VIII. *On the Embryology of a Mysid Crustacean*, Hemimysis Lamornæ.*

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Communicated by J. Stanley Gardiner, *F.R.S.*

(Received October 24, 1927,—Read February 2, 1928.)

(Plates 21–25.)

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Introduction.

The study of the embryology of *Hemimysis Lamornæ*, of which the following pages contain an account, was first undertaken with a view of tracing the later development

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* This work was partly carried out while holding a Yarrow Studentship of Girton College, Cambridge, and a Department of Scientific and Industrial Research Grant.

[Published June 28, 1928.

of the mesoderm, and the formation of the heart and segmental excretory organs. The later embryological stages of the Malacostraca have not been investigated in much detail, and usually with poor fixation of the material. In view of the recent work of CANNON (1924 and 1927) on the development of *Estheria* and *Chirocephalus*, where the presence of segmental cœlomic cavities in the mesoderm and their relation to the heart formation has been demonstrated, it became highly desirable that some Malacostracan should be examined with similar care. A Mysid, although it is not liberated as a free-swimming nauplius, can be taken as one of the least specialised Malacostraca, possessing a long tubular heart, simple antennal gland and most of the external features of the caridoid facies. For these reasons, and for the fact that abundant material is available, the type selected was *Hemimysis Lamornæ.*

However, it became evident that an examination of the earliest stages was equally necessary, and the development from segmentation stages onwards has been followed. In spite of abundant literature on Malacostracan germ-layer formation, the accounts are incomplete and often inaccurate, owing chiefly to inferior technique. In the Peracarida the origin of the germ layers and the formation and closure of the blastoporal area have not been satisfactorily worked out in any one type. Among the Decapoda the recent work of SOLLAUD (1923) on the Palæmoninæ is the most complete and careful account so far produced. Very little is known of the development of the Hoplocarida apart from the complicated metamorphosis. The embryology of the Syncarida is unknown. The literature contains much that is contradictory, especially concerning the Peracarida, so that a thorough account of the early development of any one form, and particularly of one of the Mysidacea which occupy a central position in the Peracarida, seems called for. Such a study would be useless unless a new technique was found.

Prof. H. GRAHAM CANNON originally suggested this work to me after discovering the value of the fixative used. My thanks are due to him for help and criticism, and for reading through the manuscript, and to Prof. E. W. MACBRIDE and Prof. J. STANLEY GARDINER, in whose laboratories the work was carried out. I am also indebted to Dr. L. A. BORRADAILE for advice, and to Mr. and Mrs. NEEDHAM who kindly carried out the microinjections for me.

Methods.

All previous work on yolky eggs has been based on sublimate, or worse fixatives. B. G. SMITH'S fluid, devised for Amphibian yolk (1912), which had already been used by CANNON (1920, p. 629) for *Simocephalus*, was found to be a satisfactory fixative.

Hemimysis breeds freely in the tanks at the M.B.A. Laboratory at Plymouth, where the material was obtained. The eggs are laid twelve to twenty at a time and are carried by the parent in a brood pouch. Here they hatch early from the vitelline membrane and become straightened out. The first ecdysis takes place in the brood pouch and the embryos are finally liberated as miniature adults in which nearly all the yolk has been absorbed.

Each family of embryos was taken from the brood pouch and fixed in formal bichromate. Their approximate age is easily noted in the living condition, but this is difficult after fixation. The material was stored in 5 per cent. formalin or in 70 per cent. alcohol. Fixation of the young stages was excellent, but the old embryos just about to leave the brood pouch were difficult to fix well throughout the body with any fixative. The material so fixed is very hard, and considerable difficulty was experienced in cutting the younger stages. Finally the best results were obtained by clearing in methyl salicylate from 90 per cent. alcohol and passing the embryos rapidly through clove or cedarwood oil directly into paraffin wax 52° m.p. They were then passed through two more wax baths and removed from the bath in twenty to twenty-five minutes. A longer period in the bath, a higher temperature and sometimes absolute alcohol in dehydration resulted in excessive fracturing on sectioning. Pure celloidin, or clove oil celloidin, did not prevent this. Many perfect series of sections were obtained in this manner, although a number were quite useless. The young stages were difficult to orientate, as the yolk and germinal disk do not stain differentially after this fixative. The best method was found to be to stain with alum-carmine and to orientate as an opaque object with a very strong light, preferably sunlight. Sections were cut at 8 μ thick and stained with iron hæmatoxylin or Mallory's triple stain. This stain was useful in late stages for distinguishing hæmocœlic from cœlomic spaces, the former staining blue and the latter remaining colourless. In the very young stages, where the yolk stains red, it shows up clearly the growing yolk vacuoles in the purple or blue cytoplasm of the endoderm cells. The embryos of each family were at approximately the same stage of development. This was very useful where sections in different planes at the same stage were required. Embryos freed from the parent will live under circulation for several days, so that very near stages can be obtained.

Half of each family of the younger stages was fixed with sublimate in sea water for preparing whole mounts of the germinal disk. The embryos were stained with ERHLICH'S hæmatoxylin, either at once or after treatment with sodium bicarbonate ; or, in the case of stored material, after MEYER'S bleaching mixture of potassium chlorate and hydrochloric acid. Acid alcohol then removed all stain from the yolk, leaving it only in the germinal disk. Under a binocular microscope each embryo was removed from the vitelline membrane, cut in half, and the yolk carefully scraped away from below the germinal disk. The latter was then mounted whole in balsam, but was slightly flattened by a supported coverslip. When the yolk is unstained all cells, both internal and external, can be made out. For this purpose an oil-immersion 1/7th-mm. objective and a × 7 or × 14 eyepiece were invaluable.

The figures can only show isolated stages selected from complete series of preparations.

Previous Work.

The most important researches on the early development of the Mysidacea are those of BOUTCHINSKY (1890), NUSBAUM (1887), BERGH (1893*a*) and WAGNER (1898). None of these authors, however, have examined a continuous series of stages, or the earlier differentiation of the germinal disk prior to gastrulation; and the exact details of the latter process have not been observed. WAGNER'S work is the most complete, but, unfortunately, it is in Russian (summary in German). He eliminated many errors of his predecessors concerning germ-layer formation, but his work is incomplete and unsatisfactory in the details of early development, particularly respecting the origin of the various parts of the naupliar and post-naupliar mesoderm, the genital rudiment, and the later development of the mid-gut and liver from the endodermal layer.

The teloblastic formation of the post-naupliar ectoderm and mesoderm was first described by BERGH for *Mysis flexuosa* and *M. neglecta*. He was uncertain as to the origin of the "head mesoderm" and failed to notice any preantennulary mesoderm. WAGNER attempted to analyse further the origin of the head mesoderm, but his conclusions are vague and unsatisfactory. He observed the antennal mesoderm lying laterally to the genital rudiment, but did not know if it descended from the mesodermal teloblasts or not. He thought it probable that the antennal mesoderm arose from a common origin with the teloblasts and genital rudiment (p. 178). Further, he considered that the teloblasts formed all segments behind the antennal segment (p. 178), a conclusion not substantiated for any other Peracaridan, where the teloblasts always form only the post-mandibular segments.

The greatest confusion has existed concerning the adult endoderm and yolk cells. WAGNER first showed that the yolk cells became transformed into yolk pyramids and gave rise directly to the mid-gut epithelium. He saw this transformation to epithelium taking place first near the stomodæum and proctodæum, but considered that the liver arose from outgrowths from the former, the "vordere entodermplatte." This result is not substantiated here, and was doubtless a result of unsatisfactory technique. WAGNER further doubted the previous assertions that vitellophags gave rise to blood corpuscles, although he did not observe the formation of the latter.

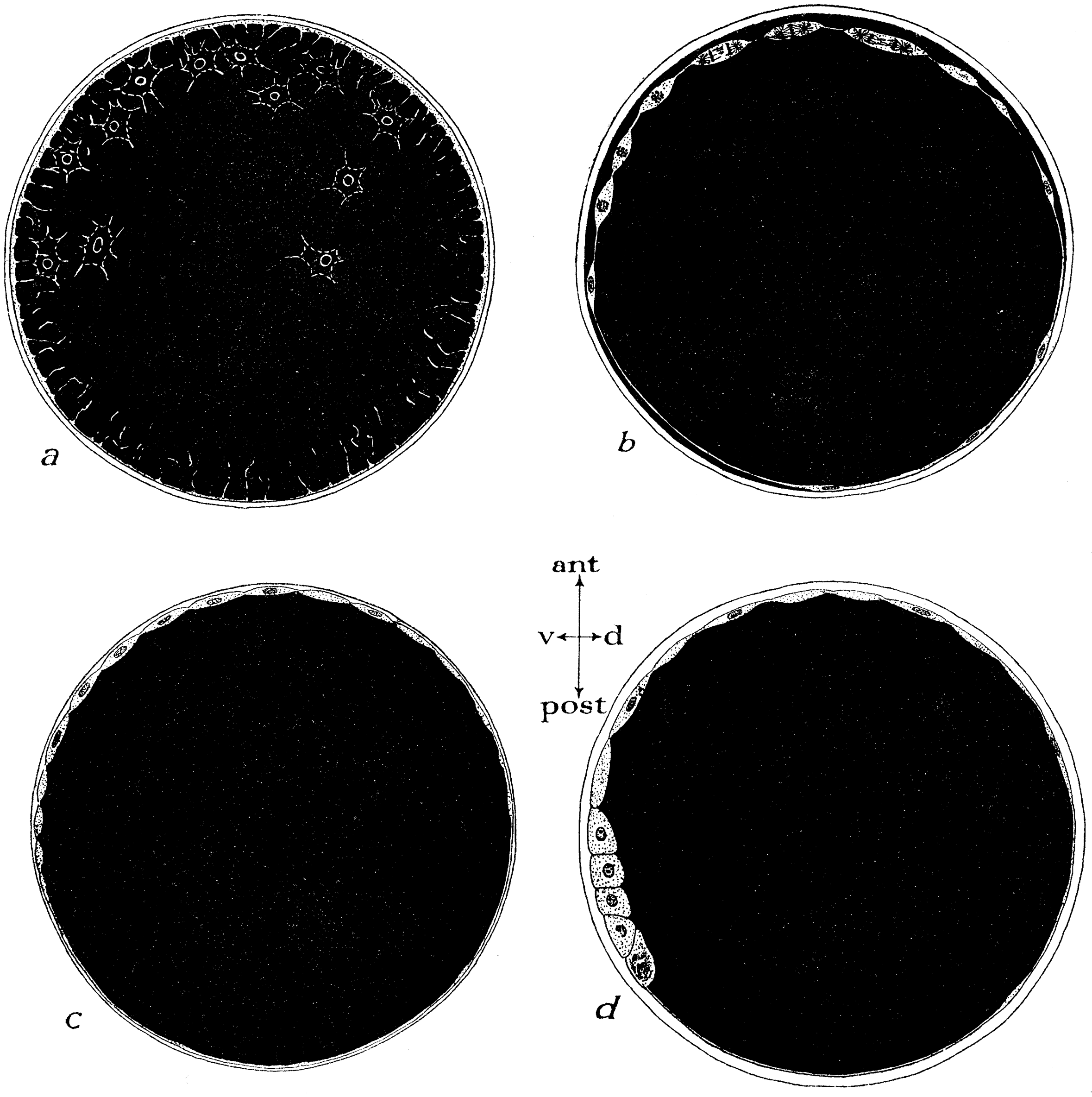
The only workers on the later development are NUSBAUM and WAGNER. NUSBAUM'S observations and interpretations of the growth of the mesoderm and heart formation are inaccurate, and he did not follow the antennal gland development. WAGNER observed some early cœlomic sacs and the division of the segmental mesoderm blocks into dorsal and ventral portions, and also the formation of the limb mesoderm. His observations on the further growth of the mesoderm and heart formation are, however, inaccurate. He correctly described the development of the antennal gland in no great detail, and observed the ectodermal origin of the V-shaped endoskeletal plate, but his conclusions concerning the origin of the mandibular tendon cannot be accepted. He observed the formation of the blood corpuscles but did not interpret them as such; and correctly followed the later growth of the genital rudiment within the body, but did not see clearly its formation.

Segmentation.

The segmentation of *Hemimysis* has not been followed in great detail, but a series of stages has been obtained showing the formation of the germinal disk. The newly laid egg measures about 440 μ in diameter and is enclosed in a delicate vitelline membrane. No chorion is present. The yolk has a peculiarly stiff inelastic consistency resulting in the young embryos being often distorted from a spherical shape by mutual pressure in the brood pouch.

The one-celled stage has not been examined, but it is probably similar to that figured by Boutchinsky (1890, Plate 1, fig. 1) for the mysid *Parapodopsis*. Here there is a central nucleus surrounded by a stellate mass of protoplasm, the yolk being covered externally by a thin protoplasmic layer. A similar condition is described by McMurrich (1895) for various Isopoda. He finds in the oocyte that the protoplasm round the central nucleus is connected to the surface layer of protoplasm by numerous strands, the yolk occupying the intervening spaces. Later, when the mass of yolk has greatly increased, the outer protoplasmic layer becomes detached from the inner mass. There is no doubt that the same process of yolk deposition in *Hemimysis* accounts for the separation of the protoplasm into inner and outer portions.

Segmentation is at first internal, the blastomeres being represented by stellate nucleated masses of protoplasm, lying deeply in the yolk. The surface layer of protoplasm is about 3–4 μ thick at the animal pole, and very much thinner at the vegetal pole. From this layer thin protoplasmic strands extend a short distance inwards, breaking up the yolk in a honeycomb-like manner. Some of these strands are connected with processes from the stellate blastomeres. The earliest embryos examined were at the four-celled stage. The blastomeres are scattered irregularly through the yolk, their centres lying at a distance of about one-sixth of the egg diameter below the surface. Subsequent cleavages occur somewhat irregularly, although blastomeres near to one another tend to divide at approximately the same moment. Thus the 16, 32, and 64-celled stages are not sharply defined, the number of blastomeres present being various. At approximately the 16-celled stage the blastomeres approach closer to the surface of the yolk. They exhibit a polarity in their distribution, the majority being grouped at the animal pole, where the superficial layer of protoplasm is thickest. Such a stage is seen in text-fig. 1 *a*, which represents a 12-celled embryo viewed as a transparent object. At about the 32-celled stage the blastomeres begin to appear on the surface. This process first takes place at the vegetal pole, and is there somewhat different from that at the animal pole. The stellate masses of protoplasm gradually rise through the yolk and fuse with the outer layer, remaining meanwhile separate from one another, or only united by long fine processes. Their protoplasm thus becomes spread out more evenly on the surface, and the fine strands both from the blastomeres themselves and from the outer layer of protoplasm with which they have fused, are completely withdrawn from the yolk. The process is completed at the vegetal pole by the 64-celled stage. At the animal pole the processes from the outer layer of protoplasm and from the blastomeres are withdrawn from the yolk before the blastomeres reach the surface. The outer protoplasmic layer becomes indistinguishable and the blastomeres rounded off while still below the surface of the yolk. They



Text-Fig. 1.—Four segmentation stages, the yolk being represented as a black mass. (*a*) Twelve-celled embryo showing the distribution of the blastomeres. The positions of all the blastomeres are projected on to one plane. (*b*) Sagittal section of about the 64-celled stage showing the blastomeres at animal and vegetal poles. (*c*) Sagittal section of about the 128-celled stage, all the blastomeres being now external to the yolk. (*d*) Sagittal section showing the ventral thickening forming the germinal disk. (Seen in surface view in text-fig. 4*a*). The orientation indicated is for stage *d* only.

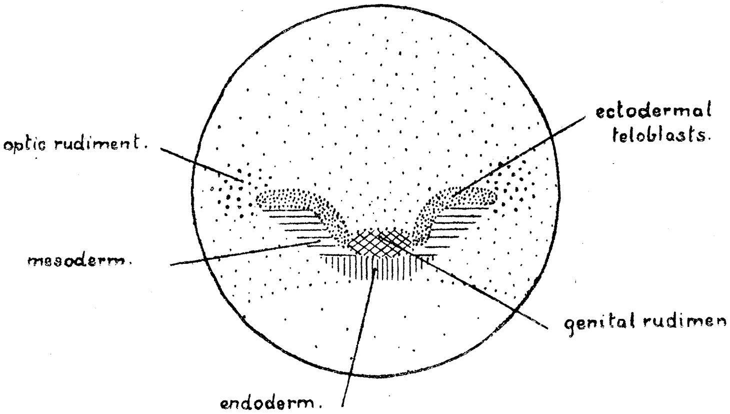
are connected to one another by thin protoplasmic bridges which, in places, may be incomplete (text-fig. 1 *b*). The regular layer of cells thus formed gradually rises bodily to the surface. The yolk, at first external to this epithelium, passes inwards between the blastomeres. Finally, at about the 128-celled stage, the yolk becomes completely internal, and is surrounded by a continuous blastoderm, composed of numerous similar thick blastomeres over the animal pole, and a few thin, much drawn out, blastomeres over the vegetal pole (text-fig. 1 *c*). The blastomeres only differ from each other in size and distribution, the condition at one pole passing insensibly into that at the other.

Differentiation of the blastodermic disk now begins. The blastomeres shift their positions over the yolk and form an accumulation at the postero-ventral edge of the animal pole. Here the cells increase in thickness (text-fig. 1 *d*). This thickening ends abruptly posteriorly against the very attenuated vegetal pole blastomeres, and merges insensibly into the surrounding blastoderm in other directions. There is as yet no nuclear differentiation (text-fig. 4 *a*).

Germ-Layer Formation.

Cells in the germinal disk previous to gastrulation show marked differentiation, and the regions destined to give rise to mesoderm, endoderm, the genital rudiment and trunk ectoderm become clearly delimited. Gastrulation is epibolic, although a slight blastoporal depression is formed. The blastoporal area comprises cells which form the whole of the endoderm and nearly all the mesoderm, including that supplying the naupliar appendages. Except for a paired extraneous source of preantennulary mesoderm no internal tissues arise from any other part of the germinal disk, and no mesenchyme is formed. The ventral thoracic and abdominal ectoderm arises from the anterior lip of the blastopore; and the ectoderm of the naupliar region, that is, of the head anterior to the maxillules, and of the dorsal side of the body is formed from the rest of the germinal disk. During gastrulation cells immigrate separately into the interior and at no point do the germ layers arise by delamination.

From the undifferentiated postero-ventral disk figured in text-fig. 4 *a* multiplication and migration of blastomeres over the yolk extends this thickened area into a transverse band. Concentration towards this transverse band results in the blastomeres being few and drawn out on the side of the embryo remote from the band. A central group of about twelve or more cells becomes characterised by small granular nuclei lacking a large nucleolus, and cytoplasm which stains lightly. These cells form the genital rudiment. Laterally a few rows of cells become distinguishable by the greater bulk of their cytoplasm, although their nuclei do not differ as yet from the remaining cells of the disk. They form on either side concave bands with the concavity directed backwards. The most anterior row of cells on each side later form the ectodermal teloblasts, and the cells behind them pass inwards to form mesoderm. Behind the genital rudiment and paired lateral thickenings a few cells absorb yolk, which is deposited in vacuoles in the cytoplasm. These cells become the yolk cells or vitellophags and later the mid-gut epithelium, and thus constitute the endoderm. Text-fig. 2 represents diagrammatically the external differentiation of the germ layers, although the mesodermal and ectodermal teloblasts are not cytologically distinguishable from one another at this stage.

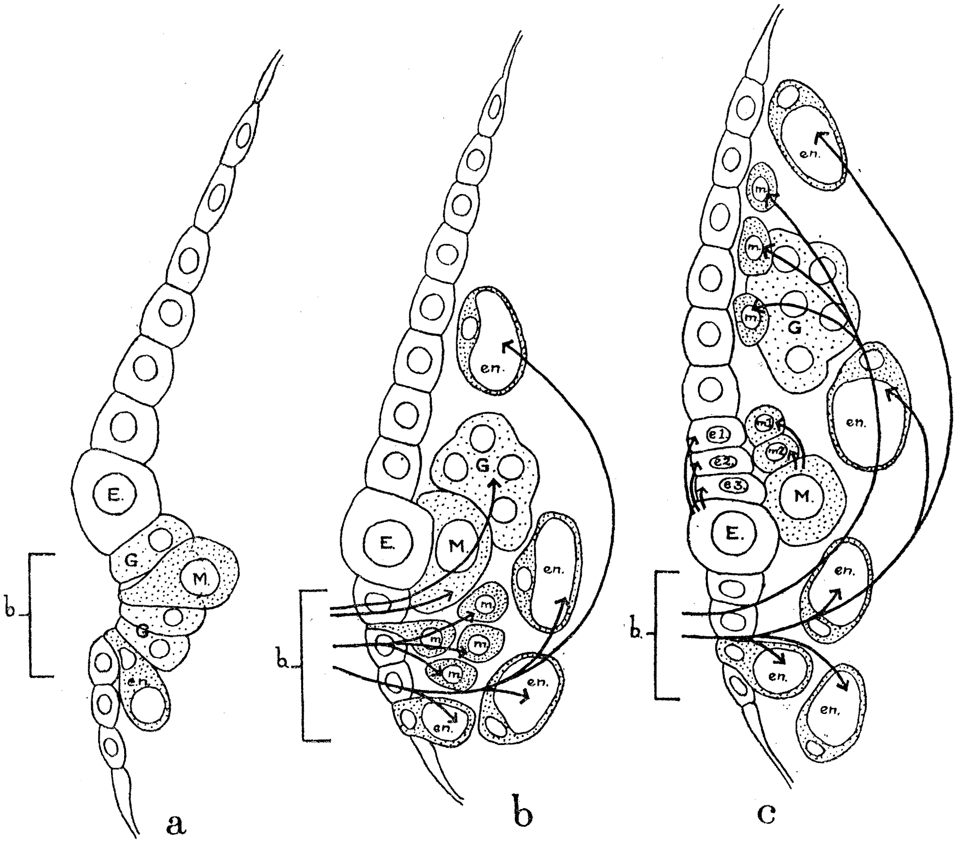


TEXT-FIG. 2.—Diagram showing the spatial relations between the genital rudiment and germinal layers before gastrulation.

Text-figs. 4 to 7 show a series of whole preparations of germinal disks from the beginning of gastrulation onwards. The cells drawn in colour are situated internal to the outer layer of cells, which are shown in black. In text-fig. 4 *b* the regions of the disk indicated in text-fig. 2 are seen, but also the first stages of gastrulation. The genital rudiment is starting to sink inwards and to be covered anteriorly by ectoderm, and one pair of mesodermal cells have slipped in from the lateral thickenings. Later, the ectodermal thickenings approach one another and meet in front of the genital rudiment (text-figs. 5 *a* and *b*). Their anterior edges form a transverse row of large cells, the ectodermal teloblasts, which shift backwards over the blastoporal area, and must be considered to be situated in the anterior lip of the blastopore (text-fig. 3). The blastoporal area behind the ectodermal teloblasts becomes sunk slightly below the general level of the disk (Plate 21, figs. 1 and 3). The growth of the various layers may now be treated separately, and those arising by gastrulation will be considered first.

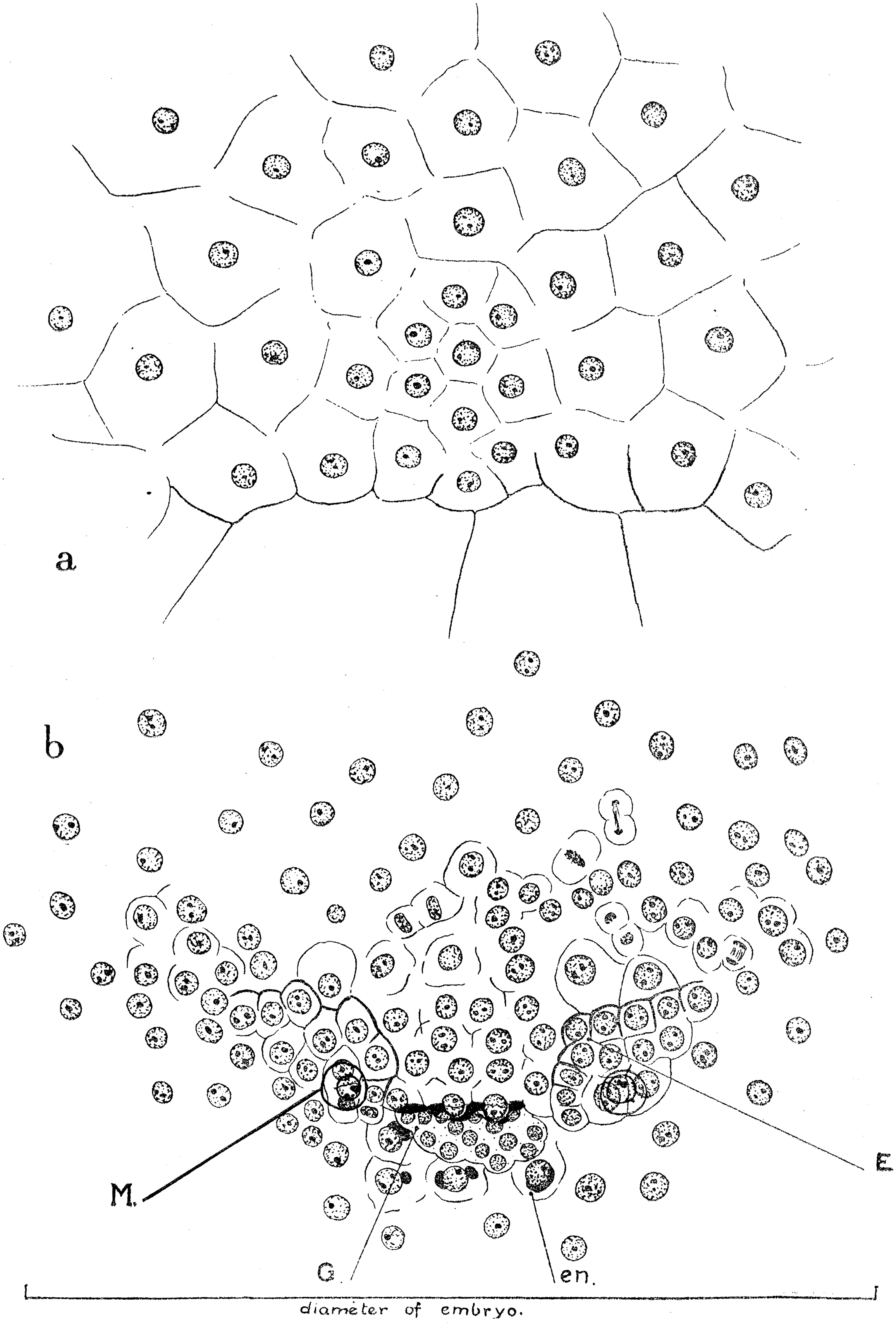
Ectodermal Teloblasts.

The origin of the ectodermal teloblasts has been described above (p. 369, text-figs. 4 *b* and 5 *a* and *b*). The paired lateral bands, at first concave, straighten out when they meet to form a continuous row (text-fig. 6 *b*). The number of cells in this row is remarkably constant. A central cell is present, lying usually a little posterior to seven lateral teloblasts on either side of it. These fifteen teloblasts are established nearly simultaneously, and this number persists unchanged during the whole functional period of these cells. Exceptions have been found, such as that seen in text-fig. 6 *a*, where twenty-one teloblasts are present. The row of teloblasts divide practically simultaneously, the central cell, however, lagging behind the rest. A wave of division seems to pass from the middle line outwards, the inner teloblasts dividing a little in advance of the outer (text-fig. 5 *b*). The divisions are unequal and give rise to a row of small cells immediately in front of the larger teloblasts (text-figs. 5 *b* and 6 *a*). Such divisions are repeated, and result in the formation of regular transverse and longitudinal rows of ectodermal cells which end abruptly against the irregular ectoderm of the rest of the germinal disk (text-figs. 6 *b* and 7 *a*). At first the anterior rows of teloblast-descendants differ from the ectodermal cells of the anterior part of the disk by their larger size (text-fig. 6 *b* and Plate 21, fig. 5 *e*), but later this distinction is lost.

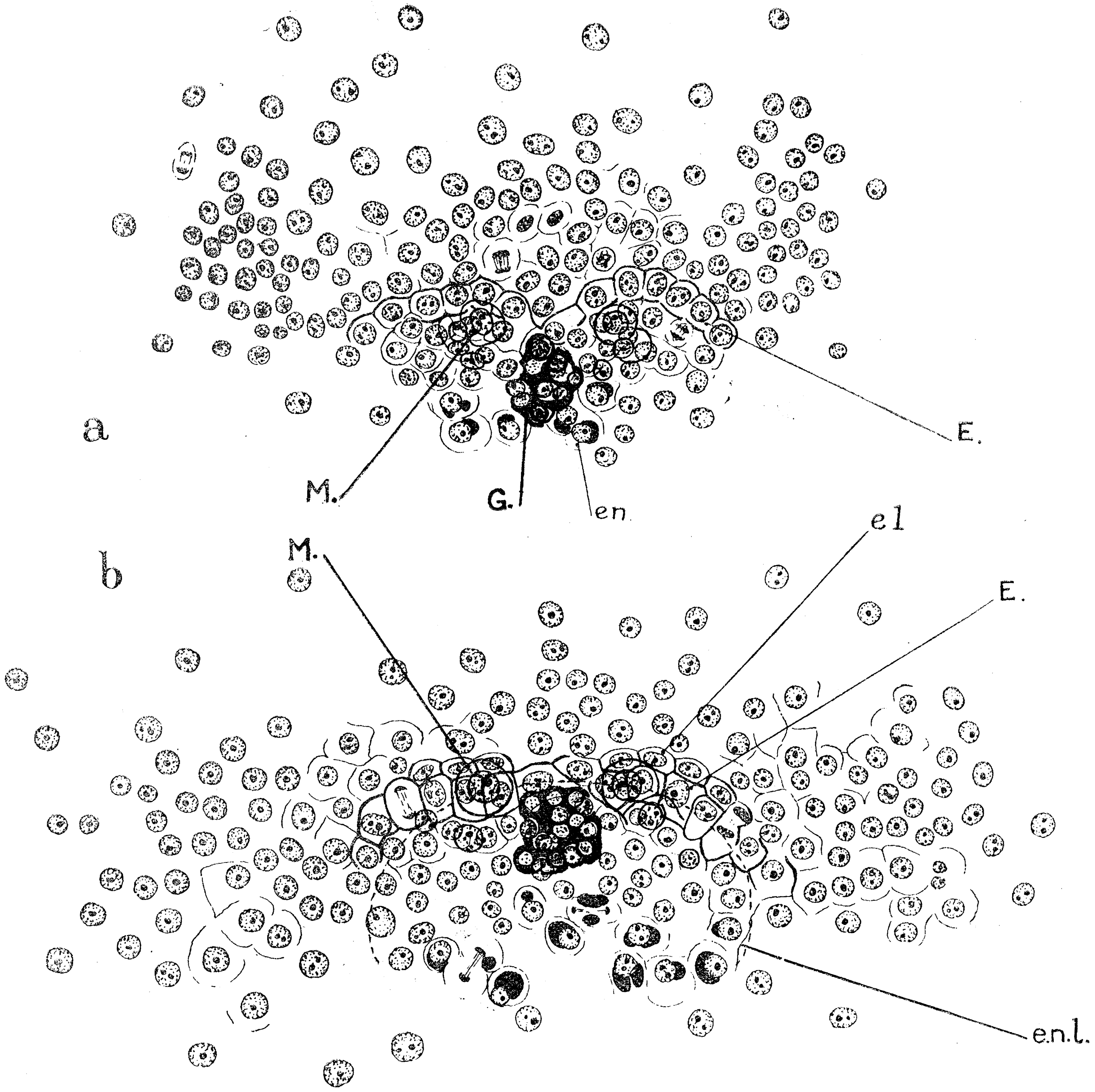


TEXT-FIG. 3.—Diagrammatic sagittal views showing the process of gastrulation by immigration from a blastoporal area. (*a*) Germ layers and blastoporal area just defined. (*b*) Gastrulation in progress. Ectodermal teloblasts differentiated in the anterior lip of the blastopore, the genital rudiment has migrated forwards and the mesodermal teloblasts, head mesoderm band and endoderm cells are passing inwards. (*c*) Gastrulation is complete except for the continued formation of endoderm. Ectodermal and mesodermal teloblasts now active, and the head mesoderm bands are being formed. *b.*, blastoporal area. *E.*, ectodermal teloblast. *en.*, endoderm cell (yolk cell or vitellophag). *e.* 1, *e.* 2, *e.* 3, descendants from ectodermal teloblasts. *G.*, genital rudiment. *M.*, mesodermal teloblast. *m.*, head mesoderm band cell. *m.* 1, *m.* 2, descendants from mesodermal teloblasts.

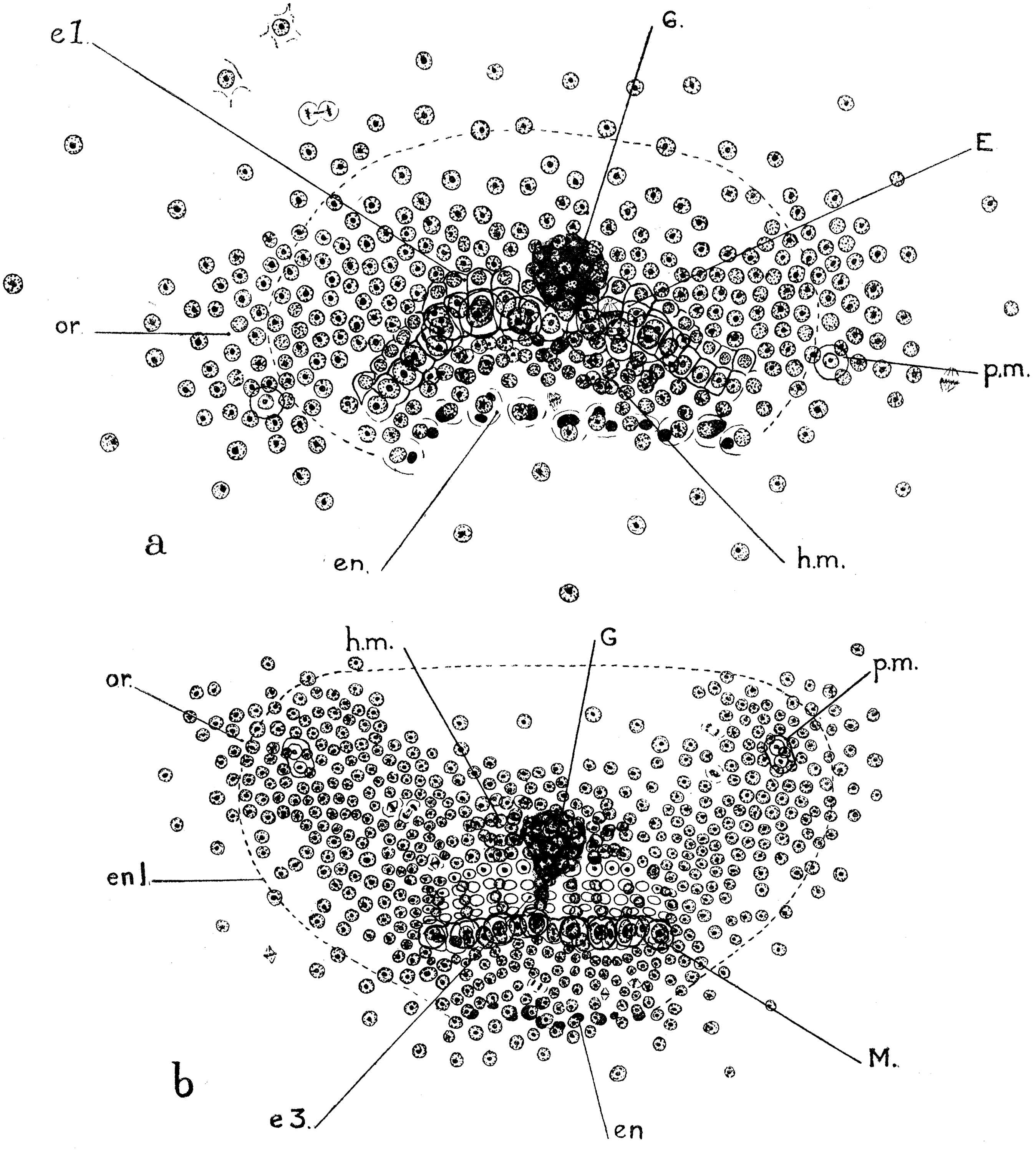
TEXT-FIGS. 4–7 show a series of whole preparations of germinal disks. Cells drawn in black are on the surface, while those which have become internal are shown in red. The red dotted line encloses the area covered by endoderm. The curved disks have been slightly flattened out in preparation.



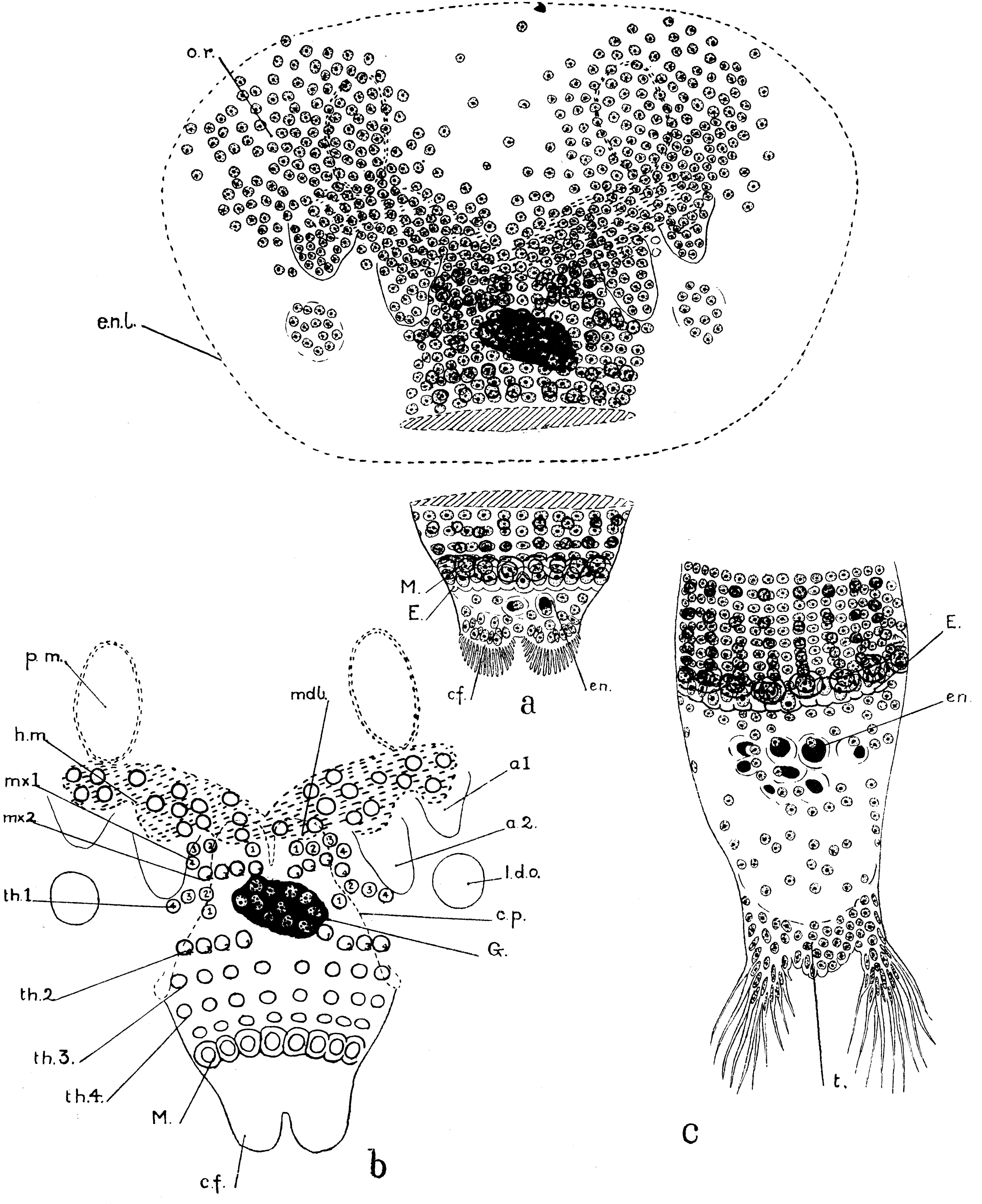
TEXT-FIG. 4.—(*a*) Undifferentiated germinal disk. (*b*) Differentiation of the germinal layers and genital rudiment and beginning of gastrulation. *E.*, ectodermal teloblasts. *en.*, endodermal cells. *G.*, genital rudiment. *M.*, mesodermal teloblast.



TEXT-FIG. 5.—(*a*) Later stage in gastrulation. The genital rudiment is internal, the curved rows of ectodermal teloblasts are approaching one another, and one pair of mesodermal teloblasts have taken up their positions below the ectodermal teloblasts. (*b*) The ectodermal teloblasts have formed a transverse row, and most of them have given one descendant. *E.*, ectodermal teloblasts; *en.*, endoderm cells; *en.l.*, boundary of area covered by endoderm cells; *e.* 1, descendant of ectodermal teloblast; *G.*, genital rudiment; *M.*, mesodermal teloblast.



Text-Fig. 6.—(*a*) Later stage. The germinal rudiment is now anterior to the teloblasts. Twenty-one instead of the normal fifteen ectodermal teloblasts are present. Three pairs of mesodermal teloblasts and many head mesoderm cells have been differentiated, and one pair preantennulary mesoderm cells have passed inwards behind the optic rudiments, which are distinguishable by their thick darkly staining cytoplasm. (*b*) The transverse germinal band is now V-shaped. Four rows of ectodermal and three rows of mesodermal teloblast descendants have been formed. The head mesoderm cells now lie in front of the latter. The ectodermal nuclei drawn in outline represent the position of a furrow appearing across germinal band. *E.*, ectodermal teloblast; *en.* endodermal cell; *en.l.*, boundary of area covered by endoderm cells; *e.* 1, *e.* 3, descendants of ectodermal teloblasts; *G.*, genital rudiment; *h.m.*, head mesoderm band cells; *M.*, mesodermal teloblast; *o.r.*, optic rudiment; *p.m.*, preantennulary mesoderm.



TEXT-FIG. 7.—Later stage, where the caudal papilla is formed. (*a*) The caudal papilla is cut off and laid back. (*b*) The mesoderm of the same embryo is figured alone, and the normal position of the caudal papilla indicated. The areas of the preantennulary, head band and teloblastic mesoderm are shown, the nuclei in the anterior rows of the latter being numbered. The genital rudiment has now moved back to the first thoracic segment. (*c*) The caudal papilla of an older embryo just before hatching. The caudal furca is well formed and endoderm formation continues. *a.* 1, antennule ; *a.* 2, antenna ; *c.f.*, caudal furca ; *c.p.*, caudal papilla ; *E.*, octodermal teloblast ; *en.*, endoderm cell ; *en.l.*, boundary of area covered by endoderm cells ; *G.*, genital rudiment ; *h.m.*, head mesoderm bands ; *l.d.o.*, dorso-lateral organ ; *mdb.*, mandible ; *mx.* 1, maxillulary mesoderm ; *mx.* 2, maxillary mesoderm ; *o.r.*, optic rudiment ; *p.m.*, preantennulary mesoderm ; *t.*, telson ; *th.* 1, *th.* 2, *th.* 3, *th.* 4, 1st 2nd, 3rd and 4th thoracic mesoderm.

Genital Rudiment.

The cells composing the genital rudiment are, from their earliest appearance as such, cytologically distinct from all other tissues. The primordium slips into the interior of the embryo (text-fig. 4 *b*) and is overgrown by ectoderm as a compact rounded mass. The nuclei are at first smaller than those of other parts, but later become relatively and actually larger. They become somewhat oval in shape and usually remain granular and without a large nucleolus. The cytoplasm remains lightly staining. The genital rudiment shifts forwards below the ectoderm and over the yolk, the ectodermal teloblasts at the same time moving backwards. The genital rudiment thus comes to lie anterior to the teloblasts (text-figs. 5 *b* and 6 *a* and *b*). Plate 21, fig. 2, represents a sagittal section of a similar stage to text-fig. 5 *b*, but shows the internal genital rudiment still connected posteriorly with the ectoderm. The number of cells in the genital rudiment is not constant, and no nuclear divisions have been observed to take place until the paired rudiments of the gonads are formed at a much later stage of development.

Mesoderm.

Mesoderm cells from the blastoporal area pass inwards in a forward direction and soon come to lie below the ectodermal teloblasts (text-fig. 3, "*M.*"). Mesoderm formation is at first active on each side of the genital rudiment, but sometimes, when the two lateral bands of ectodermal teloblasts unite well anterior to the genital rudiment, a few mesodermal cells are found passing inwards in front as well as lateral to it. The first formed lateral mesodermal elements, on passing inwards, increase in size and become arranged in a transverse row of eight cells below the ectodermal teloblasts. This row is established by the lateral addition of pairs of cell which have moved forwards from their place of origin. One pair only is seen in text-fig. 5 *b* and three pairs in text-fig. 6 *a*, and in Plate 22, fig. 10. These eight cells are the mesodermal teloblasts. Plate 21, fig. 3, shows a parasagittal section just lateral to that of fig. 2, and passes through one of the first pair of mesodermal teloblasts ("*M.*") seen in text-fig. 5 *b*. Behind it other cells are seen slipping in to form mesoderm. Text-figs. 8 *a* and *b* show the mesodermal and ectodermal teloblasts, but at a later stage.

When the eight mesodermal teloblasts have been formed, mesoderm cells continue to immigrate below the surface of the blastoporal area, but these cells are not so large as the teloblasts. They form an irregular mass below the ectoderm behind the mesodermal teloblasts (text-figs. 3 *b*, "*m.*," and 6 *a*, "*hm.*").

As soon as the eight mesodermal teloblasts have been differentiated, they all divide synchronously, each giving rise to a small descendant anteriorly. Such divisions are repeated, so that many transverse rows of eight small mesodermal cells are formed beneath the products of the ectodermal teloblasts (text-figs. 6 *b* and 7). Both mesodermal and ectodermal teloblasts, moreover, divide nearly or quite simultaneously (Plate 21, figs. 4 and 6), so that there is a corresponding number of transverse rows of ectoderm and mesoderm immediately in front of the teloblasts (text-figs. 6 *b* and 7, Plate 21, figs. 4, 5 and 6). However, the number of ectodermal rows is always one greater than the mesodermal rows, since the ectodermal teloblasts are established first (text-figs. 5 *b* and 6 *a* and *b*). The group of a dozen to twenty small mesodermal cells behind the mesodermal teloblasts now pass forward and internal to the latter, and lie at the sides of the genital rudiment in front of the zone formed by the activity of the teloblasts (text-figs. 3 and 6 *b*). Their cytoplasm often stains more deeply than that of the ectoderm (Plate 21, fig. 4). These cells are destined to form the " head bands " of mesoderm, mainly supplying the three naupliar segments. Plate 22, fig. 10, shows a transverse section of an embryo from the same family as that of text-fig. 6 *a*, passing through the posterior part of the genital rudiment and through the six mesodermal teloblasts. Internal to these teloblasts is seen the front edge of the mass of small mesodermal cells which are just starting to move forward. Later, no mesodermal cells are found behind or internal to the teloblasts, as is seen in Plate 21, fig. 4, representing a parasagittal section of an embryo of about the same age as that of text-fig. 6 *b*. The formation of the extra blastoporal preantennulary mesoderm will be considered later (p. 378).

Endoderm.

Whereas the mesodermal layer is formed rapidly from the blastoporal area, endoderm formation is a prolonged process. Cells behind the genital rudiment and lateral mesoderm absorb yolk and bulge inwards. These cells become detached from the surface and wander over the yolk internal to all other tissues (text-fig. 3 and Plate 21). At first the area covered by yolk cells is approximately that internal to the germinal disk, but later it is more extensive. This area is indicated by the dotted coloured line in text-figs. 4 to 7, only those cells still in connection with the exterior being drawn separately. When teloblastic mesoderm formation is completed, endoderm immigration continues from a region close behind the band of ectodermal teloblasts (text-figs. 7 *a* and *c* and Plate 21, fig. 6), and only ceases when the teloblasts have formed all thoracic and part of the abdominal mesoderm and ectoderm (see below). The embryo at this stage has three pairs of naupliar appendages and a well-developed abdomen, and is about to hatch from the vitelline membrane. When free within the embryo, these yolk cells become more or less spherical. The yolk vacuole continues to increase in size, and the cytoplasm becomes drawn out into a thin, sometimes scarcely visible layer over the outside, but remains thicker round the nucleus. The latter remains normal and the cytoplasm becomes darkly staining. The yolk cells never penetrate into the yolk but always lie at its surface. They divide only by mitotic division (Plate 21, fig. 6), the long axis of the spindle being always close and tangential to the surface of the cell. In these early stages the yolk cells show no signs of degeneration.

The development of the blastodermic disk outside the blastoporal area must now be considered. While gastrulation is proceeding, the cells of the rest of the disk become more concentrated, partly by division of elements already present in the transverse band (text-fig. 4 *b*) and partly by shifting of the surrounding cells up to the edges of the band. Two lateral thickenings, the optic rudiments, become distinguishable on either side of the row of teloblasts, their cells often becoming arranged in concentric arcs (text-figs. 5 *b* and 6 *a*). As the teloblasts move backwards owing to their production of ectoderm and mesoderm anteriorly, the optic rudiments shift forwards and become less lateral, so forming the ends of a V-shaped thickening continuous at its base with the region formed by the teloblasts (text-figs. 6 *b* and 7 *a* and *b*). At the posterior edges of these optic rudiments a small group of cells immigrate into the interior to form the preantennulary mesoderm (see p. 390). One cell on each side first slips in as shown in text-fig. 6 *a*. Later, several others pass inwards from the same place (text-fig. 6 *b* and Plate 24, fig. 22). A compact group of cells is thus formed, at first characterised by large nuclei and lightly staining cytoplasm.

The development has now been traced up to a stage shown in text-fig. 6 *b*, when all the germ layers are established. In no region are radial cell divisions found giving rise to endoderm or mesoderm. The only part of the outer layer which is multilaminar is found in the region of the optic rudiments. This condition is brought about partly by one cell being pushed over another by local concentration, and partly by large neuroblasts budding off smaller cells inwards (Plate 24, figs. 22 and 23). The formation of mesoderm at the hinder edge of the optic rudiments starts before the latter become multilaminar; and the localised immigration of mesodermal cells is quite distinct from, and not to be confused with, scarce and irregular immigration of cells in the rudiment itself. The positions of the large and small cells in the optic rudiments and in the ectoderm in front of the developing antennules are very constant, and the mesoderm formation always occurs at a similar place in relation to these rudiments and their constituents.

Early Development.

It is not necessary to enter at all fully into the external changes of shape of the young embryo or the development of the ectoderm, since they have been described so carefully for other Mysids as well as for various essentially similar forms. With the formation of the V-shaped band, the "germinal band," the disk becomes concentrated and occupies a smaller area than did the earlier transverse band.

"Naupliar" Region.

From the arms of the V between the optic rudiments and the teloblast descendants are formed the ectoderm of the naupliar segments with their appendages. The paired dorsal organs arise by two local concentrations of cells at the sides of the bands. The antennules and antennæ start to project from the general surface nearly simultaneously, and are followed somewhat later by the mandibles (text-figs. 7 *a* and *b*). The mandibles are formed close to the middle line and the anterior appendages more laterally. The two groups of head mesoderm cells lateral to the genital rudiment (text-fig. 6 *b*) spread forwards below the V-shaped bands (text-fig. 3, *m*, and Plate 21, fig. 5, "*h.m.*"), dividing mitotically. At first these mesoderm cells remain separate from one another, but they soon unite and form a pair of irregular loose head mesodermal bands lying to the median side of the bases of the naupliar appendages. From these bands groups of mesoderm cells bulge into the bases of the latter, which now consist of simple hollow tubes of ectoderm (text-fig. 7 *a* and Plate 21, fig. 7). Mesoderm cells rarely occur far anterior to the antennules or in the mid-ventral line. Occasionally, one or two mesodermal cells are found in the ventral anterior region between the compact preantennulary blocks. It is highly probable that such cells arose in the normal manner from the blastoporal area but anterior to the genital rudiment (see above, p. 376), so passing forward in advance of the head mesoderm, and have not been formed *in situ* from the ectoderm. As the head mesoderm spreads out below the germinal bands, the genital rudiment shifts backwards into the region formed by the teloblasts. The head mesoderm bands thus become anterior to the genital rudiment and they usually unite across the middle line posteriorly in the mandibular region (text-figs. 7 *a* and *b*). Later, after the mandibles have appeared, the mesoderm in this segment separates into two lateral masses which are larger than in the preceding segments. The two bands later break up and leave the intersegmental regions practically devoid of mesoderm. In the three naupliar segments these mesodermal bands give rise to the musculature of the limbs and connective tissues over the brain, etc., to the antennal gland in the antennal segment and to the liver in the mandibular segment. The head mesoderm never forms a cavity within itself in any other part than in the antennal gland. The subsequent development of the head mesoderm has not been followed in detail except in the formation of the antennal gland and liver.

Post-Naupliar Region.

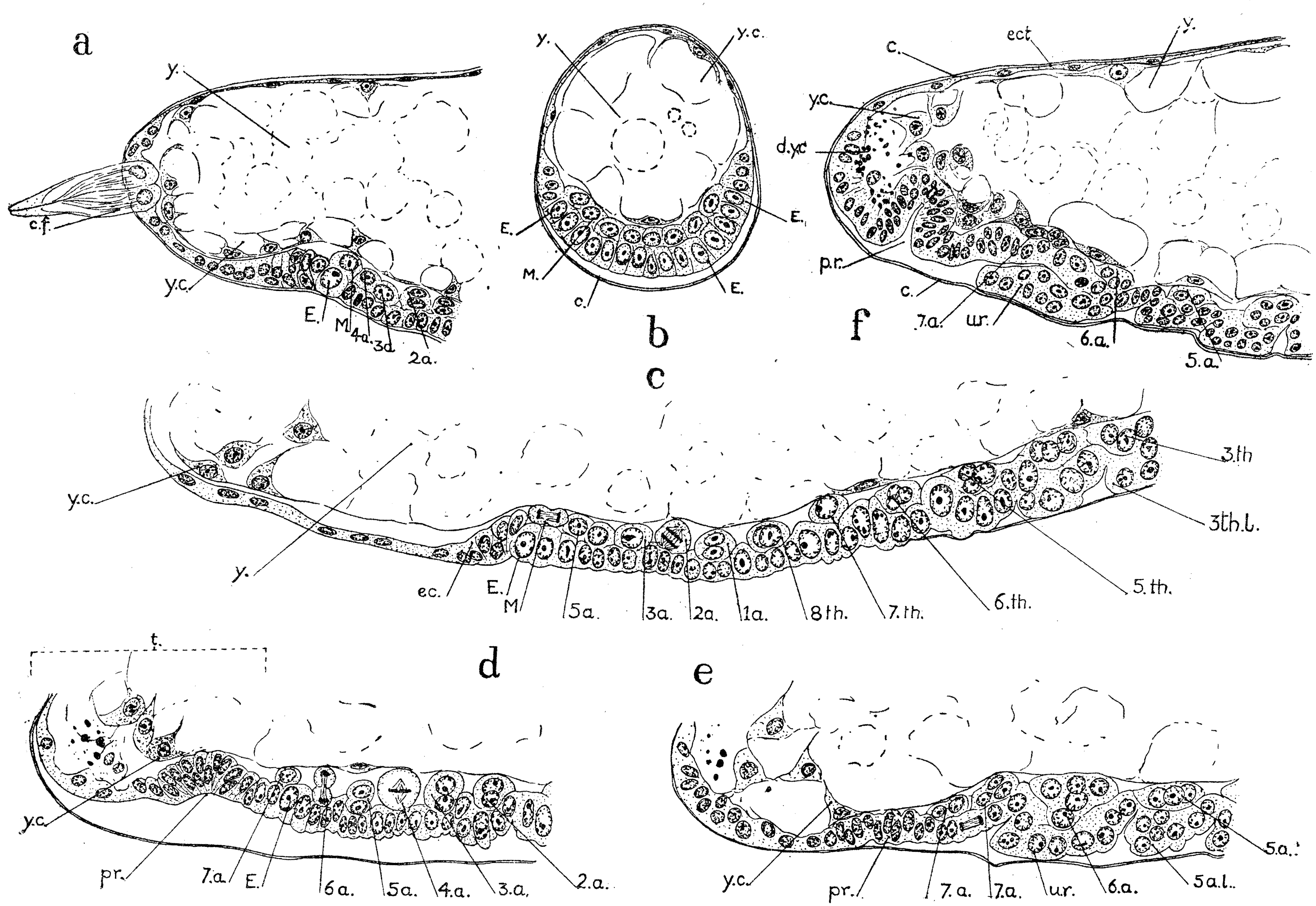
Soon after the teloblasts have become active, a transverse furrow appears anteriorly to them across the ectoderm already formed by the teloblasts. This depression is indicated in text-fig. 6 *b*, and is seen in the parasagittal sections in Plate 21, figs. 4 and 5. It is the beginning of the caudal flexure. As the tissues formed by the teloblasts increase, so this furrow deepens. It becomes crescentic, and part of the germinal disk folds forwards, so lying close against the anterior first-formed products of the teloblasts. This anteriorly directed caudal papilla is filled with yolk and represents the abdomen and part of the thorax, and from its mode of formation it is obvious that the teloblasts lie on its inner side. Text-fig. 7 *a* shows a germinal disk from which the caudal papilla has been dissected off; the dotted line in fig. 7 *b* shows the normal position of the papilla when folded forward. The parasagittal section seen in Plate 21, fig. 6, of an embryo older than that in text-fig. 7 *a*, shows the process of folding, started in Plate 21, fig. 5 carried to completion. When the fold is first formed, a few small cells lie behind the teloblasts which are transforming into endoderm cells. Posteriorly to these at the anteriorly directed tip of the papilla is a paired group of cells with elongated nuclei. These cells give rise to the provisional caudal furca. Their cytoplasm becomes drawn out into projecting processes, one from each cell (Plate 21, fig. 6). The caudal furca is thus formed from the blastodermic disk behind the blastoporal area and teloblasts. The furrow deepens and the papilla itself elongates, both by division of the teloblasts and elongation of the region between them and the caudal furca (text-fig. 7 *c*).

As already stated, the ectodermal and mesodermal teloblasts divide synchronously. The ectodermal descendants, however, soon divide again (Plate 21, fig. 6), the spindles lying parallel to the body axis. Thus approximately two transverse rows of ectodermal cells come to correspond with one row of mesodermal cells (Plate 21, fig. 6). Each segment of the thorax and abdomen is therefore represented by one transverse row of eight mesoderm cells and approximately two rows of ectoderm cells, the number in each row corresponding with that of the ectodermal teloblasts. These segmental rudiments remain unchanged until the embryo hatches from the vitelline membrane. The teloblastic mesoderm and ectoderm extend forwards as far as the maxillulary segment inclusive. The transverse rows of mesoderm cells are at first perfectly regular (text-figs. 6 *b* and 7 *a*, *b* and *c*), the cells of each row being situated at equal distances apart. In the anterior part of the thorax the eight cells of a row become disturbed. As the genital rudiment shifts backwards from the naupliar region (p. 379), the rows of post-naupliar mesoderm divide and pass on either side of the genital rudiment until it comes to lie in the first thoracic segment. The rows of mesoderm cells in this and the two preceding segments may become very irregular (Plate 21, fig. 9, and text-fig. 7 *b*).

At first the naupliar and post-naupliar parts of the mesoderm are at some distance apart (text-fig. 6 *b*). Later, when they meet, they can only be distinguished by the numbers and positions of the cells composing the latter.

The caudal flexure when first formed lies opposite the third thoracic segment. As the furrow deepens the angle of the flexure moves progressively down the body, until just before hatching it lies between the rudiments of the fifth and sixth thoracic segments. In Plate 21, fig. 6, it lies opposite the fourth thoracic segment. When the vitelline membrane ruptures, the caudal papilla is reflexed backwards, and the whole post-naupliar region is straightened out. Thus the caudal papilla gives rise to considerably more of the body than the abdomen alone.

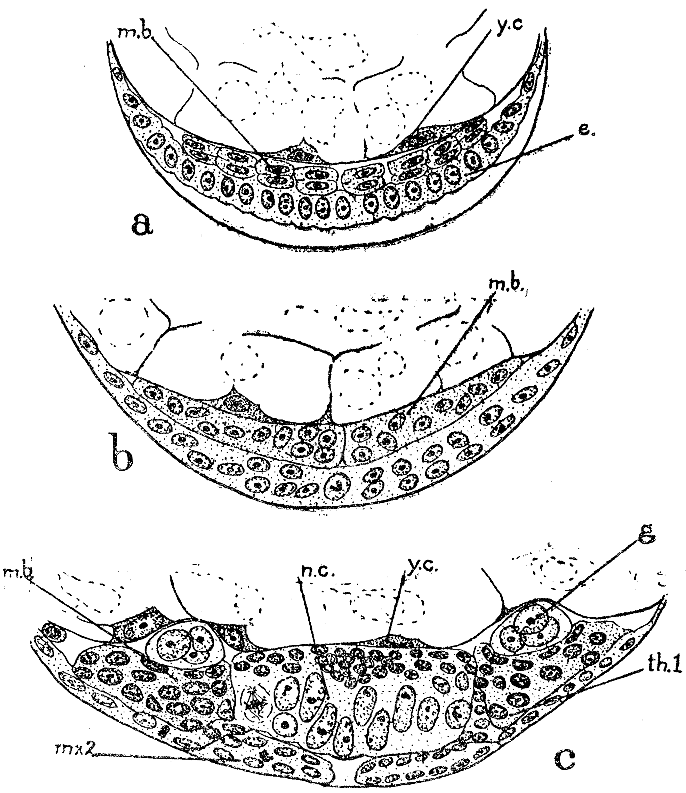
On hatching, the rudiments of about two abdominal segments are present and then endoderm formation ceases. In the production of the remaining abdominal segment rudiments the rows of teloblasts move backwards over the intervening space between them and the caudal furca (text-figs. 7 *c* and 8 *a*). The mesodermal teloblasts divide more equally so that their descendants resemble them in size (compare text-fig. 8 *a* with Plate 21, fig. 5). The ectodermal teloblasts are, however, at all times larger than the surrounding ectodermal cells. As the teloblasts shift backwards the ectodermal cells behind them on the ventral side become crowded (text-fig. 8 *c*). The last division of the mesodermal teloblasts forms two rows of eight cells, all equal in size. The anterior row gives rise to the mesoderm of the sixth abdominal segment, and the posterior row must be considered as the mesoderm of a seventh abdominal segment. This division is seen



TEXT-FIG. 8.—A series of sagittal and parasagittal sections through the posterior part of the body showing the disappearance of the teloblasts and the formation of the rudiments of the segments with their mesodermal somites, and of the proctodæum. In these embryos all segments of the body could be seen but only parts are drawn. (*a*) The primordium of the fourth abdominal segment has been formed and the mesoderm cells of the first and second abdominal segments have divided tangentially. (*b*) Transverse section of a similar stage through the fifteen ectodermal and eight mesodermal teloblasts. (*c*) Older stage, the mesodermal teloblast is dividing for the last time to form the mesoderm of the sixth and seventh abdominal segments. From the eighth thoracic segment forwards the mesoderm cells have divided irregularly to form the ventro-lateral blocks in each segment. (*d*) The mesoderm of the sixth and seventh abdominal segments is separated and an ectodermal thickening lies behind the indistinct ectodermal teloblast. (*e*) Later stage to show the fifth, sixth and seventh abdominal mesodermal somites. (*f*) The ectodermal thickening seen in (*d*) has now invaginated to form the proctodæum. The rudiment of the uropod projects below the sixth mesodermal somite. The yolk cells near the proctodæum are forming the posterior endodermal plate. *c.*, cuticle; *d.y.c.*, products of yolk cell degeneration; *E.*, ectodermal teloblast; *ec.*, ectoderm; *M.*, mesodermal teloblast; *pr.*, proctodæum; *t.*, telson; *ur.*, uropod; *y.*, yolk; *y.c.*, yolk cell; 1 *a.*, 2 *a.*, etc., first, second, etc., abdominal segment mesoderm; 5 *a.l.*, fifth abdominal limb; 1 *th.*, 2 *th.*, etc., first, second, etc., thoracic segment mesoderm.

in the parasagittal section (text-fig. 8 *c*) through one of the lateral teloblasts. The more median teloblasts of this embryo have already completed this division. The row of seventh abdominal mesoderm cells lies close to the ectodermal teloblasts (text-fig. 8 *c* and *d*). The terminal part of the body behind the seventh abdominal segment forms the telson and bears the caudal furca (for telson mesoderm, see p. 404).

The first change to take place in the segmental rows of mesoderm is a radial division of all cells so as to form a double row of sixteen cells (text-figs. 8 *a*, *c* and *d*, and 9 *a*). Further division gives rise to a pair of solid blocks of mesoderm situated ventro-laterally in each segment (text-figs. 8 *e* and *f*, and 9). The ectodermal cells also multiply and form ventro-lateral pouches round the mesoderm blocks, so that the segments are clearly visible externally by the intersegmental furrows. These changes take place from before backwards in regular sequence throughout the whole of the thorax and abdomen. Thus the establishment of segmental rudiments behind the mandibles occurs at regular intervals



Text-Fig. 9.—Transverse sections showing the formation of the paired ventro-lateral mesoderm blocks from the segmental rows of eight mesoderm cells. (*a*) Second abdominal segment, the eight cells have divided once to form a double row of sixteen cells. (*b*) Fifth thoracic segment. Further division has formed a pair of ventrally contiguous blocks of mesoderm, "*m.b.*" (*c*) First thoracic segment with the primordia of the gonads. The nerve cord and limb rudiments have appeared and the mesodermal blocks have become ventro-lateral. *e.*, ectoderm ; *g.*, genital rudiment ; *m.b.*, mesoderm block ; *mx.* 2, maxilla ; *n.c.*, nerve cord rudiment ; *th.* 1, first thoracic limb ; *y.c.*, yolk cell.

from before backwards, there being no precocious formation of the abdominal segments or delay in the appearance of the posterior thoracic ones. The thoracic and abdominal segments are at this stage precisely similar to one another and form a continuous series (text-fig. 8 *c*). The stomodæum appears soon after hatching when about three abdominal segments have been formed. It arises from the naupliar ectoderm in the mid-ventral line just anterior to the antennæ. The proctodæum appears after the seventh abdominal segment has been formed and the teloblasts have disappeared. Behind the teloblasts are about three rows of crowded ectodermal cells, often showing nucleoli (text-figs. 8 *a* and *b*), and posterior to these the ectoderm cells usually have no nucleoli. The latter multiply and become crowded mid-ventrally (text-figs. 8 *d* and *e*) and form the proctodæal invagination in the telson. The mouth subsequently shifts backwards till it lies just in front of the mandibles. A few yolk cells at the sides of the proctodæum degenerate (text-fig. 8 *f*).

Vitelline and Embryonic Membranes.

The vitelline membrane which surrounded the egg ruptures when the naupliar appendages and about half the abdominal segments have been formed. The volume occupied by the yolk prior to hatching remains approximately constant, although the growth and maintenance of the embryonic tissue must be constantly reducing the mass of yolk present. The yolk must then be absorbing water, but this absorption is limited by the space available within the vitelline membrane. When the vitelline membrane is ruptured and the embryo escapes, an immediate increase in the yolk volume occurs, until it occupies a space about 10 per cent. larger than that prior to hatching. Subsequent growth of the embryonic tissue reduces the amount of yolk present until it is all absorbed, the yolk volume decreasing steadily. The bursting of the egg membrane may be partly correlated with increasing size of the embryonic tissue and the pressure exerted by the reflexed caudal papilla, but it is probable that the increase in volume of the yolk by absorption of water is the main factor. The embryonic tissue at this stage represents only a very small portion of the mass of the whole embryo.

The sudden increase in volume of the yolk after hatching considerably stretches the blastoderm over the head region, where lies the bulk of the yolk, and the naupliar appendages and their mesodermal masses are drawn farther apart. Later, when more yolk is pushed down into the abdomen and some more is absorbed, this turgescence is lost, and the appendages approximate once more.

This phenomenon of water absorption by yolk is probably of general occurrence. GRAY (1926) has shown that the trout egg does not contain enough water for the utilisation of all the yolk, and this deficiency of water is made up by absorption during development. A similar cause probably underlies the water absorption of *Hemimysis*; and here it is of importance incidentally in the bursting of the vitelline membrane.

After hatching, the body is enclosed by a cuticle and the three pairs of naupliar appendages and caudal furca project freely. This cuticle gradually separates from the body as a new one is formed within it in the ordinary manner. The thoracic and abdominal limb buds are formed entirely within the first cuticle, which becomes widely separated from the body ventrally. As the cuticle separates from the tip of the abdomen the caudal furca loses continuity with the ectoderm and is not re-formed. The late embryo finally sheds this cuticle and with it the caudal furca. The stalked eyes and all the thoracic and abdominal limbs are thus freed. The body expands greatly after this first ecdysis, and the eyes and antennæ are rotated upwards and forwards as the dorsal mass of yolk is absorbed and the pressure of the cuticle removed. The embryos show considerable movements of body and limbs, and the epipodites of the first trunk limbs at quite early stages vibrate. The remaining yolk in the mid-gut is moved up and down by peristaltic contractions. Finally, the embryos leave the brood pouch.

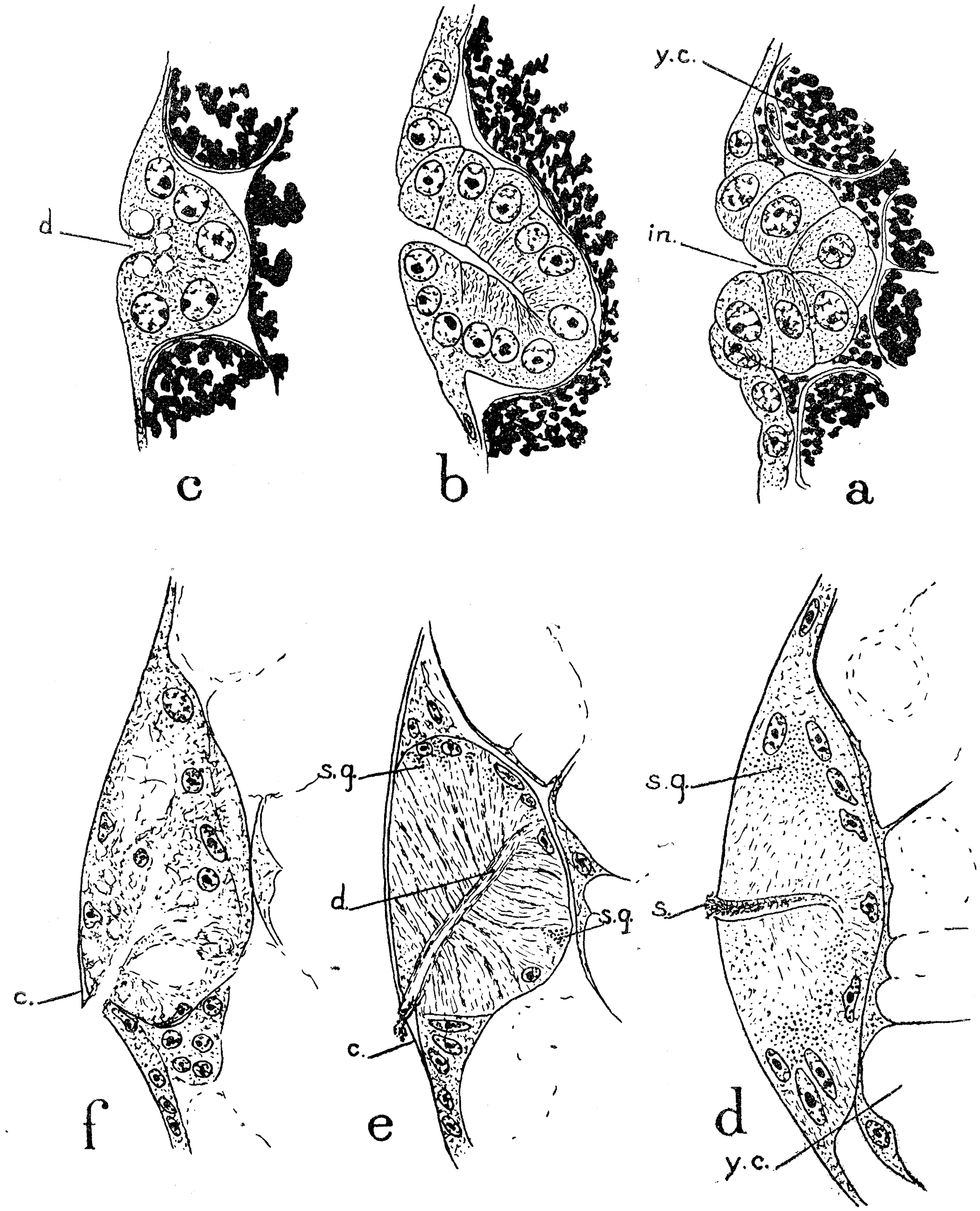
Paired Dorso-Lateral Organs.

The dorso-lateral organs of *Hemimysis* are formed as soon as the two pairs of antennæ project from the germinal bands. The ectodermal cells lateral to the antennæ form two thickenings, and these enlarged cells invaginate somewhat (text-fig. 10 *a* and *b*), the cup so formed being open to the exterior by a narrow channel. The cell boundaries are soon lost, but an intracytoplasmic duct remains in open communication with exterior (text-fig. 10 *c* and *d*). The nuclei occupy the peripheral parts of the organ. They do not divide, and do not at once degenerate as do those of the median dorsal organ (p. 392). The cytoplasm is at first homogeneous, but contains what must be secretory granules in the peripheral parts. The organ remains thus during the greater part of embryonic life. A secretion appears to be passed out of the duct (text-fig. 10 *e*). Just before the first cuticle is shed in the late embryo the activity of the organ appears to increase. The cytoplasmic granules disappear and the cytoplasm becomes strongly striated towards the duct (text-fig. 10 *e*). The organ then becomes vacuolated, presumably owing to loss of secretion (text-fig. 10 *f*), and ecdysis takes place. The organ must degenerate very rapidly as no trace is visible after the cuticle is shed. Its condition just before ecdysis is seen in text-fig. 10 *f*. As the dorso-lateral organs degenerate and the yolk is absorbed, the lateral ectoderm below these organs becomes more dorsal in position, and draws with it the muscles originally inserted below the dorso-lateral organs (p. 412).

Endoderm and Liver.

No attempt has been made to trace the later development of the alimentary canal in detail, but the early formation of the mid-gut and liver has been carefully followed. The yolk cells give rise to nothing but the mid-gut epithelium. The liver is mesodermal in origin and becomes connected with the mid-gut late in development.

The yolk cells lying at the surface of the yolk gradually spread round it and form the yolk sac. A little yolk may remain outside the yolk sac in the naupliar region and round the limb bases, where yolk globules may lie round the mesoderm. The yolk cells



TEXT-FIG. 10.—A series of transverse sections showing the growth of the dorso-lateral organs. (*a*) Enlarged cells forming a cup. (*b*) Continuation of this process. (*c*) Cell limits now lost leaving an intracellular duct to the exterior. (*d*) Shrunk nuclei and secretory granules in the periphery and secretion passing out of the duct. (*e*) As in the last, but cytoplasm striated towards the duct. (*f*) Disorganisation of the organ. *c.*, cuticle ; *d.*, duct ; *in.*, invagination forming the dorso-lateral organ ; *y.c.*, yolk cell ; *s.*, secretion ; *s.g.*, secretory granules.

absorb more yolk and become closely pressed together, forming secondary yolk pyramids.* The nuclei remain in the peripheral parts of the cells, and their cytoplasmic boundaries become very attenuated and often difficult to trace completely. In the abdomen and posterior part of the thorax the whole of the yolk becomes absorbed in this manner (text-fig. 11 *f*), but in the head region a central core of yolk is left between the pyramids. The growth of the pyramids (*y.c.*) at the expense of the central yolk mass (*y.*) is seen in text-figs. 11 *a*, *b* and *c*). In the short region traversed by the proctodæum the yolk cells do not form pyramids but degenerate (text-figs. 8 *d*, *e* and *f*, "*d.y.c.*").

Opposite the stomodæum and proctodæum, as described by WAGNER (1898), the yolk cells early become transformed into a regular epithelium. In text-fig. 11 *e* the anterior endodermal plate is well developed and continuous with the layer of yolk cells (an earlier stage of the same region is seen in Plate 22, fig. 13). The transformation of the yolk cells takes place by the peripheral protoplasmic portion containing the nucleus becoming detached from the rest of the pyramid, and the epithelial cells so formed concentrating over the posterior face of the stomodæum. A similar process takes place in contact with the proctodæum (text-figs. 8 *f* and 11 *f*).

The yolk sac becomes indented anteriorly by the vertical ectodermal septum (p. 392), which divides it into two lobes in the head. The transformation of the yolk sac into the adult mid-gut is a far simpler process than has previously been claimed. The adult mid-gut extends posteriorly to the sixth abdominal segment, the hind gut remaining short. The whole yolk sac gradually shrinks in diameter as the yolk is utilised, and the yolk cells become approximated. When the yolk sac measures about half its original diameter, the inner ends of the yolk pyramids become somewhat disorganised. As the yolk is further absorbed the outer parts of the yolk cells become more regular and form the mid-gut epithelium. This transition occurs first in the abdomen, where the yolk sac is narrower, the process spreading forwards from the posterior to the anterior endodermal plates. The latter do not form the mid-gut epithelium by growing round the yolk cells. The whole mid-gut is formed in a similar manner, the process starting first opposite the stomodæum and proctodæum.

The anterior endodermal plate remains very localised for a considerable period. It gradually extends dorsally and forms the mid-gut diverticulum. The anterior yolk lobes in the head are in connection with the dorsal diverticulum and are finally absorbed into it (text-fig. 11 *d* and 13 *k* and *l*).

The liver arises soon after the stomodæum from the posterior parts of the head mesodermal bands. After hatching, the mesoderm in the mandibular segment forms two ventro-lateral masses as in Plate 21, fig. 7. Each mass becomes divided into two parts. The lateral cells supply the mandibular mesoderm, a pair of more median groups forming the liver primordia. This separation has just occurred in Plate 22, fig. 11, and the paired liver rudiments are seen lying clearly external to the yolk cells and exactly resembling

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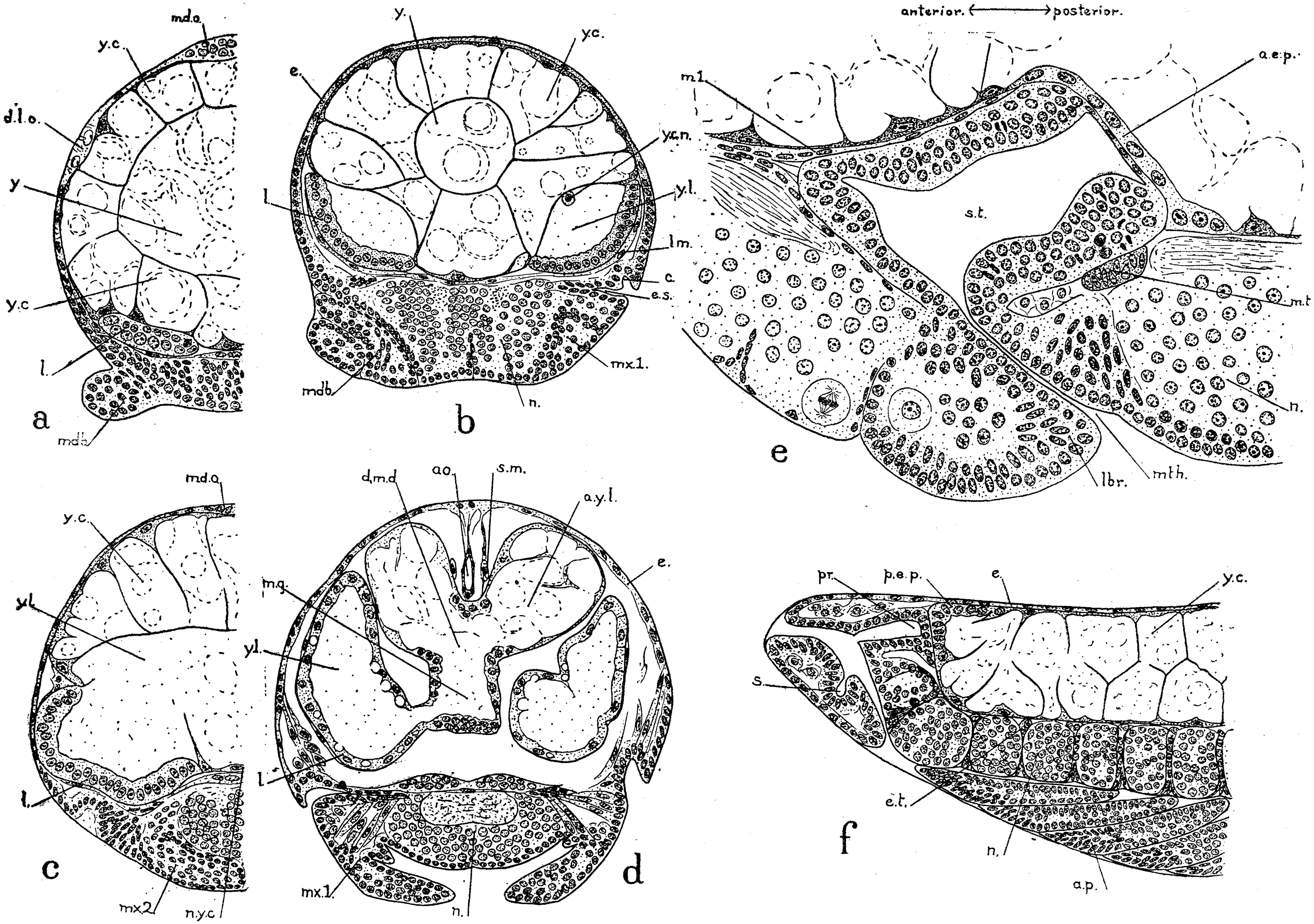
* "Secondary yolk" pyramids is used in the sense adopted for most Decapoda. There are no primary yolk pyramids in *Hemimysis*.



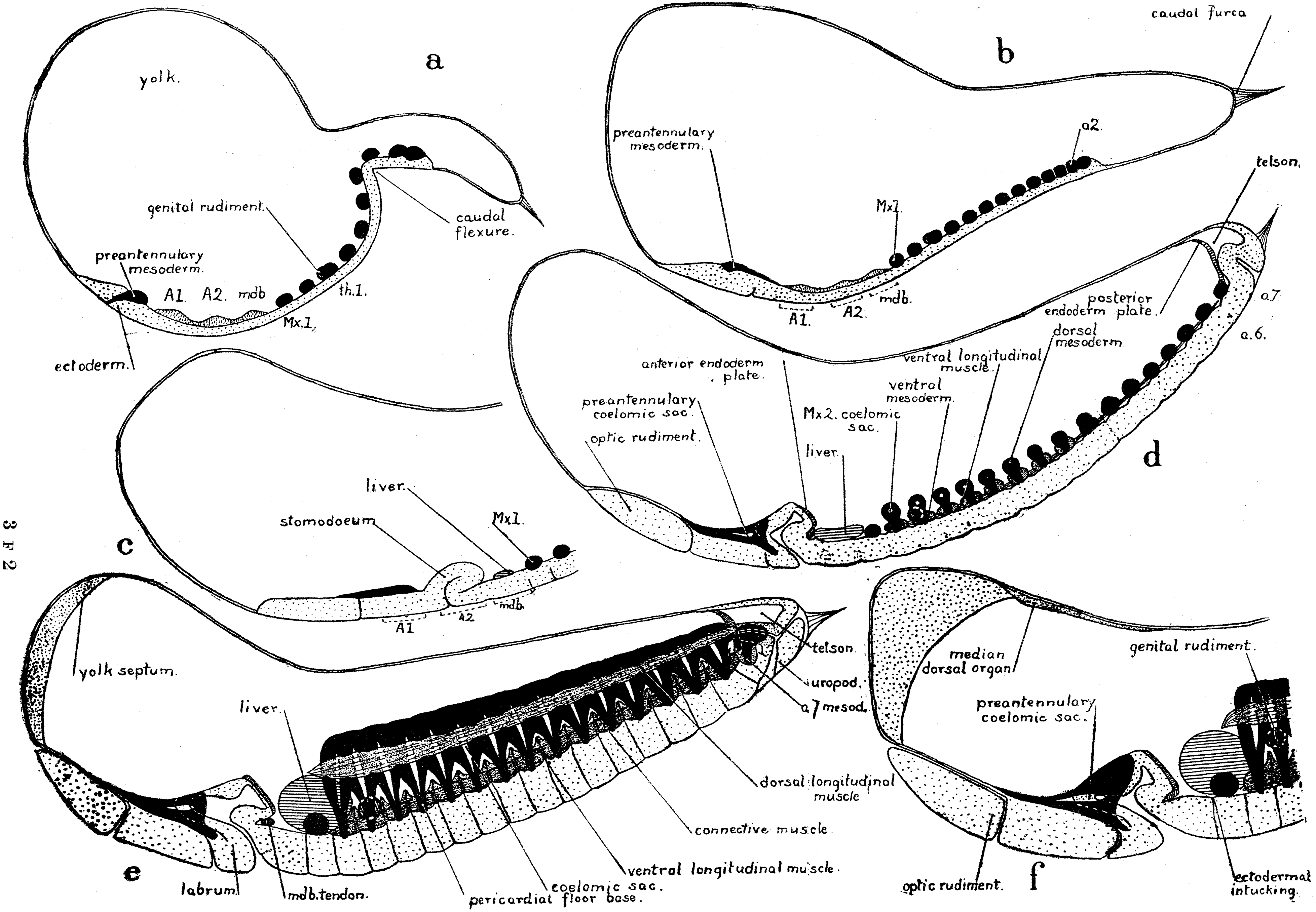
TEXT-FIG. 11.—Showing the development of the liver and mid-gut. (*a*) Transverse section through the mandibular segment showing the liver rudiment clearly external to the yolk cells. (A little older than the stage figured in Plate 22, fig. 11.) (*b*) Slightly oblique section through the maxillulary and posterior mandibular segments. The liver rudiments are larger and the yolk cells just within them are disorganised. (*c*) The liver rudiment in the maxillary segment is curling inwards to form a tube. The free yolk left by the disorganised yolk cells is abundant. (*d*) The liver tubes are formed and enclose the free yolk. The yolk cells above the developing liver are forming the mid-gut diverticulum. (*e*) Shows the formation of the anterior endodermal plate from the yolk cells against the posterior end of the stomodæum. (*f*) Posterior endoderm plate forming from the yolk cells lying against the proctodæum. The yolk cells in the abdomen have absorbed the whole of the yolk. *a.e.p.*, anterior endodermal plate; *a.o.*, anterior aorta; *a.p.*, appendages; *a.y.l.*, anterior yolk lobe; *d.l.o.*, dorso-lateral organ; *d.m.d.*, dorsal mid-gut diverticulum; *e.*, ectoderm; *e.s.*, endoskeletal intucking; *e.t.*, ectodermal tendon; *l.*, liver; *lbr.*, labrum; *l.m.*, liver mesoderm; *m.* 1, preantennulary mesoderm; *mdb.*, mandible; *md.o.*, median dorsal organ; *m.g.*, mid-gut; *m.t.*, mandibular tendon; *mth.*, mouth; *mx.* 1, maxillule; *mx.* 2, maxilla; *n.*, nerve cord; *n.y.c.*, nucleus of yolk cell; *p.e.p.*, posterior endodermal plate; *pr.*, proctodæum; *s.*, developing statocyst; *s.m.*, rudiment of stomach muscle; *s.t.*, stomodæum; *y.*, unabsorbed yolk; *y.c.*, yolk cell; *y.c.n.*, free nucleus of disorganised yolk cell; *y.l.*, free yolk left by disorganised yolk cells.

the mandibular mesoderm histologically. These liver rudiments lie in the anterior part of the mandibular segment at a little distance from the stomodæum. They grow together mid-ventrally (Plate 22, fig. 12) and form a transverse band just behind the stomodæum, which at this stage is growing backward through the antennæ to the mandibular segment. The liver rudiment is quite distinct from the yolk cells, mesoderm, and developing mandibular tendon below it. The sagittal section (Plate 22, fig. 13) shows the joined liver rudiment behind the stomodæum external to the yolk cells, the anterior endodermal plate not yet being formed. The latter has nothing to do with the formation of the liver. The lateral parts of the liver rudiment grow backwards through the mandibular and succeeding segments forming two curved epithelial plates, on the inner faces of which the outer wall of the yolk sac is clearly visible (text-fig. 11 *a*). Sooner or later these plates become separated, lying anteriorly at the sides or just behind the anterior endodermal plate (text-figs. 12, 13 and 14). The latter at this stage is never joined to the liver rudiments. These rudiments grow round the yolk sac laterally and become more cup-shaped. The yolk cells immediately on the inner faces of the liver lobes break down and their yolk is left free in this region (text-fig. 11 *b*, "*y.l.*"). The upper parts of the liver lobes gradually roll inwards (text-fig. 11 *c*) and close to form a pair of liver tubes, while the yolk sac above rounds itself off as the mid-gut. The liver tubes unite with the most anterior part of the mid-gut just behind the stomodæum, and not until then are they connected with the anterior endodermal plate (text-fig. 11 *d*). The adult liver lobes are formed by outgrowths and subdivision of the primary pair.

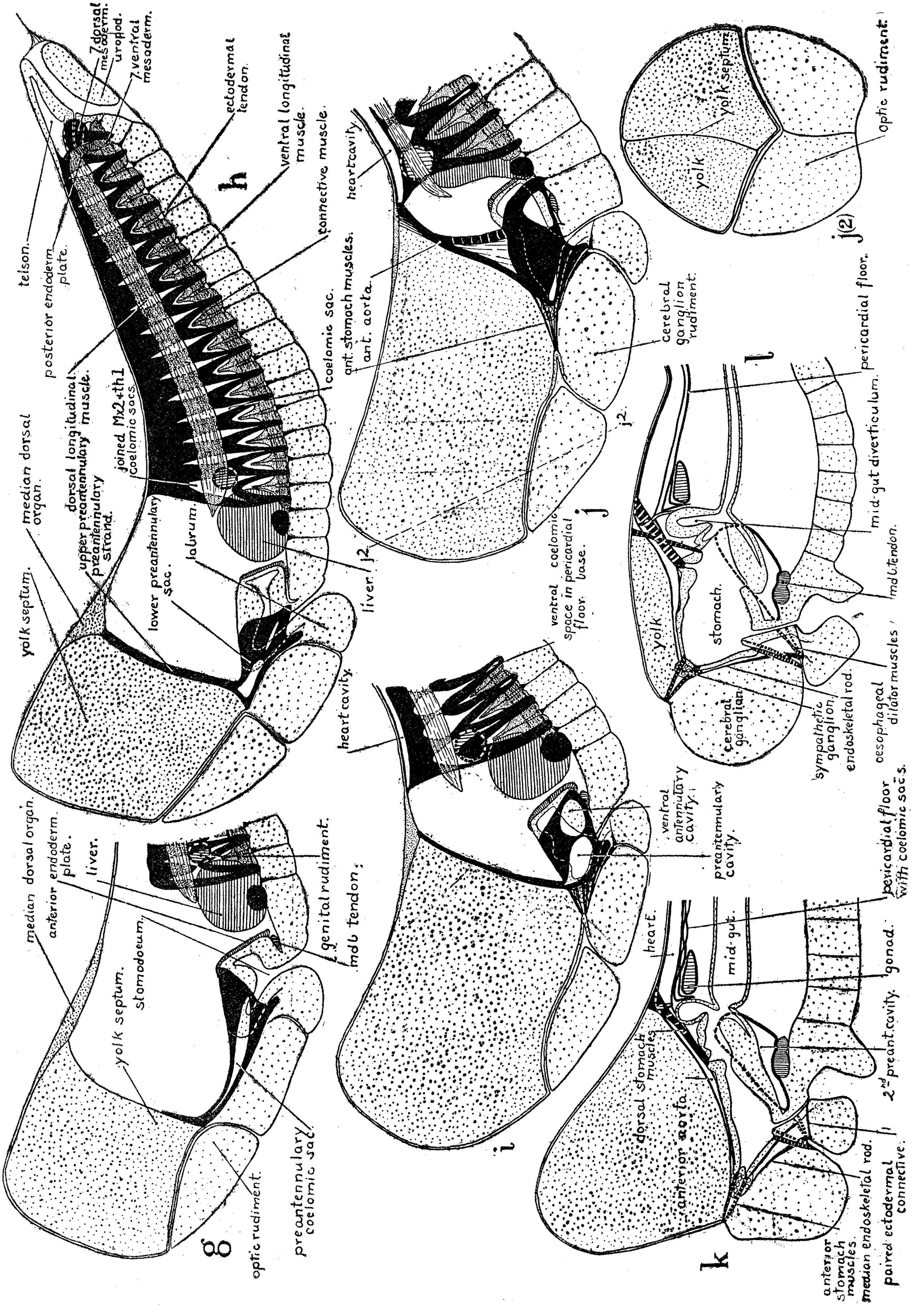
Preantennulary Mesoderm and Median Dorsal Organ.

The paired groups of mesoderm cells formed from the germinal disk behind the optic rudiments (text-fig. 6 *b*) grow progressively backwards from their point of origin as two solid strands lying immediately within the ectoderm. They remain in connection with the latter anteriorly for a considerable period, until the embryo hatches from the vitelline membrane. As the two arms of the V-shaped band approach one another, the points of origin of the preantennulary mesoderm become shifted from behind the optic rudiments (text-figs. 6 *a* and *b*) to positions internal and near to their anterior edges (text-fig. 7 *a*). With increasing age these strands tend to stain more deeply, and when the embryo hatches from the vitelline membrane they lose connection with ectoderm and grow backwards through the antennulary segment lying near the mid-ventral line (text-figs. 12, 13 and 14, and Plate 24, fig. 23). In lateral view these strands now extend forward into the cerebral region a shorter distance compared with earlier stages. This is largely an apparent rather than a real condition, since in early stages the arms of the V-shaped band are wide apart, so that a directly lateral reconstruction will exaggerate any longitudinal overlapping of parts.

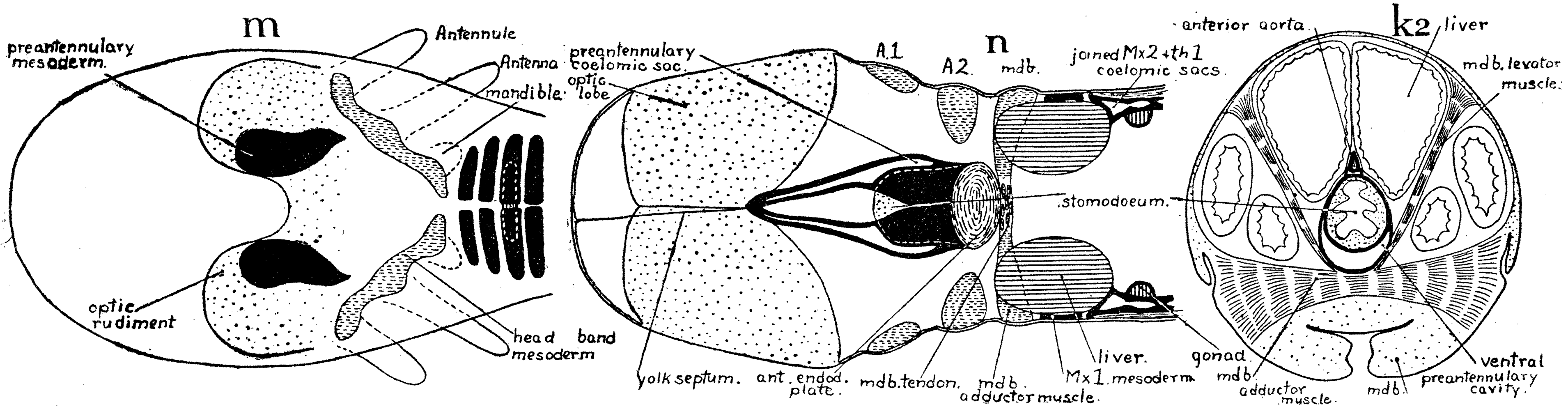
It is thus seen that these two mesoderm masses first appear behind the optic rudiments at a point in linear series with the two pairs of antennæ and mandibles which are formed



TEXT-FIG. 12.—A series of reconstructions of embryos drawn as transparent objects in side view. The preantennulary and trunk mesoderm is shown in black. The head band mesoderm is only shown in the younger stages. (*a*) An embryo just liberated from the vitelline membrane. The caudal papilla is straightening out, and the preantennulary, head mesoderm band and teloblastic mesoderm are shown. The rudiment of the seventh thoracic segment has been formed. (*b*) The second abdominal segment has now appeared and the preantennulary mesoderm is growing backwards. (*c*) The stomodæum and liver rudiments are formed and the preantennulary mesoderm has now grown through the antennulary segment. (*d*) The preantennulary mesoderm has reached the stomodæum and its cœlomic cavity is appearing. All the trunk mesodermal somites have been formed and the anterior thoracic ones have divided into dorsal and ventral portions. Cœlomic sacs are appearing in the dorsal mesoderm and the ventral longitudinal muscle is being formed by the ventral mesoderm. (*e*) The dorsal mesoderm has united above to form a continuous sheet in which lie the cœlomic sacs. The dorsal longitudinal muscle has been formed from the outer walls of the sacs and the ventral mesoderm has formed the outer connective muscles intersegmentally. Growth of the seventh abdominal somite is slower than those of the trunk. The yolk septum is being formed anteriorly. (*f*) Further growth of the yolk septum and preantennulary mesoderm, and the appearance of the median dorsal organ.


g
median dorsal organ.
anterior endoderm plate.
liver.
genital rudiment.
mdb tendon.
stomodoeum.
yolk septum.
yolk septum.
preantennulary coelomic sac
optic rudiment.
h
telson.
posterior endoderm plate.
7 dorsal mesoderm.
uropod.
7 ventral mesoderm.
ectodermal tendon.
ventral longitudinal muscle.
connective muscle.
coelomic sac.
joined Mx2+th1 coelomic sacs.
dorsal longitudinal muscle.
upper preantennulary preantennulary strand.
median dorsal organ.
yolk septum.
lower preantennulary sac.
labrum.
liver.
j2
j
ant. stomach muscles.
ant. aorta.
heart cavity.
cerebral ganglion rudiment.
ventral coelomic space in pericardial floor base.
j2
j(2)
yolk septum.
yolk.
optic rudiment.
i
heart cavity.
ventral antennulary cavity.
preantennulary cavity.
l
pericardial floor.
mid-gut diverticulum.
mdb tendon.
oesophageal dilator muscles.
endoskeletal rod.
sympathetic ganglion.
cerebral ganglion.
stomach.
yolk.
k
heart.
mid-gut.
pericardial floor with coelomic sacs.
gonad.
2nd preant. cavity.
dorsal stomach muscles.
anterior aorta.
l
paired ectodermal connective.
median endoskeletal rod.
anterior stomach muscles.

Text-Fig. 13.—(*g*) The preantennulary mesoderm has started to grow up the yolk septum, and the cœlomic cavity is at its maximum size. (*h*) The upper preantennulary strand has reached the dorsal organ and the ventral cœlomic space has appeared. The trunk mesoderm has reached the dorsal side of the body. (*i*) The dorsal organ is drawing the upper preantennulary strands back to the heart, which is being formed by the trunk mesoderm. The ventral preantennulary cavity is enlarging, and the ventral cœlomic spaces in the pericardial floor bases have appeared. (*j*) The upper preantennulary strands have reached the heart and are forming the anterior aorta and the dorsal stomach muscles. All the first-formed cœlomic spaces are shrinking. (*j* 2) Transverse section to show the position of the yolk septum. (*k*) Thick sagittal section. The trunk cœlomic sacs lie in the pericardial floor and the ventral preantennulary spaces have enlarged and united below the stomach. The yolk sac has shrunk to form the mid-gut. (*l*) Thick sagittal section after the first cuticle has been shed. The preoral region has rotated upwards and the trunk cœlomic cavities have disappeared.



Text-Fig. 14.—(*m*) Frontal view at about the same stage as text-fig. 13 *b* to show the preantennulary, head band and trunk mesoderm. (*n*) Frontal view of the same stage as text-fig. 14 *g*. The maxillary and first thoracic cœlomic sacs are uniting and the preantennulary cœlomic cavities lie at the sides of the stomodæum. (*k* 2) Transverse section through the mandibular region of the same stage as text-fig. 14 *k* to show the ventral preantennulary cœlomic space.

later. But by the time these appendages protrude, the optic rudiments have approximated, thus shifting the preantennulary mesoderm towards the middle line, and so breaking the linear series of mesoderm masses.

Growth backward of the preantennulary mesoderm strands brings them in contact with the stomodæum (text-fig. 12). They are then rather attenuated anteriorly but larger in front of the stomodæum. The strands apply themselves to the sides of the latter and spread backwards over its lateral and dorsal surfaces. Just as the strands reach the stomodæum, or occasionally a little earlier, a cavity is formed within each strand at the hinder end (text-figs. 12 and 13, and Plate 24, fig. 24). This cavity increases in size and extends along the sides of the stomodæum and forwards through the more attenuated part of the strand. It is largest just anterior to the stomodæum, and becomes much compressed laterally along its sides. The maximum development of this cavity is shown in text-figs. 13 *g* and 14 *n*. These paired mesodermal masses and their cavities represent the pair of preantennulary mesodermal somites (see p. 440).

Just after the preantennulary mesoderm strands reach the stomodæum, the median dorsal organ* makes its appearance. The head of the embryo is much distended with yolk. From the anterior end of the embryo an ectodermal intucking occurs dividing the yolk vertically into two lobes (text-figs. 12 *e* and *f*, and 13). This intucking grows progressively backwards, appearing as a very thin membrane directly continuous with the dorsal ectoderm above the yolk and with the ectoderm below the yolk and above the optic rudiments, which are being folded off from the rest of the embryo. No nuclei have been observed in this membrane. The endodermal yolk cells continue to surround the yolk in each lobe, and so lie on either side of this septum. Soon after the septum has appeared, a local concentration of ectodermal cells occurs dorsally forming the median dorsal organ. It extends from the posterior edge of the septum backwards through the mandibular region as an elongated thickening, projecting downwards into the yolk near the attachment of the septum.

The dorsal organ is a seat of cellular degeneration. No cell boundaries are visible and the nuclei become several deep and deformed in outline. The cytoplasm contains darkly staining products, presumably of nuclear breakdown, such as found in regions where the yolk cells degenerate (pp. 383 and 432), and other refringent globules (Plate 24, fig. 25). The first appearance of the dorsal organ may be correlated with progressive absorption of yolk. This must leave an excessive area of ectoderm in the head region (text-figs. 12 and 13), which is absorbed partly by means of the median dorsal organ. The septum when first formed is never median, but lies obliquely from the dorsal surface to one of the optic rudiments (text-fig. 13 *j* (2)). The septum and dorsal organ rapidly shift backwards, the latter apparently dragging the former with it. When the septum reaches the hinder limit of the optic lobes it becomes median in position.

At this stage the septum reaches the anterior limit of the preantennulary mesoderm.

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* The median dorsal organ is not to be confused with the paired dorso-lateral organs of a totally different structure (see p. 384).

The tips of the latter then turn dorsally, growing up the posterior edge of the septum and become attached to the dorsal organ (text-figs. 13 *g* and *h*, and Plate 24, fig. 25), forming the "upper strands." This growth is very rapid, and considerable differences may be found among individuals from the same family. The tension on the dorsal organ appears to be increased, and it is dragged farther down into the yolk. The dorsal organ continues to grow backwards, drawing with it the upper strands until it reaches the anterior limit of the heart tube in the maxillary segment (text-figs. 13 *i* and *j*). The mesoderm is at first attached to the anterior part of the dorsal organ, but finally the junction is shifted to the posterior end in front of the heart. The paired cavities in the preantennulary mesoderm extend upwards along the septum for a short distance. However, they soon become obliterated anterior to the stomodæum, as the front parts of the strands become drawn upwards and backwards by the dorsal organ. The cavities persist for a longer period over the sides of the stomodæum as laterally compressed spaces in the "lower preantennulary sacs." Finally, they become obliterated by the closing together of their walls.

When the upper strands have been drawn backwards till they approach the heart dorsally, the anterior aorta is formed between them. This process is seen most clearly just above the stomodæum. Here a hæmocœlic space, triangular in section, is left between the strands and the dorsal stomodæal wall. The preantennulary cavities lie in the mesoderm at the sides of this space. The floor of the aorta is formed first by outgrowths from the inner walls of the preantennulary cavities, which meet above the stomodæum (Plate 24, fig. 26). This also completes the mesodermal investment of the latter. Later, the walls of the aorta become differentiated from the inner sides of the upper strands, bounding the triangular space, after their cavities have become obliterated (Plate 24, fig. 27). Between the stomodæum and the dorsal organ the aorta is formed in a similar manner from the inner sides of the upper strands, but owing to their lateral compression the cavity in the vessel only becomes apparent later. The nuclei of the aorta differ from those of the rest of the upper strands, which are destined to form muscle, by their small size and rounded form compared with the darkly staining oval nuclei of the strands (Plate 24, fig. 27). When the dorsal organ and the upper strands reach the heart, the aorta becomes united with the latter. Its cavity then opens up, so putting the whole vessel in communication with the heart. As the strands are drawn backwards they come in contact with the upper end of the stomodæum, which later forms the stomach (text-figs. 13 *k* and *l*), so that in the adult the anterior aorta finally rests on this organ throughout its whole length.

The musculature derived from the preantennulary somites has not been followed in detail, but a few outstanding muscles may be mentioned. The upper strands give rise to two pairs of stomach muscles besides the anterior aorta. As they are drawn backwards on to the dorsal surface of the stomodæum, muscle insertions are formed at either side of the aorta on the anterior part of the pyloric portion of the developing stomach (text-fig. 13 *j* and Plate 24, fig. 27). Two pairs are formed one anterior to the other. Differentiation of the muscles takes place in the outer part of the strands, the upper ends of these muscles being attached to the dorsal organ. When the anterior aorta has united with the heart, the dorsal organ is gradually absorbed, and so these muscles become directly attached to the ectoderm. At first the two pairs of muscles lie close together (text-fig. 13 *k*), but when the dorsal organ is finally absorbed and the larval cuticle is shed, they are widely separated. The pair attached more anteriorly on the stomach are larger and lie external to the other pair, and are inserted in the dorsal ectoderm in the first thoracic segment some distance behind the anterior valve of the heart. The second and smaller pair pursues a less oblique course and passes directly upwards in front of the mid-gut diverticulum to the ectoderm at the root of the dorsal aorta (text-fig. 13 *l*). The stomach musculature of an adult mysid does not appear to have been adequately described. GELDERD (1909, p. 27, and fig. 3) describes and figures one pair of cardiac muscles running to the dorsal body wall. These seem to be the outer pair of muscles seen in *Hemimysis,* but the dorsal insertions of these muscles are not figured.

Other paired muscles are formed at the anterior end of the stomodæum. As the upper strands of preantennulary mesoderm grow upwards and backwards, the lower sacs leave strings of cells between the ectoderm behind the optic rudiment and the anterior end of the stomodæum (text-fig. 13 *i*). The furrow separating off the optic rudiments form a small median intucking towards the stomodæum on to which these strings of cells become attached. This intucking subsequently straightens out (text-figs. 13 *j* and *k*). The strings of cells form two pairs of muscles near the middle line (text-fig. 13 *k*). When the anterior part of the body is rotated upwards at the end of embryonic life, these muscles appear to keep the upper anterior angle of the stomach drawn out (text-figs. 13 *k* and *l*). Many intrinsic muscles of the stomach and longitudinal and circular œsophageal muscles are formed from the preantennulary mesoderm.

Just before the upper strands of mesoderm reach the heart paired cavities appear in the lower sacs. These arise posteriorly to the first-formed cœlomic cavities and lie along the lower lateral parts of the stomodæum behind the mouth (text-fig. 13 *i*). They do not appear to communicate directly with the original cœlomic cavities, although they are situated in a position in which these cavities must occupy were they larger (compare also the lower cœlomic spaces in the pericardial floor bases, p. 404). The first-formed cœlomic cavities then become obliterated by the sinking together of their walls (text-fig. 13 *j*), but the new cavities increase in size and spread round the stomodæum ventrally until they meet. The lower wall of this space becomes attached to the tendon of the mandibular adductor muscle and the median part of the endoskeletal plate (text-figs. 13 *k* and *l*, and 14 *k* (2)). Posteriorly this space is completely closed at the end of the plyoric stomach, and anteriorly it extends as two lateral arms round the sides of the œsophagus and ends here blindly over the circumœsophageal commissures. Before these cœlomic spaces unite, two pairs of muscle rudiments are formed from the mandibular mesoderm. The most anterior pair extends from the mid-ventral wall of the stomach to the ventro-lateral body wall just behind the antennæ and above the labrum. The next pair is inserted in the mid-ventral ectoderm behind the mouth and passes up to join the dorso-ventral mandibular muscles. When the secondary cœlomic spaces unite, these muscles are left extending across the cavity. A third pair of muscles running across this cavity seems to be formed from its walls, and extends from the middle of the mandibular tendon forwards to the ventro-lateral wall of the stomach. This cœlomic space persists in the adult. When not in contact with other organs, it is surrounded by venous spaces, from which it is separated by a cellular membrane. It is quite distinct and closed from the hæmocœl, and remains empty after micro-injection of the arterial and venous systems.

Later Development of the Post-Naupliar Mesoderm.

The development of the trunk mesoderm has been described (p. 382) up to a stage when every segment is provided with a pair of solid blocks of mesoderm. They lie at first ventrally, the two blocks being adjacent in the middle line (text-figs. 9 *b* and 14 *m*). As the ectoderm thickens to form the rudiment of the nerve cord, the paired blocks shift ventro-laterally to the bases of the ectodermal limb buds (text-fig. 9 *c*) so leaving the mid-ventral region devoid of mesoderm. Each block lies wedged between the lateral ectoderm and the nerve-cord rudiment. The block is roughly triangular in transverse section, the apex pointing downwards into the ectodermal limb bud, and the base lying against the endodermal yolk sac above. Subdivision of the blocks now takes place in all but the maxillulary segment, where the mesoderm is less compact than in the posterior segments. The cells at the apex of the triangular mass separate and form the limb mesoderm. The rest of the block divides into an outer " dorsal " and an inner " ventral " part (text-fig. 12 *d*). The former gives rise to the dorsal longitudinal muscle, heart, pericardial floor and gonoducts, while the latter forms the ventral longitudinal muscle and much of the trunk musculature.

In the dorsal mesoderm the base of the pericardial floor early becomes distinguishable as the most ventral part in the middle of each segment lying against the ectoderm at the junction of the limb and the lateral body wall. It forms a knob-like projection from the main mass of this mesoderm (text-fig. 12 *d*). In the latter a small cavity appears. The cœlomic sacs are at all stages completely closed and never contain blood. The cavities remain colourless, while all blood spaces readily stain with Mallory's triple stain or with orange G. The beginning of the subdivision of the mesoderm and the first appearance of a cœlomic sac are seen in Plate 22, fig. 14.

The changes just described take place steadily backwards from the maxillary to the sixth abdominal segment. No cœlomic spaces appear in the maxillulary segment. In the maxillary segment the knob-like bases of the pericardial floor are scarcely formed, but otherwise the mesoderm behaves in a similar manner throughout the trunk.

The limb mesoderm early becomes characterised by its very large nuclei (Plate 22, figs. 14 and 15). It spreads as a solid core of cells down the tubular ectodermal limb bud (Plate 22, fig. 15).

In the ventral mesoderm the nuclei are at first smaller than in the dorsal mesoderm. Cells from the lower parts of the ventral mesoderm grow out longitudinally and unite with those of successive segments. The rudiments of the paired ventral longitudinal muscles are thus established, and this takes place very early, just before the mesodermal blocks are clearly subdivided (text-fig. 12 *d*). The muscle rudiments become attached to the ectoderm anteriorly at the intersegmental folds between the maxillary and maxillulary segments (text-fig. 22 *d*, " *v.l.m.*").

The dorsal mesoderm grows upwards laterally, pushing its way between the ectoderm and the yolk sac, the knob-like bases remaining fixed. The outer walls of the cœlomic sacs become thickened while the inner walls remain approximately one cell thick. Cells from these thickenings grow out longitudinally and unite, forming the paired rudiments of the dorsal longitudinal muscles, which are attached to the ectoderm anteriorly in front of the maxillary segment. Later they also become attached to the ectoderm intersegmentally. The dorsal mesoderm spreads farther upwards and becomes much drawn out, especially in the lower portions, into which the cœlomic spaces do not extend, but the knob-like bases persist (Plate 23, fig. 16). The genital rudiment becomes associated with dorsal mesoderm of the first thoracic segment (see p. 410). The inner walls of the cœlomic sacs now become joined up longitudinally. Thus the upper parts of the dorsal mesoderm are joined externally by the dorsal longitudinal muscle and internally by the future pericardial floor (text-fig. 12 *e*). The thin lower parts of the dorsal mesoderm forming the lateral pericardial floor never become united (text-figs. 12 and 13). Later, the dorsal longitudinal muscle rudiment separates from the rest of the outer walls of the cœlomic sacs (Plate 23, figs. 17 and 19), which remain as segmental cavities in a continuous sheet of mesoderm.

In the thorax the lower parts of the dorsal mesoderm at first lie as ventrally projecting tongues close against the lateral ectoderm (text-fig. 24 *b* and Plate 23, fig. 16). Later, in the second to eighth thoracic segments, these tongues draw away from the ectoderm in the middle of the segments, and their edges become attached to it intersegmentally (text-fig. 24 *d* and Plate 23, fig. 17). Thus lateral tubular spaces are left between the lateral pericardial floor and the ectoderm (text-fig. 15 *c*, " *l.v.* 3," and 24 *d* and *e*, "*b.v.*"). In the first thoracic and maxillary segments the lower parts of the dorsal mesoderm remain close to the body wall, while in the abdomen the large dorsal longitudinal muscle occupies nearly all the space between the lower dorsal mesoderm and the ectoderm (text-figs. 15 *h*, *i* and *g*). At the junction between the lateral segmental pericardial floor and the continuous dorsal mesoderm, the latter becomes joined intersegmentally to the ectoderm below the dorsal longitudinal muscle (text-figs. 15 *f* and *g*, " *p.a.*," and Plate 23, figs. 20 and 21).

As soon as the dorsal mesoderm has united to form a continuous sheet on either side, the upper parts of the ventral mesoderm grow out laterally from the anterior and posterior ends of the masses, and join on to the intersegmental ectoderm (text-fig. 12 *e*) just below the attachment of the continuous bands of dorsal mesoderm. These form the rudiments of paired mesodermal connective muscles in the thorax and abdomen (text-fig. 23 *c*, "*c.m.*" and see p. 418). As the dorsal mesoderm spreads farther upwards, the ventral mesoderm and its connective muscles also grow upward (text-figs. 12, 13 and 15, and Plate 23, figs. 20 and 21).

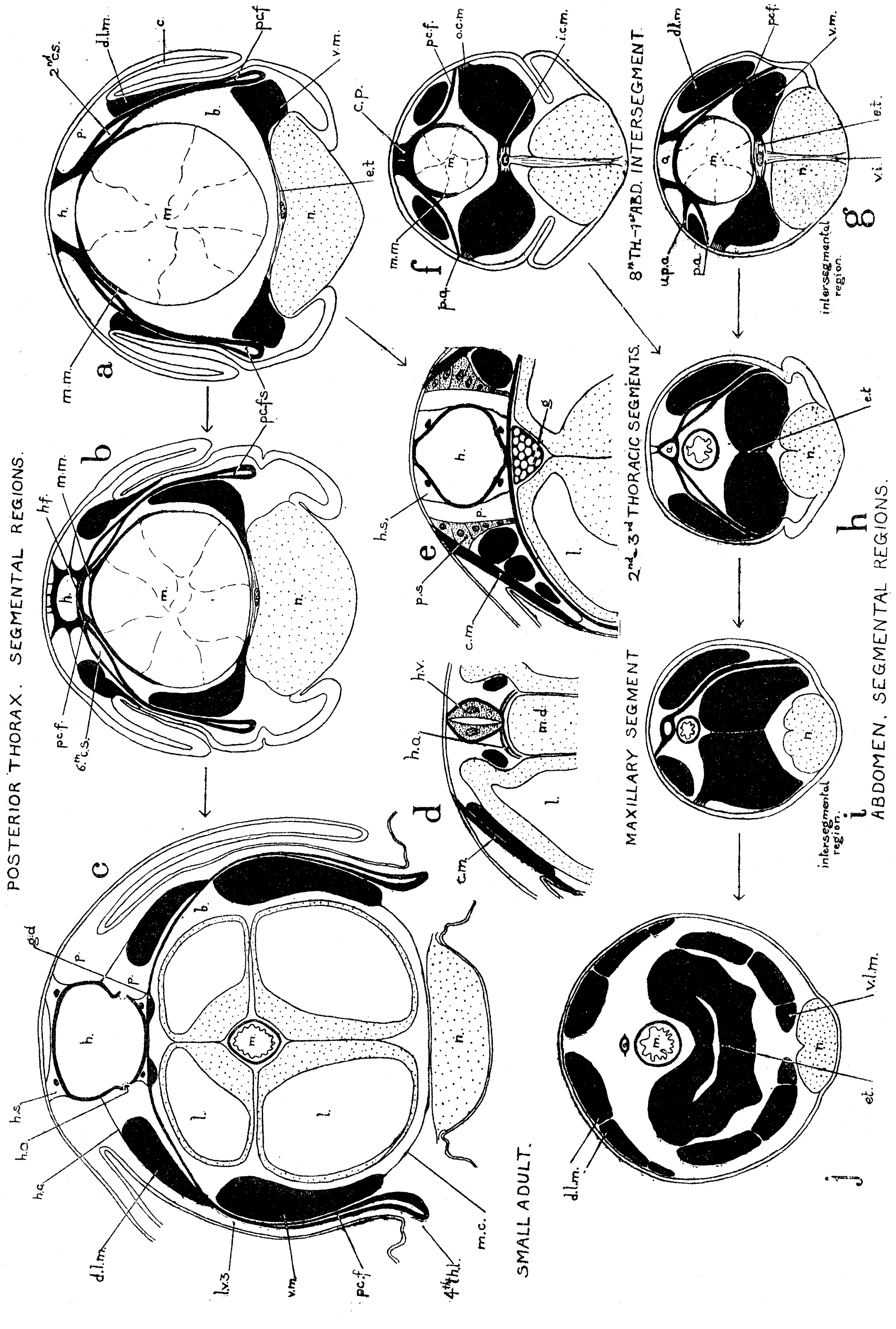
The liver at this stage extends through the maxillary segment and so compresses the maxillary mesoderm. The dorsal maxillary mesoderm tends to be squeezed backwards behind the liver and close to that of the first thoracic segment (text-figs. 12 *f* and 13 *g*). The maxillary cœlomic sacs, which are slightly larger than the rest, fuse with those of the first thoracic segment, forming one very large pair of sacs (text-figs. 13 *g*, *h*, *i* and *j*, and 14 *n*). Fusion is nearly complete in Plate 23, fig. 19.

The dorsal longitudinal muscle becomes larger in the abdomen than in the thorax, and the ventral mesoderm in the last two thoracic and all the abdominal segments becomes very bulky.

Heart and Associated Vessels and Later Development of the Cœlomic Sacs.

As the dorsal mesoderm grows upwards the dorsal longitudinal muscle remains below the attachment of the carapace fold. The mesoderm continues to creep upwards dorsal to the longitudinal muscle, where it becomes attached to the ectoderm, at first intersegmentally, from between the second and third thoracic segments backwards (Plate 23, figs. 17 and 18). Finally, the mesoderm reaches the dorsal side of the embryo. The yolk sac shrinks as the yolk is absorbed, and two spaces are formed, one between the mesoderm and the ectoderm dorso-laterally, and the other mid-dorsally between the ectoderm and the endoderm, bounded laterally by the continuous bands of dorsal mesoderm. The former space becomes the pericardial cavity and the latter the cavity of the heart and posterior aorta.

The heart is formed by the eight thoracic and maxillary segments. It develops structurally from before backwards, but the heart cavity first appears in the second or third thoracic segment owing to the large amount of yolk present in the more anterior part of the embryo. The presence of this yolk usually delays the formation of the anterior end of the heart in the maxillary segment. The walls of the heart are formed from the dorsal mesoderm above the cœlomic spaces, that is, from the upper inner angles of the fused somites. The lateral walls are first formed from the upper parts of the dorsal mesoderm (text-fig. 15 *a* and Plate 23, fig. 17). The roof and floor of the heart are formed by the growth together in the middle line of the upper and lower inner edges of the heart walls respectively. The floor forms first, but remains very thin (Plate 23, fig. 17) until the roof is complete. In this median growth the mesoderm remains connected with the ectoderm in various places, so that when the heart is completed its lateral walls and roof remain suspended from the ectoderm by numerous thin strands (Plate 23, fig. 18). The upper dorsal mesoderm containing the cœlomic spaces now forms the horizontal part of the pericardial floor. The floor of the heart is very wide at first, but as the yolk sac


POSTERIOR THORAX. SEGMENTAL REGIONS.
a
b
c
SMALL ADULT.
d
MAXILLARY SEGMENT
e
2nd-3rd THORACIC SEGMENTS.
f
g
8th TH.-1st ABD. INTERSEGMENT.
h
i
j
ABDOMEN. SEGMENTAL REGIONS.
intersegmental region.
intersegmental region.
2nd c.s.
d.l.m.
c.
pc.f.
v.m.
p.
b.
h.
m.
e.t.
n.
m.m.
pc.f.s.
h.f.
6th c.s.
g.d.
h.s.
h.a.
l.
l.v.3
4th th.l.
m.c.
h.v.
m.d.
c.m.
p.s.
g.
c.p.
o.c.m.
i.c.m.
p.a.
u.p.a.
a.
v.i.
v.l.m.

Text-Fig. 15.

TEXT-FIG. 15.—Diagrammatic sections showing the development of the heart, posterior aorta and associated structures. *a*, *b* and *c* show the heart formation in the thorax at successive stages. *g*, *h*, *i* and *j* show the development of the posterior aorta in the abdomen. The sections pass through the middle of a segment. (*a*) The dorsal mesoderm has united to form the floor but not the roof of the heart. The gut mesoderm is growing round the yolk sac. (*b*) Both floor and roof are now completed and the cœlomic sacs in the pericardial floor are at their maximum size. (*c*) Adult, through the second pair of ostia, showing the structure of the heart wall and the lateral efferent vessels to the pericardium. (*d*) Showing the valves between the heart and the anterior aorta in the maxillary segment. (*e*) Showing the strut across the pericardium and the ectodermal carapace muscles in the second and third thoracic segments. (*f*) Showing cardiac plug at the junction of the thorax and abdomen, and the intersegmental attachments of the pericardial floor. (*g*) An intersegmental region is shown on the left and a segmental region on the right. The floor of the aorta is formed but no roof. (*h*) Segmental region, aorta completed and cœlomic sacs at a maximum. (*i*) Intersegmental region on the left and segmental region on the right. The pericardial floor has lost its lower intersegmental attachment. (*j*) Adult, the pericardial floor has disappeared and the aorta is free. *a.*, posterior aorta; *b.*, hæmocœl; *c.*, carapace fold; *c.m.*, ectodermal carapace muscle; *c.p.*, cardiac plug; *d.l.m.*, dorsal longitudinal muscle; *e.t.*, ectodermal tendon; *g.*, gonad; *g.d.*, rudiment of gonoduct; *h.*, heart; *h.a.*, hepatic artery; *h.c.*, membrane between heart wall and dorsal longitudinal muscle; *h.f.*, floor of heart; *h.o.*, heart ostia; *h.s.*, space between muscular and epithelial walls of heart in which lies a longitudinal muscle; *h.v.*, valve between heart and anterior aorta; *i.c.m.*, inner connective muscle; *l.*, liver; *l.v.* 3, lateral vessel to pericardium in third thoracic segment; *m.*, mid-gut or yolk sac; *m.c.*, membrane formed by ectodermal tendon; *m.d.*, mid-gut diverticulum; *m.m.*, mid-gut mesoderm; *n.*, nerve cord; *o.c.m.*, outer connective muscle; *p.*, pericardium; *p.a.*, intersegmental connection of pericardial floor to ectoderm; *p.c.f.*, pericardial floor; *p.c.f.s.*, persistent cœlomic space in pericardial floor; *p.s.*, strut across pericardium; *u.p.a.*, upper intersegmental attachment of pericardial floor in abdomen; *v.m.* ventral mesoderm; *v.i.*, ventral ectodermal intucking to tendon; *v.l.m.*, ventral longitudinal muscle; 2*nd* and 6*th c.s.*, second and sixth thoracic cœlomic sacs; 4*th th. l.*, fourth thoracic limb.

shrinks to become the mid-gut, so the floor narrows and thickens (Plate 23, fig. 18), and can be distinguished from the now continuous pericardial floor below it (text-fig. 15 *b*).

When the heart and pericardial floor have been formed, the dorsal longitudinal muscle loses contact with them and segmentally with the ectoderm, thus lying in the pericardium. The muscle retains connection at its ventro-lateral edge with the pericardial floor except in the fifth, sixth and seventh thoracic segments (text-fig. 15 *c*). In withdrawing from the pericardial floor a supporting sheet of tissue is left between the upper part of the dorsal longitudinal muscle and the lateral heart wall across the pericardium in the last five or six thoracic segments (text-fig. 15 *b* and *c*, "*h.c.*"). The two pairs of ostia break through the continuous heart wall at a later stage just below and above the anterior end of this membrane.

In the heart wall itself the cells lining the cardiac cavity develop circular muscle fibrils, while the outer cells remain epithelial. These undifferentiated cells are absent when the heart is in direct contact with the pericardial floor. At the very end of embryonic life the epithelial covering of the heart separates from the muscular layer at the dorso-lateral and ventro-lateral corners of the heart. Four spaces are thus formed in which lie four small longitudinal muscles (text-figs. 15 *c* and *e*, and 21 *b* and *c*, "*h.s.*"). In the first and second thoracic segments in front of the heart ostia these spaces may unite laterally. Behind the ostia, where the heart is supported by a lateral strut (text-fig. 15 *b* and *c*, "*h.c.*"), the spaces are smaller, but the upper pair may unite dorsally where the heart finally pulls away from the ectoderm. A similar separation of the heart muscle from the outer epithelium has been shown by CANNON (1924, p. 411) for the anterior part of the heart of *Estheria*.

As soon as the heart is formed in the maxillary segment it unites with the anterior aorta (see p. 393). Both vessels are much compressed and closed at this point. When the lumen appears two flat cells project vertically inwards from the walls at the junction between the two, forming a valve (text-fig. 15 *d*, "*h.v.*").

The withdrawal of the dorsal longitudinal muscle from the lateral ectoderm leaves the tubular spaces between the lateral pericardial floor and the ectoderm in direct communication with the pericardium, the above dorsal longitudinal muscle, and also below the muscle in segments five, six and seven (see above). Thus the afferent venous channels are formed between the limb bases and pericardium in thoracic segments two to eight. No vessel is formed in the first segment, since the lateral pericardial floor here does not separate from the ectoderm. The first five thoracic segments become much crowded and displaced dorsally (see CANNON and MANTON, 1927, text-fig. 3) as the carapace is raised up off the body (Plate 23, fig. 18), and the venous vessels in segments two and three unite on each side just before entering the pericardium. The positions of the adult vessels in various Mysids are shown by CLAUS (1884, Plate 2) and DELAGE (1881, Plate 10). The cavity of the carapace fold becomes subdivided into various blood lacunæ, which all discharge into the pericardium along with the first three pairs of lateral vessels close to the ostia of the heart. In the first two segments the cavity of the carapace fold does not communicate with the pericardium owing to the formation of an ectodermal muscle across the opening (text-figs. 15 *d* and *e*, " *c.m.*," and see p. 421).

Where the pericardial floor is in contact with the yolk sac, mesoderm grows out round the latter and forms the mid-gut musculature (text-fig. 15 *a*, *b*, *f* and *g*, " *m.m.*," and Plate 23, fig. 17). In the posterior thoracic segments, where the yolk sac shrinks rapidly, a space may be left between it and the pericardial floor bounded laterally by downgrowing mesoderm (text-figs. 15 *b* and 18 *a*, " *x.*," and Plate 23, fig. 18). Finally, the gut mesoderm separates from the pericardial floor.

The growth of the dorsal mesoderm in the first six segments of the abdomen is at first very similar to that of the thorax. The lateral walls of the posterior aorta are at first more vertical than those of the heart in the thorax (compare text-figs. 15 *a* and 15 *g*). The roof and floor of the posterior aorta are formed in the same way as those of the heart. A transitory pericardial floor is also developed with its intersegmental connections to the ectoderm below the dorsal longitudinal muscle, but there are formed also intersegmental dorso-lateral connections to the ectoderm above the dorsal longitudinal muscle (text-fig. 15 *g*, " *u.p.a.*"). The floor of the aorta, when it first appears, is as thick as the walls while there is as yet no roof ; but in the thorax the floor does not thicken until after the roof is well formed.

Between the eighth thoracic and first abdominal segments, but sometimes extending back to the second abdominal segment, the floor and roof of the posterior aorta are formed simultaneously and very near together so that the cavity of the vessel becomes temporarily obliterated (text-fig. 15 *f*). The posterior aorta when first formed is little smaller than the heart. It rapidly shrinks and draws away from the mid-dorsal ectoderm, and the cardiac plug between the heart and aorta gradually opens up. When the posterior aorta is completed, the pericardial floor gradually disappears. At first the inter-segmental unions break down leaving tongues of pericardial floor in the middle of each segment (text-fig. 15 *i*). Later these also disappear and the posterior aorta is left quite free (text-fig. 15 *j*). The heart and aorta are thus part of a continuous structure, which is formed, as all other organs hitherto mentioned, steadily from before backwards.

The further growth of the cœlomic sacs after heart formation has started is very different. As soon as the pericardial floor becomes definitely separated from the heart and reaches a fairly dorsal position, the sacs start to expand. Expansion is only mechanically possible when the yolk sac shrinks and the pressure on the mesoderm is decreased. The sacs in the posterior part of the thorax and abdomen start to expand first, and the process spreads forwards in both regions. However, the large first pair of fused maxillary and first thoracic sacs are usually enlarged early. The condition of the cœlomic sacs once the heart formation has begun is seen for a number of embryos in Table I arranged in order of advancing development. Growth is very rapid at this period and the

TABLE I.—Expansion and final disappearance of the trunk cœlomic sacs in embryos arranged in order of advancing development.

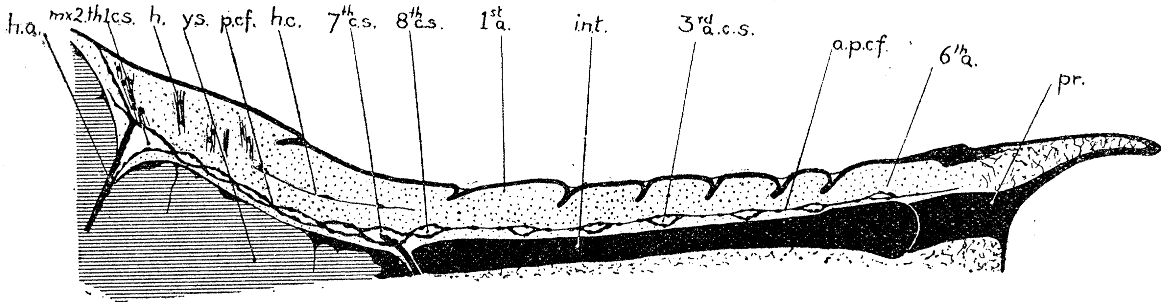
Number of embryo.	Thorax.							Abdomen.					
	max. 2 and th. 1.	th. 2.	th. 3.	th. 4.	th. 5.	th. 6.	th. 7.	th. 8.	ab. 1.	ab. 2.	ab. 3.	ab. 4.	ab. 5.	ab. 6.
6.15.1 . . .	×	/					/							
6.6.5 . . .	×			/	/	×	×	×						×
6.7.2	/				/	/	×	×			/	×	×	×
6.7.3. . . .	×	/	/	/	/	×	×	×	×	/			×	×
6.15.2 . . .	×		/	/	/	/	/		/	/	/	×	×	×
6.2.5	/				/	×	×	×	×	×	?	×	×	×
6.15.3 . . .	×			×	×	×	×	×	/	/	×	×	×	×
6.15.1 . . .	×	/	×	×	×	×	×	×	×	×	×	×	×	×
6.5.5, etc. . .	×	×	×	×	×	×	×	×	×	×	×	×	×	×
6.11	×	×	×	×	×	×	×	×				×	×	?
6.13	/					×	×	×		/	/		/	/
6.9	/					/	×	×					/	?
7.4	/						×	×						
7.3	/							/						

	compressed cœlomic sac.
/	partly expanded cœlomic sac.
×	fully expanded cœlomic sac.

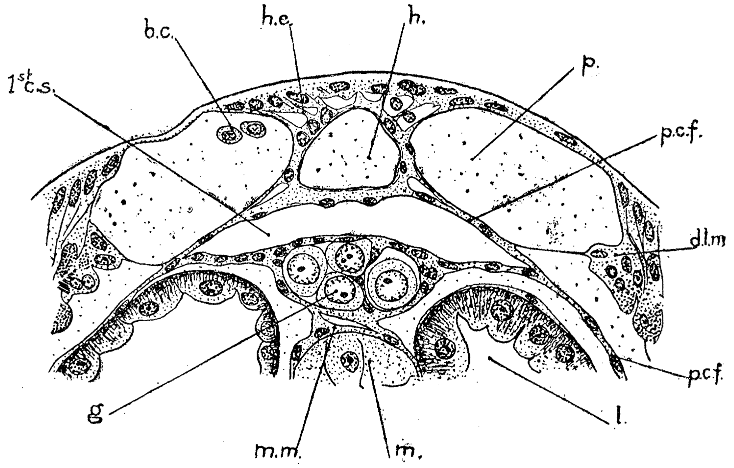
The numbers of the embryos are the index-numbers of the preparations.

maximum development of the cavities is quickly attained and persists for a short period (text-fig. 16). The cavities of the first pair of sacs are variable in size, and may become very large if the gonads lie far below the pericardial floor. They frequently unite across the middle line, forming one large space (text-fig. 17). Of the remaining thoracic cœlomic spaces the seventh pair becomes larger than the rest owing to the developing sternal arteries (see below, p. 403), and occasionally two successive spaces unite with one another. The abdominal cœlomic sacs grow relatively larger than those of the thorax with the exception of the first and seventh pairs in the thorax. The cœlomic cavities gradually become obliterated by the sinking together of their walls. This process starts from the anterior part of the thorax and abdomen and spreads backwards through the two regions (Table I). It begins just before the embryonic cuticle is shed, and is completed soon after, when nearly all the yolk is absorbed. The cavities of the first pair of sacs persist longer than those of the immediately succeeding ones on account of their larger size.

Two pairs of blood vessels are developed from the heart as soon as it is formed. Anteriorly just behind the valve and in front of the first pair of cœlomic cavities the walls of the heart grow out as two solid strands from its ventro-lateral angles. These are the rudiments of the hepatic arteries, and they grow down between the liver and the mid-gut on either side (text-fig. 16, "*h.a.*"). Later the lumen appears (text-fig. 15 *d*, "*h.a.*") and a valve in the heart wall at the root of each artery formed by a pair of distended cells. In the seventh segment a pair of sternal arteries is similarly developed,



TEXT-FIG. 16.—Diagrammatic parasagittal section of an embryo in which the cœlomic sacs in the pericardial floor are fully expanded. *a.p.c.f.*, abdominal pericardial floor; *h.*, cut heart wall; *h.a.*, hepatic artery; *h.c.*, membrane connecting; *int.*, mid-gut; *mx.* 2, *th.* 1, *c.s.*, fused maxillary and first thoracic cœlomic sacs; *p.c.f.*, pericardial floor; *pr.*, proctodæum; *y.s.*, yolk sac; 1*st a.*, 6*th a.*, first and sixth abdominal segments; 3*rd a.c.s.*, third abdominal cœlomic sac; 7*th c.s.*, 8*th c.s.*, seventh and eighth thoracic cœlomic sacs.



TEXT-FIG. 17.—Transverse section through the thorax showing the frequent fusion of the united maxillary and first thoracic cœlomic sacs in the pericardial floor. *b.c.*, blood corpuscle; *d.l.m.*, dorsal longitudinal muscle; *g.*, gonad; *h.*, heart; *h.e.*, strands connecting heart to the ectoderm; *l.*, liver; *m.*, mid-gut; *m.m.*, mid-gut mesoderm; *p.c.f.*, pericardial floor; 1*st c.s.*, first pair of cœlomic sacs fused together.

but they grow straight out through the anterior part of the cœlomic cavities in this segment, so penetrating through the pericardial floor (text-figs. 18 *a* and *b*). These two rudiments grow downwards round the sides of the mid-gut and slightly forwards to the nerve cord at the junction of the fifth and sixth segments. One or other rudimentary vessel may soon stop growing and become absorbed, the other alone passing through the nerve cord to form the sub-neural artery, or both may persist equally or unequally developed (text-figs. 18 *b* and *c*). A lumen appears in the artery and a pair of valves at its origin from the heart resembling those of the hepatic arteries. The sternal artery is thus a paired and not a median vessel. Other median and paired vessels from the heart are small and only appear late in development, and their growth has not been followed.

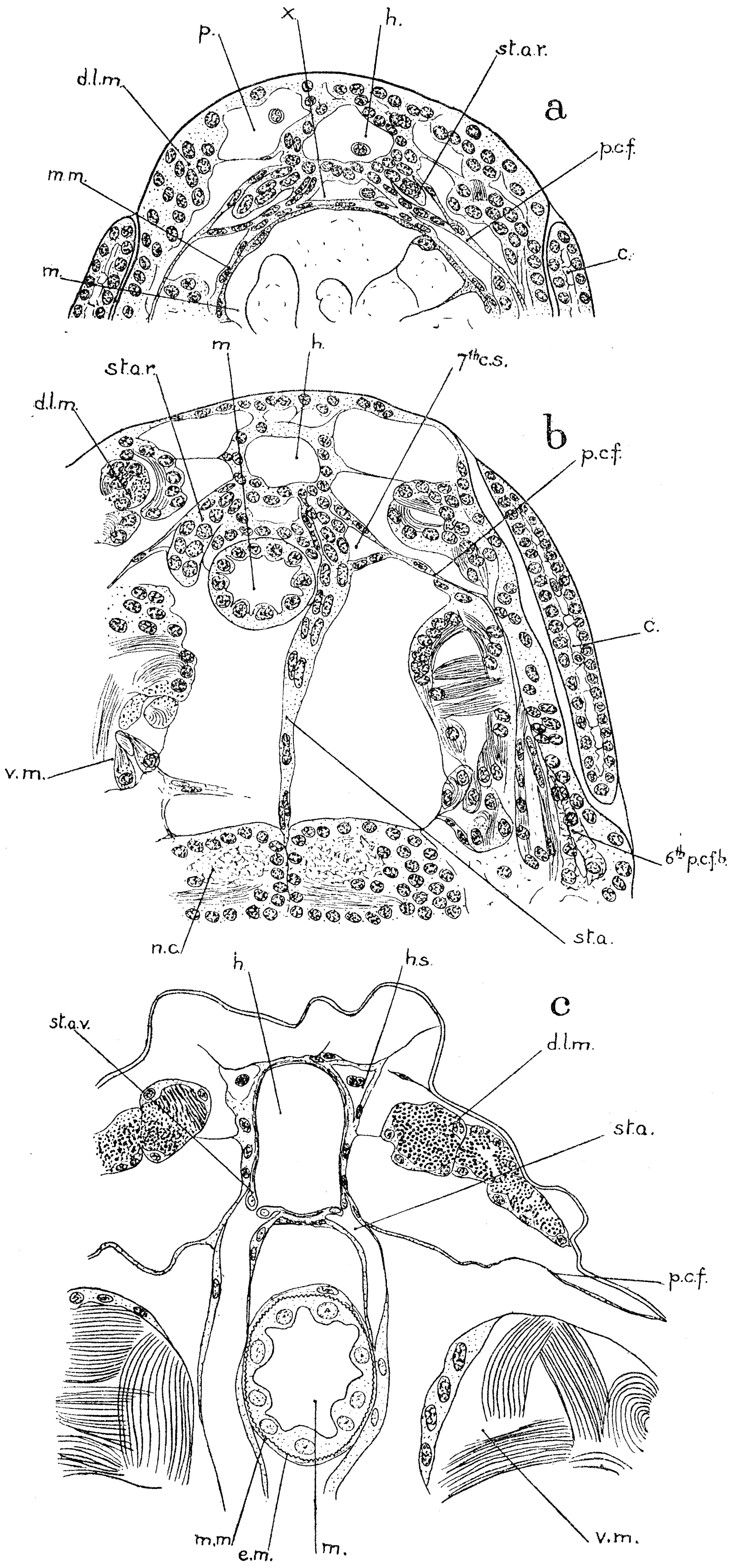
In the lateral pericardial floor which passes down to the insertion of the limbs in the middle of the thoracic segments a narrow slit-like cavity arises. These ventral cœlomic cavities appear never to be continuous with the more dorsal cœlomic spaces, although from their position they might well be the lower parts of these cavities. They are closed and U-shaped in frontal section, and their earliest appearance is seen in text-figs. 13 *i* and *j*, and 15 *a*, *b* and *c*, "*p.c.f.s.*"). These ventral cœlomic spaces persist in the adult and do not contain blood (text-figs. 24 *d* and *e*, "*p.c.f.c.*").

In the second and third thoracic segments a few cells of the dorsal mesoderm on the upper inner side of the dorsal longitudinal muscle do not become muscular, but remain undifferentiated until the very end of embryonic life. They then spread out across the pericardium and form a solid strut between the pericardial floor and the dorsal body wall (text-fig. 15 *e*, "*p.s.*").

Seventh Abdominal Segment.

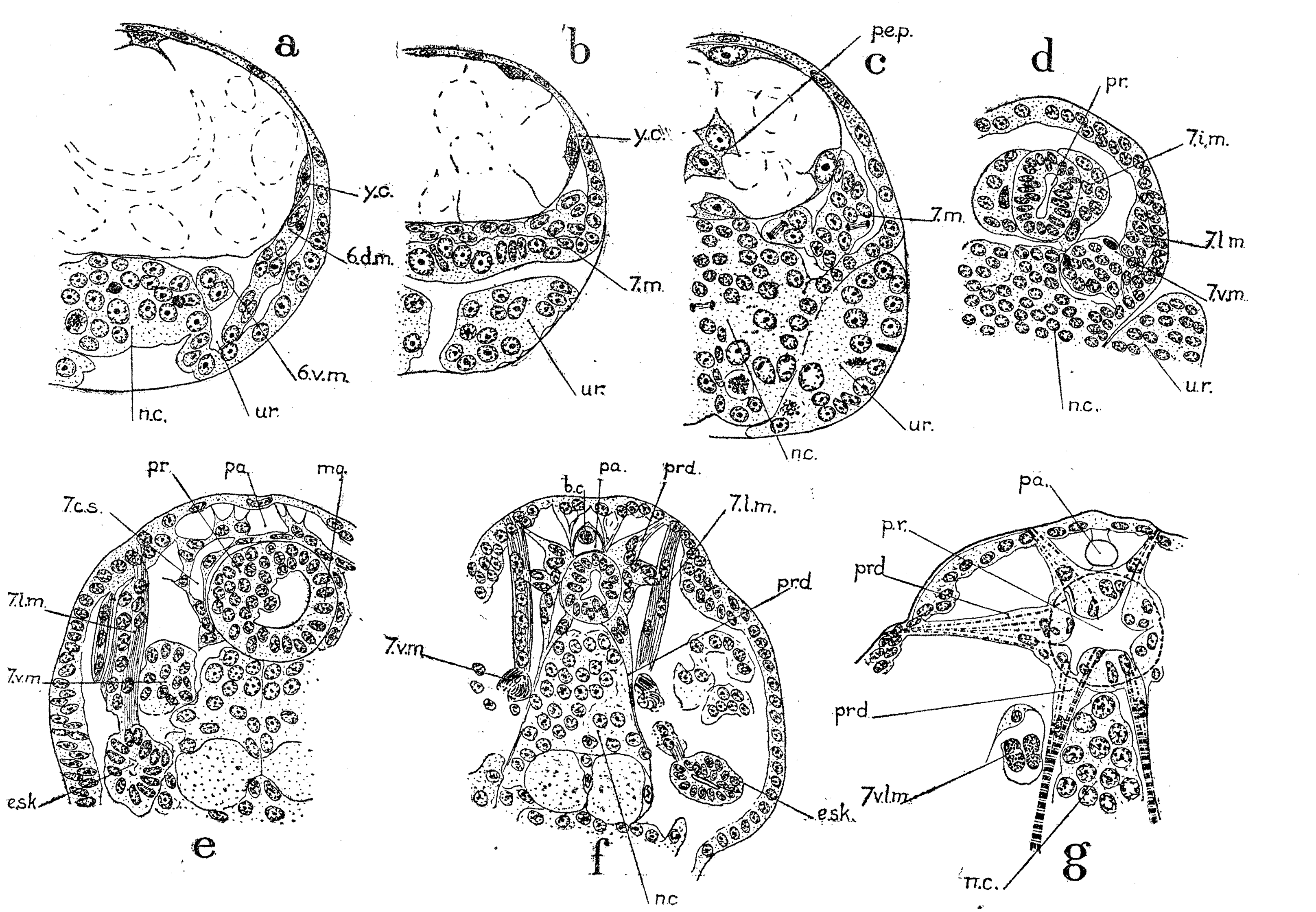
The formation of the mesoderm of the seventh abdominal segment as the most posterior transverse row of eight mesoderm cells has been described (p. 380). The subsequent growth of this mesoderm differs little from that of other segments. The first division of the row is less regular, the cells appearing much compressed between the yolk sac and the ectoderm, and a little smaller than the mesoderm cells of the preceding segments. Further division results in an accumulation of cells ventro-laterally (text-fig. 19 *b*). These are separated from the sixth abdominal block by a distance exactly corresponding with the other abdominal intersegmental gaps (text-fig. 12 *d*). Development of the seventh abdominal mesoderm is slow. In text-fig. 19 *a* the sixth mesoderm has already subdivided and grown up the sides of the body, while the seventh mesoderm has not yet formed two separate ventro-lateral blocks (text-fig. 19 *b*). Besides forming the paired blocks a few cells from the seventh mesoderm spread backwards to the end of the body, and probably form part of the telson musculature.

The seventh abdominal mesoderm blocks divide into dorsal and ventral portions; this is just starting in text-fig. 19 *c*. However, the dorsal part soon divides again. Part grows up round the proctodæum while the rest remains against the lateral ectoderm



Text-Fig. 18.—Transverse sections through the seventh thoracic segment showing the development of the sternal arteries. (*a*) Paired rudiments of the sternal arteries growing out from the heart wall through the seventh cœlomic cavities. (*b*) Both rudiments have grown through the pericardial floor, but only the one on the right has grown down to the nerve cord. (*c*) Young adult with both sternal arteries developed.

c., carapace fold; *d.l.m.*, dorsal longitudinal muscle; *e.m.*, mid-gut elastic layer; *h.*, heart; *m.*, mid-gut; *m.m.*, mid-gut musculature; *p.*, pericardium; *p.c.f.*, pericardial floor; *st.a.*, sternal artery; *st.a.r.*, rudiment of sternal artery; *st.a.v.*, valve at the junction of heart and sternal artery; *v.m.*, ventral mesoderm; *x.*, space between pericardial floor and gut mesoderm; 7*th c.s.*, 7th thoracic cœlomic sac; 6*th p.c.f.b.*, pericardial floor base in the sixth thoracic segment.



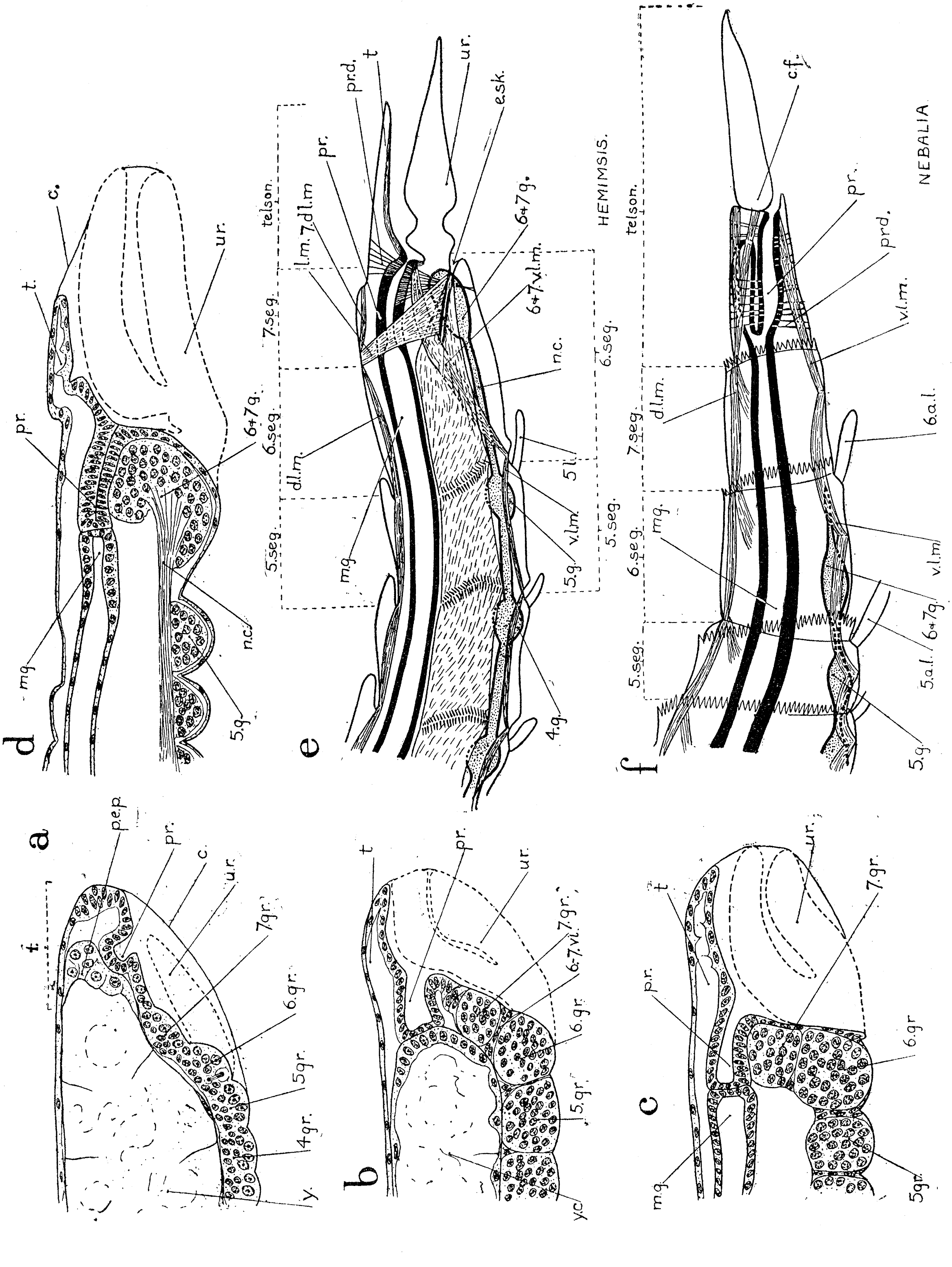
TEXT-FIG. 19.—A series of transverse sections to show the growth of the seventh abdominal mesodermal somites. (*a*) Section through the sixth abdominal segment in which the mesodermal block has divided into dorsal and ventral portions. (*b*) Section from the same embryo through the seventh abdominal mesoderm which has not yet formed ventro-lateral blocks. (*c*) Through the lateral block of seventh abdominal mesoderm at a later stage. (*d*) The seventh mesodermal block is now differentiated into a ventral, lateral and an inner portion round the proctodæum. (*e*) The seventh abdominal cœlomic cavity has appeared in the mesoderm round the proctodæum, which is forming the walls of the posterior aorta. The lateral portion has formed the rudiment of the lateral muscles from the endoskeletal tube to the body wall. (*f*) The posterior aorta is completed. The cœlomic cavity is obliterated and the rudiments of the proctodæal dilator muscles have been formed from its walls. The ventral portion of the mesoderm has formed the ventral longitudinal muscle of the seventh abdominal segment. (*g*) Small adult to show the proctodæal dilator muscles. *b.c.*, blood corpuscle; *e.s.k.*, endoskeletal tube; *m.g.*, mid-gut; *n.c.*, nerve cord; *p.a.*, posterior aorta; *p.e.p.*, posterior endodermal plate; *pr.*, proctodæum; *pr.d.*, proctodæal dilator muscles; *ur.*, uropod; *y.c.*, yolk cell; 6.*d.m.*, dorsal mesoderm of the sixth abdominal segment; 6.*v.m.*, ventral mesoderm of the sixth abdominal segment; 7.*c.s.*, seventh abdominal cœlomic sac; 7.*i.m.*, inner portion of seventh abdominal mesoderm; 7.*l.m.*, lateral portion of seventh abdominal mesoderm; 7.*m.*, seventh abdominal mesoderm; 7.*v.m.*, ventral portion of seventh abdominal mesoderm.

(text-fig. 19 *d*). The ventral parts lie close against the nerve cord and become difficult to distinguish from the nervous tissue. They finally form longitudinal muscles running from the body wall below the anus to join the ventral longitudinal musculature of the sixth segment (text-figs. 19 *e*, *f* and *g*, " *7.v.m.*," and 20 *e*, " 6 and *7.v.l.m.*"). The lateral masses chiefly form large dorso-ventral muscles from the endoskeletal tubes arising from the posterior ventro-lateral parts of the sixth abdominal segment (see p. 412, and text-fig. 20 *e*, " *l.m.*"). Small dorsal longitudinal muscles attached to the dorsal ectoderm at the anterior and posterior ends of the seventh segment are probably also formed from these lateral masses (text-fig. 20 *e*, " *7.d.l.m.*").

The ectodermal cells forming the intucked proctodæum are at all times widely separated from the body ectoderm by a hæmocœlic space. The seventh abdominal mesoderm round the proctodæum lies close against the latter, and at first quite separate from the ectoderm (text-fig. 19 *d*). As it grows round the proctodæum it unites dorsally with the sixth abdominal dorsal mesoderm. Its upper edges above the proctodæum lie close against the latter and form the posterior aorta, continuous with the aorta in the rest of the abdomen (text-figs. 19 *e* and *f*). At the same time a pair of irregular cavities appears in this mesoderm (text-fig. 19 *e*). These are the seventh cœlomic sacs. They are not formed until the cœlomic sacs in the pericardial floor are well expanded. The fixation of the cytoplasm is less good at this than at earlier stages, so that the cavities are rather ill-defined. The outer walls of the sacs become drawn out towards the ectoderm dorso-laterally, laterally and ventro-laterally, so becoming attached to the body wall. The cœlomic cavities very soon become obliterated, and their walls form groups of elongated cells stretching across the hæmocœl between the proctodæum and the ectoderm (text-fig. 19 *f*, " *pr.d.*"). These groups of cells are the rudiments of the proctodæal dilator muscles, which are formed near the end of embryonic life. Striated muscle fibrils appear in these cells, and these fibrils extend through the circular proctodæal musculature and epithelium and attach to the cuticle (text-fig. 19 *g*).

Although no attempt has been made to follow the development of the whole nervous system, that of the sixth and seventh abdominal segments has been observed. When the intersegmental furrows first appear, a ventral ectodermal thickening in each segment forms the rudiment of the ganglion and nerve cord of that segment. In the sagittal section (text-fig. 20 *a*, " *7.gr.*") is seen a seventh ganglionic thickening lying behind the sixth, and somewhat smaller in size. The uropods are attached to the sixth segment, while the seventh segment bears no appendages. Mid-ventrally the sixth and seventh ganglia become separated by an ectodermal intucking such as forms part of the ectodermal tendons at other intersegments (text-fig. 20 *b*, " *6–7.v.i.*", and see p. 414). The telson then grows back as a median lobe above the anus, forming the adult structure. The caudal furca remains on the first cuticle (text-figs. 12 and 13) and is not re-formed.

The ventral part of the sixth segment now becomes drawn backwards, and with it the uropods and the sixth ganglionic rudiment. The latter thus lies below, instead of anterior to, the seventh ganglion, and the uropods become terminal (text-fig. 20 *c*). The seventh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l.m.
telson.
7.seg.
6.seg.
5.seg.
6+7g.
6+7.vl.m.
HEMIMSIS.
n.c.
d.l.m.
mg.
5l.
v.l.m.
5.g.
4.g.
f
c.f.
pr.
prd.
NEBALIA
telson.
v.l.m.
6.a.l.
d.l.m.
7.seg.
6.seg.
5.seg.
mg.
v.l.m
6+7g.
5.a.l.
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6.gr.
5.gr.
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5gr.
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Text-Fig. 20.—*a–d*. A series of sagittal sections showing the formation and fusion of the sixth and seventh abdominal ganglia. The positions of the uropods are shown by dotted lines. (*a*) The primordia of the ganglia are seen as ventral segmental thickenings of the ectoderm. That of the seventh segment lies behind the sixth. (*b*) Intersegmental intuckings lie between all the ganglia, and the sixth segment with the uropods is being drawn backwards ventrally. (*c*) The uropods are now terminal and the sixth ganglion lies below the seventh. (*d*) Fusion of the sixth and seventh ganglia has now taken place. (*e*) Diagram of the posterior end of the adult abdomen to show the fused sixth and seventh segments, the musculature, appendages and the nervous system for comparison with (*f*), a diagram of the posterior part of *Nebalia* showing the free sixth and seventh segments, fused sixth and seventh ganglia and appendages (based on Claus' figures, 1888).

c., cuticle; *c.f.*, caudal furca; *d.l.m.*, dorsal longitudinal muscle; *e.s.k.*, endoskeletal intucking; *l.m.*, lateral muscle formed by seventh abdominal somite. *m.g.*, mid-gut; *n.c.*, nerve cord; *p.e.p.*, posterior endodermal plate; *pr.*,proctodæum; *pr.d.*, proctodæal dilator muscles formed by the seventh abdominal somite; *t.*, telson; *ur.*, uropod; *v.l.m.*, ventral longitudinal muscle; *y.*, yolk; *y.c.*, yolk cell; 5.*a.l.*, 6.*a.l.*, fifth and sixth abdominal limbs; 7.*d.l.m.*, dorsal longitudinal muscle of the seventh segment; 4.*g.*, 5.*g.*, fourth and fifth abdominal ganglia; 6 and 7.*g.*, fused sixth and seventh abdominal ganglia; 4.*g.r.*, 5.*g.r.*, etc., fourth, fifth, etc., abdominal ganglion rudiment; 5.*l.*, fifth abdominal limb; 6–7.*v.i.*, ectodermal intucking between sixth and seventh ganglion rudiments; 6 and 7.*v.l.m.*, ventral longitudinal musculature of sixth and seventh abdominal segments.

ganglion subsequently fuses with the sixth ganglion (text-figs. 20 *d* and *e*). In the adult the last segment of the body is larger than the rest and represents the fused sixth and seventh abdominal segments. Dorsally the junction between the two is marked internally by the interrupted dorsal longitudinal muscle and the muscles developed from the seventh somite to the endoskeletal tubes (text-fig. 20 *e*, " 7.*d.l.m.*" and " *l.m.*"). The whole of the ventral surface, however, is formed by the sixth segment.

Blood Corpuscles.

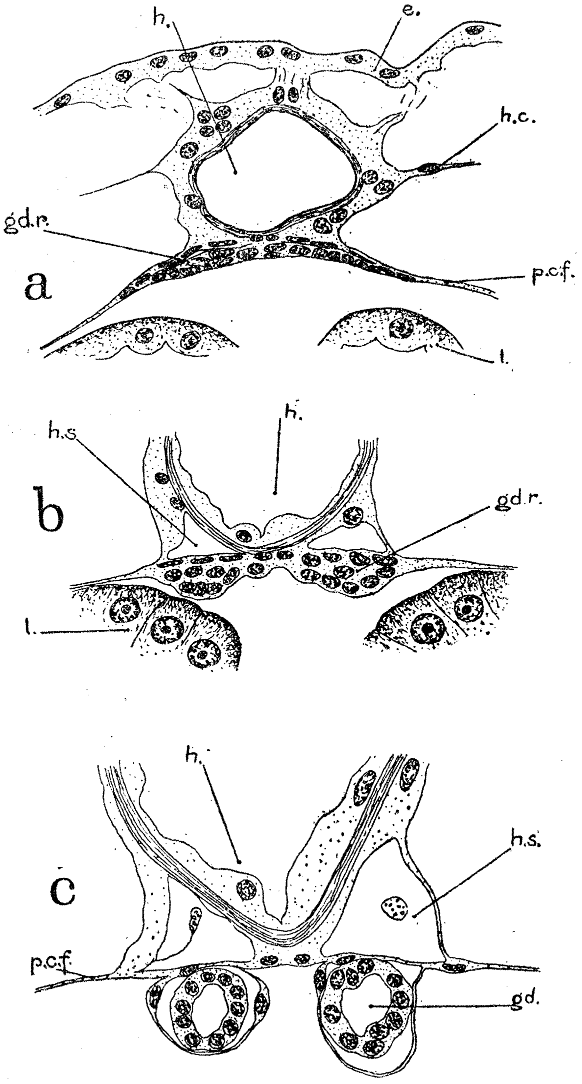
When the segmental blocks of mesoderm have been established, a few cells become separated from their upper edges and wander upwards between the yolk sac and the ectoderm, dividing mitotically as they go. They are very characteristic in appearance, the cytoplasm being small in amount and well rounded off. They are most abundant in the posterior part of the head and first few thoracic segments, but are formed sparingly in other parts. These cells spread into all the body spaces as these appear, and become blood corpuscles (Plates 22 and 23, figs. 11, 14, 17 and 18).

Genital Rudiment and Gonoduct.

The growth of the genital rudiment has been described up to a stage when it lies as a median mass in the anterior part of the first thoracic segment (p. 380). No divisions of germ cells have yet occurred. Just before or about the time of hatching the group divides, forming the rudiments of the gonads in the ventro-lateral parts of the first thoracic segment (text-fig. 9 *c*). There are now only three genital cells on either side, but about twelve cells were present in the original median rudiment. Thus some cells of the latter do not participate in the formation of the gonads. The fate of these cells could not be determined, but they probably degenerate. The nuclei of the genital cells slowly increase in size from their first appearance as such, and when they form a paired rudiment a large nucleolus appears in each (text-fig. 9 *c*).

When the dorsal mesoderm separates, the genital rudiments lie just internal to it on either side (text-figs. 12, 13 and 14). As the dorsal mesoderm grows upwards, a thin sheet of mesoderm grows out from it round each genital rudiment (Plate 23, fig. 16). The latter are thus carried upwards, and finally lie below the first pair of cœlomic spaces in the pericardial floor (text-fig. 13). The germ cells slowly multiply in number during these changes in position. The two rudiments become pressed together (text-fig. 17) and remain permanently attached to the pericardial floor. The rudiments gradually grow backwards below the heart, reaching the sixth segment or more, but a lumen only appears in the gonads when they approach maturity.

As the dorsal cœlomic spaces in the pericardial floor become obliterated towards the end of embryonic life, their ventral walls become thickened, forming a pair of longitudinal ridges near the middle line behind the gonads (text-figs. 21 *a* and *b*). In the sixth thoracic segment in the female these thickenings extend out into the pericardial floor laterally and ventrally to its bases over the insertions of the limbs. In the male this occurs in the eighth segment. These thickenings remain solid in the young animal, and only later become hollow, forming the gonoducts (text-fig. 21 *c*). The walls of the gonoducts are continuous with the mesoderm covering the germ cells and are themselves covered with a connective-tissue sheath. In the female the gonoduct extends from the base of the pericardial floor to the inner side of the limb base, and in the male this part of the limb



TEXT-FIG. 21.—Transverse sections through the thorax showing the growth of the gonoducts. (*a*) The walls of the cœlomic sacs in the pericardial floor have come together and the ventral wall is thickened. (*b*) The cœlomic sacs are completely obliterated and a cylindrical rudiment of the gonoduct, formed from the ventral walls of the sacs, lies along the pericardial floor. (*c*) Adult gonoducts with lumen. *e.*, ectoderm; *g.d.*, gonoduct; *g.d.r.*, rudiment of gonoduct; *h.*, heart; *h.c.*, membrane between heart wall and dorsal longitudinal muscle; *h.s.*, space between muscular and epithelial walls of heart; *l.*, liver; *p.c.f.*, pericardial floor.

is prolonged as the penis. It has not been possible to determine whether the short portion of the gonoduct between the base of the pericardial floor and the exterior was formed as an outgrowth from the pericardial floor or as an ectodermal intucking.

Endoskeleton and Associated Muscles.

The development of only the larger constituents of the endoskeleton has been followed, and these are entirely ectodermal. They comprise two groups. Firstly, the endoskeletal plate and various paired tubes which are apodemal in nature, and smaller solid struts not usually associated with muscles. All these structures remain connected to the exoskeleton throughout life. Secondly, segmental ectodermal tendons in the antennal to the sixth abdominal segment, and these become largely detached from the ectoderm.

The endoskeletal plate (for adult structure, see CANNON and MANTON, 1927, text-fig. 2 *a*) arises as a pair of hollow intuckings from the ectoderm in the posterior half of the maxillulary segment. They pass forwards and inwards to the transverse antennulary tendon (see below) close against the nerve cord until they meet in the middle line, so forming a horizontal V-shaped structure. Their cavities become continuous. The apex of the V is directed forwards and unites with the tendon of the mandibular adductor muscles (text-fig. 22 *d*, "*e.pl.*"). From the arms of the V just within their lateral terminations two horizontal outgrowths ("*e.pl.ex.*") pass backwards through the maxillary segment as far as the maxillary tendon ("*mx.2.t.*," and see below).

Between the mandibles and the maxillules just lateral to the nerve cord a pair of ventral finger-like intuckings grow inwards and upwards (text-fig. 22 *e*, "*e*"). They eventually extend about half-way up the body behind the mandibular adductor muscles. They become associated with a part of the mandibular mesoderm which forms muscles, joining their inner ends to the lateral body wall below the paired dorsal organs (see p. 384, and for adult structure, CANNON and MANTON, 1927, text-fig. 2 *a*). Two similar intuckings are formed between the antennules and antennæ. These tubes become invested with mesoderm, which forms large muscles inserted in the ectoderm lateral to the muscles of the above mandibular-maxillulary intuckings.* A third pair of large intuckings is formed from the ventro-lateral posterior wall of the sixth abdominal segment. These tubes project upwards and forwards. On them are attached the ventral longitudinal muscles and much of the musculature of the sixth and seventh abdominal segments (text-fig. 20 *e*, "*e.s.k.*"). Other small intuckings are formed in various parts. Finally, the endoskeletal plate and the anterior pair of tubes become partly embedded in nervous tissue. They all remain hollow with persistent epithelium and cuticle.

As the labrum is formed it becomes separated from the cerebral ganglion rudiment by a deep transverse furrow (text-figs. 12 and 13). This furrow becomes less marked in the adult as the preoral part of the body is rotated upwards. From the middle of this

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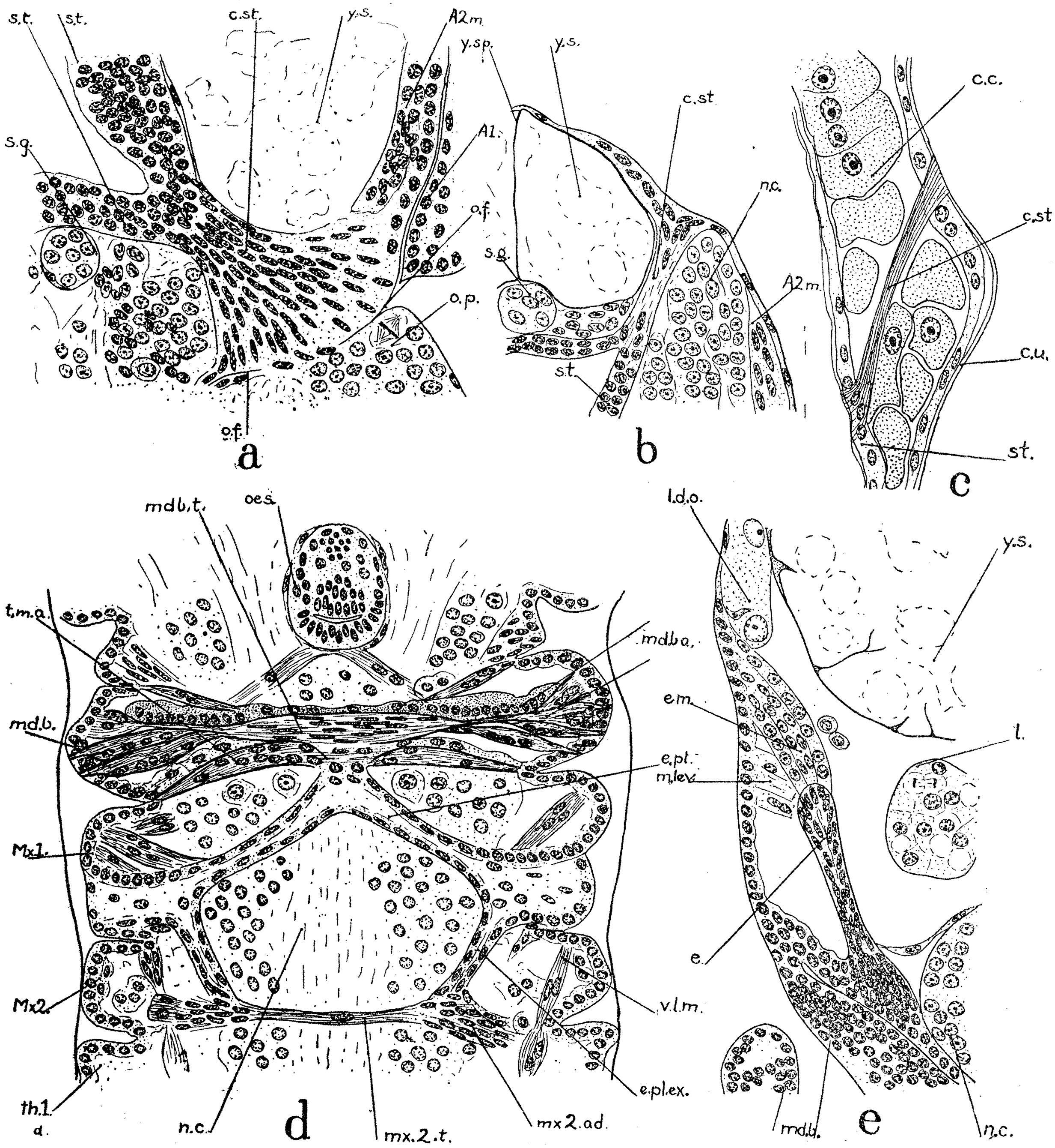
* This muscle is seen in text-figs. 2 *a* and *b*, p. 222, CANNON and MANTON, 1927, but is wrongly marked "*dlm.*"



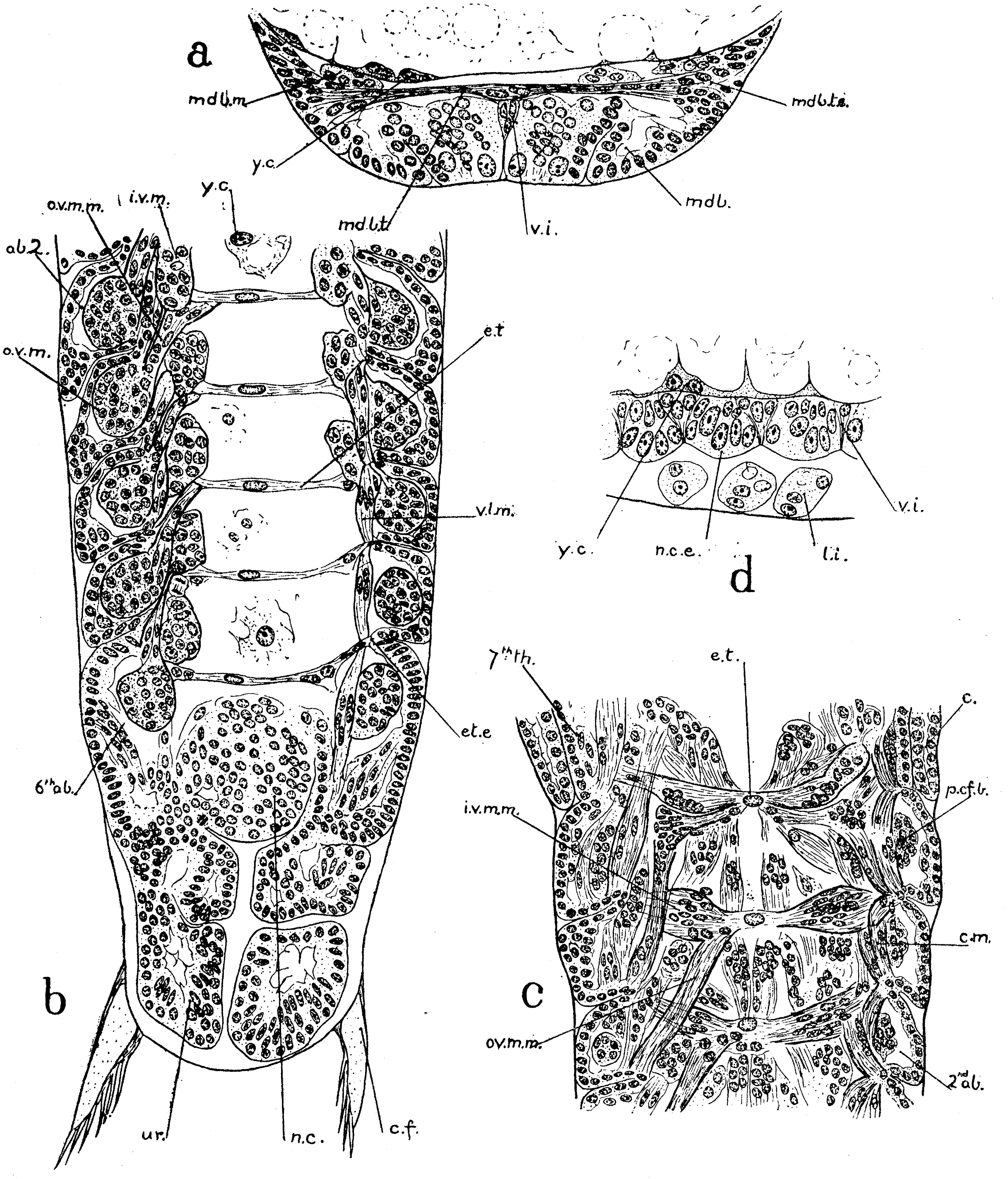
TEXT-FIG. 22.—*a–c*. Three sections to show the formation of an ectodermal strut between the cardiac stomach and the body wall. (*a*) Frontal section. Between the antennule and the optic rudiment a large ectodermal intucking has become attached to the antero-lateral angle of the stomodæum. (*b*) Transverse section of a late embryo. The ectodermal strand has now shifted dorso-laterally and is more compact. (*c*) Transverse section of a small adult. The strand has lost its nuclei and has developed fibrils attached directly to the cuticle. (*d*) Frontal section through the posterior part of the head to show the endoskeleton. The V-shaped endoskeletal plate lies in the maxillulary segment attached to the mandibular tendon anteriorly, and its posterior maxillary extensions have reached the maxillary tendon rudiment. (*e*) Transverse section through the mandibular-maxillulary intersegment to show the vertical endoskeletal tube. *A.I.*, antennule; *A.*2. *m.*, antennal mesoderm; *c.c.*, thick cells round stomach; *c.st.*, ectodermal strand between cardiac stomach and body wall; *c.u.*, cuticle; *e.*, endoskeletal tube; *e.m.*, muscle from endoskeletal tube to body wall; *e.pl.*, endoskeletal plate; *e.pl.ex.*, extension of endoskeletal plate through the maxillary segment; *l.*, liver; *l.d.o.*, dorso-lateral organ; *m.d.b.*, mandible; *m.d.b.a.*, mandibular adductor muscles; *m.d.b.t.*, tendon of mandibular adductor muscles; *mx.* 1, maxillule; *mx.* 2, maxilla; *mx.* 2 *ad.*, maxillary adductor muscles; *mx.* 2 *t.*, maxillary adductor muscle tendon; *n.c.*, nerve cord; *oes.*, œsophagus; *o.f.*, fold separating off optic rudiment; *c.c.f.b.*, base of pericardial floor; *ur.*, uropod; *v.i.*, ventral intucking forming ectodermal tendon bar; *v.l.m.*, ventral longitudinal muscle; *y.c.*, yolk cell; 2*nd ab.*, 6*th ab.*, second and sixth abdominal segments; 7*th th.*, seventh thoracic segment.

groove a solid ectodermal ingrowth takes place. A median nucleated strand of cells is formed between the anterior face of the stomodæum and the brain (text-fig. 13). In the adult this strand forms a thin rod which remains in connection with the ventral ectoderm and shows no structure beyond a few elongated nuclei. From the same furrow similar ingrowths are formed on either side of the median one. These extend backward horizontally and unite with the ectoderm near the external opening of the œsophagus (text-fig. 13). These persist as fine non-muscular struts in the adult. The finer endoskeletal membranes and struts about the brain and other parts have not been examined in detail.

At an early stage, when the post-naupliar mesoderm consists of undifferentiated lateral blocks and the ventral ectoderm is only a few cells thick, the segments are marked externally by slight intersegmental constrictions in their ventro-lateral parts. Mid-ventrally in the intersegmental regions a few ectodermal cells sink inwards. The beginning of this process is seen in the sagittal section in text-fig. 23 *d*, and it is carried farther in text-fig. 23 *a*, " *v.i.*" The thick ectoderm on either side forms the nerve cord and the intucking forms a knob of cells at the upper level of the nerve cord connected to the ventral ectoderm by a more or less attenuated neck. The formation of the ventral intuckings is followed shortly by paired lateral ones from the intersegmental folds on either side of the nerve cord. The pair in front of the mandibles are the largest, and form hollow or solid finger-like ingrowths from the ectoderm. Behind the mandibles the intuckings are smaller and usually solid. These intuckings grow inwards and slightly backwards over the ventral longitudinal muscle rudiment and the nerve cord towards the middle line (text-fig. 24 *b*, " *etr.*"). They resemble the ectoderm histologically in every way and are quite separate from the mesoderm, which is absent intersegmentally except for the rudimentary ventral longitudinal muscle. The mid-ventral and lateral intuckings then unite.

At every intersegment there is thus established a transverse ectodermal bar connected laterally and mid-ventrally with the ectoderm. Between the antennules and the antennæ it lies below the nerve cord and above the labrum, but elsewhere it lies above the nerve cord (text-figs. 23 *a* and *b*, " *m.d.b.t.*," and " *e.t.*"). The middle part of the bar is thicker than the rest and is probably formed from the ventral intucking, but growth is so rapid that the extent of the latter could not be determined. The nuclei in the middle of the bar rapidly become very large and oval, lightly staining and without nucleoli. There are numerous nuclei in the middle of the mandibular-antennal bar, but few in the other segments ; and often at a later stage only one large median nucleus is formed in all the posterior bars (text-fig. 23 *b*). Gradually each bar sinks backwards into the segment behind it and loses its lateral connections with the ectoderm.

The fate of the antennulary-antennal bar could not be determined. The antennal-manibular bar gives rise to the tendon of the mandibular adductor muscles. The bar is rarely found in one transverse plane as in text-fig. 23 *a*, even in its earliest stages, and it rapidly sags backwards into the middle of the mandibular segment (text-fig. 22 *d*,



TEXT-FIG. 23.—To show the formation of the ectodermal intersegmental tendons. (*a*) Transverse section through the anterior part of the mandibular-antennal intersegment. Lateral and ventral intuckings have formed a transverse ectodermal bar above the nerve cord, which will form the mandibular adductor muscle tendon. (*b*) Slightly oblique frontal section of the posterior part of the abdomen just above the nerve cord. Ectodermal tendon rudiments are seen attached to the intersegmental folds laterally and sagging backwards into the segment behind. Mesodermal muscle strands from the inner and outer parts of the ventral mesoderm have started to grow along these bars on the left. (*c*) Frontal section at a higher level through an older stage. The mesodermal strands have become the internal connective muscles, the ectodermal bars forming the short tendons between them. (*d*) Sagittal section through the ventral ectoderm to show the first differentiation of the mid-ventral intersegmental intuckings, a later stage being seen in fig. *a*. *ab.* 2, second abdominal segment; *c.*, carapace fold; *c.f.*, caudal furca; *c.m.*, outer connective muscles; *e.t.*, ectodermal tendon rudiment; *e.t.e.*, lateral ectodermal connection of tendon bar; *i.v.m.*, inner part of ventral mesoderm; *i.v.m.m.*, inner connective muscle from inner ventral mesoderm to the tendon of that segment; *l.i.*, limb; *m.d.b.*, mandible; *m.d.b.m.*, mandibular mesoderm; *m.d.b.t.*, ectodermal mandibular tendon rudiment; *m.d.b.t.e.*, lateral ectodermal intucking forming mandibular tendon; *n.c.*, nerve cord; *n.c.e.*, ectodermal thickening forming nerve cord; *o.v.m.*, outer part of ventral mesoderm; *o.v.m.m.*, inner connective muscle from outer ventral mesoderm to the tendon of the segment in front; *o.p.*, optic rudiments; *s.g.*, "sympathetic" ganglion; *st.*, stomodæum; *th.* 1., first thoracic limb base; *t.m.a.*, transverse mandibular adductor muscle; *v.l.m.*, ventral longitudinal muscle; *y.s.*, yolk spheres; *y.s.p.*, yolk septum.

" *m.d.b.t.*"). The middle of the bar becomes large and the nuclei crowded and flattened antero-posteriorly (text-fig. 22 *d* and Plate 24, fig. 27). As it shifts backwards it comes into association with the mandibular mesoderm (Plate 22, fig. 12). The latter remains in contact with the outer ectoderm at the base of the mandible but creeps inwards along the bar. The adductor muscles of the mandibles are differentiated in this mesoderm. The junction between the mesoderm and the bar is very clear (text-fig. 22 *d* and Plate 24, fig. 27), the mesodermal nuclei and protoplasm staining more darkly than the bar and the nuclei differing in size and shape in the two regions. Part of the mesoderm grows along the bar from each side, meeting to form a transverse muscle which is ultimately independent of the bar (text-fig. 22 *d*, " *t.m.a.*," and Plate 24, fig. 27). The latter gradually transforms to the adult mandibular adductor tendon. The nuclei in the middle portion persist until the very end of development, when the fibrils are formed. The lateral ectodermal connections lie in front and below the adductor muscles and become very attenuated, marked only by an inwardly directed cone of ectoderm. Finally they disappear. The mid-ventral ectodermal connection (text-fig. 23 *a*, " *v.i.*," and Plate 24, fig. 27, " *m.d.b.v.i.*") persists throughout life, lying between the anterior ends of the paragnaths. It shrinks in length and finally is composed of a conical group of ectodermal cells drawn out to meet the tendon (for adult structure, see CANNON and MANTON, 1927, Plate 2, and text-fix. 2 *a*).

The bar in the maxillulary segment arising between this and the mandibular segment is smaller at all stages, and the maxillary adductor muscles become attached to it as in the mandibular segment. Meanwhile, the intuckings forming the endoskeletal plate (see above) grow along the bar and fuse with it. The maxillary adductor muscles and the mid-ventral ectodermal connection of the maxillary bar thus become attached to the endoskeletal plate. The mid-ventral connection enlarges and forms the median cylindrical muscle between the endoskeleton and the groove between the paragnaths (for adult structure, see CANNON and MANTON, 1927, Plate 2, and text-fig. 2 *b*, " *g.*"). This, then, is an ectodermal muscle. Not the whole bar, however, fuses with the endoskeletal plate, but a portion shifts backwards through the maxillulary segment in the typical manner, and closely approaches the ventral intucking between the maxillulary and maxillary segments. At the end of embryonic life the bar disappears as such and spreads out as a thin covering membrane over the nerve cord.

In the maxillary segment the bar is slightly larger and forms the tendon of the maxillary adductor muscles, the ventral mesoderm becoming attached to it. The formation of this tendon is similar to that of the mandibular tendon, text fig. 22 *d* (for adult structure, see CANNON and MANTON, 1927, text-fig. 2 *c*). The tendon and its attached muscles first lies in the anterior part of the maxillary segment. It then shifts to the posterior edge of that segment close to the next ventral intucking and loses all ectodermal connections. As the tendon shifts backwards, the posterior arms of the endoskeletal plate follow, lying just above it on either side (text-fig. 22 *d*, " *e.p.l.ex.*"). The mid-ventral connection of the maxillary and at least of the anterior trunk bars persist as thin skeletal folds projecting into the nerve cord.

All the posterior bars sag backwards to the middle of the segments (text-fig. 23 *b*). Laterally the ventral mesoderm comes in contact with the bars and creeps along them to a varying extent. In the first six thoracic segments the ventral mesoderm is small in amount and remains lateral in position (Plate 23, figs. 17, "*v.m.*" and "*e.t.*"). The bars here lose their nuclei and form a thin membrane lying over the nerve cord between the lateral muscle masses (text-fig. 15 *c*, "*m.i.c.*").

In the seventh and eighth thoracic segments the ventral mesoderm is much more massive, and strands grow out from it along the bars. This process is seen starting in text-fig. 23 *b*, while the lateral ectodermal connections of the bars are still intact. Later the muscle rudiments grow right up to the central nucleus of each bar (text-fig. 23 *c*). The first muscle strands to grow out arise from the outer parts of the ventral mesoderm (text-fig. 23 *b*, "*o.v.m.*") and pass forward to the segment in front and then along the bar of that segment ("*o.v.m.m.*"). A little later muscle rudiments formed from the inner part of the ventral mesoderm ("*i.v.m.*") grow out and creep along the bar in their own segment (text-fig. 23 *c*, "*i.v.m.m.*"). The viscera in this region, unlike the rest of the thorax, are not bulky; and as the yolk sac shrinks so the bars become pulled up by the ventral mesoderm, which expands into the available space. The mid-ventral connections of the bars to the ectoderm become much stretched (text-figs. 15 *f* and *g*, "*v.i.*") until they finally break. Thus the ectodermal bar is left free between the muscles, where it is greatly shortened, and finally forms the thin median tendinous junction between the muscles masses below the intestine (text-figs. 15 *i* and *j*). A typical bar is formed between the sixth and seventh abdominal segments (text-fig. 20 *b*), but gives no adult tendon in the seventh segment. It probably forms a covering membrane over the nerve ganglia as in other parts.

Between the optic rudiments and the antennules a pair of large lateral intuckings are formed above the nerve cord. They grow inwards until they meet the anterior part of the stomodæum with which they become united (text-fig. 22 *a*, "*e.s.t.*"). These strands consolidate and shrink in length as the yolk is absorbed and the stomodæum enlarges (text-fig. 23 *b*, "*e.s.t.*"). As the preoral part of the body rotates upwards with the decrease of yolk, they appear to keep the stomodæum extended during this process. When the adult proportions have been assumed, the cardiac stomach becomes rounded and the strands lose their nuclei and develop fibrils extending between the cuticle of the lateral walls of the cardiac stomach and the body wall in the anterior antennal region (text-fig. 22 *c*, "*c.s.t.*"). The nature of the fibrils, whether muscular or otherwise, could not be determined.

Musculature.

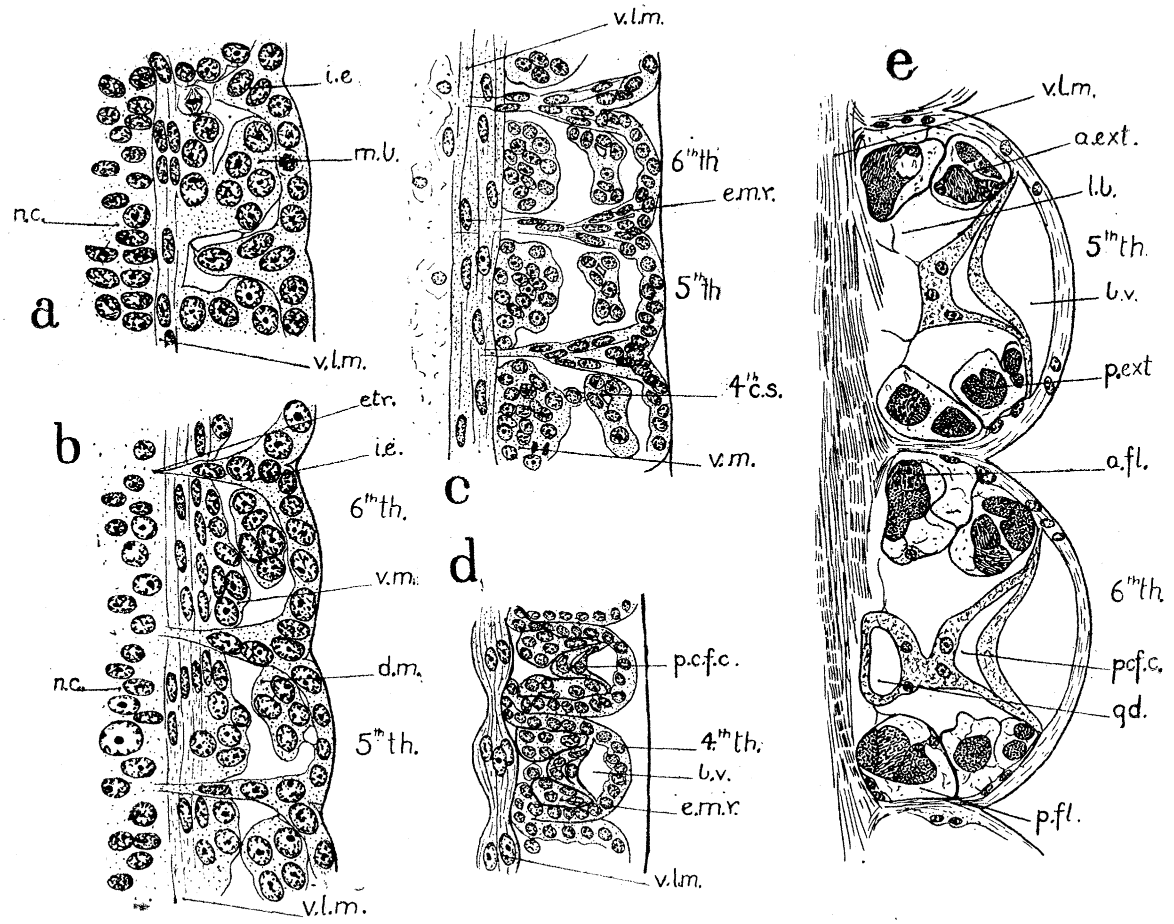
The musculature of a typical trunk segment is formed both by the mesoderm and the ectoderm. The *dorsal* and *ventral longitudinal muscles* are formed by the dorsal and ventral mesoderm respectively (p. 395). The next muscle rudiments to appear are those of the *extensor* and *flexor muscles* to the limbs. These are ectodermal in origin. After the segmental ectodermal bars have appeared a thickened intersegmental ridge is formed between the horizontal tendon rudiment and the lateral ectoderm (text-figs. 24 *a* and *b*, "*i.e.*"). The inner parts of this ridge become nipped off forming almost horizontal strands on the anterior and posterior faces of the ridges (text-fig. 24 *c*, "*e.m.r.*," and Plate 23, fig. 20, "*e.m.*"). The ends of the strands remain attached to the ectoderm, their outer attachments being more dorsal than their inner ones. These strands form rudiments of extensor and flexor limb muscles (text-fig. 25).

The mesodermal blocks are quite separate from these strands. As the mesoderm grows up the sides of the body, so the outer attachments of these muscle rudiments also shift upwards. The latter thus become more vertical and increase in size at the same time (Plate 23, fig. 21, "*e.m.*"). All the nuclei are elongated and arranged in rows. As the intersegmental furrow deepens these muscle rudiments come to lie just within the ectoderm of the limb bulge, the anterior rudiment of any intersegment lying posteriorly in the limb, while its posterior fellow lies anteriorly in the limb behind. They are now cut transversely in frontal sections (text-fig. 24 *d*, "*e.m.r.*").

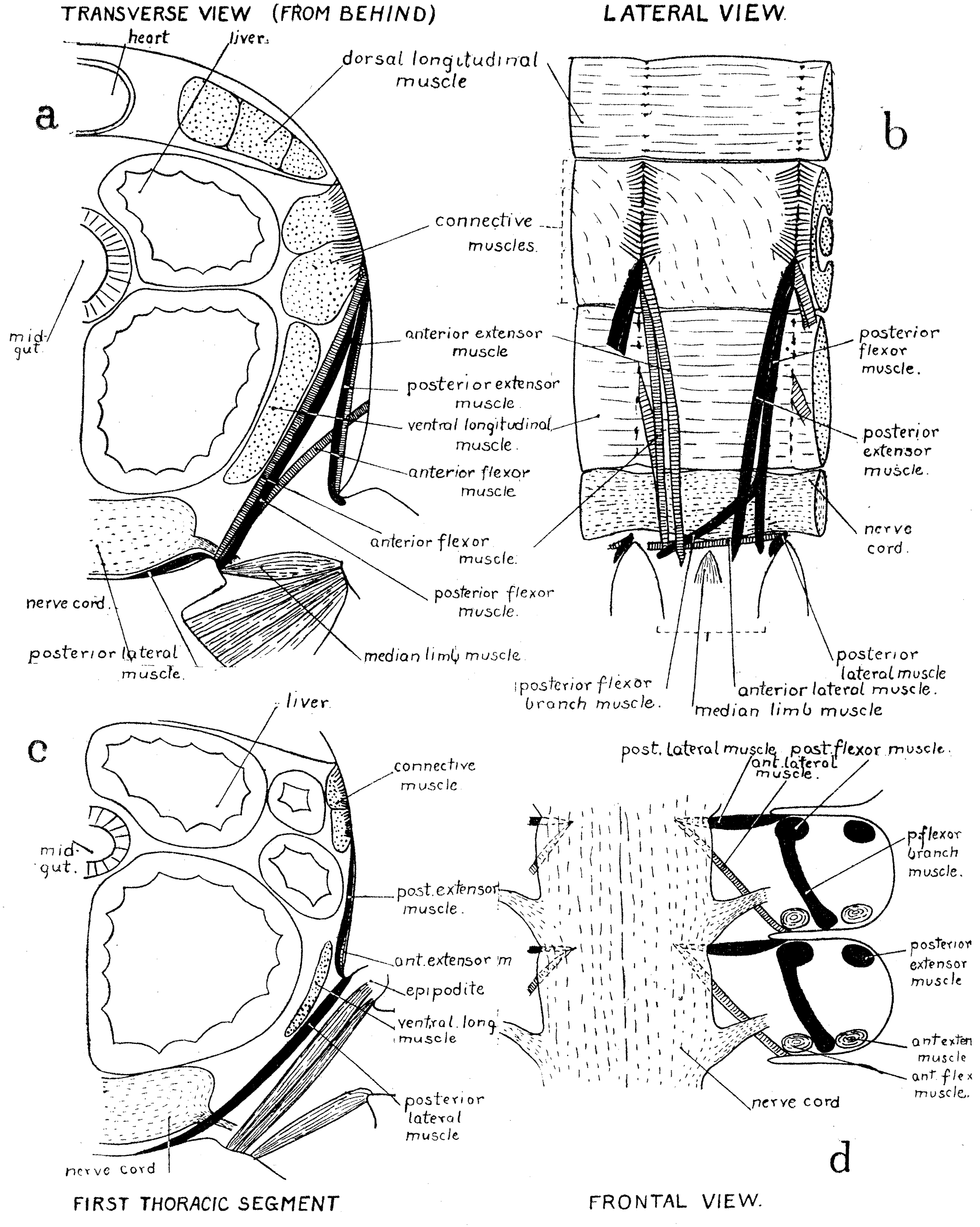
Each ectodermal muscle rudiment is conical in shape, the apex being attached to the ectoderm above, and the lower part to one side of the limb base. Below the base of the pericardial floor (text-fig. 24 *d*) the two rudiments in each limb come in contact with one another. At the end of embryonic life each conical rudiment becomes divided into inner and outer parts (text-fig. 24 *e*, "*p.ext.*" and "*a.fl.*"). The inner part forms a flexor muscle running from the angle between the limb and ventral body wall up to the intersegmental lateral ectoderm; and the outer part forms an extensor muscle from the outer part of the limb base to the intersegmental ectoderm (text-fig. 25 *a*). One pair each of extensor and flexor muscles is thus formed at the anterior and posterior ends of each segment (text-figs. 25 *b* and *d*).

In the first five abdominal segments the limb musculature is much reduced, and in the remaining segments it differs somewhat from the typical arrangement. In the thorax these four muscles to each limb are closely similar. The anterior flexors become subdivided into inner and outer strands, the outer strand being attached to the ectoderm below the inner strand (text-figs. 25 *a* and *b*). The posterior flexors in the adult divide near their lower ends, sending a branch forwards and downwards across the limb base to be inserted on its anterior side between the anterior extensors and flexors (text-figs. 25 *b* and *d*). This branch is probably formed when the two conical rudiments of one segment temporarily come in contact at their bases.

The ventral mesoderm, after separation of the ventral longitudinal muscle, forms *internal connective muscles* to the horizontal ectodermal bars (p. 396), and *external connective muscles* to the intersegmental ectoderm (text-figs. 15 *a*, *f* and *g*, "*i.c.m.*" and "*o.c.m.*"). The external connective muscles (p. 397) are formed after the ectodermal extensor and flexor rudiments have appeared, and are attached to the ectoderm directly above the latter (Plate 23, figs. 20 and 21, "*o.c.m.*"). The external connective muscles are small in the



TEXT-FIG. 24.—Frontal sections to show the development of the ectodermal extensor and flexor limb muscles. (*a*) The segments are marked by intersegmental ectodermal intuckings and the mesoderm is forming the ventral longitudinal muscle. (*b*) The mesoderm is now divided into ventral and dorsal portions, and the intersegmental ectodermal ridges have formed the intuckings giving rise to the ectodermal tendons. (*c*) Strands of cells are being separated from the anterior and posterior sides of the ectodermal intersegmental intuckings forming muscle rudiments. The mesoderm is quite separate from these strands. (*d*) The outer attachments of the strands of cells have shifted upwards and the intersegmental furrows have deepened so that the muscle rudiments are cut transversely in the anterior and posterior parts of the limb bases. The base of the dorsal mesoderm forming the lateral pericardial floor is now attached to the ectoderm intersegmentally, leaving the lateral blood vessel external to it, and the lower cœlomic spaces are appearing. (*e*) Small adult. The muscle rudiments have divided to form flexor and extensor muscles. The persistent lower cœlomic spaces lie in the pericardial floor base, and the oviduct is seen in the sixth thoracic segment. *a.fl.*, anterior flexor muscle; *a.ext.*, anterior extensor muscle; *b.v.*, lateral blood vessel from limb base to pericardium; *d.m.*, dorsal mesoderm; *e.m.r.*, ectodermal muscle rudiment forming extensor and flexor muscles; *e.t.r.*, ectodermal tendon rudiment; *g.d.*, oviduct; *i.e.*, intersegmental ectodermal intucking; *l.b.*, limb base; *m.b.*, mesoderm block; *n.c.*, nerve cord; *p.c.f.c.*, lower cœlomic cavity in base of pericardial floor; *p.ext.*, posterior extensor muscle; *p.fl.*, posterior flexor muscle; *v.l.m.*, ventral longitudinal muscle; *v.m.*, ventral mesoderm; *4th c.s.*, fourth thoracic cœlomic sac; *5th th.*, *6th th.*, fifth and sixth thoracic segments.



Text-Fig. 25.—Diagrammatic views of the musculature of a typical thoracic segment and of the first thoracic segment.

first six thoracic segments and increase in size posteriorly. The muscles derived from the ventral mesoderm are very complex and have not been worked out.

The limb mesoderm forms muscles within the limb itself and also between the base of the limb and the body. Many muscles from the limb are attached to the intersegmental ectodermal ridge, and one large muscle extends from the angle of the bifurcated basipodite inwards to a point just below the junction of the limb and ventral body wall. This muscle lies across the middle of the limb (text-figs. 25 *a* and *b*, " median limb muscle ").

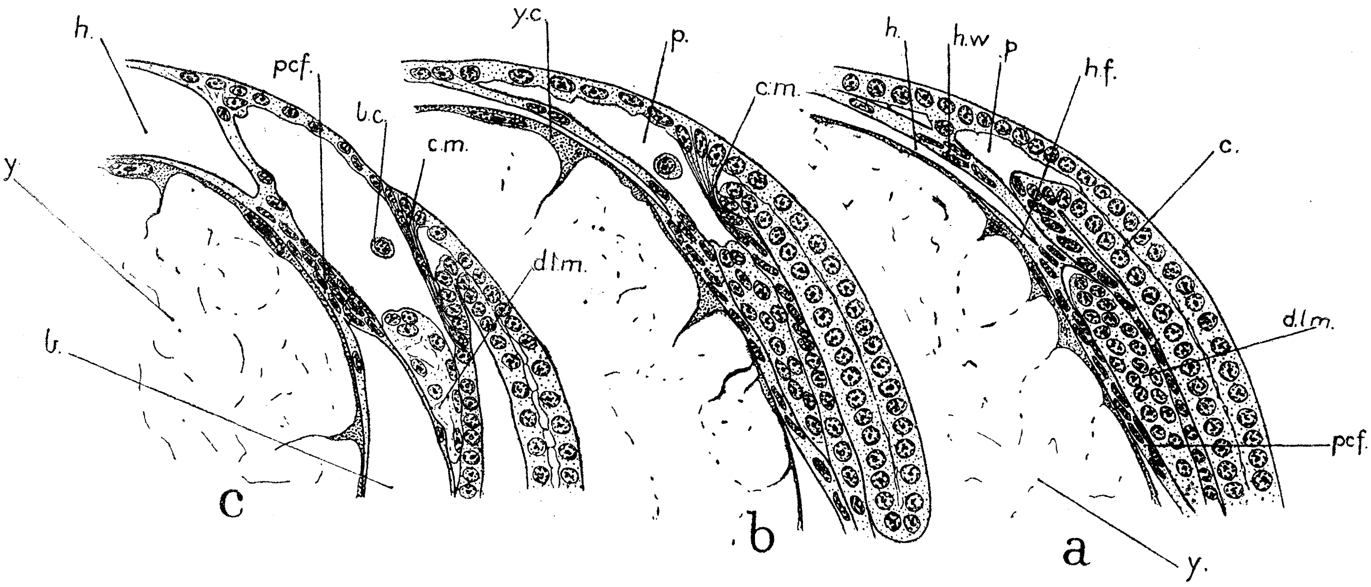
Two other muscles which may here be called *anterior* and *posterior lateral muscles* are present in the adult. They probably develop from the limb mesoderm, but their formation could not be determined accurately. They are both attached to the intersegmental ectoderm below the nerve cord. The anterior lateral muscle is very small and passes forwards to the anterior face of the limb base just internal to the anterior flexor muscle. The posterior lateral muscle is larger and passes directly outwards to the posterior face of the limb base just behind the posterior flexor muscle (text-figs. 25 *a*, *b* and *c*). Both muscles lie just within the ventral ectoderm, and appear only in the thorax.

In the first thoracic, maxillary and maxillulary segments the musculature differs somewhat from a typical trunk segment. In the first thoracic segment (text-fig. 25 *c*) the ectodermal muscle rudiments are smaller and do not divide. They form very small anterior and posterior extensor muscles. The anterior lateral muscle could not be found, but the posterior lateral muscle is large and runs across the limb base to the insertion of the epipodite.

In the maxillary and maxillulary segments lateral muscles appear to be absent. The bulk of the musculature consists of adductor muscles from all parts of the limb bases to the maxillary ectodermal tendon and the maxillulary endoskeletal plate. Flexor muscles, such as are present in the thorax, are absent from the maxillary segment. One large band of extensor muscles is here present but no separate anterior and posterior strands are recognisable. In the maxillulary segment the intucking forming the endoskeletal plate separates the upper posterior half of the limb from the body wall, so that the extensor and flexor muscles are limited to the anterior part of the segment. An extensor muscle divided into two bundles of fibres lies near the middle of the limb, and a large group of flexor muscles is present in the anterior part of the segment. A muscle strand from the flexor group passes to the lateral wall of the paragnath. The origin of the flexor and extensor muscles in the maxillary and maxillulary segments could not be determined with certainty, but there is no reason to suppose that they are formed in a manner other than that taking place in the thorax.

The mandibular adductor and levator muscles are formed from the mandibular mesoderm.

Two muscles are formed in relation to the carapace fold. In the middle of the maxillulary segment a muscle extends from the endoskeletal plate outwards and upwards to the external wall of the carapace. Secondly, in the first three thoracic segments a band of muscles is inserted below and above the attachment of the carapace to the body wall (text-figs. 15 *d* and *e*). This band of muscles is formed by the ectoderm. At the base of the carapace fold in these segments the ectoderm cells on either side become united. Text-fig. 26 *a* shows the carapace attachment just behind the third segment, and 26 *b* is through the third segment, where the muscle rudiment is just formed. The dorsal mesoderm is quite separate from the ectoderm in this region. As the furrow separating off the carapace deepens, the muscle rudiment is left inserted in the lateral ectoderm below the carapace attachment (text-fig. 26 *c*).



TEXT-FIG. 26.—Three transverse sections showing the development of the ectodermal carapace muscle. (*a*) Shows the carapace attachment to the body behind the third thoracic segment. The pericardium is freely open to the spaces within the carapace fold. (*b*) Through the third segment of the same embryo. The ectoderm cells at the base of the carapace fold have become united forming the rudiment of muscle. (*c*) An older stage where the carapace has been further folded off from the body leaving the muscle rudiment inserted in the ectoderm below the attachment of the carapace.

b., body hæmocœl; *b.c.*, blood corpuscle; *c.*, carapace fold; *c.m.*, carapace muscle; *d.l.m.*, dorsal longitudinal muscle; *h.*, heart cavity; *h.f.*, heart floor; *h.w.*, heart wall; *p.*, pericardium; *p.c.f.*, pericardial floor; *y.*, yolk; *y.c.*, yolk cell.

The larger muscles attached to the endoskeleton have already been described (p. 412). Of the stomach muscles two pairs of postero-dorsal and two pairs of antero-dorsal muscles are formed by the preantennulary mesoderm (p. 393). Other extrinsic stomach muscles appear to be mesodermal in origin. The œsophageal dilators are all mesodermal, and the development of the proctodæal dilators from the seventh abdominal somites has already been described. The formation of one or two of the cardiac stomach and œsophageal dilators may be described in detail as examples.

As the labrum protrudes from the body surface, so its cavity becomes invaded by mesoderm cells, spreading down the anterior face of the œsophagus. The ectoderm of the anterior and posterior faces of the labrum and of the œsophagus are quite separate from one another, and an undifferentiated sheet of mesoderm cells lies between them. The ectodermal nuclei are much smaller and more darkly staining than the mesodermal nuclei. The first change in this mesoderm is for certain cells to become spindle-shaped and to stretch across the space between the œsophagus, stomach and anterior wall of the labrum. Four such cells are seen in Plate 25, fig. 32, two opposite the stomach and two near the œsophagus. At either end these cells become attached to the ectoderm and fibrils appear along their whole length. When attached to the body wall or to the stomach, the mesodermal muscle cells look as if they pushed their way between the ectodermal cells to become directly attached to the cuticle (Plate 25, fig. 33). When attached to the œsophagus, however, the fibrils radiate out among the œsophageal ectoderm cells. Transverse striations do not appear till the end of embryonic life. The œsophageal as well as the proctodæal dilators are formed very late in development.

The mesodermal muscle cells so far mentioned, with the exception of the œsophageal and proctodæal dilators, are attached to the cuticle by fibrillæ passing through the hypodermis. These tendofibrillæ are always close together, and all ectodermal nuclei lie ouside the insertion, none being found between the fibrillæ. The hypodermis through which the muscle is attached may be extremely thin so that the tendofibrillæ as such are scarcely if at all distinguishable from the myofibrils. The origin of the tendofibrillæ is uncertain. A mesodermal muscle perhaps may become attached to the basement membrane of the ectoderm, the tendofibrillæ being formed by the ectodermal cells themselves; but in many cases the muscle cells appear to force their way between the ectodermal cells, and so become attached directly to the cuticle (mandibular adductors, text-fig. 22 *d*, "labral and stomach muscles," Plate 25, fig. 33).

The insertions of ectodermal muscles when fully formed cannot be distinguished from those of mesodermal muscles, as CANNON pointed out for *Chirocephalus* (1927, p. 413). The fibrils of the ectodermal extensor and flexor muscles seem to end directly against the cuticle just as they appear to do in many mesodermal muscles where the hypodermis is thin. The median ectodermal muscle from the body wall to the endoskeletal plate (see p. 416) is inserted on a fairly thick hypodermis. Here the distinct tendofibrillæ are distinguishable just as in a mesodermal muscle. The insertion of an ectodermal muscle rudiment is often very distinct from that of a mesodermal muscle, as seen in Plate 23, fig. 20, "*o.c.m.*" and "*c.m.*" Here the ectodermal muscle merges into the ectoderm, or the ectodermal nuclei may be drawn out towards the muscle; while the mesodermal muscle ends sharply against unaltered ectoderm cells. However, a mesodermal muscle attachment under considerable tension may appear misleading, the ectodermal cells and nuclei being drawn out towards the muscle, as in the levator muscles of the mandibles and antero-dorsal stomach muscles.

A second type of muscle insertion, described by CANNON (1927) for *Chirocephalus*, is seen in the inner attachments of the œsophageal and proctodæal dilators. Here the ectoderm is thick and the striated muscle fibrils are continuous as such right through the epithelium to the cuticle (text-fig. 19 *g*, and Plate 25, fig. 34). These fibrils are not grouped close together as are the tendofibrillæ, but are spread out, the ectodermal nuclei lying between them. The origin of these striated fibrils traversing the ectoderm is uncertain.

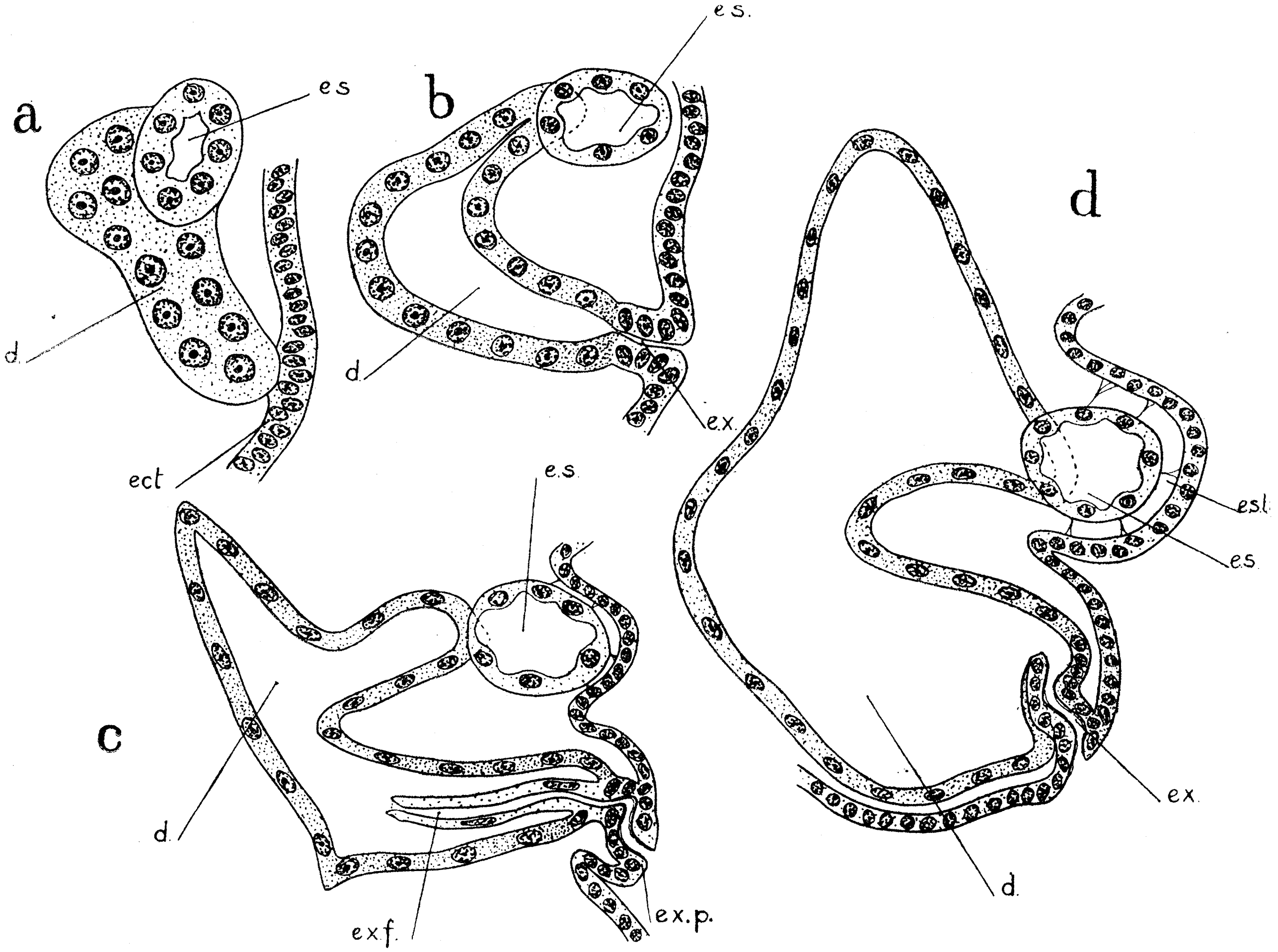
Antennal Gland.

The development of the head mesoderm bands has been followed up to a stage when the paired bands are subdivided into liver rudiments and irregular masses at the bases of the naupliar appendages. A few separate muscle rudiments are also formed from the above. When the trunk and preantennulary cœlomic cavities are appearing, the mesoderm at the base of the antenna becomes divisible into three portions. Below, an irregular mass of cells extends into the limb bulge and gives rise to the antennal musculature. Above this and on the inner side a compact group of about eight cells are distinguishable by their large nuclei and deeply staining cytoplasm from about ten small upper outer cells (Plate 25, fig. 28). The small upper cells soon arrange themselves in a sphere in the centre of which a cavity appears (Plate 25, fig. 29). This is the rudiment of the end sac of the antennal gland. The inner group of large cells becomes more compact and elongated and closely pressed against the end sac forming the rudiment of the duct of the antennal gland. Cytologically the duct cells are sharply distinguishable from the limb mesoderm and the ectoderm by their large nuclei and darkly staining cytoplasm. The rudiment of the gland now lies obliquely across the base of the antenna below the yolk sac, and remains approximately in this position in the adult.

The end sac gradually enlarges and its walls become thinner, especially between the nuclei, leaving a large central cavity (text-fig. 27). The cytoplasm remains lightly staining. The end sac becomes closely pressed against the ectoderm, with which it becomes connected by fine protoplasmic strands. The end sac lies in the posterior part of the antennal base, and the ectoderm forms small infoldings below and above it so that the end sac is lodged finally in a rounded lobe from the body wall (text-figs. 27 and 28).

The duct rudiment bulges forward in front of the end sac and also downwards and backwards below it till it touches the ectoderm of the posterior face of the limb (text-fig. 27 *a*). Here about two duct cells force their way between the ectoderm cells and reach the cuticle by narrow necks (Plate 25, fig. 30). There is no doubt that this connection to the ectoderm is formed in this way, since stages just earlier than the above show the duct cells lying just within, but quite independent of, the ectoderm cells. The duct rudiment is at first rod-like, but when the ectodermal connection is formed it becomes U-shaped in side view, the arms of the U terminating against the end sac above and the ectoderm below, the base of the U pointing forwards. The nuclei become arranged peripherally and a lumen is formed in the middle of the duct (text-fig. 27 *b*).

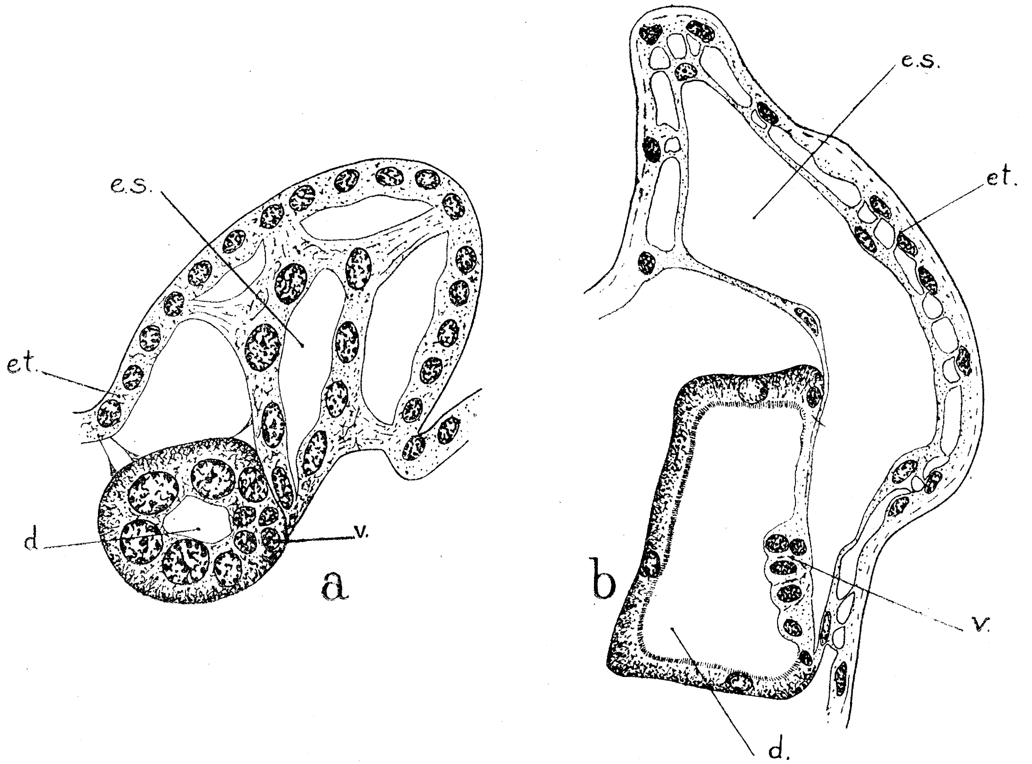
As the lumen of the duct appears the ectoderm becomes drawn inwards at its junction with the duct for a short distance (text-fig. 27 *b*). This intucking forms the rudiment of an ectodermal exit tube, although its lumen is often not formed till later. From its junction with the duct the exit tube grows inwards into the lumen of the duct, forming a long hollow chimney (text-fig. 27 *c* and Plate 25, fig. 31). Six cells participate in its formation, a longitudinal furrow indenting the outer surface between each. The nuclei of these cells pass down into the walls of the chimney. The cytoplasm of the chimney resembles that of the ectoderm and exit tube, in marked contrast to that of the darkly staining duct (Plate 25, fig. 31). This chimney is formed very rapidly when heart formation has begun, and persists until the end of embryonic life, when it is rapidly absorbed, leaving the adult duct directly continuous with the exit tube.



Text-Fig. 27.—Optical parasagittal sections showing the development of the antennal gland. (*a*) A lumen has appeared in the group of end-sac cells; and the solid duct rudiment, originally separate from the ectoderm, has now come in contact with it on the posterior side of the antennal base. (*b*) The duct has united with the ectoderm with the formation of an ectodermal exit tube. A lumen has appeared in the duct, which is now U-shaped. (*c*) An outgrowth from the upper anterior part of the duct spreads up the side of the body, and a long funnel from the inner end of the exit tube projects into the duct lumen. The exit tube is twisted and opens on a papilla. (*d*) Young adult gland, the exit tube funnel is lost, and the papilla is flattened out as the antenna is turned forwards. The end sac is lodged in a lobe of the antennal base. *d.*, duct; *ect.*, ectoderm; *e.s.*, end sac; *e.s.l.*, end-sac lobe; *e.x.*, exit tube; *e.x.f.*, exit tube funnel; *e.x.p.*, exit tube papilla.

The exit tube first connects to the exterior on the posterior upper surface of the limb in the furrow separating the end-sac lobe from the limb. Later the ectoderm is raised forming a papilla which contains the exit tube. As the papilla grows the exit tube becomes twisted, and finally opens on the lateral lower side of the papilla as an S-shaped canal lined with cuticle (text-fig. 27 *c*). At the end of embryonic life, when the antenna is rotated forwards and no longer lies close against the sides of the body, the exit tube papilla is largely obliterated (text-fig. 27 *d*).

The anterior part of the U-shaped duct forms a dorsal upgrowth extending between the stomach and the body wall (text-fig. 27 *d*). The duct itself then becomes increasingly sac-like until it reaches the adult proportions (see CANNON and MANTON, 1927 *b*, text-figs. 4 *d* and *e*). The end sac becomes drawn out against the side of the duct, where a valvular junction is formed between the two. The duct wall does not become striated opposite the end sac and remains thin and lightly staining. Here six or eight valve cells with small dense nuclei form a compact group bulging into the duct lumen (text-fig. 28 *a*). The end-sac wall at this point fuses with that of the duct. The only visible connection between duct and end sac is by fine rather vague channels passing through these valve cells, and no muscle fibrils are present in them (text-fig. 28 *b*).



TEXT-FIG. 28.—Frontal sections showing the union between the end sac and duct. (*a*) Old embryo. A group of small nuclei in the duct wall are seen at the point of contact of the duct and end sac. (*b*) Adult, the walls of the end sac and duct, where they are in contact, have coalesced, the small duct cells forming a valve. *d.*, duct ; *e.s.*, end sac ; *e.t.*, ectoderm ; *v.*, valve.

No trace of a maxillary gland could be found.

Abnormality.

Only one abnormality was found and that one was constant throughout a whole family of embryos. Here a V-shaped germinal disk with active teloblasts was found, but it was invaginated into the yolk instead of remaining on the surface. The cavity of the invagination was nearly or quite cut off from the exterior, so that the embryo was developing on the inside of a hollow cup or sphere surrounded by yolk. This condition is of interest in that it resembles the type of development shown by Insects.

Discussion.

Little need be said concerning the *segmentation* of *Hemimysis*. It resembles that found so frequently in the Peracarida and in *Nebalia* (BOUTCHINSKY, 1900) in that no cleavage furrows are formed. These appear partially in most Decapoda, and in the Amphipoda cleavage is total.

The nuclei and surrounding protoplasm of the blastomeres first rise to the surface at the vegetal pole, just as in *Leander* (SOLLAUD, 1923, p. 57) and in the Isopoda (MCMURRICH, 1895). No chorion is present, such as described by MCMURRICH for various Isopods.

In no other Malacostraca have the *spatial relations between the different germ layers* and genital rudiment been demonstrated at their earliest formation. The relative positions of the endoderm and mesoderm, however, have been seen in several instances. The plan is always similar, differences in detail being correlated with the varying degrees of determination shown by the development as a whole. Among the Isopoda, where segmentation is determinate, as in *Jæra*, the mesoderm forms a circle around the posterior endoderm,* but later contracts into a transverse band in front of the endoderm cells (text-fig. 29).

In *Hemimysis* the germ layers only become distinct when the germinal disc appears. Here the mesoderm is situated in front of the endoderm, and the liver rudiment lies between the two, as in *Jæra* (text-fig. 29). In *Asellus* the early development is slightly less determinate, the mesodermal teloblasts arising just anterior to a mesendodermal mass which is partly surrounded by ectodermal teloblasts (text-fig. 29). Finally, in *Porcellio* mesoderm and endoderm are not distinguishable on the disk and are derived from a common mesendodermal rudiment. The origin of the mesoderm in the Amphipoda has not been satisfactorily worked out, but it appears to arise anterior to the yolk cells (LANGENBECK, 1898).

In the Decapoda endoderm is formed by a blastoporal ingrowth, while the mesoderm is generally said to arise from the anterior lip of the blastopore. A detailed account of this process has been given by SOLLAUD for the Palæmoninæ, and this, in principle, may be taken as typical for the Decapoda. Yolk cells in *Leander* pass inwards from the

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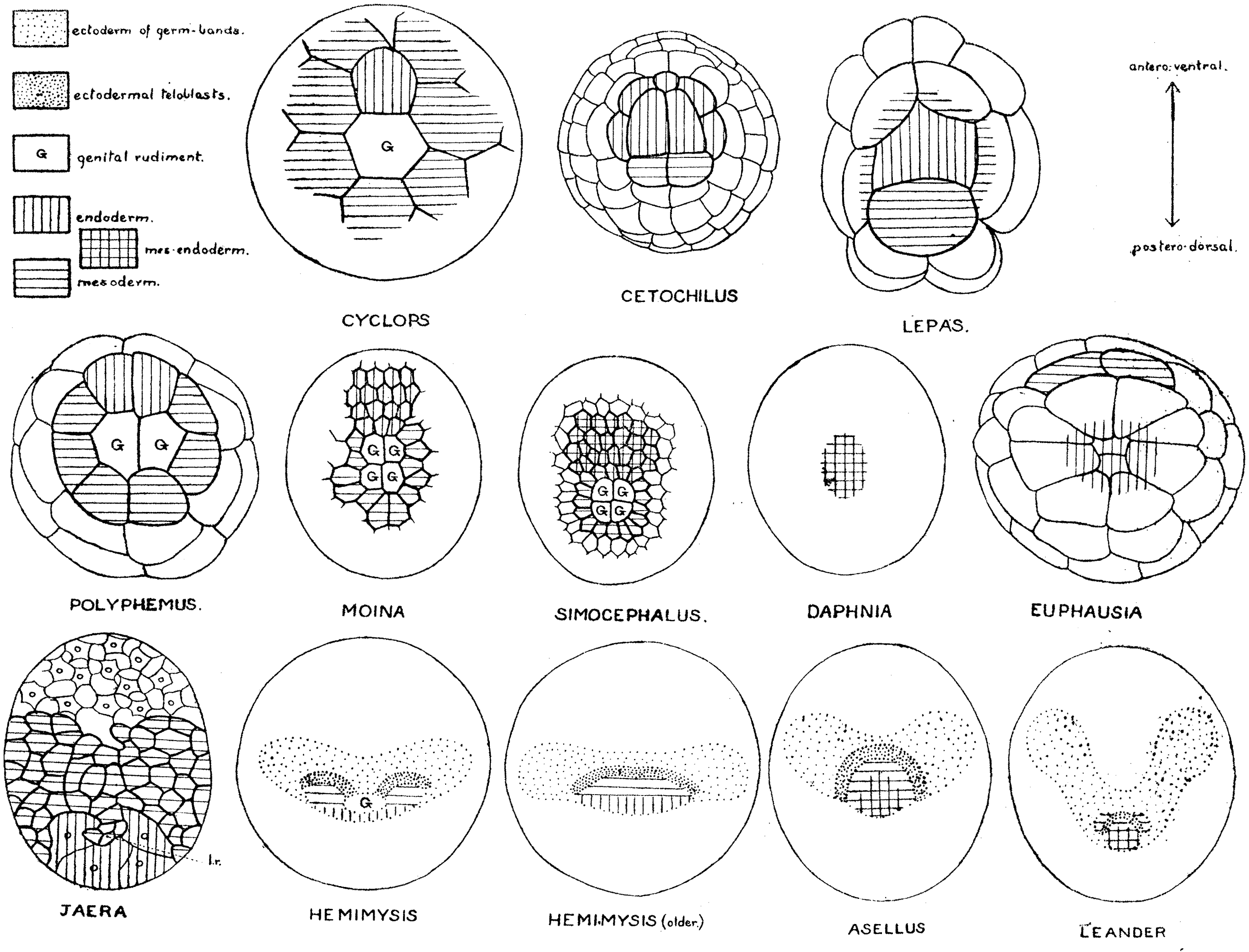
* MCMURRICH considered the "vitellophags" as mesodermal, but there is reason to believe that they represent the true endoderm (p. 433).

blastopore, and mesoderm formation starts by immigration from two thickenings at the sides of the latter. These thickenings, the " lames mesectoblastiques," are morphologically the posterior parts of the two ventral germ bands, and thus mesoderm arising here is seen to be in an equivalent position to the first-formed mesoderm in *Hemimysis* (text-figs. 4 *b* and 5 *a*). When the blastopore closes, a solid plug of cells (the " bouchon blastoporique ") is formed in this region. From the anterior part of this mass are formed



TEXT-FIG. 29.—Diagrammatic views of Crustacean embryos, to show the spatial relations between the germ layers and genital rudiment. *Cyclops* after FUCHS, *Cetochilus* after GROBBEN, *Lepas* after BIGELOW, *Polyphemus* after KÜHN, *Moina* after GROBBEN, *Simocephalus* after CANNON, *Euphausia* after TAUBE, *Jœra* and *Asellus* after MCMURRICH, and *Leander* after SOLLAUD. (FUCHS does not state the orientation of his figure of *Cyclops*, but he compares it directly with *Polyphemus*.)

mesodermal teloblasts. From the inner part yolk cells continue to be formed, and also mesodermal cells which give rise to the " lame intestinale primitive " (SOLLAUD, 1923, ch. 4, p. 77 and p. 167). The site of the " bouchon blastoporique " thus represents the blastoporal area of *Hemimysis*, and it is likewise bounded anteriorly by the ectodermal teloblasts. The spatial relations between endoderm and mesoderm are seen to be comparable in the two cases, although in *Leander* these areas overlap. Development in *Leander* is much less determinate, and the areas of mesoderm and endoderm formation are not so distinct and the former much less restricted.

In *Nebalia* the form of the germinal disk resembles that of the Decapoda and Mysidacea. At the hinder end of the germ band a solid mesendodermal plug is formed (BOUTCHINSKY, 1900), and this must be comparable with the " bouchon blastoporique " of the Palæmoninæ.

All the Decapoda and Peracarida so far considered have yolky eggs and develop by the formation of a germinal disk. Only the Euphausids (TAUBE, 1909) and *Leucifer* have eggs poor in yolk and total cleavage. In the Euphausids the mesoderm is formed from two cells situated in front of the endodermal cells (text-fig. 29). BROOKS' account of *Leucifer* does not show the relative positions of the endodermal and mesodermal rudiments.

The germ-layer formation of the Syncarida and Hoplocarida is unknown, but in the rest of the Malacostraca the endoderm appears to arise typically behind the mesoderm. If the arrangement shown by the Malacostraca be compared with those of all other Crustacea, a fundamental difference is apparent (text-fig. 29). In the Branchiopoda, as exemplified by the Cladocera, the arrangement of the rudiments shows a constant pattern when development is not extremely indeterminate. Endoderm is formed in front of the genital rudiment, and mesoderm behind it. Mesoderm may, however, spread round the genital rudiment and even in front of it, so that the anterior endoderm may be replaced by a mesendodermal mass (*Simocephalus*, text-fig. 29). In the Copepoda FUCHS (1913) has shown that the determinate cleavage of *Cyclops* closely resembles that of *Polyphemus* (text-fig. 29). Somewhat disharmonious results have been obtained by various authors on Copepod development, but all agree in finding the mesoderm arising behind the endoderm. *Lepas* among the Cirripedia (text-fig. 29) likewise shows this arrangement, but mesoderm is also formed from the cells surrounding the large endodermal cell. In the Ostracoda development is quite indeterminate, but resembles that of the indeterminate Cladocera (MÜLLER CALÉ, 1913).

Thus those forms showing determinate development among the Branchiopoda, Cirripedia and Copepoda, so far as they are known, all show the mesoderm arising primarily behind the endoderm; and when the genital rudiment is differentiated early it lies between the endoderm and the mesoderm. The arrangements of the rudiments in the known Malacostraca and Entomostraca are evidently constant in the two groups, and are shown both by microlecithal embryos with total cleavage and by yolky forms. Such a fundamental difference in the plan of development emphasises the width of the gulf that lies between the Malacostraca and the rest of the Crustacea. Attempts have been made to show a similarity between these two types of pattern. Thus BIGELOW (1902, p. 133) suggests that possibly the mesoderm of *Astacus* arising from the anterior lip of the blastopore is equivalent to the " secondary mesoderm " of *Lepas*, which is formed from the four cells round the sides and in front of the endoderm cells. In later stages he was unable to distinguish this secondary mesoderm from the primary mesoderm formed from the posterior single cell, but he considers that the former gives rise in part to the muscular and mesenchymatous tissue of the nauplius (pp. 112 and 122).

Of the two Crustacean patterns that of the Lower Crustacea, in which the mesoderm arises in the posterior lip of the blastopore, is probably the more primitive, since this arrangement is found in the Annelids and in *Peripatus*. In the Insects, Myriapods and Arachnids the mesoderm is formed, broadly speaking, from a primitive streak, that is, from all round the blastopore. A tendency for the mesoderm formation to spread round the blastopore can be seen in *Lepas* and in *Polyphemus*. A continuation of this process with the suppression of mesoderm formation in the posterior lip would culminate in the Malacostracan condition of mesoderm formation from the anterior lip only.

The shape of the young germinal disk in the Peracarida and Decapoda is always of the same type. In the less determinate forms such as *Leander* and *Astacus* it is at first a V-shaped structure, the blastoporal area lying where the arms of the V meet. When determination is greater, the germinal bands are formed earlier, and the V may be so opened out that it forms a single transverse band as in *Hemimysis*. At some early period a dislocation or migration of blastoderm cells occurs resulting in a concentration of cells on the ventral side of the embryo, where the germinal bands develop. In determinate forms such as *Jæra* this migration occurs after the germ layers are established. In *Hemimysis* a distinct concentration of blastomeres occurs before the germinal bands are formed, but in *Leander* a widespread migration of a large number of blastomeres over the yolk takes place previous to the formation of the germinal bands. Later a shrinkage of the germinal bands always takes place.

Closure of the blastopore in *Hemimysis* takes place by the backgrowth of the ectodermal teloblasts, representing the anterior lip of the blastopore, over the blastoporal area. If the posterior limit of the blastoporal area be considered to be defined by the boundary between ectoderm and endoderm cells, then the closing of the blastopore is a very prolonged process, and is only completed when the thoracic and three abdominal segments have been formed. The lateral thickenings which unite to form the anterior lip of the blastopore in *Hemimysis* are comparable with the "lames mesectoblastiques" of *Leander*, but also with the paired thoraco-abdominal rudiments of *Astacus*. In all three cases these structures form the posterior parts of the arms of the V-shaped germinal band. In *Leander* a definite blastopore closes early between the "lames mesectoblastiques." Gastrulation ceases with the completion of the ectodermal covering of the "bouchon blastoporique" by the germinal disk. This takes place early, just before the caudal papilla is formed, and later the ectodermal teloblasts shift backwards as in *Hemimysis*. In *Astacus* gastrulation is also completed early. The main process in the closure of the blastopore appears to be a backgrowth of the anterior lip, which is formed by the hinder edges of the united thoraco-abdominal rudiments (REICHENBACH, 1886, pp. 18–20). The posterior lip also grows forward to a certain extent. From REICHENBACH'S figures and from FULINSKI'S (1908) work it is seen that ectodermal and mesodermal teloblasts are present also in *Astacus* and lie partly in the anterior blastoporal lip. Thus a close similarity exists between the methods of closure of the blastopore in the three types. *Hemimysis* closely resembles *Leander*, but is remarkable in the late completion of the process due to the prolonged formation of endoderm.

The relation of the blastopore to the anus in the Malacostraca has often been considered. The relative positions of the two structures cannot be determined with accuracy since the blastopore may be a vague area and is obliterated before the anus appears. In the Decapoda most authors have considered the anus to develop just anterior to the site of the blastopore, but SOLLAUD (1923, p. 109) suggests that in reality the anus when it first appears occupies a position corresponding to the posterior part of the blastopore. A similar interpretation can be placed on the facts in *Hemimysis*. The anus pushes in behind the level of the teloblasts, and so it must be considered to be situated either over the posterior part of the blastopore or just behind it.

In *Hemimysis*, when gastrulation begins, the dorsal surface of the body is far more extensive than the ventral, which comprises only the V-shaped germinal band. Growth in length of the embryo takes place entirely by the growth backwards of the anterior ventral lip of the blastopore, interstitial growth, of course, occurring later throughout. The ventral lip of the blastopore behaves here just as does the dorsal posterior lip of the blastopore in the vertebrate embryo.

The formation of *mesodermal and ectodermal teloblasts* in the region of the anterior blastoporal lip must be general in the Decapoda and Peracarida. The ectodermal teloblasts first form a slightly curved single or paired row with the concavity directed backwards. In less determinate Isopods, such as *Asellus*, the initial concavity is much greater than in forms such as *Jæra* and *Hemimysis* (text-fig. 29). In the Mysids and Isopods the row subsequently straightens out transversely and so lies entirely on the ventral side; while in the Decapoda the condition seen in the less determinate Isopods is carried further, and the curved row becomes circular around the thoraco-abdominal papilla. In *Leander* the mesodermal teloblasts also form a circle, but in *Hemimysis*, in all other Peracarida so far described, and in *Astacus* (according to FULINSKI, 1908), only a ventral row is formed. It is probable that in all cases growth in length of the rows of teloblasts occurs by differentiation of lateral cells which become added to the rows, as seen in *Hemimysis*, and not by division of one pair of initial teloblasts as NUSBAUM claims for the mesodermal teloblasts in *Cymothoa* (1898, p. 564). In *Mysis flexuosa* BERGH (1892) found the number of ectodermal teloblasts to increase by lateral additions to the row during the growth of the post-naupliar region. In *Hemimysis*, however, the number of ectodermal teloblasts remains constant during development. The teloblasts in *Hemimysis* form all segments between the mandibles and telson, just as BERGH described for *Mysis*, whereas in *Leander*, according to SOLLAUD, only segments behind the maxilla are so formed. In *Hemimysis* one row of ectodermal and one row of mesodermal cells represent the first rudiment of each segment in the post-naupliar region. A similar result has been obtained by NUSBAUM (1898, p. 565) for *Cymothoa*. This condition probably only occurs where development is fairly determinate, for McMURRICH describes two ectodermal and one mesodermal row of teloblastic descendants in each rudiment in various Isopods. The ectodermal teloblasts thus here divide twice as frequently as the mesodermal ones. Finally, in the Palæmoninæ SOLLAUD finds each segment to be delimited secondarily from a homogeneous band composed of numerous elements.

The subsequent *changes in shape of the germinal band* with the formation of the caudal papilla appear to be a generalised character, since it occurs throughout the Decapoda and Mysidacea and also in the Leptostraca (METCHNIKOFF, 1868). In the rest of the Peracarida the thoraco-abdominal part of the germ band spreads over the yolk posteriorly and does not fold forward on itself. In the Cumacea, Tanaidacea and Isopoda the ventral germinal band always shows a dorsal curvature ; and if a folding of the embryo occurs, it is by means of a dorsal flexure and a dorsal curling of the tip of the abdomen, as seen in *Diastylis* (SARS) and *Cuma goodsiri* (DOHRN, 1870). In the Amphipoda a ventral flexure of the embryo occurs, but it is not at all comparable with that of the Mysidacea. The germinal band with the rudiments of the appendages is formed first just as in the Isopoda, and only comparatively late in development do the extremities approach one another by a ventral flexure. At a similar stage in a Mysid the ventral flexure is obliterated and the embryo straightened out.

Hemimysis, as an example of a typical Peracaridan with fairly determinate development, shows a contrast to the indeterminate Decapod type in that very few cells degenerate during embryonic growth. Cytolysis occurs only to a limited extent in the yolk cells in front of and behind the stomodæum and proctodæum respectively, within the liver rudiments and in the median dorsal organ. In *Leander*, however, much more cellular breakdown occurs. All the primary vitellophags and any cells which wander into the yolk degenerate. Also the growing edges of the " lame intestinale primitive " give products which break down at once (p. 169). BROOKS and HERRICK (1892, pp. 425–31) consider cell degeneration at length in *Homarus, Alpheus* and *Astacus*, and conclude that REICHENBACH's " secondary mesoderm " cells in *Astacus* are simply some of these degenerating cells. Amitotic division has never been observed in *Hemimysis*. It has been described in wandering cells prior to degeneration by HERRICK, and by SOLLAUD (1923, pp. 83 and 171), in the secondary yolk cells before they form the mid-gut epithelium.

In no other Peracaridan has a satisfactory account been given of the formation and development of the *endodermal layer*. The determination of the fate of the yolk cells or vitellophags and the origin of the liver in *Hemimysis* is of critical importance in the conception of endoderm formation in the Peracarida generally and in the Decapoda.

The mid-gut in *Hemimysis* is long and formed directly by yolk cells. The liver has a separate origin, arising from the mesoderm, or if the liver be considered as an endodermal organ, then the head mesoderm bands can be termed mesendodermal. The fact remains that the liver and mid-gut are not formed from a primary homogeneous endodermal layer. Now suppose that from such a form as *Hemimysis* the proctodæum became longer and the mid-gut shorter ; then the yolk cells could not all become mid-gut epithelial cells. Those lying in that part of the body traversed by the proctodæum would necessarily degenerate, as they do in *Hemimysis* at the sides of the short proctodæum. Thus the adult alimentary canal would be practically entirely ectodermal, the greater number of yolk cells degenerating and the liver being developed just as in *Hemimysis*. It will be shown that such a condition is probably found in the Isopoda, where the hind-gut is long.

The persistence or otherwise of the yolk cells in the Peracarida has been reported in such different ways that it has been difficult to interpret the real nature and function of these cells. It is probable that such difficulties are really non-existent, the yolk cells being purely endodermal elements which degenerate in proportion to the replacement of the long mid-gut by the proctodæum.

In the Cumacea (BOUTCHINSKY, 1893) and Isopoda (BOBRETSKY, 1874, etc.), and probably also in the Tanaidacea, the adult proctodæum is long. In the Amphipoda, on the other hand, it is shorter (DELLA VALLE, 1893). In the former groups the degeneration of the yolk cells is frequently claimed or implied, or they are said to form muscles, cardioblasts or blood corpuscles and not adult endoderm. In the Amphipoda and Mysidacea, however, the yolk cells have been seen to give rise to the adult mid-gut. The term " adult endoderm " as applied to the Peracarida has been used to describe the mid-gut and liver in the Mysidacea and Amphipoda ; and in forms where the mid-gut is practically absent, the liver is the main organ included under the term. Thus the " development of the endoderm " in the literature on the Isopoda refers to that of the liver, while in the Mysidacea and also the Decapoda (p. 435) it refers primarily to that of the mid-gut. Since the liver and mid-gut probably have separate origins throughout the Peracarida (see below), the confusion that has arisen by direct comparisons of " endoderm " development in the various groups is readily understood.

In the Isopoda BROBETSKY (1874) derives the liver rudiment from yolk cells surrounding the yolk, because these two structures seemed continuous. This conception is probably an error due to technique ; an examination of *Hemimysis* material fixed in the older fixatives would lead to the same conclusion. NUSBAUM (1886, p. 455) approached closer to the truth. From a sub-blastoporal ingrowth he found yolk cells wandering into the yolk and subsequently degenerating, leaving a mesendodermal mass. From two lateral thickenings of the latter in the anterior part of the embryo is formed the " endoderm " (*i.e.*, the liver). At first two tubes are formed which later divide up to give the adult liver tubes. MCMURRICH (1895) describes a liver rudiment in *Jæra* and other Isopods lying in the posterior part of the mesoderm band while this is still external (text-fig. 29). He unfortunately could not follow up the fate of this rudiment conclusively, but found it at the junction of the naupliar and post-naupliar fields. It is highly probable that this is the true liver rudiment, since it arises in a similar position to that of *Hemimysis*. A slight difference lies in its earlier differentiation and unpaired condition, both differences being correlated with the more determinate cleavage of *Jœra* compared with *Hemimysis*. If the liver rudiment were differentiated at a somewhat earlier stage in *Hemimysis*, it would necessarily be unpaired and formed from the joined posterior part of the head mesoderm bands. From sections of the embryos of the Isopod *Limnoria*, fixed in formol bichromate, the paired liver rudiments are seen in early stages to lie entirely external to the yolk cells, and the further growth of these rudiments exactly resembles that in *Hemimysis*, the yolk cells within the liver epithelium rapidly degenerating.

In the Cumacea BOUTCHINSKY (1893, p. 387) describes an inner cell mass differentiating into vitellophags which wander into the yolk, into mesoderm and endoderm, the latter forming the mid-gut. The liver arises from the sides of the "entodermalen Rinne" as a paired rudiment which forms the liver tubes. Thus there is reason to suppose that in the Isopoda and probably in the Cumacea and Tanaidacea (there appears to be no relevant literature on the latter group) the mid-gut and liver are formed as in *Hemimysis*; and that the yolk cells or true endodermal elements, few being needed to form the small mid-gut, mostly degenerate.

The Amphipoda remain to be considered, but the literature is even less satisfactory than that concerning the Isopods.

Here yolk cells pass inwards by immigration or invagination behind the median dorsal organ, that is, at the posterior end of the long germinal band (LANGENBECK, 1898, ULIANIN, 1891, PEREYASLAWZEWA, 1888). HEIDECKE (1904), however, describes immigration of endoderm cells from the germinal band itself. He finds that some of these cells absorb yolk and form vitellophags, while the rest give rise to mid-gut and liver. LANGENBECK and others consider that the adult endoderm arises only from the vitellophags. The "ventral plate" or inner layer of the germinal band has been described as arising *in situ* (LANGENBECK) or from the vitellophags (ROSSIISKAYA and KOSCHEWNIKOWA, 1891) and giving rise to mesoderm only (LANGENBECK) or to the liver rudiments (WAGNER, 1892, and ROSSIISKAYA, 1891). The development of the liver in the Amphipods seems less direct than in other Peracarida, a provisional pair of tubes being replaced by another pair which gives rise to the adult structure.

Portions of the truth can probably be found in the above conflicting accounts. The figures of the later stages of liver and mid-gut formation present striking resemblances to *Hemimysis* when allowance is made for the possibility that the liver rudiments and enclosed adjacent yolk cells have not been rightly distinguished. ROSSIISKAYA and KOSCHEWNIKOWA's figures 6 and 7, Plate 2, show two liver lobes and the mid-gut folding off from one another very much as in *Hemimysis*, the liver being epithelial and the rest of the yolk sac being composed of endoderm cells distended with yolk. No yolk spheres are seen within the formed liver epithelium. They may have been originally present and already broken down, as they do at a similar stage in *Hemimysis*, or the yolk cells may have only aggregated at the edges of the liver epithelium, as occurs round the mesodermal "lame intestinale primitive" of the Palæmoninæ (SOLLAUD, 1923).

HEIDECKE's account of *Gammarus locusta* (1904) is somewhat different but is unsatisfactory. The majority of his endodermal cells which do not become vitellophags originate later than the latter, and are said to form two longitudinal bands. The edges of these bands curl in to give the provisional liver tubes (p. 537). The adult liver and mid-gut are formed from these endodermal cells, some of which absorb much yolk. One would like to see this work repeated with better fixation before accepting the claim that all the yolk cells degenerate and have nothing to do with the yolk cells later forming the walls of the mid-gut sac ; and that the later-formed " endoderm "-giving liver, etc., has not been partly confused with the mesoderm formation. He considers that the mesoderm cells arise late, at the time of the formation of the nerve chain and after the provisional liver tubes have been formed. This seems very unlikely and his figures are not convincing.

BERGH (1892) seems to have seen more of the truth although he did not realise it. By " endoderm " he apparently means liver. He denies that it is formed by yolk cells, but rather from cells invaginated at a fixed point, the blastopore. He, moreover, recognised mesodermal (but not ectodermal) teloblasts. His figures 17 and 18, Plate 13, are most relevant. In a parasagittal section through a germinal band he shows a mesodermal teloblast and its descendants in the posterior part of the band, and anteriorly an inner layer of " endoderm." From the latter he derives the liver. Its form and position, however, appears exactly comparable to the head mesoderm of *Hemimysis,* part of which gives rise to the liver (compare Plate 4, figs. 4 and 5).

Thus in the Amphipoda there is evidence that the mid-gut alone is formed from the yolk cells, and that the liver may develop in a manner comparable with the other Peracarida. However, nothing conclusive can be said until a more critical investigation is made.

In the Decapoda it is generally accepted that at least part of the vitellophags give rise to the mid-gut and do not entirely degenerate. Work on the origin of the liver, however, is not critical. The organ is usually said to be formed from three paired rudiments arising partly or entirely from the endoderm (KINGSLEY, 1889, SOLLAUD, 1923, REICHENBACH, 1886, and BROOKS and HERRICK, 1893, etc.). It is, however, possible that the formation of the liver in the Decapoda is directly comparable with that of the Peracarida. In *Astacus* (REICHENBACH, 1886) and *Gebia* (BOUTCHINSKY, 1894) the posterior liver lobes arise from the incurled edges of the " entoderm platte," the origin of which is not described. It consists of a plate of epithelium behind the proctodæum on the posterior dorsal side of the yolk sac, and from REICHENBACH'S figures lies distinctly external to the secondary yolk pyramids. In fact, it bears exactly the same relation to the yolk pyramids as the epithelial liver rudiment does in *Hemimysis.* REICHENBACH states that the anterior and middle liver lobes arise in a similar manner, but he describes yolk cells separating from the pyramids to give the liver epithelium (pp. 107–11). His figures of this process are not convincing.

Now in the Palæmoninæ SOLLAUD (1923) has described a structure, the " lame intestinale primitive," which occupies the same relative position as the " entoderm platte " of REICHENBACH, and he emphasises the homology of the two structures (p. 181). It arises from some of the last-formed mesodermal elements in his " bouchon blastoporique." Thus if the " entoderm platte " of *Astacus* and *Gebia* is formed in a similar manner, the posterior liver tubes in these types must be mesodermal. In the Palæmoninæ SOLLAUD describes yolk cells becoming epithelial at the edges of this mesodermal plate, and from these " deux expansions laterales de l'epithelium intestinale perivitelline " develops the liver (pp. 169–72). He does not figure the process, and one would like to be sure that the " lame intestinale primitive " itself rather than the yolk cells does not give rise to the liver. If the " lame intestinale primitive " of the Palæmoninæ gives rise to the liver as in *Astacus,* then in the Peracarida and Decapoda the liver has a similar origin from the mesoderm, and only differs in that the rudiment in the Peracarida lies in the mandibular segment, while in the Decapoda it is situated above and behind the ingrowing proctodæum.

Korschelt and Heider (1909) in their classification of germ-layer formation in yolky Crustacean embryos take *Mysis* as an example of a type of development where the mid-gut is formed " unter Umwachsung des Nahrungsdotters " found in the Peracarida and Leptostraca. This group they contrast with those showing the mid-gut formed " unter Durchwanderung des Nahrungsdotters " in the majority of the Decapoda, and with the *Astacus* type " unter Filtration des Nahrungsdotters." It is evident that Korschelt and Heider are comparing the liver formation in the Peracarida with that of the mid-gut in the Decapoda ! The true mid-gut of the Peracarida is formed by yolk cells, and if the endoderm formations of the Peracarida and Decapoda are to be compared, then that comparison must lie between the yolk cells in the two groups.

In the Decapoda Sollaud (1923) has called attention to the fact that the mid-gut formed " unter Durchwanderung des Nahrungsdotters " is not separable fundamentally from the *Astacus* type " unter Filtration des Nahrungsdotters." A number of intermediate conditions occur between the yolk cells which wander entirely without order, as in the Palæmoninæ, and the united orderly migration of the endodermal elements in *Astacus* (pp. 175–78). In the Peracarida the yolk cells may wander independently through the yolk as in the Cumacean *Iphinœ* (Boutchinsky, 1897, p. 387) and various Amphipods (Heidecke, 1904, and Rossiiskaya and Koschewnikowa, 1891). In *Hemimysis* they wander independently but remain on the surface of the yolk, while in *Oniscus* (Bobretsky, 1874) at first they behave as in *Hemimysis,* but later wander directly into the yolk. Finally, in the Amphipod *Microdeutopus* (Langenbeck, 1898) the yolk cells are formed by an invagination of a regular formed layer of cells, which, however, later disorganise and spread separately through the yolk. These differences in behaviour of the yolk cells may be due in part to physical conditions, such as viscosity of the yolk. This may be too great to allow the free wandering of the yolk cells through the yolk restricting their movements to the surface, as in *Hemimysis.* The consistency of the yolk may change during development, as it absorbs water, and so the yolk cells first at the surface of the yolk may later be able to penetrate, as in *Oniscus.* It is thus apparent that there is no distinction between the methods of mid-gut formation in the Peracarida and Decapoda, similar variations in detail occurring in both groups. There is no sound evidence supporting the views that yolk cells form blood corpuscles, cardioblasts or muscles. They are true endodermal cells which may degenerate, but give rise to no other organ than the mid-gut.

Sollaud (1923) considered that in the Peracarida the vitellophags take no part in the development of the mid-gut, and represent an extreme stage of a series showing the yolk cells taking an increasingly small part in its formation (p. 178). In view of the above discussion this unqualified generalisation cannot be accepted. Sollaud further suggests that the mid-gut formation of *Astacus* should not be regarded as a filtration process. He suggests that "le vitellus filtre peu à peu entre les éléments de l'archenteron et reste tout entier extérieur à eux," and, further, that the secondary yolk pyramids represent portions of the yolk divided by zones of influence of the peripheral endodermal energids. This conception is based on his interpretation of the development of the Palæmoninæ. Here he describes the vitellophags, once they have penetrated into the yolk, as consisting of a nucleus surrounded by irregular cytoplasmic expansions; and the "secondary" vitellophags which later form the endoderm as each delimiting round it "un territoire d'influence (balles ou sphères vitellines)" (p. 183, and Plate 3, fig. 23, and text-fig. 10, 2–3); and again (p. 61), referring to the secondary yolk pyramids, he describes the vitellophags as being external and separate from the yolk segments, the latter not being comparable with cell limits. From his figures his fixation does not seem to be so good as that obtained for *Hemimysis*. A comparison with this form at once suggests that Sollaud failed to observe the true cell limits of the yolk cells, and that his yolk spheres and contained nuclei and protoplasm are in reality the yolk cells themselves, the thin protoplasmic cell boundaries outside the large yolk vacuole being unnoticed or broken down. In *Hemimysis*, after it has left the vitelline membrane, it is often difficult to observe the entire cell boundaries of the yolk cells, which are very delicate and easily displaced; but their presence round the yolk pyramids is unquestionable in view of the complete developmental series of stages examined. The vitellophags of *Hemimysis* resemble the endoderm cells of *Astacus* in every detail of structure and in the formation of yolk pyramids, and only differ in that those of *Astacus* are at first united as a continuous layer while those of *Hemimysis* are not. Thus Sollaud's evidence by comparison of the Palæmoninæ with *Astacus* does not warrant the supposition that secondary yolk pyramids so carefully described by Reichenbach are not in reality intracellular. It is possible that during gastrulation some yolk does pass between the endodermal cells as in other forms, but there is little to suggest that most of the yolk is not absorbed directly by these cells.

The *mesoderm* in Peracaridan embryos has long been recognised to consist of two portions. That lying in the naupliar region of the body is quite irregular, while the metanaupliar part comprises mesodermal teloblasts and their rows of descendants. These two parts are seen in the Decapoda (Sollaud), but the anterior limit of the teloblastic mesoderm lies behind the maxillary instead of the mandibular segment.

The development of the cœlomic cavities in *Hemimysis* in all segments except those of the antennules, mandibles and maxillules must be considered as a primitive feature, yet the formation of the mesoderm as whole is specialised in that it develops in three ways. The primitive method of mesoderm formation in yolky Arthropod embryos is probably that shown by *Peripatus* and *Scolopendra*, where the mesoderm arises by immigration from the blastoporal region, and spreads forwards as two bands of irregular cells which later break up into somites. This method is still shown by *Hemimysis* in the formation of the head mesoderm bands, but cœlomic cavities do not appear in this region, with the exception of the antennal gland end sac. In the trunk, although cœlomic cavities still appear, specialisation has taken place in the formation of teloblasts and the determinate formation of segmental rudiments from their products. In the preantennulary segment the cœlomic cavity is still formed, but the mesoderm itself arises directly from the germinal disk outside the blastoporal area. This change from the primitive condition where these somites are the first to be formed from the mesodermal bands is no more remarkable than the change to a teloblastic mesoderm formation in the trunk.

The occurrence of mesodermal teloblasts in the Arthropoda thus cannot be compared directly with those of the Annelida, as has been maintained by NUSBAUM (1898) and BERGH (1892). It is simply a secondary development from the primitive method of mesoderm formation that has occurred in the Decapoda and Peracarida and possibly in other Malacostraca, and does not represent in the Crustacea the primitive condition found in the Annelida.

The formation and development of the *naupliar mesoderm* has not been satisfactorily traced in any Peracaridan other than *Hemimysis*, and the preantennulary mesoderm, if it has been seen, has been confused with other structures. BERGH (1892) observed the head mesoderm bands in *Mysis* and considered that they probably arose *in situ* from the germinal disk, but did not neglect the possibility that their constituent parts might have wandered forwards from the post-naupliar mesoderm (p. 508). WAGNER considered all the mesoderm in *Neomysis* to arise exclusively from the hinder part of the germinal disk, but he failed to interpret the preantennulary mesoderm as such (see below). He found teloblasts forming mesoderm of the mandibular and more posterior segments, and considered the antennal mesoderm to arise from the same place as the teloblasts and shift forwards at the sides towards the antennæ. The accuracy of the former statement is doubtful, but the latter is in agreement with *Hemimysis*. NUSBAUM (1898) found the head mesoderm in *Cymothoa* arising with the teloblasts from the blastoporal region, as in *Hemimysis*. In *Ligia* and *Oniscus* he could not distinguish a sharp boundary between naupliar and post-naupliar fields, but he considered there were two distinct mesodermal origins, one from the teloblasts and the other from an ingrowth close behind the optic rudiment anterior to the main ingrowth of the germinal disk. Possibly NUSBAUM was here observing the formation of the preantennulary mesoderm as it occurs in *Hemimysis*. As already mentioned (p. 435), the layer of cells in *Gammarus* described by BERGH as endodermal corresponds in position and appearance to the head mesoderm of other forms. In the only Decapods in which the origin of the mesoderm has been carefully determined (the Palæmoninæ, SOLLAUD), the head mesoderm arises from the " lames mesectoblastiques " and " l'aire embryonnaire " after the definitive blastopore has disappeared. The areas of head mesoderm formation correspond with those of *Hemimysis*, although mesoderm from the " lames mesectoblastiques " lies outside the ectodermal teloblasts, a fact probably correlated with the late appearance of the latter after the V-shaped germinal band has been formed (text-fig. 29). Thus there is no reason to suppose that the origin of the head mesoderm bands in other Peracarida and Decapoda differs materially from that of *Hemimysis*.

Preantennulary segmental mesoderm has not been described in any other Crustacean. That its presence has been overlooked in many Malacostraca is apparent from BERGH'S figure (1892, Plate 27, fig. 10) and from WAGNER'S work. The former shows some tissue internal to the optic rudiments in the same position as the preantennulary mesoderm in text-fig. 6 *b*. No mention is made of this in the text. WAGNER (1898) finds in *Neomysis* two groups of cells in the precise positions of the preantennulary mesoderm masses in *Hemimysis*, but interprets them as parts of the cerebral ganglia. His figures 18 and 19, Plate 1, exactly represent what is found in *Hemimysis* at a stage between that of Plate 24, figs. 22 and 23. This error in interpretation is quite understandable considering the technique used at that time and the fact that the preantennulary strands are least distinct from the nervous rudiments at this period. It is in the later stages of development that the derivations of the preantennulary mesoderm are so frequently figured just as they occur in *Hemimysis*.

In *Mysis chameleo* NUSBAUM (1887) saw the strand of tissue between the dorsal organ and the stomodæum dividing the two anterior yolk lobes. However, with the general inaccuracy which characterises this work, he considers it to arise by a downgrowth from the dorsal organ, which he supposed was mesodermal, and to form within itself the heart tube (p. 190). He clearly did not distinguish between the formation of the heart and that of the anterior aorta ; nor did he follow carefully the formation of the dorsal organ and his "plis du cœur." The latter undoubtedly is the preantennulary mesoderm forming the anterior aorta. Among the Decapoda this strand of tissue has been figured by REICHENBACH (1886), KINGSLEY (1889) and BROOKS and HERRICK (1892) lying between the anterior yolk lobes of the mid-gut, and containing in its dorsal part the anterior aorta (" ophthalmic artery " of BROOKS and HERRICK, " augenarterie " of REICHENBACH). REICHENBACH shows the artery passing downwards to the stomodæum between the gut lobes anteriorly, just as in *Hemimysis*.

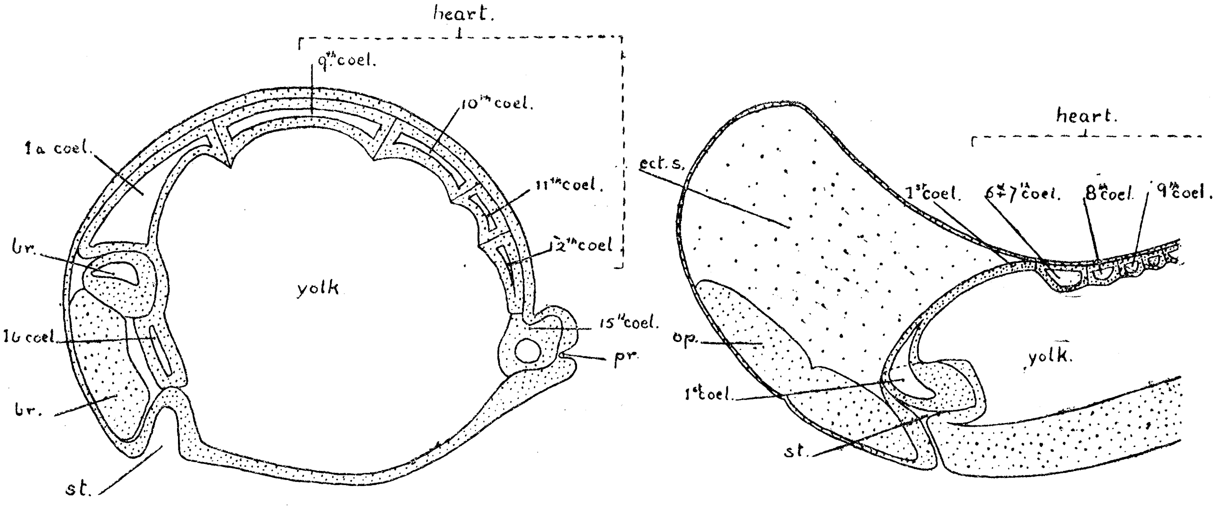
It is probable that in the Decapoda and Mysidacea, where the form of the embryo is so similar, the anterior aorta and surrounding muscles develop from homologous parts. In the Isopoda and Amphipoda no anterior yolk lobes have been shown and thus no dorso-ventral strands as in *Hemimysis*. No detailed work appears to have been done on the head mesoderm in these groups. In the Amphipoda PEREYASLAWZEWA (1888 *a* and *b*) and ROSSIISKAYA (1888, etc.) describe the heart and anterior aorta as arising separately in front of and behind the dorsal organ, the two only uniting when the dorsal organ decreases in size.

From a study of the nervous system and appendages of the Crustacea it has been established that a preantennulary segment, which must correspond to the first trunk segment of *Peripatus* and the precheliceral segment of the Arachnida is present, but no longer distinguishable in the adult. Preantennulary ganglia have been described by HOLMGREN (1916, p. 192) for the embryo of *Daphnia*. They are quite separate from the non-segmental procerebral and optic ganglia and from the median archicerebrum. In the adult *Astacus*, Isopoda and Amphipods, etc., no archicerebrum or non-segmental ganglia other than the optic lobes have been described, and the preantennulary ganglia must be represented by part or all of the protocerebral brain lobes. In the Crustacea a separation of the antennal from the rest of the preoral mesoderm has not been described ; and no transient preantennulary appendages occur. In other Arthropods the preantennulary, preantennary or first trunk segment may possess paired ganglia, cœlomic sacs and appendages, the mesoderm of this segment may be indistinguishable from that of the preoral region, or it may be separated and contain cœlomic cavities as in *Peripatus, Scolopendra, Carausius** and Spider. In other cases the preantennulary cœlomic cavities may be continuous with those of the next posterior segment as in *Limulus* (Kishinouye, 1892) and *Scorpio* (Brauer, 1895).

That the preantennulary mesoderm of *Hemimysis* represents the preantennulary somite is apparent from its situation and its later development compared with other Arthropods. Its initial position (p. 388) in front of and in series with the anterior pairs of appendages is in the region where the preantennulary somite would be expected to occur if it were developed.

The preantennulary somites of *Peripatus, Scolopendra, Limulus* and Spider lie in contact with the sides of the stomodæum. In *Peripatus* the stomodeal muscles are developed from the sides of these somites. There appear to be no formed blood vessels besides the heart, but the dorsal blood space between the first pair of somites may be comparable to the anterior aorta in *Hemimysis.* The condition here only differs from *Peripatus* in the reduced size of the somites apart from differences due to the large amount of yolk in *Hemimysis.*

The preantennulary somites in *Scolopendra* are still large, but the precheliceral somites of the Spider, which are further reduced, are extraordinarily similar to the preantennulary somites of *Hemimysis* (text-fig. 30). Each of the pair of precheliceral cœlomic cavities become divided into two portions, " one at the sides of the stomodæum (Ib. coel.) and the other below the anterior border of the semicircular groove of the brain. The



SPIDER. HEMIMYSIS.

Text-Fig. 30.—Diagram showing the cœlomic cavities in *Hemimysis* and Spider (after Kishinouye) for comparison of the preantennulary and precheliceral somites. The somites are numbered from the preantennulary and precheliceral segments backwards. *br.*, brain ; *ect.s.*, ectodermal septum ; *op.*, optic rudiment ; *pr.*, proctodæum ; *st.*, stomodæum.

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* Preantennary cœlomic sacs and appendage rudiments have been described by Weismann, 1926, for the Insect *Carausius* (see Appendix, p. 454).

former disappears soon afterwards, but the latter elongates towards the median line, and the mesodermal walls of the cavities of the two sides meeting at the median line fuse together, leaving, however, a canal between them. This canal is the aorta" (KISHINOUYE, p. 292). The cœlomic cavities at the sides of the stomodæum thus represent the "lower sacs" in *Hemimysis* which are found in this situation. The "upper strands" which grow dorsally and form the anterior aorta are comparable with the upper portions of the precheliceral somites of the Spider.

Hemimysis, then, only differs from the Spider in that the preantennulary somites do not lie against the anterior body wall, but along the ectodermal septum through the yolk in the head. The anterior aorta in other Arthropods is formed in a similar manner. In Insects it is the antennal or intercalary somites which unite to form the vessel. The adult anterior aorta of *Limulus* has been carefully described and figured by MILNE EDWARDS (1873-80), "l'artère frontal . . . elle correspond à l'artère ophthalmique des Crustacés," and its development followed by KISHINOUYE (1893). It is formed as a paired vessel lateral to the stomodæum in the first pair of somites, which are common to the cheliceral segment and the anterior part of the body. These vessels unite and communicate with the heart dorsally. According to his fig. 56, Plate 10, the aorta passes upwards through the yolk as in *Hemimysis.* The technique used was not good enough to demonstrate the presence or absence of a yolk septum, but it is possible that some such structure is used by the first pair of somites to guide them upwards to the heart. The difference in the position of the developing anterior aorta in the Spider, where it lies against the body, and in *Limulus* and *Hemimysis,* where it runs through the yolk, is probably due to the yolk remaining long and abundant in the posterior region of the body in most Arachnida, while in *Limulus* and the Crustacea it does so in the anterior region. Thus *Hemimysis* exhibits a typical pair of preantennulary somites which form muscles to the stomodæum and the anterior aorta as in other Arthropods.

The discovery of the preantennulary somites in *Hemimysis* has a direct bearing on the interpretation of the "dorsal cœlomic sac" described by ALLEN (1893) for *Palæmon, Palæmonetes* and *Crangon.* This sac "lies upon the nephroperitoneal sac and the front end of the ovary. . . . The cephalic aorta lies within the dorsal sac. The dorsal sac is formed as a hollowing out in masses of mesoderm which lie on either side of the cephalic aorta. Two lateral cavities are thus formed, which increase in size and unite below the dorsal aorta" (p. 422). It is probable that the two lateral cavities forming the dorsal sac are the cavities of the preantennulary somites, which enlarge and persist in the adult instead of becoming obliterated as in *Hemimysis.* Their position lateral to the posterior aorta corresponds with that of the preantennulary somites of *Hemimysis,* although the cavities in the latter do not extend far along the aorta in a posterior direction.

Many Arthropoda show traces in development of a primitive preoral region in front of the first somite. This region may have mesoderm of its own, but it never has a cœlomic cavity, although the cavities of the first pair of somites may invade it. It is seen typically in *Scolopendra.* Here, when the cœlomic sacs have been formed, some median mesoderm remains anteriorly, which supplies the labrum and clypeus. In *Hemimysis* the loose mesoderm from the head bands supplies the naupliar appendages and labrum and the rest of the head mesoderm. Thus any mesoderm corresponding to a primitive preoral region is not distinguishable as a separate entity. However, it arises from the blastoporal area and mesoderm bands in the same way as it does in *Scolopendra.*

In the *trunk region* the mesodermal teloblasts are usually eight in number in the Mysids (BERGH, 1892, WAGNER, 1898) and the Isopods (McMURRICH, 1895), but NUSBAUM records ten for *Ligia* and *Oniscus* (1898). Among the Amphipods mesodermal teloblasts have been observed only by BERGH (1892). He found three or four pairs of such cells in *Gammarus pulex* and figures them clearly. It is thus probable that in spite of the absence of ectodermal teloblasts in this group the post-naupliar mesoderm is formed just as in the Isopods and Mysids.

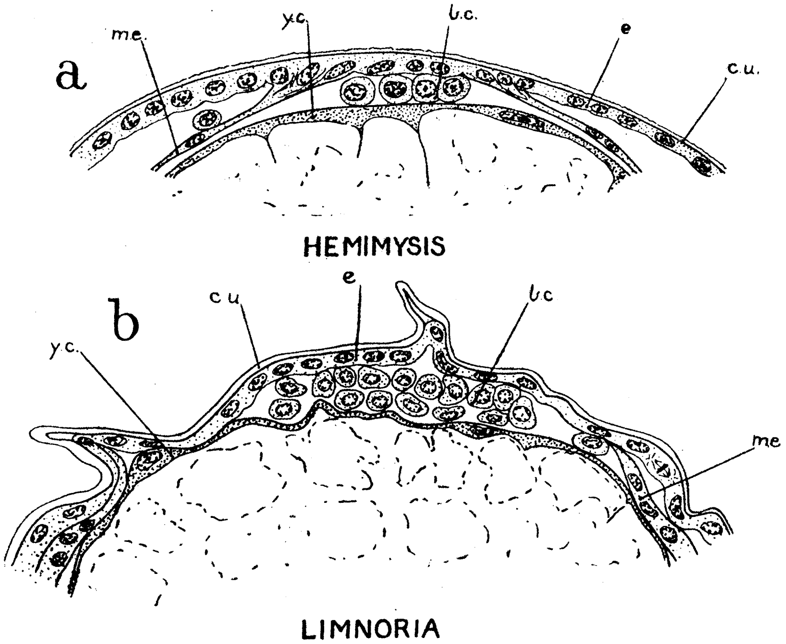
Hemimysis, as other Mysids, shows the longitudinal rows of mesodermal cells at equal distances from one another, and not arranged in two lateral groups of three rows and a median group of two, as found by McMURRICH in the Isopoda. The latter condition must be considered as a specialisation of the Mysid type, each group of mesoderm cells giving rise to different parts of the musculature and connective tissue.

WAGNER (1898) observed a few of the anterior cœlomic sacs before subdivision of the somites in *Neomysis vulgaris*. In later stages he did not find a cavity in the dorsal mesoderm, and considered the gut mesoderm to arise independently of it. These results were doubtless due to his inferior fixation, as also was his conception of heart formation by the union of originally scattered cells. NUSBAUM'S work (1889) on heart and pericardium formation is of little value, since he failed to distinguish the anterior aorta from the heart, and described the former when he thought he was dealing with the heart itself. He thus found the heart developing from behind forwards, the pericardial floor being a final outgrowth from the heart and later lost in the adult.

The little work that has been done on somite and heart formation in other Malacostraca is not at all critical, and no early cœlomic sacs have been described. That they have merely been overlooked is probable, since the Isopod *Limnoria* when fixed with formol bichromate shows cœlomic sacs from the maxillary segment backwards just as in *Hemimysis* ; and in a figure of the embryonic heart of *Astacus* (FULINSKI, 1908, text-fig. 3, p. 25) is shown a slit-like space in the pericardial floor in the typical position of the cœlomic space, although no mention is made of this in the text. Sections of a small adult *Anaspides* in Prof. H. G. CANNON'S possession show similar spaces in the pericardial floor through some segments.

The frequent reports of the initial scattered condition of the mesoderm cells previous to heart formation in the Isopods (NUSBAUM, 1886), Amphipods (PEREASLAWZEWA, 1888*a*, etc.), and in *Astacus* has probably been due to confusion between the free blood corpuscles and the somites themselves. Blood corpuscles have been variously described in the Arthropods as arising from yolk cells or from mesoderm. Their origin in *Hemimysis* is unquestionably from the upper ends of the somites, just as BRAUER described it in

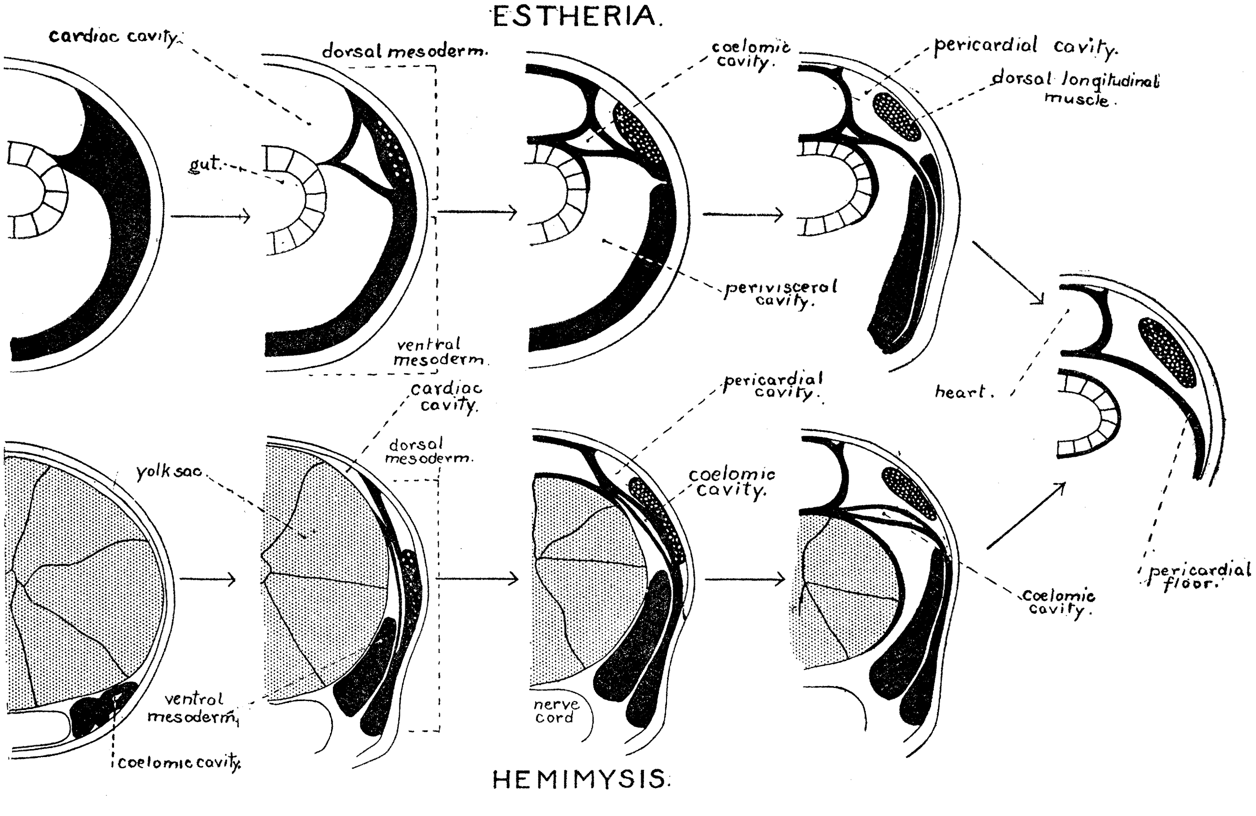
Euscorpius. These free cells always precede the somites in spreading dorsally, and in *Limnoria* they are relatively much larger and more numerous than in *Hemimysis* (text-fig. 31). Since those corpuscles lie in the cardiac and pericardial spaces before the walls of the heart are formed, their identification as cardioblasts or loose constituents of the somites themselves is understandable.



Text-Fig. 31.—Transverse sections of *Hemimysis* and *Limnoria* showing the blood corpuscles in the dorsal hæmocœlic space before the dorsal mesoderm has formed the heart walls. *b.c.*, blood corpuscles; *c.u.*, cuticle; *e.*, ectoderm; *m.e.*, dorsal mesoderm; *y.c.*, yolk cells.

The formation of segments in a regular order from before backwards in *Hemimysis* is certainly more primitive than that in many Decapod embryos of a similar shape, where the abdomen is precociously developed and the posterior thoracic region retarded. In the late expansion and final shrinkage of the cœlomic spaces, however, the thorax and abdomen behave as two separate regions.

The later development of the mesoderm of *Hemimysis* closely resembles that of *Estheria*, but differs from it in certain respects correlated with the abundant yolk present in *Hemimysis* and absent in *Estheria*. Thus in *Hemimysis* the yolk sac at first lies close against the ectoderm and restricts the mesoderm to the ventral side of the body, whereas in *Estheria* the mesoderm early fills the large space between the mid-gut and the ectoderm all round the body (text-fig. 32). The mesoderm in *Hemimysis* differentiates as it slowly grows round the yolk sac to reach the dorsal side of the embryo. The dorsal and ventral parts of the mesoderm blocks are separated ventrally, and the dorsal mesoderm with its cœlomic cavity and developing longitudinal muscle shifts gradually upwards. In *Estheria*, however, the dorsal mesoderm and its products are differentiated *in situ.* Cœlomic sacs in both are found in the maxillary segment backwards, but in *Hemimysis* they are present all the way down the body, whereas in *Estheria* CANNON only observed cavities in the first few blocks of mesoderm in the series at his disposal. However, in correspondence, Prof. CANNON suggested that in a more complete series of *Estheria* further cavities might be observed. The cœlomic cavities in *Hemimysis* are much flattened by the large yolk sac. They are absent from the tip of the somites on account of the presence of the yolk sac and developing pericardium on either side. *Chirocephalus* shows a condition more like that of *Hemimysis*, the cœlomic sac being early compressed by the developing pericardium. Owing to the early differentiation of the dorsal and ventral mesoderm in *Hemimysis*, the lateral pericardial floor is formed from the dorsal mesoderm as it grows upward. In *Estheria* the lateral pericardial floor arises later as a downgrowth from the dorsal mesoderm (text-fig. 32).



TEXT-FIG. 32.—Diagrams comparing the methods of heart formation in *Hemimysis* and in *Estheria*.

In *Chirocephalus* as well as in *Hemimysis* the roof of the dorsal vessel is well formed first in the anterior region of the body and the floor formed first in the posterior part, leaving a transient intervening “ cardiac plug.” This occlusion seems to be formed in a similar mechanical manner in both. It lies in the region of the genital segment in *Chirocephalus* and between thorax and abdomen in *Hemimysis*. These regions may correspond functionally but are not segmentally homologous.

The heart extends into the maxillary segment anteriorly in *Hemimysis* as in *Estheria*, a conclusion also reached by ALLEN for *Palæmonetes*.

Hemimysis resembles the development of most yolky Arthropodan embryos in the early formation of a series of cœlomic cavities in the ventro-lateral mesoderm blocks, these somites subsequently growing round the yolk. The cavities in *Hemimysis* are much smaller in size, and the heart grooves do not appear until the mesoderm has reached the dorsal side. The heart grooves in forms such as *Euscorpius* and the cardioblasts of *Scolopendra* and *Donacia* appear when the somites are still in the ventro-lateral position. In *Hemimysis* the cœlomic sacs reach the dorsal side and persist until the end of embryonic life, as in most Arthropods, although muscle rudiments are differentiated early.

In *Peripatus* and some Arthropods such as *Scolopendra* practically all segments participate in the formation of the dorsal vessel. Usually, however, a few somites behind the first pair do not do so, and thus the anterior aorta formed by the first pair of somites (or by the antennal or intercalary pair in Insects) has to grow backwards through several segments to reach the heart, as in *Limulus*, *Donacia* and Spider and also in *Hemimysis*. The dorsal vessel in *Hemimysis* is formed from before backwards, as in most Arthropoda, but in *Limulus* (KINGSLEY, 1893) it develops from behind forward and in *Donacia* from the two ends of the body towards the middle. In *Hemimysis* a smaller part of the dorsal vessel forms the heart than in most Arthropoda, the dorsal aorta being correspondingly longer. The roof of the dorsal vessel in the Arthropoda is usually formed before the floor, as in *Estheria*, *Scolopendra*, *Euscorpius*, *Carausius* and *Agelena*, but in *Donacia* the floor is formed first posteriorly, as in *Hemimysis* and *Chirocephalus*.

The slit-like remnants of the cœlomic sacs in the horizontal part of the pericardial floor exactly resemble those found in the later stages of *Scolopendra*, *Limulus* and *Euscorpius*. The frequent union of the first pair of cavities below the heart in *Hemimysis* is reminiscent of a similar union which occurs in all segments below the heart in *Euscorpius*. In no other Arthropod as far as I am aware has a later non-functional expansion of the cœlomic spaces been described as occurs in *Hemimysis*.

Persistent cœlomic spaces in adult Crustacea have not been noticed with the exception of the " dorsal sac " of *Palæmonetes* by ALLEN. The large preantennulary space between the stomach and the endoskeleton is certainly present in adult Euphausids, some Decapod zœæ, *Anaspides* and probably in other forms. This space and also those in the lateral parts of the pericardial floor are never in open communication with the first-formed cœlomic cavities. They appear somewhat later than the first-formed cœlomic cavities in regions where the latter would certainly be were they larger in size.

The presence of a *seventh abdominal segment* in a Eumalacostracan has never clearly been shown before. In the Isopod *Sphæroma* two ganglia are said to coalesce in the embryo forming the sixth abdominal ganglion, and in the Mysids *Lophogaster* and

Gnathophausia the long sixth abdominal segment is divided by a transverse groove in about the middle of its length. In *Hemimysis* the seventh segment is represented in the embryo by a pair of mesoblastic somites and a ganglion, although in the adult it is completely fused with the sixth segment.

Respecting *Gnathophausia*, CALMAN (1909) states "it is possible that we have here two somites in progress of coalescence, and that seven somites are represented in the abdomen of the Mysidacea as in the Leptostraca."

From a comparison of the musculature of *Hemimysis* and *Lophogaster*, there is reason to believe that the groove across the "sixth" abdominal segment of *Lophogaster* represents the junction between a sixth and seventh segment.

The terminal parts of the abdomen in *Hemimysis* and *Nebalia* are compared in text-figs. 20 *e* and *f*. In the embryo *Nebalia* the sixth and seventh ganglia are separate, but the seventh later fuses with the sixth (CLAUS, 1888). The terminal segment or telson bears the anus and a large caudal furca, and the sixth abdominal appendages are small. In *Hemimysis* fusion of the sixth and seventh segments is carried much farther. The region behind the seventh segment represents the telson, in front of which all new segments have been formed in the embryo. The telson bears the anus and a caudal furca, but the latter is lost at the first ecdysis. Finally, the telson grows backwards above the anus and the uropods enlarge. Thus the segmentation of *Nebalia* and *Hemimysis* is directly comparable, *Hemimysis* showing a greater concentration of the posterior parts. The main difference lies in the fact that in *Nebalia* the caudal furca is large, while in *Hemimysis* the uropods are large and the caudal furca embryonic, the telson forming a median outgrowth. However, it is not yet clear whether the caudal furca of *Hemimysis* embryo is the same as that of the adult *Nebalia*.

CLAUS (1872) first suggested that the last two segments and the caudal furca of *Nebalia* represented the telson of the Malacostraca, pointing out that a provisional caudal furca is present in the protozoa of *Sergestes* and *Penæus* (1884). His comparison is not quite accurate, but it is probable that the sixth and seventh abdominal segments of *Nebalia* are represented by the "sixth" abdominal segment in the Malacostraca, the telson remaining directly comparable in both groups.

CALMAN (1909, p. 167) has already drawn attention to the groove across the sixth abdominal segment in certain fossil Syncarida, recalling that of certain Mysidacea.

That *Nebalia* stands closely related to the Mysidacea is apparent from the above. CANNON (1927) has recently studied the mouth parts and feeding mechanism of *Nebalia* and has come to the same conclusion. Another point of resemblance is the change of shape passed through by the embryos.

Whether the caudal furca of *Nebalia* and *Hemimysis* is homologous with that of the adults of the lower Crustacea is uncertain. The development of *Lepidocaris* (SCOURFIELD, 1926) seems to show that the caudal furca of the adult *Lepidocaris*, and probably other Branchiopoda and Copepoda, represents a pair of true appendages on the telson (CALMAN, 1926). In *Hemimysis* the furca is purely ectodermal and does not appear to be a pair of appendages, and the development of the large jointed furca of *Nebalia* is not known.

The paired rudiments of the *gonads* are, as in *Estheria*, differentiated early and are subsequently overgrown by the dorsal mesoderm. The cavities of the gonads are thus not in direct communication with the primary cœlomic spaces, and neither are the cavities of the gonoducts, which are formed from the ventral walls of the dorsal cœlomic sacs. The small size of the cœlomic cavity probably made it impossible for the genital cells to wander directly into them as in some other Arthropods. This may also account for the duct not being formed directly from the cœlomic sacs as it is in the other forms.

WAGNER (1898) correctly observed for *Neomysis* the formation of the V-shaped *endoskeletal plate* from the ectoderm, but he was not concerned with the muscles attached to it. The paired intuckings he described in front of the mandibles appear from his figures to be those arising in front of the antennæ. A similar V-shaped endoskeletal plate and two pairs of tubes are also found in the head of *Anaspides*, of the Euphausid *Nyctiphanes*, and of the prawn *Gennadus* and probably in other forms. The plate is broadly comparable with the endophragmal system of the Crayfish (HUXLEY, 1881), and other Decapods, only it is restricted to one segment and remains hollow. WAGNER also observed the growing mandibular tendon, but his fixation was bad and he considered it to be formed by the accumulation of scattered mesoderm cells.

HUMPERDINK (1924) concluded from work on *Polyphemus* that endoskeletal structures were not nucleated or protoplasmic tissues but cell products, and that the skeleton was formed by ectodermal or mesodermal cells. In *Hemimysis* all the skeleton is ectodermal. The apodemal parts remain cellular throughout life, but other endoskeletal structures lose some or all of their nuclei in the adult. The embryonic nucleated condition of the mandibular tendon in *Chirocephalus* has been described by CANNON (1927, p. 414) and its origin from the basement membrane of the mid-ventral mandibular ectoderm. The tendon in *Hemimysis*, although arising in a slightly different manner from the ectoderm, results in a similar structure.

The series of ectodermal bars in *Hemimysis* is probably a derivative of an Annelid condition, not all these structures being now used for muscle insertions. In the Polychæte *Ophyrotrocha* there are paired transverse muscles from the sides of the body at the posterior edge of the parapodia, which pass inwards in the intersegmental regions. These muscles are attached to a mid-ventral intersegmental intucking of ectoderm between the nerve cords. This intucking is most clearly seen in the developing posterior segments of a small individual. These intuckings resemble those found mid-ventrally in *Hemimysis* between the developing nerve cords. The transverse muscles of *Ophyrotrocha* roughly correspond in *Hemimysis* with the adductor muscles as found in the mandibular, maxillulary and maxillary segments and with the internal connective muscles of other segments.

Mesodermal muscle rudiments appear to depend very generally on ectodermal structures to direct their growth and give them final attachment. The transverse ectodermal bars in each segment are used in this manner. Similarly, the ectodermal yolk septum directs the upper strands of the preantennulary mesoderm to reach the dorsal side of the body. In *Chirocephalus* the connective muscles from the ventral mesoderm grow along the ectodermal dorso-ventral muscles to the skeletal plate formed by the latter (CANNON, 1927, p. 409). In *Hemimysis* the connective muscles do not do this, since the ventral mesoderm lies against the ectoderm and above the ectodermal muscles, but simply grow straight out to the lateral body wall.

The function of the endoskeleton may be threefold at different times. It may be skeletal, serving mostly for support or muscle attachment. It may become muscular, as first pointed out by CANNON (1927*a*, p. 413). Thirdly, it may act as a temporary scaffold for the directing and supporting of developing structures.

The *musculature* of a typical trunk segment in *Hemimysis* differs somewhat from that of a Branchiopod as described by CANNON for *Chirocephalus* and *Estheria* (1924 and 1927*a*). The dorsal and ventral longitudinal muscles are similar. The connective muscles are much more complex in *Hemimysis*, where they form the bulk of the posterior trunk musculature, than they are in *Chirocephalus*. In *Hemimysis* the nerve cords lie close together and occupy the whole of the ventral side of the body between the limbs. Possibly the ectodermal flexors of *Hemimysis* are comparable with the ectodermal dorso-ventrals of *Chirocephalus*, their ventral insertions having shifted to the sides of the nerve cord, thus reaching the angle between the limb and the body wall. However, the extensor muscles of *Hemimysis* are ectodermal while those of *Estheria* are mesodermal. There are no muscles in *Hemimysis* which can be considered with certainty to represent the supra- and sub-neural lateral muscles of the Branchiopoda. The anterior and posterior lateral muscles in *Hemimysis* are the only muscles attached directly to the ventral ectoderm, and in the first thoracic segment the posterior lateral muscle extends right across the limb base to its outer side, just as the sub-neural muscle does in *Estheria*. However, the lateral muscles of *Hemimysis* are attached to the ventral body wall intersegmentally and not in the middle of a segment as in the Branchiopoda. Then the limb muscle from the bifurcation of the basipodite to the inner angle of the limb (text-figs. 25 *a* and *b*) may, perhaps, represent the supra-neural lateral muscle of *Estheria* (see CANNON, 1924, text-fig. 4, p. 406), its mid-ventral attachment having slipped sideways to the base of the limb.

Ectodermal muscles are formed from ectodermal infoldings and intuckings just as in *Chirocephalus*. The tendo- and myo-fibrils of both mesodermal and ectodermal muscles in *Hemimysis* are differentiated from the continuous unstriated fibrils which first appear in the muscle rudiment, just as CANNON described for the ectodermal muscles of *Chirocephalus* (1927*a*). In a mesodermal muscle the unstriated continuous fibrils from the cuticle through the muscle become striated in the muscle itself, leaving unstriated tendo fibrillæ through the hypodermis; or else they become striated all along to the cuticle.

Here, therefore, the myofibrils of a muscle ending directly against the cuticle cannot be considered as a criterion of an ectodermal muscle as CANNON suggested (1927*a*, p. 413). The myofibrils of the stomodæal and proctodæal dilators of *Hemimysis* and *Chirocephalus* end against the cuticle, but the muscles are mesodermal in origin in *Hemimysis* and ectodermal in *Chirocephalus*.

WAGNER shortly described the development of the *antennal gland* of *Neomysis* from the antennal mesoderm. The adult gland is of the coiled type with a narrow duct, and this is derived from an initial U-shaped condition very like *Hemimysis*, only even at this state the duct is narrower and less sac-like.

The ectodermal or mesodermal origin of the antennal and maxillary glands in the Malacostraca has been a much-debated question. In order to determine this in any one case, adequate fixation and a continuous series of stages starting before the earliest appearance of the gland are essential. These conditions have never before been fulfilled. The views put forward have been summarised by WOODLAND (1913), and the majority of workers, including WOODLAND, are of the opinion that the duct is ectodermal in origin. The earliest described stage of the duct is roughly comparable with text-fig. 21 *b*, where it is a simple tube connected with the ectoderm, as shown for the maxillary gland of Squilla by WOODLAND (1913), or where the duct rudiment is a solid rod of many cells as in the antennal glands of *Homarus* (WAITE, 1889) and *Astacus* (REICHENBACH, 1886). Such a stage is in no way a criterion for an ectodermal duct, but it is a transitory condition in the development of a mesodermal duct, whatever the final complexity of the duct may be. The whole gland was found to be mesodermal by KINGSLEY (1889) for *Crangon* and by ROBINSON (1906) for *Nebalia*. WOODLAND (p. 421) criticises the latter, and considers that "the initial clump of cells may just as well be considered ectodermal as mesodermal." In *Hemimysis* the initial cells are undoubtedly mesodermal.

The evidence put forward for the origin of the end sac directly from an ectodermal duct is also unsatisfactory, as no series of early stages has been described. The definite statements of WAITE and others of the end sac arising in a distinct mass of mesoderm are in agreement with *Hemimysis*.

The Mysid *Lophogaster* possesses antennal and maxillary glands of similar adult structure, and there is no reason to suppose that they are not both developed in a similar manner. It is probable that all the larger antennal and maxillary glands in the Malacostraca will prove to develop essentially as in *Hemimysis*, the duct and end sac being mesodermal with an ectodermal exit tube.

If the early subdivision of the mesoderm in the antennal segment be compared with that in a trunk segment, the two are seen to be very similar, although the antennal mesoderm is less compact (compare Plate 25, figs. 28 and 29, with Plate 22, fig. 14). In position the end-sac rudiment corresponds with the "dorsal" mesoderm, leaving corresponding limb mesoderm in both. This similarity may be a fortuitous one due to the position of the adult antennal gland; but if it is not, it does suggest that the end sac and its cavity really represent the whole of the dorsal cœlomic sac of this segment. The duct rudiment may then represent all or part of the " ventral " mesoderm.

The *paired and median " dorsal " organs* of a Mysid were first rightly distinguished by WAGNER (1898), and their occurrence in other Peracarida has been summarised by HEIDECKE (1904) for the Amphipoda and by NUSBAUM and SCHREIBER (1898). The latter describe these organs in *Hemimysis lamornæ* among other types, and noticed the formation of the yolk septum. This they regard as part of the dorsal organ formed by a dorsal intucking. They consider that phagocytosis by vitellophags aids the degeneration of both dorso-lateral and median dorsal organs, and that the dorso-lateral organs of *M. chameleo,* but not of *Hemimysis lamornæ,* are glandular. The primary function of both organs they suppose to be the absorption of excess ectoderm, the secretory activity being secondary.

NUSBAUM and SCHREIBER's statement that the dorso-lateral organs are non-glandular in *Hemimysis* is incorrect. In neither dorsal nor dorso-lateral organs were vitellophags observed aiding degeneration by phagocytosis, as claimed by NUSBAUM and SCHREIBER. There is no need to discuss the extraordinary speculations and statements made by NUSBAUM (for *M. chameleo,* 1887) concerning the dorso-lateral organs, since he does not again refer to these remarks in 1898. It may, however, be mentioned that his idea of these organs secreting the embryonic membrane is entirely unsupported. This membrane is simply the first-formed cuticle of the body which is shed after the embryo leaves the vitelline membrane.

NUSBAUM and SCHREIBER describe in *Hemimysis lamornæ* a pair of accessory dorsal organs lying between the median and dorso-lateral organs. From their fig. 3 it is more likely that they have here simply the bodies of the yolk cells lying close against the ectoderm, their fixation not enabling them to distinguish the thin ectoderm with its cuticle from the underlying tissues.

The median dorsal organ occurs in the Decapoda (SOLLAUD, 1923) as well as in the Peracarida. It is usually described as a seat of cellular breakdown, and any relation to the yolk septum and developing preantennulary somites has not been noticed. This relationship is probably a secondary development, and it is also probable that a similar state of affairs will be found to occur in other Malacostraca developing on the same plan as *Hemimysis.*

Summary.

(1) No cleavage furrows are formed, the blastomeres rising through the yolk to form a germinal disk.

(2) External differentiation of the germ layers and genital rudiment takes place on the disk prior to gastrulation. Mesoderm is formed anterior to endoderm.

(3) Gastrulation is effected by immigration of cells from a blastoporal area. The

anterior lip of the blastopore grows backwards across this area and forms the trunk region between the mandibles and telson.

(4) The genital rudiment passes inwards first from the germinal disk, and moves in front of the blastoporal area.

(5) A transverse row of fifteen ectodermal teloblasts is situated in the anterior lip of the blastopore. They divide simultaneously, forming rows of cells which become the ventral ectoderm of the trunk region. The ectoderm of the naupliar segments and the telson and dorsal side of the trunk is formed from the rest of the extrablastoporal ectoderm.

(6) Mesoderm is formed in three ways: (*a*) Behind the ectodermal teloblasts eight cells pass inwards and form a row of mesodermal teloblasts. They lie internal to the ectodermal teloblasts and divide synchronously with them. Each transverse row of eight mesoderm descendants forms the mesoderm of one trunk segment between the mandibles and telson. (*b*) Small cells immigrate inwards from the blastoporal area behind the mesodermal teloblasts. These pass forwards on either side of the genital rudiment and form two irregular head bands of mesoderm extending through the naupliar segments. (*c*) Preantennulary mesoderm passes in on either side from the germinal disk between the optic rudiments and the antennules.

(7) Cells on the blastoporal area behind the mesoderm absorb yolk. They pass inwards and spread over the yolk below the germinal disk as yolk cells or vitellophags. Later they completely surround the yolk and absorb most of it. The yolk sac so formed becomes the adult mid-gut, the yolk cells directly transforming to the adult endodermal epithelium. This transition takes place first opposite the stomodæum and proctodæum, forming the anterior and posterior endodermal plates.

(8) The liver is formed by a paired rudiment, which arises from parts of the head mesodermal bands in the mandibular segment.

(9) The stomodæum first appears just anterior to the antennæ. The proctodæal intucking is formed behind the anterior lip of the blastopore, but only after all the trunk segments have appeared.

(10) A preantennulary and a seventh abdominal segment are present in the embryo.

(11) Paired mesodermal somites are formed ventro-laterally in all segments. The preantennulary somites arise separately. The head bands of mesoderm become divided intersegmentally, and the rows of teloblastic mesoderm each give paired mesodermal blocks in the eight thoracic and seven abdominal segments. Somite formation in the trunk takes place steadily from before backwards.

(12) Cœlomic cavities appear in all mesodermal somites except those of the antennulary mandibular and maxillulary segments.

(13) The preantennulary somites grow backwards through the antennulary segment and invest the stomodæum. Their anterior ends then grow upwards along a median vertical " yolk septum " and reach the dorsal organ. The latter draws the yolk septum and preantennulary strands backwards to the heart. The anterior aorta is formed between

these strands, just as in *Limulus* and Spider. Much of the stomach musculature is formed by the preantennulary mesoderm. The cœlomic cavities lie on either side of the stomodæum and become obliterated. Another pair of cœlomic spaces is formed later in this mesoderm. These unite between the stomach and mandibular tendon and persist in the adult.

(14) The trunk mesoderm in the maxillary, thoracic and first six abdominal segments divides into dorsal, ventral and limb portions. Cœlomic cavities appear in the dorsal mesoderm, which then grows upwards round the yolk sac to reach the dorsal side of the body. The maxillary and first thoracic cœlomic sacs fuse on either side. The formation of a dorsal blood vessel and longitudinal muscle closely resembles that in *Estheria*, the differences being due to the large yolk sac present in *Hemimysis*. When the dorsal vessel is formed the cœlomic sacs expand, but they do so from the posterior thoracic and posterior abdominal segments forwards through each region. Finally, the sacs are obliterated from before backwards in each region. In the thorax, cœlomic spaces appear in the lateral bases of the pericardial floor and persist in the adult.

(15) The heart is formed from the dorsal vessel in the maxillary to eighth thoracic segments. In the abdomen the pericardial floor degenerates leaving the posterior aorta free. At the junction of the thorax and abdomen a transitory cardiac plug is formed much as in the genital segment of *Chirocephalus*. The sternal and hepatic arteries arise as out-growths from the heart tube and both are at first paired.

(16) The growth of the seventh abdominal mesoderm is described. It forms the end of the posterior aorta and has a pair of transitory cœlomic spaces. It gives rise to the dorsal and ventral longitudinal muscles and other muscles of the seventh abdominal segment.

(17) Blood corpuscles arise from the dorsal edges of the mesodermal somites.

(18) The development of the musculature of a typical trunk segment is described and compared with that of *Chirocephalus* and *Estheria*. Mesodermal longitudinal muscles and external and internal connective muscles are formed from the ventral mesoderm, and ectodermal extensor and flexor limb muscles from the intersegmental furrows.

(19) The larger mesodermal muscles associated with the endoskeleton are described. The œsophageal and proctodæal dilator muscles are mesodermal. A few other muscles associated with the carapace and endoskeleton are ectodermal in origin.

(20) The larger constituents of the endoskeleton are entirely ectodermal. The apodemal skeleton consists of a horizontal V-shaped plate in the maxillulary region; and paired hollow intuckings, the larger of these being in the antennal, mandibular and sixth abdominal segments. All these structures remain attached to the ectoderm, and the cuticle and hypodermis persist.

(21) Intersegmental ectodermal bars are formed from mid-ventral and lateral intuckings. Each horizontal bar shifts backwards into the segment behind it and loses connection with the ectoderm. Mesoderm then grows along these bars, which thus form tendons between the adductor muscles of the mandibles, maxillules and maxillæ and

between the internal connective muscles of other segments. The bars in the adult lose their nuclei.

(22) A ganglion is formed in the seventh abdominal segment, which later fuses with that of the sixth.

(23) The sixth abdominal segment becomes drawn out below the seventh so that the uropods become terminal. The adult "sixth" abdominal segment represents the fused sixth and seventh abdominal segments.

(24) The genital rudiment passes backwards into the first thoracic segment and divides, forming the primordia of the gonads, which consist of three cells on either side. The dorsal mesoderm of the first thoracic segment invests these primordia and draws them upwards round the yolk sac until they lie below the pericardial floor. The gonoducts are formed by hollowed-out thickenings from the ventral walls of the cœlomic sacs in the paricardial floor.

(25) The antennal gland end sac and duct are mesodermal in origin, the exit tube alone being ectodermal. The end sac closely resembles the dorsal mesoderm of a trunk segment.

(26) The spatial relations between the germ layers prior to gastrulation resembles that of other Malacostraca with total or partial cleavage, but differs fundamentally from the common plan shown by the lower Crustacea.

(27) The liver of *Hemimysis* is mesodermal in origin. That of the Peracarida generally has been described as endodermal, and this has led to an erroneous conception of the endodermal layer. The liver is probably always mesodermal, the true endoderm being represented by the yolk cells or vitellophags. In forms where the mid-gut is long, these yolk cells persist and form its epithelium, but when the mid-gut is short they largely degenerate, and there is then practically no endoderm in the adult. The true endoderm of the Peracarida is formed by cells growing round or wandering through the yolk, as in the Decapoda.

(28) The method of heart formation in *Hemimysis* is probably typical for yolky Malacostracan embryos. Accounts of heart formation by scattered cardioblasts are probably the result of a confusion between crowded blood corpuscles and the heart mesoderm itself.

(29) The segmentation of the abdomen in *Hemimysis* and *Nebalia* is directly comparable, greater concentration of the terminal parts having taken place in *Hemimysis*. The caudal furca in *Nebalia* is large, while the sixth appendages are small, but in *Hemimysis* the sixth appendages form the large uropods and the caudal furca is lost at the first ecdysis.

APPENDIX.

(*April*, 1928.)

While this paper is going through the press Dr. CALMAN has called my attention to the work of H. LEUZINGER, R. WIESMANN and F. E. LEHMANN on the embryology of a Stick insect,* and reference must be made to their results on the segmentation of the mesoderm in the head.

In this long and detailed account of the development of *Carausius*, R. WIESMANN describes the formation of 21 pairs of cœlomic sacs, 11 in the abdomen, 3 in the thorax and 7 in the head. Paired cœlomic sacs are formed in the mandibular, maxillulary and maxillary segments. They are at first separate from one another. The maxillary sacs are large, resembling those in the trunk, and form the anterior part of the heart tube. The maxillulary and mandibular sacs show progressive reduction.

A rudimentary pair of intercalary mesodermal somites are formed. They become double layered in the manner typical for other somites, but a vacuity is not formed. No rudiments of appendages appear on this segment.

The antennæ are at first post-oral in position and the antennal cœlomic sacs are large. From these sacs paired outgrowths finally reach the cardioblasts of the maxillary sacs, and then the inner walls of these outgrowths form the walls of the anterior aorta above the stomodæum.

At the sides of the stomodæum a transitory pair of preantennal appendages are formed, and below them a pair of rudimentary cœlomic sacs. Anteriorly these cœlomic sacs unite with the mesoderm covering the stomodæum. Later, their cavities shrink, and from their walls are formed muscles lying along the anterior part of the stomodæum. The protocerebral ganglion is usually considered to belong to this segment.

From part of the layer of mesoderm lying anterior to the stomodæum is developed a pair of "labral cœlomic sacs" below the paired labral rudiment. Posteriorly they are connected with the stomodæal mesoderm by a single layered sheet. A ganglion corresponding to these cœlomic sacs has not been demonstrated.

Both the preantennal and labral cœlomic sacs resemble those in other segments in the following points: (1) They arise from a one-layered plate of mesoderm which lies close against the ectoderm. The dorsal wall of the sacs is then formed by a thickening of the lateral edges of the mesoderm, which curl inwards; (2) each cœlomic rudiment is united anteriorly with its fellow by a median lamella; (3) the similar form of the cœlomic cavities and the epithelial nature of their walls. On these grounds WEISMANN considers that the insect head may consist of seven somites behind the acron.

The significance of the labral and preantennal somites of *Carausius* is discussed in

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* "Zur Kenntniss der Anatomie und Entwicklungsgeschichte der Stabheuschrecke *Carausius morosus* Br," 'Zool. Vergl. Anat. Inst., Univ. Zürich.' Jena, 1926, pp. xi + 414, 2 plates, 176 text-figures.

relation to the segmentation of the insect head. However, the bearing of these two somites, if somites they be, on the morphology of the Arthropoda as a whole, has not been considered. It is usually accepted that the first segment of *Peripatus* bearing the antennæ corresponds to the precheliceral somite of Arachnids, to the preantennulary somite of *Scolopendra* and Crustacea, and to the preantennal somite of Insects, and that the antennulary, antennal and mandibular somites of the Crustacea correspond with the antennal, intercalary and mandibular somites of Insects.

There is no evidence of any other somite lying between the acron and precheliceral, preantennulary or preantennal somite in any other form.

The evidence that the labral and preantennulary cœlomic sacs in *Carausius* represent two separate somites does not seem to be quite conclusive. In most Arthropoda the preantennulary or precheliceral somites form the anterior aorta, but in Insects this function is transferred backwards, to the antennal somite in *Carausius* and others, and to the intercalary somite in *Donacia*. When the first somite forms the aorta, two parts can be distinguished: (1) An upper or anterior part giving rise to the vessel itself; and (2) a lower posterior part forming muscles at the sides of the stomodæum. In *Scolopendra* the cœlomic cavities are large. In *Hemimysis* the reduced cavities extend through both parts of the somite, and in the Spider the two parts separate and a cœlomic space lies in each. The preantennulary sacs in *Carausius*, lying at the sides of the stomodæum and giving rise to stomodeal musculature, clearly resemble the lower preantennulary sacs of *Hemimysis*, Spider, etc.

Before concluding that the labral cœlomic sacs of *Carausius* are true mesodermal somites, it must be clear that they do not represent the upper anterior part of the preantennulary mesoderm, which is separated in the Spider. If the labral sacs do represent this mesoderm, their degeneracy may account for their initial separation from the preantennal sacs. However, from WIESMANN'S account the labral and preantennal cœlomic sacs are united via the stomodeal mesoderm, as are the two parts of the preantennulary mesoderm at a certain stage in *Hemimysis*.

Thus it is suggested that the labral cœlomic sacs of *Carausius* may represent the original anterior aorta-forming part of the preantennal somites. The anterior head segmentation of Insects and Crustacea would thus remain comparable. Further work on the head mesoderm of other Insects is needed before this point can be settled.

Other points raised by this paper cannot be considered in detail here. However, it may be mentioned that the division of each cœlomic sac into three portions, a dorsolateral giving rise to muscles, heart tube and gut mesoderm, a ventral part giving rudimentary cœlomoducts in some segments and limb musculature, and a median part forming the ventral longitudinal muscle, is more directly comparable with *Hemimysis* than with any other described form. Here a similar triple division takes place, but in the solid somite, and a rudimentary cœlomic space occurs only in the dorsal part. Further, similarity is seen to Crustacea in the maxillary somite resembling those of the trunk and forming the anterior part of the heart, the maxillulary somites being reduced.

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DESCRIPTION OF PLATES.

LIST OF ABBREVIATIONS USED.

a.a., anterior aorta.
a. 1, antennule.
a. 2, antenna.
b.c., blood corpuscle.
b.h., body hæmocœl.
bl., blastoporal area.
c.f., caudal furca.
c.fu., caudal furrow.
c.o.p., circular œsophageal muscles.
c.p., carapace.
c.pa., caudal papilla.
d., duct rudiment.
d.l.m., dorsal longitudinal muscle rudiment.
d.m., dorsal mesoderm.
d.m.c., cœlomic cavity in dorsal mesoderm.
E., ectodermal teloblast.
e., descendant of ectodermal teloblast.
ec., ectoderm.
e.m., ectodermal rudiment of extensor and flexor limb muscles.

en., endodermal or yolk cell.
e.s., end sac rudiment.
e.sk., median endoskeletal strut between brain and stomach.
e.t., ectodermal tendon.
ex., exit tube of antennal gland.
ex.c., exit tube chimney projecting into duct.
G., genital rudiment.
g.m., gut mesoderm.
h., heart cavity.
h.a., lateral attachment of heart wall to the ectoderm.
d.c., membrane connecting heart to dorsal longitudinal muscle.
h.f., heart floor.
h.m., head mesoderm.
l.b.r., labrum.
l.m., limb mesoderm.
l.o.m., longitudinal œsophageal muscles.
M., mesodermal teloblast.
M^1., immigrating mesodermal cell.
m., descendant of mesodermal teloblast.
m.d.b., mandible.
m.d.b.a., mandibular adductor muscle rudiment.
m.d.b.l., mandibular levator muscle rudiment.
m.d.b.m., mandibular mesoderm.
m.d.b.p., mandibular palp.
m.d.b.t., mandibular tendon.
m.d.b.v.i., ventral ectodermal connection of mandibular tendon.
m.t.h., mouth.
mx. 1 *m.*, maxillulary mesoderm.
mx. 2 *c.*, maxillary cœlomic sac.
mx. 2 *l.*, maxilla.
n.c., nerve cord.
n.g., nervous ganglion rudiment.
o.c.m., outer connective muscle rudiment.
oes., œsophagus.
oes.d., rudiment of œsophageal dilator muscle.
o.f., fold of ectoderm separating off the optic rudiments.
p., pericardium.
p.a.m., preantennulary mesoderm.
p.a.m.c., preantennulary cœlomic sac.
p.a.m.c. 2, late-formed preantennulary cœlomic cavity.
p.a.m.s., upper preantennulary strands.
p.b., base of pericardial floor.
s.d.m.r., insertion of dorsal stomach dilator muscle rudiment.
st., stomodæum.
st.d., rudiment of dilator muscle to cardiac stomach.
st.w., wall of cardiac stomach.
t., telson.

th. 1 *c.*, *th.* 2 *c.*, etc., cœlomic sacs of first, second, etc., thoracic segments.
th. 1 *en.*, endopodite of first thoracic segment.
th. 1 *ex.*, exopodite of first thoracic segment.
th. 1 *l.*, *th.* 2 *l.*, first, second, etc., thoracic limbs.
th. 1 *m.*, *th.* 2 *m.*, etc., mesoderm of first, second, etc., thoracic segments.
t.m.a., mandibular adductor muscle, ultimately independent of tendon.
v.m., ventral mesoderm.
y., yolk.
y.c., yolk cell, vitellophag or endoderm cell.

PLATE 21.

FIG. 1.—Sagittal section through a germinal disk of the same age as that in text-fig. 4 *b*. The genital rudiment is starting to pass inwards. × 570.

FIG. 2.—Sagittal section through an older disk where the genital rudiment is nearly entirely internal and the yolk cells are being formed from behind it and are passing inwards over the yolk. × 570.

FIG. 3.—Parasagittal section from the same embryo passing laterally to the genital rudiment. Endoderm and mesoderm cells are slipping in from the blastoporal area and an ectodermal teloblast is seen in the anterior lip of the blastopore and internal to it a mesodermal teloblast. Only one pair of mesodermal teloblasts are here present. × 570.

FIG. 4.—Parasagittal section of an older stage, a little younger than that of text-fig. 6 *b*. Mitotic figures are seen in the ectodermal and mesodermal teloblasts, their descendants lying anteriorly to them. The edges of the genital rudiment and a few head mesoderm cells are seen and also the beginning of the caudal furrow. × 570.

FIG. 5.—Parasagittal section showing five rows of mesodermal teloblast descendants touching the head band mesoderm anteriorly. The position of the genital rudiment in the sagittal plane is indicated by the dotted line. The caudal furrow is more marked. × 570.

FIG. 6.—Parasagittal section through an embryo with the caudal papilla reflexed forwards as in text-figs. 7 *a* and *b*. Endoderm is still being formed behind the teloblasts. The genital rudiment has shifted backwards into the first thoracic segment. Near the teloblasts the ectodermal and mesodermal descendants correspond in number, but in front of the third thoracic segment about two ectodermal and one mesodermal cell are seen in the primordium of each segment. × 570.

FIG. 7.—Transverse section through the mandibles of a similar stage to the last showing the irregular mandibular mesoderm from the head bands. × 570.

FIG. 8.—Transverse section from the same embryo through the maxillulary region showing the four maxillulary mesoderm cells of one side formed from the teloblasts. × 570.

FIG. 9.—Transverse section from the same embryo through the first thoracic segment showing the genital rudiment and the eight mesoderm cells of the first thoracic segment on either side. × 570.

PLATE 22.

FIG. 10.—Transverse section through an embryo of the same stage as in text-fig 6 *a*. Three pairs of mesodermal teloblasts are seen internal to the ectodermal teloblasts. The posterior edge of the genital rudiment and the anterior edge of the group of head mesoderm cells are cut. The latter are passing forwards internal to the mesodermal teloblasts. × 570.

FIG. 11.—Transverse section through the anterior mandibular region. The liver rudiments are just differentiated from the mandibular mesoderm and lie external to the yolk cells. × 570.

FIG. 12.—Transverse section through the mandibular segment of an older stage showing the liver rudiments united in the middle line. × 570.

FIG. 13.—Sagittal section through the stomodæum at about the same age as the last showing the median liver rudiment behind the stomodæum. Both are covered by unchanged yolk cells, the anterior endoderm plate not yet being formed. × 570.

FIG. 14.—Transverse section through the second thoracic segment in which differentiation of the mesodermal somite has begun. The dorsal mesoderm with its cœlomic cavity can be distinguished from the ventral mesoderm and limb portion. × 570.

FIG. 15.—Transverse section of an older stage in which the dorsal mesoderm has started to grow upwards. × 570.

PLATE 23.

FIG. 16.—Transverse section through the first thoracic segment of an older stage. It shows the further upgrowth of the dorsal mesoderm, and its association with the genital rudiment. The outer wall of the cœlomic sac is thickened. × 570.

FIG. 17.—Transverse section through the second thoracic segment. The first appearance of the cardiac and pericardial spaces is seen and the formation of the heart walls and mid-gut mesoderm from the dorsal mesoderm. The dorsal longitudinal muscle is differentiated from the outer wall of the cœlomic sac. Above the nerve-cord rudiment lies the ectodermal tendon. × 570.

FIG. 18.—Oblique transverse section through the sixth thoracic segment on the left and intersegment on the right. The heart tube is now completed. The cœlomic cavity lies in the pericardial floor on the left and the latter is connected to the lateral ectoderm intersegmentally on the right. The dorsal longitudinal muscle lies in the pericardium, and the outer connective muscle from the ventral mesoderm is attached to the ectoderm on the right. × 570.

FIG. 19.—Frontal section at the level of the cœlomic sacs at the same stage as fig. 16. The dorsal mesoderm has united to form the continuous pericardial floor, the maxillary and first thoracic cœlomic sacs are about to unite, and the rudiment of the dorsal muscle has separated from the outer walls of the sacs. × 570.

FIG. 20.—Drawn from two contiguous sections at the intersegment between the first two thoracic segments. The ectodermal rudiment of the flexor and extensor limb muscles has been nipped off from the intersegmental fold of ectoderm, and the outer connective muscle from the ventral mesoderm has grown out above to meet the lateral body wall. The dorsal longitudinal muscle and lateral attachment of the pericardial floor are seen just above these muscles. × 570.

FIG. 21.—Section through an older intersegment. The upper attachments of both ectodermal and outer connective muscles have been carried dorsally. × 570.

PLATE 24.

FIG. 22.—Transverse section of an early V-shaped germinal disk anterior to the antennules showing the preantennulary mesoderm slipping inwards. × 465.

FIG. 23.—Transverse section of a later stage through the same region showing the preantennulary mesoderm blocks lying within the thickened ectoderm. × 465.

FIG. 24.—Transverse section through the posterior part of the antenna. The preantennulary somites lie on either side at the end of the stomodæum, and their cœlomic cavities are formed. × 465.

FIG. 25.—Transverse section just anterior to the stomodæum. The upper preantennulary strands have grown up to meet the dorsal organ, and their cœlomic cavities are restricted to their lower parts. × 465.

FIG. 26.—Transverse section through the stomodæum and investing lower preantennulary sacs. Their cœlomic cavities are reduced in size and their inner walls are forming the anterior aorta. × 570.

FIG. 27.—Transverse section of an older stage. The anterior aorta is completed and the preantennulary strands are forming muscle insertions for the dorsal stomach muscles on the wall of the stomodæum on either side. The later-formed cœlomic spaces have united below the stomodæum. The ectodermal mandibular tendon is seen attached to the mid-ventral ectoderm by the intucking which partly formed it, and laterally the mesodermal mandibular adductor muscle rudiments are attached to the tendon. × 570.

PLATE 25.

FIG. 28.—Transverse section through the antennal base, showing the differentiation of the mesodermal block into end sac, duct and limb mesoderm cells. × 640.

FIG. 29.—Older stage: the end-sac cells are forming a hollow sphere and the duct rudiment is compact and solid. × 640.

FIG. 30.—Parasagittal section through the base of the antenna, a little older than the last. Two duct cells have now pushed their way between the ectodermal cells to reach the cuticle. × 640.

FIG. 31.—Frontal section of an older stage through the base of the antenna. The duct now has developed a lumen and the ectoderm has been drawn inwards to form the exit tube. A funnel formed by the latter projects into the duct lumen. × 640.

FIG. 32.—Parasagittal section through the labrum to show the development of œsophageal and cardiac stomach dilator muscles. Four spindle-shaped mesodermal cells extend across the space between the labral and œsophageal walls. × 640.

FIG. 33.—An older stage similar to the last. The four spindle-shaped cells are now inserted in the ectoderm at either end and have become striated. × 640.

FIG. 34.—Small adult through a similar region, drawn from two adjacent sections. It shows the œsophageal dilator muscles formed from the rudiments shown in the last two figures. Part of the median endoskeletal rod extending between the brain and the stomach is also seen. × 640.

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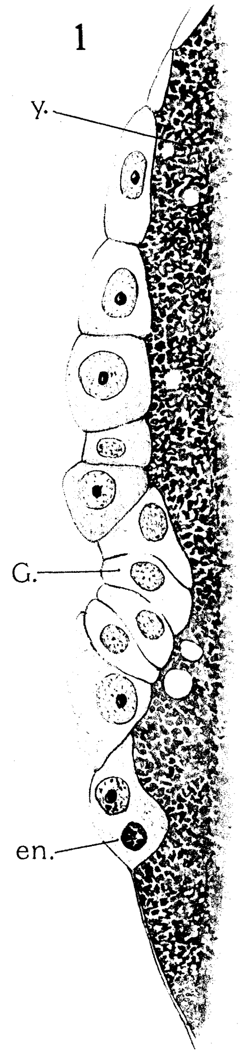

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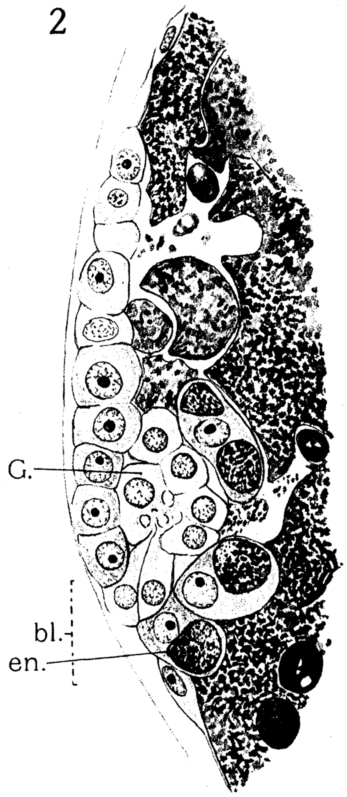

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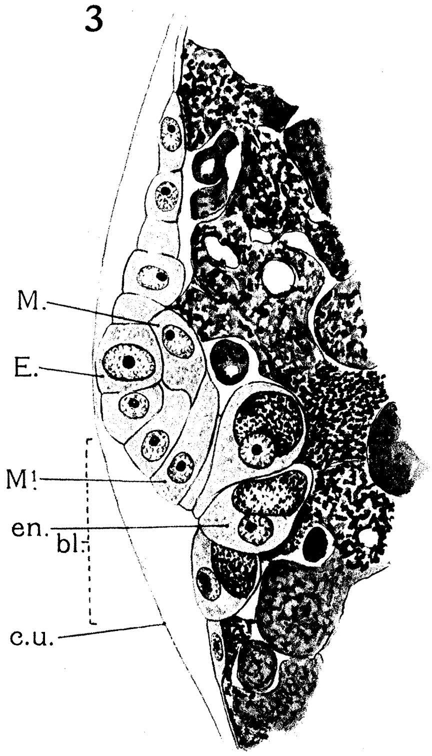

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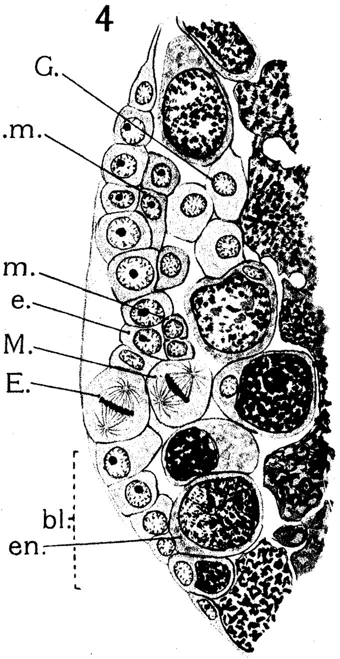

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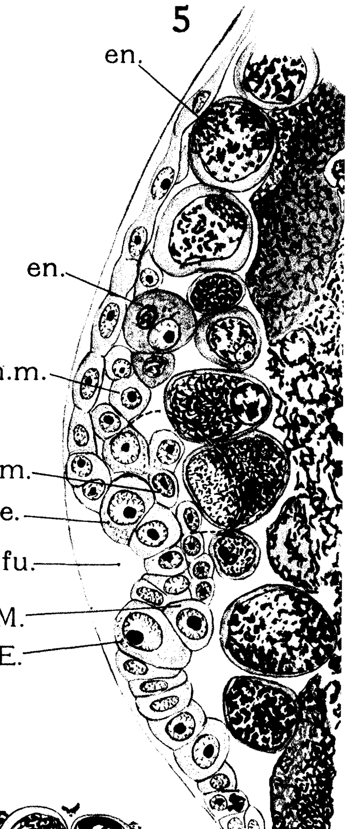

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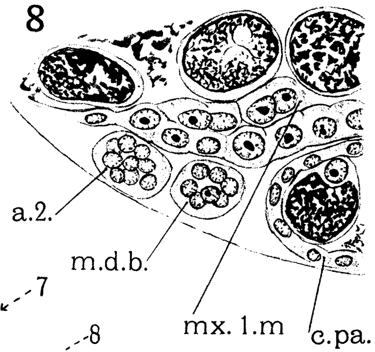

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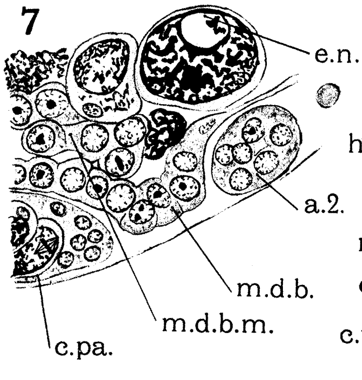

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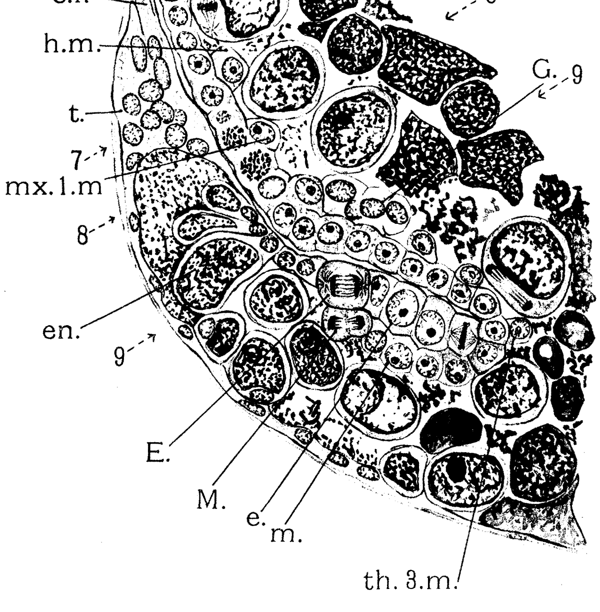

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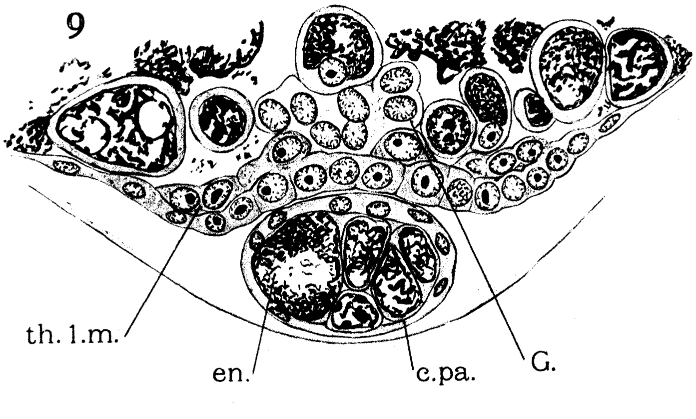

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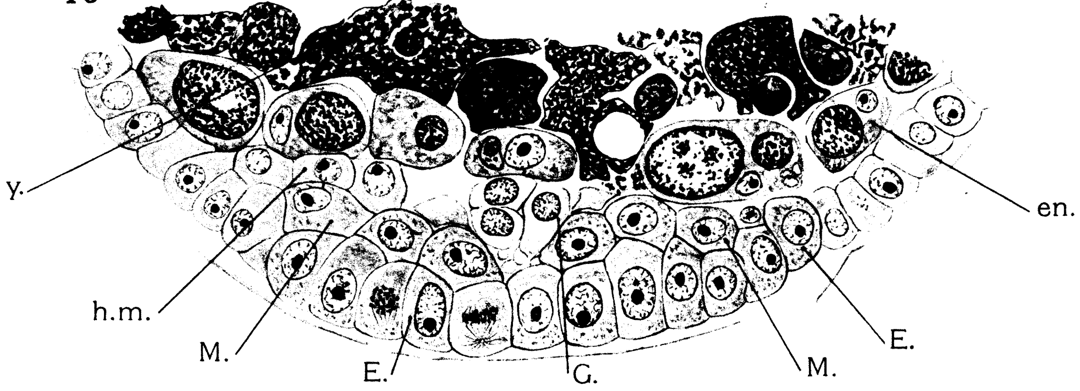

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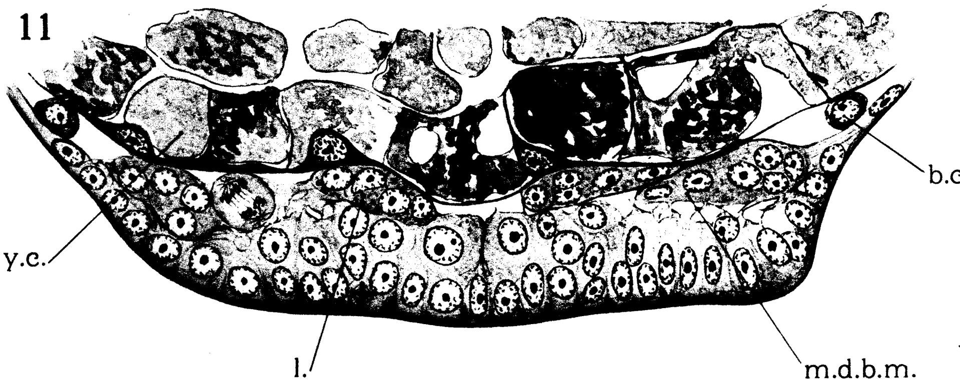

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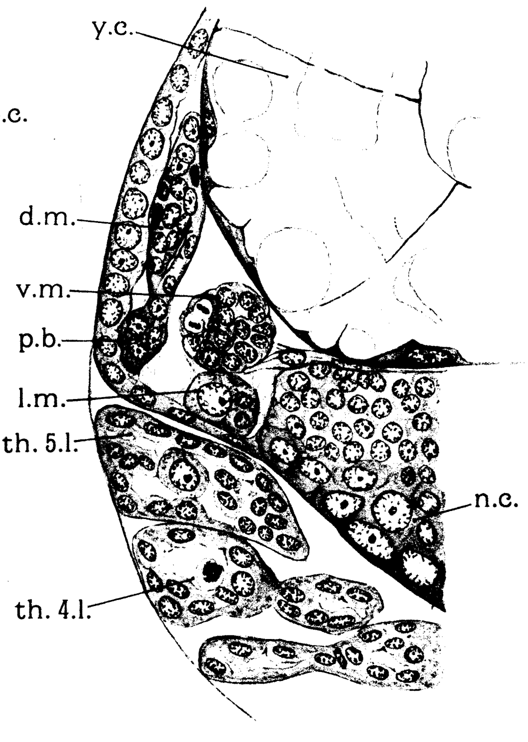

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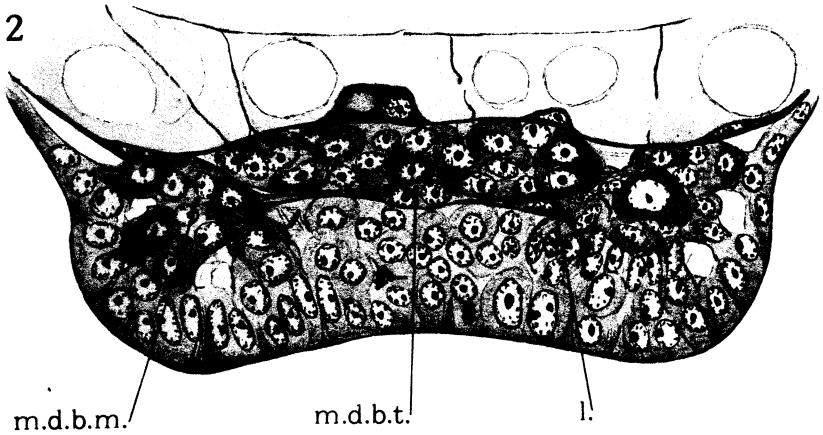

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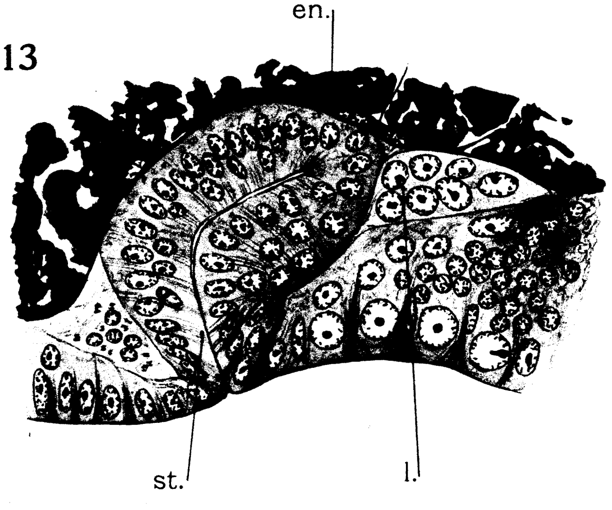

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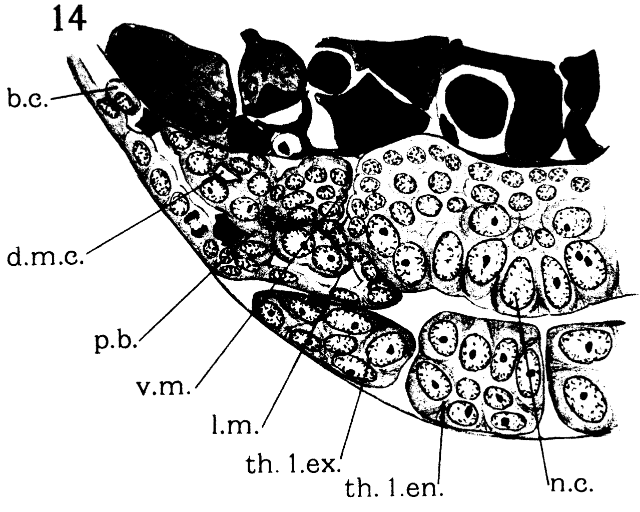

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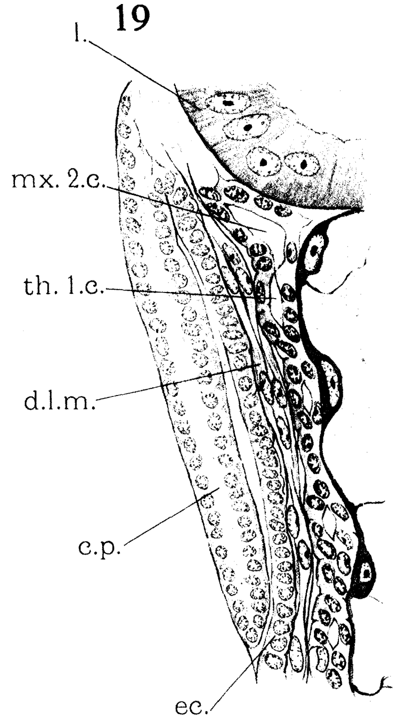

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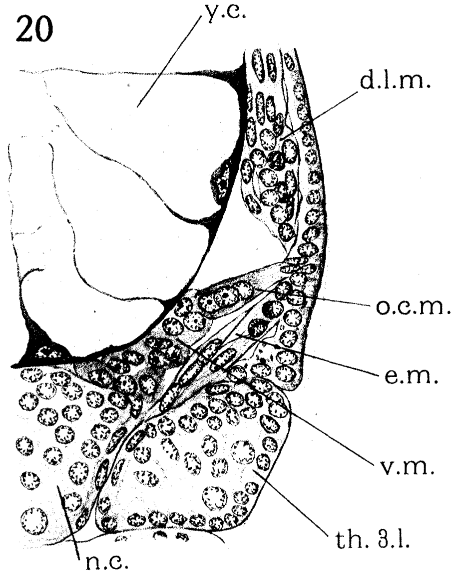

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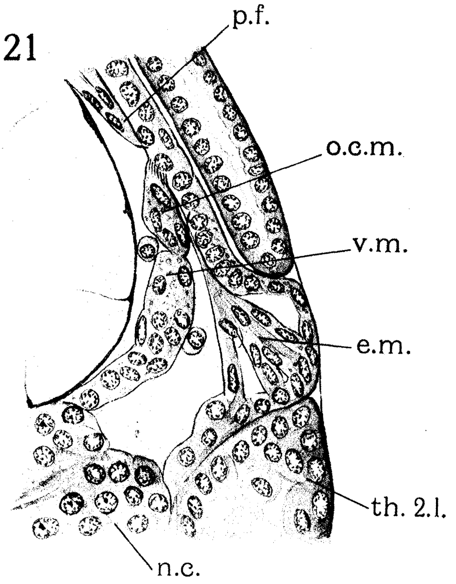

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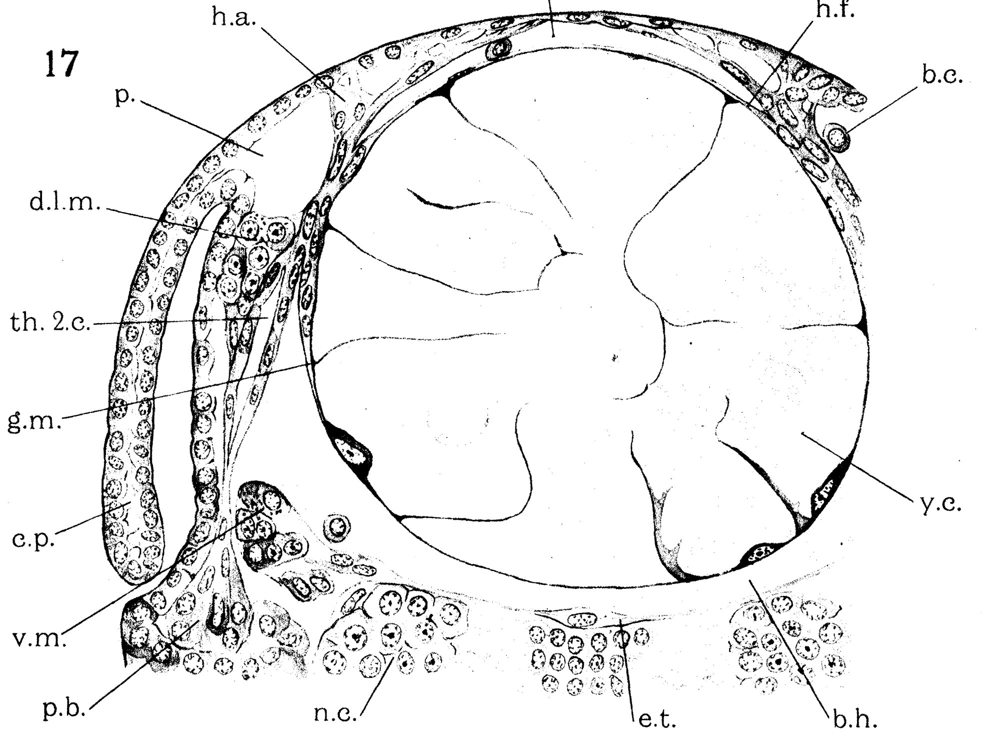

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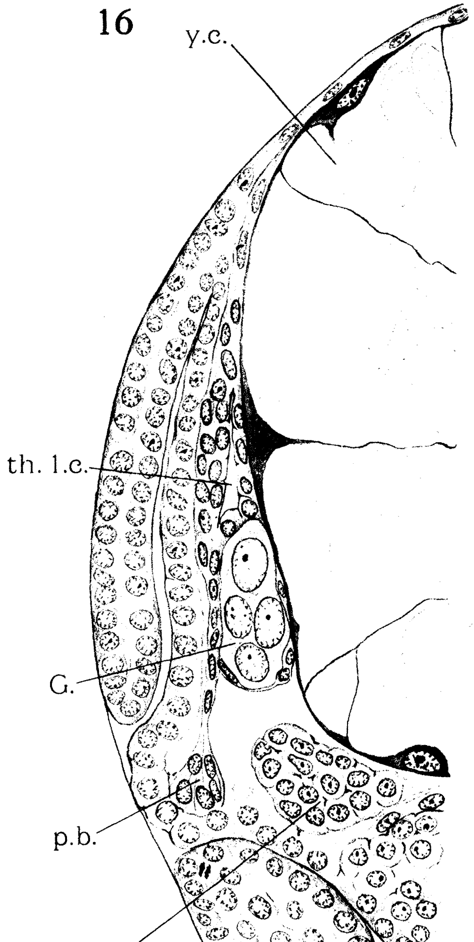

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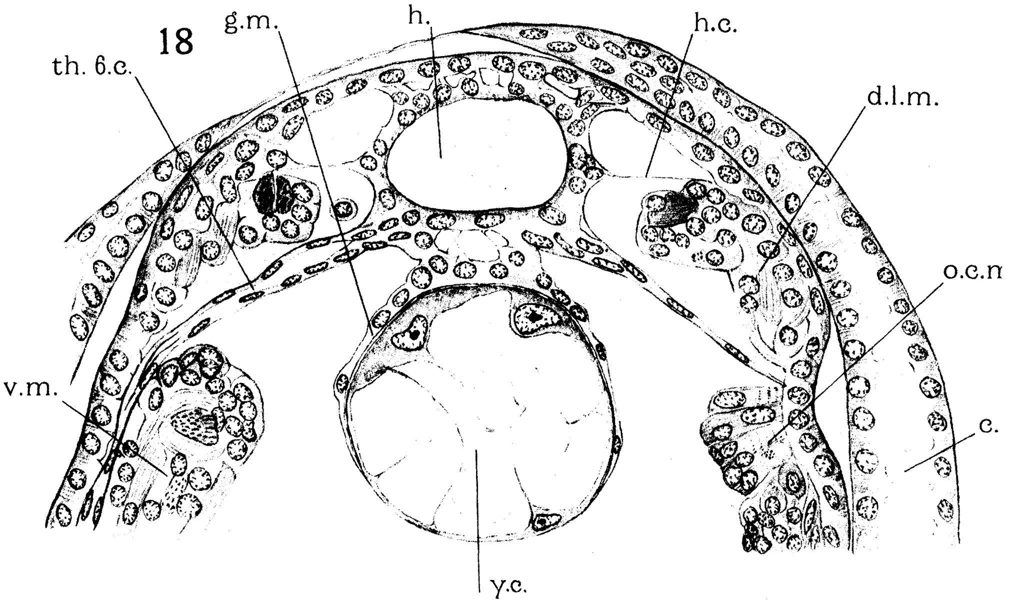

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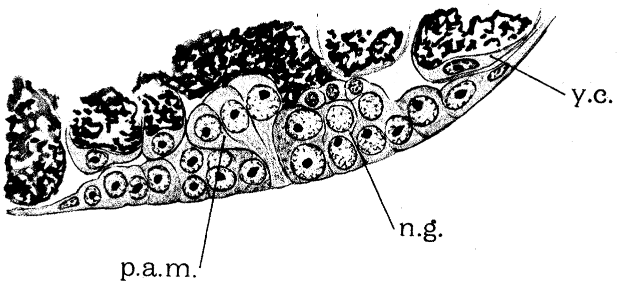

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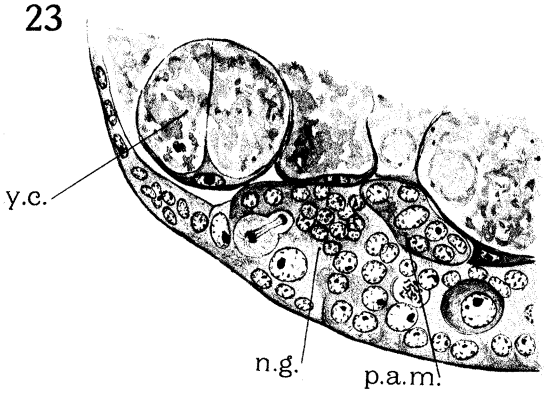

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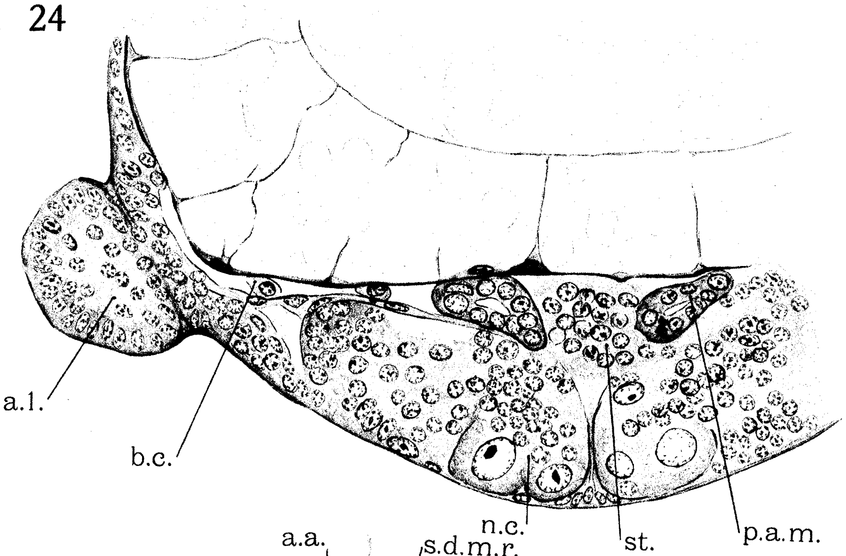

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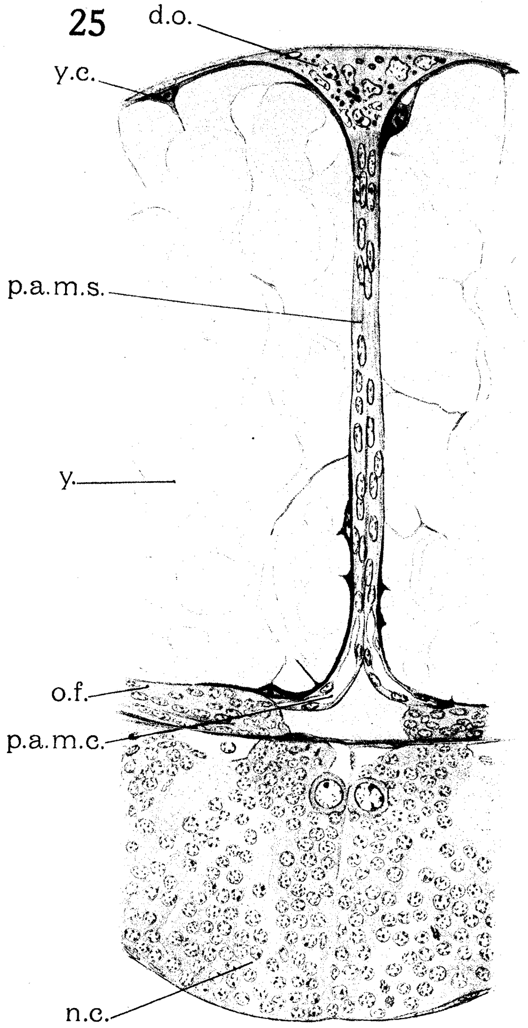

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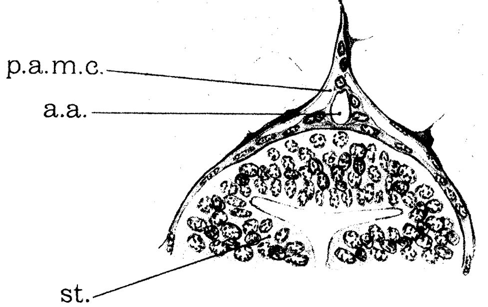

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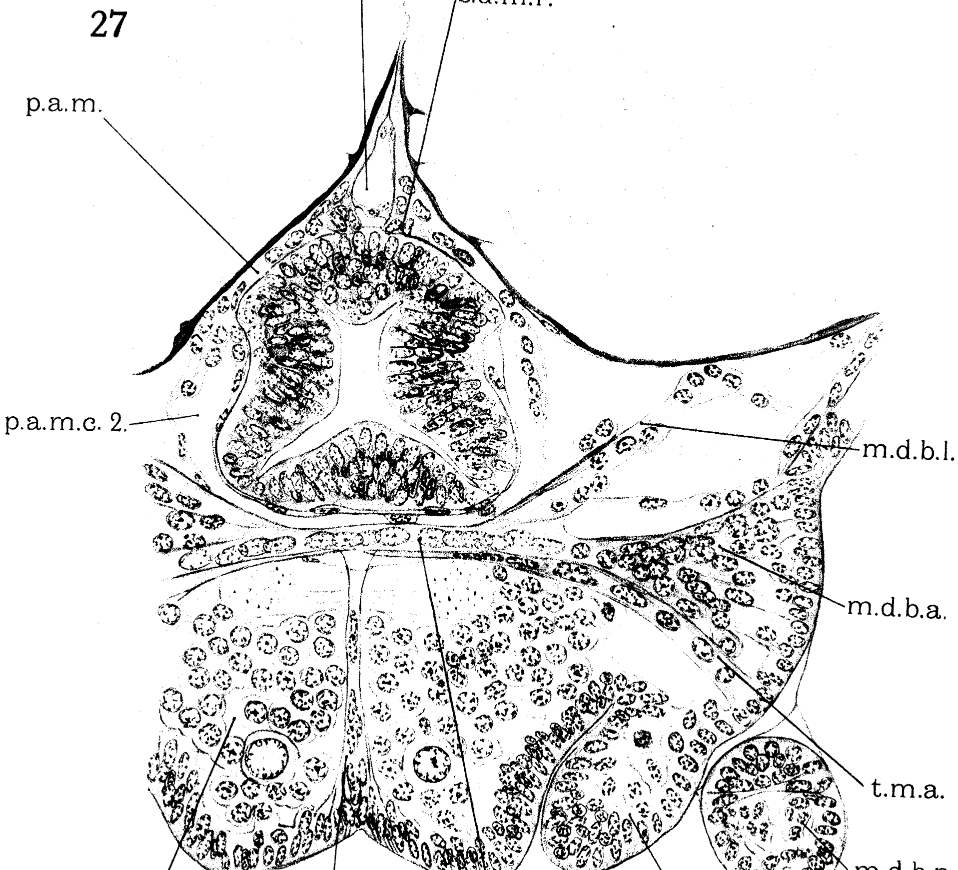

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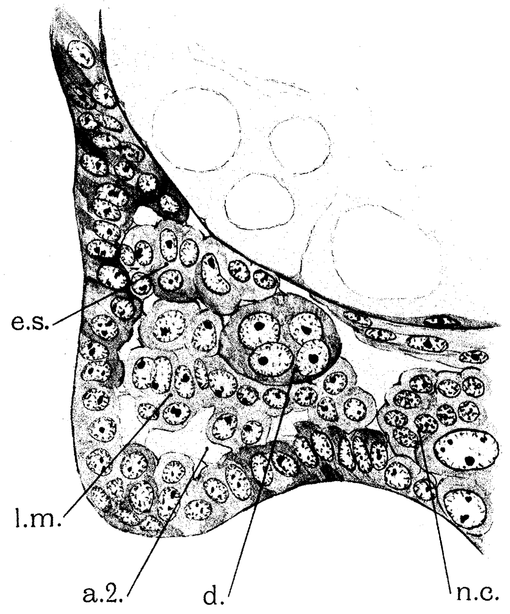

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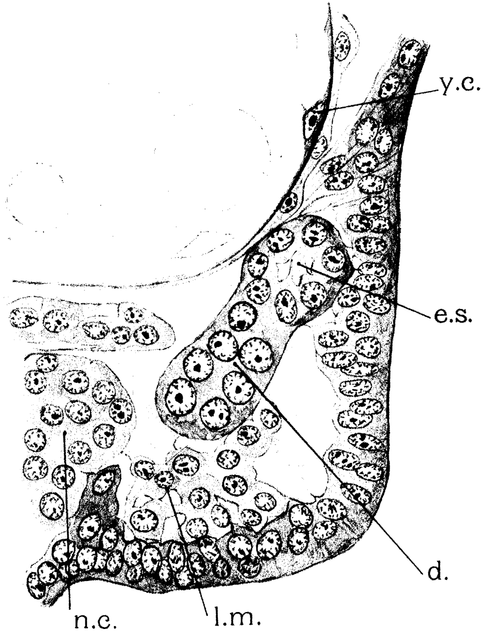

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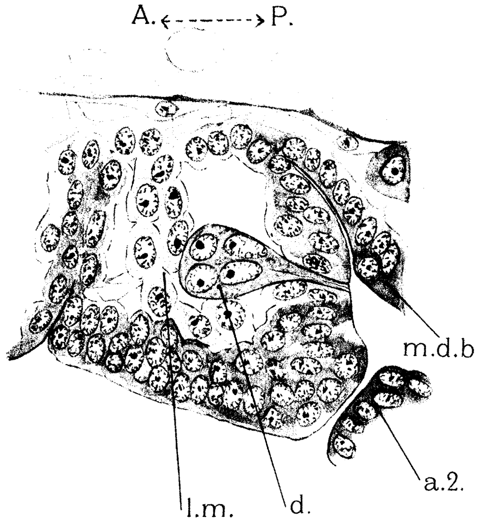

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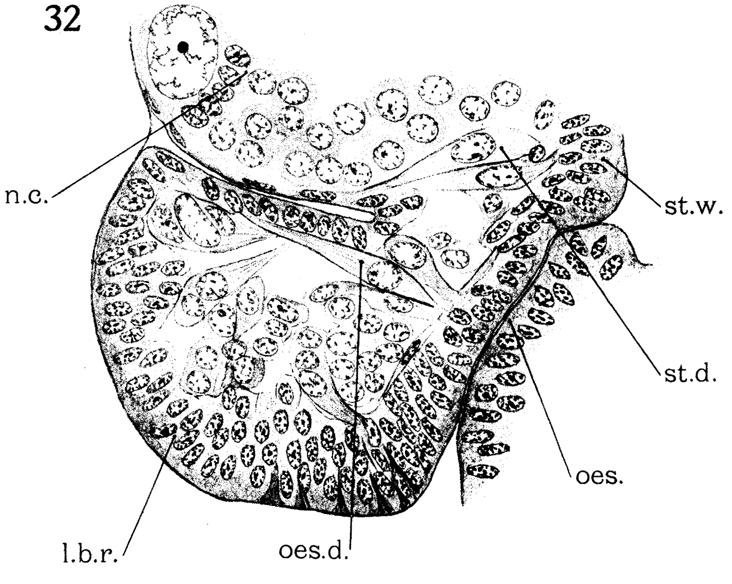

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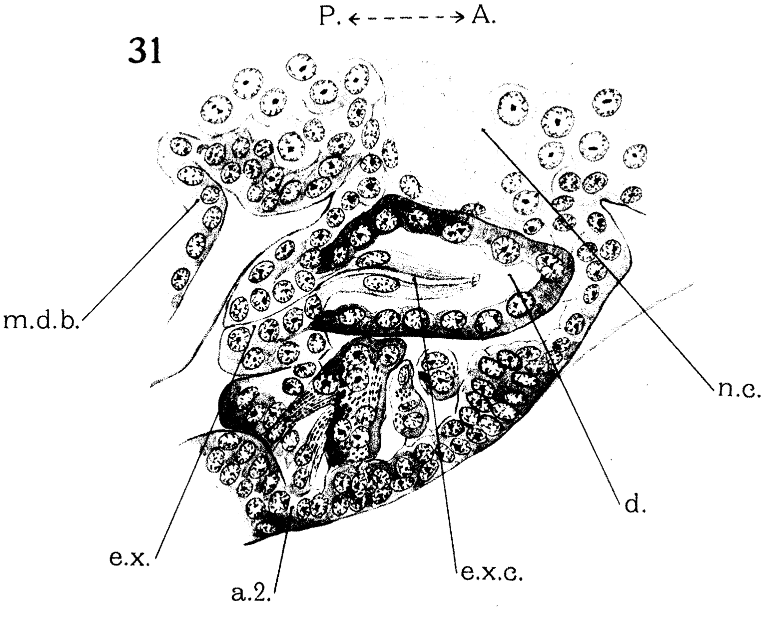

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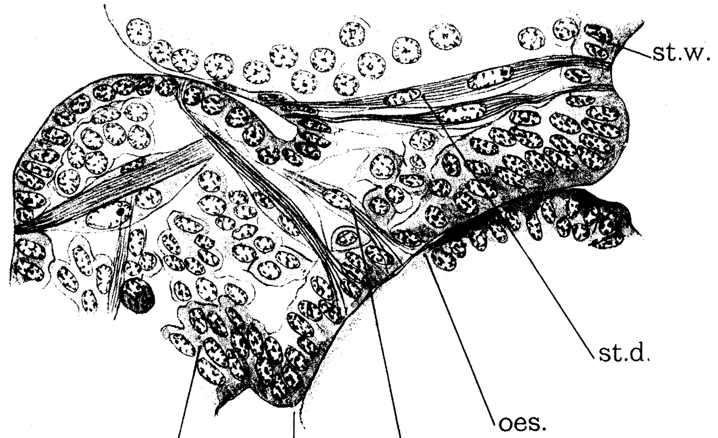

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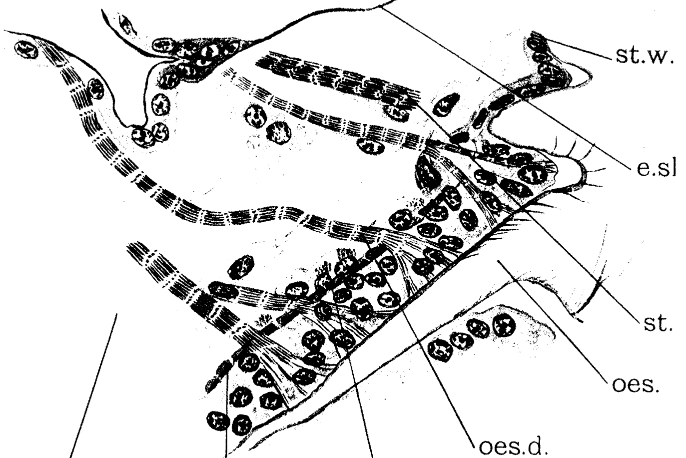

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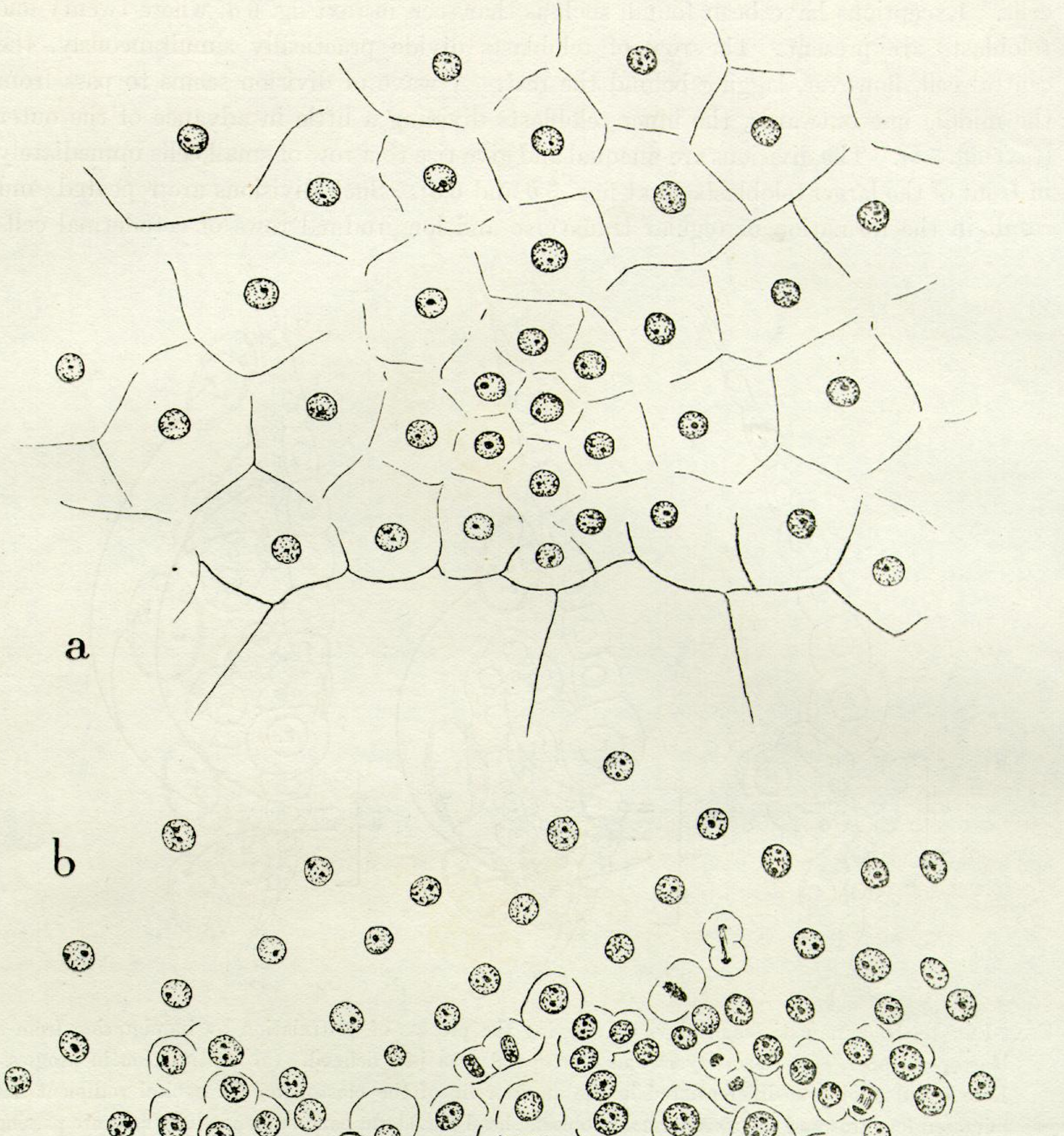
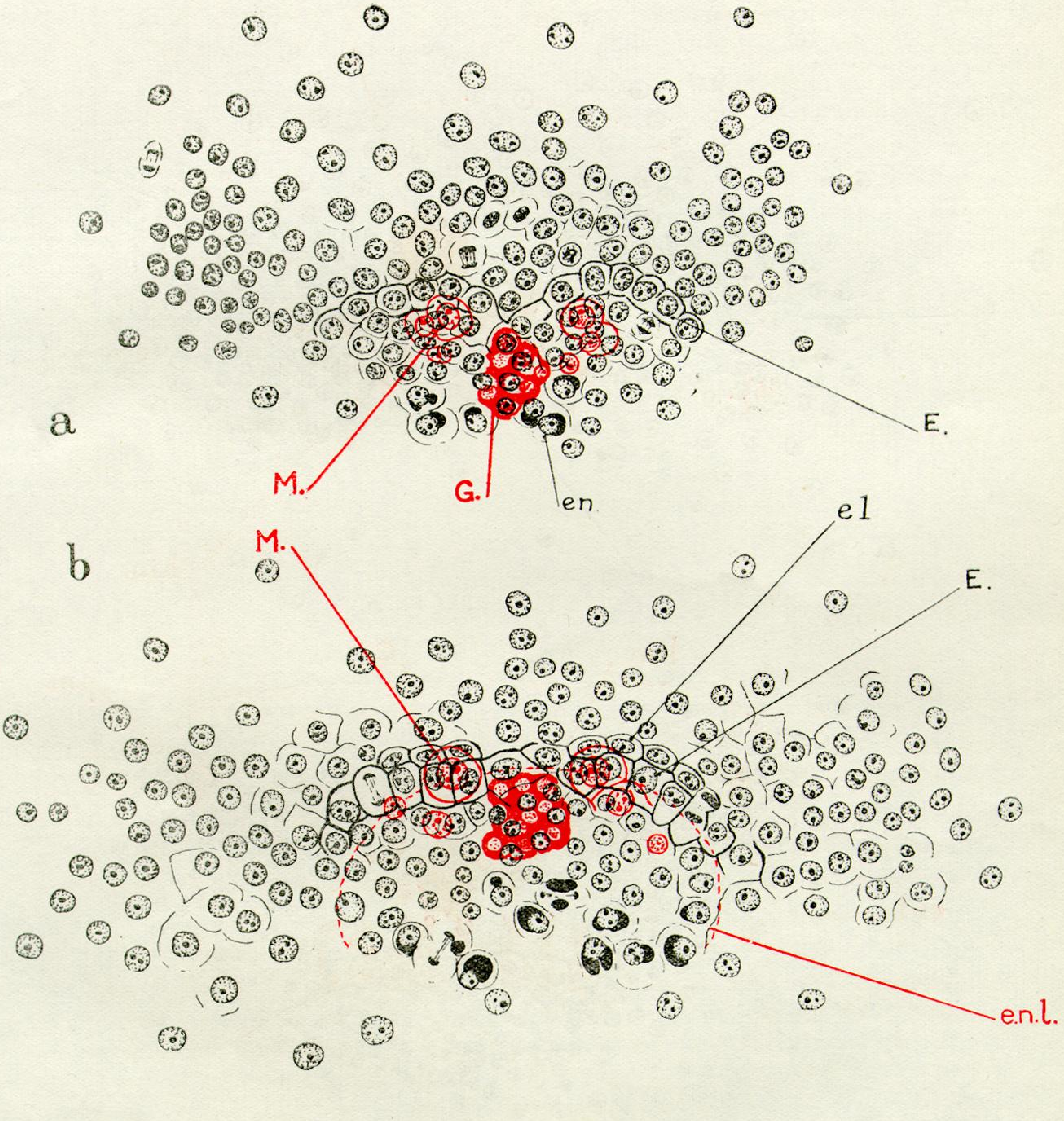
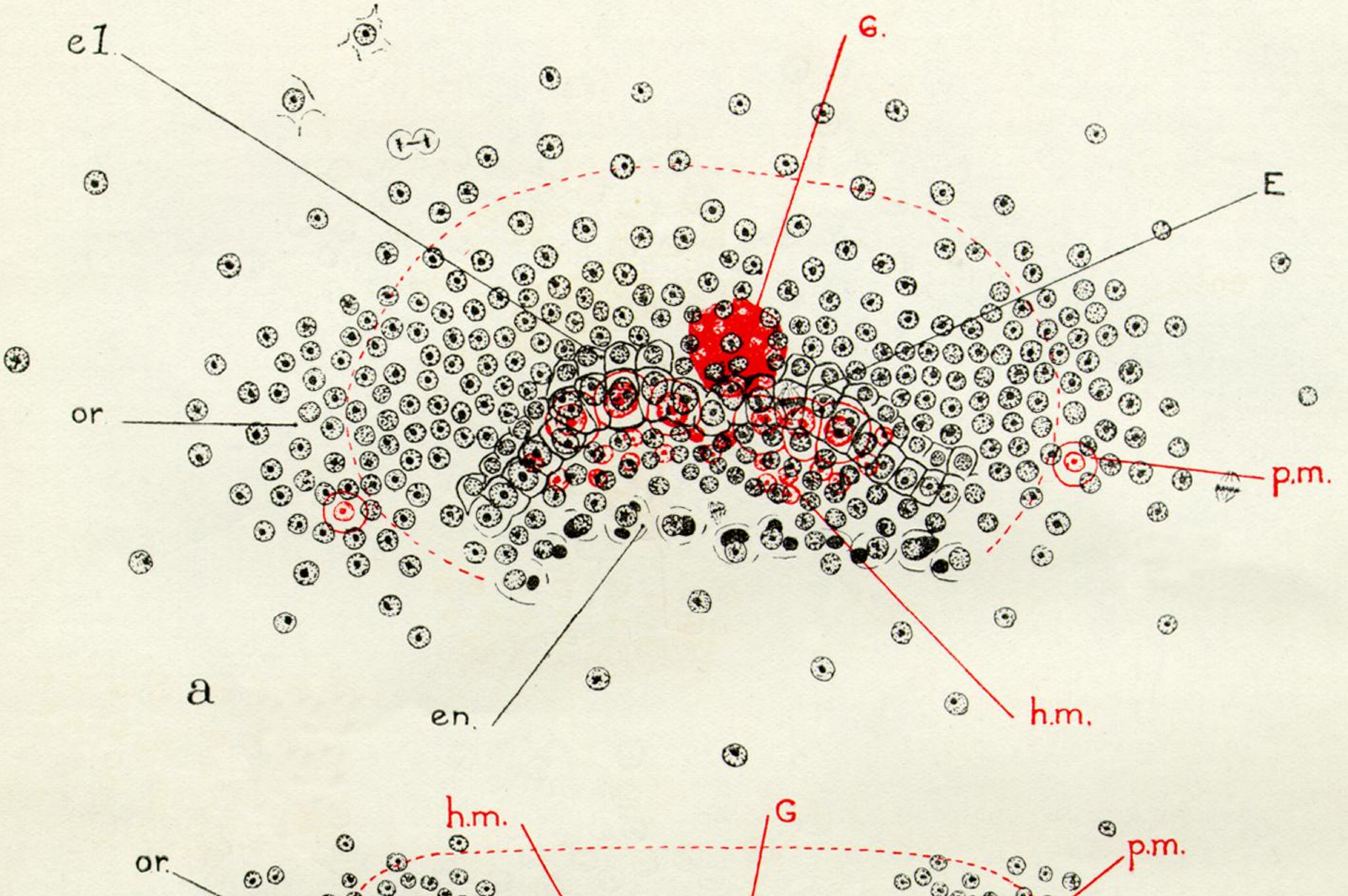
TEXT-FIGS. 4–7 show a series of whole preparations of germinal disks. Cells drawn in black are on the surface, while those which have become internal are shown in red. The red dotted line encloses the area covered by endoderm. The curved disks have been slightly flattened out in preparation.



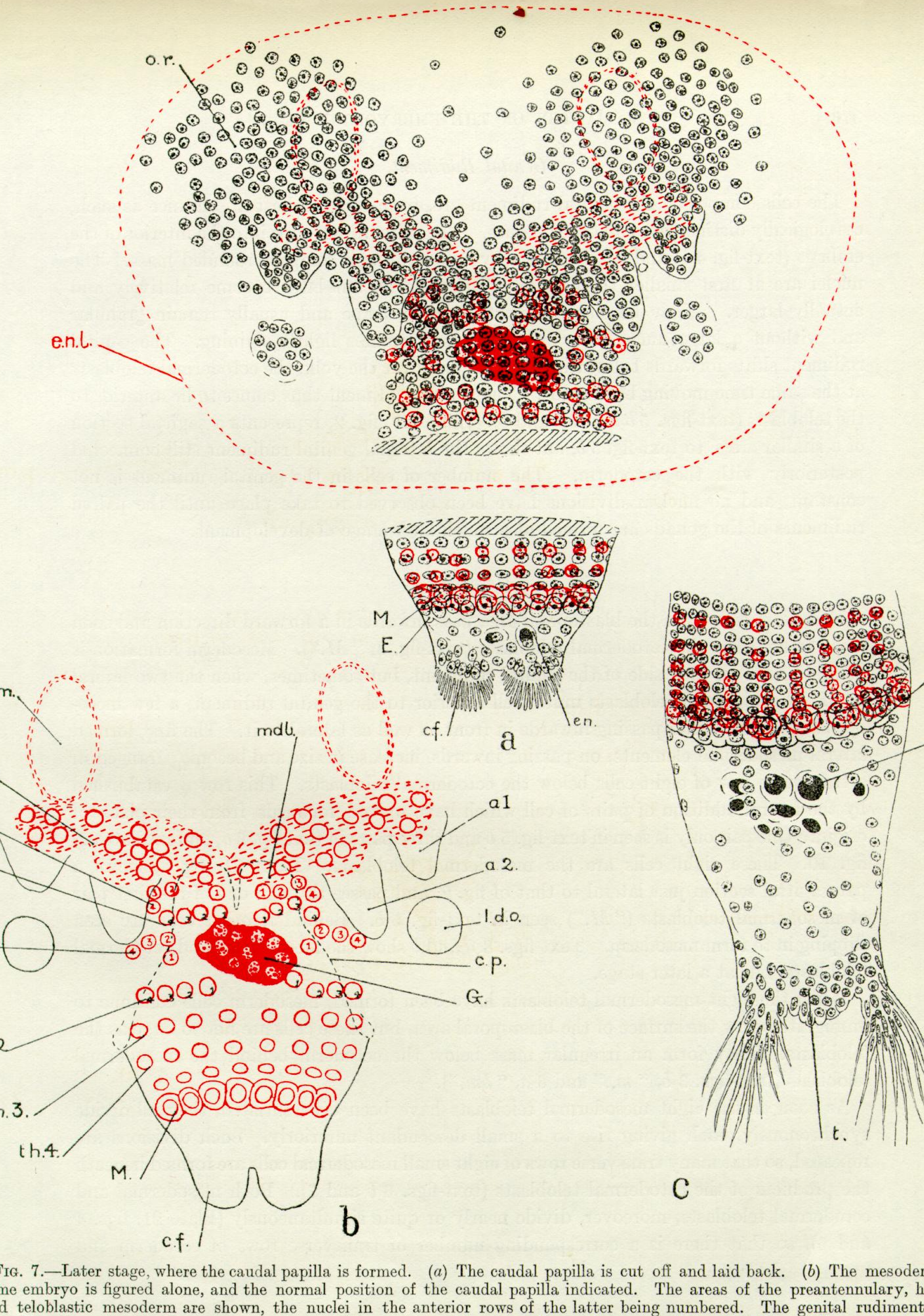
TEXT-FIG. 4.—(*a*) Undifferentiated germinal disk. (*b*) Differentiation of the germinal layers and genital rudiment and beginning of gastrulation. *E.*, ectodermal teloblasts. *en.*, endodermal cells. *G.*, genital rudiment. *M.*, mesodermal teloblast.



TEXT-FIG. 5.—(*a*) Later stage in gastrulation. The genital rudiment is internal, the curved rows of ectodermal teloblasts are approaching one another, and one pair of mesodermal teloblasts have taken up their positions below the ectodermal teloblasts. (*b*) The ectodermal teloblasts have formed a transverse row, and most of them have given one descendant. *E.*, ectodermal teloblasts ; *en.*, endoderm cells ; *en.l.*, boundary of area covered by endoderm cells ; *e.* 1, descendant of ectodermal teloblast ; *G.*, genital rudiment ; *M.*, mesodermal teloblast.



Text-Fig. 6.—(*a*) Later stage. The germinal rudiment is now anterior to the teloblasts. Twenty-one instead of the normal fifteen ectodermal teloblasts are present. Three pairs of mesodermal teloblasts and many head mesoderm cells have been differentiated, and one pair preantennulary mesoderm cells have passed inwards behind the optic rudiments, which are distinguishable by their thick darkly staining cytoplasm. (*b*) The transverse germinal band is now V-shaped. Four rows of ectodermal and three rows of mesodermal teloblast descendants have been formed. The head mesoderm cells now lie in front of the latter. The ectodermal nuclei drawn in outline represent the position of a furrow appearing across germinal band. *E.*, ectodermal teloblast ; *en.* endodermal cell ; *en.l.*, boundary of area covered by endoderm cells ; *e.* 1, *e.* 3, descendants of ectodermal teloblasts ; *G.*, genital rudiment ; *h.m.*, head mesoderm band cells ; *M.*, mesodermal teloblast ; *o.r.*, optic rudiment ; *p.m.*, preantennulary mesoderm.



TEXT-FIG. 7.—Later stage, where the caudal papilla is formed. (*a*) The caudal papilla is cut off and laid back. (*b*) The mesoderm of the same embryo is figured alone, and the normal position of the caudal papilla indicated. The areas of the preantennulary, head band and teloblastic mesoderm are shown, the nuclei in the anterior rows of the latter being numbered. The genital rudiment has now moved back to the first thoracic segment. (*c*) The caudal papilla of an older embryo just before hatching. The caudal furca is well formed and endoderm formation continues. *a.* 1, antennule ; *a.* 2, antenna ; *c.f.*, caudal furca ; *c.p.*, caudal papilla ; *E.*, octodermal teloblast ; *en.*, endoderm cell ; *en.l.*, boundary of area covered by endoderm cells ; *G.*, genital rudiment ; *h.m.*, head mesoderm bands ; *l.d.o.*, dorso-lateral organ ; *mdb.*, mandible ; *mx.* 1, maxillulary mesoderm ; *mx.* 2, maxillary mesoderm ; *o.r.*, optic rudiment ; *p.m.*, preantennulary mesoderm ; *t.*, telson ; *th.* 1, *th.* 2, *th.* 3, *th.* 4, 1st 2nd, 3rd and 4th thoracic mesoderm.

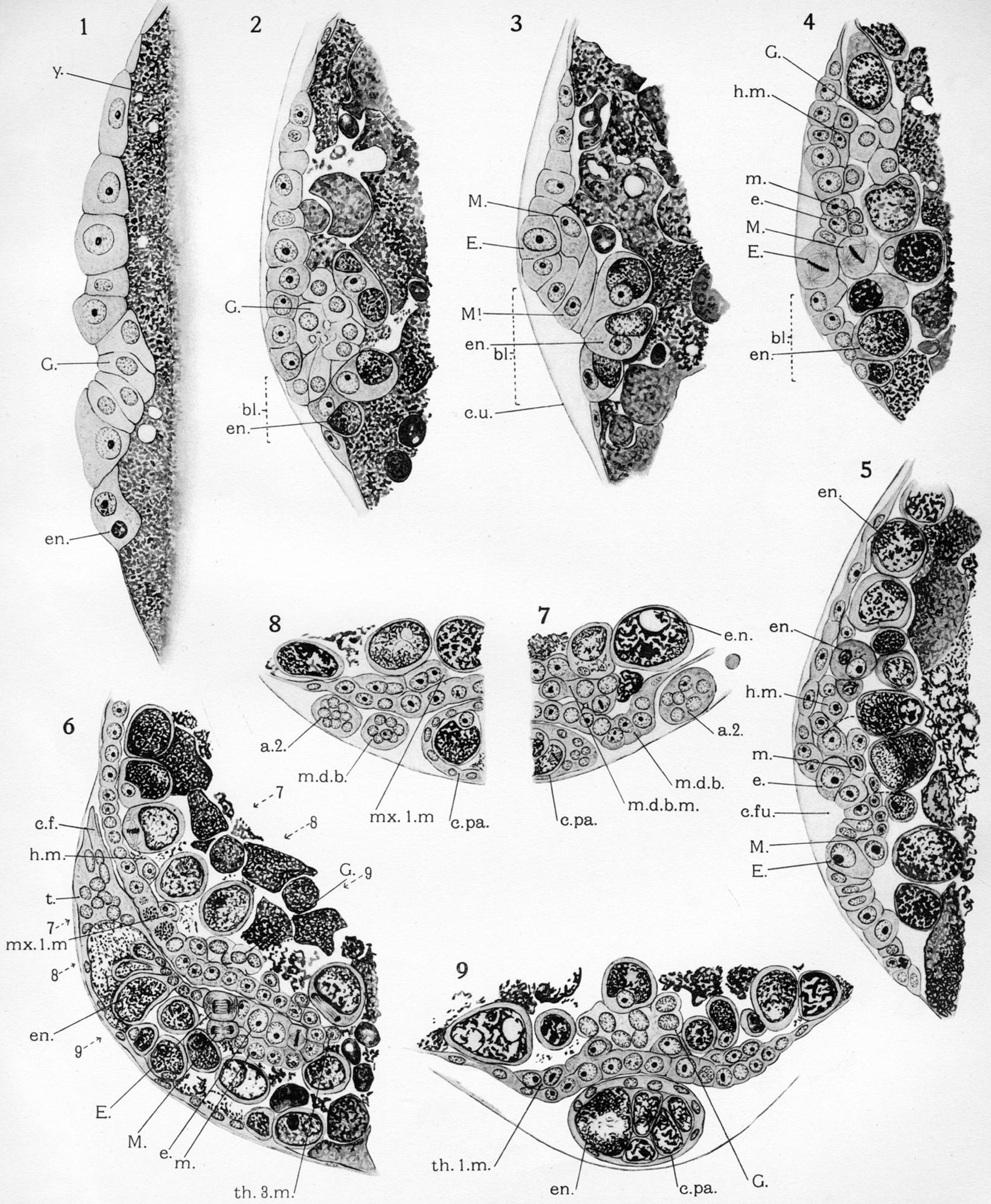


PLATE 21.

FIG. 1.—Sagittal section through a germinal disk of the same age as that in text-fig. 4 *b*. The genital rudiment is starting to pass inwards. × 570.

FIG. 2.—Sagittal section through an older disk where the genital rudiment is nearly entirely internal and the yolk cells are being formed from behind it and are passing inwards over the yolk. × 570.

FIG. 3.—Parasagittal section from the same embryo passing laterally to the genital rudiment. Endoderm and mesoderm cells are slipping in from the blastoporal area and an ectodermal teloblast is seen in the anterior lip of the blastopore and internal to it a mesodermal teloblast. Only one pair of mesodermal teloblasts are here present. × 570.

FIG. 4.—Parasagittal section of an older stage, a little younger than that of text-fig. 6 *b*. Mitotic figures are seen in the ectodermal and mesodermal teloblasts, their descendants lying anteriorly to them. The edges of the genital rudiment and a few head mesoderm cells are seen and also the beginning of the caudal furrow. × 570.

FIG. 5.—Parasagittal section showing five rows of mesodermal teloblast descendants touching the head band mesoderm anteriorly. The position of the genital rudiment in the sagittal plane is indicated by the dotted line. The caudal furrow is more marked. × 570.

FIG. 6.—Parasagittal section through an embryo with the caudal papilla reflexed forwards as in text-figs. 7 *a* and *b*. Endoderm is still being formed behind the teloblasts. The genital rudiment has shifted backwards into the first thoracic segment. Near the teloblasts the ectodermal and mesodermal descendants correspond in number, but in front of the third thoracic segment about two ectodermal and one mesodermal cell are seen in the primordium of each segment. × 570.

FIG. 7.—Transverse section through the mandibles of a similar stage to the last showing the irregular mandibular mesoderm from the head bands. × 570.

FIG. 8.—Transverse section from the same embryo through the maxillulary region showing the four maxillulary mesoderm cells of one side formed from the teloblasts. × 570.

FIG. 9.—Transverse section from the same embryo through the first thoracic segment showing the genital rudiment and the eight mesoderm cells of the first thoracic segment on either side. × 570.

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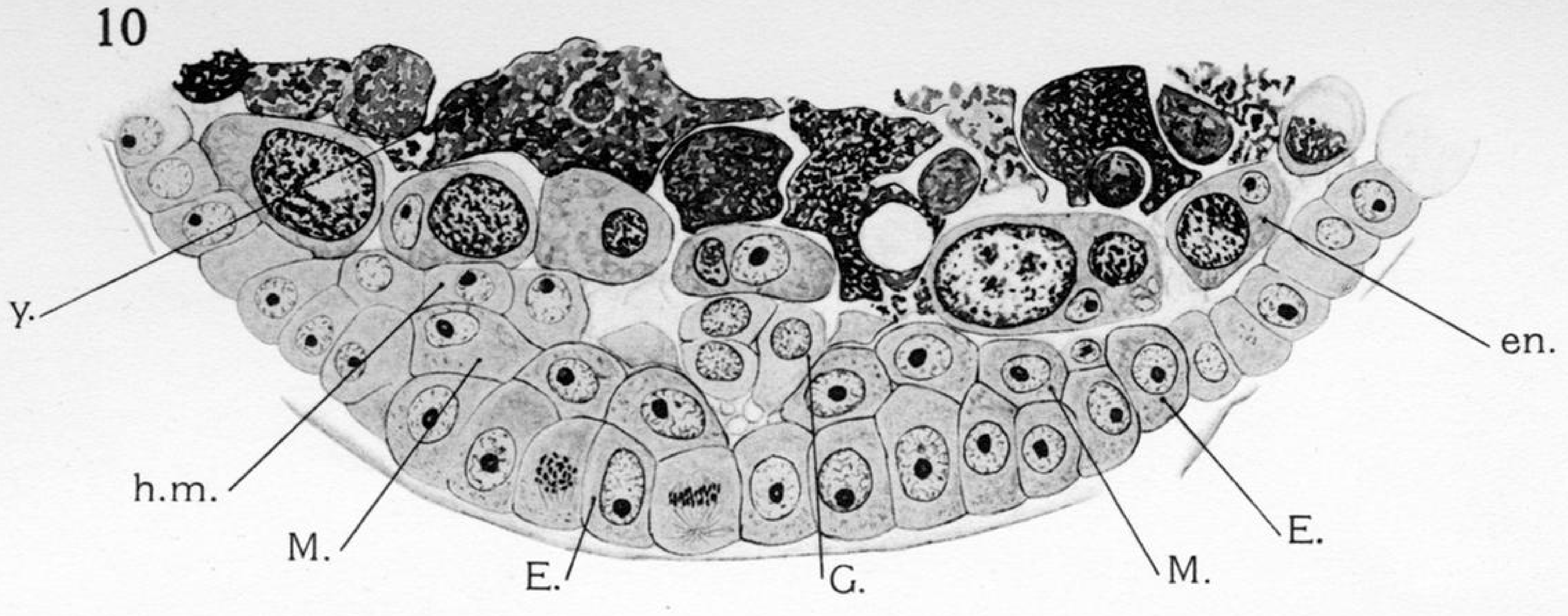

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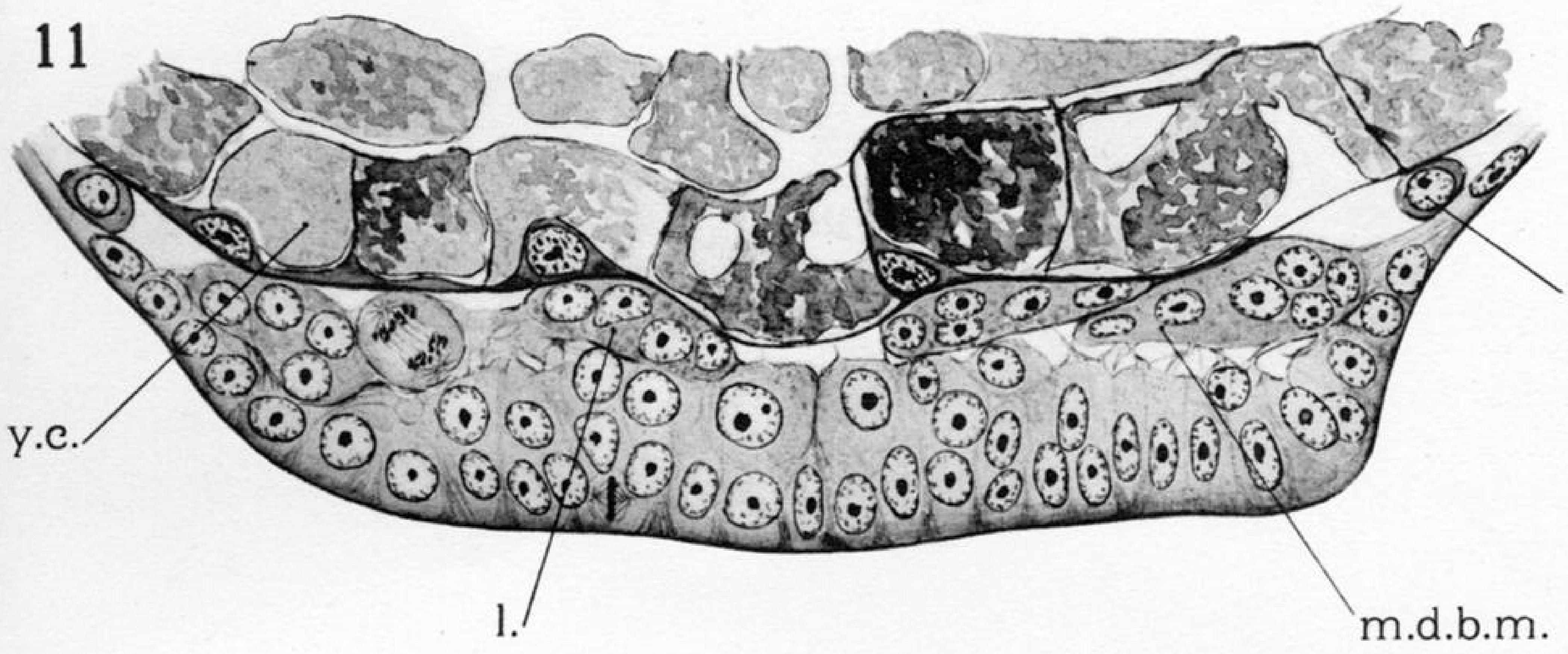

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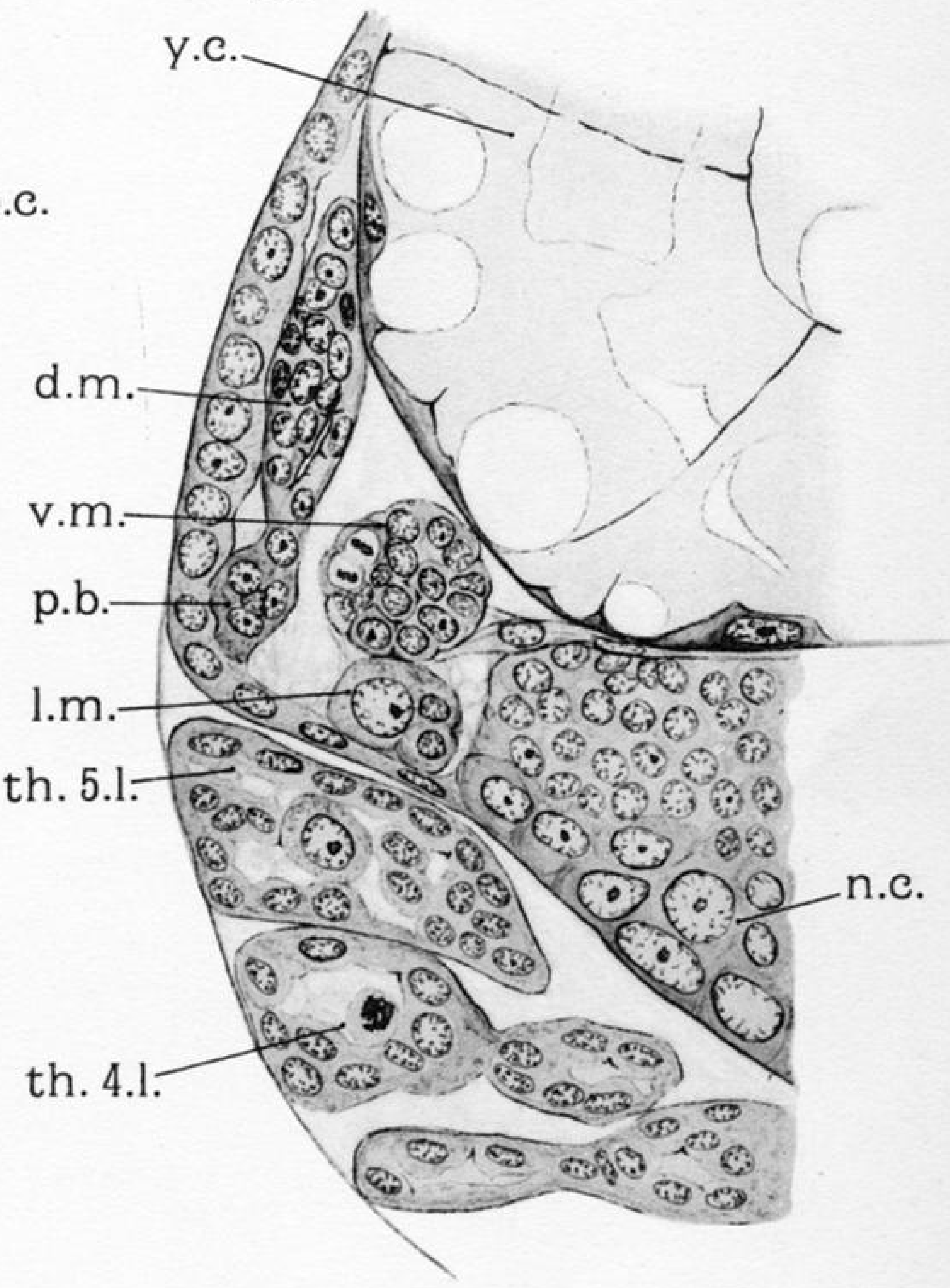

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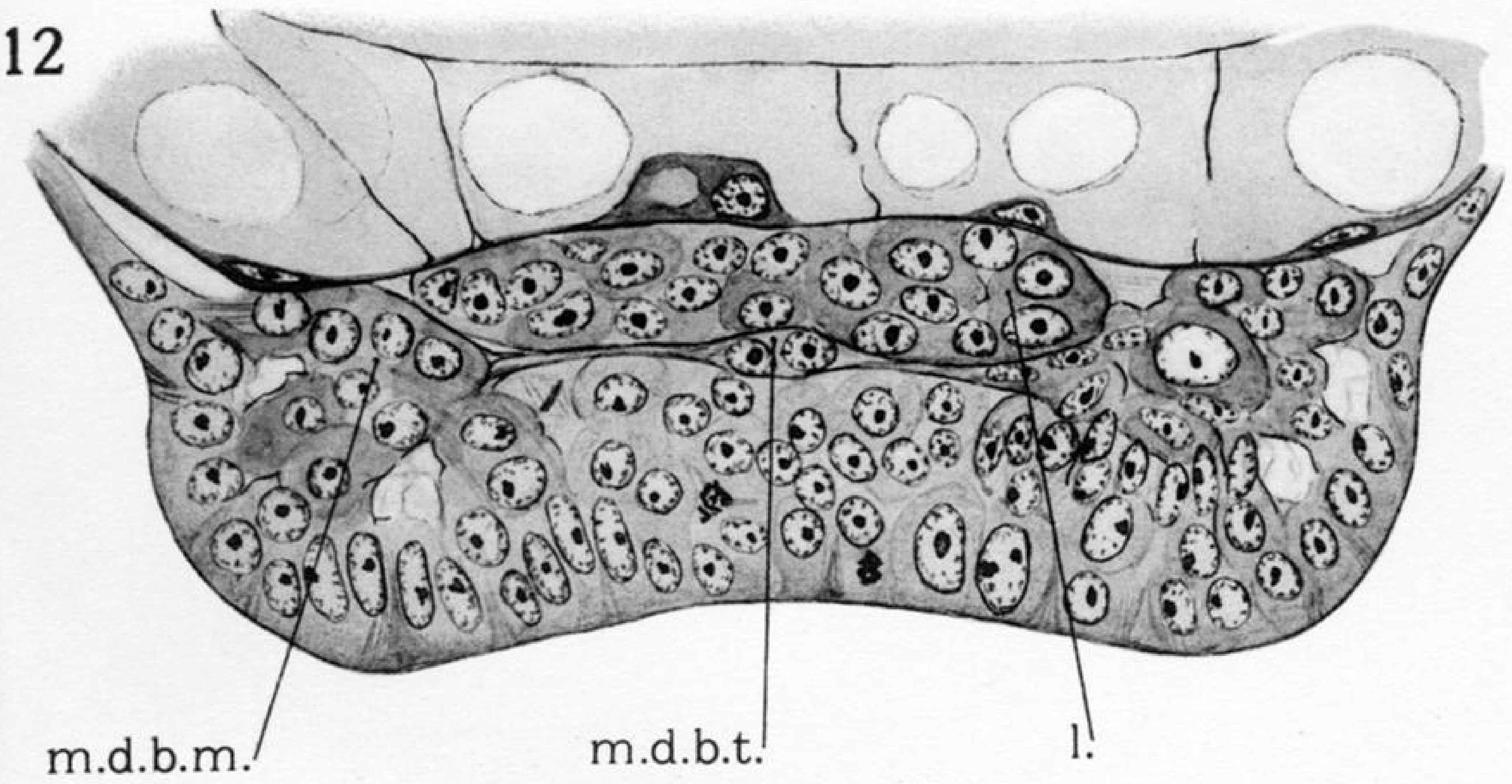

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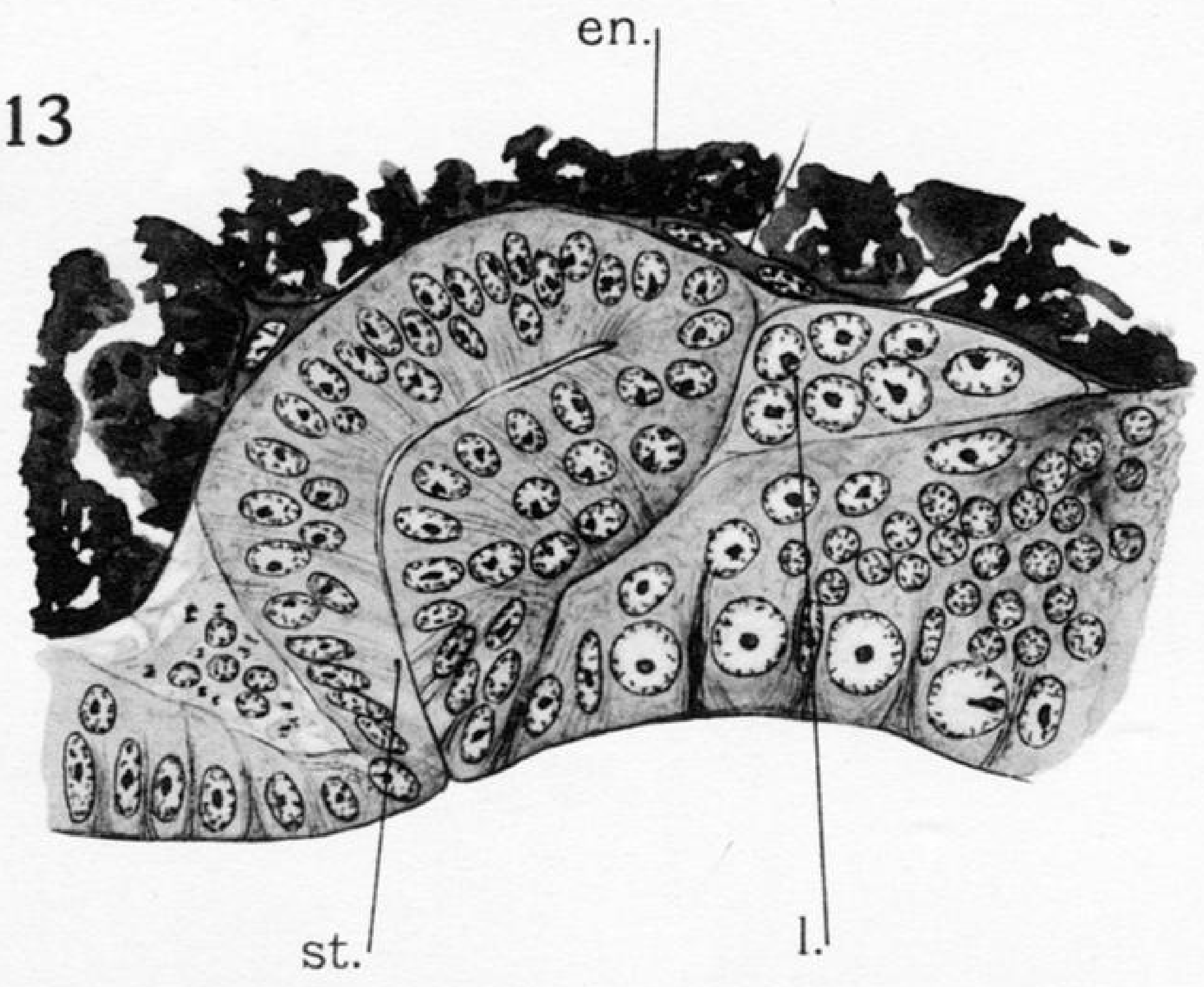

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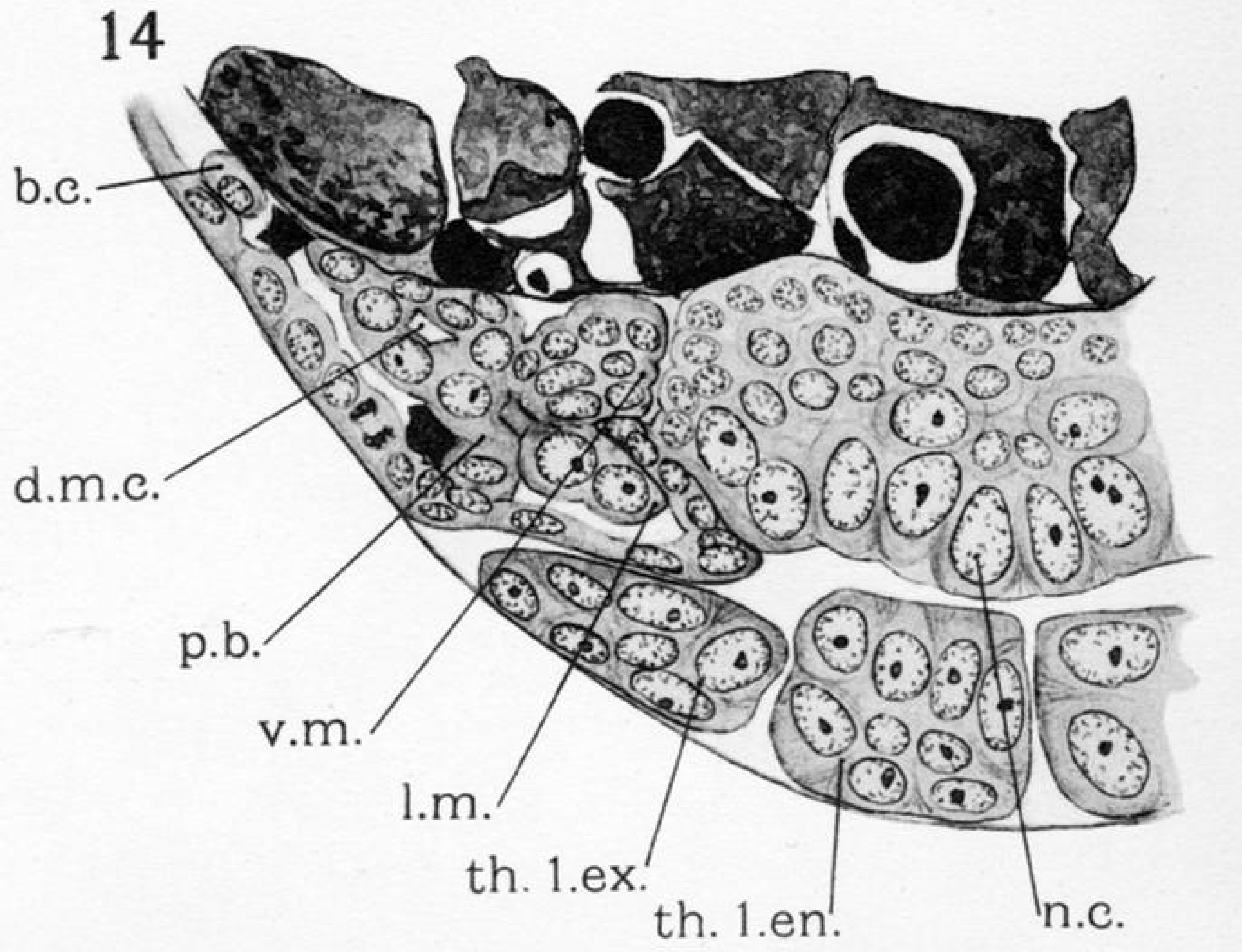

PLATE 22.

FIG. 10.—Transverse section through an embryo of the same stage as in text-fig 6 *a*. Three pairs of mesodermal teloblasts are seen internal to the ectodermal teloblasts. The posterior edge of the genital rudiment and the anterior edge of the group of head mesoderm cells are cut. The latter are passing forwards internal to the mesodermal teloblasts. × 570.

FIG. 11.—Transverse section through the anterior mandibular region. The liver rudiments are just differentiated from the mandibular mesoderm and lie external to the yolk cells. × 570.

FIG. 12.—Transverse section through the mandibular segment of an older stage showing the liver rudiments united in the middle line. × 570.

FIG. 13.—Sagittal section through the stomodæum at about the same age as the last showing the median liver rudiment behind the stomodæum. Both are covered by unchanged yolk cells, the anterior endoderm plate not yet being formed. × 570.

FIG. 14.—Transverse section through the second thoracic segment in which differentiation of the mesodermal somite has begun. The dorsal mesoderm with its cœlomic cavity can be distinguished from the ventral mesoderm and limb portion. × 570.

FIG. 15.—Transverse section of an older stage in which the dorsal mesoderm has started to grow upwards. × 570.

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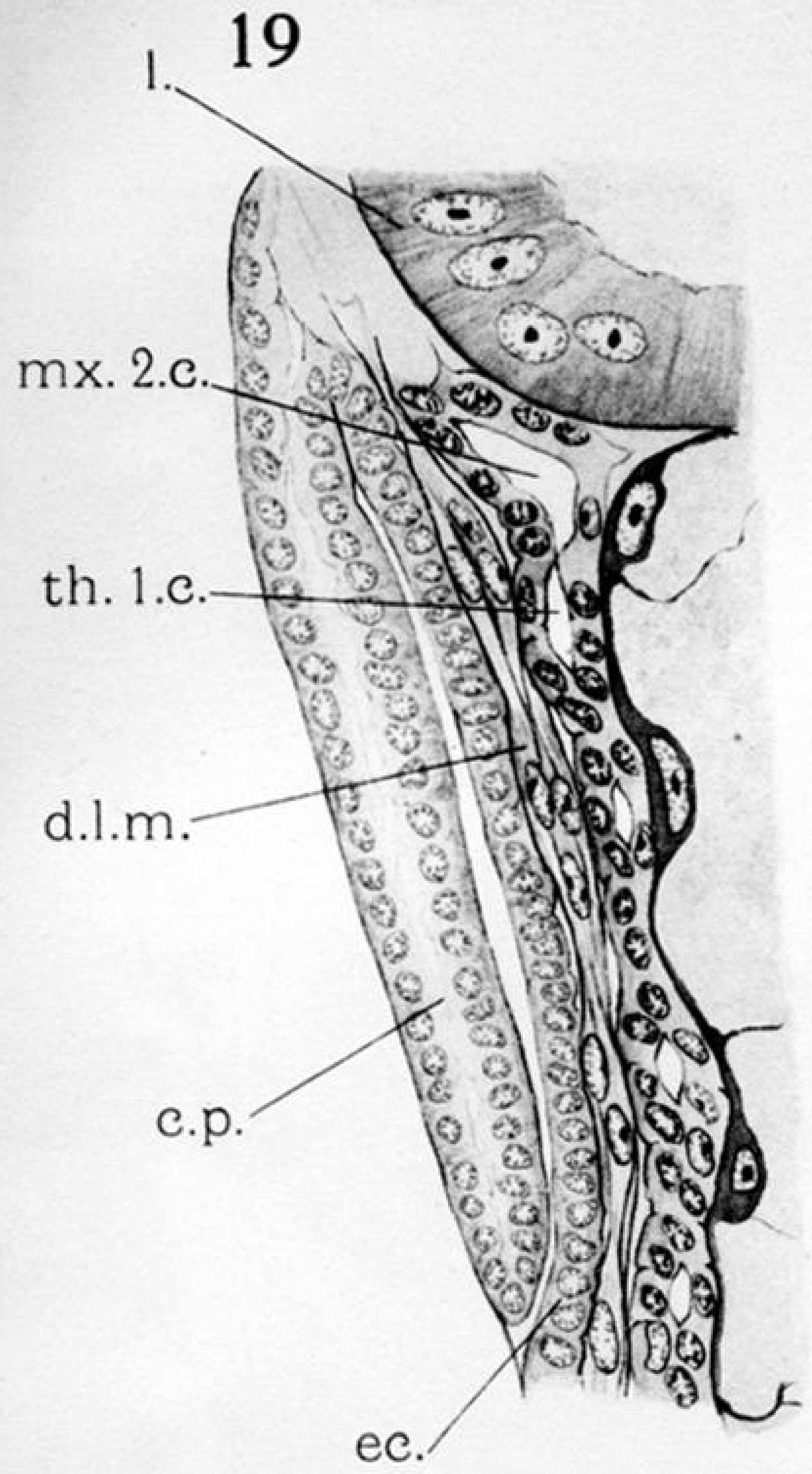

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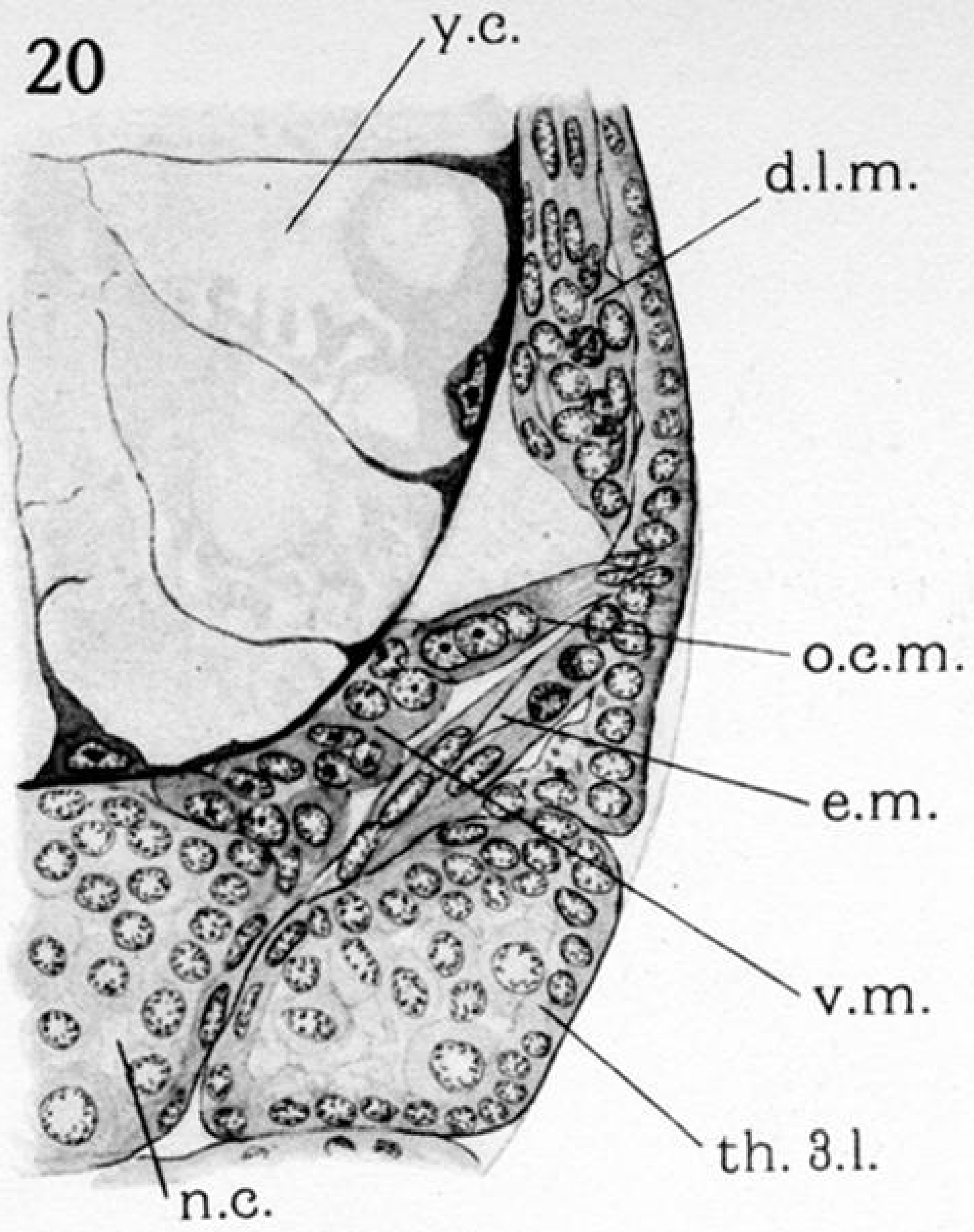

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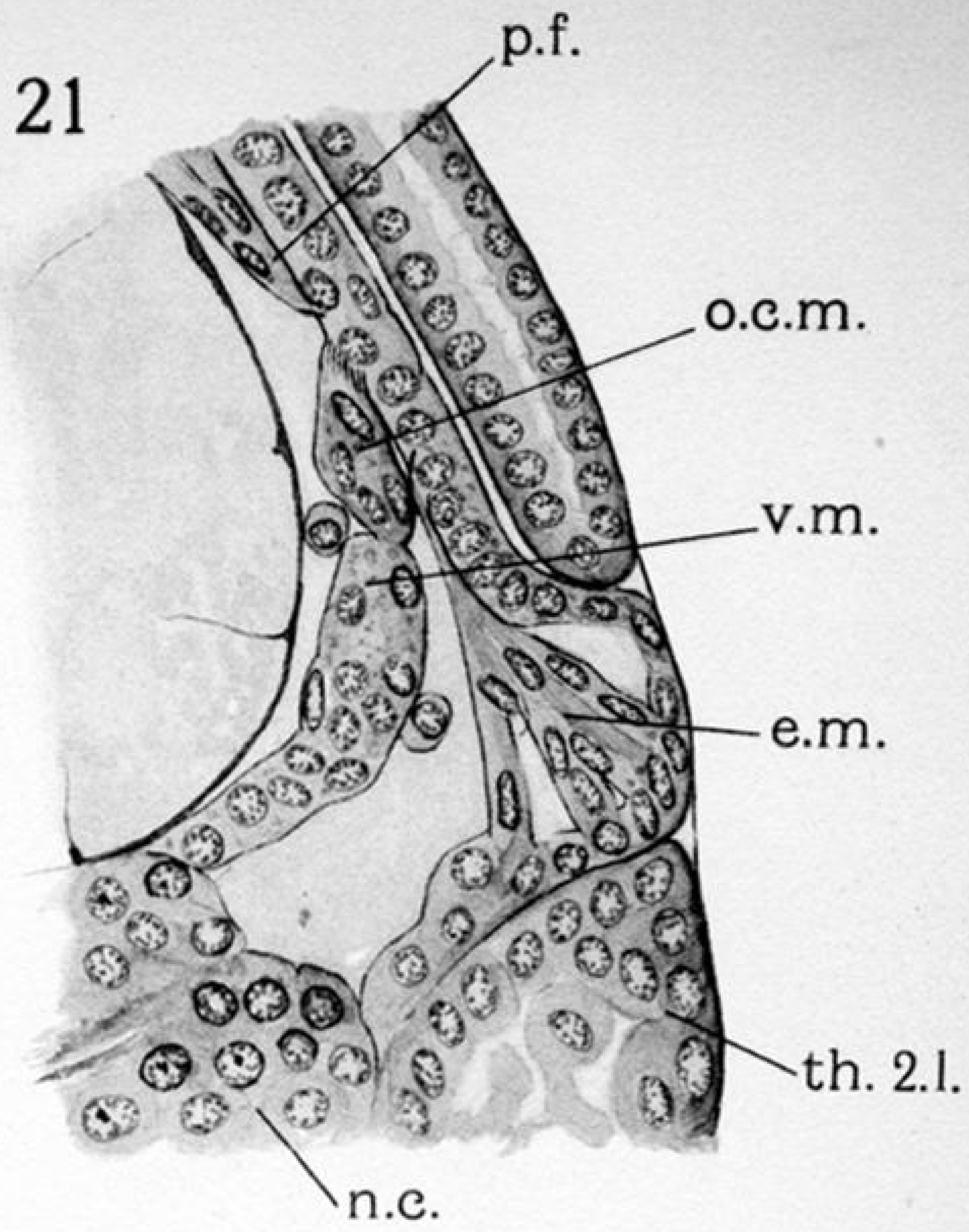

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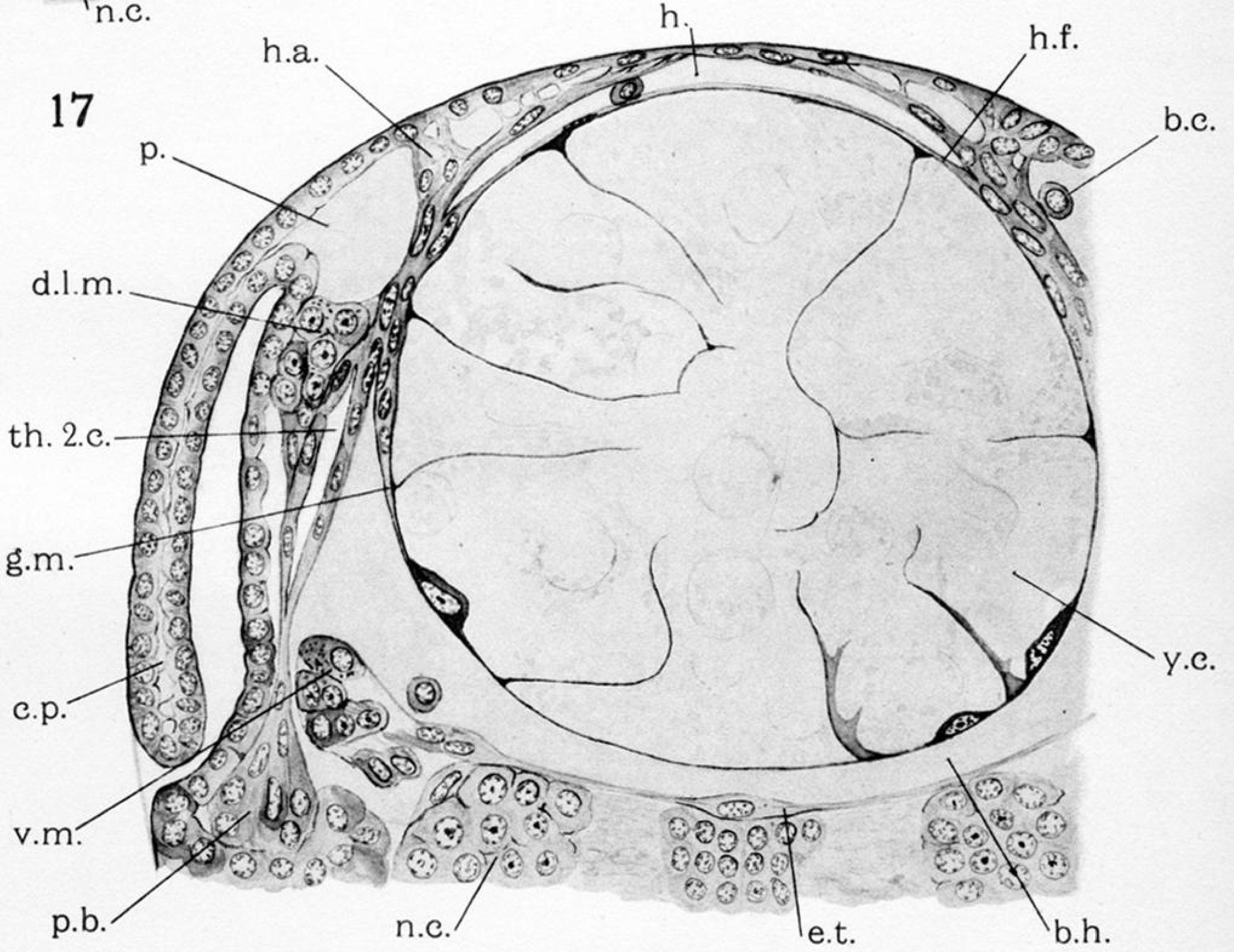

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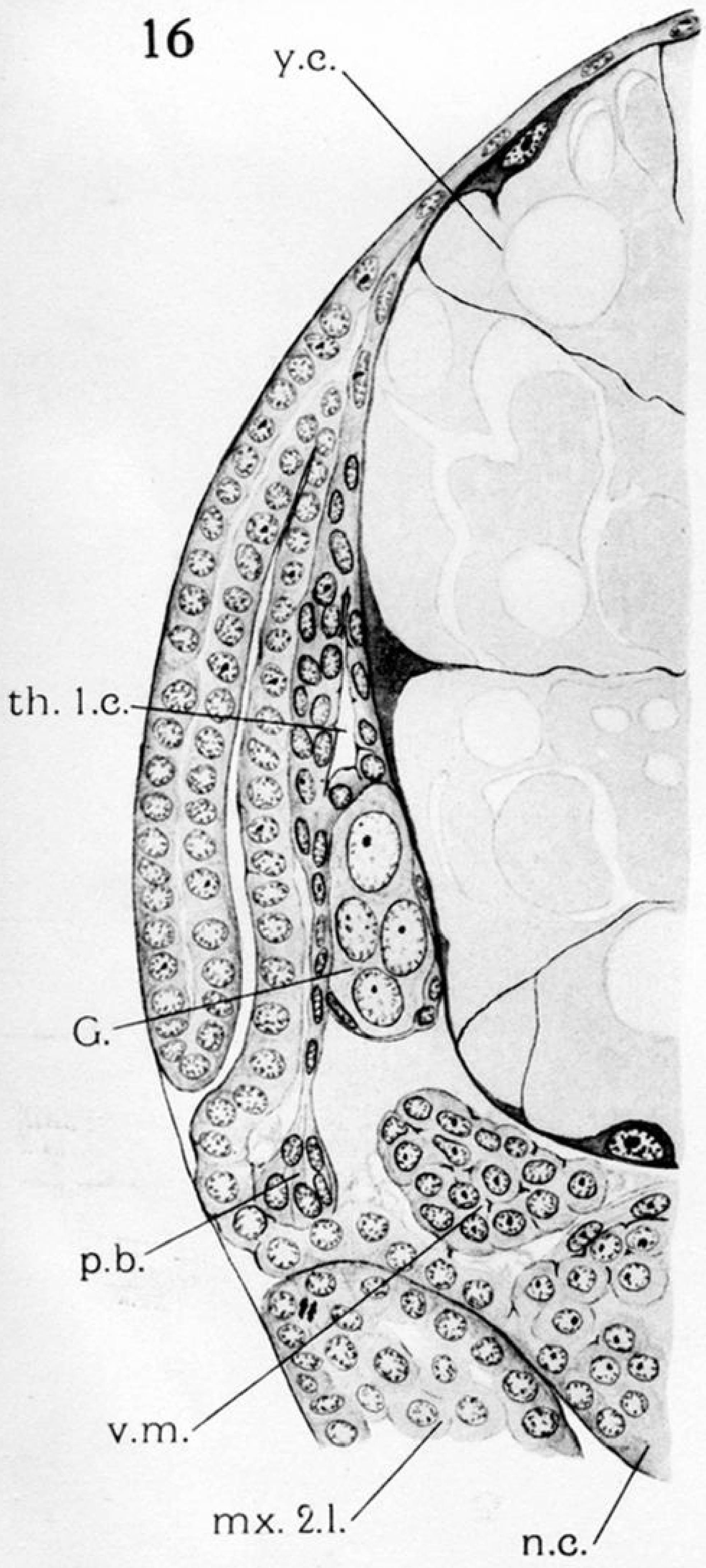

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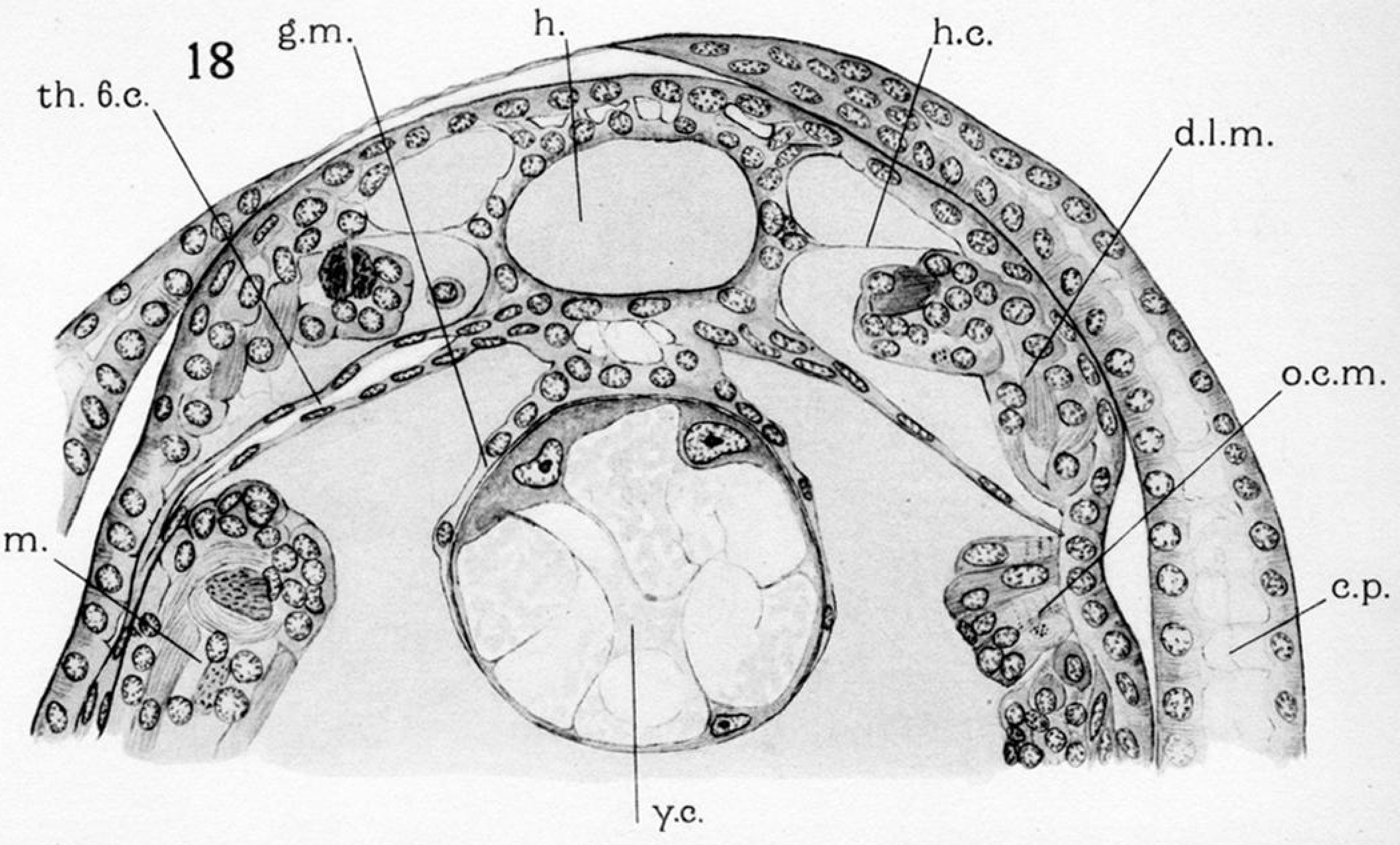

PLATE 23.

FIG. 16.—Transverse section through the first thoracic segment of an older stage. It shows the further upgrowth of the dorsal mesoderm, and its association with the genital rudiment. The outer wall of the cœlomic sac is thickened. × 570.

FIG. 17.—Transverse section through the second thoracic segment. The first appearance of the cardiac and pericardial spaces is seen and the formation of the heart walls and mid-gut mesoderm from the dorsal mesoderm. The dorsal longitudinal muscle is differentiated from the outer wall of the cœlomic sac. Above the nerve-cord rudiment lies the ectodermal tendon. × 570.

FIG. 18.—Oblique transverse section through the sixth thoracic segment on the left and intersegment on the right. The heart tube is now completed. The cœlomic cavity lies in the pericardial floor on the left and the latter is connected to the lateral ectoderm intersegmentally on the right. The dorsal longitudinal muscle lies in the pericardium, and the outer connective muscle from the ventral mesoderm is attached to the ectoderm on the right. × 570.

FIG. 19.—Frontal section at the level of the cœlomic sacs at the same stage as fig. 16. The dorsal mesoderm has united to form the continuous pericardial floor, the maxillary and first thoracic cœlomic sacs are about to unite, and the rudiment of the dorsal muscle has separated from the outer walls of the sacs. × 570.

FIG. 20.—Drawn from two contiguous sections at the intersegment between the first two thoracic segments. The ectodermal rudiment of the flexor and extensor limb muscles has been nipped off from the intersegmental fold of ectoderm, and the outer connective muscle from the ventral mesoderm has grown out above to meet the lateral body wall. The dorsal longitudinal muscle and lateral attachment of the pericardial floor are seen just above these muscles. × 570.

FIG. 21.—Section through an older intersegment. The upper attachments of both ectodermal and outer connective muscles have been carried dorsally. × 570.

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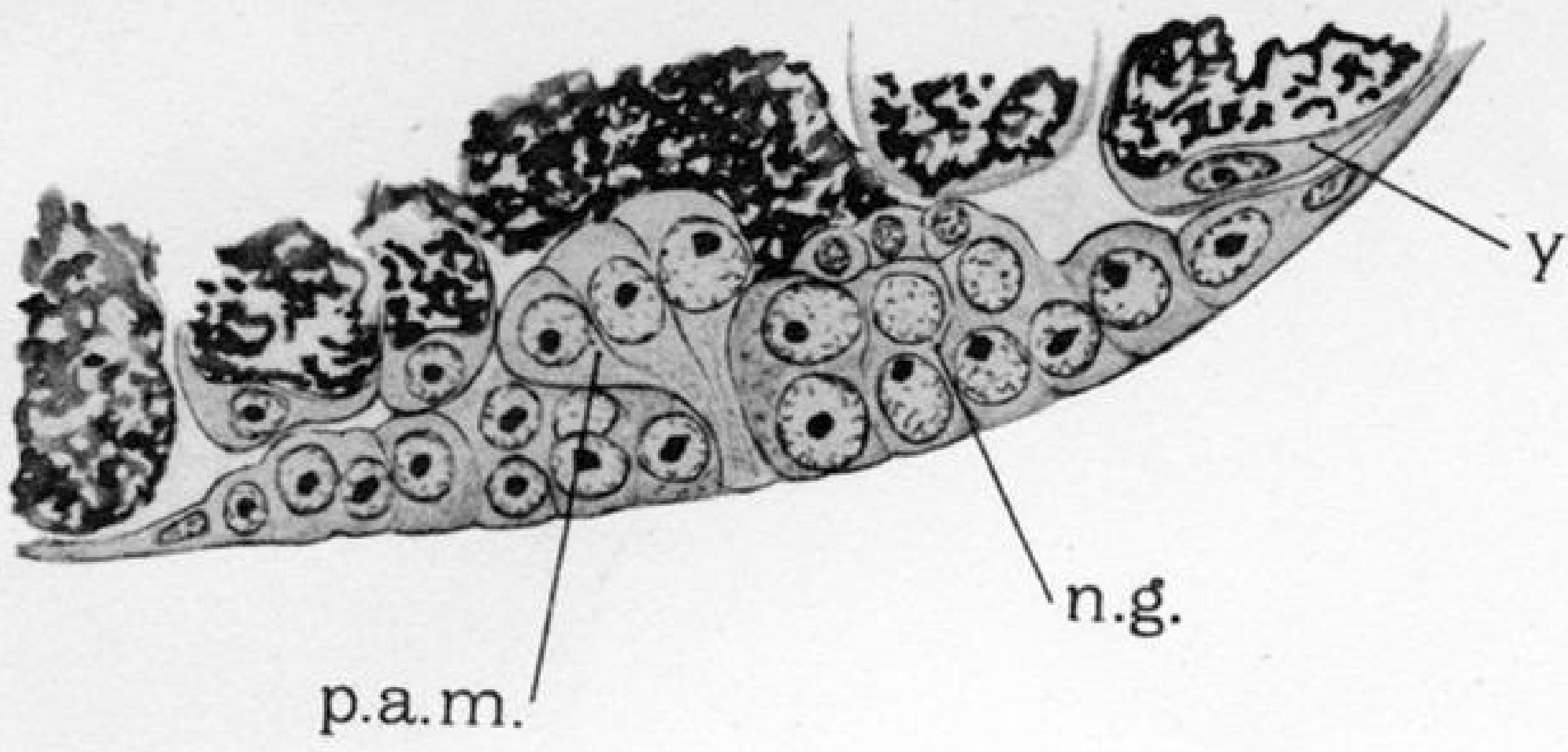

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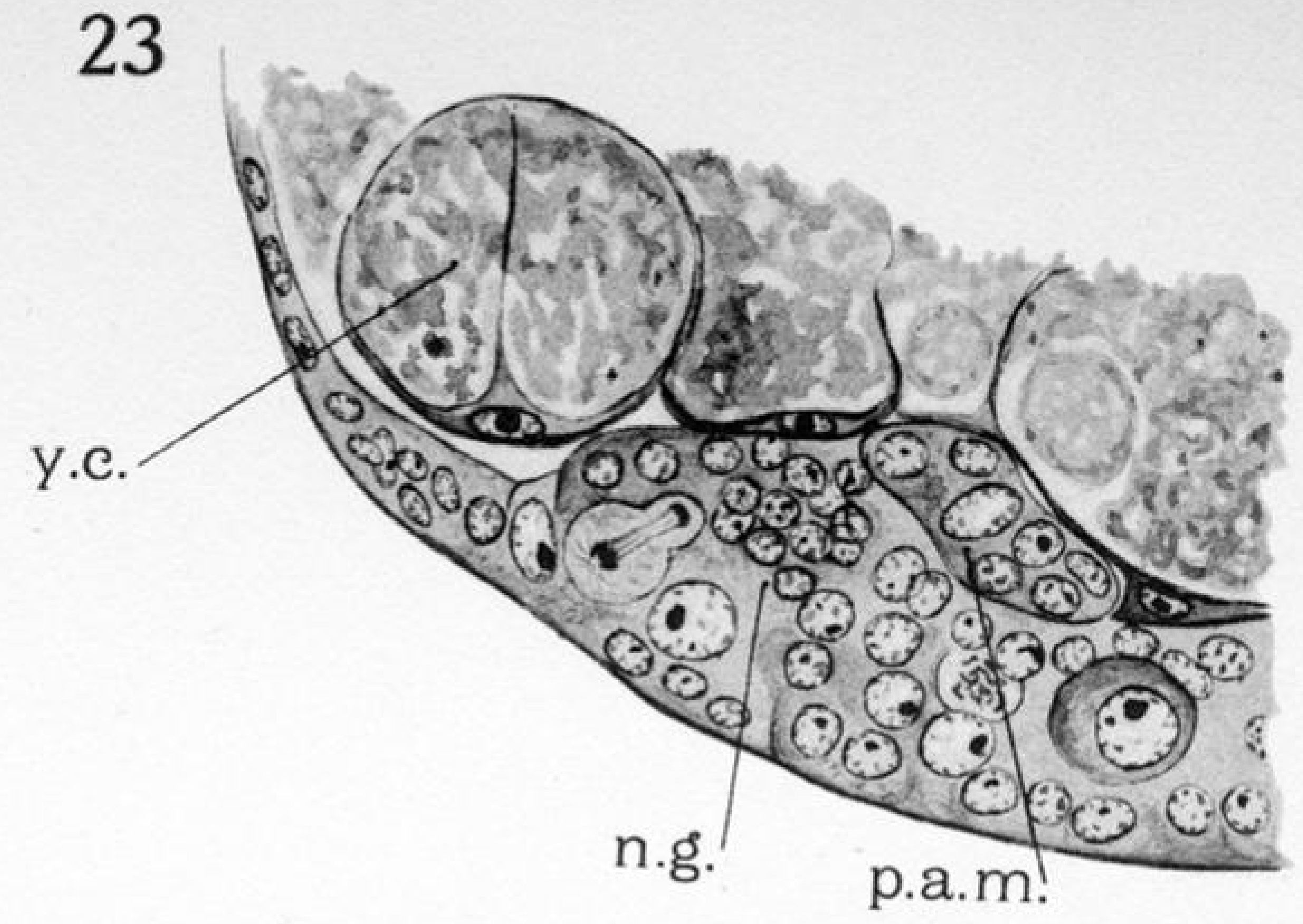

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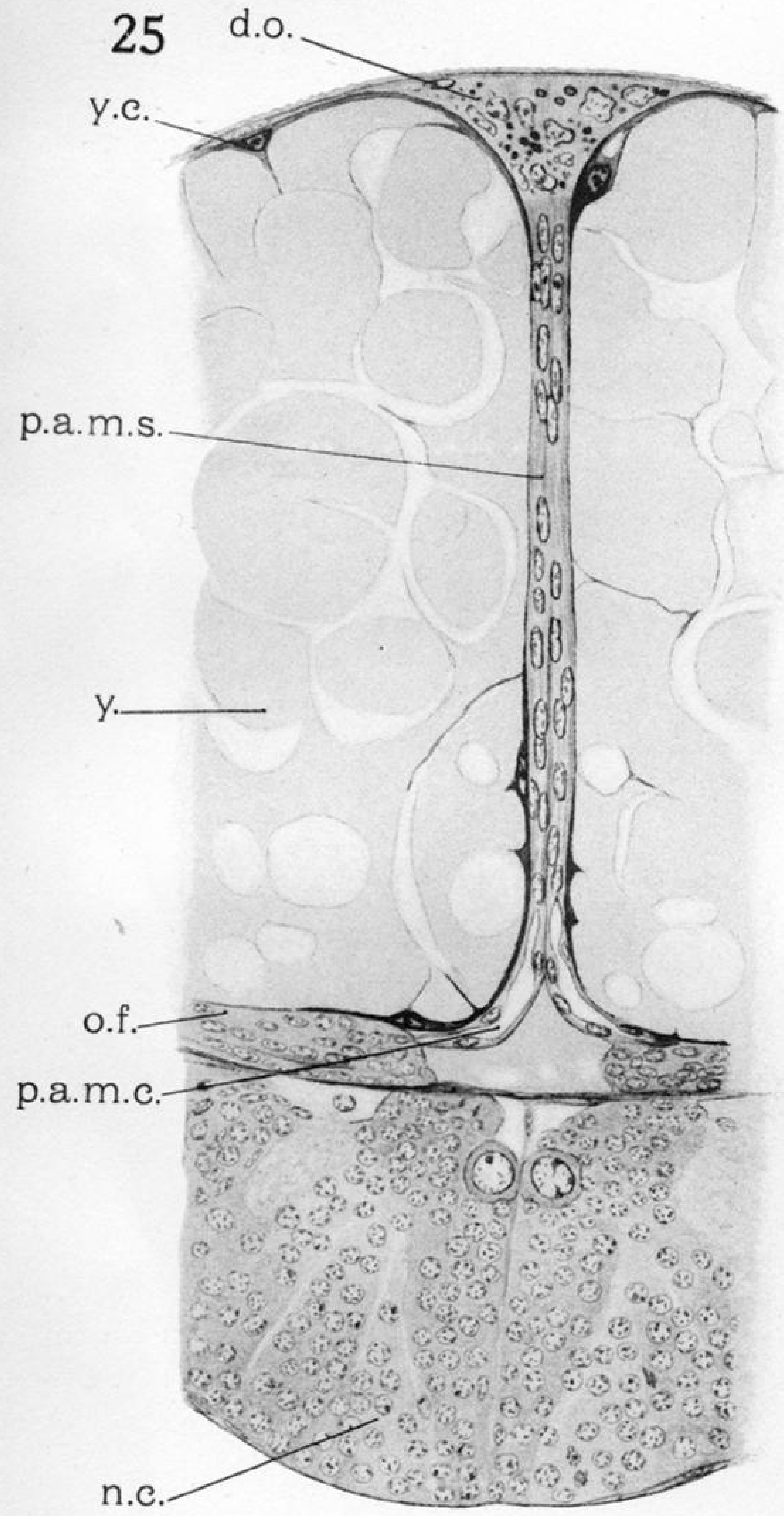

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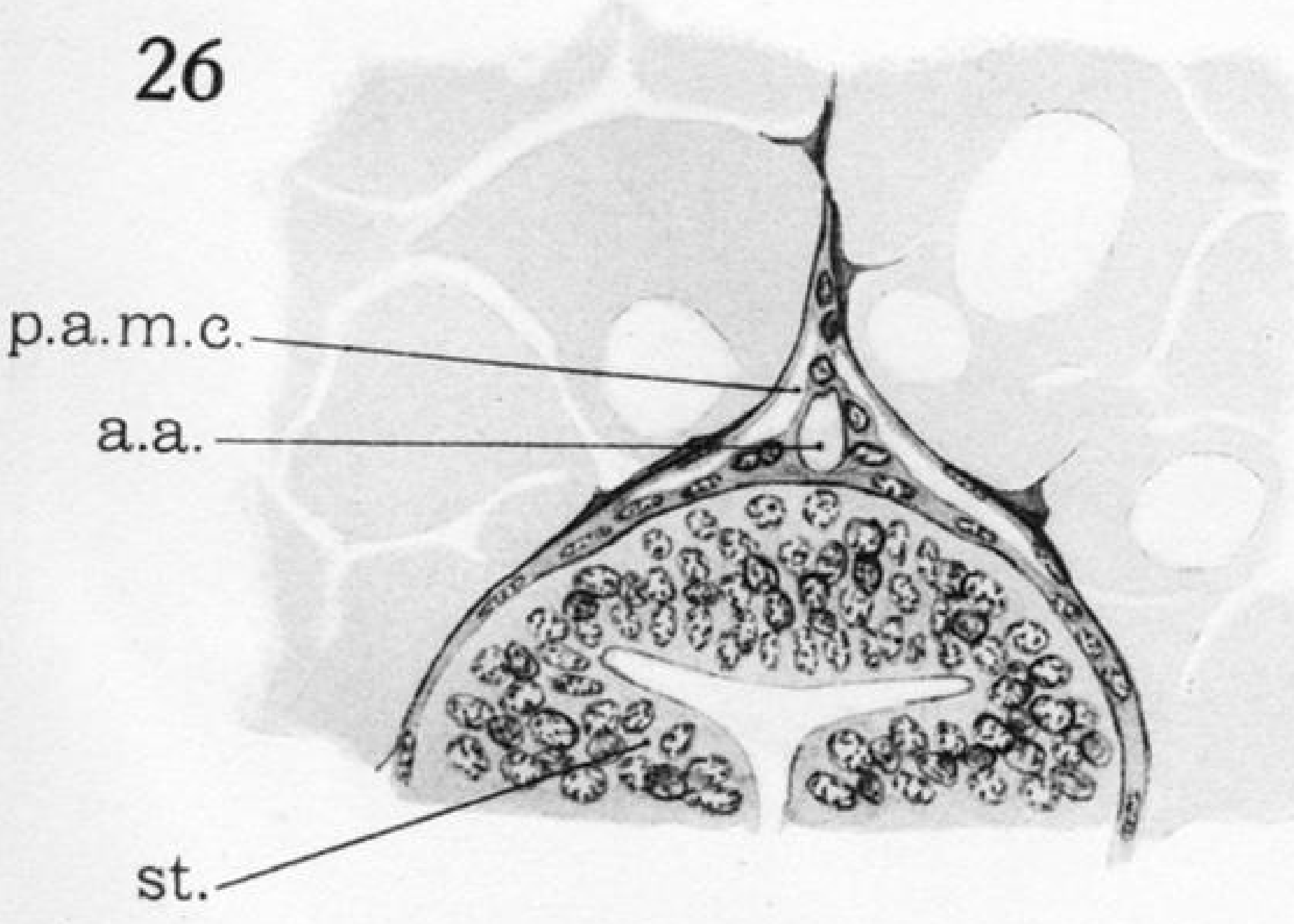

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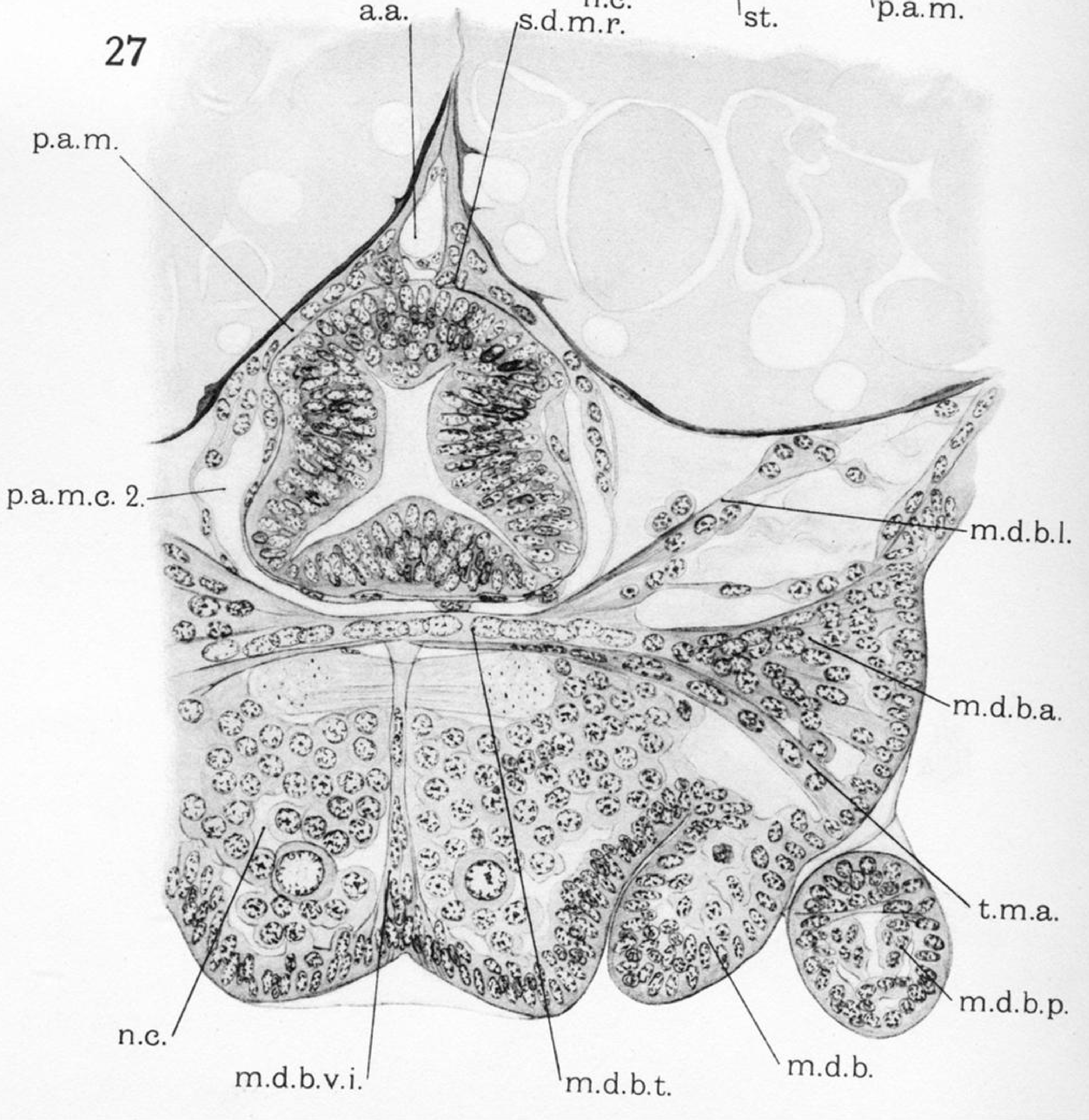

PLATE 24.

FIG. 22.—Transverse section of an early V-shaped germinal disk anterior to the antennules showing the preantennulary mesoderm slipping inwards. × 465.

FIG. 23.—Transverse section of a later stage through the same region showing the preantennulary mesoderm blocks lying within the thickened ectoderm. × 465.

FIG. 24.—Transverse section through the posterior part of the antenna. The preantennulary somites lie on either side at the end of the stomodæum, and their cœlomic cavities are formed. × 465.

FIG. 25.—Transverse section just anterior to the stomodæum. The upper preantennulary strands have grown up to meet the dorsal organ, and their cœlomic cavities are restricted to their lower parts. × 465.

FIG. 26.—Transverse section through the stomodæum and investing lower preantennulary sacs. Their cœlomic cavities are reduced in size and their inner walls are forming the anterior aorta. × 570.

FIG. 27.—Transverse section of an older stage. The anterior aorta is completed and the preantennulary strands are forming muscle insertions for the dorsal stomach muscles on the wall of the stomodæum on either side. The later-formed cœlomic spaces have united below the stomodæum. The ectodermal mandibular tendon is seen attached to the mid-ventral ectoderm by the intucking which partly formed it, and laterally the mesodermal mandibular adductor muscle rudiments are attached to the tendon. × 570.

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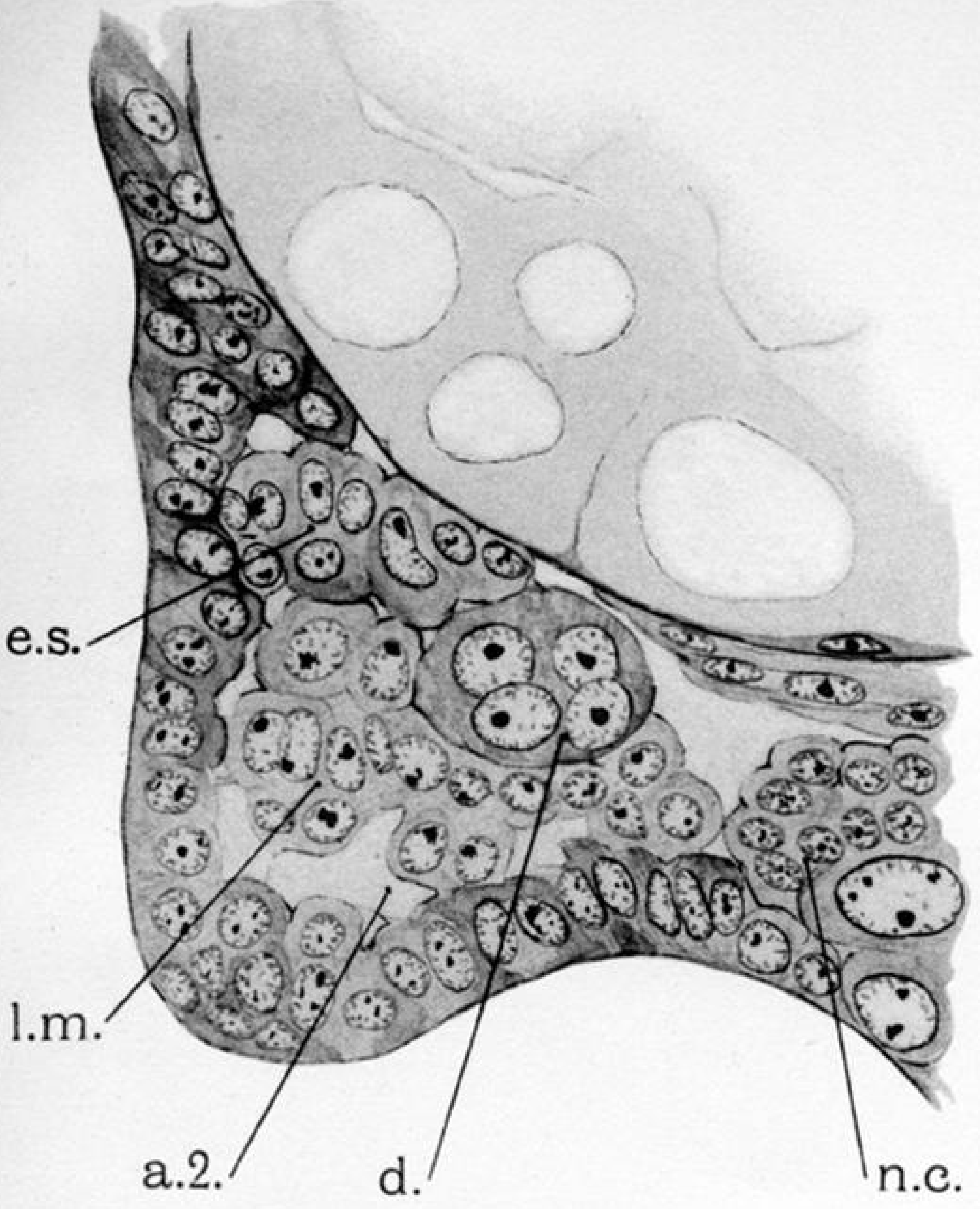

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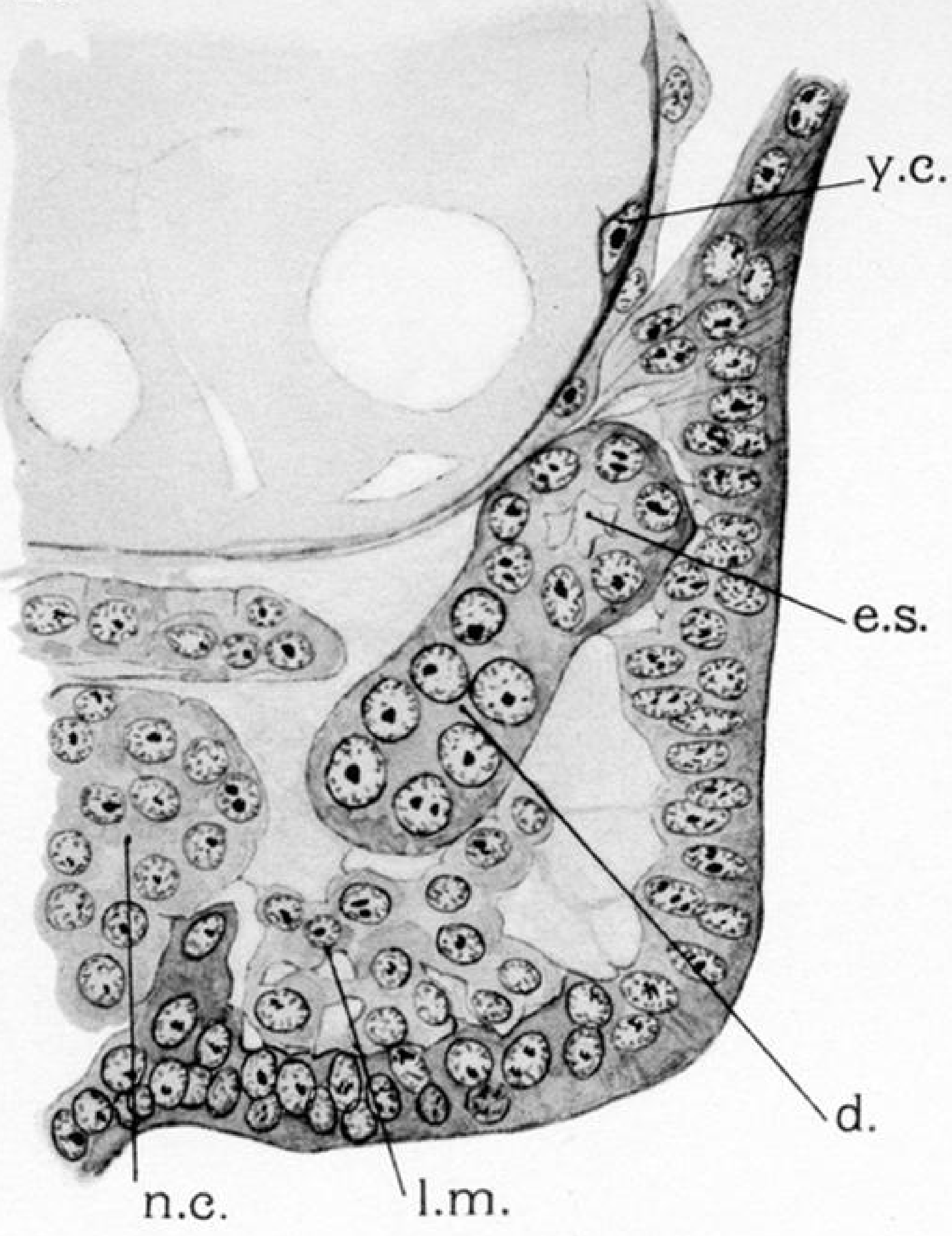

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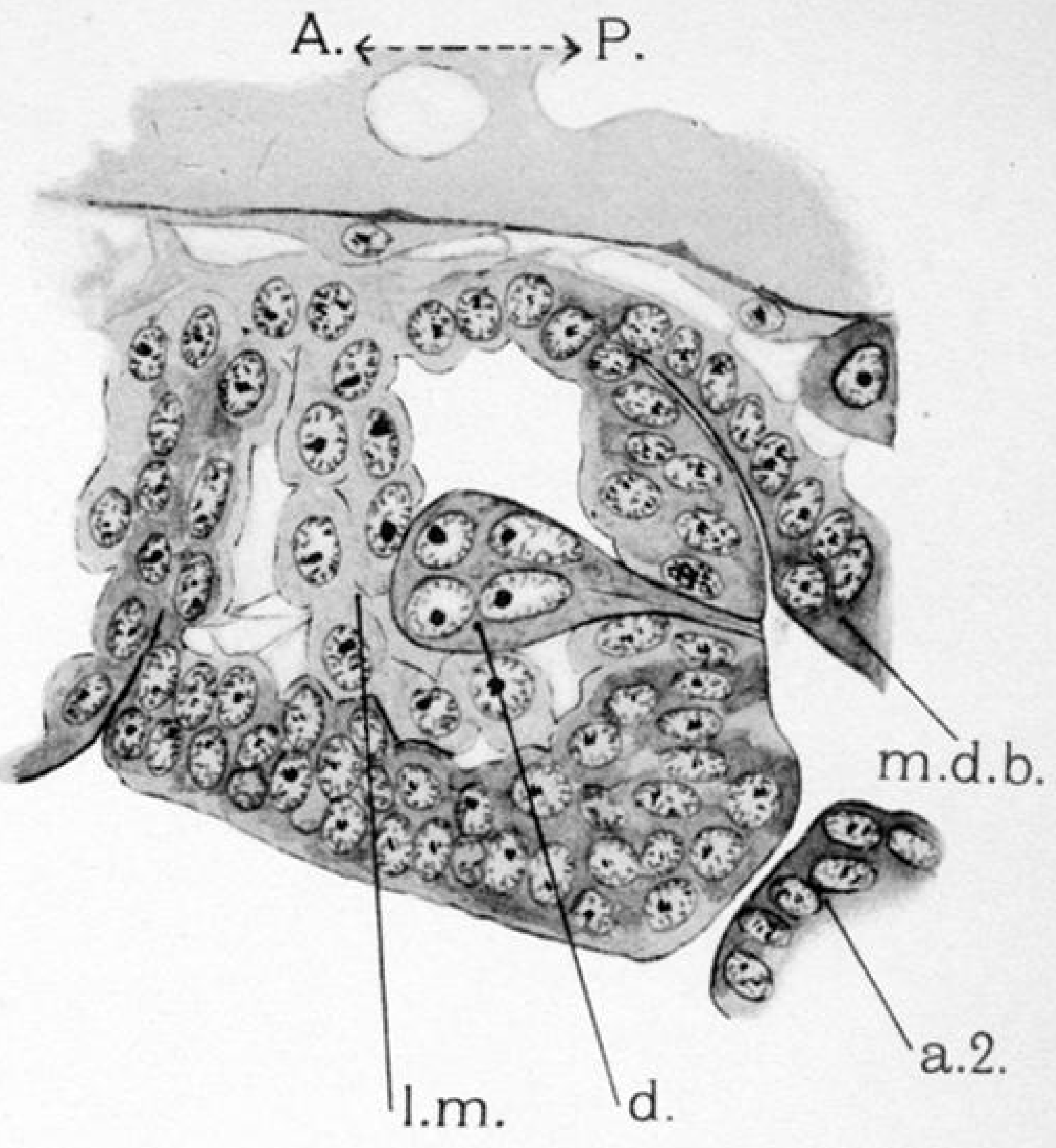

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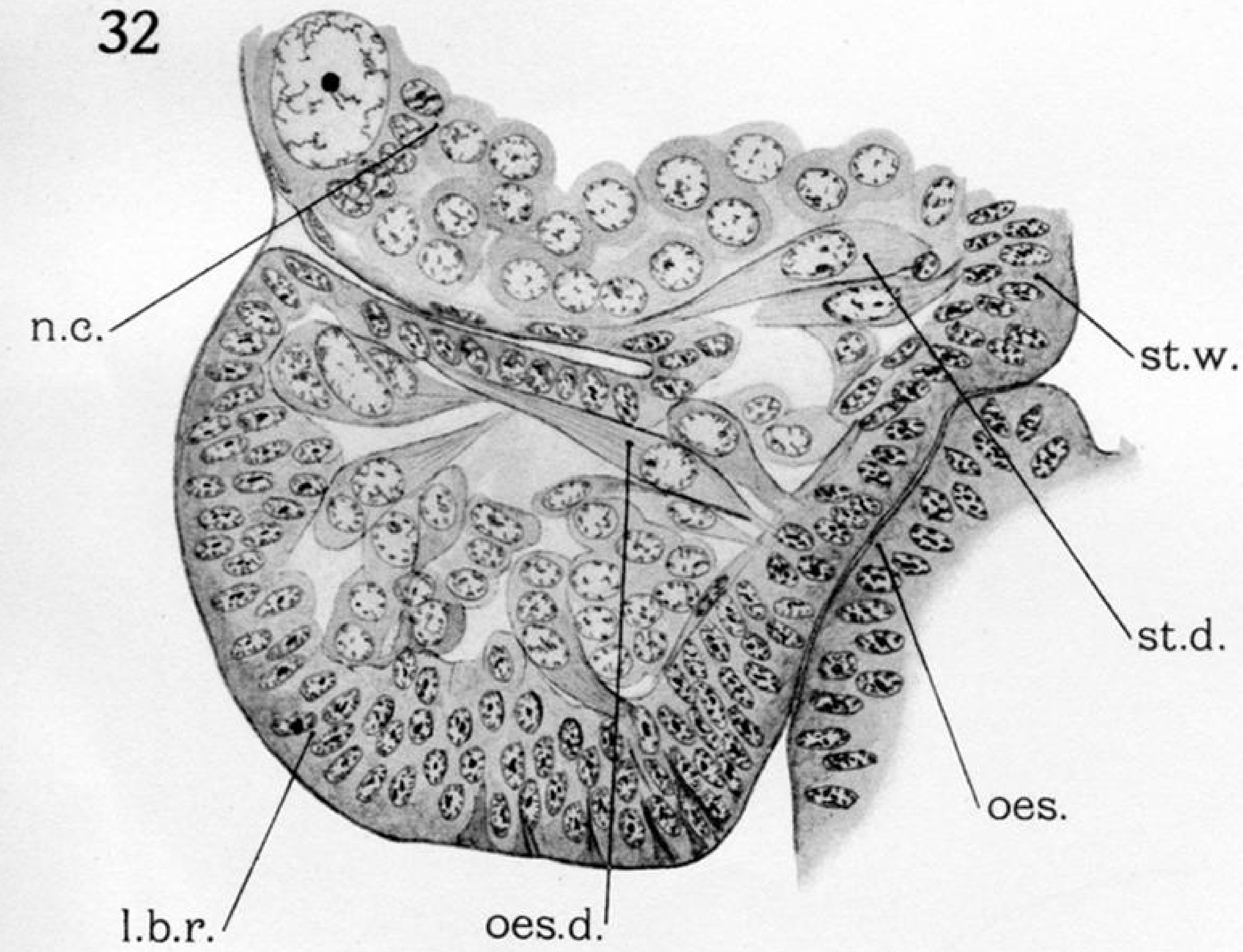

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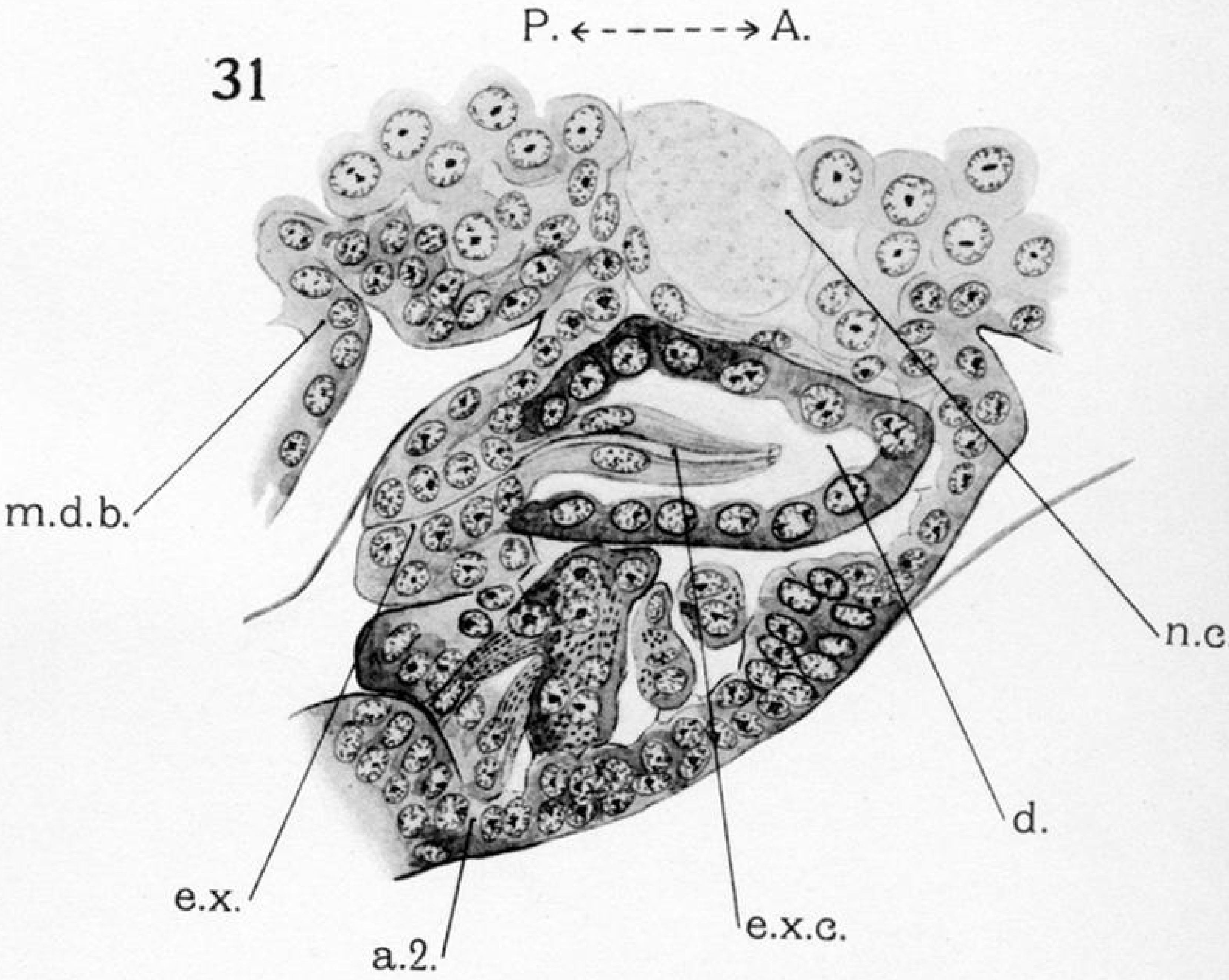

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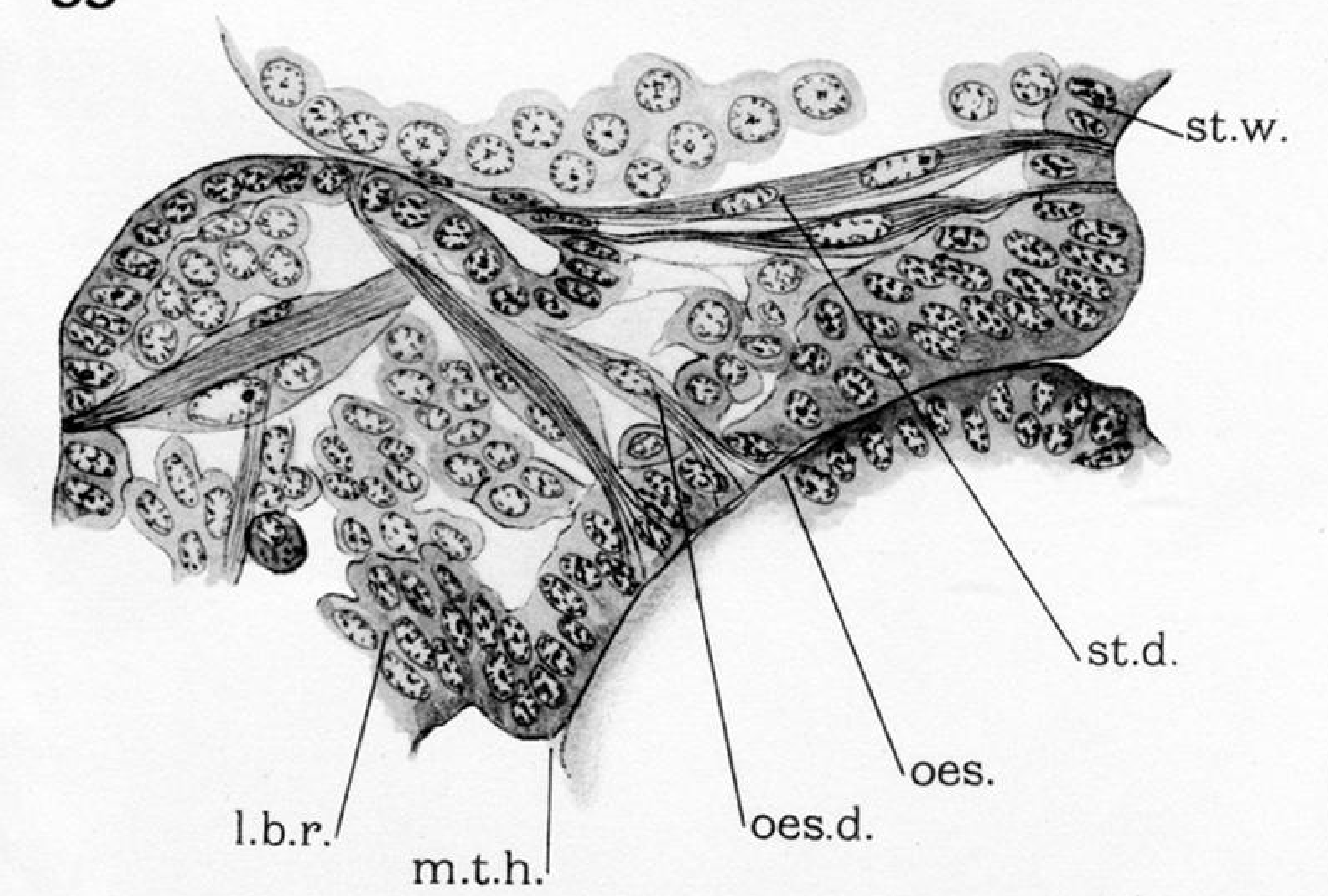

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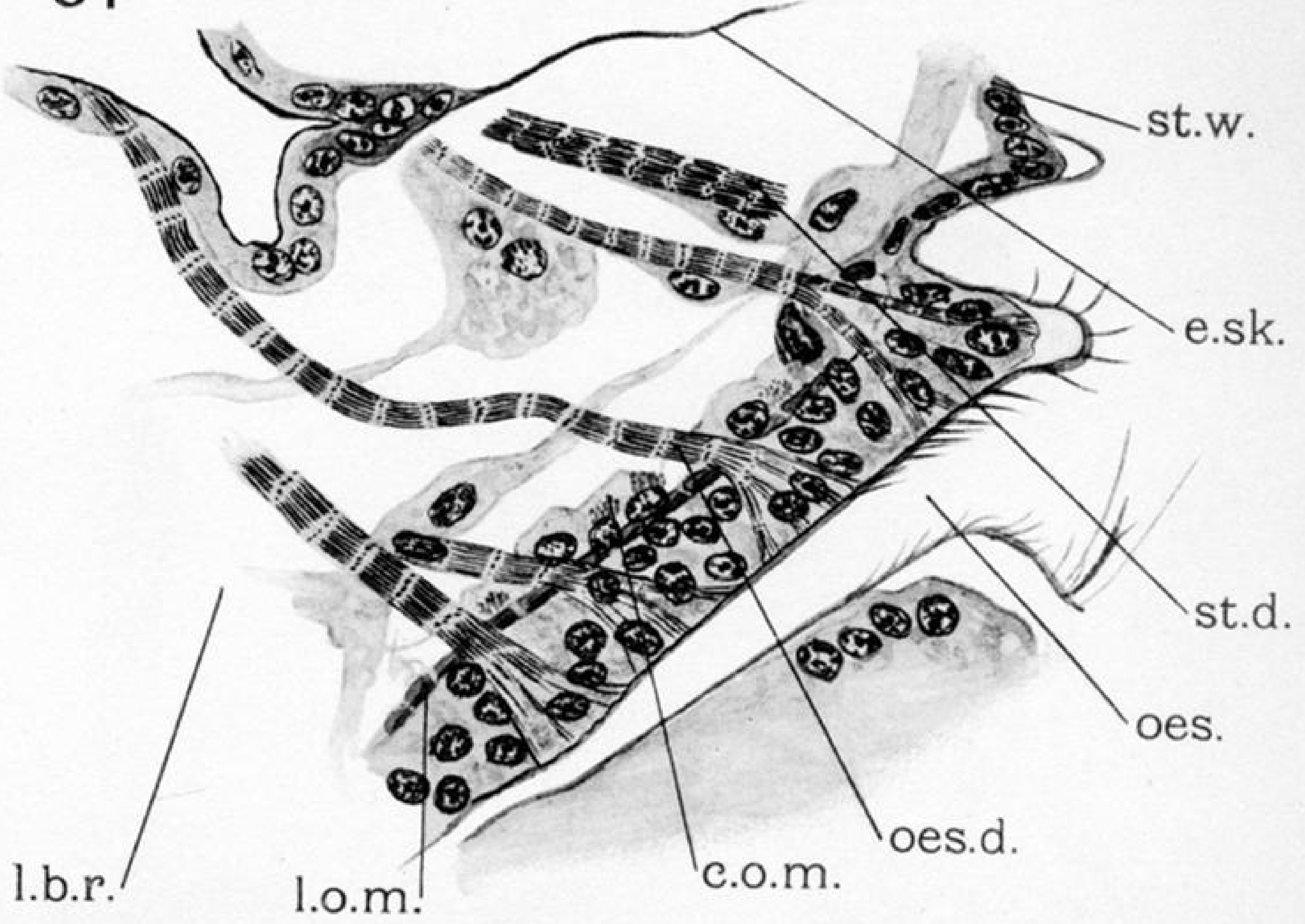

Plate 25.

Fig. 28.—Transverse section through the antennal base, showing the differentiation of the mesodermal block into end sac, duct and limb mesoderm cells. × 640.

Fig. 29.—Older stage: the end-sac cells are forming a hollow sphere and the duct rudiment is compact and solid. × 640.

Fig. 30.—Parasagittal section through the base of the antenna, a little older than the last. Two duct cells have now pushed their way between the ectodermal cells to reach the cuticle. × 640.

Fig. 31.—Frontal section of an older stage through the base of the antenna. The duct now has developed a lumen and the ectoderm has been drawn inwards to form the exit tube. A funnel formed by the latter projects into the duct lumen. × 640.

Fig. 32.—Parasagittal section through the labrum to show the development of œsophageal and cardiac stomach dilator muscles. Four spindle-shaped mesodermal cells extend across the space between the labral and œsophageal walls. × 640.

Fig. 33.—An older stage similar to the last. The four spindle-shaped cells are now inserted in the ectoderm at either end and have become striated. × 640.

Fig. 34.—Small adult through a similar region, drawn from two adjacent sections. It shows the œsophageal dilator muscles formed from the rudiments shown in the last two figures. Part of the median endo-skeletal rod extending between the brain and the stomach is also seen. × 640.