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SYNOPSIS OF STRIGEOIDEA (TREMATODA) OF FISHES AND THEIR LIFE CYCLES

BY GLENN L. HOFFMAN

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CONTENTS

ABSTRACT

This report is an aid to the identification of the strigeoid metacercaria found in the fishes of the world. It includes a condensed record of the known life cycles of those strigeoids that have fish as their second intermediate host. The parasites are placed in four metacercarial groups of strigeoids (*Tetracotyle*, *Diplostomulum*, *Neascus*, and *Prohemistomulum*), rather than grouped in the usual taxonomic fashion. The synopsis is world-wide, although keys are given only for the species of *Tetracotyle*, *Diplostomulum*, and *Neascus* of North America. Representatives of the different genera are figured and drawings are included of all available illustrations of strigeoid metacercariae of fishes.

SYNOPSIS OF STRIGEOIDEA (TREMATODA) OF FISHES AND THEIR LIFE CYCLES

By GLENN L. HOFFMAN, *Fishery Research Biologist*, BUREAU OF SPORT FISHERIES AND WILDLIFE

The object of this review is to bring together information concerning the life histories and identification of all of the known strigeoids (members of the superfamily Strigeoidea) which have fish as their second intermediate hosts. Dr. G. R. LaRue has suggested (personal communication) that the common name for this group should be "strigeoid" rather than "strigeid" because the latter might be confused with one family, Strigeidae, of the Strigeoidea. As used here, strigeoid refers to the entire superfamily, Strigeoidea Railliet 1919, which contains the families Strigeidae Railliet 1919, Diplostomatidae Poirier 1886, Cyathocotylidae Poche 1926, Proterodiplostomatidae Dubois 1937, Bolbocephalodidae Strand 1935, and Brauninidae Bosma 1931. In the examination of fish, whether for routine surveys, strigeoid life history studies, or in using the parasites for physiological, morphological, and pathological studies the immediate problem is the identification of the parasite. The larval strigeoids of the fish are often very difficult to identify and, in some instances, the species cannot be identified with certainty without rearing specimens to the adult stage in an experimental final host.

The following strigeoids have been reared to adult stage and identified:

In unfed chicks: *Posthodiplostomum minimum centrarchi* and *P. m. minimum* by Ferguson (1937), Hoffman (1958a); *Ornithodiplostomum ptychocheilus* by Hoffman (1954); *Diplostomum bacri cucaliae* by Hoffman and Hundley (1957); *Apatemon gracilis pellucidus* by Hoffman (1959); *Hysteromorpha triloba* by Hoffman (this paper); and *Linstowiella szidati* by Anderson and Cable (1950).

In domestic ducks: *Apatemon fuliginae* and *A. pellucidus* by Yamaguti (1933); *Diplostomum phoxini* by Arvy and Buttner (1954), Bell and Hopkins (1956), and Rees (1955); *Ornithodiplostomum ptychocheilus* by Van Haitsma (1930); *Cyathocotyle gravieri* (cf. Dubois, 1938); *C. melanittae* by Yamaguti (1942).

In gulls: *Cotylurus pileatus* (cf. Dubois, 1938); *Mesoophorodiplostomum pricei* (cf. Dubois, 1938).

In herons: *Hysteromorpha triloba* adults and non-ovigerous adults; *Mesostephanus odhneri* (cf. Dubois, 1938).

In hawks: *Neodiplostomum perlatum* (cf. Dubois, 1938).

In owls: *Diplostomum bacri cucaliae* by Hoffman and Hundley (1957).

In cats and dogs: *Mesostephanus appendiculatus*, *Prohemisotomum vivax* (cf. Dubois, 1938); *Prosostephanus industrius* by Tang (1941).

In mice: *Paracoenogonimus ovatus* by Komiya (1938).

In snakes: *Prohemistomum chandleri* by Vernberg (1952).

Posthodiplostomum minimum has been reared to adult stage in culture by Ferguson (1940); and *Diplostomum phoxini* has been reared by Bell and Smyth (1958). The keys by Dubois (1938, 1953) are very useful in identifying the adults.

Only one strigeoid, a cyathocotylid (*Holostephanus ictaluri*) has been recorded as an adult from fish; and only one strigeoid metacercaria, again a cyathocotylid (*Szidatia joyeuxii*) has been recorded from frogs as well as fish.

Briefly, the following routine may be used for examining fish for strigeoid metacercariae:

(1) *Skin.*—If cysts are pigmented (usually with melanin, black, or sometimes xanthine, yellow), the presence of the cysts, about 1 mm. in diameter, is obvious; if not pigmented they are often discerned by their slightly raised surfaces. The fins should be examined in a physiological salt solution under the dissection microscope.

(2) *Muscle.*—If pigmented, the cysts are easily discovered as the tissue is teased apart in the saline solution; a section is examined under the dissection microscope as the muscle is teased apart.

(3) *Gills, gill arches, and viscera.*—Examine under dissection microscope.

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(4) *Brain and anterior of spinal cord.*—Open cranium in saline solution and tease tissue apart under dissection microscope.

(5) *Eyes.*—Examine in saline solution under the microscope and tease apart.

Artificial digest is a useful method of separation when metacercariae are not numerous or are very small, particularly when the parasite is present in muscle. It is also useful for obtaining large numbers of some metacercariae for life history and physiology studies; a few species are killed, but may be recovered intact if not left in the digesting solution too long. Usually 0.5 percent pepsin, 0.5 percent hydrochloric acid in 0.65 percent saline solution is used; the amount of acid may be varied, but more than 0.25 percent kills some metacercariae. Usually 1 percent HCl is used for mammalian tissue, but fish flesh digests more readily; the fish may be ground or cut in small pieces and placed in jars with the solution at the rate of approximately 1 gram of tissue to 20 milliliters of solution. The author uses a water shaker (Hoffman, 1955a). Nearly complete digestion of the tissue can be obtained in an hour or two by this method, but cysts in the viscera are liberated in 10 to 15 minutes. The cysts settle in 5 to 15 minutes after digestion and the supernatant fluid is then decanted; usually two rinses in the saline solution facilitates examination.

Preserved material is usually unsatisfactory because the metacercariae are contracted too much for study; intact metacercariae cannot be digested from preserved material.

Some metacercariae are freed from their cysts during the pepsin digest, and some are not; at least one species, the tetracotyle of *Apatemon pellucidus*, can be freed by following the pepsin digest with a 10-minute trypsin digest (Hoffman, 1959). The trypsin solution consists of 0.1 percent trypsin in 1 percent sodium bicarbonate.

For microscopic examination in most instances the metacercariae can best be studied alive. Anesthetics are useful, such as nicotine sulfate: 1 drop of Black Leaf 40 to 400 ml. of 0.85 percent saline solution. Menthol-tween: 0.25 percent menthol in 5 percent Tween 80, one percent chlorobutanol or 0.4 percent chloretone. Cover glass pressure is probably the best method for flattening live worms to study the excretory system. Hypertonic saline solutions are sometimes useful in studying the excretory system (L. D. Nolf, personal communication). Fixed, stained mounts are necessary for some organs. The author believes that it is best to sketch the metacercaria in its characteristic live position and fill in the details later in composite fashion from stained and mounted slides. The use of hot (nearly boiling) Bouin's solution has produced the most uniform, most nearly natural shape of the metacercariae. Hot water (65° C.), followed by formalin as used for cestode larvae by M. C. Meyer (personal communication), sometimes works equally well for metacercariae. No one method has been found to work equally well on all metacercariae. The use of PVA–AFA (polyvinyl alcohol: alcohol, formalin, and acetic acid) fixative adhesive is sometimes helpful in handling small forms (Hoffman, 1954a).

It is probable that the metacercariae of strigeoid trematodes which develop in fish-eating birds and mammals are more frequently seen, and are easier to obtain than the adult worms; it would be advantageous if they could be identified easily.

There are no comprehensive publications on the freshwater fish parasites of North America. The publications of Van Cleave and Mueller (1932, 1934) and Mueller and Van Cleave (1932) are most complete, and the fish-parasite survey publications of Bangham et al. (1933–54) and Fischthal (1947–50) are also helpful. Some excellent foreign treatises on the subject, which are helpful in studying certain groups of fish parasites, are those of Dawes (1947), Plehn (1924), Yamaguti (1933), Schäperclaus (1954), Sproston (1946), Travassos, Artigas, and Pereira (1928), and the monographs of Dubois (1938, 1953) on strigeoids.

Only key references, or those not given in Dubois (1938), are given in the following synopsis, which is arranged according to the four larval strigeoid groups found in fish. Where the adult is known the parasite is placed in the proper family, and all known stages of the parasite are discussed. If the adult is unknown, the larval species is placed in alphabetical order following the known species. In the synoptic descriptions the reserve excretory system has been slighted, not because of lack of importance, but because of lack of study. LaRue (1957) has pointed out the importance of the excretory system in the classification of trematodes, and the author suggests that further study might help in the identification and

classification of the strigeoids, particularly *Diplostomulum* and *Neascus* species.

Although the synopsis is compiled from world literature, the three keys to metacercariae from fishes are restricted to North America. The keys are entirely artificial and include location in the host, as well as morphological characteristics as aids to the identification of the strigeoids. The locations in the host were found to be consistent for the larvae studied, but some may not be specific as to location. Unless stated otherwise all measurements are in microns and were made from living material. In the following synopsis the strigeoid metacercariae are placed in four larval groups (Tetracotyle, Diplostomulum, Neascus, and Prohemistomulum), which are usually treated as genera; that is, if the adult is not known, a strigeoid metacercaria may be placed in one of the four larval groups. If the adult is known, the metacercaria may be given the same name as the adult, or it may be given the larval group name. I prefer to use the two names in combination to avoid confusion.

I wish to thank Dr. G. R. LaRue, Animal Disease Parasite Research Branch, United States Agricultural Research Service, Beltsville, Md., for a critical review and for many helpful suggestions in the preparation of this paper, also, Dr. L. O. Nolf, University of Iowa, Dr. S. F. Snieszko and Dr. Ken Wolf, Eastern Fish Disease Laboratory, Leetown (P.O. Kearneysville, W. Va.), for reviewing the manuscript.

EXPLANATION OF FIGURES

ACT—accessory collecting tubule.
ALEV—anterior lateral excretory vessel.
AN—anterior nerve.
APCT—anterior primary collecting tubule.
ATCV—anterior transverse commissural vessel.
AVL—anterior of ventral lip of "cup".
BC—bursa copulatrix.
C—constriction between forebody and hindbody.
CC—calcareous corpuscles.
CCP—common collecting trunk of primary excretory system.
CH—cavity of holdfast organ.
CLS—cavity of lateral pseudosucker.
CP—cirrus pouch.
DEV—dorsolateral excretory vessel of hindbody.
E—esophagus.
EB—excretory bladder.
EC—excretory canal.
ED—excretory duct.
EG—gelatinous globule of excretory fluid.
ELN—network of extralateral excretory vessels.
EMH—external meatus of holdfast.
EO—embryonic ovary.
EP—excretory pore.
ET—embryonic testes.
FB—forebody.
GC—unicellular gland cells.
GP—genital pore.
GPr—genital primordium.
H—holdfast organ.
HB—hindbody.
HG—holdfast gland.
HV—holdfast vessel.
IC—intestinal caecum.
IL—inner lip of holdfast.
ILEV—intralateral excretory vessel.
J—apparent point of union of primary excretory apparatus with reserve bladder.
LCV—lateral collecting vessel.
LPS—lateral pseudosucker.
M—mouth.
MA—median anastomosis.
MDEV—median dorsal excretory vessel.
MEV—marginal excretory vessel.
MLS—external meatus of lateral sucker.
MVEV—median ventral excretory vessel.
O—ovary.
OL—outer lip of holdfast.
OS—oral sucker.
Ph—pharynx.
PLEV—primary lateral excretory vessel.
PLF—posterior lip of forebody.
PN—posterior nerve.
PPh—prepharynx.
PPCT—posterior primary collecting tubule.
PT—posterior tubule.
PTCV—posterior transverse commissural excretory vessel.
RE—reserve excretory system.
SCV—semicircular commissural vessels.
SPNC—suprapharyngeal nerve commissure.
T—testes.
TB—tubular portion of excretory bladder.
TCV—transverse commissural vessel.
TPEA—tubules of primary excretory apparatus.
VEV—ventrolateral excretory vessels of hindbody.
VS—ventral sucker.

I. TETRACOTYLE

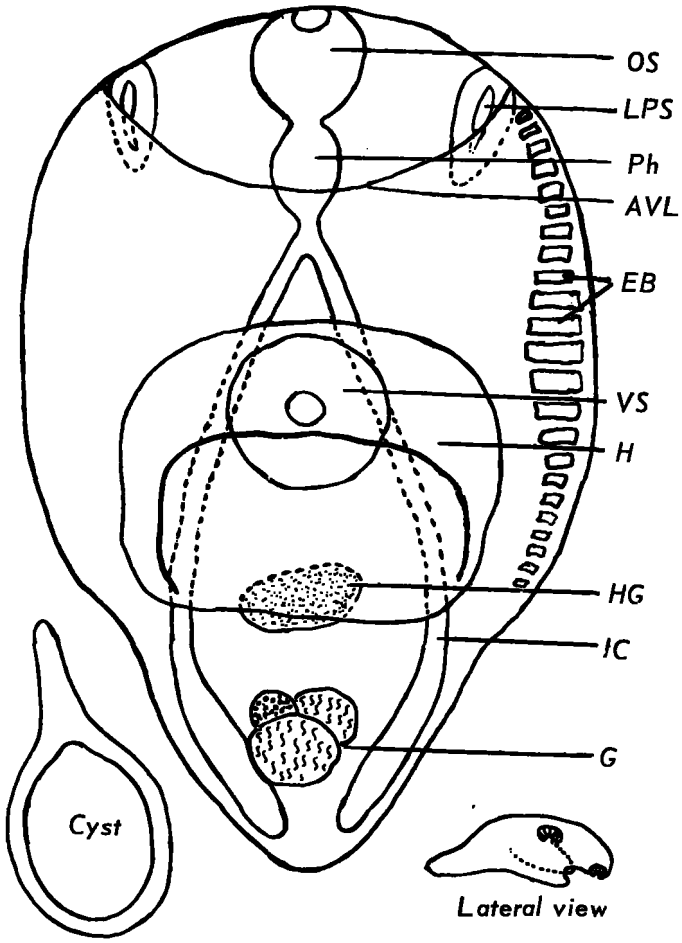

FIGURE 1.—Tetracotyle of *Apatemon gracilis pellucidus* (composite drawing from Hoffman, 1959).

This larval group has been described by Faust (1918) and Hughes (1928a, 1928d); it possesses these characteristics: (1) forebody oval or ovate-oblong in contour and relatively thick, concave ventrally or cup-shaped; (2) hindbody present as a short rounded prominence at the posterior end of the forebody, sometimes inconspicuous; (3) reserve bladder consists of a large continuous space occupying the dorsal and lateral regions of the forebody, with a sheetlike extension into the ventral lip of the anterior suctorial pocket, with small spherical calcareous concretions in the reserve excretory vessels and mostly in the anterior part of the worm; (4) a pair of lateral pseudosuckers (cotylae) on the anterolateral edges beside the oral sucker; and (5) a true cyst of parasite origin.

The last synopsis of the Tetracotyle group was by Hughes (1928d).

A. Family STRIGEIDAE Raillet.

1. *Apatemon fuligulae* Yamaguti, 1933.
Snail host and cercaria unknown.

Fish hosts: Siluridae—*Parasilurus* and *Pseudobargus*. Encysted in the skin and flesh, *Tetracotyle fuligulae* Yamaguti, 1933.

Cyst: Elongate, oval, 385 by 200μ; larvae easily liberated.

Metacercaria (fig. 2): Tetracotyliform; forebody long, flat, 540 by 380μ (Yamaguti, 1933, omitted the anterior limit of the ventral surface of the forebody); hindbody stumpy, 250 by 160μ; oral sucker 50μ; lateral pseudosuckers shallow; prepharynx short; pharynx elongated, 20μ wide; ventral sucker pre-equatorial, 60μ long; holdfast with anterior lip which extends over ventral sucker, 160 by 240μ; holdfast gland

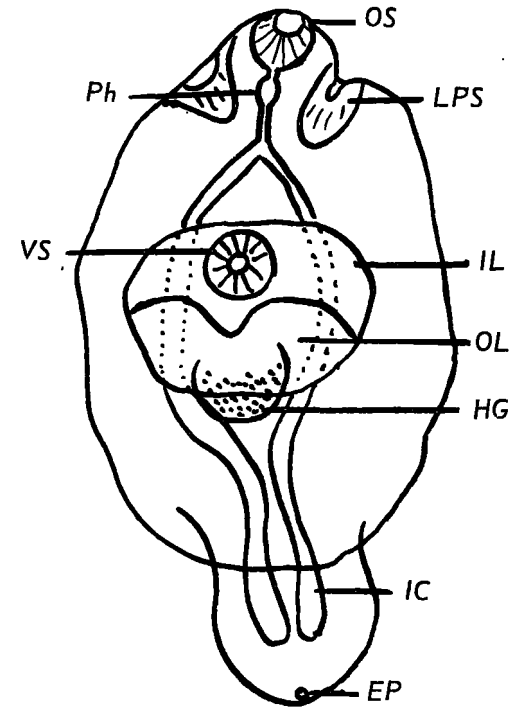

FIGURE 2.—Tetracotyle of *Apatemon fuligulae* (from Yamaguti, 1933).

prominent; genital primordia present (Yamaguti, 1933).

Final host: Anatidae–domestic duckling (experimental; Yamaguti, 1933); *Melanitta fusca stejnegeri; Nyroca fuligula.* Japan; Europe.

2. *Apatemon pellucidus* Yamaguti, 1933.
Snail host and cercaria unknown.

Fish host: Eleotridae–*Mogurnda obscura.* Encysted in body cavity. *Tetracotyle pellucida* Yamaguti.

Cyst: Oval, 650–700 by 500–600μ; host cyst fibrous, 50–80μ thick and one end generally produced into a blunt point; difficult to liberate larva.

Metacercaria (fig. 3): Tetracotyliform; 480–750μ long and divided into two distinct regions; forebody cup-shaped, 370–620 by 330–440μ; hindbody short-cylindrical, 130–200 by 150–210μ; esophagus short; lateral pseudosuckers deep and anterior wall sometimes extending forward tonguelike; ventral sucker slightly post equatorial, 80–130 by 90–140μ; holdfast divided into ventral and dorsal lobes; holdfast gland 30–40 by 50–60μ; three genital primordium bodies in hindbody; excretory system highly developed.

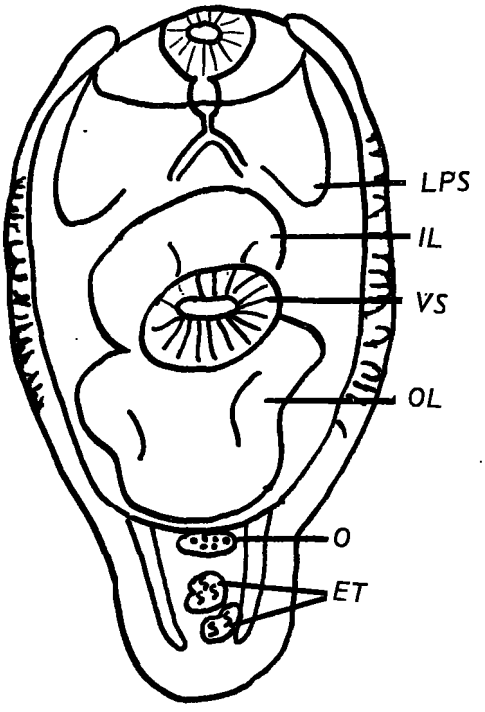

FIGURE 3.—Tetracotyle of *Apatemon pellucidus* (from Yamaguti, 1933).

Final host: domestic duck (experimental). Japan.

3. *Apatemon gracilis pellucidus* (Yamaguti, 1933) Dubois, 1953.
(This may be the same species as the preceding.)
Snail host and cercaria unknown.

Fish host: Gasterosteidae–*Eucalia inconstans.* Encysted in muscle (*Tetracotyle* species, fig. 1) described in Hoffman, 1959.

Final host: Unfed chicks; (experimental). North Dakota.

4. *Cotylurus communis* (Hughes, 1928; LaRue, 1932).
Snail host unknown, cf. Olivier and Cort (1942).

Fish host: Catostomidae–*Catostomus commersonii.* Percidae – *Stizostedion canadense griseum, S. vitreum.* Percopsidae–*Percopsis omiscomaycus.* Encysted in pericardial cavity, *Tetracotyle communis* Hughes.

Cyst: Nearly spherical, 980–1330μ in diameter; usually easy to free larva.

Metacercaria (fig. 4): Tetracotyliform; 570–950 by 570–900μ; body thick and slightly concave ventrally; hindbody very small; oral sucker 120–150μ; pharynx inconspicuous; esophagus short and narrow; lateral pseudosuckers smaller than oral sucker and not forming "ears" or "tongues" (i.e., not protrusible); ventral sucker 140–200 by 180–222μ; holdfast simple, 140–200 by 260–360μ; one genital primordium in hindbody.

Final host: Laridae (gulls)–*Larus argentatus.* Michigan.

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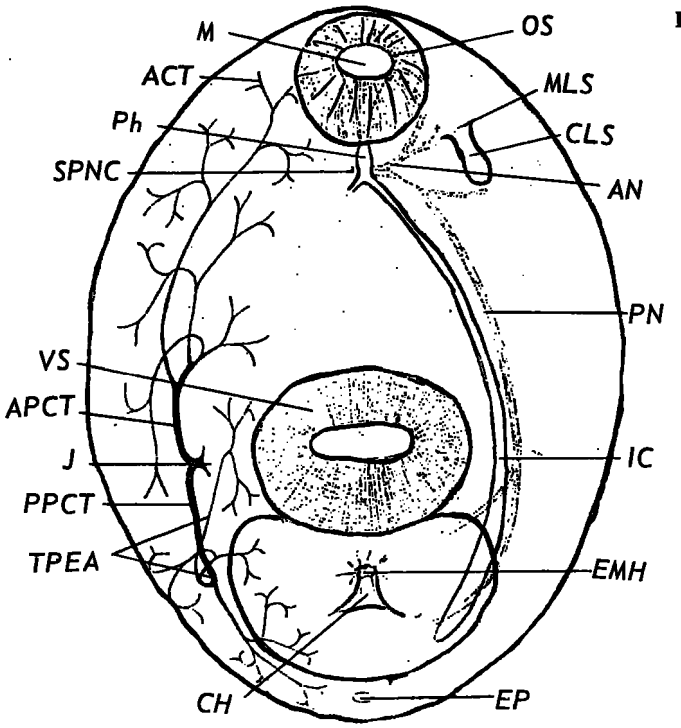

FIGURE 4.—Tetracotyle of *Cotylurus communis* showing primary excretory system (from Hughes, 1928d).

5. *Cotylurus pileatus* (Rudolphi, 1802) Dubois, 1937.

Snail host and cercaria unknown.

Fish hosts: Cyprinidae–*Abramis* species, *Alburnus alburnus*, *Phoxinus* species, *Blicca bjoerkna*. Esocidae–*Esox lucius*. Percidae–*Acerina cernua*, *Perca fluviatilis*. Encysted in the pericardial cavity, peritoneum, and eye muscles (*Tetracotyle pileata* (Rudolphi), *T. ovata*) Linst 1877, *T. variegata* (Creplin) Hughes, 1928, cf. Vickers (1951).

Cyst: Nearly spherical, ca. 1 mm. in diameter.

Metacercaria: Tetracotyliform; 840 by 570μ; oral sucker 98–130μ; ventral sucker 160–210μ.

Final host: Alcidae–*Alca torda* (auk), *Uria aalge* = *U. troille* (murre). Laridae (gulls and terns)–*Chlidonias nigra*, *Larus* species, *L. ridibundus* (experimental), *Sterna hirundo*, *S. paradisea*, *Thalasseus sandvicensis*=*Sterna* cantiaca. Europe, Asia.

B. Family undetermined, probably STRIGEIDAE.

6. *Tetracotyle biwaensis* Goto and Ozaki, 1930.

Fish host: Encysted in the body cavity of *Pseudogobio*. Japan (Yamaguti, 1942).

Cyst: Original description not available to author.

Metacercaria (fig. 5): Body oval, 850–950 by 550–700μ; oral sucker 114–130 by 120–150μ; pharynx 38–40 by 22–30μ; esophagus short; lateral pseudosuckers posterolateral to oral sucker; ventral sucker postequatorial, 150–162 by 160–170μ; holdfast organ 120–180 by 200–250μ; genital primordium present in hindbody.

7. *Tetracotyle diminuta* Hughes, 1928.

Encysted in the pericardial cavity and adipose tissue behind eyes of *Perca flavescens* and *percopsis omiscomaycus*. Michigan.

Cyst: Ovate, 330–450 by 280–420μ. Difficult to free larva.

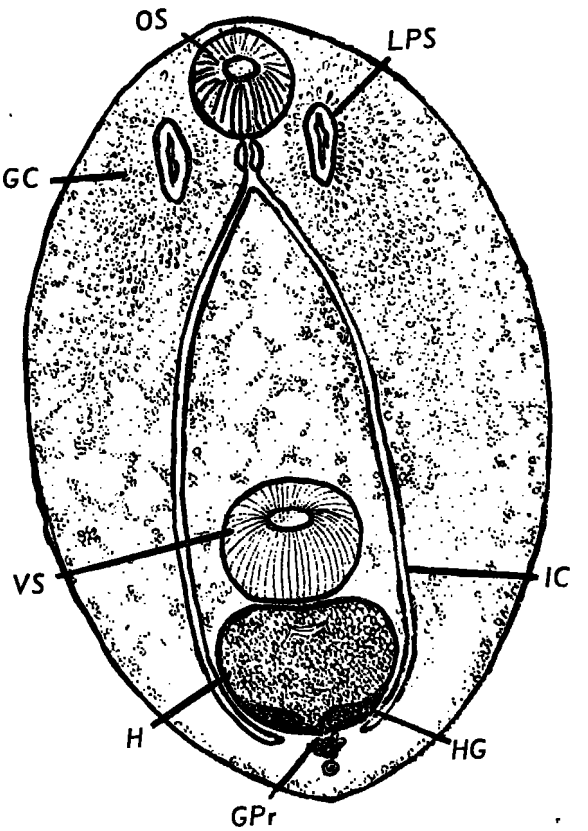

FIGURE 5.—*Tetracotyle biwaensis* (from Yamaguti, 1942).

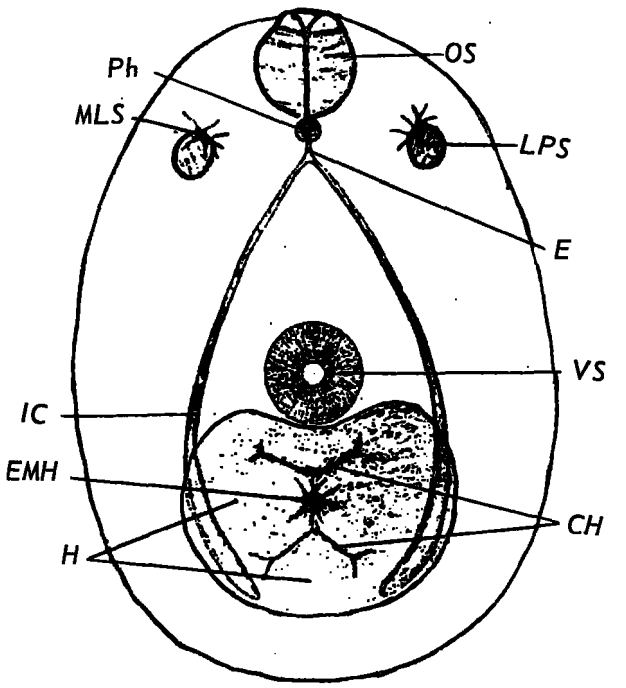

FIGURE 6.—*Tetracotyle diminuta* (from Hughes, 1928d).

Metacercaria (fig. 6): Body much like *Tetracotyle communis*. Surface appearing spinous because of mucus extrusions. 286–429 by 204–334μ; oral sucker 51–63μ; pharynx 20–23 by 15–20μ; esophagus short; lateral suckers deep and may be everted; ventral sucker 51–63μ; holdfast 78–150 by 90–180μ; reproductive and excretory systems similar to *Tetracotyle communis*.

8. *Tetracotyle echinata* Diesing, 1858.
Encysted in peritoneum of *Leuciscus* and *Acerina*. Europe.

Cyst: Oval 500–600μ in diameter.

Metacercaria: Oval, 620μ long; spines sparse, 3–4μ long. May be mucous extrusions similar to those of *T. diminuta*. This species is characterized by the large size of the hindbody.

9. *Tetracotyle indicus* Singh, 1956.
In freshwater fish. India.

10. *Tetracotyle intermedia* Hughes, 1928.
Encysted in the pericardium of *Prosopium quadrilaterale* and *Leucichthys artedi*. Michigan.

Cyst: Ovate, 550–750 by 400–560μ.

Metacercaria: Similar to *T. diminuta;* body 370–590 by 300–600μ; oral sucker 60–75 by 54–60μ; *pharynx* 24–30 by 15–18μ; lateral pseudosuckers similar to *T. diminuta;* ventral sucker 45–62 by 60–81μ; holdfast 110–116 by 150–200μ.

11. *Tetracotyle parvulum* (*Diplostomum parvulum*) (Stafford, 1904).
May be *Cotylurus communis;* cf. Hughes (1929a).

12. *Tetracotyle percae-fluviatilis* (Moulinié) von Linstow, 1877.
Encysted in the heart region of *Perca;* Europe. Carp; Russia (Astakhova, 1953).

Metacercaria: 380–880 by 300–500μ; oral sucker 60μ; lateral suckers 66 by 133μ; ventral sucker inconspicuous; holdfast 80–100μ.

13. *Tettracotyle sogdiana* Pavlovsky and Anitchkov, 1922.
Encysted in pancreas of *Schizothorax*. Turkestan.

Metacercaria: Ventral sucker anterior to the middle of the body; longitudinal invaginations in dorsal body wall.

14. *Tetracotyle sophoriensis* Singh, 1956.
In fresh water fish; India.

15. *Tetracotyle tahoensis* Haderlie, 1953.
Encysted in the pericardium of *Catostomus tahoensis*. California.

Cyst: Spherical, yellow or straw colored; ca. 630μ in diameter (fixed specimen) worms easily freed.

Metacercaria (fig. 7): 520–740 by 350–490μ; oral sucker 100–120μ; pharynx indistinct; lateral suckers ventrally located, ca. 110μ in diameter; ventral sucker 80–110 by 130–150μ; holdfast 120–140 by 160–170μ; genital primordium a small, single mass (fixed specimens).

16. *Tetracotyle* species.

Reported from many fishes by Bangham (1944), Wisconsin (1951), Wyoming (1955), Lake Huron; Bangham and Adams (1954), British Columbia; Bangham and Venard (1942), Tennessee; Fischthal (1947a, 1947b, 1950), Wisconsin; Hunter (1942), Connecticut; Sinderman (1953), Massachusetts; Van Cleave and Mueller (1934), New York; Yamaguti (1942), Japan.

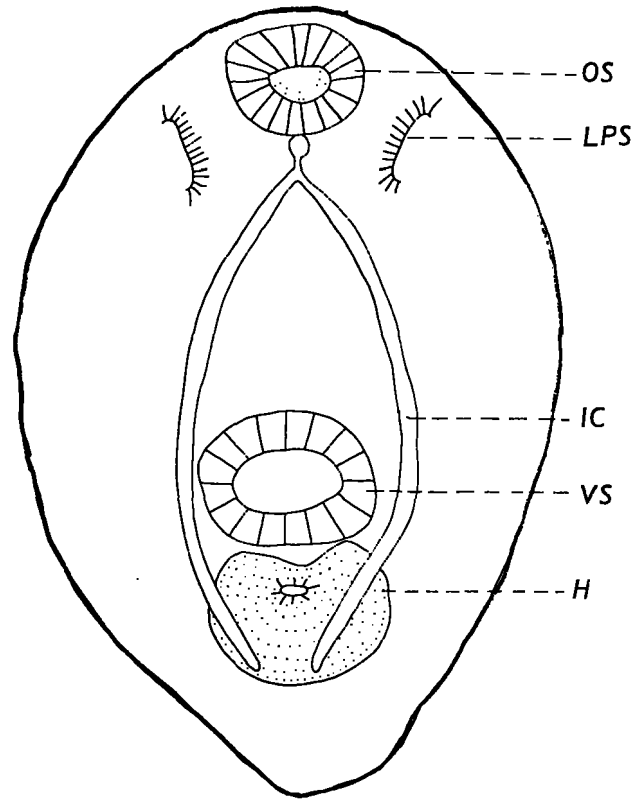

FIGURE 7.—*Tetracotyle tahoensis* (from Haderlie, 1953).

KEY TO THE KNOWN SPECIES OF TETRACOTYLE OF NORTH AMERICAN FISH

Undoubtedly there are many undescribed species of *Tetracotyle*.

1. Cyst with a prominent tail-like projection; found in musculature of *Eucalia inconstans*_____*Apatemon pellucidus*
1. Cyst without a prominent tail-like projection; not found in musculature but found in viscera, particularly pericardium _____ 2
2. Lateral cotylae as large as oral sucker_____*T. tahoensis*
2. Lateral cotylae decidedly smaller than oral sucker_____ 3
3. Diameter of holdfast organ about one-half to one-third the total length of the parasite; difficult to remove parasite from its cyst_____*T. diminuta*
3. Diameter of holdfast organ less than one-third the total length of the parasite_____ 4
4. Intact cyst about 1000μ in diameter; parasite about 700μ long; pharynx observed with difficulty; parasite easily freed from cyst_____*Cotylurus communis*
4. Intact cyst about 600μ in diameter; parasite about 450μ long; pharynx easily seen_____*T. intermedia*

II. DIPLOSTOMULUM

This larval group has been described by Hughes (1929a) and possesses these characteristics: (1) forebody foliaceous, concave ventrally; (2) hindbody present as a small conical prominence on the posterodorsal part of the forebody; (3) reserve system (bladder) consists of a system of more or less definitely arranged tubules with calcareous corpuscles, round or ellipsoidal, disposed in vesicles at the termini of small branches; (4) usually a pair of lateral organs (the so-called lateral suckers) on the anterolateral edges beside the oral sucker; and (5) no true cyst of parasite origin.

The last synopsis was that of Hughes (1929a).

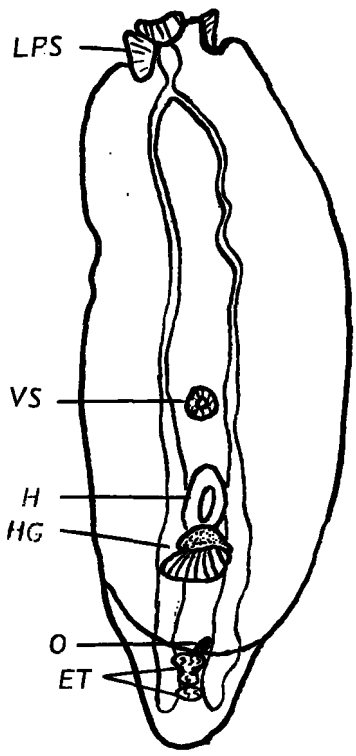

FIGURE 8.—Diplostomulum of *Bolbophorus confusus* (from Ciurea, 1930).

A. Family DIPLOSTOMATIDAE Poirer, 1886.

1. *Bolbophorus confusus* (Kraus, 1914) Dubois, 1935.

Snail host and cercaria unknown.

Fish hosts: Cyprinidae–*Abramis* species, *Idus idus*, *Scardinius erythrophthalmus*. Esocidae–*Esox lucius*. Mugilidae–*Mugil saliens*. Percidae–*Perca fluviatilis*. Encysted in the musculature (*Diplostomulum confusum* Ciurea, 1933). Europe.

Host cyst: More or less lemon shaped, 990–1390 by 690–860μ.

Metacercaria (fig. 8): 1,520–1,850 by 500–660μ; oral sucker 84–99μ; pharynx 57 by 44μ; ventral sucker 66μ; holdfast 342–343 by 150–250μ.

Final host: Pelecanidae–*Pelecanus*. Austria, Romania, Syria, Egypt, Minnesota (U.S.A.).

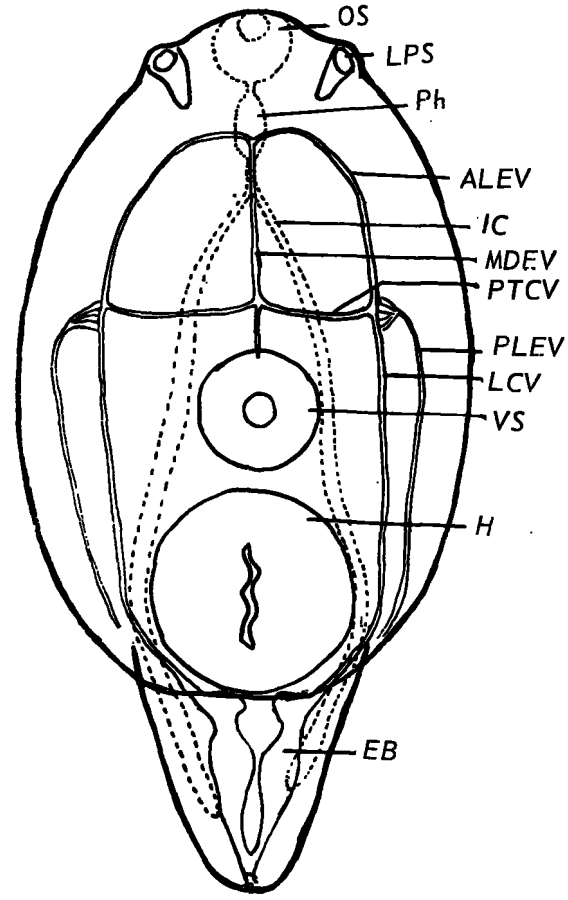

FIGURE 9.—Diplostomulum of *Diplostomum baeri eucaliae* (from Hoffman and Hundley, 1957).

2. *Diplostomum baeri eucaliae* Hoffman and Hundley, 1957.

Snail host: *Stagnicola* species.

Fish host: Gasterosteidae–*Eucalia inconstans*. Unencysted in brain (fig. 9).

Host cyst: "Pseudo-cyst" containing many larvae.

Metacercaria (fig. 9): Most like *D. phoxini;* two distinct body regions; body 500–700 by 320–380μ; hindbody 76 to 150μ long; forebody minutely spined; oral sucker ca. 65μ; prepharynx short; pharynx ca. 50μ long; esophagus ca. 20μ long; lateral pseudosuckers prominent, 30μ in diameter and 47–60μ deep; ventral sucker ca. 90μ; holdfast ca. 150μ; calcareous corpuscles round, 4–9μ in diameter.

Final host: Wild mallard duck; experimental in unfed chick (Hoffman, 1955b; Hoffman and Hundley, 1957), North Dakota.

3. *Diplostomum flexicaudum* (Cort and Brooks, 1928) Van Haitsma, 1931.

Snail hosts: *Stagnicola* species; (*Cercaria emarginatae* Cort), *Fossaria*, *Stagnicola*, *Lymnaea* (Cort, Hussey, and Ameel, 1957). Precocious metacercaria in snail (Olivier, 1940).

Fish hosts: Catostomidae–*Catostomus* species. Centrarchidae–*Lepomis macrochirus* (experimental; Ferguson, 1943b). Cyprinidae–*Pimephales promelas* (experimental; Ferguson, 1943b). Salmonidae–*Salmo irideus* (experimental; Ferguson, 1943b); experimental in tadpoles, frogs, turtles, chicks, ducklings, mice, rats, guinea pigs, and rabbits, (Olivier, 1940; Ferguson, 1943b). Lens of the eye [*Diplostomulum flexicaudum* (Cort and Brooks), (*D. gigas* Hughes and Berkhout, 1929)].

Metacercaria (fig. 10): 500–900 by 400–450μ; hindbody ca. 100μ long; oral sucker 80–90μ; pharynx 60 by 23μ; ventral sucker 90μ.

Final host: Laridae (gulls)–*Larus argentatus*. Michigan; Minnesota.

4. *Diplostomum huronense* (LaRue, 1927) Hughes and Hall, 1929.

Snail host and cercaria unknown.

Fish hosts: Percidae–*Perca flavescens*. Percopsidae–*Percopsis omiscomaycus*. Eyes [*Diplostomulum huronense* (LaRue) Hughes and Hall].

Metacercaria (fig. 11): 280–600 by 100–150μ; hindbody ca. 90μ long; oral sucker 40–50 by 28–40μ; pharynx 35–40 by 26–28μ; ventral sucker 35–40μ; holdfast 50–80 by 70–80μ.

Final host: Laridae (gulls)–*Larus argentatus*. Michigan.

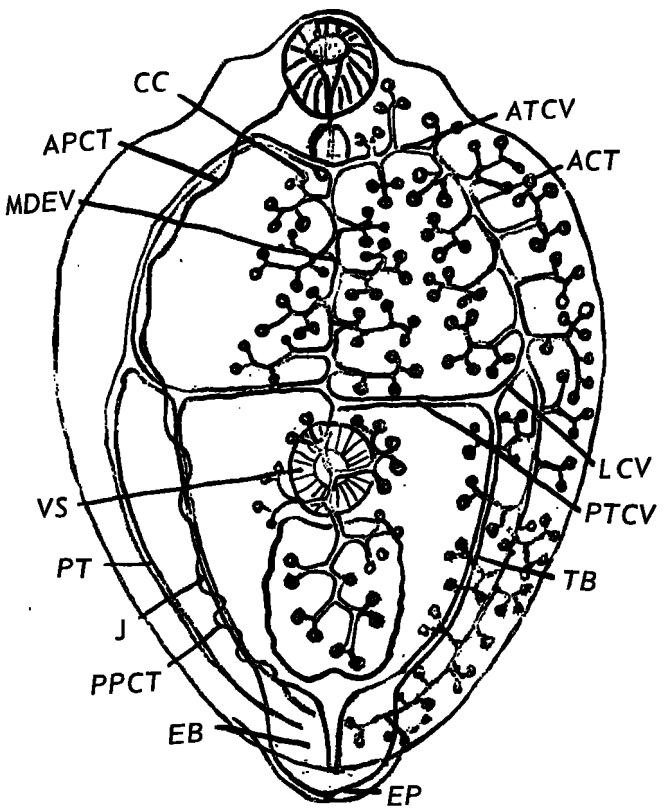

FIGURE 10.—Diplostomulum of *Diplostomum flexicaudum* showing reserve excretory system and associated calcareous corpuscles (from Hughes and Berkout, 1929).

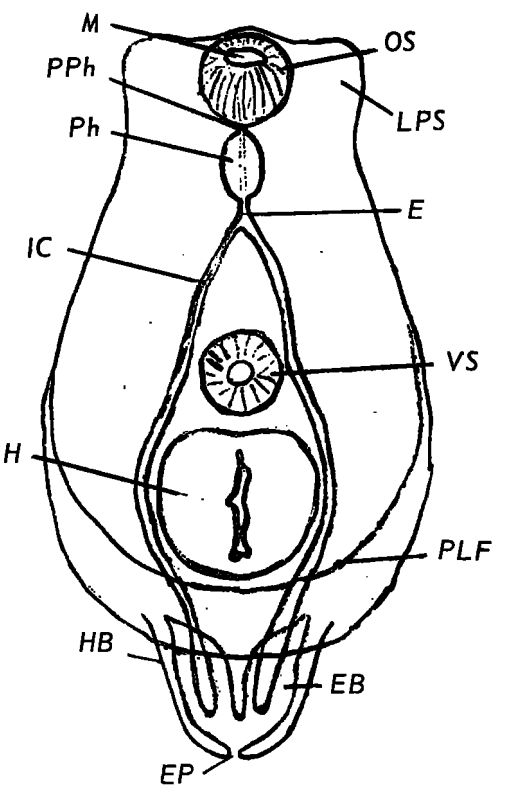

FIGURE 11.—Diplostomulum of *Diplostomum huronense* (from Hughes and Hall, 1929).

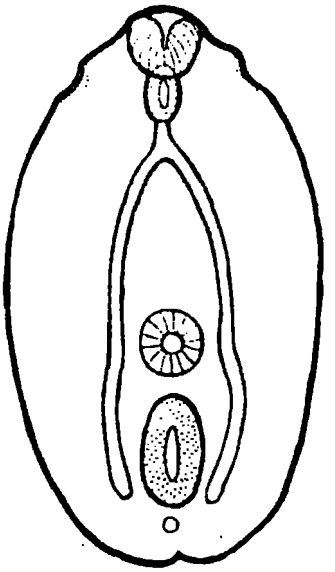

FIGURE 12.—Diplostomulum of *Diplostomum murrayense* (from Johnston and Angel, 1941).

5. *Diplostomum murrayense* Johnston and Angel, 1941.

Snail host: *Limnea lissoni.*

Fish hosts: Many species; in eyes.

Metacercaria (fig. 12): Original description (Johnston and Simpson, 1939) not seen by author.

Final host: Laridae–*Chlidonias leucopareia* (tern). Australia. (Johnston and Angel, 1941).

6. *Diplostomum pelmatoides* Dubois, 1932.
Erroneously reported as the adult of *Diplostomulum phoxini* by Rees (1955). See *Diplostomum phoxini.*

7. *Diplostomum phoxini* (Faust, 1918) Arvy and Buttner, 1954.
Snail host: *Lymnaea species* (Arvy and Buttner, 1954; Rees, 1957).

Fish host: Cyprinidae–*Phoxinus* species. Unencysted in brain, [*Diplostomulum phoxini* (Faust) Ashworth and Bannerman, 1927].

Metacercaria (figs. 13, 14): Body with two distinct regions, 247–344 by 130–215μ; spine-like striations in cuticle; oral sucker

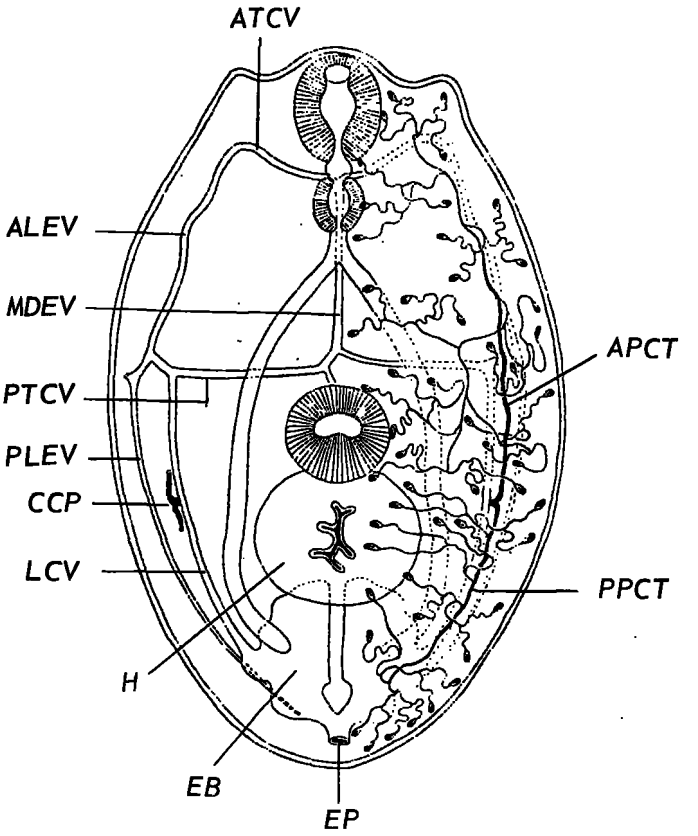

FIGURE 13.—Diplostomulum of *Diplostomum phoxini* showing primary excretory system (black) and reserve excretory system (from Rees, 1955). Note: normal shape probably similar to that of *D. baeri eucaliae* (fig. 9).

46 by 41μ; prepharynx small; esophagus short; lateral pseudosuckers prominent; ventral sucker 43 by 50μ; holdfast 66 by 83μ; calcareous corpuscles spherical or ovoid, 6–12μ in greatest diameter (Rees 1955); experimental in domestic duck. Arvy and Buttner, 1954. France. Bell and Hopkins, 1956; Rees 1955. England.

8. *Diplostomum spathaceum* (Rudolphi, 1819) Braun, 1893.
Snail host: *Lymnaea* species (*Cercaria C.* of Szidat) (Dawes, 1952).

Fish hosts: Acipenseridae–*Acipenser nudiventris.* Anguillidae–*Anguilla anguilla.* Centrarchidae–*Micropterus dolomieu.* Cichlidae–*Cichlasoma aureum* (Mexico–Caballero and Winter, 1954). Cobitidae–*Cobitis* species. Cyprinidae–*Abramis* species.

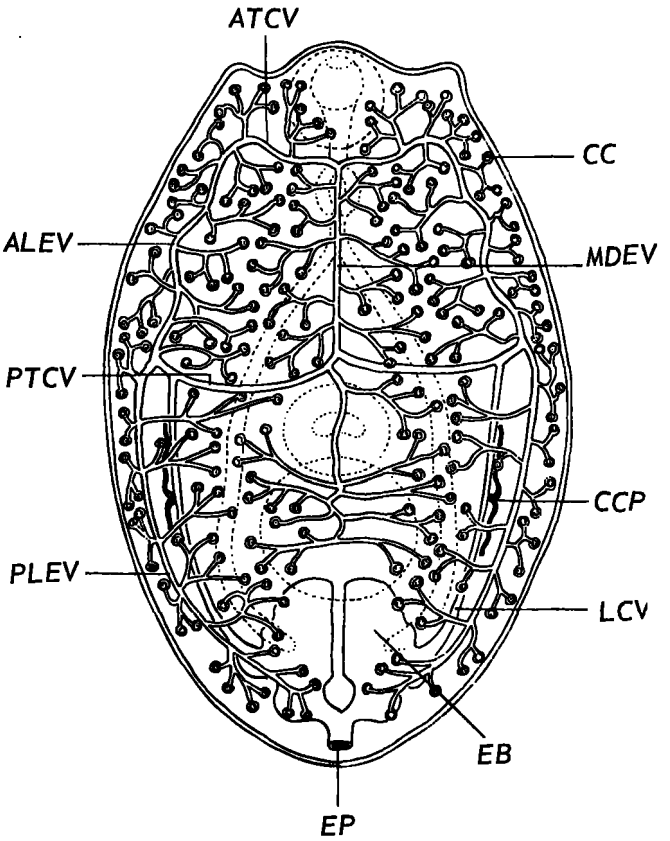

FIGURE 14.—Diplostomulum of *Diplostomum phoxini* showing reserve excretory system and associated calcareous corpuscles (from Rees, 1955).

Aspius a. erythrostomus, *Barbus* species, *Capoetobrama juschakewitschi*, *Carassius auratus gibelio*, *Chalcalburnus chalcoides*, *Chondrostoma nasus*, *Cyprinus carpio*, *Gobio fluviatilis*, *Leuciscus* species, *Pelecus cultratus*, *Phoxinus phoxinus*, *Scardinius erythrophtalmus*, *Squalius* species. Cottidae–*Cottus gobio*. Esocidae–*Esox lucius*. Gadidae–*Lota lota*. Gasterosteidae–*Gasterosteus aculeatus*, *G. pungitius*, *Pyrosteus platygaster*. Salmonidae–*Coregonus* species, *Salmo* species, *Thymallus thymallus*. Siluridae–*Silurus glanis*. *Eyes* (lens and vitreous humor) [*Diplostomulum spathaceum* (Rudolphi), Hughes 1929].

Metacercaria: Original descriptions not studied.

Final hosts: Alcidae–*Alca torda* (auk). Laridae (gulls and terns)–*Larus* species, *Rissa tridactyla*, *Stercorarius parasiticus*. Pelecanidae–*Morus bassanus*. Europe.

9. *Hysteromorpha triloba* (Rudolphi, 1819) Lutz, 1931.

Snail host: *Gyraulus hirsutus*, *Cercaria Hysteromorpha trilobae* Hugghins, 1954.

Fish hosts: Cyprinidae–*Abramis* species, *Hyborhynchus notatus*, *Idus idus*, *Leuciscus* species, *Tinca tinca*. Poeciliidae–*Poecilia vivipara*. Siluridae–*Ameiurus* species. Encysted in the musculature. (*Diplostomulum corti*) and (*D. trilobum*).

Host cyst: Delicate fibrous host cyst, 990–1320 by 830–1160μ.

Metacercaria (fig. 15): with two distinct body regions; body 1520 by 450μ (Hugghins, 1954). Body 700–880 by 400–350μ; oral sucker 62–72μ; pharynx 40–53 by 26–38μ; esophagus 15–21μ; lateral pseudosuckers deeply cupped; ventral sucker 73–86μ, pre-equatorial; holdfast trilobate; holdfast gland well developed; genital primordia well developed [fixed specimens (Hughes, 1929a).] European measurements slightly larger; cf. Dubois (1938).

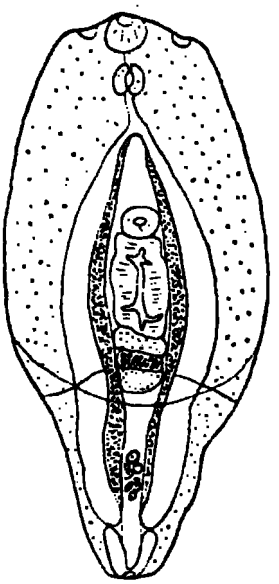

FIGURE 15.—Diplostomulum of *Hysteromorpha triloba* (from Hugghins, 1954).

Final hosts: Ardeidae (herons); *Ardea* species, *Nyctinassa* species, *Egretta* species (non-ovigerous adults; experimental). Phalacrocoracidae (cormorant)–*Phalacrocorax* species; unfed chick (experimental, North Dakota, Hoffman, this paper). Australia, Austria, Brazil, Japan, Romania, Manitoba (Canada); Illinois, Michigan, Minnesota, Wisconsin (U.S.A.), cf. Hughins, 1954.

10. *Tylodelphys clavata* (von Nordmann, 1932) Diesing, 1850.
Snail host and cercaria unknown.

Fish hosts: Cyprinidae–*Abramis* species, *Barbus branchycephalus*, *Carassius carassius*, *Leuciscus* species, *Scardinius erythrophthalmus*, *Tinca tinca*, *Aspius aspius*, *Chalcaburnus chaloides*. Esocidae–*Esox lucius*. Percidae–*Acerina cernua*, *Lucioperca volgensis*, *Perca fluviatilis*, *Sandra lucioperca*, *Aspro streber*. Salmonidae–*Coregonus* species. Vitreous humor [*Diplostomulum clavatus* (von Nordmann) Faust].

Metacercaria: Body elongate, length more than twice its width; lateral pseudosuckers sometimes "everted"; hindbody not clearly set off from forebody; body 310–520 by 100–150μ; oral sucker 41 by 33μ; prepharynx 11μ; pharynx 24 by 15μ; esophagus 33μ; ventral sucker 24μ; holdfast 59 by 37μ; excretory bladder Y-shaped and large [cf. Dubois (1938)].

B. Family undetermined, probably Diplostomatidae.

11. *Diplostomulum craniarium* (Diesing, 1850).
Cranial cavity of *Cobitis*. Europe. Reported only once.

12. *Diplostomulum* (*Tylodelphys?*) *destructor* Szidat and Nani, 1951.
Snail host: *Planorbis*. Cercaria similar to *Tylodelphys excavata*.
Fish hosts: Brain of *Basilichthys* species, *Fitzroys*, and *Salmo*. Argentina.

Metacercaria (fig. 16): Body 830 by 250μ; oral sucker 42μ; pharynx 40 by 16μ; lateral suckers not prominent; ventral sucker 42μ; holdfast 140 by 80μ; calcareous corpuscles oval [Szidat and Nani, 1951].

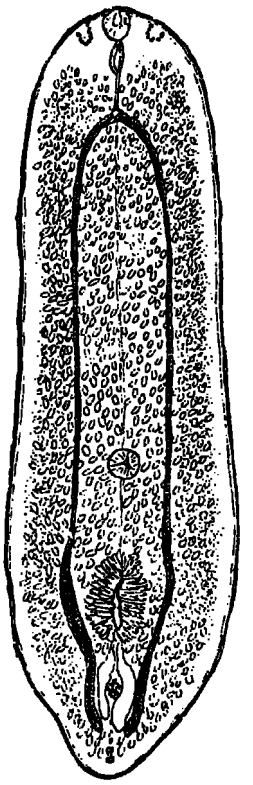

FIGURE 16.—*Diplostomulum* (*Tylodelphys?*) *destructor* (from Szidat and Nani, 1951).

13. *Diplostomulum elongatus* Singh, 1957.
Fish host: Encysted on mesenteries of the Indian freshwater fish, *Trichogaster fasciatus*.

Host cyst: 1,020 by 670μ.

Metacercaria (fig. 17): Elongate, aspinose, body division not distinct; forebody 972 by 558μ; hindbody 200μ long; oral sucker 45μ; no prepharynx; pharynx 30μ in diameter; esophagus short; lateral pseudosuckers not prominent, posterolateral to oral sucker; ventral sucker 70 by 40μ; holdfast much posterior to ventral sucker, 136μ in diameter; holdfast gland 132 by 30μ; genital primordia present; no calcareous corpuscles.

14. *Diplostomulum emarginatae* Olivier, 1942.
Similar to *D. flexicaudum*.

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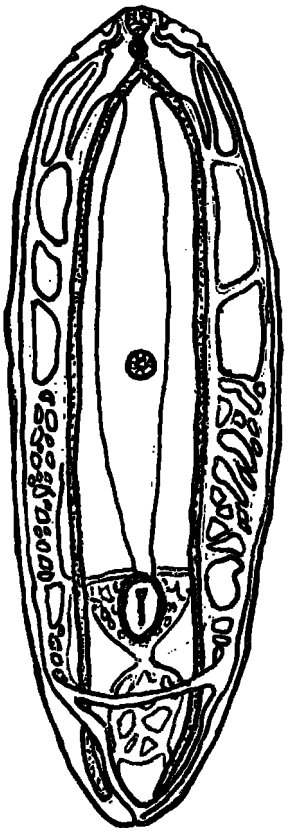

FIGURE 17.—*Diplostomulum elongatus* showing reserve excretory system (from Singh, 1957).

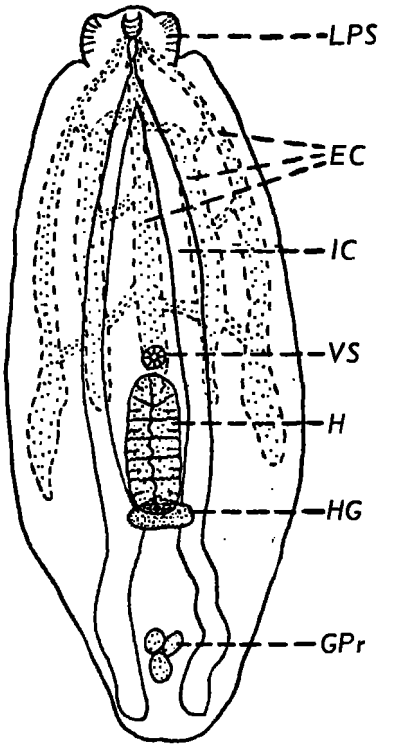

Figure 18.—*Diplostomulum ictaluri* (from Haderlie, 1953).

15. *Diplostomulum heterobranchi* (Wedl).
Fish host: In adipose tissue about brain of *Heterobranchus anguillaris*. Egypt.

16. *Diplostomulum ictaluri* Haderlie, 1953.
Fish host: Flesh of *Ictalurus catus*. California.

Host cyst: White, fibrous, and slightly spindle-shaped, ca. 1,500 by 950μ. Larva difficult to remove.

Metacercaria (fig. 18): Body regions indistinct; body 1,400-1,710 by 560–770μ; anterior end distinctly cone-shaped; oral sucker 60–90μ; no prepharynx; pharynx ca. 37μ; ventral sucker poorly defined, 40μ in diameter; holdfast 210 by 120μ; calcareous corpuscles round [fixed and stained (Haderlie, 1953)].

17. *Diplostomulum lenticola* (von Linstow, 1878).
Fish host: Lens of *Abramis*. Europe.

Metacercaria: Body outline broadly pyriform, 550 by 460μ; oral sucker 66μ; lateral pseudosuckers at extreme anterolateral reaches; ventral sucker present; holdfast 66μ.

18. *Diplostomulum metadena* Johnston and Angel, 1942.
Snail host: *Amerianna* species (also precocious metacercaria in small snail host).

Fish hosts: Natural in subcutaneous tissue of *Craterocephalus fluviatilis* and *Mugilogobius galwayi*. Experimentally in *Gambusia affinis* and *Phalloceros caudomaculatus*. Australia.

Host cyst: Thin, ovoid, 1,000–1,200 by 520–580μ. Larva easily freed.

Metacercaria (fig. 19): Body 880 by 300μ average; oral sucker 36μ; pharynx smaller than oral sucker; lateral pseudosuckers shallow but protrusible; ventral sucker ca. 25 by 20μ; holdfast ca. 120 by 80μ; genital

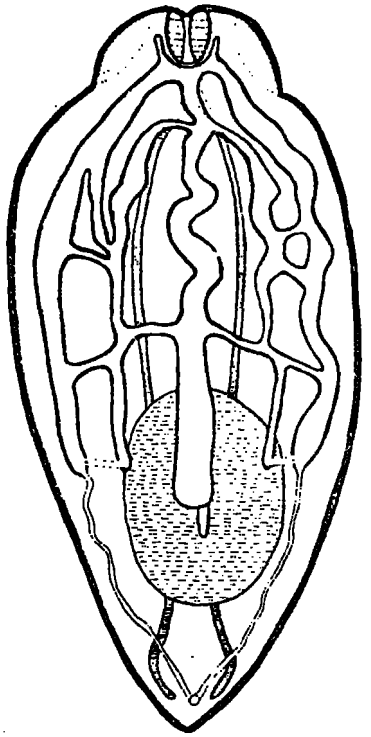

Figure 19.—*Diplostomulum metadena* showing reserve excretory system (from Johnston and Angel, 1942) [This specimen is flattened slightly.]

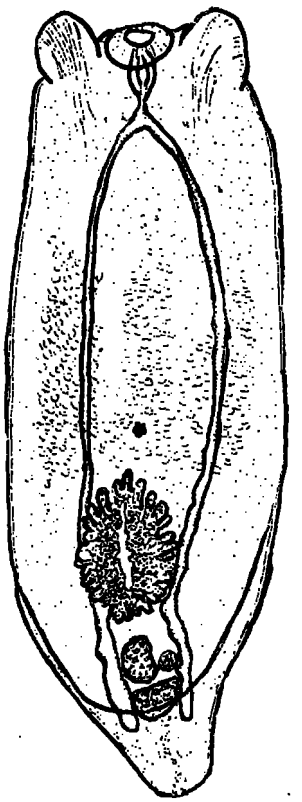

FIGURE 20.—*Diplostomulum mordax* (from Szidat and Nani, 1951).

primordia not well developed; calcareous corpuscles wanting (fixed and stained).

Final host: Adult (possibly is *Bolbophorus* of pelican).

19. *Diplostomulum mordax* Szidat and Nani, 1951.

Fish host: Brain of *Basilichthys* species.

Metacercaria (fig. 20): Body 680–880 by 330μ; oral sucker 50–80μ; pharynx 30 by 50μ; ventral sucker indistinct; genital primordia well formed (Szidat and Nani, 1951)..

Final host: Szidat and Nani suggest that the adult is *Austrodiplostomum mordax* from *Phalacrocorax*. Argentina.

20. *Diplostomulum petromyzi-fluviatilis* (Diesing, 1850).

Cyclostome host: Cranial cavity of *Petromyzon* species. Europe.

Metacercaria: Body 225–289 by 211–261μ; oral sucker 42–53μ; pharynx 31–49 by 17–25μ; cavity of lateral pseudosuckers 24–35μ deep, often spectacularly everted anteriorly; holdfast 63–109 by 105–112μ [fixed and stained (Hughes, 1929a)].

21. *Diplostomulum scheuringi* Hughes, 1929.

Has been recorded from the vitreous humor of eyes of fishes of the families Centrarchidae, Cyprinidae, Esocidae, Etheostomidae, Gadidae, Percidae, Percopsidae, Salmonidae and Siluridae by Bangham (1944), Wisconsin. Chandler (1951), Minnesota. Fischthal (1947b, 1950), Wisconsin. Haderlie (1953). Free in the coelom. California. Hughes (1929b), Michigan. Hunter (1942), Connecticut. Mueller and Van Cleave (1931), New York. Palmer (1939), Sinderman (1953), Massachusetts.

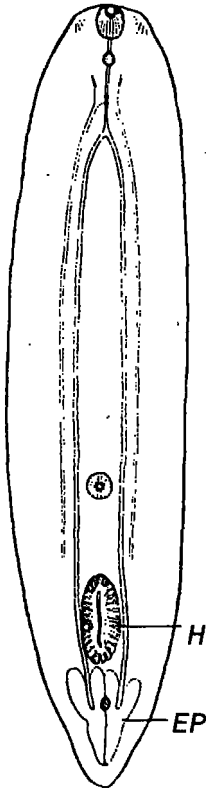

FIGURE 21.—*Diplostomulum scheuringi* (from Van Cleave and Mueller, 1934).

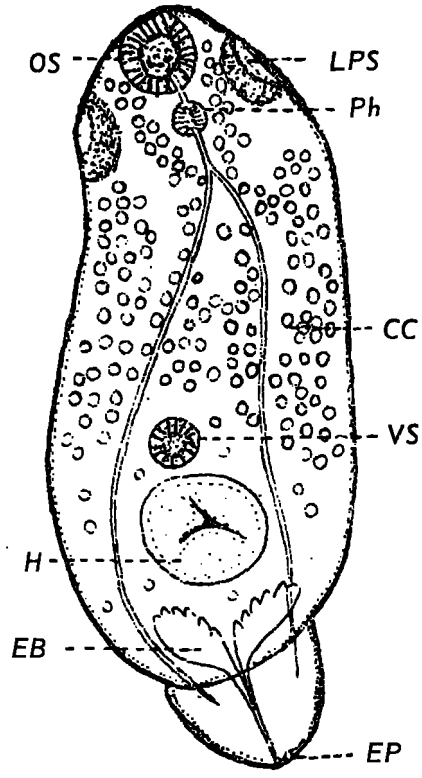

FIGURE 22.—*Diplostomulum truttae* (from Lal, 1953).

Metacercaria (fig. 21): Closely resembles *D. clavatum*; body length more than twice the width, ventral surface only slightly concave; lateral suckers and hindbody poorly differentiated; calcareous corpuscles ellipsoidal; body 885–1,155 by 210–270μ; oral sucker 30–45μ; ventral sucker 36–45μ; holdfast 96–150 by 42–75μ [fixed specimens (Hughes, 1929)].

22. *Diplostomulum truttae* Lal, 1953.
Fish host: Eyes of *Salmo trutta*. Scotland.

Metacercaria (fig. 22): Body ca. 1,000μ long and covered with minute papillae; forebody large; oral sucker 110μ; prepharynx short; esophagus short; lateral pseudosuckers deeply cupped and eversible; ventral sucker 75μ, smaller than oral sucker; holdfast well developed; calcareous corpuscles spherical.

23. *Diplostomulum* species.
Recorded from the eyes of many species of fish; it is often difficult to make a more specific identification.

KEY TO THE KNOWN *DIPLOSTOMULUM* SPECIES OF NORTH AMERICAN FRESHWATER FISH

Undoubtedly there are many undescribed species of *Diplostomulum*.

1. Found in eyes; hindbody indistinct (except *Diplostomum spathaceum*) ---------- 2
1. Found in the musculature or brain; hindbody distinct ---------- 5
2. Hindbody distinct-- *Diplostomum spathaceum*
2. Hindbody very small or not apparent------ 3
3. Found in the lens-- *Diplostomum flexicaudum*
3. Found in the vitreous humor---------- 4
4. Worm three times as long as broad. *Diplostomulum scheuringi*
4. Worm less than three times as long as broad ---------- *Diplostomum huronense*
5. Found in the brain of *Eucalia inconstans*------ *Diplostomum baeri eucaliae*

5. Found in the musculature 6
6. Ventral sucker nearly as large as oral sucker ... *Hysteromorpha triloba* (*D. corti*)
6. Ventral sucker about half as large as oral sucker ..... *Bolbophorus confusus* and *Diplostomulum ictaluri*

III. NEASCUS

This larval group has been described by Hughes (1927) and possesses these characteristics: (1) forebody much like *Diplostomulum*; (2) hindbody more extensively developed than in *Diplostomulum*; (3) reserve bladder more extensively developed than in *Diplostomulum* and with calcareous granules not confined to the termini of the small branches which do not end blindly but constitute anastomoses; (4) no lateral pseudosuckers or earlike processes; and (5) generally encysted with a true cyst of parasite origin.

The last synopsis of the group is that of Hughes (1928b).

A. Family *Diplostomatidae* Poirier, 1886.

1. *Crassiphiala bulboglossa* Van Haitsma, 1925. Snail host: *Helisoma* species.

Fish hosts: Cyprinidae–*Ericymba buccata*, *Leucosomus corporalis*, *Notemigonus crysoleucas*, *Notropis cornutus frontalis*, *Pimephales p. promelas*, *Semotilus a. atromaculatus*. Cyprinodontidae – *Fundulus diaphanus*. Etheostomidae–*Boleosoma nigrum olmstedi*. Percidae–*Perca flavescens*, *Stizostedion vitreum*. Umbridae–*Umbra limi*. Black cysts in skin, branchial arches, and myotomes [*Neascus bulboglossa* (Van Haitsma) Hughes, 1928].

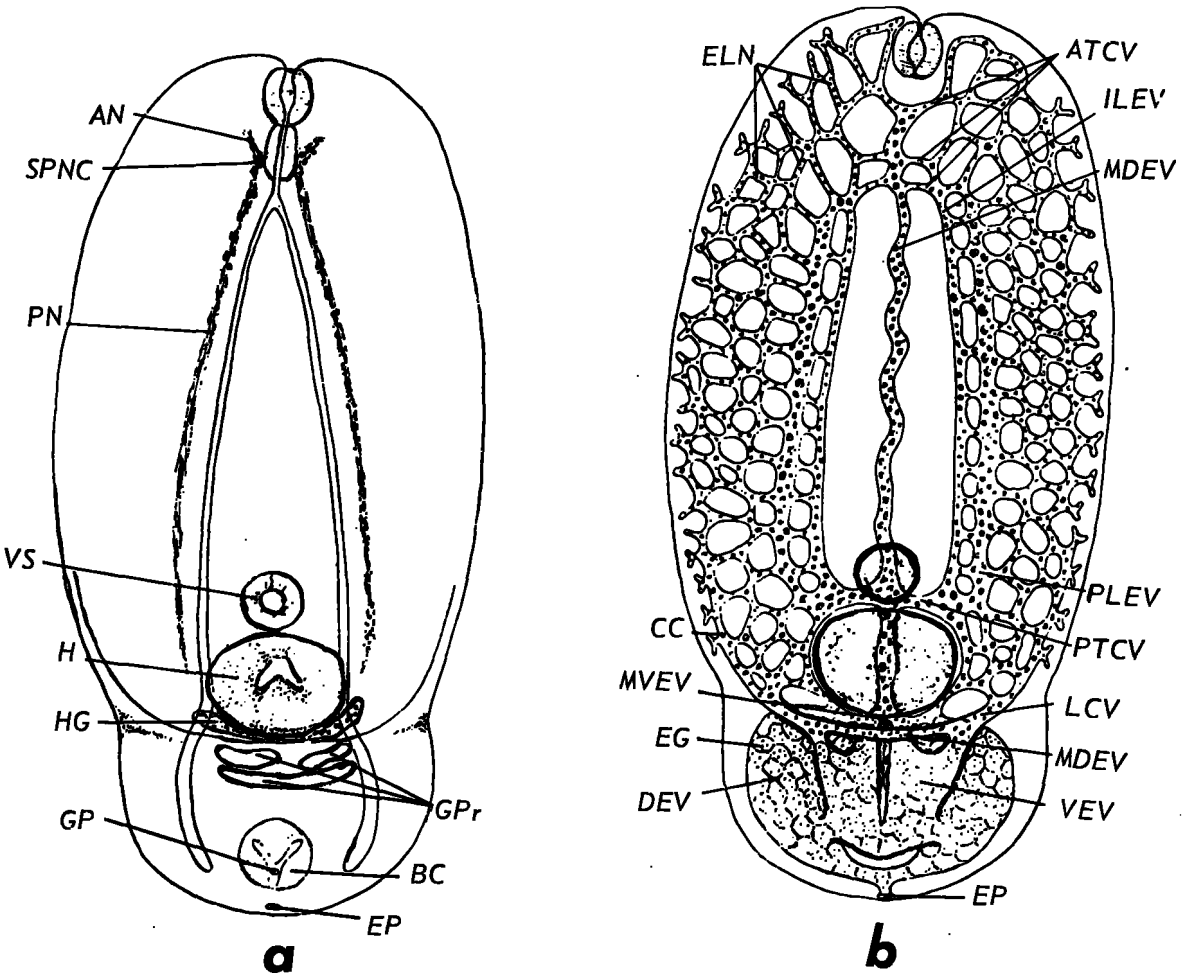

FIGURE 23.—Neascus of *Ornithodiplostomum ptychocheilus*. *A*. Ventral view, composite drawing. *B*. Ventral view of principal vessels of reserve bladder (from Hughes and Piszczek, 1928).

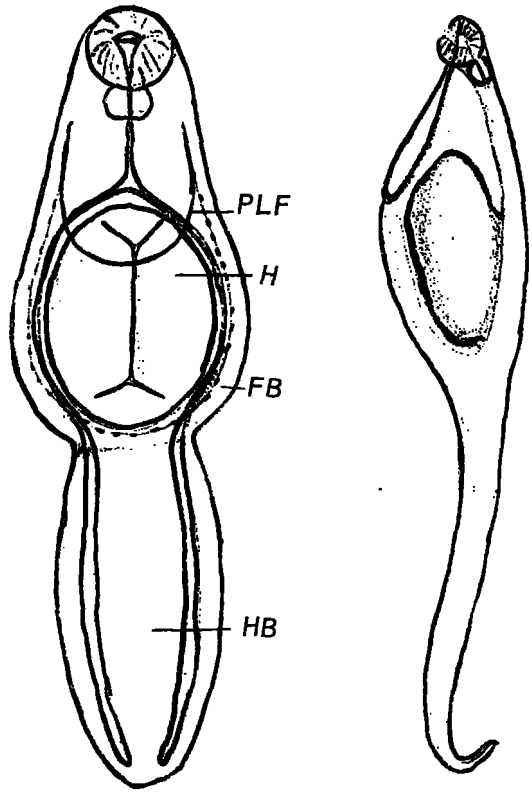

FIGURE 24.—Neascus *of Crassiphiala bulboglossa* (from Hughes, 1928c).

Host cyst: Pigmented, 360–680μ.

Parasite cyst: Ovate, 180–220 by 140–180μ; parasite folded and filling cyst; difficult to remove parasite without using enzymes.

Metacercaria (fig. 24): Two distinct body regions; body 310–400 by 125–174μ; forebody deeply cupped, 167–218μ long; hindbody conical; oral sucker 39–45μ; pharynx 21–24μ; esophagus long; ventral sucker wanting; holdfast 84–111μ long; holdfast gland wanting; genital primordia wanting (Hughes, 1928c).

Final host: Alcedinidae (kingfishers)–*Ceryle alcyon*. North Dakota and elsewhere (cf. Hoffman, 1956).

2. *Mesoophorodiplostomum pricei* (*Neodiplostomum pricei* (Krull, 1934) Dubois, 1936.
Snail host and cercaria unknown.

Fish host: *Fundulus* spp. [(*Neascus pricei*) Krull, 1934]. No description of the metacercaria was published.

Final host: Laridae (gulls)–*Larus* species (experimental). United States.

3. *Neodiplostomum perlatum* (Ciurea, 1911), 1929.
Snail host and cercaria unknown.

Fish host: Cyprinidae–*Cyprinus carpio*. Encysted in the fins and musculature [*Neascus perlatus* Ciurea (1911) 1929].

Cyst: Spherical to slightly ellipsoidal, pearl-like, 1,820–2,300 by 1,680–1,980μ.

Metacercaria (fig. 25): Forebody 910–940 by 540–670μ; hindbody 260 by 290–340μ; oral sucker 77–88μ; pharynx 59–66 by 44–55μ; ventral sucker 66–77μ; holdfast 130–180μ.

Final hosts: Accipitridae (hawks)–*Circus aeruginosus* (experimental); *Haliaetus albicilla; Falco subbuteo; Milvus migrans* (experimental). Romania.

4. *Ornithodiplostomum ptychocheilus* (Faust, 1917) Dubois, 1936.
Snail host: *Physa* species (Hoffman, 1958b).

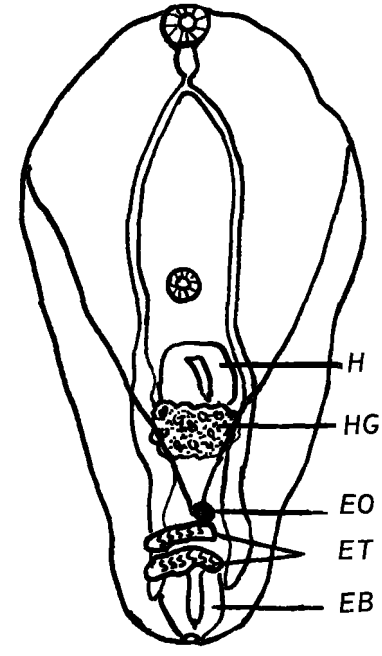

FIGURE 25.—Neascus of *Neodiplostomum perlatum* (from Ciurea, 1930).

Fish hosts: Cyprinidae–*Notropis* species, *Pimephales promelas*, *Ptychocheilus oregonensis*, *Semotilus a. atromaculatus*. Encysted in the peritoneum, viscera, and cysts free in the ovaries; on the brain of some species. [*Neascus ptychocheilus* (Faust) Hughes and Piszczek, 1928.]

Cyst: Often much larger than parasite, oval, 675–900 by 400–630μ.

Metacercaria (fig. 23): Very similar to *Posthodiplostomum minimum* but smaller and strigeoid constriction very shallow; forebody lacks a distinct posteroventral lip, concavity shallow or wanting; hindbody short and broad; body 548–847 by 245–399μ; oral sucker 28–37μ; pharynx 28–40μ; ventral sucker 35–42 by 35–45μ; holdfast 76–88 by 96–106μ.

Final hosts: Anatidae (ducks)–*Harelda hyemalis*, *Lophodytes cucullatus*, *Mergus* species; ducklings (experimental). Ardeidae–(herons) *Botaurus lentiginosus*, (*Hoffman*, 1956b); unfed chick (experimental) Hoffman, 1954. Illinois, Michigan, Montana, North Dakota.

5. *Posthodiplostomum cuticola* (von Nordmann, 1832) Dubois, 1936.

Snail host and cercaria unknown.

Fish hosts: Acipenseridae–*Acipenser nudiventris*. Cobitidae–*Cobitis taenia*. Cyprinidae–*Abramis* species, *Barbus brachycephalus*, *Capoetobrama kuschake-witschi*, *Carassius auratus gibelio*, *Chondrostoma nasus*, *Cyprinus carpio*, *Gobio gobio*, *Leuciscus species*, *Phoxinus phoxinus*, *Squalius cephalus*, *Aspius a. erythrostomus*, *Chalcalburnus chalcoides*, *Pelecus cultratus*. Percidae–*Perca fluviatilis*. Siluridae–*Silurus glanis*. Black cysts in the skin, superficial musculature, gills, mouth, fins, cornea of eye. [*Neascus cuticola* (von Nordmann) Hughes, 1927].

Cyst: Ovoid to spherical, pigmented, 690–990μ.

Metacercaria (fig. 26): Body 730–1,980μ; forebody 610–820 by 390–660μ; hindbody

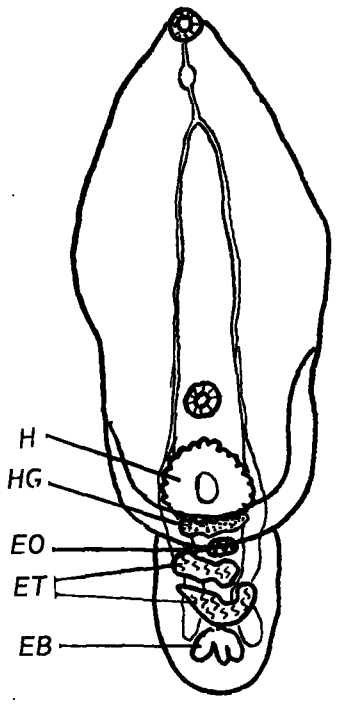

FIGURE 26.—*Neascus* of *Posthodiplostomum cuticola* (from Ciurea, 1930).

290–420 by 290–490μ; oral sucker 63–77 by 55–61μ; prepharynx 22μ; pharynx 55–61 by 30–37μ; esophagus 22–55μ; ventral sucker 68–77μ; holdfast 120–140μ.

Final hosts: Ardeidae (herons)–*Ardea* species, *Ardeola ralloides*, *Egrétta garzétta*, *Nycticorax nycticorax*. Europe.

6. *Posthodiplostomum minimum centrarchi* (MacCallum, 1921; Dubois, 1936) Hoffman, 1958.

Snail hosts: *Physa* species, Cercaria of *Posthodiplostomum minimum* Miller, 1954. (*Cercaria louisiana* Miller, 1936=*C. multicellulata* of Ferguson, 1936; Hunter and Hunter, 1940).

Fish hosts: Centrarchidae: except *Micropterus salmoides*, perhaps others (cf. Hoffman, 1958a). Encysted in kidneys, liver, pericardium, and spleen [*Neascus vancleavei* (Agersborg) Hughes, 1928].

Cyst: Usually longer than larva, 1,050–1,450 by 650–750μ.

Metacercaria (figs. 27a, 27b): Two distinct body regions; body 910–2,240μ; forebody 520–890 by 300–420μ; hindbody conical to spheroidal; oral sucker 31μ; prepharynx short; pharynx 23μ long; ventral sucker 46–62μ; holdfast 120–150μ in diameter; genital primordium well formed (Hughes, 1928b).

Final hosts: Ardeidae (herons)–*Ardea* species, *Butorides virescens*, *Herodias egretta*, *Nycticorax nycticorax* (experimental); Gaviidae (loons) *Gavia immer* (see Ferguson, 1937); unfed chicks, experimental (Ferguson, 1937; Hoffman, 1958a); United States, Canada, Cuba (Perez Vigueras, 1944).

7. *Posthodiplostomum minimum minimum* (MacCallum, 1921; Dubois, 1936) Hoffman, 1958a.

Snail host: *Physa* species (cf. Hoffman, 1958a).

Fish host: Cyprinidae (cf. Hoffman, 1958a). Encysted in the mesenteries [*Neascus vancleavei* (Agersborg) Hughes, 1928]. Very similar to *P. m. centrarchi* but smaller.

Final hosts: As above (6) perhaps (records for above are for *P. minimum*); it is not known which subspecies was concerned except for *Nycticorax*, which Ferguson experimentally infected with both strains. United States.

8. *Uvulifer ambloplitis* (Hughes, 1927), Dubois, 1938.

Snail hosts: *Helisoma campanulatum*, *Helisoma trivolvis*. (*Cercaria bessiae* Cort and Brooks). Possibly *C. flexicorpa* Collins, 1935.

Fish hosts: Centrarchidae–*Ambloplites rupestris*, *Enneacanthus obesus*, *Micropterus salmoides*, *Lepomis* species, *Micropterus dolomieu*, *Pomoxis* species, *Sclerotis punc-*

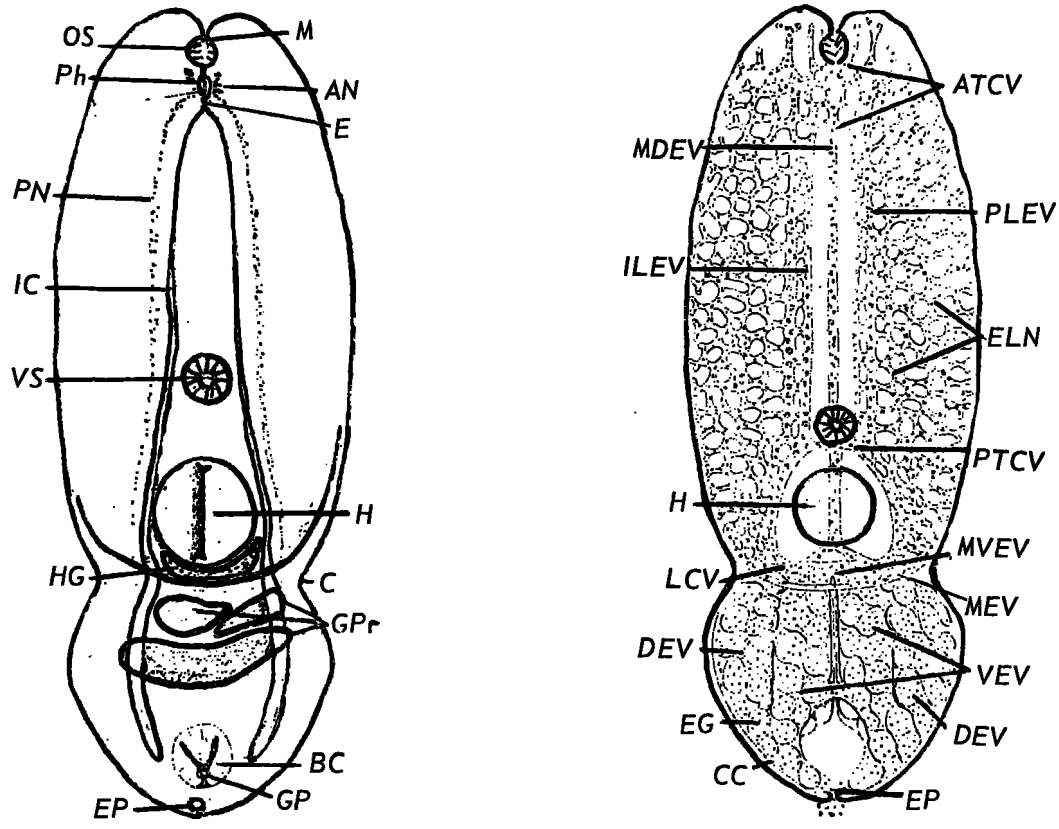

FIGURE 27.—Neascus of *Posthodiplostomum minimum* (from Hughes, 1928b). Normal shape is more like that in figure 24. Reserve excretory system shown on right.

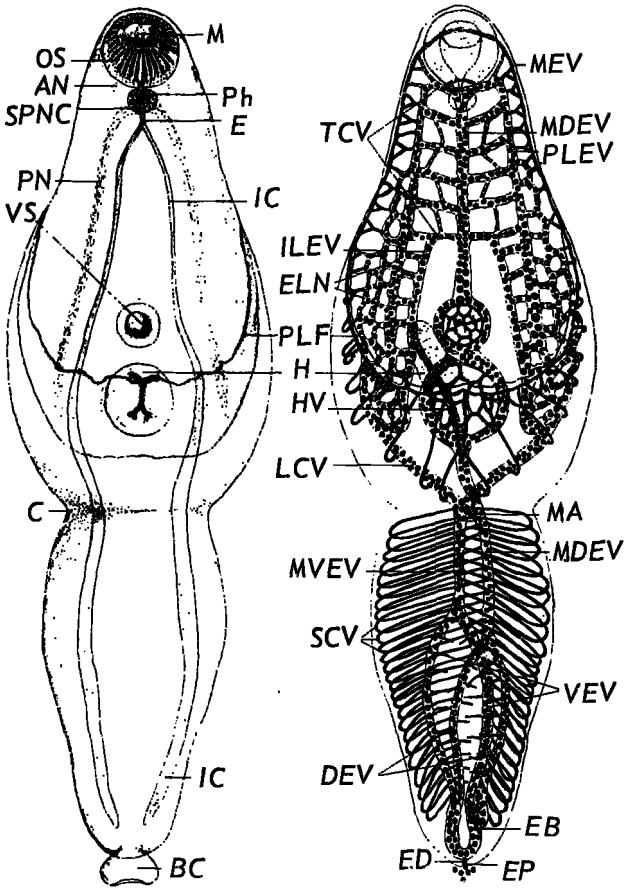

FIGURE 28.—Neascus of *Uvulifer ambloplitis* (from Hughes, 1927). Reserve excretory system shown on right.

tatus. Cyprinidae–*Chrosomus erythrogaster*, *Hybognathus hankinsoni*, *Hyborhynchus notatus*, *Margariscus margarita*, *Notemigonus chrysoleucas*, *Notropis* species, *Pfrille neogaea*, *Pimephales promelas*. Esocidae–*Esox* species. Black cysts in skin, myotomes, base of fins, around eyes, and in mouth (*Neascus ambloplitis* Hughes, 1927).

Host cyst: Pigmented.

Parasite cyst: Pyriform, distinctly flattened dorsoventrally, 360–390 by 172–236μ; difficult to free larva; parasite fills cyst.

Metacercaria (fig. 28): Two distinct body regions; forebody very thin, leaflike and deeply spoon-shaped, ventral surface spinous; 225–675 by 150–232μ; hindbody conical, 187–675 by 75–187μ; oral sucker 60–90μ; pharynx 22μ; ventral sucker 30–37μ; holdfast 52–60μ; reproductive fundament not seen (Hughes, 1927).

Final host: Alcedinidae (kingfishers)–*Ceryle alcyon*. United States.

9. *Neascus brevicaudatus* (von Nordmann, 1832), Diesing, 1850.

Fish host: In eyes of *Perca* and *Lota*; rare; not encysted (Zandt, 1924). Europe.

The author has recovered *Ornithodiplostomum ptychocheilus* metacercariae from the eyes of heavily infected experimental fish which were enclosed by the cyst of parasite origin only; in most instances this cyst ruptured so easily that the worms appeared unencysted.

Cyst: None.

Metacercaria: Forebody distinctly heart-shaped, narrowed posteriorly; ventral sucker smaller than oral sucker.

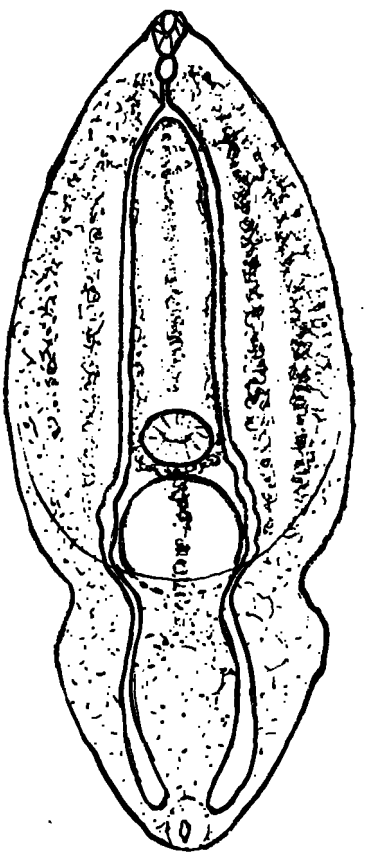

FIGURE 29.—*Neascus ellipticus* (from Chandler, 1951).

10. *Neascus ellipticus* Chandler, 1951.
Fish host: In musculature of *Perca flavescens*; cyst not pigmented. Minnesota.
Cyst: Elongate, elliptical, almost transparent, not pigmented, 735–900 by 360–500μ; parasite does not nearly fill the cyst.
Metacercaria (fig. 29): Two distinct body regions; forebody thin, shaped like a shallow spoon 450–540 by 300–325μ (stretched–750μ); hindbody 240–290 by 250–290μ with posterior end rather pointed; oral sucker 30–42 by 22–30μ; no prepharynx; pharynx 25–35 by 17–20μ; short esophagus; ventral sucker 46–55 by 55–63μ; holdfast 100–125μ; reserve excretory system resembles that of *P. minimum* (*Neascus vancleavei*) (Chandler, 1951).

11. Neascus of *Cercaria flexicorpa* Hobgood, 1938.
Very similar to Neascus of *Uvulifer ambloplitis*. Oklahoma.

12. *Neascus grandis* Mueller and Van Cleave, 1932.

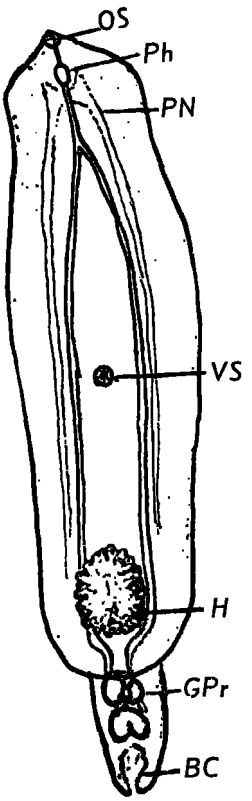

FIGURE 30.—*Neascus grandis* (from Mueller and Van Cleave, 1932).

Fish host: In viscera of *Umbra limi*. Resembles *Posthodiplostomum prosostomum* adult (Mueller and Van Cleave, 1932). New York.

Cyst: No description.

Metacercaria (fig. 30): Forebody much elongated, 1,500 by 360μ; hindbody 240 by 150μ; oral sucker ca. 22μ; pharynx 47μ long; esophagus 105μ; ventral sucker 35μ; holdfast 170 by 120μ; holdfast gland indistinct or wanting; genital primordium large (Mueller and Van Cleave, 1932).

13. *Neascus longicollis* Chandler, 1951.
Fish host: In integument of *Perca flavescens*. Minnesota.

Cyst: Oval, pigmented, 480–640 by 450–500μ, thickness 35–65μ; parasite not nearly filling cyst.

Metacercaria (fig. 31): Forebody 600–700 by 235–260μ; hindbody tail-like and narrower near forebody 170–270 by 60–120μ; anterior end of forebody terminating in a mobile finger-like process; oral sucker 38–42μ; no pharynx; ventral sucker 30 by 33–35μ; holdfast 100–110μ; reserve excretory system similar to *Neascus ambloplitis* group.

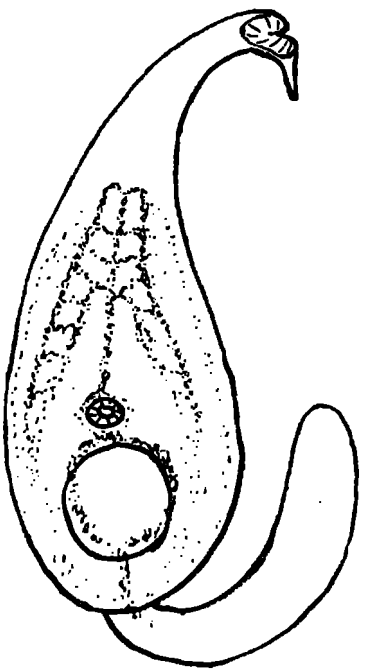

FIGURE 31.—*Neascus longicollis* (from Chandler, 1951).

14. *Neascus musculicola* (Waldenburg, 1860).
Fish host: In integument and musculature of *Perca*, *Scardinius*, *Abramis*, and *Leucisus*. Europe.

Cyst: Not pigmented.

Metacercaria: Similar to *Neascus cuticola* but the body is smaller, not folded in cyst, and hindbody is relatively larger.

15. *Neascus nolfi* Hoffman, 1955.
Fish host: In integument and musculature of *Semotilus* and *Notropis* (Hoffman, 1955a). North Dakota.

Host cyst: Spherical, pigmented, 472–576μ in diameter.

Parasite cyst: 202–324μ; cannot be easily separated from host cyst although parasite is relatively easily freed.

Metacercaria (fig. 32): Two distinct body regions; body 229–382 by 137–153μ; great width of forebody striking; forebody 229 by 147μ; hindbody 61–107 by 52–61μ; oral sucker 41 by 44μ; no prepharynx; pharynx 13 by 12μ; esophagus 24–27μ long; ventral sucker 17μ; holdfast 55μ; reserve excretory system not discernible.

16. *Neascus pyriformis* Chandler, 1951.
Fish host: In integument of *Perca flavescens*. Minnesota.

Host cyst: pigmented, spherical to ovoid, 400–550 by 300–540μ, 10–65μ thick.

Parasite cyst: Pear-shaped, 225–319 by 130–195μ ca. 7–8μ thick; difficult to free larva; parasite almost completely filling cyst.

Metacercaria (fig. 33): Forebody 435–465 by 240–255μ; hindbody 150–250 by 125–175μ; oral sucker 70 by 45μ; pharynx difficult to see, 21–23 by 17–18μ; caeca not seen; ventural sucker 38–45 by 38–40μ; holdfast 85–105 by 80–95μ; reserve bladder similar to *N. ambloplitis* group (Chandler, 1951).

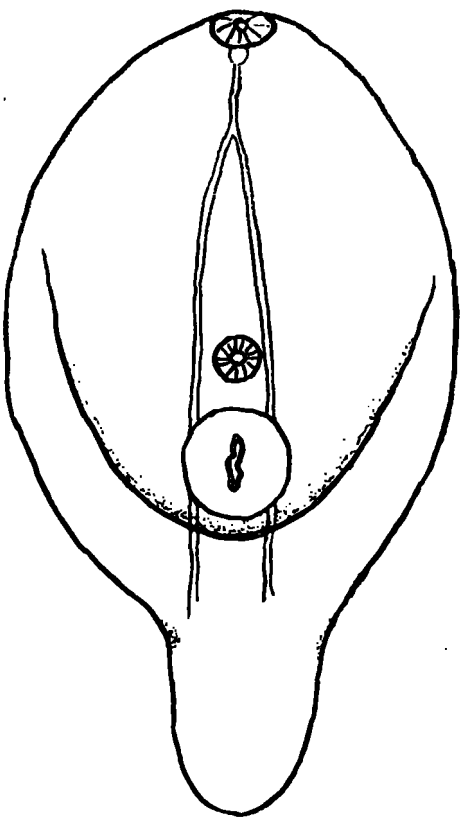

FIGURE 32.—*Neascus nolfi* (from Hoffman, 1955a).

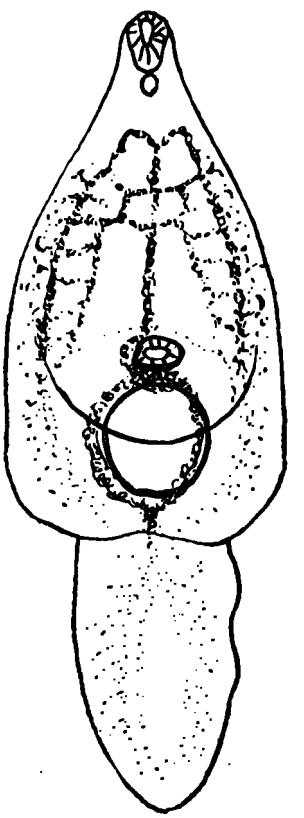

FIGURE 33.—*Neascus pyriformis* (from Chandler, 1951).

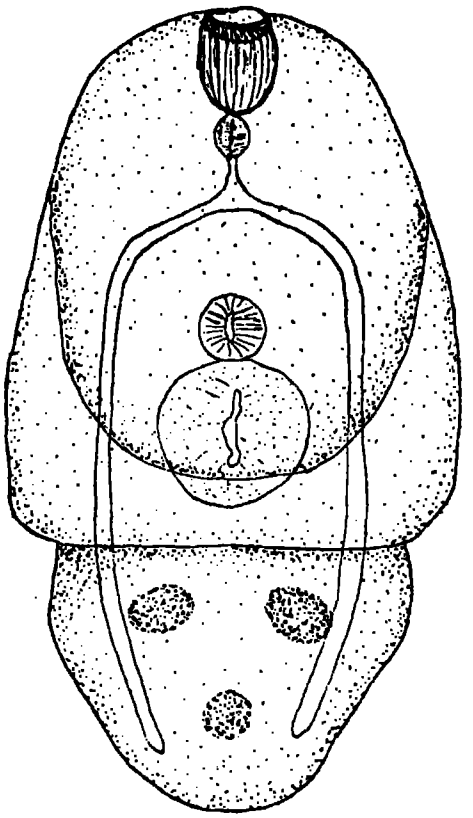

FIGURE 34.—*Neascus rhinichthysi* (from Hunter, Wanda, 1933). [This is probably from a contracted specimen.]

17. *Neascus rhinichthysi* Hunter, 1933.
Fish host: In integument of *Rhinichthys* species; New York.

Host cyst: Spherical, pigmented, 480–880μ.

Parasite cyst: Nearly spherical, 223–380μ; larva nearly fills cyst and is easily freed.

Metacercaria (fig. 34): Two distinct body regions; forebody 232–301 by 135–194μ; hindbody 97–203 by 120–135μ; oral sucker 54–63 by 48–77μ; pharynx about 20μ wide; ventral sucker 31–39μ; holdfast 69–81μ; genital primordia present; reserve bladder similar to *N. ambloplitis* (Hunter, W., 1933).

18. *Neascus wardi* Hunter, 1928.
Fish host: Encysted in *Lepomis cyanellus*. Illinois.

Host cyst: Pigmented, elliptical, 510–850μ long.

Parasite cyst: Ovoid, tough but flexible, 300–400μ long.

Metacercaria: Body 378–817 by 95–351μ; two distinct body regions; forebody 196–473 long; hindbody 115–419 by 41–236μ; oral sucker 40–79μ; pharynx 20–25 by 16–20μ; esophagus 10–15μ long; ventral sucker 22–43μ; holdfast 40–79μ; three bodies in forebody believed to be genital primordia(?); reserve excretory system similar to *N. ambloplitis* [fixed specimens (Hunter, Wanda, 1928)]; Van Cleave and Mueller (1934) state that this form is probably identical with *N. ambloplitis*.

KEY TO THE KNOWN SPECIES OF NEASCUS OF NORTH AMERICAN FRESHWATER FISH

Key extracted and slightly modified from Hoffman (1955). Undoubtedly there are many other undescribed species of *Neascus*.

1. In cranial cavity of *Notropis cornutus frontalis* and *Pimephales p. promelas;* small oval cyst; adult in chick (experimental) (Hoffman, 1954)---*Ornithodiplostomum ptychocheilus*
1. In viscera, mesenteries, peritoneum---2
1. In musculature and integument---4
2. Relatively short hindbody; constriction slight; relatively small (cyst 750μ); in mesenteries of Cyprinidae; adult in mergansers, squaw duck, and experimental in domestic duck and unfed chick (Hughes and Piszczek, 1928; Van Haitsma, 1930; Hoffman, 1954)---*Ornithodiplostomum ptychocheilus*
2. Relatively large hindbody; constriction pronounced; much larger (metacercaria more than 1 mm.); adults in herons, experimental in unfed chicks---*Neascus of Posthodiplostomum* spp.---3
3. In liver, kidneys, and on heart of centrarchids (Ferguson, 1943, Hoffman, 1958; Hughes, 1928b; Van Cleave and Mueller, 1934: 249---*P. minimum centrarchi*
3. In mesenteries of cyprinids (Hughes, 1928b; Hoffman, 1958)---*P. m. minimum*
3. In mesenteries of *Umbra limi;* forebody very large; ventral sucker in center of forebody; adult unknown (Mueller and Van Cleave, 1932: 93)---*Neascus (Posthodiplostomum?) grandis*
4. Black pigment surrounding cyst;[1] resembles *P. minimum* somewhat---5
4. No black pigment surrounding cyst---*Neascus ellipticus*
5. Metacercaria nearly fills the parasite cyst---6
5. Metacercaria does not fill the parasite cyst---9
6. Parasite cyst pyriform---7
6. Parasite cyst oval or round---8
7. Parasite cyst about 330 by 200μ; in many fish; adult in kingfisher (Hughes, 1927)---*Uvulifer ambloplitis*
7. Parasite cyst smaller (about 270 by 160μ), abruptly narrowed at one end; in perch; adult not demonstrated, possibly is *Uvulifer semicircumcisus* in kingfisher (Chandler, 1951)---*Neascus pyriformis*
8. No ventral sucker; reserve excretory system similar to that of *N. ambloplitis* but forebody greatly cup-shaped (Hughes, 1928c)---*Crassiphiala bulboglossa*
8. Ventral sucker present; reserve excretory system similar to *N. ambloplitis* although simpler; in dace; adult unknown (Hunter, Wanda, 1933)---*Neascus rhinichthysi*
9. Smaller (parasite 200 to 330μ); reserve excretory system indistinct; in *Semotilus a. atromaculatus, Notropis cornutus frontalis,* possibly others; adult unknown (Hoffman, 1955a)---*Neascus nolfi*
9. Quite large (parasite cyst 450μ long, metacercaria 870μ long); metacercaria with finger-like anterior papilla; in perch; adult unknown (Chandler, 1951)---*Neascus longicollis*

IV. PROHEMISTOMULUM

This larval group has been described by Ciurea (1933) and possesses these characteristics: (1) body round or oval, flat, and foliaceous, not separated into two parts, (2) no lateral pseudosuckers, (3) holdfast well developed, (4) reserve excretory system (bladder) consisting of two main vessels, one lateral and the other median, containing small calcareous corpuscles. Peripheral vessels bifurcate anteriorly giving rise to the median which also connects with it at the posterior extremity.

The nature of the reserve excretory system is very helpful for separating some *Prohemistomulum* species from some *Neascus* species which have indistinct hindbodies. The author's interpretation of the system of an undescribed species of cyathocotylid metacercaria is here offered as an addition to the larval group description: (4) reserve excretory system consisting of three broad vessels, continuous and looped in such a fashion as to form a crude letter "W," and fusing anteriorly in many anastomoses, and containing calcareous corpuscles throughout (fig. 35).

[1] Sometimes the pigment does not appear until 2–3 weeks after infection.

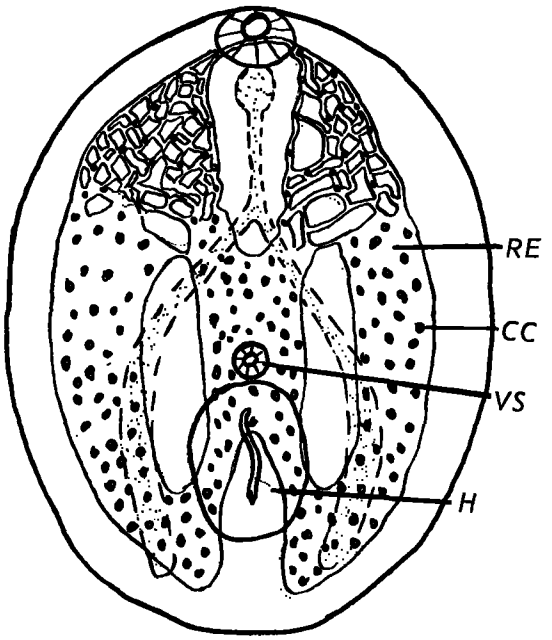

FIGURE 35.—Prohemistomulum (*cyathocotylid*) metacercaria showing "W" form of the excretory bladder.

A. Family CYATHOCOTYLIDAE Poche, 1926.

1. *Cyathocotyle gravieri* Mathias, 1935.
Snail host: *Bithynia tentaculata.*

Fish hosts: Cyprinidae–Goujons (*Gobio*) and varions (*Phoxinus*), both experimental; encysted in the musculature.

Cyst: Ovoid, wall very thick; 500 by 300μ.

Final host: Anatidae (ducks)–*Anas platyrhynchos domestica* (experimental). France.

2. *Cyathocotyle melanittae* Yamaguti, 1934.
Snail host and cercaria unknown.

Fish host: Cyprinidae–*Pseudorasbora parva;* encysted in the musculature.

Cyst: Spherical to elliptical, 198–250 by 150–250μ; consisting of 5 layers.

Metacercaria: Body 140–160 by 140–156μ, minutely spined; oral sucker 45–50μ wide (wider than long); pharynx 18–20μ; esophagus short; no ventral sucker; holdfast 80–199μ in diameter; genital primordium not seen (Yamaguti, 1942).

Final host: *Melanitta fusca;* ducklings; experimental (Yamaguti, 1942). Japan.

3. *Cyathocotyle orientalis* Faust, 1921.
Snail host: *Bulimus striatulus japonicus.*

Fish host: Cyprinidae–*Pseudorasbora parva.* Family (?)–*Sorcocheilichthys sinensis.* Encysted in muscle and connective tissue.

Cyst and metacercaria: Descriptions controversial. Faust (1921) described the metacercaria as a *Tetracotyle*, but this must be an error. Yamaguti's photograph of the encysted matacercaria, however, clearly shows the cyathocotylid type of reserve excretory system.

Final host: Anatidae–domestic mallard (experimental). Falconidae: *Milvus migrans lineatus* (kite). Japan (Yamaguti, 1940). Description not detailed enough for comparison with Faust (1921), therefore, the author is not sure that they are identical.

4. *Holostephanus ictaluri* Vernberg, 1952.
Final host: Siluridae—*Ictalurus punctatus.* Intestine.

5. *Linstowiella szidati* (Anderson) Anderson and Cable, 1950.
Snail host: *Campeloma rufum.*
Fish host: Cyprinidae–*Notropis cornutus;* encysted in the musculature.

Cyst: Nearly spherical, 400 by 300μ; difficult to remove parasite from inner cyst; peptic and tryptic digests released worms but killed them.

Metacercaria: Not described, apparently similar to immature adults.

Final host: Young chick (experimental). United States. (Anderson and Cable, 1950).

6. *Mesostephanus appendiculatoides* (Price, 1934) Lutz, 1935.
Snail host: marine snail, *Cerithium muscarum.*

Fish host: Mugilidae–*Mugil* species.

Cyst: 300–381 by 327–411μ. Description not available to author; encysted in the musculature and pericardial wall.

Final hosts: *Didelphis virginiana* (opossum); *Procyon lotor* (raccoon); *Larus delawarensis* (ring-billed gull); *Nyctocorax n. hoactli* (black-crowned night heron) (experimental); *Pelecanus occidentalis* (Hutton and Sogandares-Bernal, 1959).

7. *Mesostephanus appendiculatus* (Ciurea, 1916) Lutz, 1935.
Snail host and cercaria unknown.

Fish host: Cyprinidae–*Abramis blicca*, *Carassius carassius*, *Tinca tinca*, *Aspius aspius*.

Cyst: Description not available to author.

Final hosts: Dog and cat (experimental); cat and dog (Kuntz and Chandler, 1956). Egypt; Romania; Ukraine; United States.

8. *Mesostephanus odhneri* (Travassos, 1924) Lutz, 1935.
Snail host and cercaria unknown.

Fish host: Haemulidae (Perciformes)–*Haemulon* species; encysted beneath the skin.

Cyst: About 340μ in diameter.

Metacercaria: 300 by 190μ; oral sucker 30μ; pharynx 20 by 14μ; ventral sucker 18–20μ holdfast 80 by 60μ.

Final host: Ardeidae (herons): *Nyctanassa violacea* (experimental). Brazil.

9. *Paracoenogonimus ovatus* Katsurada, 1914.
Snail host: *Viviparus viviparus*.

Fish host: Cyprinidae–*Abramis* species, *Cyprinus carpio*, *Idus idus*, *Leuciscus rutilus*, *Scardinius erythrophthalmus*, *Tinca tinca*. Esocidae–*Esox lucius*. Encysted in the musculature. See *Prohemistomulum circulare* (fig. 37).

Final host: Mice (experimental). Europe (Komiya, 1938).

10. *Prohemistomum chandleri* Vernberg, 1952.
Snail host: *Pleurocera acuta*; Cercaria of *Prohemistomum chandleri*.

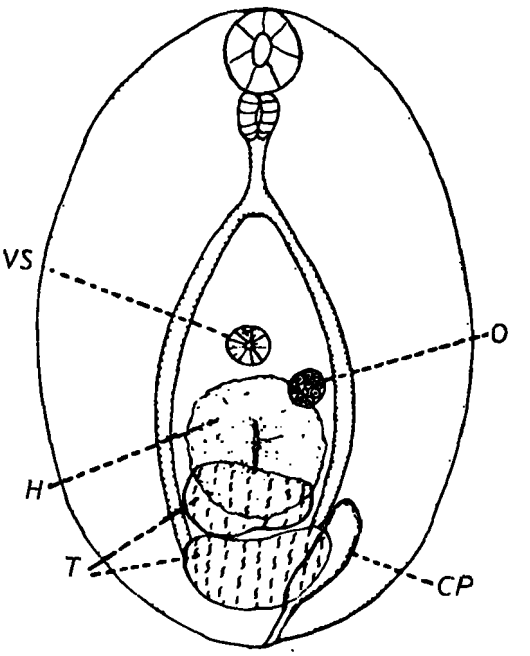

FIGURE 36.—*Prohemistomum chandleri*; adult. Prohemistomulum metacercaria not figured in original description. [The author assumes that the larval form is similar to that of the adult, but that the gonads are smaller or not yet formed (from Vernberg, 1952)].

Fish host: Centrarchidae–*Micropterus salmoides*, *M. dolomieu*.

Cyst: Spherical, pigmented, 606 by 475μ average; space between host cyst and parasite cyst filled with granular material.

Metacercaria (fig. 36): Not described, apparently similar to immature adult.

Final hosts: Siluridae–*Ictalurus punctatus* (experimental adult). Cottidae–*Cottus bairdii* (experimental adult). Snake, *Matrix sipedon* (experimental adult). United States (Vernberg, 1952).

11. *Prohemistomum vivax* (Sonsino, 1892) Azim, 1933.
Snail host: *Cleopatra bulimoides*. Cercaria *Prohemistomi vivacis* (Sonsino) Looss, 1896.

Fish hosts: Poeciliidae–*Gambusia affinis*. Cichlidae–*Tilapia nilotica*. Encysted in the muscles and peritoneal cavity [*Prohemistomulum vivax* (Sonsino) Azim, 1933].

Cyst: Spherical, pigmented, 300–320μ in diameter, cf. Dubois (1938, p. 455).

Metacercaria: Description not available to author.

Final hosts: *Milvus*. Dog, cat. Egypt.

12. *Prosostephanus industrius* (Tubangui, 1922), Lutz, 1935.

Snail host: *Parafossarulus* species.

Fish host: Cyprinidae: Crucian carp.

Cyst: Description not available to author.

Final host: Experimental in cats (Tang, 1941). China.

13. *Szidatia joyeuxii* (Hughes, 1929) Dubois, 1938.

Snail host: *Melanopsis* species. [*Cercaria vivax* (Sons, 1894); *Cercaria s. joyeuxii* Balozet, 1953].

Fish hosts: Poeciliidae–*Gambusia affinis* (experimental), encysted in the musculature. Also in toad and frog.

Cyst: Spherical, white becoming black, 450–500μ in diameter.

Metacercaria: 700 to 1000 by 450–550μ; oral sucker 60–70μ; ventral sucker 40–60μ; holdfast 175–230μ long.

Final host: Snakes, *Malpolon*, and *Tropidonotus* species. Tunisia (Balozet, 1953; Joyeux and Baer, 1941).

B. Family undetermined, probably CYATHOCOTYLIDAE.

14. *Prohemistomulum circulare* Ciurea, 1933. [Perhaps is *P. ovatus*, *cf* Dubois (1938): 452].

Fish host: Cyprinidae–*Abramis*, *Blicca*, *Cyprinus*, *Idus*, *Leuciscus*, *Scardinius*. Esocidae–*Esox lucius*. Encysted in the musculature. Europe.

Cyst: Spherical to slightly ellipsoidal, 300–440 by 290–390μ; outer cyst wall 15–44μ thick; inner cyst wall 6–13μ thick.

Metacercaria (fig. 37): Oval, 280–360 by 190–230μ; oral sucker 46–57μ; pharynx 30–37 by 28–33μ; ventral sucker 22–33μ; holdfast 72–110 by 79–99μ. Testes posterior to holdfast; ovary on left.

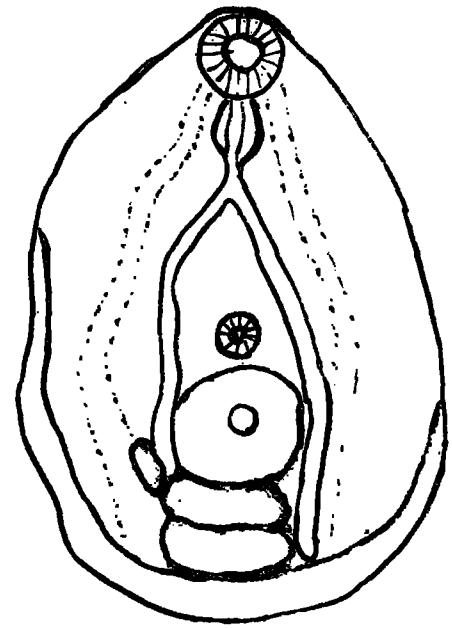

FIGURE 37.—*Prohemistomulum circulare* (from Ciurea, 1933).

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