The Anatomy and Life-history of the Fowl Tapeworm (*Amoebotaenia sphenoides*).

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In the autumn of 1924 a number of fowls in a fowl-run at Onderstepoort died, and two of them were brought to the laboratory for examination. In each case there was a severe enteritis and also about 80 specimens of *Amoebotaenia sphenoides*—the first record of this parasite in South Africa. Whether the enteritis was caused by the parasites only and whether this normally would have happened is not quite clear, as the fowls were not being properly fed at the time, due to the absence of the owner. Subsequently 95 specimens were found in a healthy, fat fowl killed for the table, where they had apparently caused no harm. Previous authors did not note any untoward symptoms, and Meggitt (1914) states that "except for a rather pronounced thinness upon the breast, the birds were normal in every way," and "none of the characteristic symptoms of tapeworm disease were present." It seems, therefore, that under normal circumstances these parasites would not cause any appreciable damage.

Since it was suspected that this tapeworm is transmitted by earthworms, experiments were undertaken to investigate this point. The fact that the discovery of this infestation was made about three months after heavy rains, when earthworms had been frequent on the surface of the soil, was considered to be in favour of the prevalent view on the nature of the intermediate host, and the first object of the experiments was, therefore, to test this point.

Morphology of the Adult Worm.

The morphology of *A. sphenoides* has been carefully studied by Meggitt (1914). My findings agree closely with these, and only a short description is, therefore, given here.

Amoebotaenia sphenoides (Raill., 1892), Cohn, 1899.
Syn. *Taenia cuneata*, v. Linstow, 1872 (nec. Batsch, 1786); *T. sphenoides*, Raill., 1892; *Dicranotaenia cuneata* (v. Linst., 1872), Raill., 1893; *Dicranotaenia sphenoides* (Raill., 1892 and 1893), Stiles and Hassall, 1897.

Diagnosis.—Body, 2 to 3.5 mm. long by 0.9 to 1.5 mm. broad; head, 220μ long by 240μ broad, with a retractile rostellum 160μ long and 37.5μ broad, which bears a single row of 14 hooks measuring 32μ in length; the dorsal and ventral roots of the hooks are relatively short and more or less equal in length, while the hook itself is long and very acute (fig. 2). The four suckers are spherical to oval in shape, prominent, unarmed, and 110μ in transverse diameter. The head is followed by a short neck, which is a little narrower than the

head, and 18 to 23 segments that gradually increase in size up to about the 14th and then again decrease (fig. 1). The ripe segments break off very easily, and hence many specimens have a smaller number of segments, and the body appears wedge-shaped as it has been described by earlier authors.

The genital pores are irregularly alternate and situated at the anterior angles of the segments. The testes are seen already in the first or second segment and rapidly increase in size; there are usually 12 to 14 in each segment lying against its posterior border dorsally in a row that extends laterally to the longitudinal excretory canals on both sides. The testes appear to be functional only in about four segments, after which they rapidly disintegrate. The *vas deferens* forms numerous coils laterally and medially to the longitudinal excretory canals. The latter take a zig-zag course through the length of the body and lie ventrally to the *vas deferens* and the vagina.

The female organs are functional in the 8th to 13th segments usually, but can be seen developing already in much younger segments. The vagina does not always curve round the cirrus sac as shown in figs. 3 and 4, but occasionally goes straight; it leads into a large pear-shaped receptaculum seminis, which is continued into a duct that is soon joined by the oviduct; the latter runs backwards from the ovary, and the combined duct now passes further in the same direction through the " shell-gland " and then proceeds forwards to the uterus. The yolk gland is bilobed and situated near the posterior border of the segment; against its anterior portion lies the " shell gland," a faintly staining spherical body; anteriorly to this lies the ovary in the form of a transversely elongated bag with irregular outline and narrower in the middle than at the two sides; it lies on the ventral side of the segment about midway between the anterior and posterior borders. The genital organs are not situated exactly in the middle of the segment, but lie towards that side on which the genital pore of the respective segment opens. The uterus is at first an empty bag situated against the anterior border of the proglottis and can be seen in sections already in the 11th segment (fig. 3). It develops rapidly, filling with eggs and displacing the ovary backwards. In about the 14th segment the uterus is large and contains numerous eggs, while there is only a thin, elongated strip left of the ovary (fig. 4). The uterus forms numerous sacculations transversely to the breadth of the proglottis, and in some specimens this is so pronounced as to present an appearance like that of the uterus of *Thysanosoma giardi*. Finally it becomes completely filled with eggs, and the sacculations disappear. In the 19th segment the uterine walls can no longer be seen, and the eggs lie scattered throughout the segment. The eggs are spherical, with a double membrane, and measure 35μ; the hooks of the oncosphere are 6μ long.

Life-history.

In 1889 Grassi and Rovelli found some cysticercoids in an earthworm (*Allolobophora foetida*), which they believed to represent the intermediate stage of *A. sphenoides*. They state that the hooks of this cysticercoid agree with the hooks of the worm in question, but evidently they did not make any experiments to prove the point. Magalhaes (1892) reports the same tapeworm from Brazil and states that, as *Allolobophora foetida* does not occur there, another species of earthworm would have to act as intermediate host. Meggitt (1914)

could not find these earthworms in the infected fields near Harborne, Birmingham, from where he obtained his material, and comes to a similar conclusion.

The infested fowl-run at Onderstepoort is on black turf, where numerous earthworms of various species come to the surface with the heavy summer rains. However, one species* is by far the most numerous in the fowl-run, and was consequently selected for the experiment. On 12th May, 1924, after keeping a patch of ground in the fowl-run moist and covered for several days, 470 earthworms were collected from about an inch below the surface. Of nine young, apparently healthy experimental fowls, three were killed and examined for intestinal worms. They each had a few adult and some young specimens of *Raillietina tetragona* and a few adult *R. echinobothrida* and *R. cesticillus*, but no *Amoebotaenia sphenoides* was found. The earthworms were then washed several times in tap-water and 150 fed to each of three of the remaining six fowls; these three were each placed in a cage together with an unfed control. The remaining 20 earthworms were then dissected, but none of them was found to harbour any cysticercoids. One of the three experimental fowls died the following night of catarrhal pneumonia, and the intestines were thoroughly examined but showed no evidence of infection with *A. sphenoides*, only a few other tapeworms were found. A second experimental fowl died after ten days, the death being preceded by diarrhœa and symptoms of anæmia, but again no *A. sphenoides* could be found, although other tapeworms were frequent, as well as specimens of *Ascaridia lineata*, *Heterakis papillosa*, *Allodapa suctoria*, and *Tropidocerca fissispina*. The third fowl was killed after fifty-three days in excellent condition and had no intestinal parasites at all. The three controls were discharged.

It seems, therefore, that if this earthworm is the intermediate host, the specimens used were probably not infected.

On 12th May a number of earthworms were again collected as above; about 40 were dissected and found uninfected, and the rest were then placed in a box of moist earth to which were added for several days the droppings of a few of the most " wormy " looking fowls of the infested lot. This experiment proved more successful, as after fourteen days the examination of some of these earthworms resulted in the finding of a number of cysticercoids, some of which were fully developed, and the hooks of these left little doubt as to their probable relationship with *A. sphenoides* (fig. 2). As these earthworms appeared to be uninfected when placed in the box, it seems reasonable to conclude that they developed the infection since that time, and that the cysticercoid appears to complete its development within fourteen days. It may be stated that the soil used was fine, dry, sandy soil taken far away from any fowl-run in the open, where it had been exposed to the sunlight, and the infection must, therefore, have come from the fowl-droppings, since the soil did certainly not contain such a large number of live tapeworm eggs.

To obtain clean chicks for further experiments, a number were hatched in an incubator and kept first in a mosquito-screened box in the laboratory and later in an insect-proof stable with a concrete floor. However, due to the advent of winter, earthworms were now becoming scarce, and the experiments were interrupted at this stage.

* Identified through the courtesy of the British Museum as *Ocnerodrilus* (*Ilyogenia*) *africanus*, Beddard, *var. nov.*

Development of the Cysticercoid.

On the 12th December, 1924, the work was resumed, and a large number of earthworms were collected in the infected fowl-run. A number were dissected, and 5 per cent. were found to harbour the same cysticercoid found previously. The earthworms were then placed in a box of soil to which were added fresh droppings from the infested fowls. On the 20th December, eight days after the earthworms had been placed in the box, a number were again dissected, and this time about 25 per cent. were found to be infested, harbouring various developmental stages of a cysticercoid, as well as some fully developed ones as found previously. We may now draw the conclusion that 20 per cent. of the earthworms appear to have got infected in the box, and that this is the second time that earthworms were infected in the laboratory by placing them in a box of soil with droppings of the infested fowls. As was noted above, the cysticercoid seems to complete its development within fourteen days, and the present experiment would appear to confirm this; the fully developed cysticercoids found at this juncture probably represent the initial infestation, while the developmental stages would be derived from the infection in the laboratory; the latter represent a series of stages that will be described presently, and from the maximum development which is attained in eight days it appears probable that complete development may take place within fourteen days. Some of the worms may, of course, have ingested tapeworm eggs shortly before they were collected, and some of the developmental stages now found may be derived from such a source. However, the bulk of them can certainly not be ascribed to such a previous infestation, as they represent all possible stages of development and some at least would have been seen at the first examination; together with the evidence of the first experiment then, the conclusions drawn above are certainly the most probable.

The youngest stages of the cysticercoid that were found were globular, solid masses of cells measuring 80μ to 200μ in diameter and surrounded by a hyaline and highly refractive membrane; the six embryonic hooklets were found lying in pairs in the cellular mass fig. 5*a*). The solid mass of cells now develops a central cavity, and we find the little bladders, measuring upwards of 230μ in diameter, still bearing the embryonic hooklets. In some no trace of further development could be found, while in others an invagination is seen to begin at a certain point and a solid papilla grows into the central cavity (fig. 5*b*). The area of invagination is very small, so that the outer membrane of the bladder does not appear to be invaginated, but only a small pore can be seen in it. The papilla grows larger and seems to raise the inner wall of the bladder with it as is shown in fig. 5*c*, representing a stage of 270μ in diameter: later, this raised portion of the wall apparently breaks down, and the invaginated mass becomes free except for a fine strand of protoplasm attaching it to the point of invagination: of the latter, nothing except this strand remains visible, as the wall of the bladder now again appears unbroken. The invaginated mass develops two constrictions, which separate distally the rostellar portion, in the middle the head portion, and proximally the "intermediate" or "neck-piece." Next, it develops a lumen, and on the inside of the wall of the rostellar portion 14 hooks begin to form, while the suckers develop on the inside of the wall of the head portion. Fig. 5*d* represents such a stage,

measuring 295μ in diameter, the most advanced of the developmental stages found on the eighth day. The calcareous corpuscles have not yet begun to form in the wall of the "neck-piece." The most proximal part of the latter is still attached to the wall of the bladder by the strand of protoplasm, and the embryonic hooklets can be seen in the wall of the bladder. These hooklets do not appear to take up any definite position; they are found near the point of invagination, as well as at the opposite pole of the bladder. The cysticercoid does not possess a tail at any stage of its development.

To attain the mature stage, the head and rostellum must become evaginated into the "neck-piece," and the latter must develop the calcareous corpuscles. The bladder of the mature cysticercoid is globular in shape or slightly oval, measuring 350μ by 310μ, and contains the scolex within the neck-piece or "inner cyst," as it may now be called, the latter measuring 230μ by 160μ, the whole being roughly oval with an opening at each end (fig. 6). This inner part is still sometimes connected by the fine strand of protoplasm to the bladder wall, but in the majority of cases this strand could not be seen, and it appeared as if the scolex, with its covering cyst, was free within the bladder or "caudal vesicle." The inner cyst contains numerous oval calcareous corpuscles in its wall; when these are dissolved in dilute acetic acid the structure of the scolex can be seen clearly. The following measurements were taken after such treatment: there are four large suckers, measuring 85μ by 50μ, although in the live specimen they are mostly circular. The rostellum bears 14 hooks (fig. 2*a*), which closely resemble those of *A. sphenoides*, and are 32μ long. The scolex is surrounded by the inner cyst, and this is again surrounded by the fluid contained in the caudal vesicle. The inner layer of the wall of the latter has grown so that the cavity has become greatly diminished; in the wall of the caudal vesicle the three pairs of embryonic hooklets can still be found. The cysticercoids are very active when placed in physiological saline; the caudal vesicle apparently does not move actively, but the scolex and its surrounding cyst, as well as the suckers and rostellum, separately can be seen to move vigorously.

It has not been definitely ascertained where exactly the cysticercoids are situated in the body of the earthworm, but, at any rate, it can be stated that they are in the body cavity, for when a worm is slit open without injuring the intestine, the cysticercoids escape. As this point is of no economic importance and only a matter of interest, it was not considered important enough to spend any time in making sections of infected earthworms to settle the question.

Infection of Chicks.

On the 13th December, after it had been found that some of the earthworms in the infested fowl-run harboured the cysticercoid, about 1,000 earthworms were again collected, and after washing them several times to remove all adhering matter, they were fed to the chicks that had been kept for the purpose. Only four chicks remained available for the experiment, and hence two were fed with about 500 earthworms each, the other two being kept as controls.

The earthworms placed in the box of soil on 12th December were left so that the cysticercoids might develop to maturity as much as possible until the 27th December, when they were also washed and

fed to the two chicks fed before, giving each chick about 300 earthworms. The droppings of the chicks were now daily examined for the presence of tapeworm eggs, but none were found until the 9th January, i.e. twenty-seven days after the first infection, when one of infected fowls passed a few eggs. On the following day, four weeks after the first infection, both infected fowls passed tapeworm eggs. The four fowls were now killed and the intestines carefully examined. Both controls were found to be free of intestinal worms, while the two infected fowls contained respectively 28 and 31 specimens of *Amoebotaenia sphenoides*, some of them being mature, but the majority not; the latter are probably from the second infection.

The result of this experiment proves then that the cysticercoid found in the earthworms is the intermediate stage of *Amoebotaenia sphenoides* and that the earthworm is the intermediate host. The number of fowls used in the experiment was certainly a minimum; but with the clear-cut result and also the previous findings, the minimum in this case was quite sufficient.

Summary.

(1) Cysticercoids, of which the hooks resemble those of *Amoebotaenia sphenoides*, were found in earthworms collected in a fowl-run infested with this tapeworm.

(2) Earthworms [*Ocnerodrilus* (*Ilyogenia*) *africanus*, Beddard, var. *nov.*] were artificially infected with this cysticercoid by placing them in a box of soil to which droppings of the infested fowls were added.

(3) The development of the cysticercoid was followed by means of a series of stages obtained from artificially infected earthworms.

(4) Clean chicks, fed with earthworms containing the cysticercoid, became infected with *Amoebotaenia sphenoides*, while the controls remained uninfected.

(5) The cysticercoid needs about fourteen days for its complete development and the tapeworm about four weeks.

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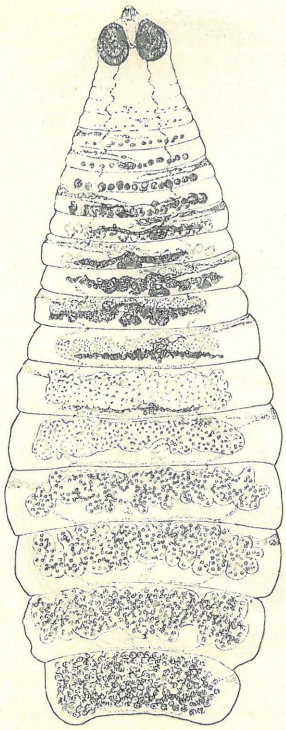

Fig. 1.—*Amoebotaenia sphenoides*. Ventral view, drawn from a stained specimen.

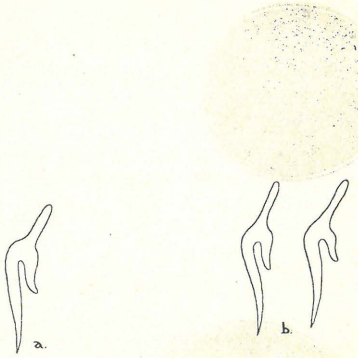

Fig. 2—(*a*) Hook from cysticercoid found in earthworm. (*b*) Hooks from rostellum of *A. sphenoides*.

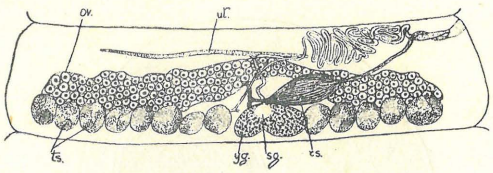

Fig. 3.—Semi-diagrammatic representation of a mature segment. Uterus is an empty bag. *ov.*, ovary; *rs.*, receptaculum seminis; *sg.*, shell-gland; *ts.*, testes; *ut.*, uterus; *yg.*, yolk-gland.

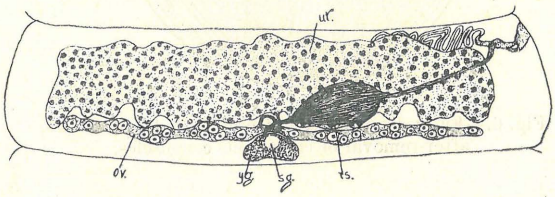

Fig. 4.—Semi-diagrammatic representation of a ripening segment. Uterus filling with eggs and displacing the ovary backward.

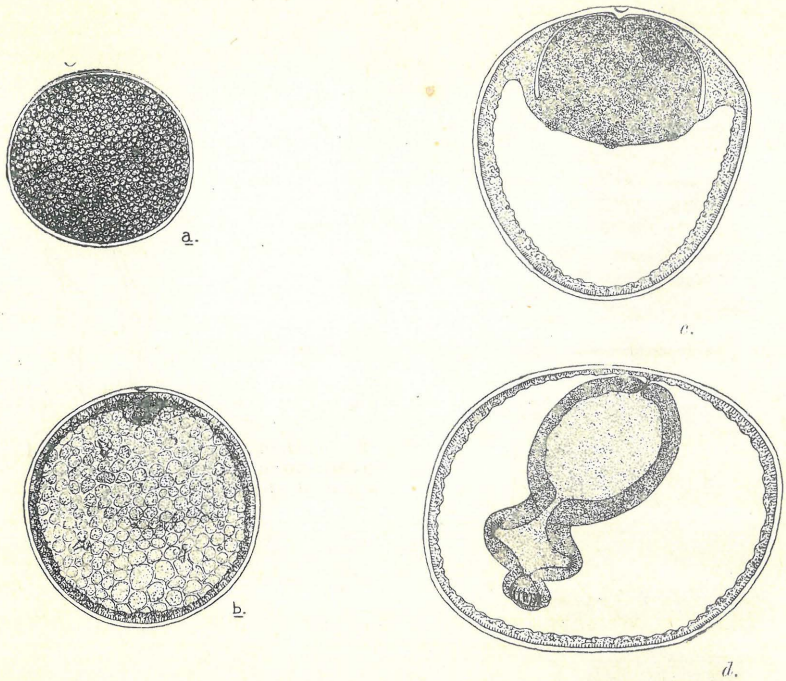

Fig. 5.—Developmental stages of cysticercoid of *A. sphenoides* in the earthworm. *a*, solid embryo; *b*, "Blastula" stage, with beginning of invagination; *c*, optical section of further developmental stage; *d*, optical section of cysticercoid before invagination.

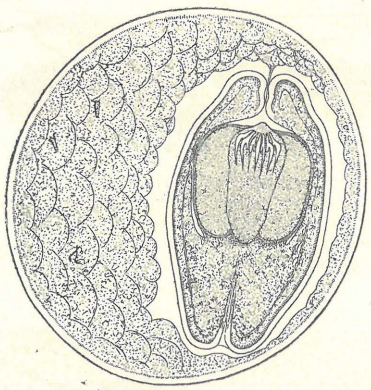

Fig. 6.—Fully developed cysticercoid of *A. sphenoides*, after removal of calcareous corpuscles.

Fowl Tapeworm.] [*H. O. Monnig.*

FIGS. 5 AND 6.