TRANSACTIONS

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W. Charles B. Wilson -

ON PENNELLA BALÆNOPTERÆ: A CRUSTACEAN, PARASITIC ON A FINNER WHALE, BALÆNOPTERA MUSCULUS.

SIR WILLIAM TURNER, K.C.B., D.C.L., F.R.S.

[WITH FOUR PLATES.]



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XVIII.—On Pennella balænopteræ: a Crustacean, parasitic on a Finner Whale, Balænoptera musculus. By Sir William Turner, K.C.B., D.C.L., F.R.S. (With Four Plates.)

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Introduction.

In September 1903 I received a bottle containing twelve specimens of a large parasite presented to me by Mr Chr. Castberg, the manager of a Norwegian whaling company which has established a fishing station at Ronasvoe in the north of Shetland.* In his letters Mr Castberg stated that the parasites were attached to a Finner whale, which, from its size, the mottled character of the whalebone and the pointed head, was obviously a Razorback—Balænoptera musculus. The parasites were numerous, and were fixed to the back of the whale, and the attached end penetrated through the skin into the blubber. Although Mr Castberg had seen many hundred whales, this is the first occasion on which he had met with this form of parasite.

From the characters of the specimens I concluded that they were a giant species of a parasitic Crustacean, of the family Lernæidæ, and on further investigation I associated them with the genus Pennella (Oken).

This genus is now regarded as including those members of the Lernæidæ which, as studied in the females, have the head stunted and club-shaped, with horn-like arms radiating from its base; the body elongated, cylindriform, not bent into a sigmoid shape; the anterior part of the body attenuated, but widening further back; a pair of genital openings with depending ova strings; the terminal part of the body caudate, giving origin to the characteristic bristle-like pennate appendages; pairs of minute rudimentary feet springing from the ventral surface of the body close to the base of the head.

From the time of Aristotle, naturalists had recognised that the Tunny and Swordfish were infested by worm-like parasites, fastened to the skin near the fin. Rondeletius,

^{*} I am indebted to my valued correspondent, Mr Thomas Anderson, merchant, of Hillswick, Shetland, for putting me into communication with Mr Castberg.

Gesner and Salvianus, in their respective treatises, written in the sixteenth century, described such parasites, and Rondeletius and Gesner figured specimens from the tunny.

Boccone published in 1674 an account of parasites found on the swordfish, Xiphias, implanted in its flesh, which he named Sangsue or "Hirudo cauda utrinque pinnata," and he gave a figure. It would seem as if this animal was different from that described by Rondeletius and Gesner. Boccone had figured a very interesting object, named by him a "poux" or "pediculus," as big as a pea, attached to the ventral surface of the parasite, immediately in front of the genital openings. He stated that it was fixed as firmly to the parasite as a limpet was to a rock. I am disposed to regard this so-called "pediculus" as the male of the female parasite to which it was attached. Its small size compared with that of the female, and its position and attachment close to the genital openings, corresponded with that of the male of the parasitic crustacean, Chondracanthus lophii, described and figured by Dr H. S. Wilson and myself in 1862.

Linnæus, in the Systema Naturæ, 1758, classed amongst the Vermes Zoophyta the genus Pennatula or Sea Pens, and he named the parasite described by Boccone, which infests Xiphias, Pennatula filosa. In 1759 J. L. Odhelius contributed to the Amanitates Academicæ of Linnæus, a dissertation entitled "Chinensia Lagerstromiana,"* in which he gave the characters of Pennatula sagitta (p. 257, and fig. 13), a parasite infesting Lophius histrio, the sea-bat of the China Sea. John Ellis reproduced in 1764 Boccone's figure of P. filosa and Odhelius's figure of P. sagitta. In 1802 Holten recognised a parasite on the flying fish, Exocætus volitans, which he named P. exocæti, specimens of which, burrowing into the abdominal cavity of that fish, have been recently described, 1901, by Mr Andrew Scott.

OKEN classed the Lernæidæ amongst the Mollusca, removed these parasites from the Sea Pens, Pennatula, and placed them in a distinct genus, Pennella, whilst DE BLAINVILLE suggested Lerneopenna as the generic name. Cuvier and naturalists generally had adopted OKEN'S term, though some preferred the spelling *Penella*.

Additional species were discovered from time to time. Chamisso and Eysenhard described Penella diodontis from the branchiæ of Diodontis mola, captured in the Pacific; Dekay named P. sagitta as adhering to Diodon pilosus, and von Nordmann, in his description of P. sagitta from Lophius marmoratus, thought that it and Dekay's specimen were the same species. Angus found a parasite on a species of Coryphæna near the gills, which William Baird named Penella pustulosa. Milne Edwards stated that Pennella sultana had been found in the mouth of Carenx ascensorius. Steenstrup and Lütken gave an account of P. varians which infested a "Dolphin," the species of which was not determined. E. Perceval Wright described Pennella orthagorisci from specimens obtained from Orthagoriscus mola caught in Cork harbour in 1869. They were implanted in the skin on either side of the dorsal fin, and the total length of the parasite from the head to the anal opening was 7 inches. He

^{*} Named after the Swedish Councillor, Magnus Lagerström.

also stated that Baird referred a Pennella from a sunfish captured in Cornwall to $P.\ filosa$. G. M. Thomson gave an account (1889) of a Pennella found on a swordfish (Histiophorus herschelii), which he named $P.\ histiophori$. Ramsay H. Traquair has called my attention to two specimens of Pennella in the Collection of the Royal Scottish Museum, which he had provisionally named $P.\ orthagorisci$. Possibly they may have been included in the Natural History Museum of the University, which was transferred many years ago to the Royal Scottish Museum, but nothing definite is known of the animal on which they were parasitic, or when they were obtained. One specimen was deprived of the head and arms; the other had a head and two lateral arms, but no dorsal arm, and it was about 5 inches long.*

Observations on the Lernæidæ during the first quarter of the last century induced naturalists to consider that these parasites were not to be regarded as Worms, Molluscs, or Zoophytes, but that they had an affinity to the Crustacea. Their position was finally adjusted in 1832 by ALEXANDER VON NORDMANN, who, from the young having the non-parasitic character of Cyclops, from the segmented structure of the male, which is a free swimming animal, though it may become attached to the female, and from the position and characters of the feet, definitely placed these curious animals amongst the Crustacea, in which they are now generally regarded by naturalists as forming a family of parasitic Copepoda.

An important extension of our knowledge of the hosts to which different species of Pennella may become attached was made when it was ascertained that specimens had been obtained imbedded in the skin of species of whales frequenting the North Atlantic Ocean. Steenstrup and Lütken published in 1861 a memoir in which a Pennella was described as attached to a Hyperoodon rostratus captured in 1855 south of the Faroe Islands; they named the parasite Pennella crassicornis. They referred to an observation made some years previously by von Düben that a Pennella, species not named, had been obtained from a Finner whale. In 1866 G. O. Sars stated that specimens of a Pennella with the head buried in the blubber were seen attached to Balænoptera musculus. In 1877 Koren and Danielssen published a memoir on a Pennella found on Balænoptera rostrata, and preserved in the museum at Bergen, which they had named Pennella balænopteræ twenty years previously. specimens from B. rostrata, buried with the head and horn-like arms in the blubber in the vicinity of the external organs of generation, had subsequently been added to this museum. Van Beneden, in his memoirs on the natural history of the Cetacea, referred to these Balænopteræ as serving as hosts for a Pennella; and he further stated, though without giving very definite authorities, that this parasitic crustacean had also been found on Balænoptera sibbaldii, and probably on B. borealis.

^{*} Dr Traquair showed at the meeting of the Royal Society at which this memoir was read two dried specimens of *Pennella exocæti*, which he had received in November 1904 from Captain Pater. It appears that when Captain Pater was on a voyage in the South Pacific a flying fish flew on to the ship; and deeply rooted in the wall of its abdomen, behind the pectoral fin, were the two specimens of Pennella, which he removed and sent to the Royal Scottish Museum.

As the memoir of Koren and Danielssen contains a description of the external characters with observations on the internal anatomy of the female *Pennella balænopteræ*, and is illustrated by a plate with nine figures, I have made a careful comparison of my specimens with their description and drawings.

EXTERNAL CHARACTERS OF THE FEMALE.

As the specimens in my possession, like those studied by Koren and Danielssen, were not uniform in length, I have measured the longest and the shortest in order to show the variation, and in the following table I have recorded their chief dimensions, alongside of the corresponding measurements of two of the specimens described by the Norwegian naturalists.

		K. & D.		TURNER.	
		A.	В.	A.	В.
Whole length of parasite .		320 m	m. 300	294 mr	n. 206
Length of head .		7	11 6	5 1	4
Breadth of head .		8	7	5 ,	4
Longest horn-like arm .		15	11 14	33 1	23
Greatest thickness of arm .		2	., 2	3 ,	3
Length of thoracico-abdominal part		315	294	289	202
Greatest thickness of same .		6	11 6	4.5	4
Length of pennated abdominal part		45	42	30 ,	25

It is obvious from these measurements that the females varied considerably in length; and as my shortest specimen had a pair of long ova strings attached to the ventral surface, it may be assumed to be adult equally with the longest. It will be noticed that neither of the two specimens is so long as the shortest of those recorded by Koren and Danielssen, whilst their longest specimen was 320 mm. ($12\frac{1}{2}$ inches). *P. balænopteræ* is therefore a giant amongst the Copepoda.

The head, both in length and breadth, slightly smaller than in their examples, had a stunted, club-shaped appearance. Its colour, that of the arms and of the upper part of the so-called thoracic region, was brownish-yellow, whilst the lower part of that region and the entire extent of the abdomen was of a dark purplish hue with a shade of green, even after the specimens had been for several months in spirit. The head, arms, and upper part of the thorax were imbedded in the skin and blubber, on the juices in which the parasite lived. The greenish-purple-tinted part of the body floated in the sea-water, and was more or less in contact with the skin of the whale. Seen through the medium of the water, it would approximate to the colour of the skin, and would furnish an example of protective mimicry.

The summit of the head was studded with numerous shallow, papilla-like tubercles; they also surrounded the cleft-like opening of the mouth, which formed a deep mesial groove extending for a small distance on the ventral surface of the head. A short groove was present on the dorsal surface, which had, at its upper end, a blunt, hook-like tubercle at each margin, but in no instance did I see a pair of pointed, claw-

like antennæ, relics of the free Cyclops stage of development, such as are represented by Koren and Danielssen in their figure 9, tab. xvi.

From the base of the head three horn-like arms arose, which extended almost horizontally outwards; they were the anchors of attachment implanted in the blubber of the whale. One sprang from the mesial dorsal surface, whilst the others were right and left lateral. They varied in length in the same specimen, and the dorsal arm was usually the shortest. They differed also in thickness and were irregular on the surface; the free end was blunt (Plate I. figs. 1, 2), and in one specimen a lateral arm was bifurcated.

The body of the parasite extended from the base of attachment of the arms to the free end of the pennated portion. It varied materially in thickness in different parts of its length. Immediately below the arms its transverse diameter was 3 to 4 mm.; it was somewhat flattened on both dorsal and ventral surfaces, and on the ventral surface, close to the mesial line, most of the specimens showed pairs of appendages. They were so minute as to be scarcely visible to the naked eye. In two specimens four pairs were seen, as had been figured by Koren and Danielssen. In others, two pairs, or even a single pair, only were recognised, and in a few they were not visible. Their recognition was assisted by the presence of a spot of dark pigment. Four is without doubt the typical number of these feet-like appendages, though it would seem as if this number was not always preserved in the process of transformation from the embryonic cyclopoid form to their retrograde condition in the adult (Plate I. fig. 2).

Eight mm. from the base of the arms the transverse diameter of the body diminished to 1.5 mm., and for a considerable distance it preserved this diameter; it was cylindrical in shape, smooth on the surface, and not unlike in form and colour a steel knitting-needle. It was an elongated neck-like division of the body, very characteristic of the parasite, and may be regarded as the thoracic segment.

The body was prolonged into the abdomen, which increased in bulk, measured 4 mm. in breadth, lost its smooth appearance, and was marked by numerous transverse constrictions, between which minute bead-like projections were arranged in rows. The abdomen was the widest and most deeply coloured part of the body; as it contained both alimentary canal and the female genital organs, it may appropriately be named the genito-abdominal segment. At the lower end two genital openings were seen on the ventral surface, from which depended the pair of ova strings. Immediately above these openings was a small rounded eminence, to which probably the male parasite may attach itself when engaged in impregnation.

The ova strings were a pair of very slender threads, yellowish-brown in colour, and of remarkable length; in one parasite each string measured 400 mm. (15.7 in.). They floated free in the surrounding medium; they were sometimes almost straight, but at others they had an undulating character.

The terminal part of the body was prolonged behind the genital openings from 25 to 30 mm., varying in the different specimens; it was only 2 mm. in transverse diameter

and came to a free end. It had a caudate appearance; but as it contained the intestinal end of the alimentary canal, it should be regarded as the caudate segment of the abdomen. The analorifice was situated in a cleft at its free end. Its dorsal surface was marked by transverse constrictions, and from its ventral surface a number of bristle-like structures arose, which gave to the terminal part of the body the pennate character which has decided the generic name.

CHITINOUS COAT.

The chitinous coat of the parasite was translucent, firm, and so tough as to turn the edge of the razor. It was for the most part homogeneous throughout its substance, but in places delicate lines, parallel to each other and to the plane of the surface, gave it a laminated appearance, as if it had been formed by superposition of layers. It varied in thickness in different regions, as was seen both in longitudinal and transverse sections. In the head, this coat was about $\frac{1}{3}$ rd of a mm. thick, but at the origin of the arms it was about $\frac{2}{3}$ rds of a mm. In the arm itself the thickness varied in different parts. In proximity to the head it formed about $\frac{2}{3}$ rds of the diameter of a transverse section, in the middle of the arm about $\frac{1}{3}$ rd, and near the free end about $\frac{1}{2}$. In the attenuated thoracic region the proportion was about $\frac{1}{2}$, in the genito-abdominal part it was less, and it was a little thinner on the ventral than on the dorsal aspect. In the pennated abdomino-caudate segment it represented about $\frac{1}{3}$ rd of the transverse diameter of the parasite.

On the outer surface of the chitinous envelope a layer of cuticle was present, which was usually closely adherent to the chitin, but in places it was partially detached, and had probably been drawn off in cutting the sections. When examined microscopically it was seen to be striated in a direction perpendicular to the plane of the surface; higher magnification showed this appearance to be due to short columnar cells, which were arranged parallel to each other. In sections where the displaced cuticle had been turned over so as to expose its free surface, the broader ends of the columnar cells were seen to be at that surface, and by their close apposition to each other to form a continuous layer.

The chitinous wall was lined by a membrane, which in various localities, to be subsequently referred to, was richly pigmented (figs. 17, 24, 26).

In the papilla-like tubercles, in the parts of the head not occupied by the muscles, in the thickened part of the body immediately below the head and in the arms, an areolated tissue was situated within the membranous lining of the wall of chitin.

STRUCTURE OF THE HEAD.

The internal structure of the head was examined in a series of transverse and longitudinal sections from its summit to the base of attachment of the arms. The

papilla-like tubercles formed the most marked feature of the summit. Each had a definite chitinous envelope, which inclosed an areolated tissue, the areolæ of which varied materially in size, and corresponded in character with the tissue in the axis of the arms to be subsequently described.

Within the tuberculated summit numerous transversely striped muscular fibres occupied a large proportion of the space dorsally and laterally inclosed by the chitinous envelope. They arose from the inner surface of the envelope, which in transverse section had a ridge and furrow-like character. The muscular fibres in this region situated laterally to the mesial plane converged from their origin and seemed to end in a common tendon, which was attached to the papilla-like tubercles situated on the side of the cleft which formed the oral aperture (figs. 5, 7, 8). Their apparent function was to draw the sides of the cleft asunder, widen the aperture, and by successive contractions and relaxations to convert the cleft into a suctorial mouth. In transverse sections of the head below the tubercles the muscular fibres were less numerous; those situated in proximity to the mesial plane converged on the dorsal wall of the alimentary canal, on which they could act directly as dilators. The fibres situated further from the mesial plane reached the dorsal aspect of a pair of bodies, to be immediately described, which stained readily with carmine. The striped muscular fibres were seen as low down as the origin of the arms, but they were absent immediately below these appendages, and their place was to a large extent taken by the areolated tissue.

I have more than once referred to a tissue, which I have named 'areolated,' situated in the head, in the part of the body immediately below the head, and in the arms into which it was prolonged at their base of attachment. In a subsequent section I shall have to call attention to a similar tissue in the abdomen. Koren and Danielsen described a layer of adipose matter, in most places not very thick, though it could form isolated fatty agglomerations; in the head, arms and the upper thoracic division of the body it formed a thick stuffing, and corresponded in its position to the areolated tissue seen in my specimens: the adipose tissue was composed of fat cells, which, they say, had one or more ramifications on the cell.

In its general characters the areolated tissue consisted of a meshwork of connective tissue, continuous with the membranous lining of the chitinous wall of the parasite. In the strands of this meshwork, more especially in its peripheral part, nucleated cells were seen in places in considerable numbers, which in size and general appearance were not unlike leucocytes. The areolæ of the meshwork varied in size, the largest being just visible to the naked eye, whilst the smallest required a magnification of two hundred to three hundred diameters. In specimens taken from the head, when the tissue was teased with needles and examined in glycerine, the areolæ were seen to contain rounded or ovoid cells, which, like fat cells, refracted the light strongly, and showed the characteristic reaction of fat with osmic acid; in the act of teasing, many of the fat cells were ruptured and oil globules escaped. In

sections through the head and arms, which had been treated with nitric acid in order to soften the chitin previous to making the section, subsequently soaked in alcohol, and then mounted in Canada balsam, the tissue was modified in appearance. Although some of the cells retained the ovoid form and to some extent the refracting character, the majority had more or less irregular outlines, and their contents had generally the appearance of a granular cell-plasm, not usually staining strongly with carmine; though sometimes the granules were relatively large, and stained more deeply with carmine, as if they had a nuclear character. It would seem as if, with the disappearance of the fat, the cell-plasm had come into view.

In certain localities the areolated tissue showed characters deserving of more detailed notice. In the arms, where they adjoined the head and where the areolated tissue was small in proportion to the thickness of the arm, two large areolæ, each containing granular cell-plasm with a nucleus, were very distinct (fig. 11). About the middle of the arm, also, a pair of areolæ, containing granular cell-plasm, similar in size and in close relation to the wall, were present; but as the areolated tissue in this part of the arm was much more abundant than near the head, a cluster of large areolæ also occupied the central area of the tissue (fig. 12). A somewhat similar appearance was seen in the relatively smaller amount of this tissue near the tip of the arm.

In some sections the areolated tissue in the arms was modified in a peculiar manner. Whilst in some of the areolæ the refracting character of fat cells was distinctive, many others, especially those of large size, were crowded with nuclei, which stained deeply with carmine. The nuclei were so closely set that the amount of cell-plasm associated with each nucleus was extremely small, and the latter dominated in quantity and distinctness over the cell-plasm. It seemed as if an extensive proliferation of the nuclei had taken place (fig. 13).

In sections through the head in proximity to the arms, where the areolated tissue was relatively abundant, the largest areolæ with their contained cells occupied the mid-area of the tissue, whilst the smaller areolæ formed its peripheral part (fig. 9). The tissue which constituted the axis of the papilla-like tubercles of the head consisted of the smaller type of areolæ, though they were not uniform in size, as some were four or five times larger than others.

It should be noted that the part of the parasite immediately below the arms had on the ventral surface the pairs of limb-like appendages already referred to. They were so extremely rudimentary that it was difficult to recognise them with the naked eye, and sometimes even they were absent. It is within this part of the body that the areolated tissue was most abundant. Had the limbs been functionally active, one cannot doubt but that an adequate amount of striped muscle would have been developed in this region as their motor apparatus; but, under the changed conditions, it was no longer required, and its place had been taken by a passive, areolated tissue containing fat cells.

In addition to the esophagus, the muscular fibres, and the areolated tissue, the

chitinous wall of the head inclosed three objects—a pair placed laterally, which were readily coloured by carmine (fig. 8, g), and one placed mesially next the ventral surface, which did not take the carmine dye (fig. 8, V).

The red stained bodies were recognised in sections through the head as high as the sides of the oral chink, and were obviously nerve ganglia. At their upper end they were separated from each other by the mesial oral chink, the tubercles connected with its walls and the areolated tissue associated with the tubercles. Each was placed close to the common tendon of attachment of the bundle of striped muscular fibres already described on each side of the head. In the upper part of a ganglion not more than six to twelve characteristic cells could be seen in the plane of section, but opposite the lower end of the oral chink the ganglion increased in size and the cells were much more numerous. Immediately below the oral cleft the ganglia were relatively large, and were situated partly to the side of the esophagus and partly ventrally to it, but they were not continuous with each other on the ventral surface, as they were separated by the mid-ventral object which did not take the carmine stain. The ganglia were traced in successive sections as far as opposite the origins of the arms, but they were not visible in the sections immediately below the arms, where their place was occupied by areolated tissue. It was noticed that where each ganglion had a wide transverse diameter, it was not unusual for the cells in its centre to show signs of disintegration; and sometimes this was so extensive that a cavity had formed, the wall of which was irregular and showed no sign of a lining membrane (fig. 8, q, q).

When examined under a high magnifying power the structure of the ganglion cells was readily recognised. The nuclei were large and oval in shape, and as they stained a deep red with carmine, they were very distinct, and an intranuclear network of fibrillæ was present in them. The cell-plasm was granulated. The best-marked cells were considerably larger than the motor cells in the lumbar enlargement of the human spinal cord, though others were very much smaller. The bodies of the cells were polygonal, and from the angles delicate processes of the cell-plasm projected. As a rule, the cells were closely aggregated, and it was difficult to trace these processes for any distance, but they were sufficiently distinct to leave no doubt of the multipolar character of the cells. In places minute intercellular intervals were visible, and the outlines of the cells were defined by a distinct wall. Although the relative proportion of the nucleus to the cell-plasm varied in the cells, it was evident that in the largest cells the cell-plasm exceeded three or even four times in quantity the size of the nucleus (fig. 15).

From the character of the cells there can, I think, be no doubt that the red stained bodies were a pair of nerve ganglia. Their position in the head, their relation to its ventral surface and to the esophagus, localise them as esophageal ganglia, situated laterally and ventrally to the gullet, though not united to each other on the ventral aspect of the esophagus. When portions of these ganglia were removed, teased with

needles, and stained with picrocarmine, delicate fibres were seen to lie between the cells and to emerge from the ganglia, which, from their association with the nerve cells, were obviously nerve fibres. Some were non-medullated; others, again, apparently contained a medullary substance, which had aggregated into little clumps within the neurilemma.

The mid-ventral object above referred to, when examined in relatively thick sections and under low magnification, seemed to be a solid cord-like body, lying mesially in the long axis of the head. It was situated between the ventral aspect of the alimentary canal and the inner surface of the ventral chitinous wall of the head. In longitudinal sections it was traced as high as the muscles of the head, the fibres of which arched above it, from their origin from the envelope of chitin to the side of the oral cleft. Its transverse diameter was greater than the antero-posterior, and it was bounded by a distinct capsule of fibrous tissue, which gave it a definite outline and differentiated it from the surrounding structures. The cesophageal ganglia were in relation to its sides, and in places even encroached on its ventral surface, and their upper ends were in the same transverse plane as the upper limit of its investing capsule. Below the ganglia it was bounded by the areolated tissue which was so abundant at and immediately below the arms. From its position it might have been taken for an axial nerve cord associated with the cesophageal ganglia, but no fibres could be detected in it, and it did not stain with carmine (fig. 8, V).

When thin sections were examined with a Zeiss lens × 250 the capsule was seen to be lined by a layer of rounded cells; in favourable sections they formed a continuous lining, but not unfrequently they were arranged in patches, separated by intervals. The cells were much smaller than the nuclei of the nerve cells in the adjoining ganglia, they were nucleated, and the cell-plasm was dimly granular. The material generally inclosed by the capsule had a granular character, and, as a rule, showed no trace of structure, and was possibly a coagulated substance. Sometimes, however, nucleated cells of great translucency were interspersed in the granular material, and fatty-looking globules were occasionally present.

In sections through the body of the parasite in the thoracic segment the corresponding arrangement, interposed between the alimentary canal and the ventral wall of chitin, was the ventral mesial space, so that the mid-ventral object above described was obviously a prolongation upwards into the head of the ventral space of the coelom.

In some of the transverse sections through the parasite made a little above the attachment of the arms a special appearance was seen. It consisted in the presence of a band or column of chitin, almost circular in outline, lying in relation to the dorsal space and interposed between the cesophagus and the inner surface of the dorsal wall of the chitinous envelope, and apparently quite independent of it. It was difficult to give a satisfactory explanation of the part which the band played in the economy of the parasite (figs. 8, 10, Ch).

ALIMENTARY CANAL.

The canal extended in a direct line from mouth to anus, and had no convolutions in any part of its course. The oral cleft passed deeply into the substance of the ventral surface of the head, and was continued at its lower part into a relatively wide esophagus, down which a bristle could readily be passed.

In transverse sections through the upper part of the cesophagus, the diameter from side to side was seen to be much greater than in the dorsi-ventral direction, and the opposite walls were almost in contact. The ventral wall of the canal was in close relation with the capsule of the mid-ventral space of the celom, which lay between it and the chitinous wall of the head, the dorsal wall was in relation to the musculature of the head, and the sides were in contact with the cesophageal ganglia (fig. 8).

In the lower part of the head, where the muscular fibres were replaced by areolated tissue, the dorsal wall of the canal was separated from the chitinous envelope by the dorsal space, which contained a granulated material, possibly a coagulum. The space was bounded by a fibrous membrane, which was lined by nucleated cells, though frequently they were in patches and did not form a continuous layer. These cells were about the size of leucocytes, and not unlike them in appearance. The muscular wall of the alimentary canal was attached to the areolated tissue at its sides by bands, formed of connective tissue and non-striped muscle, which constituted short lateral mesenteries; between these bands were narrow channels, in which blood or other nutritive fluid may have circulated.

Transverse sections through the body immediately below the arms showed the alimentary canal in the axis of the section, with a space in relation to both its dorsal and ventral surfaces. The lumen of the canal was not so compressed dorsi-ventrally as in the head. Well-marked areolated tissue surrounded the canal with its dorsal and ventral spaces, and closely packed the whole area between them and the inner surface of the chitinous wall (fig. 9). As it efficiently supported the canal, the lateral mesenteries were short and their fibres were continued into the meshwork of the areolæ, which again was continuous with the membrane lining the inner surface of the wall. A few scattered pigment cells were seen in this membrane, though not nearly so abundant as lower down in the thoracic segment of the body.

In sections through the attenuated thoracic segment the areolated tissue was no longer present, and the space inclosed by the chitinous wall was occupied by the alimentary canal and the dorsal and ventral spaces. The canal was in the axis of the section and was reniform in shape; its lateral angles were in such close relation to the lining membrane of the chitin that the mesenteries were practically absent (fig. 16). The dorsal and ventral spaces were proportionally large, almost equal in size, and were situated between the lining membrane and the corresponding wall of the alimentary canal. Each space was inclosed by a definite wall of fibrous membrane, the inner surface of which was lined by a layer of nucleated cells; the cell-plasm in some was granular

in character, though in others it was more translucent. The spaces were frequently devoid of contents, though in some sections irregular fragments, granular in appearance and possibly a coagulated substance, were present. The dorsal and ventral spaces, not only in relation to this, but to other divisions of the alimentary canal, formed the coelom or body cavity. Koren and Danielssen named the dorsal space the dorsal canal, and stated that during life it was full of red thinly-flowing blood.

The chitinous wall was lined by a definite membrane, in which was a layer of large stellate cells, full of a rich purplish-black pigment.

The alimentary canal and the associated spaces retained the characters just described as far down the body as where the attenuated thoracic part was continued into the genito-abdominal segment, in which the chitinous wall also possessed a lining membrane with large richly-pigmented cells. The alimentary canal was in the axis of the segment, and its transverse section was almost round, and so capacious that it may properly be regarded as the stomach. Each lateral aspect was attached to the adjoining pigmented membrane by a mesentery. The dorsal and ventral spaces were relatively small. Between the canal and the sides of the chitinous wall the upper ends of the two ovaries were situated (fig. 17).

Somewhat lower in the genito-abdominal segment the alimentary canal had a reniform outline in transverse section. In proximity to the genital orifices it was compressed dorsi-ventrally, and the opposite walls were almost in contact. In some sections the canal gave origin at a lateral angle to one and occasionally more diverticular prolongations, the lumen in which was continuous with that of the canal (figs. 20, 21, 22). At its lateral angles the wall of the canal was attached to the pigmented lining of the chitinous wall by fibres, apparently non-striped muscle, which formed lateral mesenteries, and the fibres formed a loose network, in the meshes of which, as well as in the interspaces of the pigmented membrane, were nucleated cells, some scattered, others in clusters, many of which resembled leucocytes, though others were elongated, caudate, and stellate, not unlike the corpuscles of connective tissue.

In the genito-abdominal segment, in relation to the lateral mesenteries and to the sides of the dorsal space, the areolated tissue was present in abundance, and the cells in the areolæ were distinctly fatty; the pigment of the pigmented lining membrane was prolonged into the strands of the meshwork, and caused them to contrast strongly with the light-refracting contents of the fat cells which they surrounded (figs. 25, 26, 27).

In the terminal caudate segment of the abdomen the intestinal division of the canal had a similar compressed appearance; the wall of chitin was lined by a membrane associated with characteristic pigment cells; lateral mesenteries and adipose areolated tissue corresponded with the arrangement described in the genito-abdominal segment (fig. 32).

In the genito-abdominal and terminal segments the dorsal and ventral spaces were well marked, and the dorsal was much more capacious than the ventral. The membrane which bounded them was lined by a layer of cells, sometimes continuous,

though at others in patches, similar in character to those previously described in the spaces of the thoracic segment, whilst the contents consisted of an indefinite granulated, possibly a coagulated, material. The existence of these spaces in front of and behind the alimentary canal permits an expansion of the walls and an increase in the size of the lumen when the animal is feeding, and their greater size in the lower end of the intestine leads one to infer that the ejecta accumulate in it prior to expulsion.

Two coats were readily recognised in the alimentary canal in its entire length —a muscular and a mucous. In favourable sections an intermediate sub-mucous coat was seen. The muscular coat consisted of the usual non-striped form of fibre arranged in two layers—an external longitudinal and an internal circular or transverse. In the abdominal and caudate divisions this coat was thickened, and had a crenulated appearance in the sections. When sections were made either longitudinally or obliquely through the canal, to enable one to obtain a view of the free surface of the mucous membrane, numerous slender, closely-set rugæ, lying parallel to each other, were seen to extend longitudinally along its surface (fig. 6). In transverse sections they were cut across, and they then had the appearance of villous processes projecting into the lumen. It was observed in these sections that the sub-mucous coat formed the core of the projections, whilst the free surface was formed of the mucosa; obviously, therefore, they were not true villi, but were permanent ruge, like the circular valvulæ conniventes in the small intestine of the mammalia. At the lower end of the canal the rugæ were more elongated and thicker than in the thoracic segment of the body. The mucous membrane was covered by a layer of epithelium, the cells of which in favourable specimens were seen to be short columns. In longitudinal or oblique sections through the canal in which the inner surface of the mucous membrane could be seen, the broader ends of the cells were recognised as forming the free surface of the mucosa. The lumen of the intestine contained epithelial and other débris.

In proximity to the anus the intestine and the structures around it were specially modified. A short distance above the anus the intestine in transverse section was flask-shaped, the stalk of which was attached to the dorsal wall of chitin by a narrow mesial dorsal mesentery, composed of non-striped muscle, which divided the dorsal space into two lateral halves. The ventral space had not at first a corresponding division. In addition, muscular fibres on each side passed from the chitinous wall to the sides of the intestine: these fibres had the form of striped muscle, but were not definitely striated. The wall of chitin was lined by a strongly pigmented membrane, in which numerous leucocyte cells were seen, either scattered or in groups. The proper muscular wall of the intestine was thicker than in the upper part of the caudate segment, and the parallel ridges of the mucous membrane were closely set together.

A little nearer the anus the section through the intestine was ellipsoidal, with the long axis directed dorsi-ventrally. The ventral space was now divided into two lateral

halves by a broad mesial mesentery formed of non-striped muscle. The walls of the dorsal and ventral spaces were lined by cells like those previously described. Strong striated muscles were situated laterally to the intestine; they arose from the wall of chitin, and were inserted by tendinous bands into the wall of the gut. Processes of the highly pigmented lining membrane passed between bundles of these fibres, and differentiated them into distinct muscles.

At the anus itself the dorsal and ventral spaces were scarcely to be recognised; the lumen of the intestine was small and laterally compressed. The submucous coat was greatly thickened and the mucous membrane showed no parallel ridges. The lateral striped muscles were well marked. The dorsal and ventral mesial bands of non-striped muscle were prolonged on to the sides of the intestine, external to its proper coat, and were arranged in an ellipse. At and near therefore the anal orifice the intestine was provided with transversely striped muscles, situated laterally, which acted as dilators; and with non-striped muscular fibres, distinct from the proper muscular coat, which formed a sphincter muscle (fig. 19).

No specially differentiated Vascular System was recognised, and no structures that could be regarded as heart, blood- or lymph-vessels. The dorsal and ventral spaces associated with the alimentary canal, and the intervals between the bundles of fibres of the mesenteries and of the lining membrane of the chitinous wall, provided channels for the distribution of a nutritive fluid.

NERVOUS SYSTEM.

In the section on the structure of the head I have described the pair of œsophageal ganglia, which, from their size, constituted the most important divisions of the nervous system. Their relation and structure having already been narrated, it is unnecessary to repeat them; but it may be stated that the position of the ganglia enabled them readily to supply nerve fibres to the wall of the œsophagus and to the striped muscular fibres, which formed important constituent parts of the head. Associated with the ganglia was a relatively large nervous cord, composed of numbers of delicate nerve fibres.

In transverse sections through the elongated thoracic segment clusters of cells were seen at intervals in close relation to the pigmented lining membrane of the ventral part of the wall of chitin and to the ventral space. The cells coloured readily with carmine, and the nuclei stained deeply and were relatively large. In some sections at least one process could be seen to arise from the cell body; in others a process arose from opposite aspects of the cell body, and the cells appeared to be fusiform or bipolar; other cells, again, were multipolar, and with delicate processes extending for a recognisable distance. In one specimen a process could be traced so far undivided as to be obviously the axon of the cell. Each cluster of cells formed a small nerve ganglion, the cells in which were smaller than in

the cesophageal ganglia. From cells of this character being seen so frequently in the transverse sections, it was clear that a chain of ganglia extended longitudinally along the ventral aspect of the thoracic segment of the parasite, immediately internal to the chitinous envelope, and that from the ganglia nerves could readily be distributed to the wall of the adjoining parts of the alimentary canal.

In transverse sections through the genito-abdominal segment collections of cells were seen immediately internal to the pigmented lining of the ventral part of the wall of chitin. They were arranged in a crescentic row, which followed the curvature of the wall, and the concavity of the crescent was directed towards the cement ducts, but was separated from them by a definite interval. The cells were nucleated, the cell-plasm was granulated, and two or three times greater in amount than the nucleus, which, again, was as big or even somewhat larger than the leucocytes, so abundant in the lateral mesenteries of the alimentary canal. Some of the cells were globular, others were elongated and rounded at the ends; occasionally I saw a multipolar cell, or one with a single pole, and frequently the cells were fusiform, with attenuated poles. From the position of the groups of cells in relation to the ventral wall of the parasite, and from their size and general character, I am of opinion that they form the abdominal chain of the nervous axis, and are engaged in the innervation of the organs contained in the genito-abdominal segment.

In many of the sections a cell was situated beyond the termination of each horn of the crescent, which was greatly elongated, and its outer pole was prolonged as far as the wall of the cement duct, which protruded a pointed process to meet it. In some sections I observed that this pole bifurcated, and its limbs embraced and were prolonged into the wall of the cement duct. This cell was placed at the side of the ventral space and seemed to be in its wall.

PENNATE APPENDAGES.

These appendages, which constituted one of the most characteristic features of the genus, grew from the ventral surface of the terminal caudate segment of the abdomen, whilst an occasional one sprang from the sides of the genito-abdominal segment near the genital openings. They formed a closely-set brush-like arrangement, the bristles of which varied in length and projected from 4 to 7 mm. from the base of their attachment, which was continuous with the wall of the segment, and had the character of a papillary outgrowth of the wall. Branches arose from the stunted basal papillæ, and these almost immediately again divided, so that from six to ten secondary branches might proceed from a common stem. Each branch had a pigmented core, inclosed in a translucent wall of chitin (Pl. I. fig. 4).

In sections made through the caudate segment the knife sometimes passed through the chitinous wall at the spot where the base of a papilla sprang from it (fig. 18). The chitin of the segment was prolonged into the wall of the bristles, and the pigmented membrane lining the wall of the segment was continued directly into their axis, and thence into the branches. In transverse sections through the bristles the pigmented core was frequently partially or wholly divided into two portions, which were either close together, or were partially fused and formed a dumbbell-like figure.

REPRODUCTIVE ORGANS.

Koren and Danielssen, in their account of *Pennella balænopteræ*, figured a dissection of the genito-abdominal segment. They described as present in it a pair of ovaries with oviducts, a pair of cement glands with excretion canals, the latter of which were nearer to the ventral surface than the oviducts, and two short canals. No mention is made of the receptacula, and the ova strings were wanting in most of their specimens.

Ovaries.—The ovaries were situated in the upper part of the genito-abdominal segment. At and near its junction with the thoracic segment, where the alimentary canal was dilated, and the dorsal and ventral spaces were relatively small, short lengths of a divided tube were seen in transverse sections to occupy a relatively large region on each side of the canal, dorsal to the lateral mesentery, and laterally to the dorsal space; the portions of each tube were scattered in the region, and were, I believe, the upper end of the ovary, for they were occupied by nucleated cells which resembled rudimentary ova. The oviducts and cement ducts were not present (fig. 17).

In sections a little lower down the parts of the divided ovary were in greater lengths and more continuous with each other, the tube was cylindriform in shape, and had reached or almost reached the mesial plane of the parasite, so as to lie immediately internal and parallel to the pigmented lining of the chitinous wall, but separated from the alimentary canal by the dorsal space. The part of each tube which lay next the wall followed its curvature. Somewhat lower down the wall of the tube next to the dorsal space bulged into diverticula and lost its cylindriform character. Whilst each ovary was in many sections situated entirely on its own side of the mesial plane of the parasite, in others the inner ends of the tubes from the opposite sides crossed the mesial plane and slightly overlapped each other. In all these sections the oviducts and cement ducts were present and were transversely divided (figs. 20, 21).

The wall of the tube was formed of a delicate membrane, and the lumen contained unfertilised ova (fig. 24). In many instances they were so closely packed together that the outlines of the individual cells were obscure. The ova were larger and more precisely differentiated when in proximity to the wall of the tube, which, from its surface being slightly crenulated, and from the passage of slender processes from the membranous wall into the lumen, seemed to be partially divided into compartments, in each of which an ovum was lodged. Each ovum contained a relatively large, well-defined germinal vesicle, situated at or near the centre of the cell-plasm, and in each vesicle, about its centre, was at least one germinal spot; not unfrequently two spots were present, and in some instances I saw three spots in a germinal vesicle.

Cement Glands.—The pair of cement glands were situated in the upper part of the genito-abdominal segment. In a considerable part of their extent they were alongside the ovaries, and corresponded in their general relations; but in some of the transverse sections ovarian tubes were present without adjoining cement glands, and in others portions of the cement glands were seen with no ovarian tubes in proximity to them. The ovaries and the cement glands were therefore not quite equal in extent. When both were present in the same transverse section the ovaries lay across the mesial plane, between the two cement glands, the latter of which were placed in close relation to the dorsal surface of the lateral mesenteries. When the cement glands alone were present they lay close to the mesial plane of the parasite, and were separated from each other by a prolongation of the dorsal space (figs. 22, 23).

Each cement gland consisted of a coiled tube inclosed in a membranous capsule, from the inner surface of which fibrous processes passed between the coils of the tubes. Lying close to the outer surface of that part of each capsule which was next the interposed dorsal space, well-marked nucleated cells, which possessed one or more processes, were seen; and as similar cells were present in the membranous wall of the space where it was next the pigmented lining membrane of the chitinous envelope, these cells should be regarded as belonging to the wall of the space rather than to the capsule of the cement gland. The coiled tube of the cement gland, in making the section, had been cut into short pieces, transversely, obliquely and longitudinally. It had a well-defined wall, which was lined by a layer of short cubical cells. The lumen of the tube contained a dimly granular substance which stained with carmine and with hæmatoxylin. No sign of an ovum could be seen in the tube.

Oviducts, Cement ducts, Receptacula, Ova strings.—Each ovary and cement gland had a characteristic duct. In the numerous transverse sections made through the genito-abdominal segment, except at the highest part of the ovary, an oviduct and a. cement duct were seen on each side of the mesial plane. They were placed ventrally to the lateral mesenteries, and in relation to the sides of the ventral mesial space. They had evidently emerged near the upper ends of their respective organs, and had passed forward into the ventral region of the segment, down which they ran to the The cement duct on each side was in front of the oviduct, and was separated from it in the upper part of their course by a slight interval. A slender intermediate band passed from the wall of one to that of the other, and at its junction with the cement duct the wall of that duct was much thinner than in other parts of its circumference. Lower down in the segment the walls of the two ducts came in contact with each other and fused together. Before their lumina became continuous with each other, the oviduct diminished in its calibre, and the cement duct became elongated antero-posteriorly. The intermediate part of the common wall then disappeared, and the receptaculum was formed a little above the genital openings (figs. 20-23, 25, 26).

The ducts were readily distinguished from each other, both by their relative position and their characters. The wall of the oviduct was much the thinner, and was

generally cylindriform, though it showed in each transverse section from four to ten or twelve bulgings on the outer surface of its wall. In many sections each bulging seemed to contain a nucleated cell, but under higher powers this was not so evident. In some sections a sharp line, apparently the lining membrane of the duct, was continued round the wall, as if to shut off the bulgings with their contents from the lumen. In others, again, the bulgings projected into the lumen, and were not shut off by a lining membrane. When the wall of the oviduct had fused with that of the cement duct, a layer of nucleated cells was traced from the outer surface of one duct to that of the other. In some transverse sections through the oviducts the lumen contained a delicate network of fibres which radiated from the centre to the periphery. The wall of the cement duct was several times thicker than that of the oviduct, except at the spot where it was joined either by the intermediate band or by the wall of the oviduct. The lumen of the cement duct, especially near its lower end, frequently contained a plug of cement which almost filled the tube (figs. 20–23).

Receptacula.—Each receptaculum seminis was situated at the side of the ventral space near its anterior part. Its antero-posterior diameter was longer than the transverse, and the wall lying next the ventral space was sometimes thinner, at others thicker, than the opposite wall; the anterior part both of wall and lumen had frequently a tortuous appearance, as if slightly convoluted, and from its lower end a short canal arose, which ended in the genital orifice. The lumen almost invariably contained a plug of cement, antero-posteriorly elongated like the receptaculum itself (figs. 29, 30).

Associated with the lower part of the genito-abdominal segment was a distinct muscular arrangement, the fibres of which were transversely striped, but in addition some bands belonging to the lateral mesenteries consisted of unstriped fibre. The striped muscles arose from the chitinous wall, some bundles ventral to the mesentery, others within its substance; they passed downwards and inwards, and in the transverse sections the fibres were usually cut through transversely or obliquely. Some fibres were attached to the wall of the oviducts; but the greater number reached the posterior end and outer wall of the receptacula, to which they were attached by tendon-like structures (fig. 28). Owing to this arrangement, the wall could be drawn outwards and the lumen of the receptaculum made larger, a condition which doubtless prevailed when the ova, the cement, and probably the spermatic fluid also, passed into it.

Ova strings.—These were about the thickness of fine sewing-thread. They began at the genital orifices and floated in the sea in which the animal lived. The outer part of each string was formed of cement, and the space which it inclosed would have contained the ova had they been ripe for extrusion. When examined microscopically, transverse lines closely set together were seen to pass from one to the other side of the inclosing cement. In my specimens I saw no ova in the ova strings. The ovarian ova were unripe, and there was an absence of ova in the oviducts and receptacula. When sections were made through the ova strings, the space inclosed by the cement was seen

to contain a quantity of minute fatty particles, the products of degeneration. It should be remembered that the parasites were taken in the autumn, after they had, in all probability, shed a crop of ova, and before the next crop was ripe for impregnation.

THE MALE.

It is well known that in the parasitic Copepoda the male is insignificant in size as compared with the female. In Chondracanthus and some other genera it has been ascertained that the male is attached to the female, close to the apertures for the ova strings. I consequently made a close examination of the ventral surface of the body of all my specimens of Pennella, with the object of observing if a male were present in any of them, but I failed to recognise one. Koren and Danielssen stated definitely in their memoir on P. balænopteræ that they had not seen any males attached to their specimens, so that the male of P. balænopteræ is as yet unknown. It would, indeed, appear that the recognition of the male in any species of Pennella is a rare occurrence. I have stated in the introductory section that BOCCONE, so long ago as 1674, figured, firmly affixed to the Pennella, which is now regarded as P. filosa, a small object which he spoke of as a "pediculus" or louse. I have no doubt, from its relative size and the place of attachment, that it was the male of the species. Boccone, therefore, should have the credit of being the first to see and figure a male Pennella, though he did not realise its sexual significance. In Pennella exocati and in P. varians the male has also been recognised and figured.

The habitat of the male Copepod, as in the case of Pennella, when not attached to the female, is uncertain. In a species like Lernwa branchialis affixed to the gills of the Gadidæ and flounders, males have been found within the gill-chamber, some attached independently to the branchiæ, others to the bodies of the females. In P. balænopteræ the females were affixed to the extensive surface of the smooth back of a great whale, to which they had doubtless attached themselves in the Cyclops phase, through which the female passes before she becomes adult and assumes relatively gigantic proportions, though in many respects retrograde characters. If the males of Pennella be provided with hooked antennæ, like those found in the male Lernæa, as there is no adjoining chamber for their lodgment, they may become directly attached to the skin of the whale in proximity to the females, until the time arrives when they are required to affix themselves to the females for the purpose of fertilising the ova when these are ripe for impregnation. If the male Pennella, as is very probable, is insignificant in size, when unattached though perhaps in close proximity to the female, it would easily be overlooked.

In considering the question where and when the ovarian ova are impregnated in the parasitic Copepoda, it has to be kept in mind that whilst the female is fixed to its host, the male retains for a considerable time the character of a free swimming Crustacean, though subsequently it affixes itself in many of, and possibly in all, the species to the female, close to the genital openings, with probably the power of again detaching itself when insemination is completed. It is possible, as has been shown by Andrew Scott in Lernæa, that fertilisation of the female may take place in the Cyclops stage when she has become attached to the host. Naturalists have expressed different opinions on the locality where the spermatic fluid comes in contact with the ova and impregnates them. Some have thought that as they pass out of the genital openings the proximity of the male, from its attachment close to the openings, allows the sperm to bathe the wall of the ovum and the spermatic threads to penetrate it. This, however, is doubtful, as the sea-water in which the parasite lives would, possibly, in such a case have washed away the sperm and impeded or prevented impregnation.

Others, again, consider that the sperm enters the genital orifices, passes into the receptacula, distends them and ascends the ovarian ducts, so as to meet the ova in their descent. It is obvious that penetration of the ovum by the sperm filaments, which is essential to impregnation, must occur before the ovum meets with the cement and is coated by it. This can only take place in the oviduct, for the secretion of the cement gland flows into the receptaculum and can envelop the ova as they enter it. The observations recorded in this memoir show that the receptaculum and its short excretory canal, even in the unimpregnated female, contained cement, so that the ova could have been coated by it before they had passed out of the genital opening to form, along with the cement, the ova string. It would seem, therefore, that fertilisation of the ovum must occur in the oviduct. The non-attachment of males to my female specimens should be associated with the unripe condition of the ova, and the consequent impossibility of fertilisation being effected at the time when the parasites were collected.*

COMPARISON WITH OTHER SPECIES.

A careful comparison of the characters of my specimens, with the description and figures by Koren and Danielssen in their excellent memoir, has satisfied me of their identity with the species which they have named *Pennella balænopteræ*. This species therefore infests both *Balænoptera musculus* and *B. rostrata*.

I have not seen the species which Steenstrup and Lütken described and delineated as found on Hypercodon rostratus, and which they named Pennella crassicornis. Koren and Danielsen, however, after comparing original specimens, considered that their Pennella balænopteræ was quite distinct from Pennella crassicornis, as it was half as long again; had a broader and longer head; the horns were nearly horizontal and very slender, whilst in Pennella crassicornis the dorsal horn was inclined almost perpendicularly downwards.

When compared with the species of Pennella infesting fish, P. balænopteræ is very much longer. Odhelius regarded the length of P. sagitta as equal to the breadth of

^{*} Ova which had developed to the nauplius stage were seen by H. S. Wilson and myself in *Chondracanthus lophii* collected in August, and in *Lerneopoda dalmanni* collected early in the year. See our Memoirs in *Trans. R.S. Edinburgh*, 1862.

the thumb. Dekay's specimen of P. sagitta was little more than half an inch long, but it is obvious from his figure that the head and arms had been torn off: the length was probably one inch. V. Nordmann stated (Heft 2, S. 122) that P. sagitta found on Lophius marmoratus was only ten lines long, and with the ova strings 1 inch 4 lines. Steenstrup and Lütken measured nine specimens of P. varians and found them to vary in length from 18 to 27.5 mm. (0.7 to 1.1 inch). These species are the most diminutive known. Boccone stated that his specimens were usually about 4 inches long. Baird gave 4 inches as the length of his Penella pustulosa, Chamisso and Eysenhard's specimen P. diodontis, Thomson's P. histiophori, and also P. exocæti, were about the same length. Perceval Wright's specimen, P. orthagorisci, was 7 inches long.

Species differed in the number of horn-like arms which radiated from the base of the head. In Boccone's figure neither head nor arms were depicted, and I am disposed to think that they had been broken off in the process of detaching the parasite from the Swordfish, in the flesh of which they were buried; the abdominal segment of the body was shown to be longer than the short thoracic segment. In Odhelius' figure of P. sagitta neither head nor arms were represented, probably for the same reason. In the Pennella sagitta described by von Nordmann, and in P. pustulosa, diodontis, and orthagorisci, two arms were said by their respective describers to have been present. Thomson states that P. histiophori had two lateral arms, but projecting between them posteriorly was a rounded protuberance; which, without doubt, was a rudimentary dorsal arm. P. sultana, exocæti, crassicornis, and balænopteræ had each three arms. In eighteen specimens of P. varians examined by Steenstrup and Lütken, one-third were said to have had three arms, two-thirds only two arms. The lateral arms were constant, but the dorsal arm was variable in the same species. The presence of a dorsal arm is not therefore a constant element in the establishment of specific differences. A specific character, which is obviously of importance, is the relative length of the thoracic and genito-abdominal segments. In P. balanopteræ the thoracic was twice the length of the conjoined genito-abdominal and caudate abdominal segments, and nearly three times the length of the genito-abdominal segment. By way of contrast in von Nordmann's P. sagitta and in Thomson's P. histiophori the thoracic and genitoabdominal segments did not seem to be distinctly differentiated from each other; in Perceval Wright's P. orthagorisci and in P. exocæti the genito-abdominal and thoracic segments were about equal in length, and in Chamisso and Eysenhard's P. diodontis the genito-abdominal segment was nearly twice the length of the thoracic. Although there seems to be no doubt that P. balænopteræ is a species quite distinct from those that are parasitic on fish, it is difficult to say definitely, in the absence of the type specimens for comparison, if all the fish-infesting forms of Pennella that have been described by different specific names have a true claim to this distinction, though it is, I think, probable, if a careful comparison were made, that the number of so-called species would be diminished.

CONCHODERMA.

Several naturalists have observed that species of Pennella have occasionally attached to them animals belonging to the sub-class Cirripedia. Chamisso and Eysenhardt seem to have been amongst, if not the first naturalists to describe a Cirriped attached In 1821 they stated that a Lernæa (Pennella) diodontis, from the to a Pennella. branchiæ of Diodontis mola, captured in the Pacific, had Lepas anatifera affixed to it. G. O. SARS described, 1865, a Pennella, with the head buried in the blubber of Balænoptera musculus, to which Cineras vittata (Conchoderma virgata) was attached. Koren and Danielssen figured two specimens of Conchoderma virgata affixed close to the genital orifices of Pennella balanoptera, and they stated that in another example as many as seven specimens were attached to the thin thoracic part. Paul Meyer saw in the collection at Naples six examples of a Pennella from Xiphias gladius, to one of which Conchoderma virgata was affixed: owing to the Pennella being imperfect, the species was not determined. To one of the examples of Pennella orthagorisci in the Royal Scottish Museum, already referred to, three specimens of Conchoderma virgata were cemented at or near the junction of the thoracic and abdominal segments. Also the P. exocæti in the same museum were similarly infested.

It is interesting to note that cases have been recorded of a direct attachment of Conchoderma to the skin of whales. Thus, Charles Darwin, p. 66, stated that he had seen the basal end of the peduncle of Conchoderma aurita sunk into the skin of Cetacea. G. O. Sars had described the same species attached to the humpbacked whale, Megaptera boops, and a similar attachment had also been noticed by Sophus Hallas.

One of my specimens of P. balænopteræ had an example of Conchoderma virgata cemented at the junction of the thoracic and genito-abdominal segments (Plate I. fig. 3). It is unnecessary to describe the generic characters of Conchoderma, or the specific characters of C. virgata, as they have been so fully narrated in the classical treatise of CHARLES DARWIN: but in order to identify the species, I may briefly refer to the external appearance of my specimen. It measured 46 mm. (1.8 in.) in extreme length, 15 mm. in the greatest dorsi-ventral diameter, and 15 mm. in greatest breadth. Though the peduncle blended with the capitulum they could be differentiated, and the former was found to be slightly longer than the latter. The dorsal carinal plate was 16 mm. long and 3 wide, and reached the anterior end of the capitulum. The scutal plate was three-lobed and 7 mm. in length. The tergal plate was 5 mm. long and only 1 mm. in width. The interval between the upper lobe of the scutum and the carina was 8 mm., and between the anterior lobe of the scutum and the tergum 6 mm. The coat in the intervals between the plates was not calcified, and was yellowish-grey in colour, with three purple bands on each side extending antero-posteriorly. The highest band on each side reached the dorsal border behind the carina, where it blended with its fellow. The other bands ran independently the whole length of the animal, and did not branch. pair of stunted processes at the anterior end of the carina represented the pair of earlike appendages so characteristic of Conchoderma aurita. My specimen in general form and characters resembled that figured by DARWIN in plate iii. fig. 2, but it had three, and not four, purple stripes in the mantle.

In conclusion, I would express my acknowledgments and thanks to Mr John Henderson, Assistant Keeper of the University Anatomical Museum, for the aid which he has given me in preparing the numerous sections examined in the course of my research, and for photographing those which illustrate the internal anatomy of the parasite, many of which have been reproduced in three of the plates.

BIBLIOGRAPHY.

BAIRD, W., "On a new Species of Penella," Annals and Magazine of Natural History, vol. xix. p. 280.

Baird, W., "Natural History of British Entomostraca," Ray Society. London, 1850.

Bassett-Smith, P. W., "Systematic Description of Parasitic Copepoda found on Fishes," Proc. Zool. Soc. Lond., p. 482. 18th April 1899.

VAN BENEDEN, P. J., "Animal Parasites and Messmates." London, 1876.

VAN BENEDEN, P. J., "Histoire naturelle des Balénoptères, Mémoires couronnés et autres Mémoires," Acad. Roy. de Belgique, vol. xli. 1887.

DE BLAINVILLE, "Mémoire sur les Lernées," in Journal de physique, de chimie et d'histoire naturelle, vol. xev. p. 372 and p. 437, plate. 1822.

De Blainville, Art. Lernæa, Dict. d. Scien. Nat., vol. xxvi. p. 112. 1823.

Boccone, "Recherches et Observations naturelles de Monsieur Boccone, Gentilhomme Sicilien," figure opposite p. 284. Vingt-cinquième Lettre. Amsterdam, 1674.

Burmeister, H., "Beschreibung einiger neuen oder weniger bekannten Schmarotzerkrebse," Nova acta physico-medica Acad. Coes. Leop. Carol., vol. xvii. p. 269. 1835.

CHAMISSO and Eysenhardt, Penella diodontis in Nova acta physico-medica Acad. Coes. Leop. Carol., vol. x., pl. xxiv. fig. 3, p. 350. 1821.

CLAUS, C., Elementary Text-book of Zoology, translated by A. Sedgwick and F. G. Heathcote. London,

Cuvier, Les Pennelles. (Pennella, Oken.) Le Règne animal, vol. iii. p. 256. 1830.

Dekay, J. E., Observations on the Pennatule fleche (P. sagitta of La Marck) in the cabinet of Dr Mitchill. Silliman's American Journal of Science, vol. iv. p. 87. 1822.

Ellis, John, P. filosa and P. sagitta in Philosophical Transactions, vol. liii. fig. 16. 1763.

Gerstaecker, A., "Crustacea Spaltfüssler," in Bronn's Thier-reichs, Bd. v. 1st Abth. Leipzig and Heidelberg, 1866-1879. Figured in Tab. vii., Penella sagitta and Penella varians.

Guérin, Iconograph. Zooph., pl. ix. fig. 3, quoted by Bassett-Smith.

Holten, Acta danica, Naturhist. Skrifter, 136, pl. iii. fig. 3. Holmiæ, 1802.

Koren, J., and Danielssen, D. C., "On Pennella balænopteræ," in Fauna littoralis Norvegiæ, 3rd part, plate xvi. p. 157. Bergen, 1877.

KROYER, H., "Systematische Uebersicht der Schmarotzer Krebse," Oken's Isis, 1840, p. 702 e.s.

LINNÆUS, C., Systema Natura, 10th ed., vol. i. p. 819, 1758; also a later edition, vol. i. parts vi., vii., pp. 3864, 3865.

Meyer, Paul, Mittheil. aus der Zoolog. Station zu Neapel, vol. i. p. 53. Leipzig, 1879.

MILNE-EDWARDS, Penellus. Crustacés, vol. iii. p. 522. 1840.

Modeer, Acta Suecica, 1786, p. 256, P. sagitta and filosa, quoted by von Nordmann.

NORDMANN, A. von, Mikrographische Beiträge zur Naturgeschichte der wirbellosen Thiere, zweites Heft.

Berlin, 1832. Pennella sagitta, p. 121, pl. x. figs. 6, 7, 8.

Odhelius, J. L., Chinensia lagerstromiana, published in a collection of Theses entitled "Amoenitates Academicæ of Linnæus," vol. iv. p. 257, fig. 3. Holmiæ, 1759. He gives a description of P. sagitta. In the references which I have seen to this species it is made to appear as if it had been described by Linnæus himself, and the name of his pupil Odhelius is not given.

OKEN, Lehrbuch der Naturgeschichte, 1815, part iii. Allgemeine Naturgeschichte, vol. v. part ii. p. 564;

oder Thierreich, vol. ii. 2nd part. Stuttgart, 1835.

Sars, G. O., "Beskrivelse af en ved Lofoten indbjerget Rørhval (Balænoptera musculus)," Forhandlinger i Videnskabs-selskabet i Christiana, p. 280. 1866.

Scott, Andrew, "Lepeophtheirus and Lernæa," Memoirs of Liverpool Marine Biological Committee.

Steenstrup and Lütken, Om Slægten Pennella, in Dansk. Vid. Selsk. Skriv., vol. v. p. 408, pl. xiv. 1861. THOMSON, G. M., "Parasitic Copepoda of New Zealand," Trans. New Zealand Inst., vol. xxii. p. 353,

pl. xxviii. fig. 2, 1889. Describes Pennella histiophori.

Turner, Wm., and Wilson, H. S., "On Chondracanthus lophii," also "On Lernxopoda dalmanni," Trans. Roy. Soc. Edin., vol. xxiii. p. 67, pl. iii. and p. 77, pl. iv. 1862.

WRIGHT, E. PERCEVAL, "On a new species of the Genus Pennella," Ann. and Mag. Nat. Hist., 4th series, vol. v. p. 43, plate i. 1870.

CONCHODERMA.

DARWIN, C., Monograph on the sub-class Cirripedia. Part 1. The Lepadidæ. Ray Soc. London, 1851.

Hallas, Sophus, Vidensk. Medd. jra den Naturhist., vol. ix. Copenhagen, 1868.

MEYER, PAUL, "Carcinologische Mittheil.," p. 53. Mittheilung. aus der Zoolog. Station zu Neapel, vol. i. Leipzig, 1879.

HOEK, P. P. C., "Account of Conchoderma Virgatum, var. chelonophilus, obtained from the carapace of a Chelone," Challenger Reports, part xxv. p. 55, pl. ii. figs. 13-15. 1883.

SARS, G. O., Forhandling. i Vidensk. Selsk., p. 280. Christiania, 1866, also 1880.

EXPLANATION OF PLATES.

PLATE I.

The drawings in this plate were made from nature by Mr James T. Murray.

Fig. 1. Pennella balænopteræ seen from its ventral surface. Natural size.

Fig. 2. Head, arms, and upper part of thoracic segment, to show the four pairs of rudimentary feet-like appendages; enlarged.

Fig. 3. Abdomen, showing the attachment of Conchoderma virgata to the upper end of the genito-

abdominal segment. Natural size.

Fig. 4. Pennate bristles detached from the caudate abdominal segment. × 10. p. 423.

PLATE II.

Fig. 5. Longitudinal dorsi-ventral section through the head and upper end of the body of Pennella. The arrangement of the striped muscles s.m. in the head, the relations of the cesophagus Œ. to the midventral space V., to an esophageal ganglion g, and to the areolated tissue ar, are shown, $\times 8$. p. 419.

Fig. 6. A more highly magnified section through a part of the esophagus Œ., in which a portion of the free surface of its mucous lining with the longitudinal folds parallel to each other, also the fibres of the nonstriped muscular wall, n.m., passing into the surrounding areolated tissue, ar., and forming mesenteries, are shown. ×14. p. 421.

Fig. 7. Transverse section through the upper part of the head. The oral cleft on the ventral surface,

the tubercles and the arrangement of the striped muscles are shown. ×13. p. 415.

Fig. 8. Transverse section through the head below the oral cleft, showing the relation of the alimentary canal A. to the midventral and dorsal spaces, the pair of œsophageal ganglia, each of which has a cavity in the centre, and the striped muscles. Ch. marks a transversely divided column of chitin, lying in relation to the dorsal space. $\times 13$. pp. 418, 419.

Fig. 9. Transverse section through the parasite close to the origin of the arms. The relations of the alimentary canal with the ventral and dorsal spaces and the large amount of areolated tissue are shown.

×13. p. 416.

Fig. 10. An oblique section through the parasite at the origin of an arm, showing the relations of the alimentary canal to the dorsal and ventral spaces, and to a mass of areolated tissue. The position of the inner column of chitin, Ch., is also shown. ×13. p. 418.

Fig. 11. Transverse section through the arm close to its origin to show the two large areolæ and those

of smaller size. ×13. p. 416.

Fig. 12. Transverse section through the arm about its middle. ×13. p. 416.

Fig. 13. Another transverse section through the arm, in which many of the areolæ were crowded with nuclei. × 13. p. 416.

Fig. 14. Transverse section through the body a short distance below the arms, showing the areolated tissue which surrounded the alimentary canal and dorsal and ventral spaces. ×13. p. 419.

PLATE III.

Fig. 15. Section through an esophageal ganglion, showing the nucleated nerve cells. p. 417.

Fig. 16. Transverse section through the attenuated thoracic region, showing the alimentary canal and

the dorsal and ventral spaces. $\times 13$. p. 419.

Fig. 17. Transverse section through the body at the junction of the thoracic and genito-abdominal segments. The upper end of the pair of ovaries can be seen at the sides of the alimentary canal, the mucous lining of which was torn off in making the section. ×13. p. 420.

Fig. 18. Transverse section through the caudate abdominal segment, showing the relation of the alimentary canal to the dorsal and ventral spaces and the origin of one of the pennate bristles. ×13. p. 423.

Fig. 19. Transverse section through the intestine at the anal orifice. On each side of the gut is a pair of large transversely striped muscles; on the ventral aspect a pair of non-striped muscles which form a sphincter arrangement around the intestine. × 50. p. 422.

Fig. 20. Transverse section through the upper part of the genito-abdominal segment, showing the two ovaries placed dorsally, with a cement and an oviduct on each side of the ventral space, separated from each

other by an interval; also the alimentary canal with its foldings or diverticula. × 15. p. 423.

Fig. 21. Transverse section through the same region, showing the same parts, but with a less complicated alimentary canal. ×13.

Fig. 22. Transverse section through the upper part of the genito-abdominal segment, showing ovaries

and cement glands in the same plane, also oviducts and cement ducts. × 15. p. 425.

Fig. 23. Transverse section through the genito-abdominal segment, showing the pair of cement glands at the sides of the dorsal space; the cement ducts and oviducts are near the ventral space: the walls of the ducts on each side are connected by an intermediate band. The pigmented lining membrane has shrunk away from the wall of chitin. The alimentary canal is reniform in section. ×13. p. 425.

PLATE IV.

Fig. 24. Section through an ovary, showing the contained ova. p. 424.

Fig. 25. Transverse section through the lower part of genito-abdominal segment, no ovaries or cement glands, but the walls of the oviduct and cement duct on each side are in contact: bundles of striped muscles, s.m., are also seen. $\times 13$. p. 425.

Fig. 26. A similar transverse section, showing fusion of the oviduct with the cement duct. × 13.

Fig. 27. A similar transverse section, where the two ducts on each side are blended, and form a receptaculum. A loop-like arrangement across the mesial plane connects the two receptacula. × 13.

Fig. 28. A transverse section a little above the genital openings. Striped muscles are attached by distinct tendons to the outer wall of each receptaculum. × 9. p. 426.

Figs. 29, 30, 31. Three transverse sections in succession from above downward in proximity to the genital openings. They show the receptacula, each containing a plug of cement. In 29 is also seen the short canal of the receptaculum which leads to the genital opening; and in 30 the opening itself is visible with a plug of cement protruding through it. ×13.

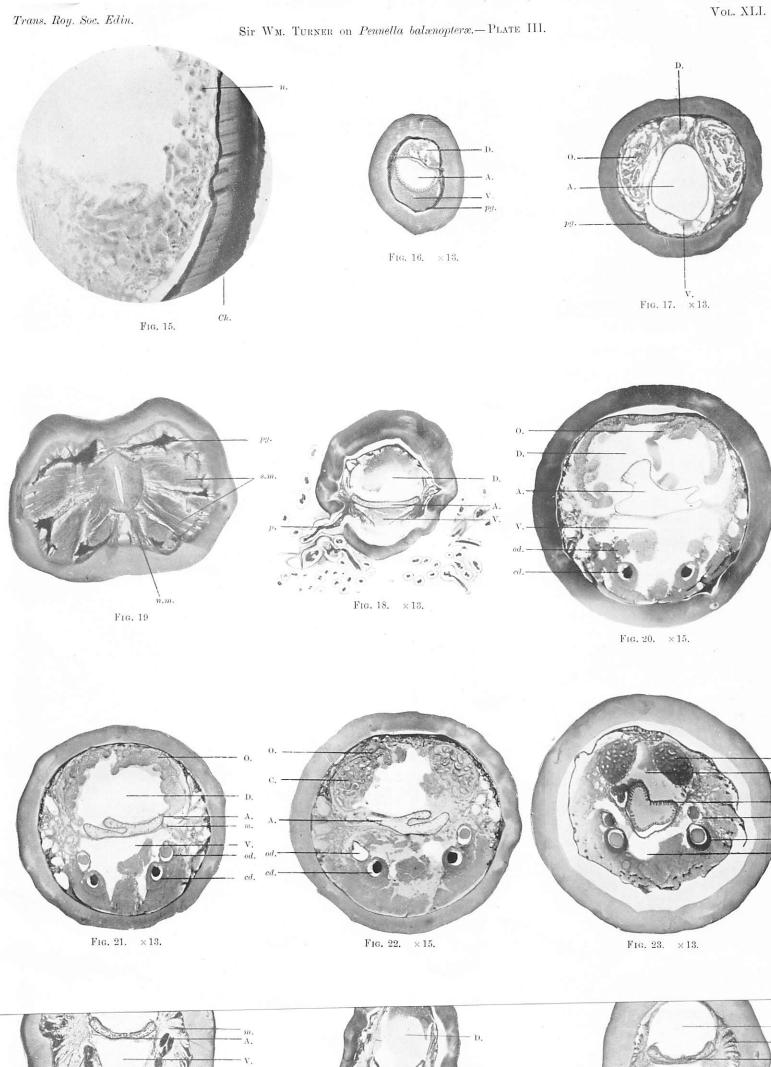
Fig. 32. Transverse section through the upper part of the caudate abdominal segment. The origin of a pair of bristles is seen and the pair of ova strings lie ventrally to the segment. ×13.

Lettering of Plates II., III., IV., the figures in which are reproductions by Messrs M. & T. Scorr of photographs of sections through Pennella.

- A. Alimentary canal.
- ar. Areolated tissue.
- C. Cement gland.
- c.d. ,, duct.
- Ch. Chitin.
- D. Dorsal space.
- g. Œsophageal nerve ganglion.
- g.o. Genital opening.
- m. Mesentery
- n.m. Non-striped sphincter muscle.
 - n. Nerve cells.
 - O. Ovary.

- oa. Ova.
- od. Oviduct.
- Œ. Œsophagus.
- or. Oral cleft.
- o.s. Ova string.
- p. Pinnate bristles.
- pg. Pigmented lining membrane.
- R. Receptaculum.
- s.m. Striped muscles.
 - t, Tubercles.
 - V. Ventral space.





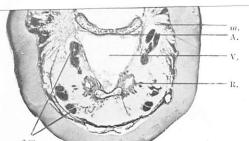


Fig. 27. ×13.

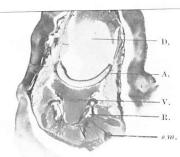


Fig. 28. \times 9.

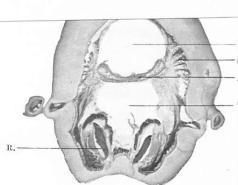
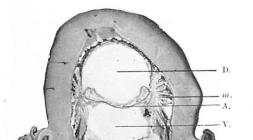
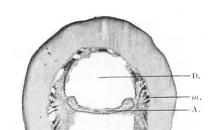
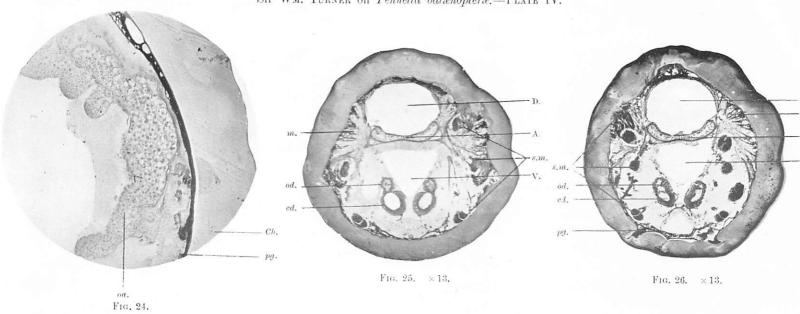


Fig. 29. ×13.









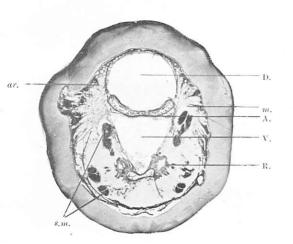


Fig. 27. ×13.

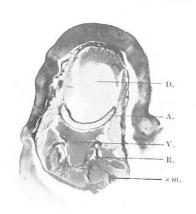


Fig. 28. \times 9.

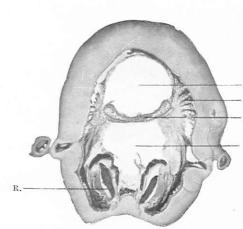


Fig. 29. $\times 13$.

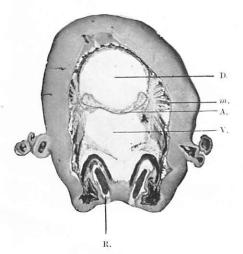


Fig. 30 \times 13.

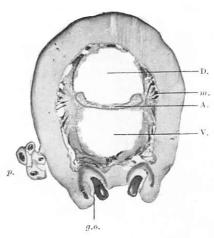


Fig. 31. ×13.

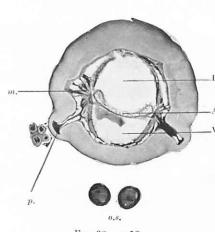


Fig. 32. \times 13.