

CHAPTER XV

ORGANS FROM THE ECTODERM

THE outer covering-layer of the embryo, the ectoderm, gives rise to the nervous system and organs of special sense (eyes, ears, nose). The adhesive glands or "suckers" are also formed by this layer; and the anterior and posterior divisions of the digestive tract, the stomodæum and proctodæum, have a lining of ectoderm.

In the present chapter we shall follow the development of these organs.

THE CENTRAL NERVOUS SYSTEM

The medullary plate appears on the surface of the young embryo at the time when the yolk-plug is about to be drawn in from the surface. It extends over about one-third of the circumference of the egg and is, at first, quite broad. It is slowly converted into a tube by the drawing together of its material, and by a subsequent over-rolling of its sides to meet in the mid-dorsal line. This change into a furrow, and then into a closed tube, involves extensive *movements* of the material of the plate. Whether the plate moves as a whole, or whether the movement is only the sum-total of changes in shape and position of the individual cells, is not known (compare Figs. 26, 42, 50). While the medullary tube is developing, the embryo as a whole is changing its spherical shape into a more elongated form and the medullary tube is also drawn out.

The medullary plate is formed, for the most part, from a thickening of the *inner layer of the ectoderm* (Figs. 26 and 42). It is continuous on each side with a broad flange or ridge of thickened ectoderm (Fig. 42, Nc). This ridge of cells, the neural crest or ridge, is also lifted up during the formation of

the tube, forming a broad sheet of cells on each side, continuous with the dorsal edges of the closing tube. These lateral sheets are very large and conspicuous at the anterior end of the nerve-tube. The subsequent history of these structures will be followed later.

The first part of the medullary tube to close, is the antero-median portion, and from this point the closure of the tube extends anteriorly and posteriorly. At the anterior end, the tube remains open latest; at the posterior end, the medullary folds arch over the blastopore, as already described.

When the medullary folds have met along the mid-dorsal line, the apposed edges fuse, and the outer layer of ectoderm then becomes continuous over the outer surface of the embryo. A part of the same layer has been cut off and lines the cavity of the neural tube. The nerve-tube soon loses all connection with the overlying ectoderm (Fig. 40).

The anterior end of the nerve tube is larger than the rest, and this end is at first bent down nearly at right angles to the long axis of the more posterior portion (Fig. 37, A). The bending begins at the front end of the notochord. A slight transverse infolding of the wall of the anterior end of the tube takes place soon after its closure, and later another transverse infolding occurs, still further forward. As a result three divisions or vesicles of this region are produced. They correspond to the fore-brain, mid-brain, and hind-brain respectively. The fore-brain (Fig. 37, FB) is the large anterior vesicle. From it develops later the third ventricle, the pineal body, the infundibulum, the optic vesicles, and the cerebral hemispheres. The mid-brain (Fig. 37, B) is the smallest of the three divisions, and gives rise to the optic lobes and to the Sylvian aqueduct. The hind-brain is continued into the more posterior medullary tube. It lies in the same plane with the medullary tube, and represents only a somewhat enlarged part of the tube. The hind-brain becomes the medulla oblongata, and from its roof the cerebellum is formed.

The roof of the fore-brain is very thin. Near the middle of its upper margin an evagination is formed, which is, at first, only a hollow diverticulum (Fig. 37, B), but when the tadpole leaves its capsule, the peripheral end of the outgrowth forms a

small round knob. This knob, the pineal body, lies just below the surface-ectoderm. Later the structure grows forward, and becomes dilated at its distal end. The dilated end or bulb remains connected with the brain by a stalk. White particles develop in the bulb, so that it stands out in strong contrast to the dark surface of the brain.

At the time of closure of the medullary folds, a mid-ventral diverticulum forms from the floor of the fore-brain. This is the infundibulum. It is in close contact with the anterior end of the notochord (Fig. 38). The infundibulum is throughout its subsequent history a wide sac with thin walls. It soon comes into close connection with another structure, the pituitary body (Fig. 39). The pituitary body arises very early, even before the neural tube is closed, as a solid ingrowth, or cord of cells, from the ectoderm, immediately in front of the anterior end of the medullary plate (Fig. 37, A). Later, this small, solid, tongue-like process projects inward from the ectoderm beneath the brain and above the dorsal wall of the pharynx. The inner end of the ingrowth expands into a flattened mass of cells, which lies immediately beneath the anterior end of the notochord. This mass becomes later the pituitary body, while the rest of the process forms a slender stalk connected at one end with the ectoderm.

THE EYES

The eyes develop in part from the walls of the fore-brain. Even before the neural tube is closed, in the embryos of some species of frogs, two pigmented areas may be seen on the antero-lateral walls at the anterior end of the infolding medullary plate. These pigmented areas mark the region from which a pair of evaginations of the fore-brain will develop to form the *optic vesicles*. The hollow vesicles push out laterally toward the sides of the head. Each tubular evagination then becomes constricted, forming a distal hollow bulb and a proximal hollow stalk (Fig. 49). The bulb gives rise to the retina and to the pigment behind the retina, while, according to Marshall ('93), the stalk forms a path along which the fibres of the optic nerve pass from the eye to the brain. The outer hemisphere of the optic bulb flattens and then pushes in so that the former

cavity of the vesicle is nearly obliterated (Fig. 49); and at the same time the inturned wall becomes greatly thickened. There is thus formed an open, cup-shaped structure with the opening of the cup turned outward. The wall of this optic cup lying toward the brain remains thin, and pigment soon appears in it. The inturned wall becomes the retina of the eye.

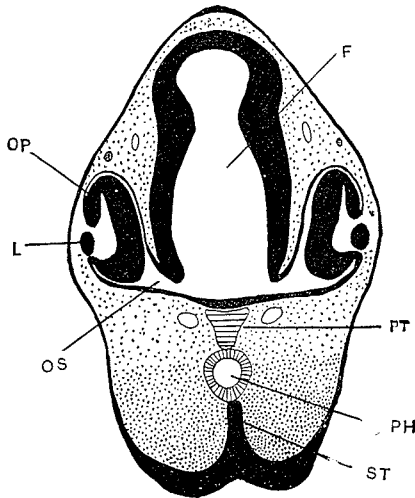


FIG. 49. — Cross-section through head and eyes. F. Fore-brain. L. Lens of eye. OP. Optic cup. OS. Optic stalk. PH. Pharynx. PT. Pituitary body. ST. Stomodæum.

At the time when the optic bulb turns in on itself, a thickening of the inner layer of ectoderm opposite the optic cup takes place. This thickening forms a solid mass of cells projecting into the open mouth of the cup. It becomes hollow and then separates from the ectoderm (Fig. 49), filling up the opening of the optic cup, and forms later the lens of

the eye. In the space left between the lens and the retinal layer the vitreous body of the eye forms. The later stages of the development of the eye take place after the embryo leaves its capsule. The nerve-fibres that develop from the retina and pass into the brain along the optic stalks have not yet appeared.

THE EARS

While the neural groove is closing, a pair of thickened circular patches of the *inner layer* of the ectoderm arises, one on each side of the head near the hind-brain. After the closure of the neural tube each area forms a shallow pit with the concavity turned outward, and each is covered by the outer layer of the ectoderm. The pit deepens, the outer edges come together, and a hollow vesicle is formed before the tadpole

leaves the capsule. These auditory vesicles separate from the surface ectoderm. "At the time of the separation the vesicle is a closed sac somewhat pyriform in shape; its lower or ventral portion being spherical and lying opposite the notochord, and its dorsal wall being prolonged upwards into a short blind diverticulum lying at the side of the hind-brain. The wall of the vesicle consists of a single layer of cubical or columnar cells." This ectodermal sac becomes the sensory lining of the inner ear (Fig. 50).

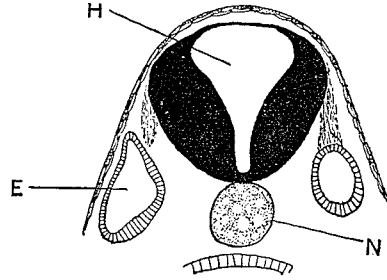


FIG. 50.—Cross-section through hind-brain (H) and inner ear (E). N. Notochord.

THE NERVES

At the time when the medullary plate forms as a thickening of the ectoderm, there also forms, as we have seen, on each side of the plate a *lateral neural ridge or plate of ectoderm*. Each neural ridge appears at first as a continuation of one side of the thickened medullary plate (Fig. 26). A slight constriction on each side marks the line of demarcation between the medullary plate and the neural ridge (Fig. 42). The neural ridges are more conspicuous at the anterior end of the medullary plate; they also develop somewhat earlier in this region. After the medullary plate has rolled up to form the medullary tube, the lateral neural ridges are also carried up, retaining for a time their primitive connection with the outer (now dorsal) part of the medullary tube (Fig. 40).

The neural ridges next become broken up into a series of dorsal nerves, the cells collecting at certain regions, and thinning out and disappearing in the intermediate regions. The dorsal nerves grow down later between the myotomes and the nerve-cord. Accumulations of cells occur at certain regions on each dorsal nerve to form the ganglion of the dorsal root, and nerve-fibres are spun out from the cells of the ganglion. The ventral roots of the spinal nerves appear much later.

Marshall ('93) says the *cranial nerves*, "which are undoubtedly derived from the neural ridges, are the trigeminal, the facial and auditory, and the sensory branches of the glosso-pharyngeal and pneumogastric nerves." These nerves, "although arising from the neural ridges in the same way as the dorsal roots of the spinal nerves, yet differ from these, and agree amongst themselves in certain important features."

"I. The nerves in question, in place of growing downwards like the spinal nerves, alongside the central nervous system, grow outwards close to the surface of the embryo between the epiblast and the mesoblast."

"II. Each of these four nerves acquires a new connection with the surface epiblast some considerable distance beyond the root of origin from the brain, and at about the horizontal level of the notochord; at this place and at any rate in part from the surface epiblast itself, the ganglion of the nerve is formed."

"III. The nerves have special relations to the gill-slits, each nerve dividing into two main branches, which embrace between them one of the gill-slits."

"IV. A special system of cutaneous nerves is developed from the surface epiblast in connection with these four nerves, forming the lateral line system of nerves."

The pneumogastric nerves are "wing-like" expansions of the neural plate, extending more than half-way down the side of the pharynx. At the time when the larva leaves the capsule, a thickening of the ectoderm on each side opposite this nerve and at the level of the notochord develops, and fuses with the nerve. From this double origin arises the ganglion of the pneumogastric. A lateral line thickening has appeared as a solid cord of cells on each side, extending from the pneumogastric backward along the side of the embryo.

It is not possible to enter here into the details of the development of the other cranial nerves enumerated above. The development of the first, third, fourth, and sixth nerves has not as yet been fully worked out. The origin of the optic nerve has been described in connection with the development of the eye.

THE APPEARANCE OF CILIA ON THE SURFACE OF THE EMBRYO

If the living embryo be examined at the time when the neural folds have appeared, it will be seen that the embryo slowly rotates within the jelly-capsule. This rotation is the result of the activity of certain ciliated ectodermal cells. The distribution of these cells over the surface of the body has been recently described by Assheton ('96). Assheton states that at the time when the medullary folds are first visible, and even after they have begun to roll in, there are no traces of cilia on

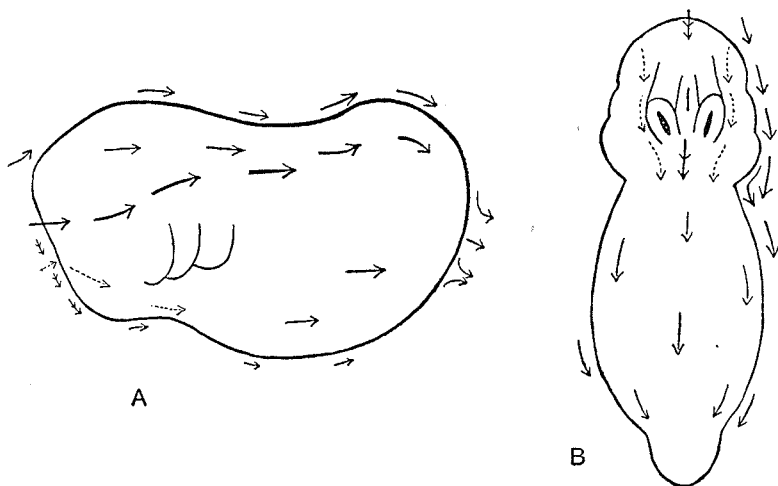


FIG. 51.—Embryo of *Rana*. The arrows show the direction of currents of water over the surface. A. Side view. B. Ventral view. (After Assheton.)

the surface of the embryo. Before the neural folds have met in the middle line the ectoderm has become ciliated in certain regions, as can be demonstrated by the streaming movement of granules of carmine placed on the surface. The arrows in Fig. 51 show the direction of the flow of granules over the surface. The lateral edges of the anterior end of the medullary folds seem to show the first traces of cilia, and a few hours later (Fig. 51, A) cilia have also appeared along the sides of the folds.

As the medullary folds grow nearer together, the ciliation extends further back along the sides of the dorsal surface. When the folds have just touched at the anterior end, cilia appear on the antero-ventral surface of the embryo, in the region where the mouth subsequently forms. The direction of the currents set up is from before backward. The whole of the dorsal surface next becomes ciliated. The ciliation spreads rapidly and at the time when seven or eight mesoblastic somites are present (when the embryo is 3 mm. in length) it has extended over the whole surface of the embryo. The currents, however, differ very much in intensity. Figure 51, A, B, shows the direction of the flow, the larger arrows indicating stronger currents. The action of the cilia is strongest at the anterior end of the body. A well-defined stream passes over the bases of the gills, which have begun to appear at this time. Over the ventral surface the currents move slowly and in eddies. At the hinder end of the embryo the action of the cilia directs the currents of water toward the blastopore and anus. When the embryo measures 4 mm., the so-called "suckers" have appeared, and the currents in that region have changed their direction. These "suckers" are in reality mucous glands that secrete a sticky substance by means of which the embryo can fix itself to objects with which it comes in contact. The edges of the glands have well-developed cilia, which direct a stream of water over the stomodæal depression, and thence backward between the glands (Fig. 51, B). In older embryos, when the glands have united to each other in the mid-ventral line, the direction of the currents in this region is altered. The central stream now turns outward around the anterior sides of the glands and passes backward along the sides. In older larvæ (8 mm.) small special currents run over the edges of the adhesive glands and into the depressions within the glands.

The cilia that cause the flow of water over the surface of the embryo are not developed by all the ectodermal cells. Even where the currents are most active, the cilia-bearing cells are slightly less abundant than the non-ciliated cells. Each ciliated cell bears on its outer surface numerous short cilia.

The gill-filaments also carry cilia in the proportion of one ciliated cell to two non-ciliated cells. The effect of the cilia becomes less conspicuous after the larvæ have reached 7 or 8 mm. in length, although even in much later stages the cilia are still found over all parts of the body. Their motion is sufficiently strong to cause the embryo (6 or 7 mm. in length) to move forward, if placed on a glass plate, at the rate of one millimetre in from four to seven seconds.