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A Study of Acanthocephala from Fish of Lake Michigan

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A STUDY OF ACANTHOCEPHALA FROM FISH OF LAKE MICHIGAN

BY

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A STUDY OF ACANTHOCEPHALA FROM FISH OF LAKE MICHIGAN

I INTRODUCTION

The present paper presents the results of a study made on the morphology of some of the Acanthocephala from fish of Lake Michigan, with the view of classifying them properly and of making additions to the knowledge of the morphology of the group. The material was collected by Dr. H. B. Ward, at Charlevoix, Michigan, in the summer of 1894.

Most of the work on this group of parasites has been done on forms found in Europe and until rather recent years practically no work at all has been carried out on this group in the United States. Joseph Leidy was the pioneer worker on the group of Acanthocephala in North America. His first work on these forms (Leidy, 1850) is devoted, in part, to a description of three new species of Echinorhynchus from various hosts. From 1850 to 1890 he published various other brief accounts in which he described four additional new species, listing all of them in the genus Echinorhynchus. Of the seven species originally described by him, four have remained valid; later he recognized that the remaining three species were identical with previously described forms. E. emydis Leidy (1851) was transferred by H. J. Van Cleave (1911) to the genus Eorhynchus as Eo. emydis (Leidy).

Edwin Linton was the next to make a report on the Acanthocephala of the United States; his first account was published in 1888. His studies have been confined almost entirely to forms found in marine fish of the Woods Hole region. However, he has reported (1893) a number of Acanthocephala from fish of Yellowstone Park. Linton's last work on this group appeared in a paper (1907) in which he de-

scribed the parasites of Bermuda fishes. It is important to note that Linton recognized only one genus, Echinorhynchus, in the group Acanthocephala. Briefly summed up, his contribution to the knowledge of the Acanthocephala consists of original descriptions of seven species of Echinorhynchus and one variety of a previously described species from the same genus. Of these seven new species, six remain as distinct species; E. serrani, which was described from a single immature female, has been included by Porta (1905) in E. aurantiacus Risso (1826). It seems doubtful, however, that E. medius Linton (1907) and E. rectus Linton (1892) constitute valid species, for E. medius was described from a fragment of one specimen and E. rectus was described from only two individuals.

H. W. Graybill published (1902) an article in which he redescribed E. thecutus Linton (1888); gave a detailed account of the morphology of this form, dealing especially with nuclear structures in the subcuticula and lemnisci; and discussed his experiments by means of which he attempted to determine the function of the lemnisci. These Echinorhynchi on which Graybill worked came from the intestine of the black bass.

In addition to the above, A. E. Verrill (1871), W. S. Marshall and N. C. Gilbert (1905), and H. B. Ward (1911) have mentioned the occurrence of Acanthocephala in various hosts in the United States. In most cases no description of the species accompanied the record.

This is the extent of the work done in the United States on this group up to the year 1913 when H. J. Van Cleave (1913) published the systematic part of an extensive work on the Acanthocephala of fresh water fauna. In this paper he described four new species of the genus Eorhynchus and redescribed one of Leidy's species which he in-

cluded in the same genus. The fact that in a single genus containing five species from hosts in this country, four of which were previously unknown, indicates the little consideration which has been given to this group in the United States.

For the past two years the writer has been making a study of the Acanthocephala from fish, considering especially those contained in Dr. Ward's collection from Charlevoix, Michigan. In this study toto mounts, transverse and sagittal sections stained in Ehrlich's acid haematoxylin, were found most useful in determining the morphological and histological structures. The technique of these forms is very difficult to perfect, for the body is covered with a dense cuticula which offers great resistance to the penetration of reagents. Another difficulty comes from the fact that in sectioning, the hard-shelled embryo often tear the more delicate internal structures. The details of the technique were carried out in the usual manner. The specimens were taken down through three grades of alcohol from 85%, in which they were preserved, into distilled water. After washing for ½ to 3/4 of an hour, they were stained for one hour in dilute Ehrlich's acid haematoxylin. The specimens were then washed for ½ hour in distilled water. Those which were to be sectioned were "blued" by washing in tap-water for 15 minutes; and then were carried up through the alcohols, cleared in xylol and embedded in paraffin at 52°C. Ten-micra sections were then mounted in series. The individuals intended for toto mounts were taken from distilled water up to 70% alcohol where they were destained by the addition of a few drops of acidified 70% alcohol (100 parts 70% alcohol & 5 parts HCl c.p.). When properly destained, the acid was washed out with 70% alcohol and the specimens "blued" by adding a few drops of ammonium

hydroxide,or sodium carbonate solution, to the alcohol. After washing out the alkali the individuals were taken up through absolute alcohol, cleared in carbol xylol or synthetic oil of wintergreen and then gradually taken into the balsam.

The records of different workers on the group of Acanthocephala are in some confusion due to the lack of uniformity in the method of recording the number and arrangement of the hooks on the proboscis. Such lack of uniformity occurs even in records of the individual writers. Porta and von Linstow describe the proboscis hooks as arranged in circular rows at right angles to the long axis of the proboscis and record the number of circles with the number of hooks in each. The difficulty in this system lies in the fact that at the anterior and at the posterior ends of the proboscis the circles are often incomplete.

Lühe and de Marval in most cases describe the hooks of the proboscis as arranged in rows which extend parallel to the long axis of the proboscis. Such rows Lühe calls "Langsreihen" and designates the number of hooks in each of these longitudinal rows. The application of this method to such probosces as are found in some of the Eorhynchi meets with greatest difficulty, since in these instances there are only a few hooks arranged in three circular rows and if recorded as longitudinal rows, alternate rows would contain but a single hook. From this evidence it seems that greater uniformity could be maintained within the entire group of Acanthocephala by strict adherence to the system of recording the number of circular rows rather than the number of longitudinal rows. In the following descriptions the writer has adopted the method of Porta and von Linstow.

A difficult in applying either system lies in the fact that in

all specimens examined in connection with the present study, the proboscs were partially inverted, making it impossible to reach a high degree of accuracy in determining the number and the arrangement of the hooks. The writer obtained the most satisfactory results from data derived from camera lucida drawings of both the everted and the inverted portions of the probosces. These results were checked by carefully counting the hooks without the aid of the camera lucida. The results of the two methods agreed in all cases.

II SYSTEMATIC ANALYSIS

a. Key to the General of Acanthocephala from Fish

1 (4) Neck with bulbous swelling - - - - 2

2 (3) Anterior part of body armed with hooks
Corynosoma Lühe

3 (2) Proboscis only possessing hooks
Pomphorhynchus Monticelli

4 (1) Neck without bulbous swelling - - - - 5

5 (6) Body, collar, and proboscis armed with hooks
Echinosoma Porta

6 (5) Body unarmed; hooks on proboscis or on both collar and proboscis - - - - - 7

7 (8) Both collar and proboscis carry hooks
Chentrosoma Monticelli

8 (7) Hooks on proboscis only; collar unarmed- - 9

9 (10) Proboscis sheath a single-layered muscular sac
Neorhynchus Hamann

10 (9) Proboscis sheath a double-layered muscular sac- 11

11 (12) Brain at posterior end of proboscis sheath
Acanthocephalus Müller

12 (11) Brain anterior to the posterior end of proboscis sheath *Echinorhynchus* Zoega

b. Characteristics which determine Species

By the use of the preceding key to the genera of Acanthocephala from fish, the forms under consideration were found to belong to the genus Echinorhynchus since they possess the following characteristics of that genus: (1) a double-walled proboscis sheath; (2) the brain anteriad to the posterior tip of the proboscis sheath.

In determing the species to which an individual of this group

belongs, it is necessary to consider what characters are most constant and hence diagnostic of the species. The writer in his own observations has confirmed the observations of H. J. Van Cleave (1913: 178) that great weight should not be given to such characteristics as body length, length of lemnisci, or length of proboscis sheath, because all of these characters very so greatly either with different stages in the development of the individual; or from the different degrees of contraction of preserved specimens or from shrinkage due to the effect of killing and preserving agents. In the 21 individuals of the two species studied, in all cases where measurements and observations on the hooks could be made, the number of circles of hooks and the number of hooks in each circle has been found constant for the species. No evidence of variation was found and there is much evidence against variation. It must be kept clearly in mind, that the inverted condition of the proboscis gives a small chance for unavoidable error in the observations. The constant agreement of the foregoing observations, however, argues strongly that the number and arrangement of the hooks on the proboscis constitute distinct specific characteristics. Earlier workers in the group did not record such constancy, but on the contrary, thought there were many wide variations in the number of rows of hooks and the number of hooks in each row. In Acanthocephalus ravae, for example, Lühe (1911: 17) gives the number of rows of hooks as varying from 12 to 20, each row containing from 4 to 6 hooks. From descriptions given by other workers in the Acanthoscephala, variability within species varies in different genera. All of the descriptions,and also the observations in this study, show that the genus Echinorhynchus is only slightly variable in the number and arrangement of proboscis hooks.

Of the internal structures the male genital organs have been found to be specificly constant in their grouping and arrangement. The relation of the testes to each other and the arrangement of the cement glands are strikingly uniform. In the nine males of E. coregoni, n.sp., and E. salvelini which were studied, the writer found the grouping of the testes and cement glands to be constant for the species.

The writer has found the embryos to vary widely: in E. coregoni, n. sp., from 51 microns to 91 microns in length and from 17 microns to 25 microns in width. In E. salvelini, the embryos measured from 115 to 165 microns in length and from 20 to 25 microns in width. In all cases the measurements were made of mature embryos which had three distinct membranes and were taken from the body of fully mature females and mounted in 85% alcohol. The descriptions of Lühe, von Linstow, Porta, and de Marval show that different species vary as to the degree of constancy in the size of the embryos. In some cases the above authors have given but a single set of measurements, while in other cases, limits of size are given, often showing a rather wide range of variability. Practically all descriptions of embryos are incomplete,for the stage of development of the embryos measured is not given. Thus in comparing the embryos of unidentified forms with earlier descriptions of embryos, there is no way of being sure that the two sets of embryos are in the same stage of development.

c. Description of Species

1. Echinorhynchus coregoni, n.sp.- Body enlarged at anterior end. Males 3.0--3.7 mm. in length. Maximum width 0.8--1.05 mm. at anterior one-fourth of body. Females 3.1--5.4 mm. in length. Widest part of body 0.6--1.5 mm. Proboscis cylindrical, carrying 20

circular rows of hooks, each circle containing 6 hooks. Hooks of adjacent rows alternate. Basal hooks 0.028--0.053 mm. in length. Hooks in middle region of proboscis 0.065--0.080 mm. in length. Terminal hooks smaller than those of middle rows. Ventral hooks larger and stronger than dorsal hooks. Embryos vary from 0.051 mm. to 0.091 mm. in length and from 0.017 mm. to 0.020 mm. in width. The common size is 0.077 x 0.019 mm.

2. Echinorhynchus salvelini, n.sp.- Body elongate; slightly enlarged anteriorly. Males 7.0--9.0 mm. in length. Maximum width 0.82--1.27 mm. in region of proboscis. Females 10.5--17.0 mm. in length. Widest part of body measures 1.19--1.58 mm. Proboscis cylindrical, armed with 26 circular rows of hooks, each circle containing 8 hooks. Hooks of adjacent rows alternate. Basal hooks 0.039--0.050 mm. in length. Hooks in middle and anterior regions of proboscis 0.044--0.068 mm. in length. Hooks in middle and anterior region with basal processes measuring 0.083 mm. Embryos vary in length from 0.115 mm. to 0.165 mm. and from 0.020 mm. to 0.025 mm. in width. Common size 0.140--0.022mm.

d. Systematic Relationships of Species

1. Echinorhynchus coregoni, n.sp.- In determining the species of E. coregoni, the writer has taken for a basis Porta's paper (1905), which lists and describes the species of Echinorhynchi parasitic in fish. The writer has compared E. coregoni not only with those described in the above paper, but also with those described by Lühe (1911), in various papers by von Linstow (1895, 1896, 1906, 1908), in de Marval's papers (1905, 1905), in Leidy's works (1850, 1851, 1852, 1887, 1888), and with Linton's described species (1889, 1892, 1893,

1907). In this comparison forms showing extreme differences have been at once eliminated, those which showed even slight likenesses have been carefully compared with E. coregoni with the following results.

E. gadi is similar to E. coregoni, n. sp.: (1) in having the hooks arranged in the same number of alternate circles, (2) in possessing embryos within the range of sizes found in E. coregoni, n.sp., (3) in a very short neck region. It differs from C. coregoni, n.sp.: (1) in the number of hooks in a circle, (2) in body size, (3) in the size of lemnisci, (4) in the grouping of the male genital organs. In E. gadi the testes are not in close contact, while in E. coregoni, n. sp., the testes are contiguous. Again, the cement glands in E. gadi, though of the same number, are arranged in a row posterior to the testes; those in E. coregoni, n. sp., are massed together posteriad to the testes.

E. borealis is similar to E. coregoni, n.sp.: (1) in body size, and in possessing a short collar. This species differs radically from E. coregoni, n.sp.: in having embryos nearly twice as long as those found in the latter, and in having more circles of hooks with more hooks in each circle.

E. oricola has the same number of circles of hooks with the same number of hooks in each circle as are found in E. coregoni, n.sp. The size of the hooks and the body length in the two forms are different, the details of which are shown in Table IV.

In E. clavula and E. coregoni, n.sp., the testes are similarly placed in the body and are in the same relation to each other. The body size is nearly the same in the two species. The number of circles of hooks and the number of hooks in each circle vary in the two

forms.

E. Salmonis is similar to E. coregoni, n.sp., in possessing a range in the number of circles of hooks which includes the number of circles found in E. coregoni, n.sp. However, E. Salmonis has one more hook in each circle. The length of the probosces in the two forms is about the same, but the width is much greater in the case of E. Salmonis. The testes in the two are in the same general relation to each other and occupy similar places in the body. The cement glands of these forms are of the same number and similarly grouped. The body size in both cases is approximately the same. The most notable difference is in the size of the embryos; those of E. Salmonis being larger than the largest embryos measured from E. coregoni, n.sp. The lemnisci in E. Salmonis are about twice as long as those in E. coregoni, n.sp.

From the above comparisons the writer holds that E. coregoni, n. sp., does not belong to any of the above forms with which it has been compared. It shows closer affinity to E. Salmonis than to any of the other species, but ever here the differences are of enough weight to warrant considering it a distinct species, for which the writer proposes the name E. coregoni. A more detailed tabulation of the relations of this species to other species of Echinorhynchus is given in the following tables.

TABLE I

E. coregoni, n.sp., compared with E. gadi

Likenesses:

Hooks: E. coregoni, n.sp.--20 alternate circles of hooks

E. gadi --20-26 alternate circles of hooks

Embryos: E. coregoni, n.sp.--0.077 by 0.019 mm.

E. gadi-- 0.076 by 0.013 mm.

Neck: E. coregoni, n.sp.-- 0.1 mm. long

E. gadi -- short.

Differences:

Hooks: E. coregoni, n.sp. -- 6 hooks in a circle

E. gadi -- 9-11 hooks in a circle

Testes: E. coregoni, n.sp. -- In close contact

E. gadi -- not in close contact

Cement glands: E. coregoni, n.sp. -- 6 massed together

E. gadi -- 6 in a row

Body length: E. coregoni, n.sp. -- female, 5.4 by 1.24 mm.; male 3.0 by 0.8 mm.

E. gadi -- female,45-80 by 0.6-0.8 mm.

male, 20 by 0.6-0.8 mm.

Lemnisci: E. coregoni, n.sp. -- 0.527-0.595 mm.

E. gadi -- 1.5 mm.

TABLE II

E. coregoni, n.sp., compared with E. truttae

Likenesses:

Hooks: E. coregoni, n.sp. -- alternate circles; 0.028-0.053 mm. (Basal hooks)

E. truttae -- alternate circles; 0.05-0.06mm.(Basal hooks)

Differences:

Embryos: E. coregoni, n.sp. -- 0.077 x 0.019mm. (0.051 x 0.017mm) (0.091 x 0.020mm)

E. truttae -- 0.10--0.11 x 0.023--0.024 mm.

Hooks: E. coregoni, n.sp.-- 20 circles; 6 hooks in a circle

E. truttae -- 26-32 circles; 10-11 hooks in a circle

Testes: E. coregoni, n.sp.-- in close contact; spherical

E. truttae -- not approaching; oval

Cement glands: E. coregoni, n.sp.-- 6, massed.

E. truttae -- 6, separated

Body size: E. coregoni, n.sp.-- female 5.4 x 1.24 mm.
male 3.0 x 0.8 mm.

E.truttae -- Female 15.0-20.0 x 1.0-1.2 mm.
male 8.0-11.0 x 1.0-1.2 mm.

Lemnisci: E. coregoni, n.sp.-- 0.527--0.595 mm.

E. truttae -- 1.4 mm.

TABLE III

E. coregoni, n.sp., compared with E. borealis

Likenesses:

Body size: E. coregoni, n.sp.--male 3.0 x 0.8 mm.
female 5.4 x 1.24 mm

E. borealis -- male 4.94 x 0.75 mm
female 7.11 x 1.03 mm

Collar: E. coregoni, n.sp.-- 0.1 mm

E. borealis -- short

Differences:

Hooks: E. coregoni, n.sp.-- 20 circles of hooks, alternate
6 hooks in a circle

E. borealis -- 25 circles of hooks, alternate
10 hooks in a circle

Hook size: E. coregoni, n.sp.-- 0.028--0.080 mm

E. borealis -- 0.042 mm.

TABLE IV

E. coregoni, n.sp., compared with E. oricola

Likenesses:

Hooks: E. coregoni, n.sp.-- 20 circles of hooks, alternate 6 hooks in a circle

E. oricola -- 20 circles of hooks, alternate 6 hooks in a circle

Differences:

Hook size: E. coregoni, n.sp.-- 0.028--0.080 mm.

E. oricola -- 0.085 mm.

Body size: E. coregoni, n.sp.-- male 3.0 x 0.8 mm.
female 5.4 x 1.24 mm.

E. oricola -- 8.75--10.27 x 0.75 mm.

Neck: E. coregoni, n.sp.-- 0.1 mm.

E. oricola -- none

TABLE V

E. coregoni, n.sp., compared with E. clavula

Likenesses:

Testes: E. coregoni, n.sp.-- located near center of body; spherical, in close contact

E. clavula -- located near center of body; spherical, in close contact

Body size: E. coregoni, n.sp.-- male 3.0 x 0.8 mm.
female 5.4 x 1.24 mm.

E. clavula -- male 3.5--4.3 x 1.0 mm.
female 7.0 x 1.0 mm.

Differences:

Hooks: E. coregoni, n.sp.-- 20 circles of hooks, alternate 6 hooks in a circle

E. clavula -- 24-26 circles of hooks, alternate 9 hooks in a circle

TABLE VI

E. coregoni, n.sp., compared with E. salmonis

Likenesses:

Hooks: E. coregoni, n.sp.-- 20 circles of hooks; each row containing 6 hooks; hooks of adjacent rows alternate

E. salmonis -- 18-22 circles of hooks, each circle containing 7 hooks

Proboscis: E. coregoni, n.sp.--0.71-1.2 x 0.17-0.26 mm.

E. salmonis -- 0.70-1.0 x 0.250-0.37 mm.

Testes: E. coregoni, n.sp.--spherical, in close contact; nearer posterior end

E. salmonis -- ovoid, in close contact; nearer posterior end

Cement glands: E. coregoni, n.sp.-- 6 grouped together
E. salmonis -- 6 grouped together

Body size: E. coregoni, n.sp.-- female 5.4 x 1.24 mm.
male 3.0 x 0.8 mm.

E. salmonis -- female 7.0-8.0 x 1.2-1.6 mm.
male 3.0-4.0 x 1.2-1.6 mm.

Differences:

Lemnisci: E. coregoni, n.sp.-- 0.527--0.595 mm.

E. salmonis -- 1.0 mm.

Embryos: E. coregoni, n.sp.-- 0.077 x 0.019 mm.

E. salmonis -- 0.095 x 0.025 mm.

2. Echinorhynchus salvelini, n.sp.: The only two species of Echinorhynchus that E. salvelini, n.sp., can be confused with are E. borealis and E. truttae. However, it differs in many important points from both of these species.

E. salvelini, n.sp., is similar to E. borealis in the following respects: (1) in possessing embryos whose range of size includes the size given for the embryos of E. borealis, (2) in possessing a neck region of approximately the same length as is found in E. borealis, (3) the probosces of the two forms are of the same size. The species are different, (1) in possessing different numbers of rows of hooks on the proboscis, (2) the number of hooks in a row is different in the two species, (3) the size of the hooks is much larger in E. salvelini, n.sp., than in E. borealis, and (4) the body size in the two disagrees.

The only point of agreement between E. salvelini, n.sp., and E. truttae is in body size. The two are markedly widely distinct in the size and arrangement of the proboscis hooks, size of the proboscis number and arrangement of the cement glands, and the size of the embryos. The details of these comparisons are shown in the following tables.

From the comparison of E. salvelini, n.sp., with other Echinorhynchi, the writer holds, that the differences are of enough importance to constitute a distinct species, to which the name Echinorhynchus salvelini has been given.

TABLE VII

E. salvelini, n.sp., compared with E. borealis

Likenesses:

Embryos: E. salvelini, n.sp.--0.115-0.165 x 0.020-0.025mm.

E. borealis -- 0.148 x 0.023 mm.

Neck: E. salvelini, n.sp.-- 0.19--0.38 mm. in length

E. borealis -- 0.2 mm. in length

Proboscis: E. salvelini, n.sp.-- 0.73-0.85 x 0.29-0.31 mm.

E. borealis -- 0.75 x 0.26 mm.

Differences:

Hooks: E. salvelini, n.sp.-- 26 circular rows; each circle containing 8 hooks.

E. borealis -- 25 circular rows; each circle containing 10 hooks

Hook size: E. salvelini, n.sp.-- 0.044-0.068 mm. in length at middle of proboscis

E. borealis -- 0.042 mm. in length at middle of proboscis

Body size: E. salvelini, n.sp.-- male 7--9 mm. in length
0.82--1.27 mm. in width.
female, 10.5--17.0 mm. in length
1.19--1.58 mm. in width

E. borealis -- male, 4.94 mm. in length
0.75 mm. in width
female, 7.11 mm. in length
1.03 mm. in width

TABLE VIII

E. salvelini, n.sp., compared with E. truttae

Likenesses:

Body size: E. salvelini, n.sp.-- male, 7.0-9.0 x 0.82-1.27mm
female, 10.7-17.0 x 1.19-1.58 mm.

E. truttae -- male, 8.0--11.0 x 1.0--1.2 mm.
female, 15.0-20.0 x 1.0-1.2 mm.

Differences:

Hook size: E. salvelini, n.sp.-- 0.044-0.068mm. in middle region of proboscis

E. truttae -- 0.061--0.080 mm.

Proboscis: E. salvelini, n.sp.--0.73-0.85 x 0.29-0.31 mm.

E. truttae -- 1.0-1.3 x 0.3-0.35 mm.

Hook arrangement: E. salvelini, n.sp.-- 26 circular rows, 8 hooks in each circle

E. truttae -- 20-22 circular rows, 13-16 hooks in each circle

Cement glands: E. salvelini, n.sp.-- 8 in a row

E. truttae -- 6 in a row

Embryos: E. salvelini, n.sp.--0.115-0.165 x 0.020-0.025mm.

E. truttae -- 0.10-0.140 x 0.023-0.026 mm.

III MORPHOLOGY

Echinorhynchus coregoni

1. Size and General Appearance.

The individuals vary in length from 6.12 mm. to 3.0 mm.--measurements being made from the posterior tip to the region of the proboscis. The maximum diameter which occurs at the anterior one-fourth of the body is 0.06 to 1.5 mm. The females are usually much larger than the males. The contracted specimens show irregular creasings which might suggest segmentation, but sections demonstrate that this condition does not extend beyond the cuticula and hence must be due only to the contracted condition of the body. The individual is divided into three regions: (1) a cylindrical proboscis armed with hooks, (fig. 1) (2) a short neck region which joins the proboscis to the posterior region, (fig. 5, a) and (3) the body proper. In all cases where measurements could be made, the neck measured 0.1 mm. This region constitutes an introvert which is drawn in by definite sets of muscle fibers which extend from the anterior edge of the neck to the interior surface of the body wall.

This species has definite dorsal and ventral surfaces. The latter is slightly flattened and the extended proboscis is always bent toward it. The dorsal surface is convex and in the region of the proboscis-sheath is markedly enlarged.

2. Body Wall

Externally, the body is covered with a dense cuticula which varies slightly in thickness in the different parts of the body, measuring from 0.003 to 0.013 mm. Beneath the cuticula is the syncitial

sub-cuticular layer which contains many nuclei irregularly arranged throughout the region. These nuclei are uniformly distributed in the body wall. They contain distinct nucleoli which vary in number and in size. In some nuclei there is a single nucleolar mass, while in others there are many nucleoli of different sizes and shapes.

The sub-cuticula is divided into two zones. The region next to the cuticula is densely granular, quite uniform in thickness, and occupies about one-third of the entire width of the sub-cuticula. In the region next to the body cavity the protoplasm is less dense but has fibrillar strands of protoplasm extending transversely across the wall.

Next to the subcuticula interiorly, is a single layer of circular muscle fibers (fig. 2b) and immediately next to the body cavity are longitudinal muscle fibers (fig 2.c) which in cross section show a definite arrangement in circular groups. Between these two layers are scattered a few large nuclei.

The subcuticula is penetrated by many transverse vessels, the Lacunae, which are irregular in arrangement and frequently anastomose. These unite to form a right and a left longitudinal canal, both of which extend the entire length of the body.

3. Proboscis and Associated Structures

When the proboscis is inverted it is held within a sheath made up of two distinct muscle layers. Extending from the inner wall of the tip of the proboscis to the posterior wall of the sheath are band of muscle fibers which serve to invert the proboscis (fig. 5,e). The proboscis retractor muscles, as shown by sagittal sections, continue through the posterior wall of the sheath and form two bands, one of which be-

comes attached to the dorsal surface and the other to the ventral surface of the body. The action of this set of muscles and the collar retractors causes the complete inversion of the introvert. Located between the proboscis retractors anteriad to the posterior end of the proboscis sheath is the brain. From this two groups of nerve fibers pass through the proboscis sheath and form the two retinacula (fig. 5,d), one of which is attached to the dorsal and the other to the ventral region of the body wall. The proboscis varies in size from 1.2 by 0.2 mm. to 0.71 by 0.2 mm. Since the proboscis was always inverted, the length had to be determined by combining the length of the extended and of the inverted portions.

The proboscis is armed with hooks arranged in 20 alternate circles, each containing 6 hooks. The circles nearer the neck are often incomplete. The hooks vary in size and shape. Those close to the neck are much straighter and more delicate than those nearer the tip of the proboscis. On the ventral surface the hooks are strikingly larger and more strongly built than on the dorsal surface. This difference is most clearly seen in the rows of hooks close to the body. The anterior rows of hooks have a definitely differentiated basal portion which is not found in the posterior hooks. Transverse sections show large nuclei at the bases of the hooks.

4. Lemnisci

The lemnisci (fig.5,c) are two large organs located at the anterior part of the body. They are attached to the collar at the point where it joins the proboscis sheath. One lemniscus is dorsal in position, the other is ventrally placed. The lemnisci show much the same structure as is found in the fibrillar part of the subcuticula. There

are large canals extending transversely through the organs, and around these canals are nuclei similar to those in the subcuticula. Those of the lemnisci, however, are much larger. Each lemniscus is surrounded by a delicate membrane which extends beyond the posterior end of the structure and is attached to the body wall. Just what connection, if there is any, exists between the two lemnisci the writer has not been able to work out definitely. A canal can be traced part way around the anterior end of the proboscis sheath, and evidence indicates that the two lemnisci open into this circular canal, although such a connection has not been demonstrated. Since there is such a marked resemblance in the canal arrangement and the general structure of the subcuticula and the lemnisci, it seems possible that there may be some connection between these parts, probably through the lateral canals of the subcuticula.

5. Reproductive Organs

In this form the two sexes are different individuals. The male apparatus consists of several parts. A pair of approximately spherical testes (fig. 5, g) are arranged one behind the other just posterior to the proboscis sheath. Posterior to the testes are six cement glands (fig. 5, h) grouped together. They are ovoid in their general outline, although there is some irregularity in this particular. Behind this the bursa begins as an elongated cup (fig. 5, i) from the posterior narrow end of which extend the cirrus (fig. 5, l). Around the cirrus is a group of large nerve cells which form a genital ganglion (fig. 5, j). The final part of the bursa is a much folded tube which has on its walls in the region of the cirrus four disc-shaped structures which I interpret as adhesive organs which aid in copulation. The whole system is swung in a clear sac which

probably is a modification of the suspensory ligament.

The female genital apparatus is held in the ligamentum suspensorum which is attached at its anterior end to the posterior tip of the proboscis sheath. Posteriorly the ligament is attached to the posterior tip of the body wall. The apparatus is divided into two distinct regions, the uterus and the vagina. The uterus consists of an anterior complicated selective apparatus by means of which only the spindle-shaped embryos are allowed to pass down the uterus to the posterior region of the structure. From the selective apparatus the uterus extends as a long tube with a single layered wall to a vaginal region which is surrounded by gland cells and sphincter muscles. In the region of the vagina, the cavity of the uterus increases in size and is abruptly narrowed into the vagina. At this place the wall of the uterus is thickened.

In the mature females no ovaries were found, but the body cavity was filled with embryos in all stages of development from egg masses to the fully developed spindle-shaped embryos with their three distinct membranes surrounding the inner granular mass. The egg masses are ovoid, but vary in size. These egg masses with the embryos were often found in such numbers as to completely fill the cavity of the female. The embryos were best studied by removing from the female and examining in 85% alcohol. Two methods were used in measuring embryos from two individuals: (1) by making camera lucida drawings of the embryos and then measuring these drawings, and (2) by direct measurement of the embryos with the ocular micrometer. One method acted as a check on the other. By the former method the greatest number of embryos measured from 0.077 mm. to 0.081 mm. in length with a range of variability from 0.063 to 0.09 mm., and by the same method

0.019 and 0.020 mm. were the most common widths, with a range of variability from 0.016 to 0.025 mm. By the latter method the most common length was found to be 0.077 mm. with extremes of 0.057 and 0.085 mm. The most common width was 0.019 mm., with extremes of 0.017 and 0.020 mm. The slight disagreement in the results obtained by the two different methods is due, in large part, to the difference in magnification used. In the direct observations, ocular micrometer #2 with 1/12th oil immersion objective were used; for the camera lucida drawing, ocular #3 and objective #5 were used.

b. Echinorhynchus salvelini

1. Size and General Appearance.

The body length in E. salvelini varies from 9 to 17 mm.; the width from 0.82 to 1.58 mm. In obtaining these measurements, the maximum diameter which occurs in the region of the proboscis sheath, was recorded as the width; the length was measured from the posterior tip of the body to the inverted collar region. In all cases the females were found to be longer than the males, but the diameter in the two sexes varied less. In the contracted specimens, the anterior region of the body and the proboscis curve sharply toward the ventral surface. The body is divided into three regions: (1) a long cylindrical proboscis carrying hooks (fig. 8, a.), (2) a well defined neck region which measures from 0.19 to 0.38 mm. in length, and (3) the body proper. The collar or neck region constitutes the introvert and is operated by muscle fibers which are attached to the collar at the place where the proboscis sheath and the collar are joined. These fibers are most numerous on the dorsal and the ventral surfaces.

2. Body Wall

The body wall is composed of distinct regions. Externally, it is covered with a dense cuticula which measures 0.003 to 0.008 mm. in thickness. Beneath this is the subcuticula which contains a densely granular region and a region in which the protoplasm is arranged in fillar strands. The subcuticula is a syncitium possessing many irregular nuclei and large lacunae. The latter unite to form two lateral vessels extending the length of the body. On the inner surface of the subcuticula, is a circular layer of muscle fibers. This is followed by a thin irregular layer of cells containing very large nuclei. This layer separates the circular band of muscle fibers from

another muscular region in which the fibers extend longitudinally. Immediately next to the body cavity is a second layer of very large cells (fig 8, h) which in section are seen to be continuous with the muscle fibers. These and the cells found between the circular and longitudinal layers are undoubtedly the cells which produce the muscle fibers.

3. Proboscis and Associated Structures

The proboscis varies in length from 0.73 mm. to 0.85 mm.; the width is from 0.29 to 0.31 mm. When inverted, the proboscis is held within a sheath made up of two distinct muscle layers. The proboscis is drawn into the sheath by the contraction of muscle fibers (fig 8 d.) which extend from the inner wall of the tip of the proboscis to the posterior wall of the probiscis sheath. These proboscis retractors (fig 8 c) continue through the sheath as two bands, one of which passes to the dorsal and the other to the ventral portion of the body wall. The contraction of these bands, the sheath retractors, causes the sheath to be drawn farther into the body. The brain is located between the fibers of the proboscis retractors, slightly posteriad to the center of the sheath. From the brain two nerve fibers branch off,--one passes through the dorsal, the other through the ventral wall of the proboscis sheath and form retinacula which attach themselves, one to the ventral and the other to the dorsal wall of the body. At the points where the nerve fibers leave the proboscis, there are large nerve calls.

The proboscis is armed with 26 circles of hooks, each circle containing 8 hooks which alternate with the hooks in adjacent circles. The hooks gradually increase in size from the smallest hooks in the incomplete circles at the posterior end of the proboscis to the larg-

est hooks found in the middle and anterior regions of the proboscis. The basal hooks measure 0.038 to 0.050 mm. in length, varying with their distance from the most posterior row. The hooks of the middle and anterior regions are 0.068 mm. in length. The hooks of the posterior region differ from the hooks of other parts of the proboscis in not having a basal or root process which projects into the substance of the proboscis. This basal process measures 0.085 mm. in length, being much longer than the projecting portion of the hook.

4. The Lemnisci

(fig. 8, b)

The long, lobed lemnisci are attached laterally at the anterior end to that part of the body wall where the anterior edge of the collar is joined to the proboscis sheath. Surrounding the lemnisci are sheaths of tissue which continue beyond the posterior tip of the organs and passing obliquely posteriad are attached to the body wall. In this species as in other forms, the function of the lemnisci has not been determined. Transverse sections of the lemnisci show that the protoplasm is arranged in fibrillar strands. Extending transversely and longitudinally through these organs are canals, similar in appearance to the lacunae found in the subcuticula. A few large irregular nuclei are conspicuous in the structure of the lemnisci. The two lemnisci are connected by a circular canal which extends around the extreme anterior end of the proboscis sheath.

5. Reproductive Organs

The male reproductive organs consist of two ovoid testes located slightly posteriad to the center of the individual. Just posterior to these is a chain of eight spherical cement glands. Immediately

following the cement glands is the bursa, the first division of which is a thick-walled, cone-shaped structure, called the Kittbental, which receives the ducts from the testes and cement glands. The Kittbental opens into the eversible portion of the bursa, which contains the cirrus surrounded by the genital ganglion. About midway between the testes and the Kittbental the wall of each vas deferens dilates into a bulbous enlargement.

The female genital organs are located in the extreme posterior end of the individual and consist of a uterus and a vagina. The important part of the uterus is the complicated selective apparatus at the anterior end of the structure. This opens into a thick uterin tube which terminates in the vagina. The vagina is surrounded by large sphincter muscles which control the passage of embryos to the exterior. Large gland cells are also found in the vaginal region.

The embryos are very long, spindle-shaped forms varying in length from 115 to 165 mm. and in width from 20 to 25 mm. The granular protoplasmic part of the developing embryos is surrounded by three membranes. No ovaries were found, but egg masses in all stages of development were numerous in the mature females. The embryos were measured by direct observation using #2 ocular in combination with 1/12 oil immersion objective.

TABLE IX

The size of the embryos in this group seems to be of enough importance to warrant a detailed study. The following table contains the measurements of embryos from two mature females of E. coregoni. The measurements were made from camera lucida drawings for which ocular #3 and objective #5 were used. The results were checked by making direct measurements of embryos from the same individuals, the combination of #2 micrometer ocular with 1/12 oil immersion were used for these measurements. Results are recorded in microns.

Individual A		Individual B	
74 x 20	82 x 19	67 x 18	77 x 19
77 x 18	82 x 20	75 x 18	81 x 19
87 x 25	77 x 19	68 x 18	81 x 19
65 x 18	71 x 19	67 x 18	70 x 18
85 x 21	90 x 19	82 x 20	80 x 20
80 x 19	63 x 19	82 x 21	81 x 19
85 x 20	82 x 20	73 x 20	83 x 20
84 x 20	86 x 21	70 x 20	80 x 19
83 x 21	75 x 19	70 x 19	78 x 19
91 x 20	77 x 18	75 x 18	85 x 20
72 x 20	77 x 18	85 x 19	83 x 20
79 x 19	81 x 21	85 x 21	83 x 21
78 x 19	77 x 19	84 x 20	80 x 19
69 x 19	85 x 20	73 x 19	80 x 20
80 x 18	80 x 20	72 x 18	77 x 18
77 x 20	81 x 19	70 x 19	70 x 20
83 x 19	80 x 20	72 x 20	70 x 18
81 x 20	73 x 18	72 x 16	80 x 19
82 x 19	73 x 20	81 x 19	81 x 19
82 x 19	74 x 20	80 x 20	73 x 17
80 x 18	83 x 18	81 x 19	78 x 19
83 x 19	90 x 20	87 x 20	83 x 20
80 x 19	83 x 20	68 x 19	77 x 19
90 x 20	79 x 20	81 x 20	80 x 19
80 x 18	79 x 19	78 x 19	67 x 18
80 x 19	86 x 18	81 x 18	
80 x 19	87 x 21		
80 x 21			

TABLE X

Measurements in microns of embryos from a mature individual of E. salvelini. Measurements made by direct observation with the aid of #2 ocular micrometer and #8 objective.

163 x 25	122 x 22	135 x 22	118 x 22
155 x 22	150 x 22	160 x 22	133 x 25
158 x 22	143 x 20	130 x 25	143 x 20
150 x 25	130 x 20	150 x 25	160 x 20
120 x 25	143 x 25	150 x 22	140 x 25
140 x 22	143 x 22	140 x 25	160 x 22
150 x 22	140 x 25	160 x 25	133 x 25
150 x 22	153 x 22	147 x 22	147 x 22
150 x 22	150 x 22	147 x 22	143 x 22
145 x 22	140 x 22	153 x 25	147 x 22
165 x 22	147 x 22	145 x 22	135 x 22
155 x 22	145 x 22	143 x 22	130 x 25
122 x 22	145 x 22	140 x 22	153 x 22
145 x 22	143 x 25	150 x 22	140 x 22
150 x 22	128 x 25	135 x 22	140 x 22
155 x 22	140 x 25	143 x 20	135 x 22
120 x 25	150 x 25	160 x 22	153 x 22
140 x 22	138 x 25	143 x 22	145 x 22
163 x 22	145 x 22	145 x 22	138 x 25
150 x 22	140 x 22	158 x 22	147 x 25
138 x 22	145 x 22	135 x 25	145 x 22
138 x 25	169 x 22	147 x 22	150 x 25
138 x 22	115 x 22	138 x 25	135 x 22
143 x 25	150 x 25	145 x 22	155 x 22
147 x 22	153 x 22	147 x 22	155 x 22
158 x 22			

EXPLANATION OF PLATES

Plate I

Representing the Morphology of Echinorhynchus coregoni

Figure 1. Proboscis (x90), showing hooks of dorsal and ventral surfaces.

Figure 2. Section of body wall (x640). a, subcuticular nuclei; b, fibers in circular muscle layer; c, fibers in longitudinal muscle layer.

Figure 3. Tangential section through subcuticula (x640), showing the irregular nuclei.

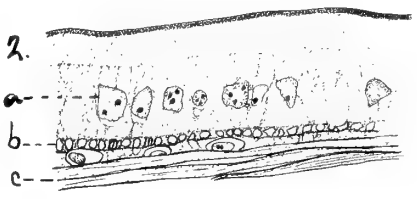
Figure 4. Hook of proboscis (x640). a, from a middle region; b, from basal rows.

Figure 5. Entire animal (x57), with part of body wall and proboscis sheath removed to show internal structure. a, collar or neck region; b, circular canal connecting the lemnisci; c, lemniscus; d, retinacula; e, proboscis retractor muscles; f, proboscis sheath retractor muscles; g, testes; h, cement glands; i, Kittbeutal; j, genital ganglion; k, adhesive organ; l, cirrus

Figure 6. Proboscis (x385), showing relative size of dorsal and ventral hooks.

Figure 7. Embryo (x890).

Plate I



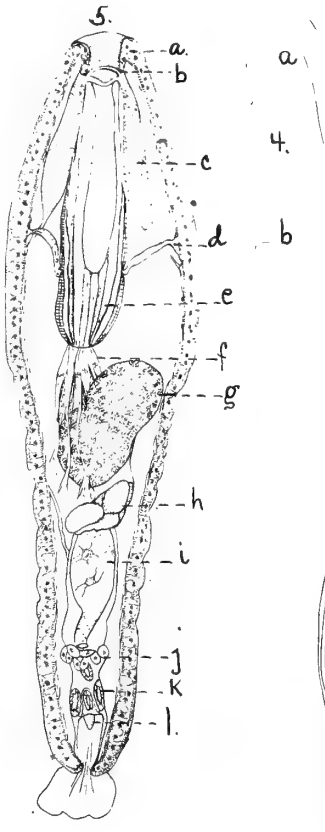


Plate II

Representing the Morphology of Echinorhynchus salvelini

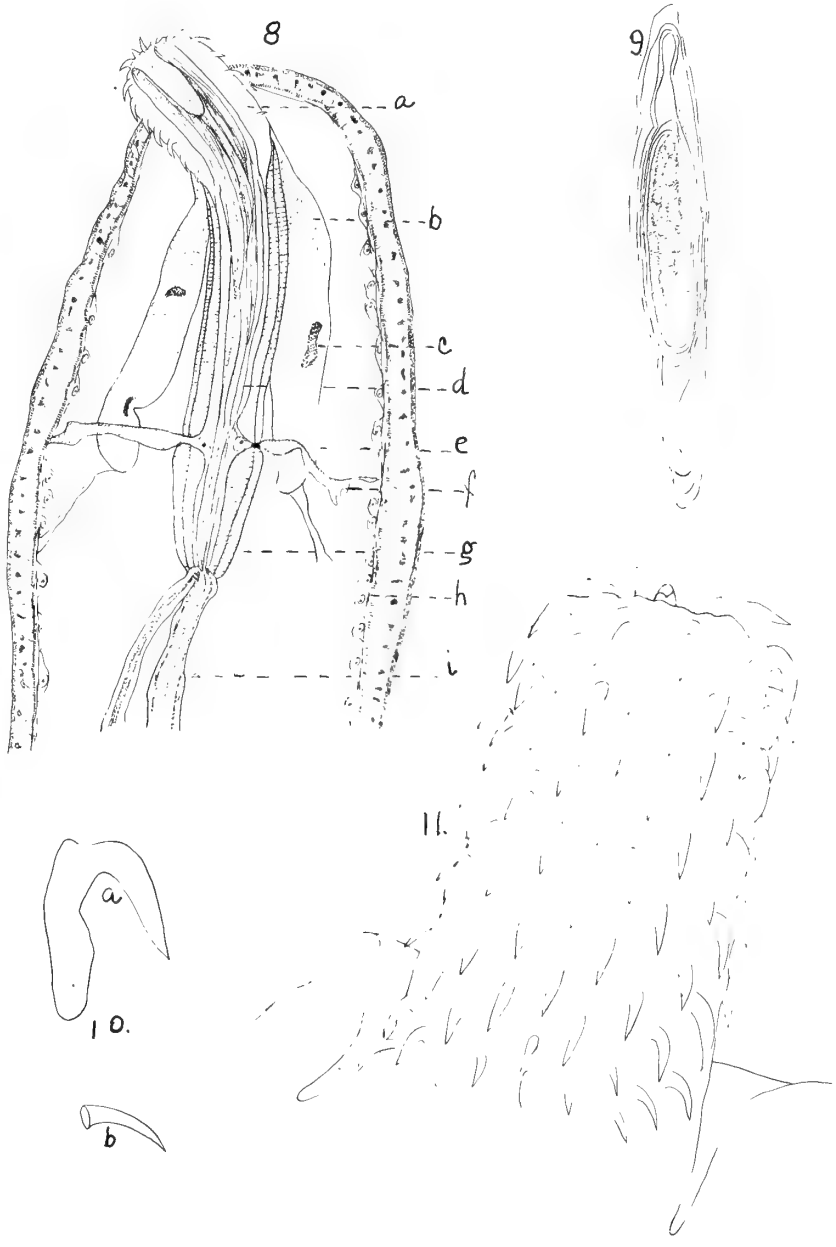
Figure 8. Optical section (x90) through anterior region of body. a, proboscis; b, lemniscus; c, one of the large irregular nuclei of lemniscus; d, proboscis retractors; e, nerve cells at base of retinacula; f, retinacula; g, proboscis sheath; h, cells associated with longitudinal muscle fibers; i, proboscis sheath retractor.

Figure 9. Embryo (x890).

Figure 10. Hooks of proboscis (x640). a, anterior hook; b, basal hook.

Figure 11. Proboscis (x285).

Plate II



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