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THE NEURONES AND SUPPORTING ELEMENTS
OF THE BRAIN OF A SELACHIAN

A Dissertation
Submitted to the Board of University Studies
of the Johns Hopkins University for the
Degree of Doctor of Philosophy

BY

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Baltimore
1901

THE NEURONES AND SUPPORTING ELEMENTS
OF THE BRAIN OF A SELACHIAN

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With Plates I-VIII.

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SECTION 1.

INTRODUCTORY.

The student of mammalian neurology has his attention fixed on a mechanism of surpassing complexity. In the pursuit of his work, he is continually touching problems, both morphological and physiological, which frequently transcend all his powers. But the complex nervous skein which he seeks to unravel is merely the final member of a series reaching backward through ever simpler and simpler conditions to the organization of the primitive vertebrate. In other words, the mammalian brain is the product of endless modifications wrought in the original plan of structure by the continual adjustment of nervous mechanisms to the play of a shifting environment. What the architecture of the ancestral vertebrate nervous system may have been we can never hope to know from actual observation. Fortunately, there are simple vertebrates existing to-day which retain many features of primitive nervous organization. To such animals, the student of neurology must ever turn for the solution of the problems which vex him in higher fields. One of these simple vertebrates is represented by a selachian of the modern seas, somewhat specialized in certain directions,

of course, but retaining, withal, much of the archaic nervous organization from which higher brains have been gradually evolved. A study of such a simple brain as that of a selachian constitutes, therefore, a necessary introduction to the more highly differentiated nervous systems of birds and mammals.

Our knowledge of the nervous system is so peculiarly dependent upon methods of investigation that the conceptions held by us might almost be said to grow out of the technique employed. The development of neurological methods during the last few years has been indeed phenomenal, and with this advance there has come the necessity for a re-investigation of many nervous systems. The results obtained by the earlier observers, while praiseworthy in themselves, simply do not furnish the precise and complete pictures of neurones which modern comparative neurology requires. And hence it is that the writer has attacked anew the structural problems of a brain which has by no means escaped the attention of investigators. The phylogenetic value usually assigned to the Selachii has caused many to examine the brain of the shark, both anatomically and microscopically. A historical review of the latter class of researches will be found in Section II, 2.

The results set forth in this paper are intended to further exact knowledge concerning the external morphology, the internal organization, and the architectural relations of the selachian neurones, while also aiming, it is hoped, in the elucidation of certain questions of a general character. The particular sela-

chian selected, *Mustelus canis* of DeKay, is one in which are combined a structure fairly representative of the Selachii as a whole, a size convenient for work, and availability in sufficient numbers to meet the rigorous demands of certain methods of investigation.

This research was begun at the Marine Biological Laboratory of Woods Holl, where two seasons were spent in the use of an abundance of living material. The principal study was continued at the University of Iowa as my regular duties permitted; while certain collateral lines were followed in the neurological laboratory of the University of Chicago. A short preliminary notice of the most important results then in hand was published in the Proceedings of the Iowa Academy of Sciences, Volume IV. The research has finally been brought to completion in the biological laboratory of the Johns Hopkins University.

It is a real pleasure to acknowledge my indebtedness to the officials of the Marine Biological Laboratory for courtesies extending over a period of several years; and to Professor Brooks, I cannot do less than express my sincere appreciation of the numerous helpful suggestions given me during the completion of my work.

SECTION II.

REVIEW OF EARLIER RESEARCHES.

1. *Anatomical Work Involving Errors of Interpretation.*

To trace the history of a misconception is a task upon which few can enter with even the least degree of enthusiasm, but it is necessary for us to notice briefly here certain erroneous views which have held sway relative to the homologies of the parts of the selachian brain. The interbrain, and along with it the midbrain and often the cerebellum as well, have been variously interpreted by the investigators of the last three decades. Wicluclo-Maclay ('70) was the first to break away from the established teachings of vonBaer ('37) concerning the possible homologies of the several brain-segments. Overlooking, in effect, the true interbrain entirely, since he regarded it as nothing more than a longitudinal commissure, Wicluclo-Maclay identified the *zwischenhirn* in that segment which we know as the midbrain; the cerebellum, being next in the longitudinal series, consequently stood for his *mittelhirn*; while he found his *hinterhirn* in the small inferior lobe of the true cerebellum. Such an interpretation appears almost inexplicable to us, but we must not allow ourselves to forget that the homol-

ologies so confidently traced by us to day are grounded on many neurological studies, the results of which were not available to the investigators of the earlier period.

Unfortunately for comparative anatomy, the conclusions of Miclucho-Maclay were accepted by Gegenbaur, and were incorporated by him in the second edition of his Grundzüge ('70), and were continued in the smaller Grundriss ('74). Appearing also, of course, in the French translation of the former work by Voët, and in the English translation of the latter by Eell, the errors were, through these several channels, given the widest possible distribution among investigators, with all the prestige of Gegenbaur's authority behind them. Gegenbaur has rectified the mistake in the latest form assumed by his text-book ('98), but it probably will be many years before the mischief is fully undone.

Stieda ('78) devoted himself to a correction of the erroneous conceptions promulgated by Miclucho-Maclay and Gegenbaur. After carefully considering the subject-matter at issue, he embodied his conclusions in a table in which the homologies of the several brain-segments are properly set forth. The work of this author had the effect, at least, of directing the attention of anatomists once more to the fact that the homologies of the fish-brain were really in question, resulting, ultimately, in the true interpretation prevailing at the present time.

Rohon ('77), although writing several years after the

publication of Stieda's paper, did not fully accept the work of that author, but took a position almost between the errors of Miclucho-Maclay on the one hand, and the truth on the other. While giving the cerebellum its proper recognition as a brain-segment, he apparently annexed his *regio ventriculo tertii* to the forebrain, thus leaving the midbrain standing for two whole segments. His *zwischenhirn*, therefore, embraced the dorsal portion of the optic lobes above, and the hypothalamus below; while he located the *mittelhirn* between and behind these two divisions of his *zwischenhirn*. Such an interpretation was certainly remarkable for the ingenuity with which a place was found where an error might be lodged, but it was almost, if not quite equaled by the general homologies drawn by Eritsch ('73), who took the whole midbrain for a secondary *vorderhirn*.

These several errors, curious as some of them certainly are, might have little more than a passing interest for us to day, were it not that they continue to reappear at intervals, tingeing the work of those making claims to a certain degree of authoritative treatment. As an instance of this kind, it may be noted that one of our most recent treatises on comparative anatomy contains a figure of the selachian brain with the cerebellum designated *lobe ottique*, and the anterior end of the oblongata the *cervelet**.

*Roule, L; L'Anatomie Comparée des Animaux, Tome 2, Fig.1137. Paris, 1898.

2. Work on the Microscopical Anatomy of the Brain.

Anatomical work on the nervous system of the *Selachii* was begun relatively early, but microscopical study lagged somewhat behind that on the bony fishes. One of the earliest researches touching the microscopical structure of the selachian brain was that of Leydig ('52). This versatile investigator was engaged in tracing the general organogeny and histology of the rays and sharks, and so his work upon the brain was not special in its character. Here, however, he discovered the olfactory glomeruli, a result altogether sufficient in itself. Of course, the nature of the microscopical methods then in use did not permit Leydig to see much more than the general outline of a glomerulus and the fibres associated therewith. It remained for later workers to trace the full significance of his discovery.

The two decades following the research of Leydig witnessed the unfolding of the germ of a special neurological technique. Stilling had introduced the method of studying the brain by means of sections as early as 1842, but the great advantages to be derived from staining the sections were not realized until 1858, when Gerlach soaked his sections in a solution of carmine. Later, 1872, Gerlach obtained such brilliant results with gold chloride as to lead to many trials with this reagent, while some of the possibilities of osmic acid were also becoming known. Finally, chromic acid and the bichromates had come

to be recognized as valuable means for hardening nervous tissues. Fortunate that man who was permitted to contribute to the inauguration of a new era in the comparative study of the nervous system, the era of microscopical research. Two investigators extended such a possibility to the field of the selachian brain at practically the same time, Viault publishing his results in 1876, and Rohon in 1877.

The research of Viault ('72) is quite broad in its scope. It includes a review of the anatomical features of the selachian nervous system; a description of the structural elements common to all nerve-centres; topographic histology, or the structure of the several parts of the brain and cord; and, finally, a consideration of the homologies of the brain-segments. The figures which accompany the paper are perfectly clear in their execution, but they represent such a low degree of magnification that they are really little more than diagrams. While the observations recorded by this author are of the most general character, he should receive great credit for interpreting the brain-segments properly at a time when there was much confusion in this respect.

In the prosecution of his research, Rohon ('77) had all the stimulating advantages of the laboratory of Claus, and his work has a high order of merit. There is a section devoted to the comparative anatomy of the cranial nerves and the several regions of the brain, in both the rays and the sharks. Certain figures illustrating this portion of the work are familiar to

all comparative anatomists through their reproduction in the text-books. The histological portion of the research is carefully written, and it is clear that the writer had seen all that the technique of the period would demonstrate. We find in his figures, therefore, nerve-cells represented with some detail of structure, nerve-fibres showing some connection with particular groups of nerve-cells, and fibre-tracts which take a certain definiteness in their courses. The most noteworthy discovery made by Rohon was the *dachherne* of the midtrain; see Section VI. But the greatest service which he has rendered consisted in his pointing out for the first time the many structural features which the brain of the selachian has in common with the organization of higher vertebrate brains.

The next research which we have to notice is that of Sanders ('82). This author seems not to have been familiar with the great advances just made in methods of research, (see *infra*); and so we find him rejecting carmine as a staining medium and expressing a preference for rosaniline because of the clearness of the pictures yielded by it, while he gives a mere hint of haematoxylin. The scale of the work is ambitious to a degree bordering on superficial treatment. There are to be included the anatomy and histology of the brain, spinal cord, and cranial nerves in both the rays and the sharks. The histological descriptions usually embrace the general distribution of the nerve-cells of a given region, followed by exhaustive measurements of their sizes. His figures are hardly more than outlines of brain-

sections, exhibiting very little detail. His most grievous mistake lay in his refusal to apply the brilliant generalization on the pallium which Batl-Rückhard ('88) had published shortly before, rejecting it as an impossible explanation of the selachian forebrain.

We now turn to the work of an investigator whose privilege it has been to lay many of the stones for the foundation of comparative neurology. Dr. Edinger has demonstrated that it is possible to carry on research in the right way in spite of the exhausting cares of a physician's life. His earlier work ('88) includes the consideration of both the embryonic and adult selachian forebrain as a part of a systematic study of the forebrain of the several groups of vertebrates. By this time there had been given to neurological workers two of the most important methods of investigation yet imagined, the chrome-silver impregnation of Golgi, and the myelin stain of Weigert. The former has led, ultimately, to the modern conception of the neurone as a structural and physiological unit; while the latter, including here the various modifications of the essential principle, has grounded our knowledge of the course of nerve-fibres in the cerebrospinal axis. In the research under consideration, ('88), Edinger was the first to apply the staining method of Weigert to the brain of the selachian. Using a counter-stain to define the nerve-cells more clearly, his results were characterized by a precision not known to the earlier workers. The chief part of the text is occupied by a description of the

fibre-tracts, and the drawings are evidently intended to illustrate this phase of the subject alone. The nerve-cells are described as to distribution and general external morphology, so far as they are made visible by the method employed. The principal aim of the research is an elucidation of fibre-tracts rather than the investigation of nerve-cells.

In a later research ('92), Edinger applied essentially the same methods to the interbrain of selachians and amphibians, and the results have a scope similar to those just noticed for the forebrain. In the later editions of his text-book (1900) he has amplified for the comparative portion of the work the results of all his own studies, together with those of others, giving us the broadest exposition of modern comparative neurology yet attempted by any writer.

To Sauerbeck ('96) belongs the credit of first publishing results from the application of chrome-silver impregnation to the selachian brain. The paper contains a very brief description of those neurones and supporting elements which had been impregnated; by far the greater number of the structures present evidently were not demonstrated at all. The treatment is quite unequal for the several regions, and the figures are drawn on a small scale. While Sauerbeck must not be given credit for the things he neither described nor portrayed, yet a first attempt in this field is certainly to be commended.

Schaper ('98), in the course of a series of studies on the cerebellum of vertebrates, has taken occasion to apply the

chrome-silver method to the selachian cerebellum. His paper records observations with a considerable degree of detail. Reference to the results of Schaper will be made more particularly under Section V.

Inspired by the elaborate classification of nerve-cells in general promulgated by Nissl in his writings, Szczawinska ('98) was impelled to make a study of the internal structure of the selachian nerve-cell. His work presents the results of his researches upon certain types of cells through the use of methylen-blue, safranin, and haematoxylin stains. The cells studied were from the sensory ganglia, motor cells from the cord and oblongata, and cells of Purkinje from the cerebellum. Szczawinska reached the conclusion that the nerve-cells of selachians have remained on a low plane of development. In support of this view he cites certain of his results-- (1) that the cell-bodies are usually bi-polar in form; (2) that there is but slight demarcation between the cell-body and its protoplasmic processes; and (3) that the chromophile substance is less differentiated than in teleosts and higher vertebrates.

SECTION III.

METHODS OF INVESTIGATION.

The technique employed in the course of this research has covered a wide range. In fact, every process holding any promise of value has been given a careful trial. It seems desirable to describe here, however, only those methods which have contributed most largely to the final results.

1. Chrome-Silver Impregnation.

The production of a chrome-silver deposit in nervous elements is far more than a simple chemical reaction between the potassium bichromate and the silver nitrate employed. There is to be added as a prime factor, the chemistry of the nervous tissues themselves. The substances present in the nervous elements enter into the reaction to such a degree that the results are either positive or negative according to the character of those substances. In the economy of the animal, serving both as the basis for nervous activity and produced as the result of it, there is a constant round of metabolic change altering the chemical composition of the nervous tissues. In my work

upon *Mustelus*, it was soon found that strict account had to be taken of the physiological state of the animal. An individual fresh from the pursuit of his prey in the open sea gave altogether different results from one which had been kept for some time in a small aquarium, simply because the reactions of the tissues in the two instances were quite different. And so, before even fair results with chrome-silver impregnation could be secured, it was necessary to make a careful study of physiological conditions.

It was also found that selachian nervous elements lend themselves but grudgingly, at best, to the reaction desired. Numerous trials were made of the several published schemes for securing impregnation, but particularly of the procedure indicated by Golgi ('94); by Ramon y Cajal ('94); by Flechsig ('89); by Cox ('91); and by Strong ('95, '96). Every application practicable was also made of formaldehyde as a constituent of the reagents employed. A general critique of these processes has already been given by me in a former paper ('97a).

The slices of perfectly fresh brain from the most active animal procurable were placed in the "rapid" hardening mixture of Golgi. The pieces were always small, not over two millimeters in thickness for, *e.g.*, a transverse section of the forebrain. The proportion of the hardening fluid used embraced one part of 1% osmic acid to four parts 2.5% potassium bichromate, and this reagent was used in liberal quantities. The proper duration of hardening was influenced by the temperature of the

room and the physiological state of the animal, but an average length of time was three days. The greatest clearness of impregnation was secured with silver nitrate solution of 0.75% strength. In the preparation of serial sections, the most desirable clearing agent was found in a mixture of oil bergamot, oil cedar-wood, and melted carbolic acid crystals, equal parts. After being hardened in chloroform, the celloidin blocks were placed in the clearing mixture, and they were kept flooded with the oil during cutting. The above mixture clears the block rapidly, it may be used repeatedly, and it has the additional advantage of allowing the preparations to be kept in it for some time without impairing the impregnation. The sections were cut 75 micra in thickness.

2. The Application of Methylen-Blue.

Methylen-blue holds so many possibilities as a neurological reagent that we are doubtless but crossing the threshold of its use to day. I have applied this aniline in every way of which I could learn, and the most important results are set forth below.

a. The Staining Method of Nissl.-- Nissl's description of his method ('94) called for the fixation of the tissues with alcohol. This has proven an unsatisfactory part of the technique for my work. Better cytological preservation by far has

been secured through the use of the chrome-oxalic mixture of Graef ('98). This reagent appears to have escaped the general attention of microscopists, at least no mention is made of it in the fifth edition of Lee (1900). The composition is here given:

Oxalic acid, 8% aq.sol.	-	-	-	200 c.c.
95% alcohol	-	-	-	150 c.c.
Chromic acid, 1% aq.sol.	-	-	-	150 c.c.
Mix in the order as named.				

Quite small pieces of the brain were fixed in this fluid for six hours, and the fixing agent was then washed out with 70% alcohol. Sections were made by the paraffin method.

The slide was taken from distilled water, and the steaming-hot stain of Nissl was poured over the sections, five minutes. The excess stain was rinsed away with distilled water for the briefest possible time, and the water clinging to the slide was absorbed with filter paper. Differentiation with the anilin-alcohol of Nissl took but a few seconds, being stopped by flooding with oil of cajeput just as soon as the sections took on a delicate rose tint. Clearing with the oil of cajeput was aided by holding the slide for a few moments in gentle heat. Mounting was done in colophonium dissolved in xylol. The staining is remarkably precise, and the color has shown no tendency to fade.

The counter-staining methods described by Held ('95), and by Warrington ('98), were also applied, with certain modifications found necessary. The erythrosin mixture of Held

was gently warmed, poured over the slide for ten seconds, and then washed away quite thoroughly with distilled water. Staining was done with either the pure stain of Nissl, or with the same diluted with an equal volume of 5% acetone; the results did not seem to differ very much. In either case, the stain was heated and allowed to act for five minutes. Differentiation with 0.1% alum solution for just a few seconds, until the sections appeared distinctly red, was followed by a brief rinsing with water. The results given by this process have been of value as an accessory to the pure methylen-blue stain, but they are far from supplanting the original method.

b. Intra-Vitum Injection.-- The coloration of the nerve-cells through intra-vitum injection of methylen-blue was given a most thorough trial, a large number of animals being utilized for this purpose. The subcutaneous injection preferred by Meyer ('96) is not practicable for *Mustelus* because of the absence of either loose areolar tissue or of lymph spaces. The syringe was therefore inserted directly into the vascular system. A 5% solution of methylen-blue, EX brand, was injected some four times during the course of an hour. Beginning with a small quantity, the amount rose successively until as much as 30 c.c. was introduced in the final injection, making some 50 c.c. in all. This whole process was governed, however, not by fixed quantities of the reagent nor by exact periods of time, but by the stopping of the heart's action and the blue-

ness of the animal. Half an hour after the final injection, the brain was removed, cut into thin slices, and then exposed to the air until the tint had become a brighter blue. In the conversion of the unstable methylen-blue stain of the fresh tissues into the insoluble form, I have not been successful with the method recommended by Eethe ('96). The use of the picrate of ammonia as a preliminary fixer has seemed to actually impair the clearness of the final preparation. I obtained the best results with the solution given by Meyer ('96):

Distilled water	-	-	-	-	-	100 c.c.
Ammonium molybdate	-	-	-	-	-	10 grams
Hydrochloric acid	-	-	-	-	-	10 drops

Heat the first two ingredients together, then add the acid.

The pieces of brain were placed in this mixture, cooled with ice, for four hours. They were then washed with iced water for two hours. Dehydration with cooled alcohols, and imbedding in paraffin were hastened as much as practicable; in fact, it is well to have the tissues in paraffin on the same day when the injection was begun. The preparations were used chiefly for the study of the architectural relations between the neurones, and so the sections were cut quite thick.

The results given by this method are characterized by exceptional clearness, due, in large measure, to the selective coloration of certain neurones, only. The attainment of the desired end is far from constant, however. After experience had shown the rule, care was always taken to apply this technique only to those animals which had been in an active condi-

tion, fresh from the open sea, if possible. But even with this precautionary recognition of physiological conditions, so far as they could be readily determined, there apparently yet remained some unknown factor which caused a negative result in some instance where it was least expected.

8. *Iron Haematoxylin.*

This reagent was imagined by Heidenhain ('92) for refined cytological work, but it truly has a place in neurological investigation. It is a most excellent stain for defining the internal structure of the nerve-cell, and also for the tracing of nerve-fibres. For the latter purpose, iron haematoxylin has proven itself preferable in this research to the stain of Weigert, since it defines the axis-cylinder instead of the myelin, permitting fibres to be followed through their ramifications entirely to the terminal arborizations.

Fixation of the tissue may be done with any good fluid. Where the tracing of axones, only, is desired, 10% formaldehyde cannot be surpassed; but where the aim is purely cytological, either the chrome-oxalic mixture of Graf or the fluid of Flemming will give superior results. For work on axis-cylinders, celloidin sections were made 30 micra thick; and for the minute study of the nerve-cell, thin sections were cut by the paraffin method.

The sections were brought from distilled water into the

mordant of 4% iron alum for two hours. The excess mordant was then rinsed away with distilled water. Staining with 0.5% aqueous haematoxylin required at least four hours for entirely satisfactory definition. Clean tap-water was used for washing out the uncombined stain, since this appears to fix the lake more firmly. The stain was differentiated with a 2% solution of iron alum, frequently renewed. This process was observed with the microscope, and when the desired effect had been obtained, the sections were transferred to tap-water. Thorough washing at this stage is necessary to prevent fading of the stain, and the slight alkalinity of ordinary tap-water appears to be a factor aiding in its preservation.

4. The Chloride of Vanadium Method.

The technique required for staining with the chloride of vanadium method of Wolters ('90) is somewhat troublesome, but the results, when obtained, certainly justify the means. Nerve-cells, axis-cylinders, ependyma, and neuroglia are all defined in one and the same section. No other method known to me gives so comprehensive a picture for general study. Its sole value lies, however, in the purely general scope of the results.

It is hardly necessary to give a description of the process here, since its essentials are outlined in Lee (1900, p.410).

SECTION IV.

THE OBLONGATA.

1. General Morphology of the Oblongata.

In *Mustelus*, the transition of the architecture of the spinal cord into that of the oblongata is traceable with a degree of definiteness which rarely obtains in other animals. It is therefore possible to contribute toward the solution of certain problems which vex the study of this highly specialized region of the mammalian brain. Only an introductory survey of the entire field will be presented here, leaving the development of details and the consideration of special questions to the following subsections.

As the *canalis centralis* widens into the fourth ventricle, the several structures of the cord lateral to it are pushed into more and more widely divergent positions, retaining, however, essentially the same mutual relations to each other. Concomitant with this divergence, the dorsal ependyma becomes broadened to form the morphological roof of the fourth ventricle (Fig. 2, t.c.p.).

In approaching the oblongata, the ventral cornua are encroached upon more and more by commissural fibres until, just

above the level of the first spinal nerve, the mammalian hypoglossus, these nuclei disappear altogether as continuous collections of nerve-cells. A small number remain associated as the nucleus of the abducens, while the remaining neurones become scattered through the formatio reticularis (Fig.2,c.n. and t.n.)

The intermediate zone and the dorsal cornu of the cord are relatively small in size, but as the paired halves diverge to right and left of the fourth ventricle they increase in mass and assume characters and functions of a special order for each region. The intermediate gray matter contributes the lobus vagi and the visceromotor nucleus of the oblongata; while the dorsal cornu becomes specialized as the general cutaneous nucleus. We will note each of these in turn.

The lobus vagi is a longitudinal elevation in the lateral wall of the fourth ventricle (Fig.1,l.vg.). Anatomically, it is one of the most striking features of the oblongata because of the row of bead-like prominences into which its surface is thrown. The position of the structure as seen in a transverse section is represented in Fig.2, l.vg. The lobus vagi is the terminal station for communis components of the VII, IX, and X nerves; see Subsection 4. Certain of these fibres, instead of passing directly to their termination here, enter a compact bundle and run posteriorly to the spinal cord. This tract is known as the fasciculus communis. Its position in the oblongata will be seen in Fig.2, f.c.

The visceromotor nucleus is a column of large nerve-cells imbedded in the lateral wall of the fourth ventricle (Fig. 2, v.m.n.). Different portions of this column are known as the nucleus ambiguus, and the motor nuclei of the VII and V, respectively. The axones for the motor roots of the V, VII, IX, and X nerves take their origin from these nerve-cells. It is a curious fact, however, that but few of the axones pass directly into their nerve-roots, but take a course first in the fasciculus longitudinalis dorsalis. This is a massive, paired tract, the two bundles lying side by side beneath the floor of the fourth ventricle (Fig. 2, f.l.d.). There are present in the dorsal longitudinal bundle nerve-fibres from several sources. Into this crowded highway the axones from the visceromotor nucleus penetrate, to finally emerge as the motor roots of their respective nerves.

The dorsal cornu of the cord is continued into the oblongata in an enlarged condition, and it becomes associated with sensory fibres of the V, IX, and X nerves to form the general cutaneous nucleus (Fig. 2, g.c.n.). The neurones of this nucleus provide a primary termination for certain general cutaneous fibres; while others turn backward to the cord as the spinal V tract. At the posterior levels of the oblongata this system appears dorsal to all other structural features, the pair forming the rounded, crest-like margins to the fourth ventricle. Proceeding anteriorly, the nucleus is pushed into a position both more ventral and more lateral by the superposition of a

new structure, the tuberculum acusticum.

The tuberculum acusticum is shown in Figs. 1 and 2, t.a. It extends posteriorly from the restiformis along the lateral margin of the fourth ventricle some three quarters of the distance to the calamus scriptorius, tapering as it proceeds. It is separated from the general cutaneous nucleus below it by a fissure which reaches well toward the limitans interna. The outer zone of the acusticum is structurally continuous with the cerebellum; it is known as the cerebellar crest (Fig. 2, cb.cr.). The acusticum is the centre for the nerves of the lateral line sense-organs and the internal ear. Its interpretation will be considered in Subsection 7.

2. Review of Nerve Components.

A proper point of view for the structure of the oblongata can best be obtained through familiarity with the problems of the cranial nerves pertaining to this region of the brain. Reference to the text-books of descriptive anatomy will discover hardly a trace of the conceptions which dominate the modern morphology of nerves. The discovery made by Sir Charles Bell as to the character of the dorsal and ventral roots of the spinal nerves was one which represented a distinct advance in sound physiology, but the application of Bell's formula to the cranial nerves has not been productive of sound morphology. The effort to compare the cranial with the spinal nerves on the

simple basis of "sensory" and "motor" could not avoid leading to many dogmatic positions concerning the real character and ultimate distribution of many fibres. An attempt to solve such intricate problems through so mechanical a method could hardly be otherwise than faulty, particularly when applied to the specialized conditions of the mammalian nerves. A thorough study of the less modified cranial nerves of the Ichthyopsida is a necessary preparation for sound morphological work in the higher field.

The views of cranial nerves held by the neurologists of to day were founded less than a decade since, but the germ of the central idea is traceable to a somewhat earlier date. Gaskell in a series of publications ('86, '88, '89) was making the attempt to solve the metamerism of the head and the origin of the vertebrate nervous system through a study of the nerves. He took occasion to show that a spinal nerve not only embraces the sensory and motor fibres of Bell, but that its structure, distribution, and function, as well as the arrangement of its central nuclei, lead to the divisibility of the nerve into two parts. One part is somatic, innervating the external surface of the body, and the muscles derived from the muscle-plates. The other division is splanchnic, supplying the internal organs and surfaces, and those muscles which Gaskell characterizes as "derived from the lateral plates of the mesoblast". Gaskell attempted to show, further, that the cranial nerves arise from

centres homologous with the spinal centres, likewise divisible into somatic and splanchnic groups.

The impetus given by Gaskell has led, ultimately, to the modern conception that a spinal nerve embraces neurones derived from four distinct sources, with as many different distributions. There are, then, to be distinguished in a spinal nerve:

(a) Somatic motor fibres. These neurones have their cell-bodies situated in the ventral cornu of the cord, their axones emerge through the ventral root, and they are distributed to the body musculature.

(b) Somatic sensory neurones, the cell-bodies of which comprise the dorsal ganglion, and their fibres connect peripheral end-organs with the dorsal cornu of the cord through the medium of the dorsal root. These two divisions of a spinal nerve comprise the principal number of fibres in the two roots.

(c) Viscero-motor; these fibres take their origin from a group of cells, the paracentral nucleus of Onuf and Collins ('98), lying lateral to the canalis centralis; they emerge through both the ventral and the dorsal roots, and are distributed to the non-striated muscles of the viscera.

(d) Viscero-sensory neurones, from the viscera, through the dorsal root, to termination in the intermediate zone of the gray matter.

A new era in the investigation of cranial nerves was inaugurated by Strong ('95) when he made the application of these principles to larval amphibians. Strong found that it is practicable to recognize certain distinct classes of fibres or

components of the cranial nerves, which are to be distinguished from each other by their size and histological characters, by their central origin or connections, and by their ultimate distribution. Kingsbury ('97) made a careful extension of these findings to several ganoids and teleosts; while Herrick ('97, '98, '99) has traced the conditions in the bony fish *Menidia* with admirable clearness. Certain conclusions reached by Johnston ('98b) from his study of the ganoid brain stand apart from the general trend of recent work, and to these we shall return further on.

The principles developed by the researches of Strong, Kingsbury, and Herrick, may now be applied to the cranial nerves of *Mustelus*. There are to be distinguished five systems of nerve components:

a. The Somatic Motor System.-- This system of neurones is homologous with the ventral-cornu neurones of the spinal cord. The fibres take origin from cells having a ventral location in the brain, and they innervate striated somatic muscles. The only representatives of this class are the nerves of the eye-muscles, the III, IV, and VI, respectively.

b. The General Cutaneous System is so called because concerned with the innervation of the skin of the head, but it is not associated with specialized peripheral sense-organs of any kind. Its fibres are components of the V, IX, and X nerves, and they are homologous with the somatic sensory spinal fibres. The cell-bodies of these neurones lie in sensory ganglia, and

the central termination is comparable to that of the somatic sensory spinal fibres. Part of the general cutaneous fibres terminate in the general cutaneous nucleus, the homologue in the head of the dorsal cornu; see Subsection 6; but others turn into the spinal V tract and take a course posteriorly for ultimate termination in the dorsal cornu of the cord. There can be no question as to the identity of this system with the somatic sensory system in its simpler condition.

c. *The Viscero-Motor System.*-- Fibres of this system form the motor roots of the V, VII, IX, and X nerves. The cell-bodies from which the axones arise form a column of cells lateral to the fourth ventricle, known, according to the level, as the nucleus ambiguus, and the motor nuclei of the VII and V, respectively. This column of cells is the cranial continuation of the paracentral nucleus of the cord, and the homology is rendered complete by the distribution of the fibres to the visceral musculature.

d. *The Communis System.*-- This term is used in the sense defined by Herrick ('99, p. 208), and as the equivalent of the fasciculus communis of Strong ('95) as applied to the system in the tadpole, and of Kingstury ('97) as used for various fishes. Communis fibres are components of the VII, IX, and X nerves. They are wholly sensory. They innervate visceral and mucous surfaces, and also taste-buds and those specialized sense-organs of the skin (end-buds) not referable to the lateral line system. The fibres are characterized by their small

size, and they are distinguishable from other components of the same nerves by this feature. They terminate in the lobus vagi. The greater number of them in *Mustelus* pass directly to their central termination without entering the fasciculus communis, using this term in the sense as originally applied by Osborn ('88) to a definite longitudinal tract.

The communis system is homologous with the visceromotor system, the lobus vagi in which central termination occurs being the continuation into the brain of the lateral or intermediate zone of gray matter in the cord. The viscerosensory system in its original condition is, however, of far less importance than its cranial representative. The communis system not only innervates visceral organs, but it has come into relations with taste-buds and peripheral end-buds, as well. It therefore is a system having a very considerable magnitude.

e. The Acustico-Lateral System is concerned exclusively with the innervation of the internal ear and the organs of the lateral line. Its fibres are components of the VII, VIII, and X nerves. They penetrate the tuberculum acusticum for immediate termination there, or for a course farther forward into the cerebellum. The significance of the latter termination will be discussed later. The components of this system in the VII and X are to be readily distinguished from other fibres associated with them by virtue of their great diameter.

The acustico-lateral system is not represented in the spinal nerves, as the four preceding cranial systems are. The

evolution of this system is bound up with that of the peculiar series of sense-organs which it supplies. Until the evidence is more nearly complete as to the embryology and affinities of the lateral line and its nerves as a whole, we really are not warranted in making any positive assertion as to its phylogeny. Some evidence as to the possible origin of its centre will be given in Subsection 7.

3. Neurones of the Ventral Cornu.

Upon reaching the level of the oblongata, the ventral cornua of the cord become broken up as distinct collections of nervous matter. Somatic motor neurones from this source are grouped into the nucleus for the VI nerve, but elsewhere there are only isolated individuals lying between the fibres of the formatio reticularis. In an earlier paper touching this subject ('97b), I left the interpretation of these scattered neurones undecided. It is now certain that they correspond to the commissural cells and the tract-cells (vorderstrangzellen), respectively, which vonLenhossek ('94) has described from the spinal cord of the selachian.

a. Tract-Neurones.-- The ventral tract-neurones are scattered over the mid-ventral field of the oblongata on each side of the raphe ventral to the dorsal longitudinal bundles (Fig. 8, t.n.). They are to be readily distinguished from all other

neurones of this region by their size, for they are really giants. Their size is exceeded only by the neurones of the midbrain roof-nucleus described in Section VI, Subsection 2.

As to external form, the tract-neurones have a wide range; a representative individual is drawn in Fig.2, t.n. There are from three to five dendrites, and their disposition controls the shape of the cell-body to a very high degree. The dendrites may be given off at opposite extremities of the cell, in which case the outline of the cell-body is a much elongated one. The form is rounded or stellate when the dendrites are spaced at equal intervals. A dendrite is always a massive process, very wide at its base, tapering quite gradually, and reaching far out into the surrounding nervous matter. It gives origin to but few branches.

The axone always arises from the body of the cell. It runs for a short distance in the transverse plane and then turns into a longitudinal bundle of fibres on the same side of the oblongata, or even on the opposite side.

The internal organization of a tract neurone is shown in Fig.44. The cytoplasm is voluminous in quantity, investing the nucleus with a thick layer on every side. The outline of the nucleus is regular, and in form may be circular or oval. There are always a remarkably small number of coarse chromatin granules, the chromatic material being distributed in the form of a delicate reticulum. Subsidiary nucleoli are rarely present.

The cytoplasm is, as already noted, great as to actual quantity. Some neurones when stained by the method of Nissl absorb the methylen-blue equally throughout all parts of the cytoplasm, and hence they appear almost homogeneous; the significance of this fact is noted below. Other neurones in the same section exhibit a large quantity of tigroid substance; the neurone represented in Fig.44 is of this type. In the vicinity of the nucleus the tigroid-bodies are usually triangular in outline, and some of them have a very considerable size. Tigroids are found far out in the dendrites, assuming here a lenticular or even a linear form, their long axes parallel with the course of the dendrite. A finely granular axone-hillock lies at the origin of the axone. In rectangular cells, as the one figured, the hillock may be spread so widely as to assume a disk-like form. The tigroids tend to become somewhat smaller in the region of the hillock.

The tract-neurones are not demonstrated readily with either chrome-silver impregnation or the intra-vitum injection of methylen-blue. The homogeneous coloration assumed by some of them with Nissl staining has already been recorded. The character of such micro-chemical reactions indicates clearly that many of these neurones are not physiologically active, at least not all of the time. The axones from some of them may enter the motor root of one of the anterior spinal nerves, and, being in an active condition, give indications of it in a well-marked store of tigroid substance. Other neurones, however, containing

together higher and lower levels of the oblongata, have come to have their functions largely usurped by the development of more specialized tracts. Such neurones are, therefore, degraded to a far lower plane of metabolic activity, and they respond but feebly to those of our stains which depend upon the presence of definite chemical constituents of the protoplasm.

b. Commissural Neurones.-- The commissural neurones are readily distinguishable from the tract-neurones by their smaller size (Fig.2,c.n.). Commissural neurones have a wide distribution. They are scattered between the tract-neurones in the vicinity of the median raphe, and they also are to be found in all parts of the lateral region as far dorsal as the base of the general cutaneous nucleus.

The external morphology of a commissural neurone is represented in Fig.3,c.n. The cell-body is relatively small in proportion to the extension of the dendrites and the axone. The form of the cell is usually an elongated oval or an irregular triangle. The dendrites are quite often only two in number, arising from the ends of the cell. The course taken by the dendrites does not seem to be affected in the least by the tracts of fibres of the formatio reticularis, since it frequently takes them obliquely through a bundle of arcuate fibres. The dendrites are stout at their bases. They give off only a few short branches. The principal axis of the dendrite pursues a rather even course for a comparatively long distance,

tapering gradually to the end. Its surface bears but few gemmules.

The axone may arise from the body of the cell, or, when the long axis of the cell is horizontal, from one of the dendrites. It takes a course directly for the opposite side of the oblongata, giving off collaterals near its point of origin and then remaining free from them. The function of such an axone is, doubtless, commissural.

The internal structure of a commissural neurone from the right side of the oblongata is drawn in Fig.45. The cytoplasm is always far less voluminous in proportion to the size of the nucleus than in the tract-neurones. The nucleus is almost invariably oval in outline, with its major axis disposed the long way of the cell. The nucleolus is not conspicuous. The chromatic material is distributed in elongated, irregularly formed strands which lie throughout all parts of the nucleus. The several masses may be connected with each other, but only the faintest suggestion of it is indicated with the highest magnification.

The cytoplasm contains a considerable quantity of tigroid substance. A few broadly triangular tigroids are scattered round the nucleus, sometimes in the condition of nuclear caps. The greater part of the tigroid substance is to be found at the wide expanse where the cell-body merges into a dendrite. Here the form of tigroid is a greatly elongated triangle. This is replaced farther along the dendrite by spindle-shaped or

linear masses. A small axone-hillock of finely granular matter lies just within the origin of the axone. The tigroid-bodies near it are smaller and more irregular than elsewhere.

The commissural neurones, in contrast with the tract-neurones, always respond to the stains applied; this indicates a uniformly active physiological condition. Commissural neurones doubtless have a not unimportant place in the economy of this region of the brain, into which so many impulses sweep through afferent nerve-fibres to great vital centres. The chaining together of the opposite halves is precisely what we should expect to find under such conditions, and the mechanism is provided by the commissural neurones just described.

4. Lobus Vagi and Fasciculus Communis.

The lobe vagi is the terminal station for the communis fibres, components of the VII, IX, and X nerves. Its general morphology has been outlined in Subsection 1.

The structure of the lobe vagi embraces a narrow zone next to the limitans interna occupied chiefly by nerve-fibres; and a deeper part in which there are both neurones and terminating fibres. The course of the nerve-fibres will be considered later.

a. Neurones of the Lobe Vagi.-- The constituent neurones of the lobe vagi are many in number and closely crowded. They

are comparatively small in size, and are referable to type II of Golgi. The external morphology of a neurone is shown in Fig.4.

The shape of the cell-body ranges from almost triangular to broadly oval. The axone may emerge directly from the cell-body, or it may spring from one of the larger dendrites. It pursues an irregular course away from the limitans interna into the deeper levels of nervous matter. Before proceeding far, it breaks up into a widely-spread arborization such as is characteristic for neurones of this type. I believe from the course of the axones that they constitute a means for transmitting impressions to the visceromotor nucleus; see Subsection 5.

The dendrites are three or four in number. They are quite stout near their origin, they taper gradually, and they do not become very fine at their terminations. Their morphology is simple, since there are only one or two branchings at most. Their lengths may be as great as that of the axone, and so the dendrites from all of the neurones here interlace to form a veritable jungle. The surface of a dendrite bears a few gemules, together with certain small knobs and elevations of various shapes.

The internal organization of a neurone from the right lobus vagi is shown in Fig.4^a. The nucleus is always large in proportion to the bulk of the cell. In some instances there is only a thin film of cytoplasm enclosing it at certain points.

The nucleus is a more or less perfect oval, holding one or more nucleoli. The chromatin is distributed in a few thin, branching strands which give the appearance of joining in some parts of the nucleus. The chromatin never stains intensely in these neurones, and so the nucleus is represented by light coloration in the figure.

The cytoplasm lies principally in the broad areas where the cell-body merges into the dendrites. Its tigroid substance is never collected into large masses. In the region of the nucleus, the tigroid material is chiefly in the condition of medium-sized granules, with a few small triangles intercalated. The dendrites have fusiform or linear tigroids scattered at irregular intervals. A very small axone-hillock gives origin to the axone. In the specimen figured, this lies at the side of the most massive dendrite, but this location is not the rule for these neurones.

b. Termination of Communis Fibres.-- By far the greater number of the communis fibres from the VII, IX, and X nerves pass directly to their termination in the lobus vagi, a few, only, entering the fasciculus communis, described below.

Fibres penetrate the lobus vagi for ultimate termination chiefly from the dorsal side (Fig. 2, c.f.). They reach this position by a sweeping curve which carries them to an ever higher level as they run inward from the exterior. These incoming fibres constitute a thin stratum next the limitans inter-

na, the neurones lying just beneath. The final arborization occurs near the body of some neurone. It is of a narrowly branching type, with fine, bristle-like twigs terminating the branches (Fig.4,c.f.).

c. *The Fasciculus Communis*.-- This remarkable tract was given the name it now bears by Osborn ('86) in recognition of the common relationship of several cranial nerves to it. Various authors had noticed the fasciculus communis previous to this time, but they had failed to grasp its significance. Stieda ('78a, p.429) had noted the presence of such a bundle in the spinal cord of the selachian; while Bohon ('77, p.42) described it from the selachian brain under the name *fasciculus longitudinalis lateralis*. The latter writer conjectured that it might pertain to the tegmental system.

In *Mustelus*, the fasciculus communis is a very sharply defined tract extending posteriorly from the VII nerve into the spinal cord, where it lies close beside the gray matter dorso-lateral to the canalis centralis. Its position in the oblongata is shown in Fig.2, f.c. During a part of its course, the visceromotor nucleus is traversed by it. Some of the communis fibres, instead of pursuing a course to the lobus vagi for termination there, turn downward into the fasciculus communis. Thence they are carried posteriorly into the spinal cord for their ultimate distribution.

From the account given by Strong ('95) of the fasciculus

communis in amphibians; and by Herrick ('99) for the bony fish, I conclude that this tract is developed in *Mustelus* to a conspicuously less degree. The significance of this smaller size for the brain of the selachian is not clear. The communis fibres are essentially viscerosensory, but there have been annexed to the system certain external sense-organs, such as taste-buds and end-buds. There are no observations indicating marked differences between the visceral connections of this system in *Mustelus* as compared with teleosts and amphibians. In fact, the archaic value and deep-seated physiological importance of such connections in all vertebrates would lead us to infer a considerable similarity in related groups. We thus appear to be thrown upon the more recent additions to the system for the explanation. It seems to me that a comparative investigation of end-buds and taste-buds will contribute much toward the solution of questions pertaining to their central tracts.

5. *The Viscero-Motor Nucleus.*

The adoption in this paper of the name visceromotor nucleus expresses the need for a general term which shall include all members of the morphologically continuous column of cells giving origin to the motor fibres of the V, VII, IX, and X nerves. This nucleus is the continuation into the oblongata of the paracentral nucleus of Onuf and Collins ('98), and the

components having their origin here innervate viscera.

The nucleus is composed of quite large neurones. The only larger ones in the oblongata are the gigantic tract-neurones described in Subsection 3, a. The cells are arranged in a compact cluster, as seen in transverse section, and this is traversed during a part of its course by the fasciculus communis. Fig. 2, v.m.n., illustrates the disposition of the neurones and their characteristic forms.

The cell-body has its form influenced by the number of its dendrites, ranging from triangular to stellate. The dendrites are always several in number. They are massive processes, often arising through such wide bases that it is difficult to say where the line of demarcation between dendrite and cell-body should be drawn. The dendrites branch freely, and the closeness with which the neurones are arranged gives, therefore, a most complicated tangle of interlacing branches.

The internal organization of a visceromotor neurone is represented in Fig. 47. The nucleus is central, or only slightly eccentric, and it has an evenly rounded contour. The nucleolus is large; there is rarely a subsidiary nucleolus. The nuclear reticulum has a coarse mesh which exhibits great clots or lumps of chromatin at the points of intersection.

The cytoplasm contains tigroid-bodies of various sizes. The largest masses lie in the field of the nucleus. The ones next to the nuclear membrane may assume the form of nuclear caps. At the periphery of the cell, the prevailing form of

tigroid is much elongated. It lies parallel with the margin of the cell. Tigroid masses are continued far along the dendrites, even into the tertiary branches. They are disposed parallel with the course of the dendrites.

In that side of the cell from which the axone arises, the tigroids have a special arrangement. The axone-hillock (Fig.47, ax.h.) is an oval mass of finely granular material, and the tigroid-bodies are packed rather densely round it. The form of tigroid is also less elongated here, merely an irregular lump.

The axone arises directly from the body of the cell. While it is destined to ultimately be a component of either the V, VII, IX, or X nerves, it generally takes quite an indirect course. The usual way is through the medium of the fasciculus longitudinalis dorsalis. An axone passes into this bundle to finally emerge at some other level. In Fig.47, the axone passes dorsal to the fasciculus communis. There is a bundle of fibres of considerable size lying here, composed chiefly of axones which have emerged from the dorsal longitudinal bundle to enter the nerve-root. Other axones, but these are few in number, may enter the nerve directly. Still others pass into a bundle of arcuate fibres and doubtless enter the nerve on the opposite side. These several paths to the nerves are shown in Fig.2, v.m.f.

The visceromotor neurones have an internal structure which is conspicuously motor in character, the large amount

of tigroid substance representing much expenditure of energy here. The large size of the neurone is evidently the correlative of the importance which the system assumes in the innervation of great vital organs. Such innervation requires a nexus with viscerosensory neurones, and the means have already been suggested in the preceding subsection, the interlacing of the axones from the lobus vagi with the dendrites of the visceromotor nucleus. This gives a complete reflex circuit for visceral innervation.

6. *General Cutaneous Nucleus and Spinal V Tract.*

The literature of the portion of the oblongata included here is in some confusion. The older writers did not have methods of investigation which would demonstrate the presence in this region of several important groups of neurones. They did see that it contains numerous bundles of nerve-fibres, however, some of which run to the cerebellum, and so *pedunculus cerebelli* appeared to be a perfectly satisfactory designation. Kingsbury ('97) extended the term *spinal Vth tract* to both the nuclei of the region and the trigeminal fibre-tract proper; such use of a term originally intended to designate a definite group of nerve-fibres is certainly to be avoided as leading to confusion. Johnston ('98b) appears to include a part of this region under his *tuberculum acusticum*. Since there appears to be need for a precise term which shall design-

nate the several nuclei of the general cutaneous system, I therefore propose that the whole be called the general cutaneous nucleus.

The general cutaneous nucleus is the continuation into the oblongata of the dorsal cornu of the spinal cord, and it carries its associated tracts with it. Its position will be seen from Fig.2,g.c.n. In structure, it is indeed complex, embracing as it does, three groups of neurones, large numbers of nerve-fibres intercrossing in several directions, the spinal V tract, and many supporting elements. The intrinsic neurones will be considered first.

a. The Molecular Layer.-- The molecular layer appears in a transverse section as a dorsal cap to the other constituents of the nucleus (Fig.2,x.1.). It is seen to be continuous with the cerebellar crest of the tuberculum acusticum.

The neurones of the molecular layer are of two varieties, the molecular neurones and the neurones of Purkinje. Both of these varieties are identical with those described in Subsection 7 for the tuberculum acusticum; their morphology will therefore not be given here.

As to distribution, the minute molecular neurones are found scattered through the whole thickness of the molecular layer. The Purkinje neurones, on the contrary, lie only in the deeper part of the layer, sending their great dendrites into the upper levels. The possible phylogenetic significance of the presence of the molecular layer in this part of the

brain will be treated in the theoretical considerations of Subsection 7.

b. *The Substantia Gelatinosa*.-- The gelatinous substance of Rolando is continued from the spinal cord into the oblongata. It takes on such an intimate relation to the terminating nerve-fibres here that Barker ('99) has proposed to call it the *nuclei tractus spinalis nervi trigemini*. The Rolandic substance occupies a position high up in the dorsal part of the general cutaneous nucleus, just beneath the cap of the molecular layer, and itself forming an investment for the bundles of fibres and larger neurones of the central mass. The complexity of its structure, and the difficulty of staining it with the usual reagents are facts well known to microscopists. The nerve-cells of Rolando's substance in the spinal cord have been studied by vonLenhossek ('94) from man, the pig, and the mouse; while Ramon y Cajal ('96) has given us an elaborate description of the oblongata of the mouse. It gives me great pleasure to be able to extend our conceptions of this peculiar formation to the field of the brain of selachians.

In *Mustelus*, the structure of the substantia gelatinosa foreshadows to a remarkable degree the organization which has been described for the higher vertebrates. The neurones are associated in groups; a representative collection is drawn in Fig.5. The axones and dendrites branch profusely and interlace so closely that the simulacrum of a fine network is given. In

this tangle, certain nerve-fibres of the general cutaneous system terminate. Such a fibre is shown in Fig.5,g.c.f.; its arborization may be distinguished from the tangle of neurones in which it lies by the somewhat greater size of its terminal twigs.

The neurones of the substantia gelatinosa, considered morphologically, are of three varieties, all of which are represented in Fig.5. The one that is present in greatest numbers, giving character to the formation as such, is of quite minute size, and is an extreme example of Golgi's second type (Fig.5,a. The cell-body is very small, polygonal in form, and there are a few short dendrites. The axone ramifies immediately into an extremely complex series of branches, constituting the principal member of the tangle mentioned in the preceding paragraph. These axones are strikingly conspicuous structures when successfully impregnated with chrome-silver.

A second form of neurone is considerably larger in size. its dendrites enter into the tangle referred to, instead of its axone. From a polygonal cell-body, some three or four dendrites radiate indifferently in all directions. The dendrite is of fine calibre, and it branches repeatedly into ever finer twigs. The branching of this system is far less profuse, however, than that of the axone of the first variety described. The difference will be readily seen by reference to Fig.5,b. The axone takes a course out of the gelatinous substance into the deeper parts of the nucleus. It gives off a number of

long collaterals during that part of its course lying in the substantia gelatinosa.

The two kinds of neurones just described evidently constitute the physical basis for the central reception of general cutaneous impressions. The first variety, with its short axone, is so concerned entirely, it would seem; while the second one described, having its axone proceeding to deeper regions, is probably involved to an equal degree in both the reception of impressions and in their distribution to deeper levels.

Still a third type of neurone remains to be described (Fig.5,c.). From an oval cell-body, a few sparsely branching dendrites arise which lead far out into the surrounding field. The axone takes a course into the deeper nervous matter, giving off only a few collaterals. This form of neurone is found outside the margins of the groups, and apparently is purely associative in function.

c. The Deeper Neurones.-- The deeper parts of the general cutaneous nucleus are occupied by fibres having courses in several different directions, and by the bundles of the spiral V tract. Neurones are scattered at intervals between the nerve-fibres, with a somewhat more closely crowded area just dorsal to the lobus vagi. Neuroglia is especially abundant in all parts of the nucleus, providing a support for the intricate maze of nervous structures.

The external morphology of a neurone from the middle region of the nucleus is shown in Fig.6. Such a neurone is considerably larger in size than any neurone from the substantia gelatinosa. From an elongated-oval or triangular cell-body, three or four dendrites proceed straight outward into the tangle of nerve-fibres and neuroglia. A dendrite is a rather stout process. It has but few branches, and these are of small size. Its surface bears scattering gemmules and minute knobs.

The axone takes its origin directly from the cell-body. It runs in a medio-ventral direction.

Two neurones stained with methylen-blue are represented in Fig.48. These are from the median collection just dorsal to the lotus vagi. The nucleus of such a neurone is proportionately quite large. It is also eccentric in its position, consequently cells are often found in which the nucleus appears to be in direct contact with the cytoplasmic pellicula at some point. The nucleoli are of some prominence. The chromatic material is also conspicuous. It is distributed in branching strands of some thickness in places, and the several strands may have slight connections.

The cytoplasm is often practically absent at the side of the nucleus. The dendrites are so thick, relatively, at their bases that the greater part of the cytoplasm appears collected in them. The tigroid substance is most abundant in the vicinity of the nucleus. The individual masses here are usually irregular in form and quite small in size. In the basal parts

of the dendrites, the tigroid-bodies become elongated. These do not reach far along the dendrites, however.

d. Termination of General Cutaneous Fibres.-- The nerve-fibres of the general cutaneous system are distributed to the skin of the head without the intervention of specialized nerve-endings. This sensory system has components in the V, IX, and X nerves. There are two principal central stations for these fibres: the general cutaneous nucleus, and the dorsal cornu of the spinal cord through the medium of the spinal V tract. The two termini are really not essentially different, however, since the general cutaneous nucleus and the dorsal cornu are morphologically continuous structures.

Fibres which have their termination directly in the general cutaneous nucleus may pass into their arborizations in relation to each of several groups of neurones. What is probably the chief mode of termination is shown in Fig. 5, g.c.f., where the fibre is seen entering the tangle of the substantia gelatinosa. At no other point in *Mustelus* is there such a bewildering maze of nervous processes as that presented by the neurones here. So far as structural features may be interpreted, it would seem that the substantia gelatinosa is well adapted for the reception of the most delicate sensory impressions. The large number of arborizations found here indicates the real importance of the group.

Terminations are also to be traced in connection with the

deeper neurones of the nucleus. In Fig. 8 there is shown an incoming nerve-fibre, g.c.f., breaking up into its arborization near one of these neurones. The arborization is of the broadly digitate variety, spreading the disturbance over some slight area. The scattered distribution of the neurones at this point is doubtless a correlative of this fact.

Finally, the molecular layer which caps the whole nucleus contains many fibres of quite minute size. This level, with its small branching neurones, and the dendrites from deeper zones, may serve to distribute impressions superficially.

Turning to the spinal V tract, this is a series of bundles of fibres which run posteriorly to the spinal cord. The bundles are scattered through the deeper part of the general cutaneous nucleus; refer to Fig. 48, sp.V. General cutaneous fibres may enter the nucleus directly from the nerve of the same side, or through the medium of the arcuate bundles from the opposite side. They may terminate at once in the nucleus, as described above; or they may turn into the spinal V tract for termination farther posteriorly. Some of those present in the tract are doubtless branches of fibres which have terminated in part in the nucleus. The spinal V tract, then, is a means for carrying great numbers of sensory nerve-fibres from cranial nerves to the dorsal cornu of the spinal cord, giving them a second and far wider hold.

The manifold central terminations of the general cutaneous system must have a significance, if we can but interpret

the facts. The system is, primarily, a tactile apparatus for the head. Any one who has watched *Mustelus* exploring with his snout every corner of a new aquarium cannot doubt that tactile impressions from this region must have a large place in the life of the animal. With practically no other check upon his visual sensations than can be derived from poking his nose into things, widely spread central terminations of cutaneous fibres is no more than should be expected.

7. *The Tuberculum Acusticum.*

The tuberculum acusticum is the *trigeminal lobe* of Viault ('72), Bohon ('77), and Sanders ('83); Kingsbury ('97) has extended the term *ceretellar crest* to the entire structure; while Johnston ('98b) appears to include under his *tuberculum acusticum* all those structures in the oblongata which are homologous with the dorsal cornu of the spinal cord. The term *trigeminal lobe* has been so variously used that it should be dropped from our nomenclature. The earlier writers on the brain of the selachian so designated the tuberculum acusticum, supposing, erroneously so, that the great trigeminal complex, which emerges just beneath its anterior end, must have the origin of its nerve-roots here.

The tuberculum acusticum is the primary terminal station for the acustico-lateral system. Fibres from the lateral line sense-organs and the internal ear are components of the VII,

VIII, and X nerves.

The structure of the tuberculum acusticum embraces a medio-central core in which bundles of nerve-fibres predominate; and an outer investing cap, the cerebellar crest (Fig.2,cb.cr.). The latter, in its outer levels, is morphologically continuous with the molecular layer of the cerebellum, so that the term *molecular layer* is very properly applied here. The neurones of the tuberculum acusticum lie chiefly in the cerebellar crest, with just a few, also, in the central core. Three varieties are to be distinguished: Purkinje neurones, granular neurones, and molecular neurones. I have so designated them because each is the equivalent in every way of the element bearing such a name from the cerebellum.

a. Molecular and Granular Neurones.-- The molecular and the granular neurones do not call for any extended description here, since they are directly comparable with the cerebellar representatives described at length in Section V.

The molecular neurones are the most numerous of the three varieties peculiar to the tuberculum acusticum. They are found scattered throughout the molecular layer, most abundantly in the deeper levels. Each has the characteristically small cell-body with slender dendrites radiating from it.

The granular neurones are far less numerous. They lie just within the base of the molecular layer, but there are not enough of them to form a distinct zone. Stained with

methylen-blue, they exhibit the typical dense nuclear structure and the small amount of cytoplasm.

b. Purkinje Neurones.-- The phylogenetic interest attaching to the presence in the oblongata of these elements calls for more special notice. The Purkinje neurones of the tuberculum acusticum are not disposed in any regular order. They lie scattered between the deeper molecular neurones, and they are also found among the granular neurones. Their dendrites are always directed toward the limitans externa, whatever the situation of the cell-body may be, although the exact course may be at a considerable angle to the perpendicular. The axone always passes inward. Refer to Fig.2, t.a.

The cell-body is slightly oval or even perfectly circular in outline (Fig.7). The particular form assumed appears to be correlated with the position of the dendrites. The gnarled character of a dendrite is quite evident. There are three or four of them, terminating in blunt tips. A dendrite bears few branches, or none at all, and its surface is studded with numerous thorny gemmules of various sizes, some of them quite large.

The axone arises from the internal border of the cell. It takes a ventral course through the intervening nervous tissue into a bundle of arcuate fibres. Its ultimate distribution has not been definitely followed.

The internal structure presents a large nucleus with deeply staining chromatin in the form of a reticulum; and cytoplasm

somewhat less in quantity than in the cerebellar neurone, and holding less tigroid substance.

From the above description of the morphology of the neurone of Purkinje from the tuberculum acusticum, it will be evident that it is strikingly like its earlier-known representative in the cerebellum. Compare, also, Fig.7 with Fig.13. The neurone from the tuberculum acusticum (Fig.7) is merely slightly smaller in size, with a dendritic top which branches somewhat less. The presence of conspicuous gemmules is characteristic of both. We shall take occasion to point out further on that the cerebellar neurone is to be regarded as the more fully developed derivative of this element from the oblongata.

c. Termination of Acustico-Lateral Fibres.-- The fibres of the acustico-lateral system enter the tuberculum acusticum through the medium of the thin neck joining the acusticum with the general cutaneous nucleus below. This fact is expressed in Fig.2, a.l.f. It appears, so far as they are traceable, that these fibres have passed over from the opposite side in the arcuate bundles. Penetrating the core of the acusticum, the fibres are at first associated in groups, but these soon become dissolved and the individual members spread through the outer levels. The fine terminal branches pass through the thorny dendritic tops of the neurones of Purkinje, and the final arborizations are to be frequently observed near the

bodies of the Purkinje cells. Such a termination is shown in Fig.7, a.l.f. The nerve-fibre divides at some distance from the cell into several twigs, and from the portions of those nearest the cell-body several small terminal twigs arise which form an arborization quite near to the cell. There is given in this way a direct nexus between the acustico-lateral fibres and the most conspicuous neurone of the tuberculum acusticum. Other fibres of minute size evidently terminate in the molecular layer between the small molecular neurones. Even here there would be an indirect connection with the Purkinje neurones, for these send their dendrites into the molecular layer.

Fibres are also to be seen in numbers which do not terminate in the tuberculum acusticum at all. Some of these remain in the central core, continuing anteriorly; while others are branches of fibres which have taken a course into the acusticum for partial termination there. All of these pass upward to the cerebellum; they will be duly considered in Section V.

1. Theoretical Conclusions.-- It has already been pointed out that acustico-lateral components are not present as such in spinal nerves. Waiving the question of the origin of the system as a whole, it will not be out of place to consider here certain problems relative to its primary centre, the tuberculum acusticum.

The position which the tuberculum acusticum occupies in the oblongata is indeed significant, superposed, as it is,

on the cranial representative of the dorsal cornu, the general cutaneous nucleus. This fact can only be taken to mean that the tuberculum acusticum is phylogenetically the younger of the two structures in question. In Subsection 8 it was shown that the general cutaneous nucleus has the archaic structural features of the dorsal cornu capped with a molecular layer continuous with the cerebellar crest of the acusticum; and that there are present here both the molecular cells and the neurones of Purkinje. Now this structural continuity may signify that the acusticum has been derived from the general cutaneous nucleus in the phylogeny of the vertebrate nervous system. Of course it will be necessary to have a thorough study of the embryology of this region in the lower vertebrates before such a conclusion can receive unqualified support. Then, too, the rise of the tuberculum acusticum has been but one feature in the evolution of the lateral line system as a whole, and so we may confidently expect some assistance from the further study of the affinities of its sense-organs.

There is somewhat more solid ground for the belief that the tuberculum acusticum has itself given origin to a very important region of the brain, the cerebellum. The full evidence on this point will be presented in Section V, Subsection 8.

8. Supporting Elements.

a. *Ependyma*.-- The ependyma of the oblongata constitutes the membrana limitans interna throughout, of course, but the degree of differentiation covers a wide range. The simplest condition is found in the tela choroidea, for the cells here do not give origin to ependymal fibres. This might be called the epithelial phase of development.

The first step in the differentiation of ependyma occurs in the dorso-lateral region of the oblongata, embracing the tuberculum acusticum and the adjacent part of the general cutaneous nucleus. The ependymal cells are rather narrow here, giving a larger number per surface area. From the tip of each cell, a very slender ependymal fibre pushes its way through the nervous matter to the limitans externa. The fibre does not branch, and its general course is a straight one, although the details of its path are very irregular indeed, sharp turns of small size occurring along its whole length. While the diameter of the fibre as a whole is quite slender, its size is increased at irregular intervals by beads and small knobs. Consult Fig. 8.

A slightly more advanced condition is to note for the ependyma of the ventral region. The ependymal cells in the floor of the fourth ventricle are larger than those described above, and their fibres are also much stouter. The general course of these fibres is shown in Fig. 2, ep.; and the details of two fibres are given in Fig. 9. It is to be noted that the

fibre extends entirely to the limitans externa, that it bears no branches, that its course is free from sharp turns, and that its diameter is varied by nodes and thickenings of various shapes and sizes. Groups of these fibres form radiating bands through the formatio reticularis, and their evident purpose is to provide stays for the vast number of longitudinal and arcuate nerve-fibres which characterize this part of the oblongata.

The ependyma attains its highest differentiation in the lobus vagi; see Fig.10. The fibres do not reach the surface, and they give origin to a most complicated series of branches at the level occupied by the neurones of the lobus. The proximal part of the fibre is quite stout and somewhat irregular in its course. The distal part becomes dissolved in branches, the terminal twigs of which are minute. The interlacing branches form a support for the neurones and nerve-fibres proper to this region.

b. Neuroglia.-- The neuroglia of the oblongata is, like the ependyma, present in great diversity of form, but the various elements are referable to two general classes. One, the well-known astrocyte, is distributed in every part of the oblongata where there are nerve-fibres in numbers-- in the roots of nerves, in special tracts, in centres where many fibres have their termination, and in the formatio reticularis. The special form of the astrocyte depends, to some extent at least, upon the density with which the nerve-fibres are arranged. At points

where there has been little pressure, the rounded form of the cell-body may be retained (Fig.3,ng.). In certain closely packed tracts, the cell is squeezed into lenticular form. In centres where many minute fibres interlace, there may be hardly any body to the cell at all, the matter being chiefly in the radiating processes (Fig.11). In every instance, the processes exhibit tortuous irregularities due to their insinuation between the nerve-fibres among which they lie.

Another type of neuroglial cell appears to be characteristic of the ventral part of the oblongata, occurring in some numbers in the formatio reticularis (Fig.3). The cell-body is large, elongated, with great processes emerging from its ends and a few smaller ones from its sides. The large processes take a course in the radius of the oblongata. They give origin to secondary and tertiary branches, the finer ones of which lie at right angles to the course of the principal branch. The whole system does not spread widely, but has the appearance of compression in one plane.

The astrocyte is evidently an important supporting element for the individual nerve-fibres between which its processes twine. The second class of neuroglial cell described seems to be adapted to the supporting of bundles of nerve-fibres. The arcuate fibres of the formatio reticularis pass in groups through the spreading brush of such neuroglial processes and are thereby given support.

9. Summary of the Oblongata.

The structural features of the oblongata of *Mustelus* may be homologized with those of the spinal cord to an unusual degree of clearness.

The ventral cornu is represented by the nucleus of the VI nerve, and by the scattered commissural and tract-neurones of the formatio reticularis.

The lobus vagi is, morphologically, the centre of the viscerosensory system, but there has been annexed to it a complex of peripheral sense-organs. It has come to be, therefore, the centre for the entire communis system, components of the VII, IX, and X nerves. Endings are found related to neurones of the Golgi II type. These send their axones toward the visceromotor nucleus. Fewer fibres of the system enter the fasciculus communis than in either the teleosts or the amphibians.

The visceromotor nucleus is the representative of the paracentral nucleus. It is a morphologically continuous column of cells giving origin to the motor fibres of the V, VII, IX, and X nerves innervating viscera. The axones do not enter their nerve-roots directly, as a rule, but through the medium of the fasciculus longitudinalis dorsalis. Some appear to cross to the opposite side. Dendrites from the nucleus come into relation with axones of the lobus vagi.

The general cutaneous nucleus is the homologue of the dorsal cornu. It is the primary centre for the general cuta-

neous components of the V, IX, and X nerves. The substantia gelatinosa contains groups of small Golgi II neurones forming dense, felt-like tangles; many terminal arborizations are found in these. Other terminations occur near larger neurones lying in the deeper parts of the nucleus. Many fibres of the system do not terminate in the nucleus, but are carried posteriorly as the spinal V tract for ultimate termination in the spinal cord.

The tuberculum acusticum is a phylogenetically young structure, not derivable from the cord directly. It is the primary centre for the acustico-lateral system, components of the VII, VIII, and X nerves. There are present, neurones of the molecular, granular, and Purkinje types, identical with those of the cerebellum. Terminations occur in the molecular layer, and near the neurones of Purkinje. The Purkinje neurones send their axones ventrally in the arcuate bundles. The cerebellar crest is morphologically continuous with the cerebellum. There is ground for believing that further investigation will derive the acusticum from dorsal cornu structures.

Supporting elements are present in the oblongata in great numbers. There is traceable a wide range of developmental forms of both neuroglia and ependyma.

SECTION V.

THE CEREBELLUM.

The cerebellum of *Mustelus* is of large size in comparison with the adjacent brain-segments. In the adult animal, it is of sufficient longitudinal extension to overhang the larger part of the midbrain in front, and also much of the oblongata behind (Fig.1,cb.). The base is only a third as great, however, indicating the smaller prototype from which the organ has been evolved. In fact, this cerebellum occupies an intermediate position in the phylogenetic scale, standing midway between the simple plate-like cerebellum of the cyclostome, the dipnoan, or amphibian, and the solid mass with radiating laminae characteristic of the mammal. It is essentially a great bulbous dilatation of the dorsal side of the neural tube, the wall of which has been thrown into folds as the process of growth thrust the vesicle against the unyielding and more slowly expanding cranium. So, instead of a solid central mass of nerve-fibres covered with layers of gray matter, we find in *Mustelus* a hollow organ, the fourth ventricle extending freely into it and ramifying through its several folds. The folds, therefore, are simply doublings in the cerebellar wall, and

are fundamentally different from the solid laminae familiar to us in higher vertebrates.

The arrangement of the structural elements of the cerebellum is readily followed, for in no other part of the brain are distinctions more clearly marked. Superficially, there is the molecular layer (Fig.12,m.l.); the granular layer lies next to the ventricle, or is separated from it only by the basal fibres (Fig.12,g.l.); between the two, there is the layer of Purkinje (Fig.12,p.l.).

The nerve-fibres of the organ are found in two well-defined groups, the basal fibres and the median fibres. The basal fibres (Fig.12,b.f.) enter the posterior region from the oblongata and soon become dissolved in the outer layers. These fibres lie next to the ventricle, and they supplant the granular layer entirely during their course, or at least displace it quite largely. The median fibres are disposed in scattered bundles which lie in the outer part of the granular layer just beneath the cells of Purkinje. The bundles take two general directions: transverse, (cut across in Fig.12,m.f'); and longitudinal, extending parallel with the structural zones (Fig.12,m.f.).

1. The Neurones of Purkinje.

The neurones of Purkinje are the largest, and by far the most impressive structural elements of the cerebellum. Their

cell-bodies are disposed in a thin stratum intercalated between the molecular and the granular layers. At those points where the granular layer is absent, the Purkinje cells come into direct contact with the layer of basal nerve-fibres, instead. As to superficial distribution, the neurones follow a well-defined rule (Fig.12,p.1.). They are most numerous on the sides of a cerebellar fold, often several cells in depth here, and not infrequently having their cell-bodies in contact. At the summit of the fold, there are wider spaces between the individual cells; and for a small space at the bottom of a fold, the cells are absent altogether. The posterior fold of the cerebellum has a part of its area without Purkinje neurones.

Fig.13 illustrates the features of external morphology characteristic of a neurone of Purkinje. The cell-body is situated, as already noted, at the base of the molecular layer. The dendrites, therefore, grow upward into the molecular layer, and to their presence here is due, in part, the marked striation perpendicular to the surface which is so characteristic of this superficial zone.

The axone always arises from the base of the cell-body, and it pursues a horizontal course for some distance. It then turns downward through the granular layer to enter the system of fibres leaving the cerebellum. Where the granular layer is absent, the axone may be traced into the layer of basal fibres for a still greater horizontal course. The axone is remarkable for the fact that it does not give off collateral branches.

The cell-body appears to have its form determined quite largely by the number and disposition of the dendrites arising from it. It may be rounded, oval, or even triangular in outline. The longer axis of the cell, while usually perpendicular to the surface of the fold, may be oblique or still farther tilted over from the orientation characteristic of it for the higher vertebrates. Even the size of the cell is influenced by its position. The diameter is greatest in those cells lying at the part of the fold where the side curves abruptly into the summit. On the sides of the fold, the size is remarkably less, and the dendrites pass outward at a wider angle, often causing the cells here to assume a horizontally elongated form. The cell studied by Szczawinska ('36) evidently was of this latter type.

The internal structure of the Purkinje cell is demonstrated less readily with methylen-blue than is the case for most nerve-cells of *Mustelus*. In successful preparations, however, the cytoplasm is found to hold tigroid masses of triangular or spindle-shaped form. These bodies are neither large in size nor many in number. There are always several of the greatest diameter arranged near to and concentric with the nuclear membrane. The thick bases of the dendrites have small, narrow, lenticular tigroids distributed sparingly as far as the level of the first great branches. The character and distribution of the tigroid-bodies will be seen by reference to Fig.49.

The nucleus of the cell lies in a basal position, but it

is always bordered by some little thickness of cytoplasm. The form is oval or circular, with an almost even contour. There is one large nucleolus, with a subsidiary nucleolus in some cells. The nuclear reticulum has a rather fine mesh; large granules of chromatin occur at the points of intersection.

The dendrites arise from the peripheral side of the cell-body, and they pass at once into the molecular layer, taking a direct course for the limitans externa. The size of a dendrite is maintained without marked diminution, the tip, in fact, being so large and blunt as to give a club-like appearance to the whole process. The mode of branching is far simpler than that of the corresponding mammalian neurone. While the dendrite of the latter ramifies to an extraordinary degree, it is rare to find branching carried beyond the tertiary divisions in *Mustelus*; compare my Fig.13 with Plates 14 and 15 of Starr's Atlas ('96). From its greater simplicity, the selachian neurone of Purkinje corresponds, in a broad way, to the embryonic condition of the higher form. The branches are spread in one plane, like a plant trained on a wall, and this plane lies transversely to the cerebellar folds. The course of the branches in this plane is less wide than for mammals, causing the whole top to present a markedly more compact appearance. The surface of a dendrite has the conspicuous roughness characteristic of this neurone wherever found. The gemmules, to which this roughened surface is due, are of several different sizes, ranging through mere points through slender spines and stouter

thorns to knobs and mushroom-like excrescences which rise far above the general level. The extent of receptive surface of the entire dendritic series is thus increased to a very considerable degree.

The part which the neurone of Purkinje takes in the economy of *Mustelus* will be discussed in Subsection 5.

3. The Molecular Layer.

This is the external layer of the cerebellum (Fig.12,m.l.). It conforms throughout to the contour of the several folds into which the cerebellar wall is thrown. Its thickness is carried with considerable uniformity, but in most of the regions the depth of matter is only about half as much as that of the granular layer within.

The molecular layer is characterized by the predominance of fibrous elements and the fewness of nerve-cells. In contrast with the mass of densely-packed, conspicuous cells of the granular layer, the outer region presented hardly more than a minutely punctate appearance to the earlier investigators who had recourse to nothing more differential than the general stains in use at that time. Hence *molecular* seemed an appropriate descriptive term for this layer.

Through the use of modern methods, we find the molecular layer to have a few proper neurones of small size, but the great mass of substance consists of fibrous material, between

the parts of which the nerve-cells are intercalated. But, it is certainly a fact worthy of mention, the fibrous constituents of the layer do not have their origin there, penetrating it, rather, from deeper levels. The dendrites of the Purkinje neurones, and the processes from the neuroglial cells comprise one great class of constituents. These take a course perpendicular to the surface and cause the vertical striation which is so marked a feature of the region. Then, too, the neurones of the granular layer send their axones outward into the molecular layer for a T-shaped division, each thus giving origin to a pair of fibres. These branches take a course across the sagittal plane of the cerebellum, parallel at once with the limitans externa and the lateral surface of a fold. To the presence of these fibres, cut across in such numbers in a sagittal section of the cerebellum, the characteristically punctate appearance of the molecular layer is chiefly due. Finally, it should also be noted, there are numerous terminations in the molecular layer of nerve-fibres which have entered the cerebellum from some other region of the nervous system. Such terminating fibres branch so as to distribute the endings over a considerable superficial area.

It will thus be seen that the molecular layer is really a tangle of nervous tissue, a series of paths where many associations may be formed. This topic will be discussed more at length in the fifth subsection.

The neurones proper to the molecular layer are, as already

noted, but few in number, and those present are scattered between the nerve-fibres. The external morphology of one of these neurones is represented in Fig.14. From a small, almost perfectly spherical cell-body, three or four dendrites radiate, branching in what is an approach to a dichotomous manner. The dendrites are not thick at their bases and they become lost to view before proceeding far, owing to the fineness of the terminal twigs. The surface of a dendrite is almost perfectly smooth, there being only the faintest indication of gemmules, but there are small varicosities at irregular intervals which produce slight variations in the thickness.

The internal organization of the cell presents a large, rounded nucleus which is enveloped by a stratum of cytoplasm of no great thickness (Fig.50). The cytoplasm contains tigroid substance distributed in granules of the most minute size, mere points even when highly magnified. The chromatin is distributed along a linin reticulum of such fine mesh that the nucleus is thereby often made to appear almost perfectly black. There is a single nucleolus.

In mammalian neurology, the molecular layer is known to have two varieties of cells: (1) Stellate cells, the processes of which lie freely in the layer; and (2) basket cells, somewhat larger in size, occupying the deeper levels of the layer, and having their axones associated with each other in such a way as to form plexuses or baskets around the cell-bodies of the Purkinje neurones. The latter type of cell is,

of course, the more specialized of the two. It is therefore interesting to note that it is not represented in *Mustelus*, but that all of the molecular cells correspond, rather, to the stellate cells of higher vertebrates. Such a result is, however, to be expected in a brain of lower phylogenetic value.

3. *The Granular Layer.*

The granular layer lies internal to both the molecular layer and the neurones of Purkinje. It is somewhat irregular in its distribution. At many places it is twice as thick as the molecular layer, notably at the summits of the great folds; while it tends to decrease in extent as the bottom of a fold is reached. A sagittal section of the entire cerebellum shows a few regions where the granular layer is absent altogether (Fig.12,g.l.).

With nuclear stains, the granular layer appears to consist of a vast number of densely packed, rounded nuclei, from which fact the names *granular* and *nuclear* have been applied as descriptive terms. It is only through the application of metallic impregnation that the real character of the elements and the relations between them have been determined. When thus demonstrated, there are to be recognized neurones of two distinct varieties, the granular, proper, and the Golgi neurones.

a. *The Granular Neurones Proper.*-- Nearly all of the

neurones comprising the granular layer are included in this class. The distinctive features of such a neurone (Fig.15) embrace a rounded cell-body having a few short dendrites, and an axone which ascends through the levels of the granular layer above its point of origin to the molecular layer, where it divides in a T-like manner.

The size of the cell-body varies slightly, but it is always smaller than a neurone of Purkinje. As to shape, there is considerable diversity. The derivative form appears to be a rounded one, but this has been subjected to much modification by the origin of the dendrites so that triangular, rectangular, and various polygonal outlines are given.

The internal structure of the cell, (Fig.51), consists chiefly of the nucleus, only the faintest halo of cytoplasm being visible at any point; even the bases of the dendrites can hardly be recognized with purely cytological stains. Demonstrated with either methylen-blue or iron haematoxylin, the nucleus is found to contain a few very coarse and irregular chromatin granules strung on fine interlacing threads of linin. The presence of a nucleolus is doubtful, at least it is difficult to distinguish one from the masses of chromatin. Fig. 51 also shows how closely these neurones are packed.

The dendrites are three or four, only, in number, arising from the cell-body at approximately equidistant points (Fig.15). A dendrite is short and nearly always relatively stout. Its course involves sinuous curves. It branches but

rarely until the tip is reached, where it dissolves into a brush or a series of hooks spreading over a relatively considerable area. There are no gemmules.

The axone is exceedingly slender. It may arise directly from the cell-body, but it usually takes its origin from one of the dendrites, either near the base or at some distance from the cell; Fig.15 illustrates the two modes of formation. The course of the axone is invariably peripheral, pushing through the intervening thickness of the granular layer into the molecular layer. At the boundary between the two layers, the course changes abruptly to a horizontal one for a short distance, and hence the entire course of an axone can rarely be traced in one section. In the molecular layer, the axone divides into two branches which, with the original stem, form a T-shaped figure (Fig.16). The two branches pursue a course parallel with the surface of the cerebellum and the sides of the fold in which they run. It is thus seen that they pass through the dendritic tops of the neurones of Purkinje, comparable to telephone wires passing through the tops of the trees along a highway.

b. Golgi Neurones.-- A few neurones of the granular layer have an altogether different character from the ones just described. These lie in the upper levels of the layer. Such a neurone is shown in Fig.17. The cell-body is always a little larger than that of the typical granule neurone, and its form

is more rounded. A few club-like dendrites radiate from it for a short distance, branching but sparsely. The size of a dendrite is increased at intervals by slight swellings.

The axone passes downward into the deeper levels of the granular layer, instead of upward. It gives off collateral branches soon after its origin, and it breaks up into a number of fine terminal twigs before any great distance has been traversed.

This neurone is homologous with the variety described by Golgi ('94) from the human cerebellum, and by him made a representative of his *second type* of nerve-cell. The branching of the axone is far less profuse, however, than in the mammal.

We thus see that the granular layer of the cerebellum of *Mustelus* is marked by the presence of the same varieties of neurones which characterize this layer in higher vertebrates. The morphology is somewhat more simple in the selachian, as should be expected, but it is a suggestive fact that the structural plan of higher forms is here outlined in its essential features.

4. Supporting Elements.

The supporting elements of the cerebellum are referable to both the ependymal and the neuroglial series, the former being limited to the granular layer, and the latter to the molecular layer. The structure in each instance appears to

be particularly adapted to the supporting of the nervous mechanisms peculiar to these regions.

a. *The Ependyma.*-- The ependyma of the cerebellum presents the usual palisade of closely crowded cells forming the membrana limitans interna (Fig.13). The cell-body is irregularly pyramidal in form, the sides rarely tapering evenly to the apex but exhibiting more or less bold curvatures of outline.

From the apex of the cell-body, a process, the ependymal fibre, arises, and this pursues a course through the structures of the granular layer to near the outer limit of that zone. I have not found a single instance where one of these fibres passed beyond the granular into the molecular layer, a fact of some possible phylogenetic value, indicating the more ancient character of the internal region.

The ependyma-fibre is relatively stout, but its diameter is far from uniform. There are fibres which have portions of the length four or five times the thickness of the intervening parts; see Fig.13,b. Occasionally, knobs and other rounded thickenings are found, particularly at angles where the course of the fibre changes abruptly. The trend of the fibre is never conspicuously irregular, only such slight turns and windings occurring as might be expected where obstructions are present during the period of growth. The general trend is directly toward the surface of the cerebellar fold, the several fibres lying more or less nearly parallel with each other.

The degree of branching exhibits wide diversity. Certain fibres (Fig.18,a) have some half-dozen principal branches of various lengths, none of them very long nor diverging widely from the main stem; besides the principal branches, there are shorter twigs distributed sparingly along both the main stem and its ramifications. Other fibres (Fig.18,c) are so beset with a multitude of small twigs, quite irregular in their branching, that the whole series is given much the appearance of a long and cylindrical brush. Between these two extremes, there are every intermediate condition of branching forms.

The ependymal fibres lie quite near to each other, and the many processes from them constitute an interlacing tangle, the profusion and extreme delicacy of which cannot be adequately represented in any drawing. In order to appreciate the significance of this dense supporting framework, the vast number of the granular neurones must be recalled. Here we find the means by which these nervous elements are given that support which is one of the primary conditions for their activity.

b. Neuroglia.-- The neuroglia provides a support for the outer structures of a cerebellar fold, just as the ependyma functions within. The characteristics of neuroglial elements are shown in Fig.19,ast and bg.f. The cell-body lies at the juncture of the molecular and granular layers, between the cells of Purkinje. Two conditions are to be distinguished. One variety (Fig.19,ast) has a cell-body of quite irregular

outline from which many processes radiate. These processes rarely branch. Some of them may proceed to a distance equal to several times the greater axis of the cell, but most of the branches are far shorter. They are placed so closely along the margin of the cell that the whole has something the effect of a halo. These cells are clearly homologous with the astrocytes of higher vertebrates.

The other type of neuroglia cell (Fig. 19, b.g.f.) is referable to the category of Bergmann's fibres of the mammalian cerebellum. The cell-body has fewer processes than the astrocyte, but it gives origin to one stout fibre which takes a peripheral course, without branching, through the entire thickness of the molecular layer. The path of the fibre is not one directly toward the surface, for it runs almost parallel with the layer of Purkinje neurones for a short distance; it then turns upward, terminating at the limitans externa in a conical expansion. During the proximal part of its length, it bears fine processes similar to those emerging from the cell-body. The distal part of the fibre has a remarkably vast number of fine processes. These may remain separate from each other, but at intervals they become matted together so closely that the whole has the appearance of felt or even that of a solid.

The account given by Schaper ('93) of what he took to be Bergmann's fibres does not correspond with my findings in several particulars. This author does not mention the processes of the cell-body, nor do his figures show them. It may be that

his preparations were insufficiently impregnated. Weight is given to such a possibility from the fact that he did not find astrocytes at all. It is certainly of some phylogenetic interest that Bergmann's fibres appear to be derived from astrocytes. I have found numerous instances where transitional forms are recognizable, linking the extremes of the simple astrocyte with the one provided with a long process, the fibre of Bergmann.

The position occupied by the cell-body of a Bergmann's fibre is also significant. Kölliker ('96, p. 363) states that at birth Bergmann's fibres in mammals lie at the boundary of the granular and molecular layers, and that during growth they normally migrate into the granular layer. Now the permanent position of Bergmann's fibre in *Mustelus* corresponds to the embryonic state in the mammal. An additional comparison may be instituted regarding the form of the fibre, the adult element of *Mustelus* remaining simple, while the mammalian fibre becomes much branched. That the condition in *Mustelus* corresponds to the embryonic stage of development in higher vertebrates is, of course, no more than should be expected.

The physiological interpretation of the cerebellar neuroglia is not difficult. The numerous processes from both the astrocytes and Bergmann's cells provide a delicate suspensory apparatus for the neurones of Purkinje. The great Bergmann's fibres, reaching upward as they do through the molecular layer, may be likened to so many telegraph poles; and the matted tan-

gles extending laterally from these are the cross-bars for the wires. The wires to be supported, following out our comparison, are the horizontal axones of the granular neurones, which, as we have already noted, extend through the molecular layer in large numbers.

5. Architecture and Physiology of the Cerebellum.

It is now a well established fact that the principal function of the cerebellum is to preside over the equilibration of the body. Moreover, a fairly direct connection is traceable between the morphology of this segment of the brain and the nature of the muscular activities which are characteristic of the animal. To the student of comparative neurology, therefore, the cerebellum holds problems of a special order, and is ever potential with no mean interest.

We have seen that the cerebellum of *Mustelus* retains an external form of a far lower order than that found in the bird or mammal. The internal organization is not so inferior, however, as we might, from this fact, be led to infer. The architectural features of the lower and the higher types are so similar that the contrast is really one of degree and not one of kind. In both instances, the same sorts of neurones are present, grouped in a similar way, and related to each other physiologically in essentially the same connections. This remarkable identity of features can only be interpreted to mean

that the cerebellum became established in its organization quite early in the history of vertebrates.

Undoubtedly, the key to the significance of cerebellar structure and physiology is to be looked for in the neurones of Purkinje. These striking cells, with their characteristic tree-like tops, apparently have all of the other structural elements present arranged contributory to them. Imbedded in the midst of the nervous matter, supported by the interlacing processes of the neuroglia there, a Purkinje neurone sends its great branching dendrites outward into a veritable maze of possible physiological connections, for such the molecular layer really proves to be. We have seen that the granular neurones contribute their axones to a series of fibres passing horizontally through a row of spreading Purkinje dendrites; that the neurones of the molecular layer are themselves radiately connecting paths; and, finally, that the incoming nerve-fibres, those arising outside the cerebellum, end, some in the granular layer, others taking a longer course into the molecular layer. These several elements evidently have no other purpose than the bringing of all incoming impressions, through one path or another, to bear upon the neurones of Purkinje. The great spreading top of a Purkinje cell is obviously a device for providing a large receptive surface for such impressions, while the many thorn-like gemmules with which the dendrites are studded serve as a greater extension still of that surface, or, perhaps, make one which is more readily impressed.

The axone of the cell takes a more or less direct course out of the cerebellum, carrying the resultant of the nervous interactions to the proper point for ultimate distribution. If it is the purpose of the whole series of cerebellar elements to provide a central mechanism of equilibration, then the neurone of Purkinje is certainly the centre of that mechanism. The various nerve-fibres sweeping into the cerebellum may terminate in several ways and at diverse levels of the organ, but everywhere there are devices for connecting them physiologically with the neurones of Purkinje, which receive all and preside over all.

The researches of Lee ('92, '93, '94, '98) upon equilibration in fishes have shown with what nice discrimination these aquatic animals balance themselves, devoid, as they are, of many sources of impressions possessed by terrestrial vertebrates. Doubtless a large number of equilibrial impressions are derived from the visual mechanism of the fish. Axones from the roof-nucleus of the midbrain pass backward into the cerebellum; and it will be shown in Section VI that there is a most intimate association between the roof-nucleus and optic terminations. Another source of equilibrial impressions is to be found in the fins and body musculature, entering the cerebellum through the tractus cerebello-spinalis. But the work of Lee clearly demonstrates the overshadowing importance of the piscine ear as a peripheral organ of equilibration. In fact, his latest research ('98) makes it clear that the great ear of

Mustelus is not a true auditory organ at all, but that its several parts are to be interpreted from the standpoint of the equilibrium sense. The large nerve-tracts from the ear to the cerebellum are, therefore, definitely significant, being the connecting fibres between the central mechanism and its most important peripheral organ. It also appears that not only does the ontogeny of the ear show its relationship to the lateral line organs, but the functions in the two instances are comparable as well.

An analysis of the habits of *Mustelus* will, it appears to me, go far toward explaining the disproportionately great development of both the ear and the cerebellum which we find the animal to have. This shark, although a comparatively small representative of the group, is, withal, a restless hunter of the seas, ever urged onward by an appetite which, apparently, has no bounds. Continually suspended in a fluid medium, and compelled to balance itself at every turn, the animal requires a precise mechanism of equilibration. This is to be found, in the main, in both an ear and a cerebellum developed to a degree out of all proportion to the scale occupied by the creature as a whole.

6. *Evolution of the Cerebellum.*

Evidence of the origin of one brain-structure from another is usually of the most meager value, but it appears as though

it were now possible to weave together a few scattered threads in the evolution of the cerebellum. Schaper ('94) has called attention to certain facts in the embryology of the teleostean cerebellum which may be taken as the starting point. The cerebellum arises in ontogeny, not as a brain-segment having the full value of the others, but as a paired thickening in the parietal walls of the neural tube at the anterior end of the oblongata. These thickenings grow upward and meet each other in the median line. Schaper has since extended his studies to all classes of vertebrates, and he finds ('99) that the anterior limit of the bilaterally symmetrical anlage may be definitely fixed, coinciding with the boundary between the primary mid- and hindbrain vesicles. The posterior limit of the future cerebellum is by no means clear, however, for it seems to merge backward into the oblongata. These are certainly significant facts.

It was shown in Section IV, Subsection 7, that the molecular layer of the cerebellum is continuous with the cerebellar crest of the tuberculum acusticum, maintaining essentially the same morphological characters throughout. It was also shown that there are present in the tuberculum acusticum neurones which are identical with those of the cerebellum-- molecular neurones, granular neurones, and Purkinje neurones; the last two varieties are not grouped into definite strata, however. The presence of granular neurones in the acusticum is worthy of remark, but the greatest weight must be attached to the

finding of Purkinje neurones here. These neurones were long supposed to characterize the cerebellum alone, and their strikingly peculiar appearance makes them readily identified. The neurones of Purkinje from the acusticum of *Mustelus* agree with those from the cerebellum as to size, general form, shape and character of dendritic top, and even in the presence of the spiny gemmules so characteristic of this nervous element. There can be no question as to their morphological identity in *Mustelus*. Johnston ('93b) has found Purkinje neurones in the acusticum of *Acipenser*, somewhat smaller and simpler than those of the cerebellum, but undoubtedly equivalent. Similar results will probably be obtained in all of the simpler vertebrates.

It may be concluded, in the light of these embryological and structural facts, that the cerebellum has arisen in the phylogeny of vertebrates as a fused outgrowth of the pair of tubercula acustica. The acusticum is the primary end-station, as we have seen, for the nerves of the ear and the lateral line organs. The cerebellum has been differentiated from the primary ending as a special centre for presiding over equilibration. Parallel with the increasing development of the equilibrational sense in vertebrates, the cerebellum has gradually acquired associations with other than the original source, so that the fibres entering the organ have ever been growing more numerous, and the bulk of the fibrous centre consequently more massive.

7. Summary of the Cerebellum.

The cerebellum of *Mustelus* is of relatively large size, and, although remaining in the primitively hollow condition, its wall has the same essential plan of structure as the organ in higher vertebrates.

Neurones of Purkinje form a zone, crowded at certain points, between the molecular and the granular layers. Such a neurone has the structural features characteristic of its mammalian representative, but with a simpler branching of dendrites. Its office is to receive incoming equilibratory impressions.

The neurones of the molecular layer are few in number. They are all of one variety.

The neurones of the granular layer are of two kinds: Golgi neurones and granular neurones. The former lie in the upper strata of the layer. The granular neurones are strikingly like those of higher vertebrates; their axis-cylinders branch in a T-shaped manner in the molecular layer, mediating between many incoming fibres and the dendrites of the neurones of Purkinje.

Ependyma is developed into a profusely branching fibre which extends through the granular layer, only.

Neuroglia provides a supporting framework for the neurones of Purkinje and the molecular layer. Both astrocytes and Bergmann's fibres may be recognized, but there are transitional forms indicating that the latter have been derived from the former.

The large size of both the ear and the cerebellum of *Mus-telus* is to be explained by the swimming habits of the animal. The structures have an equilibratory value.

The cerebellum has apparently arisen in the phylogeny of vertebrates as a fused outgrowth of the pair of tubercula acustica, a specialization of that part of the oblongata forming the original terminal station for the acustico-lateral system.

SECTION VI.

THE MIDBRAIN.

The midbrain of *Mustelus* has retained to a marked degree the features characteristic of this cerebral vesicle in its primitive condition. Its ventricle has been so little encroached upon by nervous matter that the name *aqueduct of Sylvius* would not be applied as a descriptive term were it not made necessary by usage in higher vertebrates. The aqueduct is produced laterally into a pair of spacious recesses, each of which occupies the interior of an optic lobe, while the general cavity communicates freely through narrower extensions with the third ventricle in front and the fourth ventricle behind (Fig.1,mb.). The optic lobes are two thin-walled bodies of dome-like form, separated from each other by a conspicuous median furrow, and the pair taken together are somewhat broader than the base of the midbrain on which they rest. The anterior divisions of the cerebellum lie upon and partially conceal the optic lobes from the dorsal aspect. The base of the midbrain is a direct continuation anteriorly of the great fibre-systems of the oblongata and metencephalon, showing but slight diminution in size.

The microscopical anatomy of the midbrain is really quite complicated, owing to the diversity of the terminations and connections which are established here. The base is a crowded highway between the different parts of the encephalon. The fibres of the optic nerve have their termination in the dorsal midbrain, the tectum mesencephali, with a nexus of intrinsic neurones and fibres of more distant origin associated with them. Finally, the aqueduct of Sylvius is bordered by nervous matter which is phylogenetically distinct from either the base or the tectum, and this has undergone special development at certain points as the nuclei of important motor neurones.

1. The Tectum Mesencephali.

The tectum mesencephali lies as an investing cap upon the central gray matter which surrounds the aqueduct of Sylvius, Its situation here is fraught with significance, for it represents an addition to the more ancient nervous structures made necessary by the development of lateral eyes in the vertebrate phylum. The tectum embraces the central expansions and associated connections of the nerve-fibres having their origin as axones of the retinal neurones. Certain neurones of the tectum may, also, send their axones outward into the optic nerve. The whole complex is, in fine, the primitive visual centre.

The tectum of *Mustelus* does not approach the extreme degree of differentiation which Ramón y Cajal ('89, '91) has de-

scribed from the optic lobes of birds, but it is practicable to distinguish three zones of structural elements: the layers of the superficial, the middle, and the deeper neurones, respectively, (Fig.21, sn., m.n., d.n.). VanGehuchten ('34) has described three zones from the optic lobe of the teleost, but these are not exactly equivalent to the layers noted here. his *couche moléculaire* appears to include both my superficial and middle layers; his *couche granuleuse* corresponds in position to my deeper layer; while his *couche des cellules épendymaires* is an inner zone which apparently does not include the central gray matter.

a. Termination of the Opticus. Str. Medullare Profundum.-- A great bundle of fibres may be traced dorso-posteriorly from each angle of the chiasma to the optic lobe, where it becomes dissolved through spreading over the surface. A section shows that the fibres in the outer zone lie parallel with the surface during some little part of the length of their course, and that they then pass downward into deeper parts of the tectum. Fine branches are given off in the regions occupied by the neurones of the middle and deeper layers, and many terminations appear to occur here. A certain number of fibres, however, pass to ever deeper levels, tending to become collected into bundles, and they finally blend into the stratum medullare profundum.

The stratum medullare profundum is a conspicuous feature

of the deepest part of the tectum mesencephali. At the crown of the arch which the optic lobe presents in section, the fibres are seen as great horizontal bundles interrupted at almost perfectly regular intervals by small groups of vertical fibres. The two lateral halves are united by a strong commissure just dorsal to the aqueduct of Sylvius. Fig.20,s.m.p., represents these features in a transverse section.

Traced laterally, the fibres of the stratum medullare profundum are found to pass into the base of the midbrain in two somewhat clearly marked divisions. The outer division takes a large number to the lateral surface (Fig.20,e.l.); while a markedly smaller group passes downward nearer the median line for a ventral decussation (Fig.20,i.l.). The inner division is composed of those fibres lying nearer to the central gray matter from the outset. Some of these have but a short course downward and outward, but the great mass of fibres continues near the median line as a series of intercrossing bundles which are destined to decussate ventral to the aqueduct of Sylvius (Fig.20,e.m.,i.m.).

The fibre-system composing the stratum medullare profundum must be indeed important in the economy of the brain. Into this system we have traced fibres from the cord and oblongata, fibres from the optic nerve, and from the neurones of the tectum mesencephali itself. We will subsequently have occasion to point out that a great tract sweeps into it from the inter-brain as a relay in the olfactory apparatus. Fibres are also

present here from certain of the cranial nerves. All of these fibre-systems from diverse sources are to become related to the remarkable mechanism of Reissner's fibre. It is certainly evident that there are here every means for intercommunication between different parts of the nervous system, a switch-board, so to speak, of extraordinary possibilities; but to this subject we shall return further on.

b. The Superficial Neurones.-- The outermost layer of the tectum mesencephali is characterized by the predominance of nerve-fibres and by the feeble development of its neurones. Receiving as it does the fibres of the optic nerve for their first expansion, we should hardly expect a high degree of nervous activity here. There are a few scattering nerve-cells present, however, (Fig.21,s.n.). These are quite minute in size, lenticular in form, and are disposed with their long axes tangential to the surface of the brain, as though squeezed into crevices between the mass of nerve-fibres. The internal organization of the cell presents no features which would mark it as having any degree of importance physiologically (Fig.52, s.n.).

c. The Middle Neurones.-- The neurones which lie in the middle layer of the tectum are characterized by their larger size and vastly greater numbers as compared with the outer region. In fact, the number is so great that in a section,

the nerve-cells often appear superposed one over another, and the processes make a veritable tangle of interlacing branches (Fig.21,m.n.).

The neurones of the level are to be distinguished from those of the deeper layer, on the other hand, both by their compactness and by their mode of branching, which is of the radiating type. The several processes of a nerve-cell spread out and branch freely in all directions, but they do not extend far away from their points of origin. A representative form is drawn in Fig.22. There are always several dendrites, and these may arise either from the outer end or from the side of the polygonal cell-body. The branching begins quite near the origin, so that the size diminishes rapidly from the base outward. The dendrites of the outer extremity have their finest twigs penetrating the superficial layer of nerve-fibres. The dendrites arising from the sides of a cell interlace more largely with those of other neurones. The surface of a dendrite always bears an abundance of simple gemmules.

The axone pursues an irregular course, often spreading over a considerable horizontal area, but the general trend is ever toward the center of the brain. It gives off a great profusion of collaterals as it proceeds, and the final termination is found at no great distance from the cell-body. There is here, then, an illustration of a cell of the Golgi II type. The several ramifying axones lie in the region occupied by the cells of the deeper layer.

The nucleus is a rounded, centrally located body, filling the larger part of the mass of the cell. The cytoplasm holds a few tigroid-bodies of small size, an evidence of a low order of metabolic activity in this type of cell. Fig.52,m.n., exhibits what details of internal organization are visible under the highest amplification.

The part which the neurones of this layer take in the physiology of the optic termination may be inferred with some degree of certainty. The dense tangle of dendrites just beneath the incoming optic fibres constitute a large surface for purposes of reception. The spreading axones in the layer beneath afford, with the neurones there, a physiological nexus of some superficial extent, possible paths of association, if we choose to apply the term here. We will return to this subject in the following subsection.

d. The Deeper Neurones.-- This layer is thicker than both the preceding ones put together. The neurones are less closely crowded than those of the middle layer, and they lie in groups between the bundles of optic fibres passing downward to the stratum medullare profundum (Fig.21,d.n.).

The neurones which give character to this layer are long-drawn-out, the dendrites extending nearly to the external surface of the brain, and the axone reaching well toward the limitans interna. Fig.23 shows a typical neurone considerably enlarged. The cell-body is spindle-shaped or oval in outline.

From its outer end, a single stout dendrite proceeds straight toward the periphery. This dendrite branches but sparsely, and no branches are given off for some distance beyond the point of its origin. The several branches pass outward through the middle layer of neurones, and the most delicate twigs can be traced into the superficial layer of nerve-fibres. The whole dendritic series presents a top both tall and narrow, in strong contrast to the form assumed by the neurone of the middle layer. Gemmules are scattered over the branches, but they are conspicuous neither for their size nor their numbers.

There may be other minor dendrites arising from near the base of the cell, as shown in Fig.22; but the axone always takes origin from a point opposite the principal dendrite. The axone is directed toward the *limitans interna*. It may be traced for some distance without any very marked diminution of size. Many collateral branches are given off in its course, and the ultimate destination of the principal stem appears to be a bundle of fibres contributing to the *stratum medullare profundum*.

The body of the cell is so largely filled with the nucleus that often only the thinnest investing film of cytoplasm is exhibited. Six cells from this layer have their structural features shown in Fig.53, and one of these has the thinnest enveloping cytoplasm found in this class. The nucleus of a cell is regularly oval in contour, holding one prominent nucleolus. The chromatic network is delicate and of small mesh.

The cytoplasm contains masses of tigroid substance which,

in proportion to the actual magnitude of the cell, are relatively large in size. When the nucleus lies toward one end of the cell, the largest tigroids are found in the free extremity. The prevailing form of tigroid mass is triangular, and the several masses have a rather open arrangement.

From the form of the neurone just described, we should infer that it is adapted to the part of a conducting medium between the superficial and the deeper levels of the tectum mesencephali. The internal structure also indicates that it is characterized by no slight amount of metabolic activity. Evidently, then, there is here a nervous element of considerable importance in the economy of the midbrain.

VanGehuchten ('94) has described the deeper neurones from the optic lobe of the trout (his *couche granuleuse*) as being without dendrites, and as sending their axones peripherally into the superficial levels. The character of this type of neurone in *Mustelus* certainly corresponds the more nearly with the conditions found in higher vertebrates, although much simpler of course, so that, in this respect at least, the selachian is seen to be in the direct phylogenetic line, while the teleost is divergent.

In the inner zone of the deeper layer of the tectum, at the level occupied by the numerous collaterals from the proper axones, there are to be found at intervals neurones of another character (Fig. 21). Such neurones are irregularly stellate as to general form, the dendrites and the axone radiating widely

from a polygonal cell-body. The office of this neurone may be to bring the collateral branches of the other and more numerous nervous elements into relationship. Fig.54 shows a group of five of these cells, an unusually large number to find in so limited a field.

2. *The Central Gray Matter.*

The aqueduct of Sylvius is surrounded by a layer of nerve-cells and nerve-fibres representing the most archaic part of the brain, and quite properly termed the central gray matter (Figs. 20 and 21, c.g.m.). The greater part of this nervous matter has been supplanted or overshadowed functionally by more recent additions upon its outer surface, but certain well defined groups of neurones have retained their pristine importance through the character of their ultimate connections. These are, respectively, the roof-nucleus, and the nuclei of the oculomotorius and the trochlearis.

a. The Roof-Nucleus.-- This is a collection of very large neurones lying in the roof of the aqueduct of Sylvius between the ependyma and the dorsal commissure of the stratum medullare profundum. The group has a considerable longitudinal extension, reaching from the anterior end of the optic lobes to near the juncture with the cerebellum. It is broken into two lateral halves by the median line. Fig.20,r.n. exhibits the entire

nucleus; while Fig.55 represents the distribution of the cells more in detail on the right side.

These neurones are the largest of any in the nervous organization of *Mustelus*. The size attained by the cell-body may be as great as 60 micra in transverse diameter by 100 micra lengthwise. The group, therefore, presents a very striking picture in the field of the microscope. The forms assumed by the cell-bodies are somewhat diverse, ranging from oval, through irregular outlines to a considerably elongated condition. The longer axis lies parallel, or nearly so, with the *limitans interna*.

In a thick section, the dendrites appear as two or three stout processes which push their way into the nervous matter dorsal to the group and are soon lost to view. Those cells lying very close to the median plane send their axones to the opposite side; but the remaining members of the group, comprising nearly all of the cells, have their axones extending away from the mid-line. The axones from the several cells of the same side, together with the crossed axones, run laterally for a greater or less distance, turn anteriorly, and become associated into bundles which constitute a fairly well-marked tract (Figs.20 and 55, r.n.t.). This tract extends forward to the anterior limit of the midbrain, where it unites with its fellow from the opposite side, and the united group of fibres emerges from the midbrain roof to penetrate the aqueduct of Sylvius as the fibre of Reissner. The ultimate destination will be

traced in a subsequent paragraph.

Those cells of the roof-nucleus lying in the posterior region have a different termination for their axones from the one just described. In this instance, the axones pass posteriorly, instead of anteriorly, and they take a course into the cerebellum. The significance of this fact has been considered in Section V, Subsection 5.

The cell-nucleus is a large, evenly rounded body, almost invariably eccentric in its position, sometimes, even, lying in what appears to be a special protrusion of the general cell-mass. The chromatin is distributed in the form of a reticulum of rather fine mesh which holds coarser granules at intervals. The nucleolus is evenly rounded and of conspicuous size. Many of the cells have two or even more nucleoli.

The cytoplasm, stained with methylen-blue, exhibits a minutely punctate appearance even under the highest amplification, due, chiefly, to the minute size and diffuse distribution of the tigroid substance. The tigroids are quite densely packed in the peripheral regions of the cell. In the field of the nucleus, the prevailing form of granule is rounded; farther away, the shape is a more elongated one, the long axis being tangential to the margin of the cell. Fig. 56 shows the details of cell-organization, Nissl staining.

When these cells are stained with iron haematoxylin, they exhibit what appears to be the equivalent of the perinuclear reticulum of Golgi (1900). We find the internal part of the

cytoplasm exhibiting deeply stained, massive bodies, branching, and anastomosing with each other through more slender connections. The several individual masses are disposed in such a way as to give the appearance of enclosing the nucleus as with an open network. The bodies fade away as they enter the dendrites, and there is no appearance of their having communication with the exterior such as has been described by Holmgren ('99a, '99b). Fig.57 represents the appearance of this series of structures.

It is doubtless necessary to await further researches in many distantly related fields before we attempt to pass final judgment as to the significance of the perinuclear reticulum, but the hypothesis noted by Golgi (1900) is one which certainly deserves our consideration. The appearance presented by the network may be caused, not by solid bodies at all, but by a series of communicating canaliculi filled with a fluid which is deeply colored by certain stains. Such a reticular canal-system would probably take no part in the irritable life of the cell as such, but would function on a lower plane of purely vegetative character.

The neurones of the roof-nucleus come into intimate relations with the nerve-fibres of the stratum medullare profundum. The dorsal decussation between the opposite halves of the stratum carries a strong bundle of fibres across the median plane immediately above this group of neurones (Fig.55, dc.s.m.p.) There are to be found here numerous instances of

nerve-fibres emerging from the general bundle and terminating in arborizations near the bodies of the nerve-cells. Fig. 57, ar., represents two such arborizations near the same cell. The character of the termination is exceedingly interesting. The axones are found to present a reticulo-vesicular structure throughout their whole length, the protoplasm apparently consisting of vesicles of several degrees of size united by a reticulum. Now as the axone approaches its termination, the reticulation becomes more pronounced, and the final arborization is seen to be essentially an expansion of the same thing. The ending is simply a widely-spread, digitate reticulum. There are many thorn-like branches from all of the strands, and numerous anastomoses occur between the principal ones. Consult Fig. 57, ar.

The remarkable group of nerve-cells comprising the roof-nucleus has been variously interpreted, but its true relations were not discovered until quite recently. Rohon ('77) first described this collection of cells as the *lachkerie*, a name applied, of course, from the position occupied by its paired members in the roof of the aqueduct of Sylvius. It was later recognized in the brains of various fishes, Burckhardt ('92) identifying it as the midbrain trigeminal nucleus. It has remained for Sargent (1900) to show that not only is the roof-nucleus present in all vertebrates, but that it is part of a most interesting mechanism, the fibre of Reissner ('60). Reissner's fibre is a rod-like body lying in the central canal

of the spinal cord, extending forward. It had come to be neglected entirely in recent years owing to the prevalent view that it merely represents a coagulation of the cerebrospinal fluid. Sargent (1900) demonstrated that such a view is erroneous, that Reissner's fibre is a real structure, with a perfectly definite character and distribution, and, furthermore, that it is found in all classes of vertebrates, always extending from the posterior end of the canalis centralis to the anterior end of the aqueduct of Sylvius. He has also shown (1901) that the fibre represents, in the main, the closely fused axones of the cells of the roof-nucleus. The great number of neurones comprising the anterior field of the roof-nucleus send their axones into the aqueduct of Sylvius, as noted above, whence they pass backward as Reissner's fibre through the extent of the fourth ventricle and the central canal of the spinal cord. Fine processes are given off to the nervous matter of the cord as the fibre proceeds.

An interpretation of the roof-nucleus and of Reissner's fibre arising from it may now be attempted. In the next to the last paragraph, a nexus was traced between the fibres of the stratum medullare profundum and the neurones of the roof-nucleus. There are here, it is evident, the elements of a tract through which quite direct connections may be established between the somatic motor neurones of the spinal cord and certain sensory impressions, visual and olfactory, at least. The classes of impressions noted are carried through the stratum medullare

profundum to the terminal arborizations which we have described near the cells of the roof-nucleus. The neurones of the roof-nucleus transmit such impressions through their axones, Reissner's fibre, directly to motor neurones at the several levels of the spinal cord. The apparatus of the roof-nucleus and Reissner's fibre, regarded as a thing apart, is advantageous to *Mustelus* because it is a path without relay, a short arc for motor reflexes between the eye and the olfactory organ, on the one hand, and the body musculature on the other. The giant size of the neurones of the roof-nucleus is doubtless the correlative of not only their long axones but of their importance in the economy of the animal, as well. In ascending the scale of the vertebrate series, however, it will be found that this mechanism ever takes on a progressively less and less value, owing to the development of other means for attaining the same end.

b. The Nucleus of the Oculomotorius.-- The nucleus of the III nerve lies ventral to the aqueduct of Sylvius (Fig. 58,n.III). This collection of neurones is sharply marked off from all surrounding nervous elements by the large size of its cells and by the greater intensity of stain with methylen-blue. The group extends antero-posteriorly for some distance.

The prevailing form of cell is oval, with two or three marked extensions of outline produced by the broadly triangular bases of the dendrites (Fig.59). The axone is more slen-

der by far than the dendrites; it is directed away from the limitans interna, taking the course of a sweeping curve.

The nucleus of the cell is evenly rounded in form, rather large as to proportionate size, and it has a central location. There is but a single nucleolus. The chromatin is distributed in a delicate network, the few interlacing strands visible being of great tenuity.

The cytoplasm is remarkable for the large size of its masses of tigroid substance, these bodies being visible as distinct things even under low amplification. The form of a tigroid is almost invariably triangular. The base of the triangle lies toward the nucleus, the apex pointing toward one of the dendrites. Those masses lying in contact with the nuclear membrane are somewhat broader, taking the form of a so-called nuclear cap. The size of mass decreases toward the periphery of the cell, those lying in the bases of the dendrites assuming a slender form. Reference may be made to Fig. 59.

The striking size attained by the masses of tigroid substance here is doubtless associated with the purely motor function of the III nerve, the fibres of which are the axones of these particular neurones.

c. The Nucleus of the Trochlearis.-- Rohon ('77) fell into a curious error with regards the nucleus of the IV nerve. As is well known, the root of the trochlearis passes backward and crosses over to the opposite side, appearing dorsally in the

furrow between the midbrain and the cerebellum. Rohon evidently sought for the nucleus of the nerve near its superficial origin, for he identified as such a group of cells on the border of the cerebellum.

The group of neurones constituting the nucleus of the IV nerve lies posterior and slightly ventral to the nucleus of the III nerve (Fig. 58, n. IV). The anterior end of the trochlear nucleus overlaps the posterior end of the oculomotor nucleus for a short distance.

The cells of this collection are, as compared with the cells of the oculomotor nucleus, decidedly smaller in size, and the general outline is more nearly triangular. The nucleus of the cell is relatively larger in proportion to the amount of cytoplasm. The chromatic network is so delicate as to be but faintly visible even under high magnification.

The masses of tigroid substance are few in number, relatively large in size, and wholly irregular as to form. There is a perinuclear zone of cytoplasm entirely free from tigroids. It often appears as though many of the tigroid masses are actually clinging to the limiting pellicula of the cell. Fig. 60 exhibits a condition typical for the cells of this group.

I really am unable to offer any explanation concerning the marked differences to be observed between the tigroid-bodies of the trochlear and the oculomotor neurones, respectively. The contrast in both the form and the arrangement of the tigroids is quite evident. The distinction is a real one,

not due to variation in the action of reagents, for I have several instances showing the marked contrast in one and the same section. A structural difference here is a noteworthy fact, since the two neurones are both of the somatic motor type, entirely equivalent morphologically.

3. *The Ependyma.*

The general character of the ependyma of the midbrain is represented in Fig. 21, ep., while Fig. 61 illustrates the details of cell-organization. The outline of a representative cell is somewhat lance-like, the length four times the breadth, the pointed extremity touching the ventricle and the greatest breadth at a point further removed. The interior of the cell is occupied almost entirely by the nucleus. It is really difficult to detect any cytoplasm at all except in a small area at the base of the ependymal fibre. The observer has the impression forced upon him that most of the cytoplasm during the course of growth has passed over into the cell-process. The structure of the nucleus is reticulated to an almost extreme degree. Some strands of the reticulum are relatively coarse, but many of them are so tenuous as to lie almost beyond the capacity of the microscope.

The ependymal fibre takes a course which is almost straight during the first part of its length, but toward the outer limit of the central gray matter crooked turns occur, and branches

are given off. The diameter of the process remains uniform throughout except for slight swellings which occur at intervals. The fibre terminates at the periphery of the brain.

The fact that the ependymal fibre becomes irregular and branches only after it leaves the central gray matter for the newer additions outside may have a phylogenetic significance, indicating that at one time the process had no farther course than the outer limit of this most ancient nerve-substance. But it is also entirely possible that the phenomena in question are without such deep significance, having been caused by the greater number of obstacles in the path of the fibre as it grew through the outer levels.

4. Phylogeny of Midbrain Structures.

The midbrain has ever been a stable part of the neural tube. Marked out early in ontogeny from the other brain-segments, the midbrain of *Mustelus* retains many features of organization which are really primitive in character.

The central gray matter is the most archaic of the midbrain structures, and the newer additions of the outer levels are derivable from it. The central gray matter is to be compared, both as to general functions and morphological topography, to the gray matter of the spinal cord before the latter has developed its specialized cornua. In a broad way, the ventral region of each is motor, and the dorsal part a series

of sensory centres. The homology is most readily traceable in the ventral region. The neurones of the III and IV nerves are true somatic motor neurones, corresponding entirely to those of the ventral cornua of the cord.

The dorsal region of the midbrain has become more and more specialized as an optic termination. At a phylogenetically early period, the optic fibres grew backward from their original relations to establish terminations here. Probably the most primitive connection is the one with the giant neurones constituting the apparatus of the roof-nucleus and Reissner's fibre. Through this means, the optic neurones were chained directly to the somatic motor neurones innervating the body musculature. Later, the midbrain roof became thickened by the wandering outward of neurones from the central gray matter, and by the development of new optic terminations associated with them. Thus has arisen the tectum mesencephali, an end-station which has remained important in the vertebrate series as a visual centre until secondary connections were established with the pallium. Hence the tectum is of great magnitude in the lower vertebrates, where the pallium is weak, but becomes dwarfed in the mammalian brain in which there is an overshadowing development of pallial connections.

5. Summary of the Midbrain.

The tectum mesencephali of *Mustelus* receives practically

all of the optic fibres, apparently only collateral branches being given to the interbrain. Three structural zones of the tectum are to be recognized: the superficial, the middle, and the deeper zones, respectively. The superficial layer has chiefly fibres, with a few minute, tangentially elongated neurones. The middle layer is composed of a densely crowded tangle of neurones of the Golgi II type, the axones of which spread laterally. The deeper layer has neurones which send long dendrites into the outer levels, while their axones penetrate the stratum medullare profundum. Optic terminations occur in all of these layers. The structure of the deeper layer places the selachian more nearly in the direct phylogenetic line than the teleost.

The stratum medullare profundum receives optic fibres, axones from the tectum, fibres of the olfactory mechanism from relays in the thalamus, as well as fibres from posterior regions.

The central gray matter has become differentiated at certain points to form the roof-nucleus, and the nuclei of the III and IV nerves, respectively.

The roof-nucleus is a collection of very large neurones lying dorsal to the aqueduct of Sylvius, the axones of which form, ultimately, the fibre of Reissner. Terminations of fibres from the stratum medullare profundum occur near the neurones of the roof-nucleus. The roof-nucleus and Reissner's fibre constitute a direct path for motor reflexes between certain

senses and the body musculature, involving the somatic motor neurones of the spinal cord. The senses thus mediated are, primarily, the olfactory and the visual, but the acustico-lateral and the general cutaneous systems may be represented also.

The neurones forming the nuclei of the III and IV nerves have the structure of the somatic motor neurones pertaining to the spinal cord and the oblongata.

Ependymal fibres extend through the entire thickness of the midbrain wall, branching but feebly.

SECTION VII.
THE INTERBRAIN.

The research of Edinger, *Das Zwischenhirn*, ('92), presents an account of the fibre-tracts of the interbrain of Selachii and Amphibia as demonstrated by the Weigert method. It remains for me to add to the results of that work a description of the morphology of the neurones proper to the interbrain of *Mustelus*.

1. *The Thalamus.*

The thalami of a selachian are so small in proportion to the other parts of the brain (Fig.1,th.) that certain of the older anatomists were thereby caused to overlook the interbrain entirely; see Section II. The small size of the thalamus is, I find, the expression of a low degree of organization. Several investigations have made it clear that the thalamus of a mammal has several well-defined thalamic nuclei. The thalamus of *Mustelus*, however, has remained in a condition of such primitive simplicity that it is not practicable to institute very strict comparisons between its neurones and those which are characteristic of higher forms. Before such comparisons can be of much value, a study must be made of thalami

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having intermediate degrees of development.

It has seemed to me advisable to distinguish but two collections of neurones in the thalamus of *Mustelus*. One group represents a differentiation of the ancient central gray matter; this I have designated the nucleus strati grisei. The other collection is certainly the one from which the several geniculate nuclei of higher vertebrates have been derived; this I have called the nucleus geniculatum.

a. The Nucleus Strati Grisei.-- As has just been mentioned, this collection of neurones represents a differentiation of the primitive central gray matter. The nucleus strati grisei has retained its original situation next the third ventricle (Fig. 24, n.s.g.). It forms a broad zone just within the limitans interna, comprising something like one-fourth the thickness of the entire thalamus.

The neurones of this group are the largest of the thalamus. The cell-body has a polygonal form, the several diameters not greatly unequal. The dendrites radiate freely in all directions, but they are not very long. The nucleus of the cell has an eccentric position, causing the cytoplasm to appear massed on the side from which the chief dendrites arise. The chromatic substance is disposed in a few thin strands having thickened nodes. The entire amount of chromatin is not great, and so the nucleus presents a lightly stained appearance. The tigroid substance is limited almost entirely to that part of the

cytoplasm having the greatest mass. Some of the tigroids are altogether irregular in form and are relatively quite large. Fig. 62 exhibits two neurones as they lie in place.

The nucleus strati grisei is the terminal station for those axones of the tractus strio-thalamicus having their origin in the general striatum. These sweep into the nucleus in bundles, and their terminations are to be noted between the constituent neurones (Fig. 24, f. s. t.).

The neurones of the nucleus strati grisei are, primarily, a relay in the olfacto-motor chain. The tractus strio-thalamicus terminating here is one of the links of that chain, as we shall point out in detail under Section VIII. The axones from the cells of the nucleus strati grisei pass backward into the base of the midbrain as the tractus thalamo-tectalis, and then sweep upward into the tectum to lie in the stratum medullare profundum. Here they are associated with other sensory nerve-fibres, as already noted in Section VI, and the entire group becomes related to the remarkable motor conducting path provided by the cells of the roof-nucleus and the fibre of Reissner.

It is certainly not worth while, with the knowledge which we have at present, to attempt an extensive comparison of the nucleus strati grisei with the specialized thalamic nuclei of higher vertebrates. It seems fairly safe, however, to regard the nucleus rotundus and the nucleus magnocellularis as descendants of this simple collection of cells found in the thalamus of selachians.

b. *The Nucleus Geniculatum*.-- This nucleus is imbedded in the substance of the thalamus lateral to the nucleus strati grisei. It is separated from the neurones of that group and from the external surface of the brain by bundles of fibre-tracts. In transverse section, this collection of neurones appears as a broad band curving parallel with the limitans externa (Fig.24, n.gen.).

The size of a neurone from the nucleus geniculatum is considerably less than that of one from the nucleus strati grisei, and the form is of the elongated instead of the radiating type. Fibres from the opticus leave that nerve to form a terminal zone on the periphery of the thalamus, and the dendrites of these neurones extend outward into this zone, while their axones take a course inward. The neurone, therefore, comes to be drawn out in a direction approximately at right angles to the limitans externa (Fig.24, n.gen.). The cell-body is rendered somewhat elongated by the processes taking origin at its extremities. The interior of the cell is almost wholly occupied by the nucleus, leaving but a scanty amount of cytoplasm in the bases of the cell-processes (Fig.63). The chromatin is in the condition of a fine reticulum. The tigroid substance is necessarily small in amount where there is so little cytoplasm, embracing only a few scattering granules.

Structurally considered, the neurones of the nucleus geniculatum are little specialized, remaining in an embryonic condition, so to speak. Their functional value is also of a low

order. They are certainly of far less importance as an optic termination in the selachian than are their specialized representatives in the mammal. In *Mustelus*, only collateral branches are, evidently, sent to the nucleus geniculatum, the great mass of optic fibres sweeping backward to the midbrain for termination in the tectum. With the progressive evolution of higher vertebrates, the thalamic termination of the opticus appears to have become more and more important, leading to the corresponding differentiation of geniculate nuclei. Hand in hand with the growing importance of the interbrain as a primary optic centre, however, there has been a related decline of the midbrain roof. And hence it is that the optic lobes of the fish appear so disproportionately large in comparison with the homologous parts of the mammalian brain.

2. Epithalamus: The Nuclei Habenulae.

The nuclei habenulae, or ganglia habenulae of authors, rise considerably above the level of the thalami (Fig.1, n.h.), the pair meeting each other to form a conspicuously arched bridge across the third ventricle at its posterior end. The epiphysis springs from the middle of the arch. The left nucleus is a little larger than the right one, its margin extending slightly more anteriorly.

The nucleus habenulae is an important relay-centre, and so its structure exhibits many nerve-fibres taking various direc-

tions, between which there are neurones and supporting elements. The tractus olfacto-habenularis (Section VIII, 1, c) terminates here, and the neurones of the nucleus give origin to the tractus habenulo-peduncularis, (the bundle of Meynert, and the fasciculus retroreflexus, of authors).

A representative neurone is shown in Fig. 25. The size of the entire element is rather large. The cell-body tends to retain a rounded form, although diverted from this condition more or less by the thickened bases of the dendrites. The dendrites are some three or four in number, gnarled and irregular processes, branching only a few times, and extending far outward in every direction from their points of origin. The surface of a dendrite is roughened by nodal thickenings, knobs, and a few gemmules. The axone arises directly from the cell-body in all of the instances observed. Its course is traceable for only a short distance in a transverse section, since it soon turns posteriorly into the tractus habenulo-peduncularis. This important tract takes the usual course toward the base of the midbrain. Its termination occurs there in the nucleus interpeduncularis. The significance of the tract is to be interpreted as a part of the olfacto-motor complex, discussed more particularly in Section VIII.

3. Hypothalamus: The Lobi Inferiores.

The hypothalamus is very large in *Mustelus*, projecting

far back beneath the midbrain; consult Fig.1. Its large size is merely the expression of the unusual importance which is assumed by this part of the interbrain in selachians. Intrinsic neurones, and fibres from without are to be noted in numbers in both the infundibulum and the lobi inferiores.

The wall of the infundibulum exhibits neurones separated from each other by considerable intervals (Fig.26). The cell-body is polygonal or elongated-oval in form. The dendrites are few in number. They spread widely, rarely branch, and pursue a nearly straight course.

The Lobi Inferiores are the most conspicuous features of the hypothalamus, a pair of great bulbous outpushings of the lateral wall of the infundibulum (Fig.1, l.i.). These lobes are the seat of a crowded group of neurones, a fact which is doubtless the ontogenetic cause of their large size.

Herrick ('92) has described several distinct nuclei from the lobus inferior (hypocarium) of the teleost, but I have found it impracticable to distinguish cell-groups in *Mustelus*. The neurones are disposed in a layer next to the limitans interna, the cell-bodies forming a closely-packed zone involving something like the inner fourth of the thickness of the wall (Fig. 27, i.z.). The dendrites are directed outward, forming, together with the nerve-fibres here, a fine tangle which presents the appearance of a molecular layer with general stains.

The form of a neurone is quite unlike that of any other

found in the anterior divisions of the brain. It is not dissimilar to a widely spreading bush, the cell-body being the short stem, and the dendrites the top (Fig.23). The dendrites are thick at their bases, they give origin to only a few branches, they taper gradually, and their tips usually reach almost to the limitans externa. The surface of a dendrite exhibits a multitude of spiny gemmules of various sizes.

The course taken by the axone depends upon the position of the neurone. A neurone lying in the roof gives off its axone from the base of the cell, and the axone passes ventrally, branching profusely (Fig.27). A neurone from the side-wall (Fig.28) invariably has its axone emerging from the side of the cell, taking a course toward the limitans externa for a short distance, then branching in a T-shaped manner. The fibres thus formed run parallel with the surface of the brain, one turning into the ventral part of the lobus, the other pursuing an arcuate course out of the hypothalamus (Fig.27, f.b.). Such a fibre is marked by varicosities at intervals, and it bears collateral branches (Fig.28).

The internal structure of two neurones from the lobus inferior is given in Fig.64. The figure also shows how closely these neurones are packed. The nucleus is only fairly large, and it is surrounded by a thick layer of cytoplasm on all sides. the chromatic substance is scanty in amount; it is distributed in a few thin strands. The tigroid masses are not numerous, and most of them are quite small, with just a few large ones

distributed at irregular intervals in the peripheral region of the cell.

4. Supporting Elements.

Associated with the many and crowded nerve-tracts characterizing the structure of the interbrain, there is to be noted a corresponding development of both neuroglia and ependyma.

A neuroglial element has a few stout processes radiating in every direction from the cell-body, often pursuing a markedly tortuous course. They ramify in an exceedingly complicated manner, the finest twigs interlacing to form a dense mat; see Fig. 29. Neuroglia is found in the nuclei of the interbrain, serving to support both the neurones and the terminal fibres occurring there.

Ependyma is found in all parts of the interbrain. The ependymal fibre always extends throughout the entire thickness of nervous matter, from the ventricle to the limitans externa. The fibre branches midway in its course, the several limbs often diverging considerably. The entire fibre-system bears a multitude of fine mossy processes. These features are shown in Fig. 30.

5. Summary of the Interbrain.

The thalamus is small in size and has remained on a low plane of differentiation. It is practicable to distinguish

but two thalamic nuclei. One, the nucleus strati grisei, has become defined from the central gray matter for the reception of fibre-terminations, chiefly those of the tractus strio-thalamicus from the striatum; the axones of the nucleus give origin to the tractus thalamo tectalis. The other thalamic nucleus, the nucleus geniculatum, receives collateral branches from optic fibres. It is wholly inferior to the tectum mesencephali as an optic termination, but it represents the specialized geniculate nuclei of higher forms.

The two nuclei habenulae do not exhibit great disparity in size. An olfactory tract, the tractus olfacto-habenularis, terminates here; the neurones of the nuclei give origin to the tractus habenulo-peduncularis.

The lobi inferiores are the seat of a crowded group of neurones, and the lobes are thereby given a large size. A neurone has a widely spreading dendritic top. Its axone branches in a T-shaped manner.

Supporting elements are strongly developed. The neuroglia is remarkable for the mat-like interlacing of its branches. Ependymal fibres often ramify to a striking degree; they extend through the whole thickness of the neural tube.

SECTION VIII.

THE FOREBRAIN.

The key to the understanding of the vertebrate forebrain was given by Rabl-Rückhard ('83) when he formulated the theory of the membranous pallium for the teleost. The extension of the generalization to other groups has been productive of results which fall into place in an almost schematic way. A quite remarkable series is given by the fishes. This series begins with a condition in the teleost where the entire roof of the forebrain remains non-nervous, and culminates in the dipnoid with a pallium having the essential morphological characters pertaining to all brains of a higher order.

The forebrain of *Mustelus* appears superficially to be somewhat divergent from the direct line of the series, owing to the absence of conspicuous external evidence of its bilaterality. The two striata are fused together into a solid basal mass; there is merely a broad and shallow furrow on the ventral side to mark their plane of contact. The pallium, while a thickened nervous plate as in far higher types of brains, is perfectly continuous between the right and left sides, and it is also confluent in the median plane with the striata below.

These peculiarly compacted characteristics have been the source of no little controversy. Stulnick⁴ has attempted to show as one of the dicta of a series of papers ('24a, '24b, '25, '29) that the selachian forebrain stands entirely apart from that of all other vertebrates. His conclusions were drawn from studies on *Petromyzon*, and they appear to rest upon a misconception as to the extent of the tela choroidea superior. The fallacies of his views have already been pointed out by Burckhardt ('24c), and by Rabl-Rückhardt ('24).

The lateral ventricles and the olfactory lobes of *Mustelus* really anticipate the two-lobed condition of higher forebrains in their essential characters. The lateral ventricles (Fig. 1) are derived from the outer angles of the third ventricle, and they pass the lamina terminalis some distance apart from each other. Their courses lie nearly parallel throughout. Each gives off two diverticula, the olfactory ventricle and a dorsal branch, respectively. The dorsal diverticulum, (Fig. 31, p.v.), is a short and narrow vertical cavity for the pallial eminence; see Subsection 4. This structure, while peculiar to the brains of certain selachians, is nevertheless of some comparative value, as will be evident further on.

The olfactory lobes are massive prolongations of the lateral angles of the forebrain. The primitive character of an olfactory lobe is exhibited by the sharply defined bulbus and tractus, and by the presence of the olfactory ventricle (Fig. 31, ol.v.). This is a slender cavity derived from the outer

side of the lateral ventricle at the level of the pallial diverticulum.

The recessus neuroporicus of Burckhardt ('94a) is of such interest as to deserve especial notice. It appears superficially as a well-marked depression in the median plane a little anterior to the pallial eminences (Fig.1, np.). It is rendered even more noticeable during life by the penetration of blood-vessels here, owing to which fact Bohon ('77) called it the *foramen nutritivum*. This structure is the vestige of a neuropore. Its ontogeny was first described from the ganoiid brain by vonKupffer ('90) as the *lobus olfactorius impar*. Rabl-Rückhardt described its development in the selachian embryo ('93); and Burckhardt ('94i) has identified it in many other vertebrates. The recessus neuroporicus of *Mustelus* retains the character of an open passage in the adult animal (Fig.31, np.), serving as a channel for blood- and lymph-vessels. It is accompanied by a pair of fibre-tracts, right and left, which take this primitive path from dorsum to base of the brain; see Fig.31, m.s.t.

1. The Olfactory Lobe.

It is my purpose to devote a future paper to the entire olfactory apparatus of *Mustelus*, and so a detailed description of the olfactory lobe will not be given here. For the understanding of what follows, it will be sufficient to state that,

in the bulbus, the olfactory neurones of the first order are chained to those of the second order through the usual tangles known as the olfactory glomeruli; and that the neurones of the second order, mitral cells, send their axones through the tractus to terminal stations described further on. Other neurones of the olfactory lobe, having a purely accessory value, need not detain us at present.

2. *The Striatum.*

The striatum is primarily a part of the olfactory apparatus, and its morphology must be interpreted with this fact in mind. Two groups of neurones have become defined from the general mass of the striatum for the especial reception of olfactory impressions. One of these lies next to the lateral ventricle, the epistriatum; while the other one is peripheral in its location, the nucleus postolfactorius. The structure of the principal mass, or general striatum, will be considered after that of the epistriatum.

a. *Epistriatum.*-- The epistriatum is a group of neurones lying ventral and lateral to the lateral ventricle (Fig. 31, estr.). It comprises something like the inner fifth of the entire thickness of the striatum. While not so sharply delimited from the outer levels as Binger ('92) has described for the reptilian brain, the epistriatum of *Mastelus* is readily distinguished

from the general striatum by the smaller size and more closely crowded disposition of its neurones. The neurones are not arranged in any definite order; they are of the Golgi II type, sending their axones ventro-laterally into the striatum; refer to Fig.32.

The cell-body of such a neurone ranges from triangular to polygonal in outline. There are three or four dendrites of only moderate length. These seldom branch except near their bases. They bear a very few gemmules and irregular knobs. The dendrites may extend indifferently in all directions, or they may lie tangential to the *limitans interna*.

The axone may arise from the cell-body, but in many instances observed it emerges from the thick base of a dendrite. It passes into the region of the general striatum, bearing short collateral branches along its whole length, and ultimately dividing into a widely spreading arborization between the neurones of the outer levels. Fig.33 shows the external features of one of these neurones.

The internal structure of the neurone is shown in Fig.35. The nucleus is seen to fill the greater part of the cell-body. It presents an oval form, and has chromatin disposed in a few relatively large masses, each consisting of a central clot with radiating streamers. There is a single nucleolus. The cytoplasm lies chiefly in the bases of the larger dendrites. Its tigroid-bodies are small in size, few in number, and irregular both in form and distribution. Judging from the struct-

are presented by this neurone, it is not characterized by a high degree of metabolic activity.

The epistriatum is one of the nuclei for the termination of olfactory neurones of the second order. Fibres also end here which have ascended in the tractus strio-thalamicus, and have crossed over in the anterior commissure. Some of the terminations occur near the bodies of the cells, but many of the fibres are to be traced to a narrow zone next the lateral ventricle into which the dendrites of the neurones penetrate (Fig. 22, pl. f.). Here the fibres give off branches which run parallel with the laminae interna. The significance of these terminations will be considered under the heading of the general striatum.

Comparing the description and figures given by Johnston ('98a) for the ganoid brain, it would seem that the epistriatum is the more sharply marked in *Mustelus*. Although found in an animal ranking lower in the zoological series, the fact is doubtless a correlative of the more powerful olfactory organs which characterize the selachian organization.

b. General Striatum.-- The median zone common to the pair of striata contains but few neurones. It is occupied chiefly by interlacing fibres of small calibre. The greater number of these are doubtless commissural, but in the more dorsal region there appear to be connections with the pallium.

The great mass of the striatum has neurones scattered

through it without any order of arrangement (Fig.31, str.). These neurones are never closely crowded, there usually being wide intervals between the cell-bodies. Their dendrites are very long, however, so that an interlacing plexus is given throughout the whole field. Fig.34 will illustrate these features.

An individual neurone is shown in Fig.35 drawn to a smaller scale than the other neurones of the striatum because its processes spread so widely. The cell-body may be rounded, oval, or polygonal in outline. There are numerous long and slender branching dendrites. Several dendrites often arise from a common thick stem which might almost be considered a part of the cell-body. A dendrite is noteworthy for the many little crooks which appear in its course, and also for the peculiarly spine-like gemmules which beset it. The latter feature is evidently characteristic of these neurones in fishes, as Van Gehuchten ('94) has noted their presence in the trout, and Johnston ('98a) in the sturgeon.

The cell-nucleus has its chromatin disposed in slender, branching threads, and in minute granules distributed somewhat diffusely (Fig.66). The cytoplasm forms a thick investment to the nucleus on all sides. Its tigroid masses are markedly larger than those found in the neurones of the epistriatum. The largest ones lie in the bases of the dendrites, and these have a triangular form. Other masses of smaller size and of more irregular shape are intercalated between the lar-

ger ones. Tigroids extend into the dendrites for a short distance, only.

The axone takes its origin directly from the cell-body, so far as observed (Fig. 35). It gives off collaterals during the first part of its length. The several axones descend to the base of the forebrain and run posteriorly in the tractus strio-thalamicus for ultimate termination in the thalamus; see Section VII. This conspicuous fibre-tract was described by Rohon ('77) as the *pelunculus cerebri*; by Sanders ('26) as the *crus cerebri*; and by Elinger in his earlier work ('28) as the *basale vorderhirnbündel*.

The general striatum has the type of structure and the associations which are characteristic of motor centres. The large neurones, with their long and widely spreading dendrites, enter into a nexus with the axones derived from a purely sensory centre, the epistriatum. The latter receives, chiefly, impressions of the olfactory order. The neurones of the striatum are indirectly affected through the axones of the epistriatum, carrying, in turn, the nervous disturbance to the inter-brain, whence a relay carries it to the great roof-nucleus of the midbrain for direct connection with the neurones of the body musculature. The enormous olfactory organs of *Mustelus* indicate how important the olfactory sense must be in the economy of the animal, and observation demonstrates the large place taken by olfactory impressions in the location of food. The striatum is evidently the centre for motor reflexes, of which

the sensory neurones chaining the olfactory organ to it constitute one arm, and the neurones intervening between it and the body musculature comprise the other.

c. *Nucleus Postolfactorius*.-- The nucleus postolfactorius is a collection of neurones at the ventro-lateral surface of the striatum near its anterior end (Fig. 31, n.po.). This nucleus is sharply demarcated from the general striatum by the closeness with which its neurones are arranged; Fig. 26 shows the morphology of five neurones as they lie in place. The peripheral zone is occupied by fibres, and also by the dendritic tips of the neurones themselves. The cell-bodies lie in a densely matted tangle of nervous processes just internal to the peripheral layer. A cell-body is somewhat larger than one from the epistriatum. The form ranges from pyramidal to elongated oval. The dendrites are rather few in number, relatively short, branching dichotomously once or twice. They are usually stout processes, gnarled, rough, and irregular, with but few true gemmules. Some neurones send their dendrites radiately in all directions; others take a more or less tangential course; still others are extended between the zone of nerve-fibres at the periphery and the striatum within. A conspicuously felt-like tangle is thus given by all of these interlacing dendrites.

The axone arises from one of the dendrites, so far as observed. It passes into the tractus olfacto-habenularis, cours-

ing posteriorly along the ventral border of the forebrain for ultimate termination in the nucleus habenulae of the inter-brain; see Section VII.

The internal structure of a postolfactory neurone is not of a pronounced motor type. The nucleus is always so large that it touches the periphery of the cell at one or more points, leaving the cytoplasm almost entirely in the bases of the dendrites. The chromatin lies in a fine reticulum. There may be two nucleoli. The tigroid substance is disposed in triangular or irregular bodies of smaller size than those noted for the striatum. These features are shown in Fig. 67.

The nucleus postolfactorius receives many olfactory fibres of the second order. A fibre entering for termination here is seen in Fig. 26, ol.f. This nucleus evidently holds a very different place in the olfactory apparatus from the epistriatum. The latter appears to be a sensory gateway to the striatum, while the postolfactory neurones enter into direct relations with the posterior regions of the brain.

3. *The Nucleus Neuroporicus.*

A group of neurones situated in the region of the recessus neuroporicus gives origin to a special bundle of the tractus strio-thalamicus, the *median bundle* of Klingler ('88). I shall designate this group the nucleus neuroporicus. The neurones of the nucleus neuroporicus lie chiefly behind the external

opening of the neuropore, just beneath the surface of what is really the most anterior part of the pallium. Other neurones of the same group are found at deeper levels, in the striatum, of course. The entire group is distributed, therefore, without regard to the anatomical boundaries which we seek to draw between the pallium and the striatum.

A sagittal section of the neuroporic nucleus stained by the Golgi method exhibits a bewildering nervous tangle. The components of this plexus are the processes of the intrinsic neurones, and the terminations of the olfactory fibres which sweep over from the tractus. The nucleus is seen, then, to be an additional olfactory centre.

Two neuroporic neurones are shown in Fig. 37, exclusive of the maze of nervous processes in which they lie. The cell-body is large, the largest, in fact, of any found in the fore-brain. Its form is quite distinctly polygonal, the number of sides being determined by the number of dendrites. The dendrites are very thick at their bases, and they are some three to five in number. Each one soon breaks up into large branches. The length of a dendrite is relatively short. Its surface exhibits thickenings and minute knobs sparingly distributed.

The axone may arise from the cell-body, but in most instances its origin is traceable to the thick base of one of the dendrites. The several axones from each lateral half of the nucleus run anteriorly to the level of the neuropore, where

they curve upon themselves to follow the course of that channel, forming the medianbündel of Edinger ('88); see Fig.21, m.s.t. The median bundles, right and left, are thus carried posteriorly and ventrally beside the recessus neuroporicus toward the base of the brain. Here each blends with the part of the tractus strio-thalamicus taking origin from the striatum of that side, forming its central portion.

The course taken by the median bundle, curving forward as it does to lie beside the vestige of the neuropore, is certainly fraught with significance. This is probably an ancient route which was at one time quite direct, but the phylogenetic enlargement of the forebrain has carried the recessus neuroporicus and the seat of the neurones ever farther and farther apart.

The neurones of the nucleus neuroporicus probably function as an olfacto-motor centre, supplementary to the chief one represented by the general striatum. The relations of this nucleus to the pallium will be discussed under the following subsection.

4. The Pallium.

The neurones of the pallium lie chiefly in what are called in this paper the *pallial eminences*; see Fig.1 and Fig.31, p.e. I have introduced the definitive term pallial eminence for the hemispherical roof of the dorsal diverticulum of each lateral

ventricle (Fig. 31, p.v.). The earlier anatomists had observed the presence of these elevations in certain selachian fore-brains, but their place in the organization of the pallium has not been recognized heretofore. A pallial eminence is the seat of a crowded group of neurones, and the elevated condition of the mass has probably arisen from the disproportionately rapid growth which occurs here.

The superficial zone of a pallial eminence is occupied almost exclusively by axis-cylinders, the significance of which will be noticed presently. The neurones lie in a crowded aggregate just within. Fig. 38 shows a representative group of these neurones. They are seen to embrace several varieties of form and size, all disposed without arrangement into definite layers.

a. Neurones of the Tractus Pallii.-- The external features of the largest variety of neurone of the pallial eminence will be seen by referring to Fig. 39. This type assumes a variety of guises, but it is characterized by its larger size and by the fact that its axone enters the tractus pallii. The cell-body of such a neurone ranges from broadly oval to distinctly polygonal in form. The dendrites are long and widely spreading processes, arising through thick basal masses at three or four almost equidistant points. A dendrite branches once or twice, dichotomously as a rule, and the terminal lengths become quite slender. Its surface is slightly roughened by minute gemmules. These are far less conspicuous, how-

ever, than the gemmules observed in the neurones of the striatum.

The internal structure of one of these neurones is shown in Fig. 68, p.t.n. The organization is markedly motor in type. There is an abundance of cytoplasm investing the nucleus on all sides. The nucleus is a sharply defined, central body, with a single nucleolus, and chromatin which is disposed in a condition strongly suggestive of a reticulum, although not actually appearing so. The tigroid-bodies are quite large in the region of the nucleus, the largest, in fact, of any tigroids found in the forebrain. More slender tigroids extend into the dendrites for some distance. In the cell figured, the axone exhibits a small axone-hillock of oval form.

The axone arises from the cell-body, (Fig. 68, p.t.n.), or from the thickened base of a large dendrite, (Fig. 39). It pursues a straight course, although one with many local sinuosities. The several axones of this class come to lie in the superficial zone, and they are gathered into a longitudinal bundle which lies as a broad cap on the neurone-aggregate of the pallial eminence (Fig. 31, tr.p.). This is the beginning of the tractus pallii. The pallial tract runs backward to the great posterior curve of the forebrain, where it dips ventrally to the base and enters the interbrain. Here it decussates and passes onward toward the oblongata. The tractus pallii is the mantelbündel of Gänger ('83).

b. Associative and Commissural Neurones.-- A second type of neurone found in the pallial eminence is distinguished from the preceding one by its associative or commissural value, and it is also readily recognizable by its smaller size (Fig.40). The cell-body tends to retain a globular form. It gives origin to two or three dendrites which radiate from it at equidistant points. The dendrites are only moderately stout, and they are never of great length. They branch but a few times. Their surface is sparsely studded with small gemmules. The axone may terminate on the same side of the brain; or it may enter the pallial commissure, (Fig.31,p.c.), for decussation, terminating in the opposite half. The neurone shown in Fig. 40 is an example of the commissural class.

The internal structure of a neurone of either the associative or the commissural type is drawn in Fig.68, as.n. The nucleus is a subspherical mass, so large that it occupies practically the whole of the cell-body. The only cytoplasm distinguishable is that which composes the bases of the dendrites. The nucleus stains quite deeply, owing to the dense reticulum of chromatin which pervades it. The cytoplasm has only a few tigroids of small size, an evidence of a feeble degree of activity for this type of neurone.

c. Cajal Neurones.-- Still a third type of neurone is clearly the representative of the *Cajal cell* which Ramon y Cajal ('91) described from the cerebral cortex of the rabbit,

and which Retzius ('93), and Veratti ('97) have designated after the name of the discoverer. Cajal neurones have been observed in all of the higher vertebrates by various investigators, and their identification in the brain of *Mustelus* makes it probable that they are common to all groups.

A Cajal neurone is drawn in Fig.41. This neurone occupies a superficial position, just beneath the stratum of fibres noted above; refer to Fig.31. The cell-body is an irregularly elongate-oval, with its major axis horizontal. From its opposite extremities, thick dendrites arise which run more or less nearly parallel with the *limitans externa*. A dendrite does not have marked turns in its course. It gives off branches along its upper margin which ascend toward the surface of the brain, while a few branches are derived from its under side and penetrate to deeper levels. The dendritic surface bears small gemmules and larger bosses in considerable numbers.

The axone is a direct continuation of one of the dendrites. Its point of origin is indicated by the surface becoming smooth and the course more irregular. The axone continues to hold a course tangential to the *limitans externa*, and it terminates through a few small branches at no great distance from its point of origin. This type of neurone is evidently purely associative, linking together areas not widely separated.

Structurally, the Cajal neurone is somewhat peculiar (Fig. 69). The tigroid substance is collected into a few lumps of relatively large size. These are disposed irregularly in the

great masses of cytoplasm which lie lateral to the nucleus. The nucleus is eccentric in position, leaving but a thin pellicle of cytoplasm on one of its sides. The chromatin is grouped into a few strands having conspicuously thickened nodes at intervals.

1. General Considerations on the Pallium.-- The pallium of the selachian is really a primitive representative of the stem giving origin to the pallia of amphibians, reptiles, birds, and mammals. The continuity of its two halves, contrasted with the two-lobed condition of the higher type, has caused many writers to rank the selachian pallium as a divergent branch. The correctness of the view set forth in this paper will appear when the significance of the relations which exist between certain neurones of *Mustelus* have been considered.

It has been shown that the ventral border of a lateral ventricle is the seat of one olfactory termination, the epistriatum. The epistriatum tends to become extended around the side of the ventricle toward the pallium. Axones from the marginal neurones of this olfactory centre enter the pallium, thus serving to link that region indirectly with the olfactory organ. Besides this source of impressions, the olfactory centre of the nucleus neuroporicus radiates an influence to the pallium, of which it is really a part. The pallium of *Mustelus*, therefore, is seen to have a general association with the olfactory mechanism.

It has been shown by Gdinger ('96) that the special pallial olfactory conducting path characteristic of higher vertebrates appears for the first time in the brain of the reptile. Both Gdinger and Herrick have also shown that the first sense to thus enter the field of consciousness is the olfactory one. The pallium of the selachian really anticipates the reptilian olfactory connection, although, of course, in a much simpler way. In *Mustelus*, we therefore find quite a primitive condition represented.

So far as we may be permitted to interpret morphological facts, the pallium of *Mustelus* would appear to be a long-distance motor centre of the olfactory apparatus. Other olfactomotor centres there certainly are in abundance. Both the general striatum and the nucleus neuroporicus contribute motor neurones to the tractus strico-thalamicus; while the nucleus post-olfactorius sends a tract to the nucleus habenulae. These centres obtain connection with posterior regions only through relays in both the interbrain and the midbrain. The pallium, on the other hand, sends its tract directly through the base of the interbrain toward the nuclei of the great nerves of the oblongata. The tractus pallii, therefore, gives the olfactory sense an additional hold on the nervous system, a series of connections which cannot obtain, of course, in those fishes with membranous pallia.

The phylogenetic development of the pallium of selachians would thus appear to be the outcome of the great dependence

which these fishes place upon the olfactory apparatus in the search for food. In higher vertebrates, as the olfactory sense becomes linked to the pallium through stronger bonds, and as other senses make pallial connections, one after another, this part of the brain takes on functions of an ever higher value. In *Mustelus*, there is merely an anticipation of pallial possibilities.

5. Supporting Elements.

Both neuroglial and ependymal elements are present in the forebrain of *Mustelus*.

Ependyma is found radiating from every part of the lateral ventricle, and its characters are nearly uniform for the several regions. The ependymal cells have their nuclei situated at slightly different levels, and so a broad zone next to the ventricle presents chiefly nuclei. The shape of the cell-body is influenced by the position of its nucleus, of course, but the broadened part is usually not directly in contact with the ventricle. The ependymal fibre runs straight outward from the cell-body, as a rule, and it reaches entirely to the *limitans externa*. It does not branch, its size remains nearly uniform, and its course is only slightly irregular. It bears a greater or less profusion of delicate, mossy twigs of short length. The inner portions of two ependymal elements are shown in Fig. 42.

Neuroglia is found in the several parts of the forebrain where nerve-cells are grouped in numbers. While the specific forms assumed by neuroglial elements exhibit considerable diversity, all are referable to but one type. From an irregular cell-body, numerous fine processes extend in all directions for a short distance, branching profusely as they proceed. The ultimate twigs are of quite minute size, and hence it is that the whole presents a characteristically mossy appearance. Fig.43 illustrates the features of a representative specimen.

6. Summary of the Forebrain.

A fairly well-defined epistriatum is present, receiving olfactory and other terminations. Its neurones are of the Golgi II type, sending their axones into the striatum, in the main. The axones from marginal zones enter the pallium.

Neurones with widely spreading dendrites are arranged in open order in the striatum. Their axones enter the tractus strio-thalamicus for termination in the thalamus. The striatum appears to be an olfacto-motor centre.

The nucleus postolfactorius is a densely crowded group of neurones. Olfactory fibres terminate here, and the derivative axones form the tractus olfacto-habenularis.

A group of large neurones in the vicinity of the recessus neuroporicus gives origin to the median portion of the tractus strio-thalamicus. This paired tract accompanies the neuropore

for some distance. The nucleus neuroporicus is a third olfactory centre.

The pallium has its two halves fused in the median plane. Its most important region is the pair of pallial eminences. Each of these has a special extension of a lateral ventricle. The neurones of a pallial eminence are not arranged in layers, but it is practicable to recognize three distinct forms:

(1) The neurones of the tractus pallii, the largest variety, their axones comprising the tractus pallii. (2) Commissural and associative neurones, the axones of which are distributed in the pallium itself, a special decussation of commissural fibres occurring in the median plane. (3) Cajal neurones, lying tangential to the limitans externa.

The pallium of *Mustelus* is regarded by the writer as a primitive representative of the stem giving origin to the pallia of amphibians, reptiles, birds, and mammals. It anticipates the olfactory connections of the reptilian brain. The tractus pallii is interpreted as giving the olfactory sense a hold on the nervous system in addition to that provided by the epistriatum and striatum, and the neuroporic and postolfactory nuclei. The phylogenetic development of the pallium of selachians is believed to have been the outcome of the great dependence placed upon the olfactory sense by these animals.

SECTION IX.

GENERAL SUMMARY AND CONCLUSION.

Special problems relative to the several parts of the brain have already been discussed in the foregoing pages; while summaries have been placed at the close of each of the sections. There yet remain for consideration a few topics of more general scope growing out of the study as a whole. Before proceeding to these questions, however, it will be desirable to review briefly the most important results which have been obtained.

1. *General Summary.*

The Oblongata of *Mustelus* has become only slightly divergent from the structural plan of the primitive neural tube.

The ventral cornu of the spinal cord is continued into the oblongata as the nucleus of the VI nerve, and as the scattered commissural and tract-neurones of the formatio reticularis.

The viscero-sensory system has had annexed to it a complex of peripheral sense-organs. The communis system which results from this union is represented by components of the VII, IX, and X nerves. The lobus vagi is the centre of the system.

Fewer fibres enter the fasciculus communis than in either the teleosts or the amphibians.

The visceromotor nucleus gives origin to the motor fibres of the V, VII, IX, and X nerves. The axones enter their nerves chiefly through the medium of the fasciculus longitudinalis dorsalis. The nucleus receives impressions radiated from the lobus vagi.

The general cutaneous nucleus is the homologue of the dorsal cornu of the spinal cord. General cutaneous fibres, components of the V, IX, and X nerves, terminate in both the substantia gelatinosa and the deeper part of the nucleus. Many fibres of the system enter the spinal V tract for ultimate distribution in the spinal cord.

The tuberculum acusticum is phylogenetically young. It may have been derived from the structures of the dorsal cornu. Fibres of the acustico-lateral system terminate in the tuberculum acusticum. These are components of the VII, VIII, and X nerves. Neurones are present in the tuberculum acusticum of the molecular, granular, and Purkinje types, equivalent morphologically to those of the cerebellum.

The Cerebellum is relatively large in *Mustelus*. This fact is to be interpreted from the strong development of the sense of equilibrium in the animal. The structural plan of the cerebellum is the same as that characteristic of higher vertebrates, the differences being due to greater simplicity of detail.

The evidence is for the origin of the cerebellum, in the phylogeny of the vertebrates, as a fused outgrowth of the pair of tubercula acustica. The organ represents a specialization of that part of the oblongata forming the original terminal station for the acustico-lateral system.

The Midbrain appears to have its organization arranged contributory to the roof-nucleus. This is a group of giant neurones, the axones of which enter into and very largely compose the fibre of Reissner. The roof-nucleus and Reissner's fibre, together with the motor neurones of the spinal cord, provide a direct path for motor reflexes between certain senses and the body musculature. The senses thus mediated are, primarily, the olfactory and the visual, but the acustico-lateral and the general cutaneous systems may be represented also.

The stratum medullare profundum is an important highway into which there are traceable optic fibres, axones from the tectum mesencephali, fibres of the olfactory apparatus, and fibres from posterior regions. Fibres emerge from the stratum to terminate near the cells of the roof-nucleus.

The tectum mesencephali receives practically all of the optic fibres in *Mustelus*. Three zones of neurones are recognizable in the tectum, with optic terminations in all of them. The deepest of the three layers has a more generalized structure than the corresponding zone of the teleost.

The Interbrain is the seat of several important relays between the forebrain and the posterior brain-segments.

The thalamus is but slightly differentiated. Only two thalamic nuclei are recognizable. The nucleus strati grisei receives fibres, chiefly from the tractus strio-thalamicus; its axones give origin to the tractus thalamo-tectalis. The nucleus geniculatum receives collateral optic terminations. It is wholly inferior as an optic centre to either the tectum mesencephali of *Mustelus*, or to the specialized geniculate nuclei of higher forms.

The two nuclei habenulae are not greatly unequal in size. The lobi inferiores are the seat of a crowded group of peculiar neurones.

The Forebrain is regarded by the author as anticipating the forebrains of higher vertebrates in many respects. A fairly well-defined epistriatum is present, the axones from which enter both the striatum and the pallium. The striatum is an olfacto-motor centre; its axones enter the tractus strio-thalamicus for termination in the thalamus. An accessory bundle of the tractus strio-thalamicus is derived from the nucleus neuroporicus. An additional olfactory centre is provided by the nucleus postolfactorius.

The pallium has its neurones grouped, without arrangement into layers, chiefly in the pallial eminences. Three varieties of neurones are to be distinguished. The pallium receives

impressions radiated from the adjacent olfactory nuclei; it therefore anticipates the olfactory connections of the reptilian and higher brains. The tractus pallii, arising from the pallial neurones, is regarded as giving the olfactory sense a quite direct connection with posterior regions.

3. Conclusion.

To one who has read this far, it must be evident that there is a most remarkable structural similarity between the brain of *Mustelus* and the brains of higher vertebrates. The results obtained by me do not bear out the conclusions of Szczawinska ('99) relative to the very low plane occupied by the selachian neurones; see Section II, 2. The neurones of *Mustelus* are, of course, simpler in their external morphology, and their architectural relations are of a far less complicated order, yet it is none the less true that they anticipate the conditions found in higher vertebrates in all important particulars. Such a fact is certainly the more remarkable when the great differences in the scale of general organology are taken into account. The fact can only be interpreted to mean that the nervous system of the primitive vertebrate had its essentials of organization well defined before the divergence of the several phyla occurred. A brain of the type presented by the selachian of to-day has not become sufficiently specialized during the lapse of time entirely to mask the ancestral charac-

teristics. The brain of one of the higher vertebrates embodies many modifications of the original plan, wrought in the course of its gradual evolution. These alterations may even become more conspicuous than the primary structures upon which they have been superposed, and it is only through comparisons with a less differentiated condition that we can hope to distinguish the new from the old.

A comparative study of the several brain-segments of *Mustelus* is productive of some results that might not have been anticipated. The cerebellum is marked by an organization out of all proportion to that of adjacent regions, an organization, moreover, far more highly differentiated than is presented by the cerebellum of either the amphibian or the reptile. The oblongata, on the contrary, has retained the plan of structure of the primitive neural tube without the intervention of profound changes. It is due to this fact that homologies between the oblongata and the spinal cord are so readily traced in this animal. A more extreme degree of simplicity is found in the interbrain, the thalamus having such a slight differentiation as to make comparisons between it and higher thalami somewhat difficult. Finally, the forebrain is far in advance of the forebrains of other fishes. Contrast the membranous pallium of the teleost or the ganoid with the nervous pallium of *Mustelus*, which, as has been pointed out in the preceding pages, anticipates the olfactory associations of higher brains to a noteworthy degree.

These illustrations clearly point to an underlying principle. The organization of the brain is the expression of the adjustment which has constantly taken place between the race of animals and the stimuli to which they have been subjected. This relationship between nervous organization and peculiarities in the environment is such a close one that the degree of development of the several parts of the brain may be very unequal indeed. And hence it is that the cerebellum of *Mustelus* is so highly organized, for this is the correlative of the powerful swimming capacity of the animal, requiring an adequate mechanism of equilibration. The forebrain, with its luxurious development of neurones, has arisen in connection with the large place occupied by olfactory impressions in the *Selachii*.

Morphological data in neurology must necessarily provide the foundation for all physiological work, but it is none the less important that morphological facts should have the check of experimental evidence wherever this is possible. Nowhere is there to-day a more urgent need for careful observations of this character than in the group of the fishes, where nervous processes are of such a simple order as to introduce relatively few complications. Thorndike ('99) has made at least a beginning in this field for the teleosts. This observer placed a screen with but one opening across the course in which *Fundulus* desired to swim. He found that after several repetitions the animal "learned to get out". Here, it would seem, there was a true memory of previous activities in the absence of any nervous

pallium at all, a very suggestive fact in connection with the interpretation placed in the present paper upon the pallium of *Mustelus*. An extension of the scope of experimental work on the fishes will certainly prove fruitful for comparative neurology in so many ways that the writer feels impelled to bespeak a larger place for this kind of work in our investigations.

Since the promulgation of the neurone concept by Waldeyer in 1891, no work has demanded more critical attention than that on the ultimate fibrillar structure of the nervous system, studies with which the names of Apáthy, Bethe, and Nissl will ever be connected. An investigation of neuro-fibrils obviously lies beyond the bounds set for the present research, and observations concerning them in *Mustelus* must await another opportunity for expression. In the meantime, I would join with the protest made by A. Meyer ('99), Parker (1900), and Verworn (1900) against the tendency to elevate the results of specific methods into an exclusive dogma. Although spoken from a different vantage-point, the words of Golgi (1900) may well be quoted here: "The knowledge which we possess, either anatomical or physiological, is not yet such as to permit us to interpret with certainty the greater number of the facts discovered, much less to attempt doctrinal constructions of a high order on the functional mechanism of the nervous elements".

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SECTION XI.

DESCRIPTION OF THE FIGURES.

All of the figures have been drawn with the aid of the camera lucida. A uniform scale of magnification could not be adopted because of the wide range in the sizes of the neurones. In order that comparisons may be facilitated, the scale of diameters of the drawing as reproduced is given in the description of each figure. The orientation is accurately maintained in all of the drawings, the dorsal parts being uppermost as the figure appears on the plate.

REFERENCE LETTERS.

- a.f.-- Ascending fibre
- a.l.f.-- Acustico-lateral fibre
- aq.-- Aqueduct of Sylvius
- ar.-- Terminal arborization
- as.n.-- Associative neurone
- ast.-- Astrocyte
- ax.-- Axone
- ax.h.-- Axone-hillock
- b.f.-- Basal nerve-fibre
- bv.-- Bloodvessel
- cb.-- Cerebellum
- cb.cr.-- Cerebellar crest
- cb.inf.-- Inferior lobe of the cerebellum
- c.f.-- Communis fibre
- c.g.m.-- Central gray matter
- ch.-- Chiasma

c.n.-- Commissural neurone
 dc. s.m.p.-- Decussation of the stratum medullare profundum
 d.n.-- Deeper neurones
 e.l.-- External division of the lateral ramus of the stratum medullare profundum
 e.m.-- External division of the median ramus of the stratum medullare profundum
 ep.-- Ependyma
 estr.-- Epistriatum
 ext.-- Limitans externa
 fb.-- Forebrain
 f.c.-- Fasciculus communis
 f.l.d.-- Fasciculus longitudinalis dorsalis
 f.s.t.-- Fibre of the tractus strio-thalamicus
 g.c.f.-- General cutaneous fibre
 g.c.n.-- General cutaneous nucleus
 g.l.-- Granular layer
 hy.-- Hypophysis
 III.-- The oculomotorius
 i.l.-- Internal division of the lateral ramus of the stratum medullare profundum
 i.m.-- Internal division of the median ramus of the stratum medullare profundum
 inf.-- Infundibulum
 inf.v.-- Ventricle of the infundibulum
 int.-- Limitans interna
 IX.-- The glossopharyngeus
 i.z.-- Inner zone
 l.i.-- Lobus inferior
 l.v.-- Lateral ventricle
 l.vg.-- Lobus vagi
 mb.-- Midbrain
 m.f.-- Median nerve-fibres, longitudinal bundle
 m.f'-- Median nerve-fibres, transverse bundle
 m.l.-- Molecular layer
 m.n.-- Middle neurones
 m.s.t.-- Median bundle of the tractus strio-thalamicus
 n.g.-- Neuroglia
 n.gen.-- Nucleus geniculatus

n.h.-- Nucleus habenulae
 n.III.-- Nucleus of the oculomotorius
 n.IV.-- Nucleus of the trochlearis
 np.-- Recessus neuroporicus
 n.po.-- Nucleus postolfactorius
 n.s.g.-- Nucleus strati grisei
 obl.-- Oblongata
 ol.f.-- Olfactory fibre
 ol.v.-- Olfactory ventricle
 op.f.-- Optic fibre
 p.c.-- Pallial commissure
 p.e.-- Pallial eminence
 p.l.-- Layer of the neurones of Purkinje
 p.t.n.-- Neurone of the tractus pallii
 p.v.-- Ventricle of the pallial eminence
 r.lat.X.-- Ramus lateralis vagi
 r.n.-- Roof-nucleus of the midbrain
 r.n.t.-- Tract of the midbrain roof-nucleus
 s.m.p.-- Stratum medullare profundum
 s.n.-- Superficial neurones
 sp.V.-- Spinal V tract
 str.-- General striatum
 t.a.-- Tuberculum acusticum
 t.c.p.-- Tela choroidea posterior
 t.c.s.-- Tela choroidea superior
 th.-- Thalamus
 t.n.-- Tract-neurone
 tr.cb.s.-- Tractus cerebello-spinalis
 tr.p.-- Tractus pallii
 v.m.f.-- Viscero-motor fibre
 v.m.n.-- Viscero-motor nucleus

PLATE I.

Fig.1. Median sagittal section through the brain of an adult *Mustelus*. The right lateral ventricle of the forebrain is indicated in broken outline. Natural size.

Fig.2. Composite transverse section of the oblongata at the level of the IX nerve. The Golgi method. Outline $\times 14$.

Fig.3. Structural elements from the formatio reticularis on the right side of the oblongata. The commissural neurone (c.n.) sends its axone across the median raphe. The upper neuroglial cell (ng.) has its longer axis extended in the radius of the oblongata. The Golgi method, $\times 230$.

Fig.4. Two neurones from the lobus vagi of the oblongata, and a communis fibre (c.f.) having its terminal arborization near a cell not drawn. The axones are directed into the deeper nervous matter. The Golgi method, $\times 230$.

Fig.5. Oblongata; a small area from the substantia gelatinosa of the general cutaneous nucleus. The minute neurone (a) has a profusely branching axone, with which the dendrites of (b) interlace to form a complex tangle; in this, the general cutaneous fibre (g.c.f.) has its termination. The axones of (b) and (c) penetrate the deeper levels of the nucleus. The Golgi method, $\times 230$.

Fig.6. Oblongata; a neurone from the deeper part of the left general cutaneous nucleus. A general cutaneous fibre (g.c.f.) is seen breaking up into a terminal arborization. The Golgi method, $\times 230$.

Fig.7. Oblongata. Two Purkinje neurones from the cerebellar crest of the tuberculum acusticum. An acustico-lateral fibre (a.l.f.) is seen terminating near the one on the right. The Golgi method, $\times 230$.

Fig.8. Oblongata; ependymal fibres from the outer level of the general cutaneous nucleus. The Golgi method, $\times 230$.

Fig.9. Ependymal fibres from the ventral oblongata, forming a bundle in the formatio reticularis. The Golgi method, $\times 230$.

Fig.10. Ependyma from the lobus vagi of the oblongata. The Golgi method, $\times 230$.

Fig.11. Neuroglia cell from the general cutaneous nucleus of the oblongata. The Golgi method, $\times 230$.

PLATE II.

Fig.12. Sagittal section through the entire cerebellum showing its folds, the form of its ventricle, its neurone-layers, and its principal masses of nerve-fibres. The Wolters method. Outline $\times 8$.

Fig.13. Neurone of Purkinje from the cerebellum. The Golgi method, $\times 230$.

Fig.14. Neurone from the molecular layer of the cerebellum. The greatest extension of the dendrites is parallel with the surface of the cerebellar fold. The Golgi method, $\times 230$.

Fig.15. Three representative neurones from the granular layer of the cerebellum. The intervening cell-bodies are omitted for the sake of clearness. The axones are cut across at the juncture of the granular with the molecular layer; see Fig.16, and the description in the text. The Golgi method, $\times 230$.

Fig.16. Axones in the molecular layer of the cerebellum passing transversely across the organ, derived from the neurones of the granular. Several ascending axones are to be seen just previous to their T-shaped division. The Golgi method, $\times 230$.

Fig.17. Neurone of the Golgi II type from the granular layer of the cerebellum. The Golgi method, $\times 230$.

Fig.19. Neuroglial cells from the cerebellum. The cell-bodies lie between the neurones of Purkinje. An astrocyte is seen at (ast.); and a Bergmann's fibre at (bg.f.). The Golgi method, $\times 230$.

Fig.20. Transverse section of the midbrain. The Wolters method, $\times 14$.

Fig.21. Transverse section of the entire thickness of the left optic lobe, showing the neurones of the tectum mesencephali. The Golgi method, $\times 46$.

PLATE III.

Fig.18. Ependymal elements from the cerebellum. For the sake of clearness, only a few of the fibres proper to the region have been represented. The Golgi method, $\times 230$.

Fig.22. Neurone from the middle layer of the tectum mesencephali. The Golgi method, $\times 300$.

Fig.23. Neurone from the deeper layer of the tectum mesencephali. The Golgi method, $\times 230$.

Fig.24. Interbrain. Transverse section through the left thalamus at the level of the chiasma. The dotted lines indicate the extent of the thalamic nuclei. The Golgi method. Outline $\times 30$.

Fig.25. Interbrain; a neurone from the nucleus habenulae. The Golgi method, $\times 230$.

Fig.26. Interbrain. Two neurones from the right side of the infundibulum, together with the structures adjacent to them. The Golgi method, $\times 46$.

Fig.27. Interbrain. Transverse section of the right lobus inferior. The Golgi method. Outline $\times 30$.

Fig.30. The inner half of an ependymal element from the hypothalamus. The Golgi method, $\times 150$.

PLATE IV.

Fig.28. Neurone of the hypothalamus from the right lobus inferior. The T-shaped branching lies parallel with the limitans externa. The Golgi method, $\times 230$.

Fig.29. Neuroglial element from the nucleus habenulae. The Golgi method, $\times 230$.

Fig.31. Composite transverse section of the forebrain. The Golgi method. Outline $\times 9$.

Fig.32. A small area from the left epistriatum. The neurones send their axones into deeper levels. The Golgi method, $\times 46$.

Fig.33. Neurone from the right epistriatum, its axone passing into the general striatum. The Golgi method, $\times 230$.

Fig.34. An area from the left general striatum to show the arrangement of the neurones. The Golgi method, $\times 46$.

Fig.35. Neurone from the general striatum. The Golgi method, $\times 150$.

PLATE V.

Fig.36. A small area of the nucleus postolfactorius to

show the character and arrangement of its neurones, together with the termination of an olfactory fibre. The Golgi method, × 230.

Fig.37. Two neurones from the nucleus neuroporicus. The section was taken in the sagittal plane. The Golgi method, × 230.

Fig.38. A group of neurones from the right pallial eminence. The Golgi method, × 67.

Fig.39. Neurone from the right pallial eminence. Its axone finally enters the tractus pallii. The Golgi method, × 230.

Fig.40. Neurone from the right pallial eminence sending its axone into the pallial commissure. The Golgi method, × 230.

Fig.41. A neurone of Cajal from the left pallial eminence. The Golgi method, × 230.

Fig.42. Ependyma from the left striatum. The fibres really extend entirely to the limitans externa, but only the inner portion has been represented. The Golgi method, × 230.

Fig.43. Neuroglial element from the pallial eminence. The Golgi method, × 230.

PLATE VI.

Fig.44. A tract-neurone lying just to the left of the median raphe of the oblongata, sending its axone into a tract of the opposite side. The Nissl method, × 900.

Fig.45. Commissural neurone from the right side of the oblongata; its axone passes to the left across the median raphe. The Nissl method, × 1120.

Fig.46. Neurone from the right lobus vagi. The Nissl method, $\times 1120$.

Fig.47. Neurone from the right viscero-motor nucleus of the oblongata. The axone passes dorsal to the fasciculus communis on its way to the fasciculus longitudinalis dorsalis. The Nissl method, $\times 900$.

Fig.48. Oblongata. Two of the deeper neurones from the right general cutaneous nucleus just dorsal to the lobus vagi; they lie between the bundles of the spinal V tract, indicated in outline. The Nissl method, $\times 1120$.

PLATE VII.

Fig.49. Two Purkinje neurones from the cerebellum. The Nissl method, $\times 1120$.

Fig.50. Two neurones from the molecular layer of the cerebellum. These lie unusually close together. The Nissl method, $\times 1120$.

Fig.51. Five neurones from the granular layer of the cerebellum. A nerve-fibre is seen ascending between them to the molecular layer. The Nissl method, $\times 1120$.

Fig.52. Neurones of the superficial and middle layers of the tectum mesencephali. The Nissl method, $\times 900$.

Fig.53. A group of the spindle-shaped neurones characteristic of the deeper layer of the tectum mesencephali. The Nissl method, $\times 900$.

Fig.54. A group of the stellate neurones found at intervals in the deeper layer of the tectum mesencephali. The Nissl method, $\times 900$.

Fig.55. The region immediately dorsal to the aqueduct of sylvius, showing the disposition of the neurones of the roof-nucleus. Methylene-blue, $\times 89$.

Fig.56. Neurone from the left half of the midbrain roof-nucleus. The Nissl method, $\times 900$.

Fig.57. Neurone from the roof-nucleus of the midbrain, right side, together with a part of the stratum medullare profundum. Two fibres are seen to emerge from the stratum to end in arborizations near the neurone. Iron haematoxylin staining. Outline $\times 496$; details from the homogeneous immersion.

PLATE VIII.

Fig.58. Midbrain. Sagittal section through the nuclei of the oculomotor and trochlear nerves. Methylene-blue, $\times 89$.

Fig.59. Neurone from the nucleus of the III nerve. The tigroid masses in the region of the nuclear membrane are remarkable for their large size. The Nissl method, $\times 900$.

Fig.60. Neurone from the nucleus of the IV nerve. The Nissl method, $\times 1120$.

Fig.61. Ependyma from the optic lobes. The ependymal fibres are represented to the boundary of the central gray matter, only; see Fig.21 for the entire fibre. Combination of iron haematoxylin and methylene-blue staining, $\times 1120$.

Fig.62. Interbrain. Two neurones from the nucleus strati grisei of the thalamus. The Nissl method, $\times 1120$.

Fig.63. A characteristic group of neurones from the nucleus geniculatum of the thalamus. The Nissl method, $\times 1120$.

Fig.64. Two neurones from the left lobus inferior. Their dendrites are directed toward the limitans externa. The Nissl method, $\times 1120$.

Fig.65. Forebrain. A group of three neurones from the epistriatum. The Nissl method, $\times 1120$.

Fig.66. A neurone of the general striatum. The Nissl method, $\times 1120$.

Fig.67. A group of five neurones from the nucleus postolfactorius. The Nissl method, $\times 1120$.

Fig.68. Neurones from the left pallial eminence. The neurone of the tractus pallii (p.t.n.) shows an axone-hillock. The smaller neurone (as.n.) is of the associative type. The Nissl method, $\times 1120$.

Fig.69. Cajal neurone from the lateral part of a pallial eminence. The Nissl method, $\times 1120$.

LIFE.

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I, Gilbert Logan Houser, was born on an Iowa farm in 1868. My preparatory training was given by several academies and colleges not far from home. Entering the University of Iowa, I pursued an undergraduate course in that institution for four years, receiving the degree Bachelor of Science in 1891. A year was subsequently spent in graduate study at the University of Iowa, leading to the degree Master of Science, 1892. My graduate studies have since been continued in connection with the University of Chicago and the Johns Hopkins University.

My earlier investigations were chiefly in the fields of geology and paleontology. The dissertation for the Master's degree was a critical study of the "Genera of Paleozoic Corals of the Order Madreporaria". Later, the Iowa Geological Survey commissioned me to examine certain building-stones and lime-burning rocks of eastern Iowa; my report on this subject is published in the Report of the Iowa Geological Survey, Vol.I. Receiving an appointment as Instructor of Biology in the University of Iowa, my studies have since flowed entirely in biological channels.

A biological expedition to the West Indies of three months, and four season's work at the Marine Biological Laboratory of

Woods Holl have provided both the opportunity and the inspiration for the pursuit of numerous researches. Two papers have been published as the result of these studies:-- "The Uses of Formaldehyde in Animal Morphology", and "The Nerve-Cells of the Shark's Brain".

Since my appointment as an Instructor in 1892, the University of Iowa has gradually advanced me to positions of larger and larger responsibility, culminating in my election to the Professorship of Animal Morphology and Physiology in June 1897, a position which I still hold. At my urgent request, I was granted leave of absence in September 1900 for a year of graduate study. I have chosen to spend that year at the Johns Hopkins University.

I hold membership in The American Morphological Society, The American Society of Naturalists, and The Iowa Academy of Sciences.

Baltimore, May, 1901.