METHODS OF ASEXUAL AND PARTHENOGENETIC REPRODUCTION IN CESTODES

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In the following paper we propose summarizing the various facts, known at present, regarding the different methods by which the Cestoda reproduce themselves, asexually and parthenogenetically. The formation of secondary bladders in the parent cysticercoid, like what occurs in some of the common forms such as Coenurus, Echinococcus and Polycercus, is, of course, quite well known, but though some of the more uncommon types have been described carefully, they have never received that attention which they merit. Recently, two special types of budding in larval cestodes have been described, one by Ijima (1905) and the other by Beddard (1912). These instances, together with a new case of parthenogenetic reproduction, in what we believe to be a new and adult worm recorded by us (1917), suggested the desirability of reviewing those reproductive methods (other than sexual) known to occur in the Cestoda both in the larval and adult stages. We propose to discuss each case separately, beginning with larval forms in which such reproduction takes place.

TYPE A.—WITH INTERNAL BUDDING BY PROLIFERATION

1. Monocercus Villot.—In this genus a very primitive condition in the pro-scolex, or blastogen, gives rise to a single caudal bladder by a typical method of endogenous budding.

This is to be seen clearly in the species *Monocercus* (*Cysticercus*) *arionis* (Siebold). Villot describes an original connection between the posterior part of the caudal vesicle of the cysticercoid and the cyst, in the form of "une sorte d'ombilic ou de depression infundibuliforme." In *M. didymogastris* Hill no original connection can be seen in the fully formed cysticercoid (Fig. 1). This certainly appears to be an advance on the condition in *M. arionis* described by Villot and leads to the condition in Polycercus which will now be considered.

2. Polycercus Villot.—The generic name Polycercus was proposed by Villot in 1883 for a cystic worm described in 1868 by Metchnikov. The species *P. niloticus* was so named by Willey (1907) because the

adult tapeworm stage of Metchnikov's larva is now known to be *Taenia nilotica* Krabbe, 1869, which is parasitic in *Cursorius europeus*. In its mature condition this species consists of a thin skinned bladder which contains a varying number (up to 13) of small cysticercoids of about 0.5 mm. in diameter. Although the latter lie quite free in the interior of the cyst 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 internal wall of the surrounding bladder (Fig. 2). 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 Coenurus bladder, and like these is undoubtedly to be referred to the six-hooked embryo. The first

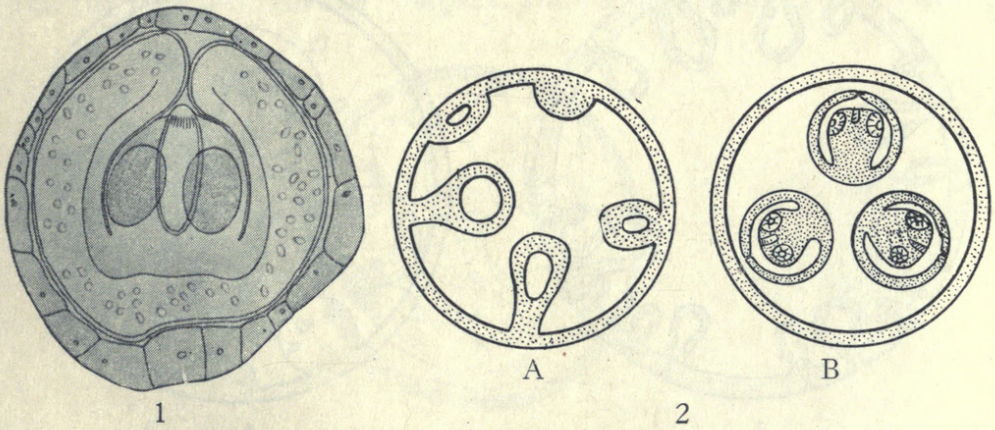
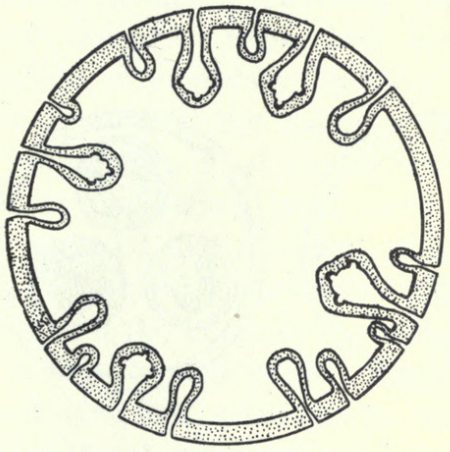


Fig. 1.—Cyst of *Monocercus didymogastris*. (After Hill.)
Fig. 2.—Cyst of *Polycercus niloticus*. (Altered from Benham.)

developmental stage observed by Metchnikov appeared as 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 of the cuticula in the form of a cellular layer. Soon the buds begin to form and at 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, detach themselves from the subsequent 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, so that at the end of its development the worm has exactly the same position as we formerly observed in *Cysticercus* (*Monocercus*) *arionis*.

From the above it will be seen that this type of budding is only an advance on the type described for Monocercus, in that more than one area of proliferation arises on the inner wall. These areas then hollow out and are later on detached when they become free in the central cavity of the parent cyst where each develops a head and becomes a *cysticercoid*. Haswell and Hill's type of Polycercus differs from the preceding type and will be dealt with later on.

3. Coenurus Rud.—In *Coenurus cerebralis* (Batsch) Rud. the stage is still further advanced than what occurs in Polycercus in that numerous scolices arise within the cavity of the parent cyst by a process of invagination of the cyst wall; but these never become detached from the cyst wall (Fig. 3).



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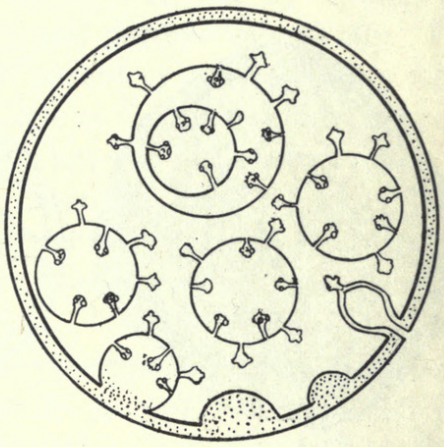

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Fig. 3.—Cyst of *Coenurus cerebralis*. (From Benham.)
Fig. 4.—Cyst of *Echinococcus* sp. (From Benham.)

4. Echinococcus Rud.—Here the condition appears to be very much more advanced, combining some of the features seen in Polycercus and Coenurus. In the cyst of this genus secondary bladders are formed as proliferations from the inner wall of the parent cyst, exactly as in Polycercus, but instead of a single head or scolex being developed in each, a large number of scolices arise in each of these secondary cysts (Fig. 4). By a continuation of the same process, tertiary bladders may also be formed from the wall of the secondary bladders, whilst still enclosed in the parent cyst.

TYPE B.—WITH INTERNAL BUDDING IN AN UNKNOWN WAY

We may now consider two distinct types of endogenous budding in cysticercoids believed to be the larval stages of *Tetrarhynchus unionifactor* Herdman and Hornell, occurring in *Placuna placenta* Linn. and *Margaritifera vulgaris* Schum. (*Avicula fucata* Gould). One of these types was first recorded by Hornell (1906) in *Placuna placenta*.

It was recorded subsequently by Willey (1907) and the cysticercus was provisionally named Merocercus. Hornell described the formation of a single secondary cyst within the parent form, but Willey later on, working on the same form from the same locality, not only confirmed Hornell's discovery, but added that the endogenously produced larvae were a very common feature of this form and that multiple formation of endogens within a single cyst was likewise common. As many as twenty secondary cysts were seen in one parent cyst (Fig. 5). Monogenetic cysts were also observed by Willey (Fig. 6), but the multiple type of proliferation was the rule. This suggests that the monogen type may only be a stage in the development of the multiple type of cysts. This multiple endogeny, however, differs from what was recorded later on (Fig. 7) by one of us (Southwell, 1910) in that the parasite from *M. vulgaris* shows simple endogeny. Multiple

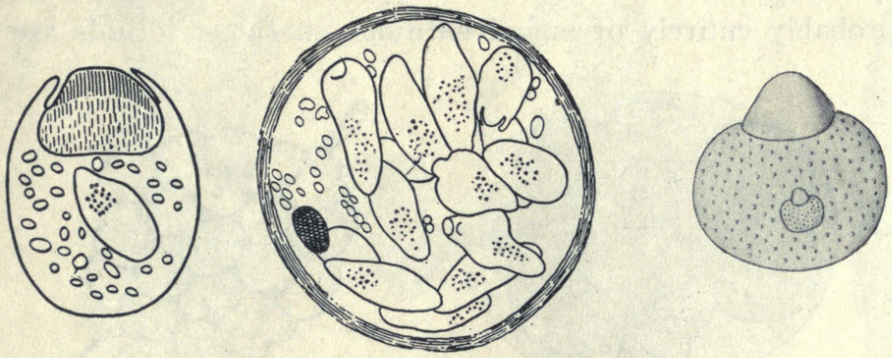

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Fig. 5.—Cyst of Merocercus with a large number of daughter cysts. (After Willey.)

Fig. 6.—Monogen cyst of *Tetrarhynchus unionifactor* (?) Monocercus. (After Willey.)

Fig. 7.—Cyst of *Tetrarhynchus unionifactor*. (After Southwell.)

endogeny was never observed, though thousands of specimens were regularly examined at different seasons of the year over a period of six years.

The type observed by Willey is certainly more advanced than the one recorded by Southwell, even though the two have previously not been distinguished from one another.

As nothing is known regarding the mode of origin of these daughter endogens from the parent cyst we are unable to say anything regarding the relation of these forms with those described in Group A. The endogens may arise either as proliferations from the epithelial lining of the mother larval form, in which it would be similar to what occurs in Monocercus. On the other hand the daughter endogens may arise from the internal intima filling up the cavity of the mother larva. In that event, this method of endogenous budding would be quite

different from the other forms. It cannot, in any case, be parthenogenetic, as no eggs or egg-like structures are shown in the figures or described in the minute account of the anatomy of the larval form given by Herdman and Hornell (1906).

TYPE C.—WITH EXTERNAL BUDDING

In the following cases, budding takes place by proliferation from the external surface.

a. Polycercus.—A species of the genus Polycercus was found by Haswell and Hill (1894) in the earthworm *Didymogaster sylvatica* Fletcher. This species of Polycercus differed from the other species of this genus in having a definite type of development which consists of a process of external proliferation from the product of the hooked embryo in the following manner. "The hooked embryo in Polycercus develops into a rounded cellular body, which becomes enclosed in a cyst, probably entirely of an adventitious character. Buds are given

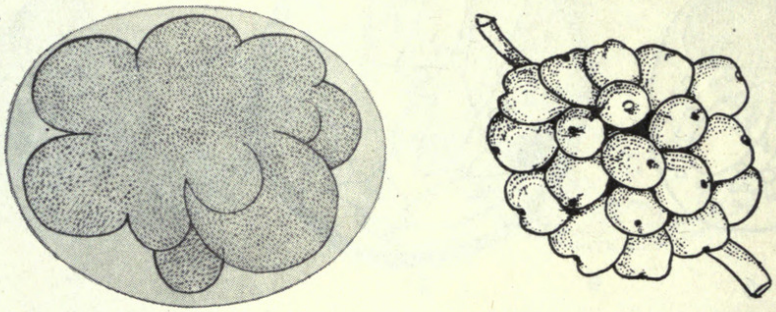

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Fig. 8.—Cyst of *Polycercus* sp. (After Haswell and Hill.)
Fig. 9.—Cyst of *Staphylocystis glomeridis*. (From Benham.)

off from the periphery of the mass and develop into cysticercoids, which soon become free in the interior of the cyst (Fig. 8). The head, with its hooks and suckers is developed from the central portion of the solid body, the middle layers form the 'body' and the outermost, the caudal vesicle" (Haswell and Hill, 1894).

b. Staphylocystis. In the species *Staphylocystis glomeridis* Villot another type of asexual reproduction is to be met with. Here by the successive branching and external proliferation of secondary cysticercoids a complex organism is produced (Fig. 9). This type of external gemmation differs from that in Polycercus described above in that there is no external cyst wall in Staphylocystis, but as the cyst in Polycercus is considered by Haswell and Hill to be only an adventitious investment, the two may be considered to be nearly related.

c. Sparganum. In *Sparganum* (*Pleurocercus*) *proliferum* Ijima (1905), found in the skin of a Japanese woman, there is a definite

kind of budding from the external surface of the larval bothriocephalid. In this case buds are given off from the parent stock in a more or less irregular manner (Fig. 10). The buds are direct outgrowths from the body of the larvae and later on they become detached. As many as seven larvae were found in the same cyst and were considered to be the detached buds.

d. Urocystidium. Beddard (1912), in examining parasites from *Fiber zibethicus,* found two tapeworms. These were considered by him to be the sexual and asexual phases of a new tapeworm. He

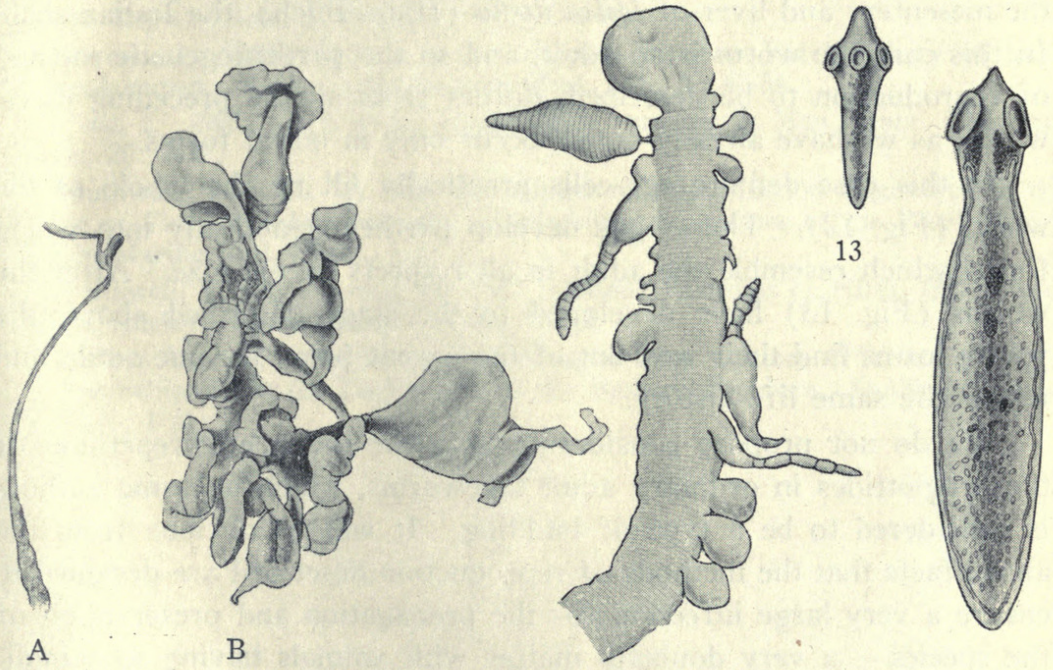

Fig. 10.—(*a*) A single individual of *Sparganum proliferum.* (After Ijima.) (*b*) A budding individual of *Sparganum proliferum.* (After Stiles.)

Fig. 11.—Asexual budding individual of *Urocystidium gemmiparum.* (After Beddard.)

Fig. 12.—An adult specimen of *Ilishia parthenogenetica* removed from the cyst. (Original.)

Fig. 13.—A young specimen of *Ilishia parthenogenetica* from the mesentery of Hilsa fish. (Original.)

regarded them as the type of a new genus which he named Urocystidium, the asexual form of which like Sparganum just referred to, buds off laterally and irregularly a series of young forms resembling the parent asexual form (Fig. 11). Beddard, however, considered his form differed from Ijima's type in that the buds were segmented. This does not appear to be an important difference, because Beddard's asexual worm is also segmented, whilst Ijima's *Sparganum proliferum* is unsegmented, and also the buds arising therefrom.

The above three types of external proliferation seem to be quite distinct from the various other types described in which buds arise from the inner walls of a cysticercoid.

TYPE D.—WITH PARTHENOGENETIC REPRODUCTION

We may now consider a method of parthenogenetic reproduction, which, as far as we are aware, is unique amongst the Cestoda and is only paralleled by what occurs in certain larval trematodes.

Ilishia parthenogenetica Southwell and Prashad, 1917.

This curious parasite was found in Bengal, India, heavily infecting the mesentery and liver of *Hilsa ilisha* (Ham. Buch), the Indian shad. In this case the worm is an adult, and so the parthenogenetic method of reproduction to be described, differs from all the preceding cases, which, as we have already noted, occur only in larval forms.

In this case definite egg-cells practically fill up the whole of the worm (Fig. 12). These eggs develop parthenogenetically into young forms which resemble the adult in all respects except size. After the worms (Fig. 13) have developed to the stage described above, the young forms find their way out of the parent form, become adult, and repeat the same life-history.

We do not propose considering here the metameric repetition of the proglottides in ordinary adult tapeworms, which by some authors is considered to be a type of budding. It will be obvious from the above facts that the methods of reproduction described are designed to ensure a very large infection for the propagation and preservation of the species — a very doubtful matter with animals having so complicated and uncertain a life-history as the forms described above. We are also of opinion that, up till now, too much attention has been paid to recording and describing new species of tapeworms, whilst in the vast majority of cases the life-histories have been utterly neglected. We are aware of the difficulty attending the elucidation of these life-histories, but it appears to us that labor in this direction would not go unrewarded and in all probability would result in the discovery of still other forms of reproduction and give results worthy of the labor and time. The field is wide and unexplored.

SUMMARY

In the above account we have discussed the followed methods of asexual and parthenogenetic reproduction amongst the Cestodes.

(1). Internal proliferation from the wall of the cysticercoid, as seen in Polycercus, Coenurus and others.

(2). Endogenous budding, as seen in Willey's Merocercus.

(3). External budding, as exemplified in Haswell and Hill's species of Polycercus, Staphylocystis, etc.

(4). Parthenogenetic reproduction in *Ilishia parthenogenetica,* an adult tapeworm of doubtful affinities.

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