PHORESIES, BIOCOENOSES AND THANATOCOENOSES IN THE *EPHEMEROPTERA*. — SUPPLEMENT

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Since publication of *Phorésies*, biocoenoses et thanatocoenoses... (ARVY, PETERS 1973), we have learned of other organisms living with *Ephemeroptera*, and new publications have appeared. In preparing this supplement, we tried to see all works cited, and discovered some errors in the bibliography to ARVY and PETERS (1973). Thus, in the references to this paper, corrections to references from ARVY and PETERS (1973) are preceded by an "*". When we were unable to verify a reference, the source is given in parentheses. We only give the author and date to references previously cited (ARVY, PETERS 1973). Unless otherwise stated, general classification of organisms is from the *Traité de Zoologie* edited by P.-P. Grassé.

Other authors have reviewed the biological relationships of mayflies. We wish to acknowledge the work of Bogoescu (1958) on mayfly parasites, Thomson (1960) on insects and *Microsporida*, Timon-David (1958) on insects as intermediate hosts of trematodes, Poinar (1975) on nematodes in insects, Brittain (1973) on life cycles of *Ephemeroptera* and vertebrate parasites, and Burton and McRae (1972) on *Simuliidae*, *Odonata*, and *Ephemeroptera*.

We also take this occasion to correct errors in the spelling of the generic names of the peritrich Zoothamnium (not Zoothamnium), the microsporidan Trichoduboscquia (not Trichoduboscquia), and the trematode Eustomos (not Eustomes).

1° FUNGI (classification from AINSWORTH, 1971)

a. Chytridiomycetes, Chytridiales

1°) Fungi invading the host:

One statement in our 1973 paper should be corrected. Codreanu (1931) assigned Endoblastidium to the family Olpidiaceae, not Chytridiaceae. In 1939, Codreanu reported an Endoblastidium sp. from Ecdyonurus lateralis (Curtis) (Heptagenia). Dr. J. W. Kimbrough has made a thorough search of all indexing books and journals on fungi, and reports that no one else has encountered Endoblastidium—in the Fungi; but this only begins the story.

Sprague (1963), revising the protozoans Haplosporidium and Minchinia, stated that species of Haplosporidiidae described from Ephemeroptera were incorrectly classified, and that figures of Haplosporidiidae

sporidium ecdyonuris Weiser, 1947 closely resembled Endoblastidium legeri Codreanu, 1931. Subsequently, Weiser (1965) assigned many Haplosporida genera to the Chytridiales, Polycaryum and Coelomycidium included; he then (1966) transferred Haplosporidium ecdyonuris to Polycaryum. Weiser (1966) also noticed the similarity between Polycaryum ecdyonuris and Endoblastidium legeri and a parallel similarity between E. caulleryi Codreanu, 1931 and Coelomycidium ephemerae Weiser, 1947. Further study may prove the species of Codreanu and of Weiser identical.

Weiser (1969) offered one suggestion to help us distinguish these "protozoa-like fungi" from true protozoa. Protozoan infections are characterized by an affinity for a single tissue, often the gut or fat bodies, while fungal infections liquify and eventually digest the whole content of the host's body. However, there are numerous exceptions. As an example, species of *Minchinia*, a true *Haplosporida*, often cause systemic infections and upon sporulation cause extensive tissue destruction (Perkins, personal communication).

2°) Fungi saprophytic on exuviae:

There is a unique collection of species which are saprophytic on invertebrate exuviae, and appear entirely confined to this habitat (Sparrow, 1938). Twelve species have been reported from mayfly exuviae, but more undoubtedly exist. Chemical substances produced by molting insects apparently attract the swimming spores, a theory supported by the selective nature of these fungi. Exuviae of craneflies and mosquitos are rarely occupied, while exuviae of mayflies, midges, and dragonflies are chosen, and pupal cases of caddisflies are especially preferred (Sparrow, 1938).

Although frequently referred to as "chitinophyllic", it seems the fungi do not actually attack chitin. Karling (1945a) found the great majority of sporangia inside of insect exuviae and Sparrow (1960) noted that fungi only flourish for a few days in the exuviae, and then form spores or become quiescent. Hanson (1946), studying *Phlyctorhiza endogena* Hanson, 1946, found that the fungus actually grows in the basement membrane, composed not of chitin but of connective tissue.

SPARROW (1960) lists the following species from mayflies:

A. Family Phlyctidiaceae

1. Phlyctorhiza endogena HANSON, 1946. Also on Odonata, Diptera; eastern USA.

B. Family Rhizidiaceae

- 2. Asterophlyctis sarcoptoides Peterson, 1903. Reported by Sparrow (1938); also on Odonata, Trichoptera, Chironomidae; Denmark, eastern USA.
- 3a. Rhizidium chitinophilum Sparrow, 1960. Reported by Sparrow (1938) (R. mycophilum); also on Chironomidae; eastern USA.
- 3b. Rhizidium ramosum Sparrow, 1938. Also on Trichoptera, Chironomidae; Denmark, eastern USA.
- 4a. Rhizoclosmatium aurantiacum Sparrow, 1938. Also on Trichoptera, Chironomidae; Denmark, eastern USA.
- 4b. Rhizoclosmatium globosum Petersen, 1903. Reported by Sparrow (1938); also on Odonata, Trichoptera, Diptera; Denmark, eastern USA.
- 5a. Siphonaria petersenii Karling, 1945 (b). Also on other insects; Amazonas, Brazil, eastern USA.
- 5b. Siphonaria sparrowii KARLING, 1945 (b). Amazonas, Brazil, eastern USA.
- 5c. Siphonaria variabilis Petersen, 1903. Reported by Sparrow (1938); also on Trichoptera, Odonata; Denmark, eastern USA.

C. Family Chytridiaceae

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- 6a. Chytriomyces aureus KARLING, 1945 (a). Amazonas, Brazil, eastern USA.
- 6b. Chytriomyces hyalinus Karling, 1945 (a). Also found on chitin and soil; Amazonas, Brazil, USA, northwestern Africa, South Africa.
- 7. Rhopalophlyctis sarcoptoides KARLING, 1945 (a). Amazonas, Brazil, eastern USA.

β. Trichomycetes

LICHTWARDT (1972) described Glotzia ephemeridarum, a new species of Harpellales (Genistellaceae), from the hindgut lining of Baetis tricaudatus Dodds nymphs in Utah, and in 1973 he discussed phylogenetic relationships in the Trichomycetes. Then Moss, LICHTWARDT and MANIER (1975) described Zygopolaris ephemeridarum, a new genus and species of Genistellaceae from nymphs of Ephemerella inermis EATON and Baetis parvus Dodds in the Rocky Mountain region of the United States. Zygopolaris superficially resembles Pteromaktron in that it projects from the anus of the mayfly host, but it is distinguished from Pteromaktron in the shapes of the thallus, holdfast, and trichospores and in the arrangement of generative cells. Zygopolaris ephemeridarum may coexist with Glotzia ephemeridarum and Paramoebidium sp. (Moss, LICHTWARDT, MANIER, 1975).

2° PROTOZOANS

In the last few years, several publications have revised the higher classification of protozoans (Honigher et al., 1964, Levine, 1970, de Puytorac et al., 1974). Following these authors, the *Protozoa* are now divided into five subphyla (or phyla – depending on the author): the *Sarcomastigophora* (flagellates and sarcodinids), the *Apicomplexa*, the *Microspora*, and the *Myxospora* (all three formerly *Sporozoa*), and the *Ciliophora* (ciliates). The electron microscope has made possible detailed study of protozoa, so that the classification of these groups is currently in a transitional stage.

2a. External

a. Phytamastogophorea, Euglenida (Sacromastigophora)

Colacium is a genus of Euglenidae distinct from Euglena in its pyrenoid structure and in its epizoic relationship with aquatic invertebrates, particularly zooplankton. Rosowski and Kugrens (1973) gave a long list of hosts from Nebraska which included unidentified nymphs of Ephemeroptera. While Cyclops and Keratella were most common natural hosts, Colacium also grew well in soilwater and media cultures. Rosowski and Kugrens (1973) worked out the life cycle, forms, and variations of the attachment structure of C. vesiculosum Ehrenberg, 1833, concluding that more than half of the named species of Colacium were variations of C. vesiculosum. They did not, however, attempt to identify the species found on Ephemeroptera.

β. Oligohymenophora, Peritrichida (Ciliophora)

There are some major papers on Peritrichida which we overlooked earlier. Stiller (1931) described Epistylis geleii from the head of an Epeorus nymph in Hungary, and Kahl (1935) described Rhabdostyla ephemerae and Vorticella ephemerae from unidentified mayflies. Sommer (1951) revised the families after studying the Peritrichida from lakes near Plön. The genera Epistylis, Rhabdostyla, and Opercularia are in Epistylidae, Vorticella and Carchesium in Vorticellidae, and Pyxicola in Vaginicolidae. She established a new family Zoothamniidae for Zoothamnium, Pseudocarchesium new genus, and others. Pseudocarchesium erlangensis (Nenninger, 1948) = Carchesium erlangensis [= Carchesium ephemera šrámek-Hušek, 1948 (according to Beigel, 1954)]. Sommer (1951) found again Opercularia nutans Ehrenberg, 1838 on Caenis nymphs and Vorticella octava Stokes, 1885 on Baetis nymphs, and added three more species to those reported from mayflies, all found on nymphs of Caenis: Vorticella convallaria L., 1758, V. campanula Ehrenberg, 1831, and Zoothamnium ramosissimum Sommer, 1951,

2b. Internal

a. Microsporea, Microsporida (Microspora)

Codreanu (1966) described Mitoplistophora angularis, a monotypic new genus and species of Nosematidae, from fat bodies of Ephemera danica (Müller) nymphs of mountain streams, Romania. Mitoplistophora is distinguished from other Microsporida by fusiform or triangular sporonts with two or three flagelliform appendages, each sporont containing 2, 8, 16, 32, 48, or 64 spores. Sporonts range in size from $7 \times 3.5 \,\mu$ (microns) to $17 \times 12 \,\mu$, appendages from $6-12 \,\mu$, the larger sporonts containing the greater number of spores.

Codreanu (1968) described Gurleya linearis, another new species, also from Ephemera danica in Romanian mountain streams, and gave additional data on Stempellia mutabilis Léger & Hesse, 1910. In 1970, Codreanu and Vavra described the ultrastructure of sporonts of Telomyxa glugeiformis Léger & Hesse, 1910.

Effects of an infection of *Thelohania* sp. on *Rhithrogena semicolorata* (Curtis) were discussed by Fahy (1975). Infected mayflies displayed characteristic white, tumor-like patches on the abdomen. The infection first appeared in the fat bodies, then spread through the abdomen converting fat bodies to sporagenous tissue. In heavily infected individuals muscle tissue was destroyed, the gut was reduced in width, but the abdomen was swollen with *Microsporida*. Nymphs died before emerging; the cause of death appeared to be fungal infections which attacked the already weakened nymphs (Fahy, 1975).

HAZARD and OLDACRE (1975) established a new family Thelohaniidae and revised Thelohania. T. mutabilis Kudo, 1923, T. baetica Kudo, 1923, T. rhithrogenae Weiser, 1946, and T. wurmi Weiser, 1946 were removed from the genus; however, lacking electron microscopic study of their spore structure, they were not assigned to other genera. Thelohania seems limited to parasites of decapod crustaceans (HAZARD, OLDACRE, 1975).

Fig. 18 (ARVY, PETERS, 1973) was from Léger (1926b). The identical paper was published again in 1927 by Léger.

β. Haplosporea, Haplosporida (Microspora)

There may be no Haplosporida in mayflies. Weiser (1965, 1966) transferred Polycaryum ecdyonuris (Haplosporidium) and Coelomycidium ephemerae to the chytrid fungi, retaining only Haplosporidium bayeri Weiser, 1947. Sprague (1963, personal communication) would also remove H. bayeri from Haplosporida.

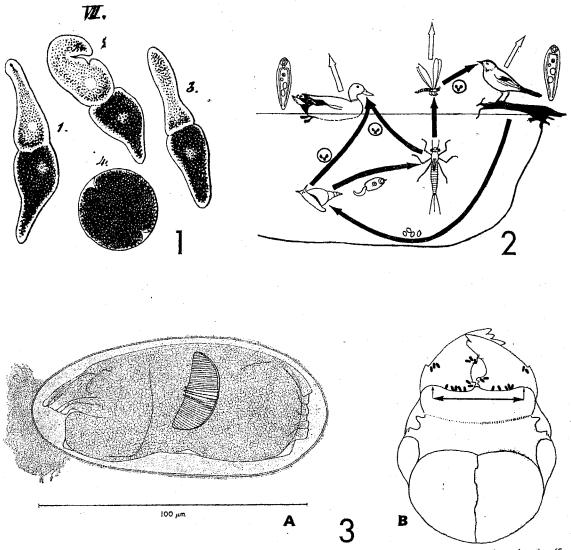
y. Sporozoea (Apicomplexa)

I. Eugregarinida

One new species of gregarine has been found in *Ephemeroptera*. Geus (1967) described *Gamocystis humilis* from the intestine of *Ephemera vulgata* L. nymphs collected in Lake Ohrid on the Yugoslavia-Albania border. Desportes (1974) published on the ultrastructure of *Enterocystis fungoides* M. Codre-Anu, 1939 and Rühl (1974) described the ultrastructure of *Gamocystis ephemerae* (Frantzius, 1848). Rühl (1974) reported that *Gamocystis* has no septum between the protomerite and the deuteromerite and should be removed from *Gregarinidae*.

The first gregarine described from Ephemeroptera was Gregarina clavata Kölliker, 1845, found in Ephemera vulgata. Frantzius (1846) then found what he thought was the same species in E. vulgata. Kölliker (1848) discussed the differences between his specimens and those of Frantzius, so Frantzius (1848) named his species Zygocystis ephemerae (now Gamocystis, Fig. 1). The two species were frequently treated as synonyms until Diesing (1859) recognized both as valid. Unfortunately, a typographical error in Diesing (1859) dated Gamocystis ephemerae as 1843 instead of 1848.

One other species from mayflies, Clepsidrina granulosa SCHNEIDER, 1887, was synonymized with Gregarina clavata by KAMM (1922). LABBÉ (1899) made Gamocystis francisci SCHNEIDER, 1882 a synonym of Gamocystis ephemerae. The Schneider synonyms have some importance as they are more detailed and better illustrated than the original works.



Figs. 1-3. 1. Gamocystis ephemerae (Frantzius): 1, 2, 3, variae formae; 4, navicellarum receptaculum (cyst). (from Frantzius, 1848); 2. Life cycle of *Plagiorchis elegans* (Rudolphi). (from Styczyńska-Jurewicz, 1966); 3. Eggs of Bdelloidea rotifera on *Povilla adusta* Navas: A, detail of egg; B, head of *Povilla* nymph showing position of eggs. (from Corbet, Sellick, Willoughby, 1974)

II. Incertae Cedis (Spiriopsis)

Spiriopsis adipophila (ARVY & Delage, 1966), parasite of the coelom of Ephemera vulgata nymphs from the Eyzies region of France, remains as mysterious now as at its discovery 10 years ago. We still do not know its origin nor, in spite of repeated investigations, its development. Its generic name was recently changed from Spirinella to Spiriopsis (ARVY, Peters, 1972), and two other pieces of information can be added to that given by ARVY and Delage (1973):

1°) Morphology. Some histological sections, favorably oriented, reveal divisions in the contents of the chamber at one extreme end of the ribbon. After staining by Feulgen-Rossenbeck method, it is possible to distinguish small punctuations which might be interpreted as divisions of the body — or as a sort of division into microspores.

2°) Distribution. Spiriopsis has been found a) in Ephemera vulgata from the Avre River by Prof. Chabaud, and b) in E. danica from Luxemburg by Prof. Hoffmann. We do not yet know if these parasites are identical with those from the Eyzies or if they represent similar species (ARVY, Proc. 2nd Int. Conf. Ephemeroptera).

3° RICKETTSIAE

Rickettsiae, classified somewhere between viruses and bacteria, have been reported only once from Ephemeroptera. Weiser (1946) listed their presence in nymphs of Baetis muticus (L.) [= B. pumilus (Burmeister)] from Czechoslovakia. The report was in tabular form.

4° PLATYHELMINTHES

a, Trematoda, Digenea

In 1971, YAMAGUTI published a revision of the digenetic trematodes of vertebrates. As he made many changes in trematode taxonomy, it seems advisable to give this rearrangement as it applies to species recorded from mayflies.

Cercaria intermedia Wunder, 1923 is insufficiently described for purposes of placement to family or cercarial type (Wesenberg-Lund, 1934). C. intermedia is not host specific and attacks any available arthropod, using only secretions from the penetration glands to penetrate gills or intersegmental membranes (in 5 min); the stylet is used to penetrate chitinized surfaces (15–30 min). C. intermedia is negatively phototactic, and Wunder (1923) believed that any host selectivity influenced solely by similarity in behavior. It definitely does not find a host by any biochemical attraction. It approaches arthropods, molluscs, and plants equally, but leaves molluscs and plants after finding the surface unsatisfactory. Wunder (1923) found pigmented cysts of C. intermedia in unidentified mayfly nymphs.

A. Allocreadiidae. — Allocreadium and Crepidostomum belong to this family (YAMAGUTI, 1971). We have reference to a report of metacercariae of Allocreadium isoporum (Looss, 1894) from nymphs of Ephemera vulgata in Karelia, USSR (SHTEIN, 1957b), and VOJTKOVÁ (1971a) reported an unidentified species of Allocreadium from Ephemera danica in Czechoslovakia. Allocreadium commune (OLSSON, 1867) was transferred to Cainocreadium (Opecoelidae), but YAMAGUTI (1971) ignored Lake Erie records of this species: thus one questionable identification is eliminated. To records already given, add FREMLING (1960) to authors finding Crepidostomum cooperi HOPKINS, 1931 in Hexagenia bilineata (SAY). When WENKE (1968) attempted to validate this tentative identification, he found C. illinoiense FAUST, 1918, but he did not confirm the presence of C. cooperi in Hexagenia. YAMAGUTI (1971) no longer considered C. hiodontos Hunter & Bangham, 1932 a synonym of C. illinoiense.

The genus Macrolecithus was placed in the Macroderoididae by YAMAGUTI (1971). LAMBERT (1974), after studying the life cycle of Macrolecithus papilliger REES, 1968 in France, returned the genus to Allocreadiidae on the strength of adult characters, the life cycle, and its oculate xiphidiocercariae. The definitive host is Phoxinus phoxinus (L.), the first intermediate Pisidium casertanum (Poll), and the only known second intermediate Caenis sp. Attempts to infect species of Heptageniidae and Baetidae were unsuccessful (LAMBERT, 1974).

B. Lepocreadiidae.—Megalogonia ictaluri Surber, 1928 is now in Lepocreadiidae (Yamaguti, 1971). Additional records are Hopkins (1933), Carlson et al. (1959), and Fremling (1960). Hopkins (1933) reported this species from mayfly gills; the latter two authors found it in Hexagenia bilineata in the Mississipi River.

C. Opecoelidae. — Having eliminated Cainocreadium commune, the species found in Leptophlebia cupida (Say) by Cooper (1915) is probably Plagioporus cooperi (Hunter & Bangham, 1932). Fish from the Great Lakes region do harbor another opecoelid trematode with mayflies as intermediate hosts, Allopodocotyle lepomis (Dobrovolny, 1939) [in Yamaguti (1971) the species is in Podocotyle]. In West Virginia, where the first intermediate host is a river snail (Nitocris dilatatus Conrad), the microcotylocercous cercariae of A. lepomis were found experimentally to penetrate Litobrancha recurvata (Morgan) through the gills and between the abdominal segments; they encysted as metacercariae in 1–8 hours, and were surrounded by a host capsule in 7 days (Lo, Hall, 1973). A. lepomis also penetrated and encysted in Sialis sp. and Chironomus attenuatus (Walker) (Tendipes), but cysts were encapsulated and killed in Chironomus (Hall, 1969). Litobrancha appears to be intermediate between an abnormal and a normal host for A. lepomis (Hall, personal communication). Definitive hosts are Lepomis megalotis (Rafinesque) and other centrarchid fishes (Yamaguti, 1971).

D. Macroderoididae. — Alloglossidium corti (LAMONT, 1921) and Eustomos chelydrae MACCALLUM, 1927 are now in Macroderoididae and Alloglossidium kenti SIMER, 1929 is no longer a synonym of A. corti (YAMAGUTI, 1971).

E. Omphalometridae. — Omphalometra, Opisthioglyphe, and Neoglyphe are placed here (Yamaguti, 1971). Neoglyphe locellus (Kossack, 1910) is the present name of the parasite of shrews reported from aquatic insects by Macy and Moore (1958). Opisthioglyphe, including once again the species O. rastellus (Olsson, 1875), has been a source of confusion in the older literature. Cercariae have frequently been assigned to more than one species; Yamaguti (1971) still gives Cercaria armata von Siebold, 1837 (discovered in Ephemera vulgata by von Siebold in 1844) as a synonym of Opisthioglyphe ranae (Frölich, 1791) in Omphalometridae and Prosthodendrium ascidia (van Beneden, 1873) in Lecithodendriidae. Having rejected Opisthioglyphe ranae and O. rastellus in our 1973 paper, we did not know where to place the Distomum endolobum of von Linstow (1893). Now there is a new possibility. Yamaguti (1971) rejected all ranae-rastellus-hystrix synonyms and recognized Opisthioglyphe hystrix (Molin, 1858), parasite of amphibians (species of Rana and Bufo). Further, he reported that larval forms of O. hystrix were found in Ephemera and Cloeon by Isaichkov (1933). We also know that Cercaria limnaeae-ovatae von Linstow, 1884 can penetrate aquatic insects (Wesenberg-Lund, 1934), and that C. limnaeae-ovatae is quite possibly the larva of O. hystrix (Dawes, 1946).

F. Plagiorchiidae.—Nine species of Plagiorchis representing two subgenera are known from mayflies. Subgenus Plagiorchis (Plagiorchis) contains P. micracanthos MACY, 1931, P. parorchis MACY, 1956 (recently raised to a species), P. proximum BARKER, 1915, and P. noblei PARK, 1936. P. noblei, a parasite of birds (Icteridae), encysted in mayflies, mosquitos [Aedes aegypti (L.)], midges, dragonflies, and caddisflies (WILLIAMS, 1964).

Four good species and one dubious species are reported from Plagiorchis (Multiglandularis). These include P. multiglandularis SEMENOV, 1927 and P. muris (TANABE, 1922). YAMAGUTI (1971) suggested that P. muris may involve two species, that of TANABE (1922) from Japan and that of McMullen (1937b) from the northwestern United States, because progenesis occurred in the specimens of McMullen but it has never been reported from Japan. P. muris was found in Ephemera strigata Eaton by HIRASAWA and ASADA (1929); this work was cited by YAMASHITA (1952). YAMAGUTI (1971) reported that P. arcuatus SHTROM, 1924 encysted in Heptagenia but cited SHTEIN (1957a) as a reference. The reference is incorrect, but the possibility exists that the information came from another source. P. laricola Skrjabin, 1924 (= P. mutationis Panova, 1927), a parasite of birds, was found experimentally to encyst in Cloeon dipterum (L.) (SHIGINA 1965). The last species, P. elegans (RUDOLPHI, 1802) has been well documented by STYCZYŃSKA-JUREWICZ (1961, 1962) from Polish and French ponds under natural and experimental conditions (Fig. 2). The first host is Limnaea stagnalis L. Xiphidiocercariae attack, penetrate, and encyst within 2 hours in a variety of aquatic invertebrates: species of Aedes, Anopheles, Culex, Corethra, Coenagrion, Lestes, Aeshna, Sialis, Ilybius, Trichoptera, some Chironomidae, Asellus, other molluscs (under rare conditions of progenesis), and Cloeon dipterum. Interestingly, young nymphs of Coenagrion sp. fed on cercariae without being invaded by combing away attacking cercariae with their legs, but less agile, older nymphs were penetrated. The cercariae even penetrated (but did not encyst) in exuviae of Cloeon, indicating some biochemical attraction (STYCZYNSKA-JUREWICZ, 1962).

Mice were used as experimental hosts and many species of birds have been reported as definitive hosts (YAMAGUTI, 1971).

G. Prosthogonomidae. - No changes.

H. Lecithodendriidae. — According to YAMAGUTI (1971), Acanthatrium is now a genus. The definitive host of A. anaplocami (ETGES, 1960) remains unknown, but two similar species suggested as synonyms of A. anoplocami (and rejected by YAMAGUTI, 1971) have a single species of bat, Eptesicus fuscus (Beauvois), as definitive host. Cercaria nyxetica Seitner, 1945 can be included in Lecithodendriidae because it has a virgulate cercaria; virgulate cercaria are known exclusively from this family.

Reactions of aquatic insects to virgulate xiphidiocercariae have been studied by J. E. Hall and his co-workers. In general these cercariae are quite selective in their choice of an intermediate host (HALL, GROVES, 1963). The species studied by HALL and GROVES (1963) formed loose or firm and compact external cysts on the abdomen or gills of the host with mucoid material from the virgula organ or outer mucoid coat. Following the progress of Cercaria adoxovirgula Hall, 1960 in Paraleptophlebia, they found that the firm, compact, external cysts were used both for attachment and leverage. The cercariae then panetrated through the gills into the fat bodies of the abdomen and formed metacercariae, but never encysted. Unfortunately, Paraleptophlebia did not survive long enough in the laboratory to determine the fate of C. adoxovirgula. The same species failed to enter Baetis spp., Ephemerella lutulenta CLEMENS, Leptophlebia nebulosa (WALKER), and Pseudocloeon dubium (WALSH) (HALL, GROVES, 1963).

Cercaria polypyreta HALL & GROVES, 1963 entered and encysted in Hexagenia limbata (SERVILLE), H. atrocaudata McDunnough, Ephemera guttulata Pictet (Hall, Groves, 1963) and Litobrancha recurvata (HALL, WITHERS, WEAVER, 1964). L. recurvata is probably a natural host (HALL, 1969), Ephemera guttulata is probably an abnormal host, and too little is known about the hostparasite relationships of the other species to guess at their associations (HALL, personal communication). Recent histochemical work on C. polypyreta has identified the enzyme N-acetyl-b-glucosaminidase, localized in the virgula organ and outer tegument. This enzyme is discharged with the mucoid material during penetration of L. recurvata and probably plays a role in the penetration process (Babu, Hall 1974b).

Cercaria tremaglandis HALL, 1960 has also been studied in natural and abnormal hosts. Cercariae, obtained from Pleurocerca acuta RAFINESQUE in Indiana and Nitocris dilatatus in West Virginia, select certain species of Ephemeroptera and Plecoptera as intermediate hosts (HALL, 1960a, HALL, GROVES, 1963). In mayflies, C. tremaglandis would not enter Stenonema or Paraleptophlebia adoptiva (McDunnough); it entered but did not encyst in Pseudocloeon sp., entered but was met by a massive defense reaction in Hexagenia limbata and Litobrancha recurvata, and entered, encysted, and developed in two species of Isonychia (HALL, 1960a, HALL, GROVES, 1963, HALL, 1969).

Defense reactions of Ephemeroptera to trematode infections

Defense reactions of insects can include external reactions, such as that of young Coenagrion to Plagiorchis elegans described by Styczyńska-Jurewicz (1962). However, the term is usually limited to physiological processes after entry, in particular "encapsulation" (SALT, 1963). According to SALT's reviews of defense reactions (1963, 1970), the hemocytes of the insect form a capsule around the cyst of the parasite, with melanin being deposited in the capsule. SALT (1970) believed that healthy insects will encapsulate any parasite that enters, unless the parasite has specific means of avoiding encapsulation. The capsule acts to deprive parasites of oxygen and other substances and to imprison the parasite. Although Hall, Weaver, and Gomez-Miranda (1969) have encountered some reactions to unencysted trematodes by stoneflies, encapsulation usually occurs in aquatic insects only after metacercariae have encysted. Some trematodes are killed; others seem to accept encapsulation as a normal part of development. In Trematoda-Ephemeroptera associations, at least three possible reactions have been documented: 1) the metacercaria doesn't encyst until the subimago molts, thus avoiding the hazards of long encapsulation; 2) the metacercaria is encapsulated, the capsula may be partly melanized, but the trematode continues to develop; and 3) the metacercaria is encapsulated and killed, and melanin is then deposited in the body of the dead trematode. Thus host reactions are clearly different for different parasites and different hosts.

Although Salt (1963) stated that unusual or abnormal hosts are more likely to encapsulate parasites than usual ones, there is no clear distinction between normal and abnormal insect hosts for trematode parasites. Hall (1969) characterized a normal host-parasite relationship as occurring when large numbers of trematodes enter an insect but the host responds to only a small number of them. Most host-parasite situations are intermediate between normal and abnormal. As an example, Cercaria polypyreta entered Litobrancha in large numbers and only 5% of the parasites had elicited a host response in mayfly nymphs examined from 8 hours to 15 days after infection (Hall, 1969). However, in cases of heavy infection there was damage to gonad and muscle tissue with increased mayfly mortality (Hall, 1969) and many metacercariae were killed by encapsulation in an insect examined after 36 days (Hall, Withers, Weaver, 1964).

Studying the reaction of Litobrancha recurvata to Cercaria tremaglandis, an abnormal host-parasite relationship, Hall (1969) found that the number of hemocytes in the blood of Litobrancha was reduced significantly after infection, indicating their involvement in defense reactions. This did not occur in similar experiments with Acroneuria. Also, comparing arbitrary indices of capsule composition, thickness, and melanization with numbers of cysts, it was discovered that the host response was less pronounced for each capsule as the number of metacercariae increased. This indicated a limit in the ability of Litobrancha to respond to the infection (Hall, 1969). Further work on the same association has proven that melanin is the pigment associated with the "melanization" of the host capsule (Babu, Hall, 1974a).

CHAMBERS, HALL and HITT (1975) studied the distribution of tyrosinase which initiates the formation of melanin about trematodes and other parasites. In *Litobrancha* this enzyme is limited to the hemocytes. In another aquatic insect, *Sialis* sp., tyrosinase activity was located in the hemolymph as well as in the hemocytes, and hemolymph tyrosinase was decreased during infection with the trematode *Allopodocotyle lepomis* (Chambers, Hall, Hitt, 1975).

β. Cestoidea, Cyclophyllidea

Kotel'nikov (1965) reported finding cysticercoids of *Fimbraria fasciolaris* (Pallas, 1781) (*Hymenolepididae*), a parasite of birds, in nymphs of *Cloeon dipterum*. He did not confirm this identification by feeding experiments.

5° NEMATHELMINTHES

a. Rotifera.

Rotifers are frequently commensal, but little is known of their associations with aquatic insects (de Beauchamp, 1965). One of the authors (LA) has frequently seen unidentified rotifers surrounding nymphs of *Ephemera vulgata* in the Avre River, France. This may be a case of commensalism, or the rotifers may coexist with *E. vulgata* in a manner similar to that reported by Degrange (1960) for the cladoceran *Alona guttata* var. *tuberculata* G. O. Sars.

I. Pseudotrocha

In 1972, Hurlbert, Mulla and Willson published a report on population dynamics of zooplankton and insects in ponds treated with an organophosphorus insecticide. Populations of the predaceous rotifer Asplanchna brightwelli Gosse (Asplanchnidae) increased in treated ponds as their principal food, herbivorous rotifers, increased and predaceous crustaceans decreased. Occasionally, a scarcity

of herbivorous rotifers forced A. brightwelli to feed on small insects, including Baetidae from $400-900 \mu$ in length.

Although commensalism in rotifers is known, only one species has been described from a mayfly. *Pleurotrocha larvarum* VLASTOV (Notommatidae) was found on *Cloeon dipterum* and *Ilybius* in a pond in the USSR (VLASTOV, 1956).

II. Bdelloidea

CORBET, SELLICK and WILLOUGHBY (1974) found numerous rotifers at the base of the cerci of *Povilla adusta* NAVAS nymphs in West African lakes. They also found bdelloid rotifer eggs at the cerci bases, the margins of the clypeus, and on the mandibles, but suggested that those eggs around the head may have been deposited as *Povilla* groomed its cerci (fig. 3).

Because of the frequent occurrence of the rotifers, some kind of regular association was indicated. Also, in Lake Barombi Mbo, Cameroon, where *Povilla* emergence is predictable by moon phase, these authors discovered that the number of eggs laid on *Povilla* decreased with approaching *Povilla* emergence. These rotifers were not identified, but possibly included species of *Philodinidae*, perhaps *Embata commensalis* (Western) Corbet, Sellick, Willoughby, 1974). According to de Beauchamp (1965), other *Bdelloidea*, often of the commensal genus *Embata*, have been found on mayflies and other aquatic insects.

β. Nematoda

I. Spirurida

Recent studies on rhabdochonid fish parasites have followed the classification of SAIDOV (1953) in which Rhabdochonidae includes Rhabdochoninae (= Cystidicolinae), Spinitectinae, and Cyclozoninae and the genus Rhabdochona contains two subgenera. Larvae found in Ephemeroptera from the subgenus Rhabdochona are R. denudata (Dujardin, 1845), R. cascadilla Wigdor, 1918, and R. decaturensis Gustafson, 1949 (originally reported in Hexagenia as Rhabdochona sp. by Gustafson, 1939). We know of two species in mayflies from the subgenus Filochona: R. cotti Gustafson, 1949, parasite of species of Cotto, found in mayfly and stonefly nymphs in the northwestern United States (Gustafson, 1949); and R. ergensi Moravec, 1968, parasite of the intestine of Noemacheilus, from nymphs of Habroleptoides modesta (Hagen) in Czechoslovakia (Moravec, 1972). H. modesta appears to be a natural host and in feeding experiments 95% of H. modesta nymphs were infected with 5-60 R. ergensi larvae per nymph (Moravec, 1972).

Moravec (1971ab) also studied the role of Ephemeroptera as an intermediate host of Cystidicoloides tenuissima (Zeder, 1800) [= Metabronema salvelini (Fujita, 1920)]. According to Maggenti and Paxman (1971) the name is now Sterliadochona tenuissima. S. tenuissima eggs containing fully developed larvae were mixed with detritus and fed to mayfly nymphs. Habrophlebia lauta Eaton, Habroleptoides modesta, and Ephemera danica were 50–100% infected. After ingestion, the first-stage larvae hatched in the mayfly gut and passed through the gut wall into the body cavity, and sometimes later into the thorax. Most first-stage larvae molted to the second stage in 17–18 days, and to infective third-stage larvae in another week. They never encysted but continued to develop, attaining a length of 4.08–7.94mm in naturally infected mayflies. Particularly heavy infections killed the intermediate host; however, Habrophlebia lauta was capable of molting to a subimago while carrying up to 15 S. tenuissima larvae (Moravec, 1971a).

In the River Bystřice, Czechoslovakia, the natural intensity of infection was 1-2 larvae per host in *Habroleptoides modesta* and 1-4 per host in *Ephemera* sp. Incidence of infection averaged 40% for *Ephemera* and only 1.7% for *Habroleptoides*; still, *H. modesta* is so abundant that it must be considered the chief host (Moravec 1971b). Moravec (1971a) found larval development required about one month at 13-15°C. Under natural conditions, development was influenced by temperature and by the life cycle of the intermediate host. There were a slow-growth winter and a rapid-growth summer generation

of Sterliachona tenuissima each year. Over winter, Salmo trutta m. fario L. were 100% infected but the rate of parasite infection and intensity dropped at the end of February and in March, following the emergence of Habroleptoides. The summer generation developed rapidly in Ephemera (and probably in Habrophlebia lauta), infected fish, and was mature enough to lay eggs (passed into the water with fish feces) in autumn as larger H. modesta nymphs returned (MORAVEC, 1971b).

Effects of an infection of Spinitectus micracanthus Christian, 1972 on an intermediate host (Hexagenia sp.) were described by Keppner (1975). At 21–23°C, eggs hatched in 6 hours, and larvae penetrated the gut wall in 12 hours, molted after 6–10 days and after 19–20 days, and continued to develop in the mayfly — unless fed to the host Lepomis macrochirus Rafinesque (at 22 days). Immediately after penetration, a first-stage larva entered into a cell of the longitudinal abdominal muscles. The cell organization was disrupted; otherwise, there was no host reaction while the larva was inside the cell. The larva grew, destroying and finally rupturing the cell after 8 days. Hexagenia reacted to further growth and tissue destruction by encapsulating the larva in a fibrotic host cyst, but this was not sufficient to stop larval growth. The size of both the host capsule and the larva continuously increased. A cyst contained 1–3 larvae and heavily infected mayflies lost the use of muscle tissue and moved but sluggishly (Keppner, 1975).

Sterliachona tenuissima was found in Ephemera danica from the River Loučka, Czechoslovakia, by Vojtková (1971b). Keppner (1975) found natural infections of Spinitectus gracilis Ward & Magath, 1917 in Hexagenia sp. from a Missouri lake, USA.

II. Enoplida, Mermithidae

Because of difficulties in rearing mermithid adults, we can still only report new host records for specimens listed as *Mermis* sp. or *Mermithidae*: from *Baetis rhodani* (PICTET) in the stream Lissuraga, France (BENECH, 1972); from *B. rhodani* in the Křtiny River, Czechoslovakia (SUKOP 1973); from *Caenis* sp. and *Callibaetis pretiosus* Banks in a Florida pond, USA (Pescador, personal communication); and from unidentified mayflies in Courland Lagoon, Baltic Sea, USSR (ZAKHIDOV, 1973). According to Poinar (1975), mermithids in mayflies were first discovered by von Linstow (1878) in nymphs of *Ephemera vulgata*.

· γ. Gordiacea, Gordioidea, Chordodidae

Poinar and Doelman (1974) experimentally infected tadpoles and insects with preparasitic larvae of *Neochordodes occidentalis* (Montgomery, 1898). *Neochordodes* successfully entered and encysted only in tadpoles and aquatic insect larvae of *Chironomidae*, *Culicidae*, and unidentified *Ephemeroptera*. Fig. 4 gives the structure of a preparasitic larva (length 47–52 μ). After ingestion, the larva penetrated the intestinal wall of the host by stretching the proboscis (pr), attaching the small anterior spines or hooklets (3 sp, 2 sp, 1 sp) to the intestinal wall, and pulling the rest of the body through the wall into the abdominal cavity. After finding a suitable location, the gordiid formed a cyst with material secreted from the intestinal gland (i.g.) through the anus (a), and applied in several overlapping layers (Poinar, Doelman, 1974).

6° MOLLUSCA. PELECYPODA, SCHIZODONTA

Most mayflies are hosts to other organisms, but with *Mollusca* the situation is reversed. Elsewhere in these Proceedings, Dr. I. MÜLLER-LIEBENAU and Dr. W. HEARD have described a new genus of *Baetidae* from Thailand which lives between the demibranchs of the clam *Hyriopsis myersiana* (LEA) (*Unionidae*). This baetid apparently feeds on the food of the clam, collecting it from the mucous of the demibranches.

H. myersiana occurs in Laos, Cambodia, and Thailand, but the collector (Dr. HEARD) found only 25 specimens in Thailand, all from one locality in Kamchanaburi Province. Six of the 25 contained baetids, one mayfly per clam.

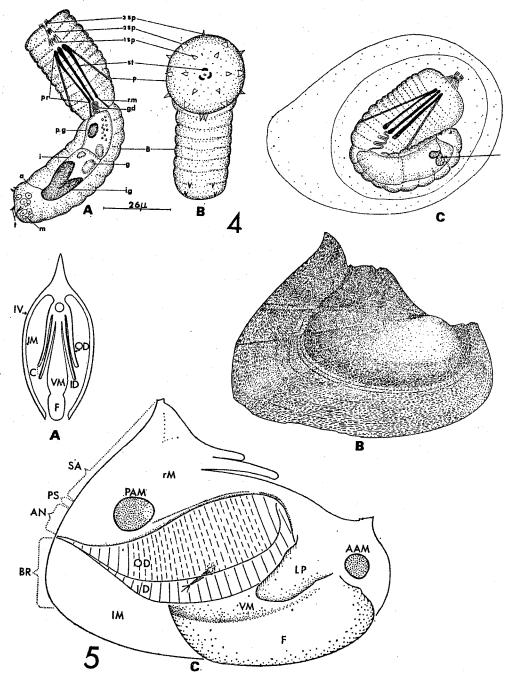


Fig. 4-5. 4. Neochordodes occidentalis (Montgomery): A, B, two views of a preparasitic larva; C, an encysted larva. Abbreviations: P, presoma; pr, evaginable proboscis; st, stylets; 1 sp, 2 sp, 3 sp, first, second and third circlet of spines and hooklets; B, body; p. g., preintestinal gland; g. d., gland duct; i, intestine; gl, globule; i. g., intestinal gland; a, anus; t, tail spines; r. m., retractor muscles; m, mesenchyme cells. (from Poinar and Doelman, 1974); 5. Hyriopsis myersiana (Lea): A, schematic medial cross section, B, right valve; C, schematic drawing with valves and mantle covering branchial chamber removed to show position of baetid. Abbreviations: V, valve, M, mantle (r = right, 1 = left); AAM, PAM, anterior and posterior adductor muscles; SA, supra-anal opening; PS, pallial suture; AN, anal opening; BR branchial opening; C, ctenidium (gill): OD, ID, outer and inner demibranches; LP, labial palp; VM visceral mass; F, foot

While no other clams examined contained mayflies, the association is not unique. The following note is from Dr. C. FROEHLICH, University of São Paulo:

"On November 10, 1965, Mr. Waldemar Catarino de Jesus, a collector of the Faculty of Biological Sciences of Botucatu, State of São Paulo, collected some mussels in a stream at Conchas (= shells), a town near Botucatu. Inside of a few of these specimens he claimed to have found nymphs of *Polymitarcidae* (either *Campsurus* or *Asthenopus*)."

Dr. Froehlich gave one of us (WLP) his specimen of this association, but it has disappeared from our collections. A clean hole had been bored through one of the valves, and the polymitarcid was living inside the shell of the already dead mussel. We suspect he was using the shell as a burrow, but lack information on other specimens of this potential mayfly-mollusc association.

Another relationship with *Unionidae* was observed by one of us (LA). A specimen of *Anodonta* sp. from the Avre River, France, was placed in an aquarium with *Ephemera vulgata*. The mayflies congregated about the clam and many were grouped around the siphon. Some even entered between the valves and crawled over the gills; they appeared to be feeding on the detritus collected by the clam. Although it seemed that the mayflies would be crushed when the valves closed, this never happened.

A similar relationship was discovered by Mr. J. RICHARDSON in a shallow, rocky stream in Maine, USA. To collect Alasmidonta varicosa (LAMARCK) (Unionidae), he was crawling upstream on his hands and knees searching for their siphonal openings. Frequently he saw Baetidae nymphs gathered around the siphonal opening and mantle. He did not see the nymphs enter the mussel, but speculated that it would be possible for them to enter and escape with ease: A. varicosa closes its valves slowly (RICHARDSON, personal communication).

7° ARTHROPODA. INSECTA, DIPTERA

A. Chironomidae. — We have one new record to add to those for Epoicocladius ephemerae (ZAVŘEL). One of us (LA) has repeatedly found larvae of all sizes of E. ephemerae on and near Ephemera vulgata nymphs in the Eyzies region of France. Also, we apologize for the omission of references to Verrier (1952) and Codreanu and Codreanu (1938) in Arvy and Peters (1973).

B. Simuliidae. — Two new African species of phoretic Simuliidae were described from Cameroon: Simulium (Phoretomyia) afronuri Lewis & Disney, 1970 from Afronurus sp. and S. (P.) baetiphilum Lewis & Disney, 1972 from Baetidae — five species of Baetis or related genera (Disney, 1973). Lewis and Disney (1972) also established a new species group, the diceros-group, for S. (P.) diceros Freeman & de Meillon and S. baetiphilum. Additional description of S. (P.) lumbwanum de Meillon was given by Lewis and Disney (1970); Garms (1972) found S. lumbwanum in Liberia. The female of S. (P.) berneri Freeman was described (Lewis, Disney, Crosskey, 1969) and its range was extended south to Angola (Luna de Carvalho, 1962) and west to Liberia (Garms, 1972).

New Himalayan species include Simulium (s.s.) jani Lewis, 1973 from Rhithrogena sp. in Pakistan, S. (s.s.) rashidi Lewis, 1973 from two-spined Iron-ally in India and Pakistan, Phoretodagmia obikumbensis Rubtsov, 1972 from Iron sp. and Rhithrogena tianschanica Brodsky in Tadzhikistan, USSR, and P. alajensis Rubtsov, 1972 from R. tianschanica in Kirgizia, USSR. Both authors gave additional descriptions of Simulium (Odagmia) ephemerophilum Rubtsov, but Lewis (1973) placed this and other phoretic Himalayan species in Simulium (s.s.) while Rubtsov (1972) made in the type species of Phoretodagmia, a new genus established for phoretic Himalayan Simuliidae.

Independent development of simuliid phoresis in two regions suggests advantages to this way of life, such as improved aeration, improved nutrition, and a high chance of survival as phoretic larvae and pupae avoid being killed by rolling rocks in mountain torrents (Rubtsov, 1962). Simuliid phoresis was once probably accidental (as in the specimens on *Baetisca rogersi* Berner found by Pescador and Peters, 1974), then facultative, then obligate, with corresponding morphological changes (Rubtsov, 1972).

Simuliidae choose their hosts (MARLIER, 1950). Factors apparently involved in host selection are

host size, host abundance, time between molts of the host, water current, protection from predators, and food (DISNEY, 1917a). In studies with Simulium berneri, S. afronuri, S. lumbwanum, and S. baetiphilum, DISNEY (1971bc, 1973) found that the dispersal of larvae on hosts is random, and concluded that it is the first-instar larvae who must choose the host. First instar S. berneri usually settled on the gills or gill-bearing terga of Elassoneuria disneyi GILLIES, later moved to the thorax, and pupated on the mesonotum or wing pads (DISNEY, 1971b). The same pattern was generally true for other species studied (DISNEY, 1971c, 1973).

Simulium baetiphilum and S. lumbwanum were more abundant on medium-sized than on large-sized nymphs (Disney, 1971c, 1973. In fact, S. lumbwanum larvae were sometimes larger than their hosts. S. afronuri avoided very young nymphs and S. lumbwanum seldom occurred on large nymphs, but the two occasionally did coexist on the same Afronurus nymph. Disney (1971c) suggested that different host sizes were an example of niche separation. Later, discovering that mature Afronurus nymphs live on the surface of stones in strong current, Disney (1973) concluded that S. lumbwanum (less modified for phoresis) was more likely to be washed away from the host than was S. afronuri. A similar movement of baetids from protected to less protected areas of a river probably caused dislodgement of many S. baetiphilum larvae (Disney 1973).

In spite of the evidence from hosts, Disney (1971bc, 1973) never found larvae of phoretic simuliids drifting freely. However, unattached larvae of *Photretodagmia ephemerophila* were found in the Ak-Bura-River (Kirgizia, USSR) by Konurbayev, Omorov and Tadzhibayev (1972). These authors reached the same conclusion — that free larvae had been dislodged from their host.

It seems G. E. HUTCHINSON (in Traver 1939) should be credited with first recognizing the habitual relationship between *Similiidae* and *Ephemeroptera*. Corbet's report (1960b) of *Simulium lumbwanum* from *Afronurus ugandanus* Kimmins was overlooked in our earlier paper (Arvy, Peters, 1973).

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SUMMARY

Phoresies, Biocoenoses and Thanatocoenoses in the Ephemeroptera. — Supplement

This paper reviews the biological associations — parasitic, symbiotic, casual, occasionally predatory — of Ephemeroptera with other organisms. Supplementing our previous work, it lists the following new groups reported in association with Ephemeroptera: Rickettsiae, chitinophilous fungi of Chytridiomycetes, the euglenoid protozoan Colacium of Phytomastigophorea, rotifers, and molluscs of Pelecypoda. In addition, it discussed the defense reactions of mayflies to trematode infections. A summary list of new species records is given in Table I.

Table 1

Species reviewed in this paper which have been reported to share some biological relationship with Ephemeroptera. Doubtful records are followed by a question mark in brackets

Class, order	Family	Species
Rickettsiae		
Chytridiomycetes, Chytridiales	Chytridiaceae	Chytriomyces aureus
,,	•	C. hyalinus
	,,	Rhopalophlyctis sarcoptoides
	Phlyctidiaceae	Phlyctorhiza endogena
	Rhizidiaceae	Asterophlyctis sarcoptoides
		Rhizidium chitinophilum
	**	R. ramosum
	"	Rhizoclosmatium aurantiacum
		R. globosum
·	73	Siphonaria petersenii
	. ,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,	S. sparrowii
	,,	S. variabilis
richomycetes Harnellalas	Genistellaceae	
Trichomycetes, Harpellales		Glotzia ephemeridarum
hytamacticanharea Euglanida	;; Euglopidos	Zygopolaris ephemeridarum
hytamastigophorea, Euglenida	Euglenidae	Colacium sp.
dicrosporea, Microsporida	Nosematidae	Gurleya linearis
T	,,	Mitoplistophora angularis
porozoea, Eugregarinida	Gregarinidae	Gamocystis humilis
ligohymenophora, Peritrichida	Epistylidae	Epistylis geleii
	***	Rhabdostyla ephemerae
	Vorticellidae	Vorticella campanula
	***	V. convallaria
	99	V. ephemerae
·	Zoothamniidae	Zoothamnium ramosissimum
rematoda, Digenea	Allocreadiidae	Allocreadium sp.
	,,	Macrolecithus papilliger
	Opecoelidae	Allopodocotyle lepomis
	Omphalometridae	Opisthioglyphe hystrix [?]
	Plagiorchiidae	Plagiorchis (s.s.) noblei
	•	P. (Multiglandularis) arcuatus [?]
	**	P. (M.) elegans
	"	P. (M.) laricola
	.,. Lecithodendrijdae	Cercaria adoxovirgula
	Documental Mane	C. polypyreta
	family unknown	C. potypyreta C. intermedia
estoidea, Cyclophyllidea	Hymenolepididae	Fimbraria fasciolaris
otifera, Pseudotrocha	Asplanchnidae	-
	Aspiancinidae Notommatidae	Asplanchna brightwelli
Bdelloidea		Pleurotrocha larvarum
!	Philodinidae?	species of Embata?
ematoda, Spirurida	Rhabdochonidae	Rhabdochona (s.s.) decaturensis
	,,	R. (Filochona) cotti
	**	R. (F.) ergensi
ondiana Cardi II	99	Spinitectus micracanthus
ordiacea, Gordioidea	Chordodidae	Neochordodes occidentalis
elecypoda, Schizodonta	Unionidae	Hyriopsis myersiana
secta, Diptera	Simuliidae	Simulium (Phoretomyia) afronuri
	,,	S. (P.) baetiphilum
	-99	S. (s.s.) jani
•	,,	S. (s.s.) rashidi
	,,	Phoretodagmia obikumbensis
	,,	P. alajensis

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