V. *On the Embryology of the Crustacean* Nebalia Bipes.

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[PLATES 20–26.]

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INTRODUCTION.

THE relation of the Leptostraca to other groups of Crustacea has long been a problem of interest, although the alliance with the Eumalacostraca has been amply justified (CLAUS, 1872, 1888, CALMAN, 1909). CLAUS discussed the essentially Malacostracan form of the appendages of *Nebalia*, and the mode of feeding by the aid of these appendages has been shown (CANNON, 1927) to be a specialized modification of the type shown by the simpler Malacostraca (CANNON and MANTON, 1927, *a*). Some of the apparent differences between the Leptostraca and the Eumalacostraca have recently been shown to be differences of degree rather than of kind. Thus the seventh abdominal segment of *Nebalia* is found also in the embryo mysid, but is partially or completely fused with the sixth segment in the adult *Lophogaster* and *Hemimysis* respectively (MANTON, 1928, *a* and *b*). Thus the basal number of abdominal segments in the Eumalacostraca as well as the Leptostraca may be seven. The presence of a large caudal furca in *Nebalia* may also be a difference of degree, if this furca is homologous with the embryonic furca of a mysid (MANTON, 1928, *a*). Other differences, such as the presence of a fully formed carapace adductor muscle, of cephalic liver lobes, etc., require further investigation. Of the resemblances between the Leptostraca and Eumalacostraca, the mode of development of the former is said to resemble that of the Mysidacea, but the embryology of no Leptostracan has been adequately followed, and the recent work on mysid development has considerably modified many previous views on this subject.

An examination of development in *Nebalia*, of which the following pages contain an account, was undertaken with a view to a comparison with that of the Eumalacostraca, special attention being devoted to the early development, the formation of the mesodermal somites and adult endoderm and liver, the further development of the mesoderm in the formation of the heart, excretory glands and genital organs, and the development of the endoskeleton and some of the associated muscles. During the course of the work it became apparent that a redescription of the external form of the various embryonic stages was essential.

The cytology of the early stages appeared to be of interest, but unfortunately an adequate supply of material for a thorough examination could not be obtained. The material available has been examined by Dr. I. MANTON, to whom I am much indebted.

I wish to record my thanks for the facilities provided by the Zoological Station at Naples during several visits. To the WORT'S Fund I am indebted for a grant towards travelling expenses. My thanks are due to Professor CANNON for helping to collect some of the material in 1926, to Dr. A. BIDDER for preparing some material for me at Naples in 1928, and to Mr. A. HUGHES for injecting fixatives into *Nebalia* with his microinjection apparatus in attempts to obtain good fixation of certain adult structures.

PREVIOUS WORK.

The most important works on the embryology of *Nebalia* are those of METCHNIKOFF (1868); BOUTCHINSKY (1897 and 1900) and ROBINSON (1906). A review of the earlier papers, and the most comprehensive account of the development, is that by ROBINSON, but it is unsatisfactory and the technique employed was inadequate. The whole preparations, judging by the figures, were almost useless; a continuous series of developmental stages was not obtained (only six are described); and the orientation and interpretation of the sections leaves much to be desired. The author could not be decisive upon many important points, and some conclusions seem to have been influenced to a considerable extent by the results obtained by NUSBAUM (1887), etc., many of which have since been shown to be erroneous. The evidence put forward by ROBINSON is here considered insufficient to support the author's conclusions.

ROBINSON leaves some uncertainty concerning the early segmentation and formation of the germinal disk, and there is reason to believe that a critical preparation was made from an abnormal embryo.

The account of the germinal disk formation by METCHNIKOFF is essentially in harmony with the present description.

There has been considerable uncertainty concerning the course of gastrulation. A mesendodermal blastoporal ingrowth has been described by BOUTCHINSKY. However, ROBINSON states that mesendodermal and yolk cells are also budded off from the blastoderm all over the germinal disk. A small groove-like blastoporal invagination is described, which becomes closed by a roofing over of the groove from the lateral walls. Several alternative suggestions for the origin of the mesoderm are put forward. The present account does not substantiate these conclusions.

The origin of the posterior liver lobes, and the formation of the mid-gut by growth of the endoderm around the yolk is described by ROBINSON, but the yolk cells are said to degenerate.

The account of the further internal development by ROBINSON is largely concerned with the nervous system, and treatment of the mesoderm is slight. No somite formation is described. Concerning the origin of the heart, the "anterior end of the heart or the dorsal aorta," p. 420, is said to arise from a group of mesodermal cells lying mid-dorsally in the anterior thoracic region. The development of the antennal gland is not followed in any way, but is described as mesodermal since no ectodermal intucking was seen in this region. Finally, germ cells are rather doubtfully described in the same position as in late embryonic stages of a mysid.

METHODS.

Part of the material was collected from the Naples Zoological station in the summer of 1926, and further work was done there in 1928 and 1931. Although *Nebalia* is a common animal around our coasts, its breeding habits are unknown, and individuals carrying embryos have not previously been recorded, although they were found breeding near Plymouth in November, 1932. In the Bay of Naples *Nebalia* breeds freely between May and November. It can often be collected abundantly with a hand net by scraping rocks and masonry which are overgrown by weed and worm tubes.

Twenty embryos or more are carried by the parent between the foliaceous thoracic limbs. The newly-laid eggs are about 330 μ in diameter, and the yolk gives a yellow colour to the thorax of the parents, rendering conspicuous those carrying embryos. The embryos were removed from the parent, fixed in formol bichromate,* and stored in 5% formalin in the dark. Fixation of the younger stages gave as excellent results as with *Hemimysis*, but the subsequent procedure had to be altered slightly from that used for *Hemimysis*. The embryos were cleared in methylsalicylate from 90% alcohol and transferred to chloroform. Paraffin wax of 52° m.p. was melted into the chloroform, and the latter evaporated somewhat for 10 minutes. The embryos were then passed through three wax baths in about 20 minutes. Orientation of the younger stages gave the usual difficulties, but the best differentiation of germinal disk from yolk was obtained by staining with strong eosin for a short time, so leaving the germinal disk unstained against the tinged yolk. Orientation was then performed in the molten

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* The method of fixation is that of B. G. SMITH (1912). The material is placed for 48 hours in

$K_2Cr_2O_7$	1 gm.
glacial acetic acid	2·5 c.c.
formalin 40%	5 c.c.
water	100 c.c.

made up at the time of using, and the fixative renewed once. The embryos are rinsed in water before transference to formalin.

wax under a high-power binocular dissecting microscope. It was usually possible to orientate four young embryos at a time, and they could thus be cut together in the same block. A great saving of labour was so effected. Sections were cut at 8 μ, except for studying the early cytology, where a thickness 14–20 μ was employed, and stained in iron hæmatoxylin or Mallory's triple stain. A complete series from the four-celled stage onwards was obtained.

Great difficulty was experienced in preparing whole mounts of young germinal disks, which had to be made from material fixed in formol bichromate. Some successful preparations were obtained either by dissecting off the vitelline membrane and then the germinal disk, or by cutting away half or three-quarters of the embryo on a microtome, and mounting the remaining fragment after removal of the vitelline membrane. The disks were stained for two days in alum-carmine, and subsequent differentiation in acid alcohol usually removed the stain from the yolk, so leaving the chromatin of the nuclei visible. Figs. 18, *a*–19, *e*, Plates 20 and 21, were prepared from whole embryos viewed as opaque objects after the yolk had been tinged with eosin.

Many changes were followed in the living state owing to the transparency of the embryos, the yolk only being opaque. The figures of various stages viewed as transparent objects, figs. 3–5, are based on camera lucida drawings of living material in which the individual yolk cells, the endodermal plate, the developing liver, preantennullary somites and anterior aorta were detectable.

Fixation of whole embryos in any fixative proved entirely inadequate for certain purposes. The origin and development of the gut mesoderm could only be seen satisfactorily in embryos removed from the villeline membrane, and then cut up so as to remove the caudal papilla intact. This was done with surgeons' needles under a binocular microscope in sea water, and the portions dissected out were fixed immediately in various fixatives. By this means much better penetration by the fixative was obtained; also the turgescence of the yolk sac was removed so that some mesodermal structures were less compressed. The best results were obtained with formol bichromate, Zenker and Dubosq-Brazil fixatives.

The older embryonic stages presented extreme difficulties in fixation, possibly caused to some extent by a cuticle not readily permeable. A large number of fixatives were tried, and at Naples an ice chest was used to keep the embryos cool during the warm weather. The best results were obtained with formol bichromate, using either the normal formula or 0·75% instead of 1% potassium bichromate, and occasionally Carnoy or Dubosq-Brazil gave useful results. Embryos were also pricked or cut up into suitable fragments before fixation. Really good fixation of the oldest stages could not be achieved. The study of the endoskeleton, segmental excretory organs, and gonad development required an examination of the adult internal anatomy. Here again good fixation was impossible to obtain, particularly in the maxillary region where a maxillary gland might be present. Of the many fixatives used, either on whole animals, on cut-up fragments, or injected into the animal before immersion in the fixative, formol bichromate and Dubosq-Brazil most frequently gave the best results, and Benoit's fluid and cold Carnoy were occasionally useful for some purposes. In investigating the structure of adult segmental excretory organs vital dyes were employed on the living animal for comparison with serial sections.

SEGMENTATION.

It has not been possible to study in detail the development of *Nebalia* between the unripe egg in the ovary, fig. 13, *d*, and the four-celled embryo. The cytological processes following the laying of the egg must occur rapidly, and their almost entire absence from the material fixed may be explained by the delay of several hours between collecting the animals in the Bay and examining them in the laboratory. Only six families out of 250 fixed and hundreds more examined contained unsegmented eggs of any kind.

The youngest stage seen, fig. 1, *a*, shows a central nucleated irregular mass of protoplasm lying within the yolk, which is surrounded by a thin peripheral protoplasmic layer. Asters are present in the inner mass. The cytoplasm then rises to the surface of the egg, but does so in more than one place, so that two or three " pseudoblastomeres " are formed at the surface, fig. 1, *b*. The nuclear material lies in only one of these pseudoblastomeres, usually the smaller, and gives rise to a division figure parallel to the surface of the egg. This division figure differs from those of the somatic cells by its large size, by the absence of visible asters at the poles, and by the irregular scattering of the chromosomes all over the spindle, fig. 1, *c*. The completion of the first cleavage has not been seen. The fate of pseudoblastomeres lacking nuclear material is unknown, and no embryos showing any phase of the second cleavage have been found.

The next stage observed is that showing four large blastomeres, and has been obtained abundantly. The four blastomeres lie together at one pole of the embryo, fig. 1, *d*. They may touch one another, as in the fig., or they may be rounded off from the yolk and pressed against each other, as are all blastomeres at later stages, fig. 1, *e*, *f*. Besides the four large blastomeres there are usually about three much smaller cells (these were also seen by BOUTCHINSKY, 1897), which lie anywhere on the surface of the embryo, fig. 1, *d*. Their origin is unknown. They have been seen in process of division, but their fate could not be determined.

From the cap of four large blastomeres cell division proceeds at right angles to the surface, and thus the blastodermal cap spreads out over the yolk, fig. 1, *e*–*h*. The small blastomeres soon become indistinguishable from the descendants of the four large ones which become progressively smaller in size, and, as the blastoderm spreads, so these small blastomeres appear to be incorporated in it. The blastoderm extends round the yolk and finally encloses the whole. The pole of the embryo last to be covered with blastoderm may be called the vegetal pole and is invested by few and much drawn-out blastomeres. Elsewhere the blastoderm is of even thickness.

Such appears to be the usual course of development, but irregular behaviour in early

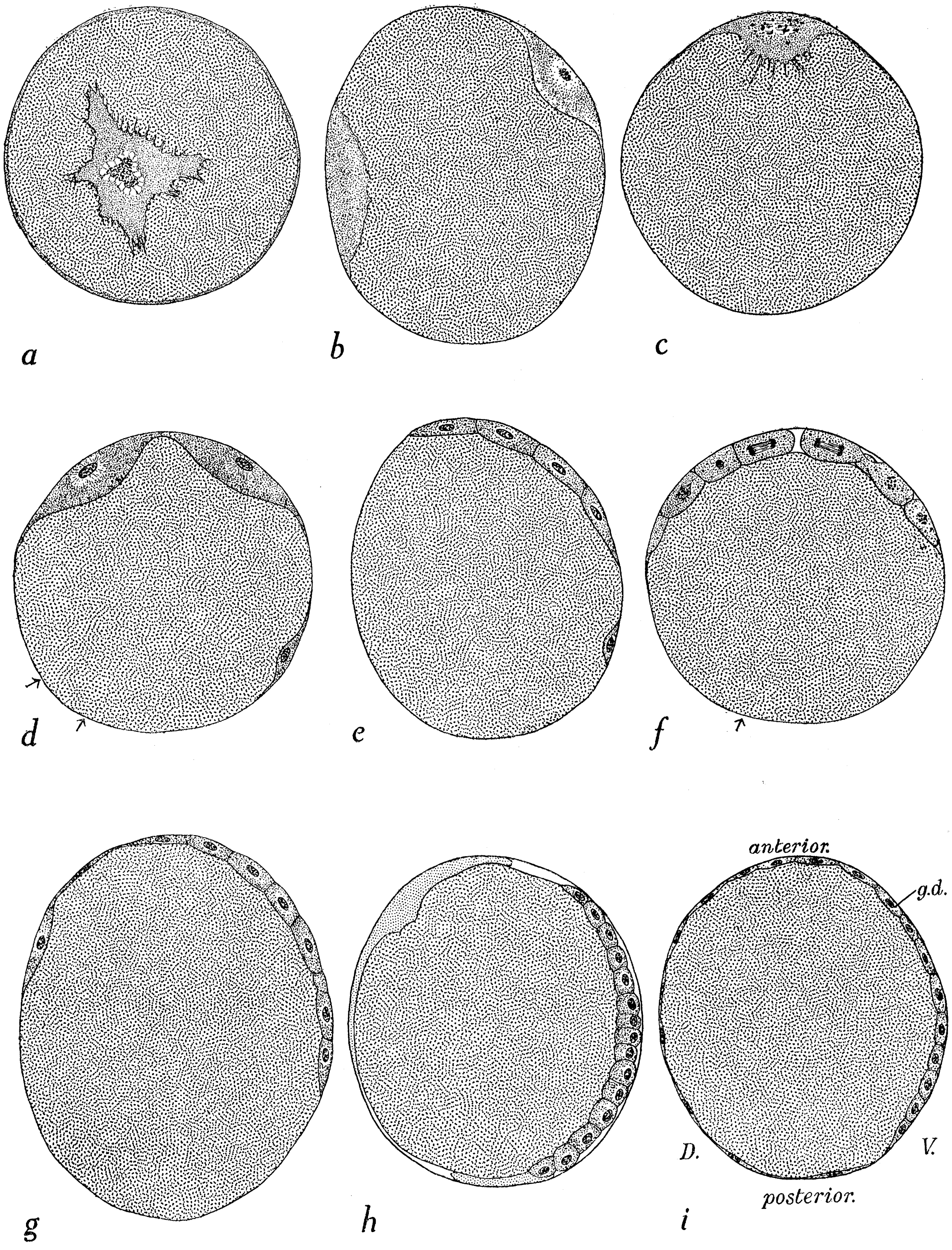

FIG. 1.—Sections of eggs and embryos showing the normal course of segmentation and formation of the blastoderm around the yolk. (*a*) Egg shortly after laying showing a thin surface layer of protoplasm and a central stellate mass containing the nucleus. (*b*) Unsegmented egg with nucleus situated in one of two peripheral masses of protoplasm (" pseudoblastomeres," see text). (*c*) The single nucleus in division (probably the first segmentation division), " pseudoblastomeres " present as in fig. *b*, but one is not cut in this section. (*d*) The result of the first few cleavages : a cap of four large blastomeres at one pole (two only seen in the section), and three small blastomeres (one seen in the section and the positions of the other two indicated by arrows). (*e*) The cap of blastomeres has proliferated and is composed of 11 cells. (*f*) Slightly older than the last and showing blastomeres in process of division. (*g*) Older stage in which the cap of blastomeres is composed of 67 cells. Three small cells are still detectable. (*h*) The blastodermal cap is composed of about 180 cells and the small blastomeres are no longer distinguishable from the rest. (*i*) Later stage in which the blastoderm has completely surrounded the yolk. The cells at the posterior vegetal pole are very thin, and those on the future ventral side are thicker than elsewhere and form the beginning of the germinal disk, *g.d.*

stages is frequent. Thus instead of a cap of four large blastomeres being formed at one pole, a number of blastomeres may lie scattered separately over the yolk (fig, 2, *j*), or a few may be aggregated together. Further division may result in a multi-laminar cap of blastomeres being formed, fig. 2, *k*, *m*, but this state seems to be transitory, as in all later stages a single layer of blastomeres only is present. Another variable feature is the state of the yolk. Part of the yolk may be replaced by a substance, possibly fluid, of different staining properties. The yolk stains black with iron hæmatoxylin and orange with Mallory, while this replacing substance appears as a faintly staining granular mass with the former, but bright blue with Mallory. This substance may form an even layer over the yolk surface or may lie in irregular accumu-

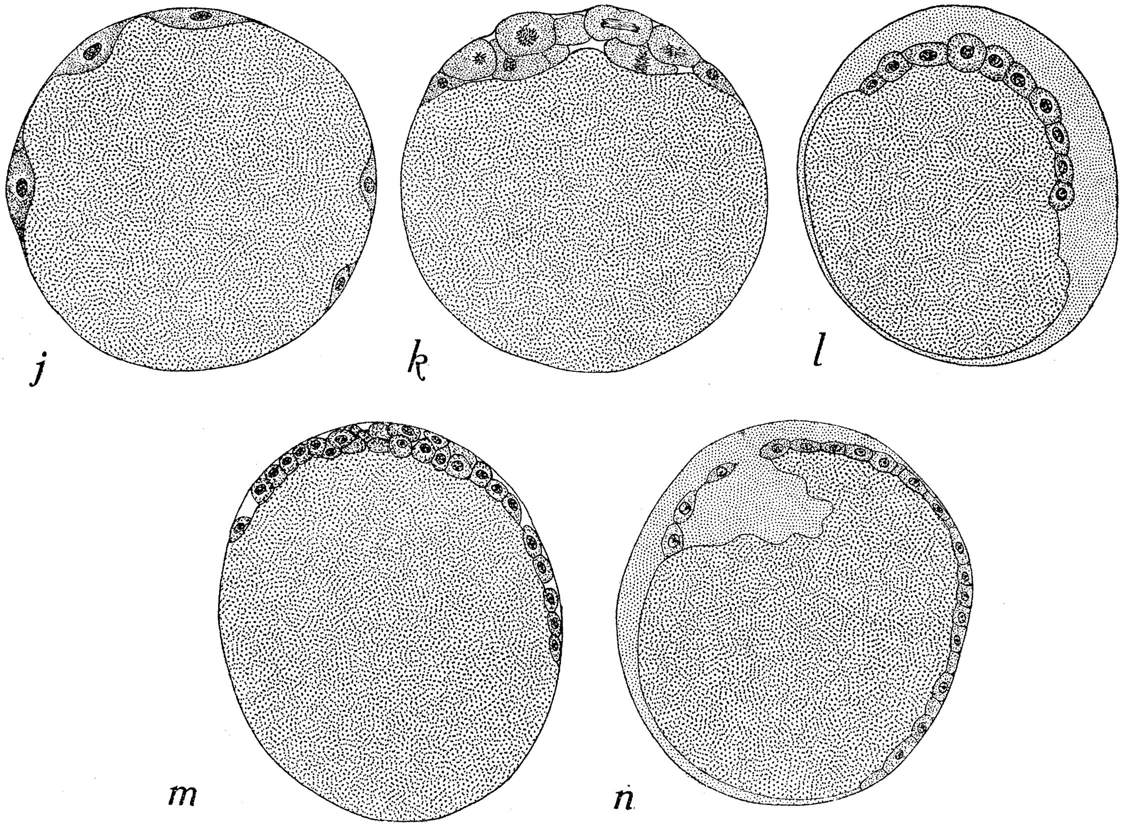

FIG. 2.—Sections of abnormally segmenting embryos showing exceptional positions and numbers of blastomeres.

(*j*) Twenty blastomeres of various sizes are scattered over the surface, and do not form a cap at one pole. From the same family as fig. 1, *e*.

(*k*) A multi-laminar cap is present. Compare the normal condition in fig. 1, *f*, from the same family.

(*l*) A considerable part of the yolk is replaced by a substance of different staining properties, and the blastomeres lie over the yolk surface below this substance.

(*m*) Cap of blastomeres which is more than one cell thick in places, and is possibly derived from an earlier stage such as seen in fig. *k*.

(*n*) Embryo of the type shown in fig. *l* at a later stage. The blastoderm does not follow entirely the contour of the yolk.

lations. Sometimes the blastoderm will lie entirely external to the yolk and to this blue staining material, or the blastomeres may sink down into the latter and follow the contour of the yolk. Some of the early stages may thus present a most unusual appearance, fig. 2, *l*, *n*. It must be supposed that these embryos either die or become normal later, as all embryos of older stages were uniform in appearance and did not show this feature.

Formation of the Germinal Disk and Subsequent Changes in External Shape of the Embryo.

Unhatched Embryo.

Shortly after the blastoderm has enclosed all the yolk the axes of the embryo become apparent. A germinal disk first appears at an elongated thickened area of blastomeres on the future ventral side of the embryo. The disk ends abruptly posteriorly, and elsewhere merges gradually into the blastodermal covering of the yolk, fig. 1, *i*. The external development of the embryo can be followed through early stages in ventral view in figs. 18 and 19, and the later stages are shown in lateral view in figs. 3–5. A blastoporal area develops at the narrow posterior end of the germinal disk, fig. 18, *a*, but no external differentiation of the germinal layers or genital rudiment takes place prior to gastrulation. The blastoderm in the anterior median part of the disk becomes thinner (compare figs. 18, *a*, and 18, *b*). This is caused by a shifting sideways of some of its cells, so that the disk becomes V-shaped, the arms of the V being separated anteriorly and remaining connected posteriorly around the blastoporal area, fig. 18, *b*. Thickenings forming the rudiments of the optic lobes and three pairs of naupliar appendages appear along the arms of the " V," and the optic thickenings then shift towards one another, fig. 18, *c*. When the limb rudiments are clearly formed, the optic rudiments become connected by a transverse thickening, fig. 19, *d*, which then enlarges posteriorly and spreads between the antennæ, where it forms the labral rudiment, fig. 19, *e*.

The trunk region between the mandibles and telson is formed by growth from teloblasts situated at the base of the V-shaped germinal disk (see below, p. 178), and all the segments are formed in series from before backwards. When the rudiments of the maxillules have appeared a transverse furrow is formed behind them, and as this furrow deepens, that part of the disk lying behind it folds forwards, so forming the caudal papilla, fig. 19, *e*, and fig. 3, A and B, *c.fu.* and *c.p.* The caudal furrow deepens as more segments are differentiated, and the angle of flexure shifts backwards until it lies opposite the third thoracic segment. The papilla elongates, and finally, when the rudiments of all segments are differentiated internally, it extends anteriorly as far as the labrum, fig. 3, E. At this stage the embryo is ready to hatch from the vitelline membrane.

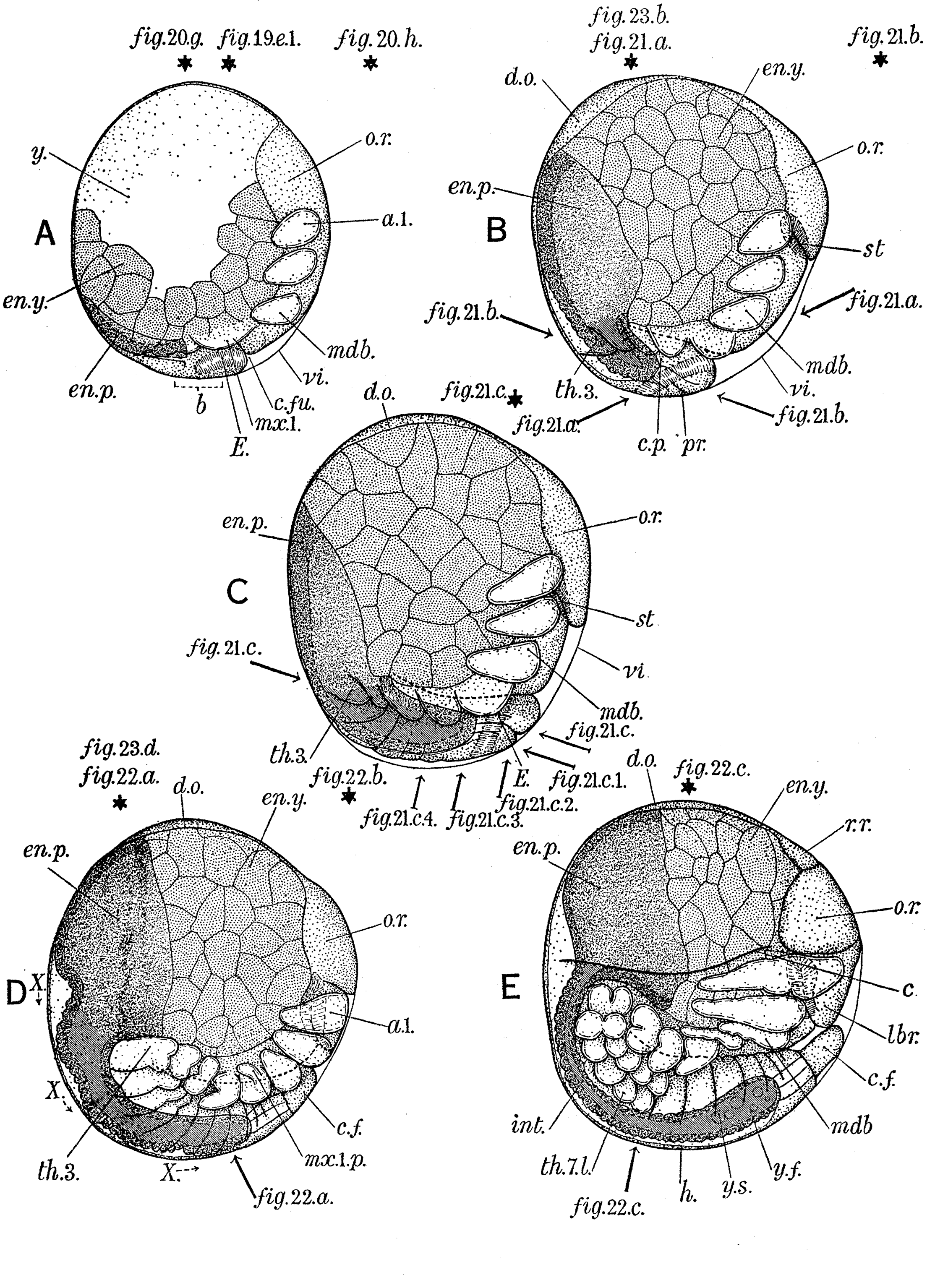
fig.20.g.
fig.19.e.1.
fig.20.h.
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o.r.
a.1.
A
en.y.
mdb.
vi.
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b
E.
fig.23.b.
fig.21.a.
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d.o.
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fig.22.c.

FIG. 3.

FIG. 3.—Figs. 3–5 show diagrams based on camera lucida drawings of living embryos drawn to the same scale (× 132 approx.). The embryos are represented as transparent objects, with the inner wall of the endodermal tube indicated in optical section by dotted lines. No mesoderm is shown other than part of the preantennullary somites where they form the anterior aorta, figs. F–I, and the trunk somites where they form the heart wall, figs. I and K. The asterisks indicate the relative ages of embryos from which sections are figured elsewhere. Thus an asterisk immediately above an embryo indicates that the section figured is of the same age as the embryo below, and an asterisk to the left or the right of an embryo indicates that the section is of an individual younger or older respectively than the embryo below. The arrows show the planes of sections figured on the plates. Figs. A–E show embryos in side view up to the age of hatching. For key to lettering see p. 230.

(A) An embryo a little younger than that shown in ventral view, fig. 19, *e*, Plate 21. The mesoderm of about four thoracic segments has been formed. The caudal furrow, *c.fu.*, has just appeared, gastrulation is still proceeding from the blastoporal area, *b.*, and the ectodermal teloblasts have not yet formed a complete ring round the caudal papilla. The endodermal yolk cells, *en.y.*, and the endodermal plate, *en.p.*, at the base of the caudal papilla are shown.

(B) The mesoderm of the eighth thoracic segment has been formed. The caudal furrow has deepened, gastrulation has ceased, and both stomodœum, *st.*, and proctodœum, *pr.*, have been formed. The endodermal yolk cells have entirely surrounded the yolk, and the endodermal plate is enlarged and tubular. The dorsal organ, *d.o.*, has appeared.

(C) The mesoderm of the third abdominal segment has been formed. The caudal papilla has elongated, but the flexure still lies at the third thoracic segment. The dorsal organ has shifted anteriorly.

(D) All the mesodermal somites have been formed and the ectodermal and mesodermal teloblasts have disappeared. Appendages as far as the sixth thoracic segment are now apparent, and the palp of the maxillule, *mx.*1.*p.*, is already directed backwards. The endodermal plate is spreading anteriorly, and within the caudal papilla shows active peristaltic constrictions. Three such contractions are seen opposite *X*. In the living animal these contractions pass progressively backwards as indicated by the dotted arrows.

(E) Embryo ready to hatch from the vitelline membrane. The caudal papilla behind the last thoracic segment has thickened and elongated. All thoracic limbs are seen and the naupliar appendages are elongated. An ectodermal rudiment of the rostrum, *r.r.*, and the beginning of the carapace fold, *c.*, are apparent. The endodermal plate has surrounded more of the yolk, and within the intestinal part of the plate lying in the caudal papilla can be seen several partly liquified yolk spheres, *y.s.*, which have been drawn into the intestine from the cephalo-thoracic yolk sac by the peristalsis. The intestine is shown in the contracted phase, peristalsis for the moment not taking place.

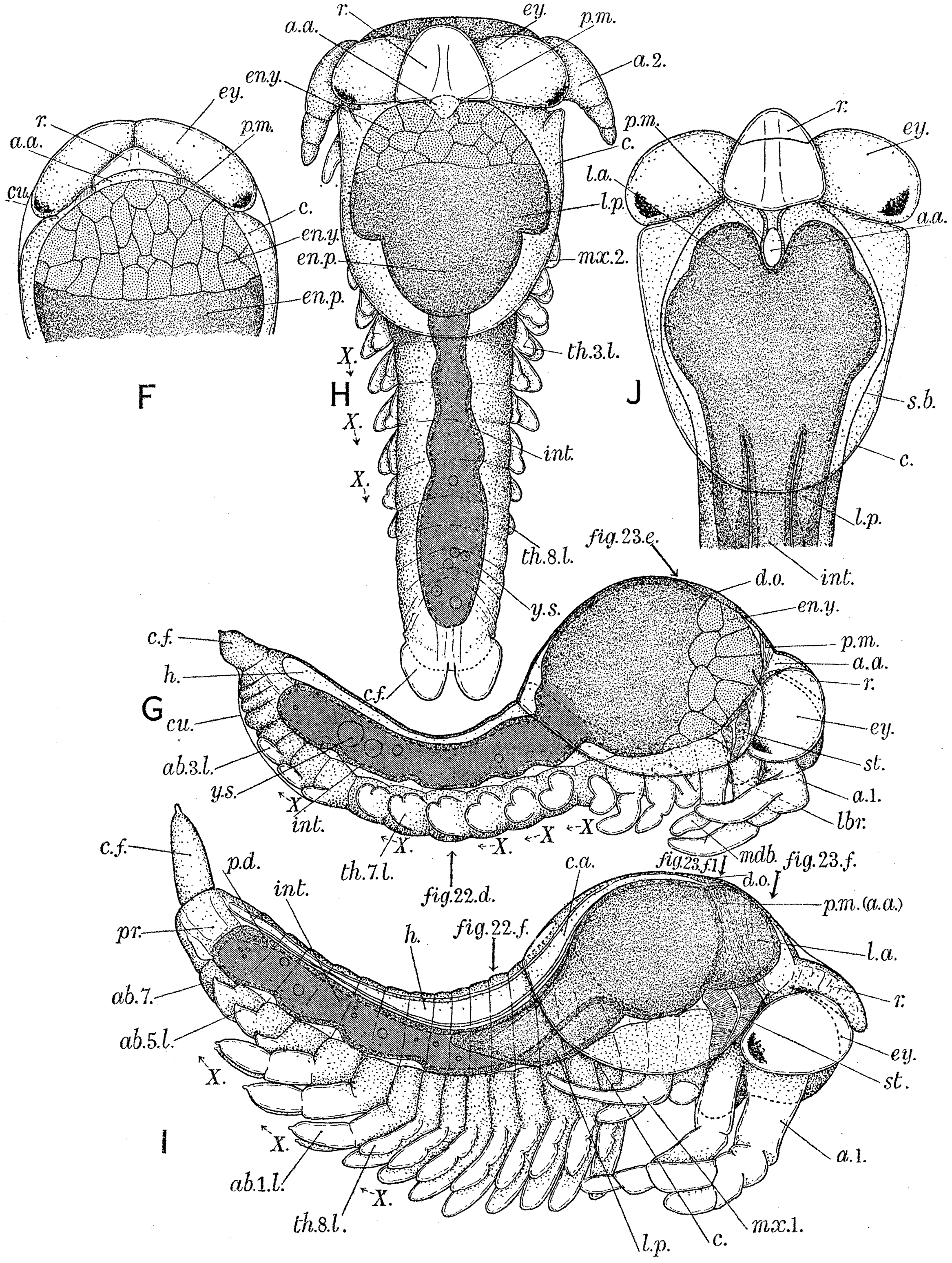

Fig. 4.—Continuation of fig. 3. For key to lettering see p. 230. The embryos have hatched from the vitelline membrane, and the order of lettering indicates their respective ages. F is just hatched, H is intermediated between G and I. F, H, and J show dorsal views, where the development of the anterior end of the yolk sac can be seen. The yolk cells, *en.y.*, gradually all become converted into the endodermal plate cells, *en.p.* (the mid-gut epithelium), and the formation of the anterior, *l.a.*, and posterior, *l.p.*, liver lobes is shown. In front of the yolk sac lies the hæmocœlic space, part of which is enclosed by the preantennullary mesoderm, *p.m.*, to form the anterior aorta, *a.a.*

Description of Fig. 4 concluded on next page.

(G) Embryo older than F and nearly ready to shed the first embryonic cuticle, *cu*. The yolk cells have nearly all formed the epithelial covering of the yolk. The cephalo-thoracic part of the yolk sac is full of stiff yolk, while the intestinal part contains fluid yolk and some stiff yolk spheres, *y.s*. Five peristaltic constrictions are seen passing backwards at *X*. Part of the preantennullary mesoderm is shown in front and above the stomodœum where it is approaching the dorsal organ (compare fig. 6, *b*). The first three abdominal limbs are seen.

(I) Older embryo some time after the first embryonic cuticle has been shed. All the yolk is now covered by the endodermal epithelium, and the dorsal rudiment of the posterior gut diverticulum, *p.d.*, is formed. The dorsal attachment of the preantennullary mesoderm has moved posteriorly so indenting the yolk sac anteriorly and leaving a pair of anterior lobes, *l.a.*, the future cephalic liver lobes, on either side, see H and J. From the maxillary segment the posterior liver lobes extend backwards through the thorax, the first origin of these lobes is seen in H. Three peristaltic constrictions at *X* are passing down the intestine. The heart is now fully formed and is continuous with the anterior aorta and is just starting to beat. An ecdysis follows this stage and then the small individual leaves the brood pouch.

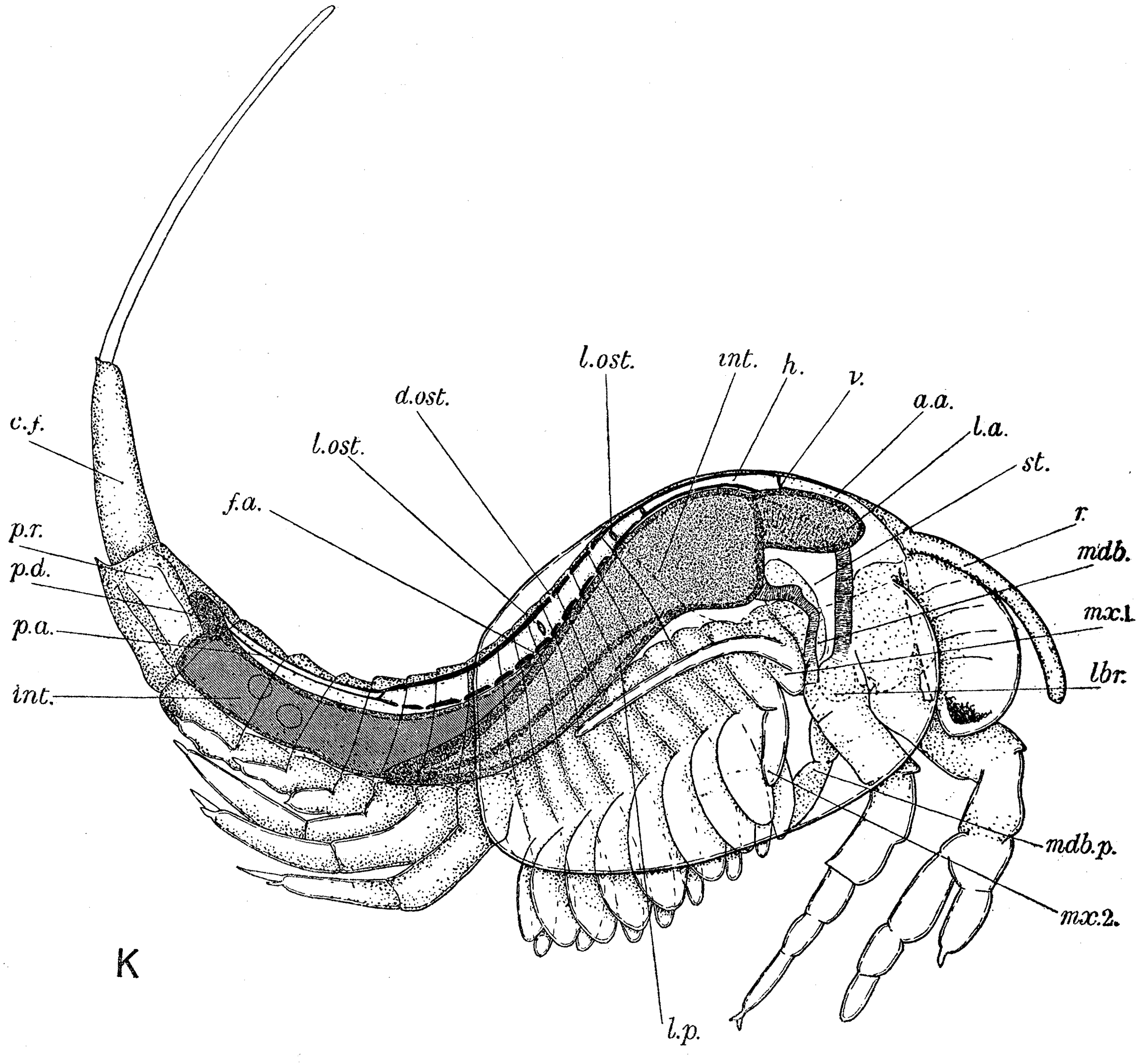

FIG. 5.—Continuation of figs. 3 and 4. The embryo K is older than in fig. 4, I, and has just shed the second embryonic cuticle. In this stage it leaves the brood pouch and becomes free swimming. The form of the alimentary canal and liver lobes is shown. Most of the yolk has been absorbed from the cephalo-thoracic part of yolk sac, which now remains as the mid-gut and anterior and posterior liver diverticula. The latter ultimately extend to the posterior end of the abdomen. A few yolk spheres still remain in the abdominal part of the intestine, but peristalsis has almost ceased. The heart and posterior aorta are shown, together with the lateral, *l.ost.*, and dorsal, *d.ost*, ostia which are present at this stage—the others being developed later—and the openings of the ventro-lateral paired arteries, *f.a.*, which leave the heart in the segments which have formed it. The valves, *v.*, between the anterior and posterior aortæ and the heart are shown.

The limb rudiments make their appearance and increase in size from before backwards along the head and thorax. The antennules, antennæ, and mandibular palps extend backwards along the sides of the body, while the maxillulary palps appear early, fig. 3, D, *mx.I.p.*, and are directed upwards and backwards (the future adult position), even before the carapace is formed. The thoracic limbs are bilobed and extend laterally. Only the first three abdominal limbs are represented before hatching, and they form ventrally directed rudiments not distinguishable in side view.

The carapace appears as a lateral fold extending from the antennal to the third thoracic segment (figs. 3, E, and 8, *a* and *b,c*).

Both stomodœum and proctodœum appear early. The proctodœum is formed over the blastoporal area after gastrulation has ceased, fig. 3, B, and shortly afterwards the stomodœal intucking passes inwards behind the labrum and between the antennæ (see below, p. 180).

After the formation of the proctodœum further growth of the unsegmented area around it, which is enclosed by the ring of teloblasts, results in the formation of the telson. The caudal furca appears as a pair of ectodermal outgrowths from the telson on either side of the anus, fig. 3, B–E.

A median dorsal organ appears at stage B, fig. 3. It lies at the anterior dorsal side of the embryo and consists of a localized accumulation of ectodermal cells which subsequently degenerate, fig. 6, just as in *Hemimysis*. No dorso-lateral organs are formed.

Between the dorsal organ and the optic rudiments another ectodermal thickening occurs at a later stage, fig. 3, E. This is composed of normal cells, and after hatching increases in size and folds off to form the rostrum, fig. 6, *a* and *b*.

During these changes in form, the volume of the whole embryo increases, and the vitelline membrane is stretched. This is due in part to the growth of embryonic tissue, but the main factor appears to be the absorption of water by the yolk causing an increase in the yolk volume. The increase in size can be seen in fig. 3, while the yolk volume is plotted in fig. 9. The bursting of the vitelline membrane is probably caused partly by the pressure exerted by the reflexed caudal papilla and partly by the yolk which is absorbing water. As so little yolk lies in the caudal papilla the pressure exerted by the papilla must be mostly muscular (compare *Hemimysis*, Manton, 1928, *a*, p. 383).

Muscular movement is first detectable when the eighth thoracic segment is visible externally at about stage D, fig. 3. Movement in the rudimentary longitudinal muscles of the caudal papilla becomes increasingly active until the vitelline membrane is ruptured at stage E. On hatching the yolk volume immediately increases by about 10% or more, causing a stretching of the embryonic tissue, as in *Hemimysis*.

Hatched Embryo.

After leaving the vitelline membrane the caudal papilla is reflexed backwards, and the embryo passes through three stages, separated by ecdyses, before leaving the brood pouch and becoming free-swimming. During these stages the yolk volume steadily decreases, figs. 4–6, until it is all absorbed. In the first stage after hatching, fig. 4, F, G, and H, the head appendages are free and have elongated, but the rostrum does not project, being covered by the cuticle next to be shed, fig. 4, G. The thoracic limbs are small and appear as before, and the first three abdominal limbs can usually be seen easily within the cuticle, but not projecting freely. The carapace fold has enlarged, and pigment is seen in the optic lobes.

When the first cuticle is shed the embryo increases in size and appears as in fig. 4, I. The rostrum, caudal furca, and appendages as far as the third abdominal segment are large and project freely, while rudiments of the last three abdominal limbs are now formed.

When the second cuticle is shed a considerable increase in size occurs, fig. 5, K, and the embryo assumes the external form of a small adult, except that the last three pairs of abdominal limbs are still rudimentary. When almost all the yolk is absorbed the embryo leaves the brood pouch, and without further ecdysis becomes free-swimming.

Gastrulation, Germ Layer Formation and Early Development.

Gastrulation takes place by immigration of cells from a blastoporal area situated in the hinder part of the germinal disk, figs. 18 and 19. All the internal tissues, with the exception of the preantennulary mesoderm, are formed from the blastoporal area alone. The process of gastrulation is seen in surface views in figs. 18 and 19, where internal cells are shown in red, and in sagittal and parasagittal sections in fig. 20, Plate 22. The positions of these sections are indicated as far as possible by arrows on figs. 18 and 19 and on fig. 3.

Mesendoderm and Head Mesodermal Bands.

The beginning of gastrulation is seen in fig. 20, *a*. Cells pass inwards singly from the blastoporal area, and come to lie between the yolk and the outer blastoderm, leaving small pits and gaps in the surface of the blastoporal area, figs. 18 and 19, *b.p.* These cells spread forwards, fig. 20, *b–d*, and fig. 18, *a*, *m.en.*, forming a compact mesendodermal mass of similar cells which may lie several deep. This mass differentiates into mesoderm anteriorly and endoderm posteriorly. As the germinal disk becomes V-shaped, so the anterior cells from the mesendodermal mass spread forwards below the arms of the disk and form the head bands of mesoderm supplying the three naupliar segments (fig. 20, *d* and *d*1, *m.en* and *n.m.*, and fig. 18, where mesoderm forming the head bands is indicated by horizontal red ruling and undifferentiated mesendoderm by interrupted ruling). This mesoderm extends as a pair of irregular strands of cells closely associated with the ectoderm in the position indicated in the figures.

Endoderm.

From the posterior part of the mesendodermal mass a few cells shift behind the germinal disk, fig. 20, *c*. These, and some of the innermost cells of the mesendodermal mass which are in contact with the yolk, form the first yolk cells or vitellophags, fig. 20, *e* and *f*, *en.y.*, by absorbing yolk which is deposited in vacuoles in the cytoplasm. The yolk vacuoles increase in size and the yolk cells wander out within the germinal disk, fig. 20, *f–h*. The edge of the area covered by a single layer of yolk cells is shown by a dotted red line in figs. 18 and 19. Yolk cells are continually being formed during the gastrulation period from the inner cells of the mesendoderm, and they finally form a continuous layer around the yolk except for the region covered by the endodermal plate (see below).

The posterior part of the mesendodermal mass remains compact, and forms a one-layered epithelial plate behind and within the posterior end of the germinal disk, fig. 20, *e*, *e*.1, and *f*, and fig. 19, *d*, *en.p.* This plate is the rudiment of the mid-gut epithelium, and the yolk cells never lie internal to it. As gastrulation proceeds, immigrating cells pass inwards anterior to the endodermal plate. Some of these become yolk cells and spread round the yolk, mainly in anterior and lateral directions, while others unite with the anterior edge of the endodermal plate, fig. 20, *g*. The plate also grows laterally and posteriorly by adjacent yolk cells becoming transformed into epithelial cells, fig. 20, *f*, *g*, *h*, and *h*.1. A yolk cell becomes closely applied to the edge of the plate, its nucleus and cytoplasm accumulating in the outer part of the cell. The thin cell wall enclosing the large yolk vacuole breaks down, so freeing the yolk, and the outer part of the cell rounds off as an epithelial cell forming part of the endodermal plate. The endoderm now comprises (i) the endodermal plate and (ii) the yolk cells.

Ectodermal and Mesodermal Teloblasts.

After formation of the head band mesoderm, differentiation at the sides of the blastoporal area leads to the formation of the teloblasts. The ectodermal teloblasts first appear as an irregular group of three or four enlarged ectodermal cells lying opposite the bases of the arms of the V-shaped disk on either side. These cells shift their positions and form a row, equal in number, on either side of the blastoporal area, fig. 18, *c* and *c*.1, *E*.1–*E*.6. The anterior ends of the rows then approximate and become united in the middle line by the differentiation of a median teloblast, fig. 19, *d* and *d*.1, *E*.0. The curved band of teloblasts so formed increases in length by lateral additions of cells in pairs, fig. 19, *e* and *e*.1, *E*.7–*E*.8. Finally, when one median and nine pairs of lateral teloblasts have been differentiated the ninth pair (*E*.9) gradually approach one another until they meet, so forming a complete circle of teloblasts around the blastoporal area, as is seen in the frontal section of a caudal papilla shown in fig. 21, *a*, Plate 23, *E*.0, *E*.1–*E*.9, which is a little older than the surface view shown in fig. 19, *e*.1.

Shortly after the appearance of the ectodermal teloblasts, four pairs of mesodermal teloblasts are formed from the anterior part of the mesendodermal mass. They lie immediately internal to the ectodermal teloblasts, and maintain constant positions below them during the migrations of the latter, fig. 19, *d*.1 and *e*.1, *M*.1–*M*.4. For the sake of clearness, no internal cells, other than the mesodermal teloblasts, are shown in these figures.

The ring of teloblasts around the blastoporal area at first lies at the edge of the rudimentary caudal papilla, fig. 19, *e*, and fig. 3, A. As the caudal furrow deepens, and the blastoporal area enclosed by the teloblasts develops (see above, p. 176), so the teloblasts come to form a ring around the papilla. The median ectodermal teloblast *E*.0 becomes mid-ventral, and the pair *E*.9 lie dorsally. The pair of mesodermal teloblasts *M*.1 usually come in contact ventrally, fig. 21, *a*.

Descendants from the ectodermal and mesodermal teloblasts are formed simultaneously and in rows, as in *Hemimysis*, as soon as the teloblasts are established, and give rise to the trunk region. Owing to the curvature of both rows of teloblasts, their descendants extend at first anteriorly, laterally, and posteriorly. This is seen in the ectodermal descendants shown in fig. 19, *d*.1 and *e*.1, the positions of the mesodermal descendants being indicated by arrows in figs. *d* and *e*. The small size of the germinal disk, and the early appearance of the caudal furrow, makes these descendants at early stages less easy to follow in sections than those of *Hemimysis*. Teloblasts (*E* and *M*) and some of their descendants (*e* and *m*) are seen in the sagittal and parasagittal sections of fig. 20, *f*, *g*, and *h*.1. The caudal papilla is formed and elongated by the activity of the teloblasts which encircle its tip. Thus the descendants of the teloblasts form the walls of the whole papilla and not only its ventral side as in *Hemimysis*.

During the differentiation of the teloblasts the ectoderm of the arms of the germinal disk forming the naupliar region becomes distinguishable from that posterior to it by the appearance of the nuclei, which are small and darkly staining, figs. 18 and 19, *c*.1, *d*.1, and *e*.1. The junction between the teloblastic and naupliar ectoderm is seen at *j* in fig. 20, *e* and *f*, and in fig. 19, *e*.1, between the mandibular and maxillulary rudiments, *mdb* and *mx*.1. All segments between the mandibular segment and the telson are formed by the teloblasts; in fig. 20, *f*, the descendants of one of the second pair of mesodermal teloblasts, *m*, are seen extending as far as the hinder border of the mandibular rudiment. As in *Hemimysis*, one transverse row of ectodermal and mesodermal descendants forms the rudiment of each trunk segment.

When the ectoderm and mesoderm of the seventh abdominal segment has been established the teloblasts disappear as in *Hemimysis*. This occurs in between stages C and D in fig. 3 when the band *E* disappears.

End of Gastrulation, Formation of Telson Mesoderm, etc.

Gastrulation continues for a time after the teloblasts are established, the immigrating cells becoming part of the endodermal plate or yolk cells. Towards the end of gastrulation a few cells from the blastoporal area remain behind the teloblasts and lie just within the ectoderm, *t.m.* in fig. 20, *h*.1 and *h*. These cells form the mesoderm of the telson and caudal furca (see below, p. 193). Gastrulation ceases quite early, just after stage A in fig. 3, and from the blastoporal area the proctodœal intucking is formed, fig. 20, *h*, and fig. 3, B, *pr*. The proctodœum is thus surrounded at first by the ring of teloblasts, fig. 20, *h*, and fig. 21, *a–c*, and the anus opens dorsally near the tip of the caudal papilla, fig. 20, *h*. As the telson develops from the unsegmented region behind the teloblasts (see p. 176) so the anus becomes terminal and posterior, and the proctodœum then runs through the telson, fig. 6. The telson mesoderm cells lie in a group on either side of the proctodœum, fig. 21, *b*, *t.m.* Their further development is described on p. 193. The stomodœum appears very slightly later than the proctodœum (see above, p. 176, and fig. 3, B).

Preantennulary Mesoderm.

The preantennulary mesoderm is formed directly from the germinal disk as in *Hemimysis*. A pair of cells pass inwards from the anterior part of the arms of the V-shaped disk, as seen in fig. 20, *d*.1, *p.m.*, and indicated in red in figs. 18, *b* and *c*. Other cells then immigrate inwards from the same region, so forming a pair of compact masses quite separate from and anterior to the head mesodermal bands.

Thus the major portion of the mesoderm, (1) the preantennulary mesoderm, (2) the head band mesoderm, and (3) the teloblastic trunk mesoderm, is formed essentially as in *Hemimysis*.

FURTHER DEVELOPMENT OF THE ENDODERM.

The endoderm towards the close of gastrulation consists, as described above, of an epithelial endodermal plate and of yolk cells, the former growing by marginal additions of (1) cells immigrating from the blastoporal area, and (2) transformed yolk cells. The extent of the endoderm can be seen in side view in fig. 3, A, *en.p.* and *en.y.*, where the yolk is only covered ventrally by yolk cells. When gastrulation has ceased, fig. 3, B, the yolk is completely enclosed in a yolk sac consisting of the enlarged endodermal plate and the yolk cells. Thereafter the endodermal plate, *en.p.*, continues to extend forwards by the transformation of the yolk cells into epithelial cells at its margin, figs. 3, 4, and 6 and fig. 20, *h*, until in the later embryonic stage, fig. 4, J and I, all the yolk cells are so transformed, and the yolk sac is entirely epithelial. The yolk cells persist longest at the anterior end of the yolk sac near the rostrum, figs. 4 and 6. They never absorb more than the outer layer of yolk into themselves, and the main mass of the yolk remains free in the middle of the yolk sac, fig. 6. From the walls of the endodermal yolk sac are developed the adult mid-gut, the posterior liver lobes, the cephalic liver lobes and the posterior mid-gut cæcum. No mesoderm takes part in the formation of the liver in *Nebalia*.

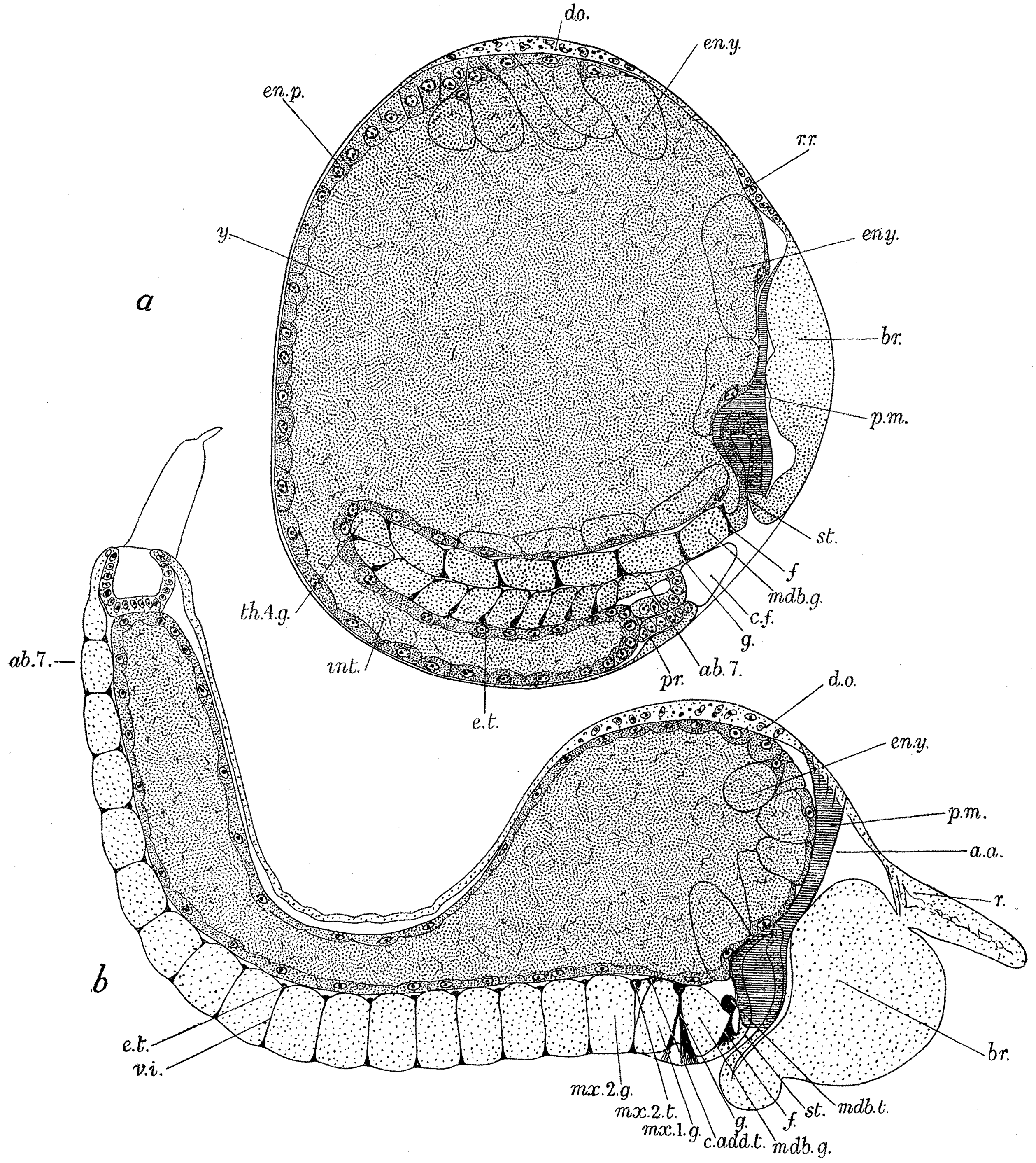

Fig. 6.—Diagrammatic sagittal sections of hatched and unhatched embryos showing the development of the yolk sac, the preantennulary somites and the segmental ectodermal bars forming the endoskeleton. × 245 approx.

(*a*) Embryo older than that in fig. 3, *D*. In the ectoderm the dorsal organ and rostral rudiment are formed, and the intersegmental ectodermal bars and their mid-ventral ectodermal connections are shown in black, *e.t.*, *g.* and *f.* The preantennulary somite, *p.m.*, covers the stomodœum and extends forward within the brain rudiment. The yolk is almost completely enclosed. The epithelial endodermal plate, *en.p.*, is tubular in the caudal papilla where it forms the intestine, *int.*, and in the cephalothoracic region the yolk cells are seen becoming attached to its edges.

(*b*) Hatched embryo younger than fig. 4, *I*. The dorsal organ, *d.o.*, and rostral rudiment, *r.r.*, have enlarged. The intersegmental ectodermal bars are only connected to the ventral ectoderm by thin strands. The mandibular bar *mdb.t.*, has enlarged and remains connected to the ectoderm mid-ventrally at *f.* The maxillulary bar has enlarged, and its ectodermal connection has divided into two parts, the anterior of which, *g.*, becomes muscular. The maxillary bar has divided, the anterior portion becoming the carapace adductor tendon, *c.add.t.*, and the remainder forming the tendon of the maxillary adductor muscles. The preantennulary somite, *p.m.*, is united to the dorsal body wall, and has reached the anterior end of the dorsal organ. The yolk is completely enclosed, and nearly all the yolk cells, *en.y.*, are converted to epithelial cells, their inner ends breaking down and liberating their contained yolk.

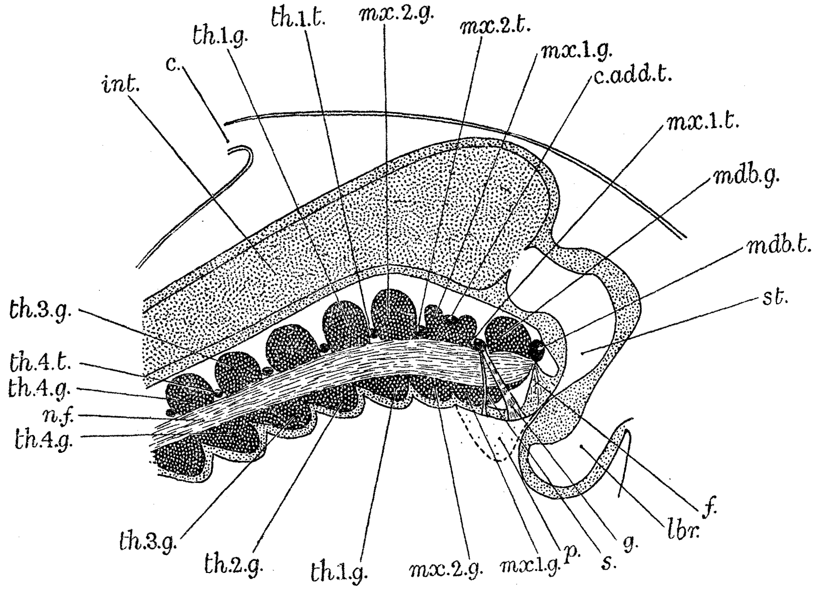

FIG. 7.—Diagrammatic sagittal section of an old embryo about to leave the brood pouch (see fig. 5), showing the relative positions of the intersegmental ectodermal bars which are forming tendons, parts of the endoskeleton, the nerve ganglia and the segmental boundaries, for comparison with fig. 6, 14, *a*, and 15. The cut bars are shown in black. In comparison with fig. 6, *b*, the relative positions of the parts have changed. The ventral insertions of the median connections to the ectoderm of the mandibular tendon, *f.*, and of the maxillulary tendon, *g.*, have been drawn forwards into the oral cavity. The carapace adductor tendon, *c.add.t.*, now indents the middle of the maxillullary ganglion. The positions of the upper parts of the ganglia and the intersegmental bars are now such that they overlie the lower parts of the succeeding ganglia; for example, the upper parts of the third thoracic ganglion, *th.3.g.*, lies above the lower parts of the fourth thoracic ganglion, *th.4.g.* This feature is here shown, as unless it is clearly appreciated the correct interpretation of transverse and frontal sections is obscured.

Mid-gut.

The endodermal plate becomes cup-shaped opposite the base of the caudal papilla (fig. 3, B), and as the latter grows, so the plate dips into it, forming a hollow finger-like extension closely apposed to the walls of the papilla and to the inner end of the short proctodœum. This extension is the rudimentary intestine or mid-gut, fig. 3, B–E, *int.*, and extends backwards from the third thoracic segment. Only a small amount of yolk passes down into the intestine, the bulk remaining in the cephalo-thoracic region, even after hatching from the vitelline membrane, figs. 3 and 4. After hatching the mass of yolk lying anterior to the third thoracic segment retards the mid-gut development in this region. The yolk cells forming the anterior walls of the yolk sac are slowly transformed into epithelial intestinal cells (see above) right up to the stomodœum, fig. 5, K. Thus the whole adult intestine from the proctodœum in the telson to the stomodœum is formed directly from the endodermal plate.

Cephalic Liver Lobes.

After hatching, changes in the shape of the cephalo-thoracic part of the yolk sac lead to the formation of the cephalic and posterior liver lobes, as well as to the front part of the intestine. The upgrowing preantennulary mesoderm at first lies above the stomodœum between the yolk sac and the anterior body wall, fig. 4, F and G, *p.m.*, and fig. 6. As the anterior aorta is formed between the preantennulary strands, they shift their insertion on the dorsal body wall in a posterior direction (see below, p. 190), and so indent the yolk sac by a vertical anterior furrow, fig. 4, H, I, and J, *p.m.* and *a.a.* A pair of " anterior yolk lobes " are so formed from the anterior end of the yolk sac, extending forwards on either side of the anterior aorta, fig. 4, H and J, *l.a.*, and the upper part of the stomodœum comes to lie between them, fig. 4, I. Towards the end of development, when little yolk remains, the yolk first disappears from these anterior yolk lobes. Their diameter decreases until the lumen is very small. Their walls thicken and remain as a single-layered epithelium, so forming the cephalic liver lobes of the adult, which lie on either side of the stomach and above the brain, opening to the mid-gut dorso-laterally immediately behind the junction of the stomach and mid-gut (see CLAUS, 1888, Plate II, figs. 6, 8–11, *vl*).

Posterior Liver Lobes.

The posterior liver lobes first appear just before the first embryonic cuticle is shed, fig. 4, H. Above the maxillæ, and within the rudimentary carapace fold, paired lateral thickenings appear in the walls of the yolk sac, fig. 8, *a*, *l.p.r.* Each thickening soon becomes a hollow thick-walled diverticulum of the yolk sac, fig. 4, H, and 8, *b*, *l.p.* and *l.p.r.* These diverticula grow posteriorly on either side of the intestine. Their distal ends are thick-walled and the lumen obliterated, but as they grow in length the yolk passes into them anteriorly and dilates the lumen, the walls becoming thin, fig. 8, *c*, *l.p.*, *l.p.r.*, and fig. 4, I and J. In fig. 22, *f*, Plate 24, the liver diverticula contain no yolk in the fifth thoracic segment, while this same segment at a later stage shows the liver full of yolk in fig. 12, *a*. As the liver lobes accommodate more yolk, so the median part of the yolk sac shrinks to form the mid-gut. Towards the end of embryonic life the posterior liver lobes extend back to the third abdominal segment, fig. 5, and later, when the animal is free-swimming, they reach the seventh abdominal segment. They open to the anterior end of the mid-gut ventro-laterally just behind the opening of the cephalic liver lobes. During the growth of the young free-swimming animal this pair of simple posterior liver lobes becomes subdivided through almost their entire length into three tubes, so forming the adult liver.

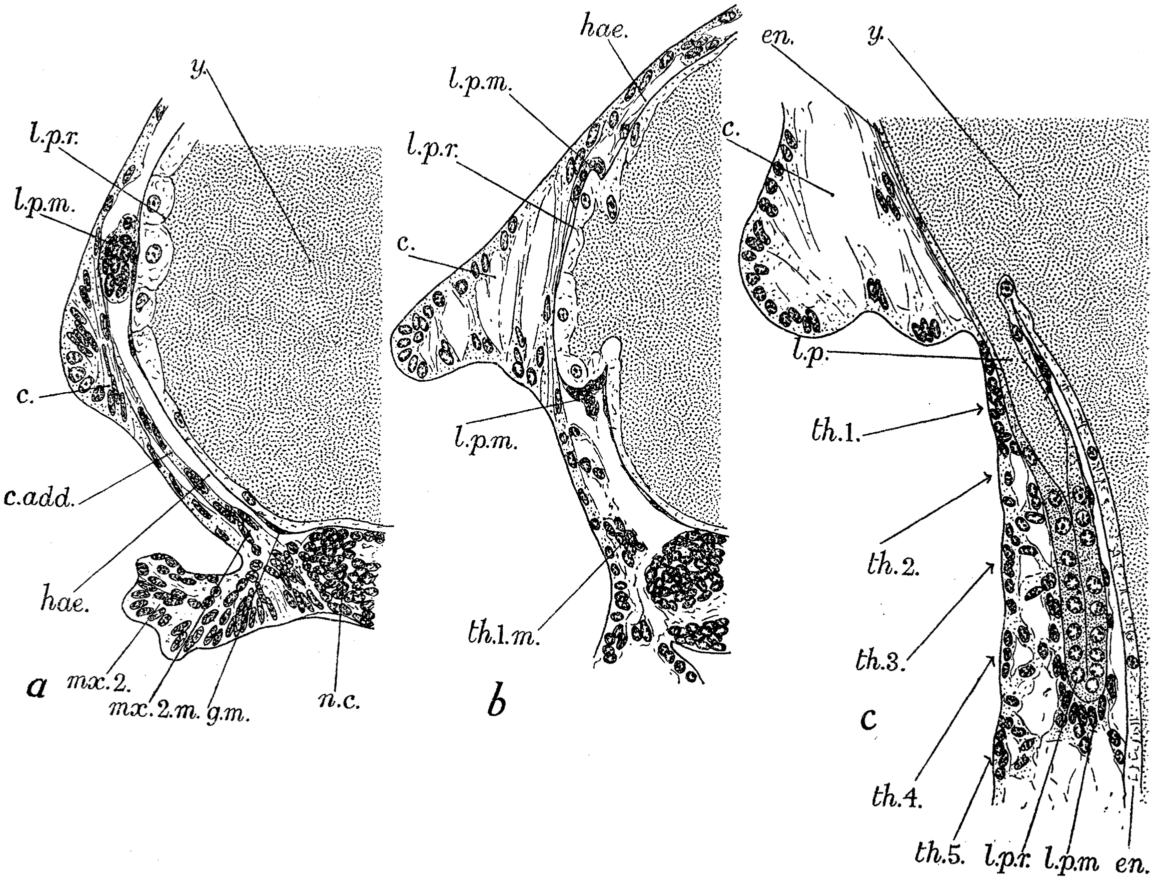

FIG. 8.—Sections showing the development of the posterior liver lobes from the endodermal yolk sac, together with the mesodermal investment of these lobes. Fixation has caused undue dilation of the carapace fold in figs. *b* and *c*. × 340 approx.

(*a*) Transverse section through the maxillary segment of an embryo slightly older than fig. 4, G., Just within the carapace rudiment, *c.*, a group of mesodermal cells, *l.p.m.*, have separated from the maxillary somite, and against them the endodermal cells of the yolk sac have thickened, *l.p.r.*, forming the rudiment of the posterior liver diverticulum. The rudiment of the carapace adductor muscle *c.add.*, is also seen.

(*b*) Transverse section through the same region of an older embryo which has shed the first cuticle fig. 4, I. The rudimentary liver is formed as a diverticulum of the yolk sac, and is surrounded by the mesoderm previously differentiated, *l.p.m.* Fig. 4, H, shows a dorsal view of a slightly younger stage.

(*c*) Frontal section of an embryo older than the last, and slightly younger than fig. 4, J. The liver diverticulum has extended posteriorly to the 4th thoracic segment, and is beginning to fill with yolk at its anterior end, *l.p.* The mesodermal investment of the diverticulum, *l.p.m.*, forms a thick cap over its distal end.

See also fig. 22, *f*, Plate 24 and fig. 12, *a*.

Posterior mid-gut Cœcum.

The hind end of the intestine is at first simple, as is seen in fig. 6. When the embryo is nearly ready to shed the second embryonic cuticle, fig. 4, I, a thickening of the epithelial wall of the gut appears dorsally just in front of the proctodœum, *p.d.* This thickening grows and forms a thick-walled diverticulum directed posteriorly above the proctodœum in the middle line, fig. 5, K. The lumen is at first virtually absent, and the diverticulum remains as the adult posterior mid-gut cæcum. No median anterior cæcum is formed at any time.

The development of the visceral mesoderm and fat body will be considered later (pp. 191 and 194).

Yolk Absorption and Yolk Sac Movements.

Changes in volume of the whole embryo have already been mentioned (p. 176). The yolk volume at successive stages is shown in fig. 9. The yolk absorbs water, and this is so rapid in early stages that the volume of the yolk sac increases, although the mass of contained yolk must be decreasing. A sudden increase in volume again occurs on hatching, when the pressure of the vitelline membrane is removed. Later the yolk volume steadily decreases, while the form of the yolk sac is being elaborated to become the liver and intestine (compare fig. 9, E′–K, with figs. 3–5, E–K).

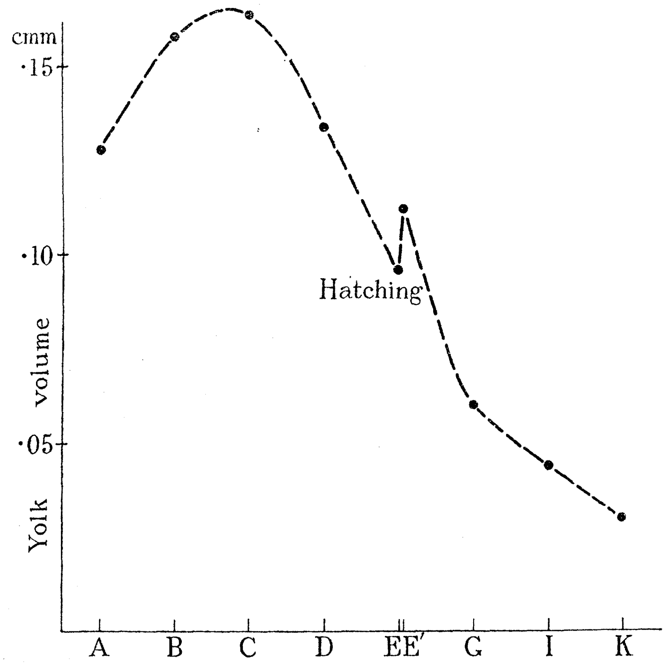

Fig. 9.—The approximate volumes of the yolk in the living embryos of figs. 3–5 are here shown. The two values E and E′ are those of the same embryo just before and just after hatching from the vitelline membrane. Yolk volumes calculated from sections of embryos of similar ages show the same main features, *i.e.*, increase in volume during early development, sudden increase in volume on hatching, and subsequent gradual reduction in volume as the yolk is absorbed. The value at K represents the volume of yolky gut contents of the embryo ready to become free. All the yolk is finally absorbed in the young free living individual.

As the mesodermal investment of the intestine is formed (see p. 191), the latter begins to show peristaltic contractions passing from before backwards. The contractions start at the base of the caudal papilla about the third thoracic segment, where the circular gut mesoderm is complete, and first appear at a stage just later than fig. 3, C. Contractions pass backwards throughout the region where gut mesoderm is developed, but not beyond. Thus fig. 21, *c*, shows the gut mesoderm formed only between thoracic segments three and seven (somites as far as the fourth abdominal have been formed), and in life the peristaltic contractions did not occur beyond the sixth thoracic segment. As new somites are formed posteriorly, so movements of the intestine extend backwards. In Table I it is seen that peristalsis never continues backwards through the most posterior and youngest somites (about five in number), where the circular gut mesodermal bands are not yet developed, fig. 21, *c*, and does not occur in the anterior region where the yolk sac is devoid of mesoderm. The contractions of the intestine are circular, but are most apparent on the ventral and lateral sides. At first they are slow and irregular, but later take place fairly regularly at a frequency of 6–10 contractions in 10 seconds, each wave of contraction taking about 6 seconds to pass down the intestine. From three to six contractions can be seen at once

TABLE I.

Stage of embryo.	Most posterior segment visible externally.	Most posterior mesodermal somite formed.	Yolk sac movement.
Unhatched— Fig. 3, C	7th thoracic	8th thoracic	No movement.
Fig. 3, C	8th thoracic	2nd abdominal	Hardly perceptible peristalsis from thoracic 3 to thoracic 5.
Fig. 3, D	2nd abdominal	7th abdominal	Peristalsis from thoracic 3 to thoracic 6.
Fig. 3, D	3rd abdominal	7th abdominal	Peristalsis from thoracic 3 to thoracic 8.
Fig. 3, E	6th abdominal	7th abdominal	Peristalsis from thoracic 3 to abdominal 5. Three or four waves along intestine at once.
Hatched— Fig. 4, G	7th abdominal	7th abdominal	Peristalsis from thoracic 3 to posterior end of intestine. Five or six waves along intestine at once.
1st cuticle shed— Fig. 4, I	7th abdominal	7th abdominal	Peristalsis from thoracic 1 to posterior end of intestine.
2nd cuticle shed— Fig. 5, K	7th abdominal	7th abdominal	No peristalsis, only local contractions.
Free-swimming young adult	7th abdominal	7th abdominal	No peristalsis.

passing down the intestine at a rate of about 0·067 mm. per second. Three such contractions are indicated opposite *X* in fig. 3, D. (In fig. 3, E, the gut is for the moment still and in a constricted condition.) After hatching peristalsis continues as before (see Table I and fig. 4, *X*), and extends along the whole length of the intestine, including the anterior part between the liver lobes, fig. 4, I. In the last embryonic stage, fig. 5, peristalsis gradually stops, only a few local twitches occurring. When the young animal first becomes free-swimming the intestine appears to be still, but in older animals movements, if present, are not clearly seen owing to the investment of the viscera by the fat body.

The peristaltic contractions of the embryonic gut are doubtless associated with yolk absorption. When the yolk sac is first formed, the contained yolk appears to be composed of a mass of droplets and to be fairly stiff in consistency. When the intestine is differentiated, its yolky contents differ from that of the rest of the yolk sac in being homogeneous and more fluid. The peristaltic contractions at the base of the caudal papilla appear to " bite " off portions of the stiff yolk from the cephalo-thoracic yolk sac, and to carry portions so separated backwards into the intestine. Here they appear as orange droplets floating in the pale yellow fluid contents of the gut, and are continually moved about by peristalsis. The droplets decrease in size, presumably becoming liquified, and finally disappear. Yolk is taken into the intestine in this manner a little before hatching and throughout later stages until it is all absorbed. No movement of the liver appears to take place in the embryo, although it is provided with circular muscles (figs. 12, *b*, and 13, *c*, *l.c.m.*).

Difficulty was at first experienced in detecting the mesodermal investment of the embryonic gut, and it was questionable whether the peristalsis was muscular in origin or was due to the contraction of the endothelial cells themselves. Variations in the technique of fixing, etc. (see p. 191), later showed an embryonic gut mesoderm consisting of minute circular bands about 1·7 μ wide and 2·5 μ apart, in which no fibrils could be detected. Peristalsis of the intestine only occurs where these mesodermal bands are developed. It is thus probable that the peristalsis is due to the contractions of these minute mesodermal bands.

The reactions of chloretone and KCl on the peristalsis of the yolk sac were investigated in order to determine whether this movement was of muscular origin or not. Families of embryos were divided up and placed in solutions of chloretone in sea water of various concentrations, and in mixtures of isotonic KCl in sea water in different proportions, some embryos being reserved as controls. The latter will live quite well for several hours in water in a watch glass. The embryos were examined every few minutes and the effects on the peristalsis noted. The results are tabulated in a condensed form in Table II. The younger embryos are more susceptible to both reagents than the older ones. Chloretone in 0·05% has little effect on peristalsis, while 0·25%–0·5% reduces or inhibits it. Isotonic KCl in sea water in concentrations above 10% causes permanent contraction, while 2% concentration either has little effect, or in a few

TABLE II.

Chloretone.	Effects on peristalsis.		
	Unhatched embryos fig. 3, D–E.	Hatched embryos fig. 4, G–H.	Embryo after first ecdysis, fig. 4, I.
0·05%	Slight inhibition. Effect wears off after 18 minutes.	Almost no effect.	No effect.
0·1%	Reduced to pulsations at base of caudal papilla.	Feebler and slower pulsations, may reach posterior end along ventral side only. Effect wears off after 20 minutes.	No effect.
0·25%	Reduced to pulsations at base of papilla, stopping intermittently.	Feebler pulsations at base of papilla. Effect wears off after 30 minutes.	Peristalsis feeble at first, recovering in 20–40 minutes.
0·5%	Stops.	Stops. Effect wears off after 60–80 minutes.	Peristalsis feeble and infrequent. Effect wears off after 50 minutes.
1·0%	Stops.	Stops.	Stops.
KCl (isotonic).			
2·0%	Intermittently stops, and pulsates at variable frequencies. After 40 minutes frequency greater than normal.	—	No effect.
10·0%	Stops, but contractions may occur and pass either forwards or backwards.	—	Stops in extreme contraction.
25·0%	Stops in extreme contraction.	—	Stops in extreme contraction.

young embryos caused an acceleration of the rate 40 minutes after immersion in the solution. Such reactions are typical of muscular action and unlike amœboid movement. Typical rhythmic muscle is accelerated by 2% isotonic KCl and goes into permanent contraction in 10–25% solutions, while amœboid movement continues in a 50% solution. Further, the acceleration effect is also paralleled by rhythmic muscle, such as that in the heart, whereas in amœboid movement potassium, in some cases at least, has been shown to possess no such action. Peristalsis thus appears to be due to the muscular contraction of the minute mesodermal bands round the yolk sac. The reactions to chloretone bear out the above conclusion.

Conduction of the impulse from one circular band to the next cannot be under nervous control, as the ventral ectoderm is undifferentiated when peristalsis first takes place. Fig. 21, *c*4, shows a section through a region in which peristalsis occurs, and the nerve cord rudiment is represented by two or three ectodermal cells on either side, *n.c.* The circular bands of mesoderm round the yolk sac are united longitudinally by a lateral strand of mesodermal cells (see p. 191 and fig. 21, *c*, and *c*4, *g.s.*). Presumably the impulse for contraction is transmitted from one circular band to the next by these lateral strands, or the contraction of one band may directly stimulate the next one beyond it to contract. Whether the circular bands and the lateral strands of cells form a syncytium could not be determined. Cell boundaries, if present, are not detectable. Comparison may perhaps be made with the syncytial heart muscle of the frog, for example, which can carry out rhythmic contractions under no nervous control. However, the rate of conduction of the impulse along the yolk sac circular bands in *Nebalia* is very slow, absolutely, compared with that of grosser muscular structures, and is almost of the same order as ciliary movement conduction. At the end of development when peristalsis of the type described above ceases, the circular mesodermal bands round the gut become fibrillar and striated (see p. 192). Possibly the independent embryonic mechanism of peristalsis is then changed over to that of movement under nervous control in the adult.

FURTHER DEVELOPMENT OF THE MESODERM.

The origin of (1) the preantennulary mesoderm, (2) the head band mesoderm, and (3) the teloblastic trunk mesoderm has been described above, pp. 177–180.

Preantennulary Mesoderm.

These somites in early stages are often difficult to distinguish from the optic and cerebral rudiments in the ectoderm, as they lie closely pressed against the latter and they also remain solid, developing no cœlomic cavities during early stages. Similar but less acute difficulties in following the early growth of these somites was experienced with *Hemimysis* (MANTON, 1928, *a*), before their cœlomic cavities appear. Figures of the preantennulary somites are here given on fig. 23, Plate 25, showing a few sections from an extensive series. These may be compared with the whole embryos shown in figs. 3 and 4, and the diagrammatic sagittal views in fig. 6. These figures may also be compared with those given for *Hemimysis*, MANTON (1928, *a*), Plate 24 and figs. 12–14.

The formation of the preantennulary somites by immigration from the germinal disk (see p. 180 and fig. 18, *b* and *c*, and fig. 20, *d*1) is of short duration, and the end of the process is seen in fig. 23, *a*, a parasagittal section showing the preantennulary mesoderm anterior to and separate from the antennulary somite. The hinder parts of the preantennulary somites then grow backwards through the antennulary segment to reach the stomodœum and labral rudiments as soon as these appear, fig. 23, *b*, *p.m.s.*

The somites may also touch the antennulary mesoderm laterally, fig. 19, *e*. With the approximation of the arms of the V-shaped germinal band the anterior parts of these somites, *p.m.a.*, come closer together, the hæmocœlic space situated between them being the cavity of the future anterior aorta. In this space free rounded mesodermal cells are found which form the future leucocytes, fig. 23, *c*, *le*. During the growth of the unhatched embryo little further change occurs. The preantennulary somites remain solid, the posterior parts, *p.m.s.*, investing the stomodœum and supplying the labrum,* and the anterior parts, *p.m.a.*, lying internal to the cerebral rudiment, the pair being separated by the anterior aorta space (compare fig. 23, *b*, *d*, and *e*, with fig. 6, *a*, *p.m.*).

On hatching, the anterior ends of the preantennulary somites grow forwards over the cerebral rudiment, and up the front of the body on either side of the rudimentary rostrum as two solid strands, fig. 23, *e*, *p.m.a.* They can often be seen in the living transparent embryo, fig. 4, F, *p.m.*, where the anterior aorta space between them is also visible, *a.a.* The ectodermal dorsal organ (see p. 176) absorbs more and more of the surplus ectodermal cells as the yolk sac shrinks, and the anterior ends of the preantennulary somites finally become inserted on the anterior edge of the dorsal organ above the rostrum, fig. 6, *b*, and fig. 23, *f*. The anterior aorta space is at first much compressed antero-posteriorly between the anterior body wall and the yolk sac, fig. 23, *e*, and fig. 4, F and G. As the preantennulary strands grow forwards and upwards, so they come closer together, and the definitive walls of the anterior aorta are differentiated between them, fig. 23, *f* and *f*1, and the cavity of the vessel opens out. At the same time the preantennulary strands indent the yolk sac anteriorly in the middle line, fig. 4, H, I, and J, leaving two lobes of the yolk sac, the future cephalic liver diverticula, *l.a.*, on either side. The shrinking dorsal organ draws the upper ends of the preantennulary strands backwards along the dorsal side of the body, so deepening the furrow on the yolk sac. Finally, the strands pass back through the mandibular segment above the stomodœum, where they unite with the anterior end of the dorsal blood vessel (see p. 195) formed by the maxillary and first thoracic somites, fig. 4, I. Thus the anterior aorta reaches the heart, and a valve develops at the junction of these two structures towards the end of embryonic life, fig. 5 and p. 195. Stomodœal muscles are developed from the outer parts of these strands after the aorta walls are formed, but they have not been followed in detail.

Towards the end of development the original postero-ventral parts of the preantennulary somites which invest the stomodœum develop a pair of cavities on either side of the stomach just behind the œsophagus, fig. 23, *f*1, *p.m.c.* In origin and position these cavities exactly resemble the " late formed preantennulary cœlomic cavities " of *Hemimysis* seen in MANTON'S (1928, *a*) Plate 24, fig. 27, *p.a.m.*, *c*2 and text-fig. 3, *i*,

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* The development of the labral mesoderm has not been followed in detail. It appears to be formed mainly from the preantennulary somites, fig. 23, *b*, Plate 25, but at this stage the preantennulary mesoderm may touch the head band mesoderm laterally, so that a precise statement is impossible.

" ventral preantennulary cavity." However, their appearance here is transitory, and they rapidly become obliterated. The musculature of the stomodœum, etc., derived from the preantennulary somites has not been followed in detail.

Trunk Mesoderm.

The formation from the teloblasts of the mesoderm of segments between the mandibles and telson has been followed (p. 179) to a stage when each segment is represented in the first place by eight mesodermal cells descended from the mesodermal teloblasts and nineteen ectodermal cells descended from the ectodermal teloblasts. These cells form a ring around the caudal papilla, fig. 21, *b* and *c*, except in segments anterior to the third thoracic, where only the ventral part of the cephalo-thorax is segmented and teloblastic in origin.

Early Development of a Trunk Somite, Formation of Gut Musculature, etc.—The development of a somite in the caudal papilla will first be described, as this may be taken as typical for the whole trunk region. Development takes place progressively from before backwards along the caudal papilla. The ectodermal cells descended from teloblasts soon divide transversely to the papilla, so forming two rows of cells in each segment. The cells shift their positions slightly, so that they lie in longitudinal zig-zag lines. Subsequent divisions become irregular; nineteen cells are still seen round the body in fig. 21, *c*3, while in *c*4, a larger number is apparent, together with the rudiment of the paired nerve cord, *n.c.* The eight mesodermal descendants, lying at first in a ring, divide tangentially to the papilla, and shift, forming two lateral groups of eight cells, fig. 21, *c*3, *ab.2.m.*, fig. *b*, *th.7.m.*, and fig. *c*, *ab.2.m.* These groups are the paired segmental somites, which by further cell division become solid blocks, fig. 21, *b* and *c*, anterior segments. The caudal papilla is somewhat flattened dorso-ventrally by pressure from the vitelline membrane, fig. 22, *a* and *b*, and the large hæmocœlic spaces between the somites seen mid-dorsally and ventrally in fig. 21, *c*3 and *c*4, are only extensive when the papilla has been fixed separately, so that this pressure is removed. With the growth in length of the papilla, by the formation of more segments and the posterior extension of the yolk sac, the somites come to lie at the side of the intestine, *en.*, instead of beside the proctodœum, fig. 21, *c*.

The first development from a somite occurs as soon as it reaches the intestine. A strand of tissue, *g.s.*, grows out towards the upper part of the intestine, fig. 21, *c* and *c*4, and cells from this strand spread out investing it. The strand is continuous from one somite to the next on the same side of the body, but the mesoderm encircling the intestine appears first as two or three narrow bands, separate from each other, in every segment. These circular bands of mesoderm (1) give rise dorsally to the floor of the dorsal blood vessel (heart and posterior aorta); usually one nucleus lies mid-dorsally in each band above the intestine, fig. 21, *c*4, *h.f.*; and (2) form minute circular muscles around the intestine. The presence of the latter could only be determined in detail after dissection of the caudal papilla from the vitelline membrane and the rest of the embryo prior to fixation. These muscle bands are about 1·7 μ wide, with gaps of 2·5 μ between them, fig. 21, *c*, *g.m.** They are present anteriorly as far as the base of the caudal papilla in the third thoracic segment; that is, up to the spherical part of the yolk sac where the somites lie ventrally below it. No fibrils or striations are visible in these circular bands at this stage. In the adult they become typical striated muscles about 2·5 μ wide and 1·3 μ apart. From their earliest appearance these circular bands of mesoderm are contractile (see p. 185).

Soon after the formation of the floor of the dorsal blood vessel and gut musculature, each somite divides into a larger dorsal portion associated with the strand, *g.s.*, and a smaller ventral portion, fig. 22, *a*, *d.m.* and *v.m.* Cells from successive blocks of ventral mesoderm elongate and unite to form the ventral longitudinal muscle, as in *Hemimysis*, *Estheria*, etc. When the limb rudiments appear in each segment as lateral ectodermal outgrowths, fig. 22, *b*, *c*, and *d*, the dorsal mesoderm spreads ventro-laterally to form the future base of the pericardial floor, *p.b.*, and the limb mesoderm, *l.m.* The floor of the dorsal blood vessel soon becomes a continuous structure longitudinally, and is now a delicate strand connecting the dorsal mesoderm on either side in each segment. The upper parts of the dorsal mesoderm in successive segments unite and become characterized by smaller nuclei, fig. 22, *b*. The dorsal longitudinal muscle, *d.l.m.*, is formed from the outer part of this mesoderm, while its further upgrowth forms the lateral walls of the dorsal vessel by the upper ends of the somites becoming U-shaped, fig. 22, *c* and *d*.

On hatching from the vitelline membrane and the removal of the pressure caused by the latter, a considerable swelling of the body occurs, and the dorsal vessel, previously almost a virtual space in many embryos, enlarges as seen in fig. 22, *d*, and the dorsal longitudinal muscle rudiment lies at its side. A cœlomic space opens out in the dorsal mesoderm below the longitudinal muscle, fig. 22, *d*, *th.*6.*c.* Traces of this space are sometimes detectable in a rudimentary state before hatching. The cœlomic cavity rapidly expands and may be extensive, as in fig. 22, *e*, *ab.*1.*c.*, where the intestine is constricted at this point. The dorsal longitudinal muscle rudiment separates from the outer wall of the cœlomic cavity; and the dorsal vessel is gradually completed by the upgrowth and ingrowth of the outer arm of the U-shaped ends of the somites. A supporting strand from the side of the vessel to the ectoderm is left as the dorsal longitudinal muscle separates, fig. 22, *f*, *h.a.* The remainder of the dorsal mesoderm now forms the pericardial floor, which extends from the vessel to the limb base segmentally, and to the lateral body wall intersegmentally, fig. 12, *a*, *p.c.f.*, right-hand side, as in *Hemimysis* (MANTON, 1928, *a*, fig. 15, *a* and *f*). The cœlomic cavity becomes smaller and lies in the upper horizontal part of the pericardial floor, where it finally disappears by the approximation of its walls. No cavity appears in the base of the pericardial

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* These circular gut muscles are not readily seen in embryos fixed whole, such as in most of those figured on fig. 22, Plate 24, etc.

floor at any stage. Lateral blood vessels are left external to the segmental bases of the pericardial floor, and they carry blood from the limbs into the pericardial space, fig. 12, *a*, *p.c.f.*, *l.v.*, left-hand side.

Early Development of Anterior Post-oral Somites.—The growth of the somites in front of the caudal papilla and of the seventh abdominal segment differ slightly from the above. Owing to the abundance of yolk in the anterior region of the body, the somites from the maxillulary to the third thoracic segment are at first restricted in position to the ventral side of the body. The maxillulary somite remains ventral in position at all times. The maxillary and first few thoracic somites grow round the yolk sac, just as do all the somites in *Hemimysis* (MANTON, 1928, *a*, text-fig. 32). The pressure of the yolk sac compresses this mesoderm considerably between the body wall and endoderm, and no cœlomic cavity has been seen anterior to the third thoracic segment. The maxillary and first few thoracic somites gradually reach the dorsal side of the body and develop essentially as do the other somites, but the formation of the dorsal blood vessel is necessarily retarded until the upgrowth is completed.

Seventh Abdominal Somite.—The growth of the seventh abdominal somites differ slightly from those of the trunk region, owing to the absence of paired limbs on this segment and to the extensive development of musculature round the proctodœum. After gastrulation has ceased the teloblasts lie in a ring round the proctodœum, fig. 21, *a*, *b*, and *c*, but with the growth of the telson from the unsegmented region behind the teloblasts (see p. 176), the latter shift anteriorly so that the seventh abdominal somites formed by the disappearing teloblasts lie at the junction of the proctodœum and intestine. A strand grows out to the intestine, fig. 24, *a*, *g.s.*, Plate 26, as in other segments, but it is here much more massive, and gives rise to a thick investment, *g.m.*, *ab.* 7, round the junction of the proctodœum and intestine. The dorsal mesoderm then separates more or less completely from the ventral block which forms the ventral longitudinal muscle, but no block corresponding to the limb mesoderm is formed; compare fig. 22, *b*, with fig. 24, *a*. The posterior end of the dorsal vessel is formed from the upper ends of the dorsal mesoderm, but the walls and roof are late in appearing, so that the somite does not appear U-shaped dorsally, fig. 24, *b*. Traces of a cœlomic space in the dorsal mesoderm can be seen occasionally, but are soon obliterated. The thick layer of mesoderm surrounding the gut spreads backwards, touching the telson mesoderm (see p. 194) round the proctodœum, and its further development will be considered with that of the telson mesoderm below.

Telson Mesoderm.—The origin of the telson mesoderm has been described above (p. 179) as a few cells which immigrate inwards from the blastoporal area and remain posterior to the teloblasts, fig. 20, *h* and *h*1, *t.m.* When the proctodœum appears these cells form two groups on either side of it, lying behind and within the mesodermal teloblasts, fig. 21, *b* and *c*1, *t.m.* These telson mesoderm cells may extend anteriorly along the whole length of the proctodœum before hatching, but usually they are quite separate from the anterior strand, *g.s.*, growing out from the somites to the intestine.

The ectodermal outgrowths forming the caudal furca lie on either side of the anus, and into these wander some of the telson mesoderm cells, fig. 21, *c*2, *t.m.*, forming a core up the middle of the developing furcal rami. The rest of the telson mesoderm forms an investment to the proctodœum and the rudiments of muscles in the telson. After hatching, when the seventh abdominal somites have differentiated into their various parts, the seventh abdominal mesoderm round the anterior end of the proctodœum, fig. 24, *b*, becomes continuous with the non-segmental telson mesoderm round the posterior part of the proctodœum. From this proctodœal investment, cells extend outwards to the ectoderm laterally, dorsally, and ventrally, to give the proctodœal dilator muscle rudiments, some of which are seen at the anterior end of the proctodœum in fig. 24, *c*. These muscles are thus derived partly from the telson mesoderm and partly from the seventh abdominal somites.

Liver Mesoderm.—The mesodermal investment of the posterior liver lobes is derived from cells early separating from the maxillary and first thoracic somites, but mainly from the former. After hatching, a few cells shift from the dorsal part of these somites up the sides of the body, and gradually form a fairly compact mass internal to the carapace fold and outside the yolk sac, fig. 8, *a*, *l.p.m.* The yolk sac here thickens, and forms the liver diverticulum (see p. 183), and these mesodermal cells then spread over the latter, fig. 8, *b*, *l.p.m.*, to form a thick cap over its distal end, and a thinner investment elsewhere. As each liver lobe grows backwards along the sides of the body, the cap of mesoderm is carried with it, and so the whole lobe is supplied with mesoderm, fig. 8, *c*, *l.p.m.*, and 12, *a*. From this investment striated circular muscles are formed in the adult. These muscles are similar to the intestinal muscles, but are less frequent and slightly smaller in size, being about 1·7 μ wide and 10·2 μ apart, figs. 12, *b*, and 13, *c*, *l.c.m.* Somites other than those mentioned above do not appear to contribute to the liver mesoderm.

Fat Body.—The formation of the adult fat body, in which the alimentary canal, liver, and gonads lie embedded, starts towards the end of embryonic life. Cells from the ventral side of the horizontal part of the pericardial floor separate from the latter, the cytoplasm becoming swollen, and fill in the interstices between the pair of liver lobes, the intestine and pericardial floor, fig. 12, *a*, *f.b.* This process continues, the cells becoming more and more swollen as they surround the viscera, fig. 12, *b* : the magnification is the same as that of 12, *a*. The fat body is not a solid structure, but the component cells are separated by a network of fine vascular spaces. These spaces are fed by paired segmental vessels from the heart (see p. 196), and open into small sinuses surrounding the ovary, liver, etc., and communicate with the general body hæmocœl by numerous pores between the fat body cells, fig. 12, *b*, *b.v.*, and *b.v.h.*

Heart and Vascular System.—The growth of a typical trunk somite to form a section of the dorsal vessel and pericardial floor has already been described (p. 191). All thoracic and abdominal and probably the maxillary somites participate in the formation of the dorsal vessel, and its posterior end is formed by the seventh abdominal somites.

Throughout the body the ventral wall of the vessel appears first, fig. 22, *a-d*, and later the sides and roof are formed by the growth of the U-shaped upper ends of the somites, fig. 22, *e* and *f*, and fig. 12, *a*. This process proceeds from before backwards, and essentially resembles that described for *Hemimysis* (compare MANTON, 1928, *a*, text-fig. 15, and Plate 23, figs. 17 and 18). The small amount of yolk in the trunk region results in much less compression of the mesoderm, and hence the cavity of the vessel appears early, and the upper ends of the somites are U-shaped and do not have to grow upwards round the yolk. However, the bulk of yolk lying in the head region, as mentioned above, delays the formation of the anterior end of the vessel in front of the third thoracic segment. Here the somites are forced to grow a considerable distance round the yolk sac in order to reach the dorsal side, as occurs along the whole trunk in *Hemimysis*. The anterior end of the dorsal vessel, when formed, grows forwards above the yolk sac towards the hinder end of the dorsal organ during the latter part of embryonic development. The formation of the anterior aorta from the preantennulary somites has been described above (p. 190). The back-growing dorsal organ brings the anterior aorta to the dorsal vessel above the stomodœum, where the two unite, figs. 4, I, and 5. The heart proper is then developed from the dorsal vessel, and extends from the anterior aorta to the middle of the fourth abdominal segment. Behind the heart the dorsal vessel remains thin-walled and becomes the posterior aorta, and the pericardial floor here breaks down or becomes indistinguishable from the outer side of the fat body. The anterior aorta also remains thin-walled. The heart walls thicken. A middle layer of cells develop circular fibrils on their outer sides, fig. 10, *a*, *h.m.*; an outer covering of connective tissue cells surrounds the heart, and a very thin endothelium of flattened cells lines it. Arteries are developed draining the heart, ostia are formed leading into it, and valves appear at all these openings.

The ostia only arise at the very end of embryonic life, and the most anterior of the three anterior lateral pairs described by CLAUS are not present in small adults. The venous valves of the dorsal and lateral ostia, fig. 5, are all of the same type, fig. 10, *a*. They are formed by a pair of thick nucleated flaps with thin attachments to the heart wall. They are directed inwards so that they allow free passage of blood into the heart cavity, but will be forced together on contraction of the heart. Fibrils, if present in the valves, have not been seen in the young adult.

Arterial valves at the base of arteries leaving the heart are also formed by paired flaps. They are, however, thin with one nucleus in each flap. Only the extreme free edge of the flap is thickened, and fibrils but no nuclei lie in this edge, which is turned away from the heart cavity and extends a short distance down the artery. Such valves are found at the origins of the anterior and posterior aortæ, fig. 10, *b*.

The further course of the anterior and posterior aortæ have been briefly described by CLAUS and others and will not be mentioned further. Other arteries leaving the heart, however, do not appear to have been recorded. From the ventro-lateral angles of the heart in the segments which have formed it arise paired vessels which pass ventro-

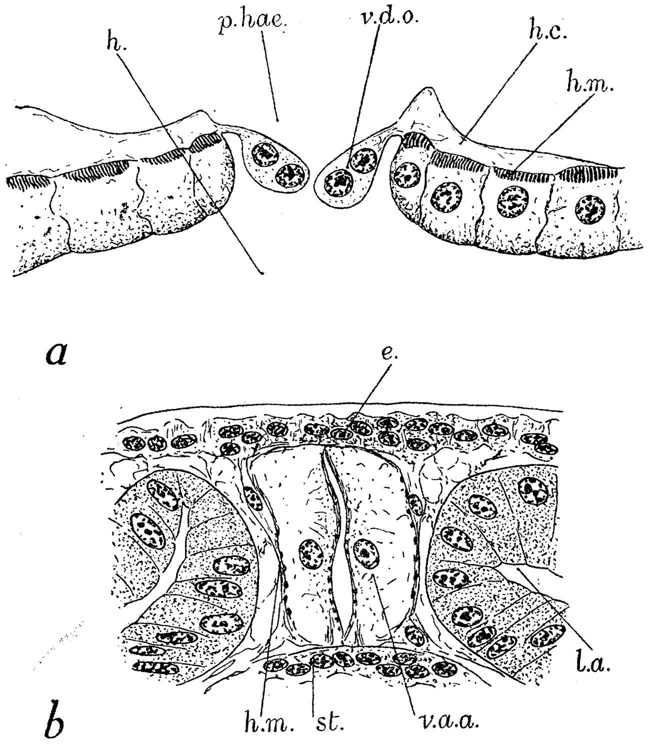


FIG. 10.—Sections of small adults showing valves of the heart.

(*a*) Sagittal section showing a typical venous ostium leading into the heart (second dorsal ostium). The valves of the ostium are cut transversely. The inner endothelium of the heart tube and the nuclei of the outer connective tissue layer, *h.c.*, are not seen in the section. × 730 approx.

(*b*) Transverse section showing typical arterial valves leading from the heart, seen in surface view (valves between heart and anterior aorta). The inner edges of the two valves, *v.a.a.*, are directed forwards into the aortic cavity, and are continued in the next anterior sections. These inner edges are thickened and fibrillar. *h.*, cavity of heart. *e.*, dorsal ectoderm. *h.c.*, connective tissue layer on outer side of heart. *h.m.*, circular muscle fibrils of heart wall. *l.a.*, anterior liver lobe. *p.hæ.*, pericardial hæmocœl. *st.*, wall of stomach. *v.a.a.*, arterial valve between heart and anterior aorta. *v.d.o.*, venous valve between pericardium and heart (second dorsal ostium).

laterally to the fat body. The openings of these vessels are indicated in fig. 5, *f.a.*, and are seen in transverse section in fig. 11, *a*, *b.v.s.* They are guarded by small longitudinal valves of the arterial type, but no fibrils have been seen in them, fig. 11, *b*, *v.b.v.s.* These vessels lead into channels between the fat body cells and communicate directly with a peri-intestinal vascular space and with similar spaces round the gonads. Anteriorly these vessels pass out sideways to the gonad sinuses, while posteriorly the main channel appears to run ventrally to the intestinal sinus. Some sections show the blood as a darkly staining precipitate, so rendering the lacunæ between the fat body cells very conspicuous. These lacunæ may be visible between every fat body cell in some parts, and they connect the peri-intestinal and genital spaces with similar vascular spaces around the liver, and finally discharge into the general body hæmocœle by pores between the fat body cells, fig. 12, *b*, *b.v.* and *b.v.h.*

Genital Rudiment.—The numbers of adult males and females are very unequal, the males being comparatively scarce. All the young adults sectioned show developing ovaries, and the sex of the late embryos and early free-swimming individuals is not apparent. The following account of the origin of the germ cells thus may only apply to the female, as no developing male has been sectioned, and it deals with the first appearance of the germ cells up to the formation of the immature ovary.

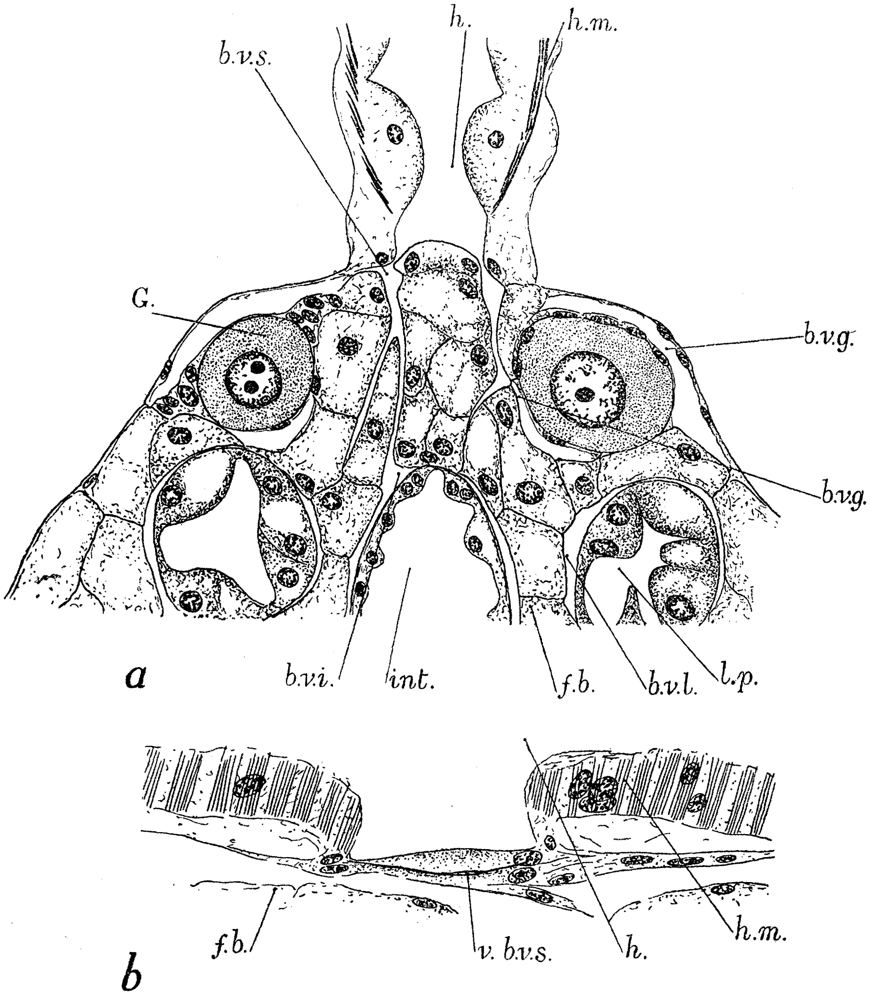


FIG. 11.—Sections showing segmental arteries leaving the heart, *h.*, in the small adult.

(*a*) Transverse section through the thorax showing the origin of one pair of segmental arteries, *b.v.s.*, leaving the heart to supply the fat body *f.b.*, and viscera. On the left one artery communicates with the peri-intestinal sinus, *b.v.i.*, and with spaces between the fat body cells. Vascular spaces can also be seen around the gonads, *b.v.g.*, and liver lobes, *b.v.l.*, and these are also fed by the segmental arteries.

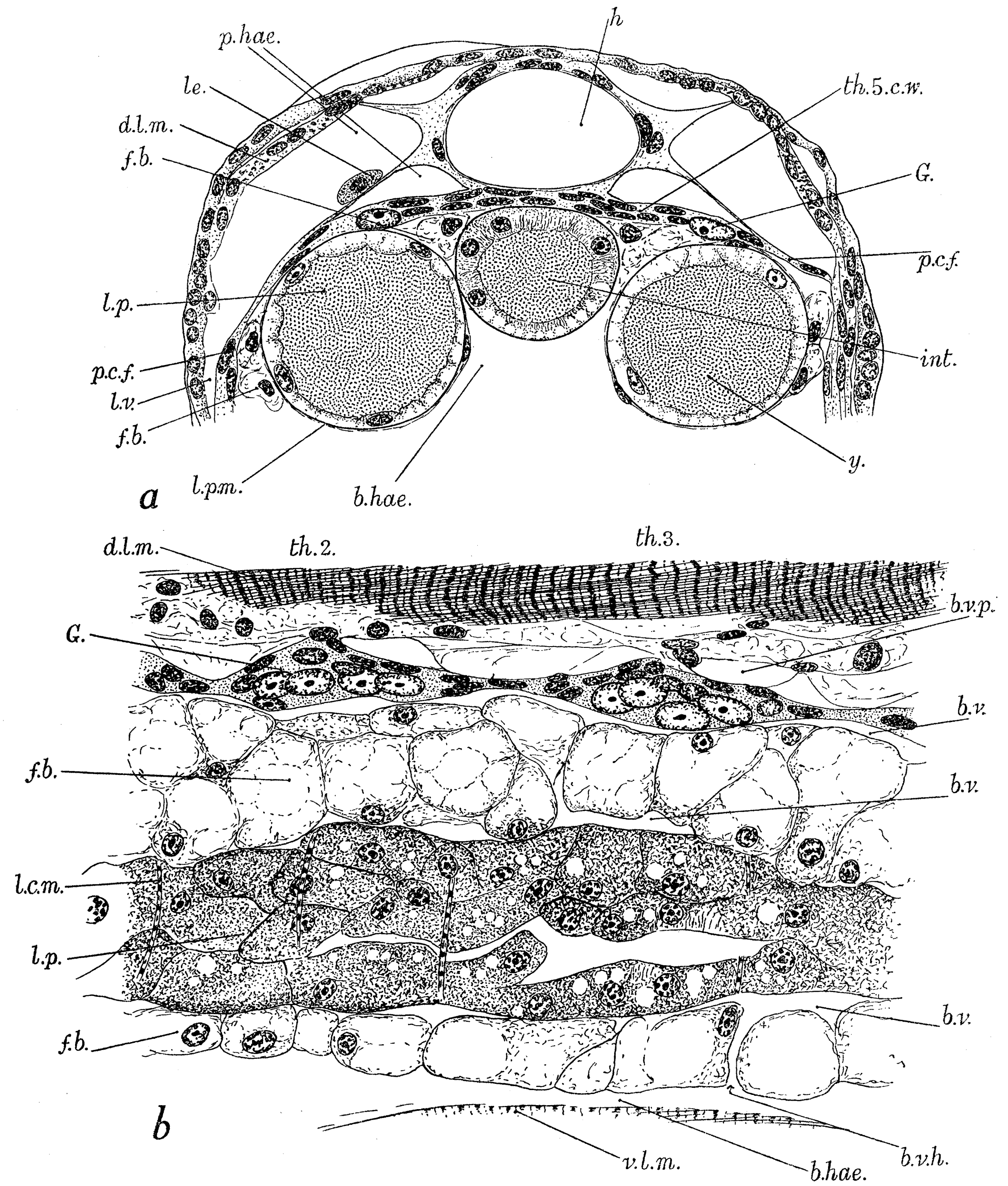
(*b*) Parasagittal section showing the valve, *v.b.v.s.*, between the segmental artery and the heart. × 730 approx.

The germ cells are not differentiated early, but appear as paired segmental gonad rudiments towards the end of embryonic development, when the dorsal blood vessel is formed and the second embryonic cuticle is about to be shed prior to the embryo leaving the brood pouch, fig. 4, I. These rudiments are differentiated segmentally from before backwards except in the anterior thoracic somites whose development is retarded by the presence of the yolk (see p. 193).

The germs cells are differentiated in the ventral walls of the cœlomic sacs in the pericardial floor. One pair of cells appears in the anterior part of each segment, lateral to the heart and above the liver lobes, fig. 22, *f*, *G*. Each germ cell gradually becomes distinguishable from the surrounding cells of the pericardial floor by the increasing size of both nucleus and cytoplasm. The former shows the chromatin in a more dispersed state, although a nucleus may be clear; thus the nucleus appears less densely staining. The earliest stage found shows one pair of germ cells in the fifth thoracic segment only, fig. 22, *f*; a slightly older embryo shows a pair in the fourth, fifth, and sixth thoracic segments, fig. 12, *a*. The cœlomic spaces have now been obliterated, and the germ cells lie in the solid pericardial floor. When the young adult leaves the brood pouch, germ cells may be present in all thoracic segments except the most anterior, and those germ cells which were formed earliest now divide, giving two pairs of cells in each segment, Table III, No. 9, xxiii. With increasing age, germ cells appear in the anterior abdominal segments also. Further division of the germ cells gives rise to paired groups of cells in each segment from the anterior part of the thorax to the middle of the abdomen, fig. 12, *b*. These groups are discontinuous in successive segments, and form thickenings in the pericardial floor. The germ cells are naked and freely exposed to the hæmocœl ventrally.

It could not be ascertained whether each group of germ cells developed entirely from division of the original single cell, or whether further germ cells are also differentiated directly from the pericardial floor in early stages. After about six germ cells are present in each rudiment, multiplication of germ cells appears to take place entirely by division of those already present.

When the animal is about 2·5 mm. long the segmental groups of germ cells have increased in size so as to become continuous from one segment to the next, forming the pair of gonads extending from the first thoracic to the sixth abdominal segment, and projecting ventrally from the pericardial floor. No germ cells arise anterior to the first thoracic or in the seventh abdominal segments. Whether separate rudiments are formed in the posterior part of the abdomen or whether the rudimentary gonad just spreads backwards into this region, as it does into the seventh abdominal segment could not be ascertained. In each segmental group of germ cells the smaller ones are seen to be in process of division, while one very large cell becomes differentiated as a future egg cell, fig. 13, *c*. With increasing size of the animal the number of large germ cells in each segment increases. They become tightly packed together in a longitudinal row in each ovary, fig. 13, *d*, so that the segmental appearance of the gonad is lost. The size of these large cells, once they are formed, remains constant until the animal becomes mature. In fig. 13, *c* and *d*, the large cells are about the same size whereas the individuals were 2·5 and 4 mm. long respectively.



FIGS. 12 and 13.—Sections of old embryos and young adults showing the development of the gonads, liver, and fat body. × 730 approx.

(*a*) Transverse section of an embryo older than fig. 4, I, and fig. 22, *f*, passing through the 5th thoracic segment. The liver diverticula, *l.p.*, have filled with yolk (compare fig. 22, *f*), and the intestine *int.*, has shrunk in diameter. The cells forming the mesodermal investment of the liver have started to enlarge in places to form the fat body, *f.b.* The cœlomic spaces in the pericardial floor have shrunk, vestiges being seen in the next posterior section. One pair of large cells lies in the pericardial floor, *p.c.f.*, on either side forming the genital rudiment of this segment, *G.* The section is slightly oblique so that on the left the pericardial floor is seen descending towards the limb base, but on the right it is uniting with the body wall near the intersegmental plane.

(*b*) Sagittal section of a small adult about 2 mm. long. The section passes through the dorsal longitudinal muscle, *d.l.m.*, above the longitudinal genital rudiment which lies in the pericardial floor, and below, the fat body, *f.b.*, surrounding the liver is cut. The enlarged genital rudiments, *G.*, of the second and third thoracic segments are seen. Vascular spaces, *b.v.*, surround the liver and permeate the fat body, and open to the general body hæmocœl by pores, *b.v.h.*

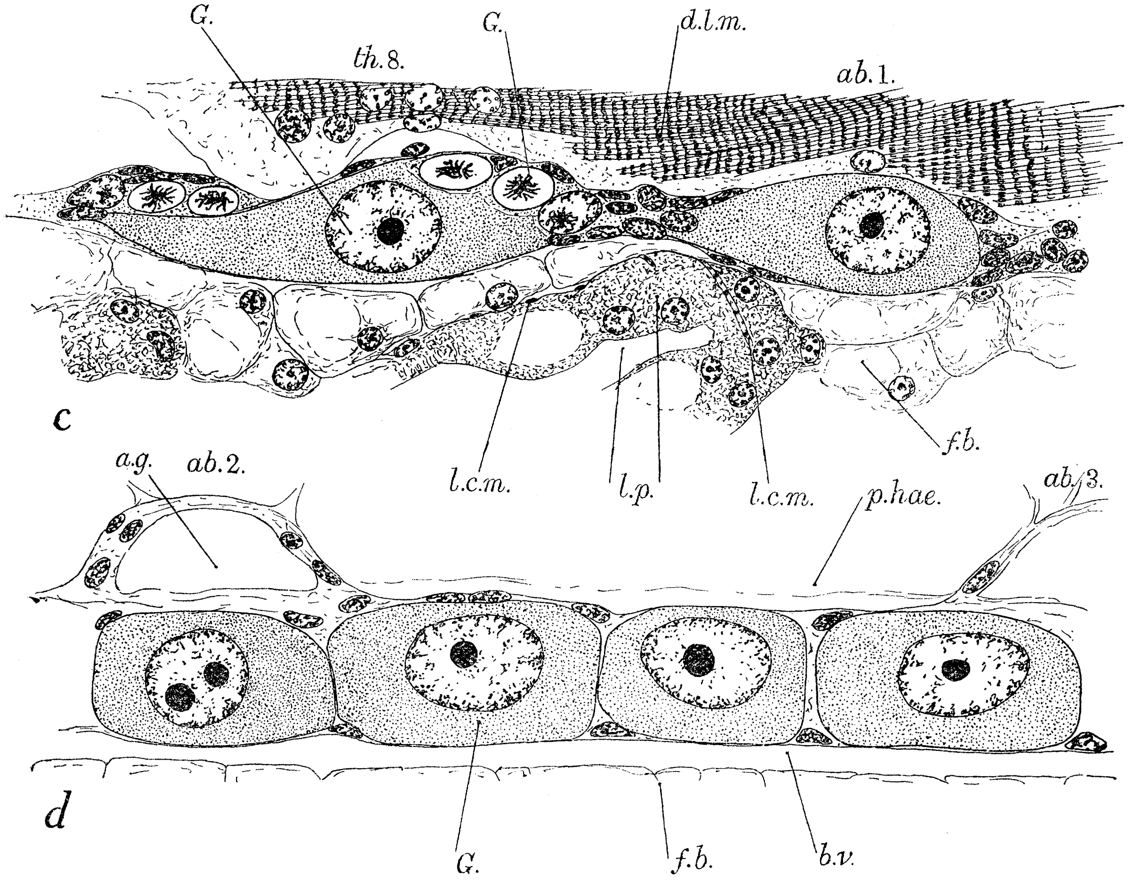


FIG. 13.—Continuation of fig. 12. × 730 approx.

(*c*) Frontal section of an adult about 2·5 mm. long, showing the genital rudiment, *G*, which is further enlarged. One large germ cell lies in each segment.

(*d*) Sagittal section of an adult about 4 mm. long showing the ovary, which is now of even diameter throughout and exhibits an even series of large germ cells.

As soon as the segmental genital rudiments become longitudinally continuous, a mesodermal investment grows round the germ cells from the pericardial floor, Table III. The paired gonads, so enclosed by mesoderm, become less closely associated with the pericardial floor, and lie below it, but loosely connected by the mesodermal investment, fig. 11, *a*.

When the animal is about 3 mm. long, the development of the oviduct starts. In the sixth thoracic segment the mesodermal investment of the gonad becomes much thickened on the outer side, and a solid outgrowth is formed which extends laterally, below the horizontal part of the pericardial floor. This outgrowth, which forms the oviduct, penetrates the pericardial floor where the latter turns down the side of the body. When the animal is about 4 mm. long the oviduct has grown down the pericardial floor to the limb base ; it becomes hollow and opens to the exterior on the inner side of the limb.

TABLE III.

Reference number of embryo or adult.	Thorax.								Abdomen.						
	1.	2.	3.	4.	5.	6.	7.	8.	1.	2.	3.	4.	5.	6.	7.
°8xviiiT.th.	—	—	—	—	1 pr. cells	—	—	—	—	—	—	—	—	—	—
^{v}°8xvii	—	—	—	1 pr. cells	1 pr. cells	1 pr. cells	—	—	—	—	—	—	—	—	—
°9xxiii	?	?	1 pr. cells	2 pr. cells	2 pr. cells	1 pr. cells	1 pr. cells	—	—	—	—	—	—	—	—
2 mm. adult . . . . Dub.T.thab.	—	G	G	G	G	G	G	G	G	G	G	G	—	—	—
2·5 mm. adult . . . . . . Dub.S.	G	G	G	G	G	G	G	G	G	G	G	—	—	—	—
2·6 mm. adult . . . . . . Dub.F.	G	G	G	G	G	G	G	G	G	G	G	G	G	G	—
3 mm. adult	—	—	G	G	G	G ov	G	G	G	G	G	G	G	G	—
4 mm. adult	?	G	G	G	G	G ov	G	G	G	G	G	G	G	G	—

Table showing the development of the ovary in late embryonic and young adult stages. In the embryos the genital rudiment is represented by one or two pairs of germ cells in a segment. In the early free-swimming stages groups of germ cells, *G*, lie segmentally. The enclosure of the rudiments, *G*, by a line indicates the formation of the mesodermal investment of the ovary, and " ov " represents the developing oviduct appearing in the sixth thoracic segment.

ENDOSKELETON AND ASSOCIATED MUSCULATURE.

In many details the musculature of *Nebalia* closely resembles that of *Hemimysis* and other Malacostraca, but a comparative and comprehensive account of the muscles of the adult *Nebalia* is here out of place and has not been attempted. The longitudinal muscles are formed much as in *Hemimysis*, and ectodermal muscles are also developed at the intersegments (see MANTON, 1928, *a*, p. 418). The growth of muscles will here be mentioned only in connection with their associated endoskeleton.

The component parts of the endoskeleton of the adult *Nebalia* are less varied than the structures found in *Hemimysis*. The latter were described under two categories (MANTON, 1928, *a*, p. 412) ; (1) the hollow maxillulary endoskeletal plate, and other tube-like ingrowths of an apodemal nature, which remain united with the outer cuticle ; and (2) segmental ectodermal bars or tendons, which become largely detached from the exoskeleton. Both these types of structure are present in *Nebalia*, the former being far simpler than in *Hemimysis*, while the latter are mainly responsible for the formation of the internal supporting structures.

In *Nebalia*, rod-like apodemal ingrowths from the outer cuticle homologous with those of *Hemimysis* are present. They occur in association with similar muscles, but tend to be smaller in size, and some are solid instead of hollow. For example, paired rods extending vertically upwards from the ventral ectoderm between the mandibles and maxillules are present in both, fig. 15, *e* (see CANNON and MANTON, 1927, *a*, text-fig. 2, *a*, *e* and MANTON, 1928, *a*, text-fig. 22, *e*, *e*). The large hollow maxillulary plate seen in *Hemimysis* is much reduced in *Nebalia*.

The bulk of the endoskeleton in *Nebalia* is formed from horizontal intersegmental ectodermal bars. These arise, as in *Hemimysis*, from lateral and ventral intuckings (see MANTON, 1928, *a*, text-fig. 23, *a* and *d*), which form horizontal bars at each intersegment, and lie between the developing ganglia of the nerve cord, fig. 6, *a*, *e.t.* These bars come to lie at the dorsal level of the nerve cord, and at first remain attached to the ectoderm both laterally and mid-ventrally, figs. 6, *b*, *e.t.* and *v.i.* and 14, *b*, *m.x.*1.*t.e.* These bars are fully formed and in their simplest state in the embryo on hatching. As in *Hemimysis*, one central nucleus lies in each bar in most segments until late in embryonic life, fig. 14, *a*. In the mandibular, maxillulary, and maxillary segments the bars are thicker, particularly in the middle where several nuclei are present, fig. 14, *a*. After hatching the relative positions of the components of the segments change. The upper part of the ganglia and the ectodermal bars sag backwards over the lower parts of the ganglia and limb bases, fig. 7. Thus the bars, which at first lie near the anterior borders of their respective segments, soon appear to be segmental instead of intersegmental in position, and in sections apparently lie in the middle or posterior part of their respective segments, fig. 14, *a*. The further development of these ectodermal bars will be considered individually.

The mandibular bar develops exactly as in *Hemimysis* (MANTON, 1928, *a*, p. 414, text-fig. 23, *a*, and Plate 24, fig. 27), and on sagging backwards to the middle of the mandibular segment forms the tendon of the mandibular adductor muscles. The rudiments of these muscles grow along the bar from the lateral mesodermal somites, fig. 14, *a*, the hindermost muscle strand growing along the bar and uniting with its fellow in the middle line, fig. 15, *t.m.a.*, as in *Hemimysis* (MANTON, 1928, *a*, Plate 24, fig. 27, *t.m.a.*). The lateral connection of the tendon to the ectoderm is lost, but the mid-ventral one remains throughout life, figs. 6, *b*, and 7, *f*. However, owing to the further intucking of the stomodœum and the oral cavity becoming more dorsally situated in the adult (compare figs. 6, *a* and *b*, and 7) this connection *f* finally extends from the tendon to the œsophagus in an anterior direction (see CLAUS, 1888, Plate 7, fig. 8, and compare *Hemimysis*, CANNON and MANTON, 1927, *a*, Plate 55, *f*). Upgrowths from the tendon on either side of the stomach become associated with muscle rudiments (see MANTON, 1928, *a*, Plate 24, fig. 27), and form the skeleton supporting the levator muscle of the

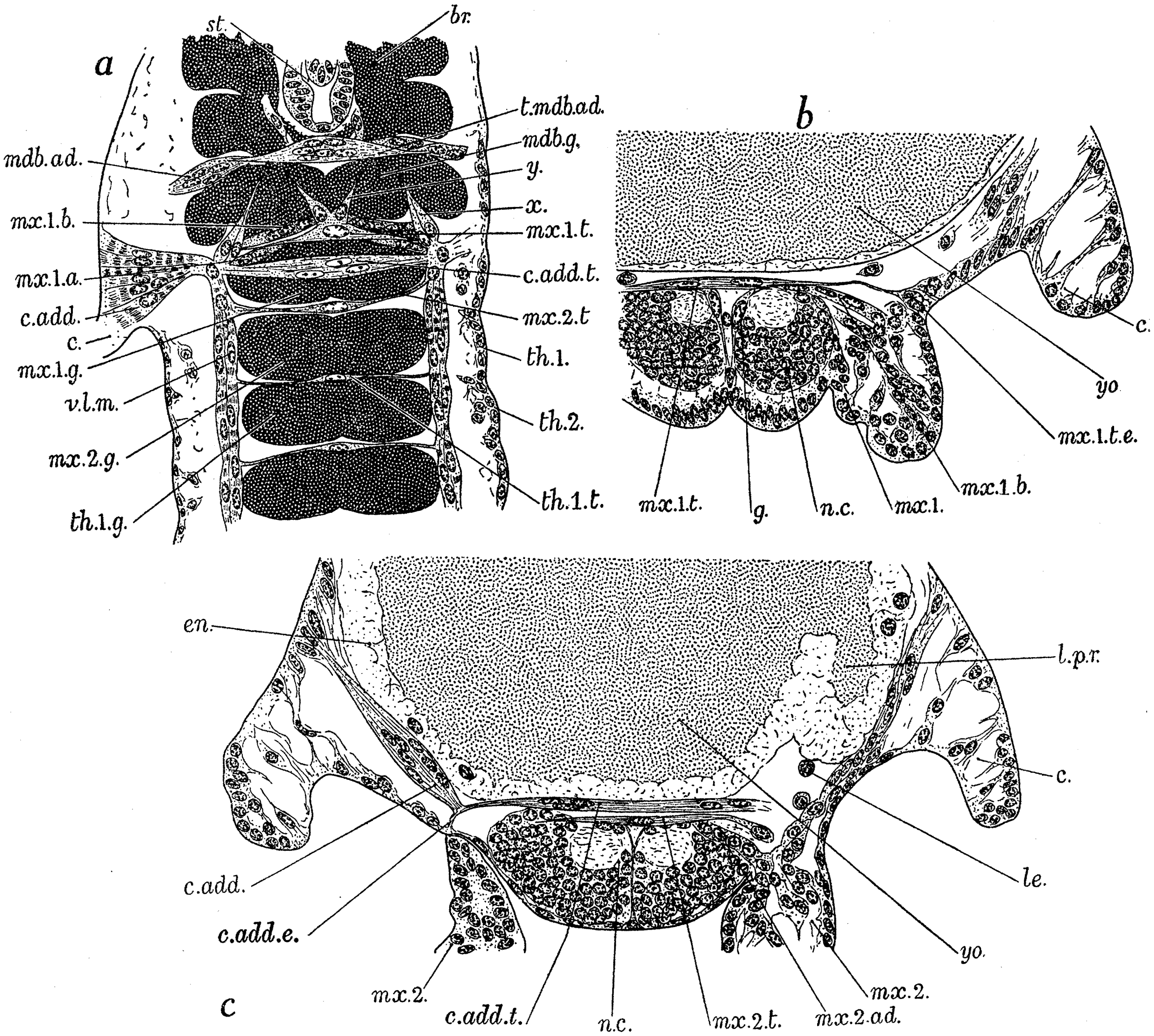


FIG. 14.—Sections of embryos showing the development of the endoskeleton. × 270 approx.

(*a*) Semi-diagrammatic figure based on three consecutive frontal sections of an embryo of about the age of that in fig. 4, I, showing the intersegmental ectodermal tendons and associated muscles for comparison with the adult, figs. 15 and 17, and with *Hemimysis*, MANTON, 1928, *a*, text-figs. 22 and 23. (N.B.—The curious relative positions of the lateral limits of the segments and of the ganglia, for example, *th.*1. and *th.*2.*g.*, will be understood after reference to fig. 7, where the lower part of *th.*4.*g.* is almost ventral to the upper part of *th.*3.*g.*, etc.)

(*b*) Transverse section of an embryo slightly younger than the last, passing through the anterior part of the maxillulary segment, and showing the ectodermal maxillulary bar attached laterally to the ectoderm at the junction of the maxillulary and mandibular segments, *mx.*1.*t.e.* Mid-ventrally the ectodermal connection *g.* forms the rudiment of the adult muscle in this position, fig. 7, *g.*, and mesodermal strands forming the rudiments of maxillulary adductor muscles are seen growing along the bar which will form the tendon between these muscles.

(*c*) Transverse section of an embryo about the same age as the last passing through the anterior edge of the maxilla on the left, and through the middle of the maxilla on the right. The upper anterior part of the maxillary bar is just separating off to form the tendon of the carapace adductor muscle, which retains the lateral intersegmental connection with the ectoderm, *c.add.e.* The maxillary mesodermal rudiment of the carapace adductor muscle is seen on the left attached to the tendon below and body-wall above (compare fig. 8, *a*), and on the right the developing maxillary adductor muscles are becoming associated with that part of the maxillary bar which remains as the tendon of the maxillary adductor muscles. *c.add.*, carapace adductor muscles. *c.add.t.*, tendon of carapace adductor muscles. *g.*, mid-ventral connection of maxillulary tendon to ectoderm. *l.p.r.*, posterior liver lobe rudiment. *le.*, leucocyte. *mdb.ad.*, mandibular adductor muscles. *mx.*1.*a.*, and *mx.*1.*b.*, posterior and anterior maxillulary adductor muscles (see fig. 15). *mx.*1.*t.*, maxillulary tendon. *mx.*2.*ad.*, maxillary adductor muscles. *mx.*2.*t.*, maxillary adductor muscle tendon. *t.mdb.ad.*, tendon of mandibular adductor muscles. *th.*1.*t.*, first thoracic ectodermal bar. *v.l.m.*, ventral longitudinal muscle. *x.*, strut between mandibular adductor tendon and carapace adductor tendon. *y.*, strut between mandibular adductor tendon and maxillulary adductor tendon. For key to further lettering see p. 230.

mandibles, fig. 15, *t.mdb.l.* The form of the mandibular endoskeleton in the mature adult is seen in fig. 17. The horizontal tendon of the adductor muscle lies below a thin transverse plate, *c.l.m.*, which unites the stout upper lateral parts of the mandibular skeleton. The latter join the adductor tendon below on either side, *l.m.md.b.*, and besides forming the skeleton for the levator muscles, *t.mbd.l.*, bear two other paired processes, one passes forwards and downwards to unite with the ventral ectoderm anterior to the mandibles, *a.*, and the other extends forwards and upwards along the sides of the stomach to the dorsal body-wall *b.*

Unlike *Hemimysis*, the maxillulary bar is large, fig. 14, *a* and *b*, *mx.*1.*t.* The mesodermal maxillulary muscle rudiments grow along the bar, fig. 14, *b*, *mx.*1.*b.* On its ventral surface are attached the anterior maxillulary muscles, fig. 14, *mx.*1.*b.* (and see Cannon, 1927, fig. 7), while a pair of posterior muscles, *mx.*1.*a.* grow along the developing bar and unite with one another in the middle line. The bar at first lies in the groove between the maxillulary and mandibular ganglia. Later it loses the nuclei, and in the adult becomes a large flat horizontal plate above the nerve cord, figs. 15 and 17. Two pairs of connections are formed by the tendon before the nuclei disappear. A pair of cells grow out from the middle portion and stretch forward above the nerve cord to the lateral part of the mandibular skeleton, fig. 14, *a*, *y.*, and form a pair of chitinous struts between the maxillulary and mandibular bars, fig. 15, Y. Laterally the maxillulary bar extends backwards and unites with that of the carapace adductor muscle (see below). The original mid-ventral connection of the maxillulary bar to the ectoderm, figs. 6 and 14, *b*, *g.*, persists in the adult. It divides into a smaller posterior and a larger anterior part. The latter forms a large median ectodermal muscle from the bar to the groove between the paragnaths, figs. 7 and 15, *g*, and with the shifting of the oral cavity (see above), finally extends from the bar antero-ventrally (see Claus, 1888, Plate 7, fig. 8, *M*). The smaller posterior part of this ventral connection remains as a chitinous strut, fig. 7, *s.*

The maxillary bar is also large. When the first embryonic cuticle is shed, fig. 4, I, the upper anterior part of the bar separates off from the rest, retains the lateral intersegmental connection to the ectoderm between the maxillary and maxillulary segments, and becomes the tendon of the carapace adductor muscles. This separation is just completed in the transverse section shown in fig. 14, *c*, *c.add.t.* and *c.add.e.* The carapace adductor tendon so formed shifts forwards over the maxillulary ganglion, fig. 6, *b*, and 14, *a*, *c.add.t.*, where it lies forming a groove across the nervous tissue in the young adult, figs. 7 and 15, *c.add.t.* The remaining part of the maxillary bar is left as the maxillary tendon in the furrow between the maxillulary and maxillary ganglia, fig. 6, *b*, 7 and 14, *a*, *mx.2.t.* The central nuclei in both parts of the bar disappear at the end of embryonic life. In the adult the maxillary tendon is attached laterally to that of the carapace adductor, figs. 15 and 17. The original lateral ectodermal connection of the carapace adductor tendon, fig. 14, *c*, *c.add.e.*, in the adult forms (1) a small solid strut passing from the tendon to the inner side of the limb bases

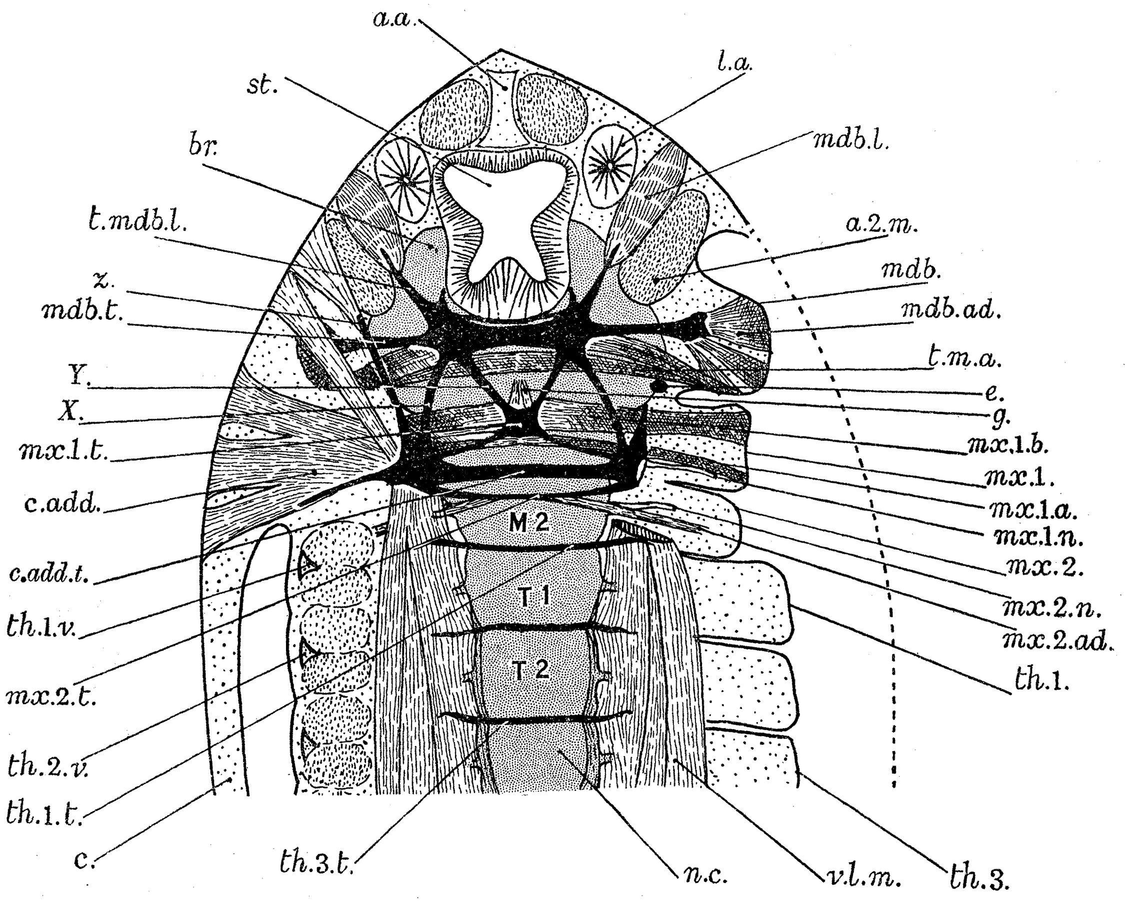


FIG. 15.—Diagrammatic reconstruction, viewed from above, of the endoskeleton and associated muscles in a small adult shortly after leaving the brood pouch. The carapace adductor muscle is shown on the left, but is omitted on the right where the ventral longitudinal muscle and carapace adductor tendon are cut short in order to expose the base of the limbs and muscles at a lower level. The endoskeleton is shown in black and the nerve cord is mechanically tinted. *a.2.m.*, muscle of antenna cut transversely. *br.*, brain. *c.add.*, carapace adductor muscle. *c.add.t.*, tendon of carapace adductor muscles. *e.*, endoskeletal strut extending vertically from mandibular-maxillulary intersegmental furrow. *g.*, mid-ventral muscle from maxillulary tendon to ventral body wall. *l.a.*, anterior liver lobe. *m.*2., maxillary ganglion. *mdb.ad.*, mandibular adductor muscles. *mdb.l.*, dorso-ventral mandibular muscle. *mdb.t.*, tendon of mandibular adductor muscles. *mx.*1.*a.*, posterior maxillulary adductor muscle uniting with its fellow in the middle line. *mx.*1.*b.*, anterior maxillulary adductor muscles uniting with the maxillulary tendon. *mx.*1.*n.*, maxillulary nerve. *mx.*1.*t.*, maxillulary tendon. *mx.*2.*ad.*, maxillary adductor muscles attached to maxillary tendon. *mx.*2.*n.*, maxillary nerve. *n.c.*, nerve cord. *st.*, stomodœum. *t.m.a.*, mandibular adductor muscle uniting with its fellow in the middle line behind the tendon (see *Hemimysis*, MANTON (1928), Plate 24, fig. 27, and text-fig. 22, *d*, *t.m.a.*). *t.mdb.l.*, tendon of dorso-ventral mandibular muscles. *T.*1., and *T.*2., first and second thoracic ganglia. *th.*1.*t.*–*th.*3.*t.*, first third thoracic tendinous bars. *th.*1.*v.* and *th.*2.*v.*, first and second lateral thoracic vessels to pericardium. *v.l.m.*, ventral longitudinal muscle. *X.*, union between carapace adductor and mandibular adductor tendon. *Y.*, union between maxillulary adductor and mandibular adductor tendons. *z.*, anterior strut from carapace adductor tendon.

at the maxillary-maxillulary intersegment, fig. 17, *h.*, and (2) a horizontal intucking which becomes hollow, passing inwards from the postero-lateral part of the maxillulary segment, just above the base of the maxillule, to unite with the carapace adductor tendon, fig. 17, *e.pl.*

The maxillary muscles become associated with the maxillary tendon, fig. 14, *c*, and 15, *mx.*2.*ad.*, much as do those of the maxillule and mandible to their respective tendons. The rudiments of the carapace adductor muscles appear early in the anterior part of maxillary segment, and presumably arise from the maxillary somites. They are first seen as a pair of compressed strands extending from the limb base to the rudiment of the carapace fold on either side of the yolk sac, fig. 8, *a*, *c.add.* The upper ends of these strands grow dorsally and become inserted on the ectoderm just above the developing carapace fold, and their lower ends become attached to the carapace adductor tendon (see above) close to its lateral ectodermal union, fig. 14, *c*, *c.add.* The adductor muscles and tendon thus form a " U " around the yolk sac. As the yolk becomes absorbed, so the muscles become less dorso-ventral in position until they lie transversely in the adult. Besides the rudiments of the carapace adductor muscles the anterior ends of the ventral longitudinal muscle rudiments also become inserted on the carapace adductor tendon. This occurs in the lateral parts of the maxillary segment close to the ectodermal connection of the tendon, figs. 14, *a*, and 15, *v.l.m.* As the carapace adductor muscles grow, so numerous extensions from the adductor tendon pass out into them. In the adult these mainly lie horizontally in the transverse adductor muscles, one is indicated in fig. 15, but a large pair extend upwards and forwards towards the dorsal body wall, fig. 15, *z.* A pair of horizontal struts are also formed between the lateral parts of the carapace adductor tendon and the mandibular adductor tendon, fig. 15, X., and remain united with the intersegmental ventral ectoderm between the mandibles and maxillules. In the adult the carapace adductor tendon broadens antero-posteriorly and forms a large flat plate in the maxillary and maxillulary segments, fig. 17, the numerous extensions from the main plate are not indicated as they overlap in dorsal view, and the comparatively small maxillary tendon lies just below the posterior border of the adductor skeleton.

Thus from the three intersegmental bars of the mandibular to maxillary segments a complex endoskeletal system is formed in the anterior part of the body, which retains to some extent its original connections with the ectoderm, either as an epithelial extension, fig. 7, *f.*; as an ectodermal muscle, fig. 7, *g.*; as a chitinous strut, figs. 7, *s.*, and 17, *h.*; or as a hollow chitinous intucking, fig. 17, *e.pl.*

Along the trunk region the ectodermal bars, as in *Hemimysis*, form transverse chitinous or tendonous rods lying above the nerve cord, and laterally entering the ventral longitudinal muscular system, fig. 15, *th.*1.*t.*, etc. The middle parts of the bars remain free from muscle insertions, unlike *Hemimysis*, where the abdominal muscles creep so far along the bars that the latter remain as thin lamellæ between the muscles of the two sides (MANTON, 1928, *a*, text-fig. 15, *g–j*, *et*). In the thorax of

Nebalia, muscles passing to the outer sides of the limb bases are inserted on these bars, and in the abdomen, in addition, large muscles running from the lateral body wall to the bars are present in the anterior segments. The latter were noted by CLAUS (1888), p. 47–8 and Plate 12, figs. 1 and 2, *T*, and he roughly indicates the adult tendonous bars in transverse section in his Plate 9, fig. 8, *Il.*, and Plate 12, fig. 2, *S*, and in sagittal view in his Plate 7, figs. 8 and 8, *Il.*

SEGMENTAL EXCRETORY ORGANS.

The study of the structure and development of the segmental excretory organs in *Nebalia* does not present many new points of interest. The form of the antennal and maxillary glands in the adult *Nebalia* has been briefly described by CLAUS (1888), but it appeared desirable to attempt to reinvestigate the adult structure besides following the development of these organs. The inferior fixation of the adult *Nebalia*, particularly in the maxillary region, even when cut in pieces, pricked, etc., made this study particularly difficult, and vital dyes, so successfully employed by GICKLHORN and KELLER (1925), and GICKLHORN (1930), in the investigation of copepod and branchiopod segmental excretory organs, were employed to confirm the appearance of sections. The best fixations obtained were those with carnoy, the head and abdomen being amputated and the body pricked as close to the carapace adductor muscle as possible.

In the adult the walls of the end sacs of both maxillary and antennal glands stain brightly with trypanrot and less regularly with vitalneurot (Grubler stains) after a period of about 13 days immersion in 0·05% solution of the dye in sea-water, fig. 16, *a*. The constant staining of the individual cells of the end sacs gave a clear indication of the position and extent of these structures for comparison with imperfectly fixed serial sections. The use of such dyes in elucidating the function of these organs, however, seems very uncertain, as so many other organs are also stained, such as the intestine, the so-called excretory patches on the thoracic limbs, the leucocytes of the blood, irregular patches of body-wall, particularly on the antennules and all parts of the body which may reasonably be regarded as respiratory, such as the carapace and outer parts of the thoracic limbs.

The use of Grubler's eosin-azur (Giemsa mixture matured 2 years) was also employed in an attempt to stain the ducts of the segmental excretory organs in the living animal. This method clearly demonstrates the cavity of the duct of the copepod and branchiopod maxillary glands (GICKLHORN and KELLER, 1925). Four drops of stain were added to 100 c.c. of sea water, and the mixture made slightly acid or alkaline by a few drops of lime-water or N/10 boric acid, and the solutions were renewed every 5 days. The general staining of the body showed up the same structures as with trypanrot, but no staining of any parts of the segmental excretory organs resulted.

The position of the antennal gland in the proximal antennal segment, and its structure, consisting of a multicellular duct and end sac, have been seen by CLAUS (1888). To this description may now be added the presence of a valve between duct and end sac and a short exit tube opening on the inner side of the limb. The whole gland is indicated diagrammatically in optical transverse section in fig. 16, *b*, and the stained end sac cells in fig. 16, *a*. The form of the end sac, which lies on the outer side of the limb, and the simple sac-like duct on its median side, is very like the simpler Malacostracan antennal glands such as in *Mysis* or *Hippolyte*, etc. Ventrally the duct narrows considerably and passes over to the inner face of the limb. Here it unites with a very short exit tube lined by chitin continuous with the outer cuticle. At the upper end of the duct a minute opening passes into the end sac. A valve is here formed by a few cells projecting into the lumen of the duct through which a narrow canal passes to the end sac, fig. 24, *f*. No fibrils have been seen in the valve, which may appear very well fixed in comparison with many adult organs.

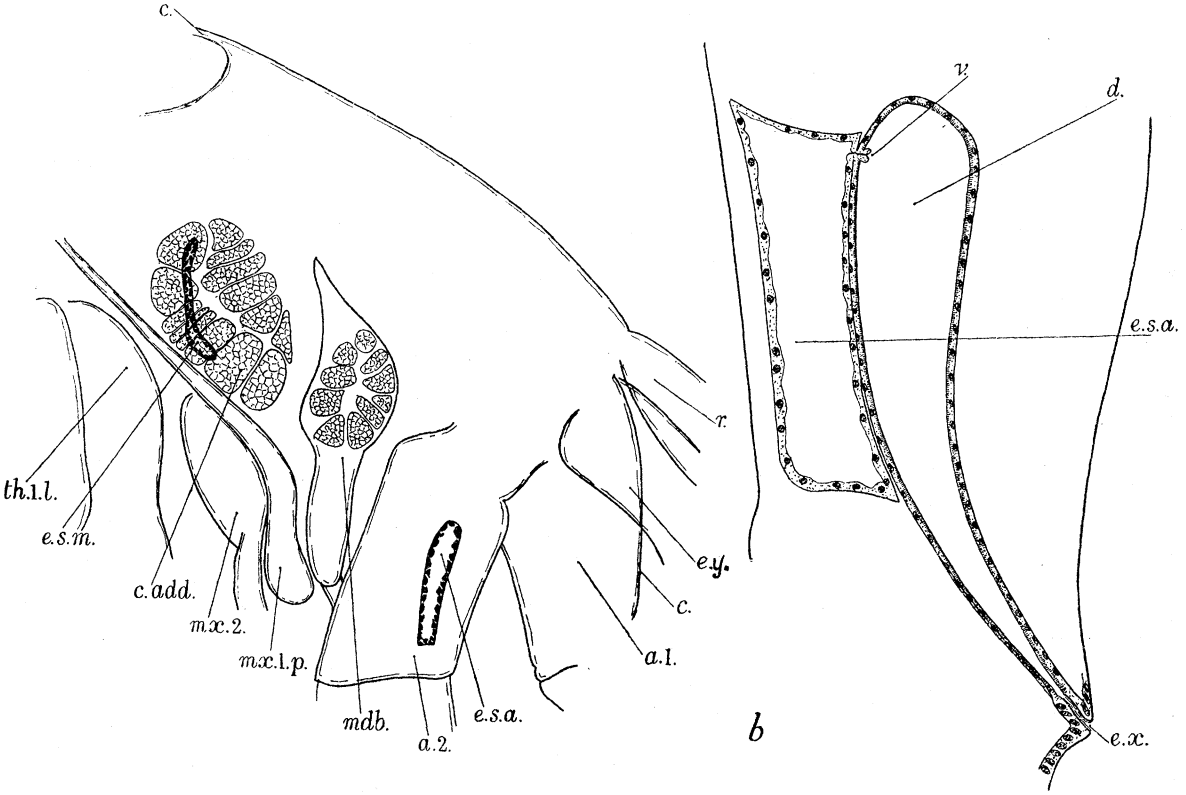


FIG. 16.—Segmental excretory organs.

(*a*) Side view of the living animal showing the end sacs of the maxillary, *e.s.m.*, and antennal, *e.s.a.*, glands. The cells composing the end sacs are stained with trypanrot. The maxillary gland is close against the tendon of the carapace adductor muscle, and is visible through the expanded lateral attachment of the adductor muscles to the carapace, *c.add.*

(*b*) Diagrammatic reconstruction of the antennal gland seen in optical transverse section. The inner side of the limb base is to the right.

The development of the antennal gland closely resembles that of *Hemimysis*, and need not be described in detail. It first appears in the embryo at the stage seen in fig. 4, G. The block of mesoderm at the antennal base becomes differentiated into three groups of cells, a small upper and outer group destined to form the end sac, an upper and inner group of larger size which will give rise to the duct, and the remaining lower and outer cells which form the limb musculature, etc., fig. 24, *d*. The end sac cells rapidly form a hollow structure which is at first closely pressed against the yolk sac. The duct cells form a solid row two or three thick, lying at the side of the end sac and extending down the limb. As the yolk sac shrinks and the nervous tissue spreads upwards, the gland is left in the antennal base. Towards the end of embryonic life the duct lumen opens out, fig. 24, *e*, and an ectodermal ingrowth forms the small exit tube. Comparison may be made with the development of the antennal gland in *Hemimysis* (MANTON, 1928, *a*, text-fig. 27 and Plate 25).

The structure of the maxillary gland is more difficult to determine owing to bad fixation in this region. The end sac stains readily with trypanrot, and is constant in position, fig. 16, *a*. It lies in the body above the maxilla and close behind the tendon of the carapace adductor muscles. It is L-shaped in transverse section. The upper and longer limb is closely pressed against the dorso-ventral extensor muscles to the posterior part of the maxillule and anterior part of the maxilla, and the shorter horizontal limb passes out sideways and forwards across the base of the maxilla close to the intersegmental intucking, *e.pl.*, between maxilla and maxillule. The lumen of the end sac is much compressed, and is usually scarcely visible in the living state, although it is larger in the lower part of the sac. The end sac appears to communicate at its outer ventral end (shorter limb of the L) with an extremely short duct or exit tube opening to the exterior above the anterior part of the maxilla, just where the carapace is attached to the body below the carapace adductor muscle. This opening could not be seen perfectly, it must be small and appears to be lined by a short chitinous intucking.

At no stage is the maxillary gland better developed. It does not appear until after the young are free-swimming. In the late embryo a small group of undifferentiated cells lie behind and against the carapace adductor muscles, just where these muscles are attached to the tendon on either side. From these cells the end sac is developed, which thus comes to be in the position described above.

Thus the structure and development of the segmental excretory organs resembles those of other Malacostraca. No ectodermal intracellular ducts are formed as in many lower crustacea, and the valve between duct and end sac of the antennal gland resembles the Malacostracan valves such as seen in *Anaspides* or the prawn *Gennadas* (CANNON and MANTON, 1927, *b*).

DISCUSSION.

Early Development and Segmentation.

The processes of maturation, of fertilization if it occurs, and of the first few cleavages require further investigation before their peculiarities can profitably be discussed. It is not impossible that *Nebalia* may prove to be parthenogenetic at Naples. Males are scarce while breeding females are abundant, a condition also found in *Trichoniscus provisorius* by VANDAL (1923). This Isopod in central and eastern France is parthenogenetic and males are few, while in southern France males and females are in normal numbers and sexual reproduction prevails.

ROBINSON'S conclusion (1906) that " the blastoderm . . . increases both by division of cells already on the ventral surface and also by the reception of additional cells which come from within the egg itself," p. 393, is not substantiated; this deduction is undoubtedly drawn from insufficient material unsuitably prepared. The early stages of *Nebalia* show considerable variation (see p. 170), the more usual distribution of blastomeres (based on examination of many individuals from an extensive series of families) is shown in fig. 1, and some of the variations in fig. 2. The granular substance, staining blue with Mallory's triple stain, which occasionally replaces part of the yolk (see p. 170), may lie external or internal to the blastoderm. The blastoderm may remain in its normal position, fig. 2, or may sink down over the contour of the yolk, as in ROBINSON'S fig. 1, Plate 16. Such a section is in no way a proof that cells from within the yolk become added to the blastoderm. Once the four large blastomeres have risen to the surface to form a cap of superficial cells, this cap only grows by the division of its component blastomeres, there being no cells which remain behind in the yolk.

Except in the rare cases when little yolk is present and total cleavage occurs, both the Decapoda and Peracarida are characterized by possessing within the egg a central stellate nucleated mass of protoplasm which divides, so that the first formed nuclei, surrounded by protoplasm, lie freely within the yolk. These nucleated masses of protoplasm then approach the surface of the yolk. In most Decapoda radial cleavage furrows appear while the nucleated masses of protoplasm are still covered by the yolk, so that each so-called " blastomere " or " primary yolk pyramid " consists of a mass of yolk containing a more or less stellate central portion of protoplasm around the nucleus (see HERRICK, 1894, for *Hommarus ;* DE CANO, 1893, for *Dromia*, etc. ; BROOKS and HERRICK, 1892, for *Alpheus, Stenopus, Hippa*, etc. ; WELDON, 1892, for *Crangon* ; SOLLAUD, 1923, for Palæmoninæ, etc.). From the central protoplasmic mass a reticulum may be visible for some distance through the yolk, and " there is little doubt that a protoplasmic reticulum extends between the yolk spherules through the whole substance of each blastomere " (WELDON for *Crangon*, p. 344, 1892 ; see also SOLLAUD, 1923). Such cleavage is typical of KORSCHELT and HEIDER'S " Superficielle Furchung. II Gruppe, Eier mit rein superficieller Furchung " (1909, p. 128). In most described Peracarida, on the contrary, the internal nucleated masses of protoplasm rise completely to the surface, and directly become the blastomeres which then lie outside the yolk, and no primary yolk pyramids are formed (MANTON, 1928, *a*, for *Hemimysis*, McMURRICH, 1895, for Isopoda, etc.). This is a very different process from that seen in most Decapoda and is not accurately included together with the Decapoda under a title of " Superficielle Furchung." The Amphipoda differ from the rest of the Peracarida in that cleavage may be total, each blastomere containing a central nucleus and protoplasmic network, which, however, is continuous with a superficial layer of protoplasm around each blastomere (HEIDECKE, 1904, etc.).

The early segmentation and formation of the germinal disk in *Nebalia* occurs in a manner essentially similar to that in *Hemimysis*. The egg in *Nebalia* contains less yolk, and the blastomeres rise to the surface at an earlier stage, so that the blastoderm investing the yolk is formed by an extension from a cap of four cells instead of first appearing as a complete layer within the yolk which gradually rises to the surface. Thus the early stages in *Nebalia* resemble the type found in the Mysidacea and other Peracarida and are unlike the Decapoda.

External Changes.

The early development of *Nebalia* is not so determinate as in *Hemimysis*, and the germinal layers are differentiated at a comparatively later stage, as in the Decapoda. Correlated with this is the early appearance of a V-shaped germinal disk, as in *Leander*, *Astacus, Dromia,* etc., instead of an almost transverse band as in *Hemimysis* which subsequently becomes V-shaped (see MANTON, 1928, *a*, p. 430). The further growth of the germinal disk of *Nebalia* is also of the Decapod type. The arms of the V-shaped band shift towards each other forming a " U," and a cross-connection is formed between their anterior ends. This is seen in *Eupagurus Prideauxi* (MAYER, 1877), *Carcinus-mœnas* (DE CANO, 1892; Plate 1, figs. 12–16), *Dromia* (DE CANO, 1893), etc., and more recently shown by SOLLAUD (1923, p. 161, and Plate 1, figs. 4–6) in the Palæmoninæ, and may be taken as typical for the Decapoda. This connection is not found in the Peracarida, where the anterior parts of the V-shaped band remain apart until the whole body has been formed, and the embryo hatches from the vitelline membrane (ex. *Mysis*, NUSBAUM, 1877, Plate 5, figs. 2–11, and Isopoda, MCMURRICH, 1895). A caudal papilla is formed and reflexed forwards in *Nebalia,* as in the Decapoda, Mysidacea, and Amphipoda, but its growth is of the Decapod type (see below, p. 213).

The body develops progressively from before backwards, as in the Peracarida, and unlike the Decapoda, where the abdomen and anterior part of the thorax are precociously formed. Hatching occurs much later than in a Mysid (see below), but the subsequent development takes place as in a Mysid in a brood pouch where embryonic ecdyses occur (two in *Nebalia* and but one in a Mysid). In both *Nebalia* and a Mysid the first free-swimming stage is a miniature adult and not a larva as in most Decapoda.

Formation of Germ Layers, Teloblasts, and Caudal Papilla.

ROBINSON'S account (1906) of gastrulation and germ layer formation in *Nebalia* is neither critical nor conclusive upon the essential points. Gastrulation in *Nebalia* takes place from a much larger area than was recognized by ROBINSON, cells immigrating inwards from most of the area enclosed by the teloblasts. No fixed blastoporal groove is present, as described by ROBINSON (1906, p. 394), although the blastoporal area may be temporarily pitted at any point where active immigration is taking place. No " roofing in " of a blastoporal groove occurs (ROBINSON, p. 397); such an impression can be gained by observing an oblique section through the blastoporal area during active immigration. ROBINSON'S further conclusion that yolk cells and mesodermal cells immigrate inwards from all over the germinal disk (pp. 396 and 399) is not substantiated, and this interpretation is in no way proved by ROBINSON'S figures 9 and 10 on his Plate 17.

In *Nebalia* the mesoderm is formed anterior to the endoderm, as in the Decapoda and Peracarida, and unlike the lower crustacea where these spatial relations are reversed (MANTON, 1928, *a*, p. 429). The degree of determination shown by the development of *Nebalia* corresponds approximately to that of the Decapoda, Palæmoninæ (SOLLAUD, 1923). The germinal layers are not differentiated externally before gastrulation, as in many Peracarida, and the mesendodermal mass below the blastoporal area of *Nebalia* resembles the " bouchon blastoporique " of the Palæmoninæ. The blastoporal area in *Nebalia* gives rise to all mesoderm and endoderm (with the exception of the preantennulary mesoderm), as in *Hemimysis*. In the Decapoda the preantennulary mesoderm has not yet been described. In the Palæmoninæ SOLLAUD describes (1923) some of the head mesoderm as being budded inwards from the posterior part of the arms of the disk in front of the blastoporal area. No such process takes place in *Nebalia*.

As in the Decapoda and Peracarida, rows of ectodermal and mesodermal teloblasts are formed in *Nebalia*, and give rise to the trunk region. The ectodermal teloblasts arise in *Nebalia* as in *Hemimysis*, from the sides of the blastoporal area, forming two rows which then unite anteriorly; and the mesodermal teloblasts are similarly formed internal to the anterior part of the blastoporal area, but in *Nebalia* this occurs after the mesoderm of the head bands has been formed and not before, a feature probably correlated with the early formation of the V-shaped germinal disk. SOLLAUD describes the ectodermal teloblasts of the Palæmoninæ as appearing first in a semi-circular row, not in two groups, while the mesodermal teloblasts are formed from the anterior part of the " bouchon blastoporique " as in *Nebalia*. In the Peracarida a median and a variable number of paired ectodermal teloblasts and usually four paired mesodermal teloblasts are present, while among the Decapoda the Palæmoninæ show 20–22 ectodermal and 14–16 mesodermal teloblasts. Whether the median ectodermal teloblast is really absent is uncertain from SOLLAUD'S figures, and all other Decapodan literature is indefinite concerning numbers of either ectodermal or mesodermal teloblasts. Possibly the Decapoda differ from the Peracarida in possessing no mid-ventral ectodermal teloblast, and in having more than four pairs of mesodermal teloblasts. If so, then both in origin and in numbers of teloblasts *Nebalia* resemble the Peracarida; and in both *Nebalia* and the Peracarida the teloblasts form all the post mandibular segments.

SOLLAUD (1923) considered the teloblasts of the Palæmoninæ to form only the post-maxillary segments. It seems desirable that this point should be reinvestigated before concluding that this is a real difference between the Peracarida and Decapoda. Some difficulty was experienced in ascertaining the anterior limit of teloblastic mesoderm and ectoderm in *Nebalia.* The embryos of the Palæmoninæ are similar in shape, and no critical figures are shown, either of whole mounts or of sections, such as are here given for *Nebalia,* a superficial examination of which might lead to a similar conclusion.

The further development from the teloblasts of *Nebalia,* however, resembles the Decapoda, as exemplified by *Astacus,** and the Palæmoniæ rather than the Peracarida, in that they form a complete ring round the blastoporal area, the telson being formed from the blastoderm enclosed by the ring, and the descendants of the teloblasts forming the walls of the caudal papilla on all sides. In the Peracarida teloblasts lie in the anterior ventral lip of the blastopore only, and their descendants form only the ventral wall of the caudal papilla.

Gastrulation in *Hemimysis* is a prolonged process, not ceasing till all thoracic and three abdominal segments have been formed. In the Decapoda, on the contrary, gastrulation ceases early, before the caudal papilla is formed (*Astacus, Palæmon,* etc.). *Nebalia* resembles the Decapoda more closely than the Peracarida in this respect, but gastrulation is continued a little later than it is in *Astacus* and *Palæmon,* and ceases just after the caudal papilla has appeared. The closure of the blastopore and the early formation of the proctodœum occur in *Nebalia* just as in the Decapoda (see MANTON, 1928, *a,* p. 430).

The arrangement of the teloblasts on the blastoporal lips, the method of growth of the caudal papilla and the relative ages on hatching in Decapoda, *Nebalia* and Mysidacea appear to be associated with the different amounts of yolk which penetrates into the caudal papilla. In *Hemimysis* the caudal papilla is distended with yolk and teloblasts are limited to the ventral lip of the blastopore, and so their descendants form only the ventral side of the papilla. In most Decapoda and in *Nebalia,* on the contrary, very little or no yolk enters the caudal papilla which is not distended, and so the teloblasts can lie all round the blastoporal lips and give rise to all sides of the papilla.

Hatching.

A few suggestions may here be made concerning the mechanism of hatching from the vitelline membrane in Malacostraca. Hatching appears to be due to three if not more factors; (1) muscular movements of the body; (2) pressure caused by uneven growth of the embryonic tissue; and (3) pressure caused by the swelling of the yolk as it absorbs water. (The absorption of water by the yolk during its utilization has been seen in *Hemimysis* (MANTON, 1928, *a*) and in the Trout (GRAY, 1926), etc.) In *Hemimysis* hatching occurs early when only seven thoracic segments have been formed, muscles are scarcely differentiated, so that the first factor is hardly operative. Hatching is probably caused mainly by the last two factors. Much yolk lies in the papilla as

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* On p. 431, MANTON, 1928, FULINSKI's work on Astacus is misquoted. He describes teloblasts in a ring round the caudal papilla, as is also indicated by the " Knospungzone " figured by REICHENBACH, 1886.

well as in the head region, the swelling of which will tend to reflex the papilla; and the increasing growth of tissue on the ventral side of the papilla will also tend to reflex it and so break the vitelline membrane. In *Nebalia* hatching occurs much later, when all segments have been formed. Here little yolk enters the papilla, which grows evenly all round, thus the second and third factors which tend to reflex the papilla in *Hemimysis* must here be less effective. Hatching appears to take place mainly as a result of active muscular movements of the papilla. In the Decapoda (ex *Carcinus*) no yolk passes into the papilla, and hatching takes place at a still later stage when nearly all the yolk is absorbed and some trunk limbs are well formed. The cause of hatching here cannot be the factors operative in *Hemimysis* and less effective in *Nebalia*; it may be due to muscular movement alone, but the possibility of hatching enzymes being present should not be overlooked. The problem of hatching in the higher Crustacea merits investigation.

Early Development of Endoderm and Formation of Alimentary Canal.

No complete account has been given of the development of the endoderm and liver in *Nebalia*, and the usual muddle prevails in the literature concerning the interpretation and fate of vitellophags or yolk cells. ROBINSON'S interpretations appear to be considerably influenced by the older work on mysids, much of which is inaccurate, and the yolk cells do not degenerate as claimed by ROBINSON.

In *Nebalia* both the yolk cells and the epithelial "endodermal plate" are here considered to represent the endoderm, and they arise from the blastoporal area only. The formation of the endoderm and alimentary tract is essentially similar to the account given by SOLLAUD (1923) for the Decapod *Leander*. In both the yolk cells from the blastoporal area wander all round the yolk mass absorbing much of it into themselves. The endodermal plate arising from the posterior part of the mesendodermal mass in *Nebalia* is clearly comparable with the "lame intestinale primitive" of *Leander*, both in origin and position, and also in its marginal growth by the yolk cells becoming epithelial and uniting with the edge of the plate, so finally enclosing the yolk in an epithelial yolk sac. However, SOLLAUD restricts the term endoderm to the yolk cells and considers the "lame intestinale primitive" to be mesodermal for no convincing reasons, and this leads to quite unjustifiable comparisons with the Peracarida, p. 228 (see also MANTON, 1928, *a*, p. 433–436). In *Hemimysis* and other Peracarida all the endodermal cells appear first as yolk cells, and only later do they become epithelial. In *Hemimysis* this occurs first opposite the stomodœum and proctodœum, and later spreads elsewhere. (The varied behaviour and fate of the yolk cells in Decapoda and Peracarida has been summarized already, MANTON, 1928, *a*, p. 433.) The epithelial yolk sac in both Decapoda and Peracarida then becomes the adult mid-gut. Thus, in the formation of the endoderm and the growth of the mid-gut *Nebalia* resembles the Decapoda rather than the Peracarida.

Liver.

The growth of the liver in *Nebalia*, as far as it has been observed, has been compared with that of Mysis (ROBINSON, 1906), but the older accounts of this process in a mysid have been shown to be erroneous (MANTON, 1928, *a*). The formation of the anterior and posterior hepatic diverticula in *Nebalia* as direct constrictions from outgrowths of the endodermal yolk sac is a simple process, and perhaps may represent a primitive method.

The posterior liver diverticula may be considered first. In *Nebalia*, as in *Hemimysis*, one primary pair of liver diverticula are formed which open to the mid-gut ventrolaterally in the maxillary segment, just behind the stomodœum; and only after the young adult becomes free-swimming does this pair of tubes subdivide to give the adult liver. The development of the liver in the Decapoda is imperfectly known. SOLLAUD describes one pair of hepatopancreatic lobes in the embryo of *Leander*, whereas in *Astacus* REICHENBACH figures the development of three pairs of liver lobes. Descriptions of the origin of the liver lobes in the Decapoda are even less precise. In *Leander* the hepatopancreatic lobes arise from concave lateral expansions of the "epithelium intestinale perivitelline" (SOLLAUD, 1923, p. 171–2), and thus resemble *Nebalia* in their direct origin from the endodermal epithelial yolk sac. In *Hemimysis*, and probably other Peracarida (MANTON, 1928, *a*, p. 433) the posterior liver lobes arise independently of the yolk sac from a pair of epithelial plates of mesoderm which grow round the yolk sac. The walls of the latter break down and so the mesodermal epithelium finally forms a pair of tubes enclosing yolk. Thus in origin from the epithelial yolk sac the posterior liver lobes of *Nebalia* resemble the Decapoda, such as *Leander*, while in shape and subsequent elaboration they are similar to the Peracaridan *Hemimysis*. However, further work on the origin of the liver in the Decapoda is needed before any sound generalizations can be made on the Decapodan methods of liver formation.

The anterior hepatic diverticula, extending forwards into the head of the adult *Nebalia*, are formed directly from the anterior lobes of the yolk sac which are separated by the developing anterior aorta. These lobes of the yolk sac are present in embryos of the Mysidacea and some Decapoda (*Alpheus*, *Crangon*, *Astacus*, etc.). In the Mysidacea they are completely absorbed during development. In *Astacus*, and at least some other forms with a schizopod larva, these lobes persist in the young free living stage and are later absorbed, whereas sections of the zoea stage of an unidentified crab show complete absorption of these lobes, if they are ever present. (The development of the paired anterior mid-gut diverticula of the crab is unknown; if they are formed from the anterior lobes of the yolk sac, the latter would probably not have disappeared by the zoea stage.) The anterior hapatic diverticula thus appear to be organs persisting in the adult *Nebalia*, which are restricted to the embryos of some Peracarida and Decapoda. The anterior hepatic diverticula found in many of the lower crustacea are extremely various in position and in form, and where the development has been recorded, even partially, it bears no resemblance to the conditions in embryonic Decapods, Mysids, and *Nebalia*.

Preantennulary Somite.

The formation and development of the paired preantennulary somite in Crustacea has previously only been followed in a mysid (MANTON, 1928, *a*), where a comparison has been given of their development in this animal and in other Arthropoda (p. 438). These somites in *Nebalia* arise and behave essentially as do those of a mysid, minor differences being due to the absence of a "yolk septum" in *Nebalia*, and the almost complete absence of cœlomic cavities within these somites; compare figs. 18, 19, 20, *d*, 1, and 23, *a* and *c*, Plates 20, 21, 22 and 25, with *Hemimysis*, MANTON, 1928, *a*, text-figs. 6 and 7 and Plate 24, figs. 22 and 23. In *Nebalia* the early forward growth of the anterior parts of the preantennulary somites takes place between the yolk sac and the ectodermal cerebral and rostral rudiments, so reaching the dorsal organ; whereas the dorsal organ in *Hemimysis* is reached by upgrowth along the ectodermal "yolk septum," a condition probably correlated with the large amount of yolk in the head region (compare fig. 6 with *Hemimysis*, MANTON, 1928, *a*, text-fig. 12, *g*, *h*, and *i*). In the spider (KISHINOUYE, 1893, and MANTON, 1928, *a*, p. 440 and text-fig. 30) where no excessive amount of yolk lies in the head, the upgrowth of the precheliceral somites resembles that *Nebalia*. In both *Nebalia* and *Hemimysis* the median dorsal organ is associated with the backgrowth of the preantennulary mesoderm to reach the heart (compare fig. 4, G and I, with *Hemimysis*, text-fig. 13, *h*, *i*, and *j*). The large cœlomic cavities formed in the preantennulary somites of *Hemimysis* are absent in *Nebalia*; compare fig. 6 and fig. 23, *e* and *f*, with *Hemimysis*, text-fig. 13 and Plate 24, figs. 24 and 25. The late formed cœlomic spaces in *Hemimysis* (MANTON, 1928, *a*, p. 394) are, however, represented in *Nebalia* (compare fig. 23, *f*, 1, *p.m.c.*, with *Hemimysis*, text-fig. 13 "ventral preantennulary cavity" and "2nd preant. cavity" and Plate 24, fig. 27, *p.m.c.*2), but they become obliterated soon after their appearance and give no large cœlomic spaces in the adult *Nebalia* as in *Hemimysis*.

Trunk Mesoderm.

The origin and growth of the trunk mesodermal somites of *Nebalia*, together with the formation of the dorsal blood vessel and gut musculature, will be recognized as extraordinarily like those of *Hemimysis* when due allowance is made for the influence of the small amount of yolk present in *Nebalia* behind the third thoracic segment at all stages in development. In *Hemimysis* the early hatching is followed by a distension of the caudal papilla with yolk, and the yolk sac in the thoracic region shrinks in diameter only late in development. Thus the mesodermal somites are at first ventral in position, and reach the dorsal side by upgrowth round the yolk sac. In *Nebalia* the trunk somites lie at the sides, extending from the dorsal to the ventral body walls, and become differentiated *in situ*. The position of the somites in *Nebalia* superficially resembles that of the trunk mesoderm in *Chirocephalus* and *Estheria* (CANNON, 1927, *a*, and 1924) where the intestine is devoid of yolk. However, the formation of these somites in

Nebalia from teloblasts, and their early development, exactly resembles *Hemimysis* (see below) and differs from the Branchiopoda, where the trunk mesoderm is at first continuous along the body and only later partially segments into successive somites, and where the dorsal and ventral mesoderm of each segment remain continuous until a later stage.

The cleavages of the eight mesodermal cells of each segment, first into a double layer of sixteen cells, eight on either side, and later into a pair of blocks, are essentially similar in *Nebalia* and *Hemimysis*, as may be seen by comparison of fig. 21, *c*3 and *c*4, with *Hemimysis*, text-fig. 9, *a* and *b* (Manton, 1928, *a*). The abundance of yolk in the latter presses both somites together on the ventral side of the body. A difference lies in the precocious formation in *Nebalia* of gut mesoderm before the division of the somite into dorsal and ventral blocks, a feature doubtless correlated with the part played by the early peristalsis of the intestinal part of the yolk sac in the yolk absorption. In *Hemimysis* the gut musculature develops at a later stage from the dorsal mesoderm, the yolk already lying in all parts of the yolk sac (Manton, 1928, *a*, Plate 23, fig. 17, *g.m.*). The division of the somites into dorsal, ventral, and limb portions ; the appearance of cœlomic spaces ; the formation of the longitudinal muscles and of the dorsal blood vessel and anterior aorta occurs essentially as in *Hemimysis*, but at an earlier stage, and from the somites in their final positions at the sides of the body, compare fig. 22, *b*, *d*, and *f*, with *Hemimysis*, Plate 22, fig. 14, and Plate 23, figs. 17 and 18, respectively. Only in the anterior trunk segments of *Nebalia* does the mass of yolk necessitate the upgrowth of somites round it, as occurs all along the body in *Hemimysis*. As in the mysid, the floor of the dorsal blood vessel appears first, and owing to the absence of yolk, the upper ends of the somites forming the vessel are U-shaped, as also in *Estheria*, instead of V-shaped as in *Hemimysis*. The form of the pericardial floor with its cœlomic spaces is similar in the two forms, but the curious order of expansion and contraction of the cœlomic spaces in *Hemimysis* occurring from behind forwards independently in both thorax and abdomen (Manton, 1928, *a*, p. 402, Table I), has not been observed in *Nebalia* where progressive development occurs along the whole body from before backwards, except for the first trunk segments which are retarded by the yolk. This progressive development is well shown by the heart and pericardium, and by the segmental genital rudiments which first appear in the middle of the thorax and are developed progressively in the hinder segments, Table III. Possibly this slight independence of thorax and abdomen in *Hemimysis* may be compared with the much more exaggerated phenomena found among the Decapoda, where the abdomen is precociously developed before the hinder part of the thorax becomes differentiated. *Nebalia* in this respect appears to be even more generalized than the mysid in that no break occurs between thorax and abdomen, the two regions behaving as a continuous whole.

The development of the seventh abdominal somites in *Nebalia* and *Hemimysis* is similar, although the seventh segment in *Nebalia* remains free from the sixth in the adult, whereas in *Hemimysis* it is fused with the sixth, and the telson and its mesoderm are much less developed. Fig. 24 *a*, *b*, and *c*, may be compared with *Hemimysis* (MANTON, 1928, *a*, text-fig. 19). In both the mesoderm is divisible into similar portions. That round the gut is massive compared with other segments, fig. 24, *a*, *ab*. 7. *g.m.*, and *Hemimysis*, text-fig. 19, *ab*, 7.*i.m.*, but the strand, *g.s.*, connecting this inner gut mesoderm with the outer part of the somite is absent in *Hemimysis*, where the inner mesoderm separates completely from the rest of the somite. The ventral mesoderm giving the longitudinal muscle, and the remaining lateral portions are comparable in the two types. The formation of the posterior end of the dorsal vessel and of the proctodœal dilator muscles is also similar, fig. 24, *b* and *c*, and *Hemimysis*, text-fig. 19, figs. *e* and *f*, but the bulk of the proctodœal dilators in *Nebalia* arise from the more extensive telson mesoderm.

The details of heart formation in *Nebalia* have been shown to be essentially like those of a mysid (p. 195), but this organ is longer, so leaving less of the dorsal vessel as a posterior aorta. The occurrence of paired segmental arteries leaving the heart is noteworthy in comparison with other Malacostraca. In *Hemimysis* it has been shown that the sternal arteries arise as a pair of vessels (MANTON, 1928, *a*, p. 403 and text-fig. 18) leaving the heart ventro-laterally in the seventh thoracic segment, and passing down the sides of the intestine. Usually only one of these persists in the adult as the sternal artery. The position in which these sternal arteries are formed exactly resembles the segmental arteries from the heart of *Nebalia*, and probably the two may be considered as homologous vessels, although the sternal artery ultimately penetrates to the subneural region, whereas the segmental arteries of *Nebalia* only extend to the viscera and fat body. The paired " hepatic arteries " of *Hemimysis* (MANTON, 1928, *a*, p. 403 and text-fig. 16), which leave the floor of the heart behind the anterior aorta valve and pass between the liver lobes and mid-gut, may be comparable to the most anterior of the segmental arteries of *Nebalia*, which leave the heart a short distance behind the anterior aorta valve and pass to the fat body, liver, and intestine. If these comparisons are justifiable, then the long heart of *Nebalia* with segmental arteries leaving it is represented in *Hemimysis* by a shorter heart and two pairs of ventral vessels, the sternal and hepatic arteries, while many of the more specialized Malacostraca possess a shortened thoracic heart, one sternal artery and a group of much modified arteries leaving the anterior end.

Genital Rudiment.

The origin of the gonads of those Crustacea in which the formation and fate of the cœlomic sacs has been followed, is of the type in which the germ cells are differentiated very early before the appearance of the somites. A mesodermal investment of the gonad is later obtained by the growth of tissue from the pericardial floor (in *Estheria*), or from the ventral wall of the cœlomic sacs (in *Hemimysis*), which gradually surrounds the gonads.

Nebalia differs from the above, and resembles the Annelids, *Peripatus*, and some other Arthropods, in showing a late origin of the germ cells, which arise in the walls of the cœlomic sacs. The origin of the germ cells in *Nebalia*, from the walls of the small dorsal cœlomic spaces below the dorsal blood vessel, is directly comparable to their development in *Peripatus* (Sedgewick, 1887) and *Scolopendra* (Heymons, 1901) (compare Sedgewick, 1887, Plate 37, fig. 43, with *Nebalia*, figs. 22 and 12). However, the cœlomic spaces in *Nebalia* become obliterated as soon as the first germ cells appear; and so the longitudinal gonad is formed by fusion of the solid segmental groups of germ cells, instead of the dorsal cœlomic sacs becoming fused to form a hollow genital rudiment, the walls of which form the germ cells, as in *Peripatus*. Thus the Crustacea in their gonad development exhibit the same methods as are found in other Arthropodan groups, these methods being modified by the very small size of the cœlomic spaces and their early obliteration.

Caudal Furca and Telson Mesoderm.

The telson in *Nebalia* is relatively larger than in most Malacostraca, and its mesoderm is more extensive. The telson arises from the blastoporal area enclosed by the teloblasts in *Nebalia*, but from a somewhat larger area in *Hemimysis*. The hollow furcal rudiment in the embryo *Nebalia* is formed in the same position on the telson as is the rudimentary solid furca of a mysid, and there is no reason to suppose that the two structures are not homologous. The difference lies in the furca of *Hemimysis* remaining ectodermal and being lost at the embryonic ecdysis, while in *Nebalia* the caudal furca continues to enlarge and is supplied by mesoderm from the telson. It has already been suggested (Manton, 1928, *a*) that the form and segmentation of the abdomen of *Nebalia* differs from the Malacostraca only in degree, and the development of the furca in *Nebalia* supports this suggestion.

The origin of the telson mesoderm in *Hemimysis* was not described as it was not clearly seen. In *Nebalia* the telson mesoderm is independent of the trunk somites of teloblastic origin, and arises directly from the blastoporal area. It may be compared with the scanty mesoderm which spreads into the non-segmental anterior end of the body from the head mesodermal bands, which also never forms a somite.

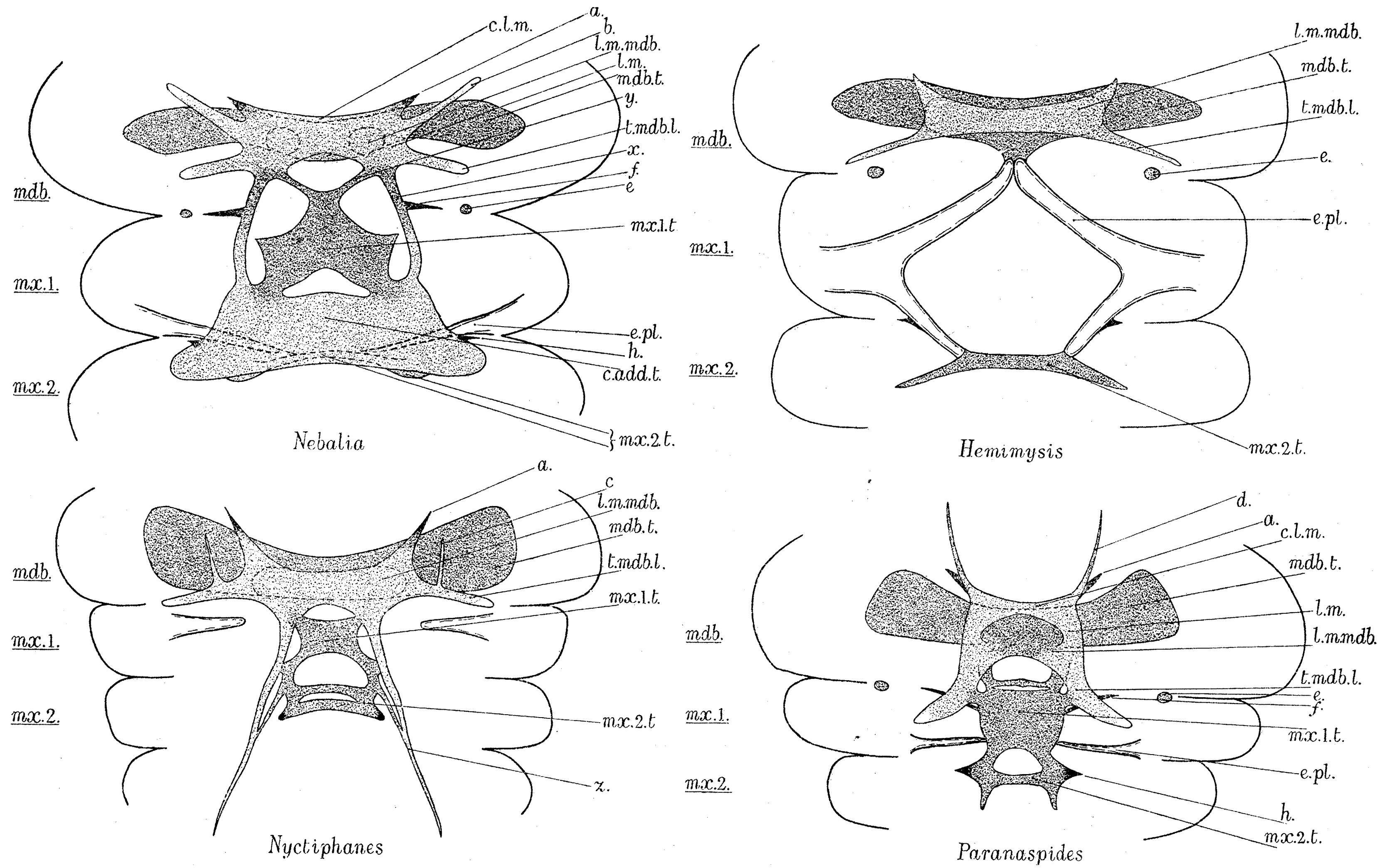
Endoskeleton and Carapace Adductor Muscle.

The finer details of the endoskeleton of *Nebalia* have not been fully described, yet in outline the structure and development of the endoskeleton closely resembles that of the Malacostraca and differs from other groups. In the lower crustacea information concerning the endoskeleton and its development is scanty (Humperdink for *Polyphemus* 1922, Cannon for *Chirocephalus*, 1926, etc.). It consists in the Branchiopoda of a system of lamellæ, buttresses, and threads, either attached to or separate from the external cuticle; and a tendonous sheet below the gut and above the nerve cord is frequent. The tendon of the mandibular adductor muscles in its form and origin resembles that of *Nebalia*, *Hemimysis*, etc., but there is no striking similarity between the arrangement of the endoskeletal elements in *Nebalia* and the Branchiopoda such as there is between *Nebalia* and the Malacostraca.

Brief reference to the endoskeleton of a mysid has already been made, p. 201, for the sake of clearness and brevity of the description. In both *Hemimysis* and *Nebalia*, besides the apodemal structures present in various parts of the body, a series of transverse intersegmental skeletal bars is formed from the ventral ectoderm all along the body. These bars lie immediately above the nerve cord; and muscles from the ventral parts of the somites, the ventral longitudinal system and the limbs become inserted upon them.

In *Nebalia* and *Hemimysis* the three bars of the mandibular, maxillulary, and maxillary segments are concerned in the elaboration of the major part of the endoskeleton which lies in the region of the mouth parts. In *Hemimysis*, owing to the formation of the apodemal endoskeletal plate in the maxillulary segment, the maxillulary bar in the adult degenerates, and that of the maxillary segment is small, fig. 14 and MANTON, 1928, *a*, text-fig. 22, *d*, *mdb.t.*, *e.pl.*, *mx.2.t.*

Information concerning the form and development of the endoskeleton of the simpler Malacostraca is scanty, and reconstructions of the endoskeleton of a *Euphausid*, *Paranaspides*, and *Anaspides* have been made for comparison with *Nebalia* and *Hemimysis*, fig. 17. *Anaspides* and *Paranaspides* are essentially similar, and only that of *Paranaspides* is figured. The endoskeleton of the prawn *Gennadas* appears to be somewhat similar to that of *Hemimysis*, and has not been figured. In *Nyctiphanes*, *Paranaspides*, and *Anaspides* the same three bars are elaborated to form the bulk of the endoskeleton, and their intersegmental connections with the ventral cuticle are retained in places. Thus the connections *a.*, *f.*, and *h.* in *Paranaspides* are probably comparable with those similarly marked in *Nebalia*. In *Nyctiphanes* the union *a.* is similar to that found in the above types, but the homologies of the other connections are doubtful. The mandibular skeleton, in *Paranaspides* and *Nyctiphanes*, as in *Nebalia*, consists of (1) the lower tendon between the adductor muscles, and (2) the upper lateral skeleton, *l.m.*, which bears the dorsal processes for the levator muscles, *t.mdb.l.*, and the processes *a.*, to the ventral cuticle, and which unite with one another by a large horizontal plate, *c.l.m.* In *Paranaspides*, as in *Nebalia*, this upper lateral skeleton is only united to the adductor tendon laterally, *l.m.mdb.*, whereas in *Nyctiphanes* and *Hemimysis* this union extends right across, and the mandibular tendon is not differentiated from the upper part of the mandibular skeleton. The maxillulary plate is large in both *Paranaspides* and *Nyctiphanes*, and is united anteriorly by lateral processes to the upper mandibular skeleton, as in *Nebalia*, and posteriorly joins the smaller maxillary plate, a union comparable with that of *Nebalia* between maxillulary and carapace adductor plates. In *Nebalia*, *Hemimysis*, and *Paranaspides* similar vertical struts, *e.*, extend upwards from the mandibular maxillulary intersegment for



Nebalia — *Hemimysis* — *Nyctiphanes* — *Paranaspides*

Fig. 17.—Reconstructions of the endoskeleton of the adult *Nebalia* (compare fig. 15 of a young specimen), *Nyctiphanes couchii*, *Paranaspides lacustris*, and *Hemimysis Lamornæ* viewed from above. Only the major bars and plates are shown, the smaller extensions of the plates into the muscles being omitted; such extensions are particularly numerous in *Nebalia*, arising from the carapace adductor tendon. The skeleton lying nearer to the ventral surface is tinted more darkly than the upper extensions. The intersegmental connections of the skeleton to the ventral ectoderm on the inner sides of the limbs when well formed are indicated in black. In all four animals the endoskeleton is an elaboration of the three primary bars of the mandibular, maxillulary, and maxillary segments. For further description see the text. *a.*, anterior extension of upper lateral mandibular skeleton uniting with the exoskeleton in front of the mandible at the sides of the labrum. *b.*, anterior extension of upper lateral mandibular skeleton to dorsal body wall. *c.*, anterior extension from the tendon of the dorso-ventral mandibular muscles, lying at the ventro-lateral border of the stomach. *c.add.t.*, plate formed by tendon of carapace adductor muscles. *c.l.m.*, median transverse connection between the lateral mandibular skeleton. *d.*, anterior extension of upper lateral mandibular skeleton along the sides of the stomach. *e.*, endoskeletal strut extending vertically upwards from the mandibular-maxillulary intersegmental furrow. *e.pl.*, ectodermal intucking passing inwards from the postero-lateral part of the maxillulary segment, just above the base of the maxillule, and uniting with the major endoskeleton in *Nebalia*, *Hemimysis*, and *Paranaspides*. *f.*, intersegmental union of maxillulary endoskeleton to cuticle at sides of paragnath. *h.*, intersegmental union of maxillary endoskeleton to cuticle between maxilla and maxillule at inner sides of limb bases. *l.m.*, lateral mandibular skeleton. *l.m.mdb.*, connection of lateral mandibular skeleton to tendon of mandibular adductor muscle. *mx.1.t.*, plate formed by maxillulary tendon. *mx.2.t.*, maxillary tendon. *t.mdb.l.*, tendon of dorso-ventral mandibular muscle. *x.*, union between carapace adductor and mandibular adductor tendon. *y.*, union between maxillulary adductor and mandibular adductor tendons. *z.*, strut extending backwards to body wall.

the insertion of dorso-ventral muscles. These struts appear absent in *Nyctiphanes*. Finally, in *Paranaspides* and *Nebalia* hollow intuckings pass horizontally inwards from the outer side of the base of the maxillule in the hinder part of this segment, *e.pl*. These intuckings unite with the maxillulary plate in *Paranaspides* and with the carapace adductor tendon in *Nebalia*, and may be homologous with the larger intuckings in a similar position which form the endoskeletal plate in *Hemimysis* and *Gennadas*. In *Hemimysis* this plate is an extensive hollow structure and the maxillulary bar degenerates. Thus the endoskeleton of *Nebalia* resembles the simpler Malacostraca in essential characteristics, but is peculiar in that the maxillary bar divides into carapace and maxillary adductor muscle tendons.

The form of the adult decapod endophragmal system is more fully known, although details of its development are not available. In *Astacus*, for example, in association with the larger size of the animal, the intersegmental endophragmal components are larger in size and more firmly united to the body wall, and besides being continuous across the nerve cord, are produced into flanges and processes for muscle insertions. Support in the region of the mouth parts is provided by a large " cephalic apodeme " united with extensions from the tendons of the mandibular adductor muscle and the " musculus dorso-ventralis posterior " of SCHMIDT (see GROBBEN, 1917, Plate I). In *Penœus* these two tendons are widely separated, and between them the maxillulary muscles are seen inserted upon a median portion of the endoskeleton, which is also united with the mandibular adductor tendon by struts (GROBBEN, 1917, Plate I, fig. 4). The tendons of the mandibular adductor muscle and of the " musculus dorso-ventralis posterior " of decapods are probably homologous with the mandibular adductor and carapace adductor tendons of *Nebalia* (see below). Possibly the maxillulary skeleton figured by GROBBEN for *Penœus* represents the maxillulary bar. If this is so, then part at least of the mouth part endoskeleton of *Penœus* is comparable with that of *Nebalia*, *Hemimysis*, the Syncarida, and *Nyctiphanes*, in that it is formed by the three intersegmental bars of the mandibular to maxillary segments; and the *Astacus* condition could be readily derived from that of *Penœus* by further elaboration and fusion of parts.

Among the Eumalacostraca, a fully-formed carapace adductor muscle is absent, but the homologue of this muscle has been claimed by GROBBEN (1917) to be present in a reduced state in the Anomura and most Macrura as the " musculus dorso-ventralis posterior." This conclusion is based on adult anatomy only. GROBBEN further considers the carapace adductor of the Branchiopoda, *Nebalia* and these Eumalacostraca to be homologous muscles belonging to the maxillulary segment.

That the carapace adductor muscle is a maxillulary structure appears to be true for the Branchiopoda, where it is innervated by a dorsal nerve from the maxillulary ganglion (*Limnadia*, etc.); where the muscle rudiment arises from the maxillulary somite and corresponds with the lateral muscles of the first maxilla (*Estheria*, see CANNON, 1924); and where the tendon between the muscles arises from the ectoderm just behind the dorso-ventral mandibular muscles (CANNON, 1924), and thus probably arises from maxillulary ectoderm. In *Nebalia*, on the contrary, the muscle is developed from the maxillary somite and its tendon from that for the maxilla, and only late in development does the tendon and part of the muscle move forwards above the maxillule. At this stage a pair of dorsal nerves grow upwards from the hinder part of the maxillulary ganglion to supply the carapace adductor muscle.

Until the development of the " musculus dorso-ventralis posterior " and its tendon in the decapods has been followed, it cannot be determined with certainty whether it is homologous with the maxillary carapace adductor of *Nebalia* or the maxillulary adductor of the Branchiopoda (and also Ostracoda). The evidence put forward by GROBBEN concerning its maxillulary nature does not appear quite conclusive. The muscle (GROBBEN, 1917, p. 474) runs from the carapace behind the cervical furrow above the maxilla, and passes into a broad tendonous band inserted on to the lateral edges of the head apodeme, and is innervated from the maxillulary ganglion. *Penæus* shows the simplest head skeleton of the Natantia examined by GROBBEN, and here the mandibular and carapace adductor tendons are separate. This was taken by GROBBEN to support the agreement with *Nebalia*, assuming the tendon in the latter to be maxillulary. However, if his figure of *Penæus* (Plate 1, fig. 4) is compared with fig. 15 of *Nebalia*, the following close similarities can be seen. The mandibular adductor tendons are clearly comparable, *Mds.* and *mdb.t.* ; the maxillulary muscles, *mx.*1.*a.*, *mx.*1.*b.*, and *Dv.*, are inserted on to the maxillulary tendons *mx.*1.*t.* and the unnamed tendon in GROBBEN'S figure ; while in both animals these maxillulary tendons are united to those of the mandibular adductor, *y.* and *Li.* Finally, the carapace adductor tendon, which in *Nebalia* is part of the maxillary tendon, in position resembles the tendon of the carapace adductor " S.M." of *Penæus*, which lies well behind the maxillulary skeleton. If these comparisons are justifiable, then the carapace adductor and its tendon in *Penæus* appears truly comparable with that of *Nebalia*, and is maxillary rather than maxillulary in origin. Thus GROBBEN'S conclusion that the homologue of the carapace adductor of *Nebalia* can be found in the Decapoda would be substantiated. However, this muscle and its tendon, being maxillary in origin, cannot be comparable with that of the Branchiopoda and probably Ostracoda, where it is a maxillulary structure, while it is certainly unlike the preoral carapace adductor of the Cirripedia.

Thus, to summarize, the Malacostracan endoskeletal system appears to be composed of a series of horizontal intersegmental bars and of apodemal ingrowths. This system is elaborated first in the region of the mouth parts, and in more specialized forms a complex endophragmal system is developed in other regions. The skeleton in the mouth part region is based on the embryonic mandibular, maxillulary, and maxillary intersegmental bars which become complex in shape and may fuse together considerably. A carapace adductor tendon may be formed from the maxillary bar ; and parts of the original series of bars may be lost owing to development of apodemal structures in the maxillulary segment.

General Conclusions.

In conclusion, the main points emerging from the above discussion can be summarized. It has been shown that *Nebalia* resembles the Eumalacostraca in all its developmental processes, and differs profoundly from the other groups. Thus the spatial relations between the endoderm and mesoderm and the form of the germinal disk show a general similarity to the Eumalacostraca and direct contrast to the other sub-classes; this alone emphasizes the close connection between the Leptostraca and Eumalacostraca.

It has been seen that in some features of its development *Nebalia* resembles the Peracarida, while in others direct comparison may be made with the Decapoda. Such features are listed in Table IV, but these interpretations must be considered provisional to a certain extent. Accurate knowledge of the development of Peracarida and Decapoda is limited to a few types, and until further work is done, similarities and differences between the two groups can only be appreciated imperfectly.

Further, in some respects the development of *Nebalia* may be considered to show primitive Malacostracan features, modifications of which could give rise to conditions found in Peracarida and Decapoda. (We have no knowledge of the development of the other Malcostracan groups.) (1) The origin and form of the endodermal layer may be so interpreted. It appears first as free yolk cells and an epithelial plate. From such a type the conditions in various Peracarida could be derived. All the endoderm first appears as yolk cells in *Hemimysis*, and in forms with a long proctodœum and short mid-gut the bulk of the yolk cells degenerate, in either case all or some of the yolk cells ultimately form the mid-gut epithelium. In the Decapoda, some forms behave much as does *Nebalia*, in others some yolk cells are said to degenerate, while in *Astacus* the yolk cells remain in contact, instead of wandering freely, and so form the gut epithelium. (2) The formation of the liver in *Nebalia* by direct modification of part of the yolk sac is a very simple and probably primitive process, while the formation of a mesodermal liver in some Peracarida (*Hemimysis*, etc.) is surely a secondary phenomenon. The Decapodan liver development, in so far as it is known, either resembles that of *Nebalia* or is more complicated. (3) The absence of any discontinuity in development between thorax and abdomen, as shown by the behaviour of the somites, gonads, etc., may be a primitive feature which has become modified in many Malacostraca in accordance with precocious development of various parts.

The persistence in the adult *Nebalia* of features shown only in embryo Eumalacostraca may be noted and perhaps considered primitive. Such are (4) the presence of cephalic liver lobes, shown by some Peracaridan and Decapodan embryos as anterior lobes of the yolk sac. (5) The unconstricted posterior abdominal region, where the sixth and seventh segments are free and the caudal furca large. The development of the furca in *Nebalia* is essentially similar to that of the reduced furca of the embryo mysid, which has no mesoderm and is lost at the embryonic ecdysis. (6) Finally the long heart, extending through about 13 segments with segmental arteries leaving it, may be regarded as more primitive than other Malacostracan hearts which are shorter and in the adult show reduction and specialization of arteries leaving the organ.

TABLE IV.

Features in which *Nebalia* resembles the Peracarida.	Features in which *Nebalia* resembles the Decapoda.
Segmentation and formation of blastoderm, pp. 168–171, 211.	——
——	Late determination of germ layers, pp. 177, 211.
	Shape of early germinal disk, pp. 171, 211.
	Subsequent development of germinal disk, pp. 171, 179, 211, 213.
Origin of ectodermal teloblasts and presence of a mid-ventral ectodermal teloblast, pp. 178, 212.	——
Number of mesodermal teloblasts, pp. 179, 212.	
Even development of the body from before backwards, pp. 171, 179, 191, 217.	
——	Early cessation of gastrulation, pp. 179, 213.
	Method of closure of the blastoporal area, pp. 180, 213.
	Structure and growth of the caudal papilla and formation of the proctodœum, pp. 176, 179, 211–213.
	The endodermal cells from the blastoporal area form (1) yolk cells and (2) the endodermal plate, both of which become the mid-gut epithelium, pp. 178, 214.
	Origin of posterior liver lobes from the yolk sac epithelium, pp. 183, 215.
Shape and subsequent subdivision of posterior liver lobes, pp. 183, 215.	
Embryo develops entirely in the brood pouch, and after ecdysis becomes free as a miniature adult, pp. 177, 211.	

Thus *Nebalia* appears to be entirely Malacostracan in its affinities, and gives no assistance in any attempt to bridge the gulf between the higher Crustacea and the other groups. The Leptostraca may perhaps be considered to have separated early from the Malacostracan stem, before the divergence of its four main divisions. At the present day *Nebalia* combines some primitive Malcostracan features with others common to the Peracarida and to the Decapoda, and at the same time shows many specialized peculiarities of its own.

SUMMARY.

(1) In the freshly-laid egg the nucleus and most of the cytoplasm are central. It is not known whether fertilization occurs, and scarcity of males suggests its possible absence.

(2) The cytoplasm rises to the surface in several places, forming several " pseudo-blastomeres," only one of which contains the nucleus. The position of the nucleus and cytoplasm during all segmentation stages appears to be peripheral.

(3) A polar cap of four blastomeres is formed which proliferates to form a single-layered blastoderm covering the yolk. The vegetal pole is the last area to be covered, and the blastomeres are here very thin.

(4) A thickening of the blastoderm is formed on the future ventral side of the embryo, so establishing the germinal disk.

(5) The development of the germinal disk and the external changes in shape are described. A U-shaped germinal band is formed, from the arms of which the naupliar segments are developed. Anteriorly the arms become united, as in Decapods, to form the labral rudiment. The trunk is developed progressively, from the base of the U-shaped band, backwards. The vitelline membrane and two embryonic cuticles are shed successively.

(6) A blastoporal area of immigrating cells is established at the posterior end of the germinal disk. Germ layers and genital rudiment are not differentiated externally. Gastrulation by immigration forms an undifferentiated mesendodermal mass of cells internal to the blastoporal area.

(7) The mesendodermal mass becomes differentiated into mesoderm anteriorly and endoderm posteriorly. Such spatial relations are characteristic of the Malacostraca and unlike the lower Crustacea.

(8) Mesodermal cells spread forwards to form the head mesodermal bands which form the somites of the antennulary to mandibular segments.

(9) The endoderm (1) is differentiated from the inner cells of the mesendodermal mass which absorb yolk into large vacuoles, so becoming " yolk cells." These yolk cells spread separately round the yolk, ultimately forming a continuous layer, (2) appears as an epithelial endodermal plate internal to the blastoporal area which is differentiated directly from the posterior part of the mesendodermal mass. The yolk is thus enclosed in a yolk sac which is composed mainly of yolk cells, but posteriorly is formed by the endodermal plate.

(10) The mesoderm of the preantennulary somites immigrates inwards from the germinal disk in front of the antennules.

(11) Teloblasts are differentiated first at the sides of the blastoporal area and later lie at its anterior ventral lip. Eight mesodermal teloblasts are formed from the mesendodermal mass, and their descendants form all somites from the maxillulary segment backwards. One median and nine ectodermal teloblasts are formed. The

shape of the caudal papilla is as in the Decapoda, and the teloblasts form a complete ring around it.

(12) The formation of the mesodermal somites and of segmental ectoderm from the descendants of the teloblasts occurs much as in *Hemimysis*, but owing to the position of the teloblasts, their descendants form all sides of the caudal papilla.

(13) Some cells from the mesendodermal mass remain behind the teloblasts to form the telson mesoderm which supplies the caudal furca.

(14) Gastrulation ceases early and the proctodœum is formed from the old blastoporal area.

(15) The endodermal plate grows firstly by division of its component cells and secondly by the addition of yolk cells which become epithelial at its edges. As the caudal papilla is formed, the posterior part of the plate dips into it and forms the intestine extending along the papilla. The anterior part of the plate gradually extends forwards by transformation of the yolk cells, till finally the whole yolk sac becomes epithelial.

(16) From the epithelial yolk sac the long mid-gut and liver lobes are developed. The pair of primary posterior liver lobes arise as direct outgrowths from the yolk sac in the maxillary region. The cephalic liver lobes are the persistent anterior lobes of the yolk sac which are left on either side of the developing anterior aorta. These lobes are present in the embryos only of other Malacostraca.

(17) Peristalsis of the embryonic gut is described in relation to the yolk absorption. This movement starts very early, and by it yolk spheres are separated from the cephalothoracic yolk mass and passed into the intestine for liquifaction and absorption. The rhythmic movement is carried out by minute strands of mesoderm surrounding the gut, and is independent of nervous control. The effects of potassium chloride and chloretone on the peristalsis are described for comparison with other types of rhythmically contractile tissue.

(18) The growth of the preantennulary somites to form the anterior aorta is described. In early stages the somites are solid, and no extensive cœlomic space is developed or persists in the adult.

(19) The development of the trunk somites is described. Owing to the small amount of yolk in the caudal papilla, the somites extend from dorsal to ventral sides of the body from their earliest appearance, and thus differentiate *in situ*, instead of having to grow up the sides of the body. Gut musculature and heart floor are precociously developed. Division of somites into dorsal and ventral blocks takes place, and the dorsal blood vessel is formed by the U-shaped upper ends of the somites. Cœlomic spaces occur in all except the most anterior trunk somites (these are compressed by the distended anterior part of the yolk sac), but do not persist in the adult. The musculature is developed much as in *Hemimysis*.

(20) Part of the seventh abdominal somites and the telson mesoderm form the extensive proctodœal muscles.

(21) The development of the heart is followed, together with the formation of paired segmental arteries, leaving the heart in the thoracic and abdominal segments which have formed it. These arteries are compared with the paired sternal and hepatic arteries of a mysid.

(22) The genital rudiment appears late at the end of embryonic life. Pairs of germ cells appear segmentally in the walls of the shrinking cœlomic sacs which form the pericardial floor. These segmental rudiments enlarge and project below the pericardial floor, and in the young adult unite longitudinally. In older adults mesoderm invests the genital rudiment, and this investment then grows out to form the genital duct. Only the developing ovary has been observed.

(23) The major portion of the adult endoskeleton is described and its development followed. Horizontal intersegmental ectodermal bars are formed all along the body and become elaborated in the region of the mouth parts where the bars of the mandibular, maxillulary, and maxillary segments form the bulk of the endoskeleton.

(24) The carapace adductor muscle is maxillary in origin, and its tendon is formed from part of the ectodermal maxillary bar. The homologies of this muscle are discussed. It may be compared with the rudimentary carapace adductor of some Malacostraca, if this should prove to be maxillary in origin, but it is unlike the maxillulary carapace adductor of the Branchiopoda.

(25) The endoskeletons of some of the simpler Malacostraca, *Paranaspides,* a Euphausid and a Mysid, are described for comparison with *Nebalia.* In all, the major part of the endoskeleton is formed from the mandibular-maxillary bars. The endoskeleton of *Nebalia* resembles that of the Malacostraca and differs profoundly from those of the lower Crustacea.

(26) The structure and development of the antennal gland is described. A valve is present between duct and end sac resembling the valves of Malacostraca such as *Anaspides* and *Gennadas.* The development is essentially similar to that of *Hemimysis.*

(27) The maxillary gland consists of a large but compressed end sac, probably opening to the exterior by a very short duct. At no stage is it better developed than in the adult, and it is not formed until after the young has emerged from the brood pouch.

(28) The developmental processes of *Nebalia* resemble those of the Eumalacostraca. Some of its features may be considered to be primitive Malacostracan processes, in some it resembles the Peracarida such as a Mysid, and in others it shows features found in the Decapoda. The Eumalacostraca show certain developmental conditions which are lost in the adult, some of these are repeated in *Nebalia,* but persist throughout life.

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KEY TO LETTERING OF THE FIGURES.

a.a., hæmocœlic space of anterior aorta.
a.g., one of the paired segmental arteries leaving the heart and supplying sinuses round the ovary, intestine, etc., in the fat body.
a.t., an anterior trunk segment.
*a.*1., antennule, or base of antennule.
*a.*1.*m.*, antennulary mesoderm.
*a.*2., antenna, or base of antenna.
*a.*2.*p.e.*, posterior external angle of base of antenna.
*ab.*1.,–*ab.*7., first–seventh abdominal segment.
*ab.*4.*e.*, ectoderm of fourth abdominal segment.
*ab.*7.*g.m.*, gut mesoderm from seventh abdominal somite.
*ab.*1.*l.*,–*ab.*5.*l.*, first–fifth abdominal limb.
*ab.*7.*l.m.*, dorso-lateral mesoderm of seventh abdominal segment.
*ab.*1.*m.*,–*ab.*4.*m.*, mesoderm of first–fourth abdominal segment.
*ab.*7.*v.m.*, ventral mesoderm of seventh abdominal segment.
b., blastoporal area.
b.hæ., body hæmocœl.
b.i., cells passing inwards from blastoporal area.
b.p., pits on blastoporal area left by immigrating cells.
b.v., vascular spaces around viscera and between fat body cells.
b.v.g., vascular space around gonad.
b.v.h., vascular space of fat body opening by pore to body hæmocœl.
b.v.i., vascular space around intestine.
b.v.l., vascular space around liver.
b.v.p., venous space communicating with pericardium above and with spaces on outer side of body and limbs below.
b.v.s., segmental artery from heart to fat body.
br., brain rudiment.
c., carapace.
c.a., line of attachment of carapace fold to body.
c.add., carapace adductor muscle, or its rudiment.
c.add.e., lateral ectodermal attachment between maxilla and maxillule of carapace adductor tendon.
c.add.t., tendon of carapace adductor muscle.
c.f., caudal furca.
c.fu., caudal furrow.
c.p., caudal papilla.
c.p.e., edge of caudal papilla.

cu., cuticle shed at first ecdysis.
d., duct of antennal gland.
d.l.m., dorsal longitudinal muscle, or its rudiment.
d.m., dorsal mesoderm.
d.o., dorsal organ.
d.ost., dorsal ostium of heart.
e., ectoderm of teloblastic origin.
E., ectodermal teloblast or teloblasts.
e.s.a., end sac of antennal gland, or its rudiment.
e.s.m., end sac of maxillary gland.
e.t., horizontal ectodermal bar (tendon).
e.x., exit tube of antennal gland.
*e.*0.–*e.*9., descendants of ectodermal teloblasts *E.*0–*E.*9.
*E.*0., central (mid-ventral) ectodermal teloblast.
*E.*1–*E.*9., first–ninth paired lateral ectodermal teloblasts.
en., endodermal epithelium forming yolk sac, or mid-gut; or dotted line indicating the area over which endodermal yolk cells have wandered from the mesendodermal mass.
en.p., endodermal plate, composed of epithelial endodermal cells.
en.y., endodermal yolk cells, or endodermal cells absorbing yolk into a vacuole, so forming "yolk cells."
ey., eye, or eye stalk.
f., mid-ventral connection to ectoderm of mandibular tendon.
f.a., origins of paired segmental arteries from heart floor.
f.b., fat body.
*fig.e.*1, *fig.e.*2, levels of sections shown in figs. *e.*1 and *e.*2 on same plate.
*fig.h.*1., level of section shown in fig. *h.*1 on same plate.
g., mid-ventral ectodermal connection of maxillulary tendon, or the muscle formed from the connection.
G., gonad, genital rudiment, or germ cell.
g.b., arm of U-shaped germinal band which forms the "naupliar" region of the body.
g.d., germinal disk composed of large cells on the ventral side of the embryo.
g.m., gut mesoderm.
g.s., longitudinal strand of mesoderm from the somite to yolk sac.
h., cavity of heart, or dorsal blood vessel.
h.a., dorso-lateral connection of heart to body wall.
h.f., floor of dorsal blood vessel.
h.m., muscle fibrils of heart wall.
hœ., hæmocœl.
int., intestine (mid-gut).
j., junction of ectoderm formed by teloblasts with the ectoderm of the germinal disk.
l.a., anterior liver lobe.
l.c.m., circular muscle round liver lobe.
l.m., limb mesoderm.
l.ost., lateral ostium of heart.
l.p., posterior liver lobe.
l.p.m., mesodermal investment of posterior liver lobe.
l.p.r., rudiment of posterior liver lobe.
l.r., thickening forming rudiment of rostrum.
l.v., lateral blood vessel from limb base to pericardium.

lb.m., labral mesoderm.
lbr., labrum.
le., leucocyte.
m., teloblastic mesoderm.
m.en., mesendodermal cells within blastoporal area.
M., mesodermal teloblast.
M.E., level of ectodermal and mesodermal teloblasts which are not cut in this section of the embryo.
*M.m.*3.–*M.m.*4., etc., arrows showing positions of third and fourth mesodermal teloblasts and their descendants.
*M.*1.–*M.*4., first–fourth paired mesodermal teloblasts.
mdb., mandible or its rudiment.
mdb.g., mandibular ganglion, or its rudiment.
mdb.p., mandibular palp.
mdb.t., ectodermal tendon of mandibular adductor muscles.
*mx.*1., maxillule, or its rudiment, or level of maxillulary segment.
*mx.*1.*g.*, maxillulary ganglion.
*mx.*1.*p.*, maxillulary palp.
*mx.*1.*t.*, ectodermal tendon of maxillulary adductor muscles.
*mx.*1.*t.e.*, lateral ectodermal attachment of maxillulary tendon.
*mx.*2., maxilla.
*mx.*2.*g.*, maxillary ganglion.
*mx.*2.*m.*, mesoderm of maxillary segment.
*mx.*2.*t.*, ectodermal tendon of maxillary adductor muscles.
n.c., nerve cord.
n.f., nerve fibres.
n.m., head mesodermal bands of blastoporal origin lying below the paired arms of the germinal disk where the naupliar appendages will be formed.
o.r., optic rudiment.
p., paragnath.
p.a., posterior aorta.
p.b., rudiment of lateral base of pericardial floor.
p.c.f., pericardial floor.
p.d., rudiment of posterior gut diverticulum.
p.hæ., pericardial hæmocœl.
p.m., preantennulary mesoderm or somite of extrablastoporal origin, forming anterior aorta in fig. 5 and fig. 23 *f.* 1
p.m.a., anterior part of preantennulary somite which will form the anterior aorta.
p.m.(*a.a.*), preantennulary mesoderm with aorta between.
p.m.c., preantennulary cœlomic space.
p.m.s., posterior part of preantennulary mesoderm which invests the stomodœum and supplies the labrum.
pr., proctodœum.
pr.d., rudiment of proctodœal dilator muscles.
r., rostrum.
r.r., rostral rudiment.
s., chitinous strut from ventral ectoderm to maxillary tendon.
s.b., side margin of body visible through carapace.
s.g.b., median space between the arms of the U-shaped germinal band.

st., stomodœum.
t.m., telson mesoderm.
th.1.–*th*.8., first–eighth thoracic segment.
th.5.*c*.–*th*.6.*c*., cœlomic cavities of fifth and sixth thoracic segments.
th.5.*c.w.*, wall of fifth thoracic cœlomic space in pericardial floor.
th.1.*g*.–*th*.4.*g*., first–fourth thoracic ganglion, or its rudiment.
th.1.*l*.–*th*.8.*l*., first–eighth thoracic limb.
th.1.*m*.–*th*.8.*m*., mesoderm of first–eighth thoracic segment.
th.1.*t*.–*th*.4.*t*., ectodermal bars (tendons) of first–fourth thoracic segment.
v., valve between duct and end sac of antennal gland.
v.a., valve between heart and anterior aorta.
v.b.v.s., valve between heart and segmental artery.
v.i., remains of ventral intucking which forms part of intersegmental ectodermal bar.
v.l.m., ventral longitudinal muscle, or its rudiment.
v.m., ventral mesoderm.
vi., vitelline membrane.
X., peristaltic constriction of the intestine which is passing backwards.
y., yolk.
y.f., fluid yolk.
y.s., sphere of solid yolk from cephalo-thoracic region.

DESCRIPTION OF PLATES.

PLATES 20 AND 21.

FIGS. 18 and 19.—Figs. *a*–*e* are diagrammatic reconstructions, based on serial sections, of embryos in advancing stages of development, showing the germinal disk. In all the figures the internal cells are indicated in colour and drawn on the left side only, horizontal ruling represents the head band mesoderm, interrupted ruling represents undifferentiated mesendoderm, and the positions of blastoporal area and ectodermal teloblasts are shown by mechanical shading. In order to eliminate some of the terminal foreshortening of the germinal disk, the length of the visible long axis has been exaggerated. The black arrows indicate the planes of sagittal and parasagittal sections figured on Plates 22 and 25. Figs. *c*.1–*e*.1 are camera lucida drawings of whole mounts of the region surrounding the blastopore from embryos of the same age as in figs. *c*–*e*. The mesodermal cells could not all be satisfactorily seen in these preparations, and the positions of the mesodermal teloblasts alone have been inserted (in colour) by aid of sections.

(*a*) Embryo of the same age as fig. 21, *b*, Plate 23. The germinal disk, *g.d.*, is a thickening on one side of the embryo, and from the blastoporal area, *b.*, cells have immigrated inwards and forwards, *m.en.* Those most anterior will form the head band mesoderm, *n.m.*, while the rest of this mesendodermal mass will form both mesoderm and endoderm.

(*b*) Embryo older than the last and the same age as fig. 20, *d*, Plate 22. The germinal disk is now a U-shaped band, *g.b.* Immigration inwards from the enlarged blastoporal area has formed a more extensive mesendodermal mass, *m.en.*, which anteriorly has spread forming the head band mesoderm. A few cells from the mesendodermal mass have started to absorb yolk (not shown). From the arms of the germinal band a pair of cells have sunk below the surface, *p.m.*, forming the rudiments of the preantennulary somites (see also fig. 20, *d*, 1, Plate 22).

(*c*) Embryo older than the last and slightly younger than fig. 20, *e*, Plate 22. The rudiments of the three naupliar appendages and optic region are seen on the arms of the germinal band, the tips of which are closer together. Ectodermal teloblasts are differentiated from the sides of the blastoporal area. Endodermal yolk cells have separated off from the mesendodermal mass and spread below the disk as far as the dotted line, *en.*

(*c*, 1) Surface view of blastoporal region of the last stage. Six ectodermal teloblasts are clearly differentiated, but have not given descendants. Small crowded nuclei lie at the base of the arms of the germinal band, *g.b.*, and pits in the blastoporal area, *b.p.*, are left by the imigrating cells. No mesodermal teloblasts are yet formed. × 340 approx.

(*d*) Embryo older than the last and the same as fig. 20, *f*, Plate 22. The arms of the germinal band are united anteriorly. The ectodermal teloblasts form a continuous band round the lateral and anterior lip of the blastoporal area. The head band mesoderm shows three paired thickenings opposite the naupliar appendages. Four pairs of mesodermal teloblasts have been differentiated from the anterior edge of the mesendodermal mass, the arrows, *M.m.*4., etc., indicate the positions of the teloblasts and their rows of descendants. Endodermal yolk cells are numerous and have extended further, *en.*, and lie in the mid-ventral line as well as below the U-shaped band. The epithelial endodermal plate, *en.p.*, has been formed from the hinder part of the mesendodermal mass, and from adjacent yolk cells, and lies within and behind the blastoporal area.

(*d*, 1) Surface view of blastoporal region of the last stage. Seven paired lateral teloblasts, *E.*1–*E.*7, are united by a median teloblast, *E.*0., and some of their descendants can be seen in rows, *e.*2. The blastoporal area is pitted, and the limit of the naupliar region ectoderm is seen. Four pairs of mesodermal teloblasts are indicated, but not their descendants. × 340 approx.

(*e*) Embryo older than the last and slightly older than fig. 20, *g*, Plate 22. The union of the arms of the germinal band has enlarged and lies mainly between the antennulary rudiments, where it will form the labrum. The more numerous ectodermal teloblasts nearly enclose the blastoporal area. In front of the teloblasts the caudal furrow has appeared, *c.fu.*, so that the anterior teloblasts lie round the edge of the rudimentary caudal papilla, *c.p.e.* The enlarged preantennulary somites have shifted posteriorly and touch the head bands of mesoderm. The latter have united forming the future labral mesoderm, *l.m.* The mesodermal teloblasts have shifted to the positions indicated by the arrows, *M.m.*3., etc. Endodermal yolk cells have spread further and cover half of the yolk, *en.* The endodermal plate has enlarged, *en.p.*

(*e*, 1) Surface view of blastoporal region of the last stage. One median and eight paired ectodermal teloblasts are formed, and both mesodermal and ectodermal teloblasts tend to surround the blastoporal area. The caudal furrow and caudal papilla are seen, and the junction between teloblastic, *mx.*1. and naupliar, *mdb.*, ectoderm is clear. Gastrulation is ceasing and fewer pits lie in the blastopora area. × 340 approx.

PLATE 22.

FIG. 20.—A series of sections showing the processes of gastrulation, etc. The orientation of sagittal and parasagittal sections on the plate is shown by the arrow. × 220 approx.

(*a*) Sagittal section of an embryo slightly older than fig. 1, *i*. The blastoderm is thickened on one side of the embryo forming the germinal disk, *g.d.*, and the blastoporal area, *b.*, is just indicated by large cells, some of which are tending to immigrate inwards.

(*b*) Almost sagittal section of an embryo slightly older than the last and the same age as fig. 18, *a*, Plate 20. The ventral area of thickened blastoderm is simple, and about 12 mesendodermal cells, *m.en.*, have immigrated inwards from the blastoporal area, and are shifting forwards.

(*c*) Almost sagittal section of an embryo older than the last. Mesendodermal immigration has proceeded further, and the cells have spread in front and behind the blastoporal area. The latter will form yolk cells.

d. and *d.*1. Almost sagittal and parasagittal sections of an embryo older than the last and the same age as fig.18, *b*, Plate 20. The germinal disk has now formed the U-shaped band, so that the blastoderm is thin in the middle line anteriorly, *s.g.b.*, and thick along the arms of the band, *g.b.* The anterior cells from the mesendodermal mass have spread forwards, *n.m.*, forming the head bands of mesoderm which will supply the naupliar appendages. The first cell of the preantennulary mesoderm, *p.m.*, is passing inwards from the anterior end of the germinal band. A few mesendodermal cells (not seen in this section) are starting to absorb yolk.

(*e*) Parasagittal section of an embryo older than the last and slightly older than fig. 18, *c* and *c*, 1, Plate 20, passing through the edge of the blastoporal area. In the anterior lip of the blastoporal area lies one of the ectodermal teloblasts, *E.* Two of its descendants are seen anteriorly, *j.*, marking the junction between this teloblastic ectoderm and that of the germinal disk. Differentiation of mesodermal teloblasts, *M.*, has started in the mesendodermal mass below the ectodermal teloblasts. The posterior end of the head band mesoderm is seen at *n.m.* The inner cells from the mesendodermal mass have absorbed yolk into vacuoles so forming endodermal yolk cells, *en.y.* Immigration from the blastoporal area is still proceeding.

(*e*, 1) Section tangential to the blastoporal area of an embryo slightly older than *e*. The arrows on fig. *e* represent the plane of the section. The ectodermal teloblasts, *E.*0.–*E.*5., appear in surface view, and within them the eight mesodermal teloblasts, *M.*1.–*M.*4. Posterior to the cells passing inwards from the blastoporal area, *b.i.*, lies the beginning of the endodermal plate, *en.p.*, and beyond it many endodermal yolk cells, *en.y.*, lie over the yolk.

(*e*, 2) Transverse section of an embryo of the same age as fig. *e*, passing across the arms of the U-shaped germinal disk. The arrows on fig. *e* represent the plane of this section. The head band mesoderm, *n.m.*, and a few yolk cells are seen.

(*f*) Parasagittal section of an embryo older than the last and of the same age as fig. 19, *d* and *d*, 1, Plate 21, passing through the edge of the blastoporal area and the base of one arm of the U-shaped germinal band. All mesodermal teloblasts are now differentiated. Ectodermal and mesodermal teloblasts are seen at the margin of the blastoporal area both anteriorly and posteriorly (compare fig. 19, *d*, 1, Plate 21.) The first rudiment of the mandible, *mdb*, is seen at the base of the arm of the germinal band, and within it the head mesoderm, *n.m.* Behind the mandible lies the junction of teloblastic ectoderm and that of the germinal disk, *j.* The teloblastic mesoderm, *m.*, is clearly differentiated from head band mesoderm. Endodermal yolk cells, *en.y.*, are larger and more numerous and have spread farther round the yolk. Posteriorly they are uniting to the edge of the growing endodermal plate, *en.p.*

(*g*) Almost sagittal section of an embryo older than the last. A caudal furrow, *c.fu.*, lies behind the maxillulary segment. Immigration from the blastoporal area is less active. A dividing ectodermal teloblast, *E.*, a mesodermal teloblast, *M.*, and one of its descendants are seen at the tip of the caudal papilla, *c.p.* (Teloblasts are not seen behind the blastoporal area as the section is median, compare fig. 19, *e*, 1, Plate 21, which is slightly older.) The endodermal yolk cells have spread farther and now lie from the antennal rudiments to behind the endodermal plate. They are seen uniting with the anterior and posterior margins of the latter. A small undifferentiated mesendodermal mass is still apparent, *m.en.*

(*h*) Sagittal section of an embryo older than the last and not so old as fig. 3, B. The caudal furrow is deeper and the caudal papilla more elongated. Segments as far as the fourth thoracic have been formed by the teloblasts. Teloblasts, *M.* and *E*, of the future ventral side of the body lie at the tip of the caudal papilla, and the arrow, *M.E.*, indicates the level of teloblasts on the future dorsal side of the body, which as yet have not met in the median plane, and so are not seen in sagittal section. Gastrulation has just ceased and the proctodœal invagination, *pr.*, has been formed from the blastoporal area. The enlarged endodermal plate is cup-shaped, with yolk cells uniting to its edges. The mesendodermal mass has disappeared except for a few cells within the proctodœum which will form the telson mesoderm, *t.m.*

(*h*, 1) Transverse section of an embryo the same family as the last, but slightly less advanced. The plane of the section is indicated by arrows on fig. *h*. Gastrulation is ceasing, but the proctodœum has not yet appeared. The descendants of the ectodermal and mesodermal teloblasts, *e.* and *m.*, are seen passing out sideways from the caudal papilla, compare fig. 19, *e*, Plate 21. The endodermal plate is cut transversely and shows yolk cells uniting with its edges. A few undifferentiated mesendodermal cells lie within the blastoporal area, *m.en.* The median ones will shift forwards and become yolk cells, while the more darkly staining lateral ones, *t.m.*, will form the telson mesoderm, see also fig. *h*.

PLATE 23.

FIG. 21.—Sections showing the early development of mesodermal somites and endodermal musculature. × 530 approx.

(*a*) Oblique transverse section of the tip of the caudal papilla of an embryo slightly younger than fig. 3, B, along the plane indicated by the arrows. The mesodermal somites of all thoracic segments have been formed. The section passes through the ectodermal and mesodermal teloblasts, all of which are now differentiated, the proctodœum, *pr.*, lying within them. The median and nine paired ectodermal teloblasts form a complete ring around the caudal papilla, compare fig. 19, *e*, 1, Plate 21. (In older stages the caudal furrow deepens and the caudal papilla narrows so that its area in transverse section becomes less, as in figs. *c*, 2–*c*, 4.)

(*b*) Frontal section of the caudal papilla of an embryo older than the last in which the mesoderm of thoracic and first abdominal segments has been formed. The plane of the section is indicated by arrows on fig. 3, B. Successive stages in the formation of solid mesodermal somites, *th.*3, from the mesodermal teloblasts, *M.*, are seen. Anteriorly the dorsal longitudinal muscle, *d.l.m.*, is forming. The dorsal surface of the endodermal yolk sac or mid-gut, *en.*, has been cut. Behind the teloblasts at the side of the proctodœum lie the telson mesoderm cells, *t.m.*, compare fig. 20, *h* and *h*, 1, Plate 22.

(*c*) Frontal section of the caudal papilla of an embryo older than the last and the same age as fig. 3, C, where arrows indicate the plane of the section. This embryo was dissected out of the vitelline membrane, and the caudal papilla cut off and fixed in Zenker. Owing to the longitudinal curvature of the papilla, a frontal section is not at the same relative level throughout. The development of mesodermal somites is seen in advancing stages along the papilla, that of the fourth abdominal segment having been laid down. A strand of mesoderm, *g.s.*, passes out from the hinder somites to the gut (see also fig. *c*, 4), and anteriorly this has formed circular strands round the gut, *g.m.*, seen here cut transversely. These strands are so small, and frequently lie so close to the gut wall, that detection may be difficult. The arrows indicate the levels of transverse sections in figs. *c*, 2–*c*, 4.

(*c*, 1) The next section of the same embryo passing ventral to the last. The cavity of the proctodœum is seen. Mesodermal teloblasts on both sides are in division, and the telson mesoderm lies in the same position as in fig. *b*. The extension backwards of the ectoderm behind the teloblasts is forming the rudiment of the caudal furca.

(*c*, 2–*c*, 4) Transverse sections of the caudal papilla of an embryo the same age as fig. *c*, and fixed in the same manner. The arrows indicate the planes of the sections.

(*c*, 2) Some of the teloblasts are seen, the rest lying anterior to the section. Dorsally lies the proctodœal intucking, *pr.*, and within the teloblasts two groups of telson mesoderm cells lie opposite the base of the caudal furca, which appears in the next posterior section.

(*c*, 3) Second abdominal segment showing the blind posterior end of the endodermal mid-gut or yolk sac, and the descendants of the 19 ectodermal and eight mesodermal teloblasts (see fig. *a*). The latter have divided once giving eight mesodermal cells on either side. The somites are quite free from the gut. The descendants of ectodermal teloblast I are forming the nerve cord rudiment, *e.*1.(*n.c.*).

(*c*, 4) Eighth thoracic segment showing further development of the mesodermal somites. A longitudinal strand, *g.s.*, has grown out towards the gut (see fig. *c*), and from this a circular band of tissue has grown round the gut. Dorsally this band forms the heart floor and bears a mid-dorsal nucleus. (Several such bands of tissue with a median dorsal nucleus may be present in each segment.) The ectodermal cells have multiplied and the 19 rows of descendants from the teloblasts are no longer detectable.

PLATE 24.

FIG. 22.—Transverse sections showing further development of the mesodermal somites. Figs. *a–c* are parts of sections of whole unhatched embryos, and figs. *d–f* are from whole-hatched embryos. The embryos do not show the gut mesoderm clearly, as in fig. 21, *c–c*, 4, Plate 23, in which the embryos were cut up before fixation. × 530 approx.

(*a*) Transverse section through the caudal papilla of an embryo just younger than text-fig. 3, D, where arrows indicate the plane of the section. The second abdominal somite here seen is more advanced than in fig. 21, *c*, 4, Plate 23. The strand from somite to gut, *g.s.*, and the heart floor are seen as before, but the somite has divided into dorsal and ventral parts, *d.m.* and *v.m.*

(*b*) Transverse section of third abdominal segment of an embryo older than the last. The dorsal mesoderm has extended latero-ventrally into the lateral limb bulge, where it forms the base of the pericardial floor, *p.b.*, and the rudiment of the limb mesoderm, *l.m.* The nerve cord, *n.c.*, is developing.

(*c*) Transverse section of the eighth thoracic segment of an older embryo ready to hatch, see fig. 3, E, where arrows indicate the plane of the section. The dorsal longitudinal muscle rudiment, *d.l.m.*, in the dorsal mesoderm is larger, the caudal papilla is thickened and the dorsal blood vessel cavity is enlarged.

(*d*) Transverse section through the sixth thoracic segment of an embryo older than the last which hatched on fixing. The plane of the section is indicated by the arrow in fig. 4, G. The dorsal mesoderm has developed further and extended dorsally, so forming the lateral wall of the dorsal blood vessel, and the cœlomic cavity has appeared laterally, *th.*6.*c.*

(*e*) Transverse section through the first abdominal segment of an embryo older than the last. The gut is constricted at this level, but not elsewhere in the embryo. The body has enlarged. The dorsal longitudinal muscle rudiment is separating from the outer wall of the much enlarged cœlomic sac, and muscle fibrils have appeared in both dorsal and ventral longitudinal muscle rudiments, *d.l.m.* and *v.l.m.* The cœlomic sac, *ab.*1.*c.*, has pulled away from the ectoderm, so leaving the lateral wall of the dorsal blood vessel attached to the body wall by delicate strands.

(*f*) Transverse section of an embryo after the first ecdysis, through the fifth thoracic segment, see fig. 4, I, where an arrow indicates the plane of the section. The roof of the dorsal blood vessel has been formed by the approximation of its lateral walls, and the cœlomic spaces, *th.*5.*c.*, are much reduced and restricted to the horizontal part of the pericardial floor. The latter, *p.c.f.*, extends ventrally to the limb base. The dorsal longitudinal muscle, *d.l.m.*, is separated from the cœlomic sac. The paired posterior liver diverticula, *l.p.*, lie at the sides of the mid-gut and are invested with mesoderm, *l.p.m.*, some of which later forms the fat body.

PLATE 25.

FIG. 23.—Sections showing the development of the preantennulary mesoderm. The first appearance of this somite is seen in fig. 20, *d*, 1, Plate 22.

(*a*) Parasagittal section through an embryo younger than fig. 3, A, and older than fig. 19, *d*, Plate 21, where an arrow indicates the plane of the section. The preantennulary cells, *p.m.*, passing in from the germinal disk are spreading backwards, but have not yet reached the anterior end of the head mesodermal band which forms the antennulary mesoderm, *a.*1.*m.* × 436 approx.

(*b*) Parasagittal section through the side of the stomodœum of an older embryo, the same age as fig. 3, B. Formation of preantennulary mesoderm has ceased, and the solid somites have spread back, *p.m.s.*, to the stomodœum, *st.*, and labral rudiment, *lbr.* The anterior part of the somite, *p.m.a.*, remains in its original position to form the anterior aorta. × 436 approx.

(*c*) Transverse section of an embryo older than the last showing the anterior parts of the preantennulary somites, *p.m.a.*, lying within the optic rudiments. A leucocyte, *le.*, already lies in the space of the future anterior aorta between the somites. × 436 approx.

(*d*) Parasagittal section, similar to fig. *b*, but of an older embryo, see fig. 3, D. The brain region is further developed and the same two portions of the preantennulary mesoderm, *p.m.a.*, and *p.m.s.*, are visible. × 245 approx.

(*e*) Transverse section, similar to fig. *c*, through an older embryo, see fig. 4, G. The anterior parts of the preantennulary somites, *p.m.a.*, lie within the optic and brain rudiments, and the anterior aorta space lies between them, *a.a.* × 245 approx.

(*f*) Transverse section through the anterior end of an embryo older than the last and slightly older than fig. 4, I. The anterior parts of the preantennulary somites, *p.m.a.*, now reach the dorsal side of the body and lie between the anterior liver lobes, *l.a.* Between them they enclose the anterior aorta space, *a.a.* × 245 approx.

(*f*, 1) A more posterior transverse section of the same embryo through the mandibular segment. The walls of the aorta, *a.a.*, have been formed by the anterior (now upper) parts of the preantennulary somites. That part of the somites investing the stomodœum now shows a small cœlomic space, *p.m.c.*, on either side. This cavity is soon obliterated. × 245 approx.

PLATE 26.

FIG. 24.—Sections showing the development of the seventh abdominal somites, and the formation and growth of the antennal gland.

(*a*) Transverse section through the seventh abdominal segment of an embryo younger than fig. 3, E. The mesodermal somite is differentiated into large dorso-lateral blocks, *ab.*7.*l.m.*, these are connected by the longitudinal strands, *g.s.*, to the gut mesoderm, *ab.*7.*g.m.*, lying at the junction of the mid-gut and proctodœum, and below lies the small block of ventral mesoderm, *ab.*7.*v.m.*, on either side. × 530 approx.

(*b* and *c*) Consecutive transverse sections of an embryo shortly after hatching, and passing through the seventh abdominal segment. *b* lies anterior to *c*. In both sections the ventral mesoderm, *ab.*7.*v.m.*, forming the posterior end of the ventral longitudinal muscle, and the gut mesoderm, *ab.*7.*g.m.*, are seen. *b* shows the dorso-lateral mesoderm forming the posterior end of the dorsal blood vessel, the floor of which only has been formed, *h.f.* In *c* the gut mesoderm shows lateral, ventral, and dorsal extensions to the ectoderm, *pr.d.* These are rudiments of the proctodœal dilator muscles. × 530 approx.

(*d*) Transverse section through the base of the antenna of an embryo of the same age as fig. 4, G. The antennal somite is differentiating into antennal gland end sac, *e.s.*, into a group of duct cells, *d.*, and into limb mesoderm cells, *l.m.* × 726 approx.

(*e*) Transverse section similar to the last through an older embryo of the same age as fig. 4, I. The duct, *d.*, and end sac, *e.s.*, of the antennal gland are well formed. × 726 approx.

(*f*) Frontal section of a small adult showing the valve, *v*, and canal between the duct and end sac of the antennal gland. × 726 approx.

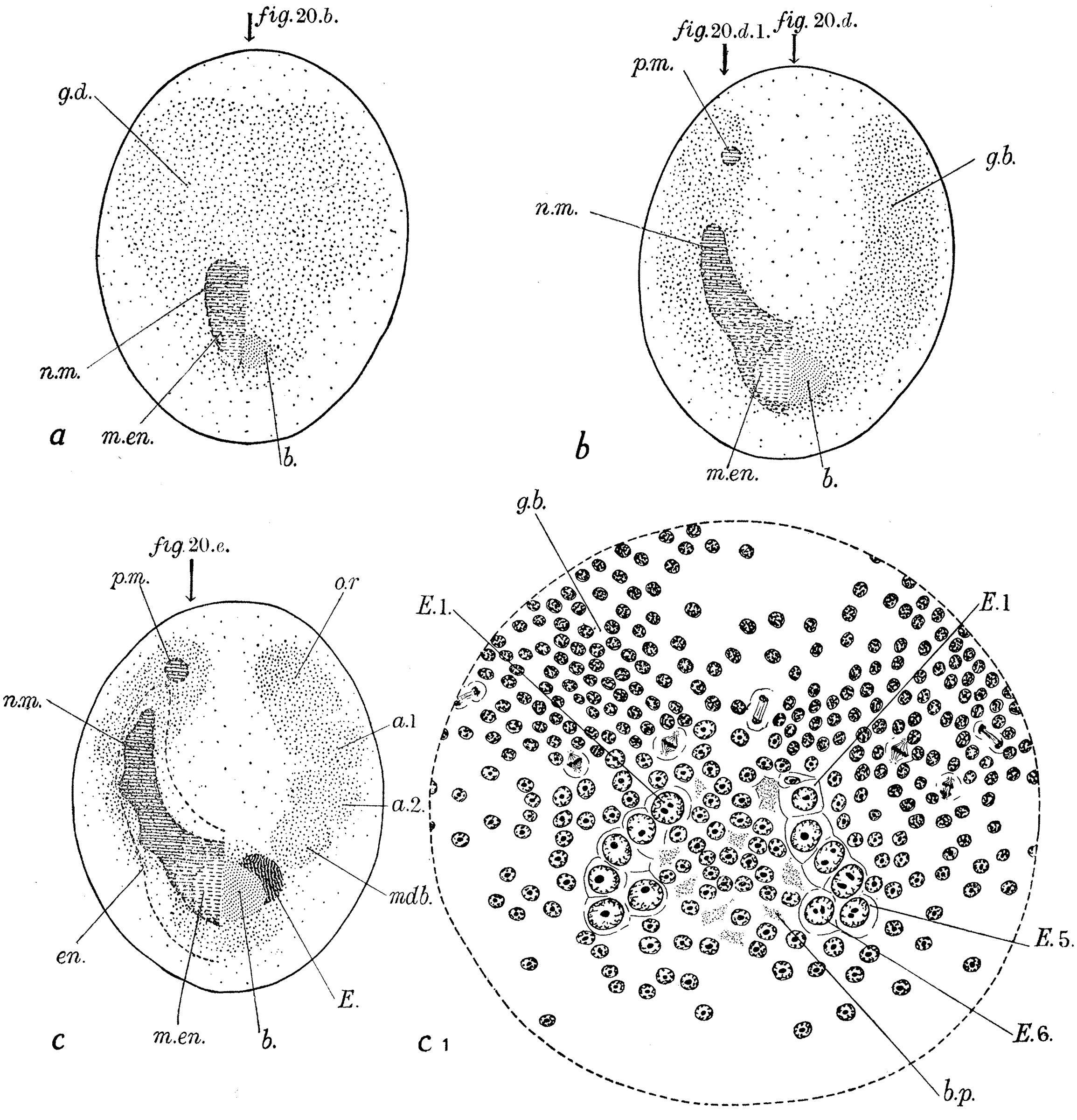
fig. 20.b.
g.d.
n.m.
m.en.
b.
a
fig. 20.d.1.
fig. 20.d.
p.m.
g.b.
n.m.
m.en.
b.
b
fig. 20.e.
p.m.
o.r
n.m.
a.1
a.2.
mdb.
en.
m.en.
b.
E.
c
g.b.
E.1.
E.1
E.5.
E.6.
b.p.
c 1

Fig. 18.

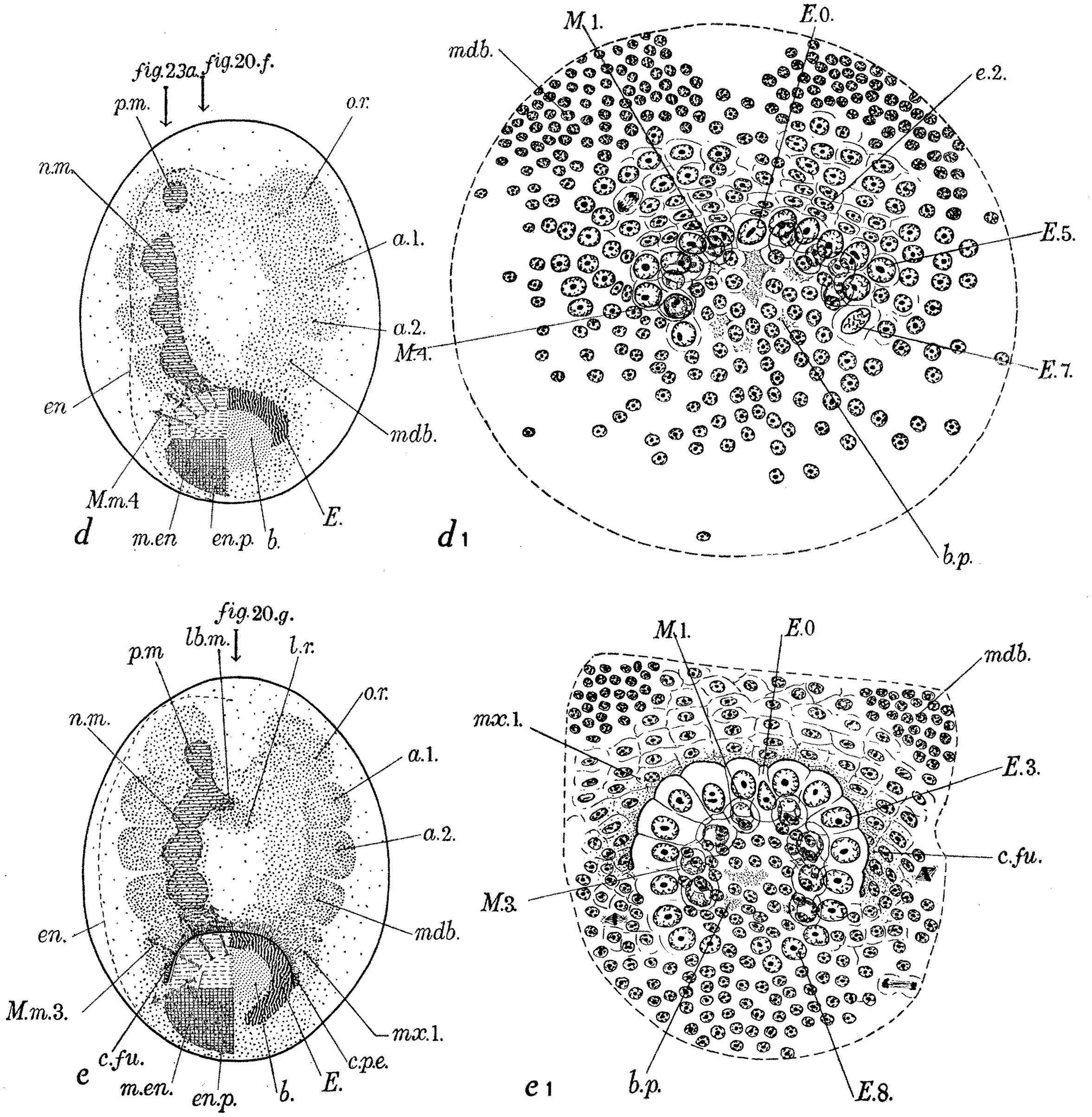
fig.23a.
fig.20.f.
p.m.
o.r.
n.m.
a.1.
a.2.
en
mdb.
M.m.4
E.
m.en
en.p.
b.
d
M.1.
E.0.
mdb.
e.2.
E.5.
M.1.
E.7.
b.p.
d1
fig.20.g.
lb.m.
l.r.
p.m
o.r.
n.m.
a.1.
a.2.
en.
mdb.
M.m.3.
mx.1.
c.fu.
c.p.e.
e
m.en.
en.p.
b.
E.
M.1.
E.0
mdb.
mx.1.
E.3.
c.fu.
M.3.
e1
b.p.
E.8.

FIG. 19.

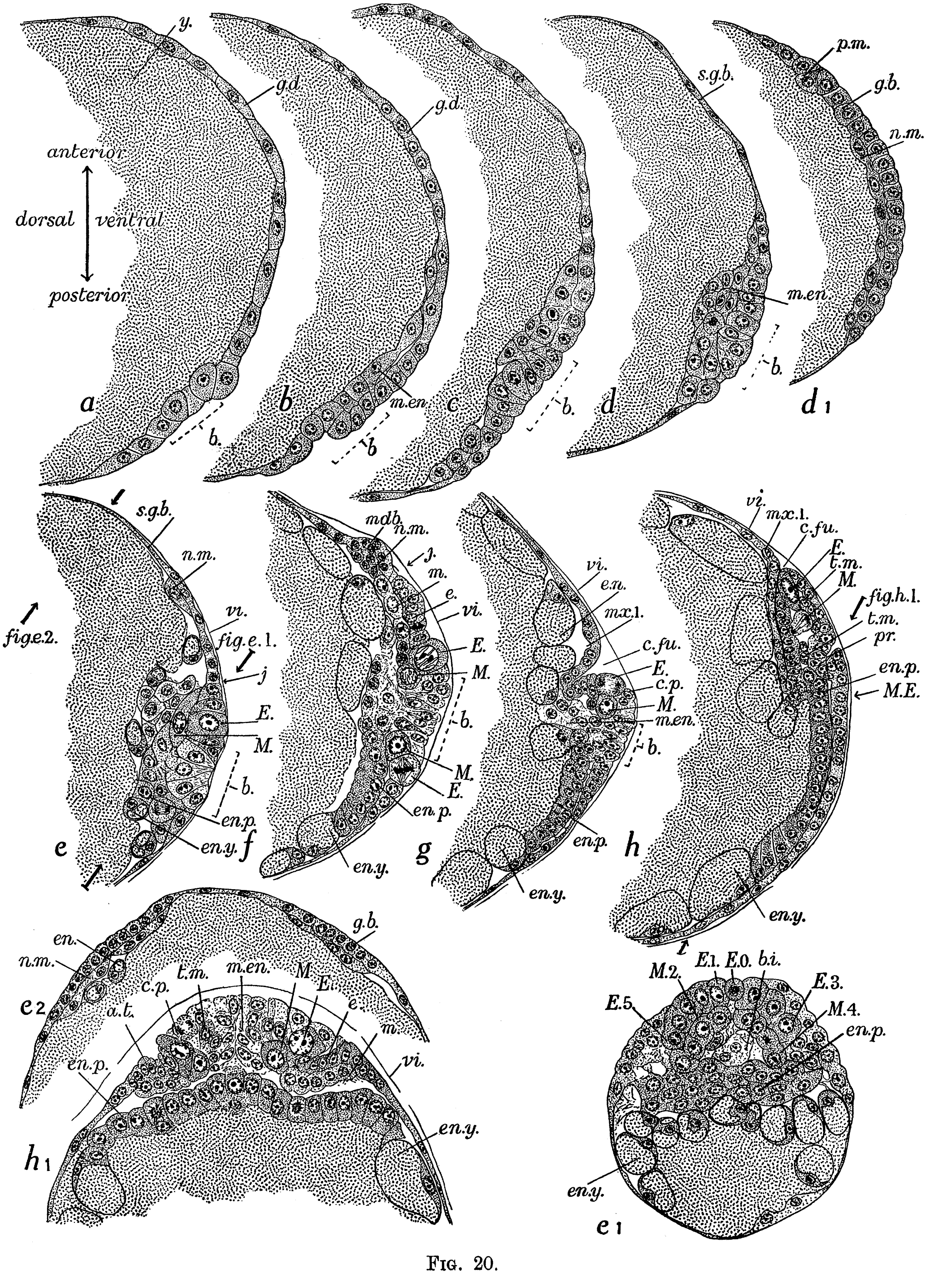
y.
g.d.
anterior
dorsal
ventral
posterior
a
b.
g.d.
m.en
b
b
c
b.
s.g.b.
m.en
d
b.
p.m.
g.b.
n.m.
d1
s.g.b.
n.m.
fig.e.2.
vi.
fig.e.1.
j
E.
M.
b.
en.p.
en.y.
e
mdb.
n.m.
j.
m.
e.
vi.
E.
M.
b.
M.
E.
en.p.
en.y.
f
vi.
e.n.
mx.1.
c.fu.
E.
c.p.
M.
m.en.
b.
en.p.
en.y.
g
vi.
mx.1.
c.fu.
E.
t.m.
M.
fig.h.1.
t.m.
pr.
en.p.
M.E.
en.y.
h
en.
g.b.
n.m.
e2
c.p.
t.m.
m.en.
M
E
e
a.t.
m.
vi.
en.p.
en.y.
h1
E.1.
E.0.
b.i.
M.2.
E.3.
E.5.
M.4.
en.p.
en.y.
e1

FIG. 20.

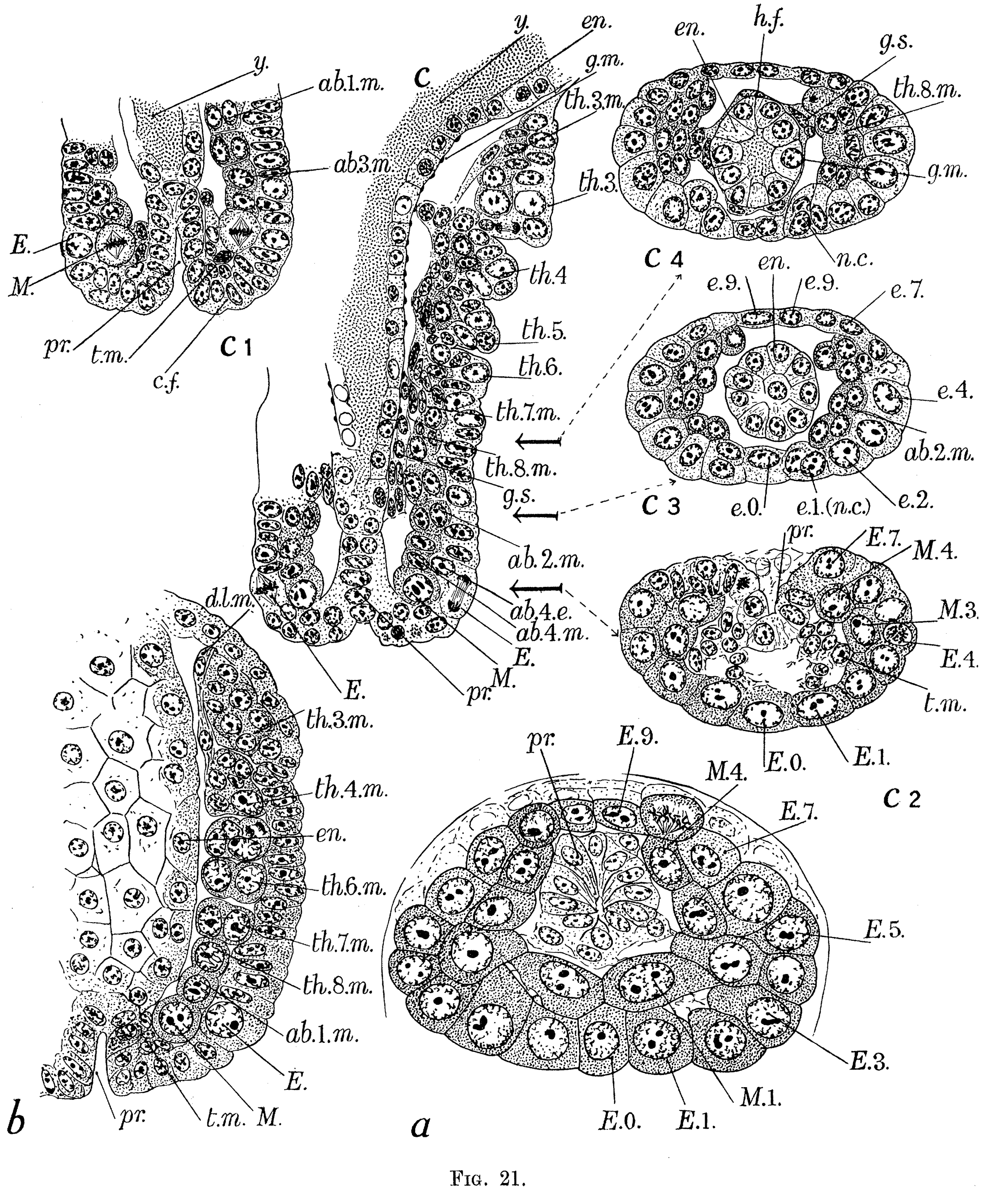
y.
ab.1.m.
ab3.m.
E.
M.
pr.
t.m.
c.f.
C 1
C
y.
en.
g.m.
th.3.m.
th.3.
th.4
th.5.
th.6.
th.7.m.
th.8.m.
g.s.
ab.2.m.
ab.4.e.
ab.4.m.
E.
M.
pr.
E.
en.
h.f.
g.s.
th.8.m.
g.m.
n.c.
C 4
e.9.
en.
e.9.
e.7.
e.4.
ab.2.m.
e.0.
e.1.(n.c.)
e.2.
C 3
pr.
E.7.
M.4.
M.3.
E.4.
t.m.
E.0.
E.1.
C 2
d.l.m.
th.3.m.
th.4.m.
en.
th.6.m.
th.7.m.
th.8.m.
ab.1.m.
E.
pr.
t.m.
M.
b
pr.
E.9.
M.4.
E.7.
E.5.
E.3.
M.1.
E.1.
E.0.
a

FIG. 21.

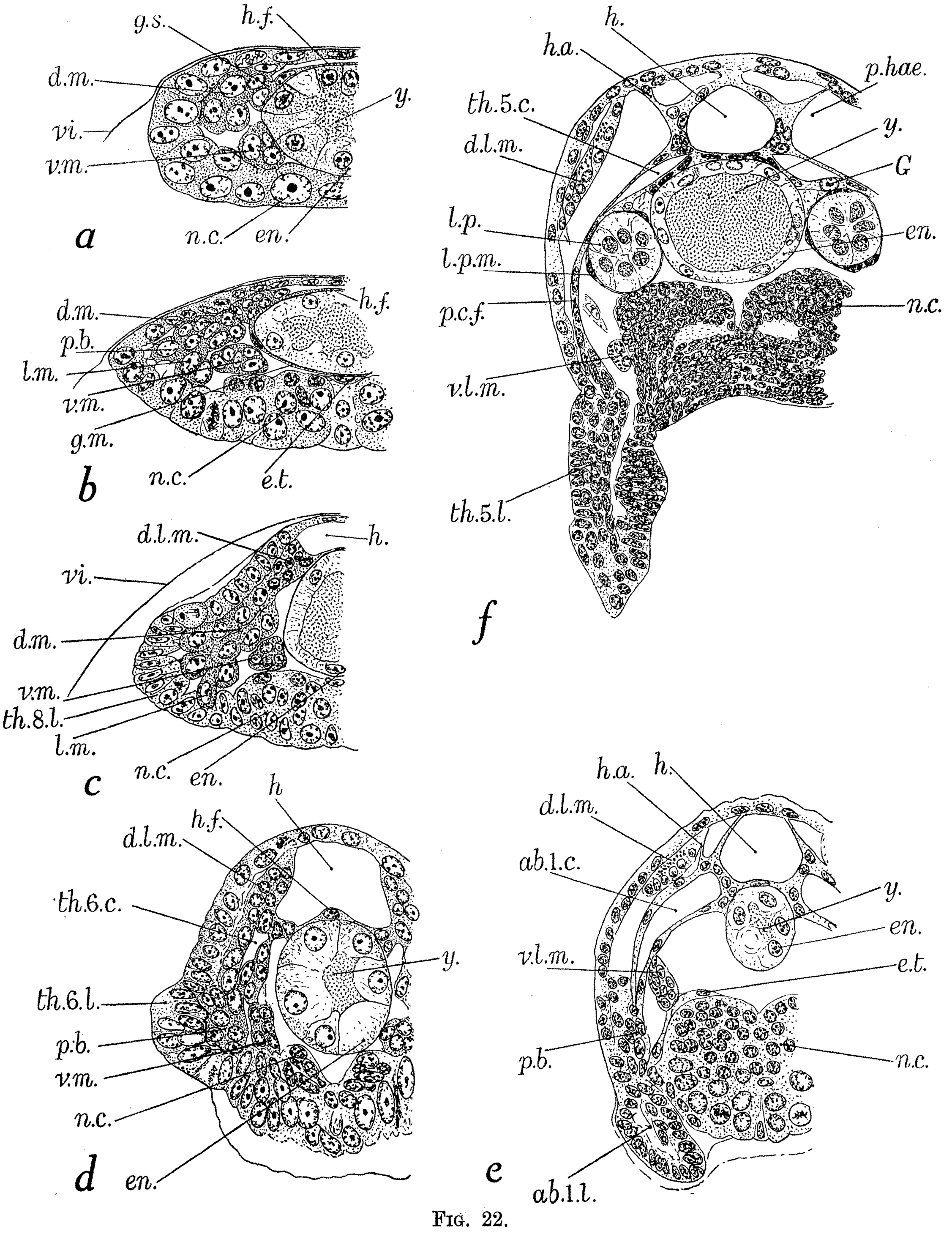
g.s.
h.f.
d.m.
vi.
v.m.
y.
n.c.
en.
a
d.m.
h.f.
p.b.
l.m.
v.m.
g.m.
n.c.
e.t.
b
d.l.m.
h.
vi.
d.m.
v.m.
th.8.l.
l.m.
n.c.
en.
c
h
h.f.
d.l.m.
th.6.c.
y.
th.6.l.
p.b.
v.m.
n.c.
d
en.
h.
h.a.
p.hae.
th.5.c.
y.
d.l.m.
G
l.p.
en.
l.p.m.
p.c.f.
n.c.
v.l.m.
th.5.l.
f
h.a.
h.
d.l.m.
ab.1.c.
y.
en.
v.l.m.
e.t.
p.b.
n.c.
e
ab.1.l.

FIG. 22.

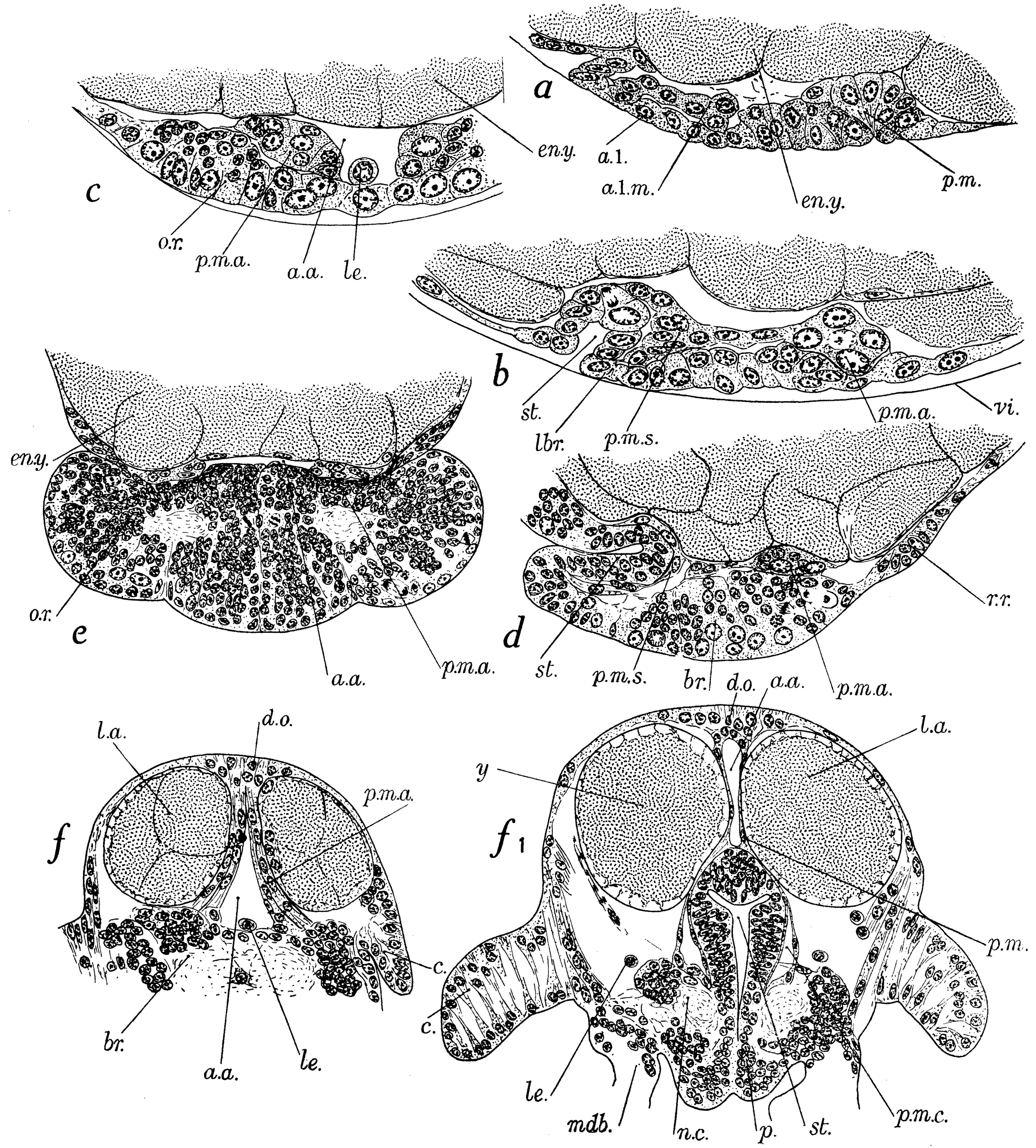
a
en.y.
a.1.
a.1.m.
en.y.
p.m.
c
en.y.
o.r.
p.m.a.
a.a.
le.
b
st.
lbr.
p.m.s.
p.m.a.
vi.
e
en.y.
o.r.
a.a.
p.m.a.
d
r.r.
st.
p.m.s.
br.
d.o.
a.a.
p.m.a.
f
l.a.
d.o.
p.m.a.
c.
br.
a.a.
le.
f1
l.a.
y
p.m.
c.
le.
mdb.
n.c.
p.
st.
p.m.c.

Fig. 23.

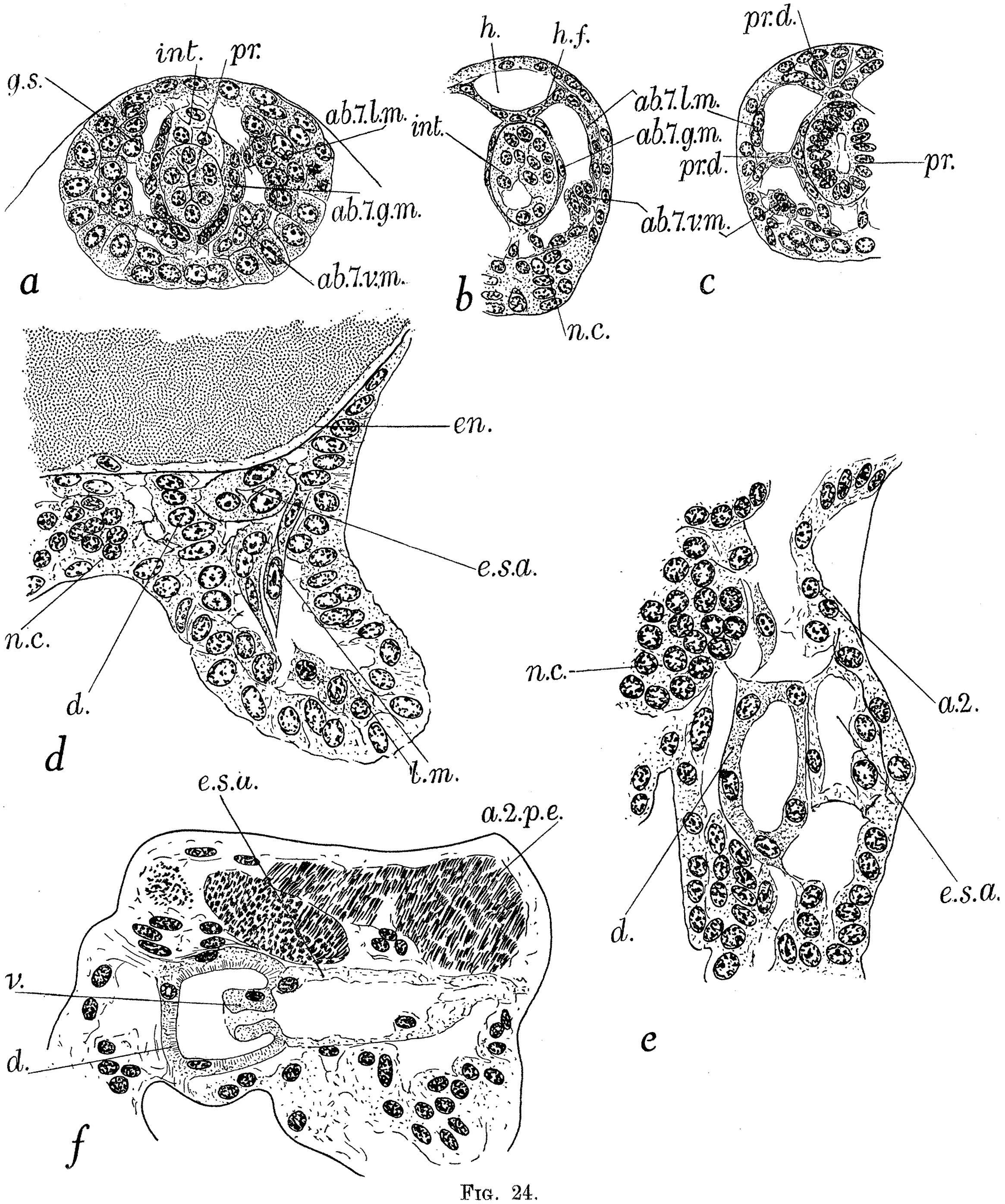
g.s.
int.
pr.
ab.7.l.m.
ab.7.g.m.
ab.7.v.m.
a
h.
h.f.
int.
ab.7.l.m.
ab.7.g.m.
ab.7.v.m.
n.c.
b
pr.d.
ab.7.l.m.
pr.d.
pr.
ab.7.v.m.
c
en.
e.s.a.
n.c.
d.
l.m.
d
n.c.
a.2.
d.
e.s.a.
e
e.s.a.
a.2.p.e.
v.
d.
f

FIG. 24.

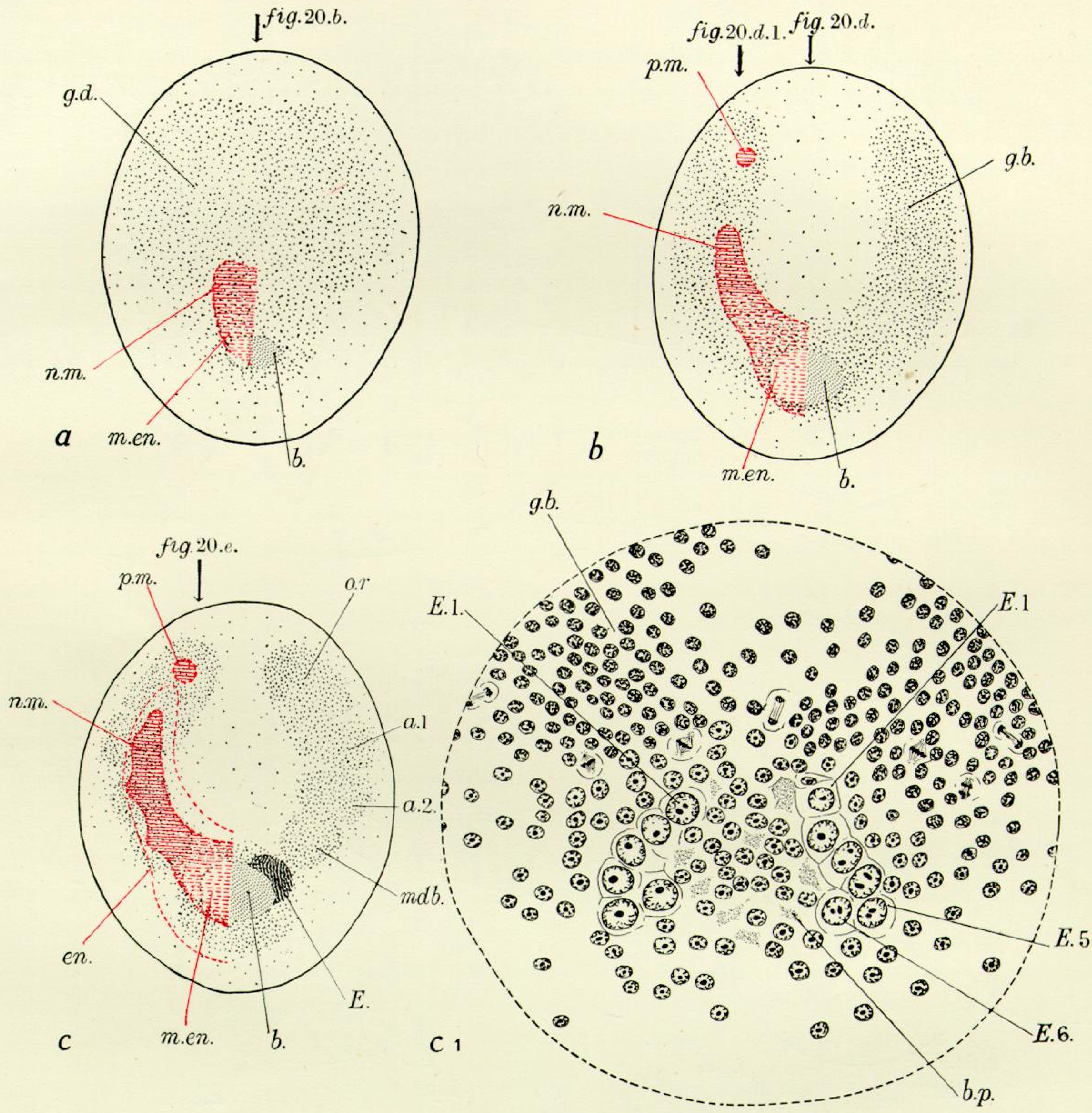

FIG. 18.

PLATES 20 AND 21.

FIGS. 18 and 19.—Figs. *a–e* are diagrammatic reconstructions, based on serial sections, of embryos in advancing stages of development, showing the germinal disk. In all the figures the internal cells are indicated in colour and drawn on the left side only, horizontal ruling represents the head band mesoderm, interrupted ruling represents undifferentiated mesendoderm, and the positions of blastoporal area and ectodermal teloblasts are shown by mechanical shading. In order to eliminate some of the terminal foreshortening of the germinal disk, the length of the visible long axis has been exaggerated. The black arrows indicate the planes of sagittal and parasagittal sections figured on Plates 22 and 25. Figs. *c*.1–*e*.1 are camera lucida drawings of whole mounts of the region surrounding the blastopore from embryos of the same age as in figs. *c–e*. The mesodermal cells could not all be satisfactorily seen in these preparations, and the positions of the mesodermal teloblasts alone have been inserted (in colour) by aid of sections.

(*a*) Embryo of the same age as fig. 21, *b*, Plate 23. The germinal disk, *g.d.*, is a thickening on one side of the embryo, and from the blastoporal area, *b.*, cells have immigrated inwards and forwards, *m.en.* Those most anterior will form the head band mesoderm, *n.m.*, while the rest of this mesendodermal mass will form both mesoderm and endoderm.

(*b*) Embryo older than the last and the same age as fig. 20, *d*, Plate 22. The germinal disk is now a U-shaped band, *g.b.* Immigration inwards from the enlarged blastoporal area has formed a more extensive mesendodermal mass, *m.en.*, which anteriorly has spread forming the head band mesoderm. A few cells from the mesendodermal mass have started to absorb yolk (not shown). From the arms of the germinal band a pair of cells have sunk below the surface, *p.m.*, forming the rudiments of the preantennulary somites (see also fig. 20, *d*, 1, Plate 22).

(*c*) Embryo older than the last and slightly younger than fig. 20, *e*, Plate 22. The rudiments of the three naupliar appendages and optic region are seen on the arms of the germinal band, the tips of which are closer together. Ectodermal teloblasts are differentiated from the sides of the blastoporal area. Endodermal yolk cells have separated off from the mesendodermal mass and spread below the disk as far as the dotted line, *en*.

(*c*, 1) Surface view of blastoporal region of the last stage. Six ectodermal teloblasts are clearly differentiated, but have not given descendants. Small crowded nuclei lie at the base of the arms of the germinal band, *g.b.*, and pits in the blastoporal area, *b.p.*, are left by the imigrating cells. No mesodermal teloblasts are yet formed. × 340 approx.

(*d*) Embryo older than the last and the same as fig. 20, *f*, Plate 22. The arms of the germinal band are united anteriorly. The ectodermal teloblasts form a continuous band round the lateral and anterior lip of the blastoporal area. The head band mesoderm shows three paired thickenings opposite the naupliar appendages. Four pairs of mesodermal teloblasts have been differentiated from the anterior edge of the mesendodermal mass, the arrows, *M.m.*4., etc., indicate the positions of the teloblasts and their rows of descendants. Endodermal yolk cells are numerous and have extended further, *en.*, and lie in the mid-ventral line as well as below the U-shaped band. The epithelial endodermal plate, *en.p.*, has been formed from the hinder part of the mesendodermal mass, and from adjacent yolk cells, and lies within and behind the blastoporal area.

(*d*, 1) Surface view of blastoporal region of the last stage. Seven paired lateral teloblasts, *E.*1–*E.*7, are united by a median teloblast, *E.*0., and some of their descendants can be seen in rows, *e.*2. The blastoporal area is pitted, and the limit of the naupliar region ectoderm is seen. Four pairs of mesodermal teloblasts are indicated, but not their descendants. × 340 approx.

(*e*) Embryo older than the last and slightly older than fig. 20, *g*, Plate 22. The union of the arms of the germinal band has enlarged and lies mainly between the antennulary rudiments, where it will form the labrum. The more numerous ectodermal teloblasts nearly enclose the blastoporal area. In front of the teloblasts the caudal furrow has appeared, *c.fu.*, so that the anterior teloblasts lie round the edge of the rudimentary caudal papilla, *c.p.e.* The enlarged preantennulary somites have shifted posteriorly and touch the head bands of mesoderm. The latter have united forming the future labral mesoderm, *l.m.* The mesodermal teloblasts have shifted to the positions indicated by the arrows, *M.m.*3., etc. Endodermal yolk cells have spread further and cover half of the yolk, *en.* The endodermal plate has enlarged, *en.p.*

(*e*, 1) Surface view of blastoporal region of the last stage. One median and eight paired ectodermal teloblasts are formed, and both mesodermal and ectodermal teloblasts tend to surround the blastoporal area. The caudal furrow and caudal papilla are seen, and the junction between teloblastic, *mx.*1. and naupliar, *mdb.*, ectoderm is clear. Gastrulation is ceasing and fewer pits lie in the blastopora area. × 340 approx.

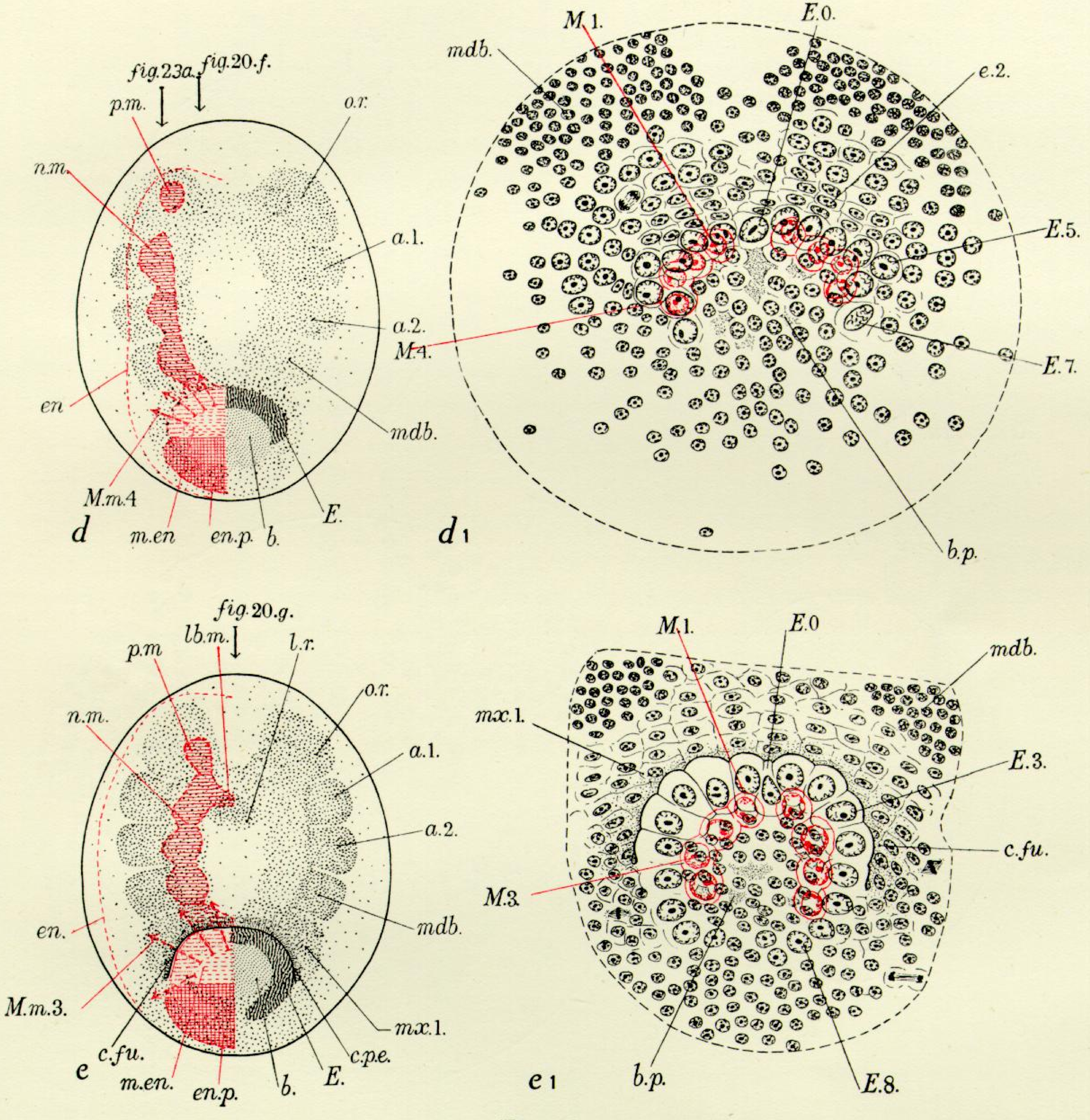

fig.23a.
fig.20.f.
p.m.
o.r.
n.m.
a.1.
a.2.
en
mdb.
M.m.4
m.en
en.p.
b.
E.
d
M.1.
E.0.
mdb.
e.2.
E.5.
M.4.
E.7.
b.p.
d1
fig.20.g.
lb.m.
l.r.
p.m
o.r.
n.m.
a.1.
a.2.
mdb.
en.
M.m.3.
c.fu.
m.en.
en.p.
b.
E.
c.p.e.
mx.1.
e
M.1.
E.0
mdb.
mx.1.
E.3.
c.fu.
M.3.
b.p.
E.8.
e1

FIG. 19.