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have been made of the frog populations and their migratory behavior in what was an ideal natural situation.

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Larval Development of Four Caryophyllaeid Cestodes[1]

ROBERT L. CALENTINE[2]

Abstract. Adults of the caryophyllaeid cestodes *Glaridacris catostomi, Hunterella nodulosa, Monobothrium hunteri* and *Monobothrium ingens* were recovered from naturally infected fishes. The oligochaete annelid intermediate hosts were experimentally infected with embryonated eggs of these cestodes. Fully developed procercoids were characterized by a scolex similar to that of the adult, also by a cercomer and primordia of reproductive organs.

Caryophyllaeid cestodes are unsegmented helminths possessing a single set of reproductive organs and which vary in length from one to 75 mm. Adults are common parasites of catostomid and cyprinid fishes in North America, but their life cycles are poorly known. Experimental life history accounts of the American species are limited to McCrae (1961) and Calentine (1964, 1965). The present report involves the intermediate hosts and larval development of *Glaridacris catostomi* Cooper, *Hunterella nodulosa* Mackiewicz and McCrae, *Monobothrium hunteri* Mackiewicz and *Monobothrium ingens* Hunter. The periodicity of the first three species in Iowa fish hosts was presented earlier (Calentine and Fredrickson, 1965). McCrae (1961) studied the larval development of *G. catostomi* and *H. nodulosa,* but certain of my results differ from his findings.

MATERIALS AND METHODS

Adults of *G. catostomi, H. nodulosa* and *M. hunteri* were taken from white suckers, *Catostomus commersoni* (Lacépède), in the Iowa River, Franklin and Hardin Counties, Iowa. Adults of *M. ingens* were recovered from smallmouth buffalo, *Ictiobus*

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bubalus (Raf.), in the St. Croix River, St. Croix County, Wisconsin. Cestode eggs were obtained by keeping gravid worms in distilled water or by dissection, and were maintained in stream water in covered stender dishes. Observations and experiments were conducted at 18 to 22 degrees C, unless otherwise specified. Feeding experiments involving embryonated eggs and annelids were conducted in a mud medium. Annelids of two or more species were often exposed to embryonated eggs in the same container. All annelids were maintained in mud under aeration and were fed a mixture of oatmeal, cornmeal and commercial fish food. Annelids of the genera *Dero* and *Tubifex* used in experiments were laboratory reared; members of other genera were collected in nature and held in the laboratory at least one month prior to use.

Cestodes were fixed in AFA and stained in Mayer's paracarmine. Oligochaetes were fixed in hot 70% ethanol or in Bouin's fluid. Experiments with the definitive hosts were not conducted because of a lack of uninfected fish. Worm measurements were taken from fixed, unflattened specimens; eggs and oncospheres (N=20) were measured in water, unless otherwise specified.

Results

Glaridacris catostomi

Eggs. The operculate eggs averaged 42 (39-46) by 60 (53-67)μ and were undeveloped when shed. Embryonation required 19 days and oncospheres averaged 24 (21-25) by 43 (35-49μ). Embryonated eggs were viable 70-90 days at room temperature and at least 217 days when maintained at 5-10 degrees C.

Intermediate hosts and procercoids. During the course of nine feeding experiments, the oligochaetes *Limnodrilus hoffmeisteri* Claparède, *Limnodrilus* sp. (probably *L. udekemianus* Claparede), *Tubifex tubifex* O. F. Müller, *T. templetoni* Southern, *Dero limosa* Leidy and *Branchiura sowerbyi* Beddard were exposed to embryonated eggs. Procercoids developed in both species of *Tubifex* and in both species of *Limnodrilus.* Although young larvae were observed in the body cavity of *Branchiura,* they underwent little development and survived no longer than three weeks. Embryonated eggs were eaten by members of *Dero,* but infections did not occur.

Members of *T. templetoni* were used in seven feeding experiments and those of *L. hoffmeisteri* in four. In a typical experiment, 38 (76%) of 50 *T. templetoni* and 25 (50%) of 50 *L. hoffmeisteri* acquired infections when exposed to eggs for 48 hours. In annelids of both genera, oncospheres penetrated the host's

intestinal wall in the mid-body region; procercoids developed in the body cavity near this site. Larvae localized between segments 19-30. Fully developed procercoids (Figure 6) averaged 1.2 (1.0-1.7) mm in body length with a cercomer 0.3 (0.1-0.4)mm long. The scolex was similar to that of the adult, but only primordia of gonads were present.

Longitudinally arranged excretory ducts originate at the posterior of the procercoid's body and extend anteriad. In the neck region they untie to form two conspicuously larger ducts which pass into the medullary region and extend to the tip of the scolex. Here, the two ducts emerge into the cortical region and give rise to many branches ramifying over the surface of the scolex. They coalesce in the neck region, forming longitudinal descending canals. The descending ducts, lying in close association with the ascending ones, empty into the cavity surrounding the proximal end of the cercomer.

Host-parasite relationships. Procercoids from the four host species were indistinguishable, but the rate of larval development varied somewhat in accordance with the size of the annelid host species. Larvae in *L. hoffmeisteri* (the largest host species) averaged 1.2 mm in length by 46 days. Two procercoids from *Limnodrilus* sp. (similar in size to the one above) measured 0.8 and 1.1 mm at 43 days. Procercoids in *T. tubifex* (a somewhat smaller annelid) averaged 0.7 (0.4-0.9) mm at 46 days; development here required about 58 days. Larvae from *T. templetoni* (the smallest host) averaged 0.9 (0.7-1.1) mm at 63 days and required about 70 days to complete development.

Experimentally infected tubificids harbored as many as three fully developed procercoids. Infected annelids (*T. tubifex,* 30 days post-infection) acquired new parasites when re-exposed to eggs. Young annelids acquired infections more readily than did older, larger ones. Infected annelids were rather short-lived; of 38 infected *T. templetoni* and 25 infected *L. hoffmeisteri* in one experiment (26 days post-infection), only one infected oligochaete of each species was present at 144 days when the experiment was terminated.

Procercoids destroyed septal walls at the site of infection, and those at the posterior of the body often caused rupture of the body wall and death of the host, especially in *Tubifex.* Infected annelids did not become sexually mature.

Hunterella nodulosa

Eggs. The operculate eggs, measuring 33 (28-39) by 54 (51-63)μ (from sections), required 14 days development; oncosphere size was not determined.

Intermediate host and procercoids. In the one feeding experiment conducted, 18 (36%) of *L. hoffmeisteri,* but none of 50 *T. templetoni,* acquired infections. Oncospheres penetrated the annelid's intestinal wall in the mid-body region. Most larvae then migrated anteriad and developed within the posterior seminal vesicle, but some developed in the body cavity near the site of penetration. Larval development required about 46 days and procercoids (Figure 5) averaged 0.9 (0.7-1.2)mm in body length with a cercomer 0.6 (0.5-1.0)mm long (N=20). The scolex of the procercoid, like that of the adult, is unspecialized; only primordia of gonads are present.

Of the 13 infected annelids in the experiment (247 days post-infection), two survived for 466 days, at which time the experiment was terminated. As many as three fully developed procercoids were present in a single host. These comparatively small larvae appeared to cause little damage to the host. Some infected oligochaetes became sexually mature, a condition seldom observed in annelids infected with larvae of other caryophyllaeid species.

There is no longitudinal orientation of the excretory ducts in *H. nodulosa;* the ascending and descending canals are not in close association.

Monobothrium hunteri

Eggs. The operculate eggs averaged 38 (37-39) by 56 (53-61)μ and required 18 days for development; onospheres averaged 19 (14-21) by 45 (42-49)μ.

Intermediate host and procercoids. One feeding experiment was established; 29 (38%) of 76 *L. hoffmeisteri,* but none of 52 *T. templetoni,* became infected. Procercoids developed in the host's coelom near the site of oncosphere penetration (segments 18-37). Larval development (Figures 1-3) required 50 days. Fully developed procercoids averaged 0.8 (0.7-1.0) mm in length with a cercomer of 1.0 (0.8-1.2) mm. The scolex of the procercoid, while generally similar to that of the adult, was quite variable in shape (Figures 7-8). Its appearance in fixed specimens depended upon the degree of contraction at the time of fixation. A shallow median loculus was observed as a temporary structure on the dorsal and ventral surface of the scolex in living specimens, but it was seldom evident on preserved ones. Only primordia of gonads were present.

A striking feature of *M. hunteri* procercoids is the nature of the cercomer (Figure 3), which is much larger than that of any other known caryophllaeid procercoid. However, later experi-

ments with two other species of *Monobothrium* (*M. ingens* and another, undescribed, species) showed that this type of cercomer is not a generic trait.

Oligochaetes harbored as many as four fully developed procercoids; all infected annelids were preserved by 75 days. Procercoids were responsible for localized tissue destruction in the host; septal walls were destroyed at the site of infection and much of the body wall musculature was also damaged or destroyed.

Monobothrium ingens

Eggs. Eggs measured 36 (28-46) by 54 (46-61)μ (*in utero,* whole mount preparations) and required 22-25 days in water for development; oncosphere size was not determined.

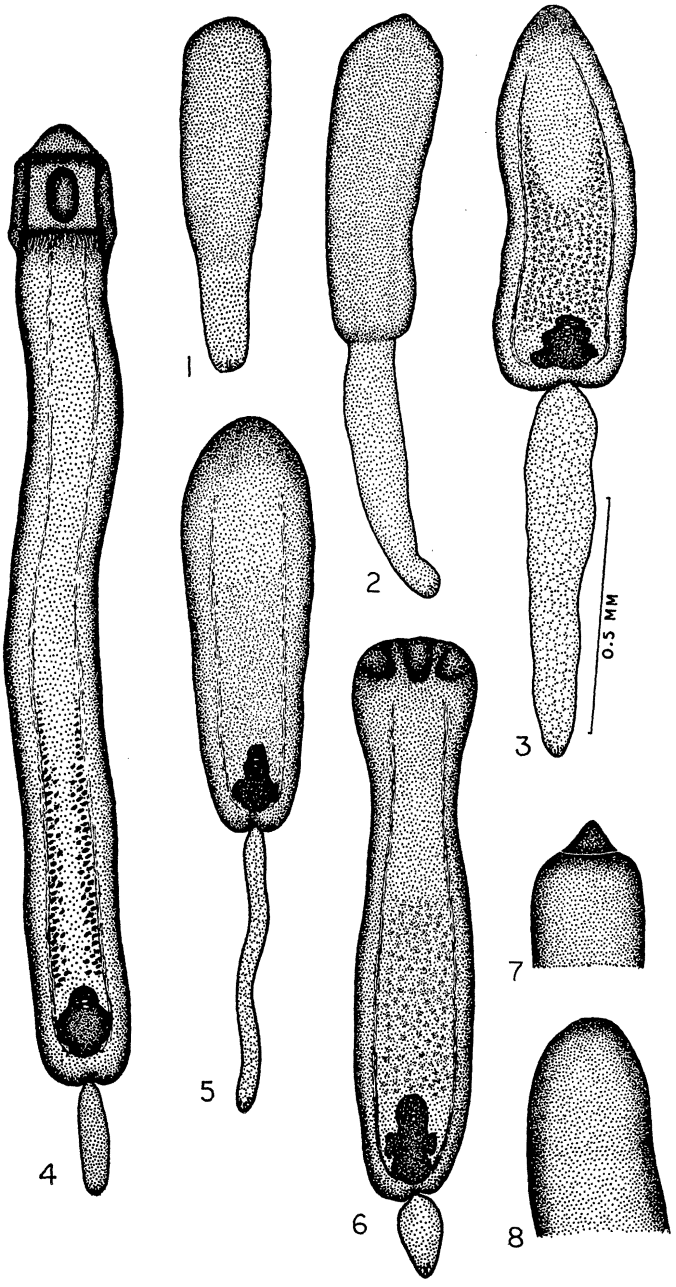
Intermediate host and procercoids. Two feeding experiments were established; in one, 20 (40%) of 50 *L. hoffmeisteri,* but none of 52 *T. templetoni,* became infected. Procercoid development required approximately 45 days and procercoids (N=8) averaged 2.1 (1.7-2.5) mm in body length with a cercomer 0.2 (0.1-0.3) mm long. Only primordia of gonads were present. Fully developed larvae (Figure 4) localized in the body cavity of the host, between segments 9 to 34. As many as eight procercoids were present in a single host (65 days post-infection). All infected tubificids were preserved at 65 days.

The scolex of the procercoid is essentially similar to that of the adult; a shallow groove occurs on the dorsal and ventral surfaces when the scolex is contracted. Longitudinal, lateral grooves are present when the scolex is extended.

Discussion

McCrae's studies with *Hunterella nodulosa* and *Glaridacris catostomi* have appeared only in abstract (1961). He found that *H. nodulosa* developed in *L. udekemianus* but not in *T. tubifex* nor in *L. hoffmeisteri.* While I found procercoids of this species did develop in *L. hoffmeisteri,* procercoid development was essentially similar in the two studies.

With respect to *G. catostomi,* however, there is a more significant difference between the two studies. Although there is again a difference of hosts (McCrae's experiments with *L. hoffmeisteri* and *T. tubifex* were negative), there is also a difference in the nature of the procercoid. None of the procercoids resulting from my experiments possessed a cercomer similar to that illustrated by McCrae (1960 Ph. D. thesis, Colorado State Univ., microfilm No. 60-6797, University Microfilms) for this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All larvae were taken from experimentally infected hosts; scale as in Figure 3.

Figures 1-3. Larval development of *Monobothrium hunteri.*
Figure 1. Procercoid at 30 days.
Figure 2. Procercoid at 40 days.
Figure 3. Procercoid at 50 days, development complete.
Figure 4. *Monobothrium ingens* procercoid.
Figure 5. *Hunterella nodulosa* procercoid.
Figure 6. *Glaridacris catostomi* procercoid.
Figures 7-8. Scolex variations in *M. hunteri* procercoids.

species. Personal correspondence with McCrae did not resolve this apparent discrepancy.

Feeding experiments conducted with two other caryophyllaeid species were not successful. Six experiments involving embryonated eggs of *Khawia iowensis* Calentine and Ulmer (from *Cyprinus carpio* L.) and the oligochaetes *L hoffmeisteri, T. templetoni, Branchiura sowerbyi* and *Dero limosa* were all negative. Likewise, six feeding experiments with embryonated eggs of *Spartoides wardi* Hunter (from *Carpiodes* spp.) and the annelids *L. hoffmeisteri, Limnodrilus* sp., *T. templetoni* and *D. limosa* were negative. Kulakowskaja (1962), however, found that *Khawia sinensis* Hsü developed in the annelids *L. hoffmeisteri, L. udekemianus, T. tubifex* and *Iliodrilus hammoniensis.*

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