STUDIES ON LIFE-CYCLES OF DIGENETIC TREMATODES

A Thesis presented for the Degree of Doctor of Philosophy

by

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ABSTRACT

30,530 specimens of freshwater molluscs belonging to eleven genera and eighteen species including gastropods and bivalves, have been examined for infection with larval trematodes. Thirty species of cercariae have been found. Of these two are described as 'Monostome', three 'Gymnocephalous', one 'Pleurolophocercous', eleven 'Furcocercous', one 'Microcercous', one 'Cystocercous', five 'Echinostome', and six Xiphidiocercaria'. These specimens were collected on different dates from 21 different places in West Yorkshire.

Eighteen of these cercariae are comsidered to be new to science, one is described for the first time in Great Britain and the remaining eleven have already been described in this country by previous authors.

A short review of each group of cercariae found during this study is presented.

The life cycles of eight species have been completed under laboratory conditions. The species involved are:

Echinoparyphium recurvatum (Linstow, 1873)

Hypoderaeum conoideum (Bloch, 1782)

Notocotylus imbricatus (Looss, 1893) Szidat, 1935

Notocotylus attenuatus (Rudolphi, 1809)

Plagiorchis farnleyensis n.sp.

Plagiorchis kirkstallensis n,sp.

Sphaeridiotrema wintersettensis n.sp.

Dolichosaccus rastellus (Olsson, 1876)

The life cycle of the latter species is the first record from Great Britain.

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INTRODUCTION

Thomas (1883) and Leuckart (1882) independently established and published the first trematode life cycle, that of the liver fluke Fasciola hepatica from Great Britain and Germany respectively. Since that time no more accounts of freshwater larval trematodes were published by British workers until 1923, when Hesse, from Scotland, reported two cercariae emerging from Lymnaea peregeer. One was a furcocercous cercaria and the other a xiphidiocercous cercaria. Hesse gave a description of the cercariae and of some aspects of their biology but did not name them. In the same year, 1923, Vevers fed ducklings with the hepatopancreas of L. peregeer infested with a tetracotyle stage that he thought to belong to Tetracotyle typica (Diesing, 1835), and the hepatopancreas of L. stagnalis naturally infected with echinostome cercariae that he identified as C. echinata (Siebold, 1837). Twenty days after feeding he obtained adults of Hypoderaeum conoideum (Bloch, 1782) and immature forms of Echinostoma revolutum (Frolich, 1802), but the tetracotyle cysts failed to develop. He stated that H. conoideum must have developed from other cercariae also encysted in L. peregeer.

In 1926 Brown investigated larval trematodes in Birmingham and Leeds. As results of these studies, nine species of cercariae from L. peregeer and L. stagnalis were added to the British fauna, of which Cercaria granulosa, C. equispinosa, C. pucilis, C. pseudarmata, C. leptosoma, C. macrosoma, C. micromorpha were new to science, while the remaining two species, C. echinata and C. fissicauda (La Val, 1855), had been previously described. He attempted to investigate their life cycle of some of these forms, but without conducting experiments. Brown (1927) obtained a xiphidiocercaria with eyespots emerging from Pisidium amnicum and Sphaerium corneum from a Yorkshire river (R. Wharfe), and he experimentally infected larvae of the may-fly, Ephemera danica, which were fed to a trout. Juvenile forms of Crepidostomum farionis (Muller, 1784) were recovered from its pyloric caeca. Adults of C. farionis were found in trout and grayling from the River Wharfe. Brown (1931) described five additional cercariae from Cheshire; two were echinostome (Cercaria oscillatoria n. sp.

and C. limbifera (Seifert, 1926) and three were new species of furcocercariae (C. echinomorpha, C. chromatophora and C. pygocytophora). Two years later Brown (1933) described the life cycle of Lecithodendrium chilostomum (Mehlis, 1831) and also briefly described the life cycle of Dicrocoelium dendriticum (Rudolphi, 1819).

Wright (1927) added additional information on the precercarial, cercarial and metacercarial stages of Fasciola hepatica. He also described two xiphidiocercariae, Cercaria cambrensis I and C. cambrensis II, from L. truncatula and L. pereger respectively. Harper (1929) published a brief account of some observations on the life cycles of Notocotylus seineti (Fuhrman, 1919) and Echinoparyphium recurvatum (Linstow, 1873). He also described four new species of xiphidiocercariae and gave some information on their biology, penetration and encystment in a variety of invertebrates. The same author (1931) described three species of furcocercariae and traced the development of two of these species into the corresponding tetracotyle stages, one of which was new species. He also established the life cycle of Strigea tarda (Steenstrups), from sporocyst to adult form.

In 1930 Matheson reported an outbreak of dermatitis caused by Echistosomatid cercaria which he identified as Cercaria elvae (Miller, 1926). Taylor and Baylis (1930) identified Matheson's material as C. ocellata (La Val, 1885). The same authors (Taylor and Baylis) described some experiments with C. ocellata and another additional furcocercaria that they referred to as "Cercaria X".

Rees (1932) published the most outstanding contribution to the study of larval trematodes of freshwater molluscs in Britain. She reported ten different species of cercariae from several species of Lymnaea of which Cercaria "Y", and Cercaria "Z" and Cercaria cambrensis III were new species. She gave details of the incidence of infection of the first intermediate hosts by the cercariae, together with the occurrence, structure and some aspects of their life cycle. She also added descriptions of various structural details to those previously described for Cercaria monostomi (Linst.), C. Fasciola hepatica (L.), C. cambrensis I (Wright), C. limbifera (Seifert), C. acellata (La Val.,), C. macrosoma(Brown)

and Cercaria "X" (Baylis). Subsequently Rees published a series of interesting papers (1932, 1940, 1952, 1955, 1957) dealing with several aspects of the biology and life cycles of larval trematodes of British Freshwater molluscs.

After the Rees (1932) paper and until 1960, only isolated accounts of British freshwater larval trematodes have been published, Vickers (1940), Dawes (1952), Erasmus (1957, 1958a, 1960) and Thomas (1958).

Iles (1959) found Cercaria pseudocellata (Szidat, 1942) under which she put as synonyms, Cercaria elvae (Miller, 1926; Matheson, 1930), C. ocellata (Vogel, 1930) and C. ocellata (Taylor and Baylis, 1930; Rees, 1932). She also reported seven different species of furcocercariae four of which were new and the remaining three had previously been described. One year later Iles gave a detailed study of the life cycle of Apatemon gracilis minor (Yamaguti, 1933) and some observations on the life cycles of C. paracauda and C. tetraglandis Iles (1959).

Nasir (1957-1958) examined over 3,000 specimens of L. stagnalis from Edgbaston Pool, in Birmingham and found eight different species of cercariae - three echinostome (E. nudicaudatum n. sp., E. pinnicaudatum n. sp., and H. conoideum (Bloch)) two furcocercariae, one strigeid (C. Cotylurus brevis Dubois and Raush, 1950) and three stylet cercariae (C. pseudermata (Brown), Plagiorchis (Multiglandularis) megalorchis (Rees, 1952) and C. edgbastonensis n.sp.). He described the life cycle of Echinostoma nudicaudatum and E. pinnicaudatum and also established the identity of the previously known C. helvetica XXXIV Dubois (1934) with the strigeid adult Cotylurus brevis. Later (1962) he reported the presance of two giant-tailed echinostome cercariae found at the same place (Edgbaston Pool) which he described and figured as new species. Nasir and Erasmus (1964) gave a key for the identification of 81 of the species of cercariae from British freshwater molluscs then known.

Khan (1960 (a) and (b); 1961 (a), (b), (c) and (d); 1962(a), (b) and (c), during a survey of larval tramatodes carried out in London and some parts of Essex, Middlesex, Surrey and Hertfordshire, reported 35 different cercarial

species of which 23 were new. This list comprised 7 echinostome, 3 gymnocephalous, 17 furcocercariae, 6 xiphidiocercariae and 2 cercariae. He completed the life cycle of three of them - C. londonensis, C. essexensis and C. bushiensis - which developed into adults of the genera Echinostoma, Hypoderaeum and Cyathocotyle respectively.

Berrie (1960) elucidated the life cycle of Diplostomum spathaceum (Rud.) and D. phoxini (Faust) from two Diplostomulum larvae in the eyes of Gasterosteus aculeatus. The same author (1960) studied the variation of D. phoxini in different definitive laboratory hosts.

Probert (1965(a) and (b); 1966) studied the larval trematodes infecting the freshwater molluscs of a lake in Breconshire (Llangorse Lake) and reported twenty-one species of cercariae, twelve of which were considered to be new. At the same time he investigated the incidence of larval trematodes from the same lake. Williams (1966) during studies of the incidence of larval trematodes in L. pereger from a pond in Milngavie near Glasgow, Scotland recorded four species of furcocercariae, one echinostome and a monostome cercaria all of which except the cercaria of Diplostomum gasterostei Williams (1966) was new. He studied the development of Cotylurus cornutus (Rudolphi, 1809) in ducks and gave brief accounts of the life cycle of all cercariae encountered except that of Haplometra cylindracea.

Pike (1967) studied some stylet cercariae and a microphallid type in freshwater molluscs from Wentloog level near Cardiff, South Wales. He redescribed C. helvetica XXXIII Dubois (1931) and the cercaria of Sphaerostoma bramae (Mull) and their metacercariae. He also recorded a further six species of cercariae - C. parvus (Khan (1961d) and C. tarda Khan (1961d) on which he gave additional information together with a description of their metacercariae and four new species - C. wentlogensis, C. rumniensis, C. octoglandulata and a Microphallid cercaria sp. One year later Pike (1968a) found the cercaria of Psilotrema oligoon (Linstow, 1887). He experimentally obtained the adult from ducklings and discussed the taxonomy of this fluke. He also described two new species of Gymnocephalous cercariae - C. frondicola and C. granocutis. In the same year (1968b) he studied

the distribution and incidence of larval trematodes in the freshwater fauna from the Wentloog level, and gave some information on the distribution of cercarial stages in the host fauna and some indication of their specificity as well as the percentage throughout the year of each host species infected with these larvae. In 1969 Pike gave an account of the life cycles of two notocotylid trematodes - Notocotylus triserialis Dies, 1839 (= N. attenuatus, Rud. 1809) and N. imbricatus (Looss, 1893) Szidat, 1935.

In Europe the most outstanding contributions to the study of trematode larvae were undertaken by Nitzsch (1816), Ercolani (1881, 1882), Siebold (1854), Filippi (1854, 1857), La Valette St. George (1855), Moulinie (1856) and Luhe (1909). Several years later, additional interesting accounts were added to this field by Mathias (1922, 1924, 1925, 1930, 1935), Dubois (1928, 1929, 1931), Dollfus (1938 and 1960), Szidat (1924, 1928, 1931, 1933, 1935), Wesenberg-Lund (1934) and Wikgren (1956).

In North America, a great amount of work on larval trematodes has been done mainly by Cort (1915, 1917, 1918), Faust (1917, 1918, 1919), H.M. Miller (1926), E.L. Miller (1936), Brooks (1930, 1943, 1948) and Cable (1935, 1938).

The study of freshwater larval trematodes in Japan was initiated by Osafane in 1898 and continued by Senoo (1903), Fujita (1906), Kobayashi (1911, 1922), Tanabe (1922, 1948), Takahashi (1927), Komiya (1938, 1939, 1941), Yamaguti (1938, 1940, 1942, 1943) and many others.

In Africa, Cawston (1915, 1917, 1922), Porter (1921, 1938), Fain (1953) and Vercammen-Grendjean (1960) have made significant contributions to knowledge in this field.

Sewell (1922) published a comprehensive account of Indian larval trematodes. Other contributions of recent years have been made by Singh (1952, 1955). Agarwall (1956), Premvati (1965), Pande (1967), Srivastava (1968) and Tapar (1970).

In many countries the study of freshwater larval trematodes has also been carried out by many workers. The major works have been those of Looss (1896, 1899) and Leiper (1915) in Egypt, Johnston, 1938, Johnston and Angel (1940)

and Johnston and Simpson (1944) in Australia, McLeod (1936, 1940) in Canada, Tubangui (1928, 1932) and Velasquez (1961, 1963, 1973) in Phillippines, Lie (1963, 1964, 1965) in Malaya, Zajicek (1963) and Zdařska (1963) in Czechoslovakia, Nakagawa (1951), Faust (1922, 1924), Tsuchimochi (1926) and Komiya (1941, 1952) in China, Uribe (1925) and Nasir and Diaz (1967, 1968(a) and (b), 1973) in Venezuela.

MATERIALS AND METHODS

(i) The host molluscs

During the period from 1972 to 1976 more than 30,530 freshwater molluscs representing 11 genera and 18 species were examined. The molluscs, which included both bivalves and gastropods, were collected from a variety of freshwater bodies (lakes, reservoirs, canals and rivers). They were caught by fishing net, by hand and, in some inaccessible localities, by the use of a grappling hook tied to a piece of rope which was thrown out into the lake or canal then hauled back dragging with it submerged vegetation or broken branches from which the molluscs were removed. The species Bithynia tentaculata (Linn.), Dreissena polymorpha (Pallas) and Acroloxus lacustris (Linn.) were principally obtained in this manner.

Once brought back to the laboratory the specimens were washed in tap water and placed in aquaria measuring about 30 by 45 cm containing aerated water and various aquatic plants obtained from the same locality as the molluscs. The aquaria were kept at a temperature of 13 to 15°C in an aquarium room. The molluscs were fed a varied diet comprising fresh and dry lettuce leaves, carrots and cabbage. The water in each aquarium was changed once or twice per week. In these conditions some of the molluscs survived for more than 8 months.

Some species such as Limnaea pereger (Mull.), L. stagnalis (Linn.), Planorbis corneus (Linn.), Bithynia tentaculata, Potamopyrgus jenkinsi (Smith) and Sphaerium corneum (Linn.) were reared in the laboratory for experimental purposes. The eggs of these species, with the exception of P. jenkinsi and S. corneum were collected at various localities and kept in aquaria in suitable conditions. P. jenkinsi and S. corneum were collected in great numbers and kept in aquaria as described above. After 25 to 30 days they were removed and transferred to other vessels where they were left for a variable period of time after which the small P. jenkinsi could be found at the surface and the small S. corneum could be found at the bottom of the vessel. In both cases ground snail shell and pieces of chalk were added as a source of calcium

(calcium carbonate). However, some of the mollusc shells were very thin and the animals soon died. The survival rate of molluscs reared in this way was about 30 to 40%, although this was greater than that of the other species raised in the laboratory.

(ii) Cercariae

In order to determine the presence of cercarial infections the molluscs were placed individually in glass vessels measuring about 5 by 7 cm which were half full of tap water. After 4, 8, 12 and 24 h they were examined for cercariae under a stereo dissecting microscope. Those giving a positive result (cercariae present) were placed in holding aquaria; those giving a negative result were discarded. The infected molluscs were examined again to confirm that they continued to release the same species of cercaria as originally determined so that possible errors caused by the presence of double infections could be eliminated. Recently released cercariae were studied *in vivo* in tapwater and 0.75% saline solution between slide and coverslip.

The excretory system of the cercariae was studied in three ways. The first method was to study the cercariae on a slide under a coverslip in 0.85% saline solution adding drops of the saline from time to time to ensure that the specimen did not dry out. It was found that the high saline concentration induces an increase in the activity of the flame cells which facilitated observation of these cells.

The second method consisted of placing the vessel containing the cercariae in the freezing compartment of a refrigerator (about - 4°C) for 15 to 20 minutes. The low temperature causes a decrease in the activity of the cercariae which sink to the bottom of the vessel. When the cercariae were mounted on a slide their movements were still very slow and the flame cells displayed little activity. As the temperature was raised by the heat of the microscope lamp the cercariae resumed their normal activity and the increase in activity of the flame cells made them more easily visible.

The third method was to use a mixture of intravital stains, normally 1% malachite green, 1% methyl blue, 1% neutral red and 1% bismark brown. This

combination of stains also caused a considerable increase in the activity of the flame cells and has the added advantage of displaying certain internal structures of the cercaria.

The study of the penetration gland-cells of the cercariae was carried out using cercariae extracted from dissected snails as well as recently emitted cercariae. In this study staining with 1% neutral red and 1% bismark brown gave the best results. 1% malachite green was used to help determine the arrangement of spines on the body of the cercariae and to display the 'collar of spines' of the echinostome cercariae.

Measurements (in mm) of the cercariae were taken from 25 to 30 specimens fixed in 10% formalin. Drawings were made freehand and the dimensions of structural features were arranged proportionally to the mean measurements of the specimens.

(iii) Sporocysts, Rediae and Metacercariae

Sporocysts, rediae and metacercariae were studied *in vivo* on a slide in tap water and 0.75% saline solution. One per cent methyl blue, 1% malachite green and 1% neutral red were used as intravital stains to highlight certain structures. Measurements of sporocysts and rediae were taken from 15 to 20 specimens immediately after fixation in 10% formalin. Measurements (in mm) of similar numbers of metacercariae were taken on live specimens. Drawings were made freehand as described for the cercariae.

(iv) Life Cycle Studies.

A number of different species of animal was used in experimental studies on the life cycles of the parasites. These animals were used both as secondary intermediate hosts and as final hosts. Among the secondary intermediate hosts used were various aquatic larvae of insects belonging to the orders Trichoptera, Odonata, Ephemeroptera, Coleoptera and Diptera. Frog and toad tadpoles and freshwater fishes were also used. The first four groups of insect larvae were collected from Durkar (near Wakefield) from a semi-permanent freshwater pool. None of these larvae ever harboured a trematode infection. The larvae of Chironomus were obtained partly from Durkar and

partly from commercial sources. Of the latter 50% were examined for the presence of trematode infections but none was ever found. The remaining 50% were used in two groups, one to infect the final hosts and the other as a control. The larvae of Aedes aegypti, fishes of the species Lebistes reticulatus (Peters) and Tilapia mosambica, tadpoles and young adults of Bufo bufo (common toad and tadpoles, young adults and adults of Xenopus laevis (South African clawed toad) were reared in the Zoology Department at Leeds University. Other fishes were obtained from commercial sources and from Mr. S. Axford of the Yorkshire River Authority.

The definitive experimental hosts - Mus musculus, Rattus norvegicus and Columba livia - were supplied by the Zoology Department. The ducklings, chicks and canaries used in these experiments were purchased commercially. The control and experimentally infected animals were kept in suitable cages in the animal house of Zoology Department and fed on commercial prepared food.

The faeces were examined by sedimentation, and the resultant sediment was examined beneath low-power and high-power microscopes. The faeces of all these animals were examined for at least 3 consecutive days prior to the beginning of the experiments in order to avoid possible errors from natural infections. No natural trematode infections of experimental hosts were found.

All birds were force-fed by means of a medicinal pipette while the mammals were slightly anesthetized with ether before force-feeding, and the cysts were introduced using a hypodermic syringe with a plastic tube on the end of the needle.

The age of all experimental animals used during this investigation ranged between 9 to 169 days old, except that the age of the canaries was unknown.

(v) Adults

To recover both the preadults and the adults of the parasites the different hosts were killed with chloroform and the alimentary canal was dissected out. It was placed into suitable saline solution in a petri dish and washed several times before being examined under dissecting microscope. The trematodes were fixed either by dropping them into warm (60° to 70° C) Bouin solution or by

flattening them between slide and coverslip. For the latter method the specimens were heat-killed in saline and fixed either in alcohol-formalin-acetic acid (AFA) or Bouin at normal temperature under slight coverslip pressure. The fixed specimens were measured and studied anatomically both before and after staining with celestin blue, borax carmine and alum carmine.

Some adults were fixed in Bouin solution and used for histological studies. Serial sections were cut at 5 - 8μm and stained with haematoxylin and Eosin. The sections were then mounted in Canada balsam or Xam. The parasites were studied *in vivo*, fixed and as serial sections. Measurements were taken from fixed specimens and are based on 20 to 70 individuals. Drawings were made with the aid of a *camera lucida* and certain morphological features were added subsequently.

(vi) *Eggs and Miracidia*

Parasite eggs were collected from the faeces of the host and from petri dishes in which the alimentary canal was washed, or sometimes by teasing apart the sexually mature worms. The eggs were kept in glass vessels in the laboratory immersed in tap water, distilled water or 0.85% physiological saline. The vessels were maintained at a temperature of 19 to 22°C and were constantly aerated to permit the development of the eggs. Of the three media distilled water gave the best results because in both tap water and saline cultures protozoal growth had an adverse effect on the trematode eggs.

Miracidia were studied alive in 0.75% saline solution. Drawings were made with the aid of a camera lucida and additional details were incorporated freehand.

Measurements were made with the aid of an ocular micrometer, the mean is given, normally followed by minima and maxima in parentheses.

LIST OF FRESHWATER MOLLUSCS EXAMINED AND LOCALITIES FROM WHICH THEY WERE COLLECTED

Since I arrived in Leeds I have visited 34 different places to collect freshwater molluscs. In 21 of these 34 collecting sites I have obtained molluscs.

The gastropod and bivalve molluscs have been identified with the aid of keys developed by Ellis (1926), Janus (1965) and Macan and Cooper (1969), and texts of Macan (1959) and Mellanby (1963) dealing with British freshwater invertebrate animals.

The number and species of molluscs examined, localities, dates and cercarial infections are listed below.

Species of molluscs examined

Class GASTROPODA

Sub-class PROSOBRANCHIA

Order Mesogastropoda

Family Viviparidae

Genus Viviparus

Viviparus viviparus (Linn.)

Family Hydrobiidae

Genus Potomopyrgus

Potomopyrgus jenkinsi (Smith)

Genus Bithynia

Bithynia tentaculata (Linn.)

Bithynia leachi (Sheppar)

Sub-class PULMONATA

Order Basommatophora

Family Lymnaeidae

Genus Lymnaea

Lymnaea auricularia (Linn.)

Lymnaea pereger (Mull.)

Lymnaea stagnalis (Linn.)

Family Physidae

Genus Physa

Physa fontinalis (Linn.)

Family Planorbidae

Genus Planorbis

Planorbis carinatus (Mull.)

Planorbis corneus (Linn.)

Planorbis crista (Linn.)

Planorbis planorbis (Linn.)

Planorbis vortex (Linn.)

Family Ancylidae

Genus Acroloxus

Acroloxus lacustris (Linn.)

Freshwater Bivalve Molluscs

Class LAMELLIBRANCHIATA

Order Eulamellibranchiata

Family Margaritiferidae

Genus Anodonta

Anodonta cygnea (Linn.)

Family Sphaeriidae

Genus Sphaerium

Sphaerium corneum (Linn.)

Genus Pisidium

Pisidium amnicum (Mull.)

Family Dreissenidae

Genus Dreissena

Dreissena polymorpha (Pallas)

Location and number of molluscs species examined and the cercarial and metacercarial infections observed

Viviparus viviparus (Linn.)

550

Kirkstall Power Station (Leeds-Liverpool Canal)

October, November 1972; January, February, August, October 1973; April, June, July 1974; January, February, November 1975; January, February 1976.

Infections: Echinostomes (cysts)

Potamopyrgus jenkinsi (Smith)

7000

Kirkstall Power Station (Leeds-Liverpool Canal); Gledhow Valley Road; Cowthorne Park.

October, November 1972; January, February, August, October 1973; April, June, July 1974; January, February, November 1975; January, February 1976.

Infections: Echinostomes (cysts); Microcercous (cysts).

Bithynia tentaculata (Linn.)

2500

Kirkstall Power Station (Leeds-Liverpool Canal); Newmillerdam Lake; Wintersett Lake; West Bretton Lake; Walton Park; Gledhow Valley Road.

October, November 1972; January, February, March, April, May; August; October 1973; January, April, June, July 1974; January, February, April, July, August, September, November 1975; January, February, 1976.

Infections: Cercaria Notocotylus imbricatus; C. pleurolophocerca I C. Sphaeridiotrema wintersettensis; C. gymnocephalous II; C. gymnocephalous III; C. vivax I; C. vivax II; C. microcotylea I; C. tarda; C. microcercous I; C. magnacauda II.

Bithynia leachi (Sheppar)

59

Newmillerdam Lake.

October 1972; January, March 1973; July 1974; April, August; September, November 1975; January, February 1976.

Infections: C. sphaeridiotrema wintersettensis.

Limnaea auricularia (Linn.)

600

Kirkstall Power Station (Leeds-Liverpool Canal); Wintersett Lake: Newmillerdam Lake, Kirklington; Riffa Beck, Pool-in Wharfedale.

November 1972; January, May 1973; January 1974; January, April 1975.

Infections: Cercaria xiphidiocercaria IX.

Limnaea peregra (Mull.)

6002

Kirkstall Power Station (Leeds-Liverpool Canal); Wintersett Lake; Newmillerdam Lake; Riffa Beck Pool-in-Wharfedale; Ilkley Moor; Durkar; Gledhow Valley Road; Kirklington; Walton Park; West Bretton Lake; Rawdon; Enroy; Roundhay Park; Eccup Reservoir; Ferrybridge; Otley; Carnforth.

October; November 1972; January, February, May, August, October 1973; January, April, June, July, November 1974; January, February, March, April, May 1975; January, February 1976.

Infections: Cercaria Plagiorchis Kirkstallensis; C. plagiorchis farnleyensis; C. Notocotylus attenuatus; C. Hypoderneum conoideum; C. echinoparyphium recurvatum; C. furcocercaria VII; C. furcocercaria IV; C. furcocercaria II; C. Diplostomum phoxini; C. paracauda; C. Cotylurus brevis; C. petifera; C. Dolichosaccus rastellus; C. Apatemon gracilis minor.

Limnaea stagnalis (Linn.)

4058

Kirkstall Power Station (Leeds-Liverpool Canal); Wintersett Lake; Newmillerdam Lake: Walton Park; New Farnley; Gledhow Valley Road; Cowthorne Park; Enroy;

Eccup Reservoir; Otley.

October, November 1972; January, February, March, April, May, August 1973; January, February, April, May, July 1974; January, February, March, April, May 1975; January, February 1976.

Infections: C. Plagiorchis kirkstallensis; C. Plagiorchis farnleyensis; C. Dolichosaccus rastellus; C. Hypoderaeum conoideum; C. echinostoma III; C. Apatemon gracilis minor; C. paracauda; C. xiphidiocercaria IX.

Physa fontinalis (Linn.)

1979

Kirkstall Power Station (Leeds-Liverpool Canal).

October, November 1972; January, February, August, October, 1973. April, June, July 1974; January, February, November 1975; January, February 1976.

Infections: Echinostomes (cysts); Microcercous (cysts)

Planorbis carinatus (Mull.)

458

Kirkstall Power Station (Leeds-Liverpool Canal); West Bretton Lake; Enroy; Cowthorne Park; Walton Park.

October, November 1972; January, February, March, April, August 1973; January, April, June, July 1974; January, February, November 1975; January, February 1976.

Infections: Echinostomes (cysts); Microcercous (cysts).

Planorbis corneus (Linn.)

530

Kirkstall Power Station (Leeds-Liverpool Canal); West Bretton Lake; Walton Park.

October, November 1972; January, March, April 1973; April, June, July 1974; January, February 1975; January, February 1976.

Infections: Echinostomes (cysts).

Planorbis crista (Linn.)

2500

Durkar, Enroy.

February, April 1973; January 1974.

Infections: Echinostomes (cysts)

Planorbis planorbis (Linn.)

472

Kirkstall Power Station (Leeds-Liverpool Canal); Walton Park; New Farnley; Cowthorne Park; West Bretton Lake; Enroy; Wintersett Lake.

October, November, 1972; January, March, April 1973; April, June 1974; January, February 1975; January, February 1976.

Infections: C. Bilharzielae polonicae; C. magnacauda I.

Planorbis vortex (Linn.)

420

Kirkstall Power Station (Leeds-Liverpool Canal); Cowthorne Park; West-Bretton Lake; Wintersett Lake.

October, November 1972; February, March, June, July 1973; April, June, July 1974; January, February 1975; January, February 1976.

Infections: C. Apatemon gracilis minor.

Acroloxus lacustris (Linn.)

190

Kirkstall Power Station (Leeds-Liverpool Canal); Newmillerdam Lake; Riffa Beck, Pool-in-Wharfedale.

November, October 1972; January, February, August, October, 1973. April, June, July 1974; January, April, September, December 1975. January, February 1976.

Infections: Echinostomes (cysts).

Anodonta cygnea (Linn.)

480

Wintersett Lake; Newmillerdam Lake; Harewood.

October, November 1972; January, March, April, June, July, August 1973; January, February, April, June, July 1974; January 1975.

Infections: None.

Sphaerium corneum (Linn.)

1200

Kirkstall Power Station (Leeds-Liverpool Canal); Wintersett Lake; Newmillerdam Lake.

October, November 1972; January, March, April, August 1973; January, April, June, July 1974; January, February, May 1975.

Infections: Cercaria macrocerca I

Pisidium amnicum (Mull.)

32

Kirkstall Power Station (Leeds-Liverpool Canal); Wintersett Lake.

October, November, 1972; January, April, May, August 1973; January, April, June, July 1974; January, February, May 1975.

Infections: None.

Dreissena polimorpha (Pallas)

1500

Newmillerdam Lake; Wintersett Lake.

February, May, August 1973; January 1974; January 1975.

Infections: None.

Monostome cercariae

Luhe (1909) defined Monostome cercariae as cercariae in which the acetabulum was absent, eyespots were present, a long slender undivided tail was without setae and which developed in rediae and encysted in the open. Faust (1917b) divided the Monostome cercariae according to the size of the body and the number of eyespots into two sub-groups; Binoculate which were characterized by having two lateral eyespots and Trioculate possessing a third additional median eyespot. Sewell (1922), basing his interpretation on the meaning of "Monostome" and using it in its widest sense, divided Monostome cercariae into six sub-groups, comprising all the forms without an acetabulum:- (1) Pleurolophocerca (Cercaria pleurolophocerca Sons. as the type of this group); (2) Urbanensis (C. urbanensis Cort.); (3) Ephermera (C. ephemera Nitzsch.); (4) Lophocerca (included C. indicae IX, XIII, XXXIX and LV.); (5) Lophoides (C. indicae XXVII.) and (6) Ubiquita (C. indicae LII and LXI.). At present only the Urbanensis and Ephemera groups are considered to be true Monostome cercariae and are very closely related to the Binoculate and Trioculate Groups of Faust (1917). According to Dubois (1929) Cercaria urbanensis is a trioculate form and therefore should belong to the Ephemera group.

Cercaria pleurolophocerca Sons. was the type of the first sub-group and is characterized by having a well-developed acetabulum (Langeron, 1920). The Lophocerca was removed by Luhe (1909) from the Monostomes because it possessed a divided tail and a fin-fold on the body. Miller (1926) placed it in the Apharyngeal brevifurcate monostome cercariae. Dubois (1929) pointed out that the absence of the acetabulum in the members of this group is not sufficient reason to keep them in the Monostome group because its organization and evolution are quite different. The members of the Lophoides group are also Furcocercariae characterized by the possession of a penetration organ and excretory system similar to that of the Schistosome cercariae. The Ubiquita group includes cercariae with a stylet, without an oesophagus or intestinal caeca and with three to six pairs of penetration gland-cells. Dubois (1929), Wesenberg-Lund (1934) and Nasir, Hamana and Diaz (1969) considered that the members of this

group belong to the true Xiphidiocercaria. Therefore this group should be transferred to the Xiphidiocercous cercariae.

Rothschild (1938d) redefined the characters of Notocotyloidea cercariae, and divided them into two sub-groups, the Notocotylidae and the Pronocephalidae. The Notocotylidae comprises all the cercaria without aural lappets or collar arranged into three groups according to the structure of the anterior portion of the excretory bladder; 1. Monostomi group in which the anterior transverse portion of the main excretory vessel is situated posterior to the median eyespot, 2. Imbricata group in which the anterior transverse portion of the excretory vesicle forms a loop between the lateral eyespots and passes anterior to the median eyespot, 3. Yenchingensis group, the cercariae of which are characterized by having an unpaired finger-like diverticulum on the anterior transverse portion of the bladder, extending anteriorly generally a little to one side of the median eyespot. The Pronocephalidae includes all the cercariae with aural lappets or a collar and comprises a single group - the Indicae XI group. In this group the transverse excretory canal is situated posterior to the median eyespot.

Dubois (1951) divided monostome cercariae into two groups, the Triserialis sub-group which develop in pulmonate gastropods and the Imbricata sub-group which develop in prosobranchiate gastropods.

I have adopted Rothschild's (1938) classification of the Monostome cercaria and the species described below represent the Monostomi and Yenchingensis groups respectively.

Cercaria of Notocotylus imbricatus

The cercaria of Notocotylus imbricatus (Looss, 1893) Szidat, 1935.

The cercaria of N. imbricatus was found during May and July, 1973 and 1974 emerging from Bithynia tentaculata obtained from Newmillerdam Lake. It was found again in August 1975 in the same host collected at Kirkstall Power Station (Leeds-Liverpool Canal) but since then it has been found only in the first locality. The infection rate was higher at Newmillerdam than at Kirkstall Power Station, being 9.3% - 14% at the former site and 1.4% at the latter.

The cercariae emerge in large numbers throughout the day, particularly in the afternoon. They are very active swimmers and do not appear to be reacting directionally to any particular stimulus. The body is bent ventrally and contracted, and the tail lashes violently, as in the cercaria of N. attenuatus. After a short period of swimming (4 to 12 min.) they encyst on any available substrate.

Description (Plate1-4 Figs.1-3)

Body elongate oval in outline, concave ventrally and very contractile. Cuticle thick, with fine granular contents, bearing 14-16 hair-like projections on papillae arranged in a single semi-circular row at anterior end of body. Approximately 10 pairs of long hair-like projections present on either side of body just posterior to this row, extending almost to posterior extremity of body. Dense groups of brown pigment granules scattered irregularly over body giving a characteristic brown colouration. Tail non-spinose, subterminal, w with a prominent pointed tip and capable of great contraction and extension. Cuticle of tail granular, armed on each side with 3 hair-like projections on papillae. Tail composed of two types of transversely elongate cells (1) small cells arranged in a linear series on each side, connected to inner wall of tail and extending along its entire length, (2) large cells concentrated in central core of tail but not reaching to its distal tip. Both cell types nucleate, with fine granular cytoplasm. Bright pigment spots present, in tail, more numerous posteriorly. Longitudinal muscles of tail formed by two bands each

consisting of numerous fibres extending from base to tip. A pair of small locomotory pockets situated at posterior end on either side of tail insertion and connected with gland cells like those described in the cercaria of Notocotylus attenuatus.

Oral sucker rounded, muscular and subterminal. Mouth situated almost eentrally on oral sucker, bordered with a single row of 10-11 setae on papillae. Narrow oesophagus divided into two long caeca immediately posterior to transverse canal. Pharynx absent. Intestinal caeca extending posteriorly and terminating antero-lateral to bladder. Anterior margin of body with 3 apertures each side of oral sucker, leading into 3 ducts but no gland-cells observed. Cystogenous gland-cells numerous throughout body except in region surrounding mouth opening. No genital primordium or nervous system observed. Three eyespots located slightly anterior to oesophageal bifurcation. Lateral eyespots almost circular and larger than median eyespot, which is transversely elongate and with both a lower concentration of pigment and a central area devoid of pigment; eyespots lie immediately posterior to oral sucker.

Excretory bladder small and almost oblong in shape, opening by small dorsal excretory pore located at junction of body and tail. Long primary excretory ducts arise antero-laterally and pass anteriorly external and parallel to the caeca on each side of body; these ducts curving inwards between posterior margin of median eyespot and oesophageal bifurcation and uniting to form a transverse commissure.

Finger-like diverticulum originating from transverse commissure and extending forwards almost to middle of oral sucker. Main excretory ducts, including diverticulum, filled with numerous refractile granules. Eighteen pairs of flame cells present, arranged in groups of three. Flame cells only clearly observable after extrusion of cystogenous gland-cell contents although their capillaries could not be traced. Caudal excretory duct passing into tail and extending almost to middle of tail where a small lateral excretory pore is situated.

Redia (Plate 1 Figs. 4-5)

The rediae are found in large numbers in the hepatopancreas of Bithynia tentaculata. They are elongate and sac-shaped, sometimes broadest in the middle according to the degree of contraction of the body. The body cuticle is thick, collar and locomotory appendages are absent and inconspicuous birth pore is located on one side slightly anterior to the posterior margin of the pharynx. The anterior end of the body is occupied by a well-developed and highly protrusible muscular pharynx which leads back into the long wide intestine which extends nearly to the posterior end of the body and is filled with brownish-yellow granular material. The redia contains 3-6 fully developed cercariae, developing cercariae and some germ balls. In some rediae a small daughter redia may be present. Only 2 flame cells were seen near the anterior of the body and the rest of the protonephridial system could not be elucidated. The daughter rediae are very active and are capable of independent contraction and elongation. They each possess a small pharynx and a relatively long intestine, and the body contains a few germ balls. No birth pore could be detected.

The adult form of this cercaria was obtained experimentally in ducklings and chickens as described below (p. 27).

Measurements of the cercaria and redia of Notocotylus imbricatus from Bithynia tentaculata

Body	0.221 (0.212 - 0.239) long x 0.116 (0.114 - 0.121) wide
Tail	0.327 (0.300 - 0.364) long x 0.028 (0.026 - 0.030) wide
Oral sucker	0.026 (0.026 - 0.026) long x 0.026 (0.026 - 0.026) wide
Oesophagus	0.019 (0.015 - 0.022) long
Eyespots	0.013 (0.011 - 0.015) long x 0.013 (0.011 - 0.015) wide
Redia	0.424 (0.238 - 0.602) long x 0.196 (0.168 - 0.224) wide
Pharynx	0.062 (0.049 - 0.076) long x 0.058 (0.049 - 0.060) wide

Encystment

Encystment has been observed occurring on aquatic vegetation and on mollusc shells. The gastropods Lymnaea pereger, L. auricularia, L. stagnalis, Planorbis corneus, P. planorbis, Physa fontinalis and the bivalve Sphaerium corneum.

In the laboratory however the most frequent sites are the bottom and sides of the container.

The cercaria may swim around for a short period of time but when it comes into contact with any substrate it attaches itself by means of the oral sucker and caudal pockets which excrete a sticky substance aiding adhesion. The body of the cercaria contracts several times then the cystogenous material is secreted over the whole body to form a transparent layer around it which soon hardens to form a compact cyst wall. The tail remains attached to the external surface of the cyst wall for a certain time during which it lashes violently. When it separates it continues to make swimming movements for about 20 minutes until it sinks to the bottom and finally disintegrates. The encysted metacercaria undergoes a series of rotating movements within the cyst which become less frequent with age. The cyst is fully-formed between 2 and 3.5 minutes after the beginning of encystment.

Exposure to warm temperature and the use of combinations of two intravital stains for example 1% neutral red and 1% bismark brown, considerably increased the rate of the encystment process. When several cercariae were mounted on a microscope slide and placed near the lamp for approximately 5 seconds encystment was completed in about 45 seconds. After adding two to three drops of the mixture of stains to cercariae mounted on a microscope slide encystment was completed in 30 to 40 seconds.

Several newly-formed encysted metacercariae which had been mechanically removed from their cysts were able to crawl in a leech-like manner by means of the oral sucker and caudal pockets, but re-encystment was never observed.

The adhesive substance secreted by the gland cells associated with the caudal pockets plays an important role in the encystment process. On several

occasions when cercariae were seen attached to a surface the contents of these glands were apparently not excluded and the cercariae did not encyst. When the contents of the caudal pocket gland-cells were secreted the cercariae were observed to encyst on the substrate on every occasion.

Metacercaria (Plate 1 Fig. 6)

The cysts are subspherical and the main cyst wall comprises two layers, an outer fibrous layer and inner thick layer.

The enclosed cercarial body is folded within the cyst. In one-week-old metacercariae no increase in size was apparent but the median eyespot had disappeared and the pigment of the lateral eyespots had become more dispersed. The main excretory ducts were wider and the refractile granules which had decreased in number, were seen moving freely within them. The oral sucker had become less prominent. In two-and-half-week-old metacercariae the lateral eyespots had completely disappeared and no trace of the caudal pockets was observed. Other metacercarial structures remained at the same level of development as in the cercaria. The activity of the coiled metacercaria then gradually diminished and it lay almost motionless. No genital rudiments or ventral glands were seen in 60-day-old metacercariae. Mortality of about 10% of these 60-day-old metacercariae was recorded. No intermediate host is required and encystment takes place in the open or upon any substrate.

Measurements of 7 day-old metacercariae of Notocotylus imbricatus experimentally obtained from several mollusc shells.

Cyst	0.121 (0.117 - 0.125) long x 0.118 (0.117 - 0.121) wide
Outer wall	0.017 (0.015 - 0.019) thick
Inner wall	0.009 (0.007 - 0.011) thick
Oral sucker	0.024 (0.022 - 0.026) long x 0.028 (0.026 - 0.030) wide

Infection of the final host

Eight naturally infected Bithynia tentaculata were placed in a vessel together with 42 empty shells of large Lymnaea peregeer (previously boiled for about 25 minutes, to avoid any natural encysted stages) for 24 h. Many cercariae

settled on the shell and the sides and bottom of the container and the resulting cysts were mechanically removed as far as possible without damage to the metacercarial body. It was found that newly-formed cysts are very fragile and it is difficult to remove them without damage to the young metacercariae inside. Old cysts are firmly attached to the substrate but usually remain whole when scraped off and the contained metacercariae survive unharmed.

1-, 10-, 25- and 60-day old cysts were used for infection experiments which were fed to 6 ducklings, 6 chickens, 4 pigeons, 4 mice and 4 rats. An additional member of each of these species was kept as a control. When examined 10-14 days after the commencement of the experiments all the controls were negative for helminth infection. Faecal samples of all experimental animals were examined for the presence of trematode eggs daily.

The data of Table 1 show that the encysted metacercaria develop into adult flukes in the caeca of ducklings and chickens but not in pigeons, rats and mice.

Immature trematodes were found after 10 days in both a chicken and duckling, indicating that metacercarial cysts are infective one day after formation. Notocotylid eggs were first seen in the faeces of a chicken (No. 2) after 12 days, and when killed this bird was found to contain 47 juvenile and 8 adult flukes. Notocotylid eggs were not seen in faecal samples from a duck until the 14th day.

In both bird species the duration of infection is relatively short - possibly longer in the duck than the chicken, the percentage recovery is also greater in the former and together these observations suggest that the duckling is the slightly more suitable host.

The egg (Plate 4 Figs. 20-22)

Twenty five sexually mature worms were removed from the caeca of experimentally infected laboratory hosts and placed in tapwater to allow the gravid worms to extrude the eggs. The worms were removed and the eggs were incubated in dishes of aerated water at 19 to 22°C for five weeks. No development occurred inside the eggs which were observed every other day during incubation and none of them hatched. Several similar experiments were performed but the results were all negative.

Additional freshly extruded eggs were exposed for 24 hr to 7 laboratory raised Bithynia tentaculata. The snails were kept in an aquarium and observed periodically for 36 days after exposure. After 45 days the snails were killed and examined but no precercarial stages were found.

The adult Notocotylus imbricatus obtained from experimentally infected ducks and chickens in the present study agree in all essential points with that described by Pike (1969), with only the following slight differences in N. imbricatus of Pike (1969), there are 15 to 16 ventral glands on each lateral row against 14 to 17 in my material, testes with 4 to 7 lobes on the lateral margins against 6 to 8 and ovary with 3 to 6 lobes against 3 to 5.

Mature eggs with 2 or 3 filaments on one pole, without filaments on either pole or with an additional internal filament were observed. (See Fig. 20-22). This variation in the number of egg-filaments is the first record for this species.

The life cycle of the present study is similar to that reported by Pike (1969) for N. imbricatus, but a comparison in certain aspects cannot be made owing to lack of information as stated in page 41 .

Measurements of adults of Notocotylus imbricatus experimentally obtained from ducklings and chickens

Body	1.705 (1.104 - 2.130) long x 0.681 (0.578 - 0.786) wide
Oral sucker	0.095 (0.084 - 0.126) long x 0.122 (0.105 - 0.137) wide
Oesophagus	0.049 (0.019 - 0.095) long x 0.016 (0.011 - 0.019) wide
Right testis	0.283 (0.168 - 0.420) long x 0.127 (0.098 - 0.168) wide
Left testis	0.290 (0.210 - 0.392) long x 0.136 (0.084 - 0.168) wide
Ovary	0.140 (0.098 - 0.154) long x 0.172 (0.112 - 0.210) wide
Mehlis' complex	0.093 (0.070 - 0.126) long x 0.139 (0.112 - 0.182) wide
Cirrus sac	0.429 (0.280 - 0.602) long x 0.045 (0.028 - 0.056) wide
Metraterm	0.276 (0.140 - 0.350) long
Eggs	0.022 (0.019 - 0.022) long x 0.010 (0.007 - 0.011) wide
Polar filaments	0.068 (0.038 - 0.106) long

Discussion

The life cycle of Notocotylus imbricatus was first completed by Szidat (1935) in Germany, working with monostome cercariae released from Bithynia tentaculata. She regarded these cercariae as belonging to the species Cercaria imbricata from Paludina immura (= Bithynia tentaculata) named by Looss in 1893, but Rothschild (1940) suggested that this designation must be regarded as Nomen nudum as Looss 's description was inadequate. However, Rothschild did accept as valid a cercaria reported from Melania tuberculata by Looss (1896) and named Cercaria imbricata.

Rothschild (1940) went on to propose that the cercaria found by Szidat

(1935) differed from that described as Cercaria imbricata by Looss (1896) and in fact that the two cercariae belonged to different monostome sub-groups. While Cercaria imbricata (Looss, 1896) was shown by Rothschild (1938) to belong to the Imbricata sub-group, the cercaria of the present study together with Cercaria Fennica Wikgren 1956 (= Cercaria imbricata) Odening (1963), C. imbricata of Donges (1962), C. imbricata of Palm (1967), C. imbricata of Pike (1969) and C. imbricata of Odening (1963) all belong to the Yenchingensis sub-group. Both Cercaria helvetica I Dubois, 1929 (= Cercaria imbricata) Doubois (1951) and C. imbricata of Wesenberg-Lund (1934) were described only briefly, without reference to details of the protonephridial system and it is not possible to assign them to a cercarial sub-group. Cercariae of the two sub-groups, Imbricata and Yenchingensis are very difficult to separate on morphological criteria and their differentiation depends upon the form of the anterior excretory duct, particularly of the transverse commissure. In cercariae of the Yenchingensis sub-group an unpaired finger-like diverticulum extends forwards from the transverse commissure; no such structure is present in cercaria of the imbricata sub-group.

It is widely accepted, as suggested by various authors including Szidat (1936) and Odening (1968), that the larval stages of trematodes show a high level of specificity concerning the molluscan first intermediate host. Odening (1968) pointed out that only one monostome cercaria has been found in Europe from Bithynia tentaculata-Cercaria imbricata- and all the experimental investigations of Szidat (1935), Donges (1962) and Odening (1968) show that this is the cercaria of Notocotylus imbricatus. It therefore appears highly probable that the cercaria found by Looss (1893) in Paludina impura (= Bithynia tentaculata) in Germany was that of Notocotylus imbricatus. The true position of the cercaria found by the same author (1896) in Melania tuberculata in Egypt remains problematical.

The cercaria described in the present study exhibits a high degree of specificity in relation to its primary intermediate host. The molluscan fauna of the habitat from which the infected snails were collected comprised Lymnaea pereger, L. stagnalis, L. auricularia, Planorbis planorbis, P. carinatus,

Physa fontinalis, Bithynia tentaculata, Viviparus viviparus, Potomopyrgus jenkinsi, Acroloxus lacustris, Anodonta cygnea, Sphaerium corneum, Pisidium amniculum. Only B. tentaculata was found to harbour Cercaria imbricata.

The only monostome cercariae belonging to the Yenchingensis sub-group previously recorded in Britain are Cercaria unistoma Llewellyn (1957), C. middlesexensis Khan (1961c) and Cercaria imbricata as described by Pike (1969). The first two of these cercariae are very similar to the present cercaria in the following points:

(1) Molluscan first intermediate host of same species (Bithynia tentaculata),

(2) Similarity of cercariae emergence and behaviour patterns.

(3) Similarity of morphology and dimensions (see Table 2).

It is therefore proposed that Cercaria unistoma and C. middlesexensis be regarded as synonyms of C. imbricata Looss (1893). The C. imbricata of Pike (1969) also obtained from Bithynia tentaculata, shows differences from these cercariae and from that the present account. These differences are given below.

Present study	C. imbricata of Pike (1969)
Redia	Redia
Birth Pore present	Birth pore absent.
Rediae containing both daughter rediae and cercariae.	Daughter rediae contain only cercariae.
Cercaria	Cercaria
Anterior end of body bearing 14-16 hair-like projections on papillae. Additionally, 10 pairs of hair-like projections on either side of the body.	Three pair hair-like processes near oral sucker. Additional structures body absent.
Each side of tail armed with three hair-like projections on papillae.	Tail without hair-like processes.
Mouth opening bordered with a single row of 10-11 setae on papillae.	Mouth opening lacking these structures

Pigment granules scattered irregularly over the body	Pigment granules arranged in six longitudinal rows along the body.
Tail without glandular cells.	Six pairs of elongate cells (glandular cells) located along the tail.
Undivided caudal excretory duct.	Caudal excretory duct divided.

These differences shown by C. imbricata of Pike (1969) and C. imbricata of the present study may be considered of sufficient weight for the two to be regarded as separate species. However, the most convincing evidence that C. imbricata of Pike (1969) and of the present study are conspecific is that they both develop into adults of the same species - Notocotylus imbricatus.

Pike (1969) fed 150 metacercariae aged 1 to 21 days to a duckling and after 17 days recovered approximately 40 mature and immature specimens of Notocotylus imbricatus from the intestinal caeca. He believed that this variation in the degree of sexual maturity may be related to differences in the ages of the metacercariae fed and stated that in this species at least there may be some development of the metacercaria within the cyst. Pike's statement is probably right when he said that these differences in the attainment of sexual maturity are accounted for by the age of the cysts since he fed a single duckling with metacercariae of mixed age. The age-range of metacercariae used in the present study was 1-60 day-old and the number of birds, including ducklings and chickens, was 12 (see Table 1). The minimum length of time required to reach sexual maturity in the two species was slightly different - 12 days in chickens and 14 days in ducklings. However, results similar to those of Pike (infection with mature and immature forms) were obtained by the present writer in both chickens and ducks even when they were fed cysts of uniform age. No growth or development was observed by the writer in metacercarial cysts after 1 day. According to Herber (1942), Erkina (1954), Odening (1966) and Acholonu and Olsen (1967) the metacercariae of notocotylid trematodes are infective immediately after their formation.

The occurrence of immature forms along with mature specimens of the same age is difficult to explain and may be related to some factor of the host parasite relationship requiring further work to elucidate.

Table 1

Experimental infection of domestic birds with approximately 140 Metacercariae of Notocotylus imbricatus (Looss, 1893) Szidat, 1935.

Experimental definitive host	Age of Cysts (Days)	Host autopsied after - (Days)	Number and % of trematodes recovered	Degree of development of Trematodes	
				Immature	Mature
Chicken 1	1	10	52 (32%)	52	0
Chicken 2	10	12	55 (32%)	47	8
Chicken 3	25	15	43 (27%)	12	31
Chicken 4	25	16	28 (18%)	8	20
Chicken 5	60	18	0	0	0
Chicken 6	60	22	0	0	0
Duckling 1	1	10	74 (46%)	74	0
Duckling 2	10	14	68 (42%)	17	51
Duckling 3	25	15	85 (53%)	13	72
Duckling 4	25	16	58 (37%)	8	50
Duckling 5	60	21	22 (14%)	0	22
Duckling 6	60	24	0	0	0
Pigeon 1	1	9	0	0	0
Pigeon 2	10	9	0	0	0
Pigeon 3	25	18	0	0	0
Pigeon 4	60	22	0	0	0
Mouse 1	1	9	0	0	0
Mouse 2	10	9	0	0	0
Mouse 3	25	18	0	0	0
Mouse 4	60	18	0	0	0
Rat 1	1	9	0	0	0
Rat 2	10	9	0	0	0
Rat 3	25	18	0	0	0
Rat 4	60	18	0	0	0

Table 2

Comparative measurements of Cercaria imbricta (present study), C. unistoma (Llewellyn (1957)) and C. middlesexensis (Khan (1960)), in m.m.

C. unistoma Llewellyn (1957)

Cercaria

Body	0.221 (0.21 - 0.27) long x 0.123 (0.10 - 0.14) wide
Tail	0.216 (0.20 - 0.26) long x 0.042 (0.04 - 0.05) wide
Oral sucker	0.031 (0.03 - 0.04) long x 0.031 (0.03 - 0.035) wide

Redia

Body	0.760 (0.51 - 0.105) long x 0.218 (0.18 - 0.27) wide
Pharynx	0.073 (0.07 - 0.08) long x 0.069 (0.060 - 0.07) wide

C. middlesexensis Khan (1960)

Cercaria

Body	0.284 (0.270- 0.316) long x 0.132 (0.116 - 0.166) wide
Tail	0.421 (0.383 - 0.463) long x 0.03 (0.026 - 0.033) wide
Oral sucker	0.031 (0.026 - 0.033) diameter

Redia

Body	0.675 - 1.5 x 0.135 - 0.195
Pharynx	0.056 - 0.083 in diameter

C. imbricata (Present study)

Cercaria

Body	0.221 (0.212 - 0.239) long x 0.116 (0.114 - 0.121) wide
Tail	0.327 (0.300 - 0.364) long x 0.028 (0.026 - 0.030) wide
Oral sucker	0.026 (0.026 - 0.026) long x 0.026 (0.026 - 0.026) wide

Redia

Body	0.424 (0.238 - 0.602) long x 0.196 (0.168 - 0.224) wide
Pharynx	0.062 (0.049 - 0.076) long x 0.058 (0.049 - 0.060) wide

Cercaria of Notocotylus attenuatus

Some specimens of Lymnaea pereger collected at Gledhow Valley Road, Kirkstall Power Station (Leeds-Liverpool Canal), West Bretton Lake, Cawthorne, and Riffa Beck at Pool in October 1972, April 1973 and March, April and May 1975 were releasing large monostome cercariae. The incidence of infection at Pool and West Bretton Lake was very high (between 21 and 40%) whereas at the remaining localities it was relatively low (between 4.1 and 8%).

The cercariae were liberated throughout the day, in greatest numbers between 11:00 h. and 14:00 h. After emergence the cercariae swim very rapidly by violent beating of the tail and during this period the body is bent ventrally and contracted. They swim for a short period (up to about 2 to 3 min.) and, after coming into contact with any substratum cease swimming, attach by means of the oral sucker and locomotory pockets and encyst.

Description (Plate 5 Figs.1-5)

Body elongate and somewhat cylindrical when extended. Body surface completely covered with minute spines. Cuticle thick, provided with hair-like projections and papillae arranged regularly around periphery of body. Dark brown pigment granules scattered irregularly throughout body and connected together by fine strands of pigment giving the body a dark-brown appearance. Tail non-spinose, slender, subterminal, granually tapering distally and very contractile; about twice of length of body. Tail cuticle thin and containing fine granules. Longitudinal and circular muscles extending along its entire length, the former originating at base of tail and comprising bands of 15-17 muscle fibers each. Seven pairs of elongate glandular cells with fine granular cytoplasm arranged regularly along length of tail and situated laterally. Two locomotory pockets located ventrally at postero-lateral margin of body; each containing a group of numerous glandular cells capable of secreting sticky material to facilitate adhesion of these structures to substratum. Locomotory pockets invaginated during swimming and projected as two conical projections during creeping movements.

Oral sucker circular, subterminal and slightly protrusible, with 7 to 8 papillae on setae situated around mouth opening; border of sucker armed with a row of closely set minute spines. Mouth slightly subterminal, opening on oral sucker and communicating with a narrow and relatively long thin-walled oesophagus. Pharynx absent. Oesophagus divided posterior to median eyespot; intestinal caeca extending to near posterior end of body before bending laterally and terminating anterior to locomotory pockets.

Three small apertures present antero-lateral to oral sucker, leading into three duct-like extensions, but no gland cells observed. Body filled with cystogenous gland-cells from lateral region of oral sucker to posterior end of body; each cell containing numerous short rods, each with very fine grey-green granular contents. No trace of genital primordium observed.

Nervous system comprising a transverse commissure immediately anterior to oesophageal bifurcation and two cerebral ganglia each giving rise to 2 antero- and 2 postero-lateral nerves. The 2 postero-lateral nerves extending posteriorly and internal to main excretory ducts as far as anterior level of locomotory pockets where they became obscured by dense cystogenous gland-cells. Anterior nerves passing to antero-lateral margin of oral sucker. Between posterior margin of oral sucker and oesophageal bifurcation 3 pigmented eyespots located, each one formed of clusters of dark-brown granules. In cercariae obtained by dissection of snail hosts only 2 eyespots present. Median eyespot fully formed only in well-developed cercariae when it is similar in size to the lateral ones and with a rounded central region devoid of pigment. On one occasion a well-developed cercaria with only 2 eyespots was seen.

Protonephridial system consisting of a short broad excretory bladder with a deep median constriction opening to exterior via pore located on dorsal surface at base of bladder. When fully expanded bladder appears spherical. Primary excretory ducts originating from anterior part of bladder, passing anteriorly and uniting by a transverse commissure just anterior to oesophageal bifurcation. A large number of refractile granules occupying whole excretory circuit, sometimes observed moving freely inside bladder. Flame cell pattern

could not be elucidated due to the presence of cystogenous gland-cells. Only 16 pairs of flame cells were seen on each side of the body, but this probably an underestimate. Caudal excretory duct arising from posterior end of bladder, extending posteriorly and opening in proximal half of tail by a small lateral secondary excretory pore. It was not possible to trace further details of the excretory system.

Redia (Plate 5 Fig. 6)

This cercaria develops in rediae found in the hepatopancreas of Lymnaea pereger. They are sausage-shaped, attenuated posteriorly, very motile and capable of extension and contraction mainly in the posterior part. The cuticle of the body is thick and is furnished with 10-12 short hair-like projections on papillae at the anterior end of the body but both a collar and locomotory appendages are absent. The birth pore is conspicuous in some rediae while in others it can hardly be seen. It is located on one side of the body a little posterior to the level of the pharynx. The anterior end of the body on either side of the pharynx is occupied by numerous gland-cells with fine granular contents.

The pharynx is almost circular in outline; behind it lies a short oesophagus which widens out into a long saccate intestine extending about two thirds of the length of the body in some rediae and occasionally almost reaching the posterior end. It contains a transparent fluid and some granular material, probably digested snail tissue. The body cavity contains cercariae at different stages of development of which only 3-5 were mature. The germ balls are usually found at the posterior extremity.

The protonephridial system comprises a wide tubular excretory bladder from which one anterior and two posterior collecting excretory ducts arise. The anterior collecting duct passes anteriorly to the level of postero-lateral margin of the pharynx, where it receives a capillary from a flame cell. The two posterior collecting ducts pass backwards and each ends in a flame cell near the distal part of the intestine. The excretory bladder contains

dispersed refractile granular material. On two occasions rediae were seen free on the bottom of the vessel in which infected snails were isolated.

Measurements of the cercaria and redia of Notocotylus attenuatus from Lymnaea pereger

Body	0.428 (0.392 - 0.504) long x 0.154 (0.126 - 0.182) wide
Tail	0.798 (0.756 - 0.882) long x 0.056 (0.056 - 0.056) wide
Oral sucker	0.042 (0.041 - 0.045) long x 0.042 (0.041 - 0.045) wide
Oesophagus	0.026 (0.021 - 0.037) long
Eyespots	0.015 (0.015 - 0.019) long x 0.015 (0.015 - 0.019) wide
Redia	0.818 (0.700 - 1.190) long x 0.222 (0.210 - 0.252) wide
Pharynx (of redia)	0.076 (0.068 - 0.087) long x 0.076 (0.068 - 0.083) wide

Encystment

The cercariae encyst on various substrates soon after being discharged by the snail host and the encystment metacercariae are found on vegetation, stones, shells of several species of snails (including its own host species) and in the laboratory on the bottom and wall of the container and microscope slides.

After a brief period of swimming (2 to 4 min.) the cercariae settle down and encyst; the whole process of encystment is similar to that in the cercaria of Notocotylus imbricatus but requires more time (4-8 min.).

Metacercaria (Plate 5 Fig. 7)

The cysts are subspherical. There are two cyst walls; the outer is fragile and easily ruptured and the inner is rather thick and difficult to break without causing injury to the worm. In the freshly formed cyst the body of the metacercaria does not differ essentially from that of the cercaria. It is rolled up within the cyst displaying constant rotating movements, and the three eye-spots still persist. As the metacercaria ages the cyst becomes brown in colour but there is no apparent sign of growth. The pigment of the eyespots begins to be dissipated with the median eyespot the first to disappear.

After 56 days there is still no growth and the encysted metacercariae do not exhibit any kind of movement except when gentle pressure is applied with a coverslip or on some accasions when subject to strong light. The cyst wall is by this time more opaque, the lateral eyespots have been lost and the refractile granules of the cercaria have decreased in number. The mortality rate of the metacercariae at this stage is about 25%.

Twelve naturally infected snails were placed in vessels containing water. Cercariae emerged in great numbers and, on coming into contact with the walls or bottom of the vessel, or with the lettuce leaves placed in it as food for the snails, began to encyst. In a few hours large numbers of cysts had formed adhering to the container or to the lettuce leaves. The cercariae rarely failed to encyst and it was difficult to find dead non-encysted specimens.

Measurements of 3 day-old metacercariae of Notocotylus attenuatus experimentally obtained from the shells of several species of snails.

Cyst	0.167 (0.155 - 0.171) long x 0.166 (0.163 - 0.172) wide
Outer wall	0.047 (0.030 - 0.060) thick
Inner wall	0.015 (0.014 - 0.019) thick
Oral sucker	0.044 (0.041 - 0.049) long x 0.042 (0.038 - 0.049) wide

Infection of the final host

The experimentally obtained cysts used in these experiments were 1, 3, 25 and 37 days old and were fed to 6 ducklings, 6 chickens, 4 pigeons, 4 rats and 6 mice. Two additional representatives of each species were kept as control but none of these was infected when examined after 4 days.

The results (see Table 3) indicate that pigeons, rats and mice are not susceptible to infection by this species as no trematodes were found at autopsy following the ingestion of metacercariae.

On the other hand both chickens and ducklings are readily infectable and in them the worms reach maturity within 8 days. Metacercariae as young as 24 h are infective to both these species. Ducklings appear to be the more suitable hosts since the percentage recovery of metacercariae as adults worms

after 4-6 days was 36.6% compared with 14.2% in chickens. Further, worms appeared to survive in larger numbers up to and beyond 16 days in the former hosts.

All the worms in both host species were recovered from the caeca.

The egg. (Plate 7 Figs 12-15)

Numerous eggs were obtained from gravid worms in experimental infections of laboratory hosts. Batches were isolated in small vessels containing either pond water or tap water and maintained at room temperature (19 - 22°C) for 3 weeks. The eggs were examined periodically during incubation but no development was observed in either series. Other eggs of the same batch were placed immediately after collection with 12 laboratory raised Lymnaea pereger most of which were seen ingesting eggs. The snails were kept in an aquarium and examined 2 and 3 weeks later but were found to be uninfected. Several attempts made to observe hatching were unsuccessful. Attempts to infect snails by ingestion of eggs also give negative results.

? The adult Notocotylus triseriales (= N. attenuatus) Pike (1969), experimentally obtained from a duck are morphologically identical with adult N. attenuatus experimentally obtained in this study. There was some variations in the number of testes lobes and the number of ventral glands. These variations are given below.

	N. triseriales (= N. attenuatus) of Pike (1969)	Present study
Ventral glands		
Lateral rows	14 to 15	14 to 18
Median row	14 to 15 (one specimen only with 12)	13 to 15
Testes		
Lobes	4 to 8	6 to 12

These minute discrepancies observed between N. triseriales (= N. attenuatus) of Pike (1969) and N. attenuatus of the present study cannot be regarded as a sufficient basis for specific distinction and can be interpreted only as intra-specific variation.

The life cycle described during the present study is very similar to that reported by Pike (1969), but since Pike used only a single duckling and 2-week old metacercariae some comparison cannot be made; these include (1) the time required for metacercariae to become infective (2) viability of the metacercariae (3) time required for attainment of sexual maturity in the final host and (4) longivity of the adult phase.

The finding of mature eggs with 1, 2 or 3 filaments at one pole and an additional internal filament constituted the first record for this species (see Figs. 12-15. This variation in the number of filaments has also been reported in other members of the family notocotylidae by (Wu, 1953; Erkina, 1958; Ameel, 1962).

The morphology of adult specimens obtained during the present work was similar to that described by Pike (1969).

Measurements of adult Notocotylus attenuatus obtained from laboratory birds.

Body	2.665 (1.444 - 4.103) long x 0.717 (0.552 - 0.999) wide
Oral sucker	0.128 (0.098 - 0.182) long x 0.136 (0.098 - 0.210) wide
Oesophagus	0.096 (0.056 - 0.140) long x 0.025 (0.014 - 0.056) wide
Right testis	0.409 (0.238 - 0.602) long x 0.199 (0.140 - 0.308) wide
Left testis	0.411 (0.252 - 0.602) long x 0.194 (0.140 - 0.322) wide
Ovary	0.202 (0.140 - 0.294) long x 0.220 (0.140 - 0.294) wide
Mehlis' complex	0.115 (0.056 - 0.182) long x 0.194 (0.140 - 0.238) wide
Cirrus sac	0.764 (0.490 - 1.218) long x 0.100 (0.070 - 0.168) wide
Metraterm	0.458 (0.322 - 0.686) long
Eggs	0.022 (0.019 - 0.023) long x 0.013 (0.011 - 0.015) wide
Polar filaments	0.160 90.114 - 0.228) long

Discussion

The genus Notocotylus was founded by Diesing (1839) to contain Catatropis verrucosa (Frolich, 1789) and gave Notocotylus triserialis Diesing, 1839 (= N. attenuatus) (Rudolphi, 1804) Kossack, 1911 as type species. Dubois (1951), in his revision of the genus Notocotylus, stated that the original material of

N. attenuatus (Rud., 1809) examined by Kossack (1911) must have been destroyed during the 1939-49 world war and our knowledge about N. attenuatus is therefore limited to Rudolphi's diagnosis which was very brief and without illustration. Therefore Dubois considered N. attenuatus (Rud., 1809) as a species inquirenda and placed N. triserialis (Dies, 1839) as the type species. The present author does not agree with Dubois's opinion and supports the contentions of Yamaguti (1958) and Beverley-Burton (1961) that the name Notocotylus attenuatus should be retained.

Joyeux (1922) found an unusual monostome cercaria from Planorbis rotunda in France characterized by having a very small tail, lacking eyespots and encysting without leaving the snail. He experimentally infected ducklings and obtained adult trematodes which he identified as Notocotylus attenuatus Rudolphi, 1809. Mathias (1930) described a monostome cercaria from Lymnaea limosa also in France. Metacercariae were on several occasions fed to ducklings and the flukes obtained were regarded as Notocotylus attenuatus. Mathias's cercaria had a long tail, always longer than the body, three eyespots and it encysted on any substratum after leaving the snail host. Mathias examined Joyeux's adult specimens and found marked differences in the size of the body, vagina and cirrus pouch. Both he and Joyeux concluded that the two sets of specimens belonged to different species. Dubois (1951), after examining the specimens of Joyeux suggested that they were identical to Catatropis verrucosa (Frolich, 1789). Odening (1966) found a monostome cercaria in Segmentina nitida and Gyraulus albus similar to that found by Joyeux (1922) from France. He experimentally obtained adult parasites and recorded them as Catatropis verrucosa (Frolich, 1789) thus corroborating Dubois's opinion.

Szidat and Szidat (1933) found two monostome cercariae in Germany emerging from Lymnaea palustris and Planorbis corneus. The first was named Cercaria vaga n.sp., and its adult form obtained experimentally was Notocotylus attenuatus Rud. 1809. The second was C. ephemera Nitzch, 1807 and the corresponding adult trematodes were named Notocotylus thienemanni n.sp. "According to the rules of Zoological nomenclature the latter parasite should be named Notocotylus ephemera

(Nitzch, 1807). Kupriyanova-Shahmatova (1959) working in the USSR, found the same cercariae that Szidat and Szidat (1933) had found in Germany and emerging from the same hosts, and on the basis of experimental evidence considered that Notocotylus thienemanni was a synonym of N. attenuatus. But Zdarska (1964), who recorded the cercaria of N. attenuatus from several species of Lymnaeid snails and C. ephemera from a Planorbid also differentiated between the two species. Yamaguti (1938) reported a monostome cercaria from Bulimus striatulus japonicus in Okayama, Japan. He fed ducklings with cysts obtained experimentally from the snails B. s. japonicus and Semisulcospira libertina and recovered adults trematodes which he identified as Notocotylus attenuatus. According to Yamaguti the main excretory ducts in the cercaria unite at the level of the intestinal bifurcation to form the transverse commissure which gives rise to a branch (finger-like diverticulum) extending to the equatorial level of the oral sucker. He thereby placed this species in the Yenchingensis group. The body length is less than half that of the cercaria of N. attenuatus and the first intermediate host belongs to the same genus Bulimus (= Bithynia). Undoubtedly Yamaguti was working with the Cercaria of Notocotylus imbricatus and not with that of N. attenuatus.

The number and arrangement of glands in the three ventral rows have been widely utilized as taxonomic criteria within the genus Notocotylus. Baylis (1928) considered that the number of these glands is not very constant within the species of this genus, and the number of them increased with the length and age of the worms. Similar observations were given by Duthoit (1931) and Noble (1933). Baylis used this feature to separate N. chionis Baylis (1928) from its most closely related species (N. attenuatus, N. aegyptiacus and N. gibbus) but later (1936) stated that the number of these glands does not vary according to the length or age of the worm. Although he believed that this character was not reliable in distinguishing existing species in this genus he again used it for specific identification of N. ralli Baylis (1936). Szidat and Szidat (1933) Herber (1942) and Pike (1969) shared the opinion that the ventral gland relationships could be utilized as a taxonomic criterion. William (1963) after

comparing mature and immature specimens of Notocotylus stagnicolae Herber, 1942, experimentally recovered from chickens, showed some differences in the number and arrangement of ventral glands. The pattern in 8- and 10-day-old worms varied from that of mature 12-day-old worms. In the former each lateral row consisted of 14 to 16 glands (usually 15), the median row consisted of 13 to 14 glands (usually 14) whereas the latter characteristically have the arrangement 16-15-16. Therefore he concluded that only sexually mature worms should be used in distinguishing closely related species.

In the present material the ventral gland relationships in adult worms experimentally obtained from ducklings and chickens showed great variation. In 52 worms studied the number of glands in the lateral rows varied from 14 to 18 (usually 15) and in the median row 13 to 15 (usually 15). This variation was more markedly in the glands of the median row. In most of the worms there is one gland (sometimes two) in the median rows anterior to the most anterior glands in the lateral rows (Figs. 16, 17, 19, 23). Less frequently in the most anterior gland in the median row is absent.

Herber (1942) during studies of life cycles of two species of notocotylid trematodes, Quinqueserialis quinqueserialis (Barker and Langhlin, 1911) and Notocotylus stagnicolae n. sp. pointed out the great difficulty of distinguishing the adult species of the subfamily Notocotylinae and specially of the genus Notocotylus in which the worms are morphologically very similar and there are few good characters for differentiation. He suggested that the lobed lateral border of each testis, the number of uterine loops and the position of the vitellaria can be used as good diagnostic characters.

In the specimens of the present study great variability was found in the number of testis lobes (6 to 12) and in the anterior limits of the vitellaria; in some specimens the vitelline follicles extended to the midline of the body while in others they did not. Additional variation was noted in the shape of the ovary and in the number of lobes (Fig. 11). In my opinion these features suggested by Herber (1942) do not enable separation between these

closely related trematodes and I consider these morphological variations as intraspecific until more data regarding life cycles are available for the species of the genus Notocotylus.

In Britain Wright and Bennet (1964) recovered adults of Notocotylus attenuatus by feeding duckling and chickens with cysts obtained experimentally from Lymnaea pereger, but they did not give any description of the larval stages or the adults, they merely pointed out the presence, in some cercariae, of 2 eyespots and an anterior ring-shaped diverticulum but they did not state whether the diverticulum arose laterally or centrally from the transverse commissure. They also described variation in the number of ventral and lateral glands in the adults. Williams (1966) obtained the cercaria of N. attenuatus from L. pereger and its adult form from ducklings in Glasgow, Scotland, but no description of the cercaria and adult was given. Pike (1969) working in South Wales reported the life cycle of Notocotylus triserialis Diesing 1839 (= N. attenuatus).

Table 3

Experimental infection of mammals and birds with Notocotylus attenuatus (Rud, 1809), Kossack, 1911

Experimental Definitive Host	Number of Cysts fed to host	Age of cysts (Days)	Host autopsied after - (Days)	Number of trematodes recovered	Degree of development of Trematodes	
					Immature	Mature
Chicken 1	165	1	4	43	43	0
Chicken 2	185	3	6	62	62	0
Chicken 3	168	25	8	37	11	26
Chicken 4	175	25	16	7	0	7
Chicken 5	185	37	39	0	0	0
Chicken 6	170	37	39	0	0	0
Pigeon 1	160	1	4	0	0	0
Pigeon 2	170	1	6	0	0	0
Pigeon 3	160	3	8	0	0	0
Pigeon 4	150	25	39	0	0	0
Rat 1	160	1	4	0	0	0
Rat 2	155	3	6	0	0	0
Rat 3	155	25	8	0	0	0
Rat 4	158	37	39	0	0	0
Mouse 1	170	1	4	0	0	0
Mouse 2	138	3	6	0	0	0
Mouse 3	145	25	8	0	0	0
Mouse 4	152	37	16	0	0	0
Mouse 5	150	37	39	0	0	0
Duckling 1	175	1	4	94	94	0
Duckling 2	175	1	4	83	83	0
Duckling 3	180	3	6	88	88	0
Duckling 4	170	25	8	76	8	68
Duckling 5	165	25	16	78	0	78
Duckling 6	180	37	39	12	0	12
Duckling 7	178	37	39	4	0	4

Gymnocephalous cercariae

Luhe (1909) created a super-group "Leptocercous cercariae" for distome cercariae with undivided tails which were narrower than the bodies at their insertion, even when the tails were contracted. He included in this super group the "Gymnocephalous cercariae" which were unarmed, the "Echinostomes" with a cephalic collar of spines and the "Xiphidiocercariae" with a stylet embedded in the oral sucker. Luhe defined "Gymnocephalous cercariae" as distome cercariae having no collar spines or stylet, with an undivided tail, and developing in rediae.

Sewell (1922) considered that "Gymnocephalous cercariae are not a natural group and subdivided them to be four sub-groups; the "parapleurolophocerca", "Agilis", "Reflexae" and the "Isopori". The major characters of the cercariae contained in these subgroups are given below.

(1) Parapleurolophocerca.

1. Small cercariae, body length about 0.175-0.263 mm.
2. Tail longer than the body and furnished with a finfold.
3. A pair of pigmented eyespots is usually present.
4. The anterior region of the surface of the body is entirely or partially armed with spines.
5. Oral sucker protractile, a well-developed pharynx, oesophagus and caeca may be present or absent.
6. Acetabulum may be present, rudimentary or absent.
7. Penetration gland cells with ducts opening on the anterior end of the body.
8. Large excretory bladder with thick wall reniform or globular in outline.
9. Development in elongated, saccular rediae, provided with an intestine and a birth pore but devoid of locomotory appendages. These cercariae leave the rediae and complete their development in the tissues of the mollusc host.

(2) Agilis.

1. These cercariae look like Echinostome cercariae but have no collar

of spines; large size, body length about 0.4 to 0.6 mm. in oval or pyriform shape.

2. Cystogenous cells containing rod-like granules.
3. Oral sucker situated anteriorly. The digestive system comprises a short prepharynx and a well-developed pharynx. An oesophagus and intestinal caeca may be present or absent.
4. Excretory bladder composed of anterior and posterior chambers. Main excretory ducts arise from the anterior chamber forming a loop at either side of the pharynx and contain refractile granules.
5. Development in rediae with conspicuous collar, locomotory appendages, birth pore, muscular pharynx, and long intestine.

(3) Reflexae - the members of this subgroup are close to those of the Agilis group but they have a finfold in the distal part of the tail. Oesophagus and intestinal caeca present.

(4) Isopori;

1. Medium-sized cercariae with proportionally very large tails.
2. A pair of pigmented eyespots.
3. A complex stylet embedded in the oral sucker. An acetabulum is small and situated near the mid-line of the body.
4. Prominent pharynx and a rhabdocoel gut, penetration gland cells present, ducts open at the base of the stylet.
5. Excretory bladder is oval or elongate in outline. Its wall consists of a single layer of large granular cells. The main excretory duct arises anteriorly from the excretory bladder and passes to the level of the acetabulum, then divides into anterior and posterior collecting ducts. Flame cell formula 2 x 4 x 2 = 16.
6. Development occurs in elongated sausage-shape rediae without locomotory appendages. Well-developed pharynx and a short intestine.

Wesenberg-Lund (1934) did not consider that Sewell's classification of Gymnocephous cercariae into four different groups could be used to separate the European gymnocephalic cercariae since the features shown by the Indian and North American cercariae were not shared by the previously described forms.

Porter (1938) found five gymnocephalous cercariae in South Africa two of which were placed in the Agilis group of Sewell (1922). The rest she could not classify in any of the groups mentioned above, mainly because of the presence of an oesophagus and intestinal caeca. She erected a new sub-group "Paragilis" to include those three species which she could not place in the Agilis group, and also suggested that Cercaria fusiformis O'Roke (1917) and Cercaria agilis Filippi as described by Sonsino (1892) should be included in this new subgroup "Paragilis".

Fain (1953) in view of the unstable classification of the Gymnocephalous group pointed out that it is not possible to give a reliable system, and he therefore, gave a temporary list of the groups of Gymnocephalous cercariae which can be recognised at present, as follows:

1. Pleurolophocerca and Parapleurolophocerca group.
2. Agilis group.
3. Paragilis group.
4. Reflexae group.
5. Megalura group.
6. Gymnocephale s. str. group.

The Megalura group was first placed in the Gymnocephalous group by Cort (1915) to include three cercariae which exhibited a close relationship namely, Cercaria distomata Sonsino, C. megalura Cort and Cercaria sp. Lutz. Sewell (1922) considered that this group of cercariae is more closely related to the Echinostome cercariae. Fain (1953) noted the importance of Gymnocephale group and pointed out that it includes the larvae of Fasciola hepatica and F. gigantica.

Cable (1938) considered that the basis for the division of the Gymnocephalous cercariae, especially in the Agilis and Reflexae group, is still uncertain

because the presence or absence of collar spines alone is not sufficient to separate these Echinostome-like forms from the true echinostomes and he redefined the above two groups to accommodate Cercariae ornatosoma Cable (1935b). Nasir and Diaz (1968) confirmed the observation of Cable (1938) in their study of the life cycle of Echinochasmus zubedakhaname, the larval stage of which is absolutely devoid of collar spines whereas these are invariably present through metacercaria to adult. The same situation occurred in Stephanoprora paradenticulata Nasir and Rodriguez (1969). On the contrary, the cercaria, metacercaria and adult of Stephanoprora denticulata (Rudolphi, 1802) Nasir and Scorza (1968) all have a constant number of collar spines.

I have followed the classification scheme of Sewell (1922) as modified by Cable (1938).

The gymnocephalous cercariae, the cercaria of Sphaeridiotrema wintersettensis, C. gymnocephalous II and C. gymnocephalous III found during the present survey are described below belong to the Agilis division.

Cercaria of Sphaeridiotrema wintersettensis

In July 1973, 250 specimens of Bithynia tentaculata were collected at Newmillerdam Lake; 30 were infected with gymnocephalous cercariae.* These cercariae at first appeared to be conspecific but detailed anatomical studies revealed that 2 different species were present. These are named Cercaria of S. wintersettensis and C. gymnocephalous II. Seventeen of the infected snails carried C. gymnocephalous II and 13 carried the cercaria of S. wintersettensis. No snails carried both species.

The cercariae are discharged throughout the whole 24 hr., but in greatest numbers in the early morning. Initially they swim relatively rapidly but they eventually settle and begin creeping rapidly over the substratum.

Description (Plate 9; Figs. 1-4)

Body flattened, oval and nonspinose. Cuticle thick, with fine granular contents bearing papillae with hair-like processes; 12 small papillae located at anterior end and 10 large papillae on each side. Tail subterminal. Cuticle thin, provided with small papillae with hair-like processes laterally along its entire length. Longitudinal muscles of tail formed by two bands each comprising 10-12 strands and with both longitudinal and circular muscles extending from the base to the tip. Proximal part of the tail occupied by a mass of cells containing a clear fluid giving them the appearance of vesicles; two rows of such cells, each cell having a prominent nucleus and fine granular cytoplasma, extending almost to tip of tail, becoming more abundant in distal two-thirds.

Oral sucker terminal or subterminal. Eleven papillae with setae situated around mouth opening. Posterior margin of oral sucker provided with a trilobed cephalic gland. Prepharynx present. Pharynx muscular, opening into oesophagus; narrow intestinal caeca extending to anterior region of excretory bladder. Lumen of oesophagus and caeca filled with rather thick granular contents.

Acetabulum situated slightly posterior to centre of body, protusible and surrounded with a very thick outer membrane lined with circular muscles;

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*Note added after preparation of account. Cercaria of Sphaeridiotrema wintersettensis also recorded in Bithynia leachi (1 snail out of 59 examined)

its border provided with a row of very minute spines set close together.

Penetration gland-cells arranged in two rows of 10 cells each, situated between the anterior half of the primary excretory ducts and the oesophagus. Each cell with coarsely granular cytoplasm and a small round nucleus; ducts opening anteriorly on the body.

Numerous large cystogenous gland-cells with rhabditiform contents located beneath the cuticle and distributed throughout the body.

Rudiments of genital system present, consisting of 3 masses of undifferentiated cells; one small mass located anterior of the acetabulum probably representing the cirrus pouch and two large masses located behind acetabulum probably representing testes.

Excretory bladder situated at posterior end of body; transversely elongated. Primary excretory duct on each side dilated containing 12-16 large refractile granules and passing anteriorly to the anterior level of pharynx, then posteriorly, as secondary ducts, following a sinuous course as far as the level of the anterior margin of the acetabulum, where the division into anterior and posterior collecting ducts occurs. Each collecting duct has 3 groups of 2 flame cells. Caudal excretory duct branching at the middle of the tail and opening laterally. Flame cell formula: $2\left[\overline{(2+2+2)+(2+2+2)}\right]=24$.

This cercaria developed into an adult trematode belonging to the genus Sphaeridiotrema; Further details are given below.

Redia (Plate 9; Fig. 5)

Rediae were observed in different stages of development they showed very little motility. The anterior margin of the body is notched; the collar is undivided and a birth pore present, just behind the collar. A pair of locomotory appendages is located almost at the end of the body. The pharynx is oval leading to a wide intestine which extends posteriorly for about two-thirds of the body length. The intestine lumen containing a brown-yellow granular material and the body cavity of the rediae is occupied by numerous germ balls and partly developed cercariae of which only 2-4 specimens were

mature in each redia.

Measurements of the cercaria and redia of Sphaeridiotrema wintersettensis from Bithynia tentaculata

Body	0.206 (0.190 - 0.220) long x 0.117 (0.106 - 0.144) wide
Tail	0.344 (0.334 - 0.353) long x 0.041 (0.041 - 0.041) wide
Oral sucker	0.039 (0.038 - 0.041) long x 0.039 (0.038 - 0.041) wide
Acetabulum	0.039 (0.038 - 0.092) long x 0.047 (0.045 - 0.049) wide
Prepharynx	0.016 (0.015 - 0.019) long
Pharynx	0.022 (0.019 - 0.026) long x 0.023 (0.019 - 0.022) wide
Oesophagus	0.022 (0.015 - 0.026) long
Preacetabular extent	0.109 (0.098 - 0.117) long
Postacetabular extent	0.050 (0.057 - 0.060) long
Redia	0.928 (0.490 - 1.190) long x 0.226 (0.140 - 0.266) wide
Pharynx	0.073 (0.064 - 0.095) long x 0.070 (0.060 - 0.102) wide

Metacercaria and Location in the snail host

After leaving the snail host (Bithynia tentaculata) the cercariae of S. wintersettensis re-entered either the same snail or a different individual of the same or another species and encysted on the inner surface of the shell.

The metacercarial cysts of this trematode were first encountered on the inner surface of the shell of a B. tentaculata which was infected with precercarial stages (rediae) of Cercaria pleurolophacerca I. Cysts were also found on a snail individual infected with the cercariae of S. wintersettensis.

Previous workers (Szidat, 1937; Burns, 1961) have shown that the cercariae of Sphaeridiotrema encyst on the inner surface of the shell of its first intermediate host. A variety of freshwater molluscs - Lymnaea stagnalis, L. pereger, Physa fontinalis, Hydrobia jenkinsi, Planorbis corneus, B. tentaculata and Ancylus lacustris (all obtained from Kirkstall Power station where the cercaria of S. wintersettensis did not occur) were utilized as experimental second intermediate hosts. The snails were kept in small containers together

with naturally infected snails which were releasing a large number of cercariae of S. wintersettensis. After the cercariae had been swimming for a brief period of time they attached themselves to the shell or body surface of the snails and began to crawl over the surface. On reaching the preferred site between the mantle and the shell the tail was shed and they proceeded to encyst. The actual formation of the cysts could not be seen under the microscope.

After removal of the shells from the experimentally infected snails a number of cysts could be seen adhering to the inner surfaces of the whorls, columella, sutures and, less frequently, the aperture. On several occasions a single cyst or group of two to three cysts was found attached to the external wall of the hepatopancreas. None was ever found within the tissues of the snails.

The newly formed cysts were not firmly attached and were therefore easy to remove. The older cysts, however, were covered by successive layers of calcareous material produced by the snail which made it very much more difficult to remove them without injuring the metacercariae. After the cysts had been extracted from these depressions the empty holes resembled a honeycomb. The number of cysts per snail varied between 8 and 68.

The species P. fontinalis and H. jenkinsi proved to be the most suitable experimental hosts for this species of cercaria, and A. lacustris was also highly suitable. On several occasions a small number of L. pereger, L. stagnalis and A. lacustris were collected from the habitat where the cercariae of S. wintersettensis occurred, but they were not infected with it. Only B. tentaculata from that locality was found to be naturally infected.

Metacercaria (Plate 10; Figs. 6-8)

Each cyst is spherical to oval in outline with an active metacercaria lying within it. The wall is thin in recently formed cysts and the metacercaria is morphologically similar to the cercaria. In seventeen-day-old cysts the walls are thicker and clearly composed of two layers; an outer and an inner layer. In these cysts metacercariae are more active and lie folded on their ventral surfaces. The oral sucker and pharynx are larger than in the cercaria the intestinal caeca are wider, slightly septate and their granular contents have

become more distinct. The cystogenous gland-cells have completely disappeared, whereas two to three penetration gland-cells are still visible. The excretory bladder is unchanged but the main excretory ducts have expanded. The excretory refractile granules are almost the same size and move more freely within the ducts. Only 12 flame cells could be seen. The genital system is represented by two masses of undifferentiated cells, situated either one behind the other or overlapping, and probably representing the testes. The most prominent feature of the metacercariae is the acetabulum with its central projection.

Twenty five to thirty days after encystment some of the cysts became brown or orange-yellow in colour and the part of the shell where they were situated turned opaque white. At this stage the cephalic gland had increased in size and its content has become very much coarsely granular. It gave off two ducts from each antero-lateral margin which opened at the anterior edge of the oral sucker. A small cirrus sac was located near the oesophageal bifurcation. No seminal vesicle or other part of the male system was observed. In some of the cysts the activity of the metacercariae had increased.

Measurements of 17 day-old metacercariae of Sphaeridiotrema wintersettensis experimentally obtained from a variety of freshwater molluscs.

Cyst	0.133 (0.130 - 0.138) long x 0.133 (0.130 - 0.138) wide
Outer wall	0.005 (0.004 - 0.006) thick
Oral sucker	0.032 (0.031 - 0.033) long x 0.049 (0.048 - 0.052) wide
Pharynx	0.026 (0.025 - 0.027) long x 0.024 (0.022 - 0.027) wide
Acetabulum	0.052 (0.052 - 0.054) long x 0.054 (0.051 - 0.055) wide

Infection of final hosts

Chickens, ducklings and canaries obtained from commercial suppliers, and pigeons bred in the laboratory, were used as potential host animals (see Table 4). Faecal samples were examined every 12 h. as described above (see p 10) and the birds were fed on the appropriate commercial pellets.

Details of these are given in Table 4 . It is clear that no birds became infected after the ingestion of 2-4 day-old metacercariae. Trematodes were found only in ducklings and canaries and the observations suggest that the latter species is the more suitable since trematodes were found in the faeces of ducklings after only 3 days. Even in the canary it is possible that the duration of infection is short - in canaries 4 and 8, although trematode eggs similar to that of S. wintersettensis were seen in the faeces of the birds, no trematodes could be found. All specimens of S. wintersettensis recovered, whether from the small intestine or the faeces, had attained sexual maturity and the earliest time of appearance of eggs in the host faeces was 62 h. Metacercariae retain their viability for at least 107 days.

Sphaeridiotrema wintersettensis n.sp.

Description (plate 11 Fig. 9-11)

Body extremely small, oval, slightly tapered anteriorly and rounded posteriorly, with maximum width at equatorial level of acetabulum; Cuticle thick; anterior part of body to level of pharynx covered with small spines.

Oral sucker terminal, almost circular. Mouth situated terminally or slightly subterminally, opening directly into very short prepharynx, followed by a well-developed muscular pharynx. Short, wide oesophagus divided at anterior level of acetabulum; intestinal caeca extend to near posterior end of body.

Acetabulum almost spherical, very muscular, highly protrusible, larger than oral sucker and lying either in centre of body or slightly anterior to it. Its surface is covered with numerous spines.

Testes transversely elongated, occupying the greater part of posterior end of body and completely overlapping each other dorsoventrally. Dorsal testis larger than ventral testis.

Vasa efferentia extending anteriorly from the anterior margins of testes and uniting to form a very short vas deferens just before entering posterior end of cirrus sac. Seminal vesicle bipartite, with distal portion larger than

than proximal. Pars prostatica weakly developed and extending as a short ejaculatory duct. A few prostatic cells occupy the space around anterior portion of seminal vesicle, pars prostatica and ejaculatory duct and some extend along length of cirrus. Cirrus muscular, non-spinose and usually everted from genital pore. Cirrus sac variable in position, usually overlapping oesophagus, oval to flask-shaped, slightly broadening at its equatorial level, and thick walled. Genital pore slightly lateral of mid line either to left or right of oesophageal bifurcation.

Ovary with smooth margins, usually oval in shape but occasionally transversely elongated. Submedian, usually lying in front of dorsal testis. Oviduct extending from mid-ventral surface of ovary for a short distance, receiving duct from seminal receptable which is large and oval or pyriform in outline. Laurer's canal apparently absent. Oviduct enlarges to form ootype surrounded by inconspicuous Mehlis' gland cells. A relatively short uterus originating from distal part of ootype and passing anteriorly to acetabulum, ending in a short muscular metraterm which opens at genital pore.

Vitellaria well-developed, formed by a few large follicles lying along intestinal caeca and extending from both sides of oesophageal bifurcation almost to posterior extremity of ventral testis. In some specimens follicles fusing at level of oesophageal bifurcation. Lateral vitelline ducts unite to form a large vitelline reservoir lying between anterior edge of dorsal testis and ovary, usually overlapping seminal receptable. A common vitelline duct was not seen.

Each individual with only a single egg, very large in proportion to the size of the worm.

Protonephridial system comprising an excretory bladder similar to that of the cercaria and metacercaria and opening to exterior via a terminal pore. From bladder the main excretory ducts arise at the level of posterior testis. Further details of this system have not been traced.

Measurements of adult Sphaeridiotrema wintersettensis experimentally obtained from canaries and ducks.

Body	0.321 (0.266 - 0.376) long x 0.188 (0.155 - 0.212) wide
Oral Sucker	0.050 (0.045 - 0.057) long x 0.055 (0.049 - 0.060) wide
Prepharynx	
Pharynx	0.033 (0.030 - 0.038) long x 0.030 (0.026 - 0.034) wide
Acetabulum	0.073 (0.060 - 0.083) long x 0.077 (0.064 - 0.091) wide
Anterior testis	0.048 (0.038 - 0.057) long x 0.052 (0.041 - 0.064) wide
Posterior testis	0.058 (0.049 - 0.076) long x 0.056 (0.053 - 0.079) wide
Ovary	0.040 (0.034 - 0.049) long x 0.034 (0.030 - 0.041) wide
Cirrus sac	0.049 (0.038 - 0.060) long x 0.026 (0.022 - 0.030) wide
Preacetabular extent	0.125 (0.098 - 0.155) long
Postacetabular extent	0.126 (0.106 - 0.140) long
Posttesticular extent	0.013 (0.003 - 0.019) long
Eggs	0.082 (0.079 - 0.083) long x 0.060 (0.057 - 0.060) wide

Egg and Miracidium (Plate 12 Figs.12-17)

Live mature worms, removed from the small intestines of the experimentally infected canaries, were placed in small dishes containing tap water to allow them to discharge eggs but it was not possible to obtain eggs by this method. Some eggs were recovered from the faeces of the experimental birds. These eggs were washed several times and incubated in distilled water in order to study the miracidium.

The eggs (Fig. 12) are very large, ovoid and thin-shelled with a slight thickening at its posterior end. They are golden yellow in colour and are not embryonated when first laid.

Approximately 27 eggs were incubated at room temperature (19 to 22°C) and development was followed from 1 to 18 days in several individuals. Fourteen to eighteen days were required for full development of the miracidium but no hatching was observed.

First day. In a freshly deposited egg the ovum is located some distance posterior to the operculum and above the midline of the egg, with a large nucleus and rather homogeneous cytoplasm. A considerable number of vitelline cells are also present.

Third day. Segmentation has taken place and the ovum has increased in size. The embryo is at the morula stage, comprising many blastomeres of different sizes. The vitelline cells have begun to collapse and decrease progressively in number. Further development occurred very rapidly with a great number of cell divisions.

Fifth day. At this stage a small rounded miracidium (Fig. 13) is already formed. It is surrounded by several fat-like globules of various sizes and 2 to 3 vitelline cells. Two flame cells can be distinguished - one located near the anterior end and the other just in front of the midline of the body but no trace of their excretory ducts can be seen. An apical gland is represented by a somewhat rounded structure, with granular contents. Several polynucleated germ cells occupy the posterior half of the body. The cuticle of the miracidium is granular and covered by rather short cilia except on the apical papilla.

Seventh day. The young miracidium (Fig. 14) has increased a little in size and both the body and apical gland have changed in shape from rounded to elongate. Two eyespots formed of brown granular pigment have appeared and are fused together, each with a lens on the posterior side. They are located one third of the length along the body. The two flame cells lie just behind the midline of body and the number of germ cells has increased whereas the number of fat-like globules and vitelline cells has decreased.

Ninth day. The miracidium now occupies almost all the available space within the egg capsule (Fig. 15). The apical gland has greatly increased in size, almost extending to behind the eyespots, and with coarsely granular still remaining concentrated at the anterior end. No trace of the vitelline gland was observed. The fat-like globules have further decreased in size and in number. A group of nucleated cells located near the anterior end probably represent the germ cells. Eyespots are each oval in shape. No excretory ducts

or pores were visible.

Fourteenth day. The miracidium has increased considerably in length and its posterior end is curved to one side (Fig. 16). The granular cuticle of the body is slightly thicker and is covered with long cilia. There are 2 pairs of sensory bristles on each side of the apical papilla and the apical gland now extends almost as far as the midline of the body. Part of its granular contents can be seen in its lumen together with four nuclei with central nucleoli and its duct opens at the apex of the apical papilla. The nervous system is represented by an oblong mass of numerous, small nuclei, located at the centre of the body between the penetration gland-cells. These latter cells have hyaline contents and each possesses 2 vacuole-like structures extending half the length of the body. Their ducts open at the base of the apical papilla. The protonephridial ducts are now clearly visible and open via dorsal lateral excretory pores situated in the posterior part of the body. Four large germ cells with central nuclei and granular cytoplasm are situated at the posterior end of the body. An additional group of small cells is located behind the flame cells. Two fat-like globules are present.

Eighteenth day. The miracidium (Fig. 17) has not developed any additional structures but the fat-like globules have gradually decreased in size. There are now 3 pairs of vacuole-like structures within the penetration gland-cells and the hyaline contents of these cells have become finely granular. The 2 eyespots have become L-shaped. Several additional germ cells have appeared.

The miracidium becomes fully developed between 14 to 18 days after the start of incubation but although observations were continued for a further 18 days free-swimming miracidia were never seen.

Experimental attempts to infect the snail host were not performed because of the paucity of eggs.

Discussion

The genus *Sphaeridiotrema* was erected by Odhner (1913) to include the species *S. globulus* which was first described by Rudolphi (1814) under the name *Distomum globulum*.

Only two additional species have been described, namely Sphaeridiotrema spinoacelabulum Burns (1961) and Sphaeridiotrema macrocotyla (Macy and Bell, 1968). The latter species was first described as a new genus, Astacatrematula, which the authors separated from Sphaeridiotrema by the location of the genital pore in relation to the acetabulum, by the position of testes and by the sac-like structure of the acetabulum. These two genera were synonymised by Yamaguti (1971) who placed Astacatrematula macrocotyla in the genus Sphaeridiotrema Odhner (1913).

Burns (1961) elucidated the life cycle of S. spinoacetabulum by feeding ducks with metacercariae obtained from experimentally infected snails 16 days after exposure to gymnocephalous cercaria. The adult trematodes were recovered from the caeca of the host 9 days after feeding. According to Burns, the tail of the cercaria of S. spinoacetabulum exhibits the following characteristic - "margins clear, suggesting short lateral fins". If this is the true structure of the tail then this cercaria will be readily distinguishable. It differs from the Cercaria of S. wintersettensis in the cystogenous gland-cells contents, in the number of flame cells and in the absence of both refractile granules and main excretory ducts. But these two cercariae are similar in their mode of encystment and in the location of the cysts within the snail host.

Sphaeridiotrema wintersettensis and S. spinoacetabulum are characterized by the possession of spines around the opening of the acetabulum, a condition not found in the other two species of the genus. The adult of Sphaeridiotrema wintersettensis can be readily distinguished from that of S. spinoacetabulum by the larger size of certain body structures such as the oral sucker and acetabulum whereas its ovary and testes are two to three times smaller than those of S. spinoacetabulum. Additionally, the length of the egg of S. spinoacetabulum is less than half the diameter of the acetabulum, whereas in Sphaeridiotrema wintersettensis egg length and the diameter of the acetabulum are almost the same.

As stated above the adults of S. spinoacetabulum were obtained from the caeca of ducklings 9 days after feeding whereas adults of Sphaeridiotrema

wintersettensis were found in the small intestine of canaries and ducklings after 62 and 72 h. respectively. In the latter host on only one occasion were a few mature worms recovered from the intestine, and it is probable that after 9 days all the worms had been passed out with the faeces.

Szidat (1937) experimentally connected Cercaria helvetica XVII Dubois, 1929, with Sphaeridiotrema globulus (Rudolphi, 1814). Probert (1965b), during studies of trematode larvae in Breconshire (Llangorse Lake) in Wales, found a gymnocephalous cercaria from Bithynia tentaculata and without any experimental evidence, thought it to be the cercaria of S. globulus. In the original description (Dubois, 1929) the presence of an undulating membrane along the length of the tail was noted. Probert however, considered that "the fin-fold of C. helvetica XVII had been mistaken for the much folded cuticle of the tail by Dubois", and established that the cercaria which he had found differed only in the presence of body 'hair' and in the shape of the bladder. The latter two diagnostic characters were used by Probert (1965) to separate C. cystogenata from C. helvetica XVIII Dubois, 1929. Probert is apparently dealing with another species, distinct from Sphaeridiotrema globulus.

The cercaria of S. globulus had been the subject of much confusion. According to Dubois (1929) and Szidat (1937) this cercaria is characterized by having its main excretory ducts filled with refractile granules. Macy and Ford (1964) found a gymnocephalous cercaria emerging from Flumenicola virens in Oregon, U.S.A. which they reported as the true cercaria of S. globulus. They also found cysts in the same snail host, which when fed to Peking ducklings, gave rise to adult worms, identified as S. globulus, in the caeca 2 days after infection. They stated that their cercaria differs in the relative sizes of the oral sucker (55 μm in diameter) and 79 μm in diameter) from that described by Szidat (1937) as C. helvetica Dubois, 1929, in which these two organs have the same diameter (30 μm). They also pointed out that refractile granules were not present in the main excretory ducts in their cercaria.

Sphaeridiotrema globulus is very closely related to S. spinoacetabulum and according to Burns (1961) the measurements and relative position of the

major organs in S. spinoacetabulum agree with those given by Braun (1902) and Odhner (1913) for S. globulus. Burns (1961) also stated that his specimens were very similar to those found by Price (1934) in U.S.A., but neither of these two authors was able to find any cuticular spines around the opening of the acetabulum or a Laurer's canal. Price (1934) reported that the uterus of S. globulus contained 60 eggs. This is a significant difference between S. globulus and the adult of Sphaeridiotrema wintersettensis, the most striking feature of which is the possession of only one egg in its uterus.

Francalanci and Manfredini (1969) reported S. globulus from Italy in ducks, guinea fowls and turkeys. The relative sizes of body and pharynx in this species are almost three times greater, the oral sucker is about 4 times longer and the acetabulum is about seven times longer than in Sphaeridiotrema wintersettensis.

The cercaria of Sphaeridiotrema macrocotyla Macy and Bell (1968) is rather inadequately described. Some details of the protonephridial system, such as anterior excretory loops, division of secondary ducts and number and arrangement of flame cells are not given. Therefore comparison from this point of view cannot be made. On the other hand, the cercaria of Sphaeridiotrema wintersettensis differs from this species in the following respects:

S. wintersettensis	S. macrocotyla
1. Few refractile granules in the main excretory ducts.	1. Main excretory ducts filled with numerous refractile granules.
2. Rhabditiform contents of cystogenous gland-cells.	2. Cystogenous gland-cells with granular contents.
3. Papillae on setae surrounding cuticle of body and tail, and opening of mouth.	3. Body, tail and opening mouth devoid of such structures.
4. Thick layer of circular muscles surrounding outer margin of acetabulum and minute spines present around inner margin of acetabulum.	4. Conditions lacking in the acetabulum of S. macrocotyla.

The life cycle of Sphaeridiotrema wintersettensis differs from that of S. macrocotyla in the following points:

1. The cercarial stages of S. macrocotyla encyst on the gills and sternites of the crayfish Astracus trowbridgi. They also encyst in the open (in water) but not in snails. The cercariae of Sphaeridiotrema wintersettensis do not encyst in the open but in snails.

2. Sphaeridiotrema macrocotyla matures in chickens but not in ducks while Sphaeridiotrema wintersettensis matures in ducks but not in chickens.

3. Macy and Bell (1968) stated that S. macrocotyla reached sexual maturity 3 days after feeding but, according to the published description of the infection experiments, a one day-old chick killed and examined 2 days after infection with about 100 14 day-old cysts harboured only immature worms and mature worms were obtained 5 days postinfection. On the other hand Sphaeridiotrema wintersettensis attained sexual maturity in canaries 62 hr. after infection.

The adult of Sphaeridiotrema wintersettensis can be separated by the following characters from the adult of S. macrocotyla:

S. wintersettensis	S. macrocotyla
Body 0.266-0.376 x 0.155-0.212 mm	0.650-0.850 x 0.350-0.510 mm
Dorsal testis 0.049 -0.076 x 0.053-0.079 mm	0.088-0.189 x 0.094-0.198 mm
Ventral testis 0.038-0.057 x 0.041-0.064 mm	0.111-0.159 x 0.72-0.210 mm
Acetabulum 0.060-0.083 x 0.064-0.091 mm	0.180-0.236 x 0.177-0.219 mm
Ovary 0.034-0.049 x 0.030-0.041 mm	0.066-0.135 x 0.054-0.084 mm
Cirrus sac 0.038-0.060 x 0.022-0.030 mm	0.135-0.285 x 0.033-0.090 mm
Bipartite seminal vesicle	Globular seminal vesicle
Seminal receptaole present	Posterior third of the uterus enlarged to serve as a seminal receptacle.

Pike (1968a) completed the life cycle of Psilotrema oligoon in Britain. His cercariae have a body with spines, the main excretory ducts are filled with

numerous small refractile granules and there are 6 pairs of penetration gland-cells and 16 flame cells on each side of the body. In contrast C. of S. wintersettensis is not spinose, it has 12-16 refractile granules and there are 10 pairs of penetration gland-cells and 12 flame cells on either side of body. These characters serve to discriminate between the two species.

The cercaria of Ribeiroia marini and that of Psilostomum ondratae can be distinguished from the cercaria of S. wintersettensis, by the occurrence in the former two species of an oesophagus with a pair of lateral diverticula, by the number of flame cells and by the utilization of fishes as the secondary intermediate hosts.

The cercaria of Psilostomum reflexae differs from the present species in the possession of an undulating membrane on the tail.

Cercaria nuda Komiya, 1952, C. miyagiensis Komiya, 1967 and C. cystogenata Probert, 1965b can all be separated from the present cercaria in having two different kinds of cystogenous gland-cells.

Cercaria macarapenensis Nasir and Acuna, 1966 and C. sanlorenzensis Nasir and Acuna, 1964 both possess 24 flame cells as in the cercaria of Sphaeridiotrema wintersettensis but the intestinal caeca are very short, not extending beyond the acetabulum.

Cercaria sensa Komiya, 1952, is provided with approximately 25 cephalic gland-cells (= probably these are penetration gland-cells) while in the present cercaria there are only 20 penetration gland-cells. C. sensa also differs in the absence of a caudal excretory duct.

Cercaria sucrensis Nasir and Acuna, 1965, can readily be separated from the present form, having a finfold on the posterior third of the tail.

Cercaria albinea Khan, 1960b and C. densacutis Khan, 1960b are similar to the cercaria of S. wintersettensis in the possession of cystogenous gland-cells with rhabditiform contents, in having 24 flame cells and in the extent of the intestinal caeca. However, these 2 forms differ from the present species in having an accessory excretory bladder lying antero-dorsal to the main excretory bladder and in lacking both cephalic glands and papillae with hair-like processes.

Cercaria gymnocephalous II and C. gymnocephalous III differ from the cercaria of S. wintersettensis in the size of the body, in the number of penetration gland-cells and, in the case of C. gymnocephalous III in the number of flame cells and the possession of two types of cystogenous gland-cells.

As a result of these comparative studies the present material is considered to represent a new species and named Sphaeridiotrema wintersettensis.

Table 4

Experimental infection of birds fed with 40 to 50 day old metacercariae of Sphaeridiotrema wintersettensis n.sp.

Experimental definitive host	Age of Cysts (Days)	Eggs detected in faeces after - (Hours)	Host autopsied after - (days)	Number of Trematodes recovered
Chicken 1	2 to 4	-	7	0
Chicken 2	2 to 4	-	7	0
Chicken 3	25 to 35	-	4	0
Chicken 4	25 to 35	-	5	0
Chicken 5	62 to 68	-	5	0
Chicken 6	62 to 68	-	4	0
Chicken 7	62 to 68	-	4	0
Chicken 8	107	-	4	0
Pigeon 1	2 to 4	-	7	0
Pigeon 2	2 to 4	-	7	0
Pigeon 3	25 to 35	-	4	0
Pigeon 4	25 to 35	-	5	0
Pigeon 5	62 to 68	-	5	0
Pigeon 6	107	-	4	0
Duckling 1	2 to 4	-	7	0
Duckling 2	2 to 4	-	7	0
Duckling 3	25 to 35	72	3	0
Duckling 4	25 to 35	96	4	3 (F)
Duckling 5	62 to 68	-	4	0
Duckling 6	107	-	6	0
Duckling 7	107	72	3	7(2 S.I 5 F)
Canary 1	2 to 4	-	7	0
Canary 2	2 to 4	-	7	0
Canary 3	25 to 35	72	3	8 (S.I)
Canary 4	25 to 35	72	3	0
Canary 5	62 to 68	72	3	12 (S.I.)

Canary 6	62 to 68	72	3	7 (S.I.)
Canary 7	107	62	2½	10 (S.I.)
Canary 8	107	62	2½	0
Canary 9	107	62	2½	6 (S.I.)

F = faeces

S.I. = small intestine

- = no eggs in faeces

Cercaria gymnocephalous II

These cercariae were released from Bithynia tentaculata collected from Newmillerdam Lake in July 1973, (see p. 51).

After emerging from the host the cercariae at first swim vigorously by means of lashing movements of the tail, similar to those of echinostome cercariae. After a few hours some cercariae can be seen at the bottom of the vessel creeping by means of their suckers. Sixteen to twenty hours after emergence they aggregate at the bottom exhibiting slow movements until their death.

The cercariae emerge during the whole day, with one maximum occurring early in the morning and another in the late evening.

Description (Plate 13 Figs.1-4)

Body flat and ovoid; cuticle thick, nonspinose, with fine granular contents and covered on both sides with papillae bearing hair-like processes; number of papillae difficult to count. Tail subterminal, without spines and bearing 5 pairs of papillae with hair-like processes located posterior to branching of the caudal excretory duct on both sides. Tail possesses longitudinal and circular muscles and contains 2 masses of nucleate cells with fine granular cytoplasm, one proximally and the other distally.

Oral sucker terminal; its posterior margin occupied by a trilobed cephalic gland filled with a very fine granular substance. Posterior border of cephalic gland clearly visible behind posterior margin of the oral sucker when pressure applied to coverslip. Prepharynx present, pharynx muscular. Oesophagus slender, relatively long and divided to form intestinal caeca extending almost to posterior end of body. Both oesophagus and caeca with granular contents. Acetabulum very muscular, located slightly posterior to middle of body and surrounded by muscle bands. Thirteen pairs of penetration gland-cells situated lateral to oesophagus; each cell with coarse granular contents and a spherical nucleus; their ducts could not be traced. Numerous cystogenous gland-cells present beneath body cuticle under almost whole body surface; Each cell with Rhabditiform contents. Genital primordium represanted by mass of

undifferentiated between posterior margin of acetabulum and excretory bladder.

Protonephridial system comprising a V-shaped excretory bladder, with primary excretory ducts arising from the anterolateral arms. Each extends anteriorly around acetabulum, expanding to accommodate 15-18 refractile granules and continuing forwards to level of pharynx where duct is constricted; it then loops and turns posteriorly bifurcating behind acetabulum into anterior and posterior collecting ducts. Each collecting duct with two groups of three flame cells. Flame cell formula $2\left[(3 + 3) + (3 + 3)\right] = 24$. Caudal excretory duct divided in posterior half of tail, into two branches, each opening laterally.

Redia (Plate 13; Fig. 5)

The rediae were present in the hepatopancreas of the infected snails. They are elongate and sac-like in form, narrowest anteriorly and widest at short distance in front of the posterior extremity. The pharynx is muscular, well developed and continuing into a long, slender gut which extends almost as far as the locomotory appendages. Its cavity is filled with a brown granular material. The collar is undivided and the birth pore which is protruded in some specimens is situated behind it, to one side of the body. A pair of locomotory appendages is situated at the posterior end. The redia usually contains 8-12 cercariae at different stages of development as well as numerous germinal masses which vary in size.

Encystment

The cercariae have never been seen encysted free in the water, on the external or internal surface of mollusc shells or on vegetation.

The further development of this cercaria is not known.

Measurements of Cercaria gymnocephalous II from Bithynia tentaculata

Body	0.237 (0.228 - 0.247) long x 0.157 (0.152 - 0.167) wide
Tail	0.400 (0.387 - 0.414) long x 0.053 (0.049 - 0.057) wide
Oral sucker	0.044 (0.041 - 0.045) long x 0.044 (0.041 - 0.045) wide
Acetabulum	0.059 (0.057 - 0.060) long x 0.070 (0.064 - 0.076) wide
Prepharynx	0.0027 (0.003 - 0.003) long
Pharynx	0.025 (0.022 - 0.026) long x 0.022 (0.022 - 0.022) wide
Oesophagus	
Preacetabular extent	0.126 (0.121 - 0.129) long
Postacetabular extent	0.055 (0.053 - 0.057) long
Redia	1.393 (1.183 - 1.656) long x 0.273 (0.210 - 0.341) wide
Pharynx	0.109 (0.095 - 0.129) long x 0.112 (0.083 - 0.136) wide

Discussion

The freshwater Gymnocephalous cercariae similar to Cercaria gymnocephalous II are:

Cercaria of Fasciola hepatica Linnaeus, 1758 (Rees, 1932)

Cercaria of Guaicaipuria pseudoconcilia (Nasir, Diaz and Lemus de guevara, 1969) Nasir, Diaz and Marcano, 1971 [= Cercaria pseudoconcilia Nasir, Diaz and Lemus de Guevara, 1969]

Cercaria of Psilotrema oligooon (Linstow, 1887) Odhner, 1913 (Pike, 1968).

Cercaria of Ribeiroia marini (Faust and Hoffman, 1934) Basch and Sturrock, 1962 [syn. Cercaria III Marin , 1928 [= Cercaria marini Faust and Hoffman, 1934]

Cercaria of Sphaeridiotrema globulus (Rudolphi, 1819) Odhner (1913), as described by Szidat (1937), Probert, 1966.

Cercaria of Guicaipuria parapseudoconcilia Nasir and Silva, 1972.

Cercaria of Stephanoprora paradenticulata Nasir and Rodriguez, 1969.

Cercaria of Sphaeridiotrema spinoacetabulum Burns, 1961.

Cercaria of Sphaeridiotrema macrocotyla Macy and Bell, 1968,

Cercaria of Echinochasmus perfoliatus Komiya, 1951.

Cercaria of Echinochasmus japonicus Ito, 1962.

Cercaria of Rebeiroia (= Psilostomum) ondratae (Mcmullen, 1938) (as described by Beaver, 1939).

Cercaria of Psilostomum reflexae Feldman, 1941.

Cercaria gigantica Cobbold, 1855 [= Cercaria pigmentosa Cawston, 1919 (Faust, 1920; Porter, 1938)].

Cercaria albinea Khan, 1960b.

Cercaria circumstricta Faust, 1922.

Cercaria concilia Nasir, Diaz and Lemus de Guevara, 1969.

Cercaria cystogenata Probert, 1965.

Cercaria densacutis Khan, 1960.

Cercaria dollfusi Fain, 1953.

Cercaria edmonddartevellei Vercammen-Grandjean, 1960.

Cercaria frondicola Pike, 1968a.

Cercaria granocutis Pike, 1968a.

Cercaria lileta Fain, 1953.

Cercaria llangorsensis Probert, 1965b.

Cercaria miyagiensis Komiya, 1967.

Cercaria nuda Komiya, 1952.

Cercaria paraudoi Nasir, Diaz and Hamana, 1969.

Cercaria pauldebrauweri Vercammen-Grandjean, 1960.

Cercaria sensa Komiya, 1952.

Cercaria sudanensis No. 3 Archibald and Marshall, 1931.

Cercaria indicae XLI Sewell, 1922.

Cercaria helvetica XIX Dubois, 1929.

Cercaria complicata Faust, 1930.

Cercaria tuberculata Filippi (1854) as described by Wesenberg-Lund, 1934.

Cercaria sanlorenzensis Nasir and Acuna, 1964.

Cercaria macarapanensis Nasir and Acuna, 1968.

Cercaria barceloica Nasir, 1971.

Cercaria asaguensis Nasir, Hamana and Diaz, 1969.

Cercaria pliepuicauda Nasir and Diaz, 1973.

Cercaria penthesilia Faust, 1921.

Cercaria sucrensis Nasir and Acuna, 1965.

Cercaria sudanensis No. 4 Archibald and Marshall, 1931.

Cercaria ornaticauda Brooks, 1943.

Cercaria stenophysae Nasir and Diaz, 1973.

Cercaria armkuniani Nasir and Diaz, 1973.

Cercaria laurotravassosi Nasir and Diaz, 1973.

Cercaria redicystica Tubangui, 1928.

Cercaria synphoriani Fain, 1953.

Cercaria ituriensis Fain, 1953.

Cercaria neerlandica I Honer, 1963.

Cercaria grandis Wesenberg-Lund, 1934.

Cercaria broederstroomae Porter, 1938.

Cercaria semirobusta Faust, 1924b.

Cercaria congolae Porter, 1938.

Cercaria santacruzia Nasir, 1973.

Of the above mentioned cercariae, only Cercaria albinea, C. densacutis, C. cystogenata, C. sensa, C. miyagiensis, C. macarapanensis, C. sanlorenzensis and C. sucrensis have the same number of 24 flame cells as C. gymnocephalous II.

In Cercaria sucrensis, the posterior third of the tail is provided with a thin membrane and intestinal caeca do not reach the equatorial level of the acetabulum. C. sanlorenzensis and C. macarapanensis are, like C. gymnocephalous II characterised by the rhabditiform contents of their cystogenous gland-cells, but the intestinal caeca of the first two do not extend posterior to the acetabulum.

Cercaria cystogenata, C. nuda and C. miyagiensis can be distinguished from the present form by their possession of 2 types of cystogenous gland-cells; one with rhabditiform content and the other with granular contents. C. sensa differs from C. gymnocephalous II in the absence of a caudal excretory duct and in the presence of sensory hair-like structures surrounding the mouth opening,

a spinose border to the acetabulum and approximately 25 cephalic glands, between the pharynx and acetabulum.

Cercaria albinea can be separated by the presence of an accessory excretory bladder and a well-differentiated genital primordium, and by the arrangement of the flame cells. C. densacutis differs by having an accessory bladder, in the arrangement of the flame cells in the number of excretory granules in the primary ducts. In addition both species lackpapillae with hair-like processes on the body and tail.

Archibald and Marshall (1931) described a gymnocephalous cercaria from Bullinus contortus in the Sudan and named it cercaria sudanensis No. 3. In this cercaria, the posterior margin of the oral sucker is occupied by two cephalic glands. Probert (1965) reported C. llangorsensis from Bithynia tentaculata in Britain. His form has oral refractive structures at the posterior border of the oral sucker, one on either side of the pharynx. These structures are similar to those described by Archibald and Marshall in C. sudanensis No. 3. Pike (1968) described Cercaria of Psilotrema oligoon, C. frondicola and C. granocutis from B. tentaculata in Britain. In his cercariae he observed two small transparent crescent-shaped structures lying against the posterior margin of the oral sucker. These structures are probably the borders of the cephalic glands which I have described in the cercaria of S. wintersettensis, C. gymnocephalous II and C. gymnocephalous III. The appearance of these glands in the latter cercariae is similar when pressure is exerted upon a living specimen between slide and coverslip, but there are 3 lobes in the gland as compared to two in Probert's (1965) and Pike's (1968) specimens.

Cercaria sudanensis No. 3 can be easily separated from C. gymnocephalous II, in having a different number of flame cells, a tripartite excretory bladder, and an unbranched caudal excretory duct which almost reaches the posterior end of the tail. In C. llangorsensis the main excretory ducts are filled with several hundred refractile excretory granules, the flame cell formula is:

$2\,[(3 + 3 + 3 + 3)] = 30$, the excretory bladder is composed of two distinct chambers and spines are present anteriorly on the body. The cercaria of Psilotrema oligoon, C. frondicola and C. granocutis differs from C. gymnocephalous II in the following characters; the number of refractile granules in the primary excretory ducts, the number of penetration glands, the absence of apapillae with hair-like structures on the body and tail, the possession of a spinose body and the number of flame cells. The preparation of C. sensa and C. gymnocephalous II has already been discussed above.

Cercaria gymnocephalous III

This cercaria was found emerging from Bithynia tentaculata obtained from Newmillerdam Lake on 11.9.73. Of 85 snails collected only one was infected with C. gymnocephalous III.

The cercariae are normally discharged in small numbers during the early hours of light each day but occasionally the period of release is late in the day. They swim vigorously for a period of between 20 minutes and one hour, but soon sink to the bottom where they begin crawling, using their suckers. The cercariae have never been observed to congregate on the bottom of the container.

Description (Plate 14; Figs. 1-5)

Body oval and spinose from anterior end to posterior level of pharynx. Cuticle very thick, with coarsely granular contents; provided with small spines and a pair of papillae with hair-like processes on each side of oral sucker. Tail subterminal, nonspinose, bearing a pair of papillae with hair-like processes, located posterior to bifurcation of caudal excretory duct. Tail with longitudinal and circular muscles along its length; the former arranged in two bands of 10-12 fibres each and the latter very numerous and difficult to count; central area of tail occupied by numerous cells with a central nucleus and granular cytoplasm which are more abundant in the anterior half; a characteristic small hole situated almost at distal tip of tail and visible only when larva is observed in ventral view.

Oral sucker terminal, with a row of 7-9 papillae with setae surrounding the mouth opening; posterior wall occupied by a trilobed cephalic gland as in the cercaria of S. wintersettensis and C. gymnocephalous II. Prepharynx relatively long. Pharynx muscular, followed by oesophagous branching immediately anterior to the acetabulum into two wide caeca extending almost to posterior end of body. Both oesophagus and caeca with granular contents.

Acetabulum circular, located behind middle of body and with its border surrounded by circular muscles as in the cercaria of S. wintersettensis and C. gymnocephalous II Two groups of six lobed penetration gland cells present

between pharynx and acetabulum. Each gland-cell with coarsely granular contents and 2 rounded nuclei. Ducts of cells pass to anterior end of body and open to exterior.

Cystogenous gland-cells of two cell types: (1) a very small oval cell type with very fine granular contents distributed over whole ventral surface of body and (2) a large cell type with rhabditiform contents found towards dorsal surface. Some of large cells with a visible central nucleus.

Protonephridial system formed by an elongate excretory bladder divided into two by a deep latero-median construction, with two long narrow primary excretory ducts arising from its anterior margin and passing towards the acetabulum, where they dilate considerably and include numerous refractile granules also found in the bladder. Ducts continue anteriorly almost to posterior level of oral sucker where they reflex as narrow secondary ducts, each containing eleven ciliated patches, and pass posteriorly into anterior and posterior collecting ducts near the excretory bladder. Anterior collecting duct receiving eight groups of two flame cells and posterior duct receiving one group of two flame cells. Caudal excretory duct divided into two short ducts with lateral openings positioned two thirds along length of tail. Flame cell formula:

$$2\,[2 + 2 + 2 + 2 + 2 + 2 + 2 + 2 + (2)] = 36.$$

Redia (Plate 14; Fig. 6)

The liver of the infected snail was full of numerous redia. Body elongate and capable of certain degree of movement. Mouth subterminal, leading into a well developed muscular pharynx, followed by a long intestine which extends almost two thirds of the length of the redia and has brown-yellow granular contents.

Collar undivided. No birth pore was observed. Two prominent locomotor appendages situated at the posterior end. Each redia contained several cercariae in different stages of development together with a considerable number of germ cells. Only 3-5 cercariae were fully mature.

Encystment

The encystment process was observed under the microscope. This cercaria was found to encyst very rapidly when placed on a slide. It suddenly loses its tail, the contents of the cystogenous glands are secreted, its body becomes rounded and enveloped in a fine transparent membrane. Once the cyst was formed the metacercaria was observed moving freely within it. After two hours, the cystogenous gland-cells were no longer visible. During this process, the rhabditiform contents were not used. Encystment was also seen to occur on the surface film of the water. Some cysts were found at the bottom of the container, but none was found on either inner or outer surfaces of mollusc shell.

Measurements of Cercaria Gymnocephalous III from Bithynia tentaculata

Body	0.256 (0.243 - 0.266) long x 0.138 (0.121 - 0.152) wide
Tail	0.449 (0.418 - 0.478) long x 0.052 (0.045 - 0.057) wide
Oral sucker	0.055 (0.053 - 0.057) long x 0.059 -(0.057 - 0.064) wide
Acetabulum	0.041 (0.038 - 0.045) long x 0.041 (0.038 - 0.045) wide
Prepharynx	0.035 (0.022) 0.048) long
Pharynx	0.040 (0.039 - 0.045) long x 0.028 (0.024 - 0.033) wide
Oesophagus	0.029 (0.022 - 0.042) long
Preacetabular extent	0.140 (0.133 - 0.152) long
Postacetabular extent	0.073 (0.068 - 0.076) long
Rediae	1.372 (1.104 - 1.919) long x 0.273 (0.210 - 0.315) wide
Pharynx	0.094 (0.076 - 0.114) long x 0.103 (0.095 - 0.121) wide
Cysts	0.224 (0.220 - 0.228) long x 0.224 (0.216 - 0.231) wide

Discussion

Of the Gymnocephalous cercariae previously described only Cercaria armykuhniani, C. cystogenata, C. lileta, the cercaria of Fasciola hepatica, C. complicata, C. nuda and C. miyagiensis resemble Cercaria gymnocephalous III in the possession of two kinds of cystogenous gland-cells. The Cercaria gymnocephalous III can be readily distinguished from all these forms by reference to the following characters:

1. Cercaria armikuhniani and C. lileta differ from C. gymnocephalous III by having two oesophageal diverticula.

2. In C. nuda, C. miyagiensis and C. complicata, the excretory bladder is composed of two chambers and the acetabulum is smaller than the oral sucker whereas in C. gymnocephalous III the excretory bladder is single chambered and the acetabulum is larger than the oral sucker.

3. Cercaria cystogenata is characterized by having a nonspinose body, no more than 25 refractile granules (average 18) in each of the primary excretory ducts and the flame cell formula of $2(2 + 2 + 2 + 2 + 2 + 2) = 24$, where C. gymnocephalous III possesses a spinose body, very numerous (>100) refractile granules in the primary excretory duct and the flame cell formula is $2\{(2 + 2 + 2 + 2 + 2 + 2 + 2 + 2 + (2)\} = 36$.

4. The cercaria of Fasciola hepatica has 10 flame cells on each side of the body, the caudal excretory duct bifurcates at about one third of the tail length and the secondary ducts form posterior excretory loops at the posterior end of the intestinal caeca. Cercaria gymnocephalous III has 36 flame cells, the caudal excretory duct forks at about two thirds of the length of the tail and the secondary ducts do not form posterior excretory loops.

Nasir and Diaz (1968) and Nasir and Rodriguez (1969) described Cercaria pomacea in Pomacea glauca and the cercaria of Stephanoprora paradenticulata in Marisa cornuarietis and P. glauca, both from Venezuela. These two species are, with Cercaria gymnocephalous III, the only gymnocephalous cercariae with 36 flame cells. The 3 species are probably closely related but they can be easily distinguished on the basis of the presence of different types of cystogenous gland-cells, number of refractile granules and details of the digestive system. In C. pomacea the oesophagus and caeca are absent, whereas in the cercaria of Stephanoprora denticulata they are present but do not extend posteriorly to the equatorial level of the acetabulum.

Cercaria gymnocephalous III is clearly different from C. gymnocephalous I and C. gymnocephalous II in body size, in the nature of the cystogenous gland-cells and the flame cell formula.

Pleurolophocercous cercariae

Sewell (1922) created the Pleurolophocercous group to accommodate the monostomes Cercaria indicae VII, C. indicae VIII, C. indicae III, C. lophocerca Fil, C. lophocerca Lebour (nec. Fil.) and C. pleurolophocerca Sonsino, which he named as the type species of this group. Sewell (1922) found that Cercaria indicae XXXI and C. indicae L were strikingly similar in all anatomical features to the members of his Pleurolophocercous group except that they possessed a well-developed acetabulum. He created the Parapleurolophocercous group to accommodate these two problematic species. Sewell placed the Pleurolophocercous group within the large Monostome group of Luhe (1909) and suggested that it was related to the Gymnocephalous cercariae.

Langeron (1924) redescribed Cercaria pleurolophocera Sonsino and noted the presence of a well-developed acetabulum. Dubois (1929) found Cercaria Lophocerca (Fil.) and in it described a very small acetabulum. Dubois considered that the presence of this organ in C. pleurolophocerca and C. lophocerca has great importance; it is responsible for the separation of the whole Pleurolophocercous group from the monostomes and it also illustrates the phenomenon of acetabulum reduction referred to by Odhner (1911). Vogel (1934) redefined the Pleurolophocercous group because he considered that, as constituted by Sewell (1922), it was not based on valid criteria and Wesenberg-Lund (1934) removed it from the Monostome cercariae. Porter (1938) found Cercaria britsiae in South Africa; although this species is very closely related to members of the Parapleurolophocercous group it possessed a well-developed digestive system. Porter therefore suggested that the Parapleurolophocercous group of Sewell should be revised to include those forms with intestinal caeca. Cable (1938) improved Vogel's definition and pointed out that the Pleurolophocercous and Parapleurolophocercous groups (Sewell, 1922) are closely related, stating "It is indeed possible that if a natural classification is to be offered, certain members of each group should be combined". Rothschild (1938a) considered that there were insufficient grounds for separating the Pleurolophocercous and Parapleurolophocercous groups and combined them, giving the following diagnosis:

1. A pair of pigmented eyespots is generally present, but may be lacking altogether.

2. The anterior end of the body, or the whole body, is armed with backwardly directed spines.

3. The anterior sucker is modified to form a protusible penetration organ.

4. The acetabulum may be absent or only poorly developed.

5. A pharynx is always present, but the alimentary canal is absent or only poorly developed.

6. Penetration glands, with ducts opening anteriorly, are present.

7. The bladder is reniform or roughly globular, with thick walls. The lateral excretory ducts enter the bladder antero-laterally.

8. The tail is longer than the body, and powerful, and is provided with cuticular fin-folds or a cuticular sheath.

9. The cercariae are phototropic. They swim by short dashes, followed in each case by a pause, during which the body hangs below the tail in the water.

10. Development occurs in rediae with an intestine and birth pore but no locomotory appendages. The cercariae leave the rediae at an early stage and continue development within the tissues of the first intermediate host.

11. First intermediate host: fresh water, brackish water or marine gastropods. Second intermediate host: generally a fish, but exceptionally an amphibian. Encystment may occur in the first intermediate host.

Martin (1950) sub-divided the Pleurolophocercous group according to the arrangement of the tail fin-folds into four groups. The type species of each group was as follows: group A. Euhaplorchis californiensis and Parastictodora hancocki cercariae; group B. Cercaria sp Rothschild; group C. another Cercaria sp Rothschild; and group D. Haplorchis cercariae. Ulman (1954) also sub-divided the group on the basis of the tail fin-folds calling it the Velocercariae for those cercariae characterized by having the dorsal fin which was longer than the ventral and may run on around the tip of the tail. Vercammen-Grandjean (1960) considered the Pleurolophocercous and Parapleurolophocercous groups to be synonymous and regarded them as intermediate between the

Echinostomidae and the Gymnocephala. Dawes (1946) placed these two groups in the Gymnocephalous cercariae.

I consider the classification scheme proposed by Rothchild (1938) to be the most natural and I have adopted it in the present account.

Only one member of the Pleurolophocercous group was found in the present study.

Cercaria pleurolophocera I

During the summers of 1973, 1974 and 1975 various collections were carried out in areas where the gastropod Bithynia tentaculata occurs; but only at Newmillerdam Lake and Kirkstall Power Station (Leeds-Liverpool Canal) were some snails infected with pleurolophocercous cercariae. The rate of infection varied between 2 and 5%.

The cercariae are emitted throughout the day, with the highest productivity in the morning and decreasing towards the late evening. Periods of vigorous swimming alternate with short rest periods. After being emitted they have a relatively long life-span of between 24 and 35 hours.

Description (Plate 15; Fig. 1-3 and 6)

Body elongate, with on each side a row of 7 hair-like projections. Oral sucker well-developed and subterminal; provided on a protusible region with five rows of spines apparently lying on dorsal wall; the number of spines in each row from anterior is 15, 11-12, 11-12, 7-8 and 7-8 respectively.

Tail subterminal, containing both longitudinal and circular muscle fibres. Two well-developed fin-folds; one a lateral membrane originating at union between body and tail, gradually widening to a maximum width near middle of tail, then decreasing considerably towards distal end where it becomes difficult to perceive; the second a dorsoventral membrane extending from middle of tail to its posterior extremity.

Two eyespots containing dark brown pigments, one on each side of body, between posterior margin of oral sucker and pharynx. Prepharynx followed by spherical, muscular pharynx. No other digestive structures present.

Twelve penetration gland-cells, arranged in 3 transverse rows (3, 4 and 5 cells per row respectively) and situated between posterior end of pharynx and anterior end of rudimentary acetabulum; each gland-cell with a coarsely granular content and a central spherical nucleus; ducts extend anteriorly, passing between eyespots and continuing towards region of oral sucker where they open to the

exterior in 4 groups of 3. Acetabulum not well-developed and appearing only as an undifferentiated mass of cells in newly emerged cercariae; its orifice becomes visible after 24 hours. No rudiments of genital organs present.

Cystogenous gland-cells with a coarsely granular content located in posterior 3-fifths of the body except in region occupied by excretory bladder.

Excretory bladder of triangular form and with its walls composed of large anucleate cells with granular cytoplasm. Principal primary ducts open anteriorly from anterolateral margin of excretory bladder extending a little behind level of pharynx, where they receive anterior and posterior collecting ducts from the flame cells. Flame cell formula: $2\left[(2+2)+(2+2+2+2+2+2+2)\right]=40$. Caudal excretory duct extending to end of tail.

Redia (Plate 15 ; Fig.4)

The rediae extracted from infected snails were not very numerous and almost all were at the same stage of development. The pharynx is very small in proportion to the length of the body; at each side of its aperture there is a pair of hair-like projections. The intestine is small and contains a brown substance similar to material of the hepatopancreas of the snail. The birth pore is situated to one side behind the pharynx, and a neck and locomotory appendages are absent. The body of the redia is full of numerous germinal masses and cercariae in different stages of development including 3 to 6 fully-formed cercariae. Apparently most cercariae leave the rediae at a very early stage, completing their development in the tissues of the snail. The excretory system of the redia consists of numerous flame cells forming 2 rows, one on each side of the body. The number and arrangement of these cells is difficult to determine, but there appear to be at least 24 on each side. A single duct can be seen opening outwards through a small excretory pore situated towards one side in the anterior part of the body.

Infection of second intermediate host

To determine the possible secondary host of Cercaria pleurolophocerca I, different species of freshwater fishes - 12 guppies, 8 Tilapia and 5 chub were

isolated with infected snails in glass vessels containing tap water.

After 24 hours, a specimen of each fish species was examined for the presence of metacercaria cysts. They were found only in the chub.

The remaining tilapia and guppies gave negative results on dissection, while the chub, which were examined alive under a dissecting microscope, showed cysts at the base of the tail, under the epidermis and scales. These fishes were maintained in aquaria to permit the development of the metacercariae.

The cysts were extracted from the musculature of the base of the tail and from the connective tissue around the bases of the fins. They displayed the following characteristics:- oval form with a fine wall within which the metacercariae is contained, showing rotating movements. The penetration ducts and glands are still visible but their contents have dwindled, presumably having been used in the process of penetration. The excretory bladder is similar in size and shape to that of the cercaria but the rest of the system is difficult to discern, although some flame cells are visible in the postacetabular region. The eyespots are still visible but there is no evidence of the oesophagus and intestinal caeca. The acetabulum shows no additional development over that of the cercaria.

The remainder of the infected fishes survived for only a few days so further details of the life cycle could not be investigated.

Measurements of Cercaria pleurolophocerca I from Bithynia tentaculata

Body	0.147 (0.140 - 0.152) long x 0.044 (0.041 - 0.049) wide
Tail	0.293 (0.273 = 0.307) long x 0.025 (0.022 - 0.026) wide
Oral sucker	0.026 (0.022 - 0.026)long x 0.022 (0.022 - 0.026) wide
Acetabulum	0.013 (0.011 - 0.015) long x 0.016 (0.015 - 0.019) wide
Prepharynx	0.016 (0.015 - 0.019) long
Pharynx	0.011 (0.011 - 0.011) long x 0.010 (0.007 - 0.011) wide
Oesophagus	
Preacetabular extent	0.083 (0.079 - 0.087) long
Postacetabulur extent	0.048 (0.041 - 0.057) long

Redia	0.808 (0.560 - 1.442) long x 0.098 (0.084 - 0.112) wide
Pharynx	0.021 (0.019 - 0.022) long x 0.022 (0.019 - 0.022) wide
Cyst	0.112 (0.106 - 0.121) long x 0.071 (0.069 - 0.079) wide
Oral sucker	0.023 (0.022 - 0.026) long x 0.024 (0.022 - 0.026) wide
Acetabulum	0.013 (0.011 - 0.015)long x 0.012 (0.011 - 0.015) wide
Prepharynx	0.012 (0.011 - 0.015 long
Pharynx	0.011 (0.011 - 0.011) long x 0.012 (0.011 - 0.015) long
Preacetabular extent	0.056 (0.053 - 0.060) long

Discussion

All previously described cercariae of the group Pleurophocerca Sewell, 1922 (= Parapleurolophocerca Sewell, 1922) are listed below.

Cercaria of Apophallus brevis Ransom, 1920 (Miller, 1941, 1946).

Cercaria of A. donicus (Skrjabin and Lindtrop, 1919) as described by Niemi and Macy, 1974.

Cercaria of A. muehlingi (Jagerskiold, 1899) Luhe, 1909 (Odening, 1970).

Cercaria of A. venustus (Ransom, 1920) as described by Cameron, 1937.

Cercaria of Ascocotyle pachycystis Schroeder and Leigh, 1965.

Cercaria of Clonorchis sinensis (Cobbold, 1875) Looss, 1907 (Komiya and Tajimi, 1940).

Cercaria of Euhaplorchis californiensis Martin, 1950.

Cercaria of Euryhelmis squamula (Rudolphi, 1819) Poche, 1926 (Anderson and Pratt, 1965).

Cercaria of Haplorchis taichui (Nishigori, 1924) Witenberg, 1930 (Martin, 1958).

Cercaria of H. yokogawai (Katsuta, 1932) Chen, 1936 (Martin, 1958).

Cercaria of Heterophyid sp. Hopkins, 1940.

Cercaria of Metagonimus yokogawai (Katsurada, 1913) Katsurada, 1912, (in Gupta and Taneja, 1970a).

Cercaria of Metorchis conjunctus (Cobbold, 1860) as described by Cameron, 1944.

Cercaria of Opisthorchis felineus (Rivolta, 1884) Blanchard, 1895 syn. O. tenuicollis (Rudolphi, 1819) of Ejsmont, 1937 in Faust and Russel, 1958).

Cercaria of O. viverrini (Poirier, 1886) Stiles and Hassall, 1896, (Wykoff, Harinasuta, Juttijudada, and Winn, 1965) (Itoh Papasarathorn and Tonkoom, 1962).

Cercaria of Phocitremoides ovale (Maxon and Pequegnat, 1949) Martin, 1958 (Cerca. .ria 'Pleurolophocercous II' Maxon and Pequegnat, 1949).

Cercaria of Stellantchasmus falcatus Onji and Nishio, 1942 (Martin 1958).

Cercaria Nr. 2 Petersen, 1931.

Cercaria atomica Fain, 1953.

Cercaria atomica kivuensis Vercammen-Grandjean, 1960.

Cercaria bhimtalensis Malaki and Singh, 1962.

Cercaria bithyniella, Fain 1953.

Cercaria bristiae Porter, 1938.

Cercaria chromophila Faust, 1922.

Cercaria constrictovesica Cable and Wheeler, 1939.

Cercaria flavidusi Premvati, 1965.

Cercaria gomtiensis Premvati, 1965.

Cercaria indicae VIII Sewell, 1922.

Cercaria indicae XXXI Sewell, 1922.

Cercaria indicae L Sewell, 1922.

Cercaria lophocerca Filippi, 1857 (Dubois, 1929, Khan, 1960; Meyer, 1964, Probert, 1965, Wesenberg-Lund, 1934).

Cercaria melanoides Porter, 1938.

Cercaria opacocorpa Cable and Wheeler, 1939.

Cercaria nicobaricae Sewell, 1931.

Cercaria parvomelaniae Tubangui, 1928.

Cercaria pinjorensis Gupta and Taneja, 1970a.

Cercaria pleurolophocerca Sonsino, 1892 (syn. C. indicae VII Sewell, 1922 (Langeron, 1924);

Cercaria pleuroloparapleuriformis Nasir and Diaz, 1973.

Cercaria plotiopsis Johnston and Simpson, 1939.

Cercaria of Parasitictora hancocki (Maxon and Pequegnat, 1949)

Martin, 1950 (Cercaria 'Pleurolophocercous I' Maxon and Pequegnat, 1949).

Cercaria of Procerovum calderoni (Africa and Garcia, 1935), Price, 1949 (Velasquez, 1973).

Cercaria quadripterygia Sinitsin, 1911.

Cercaria semicarinata Cable and Wheeler, 1939.

Cercaria sigmoidea Fain, 1953.

Cercaria spinostoma Cable, 1937.

Cercaria vogeli Cable, 1935 (Cable, 1938; Cable and Wheeler, 1939).

Of these 46 species only Clonorchis sinensis, Eurvhelmis squamula, C. atomica and C. pleuroloparapleuriformis are equipped with 12 penetration gland-cells but these four species are easily distinguished by their flame cell formulae from C. pleurolophocerca I $2\,[(2+2)+(2+2+2+2+2+2+2+2)] = 40$, being $2\,[(3+3)+(3+3+3)] = 30$ in C. sinensis, $2\,[(2+2+3+2)] = 18$ in E. squamula, $2\,[(5+6)+(6+6+6)] = 58$ in C. atomica. In C. pleuroloparapleuriformis the total numbers of flame cells is 36, but their connections with their respective capillaries have not been determined.

The cercaria of Parasitictora hancocki (Martin, 1950) was originally described by Maxon and Pequenat (1949) who referred to it as 'Pleurolophocercous I' without giving it a specific name. Later its life cycle was clarified by Martin (1950). In the original description of Maxon and Pequegnat there are stated to be 12 penetration gland ducts, which divide into four groups of 3; the glands are situated in the medial and postero-lateral region of the body but their number was not determined. Martin (1950) did not agree with Maxon and Pequenats' observations and gave the number of penetration gland ducts as 14 (groups of 3, 4, 4 and 3), corresponding to the 14 glands situated in the medial region of the body, partially surrounding the rudimentary acetabulum. In Cercaria pleulorolophocerca I described above there are 12 ducts of penetration glands divided into 4 groups of 3 and connected to 12 glands arranged in 3 transverse rows, comprising respectively 3, 4 and 5 glands, between the pharynx and the rudimentary acetabulum.

Dunagan (1960), in his key for the identification of cercariae of the superfamily Opisthorchioidea, classified Cercaria quadripterygia Sinitsin, 1911 amongst those with a lateral and dorso-ventral fin fold, a rudimentary acebabulum and possibly 12 penetration gland-cells characteristics which coincide with those of Cercaria pleurolophocerca I described by the writer. However, C. quadripterygia parasitizes a marine mollusc (Hydrobia ventrosa)in the Black Sea, and some doubt exists concerning the number of its penetration gland-cells, the existence of a pharynx and the number and arrangement of its flame cells. In C. pleurolophocerca I the primary host is a fresh water mollusc, Bithynia tentaculata, there is a definitive number of 12 penetration gland-cells, a pharynx is present and the number and arrangement of flame cells is expressed by the formula $2\left[(2+2)+(2+2+2+2+2+2+2+2)\right]=40$.

Llewelyn (1957), Khan (1960) and Probert (1965) recorded Cercaria lophocerca, Filippi, 1859 from Bithynia tentaculata, this being the only representative of the group Pleurolophocerca, Sewell, 1922 (=Parapleurolophocerca, Sewell 1922 in this country. C. lophocerca has already been distinguished from C. pleurolophocerca I described above on the basis of the number of penetration gland-cells. Moreover, other characteristics of C. pleurolophocerca I, such as the flame cell formula, extension of the lateral membrane along the tail and presence of a short oesophagus make the distinction between these two forms more convincing.

Consequently this cercaria is recorded as new and is named *Cercaria pleurolophocerca I*.

Echinostome Cercariae

The members of this group of cercariae are easily identified by the presence of a cephalic collar provided with spines around its margin. Luhe (1909) placed this group in the Leptocercous cercariae and divided it according to the length of the gut in the redia and presence or absence of a fin-fold on the tail. He also described Cercaria echinatoides, C. coronata, C. echinata and C. spinifera. Cort (1915) suggested that Echinostome cercariae cannot be sub-divided into smaller natural groups. Sewell (1922) in view of the marked differences in the excretory system and the presence or absence of a fin-fold on the tail shown by these cercariae, divided Echinostome cercariae into four sub-groups three of which are named after Luhe's species. The sub-groups are:

(1) Sub-group Coronata: without a caudal fin-fold.
In the members of this group the main collecting ducts arise from the bladder, pass forwards to the level of pharynx (the portion in front of the acetabulum is wide and contains numerous refractile granules) where they form loops and continue back as far as the level of acetabulum where they divide into anterior and posterior collecting tubes. The caudal excretory canal passes backwards through the greater part of the length of the tail and opens on the surface about at its proximal end.

(2) Sub-group Echinatoides: with a caudal fin-fold, and an excretory system similar to that of the Coronata.

(3) Sub-group Echinata: without a caudal fin-fold.
The main collecting ducts arise from a common secondary bladder and each passes forwards to the side of the pharynx. The portion of the duct in front of the acetabulum is wide and contains numerous refractile granules. At the side of the

pharynx the tubes form loops and continue back to the posterior end of the body. At the side of the bladder the main duct apparently divides into anterior and posterior collecting tubes. The caudal excretory canal opens via short lateral branches near the base of the tail.

(4) Sub-group Megalura: Without a caudal fin-fold. A glandular adhesive-organ is located at the distal end of the tail. The main excretory ducts arise from the small excretory bladder and runs anteriorly to the level of the pharynx. Here they turn back as far as the acetabulum where they divide into anterior and posterior collecting ducts. The main excretory ducts do not contain refractile granules. No caudal excretory canal is present.

Sewell (1922) separated Cercaria agilis Filippi (1859) and Cercaria reflexae Cort (1915) from the Echinostome group and created two new groups, Agilis and Reflexae, to include these echinostome-like cercariae. The two groups were separable on the basis of the presence of a caudal fin-fold in the Reflexae and its absence in Agilis.

Faust (1924a) introduced ten groups distinguished by the nature of their excretory system, and placed the Agilis and Reflexae groups of Sewell (1922) in the Echinostome cercariae. Miller (1936) classified the Echinostome cercariae on the basis of presence or absence of collar spines and caudal fin-fold, but did not include any of the members of Megalura group of Sewell (1922) as he did not consider that there was sufficient evidence to relate them to the Echinostome cercariae. Miller also added Cercaria agilis and C. reflexae to this group, because they had already been shown to be true echinostome types.

Dubois (1929), Wesenberg-Lund (1934) and Miller (1936) all suggested that the Echinostome cercariae cannot be reliably subdivided into smaller groups.

Porter (1938) found certain cercariae which were closely related to the

Echinatoides, Coronata and Echinata groups (Sewell, 1922) and on the basis of morphological differences she created three new sub-groups named Sub-echinatoides, Echinocrenata and Cucumeriformes groups. Khan (1960a) stated "Echinata, Echinatoides and Coronata groups of Sewell (1922) seem to be unnatural and should remain a single group until more suitable characters for their sub-division are discovered".

Jain and Yadav (1968) on the basis of the arrangement of the caudal excretory duct attempted to divide the Echinostome cercariae into three groups defined as follows:

1. Echinosolenata group

   The caudal excretory duct is single, median and unbranched throughout its entire course.

2. Echinobisolenata

   The caudal excretory duct forks into two branches.

3. Echinopolysolenata

   The caudal excretory duct forks into three branches, two lateral and one median which runs backwards in the tail.

Of these three new groups only the Echinobisolenata appears to be represented in Britain. However such a division is obviously not practicable for those cercariae (for example some Magnacauda) in which the caudal excretory duct is not present.

The use of the flame cell formulae, type of excretory system, presence or absence of a caudal fin-fold and number of collar spines as diagnostic characters in Echinostome cercariae classification has been proved to be of little value by several workers. For example, the cercariae of Echinostoma nudicaudatum Nasir (1960) is characterized by the absence of a caudal fin-fold and the presence of an excretory system of the Echinata type, while the cercaria of Echinostoma pinnicaudatum Nasir (1961) possesses a caudal fin-fold and the excretory system is the Echinata type. However, despite these structural differences in the cercariae, the adults are both referred to the same genus. A second example concerns the genus Hypoderaeum. In the cercaria of

Hypoderaeum essexensis Khan (1960a) the fin-fold is lacking and the excretory system is of the Coronata type whereas the cercaria of Hypoderaeum conoideum (present study) lacks a caudal fin-fold and possesses an excretory system of the Echinata type. Again the adult forms belong to the same genus despite large differences in cercarial structure.

The number of flame cells in Echinostome cercariae is difficult to determine as the body is opaque owing to the presence of numerous cystogenous gland-cells, penetration gland-cells, the nature of the digestive system and the presence of refractile granules in the main excretory ducts. Mathias (1925) described the cercaria of Hypoderaeum conoideum with 50-54 spines, but did not give the number of flame cells; Dubois (1929) gave 49 (47-53) spines and 48 flame cells; Rees (1932) 43,44 and 45 spines in the metacercariae, but no flame cells; Wesenberg-Lund (1934) 50 spines and 13 flame cells; Wikgren (1956) 25-26 spines on the ventral side and 7 spines on each lateral row and 16 flame cells in all; Meyer (1964) 49 spines and 48 flame cells; in the present study 47-52 spines and at least 40 flame cells.

The variation in number of collar spines and flame cells in Echinostome cercariae makes their identification difficult and the taxonomic significance of such characters can be only determined after the life cycles of the different species have been elucidated and the correspondence of cercaria and adult established.

The Magnacauda sub-group was erected by Byrd and Reider (1940) to accommodate a large-tailed echinostome cercaria. In these forms a small number of collar spines may be present or absent and if absent in the cercaria the spines are developed after encystment. These cercariae have experimentally been shown to develop into adults which belong to the genera Petasiger Dietz, 1909 and Stephanoprora Odhner, 1902. The excretory system of these cercariae exhibits a greater affinity to the Echinata type, but in the species hitherto described the caudal excretory duct is either absent or non-functional (lacks an excretory pore). They develop in rediae with divided or undivided collars.

I agree with Byrd and Reider (1940), Llewellyn (1957) and Khan (1960a)

that in view of the marked differences from the other members of the Echinostome cercariae, the Magnacauda sub-group should be treated separately.

During the course of this investigation, 3 cercariae of the Echinata sub-group and 2 of the Magnacauda have been found.

Cercaria of Hypoderaeum conoideum (Block, 1782) Dietz, 1909

This cercaria was obtained in autumn 1972 from Lymnaea stagnalis collected at Gledhow Valley Road and in winter 1972 from both L. pereger and L. stagnalis collected at Kirkstall Power Station (Leeds-Liverpool Canal). The rate of infection in L. pereger was 12.5% and in L. Stagnalis between 4.1 and 8.3% l.c. depending on the locality.

The cercariae are discharged intermittently throughout the day. They swim actively by vigorous movements of the tail and during swimming the body is bent ventrally and contracted. They typically swim near the bottom of the vessel and when swimming ceases they sink gradually. Touching any surface initiates rapid creeping movements executed by the alternate use of oral sucker and acetabulum. The cercariae survive for 24 - 32 hours.

Description (Plate 16, Figs. 1-4 and 6)

Body elongate, pyriform in outline and capable of considerable deformation. Body surface armed with small spines arranged in transverse rows. Cuticle thick, bearing spines on anterior and lateral margins as far as level of acetabulum and on posterior margin of body. Approximately 10-12 pairs of long hair-like projections present on each side of body. Collar well-developed, bearing 47-52 inconspicuous spines including 4 corner spines (2 oral and 2 aboral). Remaining spines arranged in a single row. Tail larger than body inserted subterminally. Both longitudinal and circular muscles extending length of tail, similar to those described in C. echinostoma III. Core of tail containing small elongate cellular bodies with fine granular contents; these bodies more abundant proximally cuticle of tail provided with numerous hair-like projections laterally; finfold and spines absent.

Oral sucker circular, slightly smaller than acetabulum, and situated terminally or subterminally. Digestive system comprising mouth, prepharynx, an elongate oval pharynx and a large slender oesophagus. Oesophagus divided just anterior to acetabulum into intestinal caeca extending to posterior end of body. Lumen of oesophagus and intestinal caeca containing granular material.

Acetabulum highly protrusible, situated posterior to middle of body; its

surface provided with one row of spines.

Anterior margin of body with apertures of 6 narrow ducts which extend to posterior margin of oral sucker before becoming too difficult to trace. Ducts apparently connected to 6 penetration gland-cells located lateral to Oesophagus; each gland-cell with coarse granular cytoplasm and without a nucleus.

Cystogenous gland-cells with coarse granular contents packing body from pharynx to posterior end. Genital primordium represented by two clusters of undifferentiated cells, one anterior and one posterior to acetabulum.

Excretory bladder consisting of two short, wide chambers, a large basal chamber opening to exterior via a dorsal pore and a small anterior chamber; chambers connected by a narrow canal. Large primary excretory ducts arising from anterior chamber; containing numerous refractile granules. Ducts initially narrow but widening at level of acetabulum, continuing as far as pharynx and forming anterior loops lateral to posterior margin of oral sucker before passing posteriorly as secondary ducts. Secondary ducts following a slightly sinuous course almost to posterior end of body, forming posterior loops at this level, then passing anteriorly to posterior level of acetabulum where bifurcation into anterior and posterior collecting ducts located. Secondary ducts each containing 11-12 ciliary patches along their lengths. At least 20 flame cells present each side of body but capillaries very difficult to observe. Caudal excretory duct arising from base of posterior chamber and giving off two lateral branches in proximal part of tail. Flame cell formula not known.

Redia (Plate 16 Fig. 5)

This cercaria developed in rediae in the hepatopancreas of the snail hosts. The redia is elongate and very active. The body cuticle is thick and filled with fine granular material; its whole surface containing scattered yellowish brown pigment. The collar is conspicuous just behind the pharynx and the birth pore is found immediately posterior to it.

The pharynx is well developed, muscular and protrusible. It leads into a short sac-like intestine which extends for about a third of the body length

and is filled with dark brown material. There are two prominent locomotory appendages located near the posterior end. The body cavity contains 7-8 cercariae at different stages of development of which 2 or 3 are fully developed at any one time. Germ balls are also abundant and vary in size.

This cercaria was found experimentally to develop into adults of Hypoderaeum conoideum. Details of subsequent life cycle stages are given elsewhere (page 100).

Measurements of the cercaria of Hypoderaeum conoideum from Lymnaea pereger and L. stagnalis

Body	0.342 (0.304 - 0.399) long x 0.112 (0.106 - 0.136) wide
Tail	0.414 (0.410 - 0.418) long x 0.039 (0.038 - 0.041) wide
Oral sucker	0.041 (0.041 - 0.041) long x 0.041 (0.041 - 0.041) wide
Acetabulum	0.053 (0.049 - 0.057) long x 0.053 (0.049 - 0.057) wide
Prepharynx	0.019 (0.007 - 0.026) long
Pharynx	0.025 (0.022 - 0.030) long x 0.019 (0.019 - 0.019) wide
Oesophagus	0.091 (0.053 - 0.063) long
Preacetabular extent	0.182 (0.133 - 0.220) long
Postacetabular extent	0.076 (0.068 - 0.087) long
Redia	0.917 (0.545 - 1.400) long x 0.231 (0.196 - 0.280) wide
Pharynx	0.074 (0.053 - 0.102) long x 0.078 (0.064 - 0.106) wide

Location of metacercariae in the second intermediate host

Freshwater snails of the species Lymnaea stagnalis, L. pereger, Planorbis corneus, Physa fontinalis and Potomopyrgus jenkinsi were collected from the Leeds-Liverpool Canal (Kirkstall Power Station) and were isolated in glass dishes containing tapwater. After 24 hours it was observed that some specimens of L. pereger were shedding large numbers of cercariae which were subsequently identified as the cercariae of Hypoderaeum conoideum (see page 95).

Whilst examining specimens of L. pereger for the occurrence of precercarial stages (in this case rediae) of H. conoideum in the digestive gland, I noted the presence of many cysts in the digestive gland, kidney, mantle wall and

some possible loose in the mantle cavity. These cysts possessed a collar with 47 to 52 spines, main excretory tubules with refractile granules, a long oesophagus and cystogenous gland-cells with coarsely granular contents. These characters are similar to those of the cercariae of Hypoderaeum conoideum, indicating that the cercariae penetrate snails and became encysted metacercariae. Similar cysts were also found in P. corneus, P. fontinalis, Potomopyrgus jenkinsi, L. stagnalis and B. tentaculata.

Laboratory reared specimens of P. corneus, P. fontinalis, L. pereger and L. stagnalis were exposed to H. conoideum cercariae. The cercariae swim actively after being released by the primary intermediate host and do not appear to be attracted to either L. pereger or other snail species. Upon making contact, apparently accidentally, with their snail host or other snails of different species they commence crawling about with the aid of their suckers. Some were observed passing between the inner surface of the shell and the host tissue where they disappeared. Several minutes latter they had apparently lost their tails since some detached tails were seen at the bottom of the container. Six hours later the majority of the cercariae had disappeared with only a few still freely swimming. Twenty four hours after penetration the snails were carefully examined to determine the location of the cysts. All the snails were infected and the cysts were found in the same organs as in the wild snails. These cysts showed the same characters as those found in the naturally infected snails. The precise site of entry into the second intermediate host has not been determined, but it is believed that the cercariae penetrate anywhere on the body of the snails and then migrate to encyst in the preferred site. The number of cysts in each snail varied from 12 to 187, being more numerous in L. pereger and P. fontinalis than in P. corneus and P. jenkinsi.

On one occasion three cysts were found at the bottom of a container containing 6 L. pereger which had been brought from Kirkstall and isolated for experimental infection by cercariae. It was believed initially that these cercariae had encysted in the open but daily examination for five days failed to detect the presence of any free-swimming cercariae. Five of the snails were killed and

examined but no precercarial stages were found although 2 snails were found to be harbouring cysts of this species. Approximately 150 recently-emitted cercariae were pipetted in about 100 cc water into three small glass dishes. They were examined many times during the next 24 hour period but no cysts were seen. It is probable that some of the cercariae were not able to penetrate the tissues of the snails and encysted in the mantle epithelium, under the shell. Later they may have been dislodged by the scraping action of the shell against the mantle as the body withdrew into the shell. This is probably how some free cysts observed on one occasion originated. The cercaria of H. conoideum were never found to encyst in the open; they normally left their primary intermediate host and re-entered either the same snail individual or another specimen of the same or a different species.

Metacercariae (Plate 17, Fig. 7)

The cysts are nearly spherical. The cyst wall is smooth, transparent and comprising two layers - an inner layer which is tough, difficult to remove without injuring the encysted metacercaria and both narrower and more opaque than the outer layer which is almost hyaline and easily reptured.

In cysts aged 24 h the encysted metacercariae lie bent back upon themselves and are usually in constant motion. The metacercariae are morphologically similar to the cercariae and the main differences noted were a slight increase in size of the main excretory ducts and the fact that the contents of the cystogenous gland-cells where less dense.

In a 15 day-old cyst the metacercaria is almost inactive and markedly more opaque. Its length has increased and the anterior and posterior ends of the body which is still folded double almost touch each other. The body spines and collar spines are more conspicuous, the former being more prominent anteriorly but the cystogenous and penetration gland-cells are no longer visible. The caeca are slightly longer, the excretory granules less numerous and there has been slight growth of both the sucker and pharynx.

Measurements of 15 day-old metacercariae of Hypoderaeum conoideum experimentally obtained from laboratory reared snails.

Cyst	0.163 (0.152 - 0.174) long x 0.153 (0.149 - 0.171) wide
Outer wall	0.024 (0.019 - 0.030) thick
Inner wall	0.009 (0.007 - 0.013) thick
Oral sucker	0.047 (0.045 - 0.049) long x 0.047 (0.045 - 0.049) wide
Pharynx	0.033 (0.030 - 0.038) long x 0.029 (0.026 - 0.034) wide
Acetabulum	0.066 (0.064 - 0.068) long x 0.066 (0.064 - 0.072) wide

Infection of the final host

The metacercariae used in the feeding experiments were 2, 5, 15, 66 and 120 days old and they were obtained from Lymnaea pereger, L. stagnalis and Physa fontinalis which were experimentally infected under laboratory conditions. Mice, rats and pigeon were reared in the animal house of the Zoology Department. Faecal samples were examined daily as described above (see p.10). The number of metacercariae fed to each host was 80.

All the attempts to infect mice and rats were unsuccessful (see Table 5).

None of the birds that had been fed with 2 to 5 day-old metacercariae produced any worms. However trematode eggs similar to those of H. conoideum appeared in the faeces of chicken 3, pigeon 3 and duckling 3 on the 12th day following the ingestion of 15 day old metacercariae. They were killed and examined on the same day and both immature and mature worms were recovered from the duodenum. In another series of experiments (chicken 4, pigeon 4 and duckling 4) all rematodes harboured were mature on the 15th after infection and were located in the first third of the small intestine.

The administration of cysts aged 66 and 120 days showed that the capacity to develop in the final was retained to some extend in cysts of these ages. In pigeon and duckling a few trematodes persisted for 28 days.

These feeding experiments demonstrated that mice and rats are probably unsuitable definitive hosts for this species. The number of worms experimentally obtained from chickens, pigeons and ducklings was low compared to the number of

metacercariae administered. Metacercariae between 2 and 5 days old did not appear to have become infective but had done so by the 12th. Metacercariae viability is retained in some individuals for at least 120 days.

Rees (1932) has adequately described the adult Hypoderaeum conoideum. My observations agree largely with those of Rees; the only point of difference is that I have found a large receptaculum seminis uterinum as an enlargement of the ootype and did see in any specimen (82 examined) a receptaculum seminis.

Adult as described by Rees.

Measurements of Hypoderaeum conoideum from experimental infections of laboratory birds

Body	6.520 (5.049 - 7.811) long x 1.194 (0.841 - 1.315) wide
Oral sucker	0.177 (0.168 - 0.210) long x 0.201 (0.168 - 0.280) wide
Prepharynx	0.015 (0.007 - 0.030) long
Pharynx	0.162 (0.112 - 0.189) long x 0.139 (0.112 - 0.168) wide
Acetabulum	0.697 (0.504 - 0.812) long x 0.736 (0.532 - 0.868) wide
Anterior testis	0.714 (0.490 - 0.882) long x 0.378 (0.280 - 0.462) wide
Posterior testis	0.751 (0.560 - 0.924) long x 0.350 (0.280 - 0.490) wide
Ovary	0.246 (0.140 - 0.294) long x 0.293 (0.182 - 0.364) wide
Cirrus Sac	0.657 (0.476 - 0.938) long x 0.203 (0.140 - 0.294) wide
Preacetabular extent	0.709 (0.553 - 1.053) long
Postacetabular extent	5.566 (3.997 - 6.316) long
Eggs	0.090 (0.087 - 0.098) long x 0.060 (0.049 - 0.068) wide
Collar	0.388 (0.350 - 0.420) long
Lateral spines	0.022 (0.020 - 0.026) long x 0.007 (0.007 - 0.008) wide
Dorsal spines	0.013 (0.013 - 0.015) long x 0.007 (0.007 - 0.007) wide
Corner spines	0.026 (0.024 - 0.028) long x 0.010 (0.009 - 0.011) wide

Egg and Miracidium (Plate 18, Figs. 12-13)

The mature worms were kept in small containers in 0.75% normal saline. The number of eggs passed was very small and most of the eggs used in these

experiments were obtained from the faeces of experimentally infected hosts.

The eggs are yellowish, oval in outline, thin-walled, operculated and not embryonated. The newly laid eggs comprise a rounded ovum with rather central nucleus and clear undivided cytoplasm. The ovum is surrounded by numerous vitelline cells.

The eggs were incubated in distilled water and tapwater at room temperature (19 to 22°C). Development was observed periodically, and after 16 to 18 days the miracidia are fully developed. A few miracidia were able to hatch from the eggs as several empty shells were found at the bottom of the container but no free swimming miracidia were seen. Some of them died without hatching. On three occasions hatching was induced by applying slight pressure thereby forcing the operculum open but in the majority of cases the miracidia were crushed by this process. The miracidia only escaped from the egg with great difficulty because of the small size of the operculum. The water, the miracidia became more active and the cilia commenced very rapid beating. The free miracidia usually exhibited rotating movements along their longitudinal axis or swam in small circles. After 2 to 5 minutes they become rather inactive, shed their cilia and become rounded. This process was observed twice and the miracidia remained alive for 10 to 15 minutes before starting to disintegrate. The flame cells of the disintegrating miracidia continued beating for between 2 and 5 minutes. Natural, un-induced hatching was not observed. No attempts were made to infect snails because no free swimming miracidia were available.

The fully developed miracidium is slightly longer than the egg and usually has its posterior end curved to one side. The miracidium occupied more than half of the space within the egg, the remainder of the space generally being filled by two or three large vacuoles and a small amount of granular material, probably derived from the vitelline glands.

Its body is elongate or oval and somewhat pointed anteriorly. Its anterior end has a protrusible apical papilla. The surface of the miracidium is ciliated except the extreme anterior end which is naked. There is an

apical gland which is flask-shaped in outline, extending some distance anterior of the eyespots and filled with rather coarsely granular contents. Its duct opens by a very small aperture located at the anterior tip of the apical papilla. There are two L-shaped eyespots formed of dark brown pigment granules. Just posterior to the eyespots, there is a rounded mass of nucleated cells which represents the nervous system.

The protonephridial system comprises two large flame cells which are rather variable in position but are usually situated behind midline of the body. Their excretory ducts follow a sinuous course forming one or two loops and then each opens separately via a small lateral excretory pore situated near the posterior end of the body. No penetration gland cells were observed. The germ cells are situated at the posterior end of the body; they are nucleated and contain a fine granular cytoplasm.

Discussion

This is a widely distributed species of trematode. It was first described by Bloch (1782) under the name of Cucullamus conoides. Dietz (1910) established the genus Hypoderaeum and included the trematode as Hypoderaeum conoideum.

The cercaria of H. conoideum was first described by Mathias (1925) from Lymnaea stagnalis and Radix ovata in France. Dubois (1929) reported it from Lymnaea palustris and L. stagnalis in Switzerland and provided further details of the protonephrideal system, which had been inadequately described by Mathias. Wesenberg-Lund (1934) found the same cercaria in R. ovata from Denmark.

It has subsequently been recorded from Finland (Wikgren, 1956), Switzerland (Meyer, 1964), Western Kazakhstan USSR (Smirnova and Ibrasheva, 1967) and Britain (Nasir, (1957-1958, Williams, 1966).

A great deal of intraspecific variation is apparent if the published descriptions of this cercaria from different localities are compared. A comparison of certain characters, including numbers of collar spines and flame cells, is presented in Table 6. Wesenberg-Lund (1934) described six small apertures located on the anterior margin of the mouth and regarded

them as the penetration gland openings but the actual glands and their ducts were not observed. In the present specimens these 6 apertures were observed to lead into 6 narrow ducts which extended as far as the posterior margin of the oral sucker. The penetration gland-cells were also visible lying lateral to the oesophagus.

Observations on the life cycle of this fluke were first presented by Railliet (1893) who found the larval stages in several species of Lymnaea, Planorbis and Paludina. Vevers (1923) fed ducklings with both the liver of L. pereger infected with Tetracotyle stages which he believed to belong to Tetracotyle typica Diesing, 1853 and the liver of L. stagnalis naturally infected with echinostome cercariae which he identified as C. echinata (Siebold, 1835) the larval stage of Echinostoma revolutum (Frolich, 1802). Twenty days postinfection adult forms of H. conoideum and immature forms of E. revolutum were recovered from the small intestine and cloaca respectively. No other trematodes were obtained. He stated that "the specimens of H. conoideum recovered from ducks must have developed from some other cercariae also encysted in Lymnaea pereger, but not detected at the time of the examination of the snails". Vevers gave a brief description of the immature forms of E. revolutum but not of H. conoideum. The life cycle was first completed by Mathias (1925) who obtained the adult parasites by feeding ducks with experimentally encysted metacercariae collected from L. limosa and P. corneus. Mathias also infected species of Lymnaea with miracidia reared experimentally from eggs.

Rees (1932) found encysted echinostome metacercariae in the mantle cavity and digestive gland of L. pereger in South Wales. The cysts were characterised by having 43-45 collar spines and she, therefore, considered that they belonged to cercaria "Z" which had previously been described from the same locality (Rees, 1932) and which also carried with 43-45 collar spines. Duckling were fed with the cysts from L. pereger and adults forms of H. conoideum were obtained from the small intestine. Rees concluded that the cysts used in the feeding experiments were those of the cercaria of H. conoideum and not those of

cercaria "Z". No free swimming cercariae of H. conoideum were found. Rees gave a full account of the morphological characters of this species.

Subsequently the life cycle of H. conoideum has been completed by several authors e.g. Hsu and Chow (1938) in China and Kumaran and Peter (1973) in India,

Williams (1966) reported an incidence rate of 3.62% for the cercaria of H. conoideum in Lymnaea pereger in a pond near Glasgow. These cercariae encysted in young L. pereger and when cysts were fed to day-old ducklings, adult parasites were recovered about 18 days later. Williams neither described nor figured any life cycle stages, giving only the diameter of the cysts.

The variation in number of collar spines in the cercarial and metacercarial stages is reflected by similar variation between adults of H. conoideum. In most specimens there were 47 or 48 spines but a few had 52 spines. In Rees' specimens the number varied from 43-45 as compared to the range of 47 to 53 given by Mathias (1925) for H. conoideum. Beverley-Burton (1961) found H. conoideum in several species of ducks near Ipswich, Suffolk. Her specimens had 47-49 spines and she suggested that the known range for H. conoideum should be extended from 45-53 (as stated by Skrjabin, 1956) to 43-53. She compared her specimens of H. conoideum with those of H. gnidini Bashkirova, 1941 from Anas sp. and with those of H. skrjabini Oschmarin, 1947 from Aythya ferina and concluded that "An examination of the specimens of these two forms would possibly result in their being synonymised with H. conoideum".

Yamaguti (1971) listed 13 species belonging to the genus Hypoderaeum, of which H. essexensis Khan (1962b) (obtained experimentally in duckling, pigeon and chicken from Great Britain) and H. dingeri Lie (1964) (obtained experimentally from duck and goslings from Malaysia) are characterized by having 49 and 49-56 collar spines respectively. The precercarial, cercarial and adult stages are very similar to those found in the present study. The number of collar spines (which falls within the range of spines for H. conoideum) could be interpreted as instraspecific variation and it would be possible to mistakenly regard them as conspecific. Fortunately, life cycle data are available for these two

species, and show that all three are separate species. It is apparent that the lack of life cycle data could lead to the erroneous designation of synonyms.

The adult of Hypoderaeum conoideum obtained experimentally from chicken, pigeon and duckling agrees in all essential features to the description given by Rees (1932) except that she reported the presence of a large elongated "receptaculum seminis" often filled with spermatozoa, which arises from the oviduct and opens into the ootype. However, in none of my specimens was this structure present. In my specimens the ootype enlarges to form a wide sperm-filled "receptaculum seminis uterinum", which is a part of the uterus, but a true receptaculum seminis is absent. Rees must have interpreted this enlargement of the cotype as a true receptaculum seminis. The ovicapt is also present in my specimens and may have been overlooked by Rees.

Hypoderaeum conoideum (Bloch, 1782) has also been recorded in Britain by Owen (1951) in the domestic ducks, Cairina moschata and Anas platyrhyncha dom., and by Soliman (1955) in the Khaki Campbell duck.

Table 5

Experimental infection of mammals and birds with metacercariae of Hypoderaeum conoideum (Bloch, 1782)

Experimental definitive host	Age of cysts (Days)	Eggs detected in faeces (+ or -) (Days)	Host autopsied after - (Days)	Number of trematodes recovered	Degree of development of trematodes: Immature	Mature	Location in host
Mouse 1	2	-	12	0	0	0	
Mouse 2	5	-	12	0	0	0	
Mouse 3	15	-	15	0	0	0	
Mouse 4	66	-	15	0	0	0	
Mouse 5	66	-	15	0	0	0	
Rat 1	2	-	12	0	0	0	
Rat 2	5	-	12	0	0	0	
Rat 3	15	-	15	0	0	0	
Rat 4	66	-	15	0	0	0	
Rat 5	66	-	15	0	0	0	
Chicken 1	2	-	12	0	0	0	
Chicken 2	5	-	12	0	0	0	
Chicken 3	15	12+	12	20	5	15	Duodenum
Chicken 4	15	15+	15	13	0	13	Jejunum
Chicken 5	66	-	15	0	0	0	
Chicken 6	120	15+	15	5	0	5	Jejunum
Chicken 7	120	28-	28	0	0	0	
Pigeon 1	2	-	12	0	0	0	
Pigeon 2	5	-	12	0	0	0	
Pigeon 3	15	12+	12	16	4	12	Duodenum and jejunum
Pigeon 4	15	15+	15	10	0	10	Jejunum
Pigeon 5	66	-	15	0	0	0	
Pigeon 6	120	15+	15	7	0	7	Duodenum
Pigeon 7	120	28+	28	1	0	1	Jejunum
Duckling 1	2	-	12	0	0	0	
Duckling 2	5	-	12	0	0	0	
Duckling 3	15	12+	12	21	14	7	Duodenum
Duckling 4	15	15+	15	14	0	14	Jejunum
Duckling 5		15+			0	10	Duodenum and jejunum
Duckling 6		15+			0	9	Duodenum and jejunum
Duckling 7		28+			0	2	Jejunum

Table 6

A comparison between the published descriptions of the cercaria of Hypoderaeum conoideum

	No. of collar spines	No. of corner spines	No. of flame cells	Ciliary patches in secondary ducts	Anterior & posterior loops in excretory ducts
Present account	47-52	4(occasionally 5) each side	at least 20 each side	present	present
Mathias (1925)	50-54	-	not determined	-	-
Dubois (1929)	49(47-53)	5 each side	24 each side	-	?
Meyer (1964)	49 (5)+19+1+19+(5)	5 each side	24 each side	present	posterior loop absent
Wesenberg-Lund (1934)	50	-	13	-	present
Wikgren (1956)	39-40 (25-26 in ventral row & 2 lateral rows of 7)		8 pairs	-	present
Rees (1932) as metacercaria of Cercaria Z	43-45	-	-	-	-
Nasir (1957-1958)	49-51	no differentiation into corner spines	at least 18 pairs	present	present

Cercaria of Echinoparyphium recurvatum (Linstow, 1873) Dietz, 1909

The cercaria of Echinoparyphium recurvatum has only been found twice, present survey, parasitising Lymnaea pereger. During spring and summer 1975, between 6.2 and 28% of L. pereger collected from Kirkstall Power Station (Leeds-Liverpool Canal) and Riffa Beck Pool-in-Wharfedale respectively, harboured this cercaria.

The cercariae emerge throughout the day in a moderate number, but the greatest number are shed between 9 and 12 in the morning. They swim actively and may be seen swimming most commonly in the lower part of the container. During the swimming periods and the creeping movements the cercariae behave like those of Hypoderaeum conoideum. They remain alive for about 24 hours.

Description (Plate 20, Figs. 1-5)

Body oval to elongate. Entire body surface provided with prominent, closely-set, backwardly-directed spines arranged in transverse rows and decreasing in size posteriorly. Cuticle thick, furnished with numerous short hair-like projections on papillae arranged fairly regularly around body but denser at anterior end. Collar well-developed, provided with 44-45 spines, including a group of 4 corner spines on each side of pharynx and 37 spines arranged in a single row. Tail subterminal on ventral aspect of body; capable of great extension and contraction. Tail provided with 12-14 long hair-like projections but surface non-spinose and without fin-fold.

Oral sucker terminal, smaller than acetabulum and protrusible. Mouth subterminal, opening into prepharynx, followed by well-developed, muscular pharynx, and long oesophagus. Oesophagus divided just anterior to acetabulum. Long intestinal caeca extending to posterior extremity of body, terminating at level of base of bladder. Lumen of oesophagus and caeca containing a single row of short, broad cells with rounded nuclei and coarse granular cytoplasm.

Acetabulum protrusible, well developed, almost circular in outline located slightly behind middle of body and surrounded by a muscular fold.

Penetration gland-cells inconspicuous, arranged in a linear row each side of oesophagus. Six pairs of gland-cells present, each with rather coarse, granular cytoplasm and devoid of a nucleus. Ducts narrow, opening on antero-lateral region of mouth. Many cystogenous gland-cells with coarsely granular contents scattered throughout body from posterior margin of pharynx to posterior end of body. Genital primordium comprising an undifferentiated mass of cells located immediately anterior to acetabulum and joined by a column of cells to a similar mass of cells lying between acetabulum and bladder. Nervous system clearly visible and consisting of two cerebral ganglia connected by a dorsal commissure. Anterior pair of nerves from ganglia passing lateral to oral sucker; postero-lateral nerves large and extending almost to distal tip of intestinal caeca..

Excretory bladder two-chambered, a large round basal chamber which opens dorsally through excretory pore located at its base and small anterior latero-transversally chamber; chambers connected by a narrow canal. Two wide, slightly coiled primary excretory ducts arising separately from anterior part of anterior chamber and passing to level of acetabulum, there becoming dilated to accommodate numerous refractile granules. Small refractile granules frequently present in lower parts of ducts. Primary ducts continuing to level of oral sucker, forming anterior loops then passing posteriorly as narrow secondary ducts containing 17-18 ciliated patches. At equatorial level of posterior chamber secondary ducts divided into anterior and posterior collecting ducts. Anterior collecting duct receiving eleven groups of two flame cells and posterior collecting duct receiving two groups of 2 flame cells. Caudal excretory duct divided into two short ducts opening laterally one third along length of tail. Flame cell formula: $2\left[(2+2+2+2+2+2+2+2+2+2+2)+(2+2)\right]=52$.

Redia (Plate 20 Fig.6)

The digestive gland of Lymnaea pereger was found to be packed with numerous elongate rediae of various sizes. The redia are very active, especially the small ones. The body cuticle is thick and in mature rediae it is covered with

small dark-green pigment spots whereas the younger rediae are almost colourless. The collar is well-developed and located between the pharynx and the birth pore the latter of which is protusible and lies on one side. There is a prominent muscular pharynx which is capable of protrusion. This is followed by a short intestine filled with brown material. A pair of locomotory appendages is situated near to the posterior extremity. Eight to nine mature cercariae were present at the same time, together with a small number of immature cercariae. The rest of the body was filled with numerous germ balls which were more abundant at the posterior end.

This cercaria has been experimentally linked to the adult of Echinoparyphium recurvatum.

Measurements of the cercaria of Echinoparyphium recurvatum from Lymnaea peregger

Body	0.373 (0.296 - 0.426) long x 0.104 (0.096 - 0.144) wide
Tail	0.423 (0.395 - 0.444) long x 0.039 (0.038 - 0.045) wide
Oral sucker	0.042 (0.038 - 0.053) long x 0.041 (0.034 - 0.049) wide
Acetabulum	0.056 (0.049 - 0.065) long x 0.051 (0.049 - 0.053) wide
Prepharynx	0.016 (0.015 - 0.019) long
Pharynx	0.024 (0.023 - 0.027) long x 0.020 (0.015 - 0.023) wide
Oesophagus	0.047 (0.106 - 0.171) long
Preacetabular extent	0.209 (0.175 - 0.258) long
Postacetabular extent	0.095 (0.057 - 0.118) long
Redia	2.577 (2.232 - 2.893) long x 0.449 (0.342 - 0.579) wide
Pharynx	0.120 (0.114 - 0.113) long x 0.119 (0.106 - 0.129) wide

Metacercaria and Location in the snail host

As soon as the cercariae emerged from the snail host, they began swimming movements which continues until they made contact with a snail of any species avilable. They crawled about on the surface of the snail using the oral sucker and acetabulum until penetration was effected and encystment took place.

The snail Lymnaea peregger is utilized by the cercaria of Echinoparyphium recurvatum as both primary and secondary intermediate host. All attempts to

infect individuals of this species which had been reared in the laboratory were successful. Additional laboratory-bred snails belonging to the species L. stagnalis, Physa fontinalis, Planorbis carinatus and P. corneus were exposed to these cercariae and became infected. Collections of all these snail specimens, together with Potomopyrgus jenkinsi, from the localities where the cercaria of E. recurvatum occurs, exhibited natural infections. It is therefore evident that the cercaria of E. recurvatum has a low host specificity as it can use any of the snails investigated as secondary intermediate host.

The encysted metacercariae in both naturally and experimentally infected snails were usually located in the mantle cavity and digestive gland but were occasionally found in the wall of oesophagus and intestine.

The metacercaria (Plate 20, Fig. 7)

The cyst is almost circular in outline, and contains a relatively inactive metacercaria which is tightly coiled and occupies the whole of the lumen of the cyst. The cyst wall is transparent and consists of an outer hyaline layer and thick inner layer. After 15 days the oral sucker, pharynx, and acetabulum had slightly increased in size and although the collar spines had become more conspicuous they were difficult to count on the coiled body of the metacercaria. The penetration and cystogenous gland-cells had completely disappeared and the intestinal caeca had become indistinct. The most prominent features of the metacercariae were the main excretory ducts, their contents and the beating cilia in the secondary ducts. No trace of an excretory bladder was found. The size of the cysts remained essentially unchanged during development although in a few cysts the outer layer showed a slight increase in thickness, probably due to a host response.

Measurements of 15 day-old metacercariae of Echinoparyphium recurvatum from experimentally infected snails

Cyst	0.159 (0.155 - 0.163) long x 0.160 (0.159 - 0.163) wide
Oral sucker	0.043 (0.038 - 0.049) long x 0.043 (0.041 - 0.045) wide
Pharynx	0.024 (0.022 - 0.026) long x 0.018 (0.015 - 0.022) wide
Acetabulum	0.052 (0.049 - 0.057) long x 0.048 (0.045 - 0.049) wide

Infection of the final host

Cysts between 2 and 30 days old were obtained from experimentally infected Lymnaea pereger reared in the laboratory and were were fed in a humber of 60 to each experimental bird hosts (see Table 7). All the birds were purchased commercially except the pigeons which were laboratory-bred.

1 chicken, 2 pigeons and 2 ducklings were each fed forty 2 to 4 day cysts. Faecal examinations were made daily for 20 days, but no trematode eggs appeared. The birds were then killed and were found not to be infected with trematodes. These experiments suggest that 2 to 4 day metacercariae were not sufficiently developed and therefore were not infective. Subsequent experiments were performed in which 7 pigeons, 3 chickens and 3 ducklings were fed metacercariae between 25 and 30 days old. Mature E. recurvatum were found in the small intestine of 4 pigeons, 1 chicken and 3 ducklings between 10 and 19 days later.

In view of the results of these feeding experiments, several conclusions can be drawn.

1. Adult worms were obtained in all three host species when fed with infective metacercariae. This indicated that E. recurvatum has a low host specificity, since it was able to attain sexually maturity in all the experimental hosts tried in the laboratory.
2. Ducklings proved to be the most appropriate experimental hosts since, when fed with infective metacercariae, none of them failed to yield adult worms.
3. Chickens proved to be the least suitable experimental hosts. Only in chicken 3, did mature trematodes develop.

4. The number of worms obtained from the feeding experiments was low (not exceeding 20%) in comparison to the number of cysts introduced.
5. The rate of development was similar in all the birds, with eggs first appearing in the faeces 10 days after having been fed infective metacercariae.
6. Although no feeding experiments were designed to determine the longevity of the worms in experimental hosts, it seems likely that they do not remain in these experimental hosts for a long period of time.

Table 7

Experimental infection with metacercariae of Echinoparyphium recurvatum (Linstow, 1873) experimentally obtained from Lymnaea peregra.

Experimental definitive host	Age of cysts (Days)	Eggs detected in faeces (+ or -) after 10 days	Host autopsied after - (Days)	Number of trematodes recovered
Pigeon 1	2	-	20	0
Pigeon 2	4	-	20	0
Pigeon 3	25	+	10	8
Pigeon 4	30	-	15	0
Pigeon 5	25	+	18	12
Pigeon 6	30	-	15	0
Pigeon 7	27	-	15	0
Pigeon 8	27	+	15	3
Pigeon 9	27	+	19	1
Chicken 1	2	-	20	0
Chicken 2	25	-	10	0
Chicken 3	25	+	10	5
Chicken 4	30	-	15	0
Chicken 5	27	-	15	0
Duckling 1	2	-	20	0
Duckling 2	4	-	20	0
Duckling 3	25	+	10	7
Duckling 4	30	+	15	3
Duckling 5	27	+	19	11

Description (Plate21-22,Figs. 8-12)

Body elongate, gradually tapering anteriorly and slightly rounded posteriorly, with the maximum width at the level of acetabulum. Cuticle covered with relatively large spines between level of pharynx and of ovary. Both dorsal and ventral body surfaces provided with transverse rows of scale like-spines extending to posterior end of acetabulum. Cephalic collar well-developed and armed with 45 spines arranged in a double uninterrupted row, including a group of 4 corner spines on each side of pharynx.

Oral sucker small, spherical usually terminal or slightly subterminal. Mouth subterminal, leading back into small prepharynx which is easily visible in well-extended specimens; pharynx muscular, oval in shape. Oesophagus very long and gradually enlarging near the anterior border of cirrus sac where it branches into two long slender caeca extending almost to posterior end of body.

Acetabulum very muscular, slightly protrusible and with its inner margin serrated.

Testes oval to elongate in shape, with smooth margins and lying in tandem in middle of posterior half of body.

Vasa efferential arising from antero-lateral borders of testes and passing anteriorly for a considerable distance. At the posterior margin of acetabulum the right was efferens bends to run alongside and both enter separately into posterior end of cirrus sac where they join to form a swollen seminal vesicle, filling most of the space within the cirrus sac. No well-developed pars prostatica and a long ejaculatory duct present. Several prostatic cells surround anterior portion of seminal vesicle, ejaculatory duct and cirrus. This latter organ not armed with spines but with a thick cuticular lining and markedly protusible. Cirrus sac thick-walled, oval to flask-shaped in outline and variable in position; usually extending from anterior region of acetabulum to common genital pore lying at about level of oesophageal bifurcation slightly to one side of body.

Ovary pretesticular, rounded and lying in middle of body, with a broad ovicapt originating from its postero-ventral area and soon given rise to oviduct.

Laurer's canal relatively long and slender arising near proximal end of oviduct looping on itself and ascending to posterior margin of ovary where it opens onto dorsal body surface. Oviduct extending dorsally and diagonally, passing below ovary then turning to right receiving common viteline duct just before ootype expansion. Ootype surrounded by a well-devebped Mehlis' complex lying between ovary and anterior testis. It extends backwards a short distance and then enlarges into a broad and coiled receptaculum seminis uterinum (proximal part of uterus) filled with spermatozoa; a true receptaculum seminis is absent. Uterus extending anteriorly forming several intracaecal uterine coils and continuing to posterior level of acetabulum where it forms the muscular metraterm opening at common genital pore.

Vitellaria well-developed and comprising large follicles lying in lateral body area, and extending from just behind acetabulum to posterior end of body; lateral fields joining behind testes and overlapping intestinal caeca and excretory bladder, lateral vitelline ducts unite in front of anterior testis and ovary to form vitelline reservoir; short common vitelline duct arising from vitelline reservoir and jointing oviduct just before the latter becomes the ootype. Eggs few but relatively large.

Nervous system consists of a dorsal commissure lying at the level of pre-pharynx and anterior and posterior pairs of nerves. Anterior nerves pass anteriorly around mergin of oral sucker. Posterior nerves pass posteriorly to posterior margin of acetabulum where they are difficult to observe due to presence of vitelline follicles.

Protonephridial system consisting of a tubular, Y-shaped excretory bladder opening by an excretory pore situated at its base; main stem of bladder extending to posterior margin of posterior testis where it divides into two main excretory ducts which pass anteriorly to level of pharynx. Flame cell formula not determined.

Measurements of adults of Echinoparyphium recurvatum obtained from experimental infections of laboratory birds.

Body	2.863 (2.282 - 3.164) long x 0.581 (0.490 - 0.644) wide
Oral sucker	0.116 (0.106 - 0.125) long x 0.115 (0.106 - 0.126) wide
Prepharynx	0.011 (0.003 - 0.030) long
Pharynx	0.094 (0.087 - 0.106) long x 0.080 (0.072 - 0.102) wide
Acetabulum	0.357 (0.258 - 0.391) long x 0.354 (0.285 - 0.380) wide
Anterior testis	0.345 (0.285 - 0.395) long x 0.215 (0.163 - 0.254) wide
Posterior testis	0.342 (0.304 - 0.368) long x 0.209 (0.159 - 0.250) wide
Ovary	0.156 (0.121 - 0.171) long x 0.141 (0.102 - 0.174) wide
Preacetabular extent	0.714 (0.588 - 0.798) long
Postacetabular extent	1.859 (1.400 - 2.240) long
Posttesticular extent	0.494 (0.418 - 0.684) long
Eggs	0.098 (0.091 - 0.114) long x 0.058 (0.057 - 0.064) wide
Corner spines	0.048 (0.045 - 0.053) long x 0.012 (0.011 - 0.015) wide
Lateral spines	0.040 (0.034 - 0.045) long x 0.010 (0.008 - 0.011) wide
Dorsal spines	0.039 (0.038 - 0.041) long x 0.012 (0.010 - 0.011) wide

Eggs (Plate 22 Figs.13-14)

Since few eggs are produced by this species and are difficult to find in the faeces of the host specimens for examination were obtained by teasing mature worms apart in water.

The eggs are unembryonated when laid, golden yellow in colour, thin-shelled and operculate (see fig.13-14).

Attempts to incubate eggs to obtain miracidia failed owing to fungal and bacterial contamination

Discussion

This form was first described under the binomen Distomum recurvatum by von Linstow (1873) using material collected from the small intestine of Fuligula marila. Dietz (1909) reviewed the family Echinostomidae (Poche, 1925)

and erected several new genera, including Echinoparyphium. Luhe (1909) proposed the new combination Echinoparyphium recurvatum (von Linstow, 1873).

The life cycle of cercaria of Echinoparyphium recurvatum has been elucidated by Mathias (1926) after feeding encysted stages of an echinostome cercaria from Planorbis planorbis to ducks. Unfortunately his descriptions of the larval stages and rediae were not adequate. Harper (1929) experimentally completed the life cycle of this species but again the cercaria was not adequately described. Azim (1930) obtained the adult parasites after feeding dogs, white rats and wild rats with metacercariae from several species of Bulinus but he did not study the cercaria in detail. Rasin (1933) gave a complete account of the life cycle. Since then this species has been recorded by many workers; - Wesenberg-Lund (1934), Dinulesco (1939), Kuntz (1953), Senger (1954), Llewelyn (1957), Khan (1960), Probert (1966), Williams (1966), Butenko (1967), Bisseru (1967) and Murar (1973).

In Britain this cercaria has been found to parasitize two different species of gastropod. Harper (1929) in Dundee and North Fifeshire, and Khan (1960) in Bushy Park, London, recorded it from the prosobranch Valvata piscinalis. Llewelyn (1957) in Rumney, South Wales, Probert (1966) in Langorse Lake, South Wales and Williams (1966) in Milgavie near Glasgow, Scotland, recorded it from the pulmonate Lymnaea pegreger. The cercaria described in the present study was also obtained from L. peregeer. Of the above-mentioned authors only Harper gave a description of the cercaria.

The shape, number of collar spines, spination of the body and digestive system agree with the description of the cercaria of Echinoparyphium recurvatum given by Harper (1929). The body measurements cannot be compared as he did not state if his measurements were taken from living or fixed specimens. In Harper's specimens the secondary excretory ducts form a posterior loop at the posterior end of the body and end at the region of the oral sucker. In my specimens there are no posterior loops and the secondary ducts divide into anterior and posterior collecting ducts just anterior to posterior end of body. The absence of these loops has been reported by Wesenberg-Lund (1934), Kuntz (1953) and Khan (1960). Harper also stated that the caudal excretory

duct extended about three-quarters the length of the tail before dividing. In the present study it is a short duct which branches at about one-third of the tail length. Wesenberg-Lund also described a similar duct whereas in the specimens of Kuntz and Llewellyn the caudal excretory duct was represented by a single short undivided tubule. Kuntz gave the first account of the protonephridial system and affirmed that it was non-functional in the developed cercaria, only becoming visible when the liquid contained inside the bladder is forced into it. Harper mentioned the presence of ciliary patches within the lower part of the secondary excretory ducts, but he did not determine their number. Kuntz and Llewellyn observed 11 and 13 respectively whereas I have observed 17-18 within these ducts. Kuntz reported the flame cell formula to be $2\left[(3+3+3+3)+(3+3+3+3)\right] = 54$, but he was not able to determine accurately where the capillaries drain the flame cells. In the present specimens the flame cells are arranged in groups of two making a total of 52. Harper described only 16 flame cells on each side of the body; Llewellyn, Khan, Probert and Williams did not mention them.

There are clearly some substantial differences between the descriptions given by different authors of the cercaria of Echinoparyphium recurvatum, particularly concerning the protonephridial system. Some of these discrepancies are probably due to variation within this highly cosmopolitan species. Others are possibly accountable for by the different interpretations of different authors working on material which is notoriously difficult to study. By no means all of these workers have demonstrated that the cercariae under examination will develop into adults of the well-defined species Echinoparyphium recurvatum, and the actual extent of variability of cercarial structures within this species must therefore remain confused.

It is also evident that there is great variability in body size, in internal organs and even some variation in the extent of the vitellaria of E. recurvatum. Tubangui (1932) found E. recurvatum in domestic ducks in the Phillippines. His specimens differed in the size of its various organs and its eggs from those described by von Linstow (1873) and Dietz (1910). Yamaguti

(1938) reported E. recurvatum in Japan from Scolopax rusticola, and he considered his specimens to be larger than others previously described. Later Yamaguti (1971) gave a range for the body size of E. recurvatum of 1.9 - 7.3 x 0.4 - 0.85 mm. The specimens obtained experimentally in the present study fall within this size range and in addition the anterior extension of vitelline follicles originated either a short distance behind or immediately behind the acetabulum.

Verma (1936) described a new variety, Echinoparyphium recurvatum. var. indiana in a common snipe and brahmany duck from India. He distinguished his variety from typical E. recurvatum mainly by its much larger cirrus sac which measured 0.42 mm instead of 0.24 - 0.25 mm as in typical E. recurvatum). Verma also stated that the cirrus sac reached to near the posterior margin of the testes. In typical specimens of E. recurvatum, the posterior end of the cirrus sac usually extended to about the middle of the acetabulum. The position of the cirrus sac anterior or antero-dorsal to the acetabulum is a diagnostic character of the genus. Verma did not give complete details of this species because he had found another similar species in one of the snipes, bearing 47 spines instead of 45. It is clear that the great extension would probably be to the anterior margin of the anterior testis. Even so it is likely that Verma was dealing with more than one echinostome species rather than E. recurvatum alone.

Yamaguti (1939) reported Echinoparyphium recurvatum var. vanelli from the small intestine of Vanellus vanellus in Japan. He stated that it differed from typical E. recurvatum (von Linstow, 1873) because in a few specimens the vitelline follicles reached as far as the posterior end of the acetabulum while in von Linstow's specimens they never reached that level. As already pointed out the character of the vitellaria is variable within the present species and such minor discrepancies probably represent intraspecific variation and should not be used for diagnosing new varieties. Subsequently E.r. var. vanelli should be considered a synonym of E. recurvatum von Linstow (1873).

Many authors, including Tubangui, 1932; Beaver, 1937; Dollfus, 1953; Yamaguti, 1958; Nasir, 1960; Lie, 1963 and Nasir and Diaz, 1968 have expressed the opinion that the number size and arrangement of the collar spines, are the most important characters in distinguishing between closely related forms of echinostome. According to Skrjabin (1956), the subspecies Echinoparyphium recurvatum var. cerci described by Oschmarin (1956) from Cercus melanoleucos is also adorned with 45 spines. According to Yamaguti (1971), the body measurements given by Oschmarin fall within the range for E. recurvatum. In the writer's opinion, the creation of a subspecies based on a single specimen of a very variable species is unsound. Therefore this subspecies E. recurvatum var cerci Oschmarin (1956) is considered as a synonym of E. recurvatum von Linstow (1873).

The validity of these three varieties has previously been questioned by Beverly-Burton (1960).

Echinoparyphium recurvatum (von Linstow, 1873) has also been reported from Britain by Owen (1951) in the domestic ducks, Cairina moschata and Anas platyrhyncha dom., Soliman (1955) in the Khaki Campbell duck and Muscovy ducks and Beverly-Burton (196.) in Anas p. platyrhyncha and Aythya fuligula.

Cercaria echinostoma III

Only one out of a sample of 47 Lymnaea stagnalis taken from Wintersett Lake during the summer of 1973 was infested with Cercaria echinostoma III.

The cercariae are shed in moderate numbers throughout the day. They swim vigorously, lashing the tail violently and they swim near the bottom, around the edge, of the vessel. When swimming ceases they sink to the bottom and crawl rapidly using their suckers, before resuming swimming. The cercariae after 24 hours are found at the bottom and show only very slow movements of the body and tail until they die.

Description (Plate 23, Figs. 1-3 and 5)

Body elongate, oval, tapering at anterior end, with a constriction behind the collar, and very contractile. Body surface covered with small spines; cuticle thick, devoid of spines and composed of fine granular material. Collar well-developed and armed with rows of 38 spines; of these 6 form corner spines, 3 oral and 3 aboral on each side of pharynx, 2 groups of 6 lateral spines arranged in rows, and 14 dorsal spines present in 2 alternating rows. Tail larger than body, attached slightly subterminally, capable of great degree of contraction and very muscular, with two bands of well-developed longitudinal muscles arising from proximal part and passing almost entire length of tail, each band comprising 8-12 muscle-fibres. Circular muscles arranged in pairs orientated transversely and forming a slight ridge; each ridge formed by 7-8 pairs of muscle-fibres, extending almost its whole length. Tail non-spinose and without fin-fold.

Oral sucker smaller than acetabulum, situated slightly subterminally. Mouth circular; prepharynx followed directly by a relatively small muscular pharynx, leading into long oesophagus. Oesophagus divided just anterior to acetabulum, forming two prominent caeca extending to posterior end of body. Both oesophagus and caeca filled with granular material and additionally containing small elongate vesicle-like structures of varying shape.

Acetabulum protrusible, well-developed and nearly circular in outline; located posterior to middle of body and encircled by a muscular ring.

Anterior margin of body with 5 pairs of small apertures, each with internal duct-like extensions - presumably ducts of penetration gland cells. Region of body between posterior level of pharynx and posterior end of body occupied by excretory bladder surrounded by large cystogenous gland-cells with coarse, granular contents. Two groups of refractile granules located either side of pharynx. No trace of genital primordium observed.

Excretory bladder divided into two chambers; a large rounded posterior chamber at base of tail opening to exterior by a small dorsal excretory pore anterior to base of tail and a small transversely elongate anterior chamber. The two primary excretory ducts arising from anterior chamber. Ducts passing anteriorly, dilated considerably lateral to acetabulum to enclose numerous refractile granules, then continuing to posterior level of oral sucker, there forming a loop. Secondary excretory ducts passing posteriorly to equatorial level of posterior chamber before dividing into anterior and posterior collecting ducts; secondary ducts containing ciliary patches along entire length. Connection of flame cells with capillaries not discerned owing to density of cystogenous gland-cells. Fifty-one flame cells observed on each side. Caudal excretory duct forks into two branches about one third along length of tail. Flame cell formula not known.

Redia (Plate 23 Fig. 5)

The rediae were numerous in the digestive gland of Lymnaea stagnalis. They are elongate and narrower at their anterior and posterior extremities. The body of the redia exhibits some movement as well as contractions. Anteriorly there is a well-developed collar and immediately behind the collar on one side the birth pore is located. The large pharynx is very muscular and protrusible, communicating with a short sac-like intestine which extends only a short distance behind the level of the collar and which contains granular material, probably from the digestive gland of the host. The locomotory appendages are situated two-thirds of the length along the body. The body of the redia contains numerous germinal masses and cercariae at different stages of development, including 8-12 fully mature cercariae.

Infection of the second intermediate host

In order to determine the second intermediate host of Cercaria echinostoma III, various species of freshwater snails (Bithynia tentaculata, Physa fontinalis, Lymnaea stagnalis, L. peregor, Planorbis corneus, P. planorbis), tadpoles of Bufo bufo, guppies and sticklebacks were exposed for 24 hr. in groups of five to between 50 and 80 cercariae in a glass vessel containing tap water. The sticklebacks were collected from a source where neither L. stagnalis nor Cercaria echinostome III has been found, the guppies and the tadpoles were reared in the laboratory.

Penetration and encystment were effected in all the gastropods and the cysts were found in the kidney. The number of cysts found in P. fontinalis was much greater than in the other species suggesting that it was possibly the most suitable secondary intermediate host. Three tail-less and moribund cercaria were recovered from the abdominal cavity of the tadpoles but no encysted metacercariae were found. In the guppies and sticklebacks no traces either of cysts or of cercariae were seen.

In further experiments approximately twelve 15-day-old metacercarial cysts from P. fontinalis were fed to three 7-day-old chicks, four 45-day-old mice, 2 pigeons approximately 6 months old and 2 canaries, all laboratory bred except the canaries were purchased commercially. The faeces of these animals were examined daily for trematodes eggs. After 14 days 2 trematodes eggs were found in the faeces of one canary. All the experimental animals were then killed and examined but no trematodes were found.

The single snail infected with C. echinostome III died soon after the experiments described above. Further collections were made during 1973, 1974, 1975 and the beginning of 1976, but no other snails infected with this species were found and it was not possible to elucidate the complete life cycle.

7-day-old Metacercaria (Plate 23 Fig. 6)

The cysts are rounded and composed of two layers, an outer fine and transparent layer and an inner opaque layer. The metacercaria is folded, occupying the entire cyst. The oral sucker, acetabulum and pharynx are all

larger than in the cercaria. The spines become more clearly visible, the primary excretory ducts and refractile granules appear to be more prominent and the ciliary patches are more active than in the cercaria. The oesophagus and caeca contain less material than the cercaria. No trace of cytogenous gland-cells was observed.

Measurements of Cercaria echinostoma III from Lymnaea stagnalis

Body	0.550 (0.518 - 0.588) long x 0.196 (0.182 - 0.210) wide
Tail	0.740 (0.700 - 0.774) long x 0.074 (0.070 - 0.084) wide
Oral sucker	0.048 (0.045 - 0.049) long x 0.053 (0.049 - 0.060) wide
Acetabulum	0.082 (0.079 - 0.087) long x 0.085 (0.079 - 0.087) wide
Prepharynx	0.015 (0.015 - 0.019) long
Pharynx	0.023 (0.023 - 0.023) long x 0.020 (0.019 - 0.022) wide
Oesophagus	0.198 (0.182 - 0.297) long x 0.019 (0.015 - 0.022) wide
Preacetabular extent	0.300 (0.285 - 0.323) long
Postacetabular extent	0.176 (0.155 - 0.190) long
Redia	2.182 (1.709 - 2.630) long x 0.451 (0.394 - 0.473) wide
Pharynx	0.164 (0.114 - 0.235) long x 0.147 (0.087 - 0.228) wide

Discussion

Cercaria echinostome III is closely related to the cercaria of Echinostoma nudicaudatum Nasir, 1960 and C. deficipinnatum Khan, 1960a. These two forms are inseparable from C. echinostoma III in certain characters, such as contents and distribution of the cystogenous gland-cells, localization of the refractile granules in the main excretory ducts, extension and division of the caudal excretory duct, digestive system and development within a rediae with a short sac-like intestine. However, inthe cercaria of E. nudicaudatum and C. deficipinnatum there are anterior and posterior excretory loops, 37 collar spines, including sets of 5 corner spines, the body and tail are provided with long hair-like projections and the number of flame cells is smaller.

Brown (1926) reported several species of echinostome cercaria from Birmingham and Leeds, namely Cercaria echinata (Siebold, 1837) in Lymnaea stagnalis; C. granulosa in L. pereger and C. iquinospinosa in L. stagnalis. The former

can be eliminated as according to Brown it has a larger body, oral sucker and acetabulum, 37 collar spines, including 4 corner spines on each side of the pharynx, and there are anterior and posterior excretory loops.

Referring to Brown's description of the two latter species certain differences between each of them and C. echinostoma III can be recognized. The main ones are described below. Cercaria granulosa has a smaller body and tail, no caudal excretory duct, only 24 flame cells and possesses of 39 feebly developed spines including 4 corner spines. C. equinospinosa has a smaller body, oral sucker and acetabulum; the tail is less than the half as long as that of C. echinostoma III. It possesses 37 collar spines.

This species is regarded as new and named Cercaria echinostoma III.

Cercaria magnacauda I

In spring 1973 a collection of 45 specimens of Planorbis planorbis was made from Walton Park. Nine were infected by an echinostome cercaria with a large tail. Further collections of P. planorbis were made during 1974 and 1975 but none were found producing this cercaria.

The cercariae are released throughout the day, at a rate of about 35 to 40 per day. The swimming movements of the cercariae are characteristically in the form of a figure "8" or "S".

Description (Plate 24 Figs.1-4)

Body completely spinose, with orange pigment distributed posterior to oral sucker. Two papillae each with a hair-like projection situated at anterior end, one on either side of oral sucker. Collar of 19 spines comprising11 in continuous series dorsal and lateral to oral sucker and 4 corner spines set on each side ventral to oral sucker. Tail almost 9 times length of body, covered with spines and containing many dark granules and brilliant green pigment. Circular and longitudinal muscles (24 - 26) extend along entire tail.

Oral sucker subterminal. Prepharynx prominent. Pharynx muscular and elongate, with orange pigment in lumen. Oesophagus divides in front of acetabulum to form 2 intestinal caeca which extend to posterior limit of body. Oesophagus and caeca full of granular material.

Acetabulum situated just posterior to middle of body, unarmed. Cystogenous gland-cells throughout body but fewer anterior to posterior limit of pharynx, contents green and rhabdiliform. No penetration gland-cells or ducts visible. Rudiments of gonads present as two masses of indifferentiated cells, one anterior and one posterior to ventral sucker.

Excretory bladder 3-chambered in form of 1 accessory chamber anterior and 1 posterior (in tail) to principal chamber and communicating with it via short narrow ducts. Principal chamber with excretory pore slightly anterior to body-tail junction. On each side of the body a primary excretory duct arises from anterior accessory chamber and follows a convoluted course forwards to

level of pharynx; between the acetabulum and pharynx this duct becomes dilated and is filled with many layered refractile granules. Each duct loops back at pharynx level and gives rise to a secondary duct which continues posteriorly to the level of excretory bladder and which is ciliated between the level of acetabulum and bladder; the secondary duct loops forwards again as a tertiary duct and gives rise at level of acetabulum to antero- and postero-lateral canals, each connected to the ducts of flame cells. Excretory bladder of tail with short blind-ending canal. Flame cell formula: $2[2 + 2 + 2) + (2 + 2 + 2)] = 24$.

Redia (plate 24, Fig. 6)

The rediae show active bending movements after being extracted from the interstitial spaces of the host hepatopancreas. The mouth is terminal and the muscular pharynx is well-developed. The elongate sack-shaped intestine with dark brown granular contents extends to the region of the locomotory appendages. The neck is undivided and the birth pore is situated immediately behind it. There are between 7 and 10 cercariae present in various stages of development. The 12 flame cells are arranged in triads, but other details of the protonephridial system were not visible.

Metacercaria (Plate 24, Fig. 5)

Twenty five guppies raised in the Laboratory were used as experimental secondary hosts for Cercaria magnacauda I. On 3 occasions fish were exposed to cercariae while being observed under the binocular microscope, but at no time were cercariae seen to enter either the mouth or the branchial cavity through the opercular slit. Nevertheless, metacercarial cysts were found in the branchial filaments of several fish exposed to cercariae for 24 hours.

The cysts are ovoid and each is enveloped by a thin wall. Each metacercaria is rolled up and occupies the majority of the space within the cyst displaying the following characteristics (Plate 24; Fig. 5)

The oral sucker is transversely elongate, slightly smaller than the acetabulum. The number and arrangement of collar spines are identical with those of the cercaria. Orange pigment is distributed throughout almost the whole body and the digestive system is more clearly visible and with darker granular content than in the

cercaria. The primary excretory ducts are dilated and in living specimens contain refractile granules moving freely within. The excretory bladder is a simple chamber containing refractile granules with 2 pairs of flame cells visible on each side of the bladder.

Attempts to infect Vertebrate host

Brown (1931) reported the occurrence of encysted metacercariae of Cercaria oscillatoria in the same host individuals of the gastropod Planorbis planorbis which were giving rise to cercariae. Similarly, Johnston and Angel (1941) encountered the supposed metacercariae of Petasiger australis in two species of the gastropod genus Amerianna maintained under experimental conditions in the laboratory. These authors suggested, however, that metacercarial infection of snails was not a normal event in this species.

Khan (1960) and Nasir (1962) exposed individuals of several snail species, including Planorbis planorbis and P. carinatus to a number of different "magnacauda" cercariae but did not subsequently find any of the corresponding metacercariae in the snails. Khan came to the conclusion that the involvement of snails in this was was "highly improbable".

Several species of fresh water gastropods - Planorbis planorbis, P. carinatus, P. vortex, P. corneus, Physa fontinalis, Lymnaea pereger and L. stagnalis - some reared from eggs deposited in laboratory aquaria and others brought from different localities where the cercariae described above were known not to occur - were placed in vessels of water with snails emitting Cercaria magnacauda I. After 24, 48 and 72 hours, the molluscs were examined, but no metacercariae were found.

Two of the snails used in the above experiments were isolated (still emitting cercariae) in small vessels, one without water and the other containing damp cotton wool to which was added more water from time to time to avoid desiccation. The snail in the waterless vessel was dissected after 24 hr, and the other after 72 hr; both were free of metacercariae.

These results corroborate those obtained by Khan (1960) and Nasir (1962).

Groups of approximately 25 cysts aged 10-25 days and extracted from the

branchial filaments of experimentally infected guppies were orally introduced with a fine pipette to the following animals: 2 6 day-old Gallus domesticus, 3 12-day-old Anas platyrhyncha platyrhyncha, 2 60-day-old Columbia livia, 2 canaries, 4 21-day-old Mus musculus, 3 60-day-old Rattus norvegicus.

The faeces of the animals were examined for digenean eggs daily for 15 days. None was found.

After 15 days the animals were killed and a search made for flukes. None was found.

Measurements of Cercaria magnacauda I from Planorbis planorbis

Body	0.205 (0.193 - 0.209) long x 0.088 (0.076 - 0.099) wide
Tail	1.755 (1.680 - 1.890) long x 0.122 (0.098 - 0.140) wide
Oral sucker	0.036 (0.034 - 0.038) long x 0.036 (0.034 - 0.041) wide
Acetabulum	0.042 (0.038 - 0.045) long x 0.054 (0.053 - 0.057) wide
Prepharynx	0.009 (0.007 - 0.011) long
Pharynx	0.017 (0.015 - 0.019) long x 0.014 (0.011 - 0.015) wide
Oesophagus	
Preacetabular extent	0.111 (0.102 - 0.112) long
Postacetabular extent	0.057 (0.053 - 0.060) long
Redia	0.775 (0.630 - 1.050) long x 0.218 (0.182 - 0.238) wide
Pharynx	0.052 (0.049 - 0.057) long x 0.050 (0.045 - 0.053) wide

Discussion

Byrd and Reiber (1940) created a new sub-group "Magnacauda" to accommodate long-tailed echinostome cercariae which seemed to be different from all other members of the echinostome group. They are:

Cercaria magnacauda O'Roke, 1917, from Helisoma trivolvis.

Cercaria caudadena Faust, 1921, from Planorbis pfeifferi.

Cercaria cita, (reported by Miller in 1925 but not described until 1929), from several species of Planorbis.

Cercaria oscillatoria Brown, 1931, from Planorbis carinatus.

Cercaria paucispina Faust and Hoffman, 1934 (syn. Cercaria IV Marin, 1928), from Biomphalaria glabrata.

Cercaria of Petasiger nitidus as described by Beaver, 1939, from Helisoma antrosum percarinatus and H. campanulatum smithii (Brooks, 1945-1948, obtained these cercariae in several species of the genus Helisoma.

Cercaria oedematocauda Byrd and Reiber, 1940, from Helisoma trivolvis.

Cercaria gigantura Johnston and Angel, 1941 (the supposed larva of Petasiger australis), from Amerianna pyramidata.

Cercaria gigantura var. grandis Johnston and Simpson, 1944, from Amerianna pyramidata.

Cercaria chandleri Abdel-Malek, 1952, from Helisoma corpulento [= larva of Petasiger chandleri Abdel-Malek, 1953].

Cercaria amelli Hedrick, 1943, from Amnicola limosa.

Cercaria limosae Hedrick, 1943, from A. limosa.

Cercaria illecebrosa, Lee and Seo, 1959, from A. limosa.

Cercaria hamptonensis Khan, 1960a, from Planorbis planorbis.

Cercaria thamesensis Khan, 1960a, from P. planorbis.

Cercaria reynoldsi Etges, 1961, from Helisoma anceps.

Cercaria rashidi Nasir, 1962, from P. carinatus.

Cercaria titfordensis Nasir, 1962, from P. carinatus.

Cercaria rithonensis Mukherjee, 1963, from Gyraulus convexiusculus.

Cercaria of Stephanoprora denticulata (Rudolphi, 1802) Odhner, 1910 (Nasir and Scorza, 1968), from Biomphalaria glabrata.

Cercaria of Petasiger novemdecim Lutz (1928 (Nasir, Gonzalez and Diaz, 1972) from Biomphalaria glabrata.

Cercaria pyrgophspiralis Nasir and Diaz, 1973, from Pyrgophorus cf. spiralis.

Cercaria amarillis Nasir and Diaz, 1973, from Armigenus kuhnianus.

Of the above only C. paucispina and C. rithorensis resemble C. magnacuada I in possessing 19 collar spines and cystogenous gland-cells with rhabditiform contents. Cercaria paucispina and C. rithorensis are distinguishable from C. magnacauda I because in them the intestinal caeca do not extend behind the

acetabulum, while in C. magnacauda I they reach the posterior end of the body. Unfortunately, however, information is lacking on structural details of the protonephridial system in C. paucispina and C. rithorensis except for the occurrence in them of anterior loops in the ducts resembling those of C. magnacauda I.

The cercaria of Petasiger nitidus and P. novemdecim, as well as Cercaria gigantura var. grandis and Cercaria amarillis are all distinguishable from C. magnacauda I on the basis of their flame cell formulae.

Various species of cercariae belonging to the sub-group "Magnacauda" have been recorded from several species of Planorbis in England by Brown (1932) Khan (1960a) and Nasir (1962). They are C. oscillatoria from Cheshire, C. hamptonensis from the river Thames near Hampton Court, C. thamensis from the river Thames near Bushy Park, C. titfordensis from Titford Pool, in Birmingham and C. rashidi from Edgbaston Pool in Birmingham.

In Cercaria oscillatoria the total number of collar spines is not known and the number and arrangement of flame cells is also very poorly documented. Thus a comparison cannot be made using these criteria but certain characteristics, particularly the occurrence of 5 angled collar spines at each side of the pharynx and encystment in a mollusc host, serve to distinguish this species from C. magnacauda I described above.

Cercaria hamptonensis, C. thamensis, C. titfordensis and C. rashidi are indistinguishable from C. magnacauda I regarding the rhabditiform cystogenous gland structure, extensions of the intestinal caeca to the posterior end of the body, 4 angled spines on either side of the pharynx and in the use of several species of Planorbis as first intermediate hosts. Nevertheless diagnostic characteristics based on the total number of collar spines and the flame cell formula aid in separating C. magnacauda I from the above-mentioned cercariae. Thus C. hamptonensis and C. thamensis possess 20 collar spines, while C. magnacauda I is characterized by 19. Both C. titfordensis and C. rashidi possess a total of 36 flame-cells in triads as opposed to a total of 28 in pairs in C. magnacauda I.

As a result of the comparisons described above C. magnacauda I is considered to be a species not previously described.

Cercaria magnacauda II

Infected snails Bithynia tentaculata were collected from Newmillerdam Lake at intervals during 1973 and 1974. While B. tentaculata occurs at numerous locations Cercaria magnacauda II was found only at Newmillerdam. The rate of infection was between 3 and 5%.

Cercariae emerge from their hosts throughout the whole 24 hour period, with the greatest numbers occurring in the early hours of the morning. They each possess a short tail and are not easily seen by the naked eye; other members of the sub-group "Magnacauda", on the other hand, possess a tail which is relatively very large, making them readily visible to the naked eye.

The cercaria swims actively, describing a figure of "8", instead of an "S"-shape as in other echinostome cercariae.

Description (Plate 25 Figs.1-3)

Body lacking a collar of spines; cuticle not spinose but with hair-like projections of varying length distributed as follows: 7 on papillae anterior to oral sucker, 1 pair without papillae laterally at level of prepharynx, 5 pairs on papillae laterally between pharynx and posterior margin of acetabulum; region between mid-level of oral sucker and posterior margin of pharynx provided with many very short hair-like projections (see fig. 1). Body cuticle thick, appearing coarsely granular. Spineless tail 1.5 times as long as body; posterior end of tail with 3 pairs of large setae without papillae; tail musculature consisting of 16 - 20 bands of longitudinal muscles extending from proximal to distal end; tail contains numerous pigmented bodies with brown granules giving it a characteristic appearance. At base of tail are groups of anucleate cells with a fine, granular cytoplasm.

Pre-pharynx relatively large; pharynx muscular, and shorter than prepharynx. Oesophagus long dividing anterior to ventral sucker. Intestinal caeca extend almost to end of body. Walls of oesophagus and caeca very thin, with no visible contents, and their outlines difficult to observe.

Oral sucker terminal, its orifice edged with a circle of papillae without setae. Anterior to orifice is a semicircle of 10 small spines (N.B. not collar

spines). Acetabulum situated in posterior third of the body, its orifice edged with a row of 17-19 spines. Cystogenous gland-cells with rhabditiform content more abundant at lateral margin of body. At anterior margin of body are 4 apertures, apparently the external apertures of penetration gland ducts, connected at some point to the gland-cells but not visible owing to the darkness of the body. Genital primordia "C"-shaped, located to one side of acetabulum and consisting of masses of undifferentiated cells.

Excretory bladder 2-chambered; anterior chamber transversely elongate and communicating with the posterior (tail) chamber by a short neck. Posterior chamber adopts different shapes depending upon state of contraction and dilation of anterior chamber. Caudal excretory duct, consisting of a fine, blind tube, is connected to posterior tail chamber. Excretory pore situated at base of anterior chamber. Anterior excretory ducts arise from anterior chamber on both sides of the body (see fig. 2); they are dilated at level of acetabulum, and they continue towards the oral sucker, where they become narrower. At this level each duct forms a loop and continues as a pecondary excretory duct towards the acetabulum. It bifurcates posterior to acetabulum forming anterior and posterior collecting ducts, receiving capillaries of flame cells. Each primary excretory duct contain 20-27 irregular-shaped refractile granules which tend to be smaller in anterior part of duct. Flame cell formula:

$3\left[(3+3)+(3)\right]=18.$

<u>Redia</u> (plate 25 Fig.6)

Rediae are situated in the digestive gland of <u>Bithynia tentaculata</u>. The body of the mature redia contains brown granules in addition to small globules with very fine granular eontents. The mouth is terminal, opening posteriorly to a well-developed almost spherical pharynx followed by a large sack-shaped intestine extending to the anterior margin of the locomotory appendages and full of a brown, granular material. The birth pore is lateral, just behind the neck, which is undivided, and the body cavity contains 5 to 12 cercariae in different stages of development. The locomotory appendages are situated in the posterior half of the body. The flame cells are obscured by

the body contents, immature rediae not visible even in the colourless body of young rediae.

Infection of second intermediate host

Since it has been shown by Beaver (1939), Abdel-Malek (1953), Nasir and Scorza (1968) and Nasir, Gonzalez and Diaz (1972), among others that encystment of some magnacauda cercariae occurs in fish, some species of freshwater fish were exposed to infections as described below:

19 guppies and 14 3-spined sticklebacks were placed in water containing snails from which C. magnacauda II were being released. Observations using a low power binocular microscope demonstrated that the fish were attracted to the cercariae and actively ingested them. The fish were killed for examination at intervals of 1, 3 and 5 hr. following initial exposure and encysted metacercariae were found on the branchial filaments of all fish. All of the gills were involved and representative number on the 1st, 2nd, 3rd and 4th fills of 3 guppies are: 7, 9, 7, 9; 8, 9, 12, 6; 20, 11, 28, 12. In no case were the bodies or tails of cercariae found in any part of the alimentary canal.

Infections with metacercariae cysts were also produced experimentally in minnows, bullheads and stone loaches.

Metacercaria of 5 hours development (Plate 25, Fig. 4)

The cysts are ovoid in form (comprising a thin wall containing the metacercaria which is very motile. The content of the cystogenic gland-cells remains almost intact, giving the impression that they had not been used during the process of encystment. The 10 small spines on the oral sucker (not the collar spines) become more easily visible. The ventral sucker almost touches the excretory bladder which now is joined by a single chamber with some refractile granules moving freely in its lumen. The intestinal caeca could not be distinguished. Collar spines are still not discernible.

Metacercaria of 14 days' development

The cysts still retain their ovoid form. In the metacercaria there is a considerable increase in size of certain organs, including the oral sucker,

acetabulum and pharynx. The rudiments of the genitalia are now apparent as 2 cell masses, one above the other, posterior to the acetabulum. The cystogenous gland-cells have a diminished content and the rhaditiform bodies have become shorter. There is a prominent outfolding or swelling of the ventral body wall, sometimes located in the mid-line of the body, between the pharynx and the ventral sucker, sometimes displaced to either side. This outfolding was not observed in the cercariae or in 5-day-old metacercariae. The number of refractile granules in the primary excretory ducts becomes reduced apparently by the coalescing of 6 or 7 small granules.

A collar of 18 spines is present, including 2 angular ones on each side which are clearly separated from the rest of the group. No spines were visible in the region dorsal to the oral sucker, possibly because they were not yet developed.

Metacercaria of 20 days development (Plate 25 Fig. 5)

There is a well developed collar of 22 spines including 2 angular spines on each side. The cystogenous gland-cells have almost disappeared leaving only small granules which are apparently remnants of the rhabditiform bodies dispersed in some parts of the body. The refractile granules are closer together, concentrated around the periphery of the acetabulum. The metacercariae make only very slow movements.

Three hundred and thirty cysts of between 3 and 32 days development extracted from the branchial filaments of various freshwater fishes (guppies, bullheads, minnows and stone loaches) infected experimentally with cercaria magnacauda II were administered at the rate of 15 per host via a pipette to 4 pigeons, 6 ducklings, 6 chickens, 3 canaries and 3 mice. In no case was infection observed.

Measurements of Cercaria magnacauda II from Bithynia tentaculata

Body	0.132 (0.125 - 0.163) long x 0.069 (0.049 - 0.068) wide
Tail	0.161 (0.155 - 0.224) long x 0.035 (0.030 - 0.053) wide
Oral sucker	0.023 (0.022 - 0.026) long x 0.023 (0.022 - 0.026) wide
Acetabulum	0.026 (0.022 - 0.026) long x 0.024 (0.022 - 0.026) wide
Prepharynx	0.017 (0.015 - 0.019) long
Pharynx	0.012 (0.011 - 0.015) long x 0.011 (0.011 - 0.011) wide
Oesophagus	0.032 (0.026 - 0.041) long
Preacetabular extent	0L088 (0.083 - 0.121) long
Postacetabular extent	0.016 (0.015 - 0.022) long
Redia	0.610 (0.490 - 0.700) long x 0.246 (0.182 - 0.280) wide
Pharynx	0.102 (0.095 - 0.114) long x 0.108 (0.098 - 0.114) wide

Discussion

All described cercariae of the spineless magnacauda group of echinostomes are listed below:

Cercaria oematocauda Byrd and Reiber, 1940, Reelfoot Lake, U.S.A.

Cercaria ameeli Hedrick, 1943, Michigan, U.S.A.

Cercaria limosae Hedrick, 1943, Michigan, U.S.A.

Cercaria pyrgophspiralis Nasir and Diaz, 1973, Venezuela.

Cercaria oematocauda is inseparable from C. magnacauda II using as criteria the number and arrangement of the flame cells, the size of the pharynx and the presence of refractile granules in the primary excretory ducts. However, the length of the tail of the present specimens is 1.5 times the length of the body whereas in C. oematocauda the tail is 4 times longer than the body. In C. magnacauda II the intestinal caeca extend to the posterior end of the body whereas in C. oematocauda they reach only to the mid-level of the acetabulum. In addition the accessory excretory bladder which is located in the anterior part of the tail in C. magnacauda II, is not present in C. oematocauda. Finally in C. magnacauda II both suckers are adorned in spines and the genital primordia almost completely surround the acetabulum while in C. oematocauda neither of these characters is displayed.

In Cercaria ameeli and C. limosae the primary excretory ducts do not contain refractile granules and the flame cell formula is $2\ \overline{[(2 + 2 + 2 + 2 + 2)]} = 20$. In contract the present specimens contain 20 to 27 refractile granules in the primary excretory duct and the flame cell formula is $2\ \overline{[(3 + 3) + (3)]} = 18$.

The tail of Cercaria illecebrosa is 12 times longer than the body and this character can be utilized to separate this species from C. magnacauda II. But the existence of certain similarities between them merits detailed comparison.

Both cercariae have collar spines without discernible angular spines, and the collar spines become visible only after a certain period of encystment in the secondary host. The metacercaria of C. illecebrosa is characterized by the possession of 22 collar spines including 2 angular ones to each side of the pharynx.

In C. illecebrosa the primary excretory ducts do not contain refractile granules but they do so in the metacercaria, whereas refractile granules are present in each primary duct of C. magnacauda II.

The two species possess a row of 10 spines on the internal dorsal region of the oral sucker. They also have the same number of flame cells (18), but other details of the protonephridial system such as the secundary excretory ducts, their division and their ciliation are not known. Finally C. illecebrosa has 9 prominent penetration gland-cells but such structures were not visible in the present specimens.

Cercaria pyrgophspiralis differs from C. magnacauda II in the length of the tail, number of spines in both suckers, number and arrangement of flame cells and division of the secondary excretory ducts.

The Magnacauda cercariae, recorded in Britain are listed above (Page 130-131) All except C. oscillatoria differ from C. magnacauda II in the definitive number of collar spines and angulars, number of flame cells and length of tail. In the latter species details of collar spines and flame cell systems are not known but encystment occurs in gastropods of the same species as those in which the cercariae are produced.

Cercaria magnacauda II can be separated from C. magnacauda I encountered during the present investigation by the following characters.

I. Cercaria magnacauda II has no collar spines, although they appear in metacercariae of 18 to 20 days development, but their number and arrangement are different.

II. In the metacercaria of Cercariae magnacauda II, the number of spines is 22 including 2 angulars on each side whereas in the metacercariae of Cercaria magnacauda I there are 19 spines including 4 angulars on each side.

III. The flame cell formula in C. magnacauda II is $2\,[(3 + 3) + (3)] = 18$ while in C. magnacauda I it is $2\,[(2 + 2 + 2 + 2 + 2) + (2 + 2)] = 28$.

IV. In C. magnacauda II the tail is 1.5 times longer than the body whereas in C. magnacauda I it is 9 times longer.

The differences described above between Cercaria magnacauda II and all other known magnacauda forms are considered of sufficient magnitude to warrant the establishment of a new species here named Cercaria magnacauda II.

Xiphidiocercous cercariae

The cercariae referred to the Xiphidiocercariae (Diesing, 1855) were subdivided by Luhe (1909) into four groups; Cercaria microcotylae, C. virgulae, C. ornatae and C. armatae. They are defined as distome cercariae and are characterised by a slender tail, a stylet and penetration gland cells but lack eye spots.

Although later workers have found a similar stylet structure in some of the Microcercous and Macrocercous cercariae, the stylet in the Xiphidiocercaria. is however different from those in the Macrocercous and Microcercous cercariae. The stylets of the latter two groups are more complex, ending with several points or possessing lateral wings. The stylets of Xiphidiocercaria usually have a pointed anterior end and some may have shoulders their walls may be thin or thick and a basal bulb may or may not be present.

The absence of eyespots in the Xiphidiocercaria is not a consistent feature. Several stylet cercariae have been described as having a pair of eye spots. These species are parasites of freshwater gastropods and clams (family Sphaeridae) and develop in rediae. Llewelyn(1957) created a new subgroup named Cercaria ophthalmicae for these forms.

An additional group 'Spelotrema' of certain marine cercariae was added to the Xiphidiocercariae by Lehour (1911).

Luhe (1909) classified the Xiphidiocercariae on the basic similarities to four groups given below but only relatively small numbers of cercariae fall precisely into any of these groups.

1. Microcotylae - small-sized body (not exceeding 0.2 mm)
   acetabulum smaller than oral sucker
   2 to 4 penetration gland cells
   small, bicornuate excretory bladder
   development occurs in the sporocyst or rediae
2. Virgulae - presence of virgula organ in the oral sucker
   three to six penetration gland cells
   V-shaped excretory bladder

3. Ornatae - slender tail with a fin-fold
4 to 6 penetration gland cells
oval or rectangular shaped excretory bladder with wide cornua

4. Armatae - body length over 0.25 mm
straight and slender tail without a fin-fold, not longer than the body
acetabulum smaller than oral sucker and situated behind the mid-line of the body
Y-shaped excretory bladder

Cort (1915) created a new group 'Cercaria polyadena' belonging to the Xiphidiocercaria for the two North American species Cercaria polyadena and Cercaria isocotylea because they share the following distinct characters:

1. Development in a gastropod, elongated sac-shaped sporocysts,
2. Tail slender and less than the body length except when very much extended,
3. Acetabulum behind the mid-line of the body and smaller than the oral sucker,
4. Stylet about 0.030 mm in length, six times as long as broad and with thickening one-third of the distance from the point to the base,
5. Penetration gland cells, six or more, one each side between the acetabulum and the pharynx
6. Excretory bladder bicornuate
7. Very short prepharynx present, oesophagus when developed, of short to medium length, intestinal caeca when present reaching to the posterior end of the body

Cort also placed the two European species - Cercaria limnaea ovatae von Linstow and Cercaria secunda Ssinitzin in the Cercaria polyadena group.

Later, Sewell (1922) considered that the body size of the Polyadenous cercariae (Cort, 1915) was not sufficiently different from that of the Xiphidiocercaria armatae (Luhe, 1909) and he suggested the Polyadenous cercariae

should belong to a subgroup of the Armatae group. Sewell (1922) also introduced another subgroup 'Daswan' for the two species C. indicae X and C. indicae LIII and consequently the Armatae were divided into two subgroups - Polyadenous cercaria Cort, 1915 and the Daswan cercariae Sewell, 1922.

Faust (1924a, b) reclassified the Xiphidiocercaria according to the flame cell formula and added two more new subgroups to the Armatae group, first Tenuispina, for Cercaria tenuispina Luhe, the larva of Opisthoglyphe ranae (Frohlich, 1719) Looss, 1907 and Cercaria stylobuccalis Faust, 1922 and second Hemilophura for C. hemilophura Cort, 1914.

Porter (1938) using Faust's work (1929) as a basis grouped several South African cercariae of the Armatae group according to their family, Dicrocoeliidae Looss (1907), Plagiorchiidae Luhe (1901) and Brachycoeliidae Johnston (1912).

Brooks (1943) subdivided the Polyadena group into a subgroup Conniae including Cercaria conniae and several other Xiphidiocercariae which have in common a javelin-shaped stylet without a basal bulb.

Vercammen-Grandjean (1960) classified the Xiphidiocercaria using as criteria the excretory system together with other characters as the presence of virgula organ, fin-fold and development of the intestinal caeca. He divided it into three main groups; Micronephridiae, Heteronephridiae and Orthonephridiae.

Grabda-Kazubska (1972) prepared a new definition of the group Xiphidiocercaria Armatae according to the detailed morphology of the cercariae. She considered that the only significant feature differentiating between the groups Armatae and Ornatae is a small fin-fold at the end of the tail, therefore she included the group 'Prima' of the Xiphidiocercaria Ornatae in the Xiphidiocercariae Armatae. She created four types in the group Armatae as follows:

1. Cercariae of the Haematoloechus type
   (1) Body length not exceeding 100-200 µm
   (2) Tail shorter than the body with the dorso-ventral fin-fold at the distal apex
   (3) Caudal pockets poorly developed or absent

(4) Ventral sucker smaller than oral sucker, situated somewhat posteriorly to middle of body

(5) Stylet slender, complete, with slightly marked transverse thickening.

(6) 4 to 6 penetration gland cells with differentiated cytoplasm

(7) Alimentary system weakly developed, usually the part anterior to the bifurcation of the intestinal coeca may be seen.

(8) Primordia of the reproductive system little differentiated

(9) Small excretory vesicle situated behind the ventral sucker

(10) Lateral branches of excretory vesicles are somewhat longer than the median stem. Main collecting ducts enter the branches of the vesicle terminally.

(11) Sporocysts small, oval or rounded, contain few cercariae

(12) Cercariae penetrate larval mosquitoes, damselflies and dragonflies.

2. Cercariae of the Plagiorchis type

(1) Small to medium in size, usually 200-300 um long

(2) Tail shorter than the body, without a fin fold.

(3) Caudal pockets well developed with spines inside.

(4) Ventral sucker usually smaller than oral; situated in the middle of the body.

(5) Stylet complete with conspicuous transverse thickening at the base of the blade, sometimes dilated posteriorly.

(6) Large penetration glands clearly differentiated into two groups by their chemical composition and appearance.

(7) Number of glands is constant in a species, mostly 6 to 8 pairs.

(8) Cystogenous glands fill almost the whole body.

(9) Alimentary tract weakly developed, usually it is apparent only as far as the bifurcation of intestinal caeca.

(10) Primordia of the reproductive system are composed of only slightly differentiated groups of cells situated around the

ventral sucker,

(11) Small excretory vesicle with branches shorter or equal to the median stem part; situated behind the ventral sucker,

(12) Main collecting ducts enter lateral branches of the vesicle terminally or somewhat subterminally,

(13) Cercariae develop in elongated sporocysts usually in great numbers,

(14) They emerge from the snail during the whole day,

(15) They penetrate larval insects,

3. Cercariae of the Opisthioglyphe type

(1) Cercaria of medium or large size, 200-500 µm,

(2) Tail shorter than the body or equal to it,

(3) Caudal pockets usually well developed with spines inside,

(4) Suckers almost equal in size,

(5) Stylet simple, without transverse thickening, incomplete posteriorly,

(6) Penetration glands, 4 to 12 pairs, not apparently differentiated,

(7) Number of glands not constant, may vary within the species or even on opposite sides of the same specimen,

(8) Cystogenous glands usually concentrated in the mid-region of the body,

(9) Intestine and primordia of the genital system usually well developed,

(10) Excretory vesicle with short or fairly long lateral branches, Sometimes the lateral branches of the vesicle extend anterior to the posterior border of the ventral sucker,

(11) Main collecting ducts enter the lateral branches terminally or subterminally,

(12) Cercariae develop in sac-like, elongated or rounded sporocysts,

(13) Usually they emerge from the snail in the early morning.

(14) Most part of the free-living time they spent in a resting position on the ground or motionless in the water.

(15) Vibration of the water stimulates them to swimming.

(16) They penetrate tadpoles and adult amphibians.

4. Cercariae of the Ochetosoma type

(1) The size and the proportions of the body and suckers, structure of stylet and penetration glands are similar to those in the Opisthioglyphe type. The biological features are also similar but differ from the Opisthioglyphe type by the shape and dimensions of the excretory vesicle.

(2) The lateral branches of the vesicle are very long extending beyond the anterior border of the ventral sucker and sometimes almost touching in front of it.

(3) Main collecting ducts enter these branches in their midway along their length.

(4) Cercariae develop in sac-like sporocysts, penetrate tadpoles and adult amphibians.

Cercariae Microcotylea was created by Luhe (1909) to accommodate very small Xiphidiocercariae with the following characters -

(1) Body length less than 0.2 mm

(2) A long undivided tail

(3) Acetabulum smaller than the oral sucker situated posterior to the mid-line of the body.

(4) 2 to 4 penetration gland-cells situated anteriorly or laterally to the acetabulum

(5) An undeveloped alimentary system, usually represented by a short prepharynx and small pharynx

(6) Small bicornual excretory bladder

(7) Development in oval or rounded sporocysts

Cort (1915) improved on the characterization given by Luhe (1909). Sewell (1922) divided the Cercariae microcotylae into four further subgroups:

(1) Cellulosa - with only one pair of penetration gland cells on each side; triradiate excretory bladder and flame cell formula $2\left[(1+1)+(1+1)\right]=8$; digestive system comprising prepharynx, pharynx, short intestinal caeca present or absent; development in oval or rounded sporocysts.

(2) Pusilla - 3 to 4 pairs of penetration gland-cells; digestive system similar to cellulosa group; flame cell formula $2\left[(1+1+1)+(1+1+1)\right]=12$; development in small rounded or elongated sporocyst

(3) Vesiculosa - the members of this group are closely similar to those of the Pusilla group. The main difference between them concerns the number and arrangement of the penetration gland cells.
In the vesiculosa the 4 pairs of penetration gland-cells are arranged in two separate groups, three cells situated laterally to the acetabulum and another single cell

located in front of the acetabulum.

excretory bladder spherical or pyriform in outline.

(4) Parapusilla - Their characteristics resemble the Pusilla group except for the presence of a complete digestive system and a more advanced development of the genital system.

Porter (1938) followed a pattern based on the development of the digestive system similar to that which Sewell (1922) used to separate the groups of Pusilla and Parapusilla and she added two new subgroups, Paracellulosa and Paravesiculosa which have more fully developed digestive systems than the Cellulosa and Vesiculosa groups.

Dubois (1929) created a new subgroup "Helvetica" in the Microcotylae group. The members of this group have a more complex excretory system than others with the flame cell formula: $2\,[(2 + 2 + 2) + (2 + 2 + 2)] = 24$.

Wikgren (1956) found two Microcotylae cercariae, Cercaria cordifomis Wesenberg-Lund (1934)and Cercaria fennica II. The former belongs to the subgroup Pusilla (Sewell, 1922) but he could not place the second one in any of the existing subgroups. It possessed a single pair of penetration gland-cells and he consequently created a new subgroup named "Monoadena" for Cercaria lophocauda Faust 1930 and C. fennica II.

Fillippi (1857) described Cercaria virgula which is characterized by having bilateral, glandular, flask-like organs located in the region of the oral sucker. Luhe (1909) created the Virgulae group to accommodate those Xiphidiocercariae with this organ and Sewell (1922) subdivided the group into two subgroups "Virgula" and"Paravirgula" according to the development of the digestive system.

I have adopted Luhe's (1909) classification of the Xiphidiocercaria. Members of Microcotylae, Virgulae and Armatae groups have been found in this study.

Cercaria microcotylea I

Bithynia tentaculata, collected at Kirkstall Power Station (Leeds-Liverpool canal), Wintersett Lake and Newmillerdam Lake in August, November and December, 1973, 1974 and 1975 were found to be infected with a very small microcotylea xiphidiocercaria. The percentage infected in each locality was very similar varying from 2.2 to 2.6%.

The cercariae emerge from the snail throughout the hours of day light. After swimming for some time they sink to the bottom of the container where they aggregate in large numbers and crawl actively using their suckers. They remain alive in the container for about 18-24 hr.

Description. Body elongate and very contractile; surface covered with small spines and bearing 6 papillae with hair-like structures on each side. Tail subterminal, its lumen occupied by numerous small granules and some irregular bodies with fine granular contents distributed along its length. Tail bearing, on each side of apex, a papilla with a hair-like structure similar to those found on the body cuticle. (see Plate 26, Fig. 4)

Oral sucker large, almost circular and occupying anterior part of body. Stylet small, with basal bulb, lateral knob-like projections and pointed terminal portion. Acetabulum rounded, spinose, smaller than oral sucker and situated a little posterior to mid-point of body. Cystogenous gland-cells numerous, with thick granular contents and distributed throughout the body with concentrations around the acetabulum and posterior half of oral sucker.

Mouth situated at centre of oral sucker; prepharynx absent; pharynx isodiametric. Oesophagus long, dividing into short caeca just anterior to acetabulum; caeca extending to just beyond anterior margin of acetabulum.

Penetration gland-cells in 2 groups of 3 trilobed cells, one group on each side of body, situated antero-lateral to acetabulum. Anterior pair with thick granular cytoplasm, middle and posterior pairs with fine granular contents. Ducts opening on anterior margin of body. (see Plate 26, Fig. 3).

Genital primordia represented by 2 masses of undifferentiated cells located posterolateral to acetabulum.

Excretory bladder V-shaped and thick walled. Principal excretory ducts originating from apex of each branch of bladder; following a sinuous course and dividing into anterior and posterior collecting ducts each with 3 pairs of flame cells. Excretory pore situated at base of excretory bladder. Flame cell formula $2\,[(2 + 2 + 2) + (2 + 2 + 2)] = 24$.

Sporocyst (Plate 26, Fig. 5)

Development of the sporocysts occurs in the digestive gland of the molluscan host. They are oval or rounded in form, thin-walled, and with numerous granules distributed throughout the body. They contain between 4 and 8 cercariae at different stages of development, only 4 - 5 of which may be well developed. Germ balls of different sizes were not abundant. The birth pore and flame cells were not observed.

Encystment.

Encystment was observed under the microscope. When the cercariae were placed (in 0.75% saline solution) on a slide under a coverslip the tail and stylet were detached, the body became rounded and almost all the cystogenous gland-cell contents were secreted. The tail-less cercaria is surrounded by a fine, transparent membrane and moves continually within it. On some occasions encystment took place before the tail and stylet were discarded. These organs were subsequently discarded and remained within the cyst. In a recently formed cyst the membrane ruptures easily allowing the metacercaria to escape.

In the fully formed cysts almost all the structural details of the metacercaria are similar to those of the cercaria, with only the cystogenous gland-cells displaying marked differences. (see Plate 26, Fig. 6).

Experiments on the infection of secondary intermediate hosts.

Two attempts were made to follow the course of infection in 14 tadpoles of Bufo bufo (common toad) and in 17 Trichopteran larvae after a 12 hour exposure to c.c. 50 cercariae per host. The experimental hosts were divided into two groups. One group was dissected and examined 12 hours after exposure, when approximately 12-20 tail-less cercariae were found in the body cavity of each host examined. The second group was examined after 72 hours but no trace either of cercariae or metacercariae was found.

Measurements of Cercaria microcotylea I from Bithynia tentaculata

Body	0.163 (0.136 - 0.182) long x 0.075 (0.060 - 0.098) wide
Tail	0.131 (0.125 - 0.136) long x 0.019 (0.019 - 0.019) wide
Oral sucker	0.038 (0.034 - 0.041) long x 0.039 (0.038 - 0.045) wide
Acetabulum	0.023 (0.022 - 0.026) long x 0.023 (0.022 - 0.026) wide
Pharynx	0.010 (0.009 - 0.010) long x 0.010 (0.009 - 0.010) wide
Preacetubular extent	0.099 (0.091 - 0.110) long
Postacetabular extent	0.042 (0.030 - 0.049)long
Stylet (overall)	0.015 (0.015 - 0.015) long x 0.005 (0.004 - 0.006) wide
Stylet (shoulder)	0.004 (0.004 - 0.004) wide
Sporocyst	0.219 (0.159 - 0.304) long x 0.121 (0.114 - 0.136) wide
Cyst	0.090 (0.085 - 0.097) long x 0.081 (0.078 - 0.085) wide

Discussion

Below are listed all those xiphidiocercaria of the subgroup Microcotylea which, like C. microcotylea I, are characterized by the possession of 3 pairs of penetration gland-cells.

Cercaria indicae XL Sewell, 1922

Cercaria indicae XVI Sewell, 1922

Cercaria indicae XLVI Sewell, 1922

Cercaria indicae XIX Sewell, 1922

Cercaria indicae XVIII Sewell, 1922

Cercaria indicae V Sewell, 1922

Cercaria helnetica XII Dubois, 1929 (as described by Llewelyn, 1957)

Cercaria cordiformis Wesenberg-Lund, 1934

Cercaria micobarica IV Sewell, 1931

Cercaria vuurensis Porter, 1938

Cercaria hartebeestia Porter, 1938

Cercaria elizabethal Porter, 1938

Cercaria stonei Porter, 1938

Cercaria nymphal Porter, 1938

Cercaria veta Porter, 1938

Cercaria globelaania Porter, 1938

Cercaria uniblotuzana Porter, 1938

Cercaria digoniostomae Ito, 1962.

Some of these species can be immediately separated from C. microtylea I because they have a different flame seel formula. They are C. indicae V, C. nicobarica IV, C. hartebeestia, C. ruunensis, C. elizabethal, C. stonei, C. nymphal, C. veta, C. globelaaria, C. umnlotuzana and C. digoniostomae.

Cercaria indicae XVIII, C. indicae XIX, C. indicae XLVI, C. indioae XL and C. cordiformis lack an oesophagus and intestinal caeca, and the number of flame cells is not known. The former structures are invariably present in C. microcotylea I and they are of sufficient diagnostic significance to justify the separation of C. microcatylea I from the other species. Additional differences are the size of the body, tail and suckers, and in the form of the genital primordia.

Cercaria indicae XVI resembles C. microcotylea I in the possession of a complete digestive system but differs from it in the following characters; size of body and tail, the absence of body spines, the number of flame cells and the form and contents of the penetration glands.

Cercaria helvetica XII also has 24 flame cells and is therefore closely related to the present species. However, C. helvetica XII differs in the absence of an oesophagus, intestinal caeca, spines in the ventral sucker and papillae with hair-like structures from the body and tail, and in the size of the body, tail and suckers.

Cercaria parvus Khan, 1962; C. minuta Probert, 1965 and C. X3 Harper, 1929 are the only representatives of the sub-group Microcotylea recorded in Britain. All of these cercariae can be readily separated from the present species by the number of penetration gland-cells.

As a result of these comparative studies the present cercaria is considered to represent a new species.

Cercaria tarda Khan, 1961d

Bithynia tentaculata from Kirkstall Power Station (Leeds-Liverpool canal), Newmillerdam Lake and Wintersett Lake were found releasing Cercaria tarda Khan, 1961d. An infection rate of 3.3% (25 out of 750) was recorded for B. tentaculata collected from Kirkstall Power Station on 15/11/1972. Similar infection rates were found in collections made in the latter two localities on 15/10/1973 and 27/6/1974 respectively.

This cercaria was described in detail by Khan (1961d) in B. tentaculata, collected at Bushy Park, London.

Cercaria tarda encountered in the present investigation agrees with the original description of Khan (1961d) in the following characters:

1. Same first intermediate host (B. tentaculata)
2. Number, position and contents of the penetration glands
3. Excretory system
4. Distribution of oil globules in the body
5. Size and form of stylet
6. Form and position of genital rudiments
7. Spinose body

There are certain differences in the measurements recorded and these could either be due to intraspecific variation or could result from differences in interpretation by different authors. In Khan's original description (1961), there is no pre-pharynx. This structure is in fact present but is only visible when the cercaria is completely extended. The intestinal caeca end slightly anterior to the ventral sucker in Khan's specimens, while in the present specimens the caeca terminate anterolateral to this sucker. Khan does not mention the presence of spines on the ventral sucker or on the tail but they are numerous on these 2 organs. Khan found an infection rate of 0.6% in B. tentaculata; whereas in the 3 localities sampled in the present study it varied from 3.3 to 4.6%. Khan also suggested that C. tarda emerges prolifically during the night and that they are very poor swimmers but in my observations the cercariae are emitted in large numbers during almost all of the day and also at night, and they swim vigorously.

Pike (1967) found Cercaria tarda in the same primary host as Khan (1961) and the present author in Wentloog Level near Cardiff, South Wales. He also gave details of the encystment of cercaria and described the metacercaria.

On certain points my observations coincide with Pike's. They are: the presence of hair-like processes on the body, a longer oesophagus, the active swimming movements of the cercariae and the number of mature cercariea present within sporocysts. On other points my observations differ-the pale granular contents of the 1st and 2nd pair of penetration glands and the positioning of the flame cells between the secondary ducts and not outside them.(see Plate 27, Fig 3-4). Pike (1967) experimented with several possible second intermediate hosts and found that in the nymphs of Trichoptera (Caddis) were the most suitable for encystment. I only used a single species of Trichoptera and found approximately 60 - 80 cysts per individual. All the details of the metacercaria studied by me are in complete accord with the data given by Pike on all essential points.

Three attempts were made to complete the life-cycle of C. tarda by feeding 7-15 day-old metacercarial cysts to laboratory raised Columba livia, Gallus domesticus, Mus musculus and Rattus norvegicus, but in none of the hosts were any parasites obtained.

One of the characters which is most remarkable in the present species is the "virgula" organ, which regularly changes shape (Figs.6-8). In recently emitted cercariae it is reniform, while in those examined 24 hours after emergence the virgula changed from a kidney shape to almost oval, showing its 2 ducts which open out into the anterior part of the oral sucker, where their secretion is discharged in droplets. The "virgula", when it is full (of a moderately thick granular substance) occupies almost all the central part of the oral sucker. 24 hours after emergence this organ diminishes in size.

There are 2 other species which have been described from Britain - Cercaria lahtinensis Probert, 1965 and Cercaria octoglandula Pike, 1967, both in Bithynia tentaculata in South Wales. These 2 forms are very similar to C. tarda in the possession of 4 pairs of penetration glands; but they differ in the number of flame cells; 20 in C. lahtinensis and 36 in C. octoglandula.

Measurements of Cercaria tarda from Bithynia tentaculata

Body	0.164 (0.159 - 0.171) long x 0.060 (0.057 - 0.068) wide
Tail	0.106 (0.102 - 0.110) long x 0.019 (0.015 - 0.022) wide
Oral sucker	0.036 (0.034 - 0.038) long x 0.027 (0.026 - 0.030) wide
Acetabulum	0.024 (0.022 - 0.026) long x 0.023 (0.019 - 0.023) wide
Pharynx	0.014 (0.011 - 0.015) long x 0.012 (0.011 - 0.015) wide
Oesophagus	0.025 (0.023 - 0.030) long
Preacetabular extent	0.071 (0.068 - 0.076) long
Postacetabular extent	0.064 (0.057 - 0.068) long
Stylet (overall)	0.020 (0.019 - 0.021) long x 0.007 (0.007 - 0.007) wide
Stylet (shoulder)	0.005 (0.005 - 0.006) wide
Sporocyst	0.159 (0.125 - 0.190) long x 0.086 (0.076 - 0.126) wide
Cyst	0.105 (0.102-0.106) long x 0.104 (0.102 - 0.106) wide

Specific diagnosis

Virgulate xiphidiocercaria. Four pairs of latero-posterior penetration gland cells with coarsely granular contents. Body and tail spinose. Body with hair-like processes on papillae. Acetabulum spinose. Oesophagus long; caeca weakly developed extending to the equatorial level of acetabulum. Virgula variable in shape. Excretory bladder large, epithelial. Flame cell formula: $2[(2 + 2 + 2) + (2 + 2 + 2)] = 24$.

Cercaria xiphidocercaria IX

This cercaria was found in Lymnaea stagnalis from Wintersett Lake and in L. auricularia from Kirklington. The collections were made in June-July 1974 and the infection rate varied between 5.4 and 12%.

The cercariae are discharged throughout the day. They are very mobile and swim vigorously, with short periods of rest during which they sink to the bottom of the container and crawl using their suckers. They survive for between 20 and 24 hours.

Description (Plate 28, Figs. 1-4)

Body somewhat oval in shape being wider at level of acetabulum, show great powers of extension and contraction and with whole surface armed with small spines. Body cuticle supplied with 14 to 16 pairs of long hair-like projections on both sides. Posterior part of body folded to form a depression which includes very thick-walled caudal pocket and armed with numerous long spines. Tail inserted subterminally in a depression of body. Two short hair-like projections on papillae located on left side of tail. No spines observed. Cavity of tail containing many cellular bodies with clear central nuclei which are more abundant proximally. Stylet javelin-shaped, embedded in dorsal anterior lip of oral sucker; thick walled, with reinforced shoulders, with pointed apex and without basal bulb.

Oral sucker almost circular in outline and larger than acetabulum, situated slightly subterminal. Digestive system comprising mouth, a very short prepharynx (only seen when the cercaria is fully extended), a well developed pharynx, a slender oesophagus which divides into caeca a short distance anterior to acetabulum caeca extending as far as posterior border of acetabulum.

Acetabulum central, isodiametric, its opening provided with large spines directed inwards. Numerous cystogenous gland-cells scattered throughout the body beneath cuticle but absent from region between oral sucker and Oesophageal bifurcation and from region occupied by posterior part of bladder; each gland with granular content. Most of body filled by globular refractile bodies of different sizes: the small ones, 0.003 (0.003 - 0.004)long x 0.003 (0.003 - 0.004)

wide arranged in small groups and sparsely distributed, medium 0.009 (0.009 - 0.009) long x 0.008 (0.007 - 0.009) wide scattered mainly on suckers, and large 0.013 (0.012 - 0.015) long x 0.012 (0.009 - 0.015) wide extending along lateral edges of body; some also in region of pharynx and oesophagus.

Fourteen penetration gland-cells with coarse granular contents, arranged in 2 groups of 7- situated antero-lateral to acetabulum on either side of Oesophagus. Ducts passing anteriorly, lateral to pharynx and on each side of oral sucker to open near tip of stylet.

Nervous system comprising an elongate commissure at level of pharynx and 2 cerebral ganglia from which arise 4 nerve cords, 2 anteriorly and 2 posteriorly. Anterior nerves passing lateral to oral sucker and ending at its equatorial level; posterior nerves only traceable for a short distance at level of Oesophagus owing to the presence of numerous cystogenous gland-cells and refractile globules. Genital rudiments represented by a large C-shaped mass of cells around acetabulum.

Protonephridial system consisting of a large Y-shaped excretory bladder, opening by small excretory pore located at base. Bladder wall thick and composed of two layers of small epithelial cells. Main excretory ducts arising subterminally and passing anteriorly with slightly sinuous course as far as equatorial level of acetabulum, where they form a loop before continuing towards bifurcation at anterior level of acetabulum. Anterior and posterior collecting ducts both receiving three groups of 3 flame cells on each side; making a total of 36 flame cells. Caudal excretory duct arising from posterior end of bladder and passing backwards into tail to open at its tip. Flame cell formula: $2\left[(3 + 3 + 3) + (3 + 3 + 3)\right] = 36$.

Sporocyst. This cercaria develops in oval or sausage-shape sporocysts, wide in the digestive gland of Lymnaea auricularia and L. stagnalis. The sporocyst wall is thick and has a granular content. Each contains numerous germ balls and some cercariae. The number of mature cercariae per sporocyst varied between 5 and 7. A few sporocysts were found with germ balls only. No birth pore was observed.(see Figs. 5-6).

Encystment and feeding experiments

Thirty four chironomid larvae were exposed to approximately five hundred cercariae for 4 hours. The cercariae penetrated and encysted in these larvae. 12-day old metacercariae were fed to each of three 6 day old chickens, two pigeons (approximately 5 months old) and four mice (two months old). The chickens were purchased commercially and both pigeons and mice were raised in the animal house of the Zoology department. The faeces of these animals were examined daily but no trematodes eggs were found. On the 10th day after feeding the animals were autopsied but no parasites were found. Similar experiments were carried out using 14-20 day-old metacercariae, but the results were still negative.

Twelve-day-old Metacercariae (Plate 28, Fig. 7)

The cysts are spherical, with thick transparent walls. Some of the structures of the metacercaria are clearly visible, such as the oral sucker, acetabulum and Pharynx. In some cysts the metacercaria may be seen folded in a U-shape within the cyst, or as in Fig. 7 . About 70% of the cysts contain a stylet and in 20% of the metacercariae the stylet remains in its original position on the oral sucker. The penetration gland-cells are still present but their contents are darker and more finely granular. The excretory bladder does not contain dark refractile granules characteristic of some cercariae of the Plagiorchis and Opisthioglyphe type. During the 12 days of development the number of refractile globules in the body of the metacercaria decreased considerably but the number of flame cells remained constant at 36.

Measurements of Cercaria xiphidiocercaria IX from Lymnaea stagnalis and L. auricularia

Body	0.223 (0.209 - 0.231) long x 0.121 (0.117 - 0.125) wide
Tail	0.136 (0.125 - 0.152) long x 0.023 (0.022 - 0.026) wide
Oral sucker	0.049 (0.045 - 0.053) long x 0.050 (0.049 - 0.053) wide
Acetabulum	0.035 (0.034 - 0.038) long x 0.035 (0.034 - 0.038) wide
Pharynx	0.015 (0.015 - 0.015) long x 0.015 (0.015 - 0.015) wide

Preacetabular extent	0.104 (0.102 - 0.110) long
Postacetabular extent	0.083 (0.076 - 0.091) long
Stylet (overall)	0.031 (0.031 - 0.033) long x 0.005 (0.005 - 0.006) wide
Stylet (shoulder)	0.007 (0.007 - 0.007) wide
Stylet (base)	0.006 (0.006 - 0.006) wide
Cyst	0.197 (0.190 - 0.209) long x 0.178 (0.171 - 0.190) wide
Oral sucker	0.071 (0.068 - 0.076) long x 0.076 (0.072 - 0.079) wide
Acetabulum	0.045 (0.041 - 0.049) long x 0.047 (0.045 - 0.049) wide
Pharynx	0.026 (0.026 - 0.026) long x 0.025 (0.022 - 0.026) wide

Discussion

Among the Armatae group, Cercaria xiphidiocercaria IX is closely related to the following species:

Cercaria of Plagiorchis muris (Tanabe, 1922) as described by Yamaguti, 1943.

Cercaria peregri Khan, 1961.

Cercaria microcaeca Probert, 1965.

Cercaria helvetica XXXIII (Dubois, 1931) as described by Pike, 1967.

Cercaria elbensis Komiya, 1938,

Cercaria lagae Brooks, 1943.

Cercaria conniae Brooks, 1943.

Cercaria argenti Brooks, 1943.

Cercaria acrodonta Faust, 1922

Cercaria longicornua Llewelyn, 1957.

Cercaria dartevelli Fain, 1953.

Cercaria brachystyla Byrd and Reiber, 1940

Cercaria A. (Tsuchimochi, 1962) as described by Ito, 19

Xiphidiocercaria I (Ginetzinskaga, 1959) as described by Smirnova and Ibrasheva, 1967.

Cercaria sp. III Vietnam Odening, 1971

Cercaria helvetica XXXIII, C. lagea and C. longicornua may be readily separated from C. xiphidiocercaria IX by the extension of the arms of the excretory bladder in the first 3 species. In C. helvetica XXXIII and C. longicornua the

arms reach as far as the middle of the body while in C. lagae they almost surround the acetabulum.

In Cercaria A, C. peregri, C. microcaeca, C. acrodonta and Xiphidiocercaria I, the intestinal caeca are very short, terminating less than half-way between pharynx and acetabulum. Cercaria nolfi, C. dartevelli, C. brachystyla, the cercaria of P. muris and Cercaria sp. III Vietnam are characterized by having long intestinal caeca, more or less reaching the posterior end of the body; additionally, in C. dartevelli and C. brachystyla the acetabulum is larger than the oral sucker and in C. nolfi and C.sp. III Vietnam the division of the main excretory ducts into anterior and posterior collecting ducts takes place at the posterior level of the acetabulum. In the cercaria of P. muris the main excretory ducts arise terminally from the arms of the bladder and the contents of the penetration gland-cells are finely granular.

Cercaria elbensis, C. conniae and C. argenti are more similar to C. xiphidiocercaria in having intestinal caeca which extend just to the posterior limit of the acetabulum. However in C. conniae and C. argenti the body and tail are larger than C. xiphidiocercaria IX the main excretory ducts divide posterior to the acetabulum and in C. conniae the oesophagus branches considerably anterior to the acetabulum. In C. argenti the oesophagus and caeca are hidden by rows of small glands and by the cystogenous glands which are very abundant throughout the body. The number of flame cells in these two species is not known so comparison of this character is not possible. C. elbensis has a similar number of penetration gland-cells and flame cells but its stylet is very much smaller, the disposition and size of the penetration glands are different, also there are no refractile globules present.

On the basis of the above comparison this species is regarded as new and named Cercaria xiphidiocercaria IX

Cercaria of Dolichosaccus rastellus (Olsson, 1876) Travassos, 1930.

This cercaria was found on two occasions in Lymnaea stagnalis and L. peregeer collected from Wintersett Lake in June and July, 1974. The infection rate in these two species of snails was almost similar and varied from 4 to 6.6%.

The cercariae emerge in low numbers throughout the day. Their swimming movements are strikingly similar to those shown by cercaria of P. kirkstallensis. When they come into contact with any object they begin creeping rapidly over its surface. During this period the tail lashes around very actively; when past the object they continue creeping over the bottom of the container or resume swimming. They remained alive for about 20-24 hours.

Description (Plate 29, Figs. 1-5)

Body elongate and somewhat oval in shape. Body surface completely covered with numerous small spines arranged in transverse rows. Spines larger laterally than on dorsal and ventral surfaces and decreasing in size posteriorly. Cuticle provided with 15-17 pairs of long hair-like projections arranged regularly around body. Caudal pocket subterminal at posterior end, covered by thickened cuticle and bearing 35-40 long inwardly-directed spines on each side. Tail shorter than body, markedly subterminal and with slightly crenate margin. Two well-marked bands of longitudinal muscles originating proximally and running its entire length, parallel to caudal excretory duct; each band containing 8-9 muscle fibres. Inner walls of tail lines with anucleate cellular bodies. A small elongate collular body present at end of tail containing three oval nuclei and very fine granular cytoplasm. No spines or other structures observed. Stylet lying on dorsal wall of oral sucker; its shoulders and base re-inforced with lateral projections. Anterior tip of stylet pointed; some granular material present between shoulders and between lateral projections of stylet.

Oral sucker terminal, almost circular in outline and slightly larger than acetabulum. Mouth opening subterminally on oral sucker then leading into relatively long prepharynx and a rounded and muscular pharynx. Oesophagus provided with thicker walls than rest of digestive system; divided near to acetabulum into two long intestinal caeca lined by a conspicuous epithelial layer. Several vesicle-like

structures present in lumen of caeca which terminate at posterior extremity of body.

Acetabulum, muscular, isodiametric and situated in middle of body; moderately protrusible and unarmed. Most of body filled with cystogenous gland-cells with coarsely granular contents; these cells more abundant in preacetabular region. A few small rounded refractile globules dispersed in body.

Penetration gland-cells lying antero-lateral to acetabulum and arranged in two groups of eight cells; each cell with a small nucleus and coarse, granular cytoplasm. Ducts passing forwards to region of oral sucker, then bending medially before opening to exterior in two groups of 4. Nervous system consisting of a transverse commissure lying dorsal to the pharynx and connected to 2 cerebral ganglia. Two short anterior nerves and 2 posterior nerves arising from each ganglia. Genital primordium represented by a large mass of cells lying immediately anterior to acetabulum.

Protonephridial system comprising a large Y-shaped excretory bladder with two wide cornua extending to posterior margin of acetabulum. Cornua wall thick and its outer surface lined with conspicuous epithelial cells; each cornua giving rise to a short main excretory duct on postero-distal margin. Main excretory duct following a short sinuous course to anterior level of cornua where divided into anterior and posterior collecting ducts. Caudal excretory duct long, passing posteriorly along tail and terminating at its tip. Both bladder and caudal excretory duct contain granular material. Flame cell formula: $2\left[(3+3+3)+(3+3+3)\right]=36$.

Sporocyst (Plate 29, Fig.7)

The digestive gland of each infected snail was packed with numerous sporocysts. Each is elongate and sausage-like and enveloped by a thick external wall, brownish-yellow in colour within which they were observed moving freely. The true internal wall of the sporocyst is thin and colourless and its lumen contains numerous germ balls of different sizes together with cercariae

at various stages of development; the number of well-developed cercariae per sporocyst varied between 5 and 9. No birth pore was present.

Measurements of the Cercaria and sporocyst of Dolichosaccus rastellus from Lymnaea pereger and L. stagnalis

Body	0.318 (0.311 - 0.330) long x 0.115 (0.106 - 0.117) wide
Tail	0.280 (0.269 - 0.288) long x 0.035 (0.030 - 0.041) wide
Oral sucker	0.059 (0.057 - 0.060) long x 0.059 (0.057 - 0.064) wide
Acetabulum	0.051 (0.045 - 0.057) long x 0.049 (0.045 - 0.057) wide
Prepharynx	0.015 (0.011 - 0.019) long
Pharynx	0.022 (0.019 - 0.022) long x 0.022 (0.022 - 0.022) wide
Oesophagus	0.021 (0.019 - 0.026) long x 0.007 (0.007 - 0.007) wide
Preacetabular extent	0.147 (0.140 - 0.152) long
Postacetabular extent	0.117 (0.114 - 0.125) long
Stylet (overall)	0.031 (0.031 - 0.031) long x 0.006 (0.006 - 0.006) wide
Stylet (Shoulder)	0.008 (0.006 - 0.009) wide
Sporocyst	1.489 (1.036 - 1.960) long x 0.313 (0.253 - 0.364) wide

The cercaria found in this study has been experimentally linked with adults of the species Dolichosaccus rastellus (Olsson, 1876) Travassos, 1930. Details of the life cycle of this species are given below.

Dolichosaccus rastellus

During a short survey of the parasites of amphibia in Yorkshire intended to reveal the natural definitive hosts of certain Plagiorchidid trematodes, twelve specimens of Bufo bufo were collected from Wintersett. These specimens were found to be infected with digenetic trematodes identifiable as Dolichosaccus rastellus.

Snails of different species - (45 Lymnaea stagnalis, 17 L. glabra, 50 L. pereger and 48 Bithynia tentaculata) were collected from the same locality (Wintersett) and placed in separate glass receptacles half filled with tapwater.

After 12 h. 2 and 3 L. peregar and L. stagnalis were respectively emitting the cercaria of Dolichosaccus rastellus. None of the other snails were releasing any cercariae, even after 72 h.

Tadpoles of B. bufo which had been reared in the aquarium from eggs collected in the vicinity of New Farnley were exposed to a large number of the cercariae of D. rastellus. Penetration was observed to occur through the buccal opening; nostrils, spiracle and, less frequently, through the skin of the tadpole. Five tadpoles were dissected after 24 h. and cysts were found in the lung rudiments, small intestine wall and in the body tissues. After a further 3 days another five tadpoles were examined and several young specimens of D. rastellus were recovered from the small intestine of each.

The remaining tadpoles were maintained in aquaria at 13-15°C. through metamorphosis into the adult stage and were examined at various intervals for the presence of developing parasites. Observations were made after 3, 6, 18 21, 42, 50, 104, 106, 112, 120, 141 and 164 days from the original exposure of the tadpoles to the cercariae and are described below (page 166).

Penetration and Encystment

When the cercariae come into contact with tadpoles they attach themselves to the body of the host and commence creeping movements by the alternate use of their two suckers until they locate a nostril, the buccal cavity or spiracle. During this process the tail may be held almost parallel to the body or occasionally undergoes a very short period of lashing from side to side. After locating one of these openings, the cercariae pass into the buccal cavity then via the glottis and reach the lung rudiments where encystment occurs.

The discovery of cysts attached to the lumenal surface of the small intestine wall 24 h. exposure to the cercariae suggests that they are swallowed by the tadpoles and pass directly to the small intestine where they encyst. On the few occasions when penetration took place through the skin of the tadpole, encystment was observed with the aid of a steoreomicroscope. When the cercaria

reaches the body of the tadpole it creeps about with its body extending and contracting and some of the cercaria lose their tail before attempting penetration, but usually this organ is lost during or when this process is completed. After creeping the cercaria adheres with the oral sucker and penetrate through the skin using both the stylet and the secretion of the penetration gland-cells. Having penetrated the skin the cercaria usually moves deep through the tissue of the host and then encysts. However few cysts were occasionally found just underneath the skin.

In further experiments, 20 tadpoles and 20 young adults of Xenopus laevis bred in the animal house at Leeds University were exposed to a large number of cercariae. After 24 h 10 tadpoles and 10 adults were dissected. Seven alive encysted meracercariae were found in the lungs of one of the adults but in none of the tadpoles. The rest experimental host were examined 72 to 96 h later but no metacercariae were found.

Similar experiments were carried out in order to study an indirect route of infection involving caddis-flies and Chironomus larvae which serve as second intermediate hosts. Larvae of caddis-flies an Chironomus were isolated in groups of 5 in glass dishes containing approximately one hundred cercariae each. After 2 h two representatives of each species were removed and examined and 5 to 12 cysts were found on the surface of the Malphigian tubes of both species of insect larvae one or two cysts were also found in the tissue of Chironomus larvae. Thirty cysts between 1hh and 12 days were fed by stomach tube to each of 10 tadpoles, 10 young adults and 5 mature adults of Xenopus laevis. After 72 h, 5 tadpoles, 5 young adults and 5 mature adults were killed and examined but no parasites were found either in the lungs or the intestines. The rest of these experimental hosts were killed and examined 7 days later and were also not infected by Dolichosaccus rastellus. In additional experiments 3 pigeons, 3 chickens and 3 mice were fed with caddis-flies and Chironomus containing 15 day old metacercariae. After 8 days all the experimental hosts gave the same negative results.

Metacercariae (Plate 30, Fig. 8-9)

The metacercariae of D. rastellus occurred in the lung rudiments, small intestines and less frequently in the body tissues of tadpoles of Bufo bufo as well as on the surface of malphigian tubes of caddis-flies and Chironomus larvae. In the latter host species, a very small number of cysts was also found within the tissues.

One day-old metacercariae which had been removed from both toads and chironomids did not show any marked difference in their morpology from that of the cercariae and no growth had occurred compared with the cercariae stage. The excretory bladder was filled with dark coloured excretory granules. The cyst wall was thin and hyaline and the metacercariae were easy to remove mechanically.

In 10-day-old cysts from caddis-flies 0.231 (0.224 - 0.239) long x 0.230 (0.224 - 0.239) wide the metacercariae had undergone appreciable development. Their bodies were longer and lay folded double within the cyst. The oral sucker and acetabulum had reached a size of 0.057 (0.049 - 0.068) long x 0.085 (0.076 - 0.095) wide and 0.046 (0.038 - 0.057) long x 0.075 (0.072 - 0.076) wide; the pharynx and oesophagus had increased respectively to 0.034 (0.030 - 0.038) long x 0.044 (0.038 - 0.057) wide and 0.035 (0.027 - 0.045) long whereas the prepharynx remained unchanged. The intestinal caeca were slightly larger and their cavities were now more clearly visible. The penetration and cystogenous gland-cells had disappeared but the openings and ducts of the penetration gland-cells were still present. The single genital primordium had increased in size but no other genital primordia were yet visible. The spines of the body and caudal pocket were more prominent. The excretory bladder was still filled with refractile granules but they were a little less numerous, and some of them could be seen moving freely within the cyst.
A total of 33 flame cells was seen.

Ten day old encysted metacercariae removed from the small intestine of a tadpole were more developed than those from Caddis flies. The most prominent feature of the metacercaria was the voluminous excretory bladder. Its arms

and stem had increased in size and the former reached as far as the equatorial level of the acetabulum. The main excretory ducts remained in their subterminal position but the excretory granules were no longer present. The number of flame cells (36) was the same as that of the cercariae.

Several papillae had appeared on the surface of the oral sucker. The intestinal caeca had increased greatly in width and were filled with granular dark-brown contents. In the preacetabular region of the body, the spines were more conspicuous whereas the caudal pocket and its spines had been lost. The testes and ovary rudiments were visible, lying in the posterior third of the body and slightly to the left side near the posterior edge of acetabulum, respectively. It is probable that these very small organs in the encysted metacercariae were obscured by the intestinal caeca or excretory bladder and had been overlooked.

Encystment and Migration

The time of encystment both in the lung rudiments and in the small intestine seemed to be the same, because only empty cysts and empty cyst together with young worms were found in both sites after 72 h exposure. The route of migration to the small intestine from the lung rudiments was not identified, however, two young flukes were found in the stomach and one in the upper portion of the small intestine 72 h post infections. They were probably in the process of migrating to the small intestine. It is, therefore, reasonable to assume that following encystment the worms started their migration to the small intestine via the bronchus and glottis to the buccal cavity and then moved along the oesophagus and through the stomach, finally reaching the small intestine where maturation occurred.

Further development in the tadpole (see Plate 31, Figs. 10-22)

The growth and development of D. rastellus in tadpoles and young adults of B. bufo were studied using stained whole mounts. The different stages of organogenesis, gametogenesis and oviposition were also determined. Details are given in Table 8 . The length of time required for the worms to become

fully grown and to produce eggs was between 127 and 164 days after infection. Adult worms from naturally infected B. bufo were almost all of the same size and were at a similar stage of sexual maturity. Over the period of these observations a considerable number of tadpoles metamorphosed whereas others remained as tadpoles. It was noted that the rate of mortality was slightly higher in metamorphosed frogs than in tadpoles and that mortality was lower in uninfected specimens.

Further, uninfected tadpoles metamorphosed more rapidly than infected ones. The mature worms recovered from the young experimentally infected toads were a little longer than those found in naturally infected adult toads. Eighteen to twenty four specimens were studied in each of the stages described below.

Three days post infection

At this age, the young worms showed a slight decrease in the relative size of the body, suckers and pharynx as compared to the cercariae except for the prepharynx which had increased slightly in relative size. The genital primordia and excretory bladder were better developed than in the cercaria; the genital primordia were represented by a large cluster of undifferentiated cells located in the area of acetabulum together with the testes rudiments separated from this mass of cells and lying diagonally in the posterior third of the body. The penetration gland-cells had been lost although some of their ducts were still visible and the refractile excretory granules were no longer present. The nervous system was well-developed. The peripharyngeal glands had begun to appear and the body and cuticle spines were more distinct.

Six days post-infection

The body, suckers and pharynx of the young worms showed a greater degree of development than in the previous stage. The intestinal caeca had increased in breadth. The differentiation of the genital primordia had begun with the cirrus sac, metraterm, Mehlis' complex, oviduct and ovary becoming distinct and the testes had doubling in size. In some specimens the testes were contiguous. The cuticle of the body was slightly thicker.

Eighteen to twenty one days post-infection

Although the size of the body had increased there was little or no growth of the suckers, pharynx, testes, ovary and cirrus rudiments. The slender seminal vesicle had begun to form and displayed a small constriction of a short distance from its anterior end. The developing genital pores were surrounded by an elongate mass of tissue, probably the future genital atrium.

Forty two to fifty days post-infection

By this stage greater development had occurred in the genital system. The cirrus sac and all its constituent parts were clearly identifiable. The metraterm wall had increased in thickness and its glands were distinct. Several loops of the uterus had appeared. While the ootype, Mehlis' complex and oviduct were completely formed and the ovicapt was slightly developed, the Laurer's canal, vitelline cells, ducts and reservoir and vasa efferentia were not yet evident. Early stages of spermatogenesis and ovogenesis were observed.

One hundred-and-four to one hundred-and-twenty days post-infection

At this stage of development the body had lengthened considerably. There was however, little change in the genital organs although Laurer's canal and the vasa efferentia were now evident. The seminal vesicle was filled with spermatozoa and the ootype had become enlarged. Additional loops of the uterus had started to appear at the posttesticular region of the body but only a few could be seen lateral to the testes.

One hundred-and-twenty-seven days post-infection

The vitelline cells were more numerous and had differentiated into follicles which joined at the posttesticular region and extended into the area between the pharynx and the acetabulum. The genital atrium was fully formed and a long common vitelline duct, vitelline reservoir and latcral vitelline ducts were now present. At about this age egg-production commenced as a single was present in the uterus of one specimen.

One hundred-and-forty-one days post-infection

All the worms recovered at this stage were larger than at 127 days but their reproductive organs were either the same size or were smaller, except for the ovary which was slightly larger. No eggs were present in the uterus.

One-hundred-and-sixty-four days post-infection

At this stage, 24 worms were recovered from toads, of which 21 were developed. All the organ systems were fully recognizable and eggs were present in the uteri of these 21 worms. The immature worms were at approximately the same degree of development as those of 141 days after infection.

In all the worms examined, no seminal receptacle was detected. As shown in table no further growth occurs following the attainment of sexual maturity.

Dolichosaccus rastellus was described from Rana temporaria in Great Britain by Prudhoe (1970). While in most respects the specimens of Prudhoe and of the present writer are closely similar certain differences are evident, particularly in the male and female reproductive systems, and in the protonephridial system. A description of each of these systems in the writer's specimens is given below.

Male reproductive system (see Plate 33, Fig. 25)

Vasa efferentia arising from anterior surface of each testis and passing directly to the cirrus sac which they enter independently. Male and female genital pores open into a large genital atrium lined with thick cuticle situated anterior to acetabulum and displaced to the left of the medial line.

Female reproductive system (see Plate 33, Fig. 22)

Ovary rounded, smooth, submedian and lying to right of midline just behind acetabulum, usually slightly overlapping it; short ovicapt (sometimes difficult to see) arising from dorso-lateral surface of ovary and expanding into a muscular oviduct which gives off a wide Laurer's canal which soon tapers markedly anteriorly and opens dorsally near the anterior edge of the anterior testis; oviduct

extends anteriorly and is joined dorsally by the common vitelline duct; it then enlarges forming a thick-walled muscular ootype surrounded by closely aggregated cells of the Mehlis complex. Seminal receptacle absent. Uterus arising from ootype and describing several loops between acetabulum and testes, continuing anteriorly along lateral side of acetabulum and finally terminating in a rather long metraterm lined by a thick cuticle and provided with circular muscles. It is surrounded by numerous gland cells; proximal portion of uterus acts as receptaculum seminis.

Lateral vitelline ducts arise on each side of body and extend towards anterior margin of anterior testis, where they join the common vitelline reservoir, from which the common vitelline duct arises. The latter unites with oviduct just before it turns into the ootype.

Protonephridial system (see Plate 33, Fig. 27)

Protonephridial system consists of a well-developed tubular Y-shaped excretory bladder lined with thick cuticle and opening to the exterior through an excretory pore which lies subterminally. The bladder extends to the posterior level of the ovary where it divides into two short broad cornua.

A main excretory duct arises subterminally from each cornua and forks into anterior and posterior collecting ducts just posterior to acetabulum.

Flame cell formula: $2\,[(3 + 3 + 3) + (3 + 3 + 3)] = 36.$

Measurements of Dolichosaccus rastellus naturally infecting Bufo bufo

from Wintersett Lake (25 specimens measured)

Body	1.696 (1.428-1.901) long x 0.592 (0.518 - 0.714) wide
Oral sucker	0.179 (0.160 - 0.201) long x 0.183 (0.160 - 0.198) wide
Pharynx	0.093 (0.080 - 0.103) long x 0.110 (0.106 - 0.0122) wide
Acetabulum	0.143 (0.118 - 0.171) long x 0.133 (0.110 - 0.152) wide
Anterior testis	0.189 (0.179 - 0.209) long x 0.217 (0.213 - 0.251) wide
Posterior testis	0.198 (0.175 - 0.232) long x 0.250 (0.217 - 0.293) wide
Ovary	0.180 (0.125 - 0.228) long x 0.174 (0.149 - 0.213) wide
Cirrus sac	0.427 (0.334 - 0.471) long x 0.081 (0.068 - 0.091) wide
Preacetabular extent	0.511 (0.420 - 0.602) long
Postacetabular extent	1.068 (0.910 - 1.190) long
Posttesticular extent	0.429 (0.350 - 0.546) long
Eggs	0.043 (0.041 - 0.046) long x 0.024 (0.022 - 0.027) wide

Discussion

Joyeux and Baer (1927) obtained adult parasites which they identified as Opisthoglyphe rastellus (Olsson, 1876) from adult Rana esculenta which had been fed on tadpoles of Alytes obstetricans previously experimentally infected with a xiphidocercaria obtained from Lymnaea stagnalis and L. auricularia. They stated that the cercaria used for these experiments closely resembled C. limnaeae ovatae, described in Linstow (1884).

The present cercaria differs slightly from that described by Joyeux and Baer (1927) in the relative sizes of oral sucker and acetabulum, but differs markedly in body-length, tail-length and size of pharynx. However, most of these differences could be interpreted as being due to either differences in the state of contraction of the measured specimens or pressure on the specimens from the coverslip. The length of the stylet is the same in both cercariae. The posterior part of the body was devoid of spines in the specimens of Joyeux & Baer (1927) whereas spines are present on this part of the present cercaria although they are less prominent than on the anterior part. Joyeux

and Baer did not give any details of either flame cells or the caudal excretory duct.

The number of penetration gland-cells in C. l. ovatae has been misinterpreted by various authors. Wesenberg-Lund (1934) suggested that there are 5 impaired glands but he figured 5 pairs anterior to the acetabulum (Pl. XIII, fig. 5). Joyeux and Baer (1958) observed 4 pairs and Meyer (1964) described 5 pairs. Unfortunately, I have been unable to obtain the original description of C. l. ovatae (V. Linstow, 1884). In the present cercaria 8 pairs of penetration gland cells were seen.

Grabda-Kazubska (1969) elucidated the life cycle of Opisthoglyphe ranae and O. rastellus. Both xiphidocercariae are very similar in structure and body proportions, differing only in the following characters: number of penetration gland-cells (6-8 pairs in O. ranae and 6 pairs in O. rastellus), anterior collecting ducts (wider and less twisted in O. rastellus), genital primordium (better developed in O. ranae), stylet (25-28µm long in O. ranae, 30-31µm in O. rastellus) and there is a thickening at the base of the stylet in O. rastellus which is absent from O. ranae. The cercaria described by Grabda-Kazubska (1969) as that of O. rastellus bears a closer resemblance to the present cercaria than does the cercaria of O. ranae, although the dimensions of body structures are markedly different except for those of the stylet which coincide exactly. The cercaria found in this study has 8 pairs of penetration gland-cells.

According to Joyeux and Baer (1927) and Grabda-Kazubska (1969) Amphibia act as the second intermediate hosts for Opisthoglyphe rastellus (= Dolichosaccus rastellus). Linstow (1884) however, observed the encystment of Cercaria lymnaea ovatae in both larval Trichoptera (Limnophilus sp. and Anabolia sp.) and Ephemerida (Ephemera sp.) and Wesenberg-Lund (1934) infected Corethra larvae with C. l. ovatae from Lymnaea stagnalis, L. ovata and Planorbis planorbis. Joyeux and Baer (1927) pointed out that the habitat where L. auricularia was found contained a large number of invertebrate forms, including insect larvae, Herpobdella spl, Gammarus sp., and Pisidium sp., but none of these animals

contained any cysts of C. l. ovatae. They also reported that several attempts to infect these invertebrates in the laboratory were unsuccessful. In the present study Trichoptera larvae and Chironomus sp. were experimentally infected with C. l. ovatae.

The mode of penetration of C. l. ovatae was not described by Joyeux and Baer (1927) but the encysted metacercariae were localized in the body cavity, musculature and in the branchial sac. According to Grabda-Kazubska (1969) the cercariae passed into the buccal cavity and branchial cavities through the buccal opening and spiracles and they encysted almost exclusively in the buccal cavity and adjoining areas. They were rarely found in the anterior part of the body and never in the muscles of the dorsal part of the body. In my observations the cercariae passed into the buccal cavity through the mouth opening, nostrils and spiracles. Then they migrated to the lung rudiments where they encysted. Less frequently cysts were found in the body tissues or attached to the wall of the small intestine.

The times of encystment and migration to the intestine of the frog by the metacercariae of D. rastellus given by Grabda-Kazubska (1969) are very similar to those found in the present study, being 2-3 days and 3 days respectively. One of the most important differences between the life cycles of D. rastellus given by both Joyeux and Baer (1927) and Grabda-Kazubska (1969) and the present material relates to the length of time taken to reach sexual maturity in the frog. According to the above authors egg-production began 8-15 and 21 days postinfection, while in the present study the beginning of egg-production was first detected 127 days post infection and specimens with the uterus filled with eggs were not recovered until 164 days post infection. Undoubtedly in my specimens commencement of egg-production was retarded by unknown factors.

After comparing the adults of D. rastellus obtained in the present experiments with those described by Grabda-Kazubska, no morphological differences in the internal organs or dimensions of general body structures were found. On the other hand the material described by Joyeux and Baer differed markedly in the presence of a receptaculum seminis, in the dimensions of the body,

pharynx and oral sucker, and in that the acetabulum and cirrus sac are about twice as long as in the present specimens.

Johnston (1912) founded the genus Dolichosaccus, and described three new species - D. trypherus, D. ischyrus and D. diamesus from Australian frogs. In the former species he described a sac-like structure in fixed and stained whole mounts that he named "the fertilization-space" which would normally be called the "receptaculum seminis". After studying living worms Johnston stated that the ova are fertilized in this space. In trematodes fertilization is known to take place in or near the ootype and the spermatozoa are stored in the seminal receptacle. No other case has been described in the literature in which the ova pass into the seminal receptacle to be fertilized. Johnston also stated "If this sac does not represent the receptaculum seminis, then no such structure is present in the species of the genus". Consequently he characterized the genus by "receptaculum seminis doubtful". Yamaguti (1958) gave as a diagnostic feature of the genus "Receptaculum seminis comparatively large" and may have based this on Johnston's description of a "fertilisation space". The same author in 1971 gave a similar diagnosis "Seminal receptacle present".

Perkins (1928) in a re-examination of the sub-family Telorchinae Looss, 1899, stated that the worm described by Looss (1906) under the name Opisthoglyphe ranae Frölich (1791) was in fact O. rastellus (Olsson, 1876). He also contended that it did not belong to genus Opisthoglyphe and established a new genus, Lecithopyge, to contain it. Perkings (1928) named three varieties of Lecithopyge rastellus - L. rastellus rastellus L. r. cylindriformis and L. r. subulatus. Travassos (1930b) placed this genus in the synonymy of the genus Dolichosaccus Johnston, 1912. Prudhoe (1970) during a study of the parasites of Amphibia in the helminthological collection of the British Museum (Natural History) examined the type specimens of the sub-species of Lecithopyge Perkins, 1928 and considered L. r. rastellus to be Dolichosaccus rastellus (Olsson, 1876) and re-described it. Prudhoe also described Dolichosaccus (L.) novaezealandiae n.sp., from Leiopelma archeryi and L. hochstetteri.

The specimens of D. rastellus obtained naturally and experimentally in the present study conform closely to the re-description of this species given by Prudhoe (1970) except that a seminal receptacle is absent in the present specimens. All specimens recovered both naturally and experimentally, were carefully examined, but this organ was not detected. Therefore it is apparent to the author that the genus Dolichosaccus contains species characterized either by the presence or by the absence of the seminal receptacle.

TABLE 8

The growth of juvenile Dolichosaccus rastellus between 3 and 146 days in the small intestine of Rana temporaria tadpoles

Days after treatment	Dimensions (mm)											
	Body	Oral sucker	Pharynx	Acetabulum	Anterior testis	Posterior testis	Ovary	Cirrus sac	Preacetabular extent	Postacetabular extent	Posttesticular extent	Eggs
3	0.238-0.266 x 0.098-0.140	0.049-0.057 x 0.053-0.068	0.022-0.034 x 0.026-0.034	0.041-0.053 x 0.045-0.057	0.007-0.015 x 0.015-0.022	0.007-0.019 x 0.015-0.022	0.007-0.022 x 0.007-0.015	0.045-0.076 x 0.011-0.022	0.098-0.117	0.037-0.098	0.057-0.060	-
6	0.182-0.490 x 0.140-0.224	0.057-0.102 x 0.064-0.106	0.022-0.057 x 0.076-0.053	0.053-0.068 x 0.053-0.079	0.019-0.041 x 0.019-0.060	0.019-0.038 x 0.019-0.064	0.011-0.034 x 0.011-0.030	0.057-0.136 x 0.007-0.026	0.148-0.212	0.091-0.212	0.057-0.0125	-
18-20	0.280-0.539 x 0.119-0.231	0.056-0.092 x 0.066-0.098	0.026-0.093 x 0.026-0.051	0.095-0.077 x 0.049-0.081	0.019-0.035 x 0.026-0.052	0.019-0.032 x 0.030-0.052	0.015-0.026 x 0.015-0.022	0.049-0.131 x 0.009-0.019	0.142-0.250	0.113-0.231	0.058-0.091	-
40-50	0.343-0.672 x 0.197-0.266	0.068-0.123 x 0.083-0.127	0.035-0.056 x 0.047-0.068	0.068-0.087 x 0.058-0.081	0.028-0.070 x 0.028-0.079	0.032-0.071 x 0.024-0.079	0.029-0.045 x 0.020-0.039	0.064-0.136 x 0.017-0.028	0.161-0.260	0.132-0.336	0.076-0.151	-
104-120	0.535-0.841 x 0.203-0.318	0.101-0.135 x 0.108-0.128	0.047-0.064 x 0.053-0.076	0.077-0.099 x 0.071-0.099	0.043-0.091 x 0.062-0.117	0.042-0.084 x 0.054-0.129	0.031-0.067 x 0.026-0.057	0.096-0.179 x 0.027-0.045	0.212-0.300 x 0.210-0.300	0.246-0.424	0.116-0.186	-
127	0.910-1.120 x 0.350-0.406	0.133-0.148 x 0.140-0.152	0.064-0.064 x 0.072-0.083	0.102-0.114 x 0.095-0.114	0.125-0.167 x 0.133-0.190	0.114-0.155 x 0.129-0.167	0.060-0.102 x 0.057-0.059	0.190-0.262 x 0.049-0.049	0.315-0.338	0.482-0.630	0.163-0,277	0.041-0.020
141	0.840-1.372 x 0.336-0.448	0.121-0.148 x 0.140-0.170	0.042-0.075 x 0.075-0.105	0.095-0.121 x 0.098-0.121	0.095-0.163 x 0.117-0.171	0.102-0.163 x 0.117-0.171	0.077-0.125 x 0.060-0.102	0.140-0.307 x 0.041-0.053	0.357-0.501	0.475-0.786	0.193-0.311	-
164	0.980-2.072 x 0.308-0.658	0.133-0.197 x 0.152-0.212	0.060-0.102 x 0.079-0.129	0.098-0.159 x 0.098-0.152	0.095-0.235 x 0.106-0.304	0.095-0.235 x 0.106-0.304	0.053-0.224 x 0.053-0.190	0.159-0.494 x 0.045-0.095	0.962-0.602	0.994-1.316	0.392-0.560	0.041-0.053 x 0.022-0.026

- = no eggs in uterus

This cercaria was recovered from 3 out of 45 Lymnaea stagnalis collected at New Farnley in 1974. Although the cercariae were emitted in fairly large numbers throughout the day the greatest numbers were released during the late afternoon and at night. They are not active swimmers and spend long periods crawling on the bottom of the container. During this time most specimens lose their tails although some resume swimming activity, mostly near the bottom but sometimes near the surface. Maximum survival time was 16 to 18 hr.

Description (Plate 34, Figs. 1-5)

Body oval and capable of great contraction. Body cuticle spinose and bearing 10 - 12 pairs of hair-like projections on papillae on each side, the first 4 pairs set closer together. Conspicuous caudal pocket at posterior end provided with thick spines; body cuticle bordering caudal pocket thickened, forming 2 prominent expansions. Tail subterminal, non-spinose and without papillae; numerous cellular bodies with hyaline cytoplasm present in tail cavity, mainly along lateral margins. Stylet javelin-shaped, re-inforced along its length, with well-marked shoulders and slightly curved tip and without lateral projections and basal bulb.

Oral sucker terminal or just subterminal. Short thin-walled prepharynx leading into well defined muscular pharynx. Long, narrow oesophagus divided anterior to acetabulum into intestinal caeca; caeca extending two-thirds length of body and with very finely granular contents.

Acetabulum subspherical and located just posterior to middle of body. Cystogenous gland-cells located mainly laterally and around acetabulum; cells poorly developed and with granular cytoplasm. Body containing numerous small refractile globules, more abundant anteriorly and in region postero-lateral to acetabulum.

Two groups of eight penetration gland-cells situated lateral to acetabulum in middle of body. Each cell with a bilobed margin, a small rounded nucleus and with coarse granular contents exhibiting Brownian movement. Ducts

passing forwards around margin of oral sucker and opening on anterior margin of body.

Nervous system comprising a transverse commissure lying over prepharynx and onnected to 2 cerebral ganglia. Two short anterior nerves and 2 posterior nerves arising from each ganglion. Genital primordium identical to that of C. xiphidocercaria IX.

Excretory bladder Y-shaped, opening to exterior via a pore at base of posterior chamber; bladder walls thick, consisting of elongate epithelial cells with fine granular cytoplasm. Two wide lateral cornuae arising from anterior chamber of bladder and reaching almost to posterior margin of acetabulum. Main excretory ducts arising apically from each cornua, divided into anterior and posterior collecting ducts anterior to acetabulum. Both collecting ducts receiving 6 groups of 3 flame cells; caudal excretory duct absent. Flame cell formula: $2\,[(3 + 3 + 3) + (3 + 3 + 3)] = 36$.

Sporocyst (Plate 34, Fig. 9)

The sporocysts are found in the digestive gland of Lymnaea stagnalis. They are small, elongate and have a thick body wall which contains dispersed yellowish brown pigment. The anterior end of the sporocyst contains a mass of cells and its lumen is completely full of germ balls and cercariae at various stages of development. The mature cercariae are always found at the posterior end. There is no birth pore.

Measurements of the Cercaria and sporocyst of Plagiorchis farnleyensis from Lymnaea stagnalis

Body	0.266 (0.254 - 0.296) long x 0.124 (0.106 - 0.136) wide
Tail	0.201 (0.190 - 0.212) long x 0.029 (0.026 - 0.030) wide
Oral sucker	0.052 (0.049 - 0.053) long x 0.054 (0.049 - 0.057) wide
Acetabulum	0.030 (0.026 - 0.034) long x 0.032 (0.030 - 0.034) wide
Prepharynx	0.013 (0.007 - 0.016) long
Pharynx	0.022 (0.021 - 0.022) long x 0.023 (0.021 - 0.024) wide
Oesophagus	0.034 (0.030 - 0.040) long

Preacetabular extent	0.137 (0.125 - 0.152) long
Postacetabular extent	0.099 (0.091 - 0.106) long
Stylet (overall)	0.030 (0.030 - 0.031) long x 0.006 (0.006 - 0.007) wide
Stylet (shoulder)	0.009 (0.009 - 0.010) wide
Sporocyst	0.524 (0.238 - 0.840) long x 0.126 (0.070 - 0.168) wide

Penetration and Encystment

The larvae of various freshwater insects (caddis-flies, dragon-flies and damsel-flies) were collected from a pond in New Farnley. These larvae were found to harbour cysts of digenetic trematodes all of which displayed similar characters including a stylet or its remains lying within them and a y-shaped excretory bladder containing refractile granules which give it a dark colour.

Snails from this locality, namely Lymnaea stagnalis, L. pereger and Planorbis corneus, were isolated in glass dishes three-quarters filled with tap-water. After 24 hr. specimens of L. stagnalis were emitting cercariae but not the other species. The cercariae were identified as xiphidiocercaria of the Armatae group, bearing a stylet in the oral sucker and possessing 8 pairs of penetration gland-cells with coarsely granular contents, cystogenous gland-cells with granular contents, a Y-shaped excretory bladder and 18 flame cells on each side of the body.

Various other different equatic invertebrates, namely Dytiscus marginalis, may-flies, Tubifex sp., Corixids., Glossiphonia sp., Asellus sp. and Gammarus pulex, were collected from a small pool at Durkar in order to test their suitability as second intermediate hosts. None of these invertebrates from Durkar ever harboured any trematode infections. Additional specimens of these species were kept in individual containers and exposed to a known number of cercariae for 12 hr. Penetration and encystment were successfully induced in all experimental species except Tubifex sp., Corixids., and Glossiphonia sp. The most heavily infected organisms were D. marginalis and Asellus sp. The metacercariae obtained from different invertebrates had all achieved the same stage of development.

Studies were made of penetration and encystment of the cercariae were made in larvae of Chinonomus plumosus, Aedes Aegypti and Corynoneura sp. The former were purchased commercially, the larvae of A. aegypti were reared under laboratory conditions and Corynoneura sp. were collected from a pool in the University Campus. Many larvae of both C. plumosus and Corynoneura sp., were examined before the start of the experiments but no prior infection by trematodes was detected.

Three heavily infected L. stagnalis were isolated in small containers of water and after a considerable number of cercariae had been discharged the snails were removed. Cercariae penetration and encystment were observed under the microscope and were found to be similar in all three insect species. The following description of these two processes is based on observations made on the larvae of Corynoneura sp.

After emission the majority of the cercariae swim for a short period of time, often sinking to the bottom of the container. They commence crawling by means of their suckers and most of them lose their tails while continuing to crawl about. On coming into contact with the insect larvae they attach to them with their suckers and begin moving over their surface. The contact between swimming or tail-less cercariae and the insect larvae appears to occur by chance as the cercariae do not exhibit an obvious tactic response to the presence of insect larvae. On several occasions cercariae were seen creeping over the body of the insect without penetrating it and some resumed swimming. After a period of crawling the cercariae shed their tails and penetrate through the cuticle using both the stylet and the secretion of the penetration gland-cells. The process of penetration can apparently be detected by the insect larvae which react by swimming a short distance, flexing their bodies and then resuming swimming. After penetration the cercariae move about within the host's tissues before encysting. During encystment the body of the cercariae is elongated and the contents of the cystogenous gland-cells are poured out to form the metacercarial cyst wall. The stylet either remains embedded in the oral sucker or free within the cyst; rarely it is shed before encystment takes place.

The exact position of penetration was usually the intersegmental articulation and both penetration and encystment were completed within 4 to 10 minutes.

Encysted metacercariae were found throughout the body cavity, with the greatest number in the 1st, 2nd and 3rd thoracic segments and less frequently in the head and false legs.

Metacercaria (Plate 34 Figs.7-8)

The cysts are spherical. The wall of the newly formed cyst is thin and the metacercaria can be seen through it. The metacercaria occupies almost the whole cyst and makes slow movements. In 8 day-old metacercariae the walls are thicker, the dark refractile globules in the body more compact and the excretory bladder is larger and packed with dark refractile excretory granules. The oral sucker, pharynx and acetabulum have undergone a certain amount of development. The intestinal caeca could not be traced and the penetration gland-cells were difficult to observe as they had lost much of their granular contents during the penetration process. The stylet is often retained in the oral sucker but may sometimes be seen free within the cyst.

Measurements of 8 day-old metacercariae of P. farnleyensis, experimentally obtained from C. plumosus, A. aegypti and Corynoneura sp.

Cyst	0.204 (0.190 - 0.209) long x 0.197 (0.190 - 0.209) wide
Oral sucker	0.070 (0.066 - 0.072) Long x 0.080 (0.075 - 0.087) wide
Acetabulum	0.043 (0.042 - 0.049) long x 0.047 (0.045 - 0.052) wide
Pharynx	0.027 (0.025 - 0.028) long x 0.034 (0.030 - 0.037) wide

Infection of the final host

Twenty metacercariae of varying ages obtained from different naturally infected freshwater insect larvae were fed to each of 5 experimental mouse hosts, (Nos. 1 to 5 in Table 9). Daily examinations of their faeces for 7 days before beginning feeding experiments proved to be negative for trematode eggs. After feeding the faeces of the mice were again examined daily and on the 6th day trematode eggs appeared. All the mice were dissected the same day and all

were infected. A total of 44 sexually mature worms (14, 5, 7, 6 and 12 respectively), belonging to the genus Plagiorchis were recovered from the small intestines.

A second series of feeding experiments was performed using metacercariae from C. plumosus, A. aegypti and Corynoneura sp., infected experimentally with xiphidiocercariae from Lymnaea stagnalis from the pond.

Seven mice, 5 rats, 4 pigeons and 4 chickens were fed with 60 cysts which varied from 2 to 12 days old (see Table 9). The mice, rats and pigeons were bred in the laboratory; the chickens were purchased commercially. Faecal samples were examined daily.

On the 6th day after feeding, eggs appeared in the faeces of mice 8, 9, 10, 12; rats 2, 3, 4, 5; pigeon 2 and chickens 2 and 3. On the 6 and 7th days after feeding mice 8 and 9, rats 2 and 3, pigeon 2 and chickens 2 and 3 were all killed and examined. The sexually mature parasites removed from the small intestines of the hosts were similar to the plagiorchids from the first experiments with naturally infected insect larvae. Mice 6 and 7, rat 1, pigeon 1 and chicken 1 were killed on the 2nd and 4th day after infection and the intestines examined but no flukes were found. It would appear that the metacercariae are not fully developed at 2 to 4 days of age and were probably not infective for the definitive experimental hosts. The faeces of pigeons 3 and 4 and chicken 4 which were examined daily after infection did not contain trematode eggs. These host individuals were not infected with trematodes when autopsied after 7 or 8 days.

The faeces of the remaining hosts were examined every other day after infection. Eggs were seen on each occasion but after the 40th day their number gradually diminished in mice and rats, more rapidly in the latter. Mice 10 and 11 and rats 4 and 5 were killed and examinedoon the 50th day. A total of 12 and 10 mature flukes were taken from mice 10 and 11 respectively. A single mature fluke was recovered from rat 4, whereas rat 5 was found to be uninfected. Mouse 12 continued to pass eggs until the 55th day; it was killed and examined on the same day and no flukes were found.

The results of these experiments indicate that 6 days are required for the metacercariae to become infective in the second intermediate host and the same length of time is required for them to reach sexual maturity in the final experimental host. Although mature flukes were obtained experimentally from a pigeon and chickens, it is probable that only a few of the metacercariae reach sexual maturity in these hosts. In addition the infection lasted for a very short period which suggests that they are not suitable experimental hosts for this trematode species. However, the number of flukes reaching sexual maturity in mice and rats was higher and the infection endured for longer, at least 50 to 55 days after feeding. This indicates that they are more suitable experimental hosts.

The mature trematodes recovered from the small intestine of mice, rats, pigeons and chickens were carefully compared with those obtained from mice fed with naturally infected metacercariae and were found to be morphologically indistinguishable.

Plagiorchis farnleyensis (Plates 35-36, Figs. 10-13 and 15-17)

Description

Body flattened, oval in outline, narrower anteriorly and with the maximum width at middle of body. Cuticle thick, densely covered with spines which are larger and more prominent in the preacetabular region than those on the posterior third of the body. Numerous unicellular gland cells containing coarse granules are situated both sides of oral sucker, pharynx, oesophagus, and some are present between the oesophageal bifurcation and acetabulum.

Mouth elongate and opening on oral sucker. It leads into a short, broad, thin-walled prepharynx. Pharynx is very muscular, oval to spherical in outline with four lobes in front. There is an extremely short oesophagus which is rarely visible in whole mounts but clearly visible in live specimens; it bifurcates some distance in front of the acetabulum. The intestinal caeca follow a slightly undulating course and are charactistically curved at the level of pharynx. They extend near to posterior end of body.

Acetabulum spherical and almost equal in size to the oral sucker.

Testes with smooth margins and situated in oblique tandem in middle of posterior half of body. A vas efferens arises anterodorsally from each testis and proceeds forward as a narrow tube, both uniting to form a very short vas deferens which enters the cirrus sac. Within the sac vas deferens expands to form a seminal vesicle which is divided by a deep constriction into a proximal part and distal spherical part. Seminal vesicle opens into a pars prostatica which continues as a short tube, the ejaculatory duct; both surrounded by prostatic cells which occupy almost all the space available around these organs. Ejaculatory duct leads into the cirrus which is eversible, highly muscular and unarmed. Genital pore situated to left of anterior edge of acetabulum. Cirrus sac elongate, clavate, very muscular and thick-walled, extending obliquely along right edge of acetabulum, reaching almost to middle of body.

Ovary pretesticular, transversally elongate, somewhat ellipsoidal and usually displaced to the right. Oviduct originates from the mid-ventral surface of the ovary and turns posteriorly before enlarging to form the seminal receptacle which is oval and contains spermatozoa. Laurer's canal rung from ventral surface of seminal receptacle and passes anteriorly to open on dorsal body surface. The oviduct extends beyond entrance of Laurer's canal for a short distance and leads into ootype which is surrounded by cells of Mehlis' complex. The ootype passes dorsally and becomes continuous with the uterus which turns dorsally towards posterior end of body forming first the descending limb passing between testes then bending anteriorly and continuing forwards as the ascending limb to posterior end of cirrus sac. Here it joins the prominent muscular metraterm which is surrounded by glandular cells and curves slightly around acetabulum on the left side. Both male and female pores open into a common genital atrium. Eggs numerous.

Vitellaria consist of numerous follicles lying on both sides of intestinal caeca, extending from a part posterior to the middle of oral sucker and extending

to posterior end of the body where they join and become much denser. Vitelline follicles unite mid-ventrally anterior to acetabulum forming a transversal commissure the latter may be absent in some specimens. Median vitelline duct arises from dorsal side of oviduct, runs posteriorly and expands to form a large vitelline reservoir which receives two separate lateral vitelline ducts.

Protonephridial system remains similar to that of the cercaria except that both excretory bladder and its ducts have markedly increased in size; Y-shaped excretory bladder opening dorsally through a priminent excretory pore surrounded by gland cells. A main excretory duct arises from each cornua and passes sinuously to level of postero-lateral margin of acetabulum, where it branches into anterior and posterior collecting ducts; both receive capillaries from 3 groups of 3 flame cells. The flame cell formula is $2\,[(3 + 3 + 3) + (3 + 3 + 3)] = 36$.

Measurements of Plagiorchis farnleyensis obtained experimentally from mammals and birds.

Body	1.004 (0.889 - 1.134) long x 0.525 (0.476 - 0.560) wide
Oral sucker	0.154 (0.140 - 0.168) long x 0.152 (0.140 - 0.154) wide
Prepharynx	0.019 (0.015 - 0.022) long x 0.038 (0.026 - 0.049) wide
Pharynx	0.072 (0.068 - 0.083) long x 0.072 (0.060 - 0.079) wide
Acetabulum	0.138 (0.126 - 0.140) long x 0.148 (0.140 - 0.154) wide
Anterior testes	0.169 (0.114 - 0.216) long x 0.223 (0.190 - 0.250) wide
Posterior testis	0.153 (0.121 - 0.178) long x 0.216 (0.113 - 0.262) wide
Ovary	0.112 (0.087 - 0.152) long x 0.134 (0.114 - 0.163) wide
Cirrus sac	0.351 (0.296 - 0.395) long x 0.065 (0.038 - 0.076) wide
Preacetabular extent	0.297 (0.259 - 0.322) long
Postacetabular extent	0.130 (0.112 - 0.140) long
Eggs	0.031 (0.026 - 0.034) long x 0.016 (0.015 - 0.019) wide

Egg and Miracidium (Plate 35, Figs.14, 14a)

Several hundred eggs were collected from mature flukes recovered from different experimental hosts. The mature flukes were washed several times, then placed in shallow dishes containing either tap or distilled water to stimulate the discharge of their eggs (it was found that fungal growth was much reduced in distilled water). Eggs were also removed mechanically from the uterus.

In newly formed eggs the shell is very thin and transparent, and has a bright green-colour. The shell rapidly becomes thick, slightly opaque and yellowish or golden yellow in colour. The eggs are oval, operculated and unembrionated. Freshly deposited eggs have a large ovum, usually located at the antopercular end, with clear cytoplasm and surrounded by 6 to 7 vitelline cells. Several intra and extrauterine eggs displayed a binucleated zygote, but no indication of cytoplasmic division was observed.

Approximately 50% of the eggs collected from the mature flukes were used in attempts to infect the snail host. The remaining eggs were incubated at room temperature (19 to 22°C) in order to obtain the miracidium larva.

After 24 hours incubation the eggs do not differ essentially from newly extruded eggs and showed little development. After about 52 hr. the young embryos were at the morula stage, represented by 6 to 7 blastomeres, and the vitelline cells had already disintegrated into small and large globules surrounding the embryo. As development proceeded the globules were distributed throughout the egg capsule but were more noticeable at the anterior and posterior ends. The number of cells increased rapidly after five days incubation by which time the embryo had grown considerably and was represented by a mass of cells that occupied almost all the space within the egg capsule. The vitelline globules had decreased in size and in number.

On the 6th day certain structures such as the apical gland, penetration gland-cells and beating flame cells were evident and the miracidium commenced making slow contractions. The entire development of the miracidium in both tap water and distilled water took place in 6 to 7 days incubation. Observations were continued for 7 weeks until the movements of the miracidium were no longer

visible, but hatching did not take place. Several attempts to obtain living miracidia by mechanical hatching were made by applying slight coverslip pressure but in all cases without success.

The fully developed miracidium is oval to pear-shaped with an attenuated anterior end occupied by the apical papilla. Externally the miracidium is covered with rather long cilia evenly distributed over the body, but absent from the anterior end. There is a large sac-like apical gland filled with coarsely granular material and with its duct opening at the anterior tip of the apical papilla. Two large penetration gland-cells with fine granular cytoplasm are situated at either side of the body, slightly behind the mid-line. Their ducts open on each side of the base of the apical papilla. The nervous system comprises a small mass of nucleated cells located almost behind the apical gland. The protonephridial system consists of a single flame cell located in the posterior third of the body. A duct from the flame cell empties via a small lateral excretory pore. A small mass of germ cells is situated in the posterior half of the body.

Attempts to infect the snail host

Laboratory raised snails, Lymnaea peregrer, L. stagnalis, Physa fontinalis and Bithynia tentaculata, were placed in containers with fully embrionated eggs, and they were observed eating the eggs. Both empty egg cases and normal eggs were found in the faeces of the snails but no cercariae were produced during the 3 months of observation. During this period a number of snails was examined microscopically after crushing between two slides but no precercarial stages were seen.

Discussion

The genus Plagiorchis was erected by Luhe (1899) and comprises more than 100 species recorded from birds, mammals, reptiles and amphibians. Massino (1929) presented a key for 25 species of Plagiorchis then Schulz and Skworzow (1931) reviewed the genus and divided it into two subgenera, Plagiorchis and Multiglandularis, on the basis of the presence or absence of a vitelline

commissure anterior to the acetabulum. In the former the vitellaria fill the lateral fields of the body, extending from posterior of the body to the anterior of the acetabulum; in the latter the vitelline follicles extend to the anterior level of the acetabulum where they form an anterior vitelline commissure.

Some authors accepted the subdivision for example; Olsen (1937), Rees (1952), Skrjabin and Antipin (1958), Dollfus (1960), Vercammen-Grandjean (1960), Groschaft and Tenora (1974), but others did not, for example, Fedorava (1954), Yamaguti (1958), Najarian (1961) and Velasquez (1964).

Skrjabin and Antipin (1958) thought that this subdivision of the genus Plagiorchis was necessary but suggested that in a few cases some members of a species possessed a vitelline commissure while other members of the same species did not. Groschaft and Tenora (1974) also regarded this character as of diagnostic importance in the division of the genus, but Najarian (1961) considered that the division was not very satisfactory since the follicles of the vitelline glands in trematodes are not equally distributed ventrally or dorsally, especially in the members of the genus Plagiorchis. Blankespoor (1974) in the study of Plagiochis noblei demonstrated a great deal of variability of vitelline glands presumably induced by different final hosts. According to his observations, in worms recovered from the robin (Turdus migratorius), the anterior limit of the vitelline glands showed great variation in its position from the acetabulum to the level of the oral sucker. Worms with a vitelline commissure posterior to the acetabulum were recovered from a sora (Porzana carolina) and other birds, whereas specimens with a well developed commissure anterior to the acetabulum were obtained from a single robin. He discovered that much greater variability was displayed by the posterior limits of vitelline follicles in worms recovered from both avian and mammal hosts. Blankespoor infected 17 different hosts including birds and mammals and after the examination of more than 1500 specimens of P. noblei concluded that the only two apparently stable diagnostic features were the size-ratio of suckers and egg size, while the body and most of the internal organs of the worms showed great variability.

Styszynka-Jurewicz (1962), in a study of Plagiorchis elegans, reported that the degree of development and the extent of vitellaria depends on the age of the worms while Krasnolobova (1971a, b), during a study of the development of P. laricola, pointed out that the size of testes and ovary depends on the age of the worms or may be influenced by seasonal factors. Similar observations were made by Groschaft and Tenora (1974) in their study of morphological variability in the species P. vespertilionis and P. koreanus. They also found that the development of these worms may slow down under unfavourable conditions.

During the course of this investigation I have established the life cycles of two trematodes belonging to the genus Plagiorchis, namely P. kirkstallensis and P. farnleyensis. In the former species no commissure was found in any of the specimens examined but in the latter species, although a conspicuous anterior commissure was usually present, in three specimens the commissure was lacking. I agree with the interpretation of Fedora (1954), Yamaguti (1958) and others, and I have therefore not distinguished between the two nominal subgenera of the genus Plagiorchis Luhe (1899).

In P. farnleyensis and P. kirkstallensis some variability was observed - for example in the location of the cirrus sac and ovary with relation to the acetabulum, and in the shape of testes but this may represent distortion caused by fixation and pressure of the coverslip rather than true intraspecific variation.

Specific determination in the genus Plagiorchis is very difficult since the adult forms are all very similar. Therefore, in the writer's opinion, the larval stage could become of great importance in distinguishing between the species although some of the cercariae are inadequately described and comparison between them is almost impossible. Additionally relatively few plagiorchid life cycles have been described in detail. The cercaria of Plagiorchis farnleyensis shows close similarities to the following:

Cercaria of Plagiorchis dilimanensis Velasquez, 1964.

Cercaria of Plagiorchis (Multiglandularis) megalorchis Rees, 1952.

Cercaria of Plagiorchis muris (Tanabe, 1922) as described by Yamaguti, 1943.

Cercaria of Plagiorchis jaenschi Johnston and Angel, 1951.

Cercaria of Plagiorchis peterborensis Kavelaars and Bourns, 1968.

Cercaria of Plagiorchis cirratus (Rudolphi, 1802) as described by Buttner and Vacher, 1960.

Cercaria of Plagiorchis elegans (Rudolphi, 1802) as described by Styczynska-Jurewicz, 1962.

Cercaria of Plagiorchis laricola (Skrjabin, 1924) as described by Krasnolobova, 1971.

Cercaria of Plagiorchis vespertilionis parorchis Macy, 1960.

Cercaria of Plagiorchis proximus (Barker, 1915) as described by McMullen, 1937a.

Cercaria of Plagiorchis (Plagiorchis) berghei Vercammen Grandjean, 1960.

Cercaria of Plagiorchis (Plagiorchis) laurenti Vercammen Grandjean, 1960.

Cercaria of Plagiorchis noblei (Park, 1936) as described by Williams, 1963.

Cercaria of Plagiorchis maculosus (Rudolphi, 1802) as described by Angel, 1958.

Cercaria of Plagiorchis microcanthos (Macy, 1931) as described by McMullen, 1937a.

Cercaria of Plagiorchis fastuosus (Szidat, 1924) as described by Krasnolobova, 1973.

Cercaria of Plagiorchis goodmani Najarian, 1961.

The cercariae of Plagiorchis muris (Tanabe, 1922) as described by Yamaguti (1943), of P. proximus (Barker, 1915) as described by McMullen (1937a), of P. goodmani Najarian, 1961 and of P. elegans (Rudolphi, 1802) as described by Styczynska-Juvewicz (1962) are all known to encyst precociously in the sporocyst. The first species has 7 pairs of penetration glands and the stylet is larger and the caeca longer than in the present species. The cercaria of P. proximus has a smaller body and tail than the cercaria of P. farnleyensis. McMullen (1937a) did not give any details of the penetration gland-cells but according to the original author (Cort, 1914) they are arranged in 2 groups of 10 to 12 cells each. The cercaria of P. goodmani has a smaller stylet than the present species, it has very short caeca and its main excretory ducts arise subterminally

from the branches of the bladder. The cercaria of P. elegans can be readily separated from the present species as it possesses only 6 pairs of penetration gland-cells. The cercariae of P. cirratus (Rudolphi, 1802) as described by Buttner & Vacher (1960), of P. berghei Vercammen-Grandjean, 1960 and of P. laurentis Vercammen-Grandjean, 1960 differ from the cercaria of P. farnleyensis in the possession of a total of 12 penetration gland-cells, and, in the former, in the length of the intestinal caeca which reach the posterior end of the body. The cercaria of P. laurenti also differs from the present species in having a very much smaller stylet.

The cercaria of P. noblei closely resembles the cercaria of P. farnleyensis in the number of penetration gland-cells and in body proportions, although the body length is different. However in the former species there are no refractile globules and only a single pair of hair-like projections on papillae. Also the structure of the excretory bladder is different. It is not possible to compare the digestive systems of the two forms as the description for the cercaria of P. noblei is incomplete.

The dimensions of the tail, oral sucker, stylet and pharynx of the cercaria of P. farnleyensis agree with those given by Kavelaars & Bourn (1968) for the cercaria of P. peterborensis. However, the stylet of the former species has a larger body and 'shoulders' than the latter. The description of the cercaria of P. peterborensis is very incomplete and omits many characters of taxonomic importance so it is not possible to give a complete comparison between the two species.

The cercariae of P. fastuosus (Szidat, 1924) as described by Krasnolobova (1973) and of P. laricola (Skrjabin, 1924) as described by Krasnolobova (1971) all have 8 pairs of penetration glands and the main excretory ducts divide posterior to the acetabulum. The last species has only 7 cells on one side and 8 on the other. Asymmetry of this nature has been observed before (Dobrovolsky, 1967) in other cercariae belonging to the families Plagiorchidae and Telorchiidae. The dimensions of the body, tail and oral sucker of the cercaria of P. laricola are greater than in the cercaria of P. farnleyensis and the intestinal caeca of the former extend to the posterior end of the body.

In the cercaria of P. fastuosus the caeca extend only to the level of the acetabulum and the caudal duct bifurcates near the end of the tail.

In the cercaria of P. jaenschi Johnston and Angel, 1952, the caeca reach to the posterior end of the body, the oesophagus is very short, the body cuticle is devoided of papillae and there are at least 10 pairs of penetration gland-cells or probably more. The cercariae of P. megalorchis Rees, 1952, of P. microcanthus (Macy, 1931) as described by McMullen (1937a) and of P. verpertilionis parorchis Macy, 1960 have smaller bodies and tails than the cercaria of P. farnleyensis. These three species also differ in that the main excretory ducts divide posterior to the acetabulum and the caeca extend to the posterior end of the body (except in P. verpertilionis parorchis for which details of the caeca are not available). The cercaria of P. megalorchis can also be separated from the present species by the finely granular nature of the penetration gland-cell contents.

The cercariae of P. dilimanensis Velasquez, 1964 and of P. maculosus (Rudolphi, 1802) as described by Angel (1958) have smaller bodies and stylets than the cercaria of P. farnleyensis and their caeca reach the posterior extremity of the body. The body cuticle of both species is devoid of papillae.

Cercaria cambrensis III Rees, 1932, and C. edgbastonensis Nasir, 1960 both differ from the cercaria of P. farnleyensis in the size of the stylet. They also differ in that C. cambrensis III has only 18 flame cells and encysts both in snails and in open water and C. edgbastonensis encysts in open water.

The cercaria of P. farnleyensis and the cercaria of P. kirkstallensis both found in the present study, can be distinguished from C. xiphidocercaria IX by the number of penetration gland-cells, size of body, tail and refractile globules and site of origin of the main excretory ducts, Additionally in the cercaria of P. kirkstallensis the acetabulum and tail are larger, the stylet has lateral projections, the caudal excretory duct is present and the cystogenous gland cells are more numerous.

The adult of P. farnleyensis is most closely related to P. goodmani, P. (M) megalorchis, P. dilimanensis, P. elegans, P. jaenschi, P. peterborensis and P. muris. Plagiorchis goodmani and P (M) megalorchis can be readily separated

from P. farnleyensis by their lack of a common genital atrium, so that the male and female genital pores open separately. They can also be distinguished from the present species by their possession of larger bodies, suckers, ovaries and testes. In P. (M) megalorchis the whole descending limb of the uterus acts as a receptaculum seminis, while a true seminal receptacle is lacking.

Plagiorchis dilimanensis and P. elegans differ from P. farnleyensis in having a longer body, smaller acetabula and in the size of their cirrus sacs. The cirrus sac is smaller in P. dilimanensis than in P. farnleyensis and in P. elegans it is larger. In both species the length of testes only slightly different from that of the present species. However, they are much narrower and are of a different shape.

In Plagiorchis jaenschi the vitellaria are less developed than in P. farnleyensis, they extend from the level of the oesophagus to the end of the intestinal caeca and the two fields remain separated. According to Johnston and Angel (1951) "some scattered follicles may occur in the oesophageal region between the lateral fields". The lateral posterior fields behind the testes do not join in this species whereas in P. farnleyensis they fuse and fill almost the whole of the post-testicular region, and the anterior vitelline commissure (present in the majority of the specimens) is strongly marked. P. jaenschi is also distinguishable from P. farnleyensis by the smaller size of its testes, by its larger cirrus, and by the structure of the metraterm which is thin-walled and nonglandular.

According to Kavelaars and Bourns (1968), when 4 or 6 day-old metacercariae obtained experimentally from Aedes aegypti were fed to mice, 29 immature worms of P. peterborensis were collected 7 days post-infection. The adult worms were obtained 14 days after feeding. In P. farnleyensis mature specimens were secured from mice fed with 7 day-old metacercariae, 6 days after feeding, using the same second intermediate host A. aegypti. This biological difference together with the larger size of its suckers, pharynx, eggs and the possession of non-glandular metraterm clearly separates these two species.

The life cycle and morphology of P. muris (McMullen, 1937a) resemble P. farnleyensis more closely than the other members of Plagiorchis.

Nevertheless it can be separated from P. farnleyensis by the following characters. The body length of P. muris is more than two and half times larger and its acetabulum and ovary are almost twice as large as in P. farnleyensis. The oral sucker, pharynx and cirrus sac of P. farnleyensis are also smaller in size. The present species can further be distinguished from P. muris by having a glandular metraterm.

Several representatives of the genus Plagiorchis have been recorded in Great Britain by Nicoll (1923) and Baylis (1939) namely Plagiorchis maculosus (Rudolphi, 1802), P. cirratus (Rudolphi, 1802), P. elegans (Rudolphi, 1802), P. nanus (Rudolphi, 1802), P. triangulare (Diesing, 1850), P. vitellatus (Linstow, 1875), P. permitus (Braun, 1901) and P. notabilis Nicoll, 1909.

Foggie (1937) described an outbreak caused by a trematode in Northern Ireland which was provisionally identified as Plagiorchis laricola Skrjabin (1924). Rees (1952) found numerous trematodes belonging to the genus Plagiorchis infecting turkey poults from Radnorshire, and she initially regarded them as identical to Foggie's specimens. After comparative studies Rees, using Olsen's key, found that the trematodes were different from P. laricola and from other species described at that time and she, therefore, named it Plagiorchis (Multiglandularis) megalorchis. Fahmy, 1954, described P. lutrae from Lutra lutra in Scotland. Fahmy and Rayski (1963) reported P. (Multiglandularis) muris from sheep in Scotland. Of these twelve species recorded from Great Britain only P. notabilis is closely related to P. farnleyensis.

A complete comparison of the P. farnleyensis with P. notabilis is difficult since the anatomical studies and measurements of the latter species were based on a single specimen taken from Anthus obscurus. However, it can be separated from P. farnleyensis by the presence in it of a short and stout cirrus sac which does not reach beyond posterior level of the acetabulum by the posterior separation of the vitelline follicles and by its body length which is almost twice that of P. farnleyensis.

Table 9

Experimental infection of mammals and birds with the metacercariae of *Plagiorchis farnleyensis* n.sp.

Experimental definitive host	Number of cysts fed to host	Age of cysts (Days)	Eggs detected in faeces (+ or -) (Days)	Host autopsied after - (Days)	Number of Trematodes recovered
Mouse 1	20	Unknown	6+	6	14
Mouse 2	20	Unknown	6+	6	5
Mouse 3	20	Unknown	6+	6	7
Mouse 4	20	Unknown	6+	6	6
Mouse 5	20	Unknown	6+	6	12
Mouse 6	60	2	-	4	0
Mouse 7	60	4	-	6	0
Mouse 8	60	7	6+	6	42
Mouse 9	60	12	7+	7	39
Mouse 10	60	12	50+	50	12
Mouse 11	60	12	50+	50	10
Mouse 12	60	12	55-	55	0
Rat 1	60	2	-	4	0
Rat 2	60	7	6+	6	37
Rat 3	60	12	7+	7	35
Rat 4	60	12	50+	50	1
Rat 5	60	12	50-	50	0
Pigeon 1	60	2	-	4	0
Pigeon 2	60	12	6+	6	5
Pigeon 3	60	12	-	7	0
Pigeon 4	60	12	-	8	0
Chicken 1	60	2	-	4	0
Chicken 2	60	12	6+	6	8
Chicken 3	60	12	7+	7	3
Chicken 4	60	12	-	7	0

\- = no eggs in faeces

\+ = eggs in faeces

Cercaria of Plagiorchis kirkstallensis

This cercaria was only found in the Leeds-Liverpool Canal at Kirkstall Power Station in January and November 1975. An infection-rate of between 1.6 and 2.5% was recorded for Lymnea stagnalis, the host of this form.

The cercariae emerge from the host in small numbers throughout the day. Soon after emerging they swim up and down before settling on the bottom, ventral side up. During this resting period the body contracts and the tail is stretched and contracted several times, moving rapidly from one side to the other; then swimming is again resumed. Occasionally the cercariae were seen crawling. They remained alive for 24 hours.

Description (Plate 37 , Figs. 1-4)

Body elongate-oval, totally covered with spines and with 8 or 9 long hair-like structures present on both sides. Base of body occupied by a prominent caudal pocket and provided with long and strong spines. Tail non-spinose, subterminal and capable of considerable elongation and contraction; its margin slightly crenated. Tail provided with numerous cellular bodies each with hyaline protoplasm and without a nucleus. These cells mainly arranged linearly internal to the tail wall although several cells irregularly dispersed in central part. Tail formed by numerous transverse and longitudinal muscles, the latter formed of two bands on either side of caudal excretory duct. Stylet javelin-shaped with large shoulders and a pair of lateral projections near its base; connected to base are several very fine muscle fibres which probably control its movements.

Anterior extremity of body occupied by a well-developed oral sucker situated slightly subterminally. Mouth opening almost in middle of oral sucker and passing into a short prepharynx, followed by a large circular pharynx. Oesophagus rather short and divided at considerable distance in front of acetabulum into 2 intestinal caeca which extend almost to posterior end of body.

Acetabulum situated in middle of body, smaller than oral sucker and moderately protusible. Cystogenous gland-cells very numerous with granular contents and extending from mid-level of pharynx almost to posterior end of body.

No refractile globules observed.

Sixteen penetration gland-cells with coarse, granular contents and a small rounded nucleus arranged in two groups on each side of body; an inner group composed of three cells located anterior to acetabulum and an outer group of five cells situated antero-lateral to acetabulum. Cell ducts slightly sinuous and passing forwards to mid-level of oral sucker then turning towards stylet to open at its base.

Nervous system well-developed, formed by two cerebral ganglia connected across lower part of pharynx by a conspicuous commissure. Four lateral nerves present, two anterior reaching level of oral sucker and two posterior extending to base of bladder. Genital rudiments consisting of two masses of undifferentiated cells; one C-shaped mass lying lateral to acetabulum and another between excretory bladder and acetabulum.

Excretory bladder Y-shaped, lined with several layers of epithelial cells. Main excretory ducts arising terminally from antero-lateral margins of bladder and following a convoluted course to about mid-level of acetabulum where divided into anterior and posterior collecting ducts. Anterior collecting ducts passing anteriorly and medially following a sinuous course; receiving capillaries from 9 flame cells. Posterior collecting ducts bending backwards towards posterior end of body, also receiving capillaries from 9 flame cells. Long and wide caudal excretory duct arising from base of bladder dilated and occupying almost whole of caudal pocket, then passing posteriorly to open proximally at tip of tail. Flame cell formula: $2\overline{[(3 + 3 + 3) + (3 + 3 + 3)]} = 36$.

Sporocyst (Plate 37, Fig. 5)

The sporocysts are small, oval or sac-like in shape, and they are situated in the digestive gland of Lymnaea stagnalis. The sporocyst wall is thick and has granular contents. It encloses several mature cercariae and germ balls of different sizes. No birth pore is present.

This cercaria has been shown experimentally to develop into an adult belonging to the genus Plagiorchis. Details of the other stages are given below (Page 199).

Measurements of the cercaria and sporocyst of Plagiorchis kirkstallensis from Lymnaea stagnalis

Body	0.275 (0.266 - 0.285) long x 0.118 (0.098 - 0.129) wide
Tail	0.216 (0.201 - 0.228) long x 0.027 (0.027 - 0.030) wide
Oral sucker	0.052 (0.049 - 0.053) long x 0.053 (0.049 - 0.057) wide
Acetabulum	0.041 (0.038 - 0.046) long x 0.036 (0.034 - 0.038) wide
Prepharynx	0.005 (0.004 - 0.008) long
Pharynx	0.020 (0.019 - 0.023) long x 0.020 (0.019 - 0.023) wide
Oesophagus	
Preacetabular extent	0.130 (0.122 - 0.141) long
Postacetabular extent	0.110 (0.095 - 0.122) long
Stylet (overall)	0.032 (0.028 - 0.034) long x 0.005 (0.004 - 0.009) wide
Stylet (shoulder)	0.008 (0.008 - 0.010) wide
Stylet (base)	0.008 (0.006 - 0.011) wide
Sporocyst	1.183 (0.518 - 1.820) long x 0.196 (0.140 - 0.280) wide

Penetration and Encystment

Larvae of several freshwater insects (Chironomus plumosus, Phryganea sp., Leptocerus sp., Dytiscus marginalis and Coenagrion sp.), were collected from Kirkstall Power Station (Leeds-Liverpool Canal) and were found to be infected with metacercariae of P. kirkstallensis. Because of the difficulties of obtaining naturally uninfected larvae, a series of experiments to study penetration and encystment was performed using only the larvae of Chironomus plumosus and Aedes aegypti.

The larvae of C. plumosus were purchased commercially. They were carefully examined alive for the presence of natural infections and no metacercarial stages were found. Fifty per cent of these larvae were used as experimental controls. The larvae of A. aegypti were reared in the laboratory.

Penetration and encystment were observed in both insect species but only that in Chironomus larvae is described below.

A large number of recently emerged cercariae was placed together with the insect larvae into small vessels containing a small amount of water. The cercariae did not exhibit any obvious directional response to the presence of the insect larvae but as soon as they came into contact with the host they attached themselves by means of their suckers and started crawling over its body surface, searching with the stylet for a suitable penetration site. The cercariae penetrated the host cuticle with the aid both of their stylet and of the cystolytic contents of the penetration gland-cells which appeared to dissolve the cuticle. The insect larvae reacted to penetration by performing vigorous movements. The tail of the cercaria lashed violently during the initial phase of penetration but usually became detached before penetration was completed. On several occasions, however, cercariae were seen bearing their tails after penetration. Very few cercariae either resumed swimming after the initial attachment to the host or failed to penetrate and encyst within it. The cercariae encysted soon after effecting entry into the host, although some specimens migrated a considerable distance within the body cavity before encystment occurred. The stylet was sometimes shed during or after encystment but sometimes it persisted either embedded in the oral sucker or free within the cyst. After entry into the host the body of the tail-less cercaria underwent a series of contracting movements and the contents of the cystogenous gland-cells were completely discharged to form a thin transparent wall around the parasite.

The cercariae encysted primarily in the muscle fibres and in the fat bodies. Less frequently cysts were found in the posterior false legs. The most common sites of entry were the intersegmental articulations of the thorax and abdomen. Several cercariae were seen to pass into the anal aperture, penetrate the wall of the rectum and encyst in the body cavity. The entire process of penetration and encystment was completed in between 4 and 16 minutes.

Metacercaria (Plate 38 Fig. 7)

In newly formed cysts the metacercariae exhibited rapidly rotating movements. The oral sucker, acetabulum, pharynx, and the rest of the digestive system were

essentially unchanged from the previous larval stage. The contents of the cystogenous gland-cells were absent but those of the penetration gland-cells were still present. The stylet in some specimens lay between the metacercaria and the cyst wall, but in the majority it could be seen embedded in the oral sucker. The caudal pockets were still visible. No excretory granules were evident within the lumen of the excretory bladder. In 8 day-old cysts the oral sucker, acetabulum and pharynx had undergone a little development. The genital primordium was prepresented by an undifferentiated mass of cells lying on the right side at the equatorial acetabular level. The penetration gland-cells had lost most of their contents, but were still clearly recognizable. The outer cyst wall had accummulated yellow pigment around its margin and the bladder had increased in size and contained numerous highly refractile granules which gave it a characteristic dark colour.

Measurements of 8 day-old metacercariae of P. kirkstallensis experimentally obtained from C. plumosus and A. aegypti

Cysts	0.168 (0.167 - 0.171) long x 0.168 (0.167 - 0.171) wide
Oral sucker	0.058 (0.049 - 0.068) long x 0.073 (0.068 - 0.076) wide
Pharynx	0.032 (0.022 - 0.038) long x 0.023 (0.022 - 0.026) wide
Acetabulum	0.041 (0.041 - 0.041) long x 0.053 (0.053 - 0.053) wide

Infection of the final host

Metacercariae aged 2, 4, 8 and 16 days which had been reared experimentally in larvae of Chironomus plumosus and Aedes aegypti were fed using a stomach tube to 23 animals, including both mammals and birds, (see Table 10).

Two additional representatives of each species used in these experiments were kept as controls; none carried any helminth infection. No pigeon, chicken or duckling became infected and it appears likely that none of these is a suitable host.

Mice 1 and 2 and rat 1 probably failed to become infected because the metacercariae used were not sufficiently developed to establish themselves in the definitive hosts. The data available indicate that the metacercariae require at least 8 days in which to develop before they become infective.

Mice 5, 6 and 7 and rats 4 and 5, were each fed twenty five 16 day-old metacercariae to determine the duration of infection in the host. Faecal examination was conducted daily and eggs were first seen in the faeces of both rats and mice on the 8th day after which faecal examination was continued every other day. From the 30th day egg-production decreased gradually in both species and rat 4 and mouse 5 were killed and examined on the 32nd day; they were found to contain 5 and 12 sexually mature flukes respectively. On the 38th day, faecal examination did not reveal the presence of eggs in rat 5 although eggs were present in the faeces of mice 6 and 7. Rat 5 and mouse 6 were killed and examined; only 9 flukes were found in mouse 6 and none was found in rat 5. On the 42nd day after infection no eggs were seen in the faeces of mouse 7. It was autopsied on the same day and no flukes were found.

The results of these experiments show that the flukes reach maturity in 8 days post-infection. They did not establish themselves in the three experimental avian hosts but they reached maturity and survived in rats and mice for about 38 and 42 days respectively.

The latter hosts have proved to be the most suitable laboratory host for the development of Plagiorchis kirkstallensis.

The flukes recovered from the small intestine of the rats were morphologically indistinguishable from those obtained from the mice.

Plagiorchis kirkstallensis (Plate 38-39, Figs. 8-10 and 11, 12 and 14)

Description

Body elongated, flattened dorso-ventrally and tapering behind acetabulum. Cuticle thin and provided with minute spines, more numerous anteriorly but granually diminishing in size and number posteriorly, being absent on the posterior end of the body.

Oral sucker very muscular, subterminal, with the mouth directed ventro-anteriorly and followed by a short wide prepharynx. Pharynx spherical, with 4 lobes in front. The very short oesophagus is hardly discernible in some specimens; it bifurcates into caeca a considerable distance in front of the acetabulum. Caeca extending posteriorly and increasing in size, terminating

at the posterior extremity of the body.

Acetabulum very muscular, smaller than the oral sucker, inner margin is bordered by 9 small papillae.

Testes oval in form, with smooth edges, lying diagonally in middle of body, separated by the uterus. Vasa efferentia arising from anterior margin of each testis and passing forwards to enter cirrus sac separately. There is no vas deferens. Within cirrus sac, the ducts are enlarged to form bipartite seminal vesicle, comprising a proximal cylindrical part and distal spherical part. Seminal vesicle followed by pars prostatica, surrounded by prostatic cells occupying almost entire volume of cirrus sac and leading into a sinuous ejaculatory duct; covered with unarmed cuticle. Genital pore lies on left side of body anterior to acetabulum. Cirrus sac elongated, cylindrical, muscular and thick-walled; bent ventrally and usually extending from anterior border of ovary to genital pore.

Ovary oval or almost spherical, lying to right of the midline, behind acetabulum and from anterior margin of the anterior testis. Oviduct emerges from median lateral edge of ovary, turns dorsally and forms a loop before joining with seminal receptacle. Laurer's canal arises from lateral margin of seminal receptacle; it extends posteriorly, then anteriorly beside seminal receptacle and finally opens to exterior in the midline near posterior margin of ovary.

Oviduct continues posteriorly receiving the median vitelline duct and joins ootype which is surrounded by Mehlis's complex. From ootype the descending limb of uterus extends posteriorly describing a sinous course between the testes and almost reaching posterior end of body; ascending limb passes anteriorly close to anterior margin of anterior testis where it becomes the metraterm. This is surrounded by unicellular gland-cells, is provided with circular fibres, lines by thick cuticle and numerous gland cells and it extends to the genital pore.

Both male and female genital pores open into a shallow common genital atrium. Eggs abundant. Vitellaria consisting of numerous follicles distributed along both sides of body from slightly posterior to intestinal bifurcation to posterior

end of body. The vitelline follicles fuse post-testicularly. The transverse vitelline ducts extending in direction of middorsal line where they fuse to form vitelline reservoir lying behind ovary.

A large tubular excretory vesicle present, capable of marked expansion and opening to exterior via an excretory pore located ventrally near posterior end of body. Main excretory canal extends anteriorly between testes and divides into two ducts just behind ovary. A coiled secondary duct arises from each excretory duct and passes anteriorly to level of the posterior margin of acetabulum where it divides into anterior and posterior collecting ducts. The flame cell formula is the same as that of the cercaria - 2 [(3 + 3 + 3) + (3 + 3 + 3)] = 36.

Measurements of P. kirkstallensis obtained experimentally from rats and mice

Body	2.404 (2.340 - 2.643) long x 0.630 (0.591 - 0.736) wide
Oral sucker	0.218 (0.209 - 0.235) long x 0.213 (0.208 - 0.235) wide
Prepharynx	0.038 (0.019 - 0.058) long x 0.070 (0.062 - 0.081) wide
Pharynx	0.119 (0.110 - 0.127) long x 0.119 (0.104 - 0.138) wide
Oesophagus	0.011 (0.007 - 0.017) long
Acetabulum	0.163 (0.151 - 0.172) long x 0.162 (0.151 - 0.171) wide
Anterior testis	0.257 (0.239 - 0.296) long x 0.168 (0.155 - 0.195) wide
Posterior testis	0.282 (0.264 - 0.309) long x (0.148 - 0.182) wide
Ovary	0.195 (0.159 - 0.231) long x 0.135 (0.121 - 0.152) wide
Cirrus sac	0.508 (0.395 - 0.627) long x 0.065 (0.062 - 0.072) wide
Preacetabular extent	0.602 (0.567 - 0.671) long
Postacetabular extent	1.611 (1.582 - 1.799) long
Posttesticular extent	0.714 (0.637 - 0.892) long
Eggs	0.046 (0.043 - 0.049) long x 0.023 (0.022 - 0.024) wide

Egg and Miracidium (Plate 39, Figs.13a, b and c)

Studies on the eggs and miracidia were carried out both on extra-uterine eggs recovered from the faeces of experimentally infected mice and rats and on those collected from sexually mature worms which were allowed to oviposit in tapwater or in distilled water.

The eggs are yellowish-brown in colour, oval, operculated, and they have a small thickened projection or knob at the posterior end. The shell is thin and semi-transparent which facilitates the observation of development. The eggs are unembrionated when laid.

Newly extruded eggs include 4 to 5 vitelline cells with clear nuclei and granular cytoplasm. The ovum is located at one side (usually to the left) and slightly posterior to the operculum and is easily distinguishable from the vitelline cells.

Approximately 150 eggs were placed in water in each of 4 small glass containers which were sealed with a vaselined glass cover. Water was added from time to time to prevent desiccation due to evaporation and the eggs were incubated at room temperature (19 to 22^{o}C).

After 38 h. incubation the early embryo is in the morula stage and comprises between 4 and 6 blastomeres. The vitelline cells begin to coalesce and disintegrate. Between 2 and 3 days after incubation the number of embryonic cells increases and the vitelline cells are completely disintegrated. Their contents of the latter together with small vacuoles (probably lipoid in nature), may be seen surrounding the embryo which has increased in size to occupy much of the space within the egg capsule. The entire development of the miracidium is completed in 4 to 5 days. At this time the vitelline material is less dense and large vacuoles are formed, probably by the fusion of smaller ones. The miracidium is very active contracting and extending its body and often knocking the operculum. During three weeks observations no miracidium succeeded in emerging from its egg. In this period its movements decreased considerably and could only be induced by using intense light or slight coverslip pressure.

Several eggs which had been kept under similar laboratory conditions failed to produce a miracidium. It is probable that the eggs had not been fertilized before being laid.

The mature miracidium is ovate and somewhat pear-shaped in outline. The surface of the body is covered with cilia except for its anterior tip which is occupied by a protrusible apical papilla. The apical gland is saccular, has coarse granular contents and its duct opens at the anterior tip of the body. There are two large, symetrically-placed penetration gland-cells with fine granular cytoplasm situated slightly posterior to the equator of the body and opening at the anterior end at each side of the apex of the apical gland. The pronephridial system comprises 2 flame cells situated two thirds of the distance along the body together with their capillary ducts opening via lateral excretory pores located near the posterior end of the body. The nervous system is represented by an oval mass of cells just behind the apical gland. The germ cells are found at the posterior end of the body; they have a central nucleus and fine granular contents, but are not numerous.

Experimental infection of the first intermediate host

Since attempts to induce the hatching of eggs proved to be unsuccessful several freshwater snails, [12 Lymnaea stagnalis and 15 L. peregerj reared under laboratory conditions, were placed for 24 hours together with hundreds of incubated and non-incubated eggs in small vessels containing tap-water. The majority of the snails were seen feeding upon the eggs. The faeces of both L. stagnalis and L. peregger were examined and a few normal eggs, eggs with fully formed miracidia and empty shells were found. The presence of egg shells in the faeces suggested that some eggs had hatched in the digestive system of the snails. However, examination of the stomach, intestine and surrounding tissue of some of the snails which had ingested eggs did not reveal any mother sporocysts or other precercarial stages. The remaining snails were kept under favourable laboratory conditions. The snails were examined every other day for 5 weeks, but no cercaria were seen emerging from them. Later dissection of these snails again failed to reveal any larval trematodes.

Discussion

The absence of a seminal receptacle is one of the characteristics of the genus Plagiorchis according to Luhe (1899) and Looss (1899). However, Park (1936) in his description of P. noblei from Agelaius phoeniceus californicus in the U.S.A. recorded the presence of a seminal receptacle in young specimens. He was unable to trace this organ in old specimens and thus placed the trematodes in the genus Plagiorchis. Park suggested that the study of serial section was absolutely necessary for the generic diagnosis of Plagiorchis. Williams (1963) found a seminal receptacle in adults of P. noblei although he pointed out that this organ was difficult to observe in some specimens. Olsen (1937) set up a new genus Plagiorchoides to contain all forms having a seminal receptacle and nominated P. noblei as the type species. Also on the basis of the presence of seminal receptacle Mehra (1937) created a new genus, Neolepoderma, and included P. noblei Park, 1936 in it. The validity of the genus Plagiorchoides was accepted by Park (1939), Tubangui (1946) and Skrjabin and Antipin (1958). Yamaguti (1958) reviewed the genus Plagiorchis and included within his diagnosis trematodes without seminal receptacles or with very small ones and he regarded Neolepoderma Mehra, 1937 and Plagiorchoides Olsen, 1937, as as synonymous with Plagiorchis Luhe, 1899.

Several members of Plagiorchis have now been described with seminal receptacles. Stossich (1904) redescribed P. vespertilionis (Muller, 1784) reporting the presence of a seminal receptacle while Travassos (1927) indicated the presence of a "vesicule seminale femelle" in P. Luehi, Dollfus (1925) translated the original description of P. muris (Tanabe, 1922) and pointed out the presence of a small "receptaculum seminis" and Yamaguti (1954) found a small seminal receptacle in P. maculosus (Rudolphi, 1802). However, Angel (1958) was not able to see one either in whole mounts or serial sections and she therefore stated that "the presence or absence of a receptaculum seminis seems thus to be characteristic of doubtful value". A seminal receptacle is also present in P. rhinolophi Park (1939), P. potamonides Tubangui (1946)

P. goodmani Najarian (1961), P. dilimaneusis Velasquez (1964) and P. peterborensis Karelaars and Bourns (1968).

Several authors (Park, 1936; Williams, 1963; Kavelaars and Bourns, 1968) have expressed the opinion that the demonstration of a seminal receptacle required careful examination of serial sections, that it may be present only during the early stages of development and that it may be absent in some members of the genus. However, in my opinion, this organ seems to be a constant character within any one species of the genus Plagiorchis since all the specimens of both P. farnleyensis and P. kirkstallensis which were studied alive clearly showed the presence of a seminal receptacle filled with spermatozoa.

I agree with the opinion of Yamaguti (1958), Najarian (1961), Velasquez (1969) and Kavelaars and Bourns (1968) who suggest that the presence or absence of a seminal receptacle may be used as specific character within the genus Plagiorchis but not a generic one.

Of the Plagiorchis-type cercariae for which the life cycle has already been elucidated, the cercaria of P. kirkstallensis is closely related to those listed on page 190.

Only the cercariae of P. goodmani, P. dilimanensis, P. megalorchis and P. noblei have eight pairs of penetration gland cells and 36 flame cells. However, the cercaria of P. kirkstallensis differs from the cercariae of P. goodmani and of P. dilimanensis in the size and shape of the stylet. Further, in the cercaria of P. goodmani the caeca do not extend to the acetabulum, the tail is spinose, the main excretory duct arises subterminally from the branches of the bladder and the cercaria encysts precociously in the sporocysts, while the cercaria of P. dilimanensis differs from the cercaria of P. kirkstallensis in having a smaller body, prepharynx, acetabulum and tail.

The cercaria of P. megalorchis is separable from the cercaria of P. kirkstallensis since in the former the penetration gland-cells have fine granular contents and the base of the stylet is not reinforced. Although Rees (1952) did not give the measurements of fixed specimens, Khan (1961) found the same species emerging from Lymnaea stagnalis in sand pits at South Ockendon in London,

and provided such information. According to Khan's measurements the cercaria of P. megalorchis differs from the present species in having a smaller body, tail, oral sucker and acetabulum. In the cercaria of P. noblei there are no published details of the caudal pocket, caudal excretory duct, genital rudiments, oesophagus and caeca, so a comparison of these features is not possible, but the cercaria of P. kirkstallensis is distinguished from it in having a larger body and acetabulum, and in possessing lateral projections at the base of the stylet and long-hair like projections on the body-cuticle.

The cercaria of P. muris, was originally described by Tanabe (1922) as having four pairs of penetration gland-cells but later McMullen (1937a) suggested there are 7 or 8 pairs. Yamaguti (1943) gave some additional details of the morphology of this species and stated that there are seven pairs of penetration gland-cells with finely granular contents. Furthermore in the cercaria of P. (M) muris there is no caudal excretory duct, the body is filled with numerous refractile globules and it is known to encyst in the sporocyst.

The cercaria of P. laricola has 7 to 8 pairs of penetration gland-cells, but differs from the cercaria of P. kirkstallensis in its larger body, oral sucker and tail; in addition the main excretory ducts divide behind the acetabulum.

It is difficult to distinguish between the cercaria of P. peterborensis and the cercaria of P. kirkstallensis because for the former species there are no published details of the number of penetration gland-cells, flame cells, cystogenous gland-cells or of the morphology of oesophagus or caeca, but nevertheless this form differs from the cercaria of P. kirkstallensis in having a smaller body and in lacking both caudal excretory duct and lateral projections at the base of the stylet.

The cercaria of P. proximus and the cercaria of P. jaenschi differ from the cercaria of P. kirkstallensis in the number of penetration gland cells. Moreover the former has a smaller body and tail, and encysts in snails. In the cercaria of P. jaenschi the division of the main excretory duct takes place behind the acetabulum and its stylet lacks basal lateral projections.

Angel (1958) found variations in the length of the stylet of the cercaria of P. maculosus according to whether the measurements were made in living or formalin-fixed specimens as follows:- living 24.3 to 28.9µm, fixed 21.5 to 24 to 24.8µm. She stated "Precise length of the stylet should not be used as a diagnosis character for Plagiorchis maculosus". Even so both measurements given by Angel are smaller than for the cercaria of P. kirkstallensis. Further differences are that the body, oral sucker and acetabulum are smaller in the cercaria of P. maculosus than in the present species but full details of the penetration gland-cells and the flame cell formula are not available for P. maculosus.

The cercaria of P. microcanthos the body, tail, oral sucker and sporocysts are considerably smaller than in the cercaria of P. kirkstallensis, and the body is filled with numerous refractile granules. These differences are believed to be large enough to separate the two species.

Macy (1960) stated that certain details of the structure and size of the oesophagus and caeca and the number of penetration gland-cells and flame cells could not be seen in the cercaria of P. vespetilionis parorchis owing to the presence of numerous refractile granules and glandular cells occupying the postacetabular region of the body. However, the separation of this species from the cercaria of P. kirkstallensis can be made on the basis of measurements of certain structures such as body, tail, pharynx and acetabulum, which are considerably smaller in the cercaria of P. vespertilionis parorchis, as well as on the absence of hair-like projections and on the presence of numerous refractile globules.

The cercariae of P. berghei, P. laurenti, P. elegans and P. cirratus can each be easily separated from the cercaria of P. kirkstallensis in having six pairs of penetration gland-cells on each side, anterior to the acetabulum. Other characters which can be used to distinguish between these species include the very much smaller stylets of P. berghei and P. laurenti (27 x 5µm and 21 x 4.5µm respectively), encystment occurring in the sporocysts in P. elegans and the division of the primary excretory ducts being located posterior to the acetabulum

in P. cirratus.

The cercaria of P. fastuosus is characterized by the possession of four pairs of penetration gland-cells and intestinal caeca which are restricted to the region anterior to the acetabulum. This differs from the cercaria of P. kirkstallensis in which there are eight pairs of epenetration gland-cells and the caeca extend to near the posterior end of the body.

The life cycles of many xiphidiocercariae belonging to the Armatae group have not been yet elucidated. Some of these share with the cercaria of P. kirkstallensis the possession of eight pairs of penetration glands and 36 flame cells, namely: Cercaria guttera Fain (1953); C. holthauseni Rankin (1939); C. helvetica IV Dubois (1928); C. helvetica XXX Dubois (1928); C. blukwa Fain (1953); C. baldai Nasir (1964) and C. urceus Nasir and Acuna (1966). However, the cercaria of P. kirkstallensis differs from C. baldai, C. holthauseni and C. urceus in the size and shape of the stylet; from C. guttera, C. blukwa, C. helvetica IV and C. helvetica XXX in the nature of the contents of the penetration glands and the size of the stylet except that in C. helvetica XXX the dimensions of this structure are more or less the same as in the cercaria of P. kirkstallensis. Cercaria helvetica XXX, possesses a long oesophagus which divides immediately anterior to the acetabulum whereas in the cercaria of P. kirkstallensis there is a short oesophagus which bifurcates a considerable distance anterior to the acetabulum.

The cercaria of P. kirkstallensis resembles C. cambrensis III Rees (1932) from Wales and C. edgbastonensis Nasir (1960) from Birmingham in having the same number of penetration gland-cells but the encystment of these two latter forms take place in water whereas the cercaria of P. kirkstallensis encyst in several larvae of freshwater artropods and it has never been found to encyst in open water. Additionally C. cambrensis III, has only 18 flame cells and in C. edgbastonensis the intestinal caeca do not reach the acetabulum.

The cercaria of P. kirkstallensis closely resembles the cercaria of P. farnleyensis in morphological features and approximate measurements of body structures. However the following differences between the cercariae have been

noted:-

1. Pharynx length in P. kirkstallensis almost twice that of P. farnleyensis.
2. Acetabulum of P. kirkstallensis larger than that of P. farnleyensis.
3. Caeca of P. kirkstallensis reach posterior end of the body; in P. farnleyensis they extend just behind of the acetabulum.
4. Refractile globules of P. kirkstallensis are absent; in P. farnleyensis they are present (numerous).
5. Cystogenous gland-cells of P. kirkstallensis are numerous extending from mid-level of pharynx almost to posterior end of the body; in P. farnleyensis they are located mainly laterally and around acetabulum.
6. Sporocyst of P. kirkstallensis larger than that of P. farnleyensis.

The adult of P. kirkstallensis is closely similar to that of P. muris, P. jaenschi, P. peterborensis, P. (M) cirratus, P. elegans, P. vespertilionis, P. proximus, P. (P) berghei, P (P) laurenti, P. noblei, P. maculosus, P. dilimanensis, and P. goodmani.

1Plagiorchis kirkstallensis may be separated from P. goodmani by the following characters: (1) a genital atrium is present, (2) the testes are half the size of those of P. goodmani. P. kirkstallensis differs from P. proximus, P. elegans, P. dilimanensis and P. jaenschi in that the pharynx, acetabulum, testes and ovary are about twice or more than twice the size of these in the latter species except that in P. jaenschi the acetabulum is about equal in size. The eggs of P. kirkstallensis are distinctly larger than in those other species. P. kirkstallensis differs from P (P) berghei and P (P) laurenti in its possession of a much smaller oesophagus, by the presence of a glandular metraterm, by the absence of a vas deferens and finally because these two species are apparently restricted to amphibians.

Plagiorchis vespertilionis parorchis and P. microcanthos may be distinguished from P. kirkstallensis by the absence in them of a seminal receptacle, by the much smaller size of their eggs and by greater extent of their body spines.

Plagiorchis (M) cirratus differs from P. kirkstallensis by the absence in the former of prepharynx, oesophagus and seminal receptacle and in that the

vitelline follicles form an anterior commissure between the acetabulum and oesophageal bifurcation.

According to Yamaguti (1954) a small seminal receptacle was present in the single specimen of P. maculosus described from Sturnia philippinensis but Angel (1958) could not find this organ either in whole mounts or in serial sections. Nevertheless this species can be separated from P. kirkstallensis by the possession of suckers about the same size, or oral sucker slightly larger than acetabulum in the former species compared to the much larger size of oral sucker than the acetabulum in the latter. The egg sizes also differ (P. maculosus - 0.030 x 0.019 mm, P. kirkstallensis - 0.046 x 0.023 mm).

Biological differences similar to those used in the separation of P. farnleyensis from P. peterborensis may also be utilized to distinguish between the latter species and P. kirkstallensis. In P. peterborensis using the same secondary and final experimental hosts maturity is attained 14 days after feeding, instead of 8 days as in P. kirkstallensis. The adult forms of P. kirkstallensis and P. peterborensis can be distinguished in the following respects: in P. peterborensis the posterior extremity of the cirrus sac touches the anterior border of the anterior testis and the ovary is situated just behind the right side of the acetabulum, sometimes overlapping it, whereas in P. kirkstallensis the ovary lies farther back from the acetabulum and the posterior extremity of the cirrus sac never touch the anterior testis.

One of the important diagnostic features used by Kavelaars and Bourns (1968) to distinguish between P. peterborensis and P. muris was the size of the eggs. Egg dimensions in P. peterborensis are 0.038 - 0.041 mm x 0.020 - 0.024 mm compared with 0.038 mm x 0.019 mm for P. muris. According to the original description (Tanabe, 1922) the size of the eggs in P. muris is 0.030 mm x 0.020-0.023 mm. Both species differ from P. kirkstallensis in which egg size is 0.046 mm x 0.023 mm. The larger body and pharynx, the length of the cirrus sac, the absence of anterior commissure and the presence of a glandular metraterm additionally serve to separate P. kirkstallensis from P. muris.

Plagiorchis noblei resembles P. kirkstallensis more closely than those other species in its morphology and in the relative size of body and internal organs. Williams (1963) failed to infect mice which were fed with 3-6 and 6-8 day-old metacercariae obtained experimentally from Aedes aegypti. He obtained similar negative results after feeding a large brown bat, Eptesicus fuscus fuscus, with 6-12 day-old metacercariae from A. aegypti. His experiments clearly indicated that mammals are not suitable experimental hosts for P. noblei. The adult forms of P. noblei were experimentally obtained from chickens fed with 4-6 day-old metacercariae from A. aegypti. However mice and rats proved to be suitable experimental hosts for P. kirkstallensis while chickens, ducklings and pigeons were unsuitable. The egg size can also be used to distinguish between these two related species. In P. noblei the eggs are 0.035 - 0.040 mm x 0.019 - 0.020 mm. as compared to the dimensions given above for the eggs of P. kirkstallensis.

The adult forms of P. kirkstallensis and P. farnleyensis differ markedly in the size of body, prepharynx, testes, ovary, cirrus sac and eggs. The measurements of the eggs are as follows: P. kirkstallensis 0.046 mm x 0.023 and P. farnleyensis 0.030 mm x 0.017 mm.

The life cycles of these two species are very similar to each other in that both P. kirkstallensis and P. farnleyensis have been cultured in vivo using the same first, second and final experimental hosts. The latter species has less rigid host specificity and can develop in both mammals and birds while P. kirkstallensis has only been experimentally shown to develop in mammalian hosts.

Another interesting character which separates these two species is the protonephridial system of the miracidium in P. kirkstallensis which comprises two flame cells and one in P. farnleyensis.

Table 10

Experimental infection of mammals and birds with the metacercariae of Plagiorchis kirkstallensis n.sp. from Chironomus plumosus and Aedes aegypti (25-30 cysts administered to each host)

Experimental definitive host	Age of Cysts (Days)	Eggs detected in faeces (+ or -) (Days)	Host autopsied after - (Days)	Number of trematodes recovered
Mouse 1	2	-	2	0
Mouse 2	4	-	4	0
Mouse 3	8	8+	8	16
Mouse 4	8	8+	8	14
Mouse 5	16	32+	32	12
Mouse 6	16	38+	38	9
Mouse 7	16	42-	42	0
Rat 1	2	-	2	0
Rat 2	8	8+	8	12
Rat 3	16	8+	18	10
Rat 4	16	32+	32	5
Rat 5	16	38-	38	0
Pigeon 1	2	-	2	0
Pigeon 2	10	-	8	0
Pigeon 3	16	-	8	0
Chicken 1	2	-	2	0
Chicken 2	8	-	4	0
Chicken 3	16	-	8	0
Chicken 4	16	-	8	0
Duckling 1	2	-	2	0
Duckling 2	8	-	4	0
Duckling 3	16	-	8	0
Duckling 4	16	-	8	0

Microcercous Cercariae

Luhe (1909) defined the members of microcercous group as Distome cercariae with stumpy tails. Dollfus (1914) created a new group, Cotylocercous cercariae, which he considered to be a natural sub-division and distinguished between it and the other members of this group. He included the marine cercariae, Cercaria pachycerca Diesing (1858), C. brachyura Lespes (1857), C. cotylura Pagenstecher (1862), C. linearis Lespes (1857) and C. buccini Lebouur (1912) but excluded C. micrura Filippi (1857) as it is a freshwater form. He described this group as follows:

Cercariae developing in simple sporocysts in marine gastropods; oral sucker provided with a stylet, penetration gland cells occupying the greater part of anterior region of body; excretory bladder large, not bifurcate and wall formed by a single layer of granular cells; tail a very short cup-like organ with thick walls, provided with large cells and acting as a sucker.

Cort (1915) considered that C. micrura could not be excluded from the tylocercous group Dollfus (1914) on the sole basis of its occurrence in freshwater molluscs. Sewell (1922) created the Linearis sub-group and included in it Cercaria pachycerca Diesing, 1858 (= C. brachyura Lespes, 1857), C. linearis Lespes, 1857, C. buccini Lebour, 1912, and C. indicae XXXVIII, On the basis of certain morphological characters, i.e. the presence of the oesophagus, intestinal caeca and stylet, he referred C. micrura Filippi, 1857, C. pachycerca Pelseneer (1906) nec Diesing (1858) and C. cotylura Pagenstecher (1862) to the other sub-group.

Cable (1938) propounded a new classification of the Microcercous cercariae recognizing five groups based on the description of the larval stages and life cycles studies, and he created a new group, Cotylomicrocercous, to include Cotylocercous cercariae. Cable described these groups as follows:

Group I. Cotylomicrocercous cercariae (Cotylocercous Dullfus, 1914 in part)

Tail modified to form a sucker-like organ of adhesion.

1. Linearis Sub-group (Sewell, 1922 in part)

Stylet simple or cleft; preacetabular penetration gland

cells present; excretory vesicle large, non-bifurcated with a thick wall composed of a single layer of granular cells, glandular in appearance. Each ascending excretory ducts divided to form anterior and posterior cellecting ducts, or reflexed anterior to acetabulum with recurrent duct receiving all of the flame cell capillaries. Develops in sporocysts or possibly very simple rediae in marine or freshwater gastropods. Adult stages members of the family Allocreadiidae Stossich, 1904.

2. Cotylura Sub-group

Stylet absent. Develop in simple sporocysts in marine molluscs only, otherwise similar to the members of the Linearis sub-group.

Group II. Sulcatomicrocercous cercariae.

Tail small, triangular, grooved ventrally. Ventral aperture near posterior end of the body receiving the ducts of a cluster of unicellular glands. Stylet present, simple. Numerous penetration gland cells present. Excretory bladder heart-shaped, thick-walled; ascending excretor ducts divided, forming flame cells capillaries. Develop in rediae in freshwater snails. Adult stages members of the family Troglotrematidae Odhner, 1914.

Group III. Chaetomicrocercous cercariae.

Tail knob-like, spinose with a group of large spines at the tip. No ventral aperture with gland cells as in the Sulcatomicrocercous group. Stylet simple. Numerous penetration gland cells present. Excretory bladder oval-shaped, with thick walls. Develop in rediae in freshwater gastropods. Adult stages are mammalian lung flukes and members of the family Troglotremidae Odhner, 1914.

Group IV. Obscuromicrocercous cercariae (Sewell's Helicis Group of Cercariae in part)

Tail very small, cap-like, often indistinctly separated from the body. Stylet absent, pharynx present. Excretory bladder small, thin-walled, usually extending into the tail with paired openings at

its tip. Ascending excretory canals extend anteriorly as far as pharynx, then posteriorly almost to the end of the body, and anteriorly again before receiving the collecting ducts. Develop in branched or vermiform sporocysts which sometimes have hard cuticular spines, in terrestrial molluscs. Adults of the family Brachylaimidae Joyeux and Foley, 1930.

Group V. Ephemerocmicrocercous cercariae

Tail a knob of vesicular cells disappearing in the latter stages of cercarial development. Pharynx and stylet absent. Develop and encyst in sporocysts without escaping from them. Parasites of freshwater bivalve molluscs. Adult stages members of the family Gorgoderidae Looss, 1901.

Dobrovolny (1939a) gave a list of freshwater and marine Cotylocercous cercariae and regarded the Microcercous cercariae as an artificial group. Dollfus (1960) presented a complete list of freshwater and marine Cotylocercous cercariae together with their geographical distributions, a few remarks concerning some of the previously described forms and a list of their hosts where their encystment or penetration is known. Dollfus also pointed out that the Cotylocercous cercariae which are developed in the sporocysts do not belong to the same major group as the Allocreadioidea, which develop in radiae and do not have Cotylocercous cercariae.

I have followed Cable's (1938) classification of the Microcercous cercaria and the cercaria found in the present study belong to the group Cotylomicrocercous, Linearis sub-group.

Cercaria microcercous I

Infected Bithynia tentaculata were obtained during 1973, 1974 and 1975 from 3 localities - Kirkstall Power Station (Leeds-Liverpool Canal), Newmillerdam Lake and Wintersett Lakes. The incidence of infection was greatest at Kirkstall where it varied from 5-10% in late spring to 20-40% in late summer. At the other 2 localities infections of only approximately 3-5% were recorded.

Cercaria are released throughout the day in small numbers. They do not swim actively and are found adhering by their tail to the substrate with their bodies held vertically. The oral sucker and tail are used for locomotion in a leech-like manner.

Description (Plate 40 Figs. 1-4)

Body elongate, covered with spines. Anteriorly provided with a row of 7 setate papillae and, containing refractile globules more numerous anteriorly than posteriorly.

Tail bell-shaped with a posterior invagination forming a muscular structure resembling a sucker which is protrusible and can be used as an adhesive organ. Central part of tail occupied by gland-cells and finely granular contents which secrete a viscous substance presumably involved in adhesion of cercaria to substrate.

Oral sucker muscular, subterminal. Stylet simple and located in dorsal wall of oral sucker. Mouth subterminal, large prepharynx muscular pharynx. Oesophagus curved. Intestinal caeca terminating close to posterior margin of acetabulum and containing dense granular material.

Acetabulum behind mid-line of body; aperture surrounded by 3 irregular rows of small spines.

Penetration gland-cells arranged in 2 groups of 6 cells on each side of acetabulum and each possessing a central spherical nucleus and coarsely granular cytoplasm; their ducts opening on anterior margin of body. Cystogenous gland-cells arranged mainly in 2 large regular columns on each side of body and with finely granular contents. Rudiments of genitalia comprise 2 cell-masses located immediately anterior and posterior to acetabulum.

Excretory bladder usually rectangular, sometimes oval, its walls covered internally with several layers of granular cells with coarsely granular cytoplasma; primary excretory ducts open from bladder anteriorly and follow a sinuous course, each giving rise to anterior and posterior collecting ducts just lateral to bifurcations of oesophagus. Anterior collecting ducts divide into 2 branches each receiving 2 flame cells; posterior duct bends posteriorly dividing at level of acetabulum with 2 branches, each receiving 2 flame cells. Flame cell formula: $2\left[(2 + 2) + (2+ 2)\right] = 16$. Excretory bladder opens to exterior through a pore at its base.

Sporocyst (Plate 40 Fig. 5)

Infection occurred in the hepatopancreas of Bithynia tentaculata where the sporocysts were very numerous. They are elongate and have a thick wall full of dark brown granules. A Birth pore was not observed. The proto-nephridial system consists of a principal excretory duct from which 6 capillaries originate, each with one large mushroom-shaped flame-cell. Each cell contains numerous cilia which remain active for more than 5 hours, in saline. The sporocyst is full of cercariae as well as numerous irregular germ balls.

The metacercarial cyst (Plate 40 Fig. 6)

A small number of cercariae encyst within the sporocysts without emerging but the majority leave the primary host, penetrate and encyst in a variety of invertebrates and vertebrates.

All the mollusc species exposed experimentally to the cercariae became infected; they were Physa fontinalis, Planorbis vortex, P. carinatus, P. corneus and Lymnaea peregger. The freshwater oligochaete Chaetogaster sp. common in the Kirkstall locality where infected B. tentaculata were found, were penetrated by some cercariae which formed metacercarial systs in the body cavity. Additionally metacercariae cysts identical to those in molluscs and in Chaetogaster sp. occurred in the body cavity, some free and some adhering to the gut wall, of several stone loach (Noemacheilus barbatulus) caught in the

canal at Kirkstall. It is not known how the cercariae arrived in the body cavity of this fish but it is considered possible that they were swallowed and subsequently penetrated the gut wall.

15-day-old metacercaria

A number of 15-day old cysts were obtained from Physa fontinalis exposed to the cercaria under laboratory conditions. They are oval in form and possess a thin, transparent and flexible wall which allows some expansion of the metacercaria. The stylet moves freely within the interior of the cyst. The digestive system of the metacercaria is clearly visible and there is a considerable increase in the granular contents of the caeca. The genital rudiments exhibit no sign of development but the acetabulum is markedly larger than in the cercaria. The contents of the penetration gland-cells remain the same whereas the cystogenous gland-cells are completely empty. The excretory bladder is smaller than in the younger specimens and is full of irregular refractile bodies. The contents of the glandular cells of the bladder were totally discharged into the bladder lumen. The flame cell number remains constant. No tail is present in any of the metacercariae.

Measurements of Cercaria microcercous I from Bithynia tentaculata

Body	0.265 (0.216 - 0.296) long x 0.083 (0.079 - 0.087) wide
Tail	0.037 (0.034 - 0.038) long x 0.029 (0.026 - 0.030) wide
Oral sucker	0.040 (0.038 - 0.041) long x 0.040 (0.038 - 0.045) wide
Acetabulum	0.047 (0.041 - 0.049) long x 0.047 (0.042 - 0.049) wide
Prepharynx	0.032 (0.019 - 0.041) long
Pharynx	0.018 (0.015 - 0.019) long x 0.020 (0.019 - 0.022) wide
Oesophagus	0.038 (0.034 - 0.041) long
Preacetabular extent	0.134 (0.117 - 0.152) long
Postacetabular extent	0.079 (0.064 - 0.095) long
Stylet (overall)	0.009 (0.007 - 0.010) long x 0.003 (0.003 - 0.003) wide
Stylet (shoulder)	0.003 (0.003 - 0.003) wide
Sporocyst	0.996 (0.657 - 1.578) long x 0.236 (0.184 - 0.263) wide
Cysts	0.188 (0.169 - 0.213) long x 0.159 (0.153 - 0.172) wide

Experimental infections

A series of experiments was carried out in order to establish the life cycle of C. microcercous I. The cysts used in these experiments came from snails infected both naturally and experimentally. Some of the experimental animals were fed isolated cysts, others were fed the whole mollusc after removal of the shell.

Experiment 1.

Eighty ten-day-old cysts were introduced orally into each of

4 Rattus norvegicus

5 Mus musculus

3 Gallus domesticus

4 Columbia livia

Faeces were examined for the presence of trematodes eggs for 7 days. None were present. These animals were killed and examined but none carried trematode infections.

Experiment 2.

Eight snails containing 28 day-old cysts were fed to each of

4 Tilapia mossambica

3 Salmo trutta

9 Lebistes reticulatus

4 Cottus gobio

Faeces were examined as in experiment 1 and the animals were killed and examined after 9 days but no trematodes were found.

Experiment 3.

Six snails containing metacercarial systs between 20 and 45 days old were fed to each of

3 Barbus conchonius

4 Noemacheilus barbatulus

4 Helostoma temminchi

3 Leuciscus (Squalius) cephalus

4 Phoxinus phoxinus

4 Rutilus rutilus

Two specimens of each species were killed and examined after 8 days, when 25 immature parasites were recovered - 18 from L. (S) cephalus, 2 from P. phoxinus and 5 from R. rutilus. The remaining fishes were examined between 2 and 7 days later and 7 additional immature parasites were recovered from L. (S) cephalus.

Experiment 4.

Twenty-two snails carrying metacercarial cysts aged between 10 and 75 days were fed to

7 Leuciscus (Squalius) cephalus

The faeces of these fishes were examined 15 and 42 days after feeding, but no trematode eggs were seen. The animals were killed and examined after

days and from 2 of them 2 and 3 immature parasites were obtained respectively. The stage of development of the immature parasites was similar to those recovered from experiment 3.

It may be concluded that Leuciscus (squalius) cephalus constitutes a possible final host.

The Juvenile form (Plate 40, Fig. 7)

In 15 day-old immature parasites from chub a marked increase in the size of the suckers over that of the cercaria was observed, with the acetabulum growing more rapidly to occupy almost the whole of the middle of the body. The prepharynx shrinks, becoming almost invisible while the pharynx and oesophagus became larger and strongly muscular. The caeca show a small extension relative to the acetabulum. The penetration gland persist just to each side of the oesophagus and they contain pale yellow granules. The cuticle of the body is thicker and its spines disappear.

There are 2 small ovoid testes situated postero-laterally to the acetabulum and a short efferent duct opens postero-dorsally from each one. The ovary is small and is located on the mid-line of the body, behind the acetabulum. The oviduct originates from the central margin of the ovary and passes into

the Mehlis' complex. The currus sac is small extracaecal and situated at the antero-lateral level of the acetabulum. It is represented by aggregations of poorly differentiated cells. The rest of the reproductive system is not clearly defined. The measurements of the immature parasites are:

Body	0.358 (0.307 - 0.418) long x 0.161 (0.155 - 0.177) wide
Oral sucker	0.066 (0.045 - 0.087) long x 0.072 (0.049 - 0.091) wide
Acetabulum	0.113 (0.102 - 0.125) long x 0.116 (0.102 - 0.136) wide
Pharynx	0.034 (0.026 - 0.041) long x 0.032 (0.026 - 0.041) wide
Oesophagus	0.036 (0.030 - 0.045) long
Anterior testes	0.032 (0.015 - 0.057) long x 0.031 (0.015 - 0.045) wide
Posterior testes	0.033 (0.019 - 0.041) long x 0.028 (0.011 - 0.041) wide
Ovary	0.017 (0.011 - 0.022) long x 0.017 (0.011 - 0.022) wide
Preacetabular extent	0.148 (0.125 - 0.178) long
Postacetabular extent	0.103 (0.079 - 0.140) long
Cirrus sac	0.037 (0.034 - 0.041) long x 0.015 (0.011 - 0.019) wide

It is clear that these trematodes are members of the genus Sphaerostoma (Sub-family Sphaerostomatinae of the family Opecoelidae Ozaki, 1925).

The comparison of these specimens with other species of this genus was not possible because certain characters of taxonomic importance such as the genital system were not fully developed.

Discussion

It appears that the metacercaria of this trematode possesses a wide range of potential second intermediate hosts, cysts having been found in gastropods, an oligochaete annelid and a fish. Cable (1938) reported that cercaria sp. trichoderma will penetrate and encyst in a wide variety of invertebrates forms including Chaetogaster sp. and Tubifex sp. (Oligochaeta; Euplanaria dorotocephala (Platyhelminthes). and even other cercariae of its own species and of C. kentuckiensis Cable (1935a). The cercaria of Plagioporus lepomis Dobrovolny (1939b) penetrated and encysted in Hyalella knicherbocheri; many species of Chironomidae; Hydroporus sp. (Arthropoda, Insecta) and they penetrated

but did not develop in simuliid larvae, Ostracods and Daphnia (Arthropoda, Crustacea) Dobrovolny (1939b).

Unfortunately sexually mature specimens were not recovered during the infection experiments described above but it seems likely that Cyprinid fishes may prove to be the definitive hosts. Sphaerostoma bramae has been recorded from freshwater fishes on numerous occasions in Britain, see Chappell and Owen (1969) and Kennedy (1974) but it is clear that the cercaria described in the present account differs from that of S. bramae in several important features.

A comparison of Cercaria microcercous I with other microcercous cercariae is given below:

Microcercous cercaria recorded from freshwater molluscs are:

Cercaria micrura Filippi (1857) in Bithynia tentaculata [= larva of Sphaerostoma bramae Muller (1776) according to Sinitsin (1905)].

Cercaria myzura Pagenscher (1881) in Neritina (Theodoxia) fluvialitis [= larva of Allocreadium angusticole Hausmann (1896) according to Mathias (1937)].

Cercaria of Plagioporus silicus Sinitsin (1931) in Goniobasis plecifera

Cercaria of Plagioporus virens Sinitsin (1931) in Fluminicola virens

Cercaria of Plagioporus sinitsini Mueller (1934) according to Dobrovalny (1939) in Goniobasis livescens.

Cercaria of Plagioporus lepomis Dobrovolny (1939) in Goniobasis livescens.

Microcercous cercaria B. Kobayashi (1922) in Melania libertina.

Microcercous cercaria D. Kobayashi (1922) in Melania sp.

Cercaria incerta (Kobayashi, 1922) Faust, (1924) as described by Ito (1953) in Semisulcospira sp.

Cercaria trichoderma Cable (1935b) in Goniobasis semicarinata

Cercaria trichocephala Cable (1939) in Goniobasis depygis.

Cercaria abbrevistyla Cable (1939) in Goniobasis depygis

Cercaria dioctorenalis Dobrovolny (1939a) in Goniobasis livescens

Cercaria indicae XXXVIII Sewell (1922) in Paludomus transchorica

Cercaria Kolea Balozet (1953) in Amnicola dupotetiana

Cercaria trioctorenalis Dobrovolny (1939) in Goniovansis livescens.

Cercaria inaurata Balozet (1953) in Melanopsis algerica

Cercaria triglandularis Probert (1965) in Bithynia tentaculata

Of these C. micrura (Cercaria of Sphaerostoma bramae) Cercaria of P. sinitini, C. abbrevistyla, C. dioctorenalis, cercaria of P. lepomis, C. kolea, C. trichoderma and C. incerta possess 16 flame cells as in C. microcercous I but only C. abbrevistyla possesses 6 pairs of penetration gland-cells.

C. microcercous I also resembles C. abbrevistyla in the size of the tail and in the oral and ventral suckers but differs from it in the following respects:

1. The body of C. microcercous I measures 0.256 by 0.081 mm whereas that of C. abbrevistyla measures 0.205 by 0.115 mm.

2. The intestinal caeca of C. microcercous I just reach the posterior level of the acetabulum and they contain granular material whereas in C. abbrevistyla they extend as far as the posterior part of the body and are empty.

3. The aperture of the acetabulum is surrounded by 3 rows of spines and the aperture of the oral sucker is unarmed in C. microcercous I but both suckers are provided with 5 rows of spines in C. abbrevistyla.

4. In C. microcercous I the excretory bladder is located a considerable distance from the posterior part of the acetabulum, whereas in C. abbrevistyla the anterior part of the bladder is displaced to one side and reaches the equatorial level of the acetabulum.

5. There are 7 setate papillae on the anterior part of the body in C. microcercous I as compared with C. abbrevistyla which has delicate "articular hairs" scattered over the entire body according to Cable (1939).

These morphological and physiological differences serve to distinguish between these two species. However, several characters, such as the structure of the excretory ducts and the formation of the cyst while known for C. microcercous I have not yet been described for C. abbrevistyla.

The cercaria of S. bramae (FIL.) as described by Luhe (1909), Wesenberg-Lund (1934), Wikgren (1956) and Pike (1967) is characterized by having 4 pairs of

penetration gland-cells, so that C. microcercous I can be readily separated from this species by the presence of 6 pairs of penetration gland-cells.

Cercaria microcauda Llewellyn (1957) and C. triglandularis Probert (1965) have been described from South Wales. While these two forms are closely related to C. microcercous I, they can be distinguished from it by having 4 and 3 pairs of penetration gland-cells respectively.

Cystocercous Cercariae

Luhe (1909) described the members of this group as cercariae with a caudal appendage which is much longer than the body, an anterior end which forms a chamber into which the body of the cercariae may be retracted; without eyespots, and either with or without a stylet. He attributed to this group Cercaria mirabilis Braun (1891) and C. cystophora Wagener (1860), and the macrocercous forms (the larval stages of Gorgoderinae Looss, 1899) which were characterized by having a rather cylindrical unforked tail, piercing spines, and the development occurring in Sphaerium.

Sewell (1922) has stated that the Cystocercous cercariae group is not a natural group and has divided it into three sub-groups. The first sub-group is the Gorgodera group (type, Cercaria macrocera Filippi (1854) together with C. gorgodera cygnoides and C. Gorgodera varsoviensis Sinitsin (1905) to which he assigned the cercariae of the members of the genus Gorgodera Looss, 1899. He characterized this group as follows:

1. Tail cylindrical and tapering, without any marked swelling in its basal portion.
2. Anterior end of the tail forming a chamber with a length of one-tenth or less of the total tail-length into which the body of the worm may be retrated.
3. Stylet present, bearing several points.
4. Acetabulum considerably larger than the oral sucker; four to nine penetration gland cells.
5. Excretory bladder narrow, elongated and extending nearly to the posterior margin of the acetabulum.
6. Developed in sporocysts with complicated excretory systems.
7. Encysted in aquatic insect larvae

The second sub-group is the Gorgoderina group. This group comprises the cercariae of the members of the genus Gorgoderina Looss, 1902. It is defined as follows:

1. Anterior end of the tail forming a cavity which may enclose the body

of the cercaria, behind this is a marked pear-shaped swelling containing a number, of spherical cells. Its posterior portion is cylindrical and tapering and the dilated anterior part is approximately one-third of the total length.

2. Stylet present, bearing several spinose points.

Acetabulum equal or slightly larger than the oral sucker, several penetration gland cells.

3. Developing in sporocysts.

The third sub-group is the Appendiculata group. Sewell created this group to accommodate Cercaria appendiculata Pelseneer (1906), C. vaullegardi Pelseneer (1906) and C. indicae XXV Sewell (1922) which are all very closely related, he also considered C. cystophora Wagener (1866) to be closely related to them. This group is defined as follows:

1. Body somewhat elongate, colourless and transparent; sucker isodiametric
2. Mouth leads back to a pharynx which is followed by a triclad gut.
3. Excretory bladder elongated nearly reaching the acetabulum.
4. Tail complex, consisting of two parts, a distal flattened or cylindrical process, and a proximal rounded or oval, and much swollen portion that forms a cyst containing a long slender filament.
5. Develop usually in rediae which in turn arised from sporocysts. The redia has a pharynx and gut but no locomotory appendages.

Sewell separated Cercaria mirabilis Braun (1891) from Cystocercous cercariae of Luhe (1909) and erected a separate division named the Mirabilis group, which he included in the Furcocercous cercariae. Wesenberg-Lund (1934) agreed with Sewell's inclusion of the Mirabilis group in the Furcocercous cercariae. Wesenberg-Lund divided Cystocercous cercariae into two groups: (1) Macrocercaria which included Gorgodera and Gorgoderina groups (Sewell, 1922) and (2) Cyrstropha group. He included all the European Macrocercariae in the Gorgodera and Gorgoderina groups which he separated on the basis of the size of the chamber of the tail. The Cyrstropha group is very closely related to the Appendiculata group of Sewell (1922). In the members of this group the tail is divided into

several parts provided with various appendages and development occurs in sporocysts or rediae. He listed twelve forms, both marine and freshwater, in this group.

Miller (1936) recognised three groups of Cystocercous cercariae; Cystocercous, Cystophorous and Macrocercous (Gorgoderine) cercariae. Apparently Miller did not accept the allocation of Mirabilis group in the Furcocercous cercariae since he placed it among the Cystocercous cercariae and did not subscribe to Sewell's division of the Macrocercous cercariae into Gorgodera and Gorgoderina groups because experimental evidence for such a division was lacking. He also gave a complete list of all the Cystocercous cercariae in the three groups known at that time.

All the gorgoridid cercariae exhibit many similarities varying mainly in the structure of the tail, the presence or absence of the stylet, the excretory system and encystment behaviour.

I have followed the classification scheme of Sewell (1922). The cercaria found in this study is a Cystocercous type and falls into Gorgoderina group Sewell (1922).

Cercaria macrocerca I

In the spring and summer of 1973, 1974 and 1975, 830 specimens of Sphaerium corneum were collected from Kirkstall Power Station (Leeds-Liverpool Canal). About 15% of the bivalves examined were infected with a macrocercous cercaria but no other trematode infection was observed.

The cercariae are expelled from the exhalant siphon of the host. They are poor swimmers and are generally found on the bottom of the vessel containing them. The body of the cercaria remains for most of the time in the chamber of the tail but occasionally emerges, when, with the aid of its suckers, the cercaria creeps over the surface of the vessel. The life span of the cercaria with its body retracted into the chamber is between 24 and 28 hours while those which prematurely emerge from the chamber survive for only 3 to 8 hours.

The cercariae are emitted at certain intervals during the day and night. The number produced during the day varied between 12 and 30 whereas during the night production was much greater, between 150 and 270. In a few cases the bivalve host emitted cercariae during the night but not during the day, or vice versa.

Description (Plates 41-42, Figs. 1-7 and 13)

Body elongate, cuticle thick and granular and bearing on each side 23-25 hair like projections on papillae. Stylet, embedded in anterior part of mouth aperture; rounded posteriorly but terminating anteriorly in a point with two shoulder-like lateral projections; no posterior basal bulb.

Tail divided into 3 regions. (1) A proximal region or chamber, which contains the cercarial body. (2) A wide middle region, formed of parenchymal cells which are enlarged anteriorly and possess a central spherical nucleus and hyaline or lightly granular cytoplasm, the central part of this med-region occupied by a mass of spherical, nucleate cells. (3) A distal thin and elongate region, formed of longitudinal and circular muscles; longitudinal in 3 bands - a central band comprising 8-9 fibres and 2 lateral bands each containing 6-7 muscle fibres. The tail possess numerous cells varying in size and form with

1 or 2 nuclei and with granular cytoplasm.

Oral sucker, subterminal, with papillated surface, some papillae possessing a process, others not. Mouth large and funnel-shaped. Dorsal part of mouth cavity containing globular structures coloured opaque green. Oesophagus long, thick-walled and dividing anterior to acetabulum to form 2 intestinal caeca extending almost to posterior end of body.

Acetabulum, just posterior to mid-length of body; its orifice occupied by structures similar to those found in oral cavity; its pariphery bearing a row of 6 papillae each with 4-5 smaller projections.

Penetration gland-cells with coarsely granular contents and each with a central nucleus; arranged in 2 groups of 6 glands on each side of body, one group anterior to bifurcation of the oesophagus and the other behind this but in front of acetabulum; on each side 6 ducts arise from the posterior group of gland-cells and pass forwards receiving connections from anterior group of gland cells to open at anterior end of body on either side of stylet.

Genital primordium well developed, ovary immediately behind and to left of acetabulum; testes situated laterally, that on right level with ovary, that on left behind ovary. Additionally a mass of cells situated at posterior margin of acetabulum. Cytogenous gland-cells extend around excretory bladder, forming a conspicuous cylinder of cells with coarsely granular contents.

Excretory bladder with 2 principal ducts arising anteriorly and dividing at each side of region occupied by the first pair of penetration glands where the anterior and posterior ducts originate, anterior ducts each receives 3 groups of flame cells at preacetabular level and posterior ducts each receives 4 groups of 3 cells each at postacetabular level; excretory pore situated at posterior end of bladder. Flame cell formula $2[(3 + 3 + 3) + (3 + 3 + 3 + 3)]7 = 42$.

<u>The sporocyst</u>

The mother sporocysts (Plate 42 Fig. 10) are situated between gill lamellae. They are elongated and irregular in form. Their walls are thick and contain numerous daughter sporocysts at different stages of development.

The daughter sporocysts (Plate 42 Fig. 12) are found attached to ctenidial filaments within interlamellar spaces. They are long and tubular in form, with a thick-wall and granular contents, and showing very slow movements. Birth pore could not be seen. The contained cercaria are in an advanced state of development. Small germ balls are also present. The excretory system is visible only in very young sporocysts apparently only recently released from the mother sporocyst. It comprises a single bladder-like principal duct from which a lateral duct originates. The duct extends towards one end of the sporocyst body and then descends almost to the level of the bladder. Along its length are found 3 groups of giant flame cells, each group containing 3 cells.

Metacercaria (Plate 42 Figs. 8-9.)

Twelve nymphs of dragon-flies (Odonata, Anisoptera) and twenty-two caddis-flies (Trichoptera), were collected from ponds where Sphaerium corneum did not occur and were placed in small vessels together with sphaerids which were emitting macrocercous cercariae.

The slow tail movements of the cercariae did not appear to constitute a strong attraction for the odonatan nymphs but six nymphs were observed ingesting cercaria at different times. These insects were isolated and examined 24 hours later but encysted metacercariae were not found. Trichopteran nymphs were never observed ingesting cercariae. All the remaining nymphs exposed to infection were examined after 72 hours when 2 dragon-fly larvae were found with 2 and 2 cysts respectively, situated in the head region, and a single caddis-fly contained 1 cyst lodged in the fat body.

The metacercariae obtained from the caddis-fly was surrounded by thin wall of parasite origin and an external fibrous wall of host origin. The stylet lay discharged intact in the anterior of the cyst. The content of the penetration gland-cells have decreased while that of the cystogenous gland-cells remained almost the same. The testes, ovary and excretory bladder had all increased slightly in size but the remaining structures showed no

significant development changes. The measurements of cysts are: 0.297 (0.288 - 0.304) long x 0.328 (0.304 - 0.361) wide; oral sucker 0.069 (0.064 - 0.072) long x 0.065 (0.060 - 0.072) wide: acetabulum 0.081 (0.076 - 0.087) long x 0.072 (0.068 - 0.083) wide.

Further life cycle details of this cercariae were not realised.

Measurements of Sporocyst and Cercaria macrocerca I from Sphaerium corneum

Body	0.469 (0.452 - 0.494) long x 0.122 (0.106 - 0.140) wide
Oral sucker	0.085 (0.079 - 0.091) long x 0.060 (0.053 - 0.064) wide
Acetabulum	0.079 (0.076 - 0.083) long x 0.083 (0.076 - 0.087) wide
Oesophagus	0.090 (0.083 - 0.095) long
Preacetabular extent	0.205 (0.174 - 0.235) Long
Postacetabular extent	0.172 (0.159 - 0.182) long
Tail proximal region	0.421 (0.364 - 0.462) long x 0.291 (0.224 - 0.350) wide
Tail middle region	0.193 (0.168 - 0.210) long x 0.219 (0.196 - 0.266) wide
Tail distal region	0.913 (0.784 - 1.092) long x 0.123 (0.098 - 0.154) wide
Stylet (overall)	0.028 (0.027 - 0.030) long x 0.007 (0.006 - 0.007) wide
Stylet (shoulder)	0.005 (0.004 - 0.006) wide
Mother sporocyst	1.073 (0.700 - 1.680) long x 0.313 (0.182 - 0.532) wide
Young daughter sporocyst	0.260 (0.114 - 0.361) long x 0.103 (0.060 - 0.133) wide
Daughter sporocyst	1.211 (1.050 - 1.330) long x 0.355 (0.280 - 0.448) wide

Discussion

The Cystocercous cercariae that have been described up to now are as follows:

Cercaria macrocerca Filippi, 1854 in part:

= C. macrocerca Thiry, 1859.

= C. of Gorgodera pagenstecheri Sinitsin, 1905

= C. of Gorgoderina vitelliloba (Olsson, 1876) Looss, 1902.

Cercaria macrocerca Wagener, 1857.

= C. of Distomum cygnoides (Zeder, 1800) Looss, 1899

= C. of Gorgodera loossi Sinitsin, 1909.

Cercaria of Gorgodera varsoviensis Sinitsin, 1905.

Cercaria of Phyllodistomum staffordi Schell, 1967.

Cercaria of Phyllodistomum folium (von Olfers, 1816) Braun, 1899 = C. duplicatum von Baer, 1827 in part = C. duplicatum Reuss, 1903.

Cercaria of Gorgodera amplicava Krull, 1935

Cercaria of Phyllodistomum caudatum steelman, 1938 = C. raicauda Steelman, 1938 (according to Beilfuss (1954)).

Cercaria of Phyllodistomum lohrenzi Lowen, 1935 = C. coelocerca Steelman, 1938 (according to Beilfuss (1954)).

Cercaria of Phyllodistomum solidum Rankin, 1937 = C. conica Goodchild, 1935 (according to Goodchild (1940)).

Cercaria of Phyllodistomum simile Thomas, 1958.

Cercaria sphaerocerca Miller, 1935.

Cercaria mitocerca Miller, 1935.

Cercaria donecerca Goodchild, 1939a.

Cercaria steelmani Baker, 1943.

Cercaria filicauda Fischthal, 1951.

Cercaria pyriformis Fischthal, 1951.

Cercaria micromyae Fischthal, 1951.

Cercaria catakonki Fischthal, 1951

Cercaria honeyi Fischthal, 1951.

Cercaria eriensis Coil, 1953

Cercaria lampsilae Coil, 1954.

Cercaria pyriformoides Coil, 1954.

Cercaria anodontae Coil, 1954.

Cercaria wabashensis Coil, 1955.

Cercaria tiogae Fischthal, 1953.

Cercaria rabbi Dunagan, 1957.

Cercaria papillostoma Coil, 1960.

Cercaria ralphaudya Vercammen-Grenjean, 1960.

Cercaria latigazica Nasir., Diaz, Hamana and Guevara, 1969.

Cercaria yacalicola Nasir., Diaz, Hamana and Guevara, 1969.

Cercaria duplicatum, C. mitocerca, C. filicauda, C. pyriformis, C. micromyae, C. catakonki, C. honeyi, C. tiogae, C. anodontae, C. pyriformoides are readily separated from Cercaria macrocerca I by the absence in them of a stylet. Cercaria eriensis, C. lampsilae and C. latigazica are distinguishable from C. macrocerca I by the lack in them of a chamber in the anterior end of the tail in which the cercaria is found. The cercaria of P. simile, C. macrocerca, C. coelocerca, C. donecerca, the cercaria of P. staffordi, C. sphaerocerca, the cercaria of G. varsoviensis, the cercaria of G. amplicava, the cercaria of G. attenuata, the cercaria of P. solidum, C. wabashensis, C. papillostoma, C. rabbi and C. ralphaudya differ from C. macrocerca I in that their penetration gland-cells are arranged in only 1 group on each side of the body.

Cercaria raicauda, C. steelmani and C. yacalicola together with C. macrocerca I are the only Gorgoderid cercariae whose penetration gland-cells are arranged in 2 groups on each side of the body.

In both C. raicauda and C. steelmani the proximal part of the tail bears a pair of lateral wings. The penetration gland-cells in the former are arranged in groups of 6 and 4 on each side and the latter of groups of 8 and 4 on each side making a total of 20 in both. In C. macrocerca I there are groups of 6 and 6 at each side making a total of 24. The flame cells of C. steelmani are arranged presumably in 21 pairs in groups of 3 as in C. macrocerca I but details of the primary excretory ducts, their division in relation to the acetabulum and their connection with their respective capillaries are not known. In C. raicauda there are 25 pairs of flame cells but like C. steelmani further details are not available. In C. yacalicola the penetration gland-cells are in 2 groups of 5 and 3 at each side making a total of 16. The flame cell formula of C. yacalicola is $2\,[(3+3+3)+(3+3+3+3+3+3+3)] = 60$ compared with $2\,[(3+3+3)+(3+3+3+3)] = 42$ in the present specimens. In addition to this C. yacalicola parasites a gastropod (univalve) mollusc Pomacea glauca (L.) and C. macrocerca I parasitises a bivalve.

The cercaria of Phyllodistomum simile and C. macrocerca are the only 2 forms of the 'macrocercous' group previously described from Britain. They

have already been distinguished above from C. macrocerca I on the basis of the number and arrangement of penetration gland-cells. In the two former species these cells are arranged in a group of 6 on each side of the body and situated posterior to the bifurcation of the oesophagus and anterior to the acetabulum whereas in the present specimens the gland-cells are arranged in 2 groups of 6 and 6 at each side of the body in tandem formation. Another character used to distinguish these two species is the flame cell formula. In C. macrocerca it is $2\left[(3+3)+(3+3+3+3)\right]=36$ in the cercaria of Phyllodistomum simile $2\left[(4+4)+(4+4+4+4)\right]=48$. These 2 species clearly have different formulae from that of C. macrocerca I ($2\left[(3+3+3)+(3+3+3+3)\right]=42$).

After comparison the present cercaria is regarded as a new species and named Cercaria macrocerca I.

Furcocercous cercariae

The members of this large and complex group comprise all those cercariae with forked tails. Luhe (1901) described the group as distome cercariae with a long bifurcated tail into which the body cannot be retracted. Development occurs in sporocysts which are capable of independent movement.

Cort (1917) divided the Furcocercariae into three; his system of classification was based on the presence or absence of pharynx and eyespots and the length of the tail furcae in relation to the overall tail length. The members of Groups I and II were separated from those of Group III by the absence in the former two of a pharynx and their possession of shorter furcae; the members of group II were separated from those of Group I by the absence in the former of eyespots.

Sewell (1922) followed Cort's scheme, expanding the group to include all known distomatous furcocercariae. The monostomes were divided into two different groups, the Lophocerca and Lophoides, although Sewell recognized a relationship between monostome and distome furcocercariae. He divided the distome furcocercariae into three groups; each group was divided into series and each series was again divided into several subgroups.

An outline of his classification is given below

A. Monostomes

B. Distomes

Group 1. Apharyngeal brevifurcate

Series 1) Hollow piercing spines

Sub-group (a) Japonicum - Flame cell formula

$2 \times 3 (+1) \times 1 = 6(+2)$

" " (b) Spindalis - Flame cell formula

$2 \times 4 (+1) \times 1 = 8 (+2)$

" " (c) Douthitti - Flame cell formula

$2 \times 5 (+1) \times 1 = 10 (+2)$

Series 2) No hollow piercing spines

Sub-group a) Ocellata - Flame cell formula

2 x 4 (+1) x 1 = 8 (+1)

" " b) Gigas - Flame cell formula

2 x 10 (+1) x 1 = 20(+2)

Group 2.

Series 1) Pharyngeal longifurcate

Sub-group a) Pahila - Flame cell formula 2 x 5(+1) x = 10(+2)

" " b) Emarginate - Flame cell formula

2 x 5 (+2) x 1 = 10(+2)

" " c) Dusra - Flame cell formula 2 x 10(+2) x 1 = 20(+4)

Series 2) Pharyngeal longifurcate

Sub-group a) Vivax - Flame cell formula 2 x12 (+3) x 1 = 24(+6)

b) Tetis - Flame cell formula 2 x 5 (+2) x 1 = 10 (+4)

Sewell (1922) removed Cercaria mirabilis Braun (1891) from the Cystocercous cercariae group of Luhe (1909) and created a separate group called Mirabilis, to include it and other allied forms, and placed it in the Furcocercous cercariae. He stated that the "Cystocercous character of the tail may be merely an example of convergence and not one of true relationship".

Miller (1926) considered the possession or lack of an acetabulum to be relatively unimportant and that the presence or absence of a pharynx was of greater taxonomic significance in the establishment of a system of classification. He divided the Furcocercous cercariae into two main groups, Pharyngeal and Apharyngeal. Each of these groups was further divided into brevifurcate and longifurcate, according to the relative length of the furcae in relation to the length of the tail stem. These four groups were again sub-divided into distomes and monostomes.

An outline of his scheme of classification is given below.

Apharyngeal cercariae

(1) Apharyngeal Brevifurcate Distome

Eight sub-groups separated on the basis of flame cell pattern, penetration gland-cells, presence or absence of pigmented eyespots and furcal fin-folds.

Group A - Flame cell formula 2 x 3(+1) = 8

Variable numbers of penetration gland-cells

Group B - Flame cell formula 2 x 4 (+1) = 10

Five pairs of penetration gland-cells.

Group C - Flame cell formula 2 x 5 (+1) = 12

Group D - Flame cell formula 2 x 6 (+1) = 14

Forms similar to Schistosome cercariae but with more elongate bodies, pigmented eyespots and furcal fin-folds.

Group E - With a posterior mucin gland and numerous penetration gland-cells.

Group F - With a large number of small penetration gland-cells, in two differentiated sets. The posterior mucin gland and head gland are lacking.

Group G - Five penetration gland-cells. Numerous posterior gland-cells.

Group H - Seven pairs of penetration gland-cells. Large number of flame cells.

(2) Apharyngeal Brevifurcate Monostome

Cercariae with a fin-fold on the body, lacking both pharynx and intestinal caeca and with no flame cells in the tail stem.

(3) Apharyngeal Longifurcate Distome

(4) Apharyngeal Longifurcate Monostome

Resembling the pharyngeal longifurcate more closely than other apharyngeal larvae, either distome or monostome. Poorly described and do not seem to form a homogenous group.

Pharyngeal cercariae

(1) Pharyngeal Brevifurcate Distome

With a pharyngeal sphincter. Excretory system not known and development may occur in rediae.

(2) Pharyngeal Brevifurcate Monostome

No representatives.

(3) Pharyngeal Longifurcate Distome

A number of poorly described forms only in a few of which have the number of flame cells and of penetration gland-cells been elucidated.

(4) Pharyngeal Longifurcate Monostome

Characterized by having a complex excretory system formed by 4 ascending main excretory ducts, one pair median in position and the other lateral, united anteriorly by a commissure. Comprising three sub-groups:

Sub-group (a) Vivax - Characterized by a rudimentary acetabulum and furcal fin-folds.

(b) Tetis - With acetabulum absent and no fin-folds on furcae.

(c) Rhabdocaeca - similar to distome cercariae, excretory system not the Vivax type and with 8 pairs of flame cells in the body and 2 pairs in the tail stem.

Wesenberg-Lund (1934) established the Strigea and Proalaria groups which are pharyngeal longifurcate distome cercariae and included certain furco-cercariae which are not Bucephalids, Cystocercous or Lophocercariae. The members of these two groups have a complicated life cycle using three or possibly four different hosts. The cercariae of the former group are characterized by having preacetabular penetration gland-cells and by the excretory system developing anterior or posterior commissures. The second intermediate host is preferably a snail, leech or vertebrate in which a cyst (tetracotyle) is formed with a definitive wall. Only after passing into a third host is development completed into adult trematodes of the genus Strigea or related genera. In the representatives of the Proalaria group the penetration gland-cells are situated behind the acetabulum and the excretory system develops

a posterior commissure. The second intermediate host is generally a fish or, more rarely an amphibian in which they form a Diplostomulum stage located in the eyes or nervous system. They develop into the genus Proalaria or related genera. Members of both groups usually have their adult form in the digestive system of birds.

Erasmus (1954) subdivided the Pharyngeal longifurcate distome cercariae into three groups on the basis of the relative positions of the penetration gland cells and the acetabulum, that is whether the cells are situated anterior or anterior and posterior or posterior to the acetabulum. Each group was then subdivided according to the total number of these cells.

Since Sewell's (1922) Group 3 of Pharyngeal longifurcate monostome cercariae was sub-divided into Vivax and Tetis sub-groups, several new sub-groups have been added. Faust (1924b) added a third group, the Leptoderma (for C. leptoderma Faust (1922) which Miller placed into the Vivax group (Sewell's Group 3). Miller (1923) also created the Rhabdocaeca group. Szidat (1933) erected two new groups, the Vivipara and Tauiana, to account for the Cercaria of Linstonwiella vivparae Szidat (1933) and C. tauiana Faust (1930) respectively. Cable (1935b) could not place his larva, Cercaria kentuckiensis Cable (1935a), in any of the groups already established and he therefore redefined and simplified Group 3 of Sewell including the Leptoderma and Vivipara groups in the Vivax group. Dubois (1938) classified the Cyathocotylid cercariae into five groups Vivax, Vivipara, Tetis, Leptoderma and Tauiana. Anderson (1944) recognized only two sub-groups of Vivax furco-cercariae (1) the Vivax sub-group which includes those with flame cells in the tail stem and (2) the Tauiana sub-group whose members lack such flame cells. Maxon and Pequenat (1949) suggested the combination of Vivax and Tetis group into one, the Vivax sub-group. Goodman (1951) gave a key to the Cyathocotylid cercariae and considered that these sub-groups should be maintained "until life history studies show that the cercariae of different groups develop into adults of the same genus". Dubois (1951), on the basis of the flame cell pattern, created a new sub-group Novena. In view of the fact that several species of Cyathocotylid cercariae, like Cercaria

duplicata Premvati (1955), C. vivacis Iles (1959), C. papillosoma Khan (1962a), Cercaria of Cyathocotyle bushiensis Khan (1962), and C. hirsuticauda Probert (1966) have characters which overlap to such an extent that these forms do not fit conveniently into any of these sub-groups, Nasir, Hamana and Diaz (1969) recommended that these classifications should be discarded in favour of only one group, Vivax Sewell, 1922.

The system of Miller (1926) has been generally accepted (with minor modifications) and I have adopted this system (as given above) in the following account.

I have followed Nasir, Hamana and Diaz (1969) in regarding all the Pharyngeal longifurcate monostome cercaria as members of a single heterogenous group, the Vivax group of Sewell (1922).

Representatives of Apharyngeal brevifurcate distome, Pharyngeal longifurcate monostome and Pharyngeal longifurcate distome cercariae have been found in this investigation.

Cercaria Apatemon gracilis minor (Yamaguti, 1933) Iles, 1959

Five per cent of the Lymnaea pereger collected at Gledhow Valley Road, Leeds in October 1973 were releasing the cercaria of Apatemon gracilis minor. One per cent of a sample of Planorbis vortex from West Bretton Lake were infected with this form in June 1974 constituting the first record of this species parasitizing P. vortex in Britain.

This cercaria was first described in Britain by Iles (1959) in L. pereger from Roath Park Lake, Cardiff. Iles also obtained the adult parasite after feeding 104 to 234-day-old metacercaria from various leeches (Erpobdella sp, Glossiphonia sp and Proclepsis sp.) to laboratory-reared 1-to 13 day-old Chaki Campbell ducklings (Anas boschas). Khan (1962) reported it in L. pereger from South Ockenden (Essex), from St. Albans and from the river Thames near Bushy Park. Probert (1966) recorded it from the same host and from L. palustris, in Llangorse Lake, Breconshire.

After detailed comparative studies Iles (1959) suggested that the cercaria described by Komiya (1938) from L. ovata and L. palustris in Germany as Cercaria hamburgensis was identical to the specimens she identified as the cercaria of A.g.minor. Iles also considered that "If on re-examination of C. pygocytophora (Brown (1931)) a posterior excretory commissure is found, it may prove to be synonymous with the cercaria of A.g.minor." Without studying new live specimens these two taxa must remain distinct, saparated by the absence of a posterior excretory commissure in C. pygocytophora.

The structure features and dimensions of the cercariae found during the present study are similar to those described by previous authors but some small differences were observed and are listed below:

1. the division of the intestinal caeca by several septa in the cercaria of the present study whereas in the cercaria of Apatemon gracilis minor, the caeca are smooth and without any division.
2. The openings of the caudal excretory ducts are at the furcal tips in the cercaria of the present study whereas in the cercaria of A.g. minor described by Iles (1959) and Komiya (1938) they open

mid-way along the furcae, in Iles's specimens at the anterior margin while in Komiya's at the posterior margin.(see Plate 43, Fig.3)

3. In the cercaria of the present study a single caudal body lies between the first and second pairs of such bodies whereas in Iles's specimens the single body is situated between the third and fourth pairs. In Komiya's specimens the arrangement of these caudal bodies is regular, the two members of the pair are opposite to each other(see Plate 43, Fig. 1).

According to Iles (1959) the cercaria of A.g.minor usually emerges in the early afternoon and sometimes overnight. In my observations the cercariae were emitted both during the day and night although maximum production occurred early in the morning.

This cercaria has also been reported in Radix ovata from Switzerland (Meyer, 1964) and in Galba palustris from Kazakhstan, USSR (Smirnova and Ibrasheva, 1967).

Measurements of the Cercaria of Apatemon gracilis minor and Planorbis vortex

Body	0.127 (0.117 - 0.140) long x 0.054 (0.045 - 0.072) wide
Tail	0.141 (0.133 - 0.152) long x 0.042 (0.038 - 0.045) wide
Furcae	0.156 (0.142 - 0.161) long x 0.017 (0.015 - 0.019) wide
Anterior organ	0.036 (0.034 - 0.041) long x 0.026 (0.022 - 0.030) wide
Acetabulum	0.030 (0.026 - 0.034) long x 0.030 (0.026 - 0.034) wide
Pharynx	0.012 (0.011 - 0.015) long x 0.011 (0.011 - 0.011) wide
Preacetabular Extent	0.057 (0.053 - 0.068) long
Postacetabular extent	0.046 (0.034 - 0.053) long
Sporocyst	1.547 (0.910 - 2.100) long x 0.105 (0.098 - 0.112) wide

Specific diagnosis

Pharyngeal longifurcate distomate furcocercaria. Four pairs of posterior penetration gland cells. Posterior excretory commissure complete, anterior incomplete. Body, tail stem and furcae spinose with long hair-like projections on papillae. Acetabulum with three rows of spines. Caeca divided by several septa. Flame cell formula: $2\left[(1+1)+(1+1+1+1+(1)\right] = 14$. Eight pairs of caudal bodies.

Cercaria furcocercaria IV

In the spring of 1973 195 juveniles of Lymnaea pereger were collected from Durkar (S. Yorkshire) in one of a number of semi-permanent pools formed during wet weather. Two L. pereger were releasing small furcocercous cercariae.

The cercariae escape in large numbers during daylight and, swimming actively, soon become widely distributed in the container. When at rest the body hangs downward suspended in the water with the furcae bent downward; then the cercariae sink and may move with the aid of the suckers along the bottom of the container.

Description (Plate 44, Figs. 1-4)

Body oval, entirely spinose; cuticle provided with a row of 9 papillae with hair-like structures on each side of body. Oral cap formed by approximately 7 to 9 alternating rows of spines; spines around oral cavity thicker and more closely set; penetration spines absent.

Tail subterminal, about as long as body. Cuticle spinose, bearing 6 pairs of hair-like structures. Central core of tail occupied by numerous cell bodies arranged in 2 rows, each cell with a clear nucleus and finely granular cytoplasm; a few similar bodies scattered in furcae. Tail containing 12 caudal bodies with spherical nuclei and arranged regularly in 6 pairs. Each caudal body attached to caudal excretory duct and connected to inner wall of tail by fine connective tissue. Two bands of longitudinal muscles present; each band constituted by 15-16 muscle fibres, extending from proximal part of tail to two-thirds along length of furcae. Furcae longer than tail and bearing pairs of hair-like structures.

Anterior organ clearly divided into 2 regions - an anterior thin-walled and a posterior thick-walled region. Head gland not observed. Small mouth situated subterminally, opening into very small prepharynx from which arises a muscular pharynx followed by a short oesophagus. Oesophagus divided anterior to acetabulum into 2 wide intestinal caeca each dubdivided by six or seven very prominent septa and extending half way to postacetabular region.

Both oesophagus and caeca filled with a finely granular material.

Acetabulum well-developed, located anterior to centre of body, with three rows of small spines around its aperture. This organ capable of protrusion.

Penetration gland-cells comprising two pairs of cells on each side of oesophagus; internal pair with fine granular and external pair with coarsely granular cytoplasm, ducts of cells continued anteriorly to open through hollow conical spines located either side of anterior organ. Nucleus of cells oval.

Immediately behind postero-lateral region of anterior organ are two pairs of accessory gland-cells (similar to the escape gland cells described by Cort (1914)) with very fine granular contents. In cercariae extracted from sporocysts or in recently emitted cercariae, these cells are more clearly visible but after about 15 hours they become difficult to observe. No eyespots present. Globular particles, scattered throughout body, their central portion occupied by rounded structures, probably nuclei. These bodies not a prominent character of the cercaria. Genital primordium represented by a single mass of undifferentiated cells lying above anterior part of excretory bladder.

Excretory bladder elongate, with three main constrictions giving it a marked trilobed appearance. A pair of primary excretory ducts originate laterally and follow a slightly sinuous course forward to anterior level of acetabulum, where they fuse to form the anterior excretory commissure. At level of posterior margin of acetabulum each primary duct gives rise to a short secondary duct, which soon divides into anterior and posterior excretory ducts each connected to two pairs of three flame cells - one group of posterior cells located lateral to bladder and the other at the base of the tail. Caudal excretory duct divided into two branches one running along each furca for about half its length where it opens to the exterior through an excretory pore.

Flame cell formula: $2\,[(3 + 3) + (3 + (3)] = 24$.

Sporocyst (Plate 44, Fig. 5)

The cercariae develop in sausage-shaped sporocysts in the digestive gland of Lymnaea peregeer. The sporocysts are capable of a certain degree of contraction and extension and possess a thin wall which is dark in colour due to the numerous dark green pigment spots distributed in small dense groups along its entire length. The pigment spots are less abundant in young sporocysts.

The body of the sporocysts contains cercariae and a considerable number of germ balls; immature development stages were most abundant but 6-8 fully-formed cercariae were also present.

Further development is unknown.

Measurements of Cercaria furcocercaria IV from Lymnaea peregeer

Body	0.124 (0.091 - 0.152) long x 0.064 (0.064 - 0.068) wide
Tail	0.115 (0.095 - 0.121) long x 0.036 (0.034 - 0.038) wide
Furcae	0.160 (0.152 - 0.190) long x 0.016 (0.013 - 0.026) wide
Anterior organ	01028 (0.026 - 0.034) long x 0.031 (0.026 - 0.034) wide
Acetabulum	0.029 (0.026 - 0.034) long x 0.030 (0.026 - 0.034) wide
Pharynx	0.009 (0.007 - 0.011) long x 0.011 (0.007 - 0.015) wide
Preacetabular extent	0.049 (0.042 - 0.057) long
Postacetabular extent	0.052 (0.049 - 0.072) long
Sporocysts	1.711 (1.260 - 2.800) Long x 0.166 (0.140 - 0.210) wide

Discussion

Of the known furcocercariae only Cercaria anhweiensis Faust (1930), C. nietfontana Porter (1938) and C. marcelloricci Fain (1953) together with Cercaria furcocercaria IV are characterized by having four pairs of penetration gland-cells anterior to the acetabulum, but the latter can be readily separated from the other three species by its flame cell formula of $2[(3 + 3) + (3 + (3)] = 24$, and the presence of an anterior excretory commissure.

Cercaria furcocercaria II and Cercaria Apatemon gracilis minor found in the present study differ from Cercaria furcocercaria IV in the following points:

1. Penetration gland-cells positioned posterior to acetabulum in Cercaria Apatemon gracilis minor and C. furcocercaria II, anterior in C. furcocercaria IV.
2. 14 and 10 flame cells in Cercaria Apatemon gracilis minor and C. furcocercaria II, respectively, 24 flame cells in C. furcocercaria IV.
3. Posterior excretory commissure present in Cercaria Apatemon gracilis minor and C. furcocercaria II, absent in C. furcocercaria IV.

Brown (1931) described Cercaria pygocytophora from Planorbis carinatus in Cheshire. His form can be distinguished from the present one by its possession of the following characters:-

1. Penetration gland-cells entirely posterior to acetabulum.
2. 24 flame cells.
3. Incomplete anterior excretory commissure.

Cercaria Bilharzielae polonicae

Kowalewski, 1895 (Szidat, 1929b).

This cercaria was only found once - in Planorbis planorbis from Wintersett Lake during the summer of 1973. The infection rate was 10.6%.

Ercolani (1881) recorded a cercaria emerging from P. corneus in Italy, as Cercaria ocellata La Valette St. George (1855). Later Szidat (1929b) considered that the cercaria reported by Ercolani was the same species which he had shown to be the larval stage of Bilharziellae polonicae. Szidat found it in the same first intermediate host in Germany. Since 1929 this cercaria has been reported by many authors from other parts of Europe, USSR and Africa including Brumpt (1931), Wesenberg-Lund (1934), Porter (1938), Vergun (1956), Wisniewski (1958), Zdarska (1963), Butenko (1967), Aristanov (1968) and Khalifa (1972). All these workers have found this cercaria to parasitise species of the Planorbidae.

Iles (1959) reported it for first time in Britain from P. corneus in Roath Park Lake, Cardiff, Khan (1961c) recorded it from the same host species in Lake Meadows (Essex), London, and stated that the morphology and measurements completely agreed with those given by Iles. My specimens are morphologically similar to Iles' specimens and my measurements taken from fixed specimens are close to hers from living individuals except that the tail and furcae are larger in my specimens.

Iles figured the ducts of penetration gland-cells opening at both sides of the anterior part of the mouth, whereas in my specimens they open through five hollow conical spines on the antero-lateral margin of the body. This has also been shown by Khalifa (1972). The proximal part of the tail of Iles's specimens is wider than in mine, with a cup-shaped depression. This cup-shaped depression is normally seen in my specimens when they are resting. It was also observed by Khan (1962c).

According to Khalifa (1972), Iles's specimens differ from his in having 3 ciliated patches, rather than 2 in the primary excretory ducts and the posterior 3 flame cells arising separately. Although in my specimens there are two ciliated patches as in those described by Khalifa and Iles, their location

is different. In my specimens they are situated at the beginning of the posterior excretory ducts whereas Khalifa and Iles described them from the convoluted portion of the primary duct. The arrangement of flame cells in the post-acetabular region is similar to that described by Iles.

Khalifa (1972) reported for first time the presence of a cephalic gland and an island of Cort. In all my specimens I have observed a cephalic gland but not an island of Cort. The pattern of hair-like processes on papillae is similar to that in Khalifa's specimens but they are more numerous in my specimens. (see Plate 45, Figs. 1 and 3).

Measurements of the Cercaria of Bilharzielae polonicae from Planorbis planorbis

Body	0.302 (0.292 - 0.307) long x 0.069 (0.064 - 0.076) wide
Tail	0.505 (0.494 - 0.513) long x 0.048 (0.045 - 0.053) wide
Furcae	0.226 (0.220 - 0.226) long x 0.025 (0.02o - 0.032) wide
Anterior organ	0.102 (0.087 - 0.110) long x 0.053 (0.049 - 0.057) wide
Acetabulum	0.030 (0.030 - 0.030) long x 0.023 (0.022 - 0.026) wide
Preacetabular extent	0.181 (0.174 - 0.186) long
Postacetabular extent	0.095 (0.091 - 0.098) long
Sporocyst	2.294 (1.680 - 2.800) long x 0.150 (0.126 - 0.0068) wide

Specific diagnosis

A pharyngeal, brevifurcate, distome cercaria. Five pairs of penetration gland cells, 2 anterior (fine granular contents) and 3 posterior (coarsely granular contents) to acetabulum. Cephalic gland present. Body, tail and furcae spinose. No excretory commissure. Two pigmented eye spots. Flame cell formula 2 [(1 + 1 + 1) + (1 + 1 + 1 + (1)] = 14.

Iles (1959) reported that the cercaria of B. polonicae emerged between 17.00 and 18.00 hr. In the present study emergence was recorded throughout the day but the behaviour of the cercariae was similar to that observed by Iles (1959). The present account constitutes the first record of the cercaria of B. polonicae in Planorbis planorbis in Britain.

Cercaria letifera Fuhrmann, 1916

This cercaria has been found on two occasions in Lymnaea peregra from Wintersett Lake, In August 1973, 15% of the snails were parasitised, while in October 1974, the percentage of infestation was 25%.

After comparison of the present cercaria with other pharyngeal longifurcate cercariae which also possess two pairs of penetration gland-cells anterior to the acetabulum and 16 flame cells it has been concluded that it is identical with Cercaria letifera, originally described by Fuhrman in 1916 from Switzerland. This species has subsequently been recorded by Dubois (1929) from Neuchatel, Switzerland, Wesenberg-Lund (1934) from Denmark, Fain (1953) from Belgian Congo, Niewiadomaka (1960) from Poland, Khan (1962) from Great Britain, Meyer (1964) from Switzerland and Smirnova and Ibrasyeva (1967) from Kazakhstan, USSR.

Cercaria letifera has always been found parasitising species of Lymnaea, except by Fain (1953) who reported it from Biomphalaria alexandrina langanyicensis collected from the Belgian Congo.

Of the published descriptions, this form is extremely similar to that given by Khan (1962), except that in his specimens the branches of the caudal excretory duct open at the middle of the furca whereas in the present specimens they open at the tip of the furca. This features has also been reported by other authors. In Khan's specimens there are fewer long hair-like processes on the body and furcae and more on the tail, but they are not on papillae as in the present material. Also in my specimens the oesophagus and caeca are filled by a fine granular substance which Khan did not mention. (see Plate 46, Figs. 1 & 3

The emergence and behaviour of these cercariae are identical to those observed by Khan. This is the second record for C. letifera in Great Britain. Further details of the life cycle and the corresponding adult form are both unknown.

Measurements of Cercaria letifera from Lymnaea pereger

Body	0.188 (0.171 - 0.201) long x 0.040 (0.038 - 0.041) wide
Tail	0.232 (0.193 - 0.247) long x 0.034 (0.030 - 0.038) wide
Furca	0.203 (0.185 - 0.212) long x 0.017 (0.015 - 0.022) wide
Anterior organ	0.042 (0.038 - 0.045) long x 0.021 (0.022 - 0.030) wide
Pharynx	0.015 (0.015) Long x 0.011 (0.011) wide
Acetabulum	0.023 (0.022 - 0.026) long x 0.023 (0.022 - 0.026) wide
Preacetabular extent	0.109 (0.091 - 0.121) long
Postacetabular extent	0.054 (0.045 - 0.057) long
Sporocyst	2.030 (1.400 - 3.080) long x 0.116 (0.098 - 0.140) wide

Specific diagnosis

Pharyngeal longifurcate distome furcocercaria. Two pairs of penetration gland cells anterior to acetabulum. Flame cell formula $2[(1 + 1 + 1 + 1) + (1 + 1 + (2)] = 16$. Two rows of penetration spines. Body, tail and furcae spinose, with hair-like processes on papillae. Acetabulum bearing a row of 35-37 spines. No excretory commissures. No eye-spots. Five pairs of caudal bodies.

Cercaria paracauda Iles, 1959.

This cercaria was recorded from 6 different localities in the Yorkshire area, namely Newmillerdam Lake, Kirkstall Power Station (Leeds-Liverpool canal), Wintersett Lake, Walton Park, New Farnley and Enroy. The collections of these snails were carried out in Spring, Summer and Autumn, 1973, 1974 and 1975. L. stagnalis obtained from all of these sites harboured Cercaria paracauda, and an infection rate of 4.5-37.7% was observed. Lymnaea pereger was found to be infected by this cercaria in the first two localities only and the incidence of infection varied between 0.6 - 2.0%.

Iles (1959) described Cercaria paracauda from L. pereger in Roath Park Lake, Cardiff. Since then it has been found only by Khan (1962) in Bushy Park, Epping Forest and Richmond Park, London, and by Probert (1966) from Llangorse Lake, South Wales. The two latter authors also found L. pereger infected with this cercaria. Only Khan reported a rate of infection (between 10 and13%) and it was similar to that reported here for L. stagnalis, although it was considerably greater than that of L. pereger. It is interesting to note that the maximum infection rate recorded was 37.7% from Kirkstall Power Station where L. pereger is more abundant than L. stagnalis. Furthermore both species of Lymnaea were found in all three localities from where Iles, Khan, and Probert reported C. paracauda, but L. stagnalis was not infected with this cercaria.

The specimens I have found agree in most essential characters with those described by Iles (1959) although detailed study has revealed some differences between the two series of specimens. It is difficult to assess whether the taxonomic significance of these differences is sufficient to justify specific recognition. The characters which the two cercariae have in common are:

1. 2 pairs of postacetabular penetration gland-cells.
2. 16 flame cells.
3. Numerous caudal bodies.
4. 6 rows of spines on oral cap.

5. 3 rows of spines on acetabulum.

6. The presence of yellow pigment granules in the area of pharynx.

7. The position of the bifurcation of the oesophagus.

8. Emergence and behaviour.

The differences between the two cercariae are tabulated below:

1. Borders of penetration gland-cells smooth	1. Borders of glands deeply trilobed. (see Plate 47, Fig. 2)
2. Division of primary excretory duct immediately posterior to acetabulum.	2. Division of primary excretory duct antero-lateral to excretory bladder. (see Plate 47, Fig. 3)
3. Caudal excretory ducts opening midway along furcae.	3. Caudal excretory ducts opening at tips of furcae.
4. Two ciliated patches in primary excretory ducts.	4. Three ciliated patches in primary excretory ducts.
5. Three rows of penetration spines comprise 5, 7 and 5 spines respectively (total 17).	5. Three rows of penetration spines comprise 4, 6 and 4 spines respectively (total 14)
6. Cephalic gland not recorded.	6. Prominent Y-shaped cephalic gland present in postero-medial portion of anterior organ. (see Plate 47, Fig. 3)

Despite these differences between the present material and that of Iles (1959) I have referred this material to Cercaria paracauda Iles, 1959 on the basis of the characters they have in common. This constitutes the first record of C. paracauda from the host species, L. stagnalis in Britain.

Measurements of Cercaria paracauda from Lymnaea stagnalis

Body	0.183 (0.171 - 0.197) long x 0.041 (0.038 - 0.049) wide
Tail	0.228 (0.224 - 0.231) long x 0.037 (0.034 - 0.045) wide
Furcae	0.217 (0.214 - 0.224) long x 0.020 (0.015 - 0.022) wide
Anterior organ	0.050 (0.053 - 0.057) long x 0.026 (0.022 - 0.030) wide
Prepharynx	0.009 (0.007 - 0.011) long
Pharynx	0.014 (0.011 - 0.015) long x 0.011 (0.011 - 0.011) wide
Oesophagus	0.016 (0.007 - 0.022) long
Acetabulum	0.026 (0.026 - 0.026) long x 0.027 (0.026 - 0.030) wide
Preacetabular extent	0.093 (0.076 - 0.114) long
Postacetabular extent.	0.059 (0.057 - 0.064) long
Sporocyst	3.016 (1.841 - 4.734) long x 0.146 (0.105 - 0.184) wide

Specific diagnosis

Pharyngeal longifurcate distome furcocercaria. Two pairs of post-acetabular penetration gland cells. Three rows of penetration spines. Six rows of spines in oral cap. Three rows of spines on acetabulum. Head gland. Eyespots absent. Many caudal bodies. No excretory commissure. Body, tail and furca spinose. Yellow pigment granules. Flame cell formula: $2\left[(1 + 1 + 1) + (1 + 1 + 1 + (2)\right] = 16$. Cuticle of body, tail and furcae armed with hair-like processes on papillae. Ten to eleven transverse rows of spines extending from thick-walled part of the anterior organ to almost posterior end of acetabulum.

Cercaria Cotylurus brevis (Dubois and Rausch, 1950) Nasir, 1960 (= Cercaria helvetica XXXIV Dubois, 1934)

The first infected Lymnaea peregra were found during October and November, 1973 in collections from Gledhow Valley Road and Durkar. The infection-rate was about 15% at Gledhow and 32% at Durkar. The cercaria was obtained again in January 1974, from the same host in Kirkington where the infection rate was 10%.

The cercaria of Cotylurus brevis was originally described as Cercaria helvetica XXXIV Dubois, 1934, in Lymnaea stagnalis from Lake Neuchatel in Switzerland. Nasir (1960), during studies of trematode larvae from Edgbaston pool, Birmingham, found a fork-tailed cercaria emerging from L. stagnalis, which by controlled feeding experiments using laboratory-bred second intermediate and definitive hosts was proved to be the larval stage of C. brevis.

C. brevis was originally described by Dubois and Rausch (1950) from the Pochard Duck (Aythya affines) from North America. The cercaria has also been found by Meyer (1964) in Zurich, Switzerland, from Radix ovata and Butenko (1967) reported it in L. stagnalis from Kazakhstan, USSR.

The cercaria described by Nasir (1960) as that of C. brevis is similar to the present material in all morphological details and also in its behaviour and emergence patterns. It differs only in certain dimensions of the oesophagus and acetabulum which are more close than those given by Dubois in C. helvetica XXXIV. Also Nasir described globular bodies of variable size in the tail of the cercaria, about which he commented "They are not the true caudal bodies or glands found in some other strigeid cercariae", but detailed microscopical study undertaken by myself revealed the presence of 18 caudal bodies arranged in 9 pairs at either side of the caudal excretory duct. He described and figured fine hair-like structures on body, tail, and furcae, but only one on a papilla on each side of the body approximately at the level of the excretory bladder. In my specimens all these structures on both body and furcae are on papillae and are more numerous on the body and less numerous on the tail than in Nasir's description.(see Plate 48, Fig. 1)

According to Nasir (1960) L. stagnalis and L. pereger are among the commonest species of gastropods in Edgbaston pool, but he did not report that any specimens of L. pereger were infected with cercaria of C. brevis. In the present study this cercaria has been recorded from L. pereger collected from three different localities, and although L. stagnalis occurred in one locality it was never found to be parasitized with the cercaria of C. brevis. This is the first record of this cercaria from L. pereger in Britain.

Measurements of the cercaria of Cotylurus brevis from Lymnaea pereger

Body	0.190 (0.182 - 0.197) long x 0.049 (0.049 - 0.057) wide
Tail	0.195 (0.193 - 0.197) long x 0.038 (0.038 - 0.037) wide
Anterior organ	0.039 (0.038 - 0.041) long x 0.028 (0.026 - 0.030) wide
Acetabulum	0.027 (0.026 - 0.030) long x 0.027 (0.026 - 0.030) wide
Prepharynx	0.009 (0.007 - 0.011) long
Pharynx	0.014 (0.013 - 0.015) long x 0.013 (0.012 - 0.015) wide
Oesophagus	0.011 (0.009 - 0.013) long
Preacetabular extent	0.011 (0.095 - 0.114) long
Postacetabular extent	0.051 (0.045 - 0.057) long
Furcae	0.173 (0.171 - 0.178) long x 0.017 (0.015 - 0.019) wide
Sporocyst	5.940 (4.866 - 7.233) long x 0.300 (0.158 - 0.526) wide

Specific diagnosis

Pharyngeal longifurcate distome cercaria. Two pairs of penetration gland cells anterior to acetabulum. Two rows of penetration spines. Three to four rows of spines on acetabulum. Body and furcae with hair-like structures on papillae. Anterior commissure incomplete. Flame cell formula 2 [(2 + 2) + (2 + 2 + (2)] = 20. Unpigmented eye spots. Nine pairs of caudal bodies.

Cercaria furcocercaria VII

About 15% of the Lymnaea pereger collected from Wintersett Lake on 2 occasions during the summer of 1973 were found to harbour Cercaria furcocercaria VII.

The cercariae emerge in large numbers throughout the day, mainly early morning and late evening and after leaving the snail they swim actively for a short period followed by a period of rest. At rest the cercariae hang with their bodies downwards and with the furcae spread apart but their tips bent downwards. They remain alive for about 24 hours.

Description (Plate 49 Figs. 1-3)

Body elongate, slightly narrower at its extremities and completely covered with spines, anterior tip occupied by a group of 19 penetration spines arranged in 3 rows, one behind the other, first row consisting of 6 spines, second row seven and third row six. Oral cap with 5-6 rows of spines extending back to anterior level of thick-walled part of anterior organ. Cuticle with 6 papillae with hair-like structures on each side of body.

Tail stem almost as long as body and furcae, and slightly subterminal; eight to ten hair-like processes on each side. Two bands of longitudinal muscles extending from base of tail to mid-way along furcae. Core of tail containing twelve caudal bodies arranged in six pairs on either side of excretory duct, but attachment to this duct was not observed. Furcae spinose, without finfolds and equipped with 8 hair-like processes. Small cell bodies irregularly dispersed along entire length of furcae and a few similar bodies also present in tail.

Anterior organ oval, protrusible; anterior part thin-walled and posterior part more muscular with numerous transverse muscle fibres. Cephalic gland absent.

Digestive system well developed; mouth slightly subterminal, prepharynx short and muscular and followed by oesophagus. Oesophagus divided a considerable distance from anterior part of acetabulum into two thin and slightly septate (each with 5-6 septa) intestinal caeca extending almost to posterior extremity

of body.

Acetabulum located behind middle of body and armed with four rows of minute spines set very close together. Body cavity containing numerous small refractile granules similar to those found in wall of sporocyst. Two oval unpigmented eye spots located antero-lateral to acetabulum but difficult to observe.

Three pairs of penetration gland cells present antero-lateral to acetabulum; cells rather small with coarsely granular contents and a circular central nucleus. Ducts following a slightly undulating course and each opening via a separate hollow conical spine, at anterior margin of body.

Excretory bladder 2-chambered; accessory anterior chamber transversely elongate. Principal posterior chamber more or less oval and communicating with the former by a short neck. From each side of accessory chamber two primary excretory ducts extend forward to anterior margin of acetabulum where they join to form the anterior excretory commissure. At this point a secondary duct arises on each side, in turn dividing into anterior and posterior collecting ducts. One group of 2 flame cells on each side connected to anterior collecting duct and 4 groups of 2 to posterior collecting duct, one of these groups located in proximal region of tail. Caudal excretory duct forked distally with each branch passing into a furca to open by a small excretory pore just proximal to midpoint of furca. Flame cell formula: $2[(2) + (2 + 2 + 2 + (2)] = 20$.

Sporocyst (Plate 49 Fig. 4)

The digestive gland of Lymnaea pereger was filled with tangled sporocysts. They are thread-like in shape and vary in length as they perform contracting and elongating movements. The anterior end contains oval structures with fine granular contents. The body is constricted at irregular intervals, forming swollen areas which are full of cercariae and the conspicuous birth pore is located subterminally at one side of the anterior end. The body wall is thick, with granular contents and small refractile tranules are distributed irregularly over its surface. There are large numbers of cercariae in all stages of development, together with several germ balls.

Further developmental details are unknown.

Measurements of Cercaria furcocercaria VII from Lymnaea pereger

Body	0.175 (0.171 - 0.190) long x 0.050 (0.045 - 0.053) wide
Tail	0.173 (0.171 - 0.182) long x 0.032 (0.030 - 0.034) wide
Furcae	0.169 (0.155 - 0.178) long x 0.014 (0.011 - 0.015) wide
Anterior organ	0.035 (0.034 - 0.038) long x 0.026 (0.026 - 0.026) wide
Acetabulum	0.029(0.026 - 0.030) Long x 0.027 (0.026 - 0.034) wide
Prepharynx	0.007 (0.003 - 0.007) long
Oesophagus	0.011 (0.007 - 0.015) long
Preacetabular extent	0.101 (0.095 - 0.0114) long
Postacetabular extent	0.045 (0.041 - 0.049) long
Sporocyst	2.761 (0.526 - 3.419) long x 0.161 (0.078 - 0.210) wide

Discussion

Among the species of pharyngeal longifurcate distome cercariae, Cercaria linearis Wesenberg-Lung (1934); C. magalesia Porter (1938); C. paralinearis Goodman (1951); C. rodhaini Fain (1953); C. pseudolinearis Khan (1962) and C. cornuarietis Nasir, Hamana and Diaz (1969) resemble C. furcocercous VII in having three pairs of penetration gland-cells in front of the acetabulum. Of them only C. rodhaini and C. pseudolinearis also possess 20 flame cells. The former is easyily distinguished from the present form by the possession of a rudimentary acetabulum and very short intestinal caeca and by the absence of an anterior excretory commissure.

Cercaria pseudolinearis is the form appearing most closely related to C. furcocercaria VII. However there are certain characters of diagnostic significance which serve to separate these two species. C. pseudolinearis has 3 rows of spines around the orifice of the acetabulum and 2 rows of penetration spines in the anterior part of the body compared with 4 and 3 rows respectively in C. furcocercaria VII. In C. pseudolinearis the primary excretory ducts divide behind the acetabulum and the anterior collecting ducts receive 2 groups of flame cells, whereas in C. furcocercaria VII the primary ducts divide anterior to the acetabulum and the anterior collecting ducts each receive only a single group of flame cells. Finally in C. pseudolinearis there are

14 caudal bodies compared with 12 in C. furcocercaria VII. In Britain, in addition to C. pseudolinearis, four other species with the same number of penetration gland-cells have previosly been described from freshwater gastropods. They are Cercaria F.2 Harper (1931); C. valvata Lal (1959); C. planorbida Iles (1959) and C. roathensis Erasmus (1960). Cercaria F.2 is readily eliminated as it possesses in addition to other distinguishing features, pigmented eye spots. C. roathensis differs in having a posterior excretory commissure and 2 incomplete commissures anterior to the acetabulum.

C. planorbida also differs from C. furcocercaria VII in lacking an anterior excretory commissure and in having a total of 14 flame cells. C. valvata can be differentiated by the apparent absence of eyespots and an anterior excretory commissure, and by the disposition of penetration gland-cells behind the acetabulum.

Cercaria of Diplostomum phoxini (Faust, 1918) Arvy and Buttner, 1954.

Lymnaea pereger, collected in May and June, 1974 and 1975, from Pool-in-Wharfedale were found to be infected with this cercaria. The infection rate varied between 11.4 and 22.7%.

This cercaria was originally described by Arvy and Buttner (1954) from Lymnaea auricularia in France. They obtained the adult parasite by feeding domestic ducks (Anas Boschas and Cairina moschata var. domestica) with minnows (Phoxinus laevis) which had been experimentally exposed to cercariae infection. Rees (1955 and 1957) found this cercaria in L. pereger var ovata in Wales and also elucidated its life cycle, conducting experiments similar to those of Arvy and Buttner. Berrie (1960) reported it from Scotland in L. pereger but did not give either a description or figures.

The cercaria found in the present study is very similar both in morphology and in its measurements to cercaria of D. phoxini as described by Arvy and Buttner (1954) and by Rees (1957). The description given by the latter author is more complete and the present specimens agree with it although the following minor differences were observed:

1. Rees stated that the ducts of penetration gland-cells open by two pores on each side of the mouth whereas in my specimens these ducts open through hollow conical spines located on either side at the anterior end of the body. (see Plate 50, Fig. 2)

2. There is a cephalic gland situated at the posterior part of the anterior organ, whereas in Rees's specimens the presence of this gland was not indicated. (see Plate 50, Fig.3)

3. In my specimens the acetabulum is surrounded by a muscular ring which was not referred to by Rees. (see Plate 50, Fig. 3)

4. Rees described the anterior and posterior excretory ducts as receiving 3 flame cells each on either side of the body. In all my specimens only one group of 2 flame cells is connected to the anterior collecting ducts and two groups of 2 connected to the posterior ones on each side of the body.

5. Rees figured (but did not describe) the branches of the caudal excretory duct entering into the furcae and opening midway along the posterior margin of the furcae. In my specimens these branches open one-third of the length along each of the furcae, one opening on the anterior margin of one furca (the right), the other on the posterior margin of the second (left) furca. (see Plate 50, Fig. 4)

It is probable that the presence of a cephalic gland and a muscular ring around the acetabulum were overlooked by Rees, while the other differences could merely represent different interpretations of the same structures by different authors.

The emergence and behaviour of the cercaria described above are identical to those described by Rees for the cercaria of D. phoxini.

Measurements of the Cercaria of Diplostomum phoxini from Lymnaea pereger

Body	0.122 (0.110 - 0.133) long x 0.035 (0.034 - 0.038) wide
Tail	0.218 (0.209 - 0.224) long x 0.039 (0.034 - 0.046) wide
Furcae	0.168 (0.160 - 0.175) long x 0.013 (0.011 - 0.015) wide
Anterior organ	0.044 (0.042 - 0.046) long x 0.026 (0.023 - 0.027) wide
Acetabulum	0.019 (0.019 - 0.023) long x 0.021 (0.019 - 0.023) wide
Pharynx	0.008 (0.008 - 0.010) long x 0.009 (0.008 - 0.011) wide
Oesophagus	0.007 (0.004 - 0.011) long
Preacetabular extent	0.064 (0.053 - 0.072) long
Postacetabular extent	0.040 (0.038 - 0.53) long
Sporocyst	5.485 (2.630 - 9.205) long x 0.338 (0.210 - 0.473) wide

Specific diagnosis

Pharyngeal longifurcate distome furcocercaria. Two pairs of posterior penetration gland cells. Two rows of spines on acetabulum. No eye-spots. Tail with eight pairs of hair-like processes. Furcae spinose with four pairs of heir-like processes on papillae. Cephalic gland present. Acetabulum surrounded by a muscular ring. Flame cell formula $2\left[(2) + (2 + 2 + (2)\right] = 16$. Branches of caudal excretory duct opening on either anterior or posterior margin of furcae.

Cercaria furcocercaria II

On April 4, 1975, a sample of 40 specimens of Lymnaea pereger was taken from Riffa Beck at Pool-in-Wharfedale and 6 were found to be producing large numbersof a forked-tailed cercaria.

These cercariae are shed in great numbers during daylight. Generally they are found in the lower half of the container, and after a certain period of time they may be seen congregated at the bottom. They swim vigorously and have regular periods of rest during which the body hangs beneath the tail and they sink gradually. They remain alive for more than 24 hours.

Description (Plate 51 Figs. 1-4)

Body elongate, cylindrical in shape; covered irregularly with spines from anterior of body to region of acetabulum. One papilla with a hair-like structure located on each side of body at equatorial level of anterior organ. Oral cap provided with several regular rows of 6-7 spines, extending back about half the length of anterior organ. Two rows of penetration spines situated anterior to mouth, first row with 6 spines and second with 7 spines.

Tail terminal, spinose, with 8 long hair-like structures on each side and containing well-developed longitudinal and circular muscles. A few small cell bodies dispersed throughout tail. Six prominent caudal bodies present on each side of excretory duct and arranged regularly in pairs, first pair smaller and in a different position from the rest. Furcae spinose, without finfolds.

Anterior organ protrusible and retractile, its wall distinctly divided into an anterior portion and a thicker muscular posteriorpart. Cephalic gland absent. Mouth apening about anterior end of anterior organ, continuing into a small prepharynx then passing into small but well-developed circular pharynx. Very short oesophagus present, but difficult to observe.

Intestinal caeca not well-developed, being represented by two swollen caeca joined at their posterior tips.

Acetabulum much smaller than anterior organ and situated posterior to middle of body, moderately protrusible, its aperture area adorned with irregularly distributed spines. A few additional spines present scattered behind aperture area.

Two prominent unpigmented eyespots anterior to acetabulum. Each eyespot full of small elongate structures with very fine granules and with a short anteriorly-directed duct. No connection with the nervous system could be seen.

Nervous system consisting of oesophageal ganglion and a wide commissure which gives off two anterior and two posterior nerves; anterior nerves passing forwards lateral to anterior organ, posterior nerves longer and running backwards to almost half way between posterior margin of acetabulum and posterior end of body.

Eight penetration gland-cells with coarsely granular contents arranged in linear formation of one, two and one on each side of body, and occupying almost whole postacetabular space. Anterior and median cells pyriform in shape, posterior cells longer and more rectangular in form. Nuclei of these cells well-marked, their ducts opening on antero-lateral margins of body.

Rudiments of genital primordium situated anterior to excretory bladder and represented by a rather elongate mass of undifferentiated cells.

Excretory bladder elongate, with three main constrictions giving it a marked trilobed appearance. Primary excretory ducts leaving antero-lateral margins of bladder and extending to posterior margin of acetabulum where they fuse to form the posterior excretory commissure. Immediately behind acetabulum a short blind-ending duct arising from primary excretory duct. Primary ducts forming coiled secondary ducts posterior to acetabulum which bend posteriorly and fork into anterior and posterior collecting ducts. Anterior collecting duct receiving capillaries from 2 flame cells and posterior from 3; 2 located in postacetabular region and 1 in proximal part of tail. Each of tail capillaries with an unusual swollen section, filled with a very

finely-granular material. Caudal excretory duct arising from posterior end of bladder and passing along tail to distal end, divided into branches running into each of the two furcae. Branches opening to exterior via small excretory pores. Flame cell formula: $2[(1 + 1) + (1 + 1 + (1)] = 10$.

Sporocyst (Plate 51, Figs. 5-7)

Development occurs in elongate thread-like sporocysts, living in the digestive gland of Lymnaea pereger. The body wall is thick, well-developed, and lined by Parenchymal cells which are more abundant at the anterior end. The conspicuous birth pore is situated near the anterior end and the body cavity is full of numerous cercariae in different stages of development together with several germ balls.

The mother sporocyst is elongate and it is difficult to separate as a single specimen from the digestive gland tissue. Its body is filled by young daughter sporocysts of different sizes and there are a great number of flame cells dispersed along the body. (see Fig. 7)

The daughter sporocysts within the mother sporocyst are quite active and may be seen in constant movement. The lumen of each contains hundreds of germ balls, and small groups of dark green refractile granules are present on the surface of the body.

Further development is unknown.

Measurements of Cercaria furcocercaria II from Lymnaea peregra

Body	0.162 (0.141 - 0.171) long x 0.038 (0.034 - 0.042) wide
Tail	0.141 (0.129 - 0.144) long x 0.041 (0.034 - 0.049) wide
Furcae	0.146 (0.139 - 0.152) long x 0.012 (0.011 - 0.015) wide
Anterior organ	0.038 (0.038 - 0.042) long x 0.024 (0.023 - 0.024) wide
Acetabulum	0.017 (0.015 - 0.019) long x 0.017 (0.015 - 0.018) wide
Pharynx	0.008 (0.008 - 0.011) long x 0.008 (0.008 - 0.011) wide
Caeca	0.020 (0.019 - 0.023) long x 0.018 (0.015 - 0.020) wide
Preacetabular extent	0.089 (0.080 - 0.099) long
Postacetabular extent	0.055 (0.046 - 0.065) long
Un-pigmented eyespots	0.009 (0.008 - 0.011) long x 0.009 (0.008 - 0.011) wide
Mother sporocyst	21.653 (19.199 - 24.196) long x 0.359 (0.316 - 0.395) wide
Young daughter sporocyst	0.793 (0.140 - 1.960) long x 0.068 (0.056 - 0.084) wide
Daughter sporocyst	5.184 (2. 104 - 7.890) long x 0.157 (0.132 - 0.210) wide

Discussion

Nineteen species of apharyngeal, longifurcate, distome furcocercariae characterized by having four pairs of postacetabular penetration gland cells, as in Cercaria furcocercaria II, have been described in the literature. They are:

Cercaria pygocytophora Brown (1931).

Cercaria stephensi Brooks (1948).

Cercaria coperata Olivier (1942).

Cercaria gracillima Faust (1917)

Cercaria burti Miller (1923) as described by Cort and Brooks (1928).

Cercaria apatemon gracilis minor (Yamaguti, 1923) as described by Iles (1959).

Cercaria angelae Johnston and Simpson (1944).

Cercaria pseudoburti Ranking (1939).

Cercaria hamburgensis Komiya (1952).

Cercaria of Strigea elegans Chandler and Raush (1947) as described by Pearson (1959).

Cercaria okoboyensis Brooks (1948).

Cercaria wansoni Fain (1953).

Cercaria rafula Fain (1953).

Cercaria helvetica XXXI Dubois (1929).

Cercaria burti var. icnusae Giovannola (1937).

Cercaria lessoni Johnston and Bechwith (1947).

Cercaria Apatemon gracilis gracilis Szidat (1929a, 1931).

Cercaria longiremis Wesenberg-Lund (1934).

Cercaria of Apatemon cobitidis cobitidis (Linstow, 1890) as described by Butenko (1967).

The cercaria of Strigea elegans and of Apatemon cobitidis cobitidis, Cercaria rafula, C. longiremis and C. okoboyensis are the only species previously described having the same number of flame cells as C. furcocercaria II. Of these cercaria of S. elegans, C. longiremis and C. rafula may all be separated from C. furcocercaria II by the absence of a posterior excretory commissure. Cercaria koboyensis and the cercaria of A. c. cobitidis can be differentiated from C. furcocercaria II by their having more than twelve caudal bodies in the tail.

The cercaria of A. g. minor (Yamaguti, 1933), Iles (1959) encountered during this investigation is readily distinguished from C. furcocercaria II by differences in the complex protonephridial system, the number and arrangement of caudal bodies and the digestive system.

Cercaria vivax I

During the summer of 1973, 125 specimens of Bithynia tentaculata were collected from Newmillerdam Lake and 2 of these yielded a furcocercaria belonging to the Vivax sub-group.

Cercariae are emitted during both the morning and the afternoon but none during darkness. The swimming movements of the cercariae are followed by a long period of rest unless disturbed when they start to swim again either upwards or more usually downwards. When the cercariae are resting some can be seen sinking to the bottom, they live for a maximum of about 24 hours.

Description (Plate 52,Figs.1-3 and 5)

Somewhat pyriform in shape, being widest in the middle of the body; body surface covered with fine spines; cuticle of body and tail provided with a row of numerous papillae with hair-like structures, 3 similar papillae located laterally at base of furcae and one pair of papillae near distal tips of furcae. Tail attached to the posterior end of the body subterminally and possessing two bands of longitudinal muscles extending from anterior part of tail to tips of the furcae, together with many circular muscles. Furcae covered with spines and provided on distal half with prominent finfolds which show fine striations resembling hair-like fin-rays. Caudal bodies absent.

Three rows of penetration spines present in area of mouth; preoral region with 6-8 rows of hook-like spines. Anterior organ terminal and resembling an oral sucker more than a true anterior organ. Mouth subterminal opening into a short prepharynx, leading to a well-developed pharynx. Pharynx circular in shape, followed by relatively short oesophagus with its anterior end surrounded by a well-marked muscular wall. Oesophagus divides slightly anterior to mid-line into broad intestinal caeca which continue back to posterior end of body. Acetabulum absent.

Numerous refractile globules arranged in groups scattered throughout body.

Four penetration gland-cells with finely-granular contents located on either side of oesophagus; their ducts pass anteriorly to dorso-lateral part of anterior organ to open through hollow spines situated each side of anterior tip of body.

Cystogenous gland-cells absent. Rudiments of genital system represented by rounded undifferentiated cells situated anterior to anterior chamber of excretory bladder.

Excretory bladder 2-chambered with a large transversely-elongated anterior chamber and posterior small rounded chamber. Four excretory ducts arise from anterior chamber - two lateral and two median. Median ducts pass anteriorly to about the mid-level of body where they unite to form a single median canal continuing forwards to level of oesophageal bifurcation. Here canal joins a transverse vessel which fuses with the 2 laterals. On each side, at level of oesophageal bifurcation, a short blind pouch arises from the transverse duct and at the left and right extremities secondary excretory ducts arise and pass backwards to level of genital primordium where they divide into anterior and posterior excretory ducts found. These each receive 2 groups of 2 flame cells. Caudal excretory duct passes into tail from base of posterior chamber and divides at distal end of tail, each branch opening at tip of furca.

Flame cell formula: $2[(2 + 2) + (2 + 2)] = 16$.

Sporocyst (Plate 52, Fig. 4)

The cercariae develop in elongate sausage-shaped sporocysts in the digestive gland of Bithynia tentaculata. They are small and are capable of limited movement. The whole surface of the body contains numerous refractile globules of different sizes arranged in small groups. Lumen of sporocyst completely full of cercariae, partially or fully differentiated, together with a considerable number of germ balls. The young sporocysts are more active than mature sporocyst and germ balls may be seen moving freely in the former.

Further development is unknown.

Measurements of Cercaria vivax I from Bithynia tentaculata

Body	0.131 (0.117 - 0.140) long x 0.060 (0.057 - 0.064) wide
Tail	0.094 (0.087 - 0.098) long x 0.031 (0.030 - 0.034) wide
Furcae	0.095 (0.093 - 0.098) long x 0.016 (0.011 - 0.020) wide
Anterior organ	0.026 (0.026 - 0.026) long x 0.026 (0.026 - 0.026) wide

Pharynx	0.015 (0.015 - 0.015) long x 0.015 (0.015 - 0.015) wide
Oesophagus	0.012 (0.007 - 0.015) long
Sporocysts	1.176 (0.0840 - 1.680) long x 0.142 (0.140 - 0.154) wide

Discussion

The furcocercariae of the subgroup Vivax Sewell, 1922, emend. Dubois, 1951 which, like Cercaria vivax I and Cercaria vivax II, are characterized by having furcal finfolds are:

Cercaria vivax Sonsino (1892), Langeron (1924), Wesenberg-Lund (1934) [= larva of Prohemistomum vivax (Sonsino, 1892), Azim (1933), C. vivax Sonsino (1894), Langeron (1924) = larva of Szidatia joyeuxi (Hughes, 1929), Dubois (1938), Joyeux and Baer (1941), Balozet (1953)].

Cercaria indicae XV Sewell (1922).

Cercaria indicae LVIII Sewell (1922).

Cercaria dorsocauda Tubangui (1928).

Cercaria kentuckiensis (Cable, 1935a as described by Cable (1938) [= larva of Mesostephanus kentuckiensis (Cable, 1935a Meyer (1960)].

Cercaria tatei Johnston and Angel (1940).

Cercaria of Prohemistomum industrius (Tubangui, 1922) as described by Tang (1941).

An unnamed cercaria described by Maxon and Pequegnat (1949).

Cercaria kasenyi Fain (1953).

Cercaria vivacis Iles (1959).

Cercaria papillosoma Khan (1962a).

Cercaria of Prohemistomum chandleri Vernberg (1952).

Cercaria of Prohemistomum expeditum Balozet (1953).

Cercaria of Szidatia joyeuxi (Joyeux and Baer, 1941) as described by Balozet (1953).

Cercaria hirsuticauda Probert (1966).

Cercaria ariformis Khan (1962).

Cercaria spatula Probert (1966)

Cercaria laevissimus Nasir, Acuna and Guevara (1966).

Of the cercariae listed below only Cercaria kasenyi, an unnamed cercaria described by Maxon and Pequenat (1949), C. hirsuticauda and C. ariformis are provided with 24 flame cells like C. vivax I.

Cercaria kasenyi and the cercaria described by Maxon and Pequegnat (1949) can readily be separated from C. vivax I because they possess flame cells in the tail.

Cercaria hirsuticauda and C. ariformis are more closely allied to C. vivax I. However there are several features which set the two former species apart:

1. They lack papillae with hair-like process.
2. The arrangement of flame cells and the division of the secondary excretory ducts.
3. The absence of refractile globules in the body.
4. The absence of blind pouches on the primary excretory ducts.

Also in C. hirsuticauda there are no penetration gland-cells, and fin-folds are present along the full length of the furcae. In C. ariformis, the penetration gland-cells are numerous, and are apparently arranged in two groups, one behind the anterior organ and the other in the inter-caecal region, but unfortunately the number of these glands is not recorded.

Other cercariae belonging to the sub-group Vivax Sewell, 1922, which have been described in Britain from Bithynia tentaculata, are listed below:

Cercaria vivacis Iles (1959), from Roath Park, Cardiff.

Cercaria papillosoma Khan (1962a), from Bushy Park, London.

The cercaria of Cyathocotyle bushiensis Khan (1962a), from Bushy Park, London.

Cercaria spatula Probert (1966), from Llangorse Lake, Breconshire.

Of these cercariae, only the cercaria of C. bushiensis has 16 flame cells, as C. vivax I, but there are no fin-folds on the tail furcae.

As a result of the comparison made above, this species is regarded as new, and is named Cercaria vivax I.

Cercaria vivax II

This cercaria was found only once - in 1 Bithynia tentaculata out of 175 collected from Newmillerdam Lake in July, 1973.

Repeated collections were carried out during 1974, 1975 and early 1976 but no additional snails infected with C. vivax II were found.

The production of cercariae is small and occurs only during the day time. The swimming and behaviour are almost exactly like Cercaria vivax I but the resting period is shorter. The cercariae were observed to live for about 36 hr.

Description (Plate 53,Figs. 1-3 and 5)

Body oval, entirely covered by minute spines which are also present on furcae. Furcae bearing papillae with hair-like structures along their margins; cuticle of tail possessing a row of long hair-like structures on both sides.

Tail slightly subterminal, provided with well-developed circular and longitudinal muscles, the latter passing from anterior end of tail to tips of furcae; circular muscles extending only to bases of furcae. Tail also containing numerous cell bodies distributed irregularly, furcae bearing small finfolds restricted to their tips; caudal bodies absent.

Two thirds of anterior organ covered by a row of 5-7 spines; penetration spines absent. Anterior organ isodiametric and terminal with mouth opening located near anterior end. Prepharynx short ending in a circular, muscular pharynx; oesophagus much shorter than pharynx and divided into two wide intestinak caeca which extend to about the level of the excretory bladder. Whole digestive system filled with granular material. Acetabulum absent. Refractile globules scattered through body.

Penetration gland-cells arranged in two groups of 8, one group on each side of pharynx; cell contents finely granular; duct openings at anterior end of body. Nuclei of these cells not observed. Cystogenous gland-cells absent. Rudiments of genital system present.

Excretory bladder consisting of an oval chamber situated at posterior end of body with main lateral and median excretory ducts arising from antero-

lateral region and passing forwards to level of mid-line of body where median ducts fuse to form median canal. At level of oesophageal bifurcation median canal joins transverse canal which passes laterally to join the external duct on each side. Transverse canal gives rise on each side to a short blind-ending pouch. Secondary ducts arise from main lateral ducts about the middle of the body, dividing into antero and postero lateral collecting ducts. Antero-lateral collecting ducts with two groups of 2 flame cells, postero-lateral collecting ducts with 3 groups of 2 cells and continuing into tail where they each receive 1 group of 2 flame cells. Each flame cell in tail ending in a swollen structure with fine granular contents. Caudal excretory duct ending at tip of each furca. Flame cell formula: $2[(2 + 2) + (2 + 2 + 2 + (2)] = 24$.

Sporocyst (Plate 53, Fig. 4)

The sporocysts were located in the hepatopencreas of Bithynia tentaculata. Body elongate with thick walls which are thicker at the extremities than over the rest of the body. Mobility of sporocyst low. Body containing numerous cercariae, germ balls and refractile globules with 8-10 of the cercariae mature.

The protonephridial system has been observed only in part. There are five parallel rows of flame cells extending from one end of the body to the other. The rest of this system was difficult to observe owing to the presence of numerous cercariae, germ balls and pigments.

Further development unknown.

Measurements of Cercaria vivax II from Bithynia tentaculata

Body	0.135 (0.121 - 0.140) long x 0.078 (0.072 - 0.083) wide
Tail	0.193 (0.190 - 0.205) long x 0.038 (0.038 - 0.041) wide
Furcae	0.162 (0.159 - 0.167) long x 0.018 (0.015 - 0.019) wide
Anterior Organ	0.027 (0.026 - 0.030) long x 1.027 (0.026 - 0.030) wide
Pharynx	0.017 (0.016 - 0.019) long x 0.017 (0.015 - 0.019) wide
Oesophagus	0.006 (0.006 - 0.007) long
Sporocysts	2.367 (1.841 - 3.156)long x 0.165 (0.131 - 0.210) wide

Discussion

Of all other Vivax-type cercariae described only the cercaria of Prosostephanus industrius Tang (1941), C. papillosoma Khan (1962) and C. spatula Probert (1966) are characterized by possessing fin-folds limited to the tips of the furcae as C. vivax II.

The first two of the above species are readily separated by having a different number of flame cells, from Cercaria vivax II, respectively, while C. spatula has the same number.

In C. spatula the penetration gland-cells are arranged in two groups - an anterior group of 4 small cells with clear nuclei on each side of the anterior organ and a posterior group of 4 or more cells located on each side of the anterior region of the caeca. In C. vivax II these cells are arranged in one group of 8 on each side, postero-lateral to the pharynx, and they do not possess nuclei. In C. spatula the capillaries of the posterior collecting ducts in the tail reach almost half-way along its length whereas in C. vivax II they reach for only one-third of the length and they each end in a swollen structure with granular contents. In C. vivax II there is a blind-ending duct on each side of the main excretory ducts, at the level of the oesophageal bifurcation. These are absent from C. spatula. In C. vivax II the body and tail are devoid of papillae with hair-like structures which are present on these organs in C. spatula. Finally C. spatula differs from C. vivax II in having a larger body, tail and furcae, and its anterior organ is almost twice as big as in C. vivax II.

The present species is considered to be new and named Cercaria vivax II.

Summary

1. A survey has been conducted of the freshwater larval trematode fauna in West Yorkshire.

2. Fifty two collections of freshwater molluscs were made at 21 different places among which the 5 most important are:-

   (1) Kirkstall Power Station (Leeds-Liverpool Canal)
   (2) Wintersett Lake (Wakefield)
   (3) Newmillerdam Lake (Wakefield)
   (4) Gledhow Valley Road (Leeds)
   (5) Pool-in-Wharfedale

At least four different kinds of cercariae have been found at each of the above sites.

3. Thirty species of cercariae, emerging from one or more of Bithynia tentaculata, B. leachi, Lymnaea peregra, L. stagnalis, L. auricularia, Planorbis vortex, P. planorbis and Sphaerium corneum were found.

4. Eighteen new species have been fully described and their relationship to previously described cercariae is discussed, they are listed below:-

(i) Three Gymnocephalous cercariae (Cercaria of Sphaeridiotrema wintersettensis, C. gymnocephalous II and C. gymnocephalous III).

(ii) One Pleurolophocercous cercaria (Cercaria pleurolophocerca I).

(iii) Five Furcocercariae (Cercaria furcocercaria II, C. furcocercaria IV, C. furcocercaria VII, C. vivax I and C. vivax II).

(vi) One Microcercous cercaria (Cercaria microcercous I).

(v) One Cystocercous cercaria (Cercaria macrocera I).

(vi) Three Echinostome cercariae (Cercaria echinostoma III, C. magnacauda I and C. magnacauda II).

(vii) Four Xiphidiocercariae (Cercaria microcotylea I, Cercaria of Plagiorchis farnleyensis, Cercaria of P. kirkstallensis and C. xiphidiocercaria IX).

5. Cercaria of Dolichosaccus rastellus is described for the first time in Great Britain.

6. Eleven previously described cercariae for Great Britain were found.

They are: Cercaria paracauda Iles, 1959

Cercaria of Apatemon gracilis minor of Iles (1959)

Cercaria of Bilharzielae polonicae of Iles (1959)

Cercaria tarda Khan, 1961d

Cercaria letifera of Khan (1962)

Cercaria of Diplostomum phoxini of Rees (1955 and 1957)

Cercaria of Cotylurus brevis of Nasir (1960)

Cercaria of Echinoparyphium recurvatum of Harper (1929)

Cercaria of Hypoderaeum conoideum of Nasir (1957-58)

Cercaria of Notocotylus imbricatus of Pike (1969)

Cercaria of Notocotylus triserialis (= N. attenuatus) of Pike (1969).

7. All the previously described cercariae from Great Britain are compared with the descriptions of previous authors. Small morphological and dimensional differences are noted and their possible significance discussed.

8. New first intermediate hosts for some of the previously described cercariae have been recorded.

9. Studies of the life cycles of Plagiorchis farnleyensis n. sp., P. kirkstallensis n. sp. and Sphaeridiotrema wintersettensis n. sp. are described.

10. The life cycle of Dolichosaccus rastellus is described from Great Britain for the first time.

11. Some additional information is provided on the morphology and life-cycles of Echiparyphium recurvatum, Hypoderaeum conoideum, Notocotylus imbricatus and N. attenuatus.

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