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1911-14.
UNDER THE LEADERSHIP OF SIR DOUGLAS MAWSON, O.B.E., B.E., D.Sc., F.R.S.

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Edited by Professor T. Harvey Johnston,
University of Adelaide.

VOL. X. PART 1.

TREMATODA

BY
T. HARVEY JOHNSTON, M.A., D.Sc.
PROFESSOR OF ZOOLOGY, UNIVERSITY OF ADELAIDE.

WITH TWENTY-EIGHT FIGURES.

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REPORT ON THE TREMATODA.

By

T. Harvey Johnston, Professor of Zoology, University of Adelaide.

(With twenty-eight figures.)

Only two species of trematodes were collected by the Australian Antarctic Expedition, one from a fish at Macquarie Island, and the other from seals in Antarctica.* The former proved to be an interesting Epibdellid, the condition of the material permitting a detailed examination of the parasite. The other had been collected previously by the "Terra Nova" Expedition and identified as belonging to a species which infests whales in the Arctic and North Atlantic, but a study of its structure showed that it was a distinct, though closely related, form.

The material has been deposited in the Australian Museum, Sydney.

Hosts and Parasites referred to in this Report.

1. *Notothenia macrocephala* Gunther ... *Pseudobenedenia notothenia*e Johnston, Macquarie Island.
2. *Leptonychotes weddelli* Lesson ... *Ogmogaster antarctica* Johnston, Antarctica.

Pseudobenedenia notothenia*e Johnston*, 1931.

(Figs. 1–25.)

A few flat, semitransparent, ectoparasitic, trematodes, resembling an *Epibdella* (sensu lato), were collected from the head and body of a specimen of *Notothenia macrocephala* at Macquarie Island by H. Hamilton in November, 1912. The worms are evidently referred to by Ainsworth (in Mawson, 1915, 235). "They (the fish) were all of the same species, somewhat resembling rock cod, but, as usual, they were covered with external parasites and their flesh was full of worm cysts. Hamilton preserved a number of them . . .". Waite, 1916 (pp. 6, 69, 70), referred to them as gliding over the surface of this species of fish and mentioned that they were similar to those infesting *Notothenia colbecki* at Antipodes Island, and identified by Professor W. B. Benham as *Tristoma* (Waite, 1909, p. 594).

* Owing to the fact that this report, though accepted for printing early in 1929, had been for years awaiting publication, the two species were described briefly in 1931, the extended account of their anatomy being reserved for inclusion in this series.

All of the material had been either sectioned or flattened, stained and mounted as whole preparations by the late Professor S. J. Johnston (to whom the collection had been entrusted originally), so that the dimensions given may require amendment if additional specimens become available for study. The largest worm (compressed and with its disc expanded and lying parallel with the body) measured 7 mm. by 4, and the smallest 4·7 by 2·3. Excluding the posterior disc, the largest worm measured 6 mm. in length, its disc being 2·2 mm. in diameter when fully expanded. A specimen which had not been compressed, but had been sectioned with the posterior sucker in its natural position, possessed a body length of 2·5 mm. and a thickness of 0·4 mm. for the greater part of its median region, but diminishing rather suddenly in front of the mouth to terminate in a thin anterior extremity, while posteriorly, behind the testes, there was a gradual decrease in thickness until, in the immediate vicinity of the disc, there was a marked narrowing to form a very short pedicel ·17 mm. thick, more or less enveloped by the adjacent parts of the disc and posterior end of the body. Its disc was 1·3 mm. long.

Except for the anterolateral projections, the body is more or less broadly elliptical with the greatest width in the midregion at the back of the ovary and anterior part of the testes. In the vicinity of the pedicel the body is more truncate.

There may be a very small median projection anteriorly, while on each side in the vicinity of the anterior suckers there is a well-marked notch indicating the posterior boundary of the anterior glandular area. The mouth is a rather large, crescentic, forwardly-directed aperture immediately in front of the pharynx and near the level of the posterior margins of the anterior suckers. The common genital pore is ventral, on the left, immediately behind the corresponding anterior sucker, and slightly outwardly from its midline. The vagina opens ventrally, also on the left side, at a considerable distance behind the male and uterine pores, but much nearer the midline and a little in front of the midlength of the body (excluding the disc). The excretory pores open dorsally on either side slightly behind the level of the genital aperture and also rather nearer the median line.

The anterior region projects laterally to a slight degree as a pair of rounded lobes which more or less merge into one another at the front of the parasite. When viewed ventrally they are slightly reniform. They contain glands and are homologous with the glandular areas or so-called suckers or sucking discs of *Epibdella* (sensu stricto). In addition to these, there are two well-developed anterior suckers, one on either side of the brain region and lying mainly in front of the level of the pharynx. These measure about 0·8 mm. in diameter in the largest specimen and project freely on the ventral surface. The area of attachment to the body is about 0·25 mm. across. The suckers are seen in section to be about 0·07 mm. in maximum thickness.

The posterior disc is practically circular and bears two slight notches near its extremity in the vicinity of the third pair of hooks. There is a thin marginal membrane about 0·1 to 0·15 mm. wide, and poorly supplied with muscles. Judging from sections, this membranous portion is more or less curved with the concavity facing ventrally, the whole structure being sharply marked off from the muscular region of the organ, which varies in thickness from 0·18 mm. just behind the pedicel to 0·025 mm. at its junction with the membrane. The pedicel is attached well in front of the centre of the organ and is very narrow and circular or elliptical in section.

There are three pairs of hooks, the middle pair of which are the largest, being long and narrow, each terminating posteriorly in a strongly curved hooked part which projects from the disc. The long axes of these hooks and of the third pair are directed towards the corresponding indentation in the muscular and membranous portions of the posterior region of the organ. The third pair are very small and lie just above the terminal part of the large hooks. They consist of a relatively broadened and flattened portion which becomes bent and then rapidly narrows and forms a pronounced hook which lies behind the hook of the second, and, like it, faces anteriorly. This third hook terminates at the posterior border of the muscular region at the head of the notch.

The anterior pair of hooks are much shorter than the middle pair and their free points are anterior, being short, rather bluntly rounded, and only slightly bent. There is a slight flange on each side of the anterior half, apparently for muscle insertion, that on the outer aspect being slightly wider. The dorsal part bears a distinct rounded projection. The axes of these two hooks are inclined so as to point backwards and inwards to meet in the midline at a point behind the midlengths of the second pair, the position varying, probably on account of differences in the degree of compression or contraction of the disc. The lengths of these three pairs, anterior, middle and posterior, in the case of the largest worm are 0·23, 0·53, 0·17 mm. respectively; while in the case of the smallest worm they are 0·19, 0·38 and 0·13 mm. If the middle hook be measured from one extremity to the other, then the length is 0·61 and 0·45 mm. respectively, the bent portions being 0·08 and 0·07 mm. respectively.

Some specimens show clear, rounded, highly refracting bodies, apparently chitinous, on the disc in the vicinity of the first and second pairs of hooks, sometimes near their inner, sometimes near their outer faces. They are not necessarily bilaterally arranged, though there is a marked tendency for them to be disposed in such a way that groups of them show bilaterality. In some cases they are absent. In no instance was there any arrangement resembling that indicated by Beneden and Heath as occurring in *Epibdella hippoglòssi* and *E. squamula* respectively. Goto (1899, 265) referred to the usual presence of a group of irregular chitinous granules on the inner side of the anterior hooks in the former species.

There are six slight ridges on the disc, corresponding somewhat in the positions with the anterolateral, posterior and postero-lateral septa in *Tristoma* (i.ei *Capsala*), the posterior being below the second and third pairs of hooks, while the postero-lateral bends laterally and posteriorly from the region of the anterior hooks. The remaining pair pass laterally and slightly anteriorly from the region near the insertions of the pedicel. They appear in the sections also and are probably largely due to the presence of strong muscles above them. They are not muscular and there is no trace of definite loculi.

The cuticle is very delicate, about 2μ in thickness dorsally where it is produced with a covering of extremely abundant and very fine hairs, about 3μ long and resembling cilia. They occur on the upper surface of the posterior sucker also, but are entirely absent from the anterior suckers. They are not present on the ventral surface, except in the immediate vicinity of the vagina, where they are much thicker and longer, reaching 0·01 mm. They also line the cavity of that organ, maintaining their length, the hairs being directed towards the vaginal opening.

The subcuticular layer is about 0·02 mm. in thickness. The musculature of the body is best developed in the vicinity of the anterior and posterior suckers. The circular fibres are very abundant though small. Below them are diagonal fibres which are most marked toward either end of the parasite. The longitudinal fibres form a well-defined thin layer below these, and tend to become aggregated into very numerous small bundles. They are much more strongly marked ventrally in the vicinity of the pharynx and mouth, immediately in front of which the bundles are relatively large and underlie the brain. In this region the circular fibres are also strongly developed to form a considerably thickened layer just below the enlarged longitudinal bundles.

The dorso-ventral fibres are delicate except in the suckers, where they become thicker and more abundant. Four definite bundles pass through the brain, one on each side, outwardly from the corresponding anterior eye, and also a pair between these eyes, the latter pair extending upwards, a bundle on either side of the excretory canal, which lies above the brain.

It is in the pedicel and the posterior sucker that the muscular system is especially developed. In these the circular fibres are much thicker than in the body, and in the sucker they are seen in whole mounts to be extremely abundant and arranged as wide sheets dorsally and ventrally, parallel with the circumference. Radial fibres are abundant. The longitudinal and diagonal fibres are more powerful and are rather complex in their distribution from the pedicel to the sucker, while there is a marked crossing of fibres to become inserted into the bases of the larger hooks. Strong fibres inserted into the more superficial tissues (investing membrane) on each side become massed into a bundle which passes around the base of the corresponding anterior hook on its posterior aspect, and part then passes forwards and upwards into the pedicel to be distributed among the longitudinal and diagonal muscles of the same side of the body,

while many of the fibres join with those of the opposite side to form a transverse muscle which acts antagonistically to the other fibres. The arrangement is shown in Fig. 3, and is somewhat like that figured by Heath for *Epibdella squamula*. Associated with the anterior and middle hooks are very large cells which Goto (1899) regarded as myoblasts in the case of *Phyllonella hippoglossi*. Heath has referred to their presence in his species. The margin of membrane is provided with weak dorsoventral and circular fibres.

The musculature of the anterior suckers consists of a series of circular fibres on both surfaces, those on the ventral being more marked, also well-developed radial fibres and a large number of strong dorso-ventral fibres which in the area of attachment of the sucker to the body become continuous with those of the body. The body musculature, both longitudinal and diagonal, is well marked in the vicinity.

The anterior glandular area is obviously homologous with the structures which Heath describes as the anterior adhesive organs, and which Monticelli has called "pseudoventose." They appear to have been confused with the typical anterior suckers, which in *P. nototheniæ* are quite distinct from them. These areas lie anteriorly and slightly laterally and are practically continuous in front, though marked off postero-laterally by a definite notch from the margin of the body. The gland cells are very numerous, rather large and pyriform, with a distinct nucleolus, and lie below the dorsal longitudinal musculature of the anterior end of the parasite. Each has a relatively long duct which passes outwards and downwards through the parenchyma, the ducts becoming so closely aggregated near their outlets and their contents so deeply staining, that this portion, when viewed in section, looks like a columnar epithelium. Probably there are many narrow sensory cells lying amongst these ducts, since there is an abundant nerve supply to the ventral region of these glandular areas, more particularly to their inner parts. Heath and Braun also suggest that similar cells in related species may be sensory, and the former author indicates a rich nerve supply to these organs. The openings of these anterior glands are so arranged that the parts containing them lie in front of, and laterally to, the anterior suckers in such a position as to increase greatly the area of contact or attachment at the anterior end of the worm. The midregion anteriorly is free from ducts, though gland cells occur there.

Monticelli (1891) and Goto (1894, 1899) have called attention to similar anterior glands in related trematodes, the latter calling them "anterior sticky glands." Goto's description agrees closely with what has been observed in *P. nototheniæ*, as he stated that such glands opened on the whole ventral surface of the "anterior sucker" of *Epibdella* and that even in *Tristoma* similar cells were present, terminating in the ventral surface of the anterior suckers, as well as on papillæ on such suckers. Monticelli (1908) has shown that the so-called anterior suckers of *Nitzschia* are really "pseudoventose," consisting of groups of gland cells lying in a sucker-like depression on each side, anteriolaterally from the mouth. Groups of cells resembling those just referred to, but not associated with definite ducts like those mentioned in connection with the anterior

glands, are abundant in the parenchyma of the regions behind the testes, and similar cells were recorded and figured by Heath as occurring in *Epibdella squamula* where they communicate with the posterior sucker. Goto (1894) referred to their presence in *Tristoma*, where they are more generally distributed.

Digestive System.

The large crescentic mouth is directed forwards and lies between, and just behind, the posterior borders of the anterior suckers. It is bounded behind by a relatively thin projecting extension of the ventral body wall, like that of *Ep. squamula* in which species, according to Heath, this structure possesses considerable mobility during life and functions as a lip. The buccal cavity is fairly large and crescentic, and into it there projects the prominent pharynx surrounded, except at its free portion, by a sheath. The organ is rather broader than long and in entire mounts and sections its walls usually project into its cavity in such a way as to resemble large lobes. It extends from the ventral almost to the dorsal surface, and anteriorly it approaches closely to the brain, which it may in part underlie. The constituent cells have the same general characters as described for *Ep. squamula*. Those which project into the buccal cavity are few, very large, weakly-staining, spongy, and non-glandular, with rather large nuclei. On their outer surfaces, below their cuticle, is a layer of well-marked circular muscle fibres which, as Heath states, probably assist in protruding this portion of the pharynx through the mouth. On their inner surfaces, lining the lumen of the outer part of the pharyngeal cavity, is a similar layer of circular fibres which would act as a sphincter. Heath does not refer to their presence in *Ep. squamula*.

Just within these cells are many large cells which project to a greater or less extent into the cavity. They possess each a large nucleus with a characteristic nucleolus, the nucleus being variable in position. The cytoplasm stains lightly near the base of the cell but readily elsewhere, thus indicating a change in its contents as its secretion is manufactured. This latter appears as a wide central core which at some distance from the free extremity of the cell becomes less dense and is seen to be disposed as a series of very delicate, more or less parallel, ducts terminating in a definite depression at the top of the projecting portion of the cell, the structure thus closely resembling that described by Heath. The succeeding part of the pharynx is formed by cells somewhat similar to those just described in regard to staining reactions, but they do not project and their cell boundaries are quite indistinct. Externally as well as internally to them are circular muscle fibres, while radial fibres pass between them. The inner circular fibres are much larger than those elsewhere in the pharynx. These latter cells are regarded as being homologous with the pharyngeal glands of other trematodes.

The pharynx narrows to pass into the œsophagus which, though very short, receives the numerous ducts of the pyriform unicellular salivary glands, which stain deeply and occupy a rather dorsal position at the sides of, and posterolaterally from, the

pharynx. They occupy a triangular area, one side being adjacent to the intestinal crus and just anterolateral from the base of the penis sac; another laterally and outwardly from the main ventral nerve; the third one anterolaterally from the œsophagus. The ducts converge to constitute the inner angle of the triangle. They are relatively very long and narrow and soon become closely aggregated, their contents deeply staining with eosin, so that they form conspicuous structures in sections, but when empty they remain practically unstained. These tiny ducts open into a narrow extension of the œsophagus immediately behind the pharynx. The succeeding part of the œsophagus has some circular fibres which act as an œsophageal sphincter.

The intestine is a very conspicuous organ in whole mounts and occupies a considerable part of the animal, its branches partly covering most of the other organs of the body. From the œsophagus there are given off the two crura which soon assume a higher dorsal level. These main branches pass outwardly just behind the pharynx and soon bifurcate each into a short anterior and a long posterior crus, each of these giving off branching diverticula laterally as well as dorso-internally. The anterior crura extend almost to the anterior glands and curve towards each other so as to surround the pharynx and brain, the cæca partly overlying these organs. From each posterior crus a number of large cæca are given off laterally, and these branch more or less dichotomously three or four times to terminate some little distance from the margin of the parasite. The crura very closely invest the outer margins of the testes and, behind these, they curve inwardly and approach each other closely in the posterior part of the body. Though branches perhaps coalesce, their union has not been detected, even in sections, and the main crura remain quite separated at their posterior ends. From the inner and dorsal side of each crus, branching cæca, shorter than the laterals, are given off and come to lie above parts of the reproductive ducts, yolk reservoir, ovary and edges of the testes, while, behind the latter, the inner cæca extend towards into, and above, the septum between the organs, almost meeting branches which are given off from crura in front of the testes and extending backwards above the septum. Behind the testes, the cæca are so numerous, though normally short, as to obscure the other organs lying there. There is a well-marked region just in front of the pedicel free from cæca. The intestinal epithelial cells stain very poorly, excepting their tiny nuclei. Heath mentions that they are amœboid during life. He and Goto (1894) believe that they are zymogenic.

Nervous System.

The following account of this system is based entirely on a study of sections, consequently the finer details have not been investigated, but the results obtained agree closely with those published by Heath for *Ep. squamula*, and by Lang (1881) for *Tristoma molae*.

The brain lies immediately in front of the pharynx and may partly overlie its anterior region so as to be situated just above the buccal cavity. It is a comparatively thick band bearing the two pairs of eyes dorsally. In front of it is a well-defined semicircular commissure which is connected with the brain by three pairs of large nerves, anterior, anterolateral and posterolateral. The brain and this commissure together form a well-marked crescent, from the posterior corners of which the main body nerves arise. Given off anteriorly from the brain, not far from the median line, is a pair of stout nerves which, after connecting with the semicircular commissure, give off a few branches to supply the extreme anterior end of the parasite. Just outwardly from the points of origin of each, a lateral branch originates and joins the commissure. Behind this, near the point of origin of the dorsal and ventral longitudinal nerves, there arises another nerve which joins the posterior end of the commissure and passes to coalesce with the outer ventral cord near its origin. From the commissure and from those nerves which extend beyond it, there are given off branches to the anterior suckers and anterior glands, as well as the tissues in the vicinity. The nerve supply to this anterior region is abundant, all the main nerves as well as the commissure being ventrally situated.

The brain and commissure contain numerous nerve cells, located peripherally in one part of the brain and more centrally in another. Fibres pass from one side to the other in different positions. Decussation was observed in the posterior portion of the organ. Both Lang and Heath have referred to the bilateral arrangement of the nerve cells in *Tristoma* and *Epibdella* respectively, and the same holds good for *P. nototheniae*. The brain merges posteriorly into two large cords beside the anterior part of the pharynx, and from these arise the main longitudinal nerves. The dorsal on each side passes upwards and slightly inwards to travel directly backwards, giving off several nerves practically symmetrically, and mainly laterally. These dorsal nerves are more widely separated than in *Ep. squamula*, or in *Tristoma*. Each is much broader than it is thick and consequently is more readily followed in horizontal than in transverse sections. The posterior terminations of these nerves were not traced, but they were obvious almost to the posterior end of the body, where they possibly enter the posterior sucker. The median dorsal nerve figured by Heath was not recognised.

As in other trematodes each inner ventral nerve is larger than in the outer. It is relatively very thick. It passes over the genital ducts and travels backwardly below the intestinal crus and the excretory canal, skirting the outer border of the corresponding testes closely and then curving inwards slightly to meet a large transverse commissure just behind the ends of the crura. The outer nerve lies about midway between the inner nerve trunk and outer boundary of the intestinal and vitelline fields. It extends almost to the end of the body and is connected in front of the pedicel, with the transverse commissure. The latter, which is not indicated in the figures of Lang or Heath as occurring in the species specially studied by them, is relatively broad. The two main nerves pass beyond it and enter the pedicel to become distributed in the sucker. The two

trunks diverge on entering the disc and give off prominent nerves to the posterior half of the organ. The anterior region of the disc is supplied by nerves from a ring commissure which joins the main nerves just as they emerge from the pedicel. The arrangement of the various nerves of the disc is indicated in fig. 11. Heath figures a narrow commissure just in front of the bases of the anterior hooks, but none was observed in that situation in *P. nototheniae*, though a nerve is given off inwardly from each trunk, but there is no obvious anastomosis.

At intervals along the course of these ventral cords there are relatively thick, connecting nerves, almost symmetrically arranged. They are especially evident between the inner and outer trunks and between the inner trunks immediately behind the testes. Well-defined nerves are given off laterally from the outer cords and these branch to become distributed to the lateral parts of the body. There are also large nerves given off to the ovary, uterus and penis sac. The commissural nerves are relatively larger and fewer than Heath indicates for *Ep. squamula*. A pair of nerves are given off from the brain to supply the walls of the pharynx, as in that species. From the posterior commissure there extend forwards a pair of large ventral nerves which join the branches immediately behind the testes. Ganglion cells occur here and there along the course of the ventral nerve cords, especially near the pharynx. Large multipolar nerve cells are present in the disc and occur here and there in the subcuticular tissues of the body (fig. 14). The main nerves present an appearance in section like that figured by Taschenberg (1879) for *Tristoma papillosum*. Judging from the remarks of the last-named author, the same general plan of nervous system occurs in *Ep. hippoglossi* and *Tristoma* spp.

The two pairs of eyes lie within the dorsal portion of the brain, the anterior pair being closer to each other than the members of the posterior pair. Each organ contains a clear spherical lens on the upper surface of which is a single layer of rounded brownish yellow pigment granules. Associated with the lens is a nerve cell with at least two rather large nerve fibres arising from it, one passing inwards and downwards into the substance of the brain. The pigmented part of the anterior eyes is directed inwards and forwards, while that of the posterior pair faces backwardly and slightly outwards.

Excretory System.

The excretory network in the parenchyma eventually connects with the main excretory canals, anterior or posterior, of each side. These ducts may vary considerably in regard to their lumen as seen in sections in different parts of the worm, but the posterior are much larger than the anterior. The former travel in very close association with the inner ventral nerve trunks, lying immediately above and usually slightly outwardly from them, but slightly ventro-laterally from the corresponding intestinal canal. Each passes back as a rather narrow tube from the posterior end of the long and spacious excretory vesicle of that side, and after giving off a wide canal which travels above the ovary or the vitelline reservoir, proceeds posteriorly very close to the ventro-

lateral edge of the testes, immediately behind which another wide tube is given off to the tissues just behind the testes. The main canal then bends gradually towards the median line and enters the peduncle close to its fellow of the opposite side, inwardly from the main nerves, and in company with these the two canals curve round in opposite directions close to the outer side of the base of the large hooks and give off branches which ramify in the tissues of the sucker.

Each anterior trunk is much shorter than the posterior and joins the excretory vesicle just behind the sex ducts. At this point it is very narrow and is closely associated with the corresponding inner ventral nerve, being situated just laterally to it. The duct curves inwardly in conformity with the course of the intestine, becoming somewhat widened. It crosses the nerve and comes to lie between it and the pharynx. It then assumes a more dorsal course as it passes forwards above the large nerve trunk beside the pharynx, and eventually joins its fellow from the opposite side in front of the pharynx, between the two pairs of eyes, where it appears as a wide tube dorso-posterior to the brain. It gives off a few canals, which pass between the brain fibres, and travels forwards to become distributed to the anterior region of the worm. A branch is given off from each anterior trunk to supply the region of the sex ducts.

Several lateral canals are given off from the outer side of the main trunks, but these seem to be much fewer than Heath indicates as occurring in *Ep. squamula*.

The excretory vesicle is relatively large, lying above the inner ventral nerve and just laterally and ventrally from the intestine. It extends from the vicinity of the testes almost to the level of the posterior border of the pharynx, where it turns outwardly for a short distance, then travels dorsally and anteriorly, narrowing somewhat, until it reaches the muscular layer. At this point it becomes very suddenly constricted into an excretory duct surrounded by abundant muscle fibres which seem mainly to be modified dorsoventral fibres, though there are circular fibres lining the duct. The latter penetrates the subcuticle and opens on the upper surface nearly midway between the edge and mid-dorsal line in the vicinity of the pharynx and above the region between the two ventral nerve cords, but dorsally and somewhat mesially from the outer ventral nerve cord. There may or may not be associated with the aperture a slight projection which scarcely deserves to be called an excretory papilla. Cuticular hairs are very abundant at the excretory pores. The canals and vesicle are lined by a delicate structureless membrane. Goto (1894, 68, 69) described and figured the main canals of *Tristoma* as consisting of an inner narrow and outer wider loop which communicate posteriorly, the latter evidently corresponding to the main canal in *Benedenia*, *Epibdella* and *Pseudobenedenia*.

Male System.

The two testes lie side by side, separated in the median line by a strand of tissue into which the intestinal branches penetrate anteriorly and posteriorly. The glands each measure 1·2 mm. in length by 0·8 mm. in breadth in the largest compressed specimen, but in sections they measured 0·9 by 0·6 mm. with a dorso-ventral dimension of 0·4 mm.

They extend from the muscle layers of the one surface to those of the opposite. These glands, though appearing more or less solid in compressed sections, are more or less deeply indented marginally as well as dorsoventrally by strands of medulla, and a number of these strands pass right through the organs to perforate them, so that in some sections each testis may appear to consist of two, three or more separate portions. In horizontal section the glands may appear slightly lobed. Their inner surfaces are practically smooth and rounded, or nearly straight, according to the position of the section. Surrounding the organs is a definite sheath of mesenchyma fibres. The peripheral region of each gland, as well as the parts adjacent to the perforations, show abundant deeply-staining small cells which exhibit a marked contrast from the more lightly staining loose tissues occupying the rest of these organs.

From the inner anterior part of each testes there arises a delicate vas efferens, the two uniting to form a vas deferens behind the ovary, to the left side of which it passes in a ventral position. On reaching the level of the vitelline reservoir it travels forwards and dorsally, passing above the left-hand portion of that organ to curve round in front of it. It then skirts the vagina, gradually widens, travels across to the right side, and returns, so that it now lies between the reservoir and the shell gland. On reaching the left side again, it is thrown into a series of irregular coils and gradually narrows to pass forwards more or less parallel to, but inwardly from, the left anterior yolk duct. It then curves inwardly above the uterus and cirrus sac, travelling backwards as a delicate duct which enters the sac laterally and somewhat dorsally in the prostate region. It now continues forwards and downwards within the sac, in a thickened portion of the wall of the latter, eventually joining the wider duct from the prostate reservoir to become the ejaculatory duct. The latter is a relatively thick-walled, fairly wide tube covered with rather long hairs. The outer portion forms a cylindro-conical penis which projects for a considerable distance into the sex canal. The penis is not chitinised. Its tip can, apparently, be retracted, not introverted, into the succeeding portion. The inner circular muscle fibres of the penis sac are abundant but very delicate, as also are the longitudinal fibres. Towards the base of the organ and inserted into its inner posterior region, are oblique fibres. The outer circular fibres are rather larger than the inner, and are best developed near the base of the organ. The penis-sac is more compact than in most other species of Capsalidæ (Tristomatidæ) whose descriptions are available. That of *Ep. ovata* Goto seems to resemble it more nearly than any other. The characteristic posterior region which encloses the prostate reservoir, is incorporated as part of the sac and possesses a spherical cavity, filled with secretion, so that it is an obvious structure in whole mounts. The canal from the reservoir bends and then passes forwards, eventually joining the vas deferens, which enters it at a papilla on the inner aspect. Into this sac there enter a number of small independent ducts of characteristic appearance, some of them posteriorly, others laterally, some of them accompanying the vas deferens for part of its course, and one enters the penis just above it; another penetrates the sac dorsally; one or two travel between the prostate reservoir and the male canal. At least one of these ducts can be traced back almost to the region of the ovary. No

doubt they communicate with certain of the gland cells which are so abundant, along with the shell glands, in the region between the ovary and the base of the uterus and penis. The ducts are filled with a homogenous fluid which stains fairly deeply. The penis sac passes anterolaterally below the intestinal crus, near the posterior border of the pharynx.

Close behind the testes are two deeply-staining organs, each parallel with the curved inner posterior corner of the corresponding testis and lying between it and the intestinal branches, the latter penetrating between the two glands. Each appears to be a large multinucleate cell with finely granular cytoplasm. No ducts could be traced arising from them. They measured in sections about 0·1 mm. in length, 0·03 mm. across, and 0·15 mm. dorsoventrally. These post-testicular glands could not be recognised in whole mounts, because of the intestinal branches and vitelline follicles which cover them. Goto referred to the presence of two similar structures behind the testes of *Ep. ovata*, but described them as consisting of a mass of polygonal cells; while Heath described two pairs similarly situated in *Ep. squamula*, and considered them to be each a cell or a syncytium. These seem to be the only references to similar organs.

Female System.

The ovary is a compact organ, the greater part of which lies to the right of the midline, immediately in front of the testes and behind the vitelline reservoir, part of whose posterior border it overlies. It measures 0·65 mm. across, 0·35 mm. maximum length by 0·4 to 0·45 mm. in maximum dorsoventral diameter. The gland is traversed by groups of dorsoventral fibres. Surrounding it is a definite sheath below which the ovarian cells are comparatively small, whereas the rest of the mature organ is more or less completely filled with large egg cells, 0·035 to 0·04 mm. in diameter, with very prominent nucleus and nucleolus. As in other Capsalidæ, the oviduct arises from the more centrally situated portion of the gland. It is a wide thin-walled tube which becomes bent within the gland into a U whose inner limbs may touch in places, the duct eventually becoming suddenly narrowed to pass upwards within the ovary close to the inner anterior border, opening quite dorsally immediately behind the yolk reservoir and slightly to the right of the median line. This narrowed portion of the duct is provided with delicate radiating muscle fibres and, when empty, has a very narrow lumen which is about one-half to one-third of the diameter of a ripe egg. Close to the point of exit, it is joined by the common yolk duct, the narrow united duct skirting the dorsal surface of the ovary. It travels below the intestinal cæca and the ovarian excretory canal, and then forwards above the right side of the yolk reservoir, being thrown into a few loose convolutions en route. It passes above the wide loops of the vas deferens to become the ootype. The duct outside the ovary is lined by a flattened endothelium, and, though nuclei were seen, cell boundaries were not recognised. There is no trace of any seminal receptacles such as Heath figured as being associated with the duct of *Ep. squamula*, after it passes in front of the yolk reservoir.

The ootype or egg mould is a conspicuous organ on account of its chitinised wall, its markedly widened lumen and its abundant musculature, both circular and longitudinal. Surrounding it is a mass of very fine fibres which are perforated by the rather large ducts of the shell glands. The latter are deeply staining and occur abundantly in the region beside, behind and above the uterus and behind the prostate reservoir. The ootype which occupies a higher dorsal level than the uterus, becomes considerably narrowed before it enters that organ. The latter has a very extensive loose sheath which stains poorly and in which a number of large strongly-staining cells are to be seen. Within this tissue the female duct, which on entry is quite narrow, becomes thrown into a few convolutions in the posterior part of the organ, then widens markedly, its walls containing muscular fibres similarly arranged to those in the oviduct. This outer portion passes practically directly into the genital atrium which may be long and narrow, or short and wide, with irregularly folded walls according to the position of the penis. The atrium which is devoid of cuticular hairs, has longitudinal, oblique, and circular muscle fibres surrounding it.

The reproductive aperture is somewhat elongate in the direction of the long axis of the worm and opens ventrally a little behind the left anterior sucker at a point practically midway between the median axis and the margin of the parasite.

The yolk follicles are extremely numerous and lie amongst the branches of the intestine. They occupy a dorsal position, extending from the most anterior to the most posterior cæca and are especially abundant behind and beside the testes. They are more or less spherical, measuring 0·02 to 0·06 mm. in diameter. Their constituent cells vary in their reaction according to their age, the youngest being more protoplasmic and deeply-staining than the older, which, apart from the uterus, remain more or less unstained, and consist mainly of yolk granules. Each follicle is continuous with a delicate duct. These small ducts unite to form larger and larger canals corresponding more or less with the intestinal branches in their distribution. The yolk material is eventually collected into four main vitelline ducts, two anterior and two posterior, lying below the intestinal crura. These ducts enter separately into a large transversely placed vitelline reservoir, though there may also be some anastomosis between the anterior and posterior ducts in its vicinity. The reservoir lies immediately in front of the ovary and behind the vagina. It occupies most of the medulla in the region where it is located. Part of it underlies the anterior portion of the ovary. Arising from its posterior and dorsal surface, close to the midline, is the common yolk duct, which gradually narrows as it travels across to the right to meet the oviduct, just as the latter emerges from the ovary. This arrangement resembles that figured by Linton for *Ep. bumpusii*.

The vagina is a very short wide tube with extremely thick walls composed of circular and especially of longitudinal fibres which form a dense covering to the duct. The cavity is lined by cuticle provided with abundant, rather strong, hairs whose free ends are directed towards the vaginal aperture, which is situated to the left of the midline immediately in front of the yolk reservoir and a considerable distance behind the penis.

It lies very much nearer the median line than does the common genital pore. It travels directly dorsally and is only 0·2 mm. long, but its thick walls give it a diameter of 0·1 mm. It communicates, at its inner end, with a small thickwalled receptaculum which extends inwards and backwards and comes to project into the anterior region of the yolk reservoir, apparently uniting with it by a very delicate aperture. Within the receptacle, which is devoid of hairs, there was observed a mass of fibres resembling tails of sperms, but which may perhaps have been merely coagulated secretion. The strongly muscular nature of the vagina suggests that it has a copulatory function—certainly not that of self-fertilisation on account of its position—but the strong hairs are so directed as to afford little support to that view. The position of the organ and its consequent extreme shortness are quite different from what is described as occurring in any other Capsalid, though a few authors have either failed to find the organ, or failed to mention its presence. Deeply staining cells, probably glandular, are present near its aperture.

There is only one fully formed egg at a time in the uterus, though another may be in process of having its shell deposited. Almost all specimens examined were somewhat distorted, so that the shape became more or less quadrangular. A normal specimen is indicated in fig. 15. Its dimensions are 0·2 mm. long by about 0·1 mm. broad. At the posterior corner there is a very long delicate filament more or less twisted or coiled while in the uterus, but in an extended specimen it measures 1·2 mm.

The systematic position of the parasite has been dealt with in the original account (Johnston, 1931).

Ogmogaster antarctica *Johnston* 1931.

(Figs. 26–28.)

Syn. *O. plicatus* Leiper and Atkinson nec Creplin.

A large number of specimens of a species of *Ogmogaster*, very closely related to *O. plicatus* (Creplin), were taken from the intestine of some Weddell seals, *Leptonychotes weddelli*, in Commonwealth Bay, King George V Land, by the late Dr. A. L. McLean.

The shape varies with the degree of contraction of the worms, most of which are more or less deeply cupped with the margin and posterior end symmetrically folded and turned inwards ventrally to some extent. When most contracted, the length of these thick-bodied parasites is only a little greater than the width, but most specimens, all of them with slightly inturned edges, range from 5 to 6 mm. in length and 3·5 to 4 mm. in breadth. One specimen, which is practically flat, measures 6 mm. by 4 mm. The maximum breadth observed was 5·5 mm. and maximum length 6·7 mm., this occurring in a specimen whose mouth was anterior and whose edges were not inturned. Leiper and Atkinson (1915, 37–8) who gave a brief account of this species from the Weddell seal and the crab-eating seal, *Lobodon carcinophaga*, under the name of *O. plicatus*, mentioned that the average length was between 5 and 6 mm., some being over 8 mm., while the greatest transverse diameter varied between 4·5 and 5·5 mm. Jagerskiold (1891, 5) reported that the length of his specimens of *O. plicatus* from northern rorquals was generally 6 to 7 mm., occasionally reaching 14 mm., with a breadth of 4 mm. and a dorso-ventral thickness of about 1 mm. The new species is thus rather smaller and relatively wider, and possesses a more rounded outline.

The posterior end is broadly rounded and wider than the anterior, the greatest width being at about the mid-length. The free margin is very regularly indented or lobed, about 18 to 20 lobes on each side, these folds varying in size and form according to the state of contraction. They are largest laterally and suddenly diminish anteriorly, where they become replaced by a prominent fold, smooth, or with a slight undulating margin, lying ventrally and situated between the oral sucker and the genital aperture. When this lateral region is fully extended its appearance resembles that figured by Jagerskiold.

The dorsal surface is smooth and more or less strongly convex, according to the depth of the concavity on the opposite surface. The ventral surface is provided with deep furrows separated by prominent rugæ. There are thirteen of the latter, parallel to the median line, the outer ridges being shorter since they approximate the curved margin more rapidly than those more centrally situated. Consequently the number seen in transverse section diminishes towards either end of the parasite. Occasionally a ridge may be broken and the parts may overlap slightly so that more than thirteen may appear to be present, if judged only from such sections. The outermost may be very small and consist of several parts, and is apt to be overlooked if the edge of the worm be strongly inturned. Between the outermost ruga and the corresponding lateral margin there is a depression wider than that between adjacent ridges. These ridges are more or less flat or broadly rounded at their free extremities which measure 0·15 to 0·2 mm. across. They are separated by furrows, 0·15 to 0·2 mm. in depth and 0·1 to 0·15 mm. in width, the dimensions varying according to the state of contraction of the worm. The rugæ do not extend forwards as far as the genital pore, but posteriorly they reach almost to the end of the parasite. The median ridge passes forwards to underlie the long cirrus sac. The rugæ present a characteristic appearance in stained preparations, since the underlying groups of deeply staining gland cells are regularly arranged and surrounded by a more or less unstained area. Leiper and Atkinson record the number of rugæ as averaging fourteen to fifteen, when viewed in section. This is probably due to an overlapping of parts of a ruga, as not more than thirteen were observed in our specimens. Jagerskiold states that from fifteen to seventeen are present in *O. plicatus*. Creplin does not mention the number observed by him.

The oral sucker is relatively large, measures about 0·5 mm. in diameter and faces more or less ventrally in contracted, but forwards in fully extended, specimens. It possesses a deep cavity which diminishes in width as it approaches the very narrow œsophagus. Just behind the mouth is the common genital aperture lying in the anterior part of the concavity (formed when the ventral surface is cupped) and more or less covered by a fold of membrane separating it from the mouth. In many specimens the long spiny penis is protruded for a considerable distance.

No attempt was made to study either the nervous system or the powerful musculature.

The digestive system is simple. A pharynx is absent. The œsophagus is quite narrow, but very well-defined, due no doubt to the presence of a strong musculature surrounding it. Jagerskiold refers to the presence, in *O. plicatus*, of pyriform cells, probably salivary glands, around it. The tube passes almost directly upwards (in contracted specimens) in the region between the oral sucker and genital aperture and divides into the two intestinal crura, each of which is somewhat widened and apparently rather thinner walled in this portion than in the remainder of the tube. The crura diverge symmetrically into a series of curves, the first fairly wide, then a small one followed by two wide curves, after which each tube passes along the anterior as well as the inner border of the corresponding testis, eventually forming a small curve behind it, the ends approaching each other to terminate on either side of the excretory pore. The arrangement is thus similar to that in *O. plicatus* except that the curves are much more nearly equal in the latter species. The crura lie above the uterus.

The excretory aperture is ventral and subterminal, between the ends of the crura. It leads into a vesicle which soon branches to form two long tubes passing forwards, approximately parallel with the margin of the worm. These at first lie outwardly from the ovary, and travel below the testes and uterus to reach the level of the genital pore where they approximate, probably fusing below the œsophagus, as described for *O. plicatus*. From this point a vessel passes backwards on each side nearer the margin of the body, giving off a few branches inwardly and outwardly, and eventually reaches almost to the posterior end. Each branch terminates in what seems to be a cluster of flame cells. Though the canals thus described were readily detected in many specimens, the further course of the tubes as described by Jagerskiold was not recognised and probably does not hold good for this species.

The testes are symmetrical, deeply incised organs, lying outwardly and slightly anteriorly from the ovary. Their maximum length is 0·7 to 0·9 mm. and breadth 0·6 to 0·7 mm. The point of origin of the male ducts was not observed, though a large empty vas deferens was seen, at first more or less median and then extending further forwards, passing to the right side of the cirrus sac and reaching about as far anteriorly as the looped portion of the uterus. This part of the male duct is thrown into a few loops also, eventually travelling backwards to curve round just behind the cirrus sac which it enters terminally, as in *O. plicatus*. The male duct now becomes quite narrow and somewhat convoluted, and may be widened in some portion to form a vesicula seminalis which is followed by a narrow duct that enters the cirrus. The sac is a long tube about 1·8 mm. long and 0·34 mm. wide, lying in the median line. Its length is thus about one-third of the total body length, whereas in Jagerskiold's figure of *O. plicatus* it is two-fifths of the total and not less than 3 mm. long. The introverted cirrus occupies most of the length of the sac and is about 0·2 mm. wide, but its breadth may vary in different parts of the tube, though it usually maintains approximately the same diameter throughout. The walls are strongly muscular. The organ was seen everted in many specimens,

generally somewhat coiled and lying over the genital opening. It gradually narrows from its base to the tip. The surface is beset with abundant, rather low, broad spines, arranged more or less transversely, sometimes giving a ringed appearance to the organ. The base of these spines is broad and more or less rounded, the spine projecting about 0·01 from the surface. The length of the fully everted organ is about 1·8 mm. Between the musculature of the sac and the enclosed male duct in its posterior portion are abundant prostate gland cells.

The ovary is median, posterior and more or less surrounded by the terminal portion of the intestinal crura. The organ is rather deeply lobed as in *O. plicatus*. It measures about 0·6 mm. across by 0·4 mm. in length (1 mm. by 0·5 mm. in *O. plicatus*).

The oviduct arises from its anterior border and after a very short course joins the common vitelline duct in the shell gland and then passes to one side as a loop which travels forwards, this uterine duct being rather narrow. It becomes transversely placed in front of the shell gland and then there follows a succession of loops. The latter are not in contact but are arranged so complexly that the uterus resembles a wide reticulum occupying a region reaching from the level of the anterior border of the testes to the posterior end of the cirrus sac and extending laterally nearly to the margin of the worm. The tube also passes forwards, especially on the left side, to occupy a great part of the area lying laterally from the posterior two-thirds of the cirrus sac. The uterus which is filled with an enormous number of tiny eggs in mature specimens, eventually travels forwards to the left side of, and parallel with, the cirrus sac. Though Jagerskiold stated that the uterus of *O. plicatus* developed branching blindly-ending sacs, Kossack pointed out that it was really a simple tube, extraordinarily and irregularly twisted. Apparently the arrangement in *O. antarctica* is essentially similar. The terminal portion of the female duct widens considerably to form a short metraterm about as wide as the cirrus sac and underlying the anterior end of it. It terminates in the rather wide female aperture. It possesses abundant minute spines as in *O. plicatus* and its walls are strongly muscular. Jagerskiold referred to the presence of abundant gland cells in this region.

The yolk glands lie below the uterus and occupy a relatively narrow transverse zone in front of the shell gland and testes and extending forwards for about one-third of the distance between the shell gland and the posterior end of the cirrus sac, so that they are more restricted than in *O. plicatus*. The number of follicles varies somewhat, and as stated by Leiper and Atkinson, may range from ten to eighteen on each side, their arrangement being more or less symmetrical. The ducts are disposed as in *O. plicatus*, the yolk eventually reaching the two main canals which unite just in front of the ovary to form a common yolk duct. The latter passes upwards and then backwards and downwards through the shell gland, where it joins the oviduct or ootyp. Laurer's canal was not recognised.

Eggs are minute and very abundant and possess a long polar filament at each end. The shape is similar to that figured for *O. plicatus*. The central elliptical portion of the shell is about 0·02 mm. long by 0·012 mm. broad and this part suddenly narrows to form the tapering filaments, the total length of the egg and its filament being about 0·18 mm.

In 1892 Monticelli compared the various systems in *Ogmogaster* with those in other Monostomid genera and pointed out the similarity of the reproductive organs to those of *Notocotyle*, the main difference being that of the arrangement of the vitellaria.

Kossack (1911, 565) created the subfamily Ogmogasterinae, Notocotylidae, to receive Jagerskiold's genus, mainly on account of the longitudinal rugæ, the position of the vitellaria, and the long, irregularly twisted uterus. He re-examined Creplin's original material and pointed out that Jagerskiold was in error in stating that the uterus developed branching blindly-ending sacs, whereas it was a very irregularly twisted tube. Poche (1925) regarded this Monostomid genus as possessing characters sufficient to justify the erection of the family Ogmogasteridae.

REFERENCES TO LETTERING.

Ac, anterior commissure; aex, anterior excretory canal; ag, anterior glands; agd, ducts of anterior glands; alr, anterior lateral ridge of disc; as, anterior sucker; avd, anterior vitelline duct; b, brain; bc, buccal cavity; c, cirrus; cm, circular muscle fibres; cs, cirrus sac; cvd, common vitelline duct; dcm, dorsal layer of circular muscle fibres of sucker; dn, dorsal nerve; e, eye; ejd, ejaculatory duct; em, egg mould; ep, excretory pore; ev, excretory vesicle; ex, excretory canal; ga, ganglion cell; gp, genital pore; h, h1, h2, h3, hooks of disc; i, intestine; ivn, inner ventral nerve; l, lip; m, mouth; mm, marginal membrane of disc; mt, metraterm; n, nerve; nc, nerve commissure; nr, nerve ring; o, egg; od, oviduct; oes, œsophagus; om, oblique muscle fibres; ov, ovary; ovn, outer ventral nerve; p, penis; pd, prostate duct; ped, pedicel of disc; pex, posterior excretory canal; ph, pharynx; plr, posterior lateral ridge of disc; prs, prostate sac; pt, perforation through testis; ptg, post-testicular gland; pvd, posterior vitelline duct; r, ruga; rm, radial muscle fibres; rs, receptaculum seminis; sa, salivary; sg, shell gland; t, testis; u, uterus; ud, uterine duct; v, vagina; vd, vas deferens; vf, vitelline follicle; vr, vitelline reservoir; vtd, vitelline duct; x, outer limit of vitelline follicles and intestinal cæca.

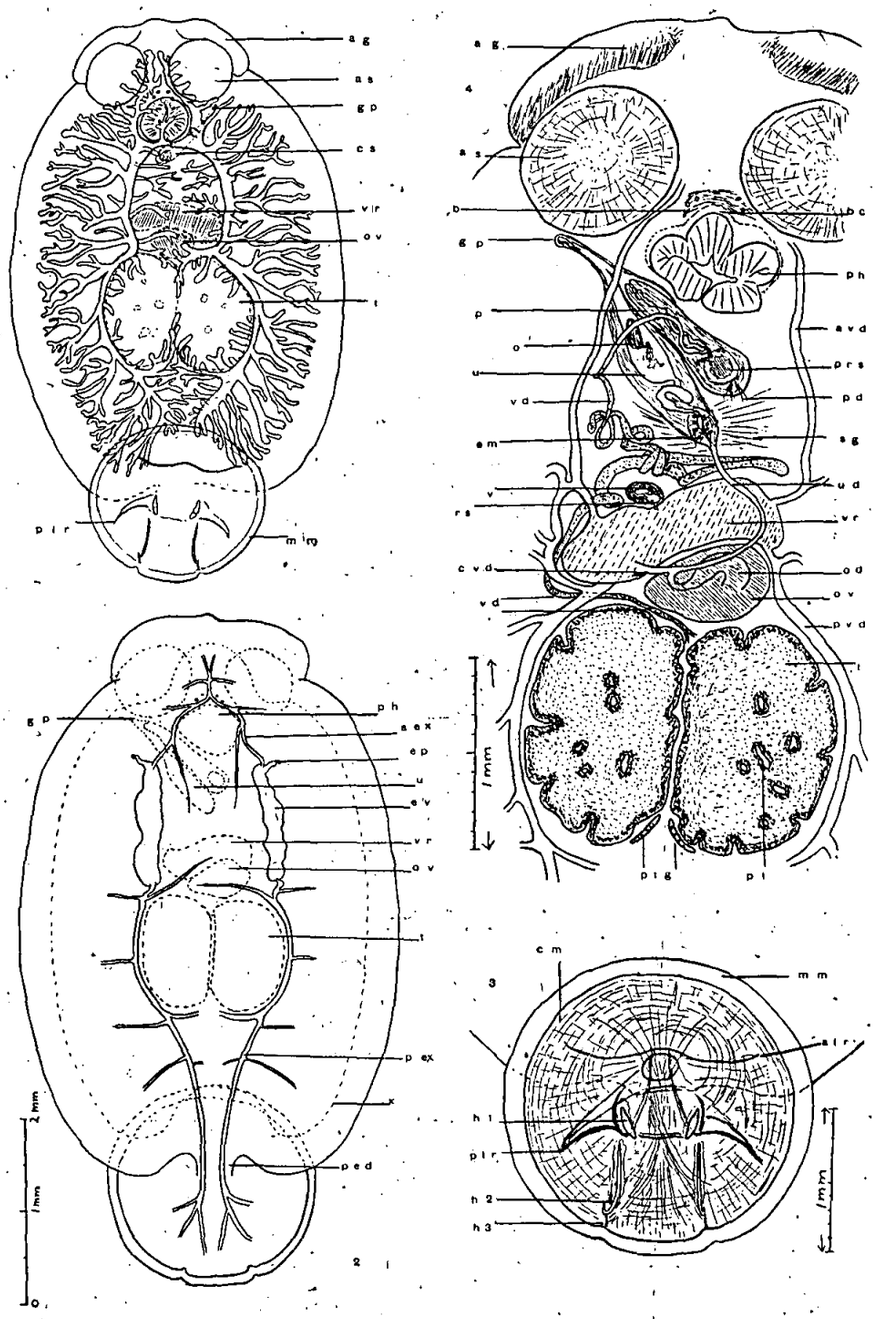
EXPLANATION OF FIGURES.

Pseudobenedenia nototheniae.

Fig. 1. General form and digestive system; reproductive system outlined.
2. Excretory system; drawn to same scale as fig. 1.
3. Reproductive system, excluding vitellaria; dorsal view.
5. Ducts of vitelline system; other reproductive organs dotted. Outer limit of vitellaria and intestinal crura dotted, also position of ridges on disc.
6. L.V.S. somewhat oblique, passing through mouth and vagina.
7. Ditto, drawn to same scale, but passing through excretory pore and pedicel of disc.
8. L.V.S. pedicel and disc.
9. L.V.S. anterior end, showing succer and anterior glands.
10. Pharynx, anterior crura, eyes, etc.—from whole mount.
Lettering as in preceding figures.
11. Nervous system; reconstruction mainly from horizontal sections.
12. L.H.S. brain.
13. L.V.S. left anterior eye.
14. Multipolar nerve cells from subcuticular tissues of body and disc, as seen in entire preparations.
15. Egg from uterus.
16. Three hooks from left side of disc—ventral view.
17. Anterior hook of right side—dorsal view. Figs. 15, 16 and 17 drawn to same scale.
18. Posterior (third) hook from left side, dorsal view.
Lettering as in preceding figures.
19. Oblique section of cirrus sac at junction of vas deferens and prostate duct.
20. Excretory pore—from T.S. body.
21. Cells from anterior part of pharynx—from L.H.S. body.
22. T.S. through region of vagina—drawn from several successive sections.
23. T.S. body showing junction of oviduct and yolk duct.
24. T.S. body near posterior edge of testes, showing post-testicular glands. Figs. 22, 23 and 24 drawn to same scale.
25. Portion of L.H.S. body, showing post-testicular glands.
Lettering as in preceding figures.

Ogmogaster antarctica.

Fig. 26. Ventral view, showing rugæ, cirrus sac and inturned margin. Position of cirrus sac dotted.
27. Ventral view, showing anatomy. Drawn to same scale as fig. 26.
28. Portion of reproductive system, dorsal view.
Lettering as in preceding figures.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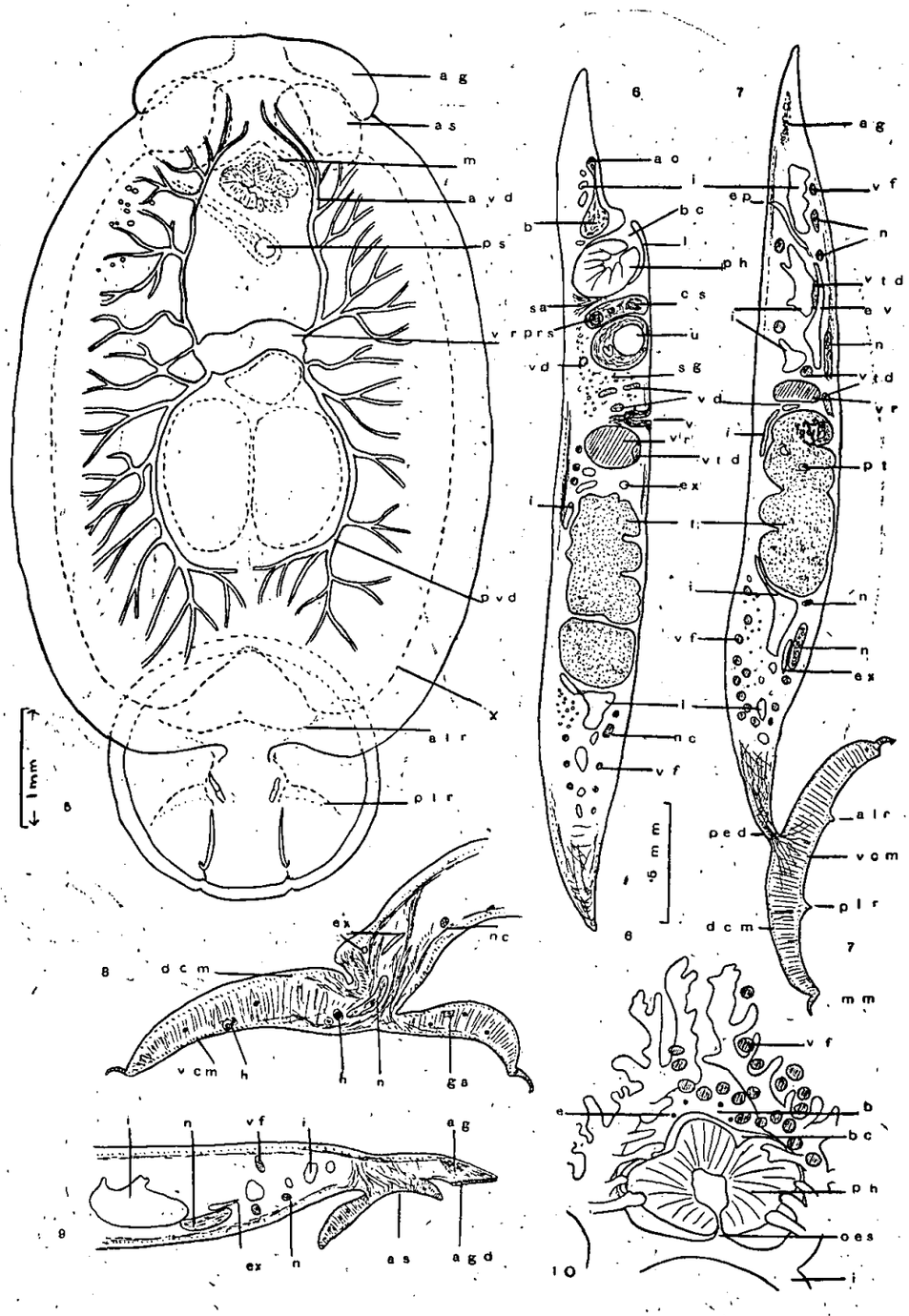
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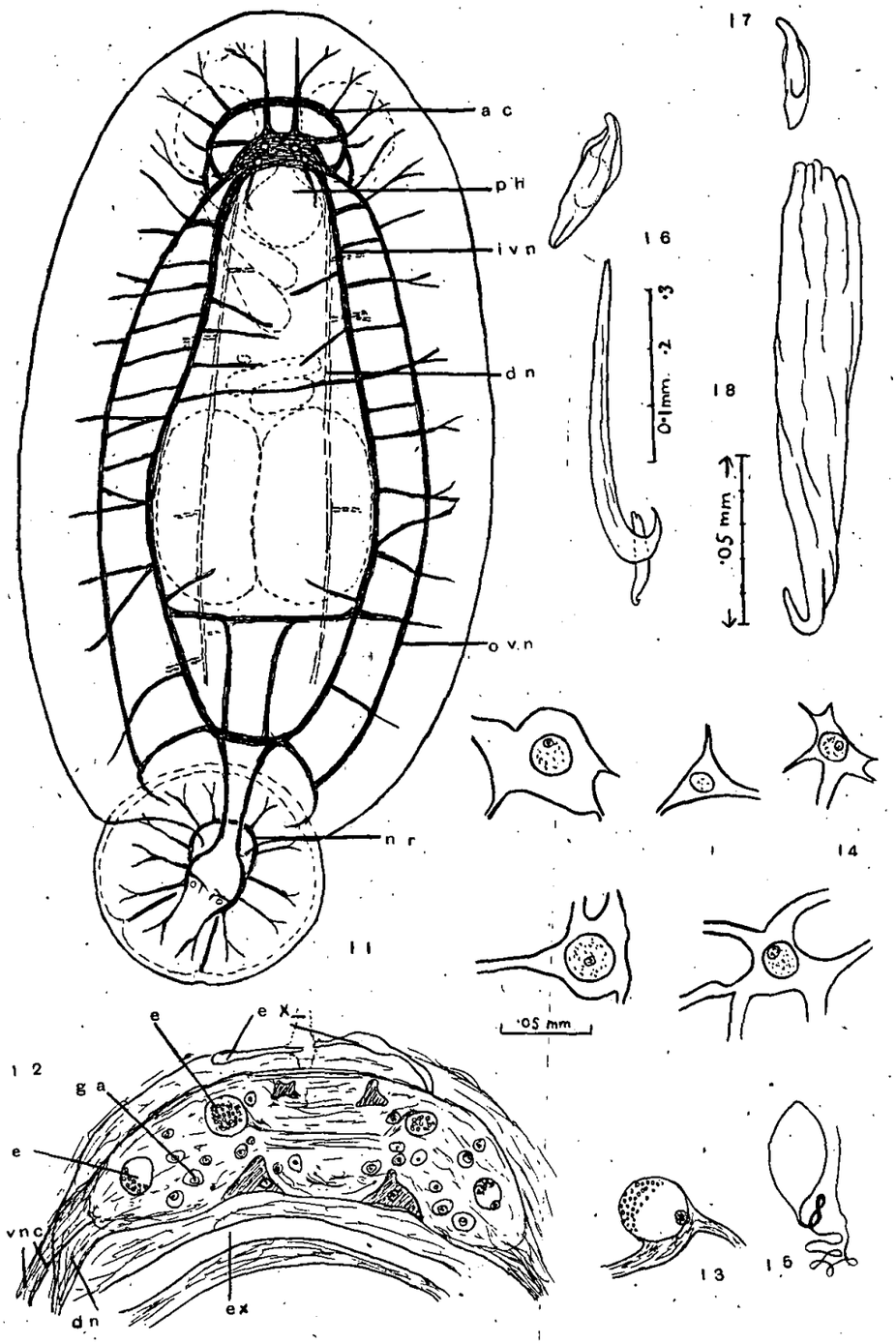
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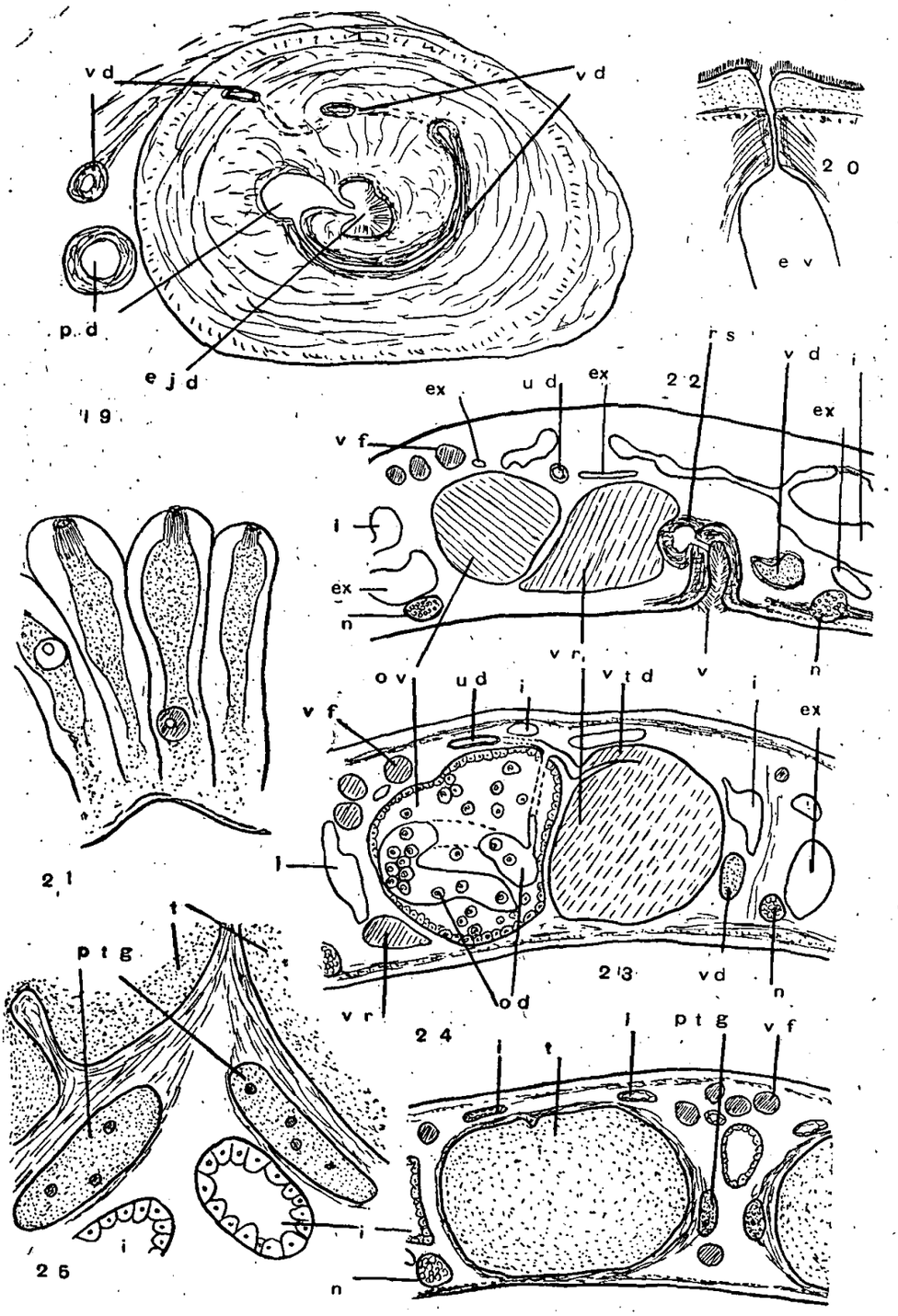
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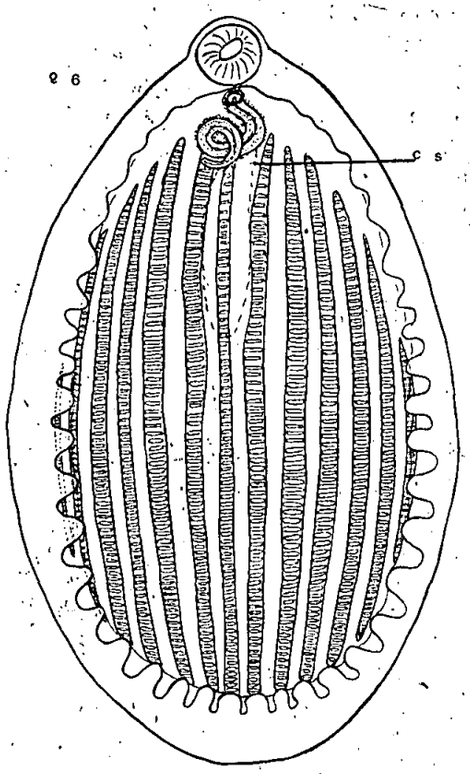

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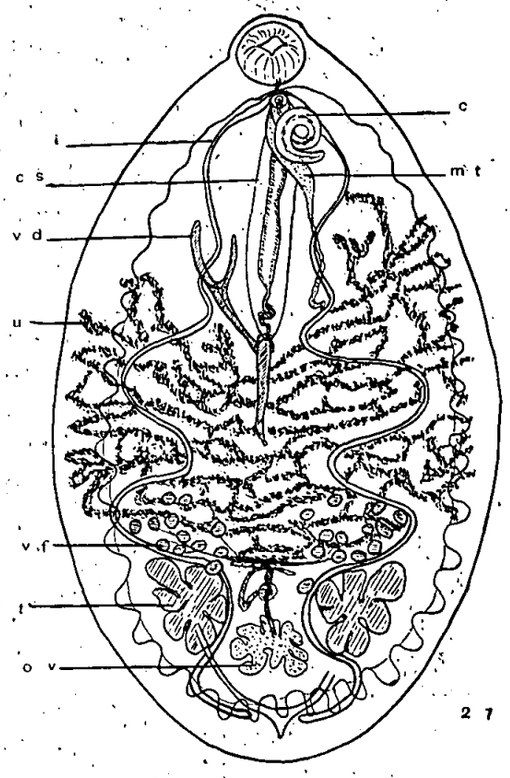

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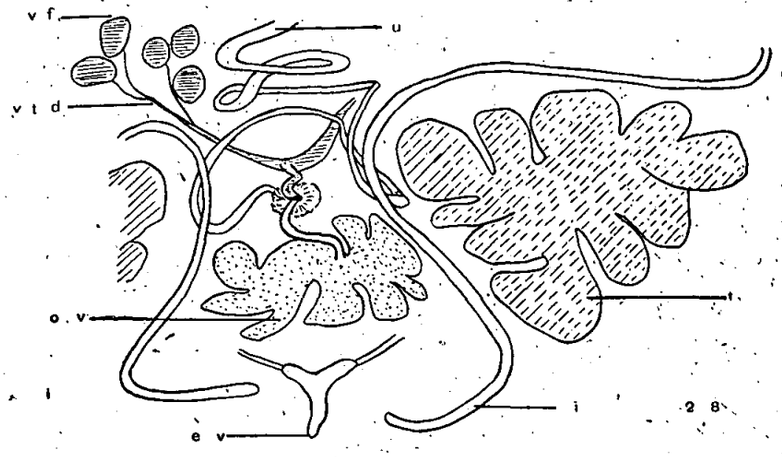

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