

Some Points in the Development of
Neomysis vulgaris.

By

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With Plates 23-4 and 3 Text-figures.

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INTRODUCTION.

THERE has been considerable difference of opinion concerning the precise application of the germ-layer theory to the development of Crustacea. For instance, while most authors (e.g. Claus, 1886; Humpferdinck, 1922) have described the muscles as being all derived from the mesoderm, others (e.g. Cannon, 1926; Manton, 1928) have maintained that some of the muscles are mesodermal and others of ectodermal origin; others again (Snetlage, 1905; Moroff, 1912) have held that the musculature in general is of ectodermal origin. This paper is an attempt to elucidate, in the development of *Neomysis vulgaris*,

J. V. Thompson, processes which have been described by Dr. S. M. Manton in her excellent and well-known paper on the related *Hemimysis lamornae* (1928) as being inconsistent with the germ-layer theory. These are (1) the origin of several distinct sets of muscles from the ectoderm, and (2) the development of the liver from the mesoderm and not from endoderm.

Other points are dealt with in the second part of the paper (pp. 579-84).

I wish to express my gratitude to Professor Goodrich who collected and preserved the material, and has given me constant assistance and valuable advice; also to Mr. B. W. Tucker and Dr. J. R. Baker for their most helpful criticism.

TECHNIQUE.

The brood-bearing females were collected in brackish water near Plymouth in the summer of 1934, and embryos of all stages fixed in Bouin's fluid.

The study was largely made from serial sections, transverse, frontal, and sagittal, 5μ thick. Of many clearing agents employed methyl benzoate was found to give best results, clearing direct from 96 per cent. alcohol (Wetzel, 1931); it readily penetrates the embryonic cuticle, 10-15 minutes in each change of fluid being sufficient. Orientation was performed in wax before cooling or on thin rectangles of lardaceous liver. Early stages were stained with iron haematoxylin, and later stages mainly with Mallory's triple stain, or with picro-nigrosin, after borax carmine differentiated with picro-indigo-carmin. The drawings of actual sections were made under the camera lucida.

PART I.

HISTORICAL.

The germ-layer theory has proved to be a very useful generalization concerning certain processes in early embryonic development of coelomate animals, and apparent exceptions to the theory, described from time to time, have usually been discredited. It describes how, in early development, there is brought about a separation of the multiplying cells of the germ

into three discrete layers, an outer ectoderm, an inner endoderm, and between them an accumulation of intermediate cells, the mesoderm. Once distinct from the others each layer gives rise to a specific set of structures, organs, and tissues. The separation takes place and is completed at a comparatively early stage, varying somewhat in different groups but having a general precision which makes the theory of value. There are complications; in the Platyhelminths, the Nemertines, and the Annelids and in the Echinoderms there is a precocious proliferation of intermediate cells from the outer layer to meet larval requirements ('mesenchyme', 'mesectoderm', &c.) and forming muscle and other tissues typical of 'mesoderm', the latter thus having a double or even a multiple origin. However the separation is completed by the same stage as in phyla where the intermediate layer has a single locus and time of origin.

The germ-layer theory may not apply to cases of regeneration (e.g. Reed, 1904), asexual budding (Tunicates, &c.), or the experimental modification of development (Stone, 1926), but this does not necessarily affect its application to embryonic development. In this connexion the Crustacea, and the Arthropoda in general, may well be a critical group, in view of the great irregularity of their early development. In most Crustacea gastrulation is a vague roughly localized immigration of cells often rendered difficult of observation by the abundance of yolk reserves; however the consensus of opinion favours the applicability of the germ-layer theory to this and to succeeding processes. A number of the immigrating cells slowly absorb all the yolk ('vitellophags') forming an epithelium (the 'yolk-sac') of large cells ('yolk-pyramids'); they form the typical endoderm and give rise to the mid-gut and its appendages, the digestive glands ('liver'). Some workers have described the vitellophags as giving rise to blood corpuscles (Nusbaum, 1887, in Mysids; Reichenbach, 1886, in Decapods), and even to the heart itself (McMurrich, 1895, in Isopods); McMurrich further believed the definitive gut to develop from paired condensations of intermediate 'mesoderm' cells. This is, in sum, a direct reversal of the theoretical processes. It is now generally agreed that the vitellophags do not, in fact, give rise to any structures not

typical of the inner layer, but it has been repeatedly suggested that the liver arises from the intermediate layer (Table II, p. 578), or even that the whole mid-gut is so derived. Miss Manton has again raised the question in tracing the origin of the liver in Hemimysis to a block of mesoderm already localized as the mesoderm of the mandibular segment.

Again some workers have maintained that there is not a complete separation of outer and intermediate layers at gastrulation, the outer layer continuing to proliferate cells which form muscle and other tissues theoretically typical of the mesoderm. Weldon (1892, Crangon), Lebedinsky (1890, Eripha), and Nusbaum (1887, Mysis) believed all the intermediate tissues to arise from the outer layer during post-gastrulation stages. Pereyaslawzew (1888, Amphipoda) postulates a more or less localized origin from the ectoderm of the limbs, which was supported by Heidecke (1904), though for part only, of the intermediate layer. These earlier descriptions, however, have been completely discredited by the discovery of mesodermal teloblasts (Bergh, 1893, Mysis; 1893, Gammarus, &c.), a transverse row of cells which buds off a regular series of rows, one to each trunk segment, as in Annelids. There is no indication in the Crustacea that any of the ectodermal teloblasts give rise to musculature, as alleged in the case of the circular musculature of Annelids (Vejdovsky, 1889, Criodrilus; Staff, 1910, Criodrilus; Bergh, 1890, Lumbricus; Penners, 1923, Tubifex). In any case these circular muscle teloblasts in Oligochaetes separate from their ectodermal sister teloblasts, completely, and sufficiently early, for essential agreement with the germ-layer theory. Other workers have derived from the outer layer only one tissue normally characteristic of the intermediate layer, namely muscular tissue. Snetlage (1905) and Moroff (1912) believed this to be true for the whole of the musculature, and though Claus (1886) and Humpferdinck (1922) have probably correctly interpreted the condition as one in which a peripheral ectodermal component ('tonofibrillen' of Humpferdinck) becomes attached to typically derived mesodermal muscles, yet the question has been reopened by Professor Cannon and Dr. Manton who describe only certain of the systems

of muscles as being ectodermal. However, as Table I shows, there is not good agreement in the evidence from different forms, and further investigation seems necessary.

TABLE I.
Ectodermal Muscles in Crustacea.

<i>Chirocephalus</i> (Cannon, 1926).	<i>Hemimysis</i> (Manton, 1928).	<i>Nebalia</i> (Manton, 1934).	<i>Estheria</i> (Cannon, 1924).	<i>Cypris</i> (Cannon, 1925).
Dorso-ventral muscles / of body	Flexor mus- cles of limbs	Intersegmen- tal muscles		
M	Extensor mus- cles of limbs			
	Carapace muscles of segments. Maxillary 2, thoracic 1, 2, 3			
	Interpara- gnath muscle	Interpara- gnath muscle		
Proctodaeal dilator mus- cles and pro- ctodaeal circu- lar muscles	M			
? Oesophageal dilator mus- cles	M			
Sphincter muscle of an- tennal gland	M		Sphincter of antennal gland	Sphincter of antennal gland
M				Sphincter muscle of maxillary gland

'M' indicates mesodermal muscles (where definitely so described) for comparison.

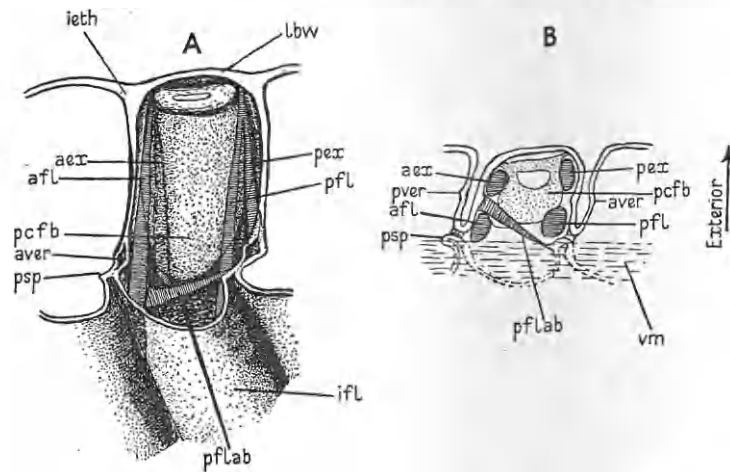
THE MUSCULATURE.

Neomysis Vulgaris.

1. Extensor and Flexor Muscles of the Limbs.

This is the most important set of muscles to which Miss Manton attributes, in *Hemimysis lamornae*, an ecto-

dermal origin. They are developed in every segment from the maxillary to the fifth abdominal, with modifications of the typical arrangement in the three most anterior of these segments and in the abdomen. The arrangement is essentially the same in *Neomysis*. In a typical segment (thoracic 2-8) there are anterior and posterior groups (Text-fig. 1), each containing a



TEXT-FIG. 1.

A. Arrangement of the extensors and flexors of the limbs in the limb-bay as seen from inside the body. B. Arrangement of the extensors and flexors as seen in frontal section of the body.

flexor and an extensor component, occupying the 'limb-bay', and pursuing (in the adult) an almost vertical course up from their attachments on the limbs close along the intersegmental ridge (cf. Manton, 1928, pp. 418-21, Text-figs. 24, 25; Pl. 23, figs. 20, 21, &c.).

The 'limb-bay' is that portion of the general body-cavity in each segment immediately above the limb, opening widely into the body-cavity above and into the limb below, and is walled off anteriorly and posteriorly by vertical intersegmental ridges which are the continuation, up the lateral body-wall, of the furrow separating each limb from that of the next segment. The intersegmental ridge eventually fades out dorsally in a

mere thickening (Text-fig. 1, *ieth.*) which serves for the attachment of these and of other muscles. The dorsal attachments of the extensor and flexor components of each group are close together, while ventrally the muscles diverge, the extensors being inserted more laterally and the flexors towards the inner side of the limb making a functional set; a forward branch from the posterior flexor is inserted between the anterior extensor and flexor.

Dr. Manton believes the muscles to be derived, in *Hemimysis*, from the intersegmental ridge they follow so closely, and therefore to be ectodermal in origin (1928, Text-fig. 24). The muscles appear to be formed by the delamination of thin sheets of cells from the ridge, later grouping themselves into the typical muscle-bundles. Between the anterior and posterior groups of any segment lies an expanded ventral prolongation of the 'dorsal mesoderm' (Manton, 1928, Text-fig. 24, 'pericardial floor base') which is left in this position as the bulk of the dorsal mesoderm moves dorsally during development. The muscles and the 'ventral expansion' together fill the limb-bay during the critical stages of development, but are apparently quite distinct from each other throughout. The anterior branch of the posterior flexor passes across the inner face of the ventral expansion and the connexion across is believed to be effected at a particular stage (Manton, Text-fig. 24 d) when the anterior and posterior groups of muscle rudiments practically meet internally to the mesoderm.

In *Neomysis* there does not appear to be good evidence of such delamination of cells from the ectodermal intersegmental ridge, nor were any division spindles of ectoderm cells of that region found to be orientated in such a way as to proliferate cells internally to the epithelium. The ectoderm of the ridge may at times appear multilaminar in frontal section (fig. 4, *ep.*, Pl. 23), but this may perhaps be explained by the oblique direction of the limbs and by the presence of approximately horizontal intuckings marking the base of the limbs and seen in surface view; it is also important that the 'outer connective' muscle of the 'ventral mesoderm' (Manton) passes out close along the intersegmental ridge (fig. 12, Pl. 24). The extensor

and flexor muscles of the limbs appear to be derived from the ventral expansion of the dorsal mesoderm, and only later become separated from it, first at their ventral attachments and later more dorsally. Figs. 1, 2, 3, and 11, Pl. 23, are a series of transverse sections of the body showing progressive stages of their development in a typical segment. Fig. 1, Pl. 23, shows a ventro-lateral quarter of a transverse section of the body at a stage when the segmental mesoderm masses on each side have divided into ventral, dorsal, and limb mesoderm blocks. The ventral end of the dorsal mesoderm (*pb.*) already shows the typical expansion, in which the muscle rudiments are developing and may be distinguished by their smaller nuclei. The dorsal longitudinal musculature is also distinguishable (*dln.*) and the whole dorsal mesoderm is seen to be closely adherent to the ectodermal epithelium. Muscle-cells push in between ectoderm cells in making their attachments on the cuticle and only with great difficulty are distinguishable from them (e.g. *mc.*). The next stage (fig. 2, Pl. 23) is drawn from a section near the posterior limit of a segment so that the forwardly directed spur (*psp.*) of the inner posterior border of the limb-bay is shown closely underlying the ventral mesoderm. The extensor-flexor groups are now differentiated (*aex.*, *afl.*, *pea.*, *pfl.*) and, owing to the position of the section and to the oblique lie of the limb, both anterior and posterior groups appear. The latter, cut almost longitudinally, clearly appear part of the ventral expansion and between them lie the rather larger nuclei (one undergoing mitosis) of the ventral expansion (*pefb.*). The former are cut more transversely near their lower ends, which are by now distinct from the central part, and are making their ventral attachments on the ectoderm. The anterior branch of the posterior flexor (*pflab.*) is distinguishable and is derived from the inner face of the expansion. In fig. 3, Pl. 23, the central part of the ventral expansion may be clearly distinguished by its large nuclei and finely granular cytoplasm from the muscle-cells along its edges, smaller, darker, and elongated. The posterior flexor is cut almost entire, but only the upper end of its extensor partner is seen, and only the lower end of the anterior extensor, while the anterior flexor is entirely absent

from the section (due to obliquity, &c., as above), and the anterior branch of the posterior flexor appears in its full extent (from *psp.* to *aver.*). The posterior extensor and flexor continue smoothly the downward sweep of the dorsal mesoderm. Fig. 11, Pl. 23, a somewhat later stage, is taken through the anterior region of a segment. The anterior extensor and flexor components are well developed yet still continuous dorsally with the rest of the dorsal mesoderm. Laterally to them is the 'lateral horn' (Manton, Text-fig. 24 e) of the ventral expansion, and between them is a vertical ectodermal intucking (*aver.*). The dorsal attachment of the muscles on the intersegmental thickening (*ietn.*) is effected about this stage just anteriorly to this section.

Fig. 4, Pl. 23, represents in frontal section of the body a slightly earlier stage than fig. 3, Pl. 23; it shows the muscles in the first five thoracic segments, the anterior segments cut more ventrally than the posterior ones. In the third the five main components of the muscles are seen still, at this stage, closely associated with the ventral expansion distinguished by its larger nuclei and granular cytoplasm. Segments four and five show the system more dorsally where the extensor and flexor components of each group are not yet separate from each other or from the central mass, whereas in segment 2, cut more ventrally, the separation of the components is almost complete. The increasing cytological difference between ectoderm and mesoderm is well shown by Ehrlich's haematoxylin. The section shows the muscles to be essentially parts of the ventral expansion, though closely lining the superficial ectoderm. This association with the overlying ectoderm becomes more intimate as development proceeds; the ectoderm is drawn in below the muscles as a shelf for their ventral attachments, and the thickening (*ietn.*) forms for their dorsal attachment; the walls of the limb-bay curve round them and vertical ectodermal ridges (fig. 4, *aver.*, *pver.*, Pl. 23) are developed between extensor and flexor components. Interpretation is especially difficult in frontal section of the body when the muscles are cut transversely, their cells then appearing small and darkly staining, very like the ectoderm cells.

Components of the Muscles and their Segmental Distribution.

Five main components of a typical segment have been described (p. 564). A second branch of the anterior flexor is described by Dr. Manton, its dorsal attachment somewhat below that of the other branch and of the anterior extensor (Manton, 1928, Text-fig. 25 a), and not following their fan-like arrangement. It seems possible that this muscle, in *Neomysis*, is derived from the ventral mesoderm, the outer connective of which passes close to the intersegmental ridge (p. 565); if this is so it is independent of the main extensor-flexor system of the limbs, though likewise mesodermal in origin.

Variations from the typical arrangement of the components occur in segments thoracic 1, and maxillary 1, 2, in correlation with the different structure and function of their appendages. In thoracic 1 the posterior flexor is present and a minute anterior flexor; in *Hemimysis* both flexors are absent though a 'posterior lateral muscle' is described having a course very similar to that of a typical posterior flexor (Manton, Text-fig. 25 c), and rather different from that of the posterior lateral muscle of other segments. The second maxilla has a very narrow limb-base, the anterior extensor-flexor group is vestigial and the components of the posterior group do not completely separate (cf. Manton, p. 421); moreover, in *Neomysis*, they remain to a very late stage united with the very distinct central part of the ventral expansion, demonstrating better than in any other segment their common origin from the expansion, and their original independence of the ectoderm. In the maxillary segment only the anterior group is well developed, an ectodermal skeletal ingrowth (Manton, Text-fig. 22 d) encroaching on the posterior region of the limb-bay, but the posterior group may possibly be represented by a carapace muscle of unquestioned mesodermal origin (cf. Manton, p. 421, Text-fig. 11 d).

It is perhaps possible to homologize with this system of muscles others in the naupliar segments which have a similar course and function and which are certainly mesodermal (e.g. Manton, Text-fig. 22 e, *em.*, &c.), and also the muscle attached to the upper posterior border of the uropods (Manton, p. 407,

Text-fig. 19 e) to a forwardly directed skeletal tube which is no doubt homologous with the small spurs (fig. 3, *psp.*, Pl. 28) jutting in medially to the posterior flexor of other segments.

2. Carapace Fold Muscles.

A second set of muscles traced by Dr. Manton to an ectodermal origin is associated with the carapace fold. There is a pair of carapace fold muscles in each of the maxillary and first three thoracic segments, in the posterior part of the segments, spanning the entrance into the carapace fold in an approximately vertical direction from the upper border of the carapace cavity (respiratory chamber) to the body-wall above (fig. 12, *cm.*, Pl. 24). Dr. Manton believed them to be derived, in *Hemimysis*, from the dorsal edge of the carapace cavity itself, by a stretching upwards of the ectodermal cells of the free edge.

In *Neomysis*, however, there is evidence that these carapace fold muscles may arise as outlying cells of the dorsal longitudinal musculature (fig. 5, Pl. 23; figs. 12, 13, Pl. 24). They appear to be part of a definite mesodermal investment passing up from the outer face of the dorsal longitudinal musculature along the dorso-lateral body-wall to the heart, a loose tissue not completely closing the entrance into the carapace fold, for the most part very closely applied to the ectoderm (fig. 5, *opm.*, Pl. 23). Dr. Manton does not describe such an extensive investment but figures parts of it (Text-figs. 15 g, *upa.*, 15 b, c, 18 a, b, c, *hc.*, &c.). The lower extent of this 'outer pericardial mesoderm' disappears except in the maxillary and first three thoracic segments where it forms the carapace fold muscles. As the dorsal mesoderm grows up the sides of the body and rounds its dorso-lateral angle the shrinkage of the yolk-sac helps to draw in the bulk of the dorsal mesoderm, consisting of the dorsal longitudinal musculature and the floor of the pericardium (fig. 5, Pl. 23; fig. 12, *pfm.*, Pl. 24), leaving the outer pericardial mesoderm adherent to the body-wall. In the four segments concerned cells of the outer layer elongate vertically as discrete muscle-strands which become attached between the carapace fold and the body-wall above. The upper portions of the outer layer in all segments forms attachments

between the heart and the body-wall and has important skeletal functions. Its share in the formation of the heart was not precisely determined, but is certainly significant.

3. The Interparagnath Muscle.

Dr. Manton has further described, as being ectodermal in origin in *Hemimysis*, an interparagnath muscle (1928, p. 416). In *Neomysis* it is a double strand of muscle (fig. 15, Pl. 24) in the mandibular-maxillulary intersegment, running vertically upwards from the mid-ventral ectoderm between the halves of the nerve-cord to the anterior ends of the skeletal plate (p. 568) which grows in from the posterior border of the maxillulary limb-bay (cf. Cannon and Manton, 1927, Text-fig. 2 b, *g.*). In other intersegments of the body there is a median vertical strand in the corresponding position, but it is merely tendinous. It is considered by Dr. Manton to be likewise ectodermal (Manton, Text-fig. 23 a, *vi.*).

It seems very possible that these median vertical strands may be truly mesodermal in *Neomysis*, continuations of the 'inner connective muscles' (Manton, p. 418) and forming their attachment on the cuticle mid-ventrally. The segmental mesoderm is at first continuous across the middle line (fig. 14, Pl. 24) and very probably establishes a connexion with a mid-ventral ectoderm cell (*mvc.*) at this early stage. As the double nerve-cords develop from the ventral ectoderm the mesodermal connexions are stretched and forced into a T-shaped structure, a median vertical component between the halves of the nerve-cord and horizontal connexions from its upper end to the main lateral masses of the ventral mesoderm. The structure is most distinct from the nervous system in the abdomen where, owing to the poorer development of the nerve-cords, it has a simpler V-shape (fig. 16, Pl. 24). The nerve-cords are likewise narrower and distinctly separated in the immediate postoral region, and mesoderm of the antennal and mandibular segments grows around and between them. Between them it forms the median vertical strand of the antennal-mandibular intersegment and the interparagnath muscle of the mandibular-maxillulary intersegment, and also connective strands along the interparagnath

groove (fig. 15, *ipg.*, Pl. 24). Fig. 6, Pl. 23, and fig. 15, Pl. 24, show stages in the development of the interparagnath muscle. In fig. 6, Pl. 23, the pale mesoderm cells form a V-shaped structure between the darker cells of the nerve-cord, the arms of the V passing out and up behind the rudiments of the mandibular adductor muscles (*madd.*) which meet across in the middle line farther forward. The arms of the V appear to give rise to the mandibular levator muscles and their tendon (fig. 15, *mdbl.*, Pl. 24) which later fuses with that of the mandibular adductors (fig. 15, Pl. 24), and eventually with the anterior ends of the endoskeletal plate (fig. 15, *ensk.*, Pl. 24) mentioned above (pp. 568-70). A segmental pigment patch (fig. 15, *pp.*, Pl. 24) lies close behind the whole complex.

Dr. Manton believes both vertical and horizontal components of the intersegmental T-shaped tendons to be ectodermal in origin, the former from cells which sink in from the mid-ventral ectoderm and the latter from ectodermal immigrations above and lateral to the nerve-cords (Manton, Text-fig. 23 a). In *Neomysis* there does not appear more than a slight indrawing of the ectoderm cells at these points (fig. 1, *eth.*, Pl. 23), as is frequently found where muscles are attached to the body-wall. The essential cellular portions of the tendons seem to be mesodermal. This question of muscular attachments has been much disputed: Claus (1886) and Humperdinck (1922) emphasize that the ectodermal contribution to the system is merely formed skeletal material not extending deeply into the body, whereas Professor Cannon (1926) describes cellular ectodermal tendons comparable to those of Dr. Manton.

THE LIVER.

In *Hemimysis*, as indicated above (p. 562), this essential appendage of the mid-gut appeared to develop from cells already localized as part of the mesoderm of the mandibular segment (Manton, Pl. 22, fig. 11). The separation of the liver rudiment from the rest of the mandibular mesoderm occurred before the formation of the stomodaeum and, as the latter invaginated and grew back through the mandibular segment, the paired liver rudiments fused to form a median mass below its blind

end. The rudiments are shown external to and clearly distinct from the yolk-sac (Manton, Pl. 22, figs. 11, 12, &c.) until a comparatively late stage when the median mass has once more divided into two lateral groups, and each has developed into an epithelial sac roughly a half-sphere in extent cupping the yolk-sac ventro-laterally in the mandibular and two maxillary segments (Manton, Text-fig. 11 c).

In the case of *Neomysis* it was not possible to demonstrate conclusively the ultimate origin of the liver which, however, may be distinguished at a rather earlier stage than that first observed in *Hemimysis*. Fig. 7, Pl. 23, shows the earliest stage identified in *Neomysis*: the rudiment, though admittedly separate from the yolk-pyramids, is equally certainly distinct from the mandibular mesoderm, and there is no serious reason to believe that its origin differs essentially from that of the anterior (fig. 20, *aep.*, Pl. 24) and posterior (fig. 9, *pep.*, Pl. 23) endodermal plates, the rudiments of the mid-gut, which are proliferated from the yolk-pyramids. Only in succeeding stages, when the stomodaeum has grown back into the mandibular segment carrying the liver rudiment with it, does the latter come into close association with the mandibular mesoderm (fig. 6, Pl. 23; fig. 19, Pl. 24). The rather distinct inner portion of the mandibular mesoderm seen earlier in this position in *Hemimysis* (Manton, Pl. 22, fig. 11) may conceivably be the rudiment of the interparagnath muscle and related structures (pp. 570-1 above). At its first appearance (fig. 7, Pl. 23), as a single rudiment, the liver is well forward in the antennal segment. The invaginating stomodaeum apparently grows back below it (fig. 17, Pl. 24), not above (Manton, p. 387), and divides it into lateral halves. This occurs shortly after hatching, and while the liver is carried back the mandibles, posterior to the invagination, are drawn relatively forward and the relations between liver and mandibular mesoderm shown in fig. 6, Pl. 23; fig. 19, Pl. 24, are established in a comparatively short space of time.

Each liver rudiment rapidly develops into an epithelium (fig. 19, Pl. 24) which separates from the yolk-pyramids, except at its edges, on account of its own rapid growth. Subsequently

the yolk-pyramids internal to the liver lobes disintegrate and the yolk passes into the liver. The anterior endodermal plate develops *between and in front of the lateral liver rudiments* and eventually becomes smoothly continuous with them (fig. 20, Pl. 24); it is histologically indistinguishable from them and it is noteworthy that in Decapods (Reichenbach, 1886) the posterior liver lobes and the posterior endodermal plate are parts of a single condensation from the yolk-pyramids. The broken appearance of the yolk-pyramids in fig. 7, Pl. 23, strongly suggests that the liver rudiment was budded off from them, and the apparent separation would possibly be increased during preparation of the sections.

DISCUSSION.

The Musculature.

The muscle systems dealt with above have been described as of ectodermal origin in *Hemimysis*; however, from a study of *Neomysis vulgaris*, the facts do appear to admit of an interpretation in conformity with the origin of musculature in general from the mesoderm. In this interpretation a factor of great importance is the intimate association which is established at various points between the ectoderm and the mesoderm. Especially is this true of that component of the mesoderm which Dr. Manton terms the dorsal mesoderm; thus the extensors and flexors of the limbs (pp. 563-9, figs. 1-4, 11, Pl. 23), derived from the anterior and posterior faces of the ventral expansion of the dorsal mesoderm, very closely underlie the ectoderm, and the carapace fold muscles of segments maxillary and thoracic 1, 2, 3 (pp. 569-70) develop from the outer pericardial mesoderm closely applied to the dorso-lateral ectoderm (fig. 5, Pl. 23; figs. 12, 13, Pl. 24). The ventral mesoderm (p. 566) is closely related to the ectoderm at the intersegments where a transverse ectodermal groove separates one limb from that of the adjoining segment; an outer connective muscle of the ventral mesoderm follows the groove outwards (p. 565, fig. 12, Pl. 24) and an inner connective passes inwards closely applied to the upper surface of the ectodermal nerve-cords (p. 570). It is from the median portions of the inner connective

muscles that the interparagnath muscle and the intersegmental tendons are derived (figs. 2, *icm.*, *ve.*, 6, *ipm.*, Pl. 23).

This association between ectoderm and mesoderm tends to become more intimate as development proceeds. The extensors and flexors of the limbs (p. 567) become so surrounded by ectodermal thickenings and shallow ingrowths that they are more or less enclosed in grooves of the ectoderm (e.g. figs. 4, *thor.* 2, 5, *pfl.*, Pl. 23), and the ectodermal thickenings *ieth.* (p. 565) to some extent surround the carapace fold muscles from behind (fig. 13, Pl. 24). The intersegmental tendons and interparagnath muscle are greatly compressed and overgrown during the active development of the nerve-cords (fig. 2, Pl. 23; fig. 15, Pl. 24).

Some help is afforded by cytological differences between the cells and tissues of ectoderm and mesoderm. Lightly staining cells and nuclei of the mesoderm, including the rudiments of the muscles in question, are distinguishable from the darker more coarsely staining nuclei of the ectoderm (see figs. 4, 5, Pl. 23). It must, however, be admitted that these differences are less marked in earlier stages, and are inappreciable at the stage of teloblast activity, and, moreover, the nervous system is an exception to the rule that ectoderm stains more deeply than mesoderm. It might in consequence be maintained that deep staining is characteristic only of an external epithelium and therefore that ectodermal muscles would not be so distinguished. Further, muscle-cells, of whatever origin, when cut in transverse section appear small and darkly staining. The evidence from cytology is thus of definite though perhaps somewhat limited value.

A further point of general importance concerns the looseness and powers of cellular migration in embryonic mesodermal tissues. The separation of the carapace fold muscles from the more internal tissues of the dorsal mesoderm is a case in point (p. 569), and the pre-antennular mesoderm (Manton, 1928, p. 388) and telson mesoderm (below pp. 579-81) present even more striking examples.

It is thus clear what factors render difficult of interpretation the origin of mesodermal structures, muscles, and tendons, here investigated. The difficulties do not arise in the case of

such major systems as the dorsal and ventral longitudinal muscles; it is only in the development of minor systems which, up to the present, have naturally not received special attention, that interpretations of different workers are likely to differ. Since Professor Cannon and Dr. Manton, whose work stands almost alone, have both found minor systems of muscles to be ectodermal in origin, it is important that their work should be extended to other types. The evidence from a study of Neomysis does not seem to lend support to their conclusions, but rather emphasizes the lack of agreement shown in Table I.

Professor Cannon advocates an homology between the ectodermal dorso-ventral muscles of *Chirocephalus* and the circular muscles of *Oligochaetes*, and would possibly extend this to such systems as the extensors and flexors of the limbs and the carapace fold muscles of Mysids which likewise stretch in the transverse plane. The suggestion is supported by the fact mentioned above (p. 562) that the teloblasts of the Annelid circular musculature are sister cells of the ectoderm teloblasts. However, as already indicated (p. 562), the time of separation of musculature from outer layer differs considerably in the two cases, a point of vital importance for the germ-layer theory. The reputed origin of systems of Crustacean musculature from fully differentiated ectoderm constitutes an undoubted exception to the theory, whereas the origin of the Annelid circular muscles at such an early stage is in essential agreement; the mesoderm in Annelids and in Arthropods arises rather from the outer layer (ectoderm) than from the inner (endoderm) as in Vertebrates and Echinoderms.

It may reasonably be maintained that *Peripatus* affords a nearer and more trustworthy comparison with the Crustacea, and the circular musculature of *Peripatus* is said to be derived from the segmental mesoderm (Sedgwick, 1888). It comes to form a close investment of the superficial ectoderm, the cells migrating as a rather loose tissue from the bulk of the mesoderm lying more medially. This is strongly reminiscent of the formation of the carapace fold muscles and outer pericardial mesoderm in Neomysis (p. 569), and in general the circular musculature of *Peripatus* corresponds with that

portion of the dorsal mesoderm of *Neomysis* which lines the lateral ectoderm.

The Tendons.

The important point at issue with regard to Crustacean tendons is whether or no there are developed cellular ectodermal tendinous structures penetrating a considerable distance into the body. There are certainly hollow ectodermal ingrowths (fig. 15, *ensk.*, Pl. 24) which form 'endoskeletal' tubes on account of the external skeleton lining them, but the ectoderm cells remain merely epithelial. It is also very probable that the attachment of muscles on the exoskeleton may involve a drawing in of cuticular material which may be formed by other than the external surfaces of ectoderm cells (Claus, Humperdinck, Grobбен). Further, the ectodermal epithelium and exoskeleton may be drawn in as shallow ridges where muscles are attached (cf. pp. 567-71, figs. 1, *ett.*, 3, *aver.*, Pl. 23, &c.). However, the formation of solid cellular ingrowths from the ectoderm serving as tendons, or even becoming contractile, can scarcely be considered as fully established. Professor Cannon suggests that ectodermal muscles may have originated phylogenetically by the ectoderm cells being drawn into the body, first as skeletal or tendinous strands and later developing powers of contraction (1926, pp. 413-14).

The interpretation of the T-shaped tendons in *Neomysis* (pp. 570-1) as derivatives of the ventral mesoderm is supported by two facts, first there is no certain evidence of immigration of ectoderm cells in that region, and secondly increasing cytological differences between ectoderm and mesoderm indicate that the tendons are mesodermal. It is further supported by comparison with other Crustacea and with other groups of Arthropods. In Phyllopoda (Cannon, 1926; Claus, 1886) and in *Peripatus* (Sedgwick, 1888) where the lateral halves of the nerve-cord are widely separated the inner connective muscles are inserted directly on to the mid-ventral ectoderm, as in the abdomen of *Neomysis*. A primitively V-shaped structure is thus converted into a T-shaped structure in the thorax of *Neomysis* (and of other Malacostraca) by the great

development of the nervous system. Korotneff (1885) has described a 'ventral diaphragm' over the nerve-cord in the insect *Gryllotalpa*, mesodermal in origin. Nusbaum (1886) describes a similar diaphragm in the Isopod *Oniscus* as a mere chitinous product of the ectoderm. Certain workers, however, have further described mesodermal tissue surrounding (McMurrich, 1895) or actually invading the nerve-cords (Grobбен, 1911, *Argulus*; Reichenbach, 1886, *Astacus*; Korotneff, 1885, *Gryllotalpa*) and it is possible that other workers have tended to underestimate the part played by the mesoderm in this region.

The Liver.

It seems almost certain that the liver of *Neomysis* is really endodermal in origin, derived with the mid-gut from a definite inner layer which gives rise to those structures alone, as in other Coelomates. In position and cell size the early liver rudiment may be distinguished from the neighbouring mesoderm (fig. 7, Pl. 23). There is evidence that it is derived from the yolk-pyramids (p. 572), in the same way as the endodermal plates which develop into the definitive mid-gut. Both liver and mid-gut condensations become separate from the yolk-sac in the sense that small yolk-free cells cannot, for mechanical reasons, remain within the heavily yolk-laden parent pyramids but move out and remain attached to their periphery (fig. 9, *pep.*, Pl. 23; figs. 19, *L.*, 20, *aep.*, Pl. 24), where they grow and enclose and absorb the yolk. In Crustacea with less yolky eggs the endodermal condensations, including that of the liver, are from the first and throughout part of the yolk-sac epithelium (e.g. *Nebalia*, Manton, 1934).

J. Wagner (1898) derives the liver of *Neomysis* from the yolk-pyramids (i.e., fig. 31).

Most workers on the development of the Malacostraca have described the liver as endodermal, the first rudiment being derived from cells of the yolk-sac (see Table II). There is less support for the theory that the liver is mesodermal in origin. In many cases it has been found from the first an integral part of the yolk-sac, in others, as in *Neomysis*, it was at first

distinctly external to a compact yolk-sac. Apart from Dr. Manton the only other worker who traced the liver back to a very early primordium not associated with the yolk-sac is McMurrich (1895) working on the Isopods. He distinguished a group of cells near the blastopore at the beginning of gastrulation distinct from the main masses of both endoderm and mesoderm and believed that it migrated forward and developed into the liver, which he found at a later stage as a paired ventrolateral rudiment in the maxillary segment, as in Mysids. As he was unable to follow the migration forwards it is possible that the group of cells observed near the blastopore was really the rudiment of the gonad which is early distinct in that region in Mysids, and which McMurrich found at a later stage in the anterior part of the thorax, as also in Mysids.

Evidence favours a common origin of liver and mid-gut in Crustacea from the yolk-sac, representing the typical endoderm

TABLE II.

The Origin of the Liver in Malacostraca.

Order.	(a) From Yolk-cells.	(b) From a Rudiment at first External to the Yolk-sac and considered to be:		
		1. Endodermal.	2. Mesodermal.	3. Mesodermal.
Leptostraca	Manton, 1934
..	Bouchinsky, 1900
Isopoda	Brobetsky, 1874	McMurrich, 1895	Nusbaum, 1886	..
Amphipoda	Rossiiskaya and Koschewnikowa, 1890	Bergh, 1893
..	C. Wagner, 1892	Heidecke, 1904
..	Langenbeck, 1898
Cumacea	..	Bouchinsky, 1893
..
Mysidacea	Nusbaum, 1887	Manton, 1928
..	J. Wagner, 1898
Decapoda	Reichenbach, 1886	Sollaud, 1923
..	Kingsley, 1889
..	Brooks and Her- rick, 1892
..	Bouchinsky, 1894
..	Lebedinsky, 1890

of the germ-layer theory. Where this has not been clearly demonstrated there is strong circumstantial evidence in the histological and cytological similarity between the various condensations. Moreover, there is the evidence of cases where the liver arises as part of the same condensation and part of the mid-gut (e.g. Reichenbach, 1886, *Astacus*). The problem may well repay further investigation.

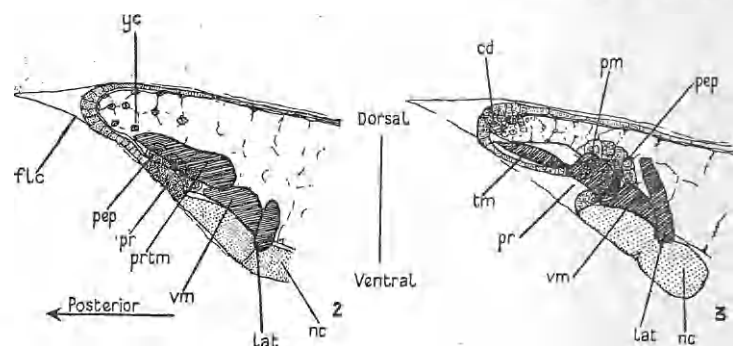
PART II.

TELSON MESODERM.

The origin of the telson mesoderm in Crustacea has been little investigated, only McMurrich (1895), Sollaud (1923), and Dr. Manton (1934) having traced it in any detail. McMurrich believed it to be derived in Isopods from the last transverse row of cells proliferated by the mesodermal teloblasts, the seventh row in the abdomen (which no doubt represents the vestigial seventh abdominal segment). Sollaud (*Palaemonidae*) and Dr. Manton (*Nebalia*), on the other hand, derive the telson mesoderm from loose post-segmental tissues invaginated at the posterior border of the blastopore, at all stages distinct from the teloblastic mesoderm. It is here worthy of note that Professor Cannon believes the post-segmental musculature of the proctodaeum in *Chirocephalus* to be derived from the ectoderm.

In *Neomysis* the telson mesoderm appears to be derived from the mesoderm of the seventh abdominal segment as in Isopods. There are no cells of the intermediate layer posterior to the teloblastic mesoderm, though the yolk-pyramids are here smaller and more numerous than elsewhere (fig. 8, Pl. 23, Text-figs. 2, 3): they degenerate as the yolk is absorbed (fig. 8, Pl. 23). As the mesoderm of the seventh abdominal segment develops it separates into two unequal portions. The smaller anterior portion ultimately gives rise to the vertical muscle (pp. 568-9) from the posterior wall of the uropods to the dorsal body-wall at the entrance into the telson; the larger posterior part consists of the future ventral mesoderm of the seventh abdominal segment (Text-fig. 2, *vm.*), and postero-dorsal to this the procto-

daedal and telson mesoderms, together representing the dorsal mesoderm of the segment (Text-fig. 2, *prtm.*). The latter reaches a dorso-lateral position comparatively early since, owing to the narrowing of the abdomen posteriorly, the eight primary mesoderm cells of the segment span not only the ventral but also the lateral surfaces, whence the telson is readily invaded by the proliferating tissue. The process is shown in Text-figs. 2, 3, and figs. 8, 9, Pl. 23; fig. 18, Pl. 24. In Text-fig. 2 the postero-



TEXT-FIGS. 2 AND 3.

Development of the telson mesoderm. (Diagrammatic parasagittal section of abdomen.)

dorsal end of the dorsal mesoderm block (*prtm.*) has already reached beyond the posterior limit of the seventh abdominal segment and lies laterally to the developing proctodaeum *pr.* The yolk-cells (*yc.*) fill the telson and are continuous with the yolk-sac farther forward. Fig. 8, Pl. 23, shows in transverse section a somewhat later stage with the telson mesoderm moving back along the lateral body-wall as the yolk-sac shrinks to the centre. On the right its cells have the typical appearance of elongating muscle-cells, on the left they are cut more posteriorly near their attachment on the ectoderm. (The median dorsal cleft and intucked ectoderm indicate the vestigial caudal furca.) The processes are seen more comprehensively in Text-fig. 3; the ingrowth of the proctodaeum is seen to be an important factor in separating the telson mesoderm proper (*tm.*) from the proctodaeal portion (*pm.*), owing to the formation

of transverse proctodaeal grooves leading out from the actual invagination. Internally the grooves appear as ridges marking the anterior limit of the floor of the telson and separating the two blocks of mesoderm. The transverse section (fig. 18, Pl. 24) shows these two mesodermal masses before complete separation is accomplished by the deepening of the grooves.

The block of mesoderm (*tm.*) here described forms the intrinsic musculature of the telson, paired longitudinal bands (fig. 9, Pl. 23) stretching back from the transverse proctodaeal groove to the tip of the furca. Part of the proctodaeal mesoderm attached to the groove in front, and the vertical muscles (pp. 568-9, 579), attached to the dorsal body-wall at the entrance to the telson, constitute extrinsic telson musculature. In addition the telson is invaded by blood-corpuscles and connective tissue from the seventh abdominal segment.

DISCUSSION.

The apparent marked difference between the origin of the telson mesoderm in Isopoda and Mysidacea, on the one hand, and in Leptostraca and Decapoda on the other, calls for further investigation. The loose cells figured by Dr. Manton (1934, fig. 21 c 2) as primordia of the telson mesoderm are much smaller than the teloblastic cells and their progeny, and undoubtedly quite distinct from them in origin (cf. also Sollaud, 1928). They penetrate between the proctodaeum and the mesoderm of the seventh abdominal segment, a position which in *Neomysis* is occupied only by endoderm cells cut off from the yolk-sac as the proctodaeum presses into it from behind (fig. 18, *pep.*, Pl. 24). The intrinsic muscles of the telson of *Nebalia* agree in disposition with those of *Neomysis*.

If, as is generally held, the telson is a post-segmental part of the body it might be expected to derive its mesoderm from special post-segmental tissue. The condition found in *Neomysis* is then a secondary one, for there is no indication in this type that it represents or includes a true segment. McMurich homologizes the telson of Isopods with the anal segment of Annelids which likewise 'probably' derives its mesoderm from the teloblasts, but he was possibly under the impression that the telson itself

represented a seventh abdominal segment, whereas it may well be that the last row of cells produced by the teloblasts form a distinct seventh abdominal segment in front of the telson, as in Mysids. This is indicated, at any rate by the segmentation of the nerve-cord, in the Isopod *Asellus aquaticus* (author, unpublished).

MEDIAN DORSAL ORGAN.

The development of the median dorsal organ is essentially as described by Nusbaum and Schreiber (1898) for *Mysis* (? *Hemimysis*) *lammournae*. An ectodermal invagination along the mid-dorsal line in the head region continues more posteriorly as a mere thickening, the whole organ, from the time of hatching onwards, being a site of cell resorption. The anterior invagination, which occurs at the time of hatching, forms a thin vertical longitudinal septum eventually reaching from the anterior end of the body to the anterior wall of the stomodaeum. The presence of distinct cells in the septum (fig. 10, Pl. 23) is, however, very transitory, and Dr. Manton was led to believe that in *Hemimysis* it is merely a cell product of the ectoderm, though cells are clearly necessary for its formation. The fact that the dorsal organ, after the formation of the septum, continues back from exactly the upper posterior corner of the latter is significant.

Before hatching the organ as seen in transverse section consists merely of two large superficial cells in the mid-dorsal line of the head region where invagination will occur. Its development at the time of hatching must be extremely rapid, and it seems highly possible that it plays some part in straightening out the ventrally flexed abdomen by drawing in the dorsal ectoderm, thus compressing the yolk and forcing it back into the abdomen. If the straightening of the abdomen, which would result from inflation with yolk, begins before hatching, it may itself be instrumental in rupturing the vitelline membrane which certainly cannot remain intact during the transition from an ovoid to a markedly elongated embryo.

The transverse section of the invagination shown in fig. 10, Pl. 23, was taken from an embryo soon after hatching, before

the stomodaeum had begun to form, so that there is little doubt as to the precise time and rapidity of the process. The sub-triangular outline of the figure also bears witness to the rapid deformation of an originally circular cross-section; moreover the yolk-pyramids *yp.* situated dorso-laterally mark the upper anterior border of the optic rudiments which, before hatching, were on the ventro-lateral surface.

It should be recalled that Brobetsky (1874), who found a distinct membranous protrusion from the dorsal organ of the Isopod *Oniscus*, believed that the organ represented the vestige of embryonic membranes comparable to those of insects which are similarly attached dorsally to the body and eventually resorbed into the body through their attachment.

DORSO-LATERAL ORGANS.

The development of the paired dorso-lateral organ is essentially as in *Hemimysis* (Manton, p. 384), and likewise suggests a significance in ecdysis. Thus they may correspond to the 'tegumental glands' described by Professor Yonge (1932, &c.) in adult crustacea. Both consist of a small cluster of gland-cells about a common duct, and are active in the secretion of a new cuticle. In *Argulus* (Pyatakof, 1926) two 'dorsal' organs are developed, one at each of the first two larval ecdyses so that there is strong evidence as to their function. The larval gland is, not unnaturally, simpler in structure than the adult tegumental glands.

GONAD.

A point of interest in connexion with the gonad of *Neomysis* is that occasionally it develops distinct metameric segmentation during a short period of development, though it arises as a single rudiment unconnected with any segment. As in *Hemimysis* it may be distinguished as early as gastrulation as a median unpaired mass in the anterior lip of the blastopore, whence it becomes localized in the first thoracic segment and divides, the halves becoming associated with the dorsal mesoderm on each side. At this stage metamerism may appear, the rudiment on each side dividing so that part becomes associated with the

dorsal mesoderm of the maxillary segment. This rather rare condition is linked with the normal by a series of intermediate conditions in which a single though bilobed rudiment on each side is associated mainly with the dorsal mesoderm of the thoracic 1 segment. All traces of segmental arrangement are lost as the gonad rudiments are carried by the dorsal mesoderm up to the dorsal side of the yolk-sac where a single median rudiment is again formed. The fusion of maxillary and thoracic 1 components is accompanied by the fusion of their respective coelomic sacs, and this occurs even when there is no distinct maxillary component; of the gonad it is likewise a normal process in *Hemimysis*, where the metameric condition of the gonad was not observed though the number of cells associated with the dorsal mesoderm of segment thoracic 1 was found to be only half the number of the original rudiment (Manton, p. 410).

In *Nebalia* the gonad first appears as a metameric series of rudiments (Manton, 1934), and this is no doubt the primitive condition (cf. *Peripatus* and *Annelids*). That in forms like the *Mysids*, where a segmental origin no longer occurs, a restricted metamerism should appear at a later stage, is of interest.

SUMMARY.

1. Certain muscle systems, alleged to be ectodermal in origin in *Hemimysis*, appear to be mesodermal in *Neomysis*. They are:

- (a) The extensor and flexor muscles of the limbs.
- (b) The carapace fold muscles of the maxillary and thoracic 1, 2, 3 segments.
- (c) The interparagnath muscle.

2. There is no clear indication of cellular ectodermal tendons.

3. Evidence is given that the liver is of endodermal origin and derived from the yolk-pyramids in *Neomysis*.

4. The telson mesoderm appears to be derived from that of the last (7th) abdominal segment, there being no post-segmental mesoderm in *Neomysis*.

5. The median dorsal organ may be an important agent in the hatching processes. Later it draws in and resorbs the superfluous extra-germinal ectoderm.

6. The dorso-lateral organs probably correspond to the 'tegumental glands' of adult Crustacea.

7. During one phase of its development the gonad of *Neomysis* sometimes shows a restricted metameric segmentation.

REFERENCES.

- Bergh, R. S., 1890.—'Z. wiss. Zool.', 50.
 — 1893a.—'Zool. Jahrb. Abt. Anat.', 6.
 — 1893b.—*Ibid.*, 7.
 Bouchinsky, P., 1893.—'Zool. Anz.', 16.
 — 1894.—*Ibid.*, 17.
 — 1900.—*Ibid.*, 23.
 Brobetsky, N., 1874.—'Z. wiss. Zool.', 24.
 Brooks, W. K., and Herrick, F. H., 1892.—'Mem. Nat. Acad. Sci. Washington', 5.
 Cannon, H. G., 1924.—'Phil. Trans. Roy. Soc. B.', 212.
 — 1925.—*Ibid.*, 214.
 — 1926.—'Journ. Lin. Soc. Zool.', 36.
 Cannon, H. G., and Manton, S. M., 1927a.—*Ibid.*, 36.
 — 1927b.—'Trans. Roy. Soc. Edinburgh', 55.
 Claus, C., 1886.—'Arch. Zool. Inst. Wien', 6.
 — 1889.—*Ibid.*, 8.
 Grobben, K., 1911.—*Ibid.*, 19.
 Heidecke, P., 1904.—'Jen. Zeitsch.', 38.
 Humperdinck, I., 1922.—'Z. wiss. Zool.', 121.
 Kingsley, J. S., 1889.—'Bull. Essex Inst. Salem', 21.
 Korotneff, A., 1885.—'Z. wiss. Zool.', 41.
 Lebedinsky, J., 1890.—'Biol. Centralbl.', 10.
 Manton, S. M., 1928.—'Phil. Trans. Roy. Soc. B.', 216.
 — 1934.—*Ibid.*, 223.
 Moroff, T., 1912.—'Zool. Jahrb. Abt. Anat.', 34.
 McMurich, J. P., 1895.—'Journ. Morph.', 11.
 Nusbaum, J., 1886.—'Zool. Anz.', 9.
 — 1887.—'Arch. Zool. Exp.', 5.
 — 1891.—'Biol. Centralbl.', 11.
 — 1902.—*Ibid.*, 22.
 Nusbaum, J., and Schreiber, W., 1898.—*Ibid.*, 18.
 Penners, A., 1923.—'Zool. Jahrb. Abt. Anat.', 45.
 Pereyaslawzew, S., 1888.—'Bull. Soc. Nat. Moscou', 2.
 Pyatakov, M. L., 1926.—'Quart. Journ. Micr. Sci.', 70.
 Reed, M. A., 1904.—'Arch. f. Entw. Mech.', 18.
 Reichenbach, H., 1886.—'Abh. Senckenb. Ges. Frankfurt', 14.
 Rossiiskaya, M., and Koschewnikowa, M., 1890.—'Bull. Soc. Nat. Moscou', 4.
 Sedgwick, A., 1888.—'Quart. Journ. Micr. Sci.', 28.

- Snetlage, E., 1905.—'Zool. Jahrb. Abt. Anat.', 21.
 Sollard, E., 1923.—'Bull. Biol. Fr. & Belg. Supplément', 5.
 Staff, F., 1910.—'Arb. Zool. Inst. Wien', 16.
 Stone, L. S., 1926.—'Journ. Exp. Zool.', 44.
 Vejdovsky, F., 1889.—'Entwicklungsgeschichtl. Untersuchungen.' Prag.
 Wagner, C., 1892.—'Bull. Soc. Nat. Moscou', 5.
 Wagner, J., 1898.—'Trudii St. Peterb. Obsch.', 26.
 Weldon, W. F. R., 1892.—'Quart. Journ. Micr. Sci.', 33.
 Wetzel, A., 1931.—'Z. wiss. Mikr.', 48.
 Yonge, C. M., 1932.—'Proc. Roy. Soc. B.', 111.

EXPLANATION OF PLATES 23 AND 24.

ABBREVIATIONS.

aep., anterior endodermal plate; *aex.*, anterior extensor muscle of the limb; *afl.*, anterior flexor muscle of the limb; *alm.*, anterior lateral muscle; *ant.*₁, first antenna (antennule); *ant.*₂, second antenna; *ant.*₃, mesoderm of second antenna; *aver.*, anterior vertical ectodermal ridge, of the limb-bay; *bc.*, blood-corpuscle; *cd.*, region of cell degeneration; *cf.*, carapace fold; *cfat.*, attachment of carapace fold to body; *cg.*, cerebral ganglion; *ch.*, chromatoid spheres; *cm.*, carapace fold muscle; *cmt.*, twig of outer connective muscle of ventral mesoderm; *di.*, invagination of dorsal organ; *dlm.*, dorsal longitudinal muscle system; *dm.*, dorsal mesoderm; *do.*, median dorsal organ; *ec.*, extra embryonic cells; *ensk.*, anterior ends of the maxillary endoskeletal tubes; *ep.*, ectodermal epithelium; *ett.*, intersegmental ectodermal thickening lateral to nerve-cord; *fl.*, first larval cuticle; *G.*, Gonad; *hc.*, strands of mesoderm between heart and dorso-lateral body-wall; *icm.*, inner connective muscle of ventral mesoderm; *icmt.*, tendon of *icm.*; *ieth.*, intersegmental thickening of ectoderm; *ifl.*, inner face of limb; *ipg.*, longitudinal interparagnath groove; *ipm.*, interparagnath muscle; *ise.*, intersegmental ectoderm; *L.*, Liver; *lat.*, lateral vertical muscle of seventh abdominal segment; *lbw.*, lateral body-wall; *lc.*, loose mesoderm cells; *li.*, limb, in section; *lm.*, limb mesoderm; *lpm.*, lateral paragnath muscles; *lwh.*, lateral wall of heart; *m.*, early segmental mesoderm; *madd.*, mandibular adductor muscle; *mc.*, mesoderm cell inserted between cells of ectodermal epithelium; *mdbl.*, mandibular levator muscle; *ms.*, mesodermal investment of liver; *mand.*, mesoderm of mandibular segment; *mst.*, mesodermal strand connecting mesoderm of antennal and mandibular segments in early stages; *mv.*, mid-ventral ectoderm cell; *mx₂cs.*, coelomic sac of maxillary segment; *nc.*, nerve-cord; *nyp.*, nucleus of yolk-pyramid; *opm.*, outer layer of pericardial mesoderm; *ovm.*, outer ventral mesoderm block; *pam.*, pre-antennular mesoderm; *pb.*, ventral expansion of dorsal mesoderm; *pbsp.*, cavity in *pcf.*; *pcf.*, central portion of ventral expansion of dorsal mesoderm; *pep.*, posterior endodermal

plate; *per.*, posterior extensor muscle of the limb; *pfl.*, posterior flexor muscle of the limb; *pflab.*, anterior branch of posterior flexor muscle; *pfm.*, inner pericardial mesoderm (= pericardial floor mesoderm); *pl.*, plasma; *plm.*, posterior lateral muscle; *pm.*, proctodaeal mesoderm; *pp.*, pigment patch; *pr.*, proctodaeum; *prtm.*, rudiment of proctodaeal and telson mesoderm; *psp.*, forwardly directed spur from inner posterior border of limb; *pver.*, posterior vertical ectodermal ridge of limb-bay; *sg.*, segmental nerve ganglion; *sn.*, peripheral segmental nerve; *stom.*, stomodaeum; *th₁c.*, *th₂c.*, dorsal coelomic sacs of segments thoracic 1, 2; *tm.*, telson musculature; *ur.*, uropods; *ve.*, median vertical mesodermal tendon; *vi.*, median ectodermal supporting cells; *vlm.*, ventral longitudinal muscles; *vm.*, ventral mesoderm; *yc.*, yolk-cells; *yp.*, yolk-pyramids; *ys.*, yolk-sac.

The dotted lines are drawn through the mid-bilateral plane. A, anterior; D, dorsal; P, posterior; V, ventral.

PLATE 23.

Fig. 1.—Lateral half of a transverse section of the body in a young embryo of *Neomysis*, showing the ventral expansion (*pb.*) of the dorsal mesoderm, from which is derived the extensor-flexor muscle system of the limbs. $\times 375$.

Fig. 2.—As fig. 1. Showing a later stage in the development of the extensor-flexor system. $\times 375$.

Fig. 3.—As figs. 1, 2. A still later stage (figs. 1, 2, 3, 11 constitute a developmental series). $\times 375$.

Fig. 4.—A frontal section of the first five thoracic segments on one side of the body at the same stage as fig. 3 showing the development of the extensor-flexor muscle system of the limbs from the ventral expansion of the dorsal mesoderm. $\times 375$.

Fig. 5.—Lateral half of a transverse section of the body in the first thoracic segment showing the separation of the outer pericardial mesoderm and carapace fold muscle from the more internal layers of the dorsal mesoderm (later stage fig. 12). $\times 375$.

Fig. 6.—Ventral half of a transverse section of the body in the posterior part of the mandibular segment showing the development of the interparagnath muscle from the mesoderm attached to the mid-ventral ectoderm (later stage fig. 15, cf. also figs. 14, 16). $\times 375$.

Fig. 7.—Ventral half of a transverse section of the body of an unhatched embryo, in the antennal segment, showing the earliest distinguished rudiment of the liver (next stage fig. 17). $\times 375$.

Fig. 8.—A transverse section of the body near the tip of the telson showing centrally the degeneration of the yolk-cells and laterally the invasion by the telson mesoderm. $\times 770$.

Fig. 9.—A parasagittal section of the telson, to follow fig. 18, and showing

the further separation of the telson mesoderm from the proctodaeal mesoderm. $\times 375$.

Fig. 10.—A transverse section of the body just anterior to the optic rudiments, in an embryo immediately after hatching, showing the deep invagination of the median dorsal organ. $\times 200$.

Fig. 11.—The last of a series of transverse sections of the body (cf. figs. 1, 2, 3) showing the development of the extensor and flexor muscles of the limbs. $\times 375$.

PLATE 24.

Fig. 12.—Lateral half of a transverse section of the body in the second thoracic segment showing the separation of the carapace fold muscle from the associated mesodermal structures. $\times 375$ (see earlier stage, fig. 5).

Fig. 13.—Frontal section of the body in the anterior part of the thorax of one side at the level of the dorsal longitudinal muscles, showing the separation from them, laterally, of the carapace fold muscles (same stage as fig. 5). $\times 375$.

Fig. 14.—Ventral half of a transverse section of the body of a newly hatched embryo showing the relation of the segmental mesoderm to the mid-ventral ectoderm, in early stages. $\times 375$.

Fig. 15.—Part of a transverse section of the body near the mandibular-maxillary intersegment showing the interparagnath muscle attached dorsally to the endoskeletal tubes which grow forward from the maxillary segment (earlier stage fig. 6). $\times 375$.

Fig. 16.—Ventral half of a transverse section of the body in an abdominal segment (same stage as fig. 6) showing the development of intersegmental tendons from the connexion between the ventral mesoderm and mid-ventral ectoderm. $\times 375$.

Fig. 17.—Ventral half of a transverse section of the body showing the liver at a stage when the stomodaeum has invaginated and grown back below it. $\times 375$.

Fig. 18.—A transverse section of the telson about the same stage as fig. 8, but farther forward, showing the separation of the telson mesoderm from the proctodaeal mesoderm. $\times 770$.

Fig. 19.—Ventral half of a transverse section of the body in the mandibular segment, at a later stage than fig. 17, showing the relation at this stage of the posterior ends of the liver rudiments to the yolk-sac and to the mandibular mesoderm. $\times 375$.

Fig. 20.—Part of a transverse section of the body at a later stage than fig. 19, in the region of the stomodaeum, when continuity has been established between the condensations of the liver and the anterior endodermal plate. $\times 375$.