ON *POLYCERCUS*: A PROLIFERATING CYSTIC PARASITE OF THE EARTHWORMS.

By William A. Haswell, M.A., D.Sc., Challis Professor of Biology, and J. P. Hill, F.L.S., Demonstrator of Biology, University of Sydney.

(Plates xix.-xx.)

The name *Polycercus* was proposed in 1883 by Villot* for a remarkable cystic worm described in 1868 by Mecznikoff.† The parasite in question was discovered by the latter at Odessa in specimens of *Lumbricus terrestris*, and does not seem to have been re-investigated since, the accounts of it and the comments on its affinities given by Moniez,‡ Leuckart,§ and Villot being all based on Mecznikoff's observations and figures.

A form exhibiting unmistakable affinities with Mecznikoff's has been found by us in a considerable proportion of specimens of an earthworm (*Didymogaster sylvatica*, Fletcher) common under stones and dead timber in certain parts of New South Wales; and an investigation of its structure and development has revealed features of some importance, which, so far as we have been enabled to ascertain, have not been previously noticed.

---

* "Mémoire sur les cystiques des Ténias." Ann. des Sci. Nat. Zool. 6me série, Tome xv. (1883).

† Verhandlungen der Petersburger Naturf. Versammlung, Zool. pp. 263-266.

‡ "Essai Monographique sur les Cysticerques." Trav. de l'Inst. Zool. de Lille, Tome iii. (1880). I have to thank Professor Giard for his kindness in sending me a copy of this work, as well as one of the "Recherches sur les Ténias" by the same author.—W.A.H.

§ "Die Menschlichen Parasiten."

Numerous attempts were made to develop the adult tape-worm by feeding cats, a bandicoot, pigeons, gulls, fowls, and lizards with the cysts; but no Tænia was found that could be assigned to the species under investigation.

The infested earthworms (Pl. XIX. fig. 1) usually contain immense numbers of cysts, the largest of which are about a millimetre in diameter, adhering in clusters to the outer surface of the alimentary canal. Each cyst (fig. 2) contains in its interior a number—usually eight to twelve, sometimes as many as thirty—of fully-formed Cysticercoids, with, sometimes, a few in early stages of development. In many cases the cavity of the cyst in the interstices between the Cysticercoids is filled with blood, showing that the cyst has been formed rather in the wall of the dorsal blood-vessel or one of its main branches than in the wall of the alimentary canal, and that there has been a communication (afterwards sometimes found to be persistent and distinguishable in sections) between the lumen of the vessel and the cavity of the cyst. A few cysts were found which contained only the earlier stages and no fully developed Cysticercoids. Nothing was seen of hooked embryos.

In the earliest stage observed the cyst contained a solid spheroidal mass of soft small-celled tissue, which was not connected in any way with the cyst-wall. The latter was mainly, if not entirely, of the character of an adventitious cyst: if any part of it had been developed from the hooked embryo, it was no longer distinguishable. In the next stage the mass had lost its former spheroidal form owing to its having become drawn out into several lobes. The lobed mass then develops a number of buds. These are at first very small blunt processes (fig. 3). Gradually they become larger (figs. 4 and 5) and assume a rounded shape, broader distally than proximally, where there is a slight constriction. As they increase in size they assume an oval form and become constricted off from the parent mass, remaining attached to it only by an isthmus or stalk (fig. 6), which in the largest becomes very narrow. Up to this point the bud has consisted of a nearly

uniform mass of small cells with only slight indications of division into an outer stratum and a central mass; but in sections these are found not to be sharply marked off from one another, the entire bud appearing as a mass of nearly uniform cells of small size. In the larger buds granules collect in the central mass, and a distinct hyaline cuticle becomes developed over the entire surface. The first trace of internal differentiation consists in the appearance in the interior, of a group of long and narrow cells (fig. 7), which lie parallel with one another in such a way as to form a circlet; these are the cells destined to form the hooks of the rostellum. At this stage vacuoles have appeared among the cells, but there is no regular cavity; a definite cavity first appears in the next stage, when the hooks have become developed.

In the next stage observed the hooks characteristic of the fully-formed Cysticercoid had appeared in the interior of the still solid mass of cells constituting the bud. Up to this point the calcareous corpuscles are not developed, and there is no trace of histological differentiation.

The next stage found is separated by a somewhat wide hiatus from that last described; but we have hitherto failed, in the many hundreds of specimens examined, to find any intermediate conditions. The calcareous corpuscles have now become formed in the outer layers of the developing Cysticercoid, and histological differentiation is well advanced. A cavity has appeared in the interior, so situated as to separate a distal, comparatively thin, wall from a proximal thick wall, on the middle of which is an inwardly projecting process—the rostellum—with a double circlet of hooks. On each side of this process on the inner surface of the proximal part of the wall are the rudiments of two of the suckers. The rostellum is at this stage entirely unconnected distally with the wall of the cysticercoid: it is capable of being to some extent invaginated within the posterior part of the rudimentary head.

The next stages (Pl. xix. fig. 9, and Pl. xx. figs. 1-3) show the rostellum more completely developed and now capable of being entirely invaginated within the posterior part of the head, which

has become developed as an elevation of the proximal wall with the suckers on its sides. The distal end of the rostellum is still quite free; along the distal edges of the sheath (fig. 2) which invests it are a number of extremely fine spinules, which may have to do with the subsequent establishment of the connection between the rostellum and the distal wall. Opposite the free end of the rostellum is a small rounded aperture perforating the distal wall of the Cysticercoid.

The next stage observed was that of the fully-formed Cysticercoid. When this is in the retracted condition (Pl. xx. fig. 4) it is an oval body with a depression at the proximal, and a rounded aperture at the distal, end. In the interior is the more or less folded rostellum and the suckers. Running from the distal end of the rostellum to the aperture is a strand, which is the sheath of the rostellum, now become firmly connected with the edges of the opening. The body wall consists of two layers, which are continuous with one another anteriorly.

Occasionally, especially if the temperature is slightly raised, the rostellum becomes protruded through the aperture (fig. 6), and a continuation of this process results in the complete protrusion of the scolex (fig. 7)—the uninverted outer layer of the wall of the Cysticercoid remaining attached to its proximal (posterior) end as the caudal vesicle, while the inverted inner layer forms the body.

One of the most remarkable features of this Cysticercoid is the great length of the rostellum, which is nearly equal to the entire length of the inverted scolex (·25 to ·3 mm.). It is narrow (about ·06 mm.) and cylindrical in form, expanded distally to form the expansion to which the hooks are attached.

The shape of this terminal enlargement varies a little in different individuals; its breadth averages ·1 mm. The hooks (fig. 5) are arranged in two alternative circlets situated close together; they are about forty in number altogether, and their length is ·035 mm. Each has two roots, one longer, anterior, in line with the free part, the other shorter, internal, nearly at right angles to the main axis.

The rostellum (figs. 8 and 9) consists of a stiffish cellular rod enclosed in a sheath and dilated terminally. The substance of the cellular rod, the size of which is subject to considerable variation, consists of vacuolated cells not unlike notochordal cells; at the anterior extremity is a mass of denser cells. Enclosing the vacuolated cells are two thin layers of muscular fibres, the fibres of the internal layer circularly disposed and those of the external layer longitudinally. Enclosing the rostellum in the retracted condition is a layer of circularly arranged muscular fibres, and outside of all a thin cuticular sheath, from which the rostellum becomes protruded when it is evaginated.

Below the cuticle in the posterior part of the head and body is a layer of circularly-arranged muscular fibres. The layer of vertically-elongated subcuticular cells characteristic of most Cestodes is not developed. The muscular fibres of the suckers are recognisable though not completely differentiated.

In some of the specimens the excretory system was to be clearly distinguished. A depression in the middle of the posterior border leading into a small cavity with very definite walls lined by a continuation of the surface cuticle, is probably the external opening of the system, though the vessels were not traced to this point. A circular vessel surrounds the rostellum, and from this are given off four longitudinal vessels with numerous branches. The flame cells are numerous, situated superficially, each terminating a minute capillary vessel; the flames are ·0075 mm. in length.

In his "Menschliche Parasiten,"* Leuckart gives an account of the cystic worm found by Mecznikoff at Odessa in the body-cavity of the common earthworm. The paper† in which this is described, which is in Russian, not being accessible to us, we have had to depend upon the account of it given (with reproduction of some of the figures) by the great German zoologist in the work referred

* English translation by W. Hoyle, p. 366.

† Verhandlungen d. Petersburger Naturf. Versammlung, Zool. pp. 263-266 (1868).

to, as well as upon the observations of Villot. The figures represent a form of Cysticercoid different from that now under consideration, and the account given of the development is not readily reconcilable with what we have found in the parasite of *Didymogaster*. We will quote here Leuckart's account in full:—

"In its mature condition it consists of a thin-skined bladder, which contains a varying number (up to thirteen) of small Cysticerci of about 0·5 mm. in diameter."

"Although the latter lie quite free in the interior and possess, like the ordinary Cysticercoids, the distinctive caudal bladder, they are of very unusual origin, inasmuch as, instead of developing directly from the six-hooked embryos, they arise by proliferation of the wall of the surrounding bladder. The bladder is thus the brood-capsule of the enclosed Cysticercoids and corresponds in some respects to the brood-capsule of the *Echinococcus*, or perhaps to a *Cœnurus*-bladder, and, like these, is undoubtedly to be referred to the six-hooked embryo. The first developmental stage observed by Mecznikoff appeared to be a solid ball of about 0·08 mm., with an unusually thick cuticular envelope and cellular contents. The latter subsequently became clear on attaining a diameter of 0·14 mm., when the embryo lies on the inner surface in the form of a cellular layer. Soon the buds begin to form, and that exclusively from the cellular wall, which becomes thicker at certain spots and sends little projections into the inner cavity. Although at first flat and connected by their broad bases with the cellular wall, the protuberances, as they grow larger, gradually detach themselves from the subjacent layer. This separation is facilitated by the development of a hollow space in the interior of the basal portion, so that after a time the bud is only connected with the mother-bladder by a thin filament. Finally this connection is destroyed, and the bud thus becomes an oval body lying freely in the interior. It then proceeds to undergo its further development. This is essentially the same as that which we have already (ob-)served in the buds situated inside the brood-capsule in the *Echinococci*, only that in this case not only head and neck are formed, but a third joint, consisting of a kind of caudal bladder.

All these parts are formed almost simultaneously, for the originally compressed and solid bud increases in length, then becomes hollow inside, and becomes jointed by the development of the hook-apparatus in front and a bladder-like expansion behind. When the suckers and hooks are completely developed, the anterior part of the body draws back into the caudal bladder by invagination of the neck, so that at the end of its development the worm has exactly the same position as we formerly observed in *Cysticercus arionis*."*

Mecznikoff thus, it would appear, describes the embryo as elongating and becoming divided into three parts, on the most anterior of which the hooks become formed, this anterior part *subsequently becoming invaginated*, with the suckers, into the posterior part or caudal bladder. This is totally at variance with what we have found to occur in the parasite of *Didymogaster*, and, taking into account certain resemblances between the two forms, we are inclined to think that it is erroneous. It is probable that, if our supposition is correct, the error arose from an attempt to reconcile the stages observed with the known developmental history of *Echinococcus*. As regards the earlier stages, Mecznikoff's figures A and B, as reproduced by Leuckart (fig. 213, p. 366), do not represent any stage that occurs in the parasite of *Didymogaster*, and it is difficult even to reconcile them with Leuckart's description. The former represents the wall of the cyst as raised up internally into three thickenings, and the latter shows three oval masses, developed from those thickenings, attached together by narrow strands, though no longer connected with the cyst wall.

Leuckart,† as already noticed, refers *Polycercus* to the type of *Echinococcus*, and so does Moniez.‡ From this view Villot§

* L.c. pp. 366 and 367 : second German edition, pp. 464 and 465.

† *Tom. cit.* p. 366.

‡ "Essai Monographique sur les Cysticerques." Travaux de l'Instit. Zool. de Lille, T. iii. (1880).

§ "Mémoire sur les cystiques des Ténias." Ann. des Sci. Nat. Zool. 6me série, Tome xv. (1883).

strongly dissents, and the history of the development, as above described, shows that his conclusion was correct. Having, however, only Mecznikoff's statements to rely upon, he was necessarily led to some wrong deductions. Thus he describes the caudal vesicle as invaginated in the "blastogène," whereas, as we have seen, the latter is really represented by a cellular mass from which the Cysticercoids are developed by proliferation. His detailed comparison with *Echinococcus* is rendered inaccurate in several particulars by a similar cause; but in its main outlines appears to us to present the true view of the case. "Le Cystique du Lombric n'appartient pas au même groupe que l'Echinocoque, et il ne représente nullement dans son groupe le type de l'Echinocoque. L'intéressant parasite découvert par Mecznikoff est un Cystique monocéphale, monosomatique et polycerque. L'Echinocoque, au contraire, est un Cystique polycéphale, polysomatique et monocerque. Les ressemblances sur lesquelles on s'est fondé pour rattacher les deux formes à un seul et même genre se réduisent en définitive à de simples analogies qui ne portent pas sur des parties homologues."*

In the Cysticercoids hitherto described there are three main types as regards the form of the completed larva: (1) those in which there is a longer or shorter caudal appendage, containing a small cavity, but in which no caudal bladder is present; (2) those in which such a caudal appendage is present and a caudal bladder as well; (3) those in which the caudal appendage is absent, but in which there is a well-formed caudal bladder.

Of the first group we have an example, it would appear from Grassi and Rovelli's account, in the Cysticercoid of *Taenia elliptica*. In *T. murina*, apparently, we have an example of the second form, in which the opening of the investing caudal bladder closes up; while in *Cysticercus tenebrionis*, according to our

* L.c. p. 34. It is to be remarked here that the description of *Echinococcus* as 'monocerque' is open to objection, the daughter-vesicles of that genus being the equivalents of the caudal vesicles of other Cestodes.

interpretation of Stein's observations, we have an example of a similar form, in which the aperture persists. Examples of the third group are *Cysticercus arionis* and the Cysticercoid of *T. infundibuliformis* (according to Grassi and Rovelli's account of it). It is to this group likewise that *Polycercus* is referable, and also, we believe, Villot's *Staphylocystis*.

In many Cysticercoids it would appear that there is a progressive invagination of the anterior parts within those lying behind: the anterior part of the head is invaginated within the posterior part; the head is invaginated within the body and the body within the caudal bladder. This condition of things is clearly a secondary one, brought about in adaptation to special circumstances. The enclosure of the head within the body and caudal bladder doubtless subserves the protection of the former; while at the same time it doubtless permits of the passage of the parasite to that part of the alimentary canal of the host in which the adult Cestode is capable of living—the hooks and suckers not coming into play for purposes of attachment until the intestinal juice has had the effect of causing evagination of the head and rostellum.

In *Polycercus* this adaptation may be said to reach its furthest known limit. Here there is no invagination in the strict sense, but the parts of the Cysticercoid are actually developed one within the other, the head within the body and the body within the caudal bladder, and it is only subsequently, when the Cysticercoid is about to pass into the adult Cestode, that by a process of evagination these parts assume their normal and primitive relations to one another. Whether this condition is exceptional or the reverse it would be impossible to say in the present condition of our knowledge of the development of the Cysticercoids. That it occurs in another form we know from the observations of Stein on the development of *Cysticercus tenebrionis**; while we

* "Beiträge zur Entwickelungsgeschichte der Eingeweidewürmer." Zeitschr. f. wiss. Zool. iv. Band (1853). Confirmed by Meissner, "Zur Entwickelungsgeschichte und Anatomie der Bandwürmer." Zeitschr. f. wiss. Zool. v. Band (1854).

also know from Grassi and Rovelli's* account of the development of the Cysticercoid of *Taenia elliptica* that the development by progressive invagination also obtains.

In some respects *Polycercus* is more nearly related to *Staphylocystis* than to any other known form of Cestode larva. In both the development is a process of *external proliferation* from the product of the hooked embryo—the essential similarity of the two cases being somewhat disguised by the development in *Polycercus* of an adventitious investment or kyst, not represented in *Staphylocystis*. But Villot's† account of the mode of formation of the Cysticercoid differs widely from what we have observed in *Polycercus*. He describes the bud as forming a hollow vesicle or cyst, within which is formed an internal hollow bud, which grows until it comes into apposition with the opposite wall of the cyst, when it becomes invaginated—the wall of the cyst giving rise to the caudal vesicle, the proximal part of the internal bud to the "body" and the invaginated part to the head.

Summary of Results.

(1) The hooked embryo in *Polycercus* develops into a rounded cellular body, which becomes enclosed in a cyst probably entirely of an adventitious character.

(2) Buds are given off from the periphery of the mass and develop into Cysticercoids, which soon become free in the interior of the cyst.

(3) The head, with its hooks and suckers, is developed from the central portion of the solid bud; the middle layers form the 'body' and the outermost the caudal vesicle.

(4) *Polycercus* is not nearly related to *Echinococcus*, but finds its closest ally in *Staphylocystis*.

---

* "Embryologische Forschungen an Cestoden." Centralbl. f. Bakteriologie u. Parasitenkunde, v. Band (1889).

† "Migrations et Métamorphoses des Ténias des Musaraignes." Ann. Sci. Nat., 6me. série, Tome viii. (1878).

EXPLANATION OF PLATES.

Plate xix.

Fig. 1.—Anterior portion of a specimen of *Didymogaster sylvatica*, Fletcher, laid open along the middle dorsal line in order to show the numerous rounded cysts containing *Polycerci*. Slightly magnified.

Fig. 2.—Five of the cysts as seen under a low magnifying power (10 diameters); the polygonal areas represent the contained Cysticercoids.

Fig. 3.—Early stage in the development of *Polycercus* from the hooked embryo; first traces of proliferation.

Fig. 4.—A somewhat later stage.

Fig. 5.—Still later stage than fig. 4, the cellular mass divided externally into numerous broad lobes. *a*, wall of cyst.

Fig. 6.—Stage in which some of the buds have assumed the general form of the future Cysticercoid and are connected to the central mass only by narrow stalks; other buds at earlier stages in their formation.

Fig. 7.—Portion of a section of a young bud, with the spindle-shaped cells from which the hooks will be developed situated in the centre of the cellular mass. Magnified about 250 diameters.

Fig. 8.—Developing Cysticercoid of *Polycercus*, in which the rostellum, with its hooks, and the suckers have become formed; the rostellum retracted within the head and not yet connected with the external aperture. *r*, anterior, and *r'*, posterior parts of rostellum; *s*, suckers; *e*, excretory aperture; *c*, internal cavity.

Plate xx.

Fig. 1.—A stage in the development of *Polycercus* similar to that represented in fig. 9 of Plate xix., but showing the external aperture and the two layers of the body-wall. *a*, aperture in wall of cyst; other letters as in preceding figure.

Fig. 2.—Sheath of the rostellum of the same more highly magnified to show the spinules along the border.

Fig. 3.—Similar stage, with the rostellum partly evaginated and extending towards the aperture. Letters as in fig. 1.

Fig. 4.—Fully developed Cysticercoid in the unextended condition, the connection between the sheath of the rostellum *(sh.)* and the edges of the aperture now established. Letters as in fig. 1.

Fig. 5.—One of the hooks of the rostellum. Highly magnified.

Fig. 6.—Cysticercoid, with the rostellum fully evaginated.

Fig. 7.—Fully extended Cysticercoid. *r*, rostellum; *s*, suckers; *b*, "body"; *c.v.*, caudal vesicle.

Fig. 8.—Transverse section through unextended Cysticercoid. *a*, central tissue of rostellum; *b*, layer of circular muscular fibres; *c*, longitudinal layer of muscular fibres; *d*, sheath; *s*, suckers; *t*, wall of cyst.

Fig. 9.—Longitudinal section. *h*, hooks; other letters as in fig. 8.