CHAPTER XIII

ORGANS FROM THE ENDODERM

WE may now turn again to the history of the development of the normal embryo.

THE CLOSURE OF THE BLASTOPORE, AND THE FORMATION OF THE NEURENTERIC CANAL

During the last stages of the closure of the blastopore its lateral lips rapidly approach each other, and it then becomes an elliptical and later a slit-like opening (Fig. 23). The posterior edge of the blastopore also grows forward for a short distance, and as a result a pocket-like continuation of the archenteron is formed (Fig. 37, A). The depth of this pocket corresponds to the extent of the forward growth of the posterior edge or ventral lip of the blastopore. If the embryo be examined in the region over which the *posterior lip of the blastopore* has advanced, there will be found at first nothing on the surface to mark the region closed over. Some observers have described faint traces of a groove in this region, but such appearances are probably exceptional. Later, however, when the outlines of the medullary folds have appeared, a distinct longitudinal groove appears in this region running posteriorly from the small blastopore (Fig. 23, B). At the ventral end of the groove a distinct depression or pit is soon formed (Fig. 37), which marks the beginning of the anus. It lies at a point opposite to the bottom of the posterior pocket of the archenteron, and corresponds therefore approximately to the region at which the first trace of the ventral lip of the blastopore was found.

As the medullary folds close in to form the nervous system, the blastopore is overarched by their posterior ends. The folds meet above and posterior to the blastopore, so that the latter can no longer be seen from the surface (Figs. 23, D, E, and 37, A). As a result the central canal of the nervous system

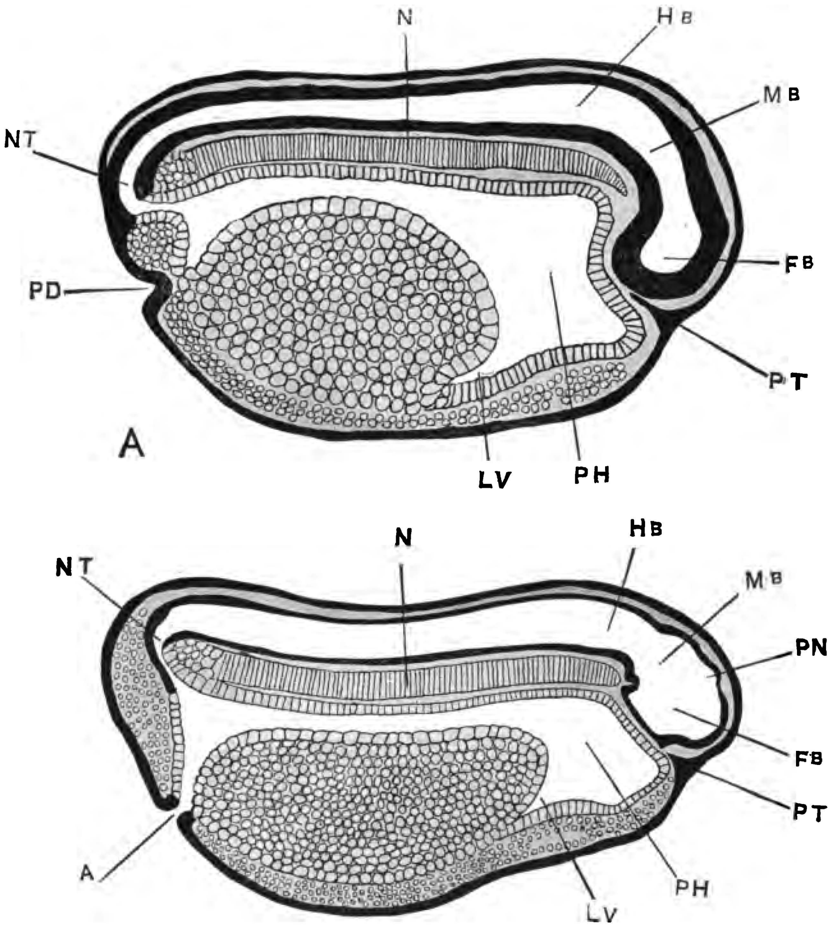

FIG. 37. — Sagittal sections through two stages: A. when blastopore is overarched; B. when anus has formed. (After Marshall, with modifications in A.) A. Anus. FB. Fore-brain. HB. Hind-brain. LV. Liver-diverticulum. MB. Mid-brain. N. Notochord. NT. Neurenteric canal. PD. Proctodæum. PH. Pharynx. PN. Pineal body. PT. Pituitary body.

becomes continuous at its posterior end with the overarched blastopore, and by means of the latter the so-called neurenteric canal, the central canal of the nerve tube, is directly continued into the archenteron (Fig. 37, A). At this time the archenteron is completely closed in from the exterior, since neither the mouth nor the anus has as yet opened.

The posterior ends of the medullary folds close just behind the blastopore. The groove lying behind the blastopore is not overarched by the folds. During this period the posterior pit of this groove has become much deeper. At first, the pit was separated from the archenteron by a thick layer of cells consisting of ectoderm, mesoderm, and endoderm. The mesodermal cells begin to pull away from this region, and the pit, in consequence, becomes deeper. Then the endodermal cells pull away beneath the pit, and only a single layer of ectodermal cells remains to separate the cavity of the archenteron from the exterior. Finally the latter cells also draw away, and the pit opens into the archenteron. The external opening becomes the anus of the frog. It is at first almost on the dorsal surface of the embryo, but it rapidly shifts[1] to a more ventral position, and at the same time the region above it elongates to form the beginning of the tail. The neurenteric canal is only a temporary structure, and is soon obliterated by the growing together of its walls, although its position may be marked in sections for some time after its actual closure by the irregular line of pigment in the region of the coalescence of its walls.

In the Urodela the changes that take place during the final stages of the blastopore are somewhat simpler. The circular blastopore is reduced to an elongated slit-like opening; but there seems to be some variation in the details of the method of its later reduction. The medullary folds *arch over only the anterior end* of the elongated blastopore, leaving free the posterior end. The anterior end becomes the neurenteric canal. The sides of the middle part of the slit-like blastopore come together and fuse at the time of overgrowth of the medullary folds. The posterior end of the blastopore always remains open to the exterior, and forms the permanent anus.

---

[1] The method by which the apparent change in position of the anal opening takes place has not been clearly made out.

The main differences that exist between the methods of formation of neurenteric canal and anus in the frog and in urodeles are these: In the frog the ventral lip of the blastopore grows forward during the closure of the blastopore, and only subsequently a new opening forms at the point from which the for-

FIG. 38. — Embryo of Rana temporaria at time of hatching.

ward growth began (Fig. 37, A, B). In the urodeles (newt and Amblystoma) the ventral lip of the blastopore remains stationary, *i.e.* it retains its first position, and the anus forms directly from its posterior end.

THE DIGESTIVE TRACT AND THE GILL-SLITS

The origin of the archenteron has been described in Chapter VI. At the time when the yolk-plug is drawn in from the surface, the archenteron has begun to enlarge (Fig. 26, A). A series of cross-sections (Fig. 26, B–E) of an embryo at this stage show that the dorsal and lateral walls of the archenteron consist of a single layer of endodermal cells, while the floor of the archenteron is formed by the upper surface of the yolk-mass. The uppermost cells of the yolk-mass show, to some extent, a tendency to arrange themselves in a single layer bounding the archenteron.

Shortly after this period the embryo increases in length, and the archenteron is correspondingly drawn out (Fig. 37). The anterior end of the archenteron enlarges, and the yolk-mass is pushed posteriorly. As a result the middle and posterior parts of the archenteric cavity become smaller than they were in the earlier stages (Figs. 39, 40). The walls of the anterior portion of the archenteron are thin, and composed of a single layer of cells. A blind diverticulum extending from this enlarged anterior portion into the yolk-mass behind (Fig. 37, A, B) forms the beginning of the liver.

The first gill-slits appear at a stage when the medullary folds have rolled over and are about to fuse. At the present stage, the gill-slits are well marked. They appear along the lateral walls of the enlarged anterior end of the archenteron as solid outgrowths of its wall. At the posterior end of the archenteric cavity the position of the blastopore, which has now closed, is marked by a diverticulum, the so-called "post-anal-gut" (Fig. 37). It is in this region that the neurenteric canal of the embryo persists for a short time after the blastopore has been covered over by the medullary folds. The pit-like invagination of ectoderm, the proctodæum, has opened into the postero-ventral portion of the archenteron (Fig. 37, B).

At the time when the tadpole is ready to emerge from the jelly-capsule (Fig. 38), the anterior portion of the archenteron has become larger and longer (Fig. 39), and in the region where the heart forms, ventral to the pharynx, an inward projection of the endodermal wall is present. In the middle region of the embryo the lumen of the archenteron is reduced to a small cavity, as seen in cross-section (Fig. 40), and is now longer from above downward than from side to side. The yolk-mass as a whole is rounded and more compact than in the earlier stages. At the posterior end of the embryo the archenteric cavity bends around the end of the yolk-mass, taking a curved course to open on the ventro-posterior surface of the body by the anus.

During the early stages of development the cells of the embryo have been exceedingly active, but no food has been taken as yet into the digestive tract, for the mouth does not open until some time after the embryo has left the egg-membranes. All the cells of the body contain yolk-granules, which serve in part, beyond doubt, to supply the energy necessary for development. A large amount of yolk is also stored up in the endoderm cells of the ventral yolk-mass, and must also long serve as a source of nourishment for the young tadpole.

The changes in shape that the archenteron passes through seem to be in part a result of the activity of the endodermal cells, and in part the necessary result of the change in shape

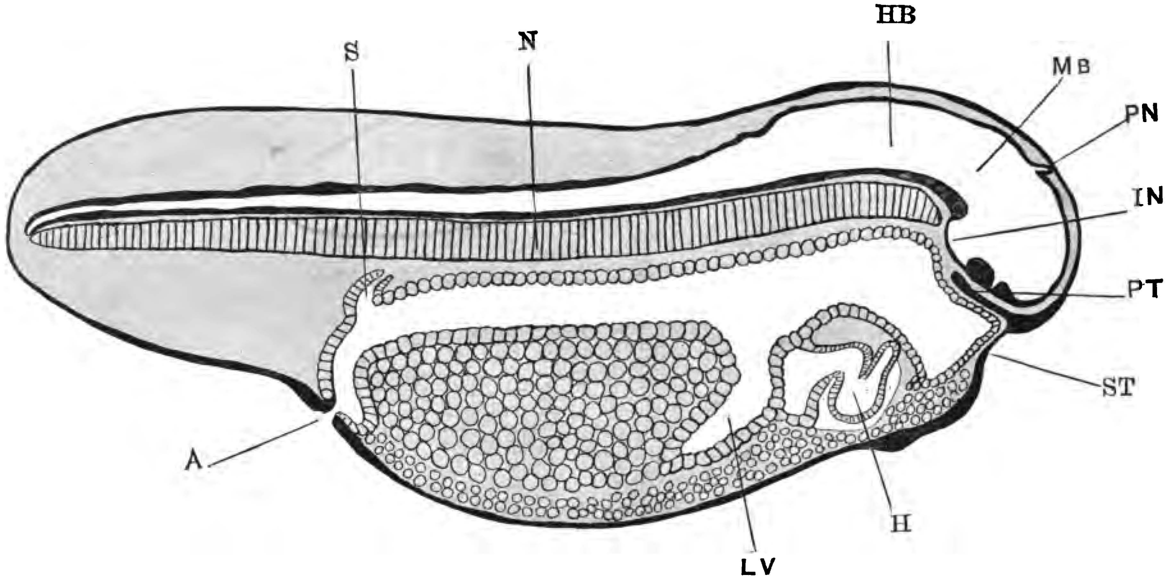

FIG. 39.—Sagittal section through middle plane of body. A. Anus. H. Heart. HB. Hind-brain. LV. Liver-diverticulum. MB. Mid-brain. N. Notochord. PN. Pineal body. PT. Pituitary body. S. Segmental duct. ST. Stomodæum. IN. Infundibulum.

that the whole embryo assumes. The early enlargement of the anterior archenteric cavity and the formation of a single-layered wall at the anterior end, with the subsequent formation of the gill-slits, would seem to be the result of the activity of the endodermal cells of those regions. On the other hand, some of the changes in shape that the lumen undergoes would seem to be due to the change in shape of the whole embryo as it elongates antero-posteriorly, and narrows from side to side. Nevertheless, even in this case the cells do not seem to be

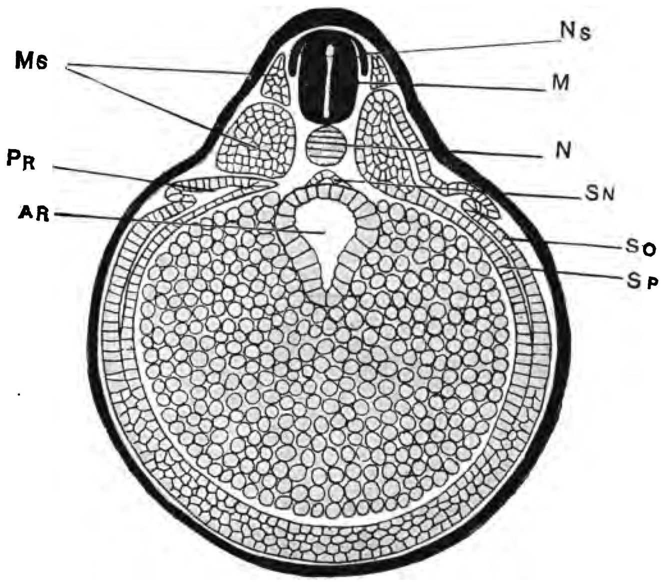

FIG. 40.—Cross-section through the middle of an embryo (3¼ mm.). AR. Archenteron. Ms. Mesoblastic somites. N. Notochord. Ns. Neural crest. M. Medullary tube. PR. Pronephros. SN. Subnotochordal rod. So, SP. Somatic and splanchnic mesoderm. (After Marshall.)

entirely passive, for the number of cells lining certain parts of the early archenteron is, in cross-section, considerably larger than the number lining the same region at a later stage. Either certain of the cells have pulled away from the surface and have passed into the yolk, or else they have changed their position relative to one another on account of the lengthening of the archenteron. In the latter case the total number of endoderm cells lining the archenteron would still be the same in the older and younger embryos, or greater in the older embryo as a result of cell-division.

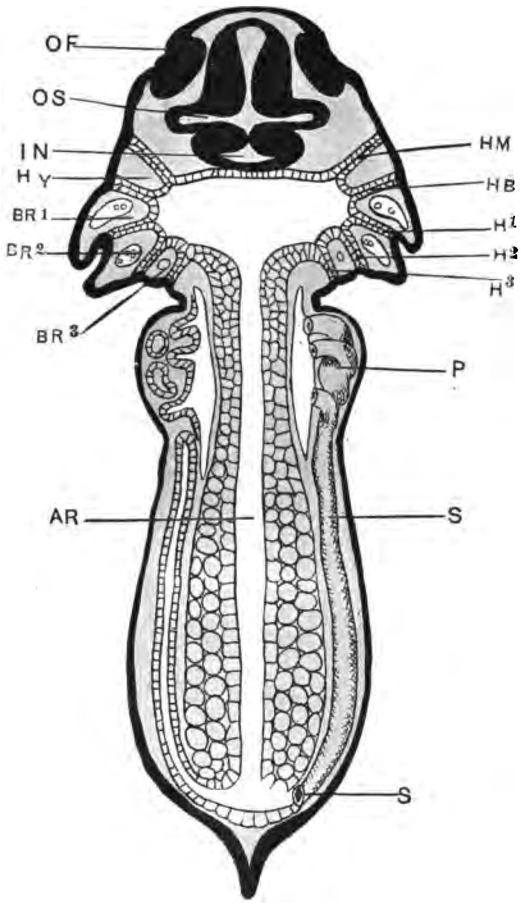

Fig. 41. — AR. Archenteron. BR[1], BR[2], BR[3]. Branchial arches. H[1], H[2], H[3]. Gill-clefts. HB. Hyoid cleft. HM. Hyomandibular cleft. HY. Hyoid arch. IN. Infundibulum. OF. Olfactory pit. OS. Optic stalk. P. Pronephros. S. Segmental duct. (After Marshall.)

The first three pairs of gill-slits appear almost simultaneously; the first two, however, before the third. When the tadpole leaves its capsule, there are five pairs of gill-slits; the two new pairs have appeared successively behind the third. A horizontal section through the larva (Fig. 41) shows to best advantage the five clefts at this stage. "The gill-pouches form vertical partitions radiating outwards from the pharynx to the surface-ectoderm. Each pouch is formed of a double fold of endoderm, the two layers of which are in close contact with each other. The outer ends of all five pairs of gill-pouches reach the ectoderm and fuse with its inner or nervous layer."[1] The most anterior pouch or cleft

[1] Marshall ('93).

is the hyomandibular cleft, and this is followed successively by the first, second, third, and fourth branchial clefts. The last is the smallest and is often imperfectly developed at this time.

The *visceral* or *gill-arches* lie between the *clefts*. The first arch between the hyomandibular and the first branchial clefts is the hyoid arch (Fig. 41). Then follow the first branchial arch (BR^1), second branchial arch (BR^2), and third branchial arch (BR^3). Behind the fourth branchial pouch there is an imperfectly defined fourth branchial arch.

When the tadpole leaves its jelly-capsule, the pouches are still double-walled, solid partitions ; but about the time when the mouth forms, the endodermal lamellæ of some of the pouches separate and place the cavity of the pharynx in communication with the exterior. The second and third branchial clefts open first. Later the first branchial cleft opens, and later still the fourth.

The hyomandibular cleft is at first like the others, but it never opens to the exterior. After its formation it separates from its ectodermal connection, and recedes from the surface. The lamellæ separate, and the cleft appears as a diverticulum of the pharynx.

Two other structures arise from the walls of the pharynx shortly before the hatching of the tadpole. "The lungs arise as a pair of pouch-like diverticula of the walls of the œsophagus. They are at first exceedingly small and have strongly pigmented walls."

The thyroid body appears about the time of hatching as a short median longitudinal groove along the wall of the pharynx. "The groove is shallow anteriorly, but deepens at the hinder end, where it leads into a small conical pit-like depression of the endoderm, forming the pharyngeal floor, just in front of the pericardial cavity. Soon after the mouth opens, the thyroid separates completely from the floor of the pharynx, remaining as a solid rounded mass of pigmented cells, in close contact with the anterior wall of the pericardium." [1]

---

[1] Marshall ('93).