
(Read 5th May 1884.)

The Norway lobster, *Nephrops norvegicus*, on account of its abundance in the Firth of Forth, and the consequent ease with which it can be obtained from the Newhaven market, is given to the practical classes in the Natural History Laboratory of Edinburgh University for dissection, as an example of the decapodous Crustacea. One day in December last, while I was superintending the work of a class engaged in the study of this animal, one of the students, whose name I have unfortunately forgotten, called my attention to some globular protuberances on the intestine of the specimen he was dissecting. At the time I was unable to answer his questions any further than to say that the protuberances were the cysts of a parasite, and I put the specimen by for subsequent examination. On opening the cysts afterwards I found in them a small white worm, which proved to be a Trematode possessing novel characteristics. In the following paper I shall describe this parasite, and show that it is so distinct from all Trematodes hitherto known as to constitute a new genus. On several occasions I had the pleasure of examining the animal in the company of my friend and former colleague, Mr Duncan Matthews, and some of the points in its structure were first noticed by him.

I will first describe the animal as completely as possible, and then deal with the manner of its occurrence and its relation to other Trematodes.

The worms when taken out of the cysts are elongated and cylindrical in shape, one surface, the ventral, being slightly flattened; they vary in length from 75 mm. to 80 mm. They are white in colour and somewhat opaque, so that there is considerable difficulty in making out their internal anatomy under the microscope. The body tapers towards each end, the thickest part being near to the oral or anterior extremity. The arrangement of the organs is bilaterally symmetrical. The mouth is a small simple circular aperture, situated on the ventral surface, close to the anterior end of the body. Behind it, along the median line of the ventral surface, is a single row of large muscular suckers, which diminish gradually in size towards the posterior end. The margins of the mouth are muscular, and its cavity can be dilated and contracted, so as to act as an additional sucker. When the animal is viewed with its ventral surface upwards, slightly compressed by a cover-glass, and under a...
low power, it presents the appearance shown in Plate XXXIX. fig. 1. The ventral series of suckers is seen along the median line; each of them has a central depression varying in size according to the state of contraction, and round this is the projecting rim, in which can be seen the radiating muscles by which the sucker is dilated. The number of suckers present varies in different individuals according to their age and size,—the smallest specimens, such as the one shown in fig. 4, may have as few as 7, the larger usually have 15 or 16, while in the largest I have counted as many as 22. No doubt specimens might be found the totals of whose suckers would supply all the intermediate numbers between these.

The suckers are always more difficult to distinguish at the posterior end of the series, where they are very small, and they evidently increase in number at this end, just as the segments of a Chaltpod. It is this approach to metamorphism which renders the creature specially interesting. The metamorphism, however, does not extend to any of the other organ systems, and consequently the animal cannot claim among the Trematodes so isolated a position as the *Gnada segmentata*, described by Lang, among the Turbellarians. From the disposition of the system of suckers, I have named the animal Stichocotyle, adding Nephropis for the specific name, from the name of its host.

The surface of the body is marked by closely set transverse folds, which are indicated in fig. 1, between the suckers. These folds, seen in optical section, give the body a crenated outline, which is also indicated in the figure. When the body is much extended, either by compression or by the muscular movements of the animal, the folds disappear; they are probably due to the presence of an inelastic cuticle, although neither in the optical nor actual section of the integument can a separation between cuticle and epidermis be distinguished. The external layer of the body wall, as seen in optical section in the living animal, is homogeneous and transparent, and of considerable thickness.

The most conspicuous of the internal organs are the main canals of the water-vessel, or excretory, system. These are two in number, one running down each side of the body through its whole length. Their size, in comparison with that of the whole animal, is extremely large; their walls are thrown into transverse folds. The interior of the canals is crowded with large spherical concretions similar to those found in the excretory system of other Trematodes and of Cestodes. These concretions, during the examination of the living animal, are continually moving with considerable rapidity, the contractions of the body forcing them suddenly from one part of the canal to another. In the middle line, between the main excretory canals, is the intestine. From the mouth can be traced a narrow oesophagus, dilating into a muscular pharynx, with thick walls, and this leads into an intestine which diminishes slightly in
diameter towards the posterior end, where it ends blindly. The intestine is quite simple, and has no branches or diverticula.

When a specimen is examined with its dorsal side upwards, and considerably compressed, the intestine and lateral excretory canals are seen with great distinctness, as there are no muscular thickenings dorsally to form suckers. Fig. 2 shows somewhat diagrammatically the view thus obtained. At the posterior end the two lateral canals terminate in muscular portions, which pass inwards behind the intestine, and unite to form a single median chamber with thick muscular walls. This chamber opens in the usual way by a pore on the dorsal surface, close to the end of the body. The rhythmical dilatation and contraction of the terminal chamber is very pronounced, and it commonly happens, when the animal is under compression, that one of the spherical bodies contained in the lateral canals passes into the terminal chamber, and is expelled from the dorsal pore with some force. The appearance of the terminal part of the excretory system under a high power is shown in fig. 3.

When the living animal is very attentively examined with an objective of high power, by careful focussing fine ciliated canals can be made out between the large lateral canals and the dorsal surface. It is probable that, like the corresponding fine canals in other Trematodes, these open into the main lateral canals, and are, on the other hand, in communication with the intercellular spaces of the body-parenchyma; but owing to the opacity of the tissues, I have not yet succeeded in tracing out these relations. The cilia, whose motion alone enables one to trace the tubules in question, are of great length, and are situated on the walls of the tubules at intervals. I have not been able to discover any "étonnoirs ciliés" at the ends of the branches of the system of tubules, like those described by Fraipont.* I have followed the ciliated tubules sometimes for considerable distances. Their course is somewhat irregular, but maintains a longitudinal direction. They branch occasionally, but the branches never extend into the median region of the body above the intestine. I have not found any tubules on the ventral side of the body, but they extend forwards beyond the anterior limit of the main lateral canals.

I have now described the general disposition of the digestive, excretory, and integumentary systems of the animal, and have hitherto mentioned nothing which cannot be made out in living specimens. No reference has been made to the generative or nervous systems. In the stage of the animal's history which is passed within the body of Nephrops neither of these systems is developed. I shall refer to structures which may be their rudiments. Special sense organs are altogether absent.

In order to examine the histological structure of the tissues, I have pre-

* "Rech. sur l'appareil excretateur des Trém. et Cestoides," Julien Fraipont, Arc. de Biologie, Tom. i. 1880.
pared transverse sections in continuous series from specimens preserved with picro-sulphuric acid, and stained with borax-carmine. The specimens chosen for this purpose were of the medium size, carrying about 16 suckers. The sections are all very similar to one another, differing chiefly in the relation which they bear to the series of suckers. In one taken from the middle of the series, the intestine is seen in the centre, elliptical in outline, the long axis of the ellipse being dorso-ventral. The epithelium of the intestine is thick, and composed of large nucleated cells, which form sometimes more than one layer, and are not quite regular in arrangement. Both in the living animal and the prepared section it can be seen that the cells of the intestinal epithelium are rapidly proliferating; the free ends of the cells project into the lumen in various degrees, and a number of detached cells are seen lying free in the interior. In the living animal these cells float about under the influence of the movements of the body, and are occasionally expelled from the mouth. Some of them contain minute round granules.

On each side of the intestine is the section of one of the main lateral excretory canals, in which there is no distinct epithelium to be seen. There are nuclei in the walls, and the cavity may be lined by an epithelium of extremely thin cells, to which these nuclei belong. The walls of the canal are extremely thin.

The parenchyma of the body, or mesenchyma, appears in the sections as a fine reticulum with deeply stained nuclei at the nodes. The actual structure of the mesenchyma in Trematodes has been much disputed,* some observers maintaining that the intercellular spaces are globular and the cells stellate; others, vice versa, that the cells are globular, and the intercellular spaces reticulate. In the living Stichocotyle the mesenchyma is seen to be crowded with minute bright refringent granules, which seem to be contained in intercellular spaces, as they move through considerable distances in parts of the animal which are in active contraction. They are shown in fig. 3.

The muscular layers of the body wall are imperfectly differentiated; they are represented by a zone of closely crowded nuclei at the periphery of the mesenchyma, and, external to this, a zone of small dots, which are probably the sections of longitudinal fibrils. The account of the muscular layers of the integument in the young of Amphilina, given by Salensky,† agrees pretty closely with the state of things in my sections, except that he mentions nuclei in the external of the two layers, and in the zone of dots I have described there are no nuclei.

The sucker is composed chiefly of elongated cells, whose long axis is perpendicular to the epidermis. These are simple muscular cells which dilate the

* Vide Fraipont, loc. cit., p. 428.
cavity of the sucker. Nuclei are scattered through the tissue, each cell probably possessing one. The muscles which contract the cavity of the sucker are not so conspicuous. The tissue of the sucker is separated from the tissues of the body by a thin limiting membrane, which is continuous at its periphery with the limiting membrane of the epidermis. This is an arrangement which is not easily explained, as, the muscles of the sucker being probably a specialisation of the ordinary muscles of the body wall, it would be expected that the continuity between the two would be maintained.

Beneath the lateral excretory canal of the right side, in the anterior sections, is an area occupied by very closely crowded nuclei. This can be traced through successive sections of the series as far as the end of the fifth sucker. It passes from its first position, under the right main canal, to the left side of the same canal, at the same time becoming thicker, and towards its termination becomes so broad as to extend beneath the intestine from the right canal to the left. There is thus an irregular cord of small unmodified cells extending through a considerable part of the length of the body, and it is possible that the generative organs of the adult are derived from this.

The most external layer of the body representing the epidermis and cuticle, is in sections, as in the living animal, quite homogeneous. I have not yet been able to distinguish in it either nuclei or cell boundaries, or a separation between epidermis and cuticle. The layer becomes thinner where it lines the cavity of the sucker. In the living animal small funnel-shaped openings are seen in the epidermis, which may be the apertures of glands, but as they are not visible in the sections it is possible that they are only fractures produced by compression.

The only trace of tissue which may belong to the nervous system is a tract composed of very fine fibrils in some of the sections anterior to the mouth. This tract forms a band extending horizontally across the body near to the dorsal side. The fibrils of which it is composed are extremely minute, and the whole tract is destitute of nuclei. It is shown in fig. 6, and may represent the cerebral ganglion. A pair of processes from this mass of tissue can be traced through the succeeding two or three sections, which are probably the rudiments of a pair of lateral nerve-cords. They pass downwards towards the under side of the main excretory canals.

The cysts in which the animal occurs are scattered on the extremely thin walls of the posterior part of the intestine of Nephrops, in the region of the abdomen. They sometimes contain more than one worm, as many as six having been taken by Mr Matthews on one occasion from a single cyst. Usually the wall of the cyst is soft and opaque, and white or light yellow in colour. It is of a cellular nature, and is apparently a pathological product of the tissue of the intestine of the host.
The cysts vary in size with the age and size of the worm within, and the youngest and smallest ones are brittle and dark brown in colour. A very young worm taken from such a cyst is shown in fig. 4. It has only seven suckers. The worm in all cases, when placed on a slide in a little water, exhibits movements of contraction and extension, and coils or straightens its body, but is not able to travel over much space. When an infected crayfish is opened which has been twenty-four hours out of water, the worms are often found to have escaped from the cyst, and are found lying on the muscles; but I think this does not take place while the Nephrops is living. The number of cysts varies considerably. I have sometimes found them covering the posterior part of the intestine completely; and in other cases only two or three of the very smallest brown cysts were present. The diameter of the cysts varies from 0.5 mm. to 2 or 3 mm. I have taken as many as forty worms from a single Nephrops.

The proportion of specimens of Nephrops infected is not small. In one case I found three out of eight contained the parasite. Usually out of a dozen opened three or four are infected; but sometimes a dozen may be searched without a single parasite being found. My observations have extended now over nearly four months, and I have not yet found any variations in the state of the parasite.

I have not found the parasite in any other part of the body of Nephrops except the intestine; and I have no evidence to show whence it is derived, what is its mature state, or in what conditions its adult stage is passed.

It seems probable that the eggs are taken into the stomach of Nephrops with its food, and that an embryo escapes from the egg, which pierces the wall of the intestine, and there develops into the stage of the worm which I have examined. The further development most likely takes place in the body of some large fish which feeds on Nephrops; but hitherto no Trematode is known living inside the body of a marine fish except the Calicotyle Kroyeri, which is found in the cloaca of rays, and Encotyllabe Pagelli in the mouth of Pagellus centrodontus.*

In passing on to consider the affinities of the parasite, it may be set down as obvious that it is in every respect a typical Trematode. The characters of the water-vessel system and of the suckers could not be found outside that class. But the arrangement of the suckers is entirely novel. A serial arrangement of the suckers is not uncommon among Trematodes; but there is no other genus in which they form a single series extending along the median ventral line through nearly the whole length of the body. The series when present is usually double. Microcotyle† has in the posterior third of its body

* Van Beneden et Hesse, Mém. Acad. Roy. de Belg., Tom. xxxiv.
† Ibid.
a series of small suckers on each side. They are very numerous, and all of the same size. In Octocotyle * there are, near the aboral extremity, four pairs of lateral suckers, one pair behind the other. The suckers of Gastrocotyle † form a single series along the edge of a projecting membrane on the right side of the body. ERNST ZELLER describes a serial repetition of pairs of suckers as an occasional abnormality in Diporpa. ‡ At the posterior extremity of this genus there is a pair of large suckers forming divergent projections. ZELLER met with a specimen in which the single pair was replaced by three pairs, one behind the other. In all these cases the suckers are provided with chitinous hooks, as in nearly all the Polystomidae. Stichocotyle is without chitinous armatures in any part of its body. Until the adult form is found and its anatomy examined, it is impossible to say anything more definite about the position of Stichocotyle than that it belongs to the Polystomidae, though it differs from all other Polystomidae in passing through an encysted stage within the body of another animal.

I hope before long to trace out the whole life history of this interesting form, as at the Granton Marine Station I shall have good opportunities for carrying on the search after its earlier and later stages. In concluding the present account I have to express my warmest thanks to Dr ARNOLD LANG, of the Naples Zoological Station, who kindly sent me some valuable suggestions and references.

EXPLANATION OF PLATE XXXIX.

Letters of Reference.

bis. Cord of blastema.
ci. ca. Ciliated tubules of water-vessel system.
cs. Spherical concretions in lateral canals.
ep. Epidermis and cuticle.
e. ap. External aperture of water-vessel system.
f. ce. Free cells in lumen of intestine.
gl. Openings of dermal glands (?).
int. Intestine.
int. cp. Epithelium of intestine.
l. ca. Lateral canals of water-vessel system.
me. Mesenchyma.
mus. Muscles of sucker.
m. Mouth.
me. gr. Granules in mesenchyma.
ne. Cerebral ganglion.
ph. Pharynx.
ps. Series of suckers.
ta ch. Terminal chamber of water-vessel system.

* VAN BENEDEN et HESSE, Mém. Acad. Roy. de Belg., Tom. xxxiv.
† Ibid.
Figs. 1, 2, 3, 4 were drawn from fresh specimens. All were drawn without the aid of a camera lucida.

Fig. 1. Ventral view of Stichocotyle, as seen under slight pressure.
Fig. 2. Optical section of the whole animal, seen with dorsal surface upwards.
Fig. 3. Optical section, showing termination of water-vessel system.
Fig. 4. Very young specimen, with seven suckers.
Fig. 5. Transverse section, passing through middle of first sucker of moderate-sized specimen.
Fig. 6. Section through pre-oral region of same specimen.

The fractions represent the relation of the diameter of the drawing to that of the object.