Family Ochetosomatidae .... p. 183

93b. Parasitic in intestine or gall bladder of vertebrates; uterus has numerous transverse and oblique folds; genital pore usually median and immediately anterior to ventral sucker; excretory vesicle Y-shaped, stem not long. 94

94a. Ceca very short and divergent; testes opposite; vitelline follicles in anterior half of body; parasitic in intestine of amphibians and reptiles. .... Family Brachycoeliidae .... p. 179

94b. Ceca long and not divergent; vitelline follicles primarily in hindbody. 95

95a. Excretory vesicle tubular; parasitic in intestine of poikilothermic vertebrates or progenetic in leeches and crustaceans. ...... Family Macroderoididae .... p. 176

95b. Excretory vesicle Y-shaped; parasitic in intestine, gall bladder or cloaca of all groups of vertebrates. .... Family Plagiorchiidae .... p. 172

Order Strigeatida (LaRue, 1926) Sudarikov, 1959

Superfamily Strigeoidea Railliet, 1919

Miracidia have two pairs flame cells; cercariae are of the longifurcate-pharyngeate type, develop in sporocysts in aquatic snails; body of adult divided into distinct fore- and hindbody, genital pore at posterior end of body; at least three hosts involved in life cycle; adults parasitic in the intestine of vertebrates. Dubois (1938 and 1968) published monographs on this group.

Family Strigeidae Railliet, 1919

Forebody cupshaped or spoonshaped, contains suckers, pharynx and foliaceous tribocytic organ; hindbody cylindrical or ovoid, contains organs of reproduction; testes usually tandem; cirrus sac absent; copulatory bursa well developed; genital pore dorso-terminal; ovary pretesticular; vitelline follicles numerous, extending into both fore- and hindbody or restricted to either fore- or hindbody; uterus short; eggs nonembryonated, operculate; excretory system composed of extensive network of tubules and reservoirs; adults parasitic in intestine of birds and mammals. Epidermal cell formula for miracidium 6, 8, 4, 3.

Key to Genera

1a. Vitelline follicles in fore- and hindbody. 2

1b. Vitelline follicles restricted to hindbody. 4

2a. Pharynx absent (fig. 224). .... **Genus** *Apharyngostrigea* **Ciurea, 1927**

Key to species in Olsen (1940) and in Ukoli (1967).

Life cycle: *A. pipientis*- Strigea cercariae (Fig. 28) develop in daughter sporocysts in the pulmonate snail, *Planorbula armigera*. They penetrate tadpoles of *Rana* and *Hyla* spp. and encyst in the coelom. The metacercaria is *Tetracotyle pipientis*. The pharynx, present in the cercaria, is lost during development to the tetracotyle stage. The adult fluke was produced experimentally in pigeons. The natural definitive hosts are heron and ibis (Olivier, 1940).

Ginetsinskaya (1961) reported the life cycle of *A. cornu*, a parasite of herons in Russia where the host snail is the planorbid *Anisus contortus*. The cercaria is *C. contorti* which encysts in the muscles of shiners and carp. Laboratory reared hosts were not used.

2b. Pharynx present. 3

3a. Forebody pyriform and expanded laterally, wider than hindbody (Fig. 225). .... **Genus** *Parastrigea* **Szidat, 1928**

Key to species in Dubois (1955).

Life cycle: *P. robusta*- Strigea cercariae develop in daughter sporocysts in several genera and species of planorbid snails. Cercariae encyst in tadpoles of *Rana arvalis, R. temporaria, Bufo bufo* and in larvae and adults of the newts, *Triturus vulgaris* and *T. cristatus*. Adults develop in the intestine of domestic and mallard ducks (Odening, 1965 and Vojtek, 1972).

3b. Forebody cupshaped, not expanded laterally and not wider than hindbody (Fig. 226). .... **Genus** *Strigea* **Abildgaard, 1790**

Key to species in Dubois (1968).

Life cycle: *S. elegans*- Miracidia develop and hatch in 11 and 14 days. Strigea cercariae develop in sporocysts in the planorbid snails, *Gyraulus parvus* and *Menetus dilatatus*. After leaving the snail, the cercariae penetrate tadpoles of the genera *Rana, Bufo* and *Ambystoma* and transform to mesocercariae (Fig. 49). Infected tadpoles are then eaten by garter and water snakes in which the metacercaria, a tetracotyle, develops. Natural definitive hosts are the snowy owl, great-horned owl and screech owl (Pearson, 1959; Miller *et al*, 1965).

4a. Hindbody at least four times longer than forebody which is heart- or spoon-shaped. 5

4b. Hindbody less than four times longer than forebody which is cupshaped or ovoid. 7

5a. Hindbody 8 to 20 times longer than spoon-shaped forebody; anterior half of hindbody distinctly narrower than posterior half; testes close to posterior end of hindbody; uterus extends far anterior to ovary; eggs numerous; genital cone and copulatory bursa large (Fig. 227). ... **Genus** *Nematostrigea* **Sandground, 1934**

5b. Fore- and hindbody not as described above. 6

6a. Forebody heart-shaped in ventral view; hindbody 4 to 8 times longer than forebody; testes oval or only slightly lobed; hermaphroditic duct long (Fig. 228). ... . **Genus** *Cardiocephalus* **Szidat, 1928**

Life cycle: *C. longicollis*- Furcocercous cercariae of the strigea group *(C. nassae)* develop in daughter sporocysts in the marine prosobranch, *Nassa corniculum*. The metacercaria is a tetracotyle infecting the optic lobes of marine fishes in the genera *Boops, Diplodus, Belone* and *Pagellus* as natural infections. Experimental infections were established in two species of *Diplodus*. Natural definitive hosts are gulls, *Larus argentatus* and *L. ridibunda* (see Prevot and Bartoli, 1980).

6b. Forebody square or rectangular in ventral view; hindbody 6 to 17 times longer than forebody; testes distinctly lobed; hermaphroditic duct short (Fig. 229). .... **Genus** *Ophiosoma* **Szidat, 1928**

7a. Copulatory bursa contains genital bulb (Fig. 230). .... **Genus** *Cotylurus* **Szidat, 1928**

Key to species in Dubois (1968).

Life cycle: *C. flabelliformis*- Miracidia develop and hatch in about three weeks after eggs are laid. They penetrate the pulmonate snails, *Stagnicola angulata, Lymnaea stagnalis, Physa parkeri, P. sayii* and Helisoma *spp. Strigea cercariae (Cercaria flabelliformis)* develop in daughter sporocysts. They encyst in the same snail and develop into tetracotyles *(Tetracotyle flabelliformis)*. The definitive hosts such as birds of the genera *Nyroca, Marila, Anas, Querquedula* and *Spatula* acquire the parasite by eating infected snails (Van Haitsma, 1931a; Cort *et al*, 1944).

Olson (1970) studied the life cycle of *C. erraticus*. Miracidia develop and hatch in 15 to 16 days at 24 C. Strigea cercariae develop in daughter sporocysts in the prosobranch, *Valvata lewisi* within 35 days. After leaving the snail they encyst in the pericardial cavity of several species of salmonid fishes and develop to the tetracotyle type of metacercaria. Gulls become infected by eating infected fishes. Sexually mature adults develop in four days following ingestion of metacercariae.

The life cycle of *C. variegatus* is similar to the above species (Odening, 1971).

7b. Genital bulb absent. 8

8a. Terminus of uterus curved forward, opening into posterior wall of copulatory bursa; genital pore on dorsal surface of body; ejaculatory pouch present (Fig. 231). .... **Genus** *Pseudapatemon* **Dubois, 1936**

8b. Terminus of uterus not curved, unites with ejaculatory duct to form long hermaphroditic duct; genital pore at end of body; ejaculatory pouch absent (Fig. 232). .. .. **Genus** *Apatemon* **Szidat, 1928**

Key to species in Dubois (1968).

Life cycle: *A. gracilis*- Strigea cercariae (= *Cercaria burti)* develop in daughter sporocysts in the snails, *Helisoma trivolvis, H. antrosum* and *Bithynia tentaculata*. The metacercaria is a tetracotyle in leeches of the genera *Herpobdella* and *Haemopis*. The adult parasite develops in the intestine of merganser and Mallard ducks, attaining sexual maturity in four days (Szidat, 1931; Stunkard *et al*, 1941).

The life cycle of this species was also studied by Blair (1956) in Scotland where different hosts are utilized.

Johnston and Angel (1951) describe the life cycle of *A. intermedius* in Australia. The cycle is similar to that of *A. gracilis* except for use of different species of hosts. The leeches are species of *Glossiphonia*. These authors comment on the difference in use of host snails by *A. gracilis* in North America, a pulmonate and a prosobranch. They suggest the possibility of two species of *Apatemon* being involved instead of only one in the North American Fauna.

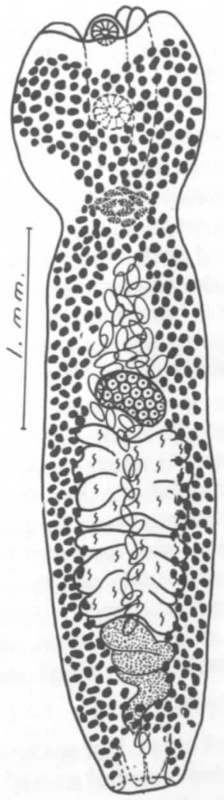


Fig. 224. *Apharyngostrigea bilobata.*

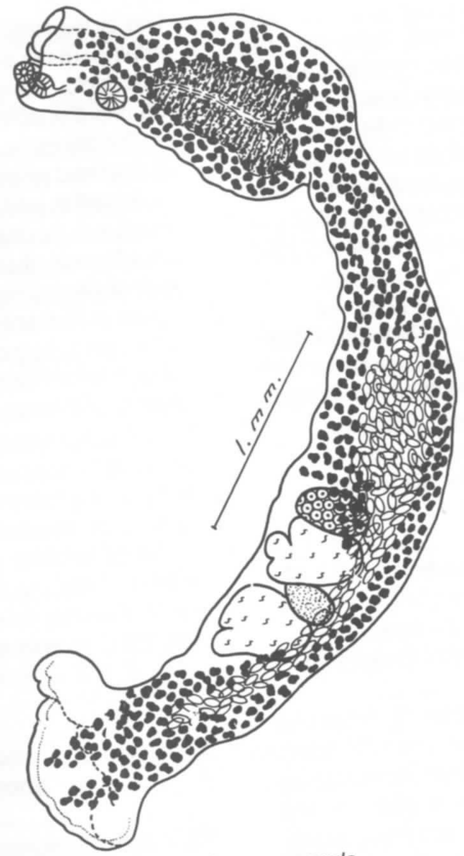


Fig. 225. *Parastrigea campanula.*

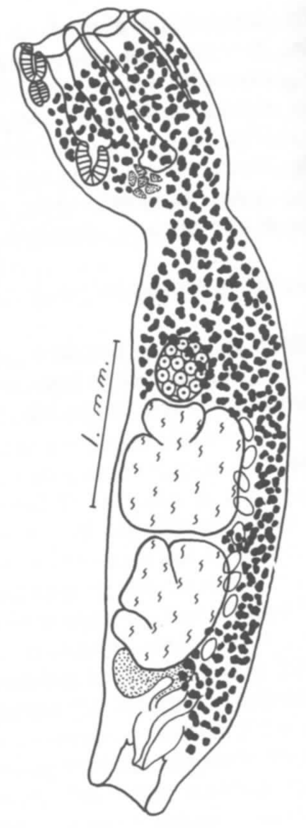


Fig. 226. *Strigea falconis.*

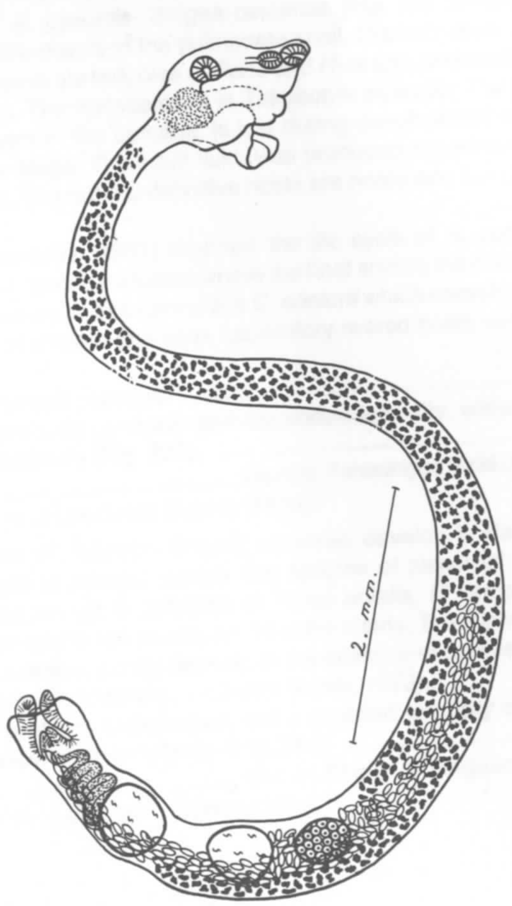


Fig. 227. *Nematostrigea serpens annulata.*

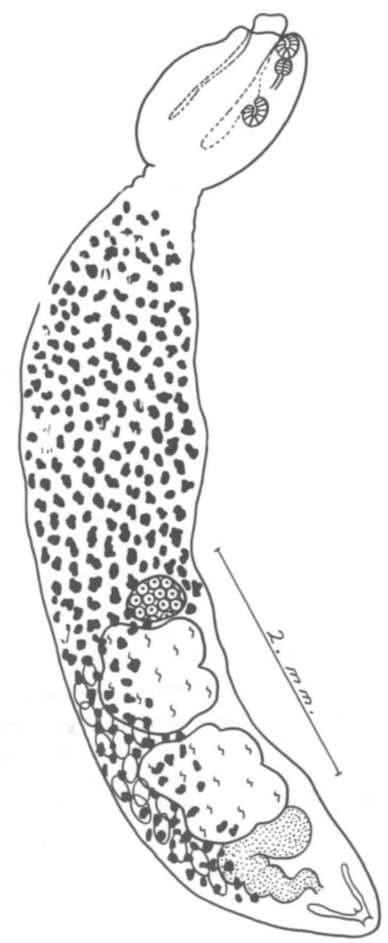


Fig. 228. *Cardiocephalus brandesi.*

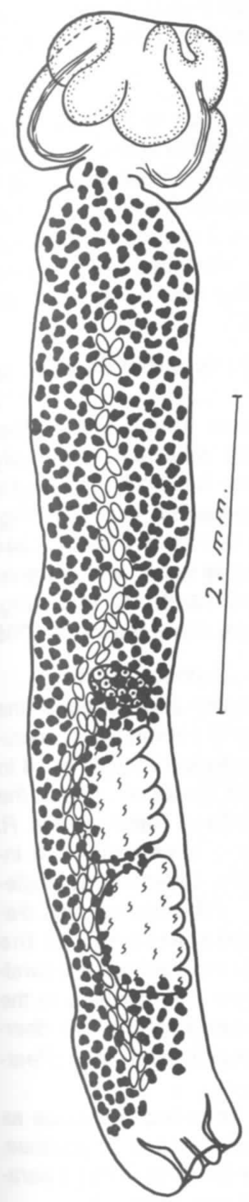


Fig. 229. *Ophiosoma crassicolle.*

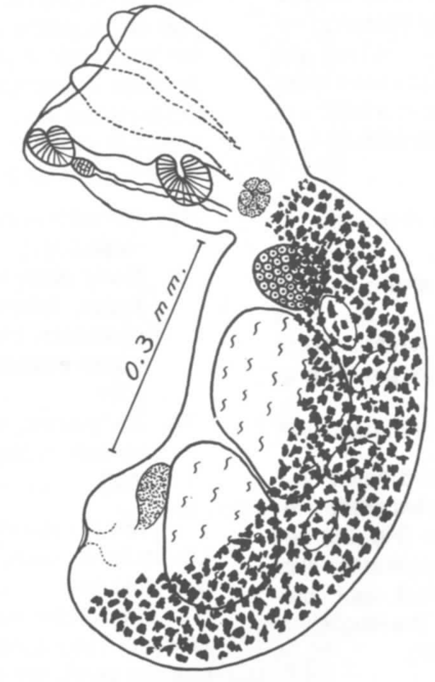


Fig. 230a. *Cotylurus flabelliformis.*

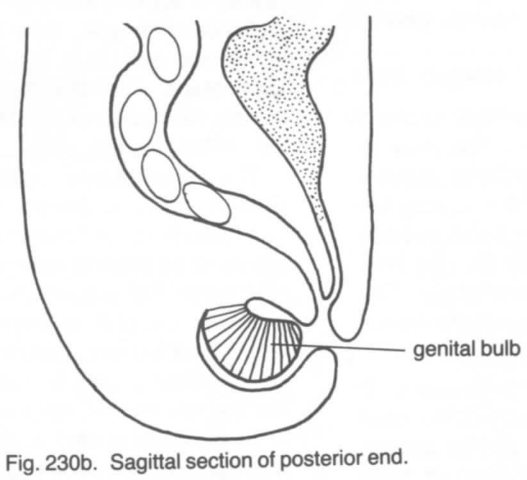


Fig. 230b. Sagittal section of posterior end.

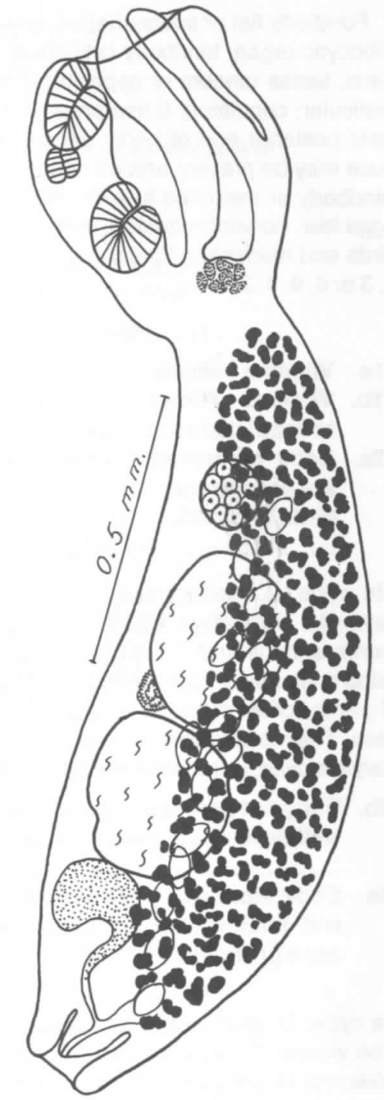


Fig. 232a. *Apatemon gracilis.*

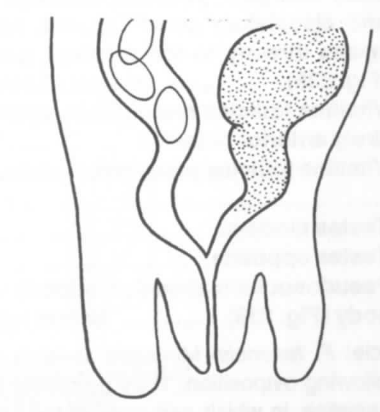


Fig. 232b. Sagittal section, posterior end.

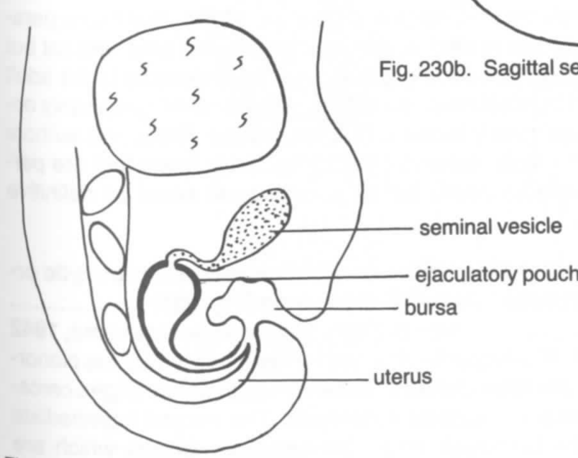


Fig. 231. *Pseudapatemon* sp., posterior end.

Family Diplostomidae Poirier, 1886

Forebody flat or spoonshaped, contains suckers and bulbous tribocytic organ; hindbody cylindrical, contains reproductive organs; testes tandem or opposite; cirrus sac absent; ovary pretesticular; copulatory bursa present, opening on dorsal surface near posterior end of body; genital cone usually present; prepuce may be present around cone; vitelline follicles in fore- and hindbody or restricted to either fore- or hindbody; uterus short, eggs few, nonembryonated, operculate; parasitic in intestine of birds and mammals. Epidermal cell formula of miracidium 6, 8, 4, 3 or 6, 9, 4, 3.

Key to Genera

1a. Vitelline follicles restricted to hindbody. 2

1b. Vitelline follicles present in both fore- and hindbody or restricted to forebody. 4

2a. Body permanently arched dorsally; pseudosuckers absent; ventral sucker vestigial or absent; parasitic in birds (Fig. 233). .... **Genus *Crassiphiala* Van Haitsma, 1925**

Life cycle: *C. bulboglossa*- Miracidia develop and hatch nine days after oviposition. After penetrating the planorbid snails, *Helisoma anceps* and *H. trivolvis*, strigea cercariae (Fig. 28) develop in daughter sporocysts in 33 days. They encyst in the skin of perch, pike, minnows and chub, causing "black spot" disease. The metacercaria is a neascus (Fig. 51b). The kingfisher, *Ceryle alcyon*, is the definitive host (Hoffman, 1956).

2b. Body not permanently arched dorsally; ventral sucker well developed; pseudosuckers present or absent. 3

3a. Body elongate; pseudosuckers absent; genital bulb and thick-walled ejaculatory pouch present; genital cone protrusible (Fig. 234). .... **Genus *Uvulifer* Yamaguti, 1934**

Life cycle: *U. ambloplites*- Miracidia develop and hatch in about three weeks. They penetrate the planorbid snails, *Helisoma trivolvis* and *H. campanulatum* in which strigea cercariae *(Cercaria bessiae)* develop in daughter sporocysts. After leaving the snails, they encyst in the muscle and skin of bass, perch, sunfish and pike, causing "black spot" disease, a condition arising from the deposition of black pigment in the cyst membrane. The metacercaria is a neascus *(Neascus amboplitis)*. Kingfishers become infected by eating the infected fish (many authors).

3b. Body elongate; pseudosuckers present; genital bulb and ejaculatory pouch absent; hermaphroditic duct opens directly to the exterior; genital atrium absent (Fig. 235). .... **Genus *Pulvinifer* Yamaguti, 1933**

4a. Vitelline follicles restricted to forebody or at least entirely anterior to testes 5

4b. Vitelline follicles present in both fore- and hindbody. 10

5a. Testes tandem. 6

5b. Testes opposite. 8

6a. Pseudosuckers absent; hindbody narrower than forebody (Fig. 236). .... **Genus *Fibricola* Dubois, 1932**

Life cycle: *F. texensis*- Miracidia develop and hatch within 12 days following oviposition. They penetrate the pulmonate snail, *Physa anatina*, in which cercariae of the strigea group develop in daughter sporocysts. The metacercaria is a diplostomulum (Fig. 51a) in the coelom and muscles of tadpoles of the genus *Rana*. The natural definitive host is the raccoon in which the parasite matures in 10 days. Experimental infections were established in chicks, mice, rats and hamsters (Chandler, 1942; Leigh, 1954).

Pearson (1961) investigated the life cycle of *Fibricola intermedius (Neodiplostomum i.)*, a parasite of the water rat, *Hydromys chrysogaster* and *Rattus assimilis*. The host gastropod is the freshwater limpet, *Pettancylus assimilis*. The diplostomulum develops in tadpoles and adults of several species of tree frogs. Diplostomula were also found in the pink-tongued skink which is regarded as a paratenic host. The earlier larval stages are like those of other species in the genus.

6b. Pseudosuckers present; hindbody about as wide as forebody. 7

7a. Body elongate, about five times longer than wide; testes lobed; tribocytic organ elliptical; forebody spatulate; hindbody longer than forebody; tribocytic organ covers ventral sucker; parasitic in otters (Fig. 237) .... **Genus *Enhydridiplostomum* Dubois, 1944**

7b. Body short, about twice as long as wide; testes transversely elongate, lobed or not; forebody oval (Fig. 238). .... **Genus *Alaria* Schrank, 1788**

Key to species of mesocercariae in Johnson (1970)

Life cycle: *A. arisaemoides*- Miracidia hatch and penetrate the planorbid snails, *Planorbula armigera* and *Promenetus exacuous*. Strigea cercariae develop in daughter sporocysts in 18 to 26 days. They penetrate and develop to mesocercariae in the muscles and connective tissue of tadpoles of *Rana pipiens*, *R. sylvatica* and *Bufo americanus*. When mesocercariae are ingested by mammals of the families Felidae, Canidae and Mustelidae they migrate to the lungs by way of the coelom and diaphragm where they change to metacercariae of the diplostomulum type. They then pass up the trachea, are swallowed and end up in the intestine where they develop to the adult stage. Paratenic hosts for the mesocercaria are deermouse, housemouse, chicken, garter snakes and frogs (Pearson, 1956; Hayden, 1969).

The above species goes through a three-host life cycle as does *A. canis*, *A. intermedia*, *A. mustelae* and *A. marcianae*. The "paratenic" or "collector" hosts are those in which a parasite survives in the same stage in which it was acquired.

In controlled experiments, transmammary infection with the mesocercaria of *A. marcianae* was found to occur in mice. The mesocercariae were present in the mammary glands of females suckling their young. In these experiments transplacental infection did not occur (Shoop and Corkum, 1983). This same parasite was found to exist as a mesocercaria in a pregnant cat but when passed to suckling young went on to develop to the adult stage in the intestine of the kittens. The same thing probably occurs in raccoons infected with *A. marcianae*. The above authors coined the term "amphiparatenic" for those hosts that are paratenic hosts as adults but as juveniles can serve as definitive host.

8a. Thick-walled ejaculatory pouch present; tribocytic organ ovoid; parasitic in raccoon (Fig. 239) .... **Genus *Pharyngostomoides* Harkema, 1942**

Life cycle: *P. procyonis*- Hatched miracidia penetrate the planorbid snail, *Menetus dilatatus buchanensis*, in which strigea cercariae develop in daughter sporocysts. The second intermediate host is the branchiobdellid, *Cambarincola osceola* which are commensals on crayfish. The adult fluke develops in the intes-

(Continued)

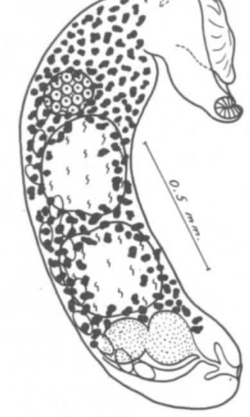


Fig. 233. *Crassiphiala bulboglossi.*

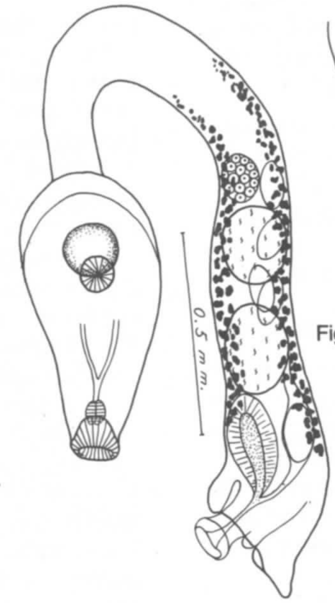


Fig. 234a. *Uvulifer ambloplitis.*

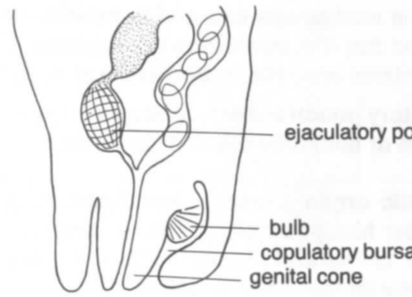


Fig. 234b. Sagittal section, posterior end.

Fig. 235a. *Pulvinifer macrostomum.*


Fig. 235b. Sagittal section, posterior end.

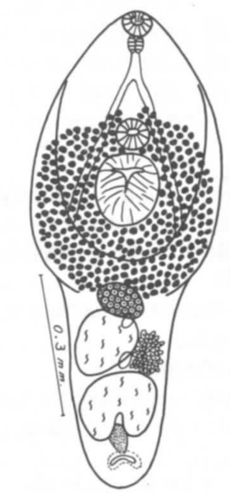


Fig. 236. *Fibricola cratera.*

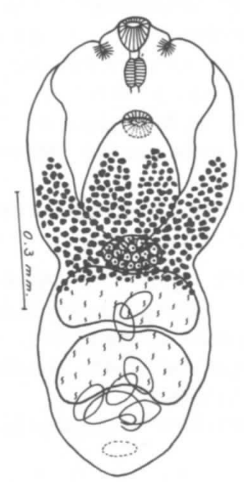


Fig. 238. *Alaria mustelae.*

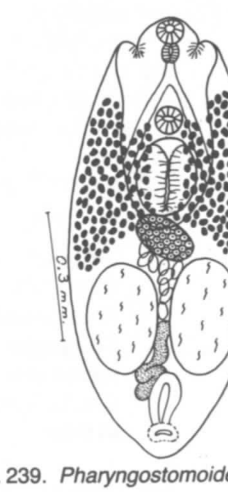


Fig. 239. *Pharyngostomoides procyonis.*

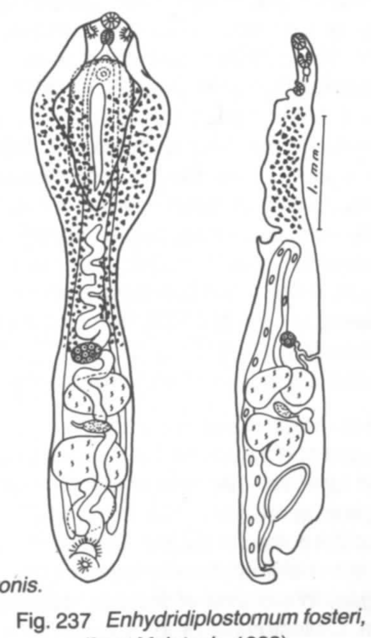


Fig. 237 *Enhydridiplostomum fosteri,* (from McIntosh, 1939)

tine of raccoon which eats the infected crayfishes. Mesocercariae of these species were found in the mothers milk. It was assumed that the mother was exposed to mesocercariae during pregnancy and that the mesocercariae migrated to the mammary glands (Harris *et al*, 1967a; Beckerdite *et al*, 1971).

8b. Ejaculatory pouch absent; tribocytic organ either very elongate or distinctly bilobed; parasitic in raccoon. 9

9a. Tribocytic organ elongate, contained in a pouch in forebody; hindbody shorter than forebody; pseudosuckers on ventral surface of body some distance from anterior margin (Fig. 240). .... Genus *Procyotrema* Harkema and Miller, 1959

Life cycle: *P. marsupiformis*- Miracidia penetrate the planorbid snail, *Promenetus exacuous* in which strigea cercariae develop in daughter sporocysts. They penetrate tadpoles of *Rana clamitans* and *R. sphenocephala* and change to mesocercariae which survive in the adult frogs. Raccoons eat the infected frogs. Diplostomula develop in the pancreas of the raccoon and then pass to the pancreatic duct where they develop to sexually mature adults in about 18 days (Harris *et al*, 1970).

9b. Tribocytic organ bilobed; hindbody longer than forebody; pseudosuckers at anterior margin of body; copulatory bursa large with genital recess and ventral papilla (Fig. 241). .... Genus *Parallelorchis* Harkema and Miller, 1961

10a. Pseudosuckers present. 11

10b. Pseudosuckers absent. 14

11a. Boundary between fore- and hindbody distinct. ... 12

11b. Boundary between fore- and hindbody barely perceptible. 13

12a. Genital bulb present in copulatory bursa; testes H-shaped; parasitic in birds (Fig. 242). .... Genus *Bolbophorus* Dubois, 1935

Life cycle: *B. confusus*- Strigea cercariae develop in sporocysts in *Helisoma trivolvis*. They encyst in numerous species of fish, causing some pathological symptoms. The metacercaria is an encysted diplostomulum. The definitive host is the pelican. This is the only known cyst-forming diplostomulum (Fox, 1966).

Paperna and Lengy (1963) studied this species in Israel where the purple heron, *Ardea purpurea* is the natural definitive host. Strigea cercariae encyst in the fish, *Tilapia nilotica* and then develops to a neascus type of metacercaria. When these were fed to supposedly trematode-free purple herons, many adult flukes were recovered 20 days later. It is possible that the "encysted" diplostomulum of Fox, 1966 is really a neascus.

12b. Genital bulb absent; testes bilobed, concave ventrally; parasitic in birds (Fig. 243). .... Genus *Diplostomum* von Nordmann, 1832

Life cycle: *D. flexicaudum*- Miracidia develop and hatch in three weeks following oviposition and penetrate the pulmonate snails, *Stagnicola angulata* and *Lymnaea stagnalis* in which strigea cercariae develop in daughter sporocysts. The cercaria *(Cercaria flexicaudum)* penetrates the common sucker, *Catostomus commersoni* and develops into a diplostomulum type of metacercaria. *(Diplostomulum gigas)* in the lens of the eye, causing cataractous lenses to form. Diplostomula of ths species have also been found in lymnaeid and physid snails.

Cercariae of *D. flexicaudum* were able to penetrate and become diplostomula in the lenses of tadpoles, frogs, turtles, chicks, ducklings, mice, rats, guinea pigs and rabbits under experimental conditions. Blindness was caused in many cases. The natural definitive hosts for this parasite are gulls and terns which eat the infected fish (Van Haitsma, 1931b).

Larvae of at least five species in the genus *Diplostomum* have been involved in causing cataractous lenses in fishes and other vertebrates. Two cases have been reported in human beings. (Ashton, Brown and Easty, 1969).

Cort and Brackett (1937, 1938) investigated the life cycle of *D. micradena* in northern Michigan where the diplostomulum causes "bloat disease" in tadpoles.

Rees (1955, 1957) and Arvy and Buttner (1954) worked on the life cycle of *D. phoxini* in Europe. The diplostomulum develops in the brain of minnows. The adult is a parasite of ducks.

13a. Pseudosuckers deep, causing anterior end of body to appear trilobed; intestinal parasites of birds (Fig. 244). .... Genus *Hysteromorpha* Lutz, 1931

Life cycle: *H. triloba*- Miracidia develop and hatch in seven days following oviposition and penetrate the freshwater snail, *Gyraulus hirsutus* in which strigea cercariae develop in daughter sporocysts. Cercariae penetrate the bullheads, *Ameiurus melas* and *A. nebulosus*, in the muscles of which they develop to diplostomula *(Diplostomulum corti)*. Adults develop within 60 hours after metacercariae are eaten by piscivorous birds such as cormorants, herons, egrets and pelicans (Hugghins, 1954).

13b. Pseudosuckers shallow, not causing body to appear trilobed at anterior end; parasite of opossum (Fig. 245). .... Genus *Didelphodiplostomum* Dubois, 1944

Life cycle: *D. variable*- Miracidia develop and hatch in 10 days. They penetrate the planorbid snail, *Menetus dilatatus* in which strigea cercariae develop in daughter sporocysts in 18 days. Cercariae penetrate the larvae of *Ambystoma opacum* and *A. maculatum* and adults of *Eurycea bislineata, Siren lacertina* and *Necturus* spp. in which diplostomula *(Diplostomulum ambystomae)* develop in the pericardial and peritoneal cavities. The natural definitive host is the opossum. Experimental infections were established in mice (Harris *et al*, 1967b).

14a. Genital cone surrounded by a prepuce; copulatory bursa evaginable; parasitic in birds (Fig. 246). .... Genus *Posthodiplostomum* Dubois, 1936

Life cycle: *P. minimum*- Strigea cercariae develop in sporocysts in *Physa gyrina* and *P. heterostropha*. The metacercaria is a neascus *(Neascus vancleavei)* in the fishes, *Lepomis gibbosus, L. megalotus* and *Ambloplites rupestris*. The mature fluke develops in the heron, *Nycticorax nycticorax*. Experimental infections were established in chicks, the mature adults developing in 32 hours after feeding metacercariae (Miller, 1954; Hoffman, 1958a).

Dönges (1964b) published an account of the life cycle of *P. cuticola* which caused "blackspot" disease in fishes in Germany.

14b. Prepuce absent; copulatory bursa not evaginable (Fig. 247). .... Genus *Neodiplostomum* Railliet, 1919
This genus has been divided into two subgenera.
Subgenus: *Neodiplostomum*- **Genital cone absent; testes unequal in size.**
Conodiplostomum- **Genital cone present; testes equal in size.**

Life cycle: *N. intermedium* - Miracidia hatch and penetrate the freshwater limpet, *Pettancylus assimilis* in which strigea cercariae develop in daughter sporocysts. After emerging, the cercariae penetrate tadpoles and adults of the tree frogs, *Hyla pear-*

(Continued)

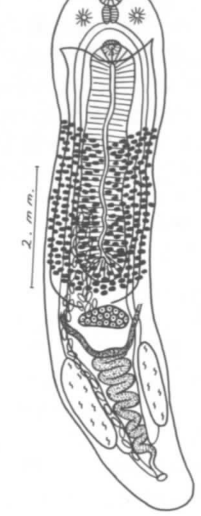


Fig. 240. *Procyotrema marsupiformis.*

Fig. 241a. *Parallelorchis diglossus.*

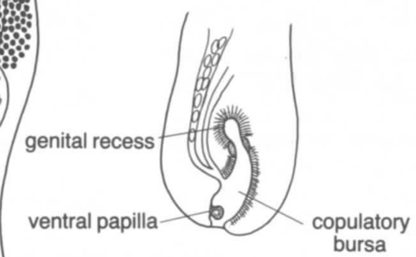


Fig. 241b. Sagittal section, posterior end.

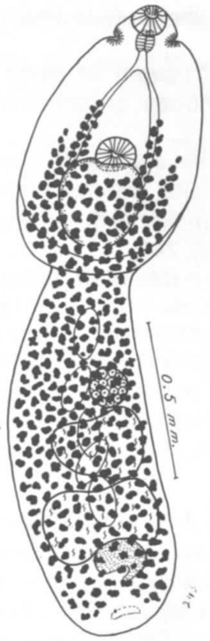


Fig. 243. *Diplostomum huronense.*

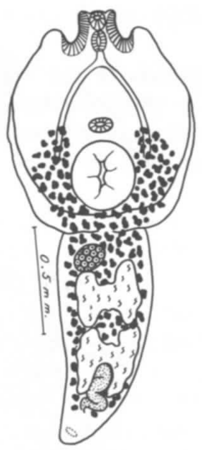


Fig. 242a. *Bolbophorus confusus.*

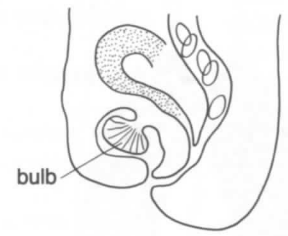


Fig. 242b. Sagittal section, posterior end.

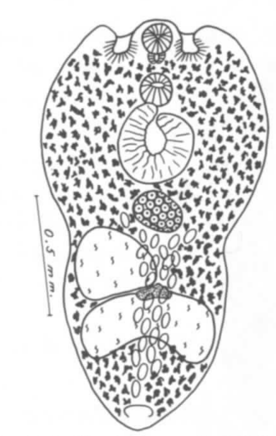


Fig. 244. *Hysteromorpha triloba.*

Fig. 245. *Didelphodiplostomum variable.*

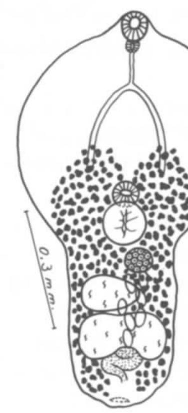


Fig. 246a. *Posthodiplostomum minimum.*

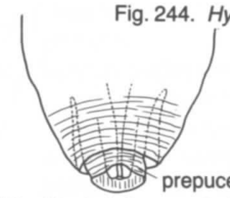


Fig. 246b. Ventral view, posterior end.

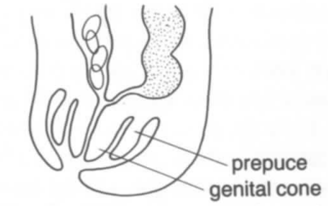


Fig. 246c. Sagittal section, posterior end.

soni and *H. caerula*. The natural definitive host is *Rattus assimilis*. The laboratory rat is a satisfactory experimental host, eggs appearing in the feces in seven to eight days (Pearson, 1961).

15a. Ovary near margin of body, wedged between the testes; hindbody of uniform thickness throughout (Fig. 248). ....**Genus *Mesophorodiplostomum* Dubois, 1936**

15b. Ovary opposite anterior testis; body becomes progressively thicker in dorso-ventral plane toward posterior end (Fig. 249). .... **Genus *Ornithodiplostomum* Dubois, 1936**

Life cycle: *O. ptychocheilus* - Miracidia develop and hatch within 10 days after eggs are released. They penetrate the pulmonate snails, *Physa anatina* and *P. gyrina* in which strigea cercariae develop in daughter sporocysts. The cercariae penetrate chubs, shiners, squawfish, fathead and bluntnose minnows and johnny darter and encyst in the brain as neascus larvae. Natural definitive hosts are several species of ducks, especially mergansers. Experimental infections were established in chicks, ducklings and English sparrow (Hoffman, 1958b; Hendrikson, 1980).

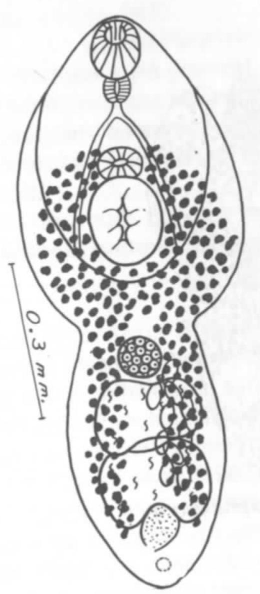


Fig. 247. *Neodiplostomum* sp.

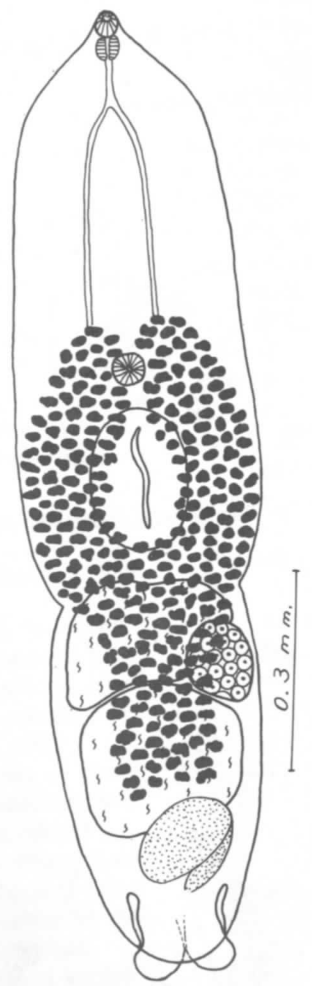


Fig. 248. *Mesophorodiplostomum pricei*.

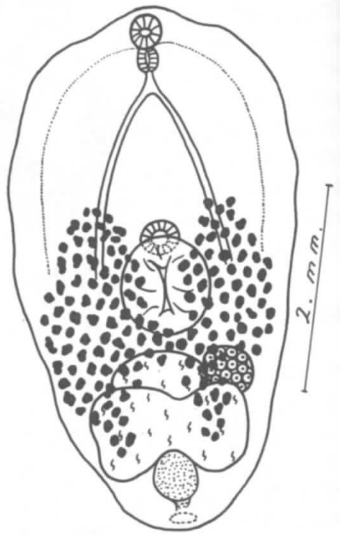


Fig. 249. *Ornithodiplostomum ptychocheilus*.

Family Cyathocotylidae Poche, 1926

Body small (less than 2 mm), round oval or elongate, usually not divided into distinct fore- and hindbody; tribocytic organ bulbous, sometimes very large; ventral sucker absent in some genera; ceca long; testes tandem, oblique or opposite; cirrus sac present, near posterior end of body; ovary either intertesticular or opposite anterior testis; genital pore at posterior end of body; vitelline follicles in both fore- and hindbody or restricted to hindbody; uterus short; eggs few, operculate, nonembryonated; parasitic in digestive tract of reptiles, birds and mammals. Epidermal cell formula of miracidium 6, 8, 4, 4; 6, 8, 4, 2 or 6, 8, 4, 3.

Key to Genera

1a. Body elongate, divided into flat forebody and conical hindbody (Figs. 250, 251). .... **Genus *Neogogatea* Chandler and Rausch, 1947**

Life cycle: *N. kentuckiensis* (= *Mesostephanus k.*) - Longifurcate pharyngeate cercariae (= *Cercaria kentuckiensis*) of the vivax type (Fig. 29) develop in daughter sporocysts in the prosobranch snails, *Anaplocamus dilatatus* and *Mudalia carinata*. They encyst in the muscles of at least 10 species of freshwater fishes. The natural definitive host is the double-crested cormorant, *Phalacrocorax auritus*. Experimental infections were established in young chicks, the parasite maturing in seven days after metacercariae were fed (Myer, 1960; Hoffman and Dunbar, 1963; Stunkard, 1972a).

1b. Body oval or round in ventral view, not divided into distinct fore- and hindbody. **2**

2a. Body oval, concave ventrally; ventral sucker some distance posterior to oral sucker; tribocytic organ small. **3**

2b. Body round; ventral sucker absent or close to oral sucker when present; tribocytic organ large or small. **4**

3a. Ovary anterior to small bulbous tribocytic organ; testes tandem; cirrus sac has thin wall (Fig. 252). .... **Genus *Prohemistomum* Odhner, 1913**

Life cycle: *P. chandleri* - Vivax cercariae (Fig. 29) develop in daughter sporocysts in the prosobranch snail, *Pleurocera acuta*. Cercariae encyst in the tissues of several species of bass. Immature specimens were recovered from the intestine of channel catfish, *Ictalurus punctata;* Northern sculpin, *Cottus bairdi* and the water snake, *Natrix sipedon,* all of which had been fed metacercariae from bass. The natural definitive host is probably a piscivorous bird. The anatomy of the mature adult is unknown (Vernberg, 1952).

3b. Ovary posterior or dorsal to tribocytic organ; testes oblique; cirrus sac has thick wall; vitelline follicles restricted to hindbody (Fig. 253, 254). .... **Genus *Mesostephanus* Lutz, 1935**

Life cycle: *M. appendiculatoides* - Vivax cercariae develop in sporocysts in the marine prosobranch snail, *Cerithium muscarum*. They encyst in the muscles of small mullet. Natural infections with metacercariae were also found in three species of mullet. Metacercariae from experimentally infected mullet were fed to a suckling opossum and partially developed flukes were recovered four days later. Experimental infections were also established in the black-crowned night heron, *Nycticorax n. hoactli*; ring-billed gull, *Larus delawarensis* and the raccoon, *Procyon lotor*. The natural definitive host is the pelican, *Pelecanus occidentalis* (see Hutton and Sogandares-Bernal, 1960).

Martin (1961) studied the life cycle of *Mesostephanus appendiculatus* which uses the prosobranch, *Cerithidea californica* as first intermediate host. Furcocercous cercariae of the vivax group develop in daughter sporocysts. Cercariae encyst in the muscles of the minnows, *Fundulus parvipinnis p.* and *Gillichthys mirabilis*. Metacercariae were fed to chicks and the adult parasite recovered nine days later from the small intestine.

Dennis and Penner (1971) and Dennis (1973) reported the life cycle of *M. yedeae* which uses the same host mollusc as *M. appendiculatus*. The cercariae encysted in *Fundulus heteroclitus, Cyprinodon variegatus* and in guppies, *Peocilia reticulata*. Experimental infections were established in chicks, the adult parasite developing in about five days after feeding infected fish. The natural definitive host is the pelican, *Pelecanus occidentalis*.

Pike (1980) studied the life cycle of *M. milvi* which uses the mollusc *Cleopatra aegyptiaca* as first host. Cercariae of the vivax group develop and eventually encyst in the tissues of the frog, *Discoglossus occipitalis*. Experimental infections were established in two wild nestlings of Abdim's stork, *Sphenorhynchus abdimii* after treatment with $CC1_4$ and liquid paraffin to eliminate previous infections. Adults were recovered seven days after feeding metacercariae.

4a. Body concave ventrally; ventral sucker plainly visible, close to oral sucker; tribocytic organ very large; genital pore in posterior fourth of body (Fig. 255). .... **Genus *Holostephanus* Szidat, 1936**

Life cycle: *H dubinini*- Mother and daughter sporocysts develop in the prosobranch, *Bithynia tentaculata*. Vivax cercariae develop and after emerging from the snail, encyst in at least six species of fishes. Metacercariae were fed to a cormorant, *Phalacrocorax carbo* and adults recovered 76 hours later (Boitek and Voitkova, 1968).

A partial life cycle is known for *H. luhei* (see Erasmus 1962; Pike, 1968).

4b. Body not concave ventrally; ventral sucker absent or covered by tribocytic organ; genital pore at posterior end of body. **5**

5a. Ventral sucker absent or covered by tribocytic organ; testes elongate and nearly opposite, near middle of body; tribocytic organ large; vitelline follicles in wreath-like design around periphery of body (Fig. 256). .... **Genus *Cyathocotyle* Mühling, 1896**

Life cycle: *C. bushiensis* - Miracidia develop and hatch in about 14 days. They enter the prosobranch, *Bithynia tentaculata* in which vivax cercariae develop in daughter sporocysts and after emerging encyst in the digestive gland of the same or a different snail. Metacercariae were fed to day-old Pekin ducks and adults recovered from the ceca six days later. Natural definitive hosts are the black duck, *Anas rubripes;* blue-wing teal, *Anas discors* and the green-wing teal, *A. carolinensis* (see Khan, 1962a; Gibson *et al*, 1972).

The life cycle of *C. opaca* was studied by Vojtek (1971). The mollusc is the same as for *C. bushiensis* but the metacercaria was found in several species of leeches and the adults inhabit the lower small intestine and colon of ducks, causing injury to the mucosa.

5b. Ventral sucker absent; testes oval, tandem or oblique; tribocytic organ small; vitelline follicles confined mainly to posterior half of body (Fig. 257). .... Genus *Linstowiella* Szidat, 1933

Life cycle: *L. szidati*- Vivax cercariae *(Cercaria szidati)* develop in daughter sporocysts in the prosobranch, *Campeloma rufum*. Cercariae encyst in the tissues of the common shiner, *Notropis cornutus*. Metacercariae were fed to baby chicks and the adults recovered three days later. The opossum has been found to be the natural definitive host for this species (Anderson and Cable, 1950; Lumsden and Winkler, 1962).

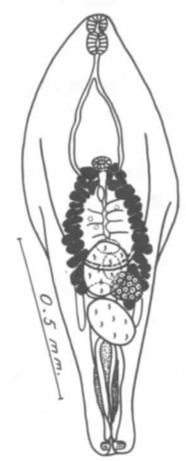


Fig. 250. *Neogogatea kentuckiensis*. (from Myer, 1960)

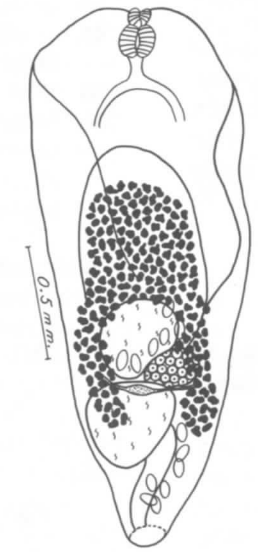


Fig. 251. *Neogogatea bubonis*. (from Chandler and Rausch, 1947)

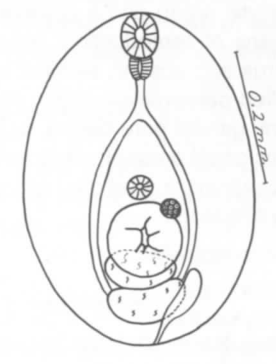


Fig. 252. *Prohemistomum chandleri*, juvenile. (from Vernberg, 1952)

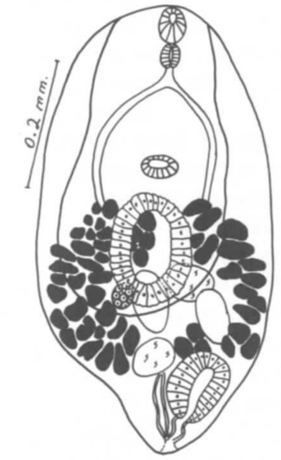


Fig. 253. *Mesostephanus appendiculatus*. (from Martin, 1961)

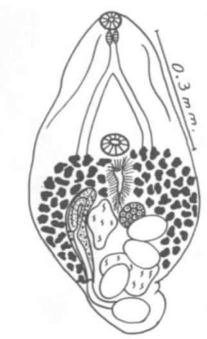


Fig. 254. *Mesostephanus appendiculatoides*. (from Cable, Connor and Balling, 1960)

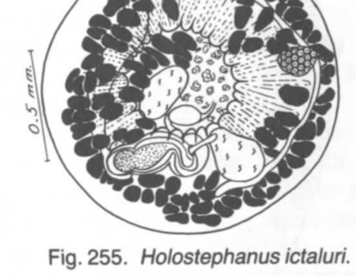


Fig. 255. *Holostephanus ictaluri*.

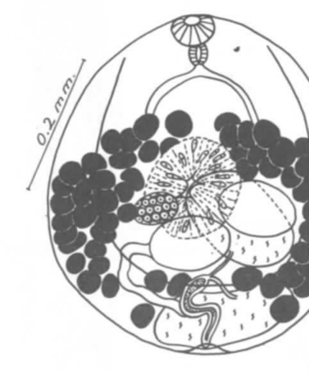


Fig. 257. *Linstowiella szidati*. (from Anderson and Cable, 1950)

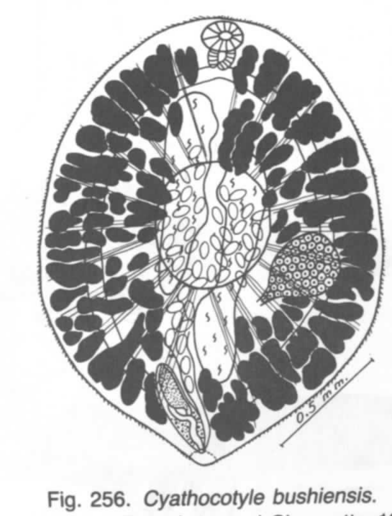


Fig. 256. *Cyathocotyle bushiensis*. (from Gilson, Broughton and Choquette, 1972)

Family Proterodiplostomidae Dubois, 1936

Body divided into flat forebody, containing the suckers and bulbous tribocytic organ and a cylindrical hindbody which contains the organs of reproduction; testes tandem, in middle of hindbody; cirrus sac absent; seminal vesicle free in parenchyma; thick-walled paraprostate organ posterior to testes; genital atrium present; genital pore dorsal, near posterior end of body; hermaphroditic canal present; vitelline follicles in both fore- and hindbody or confined to forebody; parasitic in intestine of reptiles, especially alligators.

Key to Genera

1a. **Body linguiform, division between fore- and hindbody indistinct; vitelline follicles confined to area between ovary and ventral sucker (Fig. 258) .... Genus *Crocodilicola* Poche, 1925**

1b. **Division between fore- and hindbody distinct. 2**

2a. **Vitelline follicles extend into fore- and hindbody (Fig. 259). .... Genus *Archaeodiplostomum* Dubois, 1944**

2b. **Vitelline follicles confined to forebody. 3**

3a. **Hindbody with a linear series of accessory suckers on dorsal surface; atrial sucker also present in genital atrium; ejaculatory duct fused with terminus of uterus; hermaphroditic canal thin-walled (Fig. 260). .... Genus *Polycotyle* Willemoes-Suhm, 1870**

3b. **Hindbody without accessory and atrial suckers; ejaculatory duct united with side of paraprostate organ; hermaphroditic canal has thick muscular wall (Fig. 261). .... Genus *Pseudocrocodilicola* Byrd and Reiber, 1942**

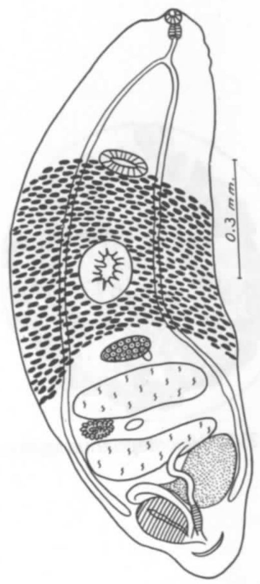


Fig. 258. *Crocodilicola pseudostoma.*

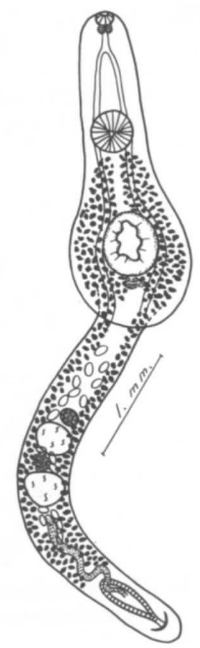


Fig. 259. *Archaeodiplostomum acetabulatum.*

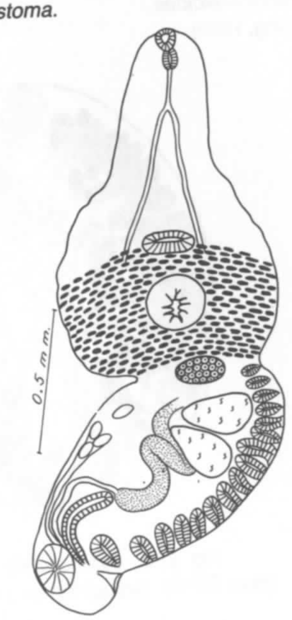


Fig. 260. *Polycotyle ornata.*

Fig. 261b. Sagittal section, posterior end.

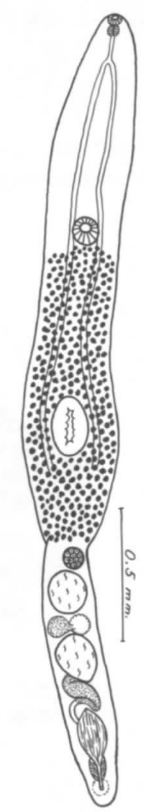


Fig. 261a. *Pseudocrocodilicola americanense.* (from Byrd and Reiber, 1942)

Superfamily Schistosomatoidea Stiles and Hassall, 1926

Miracidia have two pairs of flame cells (one pair in the family Sanguinicolidae); cercariae either brevifurcate-apharyngeate or lophocercous-apharyngeate, develop in sporocysts in aquatic snails; cercariae penetrate definitive host directly; adults monoecious or dioecious; parasitic in circulatory system of vertebrates; life cycles involve two hosts.

Family Schistosomatidae Poche, 1907

Adults dioecious with distinct sexual dimorphism; suckers present or absent; pharynx absent; ceca united in posterior part of body to form common cecum; body of male with gynaecophoric canal; testes four to multiple; cirrus sac present or absent; body of female slender; ovary ovoid or spiral shaped; vitelline follicles distributed along common cecum; uterus usually short; eggs nonoperculate, some with terminal spine, embryonated; parasitic in blood vessels of birds and mammals. Epidermal cell formula of miracidium 6, 9, 4, 3 or 6, 8, 4, 3.

Several species of the genus *Schistosoma* are parasitic in the circulatory system of human beings and domestic animals, causing schistosomiasis. The adult parasites develop in the liver and inhabit the veins associated with the digestive and urinary tracts. Distressing pathological symptoms result from infections by these parasites.

In North America species of several other genera cause schistosome dermatitis, the result of an allergic reaction to cercariae that penetrate the skin of human beings. Death of the cercariae during skin penetration provokes a tissue reaction causing formation of papules and severe itching similar to the symptoms associated with poison ivy. The disease is more commonly known as "swimmers itch" due to its occurrence in persons who frequent bathing beaches or the old swimming hole. Species of the genera *Trichobilharzia, Gigantobilharzia* and *Scistosomatium* are most frequently involved in the epidemiology of the disease in North America. The adults normally parasitize wild birds and mammals. Control measures involve the destruction of the aquatic snails in which the cercariae develop.

Key to Genera

1a. **Body of male with long gynaecophoric canal, extends through at least half of body; testes anterior to common cecum; parasitic in birds and mammals. 2**

1b. **Body of male with short gynaecophoric canal, not extending through more than one-fifth of body length or canal absent; testes located along common cecum; parasitic in birds. 7**

2a. **Testes 28 or more (up to 250). 3**

2b. **Testes 20 or less. 4**

3a. **Uterus long; eggs abundant; ovary near middle of body; ceca of female with numerous lateral branches; parasitic in mammals (Fig. 262). .... Genus *Heterobilharzia* Price, 1929**

Life cycle: *H. americana* - Miracidia hatch and enter the pulmonate snails, *Lymnaea cubensis* and *Pseudosuccinea columella.* Brevifurcate-apharyngeate cercariae develop in daughter sporocysts in 31 to 39 days. After emergence the cercariae penetrate the skin of raccoon, dog, bobcat, rabbit, nutria and mice. Developmental stages migrate through the lungs. The prepatent period in mice is 66 to 77 days. The mouse is a good experimental host. Adults inhabit the hepatic portal and the mesenteric veins (Lee, 1962; Greene, 1962).

Thrasher (1964) studied the pathology in dogs over a two-year period. In addition to histological changes in intestine and liver, symptoms such as chronic, bloody diarrhea, emaciation and anorexia were evident. Fecal examination for eggs seemed to be the only practical method of diagnosis.

3b. **Uterus short; contains one egg at a time; ovary in anterior third of body; ceca of female without lateral branches; parasitic in birds (Fig. 263). .... Genus *Ornithobilharzia* Odhner, 1912**

Key to species in Price (1929) and in Wetzel (1930).

4a. **Gynaecophoric canal extends from middle to posterior end of body; 14 to 18 testes; ceca with many lateral branches; parasitic in rodents (Fig. 264). .... Genus *Schistosomatium* Tanabe, 1923**

Life cycle: *S. douthitti* - Embryonated eggs pass in the feces of the host. Miracidia hatch and penetrate pulmonate snails, *Lymnaea stagnalis, Stagnicola palustris, S. emarginata, Physa gyrina* and *P. parkeri.* Brevifurcate-apharyngeate cercariae develop in daughter sporocysts and after leaving the snail, penetrate the skin of rabbits and rodents, eventually developing

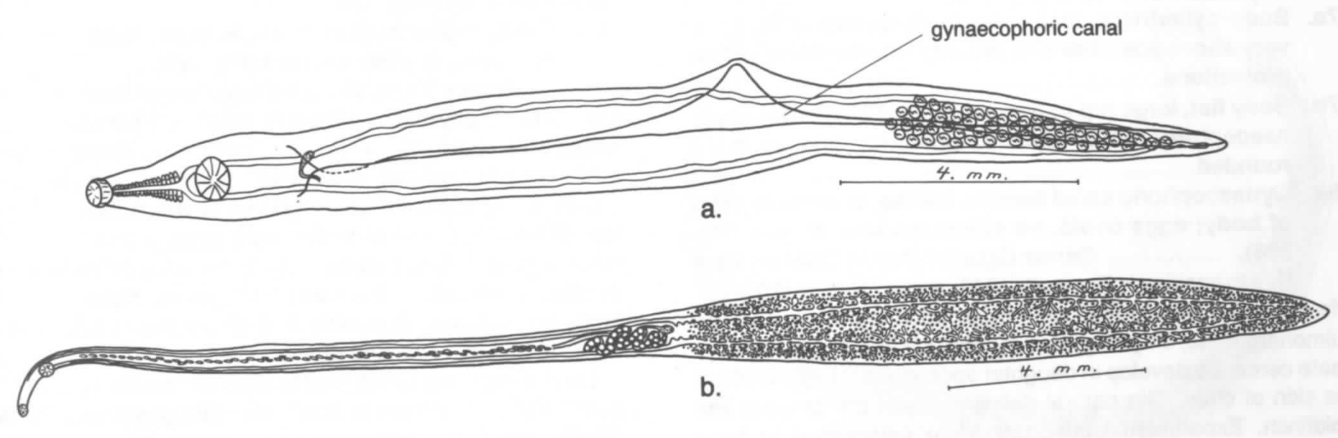


Fig. 262. *Heterobilharzia americanum.* a. male b. female

to adults in the liver. Natural definitive hosts are voles, muskrat, porcupine, rabbits and jumping mouse. Experimental infections have been established in rodents of the genera *Peromyscus, Mus, Rattus* and also in rhesus monkeys. In the latter host some sexually mature and some developing males and females were recovered from the mesenteric veins and the pulmonary blood vessels suggesting possible development in human beings (Price, H.F., 1931 and Kagan, 1953).

4b. Gynaecophoric canal extends from ventral sucker to posterior end of body; ceca without lateral branches. 5

5a. Testes 10 or less; ovary ovoid; parasitic in mammals (Fig. 265). .... **Genus** *Schistosoma* **Weinland, 1858**

Key to species in Price (1929).

Life cycle: *S. mansoni* - Natural infections by species of the genus *Schistosoma* do not occur in North America but endemic infections by *S. mansoni* occur in human beings in Puerto Rico, Jamaica and some countries in South America. The adults inhabit the mesenteric veins. Embryonated eggs pass in the feces and miracidia hatch when eggs gain access to water. They penetrate several species of planorbid snails in which brevifurcate-apharyngeate cercariae develop in daughter sporocysts. The cercariae penetrate the skin and mucous membranes of human beings, enter the blood vessels, migrate to lungs, liver and heart. Those in the liver develop to sexual maturity and migrate into the hepatic portal and mesenteric veins for mating and egg laying. Experimental infections have been established in mice, rats, hamsters, rabbits and monkeys.

5b. Testes 16 to 20; ovary has spiral shape; parasitic in birds. 6

6a. Ovary posterior to middle of body (Fig. 266). .... **Genus** *Austrobilharzia* **Johnston, 1917**

Life cycle: *A. variglandis* - Brevifurcate-apharyngeate cercariae (Cercaria variglandis) develop in daughter sporocysts in the marine snails, *Nassa obsoleta* and *Littorina pintado*. Cercariae penetrate the skin of the lesser scaup duck, *Marila affinis* and the ruddy turnstone, *Arenaria interpres*. The adult flukes inhabit the mesentric veins. Experimental infections were established in canaries, pigeons, ducklings, chickens, gulls and terns (Stunkard and Hinchcliffe, 1951, 1952; Chu and Cutress, 1954).

Bearup (1956) studied the life cycle of *A. terrigalensis*, a marine species in sea gulls.

6b. Ovary anterior to middle of body (Fig. 267). .... **Genus** *Microbilharzia* **Price, 1929**

Key to species in McLeod (1940).

7a. Body cylindrical, filamentous; gynaecophoric canal very short; posterior end of body with knoblike lateral projections. 8

7b. Body flat, large (up to 30 mm) but not filamentous; gynaecophoric canal absent; posterior end of body rounded. 9

8a. Gynaecophoric canal narrow, slitlike, in anterior third of body; eggs ovoid, no spine; suckers absent (Fig. 268). .... **Genus** *Gigantobilharzia* **Odhner, 1910**

Key to species in Brackett (1942) and in Dönges (1964a).

Life cycle: *G. huronensis* - Miracidia hatch and penetrate the pulmonate snail, *Physa gyrina* in which brevifurcate-apharyngeate cercariae develop in daughter sporocysts. They penetrate the skin of birds. The natural definitive hosts are cardinal and goldfinch. Experimental infections were established in baby chicks and canaries, the adults developing in about 30 days following exposure to cercariae (Najim, 1950, 1956).

Daniell (1979) also reported the life cycle of *G. huronensis*, paying special attention to the pathology and migration of the schistosomules from time of penetration of skin to arrival in the intestinal veins. Several additional intermediate and definitive hosts were also discovered.

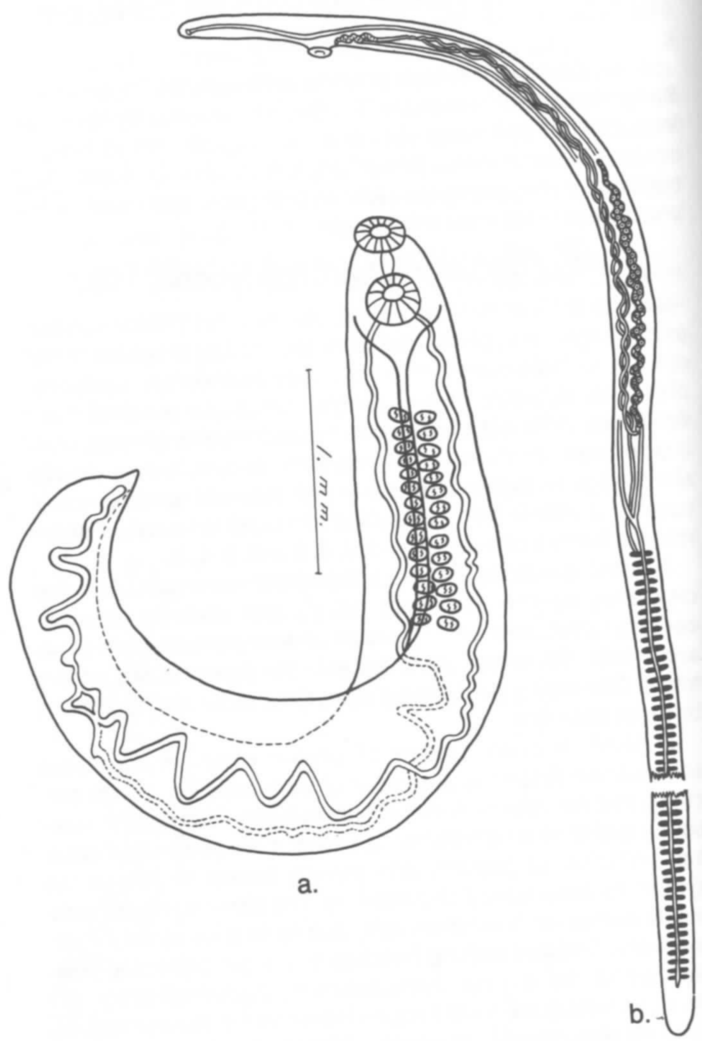


Fig. 263. *Ornithobilharzia pricei*. a. male b. female (from Wetzel, 1930)

8b. Gynaecophoric canal shallow, wide; eggs have terminal spine; suckers present (Fig. 269). .... **Genus** *Trichobilharzia* **Skrjabin and Zakharow, 1920**

Life cycle: *T. physellae* - Miracidia hatch and penetrate several species of snails of the genus *Physa*. Brevifurcate-apharyngeate cercariae develop in daughter sporocysts and after leaving the snail, penetrate the skin of ducks in which they migrate by way of the blood vessels to the heart, lungs and liver as well as other organs. Those that develop to the adult stage in the liver eventually migrate to the mesenteric veins. Natural definitive hosts are mallard, blue-wing and pintail ducks (McLeod and Little, 1942; McMullen and Beaver, 1945).

Leite, Costa and Costa (1979) reported the life cycle of *T. jequitibaensis* as it occurs in Brazil. The adult parasitizes the duck, *Cairina moschata domestica*. Experimental infections with the larval stages were established in the snails, *Aplexa rivalis* and *Lymnaea columella*. Sexual maturity was attained in ducks 12 days following exposure to cercariae.

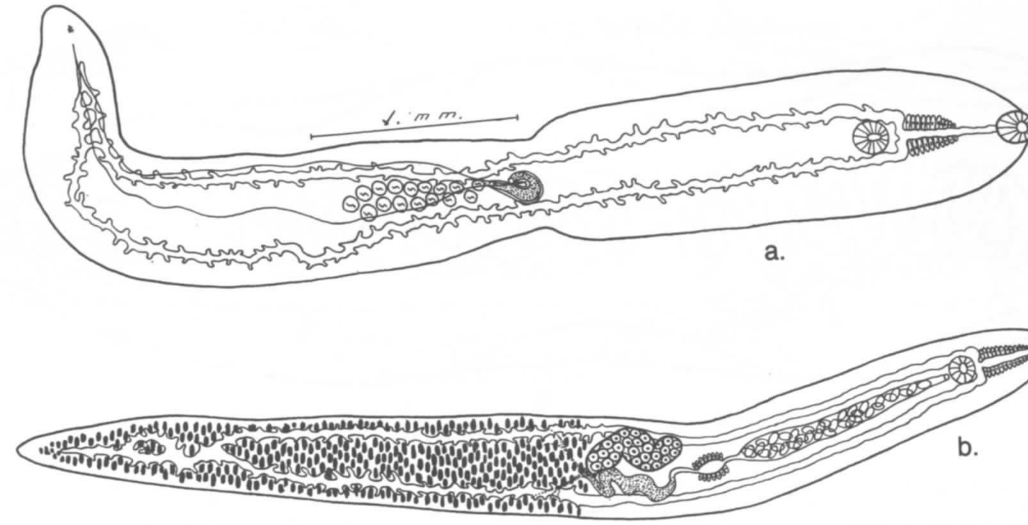


Fig. 264. *Schistosomatium douthitti*. a. male b. female

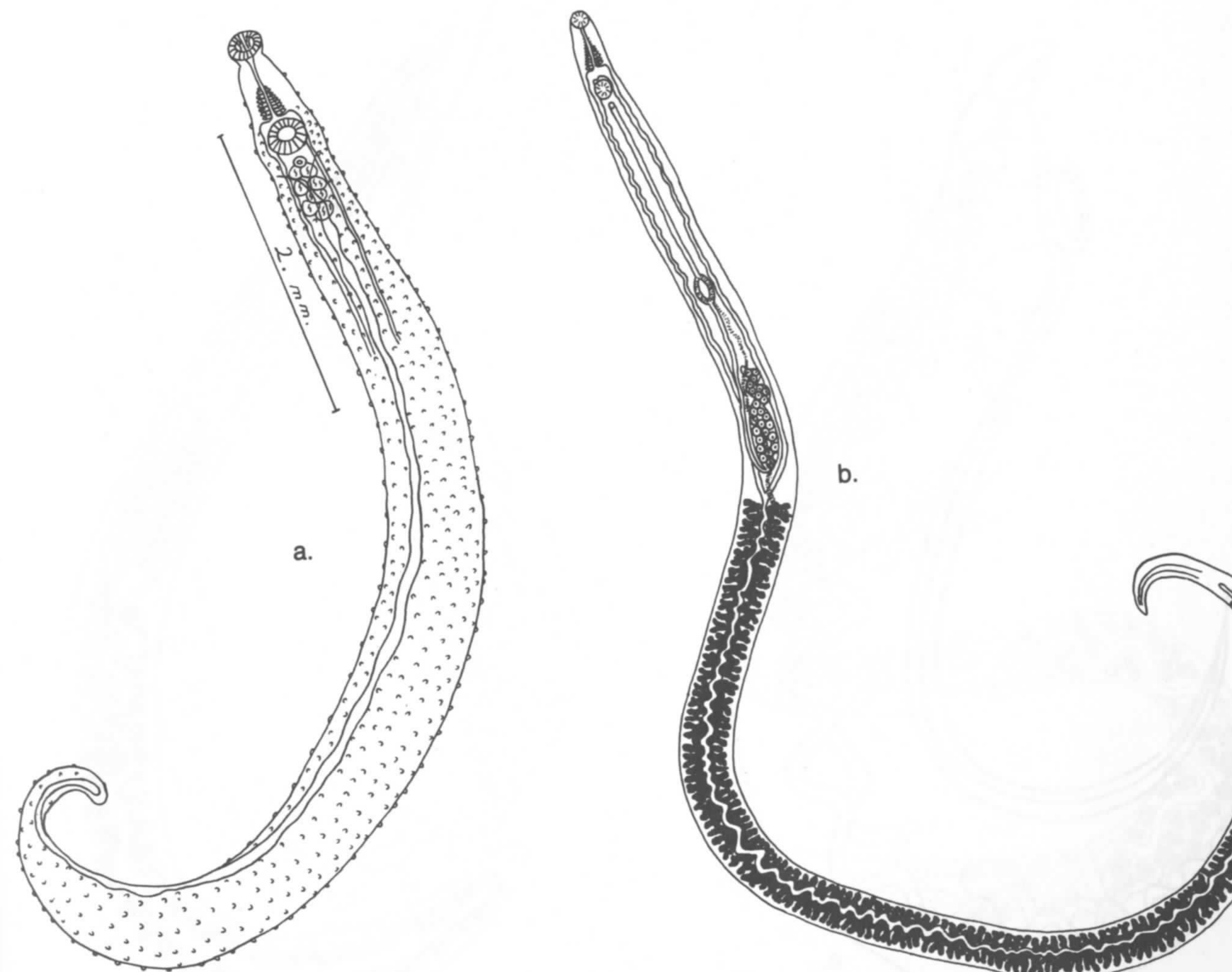


Fig. 265. *Schistosoma mansoni*. a. male b. female

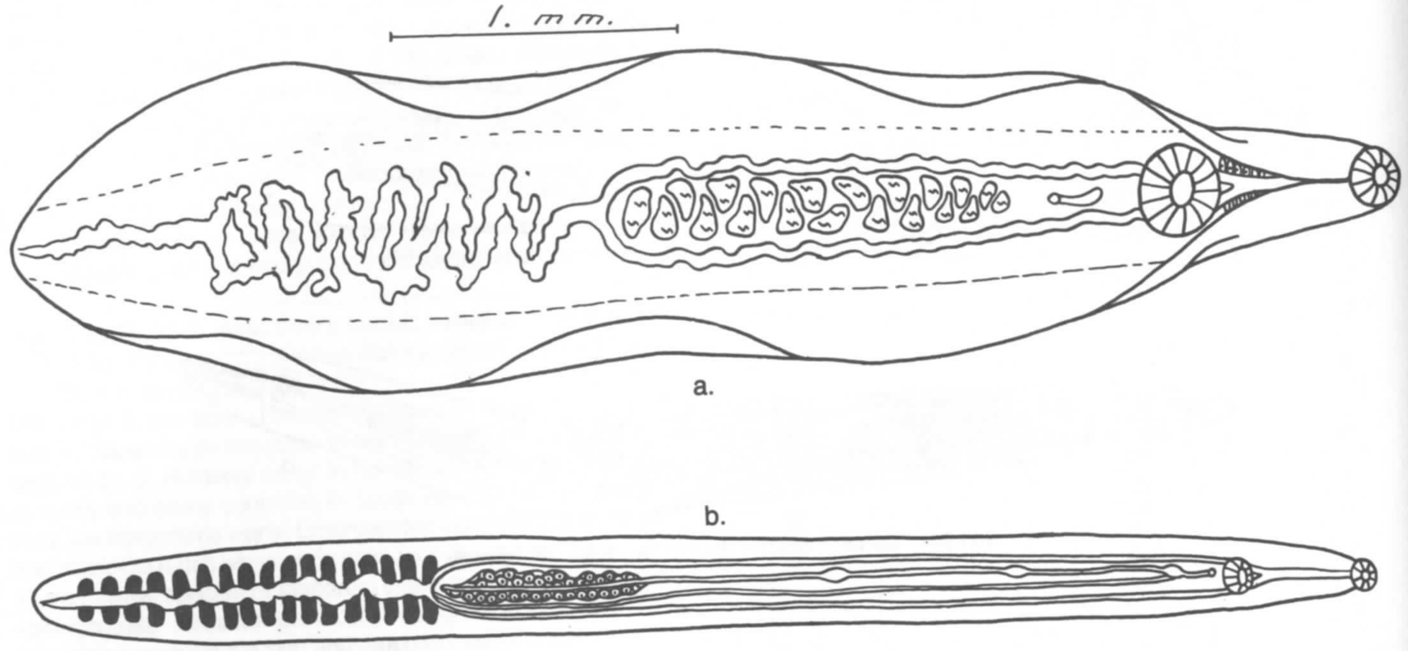


Fig. 266. *Austrobilharzia variglandis*. a. male b. female (from Chu and Cutress, 1954)

Fig. 267. *Microbilharzia lari*. a. male b. female (from McLeod, 1937)

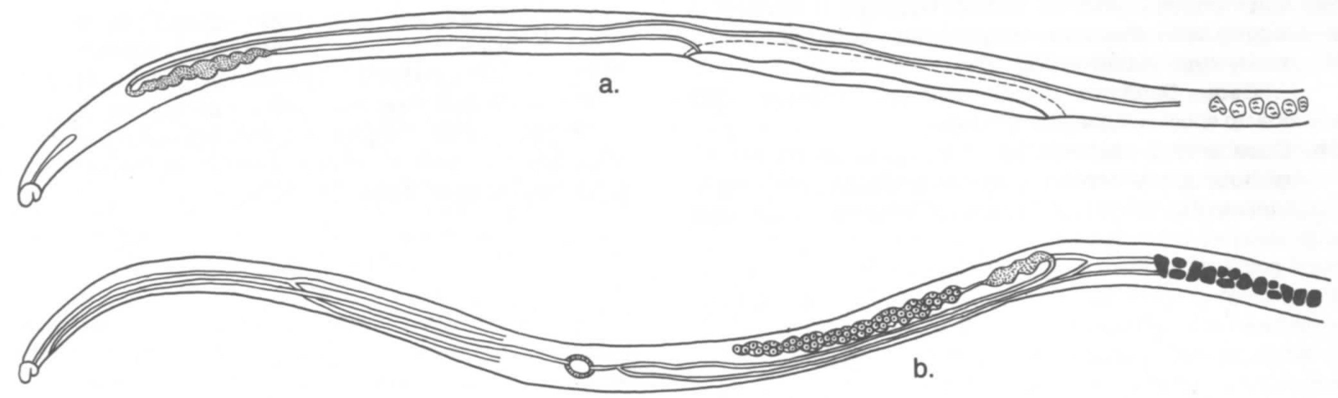


Fig. 268. *Gigantobilharzia gyrauli*. a. male b. female (from Brackett, 1942)

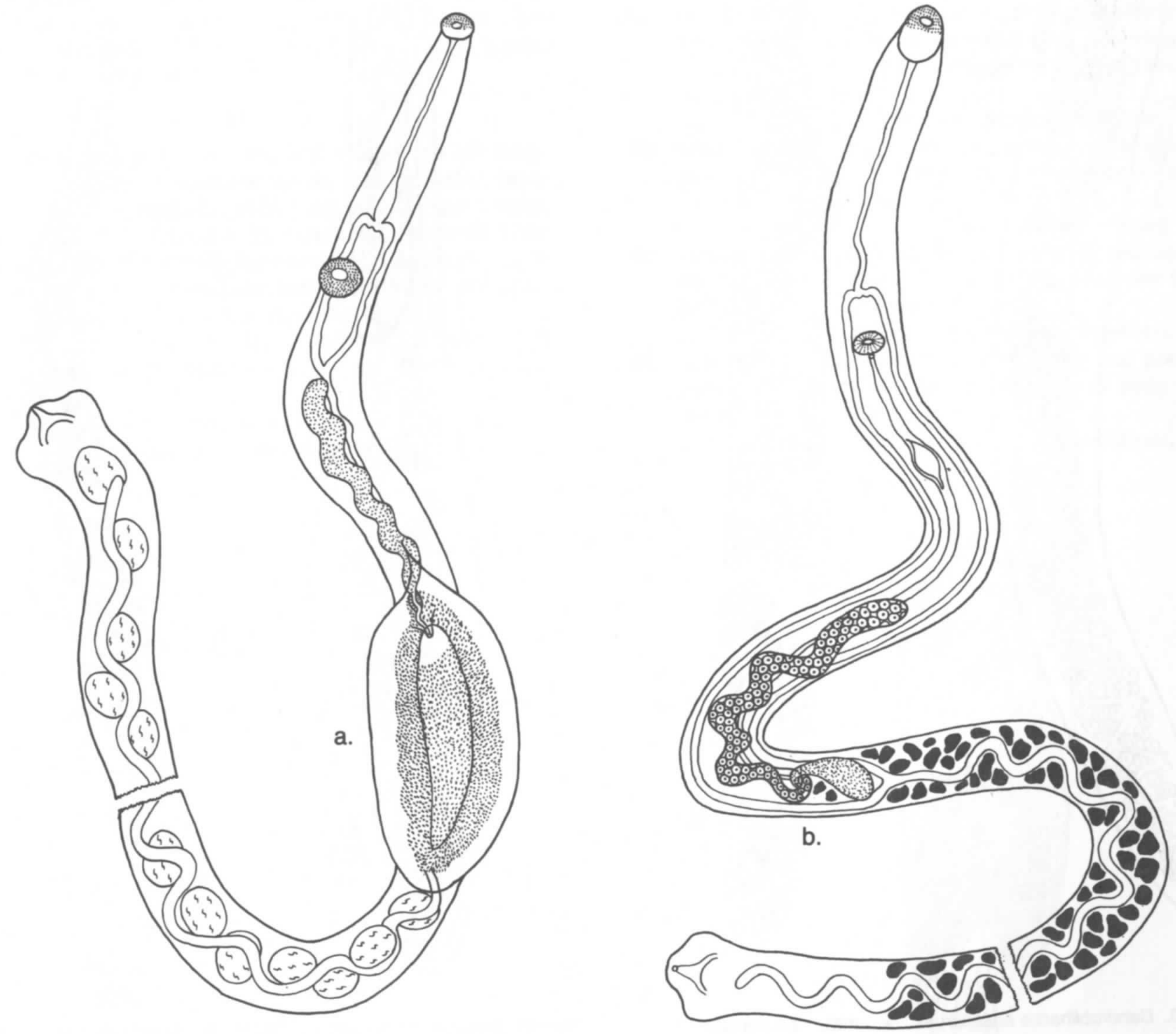


Fig. 269. *Trichobilharzia physellae*. a. male b. female

9a. Ceca united in anterior third of body; common cecum zigzag with short lateral branches; suckers absent; many eggs in uterus (Fig. 270). ....
.. **Genus *Dendrobilharzia* Skrjabin and Zakharow, 1920**
Key to species in Skrjabin (1964).

9b. Ceca united near middle of body; common cecum without lateral branches; suckers present; one egg in uterus (Fig. 271). .... **Genus *Bilharziella* Looss, 1899**

Life cycle: *B. polonica* - Brevifurcate-apharyngeate cercariae develop in sporocysts in the snails, *Bathyomphalus contortus, Planorbarius corneus* and *Planorbis planorbis.* Adults inhabit the hepatic portal and mesenteric veins of several species of ducks of the genus *Anas;* merganser ducks, *Mergus albellus* and herons, *Ardea cinerea. Anas platyrhynchos* is the most common natural definitive host (Khalifa, 1972).

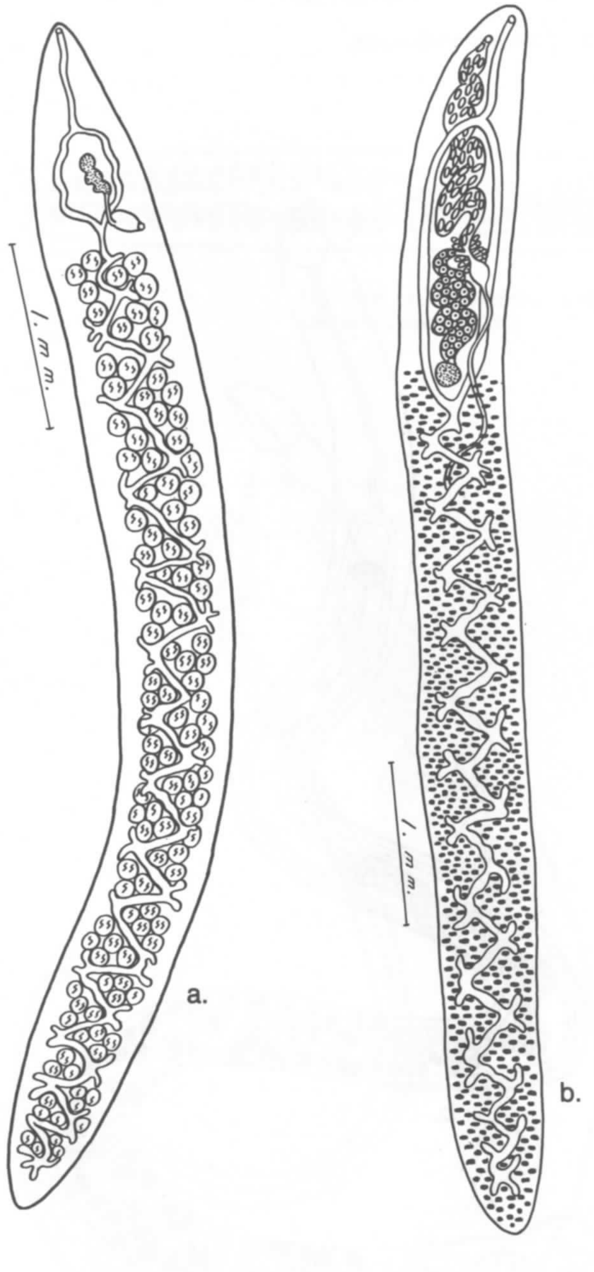


Fig. 270. *Dendrobilharzia anatinarum.* a. male b. female

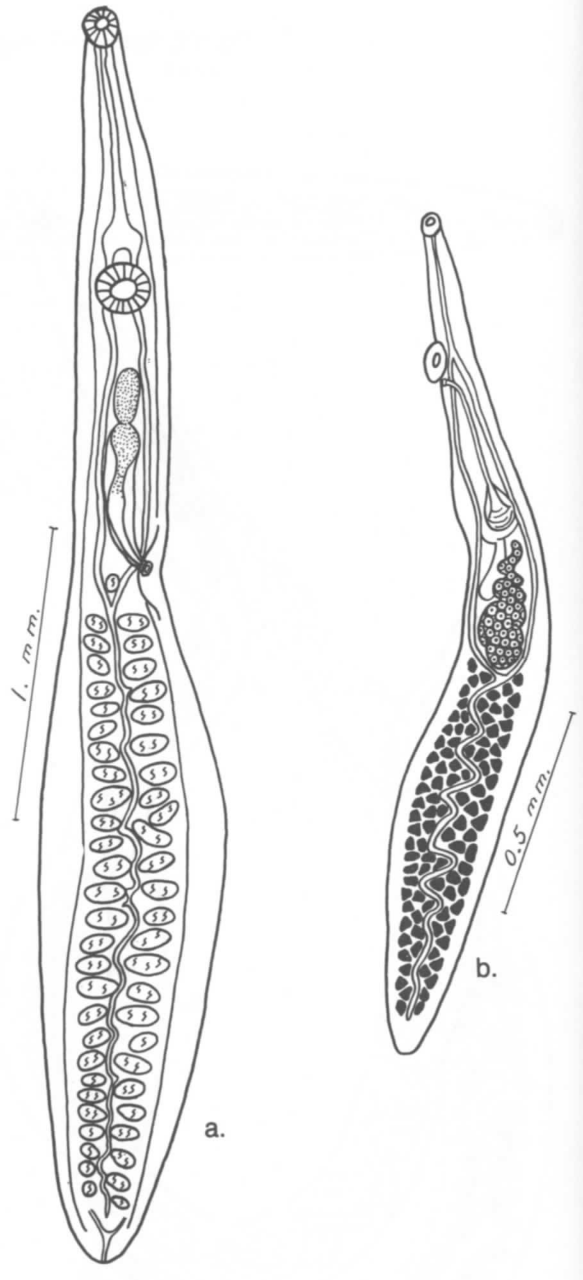


Fig. 271. *Bilharziella polonica.* a. male b. female (from Price, 1929)

Family Sanguinicolidae Graff, 1907

Body small, flat, delicate; pharynx and suckers absent; intestinal ceca X- or H-shaped or ceca short and stubby; cirrus sac usually absent; testes one, two or multiple; ovary posttesticular, in posterior third of body; male and female genital pores usually separate, on dorsal surface of body; vitelline follicles abundant, in lateral areas of body; uterus short; eggs nonoperculate, shells thin, nonembryonated; excretory system asymmetrical in some genera; parasitic in blood vessels and heart of freshwater and marine fishes.

Although the blood flukes of freshwater fishes are known to produce lophocercous-apharyngeate cercariae in prosobranch snails, several other kinds of cercariae are assumed to be the larvae of marine sanguinicolids; however, there is no experimental evidence to support these assumptions. Spinous microcercous cercariae without suckers were found to develop in sporocysts in marine lamellibranch molluscs. Brevifurcate-apharyngeate and nonfurcate-apharyngeate cerariae are known to develop in rediae in marine polychaete worms of the families Terebellidae and Ampharetidae. Lophocercous-brevifurcate-apharyngeate cercariae develop in sporocysts in tubicolous marine worms of the family Serpulidae (see Stunkard, 1929; Martin, 1944, 1952; Oglesby, 1961).

Key to Genera

1a. Body with a posterior lobe and a notch on left body margin; dorsal protuberance on lobe contains male genital pore, posterior ceca long, anterior ceca short (Fig. 272). .... **Genus *Psettarium* Goto and Ozaki, 1930**

1b. Body without posterior lobe and marginal notch. ... 2

2a. Body oval; uterus long, folded; testes indistinct; ceca X-shaped; ovary lobed, dextral (Fig. 273). ....
.... **Genus *Deontacylix* Linton, 1910**

2b. Body elongate; uterus short; testes single or multiple. 3

3a. Testis single, large, anterior to ovary. 4

3b. Testes multiple, small, intercecal. 6

4a. Ovary large, bilobed or butterfly-shaped; ceca short and stubby; testis single and deeply lobed, preovarian (Fig. 274). .... **Genus *Sanguinicola* Plehn, 1905**
Key to species in Erickson and Wallace (1959).

Life cycle: *S. idahoensis* - Eggs accumulate in the gill capillaries of young steelhead trout, *Salmo gairdneri.* Miracidia develop and hatch and penetrate the prosobranch snail, *Lithoglyphus virens* in which mother and daughter sporocysts develop. Lophocercous-apharyngeate cercariae develop in the daughter sporocysts, emerge and penetrate the tegument of fingerling trout of several species. Development to sexual maturity requires 40 to 50 days. Adults inhabit the blood vessels of the head region, some in the vascular choroid coat and iris of the eye and in vessels of the brain surface. Eggs and miracidia cause injury to the gill filaments (Schell, 1974).

The life cycle of *S. inermis* was studied by Scheuring (1922) and that of *S. alseae (Cardicola alseae)* by Meade and Pratt, 1965.

4b. Ovary small and bilobed; testis single but not lobed.
.... **5**

5a. Intestinal ceca short and stubby, X-shaped; testis single, sinistral, postcecal; common genital pore median and dorsal; parasitic in blood vessels of elasmobranchs (sharks) (Fig. 275). ....
.... **Genus *Selechohemecus* Short, 1954**

5b. Intestinal ceca long, H-shaped; testis single, median; genital pores separate and dorsal; parasitic in blood vessels of teleost fishes (Fig. 276). ....
.... **Genus *Cardicola* Short, 1953**

6a. Uterus mostly posterior to ovary, cirrus sac absent; seminal vesicle free in parenchyma; posterior tip of body with patch of spines (Fig. 277). ....
.... **Genus *Paradeontacylix* McIntosh, 1934**

6b. Uterus mostly anterior to ovary; cirrus sac present, contains seminal vesicle; posterior tip of body without spines (Fig. 278). ....
....................................**Genus *Aporocotyle* Odhner, 1900**

Fig. 272. *Psettarium sebastodorum.* (from Holmes, 1971)

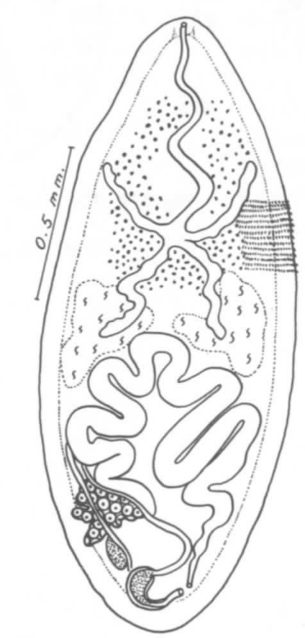


Fig. 273. *Deontacylix ovalis.*

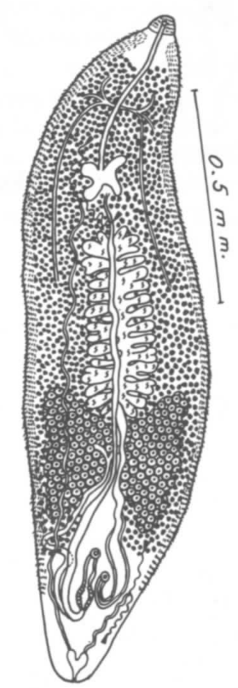


Fig. 274. *Sanguinicola idahoensis.*

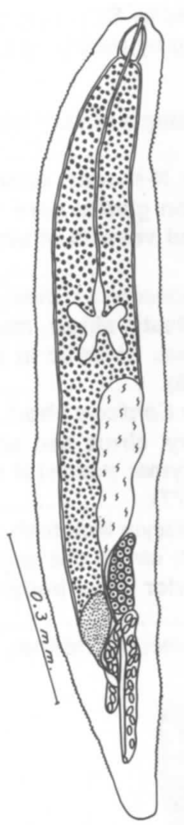


Fig. 275. *Selacohemecus olsoni.*

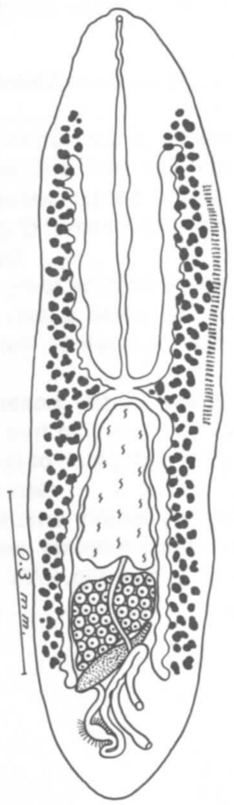


Fig. 276. *Cardicola laruei.*

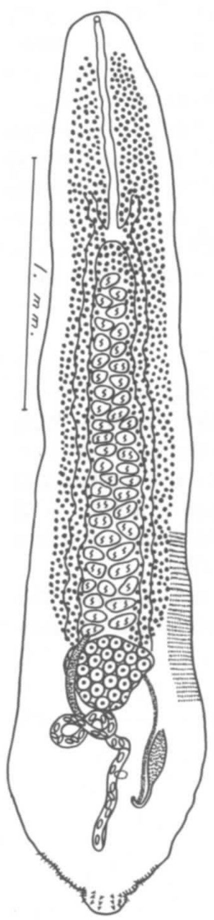


Fig. 277. *Paradeontacylix sanguinicoloides.*

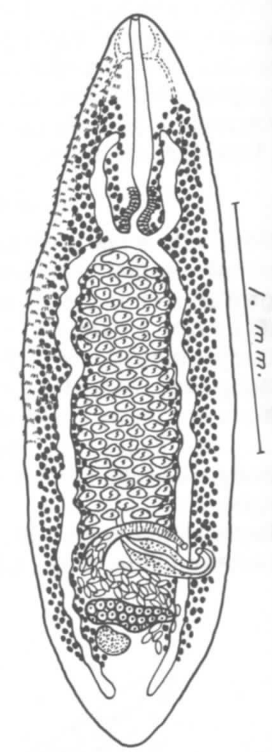


Fig. 278. *Aporocotyle macfarlani.*

Family Spirorchiidae Stunkard, 1921

Body lanceolate, flat; oral sucker present; ventral sucker present or absent; pharynx absent; ceca long, end blindly; fused in posterior part of body to form common cecum in genus *Neospirorchis,* single cecum in genus *Unicaecum;* testes one, two or multiple; genital pore either in anterior or posterior third of body, ventral, lateral or dorsal; cirrus sac present or absent; ovary inter-, pre- or posttesticular; uterus short; eggs few, operculate, embryonated; parasitic in blood vessels and heart of turtles. Epidermal cell formula of miracidium 6, 6, 4, 2.

Key to Genera

1a. Ventral sucker absent. 2

1b. Ventral sucker present. 5

2a. One intestinal cecum; one testis; seminal vesicle, ovary and uterus all long, tubular and folded; genital pore at posterior end of testis; parasitic in freshwater turtles (Fig. 279). .. **Genus** *Unicaecum* **Stunkard, 1925**

2b. Two intestinal ceca; testes multiple or a single tubular testis. 3

3a. Ceca united in midbody to form common cecum which extends to posterior end of body; testis and ovary elongate, spirally coiled; ovary posterior to testis; parasitic in marine turtles (Fig. 280). .... **Genus** *Neospirorchis* **Price, 1934**

3b. Ceca separate throughout their length; ovary not elongate; testes multiple; parasitic in freshwater turtles. 4

4a. Testes all anterior to ovary (Figs. 281, 282). .... **Genus** *Spirorchis* **MacCallum, 1919**

Key to species in Byrd (1939).

Life cycle: *S. elegans* - Embryonated eggs from the feces of turtles were incubated several days before miracidia hatched. They entered the planorbid snails, *Menetus buchanensis* and *Helisoma anceps* in which brevifurcate-apharyngeate cercariae (Fig. 25) developed in daughter sporocysts. After emergence, the cercariae penetrate the mucous membranes of the eye, nose, mouth and cloaca of turtles of the genera *Chrysemys* and *Pseudemys.* Development to sexual maturity requires six to ten weeks in the turtle. The adults inhabit the heart and larger arteries (Goodchild and Kirk, 1960).

The life cycles of *S. artericola* and *S. parvus* are similar to that of *S. elegans.*

4b. One testis posterior to ovary, the others anterior to ovary (Fig. 283). .... **Genus** *Diarmostorchis* **Ejmont, 1927**

5a. Testes multiple, fill intercecal area; parasitic in marine turtles. 6

5b. One spirally coiled testis or two testes. 10

6a. Testes separated into two groups by ovary; genital pore lateral to ovary and enclosed in a muscular genital sucker (Fig. 284). .... **Genus** *Hapalotrema* **Looss, 1899**

Key to species in Byrd (1939) and in Skrjabin (1964).

6b. Testes not separated by ovary; genital sucker absent. 7

7a. Ovary posterior to testes. 8

7b. Ovary anterior to testes. 9

8a. Testes numerous, 20 or more; esophagus at least one-third as long as body; esophageal glands present (Fig. 285). .... **Genus** *Learedius* **Price, 1934**

Key to species in Byrd (1939).

8b. Testes five to twelve; esophagus about one-fifth as long as body; esophageal glands absent (Fig. 286). ... . **Genus** *Monticellius* **Mehra, 1939**

9a. Muscular vagina present, immediately posterior to ovary; testes in single linear series between ceca (Fig. 287). ...... **Genus** *Carettacola* **Manter and Larson, 1950**

9b. Muscular vagina absent; testes in a zigzag linear series (Fig. 290). .... **Genus** *Haemoxenicon* **Martin and Bamberger, 1952**

10a. One elongate spirally-coiled testis fills intercecal area posterior to ovary; parasitic in freshwater turtles (Figs. 288, 289). ..... **Genus** *Vasotrema* **Stunkard, 1928**

Key to species in Skrjabin (1964).

Life cycle: *V. robustum* - Embryonated eggs pass in the feces of the host. Miracidia hatch and penetrate the pulmonate snails, *Physa gyrina* and *P. integra* in which brevifurcate-apharyngeate cercariae develop in daughter sporocysts. After leaving the snail, the cercariae penetrate the mucous membranes of the mouth, nose and cloaca of turtles of the genus *Amyda.* Development to sexual maturity occur in the heart and large arteries within 10 to 12 months (Wall, 1951).

10b. Two testes; ovary between testes. 11

11a. Ovary, seminal vesicle and cirrus sac between testes; parasitic in marine turtles (Fig. 291). .... **Genus** *Amphiorchis* **Price, 1934**

11b. Testes separated only by ovary; seminal vesicle and cirrus sac anterior to testes; parasitic in freshwater turtles (Fig. 292.). .... **Genus** *Hapalorhynchus* **Stunkard, 1922**

Key to species in Brooks and Mayes (1975).

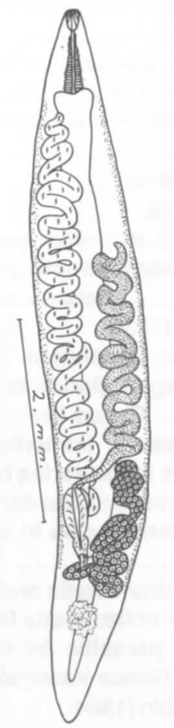


Fig. 279. *Unicaecum ruszkowskii.*

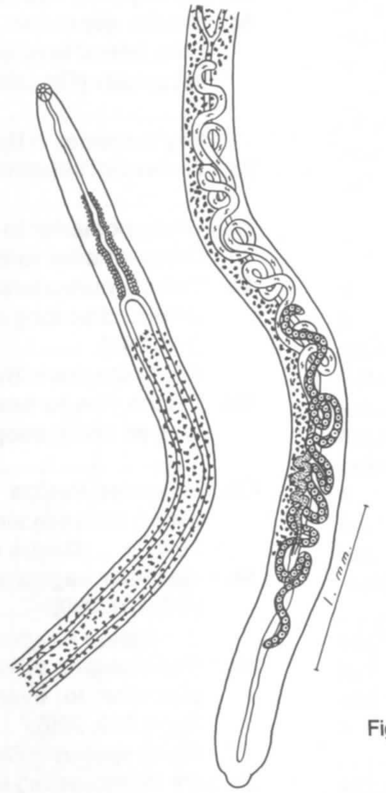


Fig. 280. *Neospirorchis schistosomatoides.*

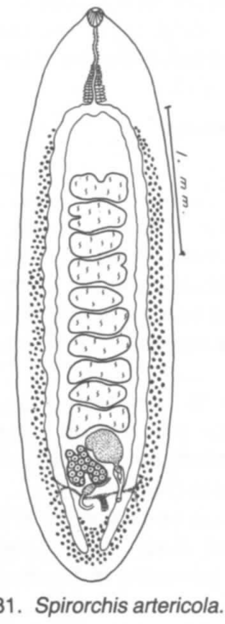


Fig. 281. *Spirorchis artericola.*

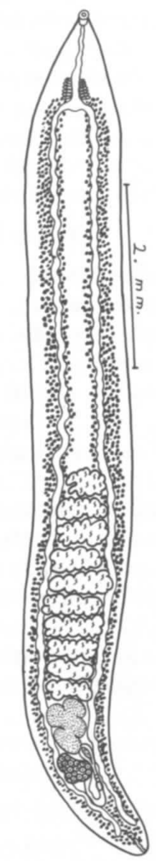


Fig. 282. *Spirorchis haematobium.*

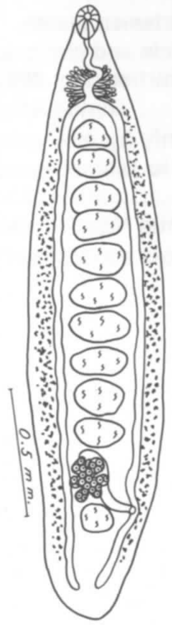


Fig. 283. *Diarmostorchis blandingi.*

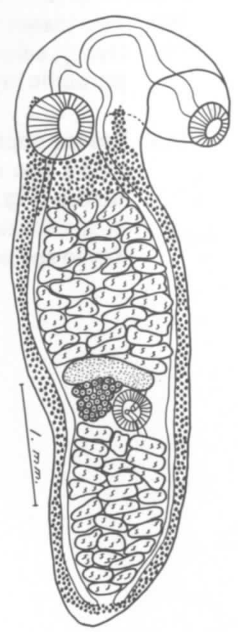


Fig. 284. *Hapalotrema synorchis.*

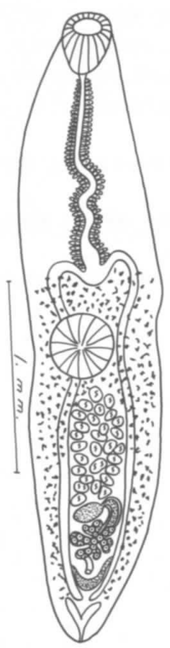


Fig. 285. *Learedius learedi.*

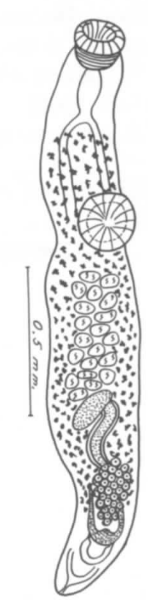


Fig. 286. *Monticellius similis.*

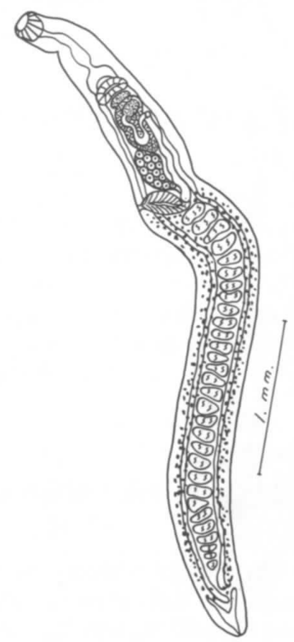


Fig. 287. *Carettacola bipora.*

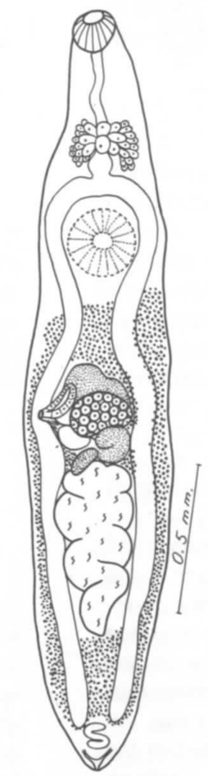


Fig. 288. *Vasotrema robustus.*
(from Stunkard, 1982)

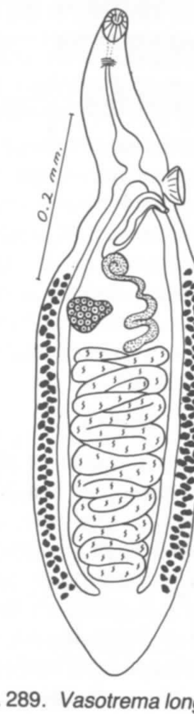


Fig. 289. *Vasotrema longitestis.*

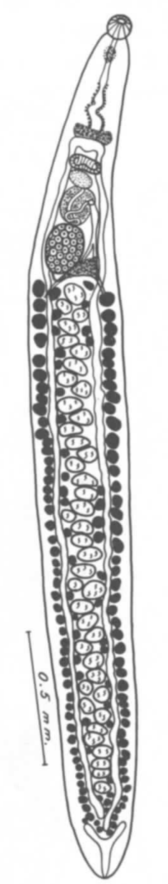


Fig. 290. *Haemoxenicon stunkardi.*
(from Martin and Bamberger, 1952)

Fig. 291. *Amphiorchis amphiorchis.*

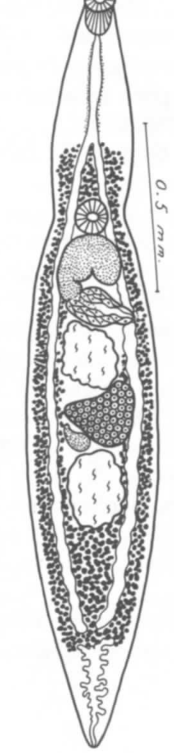


Fig. 292. *Hapalorhynchus gracilis.*

Superfamily Clinostomoidea Dollfus, 1931

Miracidia have two pairs of flame cells. The cercariae are brevifurcate-pharyngeate (clinostomoid) type, develop in a redia in aquatic snails; three hosts are involved in the life cycle; adults inhabit the mouth and esophagus of reptiles and birds.

Family Clinostomidae Lühe, 1901

Body large, flat; oral sucker small or vestigal, enveloped by a collarlike body fold; ventral sucker much larger than oral sucker, close to anterior end of body; pharynx present; intestinal ceca long; testes tandem, in posterior third of body; cirrus sac and genital pore in posterior third of body; ovary intertesticular; uterus has long ascending and descending limbs, restricted to hindbody; vitelline follicles around ceca, restricted to hindbody; parasitic in mouth and esophagus of reptiles and birds. Epidermal cell formula of miracidium is 6, 8, 4, 3.

Key to Genera

1a. Adult in mouth and esophagus of alligators; cirrus sac and genital pore between testes (Fig. 293). ....
.... **Genus** *Odhneriotrema* **Travassos, 1928**

Life cycle: *O. incommodum* - Adults of this species attach to the lining of the mouth, pharynx and the surface of the tongue of alligators. The host mollusc is still unknown but metacercariae have been found enclosed in large fibrous capsules in the ovaries, testes and mesenteries of the Florida gar, *Lepisosteus platyrhynchus.* More female gars were infected than males. After ingestion by alligators, the metacercariae excysted in the stomach or intestine then migrated up the esophagus, finally attaching in mouth pharynx or tongue. Migration required two to six days. Development to sexual maturity required 80-90 days and the life span in alligators is about two years. A fibrous nodule forms at the point of attachment (Leigh, 1978).

1b. Adult in mouth and esophagus of piscivorous birds; cirrus sac and genital pore anterior to testes or opposite to anterior testis (Fig. 294). ....
.... **Genus** *Clinostomum* **Leidy, 1856**

Key to species in Skrjabin (1964).

Life cycle: *C. marginatum*- Embryonated eggs pass in the feces of the host or are washed into water when bird drinks or eats. Miracidia hatch in water and penetrate the planorbid snails, *Helisoma antrosum* and *H. campanulatum* in which a sporocyst and two generations of rediae develop, the daughter rediae producing brevifurcate-clinostomoid cercariae which eventually encyst in the muscles and connective tissues of freshwater fishes where they develop into large yellow metacercariae. Their presence results in the "yellow grub disease" of fish. The adult parasite develops in the mouth of herons, gulls and bitterns which eat infected fish. The metacercariae are precocial as only a few days are required for development to sexual maturity after entering the definitive host (Hopkins, 1933; Hunter and Hunter, 1934; Cameron, 1945).

The life cycle of *C. attenuatum* is also known. The cercariae encyst in the tissues of frogs instead of fishes. The adult develops in the mouth of bitterns.

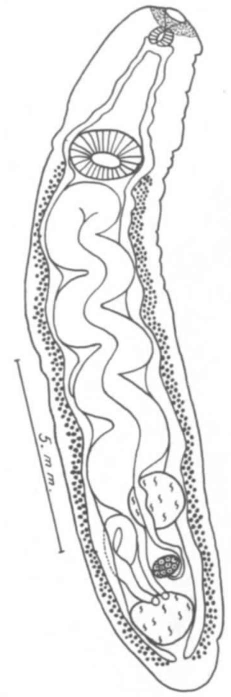


Fig. 293. *Odhneriotrema incommodum.* (from McIntosh, 1935).

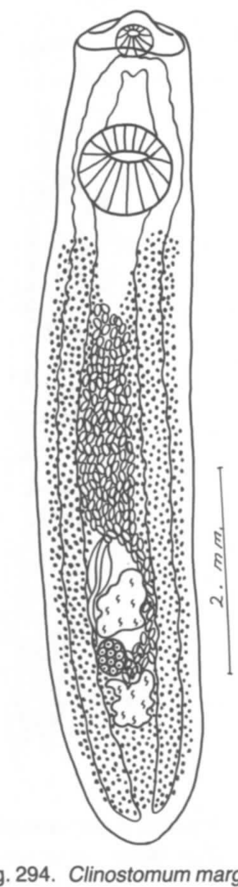


Fig. 294. *Clinostomum marginatum.*

Suborder Brachylaimata LaRue, 1957

Cercaria furcocercous, trichocercous, microcercous or tailless; develop in sporocysts in gastropod or lamellibranch molluscs; protonephridia mesostomate or stenostomate.

Superfamily Brachylaimoidea Allison, 1943

Cercaria microcercous furcocerous or tailless; develop in branched sporocysts in terrestrial or amphibious snails; protonephridia stenostomate; adults usually distomate with reproductive organs near posterior end of body; parasitic in large intestine, cloaca or bursa Fabricius of birds and mammals. Life cycle involves two or three hosts. Miracidia have one pair flame cells and long cilia in tufts or groups.

Family Brachylaimidae Joyeux and Foley, 1930

Body oval, linguiform or elongate; suckers well developed; pharynx present; ceca long; testes tandem or oblique (one testis in *Parabrachylaima);* cirrus sac and genital pore near posterior end of body; ovary pre- or intertesticular or opposite anterior testis; vitelline follicles along ceca, variable in extent; uterus usually entirely anterior to gonads, generally restricted to hindbody eggs operculate, embryonated; parasitic in colon, cecum or cloaca of birds and mammals. Life cycle involves three hosts.

Key to Genera

1a. One testis and two vasa efferentia; ovary pretesticular; vitelline follicles few; left cecum longer than right cecum; adults progenetic in terrestrial snails (Fig. 295). ....
.... **Genus** *Parabrachylaima* **Lotz and Corkum, 1975**

1b. Two testes; vitelline follicles abundant; ceca of equal length; parasitic in vertebrate hosts. **2**

2a. Ceca distinctly sinuous; body linguiform; ovary pretesticular or opposite to anterior testis (Fig. 296). ......
.... **Genus** *Postharmostomum* **Witenberg, 1923**

Key to species in McIntosh (1934b).

Life cycle: *P. helicis* - Embryonated eggs in the feces of the host are ingested by the terrestrial snails, *Anguispira alternata, Deroceras laeve* and *Polygyra* spp. Obscuromicrocercous cercariae (Fig. 15) develop in branched daughter sporocysts. The cercariae leave the sporocyst and the snail and enter the pericardial cavity of another snail of the same or a different species and develop into metacercariae without encysting. They seem to be unable to develop in the same snail that produced the sporocysts. The adult fluke develops in about eight days in the cecum of Eastern chipmunk, *Tamias strictus* and the deermouse, *Peromyscus maniculatus* (see Robinson, 1949; Ulmer, 1951).

Alicata (1940) studied the life cycle of *P. gallinum,* a parasite of chickens in Hawaii where the terrestrial snail, *Eulota similaris* is the first host. Obscuromicrocercous cercariae develop in branched sporocysts in about 60 days. The cercariae leave the snail and reenter the same or a different species of terrestrial snail *(Subulina octona)* in which they develop to infective metacercariae in 25 days. Adults develop in the ceca of chickens in about one month after ingesting metacercariae.

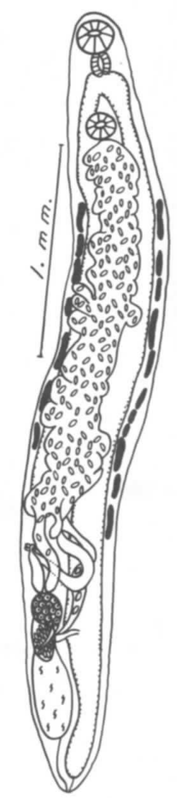


Fig. 295a. *Parabrachylaima euglandensis.*

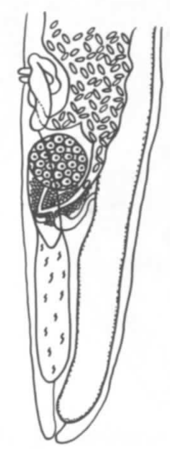


Fig. 295b. posterior end enlarged

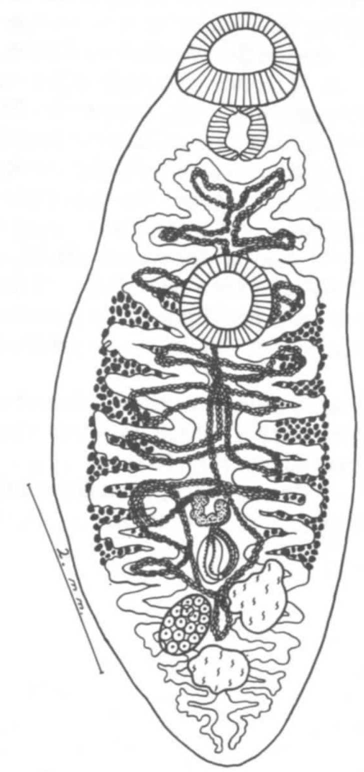


Fig. 296. *Postharmostomum gallinarum.*

2b. Ceca straight, not sinuous; body oval or elongate; ovary intertesticular. 3

3a. Genital pore and cirrus sac posterior to testes; parasitic in the intestine of mammals (Fig. 297). .... **Genus *Panopistus* Sinitzin, 1931**

Life cycle: *P. pricei* - Embryonated eggs are eaten by the terrestrial snails, *Ventridens ligera, Zonitoides arboreus, Deroceras laeve* and the slug, *Agriolimax agrestis*. Obscuromicrocercous cercariae (Fig. 15) develop in branched sporocysts and after leaving the sporocyst, creep over the surface of the snail and are transferred to another snail upon contact. Metacercariae develop in the pericardial cavity of the terrestrial snails, *Stenotrema monodon, Deroceras laeve, Zonitoides nitidus* and *Ventridens ligera*. The short-tailed shrew, *Blarina brevicauda* is the definitive host (Krull, 1934b, 1935b; Reynolds, 1938; Villella, 1954).

3b. Genital pore and cirrus sac either intertesticular or pretesticular. 4

4a. Genital pore and cirrus sac intertesticular. 5

4b. Genital pore and cirrus sac pretesticular. 6

5a. Parasitic in the intestine of birds; vitelline follicles usually extend into forebody (Fig. 298). .... **Genus *Glaphyrostomum* Braun, 1901**

Life cycle: *G. mcintoshi* - Embryonated eggs are eaten by the terrestrial snail, *Zonitoides arboreus*. Tailless cercariae (cercariaea) develop in branched sporocysts and remain in the sporocyst without encysting and develop to the metacercaria stage. Experimental infections were established in baby chicks by feeding metacercariae. The natural definitive host is the ovenbird, *Seiurus aurocapillus* (see Krull, 1935c).

5b. Parasitic in the intestine of mammals; vitelline follicles confined to lateral areas of hindbody (Fig. 299). .... **Genus *Itygonimus* Lühe, 1899**

6a. Body very elongate, filiform; uterus confined to hindbody; ventral sucker very close to oral sucker (Fig. 300). .... **Genus *Scaphiostomum* Braun, 1901**

Life cycle: *S. pancreaticum* - Embryonated eggs in the feces of the host are eaten by the terrestrial snail, *Anguispira alternata*. Miracidia, having clusters of long cilia, invade the hepatopancreas of the snail. Branched sporocysts eventually develop and produce obscuromicrocercous cercariae. Metacercariae were found unencysted in the kidneys of *A. alternata* that were not infected with sporocysts and also in *Triodopsis albolabris* and *Haplotrema concavum*. Metacercariae were fed to chipmunks that were originally free of parasites. Eggs of the parasite were present in the feces 30 days later. The adult flukes were recovered (Jensen, 1972).

6b. Body only moderately elongate; some folds of uterus anterior to ventral sucker which is some distance posterior to the oral sucker (Fig. 301). .... **Genus *Brachylaima* Dujardin, 1843**

(Synonyms: *Ectosiphonus, Entosiphonus, Harmostomum*)

Life cycle: *B. virginiana* - Embryonated eggs are eaten by the land snail, *Polygyra thyroides* which can serve as both first and second intermediate host. Obscuromicrocercous cercariae develop in branched sporocysts, leave the sporocyst, creep over the surface of the snail and transfer to another snail when contacting it. Development to the metacercarial stage and encystment occur in the kidney of the snail. Other suitable second intermediate hosts besides *P. thyroides* are *Deroceras laeve, Agriolimax columbianus, Helix pomatia, Mesomphix cupreus, Succinea* spp., *Pseudosuccinea columella* and *Helisoma trivolvis*. The adult fluke develops in the colon of the opossum (Krull, 1934a, 1935a, 1936; Hand and Voge, 1952; Ulmer, 1952).

The life cycle of *B. oesophagi* was studied by Lewis (1969) in Wales. The adult worms inhabit the esophagus and stomach of shrews. The host snail is *Zonitoides excavatus*. Metacercariae were fed to mice and shrews and the adult parasite recovered.

Villella (1953) reported the life cycle of *B. thompsoni (Entosiphonus thompsoni)*, a parasite in the intestine of short-tailed shew and white-footed mouse. Mother and daughter sporocysts develop in several species of land snails in the genera *Ventridens, Zonitoides, Retinella* and *Succinea*. The branched daughter sporocysts produce obscuromicrocercous cercariae which enter other land snails and develop to infective metacercariae. The infected snails are eaten by the definitive hosts.

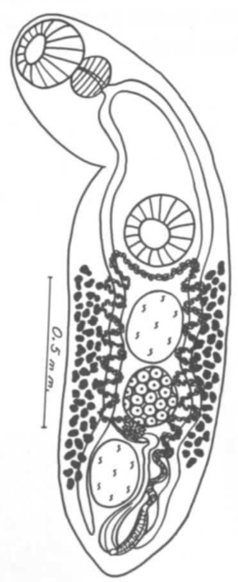


Fig. 297. *Panopistus pricei.*

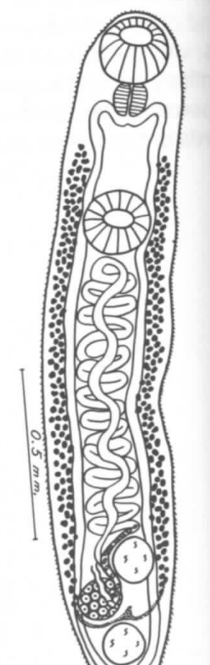


Fig. 298. *Glaphyrostomum mcintoshi.*

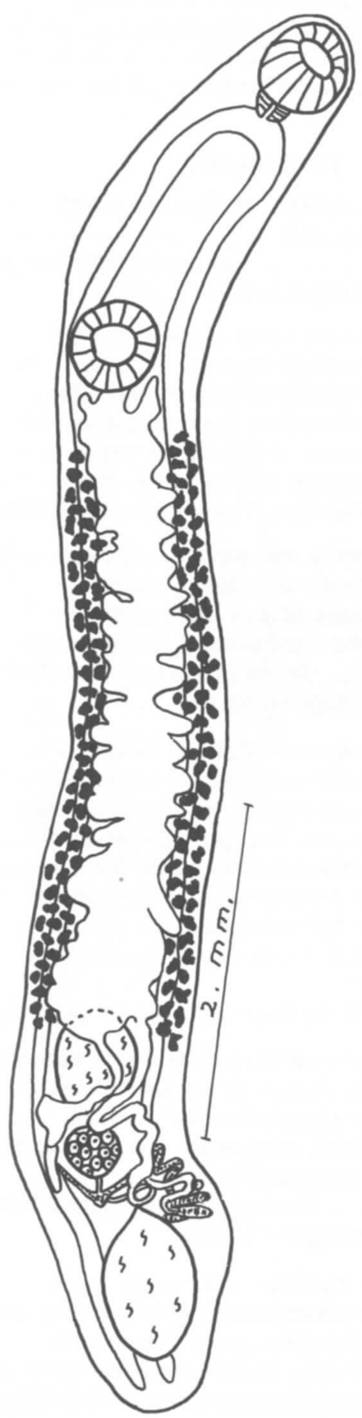


Fig. 299. *Itygonimus scalopi.*
(from Turner and McKeever, 1980).

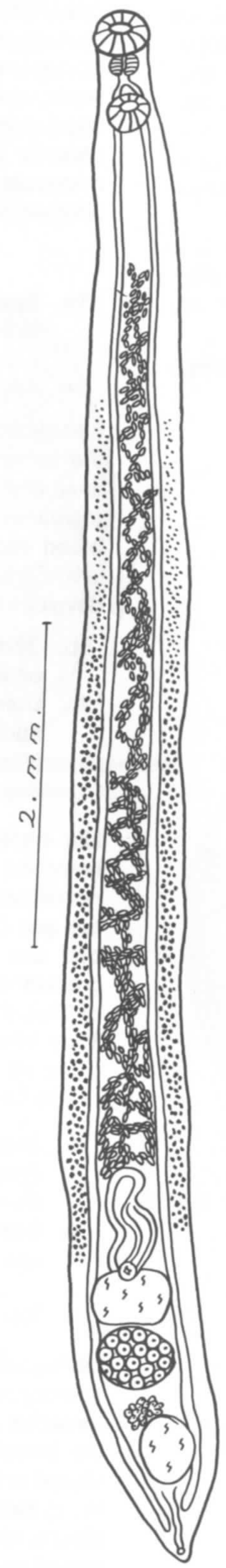


Fig. 300. *Scaphiostomum pancreaticum.*

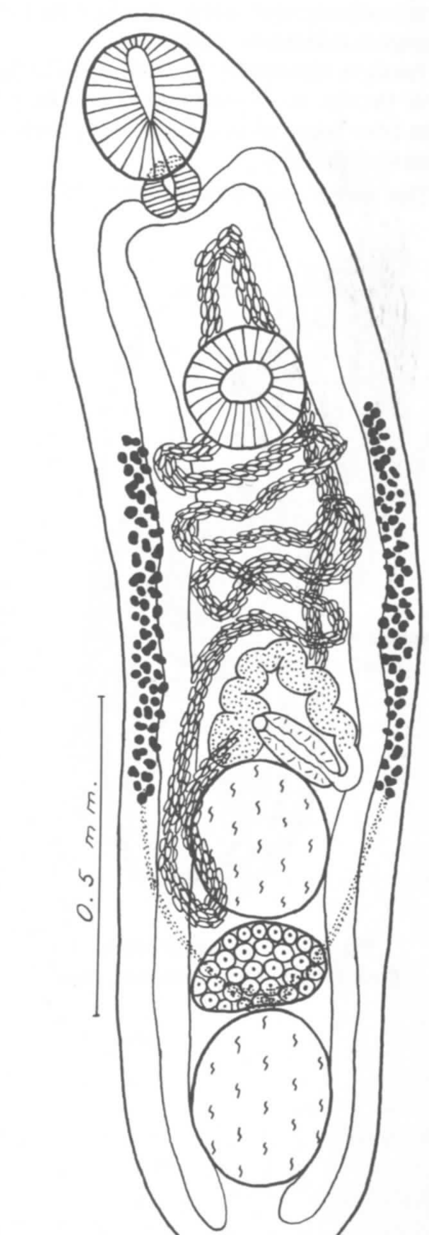


Fig. 301. *Brachylaima virginiana.*

Family Harmotrematidae (Yamaguti, 1933) Mehra, 1962

Body flat, spatulate, nonspinous; oral sucker subterminal; ventral sucker in anterior half of body; pharynx present; esophagus short; ceca long; testes tandem, in posterior third of body; ovary intertesticular; cirrus sac in hindbody, anterior to gonads; cirrus spiny; seminal vesicle bipartite, internal; genital pore in hindbody, ventral to left cecum; vitelline follicles around ceca in fore- and hindbody; uterus confined to hindbody; metraterm present. Parasitic in intestine of reptiles.

This family is represented in North America by the genus *Dracovermis* Brooks and Overstreet, 1978. *D. occidentalis* (Fig. 302) has been reported as a parasite of American alligator, *Alligator mississippiensis*.

Note: This genus was formerly assigned to the family Liolopidae.

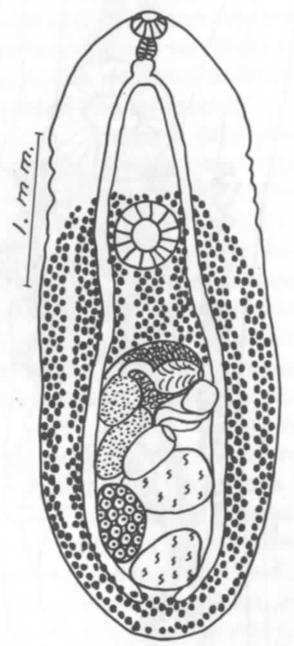


Fig. 302. *Dracovermis occidentalis*. (from Brooks and Overstreet, 1982).

Family Leucochloridiidae Dollfus, 1934

Body oval or elongate; suckers well developed except in genus *Urotocus* in which they are vestigal or absent; pharynx present; ceca long; testes tandem; cirrus sac and genital pore at posterior end of body; ovary intertesticular or opposite anterior testis; vitelline follicles lateral to ceca; uterus long, usually intercecal, some folds in forebody; eggs operculate, embryonated; parasitic in cloaca and bursa Fabricius of birds or in colon of mammals. Cercariae encyst in the sporocyst. Life cycle involves only two hosts.

Key to Genera

1a. Body elongate; suckers vestigial or absent; ovary between testes (Fig. 303). .... Genus *Urotocus* Looss, 1899
Key to species in Kagan (1952b)

Life cycle: *U. tholonetensis* - Embryonated eggs are eaten by the terrestrial snail, *Helicella arenosa*. Miracidia hatch in the snail and invade the hepatopancreas where tailless cercariae (cercariaea) develop in branched sporocysts without pigmented brood sacs. The cercariae encyst in the sporocyst. Infected snails are eaten by magpies, and by crows. The adult parasite develops in the bursa Fabricius (Timon-David, 1955b, 1957a).

1b. Body oval; suckers well developed; ovary either opposite anterior testis or between testes. 2

2a. Uterine loops pass across body posterior to ventral sucker; cirrus short and stubby; ovary between testes (Fig. 304). .... Genus *Urogonimus* Monticelli, 1888
Key to species in Kagan (1952b).

Life cycle: *U. macrostomus* - Tailless cercariae develop in branched sporocysts without pigmented brood sacs in the terrestrial snails, *Cochlicopa lubrica, Vertigo pusilla, Vallonia costata* and *Clausilia bidentata*. The cercariae remain in the sporocyst and change to metacercariae which are enclosed in a granular cyst envelope. Adult parasites developed in 14 species of birds that had been fed metacercariae from infected snails. They inhabit the cloaca, bursa Fabricius and large intestine (Schmidt, 1964, 1965).

The life cycle of *U. certhiae* was studied by Lewis (1974).

2b. Uterine loops pass across body either between pharynx and ventral sucker or dorsal to ventral sucker; cirrus long; ovary opposite anterior testis. 3

3a. Some uterine folds extracecal; cirrus long and narrow, smooth or spinous (Fig. 305). .... Genus *Leucochloridium* Carus, 1835
Key to species in Kagan (1952b).

Life cycle: *L. variae* - Tailless cercariae develop in branched sporocysts having pigmented brood sacs which extend into the tentacles of the snail, *Succinea ovalis*. The cercariae remain in the brood sacs and change to metacercariae which are enclosed in thick gelatinous cyst membranes. Metacercariae were fed to baby chicks and adult parasites were recovered from the cloaca. Natural definitive hosts are grouse, ptarmigan and warblers (Lewis, 1974).

3b. Uterine folds entirely intercecal; cirrus pustulate (blistery) (Fig. 306). .... Genus *Neoleucochloridium* Kagan, 1952
Key to species in Kagan (1952b).

(Continued)

Life cycle: *N. holostomum* - Embryonated eggs from the feces of coots were fed to the amphibious snails, *Succinea pfeifferi* and *S. elegans*. Cercariaea developed in branched sporocysts having pigmented brood sacs in the tentacles of the snail. They remain in the sporocyst and change to metacercariae which become enveloped by a cyst membrane. The natural definitive host is the coot, *Fulica atra* (see Pojmanska, 1975).

The life cycle of *N. problematicum* is similar to the above except for hosts. The snail, *Oxyloma retusa* is host for the larvae. Tentacles containing brood sacs become distended and sometimes rupture, exposing the brightly colored sacs which are thought to attract birds that eat the infected snails. Definitive hosts for this species are birds in the family Rallidae. The parasites attain sexual maturity in the cloaca of the bird in five to eight days (Kagan, 1951, 1952a).

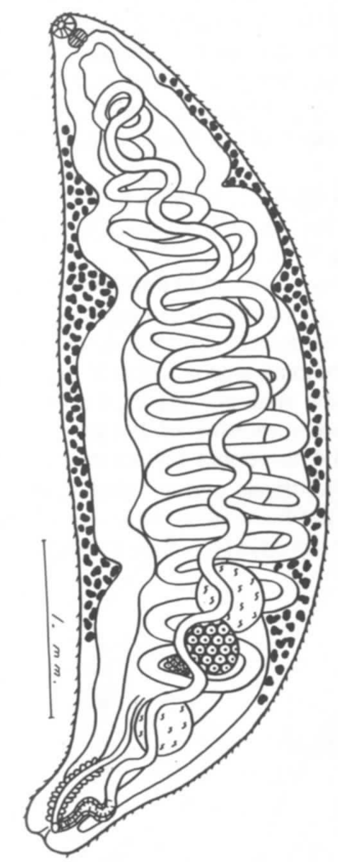


Fig. 303. *Urotocus fusiformis*.

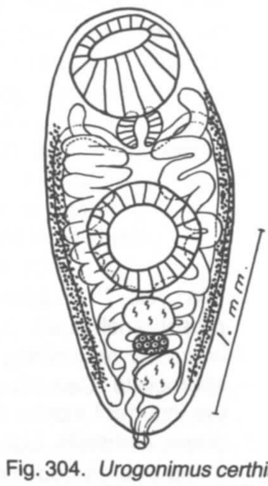


Fig. 304. *Urogonimus certhiae*. (from McIntosh, 1932)

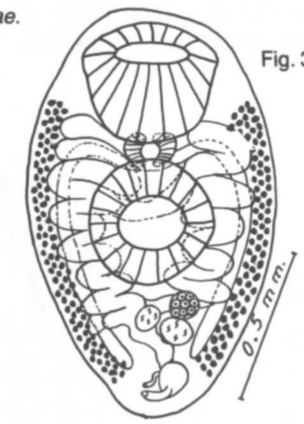


Fig. 305. *Leucochloridium melospizae*.

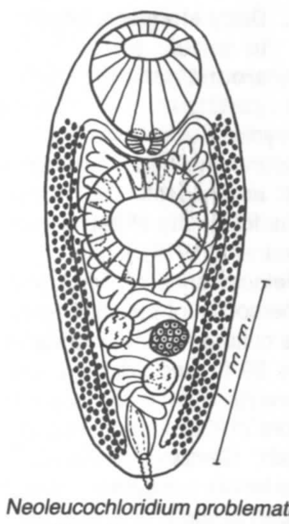


Fig. 306. *Neoleucochloridium problematicum*. (from Kagan, 1951)

Family Leucochloridiomorphidae Travassos and Kohn, 1966

Body small, elongate, fusiform or oval; ventral sucker in middle of body and larger than oral sucker; pharynx present; intestinal ceca long; testes tandem, oblique or opposite, close to posterior end of body; ovary pretesticular; cirrus sac and genital pore in hindbody; vitelline follicles in lateral clusters anterior to gonads or lateral to ventral sucker; uterus anterior to gonads; eggs operculate, embryonated; adults parasitic in bursa Fabricius of birds or in rectum and salivary glands of mammals.

Key to Genera

1a. Body elongate; vitelline follicles immediately anterior to testes; testes opposite; uterus confined to area around gonads (Fig. 308). .... **Genus *Amblosoma* Pojmanska, 1972**

Life cycle: *A. exile* - Metacercariae were found in the freshwater prosobranch snail, *Viviparus viviparus.* Feeding experiments were unsuccessful but metacercariae were compared with adults from natural infections in the duck, *Aythya fuligula* (see Pojmanska, 1972).

Metacercariae of *Amblosoma suwaense* were found free in the hemocoel of the snail *Sinotaia quadrata.* The Metacercariae were cultured in the chorioallantois of incubating hens eggs at 34 to 39 C. and adult parasites developed in about five days (Shimazu, 1974; Fried, Heyer and Pinski, 1981).

Font (1980) found unencysted metacercariae in the prosobranch, *Campeloma decisum* in Wisconsin. When some of these larvae were placed in embryonated chicken eggs they developed to adults of *A. suwaense.*

1b. Body oval or fusiform; vitelline follicles in lateral clusters some distance anterior to testes, usually lateral to ventral sucker; testes opposite or tandem; uterus mostly anterior to gonads, may extend into forebody. 2

2a. Body oval; testes opposite; vitelline follicles antero-lateral to ventral sucker; parasitic in bursa Fabricius of birds (Fig. 307). .... **Genus *Leucochloridiomorpha* Gower, 1938**

Life cycle: *L. constantiae* - Embryonated eggs are ingested by the prosobranch snail, *Campeloma decisum.* Furcocercous cercariae, resembling the dichotoma type (Fig. 27) develop in branched sporocysts. After leaving the snail, these cercariae may enter the respiratory chamber of another snail of the same species. Metacercariae gradually accumulate in the uterus of the snail. Adult flukes developed in chickens, ducks and raccoon as a result of experimental feeding of metacercariae. Natural infections occur in the bursa Fabricius of the black duck, *Anas rubripes* (see Allison, 1943).

2b. Body fusiform; testes tandem; vitelline follicles postero-lateral to ventral sucker; parasitic in the salivary glands of rodents (Fig. 309). .... **Genus *Ptyalincola* Wootton and Murrell, 1967**

Life cycle: *P. ondatrae* - Embryonated eggs are ingested by the prosobranch snail, *Campeloma decisum* in which furcocercous cercariae resembling the dichotoma type develop in branched sporocysts. Cercariae leave the snail and are then drawn into the incurrent siphon of freshwater mussels of the genera *Anodonta, Lampsilis, Ligumia* and *Alasmidonta.* Metacercariae were found unencysted between the mantle and the shell in the region of the umbo. Muskrats eat the infected mussels. Sexual maturity is attained in seven to ten days (Wootton, 1966b).

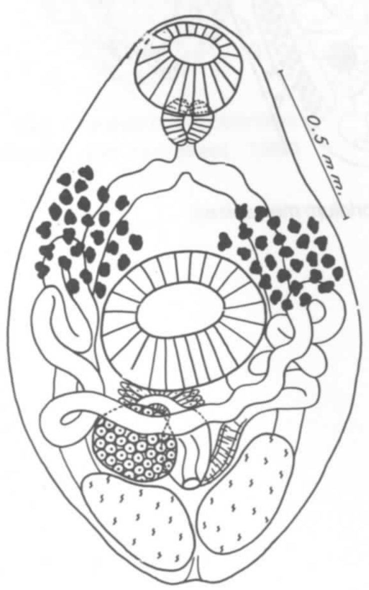


Fig. 307. *Leucochloridiomorpha constantiae.*

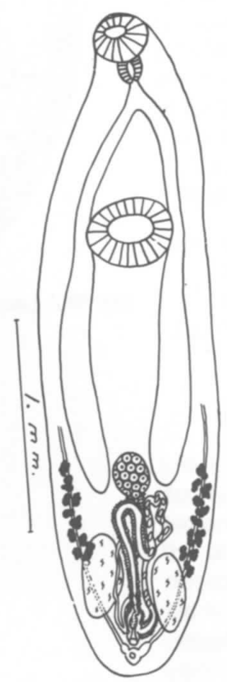


Fig. 308. *Amblosoma suwaense.* (from Shimazu, 1974)

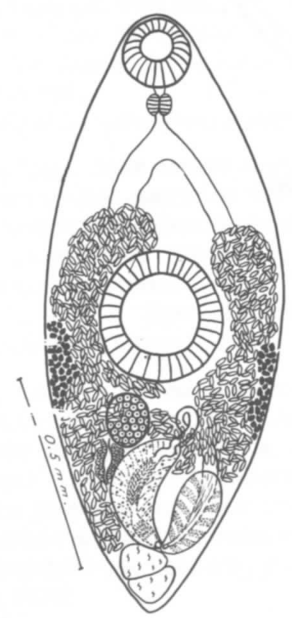


Fig. 309. *Ptyalincola ondatrae.*

Family Hasstilesiidae Hall, 1916

Body small (1 mm), spinous; suckers about equal, in anterior half of body; pharynx present; intestinal ceca long; testes oblique, in hindbody; cirrus sac near testes, the base directed anterior; genital pore in posterior third of body; ovary opposite to testes; vitelline follicles in lateral clusters along anterior half of ceca; uterus anterior to and between gonads; parasitic in intestine of hares and rabbits. Cercariae remain in sporocyst. Life cycle involves two hosts.

The genus *Hasstilesia* Hall, 1916 (Fig. 310) is represented in North America by *H. tricolor.*

Key to species in Rowan (1955).

Life cycle: *H. tricolor* - Embryonated eggs are eaten by the pupillid terrestrial snails, *Vertigo ventricosa* and *V. ovata.* The miracidia hatch in the snail intestine. Obscuromicrocercous cercariae (Fig. 15) develop in branched sporocysts and, after losing the tail, develop into metacercariae right in the sporocyst without encysting. The definitive hosts are the cottontail rabbit, *Sylvilagus floridanus* and the black-tailed jackrabbit, *Lepus californicus.* They probably eat the infected snails with vegetation (Robinson, 1953; Rowan, 1955).

The similar life cycle of *H. ochotonae,* a parasite of pikas in Russia, has been studied by Soboleva (1972).

Family Urotrematidae Poche, 1926

Body elongate, spinous; suckers small, close to anterior end of body; intestinal ceca long; testes tandem, usually in posterior third of body; cirrus sac and genital pore near posterior end of body; ovary pretesticular, separated from testes by some folds of uterus; vitelline follicles limited in extent; uterus long, folds between ovary and genital pore; parasitic in intestine of reptiles and mammals (bats).

Key to Genera

1a. Ovary and testes lobed; ventral sucker far anterior to ovary (Fig. 311). .... **Genus *Urotrematulum* Macy, 1933**

1b. Ovary and testes round or oval; ventral sucker only a short distance anterior to ovary (Fig. 312). .... **Genus *Urotrema* Braun, 1900.**

Key to species in Macy (1933) and in Skrjabin (1964).

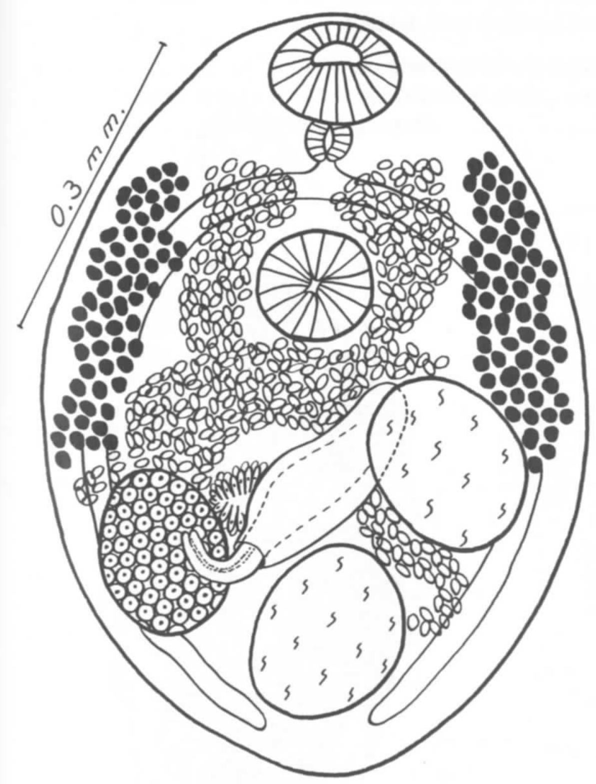


Fig. 310. *Hasstilesia tricolor.*

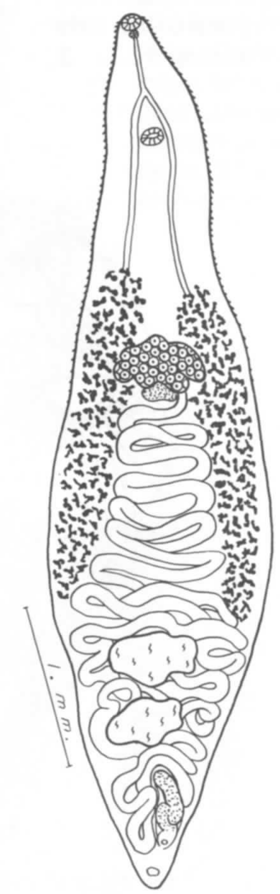


Fig. 311. *Urotrematulum attenuatum.*

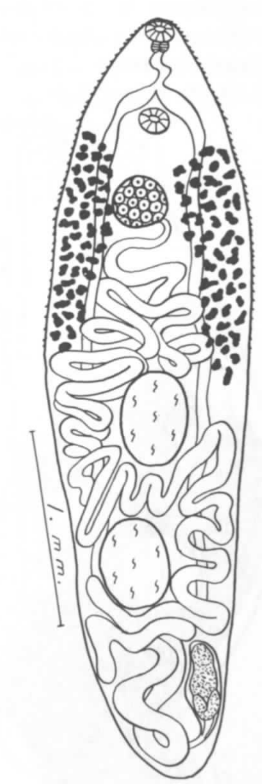


Fig. 312 *Urotrema lasiurensis.*

Superfamily Fellodistomoidea LaRue, 1957

Miracidia have one pair of flame cells. Cercariae furcocercous, microcercous or nonoculate trichocercous with large Y-, V- or U-shaped excretory vesicle, develop in sporocysts in marine lamellibranch or gastropod molluscs and encyst in a variety of marine invertebrates, sometimes encysting in the sporocyst. Life cycle involves two or three hosts. Adults parasitic in fishes and birds.

Family Fellodistomidae Nicoll, 1913

Body small, oval, fusiform or elongate; suckers well developed; pharynx present; ceca long or short; testes oblique, opposite or tandem (single testis in *Infundibulostomum*); cirrus sac present; seminal vesicle usually bipartite; genital pore anterior to ventral sucker; ovary inter-, pre- or posttesticular; vitelline follicles usually in small clusters lateral to ceca; uterus usually confined to hindbody; eggs operculate, embryonated; excretory vesicle V-, Y- or U-shaped, the arms extending forward to level of pharynx; parasitic in intestine of marine fishes. One species reported as being progenetic in marine lamellibranch molluscs.

Key to Genera

1a. One testis; external seminal vesicle present (Fig. 313). ...... Genus *Infundibulostomum* Siddiqi and Cable, 1959

1b. Two testes; external seminal vesicle absent. 2

2a. Body with muscular circumoral papillae and lateral transverse muscular folds on body immediately posterior to oral sucker; testes tandem, near posterior end of body (Fig. 314). .... Genus *Tergestia* Stossich, 1899

Key to species in Manter (1954) and in Skrjabin (1964).

Life cycle: No complete life cycle is known in this genus but three species of cercariae have been assigned to the genus *Tergestia* on the basis of comparative anatomy. *Cercaria haswelli* was obtained from *Mytilus latus* collected in New Zealand. *C. kenti* and *C. mathiasi* were found in marine plankton samples. All three are furcocercous with the base of the tail in the form of a dilated crest having crenated margins. The body has muscular circumoral processes and lateral transverse ridges behind the oral sucker. These latter features are like those of adult *Tergestia* spp. The second intermediate host is unknown; however, in the family Fellodistomidae the metacercariae are known to occur in either crustaceans or molluscs.

2b. Body without muscular papillae around oral sucker. 3

3a. Body has large muscular lobes along sides and on ventro-lateral surfaces; testes lobed, oblique; ovary lobed, anterior to right testis (Fig. 315). .... Genus *Lomasoma* Manter, 1935

3b. Body without lateral and ventrolateral lobes. 4

4a. Body oval, concave ventrally, with prominent folds near anterior and posterior ends; hindbody has five transverse muscle bands; testes lobed, oblique; ovary lobed, anterior to right testis (Fig. 316). .... Genus *Lissoloma* Manter, 1934

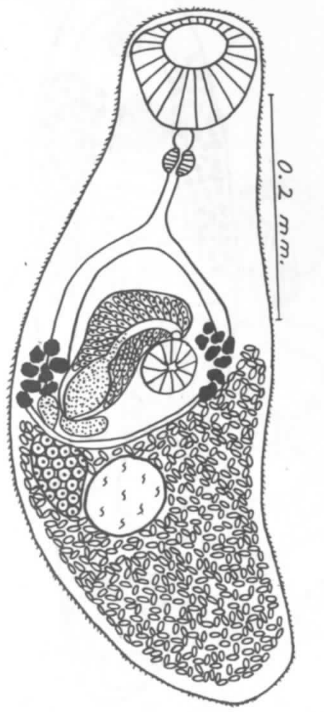


Fig. 313. *Infundibulostomum spinatum.* (from Siddiqui and Cable, 1960)

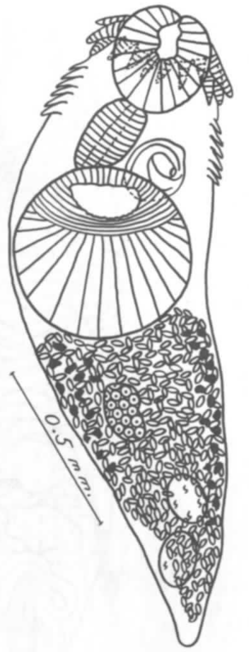


Fig. 314. *Tergestia acuta.*

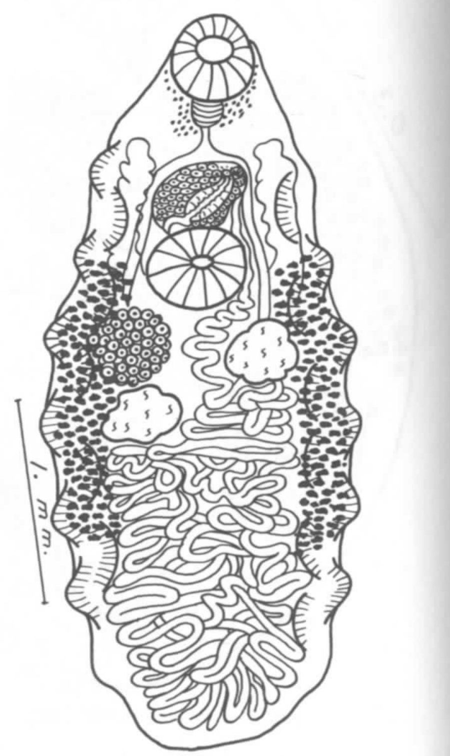


Fig. 315. *Lomasoma wardi.* (from Manter, 1934)

4b. Body without anterior and posterior folds and muscle bands. 5

5a. Oral sucker terminal. 6

5b. Oral sucker not terminal. 9

6a. Testes elongate, nearly opposite, posterior to cecal ends; uterus extends between testes (Fig. 317). .... Genus *Hexagrammia* Baeva, 1965

6b. Testes oval or round. 7

7a. Testes tandem, near posterior end of body; ovary pretesticular; uterus preovarian; oral sucker saucer-shaped (Fig. 318). .... Genus *Anisorchis* Poljansky, 1955

7b. Testes opposite, near middle of body; ovary posttesticular. 8

8a. Oral sucker saucer-shaped; vitellaria in two compact masses, postero-lateral to ventral sucker; ovary lobed (Fig. 319). .... Genus *Pseudopentagramma* Yamaguti, 1971

8b. Oral sucker funnel-shaped; vitellaria follicular, anterior to ventral sucker and lateral to ceca; ovary round (Fig. 320). .... Genus *Antorchis* Linton, 1911

9a. Testes tandem or oblique; ovary pretesticular. 10

9b. Testes usually opposite, may be slightly oblique; ovary intertesticular or anterior to right or left testis. 12

10a. Suckers about equal in size; testes tandem; vitelline follicles around ceca in area between ventral sucker and anterior testis; parasitic in parrotfishes (Fig. 321). .... Genus *Mesolecitha* Linton, 1910

10b. Ventral sucker larger than oral sucker; testes oblique; vitelline follicles either distributed along ceca or restricted to area around gonads. 11

11a. Vitelline follicles restricted to area around gonads; cirrus sac large, contains bipartite seminal vesicle, part of which is ovoid and part tubular; ovary oval (Fig. 322). .... Genus *Proctoeces* Odhner, 1911

Life cycle: *P. maculatus* - Microcercous cercariae *(Cercaria milfordensis)* develop in sporocysts in the digestive gland of the marine mussel, *Mytilus edulis*. Metacercariae were found in the coelom and in the tissues of *Nereis caudata* following exposure to cercariae from mussels. The same metacercaria has also been reported from other lamellibranchs. Metacercariae from *Nereis* were fed to the marine fishes *Coris julis, Gobius niger* and *Crenilabrus griseus*. Adults were recovered from *C. griseus* five days later. Natural infections occur in at least 10 species of marine fishes. Progenetic adults have been found in the lamellibranchs *Mytilus edulis* and *Scrobicularia plana*. (see Uzmann, 1953; Freeman and Llewellyn, 1958; Stunkard and Uzmann, 1959; Prevot, 1965; Lang and Dennis, 1976).

Wardle (1980) maintains that *Cercaria milfordensis, C. tenuans* and *C. brachidontus* are all the larvae of *P. maculatus*. He reports the hooked mussel, *Ischadium recurvum* as first intermediate host. Metacercariae were also found in this host as well as in the platform mussel, *Mytilopsis leucopheata*. Adults were found in the hindgut of sheeps head, *Archosargus probatocephalus*. There was no sign of progenesis in the mussels.

11b. Vitelline follicles distributed around ceca through about three-fourths of body length; ovary trilobed, opposite to anterior testis; cirrus sac small (Fig. 323). .... Genus *Stenakron* Stafford, 1904

Note: Chubrik (1952c, 1966) found in Russia what might be the larval stages of *S. quadrilobatum*. The host gastropods are two species of *Solariella*. Microcercous cercariae, without a stylet develop in sporocysts. It is possible that this genus might be finally placed in the family Opecoelidae.

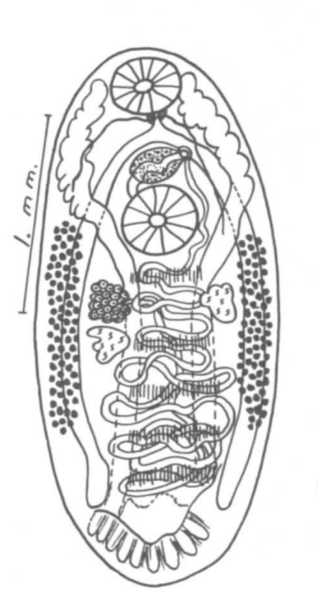


Fig. 316. *Lissoloma brotulae.* (from Manter, 1934)

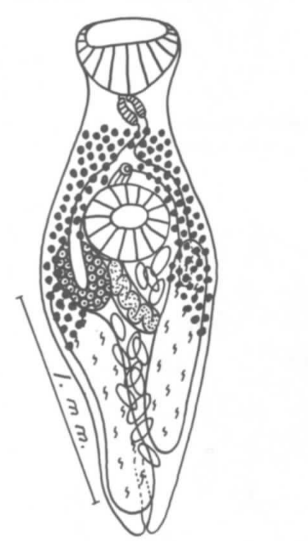


Fig. 317. *Hexagrammia longitestis.*

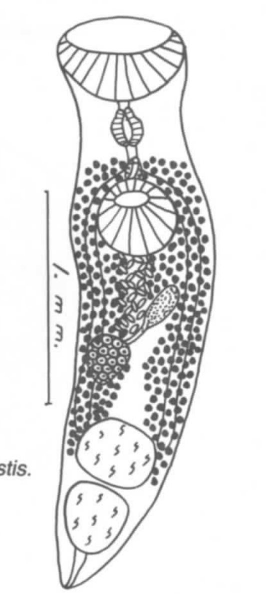


Fig. 318. *Anisorchis opisthorchis.*

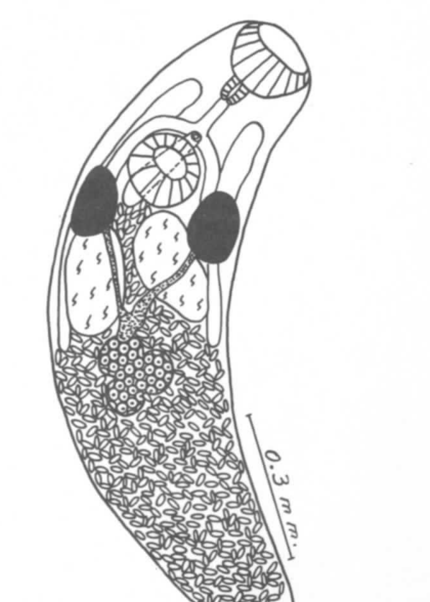


Fig. 319. *Pseudopentagramma petrovi.*

12a. **Oral sucker with zone of circular muscle fibers close to mouth; two bands of muscle fibers extend from oral sucker to sides of body; genital atrium tubular with an atrial sac; cirrus spiny; parasitic in hogfishes (Fig. 324). .... Genus *Megalomyzon* Manter, 1947**

12b. **Oral sucker without circular muscle fibers and muscle bands; genital atrium not tubular. 13**

13a. **Vitelline follicles arranged in two compact clusters lateral to ventral sucker; ovary intertesticular or posttesticular (Fig. 325). .... Genus *Pseudobacciger* Nahhas and Cable, 1964**

13b. **Vitelline follicles distributed along ceca. 14**

14a. **Body pyriform or round; vitelline follicles restricted to forebody, confluent anterior to ventral sucker; cirrus sac transverse; testes opposite; ovary trilobed, intertesticular (Fig. 326). ....Genus *Hypertrema* Manter, 1960**

14b. **Body oval; vitelline follicles restricted to hindbody or in both fore- and hindbody; testes opposite or oblique. 15**

15a. **Vitelline follicles extending posterior to testes. 16**

15b. **Vitelline follicles not extending posterior to testes. 18**

16a. **Testes oblique; ovary opposite anterior testis; vitelline follicles numerous, extend into fore- and hindbody, confluent at posterior end of body (Fig. 327). .... Genus *Pycnadena* Linton, 1910**

16b. **Testes opposite; ovary intertesticular or median and slightly anterior to testes. 17**

17a. **Body oval, small (1-2mm); ovary oval and intertesticular; vitelline follicles clustered around ends of ceca; some uterine folds anterior to testes and ovary; cirrus sac overlaps ventral sucker dorsally (Fig. 328). .... Genus *Pycnadenoides* Yamaguti, 1938**

17b. **Body fusiform, large (5-6mm); ovary lobed, median and anterior to both testes; uterus entirely posterior to both gonads; vitelline follicles in clumps lateral to ceca; cirrus sac entirely anterior to ventral sucker (Fig. 329). .... Genus *Lintonium* Stunkard and Nigrelli, 1930**

Life cycle: *L. vibex* - Nonoculate trichocercous cercariae *(C. laevicardii)* with finlets on the tail develop in elongate sporocysts in the hemocoel of the marine lammellibranch, *Laevicardium mortoni.* The metacercariae inhabit the jelly of the ctenophore, *Mnemiopsis leidyi.* The puffer, *Spheroides maculatus* harbors the adult parasite (Martin, 1945; Cable, 1954; Stunkard, 1978).

18a. **Vitelline follicles lateral to ventral sucker and gonads; ovary anterior to right testis; excretory vesicle Y-shaped (Fig. 330). .... Genus *Fellodistomum* Stafford, 1904**

Life cycle: *F. fellis* (syn. *Steringotrema ovacutum*) - Furcocercous cercariae with a large V-shaped excretory vesicle develop in sporocysts in the marine lamellibranch, *Nucula tenuis.* The cercariae are eaten by brittle stars, *Ophiura albida, O. sarci* and *Amphiura chiajei.* Metacercariae develop but do not encyst in the brittle stars. The infected brittle stars are in turn eaten by wolf fish, *Anarhichas lupus;* long rough dab, *Hippoglossoides platessoides* and by plaice, *Pleuronectes platessa* in which the adult fluke develops, inhabiting the duodenum and the gall bladder (Chubrik, 1952; Koie, 1980).

18b. **Vitelline follicles in a confluent band across body at level of ventral sucker; excretory vesicle V-shaped (Fig. 331). .... Genus *Steringotrema* Odhner, 1911**

Key to species in Skrjabin (1964).

Life cycle: *S. pagelli* - Furocercous cercariae without a tail stem develop in the marine bivalve, *Nucula nitidosa.* They bear a superficial resemblance to bucephaloid cercariae. The tail furcae are hollow and appear to serve as hydrostatic organs, enabling the cercariae to float upside down. The cercariae are taken in with water currents and swallowed by lemon sole, *Microstomus kitt* and by the dab, *Limanda limanda* in which they develop to mature flukes in less than 12 days. *Pleuronectes platessa* is also known to harbor this parasite (Koie, 1980).

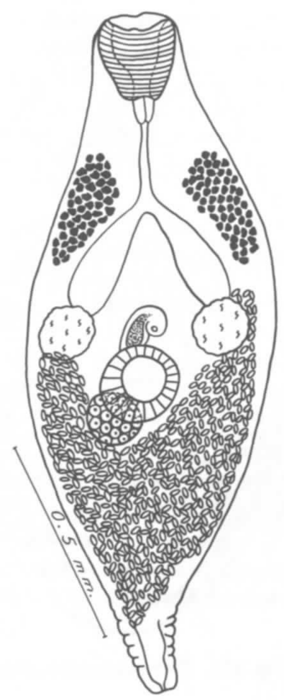


Fig. 320. *Antorchis urna.*

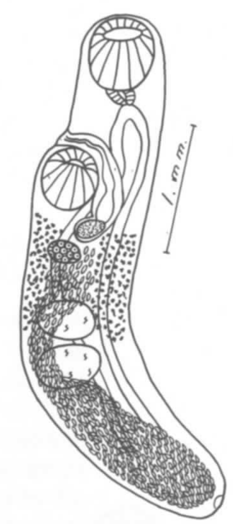


Fig. 321. *Mesolecitha linearis.*

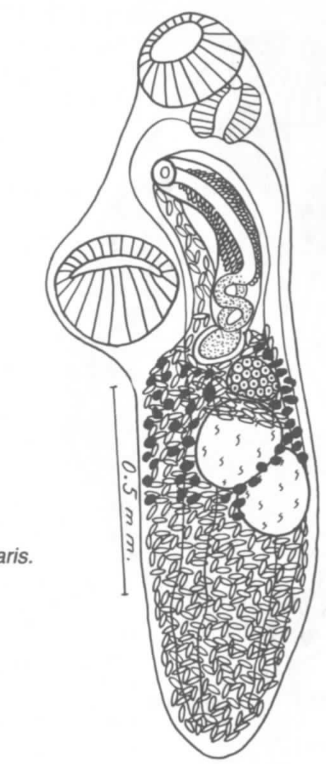


Fig. 322. *Proctoeces lintoni.*

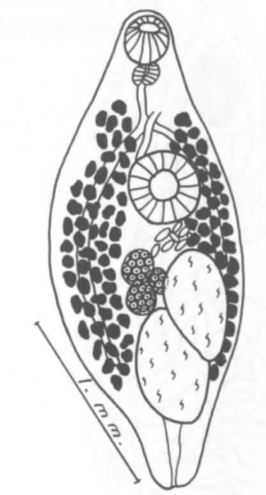


Fig. 323. *Stenakron vetustum.* (from Miller, 1941)

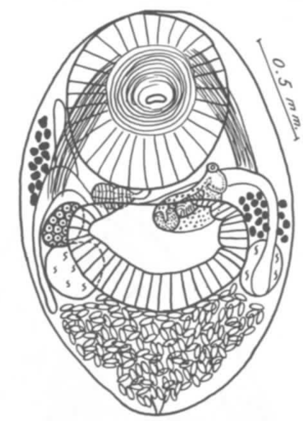


Fig. 324. *Megalomyzon robustus.* (from Manter, 1947)

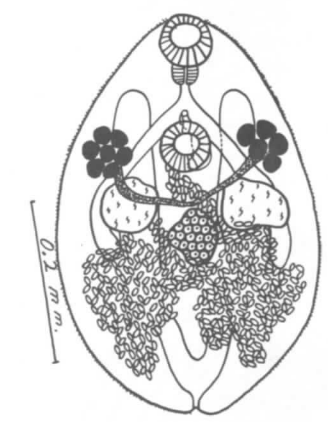


Fig. 325. *Pseudobacciger manteri.* (from Nahhas and Cable, 1964)

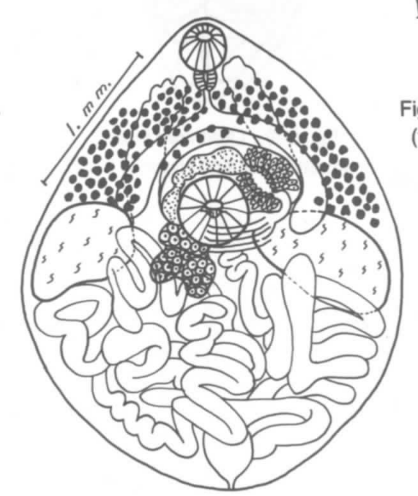


Fig. 326. *Hypertrema ambovatum.* (from Manter, 1960)

Fig. 327. *Pycnadena lata.*

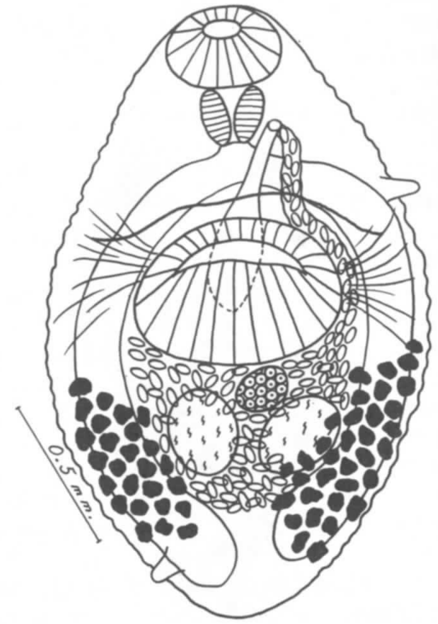


Fig. 328. *Pycnadenoides calami.*

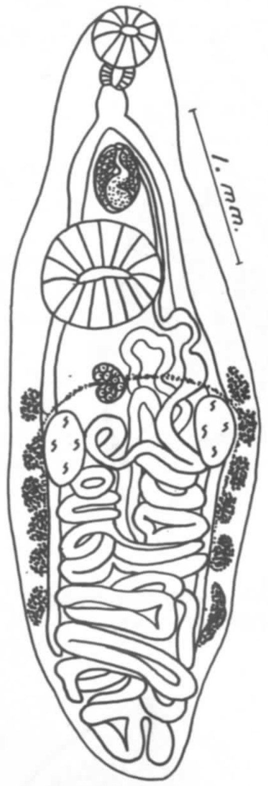


Fig. 329. *Lintonium vibex.* (from Stunkard and Nigrelli, 1930).

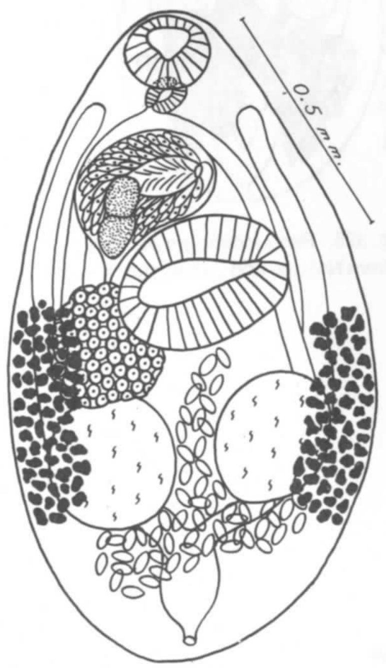


Fig. 330. *Fellodistomum brevum.*

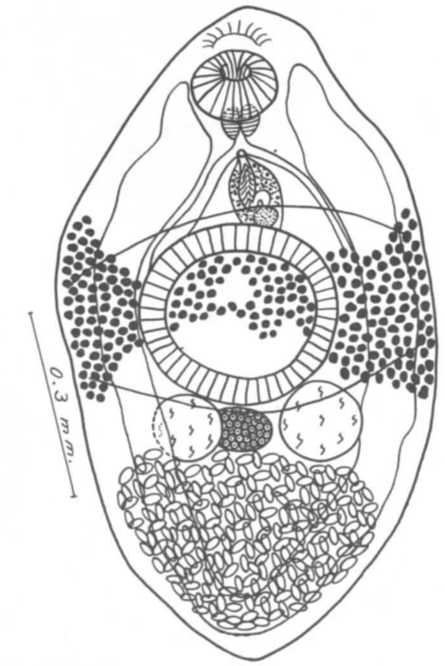


Fig. 331. *Steringotrema corpulentum.* (from Manter, 1931)

Family Monascidae Dollfus, 1952

Body elongate, cylindrical; suckers near anterior end of body; mouth a longitudinal slit; pharynx large; intestine a single cecum unites with excretory vesicle at posterior end of body; testes tandem, in middle of hindbody; seminal vesicle bipartite; genital pore and cirrus sac anterior to ventral sucker; ovary pretesticular; vitelline follicles in lateral bands between ventral sucker and testes; uterus fills most of hindbody; excretory vesicle V-shaped, arms extend to level of pharynx; parasitic in intestine of marine fishes.

The family contains only the genus *Monascus* Looss, 1907 which is represented in North America by *M. filiformis* (Fig. 332).

Life cycle: *M. filiformis* - Furcocercous cercariae with a large V-shaped excretory vesicle develop in reddish-brown, thick-walled sporocysts in the marine lamellibranch, *Nucula nitidosa.* The cercariae are eaten by the dab, *Limanda limanda* in which they develop directly to the adult stage. Some cercariae are also eaten by the crystal goby *Crystallogobius linearis* in which almost no development takes place. The latter are then eaten by the horse mackerel, *Trachurus symmetricus.* The goby can be regarded as a paratenic host.

The cercaria and the adult have a long right cecum and a vestigial left cecum which is located between the ventral sucker and the ovary (Koie, 1979).

Fig. 332. *Monascus filiformis.* (from Dollfus, 1947)

Family Gymnophallidae Morozov, 1955

Body very small (1 mm or less), oval, pyriform or fusiform, spinous; ventral sucker near middle of body, smaller than oral sucker; pharynx small; ceca extend about to midbody; testes opposite, in hindbody or lateral to ventral sucker; cirrus sac absent; seminal vesicle free in parenchyma; genital pore median, anterior to ventral sucker; ovary pretesticular; vitellaria composed of one or two compact masses or clusters of follicles, usually intertesticular; uterus fills posttesticular area of body; eggs operculate, embryonated; excretory vesicle V- or Y-shaped, arms extend forward to level of pharynx; parasitic in the intestine, gall bladder on bursa Fabricius of birds.

Key to Genera

1a. Ventral pit present anterior to genital pore; vitellaria in form of two compact masses dorsal to ventral sucker; oral sucker with pair of lateral papillae (Fig. 333). .... Genus *Lacunovermis* Ching, 1965

Life cycle: *L. conspicuous* - Furcocercous cercariae of the dichotoma type develop in sporocysts in the marine clam, *Macoma inconspicua.* They leave the sporocyst but remain in the clam, developing to the encysted metacercarial stage between the shell and mantle. Metacercariae were fed to field mice, *Peromyscus maniculatus* and adult flukes recovered. The diving ducks, *Oidemia nigra* and *Aythya marila* serve as natural definitive hosts (Ching, 1965).

1b. Ventral pit absent. 2

2a. Vitellaria in form of a single cluster of follicles. 3

2b. Vitellaria in form of two clusters of follicles or two compact masses. 4

3a. Vitellaria single transverse or V-shaped cluster of follicles; seminal vesicle bipartite; prostatic vesicle well developed; excretory vesicle Y-shaped (Fig. 334). ..... Genus *Paragymnophallus* **Ching, 1973**

3b. Vitellaria in form of a single round cluster of follicles; seminal vesicle unipartite; prostatic vesicle not well developed but prostatic gland well developed; excretory vesicle V-shaped (Fig. 335). .... Genus *Parvatrema* **Cable, 1953**

Key to species in James (1964).

Life cycle: *P. borinquenae* - Furcocercous cercariae of the dichotoma type develop in sporocysts in the marine lamellibranch, *Gemma purpurea.* After leaving the clam, the cercariae enter the marine snail, *Cerithidea costata* and develop to infective metacercariae without encysting. The adult flukes developed in baby chicks after feeding metacercariae. The natural definitive host is unknown (Cable, 1953).

4a. Excretory vesicle V-shaped; ovary anterior to right or left testis; ceca very short; seminal vesicle saccular (Fig. 337). .... Genus *Meiogymnophallus* **Ching, 1965**

Life cycle: *M. multigemmulus* - Dichotoma cercariae develop in *Macoma inconspicua,* a marine clam. The cercariae remain in the sporocyst and change to the metacercarial stage. Experimental infections were established in field mice, *Peromyscus maniculatus* after feeding metacercariae. The natural definitive hosts are ducks, *Oidemia nigra* and *Melanitta perspicillata* which probably eat the infected clams (Ching, 1965).

Bowers and James (1967) investigated the life cycle of *M. minutus* in England. The host mollusc is the cockle, *Cardium edule* in which metacercariae were found below the umbo. Natural definitive hosts are the common scoter duck and the oystercatcher. Ducklings served as experimental definitive host.

4b. Excretory vesicle Y-shaped; ceca long or half long. 5

5a. Vitelline follicles posteriolateral to ventral sucker; ovary anterior to right or left testis; ovary and testes in hindbody; seminal vesicle saccular; esophagus longer than pharynx (Fig. 336). .... Genus *Gymnophallus* **Odhner, 1900**

Life cycle: *G. choledochus* - Furcocercous cercariae of the dichotoma type develop in sporocysts in the cockle, *Cardium edule.* In the spring and summer the cercariae leave the sporocysts and the cockle and penetrate polychaete worms of the genera *Nereis, Nephthys* and *Arenicola* in which the metacercariae develop. In fall and winter the cercariae remain in the sporocysts and metamorphose to the metacercarial stage. The adult parasite develops in the gall bladder of gulls, terns and ducks which eat infected cockles and polychaete worms (Loos-Frank, 1969a and 1969b).

Bartoli (1972) studied the life cycles of *G. nereicola* and *G. fossarum* in France. The cercariae of *G. fossarum* are drawn into marine lamellibranch molluscs in water currents. There they change to infective metacercariae, lodging between the shell and the mantle. Cercariae of *G. nereicola* were found unencysted in the parapodia of polychaete worms of the genus *Nereis.*

Popova and Nikitina (1978) provide an account of the life cycle of *Gymnophallus discursata,* a parasite of gulls and terns in the Caspian Sea.

5b. Vitelline follicles anteriolateral to ventral sucker; ovary between testes; ovary and testes lateral to ventral sucker; seminal vesicle cylindrical; esophagus shorter than pharynx (Fig. 338). .... Genus *Pseudogymnophallus* **Hoberg, 1981.**

Fig. 333. *Lacunovermis conspicuous.*

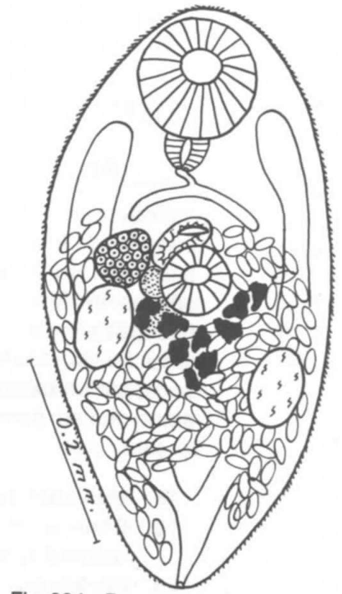


Fig. 334. *Paragymnophallus odhneri.* (from Ching, 1973)

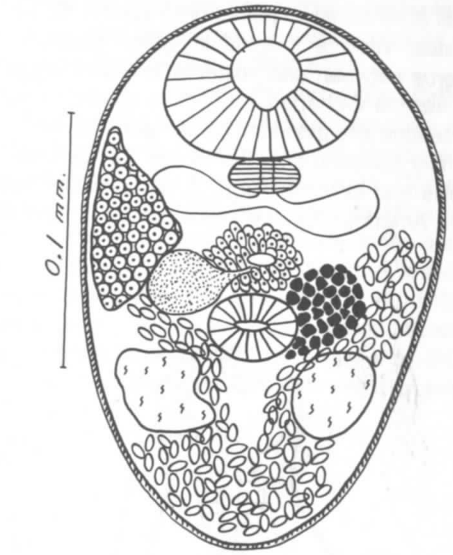


Fig. 335. *Parvatrema borinquenae.*

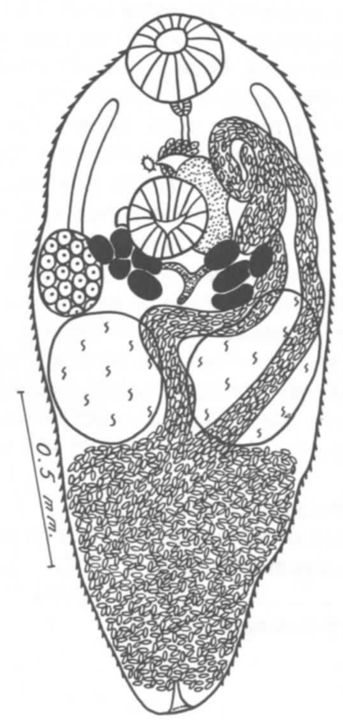


Fig. 336. *Gymnophallus deliciosus.*

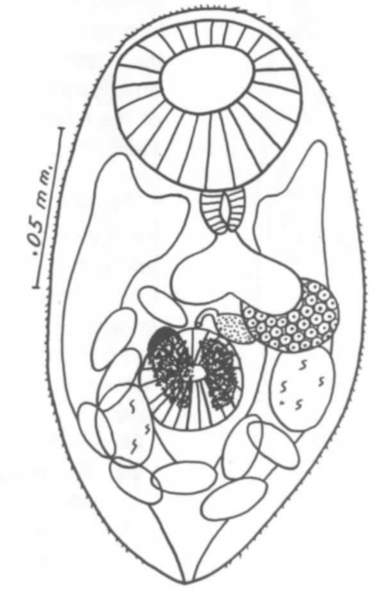


Fig. 337. *Meiogymnophallus multigemmulus.* (from Ching, 1965)

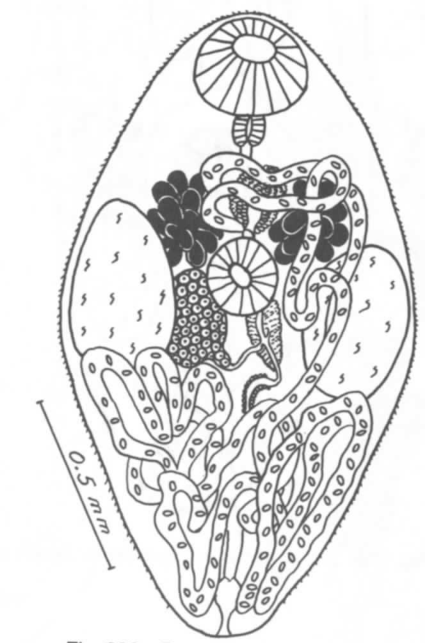


Fig. 338. *Pseudogymnophallus alcae.* (from Hoberg, 1981).

Family Botulisaccidae Yamaguti, 1971

Body oval, spinous; suckers well developed, in anterior half of body; pharynx present; esophagus has pair of lateral pouches; intestinal ceca arise at middle of body and extend a short distance beyond testes; cirrus sac posterior to ventral sucker; testes opposite, in middle of hindbody; seminal vesicle internal, bipartite; genital pore sinistral, posterior to ventral sucker; ovary between testes; vitelline follicles in lateral clusters, anterior to testes; uterus between and posterior to testes; eggs operculate; excretory vesicle V-shaped, extends to level of esophagus; parasitic in intestine and pyloric ceca of marine fishes.

The family contains only the genus *Botulisaccus* Caballero, Bravo-Hollis and Grocott, 1955. *B. pisceus* has been reported from North America (Fig. 339) as a parasite of bonefish, *Albula vulpes*.

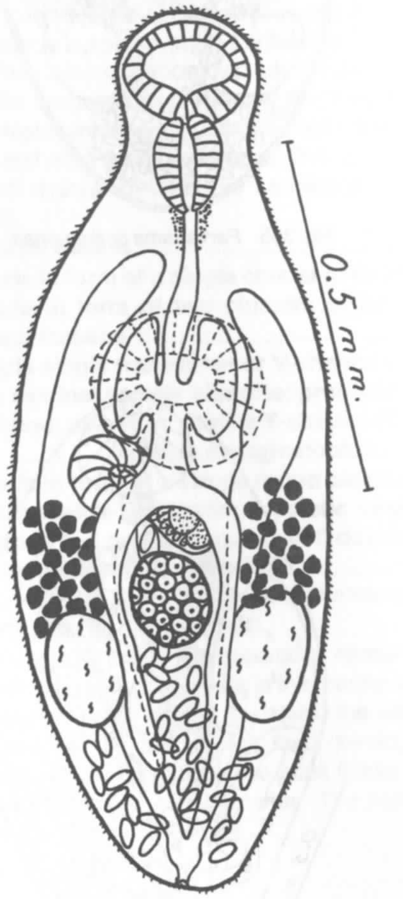


Fig. 339. *Botulisaccus pisceus.* (from Overstreet, 1969)

Superfamily Bucephaloidea LaRue, 1926

Miracidia with cilia mounted on plates or bars that extend from the body. Cercariae of the bucephaloid (gasterostome) type with contractile furcae and very short tail stem; develop in branched sporocysts in lamellibranch molluscs and encyst in fishes. Life cycles involve three hosts.

The term "bucephalus" (meaning "ox head") arises from the appearance of the cercaria which swim with the furcae foremost or uppermost and body hanging down, resembling an ox head.

Family Bucephalidae Poche, 1907

Body elongate, spinous; mouth on midventral surface of body, leads to pharynx and saccular intestine; muscular sucker or conical rhynchus at anterior end of body; testes tandem or oblique, in hindbody; cirrus sac, genital atrium and genital pore near posterior end of body; ovary pretesticular or opposite to anterior testis; vitelline follicles in lateral areas in anterior half of body; uterus extends into fore- and hindbody; eggs operculate, embryonated; parasitic in the digestive tract of fishes.

Key to Genera

1a. Muscular sucker at anterior end of body. 2

1b. Conical rhynchus at anterior end of body, with or without spines. 4

2a. Sucker surmounted by a flat hood; parasitic in marine and freshwater fishes (Fig. 340). .... Genus *Rhipidocotyle* Diesing, 1858

Key to species in Chauhan (1943).

Life cycle: *R. transversalis* and *R. lintoni* - The life cycle is the same for both species, involving the same hosts. The definitive host is the garfish, *Strongylura marina,* a littoral species that frequently ascends coastal rivers. Bucephaloid cercariae develop in branched daughter sporocysts which inhabit the gonads and the digestive gland of the marine clam, *Lyonsia hyalina.* After emergence, the cercariae penetrate and encyst in the muscles of the Atlantic silversides, *Menidia menidia.* The furcae and tail stem are discarded when the cercariae penetrate the fish. The garfish eats the infected silversides (Stunkard, 1976).

The life cycle of *R. septpapillata* was studied by Krull (1934c) and by Kniskern (1952). The adult is a parasite of pumpkinseed and smallmouth bass. Miracidia hatch and are probably swept into the incurrent siphon of the freshwater mussel, *Lampsilis siliquoidea,* in the gonads of which bucephaloid cercariae develop in branched sporocysts. Cercariae are known to encyst in the tissues of fingerling pumpkinseed, creek chub and largemouth bass.

2b. Sucker not surmounted by a flat hood. 3

3a. Sucker provided with fimbriae (tentacles); parasitic in marine and freshwater fishes (Fig. 341). .... Genus *Bucephalus* Baer, 1826

Key to species in Eckmann (1932).

Life cycle: *B. polymorphus* - Eggs in the feces of the host contain miracidia which hatch and enter the freshwater mussel, *Lampsilis iris* and *Anodonta* spp. in which bucephaloid cercariae (Fig. 23) develop in branched sporocysts. Cercariae emerge and encyst in the fins and muscles of fishes. The adult parasite develops in the intestine of bluegill, bass, perch, pike burbot and gudgeon (Woodhead, 1929, 1930).

3b. Sucker without fimbriae (Figs. 342, 343). .... Genus *Bucephalopsis* (Diesing, 1855) (= *Bucephaloides* Hopkins, 1954)

Key to species in Eckmann (1932).

Life cycle: *B. haimeana* - Bucephaloid cercariae develop in branched sporocysts in at least eight different marine lamellibranchs. Experimental infections were established in the goby, *Pomatoschistus microps* and in plaice, *Pleuronectes platessa.* The cercariae penetrate almost any part of the fish and encyst in the connective tissues and liver. The definitive host is the bass, *Morone labrax* in Europe. The metacercaria and the adult are linked only on the basis of comparative anatomy (Matthews, 1973).

4a. Rhynchus provided with several transverse rows of spines; parasite of marine fishes (Fig. 344). .... Genus *Dollfustrema* Eckmann, 1934

4b. Rhynchus without spines. 5

5a. Rhynchus elongate and provided with tentacles; parasite of marine fishes (Fig. 346). .... Genus *Alcicornis* MacCallum, 1917

5b. Rhynchus not elongate and without tentacles. 6

6a. Rhynchus well developed; testes round or oval; parastic in intestine of fishes (Fig. 345). .... Genus *Prosorhynchus* Odhner, 1905

Life cycle: *P. squamatus* - Bucephaloid cercariae develop in branched sporocysts in the marine mussel, *Mytilus edulis.* After emergence, they penetrate the marine fishes, *Cottus scorpius* and *Liparis liparis,* in which they change to metacercariae without encysting. Progenetic adults were found in the second intermediate host. Eight species of marine fishes are known to serve as natural definitive host for this species (Chubrik, 1952b).

6b. Rhynchus very small, vestigial; testes lobed; parasitic in gall bladder of freshwater fishes (Fig. 347). .... Genus *Paurorhynchus* Dickerman, 1954

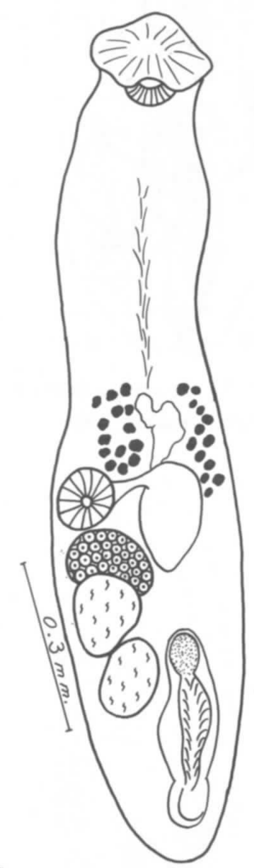


Fig. 340. *Rhipidocotyle barracudae.* (from Manter, 1940)

Fig. 341. *Bucephalus elegans*

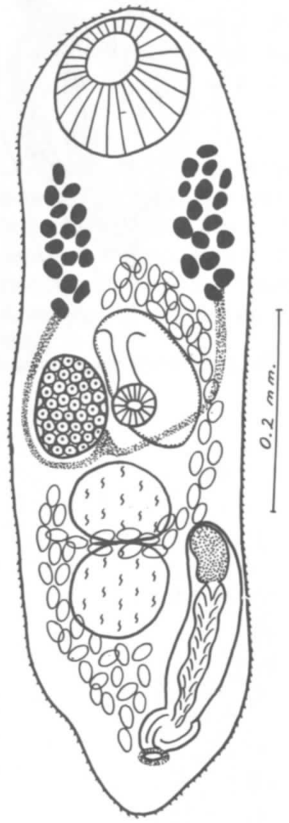


Fig. 342. *Bucephalopsis pusilla*

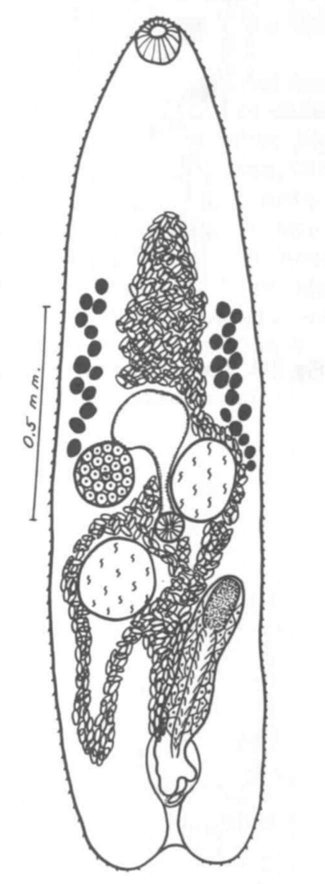


Fig. 343. *Bucephalopsis longovifera.*

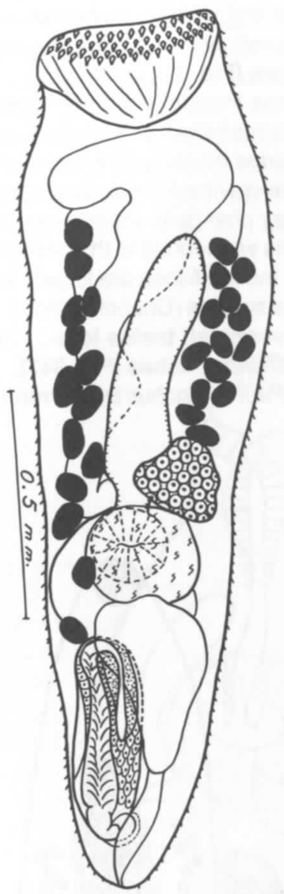


Fig. 344. *Dollfustrema macracanthus.* (from Hanson, 1950)

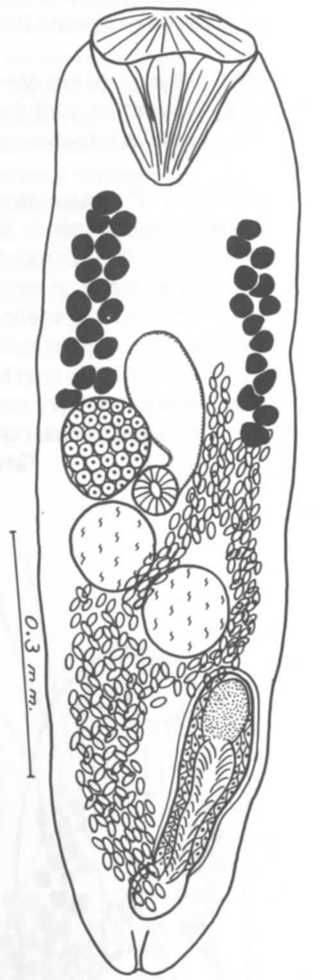


Fig. 345. *Prosorhynchus pacificus.*

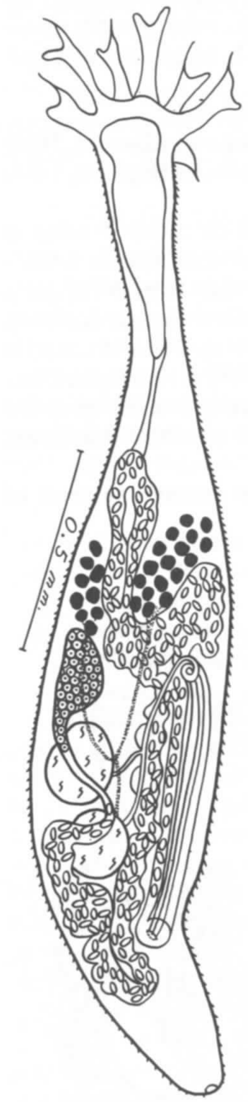


Fig. 346. *Alcicornis carangis.* (from MacCallum, 1917)

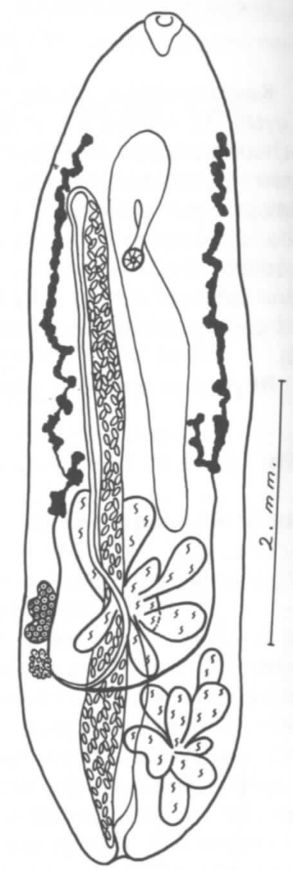


Fig. 347. *Paurorhynchus hiodontis.* (from Dickerman, 1954)

Order Azygiida Schell, 1982
Suborder Azygiata LaRue, 1957
Superfamily Azygioidea Skrjabin and Guschanskaja, 1956

Miracidia have one pair of flame cells, spines or bristles replace cilia. Cercariae furcocystocercous; develop in a redia in prosobranch or pulmonate snails; eaten directly by the definitive host. Life cycle involves two hosts. Progenetic forms occur in prosobranch snails.

Family Azygiidae Odhner, 1911

Body muscular, nonspinous, elongate oval or fusiform; suckers large; pharynx present; ceca long; testes tandem, oblique or opposite; ovary pre- or posttesticular; vitelline follicles usually lateral to ceca, confluent in some genera, usually restricted to hindbody; uterus preovarian; parasitic in stomach, intestine or coelom of fishes. Miracidia have epidermal cell formula of 5, 4 with spines or bristles replacing cilia.

Key to Genera

1a. Ovary posterior to testes; testes oblique (Fig. 348). ... . Genus *Leuceruthrus* Marshall and Gilbert, 1905

Life cycle: *L. micropteri* - Furcocystocercous cercariae (*Cercaria stephanocauda*) develop in rediae in the prosobranch snails, *Goniobasis laqueata* and *Pleurocera canaliculatum.* Cercariae were fed to *Lepomis macrochirus, Microptera salmoides* and *M. punctulatus* in which adult flukes develop in the stomach. Natural definitive hosts are *Microptera salmoides, M. dolomieui, Ambloplitis rupestris* and *Chaenobryttus gulosus* (see Patton, 1976).

1b. Ovary anterior to testes; testes opposite or oblique. 2

2a. Vitelline follicles and uterus extend anterior to ventral sucker; body oval (Fig. 349). .... Genus *Proterometra* Horsfall, 1933

Life cycle: *P. macrostoma* - Embryonated eggs are eaten by the prosobranch snails, *Pleurocera acuta* and *Goniobasis livescens.* Miracidia hatch in the snail and metamorphose to the sporocyst which produces a generation of rediae in which large furcocystocercous cercariae develop. After emergence, the cercariae are eaten by the definitive host which can be one of several species of freshwater fishes (Horsfall, 1933, 1934; Dickerman, 1934, 1945).

The life cycle of *P. dickermani* is similar to the above cycle except that it is sometimes progenetic in the host snail. When this occurs, miracidia develop and hatch in the snail, thus using a single host to complete the cycle. The life cycle cannot only be completed in a single host but can be repeated in the same snail. At least four species of *Proterometra* are known to be progenetic in prosobranch snails (Anderson and Anderson, 1963, 1967). An analysis of the degrees of variation of progenesis among different species of *Proterometra* is presented by Anderson and Anderson (1969). For life cycles of other species see Anderson and Anderson (1967).

2b. Vitelline follicles and uterus confined to hindbody. 3

3a. Vitelline follicles confluent posterior to testes; arms of excretory vesicle extend forward and unite dorsal to oral sucker; parasitic in stomach and coelom of elasmobranchs and holocephalans (Fig. 351). .... Genus *Otodistomum* Stafford, 1904

Key to species in Dollfus (1937).

3b. Vitelline follicles restricted to lateral areas, not confluent; arms of excretory vesicle long but not united anteriorly; parasitic in stomach of teleost fishes (Fig. 350). .... Genus *Azygia* Looss, 1899

Life cycle: *A. longa* - Embryonated eggs in feces of the host are eaten by the prosobranch snail, *Amnicola limosa* in which furcocystocercous cercariae develop in rediae. After emergence, the cercariae are eaten by the definitive host. This species has been reported from many species of freshwater fishes. *A. sebago* is regarded as a synonym of *A. longa* (see Stunkard, 1956; Sillman, 1962).

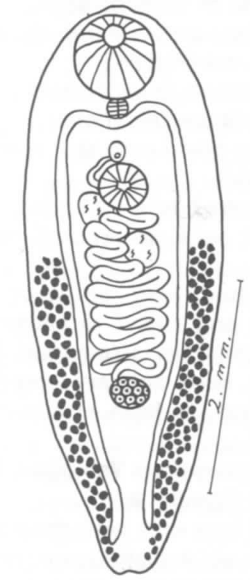


Fig. 348. *Leuceruthrus micropteri.*

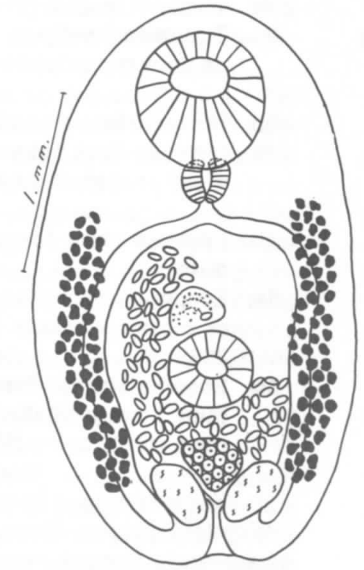


Fig. 349. *Proterometra macrostoma.*

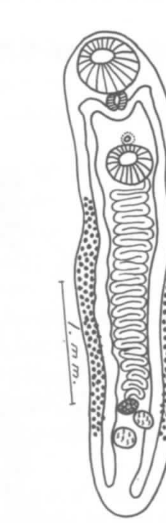


Fig. 350. *Azygia angusticauda.*

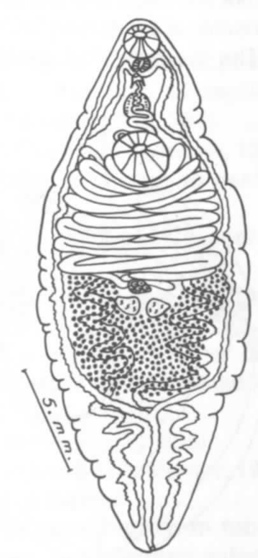


Fig. 351. *Otodistomum hydrolagi.*

The life cycle of *A. lucii* was studied by Odening (1976) who found several genera and species of pulmonate snails can serve as intermediate host. The cercaria is identical to *Cercaria splendens,* having flame cells in body, tail stem and furcae. Experimental infections with the adult were established in *Esox lucius* and *Salmo gairdneri,* the adults developing in about 63 days. The cercariae developed in a larval form that was not a typical redia since it contained a "pharynx-like structure" but no intestine. They were designated as mother and daughter parthenitae, the former developing from the miracidium, the latter producing the furcocystocercous cercariae.

Ubgade and Agarwall (1980) investigated the life cycle of *A. papillata* in India. Embryonated eggs hatched after being eaten by the prosobranch, *Vivipara bengalensis.* The miracidia metamorphosed to the sporocyst stage which was followed by two generations of rediae. The mother rediae gave rise to daughter rediae at first but later produced cercariae. The daughter rediae produced only cercarie. The furcocystocercous cercariae were fed to fish, *Channa marulius* and mature flukes recovered after 32 days.

Family Bivesiculidae Yamaguti, 1939

Body small (1 mm or less), fusiform, spinous; suckers absent; pharynx present; intestinal ceca extend to middle of body; one testis; cirrus sac large, in anterior half of body, the base directed toward anterior end of body; internal and external seminal vesicles present; ovary almost opposite to testis, near midbody region; vitelline follicles around ceca; two excretory vesicles, each extending forward to level of esophagus; parasitic in the intestine and pyloric ceca of marine fishes.

The genus *Bivesicula* Yamaguti, 1934 (Fig. 352) has been reported in North America.
Key to species in Cable and Nahhas (1962b).
Life cycle: *B. hepsetiae* - Two weeks are required for development of the miracidium following oviposition. It is not known whether the miracidia hatch before or after entrance into the snail. Furcocystocercous cercariae develop in a fork-tailed redia in several species of marine snails of the genus *Cerithium.* Cercariae are large and are eaten by the hardhead silverside, *Atherinomorus stipes* (see LeZotte, 1954).

The life cycle of *B. caribbensis* is similar to that of the above

Fig. 352a. *Bivesicula caribbensis.*

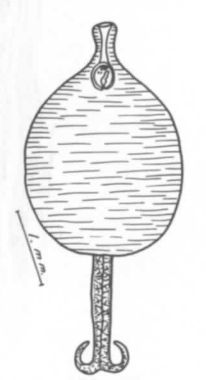


Fig. 352b. Cercaria (from Cable and Nahhas, 1962)

species. The host snail is *Cerithium literatum.* The cercariae are eaten by the big-eyed squirrel fish, *Myripristis jacobus* (see Cable and Nahhas, 1962b).

The development of furcocystocercous cercariae in a redia and the absence of a second intermediate host in the life cycle indicate relationship to the family Azygiidae.

Suborder Hemiurata Skrjabin and Guschanskaja, 1954

Miracidia spinous, nonciliated. Cercariae cystophorous, develop in a redia in gastropod molluscs, eaten by a crustacean in which the metacercaria develops. Adults either hermaphroditic or gonochoristic; parasitic in the digestive tract of fishes, amphibians and reptiles (snakes) or in the branchial cavity, coelom or swim bladder of fishes. Life cycle involves three hosts.

Superfamily Hemiuroidea Faust, 1929
Family Hemiuridae Lühe, 1901

Body oval, elongate or fusiform, flat or cylindrical; telescoping ecsoma present in some genera; cuticle nonspinous but marginal serrations, plications or flat scales may be present; ventral sucker usually larger than oral sucker, variable in position; pharynx present; ceca long, usually extend into ecsoma; testes tandem, oblique or opposite, in hindbody; cirrus sac absent; sinus sac present, encloses hermaphroditic duct; genital cone and genital atrium may be present; genital pore ventral to esophagus or pharynx; ovary usually posttesticular; vitellaria compact or tubular, lobed or unlobed, occasionally in the form of a rosette; uterus extends posterior to gonads and vitellaria; eggs operculate, embryonated; main ducts of excretory system usually united dorsal to pharynx; parasitic in the stomach of fishes, reptiles (snakes) and amphibians (amphiuma); the swim bladder of fishes; the pharynx and Eustachian tubes of amphibians. A few species are known to be progenetic.

Key to Genera

1a. **Telescoping ecsoma present (Fig. 353).** 2
1b. **Telescoping ecsoma absent.** 14
2a. **Vitellaria tubular (Fig. 353).** 3
2b. **Vitellaria in form of two round or lobed masses.** 6
3a. **Transverse cuticular plications on body surface; uterus does not extend into ecsoma (Fig. 353).** .... **Genus** *Dinurus* **Looss, 1907**
3b. **Body surface smooth, no cuticular plications.** 4
4a. **Prostate duct not very long, gland cells restricted to distal portion of duct (Fig. 354).** .... **Genus** *Ectenurus* **Looss, 1907**
4b. **Prostate duct long, gland cells present all along duct.** 5
5a. **Ecsoma longer than soma; body very elongate (2 cm or more); vitellaria tubular and lateral to ceca (Fig. 356).** .... **Genus** *Stomachicola* **Yamaguti, 1934**
5b. **Ecsoma shorter than soma; body not very long (less than 1 cm.); vitellaria tubular, in form of a rosette, posterior to ovary (Fig. 355).** .... **Genus** *Tubulovesicula* **Yamaguti, 1934**
Key to species in Sogandares-Bernal (1959).

Life cycle: *T. pinguis* - Embryonated eggs were fed to the marine prosobranch, *Nassarius trivitattus* in which cystophorous cercariae develop in daughter rediae. Emerging cercariae are eaten by the marine copepod, *Acarta tonsa* in which metacercariae then develop. The adult develops in silversides, *Menidia menidia* and numerous other marine fishes (Stunkard, 1980b).

6a. **Body surface smooth, without transverse cuticular plications or rows of scales.** 7
6b. **Body surface contains transverse cuticular plications or rows of scales.** 10
7a. **Seminal vesicle bilobed, a narrow duct connecting the lobes (Fig. 357).** .... **Genus** *Dissosaccus* **Manter, 1947**
7b. **Seminal vesicle oval or clubshaped, not bilobed.** ... 8
8a. **Seminal vesicle thick-walled; vitellaria compact, oval or round; genital pore ventral to oral sucker; oral sucker has papillae (Fig. 358).** .... **Genus** *Lethadena* **Manter, 1947**
8b. **Seminal vesicle thin-walled; vitellaria compact, lobed; genital pore ventral to pharynx or cecal bifurcation; oral sucker without papillae.** 9
9a. **Preacetabular pit present (Fig. 359).** .... **Genus** *Lecithochirium* **Lühe, 1901**
9b. **Preacetabular pit absent (Fig. 360).** .... **Genus** *Sterrhurus* **Looss, 1907**
10a. **Body contains transverse rows of scales.** 11
10b. **Body surface has transverse cuticular plications, margins serrated.** 12
11a. **Seminal vesicle bipartite, thin-walled; vitellaria lobed; body scales in close transverse rows; prostate duct short (Fig. 361).** .... **Genus** *Dinosoma* **Manter, 1934**
Key to species in Skrjabin (1964).
11b. **Seminal vesicle oval, thick-walled; vitellaria oval; body scales sparse, spine-like; prostate duct long (Fig. 362).** .... **Genus** *Anahemiurus* **Manter, 1947**
12a. **Preacetabular pit present; vitellaria in form of two lobed masses near center of soma; seminal vesicle dorsal to ventral sucker (Fig. 363).** .... **Genus** *Brachyphallus* **Odhner, 1905**
12b. **Preacetabular pit absent; vitellaria in form of two oval or round masses in posterior third of soma; seminal vesicle some distance posterior to ventral sucker.** 13
13a. **Seminal vesicle bipartite, anterior part thick-walled (Fig. 364).** .... **Genus** *Hemiurus* **Rudolphi, 1809**
13b. **Seminal vesicle unipartite, oval, thick-walled throughout (Fig. 365).** .... **Genus** *Parahemiurus* **Vaz and Pereira, 1930**

Life cycle: *P. bennettae* - The estuarine pulmonate snail, *Salinator fragilis* is the host in Australia. Sporocysts develop and in turn produce elongate rediae. The latter eventually produce rudimentary cystophorous cercariae, progenetic adults and a few daughter rediae. The caudal chamber or tail of the cercaria degenerates, the body is never withdrawn into the chamber but instead goes on to become an adult, remaining in the redia. This is an abbreviated cycle, all of it occurring within the snail without a metacercarial stage. The fate of the daughter redia is unknown (Jamieson, 1966).

14a. **Eggs have a unipolar filament.** 15
14b. **Eggs without unipolar filament.** 17
15a. **Vitellaria anterior to testes; uterus spirally coiled; testes close to posterior end of body; parasitic in fish (Fig. 366).** .... **Genus** *Hemipera* **Nicoll, 1912**
15b. **Vitellaria posterior to testes which are some distance from posterior end of body.** 16
16a. **Vitellaria in form of two clusters of follicles at posterior end of body; parasitic in pharynx and Eustachian tubes of amphibians (Fig. 368).** .... **Genus** *Halipegus* **Looss, 1899**

Life cycle: *H. eccentricus* - Embryonated eggs from the feces of frogs are eaten by pulmonate snails of the genera *Physa* and *Helisoma.* Spinous, nonciliated miracidia hatch in the intestine of the snail, penetrate the wall and then metamorphose to sporocysts which in turn produce rediae. The latter produce cystophorous cercariae which are eaten by copepods of the genera *Cyclops* and *Mesocyclops.* Metacercariae develop in the hemocoel of the copepod without encysting. Infected copepods are eaten by tadpoles in the stomach of which the parasites undergo some development until the tadpole metamorphoses, after which they migrate to the pharynx and Eustachian tubes where they mature. About three months are required for development to sexual maturity (Thomas, 1939).

Macy *et al* (1960) investigated the life cycle of *H. occidualis,* a parasite in the mouth, esophagus and stomach of *Rana aurora, Taricha granulosa* and *Dicamptodon ensatus* in Oregon. Embryonated eggs are eaten by the pulmonate snail, *Helisoma subcrenatum* in which the miracidium hatches and changes to a sporocyst which in turn produces a generation of rediae. Cystophorous cercariae develop in the rediae, emerge from the snail and are then eaten by ostracods in which metacercariae develop without encysting. Natural infections with metacercariae were also found in dragonfly nymphs. Experimental infections were established in *Taricha granulosa* which were fed infected ostracods. Note: This might be a four-host cycle like the one which follows.

The life cycle of *H. ovocaudatus* was reported by Combes and Kechemir (1978) and by Kechemir (1978) and found to be an obligatory four-host cycle. The host mollusc is *Planorbis planorbis* which eats the embryonated eggs. Spinous miracidia hatch in the snail intestine, change to sporocysts which then produce rediae which in turn produce cystophorous cercariae. The latter are eaten by copepods and ostracods in which a so called "mesocercaria" develops. This stage has gills at the caudal end of the body. When infected crustaceans are eaten by dragonfly nymphs the parasite changes to a metacercaria. The adult parasite develops in the frog, *Rana ridibunda* which feeds on dragonflies. All hosts are said to be needed for completion of the cycle.

16b. **Vitellaria in the form of two compact masses at posterior end of body; parasitic in stomach of reptiles (snakes) and amphibians (amphiuma) (Fig. 367).** .... **Genus** *Vitellotrema* **Guberlet, 1928**
17a. **Seminal vesicle long, extending posterior to ventral sucker.** 18
17b. **Seminal vesicle short, entirely anterior or dorsal to ventral sucker.** 23
18a. **Vitellaria in the form of a cluster (rosette) of digitiform or clubshaped tubes.** 19
18b. **Vitellaria in the form of two compact round or oval masses, or a cluster of six to eight lobes resembling follicles.** 21
19a. **Ovary and vitellaria anterior to testes (Fig. 369).** .... **Genus** *Macradenina* **Manter, 1947**
19b. **Ovary and vitellaria posterior to testes.** 20
20a. **Vitellaria in the form of 12 or more digitiform tubes; body elongate and cylindrical; prostate duct extends far posterior to ventral sucker; ovary round; testes tandem (Fig. 370).** ..... **Genus** *Macradena* **Linton, 1910**
20b. **Vitellaria consisting of a cluster of seven or eight clubshaped tubes, close to posterior end of body;**

body fusiform; prostate duct short, anterior to ventral sucker; ovary lobed; testes opposite (Fig. 372). .... Genus *Lecithaster* Lühe, 1901
Key to species in Srivastava (1966).

Life cycle: *L. confusus* - Cystophorous cercariae develop in rediae in the marine snail, *Odostoma trifida*. They are eaten by the marine copepod, *Acarta tonsa* in which metacercariae develop without encysting. The adult parasite develops in stickleback, *Apeltes quadracus* and in the killifish, *Fundulus heteroclitis* and *F. majalis* (see Hunninen and Cable, 1943).

21a. **Vitellaria in the form of six or eight lobes; prostate duct long, surrounded by prostate gland cells; vitellaria, ovary and testes all close to posterior end of body (Fig. 373). .... Genus *Dichadena* Linton, 1910**

21b. **Vitellaria in the form of two round or oval masses, posterior to testes. 22**

22a. **Transverse cuticular plications on body surface; vitellaria in center of body; prostatic vesicle thick-walled and glandular; seminal vesicle free in parenchyma (Fig. 371). ...... Genus *Myosaccium* Montgomery, 1957**

22b. **Body without cuticular plications; vitellaria and ovary near posterior end of body; prostatic vesicle absent; prostatic duct long, surrounded by gland cells for most of its length; seminal vesicle in a sac (Fig. 377). .... Genus *Opisthadena* Linton, 1910**

23a. **Ventral sucker posterior to middle of body; uterus fills much of forebody; gonads confined to very short hindbody. 24**

23b. **Ventral sucker anterior to middle of body or at middle of body; uterus in hindbody. 25**

24a. **Prostate gland well developed, globose (Fig. 374). .... Genus *Gonocercella* Manter, 1940**

24b. **Prostate gland small or apparently absent (Fig. 376). .... Genus *Gonocerca* Manter, 1925**

25a. **Testes opposite. 26**

25b. **Testes tandem or oblique. 30**

26a. **Vitellaria a cluster of clubshaped tubes forming a rosette or two clusters of follicles; prostate gland well developed, in forebody. 27**

26b. **Vitellaria composed of two compact oval or round masses. 28**

27a. **Vitellaria a single rosette of clubshaped tubes, posterior to ovary; most of uterus anterior to vitellaria (Fig. 375). ....Genus *Lecithophyllum* Odhner, 1905**

27b. **Vitellaria in the form of seven follicles arranged in two groups; ovary posterior to right or left testis; uterus mainly posterior to vitellaria (Fig. 378). .... Genus *Aponurus* Looss, 1907**

28a. **Ventral sucker close to oral sucker; vitellaria in form of two multilobed masses, anterior to lobed ovary; body fusiform; parasitic in swim bladder of marine fishes (Fig. 379). .... Genus *Dictysarca* Linton, 1910**

28b. **Ventral sucker in middle of body; vitellaria posterior to or opposite to ovary; ovary oval; body oval; parasitic in stomach of marine fishes. 29**

29a. **Hermaphroditic duct not enclosed in a sac; prostate gland not well developed (Fig. 380). ....** Genus *Leurodera* **Linton, 1910**

29b. **Hermaphroditic duct enclosed in a conical sinus sac; prostate gland well developed (Fig. 381). .... Genus *Derogenes* Lühe, 1900**

Note: *D. varicus* is known to be progenetic in the intestine of the parasitic copepod, *Lernaeocerca lusci* on the codfish *Gadus luscus*. It is also progenetic in the hermit crab, *Pagurus pubescens* and in several species of arrow worms, *Sagitta* spp. The hermit crabs and arrow worms probably get the parasite by eating infected free-living copepods.

30a. **Vitellaria in the form of a single lobed mass posterior to ovary; testes in anterior part of hindbody, separated from ovary by uterus; body elongate (Fig. 382). . ... Genus *Hysterolecitha* Linton, 1910**

30b. **Vitellaria in form of two compact masses; testes close to ovary. 31**

31a. **Hermaphroditic duct and sinus sac absent; pseudocirrus sac present, encloses ejaculatory duct; prostatic vesicle well developed, surrounded by prostate cells (Fig. 383). .... Genus *Intuscirrus* Acena, 1947**

31b. **Pseudocirrus sac absent; hermaphroditic duct present, enclosed in a sinus sac (hermaphroditic sac); prostatic vesicle absent; prostate gland small, posterior to sinus sac. 32**

32a. **Uterus extends posterior to vitellaria; parasitic in stomach of marine fishes (Fig. 385). .... Genus *Genolinea* Manter, 1925**

32b. **Uterus entirely anterior to vitellaria; parasitic in a stomach of freshwater fishes and amphibians (Fig. 384). .... Genus *Deropegus* McCauley and Pratt, 1961.**

Fig. 353. *Dinurus scombri.*

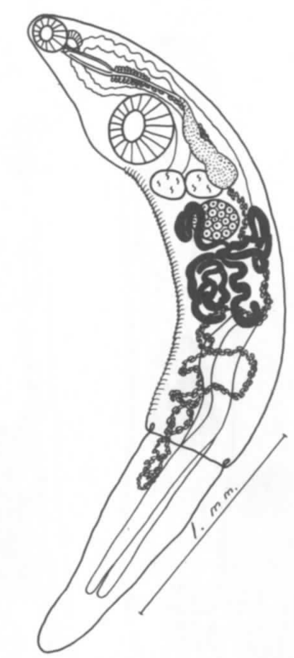


Fig. 354. *Ectenurus americanus.*

Fig. 355a. *Tubulovesicula lindbergi.*

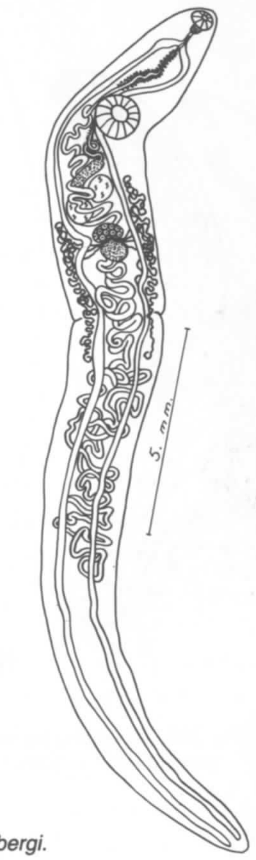


Fig. 356. *Stomachiocola magnus.*

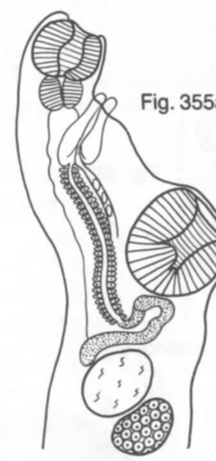


Fig. 355b. Anterior end

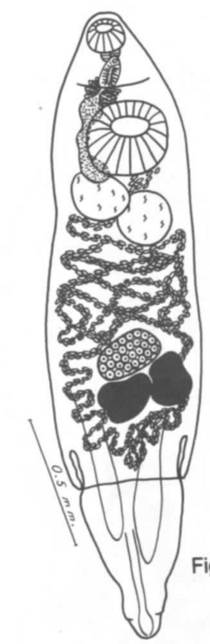


Fig. 357. *Dissosaccus laevis.*

Fig. 358a. *Lethadena profunda.* (from Manter, 1934)

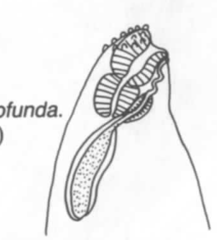


Fig. 358b. Anterior end, lateral view.

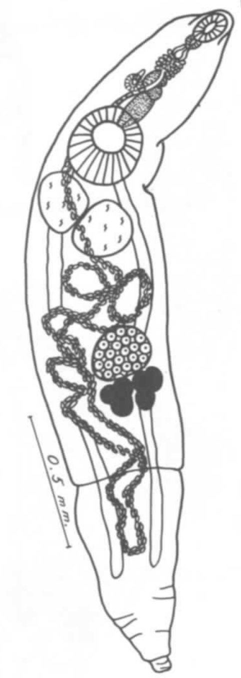


Fig. 359. *Lecithochirium microstomum.*

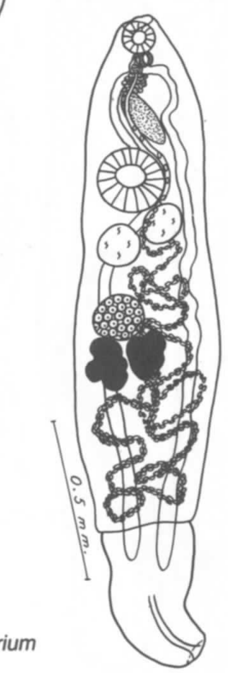


Fig. 360. *Sterrhurus musculus.*

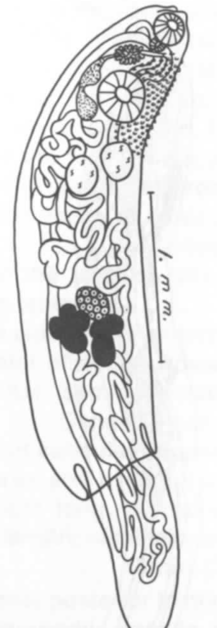


Fig. 361. *Dinosoma rubrum.* (from Manter, 1934)

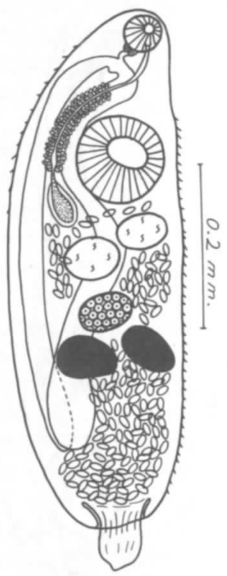
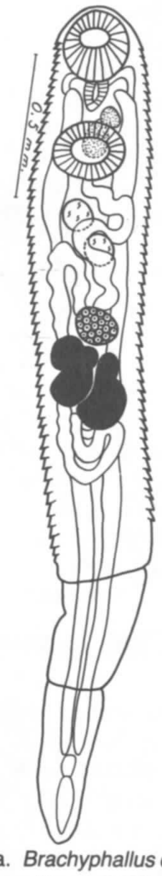


Fig. 362. *Anahemiurus microcercus.* (from Manter, 1947)



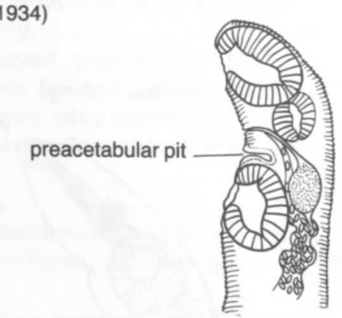


Fig. 363a. *Brachyphallus crenatus.* (from Lloyd, 1938)

Fig. 363b. Sagittal section, anterior end.

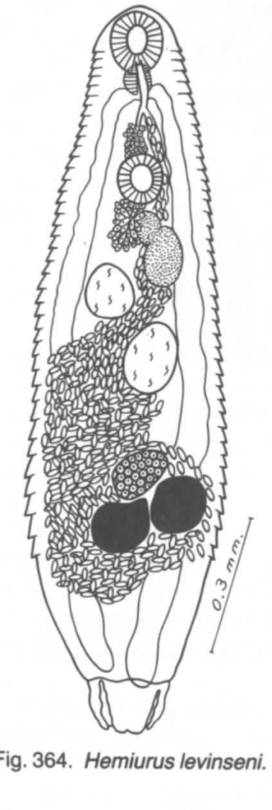


Fig. 364. *Hemiurus levinseni.*

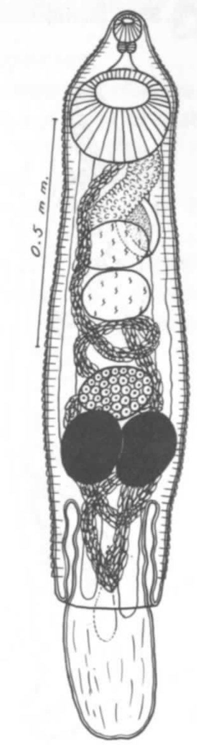


Fig. 365. *Parahemiurus merus.*

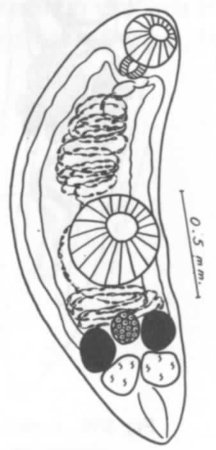


Fig. 366. *Hemipera nicolli.*

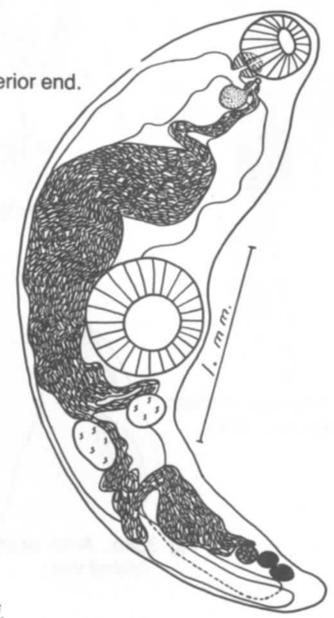


Fig. 367. *Vitellotrema fusipora.*

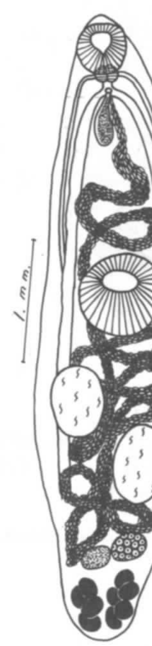


Fig. 368. *Halipegus occidualis.*

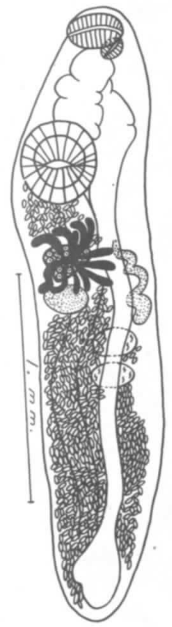


Fig. 369. *Macradenina acanthuri.* (from Manter, 1947)

Fig. 370. *Macradena perfecta.*

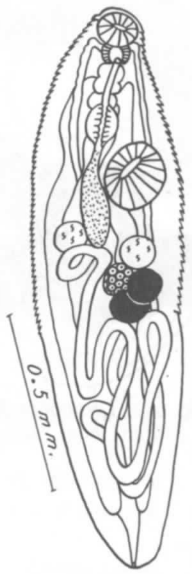


Fig. 371. *Myosaccium ecaude.* (from Montgomery, 1957)

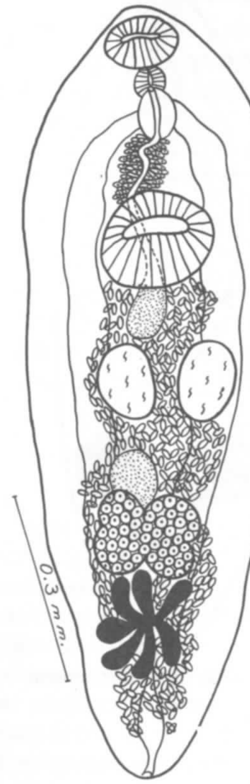


Fig. 372. *Lecithaster salmonis.*

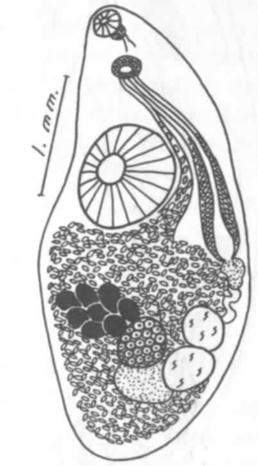


Fig. 373. *Dichadena acuta.* (from Linton, 1910)

Fig. 374. *Gonocercella trachinoti.*

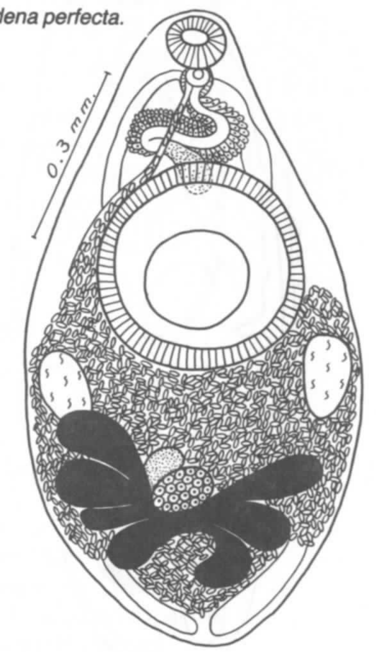


Fig. 375. *Lecithophyllum pyriforme.* (from Linton, 1910)

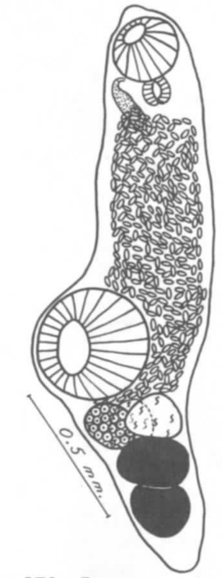


Fig. 376. *Gonocerca phycidis.*

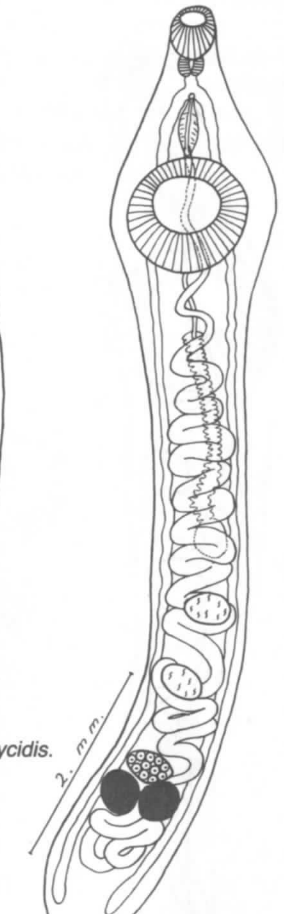


Fig. 377. *Opisthadena dimidia.*

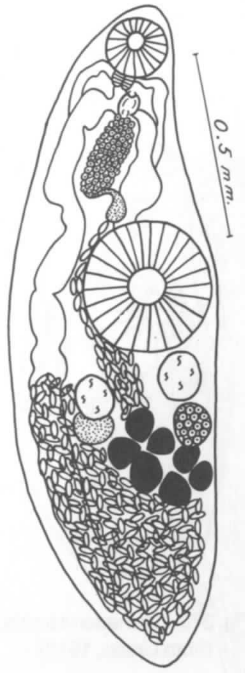


Fig. 378. *Aponurus intermedius.* (from Manter, 1934)

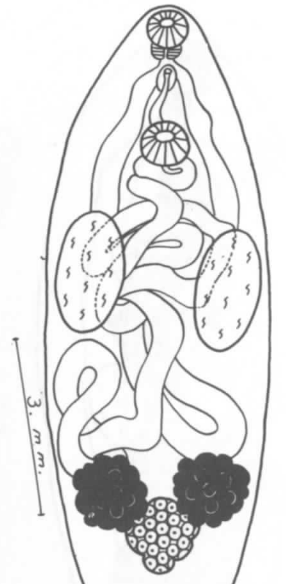


Fig. 379. *Dictysarca virens.*

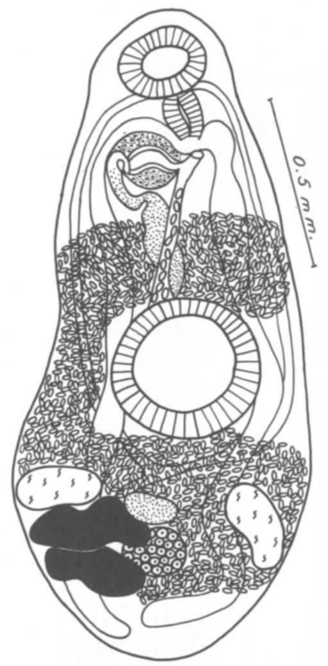


Fig. 380. *Leurodera decora.* (from Linton, 1910)

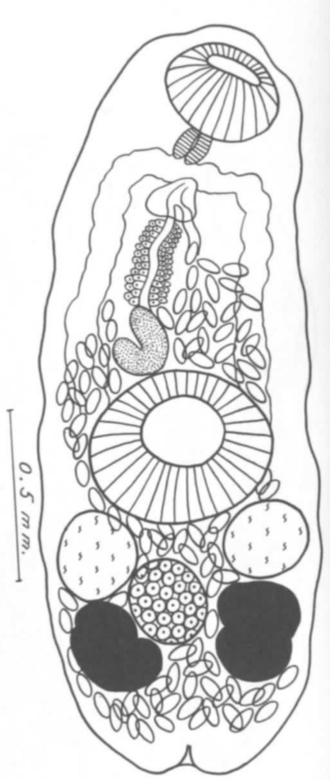


Fig. 381. *Derogenes crassus.*

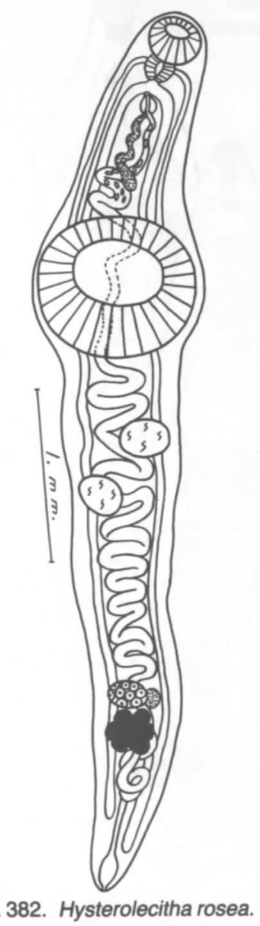


Fig. 382. *Hysterolecitha rosea.*

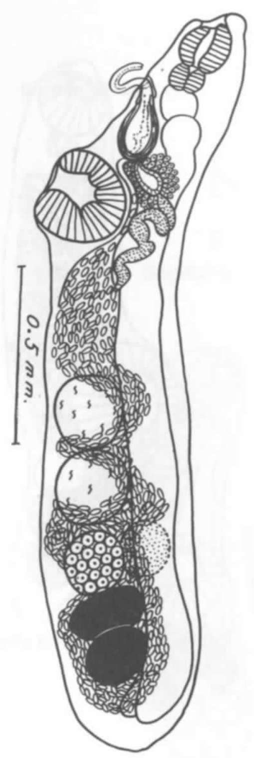


Fig. 383. *Intuscirrus aspicotti.*

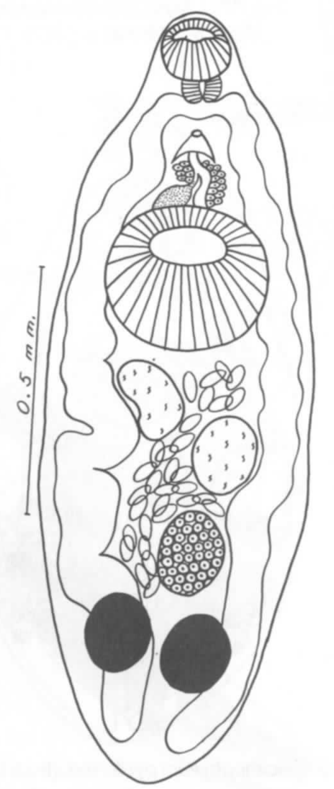


Fig. 384. *Deropegus aspina.*

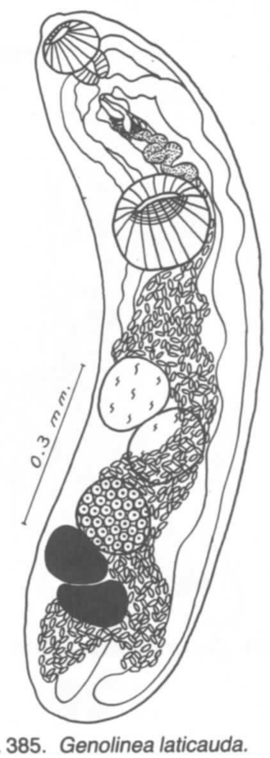


Fig. 385. *Genolinea laticauda.*

Family Bathycotylidae Dollfus, 1932

Body long (up to 18 mm), cylindrical, with preoral lobe; ventral sucker pedunculate, encircled by muscular body fold; pharynx small; ceca long; testes tandem, in middle of hindbody; cirrus sac absent; seminal vesicle tubular, free in parenchyma; hermaphroditic duct absent; genital pore ventral to oral sucker; ovary between testes; vitellaria tubular and branched, restricted to hindbody; uterus extends from pharynx to posterior end of body; eggs operculate, embryonated; main ducts of excretory system united dorsal to pharynx; parasitic in the stomach of marine fishes.

The family contains only the genus *Bathycotyle* Darr, 1902. *B. coryphaenae* is a stomach parasite of mackerel in North America (Fig. 386).

Family Ptychogonimidae Dollfus, 1937

Body muscular, nonspinous with transverse wrinkles; suckers large, subequal, the ventral sucker near middle of body; pharynx present; esophagus absent; ceca long, inflated and fused with excretory vesicle to form uroproct; testes tandem or oblique, near posterior end of body; cirrus sac absent; seminal vesicle free in parenchyma; muscular genital atrium and genital pore anterior to ventral sucker; ovary prestesticular; vitelline follicles along ceca in hindbody; uterus confined to hindbody; eggs operculate; main ducts of excretory system form ring around oral sucker; excretory vesicle small; parasitic in stomach of elasmobranchs and freshwater fishes (perch).

The family contains only the genus *Ptychogonimus* Lühe, 1900 (Fig. 387). *P. fontanus* has been reported as a parasite of yellow perch in Canada.

Life cycle: *P. megastomus* - Nonciliated miracidia with tufts of rigid bristles at the anterior end invade the mantle cavity of the tooth shell, *Dentalium alternans.* Microcercous cercariae *(C. dentali)* develop in elongate sporocysts which escape from the host mollusc and are believed to be eaten by numerous species of decapod crustaceans in which the metacercaria then develops without encysting. The infected crustaceans are probably eaten by sharks and rays the natural definitive hosts (Palombi, 1941, 1942).

Family Sclerodistomidae (Odhner, 1927) Yamaguti, 1958

Body muscular, wrinkled, nonspinous; ventral sucker larger than oral sucker, in anterior third of body; ceca long; testes small, opposite, immediately posterior to ventral sucker; cirrus sac absent; seminal vesicle convoluted, free in parenchyma; genital cone protrudes into genital atrium and contains hermaphroditic duct; genital pore close to cecal bifurcation; ovary posttesticular, in middle of hindbody; vitellaria tubular and branched, form a network lateral to ceca; uterus intercecal, restricted to hindbody; parasitic in stomach of marine fishes.

The family contains only the genus *Sclerodistomum* Looss, 1912 which is represented in North America by *S. sphoeroidis* (Fig. 388), a parasite of porcupine fish and puffers.

Family Lampritrematidae Skrjabin and Guschanskaja, 1955

Body elongate (12-50 mm), cylindrical, cuticle contains papillae; ventral sucker in anterior third of body, slightly pedunculate, larger than oral sucker; pharynx present; intestinal ceca long with dorsal diverticula; testes tandem, in middle of hindbody; cirrus and cirrus sac present; seminal vesicle long, free in parenchyma; hermaphroditic duct absent; genital pore ventral to pharynx; ovary posttesticular; vitellaria tubular, branched, posterior to ovary; uterus extends posterior to vitellaria and into forebody; metraterm opens into genital atrium; eggs operculate, embryonated; adults parasitic in stomach of marine fishes.

The family contains only the genus *Lampritrema* Yamaguti, 1940 (Fig. 389), which is represented in North America by *L. nipponicum*, a parasite of bream and salmon.

Family Syncoeliidae Dollfus, 1923

Body elongate, cylindrical, arched ventrally; ventral sucker at end of long peduncle; intestinal ceca long, fused at a posterior end to form cyclocoel; 16 to 20 testes in hindbody; cirrus sac absent; seminal vesicle long, free in parenchyma; ovary single or follicular, posttesticular; hermaphroditic duct present; genital pore ventral to oral sucker; vitelline follicles few (5 to 7), in cluster posterior to ovary; uterus long, many folds all along ceca; main excretory ducts extend forward to level of pharynx where they fuse; parasitic in branchial cavity of marine fishes.

Only the genus *Syncoelium* Looss, 1899 occurs in North America (Fig. 390). *S. filiferum* is a parasite of humpback salmon, *Onchorhynchus gorbuscha* and blueback salmon, *O. nerka* in the Pacific Northwest. Metacercariae have been found in and on the surface of marine copepods.

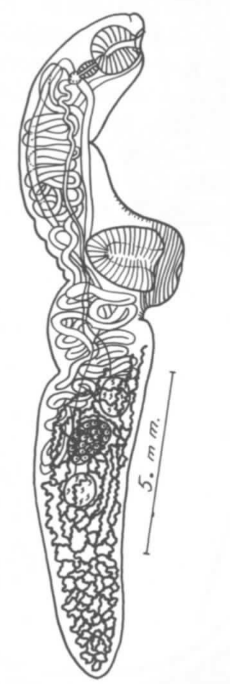


Fig. 386. *Bathycotyle coryphaenae.* (from Yamaguti, 1938)

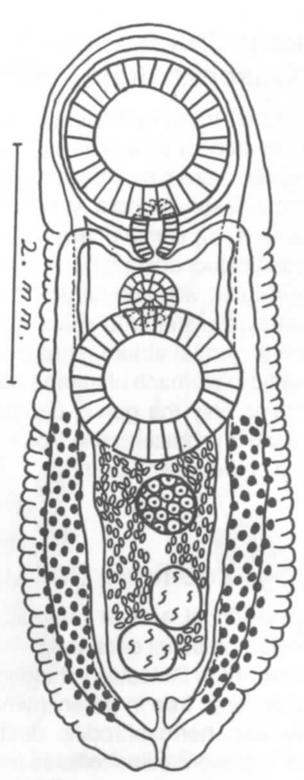


Fig. 387. *Ptychogonimus* sp.

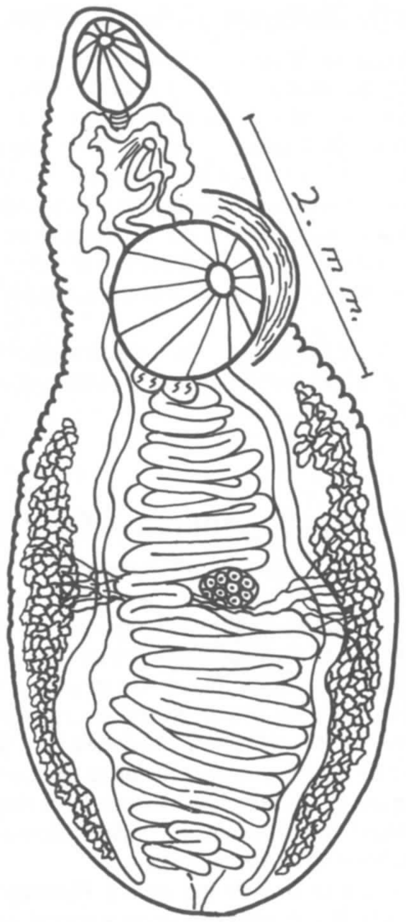


Fig. 388. *Sclerodistomum sphaeroidis*. (from Manter, 1947)

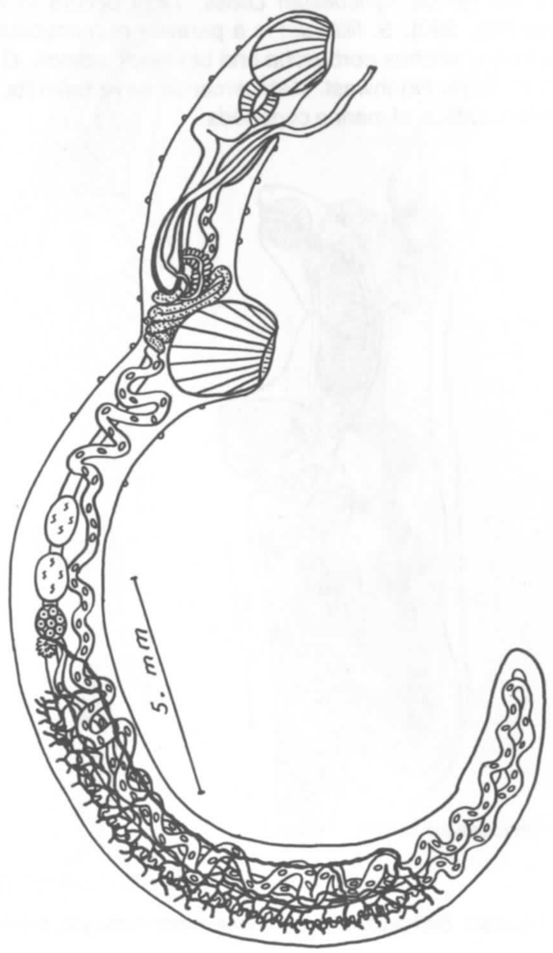


Fig. 389. *Lampritrema nipponicum*. (from Yamaguti, 1940)

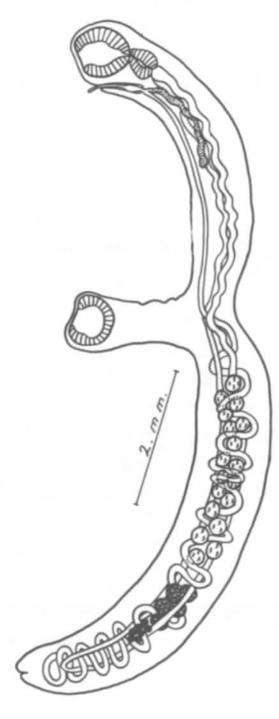


Fig. 390. *Syncoelium filiferum*.

Superfamily Accacoelioidea Dollfus, 1960
Family Accacoeliidae Looss, 1912

Body elongate, cylindrical, nonspinous; ventral sucker pedunculate, accessory suckers sometimes present; intestinal ceca with a pair of anterior branches, ceca fused posteriorly with excretory vesicle; testes tandem, in anterior half of body; ovary posttesticular; cirrus sac absent; seminal vesicle long, convoluted, free in parenchyma; hermaphroditic duct sometimes present; genital pore median, anterior to peduncle; vitelline glands filamentous; uterus with long descending and ascending limbs, extending to posterior end of body; parasitic in intestine of ocean sunfish, *Mola mola*.

Key to Genera

1a. **Several accessory suckers on anterio-dorsal surface of body and on peduncle of ventral sucker (Fig. 391).** .... **Genus *Odhnerium* Yamaguti, 1934**

1b. **Accessory suckers absent.** **2**

2a. **Vitelline glands not extending anterior to peduncle; anterior cecal diverticula unbranched (Fig. 392).** .... **Genus *Accacladium* Odhner, 1928**

2b. **Vitelline glands extend anterior to peduncle; anterior cecal diverticula branched (Fig. 393).** .... **Genus *Accacladocoelium* Odhner, 1928**

Life cycle: Unencysted metacercariae have been found in arrow worms (*Sagitta* spp.) and in the medusae of coelenterates.

Superfamily Didymozooidea (Monticelli, 1888) Yamaguti, 1971
Family Didymozoidae Poche, 1907

Body variable in size and shape, may be very long (several meters) and cylindrical or ribbonlike, or short and subdivided into narrow anterior and spherical or hemispherical posterior part, body may also be multilobed or branched; adults either hermaphroditic or gonochoristic with sexual dimorphism and are usually encysted in pairs; oral sucker vestigial or well developed; ventral sucker, pharynx and ceca present or absent; testes tubular, long or short, paired or unpaired; cirrus and cirrus sac absent; genital pore usually close to oral sucker; ovary tubular, branched or unbranched, posttesticular; vitellaria tubular, branched or unbranched, posterior to ovary and testes; uterus has many folds, extending throughout body; eggs operculate, contain a spinous nonciliated miracidium; excretory vesicle tubular; adults parasitic in muscles, skin, lining of pharynx, coelom, ovary or other visceral organs of freshwater and marine fishes.

Cable and Nahhas (1962a) reported larval didymozoids in goose barnacles (*Lepas* sp.). Unencysted metacercariae have been found in the coelom of marine copepods, coelenterates, arrow worms and fishes.

Nikolaeva (1965) suggests a possible life cycle involving marine snails as first intermediate host, barnacles as second intermediate, small fishes as third intermediate and large predatory fish as definitive host. The development of a spiny, nonciliated miracidium and the use of a crustacean second intermediate host indicate relationship to the hemiuroid trematodes.

Key to Genera

1a. **Body subdivided into narrow anterior and thick posterior portions; ventral sucker absent; hermaphroditic; parasitic in the mouth, pharynx, esophagus, stomach or coelom of marine fishes (Fig. 394).** .... **Genus *Didymocystis* Ariola, 1902**

1b. **Body very long, filiform or ribbonlike throughout.** .. **2**

2a. **Sexes separate (gonochoristic), sexual dimorphism not pronounced; testes parallel, extending through most of body; parasitic in mouth and pharynx of marine fishes (Fig. 395).** .... **Genus *Gonapodasmius* Ishii, 1935**

2b. **Hermaphroditic.** **3**

3a. **Body ribbonlike, flat; one testis; pharynx absent; parasitic in lining of pharynx of marine fishes (no illustration).** .... **Genus *Atalostrophion* MacCallum, 1915**

3b. **Body filiform, cylindrical; two tubular testes; pharynx present; ventral sucker present; parasitic in body wall or in visceral organs of fishes.** **4**

4a. **Parasitic in ovary of freshwater fishes; adults up to two and one-half meters long (Fig. 397).** .... **Genus *Ovarionematobothrium* Yamaguti, 1971**

4b. **Parasite embedded in body wall of marine sunfish (*Mola mola*); adults up to 12 meters long (Fig. 396).** .... **Genus *Nematobothrioides* Noble, 1974**

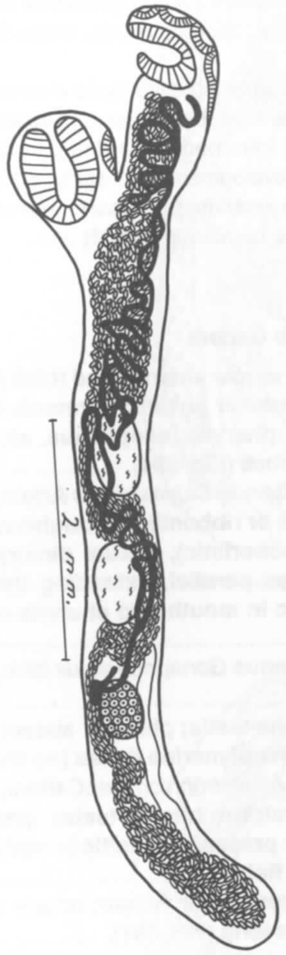


Fig. 391. *Odhnerium calyptrocotyle.* (from Lloyd, 1938)

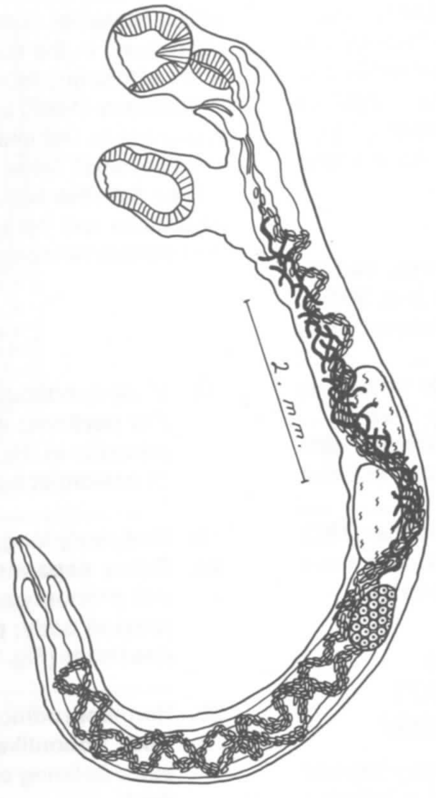


Fig. 392. *Accacladium nematulum.*

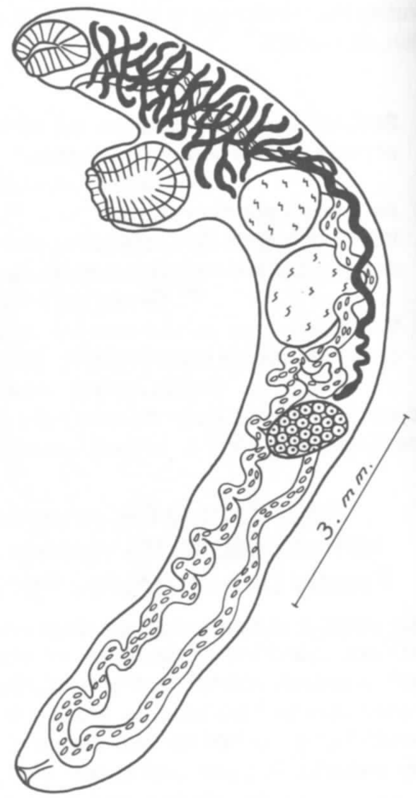


Fig. 393. *Accacladocoelium macrocotyle.*

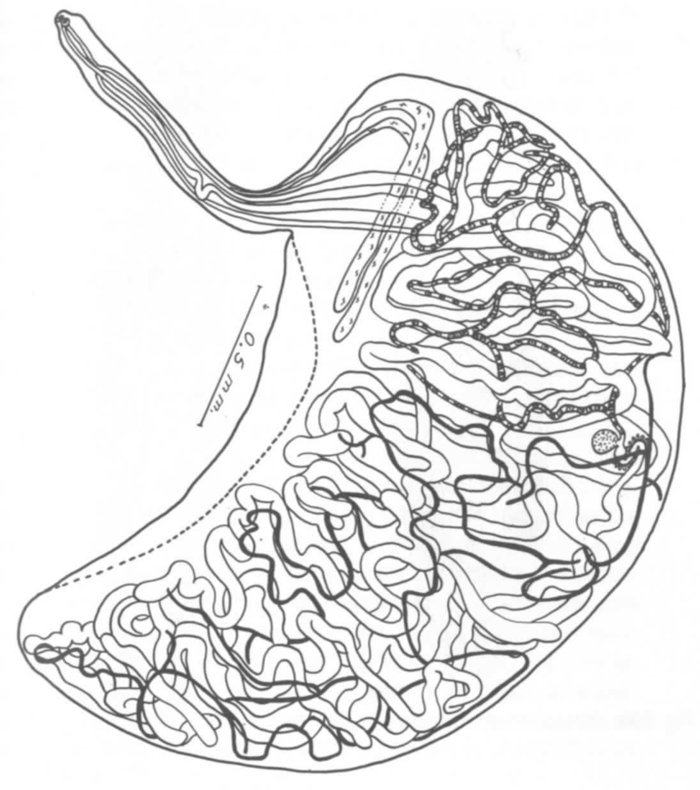


Fig. 394. *Didymocystis coatesi.* (from Nigrelli, 1939)

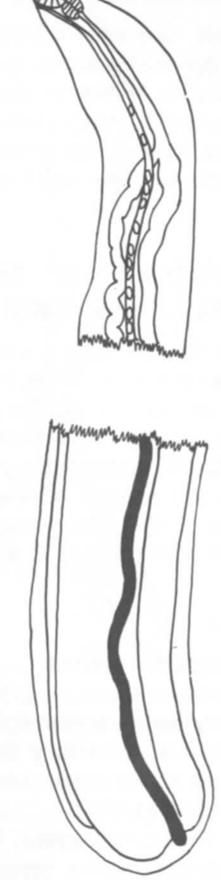


Fig. 395a. *Gonapodasmius okushimai,* female (from Ishii, 1935)

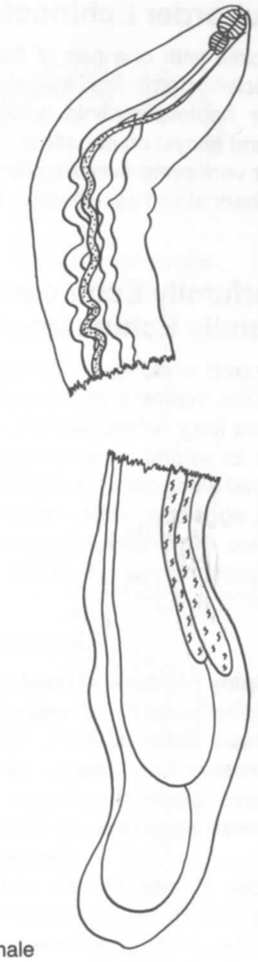


Fig. 395b. male

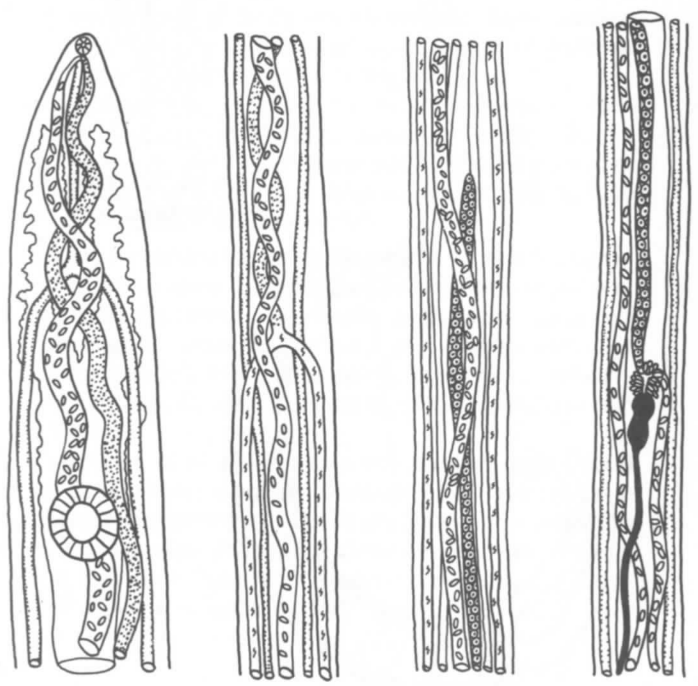


Fig. 396. *Nematobothrioides histoidii.* (from Noble, 1975)

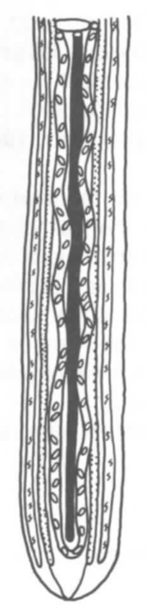
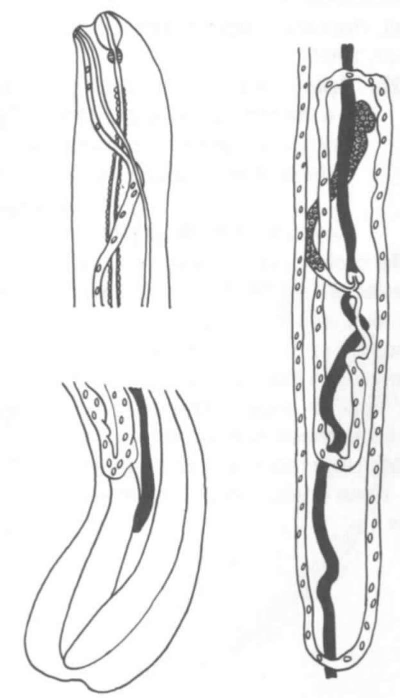



Fig. 397. *Ovarionematobothrium texomense.* (from Self, Peters and Davis, 1963)

Order Echinostomida La Rue, 1957
Suborder Echinostomata Szidat, 1939

Miracidia with one pair of flame cells. Cercariae echinostomate, echinostome-like, megalurous, gymnocephalous, megaperid or haplosplanchnid type; develop in rediae in aquatic snails and encyst on aquatic vegetation or in a variety of invertebrate or vertebrate second intermediate hosts. Cysts spherical, hemispherical or flask-shaped. Life cycle involves two or three hosts.

Superfamily Echinostomatoidea Faust, 1929
Family Echinostomatidae Looss, 1902

Body oval to elongate, spinous, usually provided with a spiny head collar; ventral sucker usually larger than oral sucker; intestinal ceca long; testes tandem; cirrus sac present; genital pore anterior to ventral sucker; ovary pretesticular; vitelline follicles distributed along ceca, confined to hindbody; uterus entirely preovarian; eggs operculate, nonembryonated; parasitic in intestine of reptiles, birds and mammals; rarely in the urinary tract of birds. Epidermal cell of formula of miracidium 6, 6, 4, 2; 6, 8, 4,2; 6, 9, 4, 2; 7, 8, 4, 2.

Key to Genera

1a. Spiny head collar weakly developed or absent. 2

1b. Spiny head collar well developed. 3

2a. Head collar absent; some very small collar spines present but tend to be deciduous; excretory ducts have lateral diverticula; suckers about equal; uterus short; eggs few; parasitic in birds (Fig. 398). .... **Genus *Protechinostoma* Beaver, 1943**

Life cycle: *P. mucronisertulatum* - Echinostome-like cercariae develop in rediae in the aquatic pulmonate snail, *Stagnicola reflexae.* These cercariae have a dorso-ventral finfold on the tail and are without a spiny collar. They encyst in *Physa gyrina, Lymnaea stagnalis* and *S. reflexae.* Experimental infections with the adult parasite were established in baby chicks by feeding metacercariae from snails. The natural definitive host is the sora rail, *Porzana carolina* (see Feldman, 1941; Redington and Ulmer, 1964).

2b. Spiny head collar weakly developed; spines tend to be deciduous; excretory ducts without lateral branches; uterus contains many eggs; ventral sucker at least five times as large as oral sucker (Fig. 399). ... . **Genus *Hypoderaeum* Dietz, 1909**

Key to species in Skrjabin (1964).

Life cycle: *H. conoideum* - About three weeks are required for development of the miracidia which penetrate the pulmonate snail, *Lymnaea stagnalis* and *L. limosa* in which sporocysts and mother and daughter rediae develop. Echinostome cercariae develop in the latter and after leaving the snail, may enter another snail to encyst. The adult fluke develops in the intestine of ducks, geese and swans. Completion of the life cycle requires about four months at 20 degrees C. (Mathias, 1925).

Khan (1960, 1962b) reports a similar life cycle for *H. essexensis.*

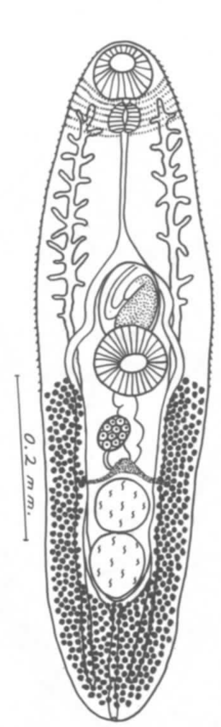


Fig. 398. *Protechinostoma mucronisertulatum.*

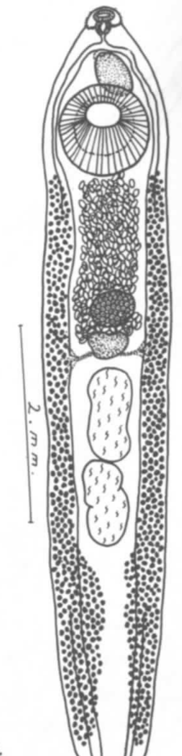


Fig. 399. *Hypoderaeum conoideum.*

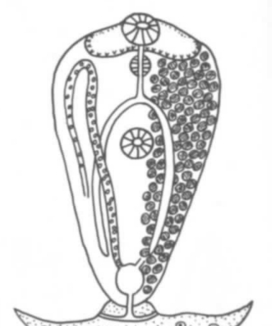


Fig. 400b. Cercaria of *Aporchis massiliensis.*

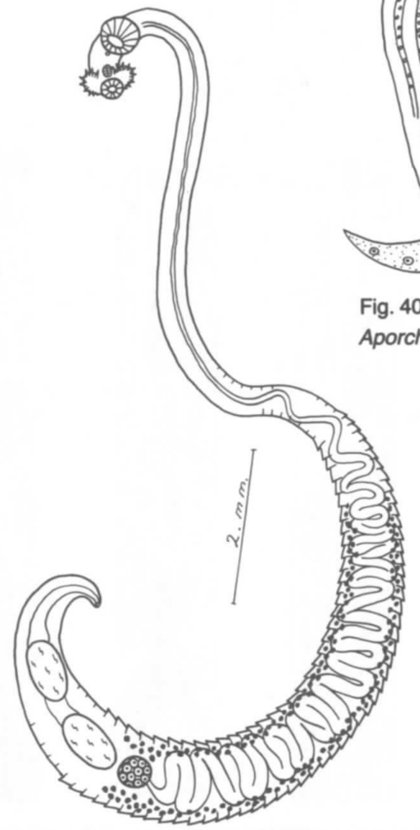


Fig. 400a. *Aporchis continuus.*

Lie (1964) studied the life cycle of *H. dingeri* in Holland. There the miracidium penetrates *Lymnaea rubiginosa* in which it changes to a sporocyst. Mother and daughter rediae develop, the latter producing echinostome cercariae. The cercariae emerge and then reenter the same or another species of snail for encystment and development to infective metacercariae. Ducks and geese serve as experimental and natural definitive hosts.

3a. Testes close to posterior end of body or at least in posterior fifth of body; body long and filamentous; ventral sucker close to oral sucker. 4

3b. Testes always some distance from posterior end of body; body long or short. 7

4a. Posterior half of body with cuticular plications and serrated margins; eggs have unipolar filament; parasitic in intestine of gulls (Fig. 400). .... **Genus *Aporchis* Stossich, 1905**

Life cycle: *A. massiliensis* - Eggs have a polar filament and contain a partially developed miracidium when laid. Miracidia become fully developed in about five days and already contain a redia which, after leaving the miracidium, penetrates the prosobranch snail, *Vermetus triqueter.* Daughter rediae produce echinostome cercariae and granddaughter rediae simultaneously. Cercaria is furcocercous with short tail stem (Fig. 400b). Cercariae eventually encyst on aquatic vegetation or other subtrates such as snail shells. Infected snails are eaten by gulls, *Larus argentatus* in which the adult parasite develops in about 40 days (Prevot, 1971).

4b. Body without plications and serrated margins; eggs without polar filament. 5

5a. Collar spines in double row and spines interrupted dorsal to oral sucker; cirrus sac unusually long, extending some distance posterior to ventral sucker (Fig. 401). .... **Genus *Pelmatostomum* Dietz, 1909**

5b. Collar spines in single row, uninterrupted dorsal to oral sucker; cirrus sac short, oval. 6

6a. Posterior part of body trough-shaped; body narrow between ventral sucker and ovary; vitelline follicles confluent posterior to testes (Fig. 402). .... **Genus *Longicollia* Bykovskaia-Pavlovskaia, 1954**

6b. Body not trough-shaped, sides of body parallel throughout; vitelline follicles not confluent posterior to testes (Fig. 403). .... **Genus *Himasthla* Dietz, 1909**

Key to species in Skrjabin (1964).

Life cycle: *H. rhigedana* - Miracidia develop in 18 days in seawater at room temperature. After hatching, they penetrate the prosobranch snail, *Cerithidia californica* in which echinostome cercariae develop in rediae. After leaving the snail the cercariae encyst on vegetation. Metacercariae are infective immediately for chicks. The natural definitive host is the curlew (Adams and Martin, 1963).

The life cycle of *H. quissetensis* was studied by Stunkard (1938a). Echinostome cercariae develop in daughter rediae in the prosobranch marine snail, *Nassa obsoleta* and encyst in the tissues of marine lamellibranchs of the genera *Mya, Mytilus, Modiolus, Cumingia, Pecten, Ensis* and in the gastropod, *Crepidula* sp. The definitive host is the herring gull.

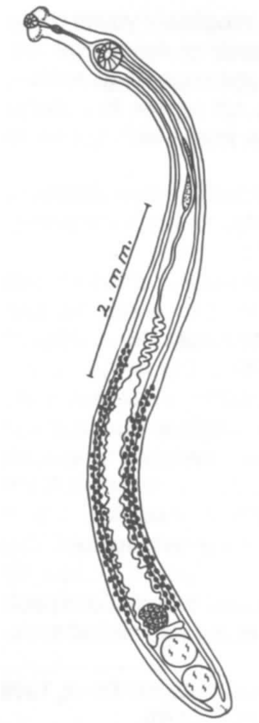


Fig. 401a. *Pelmatostomum americanum.* (from Dronen and Badley, 1979).

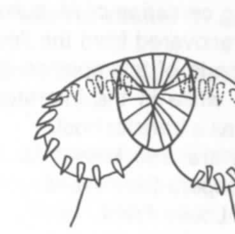


Fig. 401b. *spiny collar*

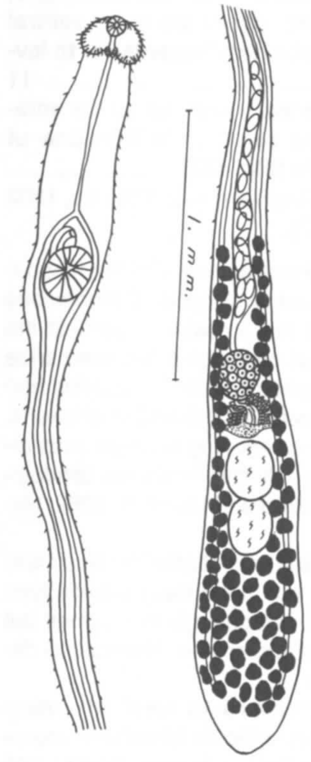


Fig. 402. *Longicollia canaanensis.*

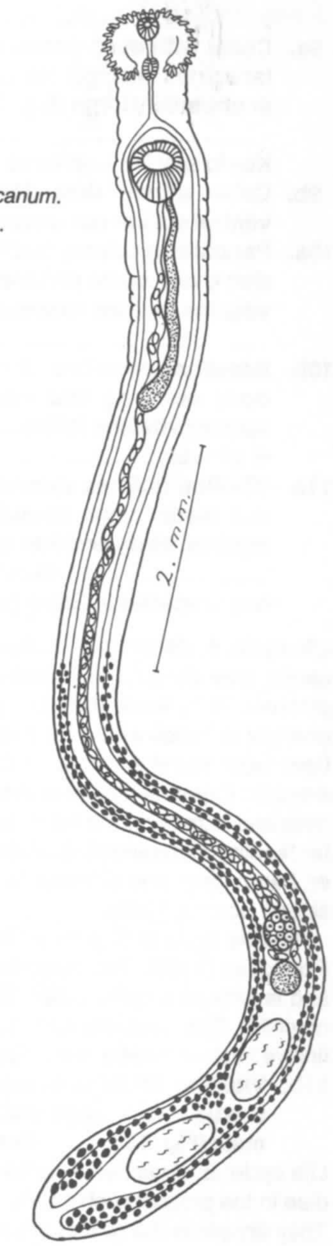


Fig. 403. *Himasthla rhigedana.*

Herman and Bacha (1978) report the infection of young chickens by placing cercariae of *H. quissetensis* on the cloacal lips. Adults were recovered from the ileum and ceca six days later. The metacercaria of this species does not appear to undergo any changes while in the intermediate host which seems to serve merely as a transfer host.

Life cycles are also known for *H. littorinae* (see Stunkard, 1966a; *H. elongata* (see Werding, 1969); *H. interrupta* and *H. continua* (see Looss-Frank, 1967).

7a. Body long and slender; ventral sucker close to oral sucker; vitelline follicles confined to testicular and posttesticular region; testes elongate, in middle of body; parasitic in intestine of otters (Fig. 404) .... Genus *Baschkirovitrema* Skrjabin, 1944

7b. Body short or only slightly elongate; suckers not close together; vitelline follicles variable in extent; not in otters. 8

8a. Collar spines interrupted dorsal to oral sucker. 9

8b. Collar spines uninterrupted dorsal to oral sucker. 12

9a. Collar with deep dorsal and ventral indentations; collar spines in single row; testes elongate; ventral sucker unusually large (Fig. 405). ....Genus *Patagifer* Dietz, 1909

Key to species in Jain and Srivastava (1970).

9b. Collar without deep dorsal and ventral indentations; ventral sucker not unusually large. 10

10a. Parasitic in urinary tract of birds; body long and slender; ovary some distance posterior to ventral sucker; vitelline follicles extend anterior to ovary (Fig. 406). .. .. Genus *Ignavia* Freitas, 1948

10b. Intestinal parasites of reptiles, birds and mammals; body not long and slender; ovary close to ventral sucker; vitelline follicles not extending anterior to level of ovary. 11

11a. Vitelline follicles extend forward only as far as anterior testis; eggs abundant; parasitic in intestine of reptiles, birds and mammals (Fig. 407). .... Genus *Stephanoprora* Odhner, 1902

Key to species in Gupta (1963).

Life cycle: *S. denticulata* - Echinostome cercariae of the magnacauda type develop in rediae in the gastropod, *Biomphalaria glabrata.* They leave the snail and are probably swept into the pharynx of fishes where they encyst on the gills. Metacercariae have been found encysted in the gills of killifish, *Fundulus heteroclitis.* Experimental infections were established in chickens, gulls and hamsters, the adult fluke developing in seven days after feeding metacercariae. Natural definitive hosts are sandpiper, heron, crow and skimmer (Stunkard and Uzmann, 1962; Nasir and Scorza, 1968).

The life cycle of *S. paradenticulata* was studied by Nasir and Rodriguez (1969). The cercaria is not of the magnacauda type and is without a spiny collar. The metacercaria has spines but no collar. The adult has both collar and spines. The natural definitive hosts are stilt and sandpiper.

11b. Vitelline follicles extend forward to level of ovary; uterus short; eggs few; parasitic in birds and mammals (Fig. 408). .... Genus *Echinochasmus* Dietz, 1909

Life cycle: *E. donaldsoni* - Echinostome cercariae develop in rediae in the prosobranch snails, *Amnicola limosa* and *A. histrica.* They encyst in the gills of several species of freshwater fishes. Metacercariae are infective after three weeks. Experimental infections were established by feeding metacercariae to pigeons. The natural definitive host is the pied-billed grebe (Beaver, 1941b).

McCauley and Pratt (1960) studied the life cycle of *E. milvi* and found that zygocercous cercariae, probably *Cercaria gorgonocephala,* develop in rediae in the prosobranch snails *Oxytrema silicula* and *Goniobasis livescens.* Cercariae emerge in clusters with tails entwined. These clusters are eaten by fish such as shiners, trout, dace, sticklebacks and guppies. They encyst in the gills of the fish which are then eaten by the definitive host. Experimental infections were established in hamsters and ducks. The natural definitive host is unknown.

12a. Lateral margins of hindbody serrated and spinous; collar reniform; testes elongate; parasitic in birds (Fig. 409). .... Genus *Prionosoma* Dietz, 1909

12b. Body margins not serrated. 13

13a. Body widest at anterior end, tapering gradually toward posterior end; corner spines of collar very large; testes lobed (Fig. 410). .... Genus *Drepanocephalus* Dietz, 1909

13b. Body and collar spines not as described above. ... 14

14a. Collar spines in a single uninterrupted row. 15

14b. Collar spine in a double uninterrupted row. 16

15a. Cirrus sac long, extending some distance posterior to ventral sucker; 23 collar spines; testes round or oval (Fig. 411). .... Genus *Acanthoparyphium* Dietz, 1909

Life cycle: *A. spinulosum* - Bearup (1960) investigated this cycle in Australia where the estuarine sandflat snail, *Pyrazus australis* serves as first intermediate host. Sporocysts were not found but mother and daughter rediae developed, the latter producing echinostome cercariae. After a brief free-living period, the cercariae encysted in the gastropods *Salinator fragilis, P. australis* and in small polychaete worms. Infected *S. fragilis* were fed to silver gulls, *Larus novaehollandiae* and adult worms recovered. *S. fragilis* seems to be the chief second intermediate host. Natural definitive hosts for this species are plovers and ducks.

Martin and Adams (1961) studied this species in California where the prosobranch, *Cerithidia californica* serves as both first and second intermediate host and the natural definitive hosts are avocet and plover which eat the infected snails.

The life cycle of *A. paracharadrii* was studied by Velasquez (1964).

15b. Cirrus sac short, anteriodorsal to ventral sucker; collar spines 26 or more; testes elongate, twisted spirally (Fig. 412). .... Genus *Euparyphium* Dietz, 1909

Key to species in Skrjabin (1964).

Life cycle: *E. beaveri* - Echinostome cercariae develop in rediae in the pulmonate snail, *Stagnicola angulata.* They encyst in the wall of the cloaca of tadpoles. Definitive hosts such as mink, otter and snowshoe hare eat the infected tadpoles or metamorphosed frogs and acquire the parasite (Beaver, 1941a).

16a. Body short (1-2mm), plump, widest at middle; testes oblique; ventral sucker in middle of body or posterior to middle; uterus short; eggs few; parasitic in birds (Fig. 413). .... Genus *Petasiger* Dietz, 1909

Life cycle *P. nitidus* - Echinostome cercariae of the magnacauda type develop in rediae in the planorbid snails, *Helisoma smithi* and *H. percarinatum.* Cercariae leave the snails and are eaten by several species of freshwater fishes in which they encyst and develop to the metacercarial stage. Experimental infections were established in canaries by feeding metacercariae. The horned grebe, *Colymbus auritis* is the natural definitive host (Beaver, 1939a).

16b. Body elongate; ventral sucker anterior to middle of body; uterus contains numerous eggs; testes tandem. 17

17a. Testes irregular in shape or lobed, in middle of hindbody; 27 collar spines (Fig. 414). .... Genus *Isthmiophora* Lühe, 1909

17b. Testes round or oval. 18

18a. Collar spines of unequal size in the two rows; ventral sucker a short distance anterior to middle of body (Fig. 415). .... Genus *Echinoparyphium* Dietz, 1909

Life cycle: *E. flexum* - Miracidia develop and hatch in about 14 days and then penetrate the pulmonate snail, *Stagnicola palustris* in which a generation of sporocysts and mother and daughter rediae develop. The latter produce echinostome cercariae which leave the snail in which they are produced and enter other snails such as *Helisoma trivolvis, Physa integra* and *Stagnicola palustris* and encyst. Some cercariae also encyst in tadpoles of *Rana, Hyla* and *Pseudacris* spp. Natural definitive hosts are bluewinged teal and American scoter ducks which probably eat the infected snails and tadpoles (McCoy, 1927; Najarian, 1953, 1954).

The life cycle of *E. dunni* was studied by Lie Kian and Umathevy (1965) and that of *E. hydromyos* by Angel (1967).

18b. Collar spines of equal size in the two rows; body elongate (10-14 mm); ventral sucker in anterior third of body (Fig. 416). .... Genus *Echinostoma* Rudolphi, 1809

Key to species in Skrjabin (1964).

Life cycle: *E. revolutum* - Miracidia develop and hatch in three to four weeks after eggs are laid. They penetrate snails of the genera *Physa, Lymnaea, Stagnicola, Helisoma* and *Pseudosuccinea* in which sporocysts and mother and daughter rediae develop. The latter produce echinostome cercariae which leave the snail and eventually encyst in the same or a different species of snail or in clams or larval amphibians. The adult fluke is parasitic in the intestine of ducks. There are rare reports of it as a parasite of human beings (Beaver, 1937).

Khan (1961) investigated the life cycle of *E. londonensis* which developed to sexual maturity in the pigeon, an experimental host, within eight days after feeding metacercariae. The host snail for the early larvae is *Planorbis corneus.* Metacercariae developed in *P. corneus* and also in *Lymnaea stagnalis* and *L. pereger.*

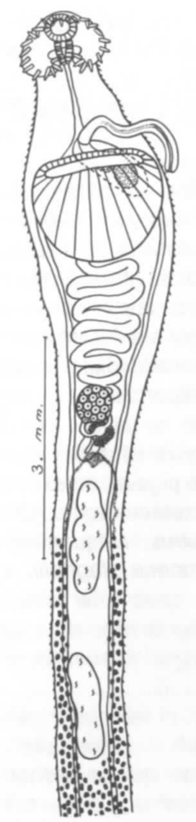


Fig. 404. *Baschkirovitrema incrassatum.*

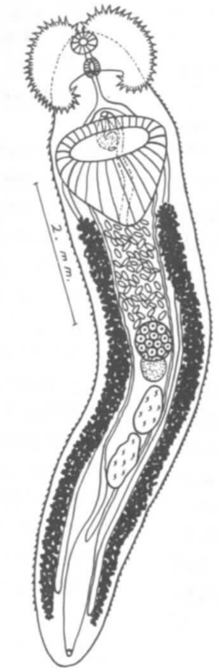


Fig. 405. *Patagifer vioscai.*

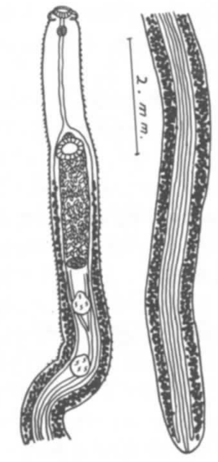


Fig. 406a. *Ignavia venusta.* (from Freitas, 1948).

Fig. 406b. spiny collar

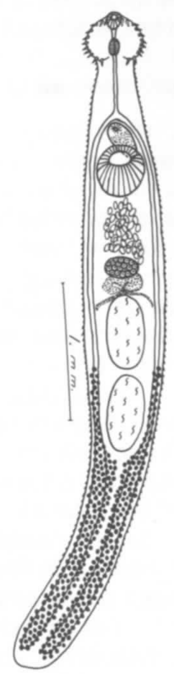


Fig. 407. *Stephanoprora pseudoechinata.*

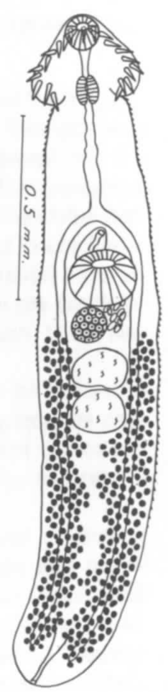


Fig. 408. *Echinochasmus donaldsoni.*

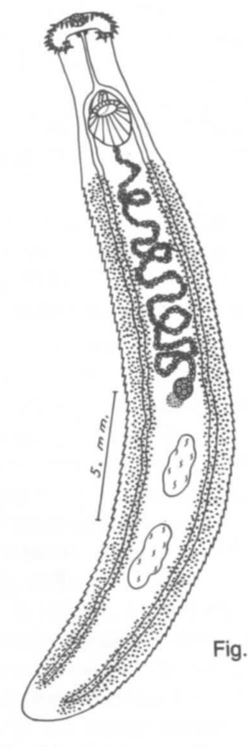


Fig. 409. *Prionosoma serratum.*

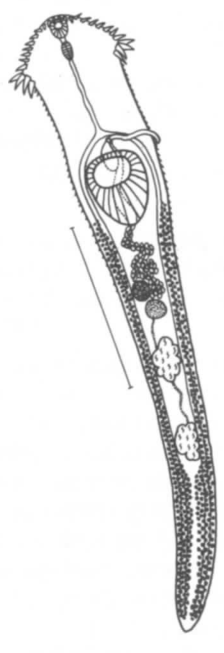


Fig. 410. *Drepanocephalus spathans.*

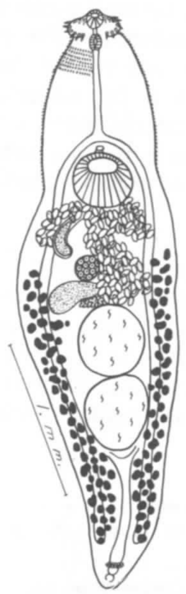


Fig. 411. *Acanthoparyphium spinullsum.*

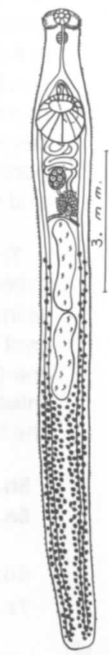


Fig. 412 *Euparyphium inermo.*

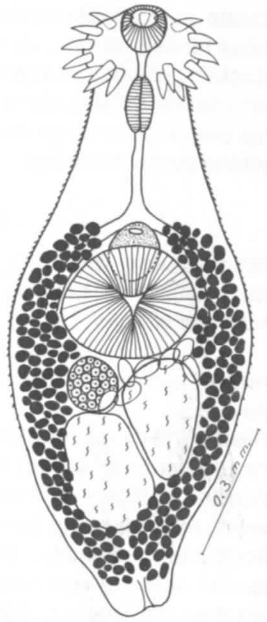


Fig. 413. *Petasiger nitidus.*

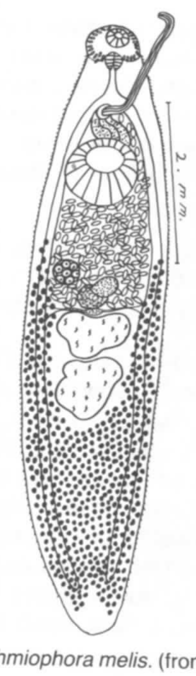


Fig. 414. *Isthmiophora melis.* (from Dietz, 1910).

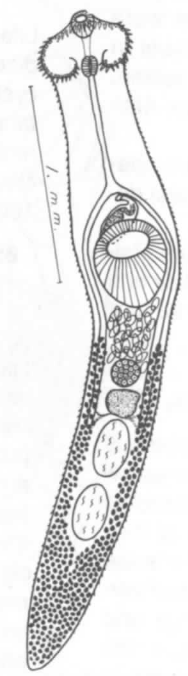


Fig. 415. *Echinoparyphium recurvatum.*

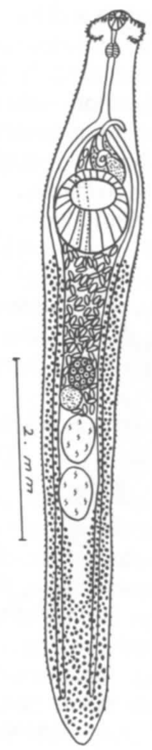


Fig. 416. *Echinostoma revolutum.*

Family Psilostomidae Odhner, 1913

Body oval, fusiform, elongate or pyriform; ventral sucker usually in anterior half of body, usually larger than oral sucker (pedunculate in *Stephanoproraoides*); pharynx present; ceca long; testes tandem or oblique; cirrus sac dorsal or anterior to ventral sucker; genital pore anterior to ventral sucker; ovary pretesticular; vitelline follicles along ceca, may extend into forebody; uterus pretesticular; eggs operculate, embryonated; parasitic in digestive tract of birds and mammals.

Key to Genera

1a. **Ventral sucker pedunculate; body cylindrical, elongate; vitelline follicles posterior to testes; parasitic in intestine of beavers (Fig. 417). .... Genus** ***Stephanoproraoides*** **Price, 1934**

1b. **Ventral sucker sessile; body oval, fusiform or elongate. 2**

2a. **Vitelline follicles confined to hindbody; cirrus sac long, extends posterior to ventral sucker. 3**

2b. **Vitelline follicles in fore- and hindbody; cirrus sac short, not extending posterior to ventral sucker. 5**

3a. **Body very elongate, sides nearly parallel; ventral sucker close to oral sucker and at least five times as large as oral sucker; testes elongate and curved (Fig. 418). .... Genus** ***Mesaulus*** **Braun, 1902**

3b. **Body elongate but sides not parallel; ventral sucker in anterior third of body, about twice as large as oral sucker; testes oval or slightly lobed. 4**

4a. **Body rounded at posterior end (Fig. 419). .... Genus** ***Psilostomum*** **Looss, 1899**

Life cycle: *P. brevicolle* - Encysted metacercariae from the cockle, *Cardium edule* and the mussel, *Mytilus edulis* were fed to an oystercatcher, *Haematopus ostralegus* and adults of *P. brevicolle* were recovered. Eggs from these specimens were used to infect laboratory-reared snails, *Hydrobia stagnalis* in which cercariae of the magnacauda type developed in rediae. Natural definitive hosts are ducks of the genera *Clangula, Melanitta, Oidemia* and *Aythya* (see Reimer, 1964).

Loos-Frank (1968b) studied the life cycle of the above species and reported a gymnocephalous cercaria for it. Natural definitive hosts are oystercatcher and herring gull.

Ching (1980) investigated the life cycle of *P. magniovum*. Psilostome cercariae developed in rediae in *Littorina scutulata* and encysted in *Mytilus edulis*. Natural definitive hosts are several species of diving ducks.

4b. **Body tapered at posterior end (Fig. 420). .... Genus** ***Psilochasmus*** **Lühe, 1909**

Life cycle: *P. oxyurus* (= *P. aglyptorchis*) - Gymnocephalous cercariae with a dorso-ventral finfold on the tail develop in yellow rediae in the prosobranch snails, *Bithynia tentaculata Littoridina australis* and *Hydrobia ulvae*. The cercariae leave the snail then encyst on the inner surface of the shell and in the mantle tissue of the same or a different species of snail such as *Spirulina vortex* and *Radix* sp. Metacercariae were fed to ducklings and chicks and mature flukes recovered in three weeks from the small intestine. Natural definitive hosts are species of ducks in the genera *Anas, Oidemia* and *Nyroca* (see Szidat, 1957; Wisniewski, 1958a; Loos-Frank, 1968a).

5a. **Esophagus with a pair of lateral diverticula; usually parasitic in birds (Fig. 421). .... Genus** ***Ribeiroia*** **Travassos, 1939**

Life cycle: *R. thomasi* (= Pseudopsilostoma ondatrae) - Miracidia develop and hatch in two to three weeks after eggs are passed in the feces of the host. They penetrate the planorbid snail, *Helisoma percarinatum*, in which echinostome-like cercariae *(Cercaria thomasi)* develop in daughter rediae. The cercariae encyst in the lateral line canal, nasal cavities and beneath the scales of perch, bluegill, pumpkinseed and bass. The cercariae and the metacercariae have esophageal diverticula like the adults which develop in the intestine of ducks, gulls, osprey and hawks. Experimental infections were established in ducks, chicks, pigeons and canaries (Beaver, 1939b).

The life cycle of *R. marini* was studied by Basch and Sturrock (1969) in the West Indies. The host snail is *Biomphalaria glabrata* in which *Cercaria marini* develops in a redia. The cerariae encyst in guppies, *Lebistes* sp. The adult fluke inhabits the wall of the proventriculus of pigeons, canaries and finches which were infected by feeding metacercariae. The natural definitive host is the blue heron, *Florida caerula*.

5b. **Esophagus without diverticula. 6**

6a. **Ventral sucker in middle or posterior to middle of body. 7**

6b. **Ventral sucker anterior to middle of body. 9**

7a. **Body fusiform; ventral sucker posterior to middle of body and smaller than oral sucker; right cecum forms permanent loop near cecal bifurcation; parasitic in wild turkeys (Fig. 422). .... Genus** ***Psilotornus*** **Byrd and Prestwood, 1969**

7b. **Body oval or pyriform; ventral sucker in middle of body and larger than oral sucker; no loop in right cecum. 8**

8a. **Genital pore posterior to cecal bifurcation; cirrus sac long, bipartite; testes oblique or nearly opposite (Fig. 423). ...... Genus** ***Astacatrematula*** **Macy and Bell, 1968**

Life cycle: *A. macrocotyla* - Psilostome cercariae develop in rediae in the freshwater prosobranch snail, *Fluminicola virens*. Encysted metacercariae from the gills and sternites of crayfish, *Astacus trowbridgi* were fed to baby chicks. Development to sexual maturity occurred within three days in the small intestine of chicks. The natural definitive host is unknown (Macy and Bell, 1968a).

8b. **Genital pore anterior to cecal bifurcation; cirrus sac short, unipartite; testes tandem (Fig. 424). .... Genus** ***Sphaeridiotrema*** **Odhner, 1913**

Life cycle: *S. globulus* - Echinostome-like cercariae *(Cercaria helvetica XVII)* develop in a redia in the prosobranch snails, *Bithynia tentaculata, Vivipara fasciata, Fluminicola virens* and in the pulmonate snails *Lymnaea palustris, L. auricularia, Physa acuta* and *Planorbis corneus*. The cercariae emerge for a brief period, then return to the snail and encyst between the mantle and shell. The adult flukes develop in the intestine of merganser, scaup, old squaw and domestic ducks which eat infected snails. Experimental infections were established in ducks, guinea fowl, geese and turkeys (Szidat, 1937; Macy and Ford, 1964; Francalanci and Manfredini, 1969).

Burns (1961a) studied the life cycle of *S. spinoacetabulum* which is a parasite of ducks. The cycle is similar to that of *S. globulus* except the adults inhabit the ceca of ducks.

(Continued)

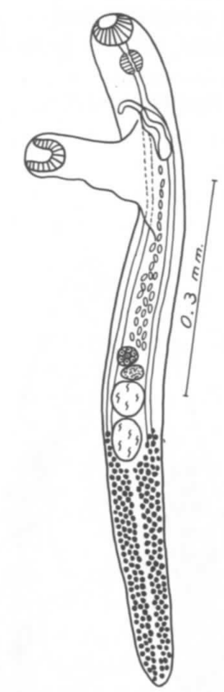


Fig. 417. *Stephanoproraoides lawi.* (from Price, 1934).

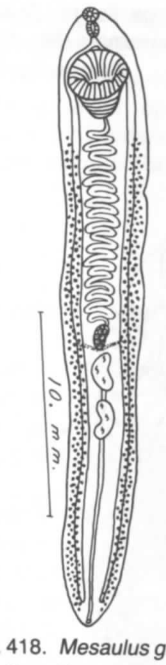


Fig. 418. *Mesaulus grandis.* (from Braun, 1902).

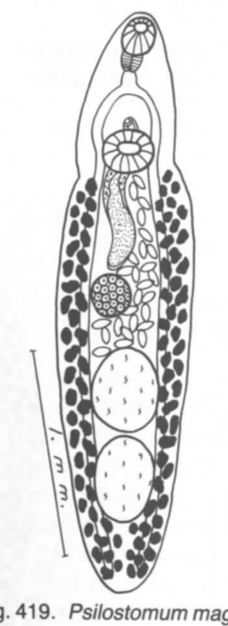


Fig. 419. *Psilostomum magniovum.*

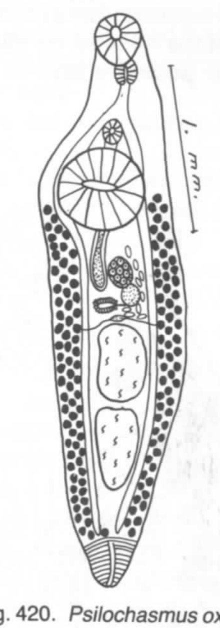


Fig. 420. *Psilochasmus oxyurus.*

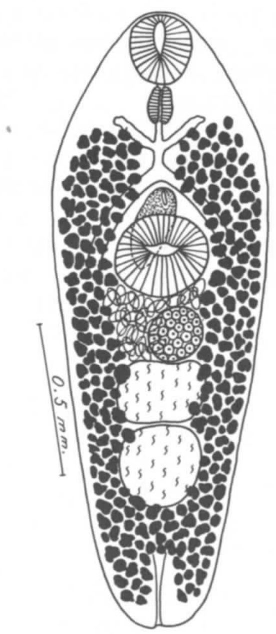


Fig. 421. *Ribeiroia thomasi.*

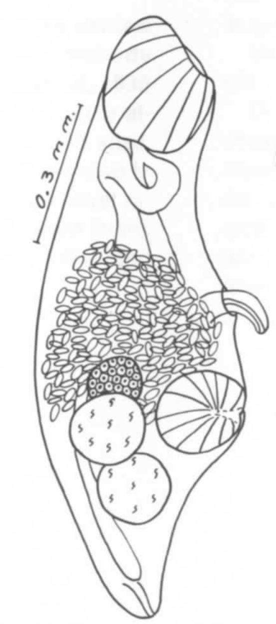


Fig. 422. *Psilotornus audacirrus.* (from Byrd and Prestwood, 1969).

Fig. 423. *Astacatrematula macrocotyla.* (from Macy and Bell, 1968).

Belyakova (1978) studied the life cycle of *S. globulus* in Russia. There the host snail is *Bithynia leachi*. Cercariae encysted in pulmonate snails of the genera *Physa, Planorbis, Planorbarius* and *Lymnaea*. Adults developed in ducklings which ingested the metacercariae with the snails. Belyakova regards *S. globulus* and *S. spinoacetabulum* as synonyms.

9a. Vitelline follicles confluent posterior to testes; testes near posterior end of body; eggs small, abundant; parasitic in proventriculus and intestine of birds (Fig. 425). .... **Genus** *Pseudopsilostoma* **Yamaguti, 1958**

9b. Vitelline follicles not confluent posterior to testes; testes some distance from posterior end of body; eggs large, few (usually one); usually parasitic in mammals (Fig. 426). .... **Genus** *Gyrosoma* **Byrd, Bogitsh and Maples, 1961**

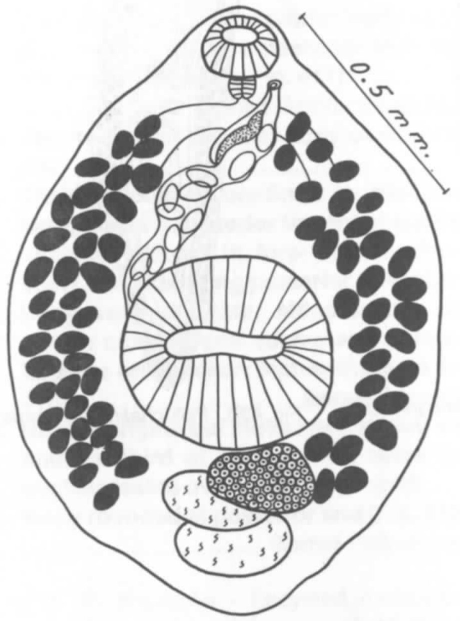


Fig. 424. *Sphaeridiotrema globulus.*

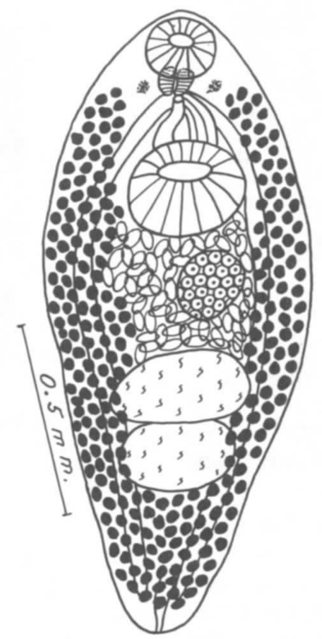


Fig. 425. *Pseudopsilostoma varium.*

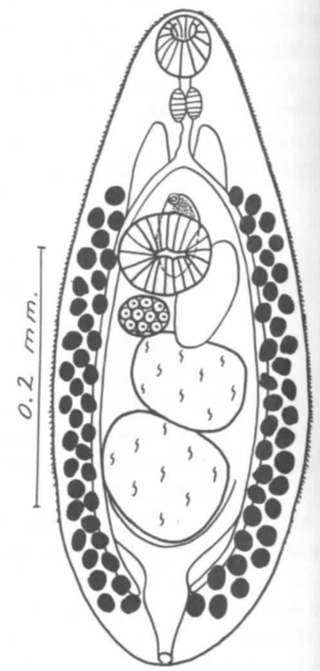


Fig. 426. *Gyrosoma singularis.*

Family Philophthalmidae Travassos, 1918

Body elongate, oval or fusiform, spinous; ventral sucker larger than oral sucker, spiny collar envelops oral sucker in some genera; pharynx present; ceca long; testes opposite or tandem, near posterior end of body; cirrus sac present; genital pore anterior to ventral sucker; ovary pretesticular; vitelline follicles arranged in a V-or U-shaped design, anterior to testes; uterus anterior to gonads, confined to hindbody; eggs operculate, embryonated; excretory vesicle has arms that extend far forward in body; parasitic in intestine, cloaca, bursa of Fabricius or conjunctival sac of birds.

Key to Genera

1a. Testes opposite; parasitic in cloaca or bursa Fabricius of birds. 2

1b. Testes tandem or oblique; parasitic in intestine or in conjunctival sac, or bursa Fabricius. 3

2a. Spiny collar around oral sucker; testes lobed; genital pore immediately anterior to ventral sucker; uterus confined to hindbody (Fig. 427). .... **Genus** *Parochis* **Nicoll, 1907**

Life cycle: *P. avitus* - Miracidia, which already contain a mother redia, hatch either before or soon after eggs are laid. Echinostome-like cercariae develop in rediae in the marine prosobranch snails, *Urosalpinx cinereus* and *Thais lapillus.* After leaving the snail, they encyst in hemispherical cyst membranes on vegetation and other substrates. The adult flukes develop in the common tern, *Sterna hirundo* and the roseate tern, *S. dougalli,* which ingest the metacercariae along with their food (Stunkard and Cable, 1932).

Angel (1954) investigated the life cycle of *P. acanthus.*

Cercariae of the megalura group (Fig. 47) develop in daughter rediae in the marine snail, *Nucella lapillus.* They encyst in the lamellibranch molluscs, *Cardium* and *Mytilus* spp. which are then eaten by gulls in which the adult parasite develops.

2b. Spiny collar absent; testes oval; genital pore ventral to pharynx; some folds of uterus extend into forebody (Fig. 428). .... **Genus** *Cloacitrema* **Yamaguti, 1935**

Life cycle: *C. michiganense* - Miracidia hatch either before or after eggs are laid and penetrate the marine prosobranch snail, *Cerithidia californica* in which megalurous cercariae develop in daughter rediae. After emerging from the snail, they encyst on vegetation or other substrates. The adult flukes develop in the cloaca of sandpipers, black-necked stilts, western willet and gulls (Robinson, 1952).

The life cycle of *C. philippinum* which was investigated by Velasquez (1969b) is similar to that of the above species.

3a. Body constricted posterior to ventral sucker; spiny collar well developed with several rows of ventral corner spines and single row of dorsal spines; parasitic in bursa Fabricius of birds (Fig. 429). .... **Genus** *Paratrema* **Dronen and Badley, 1979**

3b. Body not constricted posterior to ventral sucker; spiny collar vestigial or absent. 4

4a. Spiny collar vestigial around oral sucker; intestinal parasite of birds (Fig. 430). .... **Genus** *Echinostephilla* **Lebour, 1909**

4b. Body without a spiny collar; adults beneath nictitating membrane (conjunctiva) of birds (Fig. 431). .... **Genus** *Philophthalmus* **Looss, 1899**

Two species in the genus have been reported as parasites in the eyes of human beings.

Life cycle: *P. gralli* -Eggs contain a miracidium when laid and the miracidium contains a mother rediae. After hatching they penetrate the epidermis of the freshwater prosobranch snails, *Pleurocera acuta* and *Goniobasis* spp., then release the mother redia which migrates to the heart of the snail. Megalurous cercariae develop in daughter rediae and encyst in flask-shaped cyst membranes on the surface of aquatic arthropods which are then eaten by birds. The excysted metacercariae migrate from the mouth to the eye by way of the nasal cavities and nasolachrymal ducts. The adult flukes develop around the upper end of the ducts and beneath the nictitating membrane. Natural definitive hosts are heron, turkey, kingfisher, bittern, crow and magpie (Ching, 1961; West, 1961).

Alicata (1962) discovered that eggs leave the definitive host by way of the mouth when birds drink water. He also observed that there are three generations of rediae for this species.

The life cycle of *P. hegeneri* is similar to that of *P. gralli.* The host mollusc is *Batillaria minima* from the Gulf of Mexico. Natural definitive hosts are royal tern, yellow-crowned night heron, laughing gull and willet (Penner and Fried, 1963).

McMillan and Macy (1972) studied the life cycle of *P. megalurus.*

Dronen and Penner (1975) described the life cycle of *P. andersoni* which uses the marine prosobranch, *Cerithium stercusmuscarum* as host. The miracidium also contains a mother redia. Cyst membranes are flask-shaped. Chickens were used as experimental definitive host but the natural hosts are caspian tern, *Hydroprogne caspia* and the royal tern, *Thalasseus maximus.*

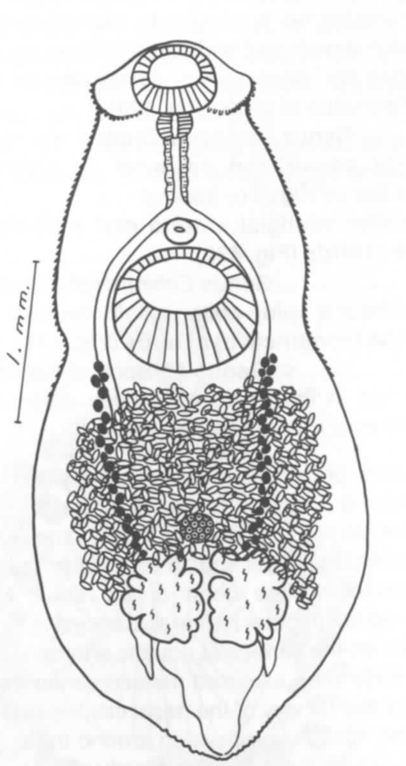


Fig. 427. *Parorchis acanthus.*

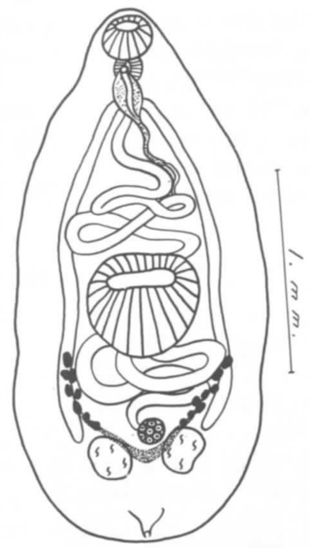


Fig. 428. *Cloacitrema michiganense.*

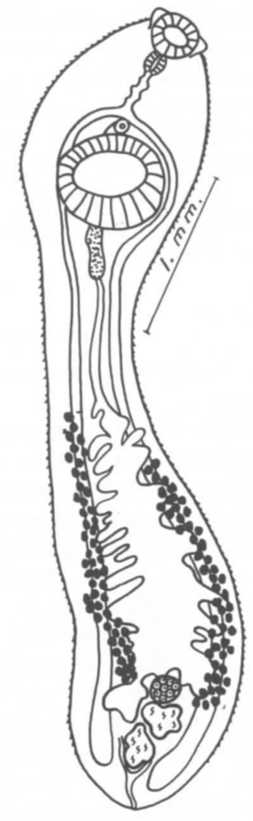


Fig. 429a. *Paratrema numenii.* (from Dronen and Badley, 1979).

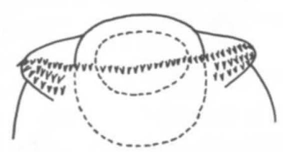


Fig. 429b. spiny collar

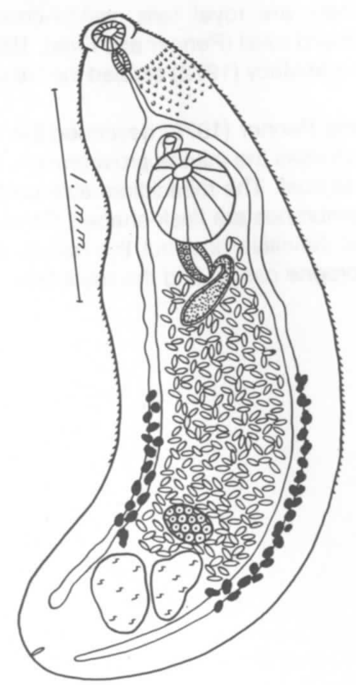


Fig. 430. *Echinostephilla haematopi.*

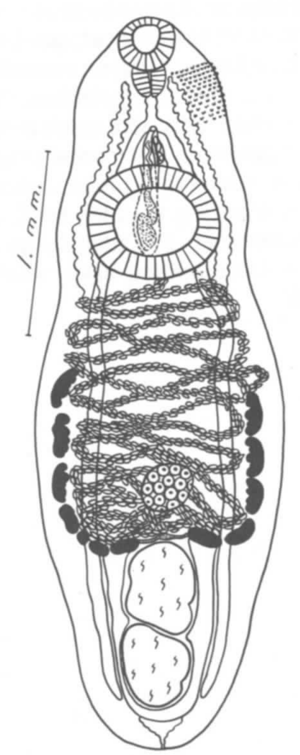


Fig. 431. *Philophthalmus hegeneri.*

Family Cathaemasiidae Fuhrmann, 1928

Body elongate; ventral sucker larger than oral sucker; intestinal ceca long; testes tandem, lobed or ovoid in middle of hindbody; cirrus sac present; ovary pretesticular; genital pore median, anterior to ventral sucker; vitelline follicles in lateral areas of hindbody; uterus entirely preovarian; parasitic in the intestine of birds.

The genus *Cathaemasia* Looss, 1899 (Fig. 432) is represented in North America by *C. nycticoracis,* a parasite of herons. Key to species in Olsen (1940) and in Skrjabin (1964).

Life cycle: *C. hians* - Miracidia hatch and penetrate freshwater pulmonate snails of the genera *Planorbis* and *Lymnaea* and also the prosobranch marine snails *Bithynia tentaculata* and *Vivipara fasciata.* Cercariae resembling those of the echinostomes and psilostomes develop in daughter rediae and after emergence from the mollusc, encyst in tadpoles of *Rana esculenta.* The adult fluke develops in herons and storks (Szidat, 1939).

Family Rhopaliidae (Looss, 1899) Viana, 1924

Body elongate, densely spinous, a retractile proboscis with large spines on each side of oral sucker; ventral sucker larger than oral sucker; intestinal ceca long; testes tandem, in middle of hindbody; cirrus sac very long, extending far posterior to ventral sucker; ovary pretesticular; genital pore median, anterior to ventral sucker; uterus entirely preovarian; vitelline follicles fill lateral areas of hindbody, confluent posterior to testes; parasitic in the intestine of opossum.

The family contains only the genus *Rhopalias* Stiles and Hassall, 1898. *R. macracanthus* (Fig. 433) has been reported from North America as a parasite of *Didelphis virginiana,* the opossum. Key to species in Siebert (1971).

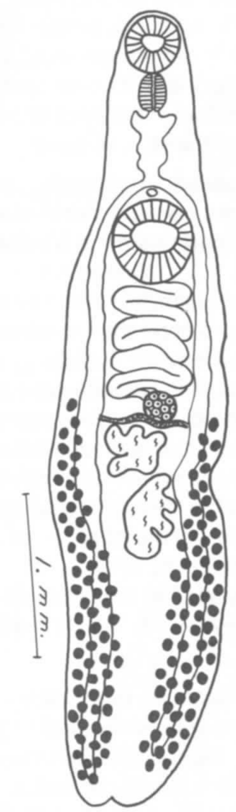


Fig. 432. *Cathaemasia nycticoracis.*

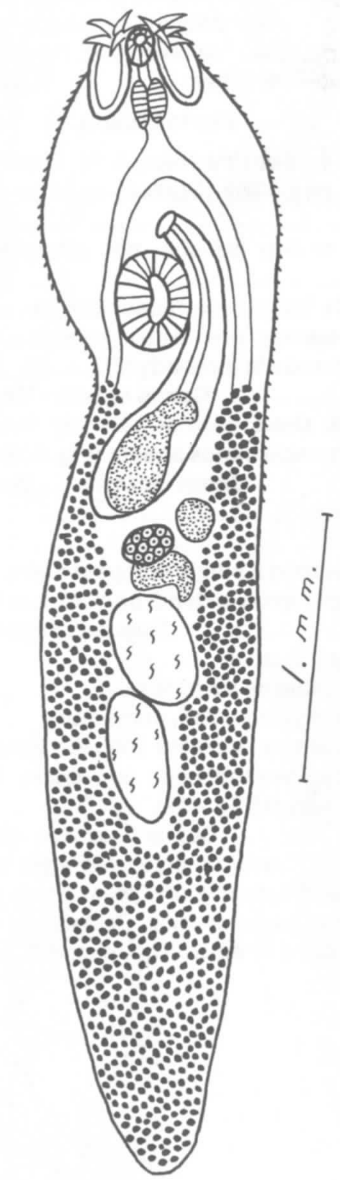


Fig. 433. *Rhopalias macracanthus.* (from Chandler, 1932)

Superfamily Haploporoidea Mehra, 1961

Miracidia have one pair of flame cells. Cercariae may be echinostome-like with unadorned tail or haplosplanchnid type with lateral finger-like processes on the tail or megaperid type with wide lateral finfolds on the tail. Cercariae develop in rediae or in sporocysts in prosobranch snails and encyst on vegetation. Life cycles involve two hosts.

Family Haploporidae Nicoll, 1914

Body small, elongate, pyriform or oval, spinous; ventral sucker in anterior half of body, pedunculate in some genera; pharynx present; ceca about half length of body; testes one or two, in hindbody; cirrus sac absent but hermaphroditic sac present, contain hermaphroditic duct, metraterm and anterior portion or bipartite seminal vesicle, remainder of seminal vesicle free in parenchyma; genital pore anterior to ventral sucker; ovary pretesticular; vitellaria either compact or follicular; uterus variable in extent; eggs operculate, embryonated; parasitic in intestine of marine and freshwater fishes.

Key to Genera

1a. Ventral sucker pedunculate, retractile, with two pointed muscular papillae; eggs have unipolar filament. 2

1b. Ventral sucker sessile, not retractile; papillae absent. 3

2a. Peduncle long; ceca fused with excretory vesicle to form uroproct; one testis; prominent dorso-ventral muscle bands in forebody (Fig. 434). .... **Genus *Myodera* Montgomery, 1957**

2b. Peduncle short; ceca end blindly; two testes; dorso-ventral muscle bands absent (Fig. 435). .... **Genus *Scorpidicola* Montgomery, 1957**

3a. One testis. 4

3b. Two testes. 8

4a. Vitelline gland a single compact mass, dorsal to ovary and testis; ceca extend only to level of testis (Fig. 436). .... **Genus *Dicrogaster* Looss, 1902**

4b. Vitellaria follicular. 5

5a. Vitelline follicles large, few. 6

5b. Vitelline follicles small, numerous. 7

6a. Body pyriform; vitelline follicles irregular in shape, distributed around ceca and testis; hermaphroditic sac small, oval (Fig. 437). .... **Genus *Saccocoelioides* Szidat, 1954**

Life cycle: *S. pearsoni* - Embryonated eggs are eaten by the freshwater snail, *Posticobia brazieri* in which a sporocyst and one generation of rediae develop. Oculate cercariae with a simple tail are produced in rediae. They encyst on freshwater algae. The mullets, *Mugil cephalus* and *Trachystoma petardi* eat the infested algae and acquire the parasite (Martin, 1973).

Cable and Isseroff (1969) described a precocial haploporid cercaria found in the prosobranch snail *Amnicola comalensis* in Texas. It is essentially an adult with a tail but lacks eggs. All reproductive organs are present. These cercariae encyst on vegetation and other solid surfaces in oval cyst membranes. They are regarded as the precocial larva of *Saccocoelioides sogandaresi*. This is the first report of a freshwater haploporid cercaria.

6b. Body elongate; vitelline follicles oval to elongate, distributed around ceca and testis; hermaphroditic sac large, extends posterior to ventral sucker (Fig. 438). .... **Genus *Carassotrema* Park, 1938**

7a. Body tapered posteriorly; ventral sucker larger than oral sucker; hermaphroditic sac at level of pharynx; vitelline follicles fill most of hindbody; eggs small, numerous (Fig. 439). .... ***Hapladena* Linton, 1910**

Key to species in Skrjabin (1964).

Life cycle: *H. varia* - Cable (1962) described an oculate cercaria (*Cercaria caribbea* LII) having some echinostome-like features such as stenostomate excretory system, cystogenous glands, no penetration glands, no stylet, simple tail and spinous body. It developed in a redia in the marine snail, *Zebina browniana* and encysted on vegetation in thick oval cyst membranes. Experimental infections resulted in the production of developing adults that bore some resemblance to *H. varia*.

7b. Body not tapered posteriorly; suckers equal; hermaphroditic sac dorsal to ventral sucker; vitelline follicles in H-shaped design in hindbody; eggs large and few (Fig. 440). .... **Genus *Saccocoelium* Looss, 1902**

Life cycle: *S. tensum* - Miracidia hatch from embryonated eggs in feces of the host and enter the prosobranch snails, *Hydrobia acuta* and *H. ventrosa* in which oculate gymnocephalous cercariae develop in a redia. The cercariae encyst on vegetation after only a brief free-living existence. Very young mullets were allowed to feed on metacercariae and adult flukes were recovered 25 to 30 days later. Metacercariae are infective shortly after the cercariae encyst. The entire life cycle requires 5 to 6 months in the laboratory. Five species of mullet serve as definitive host for this parasite (Fares and Maillard, 1974).

The same authors studied the life cycle of *S. obesum* which uses the same definitive hosts. The host mullusc is *Rissoa* sp. in Europe.

8a. Vitelline follicles in form of thick dorso-ventral bands arranged in linear series lateral to ceca (Fig. 442). .... **Genus *Vitellibaculum* Montgomery, 1957**

8b. Vitelline follicles small, abundant, distributed along inflated ceca; pigmented eyespots present (Fig. 441). .... **Genus *Megasolena* Linton, 1910**

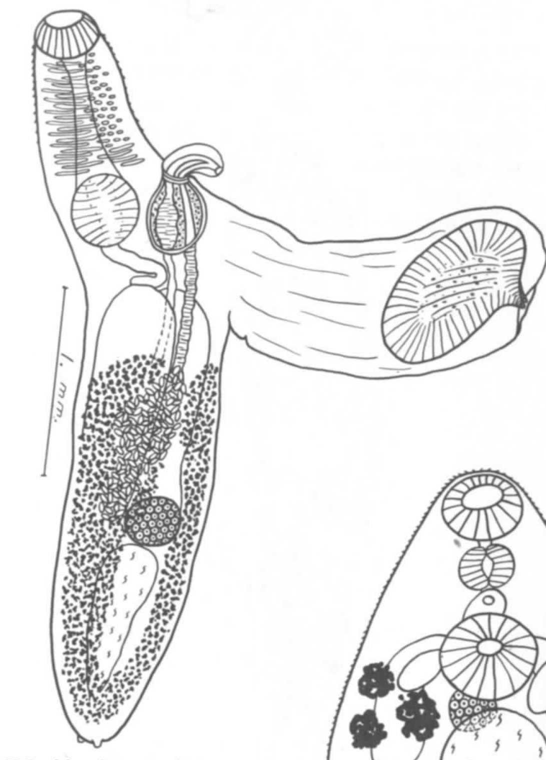


Fig. 434. *Myodera medialunae.*

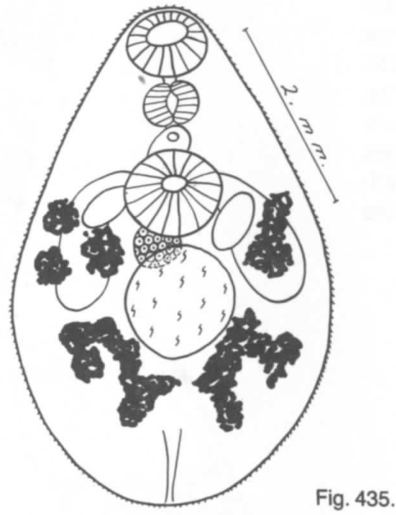


Fig. 437. *Saccocoelioides sogandaresi.*

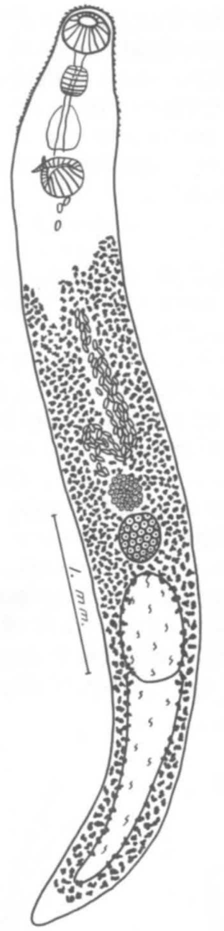


Fig. 435. *Scorpidicola californiensis.*

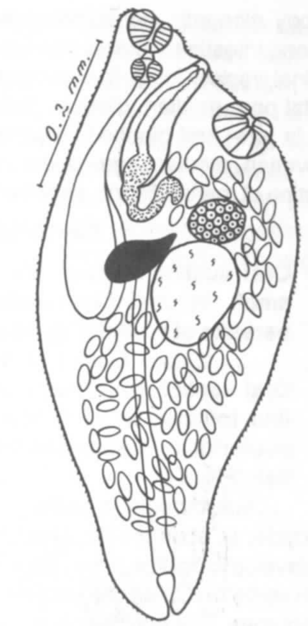


Fig. 436. *Dicrogaster fastigatus.*

Fig. 438. *Carassotrema mugilicola.*

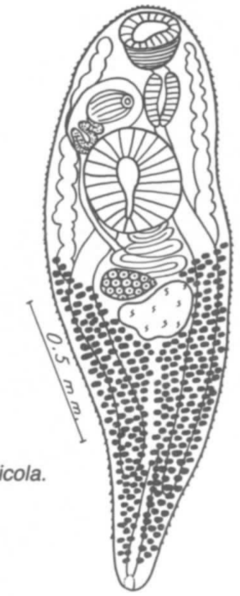


Fig. 439. *Hapladena leptotelea.*

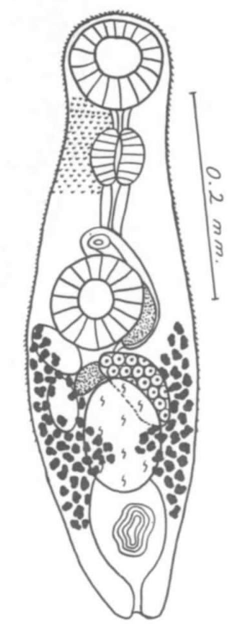


Fig. 440. *Saccocoelium beauforti.*

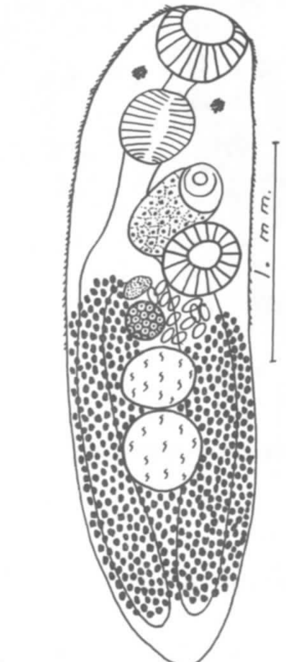


Fig. 441. *Megasolena estrix.* (from Linton, 1910)

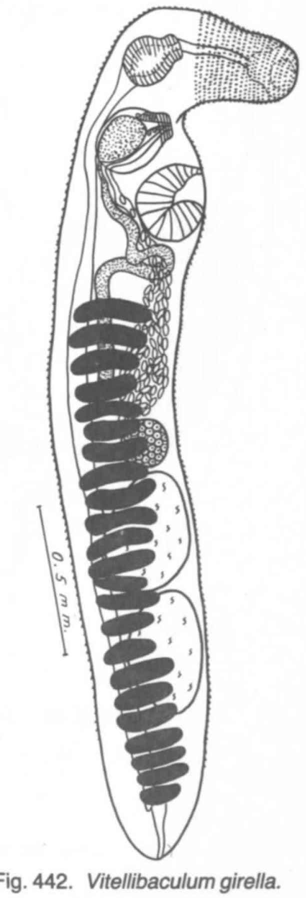


Fig. 442. *Vitellibaculum girella.*

Family Haplosplanchnidae Poche, 1925

Body elongate, nonspinous; suckers about equal; pharynx present; intestine a single cecum; one testis; cirrus sac absent; seminal vesicle long, free in parenchyma; ovary pretesticular; genital pore median, close to pharynx; vitelline follicles numerous, in fore- and hindbody, confluent posterior to testis; uterus preovarian, median; eggs operculate, embryonated; parasitic in intestine of marine fishes, especially mullet.

Key to Genera

1a. Oral sucker trilobed with papillae; vitelline follicles small, in chainlike clusters, confined to hindbody; parasite of mullet (Fig. 443). .... Genus *Hymenocottoides* Yamaguti, 1971

1b. Oral sucker doughnut-shaped, papillae absent; vitelline follicles in both fore- and hindbody, confluent posterior to testis; parasite of halfbeaks and needlefish (Fig. 444). .... Genus .....*Schikhobalotrema* Skrjabin and Guschanskaja, 1955

Life cycle: *S. acutum* - Oculate haplosplanchnid cercariae (Fig. 30) develop in sporocysts in the marine prosobranch snail, *Cerithium variable.* Cercariae encyst on vegetation in spherical cyst membranes. The adult parasite develops in the intestine of halfbeaks, *Hyporhamphus unifasciatus* and needlefish, *Strongylura* sp. which browse on the infested vegetation (Cable, 1954b).

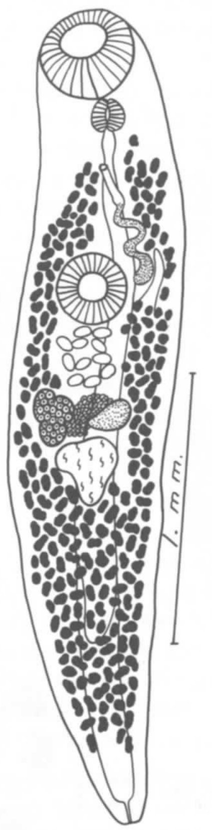


Fig. 444. *Schikhobalotrema kyphosi.* (from Manter, 1947)

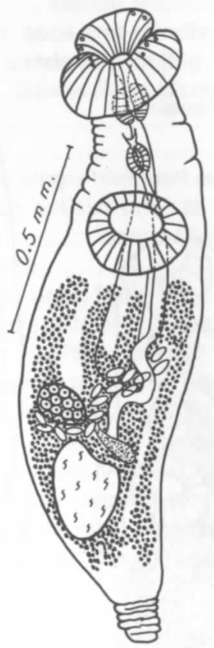


Fig. 443. *Hymenocottoides manteri.*

Family Megaperidae Manter, 1934

Body round, oval or elongate, spinous anteriorly; oral sucker larger than ventral sucker; pharynx wide, anterior margin lobed; intestinal ceca wide, opening through separate ani at posterior end of body; testes opposite, anterior to ventral sucker; cirrus sac absent; genital pore anterior to ventral sucker; ovary posttesticular, in hindbody; vitelline follicles fill most of hindbody; uterus entirely preovarian; excretory vesicle tubular parasitic in the intestine of trunk-, cow- and file-fishes.

Key to Genera

1a. Oral sucker without plasmic regions between muscle bands; oral sucker enclosed in fold of body wall (Fig. 445). .... Genus *Thysanopharynx* Manter, 1933

1b. Oral sucker with plasmic regions separating muscle bands; oral sucker not in fold of body wall (Fig. 446). . ... Genus *Megapera* Manter, 1934

Life cycle: *M. gyrina* - Oculate megaperid cercariae with ventral and lateral finfolds on the tail, develop in rediae in the gastropod, *Crepidula convexa.* Cercariae encyst on marine aquatic vegetation (Cable, 1954a).

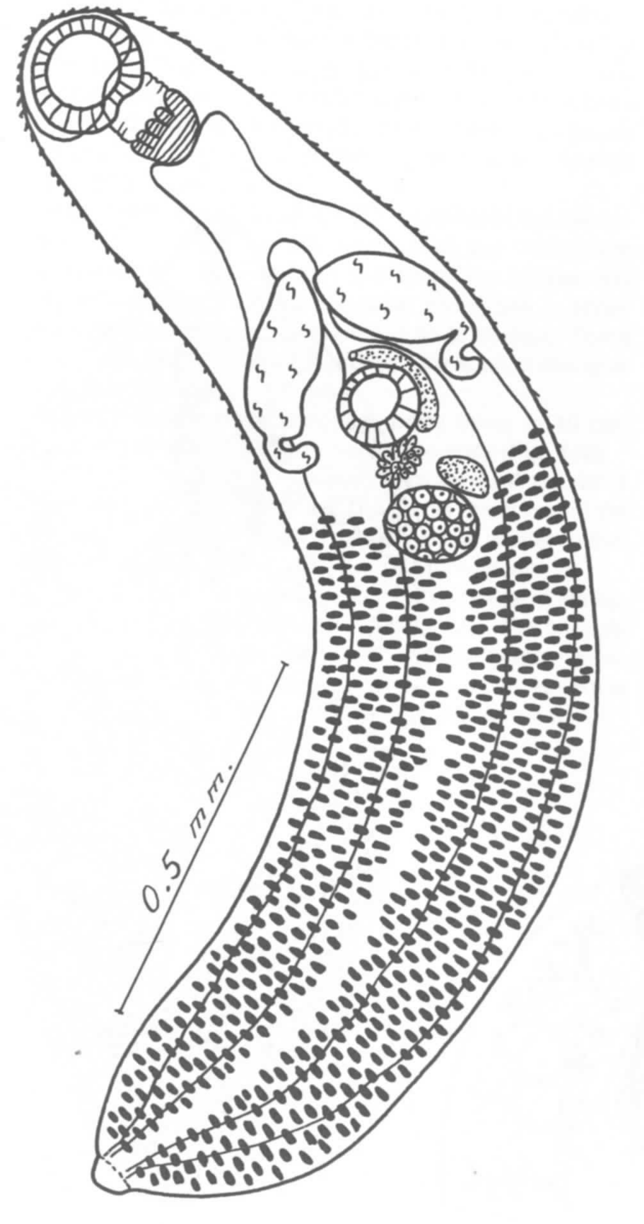


Fig. 445. *Thysanopharynx elongatus.*

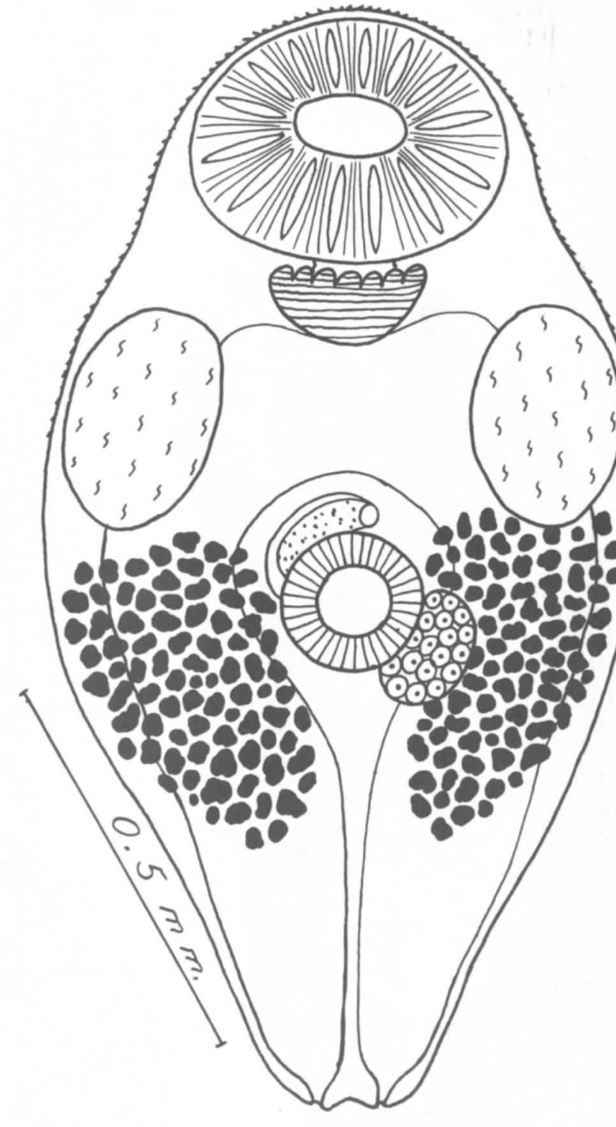


Fig. 446. *Megapera pseudura.*

Superfamily Fascioloidea Faust, 1929

Miracidia have one pair of flame cells; epidermal cell pattern is 6, 6, 3, 4, 2 or 6, 6, 6, 6, 6; cercariae are gymnocephalous, develop in a redia in gastropod molluscs and encyst on vegetation in spherical cyst membranes. Life cycle involves two hosts.

Family Fasciolidae Railliet, 1895

Body large (20 to 100 mm), flat, elliptical or oval, anterior end conical or rounded; ventral sucker in anterior fifth of body; pharynx small; ceca long, branched or unbranched; testes tandem, dendritic, in middle third of hindbody; cirrus sac anterio-dorsal to ventral sucker; genital pore median, between the suckers; ovary usually dendritic, pretesticular; vitelline follicles confined to hindbody, distributed around ceca, confluent posterior to testes; uterus preovarian; eggs operculate, nonembryonated; parasitic in liver, bile duct, gall bladder or upper small intestine of herbivorous mammals including human beings.

Key to Genera

1a. Intestinal ceca unbranched; ventral sucker much larger than oral sucker; body elliptical (Fig. 447). .... Genus *Fasciolopsis* Looss, 1899

Life cycle: *F. buski* - This genus is not represented in North America but in the Far East *F. buski* is a common parasite of swine and human beings. Miracidia develop within three to seven weeks after eggs are laid. Following hatching, they enter the planorbid snails, *Hippeutis cantori, Gyraulus saigonensis* and several species of the genus *Segmentina*. The miracidium metamorphoses to a sporocyst which then produces mother rediae which in turn produce daughter rediae. Some daughter rediae produce granddaughter rediae and cercariae simultaneously during warm weather. The latter produce gymnocephalous cercariae which after 45 days leave the snail

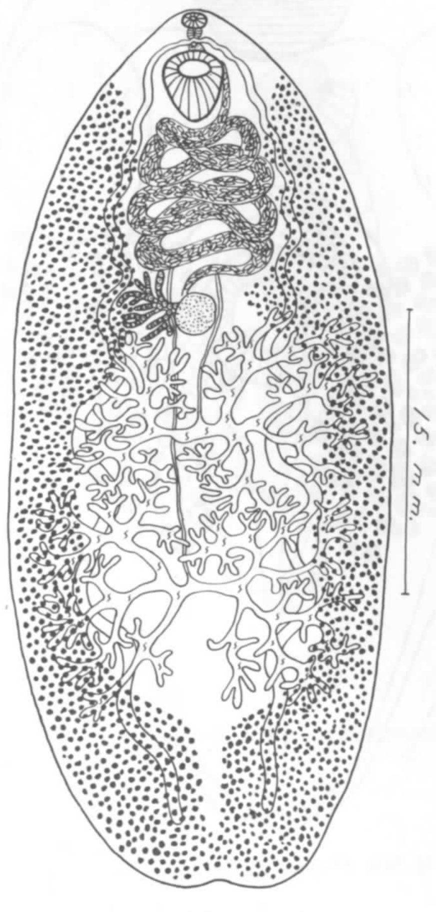


Fig. 447. *Fasciolopsis buski.*

Fig. 449. *Fascioloides magna.*

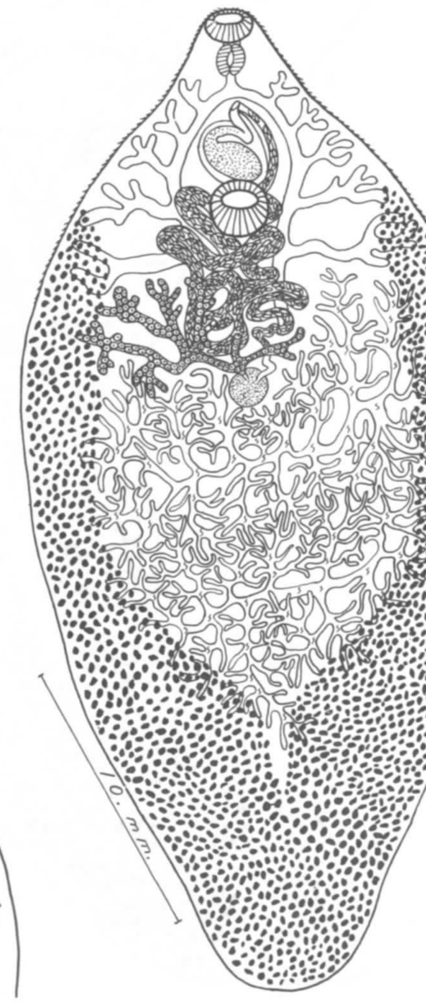


Fig. 448. *Fasciola hepatica.*

and encyst on vegetation. Important cysts are those on the seed pods of red ling and water chestnut. Human beings habitually eat the fruits by first removing the outer covering with their teeth, thus accidently ingesting metacercariae. The adult parasite develops in the upper fourth of the small intestine of swine and human beings (Barlow, 1925).

1b. Intestinal ceca have many branches; suckers about equal. 2

2a. Anterior end of body conical; body two to three cm. long; vitelline follicles dorsal and ventral to ceca (Fig. 448). .... Genus *Fasciola* Linn., 1758

Key to species in Skrjabin (1964).

Life cycle: *F. hepatica* - Miracidia develop in about 15 days after eggs are laid. They hatch and enter snails of many genera and species. Sporocysts and two generations of rediae develop in the snails. The daughter rediae produce gymnocephalous cercarae (Fig. 48) which leave the snail and encyst on aquatic vegetation. Definitive hosts such as sheep, cattle, goats, rabbits, deer and human beings accidently ingest the metacercariae with their forage. The metacercariae perforate the intestine, enter the coelom and then penetrate the outer surface of the liver. Human beings have been known to become infected by eating water cress or by using lettuce or endive grown under irrigation (Leuckart, 1882; Thomas, 1883).

Ogambo-Ongoma and Goodman (1976) investigated the larval stages of *F. gigantica* and found that the miracidium changed directly to a redia instead of a sporocyst. Mother and daughter rediae were produced, the latter giving rise to either third generation rediae and/or cercariae in 45 to 50 days. There were also some fourth generation rediae. The adult of this species attains a length of 60 to 120 mm.

2b. Anterior end of body rounded; body three to 10 cm. long; vitelline follicles only ventral to ceca (Fig. 449). .... Genus *Fascioloides* Ward, 1917

F. magna is the only species in the genus and is one of the largest known trematodes. The life cycle is similar to that of *Fasciola heptica*, using many of the same hosts.

The adults inhabit the liver and sometimes the lungs of sheep, cattle, horses, elk and deer, encapsulated in pairs. The capsule wall is sometimes calcareous. The black pigment melanin is secreted into the excretory system of the parasite. This pigment is then released into the capsules making them appear black.

Superfamily Orchipedioidea Mehra, 1961
Family Orchipedidae Skrjabin, 1924

Body elongate, nonspinous; suckers well developed; ceca long; testes multiple, intercecal; cirrus sac absent; ovary pretesticular; genital pore median, anterior to ventral sucker; vitelline follicles lateral to ceca in hindbody; uterus entirely preovarian; excretory vesicle tubular; parasitic in nasal cavities, trachea and esophagus of birds.

The genus *Orchipedum* Braun, 1901 (Fig. 450) is represented in North America by several species.

Key to species in Schell (1967b).

Life cycle: Metacercariae have been found in shrimp and crayfishes. A supposedly progenetic metacercaria was found beneath the tergites of the freshwater shrimp, *Leander fluminicola* in India. They were not encysted, only attached by suckers to the tergites. A partially developed uterus was present (Farooqi, 1958).

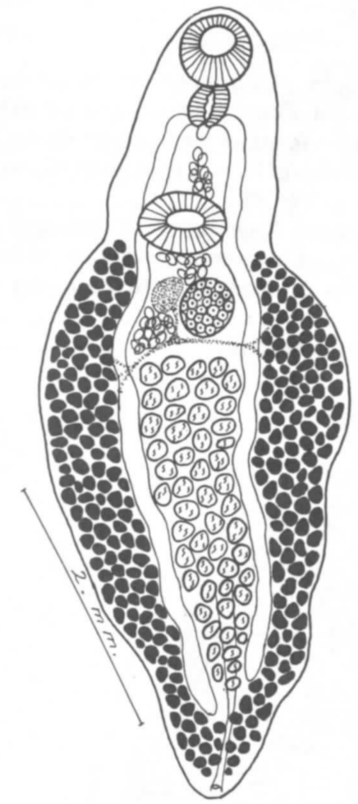


Fig. 450. *Orchipedum tracheicola.*

Suborder Cyclocoelata LaRue, 1957
Superfamily Cyclocoeloidea Nicoll, 1934

Miracidia have one pair of flame cells, contain a redia and have an epidermal cell formula of 6, 9, 4, 2 or 4, 7, 4, 2. Cercaria tailless (cercariaeum) with one, two or no suckers; develop in a redia in pulmonate snails; encyst in the redia or in tissues of the snail. Life cycle involves two hosts.

Family Cyclocoelidae Kossack, 1911

Body large (up to 15 mm), translucent, flat, oval or fusiform, nonspinous; suckers absent or vestigial; pharynx present; ceca with or without diverticula, fused posteriorly to form cyclocoel; testes two or multiple, usually close to posterior end of body; cirrus sac present; genital pore close to pharynx; ovary pre-, inter- or posttesticular; vitelline follicle along ceca, sometimes confluent posteriorly; uterus fills intercecal area anterior to gonads; eggs operculate, embryonated; parasitic in nasal sinuses and respiratory tract of birds.

Key to Genera

1a. Testes multiple, along inner margin of ceca; uterine folds intercecal; ovary median, near cecal arch; cirrus sac long, extends some distance posterior to cecal bifurcation; vitellaria form a reticulum along cyclocoel; parasite of *Ibis* (Fig. 451). .... **Genus *Polycyclorchis* Pence and Bush, 1973**

1b. Two testes, usually near posterior end of body. 2

2a. Ceca have six or more diverticula along their inner surface. 3

2b. Ceca without diverticula. 4

3a. Testes lobed, not separated by folds of uterus (Fig. 452). .... **Genus *Typhlocoelum* Stossich, 1902**

Key to species in Skrjabin (1964) and in Fotedar (1965).

3b. Testes round, separated by some folds of uterus (Fig. 453). .... **Genus *Tracheophilus* Skrjabin, 1913**

Life cycle: *T. cymbium* - Miracidia, which hatch from embryonated eggs at time of oviposition, already contain a redia. They penetrate the pulmonate snail, *Helisoma trivolvis* then release the redia which grows and eventually produces tailless cercariae. They leave the redia and encyst in the same snail. Cercariae and metacercariae have a cyclocoel. The ventral sucker is resorbed in the metacercarial stage. The definitive host becomes infected by eating the infected snails. The adult parasite develops in the mouth, nasal cavities, trachea and bronchi of ducks, geese and grebes (Stunkard, 1934).

Sreekumaran and Peters (1973) studied this species in India where the host mollusc is *Indoplanorbis exustus*. Eggs could not be found in the feces of ducks. It was assumed that they leave the bird by way of the nasal excretions when ducks drink water. Adult parasites were sometimes coughed up by the birds.

Szidat (1932) investigated the life cycle of *T. sisowi* which is considered to be a synonym of *T. cymbium*. Following the ingestion of infected snails, the metacercariae excyst then enter the blood vessels of the intestinal mucosa or invade the coelom. Those that eventually get to the lungs develop to sexual maturity in the trachea and bronchi.

4a. Ovary posterior to testes; testes some distance from posterior end of body; genital pore anterior to pharynx; uterine folds intercecal in anterior third of body but overlap ceca in remainder of body; parasitic in nasal and orbital sinuses of birds (Fig. 454). .... **Genus *Ophthalmophagus* Stossich, 1902**

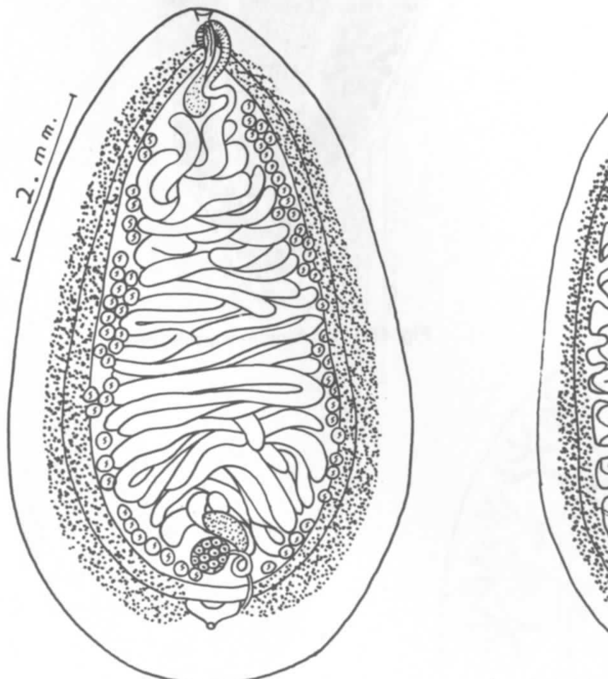


Fig. 451. *Polycyclorchis eudocimae.* (from Pence and Bush, 1973)

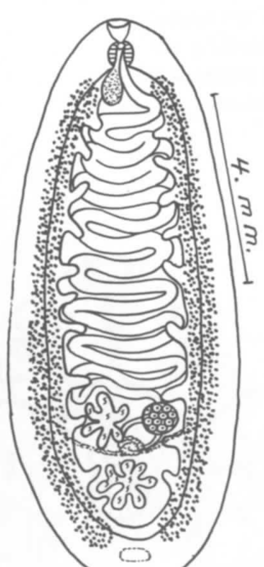


Fig. 452. *Typhlocoelum cucumerinum.*

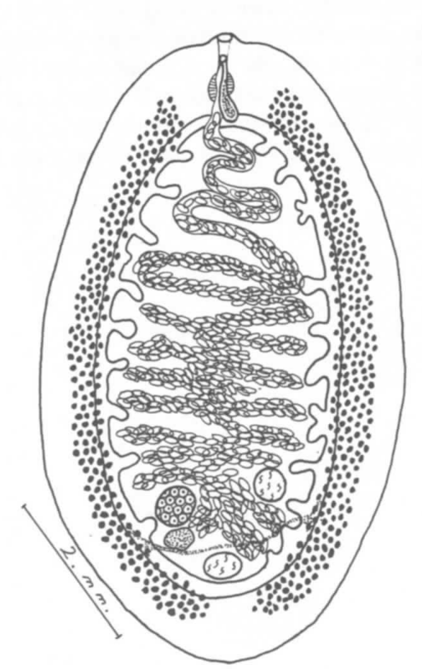


Fig. 453. *Tracheophilus sisowi.*

Life cycle: *Ophthalmophagus singularis* - The adult parasite inhabits the nasal cavities and orbits of the clapper rail, *Rallus longirostris.* The miracidium which already contains a tiny redia develops and hatches in the uterus of the adult worm. They then leave the uterus, attach to the tissues of the marine snails, *Melampus bidentatus* and *Detracia floridanus.* The redia is then released from the miracidium and penetrates the snail tissues. Only one generation of redias is produced. Tailless cercariae (cercariaea) develop and encyst in the redia. Rails are thought to become infected by eating the metacercariae in infected snails (Taft and Heard, 1978).

4b. Ovary either between or anterior to one or both testes; testes close to posterior end of body. 5

5a. Ovary between testes; gonads in a straight line; some uterine folds between testes; genital pore posterior to pharynx (Fig. 455). .... **Genus *Morishitium* Witenberg, 1928 (= *Pseudhyptiasmus* Dollfus, 1948)**

Life cycle: *M. dollfusi* - Miracidia contain a redia but they do not hatch in water. Instead, embryonated eggs were fed to the terrestrial snail, *Helicella arenosa* in which hatching apparently occurs. Cercariae with a rudimentary bilobed tail develop in the redia in which the cercariae also encyst. The metacercaria loses the tail. Experimental infections were established in pigeons, crows and sparrows. The natural definitive hosts are magpie, sparrows and crows in which the parasite inhabits the air sacs. The complete cycle requires about 140 days (Timon-David 1955a, 1957b).

5b. Ovary pretesticular or opposite anterior testis; gonads form a triangle. 6

6a. Uterine folds chevron-like, some folds embracing gonads laterally, folds may extend to body margins; no uterine folds between testes; parasitic in abdominal air sacs of avocet (Fig. 456). .... **Genus *Haematotrephus* Stossich, 1902**

6b. Uterine folds not chevron-like, mostly intercecal; some folds between testes; folds do not embrace gonads (Fig. 457). ... **Genus *Cyclocoelum* Brandes, 1892**

Key to species in Skrjabin (1964).

Life cycle: *C. mutabile* - Miracidia which already contain a redia, hatch and partially penetrate a snail. The redia escapes and enters the tissues of pulmonate snails of the genera *Helisoma, Gyraulus, Promenetus, Armigera, Physa* and *Lymnaea.* Tailless cercariae develop in the redia and later leave it and encyst in the tissues of the snail. Metacercariae are infective to coots, *Fulica americana* and *F. atra* and also to several species of ducks. Adults develop in the air sacs, trachea and bronchi within 30 days following ingestion of metacercariae. Newly excysted metacercariae penetrate the intestinal wall, enter the coelom then penetrate the liver where they remain for about 12 days. They then return to the coelom and enter the air sacs. Eggs must pass from the air sacs to the lungs for elimination from the birds (McLaughlin, 1976, 1977a).

McLaughlin (1977b) also reported a similar life cycle for *C. oculeum* which also parasitizes coots.

Taft (1973) studied the life cycle of *C. obscurum* which uses *Gyraulus hirsutus* as host mollusc. Encysted metacercariae were first observed in the redia at 14 days. Snipes, godwits and willets serve as definitive hosts.

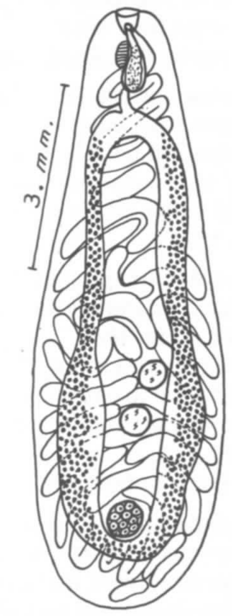


Fig. 454. *Ophthalmophagus singularis.* (from Kossack, 1911)

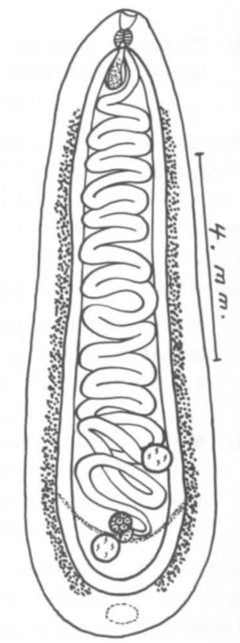


Fig. 455. *Morishitium dumetellae.*

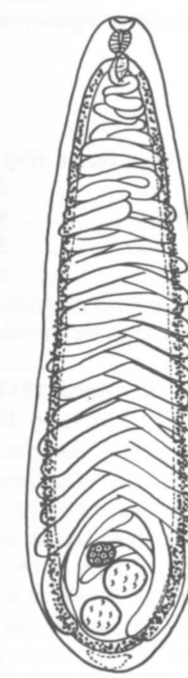


Fig. 456. *Haematotrephus lanceolatum.*

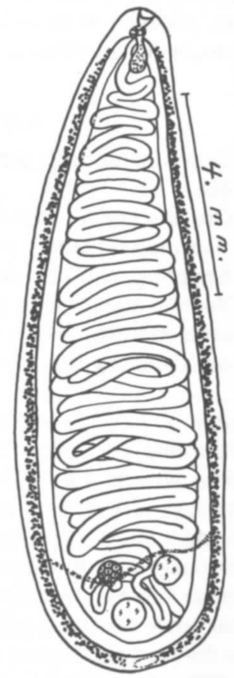


Fig. 457. *Cyclocoelum mutabile*

Suborder Paramphistomata Szidat, 1936

Miracidia have one pair of flame cells. Cercariae oculate, amphistomate or monostomate; cystogenous glands abundant; penetration glands and stylet absent; cercariae leave redia before they attain full development and complete development in tissues of snail; cercariae encyst on vegetation in hemispherical cyst membranes or remain in sporocyst (Heronimidae) and metamorphose to metacercariae without encysting; excretory system stenostomate. Life cycle involves two hosts.

Superfamily Paramphistomoidea Stiles and Goldberger, 1910

Cercaria, metacercaria and adult are all amphistomate; cercariae develop in a redia or in a branched sporocyst; no adhesive glands at posterior end of body of cercaria; main collecting ducts of excretory system not united in anterior part of body; lymph system well developed in adults.

Family Paramphistomidae Fischoeder, 1901

Body thick, muscular, nonspinous; oral sucker usually terminal, frequently with a pair of muscular diverticula; ventral sucker at posterior end of body; pharynx absent; esophagus may have muscular bulb at posterior end; ceca long; testes tandem or oblique; cirrus sac present or absent; ovary posttesticular; vitelline follicles distributed along ceca; uterus intercecal; genital pore median, ventral to esophagus or near cecal bifurcation; eggs operculate, embryonated or nonembryonated; excretory pore dorsal, near posterior end of body; extensive lymph system present; parasitic in colon or cloaca of vertebrates. Epidermal cell formula of miracidium 6, 8, 4, 2.

Key to Genera

1a. Oral sucker with a pair of muscular diverticula (Fig. 458). 2
1b. Oral sucker without muscular diverticula. 9
2a. Esophageal bulb present (Fig. 458). 3
2b. Esophageal bulb vestigial or absent. 8
3a. Ventral sucker with pair of muscular papillae on posterior margin; testes and ovary lobed; parasitic in colon or cloaca of birds (Fig. 458). .... **Genus *Zygocotyle* Stunkard, 1917**

Life cycle: *Z. lunata* - Miracidia develop and hatch in 20 to 40 days following oviposition. They penetrate the pulmonate snail, *Helisoma antrosum* in which amphistome cercariae *(Cercaria poconensis)* develop in a redia. Some rediae produce only cercariae while others produce cercariae and daughter rediae simultaneously. After emergence, the cercariae encyst on aquatic vegetation in brown hemispherical membranes. Ducks serve as the main definitive host but chickens, turkeys and geese also harbor the parasite. Sexual maturity is attained in 41 to 44 days in the colon and ceca. Experimental infections were established by feeding metacercariae to rats and sheep (Willey, 1930, 1936, 1941).

3b. Ventral sucker without muscular papillae. 4
4a. Vitelline follicles few, located either ventral or medial to ceca; parasitic in frogs, toads, newts or snakes. 5
4b. Vitelline follicles abundant, located both medial and lateral to ceca; parasitic in turtles. 7

5a. Ventral sucker about twice as large as oral sucker; vitelline follicles medial to ceca; parasitic in toads and snakes (Fig. 459). .... **Genus *Ophioxenos* Sumwalt, 1926**
5b. Ventral sucker at least four times as large as oral sucker and having a naval-like papilla in center of sucker. 6
6a. Vitelline follicles entirely medial to posterior ends of ceca; parasitic in colon of newts (Fig. 460). .... **Genus *Pseudophisthodiscus* Yamaguti, 1958 (= *Opisthodiscus* Hall, 1928)**
6b. Vitelline follicles chiefly ventral to ceca; parasitic in colon and cloaca of amphibians (Fig. 461). .... **Genus *Megalodiscus* Chandler, 1923**

Key to species in Skrjabin (1964).

Life cycle: *M. temperatus* - Eggs are embryonated when laid. Miracidia hatch and penetrate snails of three species of the genus *Helisoma* in which they change to the sporocyst stage. Amphistome cercariae develop in daughter rediae. After leaving the snail they encyst in the skin of frogs and tadpoles. Frogs become infected when they eat pieces of shed epidermis or when eating tadpoles. The adult flukes develop in the cloaca and colon of frogs. The limpet, *Ferrissia fragilis* has also been reported as a possible host mollusc for the larval stages (Krull and Price, 1932; Herber, 1938, 1939; Smith, 1967).

Macy (1960a) found the life cycle of *M. microphagus* to be similar to that of *M. temperatus* except for species of hosts. The host snails are *Menetus cooperi* and *Gyraulus* sp. The definitive hosts are *Hyla regilla, Rana aurora* and *Taricha granulosa*.

7a. Testes round, small, oblique; vitelline follicles small, abundant (Fig. 462). .... **Genus *Allassostoma* Stunkard, 1917**
7b. Posterior end of body with corner-like projections; testes multi-lobed; parasitic in turtles (Fig. 464). .... **Genus *Allassostomoides* Stunkard, 1925**

Life cycle: *A. parvus* - Amphistome cercariae develop in daughter rediae in *Helisoma trivolvis* and *H. antrosum*. After leaving the snail they encyst on aquatic vegetation and on skin of tadpoles or on exoskelton of crayfishes. The adult fluke develops in the colon, cloaca and urinary bladder of turtles which eat the cysts with their food (Beaver, 1929; Krull, 1933).

8a. Main excretory ducts united dorsal to esophagus; vitelline follicles present only along posterior half of ceca; parasitic in intestine of fishes (Fig. 463). .... **Genus *Cleptodiscus* Linton, 1910**
8b. Main excretory ducts not united dorsal to esophagus; vitelline follicles all along ceca and esophagus; parasitic in colon of muskrat (Fig. 466). .... **Genus *Wardius* Barker and East, 1915**

Life cycle: *W. zibethicus* - Amphistome cercariae develop in rediae in the freshwater snail, *Helisoma antrosum*. After leaving the snail they encyst on vegetation or other substrates. Metacercariae were fed to mice, hamsters and guinea pigs and partially developed adults recovered. The natural definitive host is muskrat (Murrell, 1963, 1965).

9a. Oral sucker retracted within body and preceded by cylindrical vestibule; esophageal bulb present; retractor muscles well developed; testes tetralobed; parasitic in mammals (Fig. 465). .... **Genus *Chiorchis* Fischoeder, 1901**
9b. Oral sucker and testes not as described above. ... 10
10a. Testes dendritic, tandem; vitelline follicles restricted to posterior half of ceca; parasitic in cecum and colon of beaver (Fig. 468). .... **Genus *Stichorchis* Fischoeder, 1901**

Life cycle: *S. subtriquetrus* - Miracidia develop and hatch in about one month after eggs are laid. The miracidium already contains a mother redia which is released as the miracidium penetrates the host gastropod. *Fossaria parva* is first intermediate host in North America. In Russia, *Planorbis vortex, Lymnaea vortex, L. ovata* and *Bithynia tentaculata* have been found to serve as hosts. The mother redia produces daughter rediae which in turn produces amphistome cercariae. After leaving the snail, the cercariae encyst on aquatic vegetation and other aquatic substrates. The adult develops in the cecum of beaver, *Castor canadensis*, which eats the infested vegetation (Bennett and Humes, 1939; Orloff, 1941; Bennett and Allison, 1957).

10b. Testes lobed or round, tandem or oblique; vitelline follicles distributed along full length of ceca. 11
11a. Testes round, small, oblique; esophagus with muscular bulb; parasitic in the intestine of fishes (Fig. 467). .... **Genus *Pisciamphistoma* Yamaguti, 1954**
11b. Testes lobed, large, tandem; esophagus without muscular bulb; parasitic in rumen of mammals. 12
12a. Muscular genital sucker encloses genital pore (Fig. 470). .... **Genus *Cotylophoron* Stiles and Goldberger, 1910**

Life cycle: *C. cotylophorum* - Miracidia develop and hatch within 10 to 29 days after eggs are laid. They penetrate the freshwater snails, *Fossaria parva* and *F. modicella* in which a generation of sporocysts and one of rediae are produced. Two redial generations are known to develop in some cases. Amphistome cercariae develop, emerge from the redia and the snail, then encyst on aquatic vegetation which is in turn eaten by the ruminant mammals. Five to eight months are required for completion of the entire cycle. The mature flukes are in the rumen of the host (many authors).

Mukherjee (1968) investigated the life cycle of *C. indicum* in India. Miracidia developed and hatched in 10 to 15 days at 32 to 35 C. They penetrate the pulmonate snail, *Indoplanorbis exustus* which were laboratory-reared and served as experimental and the natural intermediate host. Amphistome cercariae (*Cercaria indicae* XXVI) developed in 30 to 36 days. Some rediae produced cercariae and daughter rediae simultaneously. Encysted metacerariae were fed to a parasite-free goat and adult flukes were recovered from the rumen and reticulum in about five months.

12b. Muscular genital sucker absent (Fig. 469). .... **Genus *Paramphistomum* Fischoeder, 1901**

Life cycle: *P. cervi* - A generation of sporocysts followed by mother and daughter rediae develop in pulmonate snails of the genera *Physa, Bulinus, Galba* and *Pseudosuccinea*. The daughter rediae produce amphistome cercariae *(Cercaria pigmentata)* which encyst on aquatic vegetation in hemispherical cyst membranes. Sheep, cattle and goats eat the cysts with their forage. Metacercariae excyst in the duodenum then pass forward to the rumen where they develop to maturity (many authors).

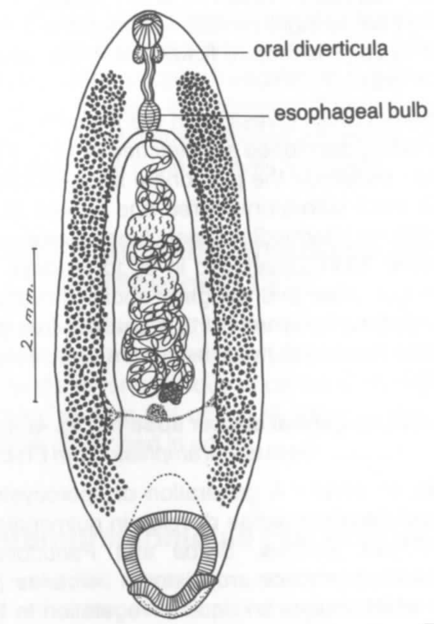


Fig. 458. *Zygocotyle lunata*

Fig. 459. *Ophioxenos dienteros.*

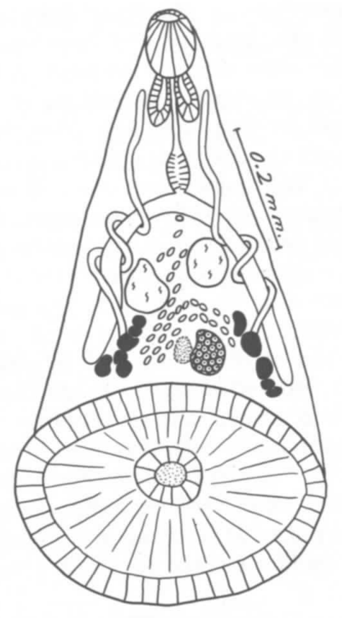


Fig. 460. *Pseudopisthodiscus americanus.* (from Holl, 1928)

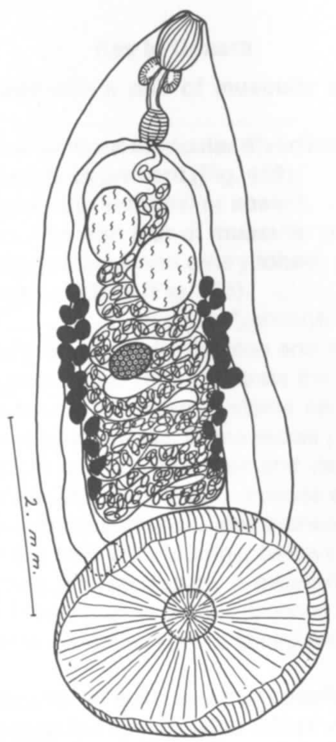


Fig. 461. *Megalodiscus temperatus.*

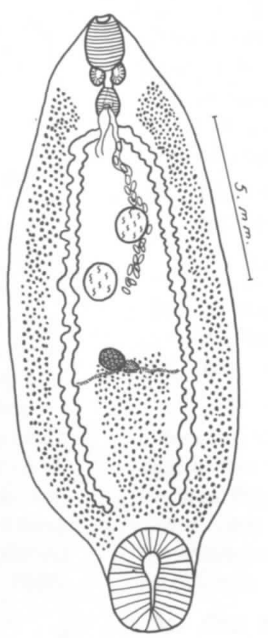


Fig. 462. *Allassostoma magnum.*

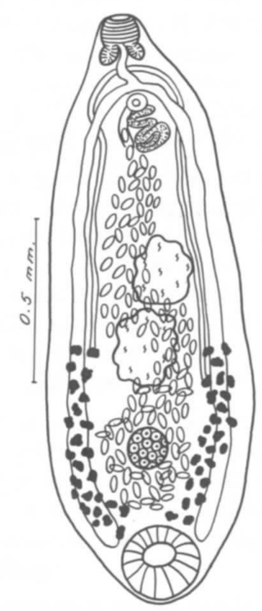


Fig. 463. *Cleptodiscus reticulatus.*

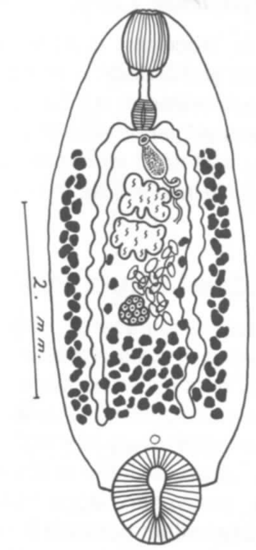


Fig. 464. *Allassostomoides chelydrae.*

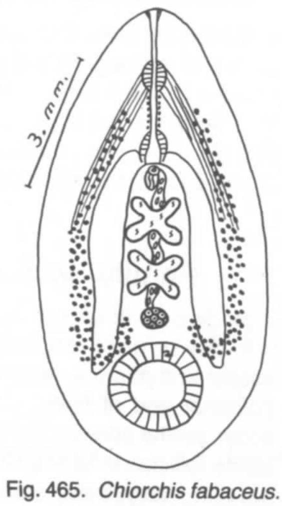


Fig. 465. *Chiorchis fabaceus.* (from Price, 1932)

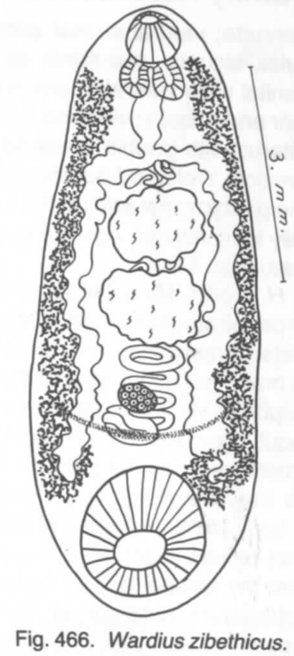


Fig. 466. *Wardius zibethicus.*

Fig. 467. *Pisciamphistoma stunkardi.*

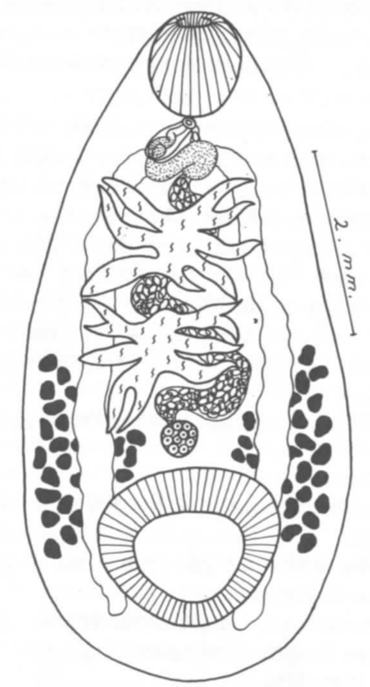


Fig. 468. *Stichorchis subtriquetrus.*

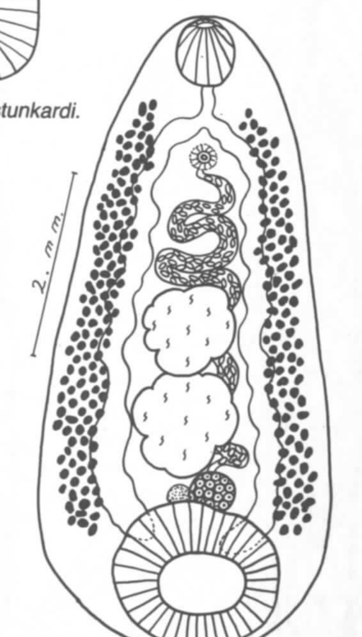


Fig. 470. *Cotylophoron cotylophorum.*

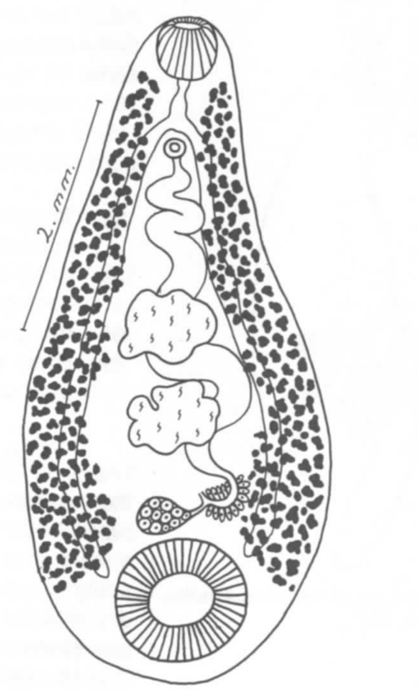


Fig. 469. *Paramphistomum cervi.*

Family Heronimidae Ward, 1917

Body elongate; ventral sucker absent; intestinal ceca long; testes tubular, sinuous, two-thirds as long as body; cirrus sac present; genital pore ventral to oral sucker; ovary pretesticular, near anterior end of body; vitellaria tubular, three-fourths as long as body; uterus with double descending and ascending limbs; excretory vesicle Y-shaped but inverted with the excretory pore dorsal to the pharynx; parasitic in the lungs of turtles.

The family is monotypic, containing only *Heronimus mollis (= H. chelydrae)* (Fig. 471).

Life cycle: *H. mollis*- Miracidia hatch while eggs are still in the uterus and penetrate pulmonate snails of the genus *Physa* upon entering water. Amphistome cercariae with flame cells in the tail, develop in branched sporocysts in the snails. The cercariae remain the sporocysts and metamorphose to the metacercaria stage without encysting. Turtles eat the infected snails. In turtles, the metacercariae migrate to the lungs by way of the esophagus larynx and trachea. As they develop to the adult stage, the body expands ventrally and the ventral sucker is resorbed. This results in shifting the excretory pore to the dorsal surface near the anterior end of the body. Three months are required for development to sexual maturity in the turtle. The amphistome cercaria indicates relationship to trematodes in the family Paramphistomatidae (Ulmer, 1960, Crandall, 1960; Lynch, 1934).

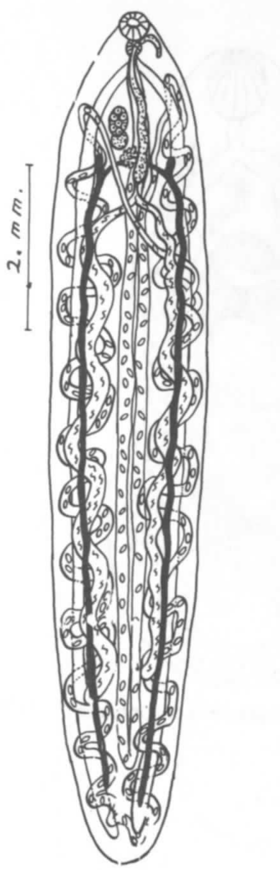


Fig. 471a. *Heronimus mollis*

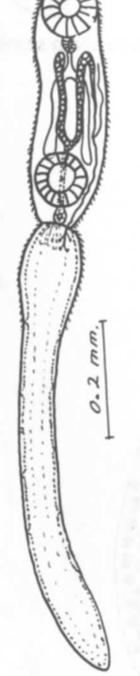


Fig. 471 b. Cercaria of *Heronimus mollis*. (from Crandall, 1960).

Superfamily Notocotyloidea LaRue, 1957

Cercariae monostomate, bi- or trioculate, usually with one pair of adhesive glands at posterior end of body; excretory pores at sides of tail; main excretory ducts united by a transverse duct in anterior part of body; cystogenous glands present; penetration glands absent; metacercaria and adult monostomate; cercariae encyst on vegetation; life cycle involves two hosts.

Family Notocotylidae LaRue, 1957

Body oval or elongate, flat; ventral surface of body usually with one or more longitudinal ridges or rows of glands; ventral sucker and pharynx absent; ceca long; testes opposite, close to posterior end of body; cirrus sac elongate, in anterior half of body; genital pore ventral to esophagus; ovary intertesticular; vitelline follicles in lateral clusters, usually anterior to testes; uterus with many transverse folds, preovarian; eggs operculate, have long bipolar filaments, embryonated; parasitic in intestine and ceca of birds and mammals.

Key to Genera

1a. Vitelline follicles anterior and lateral to testes; parasites of birds (Fig. 473). .... Genus *Hofmonostomum* Harwood, 1939
1b. Vitelline follicles entirely anterior to testes. 2
2a. Body broadly oval, without ventral longitudinal ridges or rows of glands; parasitic in birds and mammals (Fig. 474). .... Genus *Paramonostomum* Lühe, 1909

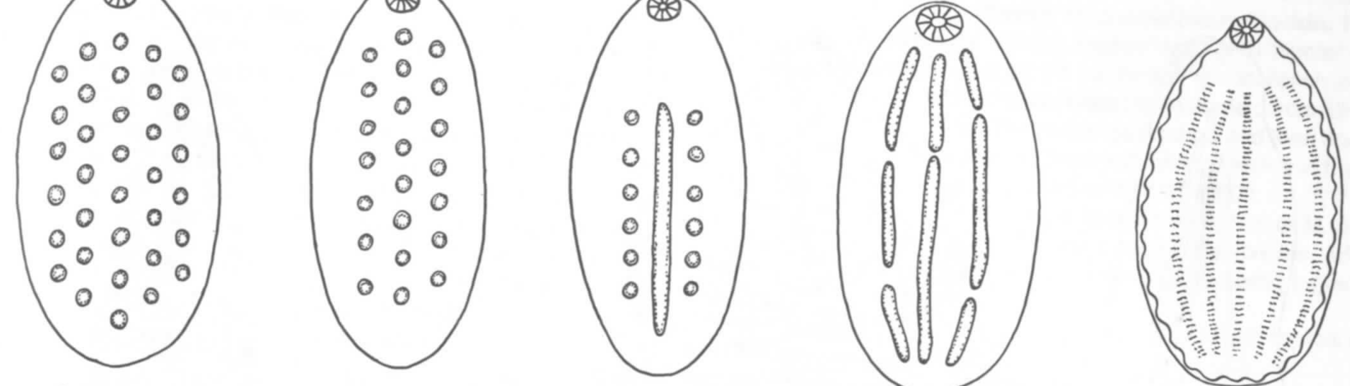
Life cycle: *P. alveatum* and *P. parvum* - Oculate monostomate cercariae develop in rediae in the prosobranch snail, *Hydrobia salsa*. They emerge from the snail and encyst on vegetation, snail shells and on other substrates. Metacercariae were fed to day-old chicks, laboratory-reared eider ducks and domestic ducklings and the adult flukes recovered from the intestine. Adults are known to penetrate between the villi and cause injury to the mucosa of the intestine. Many species of anseriform birds serve as natural definitive host for this parasite (Kulachkova, 1954; Stunkard, 1967).

The life cycle of *P. philippinensis* was investigated by Velasquez (1969a).

2b. Body oval or elongate, with longitudinal ridges or rows of glands. 3
3a. Body with two to five longitudinal rows of glands or both glands and ridges. 4
3b. Body with one to many longitudinal ridges. 6
4a. Body with five longitudinal rows of glands; parasitic in mammals (Fig. 475). .... Genus *Quinqueserialis* Skwortzow, 1935

Life cycle: *Q. quinqueserialis* - Embryonated eggs are eaten by the freshwater pulmonate snail, *Gyraulus parvus*. Miracidia hatch in the snail intestine, penetrate the intestinal wall and transform to sporocysts. Mother and daughter rediae are eventually produced, the latter give rise to monostome cercariae which leave the snail and encyst in hemispherical cyst membranes on vegetation. The adult trematodes develop in the cecum of muskrat, meadow voles and jumping mouse in about 14 days after cysts are ingested (Herber, 1942).

4b. Body with two or three longitudinal rows of glands. 5



a. *Quinqueserialis* b. *Notocotylus* c. *Catatropis* d. *Tristriata* e. *Ogmogaster*

Fig. 472. Ventral glands of notocotylids:

5a. Ventral surface of body with three longitudinal rows of glands (Fig. 476). .... Genus *Notocotylus* Diesing, 1839

Life cycle: *N. stagnicolae* - Embryonated eggs are eaten by the pulmonate snail, *Stagnicola emarginata* in which miracidia hatch and metamorphose to a mother sporocyst after penetrating the intestinal wall. Later mother and daughter rediae develop, the latter produce monostome cercariae which, after leaving the snail, encyst on vegetation in hemispherical cyst membranes. The adult parasite develops in several species of ducks and in chickens which eat the metacercariae (Herber, 1942).

Stunkard (1966b) studied the life cycle of *N. atlanticus* a marine species. The host snail is *Hydrobia salsa*, a prosobranch. The natural definitive host is the eider duck.

5b. Ventral surface of body with a median longitudinal ridge and a row of glands on each side of the ridge (Fig. 477). .... Genus *Catatropis* Odhner, 1905

Life cycle: *C. johnstoni* - Monostome cercariae develop in rediae in the marine prosobranch snail, *Cerithidea californica* and encyst on vegetation. Metacercariae, fed to baby chicks, developed to sexual maturity in 9 to 13 days (Martin, 1956)

Rohde and Lee (1967) studied the life cycle of *C. indica*.

6a. Ventral surface of body with three longitudinal ridges; parasitic in birds (Fig. 478). .... Genus *Tristriata* Belopolskaia, 1953
6b. Ventral surface of body with 3 or more longitudinal ridges, each ridge composed of numerous transverse rows of tiny glands; parasitic in marine mammals (Fig. 479). .... Genus *Ogmogaster* Jagerskiold, 1891

Family Nudacotylidae Barker, 1916

Body pyriform or oval, concave ventrally, nonspinous; ventral sucker and pharynx absent; ceca long; testes opposite, lobed, near posterior end of body; cirrus sac transverse, in posterior third of body; male and female genital pores separated, anterior to right testis; ovary lobed, intertesticular; vitelline follicles in paired lateral clusters, anterior to testes; uterus has many transverse folds, anterior to gonads; eggs have bipolar filaments; parasitic in small intestine and bile duct of mammals.

The genus *Nudacotyle* Barker, 1916 is represented in North America by *N. novicia*, a parasite of rodents (Fig. 480).

Life cycle: *N. novicia* - Embryonated eggs in feces of host are eaten by the operculate snail, *Pomatiopsis lapidaria* in which a sporocyst and two generations of rediae develop. Monostome cercariae (Fig. 31) develop in daughter rediae and after leaving the snail, encyst in hemispherical cyst membranes on aquatic vegetation. The metacercariae are eaten with the vegetation. The adult trematodes develop in the bile duct of the meadow mouse, *Microtus pennsylvanicus* or in the small intestine of the muskrat, *Ondatria zibethicus* (see Ameel, 1944).

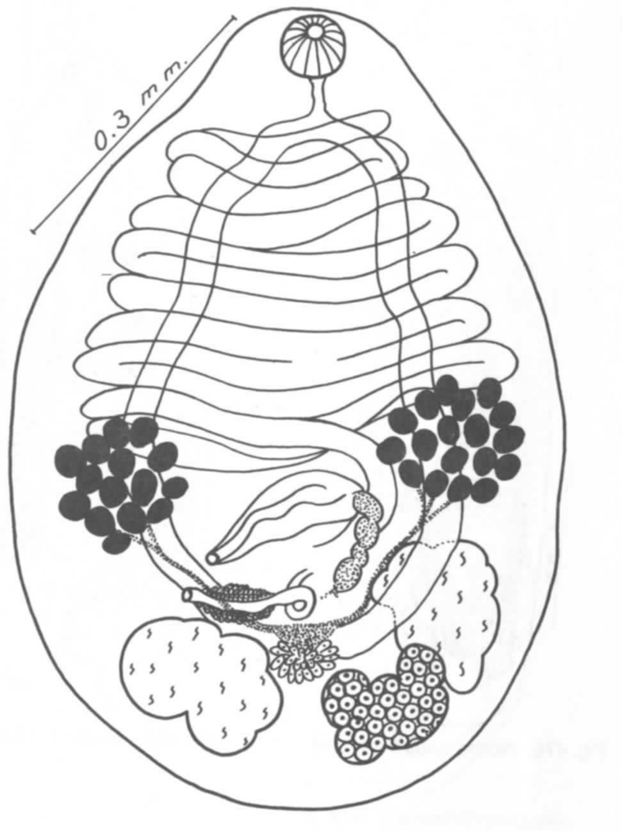


Fig. 480. *Nudacotyle novicia*.

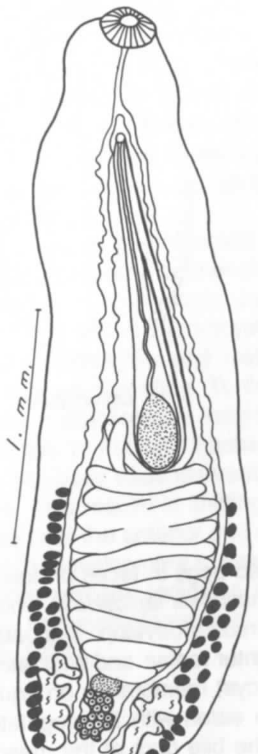


Fig. 473. *Hofmonostomum himantopodis.* (from Harwood, 1939)

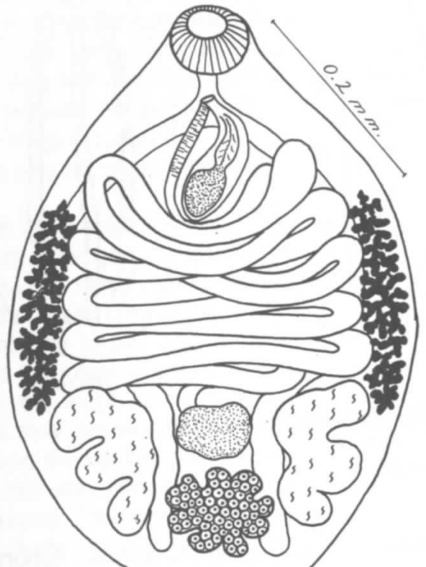


Fig. 474. *Paramonostomum alveatum.*

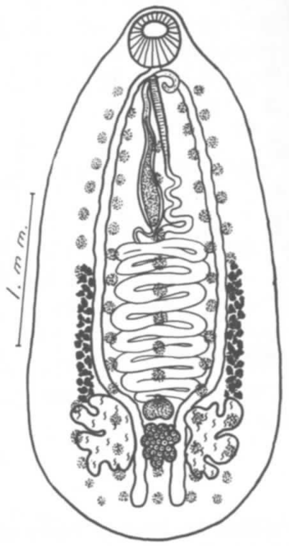


Fig. 475. *Quinqueserialis quinqueserialis.*

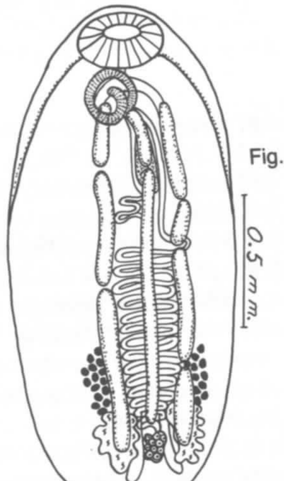


Fig. 478. *Tristriata anatis.* (from Belopolskaya in Skrjabin, 1953)

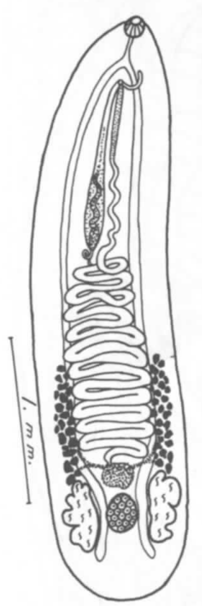


Fig. 476. *Notocotylus filamentis.*

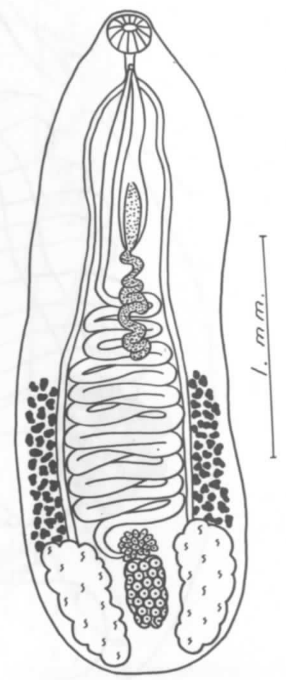


Fig. 477. *Catatropis harwoodi.*

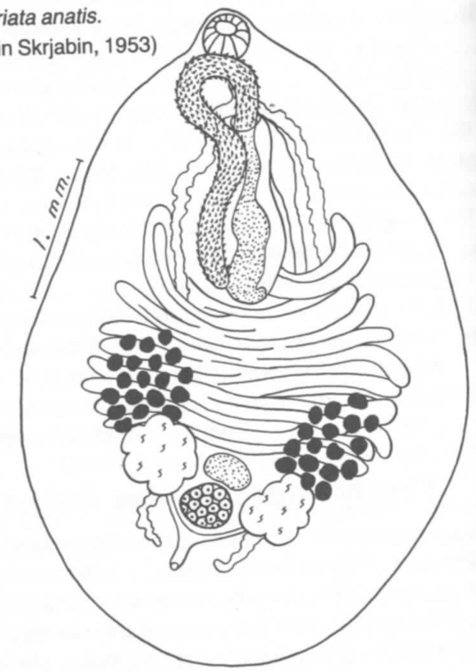


Fig. 479. *Ogmogaster trilineatus.*

Family Pronocephalidae Looss, 1902

Body elongate with parallel sides; triangular nonspinous head collar present in some genera; ventral sucker and pharynx absent; ceca long, may have lateral branches; testes two or multiple, opposite or oblique when two or in U-shaped design when multiple, close to posterior end of body; cirrus sac in anterior half of body; seminal vesicle external, long; genital pore sinistral, in anterior third of body; ovary pre- or intertesticular; vitelline follicles along ceca, pretesticular; uterus has many transverse intercecal folds, preovarian; eggs operculate, embryonated, have bipolar filaments; excretory vesicle Y- or V-shaped, arms long, united in anterior part of body, pore dorsal, near posterior end of body; parasitic in intestine, stomach or urinary bladder of turtles and birds, rarely in fishes or marine iguanids.

Key to Genera

1a. Ceca unbranched; triangular head collar distinct. .. 2

1b. Ceca with lateral branches; triangular head collar absent or weakly developed. 5

2a. Parasite of freshwater turtles; large vestibular cavity at posterior end of body; cirrus sac large; testes oblique, intercecal (Fig. 481). .... Genus *Macravestibulum* Mackin, 1930

Life cycle: *M. eversum* - Embryonated eggs with bipolar filaments are probably eaten by the freshwater prosobranch snail, *Goniobasis livescens* in which oculate monostome cercariae develop in daughter rediae. The cercariae emerge and then encyst on the operculum of the snail. The adult flukes develop in the intestine of turtles that eat infected snails (Hsü, 1937).

The life cycle of *M. obtusicaudum* is similar to that of *M. eversum. Cercaria infracaudatum* is the larva of this species. Adults develop to sexual maturity in about 60 days following ingestion of metacercariae (Horsfall, 1935).

2b. Vestibular cavity absent; cirrus sac small; testes opposite. 3

3a. Testes and vitelline follicles lateral to ceca; ceca without diverticula but main excretory ducts have diverticula; parasitic in digestive tract of birds (Figs. 482, 483). .... Genus *Parapronocephalum* Belopolskaia, 1952

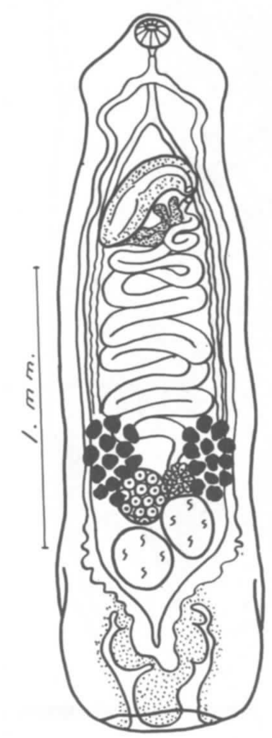


Fig. 481. *Macravestibulum obtusicaudum.*

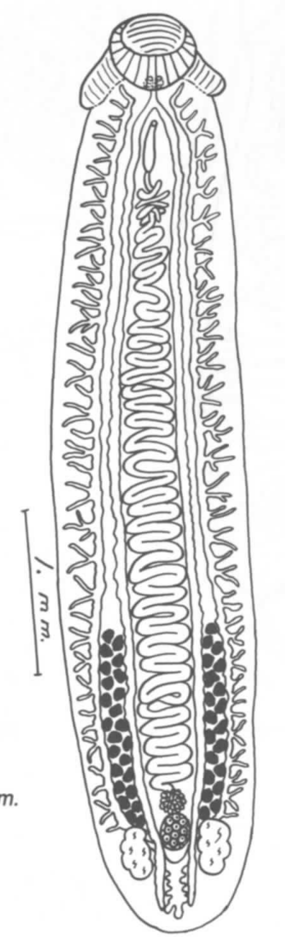


Fig. 482. *Parapronocephalum reversum.*

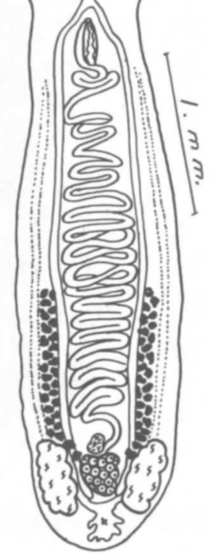


Fig. 483. *Parapronocephalum petasatum.* (from Dollfus, 1966)

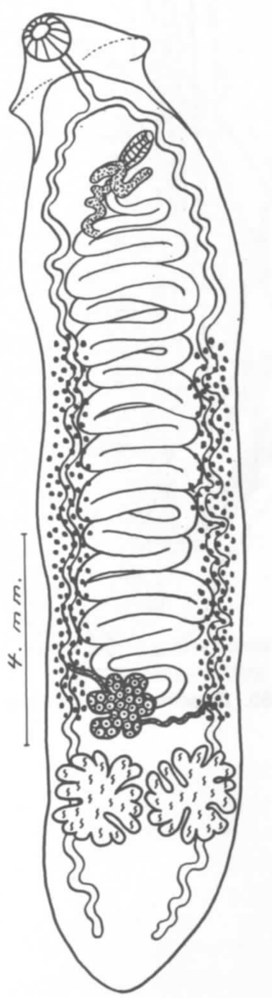


Fig. 484. *Astrorchis renicapite.*

Life cycle: *P. petasatum* (= *Notocotyloides petasatum*) Monostomate, nonoculate, microcercous cercariae with a triangular head collar develop in rediae in the marine prosobranch snail, *Littorina obtusata*. They encyst in the hemocoel of the snail in spherical cyst membranes. The natural definitive hosts are charadriforme birds which eat the infected snails. The parasite develops in the intestinal ceca of the birds (Dollfus, 1966).

3b. Testes medial to ceca and lobed; vitelline follicles around ceca; ceca sinuous. 4

4a. Body large (15 to 20 mm); vitelline follicles abundant, distributed along ceca and extending into anterior half of body (Fig. 484). .... **Genus *Astrorchis* Poche, 1925**

4b. Body six to nine mm. long; vitelline follicles around ceca in only posterior half of body (Fig. 486). .... **Genus *Pyelosomum* Looss, 1899**

5a. Head collar weakly developed; testes two, opposite; esophagus long, about one-fourth as long as body (Fig. 487). .... **Genus *Pleurogonius* Looss, 1901**

Life cycle: *P. malaclemys* - Trioculate monostome cercariae develop in rediae in the snail, *Nassarius obsoleta*. The ceca of the cercaria are branched like those of the adult. Cercariae encyst on the operculum of the snail and develop to infective metacercariae. When these were fed to the turtle, *Malaclemys centrata* partially developed adults were recovered. This was a superimposed infection. Metacercariae were also fed to a laboratory-reared *Chelonia mydas* and immature worms were recovered 10 days later (Hunter, 1967).

5b. Head collar absent; anterior end of body rounded; testes multiple, in U-shaped design near posterior end of body; esophagus very short (Fig. 485). .... **Genus *Diaschistorchis* Johnston, 1913**

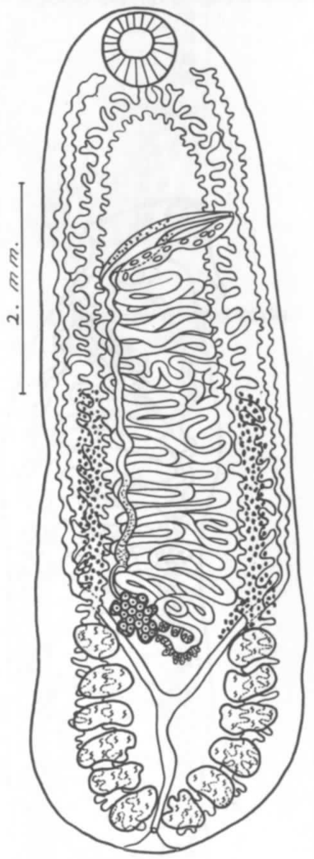


Fig. 485. *Diaschistorchis ellipticus*. (from Pratt, 1914)

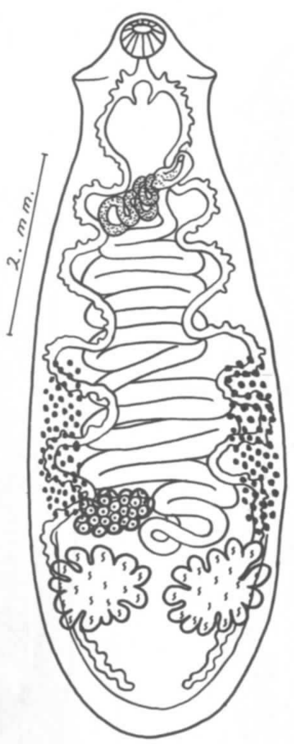


Fig. 486. *Pyelosomum longicaecum*.

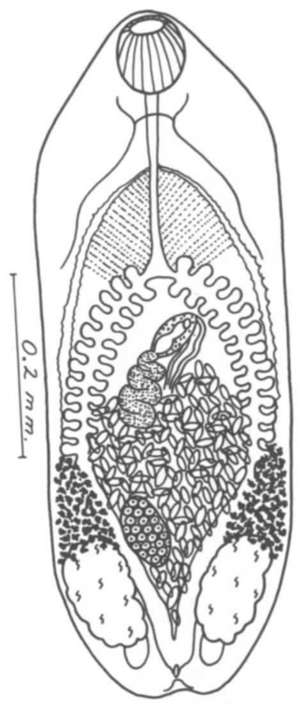


Fig. 487. *Pleurogonius malaclemmys*.

Family Opisthotrematidae Poche, 1926

Body broadly oval, concave ventrally, margins curved, spinous on ventral surface; ventral sucker and pharynx absent; ceca long, sinuous; testes opposite, lobed, in posterior third of body; cirrus sac long, at posterior end of body; genital pore at posterior end of body; ovary lobed, anterior to right testis; vitelline follicles intercecal, pretesticular; uterus occupies much of area anterior to gonads; eggs have polar filaments; parasitic in the respiratory system, esophagus, stomach and Eustachian tubes of marine mammals.

The genus *Opisthotrema* Fischer, 1883 is represented in North America by *O. cochleotrema* (Fig. 488).

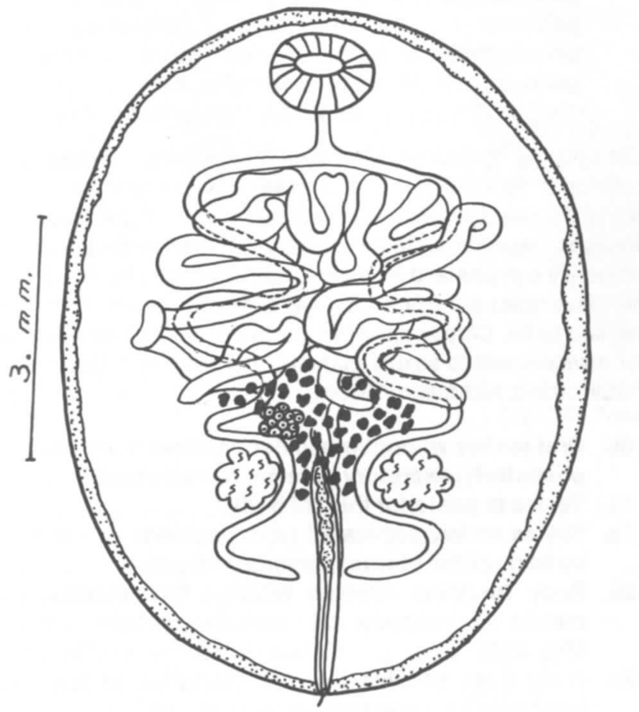


Fig. 488. *Opisthotrema cochleotrema*. (from Price, 1932)

Family Microscaphidiidae Travassos, 1922

Body elongate or fusiform, nonspinous, concave ventrally; ventral sucker and pharynx absent; esophageal bulb sometimes present; ceca long; testes tandem, in middle third of body; cirrus sac absent; seminal vesicle free in parenchyma; hermaphroditic sac present or absent; genital pore median, ventral to oral sucker or near cecal bifurcation; ovary posterior to testes; vitelline follicles lateral to ceca, variable in extent; uterus mostly preovarian, intercecal; excretory system has network of tubules through parenchyma; parasitic in large intestine of turtles.

Key to Genera

1a. Body elongate; oral sucker large with triangular projections; hermaphroditic sac absent; esophageal bulb absent; posterior end of body rounded (Fig. 489). .... **Genus *Dictyangium* Stunkard, 1943**

1b. Body fusiform; oral sucker small, without triangular projections; hermaphroditic sac present; esophageal bulb present; body with two pointed projections at posterior end (Fig. 490). .... **Genus *Hexangitrema* Price, 1937**

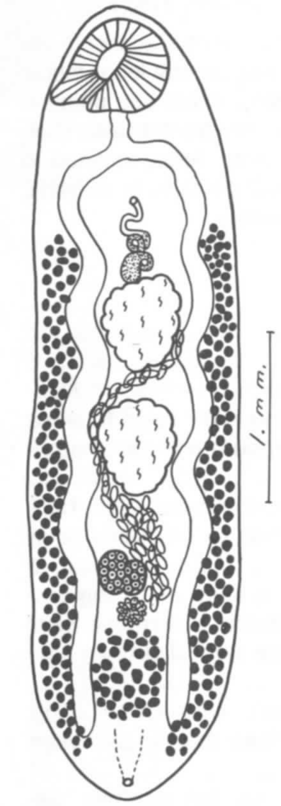


Fig. 489. *Dictyangium chelydrae*.

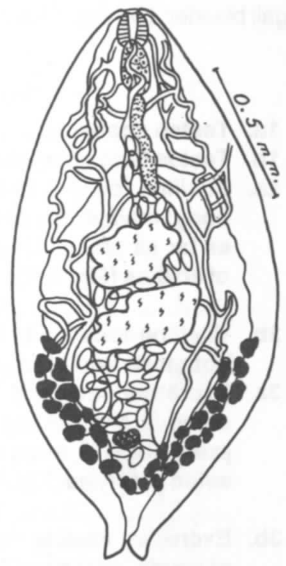


Fig. 490. *Hexangitrema pomacanthi*. (from Overstreet, 1969)

Order Plagiorchiida LaRue, 1957
Suborder Plagiorchiata LaRue, 1957

Miracidia have one pair flame cells, epidermal cell formula is 3, 3. Xiphidiocercariae of the armatae, ornatae, virgulate, ubiquita, cercariaeum or microcercous groups, develop in daughter sporocysts in gastropod molluscs; stylet horizontal; protonephridia mesostomate, no excretory vessels in tail; cercariae encyst in arthropods, molluscs or in poikilothermic vertebrates. Life cycle involves three hosts.

Superfamily Plagiorchioidea Dollfus, 1930 *emended*

Excretory vesicle Y-shaped or tubular, main excretory ducts attached at anterior end of vesicle. Cercariae of armatae or ornatae type in most species; develop in pulmonate snails; flame cell formula $[2(3+3+3)+(3+3+3)]$.

Family Plagiorchiidae Lühe, 1901

Body oval fusiform or elongate, spinous; ventral sucker in anterior half of body; pharynx present; ceca usually long; testes opposite, tandem or oblique, in hindbody; cirrus sac present; genital pore anterior to ventral sucker; ovary pretesticular; vitelline follicles along ceca, variable in extent; uterus confined to hindbody; eggs operculate, embryonated; parasitic in intestine, gall bladder, bile duct or cloaca of vertebrates.

Key to Genera

1a. Testes opposite. **2**
1b. Testes tandem or oblique. **6**
2a. Vitelline follicles in lateral clusters, confined to forebody; main ducts of excretory system extend forward as far as pharynx; parasitic in mouth and esophagus of snakes (Fig. 491). .... **Genus *Stomatrema* Guberlet, 1928**
2b. Vitelline follicles in lateral regions of hindbody or in both fore- and hindbody. **3**
3a. Excretory vesicle Y- shaped with stem of Y long and sinuous and having a pair of lateral diverticula near posterior end, arms of Y embrace ventral sucker; parasitic in turtles (Fig. 494). .... **Genus *Styphlotrema* Odhner, 1911**
3b. Excretory vesicle not as described above; parasites of newts, snakes or fishes. **4**
4a. Metraterm well developed; vitelline follicles few, lateral to gonads; ventral sucker larger than oral sucker; parasitic in snakes (Fig. 492). .... **Genus *Travtrema* Pereira, 1929**
4b. Metraterm not well developed; vitelline follicles abundant, in fore- and hindbody; suckers equal or oral sucker larger than ventral sucker. **5**
5a. Testes oval, median to ceca; ovary lobed; parasite of freshwater fishes (Fig. 493). .... **Genus *Vietosoma* Van Cleave and Mueller, 1932**
5b. Testes lobed, at ends of ceca; ovary oval; parasitic in intestine of amphibians (Fig. 495). .... **Genus *Plagitura* Holl, 1928**

Life cycle: *P. parva* - Embryonated eggs are eaten by the pulmonate snail, *Helisoma antrosa* in which xiphidiocercariae of the armatae group develop in daughter sporocysts. The cercariae encyst in snails of the genera *Helisoma, Physa, Lymnaea, Pseudosuccinea* and *Campeloma* and also in the larvae of Dobsonflies of the genus *Corydalus*. The definitive host is the newt, *Triturus viridescens* (see Stunkard, 1936).

Owens (1946) studied the life cycle of *P. salamandra* and found that the miracidia develop within one week after oviposition. Xiphidiocercariae with a finfold on the tail develop in daughter sporocysts in *Pseudosuccinea columella*. They encyst in diving beetles, dragonfly nymphs and in several species of snails. The newt, *Triturus viridescens* is the definitive host.

6a. Oral sucker with one pair of ventro-lateral muscular papillae and at least twice as large as ventral sucker; posterior end of body truncate; excretory vesicle opens through funnel-shaped muscular chamber; parasitic in intestine of turtles (Fig. 496). .... **Genus *Eustomos* Mac Callum, 1921**

Life cycle: *E. chelydrae* - Xiphidiocercariae of the armatae group develop in sporocysts in the freshwater pulmonate snails, *Helisoma antrosa, Lymnaea stagnalis, Stagnicola angulata* and *Bulimoides megasoma*. Cercariae encyst in the branchial basket of dragonfly nymphs and in several species of snails. The normal definitive hosts are snapping turtle, *Chelydra serpentina* and the painted turtle, *Chrysemys picta,* six to ten weeks being required for development to sexual maturity after feeding metacercariae (Krull, 1934d; McMullen, 1935a).

6b. Oral sucker without muscular papillae; body rounded posteriorly; excretory pore not funnel-shaped. **7**
7a. Testes in posterior third of body. **8**
7b. Testes widely separated from posterior end of body by folds of the uterus; parasitic in reptiles. **10**
8a. Body fusiform; vitelline follicles few, restricted to middle third of body, not confluent posterior to testes (Fig. 497). .... **Genus *Parastiotrema* Miller, 1940**
8b. Body oval; vitelline follicles abundant, in fore- and hindbody, confluent posterior to testes. **9**
9a. Testes tandem; cirrus sac extends some distance posterior to ventral sucker; uterus pretesticular (Fig. 498). .... **Genus *Neoglyphe* Shaldybin, 1954**

Life cycle: *N. soricis* - Xiphidiocercariae of the armatae group develop in sporocysts in the freshwater snail, *Lymnaea bulimoides.* The cercariae either encyst in the sporocysts or emerge and then encyst in water beetles, caddisfly larvae or in mayfly nymphs. Experimental infections were established in hamsters by feeding metacercariae. Natural infections occur in shrews which probably eat the infected intermediate hosts (Macy and Moore, 1958).

9b. Testes oblique; cirrus sac barely extends posterior to ventral sucker; some uterine folds between testes (Fig. 499). .... **Genus *Plagiorchis* Lühe, 1899**
Key to species in Olsen (1937).

Life cycle: *P. muris* - Embryonated eggs are eaten by the pulmonate snail, *Stagnicola emarginata* in which xiphidiocercariae of the armatae group develop in daughter sporocysts. Some cercariae encyst in the sporocyst but most of them leave the sporocysts and the snail and encyst in dipterous larvae of the family Chironomidae. Natural definitive hosts are rat, dog, nighthawk, robin, herring gull and sandpiper. Experimental infections were established in mice, rats, pigeon and human beings (McMullen, 1937).

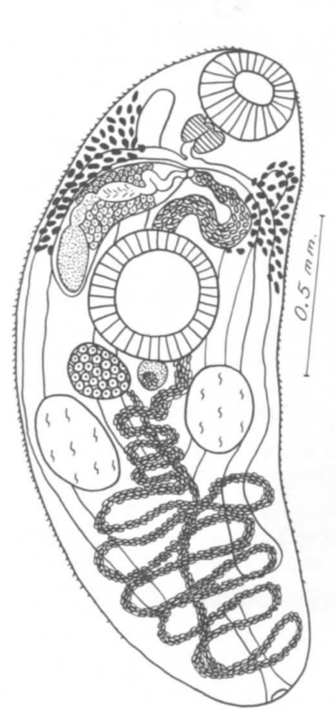


Fig. 491. *Stomatrema guberleti.*

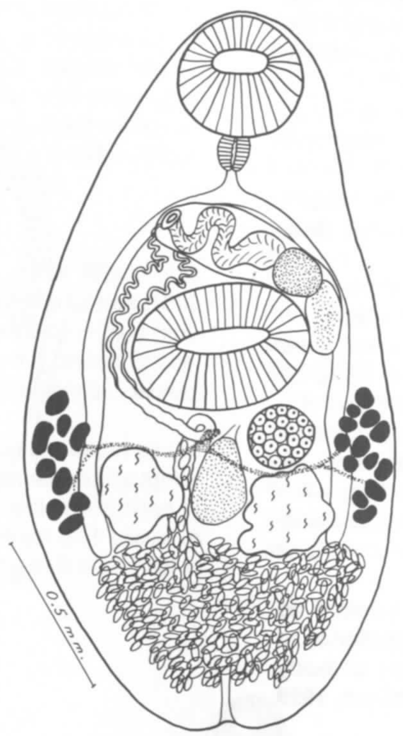


Fig. 492. *Travtrema tamiamiense.*

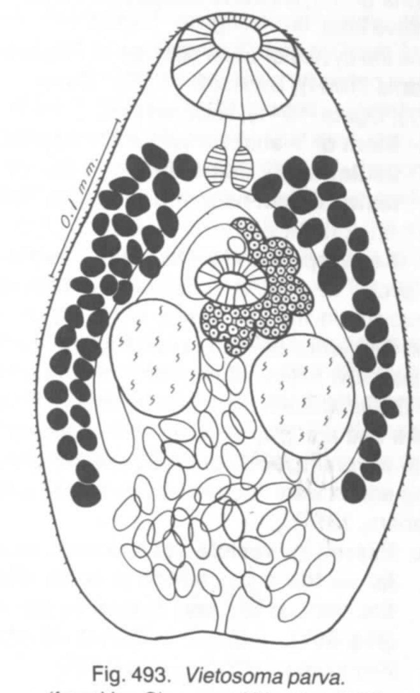


Fig. 493. *Vietosoma parva.*
(from Van Cleave and Mueller, 1932)

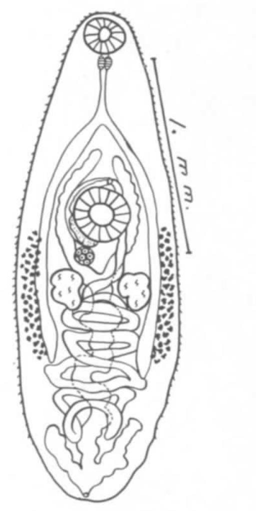


Fig. 494. *Styphlotrema solitarium.*

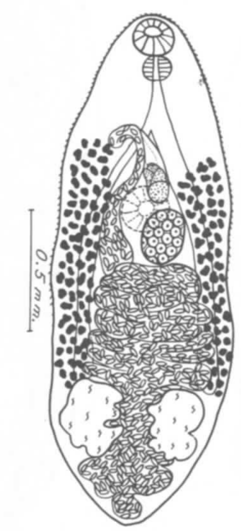


Fig. 495. *Plagitura parva.*
(from Stunkard, 1936)

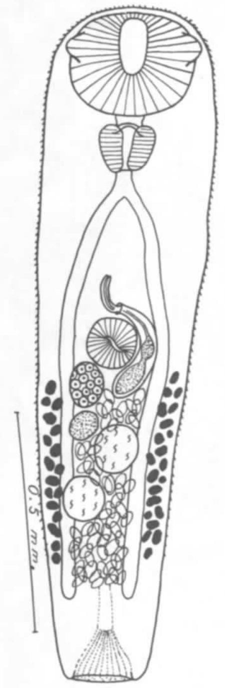


Fig. 496. *Eustomos chelydrae.*

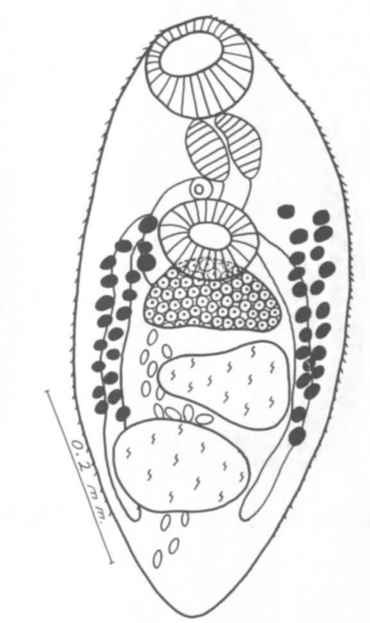


Fig. 497. *Parastiotrema ottawanense.*

Macy (1960b) published an account of the life cycle of *P. vespertilionis parorchis.* The host snail is *Lymnaea stagnalis.* The cercariae encyst in larvae of mosquitos and caddisflies and the nymphs of mayflies and dragonflies. Bats serve as the natural definitive host.

The life cycles of other species of *Plagiorchis* were studied by Williams (1964); Brendow (1970); Theron (1976); Blankespoor (1977); Ogata (1941); Najarian (1961); Rees (1952).

10a. Stem of Y-shaped excretory vesicle with lateral diverticula; ovary immediately posterior to ventral sucker; testes lobed, near midbody (Fig. 500). .... Genus *Styphlodora* Looss, 1899

Key to species in Dawes (1942) and in Skrjabin (1964).

Life cycle: *S. magna* - Xiphidiocercariae develop in daughter sporocysts in the pulmonate snail, *Physa anatina* in 35 to 40 days. Cercariae leave the snail and then penetrate and encyst in the poeciliid fishes *Mollienesia latipinna, Heterandria formosa* and *Gambusia affinis.* Metacercariae are infective in about six weeks and are found chiefly at the base of the fins. They were fed to several species of snakes of the genus *Natrix* and developing adults were recovered two weeks later from the bile duct (Graham, 1971).

10b. Excretory vesicle voluminous, extending forward as far as the ovary which is some distance posterior to the ventral sucker; testes in posterior half of body (Fig. 501). .... Genus *Allopharynx* Shtrom, 1928

Key to species in Skrjabin (1964).

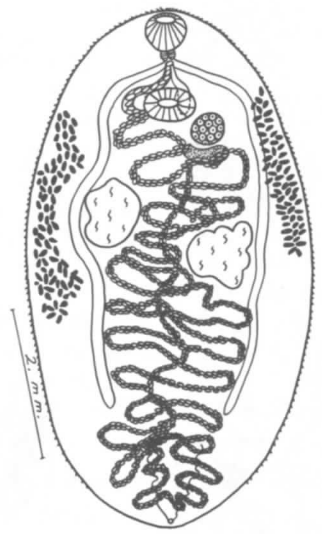


Fig. 500. *Styphlodora magna.*

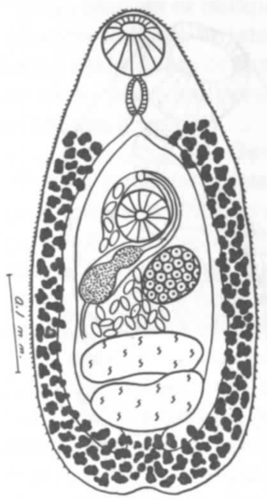


Fig. 498. *Neoglyphe soricis.*

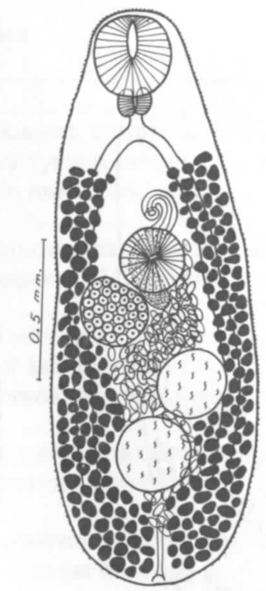


Fig. 499. *Plagiorchis proximus.*

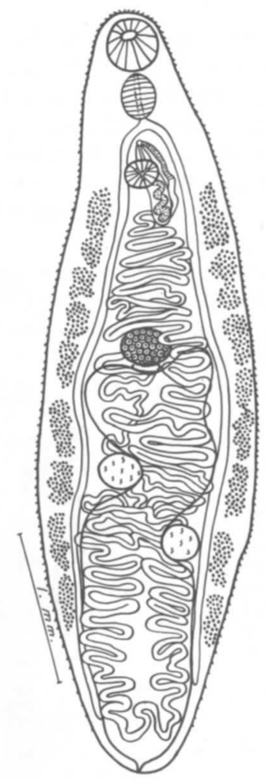


Fig. 501. *Allopharynx multispinosa.* (from Bennett, 1935)

Family Haematoloechidae Odening, 1964

Body elongate or oval; ventral sucker present, vestigial or absent; pharynx present; ceca long; testes oblique or opposite, in posterior half of body; cirrus sac elongate, near anterior end of body; genital pore ventral to esophagus or pharynx; ovary pretesticular; vitelline follicles in a series of clusters along ceca, variable in extent; uterus contains many folds; eggs small, operculate, embryonated; parasitic in lungs of amphibians.

Key to Genera

1a. Uterus has extracecal longitudinal folds (Figs. 502, 503). .... Genus *Haematoloechus* Looss, 1899

Key to species in Odening (1958). Kennedy (1981) published a key to species in Canada and the United States. Six species are thought to be valid but the genus *Ostiolum* was not recognized.

Life cycle: *H. breviplexus* - Embryonated eggs are eaten by the planorbid snail, *Gyraulus similaris* in which mother and daughter sporocysts develop, the latter giving rise to xiphidiocercariae of the ornatae group (Fig. 34). Cercariae penetrate and encyst in dragonfly nymphs of *Aeschna multicolor.* The definitive host is *Rana pretiosa.* The parasite develops in the lungs (Schell, 1965).

The life cycles of *H. parviplexus* has been investigated by Krull (1931) and *H. longiplexus* by Krull (1932).

1b. Uterus without extracecal longitudinal folds (Fig. 504). .... Genus *Ostiolum* Pratt, 1902

Life cycle: *O. medioplexus* - Embryonated eggs are eaten by the planorbid snail, *Planorbula armigera* in which ornatae cercariae develop in daughter sporocysts. After leaving the snail, the cercariae are drawn into the respiratory chamber of dragonfly nymphs in water currents and encyst in the wall of the branchial basket. *Sympetrum obtrusum* and *S. rubicundulum* are the species involved. Infected dragonflies and nymphs are eaten by the frog, *Rana clamitans.* The adult fluke develops in the lungs (Krull, 1931).

Dronen (1975) investigated the life cycle of *O. coloradensis.* Ornatae cercariae develop in daughter sporocysts in the pulmonate snail, *Physa virgata.* Cercariae encyst in dragonfly nymphs of the genera *Tramea, Libellula* and *Anax* and in damselfly nymphs of the genus *Enallagma.* The definitive host is *Rana pipiens.*

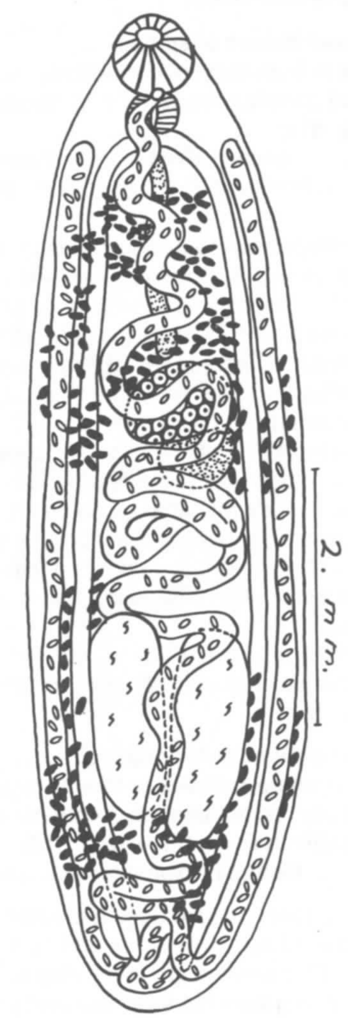


Fig. 502. *Haematoloechus longiplexus.*

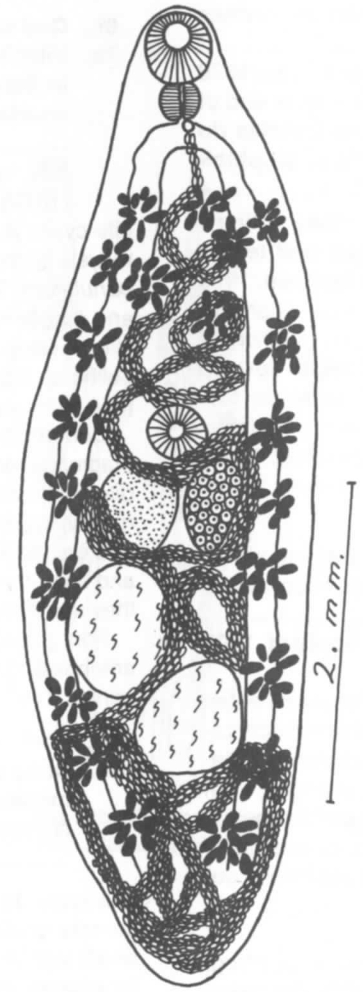


Fig. 503. *Haematoloechus similiplexus.*

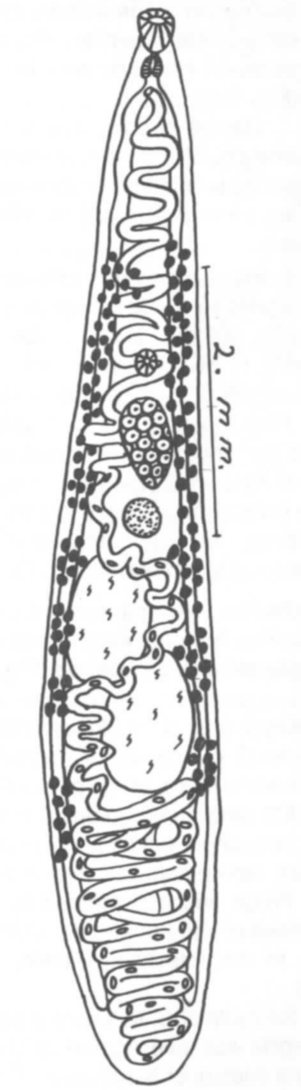


Fig. 504. *Ostiolum medioplexus.*

Family Macroderoididae McMullen, 1937

Body elongate, oval or fusiform, spinous; ventral sucker in anterior half of body, usually smaller than oral sucker; pharynx present; ceca long or short; testes tandem, oblique or opposite, in hindbody; cirrus sac present; genital pore median, anterior to ventral sucker; ovary pretesticular; vitelline follicles along ceca, variable in extent; uterus extends posterior to testes; eggs operculate, embryonated; excretory vesicle tubular; parasitic in intestine of poikilothermic vertebrates, several species progenetic in leeches and crustaceans. Epidermal cell formula of miracidium is 3, 3.

Key to Genera

1a. **Testes opposite or nearly opposite.** 2
1b. **Testes tandem or oblique.** 5
2a. **Body oval or linguiform; vitelline follicles distributed along full length of ceca in fore- and hindbody; ventral sucker close to oral sucker; parasitic in chameleons (Fig. 505).** .... **Genus *Alloglyptus* Byrd, 1950**
2b. **Body fusiform or oval; vitelline follicles distributed along about half of body length; ventral sucker in anterior half of body.** 3
3a. **Body oval; ceca extend only to middle of body; seminal vesicle bipartite; vitelline follicles lateral to ceca between pharynx and testes; progenetic in leeches (Fig. 506).** .... **Genus *Hirudicolotrema* Fish and Vande Vusse, 1976**
3b. **Body fusiform; ceca extend almost to posterior end of body; seminal vesicle unipartite; vitelline follicles do not extend forward to pharynx; parasitic in amphibians.** 4
4a. **Some uterine folds anterior to testes; vitelline follicles lateral to ceca, between cecal bifurcation and testes (Fig. 507).** .... **Genus *Hylotrema* Sullivan, 1973**

Life cycle: *H. pennsylvaniensis* (= *Choledocystus p.*) - Xiphidiocercariae develop in daughter sporocysts in the pulmonate snail, *Physa gyrina*. Cellular paletots of host origin develop around the sporocysts. Cercariae emerge and penetrate tadpoles of *Hyla crucifer* in which they develop to infective metacercariae without encysting. After the host metamorphoses to the adult stage, the metacercariae migrate to the intestine where they develop to sexual maturity (Sullivan, 1973).

4b. **Uterine folds almost entirely posttesticular; some vitelline follicles extend posterior to testes; esophageal glands well developed (Fig. 508).** .... **Genus *Glypthelmins* Stafford, 1905**
Key to species in Skrjabin (1964).

Life cycle: *G. quieta* - Embryonated eggs in frog feces are eaten by pulmonate snails of the genus *Physa* in which xiphidiocercariae of the ornatae group develop in daughter sporocysts. Paletots of host origin envelop the sporocysts. After emerging from the snail, the cercariae encyst in the skin of frogs of the genus *Rana*. Frogs become infected by eating metacercariae along with pieces of shed epidermis when molting. The adult fluke develops in the intestine (Rankin, 1944; Leigh, 1946; Schell, 1962a).

The life cycle of *G. hyloreus*, a parasite of the Pacific tree frog, *Hyla regilla* was investigated by Martin, G.W. (1969). Cercariae enter the coelom of tadpoles of *H. regilla* but do not encyst. Following metamorphosis of the frog the metacercariae migrate to the frog intestine where they develop to sexual maturity. This cycle is similar to that of *Hylotrema pennsylvaniensis*.

5a. **Body long and slender; testes widely separated; genital pore some distance anterior to ventral sucker; vitelline follicles lobed; progenetic in antennal gland of crayfish (Fig. 509).** .... **Genus *Alloglossoides* Corkum and Turner, 1977**
5b. **Body not unusually long; testes close together; genital pore immediately anterior to ventral sucker; vitelline follicles not lobed.** 6
6a. **Several circles of spines on oral sucker; vitelline follicles lateral to ceca; seminal vesicle bipartite; parasitic in garfish (Fig. 510).** .... **Genus *Paramacroderoides* Venard, 1941**

Life cycle: *P. pseudoechinus* - Embryonated eggs in the feces of the host are eaten by the pulmonate snail, *Helisoma duryi* in which xiphidiocercariae of the ornatae group develop in daughter sporocysts. Cercariae later encyst in numerous small fishes of the genera *Gambusia, Fundulus, Jordanella, Heterandria, Mollienesia* and also in the frog, *Rana sphenocephala* and in tadpoles of *R. grylio*. Of the fishes, *Gambusia affinis* is the most common intermediate host. The adult fluke develops in the intestine of the Florida gar, *Lepisosteus platyrhincus* (see Leigh and Holliman, 1956 and Leigh, 1975).

The life cycle of *P. echinus* is similar, utilizing the same hosts but the cercaria is of the armatae type and behaves differently than the cercaria of *P. pseudoechinus*.

6b. **Oral sucker without circles of spines.** 7
7a. **Vitelline follicles in both fore- and hindbody; parasitic in fishes, several species progenetic in leeches and crustaceans (Fig. 511).** .... **Genus *Alloglossidium* Simer, 1929**
Key to species in Font and Corkum (1975); Timmers (1979).

Life cycle: *A. corti* - Xiphidiocercariae develop in daughter sporocysts in the planorbid snails, *Helisoma trivolvis* and *H. campanulatum*. They encyst in the muscles and fatbody of mayfly and dragonfly nymphs and also in crustaceans. The adult parasite develops in the madtom, *Schilbeodes gyrinas;* the brown bullhead, *Ictalurus nebulosus* and the yellow bullhead, *I. natalis* (see McMullen, 1936; Crawford, 1937).

Corkum and Beckerdite (1975) studied the life cycle of *A. macrobdellensis* which is progenetic in the leech, *Macrobdella ditetra*. Xiphidiocercariae of the armatae group develop in sporocysts in *Helisoma trivolvis.* They penetrate the body of leeches and encyst temporarily in the wall of the crop. Soon they excyst and enter the lumen of the crop, then pass to the intestine where they attain sexual maturity.

Font and Corkum (1976) report adults of *A. renale* from the antennary glands of freshwater shrimp, *Palaemonetes kodiakensis*. The life cycle is unknown.

7b. **Vitelline follicles confined to hindbody.** 8
8a. **Body elongate; vitelline follicles in lateral regions of middle third of body; testes tandem; seminal receptacle present; parasitic in amphibians (Fig. 512).** .... **Genus *Haplometrana* Lucker, 1931**

Life cycle: *H. intestinalis* - Embryonated eggs are eaten by pulmonate snails of the genera *Physa, Helisoma* and *Lymnaea* in which xiphidiocercariae of the ornatae group develop in daughter sporocysts. After emerging from the snail, the cercariae encyst in the epidermis of frogs which later become infected by eating cysts in pieces of shed epidermis following a molt. *Rana pretiosa* is the definitive host (Olsen, 1937b; Schell, 1961; Current and Lang, 1975).

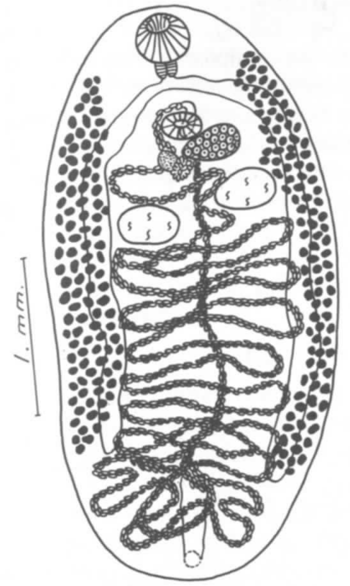


Fig. 505. *Alloglyptus crenshawi.*

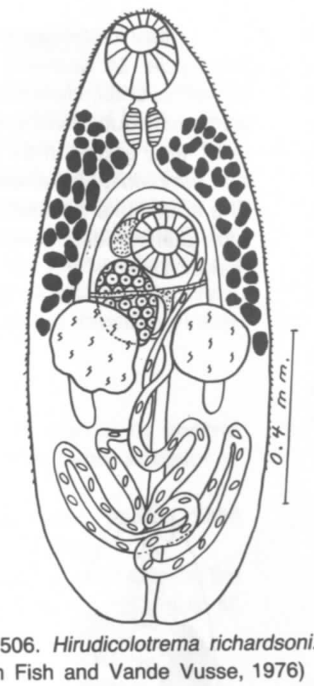


Fig. 506. *Hirudicolotrema richardsoni.* (from Fish and Vande Vusse, 1976)

Fig. 507. *Hylotrema pennsylvaniensis.* (from Byrd and Maples, 1963)

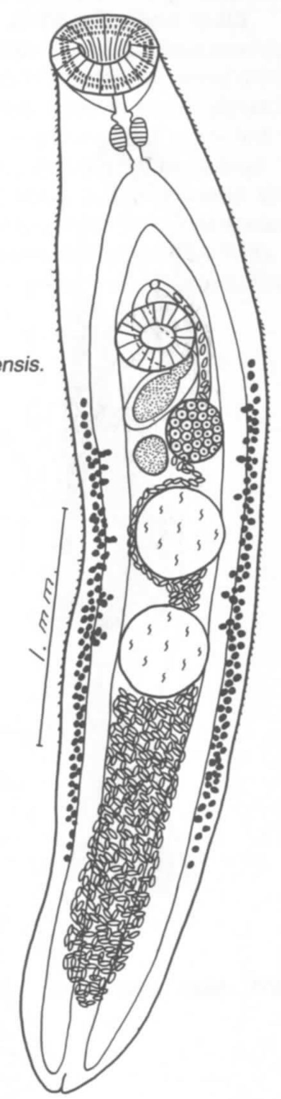


Fig. 510. *Paramacroderoides echinus.*

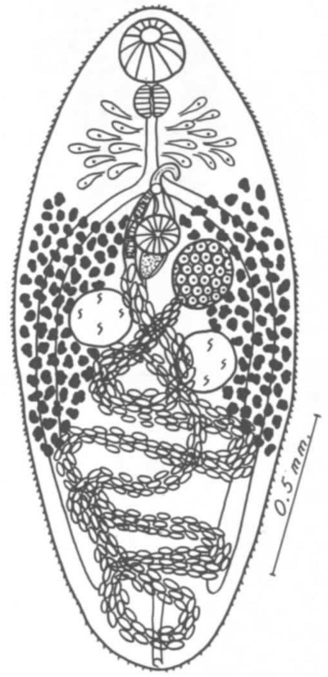


Fig. 508. *Glypthelmins quieta.*

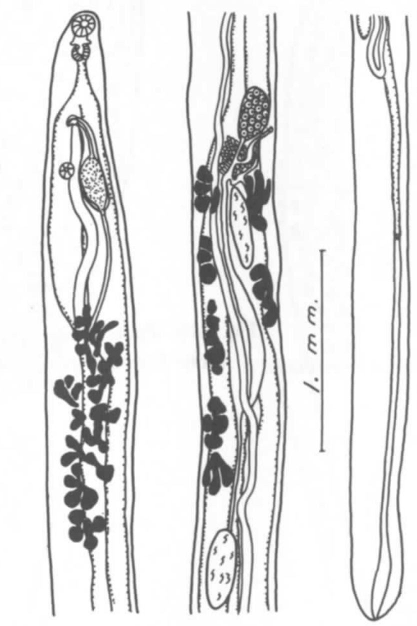


Fig. 509. *Alloglossoides cardicola.* (from Corkum and Turner, 1977)

8b. **Testes oblique; parasitic in fishes.** 9

9a. **Vitelline follicles large, in lateral region of hindbody between ventral sucker and testes; ventral sucker in anterior fourth of body, close to oral sucker (Fig. 513).** .... **Genus** *Pseudomagnivitellum* **Dronen and Underwood, 1980**

9b. **Vitelline follicles small, in lateral regions of hindbody between ventral sucker and posterior end of body, extending posterior to testes; ventral sucker near middle of body (Fig. 514).** .... **Genus** *Macroderoides* **Pearse, 1924**

Key to species in Skrjabin (1964).

Life cycle: *M. spinifera* - Embryonated eggs are eaten by the planorbid snail, *Helisoma duryi* in which xiphidiocercariae of the armatae group develop in daughter sporocysts. After leaving the snail, they encyst in the tissues of fishes of the genera *Gambusia, Fundulus, Mollienesia, Heterandria* and in tadpoles of frogs. The adult fluke develops in the intestine of the garfish, *Lepisosteus platyrhincus,* attaining sexual maturity in 10 to 12 days (Leigh, 1958).

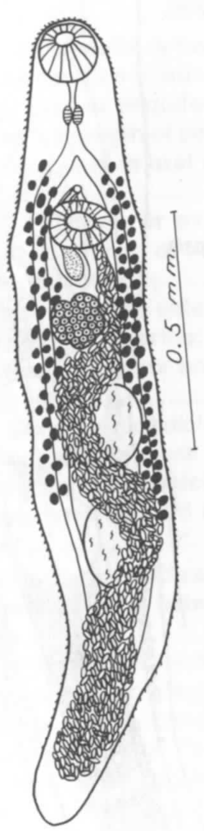


Fig. 511. *Alloglossidium corti.*

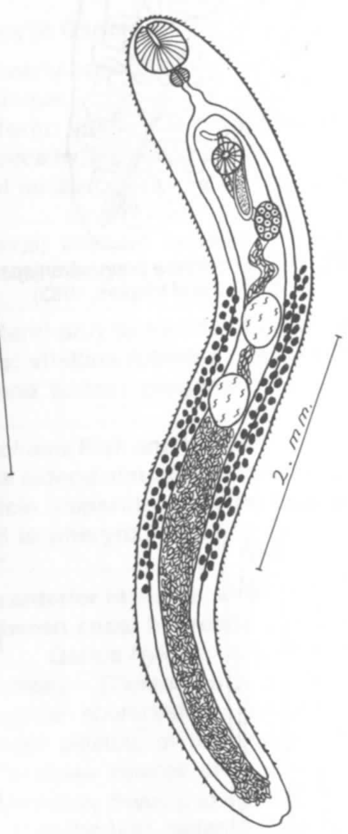


Fig. 512. *Haplometrana intestinalis.*

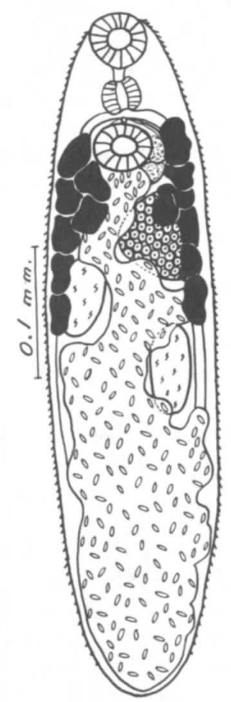


Fig. 513. *Pseudomagnivitellum ictalurum.* (from Dronen and Underwood, 1980)

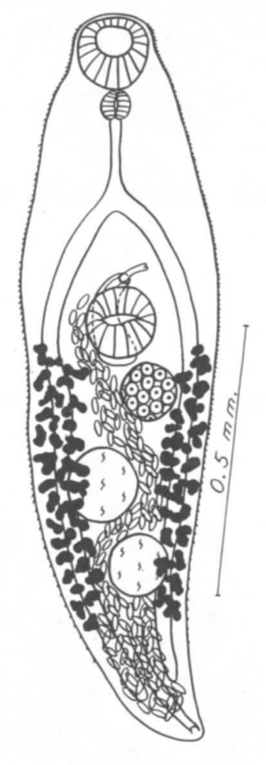


Fig. 514. *Macroderoides typica.*

Family Brachycoeliidae Odening, 1964

Body oval to elongate, tapered posteriorly, spinous; ventral sucker smaller than oral sucker, close to middle of body; pharynx present; ceca short, seldom extend beyond ventral sucker; testes opposite or oblique, in hindbody; cirrus sac present; genital pore median, anterior to ventral sucker; ovary anterior to either right or left testis or opposite anterior testis; vitelline follicles in clusters lateral to ceca and ventral sucker; uterus fills most of posttesticular and intertesticular area; eggs operculate, embryonated; excretory vesicle Y-shaped; parasitic in intestine of amphibians and reptiles.

Key to Genera

1a. **Testes opposite; cirrus sac short, dorsal to ventral sucker; seminal vesicle not bipartite; ovary anterior to right or left testis (Fig. 515).** .... **Genus** *Brachycoelium* **Stiles and Hassall, 1898**

Key to species in Byrd (1937) and in Cheng (1958).

Life cycle: *B. mesorchium* - Embryonated eggs are eaten by the terrestrial snails, *Triodopsis carolinensis, Mesodon inflectus, M. thyroidus* and *Agriolimax agrestis.* Miracidia hatch in the intestine of the snail, penetrate the wall and change to a small mother sporocyst. Tailless cercariae (Cercariaea), without a stylet, eventually develop in daughter sporocysts. As cercariae emerge from the snail, they secrete a jellylike capsule over themselves. These encapsulated cercariae are eaten by numerous species of land snails in which they encyst and develop to infective metacercariae which when fed to the salamanders, *Desmognathus fuscus* and *Eurycea bislineata cirrigera* develop to the adult stage (Denton, 1962; Jordan, 1963; Jordan and Byrd, 1967).

Cheng (1960a) investigated the life cycle of *B. obesum* which uses the snail, *Zonitoides ligerus.* Stubby-tailed cercariae with a stylet develop in sporocysts and encyst either in the hemocoel of the snail or right in the sporocyst. Metacercariae were fed to newts, *Triturus viridescens* and young adults were recovered.

1b. **Testes oblique; cirrus sac long, extends some distance posterior to the ventral sucker; seminal vesicle bipartite; ovary opposite to anterior testis (Fig. 516).** .... **Genus** *Cymatocarpus* **Looss, 1899**

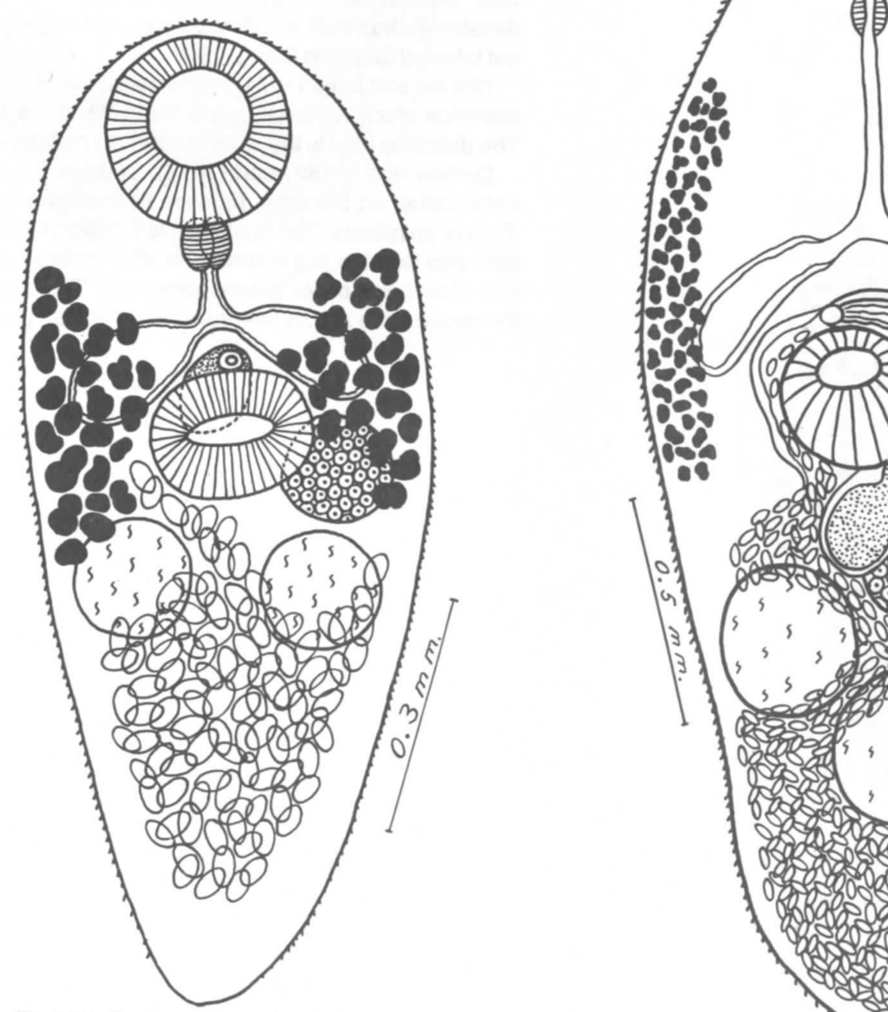


Fig. 515. *Brachycoelium salamandrae.*

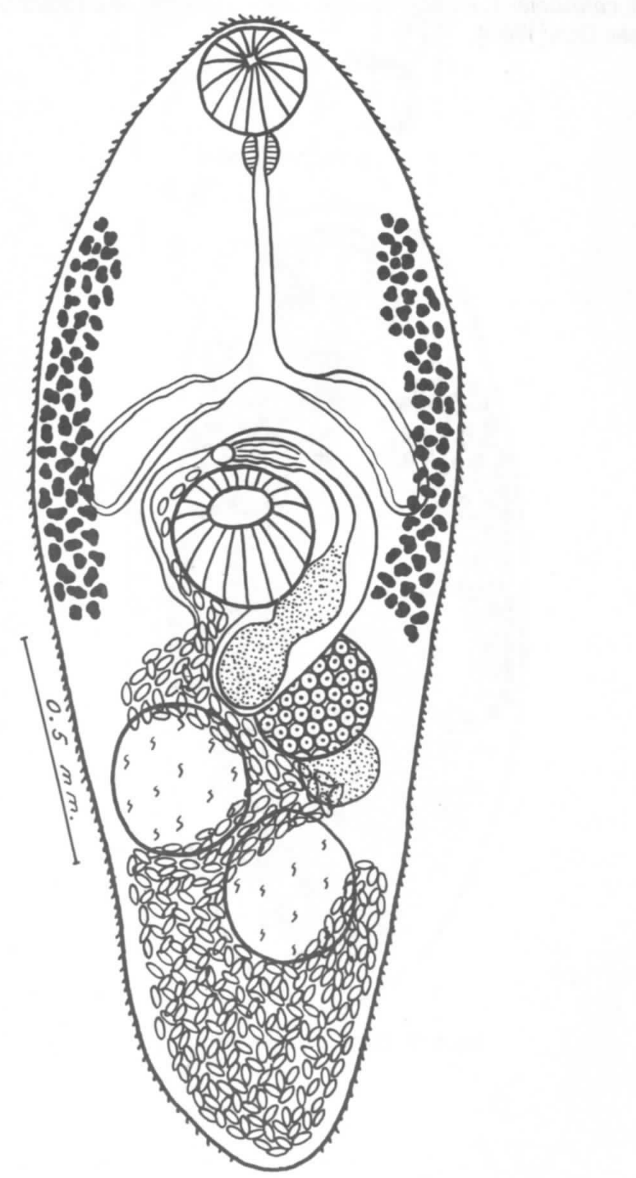


Fig. 516. *Cymatocarpus undulatus.*

Family Mesocoeliidae Dollfus, 1933

Body oval or elliptical, spinous; suckers equal, the ventral sucker in middle of body; pharynx present; ceca extend to mid-body; testes opposite, lateral to ventral sucker or immediately posterior to it; cirrus sac dorsal to ventral sucker; genital pore median, anterior to ventral sucker; ovary posttesticular; vitelline follicles lateral to ceca; uterus fills area posterior and between gonads; eggs operculate, embryonated; excretory vesicle tubular; parasitic in intestine of amphibians and reptiles.

The family contains only the genus *Mesocoelium* Odhner, 1911 (Fig. 517). Several species occur in North America.

Key to species in Cheng (1960b) and in Nasir and Diaz (1971).

Life cycle: *M. brevicaecum* - Embryonated eggs pass in the feces of the host. Tailless cercariae (Cercariaea) are produced in daughter sporocysts in the terrestrial snail, *Euhadra quaesita*. Cercariae encyst in the sporocyst and develop to the metacercarial stage. These were fed to frogs and toads. Flukes, containing a few eggs, were recovered at seven days. Development to sexual maturity requires about 25 days. Common definitive hosts are *Bufo vulgaris, Rana rugosa, R. nigromaculata, R. catesbeiana, Elaphe quadrivirgata* and *Eumeces latiscutatus* (see Ochi, 1930).

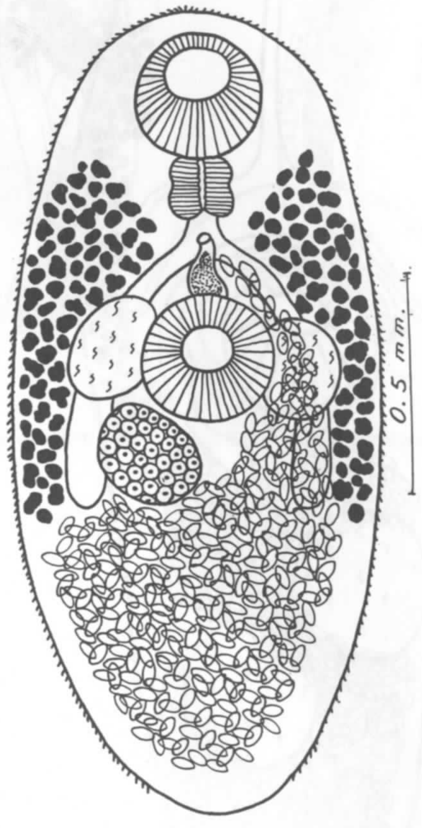


Fig. 517. *Mesocoelium waltoni.*

Family Cephalogonimidae Nicoll, 1915

Body linguiform or oval, spinous; ventral sucker in anterior half of body; suckers unequal in size; pharynx small; ceca long; testes tandem, oblique or opposite, in middle third of body; cirrus sac long; genital pore lateral or antero-dorsal to oral sucker; ovary pretesticular; vitelline follicles lateral to ceca in middle third of body; uterus fills most of posttesticular part of body; eggs operculate, embryonated; excretory vesicle Y-shaped with numerous lateral branches; parasitic in intestine of fishes, amphibians and reptiles.

Key to Genera

1a. **Body broadly oval; testes opposite; muscular prepharynx present; ventral sucker larger than oral sucker; parasite of mud eel (*Siren* sp.) (Fig. 518). .... Genus** *Cephalogonimoides* **Brooks and Buckner, 1976**

1b. **Body linguiform; testes tandem; prepharynx not muscular; suckers about equal; parasitic in frogs (Fig. 519). .... Genus** *Cephalogonimus* **Poirier, 1886**
Key to species in Ogata (1934); Caballero and Sokoloff (1936); Lamothe-Argumedo (1965).

Life cycle: *C. americanus* - Embryonated eggs are ingested by planorbid snails, *Helisoma antrosum* and *H. trivolvis*. Xiphidiocercariae of the armatae group develop in daughter sporocysts in the snail hemocoel. After leaving the snail, the cercariae penetrate tadpoles and encyst in the tissues. The adult parasites develop in the small intestine of frogs of the genus *Rana* which eat infected tadpoles (Lang, 1968).

Dronen and Lang (1974) investigated the life cycle of *C. salamandrus* which is similar to the life cycle of the above species. The definitive host is the salamander, *Ambystoma tigrinum*.

Dronen and Underwood (1977) reported the life cycle of *C. vesicaudus*, an intestinal parasite of the spiny soft-shell turtle, *Trionyx spiniferus*. The host snail is *Helisoma trivolvis*. Armatae cercariae develop in the snail, and after emergence encyst in the skin of tadpoles of *Rana sphenocephala*. The latter are eaten by the above turtle and by several other species of turtles.

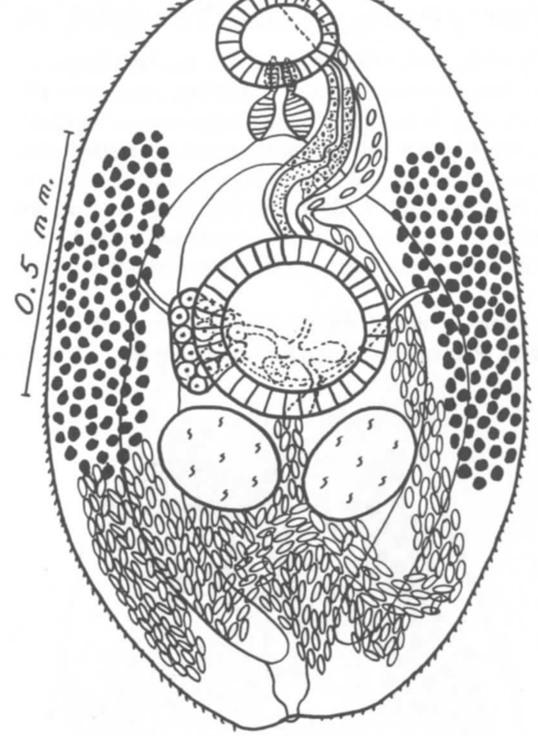


Fig. 518. *Cephalogonimoides sireni.* (from Premvati, 1969)

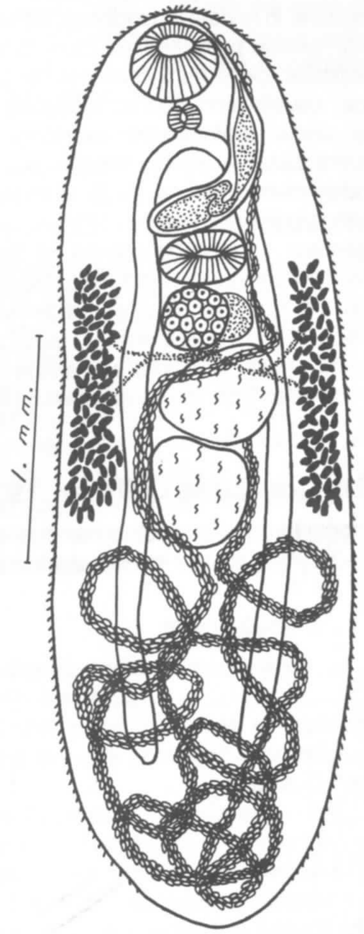


Fig. 519. *Cephalogonimus amphiumae.*

Family Auridistomidae Stunkard, 1924

Body elongate, spinous; oral sucker with paired ventro-lateral and dorso-lateral muscular papillae; ventral sucker smaller than oral sucker, in anterior third of body; pharynx present; ceca long; testes tandem or oblique, in middle of hindbody; cirrus sac anterior to ventral sucker; genital pore median, close to cecal bifurcation; ovary pretesticular, close behind ventral sucker; vitelline follicles along ceca, usually confined to hindbody, confluent posterior to testes; uterus pretesticular; excretory vesicle Y-shaped, with long stem; parasitic in intestine of turtles.

The genus *Auridistomum* Stafford, 1905 is represented in North America by two species (Fig. 520).

Life cycle: *A. chelydrae* - Xiphidiocercariae of the armatae group *(Cercaria concavocorpa)* develop in sporocysts in the freshwater snail, *Helisoma trivolvis.* They encyst in the tissues of tadpoles of the bullfrog, *Rana catesbeiana.* Metacercariae were fed to young snapping turtles, *Chelydra serpentina* and developing adults were recovered from the small intestine (Sizemore, 1936; Ralph, 1938).

Family Rhytidodidae Odhner, 1926

Body elongate, nonspinous; oral sucker has one dorsal and two ventro-lateral muscular papillae; ventral sucker in anterior third of body; pharynx present; intestinal ceca long; testes tandem, in middle third of body; cirrus sac present; genital pore anterior to ventral sucker; ovary pretesticular; seminal receptacle absent; vitelline follicles restricted to hindbody; uterus entirely preovarian; excretory vesicle Y-shaped, the main collecting ducts having many lateral branches; parasitic in the intestine of marine turtles.

The genus *Rhytidodes* Looss, 1901 (Fig. 521) is represented in North America by *R. secundus* from the intestine of *Caretta caretta,* the marine turtle.

Family Pachypsolidae Yamaguti, 1958

Body thick, oval, spinous anteriorly; suckers large, in anterior half of body; pharynx present; intestinal ceca long with lateral branches only in forebody; testes opposite, in hindbody; ovary pretesticular; cirrus sac present; genital pore submedian, anterior to ventral sucker; vitelline follicles small, in lateral regions of middle third of body; uterus mostly posttesticular; excretory vesicle Y-shaped, the main collecting ducts are branched and unite dorsal to the oral sucker; parasitic in the intestine of marine turtles.

The family contains only the genus *Pachypsolus* Looss, 1901 (Fig. 522). *P. ovalis* has been reported from North America.

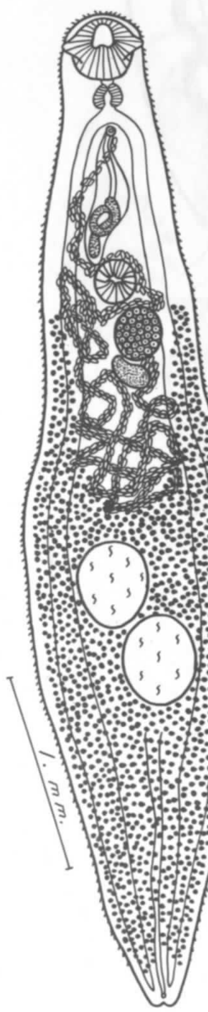


Fig. 520. *Auridistomum chelydrae.*

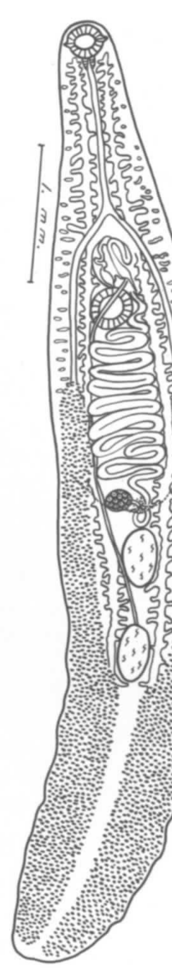


Fig. 521. *Rhytidodes secundus.* (from Pratt, 1914)

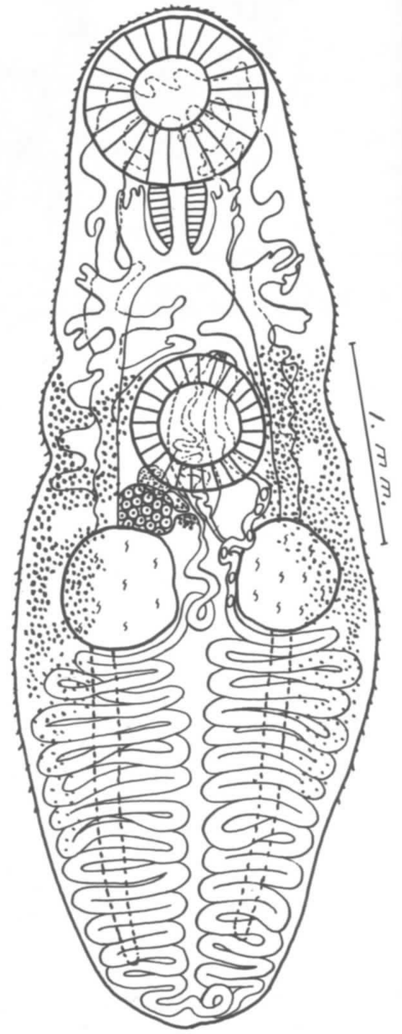


Fig. 522. *Pachypsolus ovalis.* (from Pratt, 1914)

Family Cephaloporidae Travassos, 1934

Body pyriform, spinous; ventral sucker large, near posterior end of body; pharynx present; intestinal ceca short, extend only to testes; testes opposite, dorsal to ventral sucker; cirrus sac near pharynx; genital pore close to oral sucker; ovary pretesticular; vitelline follicles in lateral areas between oral sucker and testes; uterus chiefly dorsal to ventral sucker and posterior to testes; eggs operculate, nonembryonated; parasitic in stomach and ovary (?) of marine fishes.

The genus *Plectognathotrema* Layman, 1930 is represented in North America by *P. hydrolagi,* (Fig. 523) a stomach parasite of the ratfish, *Hydrolagus colliei.*

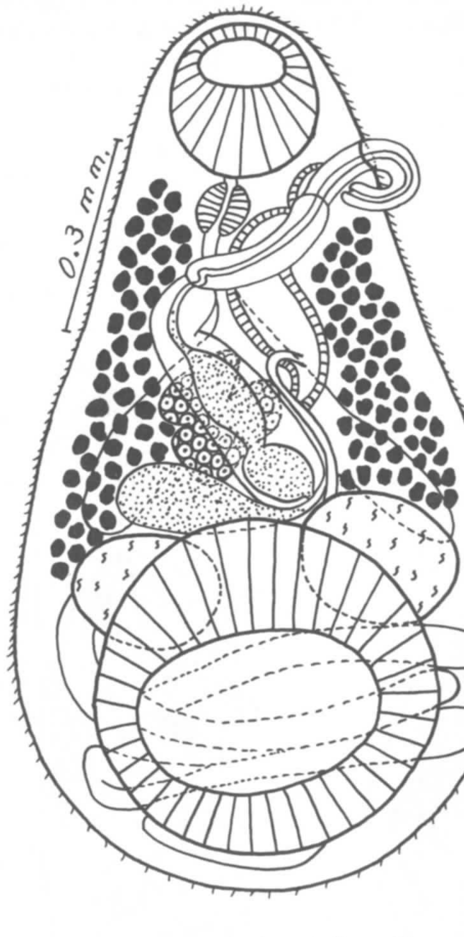


Fig. 523. *Plectognathotrema hydrolagi.* (from Olsson, Hanson and Pratt, 1970)

Superfamily Ochetosomatoidea Odening, 1964

Xiphidiocercariae of the armatae group develop in daughter sporocysts in pulmonate snails; excretory system mesostomate; excretory vesicle Y-shaped with the arms of the Y partly encircling the ventral sucker; metacercariae encysted in poikilothermic vertebrates; adults parasitic in poikilothermic vertebrates. Life cycle involves three hosts.

Family Ochetosomatidae Leao, 1944

Body elongate, linguiform or pyriform, spinous; ventral sucker in middle of body or anterior to middle; pharynx present; ceca extend to level of testes or beyond; testes opposite or oblique, in middle of hindbody or near posterior end of body; cirrus sac long, may or may not extend posterior to ventral sucker; genital pore anterior to ventral sucker, marginal, submarginal or median; ovary pretesticular; vitelline follicles along ceca in middle third of body; uterus usually with long descending and ascending limbs; eggs operculate, embryonated; excretory vesicle Y-shaped with arms encircling ventral sucker; parasitic in mouth, esophagus or respiratory tract of snakes.

Key to Genera

1a. Testes opposite or nearly so. **2**

1b. Testes oblique. **5**

2a. Genital pore marginal or submarginal; cirrus sac long, entirely anterior to ventral sucker (Fig. 524). .... **Genus** ***Ochetosoma*** **Braun, 1901**

Life cycle: *O. aniarum* (= *Renifer a.)* - Eggs in feces of host contain miracidia which hatch after eggs are eaten by the pulmonate snail, *Physa helei.* Xiphidiocercariae of the armatae group develop in daughter sporocysts. After leaving the snail, the cercariae penetrate and encyst in tadpoles of the genera *Rana, Hyla* and *Pseudacris.* Infected tadpoles were fed to snakes of the genus *Natrix* and adults recovered from the mouth and esophagus 35 days later (Byrd, 1935; Walker, 1937 and 1939).

Sogandares-Bernal and Grenier (1971) studied the life cycle of *O. kansensis* and *O. laterotrema* which use *Physella anatina* as first intermediate host. Cercariae encyst in tadpoles of *Rana pipiens.* Infected tadpoles were fed to very young cottonmouth snakes and the adult parasites were recovered from the mouth.

2b. Genital pore median or submedian; cirrus sac not entirely anterior to ventral sucker. **3**

3a. Body pyriform; testes lobed; uterus contains some transverse folds, fills most of hindbody (Fig. 525). .... **Genus** ***Pneumatophilus*** **Odhner, 1911**

Key to species in Byrd and Denton (1938) and in Skrjabin (1964).

Life cycle: *P. leidyi* - Embryonated eggs in feces of the host are eaten by the pulmonate snail, *Physa sayii* in which xiphidiocercariae of the armatae group develop in daughter sporocysts. Cercariae encyst in the tissues of tadpoles of the genus *Rana;* in mudpuppies, *Necturus maculosus;* in the cricket frog, *Acris crepitans* and in the catfish, *Schilbeodes miurus.* The definitive host is the water snake, *Natrix sipedon* which eat the infected intermediate hosts (Norris, 1945).

3b. Body linguiform; testes oval or irregular in shape. . **4**

4a. Uterus composed of several transverse folds; metraterm about as long as cirrus sac (Fig. 526). .... **Genus *Paralechriorchis* Byrd and Denton, 1938**
Key to species in Byrd and Denton (1938).

Life cycle: *P. syntomentera* - (= *Zeugorchis s.)* - Embryonated eggs are eaten by the pulmonate snails, *Physa gyrina.* Xiphidiocercariae of the armatae group develop in daughter sporocysts. After leaving the snail, the cercariae penetrate the skin of tadpoles of *Hyla regilla, Rana aurora* and *Triturus torosus* in which they encyst. The adult fluke develops in the lungs and oro-nasal cavities of snakes which eat the infected amphibians (Ingles, 1933).

4b. Uterus composed of two longitudinal folds, the ascending fold usually greatly inflated when filled with eggs; metraterm much shorter than cirrus sac (Fig. 527) .... **Genus *Lechriorchis* Stafford, 1905 (includes *Zeugorchis* Stafford, 1905)**
Key to species in Byrd and Denton (1938) and in Skrjabin (1964).

Life cycle: *L. primus* - The adult parasite inhabits the lungs of snakes of the genus *Thamnophis.* Embryonated eggs that pass forward through the trachea are swallowed and leave the body in the feces of the host. Eggs are eaten by pulmonate snails of the genus *Physa* in which miracidia hatch, penetrate the intestine and then change to the sporocyst stage. Xiphidiocercariae develop in daughter sporocysts and after leaving the snail encyst in tadpoles and frogs which are later eaten by snakes (Talbot, 1933).

5a. Body elongate; vitelline follicles in short lateral clusters in vicinity of ovary; ovary some distance posterior to ventral sucker; cirrus sac long, extends some distance posterior to ventral sucker (Fig. 528). .... **Genus *Natriodera* Mehra, 1937**

5b. Body linguiform or elliptical; vitelline follicles numerous, fill lateral areas of hindbody; ovary immediately posterior to ventral sucker; cirrus sac not extending posterior to ventral sucker (Fig. 529). .... **Genus *Dasymetra* Nicoll, 1911**
Key to species in Byrd and Denton (1938).

Life cycle: Byrd (1935) investigated the life cycle of *D. villicaeca* and found it to be very similar to that of *Ochetosoma aniarum.* Byrd and Maples (1964; 1969) described part of the life cycle of *D. conferta.*

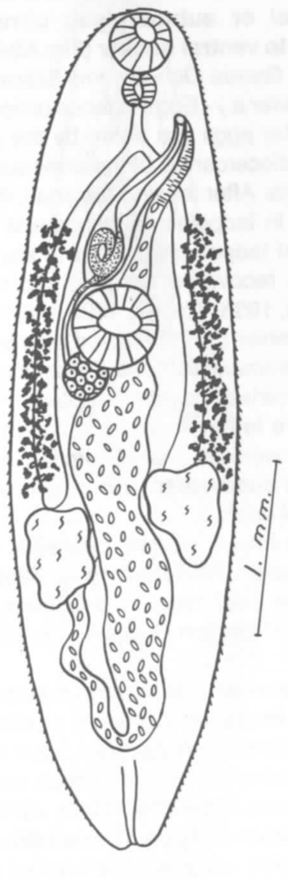


Fig. 524. *Ochetosoma ophoboli.*

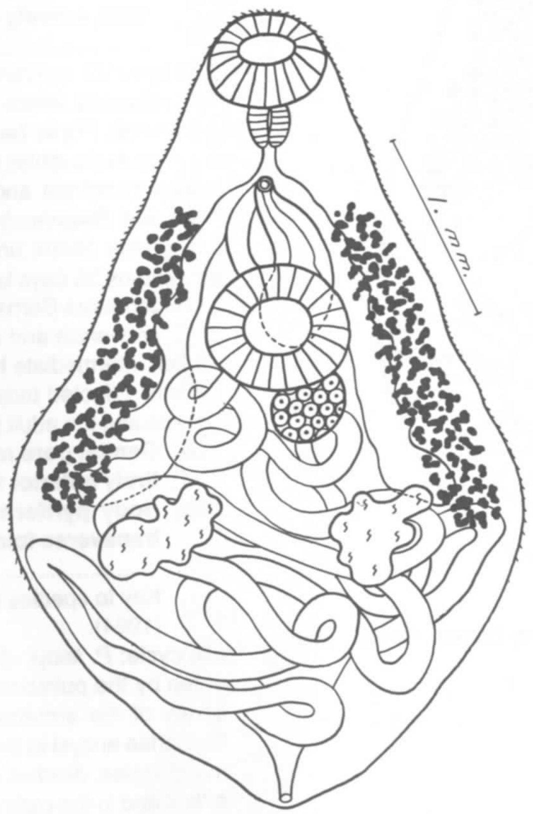


Fig. 525. *Pneumatophilus leidyi.*

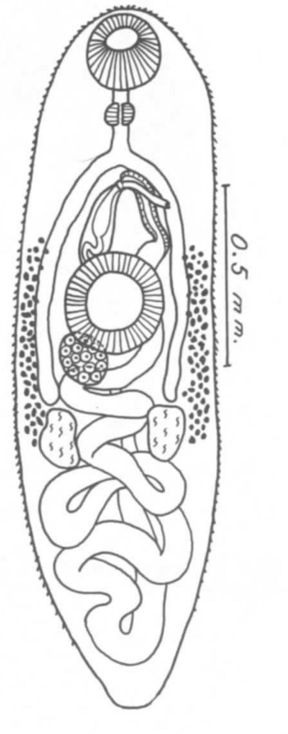


Fig. 526. *Paralechriorchis syntomentera.*

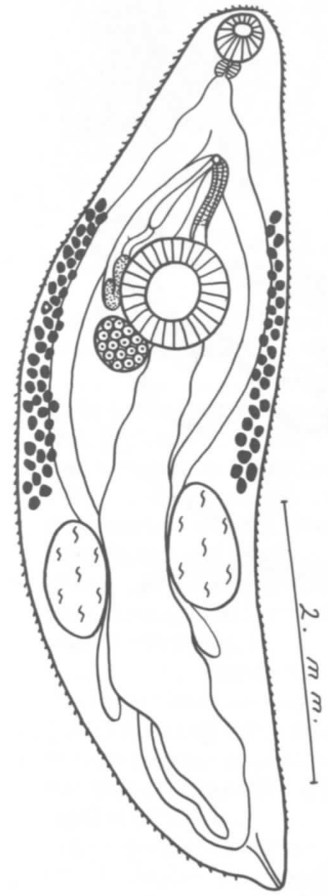


Fig. 527. *Lechriorchis primus.*

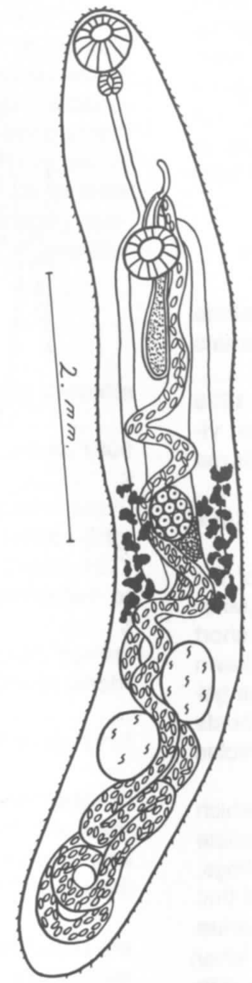


Fig. 528. *Natriodera verlata.*

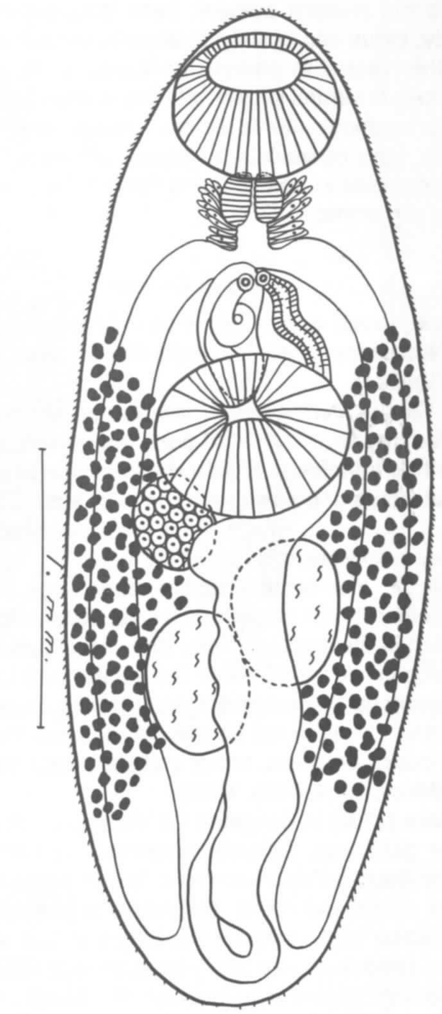


Fig. 529. *Dasymetra conferta.*

4a. Uterus composed of several transverse folds; metraterm about as long as cirrus sac (Fig. 526). .... Genus *Paralechriorchis* Byrd and Denton, 1938

Key to species in Byrd and Denton (1938).

Life cycle: *P. syntomentera* - (= *Zeugorchis s.)* - Embryonated eggs are eaten by the pulmonate snails, *Physa gyrina.* Xiphidiocercariae of the armatae group develop in daughter sporocysts. After leaving the snail, the cercariae penetrate the skin of tadpoles of *Hyla regilla, Rana aurora* and *Triturus torosus* in which they encyst. The adult fluke develops in the lungs and oro-nasal cavities of snakes which eat the infected amphibians (Ingles, 1933).

4b. Uterus composed of two longitudinal folds, the ascending fold usually greatly inflated when filled with eggs; metraterm much shorter than cirrus sac (Fig. 527) .... Genus *Lechriorchis* Stafford, 1905 (includes *Zeugorchis* Stafford, 1905)

Key to species in Byrd and Denton (1938) and in Skrjabin (1964).

Life cycle: *L. primus* - The adult parasite inhabits the lungs of snakes of the genus *Thamnophis.* Embryonated eggs that pass forward through the trachea are swallowed and leave the body in the feces of the host. Eggs are eaten by pulmonate snails of the genus *Physa* in which miracidia hatch, penetrate the intestine and then change to the sporocyst stage. Xiphidiocercariae develop in daughter sporocysts and after leaving the snail encyst in tadpoles and frogs which are later eaten by snakes (Talbot, 1933).

5a. Body elongate; vitelline follicles in short lateral clusters in vicinity of ovary; ovary some distance posterior to ventral sucker; cirrus sac long, extends some distance posterior to ventral sucker (Fig. 528). .... Genus *Natriodera* Mehra, 1937

5b. Body linguiform or elliptical; vitelline follicles numerous, fill lateral areas of hindbody; ovary immediately posterior to ventral sucker; cirrus sac not extending posterior to ventral sucker (Fig. 529). .... Genus *Dasymetra* Nicoll, 1911

Key to species in Byrd and Denton (1938).

Life cycle: Byrd (1935) investigated the life cycle of *D. villicaeca* and found it to be very similar to that of *Ochetosoma aniarum.* Byrd and Maples (1964; 1969) described part of the life cycle of *D. conferta.*

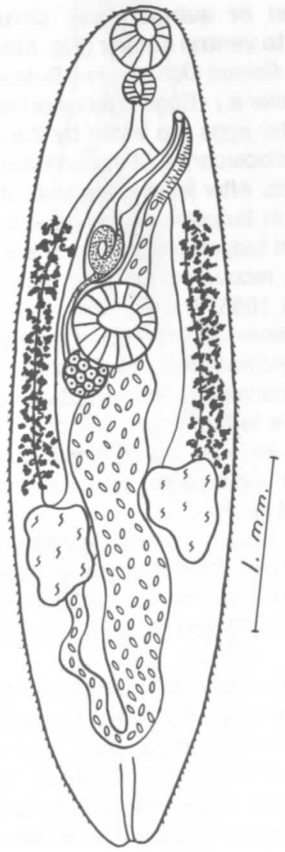


Fig. 524. *Ochetosoma ophoboli.*

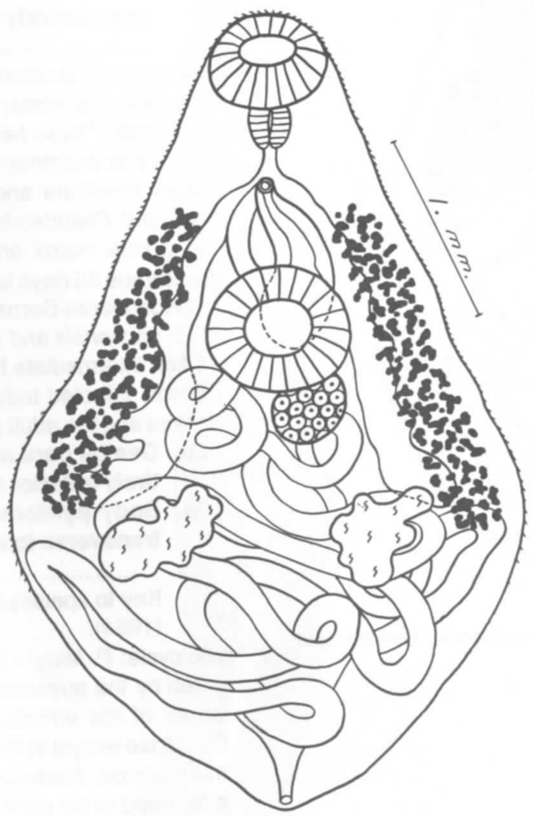


Fig. 525. *Pneumatophilus leidyi.*

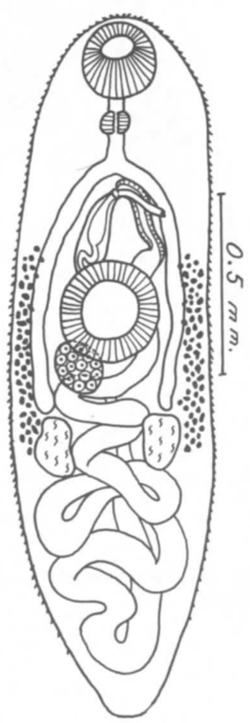


Fig. 526. *Paralechriorchis syntomentera.*

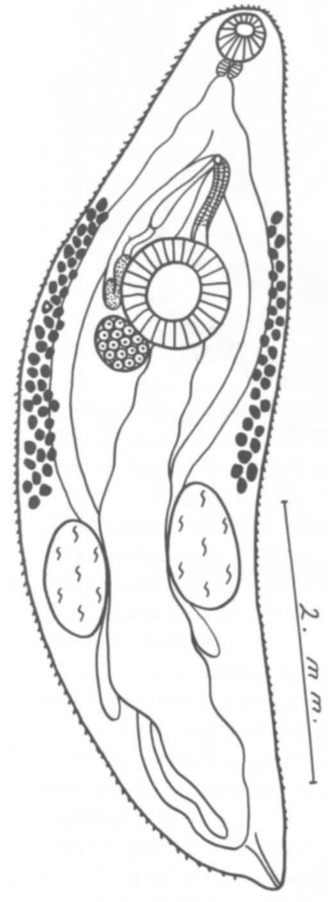


Fig. 527. *Lechriorchis primus.*

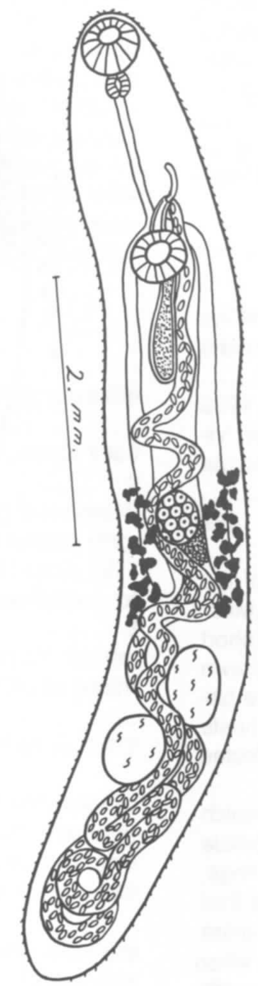


Fig. 528. *Natriodera verlata.*

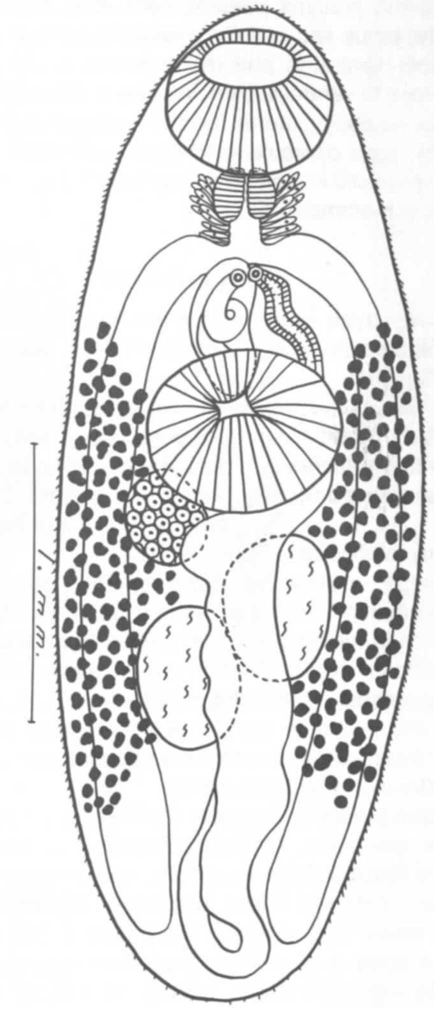


Fig. 529. *Dasymetra conferta.*

Superfamily Prosthogonimoidea Odening, 1964

Family Prosthogonimidae Nicoll, 1924

Body flat, oval or pyriform, spinous; ventral sucker in anterior half of body; pharynx present; ceca long; testes opposite, in hindbody; cirrus sac entirely anterior to ventral sucker; genital pore either ventral to pharynx or lateral to oral sucker; ovary lobed, close to ventral sucker; vitelline follicles in lateral clusters in fore- or hindbody; uterus fills post- and intertesticular areas of hindbody; eggs operculate, embryonated; excretory vesicle Y-shaped; parasitic in cloaca, bursa Fabricius and oviduct of birds and liver of mammals.

Key to Genera

1a. **Body oval; genital pore ventral to pharynx; vitelline follicles in forebody; parasitic in liver of mammals (Fig. 534).** ....
Genus *Mediogonimus* Woodhead and Malewitz, 1936

1b. **Body pyriform; genital pore lateral to oral sucker; vitelline follicles in hindbody; parasitic in cloaca, bursa Fabricius or oviduct of birds (Fig. 535).** ....
.... **Genus *Prosthogonimus* Lühe, 1899**
Key to species in Skrjabin (1964).

Life cycle: *P. macrorchis* - Embryonated eggs in feces of the host are eaten by the prosobranch snail, *Amnicola limosa*. Miracidia hatch in the snail intestine. Xiphidiocercariae with a short tail develop in sporocysts. After leaving the snail they are drawn into the branchial basket of dragonfly naiads, then enter the hemocoel and encyst in the abdominal muscles. Definitive hosts such as ducks, chickens, crows and pheasants eat the infected insects (Macy, 1934, 1939, 1940).

Boddeke (1960) investigated the life cycle of *P. ovatus* which uses the gastropod, *Bithynia tentaculata* as first intermediate host. The adult parasite develops in the oviduct of starlings, chickens, crows and ducks. Boddeke's research revealed that there is some host effect on the adults in that metacercariae from one species of laboratory-infected dragonfly naiad, when fed to starlings, crows and chickens, developed into adults with characters of *P. ovatus* in the starlings and crows but with characters of *P. pellucidus* when developing in chickens.

Adults of *P. ovatus* have been found in the eggs of chickens and ducks. Infected birds lay eggs that have a very thin shell or almost no shell. At times, egg laying stopped, the combs of the birds turned blue and at autopsy the wall of the oviduct was inflamed and thickened.

Life cycles are also known for *P. pellucidus* and *P. cuneatus* (see Krasnobolova, 1963 and Macy, 1965).

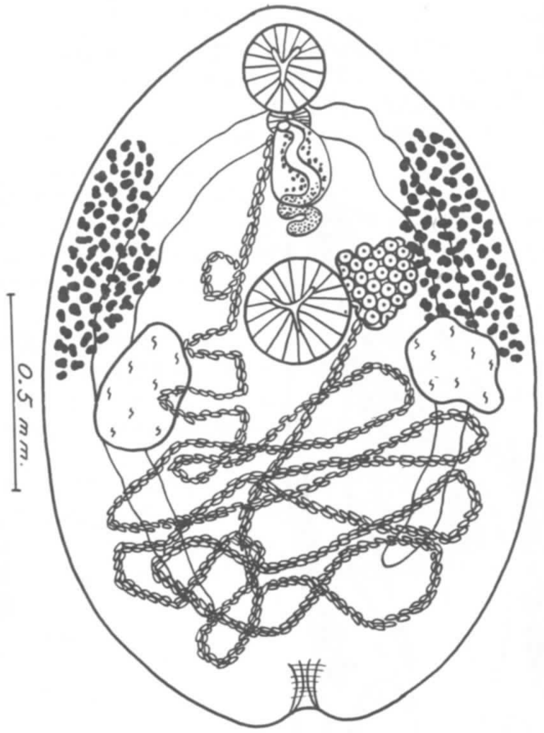


Fig. 534. *Mediogonimus ovilacus*.

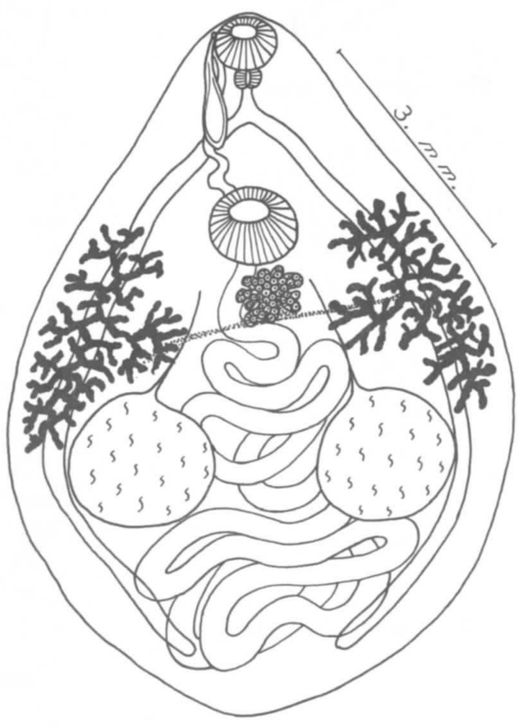


Fig. 535. *Prosthogonimus macrorchis*.

Family Telorchiidae Nicoll, 1924

Body elongate, slender, spinous; suckers in anterior third of body; the ventral sucker smaller than the oral sucker; oral sucker has paired muscular papillae in *Auritelorichis;* pharynx present; ceca long; testes tandem, both testes close to posterior end of body or testes widely separated by folds of uterus; cirrus sac long, either entirely anterior to ventral sucker or extends posterior to ventral sucker; genital pore either ventro-median and immediately anterior to ventral sucker or dorsal and sublateral and some distance anterior to ventral sucker; ovary pretesticular; vitelline follicles along ceca, confined to hindbody; uterus with many intercecal folds, either entirely pretesticular or folds between testes; eggs operculate, embryonated; excretory vesicle Y-shaped, with long stem; parasitic in intestine of amphibians and reptiles.

Key to Genera

1a. **Testes widely separated by folds of uterus; parasite of marine turtles (Fig. 530).** ....
.... **Genus *Orchidasma* Looss, 1900**

1b. **Both testes near posterior end of body.** **2**

2a. **Oral sucker with paired anterio-lateral muscular papillae; parasitic in intestine of snakes and turtles (Fig. 531).** ... **Genus *Auritelorchis* Stunkard and Franz, 1977**

2b. **Oral sucker without muscular papillae; parasites of amphibians and reptiles.** **3**

3a. **Cirrus sac entirely anterior to ventral sucker; genital pore dorsal, near left body margin; parasitic in freshwater turtles (Fig. 532).** ....
.... **Genus *Protenes* Barker and Covey, 1912**
Key to species in Bennett (1935).

3b. **Cirrus sac long, extending some distance posterior to ventral sucker; genital pore median, anterior to ventral sucker; parasitic in intestine of amphibians and reptiles (Fig. 533).** .... **Genus *Telorchis* Lühe, 1899**
Key to species in Wharton (1940).

Life cycle: *T. medius* - Embryonated eggs in feces of turtles are eaten by the pulmonate snail, *Physa integra*. Xiphidiocercariae develop in daughter sporocysts and after leaving the snail, penetrate tadpoles in which they encyst. Turtles acquire the parasite by eating the infected tadpoles (McMullen, 1934).

Schell (1962b) investigated the life cycle of *T. bonnerensis*. Embryonated eggs are eaten by the snails, *Physa gyrina, P. ampullacea* and *P. propinqua* in which miracidia hatch. Mother and daughter sporocysts develop in the snail, the latter producing xiphidiocercariae of the armatae group (Fig. 37). After leaving the snail, the cercariae encyst in other snails, in sphaeriid clams and in tadpoles of frogs and salamanders. The adult parasite develops in tadpoles of the long-toed salamander, *Ambystoma macrodactylum*, which eats the infected intermediate hosts. Adult salamanders do not harbor the parasite.

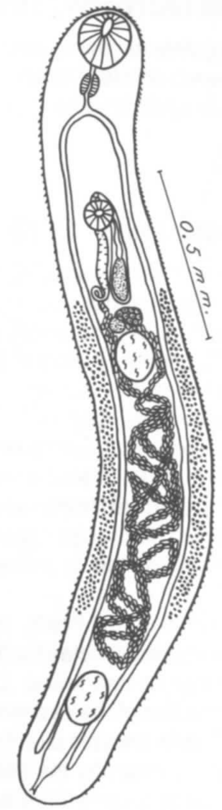


Fig. 530. *Orchidasma amphiorchis*.

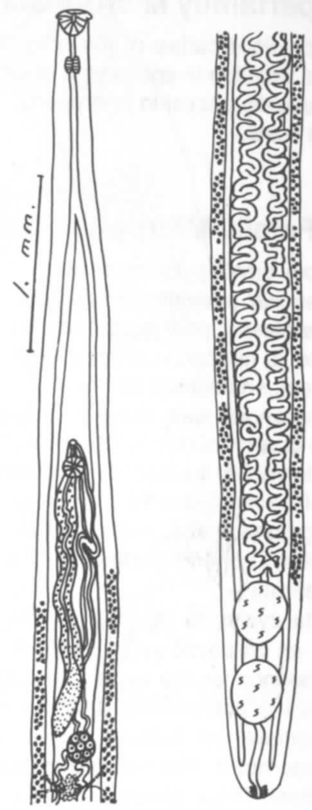


Fig. 531. *Auritelorchis dollfusi*.

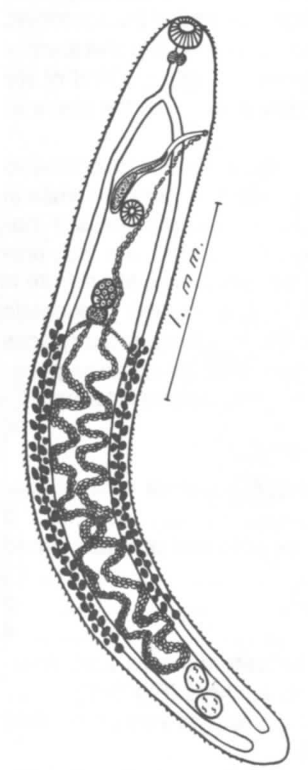


Fig. 532. *Protenes angustus*.

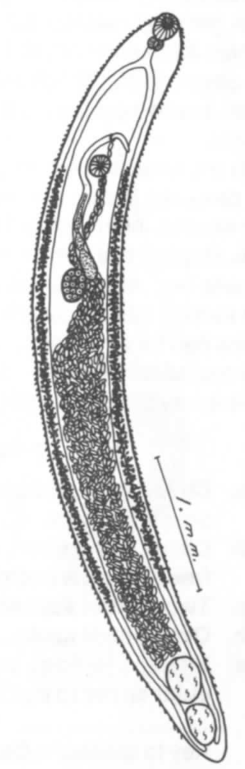


Fig. 533. *Telorchis bonnerensis*.

Superfamily Microphalloidea Morozov, 1955

Xiphidiocercariae of the ubiquita, virgulate or microcercous types, develop in sporocysts in prosobranch snails. Metacercariae usually encyst in arthropods. The life cycle involves two or three hosts.

Family Microphallidae Travassos, 1920

Body small, pyriform or oval, concave ventrally, spinous; ventral sucker posterior to middle of body; two ventral suckers in some genera; pharynx present; ceca short, divergent; testes opposite, in hindbody; cirrus sac present or absent; genital atrium present, sometimes contains pockets or alveoli or has a folded membranous wall; cirrus of the usual eversible type or in the form of a muscular bulbous structure; genital atrium opens lateral to ventral sucker; ovary anterior to right or left testis; vitelline follicles usually posterior to testes or in wreathlike design enveloping gonads and uterus; uterus confined to hindbody; eggs operculate, nonembryonated; adults parasitic in the intestine of vertebrates.

Life cycles in this family usually involve three hosts, mollusc, an arthropod and a vertebrate but in some species there is a tendency for the cycle to be abbreviated or shortened. One method of abbreviation is by way of elimination of the second intermediate host. In these species the cercaria encysts directly in the sporocyst. The infected mollusc is then eaten by the definitive host. These cercariae have a short life span and there is no free-living period. They are without penetration glands, tail and stylet and are nonmotile. They have been designated as "pseudocercariae". The life cycle of *Spelotrema pygmaeum* follows this course.

The most extreme method of abbreviation is evident in a few species that produce "blastocercariae" which are scarcely more than germinal masses that detach from the wall of the sporocyst, remain there and encyst, developing directly to the metacercarial stage. *Microphallus abortivus* goes through this kind of life cycle. In one species the blastocercaria even loses the ability to encyst.

In the usual three-host life cycles, the metacercariae tend to be precocial in that they develop gonads and genitalia while in the second intermediate host but do not become sexually mature. Beyond this condition are those species that are truly progenetic (e.g. *Microphallus opacus*), becoming sexually mature in the second intermediate host which is an arthropod. Progenetic forms can be encysted or not encysted. In *Microphallus opacus* the reproductive organs develop soon after the cerariae penetrate a crayfish and long before the cyst membrane is formed.

Key to Genera

1a. Cirrus sac present, containing seminal vesicle and prostate gland. 2
1b. Cirrus sac absent; seminal vesicle and prostate gland free in the parenchyma. 11
2a. Two ventral suckers present. 3
2b. One ventral sucker. 4
3a. Vitelline follicles posterior to testes; testes oval; muscular cirrus to right of ventral suckers (Fig. 536) .... **Genus *Gynaecotyla* Yamaguti, 1939**
Key to species in Dery (1958).

Life cycle: *G. nassicola* - Miracidia hatch and penetrate the marine prosobranch snail, *Nassa obsoleta* in which xiphidiocercariae of the ubiquita group develop in daughter sporocysts. Cercariae leave the snail and then encyst in the pericardial cavity of sand fleas, *Talorchestia longicornis.* Adult flukes develop in the intestine of shore birds such as plovers and sandpipers which eat infected sand fleas (Rankin, 1940).

3b. Vitelline follicles anterior to testes; testes lobed; muscular cirrus absent (Fig. 537). .... **Genus *Derytrema* Rebecq, 1962**
4a. Vitelline follicles confined to forebody, anterior to ceca (Fig. 538). .... **Genus *Plenosoma* Ching, 1960**
4b. Vitelline follicles in hindbody. 5
5a. Vitelline follicles form a ring, encircling testes and uterus (Fig. 539). .... **Genus *Maritrema* Nicoll, 1907**
Key to species in Deblock and Combes (1965).

Life cycle: *M. laricola* - Xiphidiocercariae of the ubiquita group develop in sporocysts in the marine prosobranch snails, *Littorina scutulata* and *L. sitkana.* They encyst in the crabs, *Hemigrapsus oregonensis* and *H. nudus.* Adults developed in gulls in 48 to 72 hours after feeding metacercariae. The glaucous-winged gull, *Larus glaucescens* is the natural definitive host (Ching, 1963).

Deblock (1975) reported an abbreviated cycle for *M. oocysta.* Ubiquita cercariae *(Cercaria oocysta)* develop and encyst directly in the sporocyst in the prosobranch, *Hydrobia ulvae.* The natural definitive host is the sandpiper, *Tringa totanus* which probably eats the infected snails.

Ching (1978) worked with the marine species, *M. megametrios* which uses the beach flea, *Orchestia traskiana* and the marine isopod, *Gnorimosphaeroma oregonense* as second intermediate host. The adult parasitec develops in the gull, *Larus philadelphia.* Ching likewise found the metacercaria of *M. gratiosum* in the barnacle, *Balanus glandula* and the adult developed in the goldeneye, *Bucephala islandica.*

Jourdane (1979) reported the life cycle of *M. pyrenaica,* a parasite of the insectivores *Neomys fodiens* and *Galemys pyrenaica* in France. Cercariae of the ubiquita group develop in daughter sporocysts in the gastropod, *Bythinella reyniesii* and later penetrate and encyst in the amphipod, *Gammarus pulex.*

Life cycles are also known for *M. setoenensis* and *M. misenensis* (see Bridgman, 1971 and Prevot *et al,* 1976).

5b. Vitelline follicles in lateral clusters in vicinity of testes. 6
6a. Transverse vitelline ducts long, prominent, pass anterior to testes (Fig. 541). .... **Genus *Longiductotrema* Deblock and Heard, 1969**
6b. Transverse vitelline ducts inconspicuous and not passing anterior to testes. 7
7a. Body elongate; vitelline follicles in narrow lateral bands; ovary and testes lobed (Fig. 540) .... **Genus *Odhneria* Travassos, 1921**

Life cycle: *Odhneria odhneri* - Microcercous cercariae develop in oval sporocysts in the marine prosobranch, *Littorina saxatilis.* The cercariae are eaten by the shrimp, *Palaemonetes vulgaris* in the muscles of which they encyst within thick cyst membranes and develop to metacercariae. The latter were fed to gulls and adult parasites recovered. Fourteen species of shore birds have been reported as host for this parasite (Stunkard, 1979a).

7b. Body oval or pyriform; vitelline follicles not in lateral bands; ovary and testes usually oval or spherical. . 8
8a. Vitelline follicles restricted to middle third of body, confluent dorsal to ceca and cirrus sac; oral sucker with anterior and lateral expansions and distinct muscle bands (Fig. 543). .... **Genus *Probolocorphe* Otagaki, 1958**

(Continued)

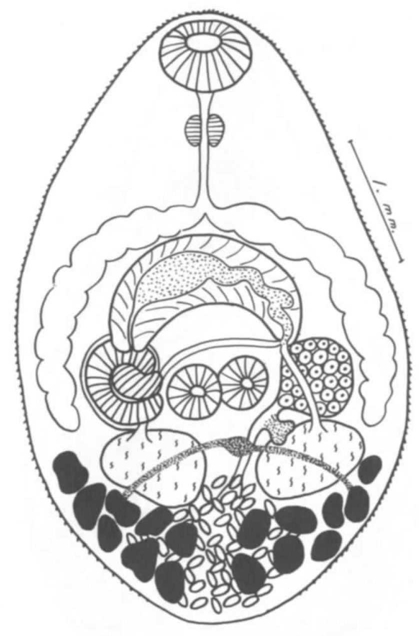


Fig. 536. *Gynaecotyla sippiwissettensis.* (from Rankin, 1939)

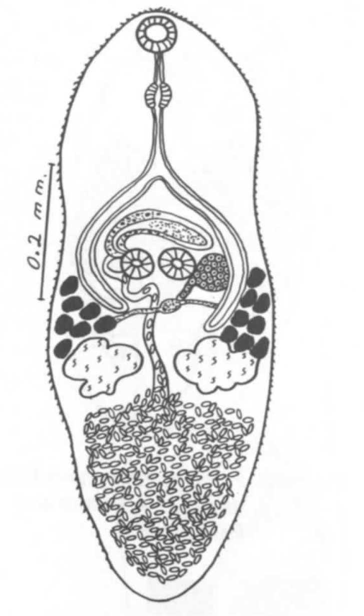


Fig. 537. *Derytrema riggini.* (from Dery, 1958)

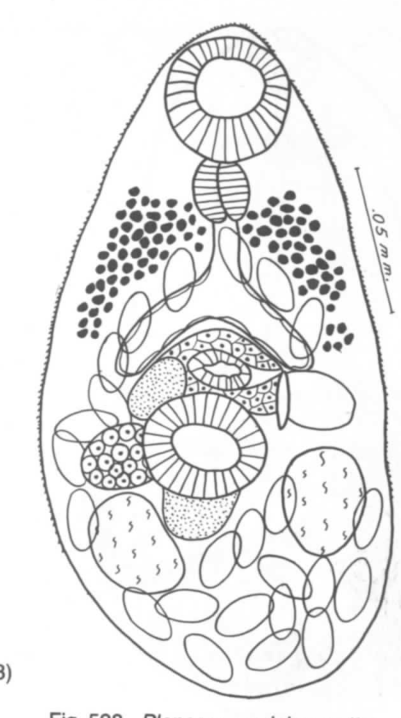


Fig. 538. *Plenosoma minimum.* (from Ching, 1960)

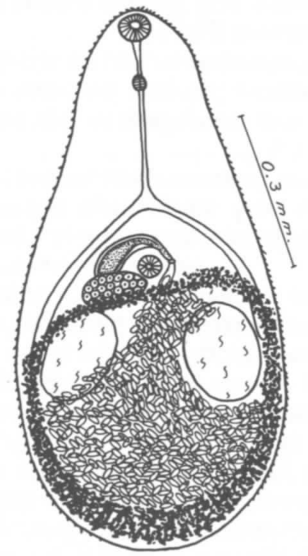


Fig. 539. *Maritrema ovatum.*

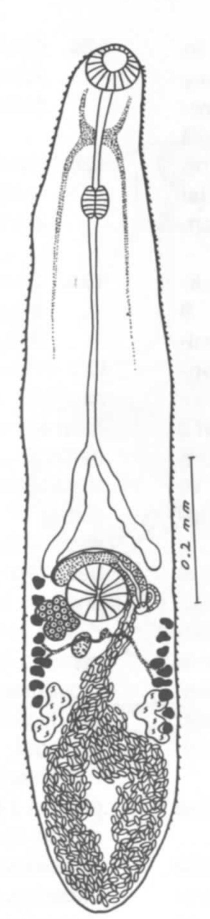


Fig. 540. *Odhneria limnodromi.*

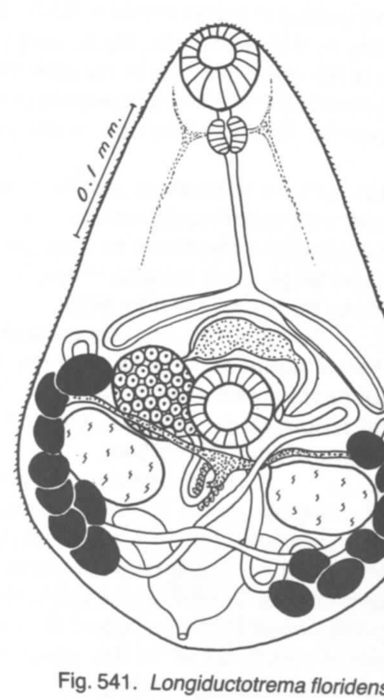


Fig. 541. *Longiductotrema floridensis.* (from Deblock and Heard, 1969)

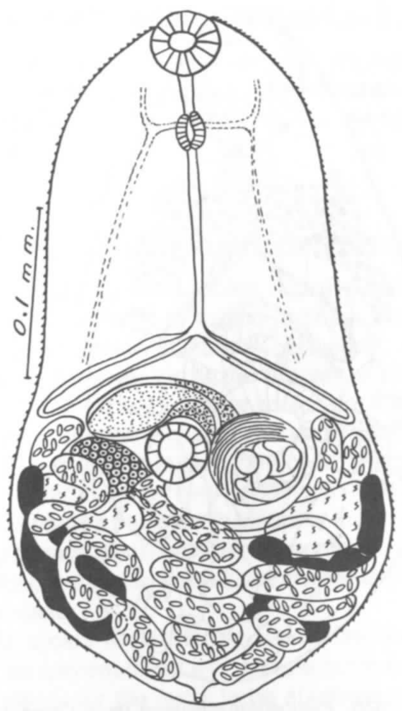


Fig. 542. *Androcotyla arenariae.* (from Deblock and Heard, 1970)

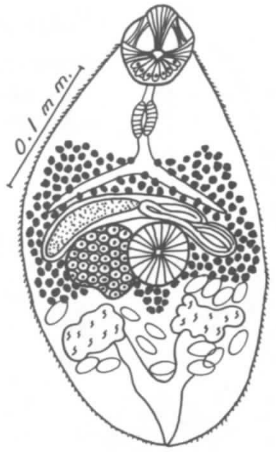


Fig. 543. *Probolocorphe glandulosa.* (from Cable, Connor and Balling, 1960)

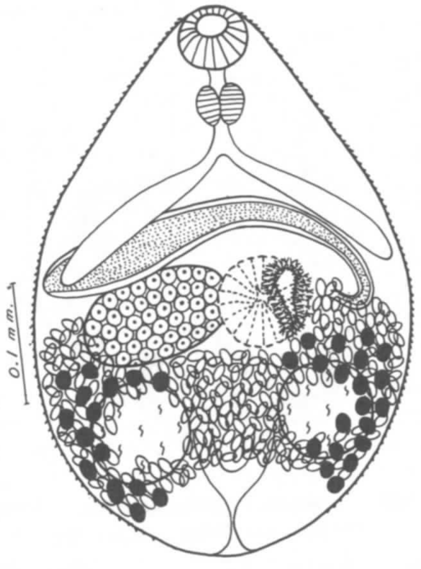


Fig. 544. *Maritreminoides nettae*, dorsal view.

Life cycle: *P. uca* - Cercariae of the ubiquita group develop in sporocysts in the prosobranch, *Cerithidia californica.* They emerge from the snail and then encyst in fiddler crabs, *Uca crenulata,* entering by way of the gills. Cysts were found in the gill tissue, base of the eyestalks and in the pericardial sinus. The species is known only from the metacercaria which is precocial but not progenetic. The definitive host is unknown (Sarkisian, 1957).

8b. Vitelline follicles in clusters around testes; oral sucker round, without muscular bands. 9

9a. Esophagus about five times as long as pharynx; genital atrium large, with muscle fibers in wall and contains three male papillae (Fig. 542). ....
.... **Genus *Androcotyla* Deblock and Heard, 1970**

9b. Esophagus about as long as pharynx; genital atrium without papillae and muscle fibers. 10

10a. Genital atrium large, spinous; cirrus sac long, anterior to ventral sucker (Fig. 544). ....
.... **Genus *Maritreminoides* Rankin, 1939**

Life cycle: *M. obstipus* - About 35 days are required for development of the miracidium after eggs are released. Eggs are eaten by the freshwater prosobranch snail, *Amnicola pilsburyi* in which xiphidiocercariae (not the ubiquita type) develop in sporocysts. Cercariae encyst in the hemocoel of aquatic freshwater isopods, *Asellus communis* which are eaten by ducks which serve as definitive host (Etges, 1953).

10b. Genital atrium small, nonspinous; cirrus sac dorsal to ventral sucker, transverse (Fig. 545). ....
.... **Genus *Pseudospelotrema* Yamaguti, 1939**

11a. Genital atrium contains male pockets (alveoli), with or without denticles or teeth. 12

11b. Genital atrium large or small, without male pockets or denticles. 13

12a. Oral sucker contains pair of ventro-lateral papillae; muscular post-oral ring present around prepharynx; female pouch absent (Fig. 546). ....
...... **Genus *Heardlevinseniella* Stiles and Hassall, 1901**

12b. Oral sucker without papillae; post-oral ring absent; male pockets well developed; female pouch usually present (Fig. 547). ....
.... **Genus *Levinseniella* Stiles and Hassall, 1901**

13a. Genital atrium very small; male copulatory organ small; parasitic in intestine of freshwater fishes (Fig. 548). .... **Genus *Microphallus* Ward, 1901**

Life cycle: *M. opacus* - Ubiquita xiphidiocercariae develop in daughter sporocysts in the prosobranch snail, *Amnicola limosa.* After emerging from the snail, the cercariae enter crayfish, *Cambarus propinquis* and undergo considerable development to the metacercarial stage before encystment occurs. Some metacercariae developed to sexual maturity in the crayfish, releasing eggs within the cyst membrane. Adults of this species have been reported from seven species of fish, two species of turtles and also from two mammalian hosts (Caveny and Etges, 1971).

The life cycle of *M. bittii* was reported by Prevot (1972). The cercaria is of the ubiquita type and develops in sporocysts in the prosobranch snail, *Bittium reticulatum.* They encyst in the appendages of the crab, *Carcinus maenas.* Gulls serve as definitive host.

Deblock (1974) studied the life cycle of *M. abortivus* which passes through an abbreviated cycle by producing blastocercariae in sporocysts in the marine prosobranch, *Hydrobia ulvae.* These cercariae are without a tail, stylet, penetration glands and excretory system. They encyst in the sporocyst where they develop directly to the metacercarial stage. Snails containing these metacercariae were fed to domestic ducklings and the adult parasites were recovered 72 hours later.

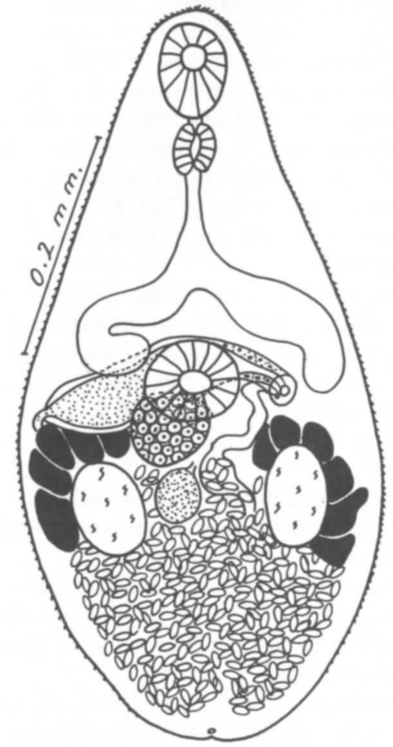


Fig. 545. *Pseudospelotrema ammospizae.* (from Hunter and Vernberg, 1953)

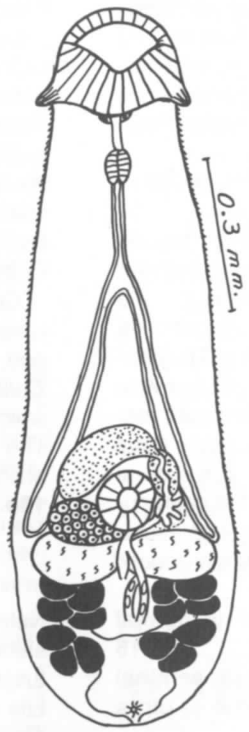


Fig. 546. *Heardlevinseniella byrdi.* (from Heard, 1968)

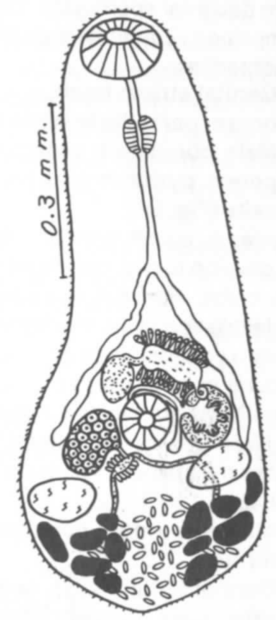


Fig. 547. *Levinseniella propinqua.* (from Rankin, 1939)

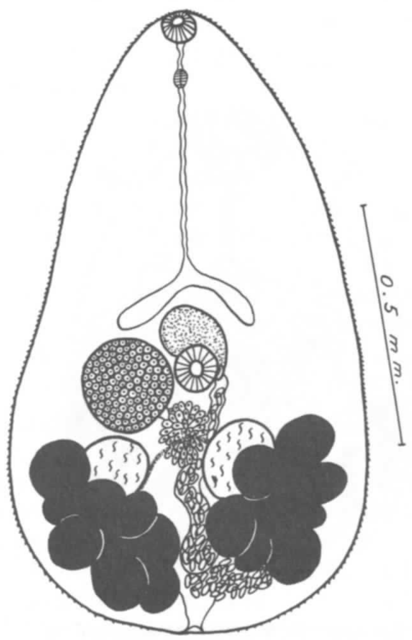


Fig. 548. *Microphallus opacus.*

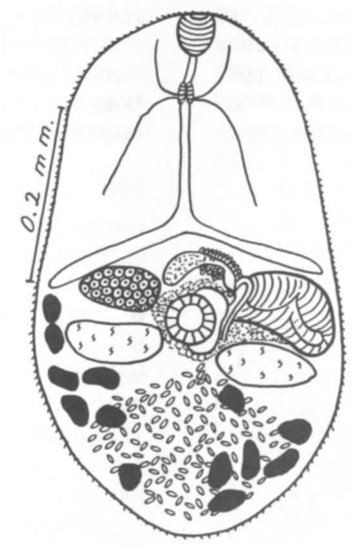


Fig. 549. *Ascorhytis charadriformis.* (from Ching, 1965)

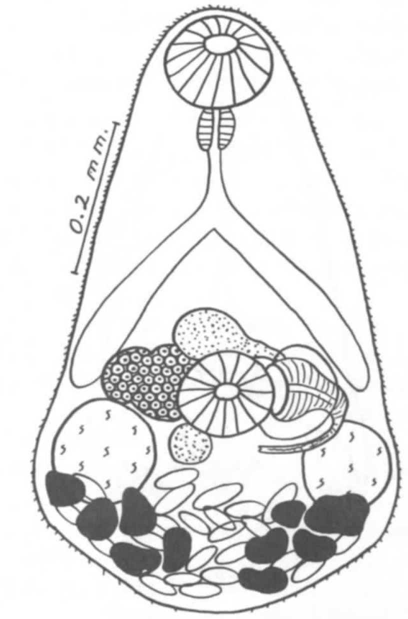


Fig. 550. *Atriophallophorus minuta.*

Jourdane (1977) studied the life cycle of *M. gracilis*, an intestinal parasite of the insectivore, *Neomys fodiens* in France. The host snail is *Bythinella reyniesii* in which ubiquita cercariae develop in daughter sporocysts. They encyst in the appendages of the amphipod, *Gammarus pulex*. The adults are protandrous hermaphrodites.

13b. Genital atrium large, cirrus a large muscular, bulbous organ; parasitic in birds and/or mammals. 14

14a. Male copulatory pouch with muscular folds; female pouch pyriform and provided with numerous gland cells (Fig. 549). .... Genus *Ascorhytis* Ching, 1965

Life cycle: *A. charadriformis* - Xiphidiocercariae of the ubiquita group develop in oval sporocysts in *Littorina scutulata*. They encyst in crabs, *Hemigrapsus oregonensis* and *H. nudus*, eventually developing to the metacercarial stage. Experimental infections were established in mice, ducklings, chicks, goldfish, frogs and young gulls to which metacercariae were fed. The natural definitive hosts are the gull, *Larus glaucescens* and the charadriforme birds *Limosa fedoa* and *Catoptrophorus inornatus*. Metacercariae maintained in seawater at 35 C for 24 hours produced eggs (Ching, 1962).

14b. Muscular, male copulatory organ present in genital atrium. 15

15a. Genital atrium large, contains conical cirrus; seminal receptacle present; parasitic in the intestine of birds (Fig. 550). .... Genus *Atriophallophorus* Deblock and Rose, 1964

Life cycle: *A. minutus* (Syn. *Levinseniella m.*) - Embryonated eggs were fed to the prosobranch snail, *Hydrobia minuta* in which somewhat degenerate, monostomate, tailless cercariae (blastocercariae) developed in sporocysts and encysted directly in the sporocysts. The adult parasite developed in one to three days in mice that were fed metacercariae (Stunkard, 1958).

15b. Genital atrium large, contains bulbous muscular cirrus; seminal receptacle absent. 16

16a. Genital atrium contains bulbous cirrus without lobes (Fig. 551). .... Genus *Spelotrema* Jagerskiold. 1901

Life cycle: *S. pygmaeum* - Pseudocercariae (*Cercaria littorinae rudis*) develop in daughter sporocysts in the marine prosobranchs, *Littorina saxatilis, L. littoralis* and *L. scutulata*. The cercariae have a rudimentary tail, pharynx and oral sucker. The remainder of the digestive system is absent as is the stylet and penetration glands. They are nonmotile and remain in the sporocysts where they develop to the metacercarial stage without encysting. The adult fluke develops in domestic ducklings and in young herring gulls in two or three days after eating infected snails. Natural definitive hosts are herring gull, *Larus argentatus* and rock pipit, *Anthus spinoletta* (see Belopolskaia, 1949; Ching, 1962; James, 1968).

Cable and Hunninen (1940) reported the life cycle of *S. nicolli*. Ubiquita cercariae develop in sporocysts in the marine gastropod, *Bittium alternatum*. They encyst in the tissues of blue crab, *Callinectes sapidus* and develop to infective metacercariae which eventually developed to adults when fed to herring gulls. The cercariae have two distinct kinds of glands with different staining characteristics.

16b. Genital atrium contains fleshy trilobed male copulatory organ; vitelline follicles overlap testes; parasitic in intestine of birds and mammals (Fig. 552). .... Genus *Carneophallus* Cable and Kuns, 1951

Note: Most species originally assigned to this genus have been shifted to the genera *Microphallus* and *Spelotrema* but their status is still somewhat uncertain.

Life cycle: *C. choanophallus* - Xiphidiocercariae of the ubiquita group develop in daughter sporocysts in the prosobranch, *Lyrodes parvula*. They encyst in the abdomen and cephalothorax of shrimp of the genera *Palaemonetes* and *Macrobrachium*. Natural definitive hosts are raccoon and the black rat, *Rattus rattus* (see Bridgman, 1969).

Velasquez (1975) investigated the life cycle of *C. brevicaeca* which also uses shrimp as second intermediate host.

The blue crab, *Callinectes sapidus*, has been involved as second host for some species, the cercariae encysting in the nervous system, causing death of the crustaceans.

C. brevicaeca has been reported as the cause of fatal involvement of heart and spinal cord of human beings in the Philippine Islands where infected crustaceans are eaten raw or undercooked (Africa and Garcia, 1935).

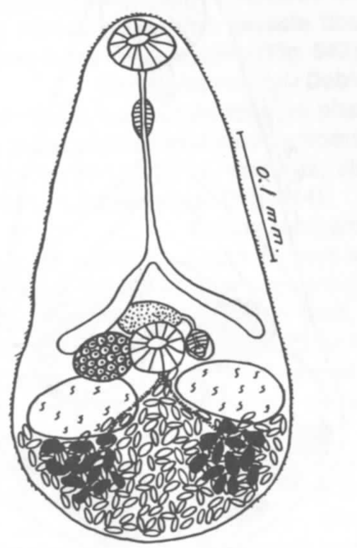


Fig. 551a. *Spelotrema pygmaeum.*

Fig. 551b. cross section through genital atrium.

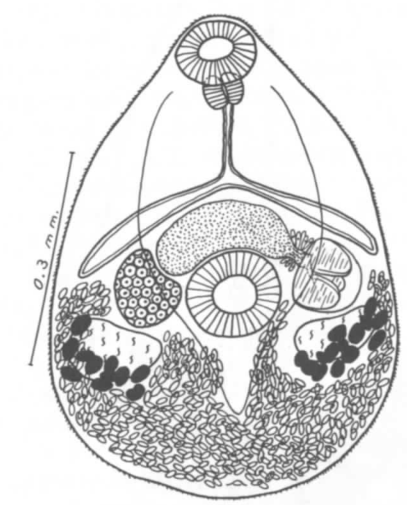


Fig. 552. *Carneophallus trilobatus.*

Family Lecithodendriidae Odhner, 1910

Body oval or pyriform, spinous; ventral sucker usually in middle of body; pharynx present; ceca variable in length; testes opposite; cirrus sac present; genital pore median, submedian or marginal; ovary pre- inter- or posttesticular; vitelline follicles in lateral clusters in forebody, rarely in hindbody; uterus fills most of hindbody, rarely extends into forebody; eggs operculate, embryonated; parasitic in digestive tract of amphibians, birds or mammals (bats). Several species have been found in human beings and other primates in the Far East.

Key to Genera

1a. Genital pore on right or left margin of body. 2

1b. Genital pore not on margin of body. 3

2a. Cirrus sac and marginal genital pore in hindbody; uterus confined to hindbody; testes posterior to ventral sucker; metraterm weakly developed (Fig. 553). .. .. Genus *Macyella* Neiland, 1951

2b. Cirrus sac and marginal genital pore in forebody; some uterine folds in forebody; testes lateral to ventral sucker; metraterm well developed (Fig. 554). .... Genus *Pseudosonsinotrema* Dollfus, 1951

3a. Genital pore on dorsal surface of body. 4

3b. Genital pore on ventral surface of body. 5

4a. Genital pore dorsal and to left of oral sucker; ovary oval, submedian, close to ventral sucker; parasitic in intestine of salamanders (Fig. 555). .... Genus *Cephalouterina* Senger and Macy, 1953

Life cycle: *C. dicamptodoni* - Xiphidiocercariae develop in daughter sporocysts in the prosobranch snail, *Bythinella hemphilli*. After leaving the snail, they encyst in nymphs of the stonefly, *Acroneuria californica*. The natural definitive host is Pacific giant salamander, *Dicamptodon ensatus* and the tailed frog, *Ascaphus truei*. Experimental infections were established in *Rana aurora* after feeding metacercariae (Anderson, Martin and Pratt, 1966).

4b. Genital pore dorsal and extracecal; ovary lobed, median, in forebody; adults encysted in wall of duodenum and stomach of frogs (Fig. 556). .... Genus *Loxogenes* Stafford, 1905

Life cycle: *L. arcanum* - Metacercariae of this species have been found encysted in the muscles of nine species of dragonfly naiads which are eaten by frogs (Crawford, 1938).

5a. Genital pore posterior or lateral to ventral sucker. . 6

5b. Genital pore anterior to ventral sucker. 9

6a. Genital pore and cirrus sac to right or left of ventral sucker; vitelline follicles in clusters at ends of short ceca (Fig. 558). .... Genus *Limatulum* Travassos, 1921

6b. Genital pore posterior to ventral sucker. 7

7a. Testes lateral to ventral sucker; ovary deeply lobed, some distance anterior to ventral sucker (Fig. 557). ... . Genus *Metoliophilus* Macy and Bell, 1968

Life cycle: *M. uvaticus* - Adults were recovered from the intestine of baby chicks five days after feeding metacercariae from nymphs of stonefly, *Acroneuria pacifica*. The water ouzel, *Cinclus mexicanus unicolor* is the natural definitive host (Macy and Bell, 1968b).

7b. Testes in hindbody; ovary dorsal to ventral sucker or anterior to right testis. 8

8a. Cirrus sac absent; ovary lobed, dorsal to ventral sucker; Parasitic in intestine of birds (Fig. 559). .... Genus *Echinuscodendrium* Skarbilovich, 1943

8b. Cirrus sac present, curved, confined to hindbody; ovary oval, anterior to right testis; parasitic in bats (Fig. 561). .... Genus *Gyrabascus* Macy, 1935

9a. Testes in hindbody. 10

9b. Testes in forebody or lateral to ventral sucker. 14

10a. Body truncate posteriorly; genital pore ventral to left cecum; cirrus sac transverse; vitelline follicles lateral to cecal bifurcation; parasitic in frogs (Fig. 560). .... Genus *Langeronia* Caballero and Bravo-Hollis, 1949

10b. Body rounded or conical posteriorly; cirrus sac not transverse. 11

11a. Vitelline follicles confluent across forebody; ceca long, arched anteriorly; ovary round, anterior to right testis; parasitic in birds (Fig. 562). .... Genus .... *Ornithodendrium* Oshmarin and Dotsenko, 1951

11b. Vitelline follicles in distinct lateral clusters, not confluent; ceca long or short. 12

12a. Ceca long, inflated; ovary lobed, dorsal to ventral sucker; uterine folds extend into forebody; parasitic in bile duct of frogs (Fig. 564). .... Genus *Loxogenoides* Kaw, 1945

Life cycle: *L. bicolor* - Virgulate cercariae (*Cercaria nyxtica*) develop in daughter sporocysts in the freshwater prosobranch, *Goniobasis depygis*. Cercariae emerge and then encyst in naiads of dragon- and mayflies. Metacercariae 40 days old were fed to frogs but without success (Seitner, 1945).

12b. Ceca short or halflong, not inflated. 13

13a. Body pyriform; ceca extend to testes; parasitic in birds (Fig. 563). .... Genus *Mosesia* Travassos, 1921

Key to species in Khotenovski (1967).

Life cycle: *M. chordeilesia* - Virgulate xiphidiocercariae (Fig. 35) develop in sporocysts in the freshwater prosobranch snails, *Goniobasis livescens* and *Pleurocera acuta*. The cercariae encyst in the hemocoel of mayfly nymphs. The adult fluke develops in the intestine of nighthawks (Hall, 1959).

13b. Body fusiform; ceca extend only to level of ventral sucker; parasitic in bats (Fig. 565). .... Genus *Tremajoannes* Saoud, 1964

14a. Testes in forebody; ceca very short and divergent; vitelline follicles in clusters lateral to oral sucker and pharynx; some uterine folds in forebody; parasitic in frogs (Fig. 567). ....Genus *Prosthopycoides* Martin, 1966

Life cycle: *P. lynchi* - Microcercous xiphidiocercariae develop in rediae (?) in the prosobranch snail, *Bythinella hemphilli*. Cercariae penetrate and encyst in the fatbody of the stonefly larvae, *Acroneuria californica*. Metacercariae were fed to frogs and the adult flukes recovered. Some progenetic adults were found in the second intermediate host. *Rana aurora* is the normal definitive host (Martin, G.W., 1966).

14b. Testes lateral to ventral sucker; parasitic in bats. . 15

15a. Vitelline follicles confined to lateral regions of hindbody, posterior to testes; ovary usually in hindbody (Fig. 566). .... Genus *Lecithodendrium* Looss, 1896

15b. Vitelline follicles confined to forebody. 16

16a. Vitelline follicles in clusters lateral to ceca, not lateral to oral sucker and pharynx. 17

16b. Vitelline follicles in clusters lateral to oral sucker, pharynx, or anterior to ceca. 19

17a. Genital atrium spinous (Fig. 568). .... Genus *Acanthatrium* Faust, 1919

Key to species in Williams (1960).

(Continued)

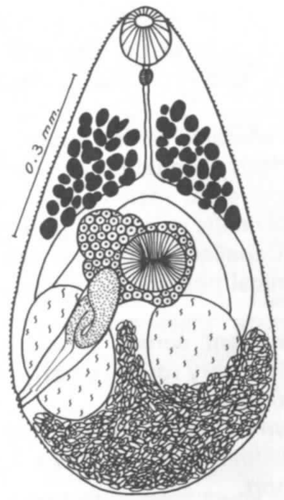


Fig. 553. *Macyella postgonoporus.*

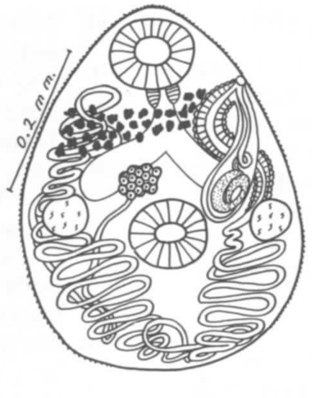


Fig. 554. *Pseudosonsinotrema catesbeianae.* (from Christian, 1971).

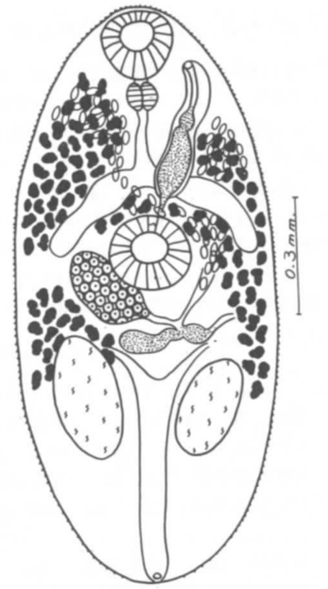


Fig. 555. *Cephalouterina dicamptodoni.*

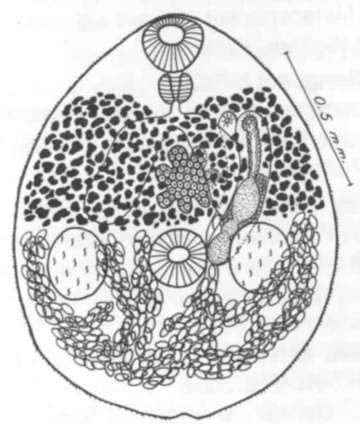


Fig. 556. *Loxogenes arcanum.*

Fig. 557. *Metoliophilus uvaticus.*

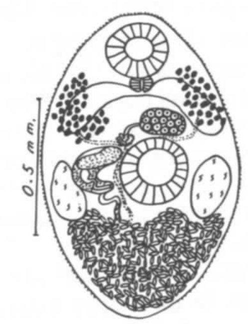


Fig. 558. *Limatulum oklahomiensis.*

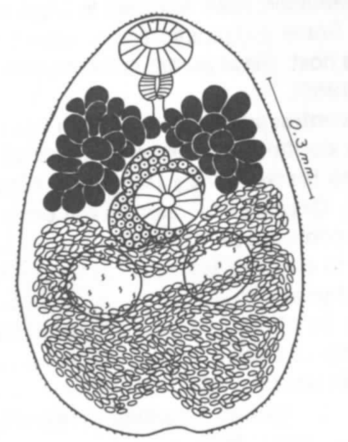


Fig. 559. *Echinuscodendrium echinus.*

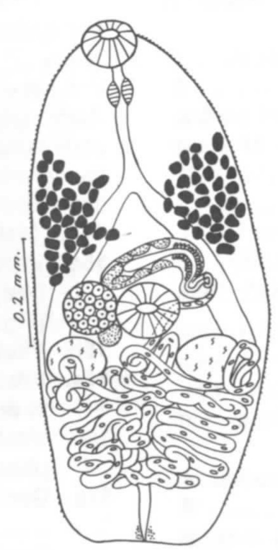


Fig. 560. *Langeronia parva.* (from Christian, 1970)

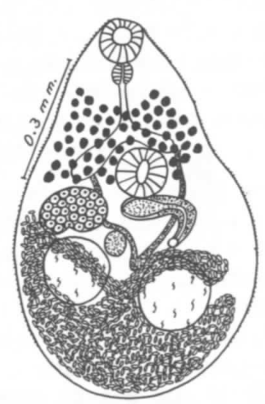


Fig. 561. *Gyrabascus brevigastrus.*

Fig. 562. *Ornithodendrium imanensis.*

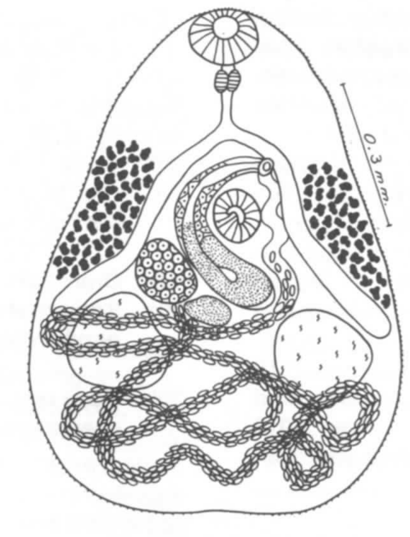


Fig. 563. *Mosesia chordeilesia.*

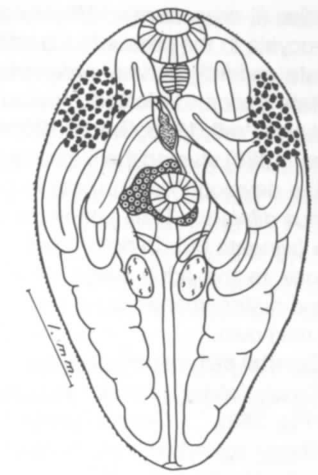


Fig. 564. *Loxogenoides bicolor.*

Fig. 565. *Tremajoannes buckleyi.* (from Cain, 1966)

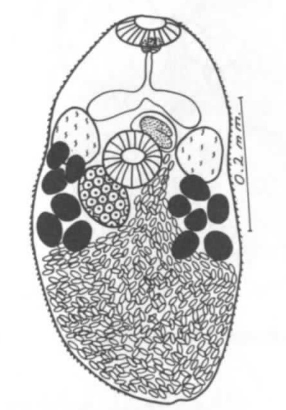


Fig. 566. *Lecithodendrium breckenridgei.*

Fig. 567. *Prosthopycoides lynchi.* (from Martin, G.W., 1966)

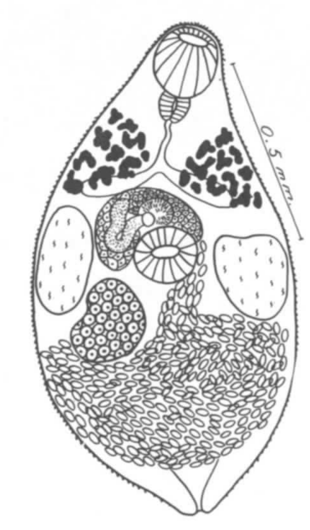


Fig. 568. *Acanthatrium micracanthium.*

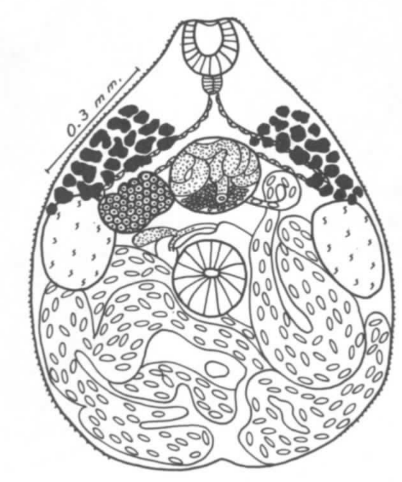


Fig. 569. *Paralecithodendrium carlsbadense.* (from Cain, 1966)

Life cycle: *A. oregonense* - Virgulate xiphidiocercariae develop in sporocysts in the prosobranch snail, *Oxytrema silicula.* They penetrate caddisfly larvae, enter the hemocoel but do not encyst. Bats become infected by eating the infected caddisflies (Knight and Pratt, 1955; Burns, 1961a).

Etges (1960) studied the life cycle of *A. anoplocami.* Virgulate cercariae develop in sporocysts in the prosobranch snail, *Anoplocamus dilatatus.* They penetrate nymphs of the mayfly, *Hexagenia bilineata* but do not encyst until after the nymphs metamorphose to the adult stage. Mice were infected by feeding encysted metacercariae in adult mayflies. The natural definitive host is unknown.

17b. Genital atrium nonspinous. **18**

18a. Ovary lobed, anterior to right testis; cirrus sac round (Fig. 569). .. **Genus** ***Paralecithodendrium*** **Odhner, 1910**

18b. Ovary round or oval, between testes; cirrus sac oval, in forebody (Fig. 570). .... **Genus** ***Prosthodendrium*** **Dollfus, 1931**

Life cycle: *P. pyramidum* - Virgulate xiphidiocercariae develop in sporocysts in the snail, *Melania tuberculata.* The cercariae are thought to be eaten by anopheline mosquito larvae in which they encyst. The adult parasite develops in the intestine of bats which probably eat the adult mosquitos (Abdel-Azim, 1936).

19a. Oral sucker with muscular ventrolateral papillae; cirrus sac oval and arcuate; ovary angular (Fig. 571). .... **Genus** ***Ototrema*** **Font, 1978**

19b. Oral sucker without muscular papillae. **20**

20a. Body round; ovary lobed; cirrus sac oval; pseudogonotyl present near ventral sucker (Fig. 572). .... **Genus** ***Ochoterenatrema*** **Caballero, 1943**

20b. Body oval; ovary oval or triangular; cirrus sac folded; pseudogonotyl absent (Fig. 573). .... **Genus** ***Glyptoporus*** **Macy, 1936**

Fig. 570. *Prosthodendrium naviculum.*

Fig. 571. *Ototrema schildti.* (from Font, 1978).

Fig. 572. *Ochoterenatrema labda.* (from Cain, 1966).

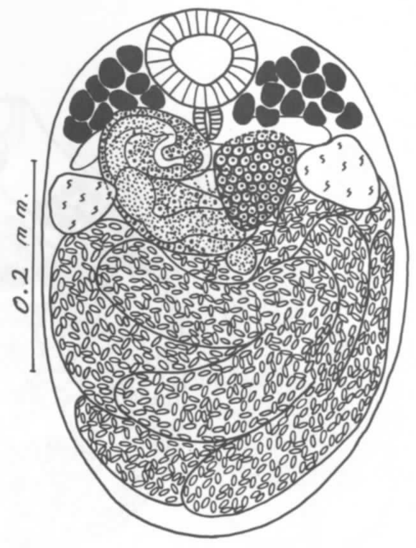


Fig. 573. *Glyptoporus noctophilus,* dorsal view. (from Macy, 1936).

Family Allassogonoporidae Odening, 1964

Body flat, pyriform or oval; suckers about equal; ventral sucker near middle of body; ceca arcuate, long or halflong; testes opposite, in hindbody; cirrus sac absent; seminal vesicle free in parenchyma; genital pore on right or left margin of body; ovary anterior to right or left testis; vitelline follicles in clusters lateral to ceca, usually in forebody; uterus confined to hindbody; eggs operculate, nonembryonated; excretory vesicle tubular; parasitic in intestine of mammals, especially bats.

Key to Genera

1a. Intestinal ceca extend only as far as ventral sucker; vitelline follicles lateral to ventral sucker (Fig. 574). ... . **Genus** ***Cephalophallus*** **Macy and Moore, 1954**

Life cycle: *C. obscurus* - Virgulate xiphidiocercariae (Fig. 35) develop in sporocysts in the prosobranch snail, *Fluminicola virens* and encyst in the muscles of crayfish, *Astacus trowbridgii.* The adult parasite develops in the small intestine of mink which eat the infected crayfish (Macy and Moore, 1954).

1b. Intestinal ceca long, extend beyond ventral sucker; vitelline follicles confined to forebody. **2**

2a. Body pyriform; genital pore on lateral margin of hindbody; vitelline follicles confluent across forebody (Fig. 575). .... **Genus** ***Allassogonoporus*** **Olivier, 1938**

Life cycle: *A. vespertilionis* - Virgulate xiphidiocercariae (Fig. 35) develop in sporocysts in the prosobranch snail, *Fluminicola virens.* The cercariae creep on the substrate and upon contacting a caddisfly larva they penetrate the gills and encyst. Metacercariae are infective in about one week. The adult parasite develops in the intestine of bats which eat the infected caddisflies (Knight and Pratt, 1955; Burns, 1961b).

2b. Body oval, anterior end conical; genital pore marginal, lateral to ventral sucker; vitelline follicles not confluent; parasitic in bats (Fig. 576). .... **Genus** ***Myotitrema*** **Macy, 1939**

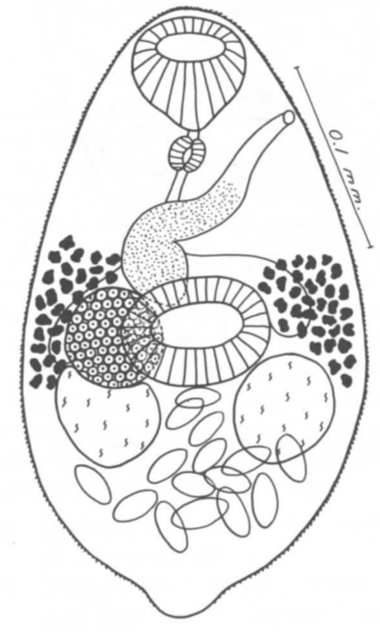


Fig. 574. *Cephalophallus obscurus.*

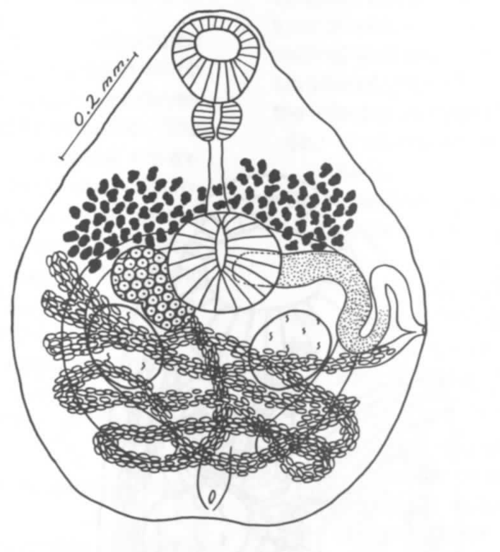


Fig. 575. *Allassogonoporus marginalis.*

Fig. 576. *Myotitrema assymetricum.*

Family Stomylotrematidae Poche, 1926

Body small (2 to 3mm), oval, nonspinous; suckers very large for size of body; ventral sucker in posterior third of body; pharynx present; ceca long; testes opposite, in forebody; cirrus sac oblique, dextral, in forebody; genital pore marginal, at level of pharynx; ovary anterior to left testis; vitelline follicles few, lateral to ceca; uterine folds surround ventral sucker; parasitic in large intestine and cloaca of birds.

The family contains only the genus *Stomylotrema* Looss, 1900 which is represented in North America by two species (Fig. 577, 578).

Life cycle: *S. vicarium* - Metacercarie were found encysted in the hemocoel of the diving beetle, *Megadytes glauca.* Some were fed to day-old chicks and to a lapwing, *Belonopterus cayennensis* and the adult parasites recovered four to seven days later. Both the metacercaria and the adult have the ventral sucker close to the posterior end of the body. In addition, the main ducts of the excretory system have lateral branches and flame cells are abundant. Very young metacercariae have a stylet which is shed. It is assumed that a virgulate cercaria in the prosobranch, *Ampullaria canaliculata* is the larva of this parasite (Ostrowski de Nunez, 1978).

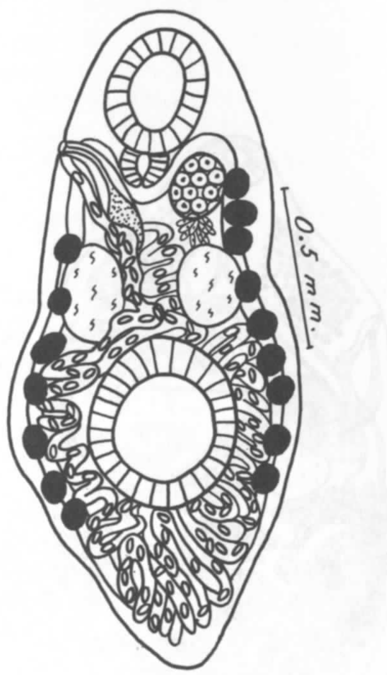


Fig. 577. *Stomylotrema gratiosum.*
(from Lumsden and Zischke, 1963).

Family Laterotrematidae Yamaguti, 1958

Body small (1 to 2mm); suckers well developed, in anterior half of body; pharynx present; intestinal ceca variable in length; testes opposite, in middle of hindbody; cirrus sac transverse, in forebody; genital pore on left margin of body; ovary anterior to right testis, usually in forebody; vitelline follicles in clusters in anterio-lateral regions of body, confined to forebody; uterus fills most of hindbody, much of it posttesticular; parasitic in digestive tract of song birds.

The genus *Laterotrema* Semenow, 1928 is represented in North America by two species (Fig. 579).

Key to species in Macy and Strong (1967).

Fig. 579. *Laterotrema americanum.*

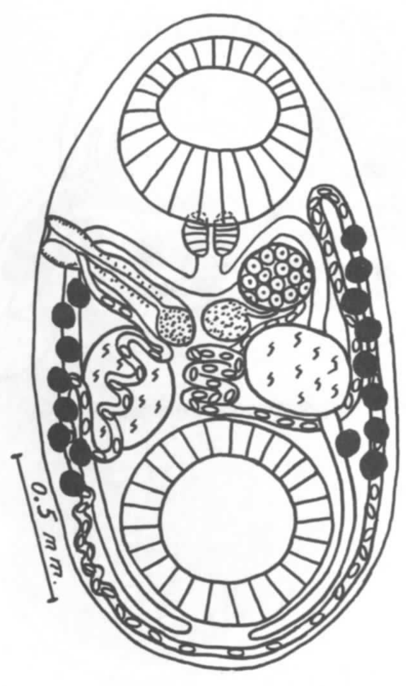


Fig. 578. *Stomylotrema vicarium.*

Superfamily Dicrocoelioidea Faust, 1929

Miracidia have one pair flame cells. Xiphidiocercariae with either a long or short tail develop in daughter sporocysts in terrestrial snails; cercariae encyst in terrestrial arthropods. Flame cell formula of cercaria is $2\ [(2+2+2)+(2+2+2)]$. Life cycle involves three hosts.

Family Dicrocoeliidae Odhner, 1910

Body filiform, elongate or fusiform, translucent; ventral sucker in anterior fourth of body, vestigial or absent in a few genera; pharynx present; ceca long, single cecum in some species of genus *Lutztrema;* testes tandem, oblique or opposite, in hindbody; cirrus sac close to ventral sucker; genital pore median, anterior to ventral sucker; ovary posttesticular; vitelline follicles lateral to ceca, usually restricted to middle third of hindbody, only on one side of body in genus *Athesmia;* uterus fills most of hindbody; eggs operculate, embryonated; parasitic in gall bladder, pancreatic, hepatic or bile duct of reptiles, birds and mammals.

This family can be divided into two groups on the basis of the type of cercaria produced. Some species produce leptocercous xiphidiocercariae which leave the snail in slime balls. The second type of cercaria is microcercous. They remain in the sporocysts which in turn is expelled from the snail in a mass of mucus.

Key to Genera

1a. Testes opposite. 2

1b. Testes tandem or oblique. 7

2a. Ventral sucker at least twice as large as oral sucker; body lanceolate, widest at level of testes (Fig. 580). .... **Genus *Zonorchis* Travassos, 1944**

Life cycle: *Z. petiolatum* (= *Dicrocoelioides p.*) - Embryonated eggs are eaten by the terrestrial snail, *Helicella arenosa* in which the miracidium hatches. Mother and daughter sporocysts develop, the latter producing microcercous xiphidiocercariae. The daughter sporocysts, each containing several cercariae, are expelled from the snail by way of the pneumostome, each sporocyst enveloped in a mass of mucus. A thick endocyst membrane then forms beneath the sporocyst wall. The endocyst probably provides extra protection for the cercariae during this free-living period. These sporocysts are eaten by terrestrial isopods, *Armadillo officinalis* and *Armadillidium vulgare* in which the cercariae then develop to infective metacercariae in about two months. Passerine birds eat infected isopods and acquire the parasite. *Passer domesticus,* the European tree sparrow is the natural definitive host (Timon-David, 1960).

2b. Suckers equal or ventral sucker only slightly larger than oral sucker. 3

3a. Ceca inflated, sinuous; parasite of reptiles and birds (Fig. 581). .... **Genus *Paradistomum* Kossack, 1910**

Life cycle: *P. mutabile* - Microcercous xiphidiocercariae develop in daughter sporocysts in *Helicella arenosa.* This mollusc is not the natural host for this species. A second intermediate host has not been found but the author suggests it might be a terrestrial anthropod. The definitive host is the lizard, *Lacerta muralis* (see Timon-David and Timon-David, 1967).

3b. Ceca narrow and straight. 4

4a. Vitelline follicles few, restricted to small lateral clusters in midbody region, extending over about one-fifth of body length. 5

4b. Vitelline follicles numerous, distributed over about half of body length. 6

5a. Testes and ovary small, oval; parasitic in mammals (Fig. 582). .... **Genus *Concinnum* Bhalerao, 1936**

Life cycle: *C. procyonis* - Embryonated eggs are eaten by the land snail, *Mesodon thyroideus* in which microcercous xiphidiocercariae develop in daughter sporocysts. The latter are expelled through the spiracle and lodge on vegetation. A second intermediate host has not been found for this species but some arthropod is thought to be involved. The adult fluke develops in the pancreatic duct of raccoon (Denton, 1944).

5b. Testes and ovary large, lobed; parasitic in birds and mammals (Fig. 583). .... **Genus *Platynosomum* Looss, 1907**

Key to species in Ku (1957).

Life cycle: *P. fastosum* - Microcercous xiphidiocercariae develop in sporocysts in the terrestrial snail, *Subulina octona.* The sporocysts leave the snail and are eaten by terrestrial isopods in which the metacercariae develops. Obligatory third intermediate hosts such as lizards and frogs also seem to be involved. Natural definitive hosts are cat, opossum, house mouse and skunk which eat the infected third intermediate hosts (Maldonado, 1945b; Eckerlin and Leigh, 1962).

6a. Ventral sucker larger than oral sucker; body narrowly fusiform (Fig. 584). .... **Genus *Conspicuum* Bhalerao, 1936**

Life cycle: *C. icteridorum* - Embryonated eggs are eaten by the terrestrial snail, *Zonitoides arboreus* and by the slug, *Deroceras laeve* in which microcercous xiphidiocercariae develop in daughter sporocysts. The latter are expelled through the spiracle of the snail and are later eaten by the terrestrial isopods, *Oniscus asellus* and *Armadillium quadrifrons,* in the digestive tract of which the cercariae are liberated. They penetrate the intestinal wall and encyst. The adult parasite develops in the gall bladder of grackles, blackbirds and meadowlarks which feed on the infected isopods (Patten, 1952).

6b. Suckers of equal size; body broadly fusiform (Fig.) 585). .... **Genus *Lubens* Travassos, 1920**

7a. Vitelline follicles unilateral; testes lobed; parasitic in birds and mammals (Fig. 586). .... **Genus *Athesmia* Looss, 1899**

Key to species in McIntosh (1937) and in Skrjabin (1964).

7b. Vitelline follicles bilateral; testes usually not lobed. 8

8a. One intestinal cecum present; body lanceolate; parasitic in birds (Fig. 587). .... **Genus *Lutztrema* Travassos, 1941**

Life cycle: *L. monenteron* - Embryonated eggs were fed to laboratory-reared specimens of the terrestrial snail, *Allogona ptychophora.* Long-tailed xiphidiocercariae left the snail in slime balls 148 days later. Four other genera and species of snails were also found to serve as first intermediate hosts for this parasite (Carney, 1966).

8b. Two ceca present. 9

9a. Body fusiform, widest at middle; testes irregular in shape; vitelline follicles restricted to short lateral zone near middle of body; parasitic in birds and mammals (Fig. 588). ... **Genus *Dicrocoelium* Dujardin, 1845**

Key to species in Macy (1931) and in Skrjabin (1964).

Life cycle: *D. dendriticum* - Embryonated eggs in the feces of the host are eaten by the terrestrial snail, *Cionella lubrica.* Miracidia hatch in the snail intestine and penetrate the intestinal wall. Xi-

(Continued)

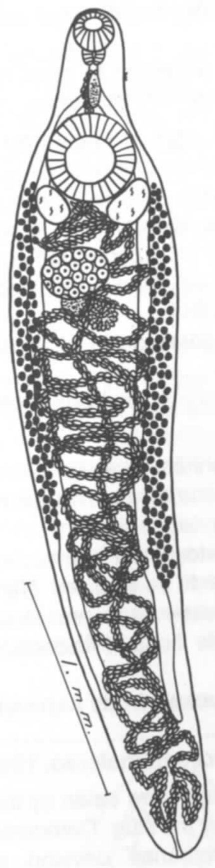


Fig. 580. *Zonorchis petiolatum.*

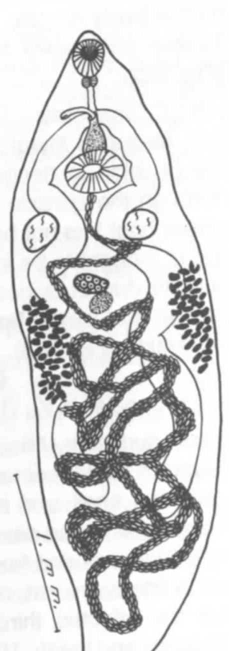


Fig. 581. *Paradistomum passerculum.*

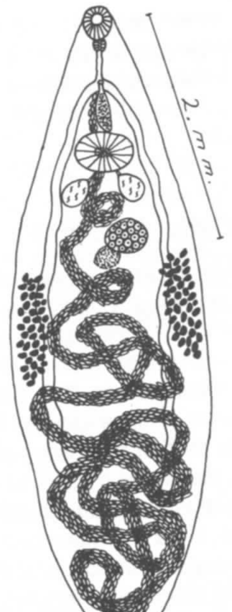


Fig. 582. *Concinnum burleighi.*

Fig. 583. *Platynosomum fastosum.*

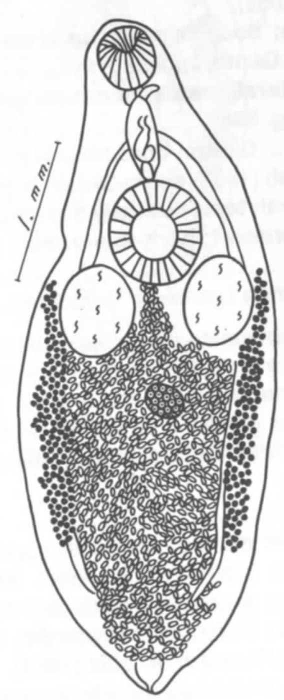


Fig. 584. *Conspicuum macrorchis.*

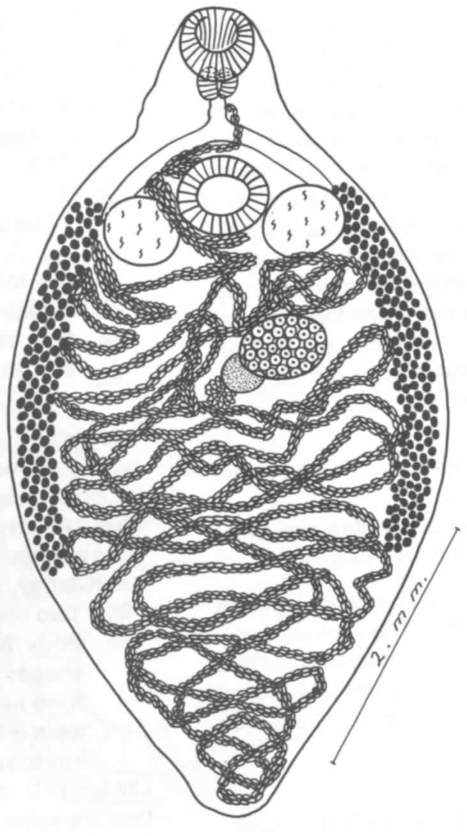


Fig. 585. *Lubens lubens.*

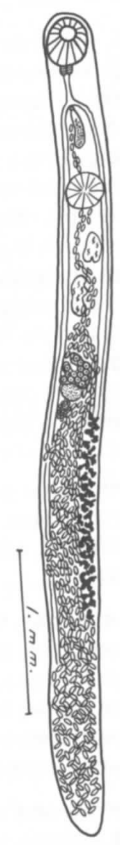


Fig. 586. *Athesmia jolliei.*

Fig. 587. *Lutztrema monenteron.*

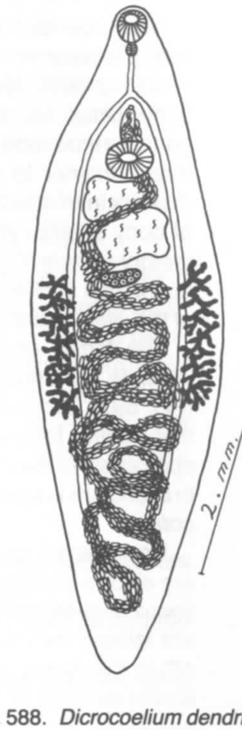


Fig. 588. *Dicrocoelium dendriticum.*

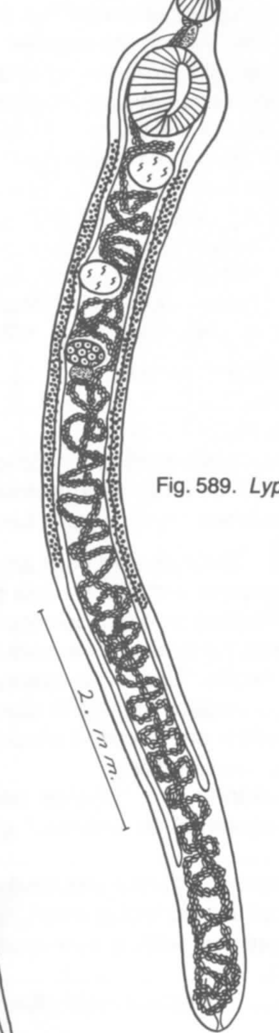


Fig. 589. *Lyperosomum oswaldi.*

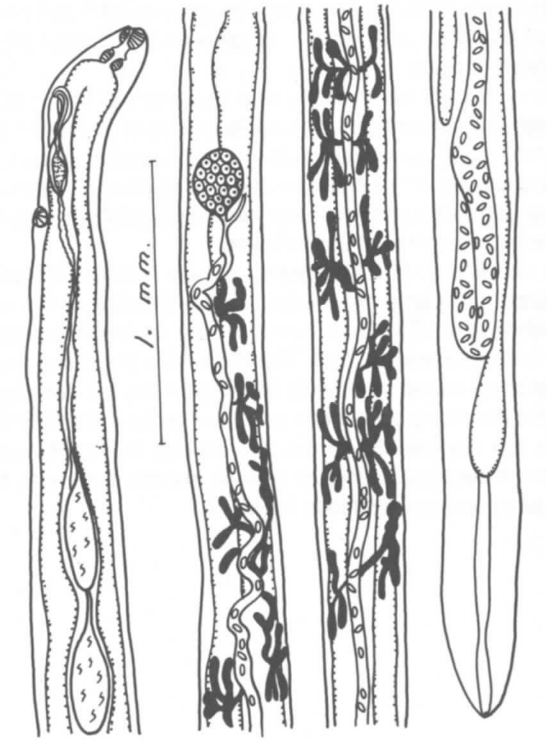


Fig. 590. *Allocorrigia filiformis.* (from Turner and Corkum, 1977)

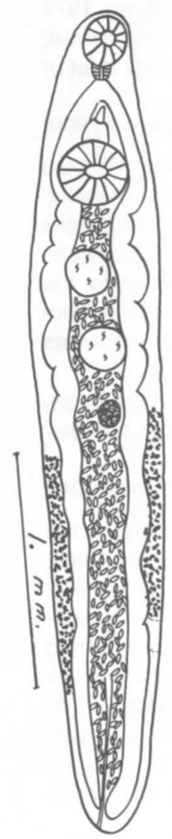


Fig. 591. *Corrigia obscura.* (from Daniels and Freeman)

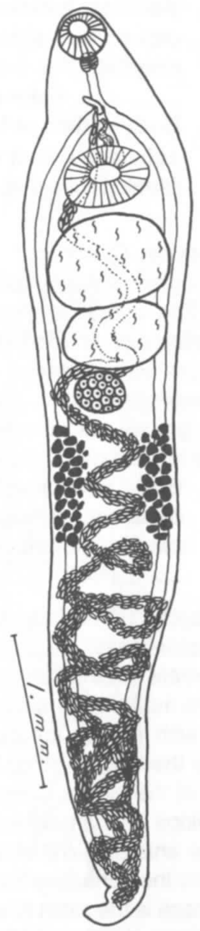


Fig. 592. *Brachylecithum mosquensis.*

xiphidiocercariae with a long tail *(Cercaria vitrina)* develop in daughter sporocysts. As the cercariae leave the sporocysts, the snail secretes mucus around masses of several hundred cercarie to form so-called "slime balls" which are expelled by way of the spiracle of the snail. Slime balls are eaten by ants, *Formica fusca* in which cercariae encyst and develop to metacercariae. Encystment is commonly in the brain of the ants, causing abnormal behavior and probably making them easier prey for the definitive host. Infected ants are eaten by herbivorous mammals such as sheep, goats, cattle, pig, deer, marmot and rabbit. Metacercariae excyst, then go to the liver by way of the bile duct. Development to sexual maturity requires six to seven weeks (Krull and Mapes 1952, 1953; Mapes 1952, 1953; Mapes, 1951; Mapes and Krull, 1951; Romig, Lucius and Frank, 1980).

9b. Body lanceolate or filiform; testes oval. 10

10a. Body filiform (Fig. 589). 11

10b. Body lanceolate (Fig. 592). 12

11a. Vitelline follicles small, abundant, some follicles anterior to ovary; parasitic in birds and mammals (Fig. 589). .... **Genus *Lyperosomum* Looss, 1899**

Life cycle: *Lyperosomum* sp. - Embryonated eggs are eaten by the land snails *Polygyra texasiana* and *Practicollela berlandieriana.* Xiphidiocercariae of the armatae group develop in daughter sporocysts. Cercariae leave the snail in slime balls which are eaten by the chrysomelid beetle, *Gastroidia cyanea.* Development to the cercarial stage requires about 100 days. Normal definitive hosts are meadowlark and bronzed grackles which feed upon the infected beetles (Denton, 1941).

11b. Vitelline follicles dendritic, no follicles anterior to ovary; parasitic (progenetic) in antennal glands of crayfish (Fig. 590). .... **Genus *Allocorrigia* Turner and Corkum, 1977**

12a. Body widest at level of testes; testes small, spherical; ceca somewhat sinuous; parasitic in pancreatic duct of black ducks (Fig. 591). .... **Genus *Corrigia* Shtrom,1940**

Life cycle: *C. corrigia* - Microcercous xiphidiocercariae develop in daughter sporocysts in the terrestrial snail, *Jaminia potaniniana.* The cercariae penetrate and encyst in the crustaceans *Hemilepistus fetschenkoi* (natural infection) and *Orthometopon planum* (experimental infection) where they develop to the metacercarial stage. Adults developed in about 75 days in *Alectoris gracea* after feeding infected crustaceans. This work was done in Kazakhstan by Panin and Romanenko (1978).

12b. Body widest at level of ventral sucker; testes large, oval; ceca straight; parasitic in liver, bile duct and gall bladder of birds and mammals (Fig. 592). .... **Genus *Brachylecithum* Shtrom, 1940**

Life cycle: *B. mosquensis* - Embryonated eggs are eaten by the terrestrial snail, *Allogona ptychophora,* in which miracidia hatch, penetrate the intestinal wall, then migrate to the digestive gland where mother and daughter sporocysts develop. Xiphidiocercariae with a long tail develop in the daughter sporocysts and leave the snail in slime balls which are then eaten by carpenter ants of the genus *Camponotus* in which the metacercaria then develops. Encysted metacercariae have been found in the brain of the ants and are believed to alter their behavior so as to increase their chances for predation by the definitive host which in this case is the robin (Carney 1967, 1969, 1970).

Carney (1972 and 1974) studied the life cycles of *B. myadestis* and *B. stunkardi* and found them to be similar to the above species. Denton (1945) investigated the life cycle of *B. americanum.*

Superfamily Renicoloidea LaRue, 1957
Family Renicolidae Dollfus, 1939

Body rounded anteriorly, conical at posterior end, spinous; ventral sucker vestigial or absent; pharynx small; ceca extend to middle of body; testes opposite or oblique, in posterior fourth of body; cirrus sac absent; seminal vesicle free in parenchyma; genital atrium and genital pore median, in anterior half of body; ovary anterior to right or left testis; vitelline follicles in lateral clusters in middle third or posterior third of body; uterus fills most of body anterior to gonads; eggs operculate, embryonated; excretory vesicle Y-shaped, the main ducts extend forward as far as the oral sucker, contain many lateral branches and join sides of the vesicle; parasitic in the kidneys and ureters of birds.

The family contains only the genus *Renicola* Cohn, 1904 which is represented in North America by at least two species (Fig. 593). Three different cercariae have been associated with this family. Leptocercous xiphidiocercariae which develop in sporocysts in marine prosobranchs and encyst in marine lamellibranchs are known to be the larval stage of one species of *Renicola.*

Nonstyleted gymnocephalous and rhodometopa cercariae are also involved in renicolid life cycles. Both of these develop in sporocysts in marine prosobranchs. Experimental evidence is still lacking for linkage of "typical" rhodometopa cercariae (Fig. 46) to this family but Prevot and Bartoli (1978) have reported a similar cercaria as being the larva of *Renicola lari* (see below).

Life cycle: *R. thaidus* - Xiphidiocercariae develop in daughter sporocysts in the marine prosobranch snail, *Thais lapillus.* Cercariae encyst in the marine lamellibranchs, *Mytilus edulis, Pecten irradians* and *Gemma gemma.* The adult parasite develops in the herring gull, *Larus argentatus* which eats the infected molluscs (Stunkard, 1964b).

Werding (1969) investigated the life cycle of *R. roscovita* in Europe. This species uses the marine snail, *Littorina littorea as* first intermediate host, *Mytilus edulis* as second host and *Larus argentatus* as definitive host. *R. roscovita* and *R. thaidus* might possibly be synonyms.

The life cycle of *R. cerithidicola* was studied by Martin (1971). Nonstyleted gymnocephalous cercariae develop in the marine prosobranch snail, *Cerithidea californica* in yellow sausage-shaped sporocysts. They encyst in the gills of killifish, *Fundulus parvipinnis.* Lamellibranch molluscs could not be infected by exposing them to cercariae of this species.

Prevot and Bartoli (1978) reported the life cycle of *R. lari,* a kidney parasite of *Larus argentatus* and *L. ridibundus.* The marine prosobranchs, *Cerithium rupestre and C. mediterraneum* serve as first intermediate host. The cercaria is large and has a much branched excretory vesicle like that of the rhodometopa cercaria but the flame cells are in groups of three instead of five and there are no finfolds on the tail. Marine fishes, *Atherina boyera* and *A. hepsetus* serve as second intermediate host, the metacercariae being encysted in the livers.

Suborder Eucotylata Odening, 1961
Superfamily Eucotyloidea Odening, 1961

Miracidia have one pair of flame cells. Cercariae tailless (cercariaea) or tail rudimentary; stylet absent; cystogenous and penetration glands present; excretory system mesostomate, vesicle tubular and thin-walled; cercariae develop in daughter sporocysts in terrestrial snails and encyst in the sporocysts.
Life cycle involves two hosts.

Family Eucotylidae Skrjabin, 1924

Body elongate, sides parallel, anterior end rounded or in form of a triangular head collar, cuticle spinous or scaly; ventral sucker vestigial or absent; pharynx small; ceca long, either end blindly or fuse to form cyclocoel; testes opposite or oblique; cirrus sac present or absent; ovary pretesticular, lobed; vitelline follicles lateral to ceca, variable in extent; uterus mostly intercecal; eggs operculate, embryonated, may be triangular in cross section; parasitic in kidneys and ureters of birds.

Key to Genera

1a. Triangular head collar at anterior end of body; testes opposite; ceca blind posteriorly (Fig. 594). .... **Genus *Eucotyle* Cohn, 1904**
Key to species in Schell (1967a).

1b. Anterior end of body rounded; testes oblique; ceca fused to form cyclocoel (Fig. 595). .... **Genus *Tanaisia* Skrjabin, 1924**
Key to species in Byrd and Denton (1950).

Life cycle: *T. bragai* - Embryonated eggs in feces of the host are eaten by the terrestrial snail, *Subulina octona,* in which cercariae with a rudimentary tail develop in sporocysts in which they encyst. The definitive host becomes infected by eating the infected snails. Development to sexual maturity takes place in the kidneys of pigeons, chickens, turkeys, grackles and oven-birds. Excysted metacercariae migrate to the kidneys by way of the cloaca and ureters. Metacercariae have a ventral sucker but it atrophies by the time the mature adult develops (Maldonado, 1945).

The life cycle of *T. zarudnyi* was studied by Kingston (1965) and by Ahmad and Gabrion (1975) in Canada and France respectively. Different species of hosts were involved in the two localities. Otherwise the cycle resembles that of *T. bragai.*

Fig. 593. *Renicola thaidus.*

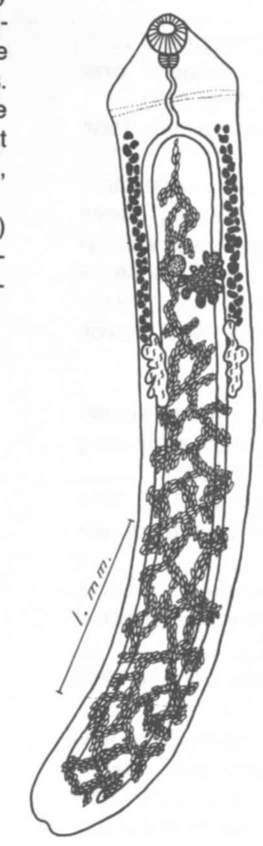


Fig. 594. *Eucotyle wehri.*

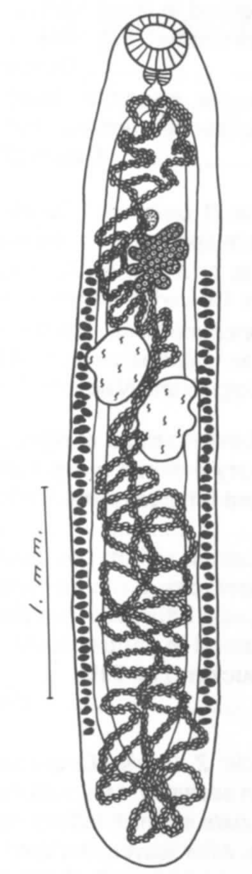


Fig. 595. *Tanaisia fedtschenkoi.*

Suborder Zoogonata Odening, 1961
Superfamily Zoogonoidea Skrjabin, 1957 *emended*

Miracidia have one pair of flame cells. Cercariae chaetomicrocercous or tailless (cercariaea); with or without a stylet; penetration and cystogenous glands present; protonephridia stenostomate; excretory vesicle has cellular wall. Cercariae develop in either a redia or a sporocyst in gastropod molluscs and encyst in marine lamellibranchs, freshwater snails, turbellarians, aquatic annelid worms or in sea urchins. Life cycle involves three hosts.

Family Zoogonidae Odhner, 1911

Body linguiform, fusiform or elongate, spinous; ventral sucker usually near middle of body; pharynx present; ceca long; testes opposite or oblique, in hindbody or lateral to ventral sucker; cirrus sac present; seminal vesicle bipartite; genital pore marginal or submarginal; genital atrium rarely present; ovary pre- or posttesticular; vitellaria in form of one or two compact masses; uterus confined to hindbody; eggs have thin shells, embryonated; parasitic in intestine of marine fishes.

Key to Genera

1a. Vitellarium a bilobed compact mass, intertesticular; ovary pretesticular. 2

1b. Vitellarium a single compact mass, posttesticular; ovary posttesticular. 3

2a. Testes oblique or nearly tandem; anterior part of body clothed in large spines; oral sucker terminal and funnel-shaped (Fig. 596). .... Genus *Glaucivermis* Overstreet, 1971

2b. Testes opposite; body spines not prominent; oral sucker subterminal, not funnel-shaped (Fig. 597). .... Genus *Diphtherostomum* Stossich, 1904

Life cycle: *D. brusinae* - Tailless cercariae *(Cercaria inconstans)* develop in sporocysts in the marine prosobranch snails, *Nassa reticulata, N. mutabilis, Natica poliana* and *Cyclonassa kamyschiensis.* Cercariae encyst in at least five genera of marine lamellibranch molluscs. The marine teleost, *Gobius niger* and *Diplodus annularis* serve as definitive host (Palombi, 1930; Prevot, 1966; Dolgikh and Naidenova, 1967).

3a. Genital atrium at right margin of body with an accessory seminal receptacle; cirrus sac flexed; ceca long and inflated; parasitic in black perch (Fig. 598). .... Genus *Neozoogonus* Arai, 1954

3b. Genital atrium and accessory seminal receptacle absent; cirrus sac not flexed. 4

4a. Cecal bifurcation far anterior to ventral sucker; testes lateral to ventral sucker; cirrus sac anterior to ventral sucker (Fig. 599). .... Genus *Zoogonoides* Odhner, 1902

Life cycle: *Z. laevis* - Embryonated eggs from feces of the host hatch in seawater. Miracidia penetrate the marine snail, *Columbella lunata* in which tailless cercariae develop in daughter sporocysts. After leaving the snail, the cercariae encyst in the parapodia and body wall of the marine polychaete, *Nereis virens.* The adult parasite develops in the tautog, *Tautoga onitis* and the Atlantic round herring, *Etrumeus sadina* (see Stunkard, 1943).

Koie (1976) investigated the life cycle of *Z. viviparus* which uses the prosobranch snail, *Buccinum undatum* for production of larval stages. Tailless cercariae encyst in brittle stars, polychaete worms, prosobranch and lamellibranch molluscs. Infected brittle stars were fed to plaice and flounders and the developing adults were recovered.

4b. Cecal bifurcation dorsal to ventral sucker; testes posterior to ventral sucker; cirrus sac lateral to ventral sucker (Fig. 600). .. Genus *Zoogonus* Looss, 1901

Life cycle: *Z. rubellus (= Z. mirus)* - Miracidia hatch in seawater and enter the marine snail, *Nassa obsoleta.* Tailless cercariae develop in daughter sporocysts and encyst in the parapodia of *Nereis virens.* The adult develops in the eel, *Anguilla chrysypa* and in the toadfish, *Opsanus tau* (see Stunkard 1938b and 1940).

Family Steganodermatidae Dollfus, 1952

Body elongate, pyriform or fusiform; ventral sucker usually in anterior half of body; pharynx present; ceca variable in length; testes opposite, in hindbody; cirrus sac in forebody; genital pore marginal or submarginal; ovary pretesticular or intertesticular; vitellaria follicular, in lateral clusters either anterior or posterior to ventral sucker; uterus fills most of hindbody; eggs embryonated, shells very thin; parasitic in intestine or urinary bladder of marine fishes.

Key to Genera

1a. Vitelline follicles restricted to hindbody. 2

1b. Vitelline follicles in forebody and/or lateral to ventral sucker. 6

2a. Ceca short, extend only to level of ventral sucker or to middle of body. 3

2b. Ceca long, inflated, extend nearly to posterior end of body. 5

3a. Ventral sucker about three times as large as oral sucker; distal end of cirrus sac surrounded by gland cells; esophagus at least six times as long as pharynx (Fig. 601). .... Genus *Proctophantastes* Odhner, 1911

3b. Suckers equal or subequal; no gland cells around end of cirrus sac; esophagus not more than three times as long as pharynx. 4

4a. Vitelline follicles at ends of ceca and some distance posterior to ventral sucker; genital pore dorsal and sublateral; body fusiform (Fig. 602). ....Genus *Lepidophyllum* Odhner, 1902

4b. Vitelline follicles along ceca between testes and ventral sucker; genital pore ventral and sublateral; body elliptical (Fig. 603). .... Genus *Steganoderma* Stafford, 1904

5a. Forebody tapered, body widest at level of testes; ovary lobed; parasitic in urinary bladder of marine fishes (Fig. 604). .. Genus *Urinatrema* Yamaguti, 1934

5b. Forebody not tapered, widest at level of ventral sucker; ovary oval; parasitic in the intestine of marine fishes (Fig. 605). .... Genus *Hudsonia* Campbell, 1975

6a. Vitelline follicles clustered lateral to ventral sucker; ceca very short, extend to level of ventral sucker (Fig. 606). .... Genus *Brachyenteron* Manter, 1934

6b. Vitelline follicles lateral and anterior to ventral sucker; ceca extend far posterior to ventral sucker (Fig. 607). .... Genus *Deretrema* Linton, 1910

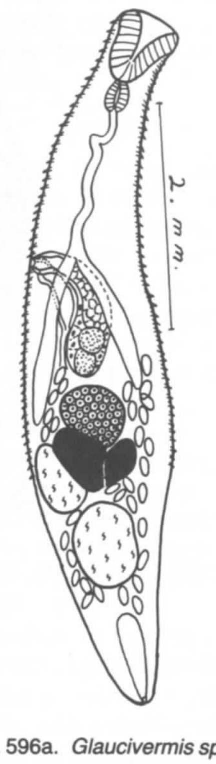


Fig. 596a. *Glaucivermis spinosus.* (from Overstreet, 1971)

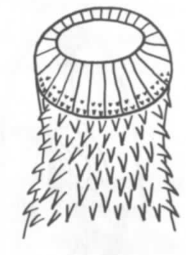


Fig. 596b. Anterior end.

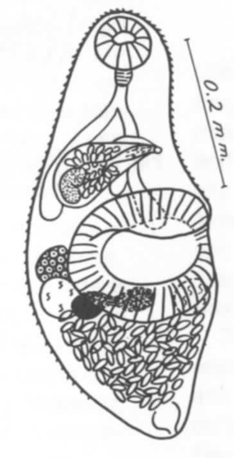


Fig. 597. *Diphtherostomum americanum.* (from Manter, 1947)

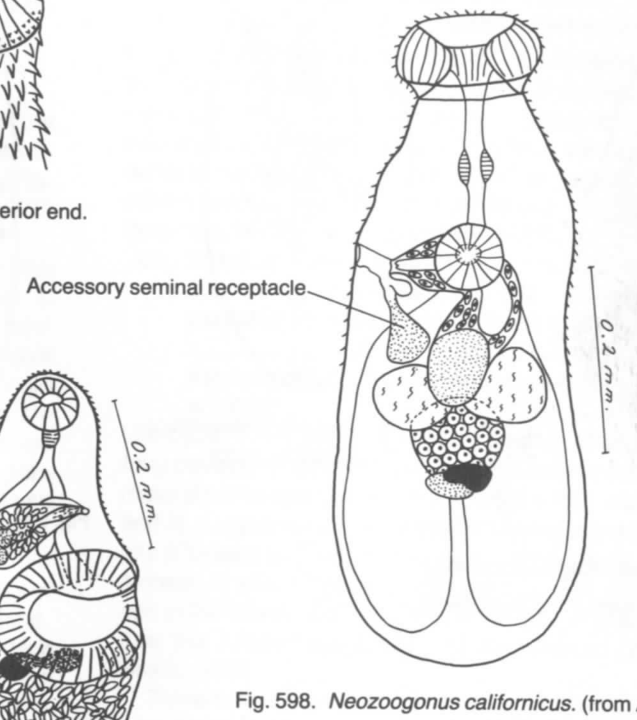


Fig. 598. *Neozoogonus californicus.* (from Arai, 1954)

Fig. 599. *Zoogonoides laevis.* (from Linton, 1940)

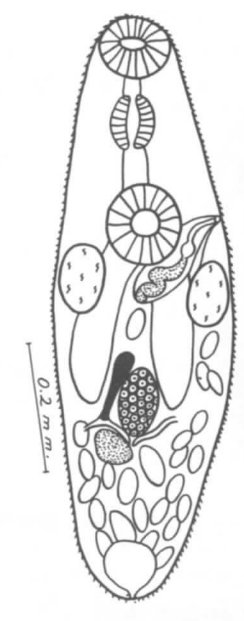
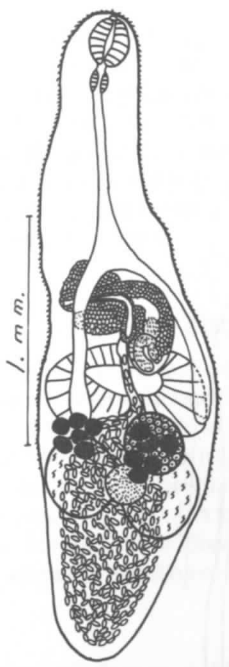


Fig. 600. *Zoogonus rubellus.* (from Odhner, 1902)



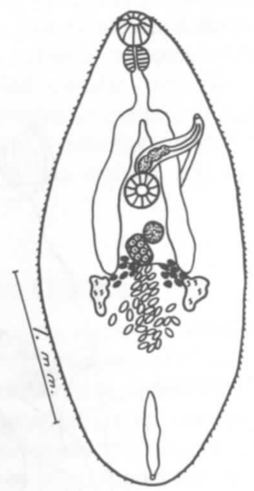


Fig. 602. *Lepidophyllum steenstrupi.* (from Odhner, 1902)

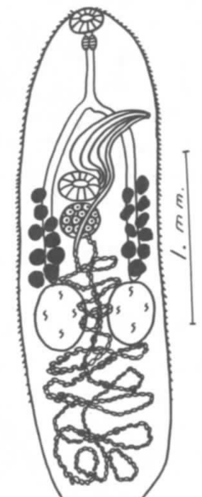


Fig. 603. *Steganoderma formosum.* (from Manter, 1925)

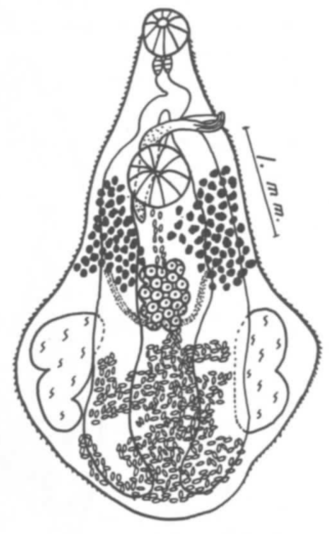


Fig. 604. *Urinatrema aspinosum.* (from Schiller, 1956)

Fig. 601. *Proctophantastes glandulosa,* dorsal view. (from Byrd, 1964)

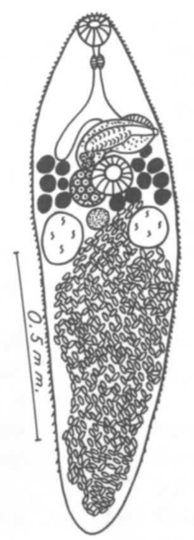


Fig. 606. *Brachyenteron peristedioni.* (from Manter, 1934)

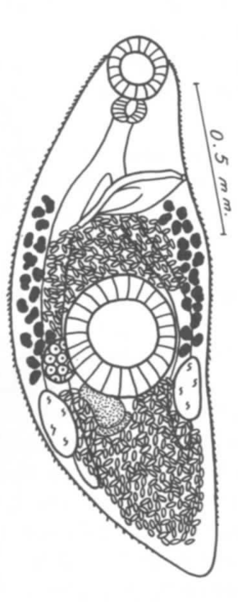


Fig. 605. *Hudsonia agassizi.* (from Campbell, 1975)

Fig. 607. *Deretrema fusillus.* (from Linton, 1910)

Family Lissorchiidae Poche, 1926 emended

Body elongate or oval, spinous; ventral sucker in anterior half of body; pharynx present; ceca usually long; one or two testes, tandem, usually in middle of hindbody; cirrus sac present; seminal vesicle usually bipartite; genital pore marginal or submarginal, lateral to oral sucker; ovary pretesticular; vitelline follicles along ceca, in hindbody, sometimes confluent dorsally; uterus long, extends posterior to testes; parasitic in intestine of freshwater and marine fishes.

Key to Genera

1a. One testis; body elongate; seminal vesicle bipartite with one part outside of cirrus sac; vitelline follicles in lateral clusters between testis and ventral sucker (Fig. 608). .... Genus ***Asymphylodora*** **Looss, 1899**

Key to species in Skrjabin, (1964).

Life cycle: *A. amnicolae* - Embryonated eggs from feces of the host are eaten by the prosobranch snail, *Amnicola limosa,* in which the miracidium hatches and changes to a sporocyst which in turn produces a generation of rediae. The latter give rise to tailless cercariae of the cercariaeum group which emerge from the snail and then reenter another uninfected snail to encyst and change to the metacercarial stage. Infected snails are eaten by fish in which the adult parasite develops. Suitable fishes are perch, killifish, smallmouth bass or pumpkinseed. Some metacercariae become sexually mature in the snails as progenetic forms (Stunkard, 1959).

Broek Van Den and De Jong (1979) reported the life history of *A. tincae,* an intestinal parasite of tench, *Tinca tinca* in Holland. The host snail is the prosobranch *Bithynia tentaculata* which serves as first and second intermediate host. Tailless cercariae (cercariaea) develop in rediae and after leaving the snail reentered the same or a different snail. Some cercariae encysted in the snails and developed to infective metacercariae; however, some do not encyst but develop to sexual maturity as free progenetic forms.

There is a tendency for species in this genus to be progenetic. *A. progenetica* and *A. tincae* mature in *B. tentaculata. A. dollfusi* is progenetic in *B. leachi. A. demeli* matures in the polychaete worm, *Nereis diversicolor* which can also serve as the normal second intermediate host (Serkova and Bychowsky, 1940; Biguet et al, 1956; Reimer, 1973). The normal definitive host for species in this genus appears to be freshwater and marine fishes.

Broek (1978) conducted experimental work on the effect of temperature on the metacercaria of *A. tincae* in the Netherlands. Water temperature above 20 C induced development of progenetic forms in *Bithynia.* She found progenetic and nonprogenetic specimens simultaneously throughout the year in warm lakes.

1b. Two testes; body oval or elliptical; seminal vesicle entirely within cirrus sac. 2

2a. Vitelline follicles confined to area around testes, confluent dorsal to testes and uterus; body oval; ceca extend to testes; testes tandem; parasitic in suckers (Fig. 609). .... Genus ***Neopaleorchis*** **Schell, 1973**

Life cycle: *N. catostomi* - Embryonated eggs are eaten by the prosobranch snail, *Lithoglyphus virens* in which the miracidia hatch and develop into delicate sporocysts which in turn produce a generation of rediae. Chaetomicrocercous cercariae develop in the rediae and after emerging from the snail reenter another gastropod such as *Physa ampullacea, Gyraulus simillaris, Ferrissia rivularis* as well as *L. virens.* The cercariae encyst and develop to the infective metacercaria stage. Infected snails are eaten by the coarsescale sucker, *Catostomus macrocheilus* in which the adult fluke develops as an intestinal parasite (Schell, 1973b).

2b. Vitelline follicles either anterior to gonads or in narrow bands lateral to ceca. 3

3a. Vitelline follicles few, large, between ovary and ventral sucker; ceca very short; testes opposite; parasitic in squawfish (Fig. 610). .... Genus ***Palaeorchis*** **Szidat, 1943**

Life cycle: *P. problematicus* - Cercariaea develop in rediae in the prosobranch snail, *Fluminicola virens.* Encysted metacercariae were also found in this snail. Some progenetic specimens were also found in the snails. Natural infections with the adult parasite occur in the intestine of squawfish. Metacercariae maintained in culture medium at 25 C developed to sexual maturity (Macy and Berntzen, 1970; Macy and English, 1975).

3b. Vitelline follicles numerous, small, lateral to ceca; ceca long; testes tandem; seminal vesicle bipartite; parasitic in catostomid fishes (Fig. 611). .... Genus ***Lissorchis*** **Magath, 1917**

Key to species in Krygier and Macy (1969); Christensen *et al* (1982).

Life cycle: *L. mutabile* - Tailless cercariae *(Cercariaeum mutabile)* develop in rediae in the limpets *Laevapex fuscus* and *Ferrissia rivularis* and also in the planorbid snails, *Helisoma trivolvis* and *H. campanulatum.* Emerged cercariae are eaten by planarians *(Dugesia* sp.) and by the aquatic oligochaete, *Chaetogaster limnaei,* in which metacercariae develop. The adult fluke develops in the intestine of chub and white sucker which probably ingest the infected planarians and oligochaetes (Wallace, 1941; Smith, 1968).

Three new cercariaea, thought to be the larvae of lissorchiids were found to encyst in *Chaetogaster limnaei* and in the planarians *Dugesia tigrina* and *Dorotocephala dorotocephala.* The cercariae developed in rediae in the limpets, *Laevapex fuscus* and *Ferrissia rivularis* (see Duncan and DeGiusti, 1976).

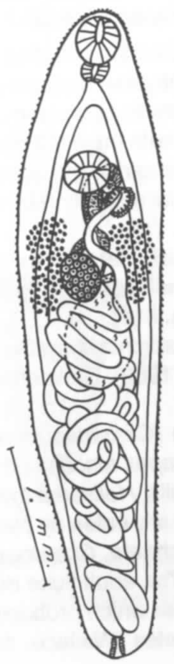


Fig. 608. *Asymphylodora atherinopsidis.* (from Olson, 1977)

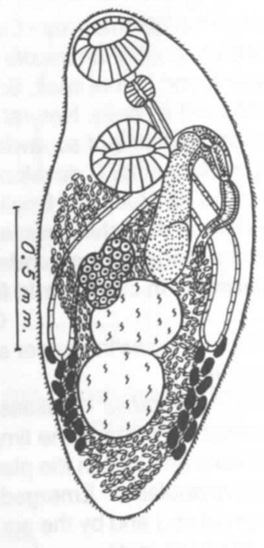


Fig. 609. *Neopaleorchis catostomi.*

Fig. 610. *Palaeorchis problematicus.*

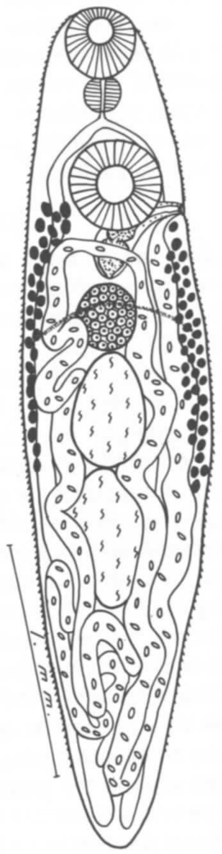


Fig. 611. *Lissorchis attenuatum.*

Superfamily Monorchioidea n. superfam.

Cercaria oculate or nonoculate, tailless or leptocercous with lappets on tail or furcocercous without tail stem, nonstyleted; develop in sporocyst in marine lamellibranchs; metacercariae encyst in lamellibranchs; adults in intestine or coelom of fishes. Life cycle involves three hosts.

Family Monorchiidae Odhner, 1911

Body variable in shape; ventral sucker in anterior half of body or near middle of body; pharynx present; ceca usually long; one testis usually present, opposite when two are present; cirrus sac present, cirrus spiny; genital pore median, usually anterior to ventral sucker; spinous genital atrium sometimes present; ovary usually pretesticular, rarely intertesticular; vitelline follicles few, in lateral clusters in hindbody; uterus confined to hindbody; metraterm in form of a spiny terminal organ in a metraterm sac; eggs operculate, nonembryonated, with or without polar filament; parasitic in intestine of marine fishes.

Note: Cercariae in this family are without a stylet and can be leptocercous, microcercous, furcocercous or tailless. All of them develop in sporocysts in marine lamellibranchs.

Key to Genera

1a. Two testes, opposite. 2

1b. One testis. 3

2a. Uterus opens into base of terminal organ; eyespots usually present; vitelline follicles arranged in H-shaped design, between and anterior to testes (Fig. 612). .... **Genus *Monorcheides* Odhner, 1905**

Key to species in Skrjabin (1964).

Life cycle: *M. cumingiae* - Oculate cercariae with lappets on the tail develop in sporocysts in the marine clams, *Cumingia tellinoides, Tellina tenera* and *Macoma tenta.* Cercariae leave by way of the excurrent siphon but may reenter the same or a different clam and encyst in the gills, foot, mantle or wall of the incurrent siphon. The adult flukes develop in the intestine of eels and flounders which might eat the infected clams (Martin, 1939b, 1940; Stunkard, 1974).

2b. Uterus opens into side of terminal organ; eyespots usually absent; vitelline follicles few, close to testes (Fig. 613). .... **Genus *Diplomonorchis* Hopkins, 1941**

3a. Vitelline follicles posterior to testis, close to posterior end of body (Fig. 615). .... **Genus *Telolecithus* Lloyd and Guberlet, 1932**

Life cycle: *T. pugetensis* - Partially embryonated eggs are eaten by the clam *Transennella tantilla* in which the miracidium completes its development. Cercariae with short furcae but no tail stem (Fig. 615b) develop in sporocysts. They leave the clam through the excurrent siphon and upon contacting any of five species of lamellibranch molluscs penetrate and encyst. Clams that most frequently serve as second intermediate host are *Tellina salmonea* and *Macoma nasuta.* Several species of sea perch serve as definitive host (De Martini and Pratt, 1964).

3b. Vitelline follicles anterior to testis. 4

4a. Eggs have monopolar filament. 5

4b. Eggs without filament. 6

5a. Ceca extend to vitelline follicles; eyespots present; vitelline follicles in lateral clusters, not confluent (Fig. 616). .... **Genus *Hurleytrema* Srivastava, 1939**

5b. Ceca extend almost to posterior end of body; vitelline follicles confluent anterior to ovary (Fig. 614). .... **Genus *Hurleytrematoides* Yamaguti, 1954.**

6a. Vitelline follicles lateral to ventral sucker; body pyriform or round (Fig. 617). .... **Genus *Monorchis* Looss, 1902**

6b. Vitelline follicles posterior to ventral sucker. 7

7a. Most of uterus pretesticular; body pyriform or oval; oral sucker subterminal (Fig. 618). .... **Genus *Postmonorchis* Hopkins, 1941**

Life cycle: *P. donacis* - Leptocercous cercariae with transverse rows of scales on the tail and spinous body develop in sporocysts in the bean clam, *Donax gouldi* which also serves as host for the metacercaria. Encysted metacercariae were fed to shiner perch, black perch and spotfin croaker and the adult flukes recovered (Young, 1953).

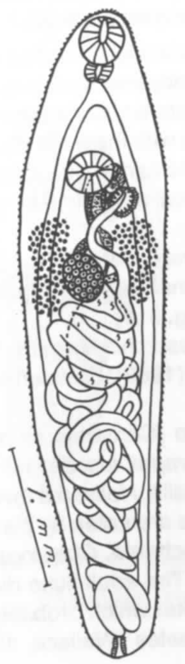
7b. Most of uterus posttesticular; body elongate or oval; oral sucker terminal, funnel-shaped or bowl-shaped. 8

8a. Genital atrium spiny; oral sucker bowl-shaped (Fig. 619). .... **Genus *Genolopa* Linton, 1910**

8b. Genital atrium not spiny; oral sucker funnel-shaped (Fig. 620). .... **Genus *Lasiotocus* Looss, 1907**

Life cycle: *L. minutus (Genolopa minuta)* - Non-styleted microcercous cercariae *(C. adranocerca)* develop in daughter sporocysts in the marine clam, *Gemma gemma.* These cercariae have numerous cystogenous glands but no penetration glands. Shortly after release from the sporocyst, they encyst directly in the clam hemocoel and then develop to the metacercariae which are extruded within a jelly-like matrix into seawater. They are apparently ingested by the silverside, *Menidia menidia.* Metacercariae were fed to silversides and a series of developmental stages were recovered from the intestine (Stunkard, 1980d and 1981b).

The life cycle of *L. elongatus* is similar, involving the same hosts (see Stunkard, 1981c).



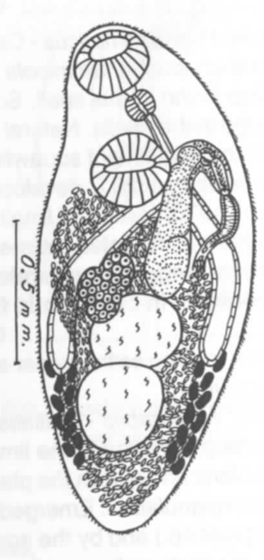


Fig. 609. *Neopaleorchis catostomi.*

Fig. 608. *Asymphylodora atherinopsidis.* (from Olson, 1977)

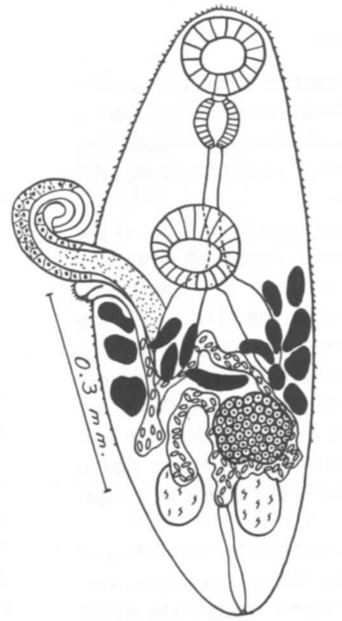


Fig. 610. *Palaeorchis problematicus.*

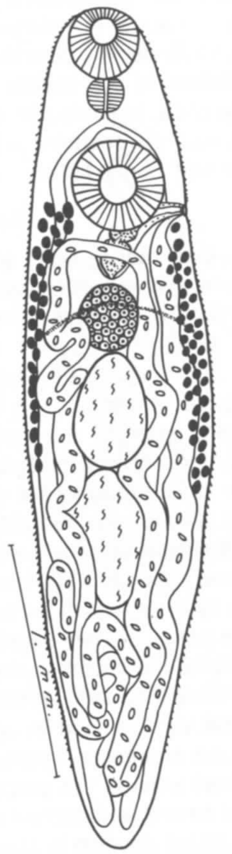


Fig. 611. *Lissorchis attenuatum.*

Superfamily Monorchioidea n. superfam.

Cercaria oculate or nonoculate, tailless or leptocercous with lappets on tail or furcocercous without tail stem, nonstyleted; develop in sporocyst in marine lamellibranchs; metacercariae encyst in lamellibranchs; adults in intestine or coelom of fishes. Life cycle involves three hosts.

Family Monorchiidae Odhner, 1911

Body variable in shape; ventral sucker in anterior half of body or near middle of body; pharynx present; ceca usually long; one testis usually present, opposite when two are present; cirrus sac present, cirrus spiny; genital pore median, usually anterior to ventral sucker; spinous genital atrium sometimes present; ovary usually pretesticular, rarely intertesticular; vitelline follicles few, in lateral clusters in hindbody; uterus confined to hindbody; metraterm in form of a spiny terminal organ in a metraterm sac; eggs operculate, nonembryonated, with or without polar filament; parasitic in intestine of marine fishes.

Note: Cercariae in this family are without a stylet and can be leptocercous, microcercous, furcocercous or tailless. All of them develop in sporocysts in marine lamellibranchs.

Key to Genera

1a. Two testes, opposite. 2

1b. One testis. 3

2a. Uterus opens into base of terminal organ; eyespots usually present; vitelline follicles arranged in H-shaped design, between and anterior to testes (Fig. 612). .... **Genus *Monorcheides* Odhner, 1905**

Key to species in Skrjabin (1964).

Life cycle: *M. cumingiae* - Oculate cercariae with lappets on the tail develop in sporocysts in the marine clams, *Cumingia tellinoides, Tellina tenera* and *Macoma tenta.* Cercariae leave by way of the excurrent siphon but may reenter the same or a different clam and encyst in the gills, foot, mantle or wall of the incurrent siphon. The adult flukes develop in the intestine of eels and flounders which might eat the infected clams (Martin, 1939b, 1940; Stunkard, 1974).

2b. Uterus opens into side of terminal organ; eyespots usually absent; vitelline follicles few, close to testes (Fig. 613). .... **Genus *Diplomonorchis* Hopkins, 1941**

3a. Vitelline follicles posterior to testis, close to posterior end of body (Fig. 615). .... **Genus *Telolecithus* Lloyd and Guberlet, 1932**

Life cycle: *T. pugetensis* - Partially embryonated eggs are eaten by the clam *Transennella tantilla* in which the miracidium completes its development. Cercariae with short furcae but no tail stem (Fig. 615b) develop in sporocysts. They leave the clam through the excurrent siphon and upon contacting any of five species of lamellibranch molluscs penetrate and encyst. Clams that most frequently serve as second intermediate host are *Tellina salmonea* and *Macoma nasuta.* Several species of sea perch serve as definitive host (De Martini and Pratt, 1964).

3b. Vitelline follicles anterior to testis. 4

4a. Eggs have monopolar filament. 5

4b. Eggs without filament. 6

5a. Ceca extend to vitelline follicles; eyespots present; vitelline follicles in lateral clusters, not confluent (Fig. 616). .... **Genus *Hurleytrema* Srivastava, 1939**

5b. Ceca extend almost to posterior end of body; vitelline follicles confluent anterior to ovary (Fig. 614). .... **Genus *Hurleytrematoides* Yamaguti, 1954.**

6a. Vitelline follicles lateral to ventral sucker; body pyriform or round (Fig. 617). .... **Genus *Monorchis* Looss, 1902**

6b. Vitelline follicles posterior to ventral sucker. 7

7a. Most of uterus pretesticular; body pyriform or oval; oral sucker subterminal (Fig. 618). .... **Genus *Postmonorchis* Hopkins,1941**

Life cycle: *P. donacis* - Leptocercous cercariae with transverse rows of scales on the tail and spinous body develop in sporocysts in the bean clam, *Donax gouldi* which also serves as host for the metacercaria. Encysted metacercariae were fed to shiner perch, black perch and spotfin croaker and the adult flukes recovered (Young, 1953).

7b. Most of uterus posttesticular; body elongate or oval; oral sucker terminal, funnel-shaped or bowl-shaped. 8

8a. Genital atrium spiny; oral sucker bowl-shaped (Fig. 619). .... **Genus *Genolopa* Linton, 1910**

8b. Genital atrium not spiny; oral sucker funnel-shaped (Fig. 620). .... **Genus *Lasiotocus* Looss, 1907**

Life cycle: *L. minutus (Genolopa minuta)* - Non-styleted microcercous cercariae *(C. adranocerca)* develop in daughter sporocysts in the marine clam, *Gemma gemma.* These cercariae have numerous cystogenous glands but no penetration glands. Shortly after release from the sporocyst, they encyst directly in the clam hemocoel and then develop to the metacercariae which are extruded within a jelly-like matrix into seawater. They are apparently ingested by the silverside, *Menidia menidia.* Metacercariae were fed to silversides and a series of developmental stages were recovered from the intestine (Stunkard, 1980d and 1981b).

The life cycle of *L. elongatus* is similar, involving the same hosts (see Stunkard, 1981c).

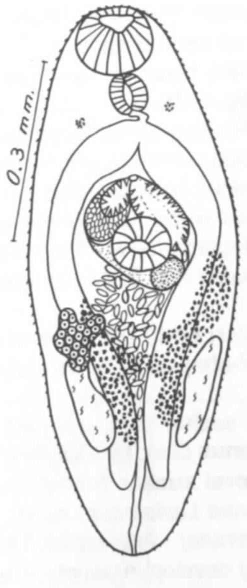


Fig. 612. *Monorcheides cummingiae.* (from Martin, 1940)

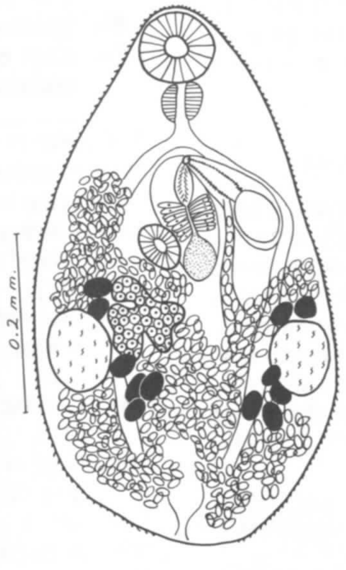


Fig. 613. *Diplomonorchis leiostomi.* (from Hopkins, 1941)

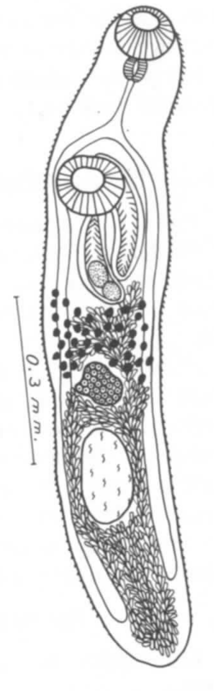


Fig. 614. *Hurleytrematoides chaetodoni.* (from Manter, 1942)

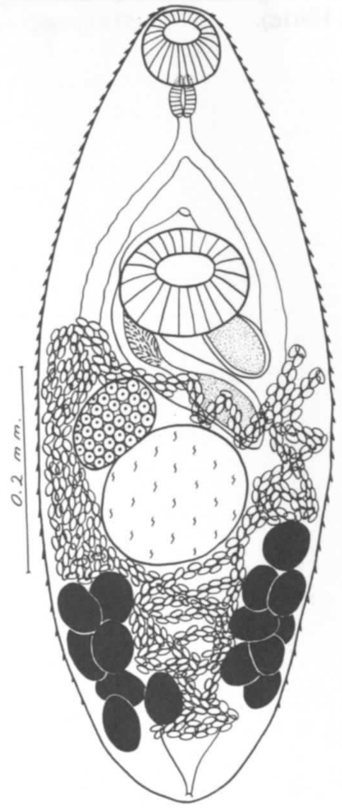


Fig. 615a. *Telolecithus pugetensis*

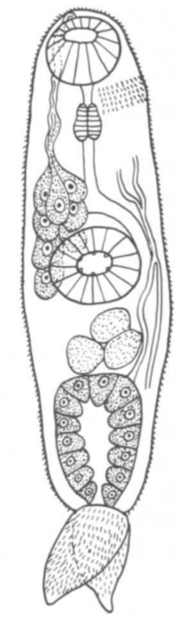


Fig. 615b. Cercaria.

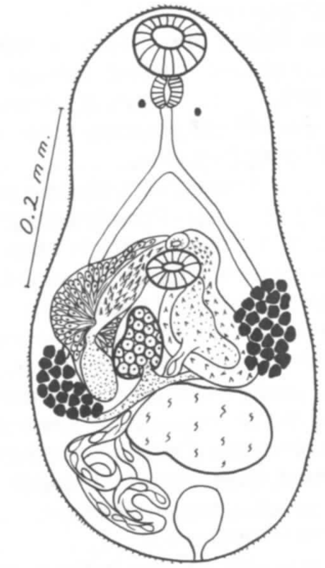


Fig. 616. *Hurleytrema pyriforme.* (from Overstreet, 1969)

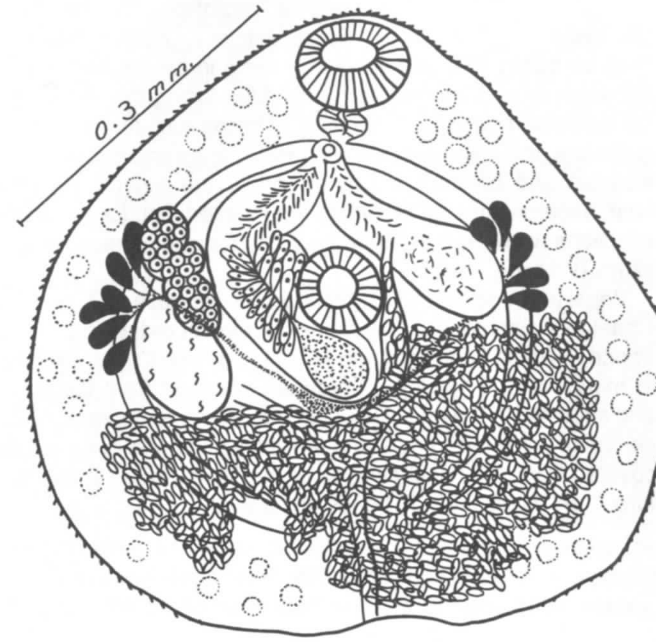


Fig. 617. *Monorchis latus.* (from Manter, 1942)

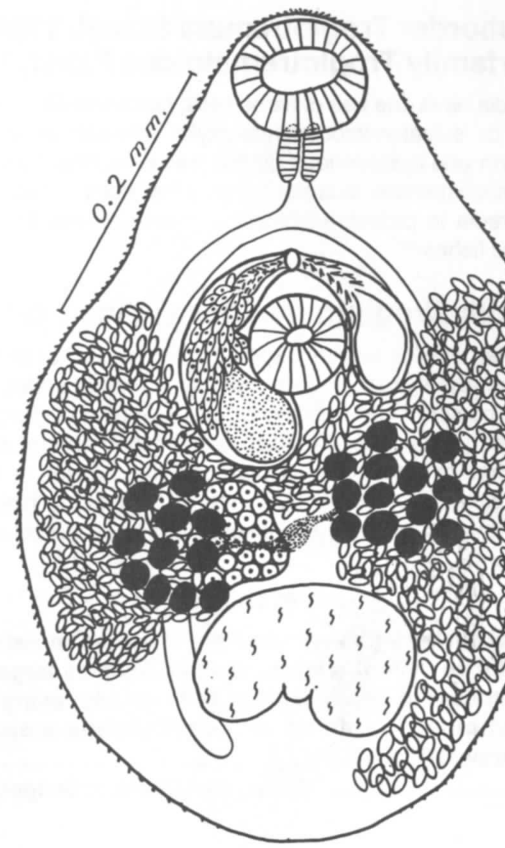


Fig. 618. *Postmonorchis orthopristis.*

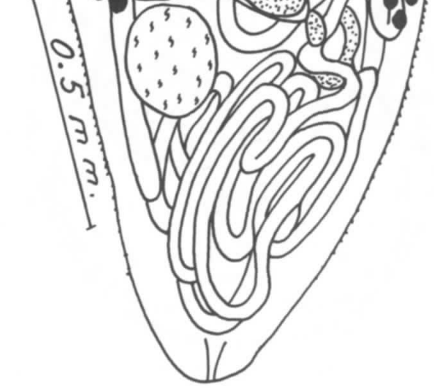


Fig. 619. *Genolopa ampullacea.*

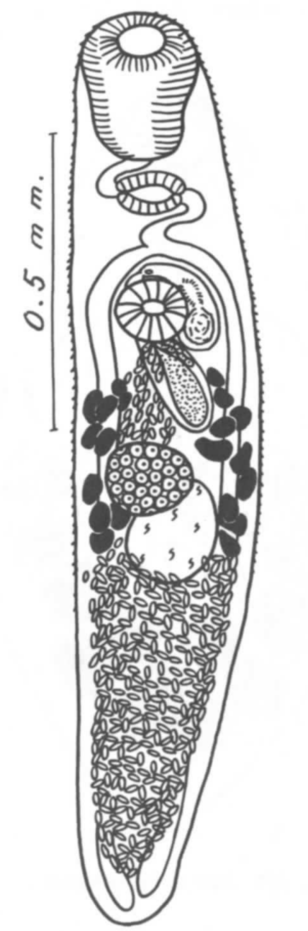


Fig. 620. *Lasiotocus longicaecum.* (from Manter, 1940)

Suborder Troglotremata Schell, 1980
Superfamily Troglotrematoidea Faust, 1929

Miracidia have one pair of flame cells; cercariae chaetomicrocercous or sulcatomicrocercous; stylet present; nonoculate; penetration and cystogenous glands well developed; excretory system mesostomate; excretory vesicle has cellular wall; develop in a redia in prosobranch snails; metacercariae in crustaceans and fishes.

Family Troglotrematidae Odhner, 1914

Body flat, oval or pyriform, spinous; ventral sucker in middle of body; pharynx present; ceca variable in length; testes opposite, near posterior end of body or close to ventral sucker; cirrus sac present; genital pore median, posterior to ventral sucker; ovary either pre- or posttesticular; vitelline follicles in lateral areas of either fore- or hindbody; uterus confined to hindbody; parasitic in intestine, frontal sinuses, kidneys or gall bladder of mammals.

Key to Genera

1a. Oral sucker with very small stylet; testes lateral or anterior to ventral sucker; vitelline follicles large, few, restricted to lateral regions of hindbody; ovary posttesticular; parasitic in insectivorous mammals (shrews) (Fig. 621). .... Genus *Xiphidiotrema* Senger, 1953

1b. Oral sucker without stylet; testes in hindbody; viteline follicles small, mostly restricted to forebody; ovary anterior to right or left testis; parasitic in frontal sinuses of mammals (Fig. 622). .... Genus *Troglotrema* Odhner, 1914

Life cycle: *T. mustelae* (= *Sellacotyle m.*) - Sulcatomicrocercous cercariae (Fig. 18) develop in redia in the freshwater prosobranch snail, *Campeloma rufum.* After losing the stubby tail, the cercariae penetrate of a variety of fishes such as pike, perch, bullheads, mudminnows, suckers and shiners and encyst in the muscles and connective tissues. Mink, the natural definitive host, become infected by eating the infected fish. Experimental infections were established in dog, cat, ferret, fox, raccoon and skunk (Wallace. 1935).

Vogel and Voelker (1978) reported the life cycle of *T. acutum.* Chaetomicrocercous (?) cercariae develop in rediae in the gastropod, *Bythinella dunkeri* and *B. alta* which had been exposed to miracidia of *T. acutum.* Cercariae emerged from the snails and encysted in the muscles of the frog, *Rana temporaria.* Metacercariae were fed to cats and ferrets. Adult parasites were recovered from the nasal sinuses of the ferret, *Mustela putorius furo.* They cause injury to bones of the skull.

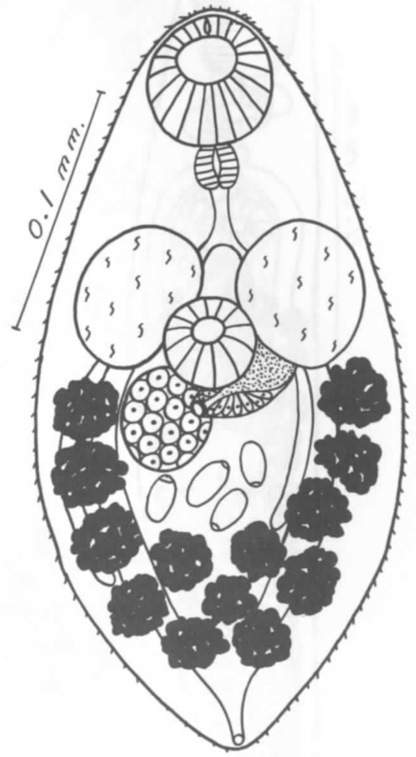


Fig. 621. *Xiphidiotrema lockerae.*

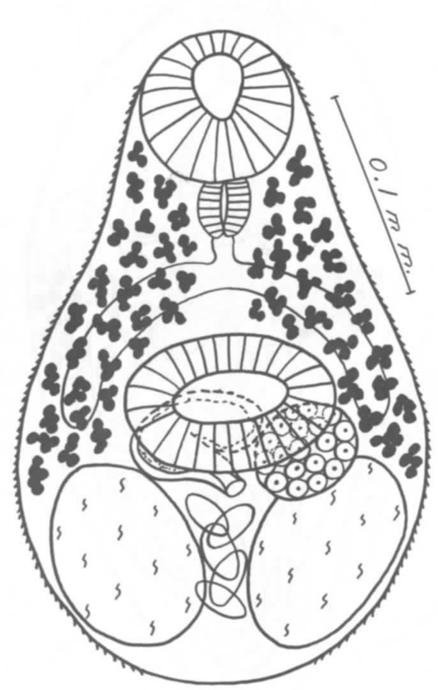


Fig. 622. *Troglotrema mustelae.*

Family Paragonimidae Dollfus, 1939

Body oval, thick, spinous; suckers nearly equal; ventral sucker near middle of body; pharynx present; ceca long; testes opposite, lobed, in middle of hindbody; cirrus sac absent; seminal vesicle free in parenchyma; genital pore posterior to ventral sucker; ovary lobed, anterior to right or left testis; vitellaria acinous, widely distributed along ceca; uterus opposite to ovary, entirely pretesticular; eggs operculate, nonembryonated; parasitic in lungs of mammals, including human beings.

The family contains only the genus *Paragonimus* Braun, 1899 and is represented in North America by *P. kellicotti* (Fig. 623). Key to species in Chen (1960).

Life cycle: *P. kellicotti* - The adult is a parasite of mink, muskrat, dog, cat, swine, fishers and fox. Eggs are swept up the trachea to the pharynx then swallowed and finally pass in the feces. Miracidia develop and hatch in about three weeks. They enter the freshwater prosobranch snail, *Pomatiopsis lapidaria* and *P. cincinnatiensis* in which sporocysts and mother and daughter rediae develop. The latter give rise to chaetomicrocercous cercariae (Fig. 17) which after leaving the snail, encyst around the heart of crayfish of the genera *Cambarus* and *Orconectes.* The definitive host eats the infected crayfish. Excysted metacercariae penetrate the intestinal wall and diaphragm and enter the outer surface of the lungs in which they finally develop to sexual maturity, loosely encapsulated in pairs (Ameel, 1934; Harley, 1972).

P. westermanni is indigenous to the Far East where it parasitizes human beings as well as feline, canine and porcine mammals.

Shimazu (1981) reported an experimental life cycle for *P. westermanni,* using the gastropod, *Semisulcospira libertina* as first intermediate host. The crab, *Geothelphusa dehaani* and the crayfish, *Procambarus clarki* seved as second intermediate hosts. The experimental definitive host was a dog in which several flukes matured within 13 weeks after feeding metacercariae.

This species is known to survive up to 20 years in the lungs of human beings.

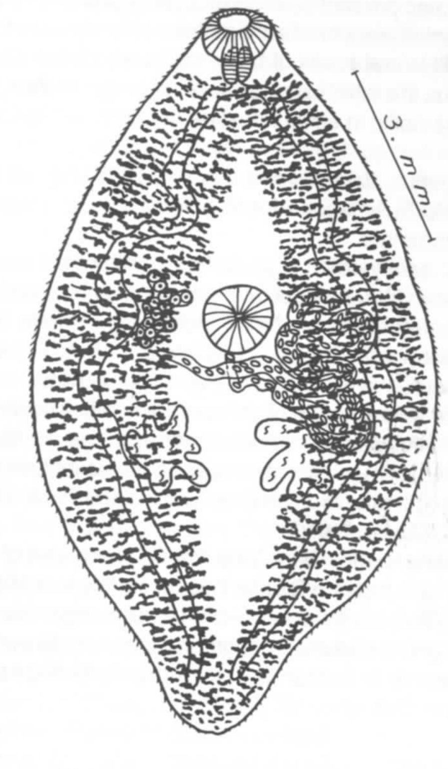


Fig. 623. *Paragonimus kellicotti.*

Family Nanophyetidae Dollfus, 1939

Body small (1 mm), oval or pyriform, nonspinous; ventral sucker in middle of body; pharynx present; ceca extend as far as testes; cirrus sac present or absent; testes opposite, in middle of hindbody; genital pore median, posterior to ventral sucker; vitelline follicles fill lateral areas of body, confluent across dorsal part of body; uterus fills intertesticular area; eggs operculate, nonembryonated; parasitic in small intestine of mammals including human beings.

Only the genus *Nanophyetus* Chapin, 1927 (Fig. 624) is represented in North America with *N. salmincola* parasitizing many species of mammals.

Life cycle: *N. salmincola* - Eggs in feces of the host are nonembryonated when laid. At least four months are required for development of the miracidium which hatch and penetrate the freshwater prosobranch snail, *Oxytrema silicula* in which chaetomicrocercous cercariae develop in a redia. Cercariae penetrate the skin and gills of salmonid and other fishes and encyst in the muscles and connective tissues. The adults develop in the intestine of many carnivorous mammals including human beings which eat infected fish (Bennington and Pratt, 1960; Mishakov, 1971; Carter, 1973).

This parasite is important in the Pacific Northwest of the United States and in eastern Siberia because of its role in the transmission of *Neorickettsia helmintheca,* the organism causing salmon-poisoning disease in dogs and other canid mammals. It is not pathogenic in human beings. Mortality in dogs can be as high as 90 percent.

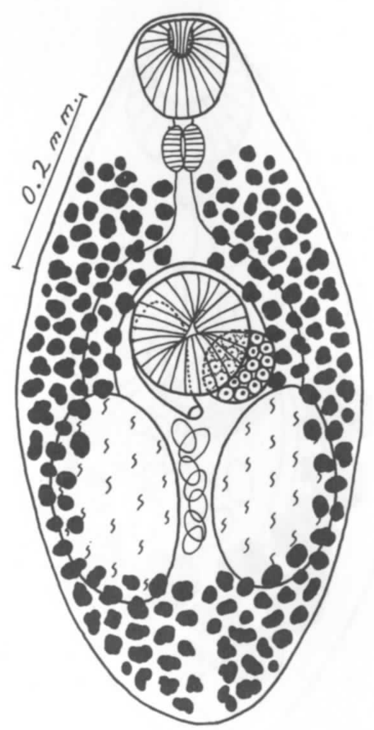


Fig. 624. *Nanophyetus salmincola.*

Family Collyriclidae Ward, 1917

Body round or oval, concave ventrally, nonspinous; ventral sucker absent; pharynx small; ceca long; testes opposite in posterior third of body; cirrus sac small, thin-walled; ovary lobed, in anterior third of body; vitelline follicles lateral to ceca in anterior half of body; uterus fills most of posterior half of body; parasitic in skin of birds.

The family contains only the genus *Collyriclum* Kossack, 1911 with two species reported from North America (Fig. 625).

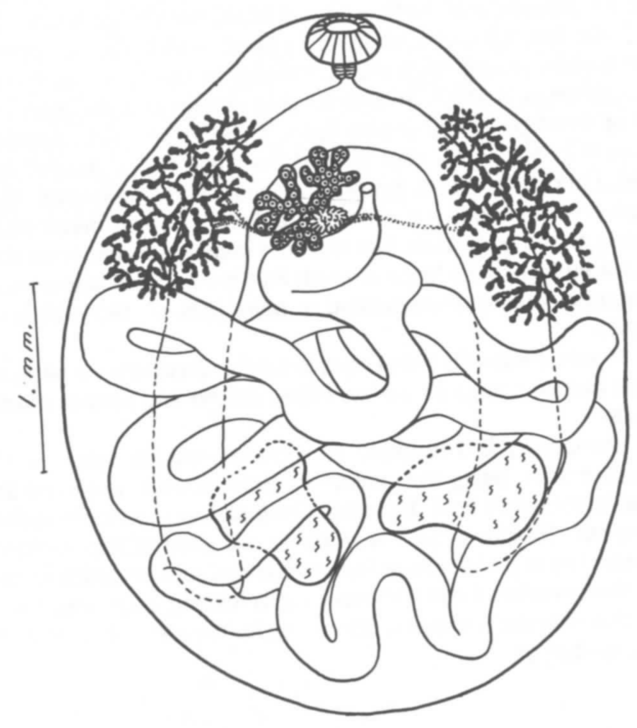


Fig. 625. *Collyriclum faba.*

Suborder Allocreadiata Skrjabin, Petrow and Koval, 1958

Miracidia with one pair of flame cells. Cercaria trichocercous, homalometronine or oculate xiphidiocercaria; penetration and cystogenous glands present; protonephridia mesostomate; excretory vesicle with cellular wall; cercaria develop in rediae in lamellibranch or gastropod molluscs.

Superfamily Allocreadioidea Nicoll, 1934

Oculate xiphidiocercariae develop in rediae in lamellibranch molluscs or occasionally in freshwater limpets; metacercariae develop in arthropods, limpets or lamellibranch molluscs.

Family Allocreadiidae Stossich, 1903

Body elongate, oval or fusiform, nonspinous; eyespots present in some species; oral sucker contains muscular papillae in some genera; ventral sucker in anterior half of body; pharynx present; ceca long; testes tandem or oblique, in hindbody; cirrus sac present; genital pore anterior to ventral sucker; ovary pretesticular; vitelline follicles distributed along ceca, limited in extent; uterus entirely pretesticular in some genera but extends posterior to testes in some genera; eggs operculate, nonembryonated; excretory vesicle tubular or saccular; parasitic in the intestine of fishes and amphibians. Epidermal cell formula of miracidium 6, 6, 4, 2 or 6, 7, 4, 2.

Key to Genera

1a. Oral sucker with one or more pairs of muscular papillae. 2
1b. Oral sucker without muscular papillae. 8
2a. Oral sucker with one pair of muscular papillae. 3
2b. Oral sucker with two or more pairs of muscular papillae. 5
3a. Four testes in opposite pairs; uterus passes median to testes (Fig. 626). .... **Genus *Megalogonia* Surber, 1928**

Life cycle: *M. ictaluri* - Ophthalmoxiphidiocercariae develop in rediae in fingernail clams (Sphaeridae) and encyst in the gills of mayfly nymphs. The adult fluke develops in the intestine of freshwater fishes of the genera *Ictalurus, Micropterus* and *Noturus* (see Hopkins, 1934a).

3b. Two testes. 4
4a. Uterus entirely pretesticular (Fig. 627). .... **Genus *Creptotrema* Travassos, Artigas and Pereira, 1928**
4b. Uterus extends posterior to testes (Fig. 628). .... **Genus *Paracreptotrematina* Amin and Myer, 1982**
5a. Oral sucker with one pair of ventro-lateral and one pair of dorsal papillae; parasitic in intestine of frogs (Fig. 629). .... **Genus *Bunoderella* Schell, 1964**

Life cycle: *B. metteri* - About 35 days are required for development of the miracidium after eggs are laid. Ophthalmoxiphidiocercariae develop in rediae in the fingernail clam, *Pisidium idahoense.* They penetrate and encyst in the hemocoel of caddisfly and chironomid larvae. The adult parasite develops in the intestine of the tailed-frog, *Ascaphus truei* which eats the infected insects (Anderson, Schell and Pratt, 1965).

5b. Oral sucker with one pair of ventro-lateral and two pairs of dorsal papillae; parasitic in freshwater fishes. 6
6a. Uterus entirely pretesticular (Fig. 630). .... **Genus *Crepidostomum* Braun, 1900**

Key to species in North America in Amin (1982).

Life cycle: *C. cooperi* - Miracidia develop and hatch in seven to ten days after eggs are laid. They penetrate fingernail clams of genus *Musculium* in which ophthalmoxiphidiocercariae develop in daughter rediae. Some mother rediae are known to produce daughter rediae and cercariae simultaneously. Cercariae encyst in the hemocoel of mayfly nymphs. The adult fluke develops in the pyloric ceca of several species of freshwater fishes (Hopkins, 1934a).

Ameel (1937) studied the life cycle of *C. cornutum.* The larvae develop in clams of the genera *Musculium* and *Sphaerium.* Cercariae encyst around the heart of the crayfish, *Cambarus immunis.*

6b. Uterus extends posterior to testes. 7
7a. Ceca extend to posterior end of body; testes tandem or nearly so; vitelline follicles all along ceca (Fig. 631). .... **Genus *Bunodera* Railliet, 1896**

Life cycle: *B. luciopercae* - Gravid worms with embryonated eggs in the uterus are passed in the feces of the host. The worms eventually rupture to release eggs which then hatch when entering water. Miracidia penetrate gills of the sphaeriid clam, *Pisidium variable* and change to the sporocyst stage which in turn produce rediae. Ophthalmoxiphidiocercariae develop in the rediae and after leaving the clam, encyst in the hemocoel of the amphipods, *Hyalella azteca* and *Crangonyx gracilis.* The adult parasites develop in the intestine of yellow perch, *Perca flavescens* within several months following ingestion of metacercariae (Cannon, 1971).

Wisniewski (1958b) studied the life cycle of *B. luciopercae* in Europe where different hosts are utilized.

Cannon (1971) also investigated the life cycle of *B. sacculata* (= *Bunoderina s.)* which parasitizes fish in the genera *Perca Stizostedion, Lepomis, Umbra, Notropis* and *Micropterus* in North America. The metacercariae develop in the cladocerans, *Daphnia similis* and *Moina affinis* which are regarded as only experimental intermediate hosts.

7b. Ceca extend only to level of testes which are nearly opposite; vitelline follicles confined to small lateral clusters, lateral to ventral sucker (Fig. 632). .... **Genus *Bunoderina* Miller, 1936**

Life cycle: *B. eucaliae* - Embryonated eggs are eaten by the sphaeriid clam, *Pisidium novebracense* in which miracidia then hatch. Ophthalmoxiphidiocercarie develop in rediae in the clam. The second intermediate host is unknown. The adult parasite develops in stickleback, *Eucalia inconstans* and in the mudminnow, *Umbra limi* (see Hoffman, 1955).

8a. Vitelline follicles few, chiefly lateral to ceca between level of ovary and ventral sucker; genital pore submedian, sinistral. 9
8b. Vitelline follicles numerous, distributed along ceca for most of their length; genital pore usually median. 10
9a. Testes tandem; hindbody longer than forebody; ovary pretesticular (Fig. 633). .... **Genus *Plagiocirrus* Van Cleave and Mueller, 1932**
9b. Testes oblique; fore- and hindbody about equal in length; ovary opposite anterior testis (Fig. 634). .... **Genus *Pseudurorchis* Yamaguti, 1971**
10a. Vitelline follicles confined to hindbody; testes tandem or oblique, ovoid or lobed; genital pore median, at cecal bifurcation; parasitic in fishes or progenetic in aquatic insects (Fig. 635). .... **Genus *Allocreadium* Looss, 1900**

(Continued)

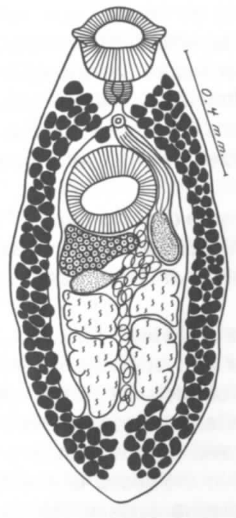


Fig. 626. *Megalogonia ictaluri.*

Fig. 627. *Creptotrema funduli.*

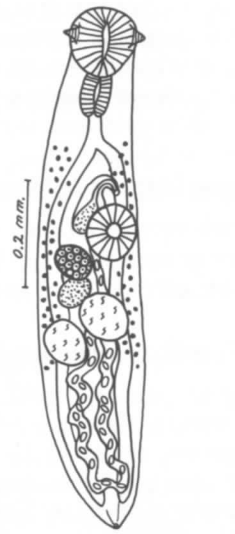


Fig. 628. *Paracreptotrematina limi,* (from Amin and Myer, 1982).

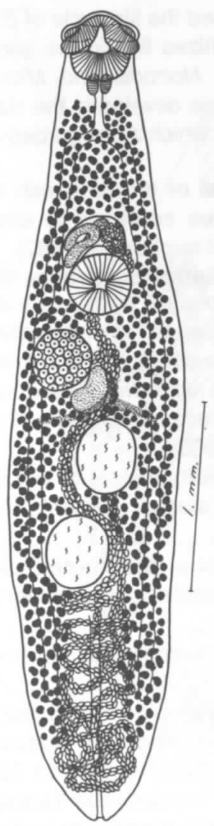


Fig. 629a. *Bunoderella metteri.*

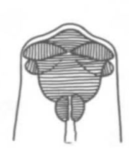


Fig. 629b. oral sucker, dorsal view

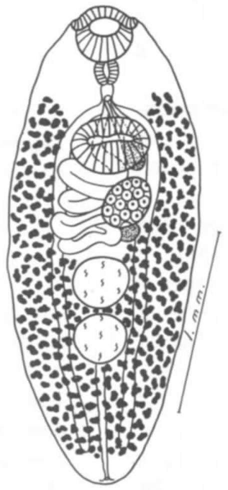


Fig. 630. *Crepidostomum farionis.*

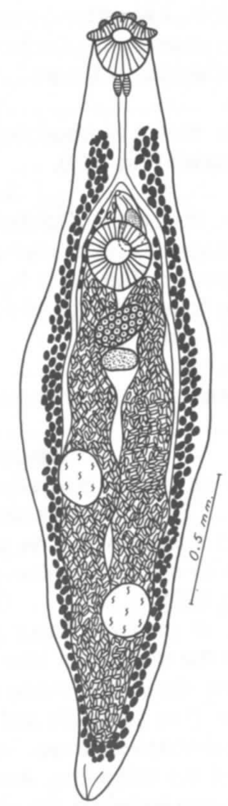


Fig. 631. *Bunodera luciopercae.*

There is a tendency for species in this genus to be "neotenic" by retaining larval features such as stylet and eyespots, and "progenetic" by developing to sexual maturity in arthropods which serve as second intermediate host.

Life cycle: *A. neotenicum* - Adults of this species develop in the hemocoel of diving beetles of the genera *Dytiscus* and *Acilius.* Miracidia develop and hatch within two weeks and penetrate sphaeriid clams of the genera *Pisidium* and *Sphaerium* in which a generation of sporocysts and then one of rediae develop. Ophthalmoxiphidiocercariae develop in the latter. Cercariae enter dytiscid beetle larvae and develop to sexually mature, neotenic adults, retaining the stylet and pigmented eyespots of the cercaria. The parasite survive the metamorphosis of the host. Eggs of the parasite are trapped until the beetle dies and decays (Crawford, 1940; Peters, 1955).

Wootton (1957) studied the life cycle of *A. alloneotenicum.* Adults develop in the hemocoel of caddisfly larvae of the genus *Limnephilus.* Miracidia hatch from eggs in debris left when larvae die and decay. They penetrate the gills of sphaeriid clams, *Pisidium abditum* in which sporocysts develop and give rise to mother rediae which in turn produce a generation of daughter rediae in which ophthalmoxiphidiocercariae develop. Some rediae produce cercariae and rediae simultaneously. The cercariae penetrate caddisfly larvae in which the adult parasite then develops.

De Giusti (1962) reported progenetic adults of *A. lobatum* in the hemocoel of the amphipods, *Gammarus pseudolimnaeus* and *Crangonyx gracilis.* Viable parasite eggs were produced but remained trapped in the hemocoel until death and decay of the host. The normal definitive hosts for this species are several species of fish.

Madhavi (1976, 1978) studied the life cycle of *A. fasciatusi* in India. This species uses the prosobranch snail *Amnicola travancorica* as first intermediate host instead of a lamellibranch. The miracidium upon hatching already contains a redia which probably is released and penetrates the gastropod, eventually producing a generation of daughter rediae. These in turn produce ophthalmoxiphidiocercariae which penetrate copepods of the genera *Mesocyclops, Microcyclops* and *Marcocyclops,* encysting in the hemocoel and developing to the metacercarial stage. The definitive host is the toothed carp, *Aplocheilus melastigma* which eats the infected copepods. The miracidium of this species differs from all other allocreadiid miracidia in containing a redia and in having epidermal cells in three tiers (6, 8, 4) instead of four tiers. Also, the excretory pores of the miracidium are dorsal and midventral instead of lateral.

The life cycle of *A. handiai* was reported by Madhavi (1980). This species parasitizes the freshwater fishes, *Channa punctata, C. orientalis* and *Clarias batrachus.* The miracidium develops and hatches in 7-12 days. The first intermediate host is the prosobranch, *Alocinna travancorica* in which ophthalmoxiphidiocercariae develop in daughter rediae. Cercariae encyst in the same or in a different snail such as, *Gyraulus convexiusculus, Lymnaea luteola* and *Thiara tuberculata.* Metacercariae from snails were fed to the freshwater fish *Channa orientalis* and partially developed specimens were recovered seven days later. The cercaria of this species has dorso-ventral finfolds on the tail as does several other allocreadiid cercariae. The species is unique in using gastropods as first and second intermediate hosts.

10b. Vitelline follicles in both fore- and hindbody. 11

11a. Ovary lobed, adjacent to anterior testis; genital pore to left of esophagus; uterus extends posterior to testes; parasitic in fishes (Fig. 636). .... **Genus** *Multivitellina* **Schell, 1974**

11b. Ovary oval or spherical, close to ventral sucker; genital pore median. 12

12a. Testes oblique; uterus extends posterior to testes; vitelline follicles not confluent posterior to testes; parasitic in the intestine of salamanders (Fig. 638). .... **Genus** *Caudouterina* **Martin, 1966**

12b. Testes tandem; uterus entirely pretesticular; vitelline follicles confluent posterior to testes; parasitic in fishes (Fig. 637). .... **Genus** *Polylekithum* **Arnold, 1934**

Life cycle: *P. ictaluri* (= *Allocreadium i.).* - Miracidia hatch and penetrate limpets, *Laevapex fusca.* Ophthalmoxiphidiocercariae develop in rediae and after emergence, encyst in the mantle of the freshwater mussel, *Lampsilis siliquoidea* and in limpets, including those that are shedding cercariae. These were assumed to be the larvae of *P. ictaluri,* a common parasite of black bullhead, *Ictalurus melas* (see Peters and Self, 1963).

Fig. 632. *Bunoderina eucaliae.*

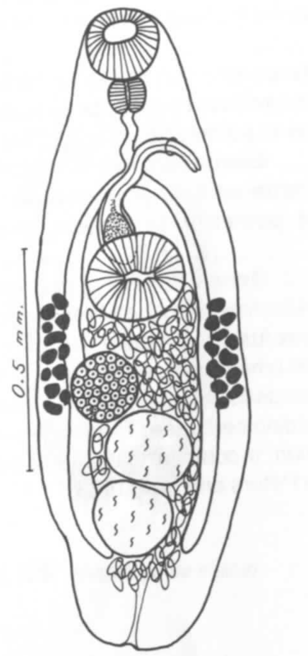


Fig. 633. *Plagiocirrus primus.*

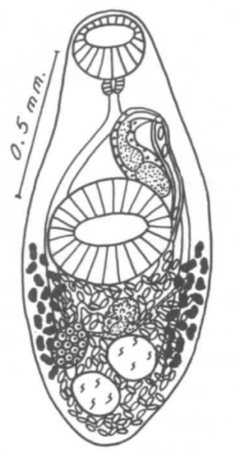


Fig. 634. *Pseudurorchis catostomi.*

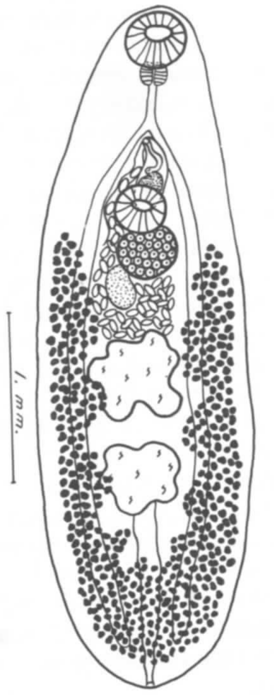


Fig. 635. *Allocreadium lobatum.*

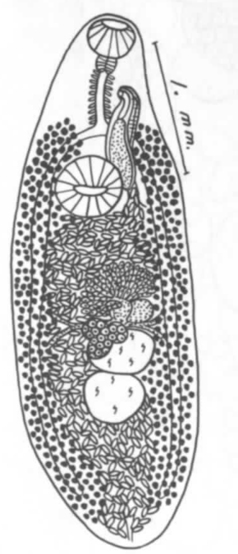


Fig. 636. *Multivitellina idahoensis.*

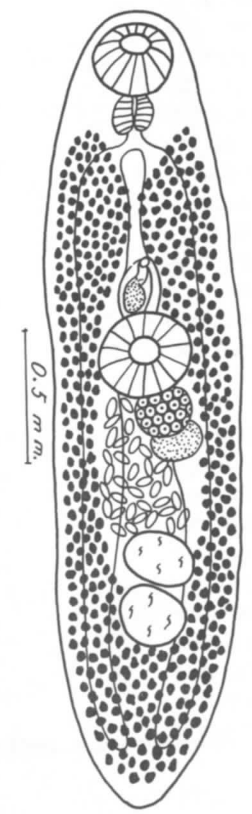


Fig. 637. *Polylekithum halli.*
(from Mueller and Van Cleave, 1932)

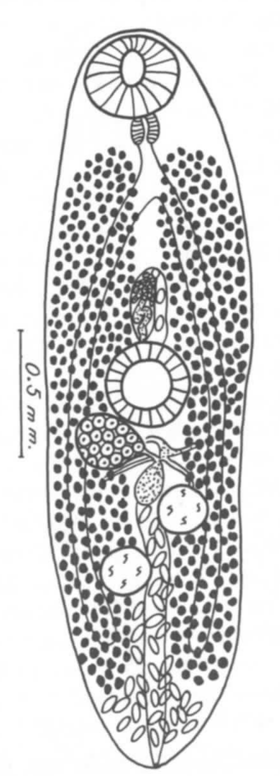


Fig. 638. *Caudouterina rhyacotriton.*
(from Martin, G., 1966)

Superfamily Lepocreadioidea Cable, 1956

Miracidia have one pair of flame cells. Cercariae are oculate trichocercous or homalometronine type; develop in a redia in prosobranch snails and encyst in molluscs, anellid worms, coelenterates, ctenophorans or in turbellarians. Life cycle involves three hosts.

Family Lepocreadiidae Nicoll, 1934

Body elongate, oval or round, spinous; pigmented eyespots in young adults; oral sucker occasionally with muscular papillae; ventral sucker sometimes contains lamellae and/or lamellar pads; pharynx present; ceca long, may open posteriorly through one or two ani or fuse with excretory vesicle to form uroproct; one, two or multiple testes, in hindbody; cirrus sac usually present; external seminal vesicle present in some genera, with or without surrounding prostate cells and membranous sac; ovary pretesticular; vitelline follicles along ceca in hindbody or in both fore- and hindbody, usually confluent posterior to testes; uterus short, pretesticular; eggs operculate, nonembryonated; excretory vesicle tubular or Y-shaped; parasitic in intestine or pyloric ceca of fishes.

Key to Genera

1a. Testes multiple (10 to 12). 2
1b. One or two testes. 3
2a. Testes in two bilateral clusters with ovary between clusters (Fig. 639). ..... **Genus** *Multitestis* **Manter, 1931**
Key to species in Skrjabin (1964).
2b. Testes in single intercecal group; ovary pretesticular; parasitic in filefishes (Fig. 640). .... **Genus** *Rhagorchis* **Manter, 1931**
3a. Body round, flat, margins curved ventrally; testes opposite, lobed; ceca arcuate; parasitic in trunkfishes. 4
3b. Body oval or elongate; testes tandem or oblique; ceca not arcuate. 5
4a. Ventral surface of body with numerous glands (Fig. 641). .... **Genus** *Dermadena* **Manter, 1946**
4b. Ventral surface of body without glands (Fig. 642). .... **Genus** *Pseudocreadium* **Layman, 1930**
5a. Ceca open through separate ani at posterior end of body; forebody flat and wider than hindbody. 6
5b. Ceca end blindly or fuse with excretory vesicle to form uroproct. 7
6a. Ovary oval; esophagus at least as long as pharynx; vitelline follicles extend forward as far as ovary; muscular metraterm absent; genital pore median (Fig. 643). .... **Genus** *Diploproctodaeum* **LaRue, 1926**
6b. Ovary lobed; esophagus very short or absent; vitelline follicles extend forward to level of ventral sucker; muscular metraterm present; genital pore submedian (Fig. 644). .... **Genus** *Bianium* **Stunkard, 1930**
7a. Oral sucker with 8 to 10 muscular papillae on anterior rim. 8
7b. Oral sucker without muscular papillae. 9
8a. One elongate testis present; one or more accessory suckers anterior to ventral sucker; ceca fused with excretory vesicle to form uroproct (Fig. 645). .... **Genus** *Cadenatella* **Dollfus, 1946**
8b. Two testes present; accessory suckers absent; ceca fused and open through a single anus (Fig. 646). .... **Genus** *Enenterum* **Linton, 1910**
9a. Ventral sucker with prominent muscular lamellae or bands on inner margin. 10
9b. Ventral sucker without muscular lamellae or lips on inner margin. 12
10a. Ventral sucker with circle of concentric lamellae or bands along inner margin (Fig. 648). .... **Genus** *Neolabrifer* **Pritchard, 1970**
10b. Ventral sucker with two semicircular lamellar pads on inner margin (Fig. 647). 11
11a. Semicircular lamellar pads and transverse lips in anterior and posterior positions on ventral sucker (Fig. 647). .... **Genus** *Labrifer* **Yamaguti, 1936**
11b. Semicircular lamellar pads and lips on lateral positions of ventral sucker (Fig. 649). .... **Genus** *Myzoxenus* **Manter, 1934**
12a. Oral sucker surrounded by circle of large spines; body elongate; ovary and testes near posterior end of body; parasitic in ocean sunfish, ***Mola mola*** **(Fig. 650).** .... **Genus** *Dihemistephanus* **Looss, 1901**
12b. Oral sucker without large circumoral spines. 13
13a. Testes oblique; external seminal vesicle absent; parasitic in urinary bladder of marine fishes (Fig. 651). .... **Genus** *Neophasis* **Stafford, 1904**
13b. Testes tandem; external seminal vesicle present; parasitic in intestine of marine fishes. 14
14a. External seminal vesicle surrounded by prostate cells. 15
14b. External seminal vesicle not surrounded by prostate cells. 16
15a. External seminal vesicle and prostate cells surrounded by membranous sac (Fig. 652). .... **Genus** *Lepidapedon* **Stafford, 1904**
15b. External seminal vesicle and prostate gland not surrounded by membranous sac (Fig. 653). .... **Genus** *Neolepidapedon* **Manter, 1954**
16a. Ceca fused with excretory vesicle to form uroproct; excretory vesicle tubular, extends forward as far as ventral sucker (Fig. 654). .... **Genus** *Neopechona* **Stunkard, 1969**

Life cycle: *N. pyriforme* - Oculate trichocercous cercariae develop in daughter rediae in the marine prosobranch snail, *Anachis avara.* Cercariae leave the snail and enter the ctenophore, *Mnemiopsis leidyi* and hydrozoan and scyphozoan medusae of the genera *Gonionemus, Bougainvillia, Nemopsis* and *Chrysaora* in which they develop to infective metacercariae without encysting. The adult parasite develops in the scup, *Stenostomus chrysops* which eat the infected intermediate hosts (Stunkard, 1969, 1974).

A similar life cycle was described by Stunkard (1980) for *N. cablei* which utilizes many of the same hosts.

16b. Ceca not fused with excretory vesicle; vesicle does not extend forward as far as ventral sucker. 17
17a. Body elongate, slender; esophagus long, partly glandular; metraterm weakly developed; external seminal vesicle oval; a few prostate cells may be outside of the cirrus sac (Fig. 657). .... **Genus** *Opechona* **Looss, 1907**
Key to species in Skrjabin (1964).

Life cycle: *O. bacillaris* - Oculate trichocercous cercariae develop in rediae in the marine prosobranch, *Nassarius pygmaeus.* After leaving the snail, they enter the ctenophore, *Pleurobrachia pileus,* the chaetognath, *Sagitta* sp. and coelenterate medusae

(Continued)

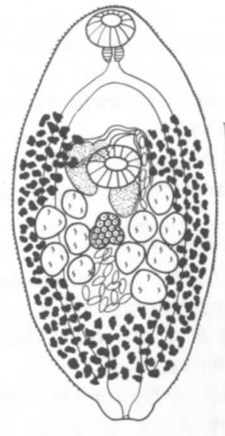


Fig. 639. *Multitestis inconstans.*

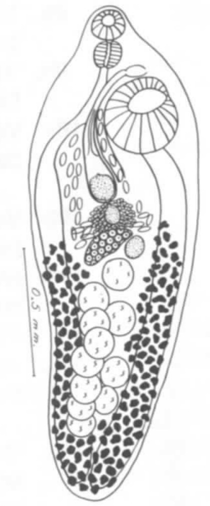


Fig. 640. *Rhagorchis odhneri.*

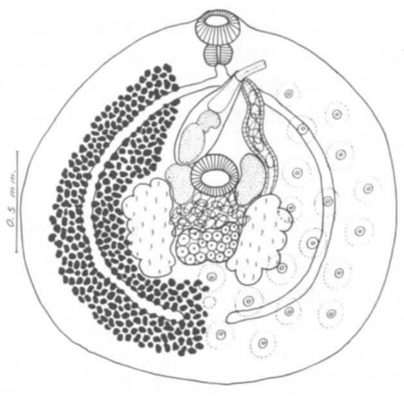


Fig. 641. *Dermadena lactophrysi.*

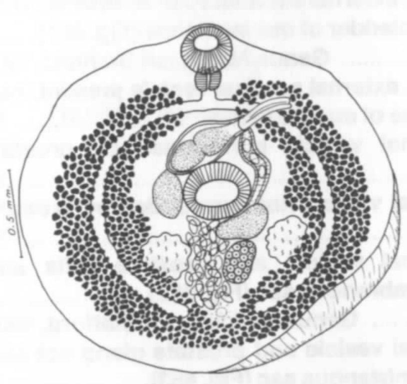


Fig. 642. *Pseudocreadium lamelliformis.*

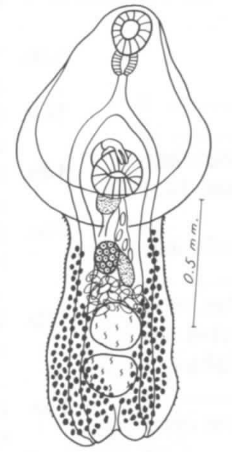


Fig. 643. *Diploproctodaeum haustrum.*

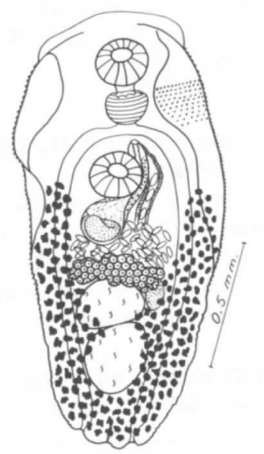


Fig. 644. *Bianium plicitum.*

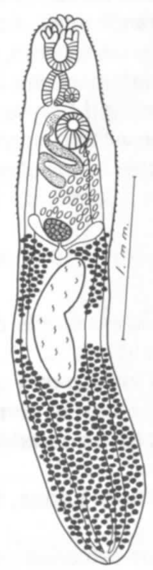


Fig. 645. *Cadenatella americana.* (from Manter, 1949)

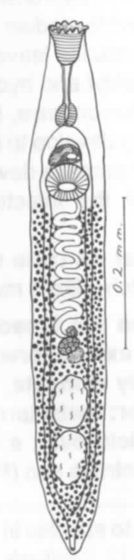


Fig. 646. *Enenterum aureum.*

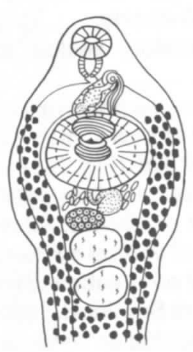


Fig. 647. *Labrifer secundus.* (from Manter, 1940)

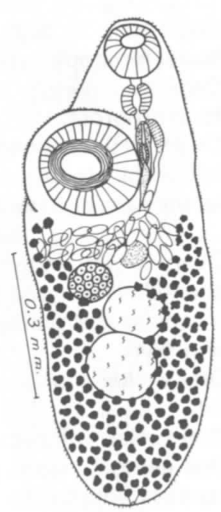


Fig. 648. *Neolabrifer bravoae.* (from Pritchard, 1972)

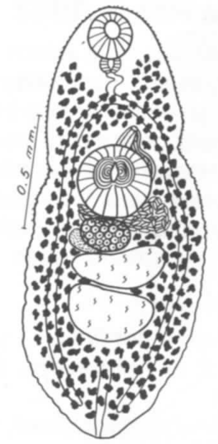


Fig. 649. *Myzoxenus vitellosus.*

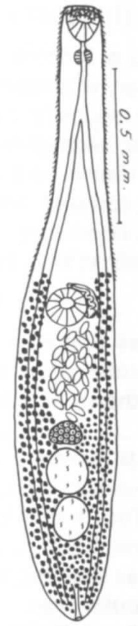


Fig. 650. *Dihemistephanus fragilis.*

Fig. 651. *Neophasis pusilla.* (from Miller, 1941)

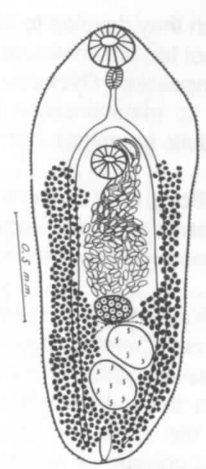


Fig. 652a. *Lepidapedon nicolli.* (from Manter, 1934)

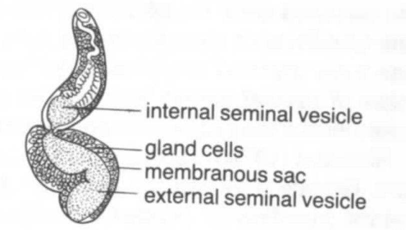


Fig. 652b. Cirrus sac and external seminal vesicle.

Fig. 653a. *Neolepidapedon medialunae.*

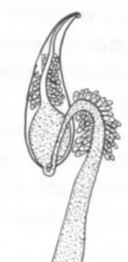


Fig. 653b. Cirrus sac and external semnial vesicle.

Fig. 654. *Neopechona pyriformis.* (from Stunkard, 1969).

Fig. 655. *Lepocreadium trulla.*

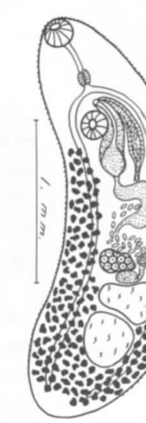


Fig. 656. *Lepocreadium retrusum.*

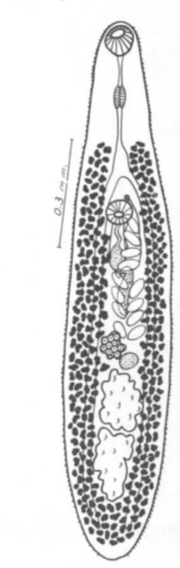


Fig. 657. *Opechona menidiae.* (from Manter, 1931)

in which they develop to infective metacercariae. Metacercariae were not fed but immature *O. bacillaris* from natural infections in the lumpsucker, *Cyclopterus lumpus* were compared and found similar to metacercariae from the second intermediate hosts. The adults parasitize marine fishes of at least five genera (Koie, 1975).

17b. Body oval or pyriform; esophagus very short; metraterm well developed; external seminal vesicle long; no prostate cells outside of cirrus sac (Fig. 655, 656).
.... **Genus *Lepocreadium* Stossich, 1904**

Key to species in Edwards and Nahhas (1968).

Life cycle: *L. setiferoides* - Oculate trichocercous cercariae *(Cercaria setiferoides)* develop in daughter and granddaughter rediae in the marine prosobranch snail, *Nassa obsoleta*. They leave the snail and enter scyphomedusae, *Chrysaora* spp.; spionid polychaete worms, *Polydora* spp.; acoelus turbellarians, *Childia* spp. and polclads of the genera *Euplana* and *Stylochus*. The metacercariae were not encysted. Some were fed to young flounder, *Pseudopleuronectes americanus* and young developing specimens of *L. setiferoides* were recovered two weeks later (Martin, 1938; Stunkard, 1972b).

Bartoli (1967) investigated the life cycle of *L. pegorchis*. Oculate trichocercous cercariae develop in rediae in the prosobranch snail, *Nassa mutabilis*. After emergence from the snail, the cercariae enter the inhalant siphon of several different marine lamellibranch molluscs but do not encyst. Free metacercariae were found in the labial palpi, mantle, foot and visceral mass of several genera and species of lamellibranchs. Adult flukes inhabit the pyloric ceca and intestine of gobies.

Stunkard (1979b, 1980a) reported the life cycle of *L. areolatum*. Oculate trichocercous cercariae develop in rediae in the marine prosobranch, *Nassarius trivittatus*. The second intermediate hosts are the medusae of the hydroid coelenterate, *Podocoryne carnea* which lives on the shells of *N. trivittatus*. Metacercariae were fed to cunners, *Tautogolabrus adspersus* and adult parasites recovered. Adults also parasitize the puffer, *Spheroides maculatus*.

Palombi (1931, 1937) described the life cycle of *L. album*.

Family Homalometridae Mehra, 1962

Body oval or fusiform, spinous; ventral sucker in anterior half of body; pharynx present; ceca long; testes tandem, oblique or opposite, in hindbody; cirrus sac absent; seminal vesicle free in parenchyma; hermaphroditic duct present; genital pore median, anterior to ventral sucker; ovary pretesticular; vitelline follicles along ceca, confluent posterior to testes; uterus entirely pretesticular; eggs operculate, nonembryonated; excretory vesicle tubular; parasitic in intestine of marine and freshwater fishes.

Key to Genera

1a. Testes opposite; vitelline follicles confined to posttesticular area; ovary anterior to right testis; body less than 1 mm. long (Fig. 658). ....
.... **Genus *Microcreadium* Simer, 1929**

Life cycle: *M. parvum* - Cercariae of the homalometronine type develop in rediae in the freshwater prosobranch snail, *Amnicola peracuta*. They encyst in the sphaeriid clam, *Musculium ferrissi* (see Hopkins, 1937).

1b. Testes tandem; vitelline follicles not confined to posttesticular area. 2

2a. Vitelline follicles in both fore- and hindbody. 3

2b. Vitelline follicles confined to hindbody. 5

3a. Cuticle thick, wrinkled; vitelline follicles confluent anterior to ventral sucker (Fig. 659). ....
.... **Genus *Crassicutis* Manter, 1936**

Key to species in Bravo-Hollis and Arroyo-Sancho (1962).

3b. Cuticle thin, not wrinkled. 4

4a. Genital pore anterior to ventral sucker; vitelline follicles confluent anterior to ventral sucker; pharynx has sphincter muscle anteriorly; oral opening a longitudinal slit (Fig. 660). ....
.... **Genus *Neoapocreadium* Siddiqi, 1959**

4b. Genital pore posterior to ventral sucker; vitelline follicles not confluent anterior to ventral sucker; pharyngeal sphincter absent; oral opening round (Fig. 661).
.... **Genus *Postporus* Manter, 1949**

5a. Oral sucker with pair of lateral muscular papillae; pigmented eyespots present; seminal vesicle bipartite, free in parenchyma (Fig. 662). ....
.... **Genus *Barbulostomum* Ramsey, 1965**

5b. Oral sucker without muscular papillae; eyespots absent or vestigial; seminal vesicle unipartite. 6

6a. Hermaphroditic duct long; ovary close to anterior testis (Fig. 663). .... **Genus *Apocreadium* Manter, 1947**

6b. Hermaphroditic duct short; ovary separated from anterior testis by about twice its diameter (Fig. 664).........
.... **Genus *Homalometron* Stafford, 1904**

Key to species in Skrjabin (1964).

Life cycle: *H. pallidum* - Embryonated eggs were fed to the marine prosobranch snail, *Hydrobia minuta* in which homalometronine cercariae (Fig. 43) developed in daughter rediae. They encysted in *H. minuta*, *Gemma gemma* and in small polychaete annelids. The natural definitive host is *Fundulus heteroclitus* (see Stunkard, 1964a).

Hopkins (1934b and 1937) described the life cycle of *H. armatum*, a parasite of freshwater fishes. Homalometronine cercariae develop in rediae in the freshwater prosobranch snail, *Amnicola peracuta* and encyst in clams of the families Unionidae and Sphaeriidae.

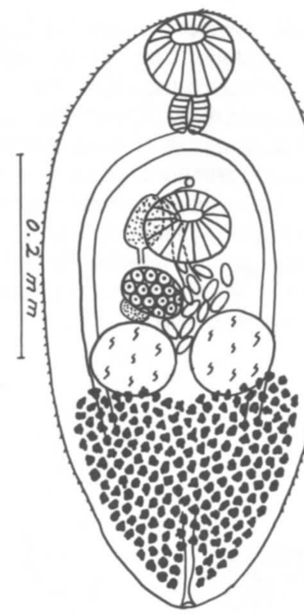


Fig. 658. *Microcreadium parvum.*

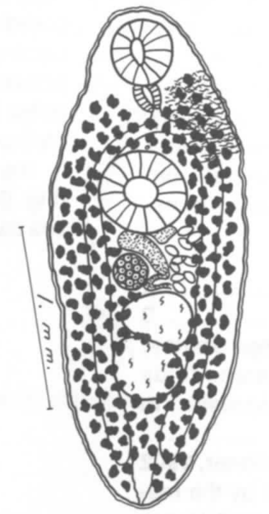


Fig. 659. *Crassicutis marina.*

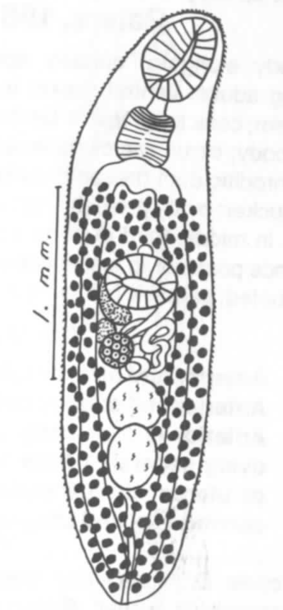


Fig. 660. *Neoapocreadium coili.* (from Sogandares-Bernal, 1959)

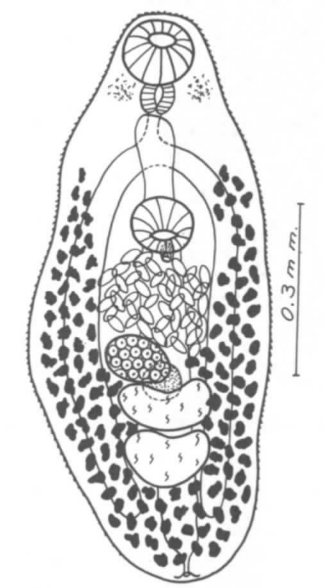


Fig. 661. *Postporus epinepheli.*

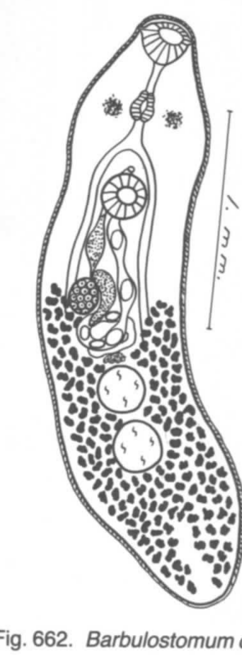


Fig. 662. *Barbulostomum cupuloris.*

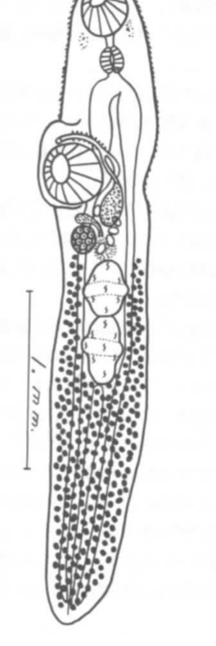


Fig. 663. *Apocreadium balistis.* (from Manter, 1947)

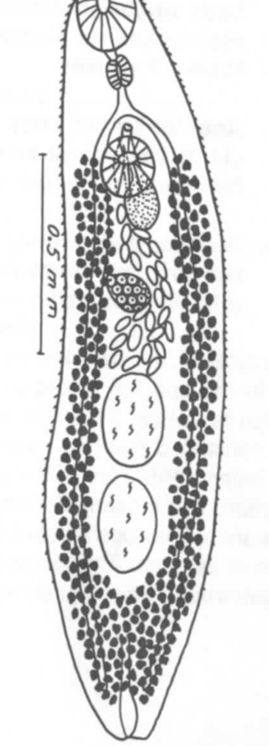


Fig. 664. *Homalometron pallidum.*

Family Deropristiidae (Skrjabin, 1958) Peters, 1961 emended

Body elongate, densely spinous; pigmented eyespots in young adults; ventral sucker in anterior half of body; pharynx present; ceca long; testes tandem or oblique, in posterior part of hindbody; cirrus sac clubshaped; seminal vesicle bipartite; hermaphroditic duct present; genital pore median, anterior to ventral sucker; ovary pretesticular; vitelline follicles distributed along ceca in middle third of body, confluent in some genera; uterus extends posterior to testes in some genera; eggs operculate, embryonated; parasitic in intestine of freshwater and marine fishes.

Key to Genera

1a. Anterior end of body inflated (widened). 2

1b. Anterior end of body not inflated. 3

2a. Anterior end of body with patches of large spines; ovary separated from seminal vesicle by some folds of uterus; uterus entirely pretesticular; parasitic in common eel and sturgeon (Fig. 665). ....
.... **Genus *Deropristis* Odhner, 1902**

Life cycle: *D. inflata* - Embryonated eggs are eaten by the marine prosobranch snail, *Bittium alternatum* in which oculate cercariae, resembling the homalometronine type develop in daughter rediae. After emerging from the snail, the cercariae encyst in the parapodia and body tissues of the marine polychaete, *Nereis virens*. The adult parasite develops in the intestine of the common eel, *Anguilla rostrata* (see Cable and Hunninen, 1942a).

Vaes (1978) studied the life cycle of what is provisionally thought to be *D. inflata* in western Europe. The host snail there is the prosobranch, *Hydrobia stagnorum*. The second intermediate host is *Nereis diversicolor*.

2b. Body without patches of large spines, anterior part of body uniformly spinous; ovary adjacent to seminal vesicle; uterus extends posterior to testes; parasitic in pike (Fig. 666). ....
.... **Genus *Cestrahelmins* Fischthal, 1957**

3a. Anterior end of body with a ventrally-interrupted circle of circumoral spines; cirrus sac, metraterm and hermaphroditic duct all long (Fig. 667). ....
.... **Genus *Pristicola* Cable, 1952**

3b. Anterior end of body without circumoral spines; cirrus sac, metraterm and hermaphroditic duct all short (Fig. 668); parasitic in sturgeon. ....
.... **Genus *Skrjabinopsolus* Ivanov, 1935**

Life cycle: *S. manteri* - Peters (1961) proposed a possible life cycle for this species, based on evidence obtained from his observation of natural infections and some experimental infections. He concluded that the oculate trichocercous cercaria reported by Seitner (1951) for *Allocreadium ictaluri* is really the larva of *S. manteri*. This cercaria develops in a redia in the freshwater prosobranch, *Pleurocera acuta*. It resembles the homalometronine type of cercaria. The metacercariae occur in freshwater oligochaetes upon which sturgeon, the natural definitive host, feeds.

Family Pleorchiidae Poche, 1926

Body linguiform to elongate, spinous; pigmented eyespots sometimes present; suckers in anterior third of body; intestinal ceca long, each with an anterior branch plus some short lateral branches; testes multiple, arranged in two dorsal and two ventral longitudinal rows, intercecal; cirrus sac present; ovary lobed, pretesticular; genital pore median; anterior to ventral sucker; vitelline follicles small, fill most of area lateral to testes; uterus entirely preovarian; intestinal parasites of marine fishes.

The family contains only the genus *Pleorchis* Railliet, 1896 (Fig. 669). Two species occur in North America as parasites of sea bass. Key to species in Skrjabin (1964).

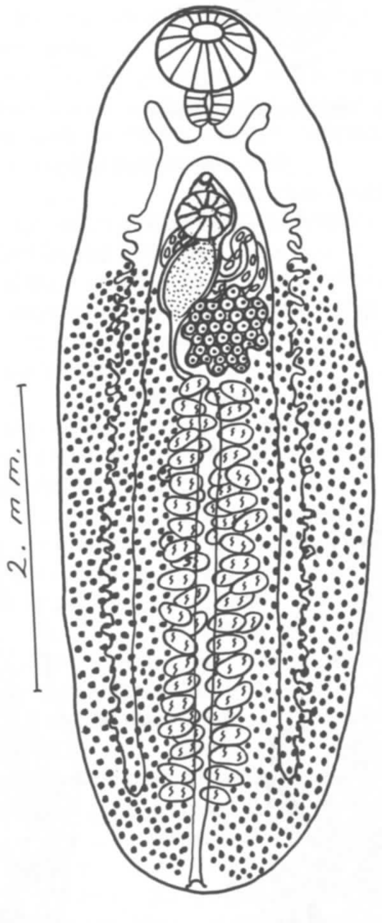


Fig. 669. *Pleorchis californiensis.*

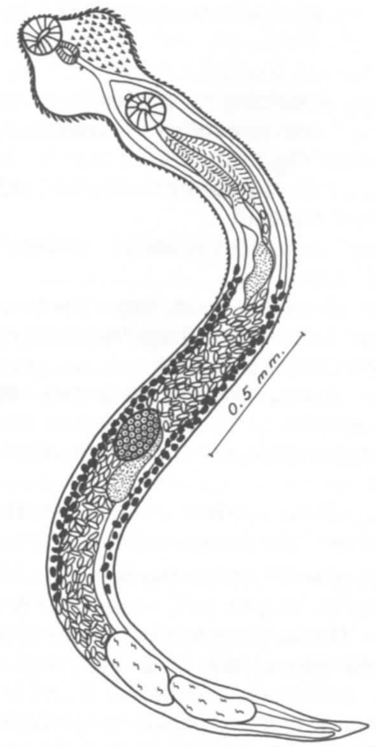


Fig. 665a. *Deropristis inflata.*

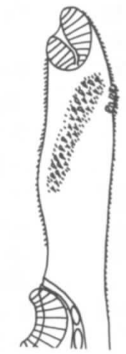


Fig. 665b. Lateral view of anterior end.

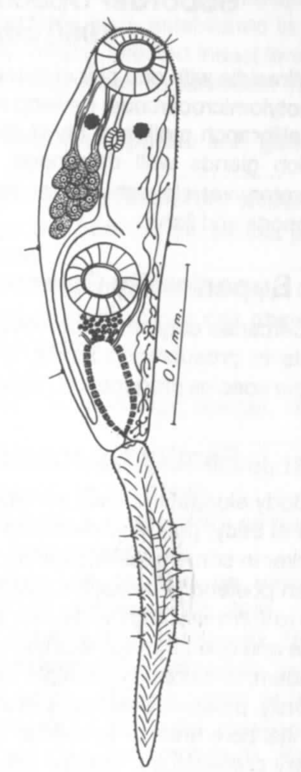


Fig. 665c. Cercaria of *D. inflata.*

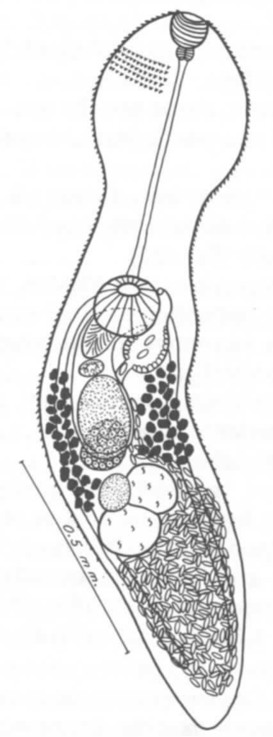


Fig. 666. *Cestrahelmins laruei.*

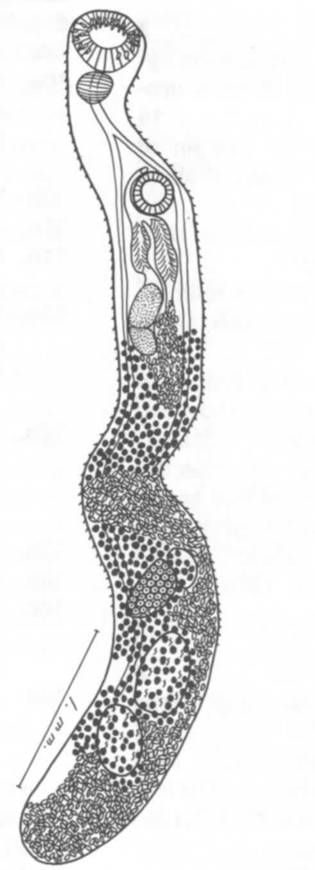


Fig. 667. *Pristicola sturionis.* (from Little, 1930)

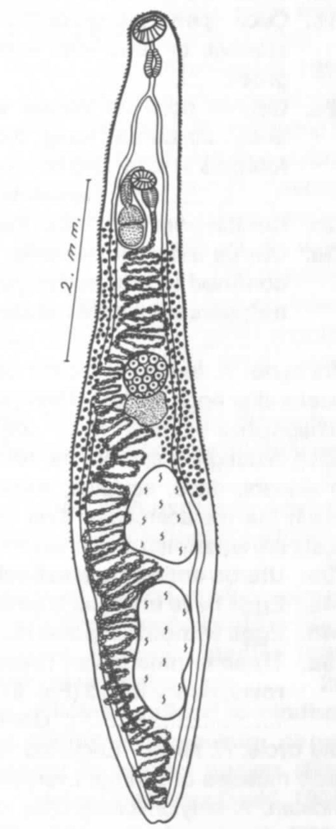


Fig. 668. *Skrjabinopsolus manteri.*

Suborder Opecoelata Odening, 1960 *emended*

Miracidia with one pair of flame cells. Cercariae cystocercous or cotylomicrocercous; develop in sporocysts in prosobranch or lamellibranch molluscs; stylet present; cystogenous and penetration glands well developed; protonephridia mesostomate, excretory vesicle with cellular wall; metacercariae in aquatic arthropods and fishes.

Superfamily Opecoeloidea Cable, 1956

Cercariae cotylomicrocercous; nonoculate; develop in sporocysts in prosobranch snails. Life cycle involves three hosts. Some species progenetic in arthropods.

Family Opecoelidae Ozaki, 1925

Body elongate or oval, nonspinous; ventral sucker in anterior half of body, pedunculate in some genera, papillae on margin of sucker in some genera; pharynx present; ceca may end blindly, open posteriorly through separate ani, fuse with excretory vesicle to form uroproct, fuse with each other to form cyclocoel or fuse and open through a single anus; testes opposite, oblique or tandem, in hindbody, multiple testes in some genera; cirrus sac usually present; external seminal vesicle sometimes present; genital pore anterior to ventral sucker (dorsal in *Neonotoporus*); ovary pretesticular; vitelline follicles along ceca, variable in extent; uterus usually pretesticular (extends posterior to testes in *Nezpercella;* eggs operculate, nonembryonated; parasitic in intestine of fishes. Epidermal cell formula of miracidium 6, 7, 4, 2.

Key to Genera

1a. Ceca end blindly at posterior end. 2

1b. Ceca open through one or two ani or unite to form cyclocoel, or fuse with excretory vesicle to form uroproct. 18

2a. Genital pore on dorsal surface near left margin of body; cirrus sac long; testes oblique lobed; vitelline follicles in fore- and hindbody (Fig. 670). .... **Genus** *Neonotoporus* **Srivastava, 1942**

2b. Genital pore on ventral surface of body. 3

3a. Uterus extends posterior to testes; vitelline follicles confined to hindbody; genital pore submedian, sinistral; parasitic in freshwater fishes (Fig. 671). .... **Genus** *Nezpercella* **Schell, 1974**

Life cycle: *N. lewisi* - Miracidia develop and hatch in about two weeks after eggs are laid. They penetrate the prosobranch snail, *Lithoglyphus virens* in which cotylomicrocercous cercariae develop in daughter sporocysts. After leaving the snail they encyst in shiners, dace, sculpins, squawfish and trout fingerlings in which the metacercariae then develop. The natural definitive hosts are squawfish and smallmouth bass (Schell, 1976).

3b. Uterus entirely pretesticular. 4

4a. Eggs have unipolar filament. 5

4b. Eggs without unipolar filaments. 8

5a. Three to nine testes (usually nine) in two longitudinal rows; ovary lobed (Fig. 672). .... **Genus** *Helicometrina* **Linton, 1910**

Life cycle: *H. nimia* - Encysted metacercariae occur in the thoracic muscles of shrimp, *Lysmata intermedia* and *Crangon formosum.* A cotylomicrocercous cercaria (Cercaria J of Miller, 1925) develops in the marine snail, *Columbella mercatoria* is thought to be the cercaria of *H. nimia.* In a laboratory experiment these cercariae encysted in *L. intermedia* which then died from overexposure (Manter, 1934).

5b. One or two testes. 6

6a. Cirrus sac very long, extending far posterior to ventral sucker; vitelline follicles confined to hindbody; parasitic in squirrelfish (Fig. 673). .... **Genus** *Stenopera* **Manter, 1933**

Key to species in Pritchard (1966).

6b. Cirrus sac short, not extending posterior to ventral sucker. 7

7a. Oral sucker terminal, funnel-shaped, larger than ventral sucker; vitelline follicles confined to hindbody, confluent posterior to testes (Fig. 674). .... **Genus** *Allostenopera* **Baeva, 1968**

7b. Oral sucker round, smaller than ventral sucker; vitelline follicles variable in extent, not confluent posterior to testes (Fig. 676). .... **Genus** *Helicometra* **Odhner, 1902**

Key to species in Manter (1934) and in Skrjabin (1964).

8a. Testes opposite; ceca short, extending only to testes; genital pore alongside of pharynx; body oval (Fig. 675). .... **Genus** *Eurycreadium* **Manter, 1934**

8b. Testes tandem or oblique; ceca extend nearly to posterior end of body. 9

9a. Small accessory sucker close to genital pore which is to left of esophagus; ventral sucker in fold of body wall; cirrus sac absent; seminal vesicle long, folded (Fig. 677). .... **Genus** *Genitocotyle* **Park, 1937**

Life cycle: *G. acirrus* - Metacercariae from the sand shrimp, *Crago stylirostris* were fed to laboratory-reared redtail surfperch, *Amphistichus rhodoterus,* the most frequently infected definitive host, and mature specimens of *G. acirrus* were recovered 14 days later. The first intermediate host is unknown (Pratt, 1970).

9b. Accessory sucker absent. 10

10a. Ventral sucker pedunculate; cirrus sac very long; genital pore to left of cecal bifurcation; body elongate (Fig. 678). .... **Genus** *Neopodocotyloides* **Pritchard, 1966**

10b. Ventral sucker not pedunculate. 11

11a. Genital pore to left of pharynx; cirrus sac absent. . 12

11b. Genital pore not to left of pharynx; cirrus sac usually present. 13

12a. Testes tandem; seminal vesicle free, extends some distance posterior to ventral sucker; vitelline follicles mostly confined to hindbody (Fig. 679). .... **Genus** *Pseudopecoelus* **von Wicklen, 1946**

12b. Testes oblique or nearly opposite; seminal vesicle does not extend posterior to ventral sucker; vitelline follicles in fore- and hindbody (Fig. 680). .... **Genus** *Manteriella* **Yamaguti, 1958**

13a. Genital pore median, posterior to pharynx. 14

13b. Genital pore submedian, sinistral. 15

14a. Vitelline follicles confined to hindbody, confluent posterior to testes; ovary irregular or oval in shape (Fig. 681). .... **Genus** *Apopodocotyle* **Pritchard, 1966**

14b. Vitelline follicles in fore- and hindbody, usually not confluent posterior to testes; ovary lobed (Fig. 682). .... **Genus** *Cainocreadium* **Nicoll, 1909**

Life cycle: *C. labracis* - Miracidia hatch and penetrate the prosobranch snail, *Gibbula adamsoni.* Cotylomicrocercous cercariae *(Cercariae cotylura)* develop in orange daughter sporocysts. After leaving the snail, the cercariae encyst in the muscles of gobiid and syngnathid marine fishes. The adult parasite develops in the intestine of the marine bass, *Morone labrax* which eats the infected intermediate hosts (Maillard, 1971).

The life cycle of *C. gulella* (= *Hamacreadium g.)* has been described by McCoy (1929, 1930).

15a. Vitelline follicles confined to hindbody. 16

15b. Vitelline follicles in both fore- and hindbody. 17

16a. Ovary round (Fig. 683). .... **Genus** *Allopodocotyle* **Pritchard, 1966**

16b. Ovary lobed (Fig. 684). .... **Genus** *Podocotyle* **Dujardin, 1845**

Life cycle: *P. atomon* - Cotylomicrocercous cercariae develop in daughter sporocysts in the marine snail, *Littorina rudis.* After leaving the snail they encyst in the hemocoel of marine amphipods of the genera *Gammarus, Amphithoe* and *Carinogammarus.* The cycle can now follow two courses. Metacercariae can be eaten by the eel, *Anguilla rostrata* or by the four-spined stickleback, *Apeltes quadracus* in which the adult fluke then develops, or they can develop into progenetic adults right in the amphipod (Hunninen and Cable, 1943a).

Ching (1979) studied the life cycle of *P. enophrysi.* Cotylomicrocercous cercariae develop in daughter sporocysts in the marine prosobranch, *Lacuna marmorata.* Cercaria encyst in the amphipod, *Hyale plumbosa.* Metacercariae from amphipods were fed to the sculpin, *Oligocottus maculosus* and the adult flukes recovered 25 days later.

The life cycle of *P. reflexa* was reported by Koei (1981). Cotylomicrocercous cercariae develop in daughter sporocysts in the marine prosobranchs, *Buccinium undatum* and *Neptunea antigua.* They encyst in the muscles of decapod crustaceans. The adult develops in cod, *Gadus morhua* which eat the infected crustaceans.

17a. Testes oblique; arms of excretory vesicle long, extend to level of cecal bifurcation; genital pore sinistral (Fig. 685). .... **Genus** *Hamacreadium* **Linton, 1910**

Life cycle: *H. mutabile* - Cotylomicrocercous cercariae develop in sporocysts in the marine prosobranch snail, *Astraea americana.* They encyst in marine fishes of the genera *Sparisoma, Halichoeres, Haemulon* and *Neomaenus.* Metacercariae become infective within three days after encystment. The adult parasites develop in the intestine of many species of marine fishes (McCoy, 1929, 1930).

17b. Testes tandem; excretory vesicle extends forward only as far as ventral sucker; genital pore to left of esophagus and pharynx (Fig. 686, 687). .... **Genus** *Plagioporus* **Stafford, 1904**

Life cycle: *P. shawi* - Miracidia develop and hatch in about two weeks after eggs are laid. They penetrate the prosobranch snail, *Lithoglyphus virens* in which mother and daughter sporocysts develop, the latter producing cotylomicrocercous cercariae. After emerging, the cercariae encyst in amphipods, nymphs of stonefly and mayfly and in chironomid larvae in which the metacercaria then develops. Metacercariae were fed to young steelhead trout and partly developed adults were recovered 26 days later. Natural definitive hosts are silver salmon, kokanee, mountain whitefish and several species of trout (Schell, 1975).

Mathias (1937) studied the life cycle of *P. angusticollis.* The host mollusc is *Neritina fluviatilis.* Cercariae encyst in freshwater amphipods and isopods. The adult fluke develops in the common eel, *Anguilla vulgaris* and in the sculpin, *Cottus gobio.*

Hendrix (1978) reported the life cycle of *P. hypentelii.* Miracidia hatch and penetrate the prosobranch, *Leptoxis carinata* in which cotylomicrocercous cercariae develop in daughter sporocysts. Cercariae emerge and then penetrate and encyst in larvae of the alderfly, *Sialis infumata* and larvae of the mosquito, *Culex pipiens.* Experimental infections were established in the swordtail, *Xiphophorus helleri* by feeding infected insect larvae. The natural definitive host is the hogsucker, *Hypentelium nigricans.*

18a. Ceca open posteriorly through separate ani; genital pore to left of pharynx. 19

18b. Ceca fused with each other or with excretory vesicle.

19a. Ventral sucker very large and conical; cirrus sac present; ovary lobed (Fig. 688). .... **Genus** *Pellamyzon* **Montgomery, 1957**

19b. Ventral sucker round, not conical; cirrus sac absent; ovary round or irregular in shape. 20

20a. Testes oval or round (Fig. 689). .... **Genus** *Neopecoelus,* **Manter, 1947**

20b. Testes lobed (Fig. 690). .... **Genus** *Apertile* **Overstreet, 1969**

21a. Ceca fused to form cyclocoel; anus absent. 22

21b. Ceca fused and open through a single anus or fused with excretory vesicle to form uroproct. 23

22a. Genital pore median; marginal papillae on ventral sucker; cirrus sac very small or absent (Fig. 691). .... **Genus** *Dactylostomum* **Woolcock, 1935**

Life cycle: *D. anaspidis* (= *Coitocaecum a.)* - Miracidia hatch and penetrate the prosobranch snails, *Potamopyrgus antipodum* and *P. badia.* Cotylomicrocercous cercariae develop in sporocysts and later encyst in the freshwater amphipods, *Paracalliope fluviatilis* and *Anaspidis tasmaniae.* Metacercariae are progenetic, developing to sexual maturity in both species of amphipods. Experimental infections were established by feeding infected amphipods to fish, *Gobiomorphus gobioides* which had been reared. Several species of marine fishes serve as natural definitive host (Macfarlane, 1939).

22b. Genital pore to left of esophagus; ventral sucker without marginal papillae; cirrus sac present (Fig. 692) .... **Genus** *Nicolla* **Wisniewski, 1934**

Life cycle: *N. gallica* - Cotylomicrocercous cercariae develop in sporocysts in the prosobranch snails, *Theodoxia fluviatilis* and in *Bythinella* sp. Natural infections with metacercariae were found in amphipods of the genera *Echinogammarus* and *Gammarus.* Some of these metacercariae were progenetic. Experimental infections were established in *Gammarus pulex* which were placed with snails that were shedding cercariae. The resulting metacercariae were identical to those found in natural infections. Natural definitive hosts are common eel, *Anguilla anguilla* and the sculpin, *Cottus gobio* (see Dollfus, 1959, 1960; Grizel and Vianey-Liaud, 1973).

23a. Cirrus sac present; ceca fused and open through a single anus; ventral sucker sessile or only slightly pedunculate. 24

23b. Cirrus sac absent; ceca fused with excretory vesicle to form uroproct; ventral sucker distinctly pedunculate. 26

24a. Papillae absent on margin of ventral sucker; cirrus sac elongate, extends posterior to ventral sucker (Fig. 694). .... **Genus** *Opecoelina* **Manter, 1934**

24b. Papillae present on margin of ventral sucker. 25

25a. Body elongate; vitelline follicles confined to hindbody; ventral sucker only slightly pedunculate; cirrus sac long, extends posterior to ventral sucker (Fig. 693). .... **Genus** *Opecoelus* **Ozaki, 1925**

Key to species in Banerjee (1965).

(Continued)

Fig. 670. *Neonotoporus yamaguti.*

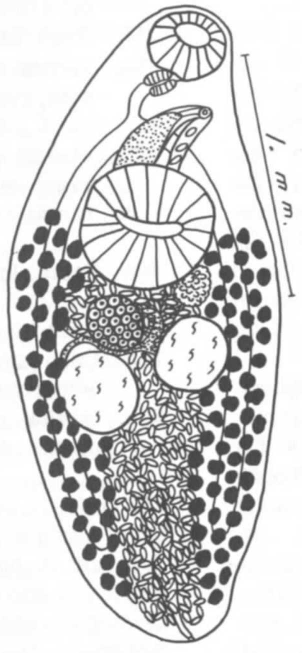


Fig. 671. *Nezpercella lewisi.*

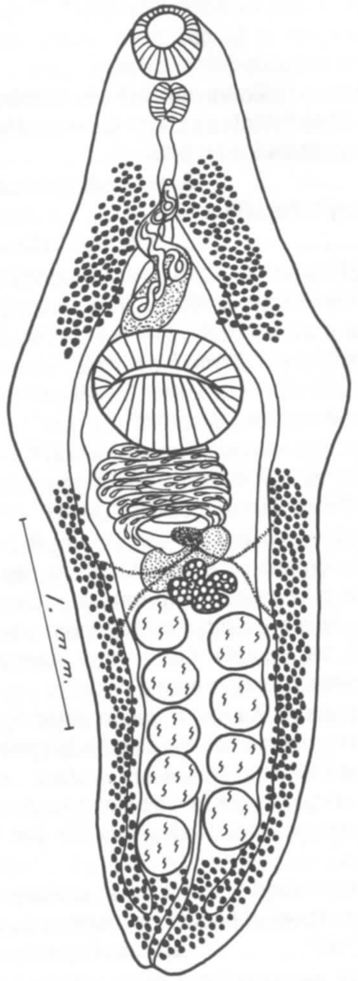


Fig. 672. *Helicometrina elongata.*
(from Noble and Park, 1937)

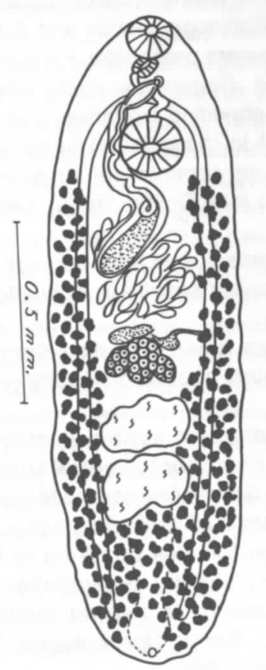


Fig. 673. *Stenopera equilata.*

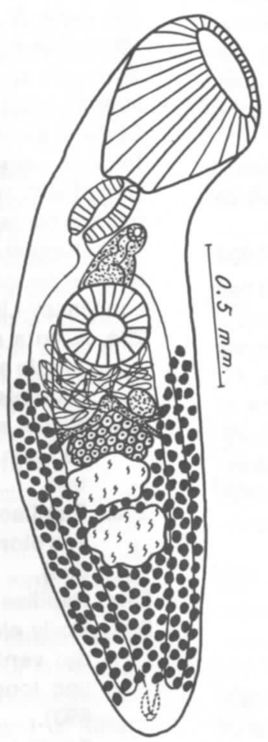


Fig. 674. *Allostenopera pugetensis.*

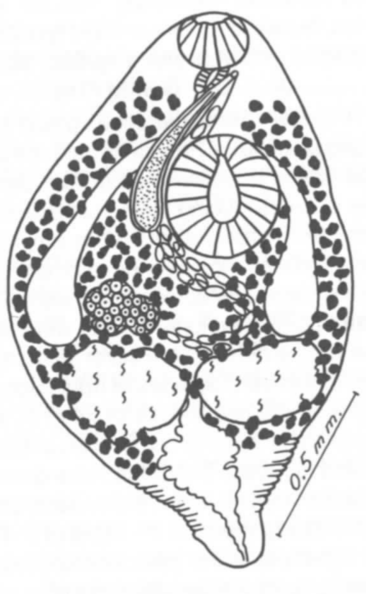


Fig. 675. *Eurycreadium vitellosum.*

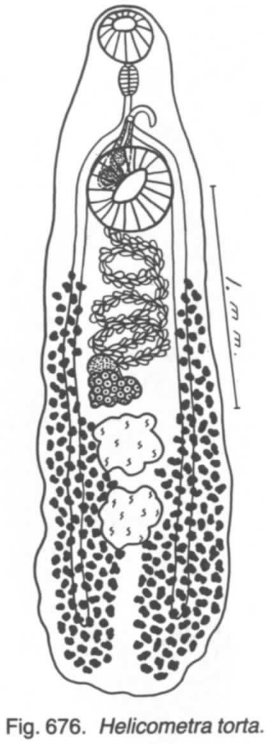


Fig. 676. *Helicometra torta.*

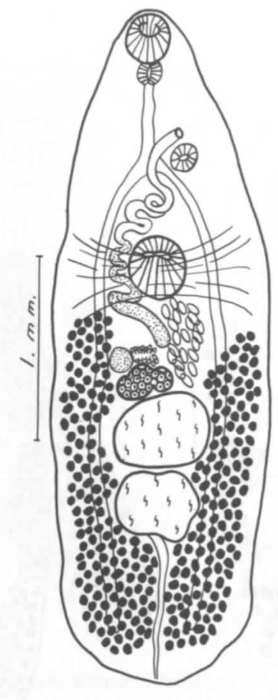


Fig. 677. *Genitocotyle acirrus.*

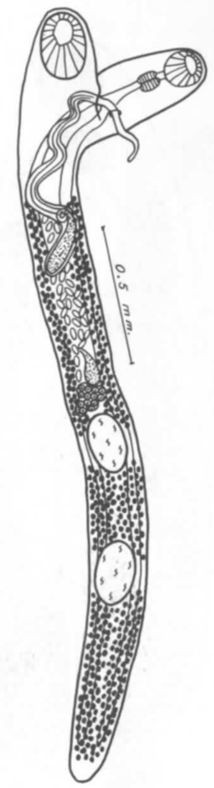


Fig. 678. *Neopodocotyloides sinusaccus.*

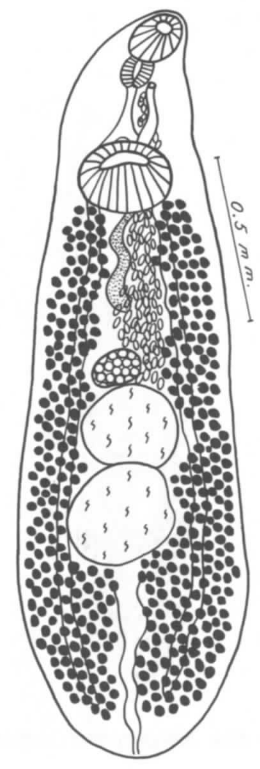


Fig. 679. *Pseudopecoelus barkeri.*

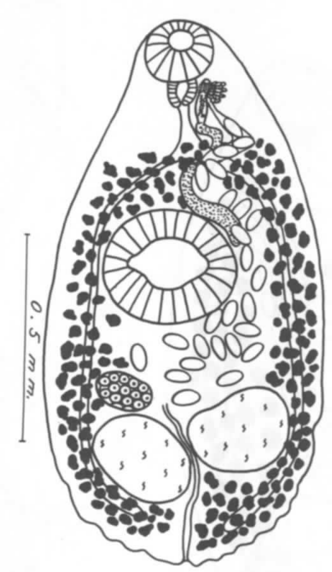


Fig. 680. *Manteriella crassum.*
(from Manter, 1947)

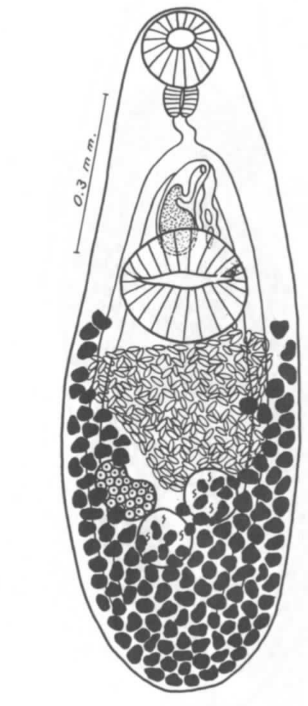


Fig. 681. *Apopodocotyle oscitans.*

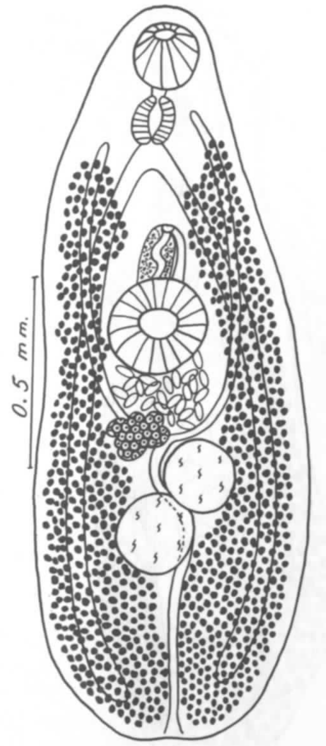


Fig. 682. *Cainocreadium gulella.* (from Linton, 1910)

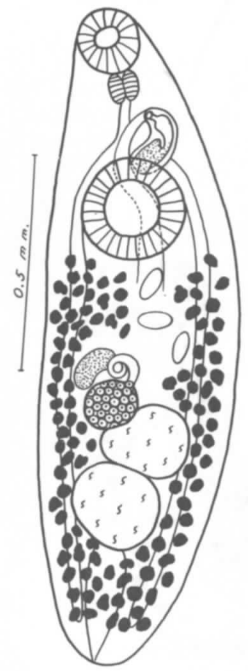


Fig. 683. *Allopodocotyle lepomis.*

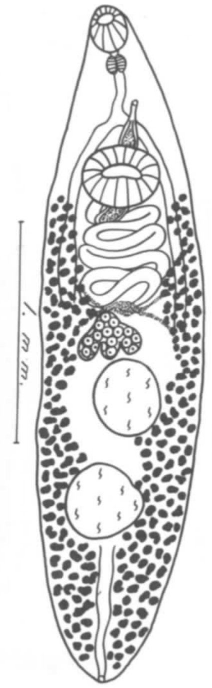


Fig. 684. *Podocotyle atomon.*

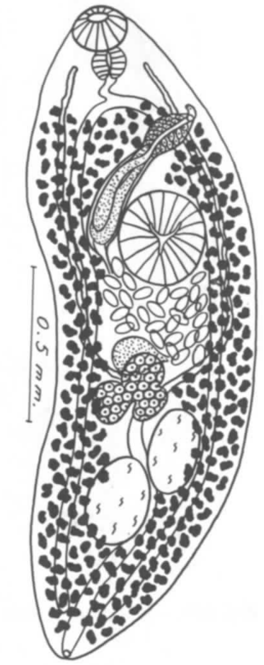


Fig. 685. *Hamacreadium mutabile.*

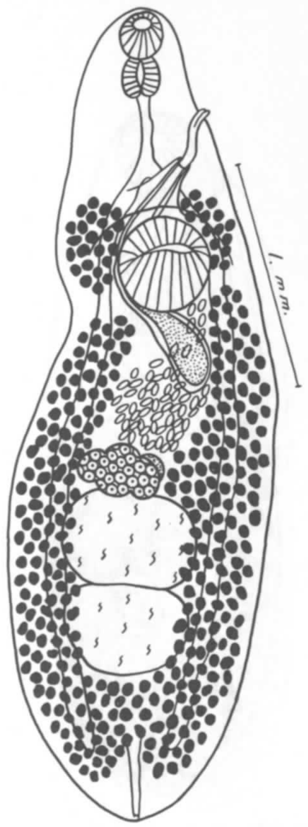


Fig. 686. *Plagioporus shawi.*

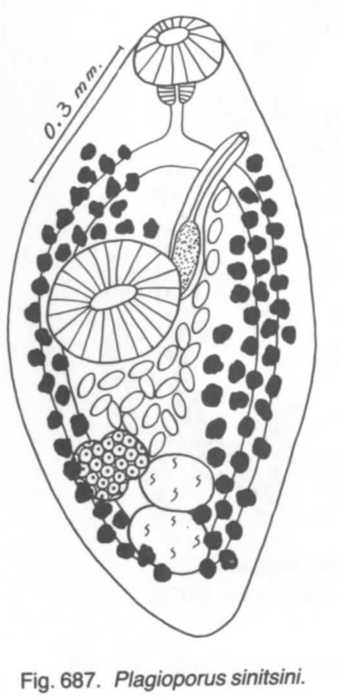


Fig. 687. *Plagioporus sinitsini.*

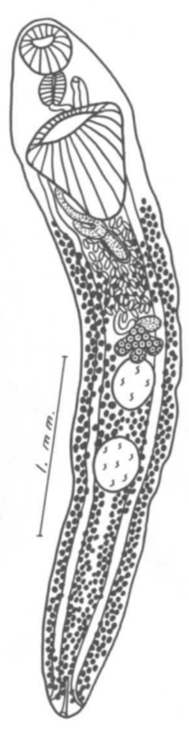


Fig. 688. *Pellamyzon sebastodis.*

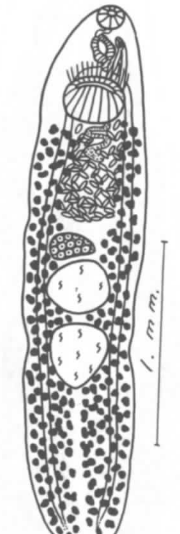


Fig. 689. *Neopecoelus scorpaenae.*

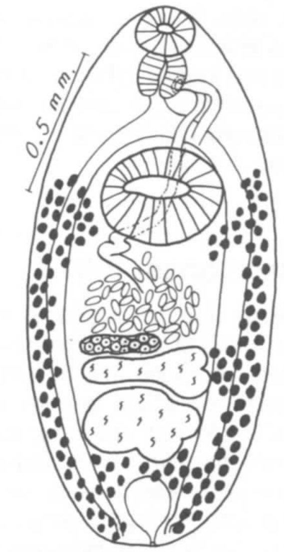


Fig. 690. *Apertile holocentri.* (from Manter, 1947)

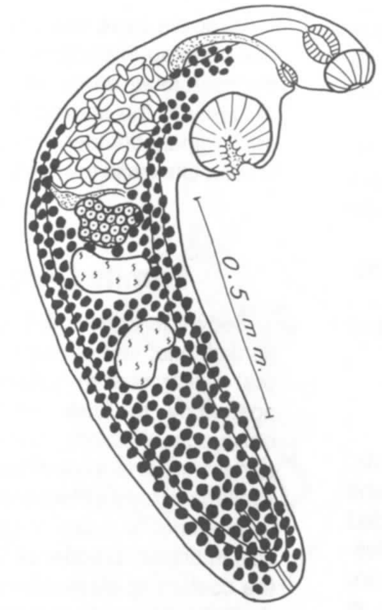


Fig. 691. *Dactylostomum vitellosum.* (from Manter, 1940)

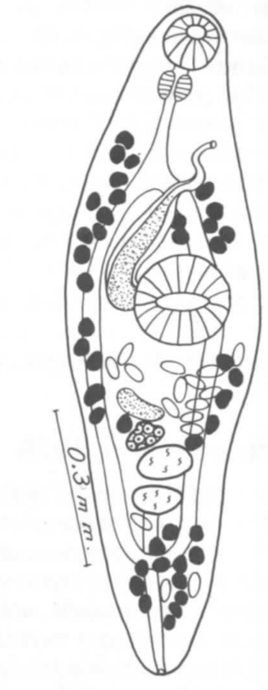


Fig. 692. *Nicolla halichoeri.*

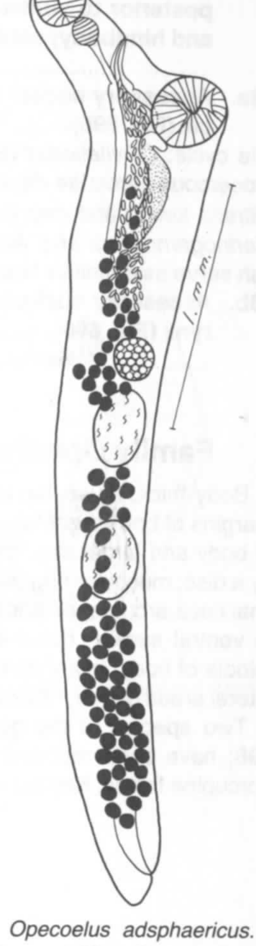


Fig. 693. *Opecoelus adsphaericus.* (from Manter and Van Cleave, 1951)

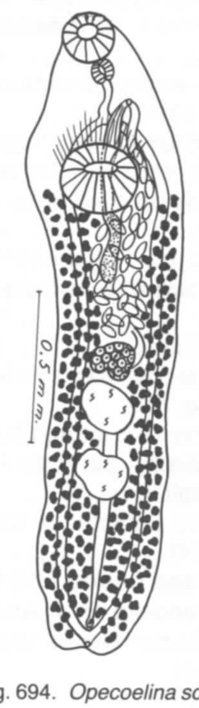


Fig. 694. *Opecoelina scorpaenae.*

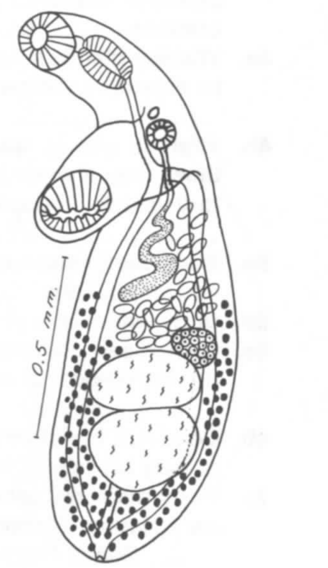


Fig. 695. *Opecoeloides brachyteleus.* (from Manter, 1947)

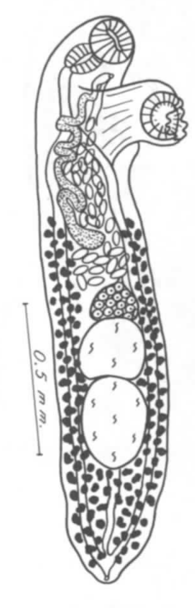


Fig. 696. *Pseudopecoeloides equesi.*

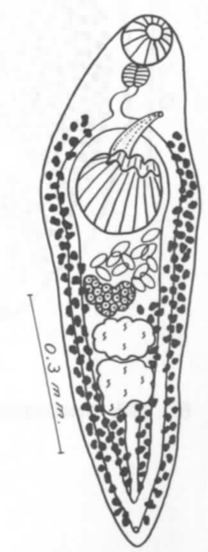


Fig. 697. *Opegaster synodi.*

25b. Body oval or fusiform; cirrus sac short, not extending posterior to ventral sucker; vitelline follicles in fore- and hindbody; ventral sucker sessile (Fig. 697). .... Genus *Opegaster* Ozaki, 1928

26a. Accessory sucker and genital pore at base of peduncle (Fig. 695). .... Genus *Opecoeloides* Odhner, 1928

Life cycle: *O. vitellosus* (Syn. *Anisoporus manteri*) - Cotylomicrocercous cercariae develop in sporocysts in the marine snail, *Mitrella lunata* and encyst in marine amphipods of the genera *Carinogammarus* and *Amphithoe.* Several species of marine fish serve as definitive host (Hunninen and Cable, 1941).

26b. Accessory sucker absent; genital pore close to pharynx (Fig. 696). .... Genus *Pseudopecoeloides* Yamaguti, 1940

Family Opistholebetidae Fukui, 1929

Body thick, muscular, round, dark pigment around vitellaria, margins of body crenulate; ventral sucker close to posterior end of body and larger than oral sucker; ventral sucker surrounded by a disc; muscular ring between oral sucker and pharynx; intestinal ceca arcuate, extending to testes; testes opposite, anterior to ventral sucker; cirrus sac present; genital pore median, in middle of body; ovary anterior to right testis; vitelline follicles fill lateral areas of body; intestinal parasites of marine fishes.

Two species of the genus *Opistholebes* Nicoll, 1915 (Fig. 698) have been reported from North America as parasites of porcupine fishes. Key to species in Cable (1956).

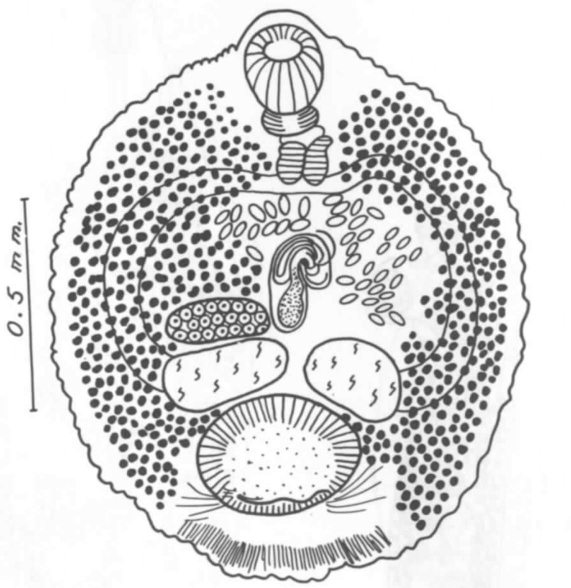


Fig. 698. *Opistholebes adcotylophorus.* (from Manter, 1947)

Superfamily Gorgoderoidea Odening, 1960 emended

Miracidia have one pair of flame cells. Cystocercous cercariae develop in daughter sporocysts in lamellibranch molluscs; metacercariae encyst in arthropods and in gastropod molluscs or rarely in the sporocyst. Adults parasitic in gall bladder, bile duct, urinary bladder, intestine or coelom of poikilothermic vertebrates. Life cycle involves three hosts.

Family Gorgoderidae Looss, 1901

Body flat, translucent, lanceolate, pyriform or banjo-shaped, nonspinous; ventral sucker in anterior half of body, larger than oral sucker; pharynx present or absent; ceca long, may be fused posteriorly to form cyclocoel; testes opposite, tandem or oblique, in hindbody, multiple testes in a few genera; cirrus sac absent; seminal vesicle free in parenchyma; ovary pretesticular; vitellaria in form of two compact masses, anterior to ovary; uterus posterior to testes; eggs nonoperculate, embryonated; parasitic in urinary bladder of fishes, amphibians and reptiles and in the coelom of elasmobranchs or in gall bladder of turtles. Epidermal cell formula of miracidium 6, 6, 3.

Key to Genera

1a. Pharynx present. 2

1b. Pharynx absent. 5

2a. Body truncate at posterior end with two pointed projections; sides of body nearly parallel; vitellaria in two compact masses; parasitic in gall bladder of turtles (Fig. 699). ....Genus *Bicornuata* Pearse, 1949

2b. Body pyriform or banjo-shaped. 3

3a. Body banjo-shaped; parasitic in urinary bladder and cloaca of sea turtles (Fig. 700). .... Genus *Plesiochorus* Looss, 1900

3b. Body broadly pyriform, foliate posteriorly; seminal receptacle present; parasitic in coelom of elasmobranchs. 4

4a. Vitelline glands lateral to ceca; ceca without diverticula; excretory vesicle Y-shaped (Fig. 701). .... Genus *Probolitrema* Looss, 1902

4b. Vitelline glands usually median to ceca but sometimes may also be lateral; diverticula on ceca; excretory vesicle Y-shaped (Fig. 702). .... Genus *Nagmia* Nagaty, 1930

5a. Body banjo-shaped or pyriform; parasitic in fishes and amphibians. 6

5b. Body lanceolate; parasitic in amphibians. 8

6a. Ceca fused posteriorly to form cyclocoel; parasitic in urinary bladder of marine fishes (Fig. 703). .... Genus *Xystretum* Linton, 1910

6b. Ceca not fused posteriorly, end blindly; parasitic in urinary bladder of fishes and amphibians. 7

7a. Body pyriform; testes multiple (5-8); parasitic in urinary bladder of common eel (Fig. 704). .... Genus *Progorgodera* Brooks and Buckner, 1976

7b. Body banjo-shaped; two testes, opposite or oblique (Fig. 705). .... Genus *Phyllodistomum* Braun, 1899

Key to species in Skrjabin (1964).

(Continued)

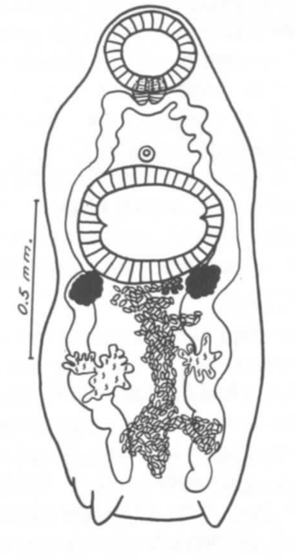


Fig. 699. *Bicornuata caretta.* (from Pearse, 1949)

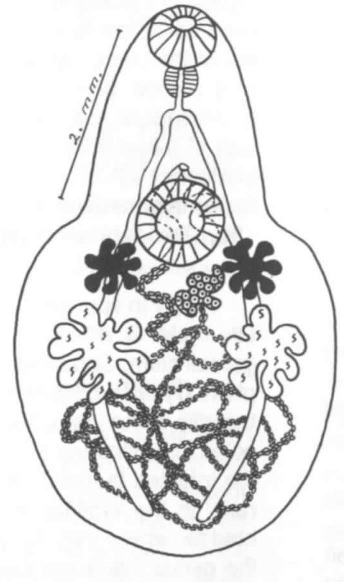


Fig. 700. *Plesiochorus cymbiformis.*

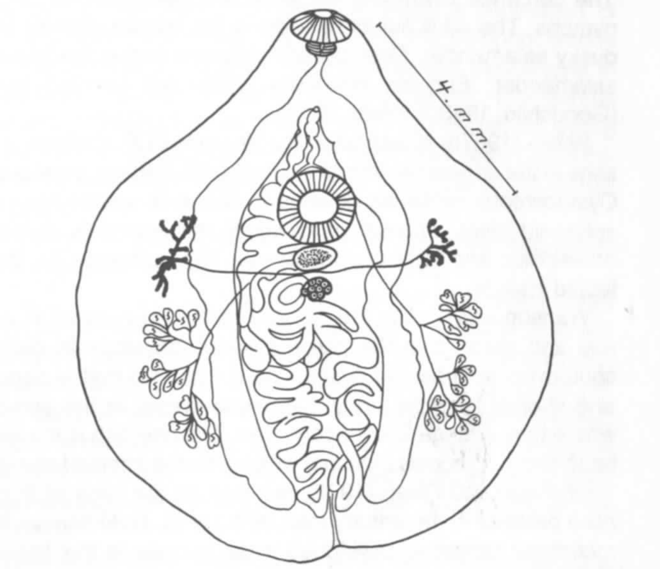


Fig. 701. *Probolitrema californiense.* (from Stunkard, 1935)

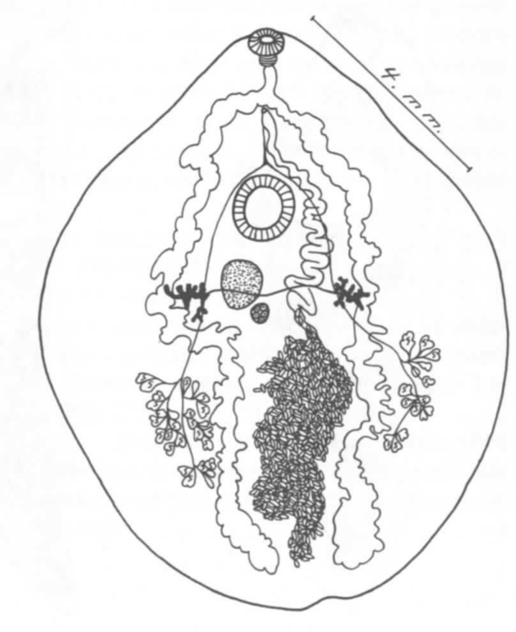


Fig. 702. *Nagmia floridensis.* (from Markell, 1953)

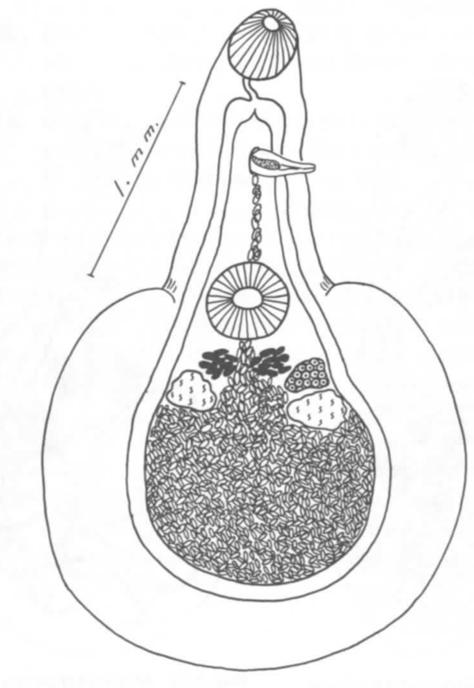


Fig. 703. *Xystretum solidum.*

Life cycle: *P. solidum* - Miracidia hatch as eggs enter water. They are drawn into the incurrent siphon of fingernail clams of the genus *Pisidium* in which cystocercous cercariae develop in daughter sporocysts which inhabit the gill lamellae of the clam. The cercariae eventually encyst in the hemocoel of dragonfly nymphs. The adult flukes develop in the urinary bladder of the dusky salamander, *Desmognathus fuscus* and in the two-lined salamander, *Eurycea bislineata* which eat infected insects (Goodchild, 1943; Groves, 1945).

Schell (1967a) investigated the life cycle of *P. staffordi*, a parasite in the urinary bladder of the bullhead, *Ameiurus nebulosus*. Cystocercous cercariae develop in daughter sporocysts in the sphaeriid clam, *Musculium ryckholti* and encyst in naiads of damselflies and trichopterous larvae. The bullheads eat the infected insects.

Wanson and Larson (1972) studied the life cycle of *P. nocomis* and report that the cercaria which develops in daughter sporocysts in sphaeriid clams, has a small tail that is narrower and shorter than the body. Cercariae encyst in the sporocyst where they change to metacercariae. The host fish is the hornyhead chub, *Hybopsis biguttata* which eats the infected clams.

Ubelaker and Olsen (1972) reported the life cycle of *P. bufonis* a parasite in the urinary tract of the toad, *Bufo boreas*. Macrocercous cercariae developed in sporocysts in the fingernail clam, *Pisidium adamsi* and after emerging encysted in dragonfly naiads of the genus *Libellula*. Some progenetic metacercariae were found in the naiads.

Wu (1938) found progenetic specimens of *P. lesteri* in the freshwater shrimps, *Palaemon asperulus* and *P. nipponensis* in China.

8a. Testes multiple (9 to 11) in two longitudinal rows (Fig. 706). .... **Genus** *Gorgodera* **Looss, 1899**

Life cyle: *G. amplicava* - Miracidia hatch from embryonated eggs passed in the feces of the host. They are swept into the incurrent siphon of the fingernail clam, *Musculium partumeium*. Cystocercous cercariae develop in daughter sporocysts in the gill lamellae of the clam. Cercariae leave the clam by way of the excurrent siphon and are then eaten by tadpoles of frogs and salamanders and by crayfishes. They encyst in the intestinal wall of these hosts. The adult parasite develops in the urinary bladder of adult frogs, toads and salamanders which eat the infected intermediate hosts (Krull, 1935d; Goodchild, 1948).

8b. Two tandem testes (Fig. 707). .... **Genus** *Gorgoderina* **Looss, 1902**

Key to species in Skrjabin (1964).

Life cycle: *G. attenuata* - Newly-hatched miracidia enter the fingernail clam, *Sphaerium occidentalis* by way of the incurrent siphon. Cystocercous cercariae develop in daughter sporocysts in the gills of the clam. They leave the clam and are eaten by tadpoles in which they encyst around the heart and liver. Frogs eat the infected tadpoles. The developing parasites remain temporarily in the Wolffian ducts of the frog, then enter the urinary bladder where they mature. Natural definitive hosts are frogs of the genus *Rana* and newts, *Triturus viridescens*. The metacercariae have nine testis primordia like trematodes in the genus *Gorgodera* but by the time they become sexually mature only two testes remain (Rankin, 1939).

The life cycle of *G. rochalimai* was studied by Jourdane and Theron (1975).

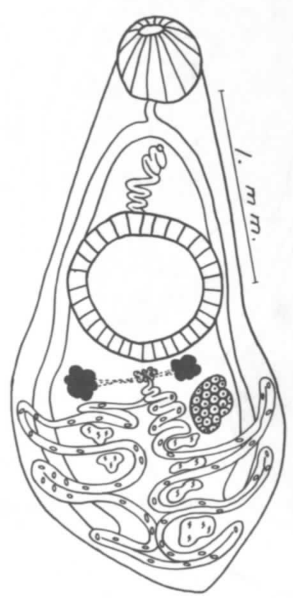


Fig. 704. *Progorgodera foliata*. (from Brooks and Buckner. 1976)

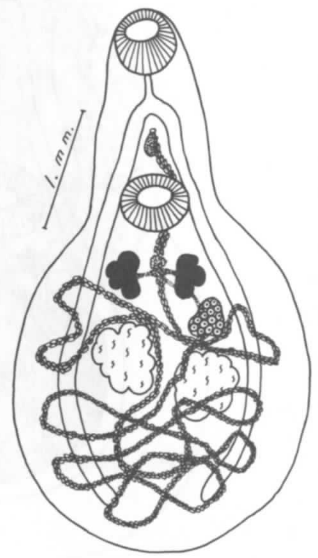


Fig. 705. *Phyllodistomum staffordi*.

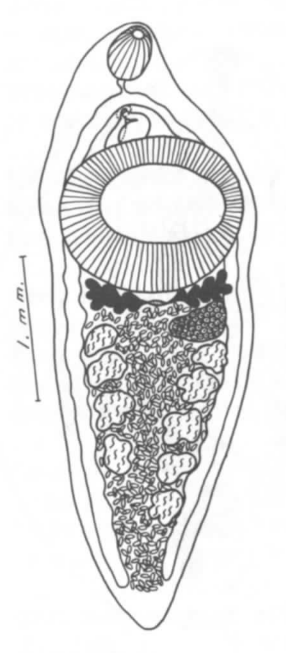


Fig. 706. *Gorgodera* sp.

Fig. 707. *Gorgoderina* sp.

Order Opisthorchiida LaRue, 1957

Miracidia with one pair flame cells. Cercariae distomate or monostomate; primary excretory vessels present in tail; stylet present or absent; tail with or without finfolds; develop in rediae in prosobranch snails; metacercariae in fishes. Life cycle involves three hosts.

Suborder Opisthorchiata LaRue, 1957
Superfamily Opisthorchioidea Faust, 1929

Cercariae pleuro- or parapleurolophocercous or gymnocephalous; oculate; cuticle spinous; protonephridia mesostomate; primary excretory pores on margins of tail close to body-tail junction; excretory vesicle with cellular wall.

Family Opisthorchiidae Braun, 1901

Body flat, translucent, fusiform or elongate; ventral sucker in anterior third of body; pharynx present; ceca long; testes tandem or oblique, near posterior end of body; cirrus sac absent; seminal vesicle free in parenchyma; genital pore median, anterior to ventral sucker; ventro-genital sac and gonotyl absent; ovary pretesticular; vitelline follicles lateral to ceca; uterus entirely preovarian, intercecal, usually confined to hindbody; eggs operculate, embryonated; parasitic in bile duct, gall bladder, liver or upper small intestine of vertebrates.

Key to Genera

1a. Testes dendritic, overlapping ceca laterally; vitelline follicles lateral to ceca between ovary and ventral sucker; parasitic in liver of mammals (Fig. 708). .... **Genus** *Clonorchis* **Looss, 1907**

Life cycle: *C. sinensis* - This is the Chinese liver fluke of human beings. It does not occur in North America but is a common parasite of cats, dogs and human beings in Asia. Embryonated eggs in feces of host are eaten by the prosobranch snails, *Parafossarulus manchouricus* and *Bulimus japonicus*. One generation of sporocysts and one of rediae develop, the latter produce pleurolophocercous cercariae. After emergence, the cercariae encyst in fishes of several species. Human beings become infected by eating metacercariae in fish flesh. Defecation by human beings in exposed places and the custom of eating raw or undercooked fish contribute to the high incidence of this parasite in the Far East.

1b. Testes lobed or oval, usually intercecal. 2

2a. Body fusiform or elliptical. 3

2b. Body elongate, slender. 5

3a. Vitelline follicles confined to lateral regions of anterior half of body, confluent anterior to ventral sucker; testes lobed, tandem; excretory vesicle passes between testes (Fig. 709). .... **Genus** *Parametorchis* **Skrjabin, 1913**

3b. Vitelline follicles lateral to ceca in middle third of body or more posterior than this, not confluent; parasitic in birds and mammals. 4

4a. Body broadly fusiform; some folds of uterus envelop ventral sucker; testes oval, oblique (Fig. 710). .... **Genus** *Metorchis* **Looss, 1899**

Life cycle: *M. conjunctus* - Embryonated eggs are eaten by the prosobranch snail, *Amnicola limosa* in which a generation of sporocysts and one of rediae are produced. Pleurolophocercous cercariae develop in the latter. After emergence, they encyst in the common sucker, *Catostomus commersoni*. Piscivorous mammals, including human beings, become infected by eating infected fish. Metacercariae excyst in the small intestine and migrate to the liver and gall bladder by way of the bile duct (Cameron, 1944).

4b. Body narrowly fusiform; uterine folds do not envelop ventral sucker (Fig. 711). .... **Genus** *Opisthorchis* **Blanchard, 1895**

Life cycle: *O. tonkae* - Embryonated eggs in feces of host are eaten by the prosobranch snail, *Amnicola limosa* in which pleurolophocercous cercariae develop in rediae. The cercariae encyst in sand shiners, pumpkinseed and blunt-nosed minnows. The natural definitive hosts are muskrat and Eastern meadow mouse. Experimental infections were established in dog, cat, rat and guinea pig (Wallace and Penner, 1939; Wallace, 1940; Sillman, 1953).

Wykoff *et al* (1965) investigated the life cycle of *O. viverrini*, a parasite in the livers of human beings in the Far East. Eggs are ingested by several species of snails of the genus *Bithynia* in which a generation of sporocysts and one of rediae are produced, the latter giving rise to oculate pleurolophocercous cercariae which encyst in at least nine species of fishes. Human beings become infected by eating raw or inadequately cooked fish.

Bourgat and Kulo (1977) described the life cycle of *O. chabaudi* in Togo. Pleurolophocercous cercariae develop in rediae in the gastropod *Gabbia neumanni* in Togo. They encyst in tadpoles and when metacercariae were fed to a kitten adults were recovered from the bile ducts seven weeks later.

5a. Body elongate, posterior end truncate, sides parallel; suckers vestigial; parasitic in birds (Fig. 714). .... **Genus** *Plotnikovia* **Skrjabin, 1945**

5b. Body elongate, posterior end rounded; at least one sucker present; vitelline follicles interrupted lateral to ovary. 6

6a. Oral and ventral suckers well developed, the oral larger than the ventral; vitelline follicles not confluent anterior to ventral sucker (Fig. 712). .... **Genus** *Amphimerus* **Barker, 1911**

Life cycle: *Amphimerus* sp. - Embryonated eggs are eaten by the prosobranch snail, *Goniobasis semicarinata*. Pleurolophocercous cercariae develop in daughter rediae in about 90 days. The second intermediate host is unknown but it is probably a fish. The mature fluke develops in the bile duct and gall bladder of the snapping turtle, *Chelydra serpentina* (see Cable, 1939).

Evans (1963) fed presumably infected flesh of the common sucker, *Catostomus commersoni* to a cat and later recovered adults of *Amphimerus pseudofelineus* from the liver.

6b. Oral sucker absent, ventral sucker very small; vitelline follicles confluent anterior to ventral sucker (Fig. 713). .... **Genus** *Pseudamphimerus* **Gower, 1940**

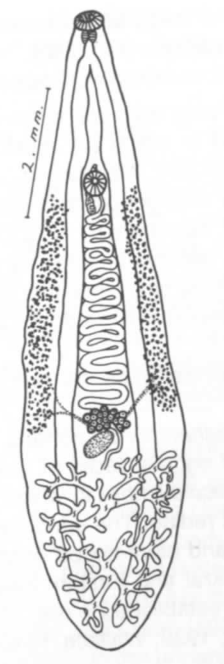


Fig. 708. *Clonorchis sinensis.*

Fig. 709. *Parametorchis complexus.*

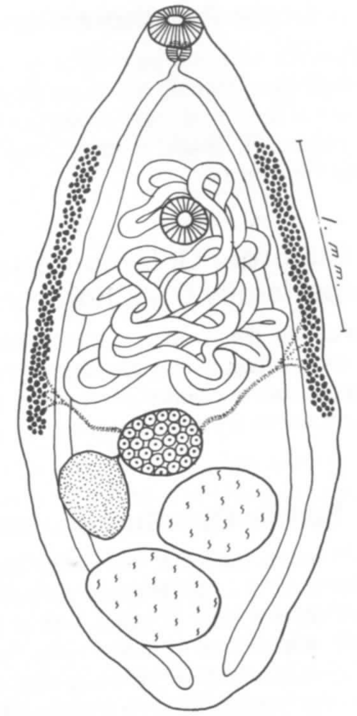


Fig. 710. *Metorchis albidus.*

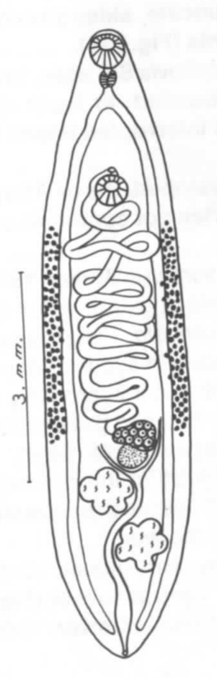


Fig. 711. *Opisthorchis tenuicollis.*

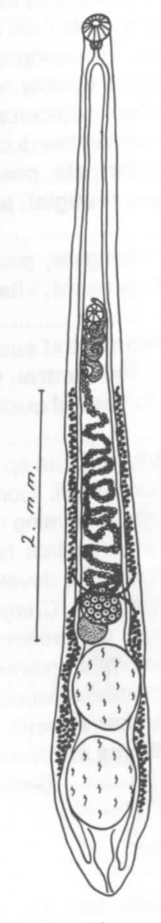


Fig. 712. *Amphimerus ovalis.*

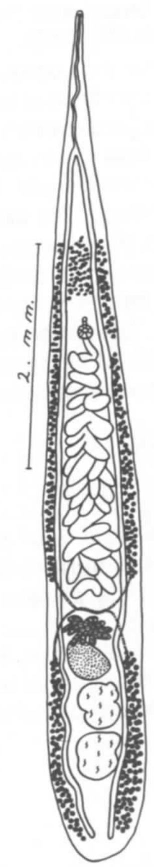


Fig. 713. *Pseudamphimerus sterni.* (from Gower, 1940)

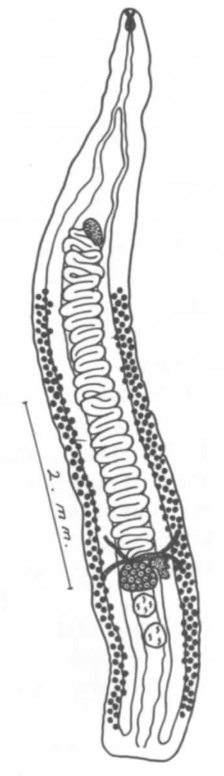


Fig. 714. *Plotnikovia podilymbae.*

Family Heterophyidae Odhner, 1914

Body small, oval, fusiform or pyriform; body spines conical or scalelike; oral and ventral suckers present; pharynx present; ceca variable in length; one or two testes; testes opposite, oblique or tandem, in hindbody; cirrus and cirrus sac absent; seminal vesicle free in parenchyma; ovary pretesticular; genital sac (containing genital pore and gonotyl if present) or ventrogenital (containing ventral sucker, genital pore and gonotyl); male and female ducts fused to form hermaphroditic duct (genital sinus); vitelline follicles along ceca or clustered around gonads; uterus usually confined to hindbody; eggs operculate, embryonated; parasitic in intestine of birds or mammals.

Note: The gonotyl is regarded as a muscular and sometimes spiny outgrowth of the wall of the genital or ventrogenital sac. The genital pore is usually adjacent to the gonotyl but in a few species it is surrounded by the gonotyl.

Key to Genera

1a. One testis. 2

1b. Two testes. 5

2a. One circle of circumoral spines present; hermaphroditic duct modified to form muscular ejector; seminal vesicle bipartite; prostatic vesicle present (Fig. 715). .... **Genus *Pygidiopsoides* Martin, 1951**

Life cycle: *P. spindalis* - Metacercariae from the gills of the California killifish, *Fundulus parvipinnis,* were fed to cats and baby chicks and mature trematodes were recovered four to six days later. The natural definitive host is unknown. Early larval stages develop in the prosobranch marine snail, *Cerithidia californica.* Cercariae, resembling the pleurolophocercous type except for the absence of finfolds on the tail, develop in a redia (Martin, 1951, 1964).

2b. Circumoral spines and muscular ejector absent. ... 3

3a. Body oval or pyriform, clothed in rows of scalelike spines; genital sac present, containing only genital pore; gonotyl absent (Fig. 716). .... **Genus *Phocitremoides* Martin, 1950**

Life cycle: *P. ovale* - Pleurolophocercous cercariae develop in rediae in the marine prosobranch, *Cerithidia californica* and after leaving the snail, encyst beneath the scales of jack smelt *Atherinopsis californica* and the California killifish, *Fundulus parvipinnis.* The natural definitive host is unknown but experimental infections were established in cats and baby chicks by feeding metacercariae (Martin, 1950a).

3b. Body fusiform or elongate; spines conical, not scalelike; ventrogenital sac present. 4

4a. Body fusiform; ceca short; ovary oval, close to testis; vitelline follicles small, clustered around gonads; ventral sucker inclined anteriorly and cavity of sucker spinous (Fig. 717). .... **Genus *Euhaplorchis* Martin, 1950**

Life cycle: *E. californiensis* - Parapleurolophocercous cercariae develop in rediae in the marine prosobranch, *Cerithidia californica* and after leaving the snail encyst in the brain of the California killifish. The natural definitive host is the California gull, *Larus californicus.* Experimental infections were established in baby chicks (Martin, 1950b).

4b. Body elongate; ceca long; ovary angular, separated from testis by some distance; testis near posterior end of body; vitelline follicles large lobed, distributed along ceca; ventral sucker not inclined anteriorly and nonspinous (Fig. 718). .... **Genus *Apophalloides* Yamaguti, 1971**

Note: This genus might not be valid. It is based on one poorly preserved specimen.

5a. Oral sucker conical with solid posterior appendix, dorsal lip present on oral sucker. .... **Ascocotyle Complex** 6

5b. Oral sucker without solid posterior appendix. 9

6a. Circumoral spines absent; ceca short; vitelline follicles near posterior end of body; short hermaphroditic duct opens into genital sac immediately posterior to gonotyl (Fig. 720). .... **Genus *Pseudascocotyle* Sogandares-Bernal and Bridgman, 1960**

Life cycle: *P. mollienisicola* - Metacercariae of this species were found encysted in the intestinal wall, gills and muscles of the sailfin molly, *Mollienisia latipinna.* Cysts were fed to hamsters and the adult parasites recovered. Other larval stages and the natural definitive host are unknown (Sogandares-Bernal and Bridgman, 1960).

6b. Circumoral spines present. 7

7a. Vitellaria restricted to testicular region (Fig. 723). .... **Genus *Phagicola* Faust, 1920**

Key to species in Burton (1958).

7b. Vitellaria distributed along lateral regions of hindbody. 8

8a. Ceca short, extend only to level of ventral sucker; uterus confined to hindbody (Fig. 721). .... **Genus *Ascocotyle* Looss, 1899**

Life cycle: *A. pachycystis* - Pleurolophocercous cercariae develop in a redia in the prosobranch, *Littoridinops tenuipes.* After leaving the snail, they penetrate the gills of killifish, *Cyprinodon variegatus,* migrate to the bulbus arteriosus where they encyst and develop in infective metacercariae in about 25 days. The infected bulbus enlarges to about 20 times normal size. The adult parasite develops in the intestine of raccoon (Schroeder and Leigh, 1965).

Ostrowski de Nunez (1976) studied the life cycle of *A. tenuicollis* in Argentina where *Littoridina piscium* is the host snail. Parapleurolophocercous cercariae develop in a redia and following emergence encyst in the bulbus arteriosus of the viviparous top minnow, *Cnesterodon decemmaculatus* in which metacercariea then develop. The latter were fed to a white mouse and adults recovered 3 to 5 days later. The natural definitive hosts are several species of herons.

Partial life cycles are known for *A. branchialis* and for *A. sexidigita* (see Timon-David and Timon-David, 1966; Martin and Steele, 1970).

8b. Ceca long extend to testes; uterus extends into forebody (Fig. 722). .... **Genus *Leighia* Sogandares-Bernal and Lumsden, 1963**

Life cycle: *L. mcintoshi* - Oculate gymnocephalous cercariae with a spiny retractile anterior end and no finfolds on the tail develop in a redia in the prosobranch, *Littoridinops monroensis.* The cercariae are eaten by small fish, *Poecilia latipinna* and *Gambusia affinis.* They penetrate the intestinal wall and finally encyst in the coelom. Adult flukes developed in baby chicks within 48-60 hours after feeding metacercariae (Leigh, 1974).

9a. Circumoral spines present; body convex dorsally; vitellaria in form of rosettes in later regions of body; adults in pairs in cysts in wall of stomach and intes-

tine of birds and mammals (Fig. 724). ....
.... **Genus *Pholeter* Odhner, 1914**

9b. Circumoral spines absent; vitellaria not in form of rosettes; adults not paired in cysts. **10**

10a. Anterior end of body truncate, wider than rest of body; testes and ovary lobed; testes tandem; arms of excretory vesicle extend into anterior part of body and united by several transverse canals in region of gonads (Fig. 725). ....
.... **Genus *Scaphanocephalus* Jagerskiold, 1903**

Life cycle: *S. expansus* - Metacercariae of this species were found in the smalltooth sawfish, *Pristis pectinata* (see Hutton, 1964).

10b. Body not as described above. **11**

11a. Ventral sucker submedian and variably lobed at apex; mouth of ventrogenital sac directed anteriorly. **12**

11b. Ventral sucker median and not lobed at apex; mouth of ventrogenital sac not directed anteriorly. **13**

12a. Vitelline follicles confined to hindbody; testes oblique; oral sucker subterminal; esophagus twice length of pharynx (Fig. 726). ....
.... **Genus *Metagonimus* Katsurada, 1913**

Life cycle: *M. yokogawai* - Although this genus is not represented in North America, it is included because of its importance as a parasite of human beings and some domestic animals in the Far East. Embryonated eggs are ingested by the snail, *Semisulcospira libertina* in which the miracidium hatches and changes to a sporocyst which in turn produces two generations of rediae. Pleurolophocercous cercariae develop in daughter rediae. After leaving the snail, they encyst beneath the skin of numerous species of freshwater fishes. The adult parasite inhabits the small intestine of cat, dog, pig and human beings.

12b. Vitelline follicles in fore- and hindbody; testes opposite; oral sucker terminal; esophagus very short or absent (Fig. 727). ....
.... **Genus *Metagonimoides* Price, 1931**

Life cycle: *M. oregonensis* - Miracidia develop within 23 days after eggs are laid. Pleurolophocercous cercariae develop in rediae in several species of prosobranch snails of the genus *Goniobasis.* Cercariae can either remain in the redia and develop to infective metacercariae or they can leave the redia and the snail and encyst in tadpoles of frogs, toads and salamanders where they then develop to metacercariae. Experimental infections have been established in hamsters but the natural definitive host is the raccoon (Ingles, 1935; Burns and Pratt, 1953; Lang and Gleason, 1967).

13a. Gonotyl postero-sinistral to ventral sucker and armed with rows of fine spines; gonotyl envelops genital pore (Fig. 728). .... **Genus *Heterophyes* Cobbold, 1886**

Life cycle: *H. heterophyes* - The genus is not represented in North America but is included because of its importance as a parasite of human beings in the Far East. The life cycle is very much like that of *Metagonimus yokogawai.* The host snails are *Pirenella conica* and *Tympanotomus microptera* which ingest the embryonated eggs. Pleurolophocercous cercariae develop and encyst in several species of fish. The adult stage develops in the small intestine of cat, dog and human being. Metacercariae and developing adults of *H. heterophyes* and *Metagonimus yokogawai* sometimes invade the intestinal mucosa, enter branches of the mesenteric blood vessels and are carried to the central nervous system and the heart where they clog blood vessels.

13b. Gonotyl without spines; genital pore usually outside of gonotyl. **14**

14a. Oral sucker with dorsal lip set off by a transverse groove; anterior wall of gonotyl provided with pockets or invaginations; vitelline follicles large, lateral to ceca; testes opposite (Fig. 729). ....
.... **Genus *Phocitrema* Goto and Ozaki, 1930**

14b. Oral sucker without dorsal lip; gonotyl without invaginations; vitelline follicles small. **15**

15a. Body linguiform; ventrogenital sac with suckerlike anterior pocket; ventral sucker small, embedded in gonotyl and in form of a nucleated knob (Fig. 730). ......
.... **Genus *Cryptocotyle* Lühe, 1899**

Key to species in Skrjabin (1964).

Life cycle: *C. lingua* - Several days are required for development of the miracidium after eggs are laid. Pleurolophocercous cercariae develop in rediae in the marine prosobranch snail, *Littorina littorea* and after leaving the snail, encyst in the subcutaneous connective tissue of cunners. Accumulation of black pigment in the cyst capsule results in "black spot" disease. The adult parasite develops in several species of piscivorous birds as well as in cat, dog and rat (Stunkard, 1930).

Ching (1978) reported new hosts for this species in British Columbia. The host snail is *Littorina scutulata.* Metacercariae developed in the sculpins, *Leptocottus armatus* and *Oligocottus maculosus* and in the starry flounder, *Platichthys stellatus.* Adults were recovered from the gull, *Larus glaucescens.*

15b. Body not linguiform; ventrogenital sac without suckerlike anterior pocket; ventral sucker muscular. ... **16**

16a. Ventral sucker armed with spines or sclerites. **17**

16b. Ventral sucker unarmed. **19**

17a. Seminal vesicle thin-walled, bi- or tripartite; ventral sucker armed with large spines or sclerites (Fig. 731, 732, 733). .... **Genus *Stictodora* Looss, 1899**

Life cycle: *S. cursitans* - Parapleurolophocercous cercariae (= *C. cursitans)* develop in rediae in the prosobranch, *Cerithidia scalariformis.* Metacercariae develop in three species of killifish of the genus *Fundulus.* Experimental infections were established by feeding metacercariae to mice, the adult flukes developing in six days. Natural definitive hosts are rice rats, opossum and raccoon (Holliman, 1961; Kinsella and Heard, 1974).

Martin (1950c) reported the life cycle of *S. hancocki* (= *Parastictodora hancocki).* Parapleurolophocercous cercariae develop in rediae in *Cerithidia californica.* Metacercariae were found in the California killifish, *Fundulus parvipinnis* and in the mudsucker, *Gillichthys mirabilis.* Experimental infections were established in baby chicks after feeding metacercariae. The natural definitive host is unknown.

17b. Seminal vesicle has thick wall; ventral sucker armed with numerous small spines. **18**

18a. Gonotyl present; envelops genital pore; hermaphroditic duct (= genital sinus) short; seminal vesicle bipartite (Fig. 734, 735). ....
.... **Genus *Galactosomum* Looss, 1899**

Key to species in Pearson (1973).

Life cycle: *G. timondavidi* - Monostomate, oculate cercariae with a very long tail without finfolds develop in rediae in the marine prosobranch, *Cerithium mediterraneum.* After leaving the snail, the cercariae encyst in the brain of mullet, *Mugil auratus* and in pipefish, *Syngnathus abaster.* The definitive host is the herring gull, *Larus argentatus* which ingests the infected fishes (Prevot, 1973).

(Continued)

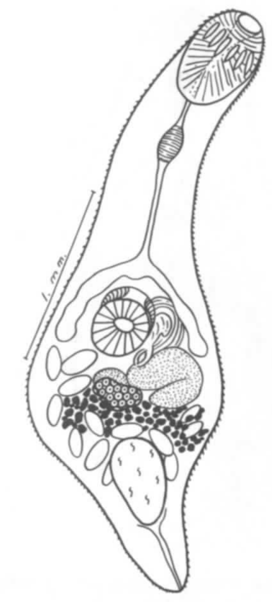


Fig. 715. *Pygidiopsoides spindalis.* (from Martin, 1951)

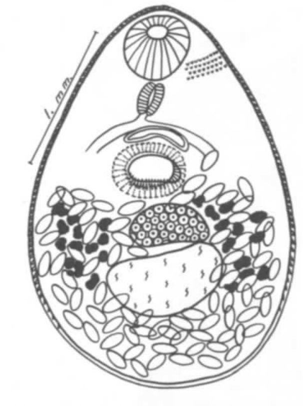


Fig. 716. *Phocitremoides ovale.*

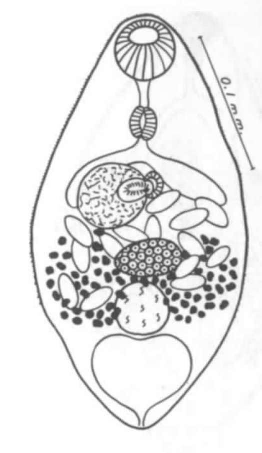


Fig. 717. *Euhaplorchis californiensis.*

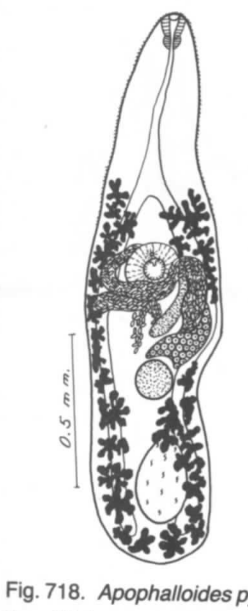


Fig. 718. *Apophalloides pyriformis.* (from Webster and Wolfgang, 1956)

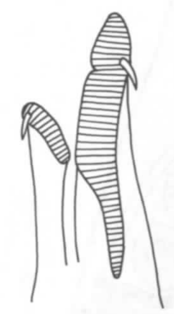


Fig. 719. *Ascocotyle angrense*, oral sucker, lateral view.

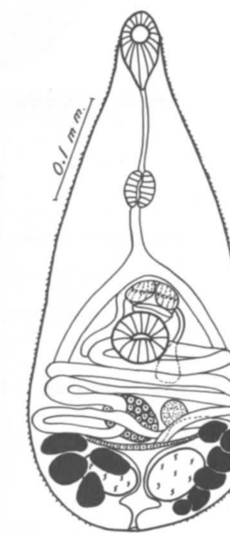


Fig. 720a. *Pseudascocotyle molliensicola.* (from Sogandares-Bernal and Bridgman, 1960)

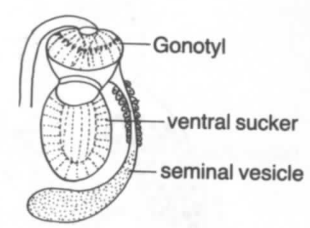


Fig. 720b.

Fig. 721b. Oral sucker lateral view.

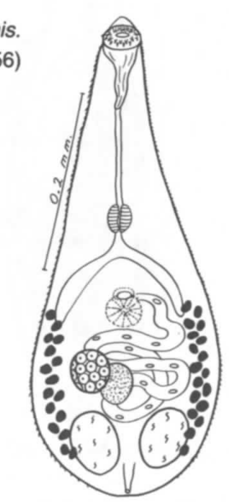


Fig. 721a. *Ascocotyle* sp.

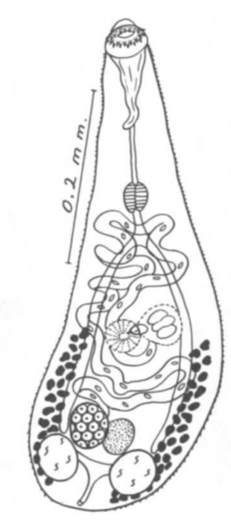


Fig. 722. *Leighia* sp.

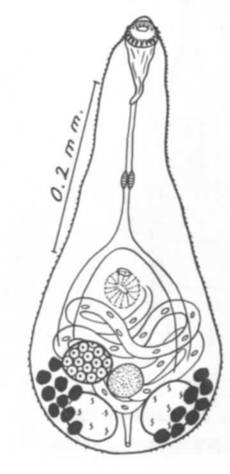


Fig. 723. *Phagicola* sp.

Fig. 724. *Pholeter gastrophilus.* (from Pearson and Courtney, 1977).

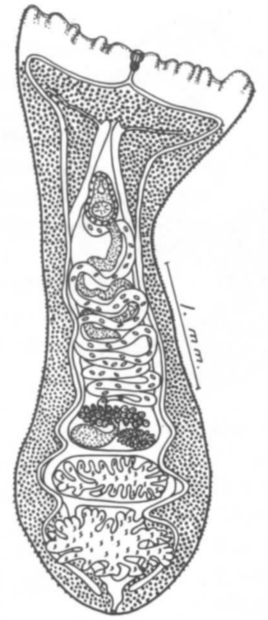


Fig. 725. *Scaphanocephalus expansus.*

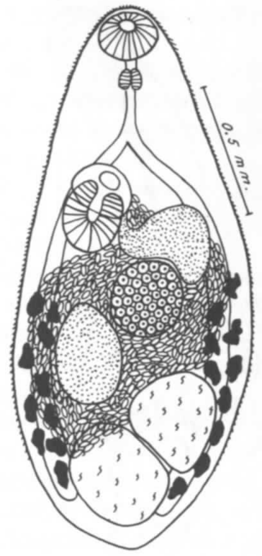


Fig. 726a. *Metagonimus yokogawai.*

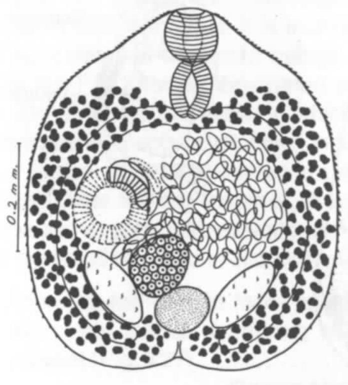


Fig. 727. *Metagonimoides oregonense.*

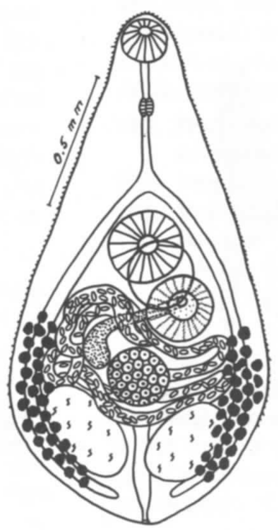


Fig. 728. *Heterophyes heterophyes.*

Fig. 726b. ventral sucker, lateral view

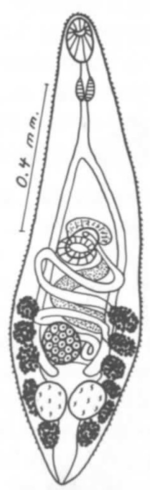


Fig. 729. *Phocitrema fusiforme.* (from Pearson and Courtney, 1977).

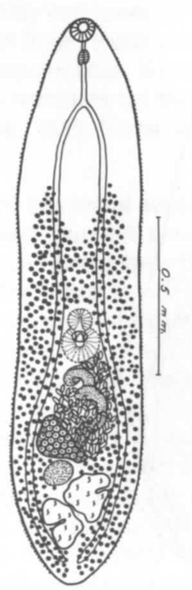


Fig. 730a. *Cryptocotyle lingua.*

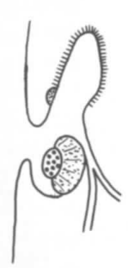


Fig. 730b. ventrogenital sac, sagittal section

Fig. 731a. *Stictodora cursitans.* (from Kinsella and Heard, 1974).

Fig. 731b. ventrogenital sac

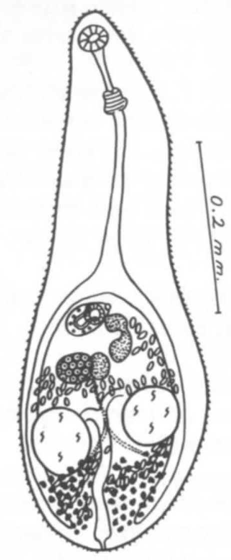


Fig. 732. *Stictodora hancocki.* (from Martin, 1950)

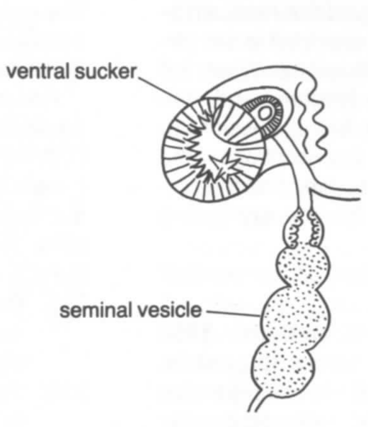


Fig. 733. *Stictodora caballeroi*

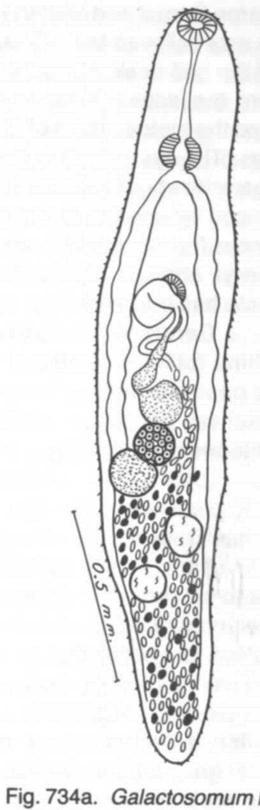


Fig. 734a. *Galactosomum humbargari.* (from Park, 1936)

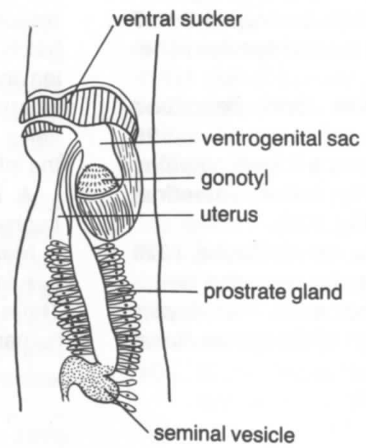


Fig. 734b. ventrogenital sac

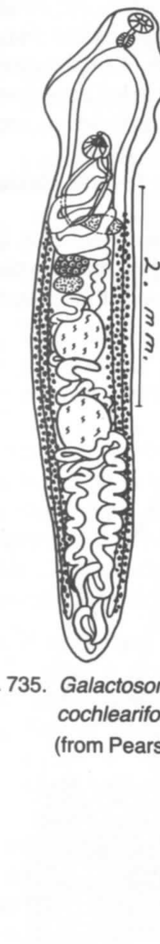


Fig. 735. *Galactosomum cochleariformum.* (from Pearson, 1973)

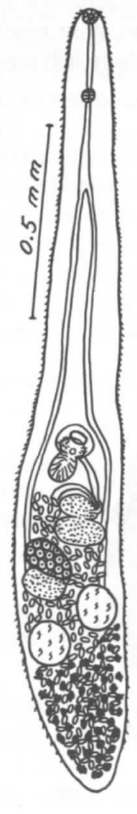


Fig. 736a. *Neostictodora nuttoni.*

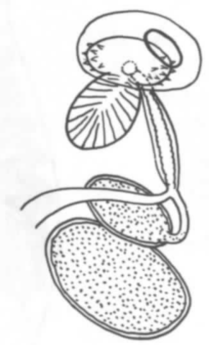


Fig. 736b. ventrogenital sac

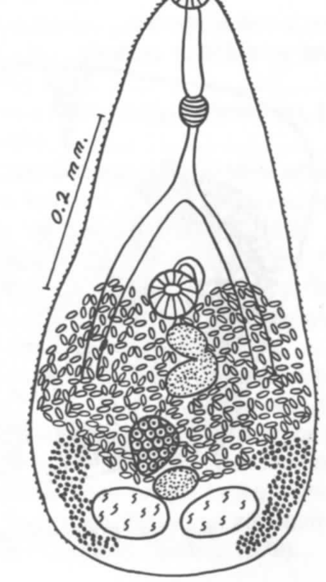


Fig. 737. *Pygidiopsis plana.* (from Linton, 1928).

Sogandares-Bernal and Hutton (1960) found the metacercaria of what was believed to be *G. spinetum* encysted in the visceral fat of the half beak, *Hyporhampus unifasciatus.* When fed to hamsters the adults failed to develop. Madhavi and Rao (1968) found the metacercaria of *G. puffini* in four species of clupeoid fishes. The cysts were in the wall of the esophagus, the adult is a parasite of gulls. Cable (1956b) proposed that the cercaria produced by species in this genus is the nonaggregating magnacercous (opisthorchioid) type.

18b. Gonotyl absent; hermaphroditic duct long; seminal vesicle has thin wall (Fig. 736). .... Genus *Neostictodora* Sogandares-Bernal, 1959

19a. Vitelline follicles confined to areas lateral to gonads, near posterior end of body; seminal vesicle bipartite; genital sac present, contains genital pore and weakly developed gonotyl (Fig. 737). .... Genus *Pygidiopsis* Looss, 1907

Life cycle: *P. pindoramensis* - The work was done in Argentina where the host snail is *Littoridina piscium.* Pleurolophocercous cercariae develop in a redia and after emerging, encyst in the gill filaments and mesenteries of the viviparous top minnow, *Cnesterodon decemmaculatus* where metacercariae develop. The latter were fed to a white mouse and adults developed 3 to 5 days later. The natural definitive hosts are several species of herons (Ostrowski de Nunez, 1976).

19b. Vitelline follicles more extensive than described above; gonotyl well developed. 20

20a. Body rectangular or pyriform; testes lobed; vitelline follicles in both fore- and hindbody; usually intestinal parasites in mustelid mammals (Fig. 738). .... Genus *Euryhelmis* Poche, 1926

Life cycle: *E. monorchis* - Pleurolophocercous cercariae develop in rediae in the freshwater prosobranch snail, *Pomatiopsis lapidaria* and encyst in tadpoles and frogs of the genus *Rana.* The natural definitive host is mink. Experimental infections were established in cats and rats, the parasite attaining sexual maturity in one week (Ameel, 1938).

Anderson and Pratt (1965) investigated the life cycle of *E. squamula.* Pleurolophocercous cercariae develop in rediae in *Bythinella hemphilli* and encyst under the skin of frogs of the genera *Rana and Ascaphus* and also in the newt, *Triturus cristatus.* Experimental infections were established in cats and hamsters. Raccoon and mink serve as natural definitive hosts in North America.

20b. Body not rectangular, either oval or pyriform; testes oval or round; parasitic in birds or in mammals other than mustelids. 21

21a. Testes opposite; seminal vesicle bipartite; vitelline follicles in fore- and hindbody; intestinal parasites of marine mammals (Fig. 739). .... Genus *Pricetrema* Ciurea, 1933

21b. Testes oblique or tandem; seminal vesicle unipartite; vitelline follicles confined to hindbody; intestinal parasites in birds and mammals (Fig. 740). .... Genus *Apophallus* Lühe, 1909

Life cycle: *A. venustus* - Embryonated eggs are eaten by the prosobranch snail, *Goniobasis livescens* in which the miracidia hatch. Pleurolophocercous cercariae develop in rediae and after leaving the snail, penetrate several species of freshwater fish where they encyst in muscles and skin. The adult parasites develop in cat, dog, raccoon and great blue heron which acquire the infection by eating infected fish (Cameron, 1937).

A. brevis causes "black spot" disease in several species of freshwater fishes.

Niemi and Macy (1974) reported the development of *A. donicus* in human volunteers who had been fed metacercariae. There have been other reports of infection with this species in human beings where fish are eaten raw.

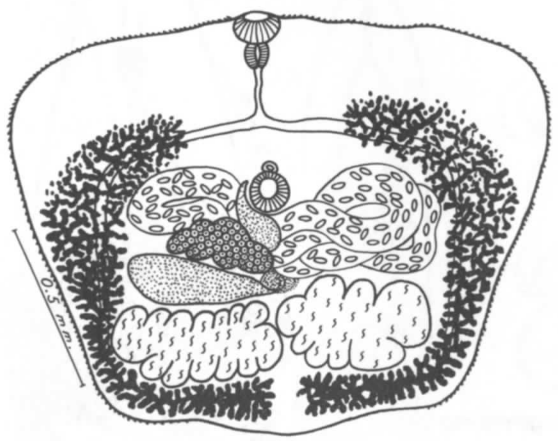


Fig. 738. *Euryhelmis squamula.*

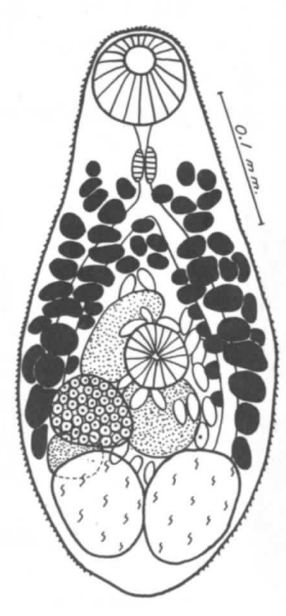


Fig. 739. *Pricetrema zalophi.*

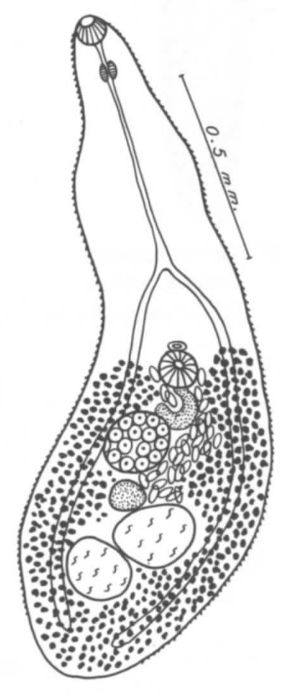


Fig. 740. *Apophallus brevis.*

Family Cryptogonimidae Ciurea, 1933

Body variable in shape; eyespots present in some genera; oral sucker terminal or not; circumoral spines present in some genera; ventral sucker usually enclosed in a ventro genital sac along with one or more gonotyls; pharynx present; ceca usually long; testes opposite, oblique or tandem (nine testes in *Siphodera*) cirrus sac absent; seminal vesicle free in parenchyma, usually bipartite; hermaphroditic duct present, opens into ventro genital sac; ovary lobed or follicular, pretesticular or intertesticular; vitelline follicles distributed along ceca; uterus confined to hindbody, extends posterior to testes; eggs operculate, embryonated, some have polar filaments; arms of excretory vesicle extend forward to level of pharynx; parasitic in intestine of fishes.

Key to Genera

1a. Oral sucker with large circumoral spines; testes opposite. 2

1b. Oral sucker without circumoral spines. 4

2a. Ovary follicular; vitelline follicles lateral to ovary and testes; intestinal parasites of freshwater fishes (Fig. 741). .... Genus *Neochasmus* Van Cleave and Mueller, 1932

2b. Ovary single, lobed. 3

3a. Ovary a transverse lobed mass; vitelline follicles along ceca between level of ovary and seminal vesicle which is some distance anterior to ventral sucker; parasitic in freshwater fishes (Fig. 742). .... Genus *Allacanthochasmus* Van Cleave, 1922

3b. Ovary a rounded lobed mass; vitelline follicles lateral to ovary and overlapping testes; seminal vesicle posterior to ventral sucker parasitic in marine fishes (Fig. 743). .... Genus *Paracryptogonimus* Yamaguti, 1934

4a. Nine testes, arranged in two longitudinal rows (5 and 4); vitelline follicles lateral to ceca, between ventral sucker and testes (Fig. 744). .... Genus *Siphodera* Linton, 1910

Life cycle: *S. vinaledwardsii* - Pleurolophocercous cercariae develop in a redia in the marine prosobranch snail, *Bittium alternatum.* They encyst in the fins and body wall of summer flounder, *Paralichthys dentatus.* The adult fluke develops in the intestine of the toadfish, *Opsanus tau* and in the pigfish, *Orthopristis chrysopterus* (see Cable and Hunninen, 1941, 1942b).

4b. Two testes. 5

5a. Testes opposite. 6

5b. Testes tandem or oblique. 11

6a. Testes elongate, lobed, close to posterior end of body; ventral sucker submedian; seminal vesicle long; parasite in ovary of catfish (Fig. 745). .... Genus *Acetodextra* Pearse, 1924

Life cycle: *A. ameiuri* - Some adult worms have been found in the swim bladder but the normal habitat is thought to be the ovary. Gravid worms retain eggs until they leave the host with fish eggs at spawning time.

6b. Testes round or oval and some distance from posterior end of body; ventral sucker median; parasitic in intestine of fishes. 7

7a. Oral sucker terminal, large, either funnel-shaped or oval. 8

7b. Oral sucker subterminal, ventral, round. 10

8a. Vitelline follicles in narrow lateral rows along ceca between ovary and ventral sucker; oral sucker oval; body with rows of scale-like spines; muscular pad immediately anterior to ventral sucker (Fig. 746). .... Genus *Cryptogonimus* Osborn, 1903

Life cycle: *C. spinovum* - Embryonated eggs are eaten by the prosobranch snail, *Cincinatia peracuta* in which pleurolophocercous cercariae develop in rediae. They encyst in the tissues of freshwater fishes such as *Micropterus salmoides* and *Elassoma zonatum* and three species of *Lepomis.* The definitive hosts are *M. salmoides* and *M. punctulatus* (see Greer and Corkum, 1979).

8b. Vitelline follicles in small clusters, lateral to pharynx; oral sucker funnel- or cup-shaped. 9

9a. Two ventral suckers present in tandem; ovary trilobed; ceca short and inflated (Fig. 748). .... Genus *Turgecaecum* Sullivan, 1975

9b. One ventral sucker present; ovary not trilobed; ceca short but not inflated (Fig. 747). .... Genus *Caecincola* Marshall and Gilbert, 1905

Life cycle: *C. parvulus* - Embryonated eggs are eaten by the freshwater prosobranch snail, *Amnicola histrica* in which pleurolophocercous cercariae develop in rediae. The cercariae encyst in the skin of several species of centrarchid and cyprinid fishes. Metacercariae are infective in about three weeks. The adult parasites develop in the pyloric ceca and intestine of largemouth and smallmouth bass (Lundahl, 1941).

Greer and Corkum (1979) studied the life cycle of *C. latostoma* which utilizes the prosobranch snail, *Cincinatia peracuta.* Pleurolophocercous cercariae encyst in the muscles of *Micropterus salmoides, Elassoma zonatum* and *Lepomis* spp. Metacercariae were fed to *M. salmoides* and *M. punctulatus* which serve as definitive hosts.

10a. Body fusiform; ovary pretesticular; suckers about equal in size (Fig. 749). .... Genus *Centrovarium* Stafford, 1904

10b. Body broadly oval; ovary intertesticular; oral sucker larger than ventral sucker (Fig. 750). .... Genus *Metadena* Linton, 1910

Key to species in Skrjabin (1964).

11a. Ten or eleven muscular, lip-like gonotyls in linear series anterior to ventral sucker; vitelline follicles in lateral clusters in forebody (Fig. 751). .... Genus *Multigonotylus* Premvati, 1967

11b. Gonotyl single, knob-like. 12

12a. Oral sucker terminal, saucer-shaped; gonotyl without large spines; vitelline follicles confined to hindbody; ovary round; parasitic in marine fishes (Fig. 752). .... Genus *Claribulla* Overstreet, 1969

12b. Oral sucker subterminal; gonotyl has several large spines; vitelline follicles confined to forebody; ovary lobed; parasitic in freshwater fishes (Fig. 753). .... Genus *Textrema* Dronen, Underwood and Suderman,1977

Life cycle: *T. hopkinsi* - Embryonated eggs are eaten by the prosobranch snail, *Cincinatia peracuta* in which pleurolophocercous cercariae develop in rediae. They encyst in the muscles, skin and fins of *Micropterus salmoides, Elassoma zonatum* and in two species of *Lepomis* (see Greer and Corkum, 1979).

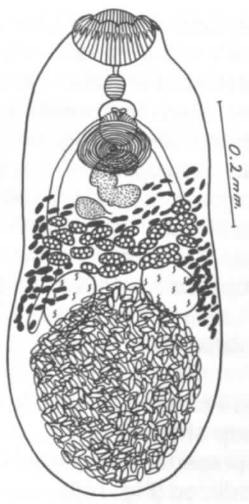


Fig. 741. *Neochasmus umbellus.*
(from Van Cleave and Mueller, 1932).

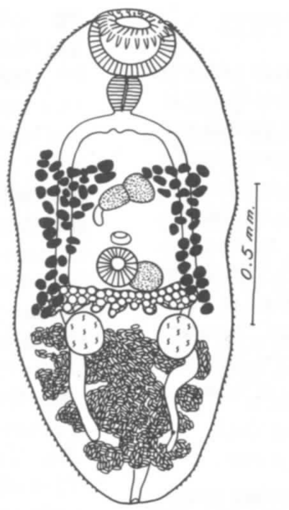


Fig. 742. *Allacanthochasmus varius.*
(from Van Cleave, 1922)

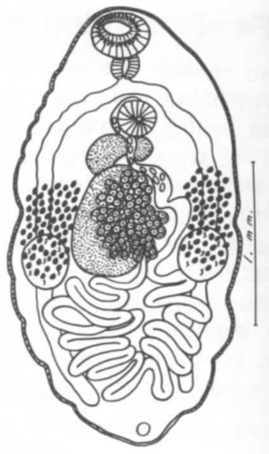


Fig. 743. *Paracryptogonimus americanus.*

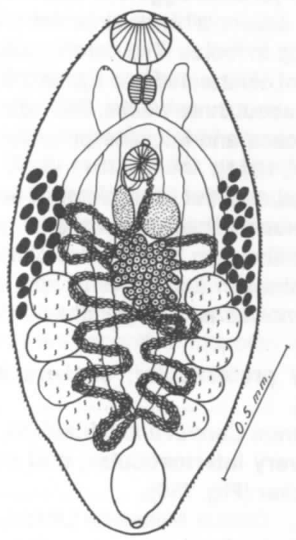


Fig. 744. *Siphodera vinaledwardsii.*

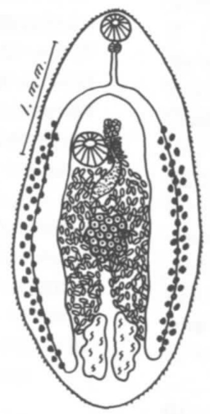


Fig. 745. *Acetodextra ameiuri.*

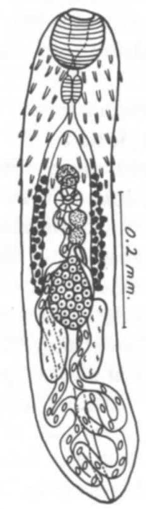


Fig. 746a. *Cryptogonimus chyli.*


Fig. 746b. ventrogenital sac

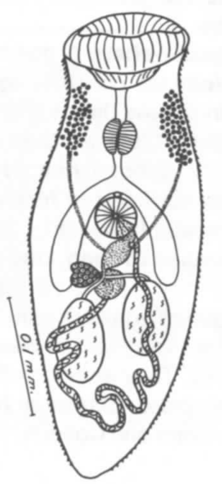


Fig. 747. *Caecincola parvulus.*
(from Marshall and Gilbert, 1905).

Fig. 748a. *Turgecaecum longifauces.*
(from Sullivan, 1975).

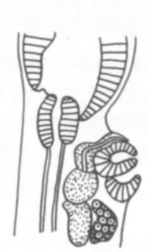


Fig. 748b. Sagittal section of ventral suckers

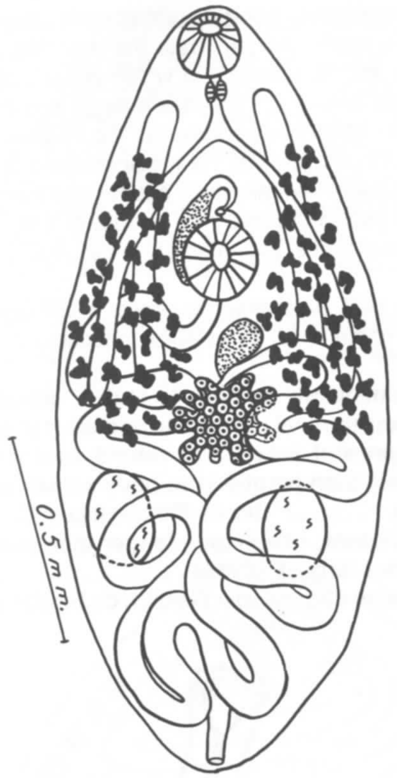


Fig. 749. *Centrovarium lobates.*

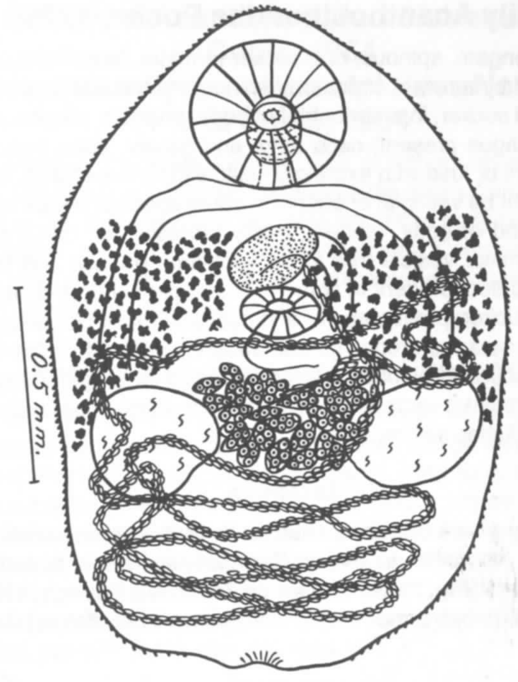


Fig. 750. *Metadena crassulata.*

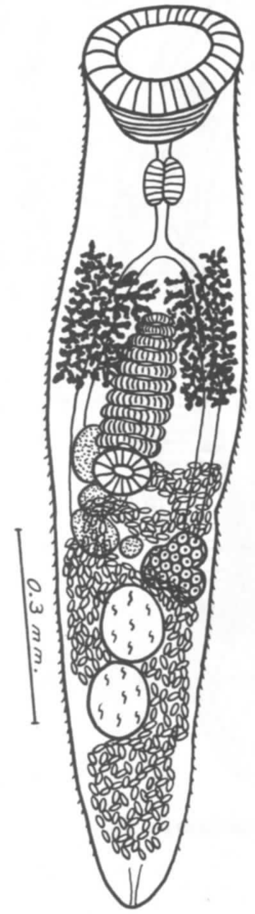


Fig. 751. *Multigonotylus micropteri.*

Fig. 752. *Claribulla longula.* (from Overstreet, 1959).

Fig. 753. *Textrema hopkinsi.*

Family Acanthostomidae Poche, 1926

Body elongate, spinous; oral sucker terminal, funnel-shaped, surrounded by a row of circumoral spines; ventral sucker smaller than oral sucker, in anterior half of body; pharynx, prepharynx and esophagus present; ceca long, end blindly, open through separate ani or fuse with excretory vesicle to form a cloaca; one cecum might be vestigial or absent in some species; testes near posterior end of body, tandem; ovary pretesticular; cirrus sac absent; seminal vesicle free in parenchyma; gonotyl and hermaphroditic duct present in some species; genital pore anterior to ventral sucker; preacetabular and postacetabular pits present in some genera; ventrogenital sac absent; vitelline follicles lateral, along ceca in hindboy; uterus pretesticular; eggs embryonated, operculate; excretory vesicle Y- or V-shaped; parasitic in intestine of fishes and reptiles.

Key to Genera

1a. Ovary some distance anterior to testes; some uterine folds posterior to ovary; Seminal receptacle anterior to ovary (Fig. 754). ... Genus *Timoniella* Rebecq, 1960

Life cycle: *T. imbutiforme* (= *Acanthostomum imbutiforme*) -The adult parasite inhabits the intestine of the marine bass, *Morone labrax.* Miracidia hatch and penetrate the prosobranch snails, *Hydrobia acuta* and *H. ventrosa* in which pleurolophocercous cercariae develop in rediae. Cercariae emerge and then encyst in the muscles of small marine fishes of the families Gobiidae, Mugilidae and Atherinidae. As the metacercariae develop the circumoral spines and ventral sucker appear and the pigmented eyespots and glands of the cercariae disappear. *Morone labrax,* the definitive host, eats the infected small fishes (Maillard, 1973).

The life cycle of *T. praeteritum* is similar, involving the same hosts but the cercaria is parapleurolophocercous (Maillard, 1974).

1b. Ovary immediately anterior to testes; uterus entirely preovarian; seminal receptacle posterior to ovary. . 2

2a. Gonotyl present anterior to ventral sucker; esophagus shorter than prepharynx; body spines very small (Fig. 755). .... Genus *Proctocaecum* Baugh, 1957

2b. Gonotyl absent; esophagus longer than prepharynx; body spines large (Fig. 756). .... Genus *Caimanicola* Teixeira de Freitas and Lent, 1938

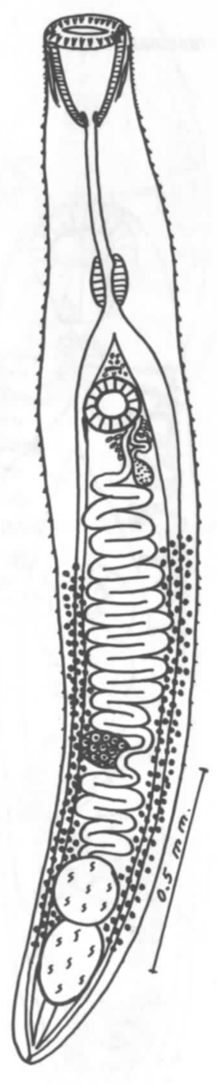


Fig. 754. *Timoniella loossi.*

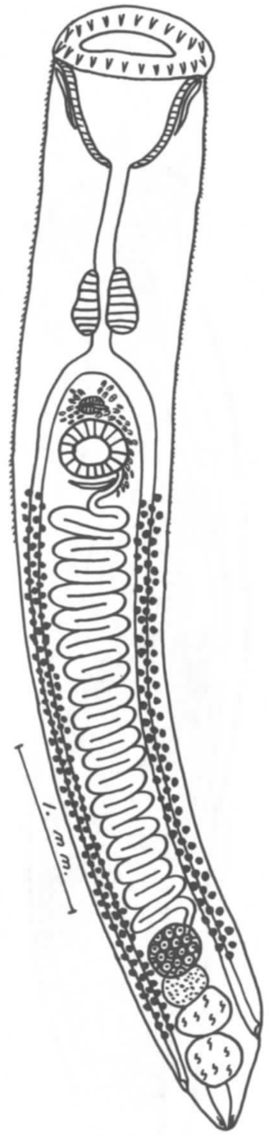


Fig. 755. *Proctocaecum coronarium.* (from Brooks and Overstreet, 1977)

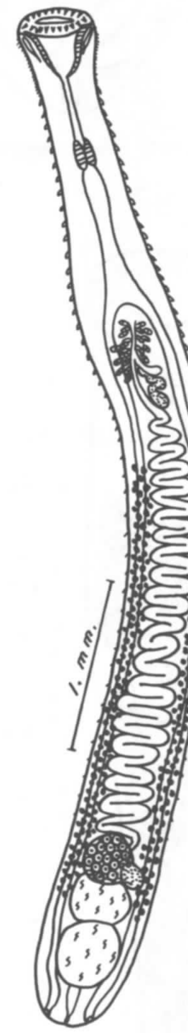


Fig. 756. *Caimanicola pavida.*

Family Pachytrematidae Baer, 1944

Body flat, broadly oval, nonspinous; suckers equal, close to anterior end of body, pharynx very small; ceca long; testes opposite, in posterior fourth of body; cirrus sac absent; seminal vesicle free in parenchyma; genital pore median, between suckers; ovary median, intertesticular or slightly posttesticular; vitelline follicles in clusters lateral to ceca; uterus very long with many transverse folds, confined to hindbody; eggs operculate, embryonated; parasitic in the gall bladder of bile duct of reptiles, birds and mammals.

The family contains only the genus *Pachytrema* Looss, 1907 which is represented in North America by *P. sanguineum* (Fig. 757). Key to species in Skrjabin (1964).

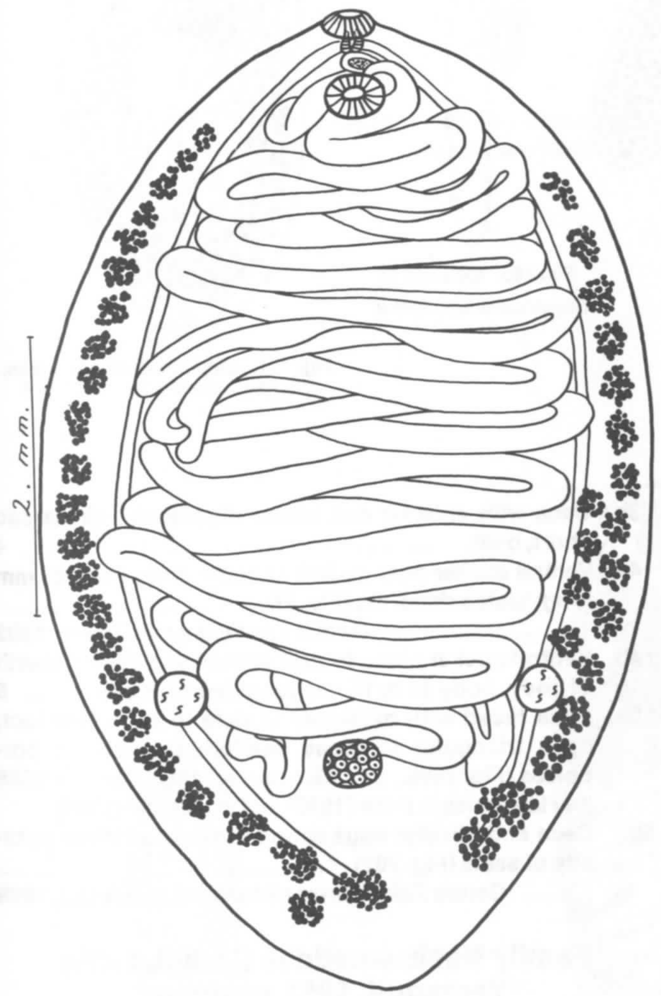


Fig. 757. *Pachytrema sanguineum.* (from Linton, 1928).

Suborder Acanthocolpiata Nahhas and Cable, 1964
Superfamily Acanthocolpioidea Nahhas and Cable, 1964

Cercariae distomate, oculate, with or without stylet; tail simple, with or without finfolds; protonephridia stenostomate, excretory pores on sides of tail well removed from body-tail junction; excretory vesicle Y-shaped with cellular wall. Cercariae develop in a redia in prosobranch snails; metacercariae encysted in fishes. Life cycle involves three hosts.

Family Acanthocolpidae Lühe, 1902

Body elongate, cuticle densely spinous, large circumoral spines in some genera; eyespots in young adults; ventral sucker in anterior half of body; pharynx present; ceca long, end blindly or fuse with excretory vesicle to form uroproct; testes tandem, in hindbody; cirrus sac present; ovary pretesticular; hermaphroditic duct present, not enclosed in a sac; genital pore anterior to ventral sucker; vitelline follicles restricted to hindbody, confluent posterior to testes; uterus preovarian; eggs operculate, embryonated; parasitic in intestine of fishes.

Key to Genera

1a. Circumoral spines absent; suckers small; ceca united with excretory vesicle to form uroproct (Fig. 758)........... .... Genus *Tormopsolus* Poche, 1926

Key to species in Skrjabin (1964).

1b. One or two rows of circumoral spines present. 2

2a. Circumoral spines in a single row; arms of excretory vesicle divided to form two convoluted tubes on each side of body; ventral sucker very close to oral sucker (Fig. 759). .... Genus *Manteria* Caballero, 1950

2b. Circumoral spines in two uninterrupted rows; arms of excretory vesicle not divided in each side of body (Fig. 761). .... Genus *Stephanostomum* Looss, 1899

Key to species in Manter and Van Cleave (1951) and in Caballero (1952).

Life cycle: *S. tenue* - Oculate xiphidiocercariae (Fig. 760) with a spiny body and cellular excretory vesicle develop in rediae in the marine prosobranch snail, *Nassa obsoleta.* After leaving the snail, they are eaten by the silverside, *Menidia notata* in which they encyst. Metacercariae were fed to Northern puffer, *Sphaeroides maculatus* and the adult flukes recovered. The natural definitive host is the striped bass, *Roccus saxatilis* (see Martin, 1939a).

Stunkard (1961) described the life cycle of *S. dentatum.* The cercaria is probably *Cercaria dipterocerca* which differs from other cercariae reported for the genus *Stephanostomum* in having lateral and ventral finfolds on the tail.

Mac Kenzie and Liversidge (1975) investigated the life cycle of *S. baccatum.* The cercaria is *C. neptunae* and the host snails are *Buccinum undatum* and *Neptunea antigua.* Cercariae encyst in plaice, *Pleuronectes platessa* and in common dabs, *Limanda limanda.* The adult is a parasite of several marine carnivorous fishes.

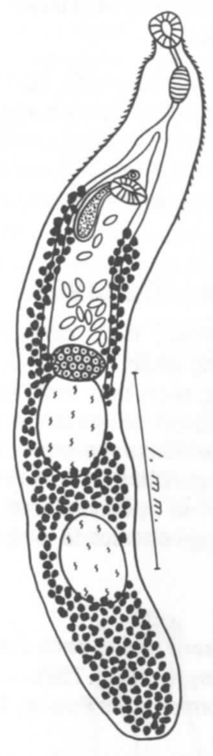


Fig. 758. *Tormopsolus lintoni.* (from Caballero, 1952).

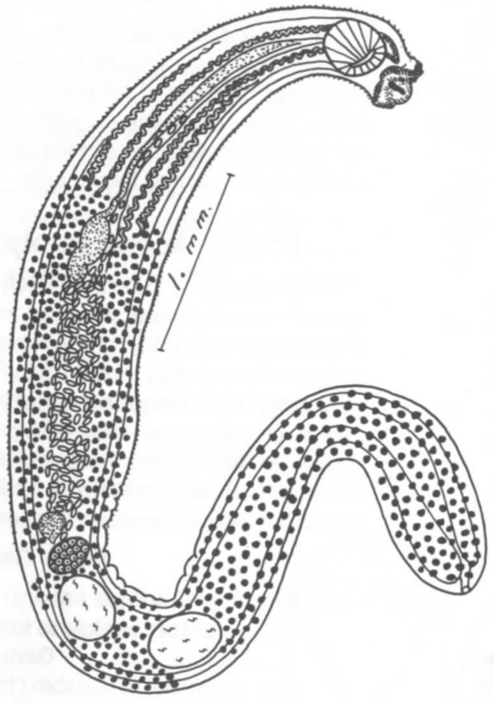
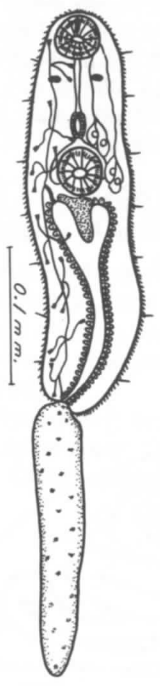


Fig. 759. *Manteria brachyderus.* (from Manter, 1940).



Figl 760. Cercaria of *Stepanostomum tenue.*

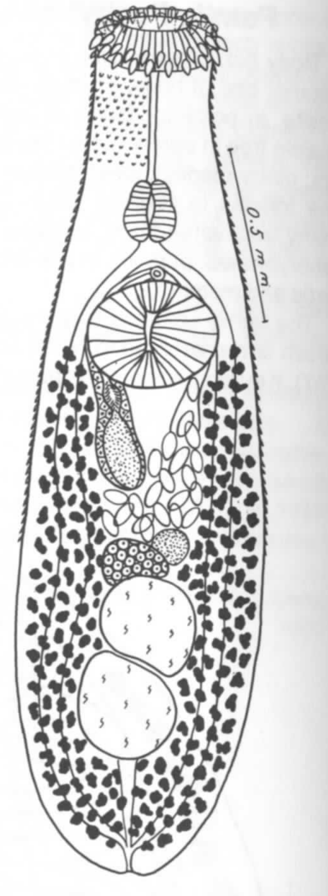


Fig. 761. *Stephanostomum casum.*

Family Campulidae Odhner, 1926

Body large, elongate, spinous; suckers about equal; pharynx present; Ceca long, with or without diverticula, either open through separate ani posteriorly or fuse with excretory vesicle to form uroproct; testes tandem, in hindbody; cirrus sac present; genital pore median, anterior to ventral sucker; ovary pretesticular; vitellaria follicular or in the form of rosettes, distributed along ceca in fore- and hindbody or confined to hindbody; uterus entirely preovarian; eggs usually triangular in cross section; excretory vesicle tubular; parasitic in bile duct and small intestine of marine mammals.

Key to Genera

1a. Ceca with a pair of anterior diverticula but no lateral diverticula. **2**

1b. Ceca without diverticula of any kind or with both anterior and lateral diverticula. **3**

2a. Vitellaria in form of rosettes and restricted to posttesticular region of body; body large (30 to 60mm); testes oval (Fig. 762). .... **Genus** *Hadwenius* **Price, 1932**

2b. Vitellaria follicular, in fore- and hindbody; body less than 15 mm long; testes lobed (Fig. 763). ....
.... **Genus** *Orthosplanchnus* **Odhner, 1905**

3a. Ceca without diverticula; vitelline follicles confined to hindbody; testes lobed; cirrus sac long, extending some distance posterior to ventral sucker (Fig. 764).
.... **Genus** *Synthesium* **Stunkard and Alvey, 1930**

3b. Ceca with anterior and lateral diverticula; cirrus sac short, oval. **4**

4a. Ventral sucker near middle of body; body 25 to 45 mm long; testes dendritic (Fig. 765). ....
.... **Genus** *Lecithodesmus* **Braun, 1902**

4b. Ventral sucker close to oral sucker, in anterior fourth of body; body 10 to 15 mm long; testes lobed. **5**

5a. Ceca fused with excretory vesicle to form uroproct; eggs triangular in cross section; parasite of porpoises (Fig. 768). ...... **Genus** *Campula* **Cobbold, 1858**
Key to species in Price (1932) and in Skrjabin (1964).

5b. Ceca end blindly; eggs round in cross section; parasite of seals (Fig. 767). ....
.... **Genus** *Zalophotrema* **Stunkard and Alvey, 1929**

Family Nasitrematidae (Ozaki, 1935) Yamaguti, 1951 *emended*

Body elongate, spinous; suckers subequal; ventral sucker in anterior fifth of body; pharynx present; ceca long, serpentine, without branches; testes lobed or dendritic, tandem, in hindbody; cirrus sac absent; seminal vesicle and prostate gland free in parenchyma; genital pore median, anterior to ventral sucker; ovary lobed, pretesticular; vitelline follicles restricted to hindbody; uterus preovarian; eggs triangular in cross section; excretory vesicle tubular; parasitic in nasal cavities of whales.

Two species of the genus *Nasitrema* Ozaki, 1935 have been reported in North America (Fig. 766).

Fig. 762. *Hadwenius seymouri.*

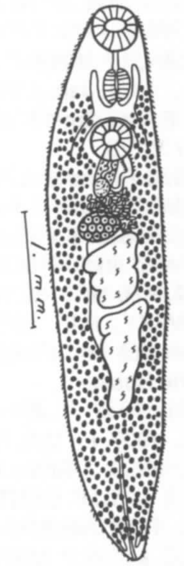


Fig. 763. *Orthosplanchnus arcticus.* (from Price, 1932).

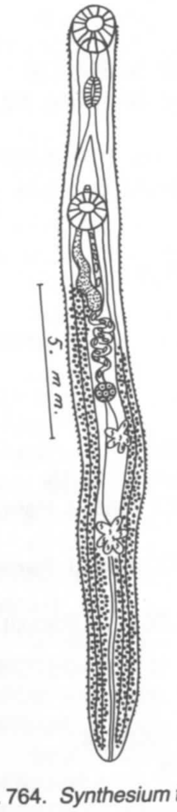


Fig. 764. *Synthesium tursionis.* (from Price, 1932).

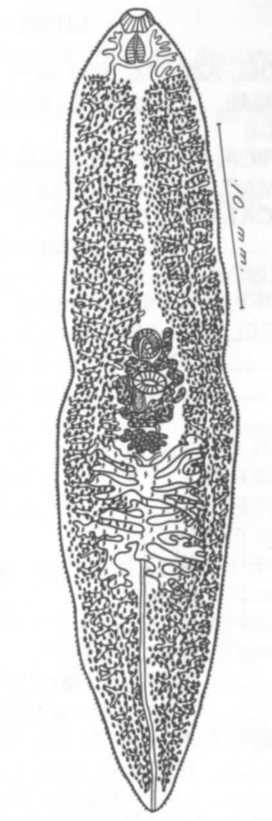


Fig. 765. *Lecithodesmus spinosus.* (from Margolis and Pike, 1955)

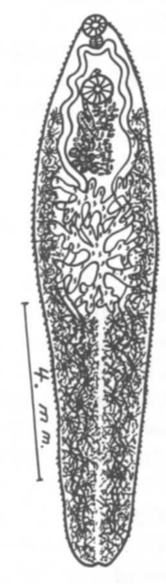


Fig. 766. *Nasitrema globicephalae.*

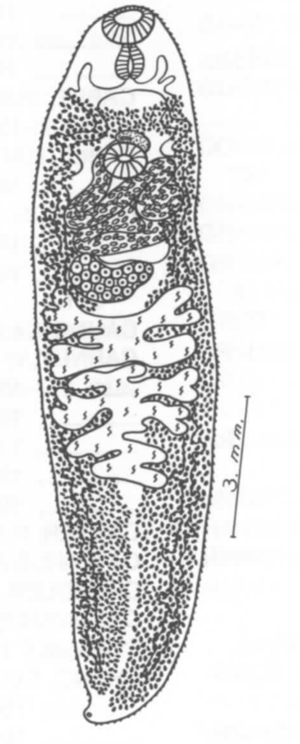


Fig. 767. *Zalophotrema hepaticum.*

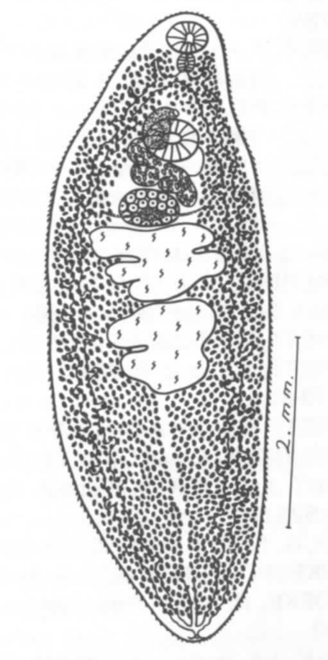


Fig. 768. *Campula oblonga.*

LITERATURE CITED

ABDEL-AZIM, M. 1936. Ann. Trop. Med. Parasit. 30:351-356.
ADAMS, J.E. and W.E. MARTIN 1963. Tr. Am. Micr. Soc. 82: 1-6
AFRICA, C. and E. GARCIA 1935. Philippine J. Sci. 57:253-267.
AHMAD, A.S. and GABRION, C. 1975. Ann. Parasit. 50:17-24.
ALICATA, J.E. 1940. J. Parasit. 26:135-143.
_______, 1962. J. Parasit. 48:47-54.
ALLISON, L.N. 1943. Tr. Am. Micr. Soc. 62:127-168.
ALVEY, C.H. 1936. Parasitol. 28:229-253.
AMEEL, D.J. 1934. Am. J. Hyg. 19:279-317.
_______, 1937, J. Parasit. 23:218-220.
_______, 1938. J. Parasit. 24:219-224.
_______, 1944, J. Parasit. 30:257-263.
AMIN, O. 1982. Pr. Helm. Soc. Wash. 49:196-206.
ANDERSON, G.A. and I. PRATT 1965. J. Parasit. 51:13-15.
ANDERSON, G.A.; G.W. MARTIN and I. PRATT 1966. J. Parasit. 52:704-706.
ANDERSON, G.A.; S.C. SCHELL and I. PRATT 1965. J. Parasit. 51:579-582.
ANDERSON, M.G. and F.M. ANDERSON 1963. J. Parasit. 49:275-280.
_______, 1967. J. Parasit. 53:31-37.
_______, 1969. J. Parasit. 55:452.
ANGEL, L.M. 1954. Tr. Roy. Soc. S. Austral. 77:164-174.
_______, 1960. Libr. Hom. Dr. Caballero. 75-86.
_______, 1967. Parasitol. 57:19-30.
ARVY, L. and A. BUTTNER 1954. C.R. Acad. Sci., Paris 239:1085-1087.
ASHTON, N.; N. BROWN and D. EASTY 1969. J. Small Animal Prac. 10:471-478.
BAKKER, K.E. and C. DAVIDS 1973. J. Helm. 47:269-276.
BANERJEE, A.C. 1965. Am. Midl. Nat. 74:451-456.
BARLOW, C.H. 1925. Am. J. Hyg., Monographic Ser. #4:98 pp.
BARTOLI, P. 1967. Ann. Parasit. 42:605-619.
_______, 1972. Ann. Parasit. 47:193-223.
BASCH, P.F. and R.F. STURROCK 1969. J. Parasit. 55:1180-1184.
BEARUP, A.J. 1956. Parsitol. 46:470-479.
_______, 1960. Austral. J. Zool. 8:217-225.
BEAVER, P.C. 1929. J. Parasit. 16:13-23.
_______, 1937. Ill. Biol. Mongor. 15:96 pp.
_______, 1939a. J. Parasit. 25:269-276.
_______, 1939b. J. Parasit. 25:383-393.
_______, 1941a. J. Parasit. 27:35-44.
_______, 1941b. J. Parasit. 27:347-355.
BECKERDITE, F.W.; G.C. MILLER and R. HARKEMA 1971. Pr. Helm. Soc. Wash. 38:149-156.
BENNETT, H.J. 1935. J. Parasit. 21:83-90.
BENNETT, H.J. and R. ALLISON 1957. Pr. Louis. Acad. Sci. 6:79-80.
BENNETT, H.J. and A.G. HUMES 1939. J. Parasit. 25:223-231.
BENNINGTON, E. and I. PRATT 1960. J. Parasit. 46:91-100.
BIGUET, J.; S. DEBLOCK and A. CAPRON 1956. Ann. Parasit. 31:525-542.
BLAIR, D. 1956. J. Helm. 50:125-132.
BLANKESPOOR, H.D. 1977. Pr. Helm. Soc. Wash. 44:44-50.
BODDEKE, R. 1960. Trop. Geogr. Med., Amsterdam 12:263-292.
BOITEK, YA. and L. VOITKOVA 1968. Astrakhn. Zapovednik Trudy 11:13-27. (in Russian).
BOURGAT, R. and S.D. KULO 1977. Ann. Parasit. 52:615-622.
BOWERS, E.A. and B.L. JAMES 1967. Parasitol. 57:281-300.
BRACKETT, S. 1942. J. Parasit. 28:25-42.
BRAVO-HOLLIS, M. and G. ARROYO-SANCHO 1962. An. Inst. Biol. Univ. Mex. 33:79-95.
BRENDOW, V. 1970. Z. Parasitenk. 33:282-313.
BRIDGMAN, J.F. 1969. Tul. Stud. Zool. 15:81-105.
_______, 1971. Jap. J. Parasit. 20:13-23.
BROEK, E. van den 1978. Pr. Brit. Soc. Parasit (Abstr. in Parasit.) 77:VI-VII.
BROOKS, D.R. and M.A. MAYES 1975. J. Parasit. 61:403-406.
BURNS, W.C. 1961a. J. Parasit. 47:933-938.
_______, 1961b. J. Parasit. 47:927-932.
BURNS, W.C. and I. PRATT 1953. J. Parasit. 39:60-69.
BURTON, P.R. 1958. Pr. Helm. Soc. Wash. 25:117-122.
BYCHOWSKY, B.E. 1957. Monogenetic Trematodes: Their Systematics and Phylogeny. Akad. Nauk. S.S.S.R. (Trans. from the Russian).
BYRD, E.E. 1935. Tr. Am. Micr. Soc. 54:196-225.
_______, 1937. Pr. U.S. Nat. Mus. 84:183-199.
_______, 1939. J. Tenn. Acad. Sci. 14:116-161.
BYRD, E.E. and J.F. DENTON 1938. J. Parasit. 24:379-401.
_______, 1950. Am. Midl. Nat. 43:32-57.
BYRD, E.E. and W.P. MAPLES 1964. Parasitol. 54:295-312.
_______, 1969. J. Parasit. 55:509-526.
CABALLERO, y.C.E. and D. SOKOLOFF 1936. Ann. Inst. Biol. 7:119-154.
CABLE, R.M. 1939. Pr. Indiana Acad. Sci. 48:201.
_______, 1953. J. Parasit. 39:408-421.
_______, 1954a. J. Parasit. 40:202-208.
_______, 1954b. J. Parasit. 40:71-76.
_______, 1954c. Biol. Bull. 106:15-20.
_______, 1956a. Parasitol. 46:1-13.
_______, 1956b. Sci. Survey Puerto Rico and Virgin Is. 16:491-577.
_______, 1962. J. Parasit. 48:419-422.
CABLE, R.M. and A.V. HUNNINEN 1940. Biol. Bull. 78:136-157.
_______, 1941. Biol. Bull. 81:279.
_______, 1942a. Biol. Bull. 82:292-312.
_______, 1942b. J. Parasit. 28:407-422.
CABLE, R.M. and ISSEROFF 1969. Pr. Helm. Soc. Wash. 36:131-135.
CABLE, R.M. and F.M. NAHHAS 1962a. J. Parasit. 48:34.
_______, 1962b. J. Parasit. 48:536-538.
CAMERON, T.W.M. 1937. Can. J. Res. Sect. D. 15:38-51.
_______, 1944. Can. J. Res. Sect. D. 22:6-16.
_______, 1945. Can. J. Comp. Med. 9:245-254, 283-286, 302-311.
CANNON, L.R.G. 1971. Can. J. Zool. 49:1417-1429.
CARNEY, W.P. 1966. Can. J. Zool. 44:343-344.
_______, 1967. Can. J. Zool. 45:131-134.
_______, 1969. Am. Midl. Nat. 82:605-611.
_______, 1970. Tr. Am. Micr. Soc. 89:233-250.
_______, 1972. J. Parasit. 58:519-523.
_______, 1974. Pr. Helm. Soc. Wash. 41:139-144.
CARTER, R.T. 1973. Diss. Abstr. Intern. 33B:4582.
CAVENY, B.A. and F.J. ETGES 1971. J. Parasit. 57:1215-1221.
CHANDLER, A.C. 1942. Tr. Am. Micr. Soc. 61:156-167.
CHAUHAN, B.S. 1943. Pr. Indian Acad. Sci. 17:97-117.
CHEN, H.T. 1960. Acta Zool. Sin. 12:27.
CHENG, T.C. 1958. Am. Midl. Nat. 59:67-81.
_______, 1960a. J. Parasit. 46:464-474.
_______, 1960b. Am. Midl. Nat. 63:439-469.
CHING, H.L. 1961. Pr. Helm. Soc. Wash. 28:130-138.
_______, 1962. Can. J. Zool. 40:889-899.
_______, 1963. Can. J. Zool. 41:881-888.
_______, 1965. Pr. Helm. Soc. Wash. 32:53-63.
_______, 1978. Can. J. Zool. 56:1877-1879.
_______, 1979. Can. J. Zool. 57:1341-1344.
_______, 1980. Pr. Helm. Soc. Wash. 47:179-185.
CHRISTENSEN, B.M.; P.K. WELLNER and L.N. GLEASON 1982. Pr. Helm. Soc. Wash. 49:22-27.
CHU, G.W.T.C. and C.E. CUTRESS 1954. J. Parasit. 40:515-524.
CHUBRIK, G.K. 1952a. Zoologicheski Zhurnal 31:653-658.
_______, 1952b. Dokl. Akad. Nauk. SSSR 83:327-329.
_______, 1952c. Dokl. Akad. Nauk. SSSR 83:981-983.
_______, 1966. Trudy Akad. Nauk. SSSR 10:78-158.
COMBES, C.; J. JOURDANE and J. RICHARD 1974. Z. Parasitenk. 44:81-92.
COMBES, C. and N. KECHEMIR 1978. Pr. 2nd. Eur. Multicolloquy Parasit. 1-6 Sept. 1975.
CORKUM, K.C. and F.W. BECKERDITE 1975. Am. Midl. Nat. 93:484-491.
CORT, W.W. and S. BRACKETT 1937. J. Parasit. 23 (Suppl.):563-564.
CORT, W.W.; S. BRACKETT and L.J. OLIVIER 1944. J. Parasit. 30:309-321.
CRANDALL, R.B. 1960. J. Parasit. 46:289-307.
CRAWFORD, W.W. 1937. J. Parasit. 23:389-399.
_______, 1938. J. Parasit. 24:35-44.
_______, 1940. J. Parasit. 26 (Sect. 2):38.
CURRENT, W.L. and B.Z. LANG 1975. J. Parasit. 61:681.
DANIELL, D.L. 1979. Diss. Abstr. 39B:3188-3189.
DAWES, B. 1942. Parasitol. 34:266-277.
DEBLOCK, S. 1974. Ann. Parasit. 49:175-184.
_______, 1975. Ann. Parasit. 50:579-589.
DEBLOCK, S. and C. COMBES 1965. Bull. Soc. Zool. France 90:101-117.
DeGIUSTI, D.L. 1962. J. Parasit. 48 (Sect. 2):22.
De MARTINI, J.D. and I. PRATT 1964. J. Parasit. 50:101-105.
DENNIS, E.A. 1973. J. Helm. 47:61-71.
DENNIS, E.A. and L.R. PENNER 1971. Occ. Papers Univ. Conn. 2:5-15.
DENTON, J.F. 1941. J. Parasit. 27 (Sect. 2):13-14.
_______, 1944. J. Parasit. 30:277-286.
_______, 1945. J. Parasit. 31:131-141.
_______, 1962. J. Parasit. 48 (Sect. 2):22.
DERY, D.W. 1958. J. Parasit. 44:110-112.
DICKERMAN, E.E. 1934. Tr. Am. Micr. Soc. 53:8-21.
_______, 1945. Tr. Am. Micr. Soc. 64:138-144.
_______, 1948. J. Parasit. 34:164.
DOLGIKH, A.V. and N.N. NAIDENOVA 1967. Zoologicheskii Zhurnal, Moscow 46:1094-1097.
DOLLFUS, R. PH. 1937. Ann. Parasit. 15:57-73; 164-176; 259-281.
_______, 1959. Ann. Parasit. 34:595-622.
_______, 1960. Ann. Parasit. 35:65-117.
_______, 1966. Ann. Parasit. 41:289-299.
DONGES, J. 1964a. Z. Parasitenk. 24:65-75.
_______, 1964b. Z. Parasitenk. 24:169-248
DRONEN, N.O. Jr. 1975. J. Parasit. 61:657-660.
DRONEN, N.O. Jr. and B.Z. LANG 1974. J. Parasit. 60:75-79.
DRONEN, N.O. Jr. and L.R. PENNER 1975. Occ. Pap. Biol. Sci. Ser. U. Connecticut 2:217-224.
DRONEN, N.O. Jr. and H.T. UNDERWOOD 1977. Pr. Helm. Soc. Wash. 44:198-200
DUBOIS, G. 1938. Mem. Soc. Neuchatel. Sci. Nat. 6:1-535.
_______, 1955. Bull. Soc. Neuchatel. Sci. Nat. 78:53-65
_______, 1968-70. Mem. Soc. Neuchatel. Sci. Nat. 10:1-258, 10:259-727.
DUNCAN, B.L. and D.L. DeGIUSTI 1976. Pr. Helm. Soc. Wash. 43:1-9.
ECKERLIN, R.P. and W.H. LEIGH 1962. J. Parasit. 48 (Sect. 2):49.
ECKMANN, F. 1932. Z. Parasitenk. 5:94-111.
EDWARDS, S.R. and F.M. NAHHAS 1968. Calif. Fish and Game 54:247-256.
ERASMUS, D. 1962. Parasitol. 52:353-374.
ERICKSON, D.G. and F.G. WALLACE 1959. J. Parasit. 45:310-322.
ETGES, F.J. 1953. J. Parasit. 39:643-662.
_______, 1960, J. Parasit. 46:235-240.
EVANS, W.S. 1963. Can. J. Zool. 41:649-651.
FARES, A. and C. MAILLARD 1974. Z. Parasitenk. 45:11-43
FAROOQI, H.U. 1958. Z. Parasitenk. 18:465-469.
FELDMAN, S.I. 1941. J. Parasit. 27:525-533.
FISCHTHAL, J.H. and L.N. ALLISON 1942. Tr. Am. Micr. Soc. 61:53-56.
FONT, W.F. 1980. J. Parasit. 66:861-862.
FONT, W.F. and K.C. CORKUM 1975. Tr. Am. Micr. Soc. 94:421-424.
FOTEDAR, D.N. 1965. Kashmir Sci. (1964) 1:44-52.
FOX, A.C. 1966. Diss. Abstr. 26:4900.
FRANCALANCI, G. and L. MANFREDINI 1969. Clinica Vet., Milana 92:339-345.
FRANKLAND, H.M.T. 1955. Parasitol. 45:313-351.
FREDERICKSEN, D.W. 1980. J. Parasit. 66:973-984.
FREEMAN, R.F.H. and J. LLEWELLYN 1958. J. Mar. Biol. Assoc. U.K. 37:435-457.
GALLIEN, L. 1932. C.R. Acad. Sci., Paris 194:1852-1854; 195:77-79.
_______, 1933. C.R. Acad. Sci., Paris 196:426-428.
GIBSON, G.G.; E. BROUGHTON and L.P.E. CHOQUETTE 1972. Can. J. Zool. 50:1351-1356.
GINETSINSKAYA, T.A. 1961. Dokl. Akad. Nauk. SSSR 135:235-239; 940-942.
GOODCHILD, C.G. 1943. Biol. Bull. 84:59-86.
_______, 1948. J. Parasit. 34:407-427.
GOODCHILD, C.G. and D.E. KIRK 1960. J. Parasit. 46:219-229.
GRAHAM, L.C. 1971. Diss. Abstr. Intern. 31B:5176.
GREENE, N.D. 1962. J Parasit. 48 (Sect. 2):48-49.
GREER, G.J. and K.C. CORKUM 1979. Pr. Helm. Soc. Wash. 46:188-200.
GRIZEL, H. and M. VIANEY-LIAUD 1973. Ann. Parasit. 48:47-53.
GROVES, R.E. 1945. Tr. Am. Micr. Soc. 64:112-132.
GUPTA, R. 1963. Zool. Anz. 171:117-130.
HALL, J.E. 1959. J. Parasit. 45:327-336.
_______, 1960. Am. Midl. Nat. 63:226-245.
HAND, C. and M. VOGE 1952. J. Parasit. 38:57-58.
HANSON, A.W. 1973. Diss. Abstr. Intern. 33B:4583-4584.
HARLEY, J.P. 1972. Am. Midl. Nat. 88:474-475.
HARRIS, A.H.; R. HARKEMA and G.C. MILLER 1967a. J. Parasit. 53:1114-1115.
_______, 1967b. J. Parasit. 53:577-583.
_______, 1970. J. Parasit. 56:297-301.
HAYDEN, D.W. 1969. J. Am. Vet. Med. Assoc. 155:889-891.
HEARD, R.W. and R.M. OVERSTREET 1983. Pr. Helm. Soc. Wash. 50:170-174
HENDRIX, S.S. 1973. Diss. Abstr. 34B:922.
_______, 1978. J. Parasit. 64:606-612.

HERBER, E.C. 1938. J. Parasit. 24:549.
______, 1939. J. Parasit. 25:189-195.
______, 1942. J. Parasit. 28:179-196.
HERMAN, S.M. and W.J. BACHA JR. 1978. J. Parasit. 64:827-830.
HOFFMAN, G.L. 1955. Pr. Iowa Acad. Sci. 62:638-639.
______, 1956. J. Parasit. 42:435-444.
HOFFMAN, G.L. 1958a. Exp. Parasit. 7:23-50.
______, 1958b. J. Parasit. 44:416-421.
HOFFMAN, G.L. and C.E. DUNBAR 1963. J. Parasit. 49:737-744.
HOLLIMAN, R.B. 1961. Tul. Stud. Zool. 9:1-74.
HOPKINS, S.H. 1931. J. Parasit. 18:79-91.
______, 1933. Tr. Am. Micr. Soc. 52:147-149.
______, 1934a. Ill. Biol. Monogr. 13(2):1-80.
______, 1934b. Science n.s. 79:385-386.
______, 1937. J. Parasit. 23:94-97.
HORSFALL, M.W. 1933. Science n.s. 78:175-176.
______, 1934. Tr. Am. Micr. Soc. 53:311-347.
______, 1935. Pr. Helm. Soc. Wash. 2:78-79.
HSU, D.Y.M. 1937. Tr. Am. Micr. Soc. 56:478-504.
HUEHNER, M.K. and F.J. ETGES 1977. J. Parasit. 63:669-674.
HUGGHINS, E.J. 1954. Tr. Am. Micr. Soc. 73:1-15; 221-236.
HUNNINEN, A.V. and R.M. CABLE 1941. Biol. Bull. 80:415-428.
______, 1943a. Tr. Am. Micr. Soc. 62:57-68.
______, 1943b. J. Parasit. 29:71-79.
HUNTER, W.S. 1967. Pr. Helm. Soc. Wash. 34:33-40.
HUNTER, W.S. and G.W. HUNTER III 1934. J. Parasit. 20:132.
HUTTON, R.F. 1964. Tr. Am. Micr. Soc. 83:439-447.
HUTTON, R.F. and F. SOGANDARES-BERNAL 1960. Bull. Mar. Sci. Gulf and Caribbean 10:40-54.
INGLES, L.G. 1933. Univ. Calif. Publ. Zool: 39:163-178.
______, 1935. Tr. Am. Micr. Soc. 54:19-21.
IVANOV, A.V. 1952. Parazit, Sborn. Zool. Inst. Akad. Nauk SSSR 14:112-163. (in Russian)
IZUMOVA, N.A. 1956. Parazit. Sborn. Zool. Inst. Akad. Nauk SSSR 16:229-243.
JAHN, T.L. and L.R. KUHN 1932. Biol. Bull. 62:89-111.
JAIN, S.P. and O.N. SRIVASTAVA 1970. Pr. Indian Acad. Sci. Sect. B. 72:156-161.
JAMES, B.L. 1964. Parasitol. 54:1-41.
JAMIESON, B.G.M. 1966. Pr. Roy. Soc. Queensland 77:81-92.
JENSEN, D.N. 1972. Can. J. Zool. 50:201-204.
JOHNSON, A.D. 1970. Tr. Am. Micr. Soc. 89:250-253.
JOHNSTON, T.H. and L.M. ANGEL 1951. Tr. Roy. Soc. S. Austral. 74:66-78.
JORDAN, H.E. 1963. Diss. Abstr. 23:4472-4473.
JORDAN, H.E. and E.E. BYRD 1967. Tr. Am. Micr. Soc. 86:67.
JOURDANE, J. 1977. Ann. Parasit. 52:403-410.
______, 1979. Ann. Parasit. 54:449-456.
JOURDANE, J. and A. THERON 1975. Ann. Parasit. 50:439-445.
KAGAN, I.G. 1951. Tr. Am. Micr. Soc. 70:281-318.
______, 1952a. Tr. Am. Micr. Soc. 71:20-44.
______, 1952b. Am. Midl. Nat. 48:257-301.
______, 1953. J. Infect. Dis. 93:200-206.
KATHERINER, L. 1904. Zool. Jahrb. Suppl 7. Festschr. 70 Geburtst. A. Weismann 7:519-550.
KEARN, G.C. 1963. Parasitol. 53:435-447.
KECHEMIR, N. 1978. Ann. Parasit. 53:75-92.
KELLY, H.M. 1926. Pr. Iowa Acad. Sci. 33:339.
KENNEDY, M.J. 1981. Can. J. Zool. 59:1836-1846.
KHALIFA, R. 1972. Acta Parasit. Polonica 20:343-365.
KHAN, D. 1960. J. Helm. 34:277-304.
______, 1961. J. Helm. 35:119-132.
______, 1962a. J. Helm. 36:67-94.
______, 1962b. J. Helm. 36:95-106.
KHOTENOVSKI, I.A. 1967. Parazitologiya 1:75-78. (in Russian)
KINGSTON, N. 1965. Can. J. Zool. 43:953-969.
KINSELLA, J.M. and R.W. HEARD III 1974. Tr. Am. Micr. Soc. 93:408-412.
KNIGHT, R.A. and I. PRATT 1955. J. Parasit. 41:248-255.
KNISKERN, V.B. 1952. Tr. Am. Micr. Soc. 71:317-340.
KOIE, M. 1975. Ophelia 13:63-86.
______, 1976. Ophelia 15:1-14.
______, 1979. Ophelia 18:113-132.
______, 1980. Ophelia 19:215-236.
______, 1981. Ophelia 20:17-43.
KRASNOBOLOVA, T.A. 1963. Helminthologia 4:213-229.
KRULL, W.H. 1931. Tr. Am. Micr. Soc. 50:215-277.
______, 1932. Zool. Anz. 99:231-239.
______, 1933. J. Parasit. 20:109.
______, 1934a. J. Wash. Acad. Sci. 24:483-485.
______, 1934b. Pr. Helm. Soc. Wash. 1:5.
______, 1934c. Tr. Am. Micr. Soc. 53:408-415.
______, 1934d. J. Parasit. 20:326-327.
______, 1935a. Tr. Am. Micr. Soc. 54:118-134.
______, 1935b. Parasitol. 27:93-100.
______, 1935c. Pr. Helm. Soc. Wash. 2:77.
______, 1935d. Pap. Mich. Acad. Sci., Arts, Letters 20:697-710.
______, 1936. Pr. Helm. Soc. Wash. 3:56-58.
KRULL, W.H. and C. MAPES 1952. Cornell Vet. 42:253-285, 339-351; 464-489; 603-604.
______, 1953. Cornell Vet. 43:199-202; 389-410.
KRULL, W.H. and H.F. PRICE 1932. Occ. Pap. Mus. Zool. Univ. Mich. 237:1-38.
KRYGIER, B.B. and R.W. MACY 1969. Pr. Helm. Soc. Wash. 36:136-139.
KU, C.T. 1957. Acta Zool. Sin. 9:206-211.
KULACHKOVA, V.G. 1954. Trudi Problemnikh Trematisheskikh Soveshchani Akad. Nauk SSSR 4:118-122.
KULWIEC, Z. 1929. Arch. Hydrobiol. Rybact. 4:277-281.
LAMOTHE-ARGUMEDO, R. 1965. An. Inst. Biol. 35:115-121.
LANG, B.Z. 1968. J. Parasit. 54:945-949.
LANG, B.Z. and L.N. GLEASON 1967. J. Parasit. 53:93.
LANG, W.H. and E.A. DENNIS 1976. Ophelia 15:65-75.
LEE, H.F. 1962. J. Parasit. 48:728-739.
LEIGH, W.H. 1946. Am. Midl. Nat. 35:460-483.
______ 1954. J. Parasit. 40 (Sect. 2):45.
______ 1958. J. Parasit. 44:379-387.
______ 1974. J. Parasit. 60:768-772.
______ 1975. J. Parasit. 61:873-876.
______ 1978. J. Parasit. 64:831-834.
LEIGH, W.H. and R.B. HOLLIMAN 1956. J. Parasit. 42:400-407.
LEITE, A.C.; H.M. de A. COSTA and J.O. COSTA 1979. Rev. Brasileira Biol. 39:341-345.
LEUCKART, R. 1882. Arch. Naturgesch. 48:80-119.
LEWIS, J.W. 1969. J. Helm. 43:79-98.
LEWIS, P.D. Jr. 1974. J. Parasit. 60:251-255
LEZOTTE, L.A. Jr. 1954. J. Parasit. 40:148-162.
LIE, K.J. 1964. Trop and Geogr. Med., Amsterdam 16:61-71.
LIE KIAN, J. and T. UMATHEVY 1965. J. Parasit. 51:793-799.
LOOS-FRANK, B. 1967. Z. Parasitenk. 28:299-351.
______ 1968a. Z. Parasitenk. 30:185-191.
______ 1968b. Z. Parasitenk. 31:122-131.
______ 1969a. Z. Parasitenk. 32:135-156.
______ 1969b. J. Ornithologie 110:471-474.

LUMSDEN, R.D. and C.A. WINKLER 1962. J. Parasit. 48:503.
LUNDAHL, W.S. 1941. Tr. Am. Micr. Soc. 60:461-484.
LYNCH, J.E. 1934. Quar. J. Micr. Sci. n.s. 76:13-33.
Mac KENZIE, K. and J.M. LIVERSIDGE 1975. J. Fish Biol. 7:247-256.
McCAULEY, J.E. and I. PRATT 1960. J. Parasit. 46 (Sect. 2):15.
McCOY, O.R. 1927. J. Parasit. 14:127-128.
______ 1929. Parasitol. 21:220-225.
______ 1930. J. Parasit. 17:1-13.
McINTOSH, A. 1934a. Parasitol. 26:463-467.
______ 1934b. Pr. Helm. Soc. Wash. 1:2-4.
______ 1937. Pr. Helm. Soc. Wash. 4:21-23.
McLAUGHLIN, J.D. 1976. Can. J. Zool. 54:48-54.
______ 1977a. Can. J. Zool. 55:274-279.
______ 1977b. Can. J. Zool. 55:1565-1567.
McLEOD, J.A. 1940. Can. J. Res. Sect. D. 18:1-28.
McLEOD, J.A. and G.E. LITTLE 1942. Can. J. Res. Sect. D. 20:170-181.
McMILLAN, T.A. and R.W. MACY 1972. J. Parasit. 58:22.
McMULLEN, D.B. 1934. J. Parasit. 20:248-250.
______ 1935a. J. Parasit. 21:52-53.
______ 1935b. J. Parasit. 21:369-380.
______ 1936. J. Parasit. 22:295-298.
______ 1937. J. Parasit. 23:235-243.
McMULLEN, D.B. and P.C. BEAVER 1945. Am. J. Hyg. 42:128-154.
MacFARLANE, W.V. 1939. Parasitol. 31:172-183.
MACY, R.W. 1931. J. Parasit. 18:28-33.
______ 1933. Tr. Am. Micr. Soc. 52:247-254.
______ 1934. Univ. Minn. Agr. Exp. Sta. Tech. Bull. #98:71pp.
______ 1939. J. Parasit. 25:281.
______ 1940. Pr. Minn. Acad. Sci. 8:39-41.
______ 1960a. J. Parasit. 46:662.
______ 1960b. J. Parasit. 46:337-345.
______ 1965. Tr. Am. Micr. Soc. 84:577-580.
MACY, R.W. and W.D. BELL 1968a. J. Parasit. 54:319-323.
______ 1968b. J. Parasit. 54:761-764.
MACY, R.W. and A.K. BERNTZEN 1970. J. Parasit. 56 (Sect. 2):445.
MACY, R.W.; W.A. COOK and W.R. DeMOTT 1960. Northwest Sci. 34:1-17.
MACY, R.W. and R.G. ENGLISH 1975. Am. Midl. Nat. 94:509-512.
MACY, R.W. and J.R. FORD 1964. J. Parasit. 50:93.
MACY, R.W. and D.J. MOORE 1954. J. Parasit. 40:328-335.
______ 1958. Tr. Am. Micr. Soc. 77:396-403.
MACY, R.W. and G.L. STRONG 1967. J. Parasit. 53:584-586.
MADHAVI, R. 1976. J. Parasit. 62:410-412.
______ 1978. J. Helm. 52:51-59.
______ 1980. Z. Parasitenk. 63:89-97.
MADHAVI, R. and K.H. RAO 1968. Curr. Sci. 37:702-703.
MAILLARD, M.C. 1971. C.R. Acad. Sci., Paris 272:3303-3306.
MAILLARD, C. 1973. Ann. Parasit. 48:33-46.
______ 1974. Bull. Soc. Zool. France 99:245-257.
MALDONADO, J.F. 1945a. J. Parasit. 31:306-314.
MALDONADO, J.F. 1945b. Puerto Rico J. Public Health and Trop. Med. 21:17-60.
MANTER, H.W. 1934. Carn. Inst. Wash. Pap. Tortugas Lab. 28:167-180.
______ 1954. Tr. Roy. Soc. N. Zealand 82:475-568.
MAPES, C.R. 1951. Cornell Vet. 41:382-432.
MAPES, C.R. and W.H. KRULL 1951. Cornell Vet. 41:433-444.
MARTIN, G.W. 1966. Diss. Abstr. 27:1658.
______ 1969. J. Parasit. 55:747-752.
MARTIN, W.E. 1938. Biol. Bull. 75:463-474.
______ 1939a. Biol. Bull. 77:65-73.
______ 1939b. J. Parasit. 25 (Sect. 2):18.
______ 1940. Biol. Bull. 79:131-144.
______ 1944. Tr. Am. Micr. Soc. 63:237-243.
______ 1945. Tr. Am. Micr. Soc. 64:203-212.
______ 1950a. J. Parasit. 36:552-558.
______ 1950b. Tr. Am. Micr. Soc. 69:194-209.
______ 1950c. J. Parasit. 36:360-370.
______ 1951. J. Parasit. 37:297-300.
______ 1952. J. Parasit. 38:356-359.
______ 1956. Tr. Am. Micr. Soc. 75:117-128.
______ 1961. Pac. Sci., Honolulu 15:278-281.
______ 1964. Tr. Am. Micr. Soc. 83:270-272.
______ 1971. Tr. Am. Micr. Soc. 90:188-194.
______ 1973. Tr. Am. Micr. Soc. 92:80-95.
MARTIN, W.E. and J.E. ADAMS 1961. J. Parasit. 47:777-782.
MARTIN, W.E. and D.F. STEEL 1970. Pr. Helm. Soc. Wash. 37:101-104.
MATHIAS, P. 1925. Bull. Biol. France and Belgique 59:1-123.
______ 1937. C.R. Acad. Sci., Paris 205:626-628.
MATTHEWS, R.A. 1973. Parasitol. 68:1-12
MEADE, T.G. and I. PRATT 1965. J. Parasit. 51:575-578.
MICHELSON, E.H. 1970. J. Parasit. 56:709-712.
MILLER, G.C.; R. HARKEMA and A. HARRIS 1965. J. Parasit. 51 (Sect. 2):22.
MILLER, J.H. 1954. J. Parasit. 40:255-270.
MILLER, M.J. 1941. J. Parasit. 27 (Sect. 2):12.
______ 1946. Can. J. Res. Sect. D. 24:27-29.
MISHAKOV, N.E. 1971. Trudy Biol. Pochvenn Inst. Vladivostok 11:236-245.
MIZELLE, J.D. and D.C. KRITSKY 1967. Tr. Am. Micr. Soc. 86:390-401.
MIZELLE, J.D. and H.D. McDOUGAL 1970. Am. Midl. Nat. 84:444-462.
MOHANDAS, A. and A.M. NADAKAL 1970. Zool. Anz. 184:233-239.
MOROZOV, F.N. 1952. Trematodes of Animals and Man by K.I. Skrjabin 6:153-615.
MUKHERJEE, R.P. 1968. J. Zool. Soc. India 20:105-122.
MURRELL, K.D. 1963. J. Parasit. 49:116.
______ 1965. J. Parasit. 51:600-604.
MYER, D.G. 1960. J. Parasit. 46:819-832.
NAJARIAN, H.H. 1953. Science n.s. 117:564-565.
______ 1954. J. Morph. 94:165-197
______ 1961. J. Parasit. 47:625-634.
NAJIM, A.T. 1950. J. Parasit. 36(Sect. 2):19.
______ 1956. Parasitol. 46:443-469.
NASIR, P. and L.M.T. DIAZ 1971. Riv. Parassit. 32:149-158.
NASIR, P. and L. RODRIGUEZ 1969. Zool. Anz. 182:230-244.
NASIR, P. and J.V. SCORZA 1968. Z. Parasitenk. 30:134-148.
NICKERSON, W.S. 1902. Zool. Jahrb. Syst. 15:597-624.
NIEMI, D.R. and R.W. MACY 1974. Pr. Helm. Soc. Wash. 41:223-229.
NIKOLAEVA, V.M. 1965. Zoologicheskii Zhurnal Moscow 44:1317-1327.
NORRIS, G.R. 1945. Doctoral Diss., Ohio State Univ. 65:527-528.
OCHI, S. 1930. Okayama Igakkai Zasshi 42:388-402.
ODENING, K. 1958. Mitt. Zool. Mus., Berlin 34:63-108.
______ 1960. Biologisches Zentralbl. 79:513-519.

______ 1965. Z. Parasitenk. 26:185-196.
______ 1970. Z. Parasitenk. 33:194-210
______ 1971. Biologisches Zentralbl: 90:49-84.
______ 1976. Biologisches Zentralbl. 95:57-94.
OGAMBO-ONGOMA, A.H. and J.D. GOODMAN 1976. J. Parasit. 62:33-38.
OGATA, T. 1934. Sci. Rep. Tokyo Bunrika Daigaku 2(B):45-53.
OGLESBY, L.C. 1961. J. Parasit. 47:233-236.
OLIVIER, L.J. 1940. J. Parasit. 26:447-477.
OLSEN, O.W. 1937a. Tr. Am. Micr. Soc. 56:311-339.
______ 1937b. J. Parasit. 23:13-28.
______ 1940. Zoologica 25:323-328.
OLSON, A.C. and M. JEFFRIES 1983. J. Parasit. 69:602-605.
OLSON, R.E. 1970. J. Parasit. 56:55-63.
ORLOFF, I.W. 1941. C.R. Akad. Sci. Dokl. USSR 31:641-643.
OSBORN, H.L. 1903. J. Morph. 18:1-44.
OSTROWSKI de NUNEZ, M 1978. Physis (Sect B.) 35 (90):51-57.
OSTROWSKI de NUNEZ, M. 1978. Physis (Sect B.) 35 (90):51-19:208-213.
OWEN, H.M. 1946. J. Parasit. 32:553-562.
PALOMBI, A. 1930. Publ. Staz. Zool., Napoli 10:111-149.
______ 1931. Boll. Zool., Torino 2:165-171.
______ 1937. Riv. Parassit. Roma 1:1-12.
______ 1941. Riv. Parassit. 5:127-128.
______ 1942. Riv. Parassit. 6:117-172.
PAPERNA, I. 1963. Bamidgeh Bull. Fish Culture Israel 15:8-28.
PAPERNA, I. and J. LENGY 1963. Israel J. Zool. 12:171-182.
PATTEN, J.A. 1952. J Parasit. 38:165-182.
PATTON, S. 1976. J. Parasit. 62:101
PAUL, A.A. 1938. J. Parasit. 24:489-510.
PEARSON, J.C. 1956. Can. J. Zool. 34:295-387.
______ 1959. J. Parasit. 45:155-174.
______ 1961. Parasitol. 51:133-172.
______ 1973. Phil. Tr. Roy. Soc. London Ser. B. 266:341-447.
PENNER, L.R. and B. FRIED 1963: J. Parasit. 49:974-977.
PETERS, L.E. Jr. 1955. J. Parasit. 41 (Sect. 2):36.
______ 1961. Am. Midl. Nat. 65:436-445.
PETERS, L. and J.T. SELF 1963. J. Parasit. 49(Sect. 2):41.
PIKE, A.W. 1968. J. Helm. 42:125-130.
______ 1980. J. Nat Hist. 14:389-399.
POJMANSKA, T. 1972. Acta Parasit. Polonica 20:35-44.
______ 1975. Acta Parasit. Polonica 23:23-36.
POPOVA, T.I. and E.N. NIKITINA 1978. Pr. 2nd. Eur. Multicolloquy Parasit. 1-6 Sept. 1975:187-188.
PRATT, I. 1970. Pr. 2nd Inter. Congr. Parasit. Pt. 1:273-274.
PREMVATI, G. 1955. J. Zool. Soc. India 7:13-24.
PREVOT, G. 1965. Bull. Soc. Zool. France 90:175-179.
______ 1966. Ann. Parasit. 41:233-242.
______ 1971. Bull. Soc. Zool. France 96:197-208.
______ 1972. Ann. Parasit. 47:687-700.
______ 1973. Ann. Parasit. 48:457-467.
PREVOT, G.; P. BARTOLI and S. DEBLOCK 1976. Ann. Parasit. 51:433-446.
PREVOT, G. and P. BARTOLI 1978. Ann. Parasit. 53:561-575.
______ 1980. Ann. Parasit. 55:407-455.
PRICE, E.W. 1929. Pr. U.S. Nat. Mus. 75:1-39.
______ 1932. Pr. U.S. Nat. Mus. 81:1-68.
______ 1938a. Pr. Helm. Soc. Wash. 5:48-49.
______ 1938b. J. Wash. Acad. Sci. 28:109-126;183-198.
______ 1939a. J. Wash. Acad. Sci. 29:63-92.
______ 1939b. Pr. Helm. Soc. Wash. 6:80-92.
______ 1942. Pr. Helm. Soc. Wash. 9:39-56.
______ 1943a. J. Wash. Acad. Sci. 33:44-54.
______ 1943b. Pr. Helm. Soc. Wash. 10:10-15.
______ 1961a. Pr. Helm. Soc. Wash. 28:4-9.
______ 1961b. Pr. Biol. Soc. Wash. 74:127-156.
PRICE, E.W. 1962a. Pr. Helm. Soc. Wash. 29:1-18.
______ 1962b. J. Parasit. 48:402-418.
PRICE, H.F. 1931. Am. J. Hyg. 13:685-727.
PRITCHARD, M.H. 1966. Zool. Jahrb. Syst. 93:173-202.
RALPH, P.H. 1938. Tr. Am. Micr. Soc. 57:376-382.
RANKIN, J.S. Jr. 1938. Am. Midl. Nat. 21:476-488.
______ 1940. Biol. Bull. 79:439-451.
______ 1944. Tr. Am. Micr. Soc. 63:30-43.
REDINGTON, B.C. and M.J. ULMER 1964. J. Parasit. 50 (Sect. 2):46.
REES, G. 1952. Parasitol. 42:92-113.
______ 1957. Parasitol. 47:126-137.
REIMER, L. 1964. Pr. Czechoslovak Acad. Sci., Prague 1962: 99-106.
______ 1973. Zool. Anz. 191:187-196.
REMLEY, L.W. 1942. Tr. Am. Micr. Soc. 61:141-155.
REYNOLDS, B.D. 1938. Parasitol. 30:320-323.
ROBINSON, E.J. Jr. 1949. J. Parasit. 35:513-533.
______ 1953. J. Parasit. 39:228.
ROBINSON, H.W. 1952. J. Parasit. 38:368.
ROHDE, K. 1973. Parasitol. 66:63-83.
ROHDE, K. and FAH ONN LEE 1967. Z. Parasitenk. 29:137-148.
ROMIG, T.; R. LUCIUS and W. FRANK 1980. Z. Parasitenk. 63:277-286.
ROWAN, W.B. 1955. Tr. Am. Micr. Soc. 74:1-21.
SARKISIAN, L.N. 1957. Wasman J. Biol. 15:35-48.
SCHELL, S.C. 1961. J. Parasit. 47:493-500.
______ 1962a. J. Parsit. 48:387-394.
______ 1962b. Tr. Am. Micr. Soc. 81:137-147.
______ 1965. J. Parasit. 51:587-593.
______ 1967a. J. Parasit. 53:569-576.
______ 1967b. J. Parasit. 53:1000-1004.
______ 1972. J. Parasit. 58:1119-1121.
______ 1973a. J. Parasit. 59:803-805.
______ 1973b. J. Parasit. 59:463-468.
______ 1974. J. Parasit. 60:561-566.
______, 1975. J. Parasit. 61:899-905.
______ 1976. J. Parasit. 62:894-898.
SCHEURING, L. 1922. Zool. Jahrb. Anat. 44:265-310.
SCHMIDT, R. 1964. Naturwissenschaften 51:444.
______ 1965. Z. Parasitenk. 26:1-17.
SCHROEDER, R.E. and W.H. LEIGH 1965. J. Parasit. 51:594-599.
SEITNER, P.G. 1945. J. Parasit. 31:272-279.
SERKOVA, O.P. and B.E. BYCHOWSKY 1940. Mag. Parasit. Inst. Zool Acad. Sci. 8:162-175.
SCHIMAZU, T. 1974. Jap. J. Parasit. 23:100-105.
______ 1981. Jap. J. Parasit. 30:173-177
SHOOP, W.L. and K.C. KORKUM 1983. J. Parasit. 69:731-735.
SIEBERT, A.E. Jr. 1971. Pr. Louisiana Acad. Sci. 33:35-37.
SILLMAN, E.I. 1953. J. Parasit. 39(Sect. 2):21.
______ 1962. Tr. Am. Micr. Soc. 81:43-65.
SINCLAIR, N.R. 1972. Can. J. Zool. 50:353-364.
SIZEMORE, P.D. 1936. Tr. Am. Micr. Soc. 55:483-486.
SKRJABIN, K.I. 1947-62. Trematodes of Animals and Man (20 volumes). Akad. Nauk S.S.S.R. Publ. Moscow-Leningrad.
______ 1964. Keys to the Trematodes of Animals and Man. (Translated from the Russian) 351 pp. Univ. Illinois Press, Urbana.

SMITH, R.J. 1967. J. Parasit. 53:287-291.
______ 1968. J. Parasit. 54:283-285.
SOBOLEVA, T.N. 1972. Parazitologiya 6:562-566.
SOGANDARES-BERNAL, F. 1959. Tul. Stud. Zool. 7:69-117.
SOGANDARES-BERNAL, F. and J.F. BRIDGMAN 1960. Tul. Stud. Zool. 8:31-39.
SOGANDARES-BERNAL, F. and H. GRENIER 1971. J. Parasit. 57:297.
SOGANDARES-BERNAL, F. and R.F. HUTTON 1960. Pr. Helm. Soc. Wash. 27:75-77
SREEKUMARAN, P. and C.T. PETER 1973 Indian Vet. J. 50:1060.
SRIVASTAVA, L.P. 1966. Parasitol. 56:543-554.
STUNKARD, H.W. 1929. Anat. Rec. 44:264.
______ 1930. J. Morph. Physiol. 50:143-191.
______ 1934. Bull. Soc. Zool. France 59:447-466.
______ 1936. J. Parasit. 22:354-374.
______ 1938a. Biol. Bull. 75:145-164.
______ 1938b. Biol. Bull. 75:308-334.
______ 1940. J. Parasit. 26(Sect. 2):33-34.
______ 1943. Biol. Bull. 85:227-237.
______ 1956. Biol. Bull, 111:248-268.
______ 1958. J. Parasit. 44:225-230.
______ 1959. Biol. Bull. 117:562-581.
______ 1961. Biol. Bull. 120:221-237.
______ 1964a. Biol. Bull. 126:163-173.
______ 1964b. Biol. Bull. 126:467-489.
______ 1966a. J. Parasit. 52:367-372.
______ 1966b. Biol. Bull. 131:501-515.
______ 1967. Biol. Bull. 132:133-145.
______ 1969. Biol. Bull. 136:96-113.
______ 1972a. J. Parasit. 58:634-635.
______ 1972b. Biol. Bull. 142:326-334.
______ 1974. J. Parasit. 60:859.
______ 1976. Biol. Bull. 150:294-317.
______ 1978. Biol. Bull. 155:383-394.
______ 1979a. Biol. Bull. 156:234-245.
______ 1979b. Biol. Bull. 157:397-398.
______ 1980a. Biol. Bull. 158:154-163.
______ 1980b. Biol. Bull. 159:737-751.
______ 1980c. J. Parasit. 66:636-641.
______ 1980d. Biol. Bull. 159:497-498.
______ 1981b. Biol. Bull. 160:146-154.
______ 1981c. Biol. Bull. 160:155-160.
STUNKARD, H.W. and R.M. CABLE 1932. Biol. Bull. 62:328-338.
STUNKARD, H.W. and M. DiSPEZIO 1975. Biol. Bull. 149:447.
STUNKARD, H.W. and M.C. HINCHCLIFFE 1951. Anat. Rec. 111:529-530.
______ 1952. J. Parasit. 38:248-265.
STUNKARD, H.W. and J.R. UZMANN 1959. Biol. Bull. 116:184-193.
______ 1962. J. Parasit. 48(Sect. 2):23.
STUNKARD, H.W.; C.H. WILLEY and Y. RABINOWITZ 1941. Tr. Am. Micr. Soc. 60:485-497.
SULLIVAN, J.J. 1973. Diss. Abstr. Intern. 33B:3392.
SZIDAT, L. 1931. Z. Parasitenk. 3:160-172.
______ 1932. Zool. Anz. 100:205-213.
______ 1937. Z. Parasitenk. 9:529-542.
______ 1939. Z. Parasitenk. 11:239-283.
______ 1957. Z. Parasitenk. 18:24-35.
TAFT, S.J. 1973. J. Parasit. 59:90-93.
TAFT, S.J. and R.W. HEARD III 1978. J. Parasit. 64:597-600.
TALBOT, S.B. 1933. Parasitol. 25:518-545.
THERON, A. 1976. Ann. Parasit. 51:329-340.
THOMAS, A.P.W. 1883. Quar. J. Micr. Sci. n.s. 23:99-133.
THOMAS, L.J. 1939. J. Parasit. 25:207-221.
THRASHER, J.P. 1964. J. Am. Vet. Med. Assoc. 144:1119-1126.
TIMON-DAVID, J. 1955a. Ann. Parasit. 30:43-61.
______ 1955b. C.R. Acad. Sci., Paris 241:2014-2015.
______ 1957a. Ann. Parasit. 32:219-242.
______ 1957b. C.R. Sceances Soc. Biol., Paris 151:592-594.
______ 1960. Ann Parasit. 35:251-267.
TIMON-DAVID, J. and P. TIMON-DAVID 1966. C.R. Acad. Sci., Paris Ser. D. 262:1261-1263.
______ 1967. Ann. Parasit. 42:187-206.
TRIPATHI, Y.R. 1957. Indian J. Helm. 7:5-22.
UBELAKER, J.E. and O.W. OLSEN 1972. Pr. Helm. Soc. Wash. 39:94-100.
UBGADE, S.R. and AGARWALL, S.M. 1980. Indian J. Parasit. 4:111-118.
UKOLI, F.M.A. 1967. J. Helm. 41:235-256.
ULMER, M.J. 1951. Tr. Am. Micr. Soc. 70:189-238; 319-347.
______ 1952. Anat. Rec. 113:613-614.
______ 1960. J. Parasit. 46:813-814.
UZMANN, J.R. 1953. J. Parasit. 39:445-451.
VAES, M. 1978. Biologische Jaarboek, Belgium 46:202-209.
VAN HAITSMA, J.P. 1931. Pap. Mich. Acad. Sci., Arts, Letters 13:447-516.
VELASQUEZ, C.C. 1964. J. Parasit. 50:261-265.
______ 1969a. J. Parasit. 55:289-292.
______ 1969b. J. Parasit. 55:540-543.
______ 1975. J. Parasit. 61:910-914.
VERNBERG, W.B. 1952. J. Parasit. 38(Sect. 2):20.
VILLELLA, J.B. 1953. J. Parasit. 39(Sect. 2):20.
______ 1954. J. Parasit. 40:470-472.
______ 1960. J. Parasit 46(Sect. 2):15.
VOGEL, H. and J. VOELKER 1978. Tropenmedizin Parasitologie 29:385-405.
VOJTEK, J. 1971. Z. Parasitenk. 36:51-61.
______ 1972. Folia Parasitologica 19:210.
WAGNER E.D. 1975. Pr. Helm. Soc. Wash. 42:97-100.
WALKER, J.H. 1937. Pr. Soc. Exp. Biol. Med. 37:245-248.
______ 1939. Tr. Am. Micr. Soc. 58:404-430.
WALL, L.D. 1951. Tr. Am. Micr. Soc. 70:173-184.
WALLACE, F.G. 1935. J. Parasit. 21:143-164.
______ 1940. J. Parasit. 26(Sect. 2):37.
WALLACE, F.G. and L.R. PENNER 1939. J. Parasit. 25:437-440.
WALLACE, H.E. 1941. Tr. Am. Micr. Soc. 60:309-326.
WANSON, W.W. and O.R. LARSON 1972. J. Parasit. 58:1106-1109.
WARDLE, W.J. 1980. Bull. Mar. Sci. 30:737-743.
WERDING, B. 1969. Mar. Biol. 3:306-333.
WEST, A.F. 1961. Am. Midl. Nat. 66:363-383.
WETZEL, R. 1930. Pr. U.S. Nat. Mus. 78:1-4.
WHARTON, G.W. 1940. J. Parasit. 26:497-518.
WILLEY, C.H. 1930. Anat. Rec. 47:364.
______ 1936. J. Parasit. 22:68-75.
______ 1941. Zoologica 26:65-88.
WILLIAMS, C.O. 1942. J. Parasit. 28:467-475.
WILLIAMS, R.R. 1960. Ohio J. Sci. 60:323-326.
______ 1964. J. Parasit. 50(Sect. 2):29.
WISNIEWSKI, W.L. 1958a. Acta Parasit. Polonica 6:273-287.
______ 1958b. Acta Parasit. Polonica 6:289-307.

WOODHEAD, A.E. 1929. Tr. Am. Micr. Soc. 48:256-275.
_______ 1930. Tr. Am. Micr. Soc. 49:1-17.
WOOTTON, D.M. 1957. Biol. Bull. 113:302-315.
_______ 1966a. Pr. 1st. Intern. Congr. Parasit. 1:547-548.
_______ 1966b. Pr. 1st. Intern. Congr. Parasit. 1:486.
WU. K. 1938. Parasitol. 30:4-19
WUNDER, W. 1926. Biol. Zentralb. 46:748-755.
WYKOFF, D.E. *et al* 1965. J. Parasit. 51:207-214.
YAMGUTI, S. 1963. Systema Helminthum: Monogenea and Aspidocotylea Vol. 4 699pp. Interscience Publ., N.Y.
_______ 1971. Synopsis of Digenetic Trematodes 2 Vols. Keigaku Publ. Co., Tokyo.
YOUNG, P.C. 1967. J. Zool., London 153:381-422.
YOUNG, R.T. 1953. J. Wash. Acad. Sci. 43:88-93.
ZELLER, E. 1872. Zschr. Wiss. Zool. 22:1-28.
_______ 1876. Zschr. Wiss. Zool. 27:238-274.

INDEX

A

B

C

D

E

F

G

H