# DEVELOPMENT OF THE BRAIN OF THE AMERICAN ALLIGATOR: <br> THE PARAPHYSIS AND HYPOPHYSIS 

WITH FIVE PLATES

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No. 1922

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# DEVELOPMENT OF THE BRAIN OF THE AMERICAN ALLIGATOR: THE PARAPHYSIS AND HYPOPHYSIS ${ }^{1}$ 

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## The Parapfysis

The literature of the pineal region of vertebrates is remarkably extensive. A considerable portion of this literature deals with the much-debated relation of the epiphysis to the pineal eye or parietal organ. It is not the purpose of this paper to enter into that discussion, for the simple reason that these structures are not present in the alligator.
O. Hertwig $(22)^{2}$ says that, except in Amphioxus, the pineal gland is not wanting in vertebrates; and Wiedersheim (54) says: "The pineal apparatus consists of the epiphysis or pineal organ proper, which persists in a more or less rudimentary condition in all vertebrates, and a more anterior ontgrowth which may be called the parietal organ."

It is not surprising, then, that various authors should have described the similarly situated structure in the alligator as the epiphysis.

Parker and Haswell, in their " Text-book of Zoology," figure 947 (from Wiedersheim), show, in a dorsal view of the brain of the alligator, a structure which they call the epiphysis.
C. L. Herrick (20) mentioned, though he did not describe in detail, the epiphysis of the brain of the alligator.

The present writer (42), in his previons paper dealing with the

[^0]general features in the development of the alligator, described what he then supposed to be the epiphysis.

Voelzkow (5I), whose paper the writer had not seen at the time of the publication of his above-mentioned paper, quotes Sorensen in the statement that, in the alligator, the paraphysis had been wrongly taken for the epiphysis. In this paper Voelzkow says that the epiphysis is absent in both the Madagascar Crocodile and the Caiman. His figures show conditions very similar to those to be described in the present paper.

For obvious reasons sagittal sections were chiefly used in studying the development of the paraphysis and hypophysis, though sections cut in other directions were used to some extent.

The earliest stage in which any sign of the paraphysis is seen is shown in figure 1 , a sagittal section of an embryo of about 7 mm . length, though the exact size, owing to the marked body flexure, could not be determined. At this stage there is not much difference in the thickness of the walls of the brain, in the different regions, except for the marked thinness of the roof of the hind-brain. A ventral depression, $v$., of the dorsal wall of the fore-brain is the beginning of the velum; a wide arch, p.a., just anterior to this marks the position of the paraphysis, and may be called the paraphysal arch. Posterior to the velum the roof of the fore-brain is slightly arched to form the beginning of what may be called the post-velar arch, v.a. (Minot), the dorsal sac or zirbelpolster of other writers. An indistinct thickening, p.c., of the dorsal wall marks the posterior limit of this arch, and also the boundary between the fore- and midbrains ; it is the future posterior commissure.

Ventral to the brain are seen the anlage of the hypophysis, $h_{\text {. }}$, to be described later, and the vacuolated notochord, ch. At this stage of development the brain cavity is very wide, dorso-ventrally, in proportion to its antero-posterior length.

Figure 2 represents the anterior end of an embryo of about 10 mm . length. It will be noticed that the brain is much longer, in proportion to its depth, than in the preceding figure, and that the cranial flexure is more marked. The section passes almost exactly through the median plane of the roof of the brain, but a little to one side of this plane in the region of the hind-brain, so that the notochord is not shown.

The fore-brain, $f . b$., is beginning to push forward to form the cerebral hemispheres, $c$., and a marked fold, the cerebellum, $c b$. ., is seen between the mid- and hind-brains. The hypophysis, h., cut slightly to one side of the median plane, has increased in size and complexity; it will be described later.

The posterior commissure, p.c., is somewhat more distinct than in the preceding stage, and the post-velar arch, $v . a$., is distinctly differentiated, partly because of the increasing thinness of its wall and partly because of the marked increase in the size of the velum, $\tau$., which now projects into the cavity of the fore-brain as a heavy transverse ridge. As seen in this plane, the velum has two lower angles, a more acute one projecting ventrad and caudad, and a thicker, more obtuse angle, projecting forward under the paraphysis.

Instead of the wide, flat arch, seen in the preceding stage, the paraphysis is here a distinct, saccular diverticulum of the fore-brain, with whose cavity it connects by a wide opening.

A section cut laterad to the paraphysal opening is shown in figure 2a. Here the paraphysis is seen as a separate, circular cavity, $p$., lying in the mesoblast between the wall of the fore-brain and the superficial ectoderm. It is not strange that, when seen in such a section, the paraphysis should have been taken for the epiphysis, because the marked forward projection of the post-velar arch, v.a., gives the impression that it and not the arch anterior to the velum is connected with this paraphysal vesicle.

In this figure the paraphysis has thick walls, with a denser layer of nuclei towards the central cavity. The velum, $v$., has here but one angle, that projecting caudad, the other angle is now continuous with the roof of the fore-brain, beneath the paraphysis.
The infundibulum is seen as a wide, shallow depression, in., in the floor of the fore-brain. The plane of the section, being more nearly median in the posterior region, cuts the side of the notochord, ch., at its extreme anterior end.

Figure 3 represents an embryo somewhat older than the one represented in figures 2 and 2a. The brain is considerably more elongated than in the preceding stage, and the cranial flexure is more marked.

In the region of the hind-brain the section is exactly median, so that the notochord, ch., and hypophysis, $h$., are cut through the median plane. In the region of the paraphysis, $p$., the section is to one side of the median plane, and the opening of that structure into the fore-brain is not seen.

The velum and paraphysis are about the same as in the preceding figure, except that the latter, in its median region, has thinner walls than in the earlier stage. The greatest change is in the post-velar arch, $v . a$., which is now much more sharply defined, mainly because its dorsal wall is much reduced in thickness. This thin roof of the post-velar arch gradually increases in thickness as it passes into the velum, but its transition into the posterior commissure, p.c., is now
very sudden, so that the latter structure is more distinct than in the preceding figure.

Figure 4 represents an embryo 2 or 3 mm . longer than the one just described. The section, which was drawn under somewhat lower magnification than was figure 3 , is almost exactly median in position, and hence does not pass through the lateral ventricles.

The cerebellum, $c b$., and posterior commissure, p.c., are more distinct in outline, the distinctness of the latter being due to the upward curvature of its anterior region, and to its now sharp differentiation from the thin roof of the post-velar arch.

The roof of the post-velar arch is thinner than in the preceding stage, and its posterior portion, where it becomes continuous with the posterior commissure, is, by the above-mentioned upbending of the anterior edge of the commissure, carried suddenly upward as a transverse furrow, seen in this figure just anterior to the posterior commissure.

The velum, $v$., is thinner in an antero-posterior direction than before, and contains, in this region, two or three small vesicles, lined with distinct cuboidal epithelium. Each cell of this epithelium contains a large, spherical nucleus.

The paraphysis, $p$., is seen as a large, thin-walled sac, connected by a very wide opening with the fore-brain.

A plane twenty-four section laterad to the one shown in figure 4 is shown in figure 4a. Here the posterior commissure, p. c., and postvelar arch, v. a., have about the same appearance as in figure 4; but the paraphysis, $p$, which is cut laterad to its opening, is seen as a small circular cavity with thicker walls than were shown in the median section. The velum, $v$., shows the most marked change over the earlier stages, and projects forward as an irregular mass into the lateral ventricle.

The paraphysis, at this stage, is a large, thin-walled vesicle, opening by a wide mouth into the fore-brain just in front of the velum. It is somewhat compressed, laterally, and, in some cases, lies more on one side of the median line than the other. The width of its opening is usually about one-third of the width of the entire vesicle, while the antero-posterior diameter is at least one-half the anteroposterior diameter of the entire vesicle.

Figure 5 represents a sagittal section of a much older embryo than the one shown in figures 4 and 4 a, though the condition of the paraphysis is not very different from the description just given. The greatest diameter of the head, from the tip of the snout to the roof of the mid-brain, is about 9 mm .

The outline of the head is begimning to assume the reptilian form,
largely because of the growth of the mandible, $m d$. The nasal cavity, $n$., opens to the pharynx through the posterior nares, $p . n$., though this connection is not shown in the figure. The cerebral hemispheres, c., are large, thick-walled structures, while the infundibulum is now relatively smaller than in the preceding stage.

The posterior commissure, cerebellum, etc., are not very different from what has been described.

The post-velar arch, $v . a$., has changed considerably; it is now higher and less wide, in an antero-posterior direction, than in figure 4. Although the length of the head has increased 50 per cent over the preceding stage, the actual diameter of the arch, from the velum to the posterior commissure, is less than is shown in figure 4.

The paraphysis, $p$., also shows signs of laving been compressed in an antero-posterior direction. The lateral diameter of its opening is still about one-third of the width of the entire structure, while the antero-posterior diameter of the opening is only one-fifth of the antero-posterior diameter. The walls of the paraphysis, as well as the roof of the post-velar arch, are somewhat thicker than they were in the preceding stage, and consist, apparently, of simple columnar epithelium, though the exact character of the cells could not be determined because of poor fixation. The paraphysis, which is now more tubular than spherical in outline, is slightly inclined caudad instead of having a slight inclination cephalad, as in the preceding stage. As will be seen, this inclination of the paraphysis away from the cerebral hemispheres becomes more marked in later development.

The velum, $v$., has undergone marked development. In the median plane, as shown in figure 5 , it is seen as a somewhat arched band of tissue forming the posterior border of the paraphysis. In this plane are seen in the velum the two or three vesicles, vs., noted in the preceding figure. These vesicles are not connected with either paraphysis or fore-brain. When followed laterally the velum is seen to expand to form, on each side, a much branched structure, the plexus of the lateral ventricle, figures 5 a and $5 \mathrm{~b}, \mathrm{c} . \mathrm{p}$.

Figure 5 a represents a section laterad to the one just described. It passes through the median edge of the choroid plexus, c. p., just described, and through the lateral portion of the paraphysis, $p$., whose walls appear thick merely because cut tangentially.

Figure 5b is a section of a somewhat older embryo than the one shown in figures 5 and 5 a . It is about, though not exactly, in the plane a-b of figure 5. It shows the laterally compressed paraphysis, $p$., and in each lateral ventricle, $c$., the much convoluted plexus, $c . p$.

Figure 6 shows the paraphysal region of an embryo of about 7 cm .
length. This embryo is several times the length of the one represented by figure 5, and has practically the external form of the adult, even the pigmentation of the skin being partially formed. In spite of this great advance in general development, about the only change in the paraphysis, $p$., is a slight increase in length. Its walls are still practically smooth and unconvoluted; they are composed of a simple columnar epithelium.

The velum, $v$. , has, in this median plane, nearly the same appearance as in figure 5 ; in it are seen four or five of the same small vesicles, vs., lined with cuboidal cells, that were seen in figures 4 and 5 . The prolongations of the velum into the lateral ventricles, the choroid plexuses, as seen in more lateral sections, are now large and much convoluted.

The post-velar arch, v. a., is much reduced in extent, so that the distance between the posterior commissure, p.c., and the velum, $v$., even in this much larger embryo, is only about two-thirds of the corresponding distance in figure 5. A greater part of the roof of the post-velar arch is considerably thickened and is somewhat convoluted.

The brain cavities are all relatively and actually smaller than in the preceding stage, and their diminution in size is made more evident by the increased thickness of the brain wall.

The oldest embryo studied was one of about 13 cm . length, nearly twice the length of the one shown in figure 6. This embryo has practically the adult form, and is fully pigmented, so that it is likely that the paraphysis has here approximated more or less closely its adult condition.

In spite of the great increase in the size of the brain over the preceding stage, there is very little change in either the size or form of the paraphysis; it is slightly longer, but it curves back over the post-velar arch in the same ways as is shown in figure $\sigma$. Its walls are of the same character and are neither more nor less wrinkled or folded than in this figure. Owing either to its increase in length or to a change in the relative positions of parts of the head the tip of the paraphysis is somewhat nearer the dorsal surface of the head ; it is, in fact, in contact with a dense layer of connective tissue which will form the roof of the skull.

The velum is somewhat longer than in the preceding stage and has rather more numerous vesicles than were there seen. It is, perhaps, partly to this increase in length of the velum that the increase in the length of the paraphysis is due.

The post-velar arch is of about the same size and outline as in figure 6 ; its dorsal wall is, perhaps, slightly more deeply wrinkled.

## The Hypophysis

The hypophysis is first seen in the alligator in embryos of about 7 mm . length. In this animal, at any rate, there is no reason for doubt as to whether it be derived from the ectoderm or the entoderm. As may be seen in figure I, $l$., the hypophysis originates as an invagination of ectoderm close under the floor of the fore-brain. The superficial ectoderm gradually thickens as it passes under the forebrain, and in the region of the invagination it is several times as thick as in other regions of the body. Followed towards the pharynx it gradually thins out again as it becomes continuous with the entoderm of the fore-gut.

Gaupp (17) says that in lizards and perhaps in all reptiles the hypophysis has a three-fold beginning: A large, round middle part, and two lateral parts, pushed in from the epithelium of the mouth cavity. In the alligator this three-fold origin cannot be made out. The conical invagination seen in figure I gradually diminishes in depth and width as it is followed laterad, until it disappears, but no lateral pouches are seen.

The general ectoderm of the body is composed of a single layer of cuboidal or even flattened cells, while the walls of the hypophysal invagination are made up of a single layer of long, narrow, columnar cells with distinct nuclei.

Just caudad to the hypophysis is seen in figure I an indefinite and smaller invagination of the thickened epithelium, p.s.; this may represent what has been called, in other forms, the pharyngeal sac. Bawden (2) says that in the duck the pharyngeal sac appears earlier than the hypophysis, reaches its maximum development in five days, and soon disappears. It lies between the hypoblast and the notochord, with the latter of which it is connected.

In the present figure no connection between the pharyngeal sac and the notochord, ch., is to be seen, unless it be represented by the slight condensation of the mesoblast that extends from the tip of the notochord to the inner surface of the sac.
Figures 2 and 2a represent the condition of the hypophysis in an embryo of about io mm. length. The general topography of the head has been described in speaking of the paraphysis of this stage.

Figure 2 is laterad to the exact median plane. It shows the main invagination of the hypophysis at the end of the reference line, $h$., caudad to which are several wrinkles of the thickened epithelium. Between the invagination just mentioned and the floor of the infundibulum, in., are two small, oval, compact masses of cells which are lateral branches of the main invagination or stalk, as it may be
called. These lateral branches are nearly solid, at this stage, though the cavity of the hypophysal stalk may be traced, in sections mediad to this, for a short distance into them, as a very narrow slit.

Figure $2 a$ is through a more nearly median region of the hypophysis, as may be seen by the section of the notochord, ch., that is shown. The region of thickened epithelium is more extensive than in figure 1 . The hypophysal stalk is at the end of the reference line, $h_{\text {., caudad the the }}$ to are seen three or four wrinkles in the epithelium. The most posterior of these wrinkles, p.s., is much deeper and more distinct than the others, and probably represents the pharyngeal sac, though no comection whatever may be seen between it and the notochord.

In figure 3 is represented a section through the median region of the lyppophysis, $h$.. now considerably more developed than in the preceding stage. The actual depth of this median invagination or stalk is about 0.3 mm ., or about one-twelfth of the greatest length of the head. The greatest width of the hypophysis is about equal to the depth of the stalk, 0.3 mm . The lateral, inside diameter of the stalk is about 0.2 mm. ; the antero-posterior diameter is about 0.12 mm .

On each side of the stalk are two lateral diverticula, seen better as a horizontal section, to be described later, figure 5 b. Of these the pair nearer the notochord are the larger and are directly continuous with the imner end of the stalk; the other and smaller pair open into the outer, lateral angles of the stalk near the opening of the latter structure.

Just candad to the stalk of the hypophysis is a distinct invagination of the epithelium, p.s., the pharyngeal sac, which shows no connection whatever with the notochord.

The walls of the hypophysis have become so much thicker, and the basal wall of the infundibulum has become so much thinner that now the former wall is, in places, thicker than the latter.
Figure 4 b is a sagittal section of an embryo of 13 mm ., " crownrump" measurement, if such a term be here permissible. The hypophysis has made considerable progress in development and has increased somewhat in size over the last stage ; its greatest lateral diameter is slightly less than 0.5 mm . ; its greatest antero-posterior diameter is practically the same.

The shape of the head las changed in several particulars. The infundibulum, in., is a more definitely outlined depression in the floor of the fore-brain, and the roof of the mouth or pharynx, whichcver it may be called, extends back of the stalk of the hypophysis instead of ending in the hypophysal invagination as in the last stage.

The most important change in the hypophysis itself is the complete closure of the wide opening to the exterior, seen in figure 3. The walls of the original opening are still distinct from each other, though they are in close contact (fig. 4, h.s.), and form a sort of solid stalk, the hypophysal stalk. The oral epithelium is still continuous with the hypophysal stalk, but it is thickened for only a short distance on either side of it.

The closure of the hypophysal opening has taken place in such a way that the stalk is at right angles to the long axis of the hypophysis proper. As seen in the present figure, the hypophysis is a hollow body of irregular outline, with thick, dense walls. The cavity consists of a central region (fig. $4 \mathrm{~b}, h_{\text {. }}$ ), and three outgrowths, the largest, o., extending back till it nearly reaches the notochord, ch.; the second, $o^{\prime}$., extending in the same direction from the base of the hypophysal stalk; and the third, $o^{\prime \prime}$., extending towards the floor of the infundibulum, in. As the sections are followed laterad these three outgrowths are found to extend for some distance on each side of the body of the hypophysis. The outgrowth $o^{\prime}$. is the largest and remains unbranched ; it is hollow throughout. The outgrowth $o^{\prime \prime}$. is also hollow and unbranched: it is the shortest of the three. The outgrowth $o$. extends laterad for some distance, and then divides into three nearly solid outgrowths which extend nearly as far as the outgrowth $o^{\prime}$.

Figure 4 c represents a section of an embryo of approximately the same size as the one under discussion. The plane of the section is nearly that of the broken line in figure $4 b$.

The section shows.one of the ontgrowths, 0. , on each side of the median cavity, $h$., the one on the left being cut tangentially so that its cavity does not show. The larger outgrowth, $o^{\prime}$., is seen on either side of the median cavity, just above the hypopliysal stalk, h. s.

The hypophysis at this stage, then, is a completely closed vesicle of irregular shape, consisting of a central cavity with three main diverticula on each side, and a solid stalk connecting it with the oral epithelium.

The pharyngeal wall, back of the hypophysis, exhibits several wellmarked wrinkles; one of these, shown at p.s., in figure $4 b$, may represent the pharyngeal sac, though it differs very little from any other of the wrinkles. In this sac the epithelium, which is somewhat thickened, almost touches the mesoblast that surrounds the notochord, ch. No connection whatever can be seen between this invagination and the notochord.

Figure 5, as was stated in connection with the paraphysis, represents a much later stage of development than the preceding. The
hypophysis is here cut laterad to its median plane, so that its stalk is not shown. The lateral outgrowths from the median body are now more numerous, more than a dozen being cut by the plane of this section. Some of these outgrowths still exhibit a small, circular lumen, while others are solid. The outgrowths lying next to the infundibular wall are crowded very close together, while those nearer the pharynx are separated by considerable connective tissuc.

No sign of the pharyngeal sac is seen in this section.
Figure 5 C is through the median plane of the hypophysis. The hypophysal stalk, $h$. s., is here cut throughout its entire length; its connection with the oral epithelium is still evident and complete, but its lumen has entirely disappeared. The stalk, though narrower than in the preceding stage, is more than twice as long, and is slightly bent towards an $S$ shape. A considerable cavity, $h$., is still seen in the body of the hypophysis, and two of the outgrowths, $o$. and $o^{\prime}$., are evident. The position of the outgrowth $o^{\prime \prime}$. is seen as a small, nearly solid projection close under the wall of the infundibulum. Just to the right and below (as seen in the figure) the outgrowth $o^{\prime \prime}$. is seen a larger mass, $a^{\prime \prime \prime}$., elongated in outline and with a narrow lumen (a small, round hole in this section). Although in close contact with the front wall of the body of the hypophysis, this thickwalled vesicle seems to have no direct connection, at this stage, with the rest of the hypophysis.

The greatest length of the body of the hypophysis is now about 0.75 mm ., an increase of 0.25 mm . over the preceding stage. Owing to a failure to record the thickness of the sections of this series the width of the hypophysis could not be determined.
A well-marked invagination, p.s., of the pharyngeal wall, a short distance back of the hypopliysal stalk, may represent the pharyngeal sac.

From the floor of the infundibulum, $i n$. , a deep, narrow pit, $i n^{\prime}$., projects down into the body of the hypophysis. The bottom wall of this pit is in close contact with the cells of the hypophysis, perhaps continuous with them, but no opening from infundibulum to hypophysis can be made out.

Figure 6a shows the condition of the hypophysis in an embryo of about 6 cm . length. The stalk, h.s., is very long and still more slender and curved than in the preceding stage; it connects with the surface at the base of a backwardly projecting fold of skin, the eustachian valve, $c$. . The stalk not only shows no sign of a lumen, but is actually discontinuous at a point near its middle region.

The body of the hypophysis is little if any larger than in the preceding stage ; its cavity has almost completely disappeared, being seen only as a narrow slit in one or two regions.

The number of lobes or branches of the hypophysis has increased considerably, and, under the low magnification used in the present figure, they appear as a collection of irregular, granular masses, separated by narrow lines of connective tissue. Higher magnification shows these masses to be composed of small, densely stained cells resembling lymphoid tissue.

The infundibular pit, $i n^{\prime}$., does not show such intimate connection with the cells of the hypophysis as was noted in the preceding stage. It is, however, more distinctly separated from the infundibulum proper by a lateral narrowing of its mouth, so that, in sections on either side of the one represented in figure 6 a, the pit is seen as a separate, circular vesicle, distinct from the infundibular wall and lying among the lobes of the hypophysis.

No sign whatever of the pharyngeal sac is to be seen in this embryo.
Figure 7 represents the hypophysis of the 13 -cn. embryo described in connection with the paraphysis. The hypophysal stalk, h.s., is here reduced to a slightly carved stump in connection with the main body of the hypophysis; its connection with the mouth is completely lost.

The body of the hypophysis still shows a narrow, slit-like lumen, $l$., on the side below the infundibular pit, in ${ }^{\prime}$.

The mass of lobules making up the hypophysis is more compact, in this median region, than in the preceding stage, so that the connective tissue septa are almost invisible, and the lobules seem to have fused together to form larger lobes. The appearance of the hypophysis under higher magnification is not different from what was seen in the preceding stage.

The infundibular pit, $\mathrm{in}^{\prime}$., has, in this figure, about the same appearance as in figure 6a, but, in sections cut laterad to the present one, the pit is found to have a branched lobe on each side. Each of these lobes is seen in parasagittal sections as two circular, thickwalled vesicles lying among the lobules of the hypophysis, entirely distinct from the zentral wall of the infundibulum proper.

## Summary

The paraphysis in the alligator has long been mistaken for the epiphysis, the latter structure being entirely absent.
The paraphysis is first seen in embryos of 7 mm . length, as a wide evagination of the roof of the fore-brain, just cephalad to a transverse fold, the velum. This evagination early becomes partially constricted off from the brain and forms a rounded, hollow mass connected with the diencephalon by a wide stalk. As growth pro-
ceeds the paraphysis becomes elongated until, in embryos of 7 cm . length, it is seen as a tubular structure, with nearly smooth walls, slightly curved away from the cerebral hemispheres and over the top of the diencephalon. In embryos of 13 cm . the paraphysis has practically the same structure as in the 7 cm . embryo.

The velum grows forward into each lateral ventricle to form its choroid plexus.

The hypophysis in the alligator begins, at about the same stage as does the paraphysis, as a single, median evagination of the roof of the mouth, just beneath the floor of the infundibulum. The original evagination becomes the stalk of a considerably branched, hollow structure which, by the lengthening of the stalk, recedes to some distance from the roof of the mouth. The stalk becomes solid and finally loses all connection with the oral epithelium. The body of the hypophysis also becomes almost completely solid, in an embryo of 13 cm ., and is seen as a lobulated mass of lymphoid tissue lying close under the floor of the infundibulum.

The material upon which this work has been done was collected by the writer, in Central Florida, with the aid of a grant from the Smithsonian Institution, for which grant acknowledgment is here made.

## BIBLIOGRAPHY.

I. Alborn, Fir, '8ł. Über die Bedeutung der Zirbeldrüse. Zeit. f. wiss. Zool., Bd. 40.
2. Bawden, H. H., '93. I. Selenka's "Pharyngeal Sac" in the Duck. Jour. Comp. Neur., Vol. 3, pp. 45-48.
3. Beard, J., '87. The Parictal Eye in Fishes. Nature, I887, July I4.
4. Beard, J., '88. The Parietal Eye of the Cyclostome Fishes. Quar. Jour. Mic. Sc., N. S., Vol. 29.
5. Béraneck, Ed., ' 87 . Über das Parietalauge der Reptilien. Jen. Zeitschr. f. Natfsch., Bd. 21, N. F., Bd. 14, S. 374-5if.
6. Béraneck, Ed., '92. Sur le nerf pariétal et la morphologie du troisième oeil des Vertébrés. Anat. Anz., Bd. 7, S. 674-687.
7. Béraneck, Ed., '93. L'Individualité de l'oeil pariétal. Résponse à M. de Klinckowström. Anat. Anz., Bd. 8, S. 669-677.
8. Burchhardt, R., 'go. Die Zirbel von Ichthyopsis glutinosus und Protopterus annecteris. Anat. Anz., 6 Jalırg., S. 348-349.
9. Burckhardt, R., '94. Die Homologien des Zwischenhirndaches bei Reptilien und Vögeln. Anat. Anz., Bd. 9, S. 320-324.
io. Dean, Bashford, '95. Fishes Living and Fossil. The Macmillan Co., New York, pp. 53-56.
ir. Dendy, A. On the Development of the Pineal Eye in Sphenodon (Hatteria). Quar. Jour. Mic. Soc., Vol. 42, p. Iti.
12. Dexter, F., '02. The Development of the Paraphysis in the Common Fowl. Amer. Jour. Anat., Vol. 2, No. I, pp. 13-24.
13. Eycleshymer, A. C., '92. Paraphysis and Epiphysis in Amblystoma. Ant. Anz., Bd. 7, S. 215-217.
I4. Eycleshymer, A. C., and Davis, B. M., '97. The Early Development of the Paraphysis and Epiphysis in Amia. Jour. Comp. Neur., Vol. 7, pp. 45-70.
15. Fleschi, M., '88. Über die Deutung der Zirbel bei den Säugetieren. Anat. Anz., 3 Jahrg., S. 173-176.
i6. Francotte, S., 'S8. Recherches sur le développement de l'épiphyse. Archiv. de Biol., Vol. 8, pp. 757-821.
17. Gaupr, E., '93. Über die Anlage des Hypophyse bei Saurien. Archiv. f. Mik. Anat., Bd. 42, S. 569-581.

I8. Gaupp, E., '97. Zirbel, Parietalatge und Paraphysis. M. and B. Ergebn. Anat. u. Entw., Bd. 7, S. 208-285.
19. de Graaf, H. W., '86. Zur Anatomie und Entwicklung der Epiphyse bei Amphibien und Reptilien. Zool. Anz., 9 Jahrg., S. 191-194.
20. Herrick, C. L., '90. Notes on the Brain of the Alligator. Jour. Cincinnati Nat. Hist. Soc., Jan. 1890, pp. I29-162.
21. Herrick, C. L., '93. Topography and Histology of the Brain of Certain Reptiles. Jour. Comp. Neur., Vol. 3, pp. 92-94 and I3I.
22. Hertwig, O., '92. Text-book of Embryology of Man and Mammals (trans.).
23. Hill, Chas., '9i. The Development of the Epiphysis in Coregonus Albus. Jour. Morph., Vol. 5, pp. 503-510.
24. Hill, Chas., '94. The Epiphysis of Teleosts and Amia. Jour. Morph., Vol. 9, pp. 237-268.
25. Hoffmann, C. K., 'S6. Weitere Untersuchungen zur Entwicklungsgeschichte der Reptilien. Morph. Jahrb., Bd. II, I886, S. I89-197.
26. Hofmann, C. K., '88. Epiphyse und Parietalauge. Bronn's Thier-Reich, Bd. 6, Pl. 3.
27. Humphrey, O. D., '94. The Brain of the Snapping Turtle (Chelydra serpentina). Jour. Comp. Neur., Vol. 4, pp. 7i-rib.
28. Kingsbury, B. F., '85. The Brain of Necturus Maculatus. Jour. Comp. Neur., Vol. 5, pp. 139-204.
29. Klinchowström, A. de, '93a. Le premier développement de l'oeil pariétal, l'épiphyse et le nerf pariétal chez Iguana tuberculata. Anat. Anz., 8 Jahrg., S. 289-298.
30. Klinckowström, A. de, '93b. Die Zirbel und das Foramen parietale bei Callichthys (asper und littoralis). Anat. Anz., 8 Jahrg., S. 561-564.
3I. Klinckowström, A. de, '94. Beiträge zur Kenntnis des Parietalauges. Zool. Jahrb., Bd. 7, S. 249-280.
32. Kraushaar, R., '84. Entwicklung der Hypophysis und Epiphysis bei Nagethieren. Zeits. f. wiss. Zool., Bd. 4I.
33. Leydig, F. von, '87. Das Parietalorgan der Wirbelthiere. Zool. Anz., Io Jahrg., S. 534-537.
34. Leydig, F. von, '90. Das Parietalorgan der Amphibien und Reptilien. Abh. d. Senchenberg. Gesell., Bd. 16, Heft 2, S. 441-551.
35. Locy, W. A., '93. The Derivation of the Pineal Eye. Anat. Anz., Bd. 9, Nr. 5 und 6, S. 169-180.
36. McKay, W. J., '88. The Development and Structure of the Pineal Eye in Hinuilia and Grammatophora. Proc. Linn. Soc. N. S. Wales, 2d S., Vol. 3 .
37. Minot, C. S., 'oi. On the Morphology of the Pincal Region, Based upon its Development in Acanthias. Amer. Jour. Anat., Vol. I, No. i, pp. 8i-98.
38. Osborn, H. S., '88. A Contribution to the Internal Structure of the Amphibian Brain. Jour. Morph., Vol. 2, pp. 5I-96.
39. Prenant, A., '93. Sur l'oeil pariétal accessoire. Anat. Anz., Bd. 9, S. 103-1I2.
40. Rabl-Rueckhardt, "78. Das Zentralnervensystem des Alligators. Zeit. wiss. Zool., Bd. 30, S. 336-372.
41. Rabl-Rueckhardt, '86. Zur Deutung der Zirbeldrüse. Zool. Anz., Bd. 9, S. 405-407.
42. Reese, A. M., 'o8. The Development of the American Alligator. Smith. Misc. Coll., Vol. 5I, pp. i-66.
43. Ritter, W. E., '91. The Parietal Eye in Some Lizards from the Western United States. Bull. Mus. Comp. Zool.. Vol. 5, No. 8.
44. Ritter, W. E., '94. On the Presence of a Parapineal Organ in Phrynosoma Coronata. Anat. Anz., Bd. 9, S. 766-772.
45. Scott, W. B., '87. Notes on the Development of Petromyzon Fluviatalis. Jour. Morph., Vol. I, pp. 253-3II.
46. Sorensen, A. D., '93a. The Pineal and Parictal Organ in Phrynosoma Coronata. Jour. Comp. Neur., Vol. 3, pp. 48-50.
47. Sorensen, A. D., '93b. The Roof of the Diencephalon. Jour. Comp. Neur., Vol. 3, pp. 50-53.
48. Sorensen, A. D., '94. Comparative Study of the Epiphysis and Roof of the Diencephalon. Jour. Comp. Neur., Vol. 4, pp. 12-72, and 153-170.
49. Spencer, W. B., '86a. The Parietal Eye of Hatteria. Nature, May 13.
50. Spencer, W. B., '86b. On the Presence and Structure of the Pineal Eye in Lacertilia. Quar. Jour. Mic. Sc., Vol. 24, pp. 165-238.
51. Voelzkow, A., '05. Epiphysis u. Paraphysis bei Krokodilien u. Schildkröten. Abh. Senckb. Naturf. Gesell., Bd. 27, Heft 2, S. 165-177.
52. Warren, John, 'o5. The Development of the Paraphysis and the Pineal Region of Necturus Maculatus. Jour. Anat., Dec., 1905, pp. I-27.
53. Wiedersheim, R., '86. Über das Parietalauge der Saurier. Anat. Anz., I Jahrg., S. 148-149.
54. Wiedersheim, R., '97. Comparative Anatomy of Vertebrates (trans. by W. N. Parker), p. 155.

## EXPLANATION OF FIGURES $1-7$, PLATES $1-5$.

All figures were drawn under a camera lucida.

Fig. I. A sagittal section through the head of a 7 mm . embryo, to show the beginning of the paraphysis and hypophysis. Objective $2 / 3$ inch; ocular 2 inch.
Figs. 2, 2a. Sagittal sections of the anterior region of a 10 mm . embryo. In Fig. 2 the section passes through the median plane of the paraphysis, but slightly laterad to the median region of the hypophysis. In Fig. 2a the section cuts the hypophysis medially, and the paraphysis to one side of the median plane. Objective 2 inch; ocular 1 inch.
Fig. 3. A sagittal section of an embryo somewhat older than the one represented in Figs. 2 and 2a. The hypophysis is cut medially, while the paraphysis is cut somewhat to one side of its median plane so that its connection with the fore-brain is not shown. Objective 2 inch; ocular I inch.

Fig. 4. A sagittal section of the anterior region of an embryo of about 13 mm . length. The paraphysis is cut sagittally, while the hypophysis is cut through its lateral edge. Objective 2 inch; ocular 2 inch.

Fig. 4a. A parasagittal section through the dorsal part of the head of the same embryo represented in the preceding figure. The paraphysis is seen as a distinct vesicle lying between the fore-brain and the superficial ectoderm. The forward growth of the velum into one of the lateral ventricles is also shown. Objective 2 inch; ocular 2 inch.

Fig. 4b. A sagittal section through the hypophysal region of an embryo of the same stage as the one shown in Figs. 4 and 4a. Objective $2 / 3$ inch; ocular I inch.

Fig. 4c. A horizontal section through the hypophysal region of an embryo of about the same age as the ones shown in Figs. 4, 4a, and 4b. The approximate plane of this section is indicated by the broken line in Fig. 4b. Objective $2 / 3$ inch; ocular I inch.

Fig. 5. A sagittal section of a much older embryo than the ones shown in Figs. 4 to 4 c . The paraphysis is cut almost exactly medially, while the hypophysis is cut laterad to its median plane. Objective 2 inch; ocular 2 inch.

Fig. 5a. A sagittal section of the paraphysal region of the same embryo shown in Fig. 5. Objective 2/3 inch; ocular 2 inch.

Fig. 5b. A horizontal section through the paraphysal region of an embryo of the stage represented by Figs. 5 and 5a. The approximate plane of the section is indicated by the broken line a-b, in Fig. 5. Objective 2 inch; ocular 2 inch.

Fig. 5c. A sagittal section through the hypophysal region of the same embryo shown in Figs. 5 and 5a. Objective $2 / 3$ inch; ocular 2 inch.

Fig. 6. A sagittal section through the paraphysal region of a 7 cm . embryo. Objective 2 inch; ocular 2 inch.

Fig. 6a. A sagittal section through the hypophysal region of the same embryo. Objective $2 / 3$ inch; ocular 2 inch.

Fig. 7. A sagittal section through the hypophysal region of a 13 cm . embryo. Objective $2 / 3$ inch; ocular 2 inch.

Lettering.
b.v., blood vessel.
c., cerebral hemispheres.
$c b$., cerebellum.
ch., notochord.
c. p., choroid plexus.
$e$., eustachian valve.
f.b., fore-brain.
h., hypophysis.
h. b., hind-brain.
ht., heart.
h. s., hypophysal stalk.
in., infundibulum.
in'., infundibular pit.
l., slit-like lumen of hypophysis.
m.b., mid-brain.
$m d .$, mandible.
n., nasal cavity.
o.- $o^{\prime \prime \prime}$., lateral diverticula of hypophysis.
p., paraphysis.
p.a., paraphysal arch.
p.c., posterior commissure.
ph., pharynx.
p.n., posterior nares.
p. s., pharyngeal sac.
v., velum.
v. a., post-velar arch (dorsal sac).
vs., velar vesicles.







[^0]:    ${ }^{1}$ The present paper is one of the results of special researches in continuation of my paper on "The Development of the American Alligator," published in 1908 in Smithsonian Miscellaneous Collections, Vol. 51, 66 pages and 23 plates, in which there was given a general outline of the whole process of development of the American alligator. There was also published in the same series, Vol. 48, pp. 381-387, an article on "Tlic breeding habits of the Florida alligator."
    ${ }^{2}$ The numeral citations in this papcr are to bibliographical references at the end of the paper.

