

DEVELOPMENT OF THE EPIPHYSIS IN
COREGONUS ALBUS.¹

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THROUGH the papers of Leydig ('90), Selenka ('90), and Hoffmann ('85), the evidence is accumulating that we have at least two outgrowths from the roof of the embryonic brain in the region where we have heretofore found only the single epiphysial outgrowth. The evidence is further strengthened by the discovery of the secondary parietal vesicle described in adult forms by Wiedersheim ('80), Ahlborn ('83), Beard, ('89), and Ritter ('91). In view of the prevailing uncertainty as to the homology of these two outgrowths, and as to their relation to the roof of the brain and to one another, it has seemed to me advisable to communicate some observations on the subject that have been made incidentally while working on the primitive segmentation of the brain of *Coregonus albus* (Günth).

In *Coregonus*² there are two epiphysial outgrowths from the roof of the primary fore-brain. These may be best seen in a sixty-day embryo (7 mm. in length). In Fig. I. there is shown the anterior part of a living embryo at this stage, as seen from

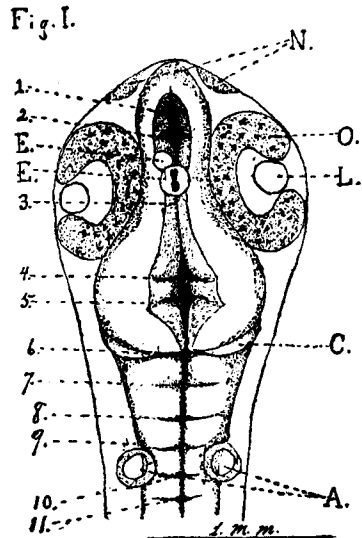


FIG. I.—Anterior portion of embryo, 7 mm. long, of *Coregonus albus*.

¹ Work from the Zoölogical Laboratory of the University of Michigan, under the direction of Professor Jacob Reighard.

² I desire to acknowledge my indebtedness to the Michigan State Board of Fish Commissioners for a liberal supply of material.

the dorsal surface and somewhat from in front. In the medulla there is represented only the floor, which shows a series of five parallel, transverse grooves, — (7), (8), (9), (10), (11). These grooves are broader and deeper towards the middle line, and become gradually narrower and shallower towards each side. They separate five transverse ridges, that are higher at the middle line and lower or less prominent towards each side. A longitudinal groove, the ventral part of the neural canal, passes along the median line of the floor of the medulla, and separates each transverse groove and ridge into two equal lateral parts. The auditory vesicles (*A*) lie on each side of the medulla, a little in front of the groove marked 10. Each one of these grooves marks the median line of a neuromere, as defined by Orr in *Lacertilia*, while lines drawn midway between these grooves, and parallel to them, indicate the limits between the individual neuromeres of Orr. Thus each of the ridges here described is equivalent to the posterior half of one of the neuromeres of Orr together with the anterior half of the next neuromere posterior to it. I adopt the nomenclature of Orr and describe these neuromeres merely for the purpose of fixing definitely this stage of development, and, for the present, do not wish to be understood as having accepted his interpretation of them.

The cerebellum (*C*) extends laterally farther than the medulla, and in the figure, owing to the point of view, appears to be partly covered by that part of the brain anterior to it. In its floor there is but one groove (6), which resembles those of the medulla. Only a part of this groove appears in the figure.

That part of the brain in front of the cerebellum tapers anteriorly; so that, in a dorsal view, it has the outline of a pear. The sides of this anterior pear-shaped portion are concave; and in these concavities, close against the brain, are the two optic vesicles. Nothing was seen, at this stage, to justify a division of this part of the brain into primary fore-brain and mid-brain. Four transverse grooves — (1), (2), (4), (5), an anterior pair and a posterior pair — mark its base. The distance between these two pairs is considerable; and while in this figure no groove is shown in the wall between these two pairs, in other embryos a fifth very small groove was seen in the position indicated by (3).

On the roof of the brain — in the median line, and in a plane passing through the middle of the optic vesicles — is seen the posterior epiphysial outgrowth *E*. It is a small spherical body, having its lateral walls thickened so that the cavity within is laterally compressed. This cavity is narrowest at the middle, on account of the greatest thickness of the lateral wall of the vesicle falling at the middle of its antero-posterior axis; consequently, in a dorsal view, the cavity has the form of a dumb-bell. Just in front of this vesicle, and a little to the left of it, is a second similar outgrowth *E'*. This anterior evagination is

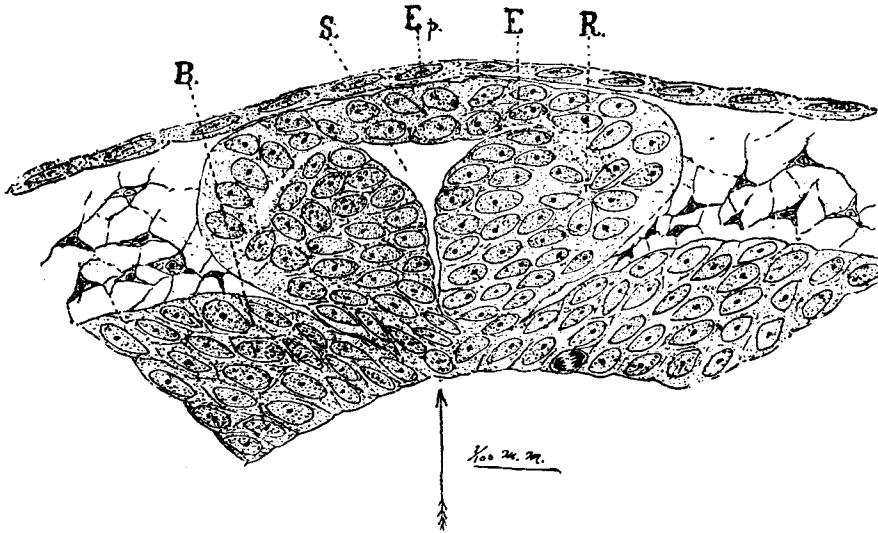


FIG. II. — Transverse section through the posterior epiphysial vesicle of *Coregonus albus*.

smaller than the posterior one, and appears to be solid. It lies close against the wall of the posterior vesicle, and is partly hidden by it.

Fig. II. shows the dorsal face of a transverse section through the middle of the posterior epiphysial vesicle. The arrow in the figure indicates the position of the median plane of the brain. The epiblast (*Ep*) lies close against the distal end of the vesicle, and is made up of a single layer of flattened epithelial cells. No mesenchyme is present between this epiblast and the dorsal surface of the posterior epiphysial vesicle. The vesicle (*E*) has the outline of a top, and is connected with the brain roof (*B*) by the apex of the top, which thus forms a very

short, thick, conical stalk. The vesicle is flattened dorso-ventrally, and has a triangular cavity (*S*). One angle of this cavity points towards the brain cavity below, into which it may be traced in the other sections, while the other two angles terminate in the lateral thickened walls of the vesicle. Some of the cells (*R*) near the middle of the thickened right lateral wall are arranged radially, while the dorsal right angle of the triangular lumen seems to form an arch which communicates with the central area, surrounded by these radiating cells. In the left half of this epiphysial vesicle there is evidence of a similar structure. The roof of the brain is thinner directly beneath

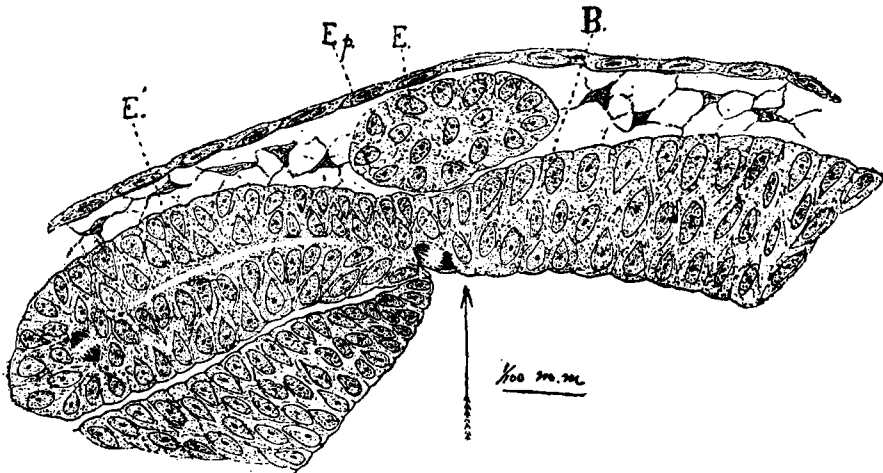


FIG. III. — Transverse section through the anterior epiphysial vesicle of *Coregonus albus*.

the posterior vesicle, and on all sides of this point it becomes gradually thicker. There is thus formed a cup-shaped depression on the dorsal surface of the brain, and in this depression the conical stalk of the vesicle lies.

Fig. III. is from the same series of sections as Fig. II. Three sections intervene between it and the section shown in Fig. II. The section passes through the middle of the anterior epiphysial vesicle (*E'*) and through the anterior part of the posterior vesicle (*E*). The sections are 10 μ . thick, and the arrow, as before, shows the position of the median plane of the brain.

The anterior vesicle (*E'*) is transversely elongated; its dorsal

surface convex; its ventral slightly concave, and closely applied to the roof of the brain. It is separated from the epiblast (*Ep*) by intervening mesenchyme. Along its middle there is a narrow cavity that communicates with the cavity of the brain, slightly to the left of the median plane. The portion (*E*) of the posterior vesicle is entirely free from the brain wall (*B*), and median in position. It is a solid mass of cells from the anterior wall of the posterior vesicle.

The stage just described shows the epiphysial vesicles ten days after their first appearance. The posterior vesicle appeared about two days before the anterior one, and could be seen in the living embryo as a small circle in the roof of the brain, in the median line. When the anterior vesicle appeared, its diameter was three-fourths the diameter of the posterior one, while it had the same position as shown in Fig. I. I was unable to study the anterior outgrowth in the living embryo for a longer period than twenty-five days, as at the end of that time it was so covered by the growth of the posterior vesicle and the surrounding brain wall that in a surface view of the brain it was entirely hidden.

Sections of stages earlier than that represented in Fig. I. show that these epiphysial vesicles arise as separate outgrowths from the roof of the brain. In each vesicle there is a cavity which opens separately into the cavity of the brain. In stages ten days earlier than that shown in Fig. I. there is, in longitudinal sections, an average of four sections that intervene between these openings, while in the transverse sections there is an average of five sections. Thus the opening of the anterior vesicle is a little more in front of the opening of the posterior vesicle than to the left of it. In stages ten days older than shown in Fig. I. these openings were obliterated, so that I was unable to establish their relation to one another.

From the study of sections it appears that the anterior vesicle shows an increase in size for about twenty days, and after that a decrease, while the posterior vesicle shows from the beginning a gradual increase. The following table is made from transverse sections, and gives the dimensions of the two vesicles in three different planes, each taken at right angles to the others:—

LENGTH.	AGE.	ANTERIOR VESICLE.			POSTERIOR VESICLE.		
		Dorso-ventral.	Transverse.	Longitudinal.	Dorso-ventral.	Transverse.	Longitudinal.
9. mm.	75 days	.037 mm.	.133 mm.	.07 mm.	.102 mm.	.135 mm.	.09 mm.
10.5 "	107 "	.027 "	.112 "	.07 "	.120 "	.147 "	.10 "
12. "	144 "	.015 "	.073 "	.05 "	.121 "	.152 "	.12 "

The first column under the anterior vesicle gives the length of the dorso-ventral diameter of the anterior vesicle. The second column gives the distance between the extreme left border of the anterior vesicle and the median plane of the brain. The measurements in the third column of the anterior vesicle are calculated from the number of transverse sections in which the vesicle appears.

The first column under the posterior vesicle gives the length of a vertical line drawn from the dorsal border of the posterior vesicle to the ventral border of the dorsal brain wall. The second column gives the length of the transverse diameter of the posterior vesicle. The third column is obtained in the same way as that for the anterior vesicle.

Besides this decrease in size of the anterior vesicle, its cells in older stages are more closely packed than in earlier stages, and show no karyokinetic figures. In early stages karyokinesis is frequently seen. I did not succeed in rearing embryos beyond 144 days, but, from the facts stated above, it seems very probable that this vesicle ultimately disappears.

In embryos seventy-five days old, the posterior epiphysial vesicle begins to grow anteriorly, so that the anterior vesicle is soon pushed to the left of the posterior one, and lies packed between it and the left brain wall. At the same time the fibres of the posterior commissure make their appearance just posterior to the union of the posterior vesicle with the brain roof. A little later there is a folding down of the brain roof anterior to these vesicles. This folding forms the posterior wall of the cerebrum, so that the epiphysial vesicles are clearly seen to be connected with the roof of the thalamencephalon.

Leydig ('90), in his recent paper, describes in *Lacertilia* two epiphysial outgrowths. He says the two lie in the median plane, the one just in front of the other; and that in the embry-

onic stage the anterior one is the larger, and partly covers the smaller posterior one. The anterior outgrowth soon separates from the brain, and develops into the eye-like parietal organ, while the posterior one remains connected with the brain roof, and forms the pineal gland (*Zirbelknopf*). My work on *Coregonus* does not cover adult forms, but, as far as studied, it is evident that while the early stages of these two epiphysial outgrowths of *Coregonus* agree in many details with the corresponding early stages of the two outgrowths in *Lacertilia*, as described by Leydig, yet the ultimate fate of these two outgrowths in the two forms is widely different. In *Coregonus* the anterior outgrowth, which is the smaller, gradually disappears, while in *Lacertilia*, according to Leydig, it develops into the adult parietal organ.

Selenka ('90), in *Lacerta* and *Anguis*, also describes two epiphysial outgrowths. The posterior outgrowth, he says, arises as a median thickening of the roof of the thalamencephalon. This he calls the epiphysis, and from its distal end he derives the parietal eye. Shortly after this there is another outgrowth, which he calls paraphysis, which comes from the roof of the prosencephalon. The paraphysis then grows backward and the epiphysis grows forward in such a way that the pineal eye comes to lie on the paraphysis as on a pillow. I could find no such outgrowth from the prosencephalon in *Coregonus*. The two outgrowths were both posterior to the depression, which, according to Rabl-Rückhard ('82), marks the anterior border of the thalamencephalon.

What relation these two epiphysial outgrowths bear to the primary and secondary parietal vesicles, described in adult *Petromyzon* by Ahlborn ('83) and in *Lacertilia* by Ritter ('91), remains yet to be worked out. It is probable that these organs will be shown to be homologous.

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