

CHAPTER XIV

ORGANS FROM THE MESODERM

THE mesoderm appears as a distinct layer over the dorsal surface of the embryo at the time when the dorsal lip of the blastopore is moving over the white hemisphere (Fig. 25). At first the mesoderm is in close contact with the endoderm, particularly along the mid-dorsal line. The notochord soon separates from the mesodermal sheets of each side by two vertical furrows, so that from this time forward there are two lateral sheets of mesoderm, separated in the mid-dorsal line by the notochord (Fig. 26, E). Around the anterior and posterior ends of the notochord, the two sheets of mesoderm are continued into each other.

These sheets of mesoderm now rapidly extend ventrally. This down-growth is brought about by additions to the ventral borders of the sheets. The new cells that are added come, probably, from the yolk-cells along the free borders of the mesoderm; the yolk-cells in this region dividing rapidly form smaller cells that are joined to the mesoderm.¹ At the time when the medullary folds appear outlined upon the surface, the lateral sheets of mesoderm have extended ventrally and to a certain extent have fused in the mid-ventral line. The cells of each sheet of mesoderm are arranged over the greater part of their extent into two layers; but on each side of the notochord the mesoderm is somewhat thickened to form the beginning of the segmental plate (Fig. 42); and in this region there is, in the early stages of development, no distinct arrangement of the cells into two layers.

¹ According to some authors the ventral extension of mesoderm results from a proliferation of the mesoderm that is first laid down over the dorsal region, but it seems to me there is little ground for such an assumption.

Over the anterior end of the embryo and around the pharynx the mesoderm forms a thin layer of cells, loosely held together (Fig. 26, B). The mesoderm over the dorsal surface of the pharynx and beneath the brain plate is represented by only a single layer of somewhat scattered cells. Around the blastopore there is a thick layer of mesodermal cells which is thickest on the dorsal surface. In general, in the posterior region of the body the mesoderm is thicker than in the middle and anterior regions.

THE MESODERMIC SOMITES

In the following stages of development of the embryo the dorsal ectodermal plate is lifted up and rolled in to form the central nervous system (Fig. 42). The mesoderm lying on

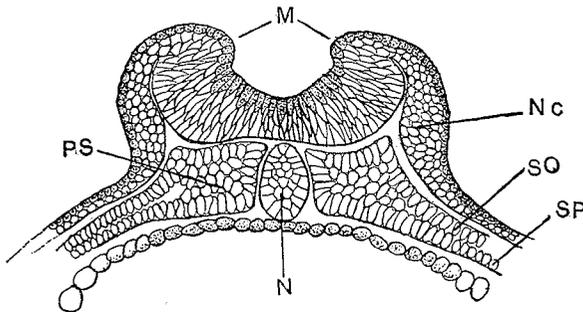


FIG. 42. — Cross-section through middle of embryo. M. Medullary plate. N. Notochord. Nc. Neural crest. PS. Primitive segment-plate. SO, SP. Somatic and splanchnic mesoderm.

each side of the notochord changes shape somewhat during this time. It forms on each side a thick, nearly solid mass of cells, the plate of the primitive segments or segmental plate (Fig. 42). The outermost cells of this mass, *i.e.* those lying nearest to the dorsal surface, now show a tendency to arrange themselves into an epithelial layer. This layer is at first continuous at the sides with the outer or somatic layer of cells of the lateral mesodermal sheets. The two layers of cells of the lateral mesodermal sheets (Fig. 42, SO and SP), the somatic and splanchnic layers, often show a tendency to separate and leave a cavity between them. This cavity filled with fluid

is the coelom, or body-cavity, and is at first continued into the segmental plate. The cavity in the segmental plate lies between the outer epithelial layer and the inner solid mass of cells.

When the medullary plate of the embryo begins to roll in to form the nerve-tube, each segmental plate begins to break up transversely into a series of blocks or mesodermic somites.

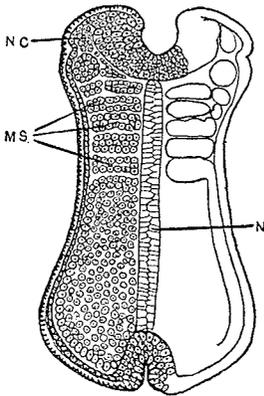


FIG. 43.—Frontal section of Bombinator. (After Götte.) MS. Mesoblastic somites. N. Notochord. NC. Neural crest.

The process begins first in the region anterior to the middle of the embryo (Fig. 43). The mesodermic somites are at first somewhat irregular in outline. The first well-marked somite lies at about the level of the ganglion of the vagus nerve. In front of this there are traces of another somite which is partially broken up into loose mesenchymatous tissue. Still further forward, the series of somites is replaced by loose mesenchyme. In the frog the number of head-somites (or structures corresponding to them) is uncertain.

At first the primitive segments or somites are not separated from the lateral sheets of mesoderm, but almost

immediately after the segmental plate has begun to break up transversely into somites, these begin to separate also from the lateral mesoderm. This separation appears first in the intersegmental borders. At this time the medullary folds have met to form a closed tube. Posterior to the fourth segment, the segmental plate is beginning to break up into blocks, but these have, as yet, no sharply marked outer or ventral boundaries. The body-cavity of the lateral mesodermal sheet is at first, as we have seen, sometimes continued into the cavity of the segmental plate, but when the constriction of the plate from the lateral sheets takes place, this communication (the communicating canal) is lost. Even in the younger stages there is a differentiation of a peripheral epithelial layer surrounding the dense central mass or kernel of the somites. This peripheral part is represented on the

outer side of each somite by the entire somatic layer. Along the ventral and median boundaries of the somites a layer having a loose epithelial character (mesenchyme) is also to be seen. Thus the central mass which is to develop into the myotome lies on the median side of the cœlom, and is wholly surrounded by an epithelial layer. Frontal sections show that this layer can also be traced inward for some distance between successive somites over both their anterior and posterior surfaces (Fig. 44).

“Not merely is mesenchyme produced by the thin peripheral layer of the somites, but in anterior regions considerable portions of the kernels of the somites also undergo a metamorphosis in this direction. Thus, if I be not mistaken, a somite immediately in front of somite 1 has been wholly converted into mesenchymatic tissue. The kernel of the succeeding somite (somite 1) has given rise to a considerable quantity of mesenchyme, and the process has been manifested, though to a less degree, even in succeeding somites.”¹

At the time when fourteen pairs of somites are present² the cells of the more anterior somites have begun to differentiate into muscle-fibres. The cells of each somite elongate in the antero-posterior direction and become cylindrical in shape, and each extends the whole length of its somite (Fig. 44, B). Each cylindrical cell has at first but a single nucleus. Around the wall of the cell a layer of fine fibrillæ appears. The original nucleus divides and re-divides into many nuclei, which lie scattered throughout the cell.

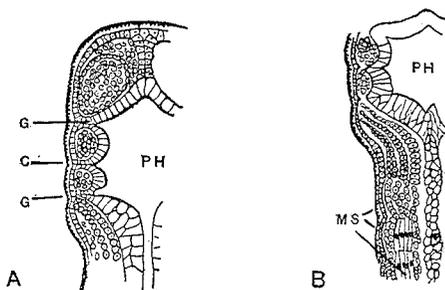


FIG. 44.—Frontal sections through the anterior end of Bombyx. (After Götze.) A. Shows three gill-pouches (G), and mesoderm of arches. B. Shows formation of mesodermic somites (MS). PH. Pharynx.

¹ Field ('91).

² Four days after fertilization of the egg, when three pairs of gills have appeared.

The development of the musculature of the head, limbs, and ventral body-wall takes place at a later stage. A description of the origin and development of these structures is beyond the limit of the present account.

THE HEART AND BLOOD-VESSELS

The heart appears at the time when the medullary folds have rolled in, and have met along the mid-dorsal line; it lies below the pharynx, and anterior to the liver (Fig. 37, B). The mesoderm in this region shows a tendency to split into two sheets and, where the heart is about to develop, a cavity, a part of

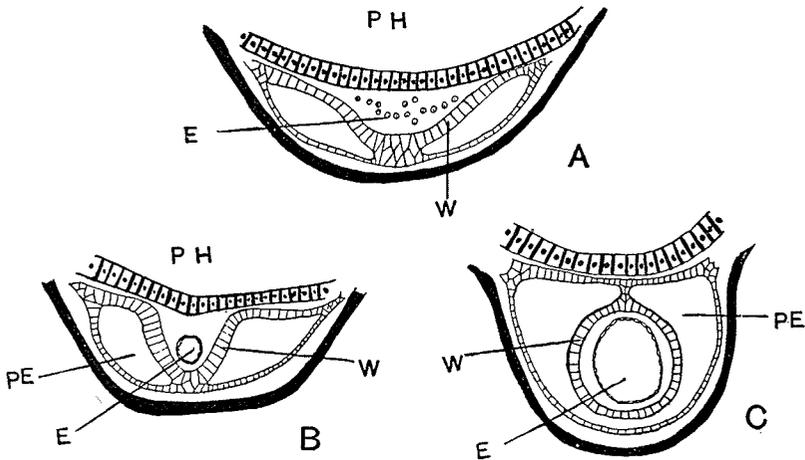


FIG. 45.—Three stages in development of heart. E. Endothelium. PE. Pericardium. PH. Pharynx. W. Wall of heart.

the cœlom, appears between the sheets. A cross-section of the larva (Fig. 45, A) shows on each side of the mid-ventral line in the region of the heart the somatic and splanchnic layers widely separated from each other. The cœlomic cavities of the right and left sides are not continuous across the middle line, but anterior and posterior to this section the cœlomic cavity is found to be continuous before and behind with the general cœlomic space on each side. A few scattered cells lie in the middle line between the splanchnic layer and the ventral wall of the pharynx (Fig. 45, A). These cells have

been described as originating from the ventral wall of the archenteron, and if so, have had a different origin from the other cells of the heart.¹

At a somewhat later stage of development the walls of the coelomic cavities of the right and left sides separate further (Fig. 45, B). The splanchnic layer thickens, and begins to surround the proliferation of scattered "endodermal cells." These endodermal cells arrange themselves into a thin-walled tube stretching throughout the heart-region (Fig. 45, B). Subsequent development shows that this tube becomes the endothelial lining of the heart. Around this endothelial tube the thickened splanchnic layers now begin to push in from the sides between the tube and the lower wall of the pharynx. The tube becomes finally entirely surrounded by mesoderm (Fig. 45, C). The mesoderm from the sides that has met beneath the pharynx forms the dorsal mesentery of the heart. The mesoderm around the tube continues to thicken, and forms later the musculature of the heart.

At first the heart has also a ventral mesentery formed by the union of the walls of the coelomic cavities below it (Fig. 45, B), but later the mesentery is in part absorbed and the coelomic cavities become continuous below from side to side, forming the pericardial chamber. The outer layer of somatic mesoderm gives rise to the pericardium itself.

The tubular heart is attached at its posterior end to the liver and anteriorly to the wall of the pharynx. It becomes free ventrally and later also dorsally along the middle of its course, and owing to an increase in length is bent on itself into an *∞*-shaped tube (Fig. 39).

When the tadpole is $4\frac{1}{2}$ mm. in length, we find a vessel opening into the posterior end of the heart, the sinus venosus, formed by the union of two large vitelline veins. These veins have appeared on each side of the liver-diverticulum and continue along the yolk-mass in a fold of the splanchnopleure. They are supposed to carry to the heart the food-material absorbed from the yolk. Into the sinus venosus empty also two

¹ At least these cells have arisen from the yolk-cells after the ventral mesoderm has been split off.

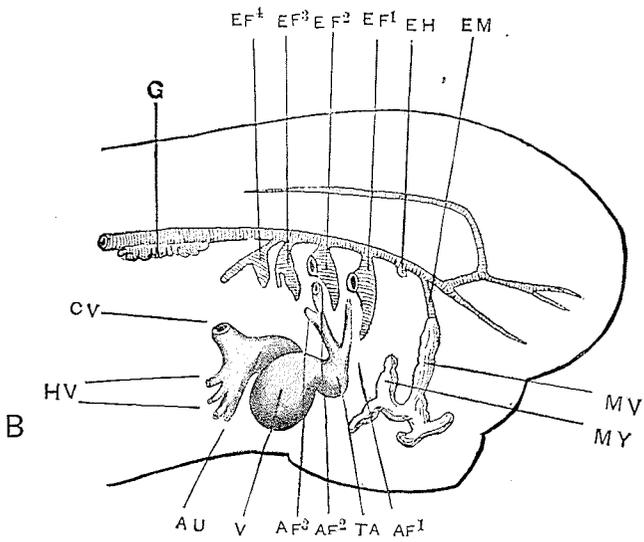
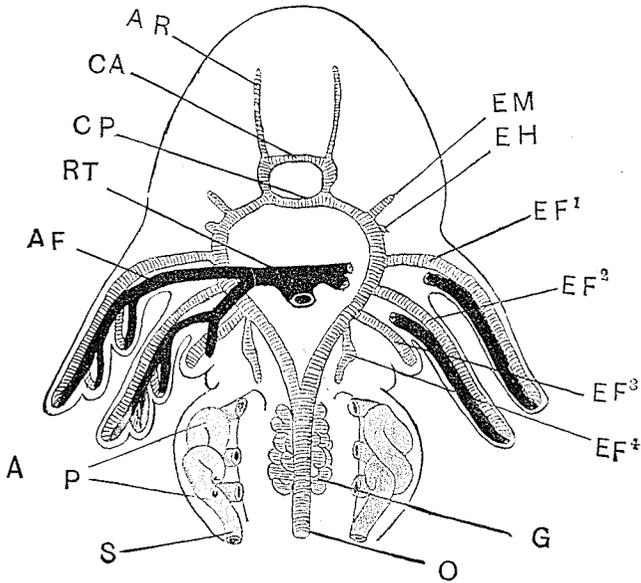


FIG. 46, A.—AF. Afferent branchial vessel. AR. Anterior cerebral artery. CA, CP. Anterior and posterior commissural vessel. EF¹, EF², EF³, EF⁴. Efferent branchial vessels of the first, second, third, and fourth branchial arches. EH. Efferent hyoid vessel. EM. Efferent mandibular vessel. G. Glomus. O. Aorta. P. Pronephros. RT. Truncus arteriosus. S. Segmental duct. (After Marshall.)
 B.—AF¹, AF², AF³. Afferent branchial vessels. AU. Auricle. CV. Cuvierian vein. EF¹, EF², EF³, EF⁴. Efferent branchial vessels. EH. Efferent hyoid vessel. EM. Efferent mandibular vessel. G. Glomus. HV. Hepatic veins. MV. Mandibular vein. MY. Hyoidean vein. TA. Truncus arteriosus. V. Ventricle. (After Marshall.)

veins that have come down from the dorso-lateral region of the embryo. These are the Cuvierian veins formed on each side by the union of the posterior and anterior cardinal veins. The posterior cardinals bring back the blood from the head-kidneys. Around the head-kidneys these veins form sinuses that are enormously large. Each posterior cardinal also receives somatic veins from the posterior part of the body-wall. The anterior cardinal veins bring back blood from the dorsal part of the head-region.

In a larva $4\frac{1}{2}$ mm. in length, the blood-vessels of the branchial region have also appeared. The anterior end of the heart, the truncus arteriosus, divides into a right and left branch, which pass forward and laterally toward the base of the gill-region. In the mandibular arch no vessels are as yet present. In the hyoid arch an irregular space appears in the mesoderm. In the first branchial arches two vessels appear, a large efferent vessel (Fig. 46, for an older embryo) connected with the dorsal aorta, and a smaller afferent vessel. The latter is at present without connection. In the second branchial arch the conditions are like those in the first. In the third branchial arch only a small efferent vessel has as yet appeared. No vessels are present at this time in the fourth branchial arch. The dorsal aorta is represented by a paired vessel in the dorso-pharyngeal region. Opposite the hyoid arch each branch of the dorsal aorta divides into a dorsal and into a ventral branch. The dorsal branches meet each other behind the infundibulum, while the ventral branch passes forward to end blindly (Fig. 46). The two aortæ unite posteriorly into a single vessel at the level of the pronephros (Fig. 46, A).

The condition of the blood-vessels shortly after the tadpole has left its envelopes (it is then 7 mm. in length) is illustrated in Figs. 46 and 47. The heart has enlarged and is further twisted on itself. The aortic bulb-portion and the auricular and ventricular portions are distinctly marked from each other by constrictions of the tube. The right and left branches of the aortic bulb have grown toward the gill-arches, and the afferent vessels of the first and second branchial arches have united with the ventral aortic branches AF^1 and AF^2 . The efferent branches, EF^1 and EF^2 , of the first and second bran-

chial arches have greatly enlarged, and the efferent and afferent vessels are now also united to each other in each arch by small vessels (Fig. 47) or capillary tubes. The efferent vessels of these two arches are also in communication with the dorsal aorta of their respective sides. There is thus established at this time a circulation of blood from the heart to the dorsal aorta by way of the first and second branchial arches.

In the third and fourth branchial arches the efferent vessels have appeared. In the third arch the beginning of an affer-

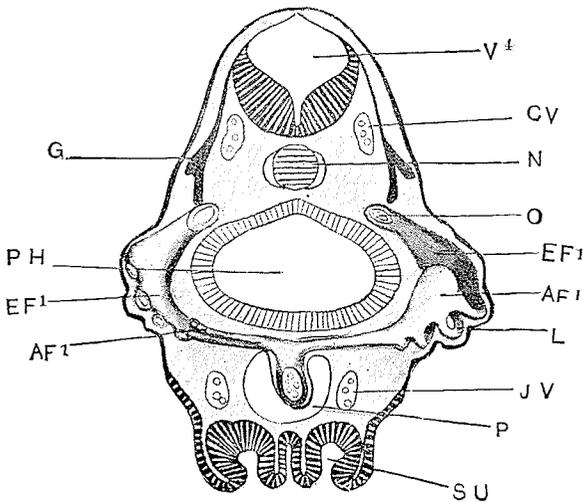


FIG. 47.—AF¹. Afferent branchial vessel. CV. Anterior cardinal vein. EF¹. Efferent branchial vein. G. Pneumogastric nerve. JV. Inferior jugular vein. L. Capillary loop connecting afferent and efferent branchial vessels. N. Notochord. O. Aorta. P. Pericardium. PH. Pharynx. SU. Suckers. V⁴. Fourth ventricle. (After Marshall.)

ent vessel is seen (Fig. 46). In the hyoid arch blood-vessels appear, as we have seen, at an early stage of development and seem to correspond to those in the branchial arches, but after developing to a certain extent, they begin to degenerate. In the mandibular arch no vessels have appeared at the time when the larva leaves its capsule. Soon after this time a vessel develops in this arch, and a small diverticulum arises from the dorsal aorta (Fig. 46, B, MV), and later the two vessels unite.

The origin of the heart has been described, but as yet *the*

method by which the blood-vessels are formed has not been fully considered. The dorsal aorta is the first vessel to arise. A series of isolated lacunæ appear in the mesoderm along the roof of the pharynx, and by opening into one another form a pair of longitudinal vessels. Vessels next appear in the first and second branchial arches. Similar vessels arise later in the third and fourth branchial arches. In the hyoid and mandibular arches the vessels appear, as we have seen, later still. These branchial blood-vessels originate in part as isolated lacunæ in the mesoderm, and in part as outgrowths of already existing vessels. For instance, *lacunar vessels* appear in the mesoderm of the gill-arches, two in each arch. One of these is the efferent lacunar vessel, and later connects with a corresponding diverticulum from the dorsal aorta, and the other lacunar vessel is the afferent vessel of the same arch. This latter vessel grows ventrally toward the diverticulum from the truncus arteriosus and unites with it.

The walls of the blood-vessels are formed directly from the mesodermal cells around the lacunæ. "The blood-corpuscles are free cells that have been left in the lacuna-spaces, or more usually are cells budded off at a later stage from the walls of the vessels into their cavities."¹ At first the blood-corpuscles are simply spherical cells containing yolk-granules. Only after the embryo is hatched do many of the corpuscles begin to acquire the shape and character of red blood-corpuscles.

THE PRONEPHROS

The excretory system of the young embryo is represented on each side by the *pronephros* and the *segmental duct*. Whether the pronephros and duct arise in part from an early ingrowth of ectoderm or whether they develop *in situ* from the somatic mesoderm is perhaps still open to doubt. Field ('91), who has worked out most recently the development of the pronephros and segmental duct in the frog, describes the organ as coming entirely from the mesoderm. We shall follow closely Field's account. The pronephros appears at a stage when the medullary

¹ Marshall ('93).

plate is first formed. It is well marked at the time when the medullary folds have rolled in, but have not yet fused. A thickening of the somatic layer of the lateral mesoderm near the second mesoblastic somite marks the beginning of the pronephros (Fig. 48, A). At a later stage, the mesodermic thickening becomes larger, and the anterior end arches over toward the cœlomic cavity, to form the first nephrostome. The ventro-posterior part of the nephrostomal thickening is continued backward as a thickening of the somatic wall as far as the seventh somite, to form the segmental duct. A canalization now takes place in the nephrostomal portion and in the segmental duct. Three short tubes or canals appear in the pronephric mass running outward from the cœlom (Fig. 41). Constrictions appear between the first and second, and between the second and third canalized tracts (Fig. 48, B), and short

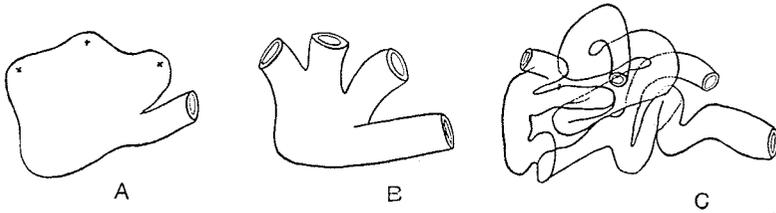


FIG. 48. — Three stages in the formation of the pronephros. (A and C after Field.)

hollow stalks are formed leading ventrally into the longitudinal canal of the segmental duct.

A proliferation of cells from the somatic layer of the mesoblastic somites, dorsal to the pronephros, gives rise to a covering of mesoderm for the pronephros, the *pronephric capsule*. A little later a protrusion of the splanchnic wall opposite to the funnels of the pronephros forms the *glomus* (Fig. 47, B). The glomus becomes filled with blood, and seems to have a direct connection with the dorsal aorta. The bulging portion of the glomus protrudes into the cœlom, and its cavity is separated from the cœlomic cavity by only a single layer of cells.

At the time when the embryo is hatched, the duct of the pronephros, the segmental duct, has fused with the wall of the cloaca, and the lumen of the duct opens into the digestive

tract (Fig. 41). Presumably the pronephros is functionally active at this time. The arrangement of the tubes of the pronephros, and their relation to the common tube or pronephric duct, is shown in Fig. 48, C. The three nephrostomes open into three collecting tubules, and these tubules have elongated independently of one another. The first collecting tubule is short; the second is thrown into several turns and opens into the pronephric duct a short distance from the first. The collecting tubule from the third nephrostome opens some distance behind the point of opening of the second. The segmental duct is thrown into a series of turns between the first and second collecting tubules; and as it leaves the pronephric region it takes at first a tortuous course, and then runs as a straight tube backward to the cloacal opening.

The posterior cardinal veins have appeared at this time, and in the region of the head-kidneys these veins widen into a sinus lying amongst the windings of the collecting tubules of the pronephric duct. The glomus of each side reaching from the region of the first to that of the third nephrostome, and lying exactly opposite the nephrostomes, is well developed (Fig. 46).

So far the description of the development of the excretory system has been that given by Field. The same author adds: "According to the account which at present receives the most general acceptance, the pronephros first appears as an outfolding of the somatopleure in the form of a longitudinal groove. The anterior end of this groove is destined to become the pronephros, the remaining portion is constricted off to form the segmental duct. Since the process of constriction advances from before backward, stages may be found in which a completed tube is continuous posteriorly with a mere groove of the somatopleure. In the anterior region the groove remains in communication with the body-cavity, and grows down toward the ventral surface of the embryo in the form of a broad pocket. The slit-like peritoneal opening of this pouch closes throughout the greater part of its length, leaving, however, two or three regions of incomplete closure, the fundamentals of the nephrostomes."

"The nephrostomal tubules are formed by the fusion of the walls of the pouch between two nephrostomes. The regions of

fusion extend in vertical lines from the nephrostomal margin of the pouch nearly to its ventral border, where there is left an unfused and therefore continuous longitudinal tract constituting the canal which I have called the collecting trunk."¹ Field continues, "In opposition to this view, I would maintain: (1) That the first trace of the excretory system consists of a solid proliferation of somatopleure, the pronephric thickening; (2) that the lumen of the system arises secondarily; and (3) that the pronephric tubules do not appear in consequence of the local fusion of the walls of a widely open pouch, but that they are differentiated at an early stage from the hitherto indifferent pronephric thickening."

The pronephric duct of the Amphibia arises, according to one view, as we have seen above, from an *evagination of somatopleure*, its lumen being therefore a detached portion of the body-cavity. A second view of the origin of the duct is, that it arises from a solid proliferation of somatopleure. Field agrees with the latter view. A third view maintains that the duct is ectodermic in origin. Field has shown, however, that in the Amphibia the excretory system develops most probably without any participation of the ectoderm in its formation.

¹"This view of the development of the pronephros, although suggested by Wilh. Müller, was first described in detail by Goette for *Bombinator*, and was later extended to other Amphibia by the researches of Fürbringer. It has been entirely confirmed by Wichmann, by Hoffmann, and still more recently by Marshall and Bles." (Field, '91, page 281.)