On the Anatomy of Prosthecocotyle torulosa (Linstow) and Prosthecocotyle heteroclita (Dies.). By Dr O Fuhrmann, University of Geneva. Communicated by Sir John Murray, K.C.B. (With a Plate.)

(Read May 1, 1899.)

In the Report on the Entozoa collected by H.M.S. "Challenger" Dr O. von Linstow * described two new tapeworms, which he named Tetrabothrium torulosum and T. auriculatum. The resemblance of the head of T. auriculatum with that of Prosthecocotyle Forsteri described by Monticelli† seemed to me to indicate that the Tetrabothrium described by Linstow probably belonged to the genus Prosthecocotyle.

Through the kindness of Sir John Murray, I received from the British Museum the original specimens for inspection, for which I wish to express here my warmest thanks. The following lines give the results of my examination; but before entering upon the description, let me say something on the systematic position of these two animals. As I have already remarked, Prof. Monticelli has rightly erected a new genus named Prosthecocotyle for the tapeworm Tænia Forsteri, Krefft. To this genus belongs, besides P. Forsteri, other parasites of birds which have been placed in the genera Tænia, Tetrabothrium, Amphoterocotyle, Bothridiotænia, Bothriocephalus. According to my researches the following species belong to the genus Prosthecocotyle:—

- 1. P. Forsteri (Krefft), (syn. Tania Forsteri, Krefft), from Delphinus Forsteri (Gray) and Delphinus delphinus, L.
 - 2. P. Monticellii, Fuhrmann (syn. Tænia erostris, ex parte, Both-
- * Linstow, O. von, Report on the Entozoa collected by H.M.S. "Challenger,"—Challenger Reports, Zoology, vol. xxiii., 1888, pl. ii. figs. 16-20.
- † Monticelli, S., "Nota intorno a due forme di Cestodi,"—Bull. dei Musei di Zoologia ed. Anat. comp. della R. Universita di Torina, vol. vii., 1892, figs. 4-13.

ridiotænia erostris, var. minor, Lönnberg), from Fulmarus glacialis, L.

- 3. P. umbrella, Fuhrmann, from Diomedea sp. (?).
- 4. P. torulosa (Linstow), (syn. Tetrabothrium torulosum, Linstow), from Diomedea brachyura, Temm.
- 5. P. macrocephala (Rud.), (syn. Tænia immerina, Abildgard (?), Rhytis immerina, Zeder (?), Bothriocephalus macrocephalus, Rud., Tetrabothrium macrocephalum, Rud., T. Zedri, Baird, T. Colymbi, Troiles Viborg (?)), from Colymbus glacialis, L., C. septentrionalis, L., C. arcticus, L., Podiceps cristatus, L., P. cornutus, Gm., Uria troile, L., Aptenodytes sp. (?), Totanus glareola, L. (?).
- 6. P. juncea (Baird), (syn. Bothriocephalus junceus, Baird, Tetrabothrium junceum, Baird), from Sarcoramphus papa, L.
- 7. P. cylindracea (Rud.), (syn. Bothriocephalus cylindraceus, Rud., Tetrabothrium cylindraceum, Rud., Bothridiotænia cylindraceu, Rud.), from Larus glaucus, Brünn, L. atricilla, L., L. ridibundus, L., L. canus, Brünn, L. marinus, L., Rissa tridactyla, L.
- 8. P. erostris (Lönnberg), (syn. Tænia erostris, Lönnberg, Bothridiotænia erostris, Lönnberg), from Larus marinus, L., L. canus, Brünn, L. fuscus, L., L. argentatus, Brünn, Rissa tridactyla, L., Sterna sp. (?).
- 9. P. eudyptidis (Lönnberg), Fuhrmann, (syn. Bothridiotænia erostris, var. eudyptidis, Lönnberg), from Eudyptes catarractes, Gm.
- 10. P. heteroclita (Dies.), (syn. Tetrabothrium heteroclitum, Dies., Amphoterocotyle elegans, Dies., Tetrabothrium auriculatum, Linstow), from Daption capensis, L., Thalassæca glacialoides (Smith).
 - 11. P. intermedia, Fuhrmann, from Procellaria sp. (?).
 - 12. P. campanulata, Fuhrmann, from Procellaria sp. (?).
- 13. P. pelecani aquilæ (Rud.), (syn. Tænia pelecani aquilæ, Rud., Tænia heterosoma, Baird, Tænia sulæ fuscæ, Baird), from Atagen aquilus, L., Sula fusca, Viellot.
- 14. P. sulciceps (Baird), (syn. Twnia sulciceps, Baird), from Diomedea exulans, L.
- 15. P. porrigens (Molin), (syn. Tetrabothrium porrigens, Molin), from Nystiardea nycticorax, L., Larus melanocephalus, Natt. (?).
- 16. P. triangulare (Dies.), (syn. Tetrabothrium triangulare, Dies.), from Delphinorhynchus rostratus, Cuv.

The genus Prosthecocotyle may be characterised as follows:— The head, without rostellum and hooks, has a quadrangular shape, which is caused by the singular structure of the suckers. Each sucker shows the peculiarity of having on the outmost end a lateral protrusion, which has the same histological structure as the oval and powerful suckers themselves. The segmentation begins not very far behind the head, and the segments are always shorter than broad, except the last segments on the The morphology of the genital organs also shows posterior end. some typical characters. Male Organs.—The cirrus-pouch is always small, and has a globular shape. It lies at some distance from the margin, and is joined with the genital cloaca by a canal which I call 'male cloacal canal.' It is rarely armed. The vas deferens is very long and without vesicula seminalis. testicles, to the number of 8 to 60 in each segment, are confined to the dorsal portion of the median field. Female Organs.—The small vitelligenous gland lies always before the great ovary. The vagina passes directly from the ventral side of the cirrus to the ovary, showing a receptaculum seminis varying in form and structure in the different species. The genital cloaca is always on the left margin of the strobila; it is very deep and possesses a very complicated musculature. The eggs are enveloped by three shells.

Prosthecocotyle torulosa (Linstow). (Tetrabothrium torulosum, Linstow.) Figs. 1-3.

This Tænia was found in Diomedea brachyura. The length is, according to O. von Linstow, 175 mm. The width behind the head is 1 mm., from there increasing gradually, and 9 cm. behind the scolex it attains 5 mm., which is the maximum width. The segmentation of the body begins immediately behind the head, but the segments are at first very short (0.022 mm.). The segments, with the genital glands well developed, are very thick; they are 0.126 mm. long by 5 mm. wide, and have a vertical diameter of about 2 mm. The measurements are almost the same for the segments crowded with eggs. The posterior border of each segment overlaps—with a prominent fold—the

succeeding one. All the specimens that I had occasion to study were strongly contracted. The measurements given above have therefore no absolute value, for they vary according to the degree of the contraction of the animal. The scolex is unarmed, without rostellum and hooks; it has the typical shape of the head of the Prosthecocotyle species. The head differs from the drawing published by O. Linstow, as may be seen by comparing fig. 17 of Linstow with my fig. 1 drawn with Abbé's drawing apparatus. The scolex is 1 mm. wide and about 2 mm. long. This singular form is produced by the prois quadrangular. trusions of the suckers characteristic of all Prosthecocotylee. These are the suckers that exhibit anteriorly and externally ear-shaped protrusions, which have the same structure as the suckers. suckers with their small openings lie on the dorsal and ventral side of the scolex; they are oval, with a long diameter of 0.34 mm. and a transverse diameter of 0.23 mm. They touch one another in the median line of the head, and are very powerful and deep. Unhappily, I cannot give information on the histological structure of this interesting scolex, because I could not make sections of it. Neither can I state whether the posterior part behind the head is normal.

The segments, which are very short and thick, and separated by a deep incision, are covered by the cuticula and the subcuticular layer of cells. The cellular structure of the parenchyma is distinct everywhere; it is not crossed over by muscular fibres. We find it so in the lateral extremities of the internal parenchyma and in the cirrus-pouch. The calcareous corpuscles are found specially in the external parenchyma, but also between the muscles and in the intermediate layer of parenchyma situated between two segments. In the ripe segments they are particularly numerous in the lateral parts of the internal parenchyma, where one can study their development out of the cells of the parenchyma.

We find directly under the cuticula a simple layer of circular and longitudinal fibres. In the parenchyma we discover two layers of longitudinal muscles. The external stratum is formed by small bundles of spindular fibres (ca. 10 fibres). This thickly laid stratum of muscles envelops completely the central part of the segment, and is only interrupted at the point where the

genital canals pass out. They go through the strobila without diminishing in thickness at the limits of the segments. muscular layer, which has a thickness of 0.038 mm., touches the cuticula only at the limits of the segments, and it follows from this disposition that the external parenchyma of each segment is completely separated. The external muscular layer is much more powerful. It consists of bundles (diameter 0.114 mm.) formed by fifty fibres at the utmost. This stratum of longitudinal muscles is separated from the external layer by a small zone of parenchyma, and only interrupted for a short space on both sides of the strobila. Inside of the longitudinal muscles we find a layer of transverse muscles. In the lateral part of the strobila these muscles radiate only in the external parenchyma, and fix themselves on the cuticula of the anterior side of the segments. The dorso-ventral fibres are specially situated where they are not disarranged by the development of the genital glands, and are therefore mostly found in the lateral sides of the proglottis and between the different These fibres can, without doubt, modify the depth segments. of the incision between the segments. As to the form of the fibres, we find it differs in the different systems. The dorsoventral fibres are very long and fine. The transverse fibres are also very long. The longitudinal fibres are, on the contrary, short and thick.

We could only study the water-vascular system in the strobila. The two pairs of longitudinal vessels are placed one above the other; the dorsal one has a diameter of about 0.01 mm.; the ventral one is much better developed, and is 0.06 mm. wide. The vessel that joins the ventrals has a diameter of 0.032 mm. The water-vascular system has a very peculiar structure, the vessels having a powerful musculature which transforms this system into a contractile organ. The dorsal vessel is especially muscular, and thus varies much in size. On the ventral vessel the circular and longitudinal fibres are neatly developed, but each one is represented by a simple stratum. Such a complex musculature has never been noticed in the water-vascular system of the cestodes. Riehm * has described circular muscles on the vessels of Dipy-

^{*} Riehm, G., "Studien an Cestoden," Zeitschrift f. d. ges. Naturwiss., Bd. 54, pp. 545-610. 1881.

lidium Leuckarti, Roboz * found on the vessels of Solenophorus a feeble stratum of circular and longitudinal fibres. The vessels which bind the ventral vessels are without muscles. I only saw the two powerful longitudinal nerves which are situated on the outside of the water-vascular system.

As the segments are separated by a deep incision, the opening of the genital cloaca is situated on the left and anterior side of The genital cloaca itself is wrinkled, and lined the proglottis. by the continuation of the cuticula of the body. On the walls of the cloaca are fixed numerous muscles descending from the transverse musculature. These muscles have the function of flattening out the cloaca; they are therefore expanders of the At the bottom of the cloaca a long canal leads genital cloaca. to the cirrus-pouch, which may be called the 'male cloacal canal.' This canal has the same structure as the 'hermaphrodite canal' described by me in Tania depressa.† This ductus has therefore a powerful circular and longitudinal musculature, surrounded by numerous nuclei pertaining to myoblasts, and parenchyma cells. Through this canal the cirrus passes to the outside. pouch, being spherical, has the typical shape of the Prosthecocotyle The wall of this organ is 0.018 mm. thick. part consists of circular, the external of longitudinal muscles. Inside this organ is the short vas deferens, which is enveloped by a feeble musculature. The penis is unarmed. The vas deferens passes nearly in a straight line under the nerve and between the two vessels of the water-vascular system. A series of circumvolutions, becoming always closer, and passing on the dorsal side of the median field to the middle of the segments, commences here. The testicles are placed on the dorsal side and are in number ca. Their diameter is in the dorso-ventral direction ca. 0.17 mm., the transverse diameter being 0.08 mm.

The female glands are, except the uterus, situated on the ventral side. The ovary is well developed and deeply lobed. The egg-cells are very large (0.057 mm.). A protoplasmic mass containing

^{*} Roboz, F. von, "Beitrage zur Kenntnis der Cestoden," Zeitschrift f. wiss. Zoologie, Bd. 37, 1882, pp. 263-285.

⁺ Fuhrmann, O., "Beitrag zur Kenntnis der Vogeltaenien," Revue Suissc de Zoologie, t. iii., 1895, pp. 454-458.

the nuclei of young egg-cells occurs at the bottom of the ovarian tubes (slightly swelled at their extremity). It is here that during a short time new eggs are produced. The vagina begins on the ventral side of the cirrus-pouch, and runs nearly in a straight line in the middle of the median field to join the oviduct. This canal dilates on two points of its course. The first widening is longish but not very considerable; it is probably the receptaculum seminis, in which I could not find spermatoids,* also the structure is not the same that one generally finds in the other cestodes for the same organ. The second widening, very short, is not far from the point where the vagina rejoins the oviduct. The structure is the same as that of the vagina, but with a much more powerful longitudinal and circular musculature. The oviduct begins with a very well developed muscular funnel. This funnel is carpeted inside by an epithelium. From this organ the oviduct goes to meet the vagina, forming distinct circumvolutions (fig. 3). The oviduct is very wide, and carpeted by an epithelium, formed partly by columnar cells, out of which issue long cilia. From the point where the oviduct meets with the vagina, it becomes very It descends towards the shell-glands, and it is there that the vitelloduct throws itself into the oviduct. The small and slightly vitelligenous gland is the sexual gland which is situated before the ovary, as in all the Prosthecocotyle. From the shellglands the oviduct leads in a straight line towards the dorsal side of the proglottis, where it opens into the uterus. The uterus is therefore situated on the dorsal side of the ovary. Its most considerable diameter is in the median line of the strobila; it diminishes promptly laterally, where it passes between the longitudinal vessels of the excretory system. This conformation of the uterus is found in the segments where the sexual glands are still well developed. It is in this state that the uterus is carpeted by very high cells. When the uterus is distended with eggs, these cells suffer a granular degeneration of which we find the remains between the eggs. Are these granules used to nourish the eggs which are for a long time devoid of an envelope, even when they have already begun their segmentation? Or do they help the

^{*} We must say that our material consisted only of a few well-preserved fragments.

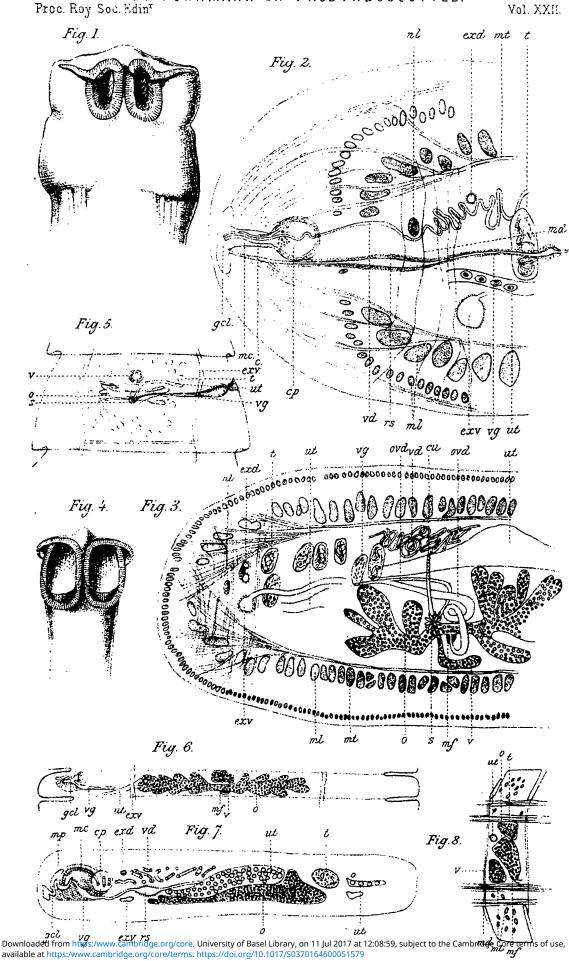
formation of the envelopes of the eggs? As I have just said, the eggs remain for a long time without shells, and are very poor in vitellus; it is only in the last segments that one finds the embryo with its six hooks enveloped by three shells (diameter of the embryo and the first envelope 0.036 mm.; hooks, 0.014 mm.; diameter of the second envelope 0.039 mm.; diameter of the third envelope 0.054 mm.). In the segments which are quite ripe, the sexual glands have completely disappeared and the uterus fills up the internal parenchyma.

Prosthecocotyle heteroclita (Dies.).

Syn. Tetrabothrium heteroclitum (Dies.), Amphoteracotyle elegans (Dies., Tetrabothrium auriculatum (Linstow). Figs. 4-7.

A serious comparative study of the originals of T. auriculatum and of Diesing's examples of T. heteroclitum has shown me that the two species are identical. This interesting Tænia was found in the intestines of Thalussæca glacialoïdes, Smith, and Daption capensis (Linn.). According to Linstow, the animal attains a length of 112 mm.; the scolex is 0.48 mm, in breadth and 0.34 mm. in length. According to my measurement the breadth of the head is of 0.38 mm. The powerful suckers occupy almost the whole of the scolex, and each one exhibits anteriorly and externally an ear-shaped protrusion. "At a distance of 0.6 mm. behind the scolex the segmentation begins. The first proglottides are 0.012 mm. long and 0.41 mm. broad; those in the middle are 0.29 mm, by 1.64 mm., while those furthest back measure 0.42 mm. in length by 2.5 mm, in breadth." This worm has not such a great thickness as P. torulosa, but is, on the contrary, very Also the proglottides are a little longer than in that species, but the separation of the proglottides is equally distinct, and the separation between each segment reaches the longitudinal muscles. In the external parenchyma numerous calcareous corpuscles are found. The internal parenchyma is reduced by the development of the sexual glands.

Besides the subcuticular musculature, which shows nothing very remarkable, we find, as in *P. torulosa*, a double zone of bundles of longitudinal muscles, the external ones of which are less strong.



The external zone is continuous, which means that it is only interrupted at the point where the sexual organs pass out. The internal zone is confined to the ventral and dorsal surfaces. On the internal side of the longitudinal musculature lies a feeble layer of transverse muscles, which assists the formation of the complicated musculature surrounding the terminal part of the sexual canals. The dorso-ventral musculature is feeble.

The nervous system consists in the strobila of two longitudinal nerves which are situated on the outside of the water-vascular system.

The vascular system, which I could only study in the segments, is situated rather far from the lateral side (in a proglottides 1.65 mm. in diameter the vascular system is 0.4 mm. distant from the side). It consists of two ventral vessels and two dorsal vessels placed above the first. These two pairs of vessels are surrounded, as in *P. torulosa*, by a musculature. The ventral vessels are joined in every segment by a large vessel.

The male sexual glands are composed of 28 testicles situated on the dorsal side of the internal parenchyma. The vas deferens is very long, and presents numerous convolutions converging towards the left side, that is to say, the side on which issues the sexual canals in all the Prosthecocotylæ. The interpretations of the male sexual apparatus given by Linstow are inexact, which is due probably from the fact that this author did not make sections. The cirrus-pouch, into which enters the vas deferens, presents a form and a structure which is, so to speak, identical in all the species of Prosthecocotyle. It is spherical, and contains a vas deferens with thick walls. The cirrus, which is very long, passes through the canal that I called in the description of P. torulosa, 'male cloacal canal.' This canal, having the shape of a very prominent papilla, has, as well as the genital cloaca, into which it enters, a complex structure. The papilla and cloaca are carpeted by the continuation of the cuticula of the body. Their muscular system is composed of internal circular fibres and of others with a radial disposition. The whole is surrounded by a system of fibres proceeding from the transverse musculature of the parenchyma. So the whole presents, in transverse sections, the structure of a sucker (figs. 6, 7). Into the deep genital cloaca, with wrinkled

VOL. XXII. 2/12/99 2 T

walls, the vagina passes out, on the ventral side of the male The vagina is large at the beginning, and surrounded by a strong musculature, essentially formed by circular fibres, which cross each other. At the entrance into the internal parenchyma, the diameter of the female canal diminishes, to swell again as soon as it has passed the water-vascular system. second extension, spindle-shaped, is equally muscular; but here it is the longitudinal fibres which prevail. It is a receptaculum seminis similar to that of P. torulosa. From this point the vagina goes towards the middle of the proglottis to meet with the canal that comes from the ovary. Before joining, the canal narrows suddenly, presenting at this point a stronger musculature. It is probably a sphincter which prevents the spermatoids returning. The sexual glands are composed of an ovary, lobed, situated ventrally, and occupying all the length and breadth of the parenchyma placed between the water-vascular system. At the origin of its canal is situated a muscular funnel: an egg-aspirator. The vitelligenous gland, situated in the middle, lies ventrally, and is small; it is placed before the ovary. Where the vitelloduct meets the oviduct is to be found a shell-gland from which the canal runs towards the dorsal side to open into the uterus, which has the same shape as in P. torulosa (fig. 7). In the last proglottides the uterus fills the whole internal parenchyma. I could not study the hooks of the embryo, the eggs not being in a sufficiently advanced state. As I had not the last proglottides, I cannot say if there are three shells surrounding the eggs.

It is very probable that in this species the fecundation of the eggs is often produced by the male organ of the same proglottid; but the very complex disposition of the musculature of the cloaca, and the peculiar development of the male papilla, lead me to believe that fecundation may also take place between different proglottides.

EXPLANATION OF THE PLATE.

- ml. longitudinal muscles.
- mt. transverse muscles.
- md. dorso-ventral muscles.
- nl. longitudinal nerve.
- ex.v. ventral canal.
- ex.d. dorsal canal.
 - gel. genital cloaca.
 - mc. male dorsal canal.
- mp. male papilla.
- cp. cirrus pouch.
 - c. cirrus.
- v.d. vas deferens.

- t. testicle.
- v. vagina.
- rs. receptaculum seminis.
- ovd. oviduct.
 - cu. canal of the uterus.
 - s. shell-gland.
- vitel. vitelloduct.
 - o. ovary.
 - mf. muscular funnel.
 - v. vitelligenous gland.
 - ut. uterus.

All the figures are drawn with Abbé's drawing apparatus.

Prosthecocotyle torulosa (Linstow).

- Fig. 1. Head of P. torulosa.
- Figs. 2, 3. Transverse sections of half of segment.

Prosthecocotyle heteroclita (Dies.).

- Fig. 4. Head of P. heteroclita.
- Fig. 5. Young segment.
- Fig. 6. Horizontal section of segment.
- Fig. 7. Transverse section of segment.
- Fig. 8. Sagittal section in the median plane of segment.