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Pollicipes spinosus Quoy and Gaimard, I: Notes on Biology and Anatomy of Adult Barnacle.

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INTRODUCTION.

Amongst modern cirripedes, the genus *Pollicipes* has frequently been regarded as lying closest to the original stock. Such views have been based rather on the arrangement of valves of the mantle than on the animal itself—its biology and anatomy. Hence it is more from this latter view-point that the New Zealand section of the genus *Pollicipes* is here examined.

Taxonomy: By priority, the genus in question should be termed *Mitella,* the name *Pollicipes* pre-dating the introduction of binomial nomenclature. But following Darwin's strong arguments for making an exception in this case (Darwin, 1851, p. 293), the term *Pollicipes* has been extensively used in geological and zoological work. Hence its employment here.

Three species —*P. spinosus* (Q. and G.), 1834, *P. sertus* Darwin 1851, and *P. darwini* Hutt, 1879— have been described for New Zealand. But field-work involving the handling of large numbers of specimens has led the present author to concur with the opinion of Jennings (1914, p. 293), namely, " To conclude, I am practically certain that the New Zealand species of *Pollicipes* so far recorded come under one species only, which, by priority, should be called *Pollicipes spinosus* Quoy and Gaimard."

Subsequent to Jennings' work, Broch (1921, pp. 247-251) has described a New Zealand species, *Protomitella paradoxa,* in which the large form (female or hermaphrodite?—penis is described as " very short," and internal anatomy is not considered) is close to some specimens of *P. spinosus.* However, he further describes two small individuals, on the " inner edge of the scuta at the apex of the rostrum " of one Plimmerton specimen, as dwarf-males. Their internal anatomy (presence or absence of testes or ovaries) is not considered. Externally they are not unlike young *P. spinosus* specimens. Fuller data would be of much interest. The present author feels hesitant to regard *Protomitella paradoxa* as distinct from *Pollicipes spinosus* until more positive evidence is available. Her own field-work at Plimmerton (one of Broch's type localities) showed a great abundance of *P. spinosus,* scattered specimens of *Calantica villosa,* and no other littoral scalpelliform cirripedes. The examination, both macroscopically and under dissecting binoculars, of large numbers of *P. spinosus* and *C. villosa,* both from there and other New Zealand localities, at various seasons, has shown no small specimens which might be dwarf males. Incidentally, this apparent total absence of complemental males in more than 100 New Zealand specimens of *C. villosa* perhaps marks it as a distinct form from the extra-New Zealand species.

Material and Methods: Abundant fresh material was available. Live specimens were kept temporarily for observation in a glass tank with a tap-driven aerating pump. Young were reared in vitro continuously from the one-cell egg to the cypris stage. An account of their development is postponed to a subsequent paper, but the times for embryonic and nauplius phases are considered here.

The anatomical portion is based partly on dissections, partly on serial sections. Both alcohol-preserved and fresh specimens were dissected under a dissecting binocular. For sections, alcoholic Bouin's and mercuric chloride were the chief fixatives used. Usually the " body " was removed from the mantle at the time of fixing, but some specimens were decalcified by changes of 1% hydrochloric acid in 70% alcohol and sectioned entire.

Paraffin-infiltration of the body was slow, 5 to 10 days in the paraffin oven giving best results. Sections were cut at from 2.5 to 50 microns. Mallory's triple stain was chiefly used. Drawings of sections and appendages were made with the aid of a camera lucida.

Acknowledgments: The present paper represents, with modifications and condensation, a thesis presented for Diploma of Honours in Zoology in the University of New Zealand. The greater part was carried out in the University of Otago, and the writer wishes to thank Professor Marples for suggesting *Pollicipes,* and for helpful advice about lines of attack.

BIOLOGY OF *P. spinosus.*

Distribution and Habitat: This species, reputedly endemic to New Zealand, has been recorded from numerous localities from North Auckland to Stewart Island. The present writer has found it ocurring around Dunedin in abundance at Bruce's Rocks and Brighton, fairly abundantly at St. Clair, Long Beach, Karitane, and other coastal-rock localities; around Wellington extremely abundantly at Island Bay and Plimmerton, present near Paekakariki and elsewhere; and at Stewart Island in moderate abundance south-east of Halfmoon Bay.

It appears confined to coastal rock localities where water surges violently. It is absent in bays and on rock points in harbours and inlets. Likewise it is absent from rock-pools, from low smooth rocks, or where an outer reef protects inner rocks from larger waves. But if great masses of inter-tidal rocks are separated by narrow channels through which water surges wildly, especially if the rock surfaces are overhung, colonies of *P. spinosus* are almost invariably found.

The chief concentration of individuals is at about half-tide level. Some occur nearly down to low tide, overlapping with the vertical distribution of *Calantica villosa.* Occasional specimens are probably above actual high-tide level. But their position is such that waves running up rock-channels would reach them long before high tide on all but the calmest days.

Specimens may occur singly, in small groups, or in colonies (Fig. 16), sometimes up to a foot or more in diameter, running into hundreds of individuals. In most cases they are attached directly to the rock. Sometimes, however, one has settled on another *Pollicipes* specimen, or on a mussel or other animal itself attached to the rock. The site of attachment of small specimens suggests that the cypris always fixes itself in a cranny and not on a flat or protruding surface of rock.

The external form appears closely related to the dwelling place. Isolated individuals on comparatively exposed rocks show numerous well-developed latera, and irregular main valves largely uncovered by integument and often spotted with black (Fig. 15). Such forms, if the terga are long, are probably Hutton's *P. darwini,* but if the tips are worn or broken they would be *P. spinosus* in its limited sense. Where many occur close together in an exposed colony, central specimens show fewer and smaller latera, probably due to friction between adjacent barnacles (Fig. 13). In more sheltered colonies the latera are even less conspicuous, being almost covered by black integument; while in extreme forms from darkest crevices even the main valves may be concealed (Fig. 14). If they are not completely covered, these valves, sheltered from wearing agencies, are smooth and regular, with unbroken tips and a well-developed rostrum (*P. sertus* of Darwin).

The length of the peduncle is also variable, ranging from about half that of the capitulum in some exposed individuals to three times its length or more in specimens in the centre of colonies or other positions where the mantle opening would otherwise be below the level of its surroundings.

Altogether, whereas considerable diversity of external form occurs, the examination of a few hundred specimens in the field indicates that this is merely epharmonic, closely related to the precise dwelling place of the individual, and with all intermediate stages connecting its several extremes.

Feeding: Neither specimens in a tank nor those in the field show the almost rhythmical extrusion and withdrawal of cirri that characterises many barnacles. Instead, the cirri remain in the extruded position for considerable lengths of time. In the tank, nothing happens unless the cirri are touched. But, if one watches a colony in its natural surroundings while the tide is coming in, about half an hour after waves begin to wash the colony first one individual and then another will slowly extrude its cirri. These are then kept continuously expanded, forming a semi-circular net through which the water rushes. Between one wave and the next the cirri may show twitching, incurling actions, by which presumably food particles are passed forwards to the trophi. But unless an animal is considerably molested, the cirri are not withdrawn into the mantle.

Conceivably it is the loss of the habit of repeatedly extruding and withdrawing the cirri that controls the type of habitat in which *P. spinosus* can survive; for the collecting of food appears to depend not so much on the activity of the animal as on the movements of the surrounding water.

Food: Judging by gut contents, smaller crustacea constitute the bulk of the diet. Most samples examined had the remains of one or more Isopod or other Malacostracous crustacean, often of no mean size. During the breeding season nauplius limbs, apparently of its own species, were not infrequent. Pieces of algae are usually present. Other recognisable remains have included polychaet setae, diatoms, nematodes, and two species of mite.

Seasonal Variations of Gonads: In June and July, the ovaries are inconspicuous in the peduncle, in most cases showing microscopically only minute, dull orange ova. Samples of barnacles examined during spring show considerable variation, ova being minute in the ovaries of some individuals, fairly large in those of others. But by November or December the upper regions of most peduncles are filled with masses of large bright orange ova, soon to become the embryos of the oncoming season. At the beginning of March, the only individuals in which ova are not readily seen in the peduncle are some which have young bright orange ovarian lamellae in their mantle cavities. At this time, specimens without ovarian lamellae mostly show peduncles filled with large eggs, while those with pale ovarian lamellae (i.e., embryos about to hatch) show moderately well developed eggs in the ovaries.

Likewise, the seminal vesicles, usually conspicuously distended with a milky mass of sperms in the early months of the year, are in the majority of specimens slender and inconspicuous from June to October. In both these months, however, some individuals have been found with moderately-extended seminal vesicles, whose contents viewed microscopically consist of a swirling mass of active, filiform sperms.

Hence it appears that eggs and sperms are slowly being formed for several months before fertilisation occurs.

One specimen of *P. spinosus* and one of *C. villosa* have been found with ova in the oviducts. These were distributed fairly evenly along them, from the peduncle to the oviduct opening, placed a millimeter or two apart. Their bright orange colour rendered the course of the ducts readily apparent.

Ovarian Lamellae: The ova are presumably fertilised as they emerge from the oviduct openings and become cemented together to form the flat paired ovarian lamellae in the mantle cavity. Earlier workers (Darwin, 1851, p. 61, and Gruvel, 1905) have presented good evidence for the occurrence of both self- and cross-fertilisation in barnacles. In the present species, whereas isolated adults presumably fertilise their own eggs, in the dense colonies commonly seen cross-fertilisation could readily occur.

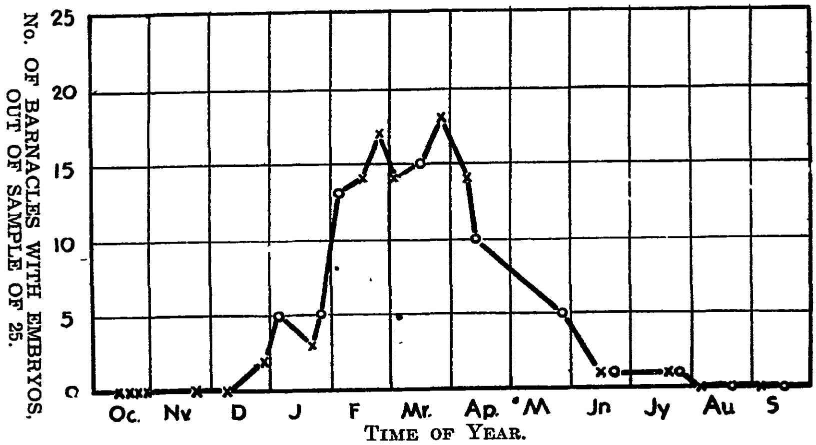
Each ovarian lamella is an irregularly oval sheet of embryos which are bound together by a transparent matrix. Direct counts made of the number of embryos per lamella (by teasing them apart and counting in a squared petrie dish) gave 806 in a fairly small lamella, 1416 in one of slightly less than average size, and 3574 in a fairly large lamella (27 x 16 mms.). Hence the number of embryos per pair of lamellae may be regarded as ranging from about 1500 to over 7000.

Two pairs of lamellae collected in mid-February, whose embryos were at the one-cell and two-cell stage, showed continuous in vitro development; natural hatching of nauplii occurring 30 and 31 days later.

Reproductive Season and Larval Periods: To get a picture of the reproductive season, samples, each of 25 large barnacles, were collected at different times of year and opened. After a preliminary examination at Dunedin during 1940, samples were taken approximately monthly (partly at Dunedin, partly at Wellington) during 1941, and less regularly subsequently. Of the 26 samples shown in graph I, circles represent 1941 samples, crosses later ones. From this it is seen that the breeding season commences in late December or early January, is at its maximum during February, March, and early April, and gradually falls to zero by August. While detailed data are not at hand for drawing comparisons, what figures are available indicate that this breeding peak follows close behind the peak of the maximum annual temperature of the sea water.

Nauplius larvae hatched from lamellae have on several occasions been reared to the cypris stage. Times taken for the nauplius phase were 13–14 days during the warmest conditions, 2½ weeks for the next, and 20–21 days when the temperature was lowest.

No cypris larvae reared from nauplii became attached and metamorphosed to the adult form. Hence the duration of the cypris phase is not known. A single attached cypris with chitinous prevalves was collected amongst *P. spinosus* adults on 26/5/40. (Direct proof is lacking, but it is almost certainly of the same species.) It was 0·9 mm. long, as compared with the length of ·84–·88 mms. of free cypres reared in vitro. The slightness of this increase, together with the date of collecting the specimen, suggest that the cypris phase is not long—probably shorter rather than longer than that for the nauplius. So it would seem probable that most of the young settle between mid-March and mid-June.



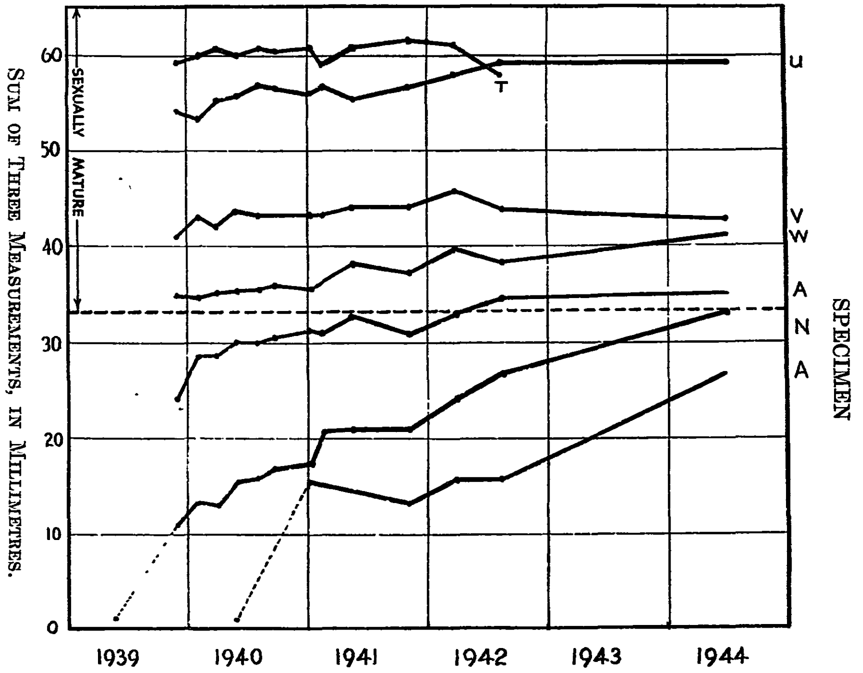
GRAPH 1.—SEASONAL OCCURRENCE OF EMBRYOS.

As during the two and a-half months' peak of the breeding season only about three-fifths of the individuals have embryos, and as one batch of embryos has been found to take one month to develop, it would appear that an average of three-fifths of a month elapses between the hatching of one lot of nauplii and the fertilising of the next series of eggs. From this data and the length of the main breeding season (Graph I), it would seem that on an average one sexually-mature adult produces two batches of larvae per season.

TABLE I.—Growth Rate.

Specimen	Measurement	Date 5/12/39	30/1/40	27/3/40	24/5/40	21/7/40	19/9/40	2/1/41	9/2/41	14/5/41	27/10/41	28/3/42	16/8/42	25/6/44
A	1	7.5	9.5	9.5	10	10.5	10.5	10.5	10	10.5	10	10	11.5	12
	2	10.5	13	13	14	13.5	13.5	14	14	14.5	14	15.5	15	15
	3	6	6	6	6	6	6.5	7	7	7.5	7	7.5	8	8
A'	1							5			5	6	6	9.5
	2							8			6	7	7	11.5
	3							2.5			2	3	3	6
D	1	9	10	10.5	10.5	10.5	10.5	10.5	11	11	11	12	12.5	15
	2			11	11	11	11	11	12	12	12	13	13	14
	3	4	6	5	6	5.5	6	6	6.5	7.5	7	9	8	9
E	1	10	10	10.5	11	12	11	11.5	12.5	13	13	12	12	12
	2				10	10.5	11	12	12	13	12.5	13	14	12.5
	3	5	5.5	5.5	6	7	7	8	7	7.5	7	8	8	7
N	1	3.5	5	4	5.5	6	6.5	6.5	7	7	7	9	11	13
	2	5	5	5.5	7	7	7.5	8	9	9	9.5	10	9	12
	3	2.5	3	3	3	3	3	3	5	5.5	5	5	7	8
T	1	21	21	23	23	23	23	23	22.5	23.5	24	23.5	21	
	2	24	24	22	22	23	22	23	22.5	22.5	22	22	23	
	3	14	15	16	15	15	15.5	15	13.5	15	16	16	14	
U	1	20	19	19.5	20	21	21	20	20	19.5	21	21	21	22
	2	22	22	23.5	24	24	24	24	25	24	24	25	25	24
	3	12	12	12	12	12	12	12	12	12	12	12	13	13
V	1	17	18	17	17.5	17.5	17.5	17.5	16.5	17	18	18	18	18.5
	2	14	15	16	16	15.5	15.5	15.5	15.5	15	15	16	15	14
	3	10	10	9	10	10	10	10	11	12	11	12	11	10
W	1	13	13	13.5	13.5	13.5	14.5	14	14	14	14	15	15	16
	2	13	13	13	13.5	13.5	13	13.5	13.5	14	14	14.5	14	13.5
	3	9	8.5	8.5	8.5	8.5	8.5	8	9	10	9	10	9	11.5

Growth Rate: The growth rate was studied by measuring several specimens in marked positions in a channel at Bruce's Rocks over a period of 4½ years. Originally, 23 specimens, ranging from the smallest accessible barnacle seen in the channel to full-sized individuals, were selected for measuring. Within three months, five young specimens (forming a small colony in a position unusually exposed for the species) died and subsequently disappeared. Soon afterwards, six others, whose environment was probably upset by the removal of a sheltering rock, also died. Of the remaining 12, the largest (T in Table I, and Fig. 15) was limp and flabby on the second-last date of measuring, had vanished by the last; and two were not certainly identifiable during the later, less frequent visits; but nine provided a continuous series of measurements. In addition, one tiny specimen (A^1) was first seen in January, '41, between two of the barnacles that were being measured, and hence was subsequently recorded. Its apparently high first figure (Graph II, A^1) was probably due to inaccurate measuring owing to its awkward position. An error of ± 1 mm. is also liable to have occurred in other measurements, as not infrequently the portion being measured was not readily accessible to the tips of the dividers.



GRAPH 2.—GROWTH RATES OF SESSILE SPECIMENS.

As total width or length of a specimen could vary with its state of contraction at the time, and as calcareous valves were liable to erode, hence not showing regular increments, it was deemed advisable to compromise by making three measurements of each specimen on each date. These were: (1) Tip tergum to tip rostrum; (2) width, base carina to base rostrum; (3) length of exposed portion of tergum, each in millimetres (Fig. 7). This data for nine specimens on 12 dates is given in Table I. For simplification, the three measurements are added and the results show graphically for seven of these (Graph II). The two smallest specimens, A^1 and N, had presumably each settled during the autumn prior to their initial measurements, when the equivalent sum of dimensions of the newly-attached cypris would be about $1\frac{1}{4}$ mms (dotted line, Graph II).

The measuring and opening of a number of specimens during the breeding season indicated that reproduction typically commenced when the sum of the above three measurements exceeded 33 mms. Hence, from Graph II it appears that about 5 years elapse between the settling of the cypris and the attaining of sexual maturity. These specimens, however, are little more than half grown. The graph indicates that at least as long again is required for " full size " to be attained while anyway as many years again may elapse before death ensues; i.e., while recognising the limitations of this data, it may probably be assumed that one individual of *P. spinosus* is producing young for a period of at least 10 years.

How Many Larvae Does One P. spinosus Adult Produce? The data provided give a basis for a rough average estimate. Taking 10 years as the length of the reproductive period (the weakest assumption, as it may be much longer), two pairs of lamellae as the annual average, and 3000 larvae as the average per pair of lamellae, then one *P. spinosus* barnacle would produce during its lifetime some 60,000 larvae.

ANATOMY OF *P. spinosus*.

Externals: The external appearance of the peduncle and capitulum is shown in Figs. 7, 13, 14, 15, and their variations have earlier been discussed. The exposed portions of the valves and spines are pale grey, sometimes with a lavender tinge. The integument is black around the valves, but pales to yellow-brown towards the base of the peduncle of more sheltered specimens. It becomes dull red on alcoholic preservation. As the capitular valves have already been described in detail by Darwin (1851, pp. 324–9) and others, they will not be further considered here.

The actual " body " of the barnacle lies inverted in the mantle-cavity, being attached anteriorly in the region of the scuta and the rostrum. It is regarded as consisting of the last three head segments and six thoracic segments of the cypris (the first, the antennulary and probably the antennary larval segments being incorporated in the peduncle). As in cirripedes generally, this " body " has rotated back dorsally at metamorphosis until its anterior end is directed towards the ventral surface of the cypris, its posterior end towards the larval dorsal surface. Hence its cirri (whose bases overlie the ventral nerve-cord) protrude through the mouth-opening which is across the posterior end of the cypris (Fig. 5).

The mouth lies in the posterior half of the body, its position being further back than in most cirripedes. This is presumably correlated with the position of the scuta and their adductor muscle, which are placed more posteriorly over the body than in the majority of pedunculates. The gut is consequently bent in a very deep U.

The swollen anterior part of the body, enclosing the bend of this U and placed beneath the adductor muscle, is termed the prosoma (Fig. 8, pr.). Between the prosoma and the mouthparts there can be seen by transparency two semi-translucent zones—the excretory organs (Fig. 8, 1 ex. and ev.). The anus, a longitudinal slit, lies just dorsal to the base of the penis, between this and the caudal appendages. The long, tapering penis is deep purple, very finely annulated, and sharply reflexed forwards between the cirri, so that its tip, bearing the male opening, usually lies close to the mouthpart projection (Fig. 10). The integument all over the body is well chitinised, staining blue with Mallory's. Over the prosoma it is smooth except for a few irregularly-placed hemispherical papillae. But over the thorax it is embossed to form oval swellings (Fig. 8). These, like narrower pads above them on coxopodites 1–5, are filled with loose connective tissue. The thin integument of the body (8 to 30 microns thick) is continuous with that lining the mantle and covering the capitulum and peduncle (except where interrupted by valves or scales). From the mantle-lining laterally, in the region of the prosoma, protrude two small papillae, the ovarian frenae. The heads of these carry numerous minute short bristles, by which they attach the ovarian lamellae to the mantle.

The Segmental Appendages: The minute antennules, embedded in the base of the peduncle, can still be seen in young sessile specimens if these are carefully removed from their substratum and boiled in caustic potash. In favourable instances (Fig. 1) there can be distinguished the long arm, the sucker, and the tiny lateral segment of the cypris antennule, while the remnants of stouter setae may also be apparent. As in other cirripedes, no vestige of the larval antennae was found.

The paired *mouthparts* lie under the broad, bullate labrum. The *mandibles* show three large teeth (Fig. 4, A, B, C). Commonly two (but sometimes three or one) smaller teeth occur between A and B, while occasionally a small one is also present between B and C. The mandibular palps are fringed terminally with numerous setae whose length varies among different individuals (Fig. 2, mn.p.). The *maxillules* and *maxillae* are shown in Figs. 6 and 2. On the posterior bases of the latter lie the openings of the excretory organs on slight projections (unlike the condition in *C. villosa,* where they project strongly).

The *cirri* each have a long coxopodite, a short, stout basipodite, and two multi-articulate rami (Fig. 3). None of the rami are markedly reduced, as in many cirripedes, and the first pair of limbs is placed close to the second (Fig. 8). The number of segments per ramus for any limb varies among different individuals and even between two sides of one specimen. Average numbers (giving legs and rami from before backwards) are: 11, 11; 13, 14; 15, 16; 16, 16; 16, 17; 17, 17.

Peduncle: The upper portion, immediately beneath the capitulum, is usually largely occupied by the ovaries. The attachment end contains the cement glands, which have not been studied in detail.

Transverse sections (Fig. 24) show an ectoderm layer of tall, clear cells, outside which lies a thick layer of faintly laminated chitin. Spaces in this in decalcified sections represent the positions of the scales. Externally bounding the chitin is a narrow, fuchsin-staining cuticular sheath. Inside the ectoderm lie three layers of muscles—diagonal, circular, and innermost a broad zone of longitudinal muscles which pass from the mantle to the base of the peduncle. Scattered through the loose connective tissue of the peduncle is a system of stout unstriated anastomosing fibres, staining a vivid red with fuchsin and more or less radially arranged (Fig. 31). From them more slender fibres pass out through the muscle layers, terminating among the ectoderm cells in fine branches attached to the integument.

Somatic Muscles (Fig. 17) : Despite the comparatively immobile life of the adult, a fairly complex muscular system is developed. Muscles may show broad zones of attachment to the body-wall surface; circumscribed origin or insertion from deep intuckings of the body-wall (termed apodemes, the chief of which occur between the mouthparts and the prosoma, at the sides of the prosoma in the U-bend of the mid-gut, and between the bases of the cirri) ; or finally may take origin from endosternites. There are three main endosternites, all median—two in the U-bend of the gut (Fig. 10 v.en. and d.en) and a slender four-horned one in the mouthpart projection posterior to the oesophagus (Fig. 11, end.). These take up aniline blue stain, but do not withstand boiling in caustic potash.

The main elements of the muscular system can be briefly functionally analysed in relation to the movements shown. *Bending and contracting of peduncle:* Its longitudinal, circular, and diagonal muscles have already been described. *Control of mantle opening:* The short cylindrical adductor muscle, attached to the centre of each scutum, is by far the stoutest in the body. It consists of fibres whose faint striations are not nearly as clear as those of many other of the somatic muscle fibres. *Raising of body in mantle:* Several pairs of stout muscles, originating at the occludent margins of the scuta and beneath the rostrum, radiate out slightly to broad insertions on the sides of the prosoma (Fig. 17, m.b.m.). *Bending of body:* Long lateral body-wall muscles, attached posteriorly to successive thoracic intuckings between limb-bases, have broad insertions anteriorly on the sides of the prosoma (Fig. 17, l.b.m.). *Movements of cirri:* Of muscles passing to the legs, some are attached basally to apodemes on the same side of the body (Fig. 17, c.m.), others cross over to the opposite side between the central body-wall and the nerve-cord (Fig. 27). *Movements of mouthparts:* The numerous short stout trophic muscles chiefly take origin from the intuckings of the integument at the base of the mouthpart projection. *Lateral contraction:* Muscles attached medianly to the upper (ventral) endosternite radiate out to intuckings of the body-wall above and below the excretory organs (Figs. 12, rad., 17, r.m.). Below the lower endosternite, two transverse muscles separate the excretory organs from the testis (Fig. 12).

Gut (Fig. 10) : Fore-, mid, and hind-gut regions are sharply differentiated. The long narrow fore-gut or oesophagus shows in section a narrow star-shaped lumen (Fig. 23), separated from the thick muscular wall by the tall ectoderm cells and layer of chitin that these secrete (Fig. 32). As well as longitudinal and circular muscles, extrinsic fibres are present which run out anteriorly to the apodeme between trophi and adductor muscle, posteriorly to the ventral endosternite (Fig. 10). At the junction with the mesenteron, the diameter of the lumen suddenly increases greatly, and the chitinous lining of the oesphagus ends as a splayed-out, expanded

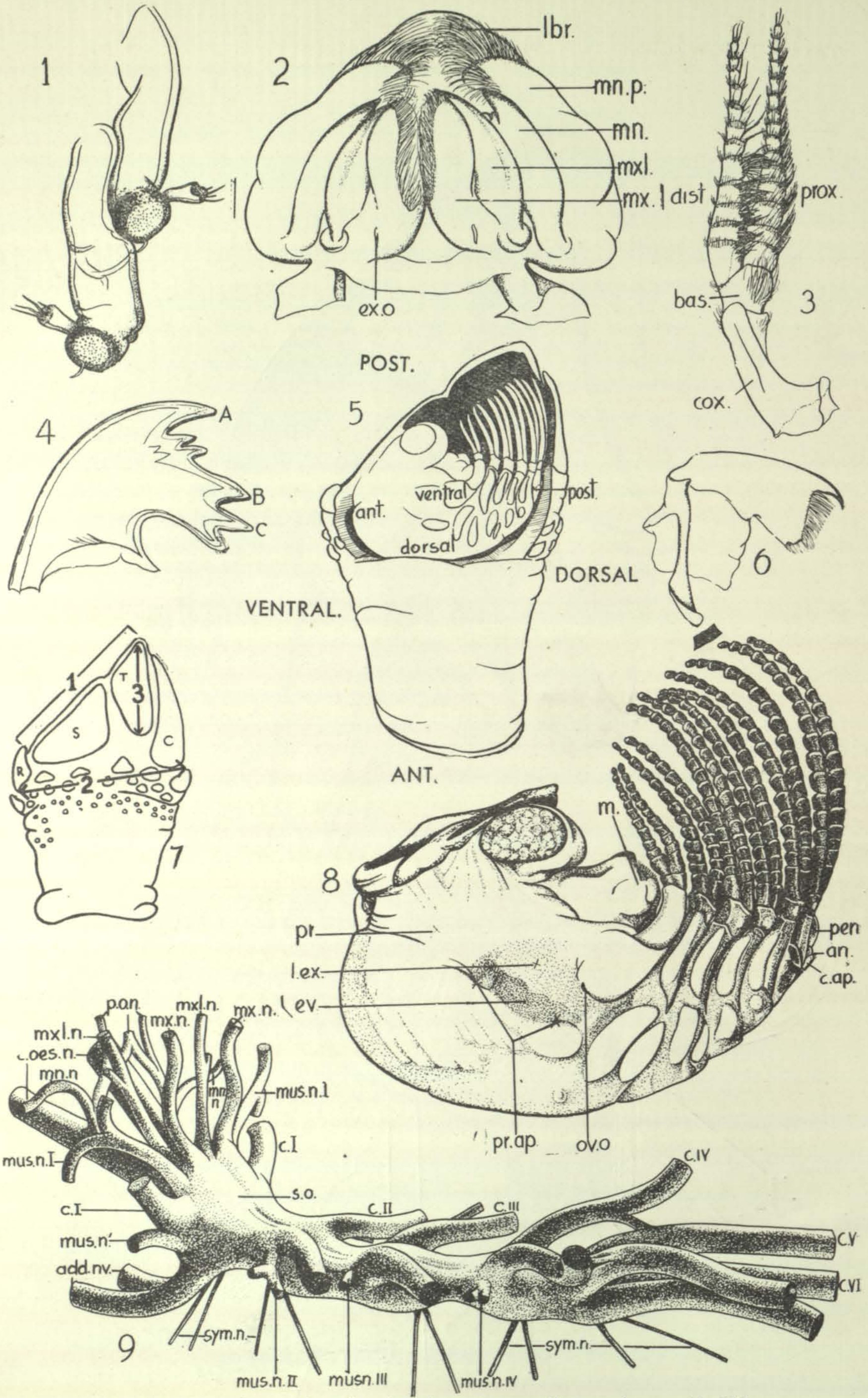


FIG. 1.—Antennules from base of peduncle of young sessile specimen, × 210.

FIG. 2.—Mouthparts in situ, viewed from behind, × 14. lbr., labrum; mn.p., mandibular palp; mn., mandible; mxl., maxillule; mx., maxilla; ex.o., excretory opening.

FIG. 3.—First right cirrus, from behind, × 7. dist., prox., distal, proximal; bas., basipodite; cox., coxopodite.

FIG. 4.—Mandible, × 14.

FIG. 5.—Adult with half of mantle removed, for comparison of orientation of cypris (capital letters) with 'body' of sessile form (small letters). Natural size.

FIG. 6.—Maxillule, × 14.

FIG. 7.—Adult, natural size, showing measurements taken in growth-rate study. R, rostrum; S, scutum; T, tergum; C, carina.

FIG. 8.—'Body,' × 4. pr., prosoma; l.ex., lateral excretory sac; ev., evacuatory sac; pr.ap., prosomal apodemes; ov.o., oviduct opening; m., mouth; pen., penis; an., anus; c.ap., caudal appendages.

FIG. 9.—Postero-lateral view of nerve cord (ventral surface uppermost); drawn from model based on dissections and serial sections. (See text for lettering.)

FIG. 10.

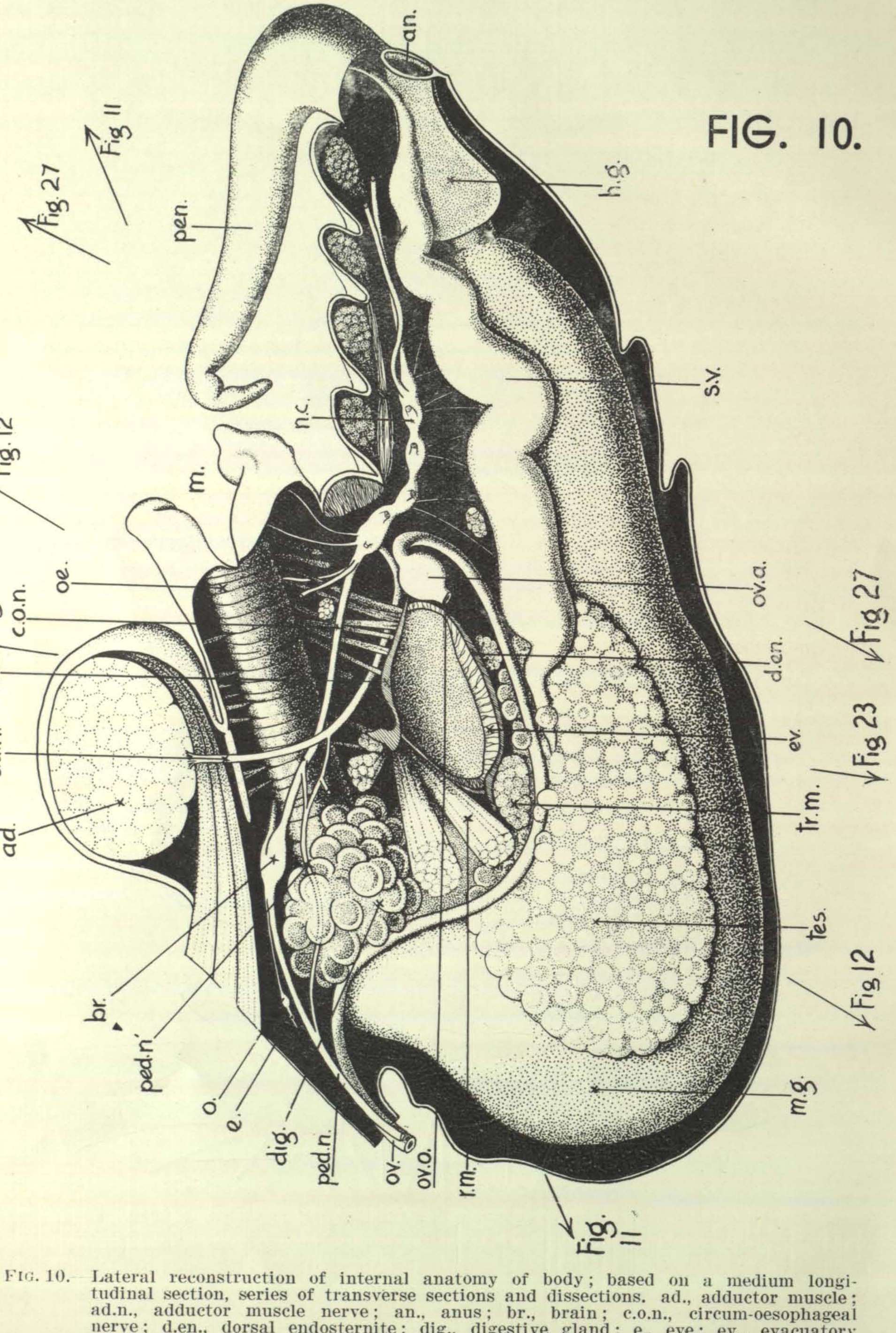
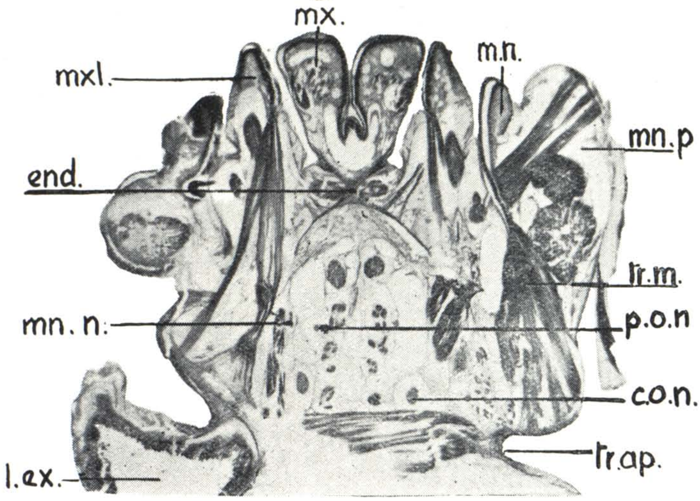


FIG. 10.—Lateral reconstruction of internal anatomy of body; based on a medium longitudinal section, series of transverse sections and dissections. ad., adductor muscle; ad.n., adductor muscle nerve; an., anus; br., brain; c.o.n., circum-oesophageal nerve; d.en., dorsal endosternite; dig., digestive gland; e., eye; ev., evacuatory sac; h.g., hind-gut; m., mouth; m.g., mid-gut; n.c., nerve cord; o., ophthalmic ganglion; oe., oesophagus; ov., oviduct; ov.a., oviduct atrium; ov.o., oviduct opening; ped.n., peduncular nerve; ped.n ., branch to last; pen., penis; r.m., radial muscles; s.v., seminal vesicle; tes., testis; tr.m., transverse muscle; v.en., ventral endosternite.

Fig. 11



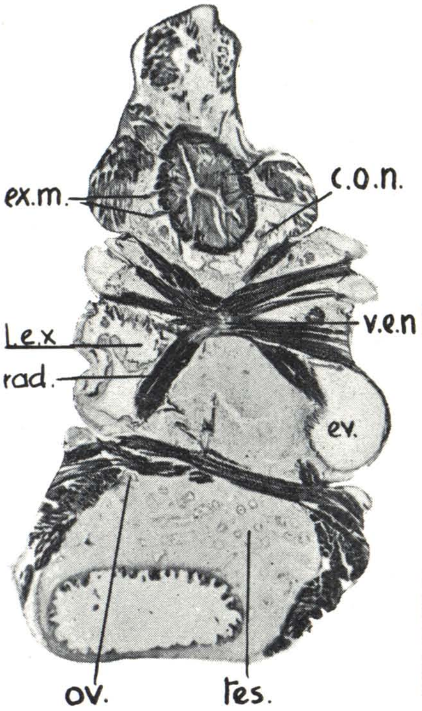


Fig. 12

Fig. 13

Fig. 14

Fig 15

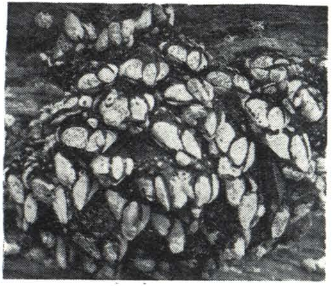


Fig. 16

FIG. 11.—T.S. Mouthparts, × 18. (For angle of section, see. Fig. 10.) c.o.n., circum-oesophageal nerve; end., endosternite; l.ex., lateral excretory sac; mn., mandible; mn.n., nerve to mandible; mn.p., mandibular palp; mx., maxillule; p.o.n., post-oesophageal nerve; tr.ap., trophic apodeme; tr.m., trophic muscles.

FIG. 12.—T.S. Body, × 9. (For angle of section, see. Figs. 10 and 17.) c.o.n., circum-oesophageal nerve; ex.m., extrinsic muscles of oesophagus; l.ex., lateral excretory organ; ov., oviduct; rad., muscle radiating from v. endosternite to body-wall.

FIGS. 13, 14, 15.—Specimens of *P. spinosus*, natural size. Fig. 13, from centre of colony; Fig. 14, sheltered form; Fig. 15, solitary exposed individual (specimen T in growth-rate study).

FIG. 16.—*P. spinosus* colony, 2/5 natural size.

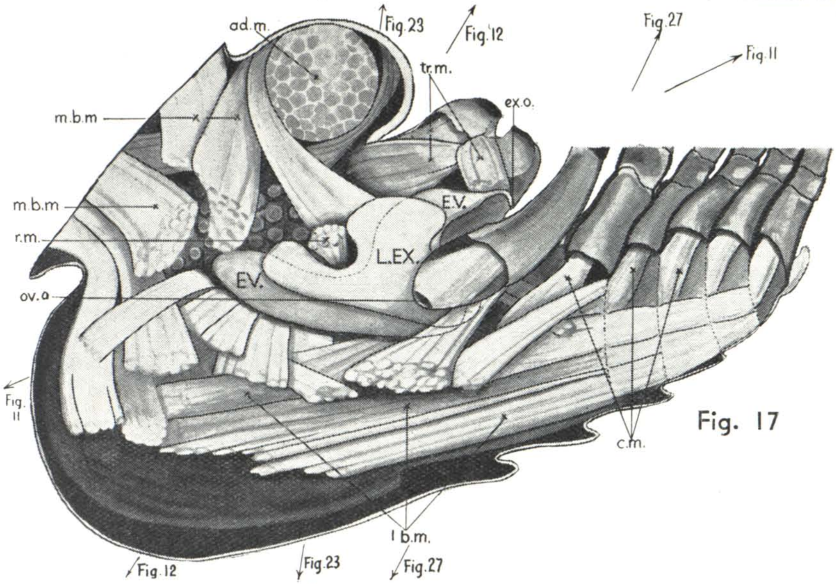


Fig. 17

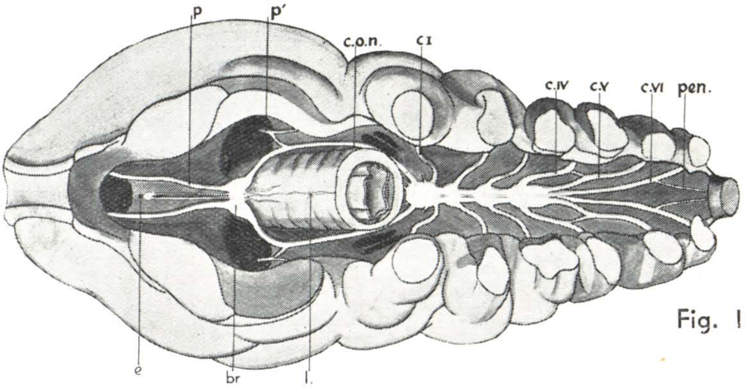


Fig. 18

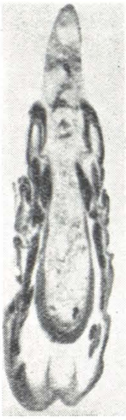


Fig. 19

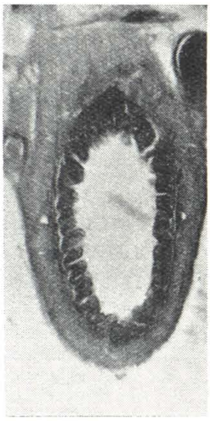


Fig. 20

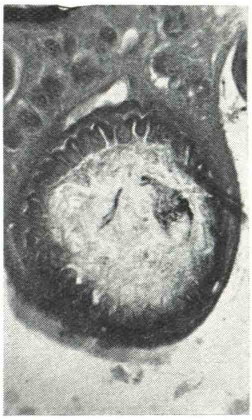


Fig. 21

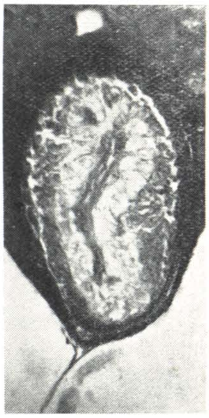


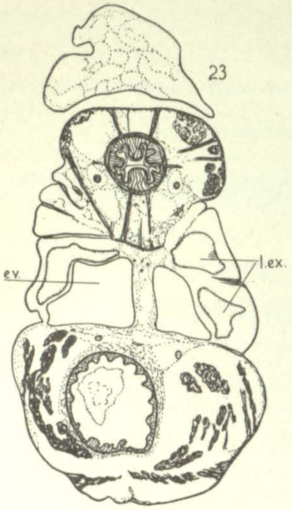
Fig. 22

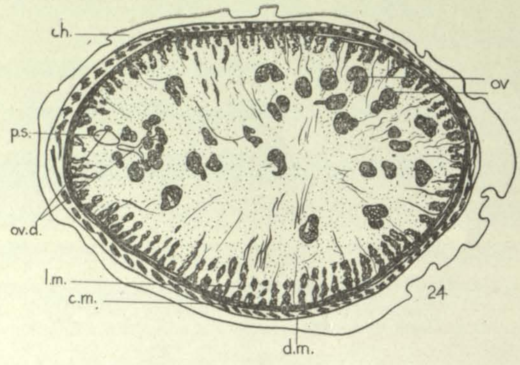
Fig. 17.—Superficial dissection of body, showing muscular and excretory systems. ad.m., adductor muscle; c.m., muscles to cirri; ev., evacuatory sac; ex.o., excretory opening; l.b.m., lateral body-wall muscles; l.ex., lateral excretory sac; m.b.m., mantle-body-wall muscles; ov.o., oviduct opening; r.m., muscles radiating from ventral endosternite; tr.m., trophic muscles.

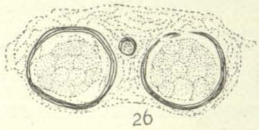
Fig. 18.—Ventral dissection, showing nervous system (adductor muscle removed). br., brain; C.I-VI, nerves to cirri; c.o.n., circum-oesophageal nerve; e., eye; l., labrum nerve; p., p′, main and accessory peduncular nerves; pen., nerves to penis.

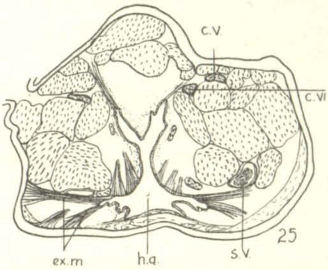
Fig. 19.—T.S. posterior end, showing discharge of peritrophic membrane, × 11.

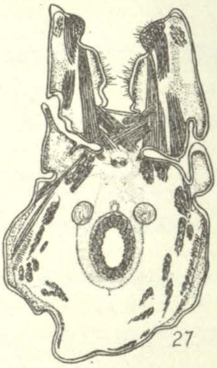
Figs. 20–22.—Successive stages in development of new peritrophic membrane, passing from behind forwards in same specimen as Fig. 19; all × 27.

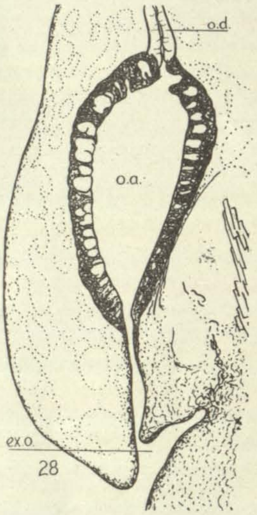


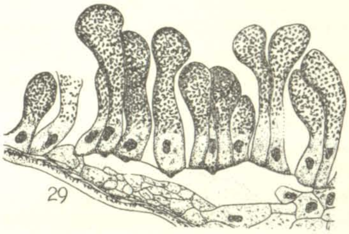


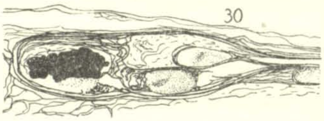


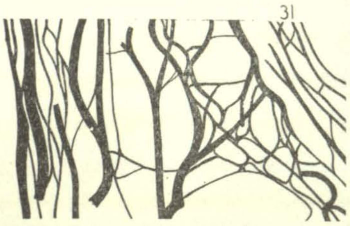












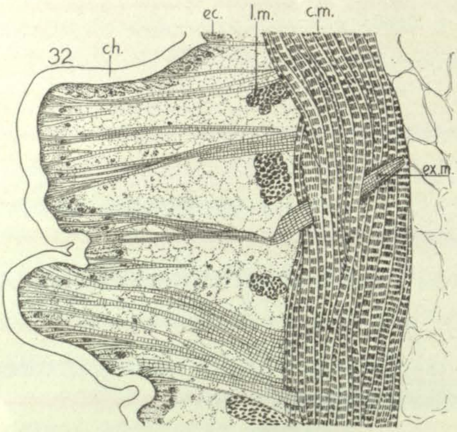


FIG. 23.—T.S. young specimen, × 22. (See Figs. 10 and 17 for angle of section.) l.ex., lateral excretory sac; ev., evacuatory sac.

FIG. 24.—T.S. peduncle, × 7½. ch., chitin; c.m., circular muscles; d.m., diagonal muscles; l.m., longitudinal muscles; ov., ovary branches; ov.d., oviducts; p.s., peduncular sinus.

FIG. 25.—T.S. thorax through hind-gut (h.g.), × 16. C.V-VI, nerves to cirri V and VI; ex.m., extrinsic muscles of hind-gut; s.v., seminal vesicle.

FIG. 26.—T.S. nerve cord, inter-ganglial region, × 76.

FIG. 27.—T.S. thorax, × 19, showing deep inter-cirral apodemes and muscles crossing from these to cirri.

FIG. 28.—T.S. oviduct atrium, × 5. od., oviduct; o.a., oviduct atrium; ex.o., external opening of oviduct, below cirrus I.

FIG. 29.—Portion of septum between excretory and evacuatory sacs, showing characteristic cells lining former, × 580.

FIG. 30.—L.S. eye and ophthalmic ganglion, × 132.

FIG. 31.—T.S. central region of peduncle, showing anastomosing fibres, × 72.

FIG. 32.—T.S. wall of oesophagus, × 160. ch., chitin; c.m., circular muscles; ec., ectoderm lining; ex.m., extrinsic muscle; l.m., longitudinal muscle.

[*To follow Plate 53.*]

structure. At the same time, the histology quickly changes to the thin-walled mid-gut arrangement. This shows a lining of tall columnar epithelium cells, thrown into numerous low papillae filled with connective tissue. Next, more especially anteriorly, come scattered diagonal muscles lying in two series at right angles to each other; while around them is a compact layer of circular muscles, running continuously into the thicker layer of oesophageal circular muscles. Surrounding the mid-gut is a broad layer of parenchyma cells with conspicuous nuclei.

A sharp constriction separates the mid-gut from the " rectum," or hind-gut, whose transectional appearance is shown in Fig. 25. The cellular wall surrounding the delicate chitinous lining is extremely thin. From among its cells, extrinsic muscles radiate out to the body-wall.

A pair of many-lobed digestive diverticula lie laterally at the junction of fore- and mid-gut (Fig. 10, dig.). Each opens into the beginning of the mesenteron posterio-laterally by a fine, short duct. The epithelial cells lining the glands are cubical. The gland contents appear granular.

Peritrophic Membrane: Food accumulates in the mid-gut, separated from its epithelial lining by a peritrophic membrane—a thin chitinous secretion.

While one peritrophic membrane is being extruded through the anus (Fig. 19), the next is already being formed in the mesenteron (which, in the temporary absence of contents, is much constricted). Its development is most advanced at the anterior end, but it appears to be being formed throughout the length of the mid-gut. In passing from behind forwards, first occurs a region with nothing inside the columnar epithelium. Then a finely granular substance appears on the surface of some, then all, of the cells (Fig. 20). A little further forward this fills the whole lumen (Fig. 21). Then it becomes separated from the epithelium and a cavity appears in its centre (Fig. 22). At this stage, before it is distended with food, the membrane appears relatively thick. Its granular outer and inner boundaries take fuchsin stain. The intervening zone is pale and irregularly stained with the aniline blue of Mallory's.

Excretory System: The paired excretory organs are placed in the U-bend of the gut. Each consists of an outer lateral excretory sac and an inner evacuatory sac (Figs. 17, 23, 1. ex. and ev.).

Each lateral excretory sac is lined with granular yellow excretory cells of characteristic appearance (Fig. 29). No opening from lateral sacs was observed, but the walls separating them from the evacuatory sacs are thin.

Each evacuatory sac, next to its lining of thin epithelial cells, has a wall of anastomosing fibres similar to those occurring in the peduncle and to a lesser extent in other parts of the body.

The short excretory ducts pass from the evacuatory sacs to the openings on the maxillae. They consist of cubical epithelium, show chitinous linings, and have an internal diameter of about 15 microns. Judging from the position of their openings, these excretory organs are probably homologous with the maxillary glands in other groups of crustacea.

Reproductive System: The *testis* is a median structure lying closely in the U-bend of the gut. Dissections show it as a compact, lobulated, dull orange organ (Fig. 10, tes.). Sections show it to consist of a mass of irregularly-branching thin-walled tubes ramifying through compact parenchyma (Fig. 12), this latter being continuous with the connective tissue of the mid-gut wall. The tubes are packed with undifferentiated cells and the various stages of developing spermatozoa.

From each side of the testis arises a duct which soon expands to form a seminal vesicle. This during summer and autumn is a smooth, conspicuous whitish-coloured, convoluted tube, thin-walled and packed with sperms (Fig. 10, s.v.). Posteriorly it tapers, fusing with its pair above (ventral to) the anus, the resulting fine duct traversing the length of the penis.

The *ovary* lies embedded in the upper part of the peduncle, usually conspicuous because of the contained bright orange eggs (Fig. 24). Whether it is really a single or paired structure is obscured in the adult by the irregular, grape-like form.

From the ovary pass a number of tubes, which soon fuse anteriorly to form the two oviducts. Each of these is slender, its wall consisting of a single layer of tall, pale, apparently vacuolated cells, whose tiny nuclei lie close to their bases. In the adult the lateral diameter of the duct is ± 80 microns, its dorso-ventral diameter about twice this. The two oviducts converge, running up close to the muscle wall of the peduncle and into the capitulum, then passing into the anterior end of the body under the rostrum. Their subsequent course, through digestive glands and testis, is shown in Fig. 10 (ov.). Each expands into an oviduct atrium at the base of cirrus I (Fig. 28). Gland cells in the wall of this presumably secrete the matrix which binds the ova into ovarian lamellae. The atrium opens to the exterior by a narrow slit (Figs. 8 and 28. ov.o. and ex.o.).

Haemocoel: In this as in other cirripedes there occurs no closed vascular system, with vessels or heart. A haemocoel, in the form of irregularly anastomosing sinuses, occurs in the loose connective tissue surrounding the various organs.

Dorsal to the posterior half of the mid-gut lies a fairly extensive sinus, interrupted medianly by a connective tissue septum from food-canal to body wall. Around the U-bend of the gut connective tissue is more copious, but this is traversed by numerous smaller sinuses, chief of which is the peri-neural sinus. Small spaces among the connective tissue surrounding prosomal viscera converge anteriorly, passing into the mantle under the rostrum as a single sinus. This at first runs immediately in front of the oviducts (Fig. 24, p.s.), then turns back in the peduncle and forks.

Nervous System (Figs. 9, 10, 18).

The central nervous system consists of an anterior supra-oesophageal ganglion or " brain " connected by a pair of circum-oesophageal nerves to a short ventral cord.

Surrounding both nerve cord and nerves is a sheath, staining blue with Mallory's. Around the sub-oesophageal ganglion especially, this appears laminated, and around nerves in longitudinal section it is clearly annulated. These features, together with the light purple colour that the enclosed nerve fibres stain, serve as useful criteria in tracing the finer branches of nerves amongst muscles. The larger nerves in cross-section are seen to consist of several bundles of fibres, each bundle surrounded by a thin blue-staining sheath.

The brain is a bilobed structure (Fig. 18, br.), histologically showing a considerable degree of complexity. From each lobe runs forward a stout peduncular nerve (Fig. 18, p.). This passes down along the junction between body and mantle, beneath the rostral sinus, receiving a composite lateral branch en route. Each nerve, after approaching an oviduct from above, swings round its outer side to enter the peduncle close behind it.

During the first part of their passage from the brain the peduncular nerves are connected by a sheet of tough tissue. Embedded in this are three extremely slender nerves, arising anteriorly from the brain (Fig. 18). The middle one of these is soon no longer traceable, but the lateral ones expand into ophthalmic ganglia placed close together. Anterior to them, sometimes in contact but at others well separated, lies an irregular mass of dense black pigment, the single median eye, without lens and of simple structure (Fig. 30).

Posteriorly from the lobes of the brain pass back the two long circum-oesophageal nerves. Each gives off a branch distally at the level of the oesophagus, and subsequently enters the front end of the sub-oesophageal ganglion.

The ventral nerve cord is obscurely double, its two elements being more or less fused in the ganglia, but separated by connective tissue and by a slender median nerve in the inter-ganglial regions (Fig. 26). There are four ganglia (Figs. 9, 18), innervating together no fewer than nine segments. Of these, the sub-oesophageal ganglion (s.o.), elongated and slightly bilobed, is the largest and most complex. From its lower surface arise the stout, paired adductor muscle nerves (Fig. 9, add. nv.). These at first pass down and forwards beneath the circum-oesophageal nerves (Fig. 10 ad.n.), running side by side medianly in the septum between the excretory organs, usually above the upper endosternite. They then diverge sharply, pass round the fore-gut on the outer side of the circum-oesophageal nerves, and sweep up to enter the adductor muscle close to its attachment to the scuta.

Each adductor muscle nerve, on approaching the fore-gut, has given off a slender branch which soon divides (Fig. 10). Of its bifurcations, the distal branch quickly enters mantle-body-wall muscles. The proximal fuses with the branch from the circum-oesophageal commissure, the resulting nerve (Fig. 10, ped.n') passing forwards among the lobes of the digestive gland to fuse with the main part of the peduncular nerve close beneath the eye.

From the region of the sub-oesophageal ganglion also arise five other pairs of nerves (Fig. 9). Those supplying the mandibles originate, not from the ganglion itself, but a short distance in front of it from the circum-oesophageal commissure. The maxillulary (mxl.n.) and the maxillary (mx.n.) nerves pass up actually from the anterior end of the ganglion. The former diverge considerably, soon forking, while the latter converge slightly. Each breaks into several branches which enter the muscles of its appendages.

The stout cirrus 1 nerves leave the sides of the ganglion, passing first slightly back and out, then swinging forwards to run up into the cirri (Fig. 18, C.I.). From the base of each a branch goes downwards (Fig. 9, mus.n'), closely following the bend of the oviduct for some distance, and finally branching to supply the lateral body-wall muscles. A further pair of nerves (Fig. 9, mus.n.I) passes outwards from the ganglion close in front of those to cirrus 1. Each soon bifurcates, one half passing up, the other down, into the muscles at the base of the first cirrus.

Similarly with the second and third ganglia (each of which innervates one segment only) there occur both main cirrus nerves running up into the limbs (C.II and III), and also more slender anterior nerves, branching to supply the muscles at the limb bases (mus.n.II and III).

The last ganglion is elongated, a slight constriction indicating its composite nature. From it arise cirri nerves IV, V, and VI, of which only the first pair is accompanied by the additional pair of basal limb-muscle nerves (mus.n.IV). Nerves IV, just before leaving the body, send in branches which fuse with V (Figs. 9, 18).

Nerves V and VI leave the ganglion terminally, the former uppermost, running back for a considerable distance in the body before entering their cirri. Immediately prior to leaving the body, nerves VI give off proximally slender penis nerves (Fig. 18, pen.). These pass along each side of the hind-gut, close above the tapering seminal vesicles. The latter fuse at the base of the penis to form a single sperm-duct, at the sides of which the nerves pass up the penis.

As in Crustacea generally, a visceral or sympathetic nervous system is present. This consists mainly of slender median nerves arising from each ganglion. From the hinder margin of the brain several strands pass directly to the underlying oesophagus, the stoutest of these running up its outer wall towards the labrum (Fig. 18). Slightly stouter nerves originate from the inner bases of the mandibular nerves (Fig. 9, p.o.n.). These bifurcate, their distal halves passing to the fore-gut muscles, their proximal halves fusing medianly, but soon breaking up to form a delicate plexus in the posterior oesophageal wall.

Dorsal nerves pass down from the ganglia of the ventral cord—two from each of the first three, four from the last, of which the final one is directed backwards (Fig. 9, sym.n.). All these lie in loose connective tissue, and are traceable in serial sections as far as the walls of the food canal.

DISCUSSION.

From the foregoing description, let us consider certain features of *Pollicipes spinosus* as compared with those of other barnacles. To begin with, there is the feeding technique, with the absence of the habit of actively extruding and withdrawing the cirri. The precise dwelling place of *P. spinosus,* where water surges violently along inter-tidal rock channels, would doubtless bring a much greater number of food particles to the cirri-net than would any currents the animal itself could create. Perhaps this species has never had a more active feeding mechanism. The wide occurrence, however, of the habit of almost rhythmically extruding and withdrawing the cirri, among both sessile and stalked barnacles, would seem against this. More probably it was superfluous in the habitat where *P. spinosus* occurs, and has secondarily been lost.

Not only in feeding, but in all its requirements this species seems unusually sluggish for a cirripede. In that the irregular blood circulation is considered to be caused by the general body movements, perhaps with a resultingly low metabolic rate in *P. spinosus* the extremely slow growth-rate is correlated.

For in its rate of growth this species seems remarkable among cirripedes. Moore (1944, p. 331) records that the operculate *Eliminius modestus* took 2½–3 months from time of attachment to the production of nauplii; Darwin (1851, p. 63) states that the yawl of the "Beagle," after 33 days in the sea, had several specimens of *Conchoderma virgata* already sexually mature; and Gruvel (1905, p. 426) maintains that the growth-rate of cirripedes generally is very rapid, pedunculates usually increasing more quickly than operculates, typically by nearly a millimeter a day until adult size is attained. Compared with this, the approximate five years that this species takes to reach sexual maturity stands in striking contrast.

In its anatomy, as compared with other cirripedes, *P. spinosus* shows no particularly noteworthy features. The adult barnacles have revealed no vestige of antennae, compound eyes, a heart, an abdomen with abdominal limb rudiments, or any of the other characters by whose absence adult thoracic cirripedes differ from less specialised crustaceans. There is, however, in its structure an absence of specialised features which collectively seem indicative of a comparatively primitive state. For instance, the cirri, unlike those of many pedunculates and operculates, are all of approximately equal length, with the first pair placed close to the second. The digestive glands consist of one pair of organs only, whose several lobes are all histologically similar. The mid-gut lacks regional structural specialisation. Branches of the testis do not ramify among the other organs, or into the limb bases. Branchial filaments have not been developed from the surface of the body or mantle lining. There is no trace of a boring, parasitic, or other specialised habit. The elaborate gastro-ophthalmic nerve plexus, occurring in certain operculates, is absent. Certain other features of the nervous system, such as the detailed segmental arrangement of the nerves, perhaps show a closer similarity to those of a generalised crustacean such as *Chirocephalus* than is shown by other cirripedes. But in the absence of sufficiently full accounts for other barnacles one hesitates to put much weight on such comparisons.

Dwarf males are absent in *Pollicipes spinosus* and other members of the genus, present in the related *Calantica, Smilium, Scalpellum, Ibla,* and reputedly in *Protomitella.* Broch appears to consider dwarf males as a basic feature of scalpelliform cirripedes. He regards his new genus *Protomitella* as primitive in this respect, considering *Pollicipes* as a specialised sideline from which dwarf males have been lost (Broch, 1921, p. 247). But, even assuming the validity of his *Protomitella,* does a wider survey of the cirripedes permit such a view? Only hermaphrodite individuals occur throughout the Balanidae, Verrucidae, and Lepadidae; while the remaining section of thoracic cirripedes, the Scalpellidae, shows many instances of this condition—for example, the genera *Pollicipes, Smilium,* and *Scalpellopsis.* The presence of complementary males associated with large hermaphrodite forms is not universal among any main section of cirripedes, but is scattered amongst various scalpellid species and genera. The unisexual condition is comparatively rare, occurring only in occasional scalpelliforms and certain *Ibla* species. Incidentally, the presence of dwarf males seems rather closely associated with a solitary habit. This suggests that their reduced parasite form has evolved in cases where cross-fertilisation could otherwise not readily occur. So it would seem that the weight of evidence is against Broch's hypothesis. Instead, it appears more logical to regard the totally hermaphrodite condition of *Pollicipes* as the typical cirripede state and the presence of dwarf males in various allied genera as a secondary future.

LITERATURE CITED.

BROCH, H., 1921. Studies in Pacific Cirripedes. *Mortensen's Pacific Expedition,* 1914–1916, Kristiana.

DARWIN, C., 1851. A Monograph of the Cirripedia. I. The Lepadidae. *Ray Society.*

GRUVEL, A., 1905. *Monographie des Cirripedes ou Thecostraces.* Paris, Masson and Cie.

HUTTON, F. W., 1878. List of the New Zealand Cirripedia in the Otago Museum. *Trans. N.Z. Inst.,* vol. xi, pp. 328–330.

JENNINGS, L. S., 1915. Pedunculate Cirripedia of N.Z. and Neighbouring Islands. *Trans. N.Z. Inst.,* vol. xlvii, pp. 285–293.

MOORE, L. B., 1944. Some Intertidal Sessile Barnacles of New Zealand. *Trans. Roy. Soc. N.Z.,* vol. lxxiii, pp. 315-334.

PILSBRY, N. A., 1908. On the Classification of Scalpelliform Barnacles. *Proc. Acad. Nat. Sci. Philad.,* lx, 1.