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Contribution No. 3 of the Harold W. Manter Laboratory,
Division of Parasitology of the Museum

Abstract

A Revision of the North American Papillose Allocreadiidae (Digenea) with Independent Cladistic Analyses of Larval and Adult Forms

N. J. Caira

Adult specimens of all 19 North American species of papillose allocreadiids were examined. A description and figure is given for the adult of each species; details of the cirrus sacs are presented for most spesies for the first time. Descriptions were emended where necessary and judgments were made on synonymies. Scanning electron micrographs of the oral sucker of 10 species are presented as is a new key to the 19 species. A cladistic analysis was performed on the group based on adult characters. The analysis indicated that the group is monophyletic on the basis of the ventral papillae associated with the oral sucker, and the following genera were substantiated: *Bunodera* Railliet, 1896, *Bunoderella* Schell, 1964, *Crepidostomum* Braun, 1900, and *Paracreptotrematina* Amin and Meyer, 1982. All available literature on the larval forms is summarized. Miracidial development was monitored in 5 species; scanning electron micrographs are presented for cercariae of 5 species, and indicate that all species possess filiform protrusions around the oral aperture and papillae on the margin of the acetabulum. Independent cladistic analyses were attempted for miracidial and cercarial data. No miracidial characters were appropriate for the analysis, but a cercarial tree is presented. This study represents the first attempt at generation of independent cladograms for separate life cycle stages at the species level. The cercarial tree was congruent but not identical to the cladogram generated from adult data. A consensus tree summarizing both cercarial and adult morphological data is presented. Based on the monophyly of the group, it is recommended that all 19 species be placed in a single subfamily, Bunoderinae.

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INTRODUCTION

Hopkins (1933) introduced the term "papillose allocreadiids" for a subgroup of the digenean family Allocreadiidae that possessed oral papillae or "six projections of the oral sucker containing strong muscle fibers like those of the sucker itself." He included 13 species in this group belonging to three genera: *Crepidostomum* Braun, 1900; *Bunodera* Railliet, 1896; and *Megalogonia* Surber, 1928. Subsequently, additional species with oral papillae (though not necessarily six) have been described or transferred to the group.

There currently exists much disagreement regarding numerous aspects of the classifiction of the papillose allocreadiids. The following examples illustrate the degree of disagreement that exists among helminthologists regarding both the taxonomy and systematics of the papillose allocreadiids. Yamaguti (1971) placed all allocreadiid species that he considered to possess oral sucker papillae into the subfamilies Bunoderinae Looss, 1902 and Crepidostominae Dollfus, 1951. He included four genera in the Bunoderinae: *Allobunodera* Yamaguti, 1971, *Bunodera*, *Bunoderella* Schell, 1964, and *Bunoderina* Miller, 1936. Yamaguti (1971) considered *Bunodera* to be monotypic. He transferred *Bunodera mediovitellata* Tsimbaliuk and Roitman, 1966 to the monotypic genus *Allobunodera*; and included *Bunodera sacculata* Van Cleave and Mueller, 1932, in the genus *Bunoderina* along with *B. eucaliae* Miller, 1936. However, the original authors of *Bunodera sacculata* and *Bunodera mediovitellata* considered these species to be members of the genus *Bunodera*.

Crepidostominae appears to be a fairly stable subfamily taxonomically in that a number of authors (e.g., Manter, 1962; Yamaguti, 1971) considered it to contain only the genus *Crepidostomum*. On the other hand, Hopkins (1934) found the monotypic genus *Megalogonia* to be closely related to *Crepidostomum*, and Van Cleave and Mueller (1934) declared them to be synonymous. Yamaguti (1971) placed *Megalogonia* in the subfamily Megalogoniinae Yamaguti, 1971, (Family Lepocreadiidae), along with *Creptotrema* Travassos, Artigas and Pereira, 1928, and *Creptotrematina* Yamaguti, 1954. Mehra (1966) advocated transferring all three genera to Crepidostminae (Allocreadiidae).

An even greater problem associated with *Crepidostomum* is species identification. Yamaguti (1971) listed 29 species in the genus, yet the descriptions of many of these species render them morphological indistinguishable. Detailed examination is necessary to determine whether or not such species are in fact valid. For example, Hopkins

(1931a) distinguished *Crepidostomum cooperi* Hopkins, 1931 from *C. cornutum* (Osborn, 1903) Stafford, 1904 on the basis of the proportionately smaller oral sucker and less conspicuous papillae in the former. Both of these character states are variable and lead one to suspect that the two species are synonymous. However, it has also been reported (Hopkins, 1934) that while the metacercariae of *C. cooperi* encyst in gammarid amphipods and mayfly larvae, the metacercariae of *C. cornutum* encyst in crayfish.

Most taxonomic decisions have been made on the basis of adult morphology, but some authors (Hopkins, 1934; Peters and La bonte, 1965; Cannon, 1971) have found the morphology of larval forms to be very valuable in resolving some difficulties in allocreadiid taxonomy. A disadvantage of dealing with the morphology of larval Digenea is their small size in relation to their complexity. Yet this problem may be circumvented with the aid of the scanning electron microscope (Lo et al., 1975). Amato (1979) successfully used scanning electron microscopy to examine four larval forms of *Megalogonia ictaluri* (=*Crepidostomum ictaluri*).

In addition, many of the systematic uncertainties associated with the papillose allocreadiids have their origins in the subjectivity of various authors. It was thought that the application of an objective analytical technique such as cladistic analysis (Hull, 1979) would aid in obtaining a better understanding of the general pattern of relationships among these species.

A major portion of this study was thus devoted to the examination of as much actual material as possible of the papillose allocreadiids. Species that were poorly known were redescribed, judgments were made on synonymies, and a cladistic analysis was performed from data gathered from adult specimens. In addition, the diversity of larval forms in the life histories of these species provided a unique opportunity to examine a question that has challenged systematists for many years: **Do the phylogenetic hypotheses constructed from larval and adult characters concur?**

In order to answer this question, larval data were collected and analyzed separately from adult data. Three outcomes are possible in a comparison of the topology of trees generated from independent data sets. (1) The trees might be identical (=congruent) (Fig. 1). (2) The trees might be consistent. A pair of consistent trees is shown in Figure 2. Although the topologies of the two trees are not identical, they are not contradictory. The trichotomy for B+C+D in tree 2b is consistent with the grouping of B+C+D in tree 2a; the former is merely less resolved. (3) The trees might be inconsistent. A pair of inconsistent trees is shown in Figure 3. Tree 3a indicates that C and D are each others' closest relatives, whereas tree 3b indicates that B and D are each others' closest relatives.

Several workers have compared phylogenies generated from independent data sets other than those of larval and adult forms. For example, Mickevich and Johnson (1976) compared morphological and allozyme data in a group of silversides, and Whalen and Caruso (1983) compared morphological and allozyme data in the shrub-like Solanaceae; Schuh and Polhemus (1980) compared morphological, ecological and biogeographic data in a group of hemipterans. Relatively few authors, however, have attempted to compare classifications or phylogenetic hypotheses generated independently from larval and adult characters. In fact, to date, only three such studies exist:

(1) Rohlf (1965) investigated the degree of congruence between classifications of *Aedes* mosquitoes based on independent studies of larval and adult morphology. He evaluated the degree of relative similarity between pairs of species for larvae and adults using numerical taxonomy and found larval and adult classifications to be quite different. Rohlf suggested that one of the conclusions from the results of his study might be that "phenetic taxonomic methods are inadequate for establishing classification."

(2) Howden (1982) cladistically examined both larval and adult characters in a group of beetles, the Scarabaeioidea. He reported finding some differences between larval and adult "character state trends." He suggested that these differences might be due either to his selection of a small number of characters (sampling error) or the fact that "selection differentially affects larval and adult characters." Neither Rohlf (1965) nor Howden (1982) produced independent cladograms of species based on larval and adult characters. As Howden did not present a cladogram of his results, it is difficult to determine exactly how his character state trends were generated.

(3) Brooks, O'Grady and Glen (1985) were the first to present a cladogram generated from adult morphological data and compare it to a cladogram generated from data on larval forms. They were working with the Digenea at the family level, and their larval tree was generated from combined data on all five larval forms: miracidium, sporocyst, redia, cercaria, and metacercaria. They found only one minor disagreement between the trees.

The Digenea are an ideal system for examining taxonomic congruence because they possess a number of morphologically distinct larval forms; the miracidium is morphologically different from the cercaria, and so on. Thus, a comparison of cladograms for adults, miracidia and cercariae was attempted in the present study.

For convenience sake all stages occurring prior to the

adult in the digenean life cycle will be referred to as "larvae." Although a current trend appears to be to restrict use of the term "larva" to life cycle stages separated by complete metamorphosis, this term has conventionally been used with reference to the various life cycle forms of the Digenea, including miracidium, sporocyst, redia, cercaria, and metacercaria (see for example Yamaguti, 1975; Schell, 1985).

MATERIALS AND METHODS

Field Studies

(1) Bluestem Lake, Lancaster Co. Nebraska (Fig. 4)

Fish: Individuals of *Ictalurus punctatus* (Rafinesque) and *Lepomis macrochirus* (Rafinesque) were seined using a 40' seine from the shore of the southwest arm of Bluestem Lake. They were transported to the Harold W. Manter Laboratory in buckets equipped with portable (battery operated) aerators. Fish were collected at monthly intervals from April through November, 1982-1984.

Clams: Up to six inches of bottom sediment 2-15' from shore were dug up and seived through ¼" mesh, copper or aluminum screening. Clams were removed from the mesh with forceps and transported to the Harold W. Manter Laboratory in plastic buckets containing lake water. The clam species examined included: *Pisidium obtusum* Sterki, *Sphaerium partumeium* Say, *S. sulcatum* Say, and *S. transversum* Say.

Mayflies: Nymphs of *Hexagenia limbata* (Serville in Guerin) were collected with an Eckman dredge from bottom debris seived through -¼" mesh screening. The nymphs were transported to the Harold W. Manter Laboratory in plastic buckets containing lake water.

Crayfish: Crayfish were collected along with the fish using a 40' seine. They were transported to the laboratory in plastic buckets containing a small amount of lake water.

(2) Wagontrain Lake, Lancaster Co., Nebraska

Fish: Individuals of *Ictalurus punctatus* and *Lepomis macrochirus* were collected during the months of January and February. Holes six inches in diameter were drilled in the ice using a Swedish ice auger, and the fish were angled. Fish were transferred to a plastic cooler containing lake water for transport to the Harold W. Manter Laboratory.

(3) Lake Keystone, Keith Co., Nebraska (Fig. 5)

Fish: Individuals of *Salmo gairdneri* Richardson were angled from the bridge near Cedar Point Biological Station at Lake Keystone in June, 1982. The fish were transported to the laboratory at Cedar Point Biological Station using a fish stringer.

(4) Tin Can Creek, Musqueum Park, Vancouver, British Columbia, Canada (Fig. 6)

Fish: Individuals of *Gasterosteus aculeatus* L. were collected with small dip nets from Tin Can Creek. They were transported to the University of British Columbia Parasitology Laboratory in plastic buckets containing stream water.

Clams: Bottom debris from calm areas at the edges of the stream was seived through the mesh of a small dip net. Forceps were used to remove the clams, *Pisidium casertanum* (Poli), from the mesh. Clams were transferred to plastic buckets containing stream water and sand for transport to the University of British Columbia Parasitology Laboratory.

Caddisflies: Larvae of the caddisflies, *Lepidostoma roafi* (Milne), and *Psychoglypha alascensis* (Banks), were collected from bottom debris at the edges of the stream using forceps. The caddisflies were transported to the University of British Columbia Parasitology Laboratory in plastic buckets filled with stream water and some bottom debris.

(5) Campbell Creek, White Rock, British Columbia, Canada (Fig. 7)

Fish: Individuals of *Gasterosteus aculeatus* were either trapped in minnow traps that were set and then checked at approximately 20 minute intervals, or they were collected with a ¼" mesh seine. They were transported to the University of British Columbia Parasitology Laboratory in plastic buckets equipped with portable aerators.

(6) Lake Opeongo, Algonquin Park, Ontario, Canada (Fig. 8)

Fish: All individuals of *Perca flavescens* (Mitchill) were trapped using Windemere traps baited with bread. The traps were suspended from a dock at the Harkness Fisheries Laboratory.

Clams: Individuals of *Pisidium casertanum*, *P. equilaterale* Prime, and *P. variabile* Prime were collected with an Eckman dredge from the bottom debris near the shore of the small cove immediately adjacent to the Harkness Fisheries Laboratory (Fig. 8). Individuals of *Pisidium ferrugineum* Prime and possibly *P. compresseum* Prime were collected with an Eckman dredge from the bottom debris in a small cove across from the Harkness Fisheries Laboratory (Fig. 8).

Mayflies: Nymphs of *Hexagenia limbata* were collected from the small cove immediately adjacent to the Harkness Fisheries Laboratory with an Eckman dredge.

Laboratory Studies

(1) Dissections, Host Identifications, and Parasite Preservation

Fish: All fish were dissected immediately after they were killed by pithing. Worms recovered from the intestine were either: (1) placed in distilled water in a refrigerator to induce egg release, and subsequently fixed in alcohol-formalin-acetic acid (A.F.A.) and preserved in 70% ethanol, (2) flattened with slight coverslip pressure and simultaneously fixed with A.F.A. and then preserved in 70% ethanol, (3) placed in distilled water in a refrigerator and then fixed in 2.5% glutaraldehyde (GTA), or (4) placed immediately into cold 2.5% GTA. In order to document the subtegumental gland system in *Crepidostomum cooperi*, worms were placed in a drop of distilled water on a slide, covered with a vasoline-rimmed coverslip, and photographed using a Nikon microscope with camera attachment—all within five minutes of removal from the host. The key of Eddy and Underhill (1979) was used as an aid to fish identification.

Clams: All clams were dissected with fine forceps. Most of the larval forms taken from the clams were fixed in cold 2.5% GTA. Some larvae were removed from the clams and examined alive in distilled water on a slide under a vasoline-rimmed coverslip. Representative clams from each locality were sent to Dr. G. L. Mackie, at Guelph University, for identification.

Mayflies: Mayfly nymphs were dissected with fine forceps. Large worms such as *Crepidostomum opeongoensis* were relaxed in refrigerated distilled water and then fixed in cold 2.5 GTA. Metacercariae were dissected from the tissue and their cyst walls were broken with fine dissecting needles. They were placed on a slide in a drop of distilled water under a vasoline-rimmed coverslip for identification. Some excysted metacercariae were preserved in 2.5% GTA. Burks' (1953) key was used for identification of mayfly nymphs.

Crayfish: Dissections were performed from the dorsal surface. In particular, the areas around the heart and digestive system were examined for metacercariae. Crayfish were identified using the key of Hobbs (1976).

Caddisflies: Caddisfly larvae were dissected with fine forceps. When the head was pulled away, the paired silk glands generally remained attached to the head and metacercariae were readily visible as expansions of the silk glands. Fine forceps were used to remove the cysts from the silk glands; fine dissecting needles were used to break open the cysts. Excysted metacercariae were preserved in 2.5% GTA. Caddisflies were previously identified (Caira, 1981) by Dr. G. B. Wiggins of the Royal Ontario Museum.

(2) Rearing Miracidia

In most cases eggs were readily released when gravid worms were placed in distilled water in the refrigerator. When this method was unsuccessful, for example with *Bunodera sacculata*, worms were dissected to remove eggs. Unembryonated eggs were pipetted into clean Stender dishes, rinsed several times with distilled water, and concentrated by swirling the distilled water several times with a probe. Dishes were covered and placed in the dark, either in a drawer or on a shelf in a darkened room, and maintained at 21–26° C.

Every 12 hours until active miracidia developed (usually for a seven day period), five eggs of each of *Crepidostomum cooperi* and *C. ictaluri* were removed from the Stender dishes and placed under a vasoline-rimmed coverslip. They were photographed using a Nikon microscope with a camera attachment and Kodak Plus-X or Tri-X film.

Eggs of *Bunodera mediovitellata* and *B. Luciopercae* often contained active miracidia while still in utero. These eggs hatched almost immediately after release from the uterus, without incubation. Five eggs of each species were photographed as given above. Hatched miracidia and some eggs containing unhatched miracidia were preserved in cold 2.5% GTA.

(3) Scanning Electron Microscopy (SEM)

Adults, Rediae, and Cercariae

Specimens fixed in cold glutaraldehyde were placed in porous teflon capsules (American Optics Co.) and dehydrated using a graded series of ethanol. They were subsequently critical point dried in a Denton DCP-1 critical point drying apparatus with liquid CO_2. Eyebrow hairs mounted on small wooden dowels were used to transfer specimens from the capsules to stubs prepared with copper adhesive tape. Smaller cercariae were stained with hematoxylin before dehydration so that they were readily visible against the white background of the capsule.

The stubs were coated with approximately 400 Å of gold/palladium, or gold using a Hummer II diode sputtering apparatus. Specimens were examined at 10 or 20 kv with a Cambridge S4-10 scanning electron microscope. Photographs were taken using Polaroid positive/negative film.

Eggs and Miracidia

Bunodera luciopercae was the only species for which eggs and miracidia were available in sufficient quantities for SEM. These specimens were transferred to a Millipore or Nucleopore filter (3-8 μ pore diameter) using a Millipore swinnex 13 mm disc filter holder (Millipore Inc.) attached

to a hypodermic syringe. They were subsequently dehydrated by injecting progressively greater concentrations of ethanol into the apparatus and letting each solution remain approximately 10 minutes. When dehydration was complete, the filter with eggs or miracidia on its surface was transferred to a small wire mesh basket, another basket was placed on top and this assemblage was critical point dried (as above). Nucleopore filters were found to be superior to Millipore filters because of their resistance to wrinkling during the drying procedure. The entire filter was then mounted on a stub using copper adhesive tape, sputter coated, and examined (as above).

(4) Light Microscopy

Many of the specimens for light microscopy were fixed in cold A.F.A., hydrated in an ethanol series, stained in Erlich's or Mayer's hematoxylin, dehydrated in an ethanol series, cleared in methyl benzoate, and mounted in Canada balsam. Much of the larval material was transferred from GTA to distilled water and examined, unstained, under a vasoline-rimmed coverslip. Some living larval material was stained with 1% neutral red to enhance epidermal plate boundaries in miracidia, and flame cells in cercariae. Some miracidia and cercariae were treated with silver nitrate following the procedure of Short and Cartrett (1973), but the technique was successful only with living material.

Five adult specimens of *Crepidostomum cooperi* were embedded in paraffin, sectioned using an American Optical rotary microtome, and mounted on slides using diluted egg albumin. They were stained in hematoxylin and eosin, cleared in xylene, and mounted in Canada balsam.

Museum and Private Collections

All specimens of papillose allocreadiids at the U.S. National Parasite Collection (Beltsville, Maryland) and the Harold W. Manter Laboratory of Parasitology (University of Nebraska State Museum) were examined. In addition, Nybelin's type material of *Crepidostomum suecicum* was requested from the Naturhistoriska Museet, Goteburg, Sweden, but no reply was received. At least one specimen of each of the 19 North American papillose allocreadiids was examined, including type specimens of 15 species. Adult specimens of *Crepidostomum farionis*, and *C. metoecus* were loaned by Dr. L. Margolis, from the Pacific Biological Station, Nanaimo, British Columbia. Cercariae and metacercariae of *Crepidostomum cornutum* were donated by Dr. H. M. Turner, of McNeese State University, Louisiana.

Descriptions

Synonyms are listed in alphabetical order. In the Materials Examined section, an author's name followed by a parenthesized date indicates a publication; an author's name followed by a date without parentheses indicates the date collected (usually obtained from Museum records or slide labels). The latter type of citation was included only when it was necessary to refer to it in the Remarks section of this paper.

The abbreviation "coll." represents "collected by", and "det." represents "determined or identified by." The U.S. National Museum Helminthological Collection numbers are abbreviated as "USNM No." and the Harold W. Manter Laboratory of Parasitology numbers are abbreviated as "HWML No.". Scientific names and authors of fishes were taken from Robins et al. (1980). In instances where host names differing from those in current usage were published, the current name is given in parentheses following that used by the investigator.

Measurements for the descriptions were taken from as many individuals as were available, up to 25. When more than 25 specimens were available, type material was measured and a random sample was chosen from additional material, up to a total of 25 specimens. For each measurement the range is given followed in parentheses by the mean, the standard deviation, the number of worms examined, and the total number of observations when more than one structure was measured per worm (e.g., papillae or eggs). All measurements are in micrometers unless otherwise stated. Curved structures such as cirrus sacs were drawn with the aid of a drawing tube and a string was used to follow the curvature of the sketch; the string was subsequently measured and the measurement converted to scale.

Unless otherwise indicated all scales and measurements are in micrometers. Original figures were drawn with the aid of a drawing tube. Figures redrawn from the original publications of previous authors are indicated with the designation "after" followed by the citation for the original figures.

A list of every host and exact locality recorded in the literature, for each species of papillose allocreadiid, was deposited at the H. W. Manter Laboratory of Parasitology. In the Remarks section following each adult description these records are generalized so that only the host families and general localities are given.

Cladistic Analysis

Data matrices were analyzed by hand as well as with the computer package "P.A.U.P." (Phylogenetic Analysis Using Parsimony) created by Dr. D. Swafford of the Illinois Natu-

ral History Survey. In the computer analysis the options "Branch and Bound" and "Mulpars" were chosen so that all most parsimonious trees would be identified.

RESULTS AND DISCUSSION

On the Monophyly of the Papillose Allocreadiids

A synapomorphy is an hypothesized, shared evolutionary *novelty*. Thus, a character state can be a synapomorphy for the members of a group only if no other organisms possess the same homologous character state. The papillose allocreadiids can be hypothesized to comprise a monophyletic group only if it can be demonstrated that the group is supported by one or more synapomorphies. An obvious set of potential synapomorphies for establishing the monophyly of the papillose allocreadiids would seem to be the muscular papillae associated with the oral sucker.

At least 14 genera of Digenea, representing eight families, possess structures that resemble the muscular oral papillae of the papillose allocreadiids. These genera include: *Cadenatella* Dollfus, 1946, *Jeancadenatia* Dollfus, 1946, and *Enenterum* Linton, 1910 (family Opecoelidae); *Waretrema* Srivastava, 1937 (family Waretrematidae); *Tetracerasta* Watson, 1984, and *Barbulostomum* Ramsey 1965 (family Lepocreadiidae); *Eustomos* MacCallum, 1921 (family Plagiorchiidae); *Auridistomum* Stafford, 1905 and *Patagium* Heyman, 1905 (family Auridistomatidae); *Rhytidodes* Looss, 1901 and *Rhytidodoides* Price, 1939 (family Rhytidodidae); *Gymnophalloides* Fujita, 1925 and *Meiogymnophallus* Ching, 1965 (family Gymnophalidae); and *Dictyangium* Stunkard, 1943 (family Microscaphiidae).

The oral suckers of these opecoelid and waretrematid genera possess terminal rather than subterminal oral apertures (Figs. 9A and 9B respectively). The six to 10 digitiform papillae are arranged around the anterior margin of the aperture; on the basis of this construction their papillae are considered to be nonhomologous with those of the papillose allocreadiids.

Watson (1984) detailed the morphology of the four retractable, dorsal "oral sucker lobes" of the monotypic lepocreadiid genus *Tetracerasta* (Fig. 9C). He demonstrated that, while the base of each oral lobe is muscular, the tip of each lobe possesses many ampullae that open to the outside via pores and are connected to gland cells in the forebody. On the basis of this unusual structure these oral lobes are considered to be nonhomologous with those of the papillose allocreadiids.

The oral sucker of the microscaphid genus *Dictyangium* has been described to possess two transverse muscular projections (Yamaguti, 1971). These projections, however, are inserted at the inner margin of the posterior border of the oral sucker (Fig. 9D) and are considered here to be more similar to the oral sucker posterior "diverticules" of other microscaphids, such as *Microscaphidium* Looss, 1900, rather than the muscular papillae of the papillose allocreadiids.

The genera *Rhytidodes* (Fig. 9E) and *Rhytidodoides* possess pointed, muscular, annular ridges that may or may not be divided. Owing to this unique structure, the ridges cannot be considered homologous with the papillae of the papillose allocreadiids.

The somewhat pointed, muscular, ventral structures associated with the oral suckers of the gymnophalid genera *Gynophalloides* (Fig. 9F), *Meiagymnophallus* and some species of *Parvatrema*, the plagiorchiid genus *Eustomos* (Fig. 9G), the lepocreadiid genus *Barbulostomum* (Fig. 9H), and the auridistomatid genera *Auridistomum* and *Patagium* cannot immediately be dismissed as nonhomologous to the ventral papillae of the papillose allocreadiids. With the exception of the two pairs of ventral papillae in the auridistomids (Fig. 9I), the muscular ventral papillae of these groups appear to differ from those of the papillose allocreadiids only in that they are conical and pointed rather than somewhat flattened and distally blunt. Nevertheless, until evidence to the contrary is presented, these conical ventral structures are considered as nonhomologous with those of the papillose allocreadiids.

In summary, (1) no structures homologous with either the dorsolateral papillae or the dorsomedial papillae of the papillose allocreadiids are currently known to exist outside of this group; thus these structures are considered as potential synapomorphies for establishing the group as monophyletic, and (2) several genera of Digenea possess structures that may be homologous with the ventral papillae found in the papillose allocreadiids, but until that homology is demonstrated, the assumption is made that they are nonhomologous. The presence of ventral papillae is therefore considered as at least a potential synapomorphy for the papillose allocreadiids.

The three papillae characters establish three self-compatible groups as monophyletic. Thus, these traits are evolutionarily consistent in the sense of Wiley (1981). The presence of dorsomedial papillae establishes the group: (*Bunodera* + *Crepidostomum*). The presence of dorsolateral papillae establishes the more inclusive group: (*Bunodera* + *Crepidostomum* + *Bunoderella*). The presence of ventral papillae establishes the even more inclusive group: (*Bunodera* + *Crepidostomum* + *Bunoderella* + *Paracreptatrematina*.)

On the basis of the presence of ventral papillae the pa-

illose allocreadiids can be considered to be a monophyletic group. If the conical ventral papillae of the groups mentioned above are in fact homologous with those found in the papillose allocreadiids (and this character is discarded from the analysis), the presence of dorsolateral papillae still establishes all papillose allocreadiids except the two species of *Paracreptotrematina* as a monophyletic group.

ADULT FORMS

Morphological Variability Among the Adult Papillose Allocreadiids

Intraspecific variability in this group of species is indicated by the measurements and ratios of the descriptions that will follow. Interspecific morphological variations are outlined in general below. These data are a combination of published accounts and details obtained in the present study.

A. *Organs of Attachment*

1. Oral Sucker and Papillae

The oral sucker may have one, two, or three pairs of blunt papillae. Serial sections of the oral sucker show that these papillae are entirely muscular and are actual extensions of the musculature of the oral sucker itself (Fig. 10A-C). In those organisms with six papillae, the papillae are arranged on the same plane in a semi-circle around the oral sucker; they include one pair of ventral papillae, one pair of dorsolateral papillae, and one pair of dorsomedial papillae (Fig. 12). In those organisms with four papillae, the ventral and dorsolateral pairs are present; in those with two papillae, only the ventral pair is present.

The oral aperture is usually oval or round (Fig. 20), but in several species it is subtriangular (Fig. 14). This difference in shape appears to be a function of the point of attachment of the ventral papillae. If the aperture is oval or round, the ventral papillae are attached on either side of the aperture; if subtriangular, the ventral papillae join together and attach along the midline anterior to the aperture, thus giving the aperture a well defined, pointed apex. In some species, *C. cooperi* in particular, the musculature of the ventral papillae is less well defined and, depending on the degree of contraction, the aperture may or may not (Fig. 23) appear to be subtriangular.

The ventral papillae vary in posterior extent. In some species they extend to near the posterior margin of the sucker (Fig. 14); in others, they do not extend posterior to the middle of the oral sucker (Fig. 19).

The relative widths of the dorsal pairs of papillae may vary. In some species the dorsolateral pair of papillae is distinctly wider than the dorsomedial pair of papillae (Fig. 24); in other species the two pairs of papillae are similar in size (Fig. 27). In most species the dorsomedial papillae are bluntly rounded, but in *C. illinoiense* these papillae are notched distally (Fig. 17).

In some species the bases of the dorsal papillae are contiguous or almost contiguous (Fig. 25); in other species the dorsal papillae may be more than one papillar width apart (Fig. 32). Relatively large papillae are more likely to be contiguous than relatively small papillae.

2. Acetabulum

The sessile acetabulum (ventral sucker) varies somewhat in size and position. The aperture is usually oval, but *C. farionis* consistently has a transverse slit. The acetabulum is larger than the oral sucker in some species, for example *C. farionis*. In other species the acetabulum is smaller than the oral sucker, for example, *C. auriculatum*. In the present study several ratios have been used in an attempt to quantify the exact size and position of the oral sucker and acetabulum. These include: oral sucker width to acetabulum width ratio, forebody length to hindbody length ratio, body width to acetabulum width ratio, forebody length to acetabulum length ratio, and hindbody length to acetabulum length ratio.

B. *Digestive System*

The digestive system from anterior to posterior consists of an oral aperture (mouth), a short prepharynx, a pharynx, an esophagus, and two blind ceca. The oral aperture and sucker are discussed above. The prepharynx is a short narrow tube that is visible only in relaxed specimens. In general, the size of the pharynx varies interspecifically as does the pharynx to oral sucker length ratio.

Esophagus length is possibly the most intraspecifically variable character. When the forebody is contracted, the esophagus tends to coil; when the forebody is relaxed, the esophagus tends to straighten. The ceca are usually long, extending to near the posterior end of the body. In a few species the ceca are short, ending in the midhindbody. This character did not vary intraspecifically.

C. *Excretory System*

The excretory vesicle is "I" shaped or saccate. It opens via a terminal pore and extends anteriorly to the region between the ovary and the posterior border of the posterior testis. Flame cells were not seen in either living or fixed material and consequently the flame cell pattern was not determined for adult specimens.

D. *Reproductive System*

1. Female

The female reproductive organs include: a single ovary, a seminal receptacle, numerous vitelline follicles, and a uterus. The ovary is generally ovoid but may appear slightly pyriform when the oviduct is visible. The ovary may be dextral, sinistral, or medial. In all species the ovary is pretesticular, and an oviduct arises from the median side of the ovary. In a few living specimens the oviduct was seen to widen into an ootype, but this detail was not visible in preserved specimens.

The ovoid or pyriform seminal receptacle is usually adjacent to the posterior margin of the ovary. The duct from the seminal receptacle joins the oviduct and the ootype, and then receives a common vitelline duct. A Laurer's canal branches off of the seminal receptacle; the length of the canal appeared to vary interspecifically. It was inconspicuous in most specimens. The cells of the Mehlis' gland were generally difficult to distinguish from parenchymal cells, but they stained well in a few specimens.

Vitelline follicles are usually distinct, but no follicles were seen in *P. limi* and they were difficult to distinguish in older specimens of *B. luciopercae*. The size of the vitelline follicles varies somewhat interspecifically, as does both their anterior and posterior extent. The extent to which the vitelline follicles are confluent in the post-testicular region is an intraspecifically variable character in *Crepidostomum*.

The uterus is generally a narrow tube that either extends to the posterior end of the body or is restricted to the testicular region. In some species, such as *B. sacculata*, the ascending ramus of the uterus expands into a sac in older individuals. When the uterine wall is not well defined, the presence or absence of a uterine sac is difficult to see even in individuals belonging to a species known to have one. Apart from the presence of eggs in some specimens, no evidence of the terminal portion of the uterus was observed. In one specimen of *Crepidostomum cooperi*, a muscular metraterm was visible (Fig. 13). Proximally, the lumen was lined with blunt projections.

2. Male

The male reproductive system usually consists of two testes that are each connected by means of a vas efferens to a collective vas deferens that enters the base of the cirrus sac. The testes may be tandem, oblique, or symmetrical. In *Crepidostomum ictaluri*, the testes are deeply lobed.

Within the papillose allocreadiids the cirrus sac is ovoid, or elongated. The details of the cirrus sac have not been presented previously for any member of the group. In general, the cirrus sac contains an anterior cirrus followed by a pars prostatica and a posterior seminal vesicle. The seminal vesicle is either very long, occupying most of the cirrus sac, or it is relatively short, occupying only the posterior third of the cirrus sac. In some species a prostatic vesicle is visible. Prostatic cells range in number from a few, to numerous cells almost entirely filling the cirrus sac. The cirrus appears to be unspined in all species examined (Fig. 11), however, details of the cirrus are difficult to see unless it is everted. An everted cirrus was seen in one or more specimens of only five of the 19 species in the group.

E. *Sensory and Secretory Systems*

Scanning electron micrographs show that all species possess numerous small papillae on the body surface. The function of these structures is currently unknown. Lasee et al. (1984) suggested that they may be either sensory or secretory in nature. Lasee et al. (1984) reported that these papillae were not arranged in any discernible patterns, but in the present study the positions and arrangements of these structures were consistent intraspecifically and differed interspecifically. For example, Figures 27 and 28 are anterior views of two different specimens of *Bunodera mediovitellata*. As can be seen, the patterns are very similar.

When metacercariae and adults of *C. cooperi* were examined alive no more than 10 minutes after removal from the host, a subtegumental network of ducts was visible (Figs. 34 & 35). These ducts were particularly numerous around the acetabulum and oral sucker, but were also present at the level of the testes. No function can currently be given to this duct system. It is not the excretory system as evidenced by the lack of flame cells at the ends of the ducts. This duct system resembles the paraesophageal gland system described by Lie (1966) in echinostome cercariae, but the ducts are not limited in distribution to the esophageal region.

DESCRIPTIONS

Bunodera Railliet, 1896

Synonyms: *Allobunodera* Yamaguti, 1971; *Bunoderina* Miller, 1936

Type species: *Bunodera luciopercae* (Mueller, 1776) Stiles and Hassall, 1898

The following diagnosis is a combination of the diagnoses of Hopkins (1934), and Yamaguti (1971), in addition to data from the present study. Diagnosis: Body elongate, oval to subcylindrical, unarmed. Oral aperture ventral. Oral sucker with six muscular papillae, four dorsal,

two ventral; bases of dorsal papillae contiguous or not. Prepharynx short; pharynx, and esophagus present. Cecal bifurcation anterior or dorsal to ventral sucker; ceca extending to near posterior end of body or terminating at midhindbody. Acetabulum in anterior half of body. Genital pore median, anterior to acetabulum, posterior to oral sucker. Common genital atrium small. Cirrus sac varying in form and size in various species, generally anterior to or in acetabular region; cirrus sac containing seminal vesicle, pars prostatica, and cirrus; prostatic vesicle visible in some species. Testes two, not divided, tandem or oblique, contiguous or not. Ovary round or pyriform, anterior to testes, dextral, sinistral or medial. Seminal receptacle adjacent to ovary posteriorly. Laurer's canal inconspicuous; Mehlis' gland inconspicuous. Vitellaria mostly lateral and ventral to ceca, rarely intercecal; extending from pharynx or posterior margin of acetabulum to posterior extremity of body or terminating at midhindbody; vitelline reservoir present. Uterus narrow and thin walled throughout, or ascending ramus expanded into sac in older individuals; extending between genital pore and posterior end of body. Metraterm inconspicuous. Intrauterine eggs several hundred to several thousand, ovoidal or elipsoidal with operculum and abopercular thickening; eggs deposited or not, embryonation occurring in uterus. Excretory pore terminal; "I" shaped excretory vesicle dorsal to testes, reaching at least as far as posterior border of posterior testis.

Bunodera luciopercae (Mueller,1776) Stiles and Hassall, 1898

(Figs. 31, 36-38)

Genotype.

Synonyms: *Asymphylodora nodulosum* (Froelich, 1791) Sewell, 1922
Bunodera nodulosa (Froelich, 1791) Railliet, 1896
Crossodera campanula (Dujardin, 1845) Cobbold, 1860
C. nodulosa (Froelich, 1791) Dujardin, 1845
Distoma campanula Dujardin, 1845
D. luciopercae) (Muller, 1776) Zeder, 1803
Distoma nodulosa (Froelich, 1791) Zeder, 1800
Fasciola lagena (Brown, 1788) Gmelin, 1790
F. luciopercae Muller, 1776
F. nodulosa Froelich, 1791
F. percae Gmelin, 1790
F. percae cernuae Mueller, 1776
F. percina Schrank, 1790
Planaria lagena Braun, 1788

Type host: *Perca lucioperca.*

Type locality: Germany.

Material examined: USNM No. 77893, ex *Perca flavescens* (Mitchill) , St. Mary's River, Missouri. USNM No. 77410, ex *Culaea inconstans,* Sioux Creek, Barron Co., Wisconsin. USNM No. 51416, ex *Perca fluviatilis* Linnaeus, Berlin, Germany; coll. by Wunder, 1910. USNM No. 51425, ex *P. flavescens,* Lake Michigan. USNM No. 8301, ex *P. flavescens,* Woods Hole, Massachusetts. HWML No. 18000, ex *P. flavescens,* Lake Opeongo, Algonquin Park, Ontario (includes one SEM stub).

Description (based on 21 specimens): Body elongate, tapering slightly anteriorly and posteriorly, length 429-1966 (905.7;362;21), width 130-933 (634;67.9;21), body length to body width ratio 3.3:1-5.3:1 (4.4: 1; 0.67; 21). Oral sucker with oval aperture and three pairs of muscular papillae, measurements excluding papillae: 113-206 (149; 32.6; 10) long by 114-187 (131.6; 54.3; 8) wide. Dorsomedial papillae 52-100 (75; 21; 20; 32) long by 38-60 (45; 13; 20; 34) wide; dorsolateral papillae 69-110 (81; 22; 20; 38) long by 43-78 (56; 15; 21; 30) wide, adjacent dorsal papillae bases contiguous; ratio of dorsolateral to dorsomedial papillae width 0.83: 1- 1.1: 1 (0.98: 1; 0.2; 20); ventral papillae extending to lateral margins of body proper, not extending past midlevel of oral sucker, width not determined. Acetabulum 97-169 (117; 24.6; 10) long by 89-150 (122; 25; 8) wide. Acetabulum to oral sucker width ratio 0.75: 1- 0.9: 1 (0.8: 1; 0.06; 8). Forebody 275-405 (319; 52.5; 7) long; hindbody 243-486 (356; 91; 7) long. Hindbody to forebody length ratio 0.9: 1- 1.66: 1 (1.1: 1; 0.18; 6). Forebody to acetabulum length ratio 2.7: 1- 3.3: 1 (3.1: 1; 0.26; 5). Body to acetabulum to body width ratio 1.6: 1- 2.2: 1 (2: 1; 0.2; 7).

Pharynx 72-143 (92; 26.6; 10) long by 56-113 (81.2; 33.9; 3) wide. Pharynx to oral sucker length ratio 1.3: 1- 2: 1 (1.6: 1; 0.22; 9); esophagus 40-113 (80; 28; 5) long, cecal bifurcation midway between oral sucker and acetabulum, to anterior margin of acetabulum; ceca extending almost to posterior end of body. Testes rounded to somewhat irregular, inconspicuous in older specimens, tandem or oblique, up to one and one-half testis diameters apart; anterior testis 89-150 (111; 33.6; 3) long by 57-120 (81.2; 33.9; 3) wide; posterior testis 73-169 (105; 55.1; 3) long by 57-94 (70.6; 20.3; 3) wide. Genital pore posterior or ventral to cecal bifurcation. Cirrus sac ovoid, anterior to acetabulum, or overlapping acetabulum to some degree,

100-248 (160.7; 53.3; 6) long by 48-75 (60.1; 10.1; 6) wide; containing: seminal vesicle in posterior half; short, prostatic element and numerous prostatic cells; cirrus. Ovary rounded, dextral, medial or sinistral; immediately posterior to or overlapping acetabulum; 72-178 (102; 51.1; 4) long by 64-178 (95; 55.2; 4) wide. Vitelline follicles lateral, extending from pharyngeal region to near posterior end of body, rarely confluent in posttesticular region; inconspicuous in older specimens; seminal receptacle adjacent to ovary posteriorly. Uterus containing 300-3000+ (16) eggs, extending almost to posterior end of body; eggs 72-80 (76; 4; 16; 28) long by 38-46 (42; 5.5; 16; 28) wide. Excretory pore terminal; excretory vesicle extending to level of ovary.

Remarks

Mueller (1776) described *Fasciola lucio-percae* from *Perca lucioperca* in Germany. Froelich (1791) described *Fasciola nodulosa* from *Perca cernua* and *P. fluviatilia* (includes *F. percae cernuae* Mueller) in Germany. Zeder (1800) moved *F. nodulosum* to *Distoma* and in 1803 moved *F. luciopercae* to *Distoma*. Dujardin (1845) erected the new genus *Crossodera* with *D. nodulosa* as the type species. However Railliet (1896) noted that *Crossodera* was preoccupied and changed the generic name to *Bunodera* with *B. nodulosa* the type by designation. Stiles and Hassall (1898) listed "*Distoma nodulosa= Fasciola luciopercae*" under the heading *Bunodera*. In recognizing the synonym of *D. nodulosum* with *Fasciola luciopercae* under the heading *Bunodera* Stiles and Hassell were actually creating the new combination. Thus credit for the new combination goes to these authors. Identity of *D. nodulosa* with *D. luciopercae* was recognized as early as 1809 by Rudolphi. Diesing (1850) discussed the synonyms of *D. nodulosa* including *F. luciopercae. F. percina, F. perca cernae. F. nodulosa. D. campanula. D. lucioperca,* and *Planaria lagena.*

To date *B. luciopercae* has been reported from the following Canadian provinces: Alberta, Newfoundland, Ontario, and Quebec; the following American states: Alabama, Alaska, Illinois, Michigan, Mississippi, New York, and Wisconsin. In addition, it has been reported from the following countries: Czechoslovakia, England, Germany, Holland, Hungary, Ireland, Lithuania, Norway, Poland, Scotland, Switzerland and Wales. The hosts reported for *B. luciopercae* include members of the following piscine families: Cyprinidae, Esocidae, Gadidae, Gasterosteidae, Percidae, and Salmonidae, It has also been reported from the following anurans: *Rana esculenta* and *Bombina bombina.*

Bunodera eucaliae (Miller, 1936) Miller, 1940
(Figs. 39-41)

Synonyms: *Bunoderina eucaliae* Miller, 1936.

Type host: *Culaea inconstans* (Kirkland), brook stickleback.

Type locality: Drainage canal, Jacques Cartier Co., Quebec.

Material examined: Paratype, USNM No. 37502, ex *C. inconstans,* Jacques Cartier Co., Quebec. USNM Nos. 76658, 76659, 76660, ex *Culaea inconstans,* Tichigan Lake Canal, Racine Co., Wisconsin. USNM No. 77409, ex *C. inconstans,* Sioux Creek, Barron Co., Wisconsin. USNM No. 78403, ex *C. inconstans,* Shell Creek, Wisconsin. HWML No. 21490, ex *C. inconstans,* O'Neil, Chippewa Co., Wisconsin.

Description (based on 25 specimens): Body oval, tapering anteriorly and posteriorly, length 454-1706 (846; 320.8; 25), width 168-533 (312; 101; 24), body length to body width ratio 2.2: 1- 3.5: 1 (2.7: 1; 0.3; 21). Oral sucker with oval oral aperture and three pairs of muscular papillae, measurements excluding papillae: 82-192 (134; 31; 21) long by 96-195 (129; 29.8; 21) wide, dorsomedial papillae 10-19 (15; 3.7; 4; 7) long by 11-29 (18; 5.7; 7; 16) wide; dorsolateral papillae 11-24 (17; 5.6; 4; 6) long by 10-20 (15; 4.7; 15; 23) wide, adjacent dorsal papillae bases not contiguous; ratio of dorsolateral to dorsomedial papillae width 0.7: 1- 1: 1 (0.9: 1; 0.11; 8); ventral papillae extending laterally to edge of body proper in anterior half of oral sucker, 8-34 (16; 7.5; 12; 21) wide. Acetabulum 120-256 (174; 42; 20) long by 114-293 (188; 47.9; 18) wide. Acetabulum to oral sucker width ratio 1.17: 1- 1.56: 1 (1: 1.4; 0.12; 16). Forebody 128-464 (256; 104.3; 17) long; hindbody 256-810 (424; 164; 17) long. Hindbody to forebody length ratio 1.08: 1- 2.75: 1 (1.78: 1; 0.43; 17). Forebody to acetabulum length ratio 0.9: 1- 2.24: 1 (1.44: 1; 0.41; 13). Body to acetabulum width ratio 1.4: 1- 1.9: 1 (1.7: 1; 0.15; 16).

Pharynx 46-90 (68; 14.8; 14) long by 36-90 (57; 15.7) wide, oral sucker to pharynx length ratio 1.4: 1- 2.6: 1 (2.1: 1; 0.33; 13); esophagus 65-161 (95; 39; 5) long, cecal bifurcation approximately midway between oral sucker and acetabulum; ceca extending into midhindbody. Testes rounded, usually oblique, occasionally symmetrical; anterior testis 81-105 (90; 12.4; 5) long by 56-97 (76; 15.9; 5) wide; posterior testis 65-105 (93; 15.9; 5) long by 70-97 (87; 10; 5) wide. Genital pore ventral or immediately posterior to cecal bifurcation. Cirrus sac ovoid, anterior to acetabulum or slightly overlapping anterior margin of acetabulum, 90-130 (109; 12.7; 7) long by 42-97 (64; 17.5; 7) wide; containing: coiled internal seminal vesicle in

posterior half; short prostatic element; cirrus. Ovary dextral, medial or sinistral; immediately posterior to or overlapping acetabulum; 54-104 (82;19.1;8) long by 52-105 (76; 21.9; 8) wide. Vitelline follicles lateral, extending from pharyngeal region into midhindbody as far as posterior border of posterior testis; seminal receptacle adjacent to ovary posteriorly. Uterus containing 2-170 (73; 45.9; 12) eggs, extending to posterior end of body; eggs 60-88 (68; 27.7; 9; 30) long by 32-52 (46; 4.6; 9; 26) wide. Excretory pore terminal; excretory vesicle extending to middle of anterior testis.

Remarks

Although this species resembles *Bunodera sacculata* in having short ceca and restricted vitellaria, Miller (1936) erected *Bunoderina* to contain the single species *B. eucaliae,* because the ascending ramus of the uterus was convoluted and tubular rather than saccate. Miller (1940) reconsidered his taxonomic decision and transferred *B. eucaliae* to *Bunodera.* Yamaguti (1958) agreed that the two species should be congeneric, but he transferred both to *Bunoderina* based on the short ceca and restricted vitellaria. Now that *Bunoderina* is considered a synonym of *Bunodera,* the two species have been transferred back to the latter genus.

To date *B. eucaliae* has been reported from members of the Gasterosteidae and the Umbriidae in the following provinces and states: British Columbia, Quebec, Ontario, Iowa, Oregon and Washington. Pratt and McCauley (1961) indicated a report of *B. eucaliae* from Maine by Mueller (1936), but this reference has not been confirmed.

Bunodera mediovitellata Tsimbaliuk and Roitman, 1966
(Figs. 20,27,28,42-44)

Synonyms: *Allobunodera mediovitellata* (Tsimbaliuk and Roitman, 1966) Yamaguti, 1971.

Type host: *Gasterosteus aculeatus* L., three-spined stickleback.

Type locality: Lake Kitovoe, Bering Island (Komandirsk Islands), Komchatka.

Material examined: HWML No. 18001 ex *G. aculeatus,* Campbell Creek, White Rock, British Columbia, USNM No. 80262, and HWML No. 18002 (includes one SEM stub), ex *G. aculeatus,* Tin Can Creek, Musqueum Park, Vancouver, British Columbia.

Description (based on 20 specimens): Body elongate, tapering anteriorly and posteriorly, length 680-3808 (1901; 750.7; ?), width 248-736 (403; 116; 18), body length to body width ratio 3: 1- 7.4: 1 (4.9: 1; 1.2; 18). Oral sucker with oval aperture and three pairs of muscular papillae, measurements excluding papillae: 152-320 (201; 38.9; 17) long by 152-320 (196; 42.5; 17) wide, Dorsomedial papillae 34-60 (47; 7.7; 12; 23) long by 40-82 (59; 12.7; 12; 23) wide; dorsolateral papillae 36-60 (46; 6.9; 11; 21) long by 36-94 (49; 12.9; 11; 21) wide, adjacent dorsal papillae bases contiguous; ratio of dorsolateral to dorsomedial papillae width 0.7: 1- 0.9: 1 (0.8: 1; 0.07; 7); ventral papillae extending laterally to edges of body proper in anterior half of oral sucker, 30-60 (42; 8.3;;19) wide. Acetabulum 160-320 (213; 45.2; 18) long by 168-320 (225; 44.4; 18) wide. Acetabulum to oral sucker width ratio 1: 1-1.33: 1 (1.14: 1; 0.12; 17). Forebody 296-800 (468; 129.5; 17) long; hindbody 672-2656 (1321; 519.8; 17) long. Hindbody to forebody length ratio 1.07: 1- 3.7: 1 (2.5: 1; 0.15; 17). Forebody to acetabulum length ratio 1.5: 1- 3: 1 (2.2: 1; 0.45; 17). Body to acetabulum width ratio 1.4: 1-2.3: 1 (1.8: 1; 0.2; 18).

Pharynx 76-144 (99; 20.3; 16) long by 44-136 (88; 31; 16) wide, oral sucker to pharynx length ratio 1.8:1-2.4:1 (2:1;0.17;16); esophagus 74-176 (114;41.3;7) long, cecal bifurcation one-half to two-thirds distance from oral sucker to acetabulum; ceca extending almost to posterior end of body. Testes rounded to somewhat irregular, tandem or oblique, up to three diameters apart; anterior testis 92-144 (121;13.4;15) long by 70-144 (101; 24; 15) wide; posterior testis 104-178 (137; 23.4; 17) long by 94-160 (115; 15.2; 17) wide. Genital pore ventral to or immediately posterior to cecal bifurcation. Cirrus sac ovoid, or elongated ovoid, entirely anterior to or overlapping acetabulum to some extent, 136-352 (232; 77.8; 10) long by 44-128 (77; 22.6; 10) wide; containing: sinuous seminal vesicle in posterior half; short prostatic element; muscular cirrus. Ovary dextral, medial or sinistral; immediately posterior to or up to two lengths posterior to acetabulum; 104-182 (153; 20.9; 18) long by 80-176 (128; 24.8; 18) wide. Vitelline follicles lateral, extending from posterior border of acetabulum to posterior border of posterior testis; seminal receptacle adjacent to ovary posteriorly. Uterus containing 117-600 (254; 231.2; 4) eggs, extending to posterior end of body; eggs 54-66 (60; 3.4; 4; 9) long by 32-38 (35; 2.8; 4; 9) wide. Excretory pore terminal; excretory vesicle extending almost to posterior border of ovary.

Remarks

The vitellaria of specimens examined in this study are slightly more extensive than those described by Tsimbaliuk

and Roitman (1966); rather than ending at the anterior border of the anterior testis, the vitellaria may extend to the posterior border of the posterior testis, and often the vitellaria are more extensive on one side of the body than the other. Although not mentioned in the original description, the uterus of *B. mediovitellata* is in the form of a long narrow tube with many convolutions extending to the posterior end of the body. The ascending ramus of the uterus in older specimens does not appear to expand into a sac as it does in *B. sacculata* and *B. luciopercae.*

Yamaguti (1971) erected the genus *Allobunodera* to contain this single species. The diagnostic characters appeared to be long ceca, vitellaria restricted both anteriorly and posteriorly, and lack of eyespots. Because *B. mediovitellata* shares long ceca with *B. luciopercae,* posteriorly restricted vitellaria with *B. sacculata* and *B. eucaliae,* and eyespots with all three species (eyespot remnants present on five specimens from British Columbia), there is no evidence to support *Allobunodera* and it is here considered a synonym of *Bunodera.*

To date *B. mediovitellata* has been reported from members of the family Gasterosteidae in British Columbia, Canada; and Komchatcha, U.S.S.R.

Bunodera sacculata Van Cleave and Mueller, 1932
(Figs. 19,33,45-47)

Synonyms: *Bunoderina sacculata* (Van Cleave and Mueller, 1932) Yamaguti, 1958.

Type host: *Perca flavescens,* yellow perch.

Type locality: Oneida lake, Syracuse, New York.

Material examined: Cotypes, USNM No. 8562 and 37501, ex *P. flavescens,* Syracuse, New York. USNM No. 78402, ex *Culaea inconstans,* Jump River, Price Co., Wisconsin. HWML No. 18003 (includes one SEM stub), ex Perca *flavescens,* Lake Opeongo, Algonquin Park, Ontario.

Description (based on 21 specimens): Body elongate, tapering anteriorly and posteriorly, length 1133-2292 (1598; 263.4; 21), width 405-800 (565; 104; 21), body length to body width ratio 2.4: 1- 4.4: 1 (3.3: 1; 0.6; 15). Oral sucker with oval aperture and three pairs of muscular papillae, measurements excluding papillae: 135-259 (192; 30.1; 23) long by 161-267 (210; 32.8; 22) wide. Dorsomedial papillae 26-60 (43; 14.4; 8; 11) long by 40-81 (68; 12.1; 20; 32) wide; dorsolateral papillae 40-64 (42; 10.8; 7; 12) long by 40-72 (46; 16.9; 15; 16) wide, adjacent dorsal papillae bases contiguous; ratio of dorsolateral to dorsomedial papillae width 0.5: 1- 0.9: 1 (0.8: 1; 0.1; 9); ventral papillae extending laterally not reaching edges of body proper, in anterior half of oral sucker, 44-72 (59; 9.3; 16; 16) wide. Acetabulum 170-251 (207; 23; 23) long by 162-267 (218; 25.9; 23) wide. Acetabulum to oral sucker width ratio 0.8: 1- 1.2: 1(1: 1; 0.09; 17). Forebody 348-761 (481; 65.5; 16) long; hindbody 429-1288 (1003; 229.5; 14) long. Hindbody to forebody length ratio 1.85: 1- 2.5: 1 (2: 1; 0.12; 14). Forebody to acetabulum length ratio 1.7: 1- 2.7: 1 (2.3: 1; 0.34; 16). Body to acetabulum width ratio 1.8: 1- 2.8: 1 (2.4: 1; 0.3; 15).

Pharynx 44-79 (62; 10.3; 22) long by 45-84 (69; 8.9; 22) wide, oral sucker to pharynx length ratio 2.5: 1- 4.3: 1 (3.3: 1; 0.5; 16); esophagus 56-304 (142; 90.1; 8) long, cecal bifurcation one-half to two-thirds distance from oral sucker to acetabulum; ceca extending into midhindbody. Testes rounded to ovoid, oblique, contiguous or nearly so; anterior testis 124-243 (170; 41.8; 8) long by 89-227 (133; 40.6; 9) wide; posterior testis 131-243 (195; 36; 10) long by 97-211 (140; 31; 11) wide. Genital pore slightly anterior, ventral or slightly posterior to cecal bifurcation. Cirrus sac ovoid, entirely anterior to or overlapping acetabulum to some extent, 141-336 (260; 55.4; 16) long by 65-154 (102; 25.3; 15) wide; containing: saccate seminal vesicle in posterior half; short prostatic vesicle with numerous prostatic cells; muscular cirrus. Ovary dextral or sinistral; immediately posterior to or overlapping acetabulum; 97-188 (145; 26.3; 21) long by 105-178 (147; 30.5; 21) wide. Vitelline follicles lateral, extending from pharyngeal region into midhindbody; seminal receptacle very small, medial to ovary, no sperm seen. Uterus containing 15-300+ (14) eggs, extending to posterior end of body, ascending ramus expanded into sac; eggs 68-88 (76; 10.7; 20; 56) long by 40-56 (43; 14.4; 8; 11) wide. Excretory pore terminal; anterior vesicle extending to posterior border of ovary.

Remarks

Bunodera sacculata was originally described by Van Cleave and Mueller (1932) from *Perca flavescens* and named for the extensive saccate uterus of mature forms. They distinguished it from the only other species of *Bunodera* known at that time, *B. luciopercae,* on the basis of the less extensive vitellaria, shorter ceca, shorter eggs, testes further forward in the body and ovary and testes not far separated.

Miller (1940) indicated that *B. sacculata* differed from *Bunoderina eucaliae* with respect to the saccate rather than narrow, tubular uterus, but was similar with respect to the posterior extent of the ceca and vitellaria. On the basis of these similarities Miller moved *B. eucaliae* to *Bunodera.*

Despite the similarity in uterine condition between *B. luciopercae* and *B. sacculata* Yamaguti (1958) removed the latter from the *Bunodera* and, on the basis of short vitellaria and ceca, placed it in the genus *Bunoderina* with *B. eucaliae*.

In fact, *B. sacculata* shares a saccate ascending ramus of the uterus with *B. luciopercae*; at the same time, it shares posteriorly restricted vitellaria with *B. mediovitellata* and *B. eucaliae*, and short ceca with *B. eucaliae*. The characters are so interrelated that the three species are here considered to be congeneric.

Hopkins (1934) reported that the seminal receptacle was either small or lacking in *B. sacculata*. Cannon (1971) observed a small, empty seminal receptacle. He reported that spermatogenesis was abortive in *B. sacculata* as no sperm were seen in the seminal receptacles, testes or seminal vesicles in any season of the year; Cannon (1971) went so far as to suggest that *B. sacculata* might in fact be a parthenogenic digenean. A small seminal receptacle was seen in several specimens collected from Algonquin Park in the present study, but no sperm were seen.

To date *B. sacculata* has been reported from the following provinces and states: Quebec, Ontario, Connecticut, Delaware, Iowa, Michigan, New York and Wisconsin. *Bunodera sacculata* is known to parasitize members of the following piscine families: Percidae, Centrarchidae, and Cyprinidae. The specimens deposited by B. Lasee at the National Parasite Collection (No. 78402) from *Culaea inconstans* represent a new host record. In several instances *B. sacculata* has been reported from *Lota lota* and *Stizostedion vitreum*, but the investigators have suggested that these reports may represent accidental infections resulting from these predaceous fish eating food fish infected with *B. sacculata*.

Bunoderella metteri Schell, 1964
(Figs. 48-50)

Synonyms: None.

Type host: *Ascaphus truei* Stejneger, tailed frog.

Type locality: Upper part of Touchet River, Columbia Co., Washington.

Material examined: Holotype and paratypes, USNM No. 60046, ex *A. truei*, Upper part of Touchet River, Columbia Co., Washington. HWML No. 18004, ex *A. truei*, Missoula, Montana (new locality record).

Description (based on 11 specimens): Body elongate, tapering anteriorly and posteriorly, length 1865-7918 (5445; 2669.8; 10), width 328-1733 (1112; 583; 10), body length to body width ratio 4.2: 1- 6.7: 1(5.4: 1; 1.1; 4). Oral sucker with subtriangular oral aperture and two pairs of muscular papillae, measurements excluding papillae: 168-627 (457; 170.7; 11) long by 184-640 (468; 187; 11) wide. Dorsolateral papillae 56-75 (61; 7.8; 11; 14) long by 72-206 (121; 45.5; 7; 14) wide; ventral papillae extending posterior to midlevel of oral sucker, not reaching edge of body proper, 32-161 (114; 47.7; 9; 18) wide. Acetabulum 152-533 (373; 147; 9) long by 168-547 (382; 153.6; 9) wide. Acetabulum to oral sucker width ratio 0.9: 1- 1.03: 1 (0.9: 1; 0.05; 4). Forebody 608-2471 (1355; 853.5; 6) long; hindbody 792-4941 (2272; 1717; 6) long. Hindbody to forebody length ratio 1.3: 1- 1.66: 1 (1.42: 1; 0.06; 4). Forebody to acetabulum length ratio 3.24: 1- 4: 1 (3.6: 1; 0.36; 4). Body to acetabulum width ratio 1.7: 1- 2.58: 1 (2: 1; 0.39; 4).

Pharynx 66-199 (145; 44.9; 9) long by 70-266 (180; 76.9; 9) wide, oral sucker to pharynx length ratio 2.5: 1- 2.9: 1 (2.7: 1; 0.18; 3); esophagus 80-600 (321; 171.7; 9) long, cecal bifurcation one-third to one-half distance from oral sucker to acetabulum; ceca extending almost to posterior end of body. Testes rounded, tandem, contiguous or up to one-half testis diameter apart; anterior testis 184-800 (502; 244; 10) long by 120-865 (464; 245.4; 10) wide; posterior testis 184-893 (571; 283; 10) long by 136-732 (462; 230.9; 10) wide. Genital pore well behind cecal bifurcation, three-fourths distance from oral sucker to acetabulum. Cirrus sac ovoid, entirely anterior to or slightly overlapping acetabulum, 160-652 (405; 189.9; 10) long by 68-400 (250; 130.3; 10) wide; containing: coiled seminal vesicle in posterior two-thirds; short prostatic element; thick walled, muscular cirrus. Ovary dextral, medial or sinistral; up to one ovary diameter posterior to acetabulum; 120-493 (322; 159; 10) long by 136-480 (342; 158.5; 10) wide. Vitelline follicles extensive, somewhat lateral, extending from posterior margin of pharynx to near posterior end of body, confluent anterior to cirrus sac, between acetabulum and ovary, between ovary and anterior testis, between testes, and in posttesticular region; seminal receptacle adjacent to ovary posteriorly. Uterus containing 21-789 (264; 305.3; 6) eggs, extending to extreme posterior end of body; eggs 36-48 (44; 2.7; 4; 15) long by 26-38 (32; 3.9; 4; 15) wide. Excretory pore terminal; excretory vesicle extending to posterior margin of ovary.

Remarks

Bunoderella is a monotypic genus. Schell described *Bunoderella metteri* from the tailed frog, *Ascaphus truei* collected from the states of Washington and Idaho. Anderson

Schell and Pratt (1965) described the life cycle of *B. metteri* and were able to experimentally infect *Rana aurora* Baird and Girard and *A. truei.* Four specimens of *B. metteri* deposited at the Manter Laboratory by G. D. Schmidt were collected from *A. truei* in the vicinity of Missoula, Montana; these specimens represent a new locality record. *Bunoderella metteri* is the only papillose allocreadiid known to parasitize anurans.

Crepidostomum Braun, 1900

Synonyms: *Acrodactyla* Stafford, 1904
Acrolichanus Ward, 1917
Megalogonia Surber, 1928
Stephanophiala Nicoll, 1909

Type species: *Crepidostomum metoecus* (Braun, 1900).

The following diagnosis is a combination of the diagnoses of Hopkins (1934) and Yamaguti (1971), as well as data from the present study.

Diagnosis: Body elongate, oval to subcylindrical, unarmed. Oral aperture ventral. Oral sucker with six muscular papillae, four dorsal and two ventral; bases of dorsal papillae contiguous or not. Prepharynx short; pharynx short; pharynx and esophagus present. Cecal bifurcation anterior or dorsal to acetabulum; ceca terminating near posterior extremity of body. Acetabulum in anterior half of body. Genital pore median, anterior to acetabulum, posterior to oral sucker. Common genital atrium very small, obliterated when cirrus is everted. Cirrus sac varying in form and size in different species, reaching only to anterior edge or center of acetabulum in some, as far as testes in others; cirrus sac containing seminal vesicle, pars prostatica, and cirrus; prostatic vesicle visible in some species. Testes two, divided or not, tandem or oblique, contiguous or not, in posterior half of body. Ovary round or pyriform, anterior to testes, dextral, sinistral or medial. Seminal receptacle adjacent to ovary posteriorly. Laurer's canal inconspicuous, loosely organized Mehlis' gland present. Vitellaria mostly lateral and ventral to ceca, extending into intercecal space between and posterior to testes, and anterior to ovary in some species; extending from different levels in forebody to posterior extremity of body; vitelline reservoir present. Uterus tubular, narrow, with thin muscular walls, between genital pore and posterior border of posterior testis. Inconspicuous metraterm present. Intrauterine eggs few to several hundred in number; ovoidal or elipsoidal, with operculum and abopercular thickening; eggs deposited while in single cell stage. Excretory pore terminal; excretory vesicle "I" shaped, dorsal to testes, reaching at least as far as posterior border of posterior testis.

Crepidostomum metoecus (Braun, 1900) Braun, 1900
(Figs. 21,30,51-53)

Genotype.

Synonyms: *Crepidostomum faeroense* Bovien, 1932
C. moeticus of Brown (1927)
C. suecicum Nybelin, 1932
Distomum metoecus Braun, 1900

Type host: *Vespertilio noctua* (=*Nyctalus noctua* (Schreber, 1774)) and *V. lasiopterus* (=*Nyctalus lasioperus* (Schreber, 1780)), bats.

Type locality: Braun described this species from specimens that he found in a vial at the Vienna Naturhistorisches Museum. Locality was not given, but the two bat species occur in Europe.

Material examined: USNM No. 80263, and HWML No. 18005 (includes one SEM stub), ex *Thymallus arcticus,* Aishihik Lake, Yukon Territory (includes one SEM stub). Additional specimens returned to Dr. L. Margolis, Pacific Biological Station, Nanaimo, British Columbia.

Description (based on 11 specimens): Body elongate, tapering anteriorly and posteriorly, length 900-2168 (1657;453;10), width 224-416 (350;78.7;8), body length to body width ratio 3.8:1-5.4:1 (4.9:1;0.56;8). Oral sucker with round oral aperture and three pairs of muscular papillae, measurements excluding papillae: 144-248 (209; 44; 9) long by 120-240 (209; 41; 7) wide. Dorsomedial papillae 40-54 (46; 5.4; 6; 10) long by 26-74 (58; 16.3; 7; 16) wide; dorsolateral papillae 22-46 (40; 6.7; 7; 10) long by 26-60 (47; 11.2; 6; 11) wide, adjacent dorsal papillae bases not contiguous; ratio of dorsolateral to dorsomedial papillae width 0.7: 1- 1.1: 1 (0.8: 1; 0.15; 6); ventral papillae extending laterally past margins of body proper, not extending past midlevel of oral sucker posteriorly, 24-50 (38; 7.7; 7; 6) wide. Acetabulum 144-272 (212; 46.5; 9) long by 160- 264 (217; 39.6; 7) wide. Acetabulum to oral sucker width ratio 1: 1- 1.4: 1 (1.13: 1; 0.14; 6). Forebody 256-568 (444; 100.8; 10) long; hindbody 496-1336 (998; 306; 10) long. Hindbody to forebody length ratio 1.6: 1- 2.7: 1 (2.17: 1; 0.09; 10). Forebody to acetabulum length ratio 1.6: 1- 2.6: 1 (2.2: 1; 0.3; 7). Body to acetabulum width ratio 1.33: 1- 1.85: 1 (1.58: 1; 0.17; 7).

Pharynx 64-96 (76;12.7;9) long by 56-96 (79;16.2;7) wide, oral sucker to pharynx length ratio 2.25:1-3.3:1 (2.76:1;0.34;7); esophagus 64-104 (91;20.1;7) long, cecal bifurcation midway between oral sucker and acetabulum;

ceca extending almost to posterior end of body. Testes rounded, tandem, contiguous or nearly so; anterior testis 80-304 (188;77.6;9) long by 80-240 (173;55.6;8) wide; posterior testis 110-288 (212;68.4;10) long by 84-216 (162;49.4;8) wide. Genital pore immediately posterior to cecal bifurcation. Cirrus sac elongated ovoid, overlapping acetabulum to some degree or extending up to one-third acetabulum length posterior to acetabulum, 230-480 (417; 89.4; 7) long by 92-120 (111; 12.3; 7) wide; containing: coiled seminal vesicle in posterior half; short prostatic element; thick walled, muscular cirrus. Ovary dextral or medial; up to one-half ovary length posterior to acetabulum; 160-224 (190; 28; 4) long by 130-216 (166; 34.8; 4) wide. Vitelline follicles lateral, extending from pharyngeal region to near posterior of body, encroaching medially at level of cecal bifurcation and between testes, confluent in posttesticular region; seminal receptacle adjacent to ovary posteriorly. Uterus containing 8-79 (30; 16.9; 10) eggs, posterior extent ranging from anterior margin of anterior testis to anterior margin of posterior testis; eggs 50-72 (64; 5.4; 9; 38) long by 38-52 (45; 2.7; 9; 38) wide. Excretory pore terminal; excretory vesicle extending to middle of anterior testis.

Remarks

Distomum metoecus was described by Braun (1900a) from specimens found in a vial at the Vienna Naturhistorisches Museum. The associated label stated that the hosts were the two species of bats listed above. Later the same year, Braun (1900b) erected the genus *Crepidostomum* to include *C. metoecus* (genotype) and *C. laureatum* (=*C. farionis*), noting that the latter species occurred in fishes and that such disparate hosts as bats and fishes might harbor the same genus of parasite if their larval stages passed through insects serving as food for both groups of hosts.

Hopkins (1934) was the first to suggest that "fish are the 'normal' hosts and that bats are only 'occasional' or 'accidental' hosts" of *C. metoecus*. He had examined Braun's type material of *C. metoecus,* compared it with Nybelin's (1932) description and figures of *C. suecicum* from freshwater fishes of Sweden, and concluded they were conspecific. Additionally, Hopkins had examined a vial of parasites from *Perca fluviatilis* from Vienna (University of Berlin Zoological Museum No. 5774) that he identified as a mix of *C. metoecus* and *C. farionis*. Based on "the abundance in fish and the apparent rarity in bats" and the greater number of eggs in specimens from fishes (8-24 rather than 1-2), he accepted *C. metoecus* as a parasite of fishes.

Since Hopkins' monograph (1934), *C. metoecus* has been reported regularly from various fish hosts (see Thomas, 1958; Slusarsky, 1958), but no further records of *C. metoecus* from bats exist. As Corbett (1955) pointed out, *V. noctua* is distributed throughout Europe and Asia, and in view of the great distribution and number of helminths reported from this bat it is unusual that the occurrence of *C. metoecus* in this host has never been confirmed.

An extremely detailed account of *C. metoecus* was presented by Slusarsky (1958). He considered *C. faeroense*) Bovien, 1932 from *Salmo trutta* and *C. brumpti*) Dinulescu, 1942 from *Salmo fario* to be synonyms of *C. metoecus*. Bovien's (1932) description of *C. faeroense* is fully consistent with *C. metoecus* and thus the two are considered synonyms in the present paper. The figure that Dinulescu (1942) presented of *C. brumpti* however, differs from *C. metoecus* in several respects: (1) the oral sucker is much smaller than the acetabulum (rather than being approximately equal to the acetabulum) (2) the body is ovoid (rather than elongated) (3) the testes are transversely ovoid (rather than round). Further evidence is necessary before the two are considered synonyms.

To date *C. metoecus* has been reported from British Columbia and the Yukon Territory in Canada, Czechoslovakia, Denmark, Italy, Luthuania, Northern Ireland, Norway, Poland, Scotland, Spain, Sweden, Wales, West Germany, Ukraine, U.S.S.R., and Yugoslavia. Most records of *C. metoecus* are from Salmonidae, but it has also occasionally been reported from Anguillidae, Gadidae, Cottidae, Esocidae, Percidae, and only once from the two species of bats *Vespertilio noctua* and *V. lasiopterus*.

Crepidostomum auriculatum (Wedl, 1858) Pratt, 1902

(Figs. 54-56)

Synonyms: *Acrodactyla auriculata* (Wedl, 1858) Odhner, 1910
A. lintoni (Pratt in Linton, 1901) Odhner, 1910
A. petalosa (Lander in Looss, 1902) Stafford, 1904
Acrolichanus (?) *auriculatus* (Wedl, 1858), Skvortsov 1927
A. lintoni (Pratt in Linton, 1901) Ward, 1918
A. petalosa (Lander in Looss, 1902) Ward, 1917
Bunodera auriculata)(Wedl, 1858) Osborn, 1903
B. lintoni Pratt in Linton, 1901
Crepidastomum auriculatum [sic] (Wedl) Linton of Pratt (1902)
Crepidostomum lintoni (Pratt in Linton, 1901) Hopkins, 1933

C. petalosum (Lander in Looss, 1902) Yamaguti, 1958
Distoma auriculatum Wedl, 1858
D. auriculatum Wedl ? of Linton (1898)
Distomum petalosum Lander in Looss, 1902

Type host: *Acipenser ruthenus* Sterle, sturgeon.

Type locality: Lake Baikal, U.S.S.R.

Material examined: USNM No. 51543, ex *Acipenser rubicundus* Auth, from St. Lawrence River, Canada; coll. and det. by Cooper (1915). USNM No. 51544, ex *A. rubicundus,* from New Baltimore, Michigan; coll. by Ward, 1893, det. by Hopkins. USNM No. 51545, ex *Acipenser fulvescens* Rafinesque, from Detroit, Michigan; coll. by C. H. Lander, 1894, det. by Hopkins. USNM No. 4845 (vial), ex *Acipenser* sp., locality unknown; coll. by Milner, det. by Linton (specimens apparently dried and subsequently returned to alcohol, uninformative). HWML No. 18006, ex. *Scaphirhynchus platorhynchus* (Rafinesque), from Lake Pepin, Wisconsin. HWML No. 22983, ex *Acipenser transmontanus* Richardson, from Nicomen Slough off the Fraser River, British Columbia; coll. by L. Margolis; additional specimens, returned to L. Margolis, Pacific Biological Station, Nanaimo, British Columbia. Lander's original drawings of *Acrodactyla petalosa* (HWML).

Description (based on 25 specimens): Body elongate, taperingposteriorly, length 1072-2840 (2182;403;25), width 320-696 (526; 92; 25), body length to body width ratio 2.89: 1- 5.75: 1 (4.15: 1; 0.76; 25). Oral sucker with subtriangular aperture and three pairs of muscular papillae, measurements excluding papillae: 224-432 (330; 55; 25) long by 200-408 (320; 54; 25) wide. Dorsomedial papillae 45-120 (84; 15.2; 18; 35) long by 96-176 (132; 22; 18; 36) wide; dorsolateral papillae 70-120 (90; 12.4; 18; 34) long by 72-144 (102; 25; 18; 34) wide; adjacent dorsal papillae bases contiguous; dorsolateral to dorsomedial papillae width ratio 0.6: 1- 0.9: 1 (0.7: 1; 0.09; 16); ventral papillae extended laterally beyond body proper and posteriorly to midlevel of oral sucker, 72-136 (105; 22.3; 14; 18) wide. Acetabulum 144-304 (249; 38.6; 24) long by 144-320 (256; 43; 24) wide. Acetabulum to oral sucker width ratio 0.38: 1- 0.95: 1 (0.77: 1; 0.3; 24). Forebody 520-1160 (845; 171; 22) long; hindbody 432-1296 (1052; 234; 25) long. Hindbody to forebody length ratio 0.83: 1- 1.85: 1 (1.2: 1; 0.19; 22). Forebody to acetabulum length ratio 2.23: 1- 4.7: 1 (3.4: 1; 0.7; 22). Body width to acetabulum width ratio 1.5: 1- 2.63: 1 (2.1: 1; 0.28; 22).

Pharynx 72-184 (139; 28; 27) long by 72-128 (108; 16; 25) wide, oral sucker to pharynx length ratio 1.6: 1- 3.1: 1 (2.39: 1; 0.43; 23); esophagus 5-120 (66; 30; 19) long, cecal bifurcation one-third to one-half distance from oral sucker to acetabulum; ceca extending almost to posterior end of body. Testes rounded to somewhat irregular, contiguous, usually tandem, occasionally oblique; anterior testis 120-248 (192; 40; 23) long by 144-360 (274; 61; 22) wide; posterior testis 120-296 (211; 53; 22) long by 112-400 (261; 72; 22) wide. Genital pore immediately posterior to cecal bifurcation. Cirrus sac median, long ovoid, overlapping acetabulum to some extent, 216-640 (460; 106; 22) long by 48-312 (184; 60; 22) wide; containing coiled seminal vesicle in posterior half; short prostatic element; thick walled, muscular cirrus, expanding distally, with conspicuous triradiate lumen. Ovary dextral, medial or sinistral; immediately posterior to or overlapping acetabulum; 110-208 (168; 31; 20) long by 90-288 (191; 50.6; 20) wide. Vitelline follicles lateral, extending from pharyngeal region to near posterior end of body, confluent in posttesticular region; seminal receptacle adjacent to ovary posteriorly. Uterus containing 4-100 (50; 27.8; 17) eggs, posterior extent ranging from anterior border of anterior testis to near posterior border of posterior testis; eggs 53-68 (62; 3.7; 17; 62) long by 32-42 (37.6; 1.2; 13; 53) wide. Excretory pore terminal; excretory vesicle extending to middle of anterior testis.

Remarks

Wedl (1858) described *Distoma auriculatum* from *Acipenser rubicundus* in Lake Baikal, U.S.S.R. This publication is consistently cited as 1857, but it was not distributed until 1858. Linton (1898) described specimens that he provisionally identified as "*Distomum auriculatum* Wedl?" These specimens, collected by J. W. Milner from *A. rubicundus* at an unknown North American locality, were deposited at the USNM (No. 4845) but had dried up by the time Hopkins (1934) examined them. Linton (1901) again reported *Distomum auriculatum* from *A. rubicundus* near the Wood's Hole region and stated that the name *Bunodera lintoni* had been proposed by Pratt for this species (presumably via personal communication). One year later, Looss (1902) published the name *Distomum petalosum* Lander (a label name on specimens sent to him by C. H. Lander from North America). According to Hopkins (1934), Looss stated that Lander's species was essentially the same as that described by Linton as "*Distomum auriculatum* Wedl?" but was distinct from the original *D. auriculatum* Wedl. Unfortunately Looss did not discuss the distinction.

In his key Pratt (1902) used the new combination *Crepidastomum auriculatum* (an obvious typographical error for *Crepidostomum*). Stafford (1904) erected the new genus *Acrodactyla,* designated *A. petalosa* as the type species, and stated that "this is the *D. auriculatum* Wedl! of Linton and it is upon the authority of Looss that I use the above specific designation." Further, Odhner (1910) suggested that *A. petalosa* was a synonym of *A. lintoni* Pratt. After examining Lander's unpublished original drawings of *A. petalosa,* Ward (1917) wrote that "A careful comparison of the details in the drawing with the evidence at hand on the other species noted is adequate to establish the distinctness of Lander's type.", but he did not elaborate on the "evidence." Ward also noted that the name *Acrodactyla* was preoccupied and replaced it with *Acrolichanus.* Faust (1918) recognized *Acrolichanus petalosa* and thought it highly probable that both *Distomum auriculatum*) Wedl? of Linton and *Bunodera lintoni* were synonyms. In addition Faust (1918) suggested that the type *D. auriculatum* Wedl from Asia was so inadequately described that it should not be given systematic position.

Skvortsov (1927) detailed the morphology of *Acrolichanus auriculatus* based on a number of specimens collected in the U.S.S.R. from *Acipenser ruthenus.* Hopkins (1933) recognized both *C. auriculatum* and *C. lintoni* and accepted *Acrolichanus petalosa* as a synonym of *C. lintoni.* In his key to the species of *Crepidostomum,* Hopkins (1933) distinguished *C. lintoni* from *C. auriculatum* on the basis of the oral sucker being much larger than the ventral sucker (rather than equal or only slightly larger) and the uterus reaching back past the anterior testis in older specimens (rather than not doing so). Hopkins' (1934) monograph contains, by far, the most detailed discussion of these species. Once again he recognized *C. auriculatum* as distinct from *C. lintoni.* He listed all European combinations, including *Distoma auriculatum* Wedl 1857 [sic] and *Acrolichanus auriculatus,* as synonyms of *C. auriculatum*; and all North American combinations, including *D. petalosum,* which he noted was published a year later than *B. lintoni,* as synonyms of *C. lintoni.* Hopkins stated that the only difference between Lander's and Linton's forms was the apparent length and position of the cirrus sac which he stated is "probably not real, and in any case is overbalanced by the agreement in all other features and the specific identity of the hosts". Hopkins combined the data of Wedl and Skvortsov to produce a specific diagnosis of *C. auriculatum.*

Present evidence supports the conspecificity of both Lander's and Linton's forms with *C. auriculatum* (Wedl, 1858): (1) Hopkins' (1933) distinction based on the extent of the uterus is not supported by specimens; some North American specimens have uteri that are pretesticular while in others the uteri may overlap one or both of the testes. (2) Hopkins' (1933) criterion of sucker ratio difference is not valid because Wedl's own Figure 2 as well as Skworzoff's Figures 1 and 2 illustrate worms in which the oral sucker is clearly larger than the ventral sucker, and North American specimens examined for this study have a sucker ratio ranging from 1:1.05-1:2.6. (3) All forms consistently possess an ovoid cirrus sac beginning well anterior to the acetabulum and overlapping the acetabulum; the cirrus in many specimens expands terminally and has a conspicuous triradiate lumen. (4) These are the only papillose allocreadiids found in sturgeon and, to date, exclusively in sturgeon. (5) The only apparent discrepancy between Wedl's description of *D. auriculatum* and other descriptions of this species is the anterior extent of the vitellaria: midway between the acetabulum and the pharynx in Wedl's description, the pharyngeal region in all other descriptions. Until additional specimens with vitellaria restricted in the fashion described by Wedl are recovered from sturgeon, it seems reasonable to assume that Wedl had an anomalous specimen(s) or that he failed to determine the true extent of the vitellaria.

In summary, *C. lintoni* is here considered to be a synonym of *C. auriculatum* Wedl, 1858, NEW SYNONYMY. The species is found exclusively in holarctic sturgeon.

Crepidostomum auritum (MacCallum, 1919) Hopkins, 1934

(Figs. 57-59)

Synonyms: *Crepidostomum cornutum* partim of Hopkins (1934)
Distomum auritus MacCallum, 1919

Type Host: *Aplodinotus grunniens* Rafinesque, freshwater drum.

Type Locality: Fresh waters near the New York Aquarium.

Material examined: Type, USNM Helm. Coll. No. 36236, ex *A. grunniens,* from fresh waters near New York Aquarium.

Description (based on 24 specimens): Body ovoid, tapering anteriorly and posteriorly, length 840-1800 (1315;281;23), width 272-720 (477;129;21), body length to body width ratio 1.95:1-3.97:1 (2.95:1;0.71;16). Oral sucker with round oral aperture and three pairs of muscular papillae, measurements excluding papillae: 104-192 (147;22.4;20) long by 120-200 (153;23.5;21) wide. Dorsomedial papillae 20-42 (34.8;6.5;7;14) long by 30-56 (41; 7.8; 9; 18) wide; dorsolateral papillae 22-40 (35.7; 7; 7; 14) long by 22-44 (34; 5.5; 9; 18) wide, adjacent dorsal

papillae bases not contiguous; ratio of dorsolateral to dorsomedial papillae width 0.7: 1- 0.94: 1 (0.8: 1; 0.07; 9); ventral papillae in anterior half of oral sucker, extending laterally slightly past margins of body proper, 28-40 (34; 4.4; 5; 7) wide. Acetabulum 144-216 (180; 28.7; 14) long by 120-200 (165; 28.6; 12) wide. Acetabulum to oral sucker width ratio 0.8: 1- 1.25: 1 (0.96: 1; 0.12; 12). Forebody 296-560 (419; 85; 17) long, hindbody 560-1200 (824; 191; 17) long. Hindbody to forebody length ratio 1.28: 1- 2.56: 1 (1.82: 1; 0.1; 14). Forebody to acetabulum length ratio 1.52: 1- 2.89: 1 (2.29: 1; 0.42; 11). Body to acetabulum width ratio 2.52: 1- 4.4: 1 (3.5: 1; 0.48; 10).

Pharynx 48-80 (65.3; 10.8; 14) long by 40-80 (60; 12.2; 14) wide, oral sucker to pharynx length ratio 1.6: 1- 3.2: 1 (2.5: 1; 0.46; 11); esophagus 70-203 (136; 42; 12) long, cecal bifurcation two-thirds distance from oral sucker to acetabulum; ceca extending almost to posterior end of body. Testes rounded, tandem, contiguous or nearly so; anterior testis 104-200 (155; 31.2; 13) long by 80-192 (140.5; 32; 13) wide; posterior testis 88-232 (161; 46; 13) long by 80-192 (137; 34.5; 13) wide. Genital pore immediately posterior to cecal bifurcation. Cirrus sac lateral to acetabulum extending up to two acetabulum lengths posterior to acetabulum, 260-680 (433; 149; 17) long by 40-112 (71; 16.8; 17) wide; containing: saccate or coiled seminal vesicle in posterior two-thirds; short, inconspicuous prostatic element; and muscular cirrus. Ovary dextral or sinistral; immediately posterior to, or slightly overlapping acetabulum, 96-176 (127; 27.7; 13) long by 80-192 (137; 32; 13) wide. Vitelline follicles lateral, extending from pharyngeal region to posterior end of body, confluent in posttesticular region; seminal receptacle adjacent to ovary posteriorly. Uterus containing 2-33 (16.3; 10.8; 17) eggs, posterior extent ranging from anterior border of anterior testis to middle of posterior testis. Eggs 68-84 (76; 4.45; 13; 49) long by 36-50 (41; 3.6; 13; 37) wide. Excretory pore terminal; anterior extent of excretory vesicle not seen.

Remarks

MacCallum's (1919) original description of *Distomum auritus* was incomplete but the accompanying figure clearly shows three pairs of muscular oral papillae and a pretesticular uterus. Hopkins (1934) listed *D. auritus* as a probable synonym of *Crepidostomum cornutum* but made no further reference to the species. Nevertheless, Hopkins' statement of synonymy implied the new combination *Crepidostomum auritum*. Examination of the 24 specimens in the type series confirms the specific identity of *Crepidostomum auritum*. It most closely resembles *C. ictaluri* but differs in its possession of two rounded testes rather than four irregular lobes. No additional records of this species currently exist.

Crepidostomum brevivitellum Hopkins, 1934
(Figs. 16,60-62)

Synonyms: None.

Type host: *Anguilla rostrata* (LeSueur), American eel.

Type locality: Maine, Sebago Lake.

Material examined: Type and paratypes, USNM Helm. Coll. No. 51518, *A. rostrata,* Maine, Lake Sebago; coll. by Ward, det. by Hopkins (1934).

Description (based on 3 specimens): Body elongate, tapering posteriorly, length 1409-2400 (1885; 496; 3), width 280-373 (342; 54; 3), body length to body width ratio 4: 1- 9: 1 (6: 1; 2.7; 3). Oral sucker with subtriangular oral aperture and three pairs of muscular papillae, measurements excluding papillae: 233-267 (253; 17.8; 3) long by 191-235 (215; 22; 3) wide. Dorsomedial papillae 76-84 (80; 3.3; 2; 4) long by 57-65 (61; 4.4; 3; 6) wide; dorsolateral papillae 76-84 (80; 2.8; 3; 6) long by 65-93 (79; 9.8; 3; 6) wide, adjacent dorsal papillae bases contiguous; ratio of dorsolateral to dorsomedial papillae width 1.27: 1- 1.34: 1 (1.3: 1; 0.04; 3); ventral papillae extending well beyond body proper and posteriorly into posterior half of oral sucker, 60-81 (71; 9.5; 3; 6) wide. Acetabulum 161-178 (173; 9.8; 3) long by 150 -219 (189; 35; 3) wide. Acetabulum to oral sucker width ratio 0.8: 1- 0.93: 1 (0.88: 1; 0.1; 3). Forebody 480-700 (557; 124; 3) long, hindbody 890-1740 (1317; 425; 3) long. Hindbody to forebody length ratio 1.81: 1- 2.75: 1 (2.35: 1; 0.48; 3). Forebody to acetabulum length ratio 2.7: 1- 4.3: 1 (3.26: 1; 0.94; 3). Body to acetabulum width ratio 1.7: 1- 1.9: 1 (1.8: 1; 0.1; 3).

Pharynx 86-92 (90; 3.3; 3) long by 80-112 (93; 17; 3) wide, oral sucker to pharynx length ratio 2.7: 1- 2.9: 1 (2.8: 1; 0.1; 3); esophagus 44-199 (104; 83; 3) long, cecal bifurcation two-thirds distance from oral sucker to acetabulum; ceca extending almost to posterior end of body. Testes ovoid to somewhat irregular, tandem, contiguous up to one testis diameter apart; anterior testis at mid hindbody, 112-206 (167; 49; 3) long by 113-172 (142; 30; 3) wide; posterior testis 160-206 (182; 23; 3) long by 120-180 (151; 30; 3) wide. Genital pore ventral or immediately posterior to cecal bifurcation. Cirrus sac sinuous, elongated, extending approximately one acetabulum length posterior to acetabulum, 589 long by 67

wide; containing: slightly coiled seminal vesicle in posterior two-thirds; short, inconspicuous prostatic element; cirrus. Ovary dextral, medial or sinistral; at least one ovarian length posterior to acetabulum; 114 long by 124 wide. Vitelline follicles lateral, extending from posterior border of acetabulum to posterior end of body, encroaching between and immediately anterior to testes, confluent in posttesticluar region; seminal receptacle adjacent to ovary posteriorly. Uterus containing 32-56 (44; 12; 3) eggs, extending to anterior border of anterior testis; eggs 52-67 (58.5; 5; 3; 14) long by 30-46 (39.2; 4.6; 3; 14) wide. Excretory pore terminal; excretory vesicle not reaching posterior testis.

Remarks

To date *C. brevivitellum* has been collected from *Anguilla rostrata* and *Lota maculosa*) (LeSueur)(=*L. lota*). Locality records for *C. brevivitellum* are restricted to North America and include the following areas: Lake Sebago in Maine, eastern Labrador, and the Central St. Lawrence Watershed in Quebec.

Crepidostomum cooperi Hopkins, 1931

(Figs. 10,11,13,23,25,34,35,63-65)

Synonyms: *Crepidostomum ambloplites* Hopkins, 1931
C. laureatum of Cooper (1915) partim
C. laureatum of Stafford (1904)
C. solidum Van Cleave and Mueller, 1932

Type locality: Go-Home Bay, Ontario.

Type host: *Perca flavescens* (Mitchill), yellow perch.

Material examined: Types (sections), USNM No. 51520, ex *P. flavescens,* Go-Home Bay, Ontario. Cotypes of *C. solidum,* ex *Perca flavescens,* Oneida Lake, New York. HWML No. 18030, ex *Lepomis cyanellus* Rafinesque, Unnamed creed, Cornhusker Boy Scout Camp, near Richardson City, Nebraska. HWML No. 18037, ex *Noturus flavus* (Rafinesque), Turkey Creek, Nebraska. HWML No. 18029, ex *Ictalurus melas* (Rafinesque), Yankee Hill Lake, Nebraska. HWML. No. 18031, ex *Ambloplites rupestris* (Rafinesque), Gull Lake, Kellogg Biological Station, Michigan. HWML No. 18028, ex *Morone americana* (Gmelin), Bluestem Lake, Nebraska. HWML No. 18034, ex *Pomoxis nigromaculatus* (LeSueur), Bluestem Lake, Nebraska. HWML No. 18032, ex *Lepomis humilis* (Girard), Pawnee Lake, Nebraska. HWML No. 18007, ex *Lepomis macrochirus* Rafinesque, Bluestem Lake, Nebraska. HWML No. 18033, ex *L. macrochirus,* Yankee Hill Lake, Nebraska. HWML No. 18036, ex *L. macrochirus,* Branched Oak Lake, Nebraska. HWML No. 18035, ex *L. cyanellus,* Pawnee Lake, Nebraska.

Description (based on 21 specimens): Body elongate, tapering anteriorly and posteriorly, 413-4160 (1883; 930; 21) long by 173-824 (444; 191.7; 21) wide, body length to body width ratio 2.4: 1- 6: 1 (3.9: 1; 0.9; 20). Oral sucker with oval aperture and three pairs of muscular papillae, measurements excluding papillae: 76-384 (221; 67.6; 21) long by 78-400 (218; 74.1; 20) wide. Dorsomedial papillae 18-120 (63; 28.8; 20; 40) long by 18-112 (61; 20.3; 20; 40) wide; dorsolateral papillae 20-120 (69; 22; 20; 39) long by 16-114 (57; 20.7; 20; 41) wide, adjacent dorsal papillae bases contiguous; ratio of dorsolateral to dorsomedial papillae width 0.7: 1- 1.15: 1 (0.9: 1; 0.1; 20); ventral papillae extending to lateral margins of body proper, not extending past midlevel of oral sucker. Acetabulum 68-384 (145; 70.9; 21) long by 95-376 (211; 74.8; 21) wide. Acetabulum to oral sucker width ratio 0.8: 1- 1.2: 1 (0.95: 1; 0.14; 18). Forebody 210-1800 (1212; 900; 19) long, hindbody 272-2800 (1800; 990; 19) long. Hindbody to forebody length ratio 1.4: 1- 2: 1 (1.66: 1; 0.13; 21). Forebody to acetabulum length ratio 2.9: 1- 4: 1 (3.1: 1; 0.3; 20). Body to acetabulum width ratio 1.3: 1- 2.8: 1 (2: 1; 0.7; 19).

Pharynx 27-120 (71; 23.1; 20) long by 27-148 (73; 28.6; 20) wide, pharynx to oral sucker length ratio 2.5: 1- 4: 1 (3.1: 1; 0.3; 18); esophagus 5.7-240 (110; 83.9; 11) long, cecal bifurcation midway to two-thirds distance from oral sucker to acetabulum; ceca extending almost to posterior end of body. Testes rounded, tandem, one-half testis diameter apart; anterior testis 65-336 (162; 87.6; 19) long by 110-376 (188; 67.2; 18) wide; posterior testis 86-400 (204; 93.8; 18) long by 95-360 (185; 74.9; 18) wide. Genital pore posterior or ventral to cecal bifurcation. Cirrus sac sinuous, extending dorsolateral to acetabulum up to one and a half acetabulum lengths posterior to acetabulum, 94-1024 (522; 305.1; 15) long by 33-104 (70; 22.8; 14) wide; containing: saccate seminal vesicle usually in posterior third; short prostatic vesicle and numerous prostatic cells; cirrus. Ovary rounded, dextral, medial or sinistral, up to one ovary length posterior to acetabulum, 88-240 (134; 46.9; 19) long by 88-320 (148; 61.8; 18) wide. Vitelline follicles lateral, extending from pharynx to near posterior end of body, confluent or not in posttesticular region; seminal receptacle adjacent to ovary posteriorly. Uterus containing 1-37 (12; 11.2; 18) eggs, extending to anterior border of anterior testis. Eggs 64-82 (57; 8.5; 4)

long by 42-60 (54; 8.2; 4) wide. Excretory pore terminal; excretory vesicle extending at least to anterior testis.

Remarks

Hopkins (1931) originally described this species from 10 specimens collected from *Perca flavescens* that Cooper (1915) had identified as *Crepidostomum laureatum*. Hopkins suggested that these specimens differed from *C. laureatum* (=*C. farionis*) in their possession of a genital pore ventral to or posterior to the crural fork, and a cirrus pouch bending over the dorsal side of the acetabulum so that its posterior end lay close to the dorsal surface of the body. He distinguished it from all other species of *Crepidostomum* by the fact that the testes lay closer to the posterior end than in any other species, the distance separating the posterior testis from the posterior end of the body being about one-tenth to one-eighth the total body length, but noted that specimens of *C. cornutum* and *C. metoecus* sometimes fall within this range. Hopkins suggested that *C. cooperi* could be distinguished from *C. cornutum* by the smaller relative size of the testes and the fact that the testes were often separated by some distance in the latter. Hopkins (1931) thought that *C. cooperi* most closely resembled *C. metoecus*. In his key he distinguished *C. cooperi* from *C. metoecus* on the basis of the ovary being dorsal to the posterior edge of the acetabulum (rather than posterior to the acetabulum) and the diameter of the suckers being about one-fifth body length (rather than one-tenth to one-eighth body length).

In the same paper Hopkins (1934) described *C. ambloplites* Hopkins, 1931 from a vial of Cooper's containing 10 specimens collected from *Ambloplites rupestris,* in Go-Home Bay, Ontario. However, in a footnote in this paper Hopkins declared this species to be a synonym of *C. cooperi*. Van Cleave and Mueller (1932) described *C. solidum* Van Cleave and Mueller, 1932 from *Perca flavescens* from Oneida Lake, New York. As a footnote to their description, they stated that after their paper had gone to press, Hopkins' (1931) paper describing *C. cooperi* and *C. ambloplites* appeared and having examined the variation of their forms considered their new species, *C. solidum,* and *C. ambloplites* both to be synonyms of *C. cooperi*. Hopkins (1934) concurred with their opinion.

Although Hopkins listed several criteria with which to distinguish *C. cooperi* from *C. cornutum* these criteria are not always consistent and variation in these characters overlaps between these two species. In his key to the North American species of *Crepidostomum,* Amin (1982) distinguished *C. cooperi* from *C. cornutum* on the basis of the suckers in the former being subequal (rather than the oral sucker larger than the acetabulum) and the vitellaria in the former being confluent posterior to the testes (rather than not confluent). It appears however, that these characters also overlap between species. As a result, although it appears that metacercariae of *C. cooperi* occur in mayflies or amphipods, and metacercariae of *C. cornutum* occur in crayfish, no single criterion was known to be consistently adequate for distinguishing the adults of these two species. In the present study however, it was discovered that the size of the seminal vesicle and subsequently the position of the pars prostatica, within the cirrus sac, may be such characters. In all specimens of *C. cooperi* examined, the seminal vesicle occupied only the posterior one-third of the cirrus sac and the pars prostatica was located in the posterior two-thirds of the sac, whereas in all specimens of *C. cornutum* examined, the seminal vesicle occupied the posterior two-thirds of the cirrus sac and the pars prostatica was located in the anterior one-third of the sac.

Van Cleave and Mueller (1932) described a winter form of *C. solidum* in which the cirrus sac reached as far back as the posterior border of the hind testis. They suggested that this excessive development of the cirrus sac might be a seasonal phenomenon as most of the individuals with this form of cirrus were collected in winter months. In the present study, in order to investigate this morphological phenomenon of winter forms, specimens of *C. cooperi* were collected from sunfish caught through the ice in the months of December and January. A total of 103 individuals from 10 different specimens of *Lepomis macrochirus* were examined. None exhibited the excessive development of the cirrus sac described by Van Cleave and Mueller (1932). It might however be interesting to examine specimens collected from *Perca flavescens* in winter as this is the host from which the unusual specimens were reported by Mueller and Van Cleave.

Crepidostomum cooperi appears to be one of the lease host specific of the papillose allocreadiids. To date it has been reported from the following piscine families: Anguillidae, Catostomidae, Centrarchidae, Cyprinidae, Cyprinidontidae, Esocidae, Gasterosteidae, Hiodontidae, Ictaluridae, Percidae, and Salmonidae. It has also been reported from the turtle *Chelydra serpentina* L. as well as the salamander *Necturus maculosus* (Rafinesque). It has been reported from the following provinces and states: Manitoba, New Brunswick, New Foundland, Nova Scotia, Ontario, Prince Edward Island, Quebec, Delaware, Georgia, Illinois, Kentucky, Louisiana, Michigan, Missouri, Nebraska, New York, Ohio, Oklahoma, Oregon, Pennsylvania, Tennessee, Texas, and Wisconsin.

Crepidostomum cornutum (Osborn, 1903) Stafford, 1904
(Figs. 15,26,66-68)

Synonyms: *Bunodera cornuta* Osborn, 1903
Distomum nodulosum Zeder of Wright (1884)
Stephanophiala cornuta (Osborn, 1903) Pigulevskii, 1932

Type host: "black bass, rock bass, catfish or bull heads."

Type locality: Chautauqua, New York.

Material examined: USNM No. 60155, ex *Lepomis gibbosus* (L.), Westhampton Lake, Virginia. USNM No. 60413, host and locality not given, det. by La Rue. USNM No. 51531, ex *Micropterus salmoides* (Lacepede), locality not given (one of specimens). USNM No. 51528, ex *Micropterus dolomieu,* Havana, Illinois. USNM No. 51527, ex *Chaenobryttus gulosus* (=*Lepomis gulosus* (Cuvier)), Money, Missouri. USNM No. 51529, ex *Ambloplites rupestris* (Rafinesque), Havana, Illinois. USNM No. 51525, ex *Ameiurus nigricans,* Mukush River, Canada. USNM No. 51524, ex *Micropterus dolomieu,* Georgian Bay, Ontario. USNM No. 51523, ex *A. rupestris.* USNM No. 51522, ex crayfish, Minneapolis, Minnesota. USNM No. 51521, ex *Amia calva* L., Put-in-Bay, Ohio. USNM No. 51526, ex *Lepomis humilis* (Girard), Money, Mass. USNM No. 60422, host and locality not given, det. by La Rue. HWML Nos. 18039 & 18040, ex *Ambloplites rupestris,* Wintergreen Lake, Kellogg Biological Station, Michigan. HWML No. 18038, ex eel, North Carolina. HWML No. 18041, ex *Ambloplites rupestris,* Gull Lake, Kellogg Biological Station, Michigan.

Description (based on 20 specimens): Body elongate, tapering anteriorly, length 623-2400 (1998; 345; 20), width 254-720 (589; 184; 20), body length to body width ratio 2.1: 1- 5: 1 (3.9: 1; 0.4; 19). Oral sucker with subtriangular oral aperture and three pairs of muscular papillae, measurements excluding papillae: 161-376 (285; 67; 20) long by 158-360 (276; 54; 20) wide. Dorsomedial papillae 56-110 (72; 28; 21) long by 51-99 (71; 24; 20) wide, dorsolateral 45-96 (79; 14; 20) long by 53-120 (80; 19; 20) wide, adjacent dorsal papillae bases contiguous; ratio of dorsolateral to dorsomedial papillae width 0.9: 1- 1.3: 1 (1.1: 1; 0.13; 19); ventral papillae extending laterally past margins of body proper, occasionally extending past midlevel of oral sucker. Acetabulum 113-236 (183; 35; 20) long by 120-263 (190; 36; 21) wide. Acetabulum to oral sucker width ratio 0.58: 1- 1.1: 1 (0.87: 1; 0.8; 20). Forebody 201-890 (670; 308; 20) long, hindbody 300-1000 (782; 260; 20) long. Hindbody to forebody length ratio 1.1: 1- 1.25: 1 (1.17: 1; 0.1; 20). Acetabulum to forebody length ratio 1.8: 1- 2.9: 1 (2: 1; 0.7; 19). Body width to acetabulum width ratio 1.7: 1- 3.4: 1 (2.15: 1; 0.5; 19).

Pharynx 45-101 (67; 22; 21) long by 38-74 (60; 15; 20) wide, oral sucker to pharynx length ratio 1.7: 1- 4.6: 1 (2.3: 1; 0.3; 21); esophagus 38-164 (101; 38; 21) long, cecal bifurcation midway to two-thirds distance from oral sucker to acetabulum; ceca extending almost to posterior end of body. Testes rounded, tandem, up to one testis diameter apart; anterior testis 66-232 (154; 68; 20) long by 80-221 (154; 34; 21) wide; posterior testis 131-394 (213; 89; 20) long. Genital pore posterior to cecal bifurcation. Cirrus sac sinuous, extending dorsolateral to acetabulum and at least one acetabulum length posterior to acetabulum, 272-960 (434; 78; 21) long by 120-216 (187; 34; 20) wide; containing: saccate seminal vesicle in posterior two-thirds; short prostatic vesicle and numerous prostatic cells. Ovary rounded, dextral, medial or sinistral, up to two ovary lengths posterior to acetabulum, 72-136 (100; 24; 21) long by 94-136 (103; 23- 21) wide. Vitelline follicles lateral, extending from pharyngeal region to near posterior end of body, usually not confluent in posttesticular region; seminal receptacle adjacent to ovary posteriorly. Uterus containing 5-38 (29; 8; 14) eggs, extending to posterior border of anterior testis. Eggs 72-84 (75; 4; 1; 5) long by 45-60 (53; 9; 14) wide. Excretory pore terminal; excretory vesicle extending at least to anterior testis.

Remarks

This species was originally described by Osborn (1903) as *Bunodera cornuta.* Stafford (1904) first used the new combination *Crepidostomum cornutum.* As discussed earlier *C. cornutum* most closely resembles *C. cooperi,* the main difference between the two being that the former occurs as a metacercaria in amphipods and mayflies, while the latter occurs in crayfish. In the present study it was discovered that, in all specimens of *C. cornutum* examined, the pars prostatica was located in the anterior one-third of the cirrus sac, whereas it was in the posterior one-third of the cirrus sac in *C. cooperi.* In order to test the reliability of this criterion for distinguishing the two species, published figures of additional specimens were examined for this character. Unfortunately, this detail has been neglected in most studies, probably because it is difficult to see in many specimens. Examination of additional specimens of both species for this character is necessary for confirmation of this potentially useful character.

Electron microscopy revealed that *C. cornutum* usually had a subtriangular oral aperture with obvious ventral pa-

pillae extending well beyond the border of the oral sucker proper, whereas *C. cooperi* generally had an oval oral aperture with less conspicuous ventral papillae (Compare Figs. 13 and 22). The small tegumental papillae patterns also differed between these two species.

To date *Crepidostomum cornutum* has been reported from the following provinces and states: Nova Scotia, Ontario, Quebec, Alabama, Arkansas, Delaware, Florida, Georgia, Illinois, Kentucky, Louisiana, Maine, Massachusetts, Michigan, Minnesota, Missouri, New York, Ohio, Oklahoma, Oregon, Pennsylvania, Tennessee, and Virginia. *Crepidostomum cornutum* has been most frequently reported from Centrarchidae and Ictaluridae, but on occasion it has been reported from Amiidae, Anguillidae, Salmonidae, once from the mudpuppy, *Amphiuma means,* and once from the frog, *Rana heckscheri.*

Crepidostomum farionis (Müller, 1784) Nicoll, 1909
(Figs. 22,32,69-71)

Synonyms: *Crepidostomum laureatum* (Zeder, 1800) Braun, 1900
C. transmarinum (Nicoll, 1909) Hunninen and Hunter, 1933
C. ussuriensis Layman, 1930
C. vitellobum (Faust, 1918) Hopkins, 1931
Creptotrema muelleri Coil and Kuntz, 1960
Crossodera laureata (Zeder, 1800) Dujardin, 1845
Distoma farionis (Muller, 1784) Blanchard, 1891
D. laureata Zeder, 1800
Fasciola farionis Muller, 1784
F. laureata (Zeder, 1800) Nordmann, 1840
F. truttae Froelich, 1789
Stephanophiala farionis)(Muller, 1784) Faust, 1918
S. laureata (Zeder, 1800) Nicoll, 1909
S. transmarina Nicoll, 1909
S. vitelloba Faust, 1918

Type host: *Salmo fario.*

Type locality: Unknown European locality.

Material examined: Holotype of *C. muelleri,* USNM No. 39143; ex *Salvelinus fontinalis* (Mitchill), Lake Abant, Turkey. Type of *C. vitellobum,* USNM no. 51841, ex. *Coregonus williamsoni* (=*Prosopium williamsoni* (Girard)), Louisiana. USNM No. 51532, ex *Trutta fario,* near Kempten, Bavaria. USNM No. 51536, ex *Salmo fario,* Hampshire, England.USNM No. 3650, ex mountain trout, Locke Creek, Park Co. Montana. USNM No. 32504, ex *Salvelinus malma* (Walbaum), Mackenzie River, Oregon. USNM No. 32506, ex *Salmo gairdneri* Richardson, Diamond Lake, Oregon. USNM No. 51533, ex *Salmo gairdneri,* Hatchery Lake, Loring, Alaska. USNM No. 51534, ex *Salmo clarki*) Richardson, Jordan Lake, Loring, Alaska. USNM No. 51535, ex *Salvelinus malma,* Jordan Lake, Loring, Alaska.USNM No. 51539, ex *Salvelinus fontinalis,* Roxbury Hatchery, Vermont. USNM No. 51538, ex *Salmo clarki,* Flathead Lake, Montana. USNM No. 51537, ex "trout", Fraser River, Colorado. USNM No. 8298, ex *Salvelinus fontinalis,* Alder Lake, New York. USNM Nos. 40270-40273, host not given, Yellowstone Park. USNM No. 8641, ex *Salmo iridens,* Northville, Michigan. HWML No. 18013, ex *Salmo gardneri,* Gretna Fish Hatchery, Nebraska. HWML No. 18011, ex *Salmo gairdneri,* Lake Keystone, Nebraska. HWML No. 18008 (includes 1 SEM stub), ex *Prosopium cylindraceum* (Pallas), Aishihik Lake, Yukon Territory. HWML No. 18009 (includes 1 SEM stub), ex *Salvalinus namaycush* (Walbaum), Aishihik Lake, Yukon Territory. HWML No. 18010 (includes 1 SEM stub), ex *Thymallus arcticus* (Pallas), Aishihik Lake, Yukon Territory. HWML No. 18011, ex *Salmo gairdneri,* Lake Keystone, Nebraska. USNM No. 8617, (labelled *C. transmarinum*) by Hunninen and Hunter. Additional specimens returned to L. Margolis, Pacific Biological Station, Nanaimo, British Columbia.

Description (based on 25 specimens): Body elongate, tapering anteriorly and posteriorly, length 1696-3680 (2560;418;25), width 512-1048 (790;189;25), body length to body width ratio 2.1:1-5:1 (3.4:1;0.7;25). Oral sucker with oval oral aperture and three pairs of muscular papillae, measurements excluding papillae: 144-320 (243;44.7;25) long by 184-311 (242;33.7;25) wide. Dorsomedial papillae 22-40 (32;5.4;8;13) long by 24-36 (31;4.1;11;19) wide; dorsolateral papillae 26-40 (34;4.2;13;20) long by 24-36 (31;4.1;11;19) wide, adjacent dorsal papillae bases not contiguous; ratio of dorsolateral to dorsomedial papillae width 0.8:1-1:1 (0.88:1;0.09;8); ventral papillae not extending to lateral margins of body proper, not extending past midlevel of oral sucker, 22-50 (36;7;23;40) wide. Acetabulum to oral sucker width ratio 1.2:1-2:1 (1.5:1;0.2;24). Forebody 400-760 (596;109;22) long, hindbody 1080-2648 (1592;342;22) long. Hindbody to forebody length ratio 1.6:1-5:1 (2.5:1;0.08;24). Forebody to acetabulum length ratio 1.3:1-2.4:1 (1.8:1;0.3;21). Body width to acetabulum width ratio 1.4:1-3.5:1 (2.2:1;0.5;25).

Pharynx 96-240 (170;34.2;25) long by 120-208 (164;27.5;25) wide, oral sucker to pharynx length ratio 1.1:1-1.8:1 (1.4:1;0.16;24); esophagus 12-336 (219;66.4;17) long, cecal bifurcation at level of anterior border of acetabulum; ceca extending almost to posterior end of body. Testes rounded, tandem, up to one-half testis diameter apart; anterior testis 184-400 (260;55;24) long by 184-440 (296;66.2;24) wide; posterior testis 192-392 (278;54.3;23) long by 192-416 (293;70;23) wide. Genital pore anterior to cecal bifurcation. Cirrus sac elongate-ovoid, extending dorsal to acetabulum, and at most, to posterior margin of acetabulum 360-760 (517;121;15) long by 56-152 (112;33.7;14) wide; containing: saccate seminal vesicle in posterior half; narrow, short prostatic element and numerous prostatic cells; cirrus. Ovary rounded, dextral, medial or sinistral, up to one-half an ovary length posterior to acetabulum, 130-304 (220;43;20) long by 112-272 (211;44.8;20) wide. Vitelline follicles lateral, extending from pharynx to near posterior end of body, confluent anterior to testes and in posttesticular region; seminal receptacle adjacent ot ovary posteriorly. Uterus containing 19-66 (45;17.7;25) eggs, extending to anterior border of anterior testis. Eggs 72-80 (75;4;1;5) long by 32-52 (44;7;15;44) wide. Excretory pore terminal; excretory vesicle extending at least to anterior testis.

Remarks

Müller (1784) originally described this species as *Fasciola farionis* Müller, 1784. Zeder (1800) compared specimens of his own with Froelich's specimens of *Fasciola truttae* Froelich, 1789 and declared that both were identical with *Fasciola farionis* which he subsequently redescribed under the new name *Distoma laureatum* Zeder, 1800. Hopkins (1934) noted that it was evident that *D. laureatum* was a synonym of *Crepidostomum farionis*.

There has been some discussion as to the identity of the North American and European forms of this species. Nicoll (1909) suggested that the North American specimens identified by Linton (1893) and Stafford (1904) as *Crepidostomum laureatum* are identical with each other but not with *Crepidostomum laureatum* (Zeder, 1800) Braun, 1900. He erected the new genus *Stephanophiala* to separate them from *C. metoecus*. He named the new species *Stephanophiala transmarina*. Hunninen and Hunter (1933) concurred and suggested that the European form was closely related to the North American forms but it was not identical with them. They redescribed the large North American form as *Crepidostomum transmarinum* and also recognized *C. vitellobum* of Faust as valid.

Faust (1918) recognized two species within the genus *Stephanophiala: S. farionis* and a new species, *S. vitellobum* Faust (1918). In addition, Faust (1918) mentioned that, although the papillose allocreadiids had been uniformly described as aspinose, he observed a small percent of specimens with "spines" on the tegument in the region dorsal and lateral to the oral sucker and he presented a figure of these structures. From the figure it is obvious that Faust was referring to the surface papillae seen clearly in the present study with scanning electron microscopy (Fig. 22). Consequently, this species should not be considered as spined.

Hopkins (1934) examined North American and European specimens and concluded that the European and American specimens differed only slightly and therefore were conspecific. Examination of numerous specimens in the present study leads me to concur with Hopkins.

To date *C. farionis* has been reported from the following Canadian Provinces: Alberta, British Columbia, Manitoba, New Brunswick, Newfoundland, Nova Scotia, Ontario, Prince Edward Island, Quebec, and the Yukon Territory. In addition, it has been reported in the U.S.A. from the following States: Alaska, California, Colorado, Georgia, Idaho, Montana, Nebraska, New York, Oregon and Wyoming. Finally, *C. farionis* has been reported from the following additional countries: Austria, Czechoslovakia, Denmark, England, Finland, France, Germany, Ireland, Norway, Poland, Rumania, Scotland, U.S.S.R, Wales, and Yugoslavia. Most records of *C. farionis* are from Salmonidae, but it has also been occasionally reported from Percidae, Acipenseridae, Cottidae, Anguillidae, Gasterosteidae, Esocidae, and Gadidae.

Crepidostomum ictaluri
(Surber, 1928) Van Cleave & Mueller, 1934
(Figs. 18,29,72-74)

Synonyms: *Megalogonia ictaluri* Surber, 1928.

Type Host: *Ictalurus punctatus* (Rafinesque), channel catfish.

Type Locality: Mississippi River, St. Paul, Minnesota.

Material examined: Holotype, USNM No. 7966, ex *I. punctatus*, Mississippi River, St. Paul, Minnesota. Paratypes, USNM No. 7967, ex *I. punctatus*, Mississippi River, St. Paul Minnesota. USNM No. 51705, ex *I. punctatus*, Mouth of Rock river, Illinois; det. by Walz (1933). USNM No. 51706, ex *I. punctatus*, Havana, Illinois; det. by Hopkins. USNM No. 51723, ex *I. punctatus*, Musatine, Iowa; det. by Hopkins. USNM No. 74750, ex *Ictalurus melas* (Rafinesque), Wild Rice River in North Dakota; det. by Sutherland

and Holloway (1979). HWML No. 21492, ex *Noturus gyrinus* (Mitchill), Red Cedar River, Barron Co., Wisconsin. HWML No. 18026 (includes one SEM stub), and HWML No. 18050 ex *I. punctatus,* Bluestem Lake, Nebraska. HWML No. 18027 ex *Lepomis macrochirus* , Bluestem Lake, Nebraska. HWML Nos. 18025 and 18049 ex *I. punctatus,* Wagontrain Lake, Nebraska.

Description (based on 20 specimens): Body tapering anteriorly, length 603-1480 (855;250;20), width 280-587 (418;88.6;20), body length to body width ratio 1.43:1-3.7:1 (2.1;1;0.66;20). Oral sucker with circular aperture and three pairs of muscular papillae, measurements excluding papillae: 94-165 (135;18.1;20) long by 108-168 (145;17.6;19) wide. Dorsomedial papillae 11-22 (17;4.1;5;9) long by 15-34 (22;6.8;8;15) wide; dorsolateral papillae 11-20 (16.2;3.2;7;9) long by 12-29 (19;4.7;10;15) wide, adjacent bases of dorsal papillae not contiguous; ratio of dorsolateral to dorsomedial papillae width 0.69:1-1.08:1 (0.86:1;0.13;7); ventral papillae not extending laterally beyond body proper, 15-28.5 (19.5;5.5;13;22) wide. Acetabulum 131-216 (171;22.4;19) long by 113-188 (156;23.4;18) wide. Acetabulum to oral sucker width ratio 0.83:1-1.23:1 (1.06:1;0.08;20). Forebody 175-325 (237;38.8;14) long; hindbody 422-660 (527;75.5;14) long. Hindbody to forebody length ratio 1.79:1-2.73:1 (2.24:1;0.27;14). Forebody to acetabulum length ratio 1.2:1-1.63:1 (1.39:1;0.17;14). Body to acetabulum width ratio 1.95:1-3.4:1 (2.7:1;0.39;18).

Pharynx 38-85 (60;11.1;19) long by 34-72 (56.5;8.2;19) wide, oral sucker to pharynx length ratio 1.94:1-3:1 (2.3:1;0.3;19); esophagus 38-90 (71;22.8;4) long, cecal bifurcation one-half distance from oral sucker to acetabulum; ceca extending almost to posterior end of body. Testes bilobed, usually appearing as one anterior and one posterior pair of opposite testes; left anterior testis 90-188 (127;45;14) long by 80-256 (145;42.5;14) wide; left posterior testis 114-263 (153;40.9;15) long by 100-224 (145;40.4;15) wide; right anterior testis 95-263 (133;41.3;14) long by 95-188 (128;26.6;14) wide; right posterior testis 115-281 (151;44.7;13) long by 80-200 (132;34.6;14) wide. Genital pore immediately posterior to, or ventral to cecal bifurcation. Cirrus sac elongated, extending to posterior border of acetabulum, ocassionally slightly beyond, 210-600 (306;103;15) long by 31-60 (47;6.9;15) wide; containing: coiled internal seminal vesicle in posterior half; short prostatic element; thick walled, muscular cirrus. Ovary dextral or sinistral; immediately posterior to, or overlapping acetabulum; 88-144 (113;21.9;15) long by 50-169 (120;29.3;15) wide. Vitelline follicles lateral, extending from oral sucker to near posterior of body, confluent in posttesticular region; seminal receptacle adjacent to ovary posteromedially. Uterus containing 1-20 (7.7;5.7;17) eggs, posterior extent ranging from anterior border of anterior testis to near posterior border of posterior testis; eggs 52-80 (64.5;7.7;12) long by 30-48 (37.6;5.5;12) wide; not embryonated when laid. Excretory pore terminal; excretory vesicle extending as far as middle of anterior testis.

Remarks

Surber (1928) erected the genus *Megalogonia* to contain *M. ictaluri* that he had described from channel catfish in Minnesota. He suggested that this species differed from *Crepidostomum* in possessing one pair of lateral papillae, four testes, and an incomplete Laurer's canal. Walz (1933) and Hopkins (1933, 1934) corrected Surber's description to include the four dorsal papillae of the oral sucker and a complete Laurer's canal.

Walz (1933) accepted the presence of four testes, but Hopkins (1933, 1934) suggested that Surber's description of four testes was a misinterpretation. Hopkins believed that there were two testes each divided by a median longitudinal constriction into right and left lobes. Both investigators presented essentially the same figure of the testes and associated ducts: short ducts that emerge from the right and left lobes of each testis and join medially; a long duct extending from each junction to the base of the cirrus sac. Walz (1933) considered the short ducts to be vasa efferentia and the long ducts to be vasa deferentia; Hopkins (1934) apparently considered the "short ducts" to be testicular bridges and the long ducts to be vasa efferentia.

Hopkins (1934) questioned the validity of *Megalogonia,* and Van Cleave and Mueller (1934) actually placed *Megalogonia* in synonymy with *Crepidostomum.* The latter authors observed that these two genera were separated on the basis of a single character that they considered to be somewhat variable; the same tendency toward testicular division had been observed by them in *C. cooperi.*

Whether *C. ictaluri* has two divided testes, or four separate testes, this single character difference is considered to be insufficient evidence to support recognition of a separate genus. The testicular condition is therefore considered to be an autapomorphy (idiosyncratic character) for *C. ictaluri.*

To date *Crepidostomum ictaluri* has been reported only from North America, including the following Provinces

and States: Quebec, Ontario, Florida, Georgia, Illinois, Indiana, Iowa, Kansas, Michigan, Minnesota, Nebraska, New York, North Dakota, Tennessee, Texas, and Wisconsin. In general, it appears to parasitize ictalurids, however it has occasionally been reported from centrarchids.

Crepidostomum illinoiense Faust, 1918
(Figs.17, 75-77)

Synonyms: *Crepidostomum hiodontos* Hunter and Bangham, 1932.

Type host: *Pomoxis sparoides* (Lacepede), crappie.

Type locality: Havana, Illinois.

Material examined: Cotypes, USNM No. 50162 (vial), 51541, ex *P. sparoides,* Havana, Illinois. Type of *C. hiodontos,* USNM No. 8609, ex *Hiodon tergisus* Lesueur, Lake Erie. USNM No. 51540, ex *H. tergisus,* Havana, Illinois. USNM No. 49413, ex *Hiodon alosoides,* Lake Texoma, Oklahoma. USNM No. 74751, ex *H. alosoides* (Rafinesque), Missouri River, North Dakota. USNM No. 7626, ex *H. tergisus,* Lake Pepin, Wisconsin. USNM No. 50143, ex *Anguilla rostrata* (anterior of one specimen prepared for SEM).

Description (based on 21 specimens): Body elongate, tapering posteriorly, length 400-3600 (1098;1030;19), width 109-656 (247;187;19), body length to width ratio 2.86:1-6.6:1 (4:1;1.12;18). Oral sucker with rounded aperture and three pairs of muscular papillae, excluding papillae 67-225 (112;54;15) long by 67-244 (114.4;62;16) wide. Dorsomedial papillae notched distally, 22-86 (46;22;16;9) long by 19-75 (39;19;16;9) wide; dorsolateral papillae 22-120 (56;29;15;9) long by 32-135 (62;32;15;9) wide, adjacent bases of dorsal papillae contiguous; ratio of dorsolateral to dorsomedial papillae width 1.4:1-1.9:1 (1.6:1;0.2;8); ventral papillae extending laterally past margins of body proper, and posteriorly to posterior border of oral sucker, 18 -90 (46;24;17;9) wide. Acetabulum 50-251 (115;70;19) long by 70-263 (129;65;19) wide. Acetabulum to oral sucker width ratio 0.9:1-1.7:1 (1.1:1;0.2;12). Forebody 104-896 (304;240;14) long; hindbody 190-2320 (732;737;13) long. Hindbody to forebody length ratio 1.25:1-3.33:1 (2:1;0.2;13). Forebody to acetabulum length ratio 1.48:1-3.2:1 (2.2:1;0.5;12). Body width to acetabulum width ratio 1.03:1- 3:1 (1.85:1;0.52;17).

Pharynx 19-83 (45.4;23;11) long by 19-94 (50;28;11) wide, oral sucker to pharynx length ratio 2.7:1-3.8:1 (3.1:1;0.45;9); esophagus 30-390 (139;115;10) long, cecal bifurcation two-thirds distance from oral sucker to acetabulum; ceca extending almost to posterior end of body. Testes rounded to somewhat irregular, tandem, occasionally oblique, contiguous; anterior testis 42-440 (192;158;10) long by 39-296 (165;127;10) wide; posterior testis 50-424 (183;147;10) long by 39-333 (159;119;10) wide. Genital pore ventral or immediately posterior to cecal bifurcation. Cirrus sac elongated, extending approximately one acetabulum length posterior to acetabulum, 90-752 (278;247;12) long by 22-96 (51;27.4;13) wide; containing: coiled seminal vesicle in posterior two-thirds; short prostatic vesicle with numerous prostatic cells filling sac; cirrus. Ovary dextral, medial or sinistral; immediately posterior to or up to one and one-half ovary lengths posterior to acetabulum; 27-280 (138;102;11) long by 25-248 (141;98;11) wide. Vitelline follicles lateral, extending from anterior border of acetabulum to near posterior end of body, confluent or not in posttesticular region; seminal receptacle adjacent to ovary posteriorly. Uterus containing 1-108 (29;39;11) eggs, posterior extent ranging from anterior border of anterior testis to middle of posterior testis; eggs 60-66 (62.5;1.95;10;7) long by 30-44 (39;5;10;7) wide. Excretory pore terminal; excretory vesicle extending to middle or anterior margin of anterior testis.

Remarks

When Bangham and Hunter (1932) originally described *C. hiodontos,* they noted that their specimens resembled *C. illinoiense* in that the median dorsal papillae were distally notched. They suggested however, that *C. hiodontos* could be distinguished from *C. illinoiense* on the basis of the following characters: sucker ratio (the acetabulum being slightly larger than the oral sucker rather than smaller), a much longer esophagus, a somewhat shorter cirrus sac, and a greater number of eggs. Hopkins (1933) listed *C. hiodontos* as a synonym of *C. illinoiense.* In 1934 Hopkins suggested that the differences between the two species were based entirely on errors in Faust's description. Hopkins corrected the description of *C. illinoiense* to include an oral sucker nearly equal to the acetabulum, an esophagus longer than the pharynx, and a cirrus sac extending only to the ovary.

Based on the Illinois specimens, *C. illinoiense* was originally characterized as a minute worm, less than a millimeter in length, with very few eggs (fewer than 10 eggs). However, Self (1954) reported specimens from *Hiodon alosoides* in Lake Texoma, Oklahoma, that were up to 5.5 mm long by 0.48 mm wide. Based on these specimens he emended the description to include: the larger body size, an esophagus up to five times as long as the pharynx, a pharynx as small

as one-fourth the diameter of the oral sucker, and a distinct neck extending from behind the oral sucker to the level of the cecal bifurcation. The larger specimens may have up to 108 eggs, and it seems possible that they are merely older and more mature than the smaller specimens reported earlier. Further study of these larger forms could however, prove interesting.

The distribution of *C. illinoiense* is restricted to North America. Locality records include the following provinces and states: Manitoba, Ontario, Illinois, New York, North Dakota, Oklahoma, and Wisconsin. Host records indicate that *C. illinoiense* parasitizes members of the following piscine families: Centrarchidae, Hiodontidae, and Percidae.

Crepidostomum isostomum Hopkins, 1931
(Figs. 78-80)

Synonyms: *Crepidostomum canadense* Hopkins, 1931
C. laureatum (Zeder) of Cooper (1915) partim.

Type host: *Aphredoderus sayanus*)(Gilliams), pirate perch.

Type locality: East Lake Fork (drainage ditch), Champaign Co., Illinois.

Material examined: Holotype, USNM No. 51542, ex *A. sayanus,* East Lake Fork, Champaign Co., Illinois. Cotype of *C. canadense* (partial specimen), USNM No. 51519, ex *Boleosoma nigrum* (Rafinesque), Go Home Bay, Ontario; coll. by Cooper. HWML No. 21493, ex *Etheostoma nigrum,* O'Neil creek, Chippewa Co., Wisconsin; HWML No. 21494, ex *Etheostoma nigrum,* Red Cedar River, Barron Co., Wisconsin.

Description (based on 4 specimens): Body elongate, tapering anteriorly and posteriorly, length 1133-2456 (1988;585;3), width 333-456 (407;65.2;3), body length to body width ratio 4:1-5.4:1 (4.8:1;0.7;3). Oral sucker with subtriangular aperture and three pairs of muscular papillae, measurements excluding papillae: 154-206 (167;40;4) long by 124-194 (165;30;4) wide. Dorsomedial papillae 26-86 (57;25;3;6) long by 51-84 (67.3;11.4;4;8) wide; dorsolateral papillae 30-74 (57.4;19;3;6) long by 38-64 (53;12;4;8) wide, adjacent dorsal papillae contiguous at bases; ratio of dorsolateral to dorsomedial papillae width 0.6:1-0.98:1 (0.77:1;0.15;4); ventral papillae extending laterally beyond body proper, and posteriorly to midlevel of oral sucker, 38-78 (60;14;4;7) wide. Acetabulum 105-200 (156;40;4) long by 114-208 (173;41;4) wide. Acetabulum to oral sucker width ratio 0.92:1-1.08:1 (0.97:1;0.07;4). Forebody 344-728 (517;195;3) long; hindbody 784-1520 (1256;409;3) long. Hindbody to forebody length ratio 2.04:1-3.13:1 (2.38:1;0.9;3). Forebody to acetabulum length ratio 2.3:1-3.6:1 (2.9:1;0.68;3). Body to acetabulum width ratio 1.9:1-2.25:1 (2.1:1;0.19;3).

Pharynx 57-84 (74;12.7;4) long by 40-86 (70;20.3;4) wide, oral sucker to pharynx length ratio 1.9:1-2.74:1 (2.29:1;0.4;4); esophagus 131-230 (167;55;3) long, cecal bifurcation dorsal to anterior border of acetabulum; ceca extending almost to posterior end of body. Testes rounded to somewhat irregular, usually tandem, contiguous; anterior testis 160-240 (187;46;3) long by 160-208 (179;26;3) wide; posterior testis 158-210 (199;41;3) long by 152-264 (196;60;3) wide. Genital pore anterior to cecal bifurcation, two-thirds distance from oral sucker to acetabulum. Cirrus sac ovoid, anterior to acetabulum or slightly overlapping anterior border of acetabulum, 68-133 (110;37;3) long by 40-99 (70.3;30;3) wide; containing: coiled seminal vesicle in posterior half; short inconspicuous prostatic element with prostatic cells; muscular cirrus. Ovary rounded, dextral or sinistral, immediately posterior to or overlapping acetabulum; 75-232 (169;83;3) long by 86-192 (149;56;3) wide. Vitelline follicles lateral, extending from anterior margin of acetabulum to near posterior end of body, encroaching between testes, confluent or not in posttesticular region; seminal receptacle adjacent to ovary posteriorly. Uterus containing 4-10 (8;3.5;3) eggs, posterior extent ranging from anterior border of anterior testis to near posterior border of posterior testis; eggs 75-94 (84;8.5;2;7) long by 45-60 (54;5.5;2;7) wide. Excretory pore terminal; excretory vesicle extending to middle of posterior testis.

Remarks

Although Hopkins (1931a, 1931b) described both *C. isostomum* and *C. canadense,* he (1934) suggested that additional material might prove them identical. *Crepidostomum canadense* differed only in having somewhat smaller oral papillae, a slightly smaller sucker ratio, and vitellaria that were not confluent in the posttesticular region. Lyster (1940) collected specimens from *Boleosoma nigrum* in Quebec that displayed the full range of characters described for both species, and consequently he (1940) placed *C. canadense* into synonymy with *C. isostomum.* In addition to the distinguishing characters for recognizing *C. isostomum* noted by Hopkins and Lyster, the conspicuously short, ovoid cirrus sac, which does not extend posterior to the middle of the acetabulum, is also characteristic.

To date reports of *C. isostomum* are restricted to North America including the following provinces and states: British Columbia, Quebec, Ontario, Georgia, Illinois, Kentucky, Louisiana, Michigan, New York, Ohio, Tennessee,

and Wisconsin. Recorded hosts include members of the following piscine families: Aphredoderidae, Cottidae, Percidae and Percopsidae.

Crepidostomum opeongoensis Caira, 1985
(Figs. 14,24,81-83)

Synonyms: None.

Type host: *Hexagenia limbata* (Serville in Guerin), burrowing mayfly.

Type locality: Lake Opeongo, Algonquin Park, Ontario.

Material examined: Holotype, USNM No. 78602 and Paratypes, USNM No. 78603, HWML No. 22863, ex *H. limbata,* Lake Opeongo, Algonquin Park, Ontario (anterior of one specimen of 22863 prepared for SEM).

Description (based on 4 specimens): Body elongate, tapering anteriorly, length 2170-2720 (2540;310;3), width 486-729 (593;101;4), body length to body width ratio 3:1-4.8:1 (4.2:1;1.0;3). Oral sucker with subtriangular aperture and three pairs of muscular papillae, measurements excluding papillae: 267-300 (286;17;3) long by 284-356 (316;37;3) wide. Dorsomedial papillae 60-72 (65;6;3;6) long by 61-81 (72;6.6;3;6) wide; dorsolateral papillae 80-88 (84;5.6;2;4) long by 122-186 (156;25;3;6) wide, adjacent dorsal papillae bases contiguous; ratio of dorsolateral to dorsomedial papillae width 1.9:1-2.4:1 (2.2:1;0.3;3); ventral papillae extending laterally past margins of body proper, and posteriorly to posterior border of oral sucker, 81-113 (90;14;3;6) wide. Acetabulum 200-267 (242;30;4) long by 196-308 (247;46;4) wide. Acetabulum to oral sucker width ratio 0.7:1-0.9:1 (0.8:1;0.12;3). Forebody 551-617 (584;47;2) long; hindbody 1029-1923 (1442;450;3) long. Hindbody to forebody length ratio 2.5:1-3.33:1 (2.85:1;0.05;2). Forebody to acetabulum length ratio 2.1:1-2.4:1 (2.2:1;0.22;2). Body to acetabulum width ratio 2.33:1-2.6:1 (2.5:1;0.13;4).

Pharynx 72-104 (91;17;3) long by 68-100 (81;17;3) wide, oral sucker to pharynx length ratio 2.8:1-3.8:1 (3.1:1;0.5;3); esophagus approximately three times pharynx length, cecal bifurcation closely preacetabular; ceca extending almost to posterior end of body. Testes rounded to somewhat irregular, tandem or oblique, contiguous or nearly so; anterior testis 64-184 (133;53;4) long by 80-172 (129;41;4) wide; posterior testis 68-184 (128;50;6) long by 88-168 (129;41;4) wide. Genital pore ventral or posterior to cecal bifurcation. Cirrus sac elongate, somewhat sinuous, extending at least one acetabulum length posterior to acetabulum, 583-729 (670;77;3) long by 73-80 (76;5;2) wide; containing: coiled seminal vesicle in posterior two-thirds; inconspicuous prostatic element; thin walled cirrus. Ovary medial or slightly sinistral; at least three ovary lengths posterior to acetabulum; 80-164 (125;37;4) long by 76-156 (124;34;4) wide. Vitelline follicles lateral, extending from near posterior margin of acetabulum to near posterior end of body, confluent in postcecal region; seminal receptacle adjacent to ovary posteriorly. Uterus containing 33-58 (45;12.5;3) eggs, posterior extent to anterior border of anterior testis; eggs 40-64 (54;7.3;3;13) long by 28-44 (39;5;3;13) wide. Excretory pore terminal, excretory vesicle extending to posterior border of posterior testis.

Remarks

The original description is the only record of *C. opeongoensis* in the literature. As discussed by Caira (1985), the discovery of ovigerous individuals in an invertebrate host is unusual though not unprecedented among the Allocreadiidae. Further investigations are necessary to determine whether *C. opeongoensis* is like *C. cornutum,* which produces eggs in both the second invertebrate host as well as in the vertebrate host, or like *Pseudoallocreadium alloneotenicum* (Wootten, 1957) Yamaguti, 1971 and *P. neotenicum* (Peters, 1957) Yamaguti, 1971, which produce eggs only in the second invertebrate host, the life cycle being completely devoid of a vertebrate host.

Crepidostomum serpentinum Talbott and Hutton, 1935
(Figs. 84-86)

Synonyms: None.

Type host: *Natrix septemvitatta,* water snake.

Type Locality: Tygart River, Randolph Co., West Virginia.

Material examined: Type, USNM Helm. Coll. No. 8968, ex *N. septemvitatta,* Tygart River, Randolph Co., West Virginia.

Description (based on 1 specimen): Body elongate, tapering anteriorly and posteriorly, length 3013, width 760, body length to body width ratio 3.96:1. Oral sucker with subtriangular oral aperture and three pairs of muscular papillae, measurements excluding papillae: 338 long by 371 wide. Dorsomedial papillae 52-60 (56;5.7;1;2) long by 104-108 (106;2.8;1;2) wide; dorsolateral papillae 52-56 (54;3;1;2) long by 84-92 (88;6;1;2) wide, adjacent dorsal papillae bases contiguous; ratio of dorsolateral to dorsolmedial papillae width 0.83:1; ventral papillae extending to lateral margins of body proper, not extending

past midlevel of oral sucker, width not determined. Acetabulum 319 long by 326 wide. Acetabulum to oral sucker width ratio 0.87:1. Forebody 923 long, hindbody 1814 long. Hindbody to forebody length ratio 1.96:1. Forebody to acetabulum to forebody length ratio 2.9:1. Body to acetabulum width ratio 1:2.3.

Pharynx 116 long by 143 wide, oral sucker to pharynx length ratio 2.9:1; esophagus 270 long, cecal bifurcation two-thirds distance from oral sucker to acetabulum; ceca extending almost to posterior end of body. Testes rounded to somewhat irregular, tandem, one-half testis diameter apart; anterior testis 206 long by 281 wide; posterior testis 210 long. Genital pore posterior to cecal bifurcation. Cirrus sac sinuous, extending dorsolateral to acetabulum and at least one acetabulum length posterior to acetabulum, 548 long by 101 wide; containing: saccate seminal vesicle in posterior half; narrow, short prostatic element and numerous prostatic cells; thin walled cirrus. Ovary rounded, dextral or slightly sinistral, two and one-half ovary lengths posterior to acetabulum, 150 long by 176 wide. Vitelline follicles lateral, extending from cecal bifurcation to near posterior end of body, confluent in posttesticular region; seminal receptacle adjacent to ovary posteriorly. Uterus containing 39 eggs, extending to anterior border of anterior testis. Eggs 72-80 (75;4;1;5) long, eggs collapsed, width not measured. Excretory pore terminal; excretory vesicle extending at least to anterior testis.

Remarks

The original description is the sole record of this species. Talbott and Hutton (1935) found 24 of 25 water snakes infected with this parasite, but only one specimen was deposited in the USNM Helminthological Collection. This specimen is damaged at the level of the ventral papillae as well as near the posterior testis. Talbot and Hutton (1935) illustrated smooth, round testes of almost equal size. It was assumed that this was the usual testes shape.

Talbot and Hutton (1935) suggested that *C. serpentinum* was most closely related to *C. cooperi* but differed with respect to the longer, more muscular cirrus sac, much larger ventral papillae, and presence in a reptilean host. The cirrus sac extends to the ovary in both species. The ventral papillae of *C. serpentinum* are neither significantly longer nor wider than those of *C. cooperi*; in both species they extend slightly beyond the body proper. Differences not mentioned by Talbott and Hutton (1935) are the position of the ovary and the anterior extent of the vitellaria. In *C. serpentinum* the ovary is two or more ovarian diameters posterior to the acetabulum whereas the ovary is either contiguous with the acetabulum or lies, at most, only one-half an ovarian diameter posterior to the acetabulum in *C. cooperi*. The vitellaria extend anteriorly to the level of the cecal bifurcation in *C. serpentinum* and the pharyngeal level or even the oral sucker in *C. cooperi*.

As most papillose allocreadiids parasitize fish as adults, the presence of one of these species in a reptilian host is somewhat unusual. This host is however substantiated by the fact that Talbott and Hutton (1935) presented data on the experimental infection of a water snake with 14 of 20 metacercariae. These authors were also able to infect a species of *Cambarus*. This fact strengthens the hypothesis that *C. serpentinum* is distinct from *C. cooperi* because the latter employs amphipods and mayflies rather than crayfish as intermediate hosts.

Paracreptotrematina Amin and Myer, 1982

Synonyms: None.

Type species: *Paracreptotrematina limi* Amin and Myer, 1982.

The following diagnosis is based on that of Amin and Myer (1982) as well as on data collected in the present study. Diagnosis: Body elongate, unarmed. Oral aperture ventral or ventroterminal. Oral sucker with two muscular ventral papillae. Prepharynx short; pharynx and esophagus present. Cecal bifurcation anterior to acetabulum; ceca terminating near posterior extremity of body. Acetabulum in anterior half of body or at midbody. Genital pore median, anterior to acetabulum, posterior to oral sucker. Common genital atrium very small. Cirrus sac varying in form and size in different species, reaching posterior margin of acetabulum in some, extending beyond in others; cirrus sac containing seminal vesicle, pars prostatica, and cirrus. Testes oblique or symmetrical. Ovary round or pyriform, anterior to testes; dextral, sinistral or medial, well removed from posterior end of body. Seminal receptacle adjacent to ovary posteriorly. Vitellaria mostly lateral and ventral to ceca, extending from cecal bifurcation to near posterior end of body, or vitelline follicles inconspicuous and extent unclear. Uterus narrow with muscular walls, between genital pore and posterior end of body. Inconspicuous metraterm present. Intrauterine eggs few to several thousand in number; ovoidal or ellipsoidal, with operculum and abopercular thickening; eggs deposited embryonated. Excretory pore terminal: excretory vesicle "I" shaped, dorsal to testes, reaching at least to level of testes.

Paracreptotrematina limi Amin & Myer, 1982
(Figs. 87-89)

Synonyms: None.

Type host: *Umbra limi* (Kirtland), mudminnow.

Type locality: Tichigan Lake, Racine Co., Wisconsin.

Material examined: Holotype, USNM No. 76643, ex *U. limi,* Tichigan Lake, Racine Co., Wisconsin. Paratypes, USNM No. 59689, ex *U. limi,* Coffee Creek, Trumbull Co., Ohio. Paratypes, USNM No. 76644, ex *U. limi,* Tichigan Lake, Racine Co., Wisconsin. Paratypes, HWML No. 21335, 21336 (sections), ex *U. limi,* Coffee Creek, Trumbull Co., Ohio. Paratypes, HWML No. 21337, 21338 (sections), ex *U. limi,* Saline, Washtenaw Co., Michigan.

Description (based on 11 specimens): Body elongate, tapering slightly anteriorly, length 429-1666 (905.7;362;11), width 130-333 (234;67.9;8), body length to body width ratio 3.3:1-5.3:1 (4.4:1;0.67;8). One set of fifteen gland cells extending on either side between pharynx and cecal bifurcation. Oral sucker with elongated, subtriangular aperture and one pair of muscular ventral papillae, measurements excluding papillae: 113-206 (149;32.6;10) long by 114-187 (131.6;54.3;8) wide. Ventral papillae extending to lateral margins of body proper at midlevel of oral sucker, 34-56 (44.6;9.3;7;11) wide. Acetabulum 97-169 (117;24.6;10) long by 89-150 (122;25;8) wide. Acetabulum to oral sucker width ratio 0.8:1-0.9:1 (0.85:1;0.06;8). Forebody 275-405 (319.52.5;7;) long; hindbody 243-486 (356;91;7) long. Hindbody to forebody length ratio 0.9:1-1.66:1 (1.1:1;0.18;6). Forebody to acetabulum length ratio 2.7:1-3.3:1 (3.1:1;0.26;5). Body to acetabulum width ratio 1.6:1-2.2:1 (2:1;0.2;7).

Pharynx 72-143 (92;26.6;10) long by 56-113 (81.2;33.9;3) wide, oral sucker to pharynx length ratio 1.3:1-2:1 (1.6:1;0.22;9); esophagus 40-113 (80;28;5) long, cecal bifurcation ranging from midway between oral sucker and acetabulum to anterior margin of acetabulum; ceca extending almost to posterior end of body. Testes rounded to somewhat irregular, usually oblique, occasionally symmetrical; anterior testis 89-150 (111;33.6;3) long by 57-120 (81.2;33.9;3) wide; posterior testis 73-169 (105;55.1;3) long by 57-94 (70.6;20.3;3) wide. Genital pore ventral or immediately posterior to cecal bifurcation. Cirrus sac ovoid, overlapping acetabulum to some degree, 100-248 (160.7;53.3;6) long by 48-75 (60.1;10.1;6) wide; containing: coiled seminal vesicle in posterior half; short, inconspicuous prostatic element; thin walled cirrus. Ovary medial or sinistral; immediately posterior to or overlapping acetabulum; 72-178 (102;51.1;4) long by 64-178 (95;55.2;4) wide. Vitelline extent unclear; seminal receptacle adjacent to ovary posteriorly. Uterus containing 11-23 (17;8.5;2) eggs, extending almost to posterior end of body; eggs 28-48 (36.8;10.6;2;12) long by 24-44 (34;5.5;2;12) wide. Excretory pore terminal; excretory vesicle extending to testicular level.

Remarks

Neither whole mounts nor sections give a clear indication of the full extent of the vitellaria in *P. limi.* Amin and Myer (1982) suggested that the vitellaria extend from the cecal bifurcation to "past testes" and illustrate the holotype specimen with this condition of vitellaria. Examination of the holotype specimen revealed dark staining nuclei extending from the anterior to the posterior end of the body, but no structures that could be positively identified as vitelline follicles.

To date *P. limi* has been reported from Michigan, Ohio and Wisconsin. Host records are restricted to the mudminnow *Umbra limi.*

Paracreptotrematina aquirrepequenoi
(Guzman, 1973) Amin and Myer, 1982
(Figs.90-92)

Synonyms: *Creptotrematina aquirrepequenoi* Guzman, 1973.

Type host: *Astyanax fasciatus mexicanus* (Filippi), Mexican tetra.

Type locality: Rodrigo Gomez Dam (before the mouth) Santiago, Nuevo Leon, México.

Material examined: USNM Nos. 75735 and 75736, HWML No. 20989, ex *A. fasciatus mexicanus,* San Marcos River, San Marcos, Hays Co., Texas.

Description (based on 12 specimens): Body elongate, tapering anteriorly and posteriorly, length 1280-3719 (1973;707.6;12), width 400-733 (507;104;12), body length to body width ratio 3:1-4.4:1 (3.8:1;0.67;12). Oral sucker with transversely oval aperture and one pair of ventral muscular papillae, measurements excluding papillae: 150-229 (182;26.3;12) long by 176-281 (209;29.5;12) wide. Ventral papillae extending laterally past margins of body proper, not extending beyond anterior third of oral sucker, 19-38 (30;7;12;21) wide. Acetabulum 154-244 (194;29.6;12) long by 152-274 (194;32.3;12) wide, with transverse aperture. Acetabulum to oral sucker width ratio

0.9:1-1.1:1 (0.95:1;0.07;12). Forebody 288-680 (421;157;5) long; hindbody 824-2160 (1339;494;5) long. Hindbody to forebody length ratio 2.5:1-4.35:1 (3.3:1;0.05;5). Forebody to acetabulum length ratio 1.7:1-3:1 (2.1:1;0.55;5). Body width to acetabulum width ratio 2.1:1-3.2:1 (2.6:1;0.33;12).

Pharynx 38-83 (87;12;12) long by 56-94 (67;11.3;12) wide, oral sucker to pharynx length ratio 2.7:1-4.5:1 (3.2:1;0.48;12); esophagus 6-188 (113;41.1;11) long, cecal bifurcation approximately midway between oral sucker and acetabulum; ceca extending almost to posterior end of body. Testes rounded or ovoid, oblique, posterior testis up to one length posterior to anterior testis; anterior testis 128-373 (264;57.5;12) long by 104-347 (187;61.2;12) wide; posterior testis 176-308 (281;79.6;12) long by 120-307 (186;53;12) wide. Genital pore ventral or immediately posterior to cecal bifurcation. Cirrus sac elongated, sinuous, curving around acetabulum, extending up to one acetabulum diameter posterior to acetabulum, 232-563 (347;124;9) long by 34-83 (54;16.2;9) wide; containing: saccate seminal vesicle in posterior three quarters; short prostatic element; short cirrus. Ovary dextral or sinistral, up to one ovary length posterior to acetabulum, 113-244 (158;41.9;11) long by 83-225 (141;49;11) wide. Vitellaria forming single or at most double row of follicles ventral or lateral to ceca, extending from level of cecal bifurcation to near posterior end of body, not confluent in posttesticular region; seminal receptacle adjacent to ovary posteriorly. Uterus containing 23 to over 1000 eggs, extending to posterior end of body; eggs 53-66 (57;4.8;6;13) long by 30-51 (35;5.3;6;13) wide. Excretory pore terminal; excretory vesicle anterior extent not determined.

Remarks

In spite of the long ceca, Guzman (1973) placed this species in the genus *Creptotrematina* Yamaguti, 1958, which is characterized by short ceca. It was therefore justifiably transferred to *Paracreptotrematina* by Amin and Myer (1982).

To date *P. aquirrepequenoi* has been reported from the Mexican tetra, family Charachidae. Locality records include Texas, U.S.A., and Nuevo Leon, México.

Key to the Adult Papillose Allocreadiids

1. a. Two muscular oral papillae 2
   b. Four or six muscular oral papillae 3
2. a. Cirrus sac extending posterior to acetabulum; vitellaria obvious ..... *Paracreptotrematina aquirrepequenoi*
   b. Cirrus sac not extending posterior to acetabulum; vitellaria indistinct ..... *Paracreptotrematina limi*
3. a. Four muscular oral papillae ..... *Bunoderella metteri*
   b. Six muscular oral papillae 4
4. a. Uterus extending to posterior end of body 5
   b. Uterus not extending posterior to posterior testis 8
5. a. Vitellaria extending to near posterior end of body ..... *Bunodera luciopercae*
   b. Vitellaria not extending posterior to posterior testis 6
6. a. Vitellaria not extending anterior to posterior margin of acetabulum; ceca extending to posterior end of body ..... *Bunodera mediovitellata*
   b. Vitellaria extending anterior at least to cecal bifurcation; ceca extending to midhindbody, never posterior to posterior testis 7
7. a. Dorsal papillae bases contiguous, or nearly so; ascending ramus of uterus saccate in mature individuals ..... *Bunodera sacculata*
   b. Dorsal papillae bases not contiguous, nearly one papilla width apart; ascending ramus of uterus a narrow tube in mature individuals ..... *Bunodera eucaliae*
8. a. Vitellaria not extending anterior to posterior margin of acetabulum 9
   b. Vitellaria extending at least to anterior margin of acetabulum 10
9. a. Dorsolateral papillae two or more times as wide as dorsomedial papillae; greatest body width in posttesticular region ..... *Crepidostomum opeongoensis*
   b. Dorsolateral papillae less than two times the width of dorsomedial papillae; greatest body width near acetabulum ..... *Crepidostomum brevivitellum*
10. a. Dorsomedial papillae notched distally ..... *Crepidostomum illinoiense*
    b. Dorsomedial papillae rounded distally 11
11. a. Each testis deeply lobed, occasionally appearing as two testes ..... *Crepidostomum ictaluri*
    b. Each testis not lobed, never appearing as two testes 12
12. a. Cirrus with conspicuous triradiate lumen ..... *Crepidostomum auriculatum*
    b. Cirrus without conspicuous triradiate lumen 13
13. a. Ventral sucker with transverse aperture; bases of dorsal papillae one or more papillar widths apart ..... *Crepidostomum farionis*

b. Ventral sucker with round or oval aperture; bases of dorsal papillae contiguous or less than one papillar width apart.....14

15. a. Bases of dorsal papillae not contiguous 16

b. Bases of dorsal papillae contiguous 17

16. a. Cirrus sac extending over one acetabulum length posterior to acetabulum; acetabulum to body width ratio greater than 1:2.....*Crepidostomum auritum*

b. Cirrus sac not extending more than one acetabulum length posterior to acetabulum; acetabulum to body width ratio less than 1:2.....*Crepidostomum metoecus*

17. a. Ventral papillae inconspicuous, not extending past margins of body proper; dorsomedial papillae wider than dorsolateral papillae.....*Crepidostomum serpentinum*

b. Ventral papillae conspicuous, extending past margins of body proper; dorsomedial papillae approximately as wide as dorsolateral papillae.....18

18. a. Pars prostatica in anterior half of cirrus sac .....*Crepidostomum cornutum*

b. Pars prostatica in posterior half of cirrus sac .....*Crepidostomum cooperi*

ADULT CHARACTER ANALYSIS

The taxa used as members of the taxonomic outgroup for taxonomic ingroup character polarization included: *Pseudoallocreadium alloneotenicum* (Wooton, 1957) Yamaguti, 1971; *P. neotenicum* (Peters, 1957) Yamaguti, 1971; *Allocreadium isosporum* (Looss 1894) Looss, 1902; *A. transversale* (Rudolphi, 1802) Odhner, 1901; *A. kamalai* Gupta, 1956; *A. mazoensis* Beverley-Burton, 1962; *A. halli* Mueller and VanCleave, 1932; *A. ictaluri* Pearse, 1924; and *A. lobatum* Wallin, 1907. The characters were divided into two groups: I. those that could be polarized using the *taxonomic* outgroup and II. those that required the use of a *functional* outgroup for polarization (see Watrous and Wheeler, 1981). In general the latter type of character is one found in two or more states only within the taxonomic ingroup, thus polarization using taxonomic outgroups is impossible; "ventral papillae posterior extent" is an example of such a character. A preliminary cladogram was produced using the characters in group I. From this tree functional outgroups were chosen and subsequently used to polarize the characters in group II. A new tree was then constructed using the augmented data matrix.

Any of the following conditions potentially resulted in a character being omitted from the cladistic analysis. This is not to say that these characters are not useful taxonomically, i.e., for distinguishing between species; they merely are uninformative as indicators of phylogenetic relationships.

Condition 1 When a character could not objectively be broken into character states. For example, continuous characters for which the species ranges overlap.

Condition 2 When the state of a character varied among the members of any one species, even though perhaps consistent for all of the members of another species.

Condition 3 When both, or all, ingroup character states were also found in the outgroup. In such cases character polarization is not possible.

Condition 4 When the derived state of a character was found in only one species of the ingroup. Autapomorphies are uninformative with respect to taxonomic groupings.

Condition 5 When the state of a character could not be determined for all members of the ingroup.

Condition 6 When the character was found in only one state both within the ingroup and within the outgroup.

The character states are listed below for each noncontinuous character. Where a character was inappropriate for the cladistic analysis, a selected example is given and the applicable condition from the list above is cited. Where a character is appropriate for the analysis it is marked with a dagger (†) in the margin and the character state found within the outgroup (plesiomorphic state) is indicated with an asterisk (*). For those characters polarized using a functional outgroup, the outgroup is also given.

In the discussion below, the character states are listed for each noncontinuous character. The characters have been divided into two groups based on the required method of polarization. Within each group the characters are listed in the order in which they appear in the species descriptions.

I. Characters Polarized Using the Taxonomic Outgroup

1. *Body length.* This was a continuous character for which no distinct states were found. For example, the range in body length for *B. mediovitellata* overlapped at least some part of the range of each of the other 18 taxa of the ingroup. (Condition 1)

2. *Body width.* This was a continuous character for which no distinct states were found. For example, the range in body width for *B. metteri* overlapped at least some part of the range of each of the other 18 taxa of the ingroup. (Condition 1)

3. *Body length to body width ratio.* This was a continuous character for which no distinct states were found. For example, the range in this ratio for *C. auriculatum* overlapped

at least some part of the range of each of the other 18 taxa of the ingroup. (Condition 1)

4. *Oral sucker aperture shape.* Two states occurred within the ingroup: (a) oval, (b) subtriangular. Most taxa consistently exhibited one state (e.g. *C. opeongoensis* consistently had a subtriangular aperture); but, other taxa, in particular *C. cooperi,* exhibited both states. (Condition 2)

5. *Oral sucker length.* This was a continuous character for which no distinct states were found. For example, the range in oral sucker length for *B. sacculata* overlapped at least some part of the range of each of the other 18 taxa of the ingroup. (Condition 1)

6. *Oral sucker width.* This was a continuous character for which no distinct states were found. For example, the range in oral sucker width for *C. metoecus* overlapped at least some part of the range of each of the other 18 taxa of the ingroup. (Condition 1)

†7. *Dorsomedial papillae.* Two states occurred within the ingroup: (a) absent*, (b) present.

†8. *Dorsolateral papillae.* Two states occurred within the ingroup. (a) absent*, (b) present.

†9. *Ventral papillae.* One state occurred within the outgroup: (a) absent*, and another state occurred within the ingroup: (b) present.

10. *Acetabulum length.* This was a continuous character for which no distinct states were found. For example, the range in acetabulum length for *C. auriculatum* overlapped at least some part of the range of each of the other 18 taxa of the ingroup. (Condition 1)

11. *Acetabulum width.* This was a continuous character for which no distinct states were found. For example, the range in acetabulum width for *B. eucaliae* overlapped at least some part of the range of each of the other 18 taxa of the ingroup. (Condition 1)

12. *Acetabulum to oral sucker width ratio.* This was a continuous character for which no distinct states were found. For example, the range in this ratio for *C. auritum* overlapped at least some part of the range of each of the other 18 taxa of the ingroup. (Condition 1)

13. *Forebody length.* This was a continuous character for which no distinct states were found. For example, the range in forebody length for *C. illinoiense* overlapped at least some part of the range of each of the other 18 taxa of the ingroup. (Condition 1)

14. *Hindbody length.* This was a continuous character for which no distinct states were found. For example, the range in hindbody length for *B. sacculata* overlapped at least some part of the range of each of the other 18 taxa of the ingroup. (Condition 1)

15. *Hindbody to forebody length ratio.* This was a continuous character for which no distinct states were found. For example, the range in this ratio for *C. metoecus* overlapped at least some part of the range of each of the other 18 taxa of the ingroup. (Condition 4)

16. *Body to acetabulum width ratio.* This was a continuous character for which no distinct states were found. For example, the range in this ratio for *C. farionis* overlapped at least some part of the range of each of the other 18 taxa of the ingroup. (Condition 1)

17. *Pharynx length.* This was a continuous character for which no distinct states were found. For example, the range in pharynx length for *B. metteri* overlapped at least some part of the ranges of all species. (Condition 1)

18. *Pharynx width.* This was a continuous character for which no distinct states were found. For example, the range in pharynx width for *C. auriculatum* overlapped some part of the ranges of all species. (Condition 1)

19. *Oral sucker to pharynx length ratio.* This was a continuous character for which no distinct states were found. For example, the range in this ratio for *C. auritum* overlapped at least some part of the range of each of the other 18 taxa of the ingroup. (Condition 1)

20. *Forebody to acetabulum length ratio.* This was a continuous character for which no distinct states were found. For example, the range in this ratio for *C. auriculatum* overlapped at least some part of the range of each of the other taxa. (Condition 1)

21. *Esophagus length.* This was a continuous character for which no distinct states were found. For example, the range in esophagus length for *C. brevivitellum* overlapped at least some part of the range of each of the other 18 taxa of the ingroup. (Condition 1)

22. *Position of cecal bifurcation.* Four states of this character were found within the ingroup: (a) one-third the distance from the oral sucker to the acetabulum, (b) one-half the distance from the oral sucker to the acetabulum, (c) two-thirds the distance from the oral sucker to the acetabulum, (d) immediately preacetabular. Some taxa consistently exhibited one state (e.g. *C. isostomum* consistently had state (d)), other taxa exhibited two or more

states (e.g. *P. limi* exhibited state (b), (c), or (d)). (Condition 2)

†23. *Posterior extent of ceca.* Two states occurred within the ingroup: (a) ceca long, almost reaching posterior end of the body*, (b) ceca short, not extending past midhindbody.

24. *Shape of testes.* Two states occurred within the ingroup: (a) testes smooth to slightly irregular in outline*, (b) testes deeply lobed, in some cases appearing as four testes. Only one taxon, *C. ictaluri* exhibited the derived state of this character. Thus, this state is an autapomorphy for this single species. (Condition 4)

25. *Relative position of testes.* Three states of this character were found within the ingroup: (a) tandem, (b) oblique, (c) symmetrical. Some taxa consistently exhibited one state; others exhibited two states. For example, *C. metoecus* consistently had tandem testes (a); *B. eucaliae* had either oblique (b) or symmetrical (c) testes. (Condition 2)

26. *Distance separating testes.* Two states were found within the ingroup: (a) contiguous, (b) not contiguous. Some taxa consistently exhibited one state; others exhibited two states. For example, the testes of *B. mediovitellata* were never contiguous (b); *C. brevivitellum* exhibited state (a) or (b). (Condition 2)

27. *Anterior testis length.* This was a continuous character for which no distinct states were found. For example, the range in anterior testis length for *C. auritum* overlapped at least some part of the range of each of the other 18 taxa of the ingroup. (Condition 1)

28. *Anterior testis width.* This was a continuous character for which no distinct states were found. For example, the range in anterior testis width for *C. auritum* overlapped at least some part of the range of each of each of the other 18 taxa of the ingroup. (Condition 1)

29. *Posterior testis length.* This was a continuous character for which no distinct states were found. For example, the range in posterior testis length for *C. auritum* overlapped at least some part of the range of each of the other 18 taxa of the ingroup. (Condition 1)

30. *Posterior testis width.* This was a continuous character for which no distinct states were found. For example the range in posterior testis width for *C. illinoiense* overlapped at least some part of the range of each of the other 18 taxa of the ingroup. (Condition 1)

31. *Position of genital pore with respect to cecal bifurcation.* Three states were found within the ingroup: (a) anterior, (b) ventral, (c) posterior. Some taxa consistently exhibited one state; other taxa exhibited two or more states. For example, the genital pore in *B. metteri* was consistently well posterior to the cecal bifurcation, (c); *B. sacculata* possessed states (a), (b), or (c). (Condition 2)

32. *Posterior extent of cirrus sac.* Two states occurred within the ingroup: (a) to ovary, (b) not to ovary. Both states were found within the outgroup: e.g. *Pseudoallocreadium alloneotenicum* possessed state (a), and *Allocreadium mazoensis* possessed state (b). (Condition 3)

33. *Cirrus sac length.* This was a continuous character for which no distinct states were found. For example, the range in cirrus sac length for *B. metteri* overlapped at least part of the ranges of all species with the exception of *B. eucaliae* and *C. isostomum.* (Condition 1)

34. *Cirrus sac width.* This was a continuous character for which no distinct states were found. For example, the range in cirrus sac width in *B. mediovitellata* overlapped at least some part of the range of each of the other 18 taxa of the ingroup. (Condition 1)

35. *Ovary position.* Three states occurred within the ingroup: (a) dextral, (b) medial, (c) sinistral. Most of the species of the ingroup exhibited two or all of these character states. (Condition 1)

36. *Ovary distance from acetabulum.* Two states occurred within the ingroup: (a) immediately posterior to, or overlapping acetabulum, (b) one or more ovary lengths posterior to acetabulum. In *C. isostomum* the ovary was consistently immediately posterior to the acetabulum; in *C. brevivitellum* it was at least one ovary length postacetabular; in *B. mediovitellata* both states occur. (Condition 2)

37. *Ovary length.* This was a continuous character for which no distinct states were found. For example, the range in ovary length for *C. isostomum* overlapped at least some part of the range of each of the other 18 taxa of the ingroup. (Condition 1)

38. *Ovary width.* This was a continuous character for which no distinct states were found. For example, the range in ovary width for *C. isostomum* overlapped at least some part of the range of each of the other 18 taxa of the ingroup. (Condition 1)

39. *Anterior extent of vitellaria.* Three states occurred within the ingroup: (a) to level of pharynx, (b) to level of anterior border of acetabulum, (c) to level of posterior border of acetabulum. All three states were found within the outgroup: e.g. *Allocreadium isosporum* possessed state (c),

A. transversale possessed state (b), and *A. kamalai* possessed state (a). (Condition 3)

†40. *Posterior extent of vitellaria.* Two states occurred within the ingroup: (a) to near posterior end of body*, (b) to midhindbody.

41. *Number of eggs.* The maximum number of eggs in some species was in the hundreds or thousands (e.g., *Bunodera* spp.), whereas the maximum number of eggs in other species was rarely greater than 100 (e.g. *Crepidostomum* spp.). Nevertheless young worms of *Bunodera* spp. and *Bunoderella* spp. at some point have only a few eggs thus explaining, for example, a range of 21-789 in *B. metteri.* Even if this character is coded as "maximum number of eggs" the character cannot be used because both states are found in the outgroup; *Allocreadium halli* generally has hundreds of eggs whereas *A. isosporum* rarely has over 50. (Conditions 3 and 1).

†42. *Posterior extent of uterus.* Two states occurred within the ingroup: (a). testicular region* (b) posterior end of the body.

†43. *Condition of ascending ramus of uterus.* Two states occurred within the ingroup: (a) narrow tube* (b) expanded sac in older individuals.

44. *Egg length.* This was a continuous character for which no distinct states were found. For example, the range in egg length for *C. opeongoensis* overlapped at least part of the ranges of all but three species of the ingroup. In addition, the range of *C. opeongoensis* overlapped at least part of the range of *C. farionis* which, in turn, overlapped the ranges of the latter three species. (Condition 1)

45. *Egg width.* This was a continuous character for which no distinct states were found. For example, the range in egg width for *B. eucaliae* overlapped at least some part of the range of each of the other 18 taxa of the ingroup. (Condition 1)

46. *Anterior extent of excretory vesicle.* three states occurred within the ingroup: (a) posterior to testes, (b) testicular region, (c) anterior to testes. Some taxa consistently exhibited one state, others possessed two of these states. For example, *B. mediovitellata* consistently exhibited state (c), *B. luciopercae* has been reported with states (b) or (c). In addition, the anterior extent of the excretory vesicle was not determined for several taxa. (Conditions 2 and 5)

47. *Position of pars prostatica.* There appear to be two states of this character within the ingroup: (a) in anterior half of cirrus sac, (b) in posterior half of cirrus sac. The state of this character was not adequately established for more than half of the taxa of the ingroup. (Condition 5)

Seven of the 47 characters in group I were appropriate for the cladistic analysis. These characters are summarized below. The codings used in the data matrix for each of the character states is given. In each case "0" is the plesiomorphic state, and "1" is the apomorphic state.

(7) Dorsomedial papillae: 0=absent; 1=present.

(8) Dorsolateral papillae: 0=absent; 1=present.

(9) Ventral papillae: 0=absent; 1=present.

(23) Posterior extent of ceca: 0=ceca long; 1=ceca short.

(40) Posterior extent of vitellaria: 0=to posterior end of body; 1=to testicular region.

(42) Posterior extent of uterus: 0=to testicular region; 1=to posterior end of body.

(43) Condition of ascending ramus of uterus: 0=narrow tube; 1= expanded into a sac.

The data matrix summarizing the states of each of the above 7 characters found in the twenty taxa of the ingroup is given in Table 1. Cladistic analysis of the data matrix in Table 1 resulted in a single most parsimonious tree (Figure 93) with a consistency index of 70%.

II. Characters Polarized Using a Functional Outgroup

48. *Dorsomedial papillae length.* This was a continuous character for which no distinct states were found. For example, the range in dorsomedial papillae length for *C. isostomum* overlapped at least some part of the range of all ingroup taxa but *B. eucaliae.* The ranges of three taxa with which *C. isostomum* overlapped, also overlapped at least part of the range of *B. eucaliae.* (Condition 1)

†49. *Dorsomedial papillae width.* Two states occurred within the ingroup: (a) less than 85 micrometers*, (b) greater than 96 micrometers. Members of the genus *Bunodera* were used as the functional outgroup.

50. *Dorsomedial papillae shape.* Two states occurred within the ingroup: (a) rounded*, (b) notched distally. Only one taxon, *C. illinoiense,* exhibited the derived state of this character. Thus, notched dorsomedial papillae is an autapomorphy for this single species. (Condition 4)

51. *Dorsolateral papillae length.* This was a continuous character for which no distinct states were found. For example, the range in dorsolateral papillae length for *C. illinoiense* overlapped at least some part of the range of each of the other 18 taxa of the ingroup (Condition 1).

Table 1. Data matrix of Group I adult characters polarized using the taxonomic outgroup. Character numbers correspond to those in the adult analysis section.

TAXA	CHARACTERS						
	7	8	9	23	40	42	43
Paracreptotrematina limi	0	0	1	0	0	1	0
P. aquirrepequenoi	0	0	1	0	0	1	0
Bunoderella metteri	0	1	1	0	0	1	0
Bunodera luciopercae	1	1	1	0	0	1	1
B. eucaliae	1	1	1	1	1	1	0
B. mediovitellata	1	1	1	0	1	1	0
B. sacculata	1	1	1	1	1	1	1
Crepidostomum metoecus	1	1	1	0	0	0	0
C. auriculatum	1	1	1	0	0	0	0
C. auritum	1	1	1	0	0	0	0
C. brevivitellum	1	1	1	0	0	0	0
C. cooperi	1	1	1	0	0	0	0
C. cornutum	1	1	1	0	0	0	0
C. farionis	1	1	1	0	0	0	0
C. ictaluri	1	1	1	0	0	0	0
C. illinoiense	1	1	1	0	0	0	0
C. isostomum	1	1	1	0	0	0	0
C. opeongoensis	1	1	1	0	0	0	0
C. serpentinum	1	1	1	0	0	0	0
OUTGROUP (see text)	0	0	0	0	0	0	0

52. *Dorsolateral papillae width.* This was a continuous character for which no distinct states were found. For example, the range in dorsolateral papillae width for *B. mediovitellata* overlapped at least some part of the ranges of all species (including *C. auritum*),except *B. eucaliae* and *C. ictaluri*. The range of *C. auritum* overlapped the ranges of the latter two species. (Condition 1)

53. *Relative positions of dorsal papillae.* Two states occurred within the ingroup: (a) bases contiguous, (b) bases not contiguous. Both states of this character occurred within the group *Bunodera* as well as within the *Crepidostomum* group. Therefore, this character cannot be polarized using the functional outgroup method. (Condition 4)

†54. *Ratio of dorsolateral papillae width to dorsomedial papillae width.* Two states occurred within the ingroup: (a) less than 1.1:1 (dorsolateral papillae approximately equal to, or narrower than dorsomedial papillae)*, (b) greater than 1.3:1 (dorsolateral papillae wider than dorsomedial papillae). Members of the genus *Bunodera* were used as the functional outgroup.

†55. *Ventral papillae posterior extent.* Two states of this character occurred within the ingroup: (a) not reaching posterior margin of oral sucker*, (b) extending to, or past posterior margin of oral sucker. Members of the following genera were used as the functional outgroup: *Bunoderella. Bunodera,* and *Paracreptotrematina.*

56. *Ventral papillae width.* This was a continuous character for which no distinct states were found. For example, the range in ventral papillae width for *B. metteri* overlapped at least some part of the range of each of the other 18 taxa of the ingroup. (Condition 1)

Three of the nine characters in group II were appropriate for the cladistic analysis. These characters are summarized below. The codings used in the data matrix for each of the character states is given. In each case "0" is the plesiomorphic state, and "1" is the apomorphic state.

(49) Dorsomedial papillae width: 0=less than 85 micrometers; 1=greater than 96 micrometers.

(54) Ratio of dorsolateral papillae width to dorsomedial papillae width: 0=less than 1.1:1; 1=greater than 1.3:1.

(55) Ventral papillae posterior extent: 0=not reaching posterior margin of oral sucker; 1=extending to, or past posterior margin of oral sucker.

Table 2. Data matrix of Group I and Group II adult characters. Group II characters were polarized using a functional outgroup. Character numbers correspond to those in the adult analysis section.

TAXA	CHARACTERS									
	7	8	9	23	40	42	43	49	54	55
Paracreptotrematina limi	0	0	1	0	0	1	0	0	0	0
P. aquirrepequenoi	0	0	1	0	0	1	0	0	0	0
Bunoderella metteri	0	1	1	0	0	1	0	0	0	0
Bunodera luciopercae	1	1	1	0	0	1	1	0	0	0
B. eucaliae	1	1	1	1	1	1	0	0	0	0
B. mediovitellata	1	1	1	0	1	1	0	0	0	0
B. sacculata	1	1	1	1	1	1	1	0	0	0
Crepidostomum metoecus	1	1	1	0	0	0	0	0	0	0
C. auriculatum	1	1	1	0	0	0	0	1	0	0
C. auritum	1	1	1	0	0	0	0	0	0	0
C. brevivitellum	1	1	1	0	0	0	0	0	1	0
C. cooperi	1	1	1	0	0	0	0	0	0	0
C. cornutum	1	1	1	0	0	0	0	0	0	0
C. farionis	1	1	1	0	0	0	0	0	0	0
C. ictaluri	1	1	1	0	0	0	0	0	0	0
C. illinoiense	1	1	1	0	0	0	0	0	1	1
C. isostomum	1	1	1	0	0	0	0	0	0	0
C. opeongoensis	1	1	1	0	0	0	0	0	1	1
C. serpentinum	1	1	1	0	0	0	0	1	0	0
OUTGROUP (see text)	0	0	0	0	0	0	0	0	0	0

The data matrix augmented with the above three characters is given in Table 2. Cladistic analysis of the data matrix in Table 2 resulted in a single most parsimonious tree (Fig. 94) with a consistency index of 77%. This cladogram allows the following systematic conclusions to be made.

(1) There is no justification for the monotypic genus *Megalogonia*. *Crepidostomum ictaluri* possesses a single autapomorphy, two subdivided testes (often appearing as four testes), which allows it to be readily distinguished from the 11 other species in the genus.

(2) The genus *Bunodera* contains four species and can be considered monophyletic on the basis of character 42 (posterior extent of the uterus). Some caution is indicated, however, because this character appears at two other points on the tree.

(3) The cladogram is consistent with Yamaguti's (1971) scheme of three genera: *Bunoderina* (consisting of 2 taxa), and the monotypic genera *Allobunodera* and *Bunodera*. However, character 43 (condition of the ascending ramus of the uterus) contradicts character 23 (posterior extent of ceca), linking *Bunodera luciopercae* with *B. sacculata*. Such a conflict in characters, with this tree topology, is best dealt with by considering the broader generic group. Thus *Allobunodera* and *Bunoderina* are considered as synonyms of *Bunodera*.

(4) While there is currently no synapomorphy for the members of the genus *Crepidostomum*, these species consistently differ from *Bunoderella* sp. and *Paracreptotrematina* spp. in their possession of dorsomedial oral papillae. In addition, members of *Crepidostomum* differ from the species in all 3 other genera in their possession of a uterus that does not extend to the posterior end of the body. Thus *Crepidostomum* should be considered to be a legitimate genus. It is predicted that future research will lead to the discovery of a synapomorphy for this group.

(5) *Crepidostomum* spp. and *Bunodera* spp. are more closely related to each other than they are to *Paracreptotrematina* spp. or *Bunoderella* sp.

(6) *Bunoderella*, although monotypic at this point, can be considered as a valid genus. It is more closely related to the group (*Crepidostomum* + *Bunodera*) than it is to *Paracreptotrematina*.

(7) The genus *Paracreptotrematina* contains two species and can be considered monophyletic on the basis of character 42 (posterior extent of the uterus). Once again caution is indicated as this character occurs at two other points on the

tree. *Paracreptotrematina* is the sister group of (*Bunodera* + *Crepidostomum* + *Bunoderella*).

LARVAL FORMS

The Life Cycle

In general, papillose allocreadiids pass through three hosts during the course of their development (Fig. 95). The life cycle usually proceeds entirely within a freshwater environment. In most cases the free-swimming miracidium enters a clam of the family Sphaeriidae where it sheds its ciliated epidermal cells, and penetrates into the host's tissue. The miracidium then develops into either a sac-like sporocyst or a sac-like redia. In general, development within the latter two larval forms is by means of polyembryony; a sporocyst produces a number of rediae, and a redia may produce a number of daughter rediae, cercariae, or a combination of the two. A daughter redia also eventually produces cercariae. It appears that sporocysts and young rediae remain near the gills and mantle of the clam, whereas mature rediae are often found near the gonads or digestive gland of the clam.

When a cercaria is released it leaves the clam and is free-swimming. It then penetrates the second intermediate host, which is generally an arthropod. It subsequently loses its tail, encysts, and develops into a metacercaria. In most cases the metacercaria excysts when the arthropod host is eaten by a vertebrate, usually a fish, less often some sort of reptile or amphibian. The metacercaria usually matures into the adult form in the digestive tract of the definitive host. In general the eggs are released into the intestine of the host and pass to the outside along with the host's fecal matter.

Apart from the fact that the presence of remnants of eyespot pigments in adult forms suggests oculate cercariae, nothing is known of the larval forms of the following species: *Crepidostomum auriculatum. C. auritum. C. brevivitellum. C. opeongoensis, Paracreptotrematina aquirrepequenoi* and *P. limi.*

Bunodera eucaliae

Larval material examined: None.

Reports in Literature: Hoffman (1950, 1955).

Miracidia

Hoffman (1950) reported miracidia within the egg 59-74 long by 23-39 wide, with cilia 6.5 long, and cephalic glands 26 long by 16 wide. He observed 12 eggs for four days and reported that none hatched. Hoffman (1950, 1955) also noted that newly deposited eggs usually contained fully formed, active miracidia, but the miracidia did not escape from the eggs.

Sporocysts None reported.

Rediae

Hoffman (1950, 1955) found that rediae developed in the fingernail clams, *Pisidium noveboracense* Prime. Hoffman (1950) noted that rediae containing cercariae were not present in April, but were present in May. He speculated that the rediae may hibernate and the cercariae may emerge only during summer months. Hoffman (1950) repoted that living rediae measured 133-197 long by 36-203 wide, and the pharynx was 23-40 long by 33-96 wide.

Cercariae

Cercariae fixed in hot 10% formalin were reported by Hoffman (1950) to have bodies 189-231 long by 63-84 wide, with tails 280-315 long by 28-42 wide: living cercariae however, had bodies 266-362 long by 43-100 wide, with tails 210-316 long by 43-72 wide. Hoffman (1950) reported that the stylet of cercariae (N=4) of *B. eucaliae* were 19-26 long by 5-8 wide.

Metacercariae

Hoffman (1950) was unable to infect caddisfly nymphs, mayfly nymphs, odonate nymphs, *Gammarus,* isopods, and sticklebacks with *B. eucaliae.* In addition, Hoffman (1955) reported that he examined *Chironomous* larvae and adults, cranefly larvae, *Anopheles* larvae, caddisfly nymphs, odonate nymphs, mayfly nymphs, beetle larvae, Belostomatidae, Gyrinidae adults, and small crayfish, but found no metacercariae. He suggested that perhaps there was no second intermediate host in the life cycle. Yamaguti (1971), however, suggested that from analogy with *B. luciopercae* it seemed almost certain that crustaceans such as Copepoda, Ostracoda, or Phylopoda would serve as second intermediate hosts for *B. eucaliae.*

Bunodera luciopercae

(Figs. 96-114)

Larval material examined: Larval forms collected from *Pisidium* variabile, *P. ferrungineum,* and *Perca flavescens* from Lake Opeongo, Algonquin Park, Ontario. HWML No. 18018.

Reports in Literature: Cannon (1970, 1971), Moravec (1969), Peters and La Bonte (1965), and Wisniewski (1958).

Miracidia

Peters and LaBonte (1965) reported that embryos were partially developed when eggs were passed, some with cilia and a fused eyespot. The epidermal cell pattern was 6,6,4,2 or 6,5,4,1. When present the 2 cells of the posterior tier were either distinctly or indistinctly separated. Up to four apical gland pores were present in a cluster on the terebratorium. A pore or pair of pores (presumably cephalic glands) were situated anteriorly, on each side of the lateral cells of the first tier; the dorsal and ventral spaces lacked pores. Three to five structures were present in the space between the cells of the first and second tiers. The excretory pores were diametrically opposite and were not accompanied by smaller round structures.

Cannon (1970, 1971) discovered that gravid *B. luciopercae* adults drop from the fish, swell in the water and then rupture, releasing the eggs; although some miracidia were fully developed in uterine eggs, the eggs were never released via the genital pore. When he mechanically released eggs into Stender dishes of water, embryonated eggs hatched, and unembryonated eggs developed normally when maintained at approximately 20 C. Cannon's description of the hatched miracidia included the following information: The body was 55-59 (55;2;5) long by 27-31 (30;2;5) wide with cilia 6 long. At least four pores were located apically in each of the spaces between the lateral cells, and three or more papillae were between the first and second tiers of plates. Additional apical structures were observed, but their number was somewhat variable. Two pigment cups formed the single, dorsal eyespot; a syncytial apical gland lay between the eyespot and the neural mass. Two flame cells, 7 long, drained into ducts that extended posteriorly, and the two excretory pores were diametrically opposite between the plates of the third and fourth tiers of plates.

Moravec (1969) found that most of the eggs obtained from adult worms contained relatively large embryos, but none contained fully developed miracidia. He reported miracidia 51-72 long by 36-42 wide with cilia 7 long, slightly longer and more dense on the anterior half of the body. The bilobed eyespot that originated as two pigmented cups was 7-9 in diameter. The apical gland was 14-16 long, and the "nerve ganglion" was near its posterior margin. He also saw two flame cells with separate ducts leading to posterior pores.

In the present study, eggs and miracidia of *B. luciopercae* were observed with SEM. The eggs had a smooth surface, and the abopercular thickening, although distinct with light microscopy, was not obvious with SEM. The terebratorium of the miracidium was ciliated, and several attempts to remove the cilia (up to 15 minutes in an ultrasonic cleaner) were unsuccessful.

Sporocysts

Wisniewski (1958) did not mention a sporocyst generation. Moravec (1969), who was able to infect *Pisidium casertanum* and *P. personatum* with miracidia of *B. luciopercae,* found that miracidia penetrated the clams and proceeded to develop into sporocysts. These sporocysts were spherical or oval, with a distinct posterior tail-like lobe. The miracidial eyespot became distinctly divided, and germ balls aggregated within the body. Fourteen days postinfection the sporocysts were 63 long by 66 wide and the tail-like extension was small but visible; after 28 days they were 75 long by 48 wide; at about a month they became spherical and the original germ balls began to develop; two months postinfection, mature sporocysts were 174 long by 237 wide (up to 312), and contained mother rediae. The surface was smooth except for a crater-like pit through which the mother rediae escaped (presumably a birth pore). The two pigmented eyespots persisted.

Cannon (1970, 1971) also reported a sporocyst stage in experimentally infected *Pisidium variabile.* He described them as thin-walled sacs surrounded by a granular coat to which host cells adhered. They grew slowly for 30 days to a maximum body size of 650 long by 200 wide and contained several rediae in various stages of development. Sporocysts degenerated after about 100 days. Cannon did not describe a birth pore in the sporocyst.

Rediae

Cannon (1970, 1971) recovered young rediae in the gill chamber of *P. variabile* that were about 120 long by 40 wide. The body wall consisted of thick, granular tegument and an inner layer of parenchymal cells. There was a shallow buccal cavity lined with minute papillae, a strong muscular pharynx, 33 in diameter, and no gut but central gland-like cells; the neural mass was posterior to the pharynx and dorsal to a clump of cells of unknown function. Young rediae had two anterior and two posterior flame cells that joined on each side to open through a lateral pore at midbody, but large rediae had up to 20 flame cells, indicating that flame cells increased in size and number as the rediae grew. Fully developed rediae entwined near the gonad, were sluggish, thin walled sacs 300-2300 long by 150-300 wide with an inconspicuous birth pore adjacent to the pharynx, and some had a distinct eyespot; they contained 25-30 cercariae and sometimes daughter rediae.

Moravec (1969) reported that mother rediae were 126-135 long by 75-78 wide, lighter in color than sporocysts and without pigmented eyespots; at the blunt

anterior end a retractable mount surrounded the mouth; the pharynx was 30-33 in diameter, a gut was lacking, and germ balls filled the posterior third of the body. Some 226 days postinfection mother rediae were 135-270 long by 54-135 wide but the pharynx remained 30-33 in diameter. Daughter rediae, which seemed to emerge through the body wall of the mother rediae, were similar to mother rediae; at 241 days postinfection they were 135-195 long by 54-90 wide with a pharynx 30 in diameter and 8 flame cells; at 303 days postinfection they were 255 long by 90 wide; daughter rediae differed from mother rediae only in the presence of numerous germ balls occupying most of the body cavity.

Cercariae

Cannon (1970, 1971) reported typical ophthalmoxiphidiocercariae 140-206(172;22;10) long by 64-80(71;7;10) wide with eyespots 11-14 (12;1;10) in diameter, stylet 17-18 (N=5) long by 7-9 (N=5) wide by 6 deep, (spine 3-4 long; N=5), and tail 166-183 (175;6;10) long by 18-24 (21;2;10) wide; tegumental inflations of the tail appeared as tail fins in lateral view. The oral sucker was 31-42 (35;3;10) in diameter with numerous small papillae; the acetabulum was 26-35 (31;3;10) in diameter with larger almost filamentous papillae that apparently secreted an adhesive substance. The digestive system with prepharynx, pharynx, esophagus, and short ceca was confined to the forebody; in the hindbody the reproductive system consisted of two diagonal testes and the female primordium. Cystogenous glands were absent and only two lateral pairs of penetration glands were present. The flame cell formula was 2[(3+3+3)+(3+3+3)] and there was an "I" shaped excretory vesicle with at least 8 glandular epithelial cells per side.

Wisniewski (1958) reported cercariae that were consistent with the cercarial size, digestive system, reproductive system and excretory system reported by Cannon (1971). However, he also described the cercariae to possess a pair of lateral tail fins, three penetration glands, the ducts of which extended lateral to the eyespots and discharged near the stylet, and glands inside the acetabulum that consisted of small pyriform cells from which a tensile substance was secreted and settled in drops around the circumference of the sucker, possibly to aid in adherence to the host.

In the present study, cercariae collected from the same host and locality as Cannon's material and conforming to Cannon's description were studied with SEM. The oral sucker was, indeed, surrounded by numerous protrusions. The acetabulum had at least five rows of tiny, filiform protrusions around its circumference; these protrusions were intermixed with seven or eight large, saccate structures. SEM indicated that the cercariae of *B. luciopercae* lack tail fins.

Metacercariae

Cannon (1970, 1971) reported experimental infections in one of 47 *Daphnia similis,* four of 10 *Hyalella azteca,* six of 11 *Crangonyx gracilis* and one of three *Siphonolurus quebecensis* that he had exposed to cercariae. Metacercariae were usually in the hemocoel adjacent to the gut. There was little change within the first three days; by the sixth day the stylet was lost, the oral sucker papillae were obvious, and the ceca extended to the posterior end of the body; fully developed metacercariae had eight lateral glands, a bladder filled with globules, and undifferentiated reproductive masses. They were infective in 12 days in *H. azteca* and measured: 265-310 (285;19;4) long, 130-180 (151;25;4) wide, oral sucker 60-85 (72;14;4) in diameter, acetabulum 60-85 (72;14;4) in diameter, anterior testis 10-20 (15;5;4) in diameter and posterior testis 14-22 (19;5;4) in diameter.

Wisniewski (1958) also reported metacercariae from the body cavity of crustaceans. Not all cercariae encysted, but those that did not, died almost instantaneously when placed in water. Metacercariae remained viable in crustaceans up to six or seven weeks, but were infective only after the oral sucker papillae had developed, which was usually after about one week.

Bunodera mediovitellata

(Figs. 115-117, 121-131)

Larval material examined: Larval forms collected from *Pisidium casertanum. Lepidostoma roafi, Psychoglypha alascensis,* and*Gasterosteus aculeatus* from Tin Can Creek, Vancouver, British Columbia. HWML No. 18020 (SEM stub of cercariae)

Reports in Literature: Caira (1981), Caira and Kennedy (In preparation).

Miracidia

According to Caira and Kennedy (in prep.) worms collected in May of 1984 were found to have many uterine eggs containing miracidia with eyespots. Worms placed in distilled water immediately began to release pale brown eggs with a relatively large operculum and an abopercular thickening. Hatched, active, miracidia were visible as soon as ten minutes after the worms were placed in a refrigerator in distilled water to induce egg release.

Caira and Kennedy found the miracidia to be variable in shape but generally tapered at both ends. The apical papilla at the anterior end was the most obvious feature of the

miracidium; it was often visible in motionless individuals still contained within the egg. Miracidia fixed in cold 2.5% glutaraldehyde were 70-100 (80;7.7;15) long by 30-40 (34;2.8;15) wide.

According to Caira and Kennedy the miracidium possessed four tiers of ciliated epidermal plates. The cilia were approximately 6 in length. The first tier consisted of six triangular plates: two dorsolateral, two lateral, and two ventrolateral. The second tier consisted of six more or less rectangular plates arranged posterior to the plates of the first tier. The third tier had two dorsolateral and two ventrolateral, somewhat square plates. The fourth tier had two squarish plates: one dorsal and one ventral. The pores and accessory papillae were not visible.

The miracidium generally had a single four-lobed eyespot dorsal to a large syncytial mass, the apical gland. Posterior to the eyespot four large cephalic gland cells were usually visible, although only two gland cells were seen in some individuals. Two flame cells lay near the posterior border of the gland cells, and their ducts extended posteriorly. A number of germinal cells were also found posterior to the large gland cells.

Sporocysts

Caira and Kennedy encountered only afew sporocysts in the gill lamellae of *Pisidium casertanum* (Poli). Sporocysts were relatively thin walled, with a layer of undifferentiated parenchymal cells. Each contained one to three rediae and generally one germ ball. Sporocysts 425-500 (458;38.2;3) long by 110-162 (134;25.2;3) wide were readily distinguished from rediae by their lack of a pharynx.

Rediae

Caira and Kennedy found young rediae in the gill lamellae as well as in the digestive gland of the clams. They ranged in body form from ovoid to elongated with a blunt or tapered posterior end. Young rediae possessed a shallow buccal cavity opening into a strong, muscular, anterior pharynx; no gut was seen. A few older rediae simultaneously containing daughter rediae and developing cercariae were occasionally seen. At least four flame cells were present in rediae of this age. The body wall consisted of a thin tegumental wall and an inner layer of undifferentiated parenchymal cells.

Mature rediae were present only in the digestive gland of the clams. These rediae were elongated, thin walled sacs, 700-1400 (1100;204;15) long by 100-350 (202;54;15) wide, that contained 14-34 (20.7;6.4;15) cercariae. The pharynxes of mature rediae were inconspicuous, as they were no larger in fully developed rediae than in young rediae.

Cercariae

According to Caira and Kennedy the cercariae were dorsoventrally flattened ophthalmoxiphidiocercariae. Specimens fixed in 2.5% glutaraldehyde had bodies 220-356 (275;35.5;15) long by 102-148 (123;15;15) wide, and tails 270-448 (333;43.5;15) long by 28-58 (41;7.3;15) wide. Scanning electron microscopy performed in the present study confirmed that lateral tail fins were lacking. The tail was covered with annular ridges that extended almost the entire circumference of the tail except for a small area along the midline of the ventral surface. This nonannular surface was ridge like in some specimens.

Caira and Kennedy described a ventral oral sucker that measured 46-66 (58;4.8;15) long by 50-64 (57;3.8;15) wide. Scanning electron microscopy performed in the present study revealed a somewhat transversely oval mouth surrounded by numerous slender protrusions. Caira and Kennedy observed a single stylet, which measured 14-22 (19;2.9;10) long by 10-12 (10.4;0.8;10) wide, located in the dorsal anterior portion of the oral sucker. The stylet was fairly robust with anterior shoulders and a tapered spine. Two distinct eyespots were present posteriolateral to the oral sucker; each was composed of many tiny pigment granules.

According to Caira and Kennedy the acetabulum, which was located approximately at midbody, was 48-76 (64;8.5;15) long by 50-72 (59;5.6;15) wide. They described the margin of the acetabulum with three to five rows of rounded protrusions that appeared to be approximately equal in size. Scanning electron microscopy in the present study confirmed this description of the acetabular protrusions. At high magnifications these protrusions appear to be filled with tiny spherical structures.

The digestive system consisted of a pharynx 14-22 (19;2.5;10) long by 16-30 (22;3.9;10) wide, an esophagus, and two short ceca that did not extend posterior to the anterior border of the acetabulum. Dorsal to the pharynx was a nerve mass. Nerve cords emerged from the left and right posterior borders of the nerve mass and extended into the tail socket. No evidence of the reproductive system was seen.

Caira and Kennedy described the excretory system as being composed of 36 flame cells, 18 on each side of the body. The flame cell formula appeared to be 2[(3+3+3)+(3+3+3)]. This formula was consistent with that found in the present study. On each side of the body the posterior three triplets of flame cells emptied into a common duct that joined a duct from the anterior three triplets of flame cells at a level posterior to the acetabulum. This common duct emptied into the excretory bladder at its anterior margin. The posterior excretory bladder was "I"

shaped and lined with a number of large, granular cells. It opened through a terminal excretory pore into the tail socket.

Caira and Kennedy observed three penetration glands on either side of the forebody of the cercaria. On each side the ducts of the outermost two gland cells entwined and passed lateral to the eyespots to open via pores near the stylet; the ducts of the innermost pair of gland cells passed medial to the eyespots and also opened via pores in the vicinity of the stylet.

Twenty-eight to 36 cystogenous glands were observed by Caira and Kennedy on either side of the body. They were generally oval in shape with large nuclei and were scattered between the eyespots and the posterior end of the body.

Metacercariae

Caira (1981) found metacercariae encysted and encapsulated within the lumen of the silk glands of larvae of the caddisflies, *Psychoglypha alascensis* Banks and *Lepidostoma roafi* Milne. She reported that the prevalence of infection was 33.7% (S=14.9; N=242) in *P. alascensis* and 3.3% (S=4.4; N=497) in *L. roafi*, and the range in the diameter of the cysts was 120-195. Six oral sucker papillae were readily visible in the metacercariae. In most metacercariae the ceca did not extend posterior to the middle of the hindbody.

Bunodera sacculata

(Figs. 118-120, 132-140)

Material examined: Larval forms collected from *Pisidium variabile* in Lake Opeongo, Algonquin Park, Ontario. HWML No. 18019 (SEM stub of cercariae).

Reports in Literature: Cannon (1971), Peters and LaBonte (1965).

Miracidia

Cannon (1971) reported that as the miracidium develops eyespot pigment is visible before flame cells or epithelial plate cells. He found that 20 C was the temperature most suitable for hatching. Formalin fixed miracidia measured 54-56 (59;7;10) long by 29-42 (34;5;10); external cilia were 6 long and arranged in four tiers of epidermal plates with a cell pattern of 6,6,4,2. At least four apical pores were present in each of the spaces adjacent to the lateral cells, and three or more papillae were present between the cells of tier one and tier two. there were two excretory pores between the third and fourth tiers; Cannon observed other apical structures (possibly gland openings) but, their number was not consistent. Internally there were two pigment cups forming a single d eyespot, a syncytial apical gland, a neural mass, two flame cells each about 7 long, with a coiled duct opening posteriorly, germinal cells and four large unicellular glands that open anteriorly.

Peters and LaBonte (1965) reported that eggs of *B. sacculata* are released undeveloped or in all stages of development. They found the epidermal plate pattern in eight specimens was 6,6,4,2 but two additional specimens had the patterns 6,6,3,2 and 6,6,5,2 respectively. There were two or more apical gland pores on the terebratorium, and cephalic gland pores, one in each of the longitudinal spaces between the cells of the first tier, up to three pores were seen in the space between the first and second tiers. In addition, there was a pair of smaller pores of unknown function in the longitudinal intercellular space at one junction of the second and third tier cells.

Sporocysts

Cannon (1971) found sporocysts predominantly in *Pisidium variabile*. The sporocysts were thin-walled sacs surrounded by a granular sporocyst coat to which host cells adhered. For the first 30 days sporocysts slowly increased in size of 200 long by 150 wide and rediae begin to escape. As the sporocysts grow miracidial eyespot pigment disperses and flame cells grow to 25-30 in diameter. No more than 21 rediae were seen at any one time in a sporocyst.

Rediae

Young rediae were elongate, 120 long by 40 wide with muscular pharynges 33 in diameter. Each had a thin granular tegument 1 thick, a layer of parenchymal cells 3 thick, a shallow buccal cavity lined with papillae, and gland-like cells that opened into the pharynx. Four lateral gland-like cells opened into the buccal cavity; there was a neural mass dorsal to a clump of cells of unknown function. On each side there were four flame cells, two anterior and two posterior that opened on each side through a midlateral pore. Young rediae were very active and were found in the gill chamber. As the rediae grew the number of flame cells increased. Large rediae had over 20 flame cells 5-20 long by 2-20 wide. Fully developed rediae were 700-1400 long by 100-200 wide, were sluggish, and generally located near the clams gonad. These rediae were elongate, thin-walled sacs with conspicuous birth pores, adjacent to the pharynges. Rediae generally contained 10-12 cercariae and occasionally contained daughter rediae.

Cercariae

Cannon (1971) reported that 10 cercariae fixed in hot formalin had the following measurements: 153-218 (174;23) long by 52-94 (75;17) wide; oral sucker 33-44 (40;3) in diameter; acetabulum 33-46(40;4) in diameter;

tail 133-200 (69;22) long by 15-28 (20;3) wide; eyespots 11-15 (13;1) in diameter. Five stylets were 15 long by 4-8 wide, 4 deep, spine 4-5 long. Cercariae were typical ophthalmoxiphidiocercariae. There was a ventrolateral nerve cord on each side from the anterior neural mass to the base of the tail. There were two diagonal testes and a female genital primordium posterior to the acetabulum. Cannon observed numerous small papillae around the oral sucker and large ones around the acetabulum. The flame cell formula was 2[(3+3+3)+(3+3+3)]. At least 16 glandular epithelial cells surrounded the "I" shaped excretory vesicle. Numerous gland-like cells occurred in the body and tail. There were three pairs of penetration glands, and cystogenous glands were present. The tail had dorsal and ventral tegumental inflations that appeared as fins in lateral view. The acetabular papillae were much more conspicuous in *B. sacculata* than in *B. luciopercae.*

In the present study cercariae of *B. sacculata* were collected from the same host and locality as those described by Cannon. Their identity was confirmed using his description. Scanning electron microscopy revealed the existence of small protrusions surrounding the oral aperture. These protrusions were villiform and were arranged in four or more rows. The protrusions on the acetabular border were much larger than the oral aperture structures, and in fact, were much larger than the acetabular protrusions in *B. luciopercae.* The acetabular protrusions were arranged in three to five rows. There appeared to be two sizes of these structures intermixed throughout the acetabular border; some protrusions were plump and round, others were slightly more slender and elongate. The size difference, however, was not as extreme as in *B. luciopercae.* Scanning electron microscopy confirmed that there were no tail fins on the cercarial tail, but there were small annular ridges throughout the length of the tail.

Metacercariae

Cannon (1971) found that metacercariae developed in 43 of 63 *Daphnia similis* and two of 20 *Moinia affinis* exposed to cercariae but not *Hyalella azteca. Crangonyx gracilis, Cambarus diogenes,* or *Siphonolurus quebecensis.* In *D. similis* the metacercariae were in the hemocoel adjacent to the gut and were infective in six days. Cannon gave the following measurements for 10 infective metacercariae: 245-290 (273;14) long by 125-210 (165;24) wide; oral sucker 65-90 (73;7) in diameter; acetabulum 65-95 (83;9) in diameter; anterior testis 26-56 (41;9) in diameter, posterior testis 50-87 (66;11) in diameter. The lateral oral papillae were visible three days after cercarial penetration and the differentiation essentially complete by the fourth day including excretory vesicle granules and light lateral glands.

Bunoderella metteri

(Figs. 141-145)

Material examined: None.

Reports in Literature: Anderson, Schell and Pratt (1965).

Miracidia

Anderson, Schell and Pratt (1965) reported that eggs were unembryonated when passed in the feces of the definitive host. In the laboratory they found that miracidia developed only in eggs kept on moist filter paper at room temperature. Thirty-five to 37 days were required for development. Miracidia were 31 to 32 long by 20 to 21 wide, and entirely covered with cilia. They contained one pair of flame cells, and four or five germ cells. Unusual though it may seem, Anderson et al. reported seeing a sac-like gut in the miracidia, but not in the rediae. They were unsuccessful in their attempts to infect young specimens of *Pisidium idahoense* Roper by allowing them to ingest embryonated eggs.

Sporocysts None reported.

Rediae

Anderson, Schell and Pratt (1965) observed rediae only in natural infections of *Pisidium idahoense.* The prevalence in clams in Oregon was 10.7% (N=128); in Idaho and Washington the prevalence was less than 1%. The greatest number of rediae found in a single clam was 18. A weakly developed pharynx was present in young rediae, but there was no gut. The pharynx was completely degenerated in mature rediae. Mature rediae were colorless, transparent, thin walled sacs that contained up to 38 cercariae and some cercarial embryos and germinal cells. The largest rediae were over 2 mm in length.

Cercariae

Anderson, Schell and Pratt (1965) reported that ophthalmoxiphidiocercariae emerged through an opening in the end of the redia. They observed a nonspinous body 340-440 long by 120-170 wide. The tail was nearly equal to the body in length when extended, but was contractile and usually drawn up towards the ventral surface of the body. The oral sucker and acetabulum were round and equal in size with diameters of 52-56. Prominent adhesive papillae were attached to the margin of the acetabulum; no papillae were seen on the oral sucker. The stylet was 17 long and had well developed shoulders at the base of a spine that curved dorsally. A pair of eyespots 6-8 in diameter were visible anterior to the pharynx.

According to Anderson et al (1965) the digestive system consisted of a prepharynx, pharynx, esophagus, and gut. The esophagus and prepharynx were each twice the length of the pharynx. The gut bifurcated midway between the pharynx and acetabulum. Four pairs of penetration glands were seen. The anterior pair had ducts that passed between the eyespot and pharynx; the posterior three pairs had ducts that passed lateral to the eyespots. No cystogenous glands were observed.

The excretory vesicle had thick cellular walls. A pair of collecting ducts joined the anterior end of the vesicle. Twenty eight pairs of flame cells were present, but a flame cell formula was not given.

Metacercariae

Anderson et al. (1965) suggested that cercariae encysted in the hemocoel of certain aquatic insects. In natural infections in Oregon, they found metacercariae in 80% of larvae and pupae of the caddisfly, *Rhyacophila grandis* Banks (N=40). The mean number of metacercariae per individual was 9.3; 35 was the greatest number found per individual. In Idaho and Washington they found chironomid larvae were also naturally infected. Mayfly nymphs (*Heptagenia* spp.) and chironomid larvae were experimentally infected, but metacercariae did not undergo further development in the mayfly nymphs.

Anderson et al. (1965) reported that metacercarial cysts from *R. grandis* had a mean diameter of 253-738 (518). Encysted metacercariae measured 707-2216 (1270) long by 239-490 (287) wide with an oral sucker diameter of 93-191 (134). Two short oral papillae projected laterally. The prepharynx was short, the pharynx was at the posterior margin of the oral sucker. The cecal bifurcation was midway between the oral sucker and the acetabulum; the ceca extended to near the posterior end of the body. An excretory bladder, filled with refractive granules, extended to the midregion of the body. Gonadal primordia were visible in mature metacercariae.

Anderson et al. (1965) were able to recover six young worms young laboratory-reared *Rana aurora* infected with fourteen metacercariae three days previously. The also successfully recovered young worms from adult *Ascaphus truei* which had been kept unfed in a cold room for three months prior to infection with metacercariae.

Crepidostomum cooperi

(Figs. 146-162)

Material examined: Larvae collected from *Sphaerium transversum* and *Hexagenia limbata* in Bluestem Lake, Nebraska. HWML No. 18021 (SEM stub with cercariae).

Reports in Literature: Choquette (1954), Esch and Hazen (1982), Hazen and Esch (1979), Hopkins (1934), Moul (1984).

Miracidia

Hopkins (1934) reported that the egg cell does not undergo cleavage while within the uterus but eggs put into pond or tap water developed: in 3 days a spherical mass without structure was formed; in five days an ovoidal embryo with two separate pigmented eyespots was formed; a mature miracidium was formed in seven days, cilia did not become active until slightly before hatching at about 10 days. He reported that the miracidium was pyriform, 65 long by 30-35 wide and 25-35 deep. Hopkins reported that the surface was completely covered with cilia, 10 long, but was not divided into plates. He noted a "pear-shaped rudimentary gut" opening at the tip of the conical papilla at the anterior end of the body, but this was probably the apical gland. The nerve mass was ventral to the eyespots; two large active flame cells were seen on either side of the body near the dorsal surface; the vibratile organelle was 7-9 long by 3-5 wide. The posterior two-thirds of the body was filled with germ cells.

In the present study miracidia from eggs released by adults taken from *Lepomis macrochirus* took five to seven days to complete their development (Fig. 154). Eyespot pigment appeared two to three days after the eggs were released from the uterus, and a fully formed eyespot was present approximately four days after release from the uterus. Specimens fixed in silver nitrate exhibited an epidermal plate pattern of 6,6,4,2. Only two pores, assumed to be excretory, were visible on the terebratorium. They were diametrically opposed between the rectangular cells of the posterior tier and the cells of the third tier. Each excretory pore was accompanied by a round, structure that stained orange-brown with silver nitrate.

Sporocysts

No sporocyst stage has been reported.

Rediae

Hopkins (1934) found rediae of *C. cooperi* in 65 of 96 *Sphaerium transversum* and one specimen of *Pisidium* sp. the rediae were of a great variety of forms. He found no regular order of mother and daughter rediae, in fact rediae often contained both daughter rediae and cercariae. Hopkins suggested that individuals containing eyespots constituted a distinct generation; they were slender, active 180-360 long by 50-70 wide with a spherical pharynx 30 in diameter and a small gut that disappeared when the rediae

matured. There were six gland cells around the pharynx with short ducts opening into the prepharyngeal invagination. Young rediae were generally found between the inner and outer layers of the gills and mantle. Rediae without eyespots had a range in form from slender to stout and contained young rediae, mature cercariae or both. As rediae were over 1000 long some reached a length of 2000. Hopkins saw no birth pore. The pharynx was 21-45 long by 21-35 wide; it did not appear to increase in size as the redia matured. The number of flame cells varied from four to 22 depending on age; they increased in size as the rediae matured. Mature rediae were generally found in the digestive gland.

In the present study one redia was examined with SEM. The ridge of the oral aperture had two cilia-like structures and the buccal cavity was lined with very minute papillae. In addition, there was a ring of cilia-like structures posterior to the oral aperture.

Cercariae

Hopkins (1934) reported an average cercarial length of 300, width of 100, and depth of 100. The tail was usually slightly longer than the body, and averaged 370 long; it lacked tail fins. The oral sucker averaged 59 long by 49 wide and the acetabulum averaged 44 long by 44 wide. Hopkins noted that both suckers were fringed with sticky protuberances that projected from the outside rim; the fringe was inconspicuous on the oral sucker but obvious on the acetabulum. The stylet was about 25 long and was embedded in a pit in the dorsal wall of the sucker. There were two large conspicuous eyespots just below the dorsal surface, lateral to the pharynx, each was about 15 in diameter. There were three large penetration glands on each side of the ventral sucker. They were pyriform or lobate and finely granular. Two of the glands had ducts that extended along the lateral margin of the body; the duct from the other gland extended forward medially; all of the ducts opened through pores on the dorsal surface near the stylet. Each gland cell was 30-45 long by 15-25 wide with a nucleus 7-9 in diameter. Forty to 50 cystogenous glands were present just below the dorsal surface from midway between the pharynx and oral sucker to the posterior end of the body. Each was 15-22 in diameter with a nucleus 5 in diameter.

According to Hopkins (1934) the narrow prepharynx was 45-60 long, the pharynx 18 long by 15 wide; there was a narrow indistinct esophagus that extended to the acetabulum and divided into two short ceca. The female primordia was in the form of a bilobed mass of small cells dorsal or immediately posterior to the acetabulum. The testes were represented by two discoidal groups of cells lying ventrally in the middle of the hindbody. The excretory bladder was a contractile tube reaching almost to the acetabulum and ending in a posterior, muscular walled outlet duct leading to a terminal pore. The wall of the bladder was composed of very large cells 20-25 long by 10-15 wide, filled with spherical granules and a spherical nucleus 5 in diameter. The flame cell formula was 2[(2+2+2)+(2+2+2)]. Each pair of flame cells consisted of one dorsal and one ventral cell.

In the present study Hopkin's cercarial description was confirmed. Scanning electron microscopy revealed that both the oral sucker and acetabulum were surrounded by protrusions. Those surrounding the oral sucker were villiform and were arranged in numerous rows. The structures surrounding the acetabulum were arranged in four to five rows and were much larger; they were of two sizes. Those on the lateral and posterior acetabular borders were large, round, plump, structures; those on the anterior border of the acetabulum were comparatively much smaller and appeared to be somewhat collapsed. Little is currently known on the structure or function of these protrusions. As mentioned by Hopkins (1934) they appear to assist the cercaria in adhering to surfaces. At high magnification (Fig. 162) these structures resemble raspberries. In one instance several protrusions were damaged and their internal contents were revealed; they appear to contain many tiny spheres, approximately 1 in diameter. They may be secretory products but further research is necessary to firmly establish this point. Scanning electron microscopy confirmed the lack of a tail fin, but revealed that the tail has numerous concentric ridges that, with the exception of a small area along the ventral surface, extend throughout the circumference of the tail surface.

Metacercaria

Hopkins (1934) reported that living, excysted metacercariae were 240-500 long and approximately one-third as wide as long. the oral sucker was 90 long by 80 wide. The acetabulum was 60 long by 70 wide, and was usually located at midbody. The oral sucker papillae were present and were similar to those in the adult except for their smaller size. There was a short prepharynx, an esophagus, and the ceca extended almost to the posterior end of the body. The cephalic glands (=penetration glands) were present but were smaller and more numerous (5-10) than in the cercariae. No cystogenous glands were seen. Long tubular cutaneous glands, abundant in the anterior end and around the sucker were present under the surface and opened to the outside through surface pores. Hopkins noted that the end of the ducts occasionally projected as small papillae on the outside surface. The excretory system

was exactly the same as that of the cercariae but the vesicle was very swollen and filled with spherical, refractive droplets. Although he examined hundreds of metacercariae at all times of the year, Hopkins never found an ovigerous metacercaria. Hopkins reported metacercariae of *C. cooperi* only from *Sphaerium transversum*, encysted within the abdominal hemocoel.

Choquette (1954) reported metacercariae of *C. cooperi* in the mayflies *Hexagenia limbata*. *H. recurvata* Morgan, and *Polymitarcys* sp. with prevalences of 80% and 20% respectively in the latter two species. Hazen and Esch (1977) reported metacercariae of *C. cooperi* in the hemocoel of the amphipod *Hyalella azteca*. Contrary to Hopkins, they reported that some of the metacercariae were ovigerous while still within the cyst.

Esch and Hazen (1982) and Moul (1984) examined the distribution of *C. cooperi* metacercariae in *H. limbata*. These investigators found that metacercariae were almost entirely restricted in distribution to the abdominal segments. Moul (1984) found that the mean intensity was 1.8 metacercariae per host, with a range of 1-5. Esch and Hazen (1982) found that the prevalence varied from 6-96% depending on the size of the host and the time of the year.

Crepidostomum cornutum
(Figs. 163-170)

Material examined: HWML No. 18017 (includes 1 SEM stub), cercariae and metacercariae collected by Turner, metacercariae ex *Procambarus clarkii*, drainage ditch near campus of McNeese State University, Lake Charles, Louisiana.

Reports in Literature: Abernathy (1937), Ameel (1937), Cheng (1957), Cheng and James (1960a, 1960b), Henderson (1938), Morrison (1969), Osborn (1903).

Miracidia

Ameel (1937) reported that on two separate occasions he was unsuccessful in his attempts to obtain miracidia from the well formed eggs laid within the cysts of old metacercariae. Ameel interpreted this result as an indication that the eggs produced by metacercariae were not fertilized. On the contrary, Morrison (1969) suggested that progenetic metacercariae of *C. cornutum* often contained viable eggs in the uterus. He noted that although these eggs occasionally contained active miracidia, they rarely hatched while under observation. The eggs usually required incubation before they hatched. Abernathy (1937) also reported that in all seasons of the year he found eggs deposited within the metacercarial cyst that were in all stages of development, some almost ready to hatch.

Ameel (1937) found that eggs collected from worms found in *Ambloplites rupestris* and *Aplites salmoides* were in the single cell stage when first laid. A large central eyespot appeared within the first week and the miracidium hatched after about two weeks incubation at 36 C. Miracidia within the eggs were approximately 60 long by 30 wide, and had a pair of flame cells and a short gut.

Sporocysts

Morrison (1969) is the only author to mention a sporocyst. Discussing the usefulness of *C. cornutum* as a laboratory animal, he suggested that "sporocysts, rediae and cercariae may be obtained from fingernail clams exposed to miracidia." However, Cheng (1957) and Cheng and James (1960b) studied the life cycle of *C. cornutum* in detail and did not observe a sporocyst.

Rediae

Henderson (1938) found 34 of 56 (60%) of *Musculium transversum texasense* Sterki infected with rediae. He described the rediae as elongate, ovoidal, and thin-walled with distinct oral and aboral thickenings, a prominent pharynx, short prepharynx, and no birth pore. Rediae contained 2-14 cercariae. Measurements of nine specimens preserved in hot 70% ethanol were 390-887 (650) long by 106-213 (160) wide.

Cheng and James (1960a, 1960b) described both first (mother) and second (daughter) generation rediae of *C. cornutum* from *Sphaerium striatinum*. According to Cheng and James (1960a), the mother rediae were found on the gills and the daughter rediae in the digestive gland (hepatopancreas); sections of the digestive gland revealed that on the average this gland enclosed 35-45 individuals.

According to Cheng and James (1960b), the mother rediae were elongate, saccular, and 352-1800 long by 68-142 wide. They reported that the degree of development did not seem to be correlated to body size; in some small specimens the body structures were more developed than in certain larger specimens. At the anterior end there was a small sucker, a short prepharynx, and a large muscular pharynx measuring 34-48 in diameter, attached to a short saccular cecum. They observed no birth pore. Fully developed specimens had a short, posterior tail.

Cheng and James (1960b) found that daughter rediae were larger, 500-2300 long by 300-500 wide than mother rediae. In one instance two cercariae were seen escaping through a birth pore located near the mouth. They estimated that the number of germ balls (presumably excluding cercariae) per redia varied from

four to 20. The number of developed cercariae ranged from two to more than 30.

Ameel (1937) found that the prevalence of infection in several thousand *Sphaerium* sp. ranged from 13-44%. He found young rediae on the gills and mantle and older rediae in the digestive gland. Ameel indicated that young rediae were motile, had a slender gut, a pharynx, and three pairs of unicellular glands next to the pharynx. Mature rediae were non-motile and elongate, with no gut, no gland cells, no birth pore and possibly even no pharynx. Rediae contained 30-40 active cercariae and some germ balls. He gave measurements of 10 mature rediae fixed in hot 10% formalin as follows: 820-1900 (995) long by 250-380 (321) wide, with an average pharynx size of 25 long by 31 wide. The pharynx size did not differ significantly between younger and older rediae.

Cercariae

Henderson (1938) experimentally correlated the cercariae and metacercariae of *C. cornutum* by exposing crayfish to cercariae. His description of the ophthalmoxiphidiocercaria is summarized here: The body was elongate and flattened dorsoventrally; the tail was slender, longer than the body proper and tapered to a point posteriorly. The tegument was covered with numerous quincuncially arranged papillae that were more numerous ventrally and laterally than dorsally. The oral sucker was subterminal, longer than wide, and the aperture was fringed with papillae that were continuous in distribution and larger than those of the body surface. The acetabulum was slightly posterior to the middle of the body, its orifice was also fringed with papillae; those around the posterior three-fourths were very large, those of the anterior fourth were much smaller. Obvious eyespots were present. The pharynx was slightly shorter than the esophagus. The cecal bifurcation was anterior to the acetabulum, and the ceca extended to the middle of the acetabulum. Three pairs of penetration glands were located lateral to the acetabulum. The ducts of the anteromedial pair extended forward medial to the eyespots, and the ducts of the others extended forward lateral to the eyespots. All three pairs open via ducts the pores of which are bunched closely around the point of the stylet. The cystogenous glands were irregular in shape but generally ovoidal and were situated near the surface of the body posterior to the eyespots; there were 49-62 (55) cystogenous glands. The female primordium was large, and posterodorsal to the acetabulum. The male primordia were small, separated by a considerable space and ventral to the excretory vesicle.

The excretory bladder, completely surrounded by large granular cells arranged in a single layer, largely filled the region posterior to the acetabulum. The lumen of the excretory bladder was continuous with the median caudal canal and variable in shape. The main collecting tubules entered the bladder anterolaterally. The flame cell formula was 2[(2+2+2)+(2+2+2)].

Henderson gave measurements of 30 specimens, killed in hot 70% ethanol, as follows: body 192-234 (213) long by 68-85 (72) wide; tail 256-291 (277) long by 24-26 (25) wide; oral sucker 43-54 (48) long by 34-42 (38) wide; acetabulum 34-42 (38) long by 30-40 (35) wide; pharynx 10-12 (11) long by 10-12 (11) wide; stylet 17-25 (21) long by 5 wide. Total cercarial length 488-525 (490); eyespot diameter 12; distance between eyespots 20-25 (23); cystogenous glands 12-17 (14) long by 5-12 (8) wide; distance from center of acetabulum to anterior end of body 102-127 (112), to posterior end 102-110 (104).

Ameel (1937) also described the cercariae of *C. cornutum*. His description was fairly consistent with that of Henderson except that he illustrated the acetabular protrusions as equal in size at all points on the margin of the sucker, whereas Henderson illustrated and verbally described two different sizes of protrusions. As Henderson's description appears to be more thorough, I am assuming that he is correct.

Cheng and James (1960b) detailed the development of the cercariae of *C. cornutum* from the germ ball stage to maturity. Their cercarial description was consistent with that of Henderson (1938), but, they did not mention the oral sucker or acetabular protrusions.

In the present study cercariae were examined with the scanning electron microscope. The presence of oral sucker protrusions was confirmed; they were slightly smaller than those of *C. cooperi*. Unfortunately, the acetabulum of each specimen was contracted making the form of the acetabular border impossible to determine.

Metacercariae

Metacercariae of *C. cornutum* were originally described from crayfish by Osborn (1903). They encysted in the heart, the gonads, and the muscles, especially those extending from the thorax to the abdomen. Osborn reported up to 40 cysts per host.

Ameel (1937) successfully infected *Cambarus immunis* with *C. cornutum*. Within two hours after exposure he found unencysted cercariae in the cardiac region; 24 hours postinfection newly encysted metacercariae were present. Ten days postinfection the metacercariae still possessed eyespots and stylets; the excretory bladder was large and conspicuous because of accumulation of many refractile granules; the oral sucker possessed papillae; and the prepharynx was shortened.

Henderson (1938) was able to experimentally infect crayfish, *Cambarus simulans* Faxon, with metacercariae of *C. cornutum*. He found that the most favorable conditions for penetration were sunlight at 38 C.

Cheng (1957) found almost 100% of *Cambarus bartoni* (Fabr.) in Sinking Creek, Virginia, infected with *C. cornutum* metacercariae. The infection ranged in intensity from 1-24 cysts per host. Each cyst measured approximately 1000 in diameter.

Abernathy (1937) found 7 of 400 males and 80% of the females of *Cambarus* sp. from Stillwater Creek, Oklahoma, infected with metacercariae of *C. cornutum*. The maximum number of cysts per male was 9; per female, 113. Most were found near the reproductive organs. She fed metacercariae to goldfish (*Carassium auratus*) and catfish (*Ameiurus melas*) and obtained a number of successful infections in both species.

Crepidostomum farionis
(Figs. 171-177)

Material examined: Eggs of *C. farionis* from *Salmo gairdneri* collected in Lake Keystone, Nebraska.

Reports in literature: Brown (1927) and Crawford (1943).

Miracidia

In the present study eggs of *C. farionis* were maintained in distilled water at room temperature and observed over a seven day period. Some zygote cleavage was seen but no eyespot development occurred during that time. This evidence suggests that the miracidia require more than seven days to complete their development.

The above result is consistent with the work of Crawford (1943) who reported that he was unable to obtain free-swimming miracidia, despite a four week observation period. Nevertheless during that time active miracidia were observed within some eggs, and empty egg shells indicated that some miracidia had escaped. The eyespot was first observed as two refractive bodies 8 in diameter that later fused into a single pigment mass; the eyespot of one miracidium measured 26 in diameter.

Sporocysts

Brown (1927) was unable to demonstrate a sporocyst stage in the life cycle of *C. farionis*.

Rediae

Crawford (1943) found elongated rediae embedded in the gills of *Pisidium* sp., of which five of 178 individuals were infected. One redia was 1750 long by 200 wide. Brown (1927) indicated that two generations of rediae were present. The mother rediae were elongate, colorless and cylindrical; they tapered at both ends and had a small anterior, sucker-like pharynx that led into a smaller, nonfunctional, sac-like intestine. Brown (1927) suggested that the mother rediae possessed a bilaterally symmetrical excretory system. On each side an anterior lateral duct received tubules from (1) a group of two large flame cells and (2) three flame cells lateral to the excretory bladder. The posterior lateral duct received tubules from eight flame cells that did not appear to be arranged in definite groups. Thus, the flame cell formula in the mother redia was given as 2[(2+3)+(8)] by Brown. Crawford (1943) suspected that as the rediae matured the number of flame cells increased but details were obscured by daughter rediae. He suggested that daughter rediae were similar in all respects with mother rediae.

Brown (1927) regularly found rediae containing cercariae attached to the gills of the *Pisidium amnicum* (Mull.), and less frequently to the gills of *Sphaerium corneum* (L.). He reported that mature rediae had a small protuberance carrying a tiny pharynx. Fully developed rediae were 2000-2500 long by 240-300 wide, and the pharynx was 60 in diameter. Brown suggested that the pharynx reached its maximum diameter of 63 in rediae measuring 650 long by 150 wide, thus further redial growth was not accompanied by pharynx growth. Brown observed a small birth pore lateral to the pharynx.

Cercariae

Brown's (1927) description of the ophthalmoxiphidiocercariae included the following information. The body was 400-520 long by 160-210 wide, and the tail was 450-600 long, or approximately equal to the body length. The two suckers were about 63 in diameter. A prepharynx was 63 long, a pharynx was 25 long, a short esophagus bifurcated anterior to the acetabulum and the ceca extended almost to the posterior end of the body. The spear-shaped stylet was dorsal to the oral sucker. Two groups of three gland cells lay anterior and lateral to the acetabulum with ducts passing anteriorly and opening via pores on either side of the stylet; on each side of the body the duct from one cell was medial to the eyespot, and ducts from the other two cells were lateral to the eyespots; finely granular, small, round cells, 48-68 in number were scattered loosely throughout the body. The excretory system on each side consisted of anterior and lateral ducts that united anterior to the ventral sucker to form a main, convoluted collecting canal. The collecting canal from each side ran posterior to the ventral sucker to enter the anterior border of the elongated excretory bladder. The flame cell

formula was 2[(2+4)+(4+3+3+3)] for a total of 38 flame cells.

Crawford's (1943) measurements of three cercariae fixed in 10% formalin were slightly smaller than those reported by Brown (1927): body 302 long by 132 wide, eyespots 20 long by 19 wide, stylet 21 long, oral sucker and acetabulum 53 in diameter, prepharynx 9 long, pharynx 22 in diameter.

Metacercariae

Brown (1927) found larvae of the mayfly, *Ephemera danica* (Mull.), infected with what appeared to be the encysted state of the cercaria described above. The cysts were pyriform, 264-400 long by 308-480 wide and usually in the fat body tissue of the larvae. Encysting cercariae favored the ventral surface of the abdomen near the bases of the seventh to fifth pairs of gills; the number of cysts per mayfly varied from one to 26, but usually there were seven to nine. Brown found that the metacercariae were usually curled within the cyst, the eyespots were usually visible, and the excretory vesicle was enlarged and filled with small spherical granules of varying sized. The oral sucker had six papillae, and the stylet had disappeared.

Crawford (1943) reported that *Ephemera* sp. hosted metacercariae of *C. farionis*. He found the cysts to be oval rather than pyriform. He reported that the excretory granules were free within the bladder lumen, or intracellular. Extruded cells were oval, had a single nucleus, and contained a large, fluid-filled vesicle. Based on experimental evidence Crawford suggested that metacercariae reach full size two to three weeks after infection.

Baylis (1931) reported metacercariae of *C. farionis* from the amphipod *Gammarus* sp. However, his figure of an excysting metacercaria is not entirely consistent with *C. farionis:* the papillae are essentially contiguous and the pharynx is very small with respect to the oral sucker. In fact, these metacercariae are much more consistent in morphology with *C. metoecus*. Baylis' only evidence for considering these metacercariae to be *C. farionis* was that *Gammarus* sp. was the principal food of trout in the area. At that time it was not known that *C. metoecus* also parasitizes salmonid fish. Further investigations are necessary before amphipods can be considered to be a second intermediate host for *C. farionis*.

Crepidostomum ictaluri

(Figs. 178-186)

Material examined: Larvae collected from *Sphaerium sulcatum* and *Hexagenia limbata* from Bluestem Lake, Nebraska. HWML No. 18022 (SEM stub with cercariae and rediae).

Reports in Literature: Amato (1979), Hopkins (1934), Moul (1984), Seitner (1951).

Miracidium

Hopkins (1934) reported that after eggs were laid in water, miracidia of *C. ictaluri* developed within the egg shell. He described the miracidia as having two fused, pigmented, concave eyespots, a rudimentary gut, two flame cells, and a coat of long cilia covering the body. Hopkins suggested that there were no "cuticular plates".

Amato (1979) reported that *C. ictaluri* had operculated eggs that were unembryonated when laid; miracidia hatched after eight to 14 days incubation at 22 C. Living miracidia were pyriform in shape and the apical papilla was not distinctly visible. She observed a pair of flame cells posterior to the middle of the larva; eyespots were located at the base of the first tier of epidermal plates. Specimens fixed in 0.5% silver nitrate measured 30-48 long by 23-30 wide, with a uniform, dense layer of cilia 6 long. Contrary to Hopkins, epidermal plates were seen; Amato observed a pattern of 6,6,4,2. She found six small duct openings at the tip of the apical papilla and six small openings at the base of the papilla at junctions of the epidermal plates of the first tier. The posterior tier was composed of two rectangular cells; the excretory pores were diagonally opposite from each other at the external corners of the plates.

In contrast to Amato (1979), Seitner (1951) found only two structures (presumably gland openings) on the terebratorium of *C. ictaluri,* and no structures between the first and second tiers. He observed that each excretory pore was flanked by a pair of smaller structures. He reported that silver impregnated miracidia measured 35 35 long by 23 wide.

In the present study eggs of *C. ictaluri* were found to be unembryonated when laid. Miracidial development took five to six days to complete at 24 C (Fig. 178). Eyespot pigment appeared between two to three days after release from the uterus; the pigment migrated to the center of the body in the anterior half of the miracidium and formed a compact mass. The beating of flame cell cilia was visible approximately three days after release from the uterus.

Sporocysts

None reported.

Rediae

Hopkins (1934) reported that rediae were long, slender, had a rudimentary gut, and a large pharynx. They

developed in fingernail clams of the family Sphaeriidae and gave rise to rediae or cercariae.

Amato (1979) found redia in the visceral cavity of *Sphaerium simile*. Young redia were in the gill tissue. They were characterized by their small size, large pharynx, possession of intestinal ceca, and lack of cercariae. Mature rediae were found in the digestive gland and other visceral organs. The pharynx was approximately the same size as that of immature rediae but appeared smaller because of the larger size of these rediae; no cecum was seen in mature rediae. The maximum number of cercariae in these rediae was 30. A birth pore was seen at the anterior region close to the oral aperture. Flame cells were obtullate, and measured 11 long by 6-16 wide at the anterior margin; a maximum of 11 flame cells was counted on one side. Scanning electron microscopy demonstrated that the tegument was rugose with numerous rows of transverse folds extending serially around the body. The collar of the oral aperture had many small knobs with a cilium-like structure. Small knobs were also seen on the body surface. A slit-like aperture (presumably a birth pore), completely covered with small papillae, was seen adjacent to the oral aperture.

Cercariae

Hopkins (1934) and Amato (1979) both reported an ophthalmoxiphidiocercaria for *C. ictaluri*. Amato (1979) recorded the following measurements for 10 living cercariae (ranges are given with means in parentheses): body 204-336 (270) long by 53-88 (70) wide; tail 240-306 (285) long by 20 wide; oral sucker 46-69 (54) long by 32-44 (37) wide; acetabulum 41-51 (46) long by 40-46 (45) wide; sucker ratio 1:1.05-1:1.25 (1:1.22); prepharynx 16-32 (24) long; pharynx 10-11 (11) long by 6-11 (8) wide; eyespot 10 long, stylet 16 long, excretory vesicle 51-93 (70) long.

According to Amato (1979) the body and tail appeared to be close to the same length. Scanning electron microscopy performed by Amato (1979) revealed a smooth tegument with numerous ciliated bulbs. The oral sucker had several rows of minute protrusions surrounding its aperture. The acetabulum was approximately equatorial and protrusible. The border of the acetabulum was encircled by numerous protrusions, which were smaller on the anterior margin then on the lateral or posterior margins. The anterior protrusions were slender, villiform, and densely packed; the larger, lateral and posterior protrusions were rounded and arranged in three parallel rows. When the acetabulum was retracted against the ventral surface the margin rolled inward. The acetabular lumen was uniformly lined with very small, knob-like structures. A narrow prepharynx, and pharynx was visible. Genital primordia were undifferentiated. the excretory vesicle was lined with tall epithelial cells; the excretory pore opened in the tail socket. The flame cell formula was 2[(2+2+2)+(2+2+2)]. Twenty-five to 45 cystogenous glands were seen per cercaria. These glands were more numerous in the posterior region of the body than in the anterior region.

In the present study the cercarial description of Amato was confirmed. In addition, the cercariae were found to possess three pairs of penetration glands. These glands were located at the anterior margin of the acetabulum in close proximity to one and other; their ducts were difficult to trace.

Metacercariae

According to Amato (1979) the oral sucker was smaller than the acetabulum and possessed six inconspicuous papillae; the acetabulum was approximately equatorial. Eyespots, or scattered pigment granules were seen in most specimens. The digestive system was similar to that of the adult. As the metacercaria matured, the ceca gradually extended to the posterior tip of the body, and the single genital primordium differentiated into an ovary and two bilobed testes. The excretory vesicle was distended with refractile excretory droplets, and the flame cell formula was the same as that of the cercaria.

Amato (1979) gave the following measurements for 10 metacercariae (the range is given followed by the mean in parentheses): Body 183-408 (231) long by 62-132 (91) wide; oral sucker 41-60 (48) long by 41-60 (47) wide; acetabulum 39-69 long by 46-74 (62) wide; sucker ratio 1:1.12-1:1.80 (1:1.35); the ventral oral papillae were 9-11 (11) long, the dorsal oral papillae were 4-6 (4) long; prepharynx 2-4 (2) long; pharynx 16-30 (21) long by 11-23 (16) wide; eyespots 9 long; ovary 20-30 (20) long by 20-30 (20) wide; anterior testes 23-46 (37) long by 23-46 (28) wide; each lobe of posterior testis 25-46 (31) long by 18-41 (23) wide.

Moul (1984) examined the distribution of the metacercariae of *C. ictaluri* on larvae of *Hexagenia limbata* and found that the prevalence was 100% in both sexes, with a mean intensity of 143.2 in females and 112.4 in males. The range in intensity was 1-444 cysts per mayfly larva. She found that metacercariae were particularly numerous on abdominal segments two through six, and were more numerous on the gills than on the abdomen proper.

In the present study Amato's metacercarial description was confirmed. However, excysted metacercariae were found to be slightly larger than those reported by Amato.

Crepidostomum illinoiense
(Figs. 187-189)

Material examined: None.
Reports in Literature: Peters (1963).

Miracidia
Peters (1963) incubated eggs at approximately 85 F and observed hatching on the fourth day. The miracidium lacked a stylet but had an eyespot. The epidermal plate pattern was 6,6,4,2 from anterior to posterior. There were two anterior structures (possibly cephalic gland openings) on each side at the anterior end of the junction between the ventrolateral and the lateral epidermal plates of the first tier. The two posterior plates were quadrangular and the two excretory pores were situated diagonally at opposite corners of the junction of the third and posterior tiers; these pores were not accompanied by smaller round structures.

The other larval forms are not known. However, the presence of eyespot remnants in some adult specimens suggests an oculate cercaria.

Crepidostomum isostomum
(Fig. 190)

Material examined: None.
Reports in Literature: Hopkins (1934).

Miracidia Not known.

Sporocysts Not known.

Rediae
Hopkins (1934) reported that rediae "probably" belonging to *C. isostomum* were found in 21 of 78 *Sphaerium notatum* Sterki. Nine of these rediae contained cercariae, the others contained rediae with immature germ balls or daughter rediae. Immature rediae were exactly like immature rediae of *C. cooperi* except that the pharynx was 40-67 long by 30-60 wide. Mature rediae were 700-1300 long by 200-300 wide with a pharynx the same size as in immature rediae. The gut disappeared at maturity. Hopkins (1934) observed six unicellular glands around the gut, and ducts running into the pharyngeal cavity in immature rediae.

Cercariae
According to Hopkins (1934) the ophthalmoxiphidiocercariae were similar to those of *C. cooperi*. He found three individuals that seemed to have developed past the cercarial stage as they had six oral papillae and a large pharynx drawn up close to the oral sucker. These cercariae were 270-360 long by 100-110 wide with tails 240-270 long, an oral sucker 70-72 long by 70-80 wide, a ventral sucker 65-75 long by 65 wide, and a pharynx 34-35 long by 30-33 wide; the compact pigment cup of the eyespot was 18 long by 15 wide, the oral papillae were 15 long. The stylet of one cercaria was 31 long and was similar in shape to that of *C. cooperi*.

Metacercariae
Metacercariae "probably" belonging to *C. isostomum* were reported by Hopkins (1934) from nymphs of *Hexagenia* sp.. He noted that they were very similar to those of *C. cooperi* except that the cirrus sac reached from near the pharynx to the anterior margin or center of the acetabulum. Hopkins (1934) noted that the only evidence to suggest that these metacercariae might not be of *C. isostomum* was the fact that the oral sucker was larger than the acetabulum in these metacercariae whereas adults of *C. isostomum* generally have suckers approximately equal in size.

Crepidostomum metoecus
(Figs. 191-192)

Material examined: None
Reports in Literature: Hopkins (1934), Noller (1925), Noller (1928), and Polyansky (1982).

Miracidia Not known.

Sporocysts Not known.

Rediae
Illustrated by Polyansky (1982) but not described.

Cercariae
Noller (1925) described *Cercaria arhopalocerca* from *Pisidium fontinale* and later (1928) assigned it to *Crepidostomum metoecus*. His decision was based on the resemblance of his cercaria to that of *C. farionis* (as described by Brown, 1927) and the complete absence of fish and other vertebrates that might serve as definitive hosts from the spring in which infected clams were found.

Metacercariae
Noller (1925) successfully infected chironomid and *Corethra* sp. larvae, and obtained metacercariae, but he presented no metacercarial description.

MIRACIDIAL CHARACTER ANALYSIS

The taxa used as members of the taxonomic outgroup for taxonomic ingroup character polarization were: *Allocreadium ictaluri, A. lobatum,* and *Pseudoallocre-*

adium neotenicum. A character conforming to any of the six conditions listed in the adult analysis section was considered inappropriate for the miracidial cladistic analysis. The following character discussion should be considered to be very preliminary because of the numerous papillose allocreadiid species for which no data on miracidial morphology were available.

Character states are listed for each noncontinuous character. For each character that conformed to one or more of the six conditions, and was therefore inappropriate for the cladistic analysis, a selected example is given and the applicable condition is cited. Characters appropriate for the analysis, are marked with a dagger (†) in the margin and the character state found within the outgroup is indicated with an asterisk (*).

57. *Body length*. Two states of this character were found within the ingroup: (a) greater than 53* (b) less than 33. Only one taxon, *Bunoderella metteri*, exhibited the derived state of this character. thus, this state is an autapomorphy for this single species. (Condition 4)

58. *Body width*. This was a continuous character for which no distinct states were found. For example, the range in body width for *B. eucaliae* overlapped at least some part of the range of each of the other taxa for which these data were available. (Condition 1)

59. *Cilia length*. this was a continuous character for which no distinct states were found. For example, the range in cilia length for *C. cooperi* overlapped at least some part of the range of each of the other taxa for which these data were available. (Condition 1)

60. *Number of epidermal cell tiers*. All ingroup and outgroup taxa exhibited only one state of this character: four tiers. (Condition 6)

61. *Number of epidermal cells in first tier*. All ingroup and outgroup taxa exhibited only one state of this character: six cells. (Condition 6)

62. *Number of epidermal cells in second tier*. Two states of this character were found within the ingroup: (a) five cells (b) six cells. Most taxa consistently exhibited state (b), but *B. luciopercae* has been reported with either state. (Condition 2)

63. *Number of epidermal cells in third tier*. Three states of this character were found within the ingroup: (a) three cells (b) four cells (c) five cells. Most taxa consistently exhibited state (b), but, records of *B. sacculata* exist with each of the three states. (Condition 2)

64. *Number of epidermal cells in fourth tier*. Two states of this character were found within the ingroup: (a) one cell (b) two cells. Most taxa consistently had state (b), but, *B. luciopercae* has been reported with either state. (Condition 2)

65. *Number of cephalic gland pores on terebratorium*. Five states of this character have been reported among the members of the ingroup: (a) zero (b) two (c) four (d) six (e) eight. Two of these states have been observed in members of the outgroup; *Allocreadium lobatum* has two cephalic gland pores, and *Pseudoallocreadium neotenicum* has no cephalic gland pores. This character could thus be recoded: (a) two or fewer pores and (b) four or more pores. However, *C. ictaluri* has been reported with no cephalic gland pores or six cephalic gland pores. (Condition 2)

66. *Cephalic gland cell length*. This was a continuous character for which no distinct states were found among the limited number of taxa for which data on this measurement were available. (Condition 1)

67. *Cephalic gland width*. This was a continuous character for which no distinct states were found among the limited number of taxa for which data on this measurement were available. (Condition 1)

68. *Number of apical gland pores on terebratorium*. Three states of this character have been reported among the members of the ingroup: (a) two pores (b) three pores (c) four pores. Two states: two pores and eight pores, have been reported among the members of the outgroup. *Bunodera sacculata* has been reported with "three or more pores" so the character could be broken down into the following states: (a) two (b) three or more. However, in this case both ingroup states are also found in the outgroup. (Condition 3)

69. *Number of flame cells*. All ingroup and outgroup taxa have been reported with only one state of this character, two cells. (Condition 6)

70. *Flame cell length*. This was a continuous character for which no distinct states were found among the limited number of taxa for which data on this measurement were available. (Condition 1)

71. *Flame cell width*. This was a continuous character for which no distinct states were found among the limited number of taxa for which data on this measurement were available. (Condition 1)

72. *Relative positions of excretory pores*. Two states of this character were found within the ingroup: (a) opposite (b)

diagonal. However, both states were found in the outgroup; e.g., *Allocreadium lobatum* has been reported with diagonal excretory pores and *Allocreadium ictaluri* has been reported with opposite excretory pores. In addition, *B. sacculata* has been reported with both states. (Conditions 2 and 3)

73. *Small papillae accompanying excretory pores.* Two states of this character were found within the ingroup: (a) absent (b) present*. Most taxa consistently exhibited either (a) or (b), but *C. ictaluri* has been reported with either state. (Condition 2)

74. *Pores (of unknown function) in spaces between first and second epidermal cell tiers.* Two states of this character have been reported within the ingroup: (a) absent (b) present. Both states have also been reported in the outgroup; e.g., *Allocreadium lobatum* has been reported with state (a), and *Pseudoallocreadium neotenicum* has been reported with state (b). (Condition 2)

75. *Embryonation time.* Two states of this character have been reported among the members of the ingroup: (a) embryonation occurs only after at least several days incubation, after leaving the host (b) embryonation occurs in the uterus. Most taxa have consistently been reported with only one of these states, however, *C. cornutum,* for example has been reported with either state. (Condition 2)

76. *Environment for miracidial hatching.* Two states of this character have been reported among the members of the ingroup: (a) able to hatch in water, (b) not able to hatch in water. Only one taxon, *Bunoderella metteri,* exhibited the derived state of this character. Thus, this state is an autapomorphy for this single species. (Condition 4)

Unfortunately, none of the 20 miracidial characters were appropriate for the cladistic analysis, and consequently a tree could not be constructed. Many of the characters may, in fact, be of some value in the future when additional information is available. Nevertheless, two miracidial autapomorphies for the monotypic genus *Bunoderella* were discovered: body length less than 33 (character 57), and miracidia unable to hatch in water (character 76). The latter character suggests that eggs must be consumed by fingernail clams before hatching can occur.

CERCARIAL CHARACTER ANALYSIS

The taxa used as members of the taxonomic outgroup for taxonomic ingroup character polarization were: *Allocreadium lobatum* and *Pseudoallocreadium neotenicum.* The character states are listed for each noncontinous character. A character conforming to any of the six conditions listed in the adult analysis section was considered inappropriate and was omitted from the cladistic analysis. For characters which were inappropriate for the cladistic analysis a selected example is given and the applicable condition from the list in the adult analysis section is cited. Where a character is appropriate for the analysis it is marked with a dagger (†) in the margin and the character state found within the outgroup is indicated with an asterisk (*). The data given in the following character discussion are true only of those species for which cercarial morphology has been described.

77. *Body length.* This was a continuous character for which no distinct states were found. For example, the range in cercarial body length for *C. cooperi* overlapped at least some part of the range of each of the other taxa of the ingroup. (Condition 1)

78. *Body width.* This was a continuous character for which no distinct states were found. For example, the range in cercarial body width for *C. cooperi* overlapped at least some part of the range of each of the other taxa of the ingroup. (Condition 1)

79. *Tail length.* This was a continuous character for which no distinct states were found. The range in tail length for *B. mediovitellata* overlapped at least some part of the range of each of the other taxa (including *C. ictaluri*) in the ingroup except *B. sacculata* and *B. luciopercae.* There was a 20 gap between the longest tail length recorded for *B. sacculata* and the shortest tail length recorded for *C. ictaluri,* but considering the contractile nature of the cercarial tail, this difference was judged to be not significant enough to warrant the recognition of 2 distinct character states. (Condition 1).

80. *Tail width.* This was a continuous character for which no distinct states were found. For example, the range in cercarial tail width for *B. mediovitellata* overlapped at least some part of the range of each of the other taxa of the ingroup. (Condition 1)

81. *Oral sucker length.* This was a continuous character for which no distinct states were found. For example, the range in oral sucker length for the cercariae of *C. ictaluri* overlapped at least some part of the range of each of the other taxa of the ingroup. (Condition 1)

82. *Oral sucker width.* This was a continuous character for which no distinct states were found. For example, the range in oral sucker width for the cercariae of *C. cooperi*

overlapped at least some part of the range of each of the other taxa of the ingroup. (Condition 1).

83. *Slender protrusions bordering oral sucker.* Two states of this character have been reported for the members of the ingroup: (a) present, (b) absent. Unfortunately, these protrusions are very tiny and they have been reported only in those species that have been examined with SEM. Under these circumstances this character was excluded from the analysis. (Condition 5).

84. *Acetabulum length.* This was a continuous character for which no distinct character states were found. For example, the range in cercarial oral sucker length for *B. mediovitellata* overlapped at least some part of the range of each of the other taxa (including *B. sacculata*) except *B. luciopercae.* The range of *B. sacculata* overlapped at least part of the range of *B. luciopercae.* (Condition 1)

85. *Acetabulum width.* This was a continuous character for which no distinct character states were found. For example, the range in acetabulum width for the cercariae of *C. cooperi* overlapped at least some part of the range of each of the other taxa in the ingroup. (Condition 1).

86. *Acetabular protrusions.* Only one state of this character was found within the members of the ingroup as well as the members of the outgroup examined: cercarial acetabular protrusions present. This character is therefore uninformative with respect to taxonomic groupings within the papillose allocreadiids. (Condition 6)

†87. *Relative sizes of anterior and posterior acetabular protrusions.* This character occurred in two states within the ingroup: (a) protrusions equal*, (b) anterior protrusions conspicuously smaller than posterior protrusions.

88. *Acetabular protrusions of two sizes throughout the entire acetabular border.* Two states of this character occurred within the ingroup: (a) no*, (b) yes. Only one taxon, *B. luciopercae,* exhibited the derived state of this character with its possession of large saccate structures intermixed with small, villiform protrusions throughout the entire circumference of the acetabulum. Thus, state (b) is an autapomorphy for this single species. (Condition 4)

89. *Shape of majority of acetabular protrusions.* Two states of this character were found among the members of the ingroup: (a) spherical* (b) villiform. Only one taxon, *B. luciopercae,* exhibited the derived state of this character. Thus, state (b) is an autapomorphy for this single species. (Condition 4)

90. *Stylet length.* This was a continuous character for which no distinct states were found. For example, the range in stylet length for *Bunodera mediovitellata* overlapped at least part of the range of each of the other taxa in the ingroup. (Condition 1)

91. *Stylet width.* This was a continuous character for which no distinct states were found. For example, the range in stylet width for *Bunodera mediovitellata* overlapped at least part of the range of each of the other taxa in the ingroup. (Condition 1).

92. *Prepharynx length.* This was a continuous character for which no distinct states were found. For example, the range in prepharynx length for *B. mediovitellata* overlapped at least part of the range of each of the other taxa in the ingroup. (Condition 1).

93. *Pharynx length.* This was a continuous character for which no distinct states were found. For example, the range in pharynx length for *C. cooperi* overlapped at least part of the range of each of the other taxa in the ingroup. (Condition 1)

94. *Pharynx width.* This was a continuous character for which no distinct states were found. For example, the range in pharynx width for *C. cooperi* overlapped at least part of the range of each of the other taxa in the ingroup. (Condition 1)

95. *Esophagus length.* This was a continuous character for which no distinct states were found. For example, the range in esophagus length for overlapped at least part of the range of each of the other taxa in the ingroup. (Condition 1).

96. *Posterior extent of ceca.* Two states of this character were found among the members of the ingroup: (a) ceca not extending past posterior margin of acetabulum*, (b) ceca extending to near posterior margin of body. Only one taxon, *C. farionis,* exhibited the derived state of this character. Thus, state (b) is an autapomorphy for this single species. (Condition 4)

†97. *Number of pairs of penetration glands.* Three states of this character were found among the members of the ingroup: (a) two pairs, (b) three pairs*, (c) four pairs. The transformation series used for this character was: 2→3→4.

98. *Cystogenous glands.* Two states of this character occurred among the members of the ingroup: (a) absent, (b) present. Both states also occurred among members of the outgroup, e.g., *Pseudoallocreadium neotenicum* has been reported to lack cystogenous glands, and *Allocreadium*

Table 3. Data matrix of cercarial characters. Character numbers correspond to those in the cercarial analysis section.

TAXA	CHARACTERS		
	87	97	99
Bunodera luciopercae	0	1	0
B. mediovitellata	0	0	0
B. sacculata	0	0	0
Bunoderella metteri	0	2	0
Crepidostomum metoecus	0	0	1
C. cooperi	1	0	1
C. cornutum	1	0	1
C. ictaluri	1	0	1
OUTGROUP (see text)	0	0	0

isosporum has been reported to possess cystogenous glands. (Condition 2).

†99. *Flame cell formula.* Two states of this character occurred among the members of the ingroup: (a) 2[(3+3+3)+(3+3+3)]*, (b) 2[(2+2+2)+(2+2+2)]. Two states of this character have been reported in the outgroup. For example, *Allocreadium isosporum* has state (a), and *Pseudoallocreadium neotenicum* has the formula 2[(4+4+4)+(4+4+4)]. Thus state (b) is considered to be the apomorphic condition.

100. *Eyespot diameter.* This was a continuous character for which no distinct states were found. For example, the range in eyespot diameter for *C. cooperi* overlapped at least part of the range of each of the other taxa in the ingroup.

Although they will undoubtedly be of some systematic use in the future, the sensory cilia found on the surface of all cercariae (Richards, 1971; Short, 1973) were not used as characters in the cercarial cladistic analysis. Their patterns appear to be fairly invariable intraspecifically and variable interspecifically. However, until a system for coding the patterns so that homologous cilia can be recognized between patterns has been developed, they cannot be informatively used in a cladistic analysis.

Three of the 24 cercarial characters were appropriate for the cladistic analysis. These characters are summarized below. The codings used in the data matrix for each of the character states is given. In each case "0" is the plesiomorphic state, and "1" or "2" are apomorphic states.

(87) Acetabular protrusions smaller anteriorly than posteriorly: 0=protrusions equal throughout; 1=anterior protrusions obviously smaller.

(97) Number of pairs of penetration glands: 0=3 pairs; 1=2 pairs; 2=4 pairs.

(99) Flame cell formula: 0= 2[(3+3+3)+(3+3+3)]; 1= 2[(2+2+2)+(2+2+2).

Sufficient data were available on the above three characters for the following species to be included in the analysis: *Bunodera luciopercae. B. mediovitellata, B. sacculata. Bunoderella metteri. Crepidostomum cooperi. C. cornutum. C. ictaluri,* and *C. metoecus.* The data matrix summarizing the states of each of the three characters for the eight taxa is given in Table 3. Cladistic analysis of the data matrix in Table 3 resulted in a single most-parsimonious tree (Fig. 193) with a consistency index of 100%.

Before proceeding with a discussion of the implications of the cercarial tree, a short discussion of monophyly is necessary. Wiley (1981; 76) defines a monophyletic group as "a group of species that includes an ancestral species (known or hypothesized) and all of its descendants." Since sufficient data on cercarial morphology was available for only eight of 19 species of papillose allocreadiids, the criticism might arise that any statements on the monophyly of the groups defined by the cercarial tree may not necessarily be in accordance with a strict definition of monophyly, as it is probable that none of the groups represent all of the descendants of an ancestor (12 of 19 known taxa were omitted from the analysis). But the unknown states of cercarial characters in these 12 species are analogous to undiscovered species, and just as undiscovered species do not pose the demand for tentativeness, neither do these unknown character states.

The cladogram can be used to make certain predictions about the character state distributions and potential monophyletic groups. The following predictions of cercarial character state distributions can be made:

(1) The cercariae of all members of the genus *Crepidostomum* possess the flame cell formula: 2[(2+2+2)+(2+2+2)].
(2) The cercariae of *Bunodera eucaliae* (the only species of *Bunodera* omitted from the cercarial analysis) and both species of *Paracreptotrematina* do not possess the flame cell formula: 2[(2+2+2)+(2+2+2)]. They most likely possess the formula: 2[(3+3+3)+(3+3+3)] or 2[(4+4+4)+(4+4+4)].
(3) The cercariae of *Bunodera eucaliae* and *Paracreptotrematina* spp. possess protrusions on their acetabulae that are not distinctly smaller anteriorly than elsewhere on the sucker.

If future research reveals that the above three predictions are correct, then the genus *Crepidostomum* can be considered monophyletic (on the basis of flame cell formula). In addition, a subgroup of taxa within the genus *Crepidostomum,* containing at least *C. cooperi. C. cornutum,* and *C. ictaluri* but not *C. metoecus,* can be considered monophyletic on the basis of the anterior acetabular protrusions being distinctly smaller than elsewhere on the sucker.

At this point, both apomorphic states of character 97, number of pairs of penetration glands, are considered as autapomorphies, two pairs for *B. luciopercae,* and four pairs for *Bunoderella metteri.* Thus, definite predictions about the number of pairs of penetration glands in other species cannot be made.

COMPARISON OF CERCARIAL AND ADULT TREES

To facilitate comparison of the results of the cercarial analysis with the results of the adult analysis, the adult cladogram is reproduced in Figure 194 with all taxa not included in the cercarial analysis omitted. While the trees are not identical, their topologies are consistent; for these eight taxa, no groupings are contradicted between the two trees. The adult analysis indicated the following groupings:

Group 1 (*B. mediovitellata* + *B. sacculata*)
Group 2 (Group 1 + *B. luciopercae*)
Group 3 (the four species of *Crepidostomum* and Group 2)
Group 4 (Group 3 + *Bunoderella metteri*)

The cercarial analysis indicated the following groupings:

Group 5 (*C. cooperi* + *C. cornutum* + *C. ictaluri*)
Group 6 (Group 5 + *C. metoecus*)
Group 7 (the three species of *Bunodera*) +
Group 6 + *Bunoderella metteri*)

This analysis suggests that larval characters are equal in importance to adult characters for resolving phylogenetic relationships. The consensus tree, constructed by combining adult and cercarial data is given in Figure 195. This tree indicates that the papillose allocreadiids, as a group, are monophyletic, as are all of the four genera currently recognized within the group. Based on these results it is recommended that the entire group be placed within the same subfamily, Bunoderinae, of the Allocreadiidae. Thus, the group Bunoderinae is a monophyletic subfamily.

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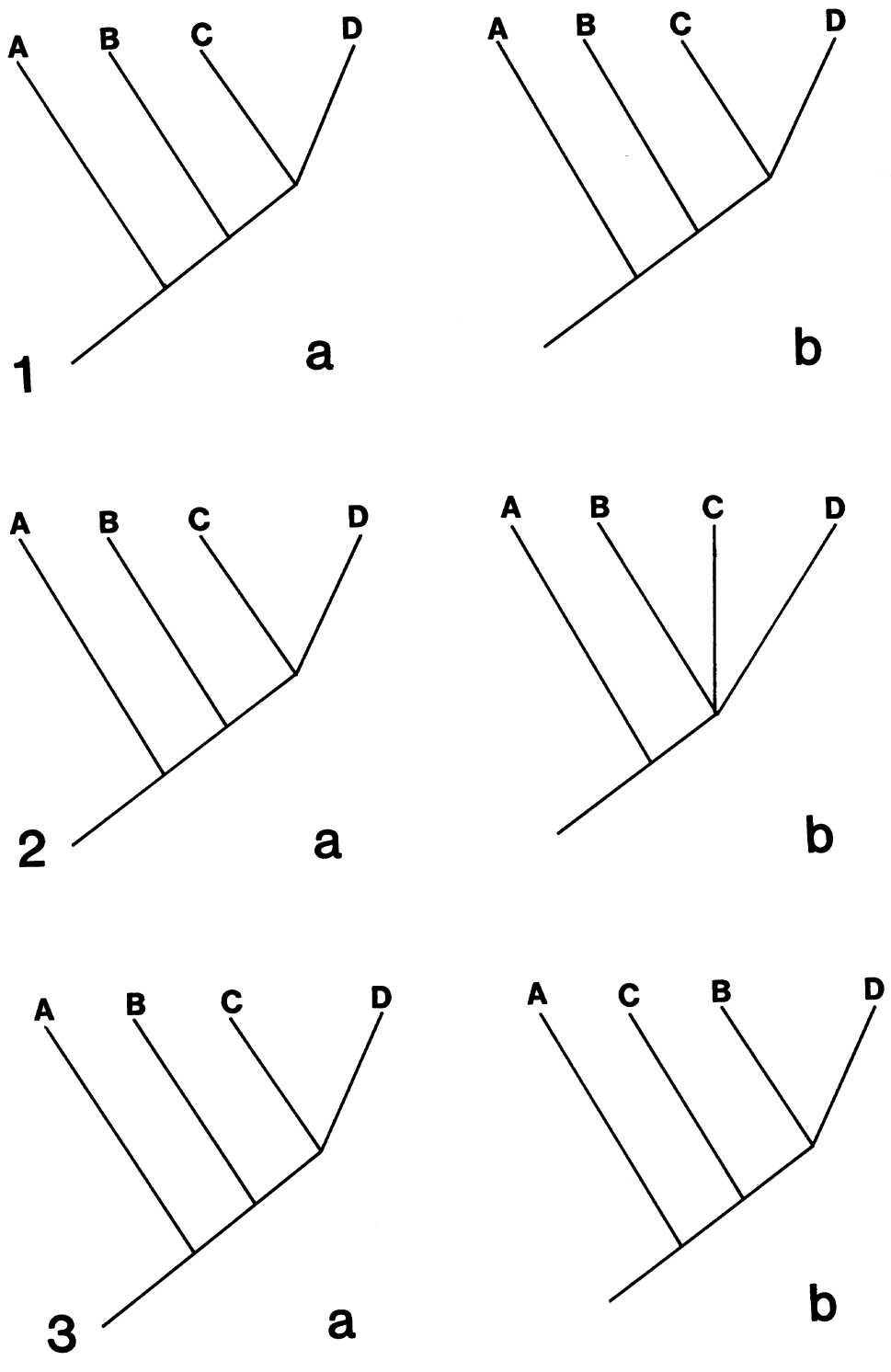
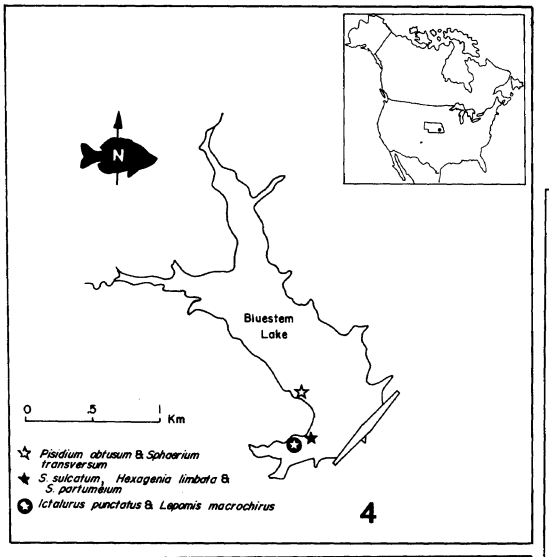
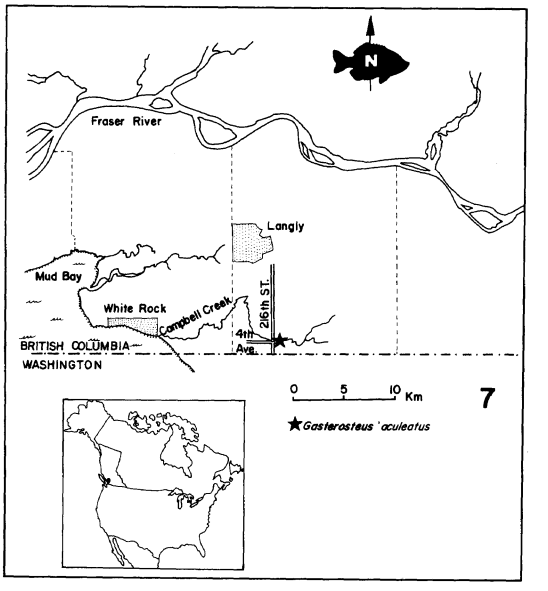
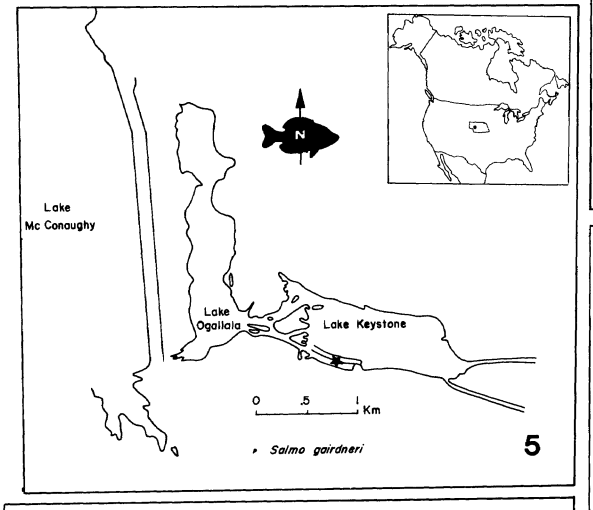
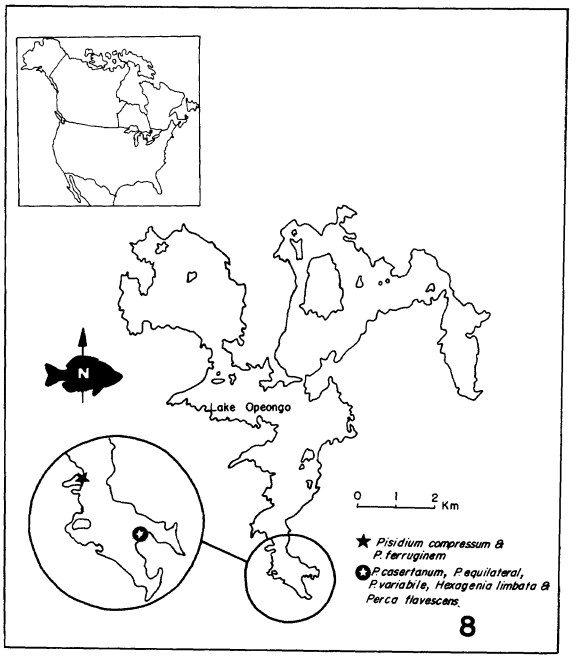


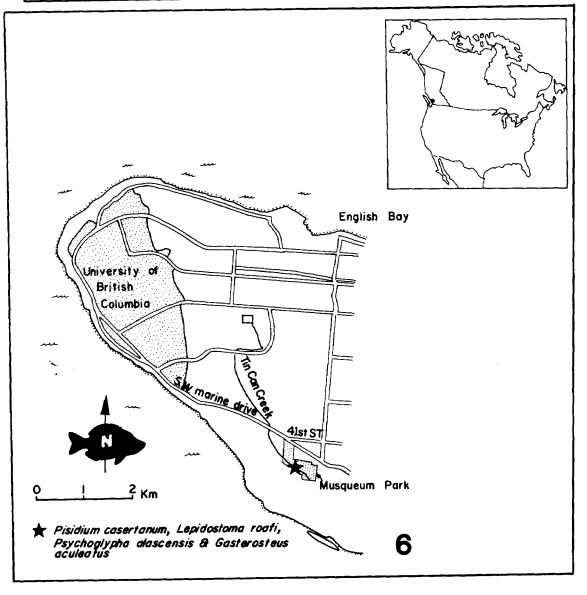
Figures 1-3. Cladogram topologies. Figs. 1a and b, cladograms with identical topologies. Figs. 2a and b, cladograms with consistent topologies. Figs. 3a and b, cladograms with inconsistent topologies.











Figures 4-8. Collecting localities. Fig. 4. Bluestem Lake, Lancaster Co., Nebraska. Fig. 5. Lake Keystone, Keith Co., Nebraska. Fig. 6. Tin Can Creek, Musqueum Park, Vancouver, British Columbia, Canada. Fig. 7. Campbell Creek, White Rock, British Columbia, Canada. Fig. 8. Lake Opeongo, Algonquin Park, Ontario, Canada.

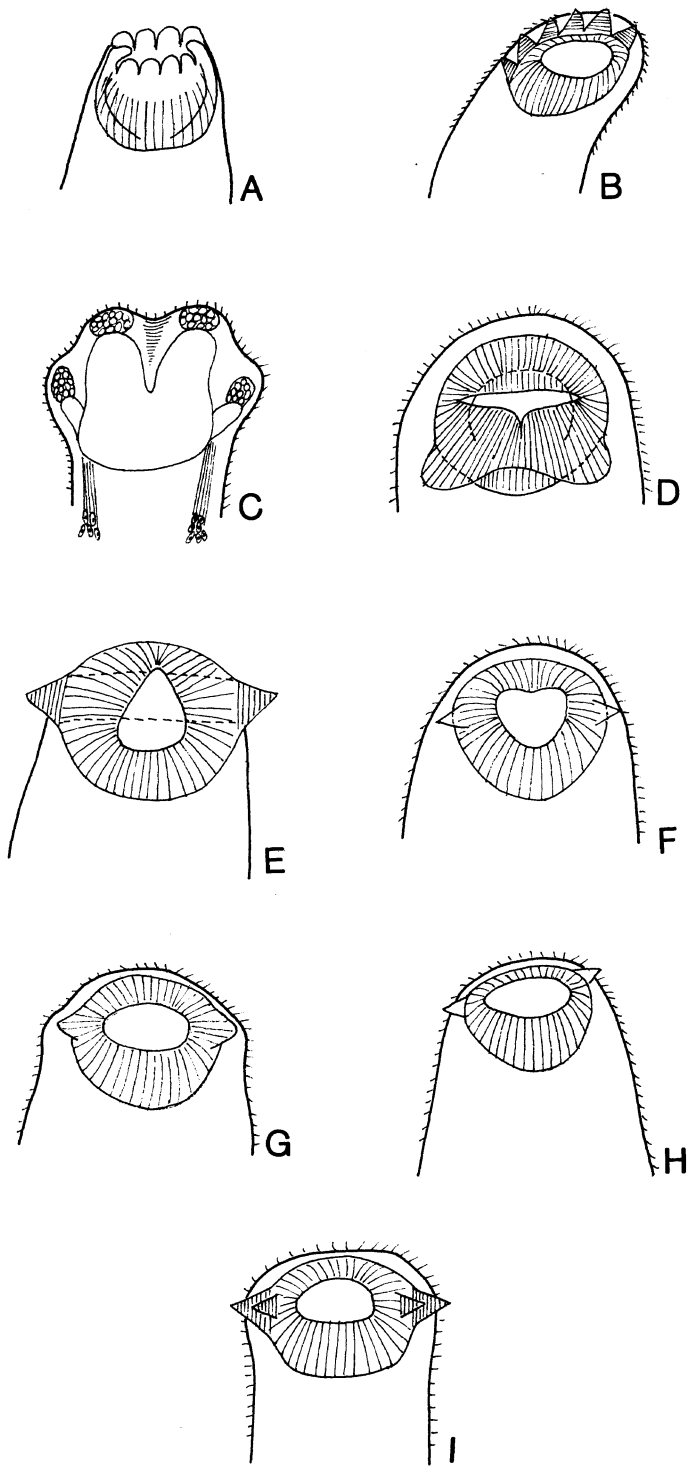
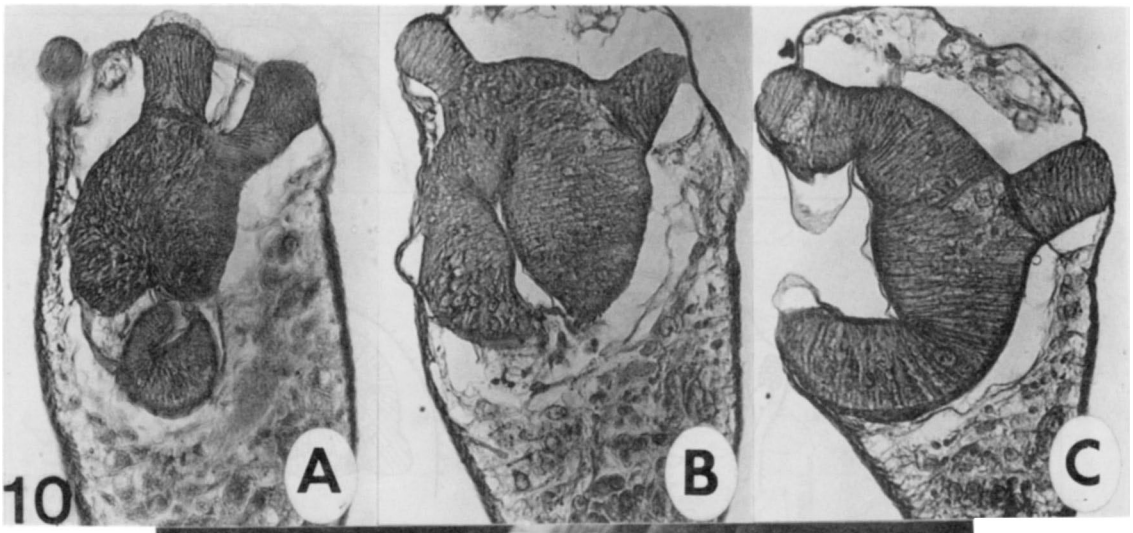


Figure 9. Digeneans with oral sucker ornamentation resembling that of the papillose allocreadiids. A, B, D-I after Yamaguti (1971). C after Watson (1984). 9A. *Enenterum sp.* 9B. *Waretrema* sp. 9C. *Tetracerasta* sp. 9D. *Dictyangium* sp. 9E. *Rhytidodes* sp. 9F. *Gymnophalloides* sp. 9G. *Eustomas* sp. 9H. *Barbulostomum* sp. 9I. *Auridistomum* sp.



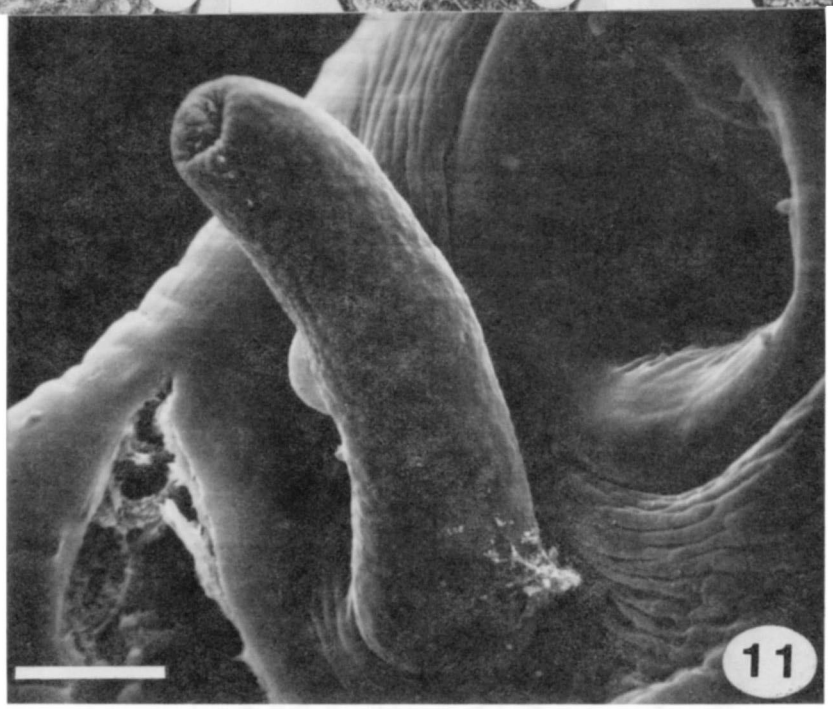
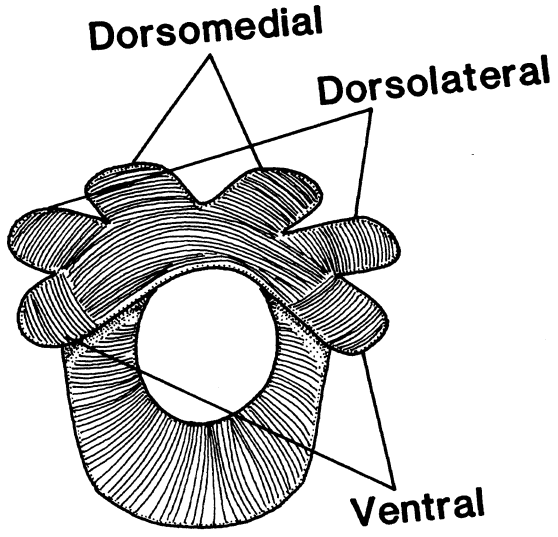


Figure 10. Serial sagittal sections through oral sucker of *Crepidostomum cooperi*. Note muscular papillae.

Figure 11. Scanning electron micrograph of everted cirrus of *Crepidostomum cooperi*. Note absence of cirrus spines. Scale bar=30μ.



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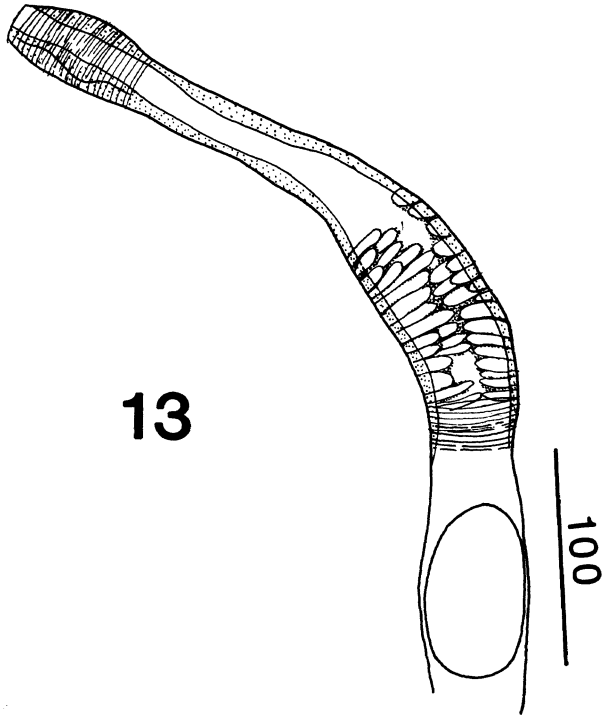

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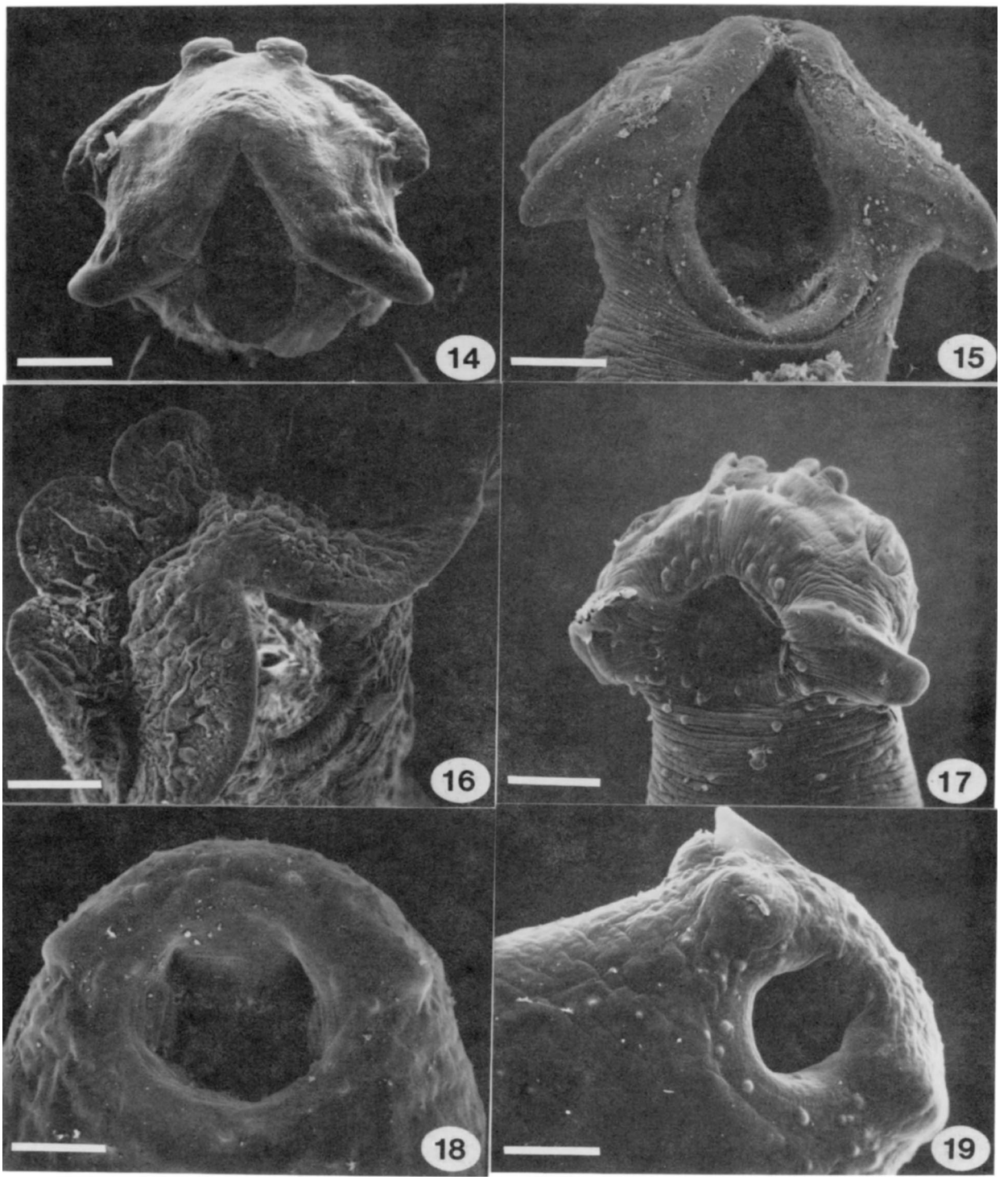
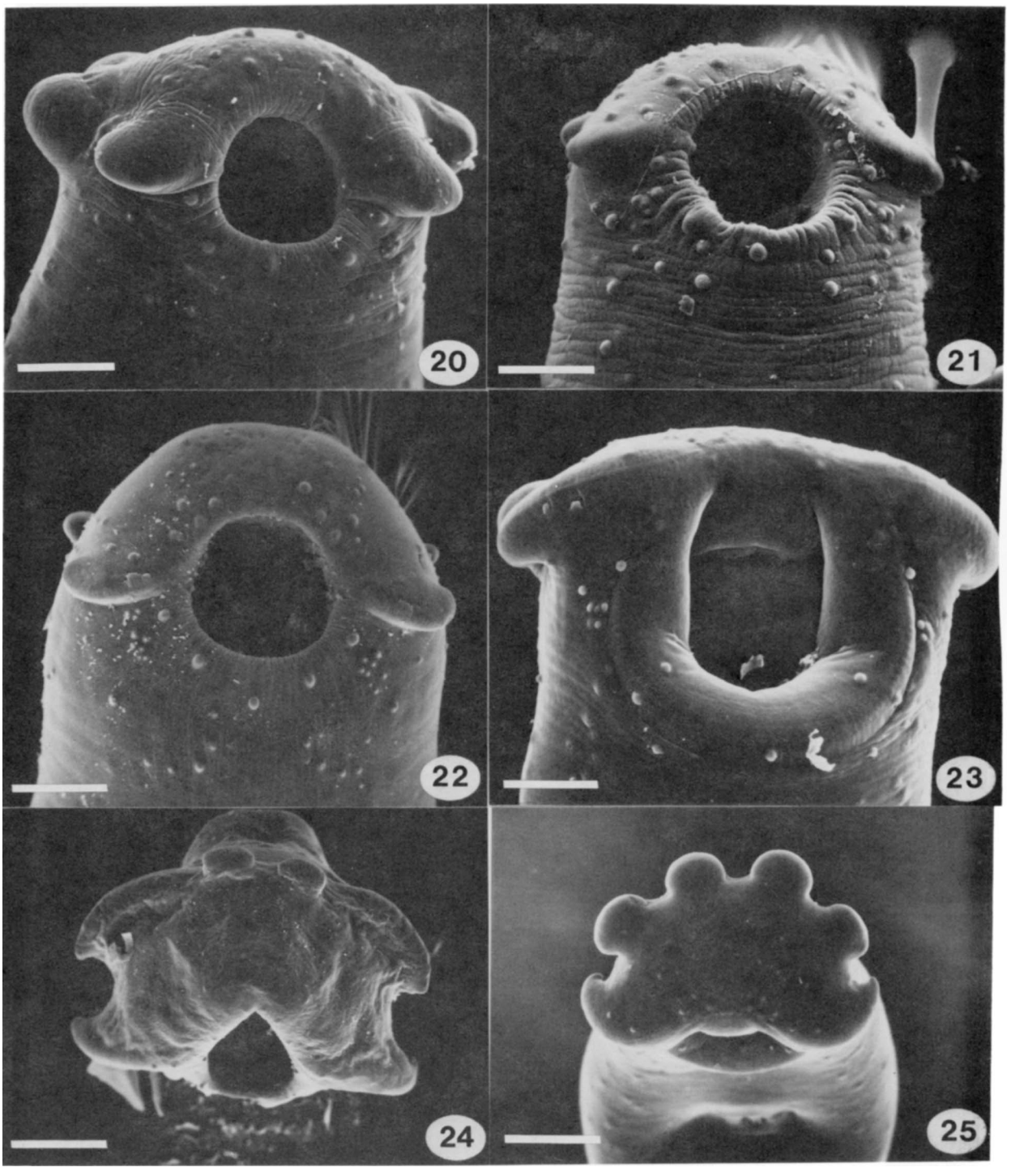
Figure 12. Schematic reconstruction of oral sucker with three pairs of muscular papillae labelled (tegument removed).

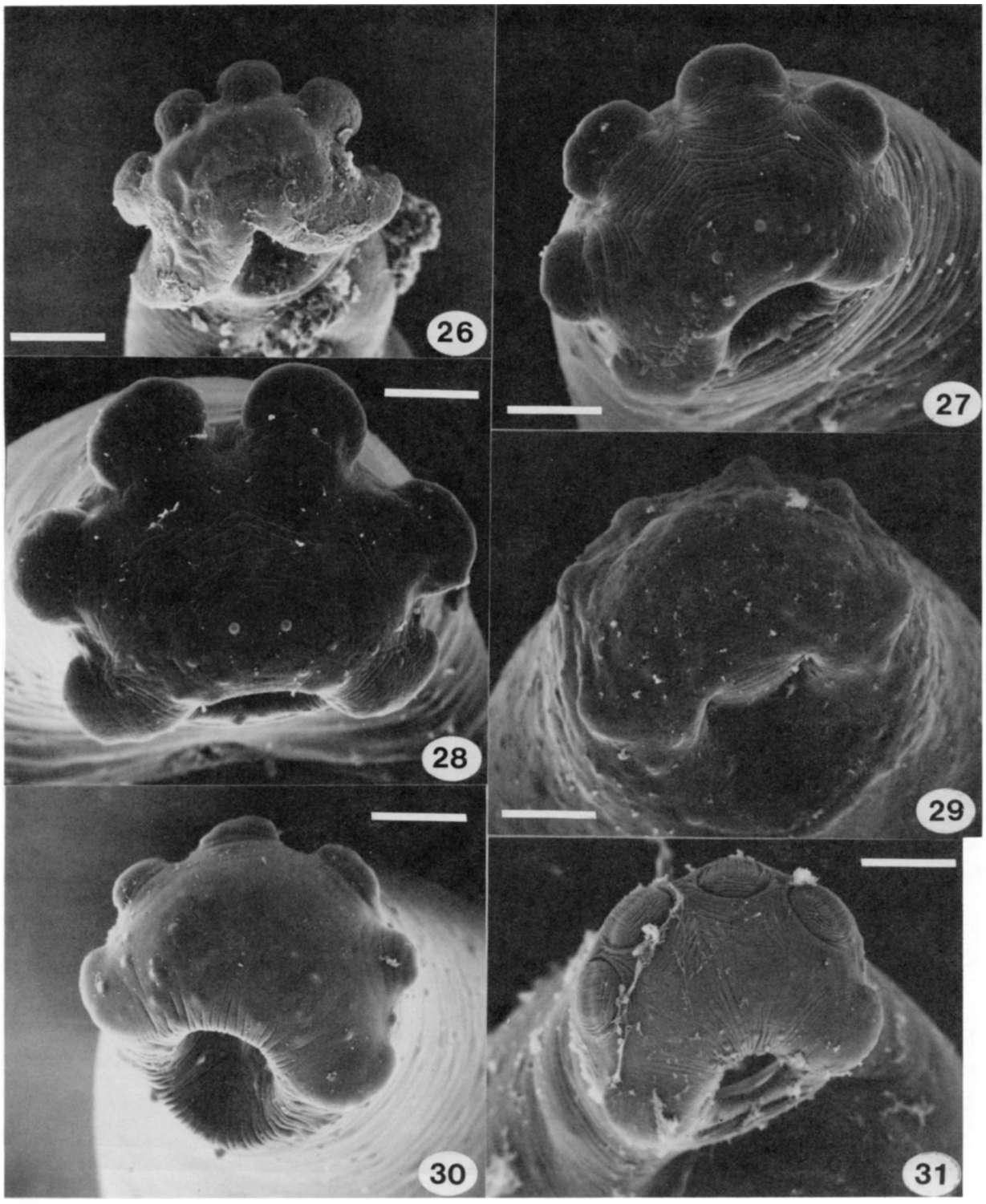
Figure 13. Detail of metraterm of *Crepidostomum cooperi*.



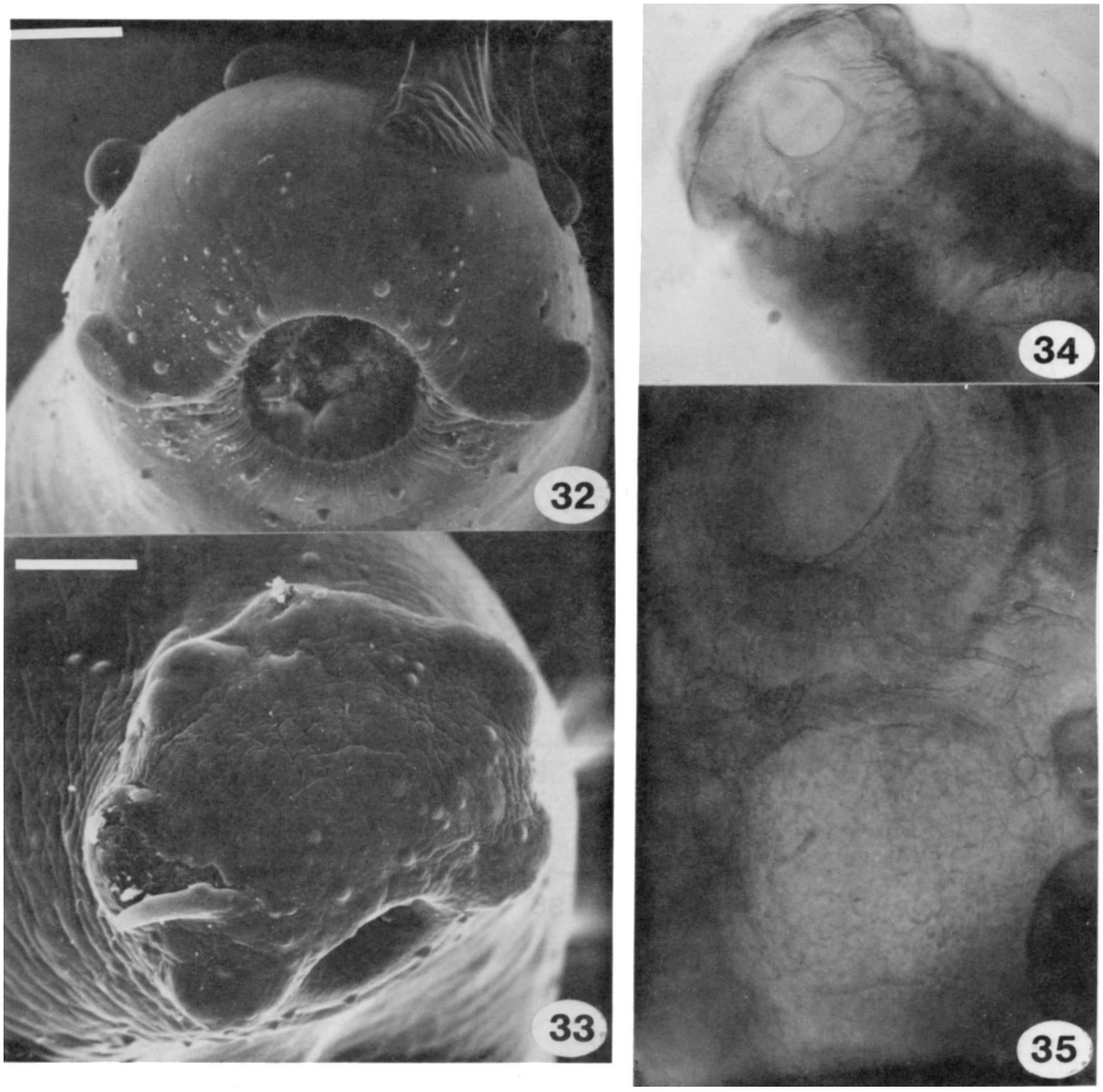
Figures 14-19. Scanning electron micrographs of oral suckers, ventral views. Fig. 14. *Crepidostomum opeongoensis*, scale bar = 90μ. Fig. 15. *C. cornutum*, scale bar = 55μ. Fig. 16. *C. brevivitellum*, scale bar = 50μ. Fig. 17. *C. illinoiense*, scale bar = 40μ. Fig. 18. *C. ictaluri*, scale bar = 20μ. Fig. 19. *Bunodera sacculata*, scale bar = 55μ.



Figures 20-25. Scanning electron micrographs of oral suckers. Figs. 20-23 ventral views, Figs 24-25 anterior views. Fig. 20. *Bunodera medioovitellata*, scale bar = 50μ. Fig. 21. *Crepidostomum metoecus*, scale bar = 45μ. Fig. 22. *C. farionis*, scale bar = 55μ. Fig. 23. *C. cooperi*, scale bar = 55μ. Fig. 24. *C. opeongoensis*, scale bar = 90μ. Fig. 25. *C. cooperi*, scale bar = 115μ.

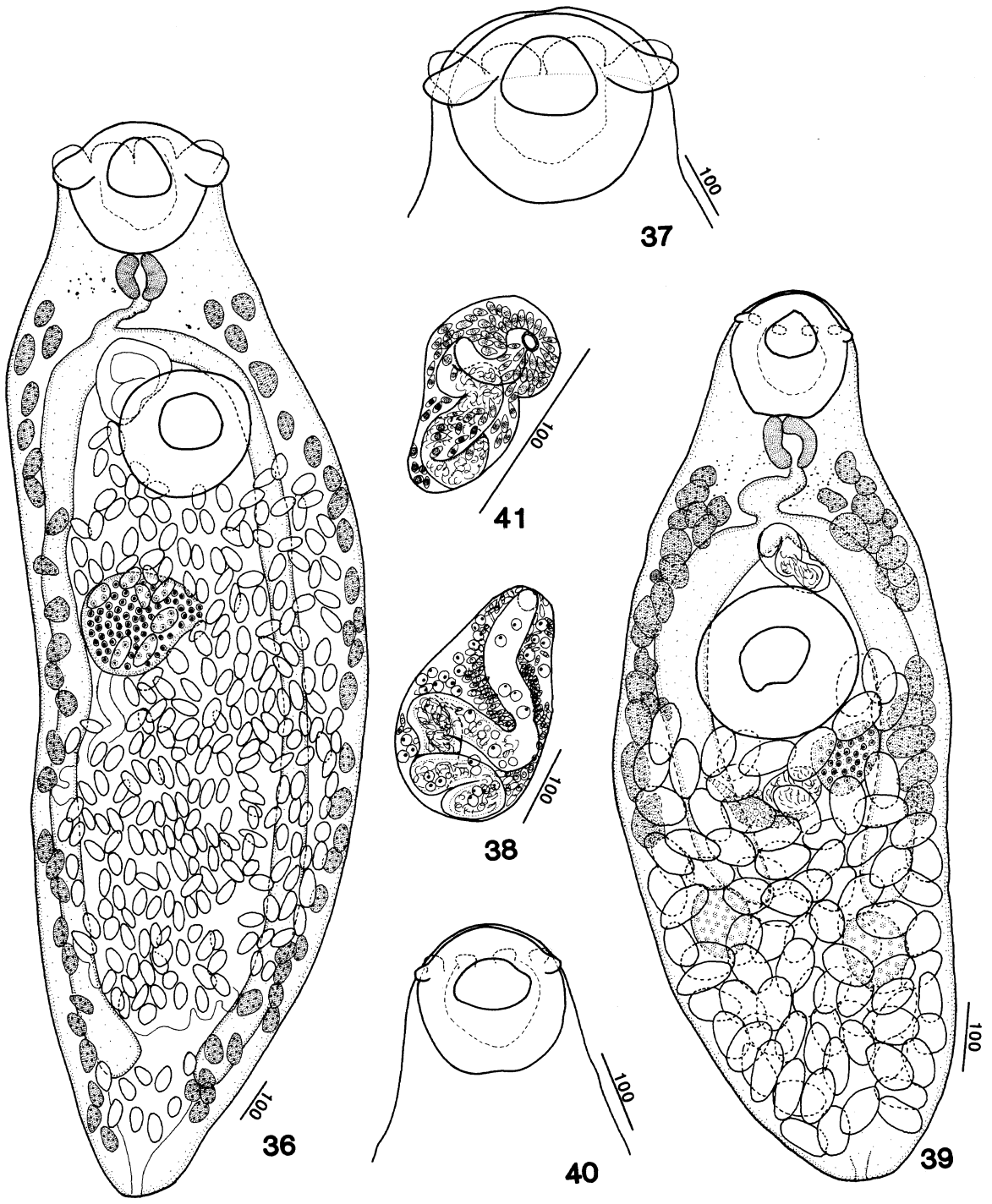


Figures 26-31. Scanning electron micrographs of oral suckers, anterior views. Fig. 26. *Crepidostomum cornutum*, scale bar = 200μ. Fig. 27. *Bunodera mediovitellata*, scale bar = 60μ. Fig. 28. *B. mediovitellata* second specimen, scale bar = 55μ. Fig. 29. *C. ictaluri*, scale bar = 20μ. Fig. 30. *C. metoecus*, scale bar = 45μ. Fig. 31. *B. luciopercae*, scale bar = 100μ.



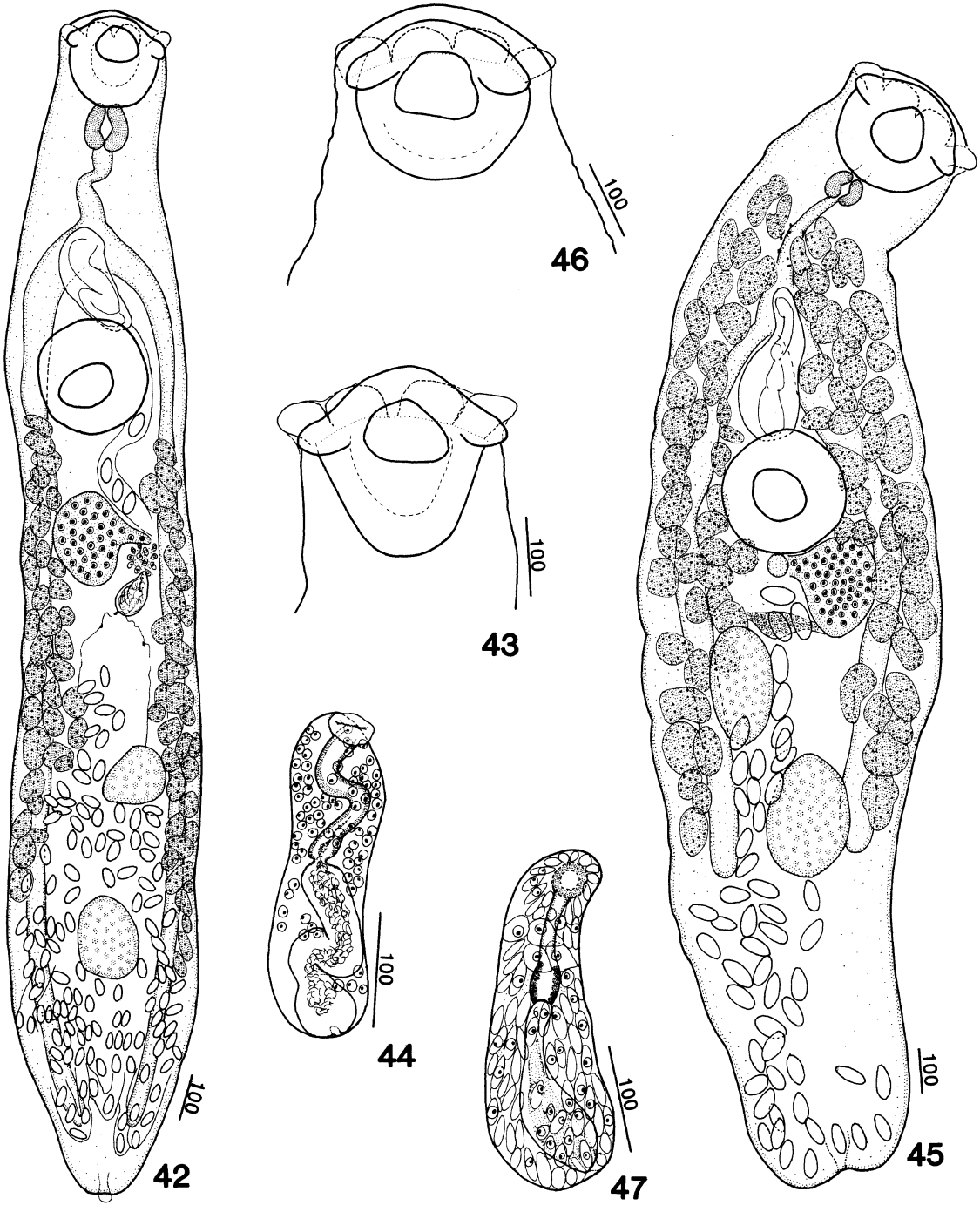
Figures 32-33. Scaning electron micrographs of oral suckers, anterior views. Fig. 32. *Crepidostomum farionis*, scale bar = 55μ. Fig. 33. *Bunodera sacculata*, scale bar = 55μ.

Figures 34-35. Photomicrographs illustrating subtegumental gland system in *Crepidostomum cooperi*. Photographs were taken of live specimens five minutes after removal from host. Fig. 34. Oral glands. Fig. 35. Glands located near acetabulum and anterior testis.



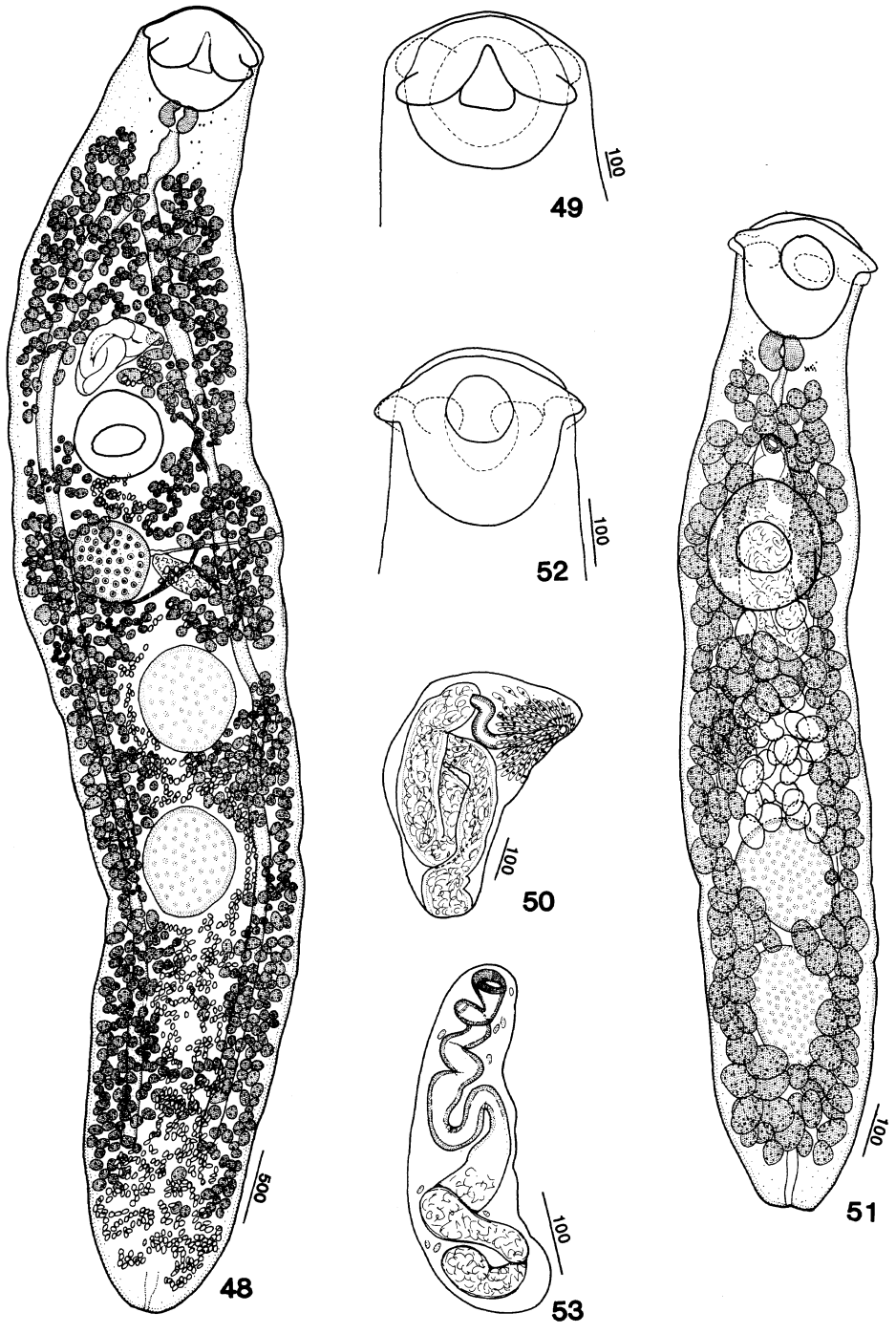
Figures 36-38. *Bunodera luciopercae,* ventral views, HWML No. 18000 (voucher). Fig. 36. Entire worm, placement of vitellaria is tentative. Fig. 37. Detail of oral sucker. Fig. 38. Detail of cirrus sac.

Figures 39-41. *Bunodera eucaliae,* ventral views, USNM No. 78403 (voucher). Fig. 39. Entire worm. Fig. 40. Detail of oral sucker. Fig. 41. Detail of cirrus sac.



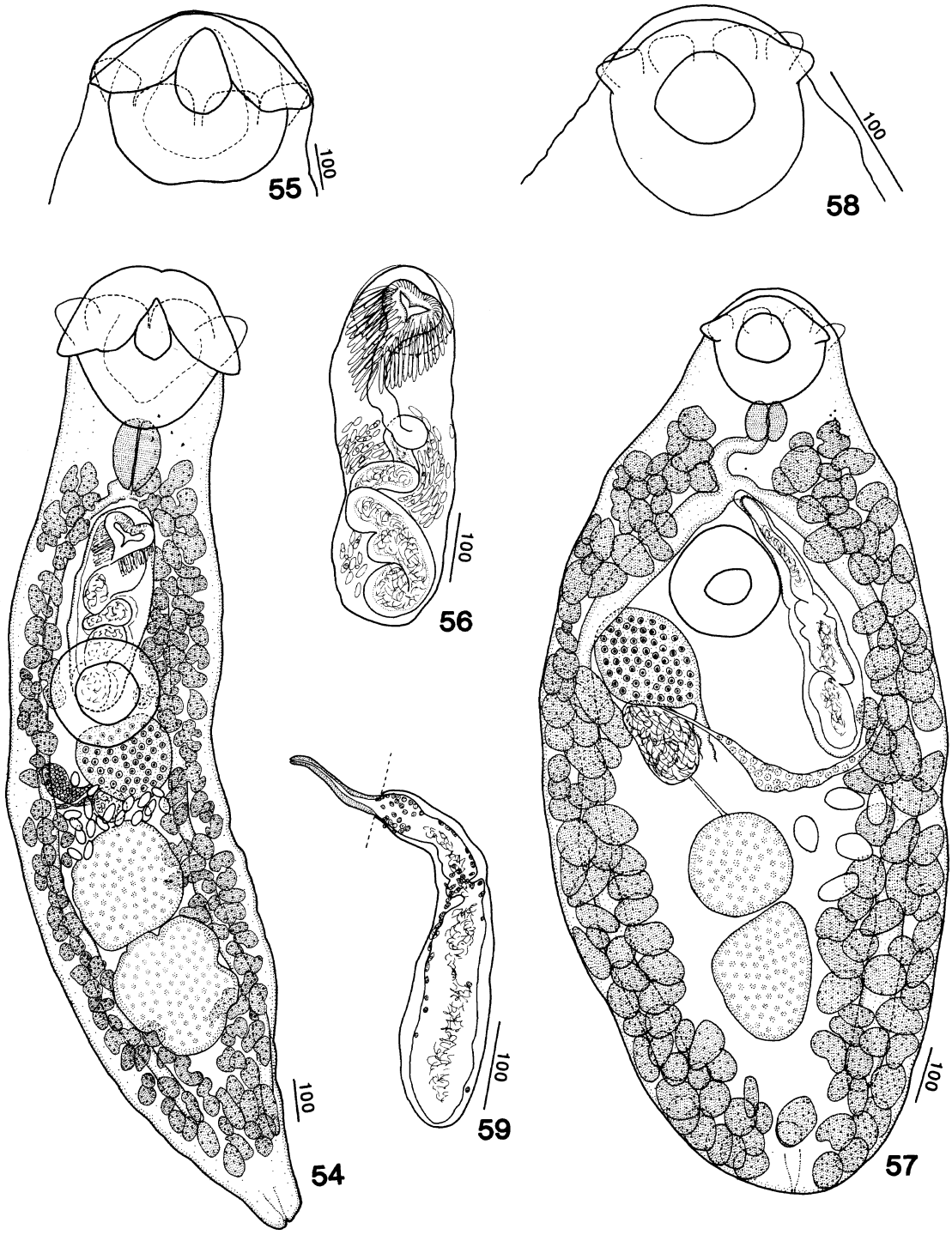
Figures 42-44. *Bunodera mediovitellata,* ventral views, HWML No. 18001 (voucher). Fig. 42. Entire worm. Fig. 43. Detail of oral sucker. Fig. 44. Detail of cirrus sac.

Figures 45-47. *Bunodera sacculata,* HWML 18003 (voucher). Fig. 45. Entire worm, ventral view. Fig. 46. Detail of oral sucker, ventral view. Fig. 47. Detail of cirrus sac, dorsal view.



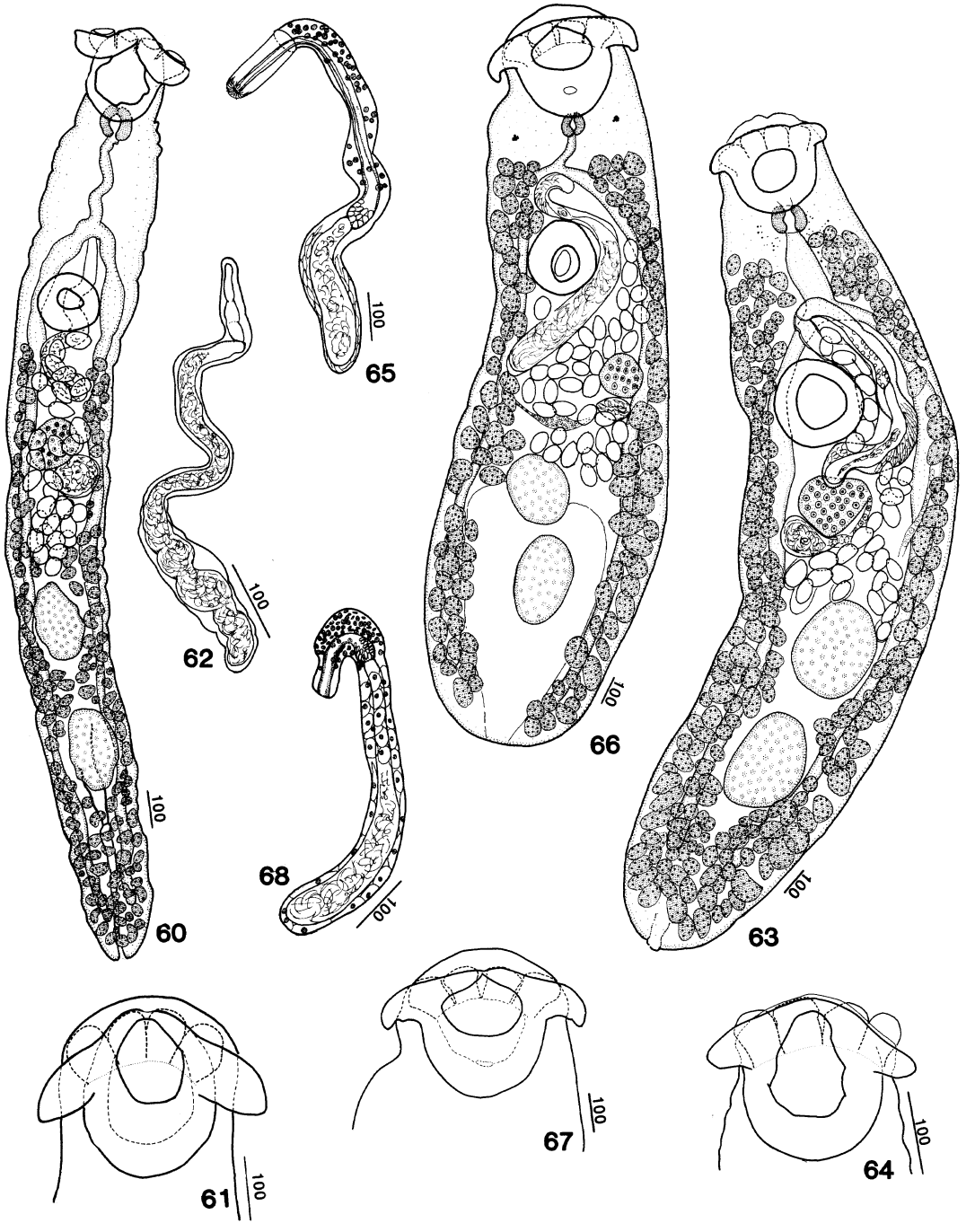
Figures 48-50. *Bunoderella metteri*, ventral views, USNM No. 60046 (paratypes). Fig. 48. Entire worm. Fig. 49. Detail of oral sucker. Fig. 50. Detail of cirrus sac.

Figures 51-53. *Crepidostomum metoecus*, ventral views, HWML No. 18005 (voucher). Fig. 51. Entire worm. Fig. 52. Detail of oral sucker. Fig. 53. Detail of cirrus sac.



Figures 54-56. *Crepidostomum auriculatum*. Fig. 54. Entire worm, ventral view, USNM No. 51543 (voucher). Fig. 55. Detail of oral sucker, ventral view, HWML No. 18006 (voucher). Fig. 56. Detail of cirrus sac, ventral view, USNM No. 51543 (voucher).

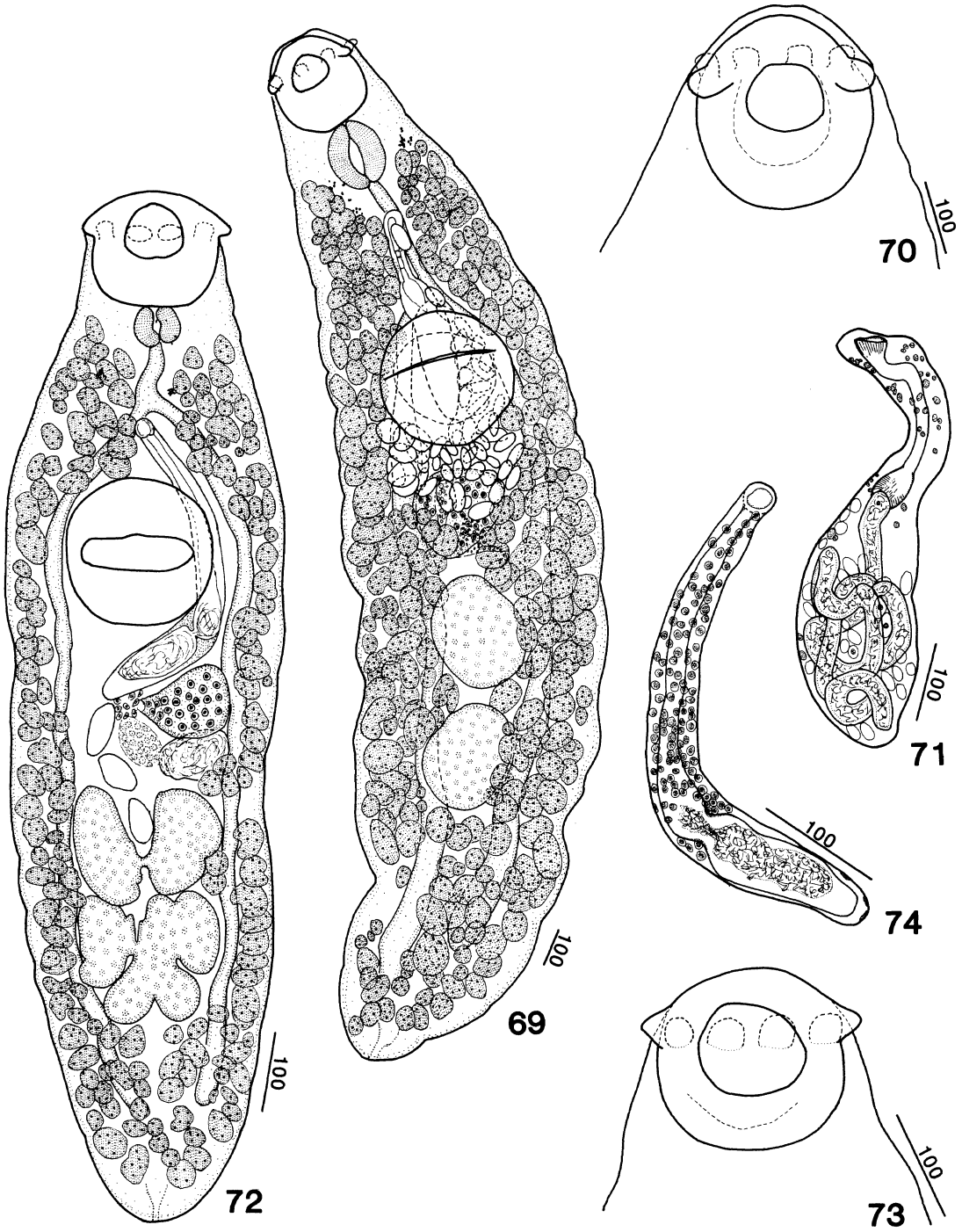
Figures 57-59. *Crepidostomum auritum*, ventral views, USNM No. 36236 (cotypes). Fig. 57. Entire worm. Fig. 58. Detail of oral sucker. Fig. 59. Detail of cirrus sac, cirrus everted.



Figures 60-62. *Crepidostomum brevivitellum,* ventral views. Fig. 60. entire worm, USNM No. 51518 (holotype). Fig. 61. Detail of oral sucker, after Caira (1985). Fig. 62. Detail of cirrus sac, USNM No. 51518 (holotype).

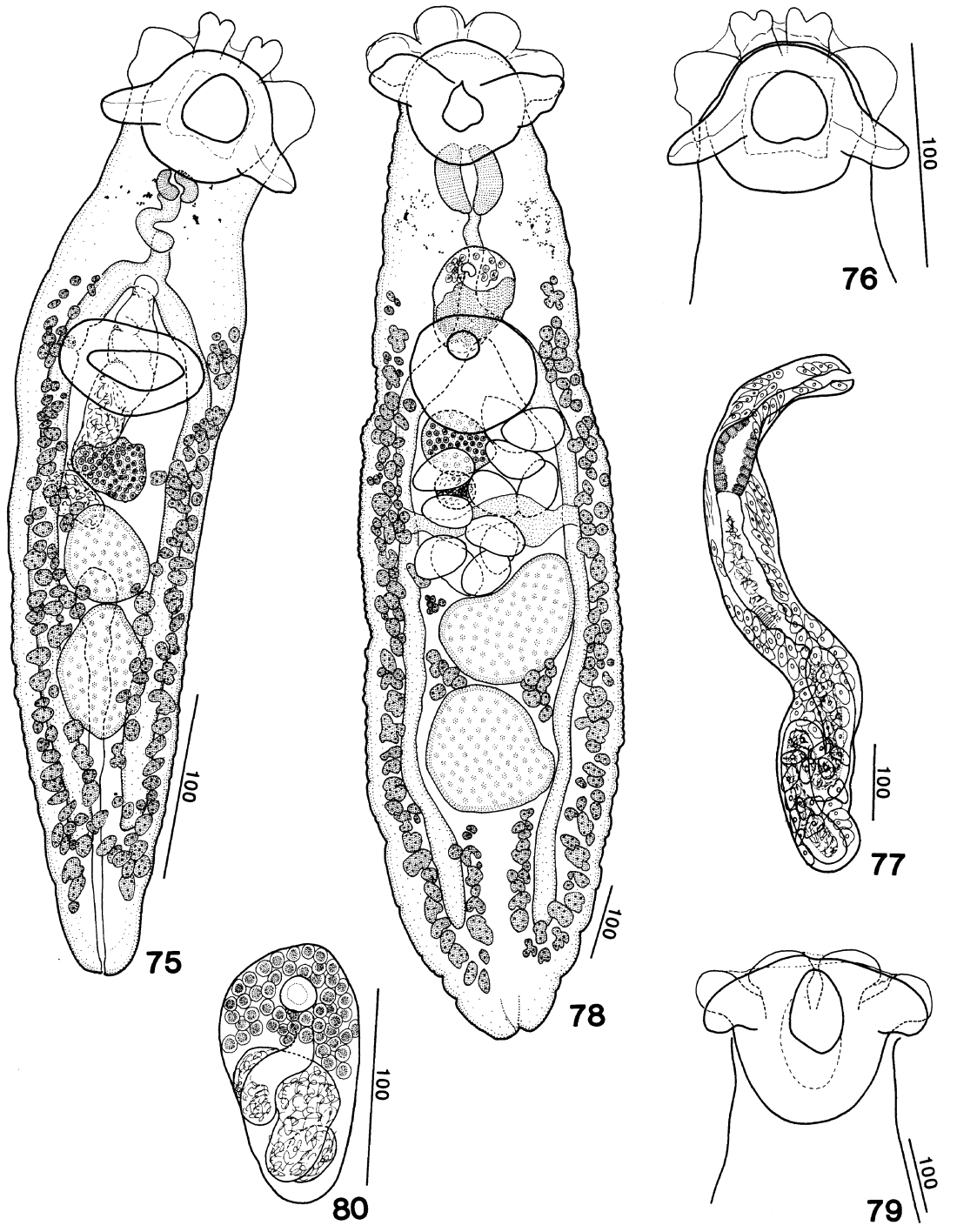
Figures 63-65. *Crepidostomum cooperi,* ventral views. Fig. 63 Entire worm. Fig. 64. Detail of oral sucker. Fig. 65. Detail of cirrus sac.

Figures 66-68. *Crepidostomum cornutum,* ventral views. HWML No. 21491 (voucher). Fig. 66. Entire worm, ventral view. Fig. 67. Detail of oral sucker, ventral view. Fig. 68. Detail of cirrus sac of metacercaria, dorsal view.



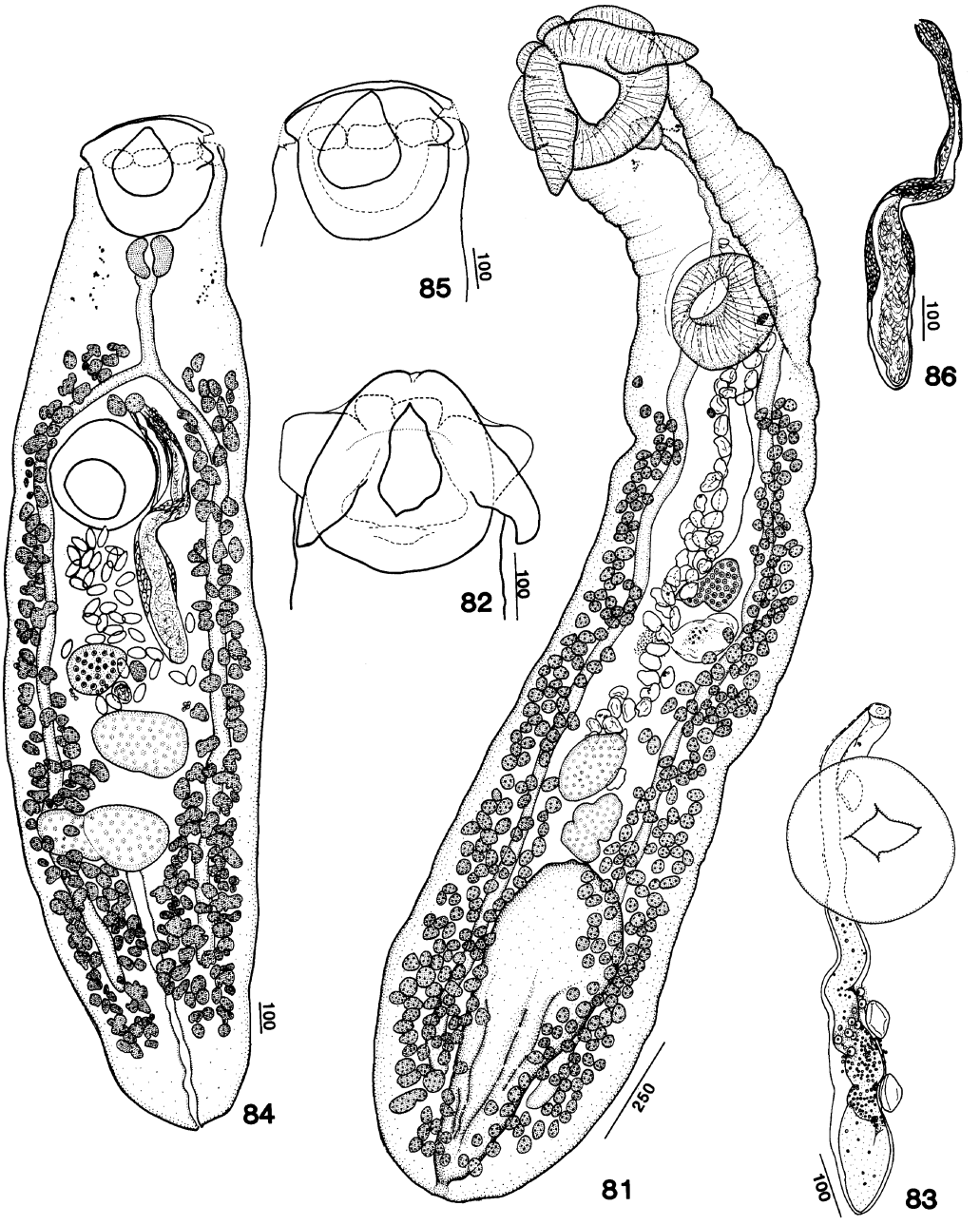
Figures 69-71. *Crepidostomum farionis,* ventral views, HWML No. 18011 (vouchers). Fig. 69. Entire worm. Fig. 70. Detail of oral sucker. Fig. 71. Detail of cirrus sac.

Figures 72-74. *Crepidostomum ictaluri,* HWML No. 21492 (voucher). Fig. 72. Entire worm, ventral view. Fig. 73. Detail of oral sucker, ventral view. Fig. 74. Detail of cirrus sac, dorsal view.



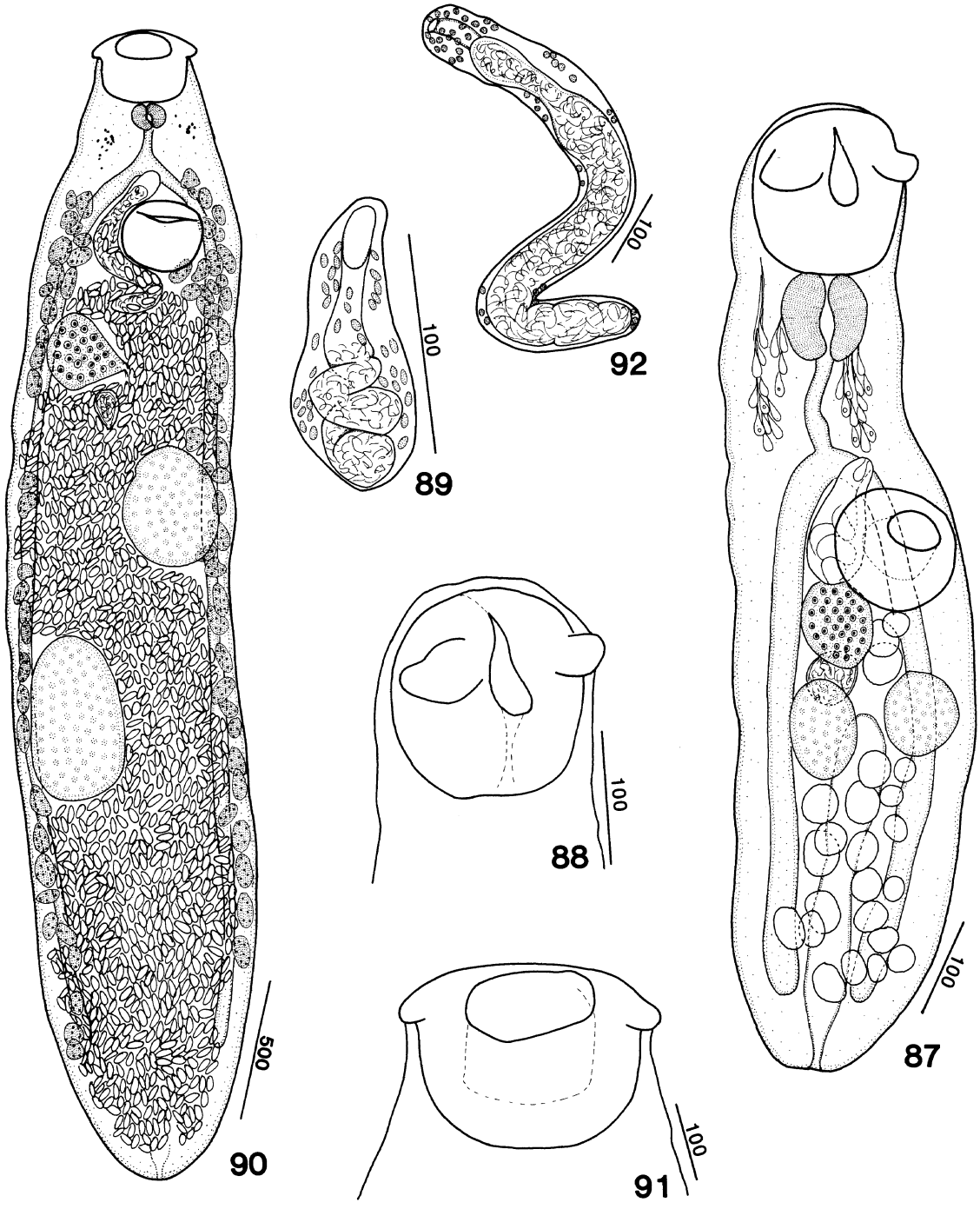
Figures 75-77. *Crepidostomum illionoiense*. Fig. 75. Entire worm, ventral view, USNM No. 51541 (cotype). Fig. 76. Detail of oral sucker, ventral view, USNM No. 51541 (cotype). Fig. 77. Detail of cirrus sac, dorsal view, USNM No. 49413 (voucyher).

Figures 78-80. *Crepidostomum isostomum*, ventral view. Fig. 78. Entire worm, USNM No. 51542 (holotype). Fig. 79. Detail of oral sucker, HWML No. 21494 (voucher). Fig. 80. Detail of cirrus sac, HWML No. 21493 (voucher).



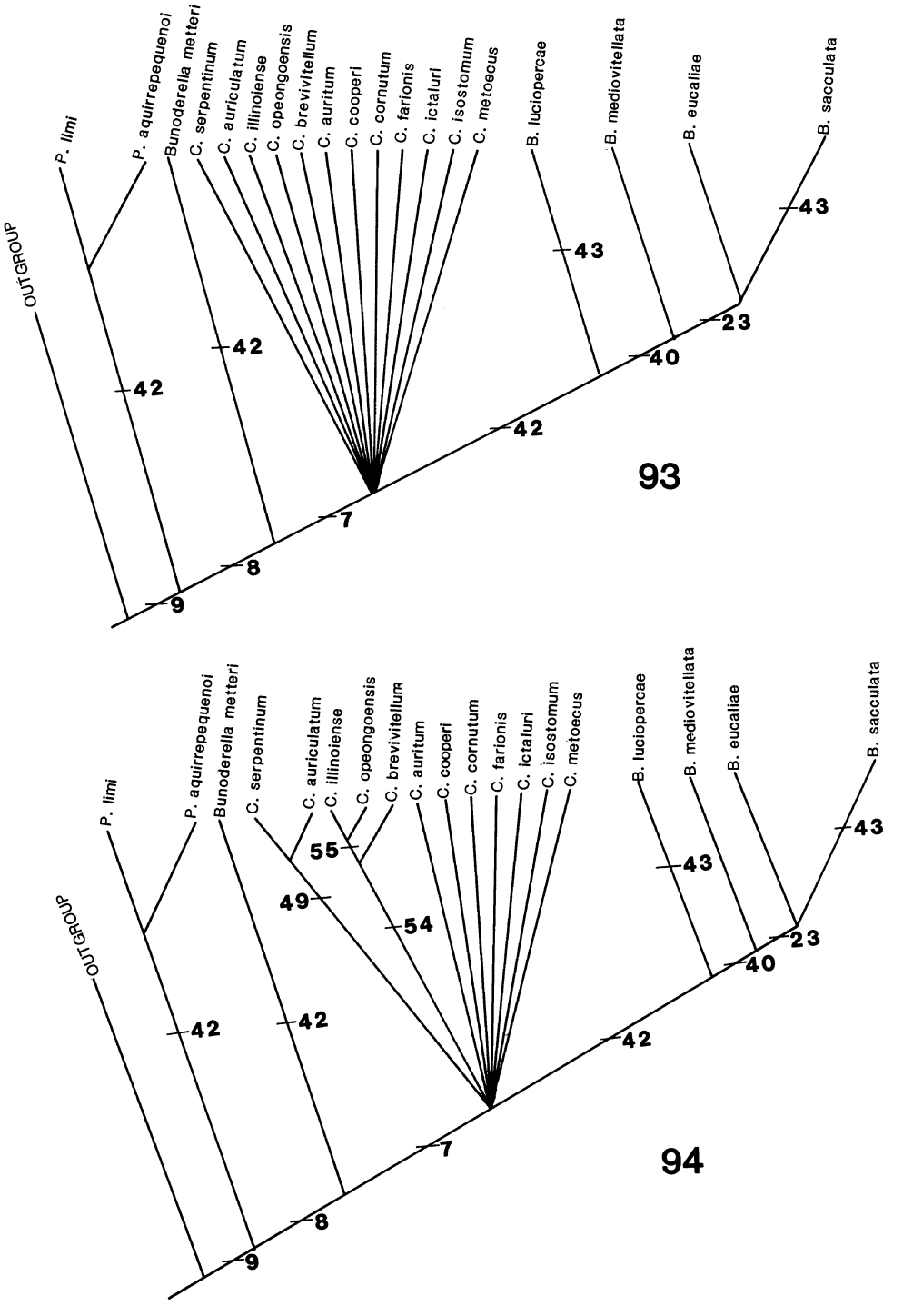
Figures 81-83. *Crepidostomum opeongoensis,* after Caira (1985). Fig. 81. Entire worm, ventral view. Fig 82. Detail of oral sucker, ventral view. Fig 83. Detail of cirrus sac, dorsal view.

Figures 84-86. *Crepidostomum serpentinum,* ventral views, USNM No. 8968 (type). Fig 84. Entire worm. Fig. 85. Detail of oral sucker. Fig 86. Detail of cirrus sac.



Figures 87-89. *Paracreptotrematina limi,* ventral views, USNM No. 59689 (paratype). Fig. 87. Entire worm. Fig. 88. Detail of oral sucker. Fig. 89. Detail of cirrus sac.

Figures 90-92. *Paracreptotrematina aquirrepequenoi,* USNM No. 75736 (voucher). Fig. 90. Entire worm, ventral view. Fig. 91. Detail of oral sucker, ventral view. Fig. 92. Detail of cirrus sac. dorsal view.



Figures 93-94. Adult cladograms. Fig. 93. Preliminary cladogram generated from analysis of adult character data matrix in Table 1. Characters are indicated following a dash; numbers correspond to the characters in the section on adult character analysis. Fig. 94. Cladogram generated from analysis of augmented data matrix in Table 2, following functional outgroup polarization of additional characters. Character numbers correspond to those in the section on adult character analysis. B.=*Bunodera*, C.=*Crepidostomum*, P.=*Paracreptotrematina*.

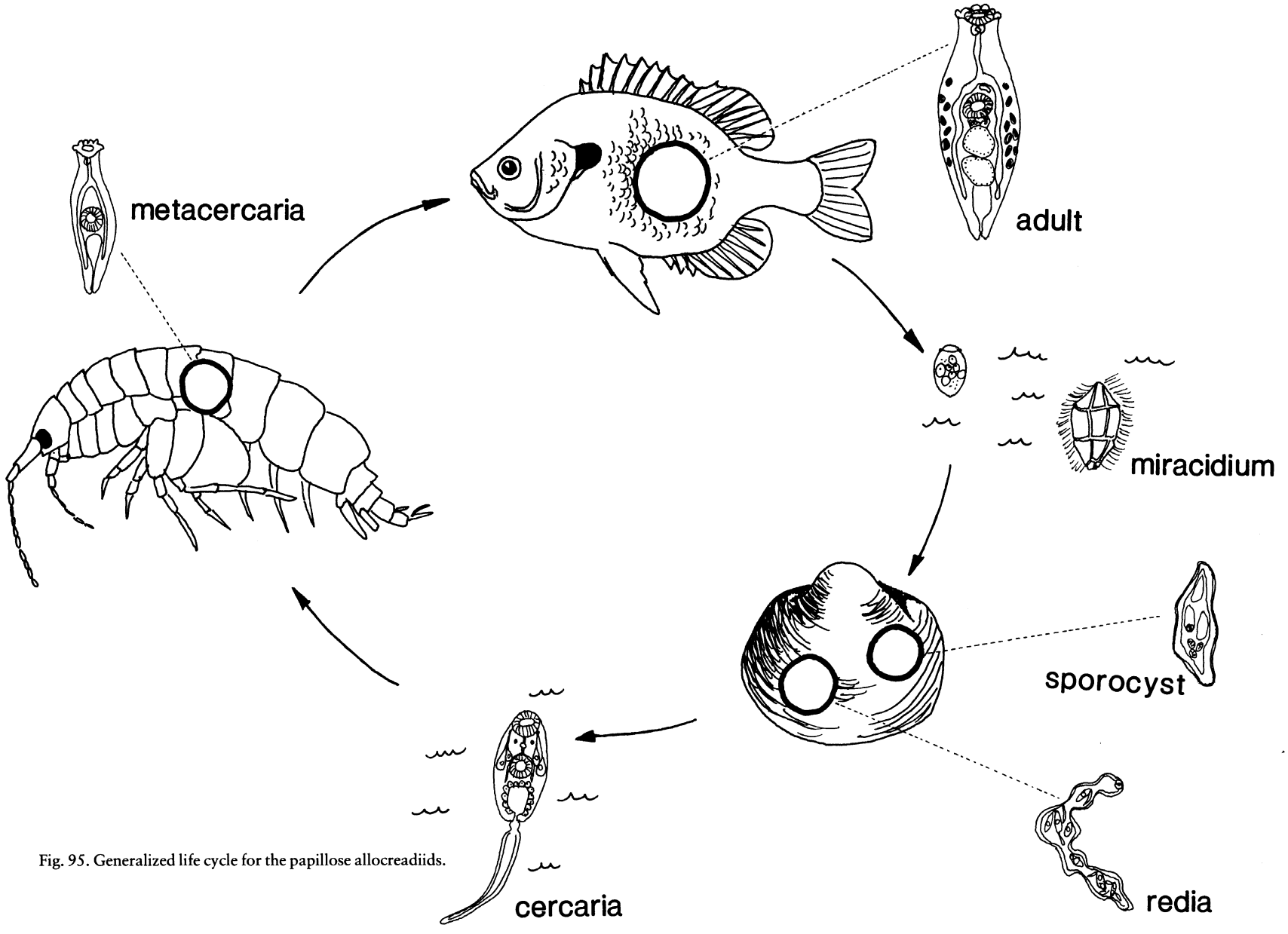
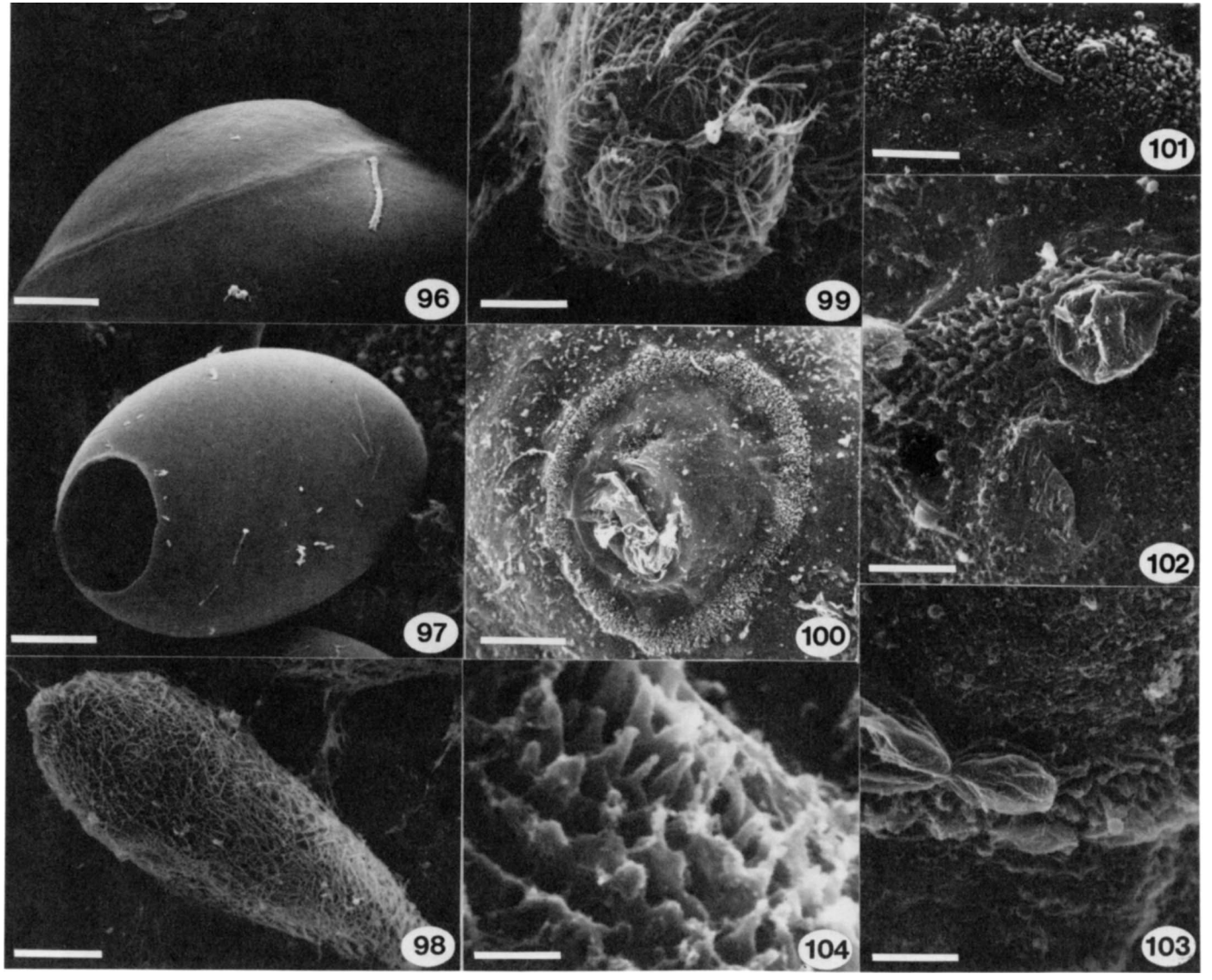
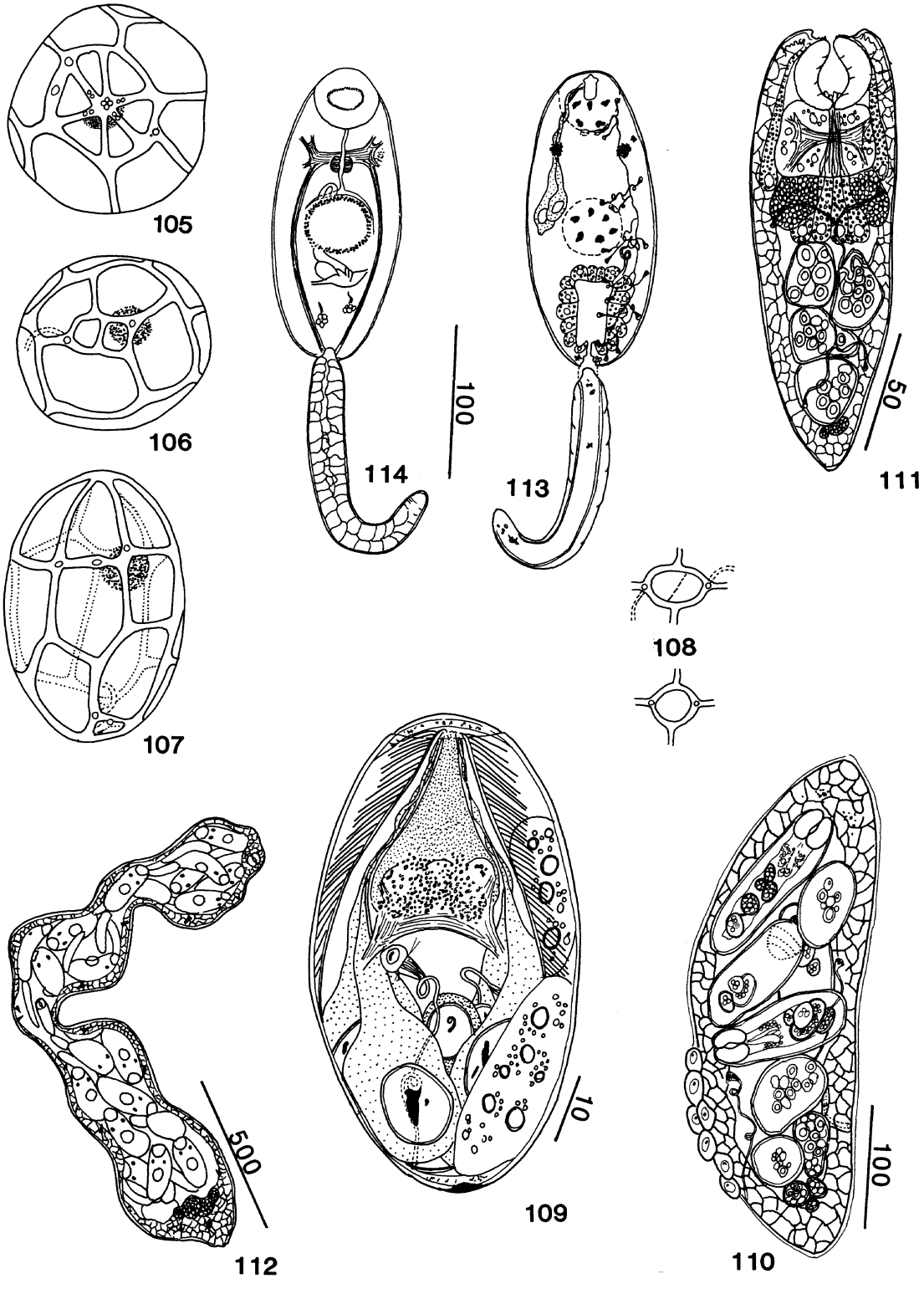


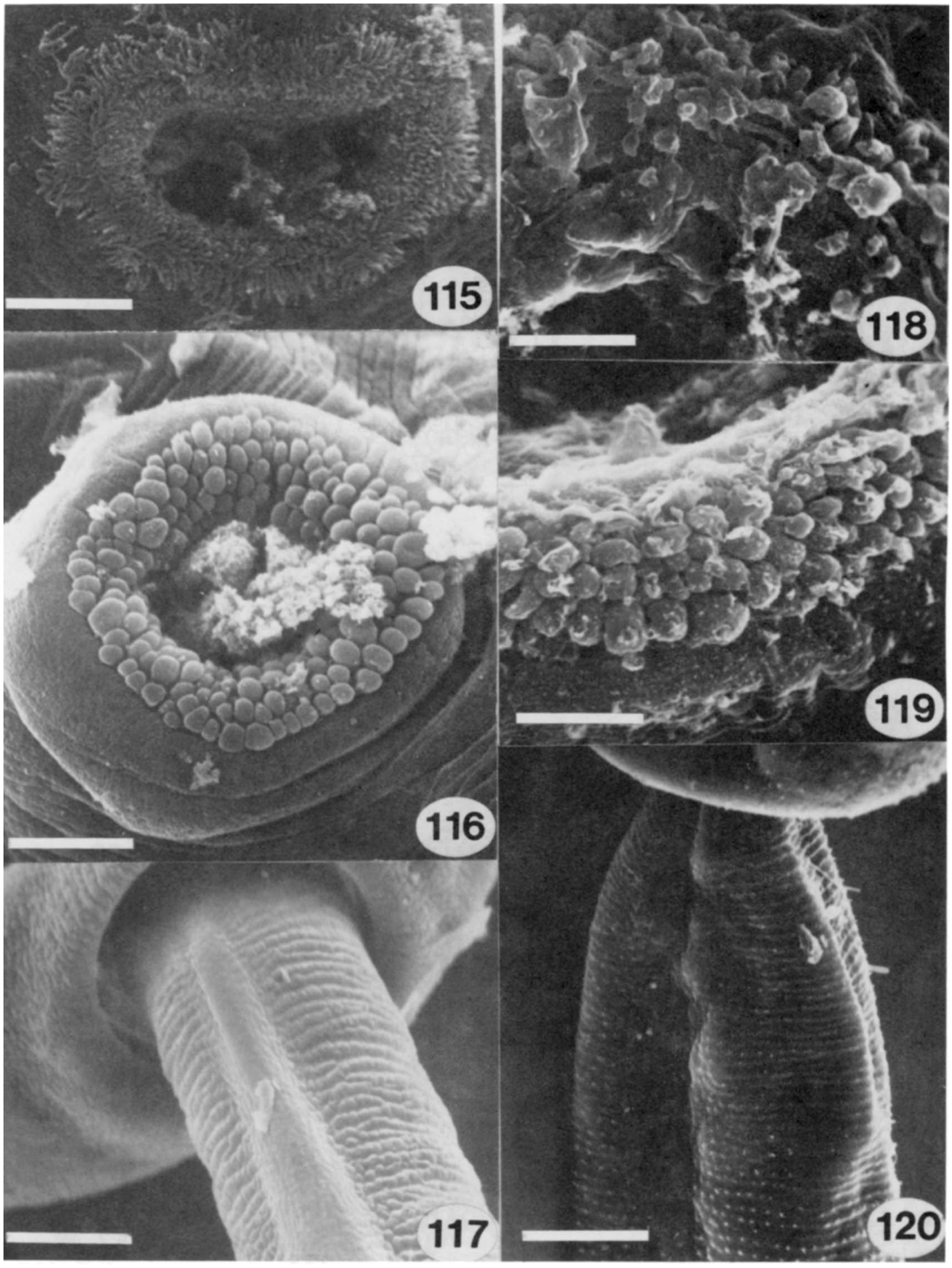
Fig. 95. Generalized life cycle for the papillose allocreadiids.



Figures 96-104. Scanning electron micrographs of life cycle stages of *Bunodera luciopercae*. Fig. 96. Detail of opercular suture of intact egg shell, scale bar = 4μ. Fig. 97. Egg shell with operculum removed, scale bar = 10μ. Fig. 98. Lateral view of miracidium, scale bar = 10μ. Fig. 99. Anterior view of terebratorium of miracidium, note presence of cilia on terebratorium, scale bar = 4μ. Figs. 100-104. Cercariae. Fig. 100. Oral aperture, scale bar = 8μ. Fig. 101. Detail of villiform protrusions surrounding oral aperture, scale bar = 3μ. Fig. 102. Detail of anterior portion of acetabulum, scale bar = 3μ. Fig. 103. Detail of posterior portion of acetabulum, scale bar = 3μ. Fig. 104. Magnified view of protrusions on posterior border of acetabulum, scale bar = 1μ.

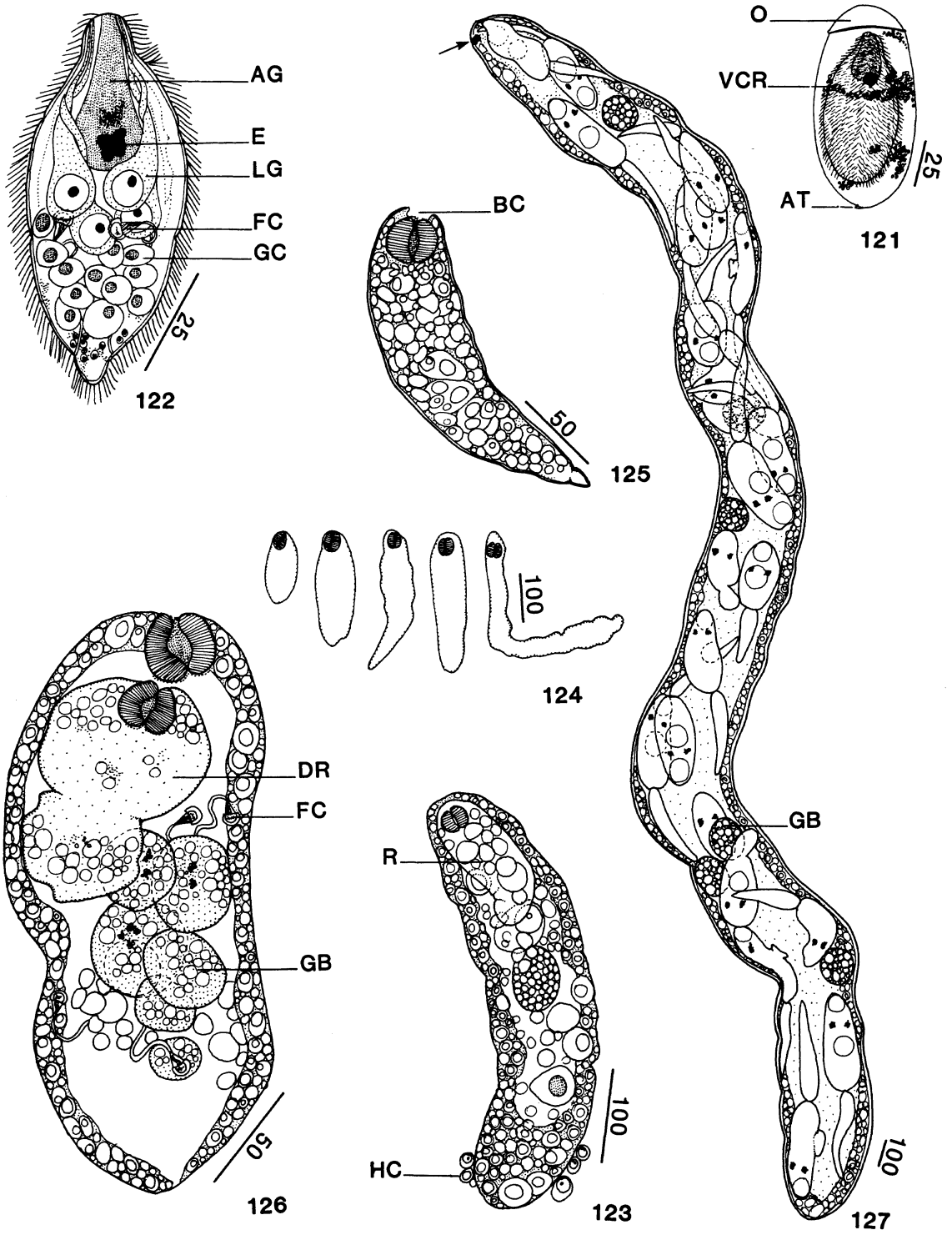


Figures 105-114. Larval forms of *Bunodera luciopercae*. Figs. 105-108. Miracidia stained with silver nitrate, after Peters and La Bonte (1965) Fig. 105. Anterior view. Fig. 106. Posterior view. Fig. 107. Lateral views. Fig. 108. Variations in posterior cells. Figs. 109-114. after Cannon (1971). Fig. 109. Miracidium within egg shell. Fig. 110. Sporocyst. Fig. 111. Young redia. Fig. 112. Mature redia. Fig. 113. Cercaria, dorsal view, excretory system is illustrated on reader's right, penetration glands on reader's left. Fig. 114. Cercaria, ventral view, note minute protrusions on acetabular margin.

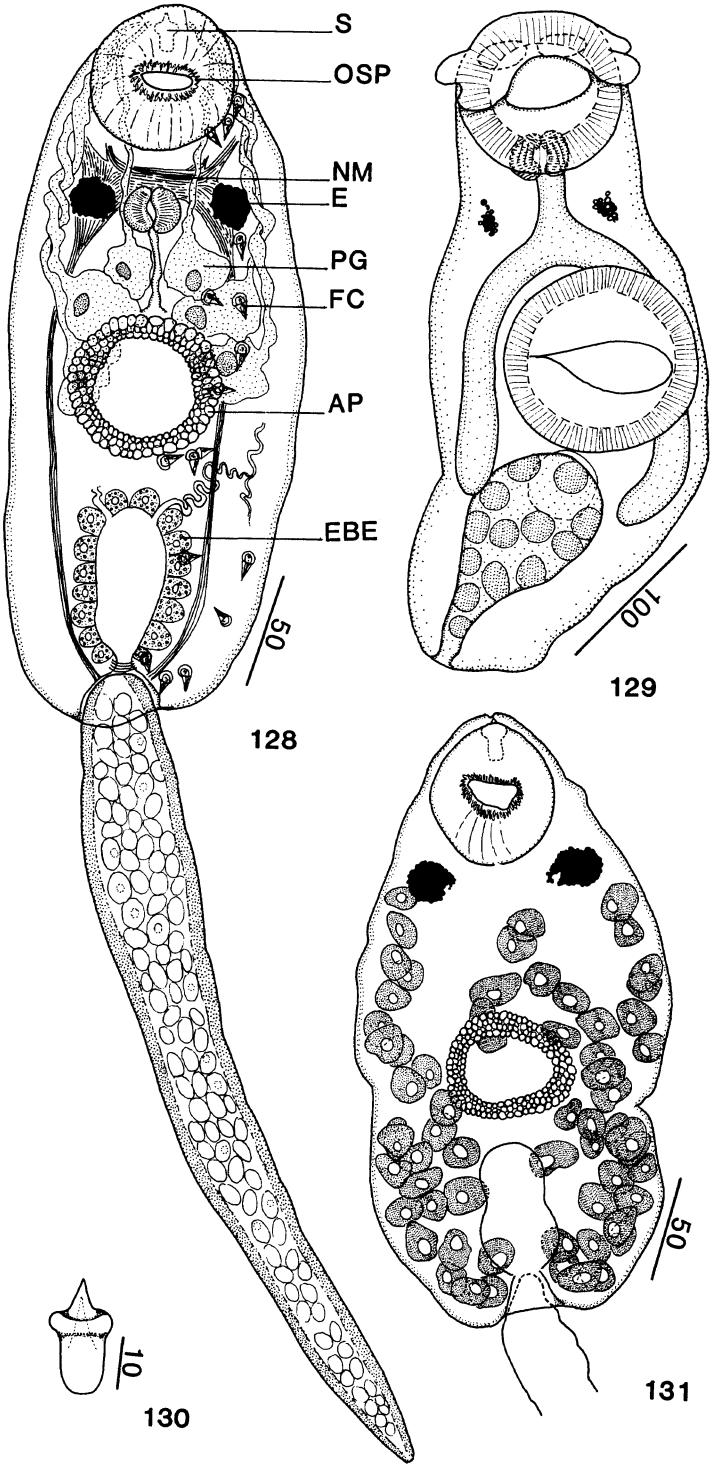


Figures 115-117. Scanning electron micrographs of cercariae of *Bunodera mediovitellata*. Fig. 115. Oral aperture, scale bar = 7μ. Fig. 116. Acetabulum, scale bar = 10μ. Fig. 117. Tail, ventral view, note absence of tail fins, scale bar = 6μ.

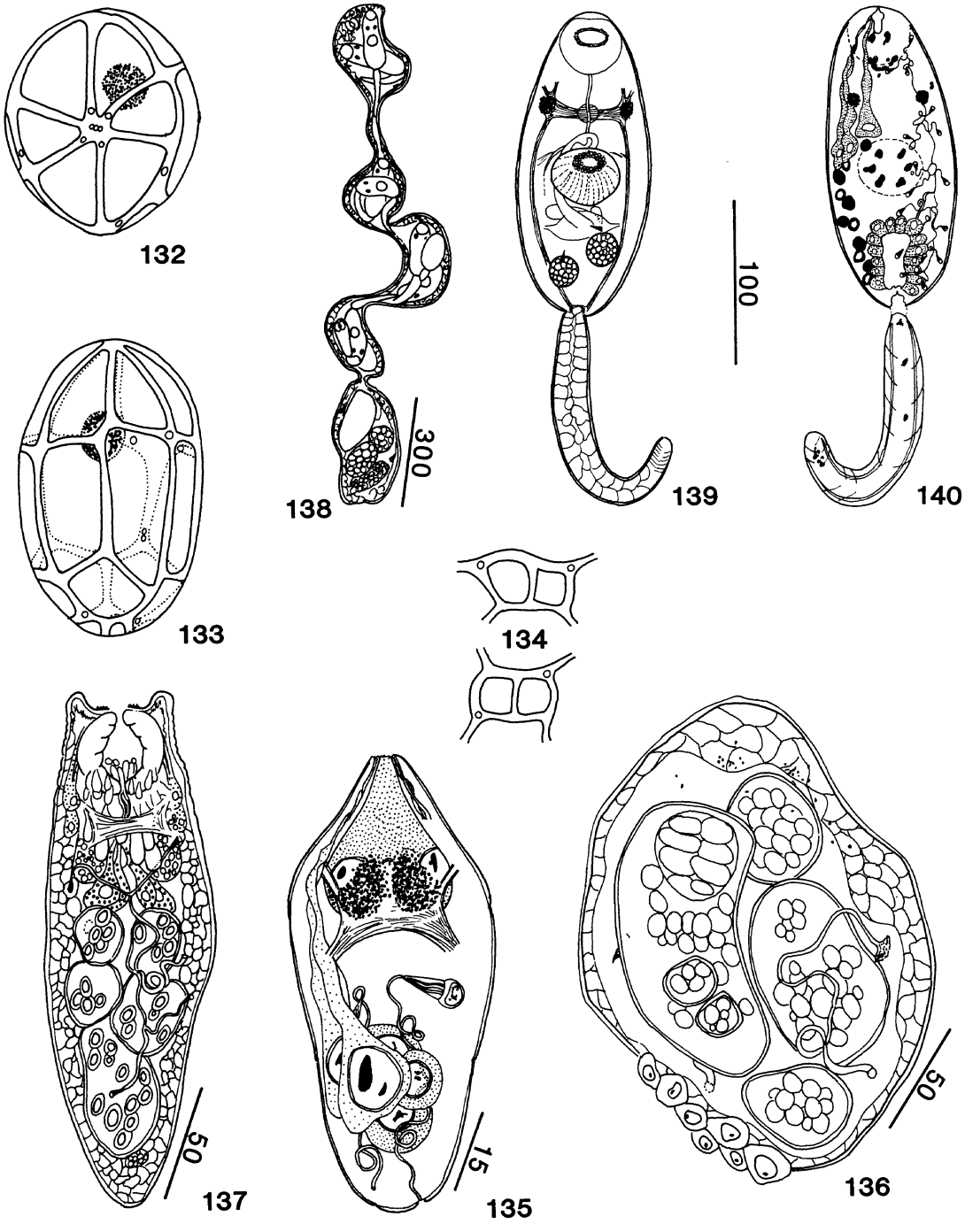
Figures 118-120. Scanning electron micrographs of cercariae of *Bunodera sacculata*. Fig. 118. Detail of anterior region of acetabulum, scale bar = 3μ. Fig. 119. Detail of posterior region of acetabulum, scale bar = 3μ. Fig. 120. Tail, note absence of tail fins, scale bar = 8μ.



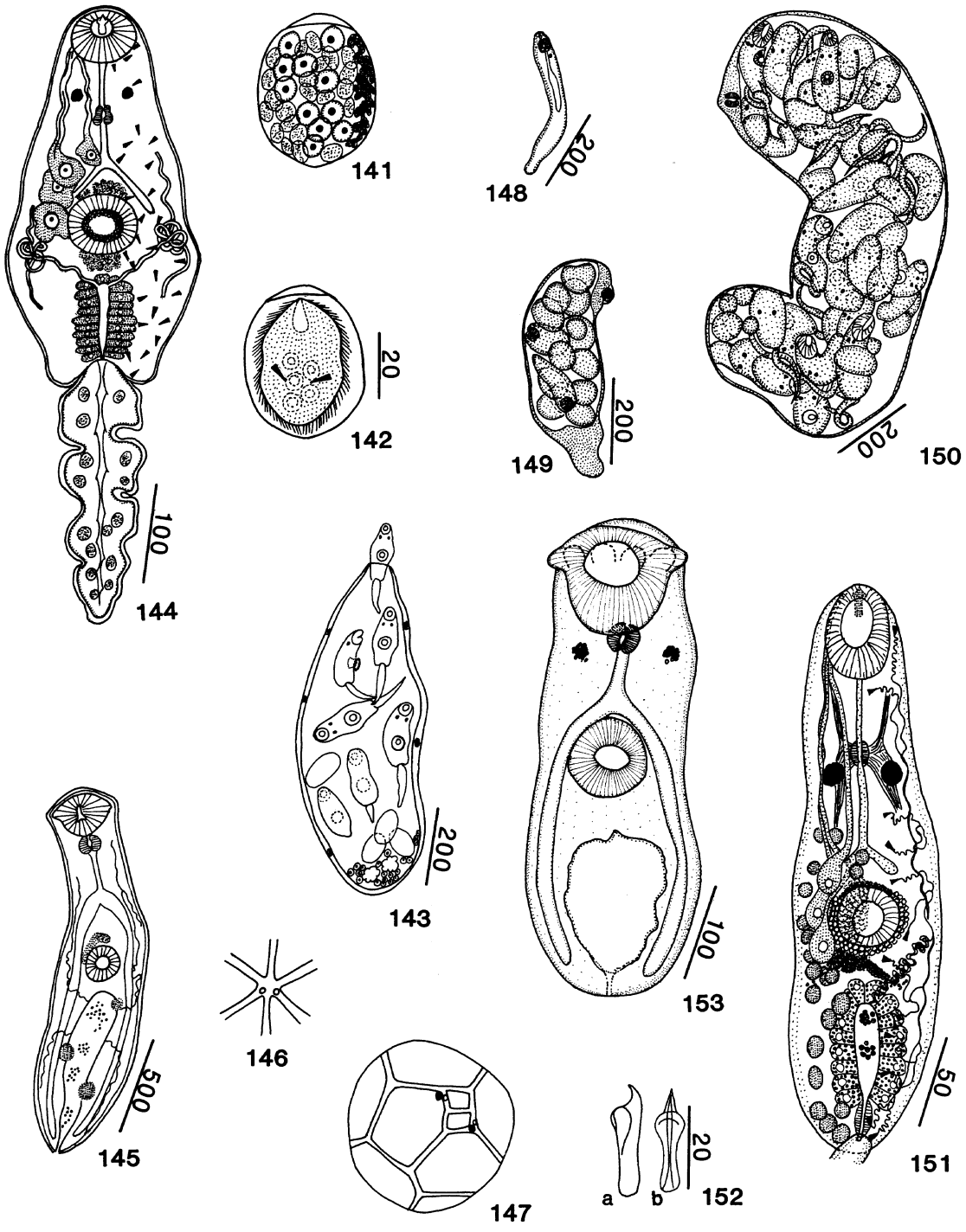
Figures 121-127. Larval forms of *Bunodera mediovitellata*, after Caira and Kennedy (in prep.). Fig. 121. Miracidium in egg at time of release from uterus. Fig. 122. Miracidium. Fig. 123. Sporocyst. Fig. 124. Various body forms of young rediae. Fig. 125. Detail of young redia. Fig. 126. Mother redia containing one daughter redia and several developing cercariae. Fig. 127. Mature redia, note pharynx at arrow.



Figures 128-131. Larval forms of *Bunodera mediovitellata*, after Caira and Kennedy (in prep.). Fig. 128. Cercaria, cystogenous glands omitted and flame cells illustrated on reader's right. Fig. 129. Cercaria illustrating cystogenous glands. Fig. 130. Stylet of cercaria. Fig. 131. Excysted metacercaria.

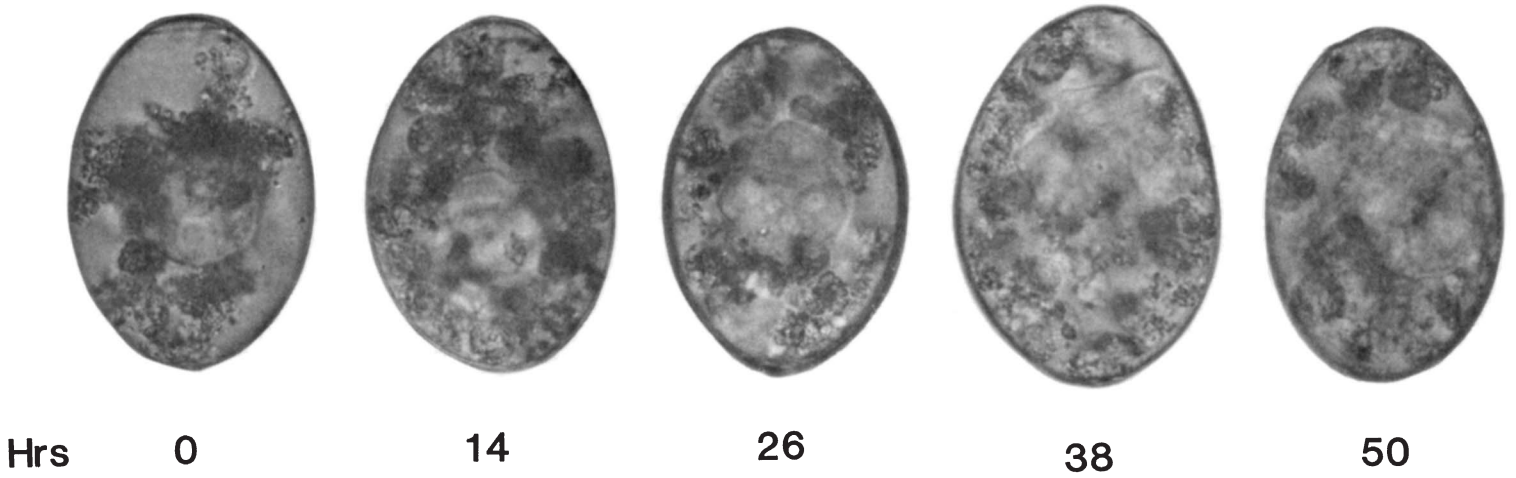


Figures 132-140. Larval forms of *Bunodera sacculata*. Figs. 132-134. Silver nitrate stained miracidia, after Peters and LaBonte (1965). Fig. 132. Anterior view. Fig. 133. Lateral view. Fig. 134. Posterior view showing two variations in excretory pore positions. Figs. 135-140. After Cannon (1971). Fig. 135. Miracidium, internal anatomy. Fig. 136. Sporocyst. Fig. 137. Young redia. Fig. 138. Mature redia. Fig. 139. Cercaria, dorsal view, flame cells are illustrated on the reader's right, penetration and cystogenous glands are illustrated on the reader's left. Fig. 140. Cercariae, ventral view, note acetabular protrusions.



Figures 141-145. Larval forms of *Bunoderella metteri,* after Anderson, Schell and Pratt (1965). Fig. 141. Egg with developing miracidium, 12 days after release from uterus. Fig. 142. Egg with developing miracidium, 37 days after release from uterus. Fig. 143. Redia. Fig. 144. Cercaria, flame cells shown on reader's right, penetration glands shown on reader's left. Fig. 145. Metacercaria.

Figures 146-153. Larval forms of *Crepidostomum cooperi.* Fig. 146. Miracidium stained with silver nitrate, anterior view. Fig. 147. Miracidium stained with silver nitrate, posterior view. Figs. 148-152. after Hopkins (1934). Fig. 148. Young redia, note gut. Fig. 149. Mother redia with daughter redia and germ balls. Fig. 150. Mature redia with cercariae. Fig. 151. Cercaria, acetabular protrusions altered to conform with SEM results. Excretory system is illustrated on reader's right, cystogenous and penetration glands on reader's left. Fig. 152. Stylet, a. lateral view, b. dorsal view. Fig. 153. Excysted metacercaria.



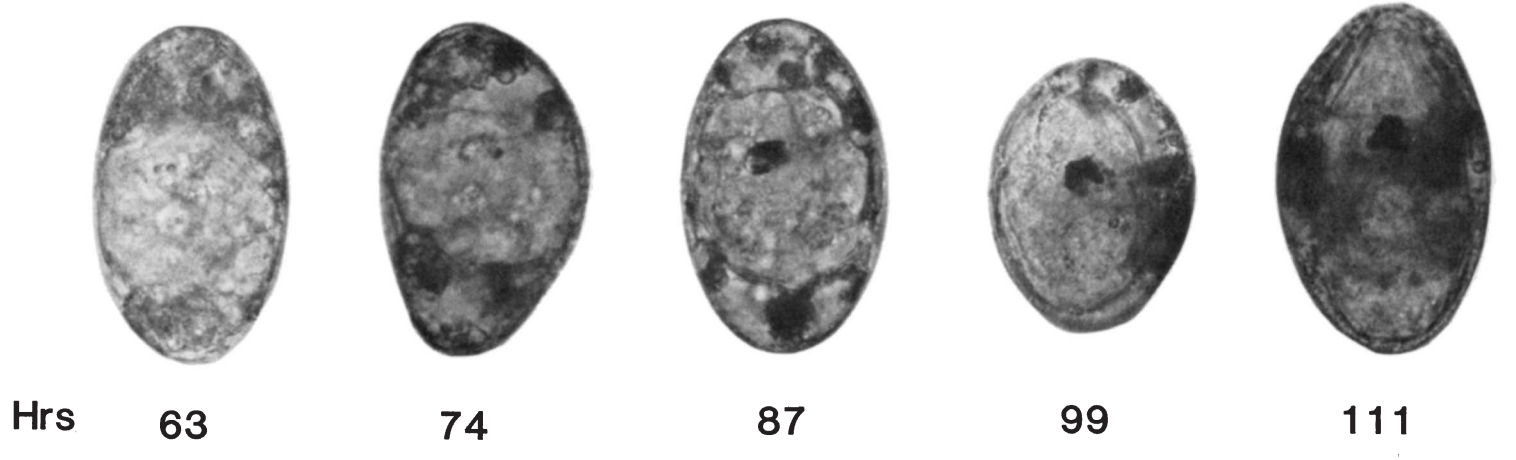


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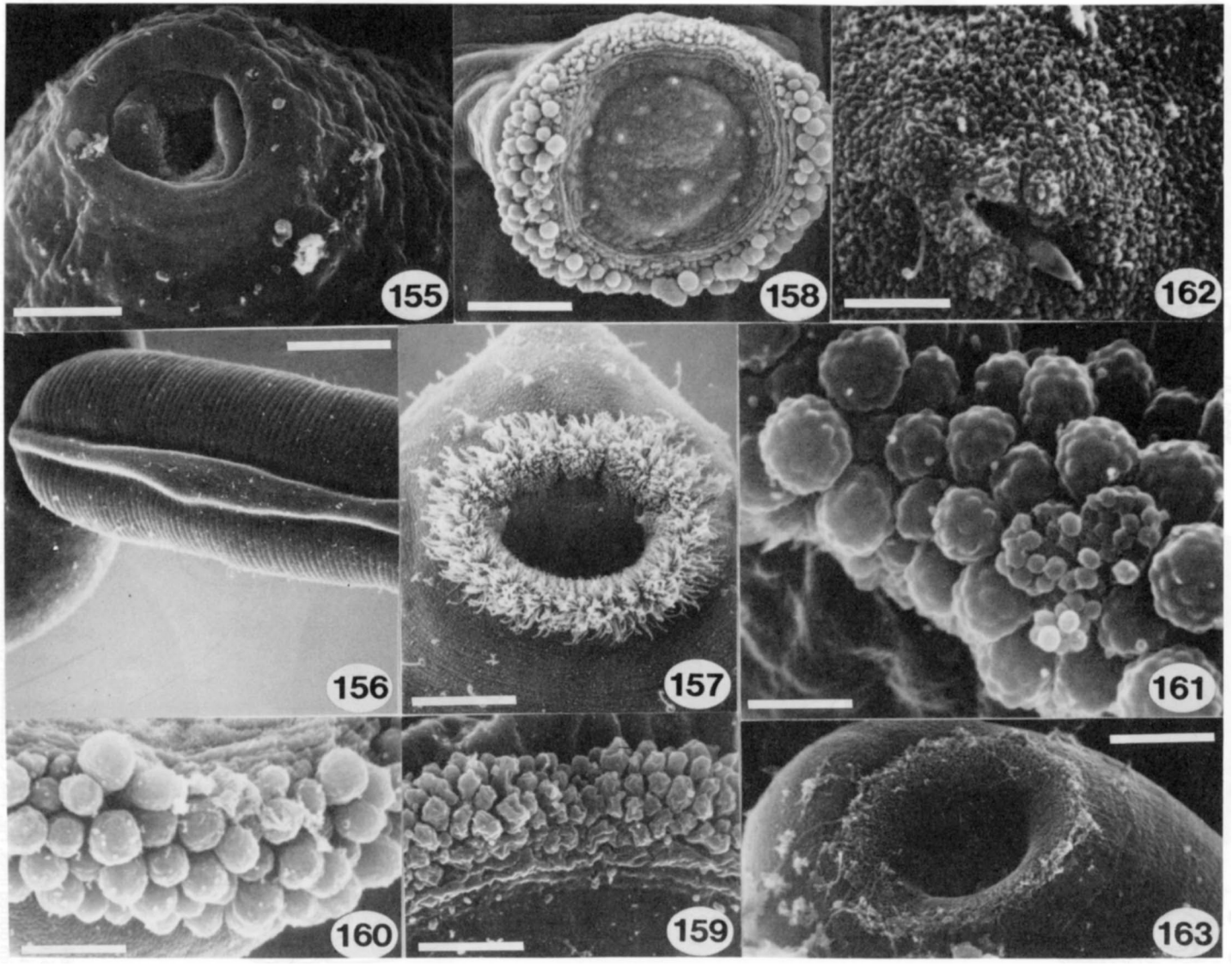
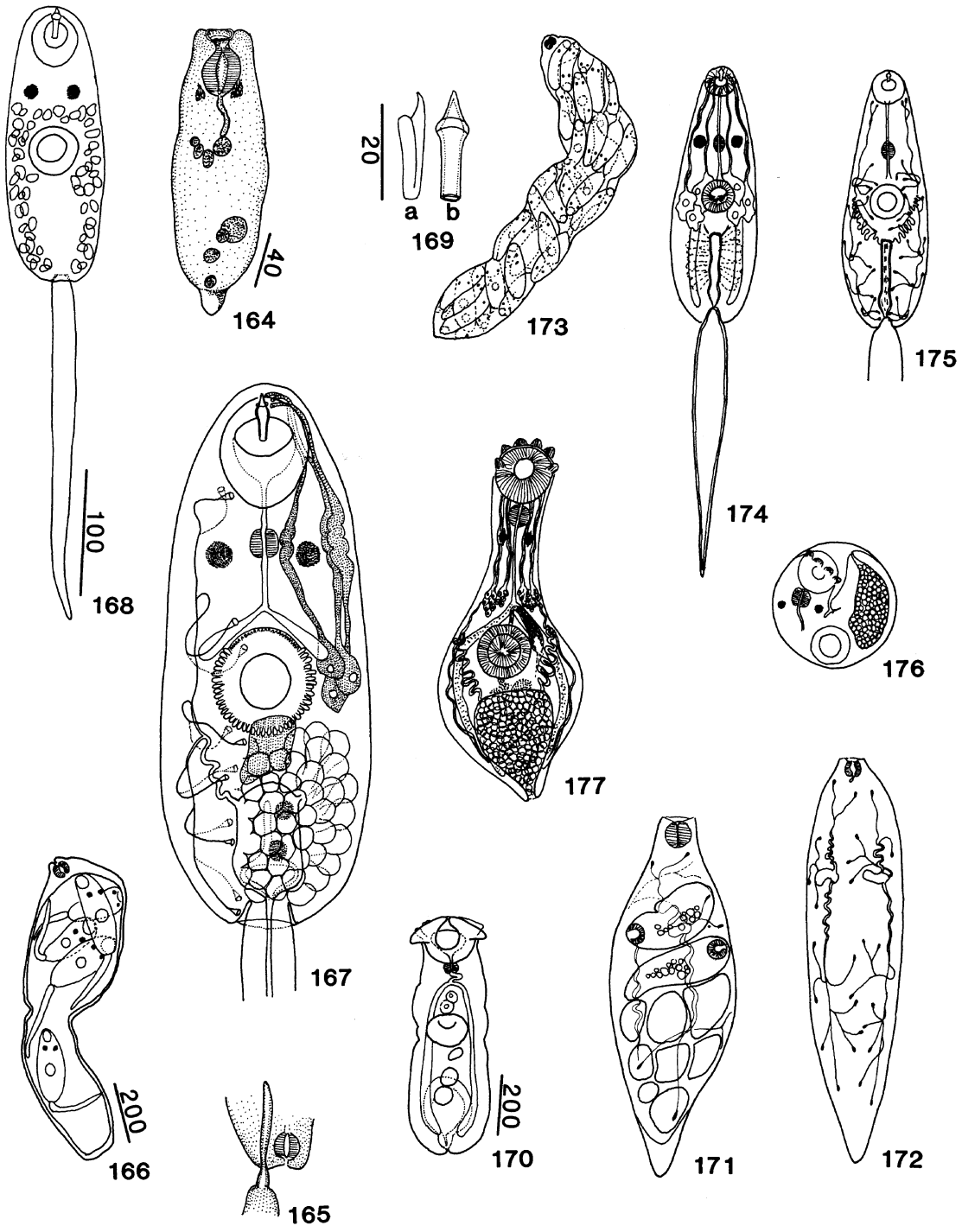
Figure 154. Stages in development of the miracidium of *Crepidostomum cooperi*. Hours after release from the uterus are given below each egg.



Figures 155-162. Scanning electron micrographs of *Crepidostomum cooperi*. Fig. 155. Redia, anterior view. Figs. 156-162. Cercariae. Fig. 156. Tail, ventral view, scale bar = 8μ. Fig. 157. Oral aperture, note numerous villiform protrusions, scale bar = 7μ. Fig. 158. Acetabulum, scale bar = 10μ. Fig. 159. Detail of anterior border of acetabulum, scale bar = 3μ. Fig. 160. Detail of posterior border of acetabulum, scale bar = 3μ. Fig. 161. Magnified view of protrusions on posterior border of acetabulum, scale bar = 2μ. Fig. 162. Partially protruding stylet, scale bar = 2μ.

Figure 163. Scanning electron micrograph of oral aperture of cercaria of *Crepidostomum cornutum*, note villiform protrusions, c.f. Fig. 159, scale bar = 7μ.



Figures 164-170. Larval forms of *Crepidostomum cornutum*. Figs. 164-165 after Cheng and James (1960b). Fig. 164. Daughter redia, note gut. Fig. 165. Cercaria escaping through birth pore of daughter redia. Figs. 166-170 after Henderson (1938). Fig. 166. Redia with cercariae. Fig. 167. Cercaria, penetration glands are shown on reader's right, flame cells on reader's left. The three typical shapes of the excretory bladder are indicated with dotted lines. Fig. 168. Cercaria with cystogenous glands. Fig. 169. Stylet, a. lateral view, b. dorsal view. Fig. 170. Excysted metacercaria.

Figures 171-177. Larval forms of *Crepidostomum farionis*, after Brown (1927). Fig. 171. Mother redia with two daughter rediae. Fig. 172. Excretory system of redia, note two excretory bladders. Fig. 173. Mature redia. Fig. 174. Cercaria. Fig. 175. Excretory system of cercaria. Fig. 176. Encysted metacercaria. Fig. 177. Excysted metacercaria.

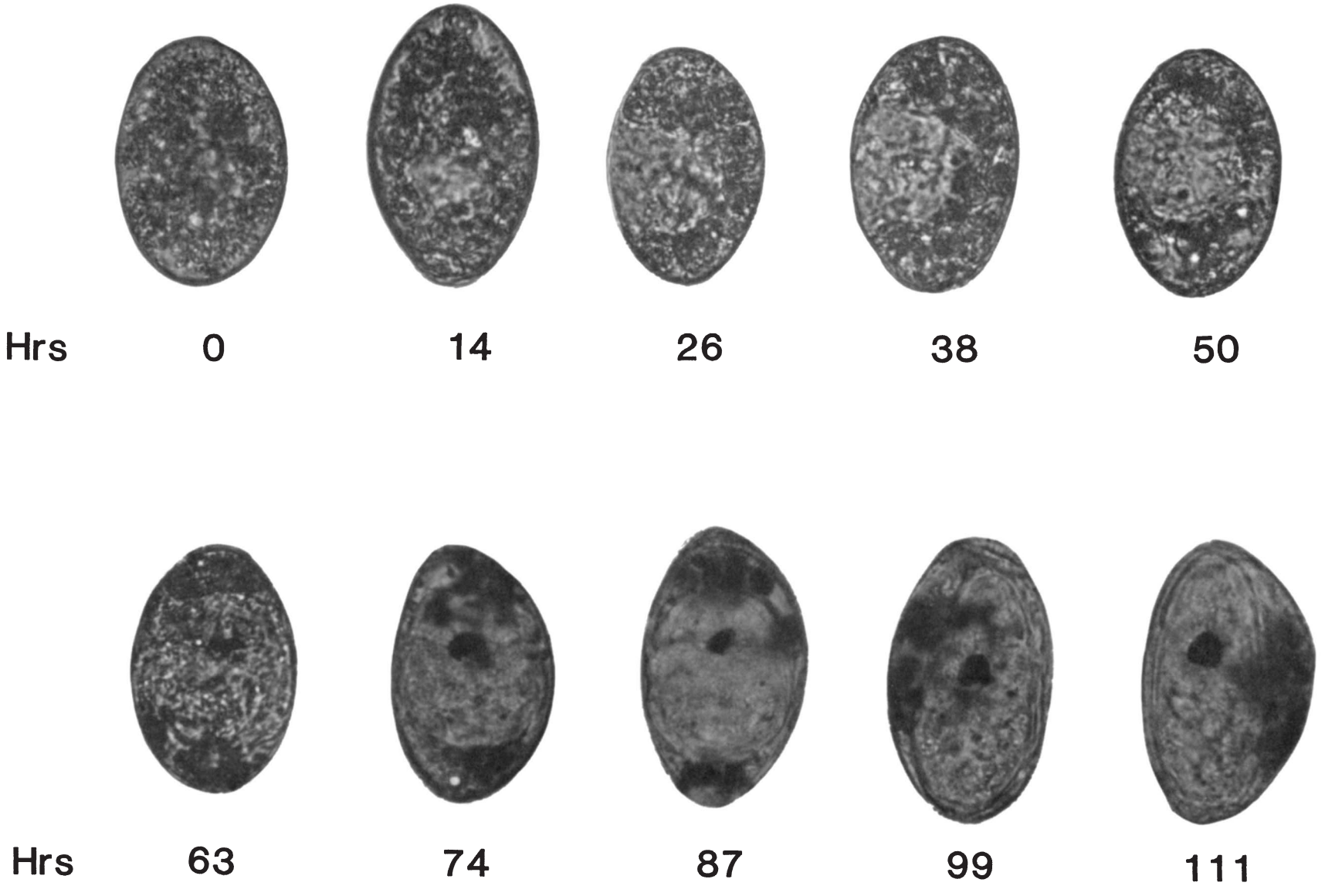
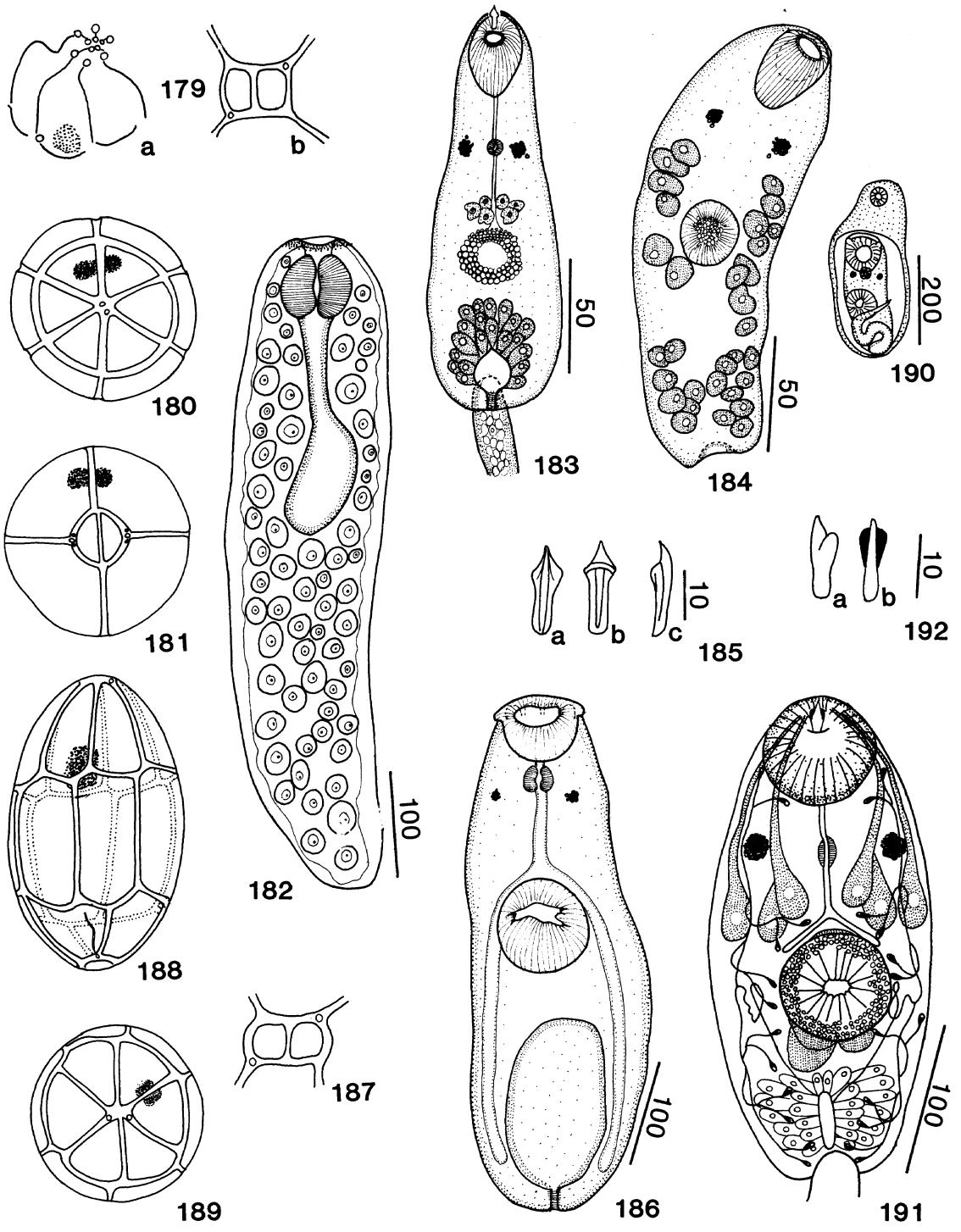


Figure 178. Stages in the development of the miracidium of *Crepidostomum ictaluri*. Time since release from the uterus is given below each egg.

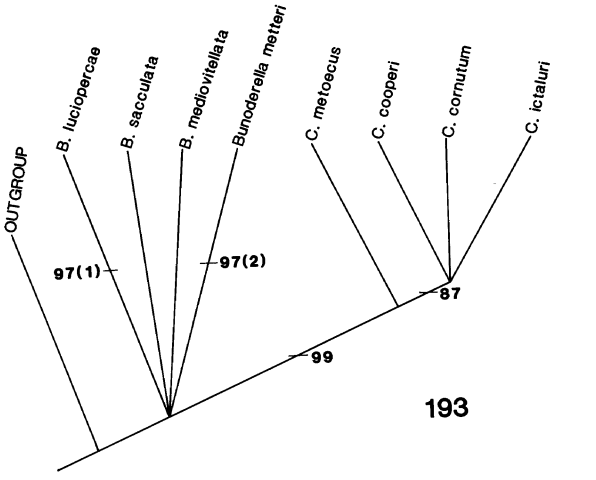


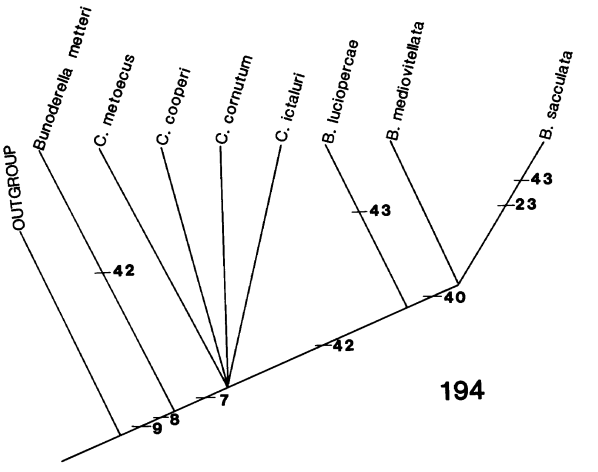
Figures 179-186. Larval forms of *Crepidostomum ictaluri*. Fig. 179. Silver nitrate stained miracidia, a. anterior view, b. posterior view, after Amato (1979). Figs. 180-181. Silver nitrate stained miracidia, after Seitner (1950). Fig. 180. Anterior view. Fig. 181. Posterior view. Fig. 182. Young redia, note gut, after Amato (1979). Fig. 183. Cercaria excluding cystogenous glands. Fig. 184. Cercaria with cystogenous glands. Fig. 185. Stylet, a. ventral view, b. dorsal view, c. lateral view, after Amato (1979). Fig. 186. Excysted metacercaria.

Figures 187-189. Miracidia of *Crepidostomum illinoiense* stained with silver nitrate, after Peters (1963). Fig. 187. Posterior view. Fig. 188. Lateral view. Fig. 189. Anterior view.

Figure 190 *Crepidostomum isostomum* (?) redia containing one cercaria with well developed oral sucker papillae, after Hopkins (1934).

Figures 191-192. Cercaria of *Crepidostomum metoecus*, after Polansky (1982). Fig. 191. Cercaria. Fig. 192. Stylet, a. lateral view, b. dorsal view.





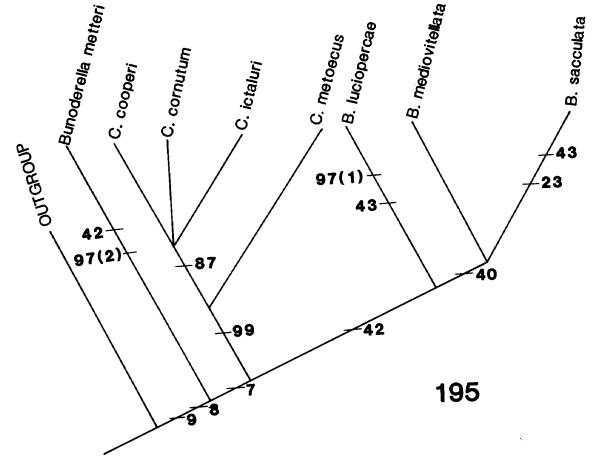


Figure 193. Cladogram generated from cercarial data in Table 3. Characters are indicated preceding or following a dash; numbers correspond to characters in the cercarial analysis section.

Figure 194. Reduced adult cladogram. Only those taxa from Fig. 94 that appear in the cercarial tree are included. Characters are indicated preceding or following a dash; numbers correspond to characters in the adult analysis section.

Figure 195. Consensus tree generated by combining cercarial and adult data. Characters are indicated preceding or following a dash; numbers correspond to characters in the cercarial or adult section.

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