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VOLUME XIII

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THE PAPILLOSE ALLOCREADIIDAE

A Study of their Morphology, Life Histories, and Relationships

WITH FOUR PLATES AND SIX TEXT-FIGURES

BY

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Contribution from the Zoological Laboratory of the
University of Illinois
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INTRODUCTION

The term "papillose Allocreadiidae" as used in this paper refers to all members of the family which are furnished with oral papillae. In the forms considered here the oral papillae are six projections of the oral sucker containing strong muscle fibers like those of the sucker itself; some of the fibers are continuous with those of the sucker wall and run more or less obliquely through the length of the papilla, and others run transversely through the papilla without connecting with fibers in the sucker; the nuclei belonging to the papilla musculature do not lie in the papillae, but in the wall of the sucker at the base of each papilla. Of the six papillae, one pair project laterally from the sucker near the ventral surface and the other four arise from the dorsal wall of the sucker. The structure of the oral papillae is the same in Crepidostomum (which includes the forms previously assigned to Acrolichanus and Stephanophiala), Megalogonia, and Bunodera, and my study has shown that the other morphological features of these genera also indicate a close relationship.

In my analysis of the morphology of these trematodes, I have placed the emphasis on resemblances or differences in the connections and in the histology of organs and parts, rather than on the exact position, size, or shape of the various structures; for a study of abundant specimens and of living material shows that the shape, size, and position of most parts are extremely variable in trematodes because of growth changes, differences in state of contraction of individuals, and other factors discussed later in this paper. I have attempted to work out the life histories and the excretory patterns of as many species as possible in order to determine whether or not the resemblances in type of larva and in type of excretory system agree with the resemblances in the gross morphology of adults on which most of the present conceptions of relationships are based. It is evident from this study that there is need of a revaluation of the importance of the various morphological features of Digenea as indicators of relationship, and that the morphology and biology of the various developmental stages, i.e., the ontogeny, must be taken into consideration before conceptions of the phylogenetic relationships of families, genera, and species of Digenea can have any true value.

The tendency of early helminthologists was to put all papillose distomes together in one group, regardless of other features or even of homologous structure of the papillae. Recently the tendency has been toward increasing separation; the latest general works on trematodes

(Poche 1926, Fuhrmann 1928) place some of the papillose Allocreadiidae in the sub-family Stephanophialinae Nicoll, distinguished only by the possession of papillae, while Bunodera is placed in a separate family, the Bunoderidae. My analysis of the morphology and ontogeny of the papillose genera and species indicates that Crepidostomum is more closely related to Allocreadium than are some of the genera now included in the Allocreadiinae and that Bunodera and Megalogonia are more closely related to Crepidostomum than some of the genera now included in the Allocreadiidae are related to each other. If the papillae were removed from any species of Crepidostomum it would be very difficult if not impossible to distinguish it from Allocreadium. The evidence now available suggests the probability that Allocreadium and Crepidostomum represent offshoots from the same ancestral stem, and that Bunodera and Megalogonia represent offshoots from the Crepidostomum branch of this stem.

MATERIALS AND METHODS

The preserved specimens used in my study were from many different sources, which are indicated in the descriptions of the species. Many specimens were collected by myself; others were borrowed from the collection of Professor Ward, from other investigators, and from American and European museums. Whenever it was possible to obtain enough living specimens of a species the animals were studied alive in order to note their actions and the changes in the shape and position of the various parts as the worms extended and contracted, and the excretory system and finer parts of the reproductive system were traced out. The study of living specimens was found to be far more satisfactory than any treatment of preserved specimens. Many specimens were also mounted in toto or sectioned; reconstructions from serial sections were used as a check on the results of study of living specimens; whole mounts were valuable for measurements, but in most cases were found not to give an adequate idea of the fundamental structure. Living specimens were studied while flattened under a cover slip in physiological salt solution, tap water, distilled water, or horse blood serum; for purposes of measurement some specimens were also studied without flattening. Infection experiments were carried out whenever enough cercariae or metacercariae could be obtained.

In the descriptive section which follows, the genus Crepidostomum and its species will be discussed first, followed by Megalogonia and Bunodera. Under each species the adult is considered first and then an account is given of the life history so far as it is known. Hosts and localities not previously reported are indicated by the asterisk (*).

MORPHOLOGY

Genus Crepidostomum Braun 1900

Since the original setting up of this genus with the two species *C. metoecus* and *C. farionis,* the addition of several more species and the extension of our knowledge of structural features and variations in structure within the genus have made it necessary to revise the generic description. The following diagnosis brings the characterization of Crepidostomum up to date.

Allocreadiidae with six muscular oral papillae projecting from oral sucker, four dorsal and two ventral. Body of adult 0.4 to 6.0 mm. long, width usually about one-fourth length. Oral sucker larger than ventral, ventral larger than oral, or both the same size. Prepharynx, pharynx, and long muscular esophagus present, esophagus often dividing just before running into crura; crural fork anterior or dorsal to ventral sucker; crura running through dorsal half of body nearly to posterior end. Genital pore ventral, median or slightly to one side of median line, between suckers; common genital sinus very small, obliterated when cirrus is everted. Cirrus sac muscular, varying in form and size in different species, reaching only to anterior edge or center of ventral sucker in some and back as far as testes in others; sac always containing seminal vesicle, pars prostatica, strongly muscular cirrus, and prostate glands; anterior end of sac protrusible. Testes two, undivided, with margins entire or slightly lobed, lying near ventral surface between ovary and posterior end of body, either tandem or oblique; vasa efferentia running forward and joining to form short vas deferens which enters posterior end of seminal vesicle. Ovary pear-shaped, near dorsal surface close behind ventral sucker, or dorsal to its posterior margin, sometimes median, more often lateral to median line on either side. Seminal receptacle pear-shaped, near dorsal surface close behind ovary. Oviduct arising from median side of ovary, almost immediately widening to fertilization chamber, receiving seminal duct from seminal receptacle at distal end of fertilization chamber, then running a short distance farther before receiving common vitelline duct, and soon afterwards entering ventral oötype; lumen of oviduct ciliated. Shell glands lying loose in parenchyma, surrounding and opening into oviduct and oötype. Laurer's canal branching off of seminal duct near receptacle and running to pore on dorsal surface usually over intestinal cecum on side farthest from ovary and receptacle. Uterus a narrow tube with thin muscular walls, usually extending back from oötype to anterior margin of anterior testis, but sometimes running back in convoluted course dorsal or lateral to testes as far as posterior edge of posterior testis before turning anteriad; terminal

part of uterus, beginning dorsal to ventral sucker, slightly modified by increased thickness of muscular wall to form metraterm, with or without projections on inner wall. Intrauterine eggs one to several hundred, but usually less than fifty; ovidal or ellipsoidal, 50 to 95 μ long, shell thin, yellowish, operculate; eggs deposited while in single cell stage. Vitellaria mostly lateral and ventral to intestinal crura, from pharynx, from crural fork, or from ventral sucker almost to posterior tip of body, extending into intercrural space between and posterior to testes and anterior to ovary in some species; longitudinal vitelline ducts joined behind posterior testis; transverse ducts meeting near ovary, usually forming vitelline reservoir, from which common vitelline duct runs to oviduct. Excretory bladder an undivided tube or pouch dorsal to testes, from anterior end of which a collecting duct on each side runs to level of ventral sucker and divides into anterior and posterior branch; three groups of flame cells tributary to each of these branches; flame cell formula 2 [(2 + 2 + 2) + (2 + 2 + 2)], perhaps modified in some species by additional divisions of flame cells in some or all groups. A pair of pigmented eyespots present in immature specimens, often persisting throughout life. Miracidium with a pair of fused pigmented eyespots, ciliated over entire surface; cuticular plates lacking; one pair of flame cells present; developing in egg free in water. Redia without ambulatory processes; pharynx large, gut rudimentary, birth pore poorly developed or lacking, flame cells four to 22 or more; developing in liver, gills, or mantle of Sphaeriidae. Cercaria a slender-tailed ophthalmoxiphidiocercaria with about three pairs of cephalic glands and a large number of cystogenous glands. Metacercaria encysted in aquatic insects or crustacea. Adults usually in intestine, sometimes in stomach, pyloric ceca, or gall bladder of freshwater fishes; occasionally in bats, urodeles, and turtles. Type species, *C. metoecus* (Braun 1900).

Crepidostomum farionis (O. F. Müller 1784)

Synonyms.—*Fasciola farionis* O. F. Müller 1784; *Fasciola truttae* Froelich 1789; *Distoma laureatum* Zeder 1800; *Fasciola laureata* (Zeder) Nordmann 1840; *Crossodera laureata* (Zeder) Cobbold 1860; *Distoma farionis* (O. F. Müller) Blanchard 1891; *Crepidostomum laureatum* (Zeder) Braun 1900a; *Stephanophiala laureata* (Zeder) Nicoll 1909; *Stephanophiala transmarina* Nicoll 1909; *Stephanophiala farionis* (O. F. Müller) Faust 1918; *Stephanophiala vitelloba* Faust 1918; *Crepidostomum ussuriense* Layman 1930; *Crepidostomum vitellobum* (Faust) Hopkins 1931a.

Hosts and Localities Reported.—*Salmo trutta* Linn. (= *Salmo fario, Trutta trutta, Trutta fario*), Great Britain; Sweden; Denmark;

France; Germany; Russia. *Salmo lacustris,* Finland. **Salmo clarkii,* *Flathead Lake, Montana. *Salmo lewisi* (= *Salmo mykiss, Salmo mykiss lewisi*), Park Co., Montana; Heart Lake and Yellowstone Lake, Yellowstone Park. *Salvelinus alpinus* (= *Salmo salvelinus, Salvelinus salvelinus*), Scandinavia; Germany. *Salvelinus fontinalis,* Canada, (Montreal market); *Vermont. *Salvelinus* sp., Peter the Great Bay, Siberia. *Coregonus oxyrhynchus,* Scandinavia; Germany. *Prosopium williamsoni* (*Coregonus williamsoni*), Bitter Root River, Montana. *Thymallus thymallus* (*Thymallus vulgaris*), Great Britain; Scandinavia; Germany. *Stenodus leucichthys,* Russia. *Coregonus lavaretus,* Europe. **Salvelinus malma,* *Jordan Lake at Loring and *Excursion Inlet, Alaska. **Salmo irideus,* *Hatchery Lake at Loring, Alaska. **Salmo mykiss,* Jordan Lake at Loring, Alaska. **Perca fluviatilis,* Vienna, Austria.

This species was first described by O. F. Müller (1784) as *Fasciola farionis.* Froelich (1789) reported as a new species *Fasciola truttae,* but Zeder (1800) compared Froelich's specimens with his own and pronounced them both identical with *Fasciola farionis* O.F.M.; this species Zeder redescribed under the new name *Distoma laureatum.* It is evident that *D. laureatum* is merely a synonym of *Crepidostomum farionis* (O.F.M.), although the former name has been used more frequently in the past.

In more modern times *C. farionis* has been described by Olsson (1876), Nicoll (1909), Faust (1918), and Brown (1927). Of these Nicoll has given the most complete description, but his specimens were too few to cover the range of variations in the species, as Odhner (1910) has already remarked. Blanchard (1891) has given a good account of the reproductive system. Faust (1918) and Linton (1893) have given the only descriptions of the American specimens, except for the brief mention of Stafford (1904).

I have studied numerous specimens of *C. farionis* in the collection of Professor Ward, from *Salmo lewisi* in Yellowstone National Park, *Salmo mykiss, Salmo irideus,* and *Salvelinus malma* in Alaska, *Salmo clarkii* in Flathead Lake, Montana, *Salvelinus fontinalis* from Roxbury Hatchery, Vermont, and "Trout" in Frazer River, Colorado. I have compared these American specimens with European specimens of *C. farionis* from *Salmo trutta* (English specimens sent to Professor Ward by Dr. H. A. Baylis) and from *Perca fluviatilis,* Austria (Univ. Berlin Mus. No. 5774), and with the descriptions of European specimens given by Olsson, Blanchard, Odhner, Nicoll, and Brown. It is evident from this study that the only differences existing between the European and the American specimens are of very minor nature and fall well within the range of individual variation. Therefore the name *Stephanophiala transmarina*

Nicoll 1909, proposed for the American form, is a synonym of *Crepidostomum farionis* (O.F.M.), as Faust has already indicated.

Hunninen and Hunter (1933) have described specimens collected by them from trout in New York as *Crepidostomum transmarinum* (Nicoll) and claim that this species is distinct from *C. farionis;* I have examined one of their specimens (8617) and find it identical with *C. farionis.*

Through the courtesy of Professor Faust and Professor Ward I have had the privilege of examining a whole mount, a series of frontal sections, and a series of tranverse sections of Faust's original specimens of *Stephanophiala vitelloba* Faust 1918 (Fig. 10). This species was described from ten specimens found in the gall bladder of *Coregonus williamsoni* from Bitter Root River at Fort Missoula, Montana. Careful examination has shown that Faust's description is wrong in some particulars, the most important of which are corrected in the following sentences: The esophagus is not especially short, being nearly twice as long as the pharynx. The cirrus sac and its included parts are exactly as in *C. farionis.* The ovary is pear-shaped. Laurer's canal opens on the dorsal surface over one of the intestinal crura. The entire reproductive system agrees with that of *C. farionis,* including the vitellaria which Faust considered the most distinctive feature. Since the size of the body agrees with that of young adults of *C. farionis* and the size of the eggs falls within the range of variation of this species, there is no characteristic left to distinguish Faust's *S. vitelloba* from *C. farionis.* It is evident, therefore, that *Stephanophiala vitelloba* Faust 1918 is a synonym of *Crepidostomum farionis* (O.F.M.), Faust's specimens being young individuals which have only recently reached the egg-forming stage, as I have previously suggested (Hopkins 1931a).

Layman (1930) gives a brief description of a "new species" of Crepidostomum from the intestine of *Salvelinus* sp. in Peter the Great Bay near Vladivostok, Siberia. The figure and all the data given for this form, *Crepidostomum ussuriensis* Layman 1930 (later in the same paper called *C. ussuriense,* which is the correct form grammatically), agree perfectly with *C. farionis,* with which it is almost certainly synonymous. It is of interest to note that Layman describes and figures the cirrus sac as extending posteriorly beyond the ventral sucker to the ovary, as it does in many but not all American specimens.

Layman's report partially fills a great gap in our knowledge of the distribution of *C. farionis.* We now know that this species occurs in Northern and Central Europe, in the Volga River in Russia, in streams and lakes of both the Atlantic and the Pacific watersheds in Northern North America, and on the Pacific coast of Siberia. The present evidence strongly suggests that the distribution of *C. farionis* is co-extensive with

the fresh-water range of salmonoid fishes in the Northern Hemisphere, except where the absence of the invertebrate hosts makes the propagation of the species impossible.

The miracidium of *C. farionis* was described by Willemoes-Suhm (1873), but little is known except that it is ciliated and has a black eyespot; the only individual studied had hatched from the egg after 34 days in water. Brown (1927) has described the other stages in the life cycle. The cercaria, a stylet-bearing cercaria with pigmented eyespots, therefore belonging to Nöller's group Ophthalmoxiphidiocercariae, develops in rediae in *Pisidium amnicum* (Müller) and less frequently in *Sphaerium corneum* (L.). The excretory formula of the cercaria is given as $2[(2+4)+(4+3+3+3)]$; the excretory system of the metacercaria and adult is on the same plan, according to Brown, but he could see only two flame cells in each of the six groups in these stages. The metacercariae were found encysted in the fat bodies and abdominal musculature of a mayfly, *Ephemera danica* (Müller). No infection experiments were reported by Brown. Baylis (1931) has reported the metacercaria of *C. farionis* from the amphipod *Gammarus pulex*. Nothing has been reported on the life history of *C. farionis* outside of Great Britain; in view of the tremendous range of the species, it seems probable that this trematode must be able to adapt itself to other invertebrate hosts in different parts of its range, though probably always remaining dependent on Sphaeriidae for its molluscan host. The ophthalmoxiphidiocercaria (Cercaria X. 4) reported by Harper (1929) may be identical with Brown's cercaria.

Specific Diagnosis.—Summing up the information now available, the following specific diagnosis may be given for *Crepidostomum farionis:*

With the characters of the genus. Length of sexually mature specimens 1 to 6 mm., body broad and thick, greatest width (in region of ventral sucker) usually one-fourth to one-third of length in preserved specimens. Suckers large, oral sucker about two-thirds as large as ventral sucker. Oral papillae relatively small; ventro-lateral pair slightly larger than the four dorsal papillae, which are approximately equal. Pharynx nearly spherical to elongate-elliptical; length of pharynx one-half to three-fourths diameter of oral sucker. Esophagus sometimes only slightly exceeding length of pharynx, sometimes twice as long, dividing just before passing over into intestinal crura. Crural fork sometimes a little anterior to level of ventral sucker, sometimes dorsal to center of ventral sucker. Common genital pore median or very slightly lateral to median line, ventral to pharynx or just behind this level, some distance anterior to level of crural fork. Cirrus sac elongate-pyriform to sausage-shaped, extending back over ventral sucker, sometimes ending near center

of sucker and sometimes reaching back past sucker as far as level of ovary. Seminal vesicle narrowed to thin duct anteriorly, nearly straight to slightly convoluted, taking up two-fifths to three-fourths length of sac; pars prostatica small; cirrus straight to slightly convoluted, with relatively thin muscular wall. Ovary pear-shaped, slightly lateral or median near dorsal surface just behind ventral sucker or dorsal to its posterior edge. Seminal receptacle pear-shaped, near dorsal surface immediately behind ovary. Laurer's canal opening on dorsal surface just above intestinal cecum on side opposite to seminal receptacle. Vitelline follicles extending along sides of body from pharynx to posterior end of body, lying lateral and ventral to intestinal crura from crural fork to ends of crura and extending inward to median line behind testes, filling in the post-testicular region solidly on the ventral side of the body; few or no follicles dorsal to level of intestinal crura. Uterus usually entirely anterior to testes, sometimes extending back dorsally to level of center of anterior testis; intrauterine eggs 65 to 85 μ long and 40 to 50 μ wide, one to about one hundred in number. Testes tandem, approximately in middle of post-acetabular region or a little farther forward. Excretory bladder a narrow elongate sac or broad tube extending forward as far as anterior edge of anterior testis or posterior edge of ovary, close to dorsal surface; flame cell formula unknown in adult, but pattern same as that of *C. cooperi*. Miracidium with complete coat of cilia and fused pigmented eyespots. Cercaria an ophthalmoxiphidiocercaria developing in rediae in the gills of *Pisidium amnicum* and *Sphaerium corneum*. Metacercaria encysted in abdomen of mayflies (*Ephemera danica*) and in amphipods (*Gammarus pulex*). Adult in intestine of fresh-water Salmonidae, rarely in other fishes.

Crepidostomum metoecus (Braun 1900)

Synonyms.—*Distomum metoecus* Braun 1900, *Crepidostomum suecicum* Nybelin 1932.

Hosts and Localities Reported.—*Nyctalus noctula* (Schreber) (*Vespertilio noctula, V. noctua*), Europe. *Nyctalus maximus* (Fatio) (*Vespertilio lasiopterus*), Europe. (Braun does not state where the specimens in the Vienna museum were collected, but both of these bats are Central European species according to Brohmer (1929) in "Die Tierwelt Mitteleuropas.") **Perca fluviatilis*, Vienna, Austria. The following were reported as hosts of *C. suecicum* by Nybelin (1932): *Thymallus thymallus*, Sweden; *Salmo trutta*, Sweden; *Lota lota*, Sweden; *Cottus gobio*, Sweden; *Salmo alpinus*, Sweden.

This species was first described by Braun (1900). Later Braun (1900a) published a more complete description and founded the genus

Crepidostomum with *C. metoecus* as type. In this paper he corrected some of the statements made in the first description and gave a fairly good figure. Odhner (1905, 1910) made some further corrections and additions after studying Braun's original specimens. Braun found his specimens in vials in the Vienna museum labeled as from the two species of bats named above, and *C. metoecus* has always since then been considered a parasite of bats; however, it has never been reported from bats since the original discovery, and until now has been known only from the type material.

Recently Nybelin (1932) has described a new species, *Crepidostomum succicum,* from Swedish fresh-water fishes, *Thymallus thymallus, Salmo trutta, Lota lota, Cottus gobio,* and *Salmo alpinus.* The specimens from *Salmo alpinus,* as described and figured by Nybelin, look very much like young specimens of *Crepidostomum farionis* except for their extremely small size (0.49 to 0.92 mm. long); the other specimens seem to me to be specifically identical with specimens from *Perca fluviatilis* which I found in one of the vials of parasites loaned to Professor Ward by the University of Berlin Zoological Museum (labeled "*Distoma nodulosum* Zed.—*Perca fluviatilis*—Wien—5774. Samml. Mehlis No. 87"). Seven of these specimens were found to agree perfectly (except for more elongated form and greater number of eggs) with two of Braun's original specimens from *Nyctalus noctula* which were loaned to Professor Ward by the Vienna Naturhistorisches Museum. There were also 12 specimens of *C. farionis* in the same vial from *Perca fluviatilis.* There is now scarcely a doubt in my mind that Nybelin's specimens and those from *Perca fluviatilis* are specifically identical with Braun's specimens from bats; I therefore consider *Crepidostomum succicum* Nybelin 1932 a synonym of *C. metoecus* (Braun). It is noteworthy that Nybelin's specimens and those from Perca contained many more eggs than the specimens from bats (8 to 24 eggs are shown in Nybelin's figures; I found up to 15 eggs in the specimens from Perca; Braun found only one or two eggs in his specimens); this fact, together with the abundance in fish and the apparent rarity in bats, makes it seem most probable that fish are the "natural hosts" of *C. metoecus* and that bats are only "occasional" or "accidental" hosts.

The two "type" specimens from bats which I studied gave the following measurements; one (Fig. 11), which was somewhat contracted but fairly straight, was 0.88 mm. long, 0.24 mm. wide at widest point (level of anterior testis), with oral sucker 0.13 by 0.11 mm., ventral sucker 0.13 by 0.14 mm., and the single egg 60 by 35 μ; the other specimen was contracted and the anterior end was bent strongly ventrad, making the apparent length only 0.73 mm.; no accurate measurements

could be made on the latter specimen, which appeared to contain only one egg. The genital pore is posterior to the level of the crural fork, as shown by Braun, and the cirrus sac turns ventrad after reaching back past the ventral sucker. The testes are very large, round, and in tandem position; they fill up the greater part of the post-acetabular region and reach nearly to the posterior end of the body. The vitelline follicles reach from oral sucker to posterior end and are mostly lateral and ventral to the intestinal crura, but also extend all the way to the dorsal surface anterior to the ovary and behind the posterior testis. The oral papillae are exactly the same shape and arrangement as in *C. cooperi*. The body is widest in the region of the testes. The ventral sucker projects a little. The other features are shown in Figs. 12 and 13.

The seven specimens of *C. metoecus* from *Perca fluviatilis* range from 1.0 to 1.22 mm. in length and from 0.17 to 0.25 mm. in width. The diameter of the oral sucker is 0.10 to 0.17 mm., and that of the ventral sucker the same. The body is widest at or near the level of the ovary in all. Except in one specimen, the anterior end of the cirrus sac is protruded and extends 0.10 to 0.20 mm. outside of the body. The genital pore is behind the level of the crural fork. The cirrus sac extends back past the level of the ventral sucker. The ovary lies close to the dorsal surface, to one side of the median line, a short distance behind the ventral sucker; the seminal receptacle lies just behind the ovary. The testes are large, tandem, and vary considerably in size and shape as in other species of the genus; they lie close to the ventral surface. The excretory bladder is an undivided sac lying close to the dorsal surface and ending over the anterior testis. The strong development of the vitellaria, which cover the sides of the body from pharynx to posterior end and also fill in nearly all the space between the other organs, is the most characteristic feature of these specimens; the same distribution of vitellaria is shown by the Vienna museum specimens from the bat and in Nybelin's figures. The eggs in the Perca specimens are about 54 by 33 μ. Most of the structural features are shown fairly well in Figs. 12 and 13.

Specific Diagnosis.—Combining all the data now available, i.e., Braun's, Odhner's, Nybelin's and my own, the following specific diagnosis of *C. metoecus* may be given:

With the characters of the genus. Length of egg-producing adults from about 0.5 to about 2.7 mm.; width one-fourth to one-tenth length; greatest width between ventral sucker and posterior testis; depth of body slightly less than width. Suckers approximately equal. Oral papillae not notched at tip. Pharynx ovoidal or ellipsoidal, one-third to one-half as long as oral sucker. Esophagus slightly longer than pharynx, much curved in contracted specimens. Crural fork anterior to ventral sucker;

crura running back through dorsal half of body on each side of ventral sucker and gonads, ending a little over half-way between posterior testis and posterior end of body. Genital pore median ventral, posterior to crural fork. Cirrus sac elongated, extending back over ventral sucker and then bending ventrad, often reaching as far as level of ovary; anterior end protrusible. Cirrus relatively long, reaching back about half the length of the cirrus sac, separated from seminal vesicle by small spherical pars prostatica; seminal vesicle not narrowed distally. Ovary pyriform, lateral and dorsal behind ventral sucker, on either right or left side; sometimes at level of posterior edge of ventral sucker, sometimes some distance behind it. Testes large, spherical or ellipsoidal, tandem in median line, about equally far from ventral sucker and posterior end of body. Uterus reaching back to anterior edge of anterior testis (or possibly in some as far as posterior testis?), then curving anteriad. Intrauterine eggs one to twenty-four in specimens observed so far, 53 to 66 μ long, 30 to 45 μ wide. Vitellaria very strongly developed; follicles extending anteriorly as far as pharynx in well-extended specimens and to oral sucker in contracted specimens, and posteriorly as far as posterior tip of body; mostly lateral and ventral to intestinal crura, but follicles also overlapping crura on dorsal side and extending to dorsal surface throughout most of the body length, sometimes meeting in median line anterior to ventral sucker and between testes; apparently always meeting in median line behind testes, where follicles pack the posterior end of the body solidly except for the narrow space occupied by the excretory bladder near the dorsal surface. Excretory bladder an undivided sac extending forward just under the dorsal surface and ending dorsal to the anterior testis; excretory pattern and flame cell formula unknown. Adults in intestine and pyloric ceca of fresh-water fishes and in intestine of bats, Central and Northern Europe.

Nöller (1925) described a new cercaria, *Cercaria arhopalocerca*, which he later (1928) assigned to *Crepidostomum metoecus*. He proposes for all distome cercariae with stylet and eyespots the new group name Ophthalmoxiphidiocercariae, into which may be placed the cercariae of *Allocreadium isoporum* and of all species of Crepidostomum, so far as known. Nöller's cercaria, which develops in rediae in *Pisidium personatum* (in Thuringia), agrees well with the cercaria of *C. cooperi;* his rediae also closely resemble the rediae of this species. The assignment of *Cercaria arhopalocerca* to *C. metoecus* is based on (1) the close resemblance of the cercaria to the cercaria of *C. farionis* as described by Brown (1927) and (2) the complete absence of fish in the spring in which the infested Pisidia were found, as well as the absence of other vertebrates which might serve as hosts for the adults. Nöller obtained metacercariae

by experimental infestation of Chironomus and Corethra larvae, but they were not described; no further experiments were made and there is no evidence that *C. metoecus* occurs in the vicinity, either in bats or in fish. I am inclined to believe that Nöller's cercaria probably does belong to *C. metoecus*, or at least to some species of Crepidostomum, but the present evidence is far from convincing.

In connection with the occurrence of *C. metoecus* in bats and the supposed occurrence of its redia and cercaria in a spring uninhabited by fish, the following suggestion may be offered. It is possible that *C. metoecus* becomes sexually mature in the second intermediate host, as *C. cornutum* and several other Allocreadiidae are known to do. If this is true, the bats reported as hosts may merely have eaten progenetic metacercariae which were already producing eggs. Sexually mature *C. metoecus* (or perhaps *C. farionis*, for that matter) encysted in flying insects such as mayflies might be carried from one stream or pond to another close by, and after the death of the insect host the eggs of the encysted worm might be released into the water, thus giving rise to infestation of the Sphaeriidae in the immediate vicinity.

Crepidostomum cooperi Hopkins 1931

Synonyms.—*Crepidostomum ambloplitis* Hopkins 1931; *Crepidostomum solidum* Van Cleave and Mueller 1932; *Crepidostomum fausti* Hunninen and Hunter 1933.

Hosts and Localities Reported.—*Perca flavescens*, Go-Home Bay, Ontario; Oneida Lake, New York; *Sebago Lake, Maine. *Ambloplites rupestris*, Go-Home Bay, Ontario; *St. Lawrence River, New York. **Lepomis cyanellus*, *Sangamon River and *Salt Fork River basin, Champaign County, Illinois. **Lepomis humilis*, Sangamon River and Salt Fork River basin, Champaign County, Illinois. **Lepomis megalotis*, Sangamon River and Salt Fork River basin, Champaign County, Illinois. **Lepomis* sp., *Baton Rouge, Louisiana. **Micropterus salmoides*, *Money, Mississippi (Tallahatchie River). **Eupomotis gibbosus*, Ragged Lake and Barnum Pond, Franklin County, New York. "Catfish," Baton Rouge, Louisiana. **Ameiurus melas*, Salt Fork River basin, Champaign County, Illinois. **Ameiurus natalis*, Salt Fork River basin, Champaign County, Illinois. *Ameiurus nebulosus*, Oneida Lake, New York. **Schilbeodes gyrinus*, experimental infestation. **Schilbeodes miurus*, experimental infestation. **Amyda mutica*, *Blue River, Connorville, Oklahoma.

This species was first described (Hopkins 1931a) from specimens collected by A. R. Cooper at Go-Home Bay and previously listed by Cooper (1915) under the name of *Crepidostomum lourcatum* (Zeder). In the same paper I described *Crepidostomum ambloplitis*. A few weeks

later Van Cleave and Mueller (1932) described a new species, *Crepidostomum solidum;* in a footnote they stated that it was their opinion that *Crepidostomum ambloplitis* and *C. cooperi* were variants of the same species, and that both *C. ambloplitis* and *C. solidum* were synonyms of *C. cooperi.* Through the courtesy of Dr. Van Cleave I have been able to examine many of the specimens on which Van Cleave and Mueller's description was based, and found that most of their specimens resemble the *C. ambloplitis* type, but some show resemblances to the *C. cooperi* type. Later I collected specimens from catfish which more completely bridged the gap between these types, leaving no morphological differences on which a specific distinction could be based; therefore I accept the view that *C. ambloplitis* and *C. solidum* are synonyms of *Crepidostomum cooperi.*

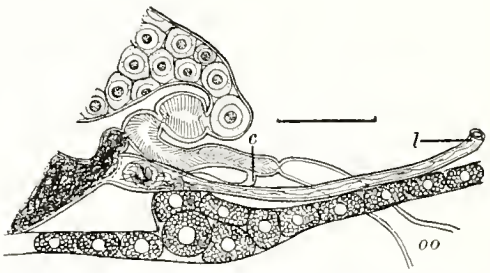
Crepidostomum fausti Hunninen and Hunter 1933, from trout, is a synonym of *C. cooperi.* I studied the type specimen of *C. fausti* (U.S.N.M. No. 8615) and paratype (U.S.N.M. No. 8616) and could find nothing to distinguish the species; the authors were misled by lack of knowledge of the variability of *C. cooperi.* Hunninen and Hunter's suggestion that some of the specimens described as *C. laureatum* or *C. farionis* by Linton and by Faust belonged to their species is a speculation with little or no foundation.

The material used in my study of this species consists mostly of specimens collected from sunfish, *Lepomis* spp., in Champaign County, Illinois, and specimens obtained from sunfish and catfish, *Schilbeodes* spp., as a result of experimental feeding with mayfly nymphs containing the metacercaria. In addition I have studied specimens from *Ameiurus* sp., Champaign County, Ill., *Lepomis* sp. and catfish, Baton Rouge, La., *Micropterus salmoides,* Tallahatchie River, Miss. (Simer's specimens), *Ambloplites rupestris* and *Eupomotis gibbosus,* New York, and *Amyda mutica,* Blue River, Oklahoma. The last mentioned lot of specimens is the first reported occurrence of any Crepidostomum in a reptile; it is possible that infestation resulted from the eating of an infested fish. Having an abundance of live material I was able to work out the excretory system and the details of the reproductive system from living specimens. In addition to this method of study, which is by far the best, I have studied whole mounts and serial sections.

Specific Diagnosis.—The information obtained in this study is summarized in the following specific diagnosis of *Crepidostomum cooperi.*

With the characters of the genus. Sexually mature specimens from about 0.40 to about 1.5 mm. in length; width varying from about one-seventh to about one-half of length according to state of contraction, averaging about one-fourth; depth varying from one-ninth to one-fourth

of length according to state of contraction; greatest width at level of ventral sucker or anterior testis. Ventral sucker one-fifth to one-half body length from anterior end according to size and state of contraction; usually slightly smaller than oral sucker, but sometimes equalling or even exceeding it in contracted specimens. Oral papillae all practically equal in size; ventral pair projecting from lateral margin of oral sucker, either directly laterad or slightly dorsad, not overlapping any part of ventral face of sucker; four dorsal papillae usually attached on transverse equator of dorsal face of sucker, but occasionally near enough to anterior margin to project anteriad beyond it; in life all papillae extend, contract,

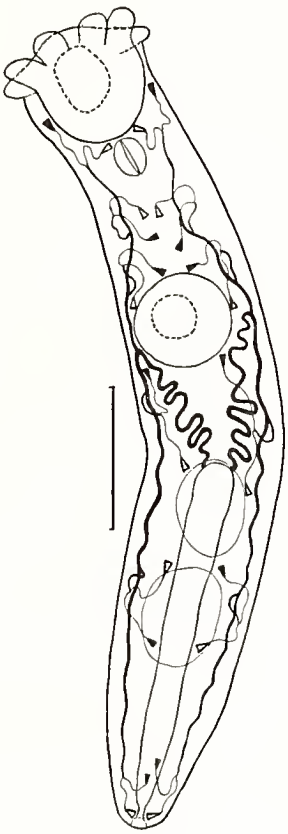


TEXT-FIG. 1.—Female reproductive organs of *C. cooperi*, drawn from living specimen, dorsal view; scale line represents 0.05 mm.; *c*, common vitelline duct; *l*, Laurer's canal; *oo*, oötype.

and bend in all directions. Pharynx ovoidal or ellipsoidal, length one-third to one-half, but usually two-fifths, of length of oral sucker. Esophagus two or three times length of pharynx but much convoluted in contracted specimens so that apparent length is less.

Genital pore usually posterior but occasionally in strongly contracted specimens ventral to crural fork; very small common genital atrium obliterated when cirrus sac is everted. Cirrus sac long and slender, tapering from near posterior end to anterior end, reaching back over ventral sucker to level of ovary or sometimes beyond, and rarely as far as posterior testis; varying from nearly straight to considerably convoluted; wall thin but muscular. Seminal vesicle two to four times as long as cirrus but so much convoluted that it occupies only two-thirds to three-fourths length of sac, tapering toward anterior end, often divided by a constriction into large posterior and small anterior chamber. Pars prostatica large, ovoidal or ellipsoidal. Cirrus slender, convoluted, with rather thin but muscular wall; lumen smooth-walled. Testes close together near ventral surface in posterior half of body, extremely variable in size and shape; twice as long as wide, spherical, or twice as wide as long according to state of contraction of body; distance from posterior testis to

posterior end one-tenth to one-fourth body length, varying according to relative size of testes and degree of contraction or extension of body. Ovary pear-shaped, dorsal, close behind and usually overlapping ventral sucker, median or slightly lateral on either side. Seminal receptacle of extremely variable size close to posterior margin of ovary. Laurer's canal running to pore on dorsal surface above intestinal cecum of opposite side. Uterus increasing in length and convolutions with age; running almost straight forward in immature specimens, back as far as anterior testis in most individuals, and back as far as center of posterior testis in a few (Simer's specimens from Micropterus); wall thin but fairly muscular; metraterm with thicker and more muscular wall beginning near posterior edge of ventral sucker, with smooth-walled lumen. Intrauterine eggs few, up to about 40; size ranging in different lots of preserved specimens from 50 to 60 μ by 30 to 40 μ, from 56 to 65 μ by 35 to 45 μ, and from 60 to 75 μ by 40 to 55 μ, and in living unflattened specimens from 62 to 75 μ by 42 to 55 μ; shells thin, yellowish, operculate. Spermatozoa about 120 μ long, with rod-shaped head 15 to 20 μ long and very slender tail. Vitellaria extending from near posterior end to about half-way between pharynx and ventral sucker, sometimes reaching posterior end of oral sucker in strongly contracted specimens (Figs. 2, 3); longitudinal vitelline ducts uniting behind posterior testis; follicles lateral and ventral to intestinal crura from center of ventral sucker to posterior testis, lateral, ventral and dorsal to esophagus and crura anterior to ventral sucker; lateral and dorsal to crura and extending clear across ventral surface behind posterior testis; a few follicles also lying median to crura between and in front of testes and above and in front of ventral sucker.



TEXT-FIG. 2.—Excretory system of *C. cooperi* adult.

Excretory bladder (Text-fig. 2) a narrow sac or broad tube close to dorsal surface, reaching forward to between anterior and posterior

edge of anterior testis; flame cell formula $2[(2+2+2)+(2+2+2)]$, vibratile organelle of flame cells about 15 μ long and 5 μ wide (in immature specimens just before attaining female maturity).

Pigmented eyespots, one on each side of pharynx or esophagus, usually present in adults, compact in some and dispersed in others.

Miracidium.—The egg cell does not undergo cleavage while within the uterus, and apparently not even after being ejected into the intestine of the host, but eggs put into pond water or tap water in a watch glass or shallow open dish soon begin cleavage; a spherical mass of cells without structure is formed in 3 days, an ovoidal embryo with two separate pigmented eyespots in 5 days, and an apparently mature miracidium in 7 days; however, the external cilia do not become active until shortly before hatching, which begins in about 10 days (Fig. 4). These results were obtained at room temperature in summer. The miracidium is pear-shaped, slightly flattened dorso-ventrally, and is about 65 μ long, 30 to 35 μ wide, and 25 to 35 μ deep while still in the shell. The cuticula is not divided into plates, but is completely covered with cilia nearly 10 μ long arranged in close-set longitudinal rows. The pear-shaped rudimentary gut opens at the tip of the conical inversible papilla at the anterior end of the body, and reaches back one-fourth to one-third the body length. Dorsal to or just behind the posterior end of the gut is a large pigment spot in the form of two shallow cups fused at their convex surfaces, forming a mass which appears V-shaped in dorsal or ventral view and round in lateral view (Fig. 4). The nerve mass lies ventral to the eyespots. Two large active flame cells lie one on each side of the body near the dorsal surface and about in the middle of the body length; they are of the same shape as in the young adults, but smaller, the vibratile organelle being 7 to 9 μ by 3 to 5 μ. The posterior two-thirds of the body is filled with germ cells.

Redia.—The redia of *C. cooperi* was found in 65 of 96 *Musculium transversum* (Say) collected in an oxbow pond formed by the dredging of Spoon River near St. Joseph, Ill., in collections made from October 8, 1931, to June 9, 1932. The infestation in this period was 67.6%. In June and July nearly all the large Sphaeriids were dead, but during July I found 18 adult Musculium; none of these were infested. The redia was also found in 2 of 3 *M. transversum* and in a single *Pisidium* sp. collected in July from Sangamon River. *Sphaerium notatum* Sterki was abundant in the Spoon River oxbow, but 60 of these were examined with completely negative results.

Each infested Musculium contains rediae of a great variety of forms, some slender and active, some very large and looking like sausage-shaped sporocysts, and some nearly spherical. Some of these are evidently growth stages of the same type of individual, while others are

apparently abnormal. There seems to be no regular order of mother and daughter rediae, for there is no constant difference between rediae containing cercariae and those producing rediae; in fact, frequently the same parent individual contains both rediae and cercariae. There are no ambulatory processes.

Individuals with eyespots, rare in comparison to the others, may constitute a distinct generation (Fig. 5). These are slender, active rediae 0.18 to 0.36 mm. long and 0.05 to 0.07 mm. wide, with a nearly spherical pharynx about 30 μ in diameter. The posterior tip is apparently adhesive, and is used for attachment while the body is pushed forward by extension, as in some rotifers. The anterior end can be inverted so that it serves as a sucker. The gut is small and does not increase as the body grows, so that it becomes proportionately smaller; apparently it disappears when the redia becomes mature. Around the pharynx are 6 gland cells with short ducts opening into the prepharyngeal invagination. I have seen one eyespotted redia, 0.37 by 0.15 mm., which contained immature cercariae; all others contained only very small germ balls. The excretory system of the eyespotted rediae was not studied in any detail. The pigmented eyespot is like that of the miracidium, but more irregular in shape; it lies near the posterior end of the pharynx. It seems probable that the eyespotted rediae develop directly from the miracidium; i.e., they are the same individuals in a more advanced stage of development.

Rediae without eyespots range from slender forms like the eyespotted type to stout sausage-shaped rediae containing young rediae, mature cercariae, or both (Figs. 6, 9). The young rediae just after leaving the parent are 0.12 to 0.25 mm. long according to the phase of contraction and extension. They usually become about 0.6 mm. long before the germ balls develop into mature cercariae, but a few nearly spherical rediae contain cercariae when only 0.3 mm. long. As a redia matures it becomes thicker and loses its motility. Some mature rediae reach a length of 2.0 mm. and most are over 1.0 mm. The gut disappears when the slender motile stage is passed, and in very old rediae the pharynx degenerates and may disappear entirely. No birth pore could be found. The pharynx varies from 21 by 21 μ to 45 by 35 μ, averaging 32 by 29 μ; there is no evidence that it increases in size after the young rediae leave the parent, small rediae having as large a pharynx as large ones. The excretory system consists of a pair of small lateral vesicles in the middle third of the body length with a tube running anteriad and another running posteriad from each; the tubes branch, and the branches divide again into capillaries, but the capillaries and flame cells have not been traced out completely. The number of flame cells varies from 4 in the youngest to 22 in the oldest; in young rediae they are of the same size and shape as in miracidium, but in mature rediae they become much larger and

broader, finally becoming fan-shaped or "toadstool-shaped" like some of the flame cells figured by Looss (1894) for adult trematodes. The smallest flame cells have a vibratile organelle 6 μ long and 2 μ wide, while the largest are 11 μ long and 33 μ wide.

Most of the young motile rediae are found in the spaces between the inner and outer layers of the gills and mantle, where they may be seen pushing their way slowly along. Many of these are only 0.15 to 0.18 mm. long, so they evidently migrate to the gills and mantle very soon after birth. All the mature rediae are found in the liver (digestive gland); the rediae in the gills and mantle contain only very small germ balls. As many as 160 mature rediae have been found in the liver of a single Musculium; the immature rediae are much less numerous. One Musculium isolated in the laboratory from December 8, 1931, to February 9, 1932, contained only 12 rediae, all immature and without eyespots; as there was no chance for infestation during this time the rediae must have been the descendants (probably of the first or second filial generation) of a miracidium which had entered the host at least two months before.

Cercaria.—The cercaria (Fig. 7) is unpigmented and transparent. The average length at rest is about 300 μ, with width and depth about 100 μ, but a creeping cercaria may vary in length from 150 to 450 μ as it contracts and extends the body. The tail is long and slender, without fins or other modifications, and tapers gradually to a sharp tip; it is usually slightly longer than the body, averaging about 370 μ long in slightly flattened living specimens. The two suckers are slightly unequal, the oral sucker averaging about 59 by 49 μ and the ventral sucker 44 by 44 μ; the ventral sucker is usually just posterior to the middle of the body, but its position varies greatly with the changes in body shape. Both suckers are fringed with crowns of sticky protruberances which project from the outside rim when the sucker is everted or flattened against a surface, and are withdrawn into the cavity when the sucker is drawn in or contracted; this fringe is inconspicuous on the oral sucker but large on the ventral sucker.

The stylet (Fig. 8a) lies near the anterior tip of the body with its base imbedded in a pit in the dorsal wall of the oral sucker; its length is about 25 μ. Two large conspicuous eyespots lie just below the dorsal surface lateral to the pharynx or a little behind this level; they are shallow cups of small elliptical brown granules which look black *en masse*; each cup is about 15 μ in diameter. Three large cephalic gland cells lie on each side of the ventral sucker, but somewhat anterior to it in extended specimens. Two of the glands give rise to ducts which run along the lateral margin of the body, while the duct from the other gland

runs forward near the median line; all of the ducts open through pores on the dorsal surface near the stylet. The gland cells are either pear-shaped or lobate; their finely granular, slightly refractive contents take only a faint yellowish tinge when treated with neutral red in life; each cell is 30 to 45 μ long by 15 to 25 μ, with a nucleus 7 to 9 μ in diameter. Forty to fifty cystogenous glands (Fig. 7) lie just below the dorsal surface from about half-way between pharynx and oral sucker to the posterior end of the body; they are each about 15 to 22 μ in diameter, with a nucleus about 5 μ in diameter; the cell contents are hyaline but take a very bright orange-red stain with neutral red in life.

The prepharynx is very narrow and about 45 to 60 μ long. The small ellipsoidal pharynx is about 18 μ long and 15 μ in diameter. A narrow, indistinct esophagus runs back nearly to the ventral sucker and divides into two short rudimentary crura, which do not extend past the level of the ventral sucker and sometimes seem to be lacking entirely.

The female reproductive complex is represented by a bilobed mass of small deep-staining cells dorsal to or just behind the posterior edge of the ventral sucker. Two strands of similar cells can sometimes be seen running anteriad over the sucker and joining just in front of it. The testes are represented by two discoidal groups of deep-staining cells lying in a tandem position close to the ventral surface in about the middle of the post-acetabular region (Fig. 7).

The excretory bladder (Fig. 7) is a contractile tube extending nearly to the ventral sucker, and ending posteriorly in a muscular-walled outlet duct leading to a terminal pore. The wall of the bladder is composed of very large cells 20 to 25 μ long and 10 to 15 μ wide, with spherical nuclei about 5 μ in diameter; these cells are filled with spherical granules or droplets as large as the nucleus. The excretory tubes, their branches, the capillaries, and the flame cells have the same arrangements as in the adult. The flame cell formula is $2[(2+2+2)+(2+2+2)]$; frequently all the capillaries and flame cells can be seen at one time in a single individual. In each pair of flame cells one cell is dorsal and the other ventral.

This cercaria is a very rapid and effective swimmer. In swimming the body is flexed ventrad, while the tail is extended to its maximum length and beats so rapidly that it may be seen only as a blurred area. Sometimes the tail leads and sometimes it pushes the body. There is a strong reaction to light: individuals which have just emerged from the host swim towards light, but after perhaps an hour they reverse this reaction and swim away from light. A swarm of cercariae may be driven from one side of a wide dish to the other in a few minutes by changing the direction of the light. When a swimming cercaria comes in contact with

a solid surface, the suckers secure a hold and progression by leech-like creeping begins. Usually the tail is cast off within a few minutes after creeping begins, and sometimes almost immediately.

Metacercaria.—The metacercaria is found encysted in the muscles and body cavity of Hexagenia nymphs, usually in the gill-bearing segments of the abdomen. A few of the infested nymphs which emerged as sub-imagos in the laboratory were identified by Doctor Herbert Ross, of the Illinois Natural History Survey, as *Hexagenia limbata* (Guerin). However, it is possible that some of the hosts belonged to other species of Hexagenia. Of 191 Hexagenia nymphs collected in the Sangamon River between Mahomet and Fisher, Ill., from July 26, 1931, to July 17, 1932, *Crepidostomum cooperi* metacercariae were found in 141, or 74%. The greatest number of cysts found in a single naturally infested individual was 13; the average number of cysts in infested hosts varied from 1.9 to 6.7 in collections made at different times and places; the lowest percentage of infestation, 61%, was found in July and August, 1931, and the highest percentage, 95%, was found in July, 1932; no statement can be made as to the seasonal variation of infestation in this case, for the infestation remained between 61% and 95% during the winter. Apparently there is an increase in the number of metacercariae per host as one goes upstream.

The metacercaria is enclosed in a thin transparent true cyst about 0.19 mm. in diameter. Except in recent infestations, the true cyst is surrounded by a layer of orange-brown granular material laid down by the host, and this in turn is usually enclosed in a wall of closely packed connective tissue. The metacercaria lies doubled in a U-shaped position, almost completely filling the true cyst.

Living metacercariae removed from the cyst average about 0.30 mm. in length, ranging from 0.24 mm. contracted to 0.50 mm. extended, the width being about one-third of the length in the resting condition. The oral sucker averages 90 by 80 μ, the ventral sucker 60 by 70 μ; the ventral sucker is usually near the center of the body length. The oral papillae are exactly as in the adult except in absolute size. The prepharynx is short as in the adult, and the pharynx is the same size, in proportion to the suckers, as in the adult. The esophagus is several times as long as the pharynx, and the crura extend nearly to the posterior end of the body except in recently encysted individuals. The cephalic glands of the cercaria are present, but are smaller and more numerous (5 to 10 on each side) and stain brownish-red with neutral red; the ducts are as in the cercaria except for the increase in number. The stylet is present, in the same position as in the cercaria, in recently encysted metacercariae, but usually not in older ones. The eyespots are still conspicuous, and usually fairly compact. There are no cystogenous glands, even in meta-

cercariae which have just completed encystment; the true cyst takes the bright orange-red stain (with neutral red) which is characteristic of the cystogenous glands in the cercaria, so there can be little doubt that the secretions of these glands take part in the formation of the cyst. Long tubular cutaneous glands, most abundant in the anterior end and around the suckers, lie just under the surface of the body and open to the outside through pores scattered over the surface; the content of these glands is a homogenous, slightly light-refractive fluid which stains yellow in neutral red; the end of the ducts sometimes project as little papillae on the outside surface. The same glands can be seen in living adults; in sections they stain deeply with eosin and Orange G.

Recently encysted metacercariae differ from the cercaria only in the absence of the tail and of the cystogenous glands and in the altered staining reaction of the cephalic glands; in older specimens the genital organs become fully developed and differ from those of the adult only in their relatively larger size in relation to the size of the adult. In *C. cooperi,* unlike *C. cornutum,* the metacercaria does not become appreciably larger as long as it remains within the cyst. In old individuals the testes are very large and are producing numerous spermatozoa, the cirrus sac is relatively larger than in most adults and is much convoluted, the cirrus, pars prostatica, prostate glands, and seminal vesicle are fully developed, the vesicle is packed with active spermatozoa, and many spermatozoa can be seen in the uterus; the ovary and seminal receptacle are of about the same relative size as in the adult and their connecting ducts are fully developed, but the ovarian cells and vitellaria are still immature. It seems evident that such an individual would begin to produce eggs very soon after entering the adult host and would have to be considered an adult in spite of its minute size; such cases may account for the forms with unusually large testes and for the individuals with abnormally large cirrus sac which Van Cleave and Mueller have designated tentatively as "winter forms." So far I have never found a progenetic metacercaria, i.e., one which produces eggs while in the second intermediate host, although I have examined hundreds of metacercariae at all seasons of the year.

The excretory system of the metacercaria is exactly the same as in the cercaria, except that the excretory bladder is enormously swollen and filled with spherical light-refractive droplets, giving a dark steel-gray appearance when seen by transmitted light. The wall of the bladder is thin; one may surmise that the large cells which surround the bladder in the cercaria have discharged their contents into the bladder, thus giving rise to the peculiar droplets characteristic of the bladder in the metacercaria. The excretory droplets are forced out through the excretory

pore from time to time after a metacercaria begins to crawl around, and become less and less abundant after an individual enters the intestine of the host fish. The flame cells are of the same shape as in the cercaria and are little if any longer.

Infestation Experiments.—A few attempts to infest young Musculium and Sphaerium by exposure to miracidia were made, but were unsuccessful.

Hexagenia nymphs were invariably infested successfully by exposing them overnight in syracuse dishes with a Musculium which was giving off cercariae. Attempts to study the process of penetration under the microscope were unsuccessful because of the sensitivity of the cercaria to light. Experimentally infested mayflies were examined alive under the microscope from time to time, and some were dissected at periods from 18 hours to 3 weeks after exposure; from 1 to 62 cysts were found on dissection. The metacercariae obtained in this way were identical with those found in naturally infested nymphs. After 24 hours, a newly encysted larva is still a cercaria to all appearances, except for the lack of a tail, and the host cyst is lacking. Within 4 days the orange-brown host cyst is formed and the excretory bladder has taken on the appearance characteristic of the metacercaria. Within 2 or 3 weeks the metacercariae are as fully developed as most of those found in natural infestations, and at this age they have been proved capable of developing into adults when fed to sunfish. The tail is never found in individuals which have penetrated into a mayfly, even in those which have not yet encysted.

A few attempts were made to infest Chironomus larvae, Sialis nymphs, dragon-fly larvae, crayfish, and Heptagenia nymphs, but without success. Cercariae penetrated into Chironomus nymphs in a few cases, but after crawling around in the body cavity for some time they all died without forming cysts. One cyst was obtained in the gill of a Heptagenia nymph, but the metacercaria died and degenerated within a few days. Cysts were occasionally obtained in the gills of Hexagenia nymphs after exposure to a heavy swarm of cercariae, but none were ever found in the gills of naturally infested hosts. No cysts were found in Heptagenia nymphs in nature, although nymphs of this genus were abundant in the Sangamon and 40 were examined. All mayfly nymphs used in infestation experiments were carefully examined under the microscope before exposure to cercariae, in order to avoid confusion with natural infestations.

Infested Hexagenia nymphs were fed to 11 sunfish, and adult or nearly mature *C. cooperi* were recovered from 8 of these. The species successfully infested were *Lepomis cyanellus, L. humilis,* and *L. megalotis.* These experiments showed that 3 to 4 weeks is the time required

by most individuals to develop into sexually mature adults after entrance into the fish host. *C. cooperi* was also obtained from 5 of 7 catfish (*Schilbeodes gyrinus, S. miurus,* and *Ameiurus melas*) which were fed infested nymphs.

The sunfish and 5 of the catfish used in these experiments came from the same Spoon River oxbow in which the cercaria of *C. cooperi* was found. These fish were kept in the laboratory from 1 to 4 months before feeding experiments were attempted. For controls I used 31 sunfish and 9 catfish from the same oxbow; of these, 6 sunfish and no catfish contained Crepidostomum. It may be worthwhile to note that no Hexagenia nymphs were ever found in this oxbow, although I searched for them many times. Probably there had been some Hexagenia here, but they had died out when the water became too stagnant.

Crepidostomum cornutum (Osborn 1903)

Synonyms.—*Bunodera cornuta* Osborn 1903; *Distomum nodulosum* Zeder of Wright 1884; *Distomum auritus* MacCallum 1918 (probably),

Hosts and Localities Reported.—

Centrarchidae: *Micropterus dolomieu,* Go-Home Bay, Flat Rock Lake, and Musquash River, Ontario; Douglas Lake, Michigan; Oneida Lake, *St. Lawrence River, and *Hatchery Pond at Ogdensburg, New York; *Middle Fork River at Penfield and *Pistakee Lake, Illinois. *Micropterus salmoides,* Money, Mississippi. "Black bass," Lake Chatauqua, New York. *Ambloplites rupestris,* Lake Chatauqua and Oneida Lake, New York; Montreal, Quebec (bought in market); Go-Home Bay, Ontario; *Put-in-Bay, Ohio; Lake Michigan, Wisconsin; St. Lawrence River. *Pomoxis annularis,* *Hetterson's Lake, Greene County, Alabama. *Lepomis* sp., Money, Mississippi. *Chaenobryttus gulosus,* Money, Mississippi.

Siluridae: "Catfish or bullhead," Lake Chatauqua, New York. "Channel cat," Lake Michigan, Wisconsin. "Yellow bullhead," Lake Michigan, Wisconsin. "Speckled bullhead," Lake Michigan, Wisconsin. *Ameiurus lacustris,* Flat Rock Lake and Musquash River, Ontario. "Catfish," *Baton Rouge, Louisiana. *Ameiurus melas,* Baton Rouge, Louisiana.

Amphibia: "Mud puppy," Lake Michigan, Wisconsin. *Amphiuma means,* Baton Rouge, Louisiana.

Invertebrates: *Cambarus* spp., Lake Chatauqua, New York; Alma, Michigan; Montreal (?), Quebec; Toronto (?), Ontario; Go Home, Killarney, and Shawanaga, Ontario; Minneapolis, Minnesota; *Madison, Wisconsin; Manhattan, Kansas; Baton Rouge, Louisiana; Mississippi (?); *Champaign County, Illinois.

C. cornutum was first described by Osborn (1903) as *Bunodera cornuta*. Stafford (1904) assigned Osborn's species to Crepidostomum. Since then numerous descriptions and reports by various investigators have made *C. cornutum* the best known American species of the genus, and have shown it to be abundant and widely distributed. The material used in my study of the adult includes Cooper's Ontario specimens and specimens collected by Hunter in New York, by H. J. Bennett in Louisiana, by myself in Illinois, by Dr. Ward at Put-in-Bay, by J. H. Walker in Alabama, by Simer in Mississippi, and by Cooper and by L. J. Thomas at Douglas Lake.

Specific Diagnosis.—The following specific diagnosis of *C. cornutum* sums up all the knowledge now available:

With the characters of the genus. Length of sexually mature specimens 1.0 to 3.7 mm. long when fairly well extended; width usually about one-fourth to one-third of length, but may be less at maximum extension; greatest width usually at level of oral sucker, sometimes at ventral sucker. Oral sucker very large; ventral sucker one-half to three-fourths as large as oral sucker, in first or second fourth of body length. Length of ventral papillae about one-half diameter of oral sucker, four dorsal papillae only slightly smaller; none notched. Pharynx one-fifth to one-third as long as oral sucker. Esophagus two to four times as long as pharynx.

Common genital pore ventral or posterior to crural fork. Cirrus sac very long, slender, often curved or convoluted; always extending back past ventral sucker, often as far as anterior testis; posterior end bent ventrad. Seminal vesicle long, convoluted, occupying posterior half or two-thirds of cirrus sac; wall muscular; pars prostatica large; cirrus slender, straight or curved, with muscular wall of moderate thickness, and lumen lined with pointed projections. Testes ventral in posterior half of body, tandem to strongly oblique, highly variable in size and shape, sometimes contiguous and sometimes separated by a space equal to diameter of testis. Vasa efferentia from testes uniting just at posterior end of cirrus sac. Ovary relatively small, pear-shaped, dorsal, median or slightly lateral on either side, sometimes touching ventral sucker and sometimes behind it a distance equal to three times its own diameter. Laurer's canal opening on dorso-lateral surface above intestinal cecum of side opposite to seminal receptacle. Uterus running back from oötype to anterior edge of anterior testis, or exceptionally as far as center or posterior edge of posterior testis, then coiling anteriad; metraterm beginning near posterior edge of ventral sucker, only slightly more thick-walled than uterus, with very prominent blunt-pointed projections in its lumen. Intrauterine eggs operculate, thin-shelled, ellipsoidal, light yellow, with germ cell in single

cell stage; numbering one to 50 or exceptionally 100; size 65 to 90 μ by 35 to 68 μ in whole mounts, with average of 81 by 56 μ. Vitellaria lateral from pharynx to posterior end, follicles mostly dorsal, lateral, and ventral to esophagus and intestinal crura with few or none median to crura, occasionally meeting near ventral surface at posterior ends of crura; longitudinal vitelline ducts joined behind posterior testis; transverse ducts near middle of body length.

Excretory bladder broad, pouch-shaped, dorsal, extending forward to level of anterior testis or ovary. Flame cell formula $2[(2+2+2)+(2+2+2)]$.

Pigmented eyespots present, one on each side of pharynx, but becoming dispersed in older individuals. Cephalic glands of cercaria persisting in adult, numerous.

Redia and cercaria unknown. Metacercaria encysted in crayfish (*Cambarus* spp.), with eyespots and (in very recently encysted individuals) a stylet; becoming sexually mature and growing to full adult size while still encysted, and producing numerous eggs of normal appearance; cysts 0.26 to 2.0 mm. in diameter, metacercaria 0.32 to about 3 or 4 mm. long, exactly similar to adult in older individuals and differing only in proportions of body and development of genital organs in younger specimens; eyespots compact in smaller specimens; cephalic glands 6 on each side of body in young metacercariae, in 2 groups of 3 each, increasing to 8 or 10 on each side in older specimens; stylet of the same form as in *C. cooperi*, 22 μ long; excretory bladder a swollen sac reaching to anterior testis or ventral sucker and filled with refractive droplets, flame cell formula $2[(2+2+2)+(2+2+2)]$.

In Osborn's original description of *C. cornutum*, his Fig. 7 shows the uterus in one specimen running back behind the testes; Faust (1918) claims that this specimen must therefore be a "Bunoderan," but the other features shown are distinctly those of *C. cornutum*. Simer (1929) reports the uterus in some specimens of *C. cornutum* reaching well past the border of the anterior testis; I have studied the specimen from which his Fig. 4 was drawn, and found it to be *C. cooperi*, but in some specimens of *C. cornutum* in Simer's collection from Micropterus the uterus does extend back dorsal to the testes as far as the posterior edge of the posterior testis. Thus in both *C. cooperi* and *C. cornutum* the uterus in exceptional cases extends back to the posterior testis, showing in this respect a tendency toward the conditions normally found in Megalogonia and Bunodera; however, the uterus in Crepidostomum always remains a narrow tube instead of becoming a sac as in Bunodera. The uterus of *C. cornutum* differs from that of *C. cooperi* by the possession of numerous blunt-pointed projections into the lumen (very large in the metraterm) which stain heavily with hematoxylin.

I have used specimens from crayfish from Louisiana, Michigan, Wisconsin, Illinois, Minnesota, Kansas, and Ontario in my study of the metacercaria. The Kansas specimens are the ones reported but not identified by Scott (1915), and the Ontario material is part of Cooper's collection. All of Scott's specimens and some of Cooper's are sexually mature, containing up to 100 eggs in the uterus; I have also studied sexually mature specimens from Louisiana and Wisconsin crayfish. Numerous living metacercariae from Illinois and Louisiana crayfish were studied alive, so that I was able to work out the excretory system of the metacercaria, but no living egg-bearing specimens from crayfish could be obtained. The flame cell of the metacercaria has a vibratile organelle 10 to 12 μ long and 4 to 6 μ wide; the vibratile organelle of flame cells in immature specimens from *Micropterus dolomieu,* on which I worked out the excretory system of the adult, is 12 to 15 μ long and 4 to 6 μ wide.

The progenetic metacercariae, i.e., those which produce eggs, are exactly like the normal adult in size and structure, except that there seems to be a tendency for more eggs to be retained in the uterus and more spermatozoa to be retained in the seminal vesicle. The vesicle becomes enormously swollen in some cases so that the cirrus sac extends back past the level of the anterior testis and is wider than the ventral sucker. In many cases the space between the worm and its cyst is packed with hundreds of eggs, but the egg cell apparently does not begin the development of an embryo as long as the eggs remain within the cyst.

The presence of pigmented eyespots and a stylet in the young metacercaria indicates that the cercaria is of the ophthalmoxiphidiocercaria type.

Crepidostomum illinoiense Faust 1918

Synonym.—*Crepidostomum hiodontos* Hunter and Bangham 1932.

Hosts and Localities Reported.—*Pomoxis sparoides,* Illinois River at Havana, Illinois. *Hiodon tergisus,* Lake Pepin (Mississippi River), Wisconsin; Lake Erie. **Boleosoma nigrum,* *Go-Home Bay (Georgian Bay), Ontario.

Faust (1918) originally described this parasite from numerous specimens taken from a single crappie, *Pomoxis sparoides* (Lac.) at Havana, Illinois, by Dr. H. J. Van Cleave. The next report of the species was made by Pearse (1924), who found sixteen specimens in the intestine of a mooneye (*Hiodon tergisus*) caught in Lake Pepin, Wisconsin, which is merely a wide stretch of the Mississippi River. Pearse figured *C. illinoiense,* but gave no description. Pearse (1924a) repeated the same record without description or figure. Hunter and Bangham (1932) have described as a new species, *Crepidostomum hiodontos,* a distome represented by seventy-three specimens from *Hiodon tergisus* in Lake Erie.

The material I have used for the study of *Crepidostomum illinoiense* consists of a slide containing 12 toto mounts, including the specimens on which Faust's description was based, and whole mounts and serial sections made by me from specimens in the vial in Dr. Ward's collection from which Faust got his specimens. One specimen of this species in Dr. Ward's collection was collected by A. R. Cooper from *Boleosoma nigrum* at Go-Home Bay, Ontario. The type specimen of *C. hiodontos* (U.S.N.M. No. 8609) and Pearse's specimens of *C. illinoiense* (U.S.N.M. No. 7626) were used for comparison.

Study of Faust's original specimens (Fig. 16) makes it evident that the supposed differences betwen *C. illinoiense* and *C. hiodontos* are based on errors in Faust's description. The oral sucker is by no means "almost twice as large" as the oral sucker, as Faust states, but is very slightly if any larger, and in a few specimens the ventral sucker is the larger. The apparent length of the esophagus as seen in whole mounts does not exceed the length of the pharynx, due to convolutions lying nearly in the dorso-ventral plane, but in sections it can be clearly seen that the esophagus is much longer, in fact, up to three times as long as the pharynx. In *C. illinoiense,* or at least in all the specimens studied, the cirrus sac ends at the level of the ovary. The uterus in the more mature specimens is coiled back as far as the anterior edge of the anterior testis, and contains up to ten eggs in Faust's material.

Study of Hunter and Bangham's type specimen of *C. hiodontos* and of another specimen which was later sent me by Dr. Hunter reveals nothing which could be used to exclude them from *C. illinoiense.* The crura are wider than in Faust's specimens and the ventral sucker is slightly larger than the oral sucker, but these are evidently merely individual differences probably due to conditions at the time of fixation. Pearse's specimens show all intermediate conditions; some have wide crura, others have crura no wider than in Faust's material; some have an oral sucker larger than the ventral, others have the reverse relationship. It is evident that Pearse was correct in assigning his specimens to *C. illinoiense,* and that *C. hiodontos* Hunter and Bangham is a synonym of *C. illinoiense* Faust. It may be noted that in Hunter and Bangham's type specimen and in one of Pearse's specimens the uterus extends back as far as the center of the anterior testis. In one of Pearse's specimens the testes are distinctly oblique, not median tandem as is usually the case in this species.

Specific Diagnosis.—An inclusive description of *C. illinoiense* may now be given as follows:

With the characters of the genus. Length of sexually mature specimens 0.45 to about 1.2 mm.; greatest width at ventral sucker or ovary,

averaging about one-fourth length. Suckers nearly equal; either oral or ventral sucker may be slightly larger than other (oral sucker averaging 0.10 by 0.09 mm., ventral sucker 0.08 by 0.10 mm. in Faust's specimens). Ventral pair of oral papillae usually curved dorsad or posteriad, length about one-half diameter of oral sucker; dorso-lateral pair slightly smaller; median dorsal pair smallest of all, length averaging about one-fourth diameter of oral sucker, shape rectangular, with a distinct vertical notch in the distal end. Pharynx ovoidal or ellipsoidal, but often directed ventrad so that it appears spherical in dorsal or ventral view, the true length being about half that of the oral sucker. Esophagus up to three times as long as pharynx, but usually looped in dorso-ventral plane so that it appears shorter. Crural fork a little in front of ventral sucker, near dorsal surface; intestinal crura running back nearly to posterior end of body, either equal or unequal in length.

Genital pore median, either ventral to crural fork or a little posterior to this level. Cirrus sac long and narrow, with thin but muscular wall, reaching back over ventral sucker to level of ovary, usually bent two or three times in its course; seminal vesicle convoluted, running through posterior two-thirds or three-fourths of sac; pars prostatica ovoid, of medium size; cirrus fairly thick-walled, either straight or slightly bent. Testes irregularly spherical or ellipsoidal, nearly equal, sometimes one or both elongated either transversely or longitudinally, close together in tandem position near ventral surface in anterior half or two-thirds of post-acetabular region. Ovary pear-shaped, dorsal, on either side of mid-line close behind ventral sucker; seminal receptacle pear-shaped, immediately behind ovary; Laurer's canal opening on dorsal surface just above intestinal cecum on side opposite to ovary (Figs. 17, 18); uterus running back to anterior edge of anterior testis and then forward over ventral sucker, becoming more convoluted with increase in age and maturity of individual; metraterm beginning at posterior edge of sucker, wall slightly thicker and more muscular than wall of uterus. Intrauterine eggs ovoidal or ellipsoidal, 56 to 65 μ by 28 to 33 μ with average of about 61 by 30 μ; egg cell not segmenting within uterus. Vitellaria lateral and ventral to intestinal crura and extending from pharynx or from level about half-way between suckers nearly to posterior end of body, a few follicles also lying dorsal to crura and extending into intercrural space between and anterior to testes; follicles filling up all available space behind testes, from one side to the other; a few follicles also lying dorsal and ventral to testes in some specimens.

Excretory bladder a narrow pouch near dorsal surface, extending forward as far as center of anterior testis; excretory pore terminal; excretory pattern and flame cell formula unknown.

Life history entirely unknown, but presence in adults of a pair of pigmented eyespots, usually somewhat dispersed, indicates that the cercaria possesses pigmented eyespots.

Crepidostomum isostomum Hopkins 1931

Synonyms.—None.

Hosts and Localities Reported.—*Aphredoderus sayanus,* East Lake Fork, Sadorus, Illinois.

Since my original description of this species (Hopkins 1931) no additional material has been obtained. It was found only in a small drainage ditch, which was subsequently dredged with the consequent destruction of the fish and Sphaeriidae; both fish and Sphaeriidae have come back to this stream since then, but there is now no Crepidostomum infestation. I have been able to learn a few more details of structure by further study of preserved material, which are added to the original description in the following specific diagnosis of *C. isostomum.*

Specific Diagnosis.—With the characters of the genus. Length of sexually mature adults about 0.8 to 2.0 mm., width usually about one-fourth length, widest in region of testes. Suckers approximately equal, average diameter about one-ninth length of body, ventral sucker one-third to one-half body length from anterior end. Oral papillae large, length about one-third to one-half diameter of oral sucker; dorsal papillae equal, ventral pair usually slightly larger. Pharynx barrel-shaped or ellipsoidal, length usually about one-half diameter of oral sucker, esophagus two to four times as long as pharynx, crural fork dorsal to ventral sucker, crura running nearly to posterior end of body. Genital pore anterior to crural fork, usually about half-way between pharynx and ventral sucker. Cirrus sac very short and broad, ovoidal or sausage-shaped, length one to three times width, usually reaching back only to center of ventral sucker; wall thin and weakly muscled. Seminal vesicle much convoluted, longer than sac but because of coiling sometimes not occupying more than half of length of sac, while in others it reaches nearly to anterior end; pars prostatica large; cirrus thick-walled and heavily muscular. Testes large, variable in shape, usually slightly oblique. Ovary pear-shaped or nearly spherical, smaller than testes, dorsal, usually overlapping posterior margin of ventral sucker, usually slightly lateral on either side but sometimes median. Laurer's canal opening dorsal to intestinal cecum on side opposite to seminal receptacle. Uterus coiling back to anterior edge of anterior testis and then forward; metraterm with muscular wall nearly as thick as that of cirrus beginning dorsal to ventral sucker and opening into posterior side of minute genital atrium.

Intrauterine eggs few (up to about 20 in specimens studied), operculate, thin-shelled, 70 to 90 μ by 40 to 60 μ with average length about 83 μ; remaining in single-cell stage while in uterus. Vitellaria from level of genital pore to posterior end; follicles lateral to esophagus and intestinal crura, and also along median sides of crura behind testes, between testes, and between ovary and testes. Excretory bladder an undivided sac, usually expanded at anterior end, reaching to seminal receptacle; flame cell formula unknown, but at least 10 and probably more flame cells present on each side of body; flame cells like those of *C. cooperi,* vibratile cone 10 to 12 μ by 4 to 5 μ.

Life History.—The life history of *C. isostomum* is still not known with certainty. Rediae probably belonging to this species were found in 21 of 78 *Sphaerium notatum* Sterki from East Lake Fork in March and April, 1930, but cercariae were found in only 9 of these, the others containing only rediae with immature germ balls or daughter rediae. Only 16 Sphaerium were found in this stream in 1931, and none of these were infested.

The immature rediae found on the gills of *S. notatum* are exactly like the immature rediae of *C. cooperi* except for the pharynx, which is 40 to 67 μ long and 30 to 60 μ wide, averaging 50 by 45 μ. Mature rediae are 0.7 to 1.3 mm. long and 0.2 to 0.3 mm. wide; the pharynx is the same size as in immature rediae. As in *C. cooperi,* the gut of the immature rediae disappears at maturity; there are 6 unicellular glands around the gut, with ducts running into the prepharyngeal cavity, in immature rediae. The excretory system is similar to that of *C. cooperi;* as many as 18 flame cells have been counted in mature rediae.

The cercaria is an ophthalmoxiphidiocercaria very similar to that of *C. cooperi.* Nearly all of those found were too immature to show the complete structure, but the eyespots were always conspicuous. Three individuals were found which were not only fully mature but had apparently developed past the cercaria stage, for they showed the 6 oral papillae typical of the genus and a large pharynx drawn up close to the oral sucker, as in the metacercaria of other species of Crepidostomum (Fig. 14). A stylet was seen in several cercariae, but only one was measured; this was 31 μ long and of the same form as in *C. cooperi.* The atypical cercariae with oral papillae were 270 to 360 μ long and 100 to 110 μ wide, with tails 240 to 270 μ long, oral sucker 70 to 72 μ by 70 to 80 μ, ventral sucker 65 to 75 μ by 65 μ, pharynx 34 to 35 μ by 30 to 33 μ and compact pigment cup of the eyespot about 18 by 15 μ; the oral papillae are about 15 μ long. As will be seen from these measurements, the pharynx is about half as long as the oral sucker; this is significant in view of the fact that metacercariae of *C. cornutum* occur in crayfish

in the same stream, since the pharynx of *C. cornutum* is less than one-third as long as the oral sucker. There is apparently a high degree of probability that the rediae and cercariae found in *S. notatum* belong to *C. isostomum.*

Crepidostomum metacercariae probably belonging to *C. isostomum* were found in a few nymphs of *Hexagenia* sp. (erroneously called *Ephoron* sp. in my 1931 paper) collected in East Lake Fork. These metacercariae are very similar to those of *C. cooperi;* the principal point of difference is the position of the cirrus sac, which in these larvae reaches from near the pharynx to the anterior edge or center of the ventral sucker. No experiments could be made because of the scarcity of material, but the only evidence against their being *C. isostomum* is the fact that the oral sucker is somewhat larger than the ventral sucker in the metacercaria, while the suckers are practically equal in the adult; however, the great range in the relative dimensions of the two suckers in *C. cooperi* shows that this is not a serious obstacle to considering the metacercaria from East Lake Fork to be the larva of *C. isostomum.* Final determination must await the finding of more abundant material.

Crepidostomum auriculatum (Wedl 1857)

Synonyms.—*Distoma auriculatum* Wedl 1857; *Acrodactyla auriculata* (Wedl) Odhner 1910; *Acrolichanus auriculatus* (?) (Wedl 1856) Skworzoff 1927; *Acrolichanus similis* Wisniewski 1933.

Hosts and Localities Reported.—*Acipenser ruthenus* L., Danube River; Volga and Oka Rivers, Russia.

Since this species was originally described by Wedl, it has been discussed by several writers whose only knowledge of the form was obtained from Wedl's description, but nothing based on a study of actual specimens (except a brief mention of the excretory bladder and cirrus sac by Odhner 1910) was published until 1924, when Skrjabin reported two specimens from Russian sterlets. More recently Skworzoff (1927, 1928) has given a detailed description of *Crepidostomum auriculatum,* based on numerous specimens from sterlets (*Acipenser ruthenus*).

There is nothing to exclude this species from the genus Crepidostomum; it differs from other species in some respects, but there is no difference on which a clear-cut generic distinction can be founded, since the peculiar features of the species are merely slight modifications of features found in other species of the genus or different in degree only. Lühe (1909) was correct in calling Wedl's species *Crepidostomum auriculatum.* Its nearest relative is *C. lintoni.*

Specific Diagnosis.—A brief diagnosis of *C. auriculatum,* combining the data of Wedl and Skworzoff, may be stated as follows:

With the characters of the genus. Adults averaging 1.87 mm. in length, sometimes as long as 3 mm.; greatest width at or behind ventral sucker, equalling about one-fourth of length. Ventral pair of oral papillae overlapping ventral surface of oral sucker, larger than other two pairs, length equalling about one-third of diameter of sucker; median dorsal pair only about one-third as long as ventral pair; dorso-lateral pair smallest, length being about one-half that of median dorsal papillae. Oral sucker round (heart-shaped when flattened), diameter about one-seventh or one-eighth length of body, equal to ventral sucker or slightly larger; oral aperture usually triangular. Ventral sucker in anterior half of body, round in outline. Pharynx longer than broad; length about half that of oral sucker. Prepharynx short. Esophagus short, length averaging less than that of pharynx. Crural fork about one-third way from oral to ventral sucker, crura reaching past testes but not to posterior end of body.

Genital pore just behind crural fork. Cirrus sac very broad and long, in some cases reaching posteriorly beyond ventral sucker; length sometimes one-third body length; wall sparsely muscular. Seminal vesicle occupying more than half of cirrus sac, convoluted; pars prostatica present; cirrus thick-walled, strongly muscular, protrusible; prostate glands strongly developed and numerous. Ovary ovoidal, near dorsal surface on either right or left side close behind ventral sucker. Oviduct, seminal receptacle, Laurer's canal, oötype, and connections as in rest of genus. Uterus with few loops, not extending posteriorly beyond anterior testis. Eggs 64 μ by 36 to 38 μ. Vitellaria along margins of body from pharynx to posterior end, meeting behind testes; transverse ducts near middle of body length, meeting to form vitelline reservoir. Excretory bladder long, sacculate-tubular, reaching anteriorly as far as ovary; main collecting tube on each side running from anterior end of bladder to level of ventral sucker, there dividing into anterior and posterior branches; flame cell formula unknown. Eyespots one on each side of pharynx. Cephalic glands numerous. Habitat, midgut of *Acipenser ruthenus*. Known distribution, rivers running into Black and Caspian Seas. Life history entirely unknown, but presence of eyespots in adults indicates that cercaria is eyespotted.

There were a few immature specimens of *C. auriculatum* in the material sent to Professor Ward from the University of Berlin Zoological Museum (Berlin No. 3247); they were collected by Collin from *Acipenser ruthenus*, locality unspecified. These are the only specimens I have had opportunity to examine, so I can add nothing to the knowledge of the species, except to say that the cephalic glands open dorsal to the oral sucker at the anterior end of the body as in other species, not into the oral cavity as Skworzoff states.

Recently Wisniewski (1933) has described a new species, *Acrolichanus similis* Wisniewski 1933, from *Salmo fario* and *Salmo irideus* in the Bosna River near Sarajevo, Jugo-Slavia. As well as I can judge without seeing specimens of this form, *A. similis* is a synonym of *Crepidostomum auriculatum*. Wisniewski admits that the differences between his species and *C. auriculatum* as described by Skworzoff are slight and of secondary importance, relating only to the slightly different shape of the body, the form and position of the testes, and the absolute dimensions of the ovary and testes, but suggests that Skworzoff's form may be identical with *A. similis* and not with the true *C. auriculatum* of Wedl. He states that the ventral sucker of Skworzoff's form was described as being larger than the oral sucker, as in his own material; it is true that Skworzoff in one place gives the dimensions of the ventral sucker as slightly larger than the oral, but in another place he states that the oral sucker is slightly the larger, and the oral sucker is also shown larger in one of his figures. All the differences which Wisniewski claims to separate his species from Wedl's can easily be accounted for by the supposition that Wedl's specimens were extended and Wisniewski's somewhat more contracted and flattened under the cover slip, as his Fig. 1 seems to show.

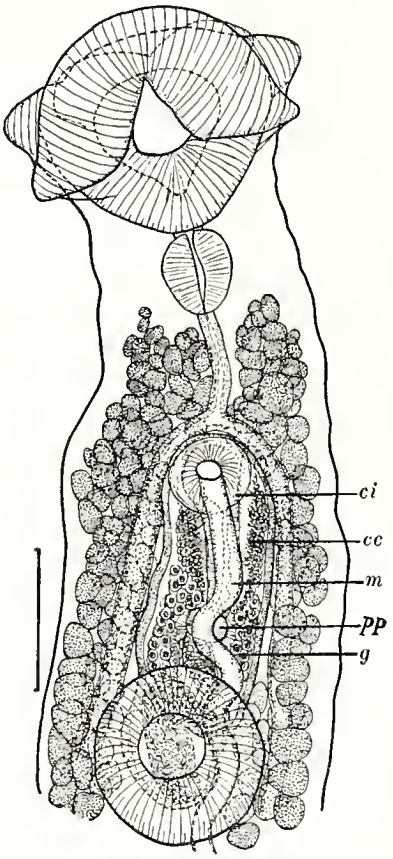
Crepidostomum lintoni (Pratt in Linton 1901)

Synonyms.—"*Distomum auriculatum* Wedl (?)" of Linton 1898; *Bunodera lintoni* Pratt in Linton 1901; "Bunodera auriculata of Wedl 1857" of Osborn 1903; "*Crepidastomum auriculatum* (Wedl) Linton" of Pratt 1902; *Distomum petalosum* Lander in Looss 1902; *Acrodactyla petalosa* (Lander) Stafford 1904; *Acrodactyla lintoni* (Pratt) Odhner 1910; *Acrolichanus petalosa* (Lander) Ward 1917.

Hosts and Localities Reported.—*Acipenser fulvescens* (*A. rubicundus*), Great Lakes and St. Lawrence River. *Scaphirhynchus platorhynchus,* Mississippi River (Lake Pepin), Wisconsin.

This species was first reported by Linton (1898) under the name of "*Distomum auriculatum* Wedl (?)," with a very brief description and vague figures. Later Linton (1901) again mentioned the species with only the comment "Pratt proposes the name *Bunodera lintoni* for this species." Pratt (1902) uses the name "*C. auriculatum* (Wedl) Linton" under the heading "Genus Crepidastomum," an obvious misprint. Looss (1902) published the name *Distomum petalosum* C. H. Lander for specimens with this label sent to him by Lander, and stated that this species was to all appearances the same as that which Linton described as "*Distomum auriculatum* Wedl (?)" but was distinct from the true *D.*

auriculatum Wedl. Stiles and Hassall (1908) and Odhner (1910) therefore consider *D. petalosum* a synonym of *Bunodera lintoni,* the latter name having been published a year earlier. Ward (1917) considers Lander's species distinct from Linton's form. Stafford (1904) proposed the new genus Acrodactyla with *A. petalosa* (Lander) as type; this generic name was later found to be preoccupied, and Ward (1917) substituted the new name Acrolichanus for the genus. I cannot find any difference of more than specific value to separate Acrolichanus from Crepidostomum, and accordingly use the name *Crepidostomum lintoni* (Pratt in Linton 1901), considering *A. petalosa* a synonym. The only difference of any importance between Lander's and Linton's forms, so far as the present evidence goes, is the apparent difference in length and position of the cirrus sac, which is figured and described by Linton as being entirely in front of the ventral sucker, while in Lander's specimens it reaches at least as far back as the anterior edge of the sucker. This difference is probably not real, and in any case is overbalanced by the agreement in all other features and the specific identity of the hosts, both lots of specimens having been found in Great Lake sturgeons. Unfortunately Linton's specimens in the U. S. National Museum are no longer available for study, having become dried up.



TEXT-FIG. 3.—Anterior end of *C. lintoni* adult; scale line represents 0.2 mm.; *cc,* cells connected with wall of cirrus; *ci,* cirrus; *g,* prostate glands; *m,* metraterm; *pp,* pars prostatica.

Although brief descriptions or notes based on study of actual specimens of *C. lintoni* have been published by Linton (1898), Looss (1902), Stafford (1904), Osborn (1903), Cooper (1915), Ward (1917), and Pearse (1924a), the only paper which

gives anything approaching a complete description is that of Faust (1918). However, Faust's inclusion of "specimens of Osborn's material from *Ambloplites rupestris*" is almost certainly erroneous.

The material used in my study of the species consists of two slides containing 5 whole mounts of Lander's original specimens from near Detroit, Michigan, numerous specimens collected by A. R. Cooper in the St. Lawrence River near Ogden Island and near Iroquois, Ontario, and Professor Ward's specimens collected in Lake St. Clair near New Baltimore, Michigan. All of these specimens are from the intestine of *Acipenser fulvescens*. They are now in the collection of Professor Henry B. Ward.

Specific Diagnosis.—The following specific diagnosis is based on my study of the specimens in Professor Ward's collection, some of which were used also by Faust in his study:

Crepidostomum lintoni: With the characters of the genus. Length of sexually mature specimens from about 1.2 to about 3.0 mm.; width averaging a little less than one-fourth of length, greatest at level of anterior testis or at ventral sucker. Oral sucker about one-third larger than ventral sucker, diameter equal to about one-fifth to one-seventh of body length. Oral papillae nearly conical with somewhat rounded tips; ventral pair largest, overlapping ventral surface of oral sucker; dorso-lateral and median dorsal pair about equal. Ventral sucker near junction of first and second thirds of body length. Pharynx ovoidal, length one-third to one-half diameter of oral sucker. Esophagus muscular, length one to two times that of pharynx; crural fork only a short distance behind pharynx and usually far in front of ventral sucker.

Genital pore median just behind crural fork. Metraterm and cirrus joining just as they reach ventral surface. Cirrus sac broad, sausage-shaped, reaching back over ventral sucker as far as center or posterior edge; wall thick, muscular. Slender convoluted seminal vesicle, usually S-shaped in dorsal view, occuping posterior half of sac; pars prostatica large, ovoidal; cirrus very strongly muscular, thick-walled, often giving the appearance in whole mounts of a genital sphincter (which does not exist); prostate glands large, numerous, filling most of the space in middle third of sac (Text-fig. 3). Testes in posterior half or posterior third of body, tandem or oblique, close together, round or slightly lobate; vasa efferentia joining after entering cirrus sac. Ovary pear-shaped, margins entire or slightly lobed, dorsal just behind ventral sucker, median or slightly lateral on either side. Oviduct, seminal receptacle, vitelline reservoir, oötype and connections as in rest of genus; Laurer's canal opening on dorsal surface only slightly to one side of median line.

Uterus running back in more or less convoluted course ventral and lateral to anterior testis, turning anteriad near anterior edge or center of posterior testis and then running forward; metraterm beginning near center of ventral sucker, with fairly thick muscular wall. Intrauterine eggs one to 30 (in specimens studied to date), ovoidal or ellipsoidal, 50 to 72 μ by 25 to 40 μ with average about 61 by 33 μ; egg cell remaining in single-cell stage until egg is laid. Vitelline follicles along margins of body from pharynx nearly to posterior end, surrounding crura on dorsal, lateral, and ventral sides and overlapping the testes to a slight extent dorsally and ventrally, but never extending inward to median line except behind testes, where they may or may not meet in median line near dorsal surface. Transverse vitelline ducts meeting to form vitelline reservoir immediately behind ovary.

Excretory bladder a long pouch lying near dorsal surface, extending anteriorly as far as seminal receptacle or ovary. Main collecting vessels running forward from each side of anterior end of bladder and dividing lateral to posterior edge of ventral sucker into an anterior and a posterior branch. Flame cell formula unknown.

Life cycle unknown; the metacercariae have been reported from cysts in crayfish (*Cambarus* sp.) but these were probably *C. cornutum*. Remnants of eyespots in immature specimens from sturgeons prove that cercaria and metacercaria must have eyespots. Cephalic glands also present in adults, opening dorsal to anterior edge of oral sucker.

Faust (1918), using Lander's unpublished notes and drawings, now in the possession of Professor Ward, says that as many as 6 flame cells have been found anterior to the forking of the excretory system and 8 have been found posterior to the forking. Later Faust (1919) gave the flame cell formula $12=(2+2)+(2+2+2+2)$ for the "larva," and later still (1924) lists the formula $2[(2+2)+(2+2+2+2)]$ for the adult. This formula is obviously inconsistent with the statements made in the 1919 paper; in a letter to me, dated Sept. 29, 1932, Faust admits this inconsistency and states that he does not now know the source of his later formula. Lander's original drawings of his crayfish specimens clearly show them to be metacercariae of *C. cornutum*. Lander's drawing of the excretory system was made from the crayfish form, not from adults; so the formula given by Faust has nothing to do with *C. lintoni*.

Faust (1919) very briefly describes and figures, from drawings made by Professor Ward, a metacercaria found by Ward in *Cambarus* sp. at Ann Arbor, Michigan. According to Faust, this is the "larva" of *C. lintoni*, but it might equally well belong to *C. cornutum*, and since no evidence is presented which would distinguish it from the latter species, its status must still be considered doubtful.

Crepidostomum canadense Hopkins 1931

Synonyms.—None.

Hosts and Localities Reported.—*Boleosoma nigrum*, Go-Home Bay, Ontario.

I have nothing more to add to my original description of this species (Hopkins 1931a). While the species appears to be distinct on the basis of the meager material at hand, it is possible that the finding of more abundant and better preserved specimens may show that *C. canadense* is identical with *C. isostomum*, with which it is undoubtedly closely related.

Crepidostomum latum (Pigulewsky 1931)

Synonym.—*Stephanophiala lata* Pigulewsky 1931.

Hosts and Localities Reported.—*Scardinius erythrophthalmus* (L.), Ukraine, U.S.S.R.

This species is known only from two specimens from the intestine of *S. erythrophthalmus*. According to Pigulewsky's brief description, the anterior end is tapered, the body being broadest in the region of the ventral sucker. The cuticula is without spines. The length is 1.03 to 1.3 mm., the breadth 0.191 to 0.195 mm. The pharynx is 65 μ long, 43 to 54 μ wide. The oral sucker is 0.143 to 0.165 mm. long, 0.056 mm. wide. The two intestinal crura are separate and do not reach the posterior end of the body. The vitelline follicles are 52 μ in diameter, and do not extend anteriorly as far as the ventral sucker. The ovary is ovoidal, 0.147 mm. long and 0.130 to 0.143 mm. wide. The uterus lies between the ventral sucker and the anterior testis. The eggs are without filament, and are 87 to 91 μ long, 43 to 56 μ wide. The testes are ovoidal; the anterior testis is 0.247 to 0.260 mm. long and 0.174 mm. wide, the posterior 0.221 to 0.260 mm. long and 0.147 to 0.174 mm. wide. The cirrus sac is sack-shaped, bent in the form of the letter S, and does not reach anteriorly past the level of the crural fork or posteriorly to the posterior edge of the ventral sucker; it is 0.108 to 0.152 mm. long. The seminal receptacle is 0.087 by 0.108 to 0.130 mm.

Pigulewsky's single figure, evidently drawn from a strongly contracted specimen, shows a distome resembling *C. farionis* in general appearance, but differing from this species in the position of the genital pore behind the crural fork, (this is not definitely shown, however), the restriction of the vitellaria to the post-acetabular region, and the positions of the ovary and seminal receptacle. The receptacle is shown dorsal and posterior to the ventral sucker in the median line, while the ovary is lateral and posterior to the receptacle. Twenty-three eggs are shown in the uterus. No esophagus is shown, but presumably the esophagus is present, though

looped in the dorso-ventral plane as in other species when the body is strongly contracted. If Pigulewsky's description and figure are correct, *C. latum* is distinctly set off from all other known species of Crepidostomum by the restriction of the vitellaria to the post-acetabular region, although its resemblance to *C. farionis* in most features is very striking.

Genus Megalogonia Surber 1928

Since the publication of Surber's (1928) description of the genus, the type and only species, *Megalogonia ictaluri,* has been restudied by Walz (1933) and by myself. These studies have shown that Surber's description of *M. ictaluri* is at fault in several instances. I give below a definition of the genus Megalogonia based on the present knowledge of the type species:

Allocreadiidae with six muscular oral papillae consisting of four dorsal and two ventral outgrowths from the oral sucker; two testes in tandem arrangement each divided by a median longitudinal constriction into a right and left lobe; uterus extending back between the lobes of the testes, sometimes to the posterior end of the body, sometimes only to the center of the anterior testis, then running forward in nearly the same course; intrauterine ova large and comparatively few as in Crepidostomum, not undergoing segmentation while in uterus; seminal receptacle, Laurer's canal, Mehlis glands, vitelline reservoir present and arranged as in Crepidostomum; genital pore median, ventral, in front of ventral sucker; cirrus sac containing seminal vesicle, pars prostatica, cirrus, and prostate glands, the long muscular cirrus taking up over half the length of the cirrus sac; excretory bladder sacculate, extending only to anterior end of posterior testis or to posterior end of anterior testis, with a collecting tube running forward from its anterior end on each side of the body and dividing near the ventral sucker into an anterior and a posterior branch which run along the margins of the body to the two ends, each of these primary branches dividing to give the flame cell formula $2[(2+2+2)+(2+2+2)]$; an eyespot on each side of the pharynx or esophagus except in older individuals. Miracidium developing within eggshell in water after laying, furnished with two fused pigmented concave eyespots, a rudimentary gut, two flame cells, and a coat of long cilia covering the body; no cuticular plates. Rediae long, slender, with large pharynx and rudimentary gut, no ambulatory processes; developing in Sphaeriidae; giving rise to more rediae or to cercariae. Cercaria a minute ophthalmoxiphidiocercaria with slender tail. Metacercaria encysted in aquatic insect larvae. Adult in intestine of fresh-water fishes. Type and only known species, *M. ictaluri.*

Megalogonia ictaluri Surber 1928

Synonyms.—None.

Hosts and Localities Reported.—*Ictalurus punctatus,* St. Croix River and Mississippi River, Minnesota; Rock River, Illinois. **Schilbeodes gyrinus,* *Spoon River at St. Joseph, Ill. **Schilbeodes miurus,* Spoon River at St. Joseph, Ill.

The material I have used in the study of the adults of *M. ictaluri* consists of about 60 specimens from *Schilbeodes gyrinus* and *S. miurus,* of which 6 were obtained from a natural infestation and the rest from experimentally fed catfish, and 20 specimens from *Ictalurus punctatus* collected by Walz at the mouth of Rock River and used in his study (Walz 1933). Living specimens were studied thoroughly; the details of the reproductive system were worked out in living specimens and checked by the study of serial sections, and the excretory system was worked out in living adults in which the vitellaria had not yet developed enough to obscure the capillaries and flame cells. Surber's type specimen, U.S.N.M. No. 7966, and two paratypes, U.S.N.M. No. 7967, were studied and compared with my material.

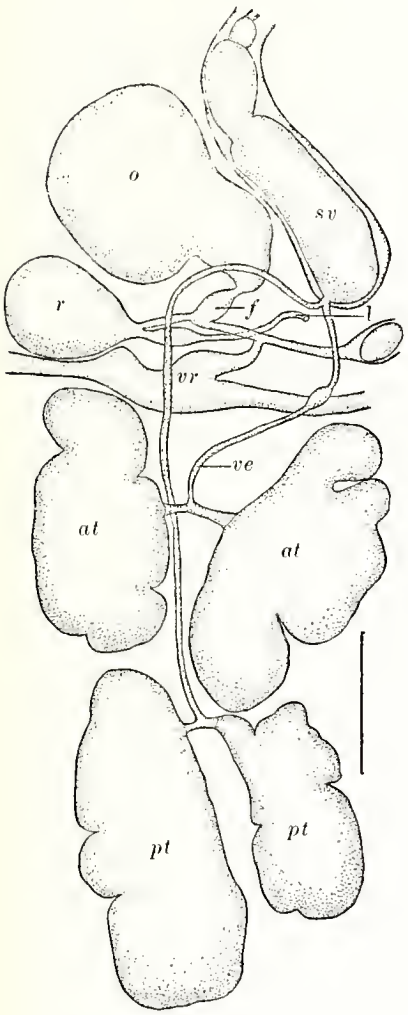
There are three major errors in Surber's description: 1. In addition to the two ventral papillae which Surber saw there are four dorsal papillae, which can be seen on Surber's type specimen, and the six papillae are arranged as in Crepidostomum and Bunodera. 2. Laurer's canal is not absent, but present and complete, opening on the dorsal surface; this is distinctly visible in the type specimen. 3. The testes are not four separate organs; there are really only two testes, each divided by a median longitudinal constriction into two lateral lobes, more or less completely separated in some specimens and broadly joined in others.

Specific Diagnosis.—A specific diagnosis of *Megalogonia ictaluri* based on my study is given below:

With the characters of the genus. Pyriform to elongate. Length of mature specimens 0.6 to 1.5 mm.; width about one-fourth of length, greatest in region between ventral sucker and posterior testis. Ventral sucker usually slightly larger than oral sucker, from anterior third to middle of body. Two ventral oral papillae projecting laterad from sides of oral sucker, four blunt dorsal papillae in line across dorsal surface of sucker and projecting dorsad; all six about equal. Prepharynx short; pharynx ovoidal or ellipsoidal, one-third to one-half as long as oral sucker. Esophagus thick-walled, two or three times as long as pharynx, usually convoluted; posterior end dividing just before running into intestinal crura. Crural fork some distance in front of ventral sucker, crura running back dorsally near lateral margins and ending about half-

way between posterior testis and posterior end of body. Genital pore median just behind crural fork. Cirrus sac with thin but muscular wall, very long and slender, either straight or bent, reaching back over ventral sucker to level of ovary; seminal vesicle usually convoluted, occupying posterior one-third or two-fifths of sac, anterior end narrowing to slender duct leading to small ovoidal or ellipsoidal pars prostatica near middle of sac; slender cirrus with strongly muscular but not very thick wall running from pars prostatica to genital pore; prostate glands comparatively few and small, lying in middle third of sac. Testes two, very large, filling nearly all intercrural space posterior to seminal receptacle; contiguous, tandem, near ventral surface; usually each divided by median longitudinal constriction into right and left lobe with only a narrow connection, but connection varying from small duct to broad bridge nearly as wide as lobes (Fig. 19, Text-fig. 4); margins of lobes usually somewhat notched or lobate but sometimes smooth; vasa efferentia from each testis joining just at posterior end of cirrus sac to form very short vas deferens which immediately enters the sac and joins the seminal vesicle. Ovary dorsal on either side of median line close behind ventral sucker, pear-shaped (Fig. 15, Text-fig. 4). Seminal receptacle large, pear-shaped, dorsal, immediately behind ovary. Laurer's canal opening on dorsal surface a little median to intestinal cecum opposite to seminal receptacle. Oviduct, oötype, shell glands and connections as in *Crepidostomum cooperi* (see p. 9). Uterus increasing in length and convolutions with age, reaching only to anterior edge of anterior testis in young adults, but in old individuals running back between lateral lobes of testes, on dorsal side, nearly to posterior end of body before turning ventrad and running anteriad; wall of uterus thicker than in Crepidostomum, lumen lined with protoplasmic projections; metraterm with thicker and more muscular wall beginning at posterior edge of ventral sucker. Intrauterine eggs one to 20 or more, operculate, about 61 by 38 μ in mounted specimens and 65 to 75 μ by 43 to 50 μ when free in water before fixation; remaining in single cell stage while in uterus. Vitellaria from posterior end of oral sucker nearly to posterior end of body; follicles from midline of dorsal surface nearly to margins of body in pre-acetabular region, dorsal and lateral to esophagus and crura; lateral and ventral to crura from ventral sucker to behind testes, with a few follicles median to crura between and in front of testes; extending completely across ventral surface behind testes; longitudinal vitelline ducts of two sides uniting ventral to excretory bladder behind testes; transverse vitelline ducts meeting to form vitelline reservoir of variable size and form ventral or posterior to seminal reservoir.

Excretory bladder narrow, sacculate or tubular, undivided, close to dorsal surface, ending between center of posterior testis and center of anterior testis. Collecting tube running forward from each side of an-



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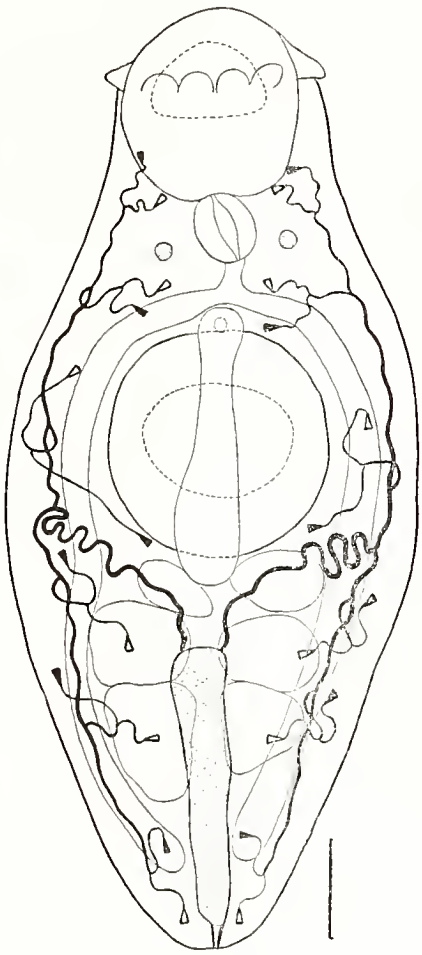


(5)

TEXT-FIG. 4.—Reproductive system of *M. ictaluri*, drawn from living specimen, ventral view; scale line represents 0.2 mm.; *at*, anterior testes; *f*, fertilization chamber; *l*, Laurer's canal; *o*, ovary; *pt*, posterior testes; *r*, seminal receptacle; *sv*, seminal vesicle; *ve*, vas efferens; *vr*, vitelline reservoir.

TEXT-FIG. 5.—Excretory system of *M. ictaluri*.

terior end of bladder, dividing lateral to posterior edge of ventral sucker into an anterior and a posterior branch; flame cell formula $2[(2+2+2)+(2+2+2)]$, one flame cell of each pair dorsal and one ventral; vibratile organelle of flame cell 15 by 8 μ in mature adults, conical.

Miracidium completely ciliated, without cuticular plates, with two fused pigmented eyespots and one pair of flame cells. Rediae in *Musculium transversum,* elongate sausage-shaped, with pharynx 40 to 52 μ by 30 to 45 μ. Cercaria of ophthalmoxiphidiocercaria type, about 200 to 250 μ long, with slender tail slightly shorter than body, stylet 15 μ long. Metacercaria encysted in gills of mayfly nymphs of genus Hexagenia, not increasing in size to any significant extent and not becoming sexually mature while in cyst. Metacercaria and young adults retaining pigment of eyespots. Adults in intestine of Siluridae.

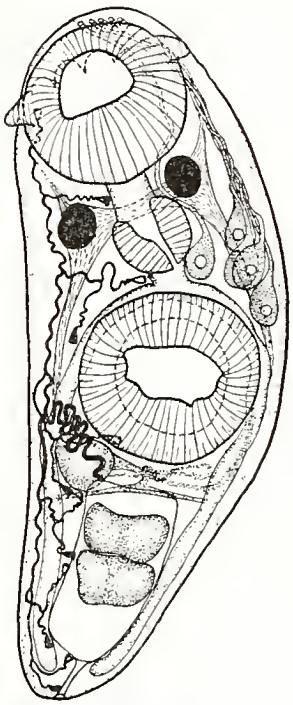
Miracidium.—Cleavage of the germ cell begins as soon as the egg is laid; a well-developed miracidium is formed within 6 days, and hatching occurs in 8 or 10 days after the egg is laid. Because of its power of extention and contraction the miracidium is variable in shape; it may be pear-shaped or ovoidal when contracted and elongate-ellipsoidal when extended, the length varying from 45 to 85 μ and the width from 30 to 40 (Figs. 20, 21). The long cilia, arranged in numerous longitudinal rows very close together, cover the entire body without a break, and there are no cuticular plates. A rudimentary pear-shaped gut, extending back only one-third or one-fourth of the body length, opens at the tip of a conical inversible papilla at the anterior tip of the body. A pair of concave pigment cups surrounding the eyespots lie dorsal to the gut, fused together on their median convex sides. A pair of large flame cells lie in the equator of the body. The posterior half of the body contains germ cells. The pigment cups of the eyespots are about 10 μ in diameter and the organelles of the flame cells are 6 to 8 μ by 3 to 4 μ.

Redia and Cercaria.—The redia and cercaria were found only once, in a *Musculium transversum* collected July 17 in the Sangamon River near Fisher, Illinois. Most of the cercariae were immature and the host died soon after being brought into the laboratory, so no adequate study could be made. The rediae are of the same type as those of *Crepidostomum cooperi,* but the mature ones are more slender; the pharynx is about 40 to 52 μ by 30 to 45 μ. The smallest immature redia measured was 200 μ long and 60 μ wide; the smallest redia containing well developed cercariae was about 0.5 mm. long and the largest was about 1.2 mm. long and 0.11 mm. wide.

The cercaria is about 200 to 250 μ long, with a slender tail somewhat shorter than the body. Identification was made by means of the stylet, which is of the same shape as that of *C. cooperi* but only 15 μ long, i.e.,

only about two-thirds as large as in *C. cooperi,* and is identical with the stylet found in the metacercariae of *M. ictaluri* (Fig. 8). Two dark pigmented eyespots lie laterally a short distance behind the oral sucker. Further than this nothing is known, as most of the cercariae were either dead or immature when studied.

METACERCARIA.—The metacercaria occurs in cysts in the gills of *Hexagenia limbata* Guerin and probably also in other species of Hexagenia; a few cysts have been found in the lateral margins of the abdomen, but not in the body cavity. From July 26, 1931, to July 17, 1932, I examined 191 Hexagenia nymphs from the Sangamon River between Mahomet and Fisher, Illinois, and found Megalogonia cysts in 91, or 48%. The highest degree of infestation, 80%, was found in the autumn and the lowest, 15%, in the spring months. The number of cysts in naturally infested hosts ranged from 1 to 40 with an average of 4.6 per host individual.



TEXT-FIG. 6.—Metacercaria of *M. ictaluri,* drawn from living specimens, ventral view.

The living metacercaria when released from the cyst is about 0.25 mm. in the resting position, 0.40 mm. when extended and 0.15 mm. when contracted, the width varying from 0.09 to 0.15 mm. The two suckers are practically equal in recently encysted individuals but the ventral sucker becomes distinctly larger than the oral in older individuals, in which the average dimensions are 47 by 54 μ for the oral sucker and 62 by 67 μ for the ventral sucker. The six oral papillae are very small, but have the same structure and arrangement as in the adult (Text-fig. 6). The digestive system is exactly the same as in the adult except in very recently encysted metacercariae, in which the crura reach only about half way from ventral sucker to posterior end. The stylet is present in the younger metacercariae; its location and shape are as in *Crepidostomum cooperi,* but it is only about 15 μ long (Fig. 8). The eyespots, one on each side of the pharynx or esophagus, are compact in most specimens; each pigment cup is about 10 μ in diameter. There are 3 to 6 cephalic glands on each side of the esophagus or crural fork; they are pear-shaped, 20 to 30 μ long and 10 to 15 μ wide;

the cytoplasmic contents are granular and stain red with neutral red in the living animal; the ducts run forward in two tracts on each side of the body and open through pores on the dorsal surface over the anterior margin of the oral sucker (Text-fig. 6). The excretory system is as in the adult except for the great distension of the excretory bladder, which fills most of the postacetabular region; the bladder is filled with excretory droplets as in Crepidostomum; the flame cells are of the same shape as in the cercaria and metacercaria of *C. cooperi,* but are smaller. The reproductive system is represented only by anlage in the younger metacercariae, but in older specimens all the organs and their ducts are present in the same arrangement as in the adult, except that the cirrus sac and uterus are shorter. There is the same variation in the shape of the testes in the metacercaria as in the adult (Text-fig. 6; Fig. 23 on Pl. IV).

Hexagenia nymphs containing Megalogonia metacercariae were fed to 7 catfish (*Schilbeodes gyrinus, S. miurus,* and *Ameiurus melas*) and 5 of these yielded Megalogonia when dissected. Sexually mature adults were found 14 to 16 days after the feeding. Two of the experimental fish were from the Salt Fork River near St. Joseph and the others were from the same oxbow of the Spoon River in which I found most of my *C. cooperi* cercariae. Two *A. melas* from this oxbow gave negative results after experimental feeding. All of the experimental fish were kept in the laboratory several weeks before feeding experiments were started. Megalogonia was found in only 1 of 9 control catfish which were caught in the same Spoon River oxbow and dissected immediately. Attempts to infest a *Pomoxis sparoides* and several *Lepomis* spp. were unsuccessful.

Genus Bunodera Railliet 1896

Until recently *B. luciopercae,* the type of the genus, has been the only species of Bunodera known, but the finding of *B. sacculata* Van Cleave and Mueller, and restudy of *B. luciopercae,* make it necessary to revise the previous conception of the genus. The present knowledge of the genus Bunodera is summarized in the diagnosis given below.

Aberrant Allocreadiidae with six muscular oral papillae projecting from the oral sucker, of which two are ventral and four dorsal. Suckers large and approximately equal. Prepharynx, pharynx, and long muscular esophagus present, the esophagus (in some at least) dividing before running into the intestinal crura; crural fork some distance anterior to ventral sucker except in strongly contracted specimens; crura running nearly to posterior end of body in some, ending in third quarter of body in others, close to dorsal surface in all. Genital pore ventral and median or slightly lateral, between suckers and anterior, ventral, or posterior to

crural fork. Cirrus sac broad and short, with thin but muscular wall; sac containing large seminal vesicle, pars prostatica, strongly muscular cirrus, and prostate glands; anterior end of sac eversible. Testes two, near ventral surface behind ovary in strongly oblique position; both close behind ovary in some, posterior testis in hind end of body in others. Vasa efferentia from testes running forward and entering vesicle separately. Ovary pear-shaped, near dorsal surface behind ventral sucker, median or lateral to median line on either right or left side. Seminal receptacle present (at least in *B. luciopercae*) near dorsal surface close behind ovary; pear-shaped, increasing in size with age. Oviduct leaving median side of ovary, soon widening to fertilization chamber, receiving seminal duct from receptacle at distal end of fertilization chamber, then running ventrad to oötype; common vitelline duct opening into oviduct between seminal duct and oötype; lumen of oviduct ciliated throughout. Laurer's canal coming off of seminal duct near seminal receptacle, running to pore on dorsal surface to one side of median line (dorsal to intestinal cecum on opposite side from ovary in *B. luciopercae*). Shell glands surrounding and opening into oviduct and oötype. Uterus running back from oötype to or nearly to posterior end of body, then turning anteriad and widening to broad pouch filling almost entire width and depth of body, narrowing again to narrow tube near posterior edge of ventral sucker; metraterm, with thick muscular wall, beginning dorsal to ventral sucker and running to genital sinus when this is present. Intrauterine eggs one to 5000 or more, ellipsoidal, 60 to 100 μ long; shell thin, yellowish, operculate; miracidium sometimes developing within intrauterine eggs. Vitellaria from pharynx to level of posterior testis or to posterior end of body, mostly lateral to intestinal crura, extending into intercrural space posterior to testes in some (*B. luciopercae*) and anterior to ovary in others (*B. sacculata*). Longitudinal vitelline ducts joined behind testes; transverse ducts meeting posterior or ventral to ovary to form vitelline reservoir, from which common vitelline duct runs to oviduct. Excretory bladder a broad dorsal sac, reaching to level of seminal receptacle or ovary; collecting tube running from each side of anterior end of bladder to level of ventral sucker, there dividing into anterior and posterior branch, each of which gives rise eventually to three groups of flame cells; excretory pattern same as that of Crepidostomum except that there are three or four flame cells in each group. Miracidium entirely ciliated, with pigmented eyespot in form of two fused cups, one pair of flame cells, no cuticular plates. Redia, cercaria and metacercaria not known, but adult has a pair of eyespots and cercaria must also have eyespots. Adults in intestine and pyloric ceca of fresh-water fishes. Type species, *B. luciopercae*. (Müller 1776)

Bunodera luciopercae (O. F. Müller 1776)

Synonyms.—*Fasciola lucio-percae* O. F. Müller 1776 (p. 223); *Fasciola percae cernuae* O. F. Müller 1776 (p. 224); *Planaria lagena* Braun 1788; *Fasciola percae* Gmelin 1790; *Fasciola percina* Schrank 1790; *Fasciola nodulosa* Froelich 1791; *Distoma nodulosum* Zeder 1800; *Crossodera nodulosa* Cobbold 1860; *Bunodera nodulosa* Looss 1899.

Hosts and Localities Reported.—*Lucioperca sandra,* Denmark; Germany. *Acerina cernua,* Denmark; Germany; Saratow, Russia. *Perca fluviatilis,* Germany; Sweden; France. *Aspro vulgaris,* Europe (fidé Schrank 1790). *Aspro zingel,* Europe (fidé Schrank 1790). *Esox lucius,* Europe (fidé Dujardin 1845). *Barbus barbus,* Germany. *Barbus fluviatilis,* France (fidé Dujardin 1845; Looss 1894 says not *B. luciopercae*). *Salmo trutta,* England; Scotland. *Perca flavescens,* Canada; United States.

The most complete description of *Bunodera luciopercae* is that given by Looss (1894), who studied both living and sectioned specimens. I have examined European specimens from the University of Berlin Zoological Museum (Vial No. 1568) and from the Königsberg Museum, and have found them to agree with Looss's description in every point except the following: (1) The excretory bladder is not forked, and does not end behind the testes as shown in his figures; instead, the bladder is a broad undivided sac, extending forward near the dorsal surface as far as the seminal receptacle. (2) The vitellaria are not dorsal to the level of the uterus, but lateral to the uterus and lateral and ventral to the intestinal crura (Figs. 22, 24, 25); they sometimes end before reaching the posterior tip of the body, as described and figured by Looss, but in most specimens the follicles extend to the posterior tip and meet behind the posterior testis, in the median line. (3) The eggs are not "nearly 100 μ long and about 50 μ wide," but only 66 to 70 μ by 43 to 51 μ in the Berlin material and 70 to 75 μ by 45 to 50 μ in the Königsberg specimens. It is possible that Looss made his measurements from living material, which would account for part but not all of this difference in egg size. The Berlin specimens were from the collection of Rudolphi.

I have also studied American specimens of *B. luciopercae* from the intestine of *Perca flavescens,* collected by Dr. A. R. Cahn from Lake Oconomowoc, Wisconsin (in January and August, 1923), and by Mr. M. A. Kemper from Lake Michigan (in April, 1913). Both of these collectors deposited numerous specimens in the collection of Professor Ward, and I have studied them both in toto and in sections. This is probably the same species that Stafford (1904) has reported from perch bought in the Montreal market and that Pearse (1924) has found abundant in the perch of Wisconsin lakes.

The American specimens which I have studied are all sexually mature (i.e., the uterus contains eggs of normal size and shape), and range from 1.0 to 3.6 mm. in length. The 1 mm. specimens are much contracted, and would probably measure about 1.5 mm. if even moderately extended. The width varies from one-fifth of the length in well-extended specimens to one-half of the length in much contracted individuals. The body is nearly round in cross-section (Fig. 22); the widest and deepest part of the body is usually about half-way between the ventral sucker and the posterior end; in well-extended individuals the pre-acetabular region is narrow and neck-like (Fig. 29), but in contracted specimens it is almost as wide as the post-acetabular region. The American specimens agree perfectly with those from Berlin and Königsberg except for the larger size of some of the American specimens, all of which however are well within the range of size given by Looss and others for European specimens. The eggs in the American material are 63 to 82 μ long and 38 to 51 μ wide, with an average of 71 by 43 μ; segmentation of the germ cell and formation of a partially developed embryo occurs within the intrauterine eggs, but so far I have not seen any which have developed to the miracidium stage.

Specific Diagnosis.—The following specific diagnosis of *Bunodera luciopercae* applies to both European and American specimens:

Bunodera luciopercae (O. F. Müller 1776). With the characters of the genus. Length of mature adults 1.0 to 4.5 mm., width one-fifth to one-half length; body round in cross-section, usually widest in middle of post-acetabular region. Suckers nearly equal, diameter one-eleventh to one-fifth length of body; ventral sucker in anterior third or half of body. Dorsal papillae slightly larger than ventral pair; length of dorsal papillae one-fifth to one-third diameter of oral sucker, length of ventral papillae one-seventh to one-fourth. Prepharynx short. Pharynx ellipsoidal, averaging two-fifths length of oral sucker with extreme range of one-third to one-half. Esophagus two or three times as long as pharynx, convoluted in contracted specimens; posterior end dividing just before running into crura. Intestinal crura running from crural fork, a short distance anterior to ventral sucker, back nearly to posterior tip of body; close to dorsal surface and lateral margins of body throughout.

Common genital pore median or slightly to one side of median line, ventral to crural fork or very slightly in front or behind this level. Male and female ducts joining almost at common pore. Cirrus sac very broad, short, seldom if ever extending back past ventral sucker; wall of sac thin but definitely muscular. Seminal vesicle long, divided by constrictions into two to several chambers; longer than sac and much convoluted in large specimens. Cirrus much shorter than vesicle, straight or

coiled, with thick muscular wall. Prostate glands up to several hundred in number; fewer in small specimens. Anterior testis near lateral margin on either side of body a little behind seminal receptacle; posterior testis on other side of body or median, near posterior ends of crura in posterior quarter of body, far behind anterior testis in larger specimens and only a little behind it in younger ones; both testes close to ventral surface. Ovary near dorsal surface slightly to one side (either right or left) of median line a short distance behind ventral sucker, which it may touch in some specimens. Seminal receptacle immediately behind ovary; larger than ovary in large specimens. Laurer's canal opening on dorsal surface over intestinal cecum on side of body farthest from ovary. Descending ramus of uterus narrow, tubular, running almost straight back from oötype in dorsal half of body, and turning ventrad near posterior end of body in old specimens or at anterior edge of posterior testis in smaller ones, immediately widening into enormously swollen ascending ramus which runs anteriad, ventral to descending ramus, taking up almost entire width and depth of body in large specimens; ascending ramus dorsal and lateral to testes and sometimes extending under edges of latter, but not ventral to center of testes. Intrauterine eggs up to 5000 or more in large specimens, much fewer in young individuals; ellipsoidal or oblong, operculate, thin-shelled, yellowish; length 63 to 82 (or 100 ?) μ, width 38 to 51 μ; miracidium developing within intrauterine eggs in very old specimens. Vitelline follicles extending in rather narrow band along lateral margins of body from near pharynx to posterior end of body (sometimes falling a little short of the posterior end in young individuals, but always reaching into posterior quarter of body); follicles lateral to esophagus, lateral and ventral to crura throughout length of latter, and meeting in median line of body behind posterior testis. Excretory bladder a broad undivided sac reaching forward immediately under dorsal surface as far as level of seminal receptacle or ovary; opening through short muscular-walled outlet duct to terminal or slightly dorsal excretory pore; main collecting ducts joining bladder on each side near its anterior end; flame cell formula probably $2[(4+4+4)+(4+4+4)]$, or at least close to this formula; excretory pattern same as that of *Allocreadium isoporum* and *Crepidostomum cooperi*. Eyespots present, one on each side of pharynx. Miracidium completely ciliated over external surface; rudimentary gut; one pair of flame cells; eyespot in form of two fused pigment cups; cuticular plates lacking. Redia, cercaria, and metacercaria unknown, but cercaria and metacercaria must have eyespots since these are present in adult.

Bunodera luciopercae is the most variable trematode I have studied; because of the great changes in form due to growth of the uterus and to

contraction or extension of the body, specimens differ so much that they could easily be regarded as distinct species except for the existence of specimens showing all intermediate conditions (Figs. 24, 25, 26, 27, 28, 29).

In regard to the life history of *B. luciopercae,* Looss (1894) shows that the cercariae previously assigned to this species by earlier authors, i.e., *Cercaria nodulosa* Linstow 1873 (which Looss says is a synonym of *Cercaria virgula* Filippi 1857) and *Distoma planorbis carinati* Filippi 1857, cannot belong to Bunodera because they lack eyespots. Schuurmans Stekhoven (1931) has reported the metacercaria of *B. luciopercae* from cysts in fishes, but in the absence of any description or recognizable figure his identification must be considered very questionable; the figure he gives does not show any resemblance to Bunodera.

Bunodera sacculata Van Cleave and Mueller 1932

Synonyms.—None.

Hosts and Localities Reported.—*Perca flavescens,* Oneida Lake, New York; *Lake Okoboji, Iowa.

Through the courtesy of Dr. Van Cleave I have been able to examine whole mounts of some of the specimens on which the original description of *B. sacculata* was based. In addition I have 5 specimens collected by Mr. H. E. Hart from *Perca flavescens* in Lake Okoboji, Iowa, Aug. 1, 1930. I can add only a few details to the original description in the specific diagnosis which follows:

Bunodera sacculata: With the characters of the genus. Length 0.5 to over 2.0 mm.; greatest width usually in post-acetabular region, about one-third of length in most preserved specimens; post-acetabular region becoming swollen and sacculate when uterus is filled with eggs. Suckers about equal. Oral papillae as in *B. luciopercae.* Prepharynx short; pharynx broad and ellipsoidal, length one-fourth to one-third diameter of oral sucker; esophagus longer than pharynx, often convoluted in contracted specimens, with thin muscular wall; crura reaching to level of posterior edge of posterior testis, never extending into posterior one-fourth of body. Genital pore ventral to crural fork or slightly farther forward. Cirrus sac short and broad, with thin muscular wall, reaching back over ventral sucker to center or posterior edge, or sometimes slightly farther; seminal vesicle straight or slightly bent, occupying posterior half or two-thirds of sac; pars prostatica small; cirrus short, thin-walled, muscular; prostate glands much less numerous than in *B. luciopercae,* mostly posterior to pars prostatica; anterior end of cirrus sac eversible. Testes strongly oblique, in anterior half or two-thirds of post-acetabular

region close to ventral surface. Ovary large, near dorsal surface close to posterior margin of ventral sucker, on either side of median line. Seminal receptacle small (possibly lacking; not seen in whole mounts examined to date). Laurer's canal opening on dorsal surface to one side of median line. Uterus running back to extreme posterior tip of body even in young specimens containing less than ten eggs; narrow throughout length in young specimens, becoming wide and sac-like (at least in ascending ramus) and filling almost entire width and depth of body in older ones; metraterm with somewhat thicker and more muscular wall beginning dorsal to ventral sucker. Intrauterine eggs numerous, up to several hundred; operculate; remaining in single-cell stage while in uterus; 65 to 85 μ by 38 to 58 μ with average about 75 by 47 μ in balsam mounts. Vitellaria from pharynx to posterior ends of crura, never reaching into posterior one-fourth of body; follicles dorsal, lateral, and ventral to crura, some extending into intercrural space in dorsal half of body. Excretory bladder a broad undivided pouch reaching forward to posterior end of ovary (according to figure published by Van Cleave and Mueller); nothing known of rest of excretory system. Life history entirely unknown, but presence of eyespots in adult shows that cercaria must have eyespots.

LIFE HISTORIES OF ALLOCREADIIDAE

Although many species and genera have been described and placed in the Allocreadiidae within the last few years, only a few authors have made any attempt to study the life histories of the forms described. *Crepidostomum cooperi* is the only species in the entire family whose life history has been worked out and all stages determined by experiment; the experimental method has been used to work out part of the life cycle in *Megalogonia ictaluri, Hamacreadium mutabile, H. gulella, Sphaerostoma globiporum,* and *Crepidostomum metoecus;* in all other cases the assignment of larval forms to specified species has been based on morphological resemblance, so that most of the life histories are still open to doubt, though tentatively acceptable until contradictory evidence is available.

The redia and type of cercaria are known for four of the nine species of Crepidostomum and for *Megalogonia ictaluri,* while nothing is known of the life cycle of Bunodera. Little is known of the development of other Allocreadiidae, but the available evidence indicates that there are three types of life cycle among the genera which have been assigned to this family by recent authors: (1) the type represented by

Allocreadium, Crepidostomum, and Megalogonia, in which the cercaria is an ophthalmoxiphidiocercaria developing in rediae in Sphaeriidae and the metacercaria encysts in crustacea, aquatic insects, or molluscs; (2) the type represented by Hamacreadium, Plagioporus, and Sphaerostoma, in which snails are the molluscan hosts and the cotylocercous cercaria, with stylet but without eyespots, develops in sporocysts; the metacercaria is always encysted, but the type of intermediate host differs greatly in the different species; (3) the type represented by Lepocreadium and Pharyngora, in which the cercaria has a long setiferous tail and develops in rediae in snails; in this type the metacercaria of each species may live in a great variety of hosts, but does not encyst. Of course there may be other types of life history in the family, for nothing is known of the larval stages in more than two-thirds of the genera and in an even larger proportion of the species.

The cercaria of Bunodera is unknown, but it is safe to assume that the cercaria has eyespots, since they are still present in young adults; recently Schuurmans Stekhoven (1931) has reported the metacercaria of *B. luciopercae* from cysts in fish, but his identification is at least doubtful. Palombi (1929) has described the metacercaria of *Helicometra fasciata* from Mediterranean shrimps of the genus Leander. Parts of the life cycles of two or possibly three other species of Allocreadium, in addition to *A. isoporum,* are now known. According to Lühe (1909) the *Distoma agamos* Linstow found in Gammarus and Asellus is probably the metacercaria of *Allocreadium transversale,* I have found the metacercaria of *A. ictaluri* Pearse encysted in the mantle of various Unionidae and Sphaeriidae, and Stafford (1931) has reported "adult" specimens of "*Allocreadium tumidulum*" from *Hexagenia variabilis. Peracreadium tumidulum* is a parasite of marine fish, so it is hardly possible that Stafford's specimens belong to this species. Professor Ward has specimens of metacercariae found encysted in the foot of Unionidae and in Gammarus which I have identified as *Anallocreadium armatum.* The life histories of *Hamacreadium gulella* and *H. mutabile* were described by McCoy (1929, 1930), the life histories of *Plagioporus siliculus* and *P. virens* by Sinitsin (1931), the life history of *Sphaerostoma globiporum* by Sinitsin (1905, 1907), and the life history of *Allocreadium isoporum* was indicated by Looss (1894) and Linstow (1897). The cercaria and metacercaria of *Lepocreadium album* and *Pharyngora bacillaris* have been reported by many authors, and a critical review of the literature on these forms has been presented by Dollfus (1925). Progenetic metacercariae of *Plagioporus cooperi* (Hunter and Bangham 1933) were found in mayfly nymphs by Cooper (1915).

It is a striking fact that the papillose Allocreadiidae agree closely with Allocreadium in life history, while Hamacreadium and Helicometra, which are usually placed in the subfamily Allocreadiinae, differ greatly from this genus in regard to life history. On the other hand, Hamacreadium agrees well with Plagiporus and Sphaerostoma, which have not been placed in Allocreadiinae. While it is useless to draw conclusions in the present state of knowledge, such facts are interesting as possible indications of relationship. When the complete life cycle of every species, or at least of one species in each genus is known, it may be possible to make a natural classification of the family, based on the characters of the developmental stages and a complete knowledge of the excretory system, as well as on such characters as the exact positions and sizes of organs, the extent of the uterus, and the lobing or nonlobing of the testes or ovary, which are obviously relatively insignificant and unreliable for taxonomic purposes. The same is true for other families of digenetic trematodes also.

EXCRETORY SYSTEM OF ALLOCREADIIDAE

The first excretory system to be completely worked out in this family was that of *Allocreadium isoporum* (Looss 1894), which was described and figured by Looss (1894). It is obvious from this account that the flame cell formula of *A. isoporum* is $2[(4+4+4)+(4+4+4)]$, and so far as I can see there is no other possible way to interpret either the figure or the description. Yet Faust (1919, 1924) gives the formula of *A. isoporum* as $2[(4+4+4+4)+(4+4)]$, and cites "Looss 1894, Fig. 103" as authority. This error seems to have influenced all of Faust's interpretations of the flame cell formula of Allocreadiidae. Faust (1919) states the formula of *Crepidostomum lintoni* (under the name of its synonym *Acrolichanus petalosa*) as $12=(2+2)+(2+2+2+2)$; this formula does not conform to the data given in his paper on Stephanophialinae and he gives no explanation of the change. As already stated, Faust obtained his information from Lander's drawing, which was really made from *C. cornutum*, not *C. lintoni*. Later Faust (1924) gives the following formulae for Allocreadiidae: "Adult Allocreadiinae *in parte* i.e., *Allocreadium isoporum* Looss: $2[(4+4+4+4)+(4+4)]$. Adult Stephanophialinae, i.e., *Acrolichanus petalosa* (Lander): $2[(2+2)+(2+2+2+2)]$. *Cercaria isopori* Looss: $2[(2+2)+(2+2)]$." In regard to *Cercaria isopori*, which Looss (1894) claimed to be the cercaria of *Allocreadium isoporum*, Faust has informed me in a letter that he based his conclusions on "Sewell's

data to the effect that *Cercaria isopori* was directly comparable to Sewell's *Cercaria indica XLIX,* which has the flame cell formula $(2 + 2) + (2 + 2)$."

I have worked out the excretory systems of *Crepidostomum cooperi, Crepidostomum cornutum, Megalogonia ictaluri,* and *Allocreadium ictaluri;* in all of these the system followed in the branching of the tubes is exactly the same as in *Allocreadium isoporum,* although the lengths and courses of the branches and the final number of flame cells in each group do differ considerably. The flame cell formula is the same for *C. cooperi, C. cornutum,* and *M. ictaluri*—$2[(2 + 2 + 2) + (2 + 2 + 2)]$, i.e., each flame cell has undergone one less division than in *A. isoporum* and there are therefore just half as many flame cells in each group. In *Allocreadium ictaluri,* on the other hand, the formula is $2[(16 + 16 + 16) + (16 + 16 + 16)]$ i.e., each flame cell has undergone two more divisions than in *A. isoporum* and three more than in *C. cooperi,* so that there are exactly four times as many flame cells as in the former and eight times as many as in the latter.

Brown (1927) gives $2[(2 + 4) + (4 + 3 + 3 + 3)]$ as the formula for the cercaria of *Crepidostomum farionis.* However, his figures show that the most anterior branch of the posterior primary branch comes off very close to the point where the main tube divides and that its point of origin is obscured by the convolutions of the main tube and its branches; so it is quite possible that he was mistaken as to the number of flame cell groups on each of the two primary branches. It is noteworthy that in the metacercaria and adult Brown could find only two flame cells in each group; this may be significant, in view of the fact that the relationship between the cercaria and the metacercaria was not established by experiment, for it is possible that the cercaria may belong to some species of Allocreadium or Bunodera.

As I interpret the description of the excretory system of *Bunodera luciopercae* given by Looss (1894), the branching of the tubes is the same in this form as in Allocreadium. He says that there seems to be three or four flame cells on each of the secondary tubes; accordingly, the formula of *B. luciopercae* may be $2[(3 + 3 + 3) + (3 + 3 + 3)]$, but more probably it is $2[(4 + 4 + 4) + (4 + 4 + 4)]$, unless there are more flame cells in some groups than in others.

Outside of the four genera Allocreadium, Crepidostomum, Megalogonia, and Bunodera, no complete excretory system is known in the Allocreadiidae; indeed in many species and several genera even the bladder is unknown. It is evident much work must be done on the excretory systems of other genera before anything more than a tentative classification can be made.

RELATIONSHIPS OF THE PAPILLOSE ALLOCREADIIDAE

As already stated, there is little use in making definite statements of relationships within the family Allocreadiidae until more is known of the structure and life histories of the genera now included in the family. The present evidence seems to indicate (1) that Crepidostomum is very closely related to Allocreadium, (2) that Megalogonia is so closely related to Crepidostomum that it is doubtful whether its status as a separate genus is justifiable, and (3) that Bunodera is closely related to Crepidostomum and Megalogonia. There is no justification for the subfamily Stephanophialinae or any placement of Crepidostomum and Allocreadium in separate subfamilies unless the possession of oral papillae is to be considered more important than all other characters combined. If any species of Crepidostomum lacked the papillae it would be extremely difficult to find any basis for excluding it from the genus Allocreadium. On the other hand, the evidence from the few life histories that are known, as well as some morphological evidence, indicates that the subfamily Allocreadiinae as conceived by modern authors and accepted by Fuhrmann (1928) is probably an artificial group which will have to be broken up when more complete knowledge is available.

The status of Bunodera is peculiar, for according to the usual conception of the family it cannot be included in the Allocreadiidae because of the extreme development of the uterus, yet it shows in every other character that it is closely related to Crepidostomum. Under the diagnosis of the family given by Winfield (1929) Bunodera easily fits into the family. According to Winfield's conception based on the structure of the uterus, Plesiocreadium Winfield is intermediate between Bunodera and the other Allocreadiidae. I do not believe that Plesiocreadium is intermediate between Bunodera and the Allocreadiinae, or even closely related to either one; it seems to me far more probable that Bunodera is related to Allocreadium through Crepidostomum or Megalogonia. As has been shown, there is a marked tendency in some species of Crepidostomum, especially *C. lintoni,* for the uterus to extend to the posterior testis, while in *Megalogonia ictaluri* it normally extends to the posterior end of the body in the older individuals. Thus the only sharp distinction on the basis of the uterus is the sacculate form in Bunodera as opposed to the tubular form in Crepidostomum; however, in young adults of *B. sacculata* the uterus is tubular (about twice as wide as the egg) although it extends to the posterior tip of the body, and Fuhrmann (1928) pictures a young adult of *B. luciopercae* in which the uterus is tubular and coils back only to the anterior edge of the posterior testis. It is evident, therefore, that there is no lack of intermediate or even

overlapping stages to connect Bunodera with the other Allocreadiidae; furthermore, the evidence seems to indicate that the shape and extent of the uterus is by no means so stable and fundamental a character as it has been considered by many workers who have attempted a systematic classification of trematodes.

The information now available does not justify the formation of a detailed theory of the phylogeny of the papillose Allocreadiidae, but it seems most plausible to suppose that Bunodera, Megalogonia, and Crepidostomum have arisen from a single ancestral line which branched off from the same stem as Allocreadium. It is possible that *Creptotrema creptotrema* Travassos, Artigas, and Pereira 1928 had its origin in the same ancestral line; this species has an expansion of the anterior wall of the oral sucker comparable to the ventral papillae of Crepidostomum, but apparently lacks the dorsal papillae. Unfortunately the description of *C. creptotrema* is incomplete and I have no specimens.

Distomum sp. Linton 1910 from cysts in *Calamus calamus* has oral papillae similar to those of Crepidostomum in general appearance. The description and figures are so incomplete that it is not possible to judge whether or not this species is related to the Allocreadiidae.

Enenterum aureum Linton 1910, a papillose species placed in the Allocreadiinae by Linton, was accepted by Poche (1926) as a member of the family Allocreadiidae with the remark that it may be closely related to Crepidostomum. However, my study of Linton's specimens (U.S.N.M. No. 8464) has revealed structural features widely different from those of Crepidostomum, and it is at least doubtful if Enenterum should be included in the Allocreadiidae. Among other features in which Enenterum differs from the true Allocreadiinae are the following: presence of cuticular spines, presence of an anus, fusion of the intestinal crura to form a single blind cecum at the posterior end, presence of a definite sac enclosing the shell glands, position of the excretory bladder ventral to the intestine, lack of eyespots even in immature specimens, and structure of oral papillae. In Enenterum the six oral papillae are muscular projections of the oral sucker as in Crepidostomum, etc., but they all arise from the margins of the oral orifice; two are on the dorsal lip, two on the ventral lip, and two on the lateral margins, the dorsal and lateral papillae each being divided into two lobes by a distal notch. The nuclei of the papilla muscles lie in the papillae, not in the wall of the sucker as in Crepidostomum.

In view of the many important differences (there are others besides those mentioned), Enenterum certainly cannot properly be included in the subfamily (Allocreadiinae) of which Allocreadium is the type, and I do not believe that it belongs in the family. Perhaps it is more closely

related to the Opecoelidae. I do not believe there is sufficient reason for the proposed placing of Opecoelidae in the family Allocreadiidae as a subfamily, but this question is outside of the scope of the present paper.

In the present state of knowledge statements of relationships within the family or of relationships to other families are statements of opinion only; until more is known of the structure, especially of the much neglected excretory system, and of the life histories of all the genera considered, any attempt at "revising" the classification is useless. The present chaotic condition of the classification of the Digenea is preferable to an iron-bound artificial system, for at least the present condition is stimulating to research and is not conducive to preconceived ideas based on paper relationships.

SUMMARY

1. Detailed, corrected generic diagnoses are given for Crepidostomum, Megalogonia, and Bunodera.

2. Acrolichanus cannot be adequately distinguished from Crepidostomum, so the generic name Acrolichanus is suppressed.

3. Bunodera belongs in the family Allocreadiidae close to Crepidostomum and Megalogonia; all three genera are closely related to Allocreadium; the three papillose genera probably represent one branch of the ancestral stem from which Allocreadium arose.

4. *Crepidostomum farionis* is reported from new hosts and localities; its known range now extends from New England to Alaska in North America, while in the Eastern Hemisphere it is known in northern Europe and the Pacific coast of Siberia.

5. *Crepidostomum ussuriensis* Layman 1930, *Stephanophiala vitelloba* Faust 1918, and *Stephanophiala transmarina* Nicoll 1909 are synonyms of *C. farionis* (O. F. Müller 1784).

6. *Crepidostomum ambloplitis* Hopkins 1931, *C. solidum* Van Cleave and Mueller 1932, and *C. Faust* Hunninen and Hunter 1933 are synonyms of *C. cooperi* Hopkins 1931.

7. New hosts and localities are reported for *C. cooperi*, showing that the species is abundant and widely distributed in central and eastern North America, and a detailed description is given, including the excretory system.

8. The life history of *C. cooperi* has been worked out. The metacercaria has a pigmented eyespot; the cercaria is a slender-tailed ophthalmoxiphidiocercaria developing in rediae in *Musculium transversum* and *Pisidium* sp.; the metacercaria is encysted in the abdominal cavity of Hexagenia nymphs and adults.

9. New hosts and localities are reported for *C. cornutum* (Osborn)

and a detailed description of structures previously neglected or misinterpreted is given, including the excretory system. A stylet has been found in the metacercaria for the first time, showing that the cercaria is an ophthalmoxiphidiocercaria.

10. Faust's description of *C. illinoiense* Faust 1918 is corrected.

11. *C. hiodontos* Hunter and Bangham 1932 is a synonym of *C. illinoiense.*

12. A few details are added to the original description of the adult *C. isostomum* and the redia, cercaria, and metacercaria probably belonging to this species are described.

13. *Crepidostomum auriculatum* (Wedl 1857) is the correct name for *D. auriculatum* Wedl 1857; a diagnosis of the species is given to include the information presented by Skworzoff (1927, 1928).

14. *Acrolichanus similis* Wisniewski 1933 is probably a synonym of *C. auriculatum.*

15. *Crepidostomum lintoni* (Pratt 1901) is apparently the correct name for *D. auriculatum* Wedl (?) of Linton 1898 = *D. petalosa* Lander 1902 = *Acrodactyla petalosa* = *Acrolichanus petalosa* = *Bunodera lintoni* Pratt 1901. A corrected description of the species is given.

16. A corrected, detailed account of *Megalogonia ictaluri* Surber 1928 is given, including the excretory system, and a few new hosts and localities are reported.

17. The miracidium, redia, cercaria, and metacercaria of *Megalogonia ictaluri* have been found. The miracidium has a pigmented eyespot; the cercaria is a slender-tailed ophthalmoxiphidiocercaria developing in rediae in *Musculium transversum;* the metacercaria is encysted in the gills of Hexagenia nymphs.

18. A few details are added to the original description of *B. sacculata* and it is reported for the first time from Iowa.

19. The known life histories of Allocreadiidae are compared; there are three types of life history within the family. Allocreadium, Crepidostomum, Megalogonia, and possibly Bunodera have an ophthalmoxiphidiocercaria developing in rediae in Sphaeriidae and encysting in various invertebrates.

20. The excretory systems of *Crepidostomum cooperi, Crepidostomum cornutum, Megalogonia ictaluri,* and *Allocreadium ictaluri* Pearse have been worked out in detail and found to have a common pattern with *Allocreadium isoporum* Looss as described by Looss. Faust's formula for Allocreadium is wrong, being founded on a mistaken interpretation of Looss' work. The fundamental formula for Crepidostomum, Megalogonia, and Allocreadium is $2[(2+2+2)+(2+2+2)]$, which is modified by additional divisions of flame cells in some species.

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EXPLANATION OF PLATES

Abbreviations

c	common vitelline duct	*p*	primordia of testes
cy	cystogenous glands	*r*	seminal receptacle
d	oviduct	*s*	seminal duct from receptacle
f	fertilization chamber	*sg*	stylet gland
g	genital anlage	*t*	transverse vitelline duct
i	intestinal cecum	*u*	uterus
l	Laurer's canal	*ua*	ascending ramus of uterus
o	ovary	*ud*	descending ramus of uterus
oo	oötype	*v*	vitellaria

All figures were drawn with the aid of a camera lucida. The scale line represents 0.2 mm. in Figures 1, 2, 3, 5, 6, 9, 10, 11, 12, 13, 14, 15, 16, 19, 22, 23, 24, 25, 26, 27, 28, 29; 0.05 mm. in Figures 4, 7, 17, 18, 20 (and 21), and 30; and 0.02 mm. in Figure 8.

PLATE I

FIG. 1.—*C. cooperi,* metacercaria drawn from living specimen, ventral view.

FIG. 2.—*C. cooperi* adult, mounted in extended condition, ventral view.

FIG. 3.—*C. cooperi* adult, mounted in contracted and slightly flattened condition, ventral view.

FIG. 4.—*C. cooperi* miracidium in egg, drawn from living specimen, dorsal view.

FIG. 5.—*C. cooperi,* young redia with eyespot, living specimen.

FIG. 6.—*C. cooperi,* mature redia containing cercariae, living specimen.

FIG. 7.—*C. cooperi* cercaria, living specimen, ventral view; glands omitted on left side, excretory tubes omitted on right; *a,* stylet, more enlarged, lateral view.

FIG. 8.—Comparison of stylets of cercariae; *a,* stylet of *C. cooperi*; *b,* stylet of *Megalogonia ictaluri.*

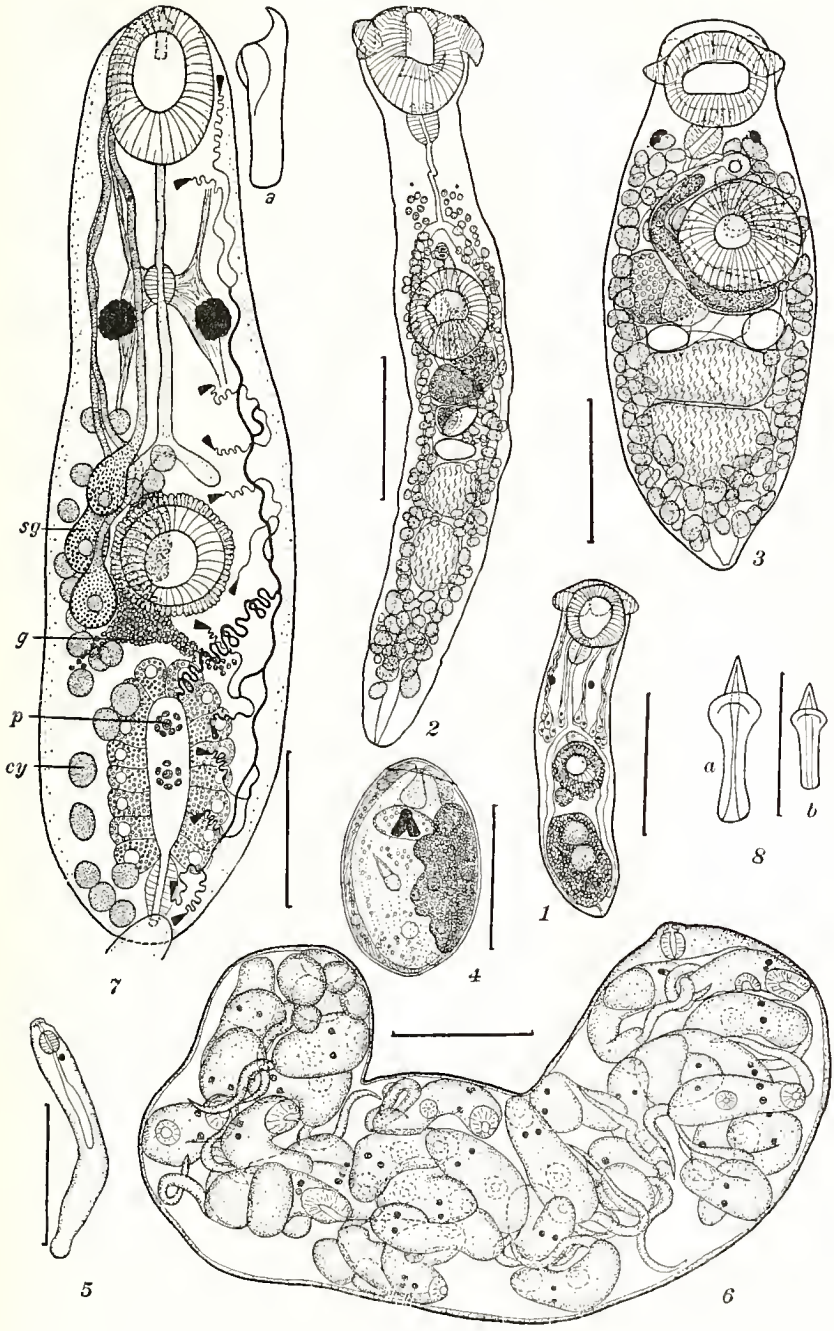

PLATE I

PLATE II

FIG. 9.—*C. cooperi,* redia containing daughter rediae, living specimen.

FIG. 10.—*C. furionis,* adult; Faust's type specimen of *"Stephanophiala vitelloba,"* whole mount, ventral view.

FIG. 11.—*C. metoecus* adult; specimen from Vienna Museum, labeled *"Crepidostomum metoecus* Braun—Type," ventral view.

FIG. 12.—*C. metoecus* adult; specimen from Berlin Museum (vial 5774), dorsal view.

FIG. 13.—*C. metoecus* adult; specimen from Berlin Museum (vial 5774), lateral view.

FIG. 14.—*C. isostomum* (?), redia containing one cercaria, whole mount.

FIG. 15.—*Megalogonia ictaluri,* adult, lateral view, whole mount.

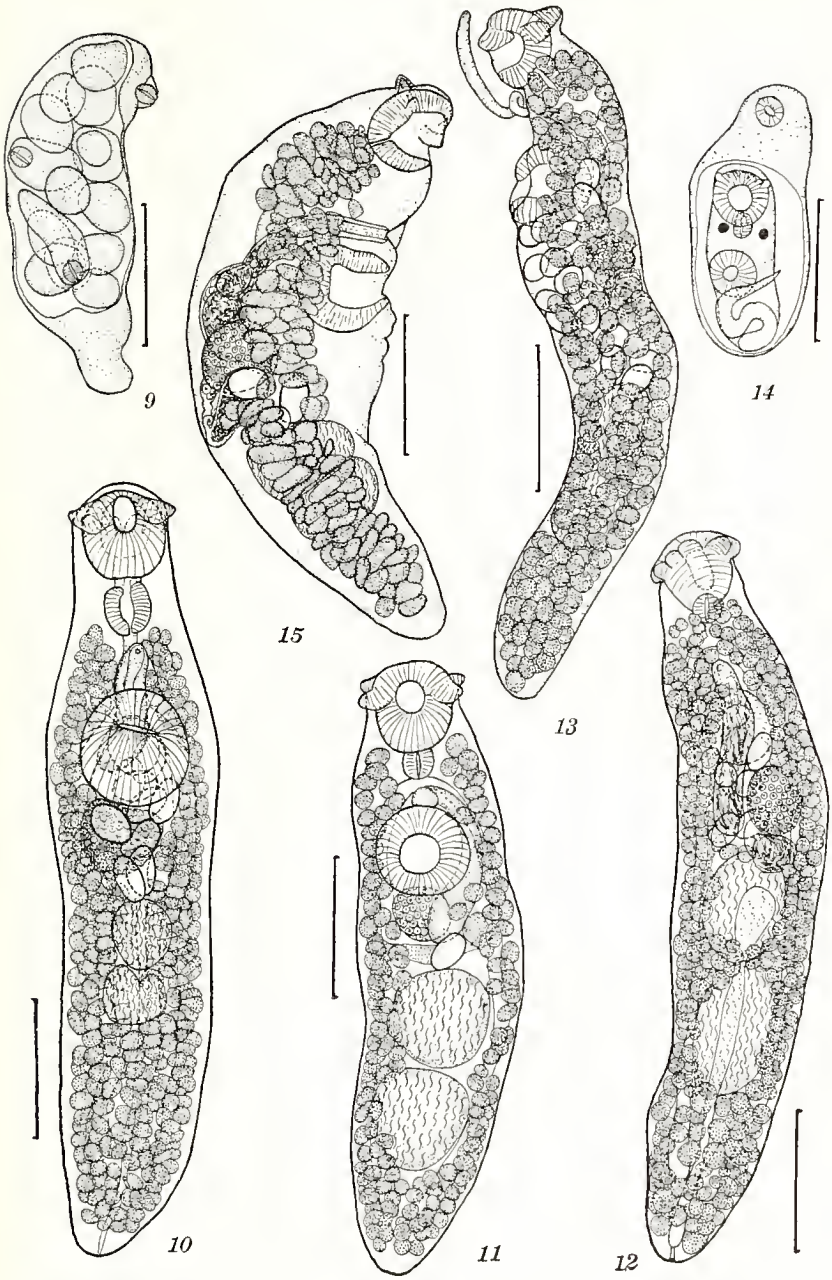

PLATE II

PLATE III

FIG. 16.—*C. illinoiense* adult; Faust's type specimen, whole mount, dorsal view.

FIG. 17.—*C. illinoiense* adult; female reproductive organs, graphic reconstruction from transverse sections, dorsal view.

FIG. 18.—*C. illinoiense* adult; diagrammatic cross section through female reproductive organs.

FIG. 19.—*Megalogonia ictaluri* adult, whole mount, dorsal view.

FIG. 20.—*M. ictaluri* miracidium in egg, living specimen, dorsal view; extended.

FIG. 21.—*M. ictaluri* miracidium in egg, living specimen, lateral view; contracted.

FIG. 22.—*Bunodera lucioperiae* adult, diagrammatic cross section through female reproductive organs.

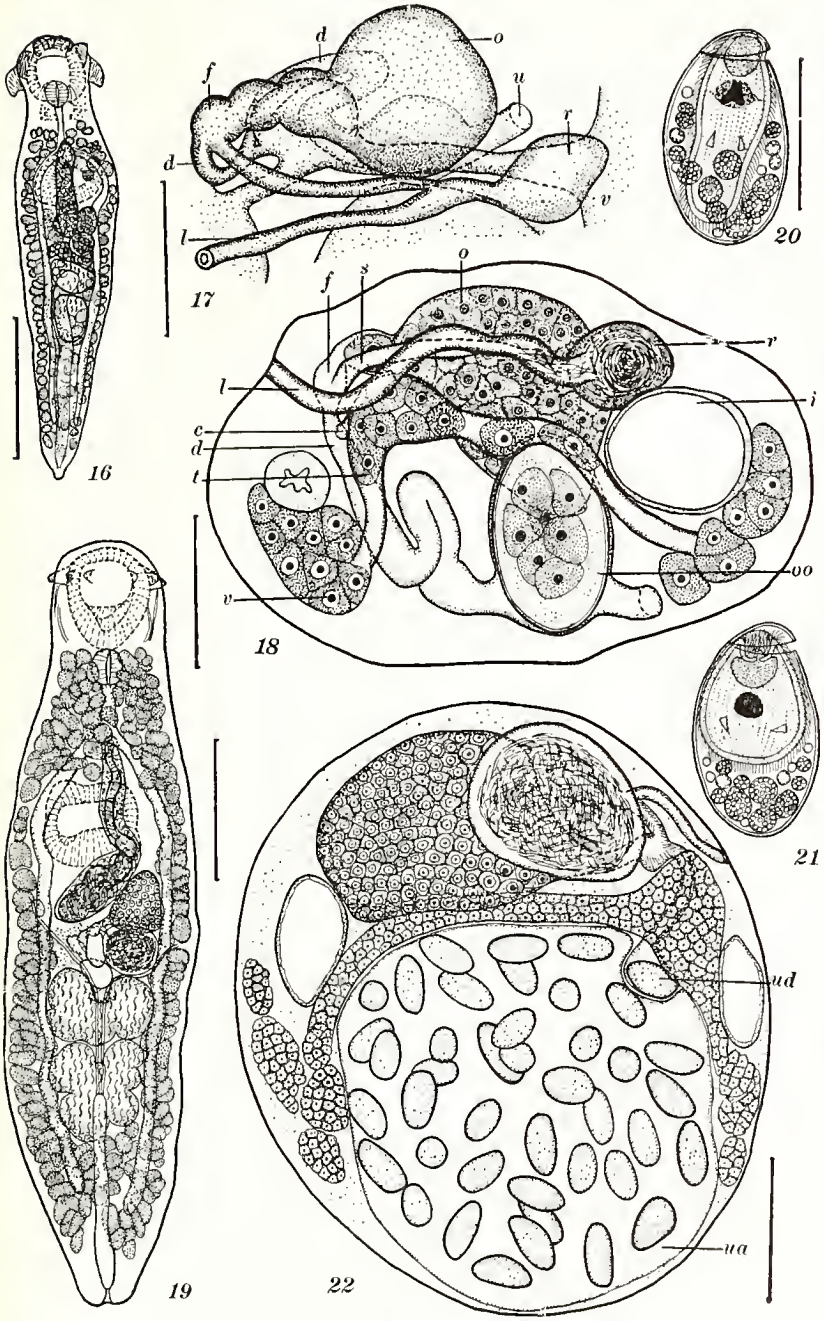

PLATE III

PLATE IV

FIG. 23.—*Megalogonia ictaluri* metacercaria, living specimen, slightly flattened; ventral view.

FIG. 24.—*Bunodera luciopercae* adult, specimen from Berlin Museum (vial 1568), lateral view.

FIG. 25.—*B. luciopercae* adult, specimen from Berlin Museum (vial 1568), lateral view.

FIG. 26.—*B. luciopercae* adult, specimen from Berlin Museum (vial 1568), dorsal view.

FIG. 27.—*B. luciopercae* adult, specimen from Königsberg Museum, dorsal view.

FIG. 28.—*B. luciopercae* adult, specimen from Königsberg Museum, lateral view.

FIG. 29.—*B. luciopercae* adult, American specimen, ventral view; contains several thousand eggs, but for the sake of clearness only one egg is shown; the rest of the uterus is indicated by stippling.

FIG. 30.—*B. luciopercae* adult; flame cells as seen in sectioned material.

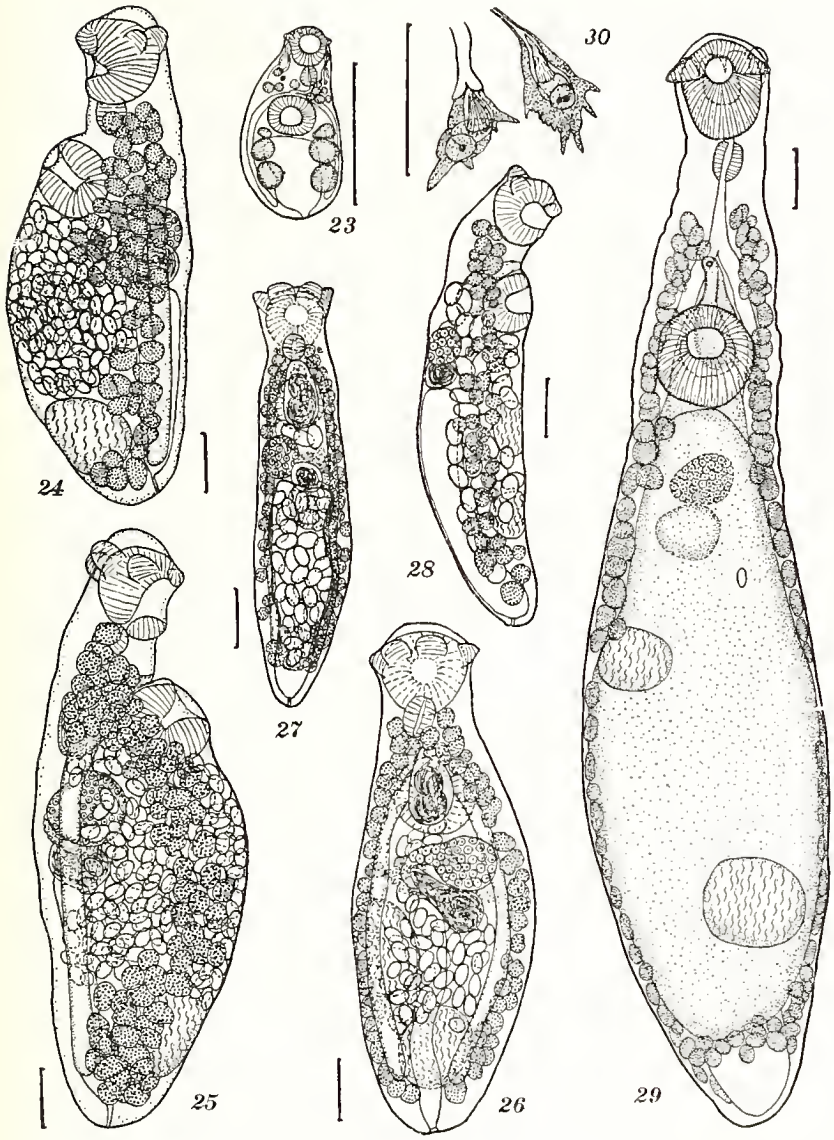

PLATE IV

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