THE MORPHOLOGY AND LIFE CYCLE OF THE TREMATODE, APATEMON INTERMEDIUS, FROM THE BLACK SWAN

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SUMMARY

1. The anatomy of the trematode, *Apatemon intermedius* (S. J. Johnston) from the duodenum of the black swan, is described.
2. Hatching time of the eggs is about 33 days in early summer.
3. *Cercaria lessoni*, from the pulmonate molluscs *Lymnaea lessoni*, *Simlimnea subaquatilis*, and *Planorbis isingi*, is its larva. Cercariae may be produced within 35 days of invasion by the miracidium.
4. The second intermediate hosts are freshwater leeches, *Glossiphonia* spp., in whose blood vascular system the encysted tetracotyle occurs.
5. 23-day-old metacercariae are compared with those of *Cercaria burti* Miller 1923 (Stunkard, Willey and Rabinowitz 1941). In *A. intermedius* they are encysted at this stage.
6. Juvenile stages found in the black swan are described.
7. Two strains of *A. intermedius*, infecting respectively *Planorbis isingi* and *Lymnaea lessoni*, are postulated.
8. In view of the wide separation between the reported types of snail host for *A gracilis*, *viz.*, *Bithynia* (Szidat) and pulmonates (Stunkard et al.) in Europe and North America respectively, we regard it as likely that two distinct species are involved.

THE ADULT

The Strigeid trematode, *Apatemon intermedius*, was described as *Hemistomum intermedium* by S. J. Johnston (1904, 109-110), whose material came from the duodenum of the black swan, *Chenopis atrata*, Lath., from the Duckmaloi River, New South Wales. Although the author placed the species under *Hemistomum*, he stated that the fusion of the lateral expansions of the body wall in the posterior region of the fore-body, together with the form of the "clinging apparatus," approached the condition occurring in *Holostomum* (*i.e.*, *Strigea* and allied genera). Dubois transferred it to *Apatemon* (1937a, 392; 1937b, 232), gave a summary (1938, 105) of the short original account, and reproduced one of Johnston's figures.

Attempts to trace S. J. Johnston's material in the Technological Museum, Sydney, where he was at the time Economic Zoologist, and in the Zoology Department of the University of Sydney, where he later became Professor, failed to locate it. Though the Australian Museum received types of most of his later species of trematodes, his *H. intermedium* was not included.

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We have found *A. intermedius* in five of eleven black swans taken from the Murray River swamps at Tailem Bend, South Australia, during the summer months between October 1939 and April 1947; and in one collected at Bow Hilll, north of Mannum, in May 1950. The worms were obtained from the duodenum and, on one occasion, from the proventriculus. Usually only a few were present in infected birds, but on one occasion, in October 1947, abundant very young stages, with adults, were obtained from the duodenum.

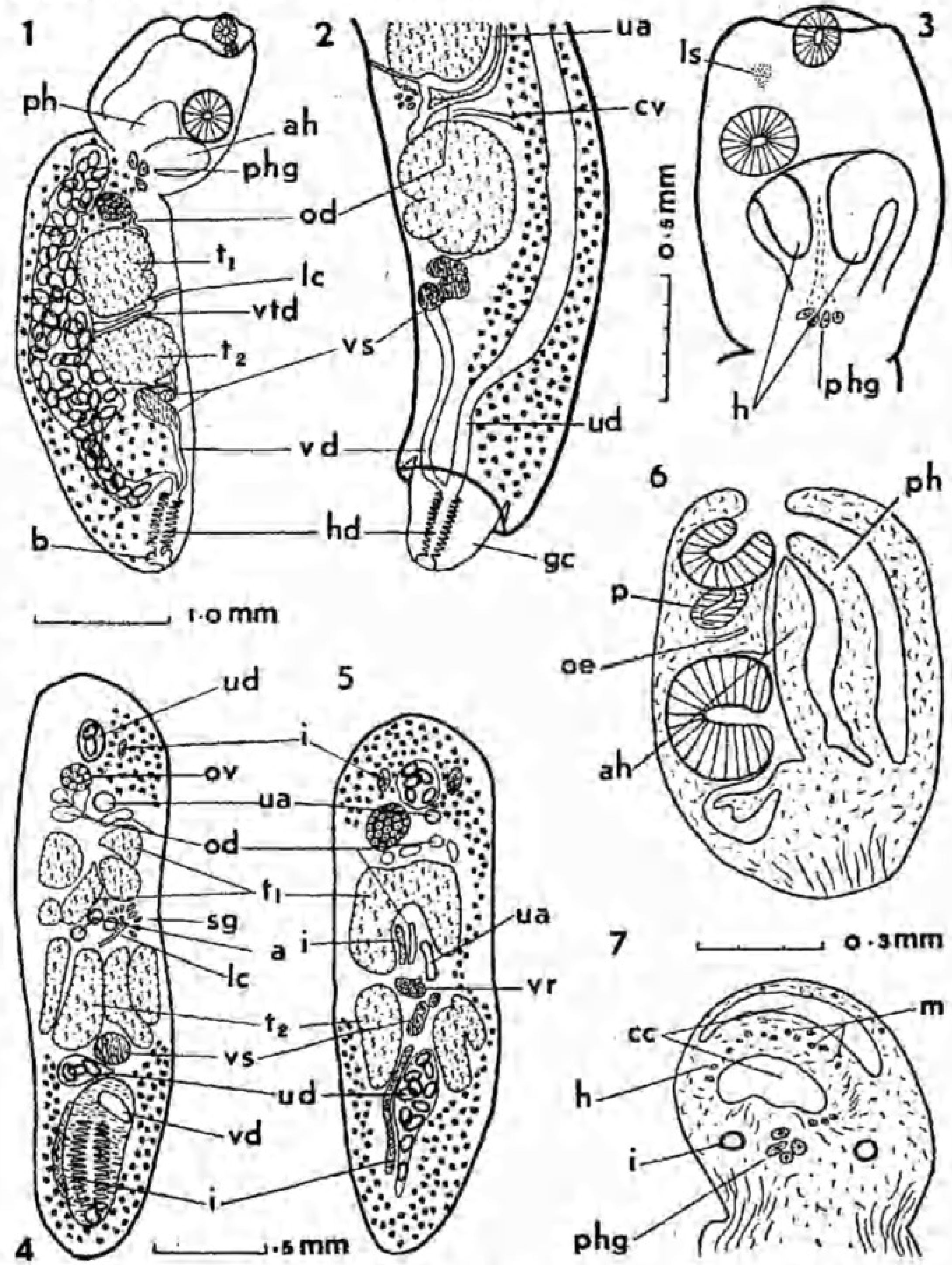

Fig. 1-7

Apatemon intermedius, adult: 1, lateral view; the vitellaria covering the testes laterally have been omitted. 2, posterior region, ventral, bursa everted. 3, fore-body, ventral. 4, 5, L.H.S. hind-body; fig. 5 represents a section more ventral than that shown in fig. 4. 6, L.V.S., fore-body. 7, oblique L.V.S., showing base of fore-body. Fig. 2 and 3 to same scale; 4 and 5; 6 and 7.

Since most adult specimens have the fore-body more or less bent back on the dorsal region of the hind-body, the neck occupies an oblique position and the dorsal and ventral surfaces of the hind-body are of unequal length. In such cases, whether adult or juvenile, the length of the fore-body has been taken as the distance between its anterior end and the middle of the neck, just behind the prominent group of glands lying behind the holdfast apparatus. The length of the hind-body is the distance between the above-mentioned point in the neck and the posterior end of the worm (with its bursa retracted). The total length of the trematode is the sum of the two measurements. All specimens were measured in glycerine or in cedar wood oil, and without coverglass or pressure, unless otherwise stated.

The fore-body was usually strongly bent back towards the dorsal part of the hind-body. Egg-bearing worms were from 3·5 to 5 mm. in length, the fore-body being 1 to 1·5 mm. long, ·9 to 1·25 mm. in maximum diameter, approximately circular in transverse section, and with its sides not quite parallel. There is a definite neck constriction. The hind-body is subcylindrical, narrowing somewhat towards each end, and its ventral surface tends to form a low arch. The posterior extremity is directed slightly dorsally and is broadly rounded when the genital papilla is withdrawn within the bursa.

The maximum widths of the fore- and hind-body are usually about the same, but there is some variation in this respect. The hind-body varied from 2·5 to 3 mm. in length and ·75 to 1·5 mm. (usually 1 – 1·25 mm.) in maximum breadth. The ratio of the length of the fore- and hind-body was about 1 : 2·2 – 2·5. The smallest egg-bearing worm, the dimensions of which have not been included in the foregoing measurements, was only 2·75 mm. in length, with a fore-body 1·0 mm. long and ·9 mm. wide, and with a narrow hind-body 1·75 mm. long and ·8 mm. in maximum breadth: the ratio of fore- to hind-body is thus 1 : 1·75. S. J. Johnston reported the following lengths:— entire worm 3·6, fore-body 0·67, and hind-body 2·93 mm., the ratio thus being about 1 : 4·4; but if we apply our method of measurement to his figure 7 (which is × 37), the total length of the specimen figured would be about 2·7 mm., that of its fore-body ·76 mm., and that of its hind-body 1·94 mm., giving a ratio of 1 : 2·5 as in our adult material.

The genital papilla, when fully protruded, is a large cone with a rounded tip, this cone measuring ·3 to ·5 mm. in length, thus being about one-tenth the total length of the worm.

The oral sucker, ·15 – ·22 mm. in diameter, is subterminal; the ventral sucker is larger, ·3 – ·33 mm. in diameter, and sometimes is stalked. The latter, when not stalked, reaches almost to the dorsal surface. The relative positions of the two suckers is indicated in the figures. The sucker ratio varies from 1 : 2 to 2 : 3. Lying laterally in the region between the two suckers, and on a level with the oesophagus and part of the pharynx, are the lateral suckers. When studied in serial sections each is seen to be an extensive wide depression lined by muscle fibres which pass to other parts of the fore-body. Unlike true suckers, they do not possess a definite basement membrane so that their inner boundary is not sharply delimited. They are obviously the persistent lateral depressions of the tetracotyle. S. J. Johnston referred to (and figured) two groups of very large unicellular glands, each group opening into a crescentic depression of the ventral body surface. We have not been able to recognise such gland cells in our material.

The cup within the fore-body is very extensive, its anterior border reaching usually almost to the posterior end of the anterior sucker. S. J. Johnston seems to have missed its anterior margin, judging from his remarks and his figure 8; but his figure 7 indicates the condition more nearly, though we have not often seen such a markedly petiolate acetabulum as he indicated in fig. 7. Projecting from the base of the cavity behind the ventral sucker, are two large complexly folded "clinging plugs" or tribocytic organs. The more posterior may be the longer, and may project slightly through the mouth of the cup. Both organs may have their margins infolded or even rolled back on their more basal portions. The anterior of these organs is grooved longi-

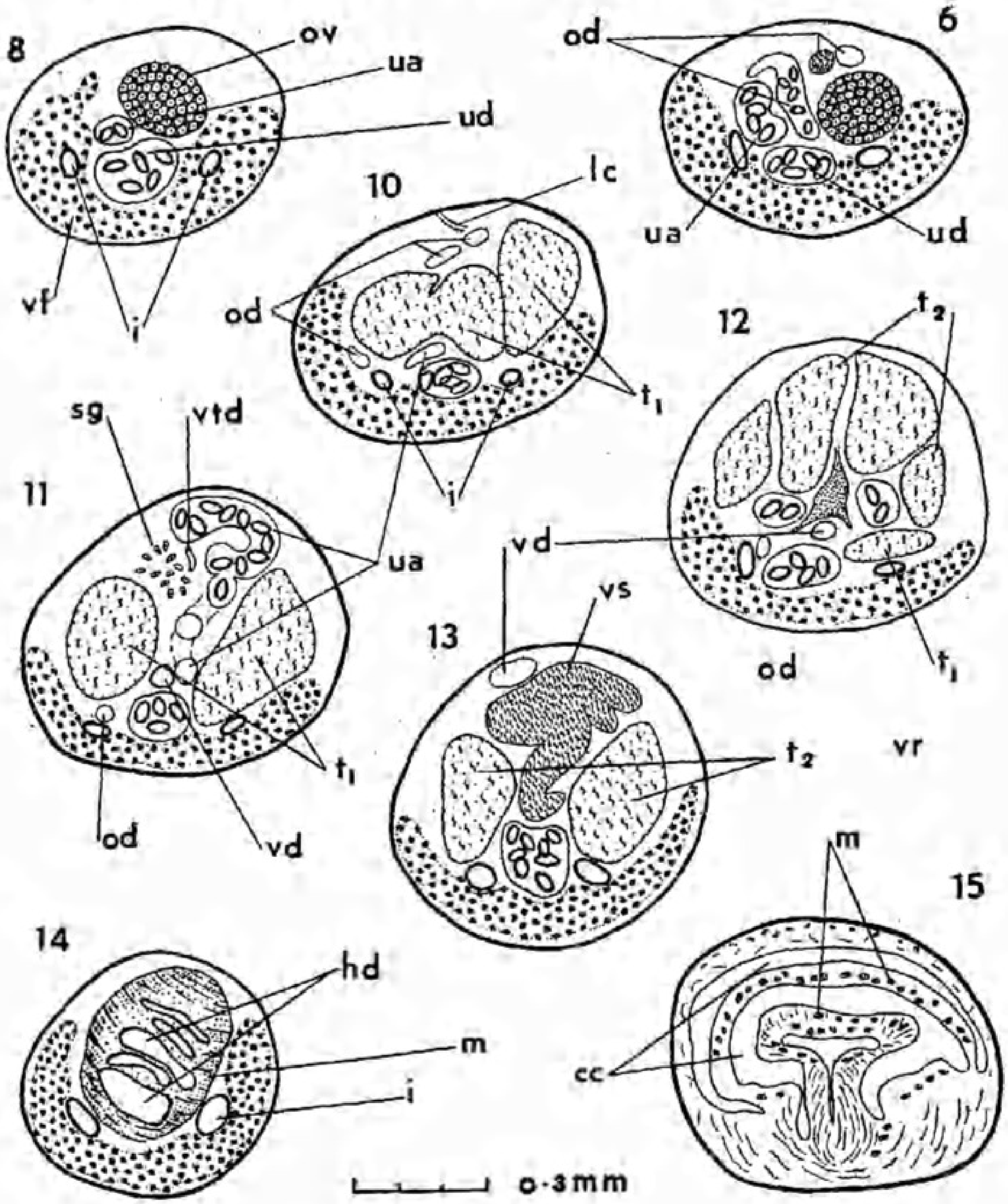

Fig. 8-15

Apatemon intermedius, T.S. hind-body of adult: 8, at level of ovary, showing caeca surrounded by vitellaria; ascending uterus about to join descending limb. 9, at level of ovary and coils of oviduct. 10, at level of anterior testis; Laurer's canal; oviduct passing upwards laterally from testis to occupy dorsal position. 11, at level of posterior part of anterior testis; ascending uterine coils moving into more ventral position between testicular lobes. 12, at level of posterior testis, showing its marked lobulation; two vitelline ducts, reservoir and common vitelline duct. 13, at level of posterior part of second testis; vesicula seminalis lying dorsally between testicular lobes. 14, through hind-body in region of hermaphrodite duct and retracted bursa. 15, through posterior region of head, showing bases of holdfast organs.

tudinally and transversely when withdrawn, and its stalk appears to have a glandular base and core. The musculature of these organs is strongly developed, the bundles of fibres being large, numerous and deeply staining. Behind these organs is a very striking group of large unicellular glands. spherical or pyriform, but the actual openings into the base of the cup were not recognized. The cytoplasm of the glands contained numerous small vacuoles which may perhaps represent the position of secretory granules in the living cells. S. J. Johnston did not mention these organs which, in unstained worms, appear as a small group of large highly refracting bodies between the base of the tribocytic apparatus and the neck of the worm. Dubois (1938, fig. 45 - 46), as well as Stunkard, Willey and Rabinowitz (1941, pl. 1, fig. 6) indicated the presence of similar structures in *Apatemon gracilis*. The hind portion of the fore-body is well supplied with longitudinal muscle fibres, which extend from the walls of the cup and from the base of the tribocytic apparatus into the body wall of the hind-body.

The oral sucker faces almost ventrally. It is succeeded by a pharynx ·08 – ·13 mm. long by ·05 – ·07 mm. wide, which is directed postero-dorsally. There is no prepharynx. The oesophagus bends ventrally in the region in front of the acetabulum, where it divides into the two crura which pass back, one on either side of the acetabulum, the two tubes approximating as they pass through the neck. In the hind-body they lie in the ventral region, below the testes and on either side of the descending uterus. In the most anterior part of the hind-body, just behind the neck, and even in part of the ovarian region, they are actually surrounded by the inner vitelline follicles, but elsewhere they lie just dorsally from the neighbouring yolk glands. The crura terminate near the posterior end of the worm and lie beside the retracted genital papilla.

The testes are large and are arranged in tandem. They are very deeply lobed, and in longitudinal and transverse sections may each appear to consist of four or five separate organs. The testes lie dorsally to the vitelline region, the caeca and the descending uterus, but ventrally to part of the ascending uterus and the shell glands. The anterior testis is about ·7 mm. long and ·6 mm. in dorsoventral diameter; the posterior testis, ·5 by ·6 mm. The testicular region occupies about 1·2 mm. in length in a worm 4·3 mm. long with a hind-body 3 mm. in length. This zone is about one quarter of the total length of the worm. The anterior margin of the anterior testis is distant from the neck about one-sixth the length of the hind-body, while the posterior end of the hind testis is distant from the end of the worm (with retracted bursa) nearly one half the length of the hind-body. The anterior vas efferens arises ventrally and travels back above the descending uterus to join the posterior vas efferens immediately behind the second testis. Here it forms the voluminous, twisted vesicula seminalis which occupies a dorsal zone behind the testes and above the uterus. Eventually it becomes the vas deferens which is joined by the uterus from below, and the wide strongly folded hermaphrodite duct so formed enters the tissues of the genital cone. The latter when retracted lies within the bursa copulatrix whose wide aperture is slightly dorsally directed. As in other species of *Apatemon* there is no well-marked bursal sphincter. The cone when fully protruded may measure ·3 to ·5 mm. in length.

The spherical ovary is about ·2 mm. in diameter and is situated on one side at about the mid-dorsoventral level, close behind the neck constriction. Its posterior border may touch the anterior testis. Between the latter organ and the ovary, and occupying a region on the anti-ovarian side, is the wide oviduct. The latter arises from the ovary just above the uterus, and then makes its way dorsally to become arranged in a number of coils in the posterior ovarian region, and especially in the region immediately in front of the anterior testis, some of the coils lying above portions of the latter. It then comes to occupy a more ventro-lateral position, below the anterior testis and on one side of the descending uterus. From here it makes its way dorsally just laterally from the end of the anterior testis, and in the narrow intertesticular region, it enters the shell gland and unites with the common yolk duct. From this point arises the narrow Laurer's canal which passes dorsally in a curved course to reach the surface above the posterior part of the anterior testis. The ascending uterus becomes thrown into a number of loops between the lobes of the anterior testis, and makes its way ventrally and forwards so as to lie just above the descending uterus and partly amonst the loops of the oviduct. Inwardly and ventrally from the ovary, the two parts of the uterus lie side by side, the descending limb being the more ventral, and in the region between the ovary and the anterior extremity of the hind-body, the ascending uterus bends down to continue back as the descending uterus. The latter occupies a median position below the testes and seminal vesicle and between the intestinal crura, but above the neighbouring vitelline glands. It eventually enters the hermaphrodite duct midventrally, while the vas deferens enters it dorsally and laterally. The hermaphrodite duct, when the bursa is withdrawn, is strongly contracted, its walls being thrown into a great number of closely arranged folds surrounded by loose tissue and muscle fibres, the whole organ terminating at the genital cone.

The yolk glands are very extensive and occupy a ventral and ventro-lateral zone extending from the neck to the posterior end of the hind-body. At either end of the latter the follicles tend to extend rather more towards the dorsal surface than they do elsewhere. As already mentioned, the vitellaria surround the crura in the pre-ovarian region. The two short main yolk ducts pass inwards and upwards in the intertesticular zone, the uterus lying between them. The two ducts soon join to form a small, more or less triangular, yolk receptacle from which there issues directly dorsally the tubular common yolk duct. The latter joins the widened oviduct near the dorsal surface. The shell glands lie between the posterior lobes of the anterior testis. Laurer's canal has already been mentioned.

An examination of S. J. Johnston's figure (pl. 5, fig. 7) indicates that the fore-body has been cut nearly sagitally, and the hind-body mainly longitudinally and horizontally. As the figure shows the two crura cut longitudinally, we would expect to see a mass of yolk glands on both sides of the posterior end of the hind-body, because of the relation of the crura to the vitelline region.

Eggs are ·072 to ·09 by ·062 - ·065 mm., showing very little variation in form and size, most of them being ·087 by ·062 - ·065 mm. They were not mentioned by S. J. Johnston.

A. intermedius seems to be nearest to *A. gracilis* (Rud.) Szidat, as figured by Dubois (1938, fig. 45-46), but is differentiated from it by having a larger size; a more forward position of the testicular region, the ovary, and the anterior end of the uterus; a much longer hermaphrodite duct; a relatively longer genital cone; and by the different sizes of the eggs. *A. gracilis* occurs in Europe as an adult in ducks; as a cercaria in *Bithynia tentaculata*, and as a tetracotyle in freshwater leeches, *Herpobdella* and *Haemopis* (Szidat 1931, 160-172; 1929, 728-730; Neveu-Lemaire 1936, 248).

Szidat (1931) reported that the larva of *A. gracilis* closely resembled, but was specifically distinct from, *Cercaria burti* Miller, and gave tabulated measurements of the two larvae (p. 165). The North American hosts of *C. burti* were *Planorbis trivolvis* (Miller 1926, 41-44), *Lymnaea stagnalis* (Miller 1927, 77), and *Lymnaea humilis* (Cort and Brooks 1928, 209-210). Willey and Rabinowitz

(1938) stated that *C. burti* had its metacercarial stage in leeches (*Herpobdella* sp.) and tentatively assigned the adult (obtained from ducks after experimental feeding of cysts) to *Apatemon sphaerocephalus*. Olivier (1940) listed *C. burti* as the larva of *A. globiceps*, giving as reference Willey and Rabinowitz's paper of 1938; but in 1941, with Cort and Brackett (Cort, Olivier and Brackett 1941, 440) he listed *C. burti* as the larva of *A. sphaerocephalus*. *A. globiceps* was a renaming by Dubois (1937, 392; 1938, 100) of *A. sphaerocephalus* (Brandes) Szidat, nec Westrumb, the latter's species being a *Strigea*. Stunkard, Willey and Rabinowitz (1941) regarded *C. burti* as the larva of *A. gracilis*, with *C. pseudoburti* Rankin 1939 as a synonym.

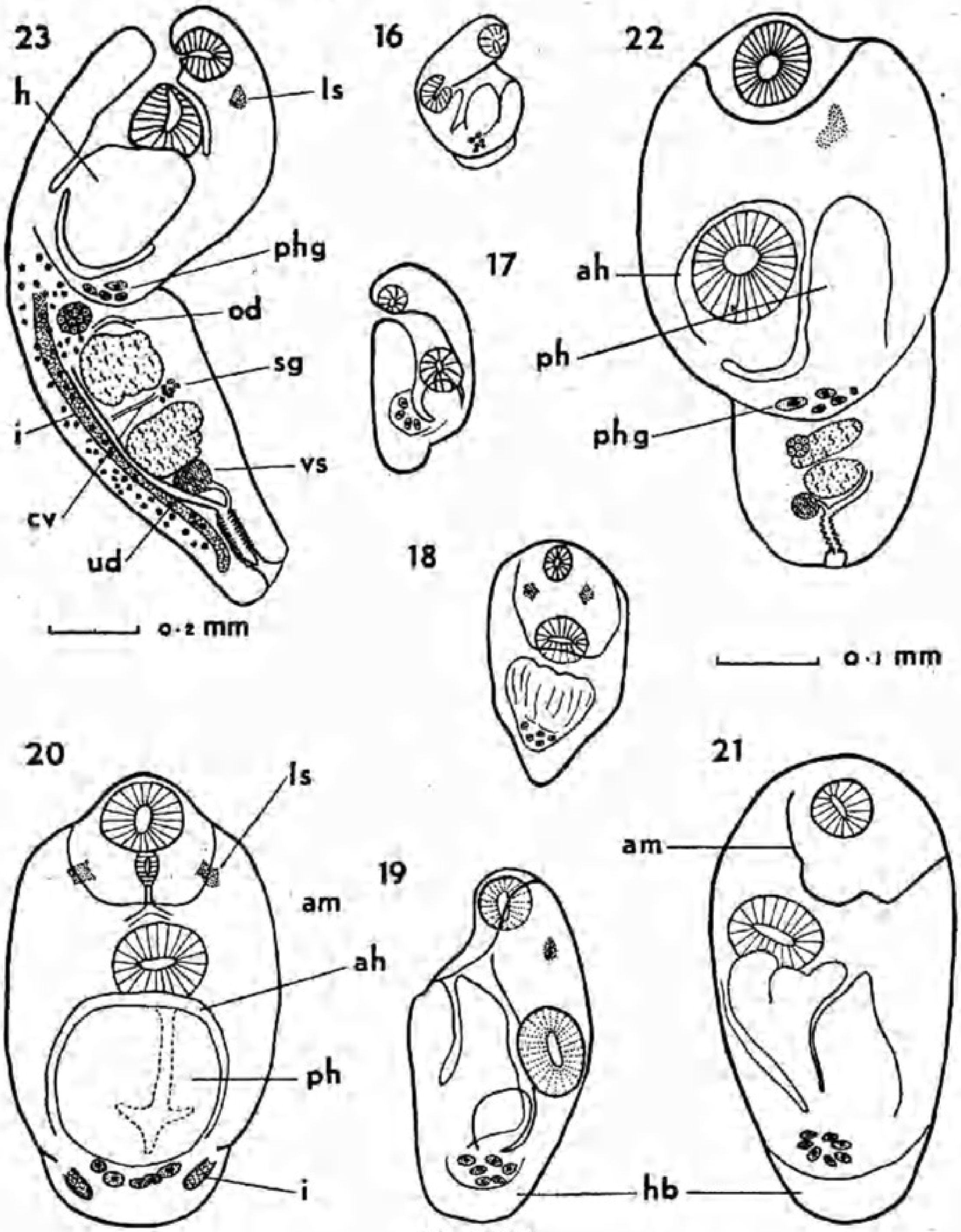

Fig. 16-23

Apatemon intermedius, young stages showing development of holdfasts and cup. 22 shows developing genitalia. 23 shows developing vitellaria.
Fig. 16-22 Drawn to same scale.

It seems to us so surprising that a furcocercaria should make use of two such widely separated types of mollusc as operculate (*Bithynia*) and pulmonate (*Lymnaea* and *Planorbis*) gastropods, that we are of the opinion that Szidat, on the one hand, and Stunkard, Willey and Rabinowitz on the other, were working with different species of the genus. The latter authors gave their reasons in a discussion in which they mentioned differences in the adults as recorded by themselves and by Dubois, as well as differences in the life histories, such as the host snails chosen by the American and European forms, and the differences in time taken for the development of the tetracotyle, although they suggested a possible explanation of the latter.

Larval Stages in Gastropods

In 1947, Johnston and Beckwith gave an account of *Cercaria lessoni*, an *Apatemon* cercaria from *Planorbis isingi*, *Lymnaea lessoni* and *Simlimnea subaquatilis*, and mentioned that *Apatemon intermedius* had been described from the black swan, a common inhabitant of the Murray swamps. It has now been shown experimentally that *Cercaria lessoni* is the larval form of *Apatemon intermedius*.

On 10 May 1947 Miss Beckwith, our former colleague, placed a number of *Lymnaea lessoni* and *Planorbis isingi* in contact with eggs of *Echinoparyphium ellisi* (Johnston and Angel 1949) and of *Apatemon intermedius*. Of eleven laboratory-bred Lymnaeae none became infected with *Apatemon intermedius*, but seven were infected with *Cercaria Echinoparyphii-ellisi*. The twelve Planorbis used were not laboratory raised, but had not been observed giving off cercariae since they had been brought to the laboratory from the Tailem Bend swamps, and were thus classed as "apparently uninfected." On dissection later four were negative, two were found to harbour other infections, while six contained sporocysts which were thought to be probably those of *Cercaria lessoni*, and which in one case contained immature cercariae of this species when dissected 110 days after exposure to the eggs. The present authors repeated this experiment in the summer months two and a half years later. On 29 October 1947 eggs from the duodenal contents of a black swan (which contained adult *Echinoparyphium ellisi* and *Apatemon intermedius*) were put in a small aquarium (A) with laboratory raised *Lymnaea lessoni* and *Planorbis isingi*. A number of the eggs were kept in a small dish and were examined daily. On 1 December 1947 the *Apatemon* eggs began to hatch, and the snails from (A) were removed to an uninfected tank (B); at various times from 21 days afterwards three Lymnaeae died, and proved on dissection to be uninfected; a fourth gave cercariae of *E. ellisi* 79 days after the snails were exposed to the eggs. Of four Planorbis, two were uninfected and two produced *Cercaria lessoni* when first tested 36 days after the miracidia had hatched. On the day when miracidia first appeared, eight Lymnaeae were put in the infected tank A; and on the following day six Lymnaeae were added. Four of the fourteen were disintegrated when found, but the remaining ten which died from 19 to 86 days afterwards, were not infected. However, six Planorbis were added to tank A on the second day, and 35 days afterwards, when they were first isolated, two of them gave off *Cercaria lessoni*; a week later a third produced cercariae. Of the remainder, two were uninfected and one was disintegrated when found 41 days after the exposure.

On the same date as that on which eggs were collected from the duodenal contents of the swan, a number of adult *Apatemon intermedius* were put in water in a small dish, and the eggs which they emitted were placed in a tank with six Lymnaeae and six Planorbis. None of the former became infected, and unfortunately only one of the Planorbis survived, to give a negative result on dissection.

Without this last experiment one might have supposed that the failure of the Lymnaeae to become infected experimentally with *Apatemon* was due perhaps to an immunity conferred by a previous infection with *Echinoparyphium ellisi*, the eggs of which hatched before those of *Apatemon intermedius*. However, in the previously mentioned experiments, a number of Lymnaeae which escaped infection with *Echinoparyphium ellisi*, also escaped a later infection with *Apatemon intermedius*, and in the last-mentioned experiment, when there was no contamination of the tank with eggs of *Echinoparyphium ellisi*, six Lymnaeae resisted infection with *Apatemon*. It must be concluded, therefore, that *Cercaria lessoni*, as described from *Planorbis isingi*, *Lymnaea lessoni* and *Simlimnea subaquatilis* exists in at least two strains, and that the strain which infects *Planorbis* does not readily infect *Lymnaea*. *Simlimnea subaquatilis* was not used in the experiments, as this snail is not often found, and we have not yet reared it under laboratory conditions.

Cort, McMullen and Brackett (1937), and Cort, Olivier and McMullen (1941) dealt at some length with the problem of multiple infestations of snails by cercariae. In 1937 Cort and his fellow-workers, in a historical survey of multiple infestations, showed that records of double infections of echinostome cercariae with other forms were comparatively uncommon. From their own observations with *Stagnicola emarginata angulata*, they thought it probable that some immunity or antagonism existed between cercariae of *Echinostomum revolutum* and some other species of cercariae (not of echinostomes), since they never appeared in double infections. In 1941 Cort et al., working with cercarial infections of *Physa parkeri*, suggested that some such condition prevented double infections of the cercaria of *Echinoparyphium recurvatum* with the schistosome, *C. physellae* Talbot 1936, and the strigeid, *C. physae* Cort and Brooks 1928, since each of the combinations, according to chance, should have occurred much more often than it actually did.

From December 1937 to September 1950 we have identified only six double infections in 7,087 *Lymnaea lessoni* examined. Three of these involved echinostomes, one of which was coupled with *Cercaria lessoni;* a fourth coupled the latter form with *C. Plagiorchis-jaenschi* Johnston and Angel 1950.

From May 1946 (the last date for which percentage infections of *C. lessoni* were recorded by Johnston and Beckwith) to September 1950, *C. lessoni* has been identified in 57 of 1,991 *Planorbis isingi*, this total comprising 38 of 1,380 from Tailem Bend, none of 417 from Wood's Flat, and 19 of 194 from Bow Hill. No *Lymnaea lessoni* have been found in the Tailem Bend swamps in this period, but four of 133 from Wood's Flat and one of 1,779 from Bow Hill, making a total of five of 1,912, have been found infected with *Cercaria lessoni*. Combining these figures with those given previously shows that *Cercaria lessoni* has been observed in 106 of 5,845 *Planorbis isingi* (1·8%) and in 117 of 5,648 *Lymnaea lessoni* (2%) from December 1937 to September 1950.

Miracidium

Twenty-two days after they were laid (October-November 1947) some eggs showed eye spots; ten days later motile miracidia were present; by the next day all had hatched. The period required for hatching in late spring was thus about 33 days. The miracidia were examined in serum diluted one-half, which had the effect of immobilizing them for examination, but which slowly killed them. The head end (fig. 26) was more distorted by the serum than was the rest of the body, as the actively swimming miracidium appeared quite sharply pointed. The eye spots are kidney-shaped and very dark. On one side, latero-posteriorly to the eye spot, was a pair of flame cells, with a collecting tube which extended nearly to the posterior end, where another flame cell was situated.

Metacercaria

Stunkard, Willey and Rabinowitz (1941) reported of *Cercaria burti* that the larvae grew and developed in the leech and did not encyst until 30 to 42 days, and that none had encysted at 23 days. This is not the case with *Apatemon inter-*

medius, 23-day-old metacercariae of which are enclosed in a thick cyst wall and can only be excysted mechanically with great difficulty. An average of ten such cysts measured 265 by 206 μ, the inner cavity being 205 by 176 μ. Johnston and Beckwith (1947) reported cysts of two sizes from leeches which had been exposed to cercariae 7 and 13 weeks before they were killed. In the smaller cysts (presumably seven weeks old) the cavity measured 205 by 180 μ, while the measurement including the cyst wall, was 295 by 246 μ. From these measurements it would seem that from 23 days to seven weeks of metacercarial development increase in size is in the thickness of the cyst wall. However, the size of the cyst may not necessarily be dependent only on age, as is indicated by a single cyst which was obtained from a leech 23 days after infection, the measurements (338 by 300 μ, with the cavity 270 by 218 μ) being substantially larger than those given for the previous series.

It is perhaps of interest to note that Stunkard et al. were unable to infect with *C. burti* three *Placobdella parasitica* and two *P. rugosa* (belonging to the Rhynchobdellida), whereas *Herpobdella* (Arhynchobdellida) was readily infected; we were not successful in attempts to infect three *Limnobdella australis* (Arhynchobellida) with *C. Apatemon intermedius*, which encysted readily in *Glossiphonia* (Rhynchobdellida). It would seem that *Apatemon* cercariae are not only selective in their choice of leech host, but that the type of leech differs for different species of the genus.

Comparison of fig. 28 with Stunkard's fig. 3 shows that the reserve excretory systems of the two forms as seen at 23 days metacercarial development is substantially the same; we did not observe the terminal vesicles or any calcareous concretions associated with them, but the system was packed with small excretory granules. In our form the median anterior canal as well as the posterior one, joined the transverse canal which lies just posterior to the ventral sucker. Johnston and Beckwith (1947) gave figures showing the commencement of the development of the secondary excretory system in the cercaria.

A series of six 23-day-old metacercariae, stained and mounted, measured from 158 by 113 μ to 225 by 165 μ, the measurements being taken across the greatest width. The metacercariae had attained much the same stage of development as that shown by Stunkard et al. in their fig. 2.

In the original account of *Cercaria lessoni*, the figures of older metacercariae freed from their cysts indicate length about ·33 mm., maximum breadth ·26, fore-body ·25 by ·26, hind-body ·08 by ·13 (at junction with fore-body) for the worm shown in fig. 7 (a ventral view), and ·42 by ·29 for that indicated in fig. 9 (a lateral view).

Juvenile Stages found in the Black Swan

As mentioned earlier, we found numerous juvenile tetracotyliform stages along with adults in the duodenum of a black swan taken at Tailem Bend in October 1947. These young worms were of different sizes and in various stages of development. On three occasions we have found in the stomach of black swans from the same locality *Glossiphonia* leeches, and one of them was heavily infected with the thick-walled cysts of *Apatemon*, distributed in its blood system from the posterior sucker almost to the anterior end. We have found natural infections in two species of *Glossiphonia*, one of them larger, thicker, more leathery and papillose, the other smaller, more slender and semi-transparent, both kinds from Tailem Bend swamps.

The youngest stage found in the swan was a tetracotyle, ·11 by ·10 mm., with the anterior two-thirds more or less spherical and the posterior third broadly rounded; while the cup and holdfast organs were present. Another (fig. 16), with the hind-body merely represented, measured ·15 by ·10 mm., its oral sucker was ·025 by ·03 mm. and the acetabulum ·03 mm. in diameter, and the cup and holdfast organs were well developed. Another was nearly spherical, ·145 by ·145 mm., with the hind-body scarcely recognisable, but it possessed a well developed cup and small holdfast organs. Measurements of other very juvenile worms were ·16 mm. long by ·10, with a very small post-body, with oral sucker ·03 by ·02 mm., and acetabulum ·05 mm. diameter; ·20 by ·10 mm., with well defined post-body (fig. 17) and with suckers ·025 and ·04 mm. diameter respectively; ·24 by ·13 mm., suckers ·03 and ·05 mm. diameter; ·36 by ·17 mm., suckers ·055 and ·08 mm.; ·43 by ·33 mm.; ·47 by ·25 mm., suckers ·06 and ·08 mm. In longer worms the hind-body becomes relatively more pronounced, but is much narrower than the fore-body—total length ·55 mm., forebody ·40 by ·30, hind-body ·15 by ·2, sex organs recognisable, oral sucker ·08 by ·07, acetabulum

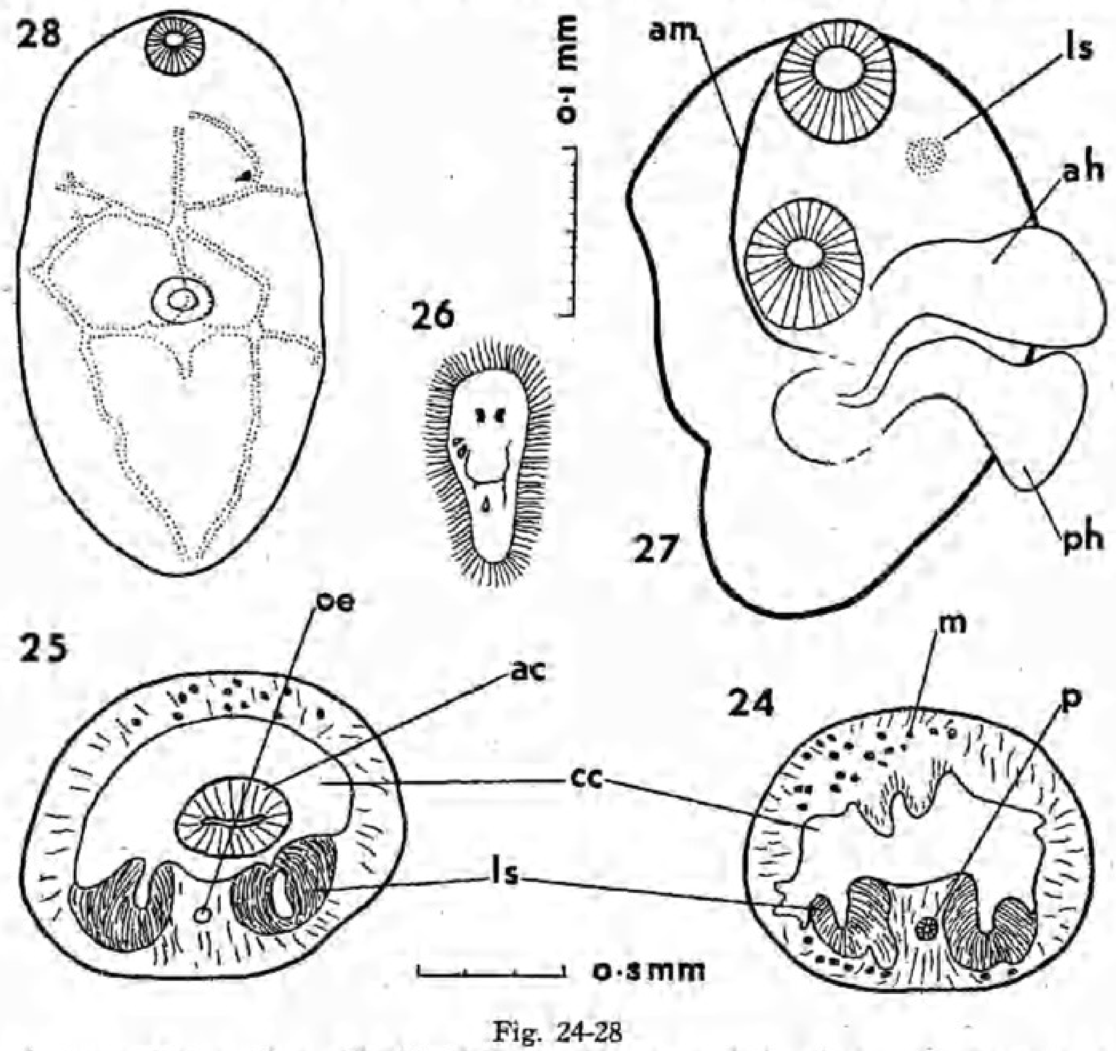

Fig. 24-28

Apatemon intermedius: 24, 25, T.S. anterior part of fore-body, showing lateral suckers; 24 lies in front of acetabulum; 25 shows stalked acetabulum in section. 26, miracidium; 27, metacercaria (tetracotyle) from 23 day-old cyst in *Glossiphonia;* stained preparation showing holdfasts. 28, metacercaria (tetracotyle) from 23 day-old cyst in *Glossiphonia;* drawn from living larva; shows excretory system. Fig. 24-25 to to same scale; 26, 28 sketches; 27, to adjacent scale.

·12 mm. diameter; ·62, fore-body ·47 by ·34, hind-body ·15 by ·25, genital organs recognisable, but closely crowded; ·71, fore-body ·46 by ·38, hind-body ·25 by ·26 mm., with genital organs as in the preceding; 1·0, fore-body, ·55 by ·5, hind-body ·46 by ·27, sex organs as in the preceding two worms. In a specimen, 1·52 mm. long, the fore-body was ·72 by ·52, and the fusiform hind-body ·80 by ·37, oral sucker ·12, acetabulum ·16 mm; vitelline follicles were present as minute scattered groups, and the gonads were no longer crowded, all the organs of the adult stage being readily recognisable (fig. 23). We have already noted that the smallest ovigerous worm was 2·75 mm. long. The youngest specimen of *A. gracilis* obtained by Szidat (1929, 145) from a duck, twenty hours after he had fed it with infected leeches, was (according to his figure 4) ·36 mm. long and about ·26 mm. in maximum width, and the gonads were already distinguishable.

Because of the presumed loss of S. J. Johnston's type material, we have designated one of our specimens as the substitute type and have deposited it, along with others, in the South Australian Museum, Adelaide.

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ac, acetabulum; ah, anterior holdfast organ; am, anterior margin of cup in fore-body; av, anterior vas efferens; b, bursa; cc, cavity of cup in fore-body; cv, common vitelline duct; e, egg; fb, fore-body; gc, genital cone; h, holdfast organ; hb, hind-body; hd, hermaphrodite duct; i, intestine; lc, Laurer's canal; ls, lateral s cker; m, muscle; od, oviduct; oe, oesophagus; os, oral sucker; ov, ovary; p, pharynx; ph, posterior holdfast organ; phg, post-holdfast glands; sg, shell glands; tl, t2, anterior and posterior testes; u, uterus; ua, ascending limb of uterus; ud, descending limb of uterus; vd, vas deferens; vf, vitelline follicles; vr, vitelline reservoir; vs, vesicula seminalis; vtd, vitelline duct.