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THE LIFE CYCLE OF THE CESTODE RODENTOLEPIS ERINACEI (GMELIN, 1789)

J. PROKOPIČ

Institute of Parasitology, Czechoslovak Academy of Sciences, Prague

Abstract. The indirect life cycle of the cestode species *Rodentolepis erinacei* (Gmelin, 1789) a parasite of the hedgehog was confirmed in experiments. The larvae develop in intermediate hosts (*Necrophorus humator*, *N. vespillo*, *Oeceoptoma thoracica*, *Geotrupes stercorosus*). These beetles collected in the field were infected with cysticercoids of *R. erinacei*. The results of these studies indicate that Joyeux (1921, 1927) was wrong in stating that *R. erinacei* develops directly without utilizing intermediate hosts.

Apart from Joyeux's (1921, 1927) generally accepted idea that *R. erinacei* develops directly without utilizing intermediate hosts, no other information on the life cycle of this cestode species has been available. During my investigations performed during the years 1965—1967 I obtained complete information on the life cycle of this cestode species from the egg to the larva developing in beetles up to the adult worm infecting the hedgehog, its definitive host.

MATERIAL AND METHODS

We examined 180 specimens of *Erinaceus europaeus* L. and 118 specimens of *E. roumanicus* Barret—Hamilton, collected in various localities of Czechoslovakia. Of these 38 specimens of *E. europaeus* (21%) and 25 specimens of *E. roumanicus* (22%) were infected with the cestode species *R. erinacei*. Eggs of adult cestodes were used for experimental infection of beetles of the species: *Necrophorus humator* (Fabr.), *N. vespillo* (L.), *Oeceoptoma thoracica* (L.) and *Geotrupes stercorosus* (Scriba). Natural infection with larvae of this cestode were found in all these beetle species.

For each experiment we used 60 beetles of each species, i.e. 240 beetles. The experiments were repeated 4 times using a total of 960 beetles. The beetles were inspected on day 1, 2, 3, 4, 5, 6, 7, 14 and 21 p.i. All developmental stages were measured and figured. On day 21, the fully developed cysticercoids were fed to 16 young hedgehogs from our laboratory breed. The various developmental stages of the cestode were obtained at autopsy from the hedgehogs on day 1, 2, 3, 7, 14, 28, 35, 42, 49 and 56 p.i.

During 1965—1967, I examined 3,942 beetles belonging to 25 species, which I collected at our field station Klec in southern Bohemia. Cysticercoids of *R. erinacei* were found in 21 specimens out of the 333 *Oeceoptoma thoracica* examined (6.5%); in 7 of the 295 *Necrophorus vespillo* examined (2.4%); in 2 of the 86 *Geotrupes stercorosus* examined (2.3%); in 3 of the 286 *Necrophorus humator* examined (1%) and in one of the 49 *Silpha obscura* examined (2%). The incidence in these beetles was 6—48 cysticercoids. We used these cysticercoids from naturally infected beetles to infect with them another group of 12 hedgehogs, which we inspected at the same intervals as the hedgehogs infected with cysticercoids from artificially infected beetles.

RESULTS

The results of artificial infection of 960 beetles with eggs of *R. erinacei* yielded information on the rate of infection of the beetles: *Oeceoptoma thoracica* (rate of infection — R. I. 70 %; incidence 40—480 cysticercoids); *Necrophorus vespillo* (R. I. 14 %; incidence 28—82 cysticercoids); *N. humator* (R. I. 5 %; incidence 7 to 140 cysticercoids); *Geotrupes stercorosus* (R. I. 2 %; incidence 8—26 cysticercoids). The exact number of eggs capable of development after ingestion by the beetles could not be established. Positive results were obtained from all hedgehogs which had been fed with an exactly determined number of cysticercoids. The percentage of attached cysticercoids ranged from 60—100 %.

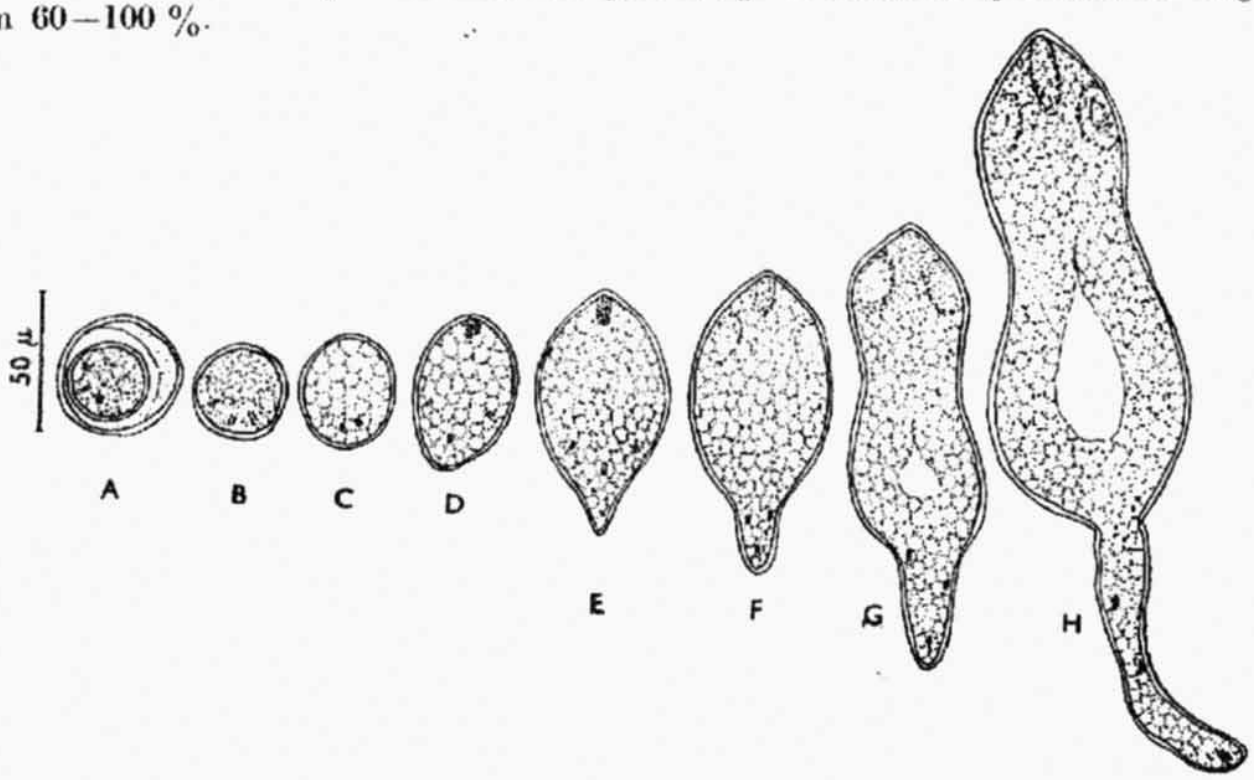

Fig. 1. A — Egg of the cestode *Rodentolepis erinacei*; B — oncosphere; C, D — growing oncosphere in the intermediate host; E, F — cestode embryo with the originating tail and rostellar rudiment; G — cestode embryo with the rudiment of the suckers, the differentiating body cavity of the cysticercoid and with the tail; H — differentiated cestode larva before scolex invagination.

DESCRIPTION OF THE LIFE CYCLE OF RODENTOLEPIS ERINACEI

Mature eggs (Fig. 1A): These are oval till spherical, size 38—42 µ in diameter. The oncosphere measures 32—36 µ in diameter (Fig. 1B) and bears 3 pairs of embryonal hooks measuring 12—16 µ. Already inside the egg the oncosphere is very mobile. After 24 hrs, liberated motile oncospheres are found in the body cavity of the beetles; these are almost unchanged in shape and size. After two days they settle in the body cavity and the cells start to divide (Fig. 1C). The rate of growth is almost uniform in all directions. The hooks remain paired, but these pairs are dispersed along the circumference of the body. Three days later (Fig. 1D) the oncospheres elongate towards the poles, the number of larger cells in their body increases and their contents becomes more translucent. The hooks are still on the circumference. Elongation continues on day 4 (Fig. 1E) and can be observed also on day 5. On one of the poles an extension (the future tail) can be viewed (Fig. 1F). On day 6 the larva stretches in longitudinal direction (Fig. 1G); the neck is forming, the cellular membranes are disappearing and the rudiment of the body cavity

of the cysticercoid is originating. Simultaneously a small elevation consisting of small cells is arising from the anterior pole; this is the rudiment of the rostellum and the suckers. The posterior pole elongates into the tail onto which the hooks are shifting. Differentiation of the larval body starts on day 8. The portion of the body with the pear-shaped elevation — the scolex anlage — is widening (Fig. 14). The differentiation of the anterior portion is completed on day 14 and the scolex starts to invaginate (Fig. 2A, B). Development continues and is completed between day 18 and 21 (Fig. 2C); the scolex and neck are invaginated into the body cavity and the surface is covered by a thin hyaline membrane.

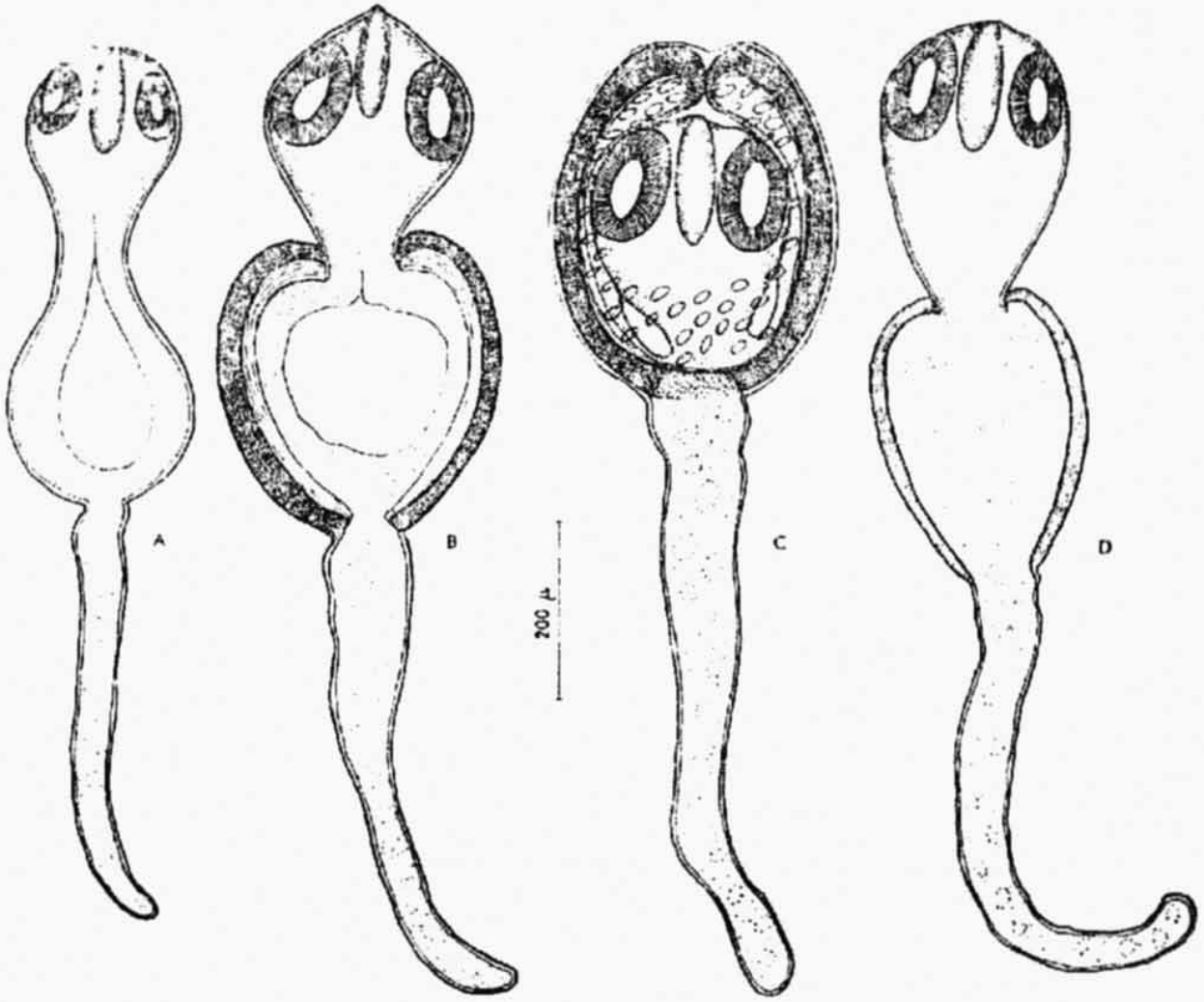

Fig. 2. A — Advanced differentiation of the cestode larva with a developed scolex before invagination; B — invagination of the cysticercoid; C — mature cysticercoid; D — evagination of the cysticercoid.

The cysticercoid: shape oval, size 550—750 × 340—360 µ. The tail is 0.2—1.5 mm long. The cyst wall has 4 layers — the superficial layer formed by a thin hyaline membrane; the 6—8 µ thick fibrous layer; the middle layer with its longitudinal fibrous structure; the last is the parenchymatous layer containing calcareous corpuscles. The neck forms the direct covering of the scolex. The centre of the cysticercoid is occupied by the scolex which measures 420—460 µ. It has a rostellum but no hooks. The suckers are oval measuring 130—140 × 80—100 µ.

Within 24 hrs after ingestion the scolex of the cysticercoid starts to evaginate in the stomach of the hedgehog (Fig. 2D). From day 2 onwards the neck grows in length and the first 2—3 segments become differentiated on it (Fig. 3A). 72 hrs p.i. the cestodes are

0.5—0.6 mm long. On day 7 there are 20—30 segments (Fig. 3B), the male sexual organs are appearing. The cestodes are 2—35 mm long, measuring 10 mm on the average. On day 14 the cestodes are 6—106 mm long (average 30 mm) (Fig. 3C, D). Their length is greatly dependent on their numbers in one host and, thus, most variable. The male and female sexual organs are clearly differentiated. On day 21 the first adult cestodes with well-developed sexual organs were observed (Fig. 3E). Eggs started to appear in the

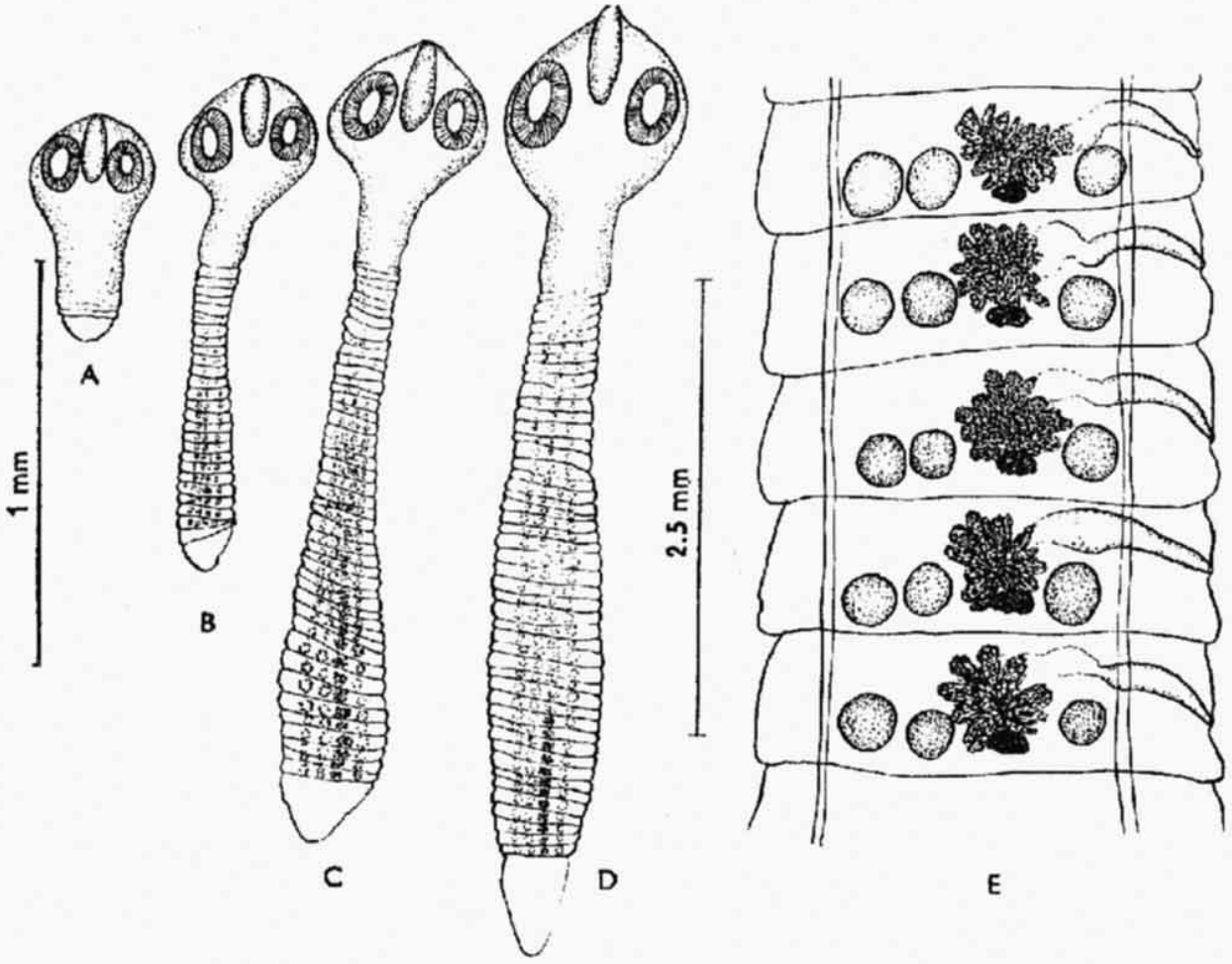

Fig. 3. A — Young cestodes 48 hrs p.i. in the intestine of the hedgehog; B — young cestode after 7 days in the intestine of the hedgehog; C, D — cestodes after 14 days in the intestine of the hedgehog; E — mature segments of cestodes after 21 days in the intestine of the hedgehog.

uteri of the last segments. On day 26, the first mature segments were shed but, generally, segments were shed from day 35 onwards. At this time we encountered the longest specimens (25—36 cm long, 1.5—3.0 mm wide). The scolex measured 400—500 μ in diameter, the suckers 250—280×180—200 μ. The rostellum was 300 μ long and not armed with hooks. The three testes were situated in one row in the posterior half of the sexually mature segment (Fig. 3E). The segments were wider than long. One testis was situated porally, two aporally. The cirrus sac extended past the lateral excretory organs. The ovary consisting of several lobes was situated in the middle of the segment with the vitelline gland below it. The genital pore is placed in the lower half of the segment. The last segments were occupied by the uterus with eggs of oval shape measuring 38—42 μ.

DISCUSSION

In France, Joyeux (1921) recorded two findings of cysticercoids (genus *Hymenolepis*) from hedgehogs. These cysticercoids measured 650—700×250 μ. Embryonal hooks (length 12 μ) were distributed over the tail. The rostellum was armed with one row of hooks (17 μ long). These hooks were consistent in shape, number and size with those of the cestode *Hymenolepis fraterna* (Stiles, 1906) which is known to have a direct life cycle. At first the author suggested that these cysticercoids are larval stages of this species but later, in view of the fact that adults of this species had never been recorded from hedgehogs of France, he expressed the opinion that this cystercoid is the larval stage of the cestode *Rodentolepis erinacei* (Gmelin, 1789) because he had recovered it once from a hedgehog. Because this cestode species has no hooks the author suggested that the hooks were shed during maturation. The scarcity of findings of this cestode species in the hedgehog are, according to Joyeux, due to its direct life cycle. Later, in order to confirm his hypothesis, Joyeux (1927) infected 7 hedgehogs with eggs of the cestode *R. erinacei*. He obtained negative results in 6 of these hosts inspecting them on day 5—8 p.i. In one of the hedgehogs, however, he found 55 mm long cestodes 100 hrs p.i., but he himself was doubtful that these cestodes had developed from the artificial infection. In my experiments, not even a cysticercoid had developed 100 hrs p.i. Both figures and descriptions of the cysticercoids recovered by Joyeux (1921, 1927) from the intestine of hedgehogs indicate that these belonged to the species *Hymenolepis fraterna*. In spite of these facts Joyeux's suggestion that the cestode *Rodentolepis* has a direct life cycle has been accepted and remained valid for the last 40 years. In Joyeux's opinion, this direct life cycle is responsible for the relatively low incidence of this cestode species (9.4 %) in the host. Having probably taken two independent species for one species only, he concluded that this species has no seasonal dynamics. By contrast, my results show a distinct curve of seasonal dynamics both in the intermediate host (April—May) and in the definitive host (June, with a peak in July). Literary references indicate that findings of *R. erinacei* in the hedgehog are not so rare as maintained by Joyeux (1927). Prokopič (1956, 1957, 1959) recovered it from 30 % of *Erinaceus europaeus* and 26 % of *E. roumanicus* in Czechoslovakia; Furmaga (1961) from 14 % of *E. roumanicus* in Poland; Dimitrova and Genov (1961) from 27 % of *E. roumanicus* in Bulgaria and Lungu and Radulescu (1957) recorded findings of this cestode species in Roumania. Merkusheva (1969) found this species in 46 % of hedgehogs in White Russia and Matsaberidze (1967) in 26.8 % of hedgehogs in Georgia.

The results of our experiments confirm that the cestode *Rodentolepis erinacei* has an indirect life cycle utilizing beetles of the species *Necrophorus humator, N. vespillo, Oeceoptoma thoracica, Silpha obscura* and *Geotrupes stercorosus* as intermediate hosts. We believe that the "Cysticercoid E" recorded by Kisielewska (1961) from *Geotrupes stercorosus* is the larval stage of this cestode species. The same cysticercoids were found in *Geotrupes stercorosus* by Prokopič and Karapchanski (1968) in Bulgaria.

CONCLUSION

Studies of the life cycle of the cestode species *Rodentolepis erinacei* (Gmelin, 1789) confirmed that the cysticercoids of this cestode species develop in beetles of the species *Necrophorus humator, N. vespillo, Oeceoptoma thoracica, Silpha obscura* and *Geotrupes stercorosus*. Of these *Oeceoptoma thoracica* seems to be the most susceptible intermediate host but it is possible that also other beetle species may act as intermediate hosts of this cestode. Development in the intermediate host is completed in 21 days, in the definitive

host (the hedgehog *Erinaceus europaeus*) in 35 days. The direct life cycle of this cestode species as suggested by Joyeux (1921, 1927) has not been confirmed. The cysticercoids found by Joyeux may have belonged to a different cestode species, possibly to the species *Hymenolepis fraterna*, and been mistaken for cysticercoids of the species *Rodentolepis erinacei*.

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J. P., Parasitologický ústav ČSAV, Flemingovo n. 2, Praha 6, ČSSR