ON THE BRAIN OF NECTURUS MACULATUS.

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(With Plates IX, X, and XI.)

CONTENTS.

INTRODUCTION.

This investigation was made in the anatomical laboratory of Cornell University. I am glad to acknowledge my indebtedness to the Anatomical Department for the material and facilities placed at my disposal: To the members of the Department, and particularly to Prof. Wilder and Dr. Fish under whose immediate supervision the work was done, I wish to express my appreciation of their interest manifested in it; the former put into my hands all his unpublished notes and drawings as well as numerous preparations of the brain made in 1873 and 1874. To Prof. Gage I am under deep obligation for material kindly obtained for me from Prof. Whitman of Chicago University and for suggestions as to methods. The series of sections through the brains of *Diemyctylus* and *Desmognathus*, which I have been enabled to examine by the kindness of Mrs. Gage and Dr. Fish have also been of great service to me. Numerous valuable suggestions have been gained from the discussions of the Neurological Conferences.

It is somewhat surprising that, although extended investigations have been made upon the nervous system of various urodeles by numerous anatomists, neither the brain of *Necturus*, nor, indeed, that of its European relative, *Proteus*, have received more than a very fragmentary treatment. The importance of these forms is obvious and has been recognized in the attention given to other parts of their structure. They are the lowest Amphibia, generally so regarded, and their perennibranchiate condition suggests at least the presence and persistence of what in other forms are larval peculiarities merely. Further, Necturus presents in its availability and the convenient size of its brain,—neither too large for convenient microscopic examination nor too small for macroscopic observation,—characters making it also well suited for the elucidation of the numerous problems connected with the amphibian, and particularly the urodele, brain. Therefore a somewhat complete treatment of this form would seem desirable.

Necturus is known to the literature of Neurology through the publications of Spitzka, Wilder, Osborn, Herrick and Fish, the attention it has received being largely confined to the interesting question of the presence of a callosum in Amphibia. So far as is known to the writer, Wilder ('84, 1) was the first to publish figures of any detail of the brain of *Necturus*.[1] Because of its simplicity it was employed by him in a lecture delivered before the Alumni Association of the College of Physicians and Surgeons, New York, February 4th, 1884, to illustrate the relations of the cavities and segments of the brain. It was one of the forms discussed by Osborn ('86) in his memorable papers on the "Origin of the Corpus Callosum"; in his subsequent article, "A Contribution to the internal Structure of the Amphibian Brain" ('88) the structure of the brain is discussed in conjunction with that of *Cryptobranchus.* Herrick's contributions to the structure of the brain of *Necturus* occur in the valuable papers by him in this journal, on the comparative morphology of the central nervous system. The mention by Fish ('95) of the relations of certain commissures in *Necturus* is merely incidental and is in connection with the question of the presence of a callosum in Amphibia. The views of these neurologists will be frequently referred to in the text.

MATERIAL AND METHODS.

The material employed in this investigation consisted chiefly of numerous brains of adult *Necturi* from 20 to 38 centimeters long. Cayuga Lake abounds in this form and fresh examples were available whenever needed. In addition to the adult, I have been enabled to examine a series of six larval *Necturi*, reared from the egg by Dr. Whitman of Chicago University. They were of the following ages and dimensions, viz.,—just hatched, 4 weeks, 6-8 weeks, 3½ months, 6½ months, and 10 months, with 22.5, 30., 28., 46.5, and 49.5

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[1] Small and diagrammatic figures of the brain of *Necturus* had been previously published by Owen (Trans. Linnean Soc., XVIII, pl. 27, fig. 6, 1839.) and by Wyman ('52) in 1852.

millimeters for their respective lengths. This series was sup-
plemented by a yet unhatched but well-developed specimen
kindly furnished by the anatomical department. The entire
heads of these were sectioned serially in three planes, sagittal,
frontal and transverse, and were extremely valuable for compar-
ison with the adult. In addition to *Necturus*, the brain of
Diemyctylus viridescens, Amblystoma punctatam, and *Desmogna-
thus fusca* were examined, especially for the oblongata and the
origin of the cranial nerves, in order to confirm and better
interpret the results obtained in *Necturus*. For the relations
of the brain and nerves to the skull, and of the nerves to each
other, serial sections were made through the entire cranium;
for the study of the form and structure of the brain itself, how-
ever, it was removed.

For fixing, were employed mercuric chloride and a
mixture devised by Dr. Fish ('93) and termed picro-aceto-sub-
limate (Formula: 50 per cent. alcohol, 1000 c. c., glacial acetic
acid 10 c. c., mercuric chloride 5 grams, picric acid 1 gram.)
The latter gave the best results. The stains employed with
brains fixed as above, were hematoxylin with Van Gieson's
picro-fuchsin as a contrast stain which gave excellent effects.
The hematoxylins employed were Gage's ('92), Delafield's and
Herrick's modification of Delafield's formula; all gave good re-
sults with possibly better figures when the last was used. Fish's
modification of Delafield's also was employed with good suc-
cess (addition of 1 c. c. of glacial acetic acid and 1 c. c. of a
saturated aqueous solution of corrosive sublimate to 100 c. c.
of the hematoxylin). For the fiber tracts were employed
Weigert's hematoxylin method, and also one which is essen-
tially a modification of Exner's perosmic acid method (Ober-
steiner) the osmium being used in conjunction with platinum
chloride and acetic acid as in Hermann's solution. The
stronger formula of this was used and the brain fixed for 24
hours, washed well in water for 4-5 hours and imbedded in
collodion as usual, cleared and cut in Fish's castor-thyme oil
mixture. It was found that the method could be employed
also when decalcification was necessary, and that the blackness

of the nerve fibers rendered the course, relation and division of the nerves easy to determine. It is not thought, however, that this method would be applicable to larger brains, on account of the expensiveness of the fluid and its low power of penetration and the brittleness of the tissue induced. It was most useful in the study of the oblongata and the origin of the cranial nerves, where the results appeared more satisfactory than those gained by the Weigert method; the caliber of the fibrers and their relations were shown with the utmost distinctness. Tissue cut in collodion by Fish's oil method ('93) could be mounted without further treatment, or a delicate nuclear stain obtained by the use of safranin. Babes' first solution was employed (Formula : concentrated alcoholic solution, 50 c. c., concentrated aqueous solution 50 c. c.). The staining required two or three minutes, and 95 per cent. alcohol was used for washing out; (Lee, '93.) The shorter silver nitrate method of Golgi was employed in the study of amyelinic fiber tracts and of cells, though the unavailabity of larval material rendered the results less satisfactory than they otherwise would have been. The usual formulas for the solutions were employed and both double and single impregnations applied.

ECTAL FEATURES.

The dorsal aspect of the brain of *Necturus* has already been well shown by Osborn and Wilder. Its extreme length is very striking and the impression of a stretching betwen the myel and the olfactory capsules is strong. The pons flexure, which is present in *Triton,* and *Diemyctylus* and is marked in *Desmognathus* is very slight in the adult *Necturus.* The cranium also is not nearly filled by the brain, and the olfactory nerves are long nearly equalling in length the combined prosencephal and rhinencephal. In the larval *Necturus* however, the cranium is quite filled by the brain and there is a decided pons flexure, as well as a weaker neck flexure. The adult condition probably indicates that the growth of the brain and skull have proceeded at quite different rates, and that this difference is much greater

in *Necturus* than in the smaller urodeles[1] above mentioned.

The greatest widths are at the olfactory lobes and at the caudal extremities of the cerebrum, at which points they are approximately the same, and much greater than in the parts farther caudad. The height (dorso-ventral diameter) does not vary greatly in the different regions ; it is least in the region of the oblongata and greatest through the infundibulum where the height exceeds the width.

On the dorsum, between the caudal portions of the cerebrum, is the supraplexus enclosing the paraphysis. Caudad of this and likewise between the caudal ends of the cerebrum, is the diatela, bounded caudally by the habenas and at the meson by the supracommissure. The epiphysis is almost circular in outline, lying dorsad of the supracommissure and extending caudad to the postcommissure and also slightly cephalad. There is no ectal distinction on the dorsum between the diencephal and mesencephal save possibly a slight transverse furrow at the postcommissure.

Pigment is generally present on the mesencephal and absent from the diencephal, but this distinction is not constant, the diencephal often being as highly pigmented as the mesencephal.

On the ventral surface is conspicuous the large hypophysis attached to the caudal portion of the infundibulum. The optic nerves are very small and the chiasma is not superficially noticeable. Cephalad of this is a subtriangular space bounded by a whitish area marking the region of the preoptic and lateral optic recesses. The metencephal is simple and very long ; indeed, it equals in length the entire remainder of the brain. It tapers gradually from its widest point at the exit of the fifth nerve to the myel.

The cerebellum is represented only by a small transverse

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[1] The restriction of Urodela and urodele by Cope to a single order of tailed Amphibia is unfortunate; it leaves no convenient term that can be applied to all the tailed Amphibia in contrast to the Anura or tailless forms,—a convenient grouping, although perhaps not of taxonomic value. *Urodele* is used here as synonymous with "tailed amphibia."

band of fibers caudad of the mesencephal. Directly caudad of this is the membranous roof of the metencephal, the metatela, a portion of which is occupied by the metaplexus which sends lateral projections cephalo-laterad on either side of the mesencephal.

Pigment is plentiful in the metaplexus and supraplexus; it also occurs upon the dorsal surface of the diencephal and mesencephal and the lips of the metacœle caudad of the metaplexus.

The meninges and blood supply of the brain have received but incidental attention here. As regards the former, however, as far as observed, the conditions in *Necturus* appeared to agree closely with those observed by Mrs. Gage ('93) in *Diemyctylus*.

The blood supply of the brain in *Amphibia* has been worked out by Schobl ('82) and Rex ('92); by the former on a number of urodeles of which *Necturus* is one. No attempt has been here made to verify his accounts, save that, as found by him, the capillary loops which penetrate the brain from the vessels lying on the surface, although generally stopping at the margin of the entocinerea, or penetrating it for a short distance only, were also occasionally seen to reach the layer of endymal cells.

CRANIAL NERVES.

No attempt has been made to study the peripheral distribution of the cranial nerves; and, in fact, the apparent need of it, existent at the time of Osborn's investigations, has been largely obviated by the later publication of Strong, Von Plessen and Herrick. The cranial nerves of *Necturus* have also been described and figured in some detail by Fischer ('64), although some evident errors occur in his work.

The description of the proximal relations of the several nerves given here is based upon a series of sections through a skull hardened in Hermann's fluid supplemented by macroscopic dissections of decalcified specimens.

I. The olfactory nerves are the largest of the cranial nerves and arise from the ventro-lateral angle of the olfactory

lobes as a single root, agreeing in this respect with *Desmogna-thus* and *Amphiuma* rather than *Cryptobranchus*, *Diemyctylus* and *Triton* in which two roots have been found to exist by Wilder ('89), Mrs. Gage ('93) and Burckhardt ('91) respectively. The nerves are quite long, dividing soon into numerous branches which are distributed to the olfactory capsules. In the larva these nerves are short, the fibers being given off laterad direct-ly to the olfactory capsule which closely adjoins the brain.

II. The rudimentary condition of the eyes in *Necturus* is naturally accompanied by a similar condition of the optic nerves. The primitive lumen of the optic vesicle is persistent and the nerves are hollow for a considerable distance periphe-rad. This fact has been already mentioned by Osborn ('88) and Herrick ('93, 2). Furthermore, the optic fibers in *Necturus* are entirely amyelinic, at least in their course in the optic tracts and the central portion of the optic nerve. This was ascer-tained both from Weigert and osmic acid preparations. The specimens were fully mature adults measuring over 30 centimet-ers in length. This condition in *Necturus* is not, however, unique; Edinger ('92) found that in young frogs and in young adult Tritons and Salamanders the optic fibers were almost entirely amyelinic.

III. The oculomotor nerve takes its origin at the usual point in the floor of the mesencephal. Though small it was always readily found.

IV. The trochlearis could always be easily detected, but I was unable to trace it to its exit from the cranium. A large number of its fibers immediately after its decussation were distibuted to the metaplexus. It is possible that such fibers represent a sensory contingent of the 4th nerve. Gegenbaur ('70) has stated that the fourth nerve contains sensory fibers in selachians and Amphibia. Strong ('90) likewise, found in the tadpole a sensory intracranial branch. No ganglion was observed, however, in *Necturus* though numerous cells occurred among the fibers of this nerve.

V. The trigeminus is of good size in *Necturus*. It arises in the usual place in *Amphibia* and passes latero-cephalad to

enter the Gasserian ganglion which is situated extra-cranial-
ly. From this ganglion arise the usual three branches,
exclusive of several small twigs composed of fibers from the
branch of the "dorsal" seventh which is associated with the
Gasserian ganglion.

VI. The abducens is quite small, being in fact the least of
the cranial nerves. It arises a short distance caudad of the
seventh, from the ventral aspect of the metencephal. It passes
laterad to the seventh, with which it is associated for a short
distance, though always distinct from it. It soon leaves it,
however, to pass cephalad to the Gasserian ganglion, immed-
iately ventrad of which it lies.

Dorsal VII. By this name, employed by Strong ('95), will
be designated a nerve which until recently has been little under-
stood. It leaves the oblongata at about the level of the exit of
the facial proper, and immediately divides, one branch joining
the trunk of the seventh and eighth nerves, the other passing
cephalad to the Gasserian ganglion, with which its ganglion is
fused, lying just dorsad of it. This nerve becomes ganglionated
slightly before the fifth, however. A very small bundle of
fibers leaves it just centrad of the ganglion to join the 7th nerve
just before it enters the ear capsule. From its ganglion two
or three small roots pass immediately dorsad; a large part of
the fibers pass cephalad in company with the ophthalmic branch
of the fifth, the ramus ophthalmicus superficialis VII, Strong.
By Von Plessen ('91) and C. J. Herrick ('94) this branch to
the Gasserian ganglion has been considered as belonging to the
trigeminus, clearly, however, without recognition of the ulti-
mate distribution of its fibers to the sense-organs of the lateral
line system, as worked out by Strong. The reference of this
nerve to the seventh is based merely on the fact of its exit from
the brain being very close to that of the seventh proper. It
belongs however to a system peculiar to the *Ichthyopsida*, and
until more is known of its origin, and of the segmental value of
the other cranial nerves, a reference of this nerve to the seventh
must be merely a matter of convenience. The other division of
the dorsal seventh will be spoken of with the following nerves.

VII, VIII. The facial and auditory arise very near together and form a single trunk which is joined by the ventral half of the dorsal VII and becomes ganglionated a short distance from the brain. From this ganglionic complex, composed of the acustic ganglion and the ganglion of the seventh (geniculate g.) one division of the eighth passes laterad to enter the auditory capsule. A very small portion of this pierces the capsule by a separate foramen but immediately unites with the larger portion. The remainder of the acustic fibers, representing presumably the *ramus utriculi*, together with the facial nerve and the dorsal VII, passes latero-cephalad to enter the otic capsule. Before it emerges there is given off the palatine nerve which leaves by a separate foramen. Immediately on its leaving the otic capsule, the seventh enters a ganglion of large cells, beyond which it divides into its several branches. This ganglion is stated by Strong to belong to the fibers of the Dorsal VII component. It is not mentioned by Herrick, but is figured by Von Plessen. The customary communicating branch between the ninth and the seventh exists in *Necturus*.

IX, X. The glossopharyngeal and vagus arise by three divisions, the more cephalic being the ninth and the representative of the lateral nerve of "fishes" (Strong), while the tenth arises farther caudad by several roots in two (or three?) groups. All these proceed latero-caudad to enter a ganglionic complex, from which six nerves emerge.

XI. The question of how far the eleventh nerve of higher forms is represented in Amphibia is a difficult one. By most investigators a spinal accessory is not recognized in Amphibia. Strong, ('90) in his preliminary paper upon the cranial nerves of Amphibia, regarded the more caudal root of the vagus as probably representing the cranial portion of the eleventh; in his final paper, no further mention is made of the eleventh, and this root is there spoken of as part of the X. Mrs. Gage ('93) and Fish ('95) both regarded the caudal root as the XI. The writer is inclined to believe that the cranial and possibly the spinal division is represented by a portion at least of this root. The morphological significance of the eleventh nerve is

however too obscure to admit of any confident homology being made.

XII. The hypoglossal in Amphibia is generally described as formed by the union of the ventral trunks of the two nerves, arising immediately caudad of the vagus group, to which dorsal roots are wanting. According to Fischer ('64) however, *Necturus* forms a single exception to this rule, and the following is quoted from him: "Der *Hypoglossus* der Perennibranchiaten und Derotremen erinnert durchaus an die Formen der Salamandrinen. Er wird überall aus den *Rami descendentes* der ersten Halsnerven zusammengesetzt und zwar meist des ersten und zweiten. Nur bei *Menobranchus* entsteht er durch Verschmelzung des zweiten und dritten. Der erste Halsnerv dieser Gattung hat nämlich einen selbständigen Verlauf. Aus nur einer ventralen Wurzel entsprungen, tritt er durch ein im Seitentheil des dem ersten Halswirbel angehörigen Körpers hervor, wendet sich dorsalwärts und verbreitet sich in dem kurzen *M. occipitalis minor* (vom ersten Halswirbel an die obere Fläche des Hinterhauptbeins). *Menobranchus* ist übrigens die einzige Gattung, bei der ich einen dem *N. accessorius Willisii* entesprechenden Nerven von ganz selbständiger Form fand. Diesem Umstande entsprechend sind es nicht der erste und zweite, sondern der zweite und dritte Halsnerv, die bei dieser Gattung sich zur Bildung des *N. hypoglossus* vereingen." The peripheral distribution of these nerves was not traced sufficiently far to render a corroboration of the above possible. The following observations, however, regarding these nerves, are of interest. The first two nerves caudad of the vago-glossopharyngeal group, have in *Necturus* no dorsal roots or ganglia. They arise in the manner customary for the ventral roots of spinal nerves, by three rootlets from the ventral aspect of the myel (or oblongata), the more cephalic at just about the point where the neuraxis enters the cranium, and indeed from the oblongata, if the metatela is regarded as demarcating its extent. The second has its origin some distance caudad. Each nerve extends caudad some distance before leaving the spinal canal, and immediately upon issuing from it divides into two branches, one of which

passes dorsad to muscles, the other caudad and ventro-laterad. The ventral root of the third nerve, which is a complete nerve with dorsal root and ganglion, arises like the first and second. It passes obliquely latero-caudad to leave the canal in company with the dorsal root, which joins its ganglion just ectad of the foramen. The ventral root, lying mesad of the ganglion, divides into three parts, each of which is joined by bundles from the ganglion. One passes directly dorsad, the second laterad to break up immediately into a number of branches, while the third and largest division passes directly caudad, fusing with the caudal portion of the ganglion. Fischer's recognition of the first of these nerves as a spinal accessory cannot be agreed to, because of its mode of origin from the extreme ventral aspect ; and its distribution, in part at least, is not comparable with that of the 11th. It is preferred here to speak of these nerves as the first, second and third spinal nerves, although the area of the hypoglossal is supplied from some of their branches. An indication of a dorsal root for the first of these has been found by Kingsley ('92) in *Amphiuma* and by Mrs. Gage ('93) in the larval *Diemyctylus*.

GENERAL MORPHOLOGY.

Rhinencephal. In the application of this term to the olfactory lobes in *Necturus*, it is not the intention to convey a prejudgement of the interesting problem as to whether or not they are entitled to recognition as constituting a separate segment of the brain. It is possible indeed that the olfactory lobes and the portions of the cerebrum which are associated with the sense of smell, constituting, it is believed, almost the entire secondary forebrain in the *Necturus*, should properly be regarded as representing a single primitive segment,—Rhinencephal. Turner, followed by Schäfer and Edinger, who extend the application, has applied the term rhinencephal to such portions in higher forms, not employing it in a segmental sense, however. As has been insisted by Wilder ('93) Rhinencephal used in its true segmental sense should include mesal (portion of aula), as well as ventral, portions of the parietes. Mrs. Gage ('93) from the

study of the brains of embryo *Diemyctylus* and the Lamprey states that "upon embryological grounds it seems as though the rhinencephal were equally entitled with the prosencephal to a share of the aula as a mesal cavity."

It is difficult to determine how much of the combined olfactory lobes and cerebrum in *Necturus,* may be considered as belonging to the former. A slight vertical furrow upon the endymal surface of the mesal walls, slightly cephalad of the caudal limit of the olfactory glomerules, may possibly be regarded as indicating its limit, in the mesal walls. The horizontal sections, Figs. 34 and 35 show the general relations. The olfactory nerves spring from the lateral and ventro-lateral portion of the lobes. Completely encircling the olfactory glomeruli, in which the nerve fibers end, is an area of ectocinerea, first appearing on the lateral aspect and spreading cephalad, both dorso-mesad and ventro-mesad, to complete the circle in the cephalic portion of the mesal surface of the apposed lobes. A slight furrow outlines this area so enclosed, more marked on the lateral surface, fainter on the dorsal and ventral aspects. Fig. 33 shows a transection through this region of the brain.

Prosencephal.—The prosencephal is of the characteristic amphibian form and structure. The extent and relations of alba and cinerea are shown in the series of transections, Figs. 28-33, 42. The ventro-lateral walls, in which the peduncular tracts are lost, representing undoubtedly the basal ganglia of Edinger, the striatums, form but faint swellings into the paracœles, these being most marked in the region of the portas. The mesal walls are spoken of subsequently in connection with the cerebral commissures. The entocinerea extends to the ectal surface of the prosencephal only in three places,—(1) at the caudal ends of the cerebrums where the walls are quite thin, (2) at the meson in the terma cephalad of the cerebral commissures, and (3) in the mesal wall cephalad of the terma; here it is quite extensive. Immediately cephalad of the terma the mesal walls of the cerebrum are formed only of pia and endyma which in the region consists of two to three layers of cells (Fig. 31). This is soon succeeded farther cephalad by true nervous parietes

in which the nerve cells extend to the exterior, generally asso-
ciated together in small clusters. It is believed that the rela-
tions in this region cephalad of the terma are important in view
of the relations in the Reptilia and the possible homology of
the hemiseptum (septum lucidum).

Paraphysis. This is quite large in Necturus, and enveloped
in and distorted by the supraplexus ; it extends cephalad closely
applied to the roof of the skull. The communication with the
cavities of the brain in the adult was constant, ageeing in this
respect with Diemyctylus. In Amblystoma ('92) the communica-
tion with the cavities of the brain was found to become inter-
rupted in larvæ twelve millimeters in length. [1] In the just
hatched larva (Necturus) the weak development of the supra-
plexus leaves the parts in a simpler condition, and the paraphy-
sis appears as an elongated sack lined by a single layer of cells,
(Fig. 8) and communicating with the encephalic cavities by a
narrow neck.

In the greatly elongated terma, which in Necturus forms in
part the floor of the brain, immediately caudad of the portas,
is a marked shelf-like elevation in which cross from side to side
two bundles of fibers, the more ventral, the precommissure, and
the dorsal, the callosum, generally recognized as such hitherto
The correctness of this homology seems doubtful, and in order
not to prejudice the question in the outset, it will be here
spoken of as the dorsal bundle or commissure. There has been
great difference in the statements made concerning the relations
of this bundle to the precommissure in Necturus. Osborn ('86)
in his memorable paper on the "Origin of the Corpus Callo-
sum" mentions and figures the dorsal bundle,—his callosum—
as completely separated from the ventral by a part of the cavity
and a fold of the plexus, and he further found the same condi-
tion in Proteus. Herrick ('93, 3) speaks as follows of the rela-
tions of these commissures in Necturus :

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[1] In his paper on the development of Amblystoma, which has just appeared
5) Eyclesheimer reiterates the statement of the obliteration of the proximal
portion of the cavity of the paraphysis, and a discussion of the significance of
the organ is given.

" In Menobranchus [Necturus] however, he [Osborn] makes the significant discovery that the upper bundle is completely separated from the lower and crosses the ventricle independently, so that a fold of the vascular plexus of the pia [*sic*], which in this genus is greatly developed, passes through the interspace. This statement of Osborn we had overlooked, but upon theoretical grounds suspected that the dorsal commissure would prove to belong to the roof and not to the floor of the ventricle. We, therefore, had introduced the accompanying drawing (Plate IX, Fig. 5) before noticing that Osborn's Fig. 14 is substantially identical. We have never found the dorsal commissure so completely separated as represented by the latter, but always in juxtaposition with the floor; it was therefore a matter of congratulation to find a clearly defined continuous film of epithelium separating it from the subjacent pre-commissure. The series being continuous and faultless and doubly stained with hematoxylin and fuchsin to differentiate epithelial from nervous elements the evidence is conclusive. Knowing, as we now do, that the plexus is but a diverticle of the roof we recognize of necessity that the commissure is morphologically dorsal." Thirdly, Fish (21) in connection with the homology of this commissure in *Amphibia* with the callosum of mammals, from the examination of a larval and adult *Necturus*, reports "a non-separation of these commissures except by a simple cellular layer." The results of my own observations differ entirely from those of the investigators mentioned above. Twelve adult brains were examined in this connection, and in no one of them was there a separation at the meson, by cells, endymal or otherwise, much less by an extension of the cavity and a fold of plexus. The dorsal bundle rested immediately upon the ventral, the precommissure. The dorsal bundle turns dorsad to the mesal wall of the hemicerebrum while the ventral passes directly laterad so that on each side of the meson cinerea becomes interpolated between them. In five larval forms examined the condition was precisely that found by Mrs. Gage in larval *Diemyctylus* ; in these the separation of the two commissures is by three or four layers of cells which in no way dif-

fered in appearance from the cells of the surrounding cinerea, nor was the more dorsal layer differentiated from the rest as a layer of endymal cells. Mrs. Gage found this condition of a separation by cinerea to persist quite late in *Diemyctylus*, and it was present even in some young adults. It is possible that the same may be true in *Necturus*, which would account for the results of Herrick and Fish, if the individuals examined by them were young. The brain upon which Osborn's figures and conclusions were based must have been abnormal in the relation of these two commissures.

The presence of cells separating the two commissures is seen from the larval conditions to be insignificant, but the recognition of these cells as endymal, as has been done by Herrick would be vital. In the distribution of the fibers of the dorsal bundle in *Necturus*, the observations of Osborn and Herrick are in the main here confirmed. Whether or not this commissure can be regarded as the representative of the mammalian callosum as first prominently advocated by Osborn seems doubtful. In view of the differences which exist in the interpretation of this bundle in Amphibia, and the importance of the question, a brief review here of the history may be warranted.

Although a callosum had been ascribed to Amphibia previously, Reissner (1864) was the first to accurately figure in *Bufo* the bundle in question, which he regarded as a callosum. Following him, Stieda ('70) rejected the homology of callosum and regarded it as the *pars olfactoria* of the precommissure. This latter view was then generally accepted by the investigators who followed him,—Goette, Bellonci ('82 and '83), Rabl-Rückhard ('83) and Osborn in his papers of 1883-4, until the appearance in 1886 of Osborn's paper on the origin of the callosum, in which occurs the statement of the peculiar relation of the dorsal bundle in *Necturus* to the precommissure, before mentioned, and also the following statement of the relations of this bundle:—" An important character is that the cerebral commissures in the Amphibia lie *behind* the foramina of Monro." Again :—"The upper bundle [his callosum] ascends in the median hemisphaeral walls, forming the posterior boundary of the

foramen of Monro, and then turns forwards roofing the foramen."

In the following year Bellonci ('87) published a paper on the anterior commissure in Amphibia and reptiles, in which he states his inability to accept Osborn's conclusions and reaffirms the declaration made in his former papers ('82 and '83) that decussational as well as commissural tracts occur in this bundle, his "*tratto superiore della commissura anteriore.*" In the Triton he found the fiber bundles which constitute the dorsal commissure coming from four regions: (1) 'those lobes which in their anterior lower and lateral parts contain the olfactory glomerules'; (2) the mesal wall of the hemispheres; (3) the caudo-lateral part of the same; and (4), the 'region of transition between the cerebrums and thalami' and especially from two ganglia dorsad of the portas.

In 1888 appeared Osborn's paper ('88) containing the following comment upon Bellonci's criticism: "I have seen reason to partly alter my views as to the nature of the commissures of the hemispheres which were described in detail in my paper on the corpus callosum. The more recent researches of Bellonci, with the aid of the Golgi method, upon these commissures, should be consulted. They show that with the purely commissural fibers, decussational fibers are intermingled. I have myself discovered that in the upper bundle or corpus callosum of *Menobranchus* [*Necturus*] there enter fibers from the diencephalon." He reaffirms, however, the entire separation of the dorsal bundle from the ventral in *Necturus* and *Proteus*.

With the exception of Bellonci and Herrick (to be mentioned presently) the investigators following Osborn,—Köppen, Edinger, Burckhardt, Mrs. Gage, and Fish, none of whom except the last discuss the question to any extent,—all recognize the homology set forth by him. Edinger ('88) states the opposed views of Osborn and Bellonci without comment, but in his figures names the tract callosum. Burckhardt ('91) seems to have recognized both a callosum and the superior tract of the anterior commissure of Bellonci, not aware apparently that the two are identical.

The views of Herrick may be gathered from his several papers in the Journal of Comparative Neurology. The dorsal commissure he considers as representing the hippocampal or fornicommissure : as representing a callosum, he figures fibers in the mesal wall cephalad of the porta, though in his last reference to the subject he considers that it might be " possible that callosal elements were bound up in the larger hippocampal commissure."

The distribution of the fibers of the commissure in question is shown in Fig's. 29-31 ; 34, 35, 38, 39 and 42, which in the main agree with those of Osborn and Herrick. The results attained also agree with those of Bellonci ; the extension of fibers into the olfactory lobes is not affirmed as definitely by him as his general statements would indicate. In *Necturus* by far the largest portion of the fibers spring from the mesal walls of the hemicerebrums both cephalad and caudad of the portas. This mesal wall has been well described by Mrs. Gage in *Diemyctylus* and the name *callosal eminence* is applied to it. It forms a prominent swelling into the paracœle, and is characterized by its scattered cells which Nakagawa ('90) considered as constituting a rudimentary cortex. By Edinger ('88), the mesal wall both in *Amphibia* and reptiles has been regarded as representing the hippocampal region in higher forms. Herrick likewise, though in his earlier papers he seemed to confine the homology to the caudal region alone, has stated in his last reference to this question ('93,3) that the caudal and mesal walls in *Necturus* may confidently be homologised with the hippocampus. Some fibers could be traced to a point slightly cephalad of the caudal limit of the olfactory glomerules on the lateral aspect, or just caudad of the endymal furrow in the mesal wall already spoken of as possibly marking the limit of the olfactory lobes.

These various tracts unite to form a single bundle which passes caudad over the porta, of which it forms the roof, and with another bundle from the dorso-mesal wall, and a small contingent from the diencephal, passes ventrad to cross in the terma or floor, immediately dorsad to the precommissure,

as stated before. The derivation of a few fibers from a nidus of the diencephal was unmistakable (Fig. 29) ; they correpond presumably with the fibers from the diencephal described by Bellonci in the Triton. These are in addition to other fibers, some medullated, which pass into the mesal wall from a more dorsal region of the diencephal,—probably the habenas. Fig. 29 shows a transection through the cephalic end of the group of cells from which the first named fibers spring. It lies dorsocaudad of the porta. Whether or not these bundles are decussational or commissural, or both, could not be determined from the specimens.

In the larva, as before stated, the dorsal commissure crosses in the floor, separated from the precommissure by several layers of cells. In the just hatched larva the fibers after crossing turn caudad and dorsad in the mesal wall of the hemicerebrum and could be followed to the point where the prosencephal and diencephal join. A derivation at this stage of some of the fibers from the diencephal was strongly suggested but not demonstrated.

Manifest difficulties attend the homology of this tract with any of the mammalian structures with which it has been compared, and the questions of the development, and relation to each other, of the callosum and hippocampal commissure are intimately connected. Herrick ('93,3) has regarded this as a purely hippocampal commissure with possibly callosal elements in it. This homology, however, he apparently made dependent on the recognition of this tract as dorsal.

It is felt that the concurrent evidence of *Diemyctylus, Desmognathus* and *Necturus* shows quite conclusively that the fibers of this commissure cross in the terma and do not belong to the roof and simply rest upon the precommissure as thought by Herrick, or cross separately and independently in *Necturus* as stated by Osborn. It is possible that the recognition of this commissure as belonging to the terma might modify Prof. Herrick's views of the strict homology with the hippocampal commissure.

The homology that has generally been recognized for this

commissure, that of a callosum, involves the general problems just mentioned. The recognition of this as a callosum, it is thought is open to serious objections. It would not be expected that a commissure which in Mammalia is very largely, at least, a cortex commissure, would be present in so well developed a condition in forms in which no true cortex exists. This suggests, of course, the question of how far ectocinereal areas may be represented by non-migrated entocinerea. The regions to which these fibers are distributed have been regarded as an incipient cortex, it is true, but they are also considered as representing the hippocamp, and the question of the homodynamy of callosum and fornicommissure arises. Far more serious than objections such as the above seems the morphologic one suggested by the relation of this bundle to the portas. The fibers collect from the mesal wall, pass ventrad, *caudad* of the porta and cross in the terma. In no way does it appear possible to homologize such a bundle with one whose fibers arise in the dorsal or mesal walls of the hemicerebrums and cross in the terma *cephalad* of the portas. This peculiar relation in Amphibia is commented on by Osborn as was noted. He evidently saw in it nothing to invalidate the homology of the tract to the callosum. The objection however seems to the writer to be a vital one.

Fish ('95) contends at some length and forcibly for the homology of the dorsal commissure with the callosum of mammals, or callosum-fornix as he believes, and presents as forming a series illustrating the transition from the condition in urodeles to that of reptiles and birds, mesal views of the region of the terma in *Desmognathus, Cryptobranchus*, frog, turtle, and bird. I cannot consider these forms as entirely comparable in this respect; the relations at the meson seem to me to be misleading. The difficulty lies not in the relations here but in the distribution of the fibers as regards the portas. In Amphibia (frog included) the fibers pass dorsad to the mesal walls *caudad* of the portas as already stated, while in reptiles they pass *cephalad* of of the portas. It is evident that however far cephalad and dorsad the terma might be bent, the relations in Amphibia could

only be directly changed into those of higher forms, by the mi
gration of the bundle in question across the portas.

It is to be regretted that no satisfactory solution of the dif-
ficulties involved can be offered here. It is believed as stated
by Herrick that the "whole question as to the relation of the
calloso-fornix structures requires special consideration on the
widest possible comparative grounds." A callosum at least
seems to be entirely absent. I fail utterly to find any trace of
a commissure in the terma cephalad of the porta where Herrick
has figured it in *Necturus.* Judging from the figures and state-
ments of Edinger, Herrick and Meyer, what has been called
the hippocampal commissure in Reptiles lies caudad of the por-
tas in the roof; hence the readiness with which Herrick consid-
ered the commissure in *Necturus* a hippocampal commissure,
since he regarded it as dorsal. A comparison with the cerebral
commissures of the reptilian brain has not been made in this in-
vestigation and an expression of opinion cannot be given as to
the comparability of the relations in Amphibia and reptiles. It
is believed, however, that this commissure will prove, in part at
least, a hippocampal commissure.

Whatever may be the result of exact comparison with the
cerebral commissures of Reptiles, it is felt that a representative
of this commissure should be looked for in other *Ichthyopsida,*
which have other characters of the brain in common. It is
hardly necessary to mention the importance of a knowledge of
the relations that the cerebral commissures have in the three
Dipnoans. Burckhardt (9) has found it in the brain of *Protop-
terus* and calls it a callosum, but he says nothing of the distri-
bution of the fibers, nor do his figures afford a solution. *Cer-
atodus* and *Lepidosiren* yet await investigation. The fact that in
Petromyzon a cerebral commissure has been recognized in ad-
dition to the precommissure, lends the hope that the conditions
there may be found to compare closely with those in urodeles,
the general resemblance between whose brains has been noted
by Wilder ('76). Mrs. Gage has contrasted transections
through the cerebral commissures in *Diemyctylus* and *Amia,* and
has suggested that the (ventrally) recurved portion of the cere-

brum may be equivalent to the mesal wall (callosal eminence) in *Diemyctylus*, in which case the membranous roof of the fish cerebrum would represent the crumpled plexuses of higher forms. This view has been endorsed by Studnicka. We might then expect to find in ganoids a commissure exactly comparable to that found in Amphibia.

The projection of the terma into the aula noticed by Mrs. Gage in Diemyctylus and Amia, to which she applied the term *crista*, (a name given by Wilder ('80) to a similarly situated object discovered by him in the mammalian brain) exists in *Necturus* merely as a slight intrusion of the pia covered by endyma. It is in this region that Herrick has figured fibers which he considered a possible callosum. As before stated, I fail to find any trace of such.

Diencephal.—This and the following segment are but slightly differentiated from each other ectally. Upon the dorsum a slight transverse furrow dorsad of the postcommissure, and the prominent caudal bend of the dorsal wall of the infundibulum on the ventral aspect, may be regarded as boundaries. Cephalad of the postcommissure, which may be considered as limiting the caudal extent of the segment in the roof, the solid walls of the diencephal become divaricated and the roof at the meson is formed by the endyma and pia alone. This consists of a single layer in its cephalic portion passing caudad into the peculiar several-layered endymal structure ventrad of the postcommissure, which has been described by Mrs. Gage ('93). At the supracommissure the walls approach to separate yet more widely cephalad of it, where the roof, diatela, is greatly expanded, limited cephalad by the velum; this is oblique, so that a large sac is formed dorsad of it, extending also laterad at each side cephalad of the habenas; it is the *postparaphysis* of Herrick ('93, 2), by whom the *paraphysis* is termed the *preparaphysis*.

Epiphysis.—This in *Necturus* consists of an aggregation of closed vesicles, forming a flattened suboval body upon the dorsum of the brain between the post- and supracommissures. Fig. 23 shows a transection of it. No connection with the dia-

cœle was found, however, as is said by Herrick to be the case.
In the just hatched larva the condition was simpler, the epiphy-
sis at that stage being a simple hollow vesicle, not communicat-
ing even at this early stage with the brain cavity. Two or three
myelinic nerve fibres, one each side, were found to pass to the
ectal surface of the brain and disappear after turning mesad be-
neath the epiphysis. They came from the mesencephal to
which they could be traced caudad. This fact is presented
without comment, but is interesting and suggestive in connec-
tion with what has been written regarding a parietal nerve.

Paraphysis, etc.—Three evaginations of the roof of the
brain have been recognized, all of which may be present in the
same form, viz., (1) the epiphysis between the post- and su-
pracommissures ; (2) cephalad of the supracommissure an
evagination which has been variously termed zirbel-polster, pol-
ster, dorsal sac, and postparaphysis ; (3) the third farther cepha-
lad, separated from the second by the velum, and here called
paraphysis. An admirable résumé of the literature of the sub-
ject is given by Sorensen ('94, 1) by whom the term *paraphysis*
includes the two more cephalic evaginations, which he considers
are caused by the division of his paraphysis by the velum into
cephalic and caudal portions, the *pre-* and *postparaphysis.* He
says of these ('94, 2): "The causes for the varied forms found
in the *paraphysis* must, we think, be sought for in the mechan-
ics of embryonic growth and development, and, as already re-
marked, to call these sac-like projections *epiphyses* is absurd, as
their structure and position prove their plexiform origin."
There is entire agreement with the above as regards what has
been called "*postparaphysis*" in Amphibia. In the just hatched
Necturus, the parts lie much nearer together. The walls of the
diencephal extend cephalad between the cerebrums quite to the
velum and there is not the extent of the tela in this region that
there is in the adult. The simple diaplexus arises from the
velum. But while there is no indication of an evagination
caudad of the velum, the *paraphysis* cephalad of it is well de-
veloped as a bulblike sac communicating with the brain cavities
by a constricted neck. In Amphibia, at least, the *preparaphysis*

and *postparaphysis* of Herrick do not seem to be structures at all
comparable. The extent of the diatela in *Necturus* appears to
be due simply to the elongated condition of the brain; the su-
praplexus extends cephalad closely applied to the roof connect-
ed with the dura. The velum extends ventro-caudad, forming
dorsad of it the apparent evagination.

Plexuses.—The plexuses of the prosencephal and dien-
cephal are greatly developed in *Necturus*; the relations, how-
ever, are as Mrs. Gage has shown in *Diemyctylus*, and the names
applied by her are here adopted. The *auliplexus* intrudes into
the cavities cephalad of the *paraphysis*. It sends extensions
through the port as into the paracoele and another division caudad
into the infundibulum. The diaplexus arises from the velum
and the diatela and extends caudad to the cerebellum, occa-
sionally protuding caudad of it into the metacoele. In the larva
the plexuses are much simpler than in the adult, and the rela-
tions set forth above are much more easily seen.

On the dorsal edge of the divaricated walls cephalad of the
supracommissure are situated the habenas. Caudad of the supra-
commissure in a similar position and extending almost to the
postcommissure is another nidus of cells similar to those of the
habenas probably representing Meynert's nidus, since Meynert's
bundle seems to spring from here. Dorso-caudad of the portas
lie the cell areas from which spring fibers which join the dorsal
cerebral commissure. This is molded about a core of alba
from which the fibers arise, and is bounded dorsally by a well
marked sulcus, which extends caudad, growing fainter to again
become distinct in the caudal region of the diencephal. On the
floor of the brain caudad of the cerebral commissures is the
cephalic projection of the cavity, the preoptic recess, from the
caudal portion of which and cephalad of the chiasma the optic
recesses project laterally to constitute the lumen of the hollow
optic nerve, as already mentioned. The infundibulum, as in
other urodeles, is large, extending caudad so as to completely
conceal the mesencephal. The hypophysis is attached to the
caudal end of the infundibulum, whose cavity extends dorsad of
it as the *saccus vasculosus*.

Mesencephal.—(Figs. 1, 4, 21, 22.) The dorsal aspect is slightly more convex than that of the preceding segment, from which it is ill defined. No mesal furrow was found indicating a pair of gemina. Upon the ventrimeson its extent is limited, extending from the infundibulum to the Mittelhirngrube of Burckhardt, the Isthmusgrube of His. Considerable morphological importance has been attached to this depression; it forms a convenient landmark and will be designated here as the mesencephalic pit. It seems to be much more marked in *Necturus* than in other urodeles, the cinerea at the meson consisting of but two layers of cells and reaching the ectal surface of the brain. Cephalad of this have been located the region of the albicantia and the *corpus interpedunculare.* The oculomotor nerves also leave the brain in this immediate neighborhood.

The entocinerea forms a continuous mass surrounding the mesocœle. A differentiation into zones such as occurs in Anura and to a less extent in certain other urodeles, is not well marked in *Necturus*; an ill defined, discontinuous stratum of alba divides the entocinerea of each tectum into an ectal and ental layer, and in places a third is suggested.

Epencephal.—The cerebellum of *Necturus* is exceedingly simple and consists, as Osborn found in *Amphiuma*, of a small band of fibers passing from one side to the other, and "containing no cells save the simple endyma."

The question as to whether or not the epencephal should be recognized as constituting a segment of equal value with the others is a difficult one, and indeed the indication of a division into segments is very obscure. Certainly, in urodeles, there is nothing except the exceedingly rudimentary cerebellum to represent that which in higher forms attains so great a development; and, viewed from the condition in urodeles alone, the inclusion of cerebellum and oblongata by His under a single segment, would appear justifiable. The term applied by him, *Rhombencephalon*, or Rhombencephal, is however open to criticism since the same name had been previously applied to the lumbar enlargement of birds. This is, how-

ever, a question for comparative and developmental study. It has been discussed somewhat by Wilder ('84) and by Stroud.

Metencephal.—This segment may be regarded provisionally as co-extensive dorsally with the membranous roof, the metatela. In *Necturus* this portion of the brain is extremely long, equalling indeed, the length of the entire brain cephalad of it, and accepting the limit here given, is not contained within the cranium but extends caudad into the first vertebral arch. The transition in structure to the myel is gradual, as usual. The myelocœle expands gradually to form the metacœle which widens cephalad to the region of the fifth nerve. On each side of the cerebellum well marked lateral recesses extend cephalad. The analogy of these to the lateral recesses or parepicœles of higher forms has been suggested, and a comparison with the similarly situated restiform bodies of sharks and rays may perhaps be made. There is a mesal sulcus in the floor of the metacœle, beginning near the exit of the 9th and becoming most marked in the region of the 5th nerve, cephalad of which point it soon disappears. This and the sulcus at the point of junction of the wall and the floor appear to be the only depressions which might be regarded as of structural importance. There is no sulcus just laterad of the fibre bundle on each side of the meson, such as occurs in many other forms.

The metaplexus occupies but a portion of the roof of the metencephal, the remainder being a simple tela. It (the metaplexus) is highly pigmented and extends from the region of the tenth nerve to slightly cephalad of the 7th, and laterally, cephalad over the lateral recesses, overlapping slightly the parts to which it is attached. Its relations and the regular arrangement of the folds which project into the metacœle can be seen from Figs. 1 and 6. The remainder of the roof is a simple tela; no metapore, or foramen of Magendie such as occurs in *Diemyctylus* (Mrs. Gage '93) was observed. In its caudal portion, however, the metatela was very thin and often ruptured.

Opposite the exit of the tenth and caudad of the meta-

plexus, the lateral edges of the walls were approximated to a greater or less degree. The same condition was observed by Osborn ('88) in *Proteus,* and Mrs. Gage in *Diemyctylus.* At this point the pia is much thicker and it is thought possible that it may be due merely to a spreading of the parts caudad, producing thus this appearance.

Endolymphatic sacs.—In *Necturus* as in other Amphibia, these come into close relations with the brain. The endolymphatic duct pierces the ear-capsule by a separate foramen and expands into a simple sac which rests upon the metaplexus in the immediate neighhorhood of the seventh and eighth nerves. Its diverticles are few and very small, attaining in no way the extent and complexity found in the frog and by Mrs. Gage in *Diemyctylus,* where there is a communication of the two sacs across the meson. Burckhardt has found the same relations of the *saccus endolymphaticus* in *Protopterus* as in Amphibia: the sacs are of great extent and divide into numerous diverticles, but do not communicate across the meson. In the larval *Necturi* examined the conditions were as in the adult,—the sacs small and simple. In connection with the simple relations of the *saccus endolymphaticus,* it may be mentioned that no periganglionic glands were observed on either the Gasserian or spinal ganglia, as in the frog.

Myel.—This has received but slight attention from me, the portion immediately adjoining the brain only being examined. In form it is subcylindrical, differing in this somewhat from *Cryptobranchus* and *Siren* (Kölliker, '93) in which it is more or less flattened. No marked cervical enlargement was observed. A dorsal furrow appeared to be wanting; the ventral one is well marked. A *ligamentum denticulatum* exists in the adult *Necturus,* where it forms a cord closely applied to the latero‐ventral aspect of the myel, which it leaves at intervals to pass to the wall of the vertebral canal, apparently at the points of articulation of the vertebrae; the myel was not studied for a sufficient distance, however, to warrant a positive statement as to the relations of the ligament.

The myel of Proteus has been studied by Klaussner ('84).

HISTOLOGY.

Oblongata.—The account of this important portion of the brain is very incomplete, from the lack of time and suitable material, as well as the natural complexity of its structure. In the adult the cells can be made to take the silver impregnation only with great difficulty, and the unavailability of fresh larval material has rendered very unsatisfactory the study of their relations. The form of the cells of the myel and oblongata in Amphibia has been shown by Fish and others. The cells of the dorsal and lateral regions are pear-shaped, the simple process extending toward the periphery and branching profusely. The motor or ganglion cells in the ventral and lateral regions are multipolar or fusiform and their processes extend peripherally into the alba and are greatly branched.

The transition from the myel to the oblongata is a gradual one ; even as far caudad as the second spinal nerve, the typical structure of the myel is somewhat modified. A transection of the cervical myel is shown in Fig. 9. In accordance with the conditions in higher forms, the alba may be divided, more conveniently than naturally perhaps, into dorsal, lateral and ventral columns. The compressed myelocœle is bordered by two or three layers of endymal cells. The dorsal and ventral cornua of the cinerea are present, but are weakly developed. The dorsal send projections ectad, interrupting and dividing into small bundles the longitudinal fibers of the alba. The cells in the myel are mostly small, their processes directed peripherally. In the ventral horns are the characteristic large cells, which also occur in the lateral region. Occasional fusiform cells were likewise observed which sent their processes into the raphé. The fibers of the ventral columns are mostly coarse, especially those immediately ventrad of the cinerea, the posterior longitudinal fasciculus and the Müllerian fibers of Osborn[1] with which are associated the large Mauthner fibers.

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[1] Osborn is not quite clear in the terms in which he speaks of the fibers of this region. The fibers immediately ventrad of the cinerea on each side of the meson, he called the posterior longitudinal fasciculus ; those farther ventrad, Müllerian fibers, presumably from a supposed homology with the fibers of that

In the region of the second spinal nerve (non-ganglion-ated), the myelinic fibers of the dorsal columns have begun to decrease in number, almost all having disappeared save such as will constitute the ascending tracts of the fifth and tenth nerves, whose fibers begin to be recognizable at this level. From this point to the beginning of the metatela the change consists merely in a migration laterad of these tracts and the dorsal ex-tension of the myelocœle. In the ventral regions of the myel changes are less marked and consist merely in a more compact arrangement of the fibers of the posterior longitudinal fasciculus. In the relations of the cell areas, the change from myel to ob-longata is not so perceptible. A general view of the distribu-tion of the cells in the oblongata may be given here. As the oblongata widens the general arrangement of cells remains much the same. The large cells of the ventral region are con-tinued cephalad for some distance, but become more scattered beyond the tenth nerve; such cells are found, how-ever, at intervals throughout the length of the oblongata, and in the region of the eighth nerves they are increased in number and size. The lateral cells of the myel become sup-planted in posision by the motor nidi of the tenth, ninth and seventh nerves, which are not so distinctly demarcated in *Nec-turus* as in *Cryptobranchus* (Osborn, '88). Farther cephalad, the compact motor nidus of the fifth nerve succeeds in the latero-ventral region. The cells occupying the remainder of the oblongata, except large, laterally situated cells near the eighth nerve and similar cells more sparsely located, are small, —so called sensory cells—especially occupying the dorso-lateral cinerea and the region on each side of the meson, where be-

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name in *Petromyzon.* If this were correct,—and it would seem but partially so, —no recognition of a distinction between the posterior longitudinal fasciculus and Müllerian fibers should be made, since in *Petromyzon* two or three Müllerian fibers continue cephalad as the axis of the posterior longitudinal fasciculus (in the restricted sense of Ahlborn). This bundle will be recognized here occupying its usual place just ventrad of the cinerea on each side of the meson, and many of the large fibers composing it seem to be comparable in their relations with the Müllerian fibers of the Lamprey.

tween the fifth and seventh nerves, they are quite abundant,
forming prominences in the floor of the oblongata,—the
nucleus centralis of Stieda.

Mauthner's Fibers.—(Figs. 9-16, 18.)   It is interesting to
observe the presence of the Mauthner's fibers in *Necturus*, add-
ing another to the forms in which their occurrence has been
noted.   They appear to be quite constantly present in Teleosts
where they have been studied by Stieda ('68), Fritsch, Mayser
('81), Kölliker ('93), and others.   They also occur in Ganoids
(*Acipenser, Amia, Polypterus, Calamoichthys, Scaphyrhynchops,*)
and in Dipnoans (*Ceratodus, Protopterus*).   On the other hand,
according to Kölliker they are absent in five genera of teleosts [1]
that have been examined and in the Elasmobranchs.   In Am-
phibia they seem to be generally present in the larval state, and
have further been observed in the adult *Triton* (Burckhardt '91),
Desmognathus (Fish '93) ; I have found them in the adult
Necturus, Amblystoma, and *Diemyctylus.*   Osborn on the other
hand states that they were not found in *Cryptobranchus* and are
not generally present in urodeles ; the last statement would
appear erroneous, however, from the enumeration above.

They are stated to be absent (as Mauthner's fibers) in the
adult *Salamandra maculosa,* (Burckhardt, '91).   In *Necturus*
they occupy their customary position in the dorsal portion of
the ventral columns, on each side of the meson.   In this posi-
tion they may be traced cephalad to their decussation just
caudad of the exit of the seventh and eighth nerves, where
they cross somewhat obliquely and turn directly laterad to end
in,—it is believed,—large cells.   They measure about 35
micra in diameter, being, it would seem, somewhat smaller
than the corresponding fibers in "fishes ;" (see Kölliker, '63).
No apparent regularity seemed to exist in their relation to
each other at the decussation, sometimes the right and some-
times the left crossing dorsad of its opposite.

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[1] These are *Orthagoriscus, Tetrodon, Mormyrus, Malapterruus,* and *Gymnotus ;*
it is interesting to note that the last three are electric or semi-electric fishes.
The relation of the first two genera to Fritsch's theory is interesting.

The Mauthner cells[1] are very large, being fusiform in shape and lying transversely to the long axis of the oblongata. The mesally directed process was not seen to branch and is thought to be continuous with the axis cylinder of the Mauthner fiber. The lateral end divided into several (at least three) processes, which extended toward the entering fibers of the auditory nerve; (see Fig. 18.) These cells resisted the silver impregnation, and the exact extent and relations of the dendrites (processes) could not be observed.

The intimate relation of the processes with the fibers of the eighth nerve has been observed by Mayser, Goronowitsch, and Burckhardt. Goronowitsch was inclined to regard the processes as giving rise directly to acustic fibers,—a condition irreconcilable with the views at present held of the relations of sensory nerve fibers. Intimately connected is the question of the relation of other large cells to the eighth nerve.

The Mauthner fibers have not been followed in *Necturus* caudad of the third spinal nerve ; as observed in other forms, however, they gradually become smaller caudad until near the caudal end of the abdomen they become indistinguishable. Stieda ('64) states further, that in Amphibia (*Axolotl*) they do not preserve their large caliber for such a distance as in fishes.

There is substantial agreement in the observations of different investigators as to the structure of the fibers in fishes and dipnoans. By all they are stated to be fibrillar and to give off twigs (collaterals?) at intervals. In dipnoans (*Protopterus* and *Ceratodus*) the fibrillar structure would seem to be particularly well marked. Sanders ('89) speaks of them in *Ceratodus* as multi-axial with axis-cylinders leaving the common sheath at intervals. In *Necturus* the fibers appear finely fibrillar, but no

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[1]There would seem but little doubt of the direct continuity of the Mauthner fiber and cell. Mayser, ('43) in his investigation of the brain of the cyprinoids, discusses both fiber and cell at some length. He states the termination of the fiber in the cell. Goronowitsch ('28) in Acipenser, states the fact, or at least his interpretation, in the following clear language : " Nach der Kreuzung verlaufen sie bogenförmig zum Unterhorne, wo sie in sehr grossen Nervenzellen enden."

Furthermore, Burckhardt ('91) found both cell and fibre in Triton, and figures the former and its connection with the Mauthner fiber.

collaterals were observed to be given off in the limited distance
that they were followed.

Of the various theories propounded to explain the function
of these interesting structures, that of Fritsch is, perhaps, most
plausible, viz., that they have to do with the co-ordination of
the action of the lateral musculature in producing the rhythmic
movements of the body and tail in swimming, coming into rela-
tion with the motor cells of the nerves by means of collaterals.

In connection with the theory of Fritsch, the discovery by
Köppen of large fibers in the caudal myel of certain reptiles is
certainly interesting and suggestive.

There would seem to be no necessary correlation between
these fibers and an aquatic life as is thought by some, since
they have been found in *Amblystoma*, which seems to lead a
terrestrial life except during the breeding season.

The Mauthner fibers correspond closely in their relations
with the median crossed Müllerian fibers of the Lamprey,[1]
which arise (Ahlborn) from large cells near the exit of the
auditory nerve, decussate, turning caudad in the myel, where
they give off collaterals (Davis) and gradually diminish in size.

Ventral Tracts.—At the beginning of the metatela, the pos-
terior longitudinal fasciculus occupies the same position as in the
myel, situated on each side of the raphé, in almost immediate
contact with the cells of the endyma, separated only by an oc-
casional nerve cell; in this position it traverses the length of
the oblongata, the course being clearly marked in the floor of
the ventricle as a white line at each side of the meson.

In Necturus, an oblique decussation of scattered fibers oc-
curs cephalad up to the exit of the caudal root of the tenth
nerve; none was observed between this and the ninth. At the
level of the ninth nerve, the root bundle of the seventh has
taken its position between this bundle and the endyma of the

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[1] The statement of Osborn ('88) and Burckhardt ('91) of the occurrence of
Mauthner fibers in *Petromyzon* is inexplicable. The idea may possibly have
been gathered from the paper of Fulliquet on the brain of *Protopterus*, where the
Müllerian fibers of the Lamprey, lateral uncrossed, median uncrossed and me-
dian crossed, are all called Mauthner fibers.

metacœle causing, apparently, a slight bulge of the floor. In the region of the eighth nerve the relations are more complicated: the root of the seventh passes laterad to its exit, and the decussation of the Mauthner fibers occurs. In connection with the latter are associated many fibers of this bundle, and other finer fibers from more ventral regions. Other coarse fibers appear to pass laterad without crossing the meson. Cephalad of the seventh and eighth nerves, the size of the bundles is much reduced owing to the loss of fibers. They, with the other longitudinal myelinic tracts, gradually become separated from each other, an amyelinic area intervening (Fig. 20). Occasional decussations still occur, however, the last just caudad of the fifth, where the large fiber could be traced to the immediate neighbood of a large isolated cell, in the extreme lateral region of the oblongata. Although actual continuity was not demonstrated, it is probable from the results attained in other forms that many of the fibers which end near the level of the eighth nerve spring from the cells of the ventral region, which, as Osborn found in *Cryptobranchus*, are particularly large and numerous in that immediate neighborhood. Likewise the origin of the decussating fibers from the large, laterally situated cells near the exit of the auditory nerve, may be tentatively held.

Some of the fibers in the ventral columns pass dorsad into the cinerea in the region of the tenth (X^1) and ninth nerves, in close relation to the nidus of the seventh and the fibers of that nerve. The relations of these fibers were much clearer in *Amblystoma* than in *Necturus*, due to their closer association into a bundle in that form. Similarly, more laterally situated fibers with thick myelinic sheaths terminated in the cinerea near the exit of the eighth nerve. A comparison of these with the lateral uncrossed Müllerian fibers of *Petromyzon*, as Köppen ('88) has done for similarly situated fibers in the frog, is attractive. In addition to the above, other coarse fibers gradually migrate dorsad and laterad to lie directly ventrad of the cinerea, and terminate, a lateral group in the region of the motor nidus of the

trigeminal, a more nearly mesal group slightly cephalad of the exit of that nerve.

A comparison with the results attained by Goronowitsch in *Acipenser* shows the relations of the ventral tracts to be very similar to those set forth above. I was unable, however, to trace any of the decussating fibers in the region of the eighth into that nerve, of which in *Acipenser* he found them to constitute one of the largest components. If indeed any acustic fibers have this origin in *Necturus*, the number does not exceed three or four.

Fasciculus communis, (Osborn).—This tract has been already treated of at some length by Strong ('95) both historically and descriptively; and no extended discussion of it is needed here. In *Necturus* this tract is relatively much smaller than in *Amblystoma*. It first appears a short distance cephalad of the beginning of the metatela as a small island of ground substance in the dorsal cinerea (Fig. 11) ; at the exit of the first spinal nerve one or two myelinic fibers appear in it. As it increases in size, it joins the adjacent alba, from which it is but partially separated by a projection of cells dorsad of it. Up to the exit of the contingent to the tenth nerve, there are but few myelinic fibers in it. Cephalad of the exit of X^1, it is hardly distinguishable from the adjacent dorsal tracts. Between X^1 and IX it joins closely the myelinic fascicle called *tract b*. Arcuate fibers penetrate, some of which turn caudad in it ; other fibers from *tract b* turn cephalad in it and possibly may be continuous with the arcuate fibers which enter it. Cephalad of the ninth it is more distinct as a separate tract and is composed almost entirely of myelinic fibers. Opposite the ninth a small fasciculus of fine fibers begins to form in the cinerea, dorso-mesad of the *fasciculus communis* which joins the bundle a short distance caudad of the seventh nerve, and with it leaves the brain to form the *fasciculus communis* component of that nerve, (VII, a. a.). I find no continuation of this bundle in *Necturus* cephalad of the seventh as it was found by Osborn ('88) in *Cryptobranchus*.

Isolated cells occur laterad and ventrad of this tract cephalad of X^1, which presumably represent what in the tadpole is

spoken of as the "so-called sensory" nidus (Strong '93). In *Necturus* the three contingents, to the seventh, ninth and tenth nerves, which leave this fasciculus are formed of fine fibers with delicate myelinic sheaths. These pass to their exit, dorsad of the ascending V, as is also the case in *Amblystoma*, differing in this respect from the condition in the tadpole (Strong '95) where they pass ventrad of it.

The homology of the *fasciculus solitarius* of man, lifted from the root bundle of X^7, has been placed by Strong upon this tract. This had been contemplated in this investigation before the appearance of Strong's work, and rejected as not capable of establishment from the facts. Although this homology is set forth by him in a most forcible and enticing manner, a hesitation is yet felt in accepting it for the following reasons: the *fasciculus solitarius* of mammals and the ascending V are regarded as entirely comparable tracts ; both become medullated early ; both may be traced caudad into the myel, and are accompanied throughout their course by gelatinous substance, chiefly on their mesal side, containing cells which constitute the end nidi of the tracts. (See Turner '94 and Kölliker '93). The *fasciculus communis* and ascending V in Amphibia appear to be quite different tracts. Further, by considering the *fasciculus communis* as representing the *fasciculus solitarius* alone, we leave unacounted for the larger end nidus of vagal sensory fibers. Strong apparently confounds this with the end nidus of the *fasciculus solitarius*. The strongest evidence in favor of the homology would be the exit of *fasciculus solitarius* fibers as the *pars intermedia Wrisbergii* now considered as a sensory root of the seventh, with the geniculate ganglion as its nidus of origin, which is affirmed by Kölliker ('93) ; by others, however, the end nidus of the glosso-pharyngeus has been stated to be the end nidus of this nerve. Brandis ('93) in speaking of the *fasciculus solitarius* in the brain of birds, stated that a portion of the fibers turned laterad to the eighth nerve and the remainder entered the trigeminal nerve.[1]

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[1] A similar relation of the bundle to the fifth is also given for man by Boettiger ('90).

In a later paper, no mention is made of such relations of the solitary bundle, and he is inclined to associate the *pars intermedia* with the vago-glossopharyngeal end nidus.   Further, regarding its central relations, the *fasciculus solitarius* is said in birds to decussate just caudad of the metatela,—a relation not as yet observed in man.   The foregoing considerations seem to warrant postponing the acceptance of the homology until a fuller comparative study of this tract is made.   Possibly the *fasciculus communis* may embody both sensory termini for vagal fibers.

Dorsal tracts.—As has already been stated, at the transition from myel to oblongata the number of myelinic fibers in the dorsal regions has greatly diminished, those remaining being almost entirely such as constitute the ascending V and X.   After the beginning of the metatela, and up to the level of the first spinal nerve, these tracts occupy the extreme dorsal position in the spreading walls of the oblongata, the fibers for the tenth the more dorsal.   Cephalad of this point the ascending V and X begin to migrate ventrad, leaving an amyelinic area to occupy the more dorsal portion.   This area is also extended by the closer apposition of the walls of the oblongata in the region of the tenth nerve.   Cephalad of X^1 the ascending V is situated in the ventro-lateral angle of the oblongata; dorsad of it begin to be distinguished the large fibers of the eighth nerve.   In this region myelinic fibers appear in the dorsal tracts, chiefly in the extreme dorsal portion and the region just dorsad of the fibers of the eighth, constituting the beginnings of the tracts named for distinction tracts *a* and *b*.   Between these two tracts the region is almost entirely amyelinic with however scattered bundles of myelinic fibers.   Into this intermediate area enter IX^1 and IX^2 and a portion of the "dorsal seventh" ($VIIb^2$).

Tract *a*, beginning in the region of the tenth nerve, reaches its fullest development between the seventh and ninth nerves.   In the region of the seventh this tract loses its extreme dorsal position, which is here occupied by an area of amyelinic substance, apparently composed largely of 'ground substance,' into which the dorsal portion of the "dorsal seventh enters" ($VIIb^1$).   This is restricted to the immediate neigh-

borhood of the seventh nerve, and cephalad tract *a* soon re-
gains its dorsal position. Slightly cephalad of the fifth nerve it
disappears, the fibers which compose it turning mesad into the
neighboring cinerea. This tract does not seem to be increased
to any extent from arcuate fibers.

Tract *b* likewise first appears in the region of the tenth
nerve reaching its strongest development between the seventh
and ninth. It lies latero-dorsad of the *fasciculus communis.* Be-
tween the ninth and tenth the tract is largely increased by arcuate
fibers which turn cephalad in it. The relation of arcuate
fibers to tract *b* continues throughout its length, but is most
marked between the ninth and X^1. Most of the bundles which
enter it turn cephalad; others, however, in the region of the
ninth nerve, turn caudad ; this is also the case in the region of
the fifth.

Between tracts *a* and *b*, the alba is almost entirely amyel-
inic. Small fascicles of myelinic fibers occur, however, in it ;
these seem to be to a large extent arcuate fibers which pene-
trate this region. Fibers also pass into this intermediate re-
gion from tracts *a* and *b*. Into it enter the dorsal division of
the ninth and the ventral portion of the "dorsal seventh"
(IX^1 and IX^2, and $VIIb^2$).

Arcuate fibers.—Arcuate bundles are well developed in
Necturus. In the myel fine myelinic fibers pass down from
the dorsal cinerea to decussate in the raphé, assuming a longi-
tudinal direction in the ventral columns. In the re-
gion of the 2nd spinal nerve and cephalad these fibers are
greatly increased in number. Up to the exit of X^1 the num-
ber of fibers is diminished ; cephalad of that point, however,
they begin to pass to the dorsal tracts, traversing the alba at all
levels, not confined to the border of the cinerea. Between the
ninth and X^1 they largely take part in the formation of tract *b*,
in which they turn both cephalad and caudad. The intermedi-
ate region between tracts *a* and *b* also receives many of them.
In the region of the seventh large bundles of arcuate fibers pass
dorsad to terminate in the lateral border of the cinerea adjacent
to the dorsal tracts, and the dorsal island of alba into which the

dorsal portion of the " dorsal seventh " enters ; and these bun-
dles are coextensive with that area.   In the region of the fifth
nerve, arcuate fibers are intimately connected with the diminish-
ing number of myelinic fibers in the dorsal tracts.   Some of
these seem to cross in the raphé and turn into the cinerea of
the opposite side.

Origin of the Cranial Nerves.   (Figs. 5, 9-20, 22.)   At
the time this investigation was undertaken the condition of our
knowledge of the origin of the cranial nerves of the tailed Am-
phibia was far from satisfactory.   Fragmentary results had been
obtained by Stieda ; more complete were the observations on
this subject made by Osborn ; still, some evident inconsistencies
in his results with those reached on other forms, and a failure
to recognized the true relations of certain nerves, rendered a
review of the subject desirable.   In respect to the homology
of the nerve components, as stated by him, interpretations de-
pended largely on the peripheral relations and distributions of
the several components, of which nothing satisfactory was
known.   The papers of Strong, however, have supplied the
necessary information ; not only has he investigated the distri-
bution and segmental value of the components but also made
extensive comparisons with the cranial nerves of other Ichthy-
opsida.   The ental or deep origins have also been discussed by
him, rendering less necessary an extended description here ;
however, as the results here attained confirm, and in part sup-
plement his, they are, in so far, at least, of value and will be
given. Where possible, the roots in Necturus have received the
names applied by him.   Instead of the terms motor and sensory
nuclei or nidi, the recent results of the impregnation methods
render preferable a terminology in which the relations of fiber
and cell are more distinctly implied, and here will be employed
those adopted by Kölliker ('93) (" Endkern " and " Ursprungs-
kern ") and Turner ('94), "nucleus of origin " and " terminal
nucleus " nidus being employed in preference to nucleus.   It is
evident that the nidus of origin of sensory nerves would be the
peripheral ganglia from the cells of which their fibers spring,
and the 'terminal nidus' within the brain, with which they

have physiologic connection, might be the nidus of origin of some intra-cerebral tract or tracts, &c.

In *Necturus*, the cranial nerves generally found in Amphibia are present. The difficulties in the recognition of the eleventh and twelfth nerves have already been spoken of. The two motor roots rising from the ventral columns caudad of the tenth (X⁷) have been termed the 1st and 2nd spinal nerves, despite the fact that they have no dorsal roots or ganglia.[1] Their mode of origin within the brain is that shown by Stieda for the motor roots of the spinal nerves in the Axolotl; some of the fibers pass directly dorsad to the ventral horns, a larger number turn cephalad in the ventral tracts, others caudad. No special nidus or origin for either of the nerves was recognized.

Vagus.—This nerve and the glossopharyngeal are closely related to each other. The vagus arises by two roots which are formed in *Necturus* of seven minor rootlets, of which the two caudal unite to form one root, the eleventh of some writers, the cephalic five forming the tenth. X¹, the largest, arises from the lateral aspect of the oblongata and derives its fibers from two sources,[2] (1) the *fasciculus communis*, whose fibers leave the brain the more dorsally, (2) ascending fibers, chiefly of large caliber, which migrate ventrad into the ascending V Some of these fibers may be traced caudad as far as the exit of the 2nd spinal nerve. Burckhardt has found in *Protopterus* a decussation of similar ascending fibers of the tenth caudad of the metatela. In *Necturus* a decussation of small fibers was observed in this region but their relation to the tenth nerve could not be determined. Strong speaks of this component in the tadpole as derived from the ascending V. In *Necturus* they

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[1] Even in man, Gray (Anatomy, Descriptive and Surgical) states that the dorsal root of the first spinal nerve is much smaller than the others and frequently has no ganglion.

[2] The true physiologic direction of the fibers is for convenience of description disregarded here, thus though really the impulse is "descending," the old term, *ascending V* is retained.

appeared rather to arise dorsad to the fibers of the ascending
V and to migrate ventrad into that tract toward their exit.
There seems to be no representative of these fibers in "fishes,"
nor, indeed in higher forms, unless it might be represented by
the *fasciculus solitarius*, a rather unsafe comparison though there
is a resemblance in the comparability of these with the fibers
of the ascending V. The decussation of certain fibers of this
component in *Protopterus*, in view of a similar decussation of
the solitary bundle observed in birds, is suggestive. The fibers
from the *fasciculus communis* are fine, with delicate myelin
sheaths, as are all fibers derived from this tract.

X^2 and X^3, which are very delicate and of few fibers each,
are undoubtedly motor, arising farther ventrad from the region
of large motor cells.

X^4 and X^5 arise slightly caudad to the three rootlets above,
and are very close to each other. X^4 is probably sensory and
its fibers like a portion of those of X^1 accompany the ascend-
ing V.

Roots X^5, X^6 and undoubtedly X^7 are motor, and arise in
much the same manner. The root fibers of the most caudal of
these roots (X^7) may be recognized as far caudad as the caudal
end of the metatela, and form an ascending fasciculus in the
lateral columns of the oblongata adjoining the cinerea. Osborn
regarded this ascending bundle as the representative of the soli-
tary bundle of the mammalian brain, but erroneously, as was
pointed out by Strong. The entire bundle turns directly laterad
to constitute X^7. Near the exit of this root fibers appear in
the adjacent cinerea among the motor cells and unite to form a
fasciculus occupying the same position as did the fibers of X^7.
The fibers leave the brain as X^6 which joins X^7, forming the
major root sometimes spoken of as the eleventh nerve. In addi-
tion to its ascending fibers, a few entered root X^7 which came
from the region of the ascending V and were presumably
sensory. In precisely the same manner as X^6 arose X^5 which
was however closely related to the roots cephalad of it.

The following Table may summarize what has been said
above concerning the roots of the tenth nerve and their origin:

VAGUS NERVE.

roots.	size.	source.	character of fibers.	function.
X¹	large	fasc. com. asc. tract.	fibers fine fibers coarse.	sensory.
X²	small	motor nidus	medium.	motor.
X³	small	" "	"	, "
X⁴	medium	asc. tract.	"	sensory.
X⁵	small	motor nidus.	"	motor.
X⁶	medium	" "	"	"
X⁷	medium	asc. lat. tract. asc. tract (few)	" "	motor ? sensory.

As compared with the origin in *Cryptobranchus* as set forth by Osborn, the following differences may be noted : his solitary bundle enters two roots in *Cryptobranchus,* but one in *Necturus.* The *fasciculus communis* enters two roots, one in *Necturus.* Further, no ascending sensory root in addition to the *fasciculus communis* was found by him ; in *Necturus* it enters three roots though in two of them the contingent was small.

Strong's results on the tadpole show slight differences, the most important of which is the changed relation of the *fasciculus communis* and (his) ascending V components, the first being ventral in the tadpole, dorsal in *Necturus.* There seem to be fewer roots, three only being recognized by him, the first drawing its fibers from the *fasciculus communis,* ascending tract (his ascending V) and a motor nidus ; the second, *fasciculus communis* and a motor nidus; the third, ascending lateral tract (solitary bundle of Osborn). The differences in the relation of the *fasciculus communis* should be noted. As to whether the ascending fibers of the tenth nerve can be said to be derived from the ascending V is merely a matter of definition ; they are, indeed, closely associated with that tract.

Glossopharyngeus.—This is closely related to the vagus, and possibly would have been better discussed with it. What are treated here under this name include the ninth nerve proper, and, from the researches of Strong, the representative of the " *Ramus lateralis vagi,*" or " *Nervus lateralis* " of other *Ichthyopsida.*

The nerve is distinct from the vagus almost up to its gang-

lions, which are fused with those of the vagus. Near the brain, however, it turns cephalad, and soon divides into two bundles, IX^{1+2} and IX^{3+4}. The first is the 1st Vago-glossopharyngeal root of Strong, (IX^1 of Osborn), and the representative of the lateral line nerve of fishes (Strong) ; IX^{3+4} is IX^{2+3} of Osborn, 2nd root of Strong.

IX^{3+4} is the more caudal and is formed of two roots. The *fasciculus communis* gives off a large contingent to form IX^3; it passes dorsad to the ascending fibers of the eighth. IX^4 springs from the motor cells in the floor of the oblongata and passes ventrad of the ascending fibers of the auditory, to its exit, joining IX^3 immediately. There is an exact agreement in the above with the results of Osborn and Strong.

The other division is composed of fibers of a very characteristic and constant appearance. They are large, with very dense myelinic sheaths, and are of the same appearance in all the forms studied. This bundle proceeds cephalad a short distance and enters the dorsal region between the tracts here called *a* and *b*, by two roots, one more dorsal and slightly cephalad of the other, and separated from it by a small fasciculus of longitudinal fibers. Some of the fibers of each root lose their myelin almost immediately on entering the brain and disappear; others may be traced cephalad for a few sections, but are lost within a quarter of a millimeter from the point of entrance. None of the fibers were observed to turn caudad within the brain.

The region into which these roots enter contains but small scattered bundles of myelinic fibers, of which the largest, on the ectal surface of the brain, separates the two roots. An interchange of fibers occurs immediately cephalad of the roots. Many arcuate fibers go to the dorsal tracts at this level. The cinerea that adjoins the dorsal tracts at and cephalad of the entrance of this nerve is composed of small cells and must be regarded as the terminal nidus.

An extensive comparative discussion of this nerve is given by Strong ('95). The lateral branch of the vagus, or more correctly perhaps the lateral nerve, has been likewise found to arise

cephalad of the ninth nerve in *Acipenser* (Goronowitsch), the *Cyprinidæ* (Mayser), sharks and Rays (*Læmargus, Lamna, Raia*) (Ewart), and *Galeocerdo* (Strong, '95), and Wright was inclined to regard its origin similar in *Amiurus.* In the *Cyprinidæ* the fibers were derived from the *tuberculum acusticum.* In *Acipenser* Goronowitsch found the lateral nerve formed of ascending and descending fibers from the "dorso-lateral" tract, of which the descending bundle was much the larger and was thought by him to come from the cerebellum. In *Necturus* the origin of these fibers was restricted to the dorsal region of the oblongata in the region caudad of the eighth nerve, which might be regarded as representing the *tuberculum acusticum* of the teleosts, although no *tuberculum acusticum* proper exists. Certainly no fibers can be traced cephalad to the cerebellum.

In *Necturus,* as compared with the other urodeles examined, this nerve was greatly developed, a condition to be expected, both from its larger size and the greater number of sense organs in *Necturus.* The ratio of IX^{1+2} to IX^{3+4} in this form is approximately 2:1. In *Amblystoma,* both roots, IX^1 and IX^2 are distinct but their ratio to IX^{3+4} is about 1:1.

Acustic Nerve.—As far caudad as the exit of the X^1 large fibers begin to appear in the region dorsad to the ascending V and between it and tract *b.* These increase in number cephalad, and at last, about 1 millimeter cephalad of the entrance of IX^1 they enter the eighth nerve. This forms a considerable and indeed the largest source of the fibers of the eighth nerve. The fibers are large with thin myelinic sheaths and are very easily traced. A far smaller portion of the acustic fibers, which are also of finer caliber, turn cephalad. Osborn ('88) regarded such in *Cryptobranchus* as decussating through the cerebellum with the corresponding fibers of the eighth nerve on the opposite side. A direct relation of acustic fibers to the cerebellum in the lower forms appears probable from the results of Mayser, Goronowitsch, and Köppen, ('88) on the species investigated by them. Ahlborn however considered that the fibers entering the cerebellum in *Petromyzon* were commissural between the acustic nidi of the two sides. In higher forms the

direct relation of acustic fibers (of the vestibular nerve) to the cerebellum, is stated by Edinger, ('86) Sala and Brandis, but disputed by Kölliker.   An ascending root of the eighth nerve is recognized by Goronowitsch, and by Stieda in the *Axolotl*.

In addition to the fibers spoken of above, others seem to end almost immediately on entering the brain, in close proximity to large cells situated in the lateral region, which have been likened to the large cells in *Petromyzon* connected with the median crossed and lateral uncrossed Müllerian fibers.   Similar cells occur caudad as far as IX^1 and may possibly represent, or be closely connected with the terminal nidus for the ascending acustic fibers.   Osborn suggests a comparison of these with Deiter's nidus of mammals.   But a single acustic root was observed in *Necturus*.   This is contrary to certain theories of the development of the ear and with results in some other, especially higher forms; it agrees however with the condition found in *Cryptobranchus* and the *Axolotl* (Steida '75).   Possibly the two roots may be represented by the ascending and descending fibers.   The eighth is $VIII^2$ of Osborn in *Cryptobranchus*.   The correspondence between the two forms would seem to be close, though his figures leave much to be desired.   The relation to the large cells is noted by him, and ascending and descending fibers, though the ascending tract apparently does not have as great extent as in *Necturus*.   The derivation of the descending fibers from the mesencephal after decussation in the cerebellum, must seem doubtful from the relations found elsewhere.

Facial Nerve.—This nerve is formed of two components, VII*aa*, a sensory root from the *fasciculus communis* of Osborn, and VII*ab*, motor, formed by two, or in some cases three, rootlets, arising from the oblongata ventrad of and at about the same transverse plane as the eighth.

VII*ab*.—At about the exit of the tenth (X^1) nerve, myelinic fibers begin to appear in the cinerea dorsad of a nidus of large cells in the ventro-lateral portion of the floor.   From here to slightly cephalad of IX^1, fibers spring continuously from this region and unite to form a close bundle which passes mesad to lie dorsad of the posterior longitudinal bundle and immediately

ectad of the endyma, causing a slight elevation. In this position they run cephalad to just caudad of the exit of the eighth where they turn laterad and ventrad, in two (or three) bundles, to leave the oblongata as the motor roots of the seventh nerve, and immediately unite with the issuing fibers of the eighth. The origin of these roots in urodeles, and the recognition of them as homologous with the facial of higher forms, have been involved in a great deal of obscurity. Stieda ('75, p. 302) recognized this bundle in the floor of the oblongata as belonging to the facial and describes its exit to form that nerve; he could not, however, discover the origin. Osborn ('88), in his study of the oblongata of *Cryptobranchus*, regarded this as belonging to the eighth instead of the seventh, and derived the fibers of VII*ab* from the posterior longitudinal fasciculus. He was not, however, certain of the correctness of the homology, and in note 3 in the appendix to his paper, seemed inclined to doubt the relation of the fibers to the posterior longitudinal bundle. He was influenced in his view of this tract by the close relation of the posterior longitudinal fasciculus and the eighth nerve in the papers of Fulliquet and Ahlborn, the last of whom his misquotes, however. The ventral division of what is here termed the dorsal VII was considered by him motor and to represent the root which would otherwise be wanting. Burckhardt ('91) following Osborn, named these roots, VIII, 3 and 4, and found them composed "mostly of Müllerian fibers." He also regarded the ventral root of the "dorsal seventh" as representing the facial. His VIII, 3 and 4 in *Protopterus* ('92) are the same, and these he derives "in part from the posterior longitudinal fasciculus, and in part from a motor nidus." Strong did not attempt a solution of the question but regarded the source of these fibers as partly from the posterior longitudinal fasiculus and partly from the trigeminal motor nidus.

In view of the importance of the matter, and the confusion with regard to this nerve in Amphibia, a somewhat extended comparative discussion seems desirable; especially since the mode of origin of this nerve is so nearly constant in widely

different forms. It is scarcely necessary to point out the exact comparability between the modes of origin of the facial nerve in Amphibia[1] and man. The nidus is situated rather deeply and begins to appear in sections just caudad of the pons. From this, fibers arise which associate themselves into a bundle upon the dorsal side of the posterior longitudinal fasciculus, in which position they run cephalad to turn sharply laterad and ventrad to their exit as the facial nerve, the two bendings constituting the well known "knee of the facial" (*genu nervi facialis*).

In his studies of the brain of teleosts, Mayser has investigated the oblongata and the origin of the nerves to a considerable extent. He describes the mode of origin of the seventh in the following words : "Die grobfaserige ventrale gekniete Quintuswurzel (*N. V. gen. vent.* [*VII*] kennt Stieda (p. 35 and 55, Knochenfische) und Fritsch (a. a. O. p. 85). Die Wurzel bildet sich bei Cyprinoiden aus zwei hinter einander entspringenden Bündeln. Das hintere legt sich der Aussenseite der aufsteigenden motorischen Vaguswurzel (*N. IX. mot.*) an und kommt aus dem hinteren Trigeminuskern Stieda's und einer Ansammlung sehr grosser blasenförmiger Zellen, welche zwischen den Kommissurenfaserzügen und zu beiden Seiten des hinteren Längsbündels liegen (*Nuc. N. V. gen. vent. post.*, Fig. 27); das vordere entspringt in derselben Weise da, wo die aufsteigende motorische Vaguswurzel (*N. IX. mot.*) nach aussen umbiegt (*Nuc. N. V. gen. vent. ant.*, Fig. 29). Vereinigt ziehen beide, fast nur vom Epithel des Centralkanale bedeckt und mit dem hinteren Längsbündel aussen oben innig verbunden nach vorn, biegen etwas vor der Umbeugungsstelle der dorsalen Kniewurzel plötzlich unter rechtem Winkel nach aussen um, wobei sie den *N. V. asc.* und die vordersten Partien der vor-

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[1] In the frog, if we may trust the observations of Stieda and Köppen, the mode of origin of the motor fibers differs entirely from that commonly found, the fibers entering the nerve directly from the trigeminal motor nidus. I find the mode of origin of this nerve in *Amblystoma* and *Diemyctylus* as described above in *Necturus*.

deren Acusticuswurzel (*N. VIII. ant.*) durchbrechen (Fig. 27-31)." No commentary is necessary upon the above. In Wright's paper upon the brain of *Amiurus*, although no attempt at tracing the internal origin of the nerves is made, it is evident from his words and figures that the larger portion of the facial fibers arise in much the same manner as set forth by Mayser. A portion of the fibers he derived from a nidus near the nerve (p. 360.).

In *Acipenser* is found precisely the same mode of origin, as may be seen from the two paragraphs below in which the origin of the facial nerve in that genus is described. The comparison with *Necturus* is close. I did not however, find any fibers of the facial to be derived from the ventral columns. It is still possible that some of the fibers before mentioned as terminating at or near the facial nidus, may pass directly into the root bundle of the facial nerve. Goronowitsch has been misquoted as to the origin he found for the facial nerve, and it has seemed best therefore to reproduce entire the portion in which it is described by him. "Proximal von der Austtrittsstelle der *N. lineae lateralis* gesellt sich zu den Bündeln ein anderes Längsfasersystem (Taf. XX, Fig. 49, *Frv.*) Die fasern desselben kommen aus der grauen Substanz des Vorderhornes, sowie aus den Ventral liegenden Theilen der weissen Substanz (Taf. XXII, Fig. 81 *Frv.*). Diese Fasern umkreisen den Boden der Vorderhirnrinne und steigen, der seitlichen Oberfläche der hinteren Längsbündel folgend, in die dorsalen Abschnitte dieser letzeren, wo sie einen runden Strang bilden. Es sind, wie wir gleich sehen werden, die Fasern der ventralen Wurzel des Facialis. Mitunter findet man, dass die Fortsätze der motorischen Zellen bis zu den Fasern des Facialis zu verfolgen sind. (Fig. 81). Ein kleiner Theil der Fasern kommt, wie gesagt, aus den ventralen Abschnitten der weissen Substanz. In den betreffenden Querschnittsebenen der Oblongata enthält die weisse Substanz viele zerstreute grosse Ganglienzellen. Ob diese Zellen als Ursprungsstätten eines Theiles der Fasern des Facialis aufzufassen sind, konnte ich nicht sicher entschei-

den.   Einige Fortsätze wenden sich in der Richtung der
Fasern.   Alle diese Verhältnisse sind in Fig. 81. dargestellt.

" Die Fasern der ventralen Wurzel des Facialis sind etwas
feiner als die der hinteren Längsbündel und sind daher sehr
leicht in proximaler Richtung zu verfolgen.   In der Nähe der
Austrittsstelle koncentrirt sich der Faserzug in einen kompak-
ten runden Strang, welcher einen Vorsprung auf der dorso-
lateralen Oberfläche der hinteren Längsbündel bildet.   Der
Strang biegt lateral unter rechtem Winkel um und durchzieht,
bogenförmig und ventralwärts verlaufend, den proximalen
Theil der austretenden Acusticusfasern (Taf. XX Fig. 50 *Frv.*)
Vor der Austrittsstelle dieses letzeren Nerven tritt die Wurzel
aus und legt sich eng ventral an die dickere dorsale Wurzel des
Facialis an. (*Frd.*)   Ein Theil der queren Bahn der ventralen
Wurzel bildet die makroskopisch wahrnehmbaren Abzwei-
gungen der hinteren Längsbündel, welche ich im anatomischen
Abschnitte besprochen habe."

In turtles, judging from the figure of Humphrey ('94), a
portion of the fibers, at least would seem to be associated with
the posterior longitudinal bundle.   In birds Brandis has found
the same origin as in mammals, with, however, the middle por-
tion, (ascending limb) reduced to a minimum.

In Elasmobranchs, the origin of a motor portion of the
facial is obscure ; Rohon's statements of the origin of the facial
are too vague and indefinite to admit of any conclusions being
founded upon them.   Sanders has found the facial to spring
from the bundle called by Rohon *fasciculus longitudinalis later-
alis*, (comparable with *fasciculus communis* ?), and it would seem
to be a sensory root.   Indeed, Jackson and Clark in speaking
of the peripheral distribution of the facial in Elasmobranchs,
state that the muscles innervated by the seventh in teleosts
do not exist in Elasmobranchs and that therefore a motor por-
tion is absent.   Equally unsatisfactory is the state of knowl-
edge of this nerve in *Petromyzon*.   Ahlborn describes the fa-
cial as arising by a single root from a nidus dorsad to the
acustic nidus.   The cells in the nidus are small and the issuing
fibers fine.   By Julin and Dohrn the facialis in *Petromyzon* is

asserted to contain motor elements (Strong '95), in which case we should expect to find another origin for a portion of the fibers.

VII*aa*, is small and arises at the level of the eighth nerve and dorsad of it, from the *fasciculus communis* and a small accessory bundle of fibers which springs from the cinerea mesodorsad of the *fasciculus communis*. The fibers are small and lightly medullated. On their way to the periphery they penetrate tract *b*, which is well developed at this level. The ganglion of this contingent is fused with that of the eighth, and represents probably the geniculate ganglion, the nerve itself representing the *pars intermedia* (Strong). Strong finds that the palatine nerve is formed by this component of the seventh. In *Necturus*, as indeed in other urodeles, this nerve (palatine) does not, as in the Anura, come into relation with the Gasserian ganglion.

Dorsal VII.—This is the VII u and l, of Osborn; VIIb or Dorsal VII of Strong. The fibers of which it is composed differ greatly in appearance from the other fibers of the facial, and indeed the other cranial nerves except IX^{1+2} with which they correspond exactly. The figures show them very inadequately; they are large and with dense myelinic sheaths. In *Necturus* the roots unite to form the dorsal seventh, and they are here spoken of as $VIIb^1$ and $VIIb^2$, VII^1 rising dorsad and slightly caudad from a region well demarcated from it. At about one-third of the distance (going cephalad) between IX^1 and VIII there begins to be formed in the extreme dorsal portion of the dorsal tracts an area of amyelinic substance of a structureless appearance—ground substance. This increases in amount to the region of the eighth nerve and decreases again cephalad of this point, disappearing entirely half a millimeter cephalad of that nerve. Into this island resting upon tract *a*, $VIIb^1$ enters at the level of the eighth. The fibers lose their myelin immediately on their entrance and disappear, turning neither cephalad or caudad. The cells immediately adjoining this area undoubtedly represent the terminal nidus of this root.

$VIIb^2$ enters the same portion of the dorsal tracts as does

IX^{1+2}; that is, the region between tracts a and b, separated therefore from $VIIb^1$ by tract a. Some of the fibers appear to terminate immediately; most of them, however, turn caudad and may be readily followed for but a short distance, since they soon lose their myelin, and become indistinguishable; some even as amyelinic fibers may be followed for a short distance farther, that is to a little caudad of the exit of the eighth nerve.

$VIIb^1$ and $VIIb^2$ unite immediately to form $VIIb$ which soon divides into two approximately equal portions, one of which joins the motor and *fasciculus communis* portions of the seventh and the eighth nerve, while the other division goes cephalad to the Gasserian ganglion.

The close comparison in origin between IX^{1+2} and $VIIb^2$ is evident: both end in approximately the same region caudad of the eighth; the fibers of IX^{1+2} turning cephalad to it, those of $VIIb^2$ caudad to it. The difference in origin between $VIIb^2$ and and $VIIb^1$, though slight, might seem to indicate that the two roots were different; that $VIIb^1$ passed to the Gasserian ganglion and should be considered as belonging to the fifth proper, as was interpreted by Herrick ('94), and representing perhaps the dorsal root of Trigeminus II of Goronowitsch in *Acipenser*. This does not seem to be the case however; the fibers of both roots are of the same size and appearance; further, the division between the roots is not the the division between the portions which join the fifth and seventh, a portion of the $VIIb^1$ undoubtedly joining the seventh and eighth. In smaller forms, *e. g.*, *Amblystoma* and *Diemyctylus*, a division into two roots is less marked, due partly to the weaker development of a tract separating them.[1]

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[1] Pinkus, '95, has examined the larvæ of *Salamandra maculosa* and *atra*, *Desmognathus fusca* and *Salamandrina*, and recognized in all the lateral line root of the VII (VIIb of Strong). In the adult of *Salamandra atra* and *Geotriton fuscus* the lateral line nerves are absent, although in the first genus a delicate strand pasess from the seventh nerve to the Gasserian ganglion and at that point atrophies. I have examined in this connection the brains of adult forms of *Amblystoma punctatum*, *Diemyctylus viridescens*, *Desmognathus fusca* and *Plethodon erythronotus*. In the first three genera the lateral nerve roots of the VII were present, although in *Desmognathus* the bundle to the Gasserian ganglion was

In fine, in *Amphibia*, the "dorsal VII" and "dorsal IX" (IX^{1+2}), both terminate in the dorsal region of the oblongata, in the immediate neighborhood of the eighth nerve and in large part slightly caudad of it.

Abducens Nerve.—This is very small in *Necturus* and arises from the ventral aspect of the oblongata by two very small roots. I was unable to trace it to its nidus. In *Amblystoma*, though the nerve is much larger and arises by three roots, no direct relation to a nidus could be observed. The fibers sprang apparently from the posterior longitudinal fasciculus. Undoubtedly the motor cells of the ventral region in this immediate neighborhood constitute the nidus of origin.

Trigeminus.—The fifth nerve is the largest of the nerves arising from the oblongata; and, save the olfactory, of all the cranial nerves. The fibers of which it is composed are drawn from four sources, and leave the brain by three ill-defined roots.

(1). Ascending V. This furnishes by far the largest portion of the fibers of the fifth in *Necturus*. It can first be distinctly recognized in the myel a slight distance caudad of the second spinal nerve, where it occupies a dorso-lateral position. In this region it is small. At the level of the first spinal nerve, it has increased in size and from this point cephalad begins to migrate ventrad. At the level of X^1 its position is lateral and the fibers of the tenth pass through it. At the eighth it is ventro-lateral, the eighth arising dorsad of it. Its fibers are mostly small, although a considerable number of large ones occur in it, some of which can be traced from its first appearance in the caudal portion of the myel. No augmentation by fibers from motor nidi was observed, and it is presumably purely sensory.

(2). Sensory nidus (terminal). Cephalad of the exit of the dorsal seventh, fibers arise among the cells adjoining the

very small. In *Plethodon* no trace of it was found and the roots of the lateral line nerves are believed to be absent. Pinkus did not examine the ental origin of the lateral line roots in *Protopterus*, but the ectal relations shown by him and the results of Burckhardt ('91) indicate a close resemblance to the conditions in the Amphibia.

ascending V, which associate themselves with that tract near the exit of the nerve. The cells among which these fibers appear presumably represent a terminal nidus, the sensory nidus of Osborn. Its extent in *Necturus* is much less however than in *Cryptobranchus*.

(3). Motor nidus. A short distance cephalad of the level shown in Fig. 19 the motor nidus of the fifth nerve appears in the floor of the metencephal, succeeding, but entirely separated from the nidus of the seventh, compared with which it is much more compact. It extends cephalad to the exit of the nerve. From this two bundles of fibers pass down to constitute the smaller roots of the fifth, V^{2+3}, which however, fuse immediately with the larger root.

(4). From the Mesencephal. As stated by Osborn, the large ganglion cells in the roof of the mesencephal which constitute the mesencephalic trigeminal nidus, are quite numerous in *Necturus*. They are found scattered throughout the extent of the roof but are massed more closely just cephalad of the cerebellum, as described by Osborn (Fig. 22). From this nidus large fibers spring which pass caudad grouping themselves in two divisions, one of which enters and passes ventrad through the cerebellum; most of these fibers enter the large root (V^1) of the nerve. Others pass the fifth without entering it, as noted by Osborn, and may be traced caudad, meso-dorsad of the ascending V, to the neighborhood of the seventh and eighth nerves.

The two smaller roots of the trigeminal are evidently not entirely the same as the motor root of man, inasmuch as from the latest evidence the mesencephalic descending tract enters the smaller motor root in man. Nor, indeed, would V^2 and V^3 in *Necturus* be the same as the rootlets in *Cryptobranchus*, which Osborn found to be formed by the descending tract.

I, II, III, and IV.—The remaining cranial nerves have received but superficial attention, and little more can be said of them than that their origins seem to be as described in other *Amphibia*.

The trochlearis (IV) is very small in *Necturus*, and I failed

utterly to trace the fibers to their nidus of origin in the base of the brain. The distribution of a portion at least of the fibers to the metaplexus has been noted before; nothing in the character of a terminal nidus was observed.

The oculomotor (III) enters the brain at the level of the mesencephalic pit and passes dorsad to its nidus in close relation to the posterior longitudinal fasciculus. Several large ganglion cells occur cephalad of this point at about the region of transition from mesencephal to diencephal, which Osborn regarded as constituting a portion of the oculomotor nidus, and also as having a relation to the fibers of the postcommissure. With Burckhardt, however, I must consider the relation of these cells to the post-commissure as of no significance, and regard as doubtful any direct connection of these with oculomotor fibers.

The undeveloped condition of the optic nerves has been commented on. The decussation of the fibers appears complete, the fibers all proceeding dorsad and caudad upon the ectal surface of the brain to the mesencephal.

The cranial nerves of Necturus cephalad of the tenth that have been more especially studied may be tabulated as follows :

nerve.	roots.	size.	source.	character of fibers.	function.*
Fifth	V¹	large	ascending V	fine and coarse	sensory.
			mesencephal	coarse	motor (?).
			sensory (terminal) nidus	fine	sensory.
	V²+V³	small	motor nidus	medium	motor.
Sixth	VI				
	(2 roots)	small	————	medium	motor.
Seventh	VIIab.	medium	motor nidus	medium	motor.
	VIIaa.	small	fasc. communis	fine	sensory.
Eighth			⎧ asc. fibers	coarse	⎫
	VIII.	large	⎨ desc. fibers	fine	⎬ sensory
			⎩ adjacent cinerea	———	⎭
"Dorsal"	VIIb¹	medium	dorsal 'Island'	coarse	sensory.
Seventh		medium	dorsal tract	coarse	
Glosso-pharyngeus	IX	medium	fasc. communis	fine	sensory.
	IX	medium	motor nidus	medium	motor.
"Dorsal"	IX	medium	dorsal tracts	coarse	sensory.
Ninth	IX	medium	dorsal tracts	coarse	sensory.

* This, of course, is only stated inferentially, since no experiments have been made to determine it empirically. In general, those roots springing from

FIBER TRACTS.

It seems best to collect under this head disconnected observations that have been made on the fiber relations in various parts of the brain, and which, due to inadequate study of the structure of related parts must be treated separately.

Lemniscus.—As far caudad in the oblongata as the exit of the tenth nerve (X¹) a denser arrangement of some of the fine fibers in the ventral region of the oblongata is apparent. This becomes more marked at the ninth and in the region of the eighth a more or less distinct bundle is formed in the alba (Fig. 17) midway between the meson and lateral aspect. This gradually becomes more marked and migrated laterad to pass dorsad into the mesencephal and there become lost. It is shown in the figures 15-17; 19-21; and 35. A large portion of the fibers which form this this tract in the oblongata cross in the raphé, and undoubtedly come from the dorsal regions as arcuate fibers, as may be seen from horizontal sections. This presumably represents the lemniscus or a portion of it as Herrick has already stated. It appears to be much better developed, as a myelinic tract at least, in *Necturus*, than in *Amblystoma* or *Diemyctylus.*

Posterior longitudinal fasciculus (Fasciculus longitudinalis dorsalis, Hintere Längsbündel).—The course and relations of the fibers of this tract in the caudal portion of the oblongata have been already described. Cephalad of the fifth nerve the tracts are represented by a few coarse fibers with which are associated finer ones. Just caudad of the mesencephalic pit other longitudinal fibers decussate and become closely associated with these bundles. Slightly cephalad of the exit of the third nerve, this tract is no longer recognizable; its disappearance in

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the ventral region of the oblongata are motor, those arising from the dorsal portion and having relation to small-celled nidi are considered sensory. There would seem to be no doubt of the correctness of the function ascribed, since it is confirmed by the study of the distribution of the nerves, and, in the case of certain of them (e. g., fifth and seventh) in which the ental origin is much as in higher forms, a double confirmation can be had.

the immediate neighborhood of the large cells in this region,—the second oculomotor nidus of Osborn,—is suggestive.

Cerebellum.—The structure of this may be reviewed here. It is very rudimentary indeed in *Necturus,* consisting simply of fibers in two groups, as described by Osborn for *Cryptobranchus*; *coarse* fibers which pass up from the oblongata and turn into the mesencephal on each side of the meson ; *fine* fibers, some of which turn caudad into the metencephal, and some cephalad into the mesencephal,—thought by Osborn to be decussating tracts from the auditory nerve. The rudimentary condition of the cerebellum did not permit me to recognize the prepeduncles [1] (Bindearme), which are present in other Amphibia, and decussate cephalad of the mesencephalic pit (Burckhardt, '91).

Postcommissure.—This is well developed. Its fibers are readily followed toward the base of the brain, but soon become dispersed, some of them appearing to assume a caudal direction. Köppen ('88) states that in the frog they end in the cinerea dorsad of the *pars peduncularis.*

Meynert's bundle is a close though small tract in *Necturus.* It arises in the region of the habenas and passes caudo-ventrad to the ectal surface of the base of the brain, where it becomes diffuse, but may be traced caudad to the mesencephalic pit. Considerable obscurity has existed concerning the relations of this tract in lower forms. It is generally described as terminating in the interpeduncular ganglion ; Ahlborn however, stated that in *Petromyzon* it might be traced into the oblongata ; Osborn ('88) traced it slightly caudad of the interpeduncular nidus in *Cryptobranchus,* while Burckhardt ('91) has apparently recognized two tracts in *Protopterus,* a *fasciculus retroflexus* terminating at the ganglion interpedunculare, and a Meynert's bundle entering the oblongata. The recent application · of the Golgi method by Gehuchten ('94) to this problem (in the trout) has shown that the fibers of Meynert's bundle spring from cells in the habenas and terminate in end-brushes in intimate relation to the cells of the interpeduncular nidus.

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[1] Herrick has called these in the frog medipeduncles. In the absence of a pons this interpretation seems to me erroneous.

Supracommissure.—This is but weakly developed in *Necturus*. As described by Herrick it consists of two bundles, a cephalic larger and a caudal smaller which cross the meson independently. Whether or not the smaller one could be regarded as a *commissura habenarum* could not be determined since the two parts of the commissure joined farther laterad. In addition to a small contingent which seemed to pass ventrad into the thalamus, this tract passed ventro-laterad into the lateral wall of the cerebrum. (Fig. 28.)

Another small number of fibers, a few of them medullated, passed down from the region of the habenas into the mesal wall of the cerebrum. They did not however, seem to come from the supracommissure.

Ventral commissures.—Considerable difficulty attends the homology of the fibers which cross in the floor of the diencephal and mesencephal. Caudad and cephalad of the mesencephalic pit myelinic fibers cross the meson; those caudad are decussational, while those cephalad seemed to be decussational in part and may be, I am inclined to believe, regarded as representing the *commissura ansulata* of teleosts.

Caudad of the optic chiasma an extensive crossing of fibers occurs, the larger portion of which, at least, are myelinic, in which Herrick has attempted to find the representatives of the commissures of the teleostean brain. The larger portion of the fibers turn dorsad and then caudad to reach the mesencephal, the *commissura transversa* (*Decussatio transversa*, Edinger). I cannot agree with Herrick in the recognition of a *commissura horizontalis*; what he figures and describes as such in *Necturus*, I find to be amyelinic bundles from the thalamus which join the basal prosencephalic tract. However, I agree with him in being unable to find any trace of the " Mantelbündel " of Edinger ; a few only of the fibers which cross caudad to the chiasma turn cephalad and suggest a possible homology.

Precommissure.—This has already been mentioned in the discussion of the question of callosum. Fibers which cross in this commissure turn, some cephalad, and some caudad, representing presumably the *pars olfactoria* and *pars temporalis* of the

precommissure of higher forms. Numbers of myelinic fibers from the basal prosencephalic tracts decussate in it and also dorsad to it. Immediately above it is the callosum of Osborn, here called for distinction 'dorsal commissure.'

Basal Prosencephalic Tract.—As has been stated by Fish ('95), the fiber bundle thus designated has received various names. Of these the term applied by Edinger, 'Basale Vorderhirnbündel' seems to the writer most appropriate and the English equivalent employed by Osborn, 'basal prosencephalic tract' (*b. p. t.* of the figures) is used. The term "peduncle" employed by Herrick and Fish is misleading since these tracts are not the equivalent of the *pedunculi cerebri*, or *crura*. Were there no false homology implied, the term peduncle would still be objectionable because of the possible confusion with the peduncles of the cerebellum.

Edinger ('93, p. 31) speaks as follows of this tract: "Das Vorderhirn der Knochenfische besitzt an der Basis ein mächtiges Stammganglion, *Corpus Striatum*, ... Das Stammganglion ändert nun von den Fischen bis hinauf zum Menschen seine Lage und sein relatives Grossenverhältniss nicht mehr wesentlich. Am gleichen Orte finden wir überall die gleichgebaute Anhäufung von Ganglionzellen, überall entspringt aus ihr ein machtiges Faserbündel, das sich caudalwärts wendet und immer in Ganglien des Zwischen- und Mittelhirn sich auflöst. Es heisst basales Vorderhirnbündel und ist für Säuger seit Langem als Linsenkernfaserung bekannt." On pages 93 and 94 is given a further discussion of the representative of this bundle in the mammalian brain.

In *Necturus* these tracts may be recognized first in the caudal portion of the diencephal where the fibers which form them are rather diffuse. Farther cephalad it is augmented by several bundles of amyelinic fibers which come from the thalamus (Fig. 23) and at the level of the optic nerve it has become a well marked round bundle (Fig. 28) containing both myelinic and amyelinic fibers. Apparently few fibers come from the mesencephal, none farther caudad; a small portion also seems to come from the infundibular region. It passes into the latero-

ventral wall of the cerebrum, which has been homologized with the striatum, and there most of its fibers terminate. Some of the fibers decussate in the precommissure as before mentioned, and a number extend into the olfactory lobes. These olfactory fibers divide into two groups, one of which passes cephalad to the olfactory lobe in the ventral wall of the cerebrum, while the other bundle passes gradually laterad, dorsad and then mesad to the extreme cephalic portion of the mesal wall. These are probably those mentioned and figured by Osborn in the dorsal aspect of the brain of *Siren*.

In the cinerea of the lateral wall just caudad of the olfactory glomeruli numbers of myelinic fibers appear which pass dorso-cephalad to the mesal wall. Whether or not these constitute a tract connecting the lateral and mesal walls of the olfactory lobe, or come cephalad from the peduncles in the cinerea, could not be determined.[1]

Upon the ventral surface of the cerebrum several small fascicles of amyelinic fibers go caudad from the olfactory lobes to the region immediately cephalad of the mesencephalic groove (mammillary region?) where they turn mesad and disappear.

They undoubtedly represent a diencephalic olfactory tract and are shown in the figures as *olf. tr.* Some of these fibers decussate below the precommissure, others do not. They are shown in Figures 27 and 36 and in the transections through the regions they traverse.

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[1]Since the above was written has appeared a paper by G. Elliot Smith in the *Anatomischer Anzeiger* (Vol. X, No. 15, pp. 470-474) on " The Connection between the Olfactory Bulb and the Hippocampus," in which is discussed a direct connection in the mesal wall, of the *fascia dentata* with the olfactory lobes, which was found in the Marsupial Brain (*Platypus*), and believed by him to be represented in the brain of the higher mammals by the striae Lancisii. Should that portion of the mesal wall in the amphibian brain to which the fibers of the dorsal commissure are distributed be shown to constitute a representative of the hippocampal region of the mammalian brain, it is suggested that the above described fibers might in that case represent a direct connection between the region of the olfactory glomerules and the mesal wall. In that event, however, the olfactory lobes would be almost entirely lateral, being represented in the mesal wall only by the extreme cephalic portion.

SUMMARY.

1. As compared with certain smaller urodeles, the brain of Necturus is greatly elongated. This appears to be due largely to a greater inequality between the rates of growth of the brain and skull. This is shown, it is thought, especially by (*a*) the almost entire absence of a pons flexure, (*b*) the length of the olfactory nerves, (*c*) the extent of the diatela.

2. A callosum is considered to be entirely absent in the amphibian brain: what has been generally regarded as such is here thought to be a hippocampal commissure, in part at least, although the homology should be dependent on comparative study.

3. An olfactory tract upon the extreme ventral surface of the cerebrum may be traced to the region just caudad of the the infundibulum,—presumably the region of the albicantia.

4. The paraphysis is well developed and in communication in the adult with the encephalic cavities. The postparaphysis of some authors is not regarded as a true evagination.

5. The fiber relations in the oblongata have been investigated to a certain extent; especial attention having been paid to the posterior longitudinal fasciculus, the dorsal tracts, lemniscus and the arcuate fibers.

6. The ental origins of the cranial nerves are worked out more or less completely. For general results Tables on pages 179 and 191 may be consulted. In particular, the motor portion of the facial nerve is shown to have the same mode of origin as in the majority, at least, of vertebrates. The first two roots of the vago-glossopharyngeal group, stated to be the representative of the lateral nerve of "fishes," and the nerve termed "dorsal seventh," are composed of fibers of the same appearance and terminate in the dorsal region of the oblongata in the neighborhood of the eighth nerve.

7. Mauthner fibers were demonstrated in the adult *Nec-turus, Amblystoma* and *Diemyctylus. Amblystoma* is a land form, hence there is no direct correlation with an aquatic mode of life

8. A *ligamentnm denticulatum* is present in *Necturus.*

9. The mesencephalic pit is well marked in *Necturus.*

10.   The fourth nerve is distributed in part to the meta-plexus (or the dura).   It is possible that such fibers are sensory, although no distinct ganglion was seen.

11.   Myelinic nerve fibers from the mesencephal pass to the ectal surface of the brain immediately ventrad of the epi-physis; these may possibly represent a parietal nerve.

12.   The optic nerve in Necturus is hollow for a portion of its length and the fibers of which it is formed are amyelinic; being in both these respects in a primitive condition.

ITHACA, N. Y., June, 1895.

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* No bibliography of the brain in Amphibia is attempted.   An apparently quite complete bibliography of the literature upon the central nervous system of the *Ichthyopsida*, comprising 395 titles, is given in a paper by A. Sanders, entitled " Researches in the Nervous System of *Myxine glutinosa*," London & Edinburgh, Williams & Norgate.   1893.

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DESCRIPTION OF FIGURES.

All the figures with exception of 1, 2, 4, and 41 were outlined by the aid
of the Abbe *camera lucida.* Figs. 1 and 2 were drawn from enlarged photo-
graphs, while 4 and 41 were reconstructed from series of sagittal sections. In
the description of each figure the approximate degree of magnification is given.
In all frontal sections and transections the right side of the figure corresponds
with the right of the observer.   Myelinic fiber tracts are given in blue, amyel-
inic in black.   An especial effort has been made to indicate clearly the contin-
uity of the endyma and the concomitant circumscription of the cavities in
accordance with the precept and example of Prof. Wilder ; see, in particular,
his note on the " Morphological Importance of the Membranous or other thin
Portions of the encephalic Cavities," *Jour. of Comp. Neurology*, Vol. I., pp.
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ABBREVIATIONS.

a.—aula (mesal part of prosocœle.)

asc. V.—ascending tract of the fifth
        nerve.

asc. X.—ascending fibers of the tenth
        nerve.

a. v. c.—anterior vertical canal.

b. p. t.—basal prosencephalic tract.

cb.—cerebrum.

ch.—chiasma.

cbl.—cerebellum.

comm. tr.—commissura transversa.

cto.—commissura tecti optici.

mf.—Mauthner fiber.

m. g.—mesencephalic pit.

mlc.—myelocœle.

mt.—metatela.

mtc.—metacœle.

mtplx.—metaplexus.

m. V.—mesencephalic tract of the fifth
        nerve.

obl.—oblongata.

of.—optic fibers.

olf.—olfactory.

olf. tr.—olfactory tract (text).

dc.—diacœle.

d. comm.—"dorsal" commissure of the text.

d. e.—ductus endolymphaticus.

Dien.—diencephal.

dplx.—diaplexus.

dt.—diatela.

e. h. c.—external horizontal canal.

Epen.—epencephal.

epiph.—epiphysis.

f. c.—fasciculus communis.

gl.—glomerule.

gln.—ganglion.

hb.—habena.

hyph.—hypophysis.

infd.—infundibulum.

l.—lemniscus.

l. r.—lateral recess.

mb.—Meynert's bundle.

m. c.—Mauthner cell.

mc.—mesocœle.

Mesen.—mesencephal.

Meten.—metencephal.

on.—optic nerve.

or.—optic recess.

p.—porta (foramen of Monro).

paraph.—paraphysis.

pc.—paracœle ('lateral ventricle').

psc.—postcommissure.

plf.—posterior longitudinal fasciculus.

por.—preoptic recess.

pplx.—prosoplexus.

prc.—prosocœle (entire cavity of prosencephal.

prcs.—precommissure.

Prosen.—prosencephal.

rc.—rhinocœle.

Rhinen.—rhinencephal.

s. e.—saccus endolymphaticus.

sp.—spinal.

spcs.—supracommissure.

splx.—supraplexus.

t.—terma.

tr. a.—tract *a.* (text)

tr. b.—tract *b.* (text)

vel.—velum (transversum).

PLATE IX.

Fig. 1. The brain of *Necturus maculatus*, dorsal aspect. x 5.4.

Fig. 2. The same from the ventral aspect. x 5.4.

Fig. 3. The same, lateral aspect. x 5.4. The cranial nerves are shown but diagrammatically, as is to a less extent their representation in Fig. 1 and 2.

Fig. 4. The mesal aspect of the brain as reconstructed from sagittal sections. x 9.

Fig. 5. Latero-ventral aspect of the oblongata to show the roots of the cranial nerves. This is a reconstruction from transections and is diagrammatic; the roots of the seventh and eighth nerves are, for the sake of clearness, separated somewhat more widely than is actually the case. (See Fig. 19.)

Fig. 6. The metaplexus from the ental aspect to show the arrangement of the folds.

Fig. 7. Transection through the brain of a larval Necturus, 6-8 weeks old, at the level of the "dorsal" commissure. The precommissure appears a few sections farther cephalad. x 31.5.

Fig. 8. Transection of the brain of a just hatched larva, at the portas, to show the paraphysis. x 31.5.

PLATE X.

Fig. 9.   Transection of the myel in the cervical region near the 3rd (1st ganglionated) spinal nerve. x 22.

Figs. 10-20.   A series of transections through the myel and oblongata, to illustrate its structure and the origin of the cranial nerves ; from a series fixed in Hermann's fluid.   The nerve cells are represented necessarily diagrammatically and somewhat enlarged.   The metatela is shown merely in outline.

Fig. 10.   Transection of the myel near the second spinal nerve.

Fig. 11.   Transection at the beginning of the metatela.   x 22.

Fig. 12.   At the level of the exit of the last root of the Vagus nerve, (X[7]).   x 22.

Fig. 13.   At the exit of the first root of the Vagus (X[1]).   x 22.

Fig. 14.   At the level of the glossopharyngeus (IX[3+4]).   x 22.

Fig. 15.   At the entrance of the " dorsal ninth " (IX[1+2]).   x 22.

Fig. 16.   Transection between IX[1] and VIII.   x 22.

Fig. 17.   At the level of the seventh and eighth nerves.   x 22.

Fig. 18.   A portion of a transection in the region of the eighth nerve showing the form and relations of the Mauthner cell.   x 42.5

Fig. 19.   A transection between the seventh and fifth nerves, at the division of the " dorsal seventh " (VIIb) one branch going to the Gasserian ganglion (½ VIIb, Fig. 1).   x 22.

Fig. 20.   At the exit of the fifth nerve.   x 22.

Fig. 21.   Transection farther cephalad, at the rising of the lemniscus, and showing the lateral extensions of the metencephal, the hypophysis and *saccus vasculosus*.   x 14+.

Fig. 22.   Transection at the mesencephalic groove and the entrance of the third nerve.   Attention is called to the large cells of the mesencephalic trigeminal nidus and the fibers from the olfactory region which end in this neighborhood.   (Tr. olf.)   x 14+.

Fig. 23.   Transection at the transverse commissure showing the epiphysis and the beginnings of the peduncular tracts; also fibers joining them from the thalamus   (walls of the diacœle).   x 18+.

Fig. 24.   A transection through the cranium and ear capsules to show the relation of the endolymphatic sac to the brain.   The walls of the membranous ear are distorted, the perilymphatic space being very large.   Compare Figs. 17 and 19.   x 8.3.

Fig. 25.   A portion of a dorsal frontal section to show the paraphysis and the extension of the diacœle simulating a more caudal evagination, lined with cells differing in appearance from those of the paraphysis.   x 14.

Fig. 26.   A section slightly farther ventrad than the section shown in Fig. 25.   x 9.

Fig. 27.   A frontal section far ventrad, following Fig. 35, Plate XI.   It passes through the precommissure and the mesencephalic groove.   Just caudad of the mesencephalic groove, fibers are shown decussating; cephalad of it are fibers from the olfactory lobes.   x 6.6.

PLATE XI.

Fig. 28. Transection at the level of the optic nerves. The tract of the supracommissure is also shown passing to the lateral walls of the cerebrum. x 18+.

Fig. 29. Transection slightly caudad of the portas. Fibers are shown collecting from the caudal mesal walls of the hemicerebrum and from the diencephal to take part in the dorsal commissure, the caudal edge of which is also shown. The diatela is greatly expanded. x 18+.

Fig. 30. Transection through the precommissure and the portas, through which extend the paraplexuses, intruding from the supraplexus, which encloses the paraphysis. The fibers of the dorsal commissure appear as a bundle roofing the portas. Compare with the more caudal section, Fig. 42. x 18+.

Fig. 31. A transection just cephalad of the terma where the paracœles are limited in the mesal walls by endymal cells alone. x 18+.

Fig. 32. Farther cephalad than section 31. The cinerea reaches the ectal surface in the mesal walls. x 14+.

Fig. 33. A transection through the olfactory lobes showing the glomerules and the ectal cinerea upon the ventral and dorsal aspects in this region. x 18+.

Fig. 34. A frontal section through the prosencephal. x 6.6.

Fig. 35. A frontal section at a more ventral level. It may be compared with the preceeding and with Figs. 44 and 42 for the relations of the dorsal commissure. x 6.6.

Fig. 36. A frontal section near the ventral surface of the brain. It shows a decussation of a portion of the olfactory fibers ventrad of the precommissure. x 6.6.

Fig. 37. A frontal section through the chiasma. x 12.5.

Figs. 38, 39 and *40.* Sagittal sections through the brain, 38 the most nearly mesal. In Figs. 38 and 39 appear fibers of the dorsal commissure, in all, the transverse commissure. Fig. 39 also shows Meynert's bundle and the postcommissure. x 11—.

Fig. 41. A mesal section through the brain of a larval Necturus, 4 weeks old. Reconstructed from sagittal sections through the head. x 9.

Fig. 42. A transection through the dorsal commissure. A portion of the precommissure only is shown, so that the relations are not well represented in transection, for which the mesal section should be consulted, Fig. 4. Fig. 42 is intermediate between Figs. 29 and 30. x 9.