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## Caryophyllaeid Cestodes from Two Species of Redhorse (*Moxostoma*)\*

LEIGH H. FREDRICKSON AND MARTIN J. ULMER

**Abstract.** Two caryophyllaeid tapeworms, *Isoglaridacris longus* sp. n., and *I. folius* sp. n., are described from two species of redhorse, namely, *Moxostoma macolepidotum* and *M. erythrurum*, respectively. Members of the genus *Isoglaridacris* appear to be host specific, since the two species mentioned in this study occur in different fish hosts collected from the same rivers.

Both *I. longus* and *I. folius* appear to exhibit seasonal periodicity, the smallest populations occurring in late summer. Their presence or absence in fish during the winter months, however, is unknown. Infected fish usually harbor a small number of cestodes, generally only a single worm. The annual per cent of infection is 38% for the northern redhorse and 37% for the golden redhorse. Eggs are operculate and oncospheres show well-defined hooks after 17 days.

A key to the three known species of the genus *Isoglaridacris* is presented.

### INTRODUCTION AND HISTORICAL REVIEW

Cestodes of the family Caryophyllaeidae are unsegmented tapeworms occurring in fresh water teleosts of Africa, Asia, Australia, Europe, and North America. Larval stages develop in aquatic oligochaetes of the family Tubificidae. Extensive historical reviews of the family have been presented by Hunter (1930), Hyman (1951), Wardle and McLeod (1952), and Yamaguti (1959).

Ten genera of the subfamily Caryophyllaeinae Nybelin 1922 are known to occur in North America, namely: *Glaridacris* Cooper, 1920 *Archigetes* Leuckart, 1878; *Biacetabulum* Hunter, 1927; *Caryophyllaeus* Muller, 1787; *Hypocaryophyllaeus* Hunter, 1927; *Pliovitellaria* Fischthal, 1951; *Bialovarium* Fischthal, 1953; *Monobothrium* Diesing, 1853; *Hunterella* Mackiewicz and McCrae, 1962; and *Isoglaridacris* Mackiewicz, 1965. The latter contains a single species, *I. bulbocirrus* described by Mackiewicz (1965) from the white sucker *Catostomus commersoni* (Lacépède) in New York. One additional genus, as yet unpublished, is indicated in Mackiewicz's doctoral dissertation (1960).

Members of the genus *Isoglaridacris* are intestinal parasites characterized by the presence of a common gonopore, an entirely medullary "A"-shaped ovary, and uterine coils not extending

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beyond the cirrus pouch. The life cycle is unknown. This study describes two additional species of the genus.

#### MATERIALS AND METHODS

Two hundred and seventy five northern redhorse [*Moxostoma macrolepidotum* (LeSueur)], and 186 golden redhorse [*M. erythrum* (Rafinesque)] ranging from 3 to 18.5 inches in total length were examined from rivers within the borders of Iowa and South Dakota between June, 1961 and January, 1963.

Both species were obtained from two main study areas in Iowa, one located near Alden in Hardin County on the Iowa River, and the other near Boone in Boone County on the Des Moines River. Northern redhorse were also taken from the Skunk River in Story County, Boone River in Hamilton County, Little Sioux River in Dickinson County near Iowa Lakeside Laboratory, Missouri River at Lewis and Clark Lake near Yankton, South Dakota, and the south fork of the Iowa River in Hardin County.

Fish were examined in the field immediately after collection. Prior to fixation, helminths removed from the intestine were placed in saline and the opened intestine was then transferred to a dish of river water for a few minutes before re-examination of the washings. Worms removed from the debris were rinsed in saline, and were fixed without pressure in A. F. A.

Examination of fish brought to the laboratory proved less desirable because nearly all hosts died during transport. Specimens of *Isoglaridacris* removed from dead fish detach from the intestinal lining and soon die. Such worms are unsuitable for critical studies due to pronounced modifications of scoleces and strobila. Field examinations of fish proved more desirable for obtaining well-fixed specimens.

Cestodes for whole mounts were stained with Mayer's paracamine, counterstained with fast green, cleared in methyl salicylate, and mounted in synthetic resin. Sagittal, frontal, and cross sections were prepared from unflattened specimens fixed in AFA, embedded in paraffin cut at 12 microns, stained with Harris' haematoxylin and counterstained with triosin or eosin.

Eggs for experimental work were collected by placing gravid worms in distilled water. Refrigerated worms shed eggs more readily than do those subjected to cooling. For developmental studies, eggs were maintained in small stender dishes at room temperature in complete darkness. To reduce bacterial and fungal growth, boiled stream water (changed daily) was used in all experimental studies.

Drawings were made with the aid of a microprojector or camera lucida.

## ISOGLARIDACRIS LONGUS

*Adults (Plates I & II)*

Specific diagnosis: *Isoglaridacris longus* sp. n. with characters of the genus. Gravid adults 14.6 mm (10 to 25) by 0.7 mm (0.6 to 1.1). Well-developed wedge-shaped scolex with three pairs of shallow loculi. Body often curved, slender, oval in cross section. Neck region short. Vitellaria in pre- and post-ovarian fields. Pre-ovarian vitellaria in two lateral rows, not continuous with post-ovarian field. Testes 124 to 170 appearing as scattered follicles between right and left preovarian vitelline fields. Posterior limit of testicular field extending to near anterior border of cirrus pouch; anterior limit of testicular field not extending to anterior limit of pre-ovarian vitellaria. Cirrus pouch large, 0.24 to 0.38 mm in diameter. Unarmed eversible cirrus. Common gonopore. Lobate ovary in form of inverted "A" whose arms may or may not be joined posteriorly. Ovarian arms measuring 1.4 mm (0.7 to 2.5). Parenchymal muscles poorly developed. Eight pairs of osmoregulatory canals in cortical parenchyma. Common excretory bladder at posterior tip. Eggs operculate, intrauterine eggs measuring 36 by 46 microns. Intestinal parasite of northern redhorse, *M. macrolepidotum*.

Holotype: USNM Helm. Coll., No. 60302 Beltsville, Maryland (from *M. macrolepidotum*).

Gravid worms (Figure 7) are elongate (10 to 25 mm in length) and in life usually appear either straight or somewhat curved. Fixed specimens are usually only slightly curved (Fig. 4). Adults are loosely attached along the greater portion of the intestinal mucosa. A distinct translucent area appears in the region of the cirrus pouch, as in *I. bulbocirrus*. The body, generally oval in cross section, becomes more rounded at the level of the cirrus pouch.

In living specimens the wedge-shaped scolex, bearing three pairs of shallow loculi, is very active, its constant extensions and contractions resembling those seen in living *Glaridacris catostomi* Cooper, 1920.

The unarmed cuticle is approximately 6 microns thick. Longitudinal subcuticular muscle fibers are quite distinct. Longitudinal fibers of the parenchymal muscles show well in cross section and are pushed outward in some areas by the pre-ovarian vitellaria (Fig. 8). Circular muscle fibers are poorly developed. Dorso-ventral muscle bands are well defined and may pass directly through organs lying in their path. Subcuticular cells fill much of the cortical area.

Eight pairs of conspicuous osmoregulatory canals (2 lateral pairs, one mid-dorsal and one mid-ventral pair) occupy the cortical parenchyma (Fig. 10). One member of each pair is much larger in diameter (27-35 microns).

The average number of testes is 145 per worm (based upon study of 22 stained whole mounts). The testicular field is situated medially, extending anteriorly from the region of the cirrus pouch but not reaching the anterior limit of the pre-ovarian vitellaria. Testes are irregularly lobate and measure 0.64 by 0.17 mm.

The large, muscular, cirrus pouch (Fig. 5) averaging 0.3 mm in diameter encloses an unarmed eversible cirrus. A large S-shaped external seminal vesicle (Fig. 12) joins the cirrus pouch on its antero-dorsal border. Extending anteriorly from the seminal vesicle is the extensively coiled vas deferens. The common genital opening (Fig. 9) lies ventrally near the posterior border of the cirrus pouch and averages 2.35 mm from the posterior tip of the worm.

Vitellaria are lobate, entirely medullary, and occupy both pre- and post-ovarian fields. Pre-ovarian follicles (Fig. 7), far more numerous, form two lateral rows extending from the neck region to the cirrus pouch, but do not touch the ovarian arms. A single group of post-ovarian follicles (Fig. 12) lies near the posterior tip of the ovary.

The lobate ovary (Fig. 12), shaped like an inverted "A" is entirely medullary, averaging 1.4 mm in length. Lateral arms of the ovary are sometimes contiguous posteriorly. The ovarian isthmus is arched ventrally against the longitudinal parenchymal muscles.

The oviduct, arising at the middle of the posterior border of the ovarian isthmus, extends directly posteriad (Fig. 11). A weakly developed muscular oöcapt is present. Immediately posterior to the isthmus, the oviduct turns anteriorly, meets the vagina, and the duct so formed turns posteriad where it joins with the common vitelline duct. The oötype is situated just posterior to the junction of the common vitelline duct and the oviduct. Mehlis' gland (Fig. 11) is very extensive, its nuclei large and conspicuous, and some of its cells extend laterad to the posterior ovarian arms.

The coiled uterus does not extend anterior to the cirrus pouch. Densely staining uterine glands (Fig. 5) surround the uterus throughout its length save for a short portion near the cirrus pouch and in the region of the oötype, where they are lacking. Immediately posterior to the cirrus pouch, vagina and uterus

unite to form a uterovaginal canal extending directly ventrad to open at the gonopore (Fig. 5). From its junction with the uterovaginal canal, the coiled vagina extends posteriad along the ventral surface of the uterus, then turns dorsally between the ovarian isthmus and uterus before joining the oviduct.

Two anterior vitelline ducts (Fig. 12) extend posteriorly from the pre-ovarian vitellaria and join medially in the region of the ovary. Both ducts are situated median to the ovarian arms and lie midway between dorsal and ventral body surfaces. In the region of the ovarian isthmus, right and left anterior vitelline ducts extend dorsally over the isthmus and unite with right and left posterior vitelline ducts to form common right and left vitelline ducts. The posterior vitelline ducts originate from the lateral borders of the post-ovarian vitellaria and extend anteriorly along the median borders of the posterior ovarian arms. Both right and left common vitelline ducts extend medially along the posterior border of the ovarian isthmus and join near the midline to form a single common vitelline reservoir. From this reservoir, a single common vitelline duct extends posteriad, joining the oviduct a short distance posterior to the junction of oviduct and vagina.

*I. longus* differs from *I. bulbocirrus* in that the wedge-shaped scolex (Fig. 6) in well-fixed specimens of the former never appears rounded. The number of testes varies between the two species, 124 to 170 occurring in the former and 100 to 149 in the latter. In *I. bulbocirrus*, testes are spherical and arranged in paired dorsal and ventral rows. However, in *I. longus*, testes are lobate and are arranged randomly in the area between the pre-ovarian vitelline fields. From the present study *I. longus* appears to be a host-specific parasite of the northern redhorse, whereas *I. bulbocirrus* has been reported only from the white sucker. Although both species of fish were taken in large numbers from one collection area during the same period, specimens of *I. bulbocirrus* were never recovered from any of the fish examined nor were *I. longus* found in white suckers.

Both helminths resemble one another in several respects, namely: the presence of eight pairs of excretory canals, occurrence of a large cirrus pouch, an "A" shaped ovary, the lack of a seminal receptacle, and the presence of pre- and post-ovarian vitellaria.

*Natural Infections.* Specimens of *I. longus* are present in small numbers in northern redhorse as indicated by the relatively large number of hosts (26) harboring but one tapeworm. The presence of more than 10 in one host is very uncommon. Of the

275 northern redhorse examined during this study, one harbored 23 *I. longus* and another 48. Of the latter, only one worm was gravid, two were mature, and the remaining 45 were immature.

Gravid helminths, first found in the intestine of redhorse in late April, were also recovered during the months of May, June, July, September, October, and November. The failure to find gravid worms in August may be associated with a periodic decline in number during the late summer months. More collections must be made on a monthly basis to verify this supposition.

Fish harbored immature tapeworms during all months in which field collections were made. Whether *I. longus* infections occur in winter is not known because of the great difficulty in collecting fish under an ice cover.

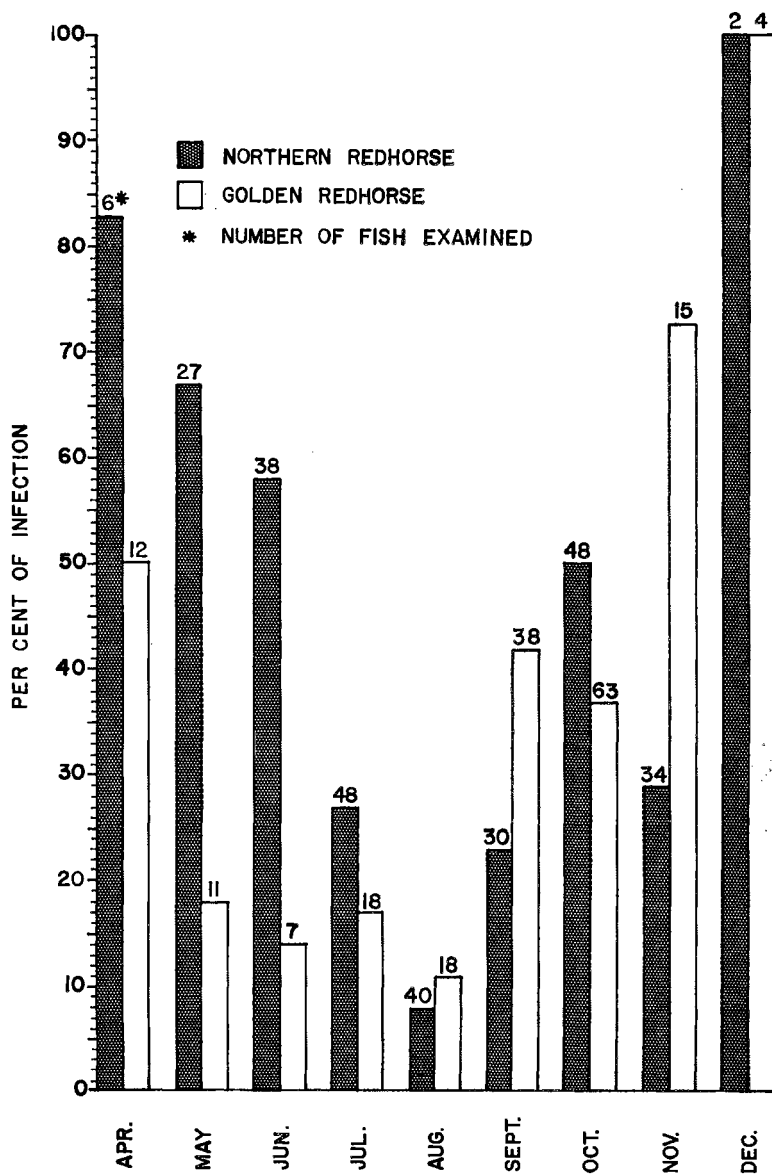
Collection records indicate that *I. longus* exhibits seasonal periodicity. The highest percentage of infection occurs in early spring (April) and from this time until August the infection declines gradually. However, in September, immature worms increase in numbers and infections reach a second peak in October. Whether or not the degree of infection remains high or drops to another low in the winter months is unknown, since only two redhorse were examined in December. Because only six fish were examined in April, the percentage of infection then may actually be somewhat different, but despite inadequate collections at certain times of the year, the variation in the per cent of infection is great enough to indicate a seasonal fluctuation.

For a more complete analysis, fish must be collected in large numbers from designated collection areas during as many months as possible. Furthermore, fish taken from portions of streams in close proximity to one another may show striking variations in percentage of infection. Such variations are probably due to ecological factors associated with the relative abundance of intermediate and fish hosts.

Total lengths of fish were recorded to determine if any relationship could be shown between size and percentage of infection. That older and younger fish harbor fewer infections was indicated by finding that fish measuring more than 16 inches and less than 8 inches in total length harbor fewer cestodes. Such variation associated with age of the hosts may be the result of changes in food habits or may be related to age immunity.

Although both male and female redhorse harbor *I. longus*, possible variations in degree of infections between the sexes may occur. These, however, were not investigated.

No intensive attempt was made to find the intermediate stage of this helminth in nature. Where life cycles have been studied, aquatic annelids serve as intermediate hosts for members of the

MONTHLY OCCURRENCE OF TWO SPECIES OF *ISOGLARIDACRIS* IN  
NORTHERN AND GOLDEN REDHORSE (1961 AND 1962)

family Caryophyllaeidae. Therefore, oligochaetes (*Limnodrilus hoffmeisteri* Claparède, *Tubifex tubifex* O. F. Müller, *Dero limosa* Leidy, and *Branchiura sowerbyi* Beddard) from the collection



areas were examined. However, none of these tubificids was infected with larval cestodes.

*Eggs.* Intrauterine eggs (from the region of the uterus surrounded by uterine glands) average 26 microns in width (range 21 to 35) by 36 microns in length (range 29 to 42). Those shed from the helminths are slightly larger, ranging from 31 to 42 microns in width (average 36) by 42 to 49 microns in length (average 46).

Freshly shed eggs (obtained by worms in distilled water) contain eight spherical yolk cells varying considerably in size (Figure 1.) Early developmental stages within the egg have not been studied.

After 17 days of development, conspicuous embryonic hooks are present on the developing oncosphere (Fig. 2). During the next five days, the oncosphere increases considerably in size (Fig. 3).

Eggs containing developing embryos are readily distinguishable under high power of the compound microscope because of their characteristic yellow-brown color.

*Experimental Studies.* Development of oncospheres was followed in the laboratory and attempts were made to determine the intermediate host of this tapeworm. Eggs of cestodes from naturally infected fish were first taken in November, 1961; however, a lack of suitable techniques and a heavy bacterial and fungal growth terminated the experiment before eggs were fully developed.

A second attempt to maintain eggs met with greater success. Eggs were collected from gravid worms in May, 1962 and fully developed oncospheres were apparent in 21 days. Adult oligochaetes, collected from the Iowa River and examined in the laboratory to make certain that none harbored larval caryophyllaeids, were exposed to the embryonated eggs of *I. longus* on June 18, 1962. These eggs were added to a glass culture jar containing water and a small amount of mud previously dried in the laboratory. One-hundred adult oligochaetes (*L. hoffmeisteri*) were added and maintained under aeration at room temperature.

After 24 hours these annelids were transferred to containers of fresh mud. One-hundred uninfected oligochaetes of the same species were then added to the original mud containing embryonated eggs. This second group of annelids was also removed after 24 hours. When oligochaetes were examined after one

week and again after three weeks, no developing procercoids could be discerned.

In the fall of 1962, large numbers of eggs obtained from four gravid *I. longus* were cultured and numerous eggs containing oncospheres showing well-defined hooks were evident by 17 days. After 23 days, all embryonated eggs were exposed to three species of oligochaetes (50 *L. hoffmeisteri*, 50 *T. tubifex*, and 15 *D. limosa*). Twenty-four hours later, all oligochaetes were examined, but oncospheres could not be seen in body cavity although eggs were present in the gut of both *L. hoffmeisteri* and *T. tubifex*. Annelids were examined again after 10 days and once more at the end of three weeks, but no larval cestodes could be discerned. A final examination made 50 days after exposure proved negative, and the experiment was terminated.

The negative results recorded in these preliminary experiments may be related to the age of the annelid host employed, as suggested by Calentine (1963, 1964) in his studies of the related genus *Archigetes*, where only very young tubificids are capable of harboring the infection.

Possibly the oncospheres of *Isoglaridacris* employed in our experiments were not viable. Calentine, however, (unpublished data) maintained viable oncospheres of other members of the same subfamily in the laboratory for periods of several months. The possibility that an intermediate host other than a tubificid may be involved in the life cycle of *I. longus* should not be overlooked, despite the fact that all published studies heretofore have involved only these invertebrates.

#### ISOGLARIDACRIS FOLIUS

##### *Adults* (Plates III & IV)

Specific diagnosis: *Isoglaridacris folius* sp. n. with characters of the genus. Gravid adults 8.8 mm (6 to 12) by 0.8 mm (0.6 to 1.14). Well-developed wedge-shaped scolex with three pairs of shallow loculi. Body often curved, widest in the region just anterior to the cirrus pouch. Neck well defined. Vitellaria in pre- and post-ovarian fields. Testes 140 to 224 in number, appearing in two dorsal and two ventral rows. Posterior limit of testicular field extending to near anterior border of cirrus pouch; anterior limit of testicular field not extending to anterior limit of pre-ovarian vitellaria. Cirrus pouch small, averaging 0.156 mm (0.105 to 0.195) in diameter. Unarmed eversible cirrus. Common gonopore. Lobate ovary in form of an inverted "A" whose arms do not fuse posteriorly. Ovarian wings measuring 1.19 mm (0.8 to 1.65). Parenchymal muscles poorly developed. Eight

pairs of osmoregulatory canals in cortical parenchyma, the smaller member of each pair being indistinct. Common excretory bladder at posterior tip. Operculate eggs 26 by 33 microns. Intestinal parasite of golden redhorse, *M. erythrurum*.

Holotype: USNM Helm. Coll., No. 60301 Beltsville, Maryland (from *M. erythrurum*).

Paratype: USNM Helm. Coll., No. 60301 Beltsville, Maryland (immature specimen from *M. erythrurum*).

In fixed specimens, gravid adults (Figure 18) appear widest in the region of the cirrus pouch. Posteriorly, the worm tapers to a blunt point while anteriorly near the neck region it is markedly narrower. A slight curvature of the body is usually present in fixed specimens giving these helminths the characteristic shape of attenuate willow leaves.

The region surrounding the cirrus pouch appears as a translucent area in immature and mature specimens, but in gravid worms the expanded uterus fills this area. The body is oval in cross section, becoming more rounded in the region of the cirrus pouch.

The wedge-shaped scolex in living specimens is very active and bears three pairs of shallow loculi (Figure 18). Adults, loosely attached to the intestinal wall, are usually found in the region of the duodenum. Comparison of specimens taken during field dissection with those taken from laboratory dissections indicates that these helminths detach from the host's mucosa and decompose soon after death of the fish. The unarmed cuticle is approximately 3 microns thick. General features of the cortical and parenchymal musculature are similar to those of *I. longus*.

Eight pairs of osmoregulatory canals arranged as in *I. longus* occupy the cortical parenchyma (Fig. 20). The larger member of each pair is easily seen in cross sections; the smaller member is indistinct. In incompletely cleared specimens, the osmoregulatory system often is remarkably apparent, appearing as an anastomosing network of canals which are more numerous near the scolex.

Distribution of vitellaria (Fig. 18) is similar to that of *I. longus*, but the posterior tips of the laterally situated bands of pre-ovarian vitellaria are often contiguous with the anterior extensions of the ovarian arms. Vitelline ducts (Figs. 22, 23) resemble those of *I. longus* in their distribution and position.

The lobate ovary, in the form of an inverted "A", is entirely medullary, and averages 1.19 mm in length. Lateral arms of the ovary, unlike those of *I. longus* and *I. bulbocirrus*, do not

join posteriorly so that the tip of the "A" is open. The shape of the ovary in preserved specimens appears to be dependent somewhat upon the state of contraction of the cestode at the time of fixation. The ovarian isthmus is arched ventrally against the longitudinal parenchymal muscles (Figure 21).

Other portions of the female reproductive system are similar in arrangement to those of *I. longus*. The extensive Mehlis' gland, however, possesses nuclei considerably smaller than those of *I. longus*. Relationships of the vagina, uterus, and uterovaginal canal are similar to those of *I. longus*.

The testicular field, lying medially between the pre-ovarian vitellaria, extends anteriorly from the cirrus pouch, but does not reach the most anterior extent of the pre-ovarian vitelline follicles (Fig. 18). Testes, varying in shape from nearly spherical to irregularly lobate, are commonly arranged in two dorsal and two ventral rows but in some specimens may be scattered irregularly throughout at least a portion of the testicular field.

Accurate determination of the number of testes is difficult, but the following procedure facilitated the task considerably. Unfixed specimens kept in distilled water overnight swelled considerably and were then fixed and stained, making the testes much more discernible. Counts made on such specimens indicate that testes average 176 in number (based on examination of 12 stained whole mounts).

The muscular cirrus pouch (Figure 16) averages 0.16 mm in diameter. The unarmed, eversible cirrus opens into the uterovaginal canal. A large S-shaped external seminal vesicle is attached to the antero-dorsal side of the cirrus pouch (Figure 23). Extending anteriorly from the vesicle is the extensively coiled vas deferens, greatly expanded by sperm in some specimens. At times this expansion of the vas deferens causes the testes located in the posterior part of the testicular field to be compressed laterally against the vitellaria. The common genital opening lies near the posterior edge of the cirrus pouch and averages 1.5 mm from the posterior tip of the worm.

Distinct morphological differences enable one to differentiate *I. folius* from *I. bulbocirrus* and *I. longus*. The most striking characteristic of *I. folius* is the small size of its cirrus pouch (0.105 to 0.195 mm) as compared to that of *I. bulbocirrus* (0.225 to 0.492 mm) and *I. longus* (0.24 to 0.38 mm). The general body shape of *I. folius* also differs from that of the other two species. Neither *I. bulbocirrus* or *I. longus* has the characteristic attenuate willow-leaf shape. The scoleces of *I. folius* and *I. longus* are similar but differ from the rounded scolex of

*I. bulbocirrus*. In gravid specimens of *I. folius*, the uterus fills the region surrounding the cirrus pouch to a much greater degree than in either of the other two species. The posterior arms of the ovary of *I. folius* are not contiguous posteriorly while in *I. longus* and *I. bulbocirrus* they may or may not join posteriorly. Pre-ovarian vitellaria touch the anterior ovarian arms in *folius* but in *longus* and *bulbocirrus* this generally does not occur. Cells of the Mehlis' gland of *I. folius* are much smaller than those in *I. longus*. Furthermore, the definitive hosts of all three species are distinctive.

*I. folius* is similar to *I. longus* and *I. bulbocirrus* in the general nature of the female reproductive complex including the presence of an A-shaped ovary, well-defined vagina and an extensive Mehlis' gland, and in the absence of a seminal receptacle.

A key to the known species of *Isoglaridacris* is given below:

1. Cirrus pouch large (0.24 mm. to 0.49 mm), more than  $\frac{1}{2}$  the width of the body at the gonopore ..... 2  
    Cirrus pouch small (0.105 mm to 0.195 mm), less than  $\frac{1}{2}$  the width of the body at the gonopore; intestinal parasite of golden redhorse *Moxostoma erythrurum* . . . *I. folius*
2. Scolex rounded, testes spherical and arranged in rows; intestinal parasite of white sucker *Catostomus commersoni* ..... *I. bulbocirrus*  
    Scolex wedge-shaped, testes lobate and arranged randomly; intestinal parasite of northern redhorse *Moxostoma macrolepidotum* ..... *I. longus*

*Natural Infections.* Collections of *I. folius* throughout the year indicate that, as in *I. longus*, seasonal periodicity is characteristic of the species, highest degree of incidence occurring in fall and spring, with pronounced declines throughout the summer. However, data on *I. folius* are less complete than those for *I. longus* for approximately half of the 186 golden redhorse collected were taken during the months of September and October. Data on incidence during winter months are lacking because of the difficulty in obtaining fish during this season.

Most infected golden redhorse harbor but a single worm per fish. Of 50 naturally infected hosts, 25 harbored only one worm. Only eight of 50 fish were parasitized by 10 or more adult *I. folius*, the maximum number of cestodes per fish being 23.

*I. folius* differs markedly from *I. longus* in its more limited distribution within the host. Cestodes of the former species are generally attached to the mucosa of the intestinal tract a short

distance posterior to the stomach, whereas specimens of *I. longus* may occur throughout the intestinal tract.

As in *I. longus*, the infection rate of *folius* varies at different collection sites. For example, in the Des Moines River, an infection rate of 75% was found at Frazer, Iowa, but only 18% of the redhorse at Boone, Iowa (several miles downstream) harbored the worms.

*Eggs.* Freshly shed operculate eggs obtained from gravid *I. folius* average 26 by 33 microns. In fixed specimens, intrauterine eggs vary from 31 to 35 microns in length and from 24 to 28 microns in width.

Study of sectioned *I. folius* with eggs *in utero* indicates that in the proximal portion of the uterus six or seven yolk cells are present in the thin-shelled eggs. Eggs in the distal portion of the uterus are much thicker-shelled. What appears to be the germinal cell in each egg stains more deeply with haematoxylin than do any of the poorly-staining yolk cells. According to Motomura (1929), yolk cells of *Archigetes appendiculatus* Ratzel do not contain chromatin and hence stain feebly. Apparently, no further development of *Isoglaridacris* eggs occurs until they pass to the outside of the body. A similar condition was noted by Motomura (1929) in *A. appendiculatus*.

Although detailed studies on the development of the oncospheres were not undertaken, occasional observation of eggs maintained in the laboratory indicates that by 11 days (Fig. 13) embryonic hooks are apparent and that fully formed hexacanth develop within a month (Fig. 14). Eggs containing developing oncospheres are characteristically yellow-brown.

*Experimental Studies.* A single feeding experiment using the eggs of *I. folius* involved the collection of eggs from gravid cestodes in October, 1962. Such eggs were allowed to develop for 32 days before exposing them to non-gravid oligochaetes (25 *T. tubifex*, 25 *L. hoffmeisteri*, and 15 *D. limosa*). These hosts, although not laboratory reared, had been maintained for several weeks in the laboratory and were carefully checked to make certain that no parasites were present before the experiment was begun. Mud used in the experiment had been completely air dried. Eggs containing fully developed oncospheres were placed in the mud and mixed thoroughly before oligochaetes were introduced.

Annelids so exposed were examined with the use of a compound microscope at the end of one-, two-, and six-week intervals, but no larval cestodes (proceroids) were observed. The failure of parasites to develop may have been due to the use of improper hosts, to the age of oligochaetes involved, or to the lack of

viability of the oncospheres used. The factors responsible for the failure of these experimental feedings involving *I. folius* are believed to be similar to those for *I. longus* noted above.

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Abbreviations used:

AVD—anterior vitelline duct	PV—post-ovarian vitellaria
CC—cortical cells	PVD—posterior vitelline duct
CP—cirrus pouch	SV—seminal vesicle
CVD—common vitelline duct	T—testes
DM—dorso-ventral muscles	U—uterus
EX—osmoregulatory canal	UG—uterine lands
GP—gonopore	UVC—utero-vaginal canal
MG—Mehlis' gland	V—vagina
OV—ovary	VF—anterior vitelline follicles
OC—oöcapt	VD—vas deferens
OD—oviduct	VI—anterior vitelline follicles
OT—oötype	VR—vitelline reservoir
PM—longitudinal parenchyma	

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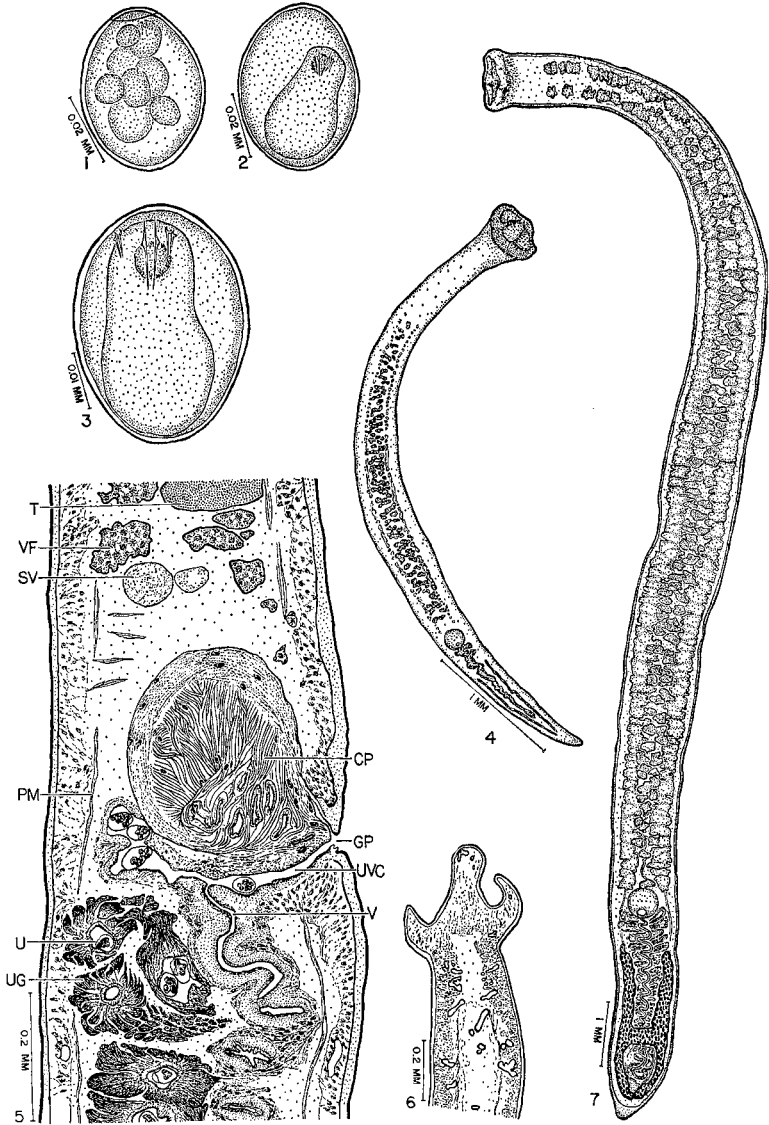


Plate I *Isoglaridacris longus*.

Figure 1. Egg after 24 hours in water. Figure 2. Egg after 17 days in water. Figure 3. Egg after 21 days in water. Figure 4. Immature specimens from northern redhorse, *M. macrolepidotum*. Figure 5. Sagittal section of adult showing gonopore and associated structures (partial reconstruction). Figure 6. Sagittal section through scolex of adult. Figure 7. Gravid specimen from northern redhorse.



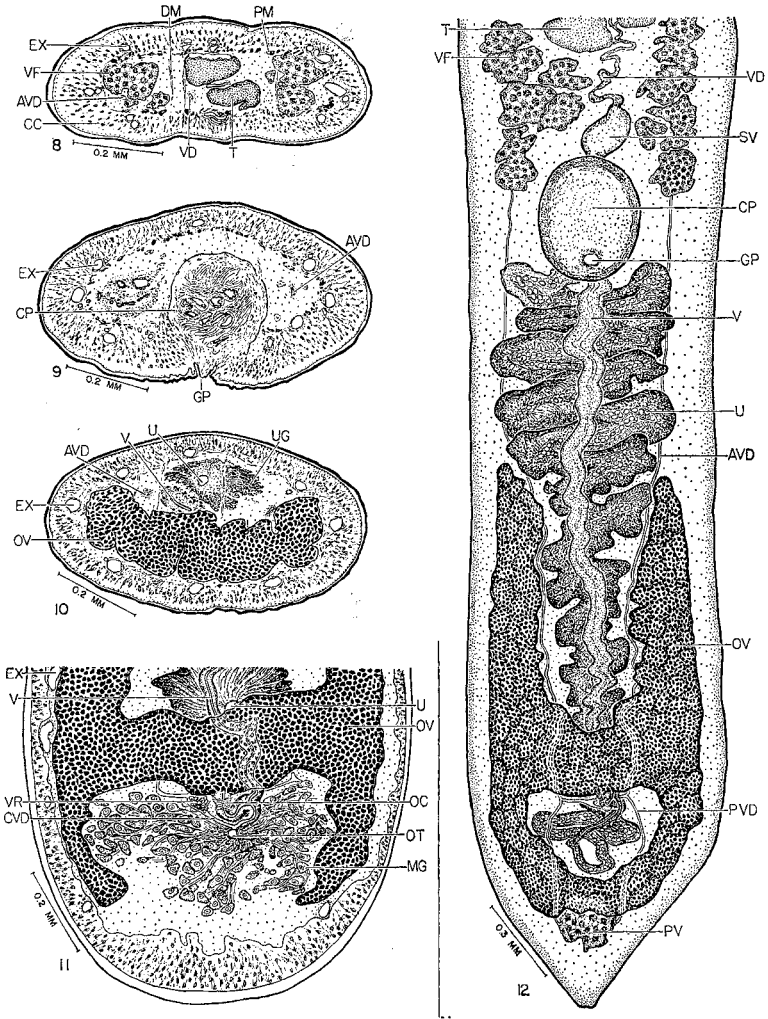


Plate II *I. longus*

Figure 8. Cross section of body in region anterior to gonopore. Figure 9. Cross section through region of cirrus pouch. Figure 10. Cross section through region of ovarian isthmus. Figure 11. Frontal section through region of oviduct and associated structures (partial reconstruction). Figure 12. Posterior portion of body, ventral view (Mehlis' gland not shown).

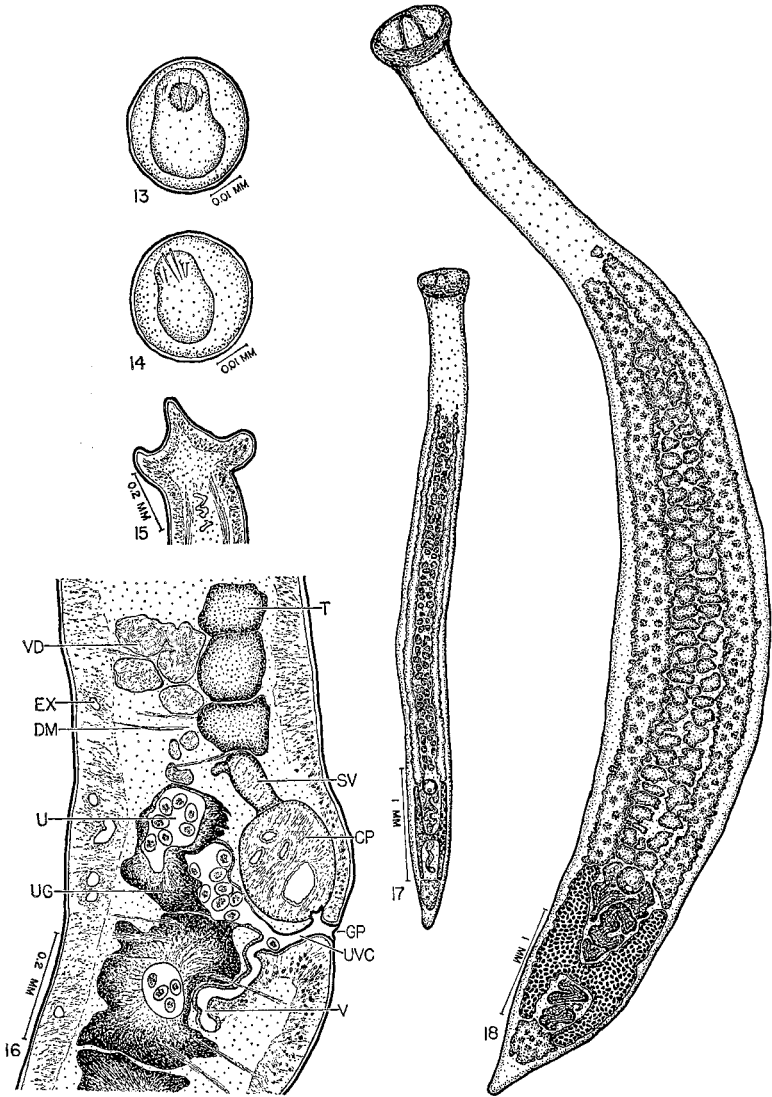


Plate III *Isoglaridacris folius*.

Figure 13. Egg after 11 days in water. Figure 14. Egg after 31 days in water. Figure 15. Sagittal section through scolex of adult. Figure 16. Sagittal section of adult showing gonopore and associated structures (partial reconstruction). Figure 17. Immature specimen from golden redhorse, *M. erythrum*. Figure 18. Gravid specimen from golden redhorse.

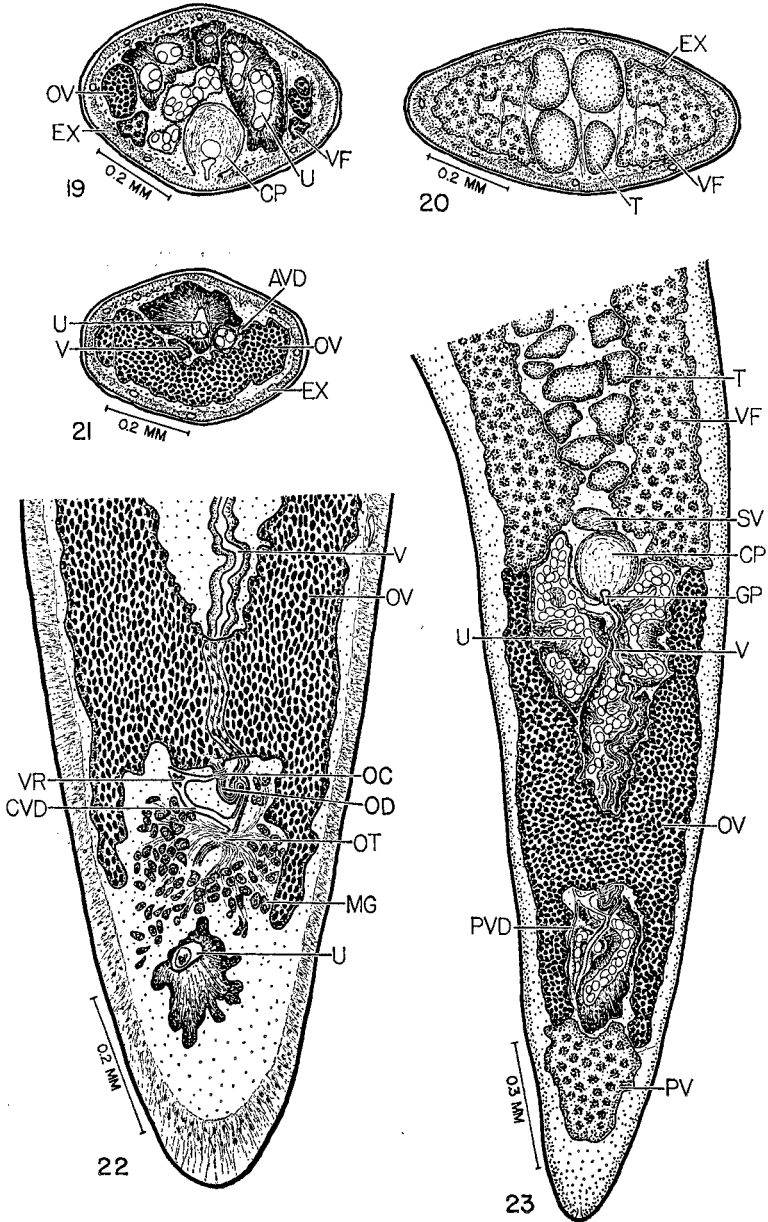


Plate IV *I. folius*.

Figure 19. Cross section through region of cirrus pouch. Figure 20. Cross section through region anterior to cirrus pouch. Figure 21. Cross section through region of ovarian isthmus. Figure 22. Frontal section through region of oviduct and associated structures (partial reconstruction). Figure 23. Posterior portion of body, ventral view (Mehlis' gland not shown).