STUDIES ON LARVAL TREMATODES

INFECTING FRESHWATER SNAILS IN LONDON

AND SOME ADJOINING AREAS

by

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ABSTRACT

A survey of the larval trematodes infecting freshwater snails in London and some parts of Essex, Middlesex, Surrey and Hertfordshire was conducted during 1958 to 1960. The results are presented in two parts.

Part I deals with the descriptioms and incidence of the cercariae encountered during this survey. Thirteen species of snails extending over six genera were examined. In all, thirty-eight species of cercariae were found. Of these two "Monostome", two "Gymnocephalous", five "Echinostome", five "Xiphiocercous", nine "Furcocercous" cercariae and two species of "Cercariaea", in all twenty-five species, are new to science.

Representatives of the "Yenchingensis" sub-group of the "Monostome", "Parapleurolophocercous" sub-group of the "Gymnocephalous" and the "Virgula" sub-groups of the "Xiphidiocercous", "Lophocercous" sub-group of the "Furcocercous" groups and the "Cercariaea" groups are recorded for the first time from Britain. Two previously known species of cercariae are described for the first time from Britain. A key to the British freshwater cercariae is given.

A brief review of the classification is given with each group whose members were found during this survey. The existing classification of the "Echinostome" and the "Vivax" groups is shown to be unnatural.

Part II deals with the life cycles of four species of cercariae.

C. londonensis n. sp. is shown to develop into a new species of the genus Echinostoma and C. essexensis n. sp. is shown to develop into a new species of the genus Hypoderaeum. The transformation of C. tetraglandis Iles into a tetracotyle in freshwater leeches is studied in detail. C. bushiensis n. sp. is shown to develop into a new species of the genus Cyathocotyle. The stages in the development of these trematodes are described.

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Part I

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PART I

Introduction

The theory of the spontaneous origin of trematodes was held till the late seventeenth century. Steenstrup (1845) realized the importance of different developmental stages in the life history of trematodes. However, Thomas (1883) was the first to show experimentally, in Fasciola hepatica Linn., the relation between these stages in the trematode life history.

Still the strigeids were regarded as possessing a metastatic mode of development, the miracidium developing directly into adult stage, until the works of Lutz (1921), Ruszkowski (1922), Mathias (1922) and Szidat (1924) proved conclusively that strigeids also possess a holometabolous development.

The study of the larval trematodes is of comparatively recent origin. This branch of study was pioneered in Europe by such workers as Filippi (1854-1859), LaValette St. George (1855), Moulinie (1856) and Ercolani (1881, 82). The first comprehensive classification of the then known larval trematodes was put forward by Lühe (1909). Lühe's scheme forms the basis of all subsequent attempts at the classification of cercariae.

During the present century considerable work on the trematode life history was done in other parts of the world, while in Europe it fell into comparative neglect. More notable works in Europe during the first half of the

present century are those of Mathias (1922, 24, 25, 27, 35), Ejsmont (1926), Dubois (1928, 29, 34), Szidat (1923, 24, 28, 29, 31, 33, 35) and a fairly large account of the Danish freshwater larval trematodes by Wesenberg-Lund (1934).

In the United States of America the field was explored by Leidy (1847, 1877) and then by Cort (1915), Faust (1917), H.M. Miller (1926) and E.L. Miller (1936). In recent years, considerable work has been done in that country and a large amount of literature is available. Particular attention has been paid by some American workers towards the classification of the furcocercous cercariae and the one proposed by Miller (1926) has generally been accepted as most adequate by later workers. Hughes (1928, 29) and Van Haitsma (1930, 31) under Professor La Rue have made valuable contributions towards our knowledge about the development of "Furcocercous" cercaria.

Looss (1895-99) studied the Egyptian fauna with some valuable addition to the basic knowledge of the subject.

Soparker (1921) described the cercarial fauna from Bombay in India and Sewell a year later published his classical memoir on the Indian forms, in which he revised and greatly extended Lühe's classification.

Our knowledge of the African freshwater larval trematodes is mainly due to the studies of Cawston (1917, 19, 23) and Porter (1938) who published a voluminous account of the South African fauna. Recently, Fain (1953) has added

fifty-six new species of cercariae from the Belgian Congo.

Johnston (1937, 38, 40, 42, 47, 49) in collaboration with other workers, published a series of papers on the Australian freshwater cercariae. Kobayashi (1918), Tsuchimochi (1924, 26), Tubangui (1928, 32) and Faust (1922, 24) described the cercarial fauna of Korea, Japan, the Philippines and China, respectively.

Faust (1919b) evolved the now well known way of expressing the flame cell pattern in the form of a mathematical formula. The importance of the excretory system in establishing the relationship among cercariae was first recognised by Cort (1917) and was further emphasized by such workers as Faust (1918, 1919, 24), Sewell (1922), Szidat (1924). Faust (1924) proposed a classification based solely on the flame cell pattern. However, difficulty in ascertaining the exact flame cell pattern in certain groups of cercariae has been experienced by several workers (i.e. Beaver, 1937, and Johnson, 1920). Miller (1926), Stunkard (1930) and Wesenberg-Lund (1934) pointed out that, in spite of the conservation of this system, its importance in the use of systematics of the larval trematodes can be exaggerated and that in certain groups of cercariae it is a very unpracticable basis for classification.

The study of the freshwater cercarial fauna and the trematode life history has received very little attention

in Britain. There is a wide gap between the publication of the life history of F. hepatica by Thomas (1883) and the description of two unidentified "Xiphidiocercariae" by Hesse (1923), during which no work has been done in Britain. Vevers also in 1923, fed the tissue of snails harbouring echinostome cysts, identified by him as those of Cercaria echinata v. Sieb. and some tetracotyles, to ducklings. He recovered some immature specimens of Echinostoma revolutum (Froel.), and Hypoderaeum conoideum Bloch., on dissecting these ducks while the tetracotyles failed to develop. The specimens of H. conoideum must have developed from cysts which escaped Vevers' notice. These infected snails, however, were received by him from Italy.

Brown (1926, 31) in his study on the British freshwater larval trematodes, which was based on snails collected from Birmingham and Cheshire areas described thirteen species of cercariae, of which five are "Echinostomes", two "Xiphidiocercariae" and six "Furcocercariae". He also tried to recover the adult stage of C. echinata v. Sieb. by rearing a young mallard in a pond where a large number of infected snails were found. Upon the dissection of this mallard, he recovered five immature specimens, which he identified as Echinostoma revolutum (Froel.). The same author (1927) described the life cycle of Crepidostomum farionis Mull and in 1933 described the life histories of some other trematodes.

Wright (1927 a & b) described two new xiphidiocercariae and made some contributions towards the structure of the cercaria of F. hepatica.

Harper (1929, 31) reported the occurrence of one "Monostome", one "Echinostome", four "Xiphidiocercariae" and three "Furcocercariae" parasitizing the freshwater snails in Dundee and Glamorgan areas. He also performed some life history studies and found that the monostome cercaria was the larva of Notocotylus seineti Fuhr. He also completed the life cycles of Echinoparyphium recurvatum V. Linst and Strigea tarda Steenstrup.

An outbreak of cercarial dermatitis was reported by Matheson (1930) among bathers in a Cardiff lake. He identified the causative agent as C. elvae Miller. The infected snails were sent to Taylor and Baylis (1930) who identified the cercaria responsible for this outbreak of dermatitis as C. ocellata and also found another furcocercaria infecting these snails.

Rees (1932) studied the occurrence of larval trematodes in four species of Limnaea in Glamorgan and Monmouth areas and described one new species each of "Echinostome", "Xiphidiocercous" and "Furcocercous" cercaria and seven species of previously known larval trematodes, with some valuable contributions towards the structure of the cercaria of F. hepatica. In the next year, she found some echinostome cysts in snails which by controlled feeding experiments

proved to be of Hypoderaeum conoideum Bloch. In 1954, again Rees described a detailed account of the life history and larval stages of Plagiorchis (Multiglandularis) megalorchis and later on (1955, 1957) the developmental stages and life cycle of Diplostomulum phoxini Faust, concurrently with some foreign workers.

Vickers (1940) described the anatomy of C. microcerca from Sphaerium corneum. Erasmus (1957) studied in detail the transformation of C. X. Baylis into diplostomulum in the eyes of several fishes. He also gave a more detailed account of the cercarial stage, but his attempts to recover the adult stages were unsuccessful. The same author has recently (1960) described a new "Furcocercaria" from Cardiff.

Dawes (1952) published a note on the life cycle of a trematode in a London pond and (1959) gave an interesting demonstration on the penetration of miracidium of F. hepatica into its snail host.

Thomas (1958) gives a detailed account of the life cycle of Phyllodistomum simile Nybelin. Iles (1959, 60) has published the first two of her intended series of freshwater larval trematodes from Cardiff. In the first paper she has described seven species of "Furcocercous" cercariae and in the second she describes the development of C. tetraglandis Iles in leeches and the life history of Apatemon gracilis minor Yamaguti.

Lal (1958) records a new "Furcocercaria" from Edinburgh.

Nasir (1960) gives an account of the life history of Cotylurus brevis Dubois and Rausch from a Birmingham pond.

Apart from Dawes' (1952) note on a trematode life cycle, no work has been done in London or adjoining areas on freshwater larval trematodes.

Material and Method

The snails were collected from different ponds, lakes, reservoirs and streams and carried in small polythene bags along with some of the water vegetation. These snails were almost always brought to the laboratory on the same day, except a few occasions when they were kept in the polythene bags overnight, which they survived without any ill effects. In the laboratory they were kept in glass tanks filled with ordinary tap-water, in which most of the local species thrived well. These tanks were constantly aerated. Water vegetation, such as weed and other water plants were also placed in the tanks to keep the water clean for a longer time. However, the water of each tank was changed twice every week. The temperature of the snail room was constantly kept at 25-27°C.

The snails were fed on lettuce only. The lettuce was used both as fresh leaves put in the tank and as dried and ground powder. Both forms were quite successful but the second method of using dried ground lettuce had the disadvantage of polluting the water more quickly.

In the laboratory *Limnaea stagnalis* (Linn.), *L. pereger* (Müll.), *L. palustris* (Müll.), *Planorbis corneus* (Linn.), *P. planorbis* (Linn.), *Physa fontinalis* (Linn.) and *Bithynia tentaculata* (Linn.) were bred for experimental purposes. All of these thrived very well on the above

method, except for L. pereger which was found to be very difficult to rear in the laboratory. All the snails reared in the laboratory had weaker shells, as compared with the snails caught in nature.

Usually the snails brought to the laboratory survived for a fairly long time, if too many snails were not congested in one tank and if the water was not allowed to pollute too much but some of the snails failed to survive in these tanks for more than a day or two without any apparent reason. This sudden death of an infected snail did not allow a detailed study of some of the larval trematodes, when a solitary infection was found.

To examine the snails for infection with trematodes, they were isolated either in 3" x 1" specimen tubes, or in jam-jars if the snails were too large for the specimen tubes, for twenty-four hours. The water of these tubes was examined against light, with the naked eye or with a hand lens, after every hour during the day and on the following morning. Some of the cercariae encyst on the walls of the container soon after their emergence and it was found to be important to note the presence of cysts in such cases. On the other hand the operculate snails may not protrude their body out of the shell for a long time, when the discharge of the cercariae is not possible. Such snails were re-examined until the snail protruded its body during the desired time.

To study the activity and the resting position of

the cercariae, a hand lens was used with considerable advantage. For such studies, the containers with cercariae were placed on a table or such other thing to avoid any disturbance caused to the cercariae by the shaking of the hand. They were also left undisturbed for some time before their resting position was examined.

A small proportion of the snails found to be uninfected by the above method were dissected under a dissecting microscope and examined for the presence of trematode infection.

The naturally emerged cercariae, or dissected from the snails, were studied both in the living and fixed conditions. The excretory system can only be studied in the living condition. As all the flame cells may not be visible in one specimen at a time and also because a small time is only available before the cercaria dies on the slide, a large number of cercariae were used to establish the flame cell pattern in each species of cercaria. In some groups of cercariae very dark pigment or a large number of cystogenous gland cells makes it extremely difficult to see the flame cell pattern with any degree of certainty. In such cases very often the use of cercariae, dissected from the snail, when both the pigment and cystogenous gland cells are poorly developed, was found to be very useful. This was also found very helpful in seeing the extent of the intestinal caeca, in

certain forms such as "Gymnocephalous" and "Xiphidiocercous" cercariae. The use of vital stains such as neutral red was utilized in making out the details of the digestive system and the penetration gland cells.

To examine the body spines and the collar spines in the echinostome cercariae, it was found best to study the living cercariae. The collar spines may also be examined in fixed specimens, cleared in glycerine to which some methylene blue has been added, as suggested by Beaver (1937), but his method of clearing the specimens in oil of wintergreen after staining them in the ordinary manner did not yield good results.

The genital primordium is best seen in fixed and stained specimens. Although haematoxyline and aceto-acetic alum carmine were both used, the carmine stain was found to be more satisfactory.

For the measurements, whenever possible, only naturally emerged cercariae were used. The measurements are based on at least twenty living and twenty fixed specimens unless otherwise stated. In the living cercariae, usually the body and tail are highly contractile and there is often a great difference between the measurements at maximum contraction and maximum extension. In this study the measurements of the living cercariae were taken from moderately extended specimens. For fixation the cercariae were concentrated in a centrifuge into a small quantity

of water to which equal volume of hot formal-saline (70 - 80°C) was added. This resulted in well stretched specimens, with remarkably uniform measurements. Cercariae fixed in this manner also provided excellent material for histological studies and whole mounts. My experience with the cercariae during the present investigation has fully convinced me that these forms, when fixed under uniform conditions provide the most reliable measurements, whereas the measurements of the living forms is affected by several factors such as degree of extension and pressure of the coverslip, etc.

After having studied the cercariae, the infected snails were dissected under a dissecting microscope, and the rediae or sporocysts recovered. These were also studied in the living as well as fixed and stained conditions. Here again, the most satisfactory fixative was found to be hot formal-saline (70 - 80°C) and the most satisfactory stain was aceto-acetic alum carmine or borax carmine.

For life history studies, four kinds of animals were used as second intermediate hosts, namely snails, insect larvae, freshwater crustaceans and leeches. The snails were all laboratory bred and undoubtedly free of previous infection. The insect larvae used were chironomid larvae and mosquito larvae. The mosquito larvae were provided by Dr. Lawrence of the Entomology Department of the London

School of Hygiene and Tropical Medicine and were laboratory bred. The chironomid larvae were mainly supplied by the Freshwater Biological Association. Half of each batch of these larvae were dissected and was always found to be free of any previous infection. The other half was presumed to be free of infection and was used in the experiments. The leeches were partly collected from a small pond, which was known to be free of any trematode infection, and were partly supplied by the Freshwater Biological Association. Several species of leeches were tried such as Haemopsis sanguisuga, Helolidella stagnalis, Protoclepsis tasselata, Erpobdella octuculata and E. testacea. The last two of these were preferred for use, because of their smaller size, ease in dissection due to thin cuticle, comparatively less pigmented body, and ease with which they can be maintained and fed in the laboratory. All these animals were kept in the snail room at 25 - 27°C.

Pigeons, day-old khaki Campbell ducklings, laboratory hatched chickens, rats and mice were used as final hosts. The pigeons were all laboratory bred and both ducklings and chickens were secured when only a day old and unfed, while rats and mice were provided by the Animal House of the London School of Hygiene and Tropical Medicine; none of these could possibly have been previously infected and they were kept on a diet which could not be a source of trematode infection. The metacercarial stages were force

fed to these animals and the faeces were examined regularly every day thereafter for the presence of eggs. If the eggs appeared after some days the animals were dissected to recover the adults, otherwise the animals were dissected after varying periods to see if the worms had developed at all in them.

Two methods for fixing the adult trematodes were tried. The use of hot 70° alcohol without pressing the animal was discarded as the worms always became coiled in it. It was found that fixing the animals in alcohol after pressing them under a coverglass was also undesirable as the worms became excessively flattened and in the case of echinostomes the arrangement of the collar spines was disturbed. Gilson's fluid yielded the best results. This fixative was heated to 80 - 90°C and the living worms were dropped into it with a dropper. The worms thus fixed always remained straight and moderately flattened. The arrangement of collar spines in the echinostomes was not disturbed. For staining borax carmine was preferred although haematoxylin and aceto-acetic alum carmine were also used occasionally. The observations made from whole mounts were confirmed and amplified by cutting 8 μ thick serial sections, which were stained with Delafield's haematoxylin and counter-stained with eosin. On the suggestion of Mr. Prudhoe of the British Museum, a solution of indigo carmine in 90 per cent alcohol was used to stain

the body and collar spines of echinostomes after staining them with borax carmine. This method was found to be most useful.

The eggs were concentrated from the faeces and washed several times in distilled water. They were kept in Petri-dishes in distilled water and allowed to embryonate at the room temperature. Very often some flagellates appeared in the Petri-dishes and killed the eggs. To avoid this, coarse particles of pigeon faeces were added to the Petri-dishes. This changed the pH of the water sufficiently to inhibit the growth of the flagellates but did not affect the eggs at all. The Petri-dishes were watched every day for the development of miracidia. The water was changed as often as it got dirty. When hatched, the miracidia were picked up with the help of a fine pipette. The miracidia were studied alive for general structure. For the epidermal plates, silver impregnation, use of neutral red in the living miracidia and fixing in Schaudin's fixative followed by staining with iron haematoxylin were used as aids. Silver impregnation was the most satisfactory method.

Laboratory bred snails were exposed to the miracidia in 3" x 1" tubes and their process of penetration studied in a watch glass under a binocular microscope.

All the drawings were made with the help of a camera lucida and were finished by me in ink, except for those

of the resting positions of the cercariae and of individual spines which are freehand sketches. The finer details of structure were also incorporated freehand.

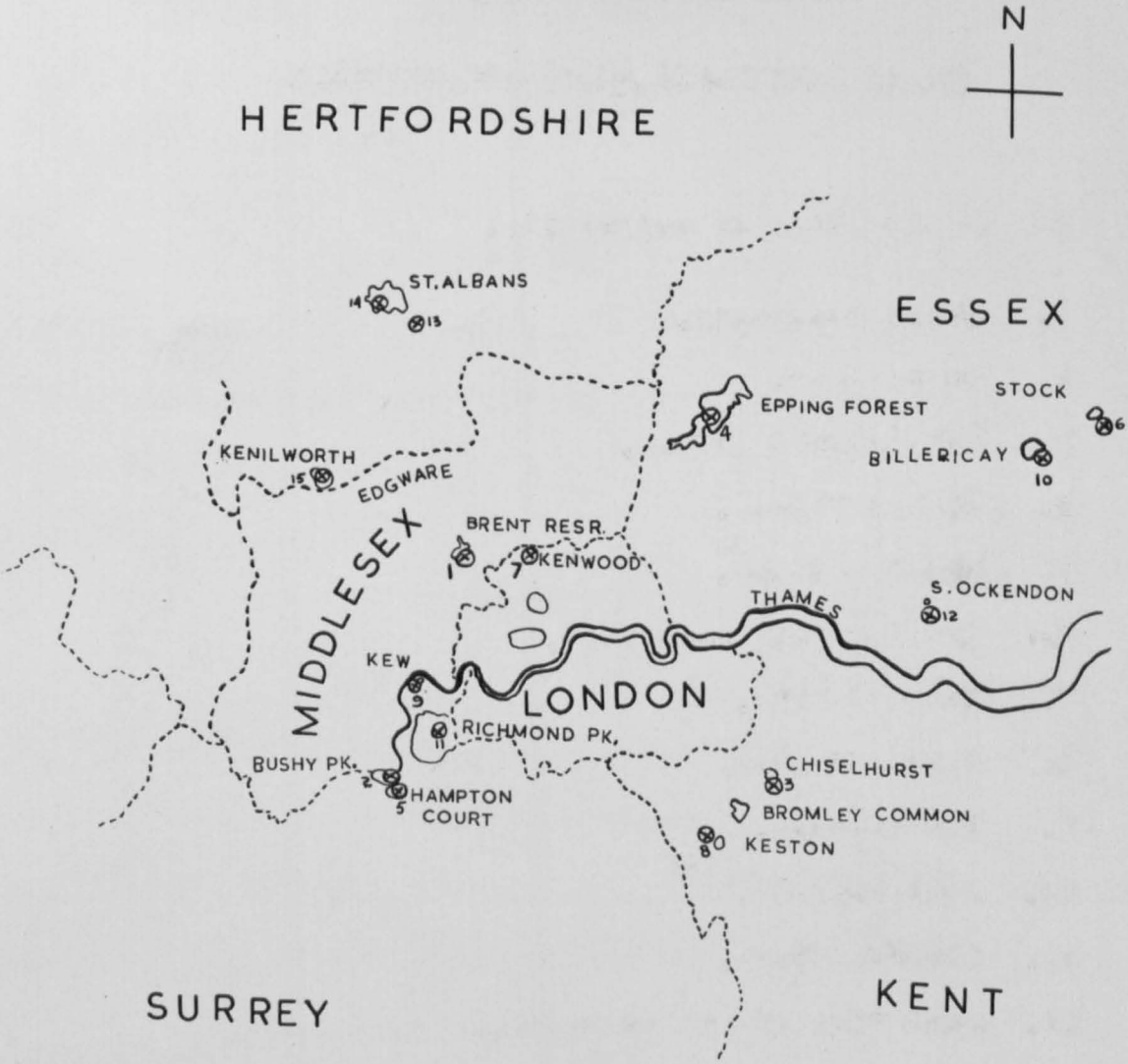
Explanation to Plate 1

Map of London and Adjoining Counties

Key to the sites of collection:

1. Brent Reservoir.
2. Bushy Park.
3. Chislehurst Common.
4. Epping Forest.
5. Hampton Court.
6. Henningfield Reservoir.
7. Kenwood Lake.
8. Keston Common.
9. Kew Gardens.
10. Lake Meadows.
11. Richmond Park.
12. Sand Pits (South Ockendon).
13. Sand Pits (St. Albans).
14. St. Albans Lake.
15. Stoneyfields Park.

Plate I



SCALE
1 INCH = 5 MILES

----- COUNTY BOUNDARIES

⊗ SITES OF COLLECTION

Localities Examined

Different localities examined during this investigation may be grouped into two categories. Firstly, those which were under regular observation, i.e. snails were collected from such places at least once in a fortnight, during March to November of every year. During colder months, snails could not be collected as they were in the state of aestivation and underground. Secondly, those places which were visited occasionally or irregularly during the collecting season.

Places under Regular Observation

1. Stoneyfields Park (Kenilworth State) Edgware

A small pond, through which the Deans Brook, a tributary of Silk Stream, passes. This pond has a molluscan fauna comprising Limnaea stagnalis, L. pereger; Planorbis corneus, P. planorbis, Physa fontinalis, Hydrobia jenkinsi.

2. Brent reservoir (Welsh Harp) (Middlesex)

This is a very large reservoir, and is not accessible at all places. Collections were made from its Southern and South Eastern banks and also from small sewage pipes discharging into the reservoir. The snails collected from here comprised L. stagnalis, L. pereger; P. corneus, P. planorbis and Physa fontinalis. During the second half of the summer in 1959, this reservoir was half dried

and could be reached from all directions.

3. Bushy Park and Hampton Court (Middlesex)

One small pond in Hampton Court and three medium sized ponds in Bushy Park provided a rich molluscan fauna and easy access to all parts of these ponds. These ponds have L. stagnalis, L. pereger; P. planorbis, P. spirorbis, Bithynia tentaculata and Valvata piscinalis.

4. Richmond Park (Surrey)

Four large ponds in this park with the same snail fauna as Bushy Park.

5. River Thames

With every visit to the Bushy Park or Richmond Park, snails were collected from adjoining parts of the River Thames. Usually, P. planorbis and L. pereger were found, but sometimes L. stagnalis and P. corneus were also collected from this river.

6. Epping Forest (Essex)

Four medium sized ponds in Epping Forest were found to contain the following molluscs: L. pereger, L. stagnalis; P. corneus, P. planorbis. All these ponds are accessible on all sides.

7. Keston Common (Kent)

There are two small ponds near which are fed by an underground river. L. stagnalis, L. pereger and L. auricularia were collected from these ponds.

8. Chiselhurst Common (Kent)

Another common near Chiselhurst with two medium sized ponds having L. stagnalis; P. corneus and P. planorbis as its molluscan fauna.

9. Lake Meadows (Essex)

This medium sized lake near Billericay has L. stagnalis, L. pereger; P. corneus, P. planorbis and B. tentaculata and is easily accessible in all directions.

10. Henningfield Reservoir (Essex)

This is a recently constructed, huge reservoir with L. stagnalis and L. pereger. It is situated near Billericay.

11. Sand Pits (South Ockendon)

Two Sand Pits on River Ham near South Ockendon (Essex) are easily accessible on most sides. The larger Sand Pit, which is about a mile from South Ockendon, was examined up to the summer of 1959 after which the larger part of it was filled.

Places from where Occasional Collections were made

1. Sand Pits (near St. Albans) (Hertfordshire)

From these Sand Pits L. stagnalis and L. pereger were collected three times in 1958 and twice in 1959.

2. St. Albans lake (Hertfordshire)

This medium sized lake had extremely polluted water,

but L. stagnalis, L. pereger; P. corneus were collected four times during 1958 and 1959 from a stream running alongside.

3. Kenwood Lake

A medium sized lake, the water is not easily accessible on the banks. Only P. planorbis were found during 1958, but in 1959 no snails were present at all.

4. Kew Gardens

The lake in Kew Gardens was visited four times throughout the tenure of this work and L. stagnalis and L. pereger were collected from it.

Apart from the places mentioned above several other ponds and lakes were tried but no snails were present in them. Particularly notable among these is the Serpentine (Hyde Park), Regents Park Lake and St. James's Park Lake.

Species of Snails Examined

During this investigation, about four thousand snails were examined. These snails belonged to thirteen species extending over six genera.

Genus Limnaea

1. L. stagnalis (Linn.)
2. L. pereger (Müll.)
3. L. palustris (Müll.)
4. L. auricularia (Linn.)
5. L. truncatula (Müll.)

Of these, L. stagnalis and L. pereger were far more common than the other three species.

Genus Planorbis

1. P. corneus (Linn.)
2. P. planorbis (Linn.)
3. P. carinatus (Müll.)
4. P. spirorbis (Linn.)

The first two species were more common than the last two.

Genus Physa

1. P. fontinalis (Linn.)

Genus Bithynia

1. B. tentaculata (Linn.)

It was found only in three localities, but was abundant in these places.

Genus Valvata

1. V. piscinalis (Müll.)

Genus Hydrobia

1. H. jenkinsi (Smith)

This species was found in enormous numbers in two places only.

Host-Parasites List of the Cercariae Encountered

L. stagnalis

Parasites	Time when infected snails were found	Percentage of infected snails	Locality
Echinostome			
C. deficipinnatum n. sp.	June to October	1-4	Sand Pits (South Ockendon)
C. essexensis n. sp.	March to November	1-4	Sand Pits (South Ockendon)
		1-4	Epping Forest
Xiphidiocercous			
C. chiselhurstensis n. sp.	March to November	1-4	Sand Pits (South Ockendon)
		1-4	Chislehurst Common
		2-5	Epping Forest
C. P. megalorchis Rees	June to September	1-5	Sand Pits (South Ockendon)
		1-2	Lake Meadows
Furcocercous			
C. X. Baylis	March to November	5-20	Henninfield reservoir
		1-2	Sand Pits (St. Albans)
		5-10	Sand Pits (South Ockendon)
C. pseudocellata Szidat	April to August, 1959	5-10	Lake Meadows

L. peregar

Monostome			
C. monostomi v. Linst	July to September	1-2	Sand Pits (South Ockendon)

		2-5	Stoneyfields Park
Echinostome			
C. Z. Rees	March to November	2-8	Lake Meadows
		5-10	Keston Common
		5-50	Bushy Park
		5-30	Stoneyfields Park
		5-10	Epping Forest
Xiphidiocercous			
C. peregeri n.sp.	March to August	Single infection	River Thames
C. meadowensis n. sp.	April to September	3-10	Lake Meadows
Furcocercous			
C. kentensis	May to July	4-50	Keston Common
		5-50	Sand Pits (South Ockendon)
C. a. g. minor (Yamaguti) Iles	July to October	2-3	River Thames
		2-5	Bushy Park
		1-4	Sand Pits (South Ockendon)
		2-5	Stoneyfields Park
C. letifera Fuhr.	September, 1959	Single infection	Sand Pits (South Ockendon)
C. paracauda Iles	August to October	10-30	Bushy Park, Richmond Park Epping Forest

L. auricularia

Echinostome			
C. Z. Rees	March to November	5-10	Keston Common

L. palustris

nil

L. truncatula

nil

P. corneus

Echinostome			
C. londonensis n. sp.	March to October	80-90	Bushy Park
		20-30	Stoneyfields Park
Furcocercous			
C. tetraglandis Iles	March to November	5-15	Bushy Park
		7	St. Albans Lake
		4-10	Epping Forest
		2-5	Stoneyfields Park
C. pseudolinearis n. sp.	August, 1959	Only 2 infected snails	Stoneyfields Park
C. bilharziellae polonicae Szidat	April to August	Only 2 occasions	Lake Meadows

P. planorbis

Monostome			
C. heterocellata n. sp.	September	2 snails	Stoneyfields Park
Echinostome			
C. hamptonensis n. sp.		10	Hampton Court

		5-50	Stoneyfields Park
C. thamesensis n.sp.	August	Single infection	River Thames
Furcocercous			
C. planorbida Iles	June to October	10-50	Bushy Park River Thames Epping Forest
C. kenilworthensis n.sp.	August and September, 1959	10	Stoneyfields Park
C. edgwarensis n. sp.	August and September, 1959	12	Stoneyfields Park
	P. carinatus		
nil			
	P. spirorbis		
Furcocercous			
C. complex-iglandulosa n.sp.	September	Single infection	Bushy Park
	P. fontinalis		
nil			
	B. tentaculata		
Monostome			
C. middlesexensis n.sp.	August to September	1-2	Bushy Park
Gymnocephalous			
C. albinea n. sp.	June to September	5-20	Bushy Park
C. densacutis n.sp.	June to September	2-10	Bushy Park
C. lophocerca Fil.	September, 1959		Bushy Park

Xiphidiocercous			
C. minor n. sp.	March to September	1-2	Bushy Park
C. tarda n. sp.	March to September	Twice only	Bushy Park
Furcocercous			
C. bushiensis n. sp.	March to October	1-4	Bushy Park
C. papillosoma n. sp.	March to October	1-5	Bushy Park
C. ariformis n.sp.	March to September	2	Bushy Park
Cercariaeum			
C. bithyneae n.sp.	March to September	1-4	Bushy Park
	V. piscinalis		
Echinostome			
C. echinoparyphii recurvati	June to October	2-5	Bushy Park
Furcocercous			
C. cristocorpa n. sp.	September, 1959	Twice only	Bushy Park
Cercariaeum			
C. internale n.sp.	September, 1960	Two snails	Bushy Park

List of Freshwater Cercariae Previously Recorded from Britain

Monostome

C. monostomi v. Linst. (Rees, 1932)
(= C. notocotylus seineti (Fuhr.) Harper, 1929)

Gymnocephalous

C. fasciolae hepaticae Thomas, 1883; Wright, 1927 and Rees, 1932

Echinostome

C. echinata Brown, 1926

C. granulosa Brown, 1926

C. equispinosa Brown, 1926

C. limbifera Brown, 1931; (Rees, 1932)

C. oscilatoria Brown, 1931

C. echinoparyphii recurvati (v. Linst.) (Harper, 1929)

C. Z. Rees, 1932

Xiphidiocercous Cercariae

C. spp. Hesse, 1923

C. pulicis Brown, 1926

C. pseudodermata Brown, 1926

C. leptostoma Brown, 1926

C. cambrensis I Wright, 1927

C. cambrensis II Wright, 1927

C. X1 Harper, 1929

C. X2 Harper, 1929

C. X3 Harper, 1929

C. X4 Harper, 1929

C. cambrensis III Rees, 1932

C. lecithodendrium chilostomum Brown, 1926

C. crepidostomum farionis Brown, 1927

Furcocercous cercariae

C. sp. Hesse, 1923

C. fissicauda Brown, 1926

C. macrosoma Brown, 1926

C. micromorpha Brown, 1926

C. X Baylis, 1930 (Syn. C. chromatophora Brown, 1931)

C. echinomorpha Brown, 1931

C. pygocytophora Brown, 1931

C. F.1 Harper, 1931

C. F.2 Harper, 1931

C. cotyturus cornutus Harper, 1931

C. Y. Rees, 1932

C. ocellata (= C. pseudocellata) Rees, 1932

C. X Baylis, 1931; (Rees, 1932; Erasmus, 1957)

C. diplostomum phoxini (Faust) Rees, 1957

C. valvatae Lal. 1958

C. tetraglandis Iles, 1959

C. paracauda Iles, 1959

C. planorbida Iles, 1959

C. apatemon gracilis minor (= C. hamburgensis Komiya, 1938) Iles, 1959

C. vivacis Iles, 1959

C. cotylurus brevis Nasir, 1960

C. roathensis Erasmus, 1960

Macrocercous cercariae

1. C. macrosoma Vickers, 1941
2. C. phyllodistomum simile Thomas, 1956

Monostome Cercariae

Lühe (1909) defined these as "cercariae without a ventral sucker, with eyespots, with long, simple and slender tail, development in redia and encystment in freedom".

Odhner (1907, 1911b) regards the Monostomes as a polyphyletic group, which have evolved, partially if not fully, from the distomes with the loss of ventral sucker.

Faust (1922) divided Lühe's "Monostome" group into two subgroups, "Binoculate" subgroup with members having two lateral eyespots and "Trioculate" subgroup in which he placed cercariae with a cyclopean third eyespot.

Sewell (1922) uses the term "Monostome" in a wider sense and has grouped under this category all the larval trematodes lacking a ventral sucker. This he postulated on the contention that in the group "Monostome" if used in the restricted sense, according to Lühe, would fall members of several subgroups, which show relationship with other groups, the members of which cannot be included in this group. He divided his "Monostome" cercariae into six subgroups; "Pleurolophocercous", "Urbanensis", "Ephemera", "Lophocerca", "Lophoides" and "Ubiquita". Of these, "Urbanensis" and "Ephemera" subgroups are roughly the same as "Binoculate" and "Trioculate" subgroups of Faust.

Later workers generally disagree with Sewell's

scheme. Dubois (1929) and Wesenberg-Lund (1934) agree with Odhner's view. Dubois (1929) also mentioned that Sewell's (1922) "Urbanensis" and "Ephemera" divisions, which he based on the size and number of eyespots, are unnatural. Miller (1926) included the "Lophocerca" and "Lophoides" subgroups among his "Apharyngeal Brevifurcate Monostome" and "Apharyngeal Longifurcate" divisions respectively. The "Ubiquita" subgroup of Sewell has been regarded as true "Xiphidiocercous" cercariae, on their close morphological similarities by Wesenberg-Lund (1934). Dubois (1929) amended the characters of the "Pleurolophocercous" subgroup in that in its members the ventral sucker may be well developed, rudimentary or completely absent. This removed this group from the "Monostome" and placed it among the "Gymnocephalous" cercariae. Later on Sewell (1931) also agreed with the amendment proposed by Dubois.

Rothschild (1938a), while discussing the classification of the cercariae of the superfamily Notocotyloidea has separated them into two main divisions. The first division includes those without an aural lappet or a collar and producing adults belonging to family Notocotylidae and the second group accommodates the cercariae with aural lappets or a collar and develop into members of family Pronocephalidae. The first group has again been subdivided into three groups, (1) "Monostomi" subgroups, with forms

having the transverse portion of the main excretory canal lying behind the median eyespots or the cerebral ganglion; (2) "Imbricata" subgroup with cercariae having their transverse portion of the main excretory duct in front of the median eyespot and (3) "Yenchingensis" sub-group including forms having an unpaired finger-like diverticulum on the transverse portion of the main excretory duct. The cercariae of the second division belonging to Pronocephalidae are placed in a single "C. Indicae XI" group. She also has suggested a list of characters for the differentiation of the species of "Monostome" cercariae.

Recently Dubois (1951) has reviewed and analysed the genus Notocotylus Diesing, 1839, and has suggested two subgeneric types, with larvae distinguishable on the morphological and biological grounds. The two groups of larvae suggested by him are:-

(1) "Triserialis" subgroup developing in pulmonate snails.

(2) "Imbricata" subgroup developing in prosobranchiate snails.

Only three "Monostome" cercariae were found in this survey. Two of them belong to the "Monostomi" subgroup and the third to the "Yenchingensis" subgroup of Rothschild.

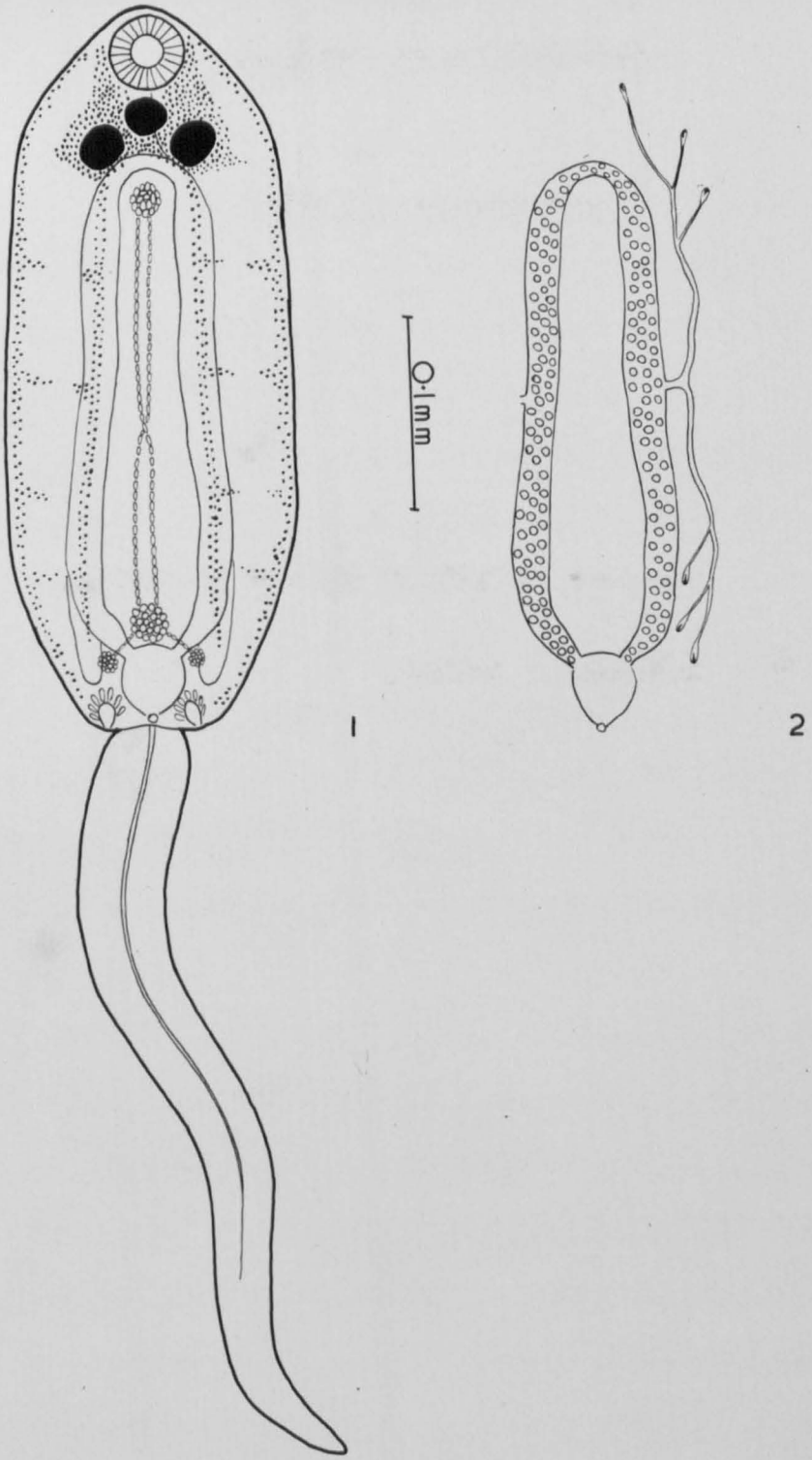
Explanation to Plate 2

Cercaria monostomi

fig. 1 General structure of the cercaria.

fig. 2 Excretory system.

Plate 2



1. Cercaria monostomi V. Linst. 1896 (Plate 2, figs. 1 and 2)
syn. C. notocotylus seineti (Fuhr, 1914) Harper, 1929

This cercaria was first recorded by Von Linstow in 1896 from L. ovata and L. pereger. Dubois (1929) reported it from Neuchatel and added L. palustris, L. stagnalis and P. carinatus to the list of its host. Wünder (1924) described the development and function of the tail and encystment, but did not give any account of the redia. Harper (1929) found a monostome cercaria from Britain which by controlled feeding experiments proved to be the larva of Notocotylus seineti Fuhr, 1914. This cercaria is identical with C. monostomi. Rees (1932) recorded it from Britain and gave a detailed account of the process of encystment. Wesenberg-Lund (1934) has reported it from Denmark. Except for one record of Dubois (1929), this cercaria was always found to parasitize species of Limnaea.

This description is given with a view to clearing some of the morphological points and to bring the description up to the level of any other cercaria recently described.

This cercaria was found on several occasions emerging from L. pereger collected during August and September, 1958 and 1959 from Bushy Park, Sand Pits near South Ockendon (Essex). At both these places P. planorbis, P. corneus were also found in abundance, but none of these species was ever found to be infected with this cercaria. The

infection rate at these two places was always different. Snails collected from Bushy Park, where there is a small pond, showed an infection rate ranging between five to ten per cent, while the infection rate among snails from Sand Pits, which occupy a larger area, never exceeded two per cent.

Redia

The rediae are long, sac-like structures in the digestive gland of the host. They are without any indentations and are colourless or hyaline and rather opaque. The lack of pigment has been attributed by Wesenberg-Lund (1934) to the probable cause of their development in snails with colourless blood as compared to the pigmented rediae of C. ephemera Nitzsch which develops in P. corneus with cherry red blood. This supposition seems to be erroneous, as several Echinostome cercariae described from lymnaeid snails have always been reported to have an orange pigment in the redia. Moreover the pigment of the redia is of a different colour from the cherry-red blood of the host, a fact which has been noted by Wesenberg-Lund himself. The muscular pharynx is followed by a short, narrow, thin-walled tube which dilates posteriorly into a wide gut. This gut of the redia was never found to extend to the extreme posterior end but always terminates some distance in front of it, leaving a space which is occupied

by germ balls. The germ balls increase in size from behind forwards as described by Wesenberg-Lund (1934). The number of developing cercaria in a redia has been given as seven to eight by Wesenberg-Lund (1934). This number never exceeded four in the present specimens and they were found in a single row or irregularly placed. The collar and the ambulatory processes are absent. Only once a redia was found to have a daughter redia inside.

The cercariae leave the rediae in an immature state to complete their development in the host-tissue. A large number of immature cercariae are always found in the digestive gland of the host, but hardly any fully developed cercariae were seen on dissecting the infected snails. The cercariae apparently leave the snail as soon as they complete their development. The largest living redia measure 2.12 mm. long and 0.39 mm. broad with a pharynx 0.1 mm. in diameter.

Emergence and Behaviour

The cercariae emerge throughout the day in fairly large numbers. They exhibit a strong positive phototropism. As soon as they come in contact with a solid object, such as the wall of the container, snail shell, lettuce or paper, they attach themselves with the help of the oral sucker and posterior suctorial pockets and begin to encyst. The cysts are formed readily and it is very difficult to

prevent it after the cercaria has once attached to a solid surface. The cysts are also formed on a slide equally quickly. It was only possible to study the cercaria by pressing the slide on the cover-glass, immediately after placing the cercaria on a slide. Heating the slide over a flame was also helpful.

Cercaria (Plate 2, figs. 1 and 2)

The shape of the body may be elongated, ovoid, spatulate or nearly circular according to the degree of contraction. The body is heavily pigmented. This pigment is concentrated more around the lateral eyespots. On the body the development of the pigment takes place along two dorsal, two ventral and two lateral lines as described by Dubois (1929) and not along only two dorsal and two ventral lines as stated by Harper (1929), Rees (1932) and Wesenberg-Lund (1934). This arrangement is more clearly seen in slightly immature cercariae after fixing and staining them. In living, fully mature cercariae it is difficult to see this concentration of the pigment.

There are three dark eyespots in the mature cercaria. Of these the median eyespot appears very late in the development of the cercariae. The majority of the cercariae dissected out of the snail have only two lateral eyespots, or occasionally a poorly developed median eye. In free-living cercariae the three eyspots are of sub-equal size

and are usually circular or slightly oval in outline. There are no spines on the body.

At the postero-lateral ends of the body on the ventral side is a pair of cuticular invaginations, the "lateral organs" or the "posterior suctorial pockets". They are borne on small conical projections of the body and are well removed from the actual junction of the body and tail. Contrary to the statements of Harper (1929) and Rees (1932) these organs are clearly visible in fixed specimens when viewed from the lateral side. Faust (1917) suggests that they have originated from similar structures, the caudal pockets, in some distome cercaria, but their position as described here makes this speculation doubtful. Dubois (1929) has mentioned the presence of "cellules glandulaires" or the cement glands associated with these structures. Both Rees (1932) and Wesenberg-Lund (1934) were unable to see them. These glands, about six in number, have been seen very clearly in fixed and stained specimens.

The anterior, sub-terminal oral sucker is followed by a short, thin-walled oesophagus, which divides just behind the median eye, forming two intestinal caeca extending to the posterior end of the body. The caeca are cellular and non-functional. Lühe (1909) describes the presence of a small pharynx, but later workers, Dubois (1929), Harper (1929), Rees (1932) and Wesenberg-Lund (1934) were unable to see any pharynx. A very careful study of

the present specimens has also failed to reveal the presence of this organ.

Nothing is known about the flame cell pattern of this species, except for a single flame cell observed by Rees (1932).

The excretory system (Plate 2, fig. 2) comprises a nearly rounded excretory bladder, which opens to the exterior dorsally at the junction of body and tail, through a transversely elongated excretory bladder. Two main excretory ducts, open independently into the excretory bladder antero-laterally. These ducts are filled with numerous rounded excretory granules and proceed anteriorly up to the posterior level of the oesophagus, where they bend inwards and join one another behind the median eyespot. A small duct opens into these main excretory ducts nearly in the middle of the body length. This duct divides into an anterior and a posterior collecting tubule, each receiving capillaries from three flame cells. The flame cells could not be seen in fully mature cercariae; this description is based on the study of immature forms. This flame cell pattern conforms to that described by Faust (1919c) for C. spatula; by Porter (1938) for C. xenopi and Fain (1953) for C. cochlea. The caudal excretory duct is unbranched and can be traced up to nearly three-fourths of its length.

The structure of the genital primordium is best seen

in fixed and stained specimens (Plate 2, fig. 1). There is a small mass of deeply staining cells just in front of the excretory bladder on the median longitudinal line. This represents the future ovary. From this, a string of cells, the oviduct, proceeds forwards up to a short distance behind the transverse part of the excretory canals where it ends in another small mass of cells which according to Faust (1917) represents the future vagina. At the postero-lateral aspects of the ovary is a pair of small larval testes. Two vasa efferentia from these testes proceed inwards joining each other at the level of the ovary, to form a vas deferens. The vas deferens proceeds anteriad along the right side of the oviduct, up to nearly the middle of the body, where it crosses over to the left side, still to continue alongside the oviduct, up to the primordium of the vagina, where it terminates in a small mass of cells, the future cirrus pouch, lying in front of and almost confluent with the vaginal primordium. This arrangement of the reproductive primordium is in accordance with the descriptions of Dubois (1929) and agrees with those described by Faust (1918b), Sewell (1922), Porter (1938) for C. monostomi, C. robusta, C. Indicae XI and C. fulvoculata, respectively, except that in C. robusta and C. Indicae XI the masses of cells representing the cirrus pouch and vagina are completely separated and in C. fulvoculata they are not shown to be present.

The tail is simple and aspinose, gradually tapering posteriorly. It may become shorter than the body when fully contracted but is, while at rest, longer than the body both in the living and fixed specimens. Rees (1932) has shown that there are six pairs of glandular cells on the sides of the caudal excretory ducts. These glands have been described for some other Monostome cercariae and Cort (1914) states that no probable function can be attributed to them. Faint outlines of these cells were observable in the present specimens.

Measurements of Cercaria (In millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length extended	0.530-0.610	0.570	0.393-0.520	0.456
Body breadth	0.280-0.300	0.290	0.150-0.250	0.190
Tail length	0.516-0.650	0.583	0.416-0.680	0.540
Tail breadth	0.066	0.066	0.043-0.060	0.050
Oral sucker diameter	0.053-0.066	0.060	0.033-0.045	0.040
Diameter of eyes	0.020-0.030	0.022	0.017-0.022	0.020
Distance between lateral eyes	0.116-0.150	0.133	0.043	0.043
Distance between median eye and anterior end of body			0.036	0.036

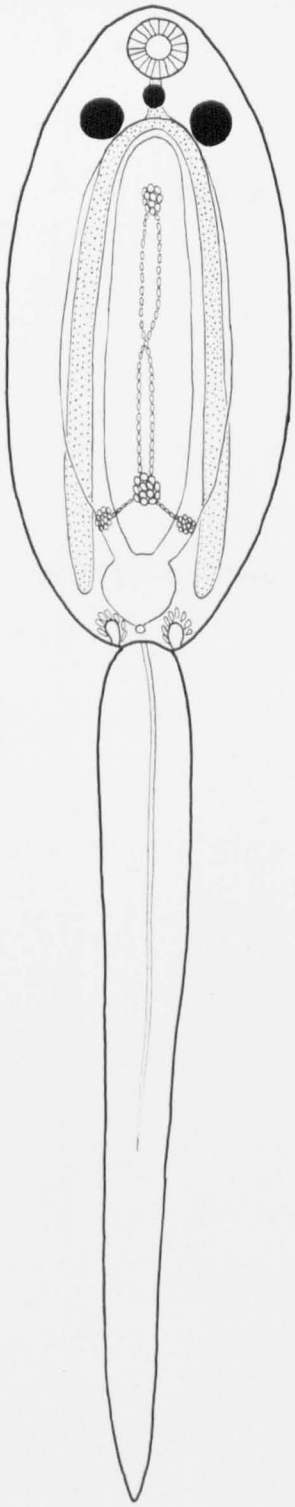
Explanation to Plate 3

Cercaria heterocellata n. sp.

fig. 1 General structure of the cercaria.

fig. 2 Excretory system.

Plate 3



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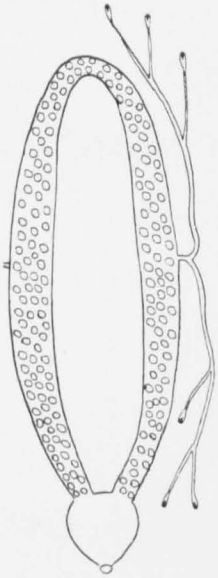


2

Cyst

The cyst formation has been studied by Wünder (1924). Wesenberg-Lund (1934), who has only figured different stages in the process, and by Rees (1932). Rees's description of the process is very accurate and my observations entirely agree with hers. The cysts are always found outside the body of the snail.

Wesenberg-Lund (1934) describes that on opening an infected snail a large number of cercariae started casting off their tails and encysting. I never had the occasion to see such a happening. Actually the majority of the cercariae which were dissected out of the snails failed to encyst.

The hemispherical cysts, with their attached sides flat, are 0.025-0.026 mm. in diameter with a double cyst wall measuring 0.015-0.025 mm. in thickness.

2. C. heterocellata n. sp. (Plate 3, figs. 1 and 2)

Only two specimens of P. planorbis collected during September, 1959 from Stoneyfields Park in Kenilworth Estate (Edgware) were found to be discharging this cercaria. This pond has a rich molluscan fauna comprising L. stagnalis, L. pereger, P. corneus and H. jenkinsi in addition to P. planorbis but none of the other species was ever found to be infected with a monostome cercaria.

Redia

The redia are simple, sac-like structures occurring in comparatively fewer numbers in the digestive gland of the host. Some of the rediae were found to be lying superficially over the surface of the gland. They are colourless, non-motile, simple sac-like structures, without a collar or ambulatory process. The bodies of the rediae are thick and with thick walls, making them opaque. A muscular pharynx is usually followed by a small thin-walled tube which dilates posteriorly to form a wide gut, extending up to the anterior limit of the germinal cells. In each redia up to 4 developing cercariae were seen. These inter-redial cercariae had only two lateral eyespots. The size of the rediae is variable. The mass of the germinal cells of the redia is confined to the posterior end of the redia. The cercariae leave the redia in an immature form and complete the development in the tissue of the host.

Living rediae vary between 0.46 and 1.20 mm. in length and 0.09-0.36 mm. in greatest width. The pharynx measured between 0.04 and 0.08 mm. in diameter.

Emergence and Behaviour

The cercariae emerge throughout the day from the snail. The largest number was seen to emerge just after

noon. After emergence the cercariae always spend a free-swimming life and do not encyst immediately as is the case with C. monostomi. The cercariae when isolated soon after their emergence, were found to take between 30 minutes and two hours before they encysted. The encystment takes place on the wall of the glass container, snail shell or other submerged objects. The wall of the glass container was the most favoured spot. All the cysts on the wall of the container were found on the lighted side, which shows that they respond to light. This phototropism however is much weaker than that exhibited by C. monostomi.

Cercaria (Plate 3, figs. 1 and 2)

The cercariae are pigmented and have a dull greyish brown colour. The pigment is not aggregated along lines on the body but is uniformly scattered all over the body. There is no concentration of pigment around the eyespots. The body is elongated when extended, but may become nearly spherical when fully contracted. Presence of pigment and numerous cystogenous gland cells which have coarsely granular contents, make the body opaque. Near the anterior end are three eyespots, two are lateral, which are circular or slightly oval, the third is median and lies just behind the oral sucker. The median eyespot is circular and is half the size of either of the lateral eyespots. All

the eyespots are dark black in colour with a lens directed dorsally and anteriorly. The body is without any spines or hair.

The tail is simple, tapering gradually posteriorly. It is muscular and when extended it is longer than the body but smaller when contracted. However, in fixed specimens it is always slightly longer than the body. There are no gland cells in the tail as described by Faust (1917, 1918b) in C. konadensis and C. robusta and seen in C. monostomi in the present study. There are patches of bright yellow or orange pigment in the tail.

Small muscular oral sucker is followed by a short, narrow oesophagus which bifurcates into two intestinal caeca, slightly posterior to the median eye. The caeca extend up to the sides of excretory bladder. I have not been able to see any cavity in the caeca nor have I been able to find the presence of a pharynx.

The excretory system (Plate 3, fig. 2) comprises a posterior, nearly circular excretory vesicle. It opens through an oval excretory pore dorsally at the junction of the body and the tail. The excretory vesicle receives two main excretory trunks antero-laterally, each opening independently into the bladder. These main excretory trunks run laterally along the body and converge at the level of the eyespots and join one another just posterior to the median eyespot. There is no median blind pouch on this

excretory commissure. The main excretory trunks are filled throughout their length with numerous refractile granules. The caudal excretory duct is unbranched. The flame cells and their capillaries are exactly the same as described for C. monostomi.

The genital rudiment (Plate 3, fig. 2) can only be seen in fixed and stained specimens. It agrees with that described by Faust for some Monostome cercariae. The ovarian cell mass lies at a small distance in front of the excretory bladder, a chain of cells arising from anterior side of the ovarian cell mass has been designated by Faust to represent the uterus which ends in a small cell mass or vagina located medially slightly behind the lateral eyes. Testes are represented by two small masses of deeply staining cells lying a small distance behind and lateral to the ovarian cell mass. A fine strand of cells, or vasa efferentia join near the ovarian rudiment to form a single vas deferens, which runs along the right side of the uterine duct up to the middle of its length, where it crosses over to the left and again continues along the uterine duct to terminate in another mass of cells, the cirrus pouch, in front. The primordium of the cirrus sac is confluent with that of the vagina; I have, however, never been able to find any trace of the vitelline glands as described by Faust (1917) for C. pellucida, C. konadensis, C. [illegible] and C. [illegible].

The encystment was observed several times. Its process is the same as has been described for C. monostomi by Rees (1932). The cysts measure 0.135-0.195 mm. in diameter with a cyst wall 0.03-0.045 mm. thick.

The tail of the cercaria after being detached, continues living and swimming for up to thirty minutes after which it settles to the bottom and disintegrates.

Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length (extended)	0.326-0.473	0.390	0.243-0.266	0.260
Body breadth	0.030-0.045	0.040	0.033-0.036	0.035
Tail length (extended)	0.333-0.500	0.416	0.336-0.350	0.346
Tail breadth at base	0.030-0.040	0.035	0.033-0.036	0.034
Oral sucker diameter	0.040-0.043	0.041	0.026-0.030	0.028
Lateral eye diameter	0.020	0.020	0.180-0.020	0.019
Median eye diameter	0.010	0.010	0.010	0.010
Distance between lateral eyes			0.033-0.036	0.034
Distance between median eye and anterior end of body			0.030-0.033	0.032

Comparison with Related Species

The cercaria under study belongs to the Monostomi sub-group of Rothschild (1938) and the Triserialis sub-group of Dubois (1951).

The complete absence of spines on the body and tail in the present species readily separates it from C. trabeculata Faust, 1914 and C. plana Faust, 1922.

Dubois (1951) has suggested that C. urbanensis Cort, 1914, C. vaga L. and U. Szidat, 1933 and C. notocotylus stagnicolae Herber, 1942, are synonyms of the cercaria of Notocotylus triserialis triserialis Dies, 1839. The present cercaria is smaller than these and also differs in having the median eye half the size of the lateral eyes in mature cercariae.

C. monostomi von Linst., 1896 is much larger than the present species, has a different type of pigment distribution on the body and also differs in having a median eye nearly of the same size as the lateral eyes.

C. ephemera Nitzsch, 1807 as described by Wesenberg-Lund (1934) and C. sp. Ahmad, 1959 have same type of the pigment distribution as in the present cercaria but both are larger and have a median eye of the same size as the lateral.

C. pellucida Faust, 1917 is larger than the present cercaria and also differs in the distribution of body pigment and in the possession of muscular bundles in the tail of the former. Both C. pellucida and C. imbricata are

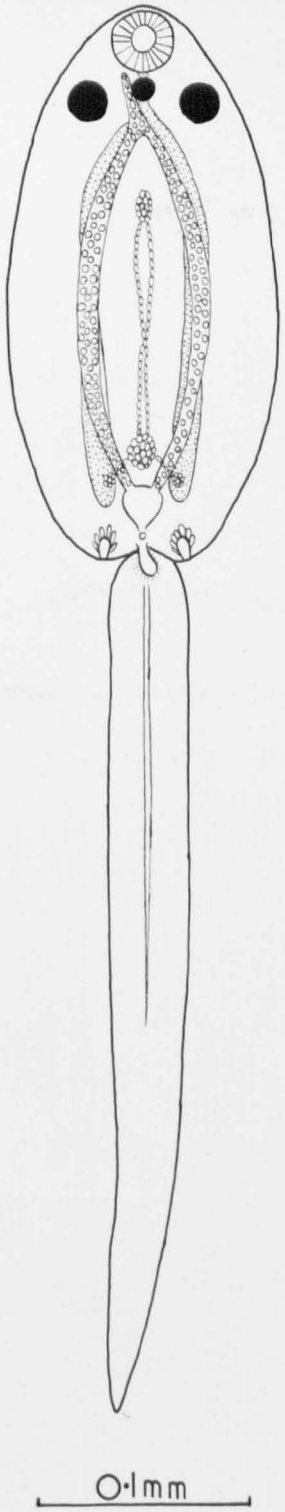
Explanation to Plate 4

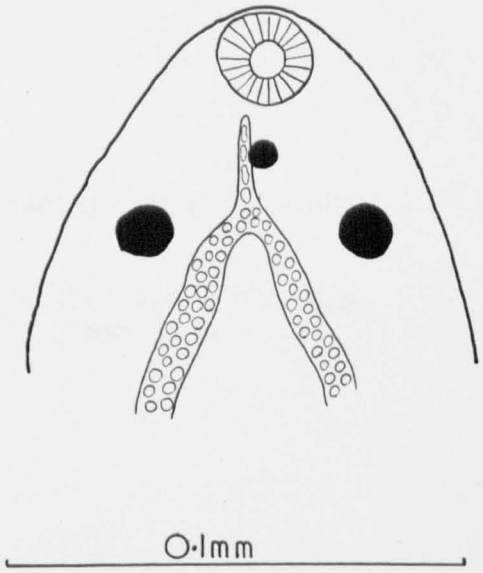
Cercaria middlesexensis n. sp.

fig. 1 General structure of the cercaria.

fig. 2 Anterior end of the body showing the blind excretory duct.

Plate 4





It also has spined internal lining and a reversible spined organ in the pharynx of the redia. The present species does not possess either of these two characters.

In view of the above comparison the present species is regarded as new and the name Cercaria heterocellata is proposed for it.

3. Cercaria middlesexensis n. sp. (Plate 4, figs. 1 and 2)

One to two per cent of B. tentaculata collected from Bushy Park were found to be infected with this cercaria.

Redia

Simple sac-like rediae are present in large numbers in the digestive gland of the host. The gut of the redia extends to about three fourths of the total length of the body and has dark or deep orange granular contents. The pharynx is well developed and slightly behind it is the birth pore. The collar and ambulatory processes are absent. The cercariae leave the rediae in an immature state and complete the development in the host tissue. Each redia may have up to four developing cercariae. The living rediae, with cercariae measure 0.675-1.5 mm. in length and 0.135-0.195 mm. in breadth with a pharynx 0.056-0.083 mm. in diameter.

Emergence and Behaviour

The cercariae are discharged in fairly large numbers during the day. They are positively phototropic and after a short free-swimming period they encyst on the wall of the container on the lighted side.

Cercaria (Plate 4, figs. 1 and 2)

The body has a dull brown pigment evenly distributed over its entire surface. There is no concentration of the pigment around the eyespots or along longitudinal lines along the body.

Near the anterior end there are three eyespots. Two lateral eyespots are jet black in colour and larger than the third median eyespot which is brown in colour and with an exposed white centre. Both the body and tail are without any spines. At the posterior end of the body are two posterior suctorial pockets. The position of these cuticular invaginations is the same as described for C. monostomi (present study). In this cercaria also these posterior suctorial pockets are without any spine and are provided with five to six small cement gland cells. The whole body is filled with cystogenous gland cells. The contents of these cells are in the form of short, thick rods with blunt ends.

The sub-terminal oral sucker is followed by a short

oesophagus which divides at the level of the excretory commissure. The intestinal caeca extend to the posterior end of the body. There is no trace of a pharynx.

The roughly pear-shaped excretory bladder is located in front of the junction of the body and the tail. It opens dorsally through a small excretory pore. Anteriorly the two main excretory ducts join at the level of the eyespots where a narrow, blind ending branch is given out which terminates near the posterior margin of the oral sucker, (Plate 4, fig. 2). This blind excretory duct is situated on the left side of the median line. The main excretory duct and the blind excretory duct are filled with numerous small refractile excretory granules.

The full complement of the excretory system could not be determined, but one pair of flame cells, postero-lateral to the oral sucker was seen.

The genital primordium is represented by masses representing an ovary, oviduct, vagina, a pair of testes, vasa efferentia, vas deferens and cirrus pouch. Their arrangement is exactly the same as described for C. monostomi and C. heterocellata (present study).

Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.35 -0.5	0.42	0.27 -0.316	0.284
Body breadth	0.116-0.26	0.15	0.116-0.166	0.132
Tail length	0.583-0.66	0.58	0.383-0.463	0.421
Tail breadth	0.033-0.066	0.05	0.026-0.033	0.03
Oral sucker diameter	0.034-0.045	0.04	0.026-0.033	0.031
Lateral eye diameter	0.015-0.023	0.019	0.016	0.016
Median eye diameter	0.011-0.019	0.15	0.010-0.013x 0.010-0.013	0.012

Comparison with Related Species

This trioculate cercaria possesses an excretory system of the "Yenchingensis" subgroup of Rothschild (1938) and in its development in a prosobranchiate snail belongs to the second group of Dubois (1951).

C. triophthalmia Faust, 1930; C. mirilli Ameel, 1939 and C. wesenberg-lundi Etges, 1956 have previously been described as trioculate forms, with yenchingensis type of excretory system and developing in prosobranchiate snails.

The present cercaria is larger in size than all three of these. It can further be differentiated from C. mirilli in having a relatively longer gut and a larger pharynx in the redia and from C. wesenberg-Lundi in having a much

larger redia.

C. triophthalmia also differs in having spines at the anterior end of the body, in pigment concentrated round the eyespots, in having a median eyespot equal in size or larger than the lateral eyespots and in having a very thin-walled redia.

The present cercaria is therefore considered as new and the name Cercaria middlesexensis is proposed for it.

Gymnocephalous cercariae

This heterogenous assemblage of cercariae comprises forms which lack a stylet or a collar of spines, possess a simple tail and develop in rediae.

Sewell (1922) regarded it as an unnatural group. He recognised four, the "Parapleurolophocerca", "Agilis", "Reflexae" and the "Isospori" sub-groups. Sewell (1922), Wesenberg-Lund (1934) and Porter (1938) agree with Lühe's (1909) view of instituting a super-group, the "Leptocerca", to accommodate the "Gymnocephalous", "Echinostome" and the "Xiphidiocercous" cercariae. Vogel (1934) observed that Sewell's (1922) characterization of the "Parapleurolophocercariae" was not entirely in accordance with recent studies on the group. He accordingly redefined the sub-group. Cable (1938) suggested further amendments to the definitions of "Parapleurolophocerca", "Agilis" and "Reflexae" sub-groups. Faust (1924) assigned the same basic flame cell formula for the "Pleurolophocerca" and "Parapleurolophocerca" sub-groups, but Cable (1938) pointed out that in view of recent studies, such a formula cannot be applied. Wesenberg-Lund (1934) however did not agree with Sewell's (1922) sub-division of the "Gymnocephalous" cercariae and pointed out that it did not serve any purpose with the European forms. He also removed the "Pleurolophocercous" sub-group of Sewell from his "Monostome" cercariae and placed it among the "Gymnocephalous" cercariae because of

their close similarity with the "Parapleurolophocerca" sub-group.

Porter (1938) agreed with previous workers in regarding the "Gymnocephalous" group as, "an assemblage of the residue from other groups", and suggested another, the "Paragilis" sub-group, differing from the "Agilis" group in having a better developed alimentary canal. She removed the "Isospori" sub-group from the "Gymnocephalous" cercariae and placed them among the "Rhopalocercous" cercariae.

Rothschild (1938b) maintained that there were insufficient grounds for the separation of the "Pleurolophocerca" and "Parapleurolophocerca" sub-groups and defined them as one group.

Fain (1953) agrees with Porter (1938) in the exclusion of the "Isospori" sub-group from the "Gymnocephalous" cercariae and includes the "Megalura" group of Sewell (1922) here.

Different sub-groups of the "Gymnocephalous" cercaria may be defined as follows:

(1) "Parapleurolophocerca" and "Pleurolophocerca" group. Cercariae with or without a pair of pigmented eyespots, body partially or wholly spined, tail longer than the body and with finfold, ventral sucker well developed, rudimentary or absent, oral sucker modified into a protrusible anterior organ, oesophagus and caeca present or absent; penetration glands present; excretory bladder reniform or globular; development in redia with a gut and birth pore but without

ambulatory processes.

Further sub-division of this group has been proposed by Martin (1950) and Ullman (1954).

Agilis group (including paragilis group of Porter)

Cercariae resembling echinostome cercariae but lacking a collar of spines, numerous cystogenous gland cells present, ventral sucker always present and situated at one third of a quarter of body length from the posterior end. The oesophagus and intestinal caeca present or absent. Excretory bladder usually two chambered, main excretory canals forming a loop at the side of pharynx. Few large excretory granules present in the pre-acetabular region of the main excretory ducts, or numerous small excretory granules present throughout their length. Development in redia with collar, birth pore and ambulatory processes.

Reflexae Sub-group

Similar to the "Agilis" sub-group but differ in having caudal finfolds and in the oesophagus and the intestinal caeca being always present.

Members of the "Agilis" and the "Parapleurolophocercous" sub-groups were encountered in the present investigations.

Explanation to Plate 5

Cercaria albinea n. sp.

fig. 1 General structure of the cercaria.

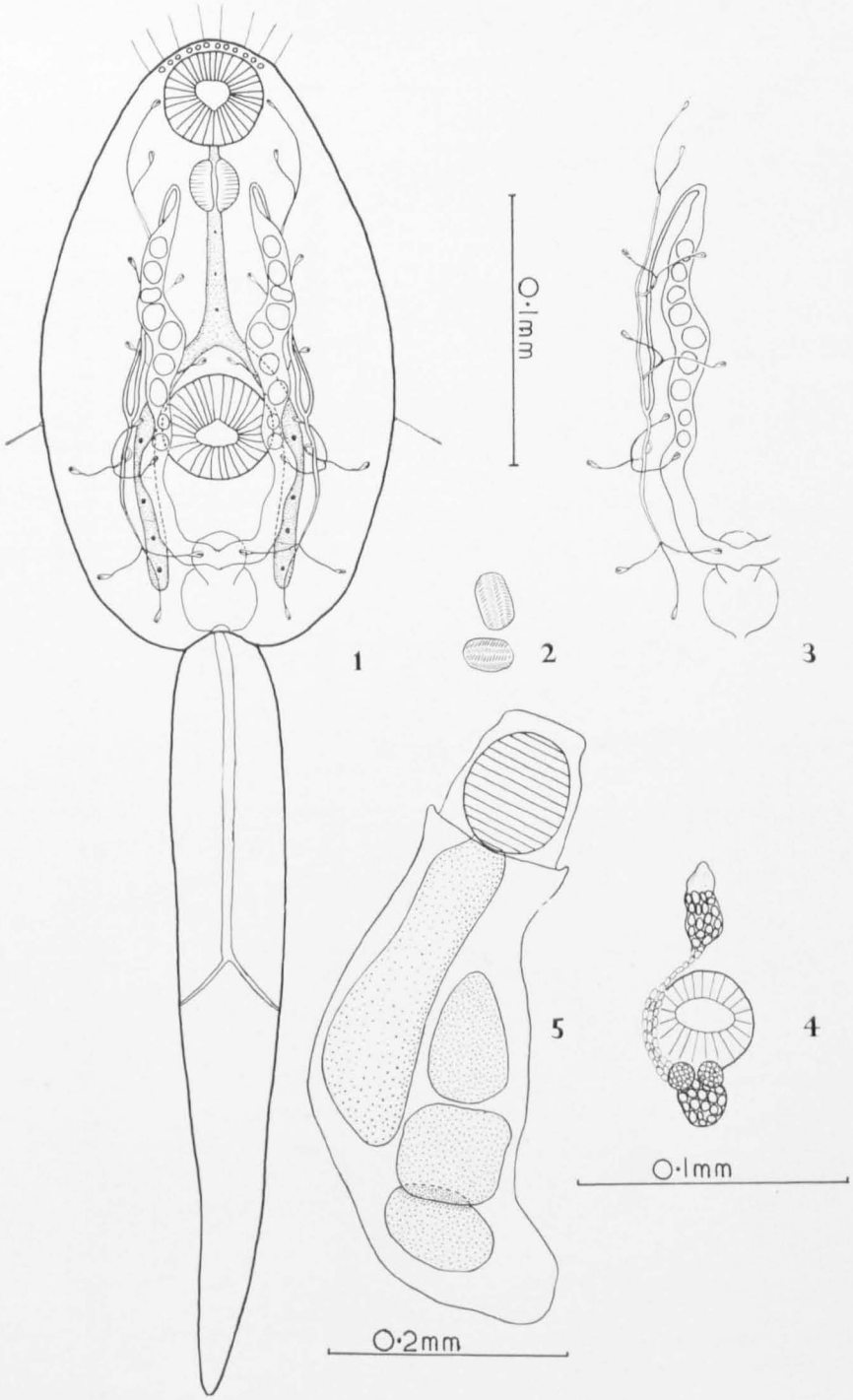
fig. 2 Cystogenous gland cells.

fig. 3 Excretory system.

fig. 4 Genital primordium (dorsal view).

fig. 5 Redia.

Plate 5



4. Cercaria albinea n. sp.+ (Plate 5, figs. 1-4)

From August to September, 1959, 10-20 per cent of B. tentaculata (Linn.) collected from Bushy Park were found to be infected with this cercaria. Among several other ponds of London and adjoining areas, this was the only place where this cercaria was found.

Redia

The sac-like rediae are loosely placed on the surface of the digestive gland of the host. They are colourless and inactive. The ambulatory processes are not well developed and are nothing but very short, stumpy projections. The collar is also poorly developed. An inconspicuous birth pore is located on the dorsal side, a short distance behind the well developed pharynx. The gut, with orange coloured liquid contents, extends about three quarters of the length of the redia. Each fully developed redia has five to six large germ balls and one to three immature cercariae. The cercariae leave the rediae in an immature stage and complete their development in the host tissue, where a large number of immature cercariae are always found. The size of the rediae is highly variable. The largest living specimen measured

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0.733 mm. in length and 0.250 mm. in breadth with a pharynx 0.116 x 0.110 mm. in size.

Emergence and Behaviour

The cercariae are shed in the afternoon. A large number is discharged between 4-5 p.m. Macroscopically these cercariae resemble echinostome cercariae; they are as white and swim in the same fashion as echinostome cercariae. They are very active and swim almost continuously after their emergence, exhibiting a tendency to concentrate near the bottom of the container.

Cercaria

The thick body is oval in shape and completely devoid of any collar or spines. There are only five pairs of long hair-like structures. Four pairs of these are situated at the anterior end of the body and one pair on the side at the level of the ventral sucker. The body is without any pigmentation and absolutely white, with no eyespots. There is a large number of cystogenous gland cells, occupying almost the whole of the body. These cells have rod-shaped contents, each cell containing four to five bundles of rods. The oral sucker is well developed and subterminal in position. A short prepharynx is followed by a muscular pharynx and a long oesophagus, which divides

just in front of the ventral sucker. The intestinal caeca extend to the posterior end of the body. Both the oesophagus and intestinal caeca are composed of a single series of cells and are non-functional.

The penetration gland cells were obscured by numerous cystogenous gland cells, but twelve ducts, presumably the penetration gland ducts open at the anterior end of the oral sucker. The ventral sucker is located behind the middle of the body and is larger than the oral.

There is an accessory excretory bladder lying antero-dorsally to the main excretory bladder, into which it opens through a wide opening. The lateral excretory ducts join together to form a short median duct before opening into the accessory excretory bladder. The lateral excretory ducts are narrow and wavy up to the ventral sucker, after which they become distended. This distended portion accommodates nine to twelve refractile excretory granules, which are irregular in shape and variable in size. A narrow loop is formed at the side of the pharynx. The descending excretory duct bifurcates at the side of the ventral sucker. The anterior collecting tubule receives three ducts, each connected with two flame cells, while the posterior receives two ducts, each connected with three flame cells. The excretory system may be expressed as $2\left[(2 + 2 + 2) + (3 + 3)\right] = 24$. The caudal excretory duct bifurcates at the middle of the tail into

two branches, each opening at the lateral side.

The genital primordium is well differentiated. There is a large mass of deeply staining cells behind the ventral sucker, this represents the future ovary. Just in front of this, there are two small circular masses of cells - the testes. A large pre-acetabular mass of cells is connected to the post-acetabular mass by a strand of cells (Plate 5, fig. 4).

The aspinose tail is simple and without a finfold. It is longer than the body both in the living and fixed specimens.

Measurements of Cercaria (In millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.283-0.400	0.341	0.216-0.253	0.236
Body breadth	0.150-0.230	0.210	0.133-0.163	0.149
Tail length	0.333-0.433	0.390	0.300-0.343	0.318
Tail breadth at base	0.050-0.065	0.060	0.040-0.050	0.045
Oral sucker	0.043-0.056x 0.050-0.056	0.050x 0.054	0.040-0.043x 0.040-0.043	0.041x 0.043
Pharynx	0.023-0.033x 0.023-0.036	0.028x 0.032	0.023x0.023	0.023x 0.023
Ventral sucker	0.056-0.070x 0.056-0.076	0.056x 0.071	0.043-0.053x 0.043-0.056	0.045x 0.051

Cyst

The encystment takes place in the body of B. tentaculata. The cysts were also found in the same snails that harboured the rediae, but in such cases the number of the cysts was always found to be small. In other snails, which were not harbouring the rediae, enormous numbers of cysts were often found. This suggests that whereas the cercariae may re-enter the same snail, they must leave the snail for a free swimming life, before encystation takes place. In light infections the cysts are found in the digestive gland, but in very heavy infections they are located on every part of the body, except those external to the shell. The encystation never takes place in the open. When a small number of cysts are present in a snail, they are always rounded, but in heavy infection they assume different shapes, due to the pressure of adjoining cysts, when most of them exhibit a roughly hexagonal or triangular outline. In such cases the size may also vary accordingly. The rounded cysts measure 0.100-0.160 mm. in diameter with a cyst wall 0.008-0.010 mm. thick.

Comparison with related species

The present cercaria differs from C. psilotremi spiculigerii Mathias, 1925; C. chitinosoma Faust, 1930; C. catenadena Faust, 1930; C. durbanensis Porter, 1938;

C. thomasi McMullen, 1938 as described by Kuntz (1951) and C. palegae Goodman, 1951, in having an unspined body.

In lacking papillae on the body, having an excretory duct branching in the middle of the tail and being absolutely white the present cercaria can be separated from C. tuberculata Fil. 1859, C. papillosa Fil. 1859 (as described by Wesenberg-Lund, 1934) and C. fasciolae hepaticae Thomas 1883. It further differs from C. tuberculata in having excretory granules limited to the pre-acetabular portion of the main excretory ducts and from C. f. hepaticae in having much smaller tail and bifurcation of the oesophagus just in front of the ventral sucker. The bifurcation of the caudal excretory duct in the middle of the tail, with its branches opening laterally in the present cercaria also separates it from C. Indicae XLI Sewell, 1922; C. gracilis O'Roke, 1917; C. fasciolae giganticae Porter, 1938; C. broederstroomiae Porter, 1938 and C. dollfusi Fain, 1953. The last of these also has a different flame cell pattern, papillae on suckers and different shape of the tail.

The presence of a pharynx, bifurcation of the oesophagus just in front of the ventral sucker and extension of the intestinal caeca to the posterior end in the present form distinguishes it from C. redicystica Tubangui, 1928; C. grandis Wesenberg-Lund, 1934; C. morijae Porter, 1938; C. klarbosiae Porter, 1938 and C. ituriensis Fain, 1953.

The present cercaria resembles C. helvetica XIX

Dubois, 1929 in lacking spines or papillae on the body and bifurcation of the caudal excretory duct in the middle of the tail, but differs in having rod-shaped contents in the cystogenous gland cells, a white body, and in being smaller in size.

Wesenberg-Lund (1934) described a cercaria from Denmark, which he has identified as C. helvetica XIX. His cercaria is nearly half the size of Dubois's species and has rod-shaped contents in the cystogenous gland cells. Wesenberg-Lund was apparently dealing with another species of cercaria. He was unable to trace the excretory system in detail or to see the intestinal caeca with certainty, but in his figure he has shown them to terminate just behind the ventral sucker. However the present cercaria differs from Wesenberg-Lund's species in having a tail longer than the body and twice as long as Wesenberg-Lund's form, in having an absolutely white body and the shape and structure of the excretory bladder.

C. helvetica XVIII Dubois, 1929 differs from the present cercaria in having a black body, a ventral sucker smaller than the oral and the nature of the contents of the cytogenous gland cells.

Cercaria of Ribeiroia (= Psilostomum) ondatrae (McMullen, 1938) as described by Beaver, 1939 and C. amnicolensis Etges, 1956, both have white bodies lacking the spines. The present cercaria can be separated from C. Ribeiroia ondatrae

Explanation to Plate 6

Cercaria densacutis n. sp.

fig. 1 General structure of the cercaria.

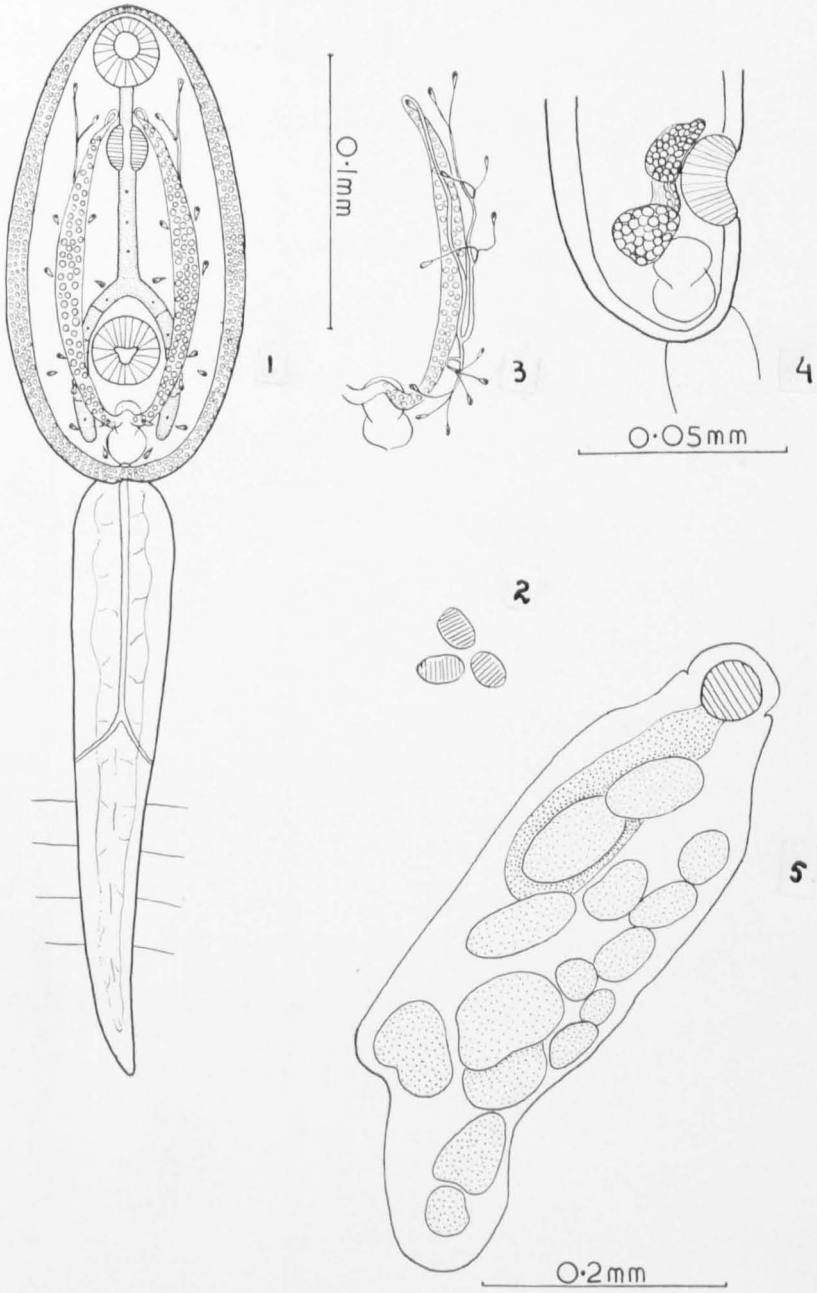
fig. 2 Cystogenous cells.

fig. 3 Excretory system.

fig. 4 Genital primordium (lateral view).

fig. 5 Redia.

Plate 6



in having only a small number of excretory granules in the main excretory ducts, in lacking diverticulae of the oesophagus, in lacking the hooks on the ventral sucker, in the smaller number of flame cells and in the bifurcation of descending excretory duct at the level of the ventral sucker. C. ammicolensis differs from the present species in its smaller size, in the extension of the excretory granules to the post-acetabular region of the main excretory duct, in having an unbranched caudal excretory duct, granular contents of the cystogenous gland cells and a ventral sucker smaller than the oral.

In view of the above comparison, the present cercaria is regarded as new and the name Cercaria albinea is given to it.

5. Cercaria densacutis n. sp.+ (Plate 6, figs. 1-4)

Between 10 and 20 per cent B. tentaculata in Bushy Park were found to be infected with this cercaria, during August to October, 1958 and 1959.

Redia

The rediae are in the digestive gland of the host. They are colourless, sac-shaped and broad at each end. The collar and ambulatory processes are poorly developed

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and the birth pore is dorsal in position. In each redia large numbers of immature cercariae are found which complete their development in the host-tissue. The gut extends to slightly less than half the length of the redia. The size is variable; the largest living redia had a length of 0.810 mm. and a breadth of 0.360 mm. with a pharynx measuring 0.055 mm. in diameter.

Emergence and Behaviour

The cercariae may be discharged throughout the day but a larger number is shed during the forenoon. Some time after their emergence, they concentrate near the surface of the water, but they also exhibit a weak negative phototropism.

Cercaria

The body of the cercaria is unpigmented and white, with a very thick body wall, composed of rounded structures. There are no spines or hairs on the body. Numerous cystogenous gland cells are present throughout the body. These have fine rod-shaped contents, each rod traversing the whole length of the cell. Fine ducts from the cystogenous gland cells open laterally on the body. There are no eyespots.

The sub-terminal oral sucker is followed by a short

prepharynx and a muscular pharynx. The oesophagus bifurcates just in front of the ventral sucker and the intestinal caeca extend to the posterior end of the body. Both the oesophagus and caeca are cellular in nature and non-functional. The main excretory ducts join to form a common duct, opening into a chamber of the excretory bladder, which in turn opens into the second chamber of the excretory bladder on its postero-ventral side. The main excretory ducts are filled with a large number of small refractile excretory granules, thoughout their length. They form a narrow loop at the side of the pharynx and the descending excretory ducts bifurcate at the level of the ventral sucker. The anterior collecting tubule receives three ducts connected with six flame cells, while the posterior collecting tubule receives two ducts also from six flame cells. The flame cell formula may be written as $2\left[(2 + 2 + 2) + (3 + 3)\right] = 24$. The caudal excretory duct bifurcates at the middle of the tail, with the two branches opening laterally.

The penetration gland cells or their ducts could not be seen.

The ventral sucker is the same size as the oral and is located between the middle and the posterior end of the body.

The genital primordium is poorly differentiated and is represented by a large post-acetabular and a large pre-acetabular mass, connected by a thick strand of cells (Plate 6, fig. 4).

The tail is simple, without a finfold. There are four pairs of long hair-like structures on it.

Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.250-0.283	0.268	0.180-0.230	0.210
Body breadth	0.116-0.166	0.141	0.096-0.130	0.120
Tail length	0.366-0.433	0.399	0.260-0.280	0.270
Tail breadth	0.046-0.050	0.048	0.036-0.046	0.040
Oral sucker diameter	0.040-0.046	0.043	0.033-0.036	0.034
Prepharynx	0.016-0.030	0.020	0.016-0.023	0.019
Pharynx	0.025-0.033x 0.020-0.030	0.030x 0.025	0.016-0.023x 0.016-0.023	0.021x 0.021
Ventral sucker diameter	0.040-0.050	0.043	0.030-0.036	0.034

Cysts

The cysts are always found in the open. They are rounded and snow-white in colour and are always located just above the water level. The cyst wall is composed of an irregular outer translucent and a uniform inner transparent layer. The cyst wall is laid down by the cystogenous material discharged through fine ducts, while the body of the cercaria continues revolving inside, which ensures a uniform inner layer of cyst wall. The tail which starts lashing briskly at the onset of encystation

is gradually detached, after which it continues lashing for some time before it decays. The outer cyst wall is notched at the anterior and the posterior ends.

The cysts are formed during late afternoon. Attempts to induce encystation earlier by placing the cercariae in the dark were not successful. The cysts measure 0.142-0.15 mm. in diameter, with a cyst wall 0.026-0.03 mm. thick.

Comparison with related species

In the lack of spines or papillae on the body, the present species can readily be separated from C. psilotremi spiculigerii Mathias, 1925; C. durbanensis Porter, 1938; C. chitinostoma Faust, 1930; C. circumstricta, Faust, 1922; C. catenadena Fuast, 1930; C. thomasi McMullen, 1938 as described by Kuntz (1951); C. palegae Goodman, 1951; C. tuberculata Fil., 1859 as described by Wesenberg-Lund (1934) and C. papillosa Fil., 1859 as described by Wesenberg-Lund (1934). The possession of a slender tail, longer than the body with the caudal excretory duct branching at its middle and opening on the sides in the cercaria under study separates it from C. Indicae XLI Sewell, 1922; C. gracilis O'Roke, 1917; C. fasciolae giganticae Porter, 1938; C. broederstroomiae Porter, 1938; C. dollfusi Pain, 1953 and C. fasciolae hepaticae Thomas, 1883.

The well developed pharynx, the oesophagus, dividing

just in front of the ventral sucker, with the caeca extending to the posterior end in the present species distinguish it from C. rediocystica Tubangui, 1928; C. klarbosiae Porter, 1938; C. congalae Porter, 1938; C. fasciolae giganticae Porter, 1938; C. morijae Porter, 1938 and C. ituriensis, Fain, 1953.

C. grandis Wesenberg-Lund, 1934 differs in having a dark body, unbranched caudal excretory duct, short intestinal caeca, granular contents of the cystogenous gland cells and in its larger size.

The present cercaria can be separated from cercaria of Riberoia (Psilostomum) ondatrae (McMullen, 1938) as described by Beaver (1939) in lacking hooks on the ventral sucker, diverticula of the oesophagus and in the bifurcation of the descending excretory duct near the ventral sucker; and from C. amnicolensis Etges, 1956 in having a ventral sucker equal to the oral, in the nature of the contents of the cystogenous gland cells, branched caudal excretory duct and in being larger.

C. helvetica XIX Dubois, 1929 has granular contents in the cystogenous gland cells, a dark body and a larger size. C. helvetica XIX of Wesenberg-Lund (1934) can be distinguished in having a thin body wall, a tail shorter than the body, a dark colour and in having few excretory granules which are limited to the pre-acetabular region of the main excretory ducts.

Explanation to Plate 7

Cercaria lophocerca

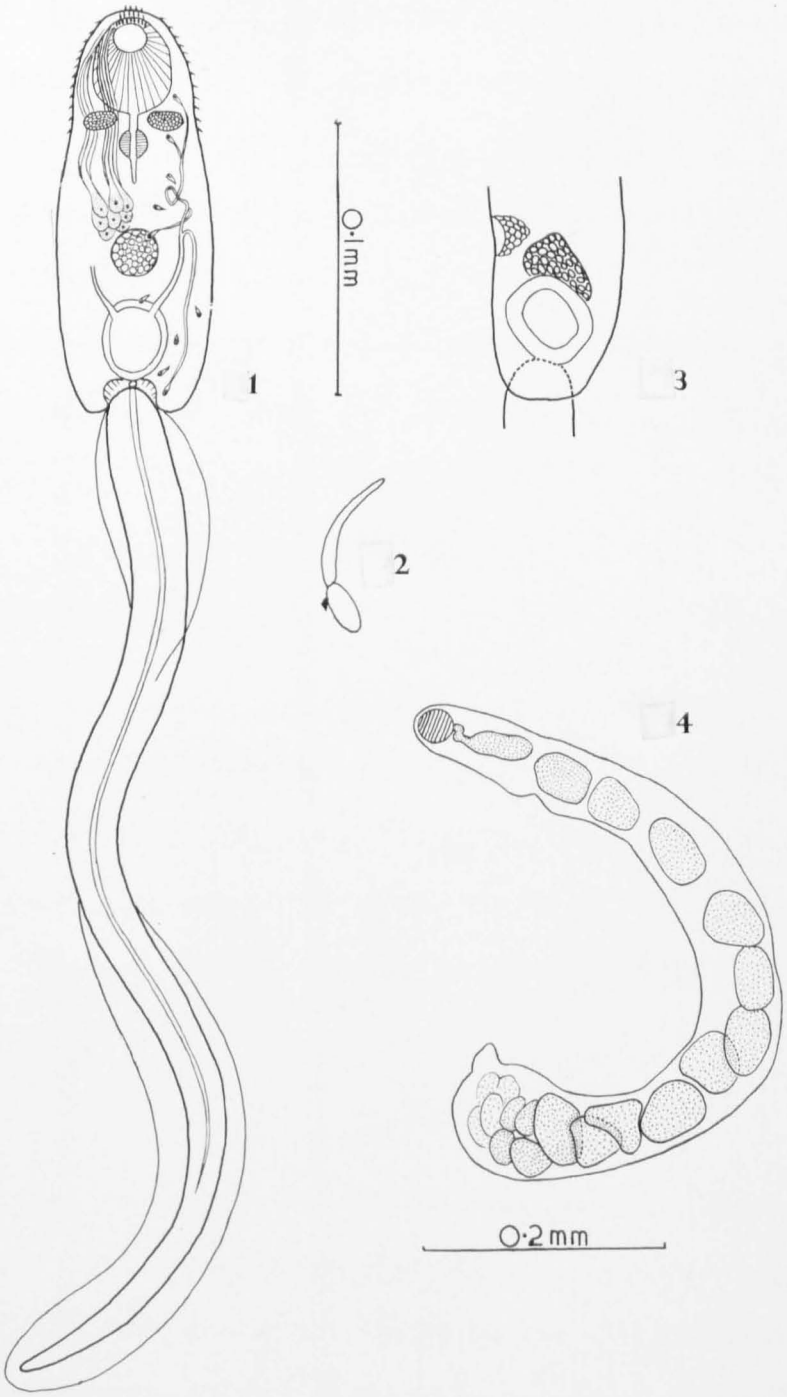
fig. 1 General structure of the cercaria.

fig. 2 Resting posture.

fig. 3 Genital primordium (lateral view).

fig. 4 Redia.

Plate 7



C. helvetica XVIII Dubois, 1929 is poorly described but can be differentiated from the present species in having a thin body wall, a ventral sucker smaller than the oral, a black body, in the nature of the contents of the cystogenous gland cells and in the limitation of the excretory granules to the pre-acetabular portions of the main excretory ducts.

It is concluded that a new species of cercaria is being dealt with for which the name Cercaria densacutis is proposed.

6. Cercaria lophocerca Filippi, 1859+ (Plate 7, figs. 1-3)

This cercaria was encountered only once, when a single specimen of B. tentaculata collected from Bushy Park on the 25th of August, 1959 was found to be infected with it. The snail survived only for a few days in the laboratory, so that a detailed study of the cercaria could not be made.

Redia

The rediae are present in the digestive gland of the host. They are long and slender with no collar or ambulatory processes. The birth pore is situated slightly behind the pharynx. The gut extends only a short distance

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behind the pharynx. In each redia a large number of germ balls were present, but no cercariae were seen. Presumably the cercariae leave the rediae in very early stage of development and mature in the host tissue as described by Wesenberg-Lund (1934).

The largest living redia measured 2.00 mm. in length and 0.23 mm. in breadth, with a pharynx measuring 0.04 mm. in diameter.

Emergence and Behaviour

The cercariae are discharged during the day in small numbers. They are bottom dwellers and show a positive phototropism. During the resting period the body is kept downwards and the tail is curved slightly.

Cercaria

The elongated body has a slightly yellow tinge. There are three rows of anteriorly directed spines at the anterior end, with nine, six and four spines respectively. About twelve rows of spines encircle the anterior end of the body. The rest of the body is without spines, but six pairs of long hair-like structures are present.

There are numerous cystogenous gland cells, with coarsely granular contents. The pigment is distributed in the body in the form of lumps. There are two darkly

pigmented eye spots, elliptical in shape. The sub-terminal oral sucker is followed by a small prepharynx and a muscular pharynx, behind which a small narrow oesophagus is seen. The caeca are absent.

Due to numerous cystogenous gland cells, pigment and scarcity of the material, the exact number of the penetration gland cells and flame cells could not be ascertained. However about seven pairs of penetration gland cells have been seen in the middle of the body. There are four groups of penetration gland ducts opening at the anterior end of the oral sucker. The two outer groups have three ducts each and two inner groups have four ducts each.

There is a large, thick-walled transversely elongated to sub-circular excretory bladder, from which two main excretory ducts proceed forwards. Ten flame cells have been observed on each side of the body. The caudal excretory duct is unbranched.

The ventral sucker in naturally emerged cercariae is rudimentary. Dubois (1929) and Wesenberg-Lund (1934) have stated that this organ is well developed in young cercariae.

The genital rudiment is represented by a single mass of deeply staining cells, lying just in front of the excretory bladder (Plate 7, fig. 3).

The tail is very long, ventral in position having caudal pockets, provided with spines. There is a well

developed lateral finfold extending throughout its length but the dorsal and ventral finfold is limited to distal half only and is continuous over the tip.

Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.150-0.280	0.220	0.110-0.160	0.139
Body breadth	0.060-0.120	0.090	0.066-0.083	0.071
Tail length	0.370-0.490	0.440	0.356-0.380	0.370
Tail breadth at base	0.035-0.055	0.040	0.026-0.030	0.029
Oral sucker	0.036-0.045x 0.030-0.040	0.042x 0.036	0.030-0.033x 0.026-0.028	0.032x 0.027
Right eye	-	-	0.010x0.006-0.008	0.010x 0.007
Left eye	-	-	0.011-0.013x 0.007-0.008	0.012x 0.008

The cercaria under study falls in Martin's group (iii) of "Parapleurolophocercous" cercariae.

The present cercaria resembles in all essential points with C. lophocerca Filippi, 1895. This cercaria has also been described by Dubois (1929) from Neuchatel and Wesenberg-Lund (1934) from Denmark.

This is the first record of this cercaria in Britain and also the first record for a member of "Parapleurolophocercous" sub-group from Britain.

Echinostome cercariae

The "Echinostome" cercariae are easily separated from other forms by the possession of a collar, bearing spines.

Lühe (1909) assigned the "Echinostome" cercariae to four groups on the nature of gut in the redia and the presence or absence of a finfold in the cercarial stage. Lühe's scheme is as follows:

I Redia with a long gut

(a) Tail of the cercaria with a finfold

(b) Tail of the cercaria without a finfold

II Redia with a short gut

(a) Tail of the cercaria with a finfold

(b) Tail of the cercaria without a finfold

Faust (1917) distinguished two types of excretory systems in the "Echinostome" cercariae. In one of these types the descending excretory duct divides into the collecting tubules near the posterior end of the body. This type was later called the "Echinata" type of excretory system. In the second type the descending excretory ducts divide near the ventral sucker. The second type later became known as the "Coronata" or the "Echinatoides" type of excretory system. Dubois (1929) has doubted the presence of the "Coronata" type of excretory system in the "Echinostome" cercariae.

Sewell (1922) discarded the length of the redia as a group character, and based his classification on the

type of the excretory system and the presence or absence of a caudal finfold in the cercaria. He recognised three groups:

(1) "Echinatoides" sub-group having a caudal finfold and an excretory system of the "Coronata" type.

(2) "Coronata" sub-group without a caudal finfold but having an excretory system of the "Coronata" type.

(3) "Echinata" sub-group lacking a caudal finfold and having an excretory system of the "Echinata" type.

Faust (1924) rearranged the classification according to the flame cell pattern only and proposed several more sub-groups of the "Echinostome" cercariae. He also included the "Agilis" and "Reflexae" sub-groups of Sewell (1922) among the "Echinostome" cercariae.

Miller (1936) agrees with Faust in the inclusion of the "Agilis" and "Reflexae" groups in the "Echinostomes".

Porter (1938) added three more groups to Sewell's classification. The "Sub-echinotoides" group for cercariae with a weak collar; the "Cucomeriformis" group for cercariae with a feeble collar and anteriorly directed oral sucker and the "Echinocrenata" group for cercariae having a lobed collar and with a heavy and clumsy tail.

The difficulty in ascertaining the exact pattern of flame cells in the "Echinostome" cercariae, due to the presence of numerous cystogenous gland cells and a large number of flame cells is well known. Workers (Johnson, 1920;

Beaver, 1937) even after studying a very large number of specimens of a single species of cercaria, were still doubtful about the exact pattern of the flame cells. The use of the flame cell pattern for the classification of the echinostome cercariae is undoubtedly most impracticable. The classification of Sewell (1922) has been accepted by most of the later workers.

Recent researches have brought to light some interesting facts about this classification. It has been established that cercariae, with a caudal finfold cercaria of Echinoparyphium spiniferum as described by Ahmad (1959) or without a caudal finfold cercariae of E. recurvatum as described by Mathias (1926) and Wesenberg-Lund (1934) and cercaria of E. flexum as described by Najarian (1954) may develop into species of the same genus.

At the same time different species of one genus of Echinostomes may have cercariae with the "Echinata" (cercaria of E. flexum in genus Echinoparyphium Dietz, 1909 and C. Hypoderaeum conoideum as described by Dubois (1929) and Wesenberg-Lund (1934) in genus Hypoderaeum Dietz, 1909) or the "Coronata" type of excretory system (cercaria of E. recurvatum as described by Wesenberg-Lund (1934) in genus Echinoparyphium and C. essexensis (present study) in genus Hypoderaeum).

In view of the above facts it is evident that both the characters used by Sewell to split up the "Echinostome"

Explanation to Plate 8

Cercaria londonensis n. sp.

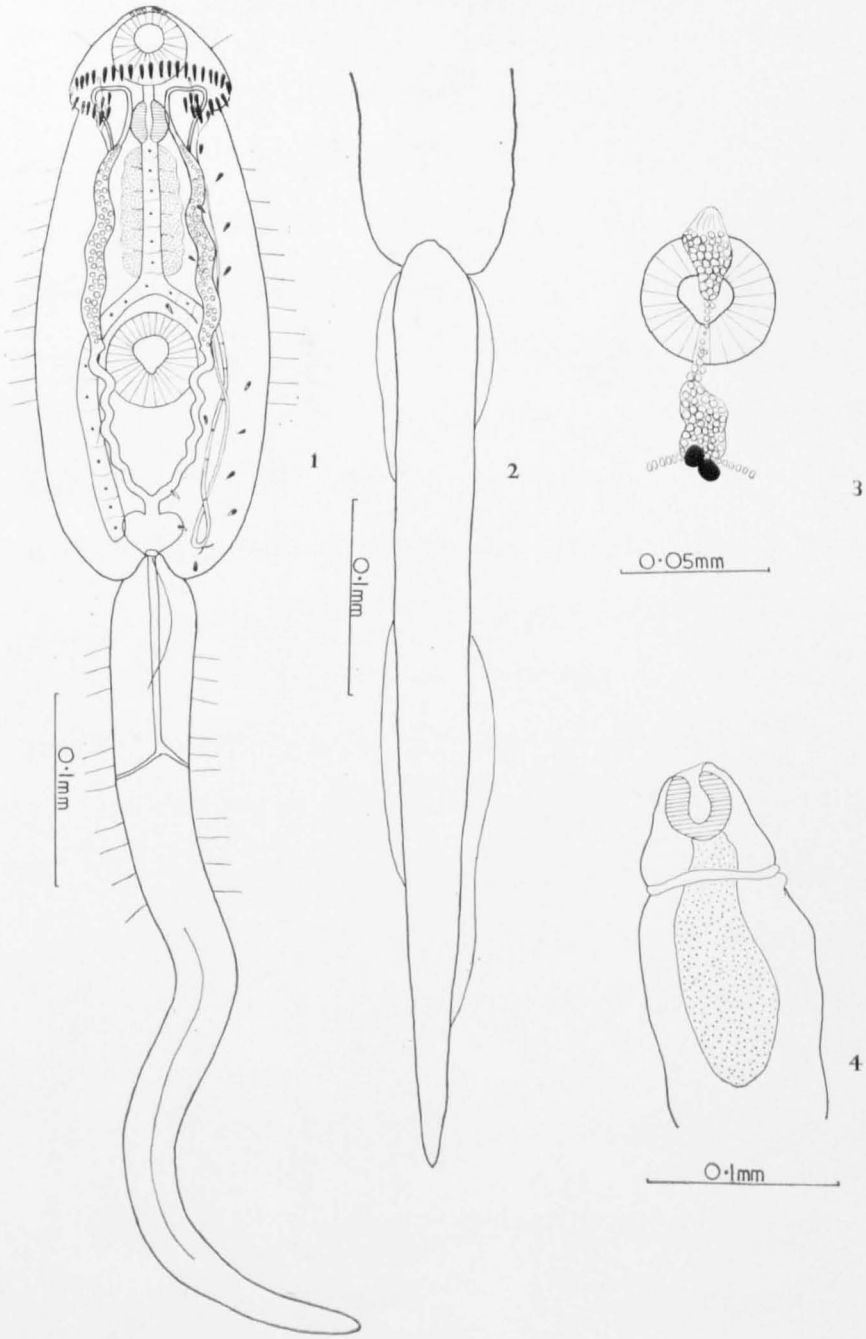
fig. 1 General structure of the cercaria.

fig. 2 Lateral view of the tail showing finfold.

fig. 3 Genital primordium (dorsal view).

fig. 4 Anterior end of the redia.

Plate 8



cercariae could only be of specific value and not suitable as group characters.

Fort (1915), Dubois (1929), Wesenberg-Lund (1934) and Miller (1936) have stated that "Echinostome" cercariae cannot be sub-divided into smaller groups.

The large-tailed "Echinostome" cercariae, with tails many times longer than the body and small number of spines, exhibit a remarkable uniformity in their structure and where the life cycle has been worked out, they were found to develop into species of Petasiger Dietz, 1909. These cercariae undoubtedly form a compact natural group, which can easily be separated from other "Echinostome" cercariae. Hence it would not be advisable to accept the view that the "Echinostome" cercariae cannot be subdivided.

However, the "Echinata", "Echinatoides" and "Coronata" groups of Sewell, as discussed above, seem to be unnatural and should remain in a single group until more suitable characters for their subdivision are discovered.

7. Cercaria londonensis n. sp.+ (Plate 8, figs. 1-4)

In Bushy Park during September of 1958 and 1959, about 90 per cent of P. corneus (Linn.) - medium to large sized - were found to be infected, with a thirty seven spined Echinostome cercaria. This pond has a rich

+In the press

fauna of molluscs, comprising L. stagnalis, L. pereger, P. planorbis, B. tentaculata and V. piscinalis along with P. corneus, but none of the other species was ever found to be parasitized by this cercaria. The only other locality where this cercaria was found among several ponds in and around London, was a small pond in Kenilworth Park. The infection rate at this place, however, was only 25 per cent.

Redia (Plate 8, fig. 4)

Very large numbers of rediae were found parasitizing every infected snail which was dissected. They almost completely replaced the tissue of the digestive gland of the host. The sac-like rediae are not very active. The bright orange pigment is only found in the larger rediae, and is scattered all over the body in the form of large spots. The gut, with homogeneous yellow contents, extends a short distance beyond the collar. The collar, birth pore and ambulatory processes are comparatively poorly developed. The older, exhausted redia becomes greatly distorted in shape and constricted several times along its length. There may be one to several cercariae in a single redia.

Along with the rediae described above, few mother rediae were seen in one of the snails examined. These have longer but more slender bodies, with thinner body

walls and one or two rediae with several undifferentiated germ balls inside.

The largest daughter redia measure 2.5 mm. long and 0.28 mm. broad, with a pharynx measuring 0.05 x 0.04 mm. The mother rediae averaged 2.82 mm. in length and 0.24 mm. in breadth, with a pharynx measuring 0.050 x 0.036 mm.

Emergence and Behaviour

The cercariae are shed throughout the day in large numbers. Soon after their emergence, they congregate near the bottom of the container and exhibit a weak negative phototropism.

Cerceria (Plate 8, fig. 1)

Both the body and the tail are very contractile. The dorsal side is somewhat convex and the ventral concave. The body is spined up to the ventral sucker. Apart from these body spines, there are long hair-like structures, similar to the "flagellets" described for several "Furcocercous" cercariae. One pair of these hair-like structures is located on the collar, and ten pairs have been seen between the collar and the ventral sucker. The well developed collar bears thirty-seven spines, of which five constitute a corner group on each side. The spines of the oral and the aboral rows of dorsal series

are of equal size. The spines of the corner group are in two series - the aboral with two and the oral with three spines. The spines of the corner group are smaller than those of the dorsal series, except one, the outer aboral corner spine which is of the same size or slightly larger. Among fifty cercariae examined solely for this purpose, the number or arrangement of the collar spines has never been seen to alter.

The tail, while at rest, and in the fixed specimens, is longer than the body, and has on its anterior half, hair-like structures similar to those found on the body. On the tail also ten such hair-like structures are present on each side. A finfold is present on the dorsal and ventral sides of the tail (Plate 8, fig. 2). On each side there is a small basal portion on the proximal end of the tail, and a distal portion situated further below. These two portions on each side are separated by a portion of the tail which is completely without any finfold. The distal portion of the finfold on the dorsal side is longer and higher than its counterpart on the ventral side, while the proximal portion on the ventral side is longer than that on the dorsal side. The tip of the tail, which again is without any finfold is invaginable and adhesive.

The body is filled with numerous cystogenous gland cells, with coarsely granular contents. The subterminal oral sucker is followed by a small prepharynx and a muscular

pharynx. The oesophagus bifurcates just in front of the ventral sucker and the intestinal caeca extend up to the posterior extremity of the body. Both the oesophagus and the caeca are cellular and non functional. The ventral sucker, slightly larger than the oral, is behind the middle of the body. In the living cercariae stained with dilute solution of neutral red, about six pairs of poorly demarcated cells - the "penetration gland cells" - become more deeply stained. These occupy nearly the whole length of the oesophagus and are situated on either side of it. Six ducts open on the anterior region of the oral sucker. These ducts can only be traced up to a short distance behind their openings. They are presumably connected with the gland cells mentioned above.

The excretory system is typical of the group. There is a pyriform excretory bladder at the posterior end, opening by a small dorsal excretory pore at the junction of the body and the tail. Anteriorly, the excretory bladder receives the two main ascending excretory ducts through a small common duct. The dilated portion of the main ascending excretory duct has several circular excretory granules with refractive walls. The excretory system is of the "Echinata" type. The caudal excretory duct bifurcates at about one-fourth of the tail length. The openings of the branches of the caudal excretory ducts could not be seen.

The genital rudiment can best be seen in the fixed

and the stained specimens. It is represented by a large post-acetabular, deeply staining, cell mass - the future ovary. At the posterior end of this larval ovary, the vitelline ducts diverge outwards. Just behind the ovary are two small, circular masses of cells, the testes. The ovarian primordium is connected by a string of cells to a large pre-acetabular cell mass, which will form the cirrus pouch of the adult (Plate 8, fig. 3).

Measurement of cercaria

(All measurements are in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.396-0.466	0.400	0.270-0.300	0.284
Body breadth	0.166-0.233	0.200	0.120-0.150	0.130
Tail length	0.400-0.510	0.460	0.460-0.510	0.486
Tail breadth (at base)	0.046-0.060	0.053	0.033-0.036	0.035
Oral sucker	0.043-0.060x 0.053-0.073	0.056x 0.060	0.036-0.050x 0.040-0.060	0.041x 0.043
Ventral sucker	0.060-0.073x 0.060-0.073	0.066x 0.066	0.040-0.050x 0.040-0.050	0.044x 0.044
Pharynx	0.020-0.030x 0.020-0.030	0.025x 0.025	0.020-0.030x 0.016-0.023	0.024x 0.021
Collar across	0.100-0.140	0.12	0.076-0.083	0.082
Outer aboral corner spine, length	0.015-0.016			
Rest of corner spines, length	0.013-0.014			
Dorsal spines, length	0.015			

Cysts

Experimentally, L. stagnalis, L. palustris (Müll.), L. pereger and P. corneus were successfully used as second intermediate hosts. The cysts are always found on the renal organs and never inside the digestive gland of the host. Circular cysts are of fairly uniform size and measure 0.100-0.123 mm. in diameter. They are invested by a double cyst-wall 0.009-0.010 mm. thick.

This cercaria develops into a species of Echinostoma Rudolphi, 1809. The complete life cycle has been worked out and is described in the second part of this thesis.

Comparison with Related Species

Some authors (Tubangui, 1932b; Sandosham, 1954) have not mentioned the presence of a caudal finfold in the cercaria of Echinostoma revolutum (Froelich, 1809) Dietz, 1909, but others (Beaver, 1937; Johnston and Angel, 1941b) have reported its presence. This cercaria which has a small finfold on the distal part of the tail on its dorsal side only, can readily be separated from the present species which has a finfold on the dorsal as well as on the ventral side.

C. helvetica XXIV Dubois, 1929, is very similar to C. echinostomi revoluti and has been considered as a synonym of the latter by Beaver (1937). C. limbifera

Seifert, 1926, was originally described to have thirty seven collar spines. Brown (1931) recorded it from Britain as having thirty-five spines. Rees (1932) also recorded it from Britain and confirmed Brown's observations. This cercaria can further be differentiated from the present species by its larger size, in lacking a separate basal part of finfold and in the finfold being continuous over the tip of the tail. The redia of C. limbifera has a long gut, while that of the present species has a short one. The cercaria of Echinostoma lindoensis Sandground and Bonne, 1940, has its caudal finfold unbroken, extending over its whole length. C. spinifera La Val., as described by Wesenberg-Lund (1934) has forty to forty-five collar spines. Recently Ahmad (1959) has described a cercaria with thirty-seven collar spines, which he has identified as C. spinifera. Ahmad's cercaria differs from the present species in lacking a separate basal part of caudal finfold, unequal size of the spines of oral and aboral series, and in having a "Coronata" type of excretory system. Moreover, this cercaria has been shown to develop into a species of Echinoparyphium Dietz, 1909.

C. cuneata Fain, 1953, has only a small collar-like finfold on the distal part of the tail. It also differs from the present species in having a "Coronata" type of excretory system and a group of four corner spines.

An un-named Echinostome cercaria with thirty-seven

Explanation to Plate 9

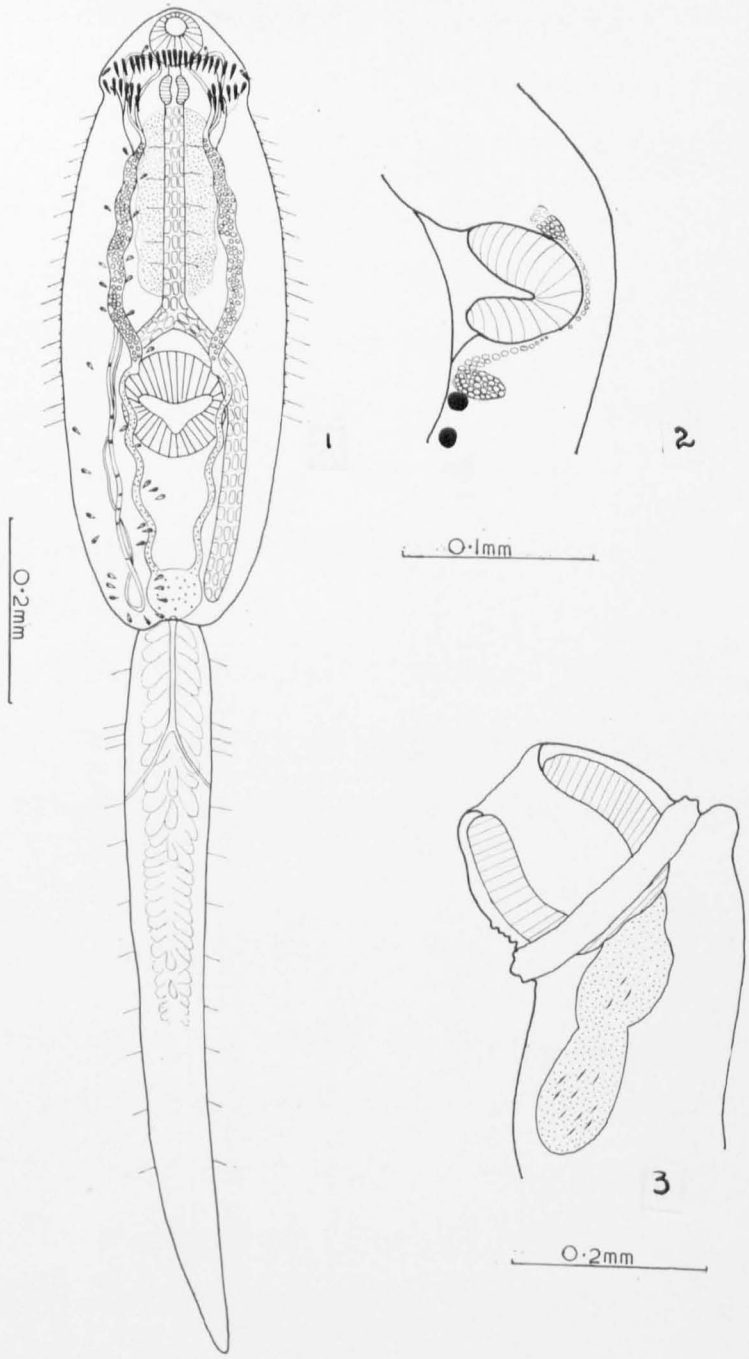
Cercaria deficipinnatum n. sp.

fig. 1 General structure of the cercaria.

fig. 2 Genital primordium (lateral view).

fig. 3 Anterior end of the redia.

Plate 9



spines described by Johnston and Muirhead (1949) has a caudal finfold similar to the present species. In the absence of any measurements or description of this cercaria a comparison is not possible. Johnston and Muirhead have stated that their cercaria is similar in structure to C. natans Johnston and Muirhead, 1949, which has thirty-five spines and an excretory system of the "Coronata" type. It is presumed that this un-named cercaria also has an excretory system of the same type, as possessed by C. natans, the "Coronata" type. The present cercaria having "Echinata" type of excretory system is regarded as different from the above mentioned species.

In view of the differences discussed above it is concluded that a new species of cercaria is being dealt with. It is proposed to name it Cercaria londonensis.

8. Cercaria deficipinnatum n. sp.+ (Plate 9, figs. 1-3)

Out of thirty-six specimens of L. stagnalis collected on 25th August 1959, from Sand Pits near South Ockendon (Essex), only two were found to be discharging this cercaria. In two subsequent collections from the same place, only one out of thirty snails (collected on 7th September, 1959) and one out of forty-three snails (collected on 25th September, 1959) were found to be infected. No infected snail was

+ In the press.

found in October or later.

Redia (Plate 9, fig. 3)

The rediae are usually found superficially over the digestive gland of the host. Only a few of them are present inside the gland. They are of deep orange colour, which is due to coarse pigment spots scattered all over the body; these are absent from younger rediae. The collar, the ambulatory processes and the birth pore are well developed. The gut of the redia extends only a short distance beyond the collar, and has homogeneous, very dark orange contents, in which a few sharp edged rods are discernible. The number of developing cercariae in a redia may vary from one to many. The motile, rediae are variable in size. The cercaria bearing rediae may vary from 1.5-2.4 mm. long and 0.36-0.495 mm. broad with a pharynx measuring 0.030-0.060 mm. in diameter. Old and exhausted rediae become greatly distorted in shape and may have several constrictions.

Emergence and Behaviour

Cercariae are shed throughout the day in large numbers. They do not exhibit any phototropism. From five to eight hours after emergence they aggregate near the bottom of the container and many of them start crawling on the

bottom with the help of their suckers. I have always found it difficult to concentrate them in a centrifuge, which suggests a negative geotropism in the active stage of life.

Cercaria (Plate 9, fig. 1)

The cercaria is comparatively large. The highly contractile body is dorsoventrally flattened with a dorsal convex and ventral concave surface. A well developed collar bears thirty-seven spines, of which five form a corner group, with three oral and two aboral in position. The spines of the oral and the aboral dorsal rows are of equal size. The body spination is visible up to the ventral sucker. Apart from the spines the body has numerous long hair-like structures, similar to those described for C. londonensis (present study). The tail is longer than the body, both in the living and in the fixed specimens and has a central cellular core. There is no finfold on the tail. The terminal part of the tail is invaginable and adhesive in nature. The aspinose tail is also beset with numerous long hair-like structures.

The oral sucker is subterminal, the prepharynx short and the pharynx muscular. The oesophagus bifurcates just in front of the ventral sucker and the intestinal caeca extend to the posterior extremity of the body. Both the oesophagus and the intestinal caeca are cellular in nature,

but unlike other cercariae described in this thesis they are composed of three to four rows of cells instead of a single row.

The body of the cercaria is packed with numerous cystogenous gland cells, with coarsely granular contents. In the living cercariae stained with neutral red, about six penetration gland cells become more deeply stained. These occupy an area on either side of the oesophagus. Only six penetration gland ducts open at the anterior end of the oral sucker.

The excretory system is of the "Echinata" type. The posterior excretory bladder is sub-circular, and opens by a small excretory pore on the dorsal side at the junction of the body with the tail. Six to eight ciliary patches have been seen in each descending excretory duct. A maximum of thirty-five flame cells have been seen on each side of the body.

The genital organs are represented by a large mass of deeply staining cells lying behind the ventral sucker. This is the future ovary. Immediately behind it and very near the ventral body wall, are the two primordia of the testes. There is a pre-acetabular mass of cells which is connected to the post-acetabular mass by a string of cells (Plate 9, fig. 2). Vitelline ducts, as seen in C. londonensis, (present study) are absent in the present species.

Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.650-0.740	0.700	0.580-0.620	0.590
Body breadth	0.280-0.340	0.330	0.220-0.240	0.226
Tail length	0.730-0.920	0.850	0.756-0.800	0.766
Tail breadth (at base)	0.100-0.120	0.110	0.083-0.090	0.086
Oral sucker	0.059-0.660x 0.063-0.088	0.063x 0.077	0.053-0.056x 0.056-0.060	0.054x 0.056
Prepharynx length	0.014-0.018	0.016	0.006-0.013	0.010
Pharynx	0.033-0.037x 0.029-0.035	0.034x 0.032	0.030-0.033x 0.023	0.031x 0.023
Ventral sucker	0.100-0.122x 0.100-0.120	0.110x 0.110	0.080-0.100x 0.900-0.110	0.086x 0.100
Collar across	0.180-0.240	0.200	0.133-0.136	0.134
Spines length	(as seen in the cyst)			
Corner spines	0.040			
Dorsal spines	0.033			

Cysts

The cysts are located on the stomach, terminal part of the alimentary canal and on the renal organs. Experimentally L. stagnalis, L. palustris and L. pereger were successfully used as second intermediate hosts. The cysts measure 0.240-0.263 mm. in diameter with a cyst wall 0.013 mm. thick. Attempts to infect ducklings, chicken and pigeons were not successful.

Comparison with Related Species

Nine species of Echinostome cercariae, with thirty-seven collar spines and without a finfold on the tail have previously been described. C. echinata V. Sieb., 1835, is a larger species differing from the present cercaria in having rod-shaped contents in the cystogenous gland cells and in having four corner spines. C. echinoparyphii aconiati Dubois, 1929, is identical with C. echinata. These two have been regarded as synonymous by Beaver (1937). C. equispinosa, Brown, 1926, is distinguishable from C. echinata only by its smaller size, and is also very much smaller than the present species. It can also be separated from the present species on the same grounds as mentioned for C. echinata. The present cercaria differs from C. rebstocki McCoy, 1929 in being larger and in having cystogenous gland cells with granular contents.

The cercaria of Echinostoma revolutum as described by Tubangui (1932) and Sandosham (1954) is without a finfold on the tail. Beaver (1937) and Johnston and Angel (1941b) who have reported this species in detail describe the presence of a small distal caudal finfold on the dorsal side. Both Tubangui and Sandosham seem to have missed it. This cercaria however is much smaller than the present species. Dubois (1929) described three species of thirty-seven spined Echinostome cercariae with the same arrangement of the spines. The nature of the cystogenous

gland cells is not known in any of these cercariae. Of these, C.helvetica XXII can easily be differentiated by the unequal size of the spines in the oral and the aboral dorsal rows. C. helvetica XXIII is nearly half the size of the present species. C. helvetica XXIV is so inadequately described that it does not lend itself for comparison with the cercaria under study. However, the former species differes from the present cercaria in having a redia with a long gut.

The present species is, therefore, regarded as new and is named Cercaria deficipinnatum.

9. Cercaria echinoparyphii recurvati Mathias, 1926

Two to five per cent V. piscinalis collected from Bushy Park were found to be infected with this cercaria.

This cercaria has been described by Mathias (1927), Azim (1930), Dinulesco (1939), Kuntz (1953), Wesenberg-Lund (1934) and Harper (1929) completed its life cycle in Britain.

Harper (1929) has figured the descending excretory ducts as dividing at the posterior end of the body. Wesenberg-Lund (1934) and Kuntz (1953) who has studied the excretory system in detail have shown them to divide near the ventral sucker. My observations on this point agree with the latter workers. Kuntz (1953) has given the flame cell formula as $2\left[(3+3+3+3)+(3+3+3+3+3)\right] = 54$.

This cercaria has been shown to parasitize species of Planorbis (Wesenberg-Lund, 1934, Mathias, 1926), Valvata (Harper, 1929), Bulinus (Azim, 1930, Kuntz, 1953) and Paluduia (Dinulesco, 1939).

Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.29 -0.43	0.35	0.2 -0.26	0.213
Body breadth	0.15 -0.23	0.19	0.13 -0.16	0.14
Tail length	0.29 -0.45	0.37	0.28 -0.43	0.35
Tail breadth	0.05 -0.06	0.055	0.04 -0.05	0.045
Oral sucker	0.04 -0.06x 0.04 -0.06	0.055x 0.055	0.035-0.05x 0.035-0.05	0.042x 0.042
Pharynx	0.016-0.025x 0.015-0.02	0.02x 0.018	0.015-0.02x 0.015-0.018	0.018x 0.016
Ventral sucker	0.05 -0.07x 0.05 -0.07	0.06x 0.06	0.04 -0.06x 0.04 -0.06	0.05x 0.05

10. Cercaria Z. Rees, 1932

This cercaria was very common in London ponds. It was found to be parasitizing L. pereger in Bushy Park, Richmond Park, Stoneyfields Park, Brent Reservoir and Sand Pits (S. Ockendon). The infection rate varied between ten and fifty per cent.

Redia

The rediae are provided with an orange pigment. The birth pore, collar and ambulatory processes are well developed. The gut, with black granular contents. The largest living redia measured 3.3 mm. long and 0.405 mm. broad, with a pharynx 0.073 mm. in diameter.

Cercaria

The collar is provided with 43-45 spines, with a group of four corner spines on each side. The descending excretory ducts divide at the posterior end of the body and are provided with ciliary patches. The contents of the cystogenous gland cells are granular. In living specimens, stained with dilute neutral red about six penetration glands on each side of the oesophagus become more prominent. The rest of the structure is the same as given by Rees (1932).

Explanation to Plate 10

Cercaria essexensis n. sp.

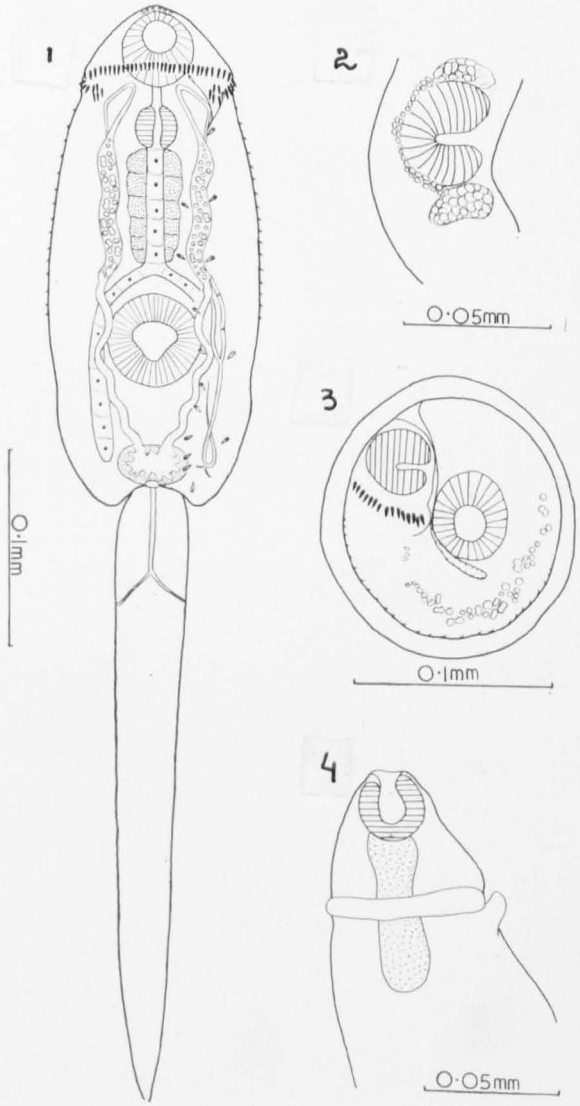
fig. 1 General structure of the cercaria.

fig. 2 Genital primordium (lateral view).

fig. 3 Cyst.

fig. 4 Anterior end of the redia.

Plate IO



Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.35 -0.5	0.445	0.33 -0.4	0.38
Body breadth	0.123-0.216	0.185	0.106-0.14	0.125
Tail length	0.433-0.55	0.476	0.33 -0.45	0.39
Tail breadth	0.043-0.066	0.056	0.03 -0.046	0.04
Oral sucker	0.05 -0.066x 0.05 -0.066	0.054x 0.054	0.04 -0.046x 0.04 -0.05	0.043x 0.045
Pharynx	0.023-0.03x 0.02 -0.023	0.026x 0.022	0.02 -0.023x 0.016-0.023	0.022x 0.019
Ventral sucker	0.066-0.083x 0.066-0.083	0.071x 0.071	0.056-0.063x 0.053-0.07	0.06x 0.06

11. Cercaria essexensis n. sp[+] (Plate 10, figs. 1-4)

Throughout the two years in which this investigation was carried out, this cercaria was encountered only once. Only one L. stagnalis collected on 7th October, 1959 was found to be infected with it. This snail was collected from Sand Pits near South Ockendon in Essex.

Redia (Plate 10, fig. 4)

The snail when brought in the laboratory was emitting large numbers of cercariae, but gradually the number decreased and within a period of two weeks stopped altogether. On dissection it was found that a large

[+]In the press.

number of rediae were present in the digestive gland. Most of the rediae were lying superficially on the gland and only a few were actually inside the tissue. All the rediae were completely exhausted, and possessed neither developing cercaria nor germ balls.

The rediae are long, sac shaped, with well developed collar, birth pore and ambulatory processes. The older rediae are yellow or pink but smaller ones are colourless. The gut extends only slightly beyond the collar. The living rediae measure 0.49-1.5 mm. long and 0.12-0.32 mm. broad, with a pharynx measuring 0.043-0.076 mm. in diameter.

Emergence and Behaviour

As pointed out above the number of cercariae being shed, fell very quickly after bringing the snail to the laboratory but most probably the cercariae are shed in large numbers before the rediae become exhausted. The cercariae are bottom dwellers and do not show any response to light.

Cercaria (Plate 10, fig. 1)

The dorso-ventrally compressed cercaria is comparatively small, with body spines visible up to the ventral sucker only. The collar is poorly developed and bears forty-seven to forty-nine small spines, most probably the number is

forty-nine. Five of these spines are corner spines on each side and the rest are arranged in two rows of alternating spines, continuous on the dorsal and the lateral sides. The tail is aspinose and longer than body both in the living and the fixed specimens. The body does not show a marked constriction immediately behind the collar.

Numerous cystogenous gland cells are present in the body. The contents of these cells are very coarsely granular. Sub-terminal oral sucker is followed by a relatively long prepharynx and muscular pharynx. The oesophagus bifurcates just in front of the ventral sucker and the intestinal caeca extend to the posterior end of the body. Both the oesophagus and the intestinal caeca are cellular in nature. The ventral sucker which is behind the middle of the body is larger than the oral sucker.

About six pairs of penetration gland cells are seen in living specimens stained with dilute neutral red. These are located on both sides of oesophagus. Their six ducts open at the anterior end of the oral sucker.

The excretory bladder is roughly rectangular and has a small accessory bladder formed by the fusion of the main ascending excretory ducts. The main ascending excretory ducts pursue a convoluted course up to the ventral sucker, in front of which they become dilated to accommodate large number of refractile excretory granules, some of which are irregular in shape and seem to be formed by the fusion of

two such granules. The excretory system is of the "Coronata" type, with seventeen flame cells on each side of the body. Six ciliary patches are present in each descending excretory duct.

The genital primordia are poorly differentiated. In the fixed and stained specimens, it is represented by a pre-acetabular and a post-acetabular mass of deeply staining cells. Both these masses are connected by a strand of cells. There is no trace of the testes or the vitelline ducts (Plate 10, fig. 2).

Measurements of Cercaria

(All measurements are in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.200-0.346	0.306	0.223-0.260	0.241
Body breadth	0.090-0.166	0.136	0.090-0.120	0.103
Tail length	0.316-0.450	0.366	0.290-0.370	0.323
Tail breadth (at base)	0.033-0.045	0.040	0.030-0.040	0.035
Oral sucker	0.040-0.060x 0.040-0.056	0.049x 0.051	0.036-0.043x 0.033-0.040	0.039x 0.037
Prepharynx length	0.013-0.030	0.022	0.003-0.013	0.010
Pharynx	0.023-0.026x 0.026	0.024x 0.026	0.020-0.023x 0.016-0.020	0.021x 0.017
Ventral sucker	0.056-0.066x 0.056-0.066	0.062x 0.062	0.040-0.056x 0.040-0.056	0.047x 0.047
Spines length				
Dorsal spines	0.009			
Corner spines	0.007-0.009			

Cyst (Plate 10, fig. 3)

The cysts are found in L. stagnalis and L. pereger. Both these snails were also infected experimentally. The cysts are rounded with unevenly thick walls and are located on the mantle of the host. The cyst wall is fairly thick but extremely delicate and can be broken very easily. The life cycle has been completed in the laboratory and will be described later. The adult is a species of Hypoderaeum Dietz, 1909. Cysts measure 0.120-0.140 mm. in diameter with a wall 0.003-0.012 mm. in thickness.

Comparison with Related Species

This cercaria is related to cercaria of Hypoderaeum conoideum (Bloch, 1782) Dietz, 1909, as described by Mathias (1925), Dubois (1929) and Wesenberg-Lund (1934); C. affinis, Wesenberg-Lund (1934) and C. densi Fain, 1953. Both Mathias (1925) and Wesenberg-Lund (1934) state that the collar spines in cercaria of H. conoideum are arranged in two rows. Wesenberg-Lund (1934) also states that there are eight lateral corner spines, while Dubois (1929) mentions the presence of five corner spines. Rees (1933) observed a group of four corner spines in both the cyst and the adult of H. conoideum. It is highly improbable that the cercaria should have a different arrangement. The present species

Explanation to Plate 11

Cercaria hamptonensis n. sp.

fig. 1 Complete cercaria showing structure of the tail.

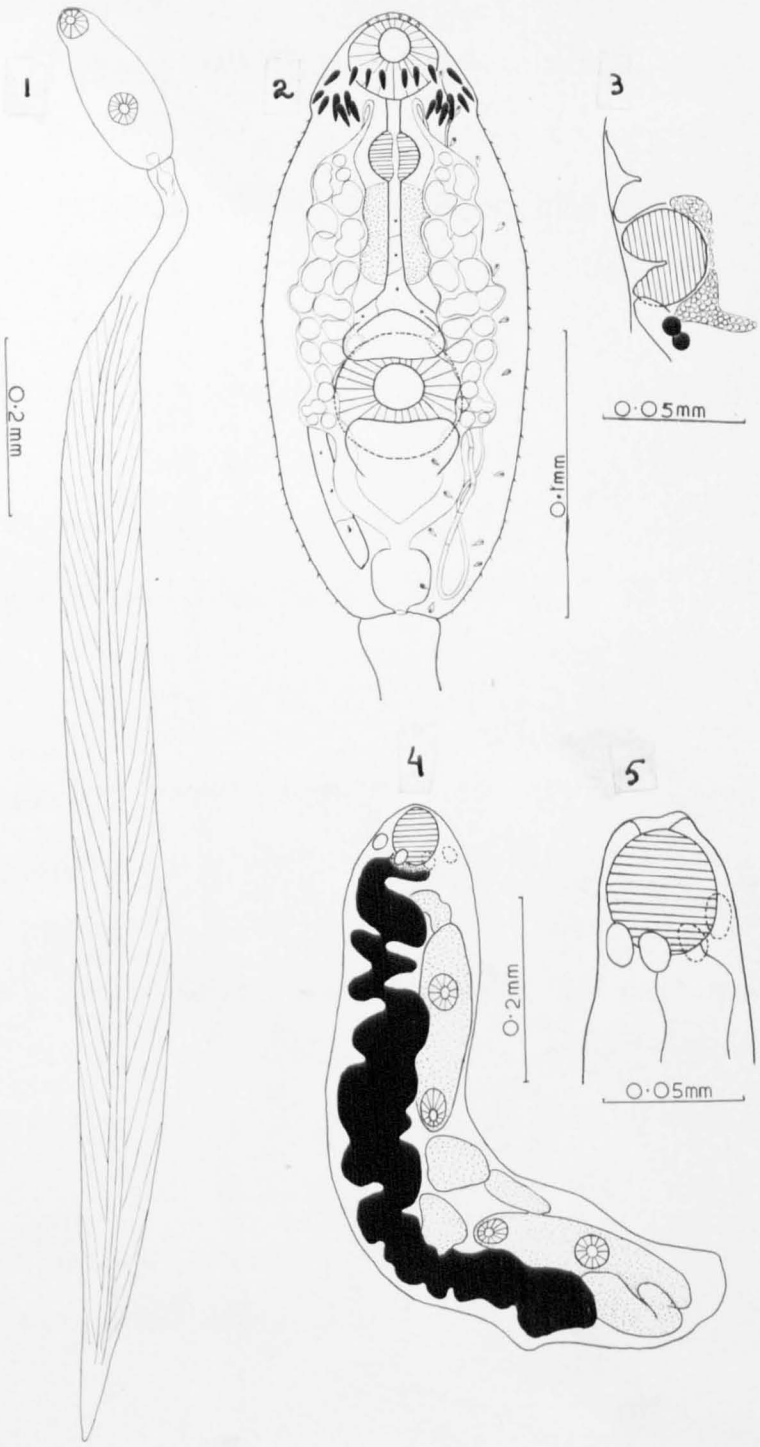
fig. 2 General structure of the body of cercaria.

fig. 3 Genital primordium (lateral view).

fig. 4 Complete redia.

fig. 5 Anterior end of the redia showing collar.

Plate II



which has a group of five corner spines also differs from the cercaria of H. conoideum in its much smaller size, smaller number of spines (which never exceeds forty-nine, while for the latter species forty-three to fifty-four spines have been described), in possessing an excretory system of the "Coronata" type, and in having a redia with a short gut.

C. densi agrees with the present species in having five corner spines and an excretory system of the "Coronata" type, but differs in having larger number of spines (fifty-three to fifty-four), in that the caudal excretory duct continues posteriorly after giving out its lateral branches, in the larger size of the body and in having a tail smaller than the body.

C. affinis has probably forty-seven spines with five lateral (corner) spines and has an excretory system of "Coronata" type but differs from the present species in having a larger body and suckers, a tail smaller than the body, in being strongly attenuated behind the collar, and in having a redia with a very long gut.

It is therefore regarded that the cercaria studied is a new species for which the name Cercaria essexensis is proposed.

12. Cercaria hamptonensis n. sp.+ (Plate 11, figs. 1-5)

On 15th September 1959, ten specimens of P. planorbis

+In the press.

were collected from the river Thames near Hampton Court. One of these snails was infected with a large-tailed "Echinostome" cercaria. In the last week of September and throughout October of the same year a large number of P. planorbis were collected from a small pond in Kenilworth Park. These snails showed an infection rate of 50 per cent with the same cercaria. No snails in either of the places were found to be infected in November or later.

Redia (Plate 11, figs. 4 and 5)

The cylindrical, motile rediae are embedded in the tissue of the digestive gland of the host. Their number in one host is comparatively small. A maximum of fifty rediae was recovered from one snail. The older rediae have a bright orange pigment, while the younger ones are colourless. The collar is broken up into four small pieces, two of these are dorsal and two ventral in position. The birth pore is on a small protuberance on the dorsal side. The ambulatory processes are poorly developed. The broad, sinuous gut has dark brown or black homogenous contents filling whole or part of it, and extends to the ambulatory process or beyond, but never to the posterior end. Two to five developing cercariae are present in an individual redia. A large number of immature cercariae were found lying free in the host tissue. The cercariae apparently leave the rediae in an immature state and

complete the development in the host tissue.

The size of the rediae is highly variable, the smallest living redia measured 0.42 mm. long and 0.195 mm. broad, with a pharynx 0.05 x 0.043 mm. in size. The largest redia had a length of 2.16 mm. and a breadth of 0.27 mm. The pharynx in this case was 0.06 x 0.076 mm.

Emergence and Behaviour

The cercariae are shed throughout the day, and in larger numbers immediately after noon. They are fairly active, swimming most of the time by lashing movements of the tail, alternating with a short resting period which may last for ten seconds. These cercariae unlike most Echinostomes exhibit a positive phototropism. They also show a tendency to aggregate in the upper half of the container. During the rest period the cercaria hangs with body downwards and the tail kept vertically upwards and motionless.

Cercaria (Plate 11, figs. 1 and 2)

The oblong, ovate body is slightly convex dorsally and concave ventrally. There is a well developed collar with twenty spines. Of these four larger spines form a corner group, on each side, while the rest are arranged in an uninterrupted row on the lateral and the dorsal sides.

The body is spined up to the posterior end. On the convex ventral side, a portion of the body wall is folded out, forming a flap which overhangs the anterior part of the ventral sucker. A similar outfolding of the body wall is present just behind the ventral sucker as well.

The aspinose tail of the cercaria is four to nine times as long as the body. There is a narrow proximal portion, interpolated between the body and the rest of the tail. After this narrow portion the tail gradually widens to reach its maximum breadth near the middle, thereafter narrowing gradually to end in a fine tip. The musculature of the tail is composed of two sets of muscles. One pair of prominent longitudinal muscle bands, originates at the posterior end of the narrow proximal portion of the tail and terminates near its distal end. Several oblique muscle fibres commence at the lateral margins and extend up to the middle of the tail. The body is filled with a large number of cystogenous gland cells with rod-shaped contents. A yellow pigment is diffused throughout the body and the tail. It is concentrated more into two large patches just behind the oral sucker and several such patches between post-acetabular region of the main ascending excretory ducts.

The subterminal oral sucker is broader than long. The prepharynx is comparatively long but is narrow and followed by a small, muscular pharynx. The oesophagus

divides just in front of the ventral sucker, which is slightly behind the middle of the body. The intestinal caeca extend to the posterior end of the body. Both the oesophagus and the intestinal caeca are composed of a single series of cells, with granular cytoplasm and clear nuclei, but the cell walls are seen only in a few places. In the living cercariae stained with dilute neutral red, the penetration gland cells, lying along the whole length of the oesophagus become more deeply stained. Their exact number could not be determined. There are probably six pairs. Six ducts, the penetration gland ducts, open at the anterior aspect of the oral sucker.

The excretory bladder is roughly triangular, with its base on the anterior side. Posteriorly the bladder opens to the exterior through a small circular opening, located at the junction of the body and the tail. Two wide main ascending excretory ducts open into it independently on the antero-lateral sides of the bladder. In front of the ventral sucker these ducts become enormously distended and have twenty five to thirty excretory granules, with doubly refractive margins. The excretory granules are irregular in shape and variable in size; some of them seem to be formed by the fusion of two or three small granules. The excretory system is of the "Echinata" type. Only fifteen flame cells on each side of the body are seen. Johnston and Angel (1941a) have reported eighteen flame

cells on each side of C. gigantura. Although they were not able to see their capillaries and exact connexions, they have suggested a flame cell formula of

$$2\ [(3 + 3 + 3) + (3 + 3 + 3)] = 36$$

The proximal narrow portion of the tail has a bladder which appears and disappears alternately with contraction and dilation of the excretory bladder in the body. No other caudal excretory ducts could be seen.

The genital primordium is represented by a large post-acetabular mass of cells, the ovary which is connected to a pre-acetabular mass by a narrow strand of cells. Just behind the ovarian primordium are two small circular masses of cells, representing the future testes (Plate 11, fig. 3).

Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.233-0.380	0.290	0.180-0.213	0.197
Body breadth	0.116-0.150	0.130	0.066-0.093	0.081
Tail length	0.975-0.195	1.350	1.350-1.485	1.400
Tail breadth (at base)	0.045	0.045	0.012-0.030	0.027
Tail breadth maximum	0.120-0.195	0.150	0.105-0.150	0.129
Oral sucker	0.043-0.050x 0.043-0.050	0.047x 0.048	0.030-0.033x 0.033-0.036	0.031x 0.035
Prepharynx length	0.016-0.033	0.022	0.006-0.013	0.012
Pharynx	0.016-0.020x 0.016-0.020	0.017x 0.017	0.016	0.016x 0.016
Ventral sucker	0.043-0.056x 0.043-0.056	0.050x 0.052	0.036-0.040x 0.040	0.038x 0.040
Collar across	0.083-0.093	0.092	0.043-0.060	0.052
Corner spines length	0.013-0.014			
Dorsal spines length	0.011-0.013			

Cysts

Brown (1931) found the cysts of C. oscilatoria in the digestive gland of P. vortex (Linn.), which also serves as the primary intermediate host. As he was unable to count the number of spines in the cercarial stage or the cysts the only criterion for identifying these cysts as those of C. oscilatoria was the compound

nature of the excretory granules. Beaver (1939) stated that Brown had probably seen the cysts of some other cercaria. Johnston and Angel (1941) also found that C. gigantura may encyst in snail hosts as well under abnormal conditions, such as lateness of season and isolation of a snail with cercariae for a long time, when the cercariae would either encyst in the snail or perish.

To establish the use of snails as second intermediate hosts by the present species, the following experiments were performed.

(1) Ten infected snails, which were known to be discharging the cercariae, were isolated in 3" x 1" containers for three days, without changing the water. These snails were dissected on the fourth day but no cysts were found in their tissue.

(2) Five laboratory bred P. planorbis were kept in 3" x 1" containers along with fifty cercariae each for a period of twenty four, thirty six and forty eight hours. On dissection, these also were found to be free from any cysts. This experiment was repeated several times, always with negative results.

The fusion of the excretory granules, which led Brown to suggest that C. oscilatoria encysts in snails, has also been observed in larval Echinostome, other than the large-tailed cercariae, i.e. C. essexensis (present study).

It is therefore concluded that the use of snails as

second intermediate host by this species of large-tailed "Echinostome" cercaria is highly improbable.

Several attempts to infect goldfish with the present cercaria were also unsuccessful.

Comparison with Related Species

Eight species of large-tailed Echinostome cercariae are known. O'Roke (1917) described the first, C. magnocanda but as he could not see any spines, he placed it among the "Megalurous" cercariae. O'Roke's material was re-examined by Miller (1929) who stated that collar spines were present in this cercaria. C. cita was reported by Miller in 1925 but was not described until 1929. In C. magnocauda, C. cita and C. oscilatoria, Brown, 1926, the number of collar spines is not known so that a comparison on this point is not possible. However, C. magnocauda has been reported to have a prominent stylet in its redial stage; the present species does not have any such structure. C. oscilatoria can be separated from the present species by having five corner spines, spines of the corner and dorsal series being of equal size and on the behaviour of the tail while at rest in the former. C. cita is smaller, with its tail quite different in shape, milky white in colour and half as long as in the present cercaria.

C. caudadena Faust, 1921, differs from the present species in having a larger number of collar spines (not

more than 24), in possessing an anteriorly dilated oral sucker and in having short intestinal caeca.

C. chandleri Abdel-Malek, 1952, has twenty-one spines. C. gigantura Johnston and Angel (1941) (cercaria of Petasiger australis Johnston and Angel, 1941), C. gigantura var, grandior Johnston and Simpson, 1944, and the cercaria of Petasiger nitidus Linton, 1928, as described by Beaver (1939), have nineteen collar spines of which four constitute a corner group. C. chandleri is smaller with its suckers nearly half the size of those in the present cercaria and has its intestinal caeca terminating just behind the ventral sucker. Cercaria of P. nitidus is smaller than the present species in the size of its body and of the suckers. It also lacks the pigment in the body or tail. C. gigantura is also smaller than the present species, differing further in the shape of the tail, in having an orange pigment in the body only, while the tail is without any pigment, the corner and the dorsal spines are of equal size and the collar spines of this species according to revised measurement of Johnston and Simpson (1944) are about half as long as those in the present species. The present cercaria has a tail similar to that of C. gigantura var.grandior but can be differentiated from it on the same grounds as discussed above for C. gigantura.

Hence the cercaria studied here is regarded as new and named Cercaria hamptonensis.

Explanation to Plate 12

Cercaria thamesensis n. sp.

fig. 1 Complete cercaria.

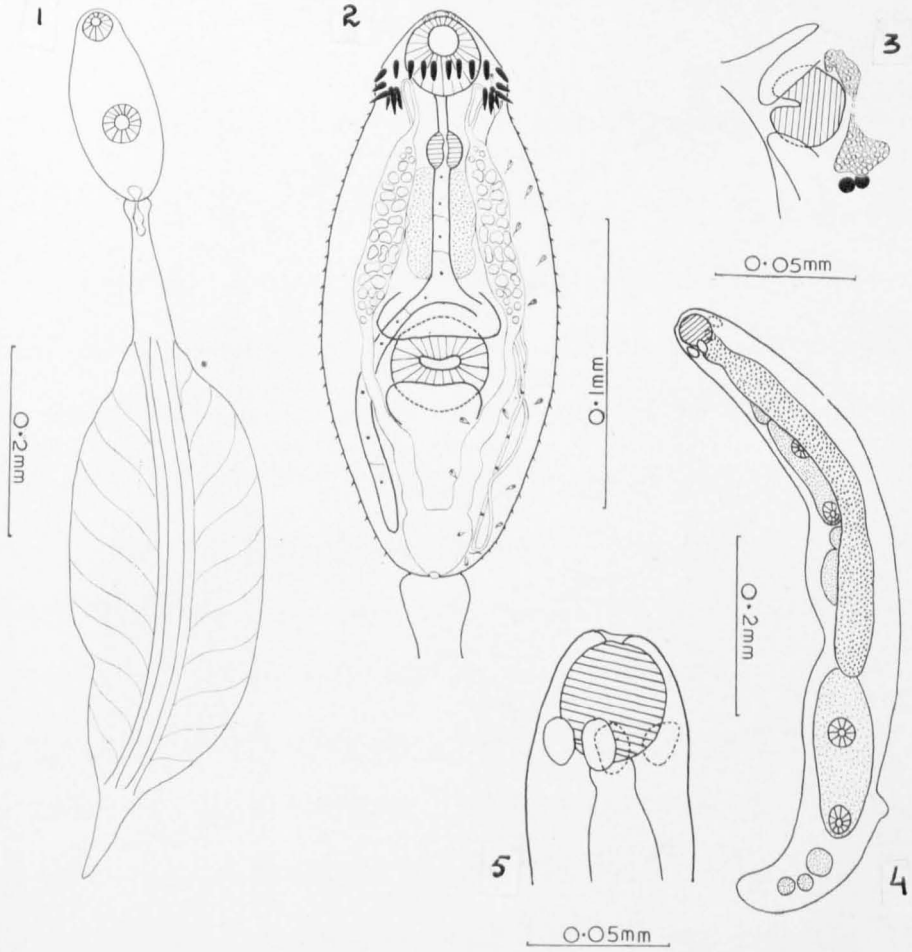
fig. 2 General structure of the body of cercaria.

fig. 3 Genital primordium (lateral view).

fig. 4 Complete redia.

fig. 5 Anterior end of the redia showing collar.

Plate I2



13. Cercaria thamesensis n. sp.+ (Plate 12, figs. 1-5)

This cercaria was encountered only once during this investigation. A single host, P. planorbis collected on 25th August 1959 was found to be emitting it. The snail was collected from the river Thames near Bushy Park.

Redia (Plate 12, figs. 4 and 5)

The rediae are superficially located on the digestive gland of the host. The most striking feature of the rediae is that irrespective of their size, they are colourless and fairly transparent. They are motile and variable in size. The collar as in C. hamptonensis is broken into four lobes. The ambulatory processes, and the birth pore are not very prominent. The gut is broad and usually terminates a short distance in front of the ambulatory processes and sometimes reaches up to these processes but never extends beyond them. The contents of the gut are in the form of masses of large black granules which may or may not fill it completely. As in C. hamptonensis the cercariae leave the rediae in an immature state and complete their development in host tissue. The smallest living redia measured 0.525 mm. long and 0.18 mm. broad with a pharynx of 0.036 mm. in diameter. The largest measured 1.225 mm. long and 0.225 mm. broad with a pharynx 0.056 x 0.05 mm.

+In the press.

Emergence and Behaviour

The cercariae are discharged in comparatively small numbers during the late afternoon. They are very sluggish with a long resting period followed by a short swimming period. The resting period may be as long as five minutes, during which it hangs motionless in the water with its body vertically downwards. This cercaria does not have a tendency to concentrate in the upper levels of the water but shows a positive phototropism.

Cercaria (Plate 12, figs. 1 and 2)

The body and tail of the cercaria is absolutely white with no trace of pigment of any kind. The oblong-ovate body is spined on its entire surface up to the posterior end except at the collar and the ventral sucker. The well developed collar bears twenty spines, of which four on each side are arranged in a corner group and the rest are disposed in an uninterrupted row on the dorsal and the ventral sides. The corner spines are larger than those of the dorsal series. The body is convex dorsally and concave ventrally with outfoldings of the ventral body-wall just in front and behind the ventral sucker. These outfoldings overlie a part of the ventral sucker at the anterior and the posterior sides respectively.

The body is filled with numerous cystogenous gland

cells with rod-shaped contents. The subterminal oral sucker is followed by a short prepharynx and a muscular pharynx. The oesophagus divides just in front of the ventral sucker into two intestinal caeca which extend to the posterior end of the body. Both the oesophagus and the intestinal caeca are cellular in nature, and non-functional. In living specimens stained with dilute neutral red, an area along the oesophagus becomes more deeply stained. It is probable that this area is occupied by the penetration glands, but their exact number could not be determined. Six penetration gland ducts open on the anterior surface of the oral sucker.

A roughly rectangular excretory bladder at the posterior end opens to the exterior through a small excretory pore, situated dorsally at the junction of the body and the tail. The two main ascending excretory ducts open, through a small median duct, into the excretory bladder. The pre-acetabular dilated portion of the main ascending excretory ducts accommodates nineteen to twenty-one large irregular excretory granules, some of which are formed by the fusion of two or three smaller granules. The excretory system is of the "Echinata" type. The descending excretory ducts are provided with ciliary patches along its course. Only six pre-acetabular and nine post-acetabular flame cells are seen on each side of the body.

The genital primordia (Plate 12, fig. 3) are similar

to those described for C. hamptonensis.

The aspinose tail is three to four times as long as the body, but much broader than in C. hamptonensis. The portion of the tail immediately behind the body is narrow, after which it quickly broadens and at the posterior end it again narrows sharply, terminating in a narrow apical portion. The anterior narrow portion of the tail has an accessory excretory bladder similar to that described for C. hamptonensis. No other caudal excretory duct is seen in this case either. The tail has a regular outline in the living and the fixed specimens, but a few irregular undulations may appear in some of the fixed specimens. There are two prominent muscles which originate at the posterior end of the narrow anterior part, and terminate at the anterior end of the narrow apical portion of the tail. There are also very fine oblique muscles originating from the lateral margins and terminating at the centre of the tail. No reticulate structure, as described for C. gigantura by Johnston and Angel (1941b), is present in this specimen.

Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.250-0.316	0.273	0.180-0.200	0.191
Body breadth	0.133-0.170	0.158	0.086-0.116	0.099
Tail length	0.925-1.125	1.065	0.600-0.705	0.654
Tail breadth (maximum)	0.300-0.375	0.345	0.180-0.330	0.225
Oral sucker	0.040-0.053x 0.040-0.053	0.045x 0.047	0.030-0.036x 0.030-0.053	0.044x 0.046
Ventral sucker	0.050-0.063x 0.050-0.066	0.056x 0.056	0.040-0.050x 0.040-0.053	0.044x 0.046
Pharynx	0.016-0.023x 0.016-0.023	0.021x 0.019	0.016-0.020x 0.010-0.016	0.017x 0.014
Collar across	0.053-0.100	0.090	0.050-0.060	0.055
Spines length				
Dorsal	0.010			
Corner	0.012			

Cysts

Attempts to infect snails and goldfish were unsuccessful.

Comparison with Related Species

The present species can be separated from C. hamptonensis in having a much shorter tail, in lacking yellow pigment in the cercaria and the orange pigment in the redia. These two also differ in the shape of the tail, the size of the collar spines and the nature of the opening of the main ascending excretory ducts into the bladder. The present

cercaria has much longer resting periods than C. hamptonensis.

In C. magnocauda, C. cita and C. oscilatoria the number of collar spines is not known. However, C. magnocauda and C. oscilatoria have a tail of quite different shape and larger proportionate size. The present species further differs from C. magnocauda in lacking a stylet in the redia and from C. oscilatoria in having a group of four corner spines, unequal size of the spines of the corner and the dorsal series and in the complete lack of pigment in the cercaria or the redia.

The form under study can be distinguished from C. cita in lacking the pigment in the body of the cercaria or the redia. The oral and the ventral suckers in C. cita are of equal size, while in the present species the ventral sucker is larger than the oral; the pharynx of the former is half the size of the pharynx in the present cercaria.

The present cercaria resembles the cercaria of Petasiger nitidus in possessing a group of four corner spines and in lack of pigment, but differs in having twenty spines as against nineteen and in possessing a larger body. The tail also is different in shape and three to four times as long as the body, while in C. petasiger nitidus it is four to nine times the length of the body.

C. caudadena has larger number of collar spines (24) and also differs from the present cercaria in having short intestinal caeca and an anteriorly dilated oral sucker.

C. chandleri has twenty-one collar spines, is smaller than the present species, has much smaller suckers and possesses a pale yellow pigment in the body. It also differs from the present species in having a tail four to ten times as long as the body, and in having shorter intestinal caeca, terminating just behind the ventral sucker.

C. gigantura and C. gigantura var. grandior have nineteen collar spines, of equal size in the corner and the dorsal series. The collar spines in these two species are about half the size of those found in the present cercaria. Both of them also differ in having an orange pigment in the cercaria and in having pigmented rediae, whereas the present cercaria has no pigment in the cercarial or the redial stage.

On the basis of the above comparison the present species is regarded as new and the name Cercaria thamesensis is proposed for it.

Xiphidiocercariae

The term "Xiphidiocercariae" was first used by Diesing (1855). Lühe (1909) included in this group distome cercariae with an anterior stylet and penetration gland cells, but without eye spots and possessing a slender tail. He divided them into four groups. These groups may be defined as follows:

(1) "Cercariae microcotylae", including forms not exceeding 0.2 mm. in length, having a ventral sucker smaller than the oral and located behind the middle of the body and lacking a caudal finfold, with two to four penetration gland cells. The flame cell formula was given by Sewell (1922) as $2\ [(1 + 1 + 1) + (1 + 1 + 1)] = 12$, while Dubois (1929) gave it as $2\ [(2 + 2 + 2) + (2 + 2 + 2)] = 24$.

(2) "Cercariae virgulae" are forms with a characteristic virgula organ, with a ventral sucker smaller than the oral, tail without finfold, three to six pairs of penetration gland cells, excretory bladder V-shaped, oval or reniform. The flame cell formula as given by Dubois (1929) is the same as given by him for "Cercariae microcotylae".

(3) "Cercariae ornatae", with a caudal finfold, four to six penetration gland cells, excretory bladder oval or rectangular, with wide cornua.

(4) "Cercaria armatae". Cercariae without a caudal finfold or virgula organ, body length more than 0.25 mm. excretory bladder bicornuate, ventral sucker

of same size as or smaller than the oral sucker and situated behind the middle.

Cort (1914) added another group, the "Polyadenous cercariae", for C. limnaeae ovatae v. Linst. 1884, C. secunda Sinitsin, 1905, C. polyadena Cort, 1914 and C. isocotylea. This group has been included as a sub-group among Cercariae armatae (Sewell, 1922; Dawes, 1946).

Lebour (1911) suggested the grouping of certain marine xiphidiocercariae with the "Spelotrema" group. Sewell (1922) was of the opinion that Lebour's arguments for this grouping are inconclusive.

Sewell (1922) pointed out that several other forms of cercariae have been described which have a stylet, but these forms ("Microcercous", "Rhopalocercous" and "Cystocercous") have a more complex stylet, with more than one point and set at right angle with the long axis of the body. He has extended the classification of the "Xiphidiocercous" cercariae, retaining all the groups of Lühe with modified "Cercariae virgulae" and the "Polyadenous" group of Cort. "Cercariae microcotylae" have been further sub-divided by Sewell (1922) into the following four sub-groups.

(1) "Cellulosa" sub-group for cercariae with only one pair of penetration gland cells on each side, with no oesophagus or caeca, triradiate excretory bladder and flame cell formula 2(2 + 2) = 8.

(2) "Pusilla" sub-group. Forms with three to four pairs of penetration gland cells, oesophagus or caeca usually absent, excretory bladder bicornuate or reniform, flame cell formula 2 $[(1 + 1 + 1) + (1 + 1 + 1)] = 12$ and development in rounded or elongated sporocysts.

(3) "Vesiculosa" sub-group. Forms with four pairs of penetration gland cells, three dorsal, with ducts in one bunch and one ventral with separate duct, excretory bladder spherical. He removed C. vesiculosa Dies., 1855 from the "Cercariae virgulae", where it was placed by Lühe (1909) and included it here.

(4) "Parapusilla" sub-group with forms differing from the members of the "Pusilla" sub-group in the possession of an oesophagus and caeca.

The "Cercariae virgulae" were divided by Sewell (1922) into two sub-groups:

(1) "Virgula" sub-group, Cercariae of small size (body less than 0.2 mm.), tail usually smaller than body, ventral sucker smaller than oral (usually half), virgula organ well developed or reduced, excretory bladder oval or reniform, oesophagus and caeca absent.

(2) "Paravirgula" sub-group, differing from "Virgula" sub-group in having oesophagus and intestinal caeca and in having a V-shaped excretory bladder.

In "Cercariae ornatae" Sewell pointed out that the definition of this group as given by Lühe was of the

briefest kind and consequently the group is a very un-natural one. He recognised one sub-group in these cercariae:

(1) "Prima" sub-group. Ventral sucker smaller than the oral and situated behind the middle of the body, tail shorter than the body and with a dorso-ventral finfold on the terminal part, the intestinal caeca terminate between the ventral sucker and the posterior end, four to five pairs of penetration glands, excretory bladder oval or rectangular, genital rudiment better developed than in the previous groups, flame cell formula probably 2 x 6 x 1 = 12.

The "Cercariae armatae" were divided into two sub-groups:

(1) "Polyadena" sub-group (of Cort, 1914). Sewell elaborated the nature of the excretory bladder and modified the characters of the group. According to the revised definition, this group would include forms with six or more pairs of penetration gland cells, stylet about 0.03 mm. long and one-sixth as broad and with a reinforcement at about one third of its length from the anterior end. Oesophagus and caeca always present, caeca extending to the posterior end, caudal pockets with spines present and the flame cell formula 2 $[(3 + 3 + 3) + (3 + 3 + 3)] = 36$.

(2) "Daswan" sub-group, moderate sized cercariae with a slender tail smaller than the body, ventral sucker

as large as or smaller than the oral sucker and just behind the middle of the body, few penetration gland cells (three pairs in both Indian forms), posterior end produced into lappets, with acicular spines, excretory bladder small and circular.

Faust (1924) rearranged the groups solely on the pattern of the flame cells and suggested several new groups.

Dubois (1929) added a new sub-group of "Cercariae microcotylae", the "Helvetica" sub-group, in which the excretory system is more complex than the other members of the group.

As has been pointed out in the account of the "Monostome" cercariae, the absence of a ventral sucker alone in a group, does not provide justifiable criterion for its inclusion among the "Monostome" cercariae. The "Ubiquita" sub-group of Sewell which he placed among his "Monostome" cercariae, as suggested by Wesenberg-Lund (1934) should be placed among the "Xiphidiocercariae". Because of their close morphological relationship with the "Parapusilla" sub-group these monostome xiphidiocercariae should be placed there.

Porter (1938) in dealing with the South African fauna has combined the classifications of Sewell (1922) and Faust (1924) and proposed two new sub-groups of "Cercariae microcotylae". The "Paracellulosa" and "Paravesiculosa" sub-groups to accommodate forms differing from the

"Cellulosa" and "Vesiculosa" sub-groups of Sewell respectively in possession of an oesophagus and intestinal caeca.

Dubois (1929) stated that Sewell (1922) has completed the definition of the "Cercariae ornatae". Sewell was actually dealing as pointed out by Wesenberg-Lund (1934) with the "Prima" sub-group of "Cercariae ornatae" and not with the whole "Cercariae ornatae". Sewell (1922) has included the "Cercariae virgulae" among the "Cercariae microcotylae".

The statement of Wesenberg-Lund (1934) that the "Paravirgulate" cercariae are not represented in Europe is also incorrect, as some virgulate cercariae have been reported from Europe with an oesophagus and intestinal caeca.

Members of "Cercariae microcotylae", "Cercariae armatae" and "Cercariae virgulae" have been found in the present investigation.

Explanation to Plate 13

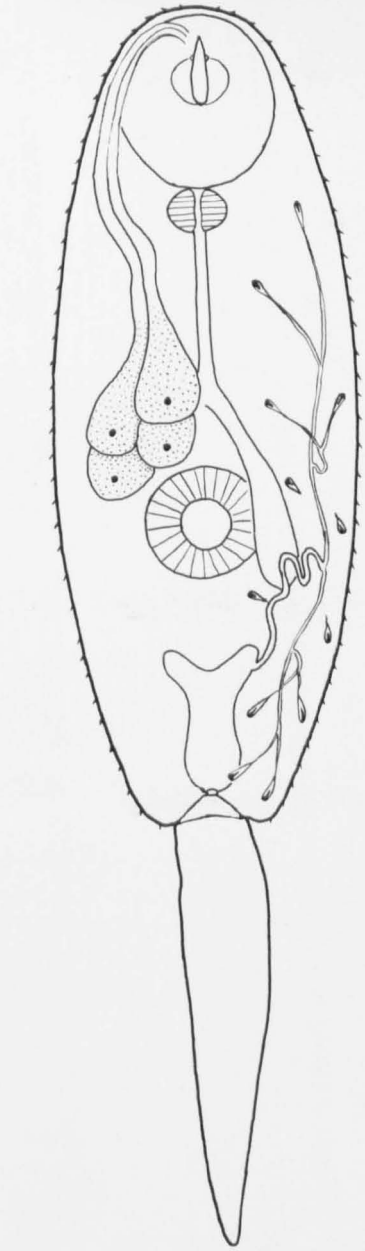
Cercaria minor n. sp.

fig. 1 General structure of the cercaria.

fig. 2 Stylet.

fig. 3 Genital primordium (lateral view).

Plate I3



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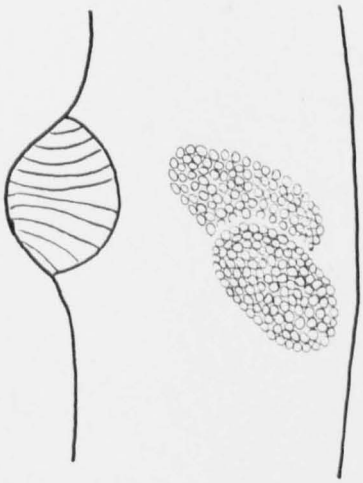

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Cercariae Microcotylae

14. Cercaria minor n. sp. (Plate 13, figs. 1-3)

One to two per cent of B. tentaculata collected from June to September, 1958 and 1959 from Bushy Park were found to be infected with this cercaria.

Sporocyst

A large number of short, stumpy sporocysts were found in the digestive gland of each infected snail. These sporocysts may be nearly rounded to slightly elongated in shape, colourless and inactive. There may be three to four developing cercariae and a few germ cells in one sporocyst. The birth pore is terminal. Both ends may be bluntly rounded off or the anterior end may be slightly drawn out. The size of living sporocysts varies between 0.146-0.366 mm. in length and 0.110-0.133 mm. in breadth.

Emergence and Behaviour

The cercariae are emitted in large numbers during the night. They are poor swimmers and tend to aggregate near the bottom of the container.

Cercaria (Plate 13, fig. 1)

The cercaria is small with a contractile body, covered over its entire surface with small backwardly directed spines. At the anterior end of the body on the dorsal side is a stylet. There are a few muscle fibres attached to the base of the stylet, which allow the stylet a lateral movement up to a right angle from longitudinal axis and an equal degree of movement on the dorso-ventral plane. The stylet has fine anterior tip and reinforcement at about one third of its length from the anterior end. The walls of the stylet are thickened up to the middle of the stylet shaft (Plate 13, fig. 2). There are numerous cystogenous gland cells throughout the body but they are more concentrated in the post-acetabular region. The contents of these gland cells are granular. There are also several refractile oil globules of variable size. The oral sucker is sub-terminal, followed by a muscular pharynx and the oesophagus bifurcates a short distance in front of the ventral sucker. The intestinal caeca are thin-walled and terminate just behind the ventral sucker. They gradually increase in diameter posteriorly. There are four pairs of penetration gland cells lying anterior to the ventral sucker. Their ducts open at the anterior end of the stylet. The ventral sucker is smaller than the oral and is situated behind the middle of the body.

The excretory system (Plate 13, fig. 1) comprises a bicornuate excretory bladder at the posterior end of the body, with a long basal part, in extended specimens. The cornua of the excretory bladder terminate between the ventral sucker and the posterior end of the body. The lateral excretory duct which originates aterminally from the cornua has a wavy course up to just behind the ventral sucker, where it forms a few coils and divides into an anterior and a posterior collecting tubule, each connected with six flame cells. The flame cell formula is $2\ [(2 + 2 + 2) + (2 + 2 + 2)] = 24$.

The genital primordium is represented by two oval masses of deeply staining cells lying dorsal and posterior to the ventral sucker, near the dorsal body wall (Plate 13, fig. 3).

The tail is simple and highly contractile. There are no spines on the tail. The caudal excretory duct is unbranched.

Measurements of Cercaria (In millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.116-0.183	0.144	0.100-0.116	0.109
Body breadth	0.050-0.066	0.061	0.033-0.040	0.036
Tail length	0.066-0.150	0.111	0.060-0.083	0.071
Tail breadth	0.011-0.016	0.014	0.013-0.016	0.015
Oral sucker	0.033-0.040x 0.030-0.040	0.037 0.035	0.023-0.030x 0.020-0.026	0.026x 0.022
Pharynx	0.011-0.013x 0.011-0.013	0.012x 0.012	0.010x0.010	0.010x 0.010
Ventral sucker	0.023-0.026x 0.023-0.026	0.024x 0.024	0.016x0.016	0.016x 0.016
Stylet length	0.02			
Breadth at shoulder	0.004			
Breadth at base	0.006			

Comparison with Related Species

C. nylstrooma Porter, 1938, C. burnupuoides, Porter, 1938, C. baakensis Porter, 1938 can all be separated from the present cercaria by their lack of an oesophagus and intestinal caeca. C. nylstrooma further differs in having an unspined body and in the shape of the stylet. C. burnupuoides has no cornua in the excretory bladder, is larger and has a different flame cell pattern and C. baakensis also has an unspined body, rounded excretory bladder and different flame cell pattern.

C. pneumata Fain, 1953 has a different flame cell

pattern, a smaller stylet of a different shape, much shorter intestinal caeca and a spined tail.

C. vesiculosa Dies. as described by Wesenberg-Lund (1934) is larger than the present cercaria and further differs in having the penetration gland cells and its ducts in two groups, in the origin of the main excretory ducts terminally from the cornua of the excretory bladder and in lacking an oesophagus or intestinal caeca.

C. helvetica XI Dubois, 1929, is larger than the species under study, but has smaller suckers and slightly smaller stylet (17-20 x 4.8-5 mm), has no oesophagus or intestinal caeca and has an alveolar dorsal side of the body, otherwise unspined. It also differs in the origin of its main excretory ducts terminally from the arms of the excretory bladder.

C. plagiorchis amurensis McCoy, 1928 (later shown to be Alloglossidium corti (Lamont) by Crawford, 1937) can be differentiated from the present species in having intestinal caeca extending to the posterior end of the body, in having a spined tail and spined caudal pockets and in that it develops in much longer sporocysts.

In view of the above comparison, the present species is regarded as new and the name Cercaria minor is proposed for it.

Explanation to Plate 14

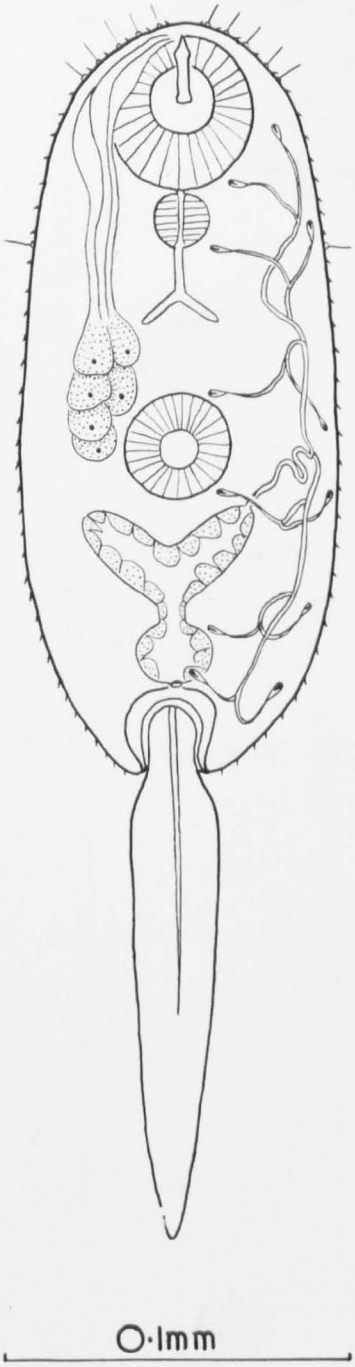
Cercaria chislehurstensis n. sp.

fig. 1 General structure of the cercaria.

fig. 2 Stylet (dorsal and lateral views).

fig. 3 Genital primordium (dorsal view).

Plate I4



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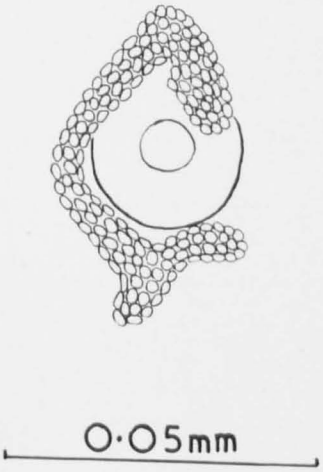

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Cercariae Armatae

15. Cercaria chislehurstensis n. sp. (Plate 14, figs. 1-3)

One to five per cent of L. stagnalis collected from Chislehurst Common (Kent), Sand Pits (South Ockendon) and Stoneyfields Park (Edgware) were found to be infected with this cercaria.

Sporocyst

A very large number of sporocysts are present in the digestive gland of the host. They are difficult to separate from the host tissue. The anterior half of the sporocyst is usually narrow as compared to the posterior half which is bulbous and accommodates two to three cercariae and germ balls. The sporocysts in fixed condition measured 0.42-0.75 mm. long with maximum breadth of 0.09-0.15 mm.

Emergence and Behaviour

The cercariae are discharged in large numbers, throughout the day. They are poor swimmers and remain near the bottom of the container.

Cercaria (Plate 14, figs. 1-3)

The body while moderately stretched is oblong. Numerous closely set, transverse rows of minute spines cover the entire body. These spines are less prominent on the posterior half of the body. Apart from these spines there are five pairs of hair-like structures on the anterior end of the body and one pair at the level of pharynx.

The junction of the aspinose tail with the body is subterminal. The caudal pockets are prominent but without any spines. A stylet is present at the dorsal side of the oral sucker. The stylet is javelin shaped with a shoulder at about one-third of its length from the anterior end, and a similar but less pronounced reinforcement at the base (Plate 14, fig. 2). Both the shoulder and basal reinforcements are continuous over the dorsal and lateral sides, but are absent from the ventral side of the stylet.

The oral sucker is larger than the ventral sucker, which is located near the middle of the body. The prepharynx is practically absent and the pharynx with poorly developed muscles. The oesophagus bifurcates between the pharynx and the ventral sucker and the short intestinal caeca, diverging outwards, terminate slightly posterior to the oesophageal bifurcation.

The cystogenous gland cells with minute rod-shaped

contents occupy most of the body behind the pharynx. Interspersed among the cystogenous gland cells are several refractile oil globules of variable size. There are six pairs of penetration gland cells antero-lateral to the ventral sucker. These glands remain unstained with neutral red. The penetration gland ducts open at the anterior end near the tip of the stylet.

The excretory bladder is bicornuate with a basal chamber, a narrow shaft and two cornua. The cornua reach the posterior end of the ventral sucker. The main excretory ducts are short and convoluted. Both the anterior and posterior collecting tubules receive capillaries from six flame cells on each side. The flame cell formula is $2\ [(2 + 2 + 2) + (2 + 2 + 2)] = 24$.

The genital rudiment is represented by a C-shaped mass of cells lying dorsal to the ventral sucker (Plate 14, fig. 3).

The tail is without any spines or finfold. The caudal excretory duct is unbranched.

Measurements of Cercaria

(All measurements in millimetres)

Body length	0.166-0.236	0.229	0.20 -0.231	0.223
Body breadth	0.10 -0.116	0.111	0.088-0.110	0.102
Tail length	0.10 -0.216	0.208	0.14 -0.156	0.138
Tail breadth	0.02 -0.023	0.022	0.02 -0.03	0.024
Oral sucker	0.04 -0.05x 0.043-0.056	0.046x 0.050	0.04 -0.043x 0.04 -0.05	0.043x 0.047
Pharynx	0.18 -0.02x 0.02 -0.023	0.019x 0.021	0.016x0.020	0.016x 0.020
Ventral sucker	0.036-0.040x 0.036-0.040	0.033x 0.033	0.030-0.036x 0.030-0.036	0.033x 0.033
Stylet length	0.026			
Stylet breadth at shoulder	0.006			
Stylet breadth at shaft	0.004			
Stylet breadth at base	0.005			

Comparison with Related Species

In possessing a bicornuate excretory bladder with a basal chamber, median shaft and cornua, the present species can be distinguished from C. Indicae XVII Sewell, 1922, C. XI Harper, 1929; C. exilis Brooks, 1930; C. mesotyphla Miller, 1936; C. acanthocoela Miller, 1936; C. herberi McMullen, 1938, C. episthoglyphae ranae Komiya, 1938; C. paracephaladena Faust, 1926, C. mafuria Porter, 1938, C. microphalloides Porter, 1938 and C. dorotti Brooks, 1943b.

C. lechiorchis primus Talbot, 1933, C. l. tygasti

Talbot, 1933 and C. cadiorchis eurimes Talbot, 1933 can all be separated in having the cornua of the excretory bladder encircling the ventral sucker and in having longer intestinal caeca.

C. amherstensis Rankin, 1939 has a stylet with no shoulders, spines in the caudal pockets, longer intestinal caeca, the cornua of the excretory bladder extending to the middle of the ventral sucker, aterminal origin of the main excretory ducts from the excretory bladder and two caudal excretory ducts nearly up to the tip of the tail. The present cercaria can be distinguished from C. talboti McMullen, 1938 in having an unspined tail, short intestinal caeca and in the position of the penetration gland cells.

C. britskalia Porter, 1938 can be separated from the present species on the shape of the excretory bladder, in having longer intestinal caeca and in having rod-shaped contents in the oesophagus and the intestinal caeca.

C. granulata Fain, 1953 is a much larger species with a larger stylet and further differs in having spines on the tail and caudal pockets and in the extension of the intestinal caeca to the posterior end of the body.

The species under study is therefore regarded as new and the name Cercaria chislehurstensis is proposed for it.

Explanation to Plate 15

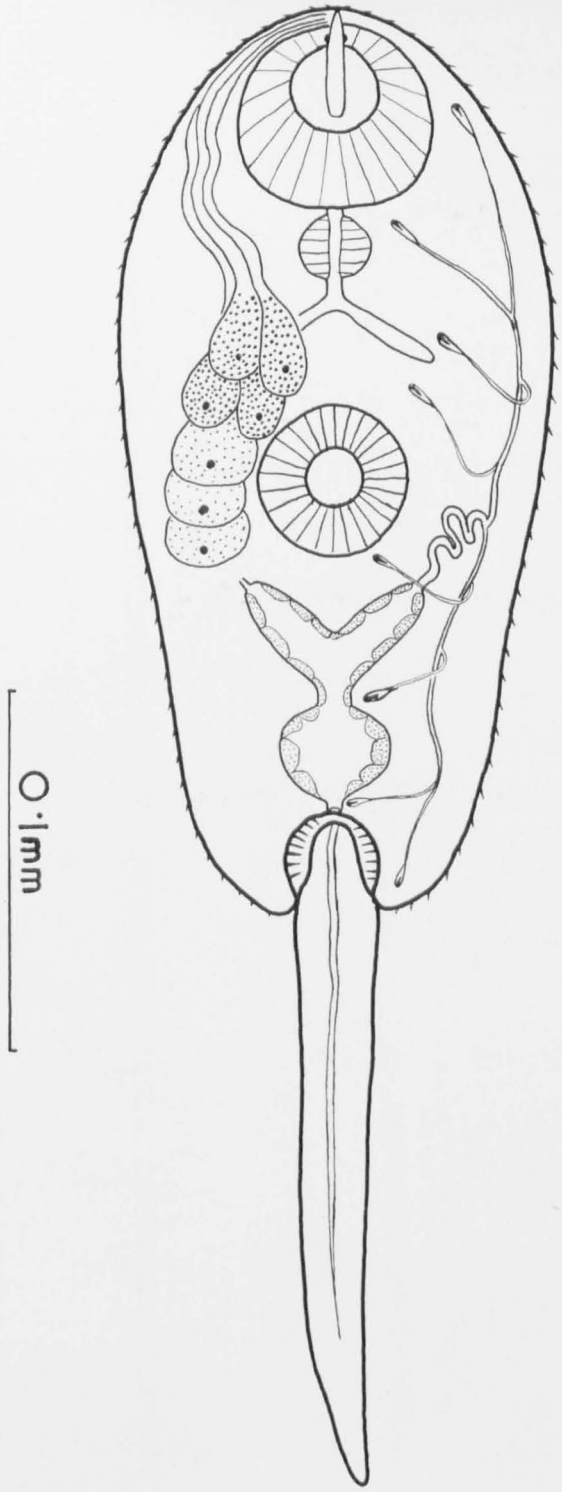
Cercaria peregeri n. sp.

fig. 1 General structure of the cercaria.

fig. 2 Stylet.

fig. 3 Genital primordium (dorsal view).

Plate I5



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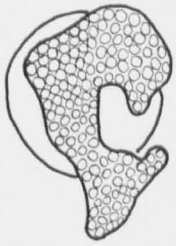

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16. Cercaria peregeri n. sp. (Plate 15, figs. 1-3)

This cercaria was encountered once when one of one hundred L. pereger collected from the river Thames on 15th June, 1960 was found to be emitting this cercaria.

Sporocysts

The sporocysts are long thread-like structures present in large numbers and deeply embedded in the digestive gland of the host. It is difficult to remove them from the tissue of the gland. A large proportion of their length is composed of narrow constricted portions, with one to three bulbous swellings, which accommodate the germ cells and the developing cercariae. The anterior end is narrow as compared with the posterior, which is swollen and rounded. The birth pore is subterminal.

The living sporocysts measured 1.50-2.1 mm. in length with the maximum breadth at bulbous portions being 0.09-0.24 mm. and the minimum breadth of 0.045 mm. at the constricted portions.

Emergence and Behaviour

The cercariae emerge during the night. They are poor swimmers and tend to concentrate near the bottom of the container. By the afternoon most of them settle to

the bottom and start crawling with help of their suckers.

Cercaria (Plate 15, figs. 1-3)

The body of the cercaria is thick and not highly contractile. The entire body is covered with small spines. The tail is subterminally attached to the body. The caudal pockets are well developed and provided with strong spines.

The subterminal oral sucker is larger than the ventral sucker, which is situated in the middle of the body. The stylet (Plate 15, fig. 2) is elongated, with a reinforcement nearly one third of its length from the anterior end. This reinforcement is continuous over the dorsal and lateral sides, but not on the ventral side. The base of the stylet is not reinforced. About three pairs of small muscle fibres inserted at the base of the stylet, manoeuvre the stylet in all directions, and it may come to point directly backwards.

A very small prepharynx follows the oral sucker and in turn is followed by a muscular pharynx. The narrow thin walled oesophagus divides a short distance behind the pharynx; small caeca, diverging outwards, terminate between the pharynx and ventral sucker.

The body of the cercaria is filled with a large number of cystogenous gland cells, with granular cytoplasm. Several rounded oil globules, of varying size are scattered

throughout the body. There are seven pairs of penetration gland cells in front of and lateral to the ventral sucker. Of these, four on each side are smaller and have coarsely granular cytoplasm, while the posterior three on each side are larger and have clear cytoplasm. Their ducts follow a wavy course anteriad and open near the tip of the stylet.

The infected snail died before a thorough examination of the excretory system could be made. As far as it was studied, it comprises a triradiate excretory bladder with a rounded basal part, elongated cornua, reaching up to the posterior end of the excretory bladder. Each cornua gives rise to a convoluted excretory duct, which divides into two collecting tubules. At least four flame cells have been seen, connected with each collecting tubule, arranged in $2 \cdot [(2 + 1 + 1) + (1 + 1 + 2)] = 16$, fashion.

The reproductive primordium (Plate 15, fig. 3) comprises an irregular mass of cells, lying on the anterior, dorsal and posterior sides of the ventral sucker.

The aspinose tail, is highly contractile, with an unbranched caudal excretory duct, which could be traced up to about three quarters of the tail length. Decaudation occurs readily and the tail after separating from the body continues moving for some time.

Measurements of cercaria (In millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.250-0.390	0.296	0.226-0.283	0.254
Body breadth	0.106-0.183	0.133	0.093-0.126	0.110
Tail length Maximum Contracted	0.066			
Extended	0.176-0.183	0.180	0.150-0.183	0.175
Tail breadth	0.026-0.050	0.044	0.020-0.026	0.022
Oral sucker	0.053-0.066x 0.053-0.066	0.060x 0.060	0.050-0.053x 0.050-0.053	0.051x 0.051
Ventral sucker	0.040-0.050x 0.040-0.050	0.044x 0.044	0.040-0.043x 0.040-0.043	0.037x 0.037
Pharynx	0.020-0.023x 0.020-0.023	0.021x 0.021	0.016-0.020x 0.016-0.020	0.018x 0.018
Stylet length	0.033			
Breadth of shaft	0.005			
Breadth of shoulder	0.0066			

Comparison with Related Species

C. acrodonta Faust, 1922 differs from the present cercaria in being smaller, in having a stylet less than half the size of that in the present species, in having very wide intestinal caeca, in the much more posterior position of the ventral sucker and in having a different arrangement of the penetration gland cells.

C. elbensis Komiya, 1938 is also smaller than the present species, has a smaller stylet and further differs in its intestinal caeca extending to the posterior end

of the ventral sucker.

The presence of excretory granules in the excretory bladder and the extension of its cornua practically around the whole of the ventral sucker in C. lajae Brooks, 1943 readily separates it from the present cercaria.

The presence of short intestinal caeca, which terminate considerably in front of the ventral sucker, the origin of the main excretory ducts terminally from the cornua of the excretory bladder, and differentiation of the penetration gland cells into two sets, in the present species separate it from C. conniae Brooks, 1943, C. argenti Brooks, 1943 and C. nolfi Brooks, 1943. The size of the stylet in all these species is also slightly different from that of the present species, while the stylet of C. conniae also has a basal thickening, which is absent in the present cercaria.

Although the complete flame cell formula could not be determined in the present cercaria, it is evident, in view of the above comparison, that a new species of cercaria is being dealt with. The name Cercaria peregeri is proposed for it.

17. Cercaria plagiorchis (multiglandularis) megalorchis Rees, 1952

Three to four per cent of L. stagnalis collected from Sand Pits (S. Ockendon) were infected with this cercaria.

This cercaria has been described in detail by Rees (1952). My observations and measurements agree completely with those given by the above author on all essential points. The breadth of the stylet shaft is given by Rees as 0.008 mm. but in the specimens examined by me this is the breadth of the shoulder, while the shaft measures 0.0048 mm. Also Rees has given the diameter of the pharynx as 0.2-0.22 mm. which is apparently a mistake and should be 0.02-0.022. Rees has not given the measurements in the fixed condition, which are given below. Rees has recorded this cercaria from L. pereger but in the present investigation only L. stagnalis were found to harbour this larval trematode. It is interesting to note that the above locality had both these species of snails. However, the place from where Rees (1952) obtained the infected snails had only L. pereger of the two species.

The only other interesting fact noted was that some of the snails collected from the same locality were discharging the cercariae during the day, while others were shedding them only during the night. No morphological difference among these two types of cercariae was found.

According to Rees (1952) very few cercariae of P. megalorchis emerge during the day, most of them emerging during the evening, night and early morning.

Explanation to Plate 16

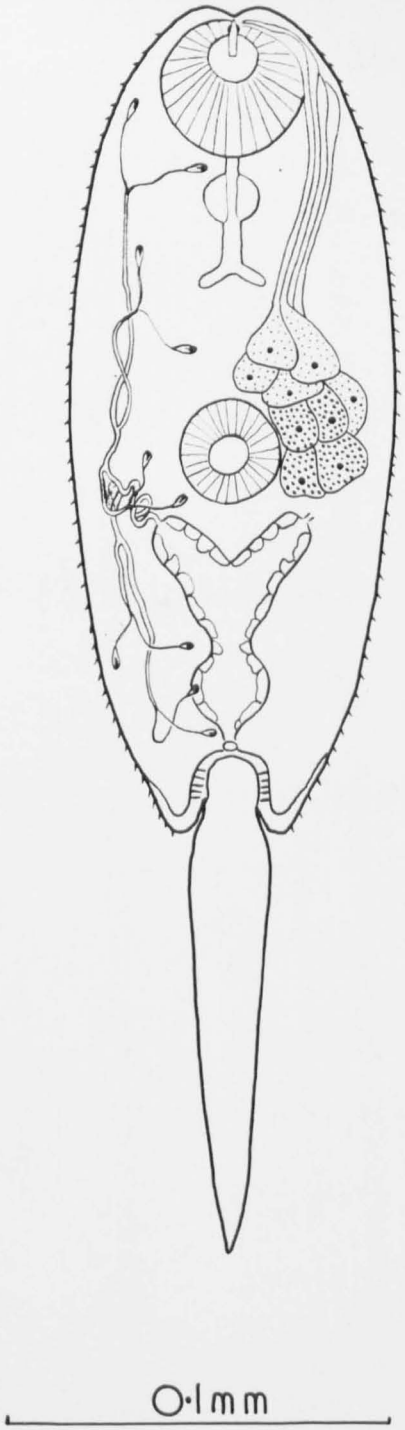
Cercaria meadowensis n. sp.

fig. 1 General structure of the cercaria.

fig. 2 Stylet.

fig. 3 Genital primordium (dorsal view).

Plate I6



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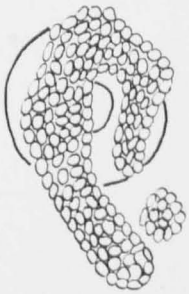


3

Specific Diagnosis

Xiphidiocercaria, with spined body and eight pairs of penetration glands anterior to the ventral sucker. Oral sucker larger than the ventral and the intestinal caeca extending to the posterior end. Excretory bladder bicornuate, cornua reaching the posterior margin of the ventral sucker. Flame cell formula $2\ [(3+3+3)+(3+3+3)] = 36$. Stylet javelin-shaped 0.31-0.33 mm. long and about one sixth as broad. Tail simple, without finfold, caudal pockets spined.

Measurements of Fixed Cercariae (In millimetres)

	Range	Average
Body length	0.206-0.223	0.213
Body breadth	0.083-0.09	0.087
Tail length	0.130-0.146	0.136
Tail breadth	0.02	0.02
Oral sucker	0.04 -0.046x 0.043-0.046	0.043 0.045
Ventral sucker	0.03 -0.033x 0.03 -0.033	0.032x 0.032
Pharynx	0.016-0.018x 0.018-0.02	0.017x 0.018

18. Cercaria meadowensis n. sp. (Plate 16, figs. 1-3)

From three to ten per cent L. pereger collected from Lake Meadows and Epping Forest were found to be infected with this cercaria.

Sporocyst

The simple, thin-walled sporocysts are present in enormous numbers in the digestive gland of the host. They are very difficult to separate from the host tissue. The birth pore is terminal. The living sporocysts measured 0.33-0.97 mm. in length and 0.15-0.27 mm. in breadth.

Emergence and Behaviour

The cercariae are discharged during the night in large numbers. The cercariae are sluggish, usually remaining near the bottom of the container, where they creep with the help of their suckers.

Cercaria (Plate 16, figs. 1-3)

The body and tail are highly contractile. Small spines cover the whole body. These spines are arranged in parallel rows starting in the middle of the body and radiating outwards and forwards.

The subterminal oral sucker is larger than the ventral sucker. The prepharynx is short and the pharynx muscular. The oesophagus is narrow and comparatively short, dividing between the pharynx and the ventral sucker, into two short intestinal caeca which terminate considerably in front of the ventral sucker.

There are nine pairs of penetration gland cells

lying in front of the ventral sucker. These cells remain unstained with neutral red. The penetration gland ducts are dilated at the side of the oral sucker and open at the anterior tip. Numerous cystogenous gland cells, with granular contents and oil globules of varying sizes, are present.

The excretory bladder is bicornuate, with its cornua extending up to slightly behind the ventral sucker. The two main excretory ducts originate terminally. These ducts are convoluted at the posterior level of the ventral sucker where each divides into anterior and posterior collecting tubules. The anterior collecting tubule receives capillaries from six flame cells and the posterior from four flame cells. The flame cell formula is

$2\ [(2 + 2 + 2) + (2 + 2)] = 20.$

The genital rudiment is represented by an irregular mass of cells lying almost covering the ventral sucker dorsally and extending behind it (Plate 16, fig. 3).

Stylet is javelin-shaped, with shoulders at about one third of its length from the anterior end and with no basal thickenings, (Plate 16, fig. 2).

The aspinose tail is simple and without finfolds. There is a pair of caudal pockets provided with several prominent spines. The caudal excretory duct is unbranched and is discernible up to two thirds of its length.

Measurements of Cercaria (In millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.216-0.333	0.295	0.223-0.266	0.200
Body breadth	0.100-0.150	0.125	0.100-0.116	0.102
Tail length	0.150-0.200	0.170	0.140-0.180	0.150
Tail breadth	0.026-0.046	0.031	0.023-0.026	0.025
Oral sucker	0.060-0.065x 0.050-0.073	0.062x 0.060	0.046-0.063x 0.050-0.063	0.056x 0.057
Prepharynx	0.013-0.016	0.015	0.008-0.016	0.012
Pharynx	0.020-0.023x 0.020-0.023	0.021x 0.021	0.016-0.020x 0.020-0.026	0.019x 0.022
Ventral sucker	0.040-0.043x 0.040-0.043	0.041x 0.041	0.036-0.040x 0.036-0.040	0.037x 0.038
Stylet length	0.027			
Breadth at shoulder	0.0053			
Breadth of shaft	0.0036			

Comparison with Related Species

Five species of cercariae with nine pairs of penetration gland cells and no finfold on the tail have been described.

C. glandulosa Faust, 1917 differs from the present cercaria in having a larger body and stylet. C. acanthocoela Miller, 1936 can be differentiated in having a larger stylet and in having thirty-six flame cells in the body. It also has been described as having six to nine penetration gland cells.

C. daymetra villicaeca Byrd, 1935 and C. tricystica Miller, 1936 both have a shorter stylet. C. d. villicaeca

can further be differentiated in having long intestinal caeca, a flame cell formula of 2 $[(3 + 3 + 3) + (3 + 3 + 3)] = 36$ while C. tricystica also differs in being smaller and in lacking spines in the caudal pockets.

In C. isocotylea Cort, 1915 the size of the stylet is not known; however, this cercaria differs from the present species in having larger number of flame cells and in having the two suckers of equal size.

The present cercaria is therefore regarded as new and the name Cercaria meadowensis is proposed for it.

Explanation to Plate 17

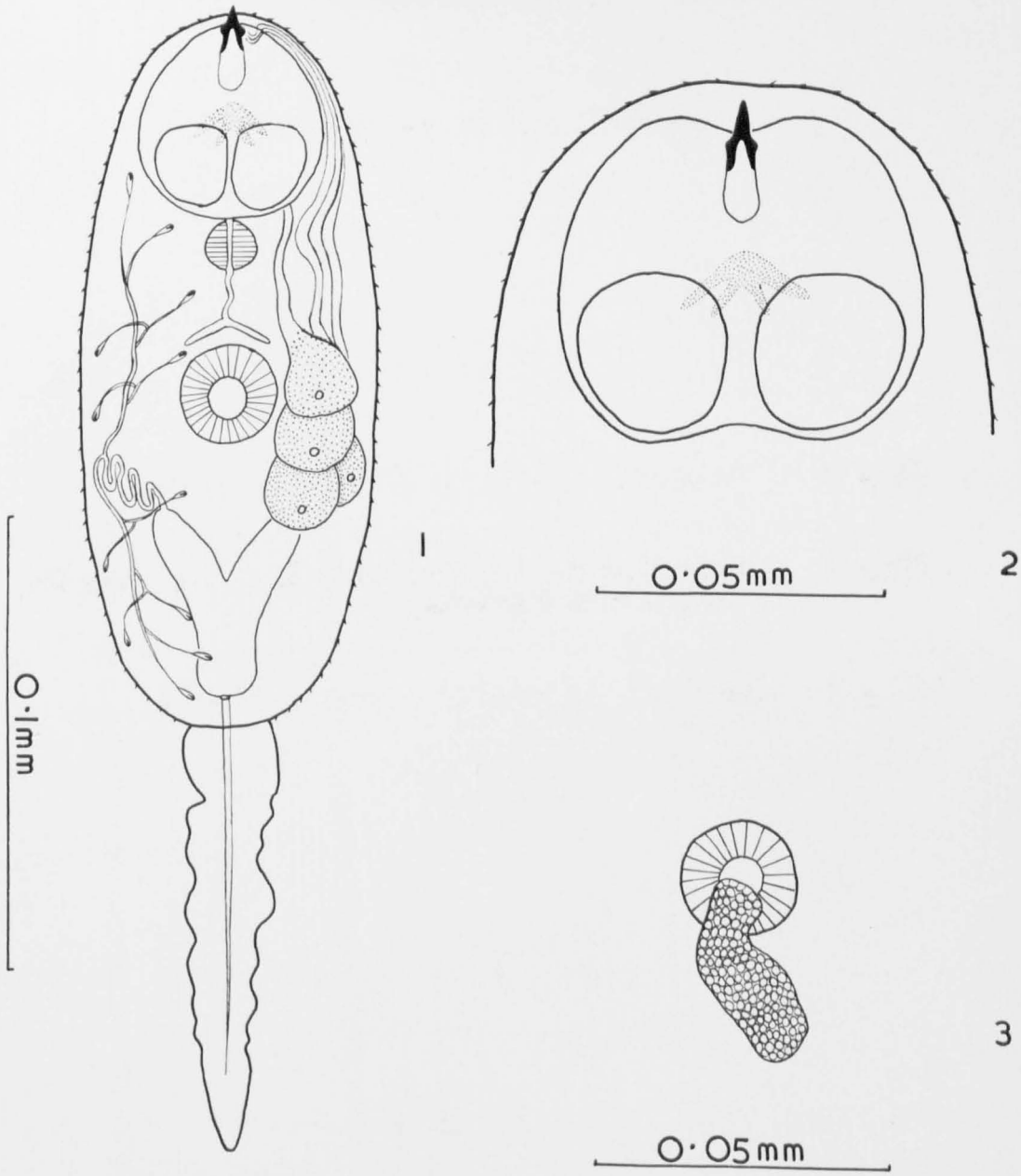
Cercaria tarda n. sp.

fig. 1 General structure of the cercaria.

fig. 2 Anterior end of the body showing virgula organ and stylet.

fig. 3 Genital primordium (dorsal view).

Plate I7



Cercariae Virgulae

19. Cercaria tarda n. sp. (Plate 17, figs. 1-3)

During June and August, 1959 about 300 specimens of B. tentaculata were collected from Bushy Park. Of these only two were found to be infected with a virgulate xiphidiocercaria.

Sporocyst

Short sac-like sporocysts are usually present in large numbers in the digestive gland. A very striking feature of most of these sporocysts is the presence of two cercariae in each, one of them immature and inactive and the other mature and constantly moving inside it. No birth pore was seen. The living sporocysts measured 0.180-0.370 mm. in length and 0.075-0.0135 mm. in maximum breadth.

Emergence and Behaviour

The cercariae are discharged in fairly large numbers during the night. They are very poor swimmers and have a weak tendency to concentrate near the top of the water, but a few cercariae may always be found at every depth of the water.

Cercaria (Plate 17, figs. 1-3)

The cercaria is small, with contractile body. Entire surface is covered with minute backwardly directed spines. At the anterior tip there is a stylet, which is moved usually in the dorso-ventral plan with the help of small muscles attached at the posterior end of it. The stylet has a fine anterior tip and a shoulder at about one third of its length from the anterior end. The walls of the stylet are reinforced up to slightly behind the shoulder. (Plate 17, fig. 2)

The body is filled with numerous cystogenous gland cells, with granular contents. There are also comparatively few oil globules, which are variable in size. The subterminal oral sucker is followed directly by a muscular pharynx and a short oesophagus, which bifurcates some distance in front of the ventral sucker, giving rise to two intestinal caeca, which extend back to the level of the ventral sucker. Inside the oral sucker, there is a virgula organ composed of two roughly triangular arms. There is an area of coarse granules just in front of the virgula organ. These granules take a deep stain with neutral red. Their exact nature could not be determined.

The ventral sucker is nearly in the middle of the body and is smaller than the oral.

There are four pairs of penetration gland cells, situated at the side of the ventral sucker. Three of

these are in one group, and one is separate. The penetration gland ducts are also divided into two groups.

The excretory system comprises a bicornuate excretory bladder, which opens to the exterior through a small excretory pore at the junction of the body and tail. When the cercaria is fully stretched the basal part of the excretory bladder becomes elongated with small cornua, but when contracted it becomes nearly rounded, with cornua longer than its base. The two lateral excretory ducts originate from the cornua aterminally and after forming a few coils each of them divides into anterior and posterior collecting tubules, at the side of the ventral sucker. Each collecting tubule receives three tributaries from six flame cells. The flame cell formula is $2\left[(2+2+2)+(2+2+2)\right]=24$.

The genital rudiment is represented by a broad, elongated mass of cells, the major part of which lies immediately behind the ventral sucker, while only a small anterior part overlies the posterior half of the ventral sucker (Plate 17, fig. 3)

The tail is highly contractile, and with very fine crenulations, particularly evident in stretched condition. These crenulations look very much like spines, but they disappear when the tail is contracted. The caudal excretory duct is unbranched.

Measurements of the Cercaria (In millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.166-0.250	0.188	0.146-0.166	0.156
Body breadth	0.070-0.123	0.108	0.056-0.076	0.064
Tail length Maximum Contracted	0.050			
Extended	0.116-0.206	0.155	0.086-0.100	0.090
Tail breadth	0.020-0.036	0.028	0.016-0.023	0.020
Oral sucker	0.043-0.053x 0.043-0.053	0.051x 0.049	0.040-0.043x 0.033-0.040	0.041x 0.035
Ventral sucker	0.023-0.026x 0.026-0.030	0.025x 0.028	0.020-0.026x 0.023-0.026	0.023x 0.024
Pharynx	0.013-0.016x 0.015-0.016	0.014x 0.016	0.013x0.016	0.013x 0.016
Arm of virgula organ	0.026x0.026		0.020x0.013	
Stylet length	0.020			
Stylet breadth at shoulder	0.005			
Stylet breadth at base	0.006			

Comparison with Related Species

Seven species have previously been described with four pairs of penetration gland cells and pyriform virgula organ.

C. helvetica VIII Dubois, 1929, C. helvetica IX Dubois, 1929 differ from the present species in their larger size, in having a longer stylet, different arrangement of the penetration gland ducts, and in having a V-shaped excretory bladder.

C. virgula Fil is also considerably larger and has a larger number of penetration gland cells and aterminal origin of the main excretory ducts. C. geddesi Cable, 1938, is smaller and also differs in having the basal part of the tail spined, in having a larger stylet, different arrangement of the penetration gland cells and in lacking an oesophagus or intestinal caeca.

C. kawa Fain, 1953, can be distinguished on the shape of the stylet, differentiation of the penetration glands in two groups of two each, arrangement of the penetration gland ducts and in having V-shaped excretory bladder.

C. cephalophallus obscurus Macy and Moore, 1954, has a larger stylet and also differs in having a tubular excretory bladder, in the position of the penetration gland cells and in the absence of a digestive tract.

C. nodulosa v. Linst. as described by Wesenberg-Lund (1934) is a larger species, with its ventral sucker nearly twice in size of that in the present cercaria. It can further be separated from the present species in being an active swimmer.

The present species is therefore regarded as new and named Cercaria tarda.

Furcocercous Cercariae

Lühe (1909) in his account of the "Furcocercous" cercariae, restricts the use of the term to the distome forms, with long bifid tails which develop in long motile sporocysts. He distinguished these cercariae from the "Mirabilis" sub-group of "Cystocercous" cercariae by adding to his definition that the body cannot be retracted into the basal part of the tail.

Lühe's account was based on nine species. A large number of widely different forms have since been described which are all placed in the "Furcocercous" cercariae, making it a very large assemblage of highly varied forms. The further sub-division of these cercariae has received the maximum attention of the workers and a number of schemes have been put forward.

Cort (1917) based his classification on the presence or absence of pharynx and eyespots and the comparative length of the furca.

Sewell (1922) was in agreement with Cort regarding the principles of the sub-division. He greatly extended and modified the classification put forward by Cort. In accordance with his scheme to separate the monostome forms completely from the distomes, Sewell placed the "Lophocercous" forms among his "Monostome" cercariae. Later workers however do not agree with Sewell and Miller (1926) included the "Lophocercous" forms among his "Apharyngeal Brevifurcate

Monostome" division of the "Furcocercous" cercariae. Sewell also agreed with Braun (1894) in regarding the "Mirabilis" cercariae as more highly evolved forms of "Furcocercous" cercariae and suggested that the similarity of the tail with the "Cystocercous" cercariae was a convergence.

Faust (1924) suggested another classification based solely on the flame cell pattern.

Miller (1926) showed that the so-called brevifurcate and longifurcate cercariae differ not only in the comparative size of the furca but also in other characters. His classification has generally been accepted by later workers as most adequate. This scheme has been adopted in this work and is outlined below:-

(a) Apharyngeal

1. "Apharyngeal Brevifurcate Distome" cercariae
(= Sewell's group I)

Group A. with flame cell formula 2 x 3 (+ 1)
(Spindale group of Sewell in part)

Group B. with flame cell formula 2 x 4 (+ 1) and five pairs of penetration gland cells.

Group C. with flame cell formula 2 x 5 (+ 1)
(douthitti group of Sewell in part)

All the above groups have 3-5 penetration gland cells on each side and differ in the complexity of the flame cell pattern.

Group D. These possess many characters of the

schistosome cercariae but differ in having pigmented eyespots, elongated bodies and furcal finfolds.
(= Elvae or Ocellata group)

Group E. (bombayensis No. 13) possessing a posterior mucin gland, large number of penetration gland cells differentiated into two groups.

Group F. (Wynaad) Similar to group E but differs in lacking the so-called posterior mucin glands, in the possession of a large number of small penetration gland cells differentiated in two sets and in lacking a head gland.

Group G. (elephantis) Five pairs of penetration gland cells, three small anterior and two large posterior, around the ventral sucker. Numerous posterior gland cells.

Group H. (gigas of Sewell, in part)
Five pairs of penetration gland cells in front of the ventral sucker and two pairs behind it, a large number of flame cells.

A key for the separation of these sub-groups of apharyngeal brevifurcate distomes has been given by Miller (1923).

2. Apharyngeal brevifurcate monostome cercariae. Lophocerca group of Sewell in part. Flame cell formula 2 x 3 (+ 0). Finfold on body and furca.

3. "Apharyngeal Longifurcate" cercariae

(a) Apharyngeal longifurcate distome cercariae.

(b) Apharyngeal longifurcate monostome cercariae.

Pharyngeal

1. "Pharyngeal Brevifurcate Distome" cercariae.

2. "Pharyngeal Brevifurcate Monostome" cercariae (no representative).

"Pharyngeal Longifurcate" cercariae

1. Distome forms

2. Monostome forms (these have been discussed in detail in the account of "Pharyngeal longifurcate monostome" cercariae in the present study)

(a) "Vivax" group of Sewell

(b) "Tetis" group of Sewell

(c) "Rhabdocaeca" group

Members of the "Apharyngeal Brevifurcate Monostome", "Apharyngeal Longifurcate Distome", "Pharyngeal Longifurcate Monostome" and "Pharyngeal Longifurcate Distome" groups have been encountered in the present study.

"Apharyngeal Brevifurcate Monostome" Cercariae

"Lophocercous" Group

The group "Lophocercous" cercariae was erected by Lühe (1909) for C. cristata La Val. 1855 and C. microcristata Ercol, 1881, both of which had a dorsal finfold on the body. He regarded this as a completely separate group of cercariae. Sewell (1922), in accordance with his scheme to divide all the cercariae into two categories on the sole basis of presence or absence of a ventral sucker, placed the "Lophocercous" cercariae among his "Monostome" Cercariae and described four species from India. This view, as already discussed in the account of "Monostome cercariae", was not accepted by later workers. However, Sewell gave a detailed definition of this group. His "Lophocercous" group includes cercariae with:

(1) Very small bodies (less than 0.2 mm.), proportionally long tail shaft (at least one and a half times the body length), furca short. Both body and furca are provided with finfold.

(2) The centre of body occupied by a group of salivary glands (penetration glands).

(3) Ventral sucker absent; anterior organ a protrusible snout.

(4) There is no trace of a pharynx or intestine.

(5) Three pairs of flame cells in the body but no flame cells in the tail.

(6) Develop in small, oval or rounded sporocysts.

Miller (1926) included these forms among his "Apharyngeal Brevifurcate Monostome" division of Furcocercariae.

Odhner (1911d) suggested that C. cristata would develop into a species of Sanguinicola Plehn. Works of Scheuring (1923) and Ejsmont (1926) have proved this to be true. The last two authors added three more species to the "Lophocercous" cercariae. Dubois (1929) treated them as a sub-group, the "Lophocerca", among "Furcocercariae" and added another species, C. helvetica XVI. Porter (1938) has described two species from Africa. More recently Johnston and Beckwith (1947) and Fain (1953) have added one species each from Australia and Belgian Congo respectively.

According to Dawes (1946) these cercariae are confined to the Old World. Some cercariae, such as C. spirorchis parvus Wall, 1941b, C. whitentoni Croft, 1933 and C. brevifurca McCoy, 1929, have been described from the United States. All these have a body finfold. Wall (1941a) also described another cercaria belonging to genus Spirorchis - C. spirorchis elephantis - which is without a body finfold. It is clear that the presence of a dorsal body finfold alone is not sufficient to justify a natural group, but none of these American forms as well as C. bamboyensis No. 8 Soparker, 1921 and C. clinostomum marginatum as described by Krull (1934) would be included in the group if Sewell's definition is adopted. This would leave in the group "Lophocercous" cercariae, which

Explanation to Plate 18

Cercaria kentensis n. sp.

fig. 1 General structure of the cercaria.

fig. 2 Resting posture of the cercaria.

Cercaria cristocorpa n. sp.

fig. 3 General structure of the cercaria.

fig. 4 Resting posture of the cercaria.

Plate I8

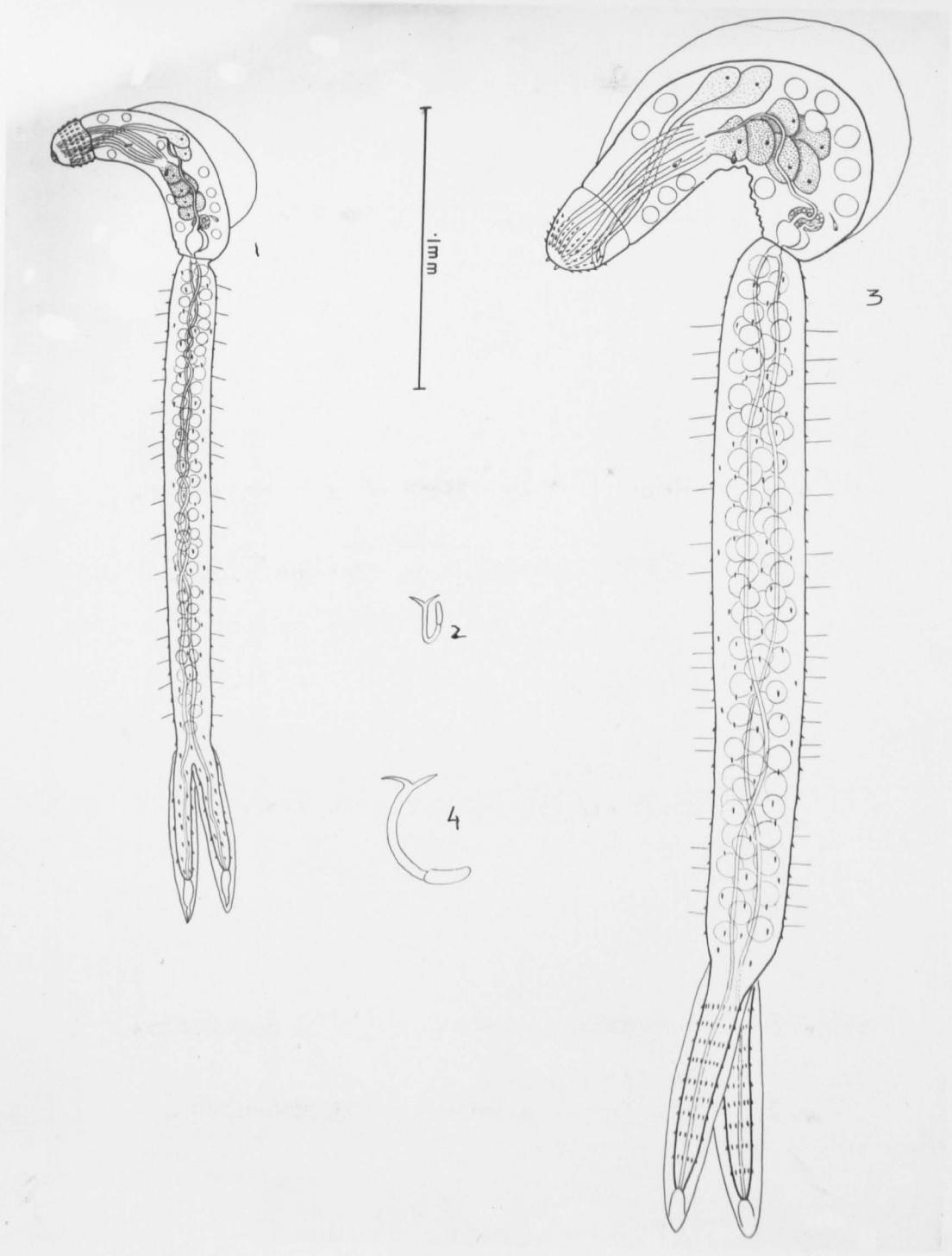


exhibit a remarkable similarity in morphology; and wherever the life cycle has been worked out, they have been shown to penetrate directly into cyprinoid fishes and develop into species of Sanguinicola, in the blood vascular system.

So far, no species of this group has been reported from Britain.

1. C. kentensis n. sp. (Plate 18, figs. 1 and 2)

From Keston Common (Kent) on 30th April, 1959, twenty L. pereger were collected and ten of them were found to be emitting this cercaria. All of the infected snails were small sized and young. An equally high percentage of infection was found among L. pereger collected on several occasions during May 1959 from Sand Pits near South Ockendon (Essex). This infection rate fell considerably in snails collected from either of above places during June (20 per cent) and was rare in snails collected during July (2 per cent). No infected snail was found in August or later in the season. Always small sized snails were found to be infected with this cercaria.

Sporocyst

Infected snails which had been kept in the laboratory for four weeks stopped discharging the cercariae. These

contents, disintegrate and leave the host completely free of infection.

Complete living sporocysts measured 1.0 - 1.12 mm. long and 0.15 - 0.16 mm. broad.

Emergence and Behaviour

The cercariae are shed in the late afternoon and perhaps during the night or early morning also. They are emitted in very large numbers. After emergence they remain well distributed throughout the depth of the container and do not show any phototropism. After emergence they hang motionless in water and do not swim for a long time until disturbed. During the rest period the furca are wide open and the tail shaft bent to such an extent that the second part of the tail stem and the body comes to lie parallel to the first portion of the tail shaft, and the tip of the body touches the furca. In this position, in which furca are kept upwards, the portion of tail stem just behind the body is twisted into a right angle, so that the ventral side of the body comes to lie against the lateral side of the tail stem (Plate 18, fig. 2). This long resting period is followed by a very short period of swimming during which the cercaria darts for a short distance, tail foremost.

snails on dissection were found to be completely free of any sporocysts or developing cercariae in the digestive gland. On the other hand, some of the snails which were still emitting the cercariae, were found to have a large number of cercariae in various stages of development lying free in the tissue of digestive gland. The snails, which were collected very early in the season (early May) had very delicate, thin-walled, elongated sac-like sporocysts, which had numerous cercariae, in very early stage of development, in the digestive gland of the host. These sporocysts were so delicate that they would rupture with the slightest touch of a dissecting needle. They are firmly embedded in the host tissue and are very difficult to separate. The sporocysts do not have a birth pore. Inside, there are large number of cercariae which, as they increase in size, rupture the sporocysts and are liberated into the host tissue, still very immature, to complete their development in the host tissue before they are discharged.

Wesenberg-Lund (1934) described the sporocyst in a closely related form C. cristata, which had daughter sporocysts in it, this was presumably a mother sporocyst. From the above observation and the fact that no large sized snail was ever found to be infected with this parasite it is suggested that there is only one or very few generations of daughter sporocysts, which after having liberated their

Cercaria (Plate 18, fig. 1)

The body of the cercaria is very small and laterally compressed. There is a finfold on the mid-dorsal line. This finfold is reduced anteriorly as well as posteriorly, it starts some distance from the anterior organ and finishes a small distance in front of the junction of the body with the tail. The lateral compression and the finfold causes the cercaria to lie on its side under a cover glass. The anterior organ is modified to form a protrusible, telescopic snout, which is demarcated from the rest of the body. At the anterior tip there are two conical, perhaps hollow conical processes, which presumably aid in its penetration into the final host. Behind a small bare anterior part there are four circular rows of spines encircling the anterior half of the anterior organ. The rest of the body is without any spines. There is no ventral sucker. For several of the related cercariae previously described a simple rhabdocoele gut has been reported C. cristata, C. microcristata, C. sanguinicola inermis, C. species (B. leechi), C. species (L. stagnalis). In the present species I have not found any trace of a gut. There are several cells inside the body, with granular cytoplasm and nuclei, these have been suggested to be the penetration gland cells. Six of these occupy an area immediately behind the middle of the body and are more

prominent, with six ducts, the penetration gland ducts opening at the anterior end. Two glands, with clearer cytoplasm are seen on the antero-dorsal aspects of the six glands just mentioned, with their ducts opening on the ventral side of the anterior organ subterminally. There are some other cells present in the body but their nature or their ducts could not be ascertained.

The excretory bladder is two chambered, with a main excretory duct proceeding forwards from each of them. Three flame cells are present on each side of the body, but their connection with excretory ducts could not be made out. Posteriorly from each chamber of the excretory bladder one caudal excretory duct originates. These ducts proceed throughout the length of the tail shaft, intercoiling, at two or three places, but never joining each other. Each of these caudal excretory ducts passes into one of the furca and opens into its cup-like tip. There are no flame cells in the tail.

The genital primordium is represented by a single mass of deeply staining cells lying just in front of the excretory bladder.

The tail shaft is nearly twice the length of the body. There is a core of numerous rounded bodies extending throughout its length. The tail shaft has spines scattered all over its surface and several fine hair-like structures, of which fifteen were counted on each side. A well

developed series of oblique muscle fibres originate at the lateral margin and terminate at the centre of the tail shaft. Furca are short, laterally compressed, blade-like structures. They are provided with a dorsal and ventral finfold, each extending over the entire length of the furca and continuous over the tip. Like the tail shaft, the furca are also provided with spines, irregularly scattered over it, but there are no flagellets.

Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.110-0.130	0.124	0.083-0.100	0.093
Body depth	0.023-0.030	0.025	0.016-0.023	0.020
Tail shaft length	0.216-0.233	0.225	0.166-0.186	0.182
Tail shaft breadth	0.021-0.026	0.023	0.012-0.020	0.018
Furca length	0.086-0.100	0.090	0.060-0.066	0.063
Furca breadth	0.013-0.016	0.014	0.010-0.013	0.011
Anterior organ length	0.016-0.023	0.020	0.016-0.020	0.019
Maximum height of body finfold	0.018-0.02	0.019		

Comparison with Related Species

C. Indicae XIII Sewell, 1922; C. Indicae XXXIX Sewell, 1922; C. Indicae LV Sewell, 1922; C. ferrisia Porter, 1938

and C. indicanonoides Porter, 1938 can all readily be separated from the present species in their possession of eyespots, which are not present in the present species.

C. cristata La Val., 1855; C. microcristata Ercol. 1881, C. sanguinicola inermis Scheuring 1923; C. species from B. leechi Ejsmont, 1926 and C. species from L. stagnalis Ejsmont, 1926, all have their body finfolds extending over the full length of the body behind the anterior organ, and have a rhabdocoele gut. Both these characters separate these species from the cercaria under study, which has a reduced body finfold and no gut at all. C. sanguinicola inermis also differs in that its furcal finfolds extend over the terminal part of tail shaft.

In the reduction of the body finfold the present cercaria agrees with C. helvetica XVI Dubois, 1929; C. lophosoma Johnstone and Beckwith, 1947 and C. muda Fain, 1953. The last of these can readily be separated from the present species in its number of flame cells, in having an alimentary canal and single caudal excretory duct in the tail shaft. The description of C. helvetica XVI is very brief. There is no mention of flagellets on its tail shaft or of the presence of a gut in the body. However, this species can be separated from the present cercaria in the reduction of the finfold on the furca and a longer tail stem and much shorter furca, but a detailed comparison is not possible for want of further knowledge about Dubois's species.

C. lophosoma agrees very closely with the present species in size, except a slightly longer tail shaft in the former. These two species also agree in the complete absence of a gut, but C. lophosoma differs in lacking anterior conical processes and in having a single caudal excretory duct in the tail shaft. These two species develop in widely different snail hosts. C. lophosoma further differs from the present species in that it develops in nearly rounded sporocysts, while the latter develops in elongated sporocysts.

The present species is therefore regarded as new and the name Cercaria kentensis is proposed for it.

21. Cercaria cristocorpa n. sp. (Plate 18, figs. 3 and 4)

This cercaria was found only twice. Out of ten V. piscinalis collected from Bushy Park on 20th September, 1959 one was found to be discharging this cercaria. On the second occasion, an infected snail was collected on 30th September, 1960.

Sporocyst

Development takes place in small, oval or sub-circular sporocysts in the digestive gland of the host. The sporocysts are very delicate and measure 0.12 - 0.195 x 0.075 - 0.105 mm. The birth pore is absent.

Emergence and Behaviour

Unlike C. kentensis, this cercaria was never found to be discharged during the day; but whenever the snail was isolated in a tube and left overnight, a large number of cercariae were found to have been discharged during the night. As in C. kentensis, this cercaria hangs motionless in water for a long time if undisturbed, followed by a very short swimming period, in which it darts for a short distance, tail foremost. The resting posture of this cercaria is different from that of C. kentensis. The furca are kept up but only slightly open and the tail shaft is also only slightly bent, keeping the furca, tail shaft and body in a semi-circle and the body never touches the tail (Plate 18, fig. 4).

The cercariae are usually well distributed in the water, but they show a weak tendency to aggregate near the top level.

Cercaria (Plate 18, fig. 3)

When alive, the highly contractile body is held in the form of a semi-circle. There is dorsal finfold starting just behind the anterior organ and extending to the junction of body and tail. The protrusible snout-like anterior organ is clearly demarcated from the body by a transverse constriction. There is a pair of conical

projections, at the anterior tip of the anterior organ. After a bare circum-oral area five rows of prominent spines encircle the anterior half of the anterior organ. The rest of the body is without spines. There is a large number of cells with granular contents and nuclei, in the body. Their exact number could not be counted, but at least 8 glands have been seen. Of these, six form a posterior group, with their ducts opening at the tip of the anterior organ, while two pairs of glands occupy a position at the middle of the body and in front of it on the dorsal side. Each pair is connected with a duct, which runs obliquely in the body to open in the middle of the anterior organ on the ventral side.

There is no trace of an alimentary canal. The excretory system and reproductive primordium is similar to that described for C. kentensis.

The tail shaft is long, with numerous rounded cells forming its core, these cells are irregularly arranged. Spines on the tail shaft are comparatively more prominent but irregularly arranged. There are 18 long hair like structures, the flagellets, on each side of the tail shaft. Furca are laterally compressed, with a finfold extending the entire length and continuous over the tip. The spines on the furca are prominent and are arranged characteristically in nine parallel rows.

Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.166-0.200	0.172	0.123-0.146	0.136
Body depth	0.050-0.066	0.060	0.031-0.041	0.036
Tail shaft length	0.283-0.316	0.300	0.240-0.250	0.245
Tail shaft breadth	0.026-0.040	0.033	0.023-0.033	0.026
Furca length	0.123-0.140	0.130	0.086-0.096	0.091
Furca breadth	0.018-0.023	0.022	0.013-0.020	0.016
Anterior organ	0.023-0.036x 0.030-0.036	0.030x 0.033	0.026x 0.018-0.021	0.026x 0.020
Height of body membrane	0.020-0.023	0.022	0.010-0.020	0.015

Comparison with Related Species

This cercaria differs from C. kentensis in its larger size, the presence of an unreduced body finfold, the number of rows of spines on the anterior organ and their arrangement on furca, the shape and size of sporocyst and their posture during rest. They also develop in quite different hosts.

C. cristata as described by Wesenberg-Lund (1934); C. microcristata; C. helvetica XVI; C. sanguinicola inermis and C. lophosoma all are smaller than the present species. All of these, except C. lophosoma and C. helvetica XVI, also differ in having a gut, which is completely absent in the present species, and in the arrangement of spines

on the furca. C. sanguinicola inermis further differs in having its furcal finfold extending over the terminal part of tail shaft. C. lophosoma does not have anterior conical processes, which are present in the present species. It also differs in having a reduced body finfold, in the arrangement of spines on furca and in the single caudal excretory duct. C. helvetica XVI is very briefly described, but can further be differentiated from the present species by the reduction of its finfold on body and furca. C. cristata according to Lavalett's (1855) original measurements has a much larger tail shaft, but much shorter furca, while according to Ercolani's (1881) measurements it has much larger body, tail shaft and furca. According to Wesenberg-Lund's measurements it is smaller than the present species. However, it further differs from the present cercaria in developing in elongated sporocysts.

C. species from B. leechi has a smaller body but a longer tail shaft. It further differs in having a rhabdocoele gut which is absent in the present species. C. species from L. stagnalis has smaller body and furca but a longer tail shaft. It also differs from the present species in having a gut.

C. muda has a larger number of flame cells in body, a reduced body finfold, single caudal excretory duct, an alimentary canal, and a much larger number of anterior conical processes; all of these characters readily

differentiate it from the present species.

It is proposed to name the present species, which is new, as Cercaria cristocorpa.

Apharyngeal ~~Longifurcate~~ Brevifurcate Distome cercariae

"Ocellata" Group

(22) Cercaria pseudocellata Szidat and Wigand, 1934

Syn. C. ocellata Vogel, 1930

C. elvae Matheson, 1930

C. ocellata Taylor and Baylis, 1931

C. ocellata Rees, 1932

C. ocellata Wesenberg-Lund, 1934

This cercaria was found to be infecting L. stagnalis collected from Lake Meadows (Essex) and Sand Pits near South Ockendon (Essex) between March and July of 1959. The rate of infection at these two places was between 5 - 10 per cent. No infected snails were found after July, 1959 and at both places only large sized snails were found to be infected. The probable explanation for this may be that these snails were infected in the preceding year and that re-infection of young snails did not occur in 1959.

Sporocysts

The infected snails harboured a very large number of long threadlike sporocysts, which are inextricably intercoiled. The birth pore is terminal and the posterior end is usually swollen. One complete sporocyst was 7.125 mm. long with a maximum breadth of 0.165 mm. and a minimum breadth of 0.03 mm. Portions of some of the sporocysts were longer

than this complete sporocyst.

Cercaria

Apharyngeal, ~~longifurcate~~ Brevefurcate, distome, ocellate furcocercaria. Naturally emerged cercaria with five pairs of penetration gland cells, differentiated into two groups. The two pre-acetabular pairs with coarse cytoplasm and the three post-acetabular pairs with clear granular cytoplasm. Flame cell formula 2 (3 + 3 + (1)) = 14. The cercaria shows a strong positive phototropism and attaches to the side of the container with its ventral sucker, keeping the pre-acetabular portion of the body and the tail stretched outwards at right angle with the side on which the cercaria is attached. They do not show any tendency to aggregate near the surface of the water.

This cercaria is distinguished from C. ocellata La Val: (s. str.) in being larger, in that it does not have a tendency to aggregate near the surface of the water and in its mode of attachment to the side of the container.

Matheson (1930) reported this cercaria from Britain as C. elvae Miller, 1923. Taylor and Baylis, 1931 identified it as C. ocellata La Val. Rees (1932) also recorded it as C. ocellata La Val. Recently, Iles (1959) again recorded it from the same locality and identified it as C. pseudocellata Szidat, 1934 and suggested the following synonymy:

1. C. elvae Miller, 1926
2. C. elvae Matheson, 1930
3. C. ocellata Vogel, 1930
4. C. ocellata Taylor and Baylis, 1931
5. C. ocellata Rees, 1932

McMullen and Beaver (1945) suggested that C. elvae Miller (1923) was identical with C. ocellata but Iles (1959) has regarded it identical with C. pseudocellata.

The species described by Wesenberg-Lund (1934) as C. ocellata also has the same mode of attachment as C. pseudocellata and has not been described to have a tendency to aggregate near the surface of the water. The measurements are also very close to those described for C. pseudocellata; particularly in the case of fixed specimens, which are more reliable than those in the living forms. It is therefore suggested to be identical with C. pseudocellata.

Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.343-0.370	0.350	0.233-0.296	0.267
Body breadth	0.100-0.120	0.110	0.050-0.070	0.058
Tail shaft length	0.400-0.483	0.405	0.320-0.350	0.330
Tail shaft breadth	0.056-0.060	0.058	0.036-0.046	0.039
Furca length	0.316-0.346	0.335	0.210-0.236	0.230
Furca breadth	0.030-0.040	0.035	0.013-0.023	0.016
Anterior organ	0.096-0.116x 0.010-0.073	0.105x 0.071	0.083-0.086x 0.036-0.056	0.085x 0.044
Ventral sucker	0.033-0.040x 0.033-0.040	0.034x 0.034	0.026-0.030x 0.026-0.030	0.028x 0.028
Eyespots			0.008x0.006	
Distance between the eyes			0.040-0.050	0.045
Distance between eyes and the anterior end of the body			0.146-0.166	0.124

23. Cercaria bilharziellae polonicae Szidat, 1929

Syn. C. ocellata Ercol. 1881

P. corneus collected on two occasions (10th and 24th June, 1959) from Lake Meadows (Essex) were found to be discharging this cercaria. This cercaria was never found in any other pond, nor in Lake Meadows after June. Here again only the large sized snails were found to be infected. This might also be for the same reason as given in the case

Explanation to Plate 19

Cercaria kenilworthensis n. sp.

fig. 1 Complete cercaria.

fig. 2 General structure of the body of cercaria.

fig. 3 Resting posture.

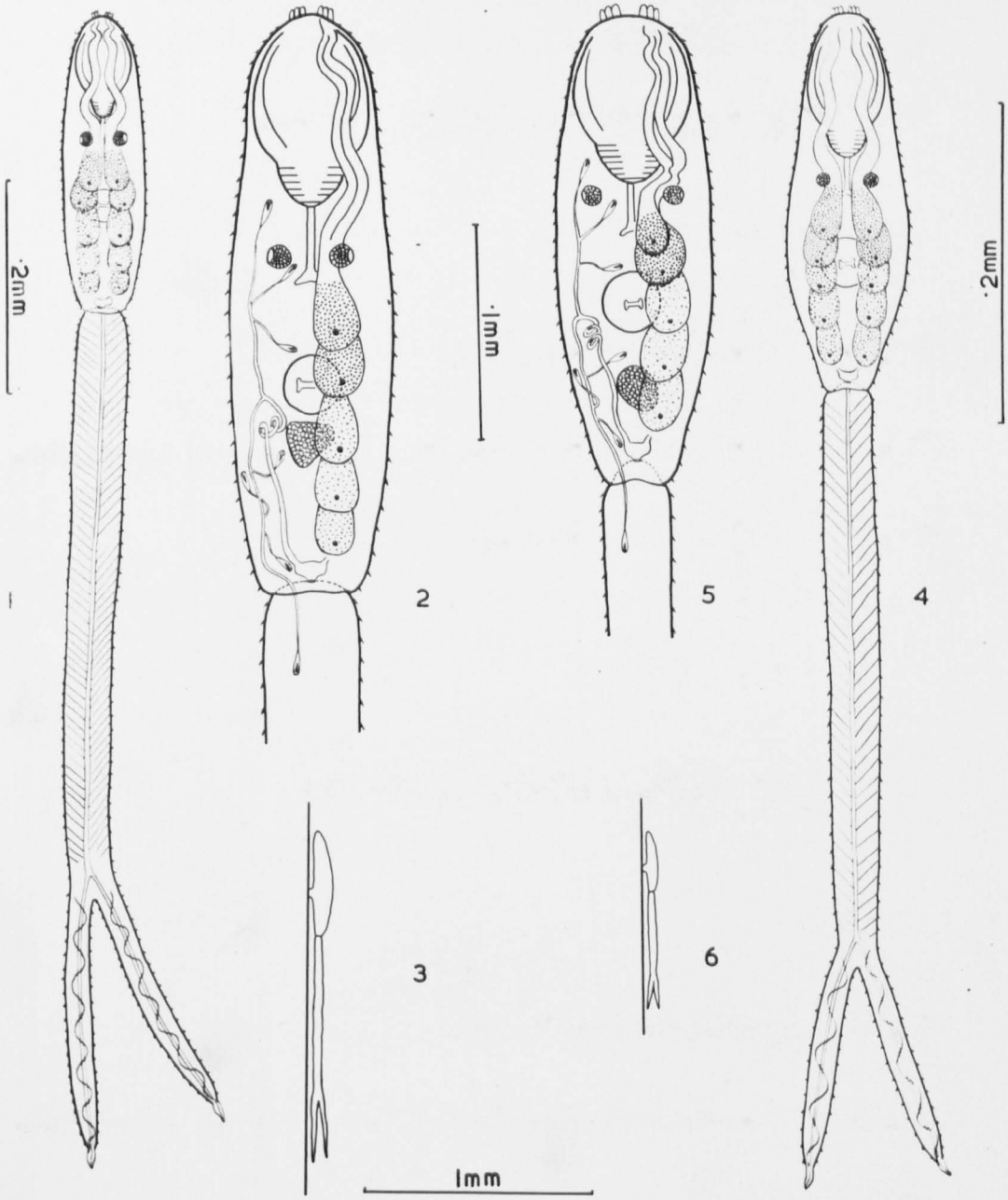
Cercaria edgwarensis n. sp.

fig. 4 Complete cercaria.

fig. 5 General structure of the body of cercaria.

fig. 6 Resting posture.

Plate I9



of C. pseudocellata.

This cercaria was first described by Szidat in 1929. Brumpt (1931), Wesenberg-Lund (1934) and Porter (1938) have recorded it from Germany, Denmark and South Africa respectively. Very recently, Iles (1959) has recorded it from Wales in Britain.

Apharyngeal, brevifurcous, distome furcocercaria of the ocellata type. The naturally emerged cercaria has five pairs of penetration gland cells, differentiated into two groups. Anterior two pairs with clear cytoplasm and the posterior three pairs with coarsely granular cytoplasm. Flame cell formula 2 [3 + 3 + (1)] = 14. Base of the tail expanded in the resting condition, with a cup-like depression. With a tendency to cling to the mucous film at the surface of the water.

My observations on the structure of this cercaria and the measurements quite agree with those given by Iles (1959) and therefore will not be repeated here.

24. Cercaria kenilworthensis n. sp. (Plate 19, figs. 1-3)

About 10 per cent of P. planorbis (Mull.) collected from a small pond in Stoneyfields Park, Kenilworth Estate (Edgware) during the last half of September and the first half of October, 1959, were found to be discharging this cercaria. The molluscan fauna of this pond comprises L. stagnalis, L. pereger, P. corneus and H. genkinsi,

apart from P. planorbis, but none of these species was ever found to be infected with this cercaria. This cercaria was never encountered from this pond during 1958, although this pond was under regular observation during that year.

Sporocysts

A comparatively small number of long, thread-like sporocysts was found in the digestive gland of the host. The fairly transparent sporocysts are very delicate and so intricately intercoiled that it was impossible to separate them, without breaking. They are constricted at several places along their length. Each constriction is followed by a bulbous portion, which accommodates one or two developing cercariae. Some of these cercariae, apparently fully developed, continue lashing their tails briskly.

The largest portion of a sporocyst was 1.1 mm. long, with a minimum breadth of 0.045 mm. and maximum breadth of 0.15 mm.

Emergence and Behaviour

The cercariae are discharged during the day in comparatively small numbers. They exhibit a positive phototropism but do not swim directly to the lighted side

of the container. During this resting period the cercaria gradually sinks, keeping its furca closed and uppermost, while the tail and the body is in a straight vertical line.

If undisturbed for some time after their emergence, practically all of the cercariae are found attached to the side of the container nearest to the light. They attach with their ventral suckers, and keep the body and the tail in a straight vertical line, very close to the side of the container. The furca in attached cercariae are kept closed but, contrary to the freely hanging cercaria, lowermost (Plate 19, fig. 3).

The cercariae also have a tendency to remain in the upper level of the water. The life of free swimming cercariae is up to seventy-two hours at room temperature.

Cercaria (Plate 19, fig. 1 and 2)

The elongated contractile body has two prominent darkly pigmented eyes, each with a lens on the outer side. The anterior organ is divided into a large glandular and a small muscular portion. There is a well developed head gland in the glandular part of the anterior organ. A narrow straight oesophagus proceeds backwards up to a short distance behind the eyespots, where it divides into two short caeca. The well developed ventral sucker is behind the middle of the body and is highly protrusible. Because of this protruded ventral sucker the cercaria always lies

on its lateral side under the coverglass on a slide. Four sets of muscles from the ventral sucker are attached to the dorsal body wall.

There are five pairs of penetration gland cells. The anterior two, with coarsely granular cytoplasm, are circum-acetabular and the posterior three, with clear cytoplasm are behind the ventral sucker. The penetration gland ducts are very prominent and open at the tip of the anterior organ. The openings of these ducts are highly reinforced and capped with prominent conical processes.

The excretory bladder is small and rectangular. The main excretory ducts are coiled at the level of the ventral sucker. These coils have ciliary patches in them. The anterior collecting duct receives capillaries from three flame cells and the posterior from four, three in the post-acetabular region of the body and one in the proximal part of the tail. The caudal excretory duct traverses the whole length of the furca and opens on its tip into a cup-like structure which is demarcated off the main part of the furca (Plate 19, fig. 2).

The genital rudiment is represented by a small mass of deeply staining cells, lying just behind the ventral sucker (Plate 19, fig. 2).

The tail shaft is longer than the body and has uncrenulated margins, with strongly developed oblique

muscles originating at lateral margins and terminating at the centre. The furca are narrow, blade-like, with a finfold extending on its whole length on the dorsal and the ventral sides and continuous over the tip. They are not markedly constricted off the tail shaft.

The body, tail shaft and the furca are uniformly spined.

Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.433-0.550	0.469	0.300-0.336	0.321
Body breadth	0.110-0.120	0.115	0.083-0.093	0.090
Tail shaft length	0.583-0.700	0.653	0.533-0.600	0.561
Tail shaft breadth	0.066-	0.066	0.053-0.063	0.057
Furca length	0.300-0.376	0.340	0.263-0.270	0.252
Furca breadth at base	0.031-0.043	0.041	0.030-0.033	0.031
Anterior organ length	0.086-0.133	0.117	0.100-0.116	0.107
Anterior organ breadth	0.070-0.080	0.075	0.053-0.063	0.055
Ventral sucker diameter	0.040-0.056	0.050	0.030-0.036	0.033
Diameter of eye	0.011-0.013	0.012	0.010-0.013	0.012
Distance between eyes			0.018-0.022	0.020
Distance between eyes and anterior end of body	0.150-0.156	0.160	0.113-0.133	0.123
Distance between centre of ventral scuker to posterior end of body			0.100-0.133	0.108

Comparison with Related Species

The present species differs from C. tuckerensis Miller, 1927; C. Indicae XLVII Sewell, 1922; C. bilharziella yokogawi Oiso, 1927; C. jaenschi Johnston and Cleland, 1937b; C. elongata Brackett, 1940; C. gigantobilharzia sturniae (Tanabe, 1948) Komiya and Ito, 1952; C. duboisi Fain, 1953 and C. turicensis Meyer and Dubois, 1954 in its flame cell formula and from C. shwetzi Fain, 1953; C. macrosoma Brown, 1926 in its number of penetration gland cells. It differs from C. variglandis Miller and Northup, 1926 and C. columbiensis Edwards and Jansch, 1955 both in the number of flame cells and penetration gland cells.

In having five pairs of penetration gland cells and a flame cell formula of 2 [3 + 3 + (1)] = 14, the present species resembles C. ocellata La Val. 1855 (= C. elvae Miller 1923 according to McMullen and Beaver (1945)); C. bilharziellae polonicae Szidat, 1929; C. echinomorpha Brown, 1931; C. parocellata Johnston and Simpson, 1939; C. pseudocellata Szidat and Wigand, 1934; C. parocellata Szidat, 1942; C. neocellata Szidat, 1942; C. longicauda McFarlane, 1944; C. oregonensis McFarlane and Macy, 1946; C. dermolestes McLeod, 1940; C. longicauda McFarlane, 1944; C. trichobilharzia adamsi Edwards and Jansch, 1955 and a marine form C. littorinallinae Penner, 1950.

The resting posture of C. herini Fain, 1955 is not known,

but it can be distinguished from the present species in having a much smaller tail shaft, in possession of an additional pair of flame cells in older cercariae and in having long hair-like structures on the body.

The present cercaria can readily be separated from all other species referred to above because of its larger size and the position of the body and tail, during its attachment to the illuminated side of the container.

It is concluded that the cercaria studied here is a new species for which the name Cercaria kenilworthensis is proposed.

25. Cercaria edgwarensis n. sp. (Plate 19, figs. 4-6)

About 12 per cent of P. planorbis collected from a small pond in Stoneyfields Park (Edgware) during September and October, 1959 were found to be discharging this cercaria. As in the case of C. kenilworthensis this cercaria was never recovered from any other species of snail from this pond, nor was it found during 1958.

Sporocyst

The digestive gland of the host was teeming with a large number of sporocysts. These are long, thread-like and very delicate with the same structure as described for C. kenilworthensis and similarly inextricably inter-coiled.

The cercaria while still enclosed in the sporocyst lashes its tail vigorously, with the result that portions of the sporocyst appear to be very motile, whereas it is actually inactive.

The largest portion of the sporocyst measured 1.8 mm. with a minimum thickness of 0.03 mm. and a maximum thickness of 0.13 mm.

Emergence and Behaviour

The cercariae are emitted during the day in large numbers. They show a strong phototropism and swim directly towards the light. The cercariae attach to the lighted side of the container in exactly the same manner as described for C. kenilworthensis (Plate 19, fig. 6). On reversing the sides of the container or stirring the water, the cercariae detach themselves, swim to the lighted side of the container and attach again. These cercariae also exhibit a tendency to aggregate near the surface of the water.

Cercaria (Plate 19, fig. 4 and 5)

The body is highly contractile and uniformly spined all over. There are two prominent darkly pigmented eyespots, with lenses on the outer sides. The anterior organ is well developed with an anterior glandular and a

posterior muscular portion. A well developed head gland is present. The gut is narrow and thin walled and terminates in two short rami slightly behind the eyespots. There is no trace of a pharynx.

The ventral sucker which is behind the middle of the body, unlike C. kenilworthensis and several other members of the group, is only very slightly protrusible and it is always possible to have the cercaria lying dorso-ventrally under the cover glass on a slide.

There are five pairs of penetration gland cells in naturally emerged cercariae. The first of each series is the smallest and partially enveloped by the second. First two of these glands are with coarsely granular cytoplasm and basophilic in reaction while the posterior three have clear cytoplasm and are acidophilic in nature. The penetration gland ducts have a slightly convoluted course and open at the anterior end. The openings of these ducts are very heavily reinforced, forming prominent cap-like projections at the anterior end.

The excretory system (Plate 19, fig. 5) is similar to that described for C. kenilworthensis.

The genital rudiment is represented by a small mass of deeply staining cells, lying between the ventral sucker and the posterior end of the body (Plate 19, fig. 5).

The tail shaft is longer than the body, with uncrenulated

margin. Several oblique muscles originate at the lateral margins and terminate near the centre of the tail. The furca are shorter than the body and are provided with a narrow finfold extending on its entire dorsal and ventral side and continuous over the tip.

Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.250-0.290	0.270	0.240-0.276	0.261
Body breadth	0.100-0.110	0.109	0.083-0.100	0.090
Tail shaft length	0.300-0.360	0.342	0.316-0.366	0.342
Tail shaft breadth	0.030-0.040	0.038	0.03 -0.04	0.036
Furca length	0.133-0.196	0.165	0.100-0.156	0.131
Furca breadth at base	0.016-0.020	0.017	0.013-0.02	0.016
Anterior organ	0.086-0.093x 0.060-0.066	0.090x 0.064	0.076-0.09x 0.046-0.053	0.085x 0.050
Ventral sucker	0.030-0.033x 0.030-0.033	0.031x 0.032	0.023-0.030x 0.030-0.036	0.026x 0.032
Distance between the eyes	0.033-0.04	0.037	0.020-0.026	0.023
Distance between eyes and anterior end	0.106-0.113	0.108	0.09 -0.106	0.099
Diameter of eye			0.009-0.01	0.010
Distance between centre of ventral sucker and posterior end of body			0.07- 0.09	0.088

Comparison with Related Species

C. tuckerensis Miller, 1927; C. Indicae XLVII Sewell, 1922; C. bilharziella yokogawai Oiso, 1927; C. jaenschi Johnston and Cleland, 1937; C. elongata Brackett, 1940; C.J. sturniae (Tanabe, 1948) Komiya and Ito, 1952 and C. duboisi Fain, 1953 and C. turicensis Meyer and Dubois, 1954 all have a flame cell pattern different from 2 [3 + 3 + (1)] = 14. C. schwetzi, Fain 1953 has been described with only four pairs of penetration gland cells and C. macrosoma Brown, 1926 with only two pairs. The present species with five pairs of penetration gland cells and a flame cell formula of 2 [3+3 + (1)] = 14 can readily be separated from all the species mentioned above, and from C. variglandis Miller and Northup, 1926 and C. columbiae Edwards and Jansch, 1955 which have different number of flame cells and penetration gland cells.

C. ocellata La Val. 1855 [= C. elvae Miller, 1923 according to McMullen and Beaver (1945)]; C. pseudocellata Szidat and Wigand, 1934; C. parocellata Szidat, 1942; C. longicauda McFarlane, 1944 and C. oregonensis McFarlane and Macy, 1946, are all larger than the present cercaria and also differ in the position of the body and tail during attachment. The cercaria under study has a shorter body and tail stem and much shorter furca than C. parocellata Johnston and Simpson, 1939 and C. neocellata Szidat, 1942 and differ also in the way of attachment.

C. t. adamsi Edwards and Jansch, 1955 has a smaller

body but a larger furca and a different posture during rest.

C. stagnicolae Talbot, 1936, with six pairs of penetration gland cells; C. dermolestes McLeod, 1940 and C. elongata Brackett, 1940 do not attach to the surface, but hang motionless near the illuminated side of the container. C. physallae Talbot, 1936 also with six pairs of penetration gland cells on the contrary attaches itself near the bottom of the container with its pre-acetabular region of the body and tail projecting upwards. The present species attaches to the side of the container, keeping its body and tail parallel to the side on which it is attached.

The present species also differs from C. bilharziellae polonicae Szidat, 1929 in having a larger body and tail shaft and much larger furca and from C. gyrauli Brackett, 1940 in having larger body and tail shaft but shorter furca. It also differs from the latter two species and a marine form C. littorinallinae Penner, 1950 in that it does not cling to the surface of the water.

C. echinomorpha Brown, 1931 is quite close to the present species in measurements, although the body and furca are slightly shorter and the tail shaft slightly longer in the former. The present cercaria differs from C. echinomorpha in that the oesophagus does not reach the ventral sucker; the penetration glands are differentiated into two groups; it does not float passively on the surface

and when attached to the side it does not continue lashing its tail. In its posture during attachment it agrees with C. kenilworthensis (present study) but is much smaller in size.

C. herini Fain, 1955 is much larger and has a different flame cell pattern in older cercariae and long hair-like structures which are absent in the present species.

It is therefore concluded that the present species is new and the name C. edgwarensis is proposed for it.

Pharyngeal Longifurcate Monostome Cercariae

("Vivax" Group)

Sewell (1922) placed the "Vivax" (s.l.) type of cercariae in his group 3 of the Furcocercous cercariae and divided them in two, the "Vivax" and "Tetis" sub-groups, on the basis of presence or absence of a furcal finfold and rudimentary ventral sucker in combination with the number of flame cells in the body and tail. Faust (1922) added the "Leptoderma" sub-group for brevifurcate forms with no furcal finfold and thirty flame cells in the body and tail. Szidat (1933) added a fourth, the "Vivipara" sub-group for cercariae with no furcal finfold, twenty-four to thirty flame cells in the body with usually six flame cells in the tail. He also considered C. tauiana Faust, 1930, as strange to all the previous groups and instituted yet another, the "Tauiana" sub-group, for it.

Cable (1938) included the "Leptoderma" and "Vivipara" sub-groups in the "Vivax" (s. str.) sub-group. Later Anderson (1944) and Maxon and Pequegnet (1949) and Anderson and Cable (1950) described forms which overlapped both the "Vivax" (s. str.) and "Tetis" sub-groups and suggested that they should also be united with the "Vivax" sub-group. Anderson (1944) also suggested that the "Tauiana" sub-group would also be shown to be inseparable from the "Vivax" (s. str.) sub-group. Goodman (1951), however,

expressed the opinion that these sub-groups be retained until more knowledge is gained about their life-histories, and the members of different sub-groups are shown to develop into species of one genus. He also pointed out that a rudimentary ventral sucker may be present or absent in members of any group.

In having furcal finfolds, penetration gland cells and in lacking a rudimentary ventral sucker and flame cells in the tail, C. ariformis (present study) overlaps both the "Vivax" and "Tauiana" sub-groups, thus providing evidence in support of Anderson's (1944) view that even the separation of the "Vivax" and "Tauiana" sub-groups is unnatural. While C. bushiensis, which has all the characters of the "Tetis" sub-group, is shown to possess a rudimentary ventral sucker and an additional pair of flame cells in the body, but develops into a species of the genus Cyathocotyle Mühling.

A better knowledge of the life history of these cercariae, as suggested by Goodman (1951), would be of no use in confirming a classification which fails to embrace successfully all the larval forms of this type. In the presence of these forms which overlap different proposed sub-groups, it seems only plausible to infer that the sub-division as proposed by Sewell (1922), Faust (1922) and Szidat (1933) is unnatural, and that all these sub-groups should remain in one group.

Explanation to Plate 20

Cercaria bushiensis n. sp.

fig. 1 Complete cercaria.

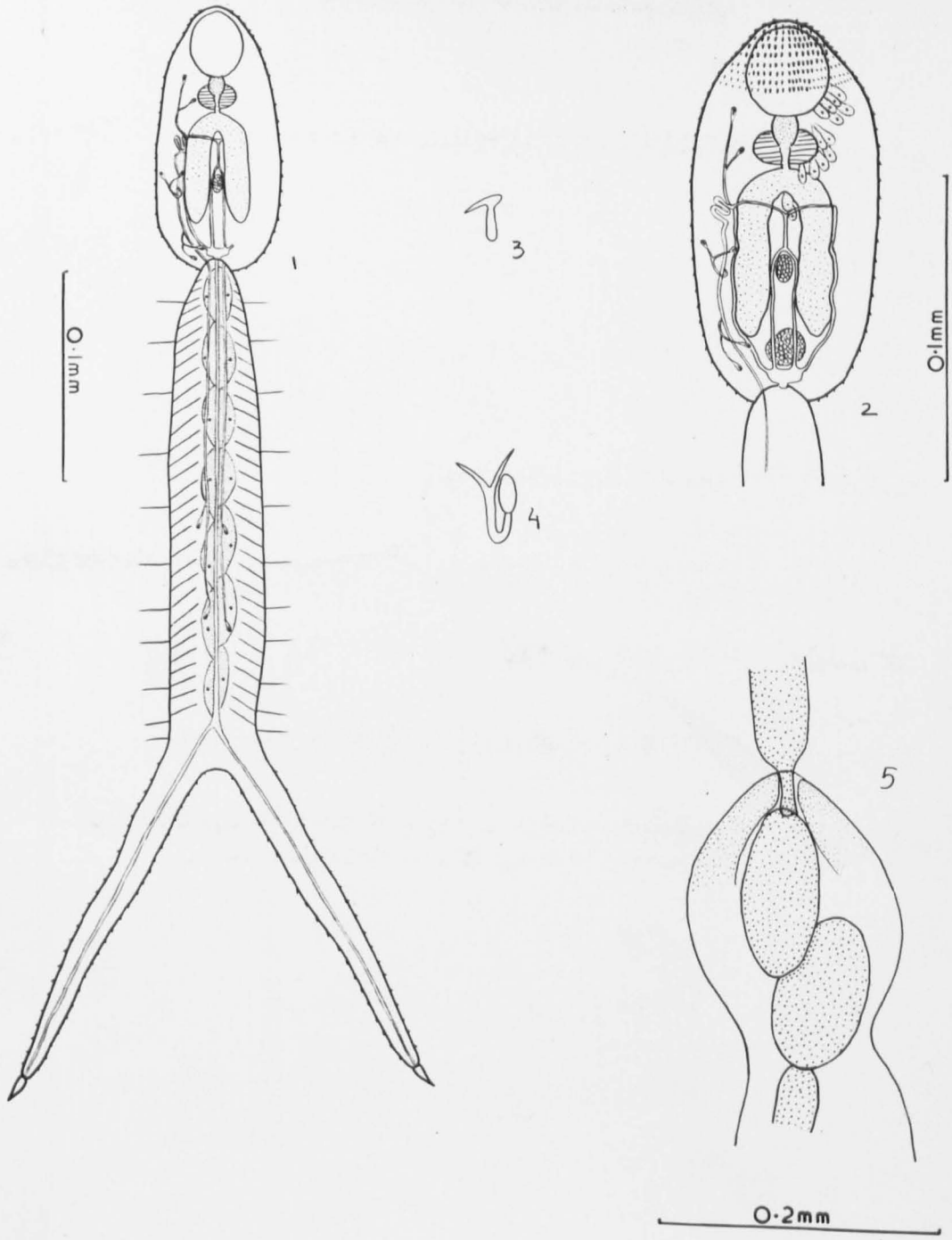
fig. 2 General structure of the body of cercaria.

fig. 3 Single spine.

fig. 4 Resting posture of the cercaria.

fig. 5 Anterior end of the sporocyst, with a cercaria emerging out of it.

Plate 20



26. Cercaria bushiensis n. sp. (Plate 20, figs. 1-5)

About 1-4 per cent of B. tentaculata collected from Bushy Park were found to be infected with this cercaria, during June to September, 1958 and 1959. This was once found as a double infection with a xiphidiocercous cercaria.

Sporocyst (Plate 20, fig. 5)

The digestive gland of the host was teeming with a large number of sporocysts. They are loosely packed and are quite easy to separate. The elongated, colourless sporocysts are very active with a protrusible anterior end, and harbour eight to twelve fully developed cercariae and a large number of immature forms. The posterior end is rounded and the anterior, when protruded, narrowed and pointed. The birth pore is terminal. Living specimens measured 1.72-3.82 mm. in length and 0.13-0.25 mm. in breadth.

Emergence and Behaviour

The cercariae are usually shed during the day, but may also be shed during the night or early morning. They are emitted in large numbers. They have a tendency to aggregate near the bottom of the container, if left undisturbed for some time. During the resting period the furca are kept open and the tail shaft bent in the

middle, so that the body and proximal half of the tail shaft come to lie opposite the distal half of the tail shaft and one of the furca (Plate 20, fig. 4). They sink swiftly downwards during the resting period, but some cercariae are always seen to be going up instead of down, while at rest.

Cercaria (Plate 20, figs. 1-4)

The body is highly contractile and covered all over with small backwardly directed spines. It is oval when stretched and circular when contracted. The pick-axe shaped spines (Plate 20, fig. 3), which cover the anterior half of the anterior organ, are more prominent than the rest. There are no penetration spines or a circum-oral spineless area. A well-developed anterior organ is followed by a small but comparatively wide prepharynx, which in the contracted specimens assumes a position on the dorsal aspect of the anterior half of the pharynx. The pharynx is muscular and followed by a short oesophagus, which divides into two prominent, wide caeca extending to a short distance in front of the excretory bladder. The intestinal caeca have only a few poorly-developed undulations on the margin, which is otherwise smooth.

The penetration gland cells are in three groups, behind the anterior organ, lateral to the pharynx and between the intestinal caeca. The exact number of these

cells could not be counted because of their poor differentiation.

A rudimentary ventral sucker 0.010 x 0.008 mm. in size is situated at nearly the middle of the body. This organ is difficult to see in the living cercariae but can easily be seen in fixed and stained specimens.

There is a small rectangular excretory bladder at the posterior end of the body which opens dorsally through a small excretory pore. Two pairs of main excretory ducts leave the excretory bladder. The outer pair proceeds forwards, closely applied to the intestinal caeca, up to slightly behind the oesophageal bifurcation, where they are joined by a transverse excretory commissure. After this the main lateral excretory duct on each side forms a few convolutions and divides into an anterior and a posterior collecting tubule. The anterior collecting tubule receives capillaries from two flame cells and the posterior collecting tubule from three pairs, of which the last is located in the distal half of the tail shaft. The two median main excretory ducts continue forwards along the inner sides of the intestinal caeca up to nearly the middle of the body, where they join to form a common median excretory duct, which opens into the transverse excretory commissure. The flame cell formula may be expressed as $2\,[2 + 4 + (2)] = 16$. The branches of the caudal excretory duct open on the tip of the furca.

The genital rudiment is represented by a single mass

of cells lying just in front of the excretory bladder.

The tail shaft is two to three times as long as the body and has finely crenulated margins. There are about eleven long hair-like structures on each side, otherwise it is aspinose.

The furca are longer than the body and are without any finfold. They are not markedly constricted off the tail shaft. There are eight longitudinal rows of spines on each side, extending along the whole length. No long hair-like structures were seen on the furca. The oblique muscle fibres of the tail shaft are well developed and the caudal excretory duct is surrounded by seven pairs of nucleated cells.

Measurement of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.106-0.200	0.146	0.103-0.133	0.120
Body breadth	0.080-0.116	0.090	0.056-0.080	0.067
Tail shaft length	0.273-0.333	0.296	0.266-0.286	0.272
Tail shaft breadth	0.040-0.053	0.048	0.040-0.056	0.044
Furca length	0.210-0.250	0.224	0.166-0.183	0.176
Furca breadth	0.020-0.036	0.026	0.020-0.030	0.023
Anterior organ	0.030-0.040x 0.030-0.040	0.036x 0.034	0.030-0.040x 0.026-0.033	0.031x 0.026
Prepharynx			0.013	0.013
Pharynx	0.013-0.020x 0.016-0.020	0.015x 0.016	0.0131-0.016x 0.0133-0.020	0.013x 0.014
Oesophagus			0.010	0.010
Length of caeca			0.040-0.048	0.046
Distance of caeca from posterior end of body			0.020-0.025	0.023

Comparison with Related Species

C. Indicae XXXIII Sewell, 1922, C. theodoxa Porter, 1938, and C. schoutedeni Fain, 1953, can all be separated from the present cercaria in lacking a rudimentary ventral sucker and in having no penetration gland cells in the intercaecal space. C. Indicae XXXIII and C. theodoxa further differ from the present species in having a different flame cell formula. C. schoutedeni and C. theodoxa

have spined tail shafts, while in the present species the tail shaft is aspinose.

C. yankapiensis Goodman, 1951, differs in being larger than the present species, in lacking a rudimentary ventral sucker, and in its body spines being limited to the anterior organ. Furcocercaria No. 4 Petersen, as described by Wesenberg-Lund (1934), is bigger than the cercaria under study, and differs also in having papillae on the body, no spines on the body behind the anterior organ and in the point of caudal insertion on the body.

The measurements of the body of Cercaria sp. Wesenberg-Lund, 1934, are not known, but it has a tail shaft smaller and furca longer than the present species. It further differs in having its body spines only on the anterior organ area, in the larger number of flame cells connected with the posterior collecting tubule and in having no penetration gland cells in the intercaecal space.

C. curonensis Szidat, 1933, and C. balthica Szidat, 1933, both can be distinguished from the present cercaria in having their intestinal caeca extending to the excretory bladder, in lacking a rudimentary ventral sucker and in having only five pairs of flame cells in the body. The present species also differs from C. curonensis in having a smaller body but larger tail shaft and furca and in its tail being inserted almost at the posterior end of the body.

C. cyathocotyle gravieri Mathias, 1935, is very

Explanation to Plate 21

Cercaria papillosoma n. sp.

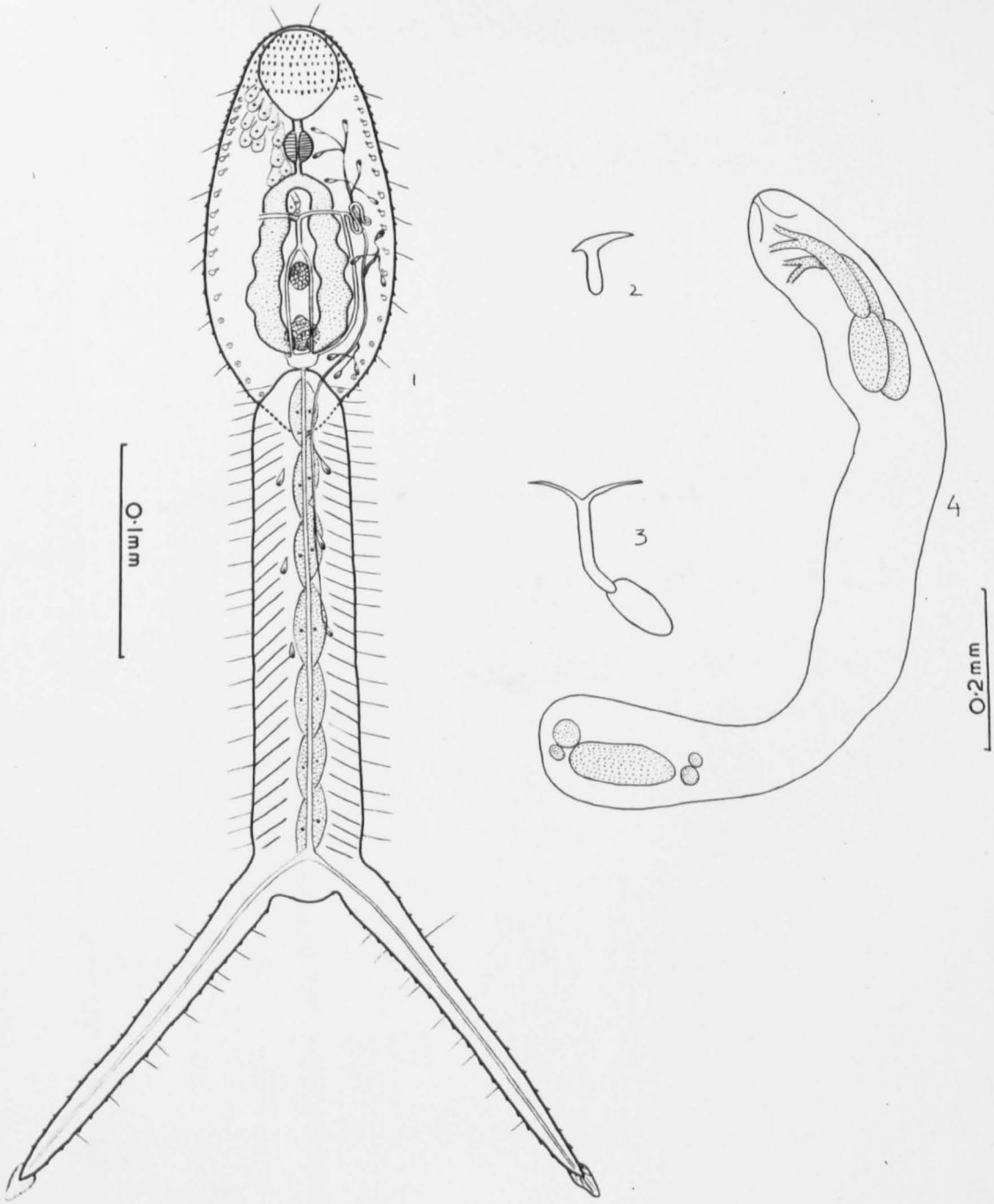
fig. 1 General structure of the cercaria.

fig. 2 Single spine.

fig. 3 Resting posture.

fig. 4 Sporocyst.

Plate 2I



poorly described and there is no figure to illustrate the account. However, the present cercaria can be distinguished from this cercaria in having a smaller body but longer tail shaft and furca, in the presence of a rudimentary ventral sucker and in the termination of the intestinal caeca at a distance from the posterior end of the body.

In view of the above comparison the present cercaria is regarded as new and the name Cercaria bushiensis is proposed for it.

This cercaria has been shown to develop into a species of Cyathocotyle. The life cycle is described in the second part of this thesis.

27. Cercaria papillosoma n. sp. (Plate 21, figs. 1-4)

One to five per cent B. tentaculata collected from Bushy Park were found to be infected with this cercaria. The highest rate of infection was found in September.

Sporocyst (Plate 21, fig. 4)

The sporocysts are simple sac-like structures in the digestive gland of the host. The anterior end is narrowish and the posterior end is rounded and broad. The birth pore is terminal. They are very easily separated from the host tissue. Each sporocyst has a few germ balls

and a maximum of eight cercariae. The living sporocysts measure 0.875-1.56 mm. long and 0.09-0.26 mm. broad.

Emergence and Behaviour

The cercariae are discharged during the day. They are not emitted in large swarms. They swim tail foremost and, during the resting period, the furca are kept wide open and the tail shaft only slightly bent so that there is always an obtuse angle between the distal half of the tail shaft and the proximal half of the tail shaft and the body (Plate 21, fig. 3).

The cercariae have a tendency to aggregate near the surface of the water. They do not exhibit any response to light.

Cercaria (Plate 21, figs. 1-3)

The thick body of the cercaria is provided with a yellow colour just under the body wall. It is oval when stretched and nearly rounded when contracted. Small spines cover the entire body, but about twelve rows covering the anterior half of the anterior organ are more prominent. These spines are pick-axe shaped with a long handle and pointed blades (Plate 21, fig. 2). There are no anterior penetration spines, nor is there a spineless circum-oral area. A pair of long hair-like structures or flagellets

are present at the anterior end and about eight pairs on the sides of the body. On the dorsal side of the body, apart from the spines and flagellets, there are numerous stumpy papillae, each with a short stalk and a swollen tip. When viewed from above these papillae appear as only rounded plates with a dark centre. They barely project outside the lateral margin of the body.

The large sub-terminal anterior organ is followed by a short thin-walled prepharynx and a well-developed nearly spherical pharynx. The oesophagus is very short and soon after its origin divides to form two wide, thin-walled caeca, with wavy margins and extending to the level of the excretory bladder.

The penetration glands are in three groups. Six pairs of glands are located at the postero-lateral margin of the anterior organ, four pairs on the sides of the pharynx and three pairs between the intestinal caeca just behind the oesophageal bifurcation. Their ducts open at the tip of the anterior organ. An oval, rudimentary ventral sucker, 0.011 x 0.008 mm. in size, is present nearly in the middle of the body.

There is a small rectangular excretory bladder in front of the caudal insertion, which opens on the dorsal side through small excretory pore. The basic pattern of the excretory ducts is the same as described for C. bushiensis (present study) but the anterior collecting

tubule receives capillaries from six flame cells arranged in two groups. The posterior collecting tubule drains capillaries from nine flame cells arranged in three groups, the last of which is situated in the tail shaft. The flame cell formula may be written as $2\ [(3 + 3) + (3 + 3) + (3)] = 30$.

The branches of the caudal excretory duct open at the tip of each furca.

The genital primordium is represented by a mass of deeply staining cells just in front of the excretory bladder.

The tail shaft is longer than the body and is inserted on the dorsal side, considerably in front of the posterior end of the body. It has slightly crenulated margins. There are no spines on the tail shaft but numerous long hair-like structures are present. Twenty-five to thirty-five of these have been seen on each side. The caudal excretory duct is surrounded by seven pairs of long nucleated cells. The oblique muscle fibres of the tail shaft are well developed.

The spined furca are nearly of the same size as the body. There is a small finfold limited to the tip of each of the furca.

Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.256-0.316	0.272	0.193-0.22	0.200
Body breadth	0.100-0.166	0.130	0.090-0.093	0.092
Tail shaft length	0.333-0.433	0.370	0.303-0.306	0.305
Tail shaft breadth	0.046-0.053	0.049	0.043-0.050	0.046
Furca length	0.250-0.310	0.272	0.200-0.216	0.209
Furca breadth	0.020-0.033	0.029	0.013-0.020	0.017
Anterior organ	0.063-0.073x 0.050-0.056	0.066x 0.054	0.043-0.046x 0.033-0.036	0.044x 0.038
Prepharynx length			0.006-0.010	0.008
Pharynx	0.016-0.020x 0.018-0.023	0.018x 0.020	0.016x0.016	0.016x 0.016
Oesophagus length			0.006-0.013	0.009
Caeca length			0.083-0.113	0.100

Comparison with Related Species

Among the cercariae of the "Vivax" (s. lat.) type, C. vivax Sonsino, 1894, C. vivax Sonsino, 1892 (= C. prohemistomum vivax Azim, 1933), C. Indicae XVIII Sewell, 1922, C. dorsocauda Tubangui, 1928, C. vivax Wesenberg-Lund, 1934; C. kentuckiensis Cable, 1935, C. tatei Johnston and Angel, 1940, C. prostephanus industrius Tang, 1941, C. kesenyi Fain, 1953, and C. vivacis Iles, 1959, have been described as possessing a finfold on the furca.

In having the finfolds limited to the tip of the furca,

Explanation to Plate 22

Cercaria ariformis n. sp.

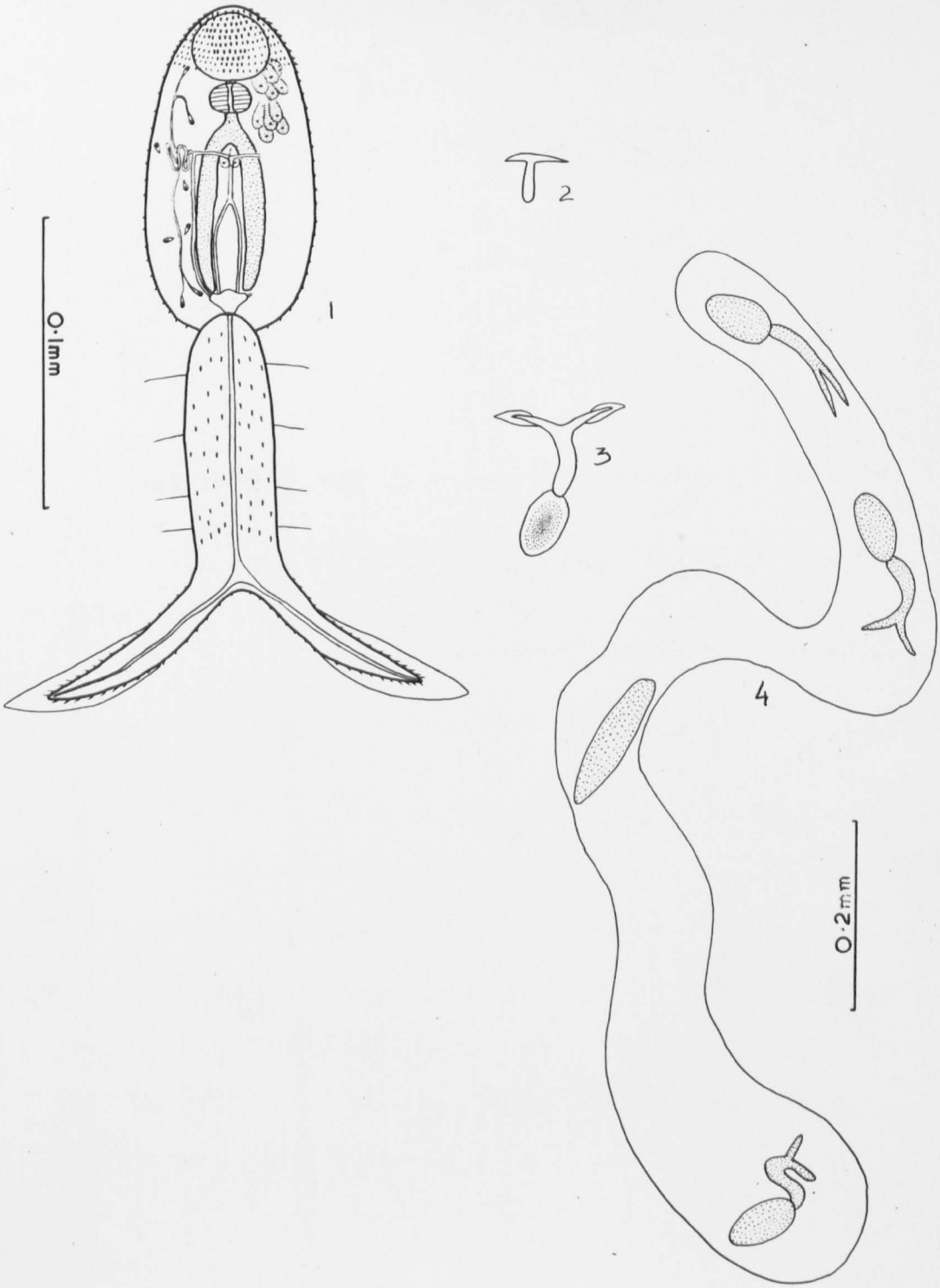
fig. 1 General structure of the cercaria.

fig. 2 Single spine.

fig. 3 Resting posture.

fig. 4 Sporocyst.

Plate 22



the present species can readily be separated from all the above species, except C. p. industrius. C. p. industrius is larger, has no papillae on the body and possesses fifteen pairs of flame cells in the body as against twelve in the present species.

In view of the above comparison, the present species is regarded as new and the name Cercaria papillosoma is proposed for it.

28. Cercaria ariformis n. sp. (Plate 22, figs. 1-4)

Only two per cent B. tentaculata collected from Bushy Park during June to September were found to be discharging this cercaria.

Sporocyst (Plate 22, fig. 4)

A large number of long, thread-like sporocysts are present in the digestive gland of the host. The sporocysts are active and each bears two to twelve developing cercariae inside. Usually the sporocysts are slender with uniform thickness and both ends rounded, but a fairly large proportion is distorted and constricted at several places. Such distorted sporocysts harbour a smaller number of cercariae (1-6). The living sporocysts range between 1.3 to 2.7 mm. in length and 0.165 to 0.225 mm. in their maximum breadth.

Emergence and Behaviour

The cercariae are shed in small numbers during the day. They confine themselves near the bottom of the container, where a short swimming period is followed by a long resting period. During the swimming period the cercariae move upwards for a short distance keeping their tails foremost. In the resting condition, the furca are kept open; the tail shaft is only very slightly curved or may remain straight and the body is kept in line with the tail shaft (Plate 22, fig. 3).

Cercaria (Plate 22, figs. 1-3)

The highly contractile body is longer than the tail shaft and the furca. There is a wide spoon-shaped concavity on the ventral side of the body, while the dorsal side is convex. The whole body except the ventral concavity is spined. The pick-axe shaped spines (Plate 22, fig. 2) lining the anterior end are more prominent than the rest, but there are no anteriorly pointed penetration spines.

The anterior organ is protrusible followed almost directly by a muscular pharynx. The oesophagus is short and the intestinal caeca reach the excretory bladder. The walls of the intestinal caeca, which become narrowed posteriorly, are smooth.

There is a large number of poorly differentiated penetration gland cells arranged behind the anterior organ, postero-lateral to the pharynx and few cells in the inter-caecal space. The exact number of these glands could not be counted.

The excretory bladder is small and tripartite. Two median excretory ducts originate at the anterior end of the bladder and extend nearly to the middle of the body, where they join to form a common median excretory duct. The lateral excretory ducts extend to near the oesophageal bifurcation where they are joined by a transverse commissure connecting the common median duct and the two lateral ducts. Just behind the level of the oesophageal bifurcation there are profound convolutions in the lateral excretory duct. Eight flame cells were seen on each side of the body. No flame cells are present in the tail. The furcal excretory ducts open at the tips of the furca.

The genital primordium is represented by a large rhomboidal mass of cells lying just in front of the excretory bladder.

There is no trace of a ventral sucker.

The tail shaft has slightly crenulated margins. There are several oblique rows of spines on the tail shaft and four pairs of long hair-like structures. The oblique muscles of the tail shaft are well developed. The furca are provided with a well-developed finfold on the distal

half, and prominent long spines on its entire length. The caudal excretory duct is not surrounded by cells.

Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.093-0.200	0.151	0.083-0.143	0.116
Body breadth	0.090-0.123	0.102	0.056-0.070	0.060
Tail length	0.110-0.123	0.114	0.093-0.116	0.100
Tail shaft length	0.023-0.035	0.035	0.026-0.033	0.029
Furca length	0.120-0.136	0.126	0.076-0.090	0.081
Furca breadth	0.016-0.020	0.020	0.010-0.013	0.012
Anterior organ	0.026-0.033x 0.036-0.040	0.031x 0.039	0.020-0.026x 0.020-0.026	0.023x 0.023
Pharynx	0.016x0.020	0.016x 0.020	0.011-0.013x 0.0133-0.016	0.012x 0.015

Comparison with Related Species

The present species differs from all previously described species, with furcal finfolds, in lacking flame cells in the tail. It further differs from C. vivax Sonsino, 1892 (= C. prohemistomum vivax Azim, 1933), C. Indicae XVIII Sewell, 1922, C. dorsocauda Tubangui, 1928, C. tatei Johnston and Angel, 1940, and C. prohemistomum expiditum Balozet, 1953, in its smaller size and in the finfolds being present on the distal half of the furca only.

C. vivax described by Wesenberg-Lund (1934) differs

from the present cercaria in having finfolds on the entire length of the furca, in having a rudimentary ventral sucker and in lacking spines from the body behind the anterior organ and the tail shaft.

C. Indicae XV Sewell, 1922, can also be separated on its aspinose nature of the body and tail shaft, the presence of concretions in the main excretory canals and on the fact that miracidia also develop in the sporocysts of this species.

C. kentuckiensis Cable, 1935, as described by Cable (1938), can further be distinguished from the cercaria under study by the aspinose nature of its tail shaft, the presence of a rudimentary ventral sucker and an unusual type of excretory system. C. vivax Sonsino, 1894, (= C. szidati joyexi Joyex and Baer, 1941) also differs in having an excretory system of unusual type and in lacking spines on the tail shaft.

An un-named cercaria described by Maxon and Pequegnat (1949) can also be separated from the present cercaria in having finfolds on the entire length of the furca, in the presence of a double transverse excretory commissure, rudimentary ventral sucker and in the comparative lengths of the body, tail shaft and furca.

C. kesenyi Fain, 1953, has long hair-like structures on the body and furca, papillae on the body, only six flame cells in the body, two transverse excretory commissures

and different posture during the resting period.

C. vivacis Iles, 1959, resembles the present cercaria in measurements. Iles (1959) was unable to see any flame cells in the tail, but she has presumed that they are present. However, this cercaria differs from the present species in lacking spines and long hair-like structures from the tail shaft, in possessing anterior penetration spines and a rudimentary ventral sucker. This cercaria also has a different posture during the resting period.

The present cercaria is therefore regarded as new and the name Cercaria ariformis is proposed for it.

Pharyngeal Longifurcate Distome Cercariae

1. Cercaria letifera Fuhrman, 1916

This cercaria was encountered only once when one out of fifty L. pereger collected from Sand Pits (South Ockendon, Essex) was found to be infected with it.

Sporocyst

The snail died and disintegrated overnight before the sporocyst could be studied.

Emergence and Behaviour

The cercariae are shed throughout the day but a much larger number is discharged during the afternoon. They are found at all depths of water, but often more cercariae are found in the upper half of the container than in the lower half. During the resting period the furca are stretched outwards at right angles with the tail shaft and the body and tail shaft hang vertically downwards. During this resting period the cercariae sink gradually. In the short swimming period which follows the cercariae usually swim vertically upwards, tail foremost.

Cercaria

The body and furca are spined and the tail shaft

aspinose. There are two rows of anterior penetration spines with eight spines in each row. The bare circum-oral area is followed by four rows of more prominent spines. The ventral sucker has only one row of spines. The spines on the ventral sucker are hook-shaped. There are two pairs of long hair-like structures on the body, eight pairs on the tail shaft and three on each of the furca.

A comparatively small anterior organ is followed by a small prepharynx and muscular pharynx. The bifurcation of the oesophagus takes place between the pharynx and ventral sucker and the intestinal caeca terminate between the ventral sucker and the posterior end of the body. The caeca increase in diameter posteriorly and diverge outwards at the posterior end.

There are two pairs of penetration gland cells in front of the ventral sucker. The anterior pair is situated one behind the other and the posterior pair opposite each other. Their ducts are swollen in the region of the anterior organ.

The excretory bladder is small and the main excretory ducts form only a few coils behind the ventral sucker. At this point each excretory duct has a ciliated patch in it. The flame cell formula is $2\,[4 + 2 + (2)] = 16$. The branches of the caudal excretory duct open at the middle of the furca. No excretory commissure or eyespots, pigmented or unpigmented, were seen.

A small mass of cells lying just in front of the excretory bladder represents the genital primordium.

The tail shaft has five pairs of prominent elongated caudal bodies, which are arranged in pairs.

Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.15 -0.283	0.196	0.19-0.223	0.203
Body breadth	0.043-0.06	0.055	0.04 -0.05	0.043
Tail shaft length	0.193-0.250	0.208	0.196-0.226	0.213
Tail shaft breadth	0.03 -0.05	0.038	0.03 -0.036	0.033
Furca length	0.216-0.246	0.227	0.203-0.22	0.211
Furca breadth	0.013-0.02	0.015	0.013-0.023	0.017
Anterior organ	0.046-0.050x 0.02 -0.03	0.045x 0.024	0.04 -0.05x 0.02 -0.03	0.045x 0.024
Pharynx diameter	0.01 -0.013	0.011	0.01 -0.013	0.011
Ventral sucker diameter	0.03 -0.04	0.034	0.02 -0.03	0.024

This cercaria was originally described by Fuhrman in 1916, from Switzerland. Dubois (1929) described it from Neûchatel and Wesenberg-Lund (1934) from Denmark. Recently Fain (1953) has recorded it from Belgian Congo. The description of this cercaria as given by Fain agrees with my observations except for more flagellets on the body and furca and less on the tail shaft, and six to

eight rows of prominent spines in the oral cap, in Fain's account. This cercaria is here recorded from Britain for the first time.

30. Cercaria tetraglandis Iles, 1959

A very common cercaria in London ponds. Between ten to fifty per cent P. planorbis collected from St. Albans Lake, Bushy Park, Stoneyfields Park, Baldwin's and Lost Ponds (Epping Forest), Lake Meadows (Essex), Sand Pits (South Ockendon, Essex) were harbouring this cercaria.

This cercaria was independently discovered and studied by me before its recent description by Iles (1959) from Roth Park Lake, Cardiff. My observations on the morphology and behaviour of this form quite agree with those of Iles.

Specific Diagnosis

Pharyngeal, longifurcous distome cercaria, with two pairs of penetration glands in front of the ventral sucker and flame cell formula of 2 [4 + 4 + (2)] = 20. Body and furca spinose, tail shaft aspinose. One row of anterior penetration spines and four rows of spines on the ventral sucker. Body and tail shaft with long hair-like structures. Oesophagus bifurcating at a distance from the ventral sucker and caeca terminating between the ventral sucker and the

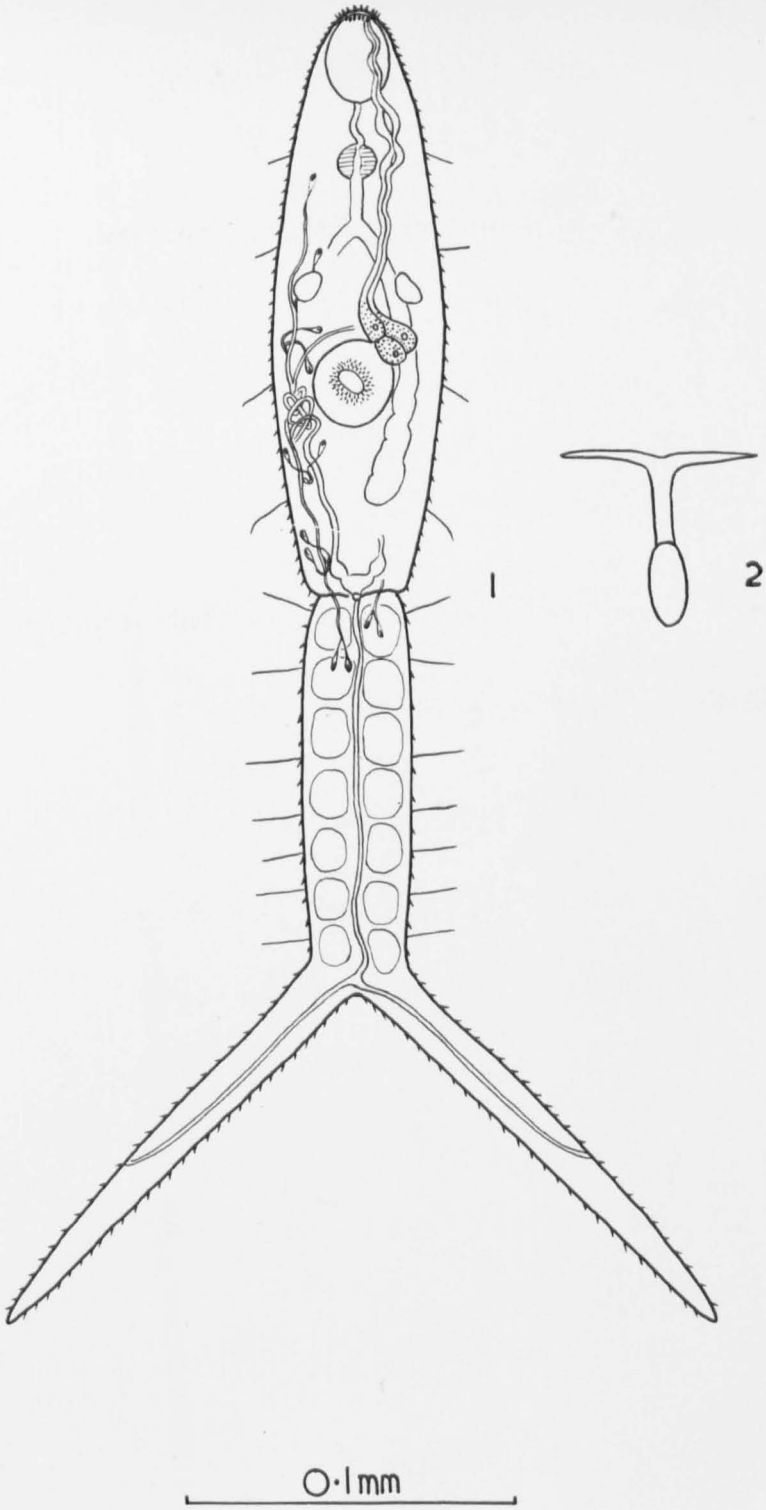
Explanation to Plate 23

Cercaria pseudolinearis n. sp.

fig. 1 General structure of the cercaria.

fig. 2 Resting posture.

Plate 23



posterior end of body. Anterior excretory commissure and a pair of unpigmented eyespots present. Several small caudal bodies in tail shaft.

Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.15 -0.18	0.165	0.14 -0.16	0.153
Body breadth	0.06 -0.08	0.072	0.033	0.033
Tail shaft length	0.133-0.15	0.143	0.11 -0.12	0.114
Tail shaft breadth	0.033-0.05	0.043	0.023-0.026	0.024
Furca length	0.18 -0.2	0.183	0.13 -0.14	0.134
Furca breadth	0.023-0.026	0.025	0.013	0.013
Anterior organ	0.033-0.036x 0.026-0.03	0.035x 0.028	0.026-0.03x 0.02 -0.023	0.029x 0.021
Pharynx diameter	0.013-0.016	0.015	0.01 -0.016	0.011
Ventral sucker diameter	0.03 -0.04	0.036	0.025-0.026	0.026

31. Cercaria pseudolinearis n. sp. (Plate 23, figs. 1-2)

One out of fifteen P. corneus collected from Stoneyfields Park on 20th August, 1959 were found to be infected with this cercaria. This was the only occasion when this cercaria was encountered.

Sporocyst

An enormous number of sporocysts were found in the digestive gland of the host. It is very difficult to separate them from each other and from the host tissue. The elongated, thread-like sporocysts are active and constricted at several places. The birth pore is sub-terminal. The living sporocysts measured 3.6-5.8 mm. long and 1.2-1.5 mm. broad.

Emergence and Behaviour

The cercariae are discharged throughout the day in large numbers. They swim tail foremost and remain well distributed throughout the water. No response to light is shown. A short swimming period alternates with a long resting period in which the cercaria keeps its furca stretched outwards at an angle of ninety degrees with the tail shaft and the body and tail hang vertically downwards (Plate 23, fig. 2).

Cercaria (Plate 23, fig. 1)

The contractile body, tail shaft and furca are spined. There are two rows of anterior penetration spines with ten and six spines respectively. There are three rows of spines on the ventral sucker. Ten rows of more prominent spines encircle the anterior region of the body behind a

bare circum-oral patch. The body has four pairs of long hair-like structures. Seven pairs of such hairs are present on the tail shaft.

The mouth is sub-terminal and ventral. The anterior organ is followed by a comparatively long prepharynx and a muscular pharynx. The oesophagus bifurcates between the pharynx and the ventral sucker and the intestinal caeca, slightly increasing in diameter posteriorly, terminate between the ventral sucker and the posterior end of the body.

Three pairs of penetration gland cells are situated in front of the ventral sucker. Their ducts, swollen just behind the anterior organ open at the anterior tip of the anterior organ.

The excretory bladder somewhat crescentric in shape opens by a small pore at the junction of the body with the tail. The two main excretory ducts are convoluted just behind the ventral sucker, where they divide into an anterior and a posterior collecting tubule. At this point the transverse excretory commissure, passing in front of the ventral sucker also joins. The flame cell formula is 2 [4 + 4 + (2)] = 20. The branches of the caudal excretory duct open at the middle of the furca. The tail shaft has seven pairs of poorly differentiated caudal bodies.

The genital rudiment is represented by a small mass

of deeply staining cells lying in front of the excretory bladder.

Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.183-0.233	0.21	0.18 -0.2	0.188
Body breadth	0.05 -0.076	0.06	0.036-0.043	0.040
Tail shaft length	0.13 -0.15	0.141	0.116-0.126	0.118
Tail shaft breadth	0.03 -0.046	0.036	0.033-0.036	0.034
Furca length	0.16 -0.183	0.17	0.15	0.15
Furca breadth	0.02 -0.03	0.025	0.013-0.020	0.016
Anterior organ	0.03 -0.033x 0.023-0.033	0.032x 0.026	0.028-0.033x 0.018-0.02	0.03x 0.019
Pharynx diameter	0.013-0.016	0.015	0.13	0.013
Ventral sucker diameter	0.03 -0.036	0.033	0.026-0.030	0.028

Comparison with Related Species

In having three pairs of pre-acetabular penetration gland cells, the present cercaria resembles C. linearis Wesenberg-Lund, 1934; C. magaliesia Porter, 1938 and C. paralinearis Goodman, 1951.

C. linearis can be distinguished from the present species in having unspined furca, in lacking spines on the ventral sucker and an anterior excretory commissure and in the bifurcation of the oesophagus just in front

of the ventral sucker.

C. magaliesia and C. paralinearis both have different excretory pattern. C. magaliesia also differs in having a long oesophagus, while C. paralinearis further differs in lacking an oesophagus.

The present species is therefore regarded as new and the name Cercaria pseudolinearis is proposed for it.

32. Cercaria X Baylis, 1930
Syn. C. chromatophora Brown, 1931

Five to twenty per cent of L. stagnalis collected from Henningfield reservoir (Essex), Sand Pits near South Ockendon (Essex), Sand Pits near St. Albans (Hertfordshire) and ponds in Epping Forest (Essex) were found to be infected with this cercaria. One interesting fact about this cercaria is that all the infected snails were of very large size. No small sized snail was ever found to be shedding it.

It was first reported by Baylis and Taylor in 1930, from snails sent to them from Roath Park Lake (Wales). They also found that the cercaria penetrated freshwater fishes and developed into diplostomulum in the eye. Their description of the development in fishes and diplostomulum was, however, inadequate. Rees (1932) recorded it from Glamorgan. Recently, Erasmus (1958) again recorded it from Roath Park Lake and gave detailed account of its development in the eye of freshwater fishes and also that of the cercaria

and the diplostomulum stages. His attempts to obtain the adults did not succeed.

Brown (1931) described a similar cercaria, C. chromatophora, which has been regarded as identical with C. X. by Erasmus (1958).

My observations and measurements agree entirely with those of Erasmus.

Specific Diagnosis

Pharyngeal, longifurcate distome cercaria with two pairs of penetration gland cells behind the ventral sucker and a flame cell formula 2 [3 + 4 + (3)] = 18. The body and furca spined, tail shaft aspinose. Three rows of anterior penetration spines and two rows of spines on the ventral sucker present. Numerous small caudal bodies in the tail shaft.

33. Cercaria planorbida Iles, 1959

About 5-50 per cent of P. planorbis collected from Bushy Park and Baldwins Pond in Epping Forest were found to be infected with this cercaria.

This cercaria was independently discovered and studied by me before its recent description by Iles (1959) from

Roath Park Lake, Cardiff. My observations on the measurements, structure and behaviour of this cercaria agree entirely with those given by Iles (1959).

Specific Diagnosis

Pharyngeal, longifurcate distome cercaria, with three pairs of penetration gland cells behind the ventral sucker, and a flame cell formula of 2 [2 + 4 + (1)] = 14. Anterior transverse excretory commissure and unpigmented eyespots present. Body and furca spinose, tail shaft aspinose, anterior penetration spines and three rows of spines on the ventral sucker. Oesophagus bifurcates just in front of the ventral sucker and the caeca extend to just behind the ventral sucker. Eight pairs of caudal bodies present. During resting period the furca are bent downwards and the body and tail shaft hang vertically downwards.

34. *Cercaria paracauda* Iles, 1959

Ten to thirty per cent *L. peregeer* collected from Bushy Park, Epping Forest, Richmond Park were found to be infected with this cercaria.

Cercaria

This cercaria was independently discovered and studied by me before its recent description by Iles (1959) from Britain. My observations and measurements agree entirely with those given by Iles.

Specific Diagnosis

Pharyngeate, longifurcate, distome furcocercariae, with two pairs of penetration gland cells behind the ventral sucker and a flame cell formula of 2 [3 + 3 + (2)] = 16. Three rows of anterior penetration spines. Body covered with transverse rows of spines. Tail shaft aspinose, furca spinose. Numerous caudal bodies. No transverse excretory commissure or unpigmented eyespots. Intestinal caeca extend to the posterior end of the body. Yellow pigment granules present at the point of oesophageal bifurcation.

35. Cercaria apatemon gracilis minor (Yamaguti, 1933) Iles, 1959
Syn. C. hamburgensis Komiya, 1938

This cercaria was found to infect L. pereger in Sand Pits (South Ockendon, Essex), Sand Pits (St. Albans), Bushy Park, Stoneyfields Park (Edgware), Richmond Park and in the River Thames near Bushy Park. The infection rate varied at different places between two to six per cent.

This cercaria resembles in all details C. a. g. minor as described by Iles (1959), except that in my specimens the intestinal caeca increase in diameter posteriorly and are constricted at two or three places; the prepharynx is much shorter than that figured by Iles.

As pointed out by Iles (1959), C. hamburgensis Komiya, 1938 is identical with this cercaria. C. pygocytophora Brown, 1931, lacks the posterior excretory commissure, and spines from the posterior half of the body and furca and the penetration gland cells are arranged in two longitudinal rows. It is, in my opinion, doubtful that this cercaria should be regarded identical with C. a. g. minor as suggested by Iles (1959).

The sporocysts are long and constricted at several places with pointed anterior and swollen, rounded posterior ends. The birth pore is sub-terminal. The swollen portions of the sporocysts harbour several cercariae. The living sporocysts measure up to 4.2 mm. in length with a maximum width of 0.29 mm.

In the cercaria the genital primordium is represented by a single small mass of deeply staining cells lying just in front of the excretory bladder.

Specific Diagnosis

Pharyngeal, longifurcate, distome cercaria, with four pairs of penetration gland cells behind the ventral

sucker and flame cell formula 2 [2 + 4 + (1)] = 14. Posterior excretory commissure and anterior blind excretory ducts present. Body and furca spined on their entire length, ventral sucker with four rows of spines. No anterior penetration spines. The oesophagus bifurcates just in front of the ventral sucker and the caeca terminate just behind it. Two unpigmented eyespots present. Tail shaft with eight pairs of caudal bodies.

Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.176-0.213	0.2	0.120-0.133	0.128
Body breadth	0.066-0.086	0.076	0.033-0.049	0.036
Tail shaft length	0.166-0.176	0.171	0.13 -0.133	0.130
Tail shaft breadth	0.043-0.050	0.047	0.033-0.04	0.036
Furca length	0.161-0.183	0.170	0.116-0.133	0.126
Furca breadth	0.026-0.030	0.029	0.013-0.016	0.015
Anterior organ	0.036-0.043x	0.041x	0.03 x0.028	0.03x 0.028
Pharynx	0.016-0.02	0.017	0.01 -0.013	0.012
Ventral sucker diameter	0.03 -0.033	0.031	0.023-0.025	0.024

Explanations to Plate 24

Cercaria complexiglandulosa n. sp.

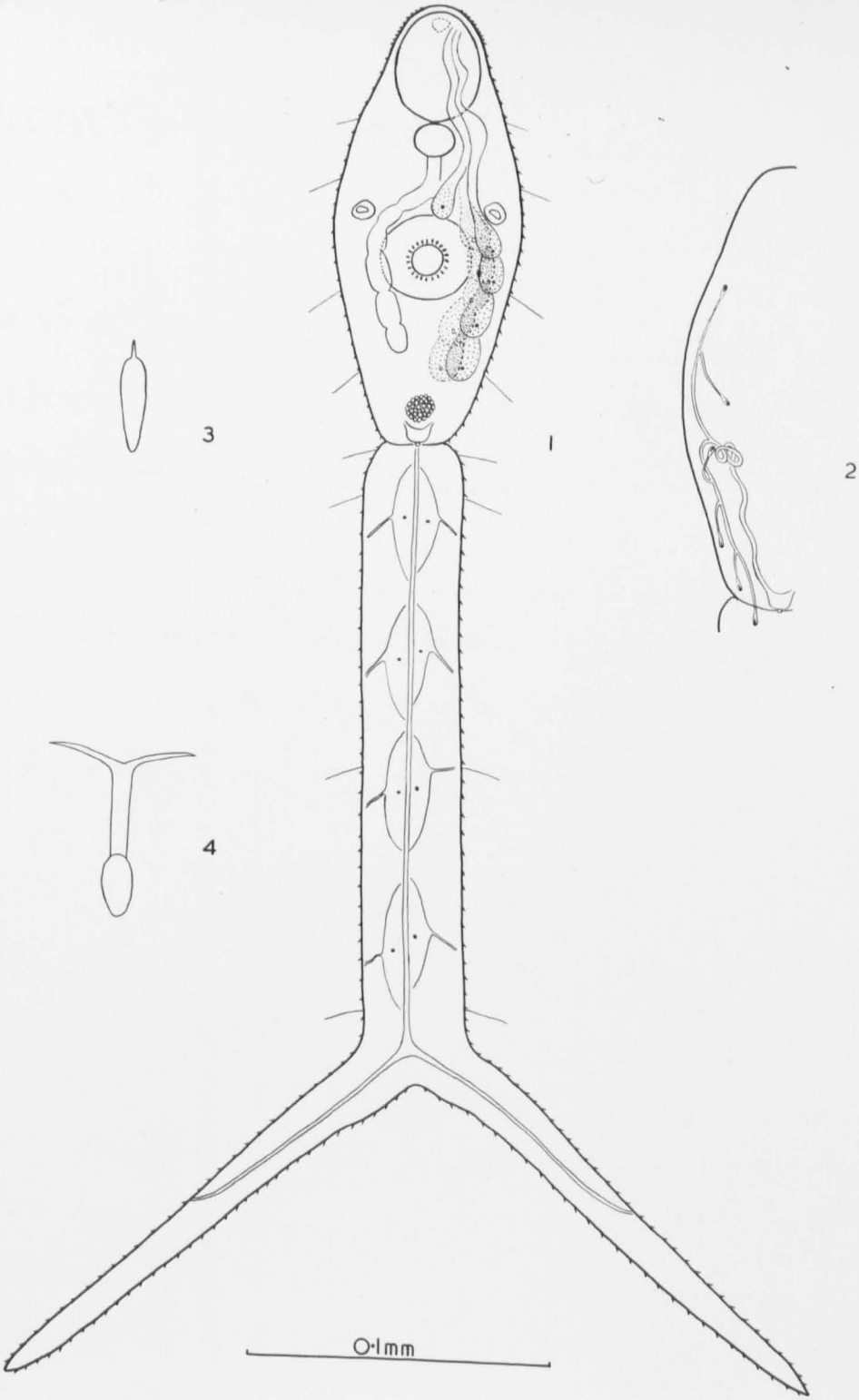
Fig. I Genral Structure of the Cercaria

Fig. 2 Excretory System of the Cercaria

Fig. 3 Single Spine from the Ventral Sucker

Fig. 4 Resting Position of the Cercaria

Plate 24



36. Cercaria complexiglandulosa n. sp. (Plate 24, figs. 1-4)

This cercaria was encountered only once, when a single P. Spirorbis collected from Bushy Park on 10th August, 1960 was found to be discharging it.

Sporocyst

The sporocysts are long thread-like structures in the digestive gland of the host. The anterior end of the sporocyst is narrow and protrusible while the posterior is rounded. The birth pore is aterminal. The sporocysts may be constricted at three or four places. Each sporocyst may have several cercariae and germ balls. The living cercaria-bearing sporocysts measured 1.27-2.1 mm. in length and 0.082-0.12 mm. in breadth.

Emergence and Behaviour

The cercariae are discharged in fairly large numbers during the night. If left undisturbed they aggregate near the bottom, but with even a slight disturbance they become distributed throughout the container. A long resting period is followed by a short swimming period, during which the cercaria darts for a short distance, tail foremost. During the resting period (Plate 24, fig. 4) the furca are kept open and the body and tail shaft hang vertically downwards. While at rest the cercariae were

seen to sink slowly or to float vertically upwards.

Cercaria (Plate 24, figs. 1-3)

The cercaria has a thick contractile body. The body, tail shaft and the furca are provided with small irregularly arranged spines. The spines covering the region of the first half of the anterior organ are more prominent. There is a bare circum-oral area but no anterior penetration spines. The ventral sucker has a single row of prominent spearhead shaped spines (Plate 24, fig. 3) round its opening. There are four pairs of long hair-like structures on the body and four pairs on the tail shaft.

The oral opening is sub-terminal and the anterior organ protrusible. The pre-pharynx is short and followed by a poorly differentiated pharynx. The oesophagus divides slightly in front of the ventral sucker and the intestinal ceaca extend up to between the ventral sucker and the posterior end of the body. The whole body is filled with a large number of rounded cells, which make the observations on the internal structures difficult.

There are two sets of five penetration gland cells, arranged one behind the other on each side of the body. The outer set is dorsal in position and the inner ventral. In each set the anteriormost cell lies in front of, the next two lateral to and the last two behind the ventral

sucker. The post-acetabular penetration gland cells are larger than the rest. The penetration gland ducts open at the tip of the anterior organ.

A small rectangular excretory bladder is located near the junction of the body with the tail. It opens dorsally through a small excretory pore. There is no island of Cort. The main excretory ducts are highly convoluted behind the ventral sucker, where they divide into anterior and posterior collecting tubules. The anterior collecting tubule receives capillaries from two flame cells and the posterior from four flame cells. The last of the posterior flame cells is located in the proximal end of the tail. The flame cell formula is $2\,[2 + 3 + (1)] = 12$. There is no transverse excretory commissure (Plate 24, fig. 4).

The tail shaft is longer than the body and furca and has crenulated margins. The furca are laterally flattened blade-like structures. The caudal excretory duct opens in the middle of the furca. There are no true caudal bodies, but the caudal excretory duct in the tail shaft is surrounded by five pairs of elongated cells, which are connected to the surface by five cytoplasmic threads. There are also few rounded nucleated cells both in the tail shaft and furca. Some of these cells were seen to move freely, according to the movements of the tail.

The genital rudiment is represented by a small mass

of deeply staining cells lying just in front of the excretory bladder.

Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.12 -0.23	0.176	0.106-0.146	0.123
Body breadth	0.04 -0.113	0.080	0.05 -0.066	0.056
Tail shaft length	0.183-0.233	0.216	0.166-0.20	0.183
Tail shaft breadth	0.036-0.050	0.042	0.033-0.043	0.038
Furca length	0.166-0.21	0.193	0.153-0.16	0.156
Furca breadth	0.030-0.040	0.037	0.013-0.023	0.016
Anterior organ	0.033-0.05x 0.03 -0.033	0.043x 0.032	0.03 -0.033x 0.026-0.028	0.032x 0.026
Pharynx	0.013-0.016x 0.013-0.016	0.015x 0.015	0.01 -0.013x 0.01-0.013	0.011x 0.011
Ventral sucker	0.036-0.043x 0.036-0.043	0.04x 0.04	0.03 -0.026x 0.33	0.03x 0.03

Comparison with Related Species

Few pharyngeate species have been described with penetration gland cells anterior and posterior to ventral sucker. C. Indicae II Sewell, 1922 and C. bombayensis 9 Soparker, 1921 which are probably identical though have the same flame cell formula as the present species, differ in having only three pairs of penetration gland cells.

C. elvaeformis Porter, 1938 and C. succinia Porter,

1938 can also be separated from the present cercaria in having a different number of penetration gland cells and a different flame cell formula.

C. bulbocauda Miller, 1927 and C. absurda Miller, 1927 both have seven pairs of posterior penetration gland cells, a flame cell formula of 2 [3 + 3 + (1)] = 14 and swollen tail shafts.

C. granula Miller, 1927 and C. hirusta Miller, 1927 differ in having a different number of penetration gland cells and six cells in the anterior organ, six pairs of caudal bodies, posterior transverse excretory commissure.

In both C. pseudovivax Faust, 1924 and C. divaricata Faust, 1924, a large number of small penetration gland cells extending from in front of the ventral sucker to behind it have been described. They also differ from the present species in having glandular cells round the prepharynx, and island of Cort and in their intestinal caeca terminating at the posterior end of the ventral sucker. C. pseudovivax also differs in having a tail shaft smaller than the body.

It is evident from the above comparison that the present cercaria is a new species for which the name Cercaria complexiglandulosa is proposed.

Cercariaea

The majority of these forms has been described from the terrestrial snail and only a few have been described from freshwater molluscs.

Lühe (1909) divided these tail-less forms into two subgroups. The "Cercariaeum" (s. str.) subgroup with forms developing in rediae or unbranched sporocysts and the "Leucochloridium" subgroup with forms developing in branched sporocysts. Cort (1918) regarded this group as an unnatural one.

Sewell (1922) proposed three, the "Mutabilis", "Helicis" and the "Leucochloridium" subgroups, developing in rediae, unbranched sporocysts and branched sporocysts, respectively.

Dubois (1929) further split up the "Mutabilis" subgroup of Sewell into three subgroups. He proposed the following classification:-

1. "Mutabile" subgroup, cercariae developing in rediae; having a tubular excretory bladder with a sinuous cavity and a flame cell formula of $2\ [(4 + 4 + 4 + 4) + (4 + 4 + 4 + 4)] = 64$; two testes present.

2. "Helveticum" subgroup. Cercariae differing from mutabile group only in having a flame cell formula of $2\ [(3 + 3 + 3) + (3 + 3 + 3)] = 36$.

3. "Squamosum" subgroup cercariae with a small pyriform or rounded excretory bladder and only one testis. Flame

Explanation to Plate 25

Cercariaeum bithyneae n. sp.

fig. 1 General structure of the cercariaeum.

fig. 2 Genital primordium (lateral view).

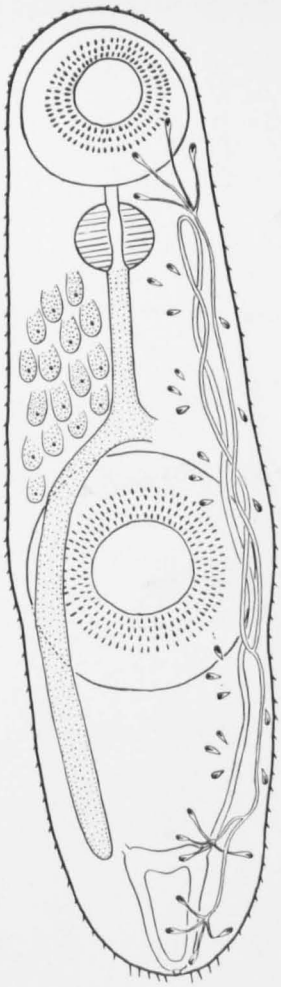
fig. 3 Cyst.

Cercariaeum internale n. sp.

fig. 4 General structure of the cercariaeum.

fig. 5 Genital primordium (lateral view).

Plate 25



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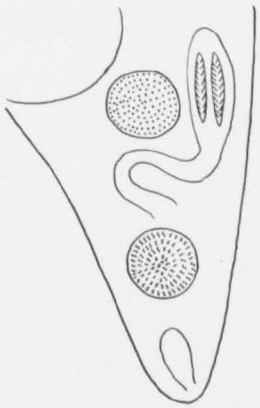

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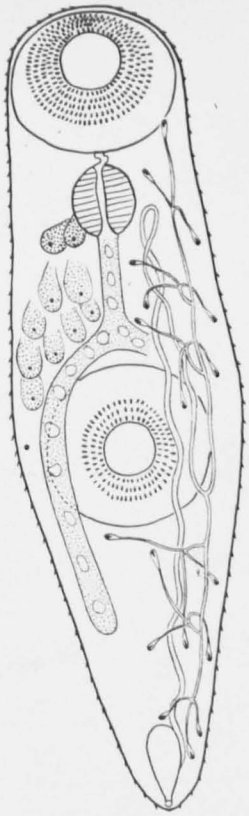

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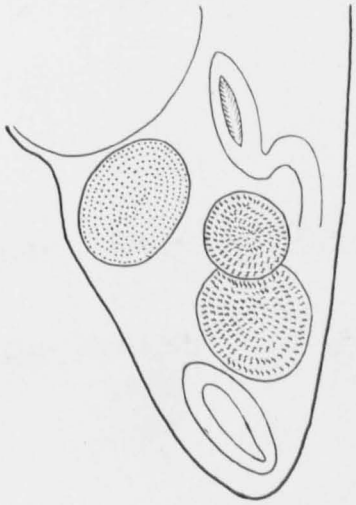

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cell formula same as mutabile group.

4. "Helicis" subgroup same as Sewell.

5. "Leucochloridium" subgroup same as Sewell.

Wesenberg-Lund (1934) disagrees with Dubois's classification and in his study of the Danish freshwater cercariae employed Sewell's scheme.

There is still much to be known about the structure and biology of these forms. The fact that a rudimentary tail may be present in immature stages has led workers (Sewell, 1922; Dubois, 1929 and Wesenberg-Lund, 1934) to the opinion that these cercariae are very closely related with the "Microcercous" cercariae. Cable (1935a) even included parts of this group among his "Obscuro-microcercous" cercariae, a sub-division of the "Microcercous" group.

37. Cercariaeum bithyneae n. sp. (Plate 25, figs. 1-3)

One to four per cent B. tentaculata collected from Bushy Park were found to be infected with this cercariaeum.

Redia

A large number of rediae is found in the digestive gland of the infected snails. The rediae are sac-like and colourless except for a short, broad gut with black contents. The collar or ambulatory processes are absent. There may be up to four developing cercariae in one redia.

The living rediae measured 0.42-0.75 mm. in length and 0.19-0.21 mm. in breadth with a pharynx 0.063-0.075 x 0.07-0.087 mm. in size.

Emergence and Behaviour

The cercariae are discharged through the siphon, after which they crawl to the tip of the tentacle of the snail. Here they attach themselves firmly with the help of the ventral sucker and keep stretching their forebodies and continue moving them from side to side. A maximum of four cercariae have been seen on each tentacle at one time. They were never seen to leave the snail and crawl on the bottom of the container. Occasionally they were found to leave the tentacle and crawl back into the body of the snail, where they probably encysted.

The movement of the cercariae on the tentacle suggests that on coming into contact with another snail, they would leave the first snail to encyst in the second as suggested by Wesenberg-Lund (1934).

When isolated in tubes, a large number of uninfected snails also had these cercariae on their tentacles. These snails apparently had received them from the infected snails before isolation, but the cercariae were repeating the same process on the tentacle, instead of encysting soon after their migration to the uninfected snails.

Cercariaeum (Plate 25, figs. 1-3)

The extremely thick body is elongated and highly contractile, with the maximum breadth at the level of the ventral sucker. The post-acetabular region of the body is bent upwards. The whole body is covered with posteriorly pointing spines, particularly prominent at the posterior tip of the body. There are a few small cuticular projections in the region of the oral sucker. Three circles of spines surround the opening of the oral sucker and four such rows are present on the ventral sucker. There is no stylet. A very strongly developed ventral sucker is located behind the middle of the body and is larger than the oral sucker.

The sub-terminal oral sucker is followed by a small prepharynx, a well developed pharynx and a long oesophagus which bifurcates just in front of the ventral sucker. The intestinal caeca extend to the vicinity of the excretory bladder. The walls of the oesophagus and intestinal caeca are thick.

A large number of penetration gland cells are located between the pharynx and the ventral sucker.

The excretory bladder is elongated and somewhat tripartite, with a wide cavity. The walls of the excretory bladder are also thick. Posteriorly the excretory bladder opens to the exterior through a small excretory pore. Antero-laterally two wide main excretory ducts open into

the excretory bladder. These ducts proceed up to the level of the pharynx, where they are reflexed backwards, forming the descending excretory duct which bifurcates into an anterior and posterior collecting tubule at the side of the ventral sucker. Thirty-two flame cells are present on each side. The flame cells are arranged in groups of four and the flame cell formula apparently is $2\left[(4+4+4+4)+(4+4+4+4)\right]=64$.

The genital organs are well developed. There is an ovary at the level of the posterior half of the ventral sucker. Behind the ovary are two unequal testes diagonally placed. A wide duct leaves the testes and opens into a well developed cirrus pouch. The cirrus pouch has spined internal surfaces (Plate 25, fig. 2).

Measurements of Cercariaeum

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.333-0.49	0.44	0.386-0.46	0.44
Body breadth	0.11 -0.25	0.2	0.16 -0.2	0.18
Oral sucker	0.083-0.086x 0.083-0.100	0.085x 0.09	0.060-0.083x 0.063-0.083	0.071x 0.07
Pharynx	0.036-0.04x 0.04 -0.048	0.04x 0.043	0.03 -0.036x 0.036-0.046	0.033x 0.038
Ventral sucker	0.12 -0.133x 0.12 -0.133	0.125x 0.125	0.083-0.116x 0.083-0.116	0.106x 0.106
Distance between the ventral sucker and the posterior end			0.116-0.140	0.128

Cysts (Plate 25, fig. 3)

The cysts were recovered from naturally infected *B. tentaculata*. They are situated near the basal part of the digestive gland of the host. The cyst wall is very thin and delicate. It does not closely infest the animal, which continues moving freely inside. The cyst wall may be withdrawn into the suckers and the cysts may assume different shapes according to the movement of the larva inside. The cyst wall can easily be broken with a slight pressure of the coverglass. The liberated metacercariae were found to have the same measurements as the cercariae. The cysts measure 0.227-0.257 mm. in diameter.

Comparison with Related Species

According to Dubois (1929) C. mutabile Cort, 1918 (= C. trigonodistomum mutabile Wallace, 1938) and C. Indicae LIV Sewell, 1922 are the species with two testes and a flame cell formula of 2 $\left[(4 + 4 + 4 + 4) + (4 + 4 + 4 + 4)\right] = 64$.

C. mutabile can be separated from the present species in the body spines being limited to the anterior end only, on the size of the oesophagus and excretory bladder and on the position of the ventral sucker. C. Indicae LIV also has its body spines limited to the anterior two thirds of the body and further differs in having a smaller number of penetration gland cells, larger excretory bladder and in the proportionate size of the two suckers.

The flame cell pattern of Cercariaeum No. 1 Petersen as described by Wesenberg-Lund (1934) is not known. It has been described to have two testes. It can be distinguished from the present species in being much larger and in having no spines on the suckers, in having a short oesophagus and very wide caeca. It also differs in developing in a different host and in the fact that it was never found to come out of the snail.

In view of the above comparison, the present species is regarded as new and the name Cercariaeum bithyneae is proposed for it.

Cercariaeum internale n. sp. (Plate 25, figs. 4 and 5)

This cercariaeum was found three times on the dissection of V. piscinalis collected from Bushy Park. It was never found to emerge from the snail. When liberated by dissection, they fall to the bottom where they continue stretching their bodies, but were not seen to move with the help of their suckers.

Redia

A large number of rediae are found in the digestive gland of the host, usually arranged in bunches. The rediae are colourless, with a short pharynx and a short but wide gut, which is filled with homogeneous bright orange contents. No birth pore, collar or ambulatory processes could be seen. There may be from two to numerous developed cercariae and one to two undifferentiated masses of cells. The size of the rediae is highly variable. Living rediae with fully developed cercariaeae in them ranged between 0.525-2.175 mm. in length and 0.195-0.300 mm. in breadth with a pharynx 0.033-0.056 mm. in diameter.

Cercariaeum (Plate 25, fig. 4)

The body of the cercariaeum is highly contractile and covered with backwardly directed spines on the entire dorsal and lateral sides. The spines are absent from the mid-ventral

surface of the body. The oral sucker is provided with five and the ventral sucker with three circles of spines. There is no stylet.

The oral sucker is smaller than the ventral and sub-terminal in position. The prepharynx is small and narrow. The well developed pharynx is followed by a prominent oesophagus which bifurcates just in front of the ventral sucker. The intestinal caeca terminate between the ventral sucker and the posterior end. Both the oesophagus and intestinal caeca have few concretions irregularly scattered among them.

There is a large number of penetration gland cells, extending from the level of the pharynx to post-acetabular region. The exact number of these glands with finely granular protoplasm and prominent nuclei could not be counted. There are also two glands at each side of the pharynx, with coarsely granular protoplasm.

There is a small pyriform excretory bladder at the posterior end of the body which opens posteriorly through a small excretory pore on the dorsal side. The two main excretory ducts originate from the sides of the excretory bladder and pursue an extremely convoluted course up to the sides of the pharynx, where they are flexed backwards. The descending excretory ducts are also highly convoluted and extend to the level of the ventral sucker where they divide into an anterior and posterior collecting tubule,

each receiving capillaries from three groups of three flame cells on each side. The flame cell formula is 2 [(3 + 3 + 3) + (3 + 3 + 3)] = 36 (Plate 25, fig. 4).

There is one testis only, with its duct and the larval cirrus pouch with spined internal surface is well developed. The ovary is slightly larger than the testis and lies just behind the ventral sucker (Plate 25, fig. 5).

Measurements of Cercariaeum

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.42 -0.533	0.494	0.333-0.436	0.38
Body breadth at ventral sucker	0.15 -0.21	0.175	0.083-0.113	0.09
Oral sucker	0.08 -0.116x 0.08 -0.116	0.096x 0.113	0.066-0.073x 0.07 -0.083	0.07x 0.076
Pharynx	0.036-0.043x 0.023-0.043	0.04x 0.036	0.033-0.04x 0.033-0.04	0.036x 0.036
Ventral sucker	0.09 -0.13x 0.096-0.133	0.118x 0.118	0.066-0.083x 0.066-0.083	0.073x 0.073

Comparison with Related Species

According to Dubois (1929), C. paludinae impurae (Armatae) Fil., 1854 and C. helveticum I Dubois 1929, have an excretory system of 2 [(3 + 3 + 3) + (3 + 3 + 3)] = 36 and one testis. Both of these cercariaeae can be distinguished from the present species in having two testes, a long tubular excretory

bladder and a stylet. The present cercariaeum is also considerably smaller than these two species.

C. crassa Wesenberg-Lund, 1934 is also much larger and develops in Pisidium amnicum. Although the excretory and reproductive systems of this cercariaeum are not known, it can further be separated from the present species in possessing a large excretory bladder and in the extension of its intestinal caeca to the posterior end.

The only other cercariaeum to be reported from V. piscinalis is C. gibba Wesenberg-Lund, 1934. No spines have been described on the suckers of this species and the flame cell pattern is unknown. This cercariaeum is smaller than the present species and is slightly spined, while the present cercariaeum is strongly spined. Six "taps" described for C. gibba are absent in the present cercariaeum. C. gibba also differs from the present species in having a very large excretory bladder, three pairs of penetration gland cells at the sides of the pharynx and in having a different size of the suckers and different proportion between the two suckers.

The present species is therefore regarded as new and the name Cercariaeum internale is proposed for it.

Key to the British Freshwater Cercariae

1.	a)	Tail absent in mature cercariae.	2
	b)	Tail present in mature cercariae.	3
2.	a)	Tail absent in mature cercariae, two testes, flame cell formula: $2\ [(4 + 4 + 4 + 4) + (4 + 4 + 4 + 4)] = 64$.	*Cercariaeum bithyneae* n. sp. +
	b)	One testis, flame cell formula: $2\ [(3 + 3 + 3) + (3 + 3 + 3)] = 36$.	*Cercariaeum internale* n. sp. +
3.	a)	Tail simple.	4
	b)	Tail bifurcate.	24
4.	a)	Tail much longer and broader than body and with a cavity at the proximal end, into which the body can be withdrawn.	5
	b)	Tail without a cavity at the anterior end.	6
5.	a)	Flame cell formula: $2\ [(3 + 3) + (3 + 3 + 3 + 3)] = 36$. Sporocyst without birth pore, encysts in chironomid larvae.	*C. macrocerca* Vickers, 1941
	b)	Flame cell formula: $2\ [(4 + 4) + (4 + 4 + 4 + 4)] = 48$. Sporocyst with a birth pore, encysts precociously in mollusc hosts.	*C. phyllodistomum simile* Thomas, 1956
6.	a)	Stylet and collar of spines absent.	7
	b)	Collar of spines present.	10
	c)	Stylet present.	14
7.	a)	Ventral sucker absent.	8
	b)	Ventral sucker rudimentary or well developed.	9
8.	a)	Three eyespots of equal size in mature cercariae; pigment arranged along six rows on the body.	*C. monostomi* (Syn. *C. N. seineti* Harper) +

+Represents the cercariae recorded in the present study.

	b)	Median eyespots smaller than the lateral in mature cercariae, pigment uniformly distributed, excretory system without a blind extension.	C. heterocellata n. sp.+
	c)	Three eyespots, median smallerthan lateral eyespots, pigment uniformly distributed, excretory system with a blind extension at the anterior end.	C. middlesexensis n. sp.+
9.	a)	Two eyespots present; ventral sucker rudimentary; tail with lateral and dorso-ventral finfolds.	C. lophocerca Fil.+
	b)	Body unspined and white. No eyespots; few large excretory granules in main excretory ducts; excretory bladder two chambered, caudal excretory duct bifurcates in the middle of the tail. Flame cell formula: 2 [(2 + 2 + 2) + (3 + 3)] = 24	C. albinea n. sp.+
	c)	Body wall very thick, unspined and white; numerous small excretory granules in main excretory ducts, excretory bladder two chambered, caudal excretory duct bifurcates in middle of tail; flame cell formula: 2 [(2 + 2 + 2) + (3 + 3)] = 24.	C. densacutis n. sp.+
10.	a)	Tail much longer and broader than body, few collar spines.	11
	b)	Tail only slightly longer but narrower than the body and without finfold.	12
	c)	Tail only slightly longer but narrower than the body and with finfold.	13
11.	a)	Number of collar spines unknown, a group of five corner spines; body and tail pigmented; tail oscilates during rest.	C. oscilatoria Brown
	b)	Twenty collar spines, a group of four corner spines on each side, body and tail pigmented; tail does not oscilate during rest.	C. hamptonensis n. sp.+
	c)	Twenty collar spines, a group of four corner spines on each side, body and tail without pigment.	C. thamesensis n. sp.+

+Represents the cercariae recorded in the present study.

12.	a)	Thirty-seven collar spines, with a group of four corner spines, cystogenous glands with rod-shaped contents.	C. echinata v. Sieb.
	b)	Same as 12(a) but much smaller.	C. equispinosa Brown
	c)	Thirty-seven collar spines, with a group of five corner spines on each side; cystogenous glands with granular contents.	C. deficipinnatum n. sp. +
	d)	Thirty-nine (?) feebly developed collar spines, five corner spines on each side, redia with short gut.	C. granulosa Brown
	e)	Thirty-eight to forty-five collar spines, excretory system of "Coronata" type.	C.e. recurvatum Mathias +
	f)	Forty-three to forty-five collar spines; excretory system of "Echinata" type.	C.Z. Rees +
	g)	Forty-nine collar spines, excretory system of "Coronata" type.	C. essexensis n. sp. +
13.	a)	Thirty-five collar spines, with unbroken caudal finfold, extending over tip.	C. limbifera (Brown, Rees)
	b)	Thirty-seven collar spines, with caudal finfold broken into two portions on each side.	C. londonensis n. sp. +
14.	a)	Size less than 0.2 mm.; three to four penetration gland cells.	15
	b)	Virgula organ present.	16
	c)	Size more than .2 mm. No virgular organ. No eyespots develop in sporocyst.	17
	d)	Eyespots present develop in redia.	
15.	a)	Four pairs of penetration gland cells, bicornuate excretory bladder, main excretory ducts originate aterminally from cornua.	C. minor n. sp. +
16.	a)	Virgula organ two rounded sacs, 4 pairs of penetration gland cells, bicornuate excretory bladder; flame cell formula: 2 [(2 + 2 + 2) + (2 + 2 + 2)] = 24.	C. tarda n. sp. +

+Represents the cercariae recorded in the present study.

17.	a)	Bicornuate excretory bladder.	18
	b)	Simple tubular excretory bladder, with no cornua.	19
18.	a)	Four pairs of penetration gland cells.	19
	b)	More than four pairs of penetration gland cells.	20
19.	a)	Oral sucker nearly twice the size of ventral sucker, caeca extend only slightly behind the ventral sucker; flame cell formula: 2 [(3 + 1 + 3) + (3 + 3)] = 26.	C. pulicis Brown, 1926
	b)	Oral sucker slightly larger than ventral sucker; caeca extend to the posterior end of body. Flame cell formula: 2 [(3 + 3) + (5)] = 22.	C. pseudodermata Brown, 1926
20.	a)	Penetration gland cells in two groups on each side.	21
	b)	Penetration gland cells in one group.	22
21.	a)	Two lateral groups with four penetration gland cells each and two median groups with two penetration gland cells each. Oral sucker much larger than ventral sucker, oesophagus bifurcates between pharynx and ventral sucker.	C. XI Harper
	b)	Lateral group with six glands each, number of cells in median group not known, suckers of sub-equal size.	C. X2 Harper
	c)	Posterior group of two cells each and anterior group of four cells each. Caeca extend to posterior end of body.	C. sp. Hesse
22.	a)	Five pairs of penetration gland cells, oral sucker larger than ventral sucker; flame cell formula: 2 [(3 + 1 + 1 + 3) + (3 + 3)] = 28.	C. leptosoma Brown
	b)	Six pairs of penetration gland cells, flame cell formula: 2 [(4 + 6)] = 20.	C. chiselhurstensis n. sp +
	c)	Seven pairs of penetration gland cells.	C. peregeri + n. sp.

+Represents the cercariae recorded in the present study.

	d)	Eight pairs of penetration gland cells, flame cell formula: 2 [(5 + 4)] = 18.	C. cambrensis Rees
	e)	Eight pairs of penetration gland cells, flame cell formula: 2 [(3 + 3 + 3) + (3 + 3 + 3)] = 36. stylet, 0·31-0·33 mm. emerge at night.	C. plagiorchis (multiglandularis) Megalorchis Rees +
	f)	Nine pairs of penetration gland cells, flame cell formula: 2 [(2 + 2 + 2) + (2 + 2 + 2)] = 20.	C. meadowensis +
	g)	Twelve pairs of penetration gland cells, flame cell formula: 2 [(3 + 1 + 3) + (3 + 3)] = 26, ventral sucker larger than oral sucker.	C. cambrensis Rees Wright
23.	a)	Eight penetration gland cells; flame cell formula: 2 [(3 + 2)] = 10.	C. X4 Harper
	b)	Six penetration gland cells, flame cell formula: 2 [(2 + 4 + 4) + (3 + 3 + 3)] = 38.	C. c. farionis Brown
24.	a)	Apharyngeal monostome, brevifurcous with threepairs of flame cells in the body and none in tail, finfold on the body and furca.	25
	b)	Apharyngeal distome, with pigmented eye-spots; flame cell formula: 2 [3 + 3 + (1)] = 14.	26
	c)	Pharyngeal, monostome.	30
	d)	Pharyngeal distome, longifurcous.	32
25.	a)	Body finfold reduced, anterior conical projections present, gut absent development in elongated sporocysts. Total size, 0·413-0·463 mm.	C. kentensis n. sp. +
	b)	Body finfold unreduced, anterior conical projections present, gut absent, development in rounded or oval sporocysts, total size, 0·572-0·656 mm.	C. cristocorpa n. sp. +

+Represents the cercariae recorded in the present study.

26.	a)	Less than five pairs of penetration gland cells behind the ventral sucker.	27
	b)	Five pairs of penetration gland cells.	28
27.	a)	Two pairs of penetration gland cells.	C. macrosoma Brown
	b)	Three pairs of circum-acetabular penetration gland cells, flame cell formula: 2 [3 + 2 + (1)] = 12.	C. F.2 Harper
28.	a)	Penetration glands not differentiated into two groups, no lens in eyespots, floats passively on surface, when attached, the tail continues lashing.	C. echinomorpha Brown
	b)	Penetration glands differentiated into two groups, eyespots with lens.	28
29.	a)	Attaches to the lighted side of container with its ventral sucker and keeps its pre-acetabular body and tail stretched straight outwards, no tendency to aggregate near the surface of the water.	C. pseudocellata+ Szidat and Wigand
	b)	Clings to the mucous membrane at the surface of the water, tail with swelling at the base.	C. bilharziellae+ polonicae (Szidat)
	c)	Attaches to the side of container with ventral sucker and keeps its body and tail close and parallel to the side on which attached.	C. kenilworthensis+ n. sp.
	d)	Same as 29(c) but much smaller.	C. edgwarensis+ n. sp.
30.	a)	Furca without finfold, rudimentary ventral sucker present, flame cell formula: 2 [(2) + (2 + 2) + (2)] = 18.	C. bushiensis+ n. sp.
	b)	Furca with finfold.	30
31.	a)	Tail aspinose, anterior penetration spines present, nine pairs flame cells in body, caudal falme cells present, acute angle between body and tail during rest, finfold on distal half of furca.	C. vivacis Iles

+Represents the cercariae recorded in the present study.

b) Tail spinose, anterior penetration spines absent, eight pairs of flame cells in body no flame cells in tail, body and tail in a straight line during rest. — C. ariformis n. sp.+

c) Body with papillae, caeca extend to excretory bladder, during resting position obtuse angle between body and tail, finfolds limited to tip of furca; flame cell formula: 2 [(3 + 3) + (3 + 3 + (3)] = 30. — C. papillosoma n. sp.+

32. a) Penetration glands in front of the ventral sucker. — 33

b) Penetration glands behind the ventral sucker. — 35

c) Penetration glands in front and behind the ventral sucker. — C. complexiglandulosa n. sp.+

33. a) Two pairs of penetration glands. — 34

b) Three pairs of penetration glands, anterior excretory commissure, seven pairs of caudal bodies, flame cell formula: 2 [4 + 4 + (2)] = 20. — C. pseudolinearis n. sp.+

34. a) Flame cell formula: 2 [3 + 4 + (2)] = 18. — C. fissicauda Brown

b) Unpigmented eyespots absent, flame cell formula: 2 [4 + 4 + (2)] = 20; oesophagus bifurcates just in front of ventral sucker, caudal bodies in tail. — C. cotylurus cornutus (Harper)

c) Unpigmented eyespots present, flame cell formula: 2 [(2 + 1 + 1) + (2 + 2) + (2)] = 20; oesophagus bifurcates nearer the ventral sucker than pharynx, numerous small caudal bodies, develops into tetracotyles in leeches. — C. tetraglandis Iles+

d) Same as 34(c) but flame cell formula: 2 [(2 + 2) + (2 + 2) + (2)] = 20; no caudal bodies, more than one row of anterior penetration spines, shorter oesophagus; develops into tetracotyles in snails. — C. cotylurus brevis (Dubois, 1934) Nasir

+Represents the cercariae recorded in the present study.

	e)	Flame cell formula: 2 [4 + 3 + (2)] = 18; oesophagus bifurcates between pharynx and ventral sucker, five pairs of caudal bodies.	C. letifera Fuhr. +
35.	a)	Two pairs of penetration gland cells.	36
	b)	Three pairs of penetration gland cells.	37
	c)	Four pairs of penetration gland cells.	38
36.	a)	Flame cell formula: 2 [3 + 3 + (2)] = 16; 12 caudal bodies.	C. diplostomiphoxini Rees
	b)	Flame cell formula: 2 [3 + 3 + (2)] = 16; numerous caudal bodies.	C. paracauda Iles, 1959 +
	c)	Flame cell formula: 2 [3 + 4 + (2)] = 18; numerous caudal bodies.	C. X. Baylis + (- C. chromatophora Brown, 1931)
	d)	Flame cell formula: 2 [2 + 4 + (1)] = 14.	C. Y. Rees
	e)	Flame cell formula: 2 [2 + 2 + (1)] = 10.	C. micromorpha Brown
37.	a)	Six pairs of caudal bodies, flame cell formula: 2 [3 + 2 + (1)] = 12; no excretory commissure.	C. valvatae Lal.
	b)	Eight pairs of caudal bodies, flame cell formula: 2 [2 + 2 + (1)] = 14; posterior excretory commissure present; rests with an acute angle between furca and tail stem.	C. planorbida Iles +
	c)	Thirteen to fourteen caudal bodies, flame cell formula: 2 [2 + 3 + (1)] = 12; posterior commissure and anterior blind excretory ducts present; rests with right angle between furca and tail shaft.	C. roathensis Erasmus
38.	a)	Posterior excretory commissure and anterior blind excretory ducts present, flame cell formula: 2 [2 + 4 + (1)] = 14.	C. a.g. minor (Iles) (- C. hamburgensis (Komiya)) +
	b)	Anterior blind excretory ducts present but no posterior commissure.	C. pygocytophora Brown

+Represents the cercariae recorded in the present study.

PART 2

The second part of this thesis deals with accounts of the life cycles of four species of the cercariae described in Part I.

C. londonensis n. sp. was found to develop into a species of the genus Echinostoma and C. essexensis into a species of Hypoderaeum. C. tetraglandis was found to develop into tetracotyle in freshwater leeches, but the attempts to obtain the adult stage were unsuccessful. C. bushiensis n. sp. developed into a species of the genus Cyathocotyle.

The stages in the life history of Echinostoma londonensis n. sp., Hypoderaeum essexensis n. sp. and Cyathocotyle bushiensis n. sp. and the transformation of C. tetraglandis into tetracotyles in leeches are described here.

Explanation to Plate 26

Echinostoma londonensis n. sp.

fig. 1 Egg capsule.

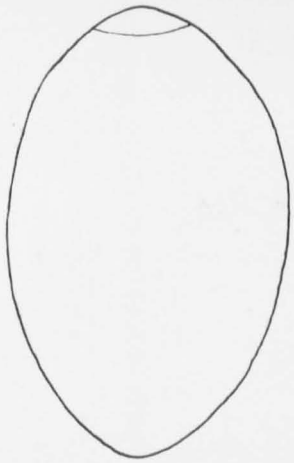
fig. 2 Egg, with fully developed miracidium inside.

fig. 3 Miracidium, general structure.

fig. 4 Anterior end of the miracidium, showing the apical papilla.

fig. 5 Epidermal plates of the miracidium (dorsal view).

Plate 26



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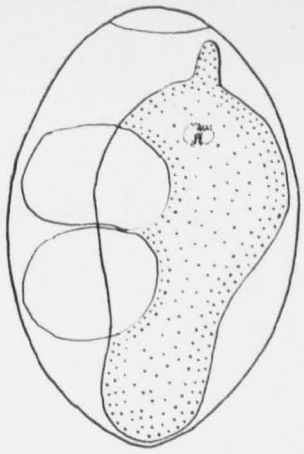

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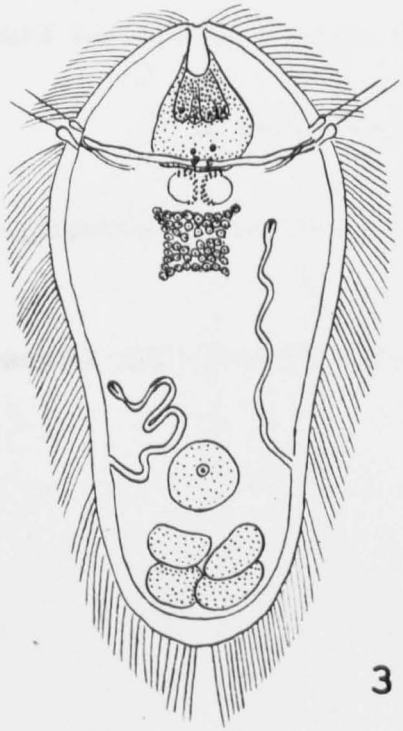

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1. Life History of Echinostoma londonensis n. sp.

C. londonensis n. sp. was found to encyst in snails. When these cysts were fed to pigeons, they developed into a species of Echinostoma. Different stages in the life history were studied and are described below.

Egg (Plate 26, fig. 1)

The eggs are oval in shape, operculate and yellowish brown in colour. The extra-uterine eggs measure 0.1 - 0.12 mm. long and 0.06 - 0.075 mm. broad and are unembryonated when laid.

Miracidium (Plate 26, figs. 2, 3 and 4)

The eggs were collected from experimentally infected pigeons, concentrated and allowed to incubate in distilled water at the room temperature. The miracidium was found to be fully formed in four weeks. At this stage, the miracidium exhibits slow movements of contraction and extension after long intervals. The essential structures such as eyespots, flame cells, cilia and, to some extent, the epidermal plates may easily be seen through the eggshell. As the miracidium is longer than the egg shell, it lies with a bend on the ventral side and occupies more than half the space inside the shell. The rest of the space is occupied by two refractile globules. The apical papilla

is almost always facing the opercular end.

The emergence of the miracidia commences after five weeks. All the miracidia do not hatch in one day and the hatching continues for about one week. The emergence of the miracidia was seen to be particularly facilitated by change of water and exposure to strong light. In the absence of these aids, very few miracidia were found to hatch.

When the miracidium is ready to hatch, it becomes very active and strikes against the operculum vigorously with the apical papilla. The body contracts and expands quickly and cilia start beating very actively.

The liberated miracidia are very active and swim in all directions. Their movement may be temporarily slowed down on striking against a solid object or on reaching the surface of the water. When swimming at a lower speed the body is seen to be rotating on its long axis along with forward movement. In a Petri-dish, although the miracidia are found in all parts and depths of the water, more of them are always found near the periphery slightly below the surface and nearest to the light source.

To determine whether the miracidia show any response to light, one half of the Petri-dish was placed in comparative darkness, while the other half was exposed to strong light. It was noticed that a much larger proportion

of the miracidia were always found in the lighted half of the container and only a few were seen in the dark area.

The miracidium is elongated with the maximum girth at about one third of its length from the anterior end. The living miracidia measure from 0.1 - 0.14 mm. in length and 0.071 - 0.08 mm. in breadth. The body is covered with long cilia born on nucleated epidermal plates. The epidermal plates (Plate 26, fig. 5) are arranged in four tiers. The first tier has six, roughly triangular plates, of which two are dorsal, two lateral and two ventral in position. The epidermal plates of the first tier measure 0.18 - 0.023 mm. long with a maximum breadth of 0.013 - 0.016 mm. The second tier also has six epidermal plates of which two are dorsal, two lateral and two ventral in position. The epidermal plates of the second tier are squarish in shape and measure 0.024 - 0.027 mm. long and 0.018 - 0.022 mm. broad.

The third tier has four rectangular epidermal plates of which two are dorso-lateral and two ventro-lateral in position. The epidermal plates of the third tier measure 0.05 - 0.07 mm. long and 0.03 - 0.037 mm. broad. There are only two epidermal plates in the last tier. One of these is dorsal in position and the other ventral, measuring 0.03 - 0.04 x 0.04 - 0.05 mm. The arrangement of the epidermal plates may be expressed as 6:6:4:2.

The distance between the first and the second tiers

of epidermal plates is greater than between other tiers. The cilia, which beat from the anterior posteriorly, are about the same size on all plates. Very often, the cilia at the anterior sides and the posterior end seem to be larger than at the other parts of the body. This is because at these places the cilia are not very sharply bent backwards and their full length may be seen.

At the anterior end of the body is a retractile apical papilla (Plate 26, fig. 4). This papilla can be completely withdrawn and may remain so for a long time. In several cases when a miracidium was being studied, this organ was found to be completely retracted. Slightly behind the tip of the apical papilla is a circle of long hair-like structures, about six to eight in number and longer than the body cilia but inactive. These hair-like structures might be sensory in function. No mouth opening could be seen.

Between the first and second tier of the epidermal plate is a collar-like fold of the body. Laterally between the first and the second tier of the epidermal plates on each side is a pair of small processes, the lateral processes. Each of these processes has a narrow stalk and a swollen apical part. The apical part of the one of these lateral processes on each side is broader than the other. Each of them bears a long hair-like process, longer and stiffer than the cilia and inactive. A very fine duct was seen

to proceed from the lateral processes towards the central nerve mass, but its connection with any internal structure could not be established. Very often, particularly when the miracidium is about to die, a small droplet was seen to extrude at the tip of these lateral processes.

Just behind the apical papilla are four glands, the penetration glands, with very coarsely granular contents and clear nuclei. The walls of the penetration gland cells are poorly developed and are difficult to see. They may often appear as a single flask-shaped structure with four nuclei at the posterior end. Their contents seem to extend, probably into their duct, up to the tip of the apical papilla.

Extending from behind the apical papilla to the level of eyespots, lying beneath the penetration glands, is a broad, saccular organ, the so called "primitive gut". The contents of this organ are finely granular and homogenous, and at the posterior end, there are four large nuclei. The walls of this organ do not exhibit a cellular nature and there are no appendages of this organ. In miracidia which are about to die under the pressure of a cover glass a small drop of clear liquid was seen to ooze out of the tip of the apical papilla. This liquid was, however, quite unlike the contents of the penetration glands or of the primitive gut. The central nervous system is represented by a quadrangular mass of nervous tissue with

several superficial nuclei, possibly of the nerve cells. On the anterior and dorsal side of the central nerve mass is a pair of prominent eyespots. Each eyespot is made up of a pair of crescents of dark granules with a clear lens on the outer concave side. These eyespots may touch each other mesially or may even overlap, but are never fused into a single mass.

There is one pair of asymmetrically placed flame cells. The anterior, on the right side, is situated at the level of the eyespots. The posterior, or the left flame cell, is nearly in the middle of the third tier of epidermal plates. The right flame cell is ventral in position while the left is dorsal. The excretory ducts of each flame cell opens independently between the third and fourth tiers of epidermal plates on the corresponding side.

The germinal cell is represented by a single large nucleated cell between the third and the fourth tiers of epidermal plates. At the posterior end of the body there are four cells more prominent and larger than the other cells in the body. Their nature is not known (Plate 26, fig. 3).

Discussion

The number and the arrangement of the epidermal plates in the miracidium has been described for six other members

of the family Echinostomatidae, i.e. Hypoderaeum conoideum by Mathias (1925), in Echinoparyphium recurvatum by Rasin (1933), in Euparyphium ilocanum by Tubangui and Pasco (1933), in Echinostoma revolutum by Beaver (1937), in Parorchis acanthus by Rees (1940) and in E. flexum by Najarian (1954). In all the above cases, the arrangement of the epidermal plates is 6:6:4:2, except in P. acanthus and E. ilocanum where it is 6:7:4:2 and 6:5:4:3 respectively.

The use of the number and arrangement of the epidermal plates in establishing the relationship between different families or between the members of the same faily as suggested by several workers (Stunkard, 1923; La Rue, 1926b; Price, 1931; Hunter and Hunter, 1934; Bennet, 1936; Beaver, 1937 and Tang, 1941b) appears to be of doubtful nature as the members of one family may have different number and arrangement of the epidermal plates. This view is further supported by the fact that variations occur in the members of even one species, as shown by Lynch (1933) in the miracidium of Heronimus chelydrae, Thomas (1883) in Fasciola hepatica and Pearson (1956) in Alaria arisaemoides. Lynch (1933) and Dobrovolny (1939) have already expressed the opinion that the number and the arrangement of the epidermal plates in the miracidium is not a reliable index of the family relationship. The fact that the members of some unrelated families may have miracidia with identical number and arrangement of the epidermal plates also supports this view.

The lateral processes between the first and the second tiers were clearly seen to be present in slightly flattened specimens. These structures have been given different names. Cort (1919) calls them "anterior ducts", Faust and Meleney (1924) describe them as "lateral ducts", Van Haitsma (1931), Price (1931), Tubangui and Pasco (1933), Rees (1940), Wall (1951) and Pearson (1956) have designated these processes as "lateral processes" while Hunter and Hunter (1935) have named them as "lateral papillae" and Reisinger (1923), Lynch (1933) and Bennet (1936) call them "sense papillae". These structures have been described for the miracidium of P. acanthus by Rees (1940) and for E. flexum by Najarian (1954). Tubangui and Pasco (1933) found only one process on each side of the miracidium of E. ilocanum. However, these processes in the present miracidium are more like those described for the strigeids in having a long hair-like structure attached to them.

Sewell (1922) suggested that the lateral processes in the miracidium of Schistosoma haematobium are the vesicular swellings of a peripheral system of canals running between the epidermal plates. Price (1931) and Pearson (1956) have refuted this view. Pearson (1956) also suggested that Sewell has mistaken the spaces between the epidermal plates for canals.

Willmott (1952) has denied the presence of any true processes in the miracidium of Paramphistomum hibernae

and regards them as nothing but cytoplasmic extrusions which appear specially in the moribund miracidia. This is not correct at least in the present miracidium. The extrusion of a droplet has also been noted in several other miracidia.

Cort (1919) and Stunkard (1923) did not find any internal associations with these processes. Price (1931), Bennet (1936) and Pearson (1956) could find a small duct leading inwards from these structures. Faust and Meleney (1924), Hunter and Hunter (1935), Rao (1937) and Sinha and Srivastava (1960) found these ducts to be connected with a vesicle, which has been called by the first authors as "lateral or mucoid glands". A similar structure has also been sketched by Van Haitsma (1931b) in the miracidium of Diplostomum flexicaudum.

Reisinger (1923) found these processes to be supplied with nerve fibres and suggested a sensory function. Lynch (1933), Bennet (1936), Rees (1940), Wall (1951) and Hugghins (1954) also suggest a sensory function for these processes. Rees (1940) also suggested that they play a role in the liberation of the miracidium from the egg-capsule.

I was unable to see a true mouth opening in the present miracidium as described in some other miracidia by Barlow (1925), Sinitsin (1931) and Rees (1940). Price (1931) and Tubangui and Pasco (1933) were also unable to see a mouth opening as described by the above authors.

The so called "primitive gut" of the miracidium has

been regarded as a functional gut full of granular contents derived from the digestion of the material received from the vitelline cells of the egg. Porter (1938) has also observed the presence of very small caeca at the posterior end of this structure in the miracidium of S. haematobium. Several authors regard it as non-functional rudimentary gut (Thomas, 1883; Looss, 1896; Ortmann, 1908, Johnson, 1920; Sewell, 1922; Stunkard, 1923; Faust and Meleney, 1924; Barlow, 1925; Sinitsin, 1931; Krull and Price, 1932; Tubangui, 1932b; Tubangui and Pasco, 1933 and Olsen, 1937). While others (Reisinger, 1923; Manter, 1926; Price, 1931; Lynch, 1933; Hunter and Hunter, 1934; Bennet, 1936; Park, 1936; Odlaug, 1940; Rees, 1940; Chandler, 1942; Hugghins, 1954 and Pearson, 1956) have regarded it as a glandular organ, which has been termed Apical gland by Lynch (1933). Van Haitsma (1931) suggests that this organ is a rudimentary gut which also serves some part in the penetration of the miracidium into the snail.

Although very often a small droplet is seen to ooze out of the tip of the apical papilla, it was never found to be similar to the contents of the "rudimentary gut". As argued by Hunter and Hunter (1935) that in its short life span, a miracidium would not need a functional gut and in the absence of a lumen in this structure it seems more plausible to regard this organ as glandular in function.

The pigment of the eyespots in the miracidia of

E. revolutum (Johnson, 1920), E. murium (Tubangui, 1932), E. ilocanum (Tubangui and Pasco, 1933) and E. flexum (Najarian, 1954) has been shown to be fused into a single mass, which was never found to be the case in the present miracidium, although the two masses may join in the middle or even overlap depending on the contraction of the body.

Penetration into Snail

When placed in a watch glass along with a prospective snail host, the miracidium does not exhibit any chemotactic reaction, nor does it swim directly towards the snail. Any contact with the snail is purely accidental, which may occur during the course of its normal swimming. Even after touching such parts of the snails, which might not be suitable for penetration, it usually swims away from it after a few seconds of probing with its apical papilla. Very often a miracidium may get entangled in the slime secreted by a snail. In such an event, the movements of the miracidium are very much slowed, but its slow forwards movement through the slime may continue for some time.

The snail reacts violently to the penetration of a miracidium. It usually withdraws itself into the shell and secretes a thick coat of slime, following the penetration of a miracidium. This secretion might be serving as a mechanical barrier against the entry of any more miracidia.

In the present study only young P. corneus were used

for the above experiments. Most of the snails which had been exposed to the miracidia were found to die after six to seven days.

The actual penetration of the miracidium into the snail was not observed.

Redia and cercaria have been described in the first part of this thesis.

Cyst

The structure and the size of the cyst has been described in the first part of this thesis. The metacercaria lies coiled inside the cyst and is capable of some movements. The flame cells are always seen to be functioning. It was not possible to break the cyst without injuring the metacercaria.

C. echinata and C.E. revolutum have been described to encyst in freedom by Wesenberg-Lund (1934) and Caballero and Larios (1940). Faust (1918) has also seen C. trisolenata to encyst in the open. Stunkard and Cable (1932) and Rees (1940) found that C.P. avitus and C.p. acanthus may also encyst in the open. This was never seen to happen in the present cercaria.

A wide variety of animals has been shown to serve as second intermediate host of the echinostomes, such as Planarians (Johnson, 1920; Macy, 1942), Leeches, turbellarians and Batrachia (Caballero and Larios, 1940), Fish (Beaver, 1937),

Tadpoles (Lutz, 1924; Tsuchimochi, 1926; Fallis, 1934; Beaver, 1937 and Johnston and Angel, 1941). However, only freshwater snails were used as second intermediate hosts in this study.

Whenever P. corneus, L. stagnalis and L. pereger are exposed to the cercariae in the same container, it was found that maximum number of cercariae encysted in L. pereger and the minimum number in P. corneus. It is suggested that when the opportunity presents itself the echinostome cercariae show a slight host preference. Such host preference was also noted by Beaver (1937) in E. revolutum.

Faust (1917, 1924a) states that C. biflexa and C. checkiensis may encyst without leaving the first intermediate host. Johnson (1926) also thinks that this shortening of the process often takes place in E. revolutum. Tubangui (1932b) describes a very short, if at all, free life for the cercaria of E. murium. Wesenberg-Lund (1934) is of the opinion that the echinostome cercariae normally leave the first intermediate host, but may encyst without leaving it under abnormal conditions. On the other hand, Chatterji (1933) (C. palustris), Krull (1935) (E. coalitum) and Miller (1936) (C. trivolvis) are of the opinion that these cercariae essentially have a free swimming life.

In the present investigation it was noted that when the snails were exposed to a large number of cercariae,

the entrance of the cercariae into them was not accomplished quickly. Always a long time (six to eight hours) passed before any noticeable number of the cercariae were found to have penetrated into the snails, although a close proximity of the snails and the cercariae occurred.

At the same time in one tank both the infected, cercariae-discharging snails and the uninfected free snails were kept together for six weeks. After this period all of these snails were dissected and it was found that cercaria-discharging snails harboured much fewer cysts than the other snails. Both these observations seem to suggest that under normal conditions at least, the cercariae of this species must leave the original host for a free swimming life, although they may subsequently re-enter the same snail for encystation.

In several other echinostome cercariae it has been noted that the cysts are found only on certain organs of the second intermediate hosts (Fillipi, 1854; Sewell, 1922; Mathias, 1925; Brown, 1926; McCoy, 1929; Wesenberg-Lund, 1934; Ono, 1935 and Johnston and Angel, 1941). The cysts of the species under study were also always found on the renal organ except two instances when five and seven cysts respectively were found in the digestive gland.

Johnson (1920) has suggested that the metacercaria of E. revolutum absorbs moisture and perhaps food through the cyst wall and Krull (1935) has stated that the cysts

of E. coalitum grow in size as they grow older. The cysts in the present study, however, were not found to grow in size with age. The cysts were found to remain alive and infective for up to six months and perhaps even longer.

As will be seen from the feeding experiments, the cysts which are at least four days old are infective and the younger cysts failed to develop into adults.

Feeding Experiments

Experiment No. 1

Animal	No. of cysts fed	Age of cysts	Examination of faeces: Days after feeding 1	2	3	4	5	6	7	8	9	Results of autopsy
Rat 1	200	4 weeks	-	-	-	-	-	-	-	-	-	Nil
Rat 2	100	4 weeks	-	-	-	-	-	-	-	-	-	Nil
Rat 3	100	4 weeks	-	-	-	-	-	-	-	-	-	Nil
Duckling 1	200	4 weeks	-	-	-	-	-	-	-	-	-	Nil
Duckling 2	100	4 weeks	-	-	-	-	-	-	-	-	-	Nil
Pigeon 1	100	4 weeks	-	-	-	-	-	-	-	+	+ +	10 adults
Pigeon 2	200	4 weeks	-	-	-	-	-	-	-	+	+ +	20 adults
Pigeon 3	500	4 weeks	-	-	-	-	-	-	died of acute enteritis			
Pigeon 4	1,000	4 weeks	-	-	-	-	-	-	died of acute enteritis			

Experiment No. 2

Animal	No. of cysts fed	Age of cysts	Examination of faeces: Days after feeding 1	2	3	4	5	6	7	8	9	Results of autopsy
Pigeon 5	100	1 day	-	-	-	-	-	-	-	-	-	Nil
Pigeon 6	200	1 day	-	-	-	-	-	-	-	-	-	Nil
Pigeon 7	100	2 days	-	-	-	-	-	-	-	-	-	Nil
Pigeon 8	200	2 days	-	-	-	-	-	-	-	-	-	Nil
Pigeon 9	100	3 days	-	-	-	-	-	-	-	-	-	Nil
Pigeon 10	200	3 days	-	-	-	-	-	-	-	-	-	Nil
Pigeon 11	100	4 days	-	-	-	-	-	-	-	+	+	15 adults
Pigeon 12	200	5 days	-	-	-	-	-	-	-	+	+	23 adults
Pigeon 13	100	6 months	-	-	-	-	-	-	-	+	+	18 adults

Experiment No. 3

Animal	No. of cysts fed	Age of cysts	Examination of faeces: Days after feeding 9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	25	27
Pigeon 14	100	2 weeks	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-
Pigeon 15	100	2 weeks	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-
Pigeon 16	100	2 weeks	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-	-
Pigeon 17	100	2 weeks	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-
Pigeon 18	100	2 weeks	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-	-
Pigeon 19	100	2 weeks	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-
Pigeon 20	100	2 weeks	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	-

+ = eggs present in faeces

- = eggs absent in faeces

Explanation to Plate 27

Echinostoma londonensis n. sp.

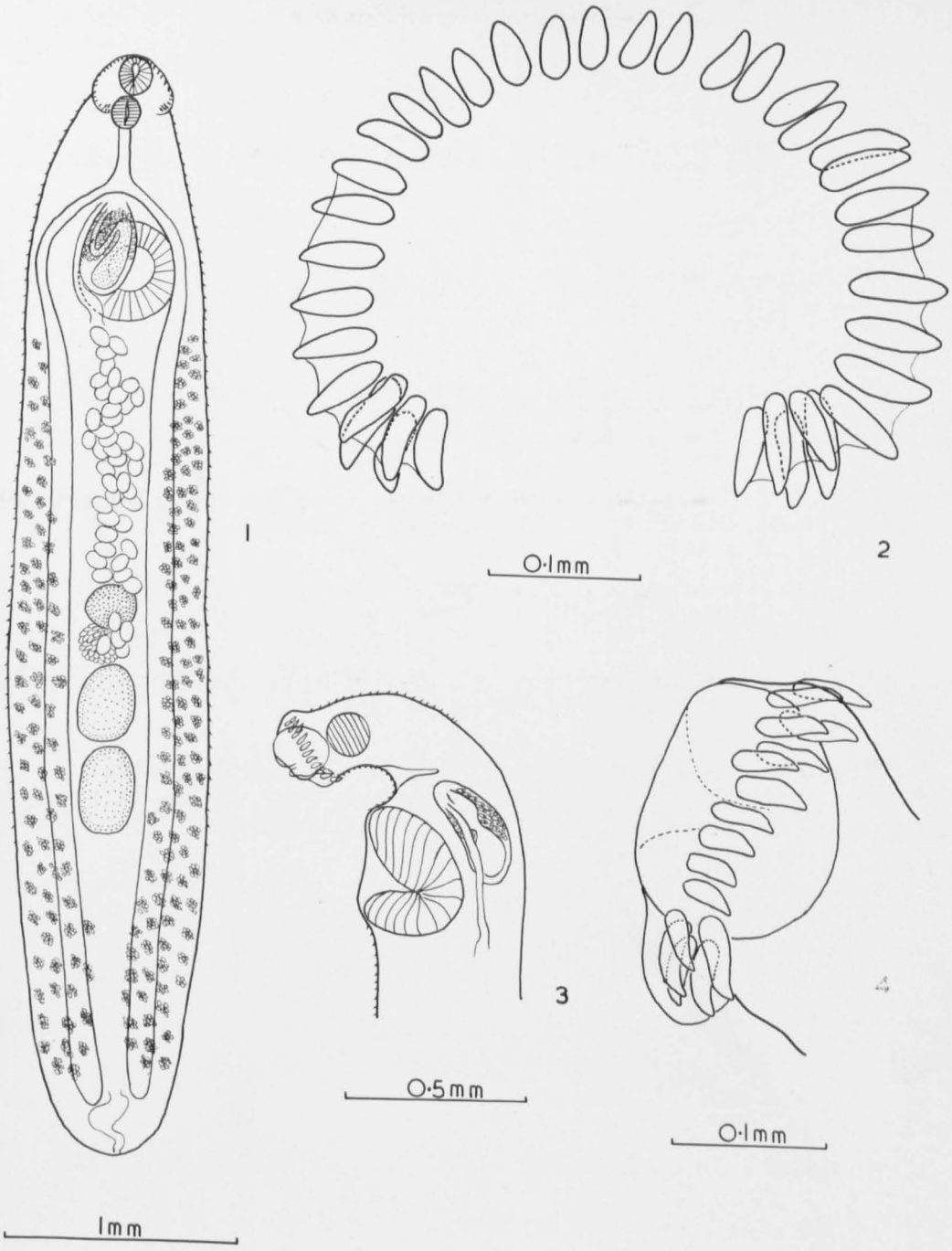
fig. 1 General structure of the adult (dorsal view).

fig. 2 Collar spination.

fig. 3 Anterior end of the adult (lateral view).

fig. 4 Collar spination from lateral side.

Plate 27



Conclusions from the feeding experiments

The following conclusions may be drawn from the above experiments:

1. Rats and ducklings do not serve as final hosts for this trematode. Pigeons are suitable hosts.
2. About 20 per cent of the cysts develop into adults.
3. The cysts which are less than four days old are not infective.
4. The trematodes attain maturity in eight days after being fed to the final host.
5. In heavy infections the trematodes cause acute enteritis and kill the host.
6. After attaining maturity, the adult trematodes remain for one to two weeks in the host after which they are passed out.

The adult echinostomes are always found in the large intestine of the host. In no pigeon which was dissected were any adults found in the small intestine.

Adult (Plate 27, figs. 1-4)

The general shape of the body is elongated, dorso-ventrally flattened with the greatest width usually in the uterine region but sometimes in the region of the ventral sucker.

There is a well developed collar at the anterior end.

The collar is continuous over the dorsal side and bears thirty-seven spines (Plate 27, figs. 2 and 4). Five of these collar spines on each side constitute a corner group, with three oral in position and two more deeply set and aboral. The outer aboral corner spine is always larger than the rest. There are four lateral unalternating spines on each side. The nineteen dorsal spines are arranged in two rows of alternating spines, the oral series with ten spines and the aboral series with nine. The rows of dorsal spines are continuous over the dorsal side. The aboral dorsal spines are continuous with the lateral spines. In properly fixed specimens, which were fixed soon after the dissection of the host, the number and the arrangement of spines was found to be constant.

The body spination extends from just behind the collar to the level of the ventral sucker on the dorsal side and to the posterior testis or sometimes beyond on the ventral and the lateral sides.

The oral sucker is sub-terminal with a uniform edge of its aperture and followed by a very short prepharynx, which is usually completely hidden in the whole mounts. The muscular pharynx is well developed and only slightly smaller than the oral sucker. The pharynx is usually longer than broad. The oesophagus divides just in front of the ventral sucker and the caeca extend to near the posterior end of the body. The ventral sucker is about

one sixth to one eighth of the body length from the anterior end and about two and a half times the size of the oral sucker. The edge of its aperture is wavy.

The testes are tendem and nearly spherical to ovoid in shape in specimens fixed without any pressure. In specimens fixed under pressure, the testes invariably become more or less lobed. They are located in the posterior half of the middle third of the body. The anterior testis is somewhat smaller than the posterior. The pyriform cirrus sac (Plate 27, fig. 3) is muscular and always lies dorsal to the ventral sucker in specimens fixed without any pressure, but in those fixed under pressure it comes to lie to the right side of the ventral sucker. In size the cirrus sac is as long as or slightly smaller than the ventral sucker but less broad. The seminal vesicle is well developed and coiled. The pars-prostatica is voluminous and the muscular, unspined cirrus when fully protruded may be even longer than the cirrus pouch.

The ovary is situated just behind the equator and is spheroidal in shape. The diffuse shell gland is well developed and nearly the same size as the ovary. The uterus has eight to ten coils up to the ventral sucker, after which it runs alongside the cirrus sac and opens into a common genital aperture, which is immediately post-bifurcal. A proper common genital atrium is not present. The

vitellaria are in the shape of small rosette-shaped clusters, extending from just behind the ventral sucker to near the posterior end of the body. In front of the anterior testis the vitellaria are extracaecal. Behind the testicular region they extend into the intercaecal space, but never meet in the middle.

Measurement of nine-days old adults

Body length	4.05 -5.4
Body breadth	0.405-0.93
Collar across	0.3 -0.375
Oral sucker	0.15 -0.195x 0.135-0.18
Prepharynx	0.015-0.048
Pharynx	0.12 -0.165x 0.12 -0.135
Oesophagus	0.225-0.345
Ventral sucker	0.36 -0.51x 0.39 -0.51
Cirrus sac	0.295-0.42x 0.18 -0.27
Ovary	0.12 -0.21x 0.165-0.255
Anterior testis	0.195-0.33x 0.195-0.285
Posterior testis	0.24 -0.375x 0.21 -0.27
Corner spines	
Inner aboral	0.040-0.046x0.013-0.016
Middle aboral	0.043-0.050x0.013-0.016
Outer aboral	0.043-0.046x0.013-0.016
Inner oral	0.040-0.046x0.016
Outer oral	0.050-0.060x0.016-0.023

Lateral spines	0.046-0.053x0.013-0.016
Dorsal spines	
Oral	0.05 -0.063x0.016-0.020
Aboral	0.046-0.056x0.016-0.020

Comparison of E. londonensis n. sp. with Related Species

Echinostoma revolutum (Froel, 1802) Dietz, 1909; E. ralli Yamaguti, 1934; E. robustum Yamaguti, 1935; E. lindoensis Sandground and Bonne, 1940; E. revolutum tenuicolis Baschkirova, 1941; E. goldi Oschmarin, 1956; E. stromi Baschkirova, 1946; E. sp. Sadovskaja, 1952 are the recognised thirty-seven spined species of the genus Echinostoma.

All these species exhibit a remarkable similarity in their morphology. Because of the considerable range of size which the adults of a species can attain, the absolute size of these trematodes is of no value in separating different species.

Beaver (1937) after an extensive study of the morphology and life history of E. revolutum, has regarded a large number of previously described species of the genus as synonymous of E. revolutum. He has recommended that the number and the arrangement of collar spines, length of the uterus and the comparative size of the two suckers and the pharynx as the reliable specific characters.

Yamaguti (1933, 1934), Bonne, Bras and Joe (1948) and

Bras, Bonne and Joe (1953) consider the size of the collar spines as of diagnostic value, while Sandground and Bonne (1940) attach considerable importance to the biological differences in determining the species among the genus Echinostoma.

E. ralli has a group of four corner spines, while E. goldi has six corner spines on each side. Both of these species differ from the present species which has a group of five corner spines. Both of these also have a different proportion between the two suckers.

The arrangement of the collar spines of E. sp. has not been described in detail but is figured to have three corner spines on one side and only one on the other, an arrangement quite different from the present species. It also differs from the present species in having considerably different proportion between the two suckers.

E. revolutum tenuicolis, E. stromiae, E. lindoensis and E. robustum all have larger collar spines than the present species. E. revolutum tenuicolis, E. lindoensis and E. robustum also have a different proportion between the two suckers, while in E. stromiae the pharynx is less than half the size of the oral sucker. E. lindoensis can also be separated in having a different cercarial stage.

E. revolutum differs from the present species in having six lateral spines on each side, in having a different proportion between the two suckers and in the larger size

of the collar spines. The present species can further be separated from E. revolutum in having a distinguishable cercaria and in its inability to develop in rats.

The present species is therefore regarded as new and named Echinostoma londonensis.

Explanation to Plate 28

Hypoderaeum essexensis n. sp.

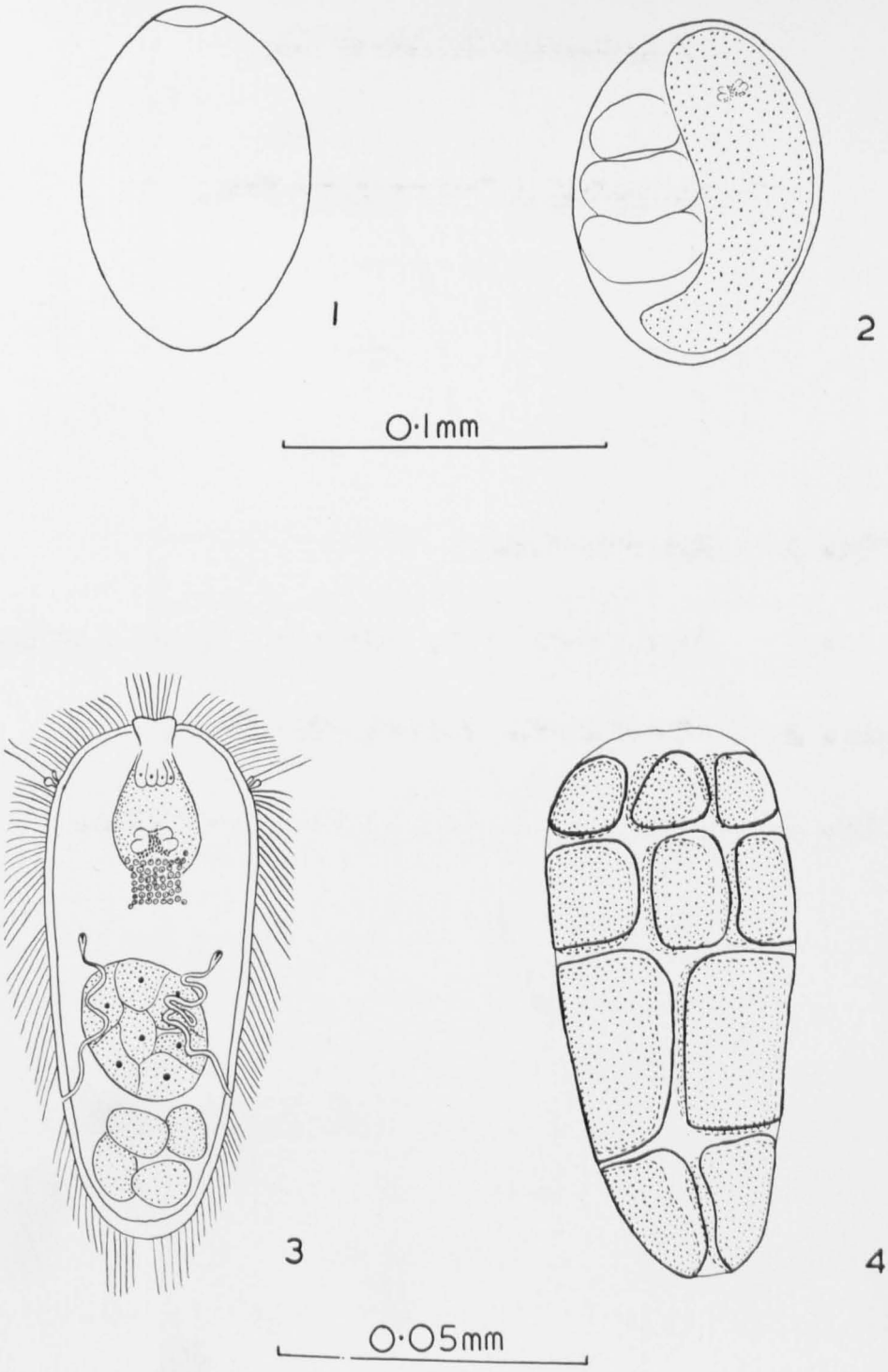
fig. 1 Egg capsule.

fig. 2 Egg, with fully developed miracidium inside.

fig. 3 Miracidium, general structure.

fig. 4 Epidermal plates of the miracidium.

Plate 28



2. Life History of Hypoderaeum essexensis n. sp.

As stated in the first part of this thesis, the life history of C. essexensis n. sp. was completed in the laboratory. The cysts from the snails when fed to ducklings, chickens or pigeons produced adults which belong to the genus Hypoderaeum. The descriptions of the different stages in the life history are given below.

Egg (Plate 28, fig. 1)

The eggs are yellowish in colour, operculate, oval in shape and unembryonated when laid. The extra-uterine eggs measure 0.103 - 0.110 mm. long and 0.073 - 0.076 mm. broad.

Miracidium (Plate 28, figs. 2, 3 and 4)

The eggs collected from the experimentally infected ducklings were repeatedly washed with distilled water and allowed to incubate in distilled water kept in Petri-dishes at room temperature. The miracidia were found to be fully developed in seven to eight days, but were not very active at this stage. The hatching of the miracidia starts on the eleventh or twelfth day. The fully developed miracidium is longer than the eggshell and is consequently curved on one side. There are two or three globules in the part of the eggshell which is not occupied by the

miracidium (Plate 28, fig. 2). When ready to hatch, the miracidium becomes very active and starts striking violently against the operculum, while there is rapid contraction and extension of the body. The hatching is stimulated by the change of old water with fresh water and exposure to strong light, without which few miracidia hatch. The hatching continues for about six days, after which a large number of empty eggshells are seen in the Petri-dish.

The free swimming miracidium is very active and is found swimming in all directions. When swimming at a low speed, they are clearly seen to be rotating on their long axis along with the forward movement. Although the miracidia are distributed to all depths and parts of the water, they are more numerous at the periphery just below the surface and nearest to the light source. When half of the Petri-dish containing the miracidia was placed in a comparative darkness a much larger proportion of the miracidia was seen in the lighted half of the Petri-dish. On striking a solid object the movements of the miracidium are slowed, a quick probing with the apical papilla takes place and the miracidium resumes its swimming actively.

The miracidium is elongated, with the maximum diameter at about one third of the body length from the anterior end. The posterior end is narrower than the anterior. The living miracidium measures 0.071 - 0.111 mm. in length

and 0.05 - 0.07 mm. in breadth, while fixed in hot formalin they measure 0.071 - 0.08 mm. long and 0.038 and 0.041 mm. broad.

At the anterior end is an apical papilla, which usually remains withdrawn and in such a state gives a wrong impression of a mouth opening at the anterior end. The mouth opening is really absent. Just behind the tip of the apical papilla is a circle of six to eight long, hair-like structures which are inactive and probably sensory in function.

The body is covered with four tiers of nucleated epidermal plates (Plate 28, fig. 4). There are six epidermal plates in the first tier, of which one is dorsal, two dorso-lateral, two ventro-lateral and one ventral in position. The roughly triangular epidermal plates of the first tier in silver impregnated specimens measure 0.014 - 0.015 mm. in length and 0.014-0.015 mm. in breadth at the base. The second tier also has six epidermal plates arranged in the same manner as the first tier. The epidermal plates of the second tier are rectangular in shape and measure 0.017 - 0.023 mm. in length and 0.016 - 0.019 mm. in breadth.

There are four rectangular epidermal plates in the third tier, of which two are dorso-lateral and two ventro-lateral in position. The epidermal plates of the third tier measure 0.028 - 0.038 mm. in length and 0.02 - 0.03

in breadth.

There are only two laterally arranged plates in the fourth tier. These roughly triangular plates with rounded angles are 0.02 - 0.027 mm. long and 0.036 - 0.041 mm. in maximum breadth.

The epidermal plates bear long cilia, which beat from forwards backwards. The cilia cover the whole body except the anterior end, the spaces between the epidermal plates and the posterior end. The cilia are all of the same length, but those at the posterior end appear to be larger in the living stage because they are fully outstretched. The cilia are 0.011 - 0.015 mm. long.

Between the first and second tiers of the epidermal plates are two lateral processes on each side. Each process has a narrow basal part and a swollen tip, with a long, stiff hair-like process which is longer than the cilia. The narrow canal leading inwards from the lateral processes could not be observed in the present miracidium. Just behind the apical papilla are four penetration gland cells with poorly demarcated walls, coarsely granular contents and with prominent nuclei. The ducts of the penetration gland cells could not be observed.

Beneath the penetration gland cells, extending from behind the apical papilla to the posterior end of the eye-spots is a broad "primitive gut" with finely granular contents and four nuclei at its posterior end. In moribund

miracidia a small drop of clear fluid was seen to ooze out of the tip of the apical papilla.

The eyespots are prominent and made up of two pairs of crystalline lenses lodged into two crescentic masses of dark brown pigment. These masses of pigment are usually independent of each other but in contracted specimens they may join each other mesially. The eyespots measure 0.006 - 0.008 mm. in diameter.

The two flame cells are nearly symmetrically placed near the middle of the body, their ducts are convoluted and open laterally between the third and fourth tiers of the epidermal plates.

The genital rudiment (Plate 28, fig. 3) is represented by a large mass of deeply staining cells lying just behind the middle of the body. At the posterior end of the body are four, more prominent cells of unknown nature.

Discussion

As in most of the other echinostome miracidia, the epidermal plates in the present miracidium are arranged in 6:6:4:2 manner. The epidermal plates of the last tier are arranged laterally in the present miracidium. This is in contrast with the miracidium of H. conoideum as described by Mathias (1925). This difference in the arrangement of the epidermal plates of the last tier in the two species of Hypoderaeum throws some doubt on the

hypothesis of Najarian (1954) that the epidermal plates of the last two tiers in the miracidia of the members of a genus of echinostomes are always similar.

However, the present miracidium and the miracidium of H. conoideum resemble in other respects the miracidia of the genus Echinoparyphium, i.e. symmetrically placed flame cells, two pairs of eyespots and in the present miracidium, the arrangement of the epidermal plates of the last tier as well.

The study of this miracidium lends further support to the fact that the echinostome miracidia do have two pairs of lateral processes, very much like those described for some strigeid miracidia in having long, hair-like processes at their tips. Although a duct connected with them could not be seen in the present miracidium as in the case of the miracidium of E. londonensis (present study), it is probable that such a structure might be present, because a small drop of fluid was seen to be extruded at the lateral processes in this case as well.

In the possession of two pairs of eyespots and symmetrically placed flame cells the present miracidium differs from the miracidium of E. londonensis (present study).

The present miracidium further differs from that of E. londonensis in possessing a large mass of several cells representing the genital primordium and in having a larger "primitive gut".

Penetration into the Snail

The miracidium does not exhibit any reaction to the presence of a snail near it and continues its usual movements. Any contact between the snail and the miracidium is purely accidental. On touching a part of the snail which might be unsuitable for penetration, a miracidium probes it with its apical papilla for a short time and swims away, as it would do on touching any other solid object in the water. However, the snail reacts violently to the penetration of a miracidium by withdrawing into the shell and by secreting a thick coat of slime which, as suggested before, might be serving as a mechanical barrier for any more miracidia penetrating into the snail. The actual penetration of the miracidium into the snail was not observed.

Redia and Cercaria

The redia and the cercaria stages have been described in the first part of this thesis. Mathias (1925) has demonstrated a sporocyst stage in the life-cycle of *H. conoideum*. A sporocyst stage has also been shown to be present in the life cycles of *E. recurvatum* (vide Rasin, 1933) and *E. flexum* (vide Najarian, 1954). On the contrary, Rees (1940) has shown that the miracidium of *P. acanthus* already has a mother redia developed in it, which would

eliminate the possibility of the existence of a sporocyst stage. No attempt was made during the present study to recover a sporocyst stage.

Cysts

For experimental purposes, only cysts from the laboratory bred snails were used. The structure of the cyst has been described in Part I.

Feeding experiment No. 1

Animal	No. of cysts fed	Age of cysts	Examination of faeces: Days after feeding 1	2	3	4	5	6	7	8	9	10	11	12	13	14	Results of autopsy
Rat 1	100	2 weeks	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Nil
Rat 2	200	2 weeks	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Nil
Pigeon 1	100	2 weeks	-	-	-	-	-	-	-	-	-	-	-	-	+	+	1 adult
Pigeon 2	100	2 weeks	-	-	-	-	-	-	-	-	-	-	-	-	+	+	1 adult
Chicken 1	100	2 weeks	-	-	-	-	-	-	-	-	-	-	-	-	+	+	1 adult
Chicken 2	100	2 weeks	-	-	-	-	-	-	-	-	-	-	-	-	-	+	Nil
Duck 1	100	2 weeks	-	-	-	-	-	-	-	-	-	-	-	-	+	+	15 adults
Duck 2	100	2 weeks	-	-	-	-	-	-	-	-	-	-	-	-	+	+	17 adults
Duck 3	100	2 weeks	-	-	-	-	-	-	-	-	-	-	-	-	+	+	14 adults

+ = eggs present in faeces

- = eggs absent in faeces

Feeding experiment No. 2

Animal	No. of cysts fed	Age of cysts	Examination of faeces: Days after feeding 13	14	15	16	17	18	19	20	21	22	23	24	25	Results of autopsy
Duck 4	100	1 day	-	-	Duck dissected (15th day); no adult found											
Duck 5	100	1 day	-	-	Duck dissected (15th day); no adult found											
Duck 6	100	2 days	-	-	Duck dissected (15th day); no adult found											
Duck 7	100	2 days	-	-	Duck dissected (15th day); no adult found											
Duck 8	100	3 days	-	-	Duck dissected (15th day); no adult found											
Duck 9	100	3 days	-	-	Duck dissected (15th day); no adult found											
Duck 10	100	4 days	+	+	+	+	+	+	+	+	+	+	+	+	+	15 adults
Duck 11	100	4 days	+	+	+	+	+	+	+	+	+	+	+	+	+	12 adults
Duck 12	100	6 days	+	+	+	+	+	+	+	+	+	+	+	+	+	17 adults
Duck 13	100	4 months	+	+	+	+	+	+	+	+	+	+	+	+	+	17 adults

+ = eggs present
− = eggs absent

From the feeding experiments tabulated above, it is evident that, although these trematodes may develop in pigeons and chickens, the percentage of the worms reaching maturity is very low and that these animals are not the proper hosts. The rats do not serve as final hosts at all.

The cysts younger than four days are not infective but the cysts which are as old as four months are infective. It is possible that the cysts remain infective as long as the snails harbouring them live.

Explanation to Plate 29

Hypoderaeum essexensis n. sp.

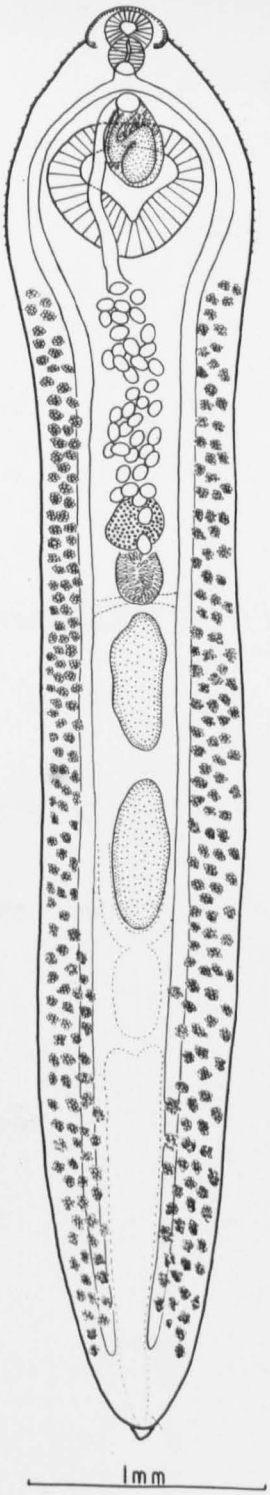
fig. 1 General structure of the adult (dorsal view).

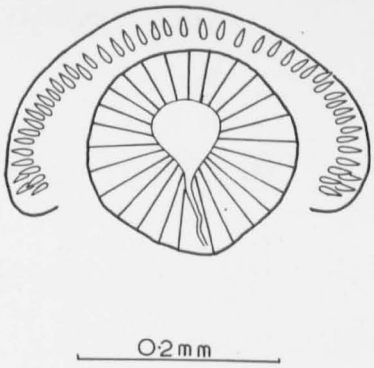
fig. 2 Collar spination.

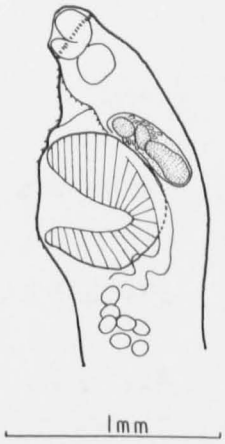
fig. 3 Anterior end of the adult (lateral view).

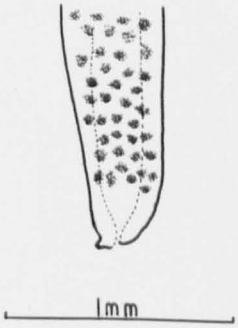
fig. 4 Posterior end of the adult (lateral view).

Plate 29









The maturity is attained in thirteen days when a small number of eggs are found in the faeces. After attaining maturity, the worms are retained by the hosts for a long time, at least two weeks as shown in the second table.

The adult trematodes are always found within three to four inches of the first part of the small intestine. Only in one case were two worms outside this area, but in this case as well they were well within the first half of the small intestine.

Adult (Plate 29, figs. 1-4)

The adult worms are elongate, dorso-ventrally flattened with the anterior end blunt and the posterior end pointed. The maximum breadth is attained at the level of the ventral sucker.

The collar is poorly developed and bears forty-nine spines, of which five on each side constitute a corner group and the rest are arranged in two rows of alternating spines (Plate 29, fig. 2). The spination of the body is arranged in diagonal rows, which extend on the ventral side up to the posterior margin of the ventral sucker. The body spines nearest to the collar extend up to near the mid-dorsal aspect, leaving a narrow naked area on the mid-dorsal surface of the worm. This naked area becomes increasingly larger posteriorly. So that there are no spines on the mid-dorsal side of the worm (Plate 29, fig. 3).

The oral sucker is sub-terminal, followed by a very short prepharynx which is often completely obliterated in fixed and stained specimens. The muscular pharynx is slightly smaller than the oral sucker and is longer than broad. The oesophagus is short and divides some distance in front of the ventral sucker. The intestinal caeca are narrow and extend to near the posterior end of the body.

The ventral sucker is cup-shaped and strongly developed, with strong muscle bands originating from its inner side and extending to the dorsal body wall. The ventral sucker is about three times the size of the oral sucker. The ventral sucker is located at about one fifteenth of the body length from the anterior end.

The two testes are elongated and occupy the third quarter of the body. In fixed specimens they seem to be slightly twisted. This is because of the uneven shrinkage of the testicular material during fixation. However, in living specimens they have a smooth uniform outline. The posterior testis is slightly longer than the anterior testis. The cirrus pouch is well developed and extends to the middle of the ventral sucker. In few cases it was found to extend only slightly behind the middle of the body but was never found to extend to the posterior end of the ventral sucker. The pars-prostatica is poorly developed.

The ovary is elliptical or rounded and is located

slightly pre-equatorial. The shell gland is diffused. The uterus is long with six to nine coils and numerous eggs. It passes over the ventral sucker slightly on the right of the middle line and opens into a common genital opening. A proper common genital atrium is absent. The common genital opening is immediately post-bifurcal.

The vitellaria are in the form of small rosette-shaped clusters starting from the posterior border of the ventral sucker and extending to near the posterior end of the body. Up to the posterior end of the posterior testis, the vitellaria are extracaecal. Behind the testes they cover the intestinal caeca and may at places extend into the intercaecal space but always leave a wide gap in between the vitellaria of two sides.

At the posterior end of the body, there is a small appendage lying above the excretory pore which is slightly on the dorsal side.

Measurements

(All measurements in millimetres)

Body length	4.05 -6.52
Body breadth	0.9 -1.11
Collar across	0.345-0.39
Oral sucker	0.195-0.21x 0.195-0.21
Pharynx	0.15 -0.18x 0.15 -0.165
Ventral sucker	0.615-0.675

Proportion between oral and ventral sucker 1:3

Cirrus sac	0.35 -0.48
Oesophagus	0.06 -0.12
Anterior testis	0.45 -0.63x 0.241-0.285
Posterior testis	0.465-0.675 0.24 -0.33
Ovary	0.195-0.255x 0.225-0.285
Spines length	
Corner spines	0.026-0.03
Edge spines	0.023-0.026

Comparison of H. essexensis n. sp. with Related Species

H. butagensis (Tubangui, 1932) Baschkirova, 1941 can readily be distinguished from the present species in having seventy-two collar spines. H. gnedini Baschkirova, 1941 has fifty-one spines of which five are in a corner group on each, but has its ventral sucker six times as big as the oral sucker which the present species has a proportion of 1:3 between its oral and ventral suckers. It also differs in the extent of its vitellaria behind the posterior testis.

In H. mainpuria Verma, 1936 and H. magnocirrusa Verma, 1936 the number of collar spines is not known. Both species differ from the present one in having a different proportion between the two suckers, in having larger cirrus sacs and in the extension of their body spination up to the region of the ovary. H. microspina (Singh, 1954) Skrjabin and Baschkirova, 1956 has forty-nine spines which

are, according to Singh (1954), arranged in a single row, although his figure shows a group of three corner spines on each side. It further differs in the proportion between its oral and ventral suckers and the size of the collar spines. H. skrjabini Oschmarin, 1946 differs in having four corner spines on each side, in a different proportion between the oral and the ventral sucker and in that its vetellaria meet in the middle behind the testes. H. vigi Baschkirova, 1941 has forty-three spines of much larger size with a group of five corner spines on each side. It can also be differentiated from the species under study in having lobed testes, a different proportion between the two suckers and a comparatively longer cirrus sac. H. sp. Oschmarin, 1956 has forty-seven spines, without any grouping of the corner spines and a different proportion between the oral and ventral sucker. H. conoideum (Bloch, 1782) Dietz, 1909 has been described as possessing forty-seven to fifty-three spines. Rees (1933) found that there is always a group of four corner spines on each side. The present species has always a group of five corner spines on each side and further differs from H. conoideum in having a proportion of 1:3 between the oral and ventral suckers as against 1:4 in H. conoideum (Skrjabin, 1956), and in having a comparatively smaller cirrus sac. The present species can also be separated from H. conoideum in always developing in the first half of the small

intestine, while the latter species always develops in the second half of the small intestine (Rees, 1933). These two species also have distinguishable miracidium, redia and cercaria stages.

The present species is therefore considered as new and the name H. essexensis is proposed for it.

3. Studies on the Development of *C. tetraglandis* Iles, 1959, in Leeches

While this work had been done independently, Iles (1960) briefly described the development of this cercaria into tetracotyles in leeches. She has not given any account of the tetracotyle stage. In the present investigation, this cercaria was also found to penetrate freshwater leeches. The transformation of the cercaria into tetracotyle stage was studied in detail, but the attempts to establish the adult stage were not successful.

Second Intermediate Host

To ascertain the second intermediate host of this cercaria, laboratory bred snails and leeches were tried. Among the snails *P. corneus*, *L. stagnalis* and *L. pereger* were exposed to the free swimming cercariae, but no cercaria was seen to penetrate the above snails. Alternatively, five snails of each species were isolated with a very large number of free swimming cercariae for twenty-four hours. These snails were dissected six days afterwards, but no developing metacercaria was found in them. It was therefore concluded that snails do not serve as second intermediate hosts.

Four species of freshwater leeches, *H. sanguisuga*, *H. stagnalis*, *P. tasselata*, *E. octuculata* and *E. testacea*

were then exposed to the free swimming cercariae. The penetration was seen to occur in all of them and on dissection after six days, developing metacercariae were also found in all of these species. Of all the species of leeches used in this experiment, E. octuculata and E. testacea were found to harbour the largest number of metacercariae. Because of the ease with which these leeches can be fed and kept in the laboratory and because they are easy to dissect, only these species were used for all subsequent experiments.

The infected leeches were kept in the laboratory at a temperature of 26°-27° C. They were dissected at varying periods of time and the metacercariae were studied both in the living as well as in the fixed and stained condition.

Penetration of the Cercaria into a Leech

The leech was placed in a small amount of water with several cercariae in a watch glass and the process of penetration was studied under a dissecting binocular microscope. The cercariae were never found to show any reaction to the presence of the leech and continued their normal swimming. The contact with the leech was always accidental. On being attacked by several cercariae at a time, the leech becomes greatly agitated and starts coiling and uncoiling its body rapidly. This reaction is accompanied by quick

secretion of a thick coat of slime which envelops the body of the leech. The slime prevents more cercariae from reaching the body of the leech.

The cercaria after attaching to the surface of the leech with its ventral sucker, continues probing the surface for a short time with its anterior tip. When the cercaria finds a suitable spot for penetration, the anterior tip of the body is forced into the skin of the leech and probably the contents of the penetration gland cells are also discharged and help in its penetration. By the time about one fifth of the body has penetrated into the leech, the ventral sucker is detached and the body is stretched outwards and becomes long and narrow. The gradual penetration is continued. The tail which continues lashing throughout the above process is cast off when about half of the cercarial body has penetrated into the leech. The complete penetration is accomplished in about ten to fifteen minutes. It is probable that the lashing of the tail helps in pushing the cercaria forwards while the backwardly directed spines on the body of the cercaria prevent it from slipping out of the body of the leech.

The leeches when heavily infected do not show any ill effects until about twenty days after infection, when most of them start dying off. In mildly infected leeches, no ill effects were noted.

Explanation to Plate 30

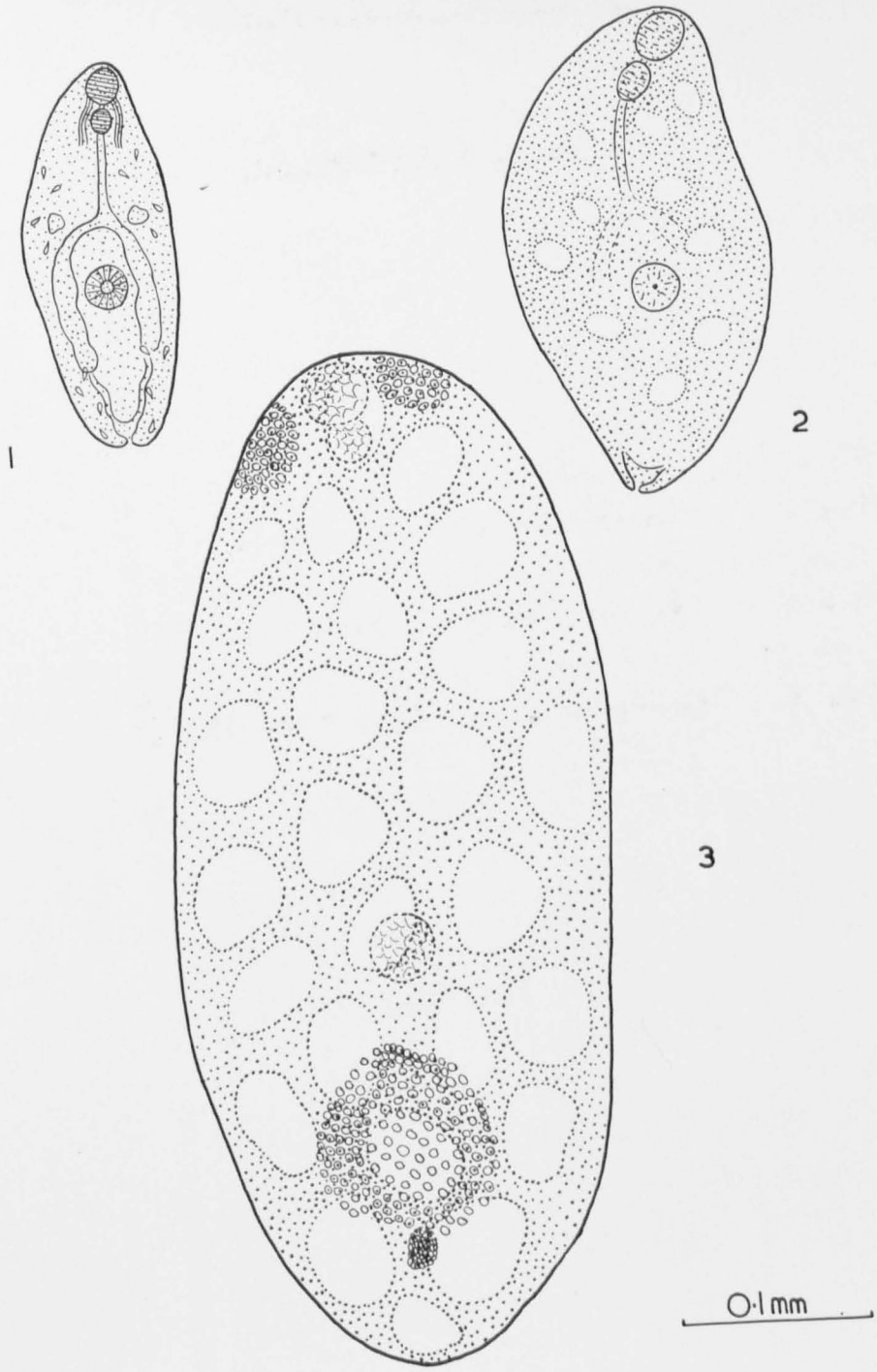
Cercaria tetraglandis

fig. 1 Six days after infection.

fig. 2 Ten days after infection.

fig. 3 Fourteen days after infection.

Plate 30



Development of the Cercaria in Leech

Six days after infection (Plate 30, fig. 1):

The larva is slightly active and larger than the cercarial body. There is no trace of spines on the body or the ventral sucker. The intestinal caeca are distended. The body is filled with numerous rounded cells of varying sizes, some of them are considerably larger than the other, are distinctly nucleated and have a faintly developed flagellum. These are the giant cells or "Riesenzellen" of Szidat (1924) or "cellules giantes" of Dubois (1934).

The excretory bladder is distorted but the flame cell pattern is the same as in the body of the cercaria. The disintegrating ducts of the penetration gland cells may be seen at the sides of the anterior organ, but no trace of the penetration gland cells is visible.

Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.28 -0.36	0.34	0.133-0.253	0.23
Body breadth	0.1 -0.16	0.13	0.056-0.1	0.08
Anterior organ	0.04 -0.048x 0.023-0.028	0.043x 0.026	0.03 -0.043x 0.018-0.026	0.04x 0.02
Pharynx	0.016x0.13	0.016x 0.013	0.01 -0.01	0.01x 0.01
Ventral sucker	0.03 -0.036x 0.03 -0.036	0.033x 0.033	0.023-0.03x 0.023-0.03	0.027x 0.027

Ten days after infection (Plate 30, fig. 2):

The body size increases further. The whole body is full of numerous rounded bodies in which no nuclei are seen. The giant cells also increase in size and their flagella are more prominent. The flagella of some of the giant cells get entangled. A few vacuoles make their appearance. Dubois (1934) has suggested that the vacuoles in the body are formed by the entangling of the flagella of the giant cells.

The excretory bladder and the flame cell pattern is unchanged. The anterior organ, pharynx intestine and the ventral sucker show signs of degeneration. The reserve excretory bladder is also developing and the excretory concretions in it are capable of considerable free movement. The larva is not motile.

Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.316-0.49	0.35	0.285-0.3	0.29
Body breadth	0.17 -0.19	0.17	0.15- 0.165	0.155
Anterior organ	0.036x0.30	0.036x 0.030	0.026x0.024	0.026x 0.024
Pharynx	0.016-0.018x 0.016-0.0183	0.017x 0.017	0.016x0.016	0.016x 0.016
Ventral sucker	0.036x0.036	0.036x 0.036	0.03 x0.03	0.03x 0.03
Giant cells	0.007-0.014			

Fourteen days after infection (Plate 30, fig. 3):

The body has considerably increased in size. The anterior organ, pharynx and ventral sucker are disintegrated. No trace of the alimentary tract could be seen. The body becomes highly vacuolated and a very large number of the flagella of the giant cells are seen to be entangled. The flame cells are mostly obscured, but a few flame cells may be seen when considerable pressure is applied to the larva. The lateral sucking cups make their appearance as a compact mass of cells at the sides of the anterior organ. Another large compact mass of cells lying just in front of the still small genital primordium represents the beginning of the holdfast organ.

Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.55 -0.7	0.065	0.045-0.07	0.057
Body breadth	0.2 -0.4	0.3	0.165-0.27	0.023
Anterior organ rudiment	0.030-0.045x 0.030-0.045	0.04x 0.04	0.03 -0.04x 0.03- 0.04	0.035x 0.035
Pharynx rudiment	0.02 -0.25x 0.02 -0.25			
Ventral sucker rudiment	0.03 -0.04x 0.03 -0.04	0.036x 0.036	0.02 -0.03x 0.02 -0.03	0.025x 0.025
Lateral sucking cup rudiment			0.05 -0.06x 0.04 -0.05	
Holdfast organ rudiment			0.09 -0.15x 0.08 -0.12	

Explanation to Plate 31

Cercaria tetraglandis

fig. 1 Eighteen days after infection.

fig. 2 Twenty-two days after infection.

Plate 3I

Eighteen days after infection (Plate 31, fig. 1)

The body is still thick and fairly opaque. The size has slightly decreased. The suckers and pharynx start reorganizing. The primordia of the lateral sucking cups and the holdfast organ become better defined. The genital primordium is still small. The number of the vacuoles decreases in number and size.

The excretory system and the alimentary tract are obscured, but a few flame cells may be seen on applying considerable pressure on the larva.

Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.43 -0.6	0.50	0.24 -0.39	0.0
Body breadth	0.2 -0.3	0.27	0.07 -0.15	0.12
Anterior organ rudiment	0.055-0.06x 0.053-0.062	0.058x 0.059	0.043x0.043	0.043x 0.043
Pharynx rudiment	0.02 -0.025x 0.02 -0.025	0.022x 0.022	0.023x0.02	0.023x 0.02
Ventral sucker rudiment	0.05 -0.062x 0.053-0.063	0.058x 0.06	0.040-0.046x 0.040-0.046	0.045x 0.045

Twenty-two days after infection (Plate 31, fig. 2):

The body becomes comparatively flattened and is nearly of the same length as that of the eighteen days old larva. A shallow concavity appears on the ventral side. Slight differentiation of the hind body may be seen. The lateral

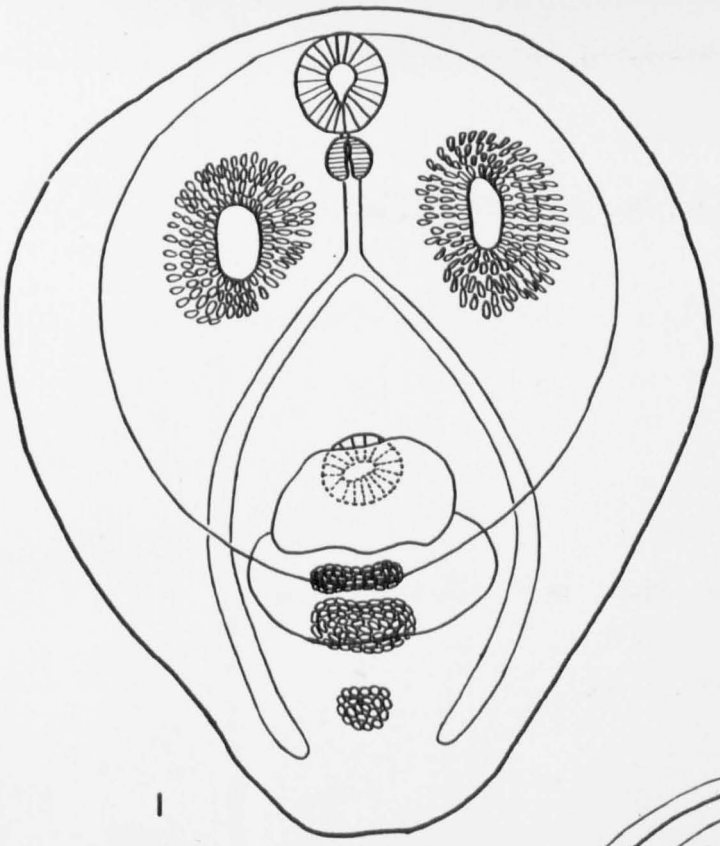
Explanation to Plate 32

Cercaria tetraglandis

fig. 1 Thirty days after infection.

fig. 2 Tetracotyle.

Plate 32



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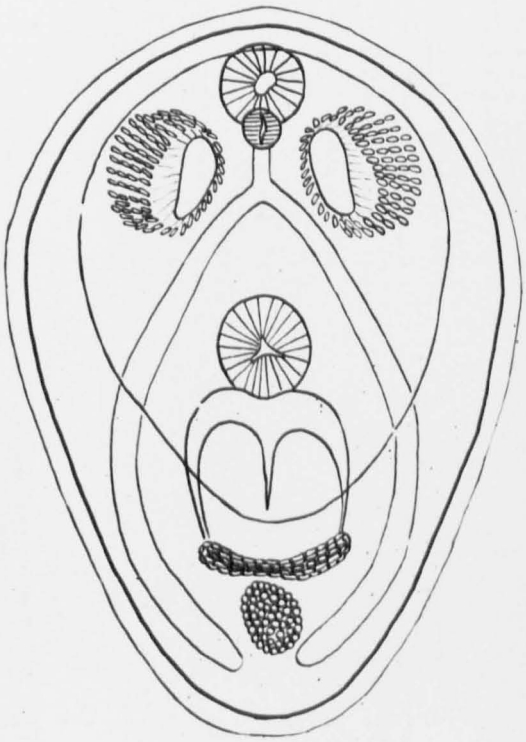

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sucking cups and the holdfast organ are better developed. The suckers and the pharynx are completely reformed, but the oesophagus can only be seen for a short distance behind the pharynx. The caeca could not be seen. The genital primordium is still small.

The vacuoles disappear from the body. Still only a few flame cells are seen in highly pressed specimens. The larva is inactive.

Measurements of Cercaria

	Living		Fixed	
	Range	Average	Range	Average
Body length	0.4 -0.6	0.50	0.39 -0.429	0.4
Body breadth	0.185-0.275	0.25	0.225-0.24	0.023
Oral sucker	0.045-0.060x 0.040-0.060	0.05x 0.05	0.04 -0.043x 0.04 -0.043	0.041x 0.041
Pharynx	0.02 -0.026x 0.02 -0.026	0.024x 0.024	0.02 -0.026x 0.02 -0.026	0.023x 0.023
Ventral sucker	0.045-0.06x 0.048-0.06	0.05x 0.048	0.036-0.04x 0.036-0.04	0.039x 0.039

Thirty days after infection (Plate 32, fig. 1):

The body is smaller than the thirty days old larva but much broader in the anterior half. The larva has assumed the general shape of the tetracotyle. The oral sucker, pharynx and ventral sucker are well developed. The oesophagus bifurcates between the pharynx and the ventral sucker. The intestinal caeca extend nearly to the posterior end of the body. The lateral sucking cups

are well formed and their openings are clearly visible. The holdfast organ has differentiated into two lobes, each with a glandular mass at its base. The genital rudiment is still undifferentiated and small.

A prominent and deep concavity is clearly noticeable on the ventral side, while the hind body is also differentiated. The number of flame cells in the body has increased enormously. Obviously the multiplication of the flame cells has taken place at this stage. The reserve excretory bladder is well formed and the excretory concretions can move freely inside it.

Measurements of Cercaria

(All measurements in millimetres)

	Living		Fixed	
	Range	Average	Range	Average
Forebody length	0.36 -0.55	0.045	0.345-0.36	0.35
Forebody breadth	0.34 -0.43	0.038	0.345-0.37	0.355
Hind body length	0.105-0.12	0.11	0.075-0.09	0.08
Hind body breadth	0.135-0.19	0.162	0.09 -0.105	0.095
Oral sucker	0.053-0.07x 0.053-0.07	0.06x 0.06	0.05 x0.05	0.05x 0.05
Pharynx	0.022-0.029x 0.022-0.029	0.025x 0.025	0.026x0.027	0.026x 0.027
Ventral sucker	0.053-0.07x 0.056-0.07	0.06x 0.06	0.04 -0.05x 0.04 -0.05	0.045 0.045

After this, the larva continues decreasing in size gradually, with increasingly better development of the

lateral sucking cups and the holdfast organ, up to the forty-eighth day, when the tetracotyle is fully formed but still unencysted. The encystment takes place on the forty-ninth day.

Tetracotyle (Plate 32, fig. 2)

The tetracotyle is pear-shaped and invested by a thick cyst wall. The tetracotyles are found in the space between the intestinal tract and the body wall, mostly among the botrioidal tissue of the host. The shape of the cyst is affected to some extent by the pressure of the surrounding tissue of the host and some of the cysts are nearly circular in shape.

The cyst wall is composed of two layers. The inner layer is thinner, tougher and transparent in colour. The outer layer is thicker and gelatinous and also transparent. The outer layer of the cyst wall is traversed by numerous, coiled thread-like structures which may protrude beyond the boundaries of the cyst wall. When fixed in hot formal-saline, the outer cyst wall completely disappears. The posterior end of both the cyst walls is traversed by a wide, posteriorly dilated aperture which is connected to the excretory pore and through which the refractile excretory concretions are periodically shot out. No such canal was observed at the anterior end of the cyst wall. The inner layer of the cyst wall has prominent apertures

opposite the openings of the oral sucker, ventral sucker, lateral sucking cups and holdfast organ.

The body of the tetracotyle has a deep concavity on the ventral side, extending from just in front of the oral sucker to behind the ventral sucker, and leaving only small area on the sides and in front of the oral sucker. The oral sucker, lateral sucking cups, ventral sucker and the holdfast organ open into this concavity.

The hind body is rather poorly demarcated from the fore body. This demarcation may not be easily seen in encysted forms. However, in excysted forms the hind body is usually bent on the underside of the fore body.

At each antero-lateral aspect of the fore body is a lateral sucking cup, formed by a compact mass of parenchymatous tissue enclosing an elongated opening which is directed inwards. The lateral sucking cups are also muscular and are capable of considerable extension.

The well developed holdfast organ is located at the posterior end of the fore body. It is composed of two lips, enclosing a radiating cavity and opening through a small oval aperture ventrally. The two glandular masses as seen in the thirty days old larva have fused into one transversely elongated mass at the base of the holdfast organ. The anterior lip of the holdfast organ is only slightly notched at its free end and usually covers the ventral sucker partly or completely. The posterior lip

has a deep notch, extending almost to its posterior end.

The oral sucker is sub-terminal and the prepharynx practically absent. The oesophagus is narrow and divides nearer to the pharynx than to the ventral sucker. The intestinal caeca extend nearly to the posterior end of the body. The genital primordium lies behind the holdfast organ and is still undifferentiated.

The primary excretory system has numerous flame cells with their associated canals. The pattern of the flame cells or their number was not studied. The reserve excretory bladder consists of an irregular network of spaces, filled with calcareous granules in a hyaline fluid, which can move freely in any direction according to the pressure or movement of the body.

The tetracotyles decrease in size as they grow older. At the same time the outer layer of the cyst wall goes on diminishing in size. In mature tetracotyles a network of highly refractile granules of varying sizes and shapes covers the surface of the metacercaria, except in the area of the suctorial pocket.

Measurements

Living

Cyst length	0.33 -0.405
Cyst breadth	0.24 -0.3
Inner cyst wall	0.005-0.007
Outer cyst wall	0.03 -0.045

Metacercaria

Fixed and Mounted Specimens

	Range	Average
Fore body length	0.2 -0.246	0.223
Forebody breadth	0.203-0.240	0.22
Hind body length	0.08 -0.113	0.1
Hind body breadth	0.106-0.116	0.11
Oral sucker	0.043-0.05x 0.043-0.05	0.046x 0.046
Lateral organs	0.080-0.1x 0.050-0.076	0.089x 0.067
Ventral sucker	0.053-0.057x 0.053-0.057	0.054x 0.054
Anterior lip of the holdfast organ	0.083-0.093x 0.090-0.093	0.088x 0.092
Posterior lip of the holdfast organ	0.053-0.063x 0.076-0.083	0.058x 0.080

Discussion

Several species of tetracotyles have been reported from leeches. The tetracotyle of Cotylurus cornutus (Rud.) has been reported from leeches (Szidat, 1929a,1931) and more frequently from mulluscs (Mathias, 1925; Hughes, 1929; Szidat, 1924). The present tetracotyle was never found to develop in gastropods.

During the transformation of the cercaria into the tetracotyle, all the cercarial structures are disintegrated and reformed while new structures are added during the transformation. The primary excretory system as is also noted by Nasir (1960) in C. brevis is retained throughout the transformation, and the flame cells increase considerably in number through the multiplication of the existing flame cells. Another notable thing in the present investigation is the complete immobility of the developing larva, except for slight powers of contraction and expansion in the early stages. This observation is in contrast to the generally accepted idea that the developing larva is motile up to the stage when the cercarial structures are lost and the larva assumes the typical sac-shaped form. It would, however, be a difficult thing for the present developing larva to be able to move among the strong tissue of the leech especially in the limited space available in small leeches such as those used in the present investigations.

The inner layer of the cyst wall is generally accepted as of parasite origin, while the outer layer is considered to be of host origin (Faust, 1918a, Hughes, 1928).

Oliver (1940), however, regards the outer layer of T.pipientis to be of parasite origin and not of host origin. The apertures in the inner cyst wall opposite the suckers, lateral sucking cups and the holdfast organ have also been described in most other tetracotyles (Diesing, 1858; Filippi, 1859; Linstow, 1894;

1898; Diesing, 1858; De Filippi, 1859; Von Linstow, 1894; Szidat, 1924; Hughes, 1928; Nasir, 1960 and Iles, 1960). Faust (1917) did not observe any apertures in the cyst wall of T. flabelliformis but Hughes (1929a) upon re-examination of Faust's co-type specimens found the apertures. Mathias (1925), however, argued that a true cyst wall should completely isolate the enclosed metacercaria from the host tissue.

The opening in the cyst walls at the posterior end was seen but its counterpart at the anterior end as shown by Szidat (1924, 1929a), Wesenberg-Lund (1934) and Nasir (1960) was not seen.

The eversion of the lateral sucking cups in the present tetracotyle was found to take place after keeping them for a long time in water and is due to excessive imbibation of water as suggested by Hughes (1929) and is not a permanent feature of the mature tetracotyles as believed by Faust (1918a).

Faust (1918a,1922) has suggested that the reserve excretory bladder consists of a regular system of canals. My observations in the present tetracotyle agree with those of Hughes (1928) that this system consists of an "irregular continuous coarse-meshed network of spaces filled with a hyaline fluid containing calcareous granules of variable sizes, which move freely in any direction in response to pressure or movement of the body"; they do not agree with

those of Faust (1918).

Recently, Iles (1960) has also studied out the development of this cercaria into tetracotyles. In her experiments which were carried out at room temperature, this cercaria was found to take a much longer time to complete its transformation into tetracotyles. This time was particularly long during winter months (153 days), while in the present study which was carried out at constant temperature of 25°- 27° C, the time was only forty-nine days, irrespective of the season in which the leeches were infected. Different species of cercariae have previously been reported to complete their transformation into tetracotyles in varying periods of time. Iles (1960) suggests that this variation may be a specific character or may be due to temperature effects. The disparity between the times as given by Iles and in the present study are apparently due to different temperatures at which the two studies were carried out. At the same time Erpobdella testacea which has been regarded as an unsuitable host for this cercaria by Iles, was found to be very suitable in the present study.

Iles (1960) has not given a detailed description of the tetracotyle but her measurements are slightly bigger than found in the present species. She also mentions that the development of the cercariae is not uniform in all her experiments and some cercariae failed to encyst

even after 153 days. This might be due to the temperature effects. In the present study which was carried out at constant temperature all the cercariae were always found to encyst on the 49th day. Another striking difference between these two studies is that in Iles' experiments the lateral sucking cups and the holdfast organ do not develop till very late in the development whereas in the present investigation the primordia of these organs make their appearance very early in the development.

As regards the differentiation of the different species of tetracotyles, the morphology does not serve as a useful character as is also noted by Nasir (1960) and Iles (1960). The tetracotyles as noted in the present study and by Hughes (1928a) and Nasir (1960) decrease in size with the increasing age. Both Hughes (1928a) and Nasir (1960) state that size variation in tetracotyles is not of any taxonomic importance.

Different tetracotyles can, therefore, be distinguished from one another only on the basis of the knowledge of other stages in their life histories as suggested by Nasir (1960) and on their biology as suggested by Iles (1960) but not on the morphology or size variation, which has generally been used to separate different species.

Explanation to Plate 33

Cyathocotyle bushiensis n. sp.

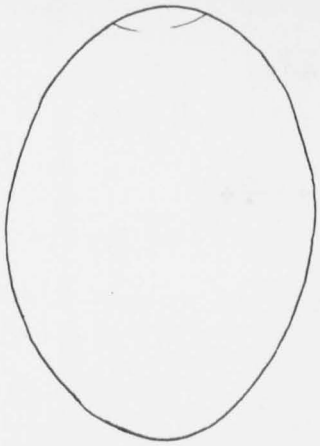
fig. 1 Egg capsule.

fig. 2 Egg, with fully developed miracidium inside.

fig. 3 Miracidium, general structure.

fig. 4 Epidermal plates of the miracidium (lateral view).

Plate 33



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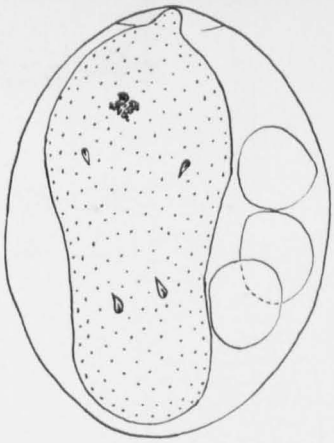

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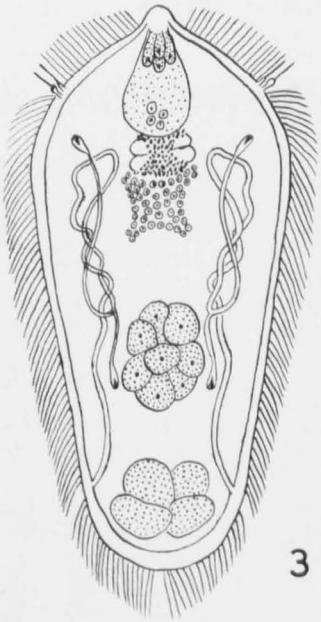

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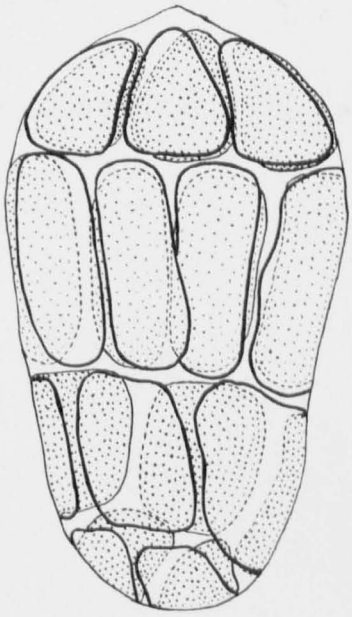

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4. Life History of Cyathocotyle bushiensis n. sp.

The cysts of this cercaria were found in the digestive gland of B. tentaculata. On feeding these cysts, adults belonging to the genus Cyathotyle (Mühling, 1896) developed in the ducklings. Other stages in the life cycle and the adults were studied and are described below.

Egg (Plate 33, fig. 1)

The eggs are oval in shape, very light yellow in colour, operculate and thin-shelled. The eggs collected from faeces are unembryonated, measuring 0.073 - 0.076 mm. long and 0.063 - 0.066 mm. broad.

Miracidium (Plate 33, figs. 2-4)

The eggs were collected from the experimentally infected ducklings. They were concentrated and washed with several changes of distilled water and incubated at room temperature. The miracidia were fully developed in eight to ten days but hatching did not start till the fourteenth day. As in E. londonensis and H. essexensis, hatching was facilitated by replacing the water with fresh water and by long exposure to strong light. Change of temperature from cold to warm also activated the miracidia.

The fully developed miracidium is longer than the eggshell and lies in it with a curve on one side, occupying more

than half the space (Plate 33, fig. 2). The rest of the space is taken up by two or three globules. With rare exceptions, the apical papilla faces the operculum of the eggshell. The miracidium when fully formed on the eighth day shows occasional slow movements of contraction and extension. The eyespots, flame cells and some other structures are easily discernible through the eggshell. On the fourteenth day, after changing the water, raising the temperature and after exposure to strong light, the movements become violent. The apical papilla is repeatedly forced against the operculum and the cilia beat rapidly. The hatching of the miracidia continues for about six days.

The free-living miracidium is very active and swims incessantly in all directions. When it touches a solid object in the water, the movements are stopped for an instant, the nature of the object seems to be probed with the apical papilla and the active movement is resumed after the object is found unsuitable for penetration. The movements of the miracidium are also slowed down when it reaches the surface film of the water. The forward movement of the miracidium is clearly seen to be accompanied by its rotation on the long axis of the body, resulting in a spiral movement of the miracidium.

More miracidia are found near the periphery of the Petri-dish and near the source of light than in the centre

or away from the source of light.

The miracidium (Plate 33, fig. 3) is elongate in shape and capable of considerable contraction and extension. The living miracidia measure from 0.1 - 0.15 mm. in length and 0.05 - 0.07 mm. in breadth. The maximum girth is attained at nearly one third of the body length from the anterior end. At the anterior end there is an invaginable apical papilla which was never found to be protruded during the active movements of the miracidium, but is at once pushed out when it touches a solid object. Slightly behind the tip of the apical papilla is a circle of six to eight long hair-like structures. They are probably sensory in function.

The epidermal plates (Plate 33, fig. 4) are arranged in four tiers. The first tier has six triangular epidermal plates of which two are dorsal, two lateral and two ventral in position. The plates of the first tier are 0.023 - 0.026 mm. long and 0.019 - 0.02 mm. broad at the base, in silver impregnated specimens.

There are eight epidermal plates in the second tier of which two are mid-dorsal, two dorso-lateral, two ventro-lateral and two ventral in position. They are rectangular and measure 0.041 - 0.042 mm. long and 0.015 - 0.019 mm. broad.

The third tier has four squarish plates with one dorsal, one ventral and two lateral in position. They measure 0.023 - 0.03 mm. long and 0.02 - 0.023 mm. broad.

Only two epidermal plates are present in the last tier. One of these is dorsal and the other ventral in position. They measure 0.015 - 0.019 mm. long and 0.02 - 0.023 mm. broad.

The cilia are borne on the epidermal plates. All the cilia are nearly of the same size but those at the posterior end appear to be larger than the rest because at this point they are completely outstretched and their complete length may be seen.

Between the first and second tiers of the epidermal plates is a pair of lateral processes, each with a narrow stalk and a swollen tip bearing a long, stiff and inactive hair-like structure which is shorter than the cilia of the epidermal plates. In miracidia which were about to die, a small droplet of liquid was very often seen extruding from these processes. No internal connection of these processes could be seen.

The most prominent structures in the miracidium are the eyespots. They are thick semi-circular masses of dark pigment which are confluent mesially. On each of the outer sides is a pair of crystalline lenses enclosed by the pigment on the anterior, mesial and posterior sides.

The "rudimentary gut" or the "apical gland" of Lynch (1933) is a sac-shaped structure, with non-cellular walls, finely granular contents and four vesicular nuclei at the posterior end. The "rudimentary gut" extends

from behind the apical papilla to the anterior end of the eyespots. The extrusion of a small, clear drop of fluid at the tip of the apical papilla was seen in many moribund miracidia but no true mouth opening was seen.

There are four penetration gland cells, just behind the apical papilla lying above the rudimentary gut. The walls of these penetration glands are not very distinct, but the contents are coarsely granular with one prominent nucleus in each cell.

The central nervous system is represented by a quadrangular mass of nervous tissue, lying just behind the eyespots. The nervous tissue is covered with several nuclei, which are probably the nuclei of the nerve cells.

A pair of flame cells is present on each side of the body. The anterior flame cell lies at the side of the eyespot and the posterior nearly in the middle of the third tier of the epidermal plates. The ducts from these two flame cells on each side join nearly in the middle of the body, forming a common excretory duct, which pursues a wavy course up to the side of the eyespots where they are looped backwards and open on the side of the body between the third and the fourth tiers of the epidermal plates.

The genital primordium is represented by a mass of deeply staining cells, just behind the middle of the body. There are four more prominent cells of unknown nature at the posterior end of the body.

Discussion

Unlike most strigeid miracidia, the present miracidium has an epidermal plate formula of 6:8:4:2. The presence of only two epidermal plates in the last tier has been observed in one interspecific variation of A. arisaemoides, which normally has an epidermal plate formula of 6:8:4:3 (Pearson, 1956). No details of the structure of the miracidium of C. gravieri have been given by Mathias (1935). The only other previously described miracidium in the family Cyathocotylidae is that of Prosostephanus industrius Tubangui, 1928, as described by Tang (1941b). The miracidium of the present species differs in several aspects from that of P. industrius. Tang (1941b) has not given the figure of the epidermal plates of the miracidium of P. industrius but in the text has described it as 6:8:4:3 while the present miracidium has an arrangement of 6:8:4:2. This gives further support to the contention that the arrangement of the epidermal plates is not always the same among the members of a family and cannot be used as an index of family relationship.

Tang (1941b) has not described any lateral processes or hair-like structures on the apical papilla which are present in the miracidium under study.

The "primitive gut" of the miracidium of P. industrius has been shown to be exceptionally long and extending more than half the length of the body of the miracidium, while

in the present species it is small and reaches only the anterior end of the eyespots. However, the four nuclei of the "primitive gut" in P. industrius, which are normally at the posterior end of this organ, are just in front of the eyespots. The penetration glands have not been described by Tang (1941b) and only one lens is shown to be present on each side. The present miracidium has distinct penetration glands and two lenses on each side.

In having two pairs of lenses the present miracidium agrees with those of Cotylurus cornutus (= strigea tarda) (Mathias, 1925), Diplostomum flexicaudum (Van Haitsma, 1931), Neodiplostomum lucidum (Park, 1936) and A. arisaemoides (Pearson, 1956). The miracidia of Hysteromorpha triloba (Hugghins, 1954) has one lens on each side, except occasionally when two lenses are found in each pigmented cup. The present miracidium also differs from the rest of strigeid miracidia, except that of A. arisaemoides, in having the pigment of the two sides fused into one mass.

Penetration into Snail

The miracidia do not show any reaction to the presence of a snail in close proximity and continue their normal movements in all directions. The contact between a miracidium and a snail is purely accidental. On coming into contact with such parts of the snail which are unsuitable for penetration, such as the foot, the miracidium probes the

Explanation to Plate 34

Cyathocotyle bushiensis n. sp.

fig. 1 Mature cyst.

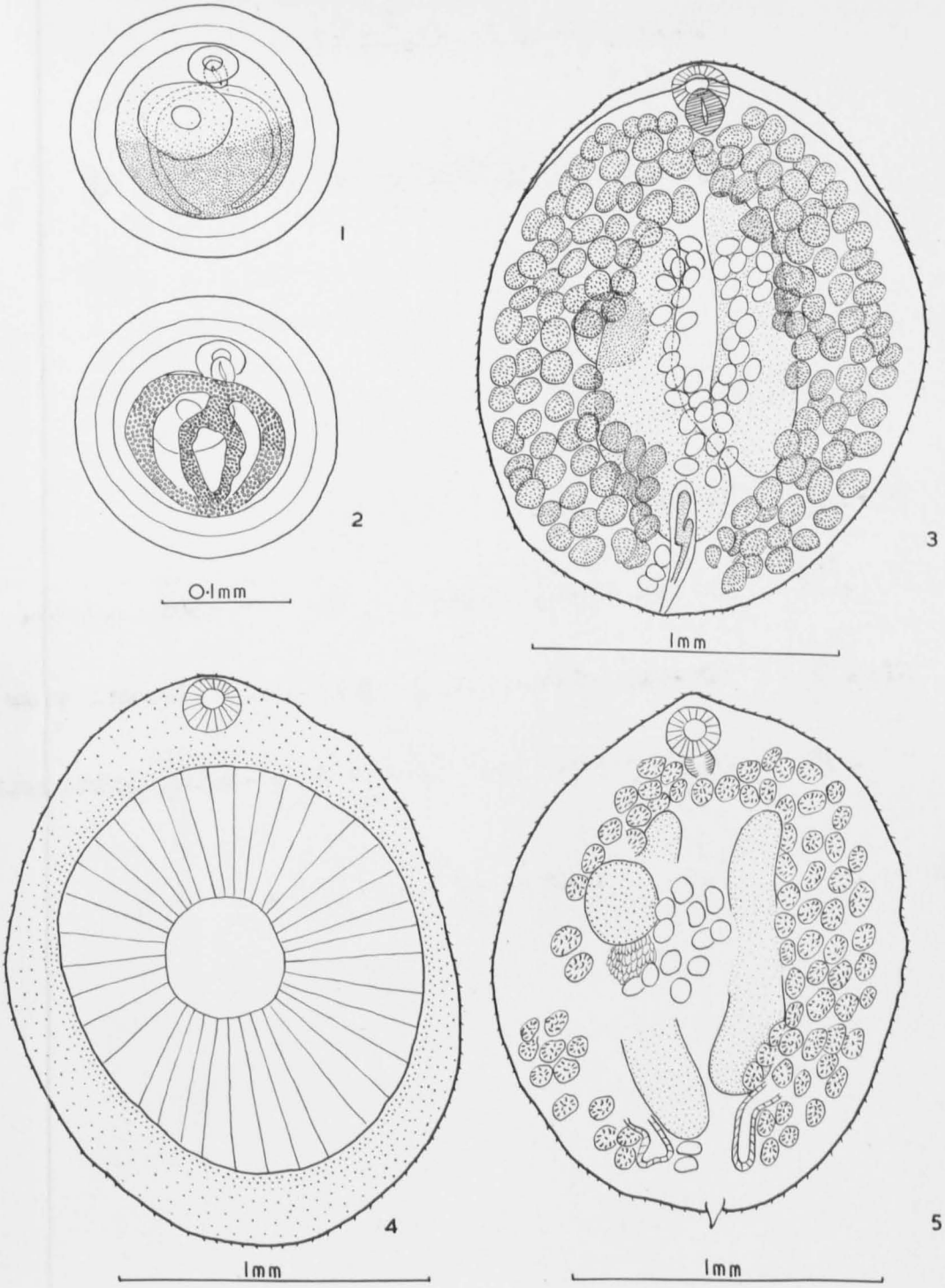
fig. 2 Mature cyst, showing main excretory ducts.

fig. 3 General structure of the adult (dorsal view).

fig. 4 Ventral view of the adult, showing tribocytic organ.

fig. 5 Facial section of the adult.

Plate 34



surface for a short time and swims away. When a miracidium touches a suitable part of the snail, such as the surface near the tentacles, penetration is quickly accomplished.

The snail reacts violently to the penetration of a miracidium by completely retracting its body into the shell and by the secretion of a thick coat of slime. Both these things might be serving as protection against the entry of other miracidia.

Only B. tentaculata were exposed to the miracidia.

Sporocyst and Cercaria

The sporocyst and the cercaria have been described in the first part of this thesis.

Cyst (Plate 34, figs. 1 and 2)

The cysts are located in the basal part of the digestive gland of the second intermediate hosts which may be B. tentaculata or V. piscinalis. Laboratory bred B. tentaculata were also successfully infected experimentally. The transformation of the cercaria into the cyst was not studied.

The cysts are spherical, with a very thick transparent double cyst wall. The metacercaria fills the cavity of the cyst completely and is capable of little free movement.

In immature cysts there is no pigment, but as the

metacercaria attains maturity a black pigment develops which gradually increases in extent and in older cysts may cover the whole surface of the metacercaria. Usually the aboral hemisphere of the metacercaria is seen to be covered with this pigment (Plate 34, fig. 1). Apart from the absence of the pigment the immature cysts can also be distinguished from the mature ones in being considerably larger and in having a much thinner cyst wall.

The cyst wall of the mature cysts is so thick and strong that it cannot be broken without causing considerable damage to the metacercaria. There are no apertures in the cyst wall comparable to those described for certain tetracotyles. However, the cyst wall is to some extent permeable as the contained metacercaria can be stained, though much more slowly, with ordinary stains.

The tribocytic organ is already well developed and can more easily be seen in slightly immature cysts which do not have any pigment.

The main excretory ducts are very much distended and are full of excretory concretions (Plate 34, fig. 2). It has been suggested that enormously distended main excretory canals filled with excretory concretions indicate that they are the tubular portions of the excretory bladder.

Each naturally infected snail may harbour as many as twenty cysts.

Measurements of living mature cysts

(All measurements in millimetres)

	Range	Average
Diameter of the cyst	0.22 -0.283	0.239
Inner cyst wall	0.006-0.016	0.013
Outer cyst wall	0.023-0.043	0.028
Oral sucker	0.03 -0.036x 0.036-0.053	0.034x 0.046
Pharynx	0.02 -0.033x 0.02 -0.026	0.026x 0.023
Tribocytic organ (diameter)	0.063-0.1	0.088

Tetracotyle orientalis Faust, 1921 has been shown to have lateral sucking cups, a holdfast organ with an anterior and a posterior lip, short intestinal caeca and a primary excretory system with a posterior excretory bladder from which two main lateral excretory ducts originate anteriorly. It also has a small ventral sucker, a ventral concavity and the body is somewhat divided into two parts.

Cyathocotyle orientalis, the adult stage of T. orientalis as claimed by Faust (1921b), on the other hand has no lateral sucking cups, a holdfast organ quite unlike that of the tetracotyle, no ventral concavity and the intestinal caeca extending to the posterior end of the body. This striking dissimilarity between the structures of the tetracotyle and the adult stages is explained by Faust by assuming that during the

transformation to the adult, the lateral sucking cups, the holdfast organ and the ventral concavity disappears while the ventral sucker, which he regarded phylogenetically as a genital pore, becomes enormously enlarged to develop into the holdfast organ of the adult.

Dubois (1938) in his monograph on strigeids has shown that a ventral sucker is present in C. orientalis. It is well known now that the lateral sucking cups and the holdfast organ in other strigeids are carried over to the adult from the metacercarial stage. It is also well known that the cyathocotylid cercariae always possess an additional pair of main median excretory ducts originating from the excretory bladder.

It is inconceivable that the lateral sucking cups, the well developed holdfast organ and the ventral concavity of T. orientalis should all disappear during its development to the adult stage in the final host. It is my opinion that T. orientalis is not the metacercarial stage of C. orientalis at all, and belongs to some other strigeid not belonging to Cyathocotylidae. This view is also supported by the fact that no trace of the median excretory ducts, a common feature of all the cyathocotylid cercariae, is present in T. orientalis.

C. orientalis recovered from the experimentally infected duck had obviously developed from some other metacercariae, undetected by Faust (1921) in the mixture of different kinds

of metacercariae which he fed to that duck.

Whereas directly opposite to T. orientalis, the metacercaria under study has a remarkable resemblance with its adult in lacking a ventral concavity, lateral sucking cups and in the structure of the holdfast organ and in the extent of the intestinal caeca. The main median excretory ducts of the cercaria are also prominent in the present metacercaria and are now greatly distended and full of excretory concretions.

The cysts of C. gravieri develop in fresh water fish. Mathias (1935) gives only a very brief account of the cyst as being ovoid and with refractile granules. He, however, found that although the cysts are formed within one day of penetration of the cercariae into the fish, they are not infective till after eight or ten days.

The present metacercaria closely resembles that of other metacercariae described in Cyathocotylidae.

Feeding Experiments

In these experiments, Rat 1, Pigeon 1, Chicken 1 and Duck 1 were fed with the cysts from laboratory infected snails. All other animals were fed with the cysts recovered from the naturally infected snails.

Examination of faeces

Animal	No. of cysts fed	Days after feeding 1	2	3	4	5	d	Results of autopsy	Location in the host
Rat 1	30	-	-	-	-	-	-	Nil	
Rat 2	50	-	-	-	-	-	-	Nil	
Pigeon 1	30	-	-	-	-	-	-	Nil	
Pigeon 2	40	-	-	-	-	-	-	Nil	
Chicken 1	30	-	-	-	-	-	-	Nil	
Chicken 2	50	-	-	-	-	-	-	Nil	
Duck 1	30	-	-	-	-	+	+	2 adults	Caecum
Duck 2	50	-	-	-	-	+	+	3 adults	Caecum
Duck 3	50	-	-	-	-	+	+	4 adults	Caecum

+ = trematode eggs present
- = trematode eggs absent

Rats, pigeons and chickens do not serve as final hosts for C. bushiensis. The ducklings were fed while they were one day old and unfed. No food was given to infected ducklings till twenty hours after feeding.

Maturity is attained by these trematodes on the fifth day after feeding, when a small number of eggs appear in the faeces. The number of eggs in the faeces increases considerably on the sixth day. Only a small proportion of the cysts develop into adults. This might be due to their unusual location in the host, which was always the caecum. In the caecum the worms are very strongly fixed with their tribocytic organ into which the mucous membrane is drawn. When removed a small haemorhaged portion of

the mucous membrane is observable at the point of attachment.

Adult (Plate 34, figs. 3-5)

Cyathocotyle bushiensis n. sp.

The body is circular and thick with a convex dorsal and almost flat ventral surface. The lateral margins of the body are not folded up. Small backwardly directed spines cover the whole body. The circular tribocytic organ is well developed and projects on the ventral side and covers a large portion of the ventral side of the body. The internal opening of the bribocytic organ is also usually circular or sometimes slightly drawn out at the anterior side (Plate 34, fig. 4).

The oral sucker is sub-terminal and the prepharynx practically absent. The pharynx is well developed and lies dorsal to the oral sucker in the fixed specimens. The oesophagus is very short and the intestinal caeca, which are completely obscured in whole mounts, extend to to the posterior end of the body. The ventral sucker is absent.

The vitellaria are in the form of medium sized follicles and are extensive. They extend from the sides of the pharynx to the posterior end of the body, leaving only a small area in the middle of the body. These glands take up a deep stain quickly and almost completely hide the reproductive organs and the intestinal caeca.

The testes are elongate, sausage-shaped, extending from behind the pharynx to some distance in front of the posterior end. The right testis is smaller than the left. The cirrus sac is narrow and about a quarter of the body length. The seminal vesicle is well developed and slightly coiled. The pars-prostatica could not be observed. The cirrus pouch opens at the posterior end slightly on the dorsal side.

The ovary is circular lying partly under the left testis, nearly on the equator of the body. Immediately behind the ovary is a diffuse shell gland. The uterus proceeds upwards on the left side of the body up to the anterior end of the left testis, then turns backwards extending to the posterior end of the right testis. Here it proceeds forwards again in the right half of the body up to the level of the anterior end of the left testis and again turns back and opens alongside the cirrus sac into a common genital pore.

Neither the vitellaria nor the reproductive organs extend into the tribocytic organ.

From forty to fifty-four eggs were seen in the uterus of each worm.

Measurements (Five specimens)

(All measurements in millimetres)

Body length	1.7 -1.83
Body breadth	1.26 -1.38
Tribocytic organ diameter	1.23 -1.63
Inner opening of the tribocytic organ	0.25 -0.30
Oral sucker	0.15 -0.16x 0.16 -0.2
Pharynx	0.133-0.15x 0.133-0.15
Right testis	0.75 -0.9 x0.18 -0.26
Left testis	1.05 -1.2 x0.15 -0.3
Ovary (diameter)	0.221-0.28
Cirrus sac	0.45 -0.55x0.07 -0.09
Eggs	0.073-0.076x0.063-0.066

Comparison of C. bushiensis with Related Species

Thirteen species of the genus Cyathocotyle Mühling, 1896 have been described from bird hosts.

C. prussica Muhling, 1896; C. orientalis Faust, 1921; C. melanittae Yamaguti, 1934; C. fusa Ishii and Matsuoka, 1935; C. gravieri, Mathias, 1935; C. oviformis Szidat, 1936; C. teganuma Ishii, 1935; C. spp. Szidat, 1936; C. szidatiana Faust and Tang, 1938 and C. anhingi Vidyarthi, 1948, are all smaller than the present species and have rounded or oval testes.

C. prussica, C. orientalis, C. fusa, C. gravieri, C. oviformis, C. szidatiana, C. anhingi and C. spp. can

also be separated from the present species in having a ventral sucker and in having fewer eggs of a larger size in the uterus. C. prussica, C. oviformis, C. orientalis and C. anhingi can further be distinguished from the present species in having comparatively larger cirrus sacs. C. melanittae and C. teganuma also have fewer but larger eggs in the uterus.

C. calvusi Verma, 1936 and C. chungkae Tang, 1941 have a different shape of the body. C. calvusi, which has been placed in the genus Holostephanus by Mehra (1943), also differs in the position of the testes in having a much smaller tribocytic organ and in having fewer but larger eggs; C. chungkae further differs in possessing a ventral sucker in the shape, size and the position of the testes and in having fewer and larger eggs in the uterus.

C. indica Mehra, 1943 can be distinguished from the present species in having a ventral sucker and in the position, shape and size of the testes and in being slightly larger than the present species.

In view of the above comparison, the present species is regarded as new and the name Cyathocotyle bushiensis is proposed.

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