ACTA ZOOLOGICA FENNICA 92

EDIDIT

SOCIETAS PRO FAUNA ET FLORA FENNICA

HISTOLOGY OF FIVE CERCARIAE
(TREMATODA: MALACOCOTYLEA)

BY

AILI SELINHEIMO

REWRITTEN AND EDITED

BY

BO-JUNGAR WIKGREN

(ZOOLOGICAL STATION, TVÄRMINNE)

WITH 9 PLATES INCLUDING 80 FIGURES

HELSINGFORSIAE 1956

HELSINGFORS 1956
PRINTED BY A.-B. TILGMANN

CONTENTS

	Page
Introduction	3
Material	4
Methods	5
Results	5
Epidermis	5
Parenchyma	6
Muscles	6
Suckers	7
Anterior organ	7
Stylet	7
Penetration glands	7
Cystogenous glands	8
Intestine	9
Nervous system	9
Excretory system	9
Gonad anlage	10
Tail	10
Summary	11
Index to figures of each cercaria species	12
References	13
Abbreviations	13

INTRODUCTION

The laboratory work, the preparation of the slides and the drawings were done by Mrs. AILI SELINHEIMO (née VALTONEN). The investigation was carried out at Tvärminne Zoological Station in 1933. The manuscript was submitted as a thesis for the degree of Cand. phil., but was not prepared for publication. WIKGREN was given the original manuscript to prepare for publication. His task has merely been that of an editor in rewriting the text, adding some details and notes on the literature, translating the manuscript into English and rearranging the figures.

Since microanatomical investigations on cercariae are very few and restricted to a few species only, it is hoped that this work will be of some value. Without doubt the microanatomical treatment of trematode larvae reveals certain features not observable in the living state.

We wish to express our sincerest thanks to Professor ALEXANDER LUTHER, Ph. D., under whose guidance both the experimental work and the final preparation have been made, for his great interest, critical advice and kindness in making available the resources of the Tvärminne Zoological Station.

We also thank Mrs. JEAN M. PERTTUNEN, B.Sc., for checking the English of the manuscript. The Figures have kindly been redrawn by Mr. V. NYSTRÖM.

February 1956.

Bo-Jungar Wikgren.

MATERIAL

The cercariae here studied have emerged from snails collected from two localities, *viz.* Krogarviken, a bay at the Tvärminne Zoological Station, and Baggby (Gloet?), a shore near the town of Ekenäs/Tammisaari. Five cercaria species have been investigated microanatomically. These species will be described in a paper by WIKGREN. Here only short descriptions and drawings of the cercariae are given.

1) *Cercaria helvetica XVII* Dubois 1929 (synonym: *Cercaria obscura* Wesenberg-Lund 1934), a Gymnocephalous cercaria with a remarkably large tail and exhibiting in extreme degree the capacity to alter the body form. Host: *Bithynia tentaculata* (L.). Fig. I, 1.

2) *Gymnocephalous cercaria C* sp. indet., a cercaria closely related to the cercaria of *Fasciola hepatica* Linnaeus 1758. The host is *Bithynia tentaculata* (L.). Fig. I, 2.

3) The cercaria of *Echinostoma revolutum* (Frölich 1802) Looss 1899 (synonym: *Cercaria echinata* Siebold 1837, etc.), a large Echinostomous cercaria emerging from *Lymnaea stagnalis* (L.). Fig. II, 5.

4) A Polyadenous *Xiphidiocercaria* sp. indet. with 7 penetration gland cells on each side. Hosts: *Lymnaea* species. Fig. II, 4.

5) The cercaria of *Diplostomum spathaceum* (Rudolphi 1815) Olsson 1876, emend. (synonym: *Cercaria C* Szidat 1924), a very common Furcocercous cercaria emerging from *Lymnaea* species. A confusion between two species has obviously occurred, since the cercaria is noted as having emerged from *Bithynia tentaculata* also. Fig. I, 3.

METHODS

The cercariae were fixed with LANG's corrosive sublimat-acetic acid. Whole mounts were stained with Borax-Carmine and sections with HEIDENHAIN's Iron Haematoxylin or HANSEN's Alum Haematoxylin. HEIDENHAIN's stain was superior in staining muscle, HANSEN's stain in staining gland cells, etc. The paraffin sections were 3—5 μ thick.

RESULTS

Epidermis

(Figs. III, 6—15)

The outermost layer is a usually thin cuticle (*c*), followed by the subcuticle (*sc*) and the basement membrane (*bm*). The epidermal cells (*ec*) lie below the basement membrane, being connected by thin protoplasmic processes with the other epidermal layers (fig. III, 6). In *Gymnocephalous cercaria C* the cuticle appears cellular, being formed of small, cuboidal cells (*ec*). The cell membranes of these have been seen only in sagittal sections, not in sections perpendicular to the surface (figs. III, 7—9). According to WALTER (1893) the ends of the dorsoventral muscles pass into the subcuticle, but BETTENDORF (1897) does not confirm this. In *Gymnocephalous cercaria C* and in the cercaria of *Echinostoma revolutum* the muscle fibres (*dvm*) do pass to the surface (figs. III, 9, 12). These fibres are not identical with the processes of the epithelial cells.

In the epidermis of *Cercaria helvetica XVII* are seen small, round structures, osmewhat resembling the rhabdites of turbellarians (figs. III, 10, 11).

Typical epidermal spines occur in the cercaria of *E. revolutum*. They stain deeply with HEIDENHAIN's, but not at all with HANSEN's Haematoxylin. The spines (*sp*) are short and pyriform and situated on the basement membrane and do not reach to the surface. They are arranged in transverse rows. Each spine has a rounded base, staining red with HANSEN's Haematoxylin. Four muscles adhere to this base. They run obliquely toward the underlying tissues (figs. III, 12, 13). The muscles are not seen to pass from spine to spine as BETTENDORF (op.c.) has reported.

In the body wall of the Xiphidiocercaria are structures which resemble spines in that they stain intensely with HEIDENHAIN's Haematoxylin. They lie very close together (figs. III, 14, 15). These spines (*sp*) do not possess either a rounded base or muscles of their own.

Gymnocephalous cercaria C possesses a circular epidermal fold (*cf*) around the ventral sucker. Many muscle fibres adhere to the inner side of this fold (fig. V, 39).

Parenchyma

(Figs. III, 16; V, 37—VI, 47; VII, 49—53; VII, 55—VIII, 57; VIII, 65; VIII, 68—IX, 71; IX, 77)

The network of the parenchymal syncytium fills all the free spaces of the body. Usually the nuclei are large and surrounded by a thin protoplasmic layer with processes to the adjacent protoplasm territories. The parenchyma occurs in all parts of the body, the suckers, the tail, etc. Protoplasmic threads are also seen between the muscle fibres, beneath the epidermis and on the surface of the nerve centres. No differences in the parenchyma of the different species are observable. *Xiphidiocercaria* sp. is richly supplied with long threads, possibly parenchymal fibrils (figs. VI, 42, 46; *pf*). The cercaria of *Echinostoma revolutum* has a unique structure between the ventral sucker and the pharynx, *viz.* a reticle with scattered nuclei (mucin glands?) (figs. VII, 55, 56; *x*).

Muscles

(Seen in most figures)

The body muscles may be divided into two main groups, *viz.* body wall muscles and dorsoventral muscles.

The muscle layers forming the muscular body wall are from the outside: longitudinal muscles (*lm*), circular muscles (*cm*) and two oblique muscle layers (*dm*) (figs. III, 16—IV, 22; IV, 29).

In *Gymnocephalous cercaria C* all the different muscles appear to be of equal thickness, in the cercaria of *Echinostoma revolutum* the longitudinal muscles are stronger than the others. In spite of the fact that *Cercaria helvetica XVII* continuously alters its form, the muscles in this species are poorly developed.

The muscle fibres are mostly unbranched, but do sometimes branch (figs. III, 17; IV, 23; V, 38, 39; VI, 41). The myoblasts (*mb*) lie scattered between the muscle fibres. Their shape is very diverse (figs. III, 7, 8, 16, 18; IV, 24—30; V, 38; VI, 41; VII, 51). In *Gymnocephalous cercaria C* two main types occur (figs. IV, 24, 25). The long processes of the muscle cells are not seen to unite with the muscle fibres. The cells assumed to be myoblasts are much smaller in the cercaria of *Echinostoma revolutum* (figs. IV, 26, 27) than in the other species. It may be noted that similar cells lie around the ventral sucker below the epidermal fold of *Gymnocephalous cercaria C* (figs. IV, 30; VII, 51).

The dorsoventral muscles run obliquely in many directions between the dorsal and ventral surfaces of the body (figs. IV, 31—V, 35; VIII, 67). The cell body is in intimate connection with the muscle fibres (fig. V, 36). On reaching the surface the fibres split up into many radiating fibrils (figs. IV, 31; V, 33).

Both smooth and striated muscles occur in the tail (p. 11).

Suckers

(Figs. IV, 28, 31; V, 33, 34, 37—VI, 42; VI, 45; VII, 51, 52, 55; VIII, 67)

The structure of the ventral and oral suckers is quite similar. The outer lining seems to be a direct continuation of the body cuticle, while the innermost layer consists of a powerful basement membrane. The suckers are made up of parenchyma cells, muscle cells and muscle fibres. The muscle layers are the same as those that FUHRMANN (1928) mentions in adult trematodes, *viz.* equatorial (*em*), meridional (*mm*) and radial muscles (*rm*). The ends of the radial muscles are seen to split up into numerous fibrils.

Anterior organ

(Fig. VI, 43)

The anterior part of the anterior organ of the cercaria of *Diplostomum spathaceum* is an invagination of the epidermis, the posterior part being very muscular. There are circular, radial and oblique muscles.

Stylet

(Figs. VI, 42; VIII, 61)

Two muscle systems operate the stylet (*s*) of *Xiphidiocercaria* sp., the one adhering to the proximal end (piercing muscles) the other to the thickenings near the distal end (shoulders) (withdrawal muscles). The muscle fibres are branched. No sheath has been seen around the stylet (compare REES, 1932, p. 21).

Penetration glands

(Figs. VI, 45, 47)

Penetration glands (*pgl*) have been seen in the Xiphidiocercaria (fig. II, 4) and the Furcocercaria (fig. I, 3). In *Xiphidiocercaria* sp. they are finely granulated, deeply staining cells with conspicuous nuclei. They lie around the ventral sucker (fig. VI, 45). The ducts (*dpgl*) stain in the same manner as the gland cells (fig. VI, 47).

Cystogenous glands

(Figs. IV, 30, 31; V, 32, 33; VI, 44—46, 48; VII, 49—56; VIII, 67)

The cystogenous cells are extremely well developed in all these cercariae except the cercaria of *Diplostomum spathaceum*. There are two main types of apparently cystogenous cells, *viz.* rod cells (*rc*) and granulated cells (*cgl*). Rod cells alone occur in *Cercaria helvetica XVII* (fig. VII, 49), both types are found in *Gymnocephalous cercaria C* (fig. VII, 53) and only granulated cells in the cercaria of *Echinostoma revolutum* (figs. VII, 55, 56) and *Xiphidiocercaria* sp. (fig. VI, 44).

The rod cells (*rc*) in *Cercaria helvetica XVII* are quadrangular with long rods, sharply pointed at the ends (fig. VII, 50), while the rod cells in the other Gymnocephalous cercaria are often drop-shaped and filled with a large number of smaller rods, arranged in rows (fig. VII, 54). The locus of the rod cells in the body seems to suggest that they secrete cystogenous material. According to LEUCKART (see REES, 1932, p. 11) these cells should be myoblasts. BRAUN (1893) states that the rod cells in the cercaria of *Fasciola hepatica* do not disappear at encystment, but form the inner membrane of the cyst.

The granulated cystogenous gland cells (*cgl*) in *Gymnocephalous cercaria C* are located in a compact mass on the ventral side of the body anterior to the ventral sucker (fig. VII, 53). In the cercaria of *Echinostoma revolutum* the cells are smaller, filling all the body spaces (fig. VII, 56). In the Xiphidiocercaria the cystogenous glands are large and the connection with the cuticle is clearly seen (figs. VI, 44, 45, 48). They stain red with HANSEN's Haematoxylin. Scattered among these larger cells are other smaller, blue-staining cells. From fig. VIII, 63 it is seen that the processes of these cells run to the body surface. These cells are probably nerve cells.

In the Xiphidiocercaria are large chromatophobe cells (*vgl*), containing scattered staining particles, situated anteriorly of the penetration gland cells (*i.e.* in front of the ventral sucker) (figs. VI, 45, 46). In the nuclei the nucleolus is clearly seen. DUBOIS (1929) called these cells »cellules giantes» and REES (1952) »ventral gland cells», arranging them among the cystogenous glands. Obviously they are mucin glands (KRUIDENIER, 1947). In transverse sections of the body in front of these cells rounded structures (*x*) staining in the same manner as the large cells are seen. These structures may be ducts. They lie beneath the ducts of the true penetration glands (*dpgl*), as is seen from fig. VI, 47 (cf. fig. VI, 42).

Intestine

(Figs. V, 35; VI, 41—43; VII, 52, 53, 55, 56—VIII, 61)

The cuticle which lines the cavity of the oral sucker is seen to be a continuation of the lining of the praepharynx (*pph*) and pharynx (*ph*) and at least partially of that of the oesophagus (*oe*) (figs. VI, 41—43; VII, 52). The praepharynx has thin layers of longitudinal and circular muscles (fig. VI, 41). According to FUHRMANN (op.c.) similar muscle layers occur in the oesophagus, too. The pharynx has the same structure as the suckers, *viz.* equatorial, meridional and radial muscles together with parenchyma cells and muscle cells (figs. VI, 41, 42). The oesophagus in all except the cercaria of *Echinostoma revolutum* is tubular; in the cercaria of *E. revolutum* it is cellular without a lumen (fig. VII, 56). The intestinal diverticula (*int*) are cellular in *Gymnocephalous cercaria C* (fig. VIII, 58), the cercaria of *E. revolutum* (fig. VIII, 59) and *Xiphidiocercaria* sp. (fig. VIII, 60), and most probably also in *Cercaria helvetica XVII* (fig. VII, 49). The diverticula of the cercaria of *Diplostomum spathaceum* are filled with a homogeneous mass. The walls are thin (fig. V, 35).

Nervous system

(Figs. VI, 47; VII, 51, 55; VIII, 57, 62—64)

The central nerves have been most clearly seen in the Xiphidiocercaria. The composition of the central nerves and the centres is clearly shown in fig. VIII, 62. All the nerves and ganglia are covered with deeply staining cells (*nc*). Some of those of *Xiphidiocercaria* sp. were provided with only two processes, some with more (figs. VIII, 63, 64). The cells are presumably nerve cells (compare p. 8). The similar cells in the cercaria of *Echinostoma revolutum* were much smaller, which is in correlation with the relatively small size of all cells in this species (fig. VII, 55).

Excretory system

(Figs. V, 32; VI, 45; VII, 49, 53, 56; VIII, 65, 68; IX, 70, 73—75, 78, 79)

The urinary bladder (*ub*) of *Cercaria helvetica XVII* is bilobed, being composed of a thin-walled bladder in the posterior end of the body and a thick-walled, muscular bladder in the proximal end of the tail (fig. VIII, 65). Apparently the posterior lobe functions as an action and suction pump and the anterior lobe serves merely as a reservoir.

In *Gymnocephalous cercaria C* the urinary bladder consists of two thin-walled lobes. In the anterior lobe are parenchyma cells (?) (figs. VIII, 66, 67).

The Y-shaped vesicle of the Xiphidiocercaria has a lining of cuboidal cells (fig. VI, 45).

Of other parts belonging to the excretory system the horns (tubes) of the vesicles (*ud*) in the two Gymnocephalous cercariae have been seen (figs. VII, 49, 53). The wall of the urethra (*ur*) in *Gymnocephalous cercaria C* seems to be composed of endothelial cells (fig. VIII, 68). See further the urethra in figs. VIII, 65; IX, 70, 72—74, 78.

Gonad anlage

(Figs. VI, 44, 45; VII, 51, 55)

Aggregates of small, deeply staining cells (*ga*) have been seen around the ventral sucker in most species. These cells most probably form the gonad anlage, but no definite arrangement into reproductive organs has been recognized.

Tail

(Figs. VIII, 65, 68; IX, 69—80)

The tail of the cercariae is an ingenious organ. The swimming behaviour and movements of the cercariae seem to be directly related to the structure of the tail. This is also shown by the occurrence of a great diversity of tail structures. These problems have been dealt with by WUNDER (1924). According to him the main layers are: the cuticle, the muscle layers, of which the outer is circular and the inner longitudinal, and the innermost parenchyma.

The tail of *Cercaria helvetica XVII* has an enormous capacity to alter its form. According to WESENBERG-LUND (1934) the tail is often flattened. The cercaria swims in a very characteristical, lazy manner. In the tail, below the cuticle, lies a thin circular muscle layer (*cm*), but the longitudinal muscles (*lm*) have been transformed to an oblique muscle system running from the urethra to the cuticle (figs. VIII, 65; IX, 69, 70). This organisation may be characteristical of flat tails. Within the tail is a granulated mass with smaller and larger nuclei. Cell membranes have not been observed.

The tails of Gymnocephalous cercariae are usually very muscular, the cercariae swimming with vigorous lashings of the tail. *Gymnocephalous cercaria C* is provided with circular and longitudinal muscles. The longitudinal muscles are grouped on opposite sides and on each side there are two muscle bunches (figs. IX, 72, 73). The myoblasts (*mb*) are large, granulated cells with large nuclei and conspicuous nucleoli. They lie beneath the muscle fibres or are connected with these by a short nec (fig. IX, 71 *a* and *b*). This is in good agreement with BETTENDORF's (op.c.) observations. In the tail there is furthermore a parenchymal syncytium.

The tail of the cercaria of *Echinostoma revolutum* is very similar to that of *Gymnocephalous cercaria C*. The muscles seem to be stronger and the longitudinal muscles are striated (*slm*). The arrangement of the longitudinal muscles is the same, but the two lateral bunches are better isolated from each other (fig. IX, 77). The muscle cells are large and chromatophobe. The nuclei are large (figs. VIII, 68; IX, 76, 77). The parenchymal network is typical. The cercaria of *E. revolutum* is a good swimmer.

In *Xiphidiocercaria* sp. the longitudinal muscles are arranged in one group on either side of the tail (fig. IX, 75); they are poorly developed in comparison with the two lastmentioned species. Myoblasts are not seen. According to CORT (1915) the longitudinal muscles in the tail of *Cercaria urbanensis* Cort 1915 and *Cercaria inhabilis* Cort 1915 form a continuous layer. In the tail of *Xiphidiocercaria* sp. are large chromatophobe cells (turgescent cells or perhaps myoblasts) (figs. IX, 74, 75). These Xiphidiocercariae are poor swimmers, swimming periods (ascents) being followed by resting periods (sinking).

The tail-stem of the Furcocercous cercaria of *Diplostomum spathaceum* is nearly rectangular in transverse section, the longitudinal striated muscle-bunches (*slm*) being concentrated in the corners (figs. IX, 78—80). Between the bunches of striated muscles non-striated longitudinal muscles (*lm*) are seen. A similar organisation in Furcocercous cercariae has been reported by MILLER (1926). The circular muscles are poorly developed. Beneath the muscle bunches are small cells, perhaps myoblasts. Around the urethra are large, faintly granulated cells with rounded nuclei and conspicuous nucleoli. There is a close relation between the structure of the Furcocercous tail and the fact that during swimming the tail only swings in one plane.

SUMMARY

The histology of five cercaria species has been studied. Of these two are Gymnocephalous, one Echinostomous, one a Xiphidiocercaria and one a Furcocercaria. The results are in good agreement with the findings of previous authors.

The epidermis in one Gymnocephalous cercaria appears to be cellular, in the other species it is of usual type, consisting of a cuticle and inverted epidermal cells. The parenchymal syncytium fills all the free spaces of the body. The muscles are of three types: body wall muscles, dorsoventral muscles and striated muscles. The cells of the body wall muscles are large with branched projections. The cells of the dorsoventral muscles are directly connected with the muscle fibres. Striated muscles occur in the tail of the Echinostomous

and the Furcocercous cercaria; the muscle cells are large and chromatophobe. The muscles of the suckers and the pharynx consist of equatorial, meridional and radial layers. There are penetration glands and cystogenous glands of various structure. The rod-cells of the Gymnocephalous cercariae appear to be cystogenous, but they may have other functions, too. A typical feature of the Xiphidiocercaria is the presence of large, chromatophobe cells in front of the ventral sucker (mucin glands). The oesophagus is in most species tubular; the diverticula in all except the Furcocercous cercaria are cellular. The nervous system has been most clearly seen in the Xiphidiocercaria. The excretory system is rather different in the different species. The tail structure in relation to the swimming behaviour is briefly discussed.

REFERENCES

BETTENDORF, H. 1897. Über Muskulatur und Sinneszellen der Trematoden. — Zool. Jb., Anat. *10*, 307—358.

BRAUN, M. 1879—1893. Vermes. A. Trematodes. In Bronn's Klassen u. Ordnungen d. Thierreichs *4* (1), 306—925.

CORT, W. W. 1915. Some North American larval trematodes. — Ill. Biol. Monogr. *1* (4), 1—86.

DUBOIS, G. 1929. Les cercaires de la région de Neuchâtel. — Bull. Soc. neuchâtel. Sci. nat. *53*, N.S. 2, Year 1928, 3—177.

FUHRMANN, O. 1928. Trematoda. In Kükenthal und Krumbach, Handbuch d. Zoologie *2* (2), 1—140.

KRUIDENIER, F. J., 1947. Mucin in developing digenetic trematodes. — J. Parasit. *33* (6; 2, Suppl.), 17.

MILLER, H. M. 1926. Comparative studies on furcocercous cercariae. — Ill. Biol. Monogr. *10* (3), 1—112.

REES, GW. 1932. An investigation into the occurrence, structure, and life-histories of the Trematode parasites of four species of *Lymnaea* (*L. truncatula* (Müll.), *L. pereger* (Müll.), *L. palustris* (Müll.), and *L. stagnalis* (Linné)), and *Hydrobia jenkinsi* (Smith) in Glamorgan and Monmouth. — Proc. Zool. Soc., London 1932 (1), 1—32.

—»— 1952. The structure of the adult and larval stages of *Plagiorchis* (*Multiglandularis*) *megalorchis* N.nom. from the turkey and an experimental demonstration of the life history. — Parasitol. *42*, 92—113.

WALTER, E. 1893. Untersuchungen über den Bau der Trematoden. — Zeitschr. wiss. Zool. *56*, 51 pp.

WESENBERG-LUND, C. 1934. Constributions to the development of the Trematoda Digenea. Part II. The biology of the freshwater cercariae in Danish freshwaters. — D. Kgl. Danske Vidensk. Selsk. Skrifter, naturv. math. Afd., *9*, Ser. 5 (3), 1—223.

WUNDER, W. 1924. Bau, Entwicklung und Funktion des Cercarienschwanzes. — Zool. Jb., Anat. *46*, 303—339.

INDEX TO FIGURES OF EACH CERCARIA SPECIES

Cercaria helvetica XVII Dubois

Figs. I, 1; III, 10, 11; V, 37; VII, 49, 50; VIII, 65; IX, 69, 70.

Gymnocephalous cercaria C sp.

Figs. I, 2; III, 7—9, 16; IV, 24, 25, 30, 31; V, 32, 33, 36, 38, 39; VI, 41; VII, 51—54; VIII, 58, 66, 67; IX, 71, 72.

Cercaria of *Echinostoma revolutum*

Figs. II, 5; III, 6, 12, 13, 17—21; IV, 26—28; V, 34, 40; VII, 55, 56; VIII, 59, 68; IX, 76, 77.

Xiphidiocercaria sp.

Figs. II, 4; III, 14, 15; IV, 22, 23, 29; VI, 42, 44—48; VIII, 60—64; IX, 73—75.

Cercaria of *Diplostomum spathaceum*

Figs. I, 3; V, 35; VI, 43; VIII, 57; IX, 78—80.

ABBREVIATIONS

ao	anterior organ
bm	basement membrane
c	cuticle
cf	circular fold
cg	cerebral ganglion
cgl	cystogenous glands
cm	circular muscles
cp	caudal pocket
dc	dorsal commissure
dm	diagonal muscles
dpgl	ducts of penetration glands
dvm	dorsoventral muscles
ec	epidermal cells
em	equatorial muscles
ep	epidermis
ff	fin-fold
ga	gonad anlage
gl	glands
int	intestine (gut)
lm	longitudinal muscles
mb	myoblasts
mm	meridional muscles
nc	nerve cells
ndp	nervus dorsalis posterior
nla	nervus lateralis anterior
nlp	nervus lateralis posterior
nva	nervus ventralis anterior
nvp	nervus ventralis posterior
oe	oesophagus
os	oral sucker
pc	parenchyma cells
pf	parenchymal fibrils
pgl	penetration glands
ph	pharynx
pph	praepharynx
rc	rod cells
rm	radial muscles
s	stylet
sc	subcuticle
slm	striated longitudinal muscles
sm	stylet muscles
sp	spines
ub	urinary bladder
ud	urinary ducts
ur	urethra
vgl	ventral gland cells
vs	ventral sucker

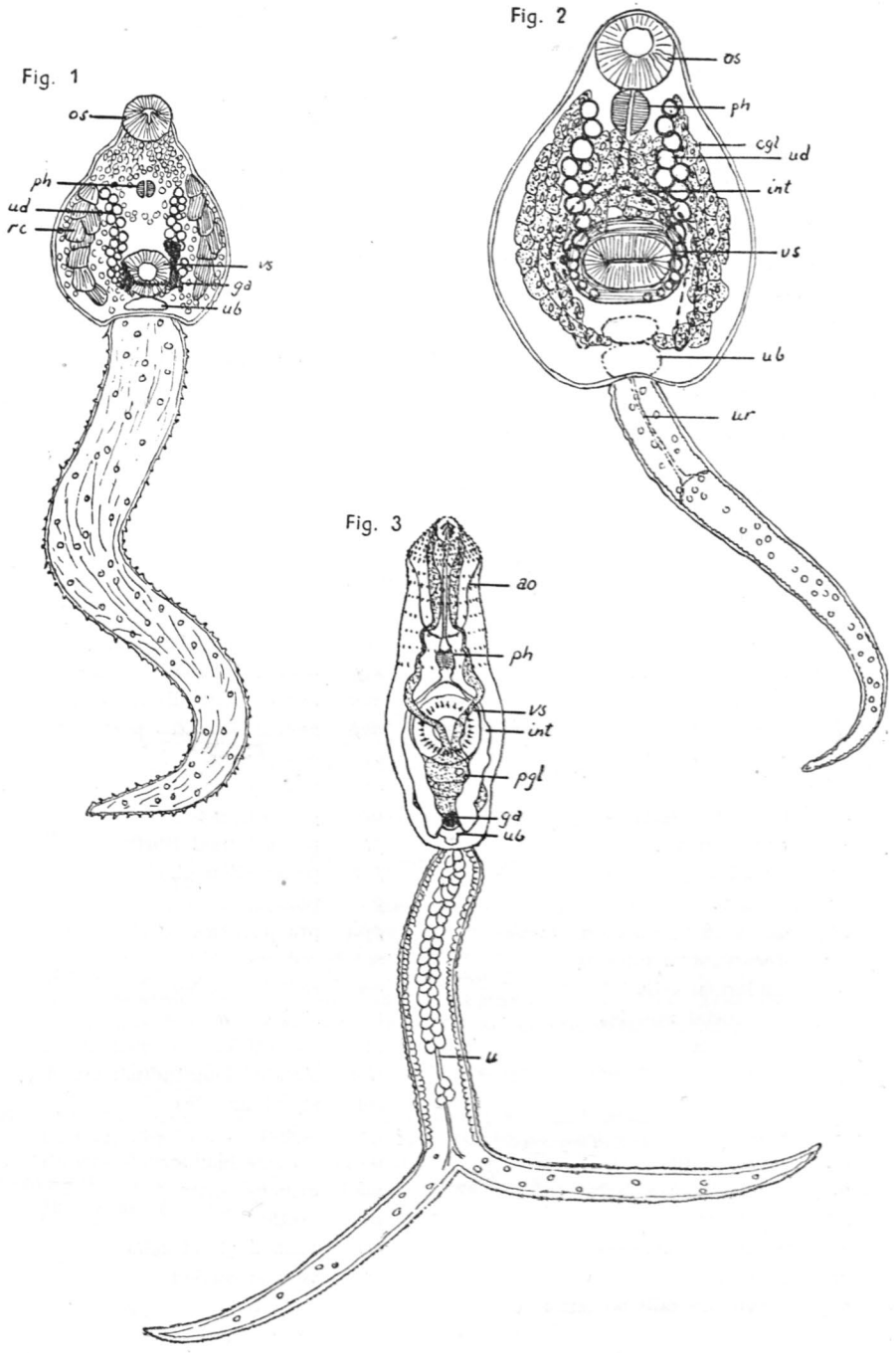


PLATE I

Fig. 1. *Cercaria helvetica XVII* Dubois 1929.
Fig. 2. *Gymnocephalous cercaria C* sp.
Fig. 3. Cercaria of *Diplostomum spathaceum* (Rudolphi 1815) Olsson 1876.

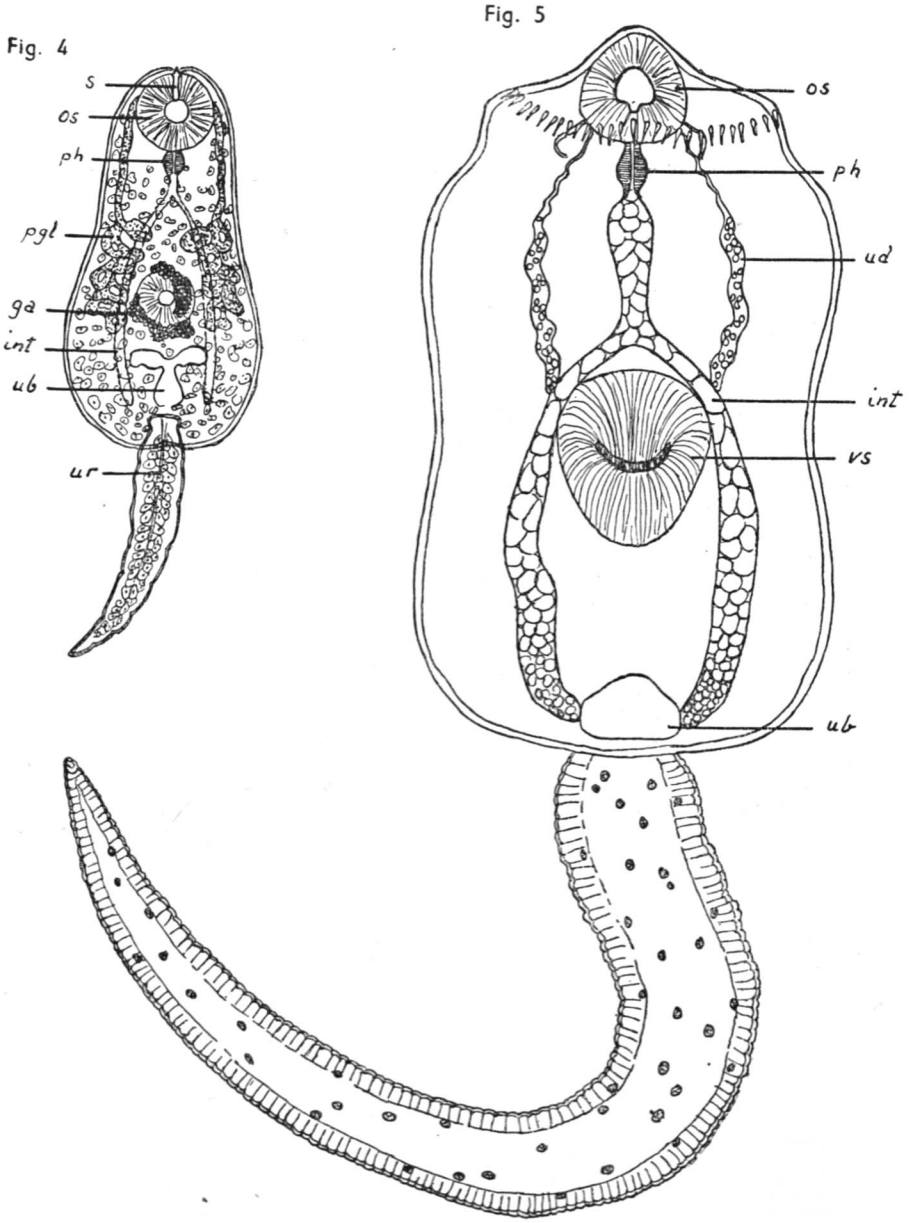


PLATE II

Fig. 4. *Xiphidiocercaria* sp.
Fig. 5. Cercaria of *Echinostoma revolutum* (Frölich 1802) Looss 1899.

PLATE III

Fig. 6. Cercaria of *Echinostoma revolutum*. Section of the epidermis. Inverted epidermis cells (*ec*) with branched protoplasmic processes.

Figs. 7 and 8. *Gymnocephalous cercaria C* sp. Sagittal section of the body wall, showing muscle fibres (*lm, cm*) beneath the epidermis, muscle cells (*mb*) and small, cuboidal epidermal cells (*ec*).

Fig. 9. *Gymnocephalous cercaria C* sp. Transverse section of the body wall.

Figs. 10 and 11. *Cercaria helvetica XVII*. Epidermis with small granules. In fig. 11 the small granules are seen at greater magnification.

Fig. 12. Cercaria of *Echinostoma revolutum*. Transverse section of the body wall, showing the minute epidermal spines (*sp*) on the basement membrane (*bm*) and the ends of the dorsoventral muscles (*dvm*).

Fig. 13. Cercaria of *Echinostoma revolutum*. Horizontal view of the body wall, showing epidermal muscles (*lm, cm*) and spines (*sp*).

Fig. 14. *Xiphidiocercaria* sp. Horizontal view of the body wall, showing epidermal spines (?).

Fig. 15. *Xiphidiocercaria* sp. Section of the body wall (compare with fig. 14).

Fig. 16. *Gymnocephalous cercaria C* sp. Sagittal section of the body wall.

Fig. 17. Cercaria of *Echinostoma revolutum*. Sagittal section of the body wall. Some of the muscle fibres are seen to branch.

Fig. 18. Cercaria of *Echinostoma revolutum*. Sagittal section of the body wall.

Fig. 19. Cercaria of *Echinostoma revolutum*. Body wall muscles.

Fig. 20. Cercaria of *Echinostoma revolutum*. Body wall muscles. The longitudinal muscles (*lm*) are contracted. Observe that the extended muscles (*cm*) are waved.

Fig. 21. Cercaria of *Echinostoma revolutum*. Body wall muscles. The circular muscles (*cm*) are contracted.

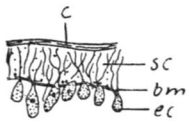


Fig. 6

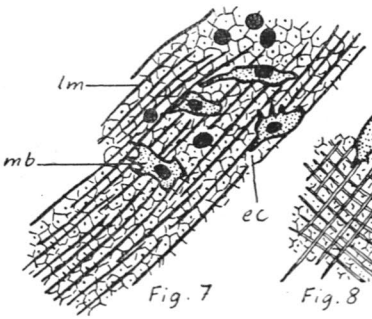


Fig. 7

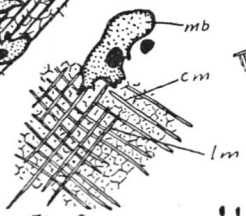


Fig. 8

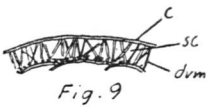


Fig. 9

Fig. 10

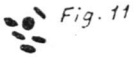


Fig. 11

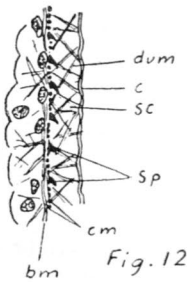


Fig. 12

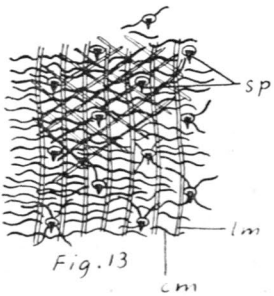


Fig. 13

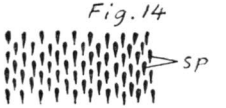


Fig. 14

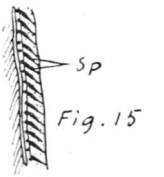


Fig. 15

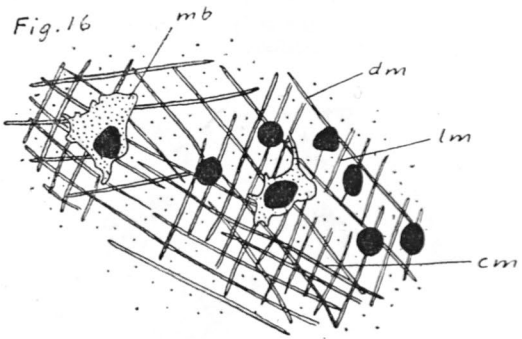


Fig. 16

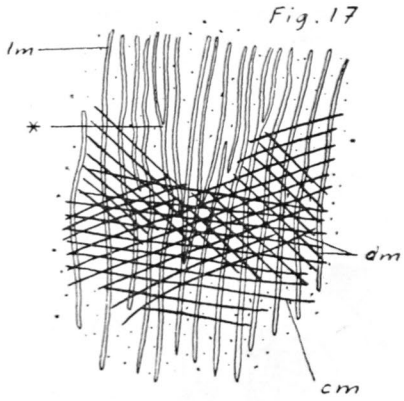


Fig. 17

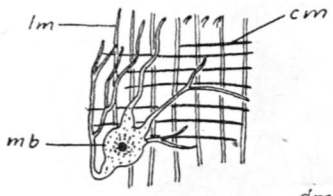


Fig. 18

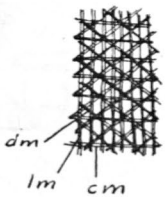


Fig. 19

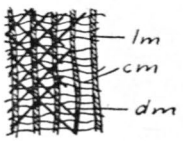


Fig. 20

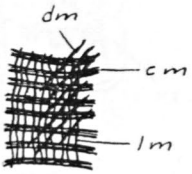


Fig. 21

PLATE IV

Fig. 22. *Xiphidiocercaria* sp. Body wall muscles.

Fig. 23. *Xiphidiocercaria* sp. Branching stylet muscles.

Figs. 24 and 25. *Gymnocephalous cercaria C* sp. Sections of the body wall, showing muscle cells (*mb*).

Fig. 26. Cercaria of *Echinostoma revolutum*. Transverse section of the body wall, showing muscle cells (*mb*) beneath the subcuticle.

Fig. 27. Cercaria of *Echinostoma revolutum*. Sagittal section of the body wall.

Fig. 28. Cercaria of *Echinostoma revolutum*. Sagittal section of the ventral sucker. Myoblasts (*mb*) lie between muscles and parenchyma cells.

Fig. 29. *Xiphidiocercaria* sp. Body wall muscles, and myoblasts.

Fig. 30. *Gymnocephalous cercaria C* sp. Sagittal section of the posterior half of the body, showing large myoblasts (*mb*) beneath the ventral sucker (*vs*), etc.

Fig. 31. *Gymnocephalous cercaria C* sp. Median section of the body showing the dorsoventral muscles (*dvm*). The figure is combined from three sections.

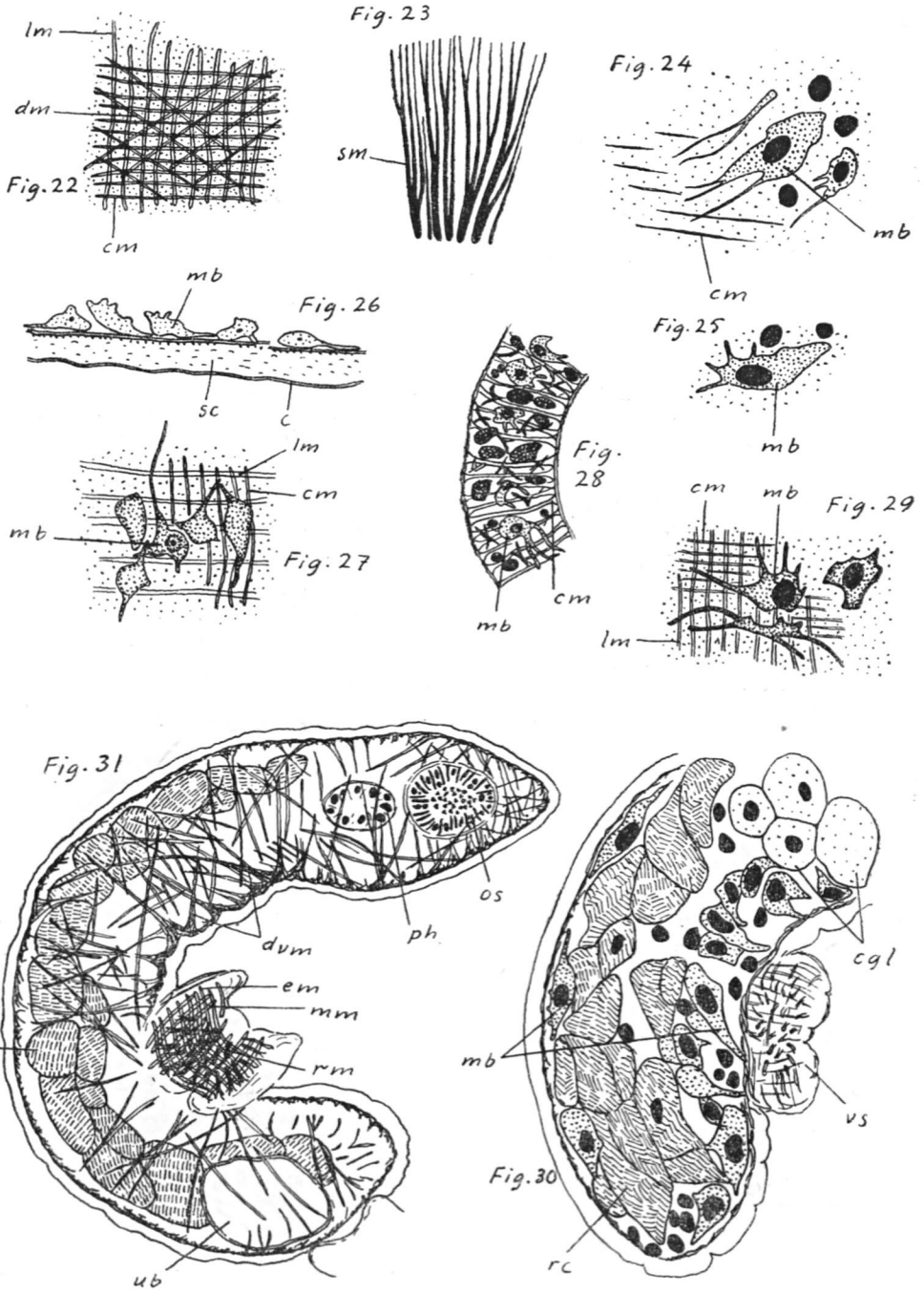

lm
dm
cm
Fig. 22
Fig. 23
sm
Fig. 24
mb
cm
mb
Fig. 26
sc
c
lm
cm
mb
Fig. 27
Fig. 28
cm
mb
Fig. 25
mb
cm
mb
Fig. 29
lm
Fig. 31
os
ph
dvm
em
mm
rm
rc
ub
cgl
mb
vs
Fig. 30
rc

PLATE V

Fig. 32. *Gymnocephalous cercaria C* sp. Transverse section of the body behind the pharynx, showing dorsoventral muscles (*dvm*). The figure is combined from three sections.

Fig. 33. *Gymnocephalous cercaria C* sp. Transverse section of the body at the ventral sucker (*vs*). The figure is combined from three sections.

Fig. 34. Cercaria of *Echinostoma revolutum*. Sagittal section of the body, showing the dorsoventral muscles (*dvm*).

Fig. 35. Cercaria of *Diplostomum spathaceum*. Transverse section of the body behind the ventral sucker.

Fig. 36. *Gymnocephalous cercaria C* sp. Cell bodies of dorsoventral muscles.

Fig. 37. *Cercaria helvetica XVII*. Horizontal section of the ventral sucker. The sucker is provided with a row of small spines.

Fig. 38. *Gymnocephalous cercaria C* sp. Horizontal section of the ventral sucker. *c* erroneous, should be *pc*.

Fig. 39. *Gymnocephalous cercaria C* sp. Transverse section of the ventral sucker. Observe the epidermal fold around the sucker.

Fig. 40. Cercaria of *Echinostoma revolutum*. Transverse section of the ventral sucker.

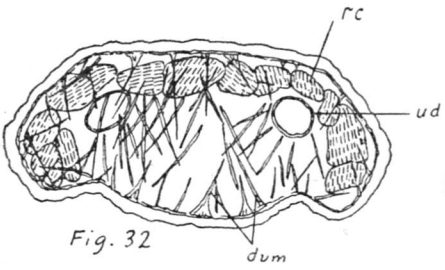


Fig. 32

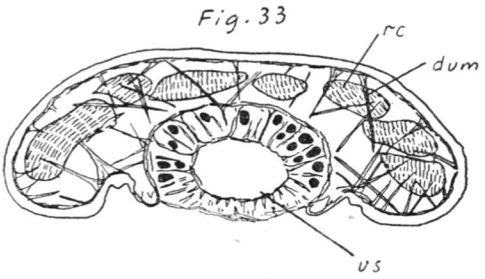


Fig. 33

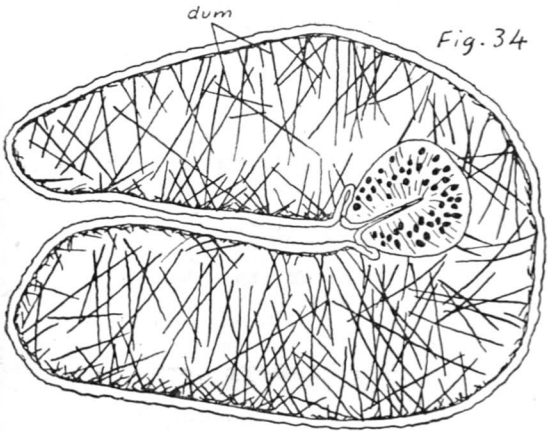


Fig. 34

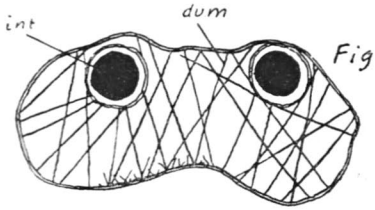
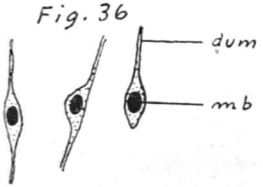


Fig. 35

Fig. 36



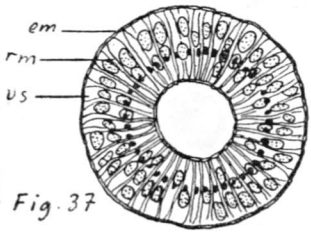


Fig. 37

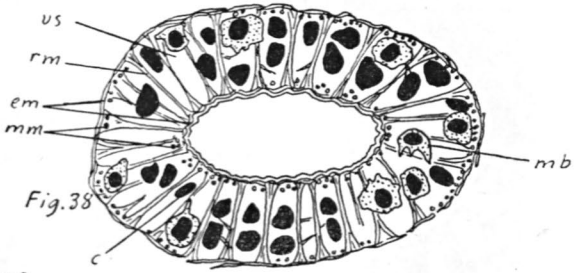


Fig. 38

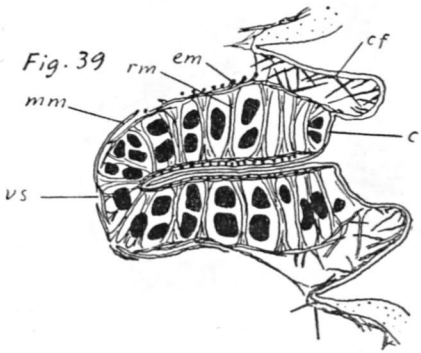


Fig. 39

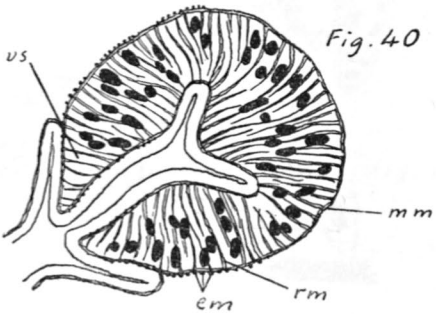


Fig. 40

PLATE VI

Fig. 41. *Gymnocephalous cercaria C* sp. Horizontal view of the oral sucker (*os*) and the pharynx (*ph*). Combined from several sections.

Fig. 42. *Xiphidiocercaria* sp. Horizontal view of the oral sucker (*os*) and the pharynx (*ph*). Combined from several sections. Observe the long fibrils (?) marked *x*. These may be part of the ducts of the penetration glands or perhaps of the large chromatophobe cells. (Compare with fig. 47).

Fig. 43. Cercaria of *Diplostomum spathaceum*. Horizontal section of the anterior organ (*ao*).

Fig. 44. *Xiphidiocercaria* sp. Horizontal section of the body near the dorsal surface.

Fig. 45. *Xiphidiocercaria* sp. Horizontal section of the body.

Fig. 46. *Xiphidiocercaria* sp. Transverse section of the body between the pharynx and the ventral sucker. Observe the parenchymatous threads (*pf*) which fill all the body spaces.

Fig. 47. *Xiphidiocercaria* sp. Transverse section of the body at the pharynx (*ph*). Observe the ducts of the penetration gland cells (*dpgl*) and the chromatophobe structures (ducts?) beneath them (*x*).

Fig. 48. *Xiphidiocercaria* sp. Granulated cystogenous gland cells.

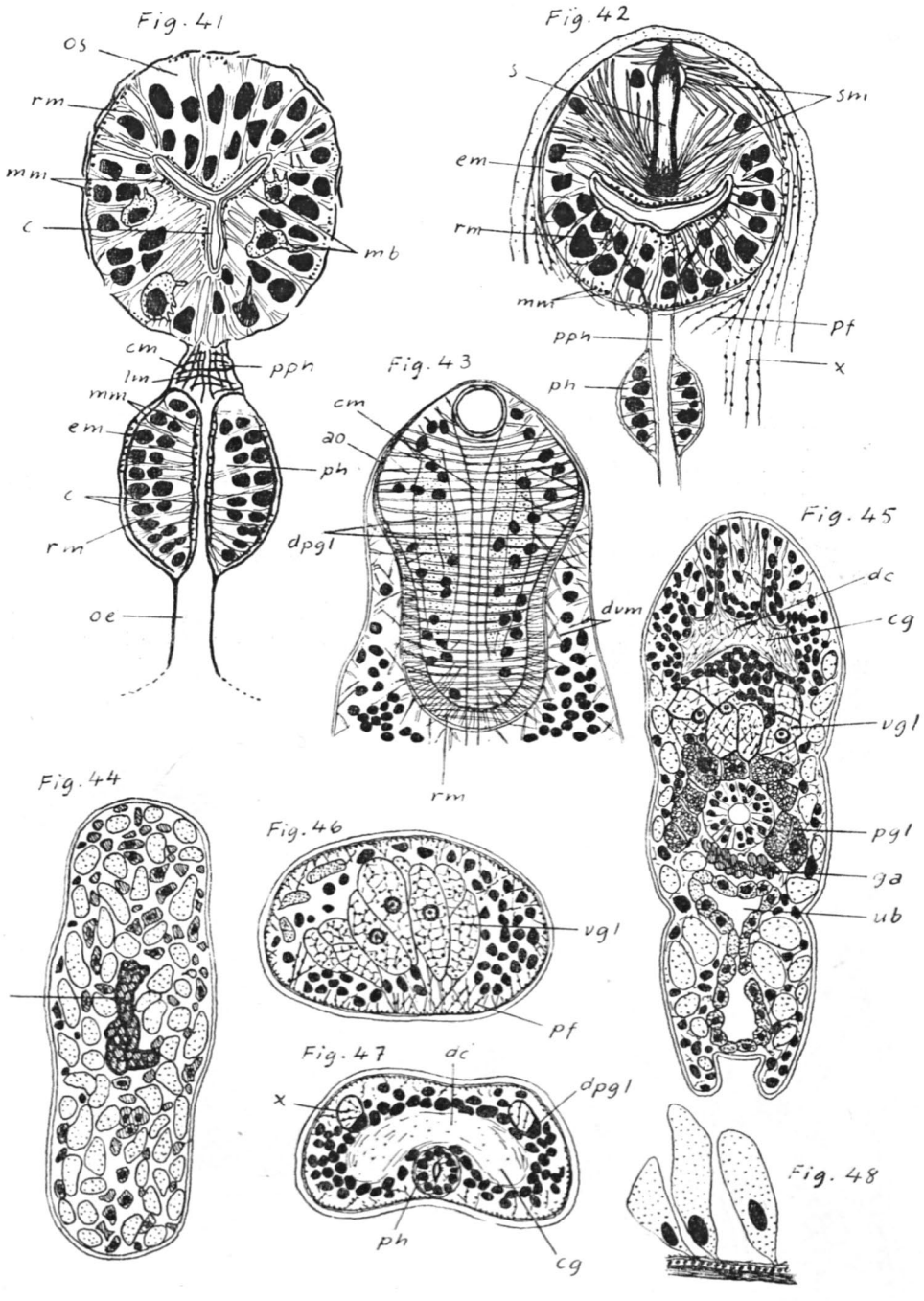


Fig. 41
os
rm
mm
c
mb
cm
ppn
lm
mm
em
ph
c
rm
oe
Fig. 42
s
sm
em
rm
mm
pph
pf
x
ph
Fig. 43
cm
ao
ph
dpgl
dvm
rm
Fig. 44
ga
Fig. 45
dc
cg
vgl
pgl
ga
ub
Fig. 46
vgl
pf
Fig. 47
ac
x
dpgl
ph
cg
Fig. 48

PLATE VII

Fig. 49. *Cercaria helvetica XVII.* Transverse section of the body in front of the ventral sucker.

Fig. 50. *Cercaria helvetica XVII.* A rod cell (*rc*).

Fig. 51. *Gymnocephalous cercaria C* sp. Horizontal section of the body. Observe the ring of large cells (myoblasts, *mb*) around the ventral sucker.

Fig. 52. *Gymnocephalous cercaria C* sp. Median view of the body.

Fig. 53. *Gymnocephalous cercaria C* sp. Transverse section of the body in front of the ventral sucker.

Fig. 54. *Gymnocephalous cercaria C* sp. Rod cells.

Fig. 55. Cercaria of *Echinostoma revolutum.* Horizontal section of the body.

Fig. 56. Cercaria of *Echinostoma revolutum.* Transverse section of the body behind the pharynx.

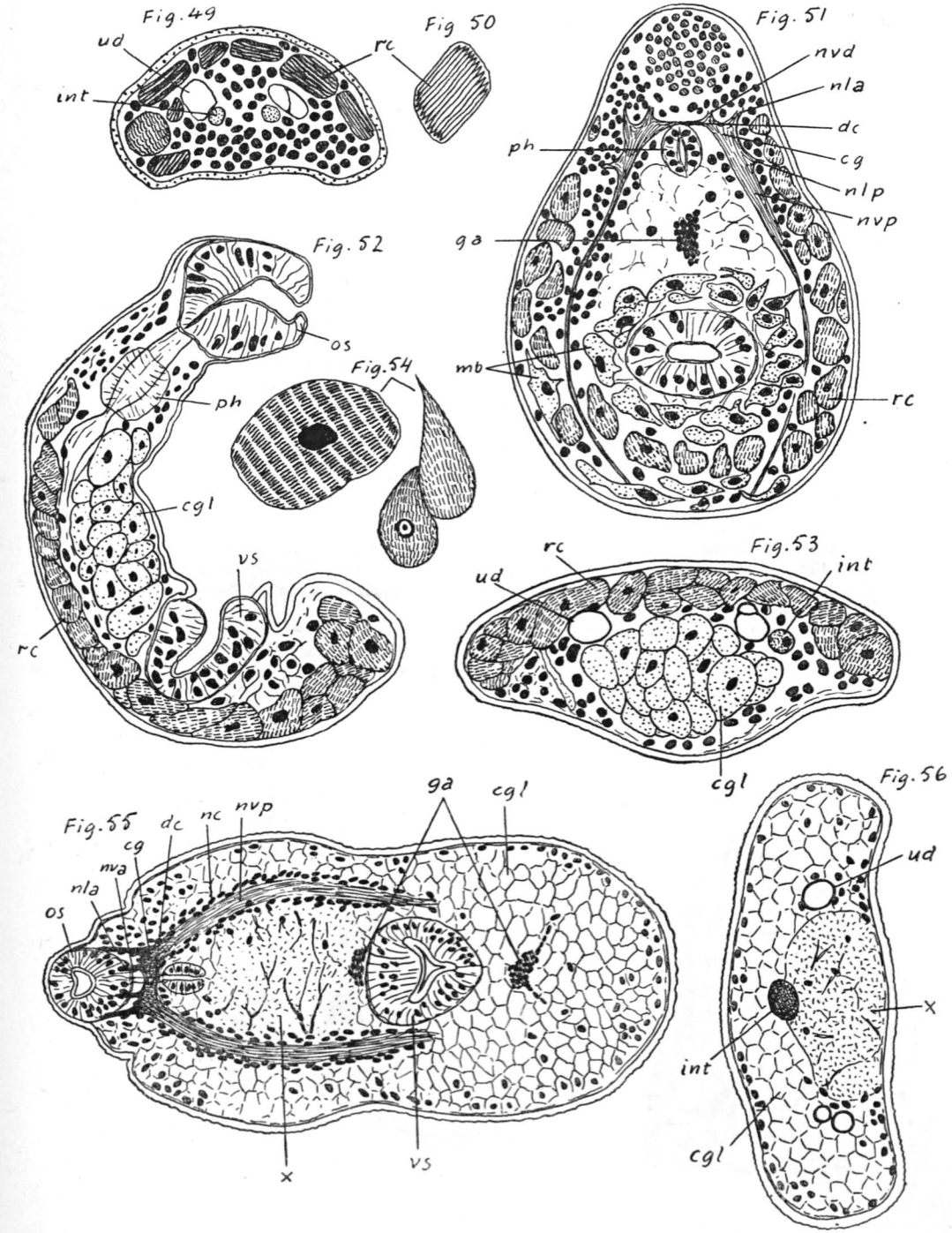


Fig. 49
ud
rc
int
Fig 50
Fig. 51
nvd
nla
dc
ph
cg
nlp
nvp
ga
mb
rc
Fig. 52
os
Fig. 54
ph
cgl
vs
rc
Fig. 53
rc
ud
int
cgl
Fig. 56
ud
x
int
cgl
Fig. 55
ga
cgl
dc
nc
nvp
cg
nva
nla
os
x
vs

PLATE VIII

Fig. 57. Cercaria of *Diplostomum spathaceum*. Horizontal section of the body, showing the region between the anterior organ (*ao*) and the ventral sucker (*vs*).

Fig. 58. *Gymnocephalous cercaria C* sp. Part of the cellular intestine (*int*).

Fig. 59. Cercaria of *Echinostoma revolutum*. Part of the cellular intestine (*int*).

Fig. 60. *Xiphidiocercaria* sp. Part of the cellular intestine (*int*).

Fig. 61. *Xiphidiocercaria* sp. Schematic drawing of the oral sucker (*os*) and the mouth opening seen from the side.

Fig. 62. *Xiphidiocercaria* sp. The ganglia and the central nerves.

Fig. 63. *Xiphidiocercaria* sp. Oblique section of the anterior end of the body, showing cerebral ganglia (*cg*) and nerve cells (*nc*).

Fig. 64. *Xiphidiocercaria* sp. Deeply staining (blue) cells assumed to be nerve cells (*nc*).

Fig. 65. *Cercaria helvetica XVII*. Horizontal section of the posterior end of the body and the proximal part of the tail, showing the bilobed urinary bladder (*ub* and *ub'*).

Fig. 66. *Gymnocephalous cercaria C* sp. Oblique sagittal section of the bilobed urinary bladder (*ub*).

Fig. 67. *Gymnocephalous cercaria C* sp. Horizontal section of the posterior half of the body. Only the posterior lobe of the urinary bladder (*ub*) is visible.

Fig. 68. Cercaria of *Echinostoma revolutum*. Longitudinal section of the tail, showing the bifurcation of the urethra (*ur*).

Fig. 57

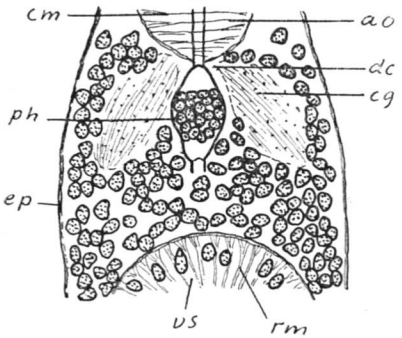


Fig. 58

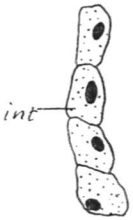


Fig. 59

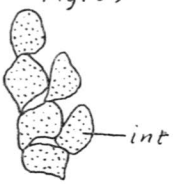
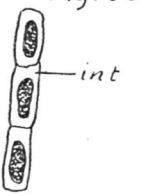


Fig. 60



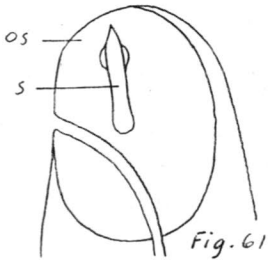


Fig. 61

Fig. 62

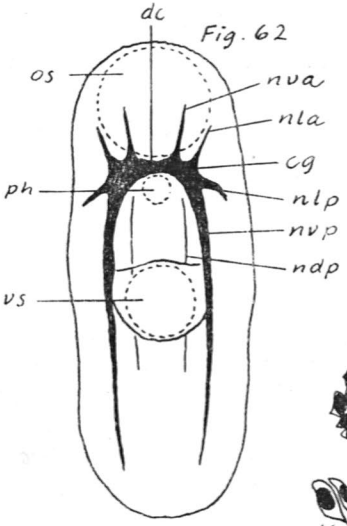


Fig. 64

Fig. 63

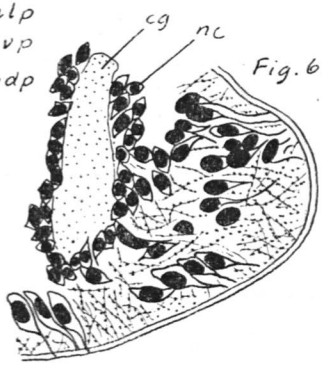


Fig. 65

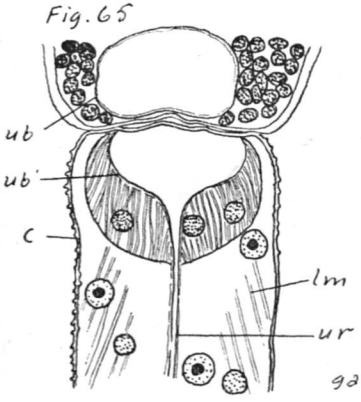


Fig. 67

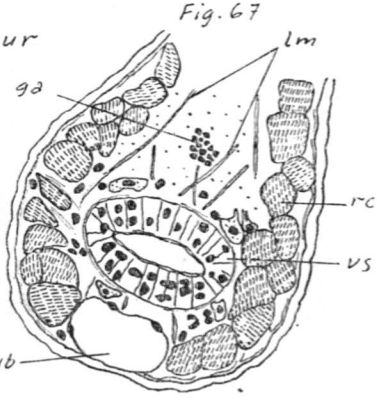


Fig. 68

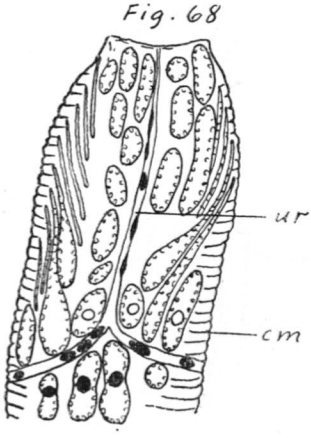


Fig. 66

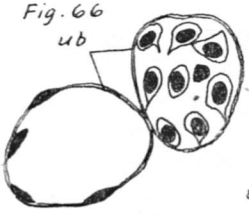


PLATE IX

Fig. 69. *Cercaria helvetica XVII.* Horizontal section of the proximal part of the tail.

Fig. 70. *Cercaria helvetica XVII.* Section of the distal end of the tail.

Fig. 71. *Gymnocephalous cercaria C* sp. Sagittal section of the middle part of the tail. Observe the two types of connections between the muscle cells and the muscle fibres (*a* and *b*).

Fig. 72. *Gymnocephalous cercaria C* sp. Transverse section of the tail.

Fig. 73. *Xiphidiocercaria* sp. Horizontal section of the proximal end of the tail, also showing the caudal pocket (*cp*).

Fig. 74. *Xiphidiocercaria* sp. Longitudinal section of the tail, showing the large chromatophobe cells (myoblasts?).

Fig. 75. *Xiphidiocercaria* sp. Transverse section of the tail.

Fig. 76. Cercaria of *Echinostoma revolutum.* Sagittal section of the middle part of the tail.

Fig. 77. Cercaria of *Echinostoma revolutum.* Transverse section of the tail.

Fig. 78. Cercaria of *Diplostomum spathaceum.* Longitudinal section of the middle of the tail-stem.

Fig. 79. Cercaria of *Diplostomum spathaceum.* Transverse section of the tail-stem.

Fig. 80. Cercaria of *Diplostomum spathaceum.* Longitudinal muscles in the tail-stem. Striated muscles (*slm*) occur only in the corners.

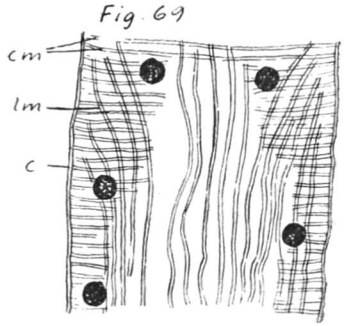


Fig. 69
cm
lm
c

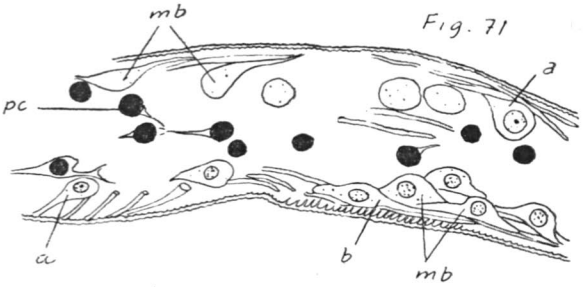


Fig. 71
mb
pc
a
a
b
mb

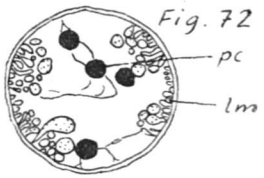


Fig. 72
pc
lm

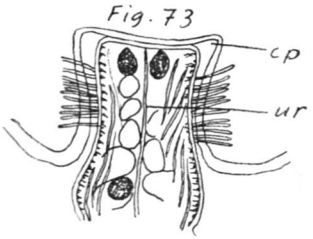


Fig. 73
cp
ur

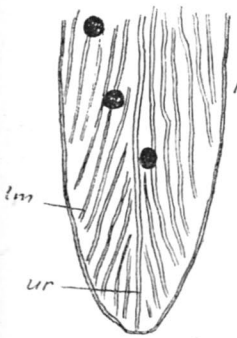


Fig. 70
lm
ur

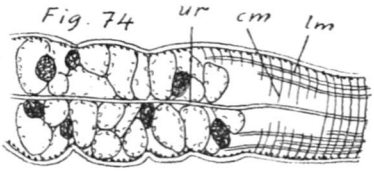


Fig. 74
ur
cm
lm

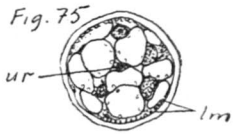


Fig. 75
ur
lm

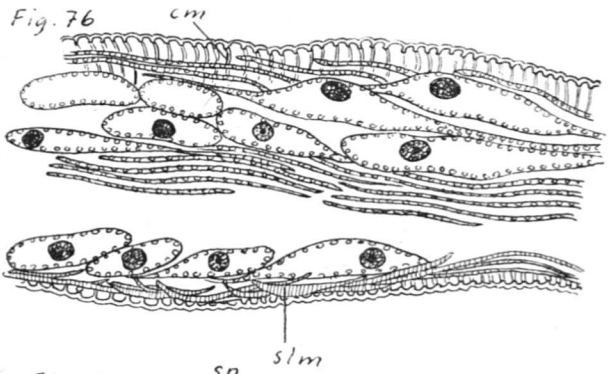


Fig. 76
cm
slm

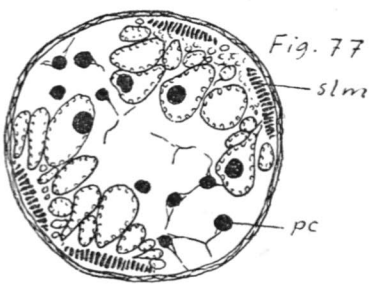


Fig. 77
slm
pc

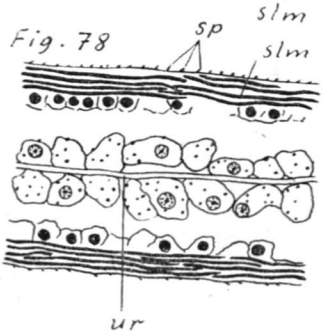


Fig. 78
sp
slm
ur

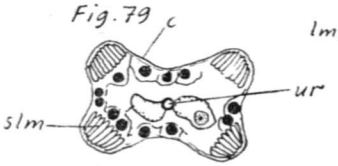


Fig. 79
c
ur
slm

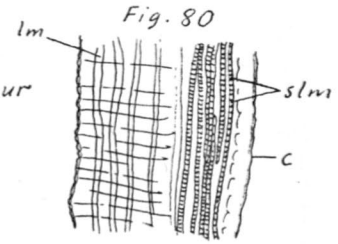


Fig. 80
lm
slm
c