The morphology of the pineal region in teleosts / Robert J. Terry.

Contributors

Terry, Robert J. 1871-1966.
Royal College of Surgeons of England

Publication/Creation

[Boston] : The Journal, [1910]

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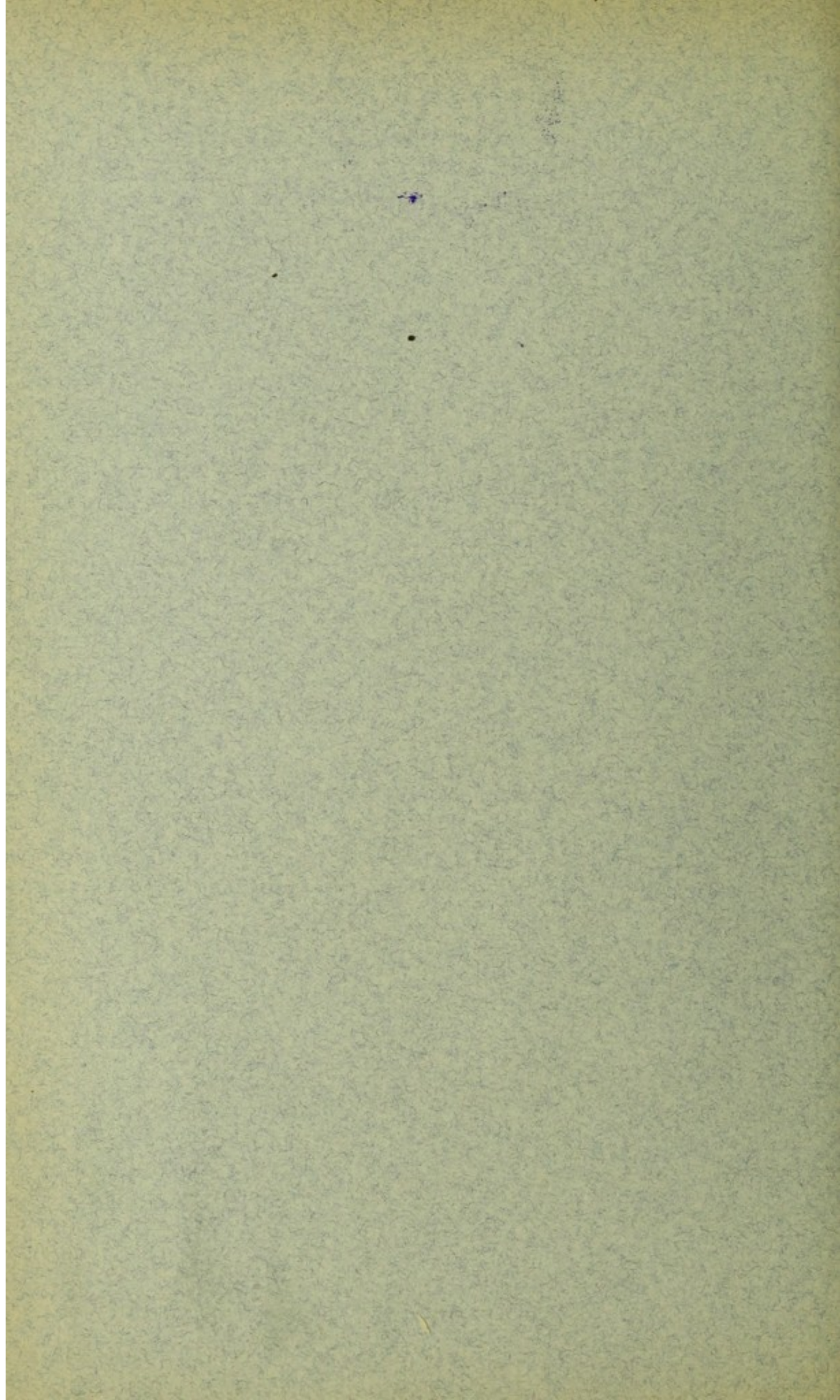
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The Morphology of the Pineal
Region in Teleosts

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School*

TWENTY TEXT FIGURES

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INTRODUCTION

In 1901 Minot published an account of the morphology of the pineal region in which it was shown that the characteristic structures included therein had their beginnings in constant well-defined divisions of the fore-brain roof. These subdivisions constitute a succession of arches and intervening projections into the ventricle, and in Acanthias are recognizable in embryos of 11.5 mm.

in length, a stage in which the diencephalon and telencephalon are demarcated. The names proposed for them, taken in order from before backward, are:

1. Paraphysal arch
2. Velum transversum
3. Post-velar arch

4. Superior commissure
5. Epiphysis
6. Posterior commissure.

According to the author, "The homologues of all these parts, exist probably in all vertebrates."

Other questions suggested and discussed in the paper concern the distinction between the paraphysis and paraphyseal arch, the genesis of the choroid plexus, the significance of the great difference of development of the post-velar arch among animals, the relations of the superior commissure and the position of the posterior commissure with reference to the diencephalon and mesencephalon.

Following the direction of research given in Minot's paper, Dexter ('02) and Warren ('05), in investigations of the avian, amphibian and reptilian brains, have supported the view of the general occurrence of the primitive subdivisions and also have noted especially the distinction between the paraphyseal arch and organ.

The present study[1] was undertaken with the object of extending the same line of inquiry to the teleostean brain. In view of the differences in the mode of formation of the medullary tube in the elasmobranchs and teleosts, misgivings were felt at the start that the early form of the fore-brain roof would necessitate an interpretation of the value of its parts in terms of the elasmobranch type rather than present parts easily identified and directly comparable with the divisions of the shark's brain. To some extent this was true, but the early appearance of the epiphysis, posterior commissure and velum was sufficient to make certain the interpretation of the remaining regions. The method of study adopted
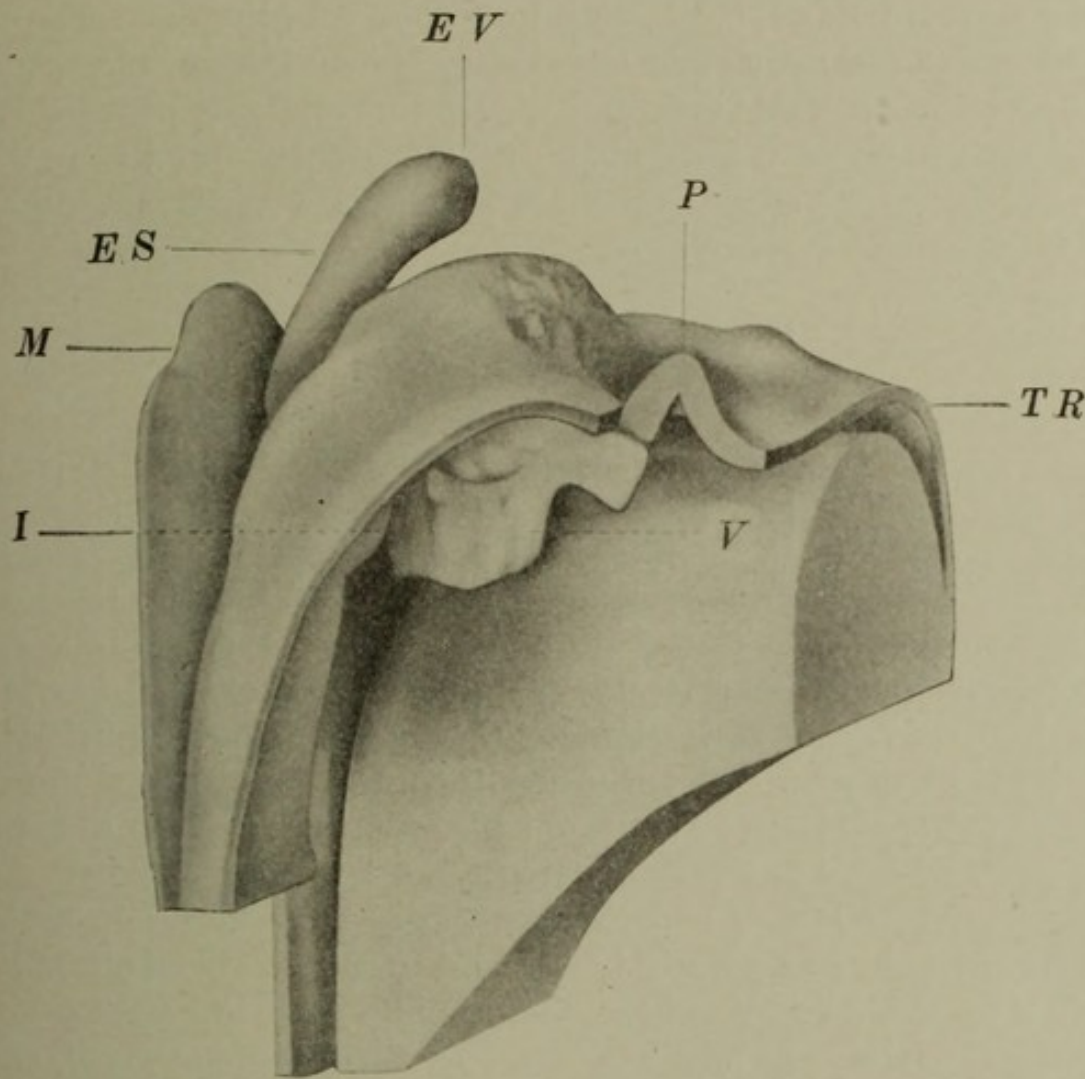
Fig. 1. Reconstruction of the pineal region of an Opsanus embryo of 11 mm. H.E.C., series no. 121. × 167. A part of the right wall of the ventricle has been removed and the paraphysis has been sectioned in the median plane.

has also helped in the identification of the regions in the smallest embryos. As the starting point, there was selected from the series an embryo in which all the structures peculiar to the pineal region could be identified beyond question. Each structure was then traced back through smaller and smaller embryos to the stage in which it was first apparent.

The material basis for most of the observations recorded is Opsanus (Batrachus) tau, the toad-fish, a teleost represented in

the Harvard Embryological Collection by an extensive series of
sections of embryonic and larval stages. In addition, the brains
of specimens half and fully grown were obtained and prepared for
dissection and microscopical study. Other fishes included in the
research are Salvelinus, Fundulus, Ameiurus, Lepidosteus, Amia,
Acanthias and Petromyzon.

I DESCRIPTION

Opsanus Embryos of 11 mm. in Length

Epiphysis. In embryos of this stage the epiphysis is located
in the middle of a depression intervening dorsally between the mid-
brain and telencephalon (fig. 1, *ES*). Its direction is nearly dorsad,
corresponding in this respect with the posterior epiphysis of Salmo
embryos of 7 mm. Hill ('94) found the posterior epiphysis in larval
salmon of 13 mm. directed forward, so that it presented dorsal
and ventral surfaces. The end of the organ lay close to the epi-
dermis, whereas in Opsanus it reaches a level half-way between
the diencephalic roof and the ectoderm. Differentiation of the
outward form has already begun and sagittal sections (fig. 2, E)
show an ovoid end-vesicle surmounting a cylindrical stalk. The
latter expands at its base where it joins the diencephalic roof, and
presents a slight curve in the sagittal plane in adaptation to the
superior commissure lying just anterior. The epiphysis of Opsanus
at the present stage, like that of Clupea (Holt '91), is a solid
structure. These teleosts differ, therefore, from the embryos of Salmo
in which, as shown by Hill, the epiphysis is hollow. Sections of the
solid epiphysis give evidence, however, of a difference in the
the structure of the peripheral and central regions, the former
appearing deeply, the latter but lightly stained. Moreover the
protoplasm of the peripheral coat is nucleated, whereas that of
the central region is non-nucleated.[2] This sort of structure is

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[2] There are no cell boundaries in the protoplasm of the epiphysis at this stage;
the organ has a syncytial structure and the nuclei are all located in the peripheral
parts, forming a more or less even layer.

Fig..2.   Median section of the pineal region of an Opsanus embryo of 11 mm.
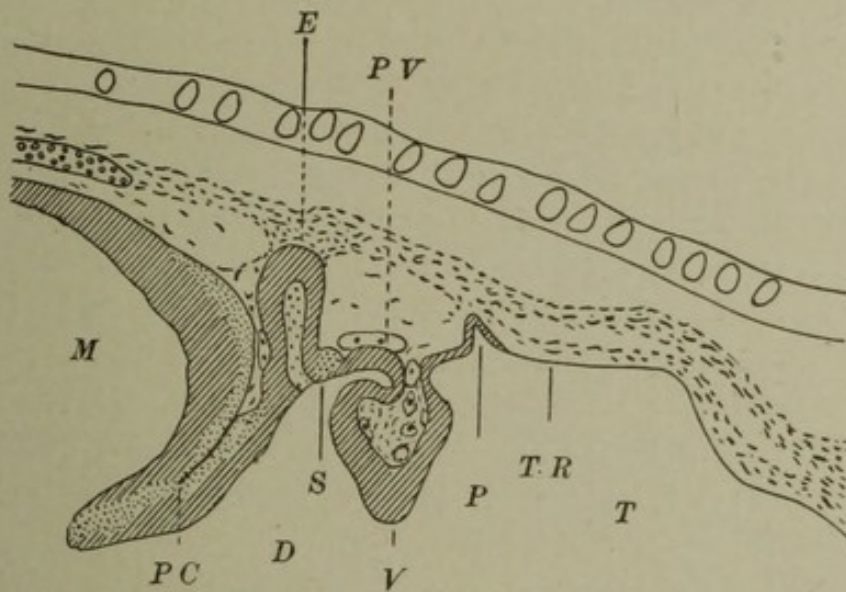H.E.C., series no. 122, section no. 118. × 130.

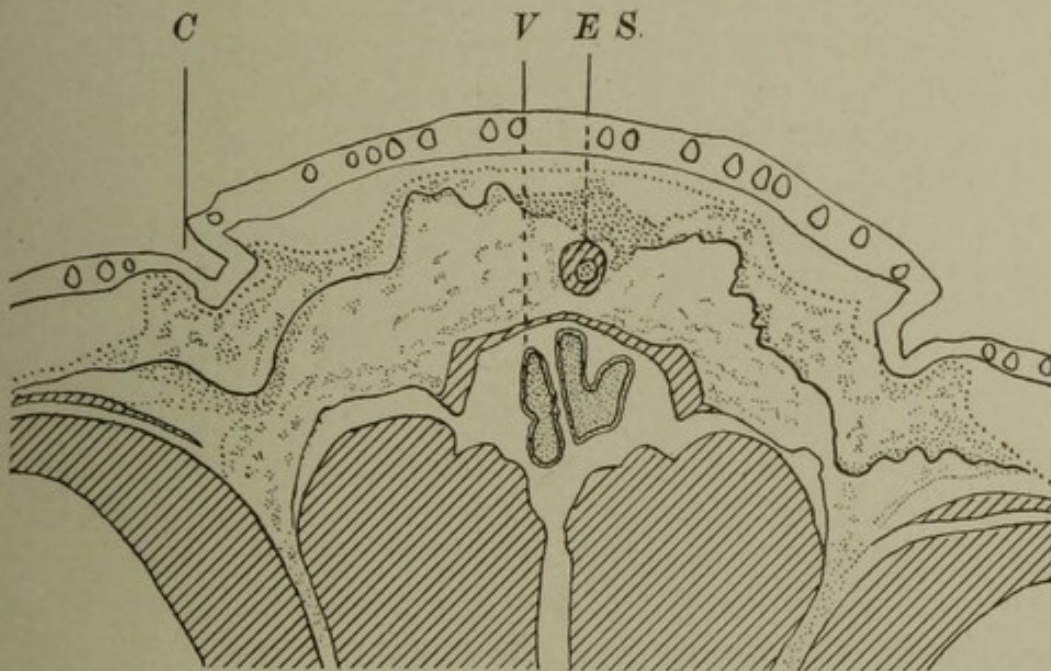
Fig. 3.   Transverse section of the pineal region of an Opsanus embryo of 11 mm.
H.E.C., series no. 121, section no. 99. × 97.

to be seen in both the end-vesicle and stalk, the clear central portion of the latter extending quite to the base and to the margin of the ventricle. In later stages a cavity forms, taking the place of the region of lightly-staining protoplasm, and the peripheral nucleated layer then becomes a surrounding wall. The thickness of the peripheral layer varies somewhat in different parts of the vesicle, but there is no marked contrast in this respect between the anterior and posterior regions of the layer. In transverse (fig. 3, ES) and in frontal sections, the epiphysis is seen to have a median position. The point of union of the stalk with the roof of the third ventricle is also midway between the intermediate tubercles; that is to say, there is no approximation of one or the other of the tubercles toward the middle line. Regarding the presence of a second epiphyseal organ, the following observation was made. In the series of transverse sections no. 121, a small rounded body was found to the left of the median line anterior to the epiphysis and surmounting the superior commissure (fig. 4, A). In section no. 101 (fig. 5, A) continuity was traced between this body and the roof of the third ventricle anterior to the commissure. Structurally it consists of a peripheral nucleated stratum surrounding a central clear area of protoplasm.

The depression on the dorsal aspect of the brain between the mesencephalon and telencephalon is filled with a loose mesenchymal network. This tissue surrounds the epiphysis and connects the end-vesicle with the membranous roof of the cranium by a dense broad band. Hill states that the end of the epiphysis in Salmo of 13 mm. projects into a mass of undifferentiated tissue lying between it and the epidermis. Blood vessels are present at the sides and at the back of the epiphyseal stalk. One of them is constant and traverses the mesenchyma in the median plane. The pigmentation of the tissues about the epiphysis described by Cattie ('82) appears in the later stages of development of Opsanus. Differentiation of the epidermis over the pineal region does not occur except in connection with the formation of the pit organs of the lateral line system.

Superior Commissure. Fig. 2, taken from a median sagittal section of the pineal region of an Opsanus embryo of 11 mm.,
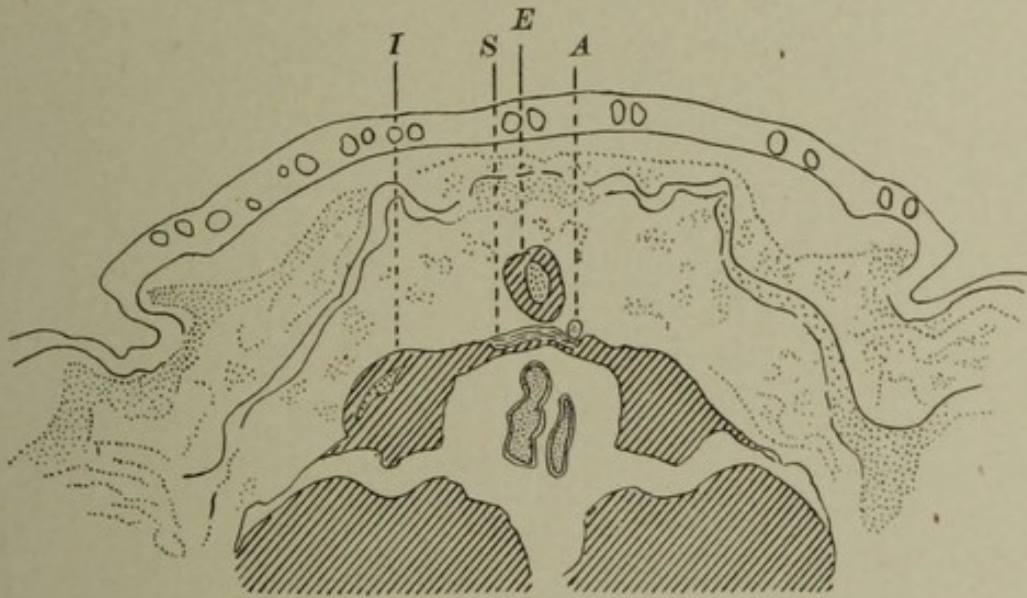
Fig. 4.   Section no. 102 of the same series as fig. 3. $\times$ 97.
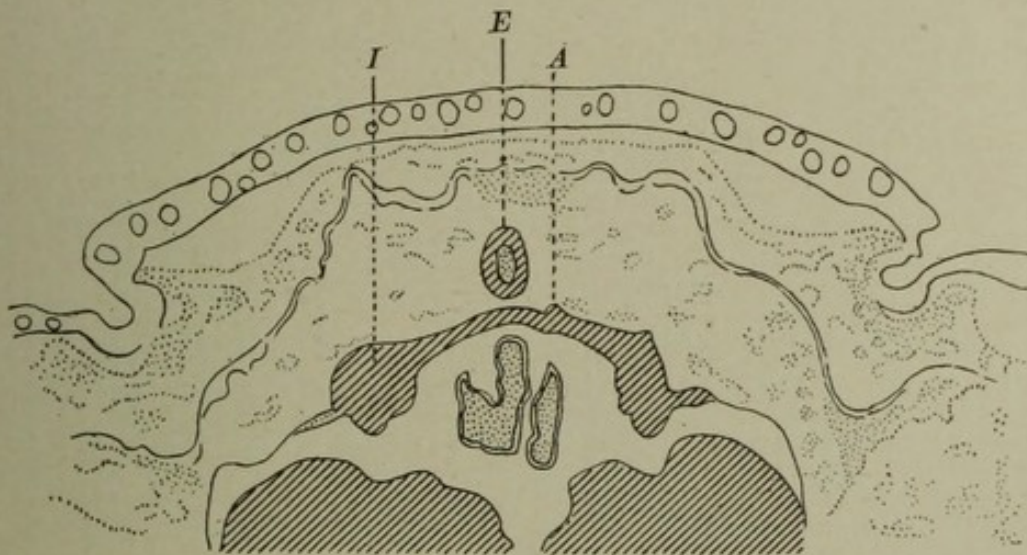

Fig. 5.   Section no. 101 of the same series as fig. 3. $\times$ 97.

shows the superior commissure (S) lying immediately anterior to and in contact with the base of the epiphysis. It occupies a position in the outer part of the diencephalic roof, resting ventrally upon a thin ependymal layer (Comp. Acanthias, 22 mm., Minot, '01). The component fibers, non-medullated at this period, pass over the surface of the post-velar arch to the intermediate tubercles.

Posterior Commissure. The posterior commissure is located in that fold of the brain-roof which is recognized as the boundary between the mid-brain and fore-brain. Sagittal sections show it to be folded transversely. The two layers resulting from this disposition of the commissure are continuous at their ventral edges. They extend from side to side and lie, the one dorso-caudad of the other (fig. 2, PC). Rabl-Rückhard ('82), Haller ('98), Mayser ('82), and other writers, have noted these two divisions in teleosts. Haller has described the commissure in Salmo as composed of a dorsal and a ventral part, the former belonging exclusively to the lobi optici and carrying fibers from lobe to lobe, the latter made up of mixed fibers of the longitudinal tracts. In the toad-fish, a septum of mesenchyma, continuous with the same tissue around the epiphysis and mid-brain, separates the two layers for a considerable distance. The ventral or anterior stratum, an even layer of fibers, is separated from the third ventricle by a thick ependyma. It reaches forward as far as the epiphysis, occupying that region of the diencephalic roof called the Schaltstück or pars intercalaris (Burckhardt). Some of the fibers pass around the base of the epiphyseal stalk. The dorsal or posterior stratum is related to the wall of the mid-brain. Its thickness varies inversely with that of the underlying epithelium in such manner that, whereas the ectal surface of the stratum is even, the deep surface is irregular. When followed in the dorsal direction, this stratum merges with the ectoglia layer of the mid-brain roof.

Velum transversum. (Fig. 1, V). This structure, projecting from the roof of the brain into the ventricle some distance in front of the superior commissure, is naturally divisible into two parts. One of these is a low, broad, transverse fold of the roof, the other a large ovoid body, hanging from the middle of the fold by a short pedicle (fig. 2, V). In the embryos of teleosts, ganoids, and elas-

mobranchs, the velum consists of a simple reduplication of the epithelium of the brain-roof. Such a velum is found in Opsanus at an earlier period of development and persists as the transverse fold of the present stage (fig. 6, VL). The median lobe, although constituting the greater part of the velum at this time, is a secondary modification of the middle part of the fold. The latter, followed anteriorly, goes over into the paraphysis, posteriorly into the post-velar arch. On either side, a prominent sagittal ridge of the fore-brain roof can be seen extending backward within the
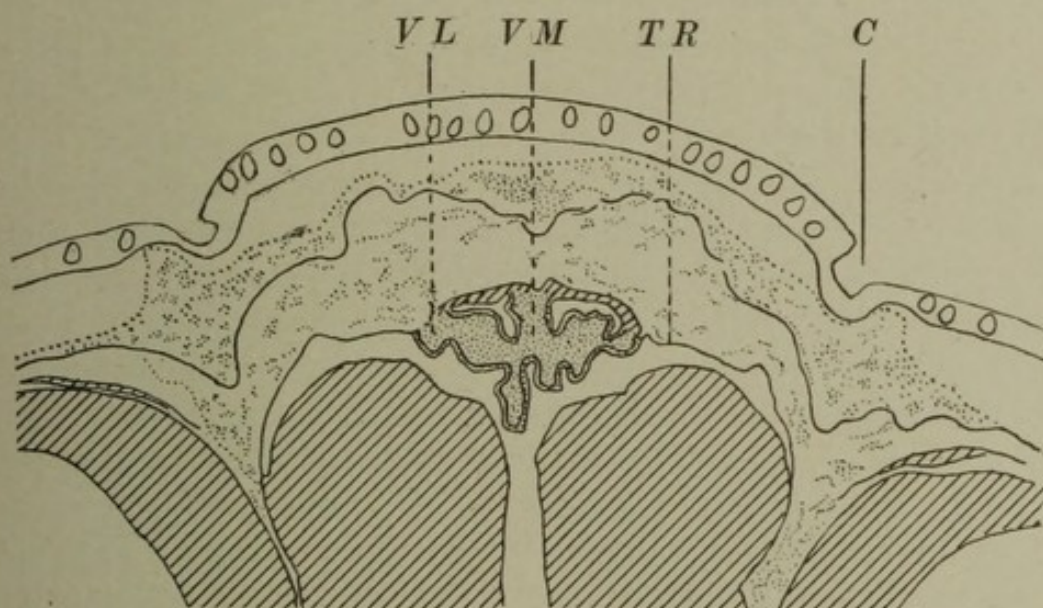
Fig. 6. Section no. 97 of the same series as fig. 3. × 97.

ventricle to the intermediate tubercle (figs. 3, 5). It marks the lateral extent both of the velum and paraphysis. Regarding the contour of the median lobe, one finds the surface broken by fissures of greater or less depth, dividing the whole mass into lobules. The part of the lobe lying behind the level of the pedicle is greater than that anterior. It will be seen by referring to fig. 2, that the lobe projects some distance caudad beneath the post-velar arch. The velum, even at this early stage, affords evidence of being adapted to a secretory function. Sections of the lobe show a peripheral thick epithelial tunic, thrown into folds and sup-

ported by mesenchyma rich in blood-vessels. The latter, continuous with vascular channels in the vicinity of the epiphysis, post-velar arch and paraphysis, are close under the velar epithelium. No difference was observed in the thickness of the epithelial coat of the anterior and posterior aspects of the velum as has been described in Acanthias by Minot ('01) and in Acipenser by Kupffer ('06).

Post-velar Arch (Fig. 2, PV). The name "post-velar arch" was given by Minot ('01) to the curve in the brain roof which lies between the velum and the epiphyseal anlage. This is the part of the diencephalic roof called Zirbelpolster by Burckhardt and the region of the post-paraphysis of Sorensen ('94). Out of this region is developed in the ganoids and some of the bony fishes the evagination called by Goronowitsch ('88) the dorsal sac. In Ospanus, the arch does not expand into a sac, but on the contrary diminishes in extent and finally disappears. In the stage under discussion, the post-velar arch is a small dome-shaped evagination of the diencephalic roof extending sagittally between the superior commissure and velum and going over laterally into the intermediate tubercles. At no time is the evagination so extensive as it is in Salmo where, as Hill ('94) states (p. 242) "it bears some resemblance in form to the epiphysis." The arch in Opsanus rises a little higher than the base of the epiphysis but not so high as the paraphyseal fold. Its simple cavity can be followed forward to the pedicle of the velum, on either side of which it becomes continuous with a short blind recess (fig. 6). In transverse sections through the posterior part of the velum, these two small recesses appear as lacunae surrounded by the velar and ependymal epithelium. In structure the post-velar arch consists of a layer of rather thick ependyma. Anteriorly, this continues with slight increase in the height of its constituent cells into the velar epithelium. Posteriorly, it changes abruptly to a very thin layer at the level of the superior commissure. The latter lies upon the epithelium of the caudal part of the arch, over which it extends in a lateral direction as far as the intermediate tubercles. Folds of the epithelium are not present, nor are there any diverticula such as Herrick ('91) has found in the walls of the dorsal sac of

Lepidosteus. In a word, there is no differentiation of this part of the diencephalic roof; it resembles the simple post-velar arch, found by Minot in Acanthias embryos. The vascularity of the dorsal sac and of the region around it was observed by Balfour ('77) and has been described by subsequent investigators. Blood sinuses of considerable size are present in Opsanus in the mesenchyma dorsad of the post-velar arch, and are connected with the vessels of the epiphysis and velum.

Paraphysis. (Fig. 2, P). Gaupp's ('97) and Studnička's ('05) reviews of the extensive literature of the pineal region contain few references to the paraphysis in teleosts. The question of its presence in the class has received little attention. Three years after Selenka's ('90) discovery of the organ, Burckhardt found a paraphyseal rudiment in the trout. Later, Studnička ('95) described a paraphysis in two teleosts, Lophius and Anguilla. In adult Lophius the paraphysis appears as an evagination of the brain wall in front of the velum. Its occurrence is not constant. In young Anguilla the organ is a relatively large, thin-walled sac connected by a narrow base with the brain. In 1905 the same investigator described the paraphysis in two other bony fishes, Cepola rubescens, in which ·it appears as a conical sac in front of the velum, and Belone acus, where a rudimentary paraphysis is indicated by uneveness of the lamina supraneuroporica. The paraphysis of Opsanus is a simple transverse fold of the roof of the telencephalon just anterior to the velum (fig. 1, P). Its walls are composed of an epithelium differing markedly in its greater thickness and staining properties from the tela of the fore-brain. In sagittal sections the paraphysis appears tent-shaped, with an anterior oblique and a posterior perpendicular wall going over into the velar fold. Of these two walls the anterior is so newhat thicker. Followed in the lateral direction the the organ is clearly defined to the same extent as the velar fold, that is, as far as the sagittal ridge of the fore-brain roof, described on p. 329. The simple cavity of the paraphysis presents no diverticula and communicates freely with the telencephalic ventricle.

Opsanus Embryos 8 mm. in Length

Epiphysis. The dorso-caudal direction of the epiphysis at this stage brings its posterior surface into contact with the mid-brain (fig. 7, E). The organ is relatively shorter now and in form
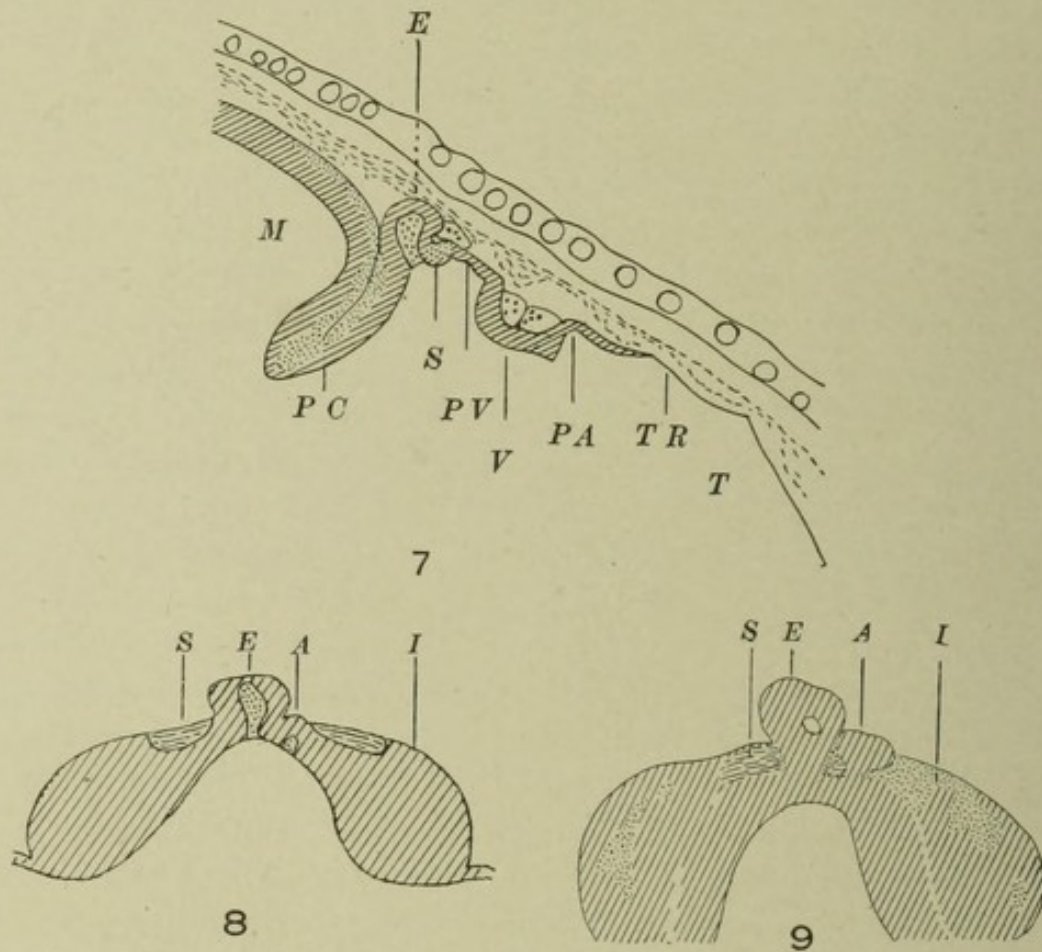
Fig. 7. Median section of the pineal region of an Opsanus embryo of 8 mm. H.E C., series no. 116, section no. 78. × 116.8.

Fig. 8. Transverse section of an Opsanus embryo of 8 mm. H.E.C., series no. 115, section no. 36. × 116.8.

Fig. 9. Transverse section of the pineal region of a Salvelinus embryo of 10 mm. H.E.C., series no. 455, section no. 42. × 84.

somewhat oval. Its structure is essentially as in the 11 mm. embryo and calls for no particular description. Just to the left of the base of the epiphysis there can be seen in transverse sections of the diencephalic roof an oval, compacted mass of nuclei pro-

jecting above the surface. The center of the mass consists of clear protoplasm, the whole structure bearing a close resemblance to the epiphysis of the 3.5 mm. embryo (fig. 8, A). This small bud is evidently the beginning of the anterior rudimentary epiphysis noted in the 11 mm. embryo. The examination of Salvelinus embryos, resulted in the discovery of two epiphyses as was anticipated in view of their presence in Salmo. They are represented in transverse section in fig. 9. It will be seen that these bodies are of unequal size, that the larger one is located in the median plane and the smaller one to the left. A cavity is present in the larger epiphysis.

Hill and other investigators have remarked upon the absence of mesodermal tissue between the epiphysis and ectoderm in very young teleost embryos. This condition was observed in the present study in the embryos of Salvelinus (fig. 10), Fundulus, and also Amia (fig. 11). It is not so however in Opsanus embryos, for there is always present between the brain and the epidermis a continuous layer of mesenchyma. Within this tissue the end of the epiphysis is to be seen (fig. 7, E). It is worthy of note that, whereas the end vesicle of this organ is pressed closely against the epidermis in the above named fishes, it is farther removed in Opsanus. A large blood sinus, lying between the superior commissure and the mesenchymal layer, is in contact with the anterior surface of the epiphysis.

Superior Commissure. It is at this stage of development that the superior commissure first appears as a clearly defined bundle of fibers. Its position relative to the epiphysis is the same as in the 11 mm. embryo. Sagittal sections show that the fibers are incompletely separated by a range of nuclei into dorsal and ventral groups.[3] In fig. 7, it will be observed that the commissure lies upon the ependyma of the post-velar arch.

Posterior Commissure. Excepting that the fibers of the commissure are spread to a relatively greater extent upon the epi-

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[3] Transverse sections reveal an intermingling of certain of the ependymal cells with fibers of the commissure, a condition interesting in connection with Mrs. Gage's ('95) observation that, in Diemyctylus, processes of the endymal cells traverse the commissure.
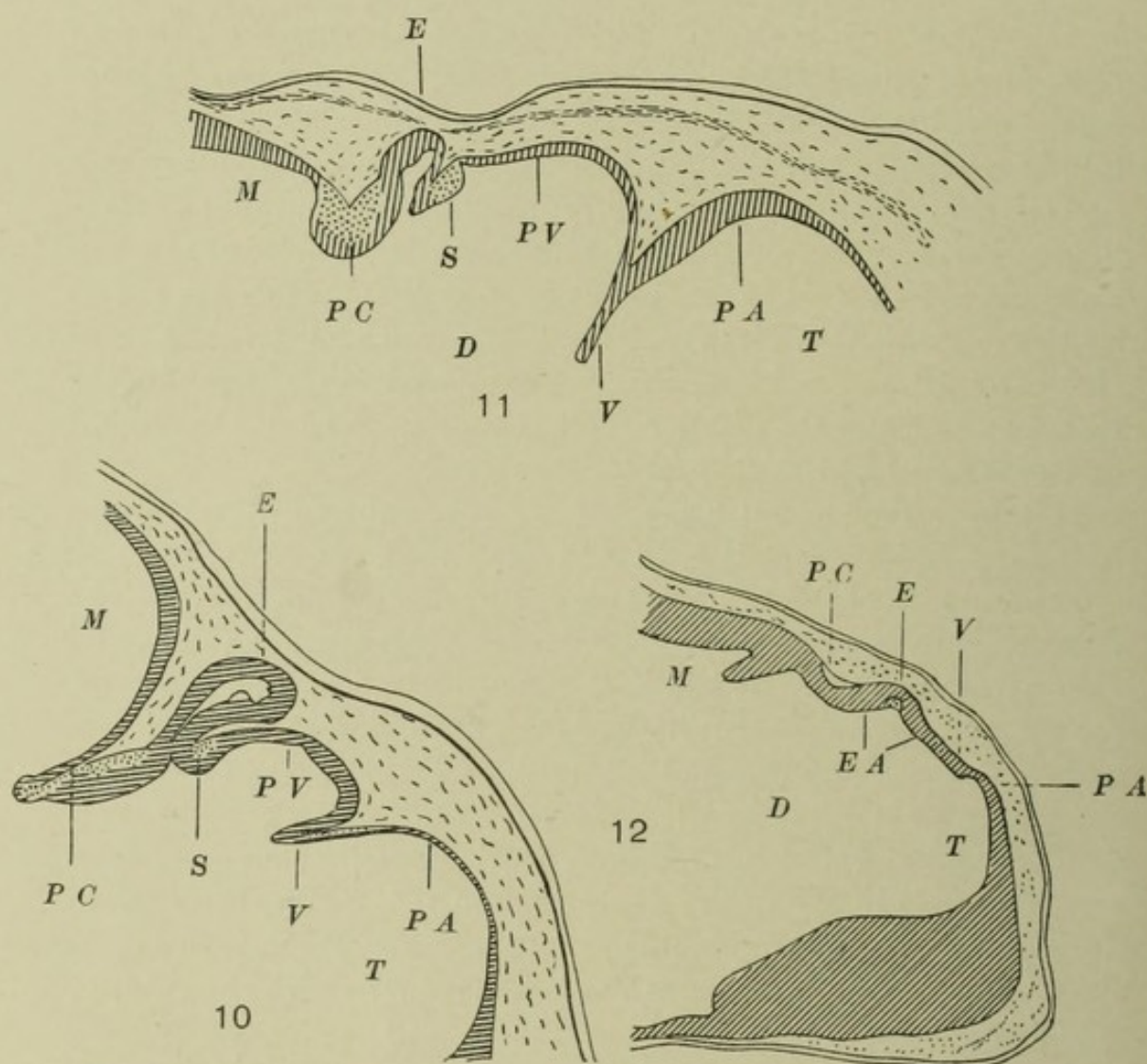
Fig. 10. Median section of the pineal region of a Salvelinus embryo of 10 mm. H.E.C., series no. 458, section no. 60. × 84.

Fig. 11. Median section of the pineal region of an Amia embryo of 10 mm. H.E.C., series no. 12, section no. 91. × 84.

Fig. 12. Median section of the fore-brain of an Opsanus embryo of 5 mm. H.E.C., series no. 110, section no. 55. × 115.

physeal stalk, the conditions described for the 11 mm. stage obtain in the specimens under discussion.

Post-velar Arch.   Compared with the 11 mm. embryo, the post-velar arch is relatively larger. The evagination is more pronounced and there is presented in consequence a considerable posterior surface over which the superior commissure is spread. This relation is very striking in Amia (fig. 11, S).

Velum Transversum.   The transverse fold and median lobe are both present, the extent and relations of the former being the same as in the 11 mm. embryo.   Differentiation in the form of the middle lobe has not begun; its surface is smooth and it is connected directly with the transverse·fold.

Paraphysis.   There is no paraphyseal evagination at this stage.   In its place the brain-roof forms a low arch or dome, sharply defined laterally and anteriorly.   This paraphyseal arch rises somewhat above the general level of the fore-brain tela, with which it contrasts in its thicker and more deeply staining epithelium.   Caudally the arch goes over into the transverse fold of the velum.

Opsanus Embryos 5 mm. in Length

Epiphysis.   Instead of the more or less conical, projecting epiphysis observed in the preceding stages, there is now present a simple, arch-like evagination of the diencephalic roof (fig. 12, EA).   The middle of this arch is differentiated both in form and structure from the rest (fig. 12, E).   It is raised slightly above the general level and presents in sections the same structural divisions, peripheral and central, as were found in the epiphysis of the older embryos.   The arrangement of the nuclei in a superficial layer is interesting in connection with Eycleshymer's ('92) observation of the migration of nuclei in the epiphyseal evagination of Amblystoma embryos and of a somewhat similar phenomenon in the optic vesicles.   The epiphyseal arch occupies the median plane, its summit lying within the mesenchyma which now fills the interval between the brain-roof and the epidermis. The latter presents no special features in this region.   A second epiphyseal outgrowth was not observed and so it appears that this smaller bud is a later development than the principal epiphyseal organ.   In Acanthias, a projection into the ventricle, seen in sagittal sections, marks the site of the future superior commissure and limits the epiphyseal arch anteriorly.   Since this projection is not well defined in Opsanus, the arch goes over without sharp limit into the post-velar region.

Superior Commissure. This tract is not present.

Posterior Commissure. In an embryo of 6.5 mm. the posterior commissure appears in sagittal sections (fig. 13, PC) as a large clear area in the ectoglia of the brain-roof, limited within the deep fold between the fore- and mid-brain. Throughout this area a network of fine processes, continuous with the ependyma, can be seen. The dorsal surface of the commissure presents an indentation, the beginning of the division into the two parts seen in later stages. This indentation is found in Amia (fig. 11, P.C) and in the trout as represented in Kupffer's ('06) fig. 150. This investigator says, (p. 131): "Sowohl die Commissura anterior wie die posterior lassen bei der Forelle anfänglich zwei scharf geschiedene Portionen erkennen." In Opsanus the anterior part reaches the epiphysis and lies in contact with its posterior surface.

In embryos of 5 mm. the commissure is stretched out in the superficial or ectoglia layer of the brain-roof, caudad of the epiphyseal arch (fig. 12, P C). Haller ('98) has seen a similar disposition in selachians and remarks that it is transitory in the teleosts. The extended posterior commissure has been observed in other forms, as, for example, Ammocoetes (See Kupffer, '06, fig. 47), and it has been found in the present investigation in Fundulus embryos of 7 mm. The fore-brain in front of the epiphysis presents in sagittal sections an angular bend dividing it into a longer posterior and a shorter anterior segment (fig. 12). Behind the bend a large blood sinus lies in contact with the roof which at this point projects into the ventricle. This is the beginning of the velum transversum. The epithelial roof in front of the angle goes over anteriorly by a slight curve into the thicker terminal wall of the ventricle. This curve is to be compared with Minot's paraphyseal arch.

Opsanus Embryos 3.5 mm. in Length

Sagittal sections show the brain roof considerably thickened in the epiphyseal region where a slight folding represents the beginning of the epiphyseal arch (fig. 14, EA). A short distance

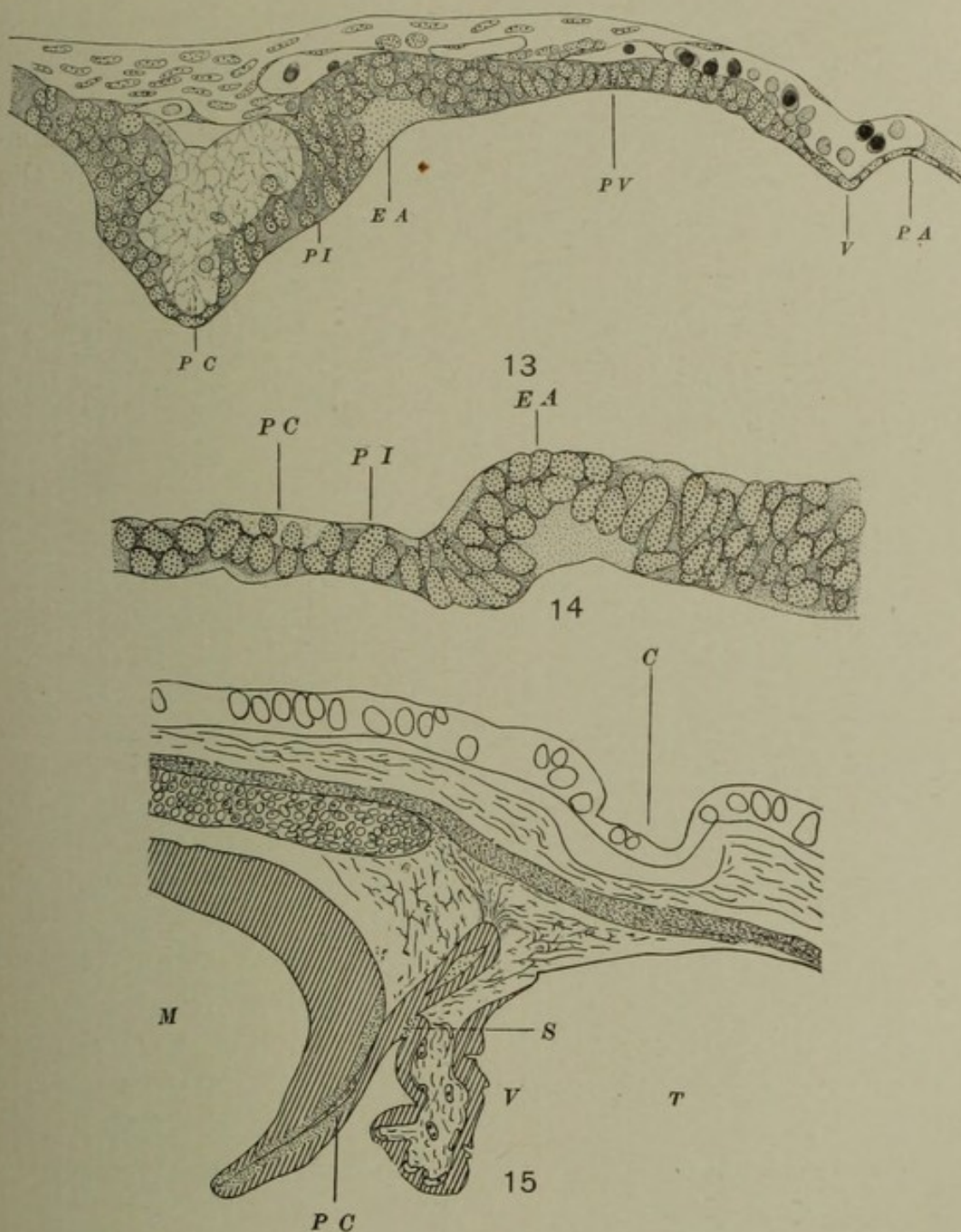Fig. 13. Median section of the pineal region of Opsanus. Length 6.5 mm. H.E.C., series no. 113, section no. 67. × 400.

Fig. 14. Median section of the pineal region of an embryo Opsanus. Length 3.5 mm. H.E.C., series no. 107, section no. 50. × 500.

Fig. 15. Pineal region of an Opsanus embryo of 15 mm. Median section. H.E.C., series no. 1183, section no. 145. × 84.

caudad, the site of the posterior commissure is indicated by a slight projection of the roof into the ventricle and the presence of a small elongate area of clear protoplasm (Comp. Hill, '99). Between the epiphyseal arch and the site of the posterior commissure, there appears a segment of the brain-roof not seen in the older embryos as a separate region. Its relations identify it as the pars intercalaris (fig. 14, PI). The segment of the roof anterior to the epiphyseal arch is thicker than that which is posterior; also it is relatively and absolutely thicker than the corresponding part in older stages. It presents, as in the 5 mm. embryo, a flexure in the sagittal plane, but exhibits no trace of the subdivisions evident at that stage.

Opsanus Larvae 15 mm. in Length

Epiphysis. In fig. 15, taken from a section a little to one side of the median plane, the epiphysis is seen to be inclined well forward over the paraphyseal region of the fore-brain. The epidermis is now folded to form a deep, wide groove extending transversely between the lines of the supraorbital pit organs (fig. 15C,). Although standing in a position posterior to the level of groove, the epiphysis is inclined forward so that its axis, if prolonged, would meet the groove. This topographical relation is the only one which was observed between the two organs. The small epiphyseal bud, noted in younger stages, is not present. A mesenchymal layer, in which the bony cranial roof is to form, now covers the great dorsal fontanelle of the chondrocranium. Over a considerable area of this layer are attached strands of connective tissue which radiate from the end of the epiphysis.

Superior Commissure. Owing to the disappearance of the postvelar arch, the superior commissure now lies between the velum and the epiphyseal stalk.

Posterior Commissure. The two divisions are even more sharply limited toward each other than is the case in the earlier stages. The mesenchymal septum is a well defined fold in a membrane which, followed posteriorly, covers the mid-brain, and anteriorly joins with the connective tissue over the diencephalon. The

anterior part of the commissure rests upon the intercalated division of the diencephalic roof, reaching forward to the base of the epiphysis. The posterior division forms a superficial fiber layer of the mid-brain in this region.

Velum Transversum. The middle lobe of the velum is relatively larger than in the preceding stage. In its growth backward it has invaded the region of the post-velar arch and has come therefore to lie below the epiphyseal stalk and the intercalated part of the diencephalon. The lobules comprising it are numerous and each includes a blood sinus whose walls are closely related with the epithelial covering of the velum.

Post-velar Arch. The reduction of this region, already referred to, goes hand in hand with the backward growth of the velum. The latter appears to have taken up and included the epithelium of the arch. That this process takes place was however not proved, for the epithelium of the arch presents no characters by which it can be distinguished from that of the pedicle and base of the velum.

Paraphysis. The thick epithelial coat of the velum passes over into the roof of the telencephalon for a short distance, giving place to the flat epithelium of the tela. Where this change occurs the roof is elevated into a slight but conspicuous transverse fold lying just beneath the end of the epiphysis. This rudimentary paraphysis presents a simple structure, consisting, as in the preceding stages, of a rather high epithelium, resting upon a thin stratum of connective tissue which contains but few vessels.

Opsanus Larvae of 19 mm. in Length

Epiphysis. The forward inclination of the epiphysis is more marked than in the preceding stage. The elongated stalk, bent over the superior commissure, is continued into the now much enlarged end-vesicle. In the latter a cavity is to be seen for the first time. This space, occupying the region which in earlier stages was characterized by the presence of clear, non-nucleated protoplasm, is traversed by fine fibrillae continuous with the surrounding walls (fig. 16). The conclusion that these fibrils

from a protoplasmic syncytium, derived from the central clear protoplasm and continuous with the walls of the epiphysis rests on the following evidence. The fibrils are first seen at the time of the appearance of the central cavity, not after it is formed. The cavity of the stalk is completed after that of the vesicle and a syncytium of fibrils is seen as the central axis of protoplasm disappears in the process of cavity formation. In staining reactions and in structure the fibrils agree with the central protoplasmic mass, except at the periphery where they resemble, in
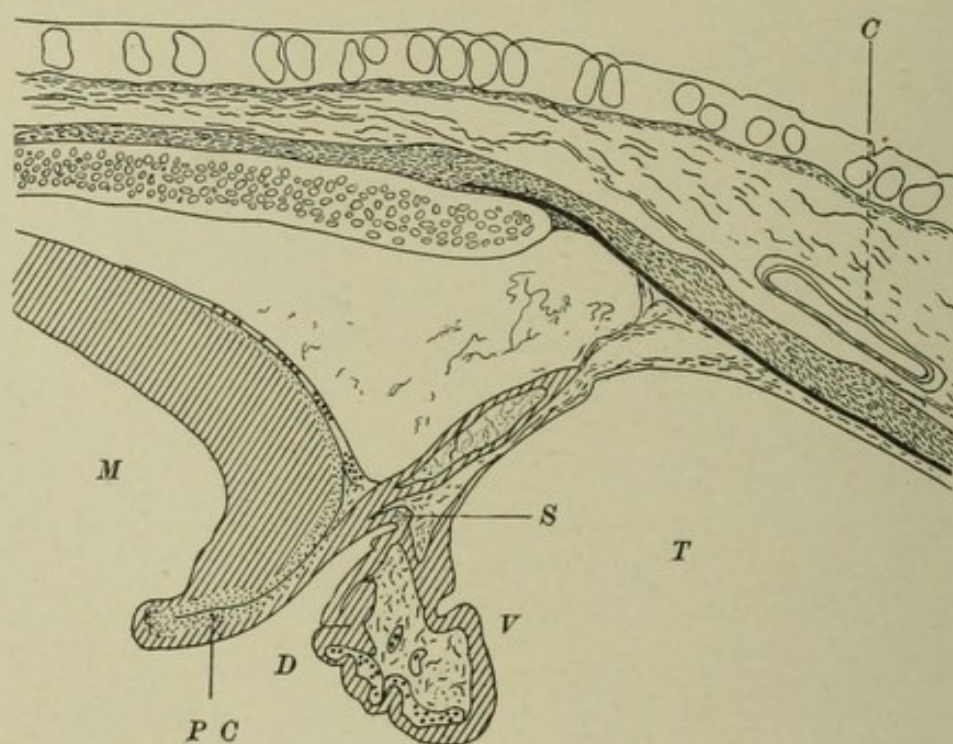
Fig. 16. Pineal region in median section. Opsanus of 19 mm. H.E.C., series no. 1188, section no. 203. × 84.

these respects, the surrounding walls. There is, therefore, no line of demarcation between the net-work and the protoplasm of the walls. The latter have undergone no differentiation at this time; there are as yet no cell boundaries. Bone has appeared in the cranial roof and to its under side are fixed the connective tissue bundles that radiate from the tip of the epiphysis. A commissural canal has replaced the transverse groove of the integument, seen in the 15 mm. larva, lying somewhat further in advance of the end vesicle of the epiphysis than did the groove (fig. 16 C).
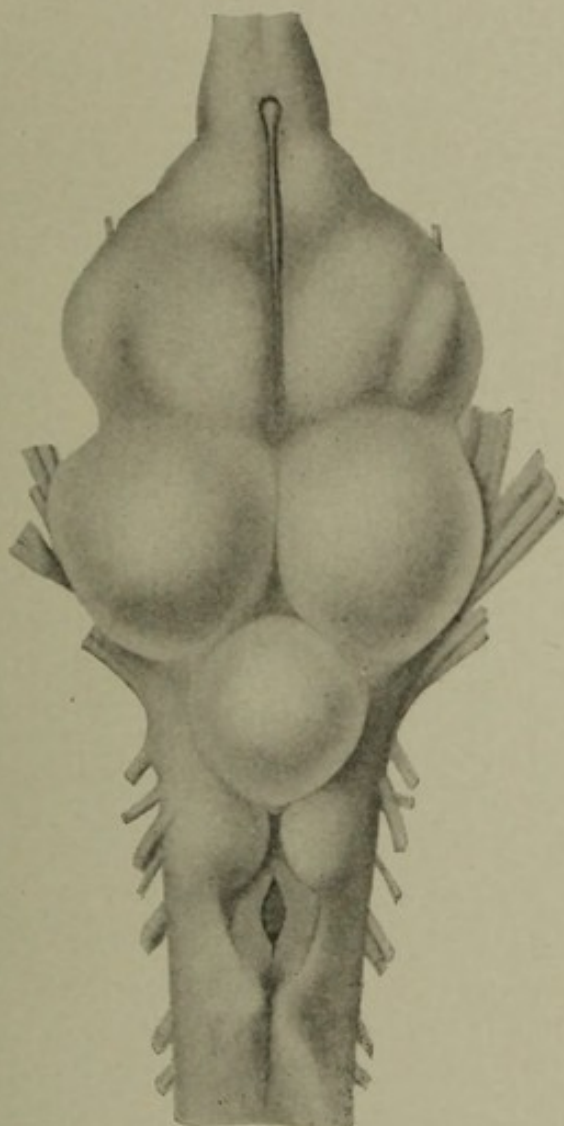
Fig. 17. Dorsal aspect of the brain of adult Opsanus. × 7.

Superior Commissure. This remains as in the preceding stage.

Posterior Commissure. The fibers of the commissure are now separated into bundles by delicate septa continuous with the underlying endyma.

Velum Transversum. The pedicle of the median lobe now extends backward to the level of the superior commissure. As a consequence of the backward growth of the velum the dorsal part of the diencephalic cavity has been reduced to a mere cleft extending transversely between the intermediate tubercles. The epithelium of the lobules is everywhere elevated into tufts supported by vascular connective tissue.

Paraphysis. Velar epithelium extends forward toward the para-physeal region where there is to be seen a slight transverse fold of the brain-roof. This fold, which appears to be the remains of the paraphysis, forms the anterior end of a median longitudinal groove of the tela, evident in transverse sections. The groove is the beginning of a deep median invagination which in the adult toad-fish separates two diverticula of the caudal end of the telen-cephalic ventricle.

Adult Opsanus

Epiphysis. The fully developed epiphysis presents a form not uncommon among the teleosts (fig. 17). It consists of an oval end-vesicle terminating a long slender stalk, the whole structure being directed cephalad in the median plane and suspended in the meninges between the fore-brain tela and the cranial roof. The stalk, which is slightly fusiform, measures 6 mm. in length and 0.08 mm. in its greatest diameter. The end-vesicle measures 0.6 mm. in length and 0.38 mm. in greatest breadth. There is no angle between the stalk and vesicle but a gentle curve extends throughout the length of the organ. The cavity, present in both stalk and vesicle, does not communicate with the ventricle. It is traversed by protoplasmic processes forming a wide mesh-work from wall to wall. An artery and vein are associated with the epiphysis throughout its whole extent. In the connective tissue along these vessels and around the distal half of the organ black pigment is present in considerable amount. The commissural canal of the lateral line system is now far anterior to the end of the epiphysis and there seems to be no further relation between these organs. A parietal foramen or fossa of the osseous cranial roof is not present.

Superior Commissure. There is no change in the structure and relations of this commissure from what was last observed.

Posterior Commissure. The two divisions of the posterior commissure are still recognizable; the intervening connective tissue septum now is less distinct. The anterior division contains some longitudinal fibers which extend in a thin layer around the base of the epiphyseal stalk and on to the intermediate tubercles.
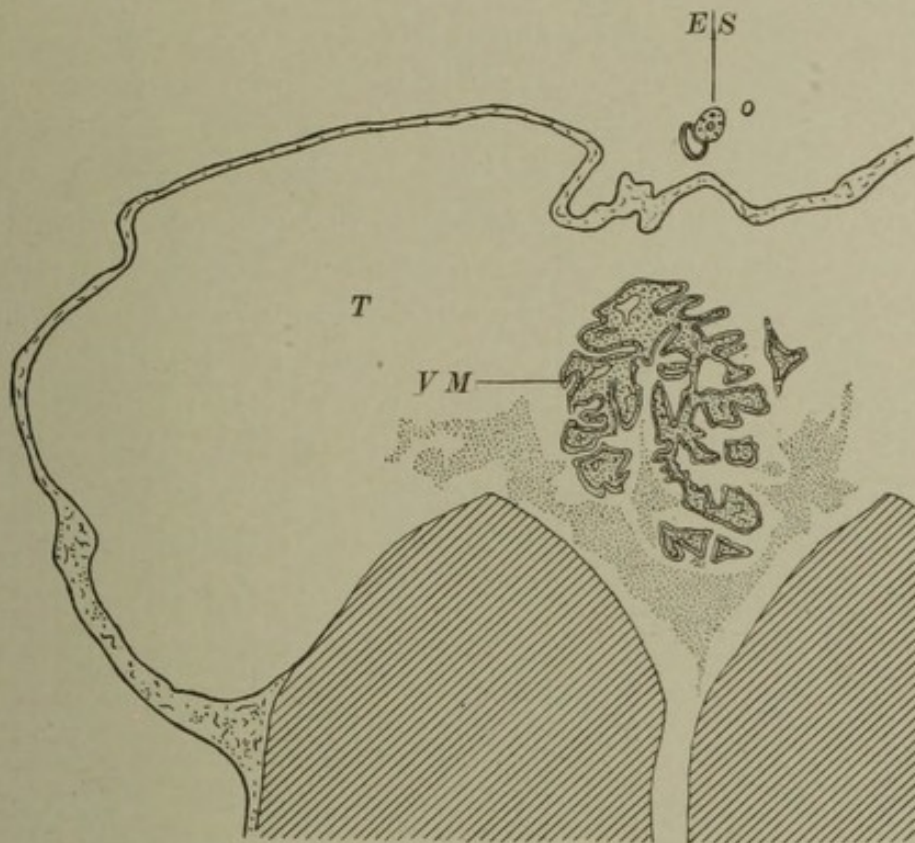
Fig. 18.   Transverse section through the pineal region of an adult Opsanus. W.U.C., series no. 13, section no. 517.   × 21.

Velum Transversum. The appearance of the median lobe of the velum is much the same as that of the 19 mm. larva. The covering epithelium consists of a single layer of long club–shaped cells, grouped into prominent tufts. The larger free end of the cell is often irregular, fringed or lacerated, sometimes rounded and regular. Neither cilia nor cuticulae are present, but long shreds of some substance extend from the ends of the cells into the ventricle there to become continuous with a coagulum which is always found close about the velum. In the coagulum are rounded bodies and masses which are stained like the clubbed ends of the cells. The nucleus is located near the free end of the cell and, between it and the base, granules are sometimes to be seen which stain deeply. The epithelium rests upon a rather thick reticular membrane, separating it from numerous underlying blood-vessels.

Post-velar Arch. This structure can no longer be said to exist, its place being occupied by the velum.

Paraphysis. There is no trace of a paraphyseal differentiation of the fore-brain tela. The latter, in its posterior part, has, however, been changed from the simple dome-form of the larval stages by the appearance of bilateral diverticula. In fig. 18, it will be seen that the ventricle is continuous from side to side, but that the tela is depressed in the mid-line to form a broad, shallow groove opposite the stalk of the epiphysis. Fig. 19, which is taken from a section at the level of the velar pedicle, shows a median partition between the two wide diverticula of the fore-brain ventricle. This septum extends from the bottom of the groove, noticed in the previous figure, and contains, besides some large blood-vessels going to and away from the velum, the stalk of the epiphysis.

II Discussion

Morphological Divisions of the Fore-brain Roof

Burckhardt ('94, a & b) recognized in types of all vertebrate classes the presence and constant relations of the following structures:

Paraphysis	Epiphysis
Velum Transversum	Pars Intercalaris
Zirbelpolster	Posterior Commissure.
Superior Commissure	

The forecast of these structures in the embryonic brain has been described by Minot ('01) who, as mentioned in the beginning of this paper, found that the pineal region of Acanthias at an early stage presented six constant divisions. The divisions, in the form of arch-like evaginations and alternating depressions into the ventricle, were named by this author according to their subsequent differentiation. Further observations upon the pineal region of embryos of other animals led to the belief that they were fundamental and that homologous parts might be found in all vertebrates.
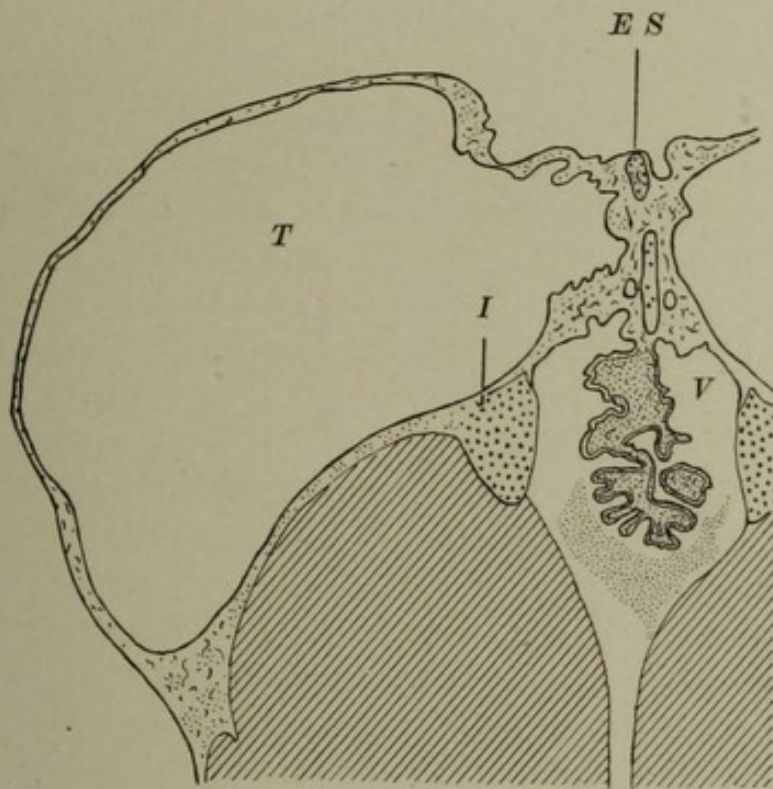
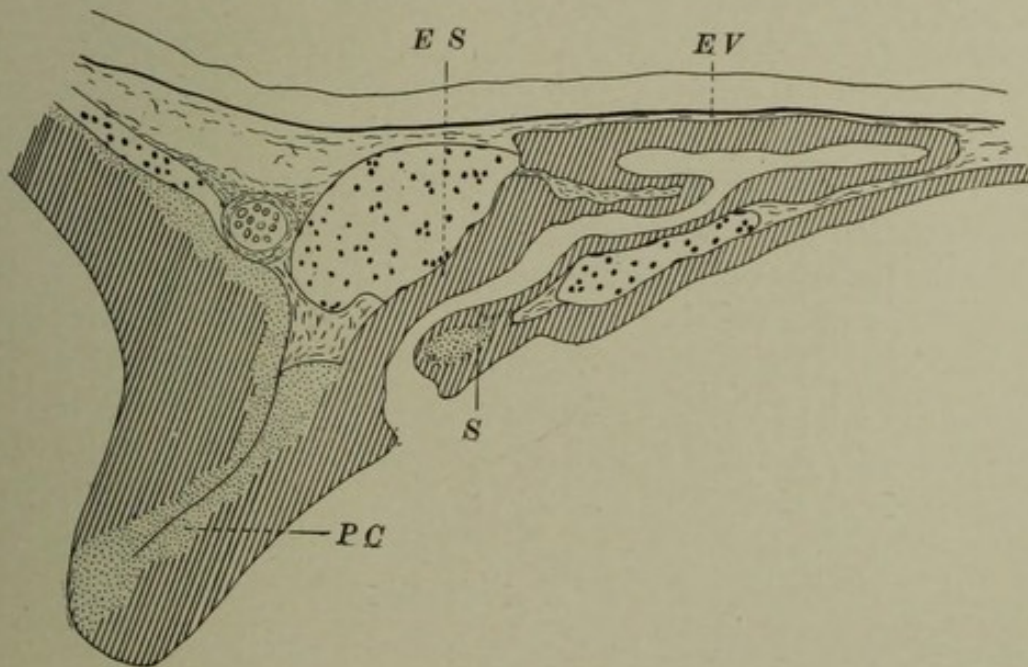Fig. 19. Section no. 542 of the same series as in figure 18. × 21.

Fig. 20. Median section of the pineal region of Ameiurus. Length 10 mm. H.E.C., series no. 388, constructed from sections nos. 89–92. × 290.

Dexter ('02), in his study of the development of the paraphysis
in the fowl, has identified and figured subdivisions of the fore-
brain roof, comparable with those described by Minot; and Warren
('05), who has found the arches in Necturus, has shown a very
striking resemblance between the embryonic pineal regions of this
amphibian and Acanthias.

In regard to teleosts it is probable that Minot's subdivisions of
the embryonic fore-brain are present throughout the class.   In
Kupffer's ('06) figure of a trout embryo of 53 days, the epiphysis is
represented as an elongate evagination, but the other subdivisions
of the the roof are shown to have the form of arches and inter-
vening folds.   A post-velar arch and the invaginations of the
velum and the posterior commissure are shown in Hill's ('94)
figure of Salmo fontinalis of 42 days. Opsanus embryos present
the six subdivisions and also a pars intercalaris. The intercalated
part first appears as a distinct segment in embryos of 3.5 mm.
lying between the posterior commissure and the epiphyseal arch.
As the result of forward growth of the commissure over the inter-
calated part, the latter as such disappears; that is to say, it no
longer remains a segment interposed between the posterior com-
missure and the epiphysis. It can be recognized, however, in all
later stages in the stretch of ependyma underlying the anterior
division of the posterior commissure. The fundamental divisions
appear less clearly defined than they do in Acanthias and, more-
over, they are not all evident at the same time as is the case in the
dog-fish. In Opsanus, the epiphyseal arch is present in the
smallest embryo studied as are also the posterior commissure
and intercalated part; all three can be seen during a brief period
(embryos of 3.5 to 5 mm.).   By the time the posterior commissure
has grown over the pars intercalaris (embryo of 6.5 mm.), the velar
invagination is seen. The epiphyseal arch disappears with the
formation of the main epiphysis, the post-velar and paraphyseal
arches and the superior commissure presenting themselves at this
time (embryos of 8 mm.).

As to the relation which these divisions bear to the neuromeres,
no direct evidence was obtained in the present study. Kupffer
('06) has identified the region of Burckhardt's Zirbelpolster (Minot's

post-velar arch) as the median dorsal part of his parencephalic segment which in turn, he derives from the second neuromere. The same author finds the intercalated part to be the roof of his synencephalic segment, derived from the third neuromere. Regarding the relation of the epiphysis to these segments, Kupffer ('06) says: "Es tritt nämlich die Commissura posterior, die man als dorsale Grenzmarke zwischen dem Vorder und Mittelhirne festzuhalten hat, nicht zwischen den Segmenten *p* and *se* auf— hier entsteht die Epiphyse" (p. 175). The segments *p* and *se* are the parencephalic and synencephalic segments. The paraphysis is the product of the telencephalic segment derived from the first neuromere, and the velum marks the dorsal boundary between the telencephalic and parencephalic segments. According to Johnston ('05) the second neuromere gives rise to the optic vesicles; from its narrow dorsal part is formed the velum. The epiphysis, according to this author, belongs to the third neuromere.

Epiphysis

The two epiphyseal outgrowths of Opsanus differ in their early form and relations from those of Salmo, Coregonus and the other teleosts which Hill ('91, '94) studied. In the first place they are not true evaginations but solid outgrowths of the brain-roof. As in the case of the solid epiphysis of Clupea, a cavity traversed by fibers is later formed in the main organ. Holt ('91) regarded the fibers as a coagulum and found no eye-like structure in the epiphysis, but Studnička ('05), who looks upon the two walls of the pineal vesicle of Petromyzon as retina and pellucida, hints at a comparison of these syncytial nets with the remains of a corpus vitreum of the parietal organ. The network in Opsanus is derived, as already shown, from the lightly staining protoplasm occupying the axis of the epiphysis, and it therefore cannot be considered a coagulum of some possible secretion of the walls of the organ. A secretion discharged into the cavity of the epiphysis of Opsanus would have no outlet. While the organ is moderately vascular it does not conform in structure with any of the ductless glands. On the other hand there is little evidence

in support of the theory of the epiphysis of this teleost being an ocular organ, either rudimentary or degenerate. Whatever may be the significance of the syncytial network, its formation in Opsanus goes hand in hand with the development of the epiphyseal cavity, a process analogous with that which produces the cavities of the central nervous system in the teleosts.

As to the fundamental question of the independence of origin of the two epiphyseal vesicles, the evidence afforded by Hill's material is not convincing. In Opsanus the two outgrowths are entirely separate and there is no question of one of them being developed from the other. The smaller bud appears later than the definitive epiphysis and arises from the diencephalic roof. It lies at first to the left and a little in advance of the main organ but secondarily comes into connection with the superior commissure and the post-velar arch. This forward migration recalls the shifting of the anterior vesicle of Amia and Lacerta.

The end of the epiphysis, from the time it is first seen in Opsanus, is closely related with the overlying tissues. In the smallest embryo the cranial mesenchyma extends between the epiphysis and ectoderm. In larger embryos and in larvae, strands of this tissue and finally connective tissue fibers proceed from the epiphysis to the roof of the cranium. There is no evidence to show that the function of these connecting strands is anything more than a passive one in fixing the epiphysis, but the early appearance of a bond between the end-vesicle and the overlying parts is suggestive of some other relation. Dean '95) has expressed the opinion that the epiphysis of fishes is connected with the innervation of the sensory canals of the head, at the same time opposing the theory of its relation to a median eye. In the present study attention was specially directed to a search for evidence in support in this view, but there was nothing observed which pointed to a relation between the epiphysis and the lateral line system, beyond the fact that the former is at one time directed toward the supraorbital commissural canal and is approximated rather closely to it.

The forward inclination of the epiphysis, occurring at the time when the roof of the cranium is first laid out in the mesenchyma,

points to the influence of cranial development on the position of this organ.

The statement made by Goette ('75) that the pineal body in Bombinator arises from a bridge which connects the brain and ectoderm has repeatedly been reaffirmed and denied. Van Wijhe ('83) and Hoffmann ('84) have presented evidence in support of the connection; Mihalkovics ('77), Balfour ('85), and later investigators assert that the epidermal bridge has no existence. Locy ('93) claims that the beginning of the epiphysis in the shark can be seen in the medullary plate. No recent investigator has found a continuity between the epiphysis and ectoderm after the formation of the medullary tube, although a close relationship has often been observed between the end of the pineal body and the outer germ layer. This condition and the absence of any intervening mesoderm led Hoffman to believe that the epiphyseal anlage was laid out before mesodermal formation had commenced. In Opsanus of 3.5 mm., when the epiphysis is just discernible, a mesenchymal stratum stands between it and the ectoderm and there is no evidence of continuity between these parts.

Posterior Commissure

It was shown in the descriptive part of this paper that the posterior commissure, arising in the ectoglia layer of the brain-roof, is, at first, located posteriorly to a pars intercalaris, that it spreads forward over this region and finally becomes included within the fold that intervenes between the mid-brain and diencephalon. Moreover, it was found that the commissure in the older embryos, in all stages, and in the adult fish, presents two distinct divisions, anterior and posterior, separated by a connective tissue septum. This mode of development has been observed in other bony fishes, to which reference has been made above (p. 336), and its division into strata has been described and represented in figures of the teleostean brain. It appears, therefore, that a type of posterior commissure appears among bony fishes, characterized by the presence of two strata of fibers separated by a partition. The commissure lies neither altogether in the wall

of the mid-brain nor in the diencephalon, but is so situated that its posterior layer stands in connection with the former, while its anterior stratum is spread out in the roof of the latter caudad to the epiphysis. In form and position, therefore, it differs from the corresponding tract of the elasmobranchs, in which fishes it has been shown to be a fiber bundle associated wholly with the midbrain (Ehlers, '78; Edinger, '99; Minot, '01). With this difference in the commissures of the two classes of fishes is correlated the difference presented by the pars intercalaris, which is extensive in the teleosts, small or absent in the elasmobranchs.

Regarding a pineal nerve, the evidence was insufficient to warrant the statement that such a structure is present in Opsanus. There is that close relationship between the posterior commissure and the epiphysis which has been described by Edinger ('99) in Scyllium and sturgeon, by Kupffer ('93, '06) in the trout; and shown by Dean ('96) in his figure of Amia (Comp. fig. 11). In the smaller embryos of Opsanus the posterior commissure extends further upon the base of the epiphysis than it does in the adult, recalling the relation of a tractus pinealis. Many fibers were followed to the base of the epiphyseal stalk but their terminal relations were not discovered.

Superior Commissure

The observation made by Osborn ('84) on the position of the superior commissure in front of the epiphysis has been many times confirmed and in recent years emphasized by Minot ('01) and Dexter ('02). Cameron ('04), however, appears unwilling to concede that the commissure should be considered as closely related to the epiphysis. He states that in all vertebrates it is situated behind the root of the choroid plexus of the third ventricle. The definition of the position of the commissure given by Osborn, Minot and Dexter implies a topographical relation to a constant organ. The structural relationship between the commissure and the epiphysis in the ganoids described by Herrick ('91) and by Eycleshymer and Davis ('97) is another reason, beyond that of mere topography ,for associating the two parts. Yet, the position

of this fiber bundle immediately in front of the epiphysis does not always obtain, as Cameron points out, and a definition of its relations applicable to all cases must wait until more observations have been made. One relation appears to be constant, namely, that the commissure is associated with the post-velar arch. This relationship is shown in median sagittal sections of the brain where it appears that the diencephalic roof in front of the epiphysis is composed of two strata, the cellular ependyma and the narrow fiber layer of the superior commissure. When these are followed in a direction away from the median plane they are found to pass over to the intermediate tubercles. Here all three of the fundamental layers of the brain wall, as recognized by His ('89) and Minot ('92, '03) can be seen, the Randschleier or ectoglia layer being formed by the fibers of the superior commissure. The latter may therefore be regarded as the ectoglia layer of the post-velar arch, small and limited to the posterior aspect of this region in Opsanus, but more extensive in Amia and Petromyzon. The origin and early disposition of the posterior commissure would warrant the same conclusion respecting its relation in the brain wall.

Post-velar Arch

The post-velar arch reaches its highest development in Opsanus when the embryos are about 8 mm. long, and subsequently disappears, probably by incorporation with the velum. The epithelium of the arch is like that of the median lobe of the velum and probably functions as a secreting surface. Hill ('94) and Leydig ('96) have found that this part of the brain-roof in teleosts is specially differentiated to form ridges and secondary folds of the epithelium resting upon a connective tissue foundation, in some cases vascular. Leydig states that in the trout the cells are higher toward the summit of the arch. The great expansion of the post-velar region in the ganoids is well known through the writings of Balfour, Huxley, Wiedersheim, Goronowitsch, Wilder and others in recent years. In Amia and Lepidosteus, Kingsbury ('97) found the dorsal sac, velum and metaplexus lined with an

ependymal epithelium which appears to consist of secreting cells, and Herrick ('91) describes the pouch of the diatela as possesed of a wall composed of a single row of cells with long cilia or flagella. It appears, therefore, that in these ganoids the epithelium of the arch is especially modified and lines a great evagination of the diencephalic roof. Regarding the elasmobranchs, Minot ('01) says " . . . . . the post-velar arch remains small, hence the velum seems to arise later very close to the mouth of the epiphysis."

The connection of the smaller epiphyseal bud with the post-velar arch by forward shifting brings up the question of its possible relationship with those large outgrowths of this region which have been observed by Schauinsland (See Kupffer, '06) in Callorhynchus, by Gierse ('04) in Cyclothone, and by Handrick (See Studnička, '05) in Argyropelecus. Commenting on the latter, Studnička, ('05) says: "Der Fall ist sehr wichtig, da er zeigt, dass der *de norma* breitere Dorsalsack unter Umständen sich in ein enges schlauchförmiges Gebilde verwandeln kann. Dieselbe Erscheinung kann man bekanntlich auch bei der Paraphyse beobachten; auch diese tritt einmal als ein enger Schlauch, ein anderes Mal wieder in der Gestalt eines breiten Sackes (Paraphyseal-bogen—Sedgwick Minot) auf."

Velum Transversum

The velum transversum of the teleosts, according to the current descriptions, consists of a simple transverse fold of the fore-brain roof, having smooth surfaces and a free ventral margin. Rabl-Rückhard ('82) regards the velum as the starting point, phylogenetically, of the choroid plexus, although he found no differentiation in this direction in the bony fishes. In them this organ seems to be less advanced in its development than it is among the selachians, where it has been shown that projections are formed on either side which are regarded by Minot ('01) as the anlages of the choroid plexuses of the lateral ventricles. In Acanthias a superficial coat appears upon the ependyma of the anterior surface of the velum, the nature of which is uncertain, but as

Minot says ('01, p. 91), " . . . suggests . . . the formation of secretory spherules." Gentès ('08) regards the velum of torpedo as a true choroid plexus. The enormous development of the velum of Opsanus is a striking peculiarity of the brain of this bony fish. The more important structural characters which have been described on p. 342, seen in all the adult and larval specimens, are those belonging to the true choroid plexus and establish the velum of the toad-fish as such an organ.

Among the teleosts possessing a rudimentary velum, Belone acus has been cited by Studnička ('05). In the brain of the Ameiurus embryo, shown in fig. 20, the velum is rudimentary and there is a further resemblance to Belone in the peculiar form of the epiphysis. This consists of a large flattened end-vesicle supported upon a rather slender and tortuous stalk. As to the significance of the primitive velum the view recently expressed by Johnston ('09) is interesting, namely, that the velar invagination begins early "on account of the withdrawal of material from the alar plate to form the optic vesicle." With such a relationship between these structures, some variation in the development of the optic vesicle might be expected in those animals where the velum is rudimentary or absent.

Paraphysis

The occurrence of a paraphysis in a number of teleosts, as discovered by Burckhardt and Studnicka, lends support to the interpretation that has been given to the fold of the fore-brain roof in Opsanus. The higher epithelium of the fold differentiates this rudimentary organ from the tela anterior to it, and its position, immediately in front of the velum, corresponds with the location of the paraphysis in all forms in which it has been observed. This relation of paraphysis and velum or choroid plexus is responsible for the identity of the former organ remaining hidden for so long a time. In Opsanus the paraphyseal fold is clearly no part of the velum for it appears after the latter has been formed, differs from it in structure and has only a brief existence.

The part of the embryonic fore-brain roof which is to give rise

to the paraphysis has usually the form of a dome. Since Minot
('01) named it the paraphyseal arch and demonstrated that the
paraphysis arises from it, its presence has been recognized in
all the vertebrate classes. (Comp. Dexter, '02; Warren,[4] '05;
Kerr, '03; Johnston, '09).

III Conclusions

1. A. The six morphological divisions of the fore-brain roof
recognized by Minot are present in Opsanus, and probably also
in Salmo, Salvelinus and Amia.

B. These divisions, in the form of arches and alternating
projections into the ventricle, are not all present at the same
time in Opsanus as in Acanthias.

2. A. A pars intercalaris is to be seen as an independent segment
of the brain-roof between the posterior commissure and the epi-
physis in embryos of Opsanus 3.5 mm. long.

B. In the adult it remains as a thick stretch of ependyma,
supporting the anterior stratum of the posterior commissure.

3. A. There are two epiphyses connected with the brain of the
toad-fish, one of them being a mere rudiment.

B. The main epiphysis lies in the mid-line and develops a
stalk and end-vesicle.

C. The rudimentary organ makes its appearance some time
after the definitive epiphysis is differentiated, lies at first to the
left and a little in advance of it and subsequently migrates
forward into the region of the post-velar arch.

D. The origin of these organs is entirely independent, the
one from the other.

E. Both epiphyses are originally solid outgrowths, the main
organ springing from the epiphyseal arch, the rudiment from
the diencephalic roof behind the superior commissure after
the disappearance of the epiphyseal arch.

F. The cavity which develops secondarily in the end-vesicle

[4] Warren, John. On the paraphysis and pineal region in Lacerta and Chrysemis
marginata. Assoc. Am. Anat. 25th Session. Boston, December 30, 1909.

and stalk of the main epiphysis includes a weak meshwork of protoplasmic processes continuous with the surrounding walls.

G. Continuity between the epiphysis and ectoderm was not observed; the fibers that extend between the end-vesicle and the overlying parts are mesenchymal in origin.

H. There is no parietal foramen and no differentiation of the epidermis of the epiphyseal region in Opsanus.

I. A nerve connection between the epiphysis and lateral line system does not obtain.

J. A pineal nerve was not discovered.

K. There are two epiphyses in Salvelinus, the chief organ being median in position, the subordinate outgrowth to the left of the former.

4. A. The posterior commissure of Opsanus has its origin in the ectoglia of the brain-roof.

B. In teleosts the commissure is divided into two parts, the one associated with the mid-brain, the other with the intercalated part of the diencephalon.

5. A. The superior commissure lies, in the toad-fish, immediately anterior to the base of the epiphysis.

B. It arises in the ectoglia of the diencephalic roof, retains the relation of an ectoglia layer in the brain-wall of the adult and may be regarded as an incomplete ectoglia stratum of the post-velar arch.

6. A. The post-velar arch attains its maximum extent in the embryos of Opsanus and early begins to diminish and finally disappears.

B. Its place is taken by the velum in its backward growth.

C. Its epithelium probably becomes incorporated with the velum.

7. A. In the development of the velum of Opsanus, a transverse fold and a median lobe are formed, the latter differentiating as a choroid plexus of the fore-brain ventricle.

B. The velum of Amieurus embryos is rudimentary.

8. A rudimentary paraphyseal organ is developed from the paraphyseal arch, appearing later than the epiphysis and disappearing during the early larval life of the toad-fish.

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REFERENCE LETTERS

A   anterior epiphysis
C   commissural canal of the lateral line system
D   diencephalon
DI   diverticulum of the telencephalic ventricle
E   epiphysis
EA   epiphyseal arch
ES   epiphyseal stalk
EV   epiphyseal end-vesicle
I   intermediate tubercle
M   mesencephalon
P   paraphysis

PA   paraphyseal arch
PC   posterior commissure
PI   pars intercalaris
PV   post-velar arch
S   superior commissure
T   telencephalon
TR   telencephalic roof
V   velum transversum
VM   median lobe of velum transversum
VL   transverse fold of velum transversum.