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OBSERVATIONS ON THE INNERVATION OF THE INTRACRANIAL VESSELS.

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With Plate I.

The research, the results of which are here given, was begun some two years ago, at which time the only observations, familiar to me, dealing with the innervation of the vessels of the pia-mater and brain, were those of Lovell Gulland (1) and Obersteiner (2). Gulland (1), at the suggestion of Dr. Batty Tuke, examined the brain vessels, with a view of ascertaining "whether it was possible to demonstrate nerve-fibrils in the walls of the intracranial bloodvessels." " The methods employed were the Golgi method with various modifications and the Ehrlich methylene blue method. The brains examined were those of cats and rabbits, adult, young and embryonic and a number of human brains obtained as fresh as possible from the post-mortem room." His results are summarized by himself as follows: " The net result of all these observations was that neither by the silver, the mercury, nor the methylene blue method could I succeed in demonstrating any nerve-fibers in the walls of the pial vessels nor of the intracerebral vessels. In Golgi preparations, the bloodvessels, especially the smaller ones, are often impregnated as a whole; sometimes a partial impregnation of this sort gives an appearance like a nerve plexus. Again in the larger vessels especially, the longitudinal network of elastic fibers is often impregnated, but it is easy to distinguish this from the nerve plexus of ordinary arteries. The processes of the neuroglia cells attached to an artery and running along it, as they often do, for a little way, might also give rise to error."

Obersteiner (2) describes a preparation of the pia-mater, taken from the convexity of the human brain, stained in gold chloride, which has been in his collection for many years, and which contained a small vessel (figured by him), on which a number of relatively large nerve-fibrils were found. He states that in this preparation, only the coarser nerve-branches seemed stained, the finer branches, with their terminations remaining unstained. "Es ist also" (he adds) "damit der directe anatomische Beweis geliefert, dass die feineren intracraniellen Gefässe, wenigstens innerhalb der Pia mater, ihre eigenen Nerven besitzen. Daraus darf doch ohneweiters der Schluss gezogen werden, dass diesen Gefässen auch die Fähigkeit zukommt, sich activ, selbstständig zu contrahiren, respective zu dilatiren."

These contradictory statements, taken in connection with the fact that physiologists very generally deny the existence of vaso-motor fibers in the intracranial vessels—if one may be allowed to judge from their writings—led me to re-investigate the question under consideration. Sometime after the completion of my own observations, I was gratified to see a short abstract, in which Gulland (3) states that on renewed investigation he had been able to find nerves on the intracranial vessels. He there states that: "In material from human brains and those of dogs prepared by the Cox's method, given him by Dr. W. Ford Robertson, he found nerves on a number of the vessels, and saw that they presented the usual appearance of perivascular nerve plexuses." At the Edinborough meeting of the British Medical Association, microscopical specimens were shown in proof of this fact. This abstract further states, that Dr. H. Morrison, of London, had also been able to demonstrate these nerves by Sihler's hæmatoxylin method. In consideration of the fact that my own work was practically completed before I became cognizant of the observations just given, and further, since the methods adopted by me seem to differ in every respect from those followed by the English observers, I see no inconsistency in presenting my own results at this time. The answer to the question of the existence or non-existence of vaso-motor nerves on the intracranial vessels is so necessary to a

correct understanding of the circulation of the brain, both in its physiological and pathological aspect, that corroborative results obtained in the investigation of this fundamental anatomic fact, can but extend and substantiate our knowledge of brain physiology.

In my own experiments I have used dogs, rabbits and cats. For staining the nerves I have used the methylen blue method of Ehrlich. After anaesthetizing the animal, the carotid was exposed in the neck, on one side, and a canula inserted cerebralward. I then injected of a 1% methylen blue solution, made up in normal salt solution, a quantity sufficient to tinge lightly blue the ear and eye of the side on which the injection was made. It was found expedient to remove the thoracic and abdominal viscera, and elevate the head of the injected animal for a few moments after the injection, to allow as much of the blood, as would do so, to drain from the head. Unless this is done there is always oozing and bleeding during the removing of the brain. Some thirty to forty-five minutes after the injection, the brain and cervical cord were exposed, and to insure against lacerating the pia-mater, the dura was, during this step, injured as little as possible. After removing the dura, the cord was cut about one inch below the junction of the vertebral arteries and the brain removed. The cerebellum was then cut off and an incision made into each cerebral hemisphere, and these reflected outward. The brain was then placed on a glass plate, base uppermost and exposed to the air for a period varying from five to thirty minutes or until it was found that the nerve fibers sought were stained. After some experimentation it was found that preparations of the pia-mater could be most easily made by dissecting off with curved scissors, pieces of the brain cortex, and after placing these on a large slide, pial surface uppermost, and covering them with a large cover glass, exerting pressure sufficient to press the brain tissue out from under the pia-mater.

Even a delicate pia-mater—from the rabbit for instance—may be treated in this way without laceration. This simple method has the advantage of giving preparations which may at

once be examined microscopically. Relatively large pieces of pia-mater may in this way be obtained, practically free from brain tissue. I have for instance a number of times been able to obtain, in one piece, the pia-mater from the base of the brain of a cat, with that covering the lower surface of the medulla and upper cervical cord, which, although slightly lacerated, would contain a complete circle of Willis with its main branches, the basilar and a portion of the vertebrals. When it was found that the perivascular nerves were well stained, the pieces of pia-mater were fixed either in an ammonium picrate solution, (Dogiel) or in the ammonium molybdate solution (Bethe). Some of the ammonium molybdate fixed tissue was hardened in alcohol, sectioned and counterstained in alum-carmine. I have given the method used by me somewhat in detail, since Gulland (1) mentions having used the methylen blue method in his research, without success however. If I read his account correctly, the methylen blue method used by Gulland, was the modification of Ehrlich's method suggested by Dogiel, according to which a dilute solution of methylen blue, made with normal salt solution, (1-1000 used by Gulland) is applied to the tissues. This method was used by me, with negative results.

The existence of a perivascular plexus in the arteries carrying blood to the brain, seems beyond question. A number of anatomies consulted with reference to this point mention them. We read in Quain that the ascending carotid branches of the superior cervical ganglion, as they ascend into the skull with the internal carotid artery, divide into two parts, known respectively as the internal and external division. The terminal parts of these two divisions extend to the cerebral and ophthalmic arteries, around which they form secondary plexuses, those on the cerebral arteries ascending to the pia mater.

And again : " From the lowest cervical and first dorsal ganglion, slender grey branches ascend along the vertebral artery in its canal, forming a plexus (plexus vertebralis) around the vessels by their intercommunications, and supplying it with offsets. This plexus is connected with the cervical spinal nerves as they cross the vertebral artery, and its ultimate ramifications

are continued on the intracranial branches of the vertebral and basilar arteries."

Testus states that "in the course of the arteries of the cranial pia-mater numerous nerves, arising probably from the carotid plexus, may be found. Their branches have been found on the small branches of the pial vessels, even such as penetrate the convolutions. Nothing however is known about their mode of ending." He asks the question,—"What is the anatomical significance of the nerve plexus on the pial vessels?" And answers, "It is very rational to think, they terminate in the smooth muscle of the arteries, and that they become here, as in other parts of the body, regulators of the circulation." He further suggests the probability of there being nerves other than vaso-motor on the vessels of the pia-mater, namely sensory nerves, susceptible of being stimulated in the periphery and thus becoming, both in normal and pathological conditions, points of departure of reflexes. Kölliker refers to the nerves on the cranial vessels in the following words.—"An der Hirnbasis finden sich an den Arterien des Circulus Willisii viele ähnliche Geflechte" [Reference is here made to nerve plexuses on the vessels of the pia of the cord, first described by Purkinje] "welche mit Stämmchen von höchtens 67μ mit den verschiedenen Arterien, mit Ausnahme derer des Cerebellum, immer dem Verlaufe desselben folgend, durch die ganze Pia des Gehirnes sich ausbreiten, gedoch in ihren Enden nirgends erkennen lassen; doch verfolgte ich dieselben bis zu Arterien von 90μ und darunter in die Substanz des Gehirns hinein."

He further states that in the pia-mater of the brain, other than sympathetic fibers (Plexus caroticus internus, Plexus vertebralis), are to be found; quoting Bochdalek to the effect that he had traced numerous branches from the roots of four of the cranial nerves to the perivascular plexuses on the vessels of the base of the brain and the cerebellum. That there are nerve plexuses on the larger vessels of the base of the brain, has long been known. This is shown by the fact that Bourgery and Arnold described very delicate nerve fibrils passing from the carotid plexus to the anterior and middle cerebral and posterior communicating. In

successfully stained methylen blue preparations, perivascular
nerves may be clearly seen on the vessels constituting the circle
of Willis, and on the larger arterial branches that proceed from
it, and may from here be traced on to the arteries of the pia-
mater of the hemispheres. Even under low magnification, how-
ever, it becomes obvious that such perivascular nerves do not
all present the same characteristics. On the one hand, and this
more particularly on the larger vessels, well formed bundles of
medullated nerve fibers are observed ; on the other, plexuses
of non-medullated nerve fibers. To anticipate somewhat, I may
state, for considerations which will follow, that I have come to
regard the medullated nerve fibers as sensory nerve fibers, the
perivascular plexuses of non-medullated fibers as vaso-motor
fibers. I shall therefore consider the nerves associated with the
arteries of the cranial pia-mater under these two heads.

Sensory nerves. In all well stained methylen blue prepara-
tions of the pia-mater, whether of the dog, cat or rabbit, I have
observed relatively large medullated nerve fibers accompanying
the blood vessels, not only the larger vessels found on the base
of the brain and medulla, but following the vessels over the con-
vexity of the cerebrum to the great longitudinal fissure. These
medullated nerve fibers reach the pial vessels, so far as I have
been able to determine, from two main sources. A relatively
large bundle of medullated nerves—sometimes several small
ones—joins the middle cerebral just after it gives off the pos-
terior communicating branch. This, as a rule, divides into two
branches, one joining the middle cerebral, the other the pos-
terior communicating artery. The other source of medullated
nerve fibers is from one or several bundles of medullated nerve
fibers, which proceeds upwards on the basilar artery until it
divides into the posterior cerebrals; the nerve-bundles on the
basilar undergo a similar division and follow the branches
of this artery. The bundles of medullated nerves on the
basilar artery are formed from such found on the vertebral
arteries. Fig. 1 may serve to illustrate these statements. In
the figure the circle of Willis with a portion of the basilar artery,

removed from the base of a cat's brain, was reflected by camera lucida. From the same preparation the nerve bundles are sketched in semi-diagrammatically, only a sufficient number of nerve fibers being sketched to give the general course of the larger bundles of medullated nerves. In the preparation a relatively large bundle of medullated nerves divides into two branches, the one, *a*, accompanying the posterior communicating branch. This bundle and its branches could be followed along this artery on to the posterior cerebral of the side on which the nerves are sketched and on to the posterior cerebral of the opposite side. In this bundle, I was able to count, at its origin, some twenty relatively large medullated fibers. The other branch, *b*, containing ten large medullated fibers, accompanies the middle cerebral. The nerve bundle, *c*, I regarded as a continuation of *b*, although the connection is not apparent, as the nerves on the intervening portion of the vessels were practically unstained. The bundle of medullated nerves on the basilar artery, in which I was able to count 15 large nerve fibers, divides into branches which follow the right and left posterior cerebral. The branch on the left side was traced to the middle of the posterior communicating artery. There are then, and this may be emphasized, no distinct areas of distribution for the medullated nerve fibers, accompanying the pial vessels and coming from the two sources above mentioned. The bundles of medullated nerve fibers on the vessels forming the anterior part of the circle of Willis, are distributed to half of the circle of Willis and from this to the arteries arising from it, and to some extent to the opposite side of the circle of Willis; the medullated nerves entering with the basilar artery are distributed, in part, at least, to the anterior portion of the circle of Willis.

The medullated nerve fibers here under discussion undergo repeated division, such division taking place at the nodes of Ranvier; the resulting branches now and then seem to run parallel for a distance, again diverging at acute or obtuse angles. Such branching is repeatedly observed at places where the artery divides, one branch of a dividing medullated nerve accompany-

ing respectively, each of the arterial branches.   In the preparation from which Figure I was drawn, at the place of division of the nerve bundle into branches *a* and *b*, a number of dividing medullated nerves may be observed in which one branch passes to the middle cerebral, the other to the posterior communicating. Similar observations I have repeatedly made. Attention is drawn to this fact to show over how large an area a single medullated fiber (sensory fiber) may be distributed, and to show how futile it would be to attempt to localize pain in the pia-mater ; for it must be understood that such diverging branches may now and then be traced in the pia-mater of the cat, for distances approaching an inch, without reaching their termination.

In preparations of the pia-mater, coming from the base of the brain and embracing the circle of Willis and the anterior and middle cerebrals and their main branches, the medullated nerve fibers, above described as found in connection with the arteries of the circle of Willis, may be traced in connection with the branches of the anterior and middle cerebral to the borders of the preparation.   In preparation of the pia-mater from the lateral aspect of the hemispheres they are again found with the vessels and in suitable preparations may be traced to the longitudinal fissures. On the lateral surfaces of the cerebral hemispheres the medullated fibers accompanying the pial vessels appear as single fibers or small bundles consisting of two, three, four or five medullated fibers. The bundles of medullated nerve fibers, as also single fibers, accompanying the pial vessels undergo, as before said, repeated division, not only at points of division of the arterial branches but at other points along the course of the vessels.   The branches of bundles of medullated fibers or single fibers wind around the vessels in long sweeps, and here and there exchange fibers, and in this way form plexuses of large irregular meshes, which surrounds the vessels.

I have in a number of experiments been able to obtain methylen blue preparations which show most clearly the mode of termination of the medullated nerve fibers under discussion. The most successful preparations come from the cat, through a

sufficient number of observations have been made on the dog and rabbit to enable me to say that the endings described for the cat hold good for these animals also.

The most successful preparation obtained, showing the mode of termination of the medullated fibers accompanying the pial vessels is reproduced in Fig. 2, which gives the ending of a single medullated nerve fiber as seen under the 1-12 in. oil immersion. The preparation was unusually fortunate, as owing to the caprice of the methylen blue method, in the region of the vessel—posterior cerebral—from which the drawing was made, beside the branches of this one nerve, only a few coarse medullated branches with some few non-medullated fibers were stained. As may be seen from this figure, the medullated fiber, after reaching the vessel, gives off a number of relatively large medullated branches which leave the parent fiber at nodes of Ranvier; these primary branches divide further into medullated fibers of a second order, and of somewhat smaller size, some of which divide still further into still smaller medullated branches. The medullated branches terminate at a longer or shorter distance from the parent fiber in fine, varicose, non-medullated, terminal fibrils, which may often be traced for relatively long distances before they end, and this usually in a small granule or nodule. Similar non-medullated fibrils proceed from the medullated fibers, at nodes of Ranvier. These terminal, varicose fibrils have, as the figure may serve to show, a course which may be parallel or oblique to the long axis of the vessel, and therefore not parallel to the long axis of the non-striated muscle cells of the vessel wall, a fact to which I draw attention at this time, for reasons which will appear later. Complete, or even nearly complete endings such as shown here I have not often met. In well stained preparations, varicose fibrils such as above described and having a similar course, are met with in connection with the pial vessels in all parts of the pia-mater of the cerebral hemisphere, even on vessels with a musculature consisting at most of two or three layers of non-striated muscle cells. It is often somewhat difficult, however, and again impossible, to trace them for distances long enough to ascertain their

origin.   So that relatively infrequently can they be traced to medullated fibers, from which I believe they proceed.   I believe that these varicose fibers may be differentiated from the vascular nerves which terminate in the non-striated muscle tissue and which will be considered under the head of vaso-motor nerves. As to the relation of the medullated nerves and their endings to the vessels and their structural elements, my observations are not so conclusive as to be entirely beyond question, especially as concerns their ending.   In methylen blue stained preparations of the pia, mounted in ammonium picrate-glycerine, especially if such preparations have been mounted some days, in which case even relatively thick pieces of tissue become quite transparent, it may be seen that the larger and smaller bundles of medullated nerve fibers and the majority of the single medullated fibers are situated in the connective tissue adventitia of the vessels or in the neighboring fibrous tissue.   This is especially well shown, when, in the field of observation, the nerves happen to lie by the side of the artery.   As is well known, non-striated muscle cells are readily stained by methylen blue when applied to the fresh tissue. Such cells retain their color after fixation.   This fact makes it easy to determine the relation of the medullated nerve fibers to the muscular coat of the vessel.

This relation holds good for the smaller as well as the larger pial vessels.   However, to make certain of this fact, especial attention was paid to it, in a number of series of sections of pia containing vessels.   The tissue was stained in methylen blue, controlled under the microscope before fixing, fixed in ammonium molybdate, hardened in alcohol, embedded in paraffine and cut serially.   The sections were then fixed to slides and counter-stained in alum carmine.   In cross or oblique sections of vessels, in pial tissue thus prepared, the medullated nerve fibers were found in the adventitia. It was however much more difficult to reach a definite conclusion as to the disposition of the terminal branches of these medullated fibers, and their relation to the structure of the vessel wall.   By studying surface preparations of the pia, the conviction is gained that the

majority of the slender, varicose fibrils, terminal branches of the medullated nerves, end in the adventitia of the vessel or in the surrounding connective tissue. When such varicose fibrils are seen by the side of the vessel, their termination in the connective tissue seems often easy to make out. When on the surface of the vessel presented to the observer, careful focusing will usually enable one to determine that, for the greater portion of their course, at least, they are not in the muscular layer of the vessel, although they are often in focus at the same time as is the superficial part of the muscular coat. This statement has reference especially to the larger vessels. In sections, prepared as above mentioned, I have now and again found relatively long segments of varicose nerve fibres in the adventitia, having a course parallel to the long axis of the vessels. Sections are however not so serviceable as surface preparations in the elucidation of this point, as it is impossible to obtain in a section segments of nerve long enough to form an idea concerning their course and relation to other nerve fibers.

So far as I may judge from my own observations, I believe I am warranted in making the statement that many at least of the non-medullated, terminal branches of the medullated fibers accompanying the vessels of the pia, end in the adventitia of the vessels or the fibrous tissue surrounding them ; whether all do or whether some of them terminate in the muscular coat or even under the endothelium, I must leave as an open question.

In a number of preparations, medullated nerve fibers and their terminal branches were seen in the pia-mater some distance removed from vessels. This I have seen more frequently in the pia of the base of the brain and especially that portion enclosed in the circle of Willis. In the pia covering the lateral surfaces of the cerebral hemispheres such medullated nerve fibers have not been found frequently, but often enough to warrant the statement that here also the medullated nerves terminate in the pia in regions free from vessels. No medullated nerve fibers were found accompanying the veins of the pia. These veins, as is well known, have no muscular coat, and are therefore easily distinguished from the arteries in which the

muscle cells are readily stained. As previously stated, the medullated nerve fibers found in the pia-mater have been interpreted as sensory in function. My reasons for this assumption are based on their histological appearances, the nature of their endings and their distribution, and may be summarized as follows:

1.   These nerves are distinctly medullated, a fact which is readily made out in methylen blue preparations, although as a rule only the neuraxes are stained. In methylen blue preparations the neuraxes of the medullated fibers stain more deeply at the nodes of Ranvier, and at the nodes present an appearance which suggests the Fromman's crosses obtained when treating medullated nerves with a silver nitrate solution. In more deeply stained methylen blue preparations the myelin of medullated nerves stains faintly blue and may then be readily recognized.

2.   The medullated nerves in the pia appear, as has been stated, in relatively large bundles, especially in connection with larger vessels at the base of the brain; these bundles branch and anastomose forming plexuses, with wide meshes, which surround the vessels.

3.   The neuraxes of these medullated fibers are much larger than the neuraxes of sympathetic neurons or white rami fibers known to me. Accurate measurements have not been made, yet I feel justified in making this comparison, basing my judgment on a somewhat extended experience with the size and appearance of sympathetic and white rami nerves as seen when stained with methylen blue. The possibility of their being cerebro-spinal motor fibers may, I believe, be dismissed without further comment.

4.   These medullated fibers branch and re-branch and present the short internodal segments, usually observed when sensory nerve fibers approach their termination.

5.   The non-medullated, varicose, terminal branches of the medullated fibers, the majority of them, at least, end in fibrous tissue—adventitia of vessels or in pia. These terminal fibrils are in the main parallel to the vessels or cross them

obliquely, and are thus unlike the terminal branches of the vaso-motor fibers which end in the muscular coat. These latter course along in the intercellular cement between the muscle cells and are parallel to them, that is, at right angles to the long axis of the vessels. This difference—the mode of distribution of the medullated nerve fibers and the vaso-motor is clearly seen in methylen blue preparations of the pia-mater, in which both sets of endings are stained on the same vessel.

6. Where the entire ending of the medullated fibers is made out, as in the preparation from which Fig. 2 was drawn, the ending resembles the peripheral termination of sensory nerves with free endings in other parts of the body, and is identical with the ending of sensory nerves found in the dura mater, to be described later. I have therefore looked upon the medullated nerve fibers found in the pia as sensory, since their arrangement, size and mode of ending make it improbable that they are the neuraxes of sympathetic neurons or of white rami neurons. The term *sensory nerve fibers* is here used in the sense commonly ascribed to it. Reference is had, to the dendrites of neurons in the cerebral or spinal ganglia with T-shaped processes.

Vaso-motor nerves. On the vessels of the pia-mater, from the larger vessels constituting the circle of Willis, to vessels with a muscular coat of not more than two layers of involuntary muscle cells, I have found perivascular nerves arranged in the form of a plexus, which in every respect resemble the perivascular nerves—vaso-motor nerves—found in the wall of vessels in other parts of the body. They are non-medullated and arranged in the form of plexuses which surround the vessels. On the internal carotid artery, as soon as it leaves the carotid canal, and on the vertebral after appearing in the spinal canal, such perivascular plexuses are observed, and these may in suitable preparations be traced on to the anterior and middle cerebral and posterior communicating on the one hand, and basilar and posterior cerebral on the other hand, and from the vessels of the circle of Willis to the branches that arise therefrom. On the

larger pial vessels, these non-medullated, varicose nerves form a
primary plexus in the adventitia, the strands of which consist of
small bundles of non-medullated fibers, and of single fibers. The
small bundles of non-medullated nerves undergo repeated
division; these, with the single fibers which also branch fre-
quently, form an interlacing network—a nerve plexus. Within
this plexus is formed a second, though not so well defined plexus.
which would seem to lie just external to the muscular coat.
From this, the terminal fibrils which end in the muscular tissues
of the vessels, are given off. In Fig. 3 is sketched a short seg-
ment of one of the larger branches of the middle cerebral in the
pia of a cat. In the figure the nerve plexus on that portion of the
wall of the vessel turned toward the observer is reproduced. In
the preparation from which this sketch was made, the sensory
fibers were not well stained, their endings not at all, in the region
of the vessel shown in the figure. It may serve to show the
richness of the nerve supply of the pial vessels. The plexus
in the adventitia being particularly well shown, the terminal
fibrils could not be clearly made out with the magnification used,
and are therefore not shown in the figure. In the smaller pial
vessels with a muscular coat consisting of two to four layers of
involuntary cells, only one plexus of non-medullated nerves is
made out. In Fig. 4 is reproduced such a plexus. The sketch
was made from a methylen blue preparation of the pia of
a dog as seen under the 1-12 in. oil immersion. In one
portion of this small artery, the non-striated muscle cells
were well stained — not shown in figure — and in optical
section it was made out that in this portion of the vessel
there were present two layers of involuntary muscle cells
in the media. I have found it much more difficult to stain
the perivascular nerves on the smaller vessels of the pia; yet
they have been found often enough in the dog, cat and rabbit
in the pia-mater removed from various regions of the cere-
bral hemispheres so that I conclude that they are generally pres-
ent, and that the difficulty experienced in staining them is due
largely to the uncertainty of the method used.

That the ultimate branches of the fibers forming the perivas-

cular plexuses here discussed terminate in the muscular coat of the pial vessels, one may often observe in well-stained methylen blue preparations mounted in ammonium picrate-glycerine. In such preparations, by careful focusing, very delicate varicose threads are now and then found in the muscular coat, running parallel to the long axis of the involuntary muscle cells. To make certain, however, the serial sections, to which reference has previously been made, were studied with special reference to this point. In such sections—double-stained in methylen blue and alum carmine—very delicate varicose fibrils, stained blue, are found between the non-striated muscle cells of the vessel wall, which are stained red. And here and there in fortunate sections, these were seen to give off short lateral twigs terminating in fine granules on the muscle cells; in other words, the ultimate ending of the nerves in involuntary muscle tissue. To one familiar with the appearance of methylen blue preparations, fixed, hardened, sectioned and counterstained as above described, blue granules or even short blue fibrils do not of necessity indicate the presence of a nerve ending; for, unfortunately, tissues other than nervous stain blue and blue granules which appear to be nothing but precipitate are often seen. This I have tried to bear in mind, and only such granules or small end-discs, were accepted as the ultimate ending of perivascular nerves in the muscular coat of the pial vessels, when I was able to trace a connection between them and a blue fibril which from its varicosity, color reaction and other appearances I was led to regard as a nerve fibril. The arrangement and mode of ending of the perivascular nerves in the pia-mater being in every respect like that of vaso-motor nerves in other parts of the body, I feel warranted in placing them in the same category.

Assuming that the non-medullated nerve fibers of the perivascular plexus found on the carotid artery were the neuraxes of sympathetic neurons, the cell bodies of which were situated in the superior cervical ganglion, and that those found on the vertebral arteries were the neuraxes of neurons, the cell bodies of which were to be found in the inferior cervical and stellate ganglia, I extirpated these ganglia in pairs, with the hope that the

resulting degeneration would enable me, by exclusion, to ascertain the area of distribution of the neuraxes of the sympathetic neurons removed in the respective ganglia extirpated. Tuckett (8) has shown,—"that where non-medullated nerves degenerate, the core of the fibers of Remak, staining with methylen blue, disappears, while the sheath and nuclei are unaffected by cutting them off from their trophic nerve-cells. Degeneration is shown, by the histological changes and physiological phenomena, to begin about the twenty-fourth, while loss of irritability and conductivity is complete by the fortieth hour." The experiments on *extirpation* of the ganglia were all made on cats. The operated animals were kept for a time varying from 3 to 49 days (see table) after *extirpation* of the ganglia. The results obtained in this portion of my investigation are so meager, that it does not appear to me advisable to give the protocol of these experiments in detail; I have therefore grouped the salient points in the table opposite.

In summarizing the results given in this table, attention may be drawn to the fact that in experiments where nerves in the pial vessels were stained, after the *extirpation* of sympathetic ganglia in the neck or thorax, the medullated nerve fibers accompanying the basilar or internal carotid and its branches were stained. The *extirpation* of the ganglia, did in no way alter their reaction to the methylen blue. This I take it may be put forth as an additional argument, to those already given, that these medullary nerve fibers are sensory. As to the distribution of the vaso-motor fibers, the results are not conclusive. A study of the table will show, that after *extirpation* of the superior cervical ganglia the vaso-motor fibers on the anterior half of the circle of Willis and the branches of the middle cerebral seem less numerous or entirely wanting; the same is true of the basilar artery and its branches after *extirpating* the inferior cervicals or stellates or both. Yet after making comparisons between the preparations obtained in these experiments and those obtained from normal animals, I am free to admit that the above conclusions do not seem justified. It should be stated that in this research some sixty animals were used, and of this number

TABLE I. GIVING SYNOPSIS OF EXPERIMENTS ON EXTIRPATION OF SYMPATHETIC GANGLIA.

No.	Ganglia removed.	Length of time intervening between extirp. of ganglia and meth. blue injection.	Examination of pial vessels resulted as follows:			Remarks.
			Vertebral and basilar.	Circle of Willis.	Middle cerebral and branches.	
1 2 3	L. and R. Sup. cerv.	Cat dead next morn. Cat dead next morn. 25 days.	Sensory fibers well stained. A few vaso-motor fibers	Sensory fibers well stained. Some few vaso-motor fibers on the internal carotid branches of the circle of Willis, especially post-com.	Sensory fibers well stained. No vaso-motor on the middle cerebral on convexity of hemispheres	Methylen blue staining unsuccessful. Vessels stained deeply and diffusely blue
4 5	" "	Cat dead second day 3 days	—	—	—	Methylen blue staining unsuccessful. Vessels stained deeply blue
6	" "	49 days	—	·	—	No nerves stained
7	" "	Dead third day	—	—	—	No nerves stained
8	L. and R. superior and middle cervical	9 days	—	—	—	No nerves stained
9 10 11	L. and R. stellate L. and R. stellate "	5 days 8 days 4 days	—	—	Right side sensory nerves. None left side	No nerves stained " " " " Basilar and circle of Willis stained deeply and diffusely blue
12	"	7 days	—	Sensory and vaso-motor fibers on anterior half of circle of Willis.	Sensory and vaso-motor fibers	Sensory and vaso-motor nerves. None left side. Right side sensory nerves
13	L. and R. sup. cerv.	9 days	—	—	Right side sensory fibers well stained. Left side only a few	Circle of Willis stained deeply blue
14 15	" " L. and R. stellate	3 days 9 days	Sensory fibers. Vasomotor fib'rs?	No nerves stained	—	Nerves not well stained

only in a small percent. did I obtain results which might be looked upon as satisfactory, and by this is meant that only in a few experiments were the nerves on the larger as well as the smaller vessels, and in different regions of the pia-mater well stained.   In a much larger number of experiments they were well stained in certain regions, sometimes on one side and not on the other, again on one portion of the circle of Willis and not on the remaining portion, sometimes medullated, sensory fibers and not vaso-motor or vice versa, etc.; although after some preliminary experimentation, the same method—strength of solution, quantity, time of exposure, etc.—was used in all the experiments.

It seemed therefore ill-advised to continue this line of experimentation.   Before leaving, however, these experiments, attention may be drawn to the fact that after the *extirpation* of the ganglia as above described, in nearly every experiment certain vessels of the pia stained a peculiar, greenish blue color, quite unlike the deep blue color seen after the injection of methylen blue into normal vessels.   It is to be born in mind that the muscle cells of the vessels show a selective action toward the methylen blue.   I am not prepared to say that this change in the reaction of the muscle cells toward the methylen blue, after the *extirpation* of the sympathetic ganglia of the neck, indicates a chemical change in the protoplasm of these muscle cells, perhaps as a result of trophic influences interrupted at the removal of the cell bodies of sympathetic neurons, sending neuraxes to these vessels.   I offer this as a possible explanation of a phenomenon observed in many of the experiments here under discussion.

In the preceding pages I have drawn attention to the nerves in the pia-mater of the cerebral hemispheres, and more particularly to the nerves,—sensory and vaso-motor,—found in conjunction with the middle cerebral and its branches.   I can not state positively that I have been able to trace any such nerves into the substance of the brain.   In preparations of the pia, prepared after the method described (namely, removing the pia-mater with a portion of the brain cortex to a slide and

pressing the brain tissue out from under the pia) it is often impossible to differentiate between the small arterial branches in the pia-mater and those which penetrate the brain substance—intracerebral branches. As previously stated, small vessels with two to three layers of involuntary muscle cells in the media possess vaso-motor nerves. Whether some of these arterioles were intracerebral, I can not say; it seems however very probable, as such vessels correspond in size and structure of coats to many of the intra-cerebral arterioles found in the cortex. Kölliker (6) states that he was able to trace perivascular nerves into the substance of the brain.

I have repeatedly attempted to ascertain whether perivascular nerves were to be found on the vessels of the choroid plexus in the lateral ventricles. My results have thus far, however, been negative. This, I believe, is in part at least due to the fact that in methylen blue preparations—both when the methylen blue is injected into the circulation and when applied in very dilute solution (1 to 1000 in normal salt solution) to the fresh choroid plexus—the epithelial cells covering the vessels of the choroid plexus stained so deeply that the underlying structures could not be made out with any degree of clearness.

As to the nerves in the pia-mater of the cerebellum, my results have not been so conclusive as might be desired. Sensory nerves have now and then been traced by the side of the arteries of the pia-mater of the cerebellum; these end as do similar nerves in the pia-mater of the cerebral hemispheres. Vaso-motor nerves have been met with in only a few cases, and then only in small numbers and not so clearly stained as in other parts of the pia.

Nerves of the Dura-mater. The presence of nerves in the dura-mater seems beyond question. Their origin, course and to some extent distribution have been known to anatomists for many years. It is not my purpose at this time to concern myself with these grosser anatomic facts, as my observations have not been of a nature to give me data for this purpose. In a number of experiments on dogs, cats and rabbits, I have

obtained well-stained preparations of the dura-mater after the injection of a methylen blue solution with a view of staining the nerves of the pia-mater.

In a number of such preparations the terminations of the dural nerves were well stained and it is to this that I propose to confine my remarks. Alexander (9) made observations with the gold chloride method on the nerves in the dura of the dog, Guinea-pig, rabbit, rat, mouse, dove and frog, and found two kinds of nerves,—vessel-nerves and dural-nerves. He then states that the arteries of the dura, to their microscopic branches are accompanied by two small nerve bundles which run parallel to the vessel. These bundles become smaller toward the periphery until ultimately only single, medullated nerves are found by the side of the vessels. From these medullated fibers, non-medullated branches are given off which go toward the vessels and terminate thereon ; their mode of ending he could not ascertain. The dural nerves, he states, have their origin directly from the larger nerve bundles or from those following the vessels. These bundles of medullated nerves, after division, end in non-medullated fibers which form plexuses, often with very narrow meshes. These plexuses seemed in no way connected with the vessels. Whether this was a true plexus or only a network could not be ascertained. Alexander, however, if I read him correctly, inclines to the former view.

My own observations led me to the conclusion that in the dura mater of the dog, cat and rabbit two kinds of nerves were to be found :

a. Sympathetic nerves forming peri-vascular plexuses.

b. Medullated, sensory nerves terminating in the dura.

The sympathetic nerves form peri-vascular plexuses, which in every respect resemble those already described for the pia-mater and those found about arteries in other parts of the body. They have been found most clearly stained on the middle meningeal artery ; this seemed to me, however, accidental, as the portion of the dura containing this vessel and its branches is more easily removed and seemed better stained than other parts of the dura.

The peri-vascular plexus on the middle meningeal has been observed on this vessel as soon as it reaches the dura, and I have been able to trace it along its course until the arterial branches were reached having a musculature consisting of two layers of involuntary cells. My reason for believing the non-medullated nerves, which form this peri-vascular plexus, to be neuraxes of sympathetic neurons, is the fact that in some of the best stained preparations, fine nerve fibrils, coming off from the perivascular plexus, could be traced into the muscular coat of the vessels, where such fine nerve fibrils assumed a course parallel to the long axis of the involuntary muscle cells of the vessel wall, between which they seemed to terminate. For such a perivascular plexus see Fig. 5.

The medullated nerves of the dura which, with other observers, I regard as sensory, comprise the two kinds of nerves described by Alexander. Bundles of medullated nerves accompanying the arteries are readily stained in methylen blue; two such bundles are shown in Fig. 5. In portions of the dura free from larger vessels, are found bundles of medullated nerves (see Fig. 6) having a course quite independent of the vessels; these I take to be the dural nerves described by Alexander. In their mode of ending I find no difference between the medullated nerves of the dura accompanying the vessels and those having a course independent of them. In each case the medullated nerves, after branching here and there at the nodes of Ranvier, lose their myelin and continue as non-medullated fibers. These non-medullated fibers after further branching, terminate in long varicose fibrils, which may now and then be traced through several fields of the microscope when the preparation is viewed under a magnification of about 400 diameters.

These non-medullated terminal branches interlace in every possible manner, as may be seen in Fig. 6, giving an appearance which is commonly termed a nerve plexus; the identity of the nerve fibrils is, however, not lost in this "plexus" as one meets with no anastomoses of the nerve fibrils. The medullated fibers accompanying the arteries of the dura often terminate over them or in such a way as to surround the vessels; their term-

inal branches do not however form perivascular plexuses; the plexus formed by the sympathetic fibers seems quite independent of them.   The one set of fibers—vaso-motor or sensory— is often stained to the exclusion of the other, the sensory fibers staining more readily than the vaso-motor nerves.

I have not been able to trace in its entirety the end-brush of a single medullated nerve fiber terminating in the dura.   In a well stained preparation, the varicose terminal branches of the sensory fibers are so interwoven that the ones coming from a single medullated nerve fiber can not be separated from the others.   There would seem to be no doubt, however, that the termination of the sensory fibers of the dura is an end-brush spread over a relatively large area, the component parts of this end-brush being very slender, varicose fibrils which terminate in the connective tissue of the dura.

As the preceding pages have shown, the writer has endeavored to answer the question of the existence or non-existence of vaso-motor nerves on the intracranial vessels, not by results obtained in physiological experimentation, but rather from observations made by the aid of our modern histological methods and the microscope.   A knowledge of the existence of vaso-motor nerves on the intra-cranial vessels must of necessity weaken the position of physiologists, who, as a result of physiological experimentation, no matter how carefully planned and well executed such experiments may seem to be, deny the existence of such nerves. As the writer has conducted no physiological experiments in the investigation, for the reason that he has felt himself incapable of undertaking them, he deems it presumptuous to discuss the results and conclusions of physiologists, who, from their observations, have gained the conviction that the intra-cranial vessels were lacking in a vaso-motor nerve supply.   For a consideration of this phase of the question under discussion I would refer the reader to the recent communication of Leonard Hill (10), in which admirable work, he has summarized his own numerous investigations in this field and those of his co-workers and has given us a most critical digest

of the literature bearing on this subject. Before concluding this paper it may, however, not be amiss to state briefly what may be regarded as the consensus of the opinions of physiologists on the question of the vaso-motor nerve supply of the intracranial vessels, and in doing this I quote from Hill, whose extended observation and knowledge of the literature enable him to make such a summary much better than I can.

"No evidence has been found of the existence of cerebral vaso-motor nerves: either by means of stimulation of the vaso-motor center, or central end of the spinal cord after division of the cord in the upper dorsal region: or by stimulating the stellate ganglion, and, that is to say, the whole sympathetic supply to the carotid and vertebral arteries." "In every experimental condition the cerebral circulation passively follows the changes in the general arterial and venous pressures." "There is no compensatory mechanism by which the intracranial pressure is kept constant." And to quote still further, Hill states that in "turning to the evidence of past workers, I find that Nothnagel and Akermann obtained at times, on stimulating the cervical sympathetic, evidence of dilatation of the pial vessels. Recently Cavazzani found evidence of both cerebral constrictor and dilator fibers in this nerve; the methods of these workers are valueless in deciding such a question. Schultz, Riegel and Jolly, Cramer, v. Schultén, Gaertner and Wagner, Hürthle, Roy and Sherrington have obtained no positive evidence of any active cerebral effect from stimulation of this nerve." In this connection it may be interesting to note that Hill states that "in a recent exhaustive research, Gulland has failed to demonstrate by every known histological means the existence of any vaso-motor nerves in the pial vessels." This latter statement at least needs modification, since, as has previously been shown Gulland himself admits the presence of perivascular nerves on the pial vessels.

The statement above made may serve to emphasize the view previously expressed, that physiologists very generally deny the existence of vaso-motor nerves in the pial vessels. The fact that nerves, which in every respect—considered struc-

turally—resemble vaso-motor nerves found in other organs, have in a number of instances been found in the pial vessels, suggests at least the advisability of a renewed investigation of this problem at the hands of the physiologist, if indeed, considering the complexity of the problem, the question may be decided from this standpoint. I am reminded here of a similar doubt expressed by Obersteiner (2) in the article from which I have already quoted freely. After stating, and agreeing in this respect with Mosso, that the vessel-nerves of the brain are easily fatigued and fail to respond at a time when vaso-motor nerves still react in other organs, he adds: "Diese besondere Ermüdbarkeit könnte vielleicht auch zur Erklärung der negativen Versuchresultate mancher Forscher herangezogen werden. Jedenfalls gestatten alle derartigen experimentellen Ergebnisse mancherlei Auslegung und sind nicht geeignet eine entschiedene Beantwortung der Frage nach dem Vorhandensein von Nerven an den Gehirngefässen zu ermöglichen."

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8. *Tuckett*: On the structure and degeneration of non-medullated nerve fibers. Journal of Physiology. Vol. XIX. Page 267.

9. *Alexander*: Bermerkungen über die Nerven der dura Mater. Archiv für Mikroscopische Anatomie. Vol. XI, 1875. Page 231.

10. *Leonard Hill*: The physiology and pathology of the cerebral circulation. London, 1896. References to other papers mentioned may be found in this volume on pages 202-204.

DESCRIPTION OF FIGURES.

PLATE I.

Fig. 1. Circle of Willis and basilar artery of cat. Showing in a semi-diagrammatic way the distribution of the sensory nerve fibers. Only a few of the stained fibers sketched to give their course and distribution. 1. anterior cerebral ; 2. middle cerebral; 3. posterior communicating; 4. posterior cerebral; 5. basilar. For letters see text.

Fig. 2. Portion of posterior cerebral artery of left side of cat showing the termination of a sensory nerve fiber. Nerve with ending in the adventitia of vessel. Methylen blue preparation fixed in ammonium picrate and mounted in ammonium picrate glycerine. Magnification 900 diameters. Reduced to one-fourth.

Fig. 3. One of the larger branches of middle cerebral of a cat. Methylen blue stain. Shows perivascular vaso-motor plexus. Magnification 450 diameters. Reduced to one-half.

Fig. 4. Small pial vessel from dog. Vessel has two layers of involuntary muscle cells. Shows perivascular vaso-motor plexus. Magnification 900 diameters. Reduced to one-half.

Fig. 5. Middle meningeal of cat. Methylen blue stain. Two bundles of medullated nerve-fibers—sensory fibers—accompanying it ; *m.* vaso-motor plexus in vessel. Magnification 150 diameters. Vaso-motor plexus sketched in from higher power. Reduced to one-half.

Fig. 6. From surface preparation of dura of cat. Methylen blue preparation. *M.* bundles of sensory, medullated fibers. Varicose fibers in sketch terminal branches of sensory dural nerves. Magnification 450 diameters. Reduced to one-half.

OBSERVATIONS ON THE BLOOD CAPILLARIES IN THE CEREBELLAR CORTEX OF NORMAL YOUNG ADULT DOMESTIC CATS.

By Frank S. Aby, Ph.B., M.D.

With Plate II.

CONTENTS.

I.   Summary.

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 A.   A set of small arterioles which pass through both molecular and granule layer to the medullary portion.

 B.   A set of small arterioles which pass through the molecular layer into the granule layer.

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 IV.   Capillaries from arterioles A of opposite side of lamina.

Third.   The molecular layer has *three* sources of blood supply.

 I.   Collateral capillaries from arterioles A.

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 III.   Capillaries C.

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    III.   Capillaries are not especially abundant about the cells of Purkinje.

Seventh.   The cerebellar cortex is to be considered as a distinct vascular organ.

Eighth.   Although this report is primarily and essentially a record of observation, it is certainly not out of place to formulate a hypothesis which may serve as a basis for future work.   The granule layer appears to be more highly vascular than any other portion of the cortex, and the layer of cells of Purkinje is indifferent.   Reasoning deductively from what we know of relative blood supply in other organs, it appears fairly safe to conclude; first, that volume for volume, metabolic processes are more extensive in the cells of the granule layer than in any other region of the cortex ; second, that metabolic processes are not especially active in the cells of Purkinje, in this particular animal. This hypothesis presupposes a principle, which I will state tentatively as follows :

Ninth.   Formulation of a Principle of Histologic Angiology. At a given age, in a given organ, the relative number of blood capillaries in two regions is a certain index to the relative intensity of metabolic changes in those regions.

As a corollary to the above, at various ages of a given species, in a given organ or portion of an organ, the relative abundance of blood capillaries is a certain index to the relative intensity of metabolic changes.

II.   Introduction.

The present communication is presented merely as a record of observations upon blood distribution in one particular animal form, at a definite age, and in the normal cerebellum.   To state the matter in another form, questions regarding the comparative arrangement in different species, in the same species at different ages, or under abnormal conditions are not included within the scope of this paper.

This record is based upon a series of observations extending over a period of ten years.   The observations were first made during the winter and spring of 1889, in preparations made by myself. Professor S. Calvin then pointed out from these preparations that there was a difference in the blood supply of the granule and molecular layers.   From this point the observations were extended by the writer, and the arrangement presented in the summary to this paper was recognized as being probably the true arrangement under the conditions mentioned in the title.   This arrangement has been demonstrated to classes and to private individuals year after year since 1889, in various cats and with various injection masses.

In what I propose to designate as a complete injection, a term which will be explained later, the three classes of vessels about to be described have always appeared.   This fact having been demonstrated again and again, it may be deemed unnecessary to state that it appears reasonably certain that this arrangement is the true one, and that it may be demonstrated at any time if the previously mentioned conditions are taken into consideration.

III.   Methods.

It is unnecessary to enter upon an extended discussion of technique, inasmuch as no method was used which has not been the common property of histologists for years.   Nevertheless, there is a necessity for outlining the technique.

The logical basis for the technique of injecting blood capillaries is as follows: We know from observing thin animal

membranes in living animals that there are certain minute tubes called capillaries through which blood may be seen to flow. Having observed the size and arrangement of these capillaries in the living animal while the blood is still flowing through the tubes, we may next proceed to find the artery leading to that region, or the vein leading from it, introduce a canula into the vessel, pointing it toward the region under consideration. Next we may inject some colored fluid into the vessel, and by actual inspection may see this fluid fill every capillary which was observed during the life of the animal. More than this, if the pressure be exactly equal to the normal blood pressure, other conditions remaining the same, the *size* of the capillaries should be equal to their size in the living animal. As the caliber of capillaries may vary from moment to moment in the living animal, so may the caliber vary at the time of injection, giving us apparently a capillary of large size, or a capillary of small size. Under the circumstances quoted above, the tubes may all remain free from emboli, the pressure may be about equal to the normal blood pressure, and *every* tube which contained blood in the living animal, be that tube large or small, may be exactly filled. These are the ideal conditions, the result an ideal result. It is to an injection of this kind that I apply the term *complete injection*. It is very clear to the practical histologist that this ideal result, a *complete injection*, is not a very frequent occurrence.

If now a small embolus plug up an artery or an arteriole, and the pressure is not sufficient to drive the injection mass around through the collateral circulation, it is clear that there will be areas where every capillary is not filled. Even if no embolus interfere, the pressure may be insufficient, and certain capillaries are not filled. Still again, embolism may be absent, the pressure approximate the normal blood pressure, but some or all the vessels may be contracted because of post mortem changes, and in this case again certain capillaries may remain empty, or partly filled. Any one or any combination of these factors may result in something less than a complete injection, and to this result I apply the term *under-injection*.

Still another phenomenon may occur. The pressure may be too great. In this case the various tubes will become distended, and at the point or points of least resistance ruptures may occur. It is obvious, however, reasoning from previous knowledge and experience, that *no new capillaries can possibly be formed by injection.* Experience shows that the injection mass pours out into the extra-vascular areas in a confused mass. This is what I desire to designate *over-injection.*

Perhaps I have entered into this tedious explanation at greater length than the nature of the circumstances seem to warrant. My defense is that I have been asked frequently, " How do you *know* that those rods of colored gelatine indicate the actual size, number and arrangement of the minute blood streams ? " The basis for the technique is outlined above, and shows that we may safely draw conclusions through the application of induction as to *number* and *arrangement* of capillaries, but not as to *caliber.*

In prosecuting these studies several injection masses have been used,—gelatin, glycerine, warm, cold, and of various colors. The mass used in making the injection from which the plate was made was carmine gelatin, a formula very near Carter's Carmine Gelatine Mass, given in Beale, page 113.

As to methods of making the injection, the canula was always introduced into the carotid, sometimes right, sometimes left, and directed toward the head. I have used several forms of apparatus employing hydrostatic pressure, but in my hands the syringe has given better results than any other means of injecting. I will state that the percentage of failures is always high, and usually many trials must be made before obtaining a complete injection.

IV. Observations.

In longitudinal vertical sections of a completely injected cerebellum three sets of vessels may be observed to be distributed from the *pia mater.* First, a set of small arterioles passing through the cortex into the medulla ; second, a set of small arterioles passing through the molecular layer and breaking up

into capiliaries in the granule layer; and third, a set of capillaries distributed immediately through the molecular layer. For the sake of clearness and brevity, I propose here to designate these by the letters A, B and C. These are arranged in order in the summary.

In the plate, which is produced by photographic processes, from the section itself, examples of these three types may be seen. At 1, 6, 10, 11 and 13 are examples of class A. At 2, 9 and in various other situations, examples of class B. Above the X to which lines 4 and 7 lead are examples of class C.

It is to be clearly understood now that no sharp line separates these three classes. The classes merge one into another, and frequently it is difficult to assign a given vessel to its proper class. By a careful study of the plate there will be observed in several situations vessels which may be classed as either B or C. Such a study will also demonstrate that not much reliance can be placed on *size* as a basis of classification. As to the relative *numbers* of vessels of these three classes, it is possible to arrive at only a rather indefinite approximation. The average of a number of enumerations show the following rates. One vessel of class A to about twenty vessels of class B, and one vessel of class B to about fifteen of class C.

Considering the arrangement of vessels in the various layers of the cortex, we may state the proposition that the granule layer has *four* sources of blood supply. An arteriole of class A may be seen to pass into the medullary layer, and at a greater or less distance from its point of departure from the granule layer, send a recurrent branch to the granule layer of its own side. In the plate, this may be seen at 1 and 11. But the greater part of its blood supply is derived from vessels of class B. Numerous instances of this may be seen in all parts of the plate. But if all the vessels of class B, should become obliterated, and all the recurrent branches from class A failed, still the granule layer could receive a supply of blood from the anastomosing capillaries from class C. This anastomosis may be studied by means of a magnifier in various parts of the plate.

Aside from the three sources of blood enumerated above, the capillaries in the granule layer may receive a supply of blood from certain vessels of class A, some of which may be seen to give branches to *the opposite side* of the lamina. In other cases the arteriole itself may be seen to cross the medullary layer and distribute itself into capillaries in the granule layer of the opposite side. No example of this appears in the plate.

From these observations it appears that the vessels in the *pia mater* on one side of a lamina may be completely occluded, still blood may reach every part of the cortex on that side through certain vessels of class A from the opposite side.

Directing attention now to the molecular layer, *three* sources of blood supply may be recognized. Occasionally arterioles of class A may be observed to give off collateral branches while passing through the molecular layer. No instance of this can be shown in the plate. Collateral branches from arterioles B can be observed more frequently. The plate shows good instances of this at 2 and 9. But it may be asserted that the molecular layer depends largely upon the capillaries of class C for blood, and as previously stated, there are about fifteen of these to one vessel of class B. Examples of this may be seen at 4 and 7.

In normal adult domestic cats, so far as my observations extend (and upon this point I have been particularly careful to extend my observations) no peculiarity in the number, size or arrangement of blood vessels marks the layer or region occupied by the cells of Purkinje. In other words, the layer of the cells of Purkinje does not constitute a distinct vascular region.

It may be stated in connection with the subject matter of this paper that the medullary portion is occupied by blood vessels arranged in two ways. In the lamina the mesh is elongated, while in the deeper portions the mesh is not elongated.

Comparing now the layers of the cortex one with another, as regards relative number of capillaries, the arrangement of capillaries, and the relative size of mesh, we may state the following propositions. Comparing a like volume of granule layer and molecular layer, the number of capillaries in the granule layer

exceeds those in the molecular layer. As to arrangement, it may be stated in general that the vessels of the molecular layer stand at right angles to the pia mater, while the vessels of the granule layer lie in planes parallel to the pia mater. The mesh in the molecular layer is of the elongated type, while that in the granule layer is not elongated.

It may be stated in general that the mesh in the granule layer is closer than in the molecular layer, this following as a corollary to the proposition regarding the relative number of capillaries, provided the calibers are approximately equal.

From what I have previously stated regarding the layer of Purkinje's cells, it is clear there is not much possibility of instituting a comparison between that layer and the others, regarding the question of vascularity.

Considering the cortex as a whole, it may be regarded as a distinct vascular organ, sharply defined from the medullary layer. It is a remarkable fact that the capillaries of the granule layer, at the boundary zone between the granule layer and the medullary layer, turn upon themselves and form loops which very strongly remind one of the arrangement of capillaries at the inner surface of the gastric mucosa ! In the plate, 3 and 5 point to situations showing this peculiarity. The plate shows in all parts how clearly defined the cortex is from the medullary portion.

It remains to call attention to certain regions where separation of the granule layer from the molecular layer has occurred. At 8 and 12 may be seen elongated clearer spaces, the line 11 also traverses such a space. These are probably to be regarded as artificial, but they serve to point out that the granule layer and molecular layer of the cortex are really two organs, considered as to vascularity.

V.   Explanation of Plate II.

Cerebellum of normal young adult domestic cat, age about one year. Cat injected through carotid artery with gelatin-carmine. Longitudinal vertical section near the median line, section adout 1-50 inch in thickness. Photographic negative× 20. Plate× 1. No retouching at any stage of the process. Preparation by Frank S. Aby. Photograph by W. H. Knap. Plate by A. Jahn. The heavy color indicates the *pia mater*.

1.   Vessels of class A.   Shows recurrent capillaries to granule layer.
2.   Vessel of class B.   Shows recurrent capillaries to molecular layer.
3.   Along this line the vessels form loops, sharply defining cortex from medullary portion.
4.   Vessels of class C.
5.   Region similar to 4 of plate.
6.   Vessel of class A.
7.   Vessels of class C.
8.   Showing separation of granule layer and molecular layer along region of Purkinje's cells.
9.   Recurrent capillaries from vessels of class B.
10.   Vessel of class A.
11.   Vessel of class A, showing recurrent capillaries to granule layer.
12.   Line of separation similar to 8 of plate.
13.   Vessel of class A.

Private Laboratory of Frank S. Aby, Chicago, January, 1899.

AN ANOMALY IN THE INTERNAL COURSE OF THE TROCHLEAR NERVE.

By Richard Weil.

With Plate III.

Although variations in the course and distribution of the external portion of the Trochlear nerve are by no means unknown the present case represents, as far as the writer has been able to discover, the only recorded instance of an internal anomaly. This is probably to be attributed to the relative infrequency with which histological examinations of the internal structure of the midbrain are made. It is certainly true that the morphological peculiarities of this nerve—embracing the character of its cells of origin, of its decussation, of its exit, and also of its development—mark it as the most aberrant of the cranial nerves, and might lead *à priori* to an expectation of considerable variability.

The material[1] was a human foetus, of the eighth to the ninth month, of which one-half the brain above the medulla was preserved in bichromate, and stained according to the Weigert procedure. The bundles which took the stain in the midbrain were the nerves: oculomotor, trochlear, and trigeminus; the long sensory tracts: superior and inferior fillets, and the posterior longitudinal bundle, and some of the intracerebral commisural tracts, such as the brachium conjunctivum. The origin of the trochlear nerve is, as normally, in the floor of the Sylvian aqueduct, dorsal to the posterior longitudinal bundle. All the fibers are given off in one or two bundles, and run obliquely dorsally and backwards to the decussation. The relations of the nerve in this part of its course, both to the mesencephalic root of the fifth nerve and to the superior brachium

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[1]For this I am indebted to the Pathological Laboratory of the New York State Hospitals.

are normal.   The decussation occurs in the posterior medullary velum.   From this point onwards the course of the nerve is anomalous.   It is the rule for the nerve to make its exit at the level of the decussation, either from the dorsum, or occasionally from the side, of the velum.   In this case, however, the nerve fails to do so ; instead, it turns upon its course, and runs forwards and outwards, traversing first the velum, then the base of the posterior quadrigeminal bodies.   Its exit occurs in the superficial sulcus of the midbrain, situated between the posterior quadrigemina above, and the lateral convexity made by the inferior fillet below.

The explanation of this variation is coupled, in the present state of our knowledge, with considerable difficulty.   If we adopt the grouping of variations suggested by Cunningham, we shall, provisionally at any rate, place this among the " pragonic " variations, the unclassified residuum.   In the first place, it corresponds with no stage in the normal embryogenesis of the fourth nerve in the human species.   Nor does it, so far as we know, represent an atavistic condition, for it is a striking fact that the essential relations of the internal course of the nerve are identical in all vertebrates.

The anomaly appears, therefore, to be inexplicable, or fortuitous.   Nevertheless, there are certain circumstances which indicate that it may afford a possible clue to the original course of the Trochlear nerve.   The foetal segmentation of the brain is violated by this nerve, in that its origin and exit are separated by one of the primary constrictions of the foetal brain.   It has its nucleus in the adult midbrain, or second cerebral vesicle, while it leaves the brain in the anterior portion of the foetal third cerebral vesicle, the so-called Isthmus Rhombencephali. This origin and exit are constant throughout the vertebrate series.   If the posterior limit of the adult midbrain coincides with that of the so-called mesencephalic segment of craniologists, it is evident that certain of the internal relations of the fourth nerve must have been secondarily acquired.   The segmental nerve must, of course, leave the central system from that segment in which it originates.   This throws the difficulty

one step further back, since it is not yet clear, whether the nerve is to be regarded as a "mesencephalic" segmental nerve (Locy), in which case the anomaly would be imperfectly atavistic, and so conservative, or "epigonic" as Cunningham says; or, as belonging to the post-mesencephalic segment (van Wijhe, etc.), in which case the nucleus of origin has been displaced forwards. Finally, it is conceivable that the second primary cerebral incisure has no real segmental value, and that the fourth nerve, though crossing it, is still within the boundaries of a single cranial segment. Under this last supposition, the anomaly is, of course, entirely without significance.

For other theories of the original course of the Trochlear nerve, which do not, however, deal with this phase of the question, Fürbringer's article may be consulted, in Gegenbaur's Festschrift.

DESCRIPTION OF PLATE III.

Figure 1 is taken through the posterior quadrigemina; *figure 3*, through the velum; *figure 2* occupies an intermediate level. *IV.L*, Trochlear Nerve of left side; *IV.R*, Trochlear of right side; *V.M.*, Mesencephalic root of trigeminus; *P.L.B.*, Posterior longitudinal bundle; *I.F.*, Inferior fillet; *S.F.*, Superior fillet; *B.C.*, Brachium conjunctivum.

In figures 1 and 2, IV.R. is traveling back from its origin to the decussation; IV.L. is traveling forwards, from the decussation to its exit.

CRITICAL REVIEW OF RECENT PUBLICATIONS OF BETHE AND NISSL.

By Adolf Meyer, *Worcester, Mass.*

Since my "Critical Review of the data, etc. of Modern Neurology" was written, April, 1898, several publications apart from the one of Apáthy have appeared which claim a complete change in the current views. Apáthy's work deals so exclusively with invertebrate material that I leave its review to one better prepared. The articles here referred to are those of Bethe and Nissl.

Bethe (1) mentions as the most important findings of Apáthy the discovery of the numerous fine fibrils in the afferent fibers, and the peculiar origin of the one large fibril of the efferent fibers from a net-work around the nucleus of a ganglion cell. This inner net-work anastomoses with a more superficial net-work of finer fibrils which collect there from the splitting up of afferent fibers.

Bethe's fibril-stain shows clearly the existence of individual fibrils in the nerve fibers of vertebrates, embedded in a homogeneous substance. At the bifurcation of posterior root-fibers part of the fibrils go into one branch and part into the other. In such bifurcations Bethe has never observed any fibrils passing from one branch into the other, such as is the case in dendrites. It is, moreover, easy in these specimens to say which is the course of a fiber, because the collaterals always leave with the same distal divergence.

The cell pictures are in many respects the negatives of the Nissl specimens; but the eagerness with which the nucleus attracts the stain makes it difficult to bring out the fibers near the nucleus. In small bipolar cells the fascicles of fibrils pass through from one dendrite to the other, dividing into bundles

at the subsequent subdivision of the dendrites without any splitting up of individual fibrils. From the long description of the conditions in other cell types the following data are important:

1. Fibrils are present not only in the neurite, but in the dendrites, passing through the cell-body from one dendrite to the neurite or from one dendrite to another.

2. Intracellular net-works as described by Apáthy in invertebrates are probably not present in vertebrates. At best there is an occasional bifurcation of a fibril, the two branches going into different dendrites.

The origin or final distribution of the fibrils is not established; the fibrils are claimed as the unique 'conductors,' although no experience with experiments on vertebrate material is brought forth.

Bethe (2) further reports the remarkable results of his studies on the nervous system of arthropods, and especially the interesting fact that in Carcinus he was able to cut out the 'cells' of the motor fibers of the second antenna, without destroying the neuropil connecting the receptory and the motor fibers, although the operation severed the neuropil also from the brain and from the abdominal ganglia. After twelve to twenty-four hours, the tonus, reflex-irritability, and even the summation of stimuli, could be demonstrated again; the only obvious abnormality was an exaggeration of reflex-irritability. On the third or fourth day the phenomenon disappeared and the antenna became paralyzed and remained so. On this result Bethe bases his view that the nerve cells have merely trophic functions and are, perhaps, the bearers of reflex inhibition. He uses the word 'nerve-cell' in the 'preneuronic' sense, meaning by it merely the nucleus with the surrounding protoplasm, but not the processes.

Such a division is easy in the arthropods; but in vertebrates it would meet considerable difficulty. It would certainly be necessary to remember that the 'cell body' in arthropods comprehends a much smaller part of the neurone (using this word for what grows out of a cell-unit of the embryonic tissue) than that of a vertebrate. This point is, of course, duly con-

sidered by Bethe; but many a neurologist who is not acquaint-
ed with the nervous system of invertebrates is apt to become a
victim to the ignorance of this difference. The very fact that
Bethe goes to the text-books of physiology and anatomy for his
'authority' of the use of the word 'nerve-cell'; and that he
seems to seriously believe that men familiar with the 'neurone-
theory' proper, speak of memory-cells, etc. in the sense of
'cell-bodies' for memories, ignoring the processes, would force
us not to take his word 'Nervenzelle' as a serious histological
expression. A 'nerve-cell' of an arthropod after Bethe's
nomenclature is only a very small part of a 'nerve-cell' in the
modern sense of the word neurone; the size of the *processes* of
those small cell-bodies is such as to warrant the viability of the
tissue for a period of two to three days, just as we know that a
peripheral nerve in man, when cut through, preserves its elec-
trical excitability for at least two days, during which period the
excitability both to the faradic and to the galvanic current may
even be slightly increased (similar to what is mentioned in the
experiment on the arthropod); then begins a gradual diminu-
tion and only at the end of the first week or even as late as the
middle of the second, do we find the minimum excitability.
With perfect knowledge of this fact, we maintain what we said
concerning the 'motor neurone,' and the only consequence of
Bethe's experiment on our general view would be this : that, if
we could destroy the nucleus of the segmental efferent neurones
without injuring the rest of the cell, the function of the cell
would probably last at least as long as the excitability of a cut
nerve. Between this and the extermination of the 'neurone-
theory' there is a long distance.

The rest of the paper is devoted to a noteworthy sketch
of a physiological conception of psychic activity, culminating
in the idea, that all psychic activity is the play of the outside
world on the fibril net-work of the nervous system.

While Bethe keeps in the main carefully to the description
of the fibrils and to his experiment, Nissl (3) takes a far broader
sweep in his apotheosis of the 'gray matter.' The article is
psychologically interesting, but difficult to render in abstract.

The sum total of the results of his studies of the cell-bodies in poisoning and disease has convinced Nissl that the real core of nervous function is only imperfectly touched by the histological findings.   Apáthy and Bethe have established the view of M. Schultze, that the fibrillary substance is the highest degree of differentiation of cell-plasm of the animal body.   It develops to a great extent beyond the cell and persists outside of it. 'Ich schneide damit die hochwichtige und zur Zeit absolut un-gelöste Frage nach dem Wesen der grauen Substanz an.' Nerve cells and their ramifications are not the essential criterion of the gray matter.   It is characterized wholly by the presence of 'molecular' substance in which the other elements are embed-ded.   Apáthy claims that in the invertebrates the probably ho-mologous neuropil is a continuous (anastomosing) net-work of elementary fibrils.   This condition is not established for the vertebrates, but we have proof for the view that the functionally highest parts of the nervous central organ contain large amounts of this substance which cannot be glia and the existence of which 'cannot possibly be simulated by the sum of nerve-cell pro-cesses plus the non-nucleated glia in connection with non-medul-lated and medullated nerve fibers.'   The proof of this consists in the consideration that the dendrites in Bethe's specimens ramify without division of the fibrils and that the number of fibrils in the dendrites is so small after a few bifurcations that the ex-tremely numerous ramifications of the dendrites in many Golgi pictures is sheer impossibility.   'They cannot be the expression of division of dendrites but must have another meaning.'   At least a part of the Golgi dendrites are supposed by Nissl to be neurites which originate in the gray matter and go the nerve cells to form the pericellular net of Held, demonstrable also in Bethe specimens.   Nissl goes so far as to say that the cells ex-tend only as far as they are visible in the 'acute alteration' in Nissl specimens.

Nissl finds himself forced to give up the neurone-theory and to assume the following elements in the central nervous system :

"(1) nerve-cells and (2) a specifically nervous substance

which is no real nerve-cell protoplasm, but a modified cell pro-
toplasm which is found partly within the nerve cell in the form
of fibrils, partly outside forming the enormous masses of (inter-
cellular) gray matter which is, anatomically, to be considered a
very delicate continuous net-work ('Gitterwerk') of elementary
fibrils, together with the much coarser pericellular net which
probably also consists of fibrillary substance and belongs al-
ready to the central gray matter, not to the cell-body; secondly,
it appears in the form of fibrils as the most essential constituent
of the nerve fibers." Nissl gives two remarkably striking pic-
tures of pericellular nets from Bethe specimens, and three illus-
trations of cortex of the mole, of the dog, and of man, from
corresponding regions, showing very clearly the greater amount
of 'gray matter' between the cells in man. (The higher the
development of an animal, the fewer the nerve-cells in an equally
large space of cortex.) The comparison shows that the superficial
layer of the cortex varies least; an increase in 'gray matter'
is largely visible in the second and third layer. Nissl says (page
1028) correctly that any hypothesis must be dropped (we should
say modified) as soon as even one single fact has been demon-
strated to disagree with it. With this insight he proceeds to
undo the neurone-theory 'once forever,' and even his own hy-
pothesis of specific nerve-cell function, since he has 'discov-
ered' the 'gray substance' and the fact that the cell-changes
described by him cannot be an expression of disturbed function
but merely that of a chemical or physical alteration. The ex-
istence of various cell-types in the nervous system is none the
less evident to him. The more elaborate forms of function in
the highest species of the animal series undoubtedly depend on
an increasing division of labor of the cells in the higher cell-
communities. 'From this point of view the idea, somewhat
strange to our usual thought, becomes intelligible (?), that the
highest functions of the vertebrate body are not directly at-
tached to cells, but to a living substance, the morphological
arrangement of which reminds one much rather of anything
else than of cells. We need only look into our body carefully

to convince ourselves readily that the most differentiated sense-organs, or the voluntary muscles, offer similar relations.'

Everthing seems to indicate that there is a division of labor in the nervous system in this sense, that the nutrition, metabolism and the elimination of effete material in the gray matter and in the tracts of fibrils is attended to by the nerve-cells, and also the task of accumulating the necessary energies for the production of heavy work, so that enough vital power is ready for the real nervous substance even in answer to the slightest stimuli.   This view of such a dualism is necessary to explain the apparent contradiction between the intimate spacial relationship between nervous substance and nerve-cells and on the other hand the independence of the two morphological components of the nervous system.

This short sketch merely presents the general trend of argument of Nissl.   His long and not lucid paper contains many hints of things which must as yet be withheld from the world ; many of the ' facts ' are obtainable only with Bethe's method which is also withheld.   Many expressions are given meanings which seem to be the fountain-head of confusion ; I mention only his use of the term ' cell.'   Nissl's cell is a decidedly expurgated affair, a sponge through the holes of which the ' real nervous substance ' grows quite irrespective of the fact that the fibrils and the expurgated cell-concept are together that which we are accustomed to call cell for reasons too simple to be offered to Dr. Nissl.   The same holds for ' gray matter ' of which nobody would ever think that it meant what Nissl wants it to mean.   Perhaps this terminology is necessary to produce the degree of obscurity so popular for certain kinds of ' demonstrations.'

The experiment of Bethe establishes physiologically the correctness of the view of Nansen (see page 124 of my review and plate 15, fig. 1) of which both Bethe and Nissl seem ignorant ; and Nissl's ' gray matter ' is a realization of what Golgi puts forth as the greatest obstacle to the neurone-theory, his réseau nerveux diffus (my review, page 126) not mentioned with one word by Nissl who seems in more than one way to make

an easy fight with the uncomfortable results of Golgi's method. Nissl's gray matter is supposed to consist of fibrils yet to be discovered, but it is already made the sanctum of the omnipotent unknown 'nervous function.' And Bethe tries to make us forget the pangs of not knowing any material memory-substrata by drawing before our eyes a very plausible picture of general biological concepts, which has not a word to say concerning the essential problems of functional organization and differentiation. Nissl's dictum of the extermination of the neurone-theory reminds one of boys who make a snow man, decapitate him and declare solemnly that they have killed him. It would be interesting to know what life the snow man had and what Nissl's (and Bethe's) neurone-theory looked like before its light began to fail. The motto which Nissl puts at the head of his article seems to be intended for other people only; or will it be said to apply to Nissl himself as well? 'Wer die Geschichte der Nervenanatomie und Nervenphysiologie des letzten Jahrzehnts prüft und durchgeht, der muss in der That in den vielen, mit grosser Zuversicht aufgebauten und durch alsbald bekannt gewordene, an die Ironie des Schicksals mahnende neue Thatsachen enttäuschten und widerlegten Theorien eine Warnung erblicken, jetzt schon Ansichten über die Funktion von Theilen aufstellen zu wollen deren Erkenntniss noch weit—weit von einem wünschenswerthen Ziele entfernt ist. (B. Stilling, 1856).'

The status of the neurone-problem developed a year ago is not changed essentially to-day. It will be a difficult task—but one which must be worked over—to bring into harmony the widely differing pictures produced by the methods of Golgi, of Ehrlich, of Bethe, of Nissl, etc., to work through all the important experimental reactions with these methods and to refrain from putting bright guesses down as statements of facts. It is quite evident that we are still very far from a complete picture of the architecture of the nervous system; but not so far that we should allow ourselves to be thrown out of the saddle by every little addition of detail. The neurone-theory deals primarily with genetic and trophic relations, and as such it is a

good working hypothesis, though full of unsolved problems. The question of function of the nervous system is today at best one of activity of aggregates of neurones, and if we want to specialize further, we will do best to start from the known and not from the unknown. Many of us have the feeling that notwithstanding the veto of Golgi and the considerations of Nissl we are perhaps not forced to accept a 'réseau diffus' outside of what we know as processes of cells and certainly few people will follow Nissl in willingly despising what we have and in putting the sole emphasis on the 'non-classified residium,' the storehouse from which the supplies for all the hopes and the remedies for all the woes are expected to be furnished to those disappointed with what is safely established and with the usual methods of acquiring new knowledge.

LITERATURE.

1. Bethe, Ueber die Primitivfibrillen in den Ganglienzellen von Menschen und anderen Wirbelthieren. Morph. Arbeiten von Schwalbe. Vol. VIII, p. 95-116, Tafel IX and X.

2. Bethe, Die anatomischen Elemente des Nervensystems und ihre physiologische Bedeutung. Biolog. Centralblatt. Vol. XVIII, p. 843.

3. Nissl, Nervenzellen und graue Substanz. Münch. Med. Woch. 1898.

REPORT OF THE ASSOCIATION OF AMERICAN ANATOMISTS.

The eleventh annual session was held in New York City, Dec. 28-30, in conjunction with the "Naturalists" and other affiliated societies. Most of the meetings were held at the Medical Department of Columbia University. Forty-one members attended and twenty new members joined, making a total membership of one hundred and forty-one, of whom ten are honorary. The localities and names of the new memberf are as follows : From Ann Arbor, Prof. J. P. McMurrich, Univ. of Michigan ; from Baltimore, Professors F. P. Mall and L. F. Barker, and Associate R. G. Harrison, of the Johns Hopkins University; from Buffalo, Dr. N. S. Russell, assistant in anatomy, Univ. of Buffalo; from Ithaca, Dr. L. Colville, lecturer and demonstrator in anatomy, Cornell University Med. College; from Montreal, Dr. J. G. Mac-Carthy, senior demonstrator of anatomy, McGill University; from New York City, Prof. J. D. Erdmann of Bellevue Med. College ; Dr. Evelyn Garrigues, assistant demonstrator of anatomy, Womans Medical College ; Dr. Ales Hrdlicka, associate in anthropology, Pathological Institute of N. Y. Hospitals ; and the following assistant demonstrators of anatomy in Columbia University : Doctors G. E. Brewer, C. Carmalt, H. D. Collins, G. W. Craig, W. Martin, W. H. Rockwell, and A. S. Vosburgh; from Philadelphia, Prof. J. C. Heisler of the Medico-Chirurgical College ; from Savannah, Dr. E. R. Corson ; from Washington, D. C., Dr. C. I. West, demonstrator and lecturer in topographical anatomy, Howard University.

The address of the president, Dr. Burt G. Wilder, discussed "Misapprehensions as to the Simplified Nomenclature"; the speaker urged especially a fuller recognition of what had been done by the English anatomists, Barclay, Owen, Pye-Smith and T. Jeffery Parker, and hoped the nomenclature of the future would be called the "Anglo-American."

The Association voted that abstracts of papers be required in advance, and that brief abstracts be included in the program ; that the time for reading papers be limited to thirty minutes; that the Secretary-Treasurer be allowed his railroad fare and ten dollars toward his hotel expenses at each meeting. The Association also accepted the propo-

sitions of the editors of the (English) *Journal of Anatomy and Physiology* as to making that journal the official organ of the Association, and nominated Prof. George S. Huntington as the American editor. The details of the arrangement will be given in a circular to be issued by the secretary of the Association. Dr. E W. Holmes, of Philadelphia, was elected a member of the Executive Committee, and the president was authorized to fill the vacancy in the Committee on Anatomical Nomenclature caused by the resignation of Dr. Dwight.[1]

The subject assigned for discussion, "The teaching of Anatomy in our Medical Schools," was opened by Dr. Holmes in "The defects of our present methods," and further considered under ten divisions viz., 1. Preparatory education; 2. The value and place of General Biology and Comparative Anatomy; 3. Histology and Embryology in the medical course; 4. The relative value of didactic methods; 5. Practical anatomy and how to teach it; 6. The order of topics; 7. The correlation of structure and function in teaching; 8. The use of charts and blackboards; 9. The qualifications requisite for a teacher of anatomy; 10. The desirability of terminologic consistency; by Dr. Gerrish (4, 6 and 8), by Dr. Huntington (2, 3, 5 and 6), and Dr. Wilder (10). In view of the extent and importance of the subject it was suggested that at future meetings a smaller number of divisions be more fully considered.

The following papers were read and discussed; all were illustrated by specimens, and charts or photographs, and several by lantern-slides or enlarged photographic projections: By J. A. Blake, " The roof and lateral recesses of the fourth ventricle considered morphologically and embryologically;" by G. E. Brewer, " Preliminary report on the surgical relations of the duodenal orifice of the common bile-duct;" by E. R. Corson, " An X-ray study of the normal movements of the carpal bones and wrist;" by F. Dexter, " Morphology of the digestive tract of the cat;" by T. Dwight, " The origin of numerical variations of the vertebrae;" and " The living model showing the platysma in contraction;" by S. H. Gage, " Further notes on the relation of the ureters and great veins;" by I. S. Haynes, " An explanation of a new method of cutting gross sections of the cadaver, with demonstration of the technique;" by Ales Hrdlicka, " The normal human tibia;" by G. S. Huntington, " Morphology and phylogeny of the vertebrate ileocolic junction," " Visceral and vascular variations in human anatomy;" and "The sternalis muscle;" by W. Martin, "The caecum and appen-

[1] Dr. E. C. Spitzka of New York city has since been selected.

dix in 100 subjects ;" by J. G. MacCarthy, ''The internal structure of the hippocampus ;" by B. B. Stroud, "Note on the staining of isolated nerve-cells," and '' Preliminary account of the degenerations in the central nervous system of frogs deprived of the cerebrum ;" by B. G. Wilder, '' Some current misapprehensions as to the objects of the Cornell collection of brains." For lack of time there were read by title only, Dr. Wilder's paper, ''Further tabulation and interpretation of the paroccipital fissure (occipital division of the intraparietal complex) ;" three papers by Dr. Huntington, '' The genito-urinary system of the American pit-viper ;" '' Contribution to the anatomy of the reptilian vascular system ;" '' Cerebral fissures and visceral anatomy of the Eskimo from Smith's Sound ;" and Dr. Haynes' discussion of Teaching.

At its closing session, Dec. 30, the Association adopted without dissent the report of the Committee on Anatomical Nomenclature presented by the majority (Gerrish, Huntington and Wilder). It comprises four divisions, viz.:

A.   Brief statement of reasons for preferring certain terms (about fifty in number) already adopted by the Association.

B.   Recommendation of *mesocoelia* as a name for the cavity of the mesencephalon, with reasons therefor.

C.   Recommendation of 181 names of bones (120) and muscles (61) identical with those in the B. N. A. (Basel Nomina anatomica).[1]

D.   Recommendation of 17 names of bones and muscles differing from those of the B. N. A.

REPORT.

A.   *Brief statement of reasons for preferring certain neural terms included in the report adopted at the last meeting of the Association.*[2]

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[1] Die anatomische Nomenclatur. Nomina anatomica, Verzeichniss der von der Anatomischen Gesellschaft auf ihrer IX. Versammlung in Basel angenommenen Namen. Eingeleitet und im Einverständniss mit dem Redactionsausschuss erläutert von Wilhelm His. Archiv für Anatomie und physiologie. Anat. Abth., Supplement Band, 1895.

[2] This portion was already written last year, but was not printed on account of the supposed necessity of having the last report ready for distribution at a certain date. The numbers in parentheses correspond with the serial numbers i n that report (*Proceedings of the tenth annual session*, pp. 9, 47-53). Some of these terms are more fully discussed by the secretary of the committee, in ''Neural Terms, International and National," *Journal of Comparative Neurology*, VI, December, 1896, pp. 216-352, including seven tables. Parts VII-IX have also been reprinted under the title '' Table of Neural Terms, with Comments and Bibliography."

Alba (1); cinerea (2); gelatinosa (3); reticularis alba (77); cauda-tum (89); pallidum (108); albicans (123); entocinerea (143); intercala-tum (144); and arachnoidea (208), are neuter or feminine adjectives used as substantives, and comparable in that respect with cases already discussed, viz., callosum (§13) and dura (§15); special points con-nected with them may be considered hereafter.

Limen (6); caput (90); cauda (91); fimbria (94); splenium (96); genu (97); rostrum (98); corona (110); tuber (124); valvula (148); frenulum (149); lingula (154); arbor (166); calamus (173); ligula (176); pyramis (181); conus (189); filum (190); cisternae (209); glomus (217); circulus (231); torcular (251), are more or less closely comparable with calcar, chiasma, tentorium, and falx (§§9-12) in that, even when not absolute idionyms, their signification would be determined by the con-text or could be indicated by a word that need not be repeated.

In replacing " substantia corticalis " by cortex (105); " nucleus lentiformis " by lenticula (107); " corpus geniculatum " by geniculum (116, 117); " lamina terminalis " by terma (128); "corpus trapezoid-eum " by trapezium (165); "nucleus emboliformis" and " n. globosus" by embolus and globulus (170, 171); " corpus restiforme " by restis (184); " formatio reticularis " by reticula (206), we simply replace phrases including adjectives that suggest resemblance to objects (simile names) by the substantive names of the objects themselves. In so do-ing we follow the actual example of the B. N. A. in preferring (§6) oliva to " corpus olivare," clava to " processus clavatus," vermis to " processus vermiformis ;" and pyramis to " corpus pyramidale." In-deed, the logical extension of the system embodied in the retention of " corpus restiforme " when restis is available would burden anatomy with gyrus insuliformis, corpus pontiforme, and corpus hippocampoides none of which, fortunately, has materialized.

Endyma (4). As well stated by Hyrtl (" Onomatologia," p. 200) the initial syllable of " ependyma " is quite superfluous. If, on the other hand, the qualifying genitive " ventriculi " is required, as in the B. N. A., why not " cerebri " also in order to secure absolute explicit-ness? As a matter of fact both endyma and " ependyma " are idio-nyms, and the former is as much better as it is shorter.

Habena (120), vallis (153), and acervus (218) are preferred to the diminutives " habenula, vallecula " and " acervulus " because they are shorter; " acervulus," moreover, is a modern coinage.

Gyrus subcalcarinus (61) and Gyrus subcollateralis (60). These terms are recommended in place of " Gyrus lingualis " and " Gyrus fusiformis " respectively. The difficulty of applying the latter is well-

known; indeed, so vague are the resemblances implied in them that certainty can hardly be insured without resort to the rather puerile mnemonic device of associating the letter n in calcarina and lingualis. But since Fissura calcarina and Fissura collateralis are now almost universally employed, and no new words have to be introduced, there seem to us to be several advantages and no disadvantages in designating the gyri just ventrad of the two fissures respectively by terms indicating their relative positions.

Gyrus subfrontalis (46). In the B. N. A. was adopted "Gyrus frontalis inferior" to the exclusion of the common synonyms, "convolutio Brocae" and "Gyrus frontalis tertius."[1] The question is therefore narrowed down to the relative merits of "Gyrus frontalis inferior" as adopted in the B. N. A. and Gyrus subfrontalis as preferred by us; and since this is a type of a large number of cases of difference between the two lists, it will be presented in some detail.

The two terms agree in being both distinctly Locative Names. The location of a part is a general and comprehensive attribute, and, as remarked by Owen, "signifies its totality without calling prominently to mind any one particular quality, which is apt thereby to be deemed, undeservedly, more essential than the rest." Locative names form two natural groups, Prepositional and Adjectival. Prepositional Locatives.—With these the qualifying prefix, a preposition or adverb, indicates the location of a part relatively to some other part, more important, more easily recognized, or previously designated. Praecuneus designates a cortical area just "in front of" the cuneus; subcalcarinus and subcollateralis are prepositional locatives. Adjectival Locatives.— These indicate either the location of a part within some general region, or its membership of a series. Vertebra thoracalis designates a spinal segment in the thorax. Commissura anterior, cm. media and cm. posterior distinguish members of a series. Subfrontalis is an adjectival locative, and the preposition *sub* is employed as a prefix in the sense of inferior or lower; it is also a true monoymic adjective, and not a

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[1] Both these names were rejected by the secretary of this Committee in 1885 ("On two little known cerebral fissures, with suggestions as to fissural and gyral names," *Amer. Neurol. Trans.; Jour. Nerv. and Mental Disease*, XII.; abst. in Neurolog. Centralblatt, Dec. 15, 1885), the former as an eponym and as including the needlessly long word convolutio, and the latter as a trionym and because the enumeration of the three concentric frontal arches might quite as naturally begin with the "inferior" as with the "superior;" indeed, this was done by Meynert ("Psychiatry," Fig. 9); likewise by Leuret in the analogous case of the arches about the Sylvian fissure of Carnivora.

quasi-mononym like the hyphenated " infero-frontalis " sometimes employed.

B. Mesocoelia (English mesocoele or mesocele).— This single word is recommended as a name for the entire cavity of the mesencephalon, the region including the crura and the quadrigeminum.

The following considerations apply to the general use of coelia (English coele or cele) in place of ventriculus.

(1). Its Greek origin renders it compoundable regularly and euphoniously with the characteristic prefixes already employed in the segmental names, e. g., mesencephalon etc. (2). These compounds are mononyms, and therefore capable of inflection (e. g., mesocoeliae), derivation (e. g., mesocoeliana), and adoption into other languages without material change; e. g., English, mesocele; French, mesocoelie; German, Mesokölie; Italian, mesocelia. (3). The various national paronyms thus formed are likewise capable of derivation; e. g., mesocelian. (4). There is classic authority for use of coelia in the sense of encephalic cavity. In the lexicon of Liddell and Scott κοιλία ἐγκεφάλου is quoted as in good and regular standing among Greek medical writers. According to Burdach ("von Baue und Leben des Gehirns", 1819-22, II, 301, 378, 380), Galen designated the "fourth ventricle" as κοιλία ὀπισθίου ἐγκεφάλου, τετάρτη κοιλία, and ὀπισθία κοιλία (De usu partium, Lib. VIII, cxii, p. 170); the "third ventricle" as μέση, τρίτη κοιλία (idem. IX, III, 172); and the "lateral ventricles" as προσθίαι κοιλίαι (De odoratus instrumento, II, 110). Coelia is then certainly not "new."[1] (5) These ancient usages are assumed to be familiar to most anatomists, who therefore should recognize the compounds with little or no hesitation. (6) The compounds are so euphonious and so obviously correlated with the segmental names as to be learned and remembered easily even by general students and by such as may not have had a classical training. (7). In recent times coelia has been independently proposed by two anatomists, teachers as well as investigators.[2] (8). It has been adopted more or less completely

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[1] Dr. Achilles Rose, of New York City, informs the secretary of the Committee that in the modern Greek treatise on Anatomy by Παπαϊωάννου (Athens, 1888-1890, 3 vols.) the encephalic cavities are designated by ἀι πλάγιαι κοιλίαι; τρίτη ἢ μέση κοιλίαι; τετάρτη κοιλία.

[2] The secretary of this committee, March, 1881 ; Prof. T. Jeffery Parker, of Otago, New Zealand, August, 1882 ; in addition to the three publications enumerated in the Bibliography of " Neural Terms," there should be named his two papers on Apteryx (Philos. Trans., 1891 and 1892) and Parker and Haswell's " Zoology," 1897.

by four of the older American neurologists, C. K. Mills ('97), Henry F. Osborn ('82, '84, '88), E. C. Spitzka ('81, '84), and R. Ramsay Wright ('84, '85); and unreservedly by eight of the younger, W. Browning, T. E. Clark, P. A. Fish, Mrs. S. P. Gage, O. D. Humphrey, B. F. Kingsbury, T. B. Stowell, and B. B. Stroud. (9). Coelia and its compounds are idionyms, i. e., used in no other sense in normal vertebrate anatomy; hence, unlike ventriculus and its compounds, they are free of ambiguity. This argument is stated last because it seems to the committee of comparatively slight importance. Theoretically, of course, ventriculus (encephali) might be mistaken for ventriculus (cardiae s. cordis). Practically, however, the context would almost infallibly obviate misapprehension. Hence the absolute unambiguity of coelia and its compounds would not in itself justify its replacement of ventriculus. It would be a *causa vera*, but hardly a *causa sufficiens*.

The special arguments for the adoption of mesocoelia in advance of the other coelian compounds are four :

(1).   There is substantial agreement among anatomists in recognizing a definite encephalic segment under the title mesencephalon ; this cannot yet be said of the other regions.

(2).   The cavity of this segment has no common ventricular dessignation like "quartus," "tertius," and "lateralis."

(3).   The terms, ventriculus mesencephali or v. mesencephalicus (English, mesencephalic ventricle or cavity), are seldom used and are somewhat clumsy. Even less convenient are the phrases "aquaeductus cerebri Sylvii" and "iter a tertio ad quartum ventriculum."

(4).   The abbreviations, iter and aqueduct, while sufficiently descriptive of the adult conditions in man and other mammals, are quite inappropriate to the " vast and spacious cavity" of the embryonic mesencephalon, and to the lateral extensions in frogs, reptiles, and birds.

Sections C and D of the Report give the lists of names of bones and muscles recommended by the committee, which are identical with those in the B. N. A. and of those which differ from those of the B. N. A. For these lists consult the full Proceedings of the Association.[1]

D. S. LAMB, Secretary.

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[1] Also the *Philadelphia Medical Journal*, Feb. 25, 1899. Copies of the Report will be mailed upon application to the secretary of the committee, Dr. B. G. Wilder, Ithaca, N. Y.
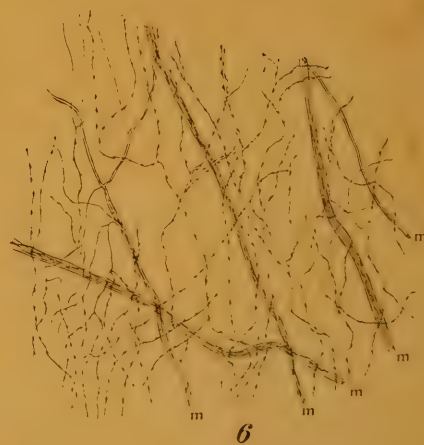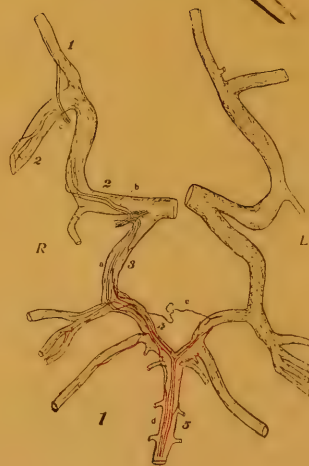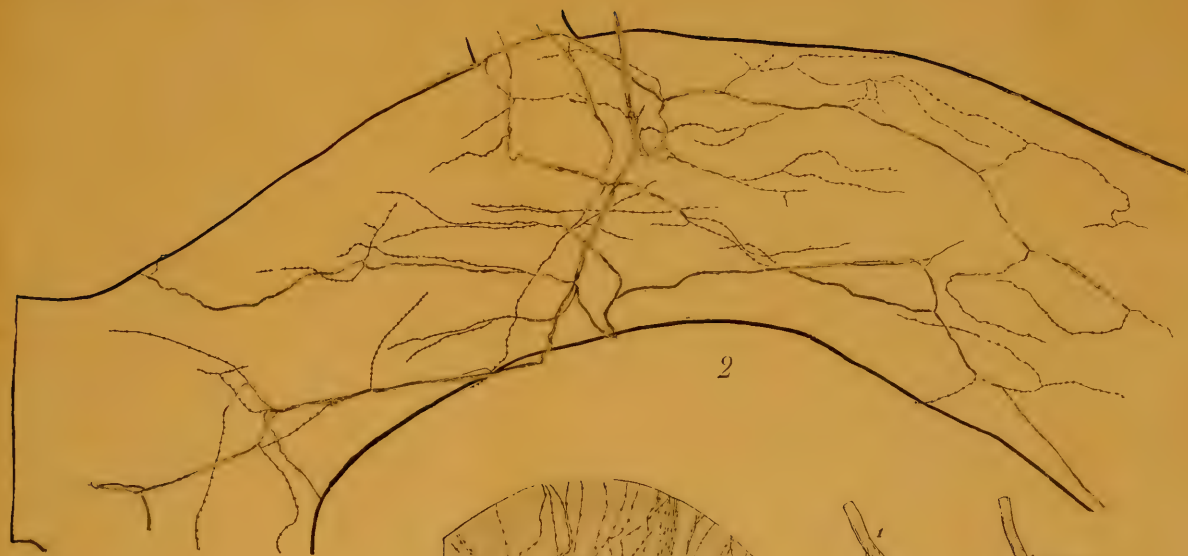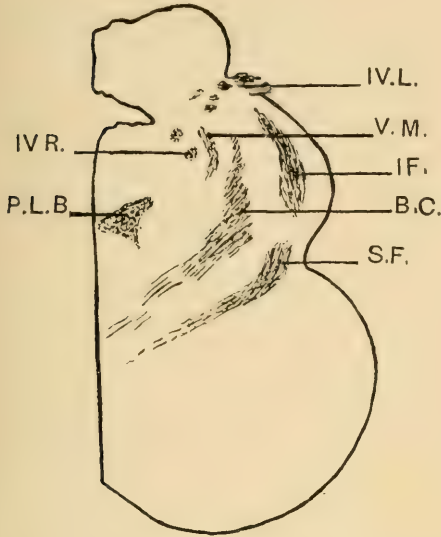
PLATE I.

Fig. 1
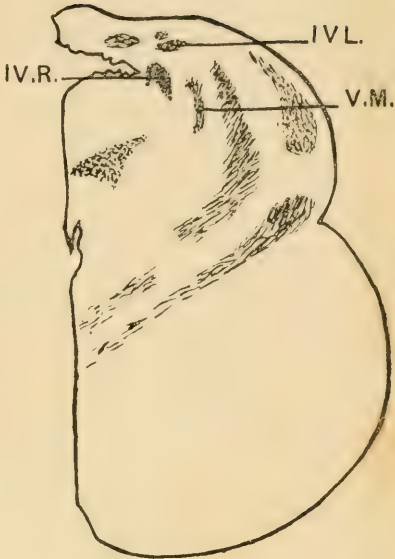
Fig. 2
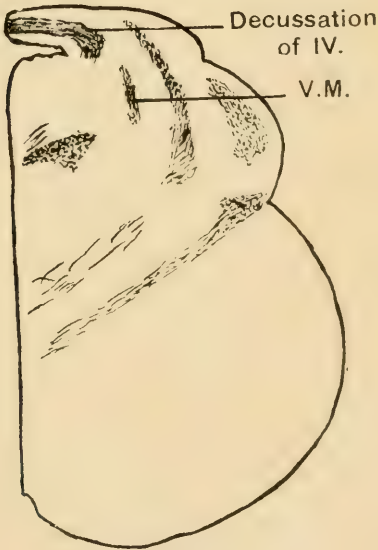
Fig. 3

NERVE TERMINI IN THE SKIN OF THE COMMON FROG.[1]

By G. E. Coghill.

PART I.

With Plates IV and V.

The study here presented is a continuation of that which was begun last year under the direction of President Herrick and the results of which were published in Vol. VIII, Nos. 1 and 2 (combined) of this JOURNAL, under the caption, "The Somatic Equilibrium and the Nerve Endings in the Skin."[2] In this discussion we dealt with the skin of both Anura and Urodela. In the present study the frog only is considered; and the points further discussed here which were presented on pp. 37-51 of the volume referred to are: the isolated sensory cell or terminal cell, the ganglionic plexuses, and nerve termini on glands. Our belief with reference to these structures is supported by methods not used formerly, and other conditions related to them have come to our notice. The latter have to do chiefly with the musculation and innervation of certain glands.

The results of our earlier study of the nerve endings were obtained by the haematoxylin, picrocarmine and methylene blue stains, and by the use of chrom-acetic acid solutions as fixing agents. For fixing we have since used other modifications of the chrom-acetic acid preparations, and Flemming's solution in

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[1] Thesis presented for the degree of Master of Science at the University of New Mexico.

[2] The present installment includes simply the author's results; an historical résumé may be expected with the second part which will be devoted to the embryogenesis of the skin.

addition; with application of Delafield's haematoxylin, Benda's Sulphate of Iron Haematoxylin, and Weigert's Haematoxylin. Further use has been made of methylene blue intra vitam preparations, and the silver method has also been employed.

The methods just mentioned show that free-ending nerve cells occur in large numbers in the skin on the head of the frog, that these are usually found in clusters of three or more, and that these clusters tend to be grouped to such an extent that they appear, in our best preparations, over a comparatively large field with varied frequency, while in an adjacent area they are entirely absent. For their distribution and general arrangement in the surrounding parts, the best results have been obtained from tissues hardened in the chrom-acetic acid and Flemming solutions and stained with Weigert's Haematoxylin. (Fig. 1.) In this preparation numerous clusters of fibers are seen to pass ectad through the corium and terminate in long rod-like cells in the Malpighian layer. The continuity of the terminal cell with the nerve is certain. In instances otherwise clear this point is made doubtful by the presence of pigment, but such evidence is now in hand that the continuity of cell with nerve must be accepted. This is shown also in the methylene blue preparations, in which case the deeply impregnated fiber has been seen to pass in a similar manner through the corium and, clearly differentiated from the neighboring pigment, to continue into the terminal cell, the wall of which is continuous with the sheath of the fiber. (Fig. 4.) The terminal cells are clearly differentiated from the neighboring epithelial cells. They are much longer than the latter, extending through nearly the entire height of the Malpighian layer, usually appearing to end just short of the horny surface of the skin. Their special cavity through the epithelial layer and opening on the surface which has been seen in other instances is not found in the later preparations. On the contrary, the terminal cells often diverge at the base of the Malpighian layer, the epithelium cells crowding in between them. This discrepancy in results may be due to the difference in the methods employed in the two instances, though it more likely indicates that the structure in question is

of a primitive and embryonic nature, becoming obscured in older tissue. The nucleus of the terminal cell, in accordance with earlier descriptions, is long and narrow, as are also those which appear in the nerve in its passage through the corium. Here the nerve is shown by both Flemming and chrom-acetic acid preparations stained with the Delafield, Benda and Weigert haematoxylins, and also by the methylene blue and silver impregnations. (Figs. 1-6.) The Weigert being primarily a sheath stain, the fibers are frequently seen with difficulty by that method, and to be seen at all require an exact decolorization. In special instances this process was observed under the microscope and the tissue removed at the proper stage of differentiation. The best results, however, for showing the structure of the nerve in its passage through the corium came from a teased methylene blue preparation (Fig. 3). In this special case the Malpighian layer was in part torn away, but the glands and other structures of the skin further entad were intact, so that the fiber could be traced with but one short interruption from immediately beneath the Malpighian layer to near the base of the corium. The sheath, also, for the greater part of this distance, was clearly differentiated from the fiber. Other similar fibers associated with it were tracable for a shorter distance.

The ental destination of these fibers from the terminal cells is difficult to determine with absolute certainty. However, in methylene blue and silver impregnations, they are traced for some distance beneath the corium and in a plane nearly parallel with it (Figs. 5 and 6), while with the Weigert method they have been seen to enter small bundles of fibers immediately beneath the skin. (Fig. 2.) This indicates that they are branches from the plexus of nerve fibers and bundles which is known to exist in this region. If they are such, the innervation of the terminal cells on the head, as has been demonstrated from the head of the tree frog for this study especially, must be by the frontal branch of the fifth nerve.

A discussion of the nerve termini on the glands requires first a reference to other structures related to them. The glands in the skin of the frog, as is well known, are of two classes,

distinguished here as the ental and the ectal series. The glands of the ectal series are distributed quite regularly throughout the skin of the head, and occur together with those of the ental series. In the latter case they are much smaller than the glands of the ental series, being forced peripherad into the interstices of the ental group which in places constitutes nearly the entire integument beneath the Malpighian layer.

Where the ental glands do not occur, those of the ectal series may become very large in some instances, extending through nearly the entire height of the corium and becoming very closely crowded together. But regardless of position or size, their structure is universally the same, and they are thus easily distinguished from those of the ental series. The peripheral cells of the ectal series are approximately cubical, becoming lengthened or depressed according to the shape of the gland and their position in it. The walls of these glands are made up of such cells, supported externally by fibers of connective tissue. There appear no differentiated muscular elements connected with them. On the glands of the ental series the peripheral structure is entirely different. As with the ectal series, there is a tendency for the connective tissue to fold about them, but within this tissue, lying compactly on the surface of the gland, is a complete tunic of non-striated muscle cells. In a section through the median plane of the gland this arrangement is not noticable, but in sections just denuding the periphery of the organ the form of these cells is plainly shown. They are broad in their middle part and taper to a more or less acute point at either end, being very much flattened throughout their entire length. Their nuclei are large, elongated and rounded at the ends. Each cell seems to be entirely separate from its neighbor, there being frequently a considerable space between them. This structure was first observed in tissues fixed in Flemming's solution and stained by the Weigert method. (Fig. 7). It has since been verified by sections of the same preparation stained by the Delafield and Benda methods; in similar preparations double stained with picrocarmine; also by the same stains applied to tissues fixed in the chrom-acetic acid solution,

and by the methylene blue method. The normal position of these cells seems to be with their axis approximately perpendicular to the surface of the skin, though in one instance a part of them seemed to lie obliquely. This single exception to the rule may, however, be interpreted as an artificial arrangement. It can be affirmed with certainty of these cells that their function is muscular. This position is sustained by the application of methylene blue which reveals a liberal nerve supply to them, and the typical form of muscular nerve endings on their periphery. (G. C. Huber and DeWitte, this JOURNAL, Vol. VII, 3-4, Fig. 25.) In one instance (Fig. 9), sketched under the oil immersion lense, the evidence by lower powers was sustained. Nodosities, stained a deep blue, are seen to be connected by a fine fiber, lying in a position corresponding with that of the tunic cells. At first there seemed to be a possibility that this appearance was due to a precipitation between the cells, and that it sustained no definite relation to them. But on closer examination it was discovered that there were a number of these cells sufficiently impregnated to show conclusively that the fibers with their varicosities lie, not between the cells, but upon them. In another instance, an individual cell teased from the gland showed the same arrangement. Two plainly differentiated nerve fibers with occasional nodules lie on the surface of the cell as if firmly attached to it. Furthermore, on three successive glands of this series non-medullated nerve fibers were seen to pass from the ental portion of the corium to the glands, and to distribute themselves there among the fibers and nodules on the cells, and in some cases the fiber itself assumed the varicose form and became very diminutive. These fibers going to the glands are smaller than those going to the terminal cells, and their nuclei are also smaller and shorter. This nerve connection is apparently sustained by the other methods employed, excepting only the Golgi, but the evidence from these methods is not such as to be of itself convincing.

As yet it has not been possible to trace these fibers to an entrance into a bundle or as a single fiber for any distance beneath the corium, as was done in the case of the terminal fibers.

The problem of their ental destination is probably involved with
that of the ganglionic plexus, to be described.

In the skin from the head of the frog treated with the
silver method, there is found at the base of the corium, a rela-
tively thick stratum containing a most intricate plexus of gang-
lion-like cells with their fibers. This plexus is to be distin-
guished from that which was mentioned in connection with the
ental course of the fibers from the terminal cells. The latter
lies farther entad, and is composed wholly of nerve bundles
with their ramifications. The ganglionic plexus occupies the
base of the corium. In some instances the elements of the two
may mingle, but their structures are wholly different. In many
instances the fibers of the ganglionic plexus are so numerous
that the central portion of the stratum becomes perfectly opaque
with the stain, while the ental and ectal edges show a purely
fibrous arrangement. In other localities of the stratum there
are blackened areas showing the structure just described but
united with each other by numerous plainly differentiated fibers.
In still other instances there are large areas in which the struc-
ture is purely fibrous. (Fig. 11 and 12.) At first sight there
seemed to be a possibility that this appearance might be due to
the presence of extensive pigmentation; but examination of sec-
tions of the skin from the same region fixed in the chrom-acetic
acid and Flemming solutions and stained as previously men-
tioned showed no pigmentation whatever in this part of the skin,
while sections treated in methylene blue showed that there
might be occasionally a granular pigmentation in this region
and that typical chromatophores occur very seldom. By refer-
ence again to the sections treated with the Golgi method, it
was found that the stratum impregnated universally had a
fibrous structure in part, and that, in relatively large areas
where there was the clearest differentiation of the stain, the
structure was purely fibrous. In the latter instance, if the ap-
pearance in question were due to the impregnation of chroma-
tophore elements, it would be expected that the stain would
first select the body of the chromatophore and not bring to
light its phenominally long ramifications, if the fibers could

possibly be interpreted as such. Furthermore, an occasional chromatophore was found in the immediate vicinity of these elements, which differed widely, both in structure and in reaction to the stain, from the cells and fibers under consideration (Fig. 14). Frequently a number of these cells are matted together in such a way as to form an irregularly shaped body, from which numerous fibers of variable length ramify in all directions. Often the fibers from different bundles are so closely woven together that they appear to be continuous from one cluster to the other, as indeed they may be. This type of cell, however, is not confined to the stratum at the base of the corium. It tends to wander peripherad. In such cases fibers from one end of the cell have been traced for long distances till they became lost in a complex of fibers, the destination of which is in the stratum just described. (Fig. 13.) From the other end of the cell, shorter fibers ramify among the surrounding tissue. In some instances they seem to attach themselves to the periphery of the glands of the ectal series.

The function of the fibers arising from the lower stratum, however, seems to be more intimately related to the glands of ental series, for these fibers pass ectad in marvelous numbers and embrace the entire surface of the glands. This condition was demonstrated by the projection upon a median plane of drawings made with the camera lucida from consecutive sections. (Fig. 8, A-E).

These fibers do not seem to be identical with those described as innervating the tunic cells of the ental gland. They differ from these in their distribution and relative positions. They correspond, however, with the structures described by President C. L. Herrick, in this JOURNAL, Vol. VIII, p. 51 (Fig. 40, reproduced as Fig. 15, Plate V, of this article). In this instance it was found that a net-work of non-medullated fibers crossing at slightly different levels appeared on glands in the toad, and that these fibers apparently were connected with the ganglionic plexus at the base of the corium, though the latter point was not certain. This relation, however, is now satisfactorily demonstrated. It seems, there-

fore, that there are two groups of nerves passing to the glands of the ental series ; the one attaching by the typical endings to the enveloping muscle cells, the other ramifying promiscuously over the surface of the gland.

It should be noted further that nerve bundles enter the ganglionic stratum on its ental aspect, and that fibers, either singly or in clusters, pass out of them and distribute themselves among the fibers and cells of the plexus. The exact destination of these fibers cannot be determined, though it seems plausible that a part of them at least terminate in the ganglion cells, since the cells in the more peripheral parts of the skin send long fibers into the plexus. Furthermore, in the skin of the Axolotl it is known that such a relation exists between similar cells and the nerve bundle.

In submitting the above results, the writer gratefully acknowledges the aid given him by President Herrick, under whose supervision the investigations were made.

METHODS.

1.   CHROM-ACETIC ACID.   The skin was removed from the top of the head of the frog on one side the median line and fixed seven hours in the following solution : chrom-acetic acid (Fol's formula), two parts ; water, one part; 10% solution of platinic chloride, ten drops to about two ounces of the preparation.

2.   FLEMMING'S STRONGER SOLUTION.   The skin from the top of the head of the same specimen as in No. 1, on the other side of the median line, was fixed seven hours in Flemming's stronger solution.

For tissues fixed in both these solutions the usual methods of paraffin embedding were employed, and the sections were cut serially.   The stains used were as follows:

(a).   Delafield's alum haematoxylin and picrocarmine. On a number of slides, the haematoxylin alone was applied.

(b).   Benda's sulphate of iron haematoxylin.   With this stain the best results were obtained by mordanting about one

hour in the solution usually employed, and destaining with a thirty per cent. solution of acetic acid.

(c). Weigert's haematoxylin. The tissues were mordanted three hours in a one-half saturate solution of copper acetate, stained three three to four hours in Weigert's haematoxylin, and differentiated in Weigert's decolorizer. Three hours in the stain for Amphibian tissue has proved sufficient, and no doubt less time would give good results.

3. Methylene Blue. The solutions used in this method were those employed by Prof. Huber, viz., one-tenth per cent. solution of methylene blue in normal salt, fixed either in a saturated solution of ammonium picrate or in a solution of ammonium molybdate as follows : distilled water, 10 cc.; ammonium molybdate, 1 gram ; hydrochloric acid, 1 drop. For sectioning, the latter was used; for examining *in toto*, the former. The stain was injected beneath the skin of the head by means of a hypodermic syringe. About six hours after the injection the frog was killed and the skin removed. After exposure to the air till the nerves were well differentiated, the tissues were placed for one day in the fixatives mentioned. Those in ammonium picrate were then changed to glycerine. Those in the ammonium molybdate solution, were treated in the following manner : one hour in 95 % alcohol, one hour in absolute alcohol, one hour in warm turpentine, and embedded in paraffin in an oven at a temperature of 70° C. This method of dehydrating and embedding involves some decolorization. Nevertheless, it gives good results if the process be hastened as much as is permissible.

4. Golgi. Strong's modification of the silver method was followed in the main. Small fragments of skin were placed for 48 hours or more in a solution of 3½ % potassium bichromate four volumes and 1 % osmic acid one volume. After four days in a 1 % solution of nitrate of silver, they were washed two hours in 95 % alcohol, one half hour in equal parts absolute alcohol and ether, and one hour in warm turpentine. For embedding, paraffin was used as with the methylene blue method.

DESCRIPTION OF PLATES IV AND V.

PLATE IV.

Fig. 1. Section of skin fixed in the chrom-acetic acid solution and stained by the Weigert method, showing the terminal cells (a) in continuity with fibers (b) passing through the corium.

Fig. 2. Section of the same showing terminal fibers (a) connecting with a bundle (b) beneath the corium, also ental gland (c) showing partially the tunic of muscle cells.

Fig. 3. Teased preparation of skin stained intra vitam with methylene blue, showing structure of the nerves passing to the terminal cells. Fiber at *a*.

Fig. 4. Section through skin stained with methylene blue, showing terminal cells (a) with fibers through corium. Other fibers appear in the middle portion of the corium.

Fig. 5. Section of same, showing course of fiber beneath the corium. The fiber and its sheath are plainly distinguished throughout this extent.

Fig. 6. Section stained by the silver method, showing nerve (a) passing ectad through the corium and becoming obscured at the ental portion of the Malpighian layer by a chromataphore (b). The ental part of the nerve (c) by a less perfect impregnation is shown to extend beneath the corium for some distance.

Fig. 7. Section fixed in Flemming's solution and stained by the Weigert method, showing the periphery of a gland of the ental series with its envelope of muscle cells (a); *b*, gland of the ectal series; also terminal fibers at *c*.

Fig. 8. A-E. Five consecutive sections stained by the Golgi method, showing glands of the ental series (a) with enveloping fibers (b) from the plexus (c) at the base of the corium. Ectal glands at *d*.

PLATE V.

Fig. 9. Section stained by the methylene blue method, showing tunic cell at *a*, and nerve endings at *b*.

Fig. 10. Similar section, showing nerves (a) passing to ental glands, with typical endings at *b*; *c*, blood vessel; *d*, nerve bundle.

Fig. 11. Section stained by the silver method, showing the structure of the ganglionic plexus at the base of the corium; *a*, opaque central portion with fibrous arrangement at the ental and ectal edges; *b*, nerve bundles entering the ental aspect of the plexus.

Fig. 12. Section stained by the silver method, showing purely fibrous structure of the plexus at the base of the corium; *a*, ganglion cell; *b*, nerve bundle passing into the plexus and becoming obscured by a more densely stained portion.

Fig. 13. Section stained by the silver method, showing ganglion cells located in the ectal portion of the corium; *a*, several cells matted together; *b*,

fibers passing from the cell into the plexus; *d*, a typical ganglion cell; *e*, group of fibers entering the plexus; *f*, ental gland; *g*, ectal gland.

Fig. 14. Section stained by the silver method, showing a typical chromatophore in the ganglionic stratum at the base of the corium; *a*, chromatophore; *b*, single ganglionic cell; *c*, a number of ganglion cells matted together.

Fig. 15. "Section of the skin of the head of a toad (Bufo) after *intra vitam* injection with methylene blue and fixation with Bethe's solution of molybdate of ammonia. Examined in glycerine. The section is somewhat oblique so that the duct and part of the body of the gland is removed. The delicate non-medullated fibers are seen generously distributed over the uncut surface of the gland. Coarser fibers are also seen in the lower and upper plexuses, also a bundle of sensory rods at the left."

Fig. 16. "Intra vitam methylene blue preparation of skin of axolotl, showing cell of the ganglionic meshwork beneath the corium with the epidermis. *a*, fiber passing to cells of the intracellular reticulum ; *b*, non-medullated fibers from a nerve piercing the corium; *c, c1, c2* and *c3*, ganglion cells of the plexus beneath the corium."

NOTE: Figures 15 and 16 were drawn by Prof. C. L. Herrick, and are reproduced with their descriptions from Vol. VIII, Plate IX, of this JOURNAL.

THE NUMBER AND ARRANGEMENT OF THE FIBERS FORMING THE SPINAL NERVES OF THE FROG (RANA VIRESCENS).

By Irving Hardesty.

(From the Neurological Laboratory of the University of Chicago.)

With Plates VI to XIII.

I. SUMMARY.

1. A gross examination of the different spinal nerves shows marked variations in their architecture (Plate VI).

2. The number of fibers in the ventral roots decreases from the spinal cord towards the spinal ganglion.

3. The number of fibers in the dorsal roots decreases from the spinal ganglion towards the spinal cord.

4. The section of the nerve trunk immediately distal to the spinal ganglion (dorsal branches excluded) contains a greater number of fibers than are fouud in a section of the trunk further distal.

5. The decrease in the number occurs among the smaller fibers of the nerve.

6. The general explanation of these relations is found in the fact that the fibers arising from the spinal ganglion grow, on the one hand, towards the spinal cord by way of the dorsal root and, on the other, towards the periphery by way of the nerve trunk ; and, that the fibers of the ventral root grow from the spinal cord towards the periphery.

7. In frogs of increasing weight, the fibers of the dorsal root increase in number more rapidly than do those of the ventral root.

8. The sum of the fibers in the trunk and dorsal branches combined, exceeds in every case and by a considerable amount the sum of the fibers in the two roots.

9. The excess of fibers in the trunk and dorsal branches seems to be correlated both with the absolute and proportional size of the dorsal branches.

10. The method herein employed for the enumeration of nerve fibers possesses several features which commend it as more trustworthy than any of those previously employed.

II. INTRODUCTION.

The number, size and arrangement of the medullated nerve fibers constituting the peripheral nervous system in vertebrates presents many problems worthy of investigation.

The problem which forms the basis of this paper is a de-

termination of the length of some of the nerve fibers arising from the cells of origin situated in the ventral horns of the spinal cord and in the spinal ganglia.

The region chosen for the study of this extension of the nerve fibers is, on the one hand, that formed by the roots of the spinal nerves, and on the other, that formed by the spinal nerve trunks as far as their union with the rami communicantes. The study involves first, an enumeration of the fibers contained in each nerve root at different levels, and second, a determination of the number of fibers contained in a section of the trunk and dorsal branches immediately distal to the spinal ganglion and in a section of the trunk further distal.

The animal examined was the common leopard frog, *Rana virescens.*

III. THE GROSS ANATOMY OF THE SPINAL NERVES.

The gross appearance of the different spinal nerves when dissected out and freed from adherent connective tissue is exhibited in Plate VI. The sketches there produced are drawn to scale.

Passing from the Xth to the Ist nerve, three chief features of variation are to be noted.

1. The most marked variation is exhibited in the abundance of the dorsal branches. It is seen that for the Xth these branches are few, for the IXth they are more abundant, while for the VIIIth there is seldom more than one, and this is relatively very small and arises directly out of the mass of the ganglion instead of springing from the nerve trunk at the distal end of the ganglion as it does in case of the IXth and Xth. For the VIIth, again, the condition is much as it is in the IXth. The dorsal divisions of the VIth, Vth, and IVth are both relatively and absolutely larger than those of any of the other nerves. For the IIIrd nerve the branches are less than for the three nerves caudad to it, and the larger branches of it usually arise out of the ganglion and at right angles to the long axis of the nerve trunk. The IInd gives off many very small branches but in a very irregular manner, while the Ist returns to the general type of those most caudad.

2. The dorsal and ventral roots vary both in length for the different nerves and in relative size for the same nerve. As a result of the difference between the rate of growth of the spinal cord and the canal in which it lies, the more caudal nerves possess the longer roots, since in the frog the spinal ganglia always remain in the intervertebral foramena. The length of the roots thus gradually decreases until, passing cephalad, the roots of the IInd and Ist nerves are merely long enough to reach at almost right angles their zones of exit and entrance upon the cord. The relation between the size of the two roots of a nerve is more constant than the relation between the size of the roots of any two successive nerves. The most striking and constant difference between the two roots is presented in the Ist or hypoglossal, the dorsal root being not only relatively but absolutely smaller than that of any other nerve.

3. The distance between the spinal ganglion and the ramus communicans (*c*, Plate VI) undergoes a very considerable variation for the different nerves. As shown in the plate, this distance decreases rapidly between the VIIth and IIIrd nerves, the ramus being given off much closer to the ganglion in case of the IVth, IIIrd, IInd and Ist nerves.

The relative size of any two or three successive nerves can often be observed as decidedly different in different frogs or indeed, on the two sides of the same individual. The VIIth, VIIIth and IXth have been more often noticed as varying in this respect. When the IXth is proportionately small, the VIIIth is generally large and when the VIIIth is smaller than usual, the VIIth and IXth appear more than ordinarily large. Quite often the VIth, VIIth, VIIIth and IXth nerves were noticeably larger on one side than on the other of the same individual. In these cases, the larger nerves were most often on the left side of the animal.

IV. THE NERVES WHICH WERE INVESTIGATED.

An enumeration of the fibers was made for all the spinal nerves except the IInd and Xth. The IInd was neglected for the time being, because of its large but very short roots, be-

cause numerous small branches are given off and received all along the short distance between its ganglion and its ramus communicans, and for the reason that, owing to its large size, it is penetrated by osmic acid with great difficulty.

The Xth, unlike the other nerves, passes out of the spinal canal through a long foramen in the *urostyle* (canalis coccygeus). This position renders its necessary exposure to the reagent and its removal without injury very difficult and justified its exclusion at this time also.

V.   THE NUMBER AND ARRANGEMENT OF THE NERVE FIBERS IN THE DORSAL AND VENTRAL ROOTS AND IN THE BEGINNING NERVE TRUNK.

1.   The examination of the roots consisted in counting the fibers in sections taken from two or three different levels of each root; i. e., the fibers of each root were counted at different distances from their cells of origin.   The points at which the sections were taken are indicated by the numbers 1, 2 and 3, Plate VI.   The Plate shows also that in case of the longer roots three counts were made, while for the shorter, for obvious reasons, two counts were thought sufficient.

2.   Counts were made of a section of the trunk taken immediately distal to the spinal ganglion and of a section of the dorsal branches made as close up to the ganglion as possible.   (Sections 4 and 6, Plate VI).

3.   Another enumeration was made of the fibers contained in the trunk at a point just central to its junction with the ramus communicans.   (Section 5, Plate VI).

The results of such enumerations are presented in Tables I and II.   These tables contain results obtained from two different specimens.   They show (1) that, as indicated in the columns A, B and C, the number of fibers in the ventral root remains constant or decreases in the course of the root from the spinal cord towards the dorsal root ganglion ; (2) that the number of fibers in the dorsal root remains constant or decreases in the course of the root from the ganglion towards the spinal cord.   Leaving the roots and turning to the trunk, the tables

show (3) that the section of the trunk taken next to the ganglion (dorsal branches excluded) contains more fibers than are contained in a section taken further distal (columns J and K). Further, Table I shows that the sum of the fibers in the trunk and dorsal branches taken immediately distal to the ganglion is always considerably greater than the sum of the fibers contained in the ventral and dorsal roots just distal to the ganglion. This fact of the excess of fibers in the trunk and branches is especially presented in Table III.

TABLE I.

FROG, FEMALE, WEIGHT 48.2 GRAMS.

Level of section		Roots							Trunk					
		A	B	C	D	E	F	G	H	I	J	K	L	M
		Sections of the Roots			Excess		Length between 1 and 3	Sum of Roots at	Excess of sum of trunk and branches at	Sum of trunk and branches at	Trunk and sum of branches at	Trunk at	Excess of trunk at	Length between 4 and 5
					at	at								
		1	2	3	3	1	mm	3	4	4	4	5	4	mm
I R.	D.	132		132	0		.75		78	1255	1173	1168	5	1
	V.	1046		1045		1	.75	1177			82			
II	--	----	----	----	---	---	---	----	----	----	----	----	---	---
III R.	D.	317		329	12		I		170	878	653	572	81	1
	V.	397		379		18	I	708			225			
IV L.	D.	367		371	4		2.5		103	637	378	324	54	2
	V.	163		163		0	3	534			259			
V L.	D.	288	290	299	11		3.5		145	571	279	262	17	2.5
	V.	133	132	127		6	3.5	426			292			
VI R.	D.	341	350	350	9		4		220	845	475	469	9	4
	V.	261	259	251		10	4	601			370			
VII L.	D.	1043	1102	1108	65		4.5		212	1697	1556	1530	26	6
	V.	398	391	377		21	5	1485			141			
VIII L.	D.	2051	2083	2108	57		6		217	3620	3534	3501	33	8
	V.	1316	1301	1295		21	6.5	3403			86			
IX L.	D.	1106	1167	1171	65		7		257	2149	1881	1854	27	7
	V.	757	752	721		36	7.5	1892			268			

TABLE II.

FROG, FEMALE, WEIGHT 59.5 GRAMS.

		Roots							Trunk					
		A	B	C	D	E	F	G	H	I	J	K	L	M
		Sections of the Roots			Excess		Length between 1 and 3	Sum of Roots at	Excess of sum of trunk and branches at	Sum of trunk and branches at	Trunk and sum of branches at	Trunk at	Excess of trunk at	Length between 4 and 5
					at	at								
Level of section		1	2	3	3	1	mm	3	4	4	4	5	4	mm
VI R.	D.	235	243	246	11		6		138	513	227	223	4	2
	V.	134	132	129		5	6.5	357			286			
VII R.	D.	791	798	814	23		7		199	1263	1108	1039	69	7
	V.	259	256	250		9	7	1064			155			
VIII R.	D.	1649	1714	1732	88		8		86	2838	2789	2743	46	7.5
	V.	1037	1023	1020		17	8.5	2752			49			
IX R.	D.	1437	1454	----	17		4.5		109	2536	2297	2285	12	8.5
	V.	991	973	955		36	9	2427			239			

EXPLANATION OF TABLES I AND II.—These tables contain the records of the enumeration of the fibers at different levels of the ventral and dorsal roots and of the nerve trunk of the spinal nerves of the frog. Table I contains counts made upon eight of the spinal nerves of a frog weighing 48.2 grams. Table II, counts of four nerves of a 59.5 gram frog. The figures at the head of the columns indicate the level of the section at which a count was made. For convenience of reference, each column is designated by a letter.

The point of principal interest which is claimed for these results lies in the change in the number of fibers to be found in the course of the dorsal and ventral roots and in the course of the trunk between the limits chosen.

It is first desired to determine whether there is any regularity in these variations such as would be exhibited by a percentage change in the number of fibers for a unit of length. Table I gives the absolute amount of variation in the number of fibers found between the different levels at which the counts were made and thus does not take into account the length of the root nor the distance between the points at which the sections of the trunk were taken. Plate VI will show that these distances through which the changes occur vary greatly for the

different nerves. In order therefore to determine the variations more exactly it was necessary to compute for each nerve, the average amount of variation occurring in a unit of length and convert the variations thus obtained into percentage values. To do this the total amount of variation in a given case was divided by the number of millimeters through which it occurs. In a ventral root, for example, the number of fibers found in the section nearest the ganglion was subtracted from the number found in the most proximal, or section nearest the cord. The difference thus obtained was divided by the number of millimeters between these points (sections 1 and 3, Plate VI). This average variation per millimeter having been found, its percentage value of the entire number of fibers contained in the *most proximal* section was determined. For the dorsal root, of course, since the variation occurs in the opposite direction, the number found nearest the ganglion (section 3) was used as that on which to compute the percentage of variation; and for the trunk, the number in section 4, the section containing the largest number of fibers.

The percentages of the average amounts of variation per millimeter of length obtained for the several spinal nerves included in Tables I and II are as follows:

TABLE III.

FROG, FEMALE, WEIGHT 48.2 GRAMS.

	Average percentage decrease per mm.		
The nerve	In ventral root	In dorsal root	In trunk
I	0.12%	0.00	0.42%
II	------	------	
III	4.60%	3.60%	12.04%
IV	0.00%	0.43%	7.10%
V	1.30%	1.05%	2.44%
VI	0.96%	0.64%	0.48%
VII	1.05%	1.30%	0.28%
VIII	0.24%	0.45%	0.12%
IX	0.63%	0.79%	0.20%

FROG, FEMALE, WEIGHT 59.5 GRAMS.

	Average percentage decrease per mm.		
VI	0.57%	0.70%	0.88%
VII	0.50%	0.38%	0.79%
VIII	0.19%	0.60%	0.22%
IX	0.40%	0.26%	0.06%

These conditions of average variation per millimeter in the number of fibers found at different distances from their cells of origin, are illustrated by curves in Chart I.
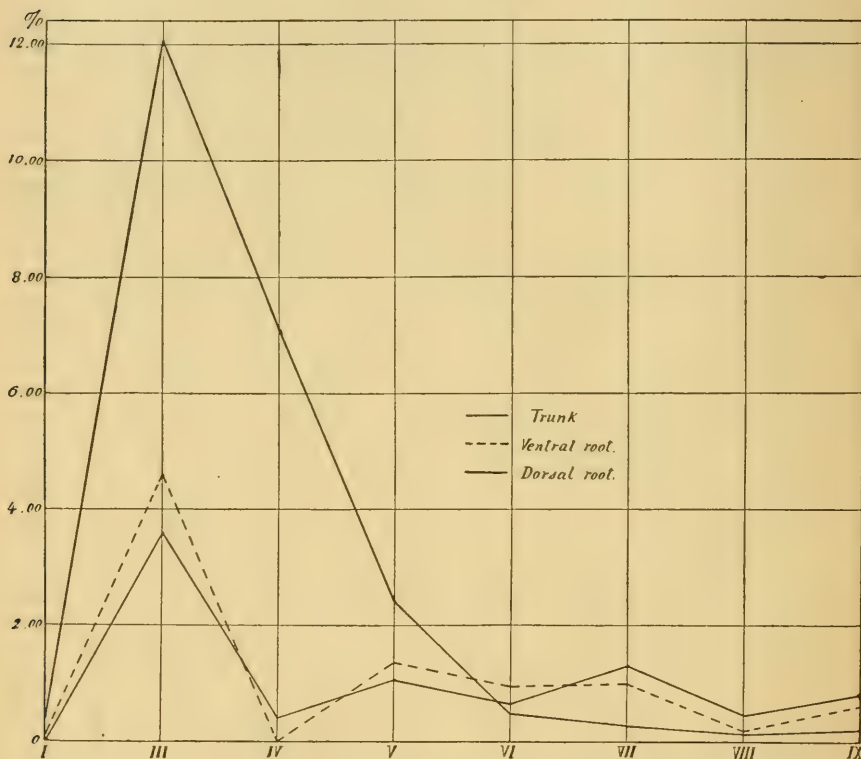
CHART I, showing, in the different spinal nerves of one specimen, the relations of the percentage values of the average change per millimeter in the number of fibers in the dorsal and ventral roots and in the trunk. The distances in which the changes occur and the numbers from which the percentages are computed are given in Table I.

The curves of this chart, constructed from the values in Table III, show more readily than does Table I, (1) that the changes in *the two roots* of a given nerve do not differ very considerably from each other; (2) that in the several nerves there is no regularity in the amount of variation occurring in a given root, the curves for the two roots crossing each other repeatedly; (3) that the percentage variation per millimeter in the

trunk is greater than that in the roots in case of the Ist, IIIrd, IVth and Vth, and below that in the roots in case of the VIth, VIIth, VIIIth and IXth. Values obtained from the second specimen, however, show that this cannot be considered at all as a general condition. As a whole, (4) the greatest variations are seen to occur in the IIIrd, IVth and Vth, while the VIth, VIIth, VIIIth and IXth are more similar to one another.

The absence of data from nerves II and X is to be deplored. The abrupt rise from the Ist to the IIIrd nerves might be broken by data from the IInd. The explanation of why the changes in the IIIrd rank so much higher than those in the other nerves must be deferred till further investigation of this nerve can be made. As is well known, the IIIrd is the spinal nerve which, in the frog, contains the greatest percentage of fibers which pass to the sympathetic system, and therefore the nerve contains a greater percentage of small fibers than any other nerve. But, at present, no adequate explanation based upon this fact can be suggested.

To explain the decrease in the number of fibers of the ventral root as it passes from the spinal cord toward the point of its junction with the dorsal root, we assume that those fibers, which grow out from the ventral horn cells have extended unequal distances from the cord. In the dorsal root, the variation in the number of fibers is to be explained in the same way. Here the decrease is in the opposite direction from that in the ventral root, and naturally so since, as is now known, very nearly all the fibers comprising the dorsal root are the central prolongations of the outgrowths of the spinal ganglion cells.

This explanation is also applied to the decrease in the number of fibers found in the trunk between the section next the ganglion and that most distal. In the trunk the great mass of the fibers, at least, being of the same origin as those composing the roots, the changes in the roots demand that the decrease in the trunk should occur, as it does, towards the periphery. As is well known, no branches are given off from the roots, nor, with the exception of the IInd nerve, are any branches given off from the trunk between the spinal ganglion

and the ramus communicans.   This explanation of the changes as due to growth will be discussed later.

VI.   The Rôle Played by the Smaller Fibers.

It was suggested that it would be well worth while to determine whether the decrease in the number of fibers in the roots and trunk occurs through variations in the number of the large or the small fibers.   It is known from previous descriptions that the two roots differ from each other in the general appearance of their transverse sections.   The ventral root shows much more uniformity in the diameter of its fibers than does the dorsal.   The ventral roots of the spinal nerves of the frog, while not possessing the very largest fibers, yet, with the exception of the ventral root of the IIIrd nerve, have the great majority of their fibers uniformly large.   This excess of large fibers is interspersed with fibers distinctly small and with a very few intermediate in size.   Plates VIII, X, and XII represent sections of the ventral root of the VIIIth nerve which is quite typical.

The dorsal root, on the other hand, shows no uniformity as to the diameter of its fibers.   It is rather a mixture of fibers of all sizes from the very small up to a few larger than any found in the ventral root.

In order, therefore, to find if possible, in fibers of what general diameter the above changes in number occur, a second count was made of ten of the sections of the roots.   Sections of the smaller roots were chosen since the labor of counting would be less and the results obtained would be fully as significant as in case of larger ones.

As will be explained in that part of this paper which deals with the methods employed, each count was made from a photograph of the section and controlled by having the section at at the same time under the microscope and highly magnified. Thus the use of the photograph guarded against any fibers being overlooked or recounted, and all doubtful cases could be settled at once and accurately by an appeal to the microscope. In the investigation with regard to the small fibers, all those

having a diameter of 5 micra and under were considered as small fibers, and in order to have but two classes, all those above 5 micra were considered as large. With a combination of lenses producing a magnification of 800 diameters (Zeiss—obj. 8 mm, oc. 12), each division of the occular micrometer used was equivalent to exactly 5 micra. By the aid of a mechanical stage any fiber the diameter of which was questionable could be quickly tested. Each section was counted by fields marked out on the photograph. In case of a section containing fewer small than large fibers, the section was first examined by counting the small fibers. Then the large fibers were counted as a matter of control. In every case, when the numbers for large and small fibers were added, the sum was the same as that obtained in the previous counts and recorded in Table I.

The enumerations thus made were as follows in Table IV :

TABLE IV.

				Counts made for small fibers.			Counts recorded in Table I.		
				Sec. 1	Sec. 3	Dif.	Dif.	Sec. 3	Sec. 1
IIIrd N.	Dorsal root	small		155	164	9	12	329	317
		large		162	165	3			
	Ventral root	small		306	289	17	18	379	397
		large		91	90	1			
Vth N.	Dorsal root	small		193	203	10	11	299	288
		large		95	96	1			
	Ventral root	small		45	39	6	6	127	133
		large		88	88	0			
VIIth N.	Ventral root	small		107*	95	12	14	377	391*
		large		284	282	2			

TABLE IV, containing the results of a separate enumeration of the large and small fibers in the various dorsal and ventral roots indicated. In order to compare the results of these counts with those previously obtained in counts of the same sections and recorded in Table I, the corresponding numbers of that table are placed in parallel columns. The numbers of nerve VII, indicated by a star, are those found for section 2, Plate I, instead of section 1, as the column reads.

While in most of the cases, the differences in the number of small fibers do not accord with the differences between the

entire numbers previously found, yet it is seen that by far the greater portion of a difference does occur among the small fibers ; i. e., those 5 micra or less in diameter. The lack of complete accordance is perhaps due to fibers whose diameters were so near the border line between large and small that a slight distortion, or the lack of it, resulted in their being classed in the one category at one level and in the other at another.

These counts for small fibers were of dorsal and ventral roots exclusively. If the variations in the number of fibers in the roots can be shown to take place in the smaller fibers, it is reasonable to assume that the variations found in the trunk, occur among the small fibers also.

Birge ('82) made counts of the fibers at a single level of the two roots and of the trunk of frogs of different weights or ages. In regard to the fibers of the ventral roots, he found upon summing up the entire number of motor fibers determined for one side of each animal, that there existed such proportions between the numbers of these fibers and the weights of the frogs, that, given the one he could compute the other approximately. Assuming the number of ventral root fibers to be the same for the two sides of the animal, he found that an increase in the weight of the frog was accompanied by an increase of about 55 ventral root fibers for each gram of body weight.

This author also determined that the average diameter of the fibers in the roots of the younger specimens was less than that in the older and expressed the opinion that, during growth, small fibers thicken into larger ones.

Korybutt-Daskiewicz ('78) as early as 1878 described the ingrowing of new fibers in the sciatic nerve of the frog. He pictures the first formation of the medullary sheath about the outgrowing neuraxone, either as fine varicosities which blacken with osmic acid, or as first a thin layer of myelin which gradually thickens. These changes were noted near the end of the growing fiber. The sheath was observed to cease, not gradually, but more as the wood portion of a sharpened lead pencil,

the axis cylinder preceeding the myelin sheath by short but varying distances.

Kolster ('93) in studying the regeneration of fibers following the section of the nerve, pictures the myelin sheath as being reformed a node at a time, the regenerating axis cylinder preceding the development of the myelin. Accepting the above description that the sheath forms, node by node, the sheath would necessarily cease bluntly and transverse sections stained with osmic acid alone would only show the growing fiber appearing or disappearing suddenly, the axis cylinder portion being invisible.

Whatever the source of the medullary sheath, it was thought highly probable that among the small fibers of the transverse sections here counted, there might be observed some fibers cut at the point at which this sheath was just being acquired. In examing the preparations with this object in view, certain difficulties had to be recognized.

1. The preparations not having been made with this point in mind, in the mounting, good sections rather than serial sections had been chosen.

2. Since it was desired that the section chosen for counting should be one from within a fraction of a millimeter of a certain point along the course of a root or trunk, but few sections were usually mounted.

3. The average of the decreases in number even in the roots being about 1 fiber to each 100 in a millimeter of length, it is evident that in the necessarily very thin sections, the opportunities of observing a disappearing fiber are rare. For these reasons it may be, very few satisfactory cases of a disappearing fiber have been observed. One of these is represented in Figs. 1-6, Plate VII. In the search for disappearing fibers, sections were now and then observed which were evidently cut so as to contain only the node of Ranvier. These of course when followed in the series showed in both directions a reappearance of the myelin sheath.

VII.   The Relations of the Ventral and Dorsal Roots
to each other.

The absolute numbers of the fibers enumerated in the ven-
tral and in the dorsal roots and in the trunks and dorsal branch-
es are represented in the curves of Chart II.   This chart is con-
structed directly from Table I, and is but a charted expression of
the numbers given there.   In order to complete the chart, the
data for the IInd and Xth nerves are computed from the results
obtained by Birge in the work above cited.

This interpolation in the curves was made on the basis of the
following calculation.   The total number of fibers found by Birge
in the spinal nerves of a 63 gram frog was taken and the pro-
portional values of the numbers for the nerves in question was
determined.   Then the same proportional values were found of
the numbers recorded in Table I.   The amounts thus deter-
mined for the ventral and dorsal roots and for the trunk of the
IInd and Xth nerves were inserted to complete the chart.   The
number of fibers ‘in the dorsal branches of these two nerves
could only be roughly estimated, since Birge did not deal with
with them at all.

Birge used a different species of frog (*esculenta*) from the
one used in this work and, that the proportion of fibers con-
tained in a given nerve is even approximately the same for the
two species, can only be assumed.   From observations made
by Professor Donaldson in this laboratory, it appears that the
European *Rana esculenta* has a central nervous system of pro-
portionally smaller weight than the American *Rana virescens*.
This relation is also indicated by comparing Birge's results with
those mentioned in this paper.

Birge counted in a frog of 63 grams, a much smaller num-
ber of fibers than were here found for one of 48 grams, as re-
corded in Table I.   For the ten spinal nerves of one side of a
63 gram frog, Birge found in the two roots a total of 9,618
fibers.   Of the species here used, a frog weighing 48 grams was
found to possess 14,783 fibers in the roots of the ten spinal
nerves of one side.   While the two sides of the same specimen

may vary considerably, even in the total number of fibers, it is evidently not reasonable to suppose the variation can account for this difference which amounts to 5,175 fibers.

Chart II, more readily than Table I, conveys an idea of the absolute relations existing between the numbers of fibers in the trunk and dorsal branches of the ten spinal nerves and the numbers of fibers in the dorsal and in the ventral roots. It shows (1) the abrupt rise in the number of fibers at those regions of the spinal system from which the limbs are supplied; (2) as might be expected, the curves for the roots follow that for the trunk and dorsal branches fairly closely, and (3) that the curves for the two roots follow each other but roughly, crossing between the Ist and IInd nerves, between the IInd and IIIrd, IIIrd and IVth, and between the IXth and Xth. The dorsal root of the IInd contains the greatest number of root fibers and the dorsal root of the Xth the least number, both of which however are interpolations.
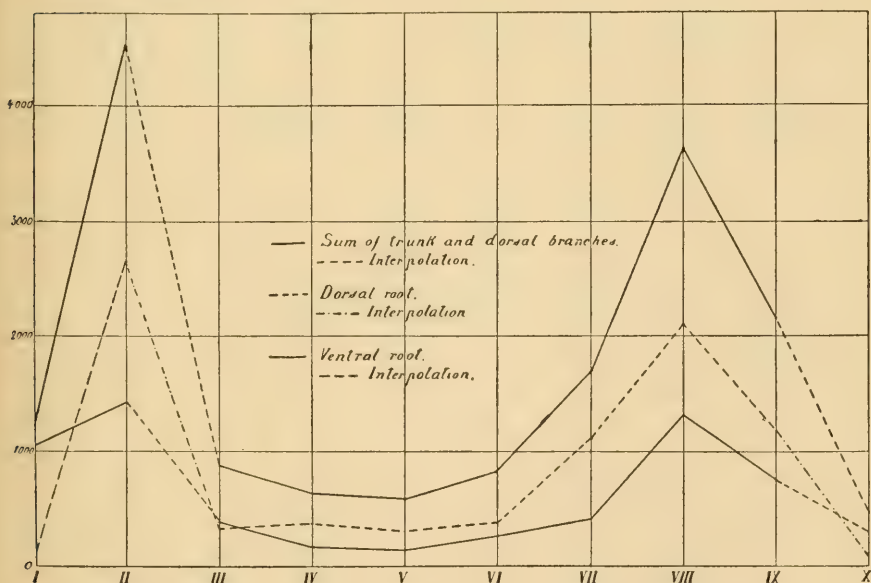

CHART II, showing the number of fibers in the dorsal roots, and in the ventral roots and the sum of those in the trunk and dorsal branches of the different spinal nerves. The parts of the curves in broken and dotted lines which represent the IInd and Xth nerves are interpolations from the records of Birge.

The relations existing between the two roots, as shown here, correspond in the main with those found by Birge.

1. The number of dorsal root fibers in the same animal is greater than that of ventral root fibers. A frog of 48 grams has for one side approximately 8572 dorsal root fibers against 6211 in the ventral roots. This is an excess of 38%. This excess in the dorsal roots however is greater than that obtained by Birge in a frog of 63 grams.

2. The apportionment of fibers to the different roots is widely different. Only in case of the Ist, IIIrd and Xth nerves, do ventral root fibers exceed those of the dorsal root. In the remaining nerves, dorsal root fibers predominate, but in very unequal degrees. Of all the nerves here investigated, the greatest percentage of dorsal root fibers in excess of those of the ventral root is found in case of the VIIth nerve. In Table I this nerve possesses an excess of 178% and in Table II an excess of 214%.

The percentage values of the excess of the larger root of each nerve represented in Chart II are given in Table V. For contrast the cases in which the ventral root contains the greater number of fibers are placed in a separate column.

TABLE V.

FROG, WEIGHT 48.2 GRAMS.

Number of the Nerve	Excess	
	Occurring in dorsal root	Occurring in ventral root
I		692%
II	83%	
III		20%
IV	127%	
V	125%	
VI	34%	
VII	178%	
VIII	60%	
IX	54%	
X		370%

The percentage values given in Table V are presented in the form of a curve in Chart III. In the Chart the cases of an excess of dorsal root fibers are recorded above the base line and those of an excess of ventral root fibers below it. It is seen

that the curve begins far below the line of the Ist nerve, rises
well above it for the IVth and Vth, falls again for the VIth,
rises highest for the VIIth and ends below the line for the
Xth.
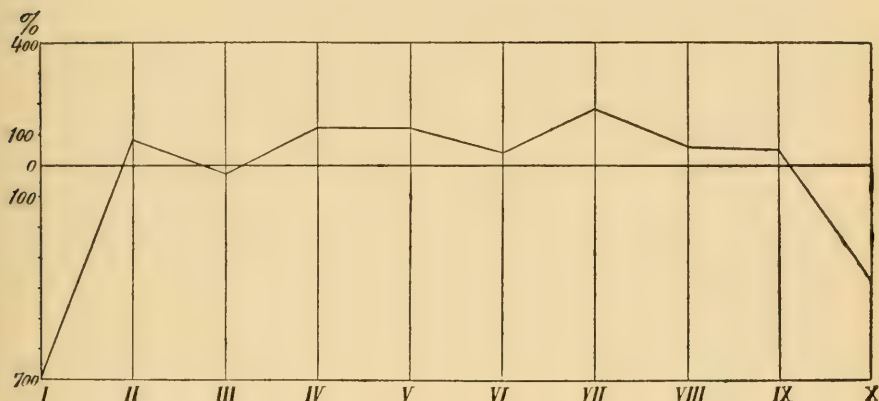
CHART III, exhibiting the excess in the larger root of the several spinal
nerves. The records show the percentage value of the excess of the larger root.
The records for the dorsal root appear above the base line and those for the
ventral root, below it.

3. In regard to the relations existing between the two
roots, it can also be shown that during growth the dorsal root
fibers increase in number more rapidly than do those of the
ventral root [Birge ('82)]. This is seen to be true even for
slight differences in weight. Table II contains a record of
counts made of four nerves from a specimen of somewhat greater
weight than that entered in Table I. A comparison of the per-
centage values of the excess of dorsal root fibers in these four
nerves as recorded in the two tables is give in Table VI.

TABLE VI.

Number of the nerve	Percentage of excess of dorsal root fibers from records of	
	Table I, frog wt. 48.2 grams	Table II, frog wt. 59.52 grams
VI	34%	83%
VII	178%	214%
VIII	60%	67%
IX	54%	49%

Table shows at a glance that for the heavier frog, there is a decided gain in the excess of the dorsal root fibers. That the percentage of the excess in the IXth nerve fails to show an increase is probably due to an unequal distribution of root fibers in the VIIIth, VIIth and IXth nerves. The gain in the VII is more than ample to balance the deficiency.

To determine whether the relation exhibited by these four nerves is true for the entire ten, we must again draw upon the records of Birge. To determine the increase in the number of fibers with increase in size of the animal, Birge counted the ten nerves of several specimens chosen with reference to their weight. Using his figures for the total numbers of dorsal root fibers and of ventral root fibers found for one side of the specimen, and computing the percentage of the excesss of dorsal root fibers in each case, we get

TABLE VII.

From Birge—*Rana esculenta*.

Weight of frog	Total number of dorsal root fibers	Total number of ventral root fibers	Excess of dorsal root fibers	%
23 grams	3781	3524	257	7.3
63 grams	5335	4283	1052	24.5

Taking the total number of fibers in each root of the VIth, VIIth, VIIIth and IXth nerve of the same specimens used in Table VII we get,

TABLE VIII.

From Birge—*Rana esculenta*.

Wt. of frog.	Total number fibers in Dorsal Roots.	Total number fibers in Ventral Roots.	Excess of Dorsal Root fibers.	Percentage.
23 grams.	1930	1225	705	55.5
63 grams.	2840	1612	1228	76.1

Thus it is seen that there is an increase in the excess of dorsal root fibers for the larger specimen when we consider the VIth, VIIth, VIIIth and IXth nerves as well as when we consider the entire ten nerves.

Then taking the sums of the dorsal root fibers and the sums of the ventral root fibers found in the VIth, VIIth, VIIIth

and IXth nerves of the two specimens employed in Tables I
and II, and determining the percentage of the excess of the
fibers of the dorsal roots indicated by these sums we get

TABLE IX.

Rana virescens.

Wt. of frog.	Total number fibers in Dorsal Roots.	Total number fibers in Ventral Roots.	Excess of Dorsal Root fibers.	Percentage.
48.2 grams.	4737	2732	2005	73.7
59.52 grams.	4246	2421	1825	75.4

Thus, an increase in the excess of fibers in the dorsal root
is found not only for an increase of 40 grams in weight but also
for an increase of only 11 grams in weight.   Also the increase
in weight being slight, the increase in the excess of dorsal root
fibers is correspondingly slight.   So, it is hoped that some evi-
dence is added to that brought forth by Birge to the effect that
as the animal increases in size, the number of dorsal root fibers
increases more rapidly than that of the ventral root.

It may be fairly asserted that by far the greater part of the
sensory or dorsal root fibers of the frog go to innervate the skin.
As the animal grows the skin of course increases in area, but
exactly what relation this increase in the excess of sensory
over motor fibers has to the increase in the area of the skin, is
yet to be investigated.

A very interesting relation is found to exist between the
numbers of the dorsal and ventral root fibers present in those
nerves which contribute their fibers to the inervation of the leg.
It is known that, in the frog, the VIIth, VIIIth and IXth
nerves give nearly all their trunk fibers to the formation of the
sciatic nerve.   If the sums of the dorsal and ventral root fibers
of these three nerves be taken and the one divided by the oth-
er, there is obtained for each of the above specimens the pro-
prortions represented in Table X.

TABLE X.

The proportion of ventral root to dorsal root fibers contained in the VIIth, VIIIth, and IXth nerves of four specimens.

Wt. of frog, grams.	Ventral root fibers.	Dorsal root fibers.	Proportion.	
23	1088	1754	1—1.7	} *R. esculenta.*
63	1453	2656	1—1.8	
48	2471	4387	1–1.77	} *R. virescens.*
59	2287	4000	1–1.75	

These proportions are interesting because they seem to indicate that, whatever the size of the animal, there exists an almost fixed relation between the inervation of the tissue of the leg by sensory and motor fibers. This similarity in the proportion of ventral to dorsal root fibers fails if there be included in the sums, the ventral and dorsal root fibers of other nerves than those which go to form the sciatic. Even when the VIth nerve alone is included the proportions become more varied.

Another point may be noted with regard to the roots. The average diameter of the fibers of the same root differs for the different nerves. Birge noted for the European frog that the greatest average diameter for ventral root fibers is possessed by the VIIth nerve and the least average diameter of ventral root fibers by the IIIrd. This is found to be true also for the specimens here investigated. In addition it may be added that the least average diameter of dorsal root fibers is to be found in the dorsal root of the Ist nerve and usually the largest of those very large dorsal root fibers before mentioned are to be found in the dorsal root of the VIIth. For the ventral root of the IIIrd, it may be said that the few fibers it contains of the ordinary ventral root type are as large as the average of those of the ventral roots of the other nerves. Its fibers however are sharply divided into two types and the average diameter of its fibers is reduced because of the presence of a very large number of that type of small fibers which Gaskell ('89) and others have described as destined to pass to the sympathetic system and which, in the preparations here used, can be seen to largely compose the rami communicantes.

Birge obtained the average diameter of the fibers of a

root by dividing the area of the transverse section of the root by the number of fibers contained in it.

Schwalbe ('82) made some determinations of the diameter of the fibers of the two nerve roots of the frog by actually measuring a few fibers of each root and taking the average diameter of the fibers thus measured. Schwalbe, like Birge, obtains the least diameter for the motor root of the IIIrd nerve, but unlike Birge, he finds the greatest average diameter for dorsal as well as ventral root fibers possessed by the roots of the VIIIth and IXth nerves. The species of frog used by Schwalbe was the same as that used by Birge.

VIII. THE RELATION OF THE ROOTS TO THE TRUNK.

In presenting Tables I and II, attention was called to the fact that in every case the sum of the fibers in the trunk and dorsal branches taken just distal to the spinal ganglion, exceeds by a considerable amount the sum of the fibers in the two roots
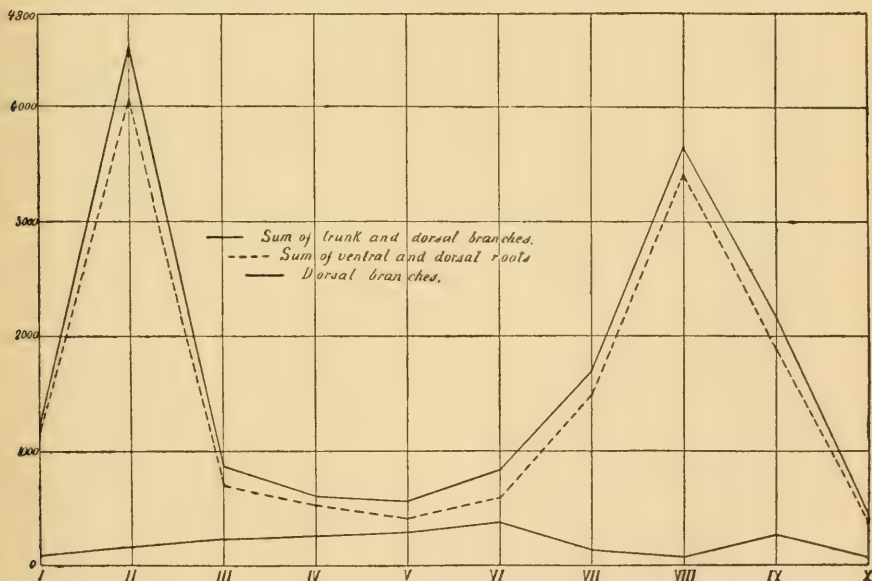

CHART IV. Curves showing the relation existing between the sum of the fibers in the two roots taken close up to the spinal ganglia and the sum of the trunk and dorsal branches taken just distal to the spinal ganglion. The lowest curve represents the sum of the dorsal branches alone.

taken just central to the ganglion, or at any point along the course of the roots. This relation is especially presented in Chart IV. This chart is constructed from the data employed for Chart II. It differs from the latter by the fact that the sum of the fibers in the two roots taken just central to the ganglion, is employed instead of plotting the roots separately. The relations presented, therefore, are those of absolute values. The lower curve represents the number of fibers separately contained in the dorsal branches of each nerve.

Attention is called to the chart as showing (1) the fact that the sum of the roots is always below the sum of the trunk and dorsal branches; (2) that the curve for the two roots runs nearly parallel with that of the sum of the trunk and branches; (3) that the greatest amount of deviation between the two curves does not occur in the larger nerves; and (4) that the dorsal branches attain their highest absolute values in the smaller nerves. Also, it is to be noted, that, though the value of the dorsal branches does not always coincide with the amount of the excess of fibers which these branches together with the trunk contain above the sum contained in the two roots, yet the curve for the branches suggests that there may exist some relation between the number of fibers contained in them and the amount of the excess. On comparing the percentage values of this excess of the trunk and branches over the sum of the roots for the different nerves, this probability presents itself still more strongly.

Table XI, here given, is derived from the numbers in Table I and is designed to show first, the amount of the excess of this sum of the trunk and branches over the sum of the roots and the percentage values of the excess based upon the sum of the roots; and second, the relation or coincidence between this excess and the absolute number of fibers in the dorsal branches.

TABLE XI.

FROG, WEIGHT 48.2 GRAMS.

Number of the nerve	A Excess of fibers in trunk and dorsal branches over sum of roots	B Percentage of the excess	C Percentage of dorsal branches	D The number of fibers in dorsal branches
I	78	6.6	6.9	82
II				
III	170	24.2	31.7	225
IV	103	19.3	48.5	259
V	145	34.0	68.5	292
VI	220	38.3	61.4	370
VII	212	14.3	9.5	141
VIII	217	6.37	2.5	86
IX	257	13.6	14.1	268

TABLE XI, giving the percentages of the amount by which the sum of the trunk and dorsal branches taken just distal to the spinal ganglion, exceeds the sum of the ventral and dorsal roots taken just central to the ganglion. Column A contains the absolute number of the excess of fibers found in the trunk and dorsal branches, column B the percentage of this excess based upon the sum of the dorsal and ventral roots. In column C the percentage of the absolute number of fibers contained in dorsal branches is given based upon the sum of the fibers in the ventral and dorsal roots, and column D contains the absolute number of these fibers composing the dorsal branches.

From the table it is at once seen that those nerves which have the greatest amount of excess in the number of fibers distal to the ganglion, have also the greatest number of fibers in their dorsal branches. The VIIIth nerve has the lowest percentage of excess and has also the smallest dorsal branch, while both the greatest amount of excess and the greatest number of fibers in their dorsal branches are possessed by the VIth. This nerve shows an excess of 38.3% and its dorsal branches amount to 370 fibers.

Again, if column C of the table is brought in, it is seen that those nerves which have not only absolutely but proportionally the largest dorsal branches, have also the greatest percentage of an excess of fibers in the trunk and dorsal branches. The dorsal branches of the IVth, Vth and VIth are 48%, 68% and 61% respectively of the sum of the root fibers of the nerves to which they belong. These are the nerves which show the greatest excesses of fibers distal to their spinal ganglia. In

the IXth the excess is very nearly the same as the dorsal branches ; that is, 257 against 268 fibers or 13% against 14%.

The specimen used for the four sets of counts recorded in Table II, while being heavier, gives excesses in the trunk and dorsal branches absolutely less than those obtained in Table I, although the number of fibers contained in the four nerves involved is somewhat less. However, while the excesses are less, the dorsal branches are also both absolutely and proportionally less. The values obtained for the four nerves recorded in Table II, are given in Table XII.

TABLE XII.

FROG, WEIGHT 59.52 GRAMS.

Number of nerve	Excess of fibers in trunk and dorsal branches over sum of roots	Percentage of the excess	Number of fibers in dorsal branches	Percentage of dorsal branches
VI	138	36.7	286	76.2
VII	199	18.7	155	14.5
VIII	86	3.1	49	2.1
IX	109	4.4	239	9.8

On comparing Table XII with Table XI it is seen that the two specimens, differing in weight and in the number of fibers, agree in the general relation existing between the excess of fibers in the trunk and dorsal branches and the amount of the dorsal branches.

This approach to a conformity or correlation between the excess of fibers distal to the spinal ganglion and the number of fibers which do not enter into the formation of the trunk, may be a mere coincidence and entirely without significance. Indeed, in the VIIIth nerve (Table I), for example, as many as 131 fibers of the excess, are necessarily contained in the trunk; and, in case of the VIth, on the other hand, the trunk lacks 126 fibers of containing as many as there are in the two roots.

IX.   DISCUSSION OF THE OBSERVATIONS AND COMPARISONS WITH THE RESULTS OF OTHER OBSERVERS.

    1.   The excess.

That there does occur a greater number of fibers distal to

the spinal ganglion than is contained in the two roots central to it, is very evident. In several instances an excess has been obtained by previous observes.

Holl ('75) counted the fibers in the two roots and in the trunk of three of the lumbar nerves of the frog. In every case his counts showed a slight excess in favor of the trunk. This excess, however, never exceeded 2 % and the author concluded that the number of fibers on the two sides of the spinal ganglion was the same. He explained the excess as due to errors in counting.

Freud ('78), in investigating the spinal ganglia of Petromyzon, reached the general conclusion that the number of dorsal root fibers was equivalent to the number of spinal ganglion cells. However, he barely mentions on page 79 that, in Petromyzon, he found an increase of fibers in the trunk. This increase he regards as occurring within the ganglion and considers it of little importance, thinking it due to a splitting of the processes of the spinal ganglion cells. Figures illustrating this splitting are give in his plates. Freud's counts were made from teased preparations.

Stienon ('80) in studying the relation of the dorsal root fibers to the cells of the spinal ganglion, made two counts of the fibers in the two roots and in the trunk. In one of these counts, a cervical nerve of the dog was used and in the other a lumbar nerve of the frog. In both he obtained a slight excess in the trunk (1.2 % for the frog) and, like Holl, explained the excess as due to errors in technique.

Birge ('82) who, as before mentioned, made counts of the several spinal nerves of the frog, obtained for two of the nerves quite an appreciable excess of fibers in the trunk. In one (IInd) there were found nearly 16 % more fibers in the trunk than in the two roots, and in the other (IXth) an excess of nearly 14 %. Birge is the first to attach a significance to the excess found. While admitting that the differences obtained might lie within the bounds of error in technique, yet he did not think this probable and suggests that the matter be further investigated.

Gaule and Lewin ('96) in a preliminary paper, give some enumerations upon the nerves of the rabbit. At the time of publication counts had been made of the fibers contained in the two roots and in the trunk and dorsal branches of three of the sacral nerves. These counts revealed respectively, 19%, 11% and 15% more fibers in the trunk and branches combined, than there were in the sums of the two roots. They are the first to mention having included the dorsal branches in the enumeration.

Bühle ('98), in a study of the spinal ganglia of the frog, counted the fibers to be found on the central and distal sides of the spinal ganglion. The original of this paper of Bühle has unfortunately not yet been obtainable. According to a review by Lenhossék ('97), Bühle obtained an excess of fibers on the distal side of the ganglion which in one case amounted to as much as 25.5%. Even this, however, is less than the excess here found for the Vth and VIth nerves of the American frog (*R. virescens*).

To explain the excess of fibers on the distal side of the spinal ganglion, Gaule ('96) suggested the only two possibilities: (1) Fibers coming from the periphery may end in the ganglion and thus not pass over into the dorsal root; or, (2) fibers may arise in the ganglion and pass toward the periphery without there being a corresponding central process.

Since the excess can be looked upon as well established, the two possibilities suggested by Gaule may be presented in some detail.

1.   Medullated fibers arising from the cells of the sympathetic ganglia pass, by way of the ramus communicans and the nerve trunk, to the spinal ganglion and end there. For the existence of such fibers the evidence is as follows:

Bidder and Volkmann ('42), noting the great number of small medullated fibers present in the peripheral nerves of the frog and especially in the sympathetic system, arrived at the conclusion that these small medullated fibers originated in the cells of the sympathetic ganglia, and they suggested the small diameter as the characteristic by which the fibers of the sympa-

thetic system could be distinguished from those of the spinal system.

Kölliker ('45), opposing this idea of Bidder and Volkmann, undertook a series of investigations which resulted in his being forced to agree with them to the extent that, in addition to the many non-medullated nerve fibers having their origin in the sympathetic system there do arise from the cells of the sympathetic ganglia quite a number of medullated fibers also.   Kölliker found this to be true, not only for the frog but also for other vertebrates.   In a later paper, Kölliker ('94) calls especial attention to these medullated sympathetic fibers.   He describes them as " dunkle randige Fasern "— fibers possessing a thinner myelin sheath than that of the cerebro-spinal fibers, which sheath stains less black with osmic acid. Kölliker also states that, while the great majority of sympathetic fibers are " motor " in function, it is possible that there are also among them "sensory " fibers which may play a rôle in reflexes occurring in the domain of the sympathetic system. Since Kölliker ('94), medullated fibers of sympathetic origin have been often observed by Dogiel ('95 and '96) and others. There is no doubt that for both mammals and the frog, some sympathetic fibers are medullated.

Some fibers from the sympathetic ganglia pass by way of the nerve trunk to the spinal ganglia.   By the observations of Cajal ('93), Retzius ('94), Huber ('96), Dogiel ('96 and '97), Cajal and Olóriz ('98) and others, it has been established that for the frog and certain mammals at least, fibers having their origin in the cells of the sympathetic ganglia, pass by way of the ramus communicans and nerve trunk to the spinal ganglia and end in pericellular plexuses about the cells there.   Dogiel's observations on medullated sympathetic fibers have been made especially upon certain of these fibers going to and found in the spinal ganglion.

If sympathetic fibers pass to the spinal ganglia and end there and if some of these fibers are medullated, then an enumeration of the medullated fibers on the distal side of the spinal ganglion would include these medullated fibers which do not

pass through it, and an excess in the trunk would be the natural result. This explanation of the excess is illustrated in scheme I.
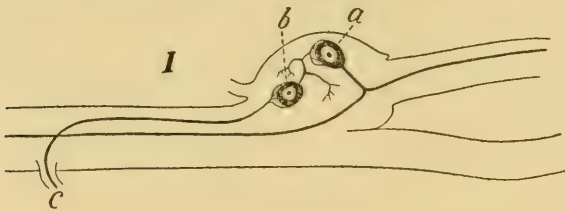

According to this scheme the medullated sympathetic fiber enters the ramus (*c*) and passes to the ganglion where it terminates in an end-brush about the body (*b*) of a Dogiel spinal ganglion cell of type II.   Thus it is seen that a section taken immediately distal to the ganglion would contain two fibers, whereas one taken central to the ganglion would include only the central process of the ordinary spinal ganglion cell, or Dogiel's cell of type I, (*a*).

How numerous these medullated sympathetic fibers are, which are present only on the distal side of the ganglion would be difficult to determine. None of the observations so far made have been attempts to determine their number.   But none of the descriptions of these fibers, nor Dogiel's ('96) description of what he considers sensory cells in the sympathetic ganglia, seem to justify the assumption that they are numerous enough to account for the excesses which have been found.   It seems necessary therefore, to assume that, in addition to the fibers arising in the sympathetic ganglia, there are also other fibers present in the nerve trunk which do not occur in the roots. The other possibility is the second one suggested by Gaule ; namely, that fibers may arise in the spinal ganglion and pass to the periphery without there being corresponding central processes in the dorsal root.

Three possible ways suggest themselves by which an excess in the trunk may occur according to this second suggestion by Gaule.   These possibilities can be illustrated by three schemes.
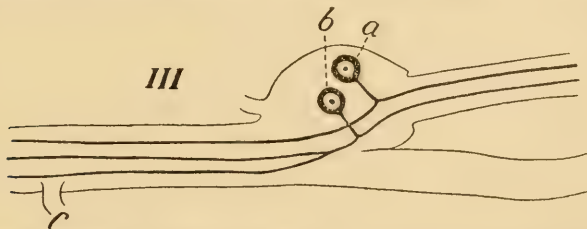
1.   Scheme II is intended to illustrate a probability that on approaching maturity the peripheral process of a spinal ganglion cell (*b*) becomes medullated first.   The mature cell (*a*) has sent a process in both directions and consequently in
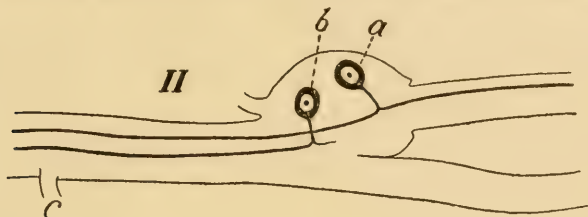
that case a fiber would be counted on both sides of the ganglion.   Direct histological evidence in favor of Scheme II is lacking.   Some observations however may be considered as having an indirect bearing upon this point:

In addition to the work of Wagner ('48) on the spinal ganglia of fishes, the more recent observations of van Gehuchten ('91), Kölliker ('93), Cajal ('93 and '94), Lenhossék ('95) and Dogiel ('97), made chiefly upon foetal material, indicate that the central process of the T-fiber is often much thinner than the peripheral one.   And the observations of Ambronn and Held ('96) seem to indicate that as a whole the peripheral system is medullated before the central and thus perhaps the peripheral process of the spinal ganglion cell acquires its medullary sheath before the central one which goes to form the dorsal root.

2.   Scheme III illustrates a possibility of one source of the excess of fibers distal to the spinal ganglion.   This sugges-

tion was offered by Bühle ('98).   It is based upon the fact that in certain cases a splitting of the processes has been observed within the spinal ganglion.

A splitting of the peripheral process of the cell (*b*) would give two fibers on the distal side of the ganglion corresponding to one fiber on the central side. This splitting or division of the fiber has been observed by Stannius ('49) for fishes, Freud ('78) for Petromyzon, and by Dogiel ('97) for mammals. Dogiel's observations however lead him to think that the splitting more often occurs in the central rather than in the peripheral outgrowth of the spinal ganglion cell. Freud, on the other hand, positively states that for Petromyzon the splitting occurs in the peripheral process.

That a splitting or division of fibers may be one cause of the excess found on the distal side of the ganglion, is an explanation which may have a better foundation than at first appears. Dr. Elizabeth Dunn has just made, in this Laboratory, some enumerations of the fibers contained in the trunk of the sciatic nerve of the frog and also of the fibers contained in the several branches into which this nerve divides for the innervation of the leg. She kindly permits reference to be made to the fact that she finds an appreciable excess of fibers in the branches. In a frog (*Rana virescens*) of about 50 grams weight there were found in the trunk of the sciatic of one side, before any branches are given off, 4293 fibers, while the sum of the fibers found in the several muscular and cutaneous divisions to the thigh and in the *tibialis* and *peroneus* branches to the lower leg, amounted to 4511 fibers—an excess of 218. This excess of fibers in the branches was found to be very similar for the two sides of the same frog.

The only explanation which suggested itself for this greater number of fibers in the branches is that it was due to a splitting of the fibers of the trunk of the sciatic. This probable and evidently necessary splitting of the fibers called for by the results of Dr. Dunn suggested an examination of the sciatic nerve especially at the points at which the branches are given off, for it was thought that in these regions the splitting would most probably occur. This investigation is as yet incomplete. However at this stage abundant cases of divided fibers have been observed in the branches of the sciatic of the second and

third order. They have been demonstrated both after treatment with osmic acid followed by maceration in a mixture of glycerine and hydrochloric acid and by means of methylene blue. In preparations pressed out under the cover glass rather than teased, numerous cases have been observed in which the fiber splits at the angle formed by the division of the nerve branch, one branch of the divided fiber passing into each branch of the divided nerve.

The splitting of the fiber occurs, as would be expected, at a node, and there is no diminution in the diameter of the fibers which result from the splitting. Each of the fibers— sometimes three in number—which result from the division possesses a diameter about the same as that of the fiber which divided to form them.

It has already been noted in this paper (Table XI) that there is a marked correlation between the actual number of fibers in the dorsal branches of the spinal nerves and the amount of the excess of fibers in the sum of the trunk and these dorsal branches above the sum of the fibers contained in the two roots. In those nerves in which the excess is greater the number of fibers in the dorsal branches is both absolutely and proportionately greater. The dorsal branches going to the dorsal muscles and to the skin of the back may be looked upon as branches of the spinal nerve just as well as the branches to the muscles and skin of the leg are branches of the sciatic nerve, and if some of the fibers in the branches of the sciatic are the result of splitting then some of the fibers in the dorsal branches of the spinal nerves may be the result of splitting and hence a splitting of fibers in and on the distal side of the spinal ganglion may be one cause for the excess of fibers present on the distal side of the spinal ganglion.

In order to determine the truth of this assumption an examination of the fibers in the region of the spinal ganglion is now in progress. At the present stage of this investigation a statement may be here inserted to the effect that divided fibers have been frequently noted in the dorsal branches well outside the limits of the ganglion but so far, such cases have been much

less frequently observed within the boundaries of the ganglion. The fibers which pass to the dorsal branches from the ventral root cross the greater mass of fibers which go to form the nerve trunk and this interweaving results in a tangle which renders a sufficiently disassociated preparation quite difficult to obtain. A few cases however have been found in which a ventral root fiber was seen to split into two. That one of these passed to the dorsal branches could not be clearly determined owing to injury in the disassociation ; that they were ventral root fibers, however, there is no question. This splitting of ventral root fibers is not included in the possibilities suggested by Gaule.

As to the splitting of fibers arising from the cells of the spinal ganglion, while many divided fibers have been observed, none have yet been seen concerning which it can satisfactorily be asserted that both the products of the division pass to the periphery. Unless each can be followed separately either into the nerve trunk or into the dorsal branches there is nothing to show that the structure is not the characteristic T-fiber, or one of the numerous divisions which Dogiel claims for the processes of his ganglion cell of the IInd type. However it must be remembered that the investigation is only just begun. But it should also be remembered that an occasional division of the peripheral process of the spinal ganglion cell has already been noted by previous observers.

3. The possibility to be suggested by Scheme IV is that among the spinal ganglion cells which never send processes to the dorsal root, there are some which send processes to the periphery.
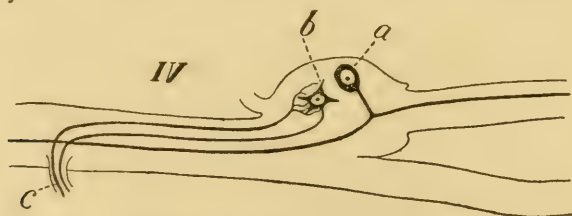
There are no histological observations which directly support this scheme. The investigations of Hodge ('89) and

Bühle ('98) show that in the spinal ganglia of the frog there are from two to five times as many cells in a spinal ganglion as there are fibers in the dorsal root. Of this excess of cells many are no doubt latent ganglion cells, others are of the Dogiel spinal ganglion cell of Type II, but still others may be multipolar cells. Multipolar cells have been observed in spinal ganglia by Kölliker ('93), Disse ('93), Lenhossék ('94), Spirlas ('96), Dogiel ('97) and Cajal and Olóriz ('98), and the possibility presented by Scheme IV is that some of these multipolar cells are of the sympathetic type which have developed within the spinal ganglion. Such a cell (*b*) is assumed to be under the control of one of the medullated sympathetic fibers (*c*) which have been observed to pass from the sympathetic system to end in the spinal ganglia—an arrangement which would give an excess of at least two fibers in the nerve trunk.

Another barely possible arrangement might be noted : Although histological evidence for the frog is lacking, certain experimental evidence brought forth chiefly by Steinach ('95) and Horton-Smith ('97) seems to indicate that there are in the dorsal root certain fibers of intra-spinal origin which when stimulated produce disturbances in the domain of the sympathetic system. This evidence might be interpreted to mean that some of these fibers, instead of passing through the spinal ganglion, terminate in the spinal ganglion and control some of the multipolar cells there of presupposed sympathetic type. Such a fiber might break up into a number of branches and thus control a number of these cells each of which would send a process to the periphery and thus an excess of fibers in the nerve trunk would be produced.

Against the probability that the multipolar spinal ganglion cells play the rôle above assigned them, it must be stated that Dogiel ('97) who has made a careful study of these cells in mammals, in the maze of fibers present, was unable to follow any of their processes outside the bounds of the ganglion. He suggests that they are either cells of a sympathetic type or are modifications of his spinal ganglion cells of type II.

2. THE VARIATIONS IN THE NUMBER OF FIBERS FOUND AT DIFFERENT LEVELS IN THE ROOTS AND TRUNK.

As before mentioned, these differences are explained on the supposition that fibers growing into the roots and into the trunk have proceeded unequal distances from their cells of origin.

Ever since the investigations of His ('86 and '89) it has been admitted that the medullated fibers forming the spinal nerves are the outgrowths, on the one hand, of the cells of the dorsal root ganglia, and on the other, of those situated in the gray matter of the spinal cord.

Kaiser ('91) has shown that the number of mature nerve cells in the cord increases with the growth of the animal, and the work of Birge ('82) is sufficient to show that the fibers of a nerve increase in number during the growth of the frog. Birge found for the frog that the increase in the number of fibers in the spinal nerves was quite proportional to the increase in the weight of the animal.

Donaldson ('97) determines the fact that the entire neurone, the nerve fiber as well as the cell body, increases in size during the growth of the animal.

Korybutt-Daskiewicz ('78) observed growing fibers along the sciatic nerve of the frog. This investigator also described the myelin sheath in its formation about the growing axis cylinder as tapering bluntly and ceasing a short distance behind the growing tip.

Kolster ('93) in a study of the regeneration of fibers following the section of the nerve, pictures the sheath as being acquired a node at a time and consequently as ending bluntly —the axis cylinder preceding the formation of the sheath. Both observers describe the myelin as first appearing either as a thin layer blackening with osmic acid or as fine irregularly accumulated droplets. Stroebe ('93) observed the sheath as making its appearance in much the same way.

These descriptions accord fairly well with the results of searches made here for growing nerve fibers, one of which is represented in Plate VII, figs. 1 to 6.

It is concluded therefore, that the variations found to occur in the number of fibers at different levels of the dorsal and ventral roots and in the nerve trunk as recorded in Tables I and II are but the natural result of the growth of the nerve fibers.

X. METHODS AND TECHNIQUE.

If a detailed account were given of the difficulties experienced before obtaining satisfactory preparations, this division of the paper would be much more lengthy than it is intended to make it.

The first and prime object was not only to obtain preparations in which medullated nerve fibers were so sharply differentiated that each one stained could be readily distinguished as such, but also to obtain preparations in which it could be satisfactorily asserted that all the medullated fibers were distinguishable.

Little can be said concerning the effect that the general nutritive condition of the animal, the season of the year etc., may have upon the staining properties of its medullated fibers. It is reasonable to suppose that pathological or even certain natural conditions may influence to some extent at least, the stain reactions of nerve fibers as well as those of other tissues. Gaule ('89) recognized season as having an influence and recommended *Rana temporaria* in May and *Rana esculenta* in June for the clearness with which their nerve fibers might be stained by the Weigert method. Little more can be said here however, than that the best results were obtained with freshly caught specimens, and that while the experiments for a satisfactory staining method extended through several seasons, both the specimens from which the results recorded in this paper were obtained were killed in October.

For bringing out medullated nerve fibers, treatment with osmic acid was of course, the first that suggested itself. Osmic acid however was found to possess several defects. These de-

fects were principally due to the well known slowness with which osmic acid penetrates and to the distortion of the nerve fibers which it often produces either by a swelling effect upon the myelin sheaths or by a shrinkage of the perineuric investment of connective tissue. The myelin sheath seems to undergo some form of disintegration shortly after death and unless the osmic acid penetrates the sheath before this occurs, the reduction of the osmium is incomplete and indefinite structures are the result. To avoid this the nerve must be exposed to the action of the reagent as quickly as possible. For the entire ten spinal nerves, it was found difficult to accomplish this, especially in case of the intervertebral portions of the nerves, without some pulling or crushing or the loss of some of the smaller dorsal branches. It is well known that the action of osmic acid upon the medullary sheaths of fibers which have been injured results in very abnormal appearances.

Little difficulty was met in obtaining with osmic acid well stained sections from those portions of the nerve roots lying free in the spinal canal, or in obtaining fairly satisfactory sections from that part of the nerve trunk lying exposed in the body cavity. The great difficulty was experienced in getting sections well blackened and intact of those portions of the nerve immediately central and distal to the spinal ganglion. Even if removed from the intervertebral foramen without injury or loss of some of the branches, there still remained the periganglionic capsule of connective tissue and the "periganglionic gland." If this was left on, it interfered with the penetration of the osmic acid and the contraction of the capsule produced by the reagent resulted in an injurious condensation of the nerve fibers which it enclosed. If removed, its removal in the fresh state was well nigh impossible without injury to the nerve. The use of osmic acid being thus beset with difficulties, other methods of treatment were resorted to. However, after trying both the Pal-Weigert method and a modification of the iron haematoxylin method, neither of which gave preparations so suitable for photographing nor, after the required decolorization, preparations in which the small fibers appeared satisfactorily distinct, it be-

came necessary to return to osmic acid as offering the greatest possibilities of obtaining satisfactory results.

In order to obviate the difficulties attending its use, several osmic acid mixtures were tried. These again had to be abandoned as inefficient. Where one was an advantage in one respect it was a drawback in another. Various mixtures of osmic acid and formalin were tried, but, while giving cylindrical and well blackened fibers, had to be abandoned because formalin was found not only to accelerate the reduction of the osmium but, what was not desired, also to produce a brittleness which made it more difficult to obtain sections thin enough for photographing and reliable counting.

The most promising combinations with osmic acid were found in the application of a reducing agent after the exposure to the action of the acid. After trying several of the reducing reagents used in the ordinary photographic developers, the best results were obtained with a 0.5 % water solution of pyrogallic acid. If the nerve be washed for two and a half or three hours in distilled water after removal from the osmic acid and then placed for an hour or so in this solution of pyrogallic acid, a decided increase is noticeable in the intensity with which the medullary sheath is blackened, without any indication of a reduction of the osmium in the other structures of the nerve. Some of the nerves used in making the counts of fibers recorded in this paper had been treated in this way.

The method of procedure which proved the most satisfactory is the following.

DISSECTION.

The animal was killed and weighed and, if female, the weight of the ovaries deducted. Then the viscera, the skin, the limbs and a portion of the abdominal and thoracic muscles were removed. This left only the head and the more dorsal portion of the body. From the ventral side, the spinal cord was now laid bare by carefully severing the pedicles of each vertebra and thus removing the centra of the entire vertebral column. This also lays open the intervertebral foramena. Then

with small scissors or fine bone forceps incisions were made in the dorsal muscles just under the position of each spinal ganglion in order to allow the reagent to reach the dorsal branches more freely.

The head was next severed well above the origin of the first spinal nerve and, with a fine pipette, 1 % osmic acid was forced under the cord washing out the cerebro-spinal fluid and replacing it with osmic acid. The cord was left in position at this stage lest its removal should disturb the normal tension of the nerve roots or otherwise injure them. The whole was then placed for 10 or 15 minutes in a vial containing a one-fifth one per cent. solution of osmic acid and this was frequently agitated. The idea in using the weaker solution was to insure a slower fixation of the connective tissue investments. It was thought that a slower fixation would result in a less violent contraction and consequent condensation of the nerve bundles and thus also allow a more rapid penetration of the stronger solution which follows.

At the end of the 15 minutes the specimen together with the weaker osmic solution was transferred to a dish under a dissecting microscope. With the eyes and nose of the observer protected from the fumes of the acid, each nerve root was gently severed from its connection with the spinal cord and the cord removed. Next each nerve trunk was severed a few millimeters distal to its connection with the ramus communicans and the ramus itself cut. Then with the aid of a fine tentaculum and small spring scissors (under an enlargement of 16 diameters) each nerve was detached and removed from the intervertebral foramen, especial care being taken not to injure nor lose any of the dorsal branches. The periganglionic capsule was now opened and partially teased away and the nerve transferred to a 1 % solution of osmic acid.

At the end of from 12 to 24 hours the nerves were removed from the osmic acid solution to distilled water. Again under a dissecting lens, the teasing away of the periganglionic capsule and other loosely attached connective tissue was carefully completed and camera outlines were made of the dissected

nerve and roots under a known magnification. The length of the roots and trunk was then determined in millimeters and indicated on the drawings.

The washing in water was continued from 4 to 12 hours, or long enough to remove all the surplus osmic acid. The material was then transferred to 70 % alcohol, dehydrated in alcohol of about 97 %, cleared in a mixture of 3 parts pure xylol and one part carbolic acid and embedded in very hard paraffin (melting point about 56°). Absolute alcohol was usually avoided, since in the previous experiments there were occasional indications of the myelin having been slightly dissolved. Clove and cedar oils were also avoided for the same reason.

Sections 3 micra in thickness were taken at each of the prescribed levels of the roots and nerve trunk. Those from each level were mounted on separate slides as soon as cut. The sections were fastened to the slide by means of the "albumen water method." For photographic purposes it is absolutely necessary that the sections be flat on the slide. The flattening was accomplished by placing the slide with the sections floating upon it, upon a water bath the temperature of which was just below the melting point of the paraffin. Here, the sections having flattened out, the slide remained with the paraffin in a plastic state till the water had practically dried out from under the sections. Then the slide was placed aside for several hours longer to allow the drying to become complete.

After mounting in balsam, the sections on each slide were examined as to their fitness for photographing and counting and those chosen were marked by a small square on the cover glass.

THE PHOTOGRAPHY.

As can be readily seen, the object striven for in the photography was to get the greatest amount of contrast and at the same time precision as to outline. Of the three brands of photographic plates tried, that made by the Cramer Dry Plate Works of St. Louis, Mo., and sold under the name of "Cramer's Contrast Plate," was by far the best for the purpose.

Also, after trying several formulae, the developer which gave the best satisfaction was made according to the "Bromo-hydro-chinon" formula which accompanies these plates.

The apparatus used was the large photographic and projection outfit manufactured by Zeiss. This was mounted on a large stone pillar which insured the perfect steadiness of the apparatus.

The sections were photographed under a magnification of from 500 to 800 diameters and the exposure made according to the intensity of the light. A small diaphragm and long exposure gave the best results. The source of light was an ordinary Welsbach burner.

THE PRINTING.

Each negative of a section was labeled with the weight of the frog, the number of the nerve and with the region and level from which the section was taken. This label was cut through the film on one corner of the negative so that in the printing the label would print also.

That grade of velox paper sold under the name "Carbon Velox" was found best suited for reproduction, since pure blacks and whites can be obtained with it. Plates IX, XI, and XIII are reproductions of prints made with this paper. Blue prints were used almost exclusively in the counting procedure. Blue print paper is easier to manipulate and if a good quality be used, prints can be obtained possessing a high degree of sharpness and detail.

THE METHOD OF COUNTING.

The method employed was devised in this laboratory and has not been previously described. In order to count a given section, a photograph of it was fastened upon a small board of soft wood, the section itself placed under the microscope and the two oriented. With a sharp pointed pencil, the photograph was marked off into fields of small area the boundaries of which were determined by the grouping of the fibers.

The section, kept under the microscope for reference, was subjected to an enlargement of 640 diameters or an enlarge-

ment usually above that under which the photograph had been made.

After a short study of the section under the microscope, it was found suprisingly easy to identify any fiber in a field of the photograph with its original in the section. Thus, also, the boundaries of the fields marked off on the photograph could be readily determined in the microscope.

The counting itself was largely mechanical. An automatic registering machine, one common use of which is to count telegraph poles, was modified by attaching to its finger press a short steel rod. Into the end of this rod was inserted a needle so arranged with a set screw that the point could be protruded any distance required. Plate VII, Fig. 7, represents a photograph of the machine as it was here employed. In want of a better name it will be referred to as the "counter." When the rod is pushed up, the counter with an audible "click" registers one ; the pressure removed, the rod springs back to its first position. The machine registers up to 1000 and repeats. By piercing with the needle the center of a fiber in the photograph, the rod is pushed up and the counter records. Thus when each fiber represented in a photograph has been punched, the counter has recorded on its register the total number of fibers in the section. When a section contained more than 1000 fibers, each thousand when indicated by the register, was noted and the counting continued. Since the counter began to repeat immediately upon reaching 1000, there was absolutely no danger of loss or mistake.

Each field as marked off on the photograph was counted separately. Not till all the fibers in one field had been counted, was the counting of those in an adjacent field begun. The aid of the microscope was most necessary in counting the small fibers ; large blood vessels were distinguishable on the photograph as well as in the microscope. Every case which occasioned the least doubt was quickly and finally settled by an appeal to the microscope. Sometimes, among the smaller fibers, there appeared in the photograph what seemed to be two fibers lying in such close contact as to resemble the figure 8. These

cases were always referred to the microscope which often showed them to be one fiber collapsed in such a way as to give its section this form.

In using the counter, the eye of the observer naturally follows the point of the needle. Since a puncture is made in the center of each fiber at the time it is counted, this puncture is readily seen and protects the fiber from being counted a second time.

After a photograph had been counted in this way, each field was examined a second time. This time the microscope was used even more frequently than the first and especial search was made for small fibers which might have been overlooked. This search seldom added more than 2 % to the first count. Finally each field of the photograph was examined with a hand lens, search being made for unpunched large fibers. The hand lens was an advantage both in reducing the field of view and in so magnifying the fibers that one with an unpunctured center could be quickly discerned. Strange to say, if any of the larger fibers had been omitted in the previous counts, they were usually found to be the very large ones.

When a count had been completed the number of fibers found in the photograph was written below the label which had been printed on it and the photograph was filed. In order to more thoroughly guard against any personal equation, no two sections from consecutive levels were counted in succession. Sometimes the counting of two nerves was carried on simultaneously and thus in the large number of sections involved, the number of fibers contained in a section from a given level had passed out of mind before determining the number contained at an adjacent level.

In order to test the accuracy of the enumeration, in quite a number of cases a second photograph was counted. In almost every case the second number obtained was identical with that of the first count. If there did result a difference in the two counts it seldom amounted to 1 % and the fibers causing the difference were always found.

The advantages claimed for this method of counting are notably three :

1. The method reduces the mental stain to a minimum. The ordinary ''net'' method ¡used by earlier observers, and even as improved by Gaule ('96), involves many difficulties which are entirely avoided by the used of a photograph.

2. The method is largely mechanical. The work of carrying numbers in the mind and the final addition of the numbers so carried, is transferred to the machine.

3. The work of counting a section may be interrupted at any time without the least danger of loss in the accuracy of the number finally obtained. One who has ever attempted to count a section containing several thousand fibers will immediately realize this advantage.

By reason of the accuracy attainable with this method it is justifiable to attach great weight to the small numerical differences found to occur in the course of the nerve roots and trunk.

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XII.   EXPLANATION OF PLATES.

PLATE VI.

The ten spinal nerves of *Rana virescens*. Left side. Drawn to scale and enlarged six diameters.

The Roman numbers indicate the number of the nerve.

The Arabic numbers indicate the levels at which the sections were taken for the enumeration of fibers recorded in Tables I and II. The Arabic number 6 indicates the region at which the sections of the dorsal branches were taken. In case of the VIIIth and IXth nerves the branches are here so arranged that the transverse section of the trunk may also involve a transverse section of the branches.

C.—Ramus communicans.

D. r.—Dorsal root.

V. r.—Ventral root.

PLATE VII.

Figs. 1-6. A series of transverse sections which show a growing fiber. Taken from ventral root of VIth nerve of frog used in Table I. The series, beginning at Fig. 1, passes toward the spinal cord and includes a length of about 30 micra.

The smallest fiber of the group, the growing fiber, makes its first appearance as a brown ring and soon acquires its medullary sheath.

Camera drawings. Magnification, 466 diameters.

Fig. 7. Automatic registering apparatus used in counting technique. When rod containing the needle is pressed inward the machine records.

½ natural size.

PLATES VIII TO XIII.

General explanation :

Plates IX, XI and XIII represent sections from the ventral root of the VIIIth nerve of a frog of 48.2 grams. The plates are made from the identical photographs employed for the enumeration of the fibers of this root as recorded in Table I and correspond respectively to columns A, B and C of that table or to levels 1, 2 and 3, Plate VI.

Plates IX and XI contain two sections each as the root is divided in the same manner as the ventral root of IXth nerve, Plate VI.

All the figures are reduced to about ½ the size of the photographs from which they were made.

Plates VIII, X and XII are companions to Plates IX, XI and XIII respectively. They show the fields as marked out on the photographs during the counting and also the number of fibers determined for each field. The boundaries of each figure coincide with those of the companion photograph. The total number of fibers determined for each section is placed at the lower right hand of each figure.

The black dots in the center of each fiber represent the holes made by the needle of the "counter," Plate VII, Fig. 7. This dot is sometimes obscured in the reproduction, especially in case of some of the smallest fibers where the small white axis cylinder space is obliterated by the puncture which is reproduced in black like the medullary sheath.

Blood vessels are also reproduced in black.

A hand lens will facilitate the examination of the prints.

PLATE VIII.

Fig. 1. Companion figure to Fig. 1, Plate IX.

Fig. 2. Companion to Fig. 2, Plate IX.

PLATE IX.

Figs. 1 and 2. Transverse sections of ventral root, VIIIth nerve, from region corresponding to level 1, Plate VI.

Magnification : $\begin{cases} \text{Fig. 1.} & \text{300 diameters.} \\ \text{Fig. 2.} & \text{310 diameters.} \end{cases}$

PLATE X.

Fig. 1. Companion to Fig. 1, Plate XI.

Fig. 2. Companion to Fig. 2, Plate XI.

PLATE XI.

Figs. 1 and 2. Transverse sections of same ventral root but from region corresponding to Level 2, Plate VI.

Magnification : $\begin{cases} \text{Fig. 1.} & \text{284 diameters.} \\ \text{Fig. 2.} & \text{275 diameters.} \end{cases}$

PLATE XII.

Companion to Plate XIII.

PLATE XIII.

Transverse section from same ventral root, taken from region corresponding to Level 3, Plate VI. The two divisions represented in Plates IX and XI have here fused.

Magnification, 307 diameters.

THE TOTAL NUMBER OF FUNCTIONAL CELLS IN THE CEREBRAL CORTEX OF MAN, AND THE PERCENTAGE OF THE TOTAL VOLUME OF THE CORTEX COMPOSED OF NERVE CELL BODIES, CALCULATED FROM KARL HAMMARBERG'S DATA ; TOGETHER WITH A COMPARISON OF THE NUMBER OF GIANT CELLS WITH THE NUMBER OF PYRAMIDAL FIBERS.

By Helen Bradford Thompson.

(From the Neurological Laboratory of the University of Chicago.)

CONTENTS.

SUMMARY.

I.   The total number of functional nerve cells in the cere-
bral cortex of the adult man is, in round numbers, 9200 mil-
lion.

II.   The proportion of the total volume of the cerebral
cortex of the adult man composed of functional nerve cell bod-
ies, is 1.37 %.

III.   The number of giant cells in the cerebral cortex of
man is almost the same as the number of pyramidal fibers pass-
ing to the spinal cord.

I.   INTRODUCTION.

A.   The most minute and careful work upon the size and
arrangement of the cells in the human cerebral cortex which
has as yet been given to the public, is that contained in a mon-
ograph by Karl Hammarberg, entitled "Studien über Klinik
und Pathologie der Idiotie, nebst Untersuchungen über die nor-
male Anatomie der Hirnrinde," Upsala, 1895.   The data
which appear in this monograph with regard to the size and
frequency of the functional nerve cells, and the thickness of the
layers in the various regions of the cerebral cortex, give oppor-
tunity for far greater accuracy than has before been attained in
the determination of two important and interesting points with
regard to the cortex ; first the number of nerve cells contained
in the cortex as a whole, and in its several parts, and second
the proportion of the total volume of the cortex composed of

nerve cell bodies. When compared with the previous compu-
tations upon these two points, for which the available data were
comparatively incomplete, the outcome of calculations based
upon Hammarberg's material, is very surprising. Meynert[1] es-
timates that there are, in round numbers, 612 million nerve
cells in the convex surface of the cerebral cortex. This esti-
mate, he states, is based upon two sets of data, first, his own
enumeration of the cells of the various layers as they appear in
sections of known thickness, and second, the area of the entire
convex surface of the hemispheres as determined by Rudolph
Wagner.[2] He is willing to admit a possible error of a million
or two in his calculation, but considers it reliable within those
limits. Taking Meynert's estimation as a starting point, Don-
aldson[3] calculated that there were 1200 million nerve cells in
the entire cerebral cortex, and that 3000 million would be a
moderate estimate for the number of cells in the entire Central
Nervous System. The present calculation, based upon Ham-
marberg's data, gives the astounding result that there are over
9200 million nerve cells in the cerebral cortex alone, or about
eight times as many as the largest previous estimate.[4] The
proportion of the total volume of cortical substance composed
of nerve cell bodies was determined by Donaldson[5] to be cer-

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[1] Der Bau der Gross-Hirnrinde und seine örtlichen Verschiedenheiten.
Separat-Abdruck aus der " Vierteljahrschrift für Psychiatrie etc.," 1872, vide
p. 18.

[2] Vorstudien zu einer wissenschaftlichen Morphologie und Physiologie des
menschlichen Gehirns als Seelenorgan. Zweite Abhandlung ; Göttingen, 1862,
vide p. 18.

[3] The Growth of the Brain. London and New York, 1895, vide p. 159.

[4] Barker (The Anatomy and Physiology of the Nervous System and its Con-
stituent Neurones, as revealed by recent investigations. The N. Y. Med. Jour,
1897, vide p. 686, note) suggested that Donaldson's estimate of the total num-
ber of cells in the central nervous system was too small rather than too large,
because 3000 million is too small a proportion of the total number of fixed body
cells, estimated by Francke as 3,996,000 million (Die Menschliche Zelle, 1891,
p. 27).

[5] l. c., p. 169 ff.

tainly less than 10 %, while Hammarberg's figures yield 1.37 % as the correct proportion.

B.   The great discrepancy in these results makes it a matter of interest to look with some care both into Hammarberg's methods of preparing material, making observations and tabulating results, and also into the way in which his results have been used in the present calculation.   His study of the size and frequency of nerve cells in the normal cortex included a careful microscopic examination of twelve brains of both sexes, ranging in age from a five month's foetus to middle aged adults. The numbers given in his text are only those for the six adult male brains he examined, and the calculations reported in this paper apply, therefore, to adult male brains alone. His method of preparation was to harden the brains in 95 % alcohol, stain with methylene blue, clear in xylol and imbed in paraffin. The shrinkage due to this process, would of course have no bearing upon the number of cells in the cortex, but would, on the other hand, affect the size of the cells and the thickness of the cortex as a whole.[1] If however the separate cells shrink nearly proportionately to the entire mass of the cortex, as they probably do, the calculation of the percentage of the entire volume composed of nerve cells would also be practically unaffected. Hammarberg reports that careful measurements made upon the thickness of the cortex before and after the processes of hardening, imbedding and staining, show that the shrinkage involved is less than .2 mm.   The difference is so slight, he says, that it cannot be detected by macroscopic measurements.   Since the errors due to methods of preparation are very small in absolute amount, and are of such a nature that they would not modify the results essentially, they have been neglected in making the calculations.

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[1] The thickness of the cortex as given by Hammarberg is less, on an average, than that determined by Donaldson, l. c., p. 206. Donaldson's average thickness of the cortex is 3.24 mm. for the summits of the gyri, Hammarberg's 2.48 mm.   Hammarberg's data show a very wide range of variation, amounting to 100%.

Hammarberg's method in handling the material after it was prepared, was as follows: He made serial sections of all the gyri of the cortex, some of them 10 μ, and some of them 20 μ, thick. He then recorded the thickness of each layer in each region of the cortex, in tenths of a millimeter, and also the two diameters of the average cell in each layer, in micra. As his unit of measurement for the frequency of the cells, he used the number of cells contained in a cube measuring one tenth of a millimeter on a side. If his sections were cut 20 μ thick, each little cube (0.1 mm.)³ of which his total mass was theoretically built up, would be divided into five slices by sectioning. In order to count the number of cells in his five slices and so obtain the number of cells in any particular unit cube, he counted the number of cells which appeared in corresponding areas, 0.1 mm., square, in five successive sections. To avoid counting more than once the large cells which appear through several sections, he counted in any section only those cells in which nuclei were present. The frequency of the cells for each layer is recorded, then, in terms of the number of cells per unit cube (0.1 mm.)³. The numbers which appear in the text are not based on single determinations taken hap-hazard from some portion of the region, but are averages made up from several enumerations and measurements, and are representative of the entire region for which they stand.

C. The division of the cortex into regions adopted in this paper is determined by the number of different sets of measurements Hammarberg found it necessary to record in order to represent the entire cortex. That is to say, any portion of the cortex which is uniform enough in structure to be fairly represented by a single average set of measurements, including the thickness of the layers, the size of cells, and the frequency of cells, is called a single region. In making his examinations, Hammarberg followed the division of the cortex into gyri as given by Ecker[1]. The orbital surface of the frontal lobe, for

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[1] In writing this paper, Hammarberg's nomenclature for the gyri has been used.

instance, belongs partly to the first, partly to the second, and partly to the third frontal gyrus, and was examined in connection with these three divisions.   But the entire orbital surface shows such uniformity of structure that it requires but a single set of measurements, and is therefore treated in this paper as a single region. The first frontal gyrus, on the other hand, which in the customary division of the cortex is treated as one region, shows such variations in structure that it is necessary to break it up into four separate parts ; first the orbital surface which is included in the orbital region ; second the anterior third of the lateral surface together with the adjoining portion of the mesial surface, which form an entire region by themselves ; third the posterior two-thirds of the lateral surface which forms another single region ; and fourth the portion of the mesial surface bordering on the sulcus calloso-marginalis, which is included with the gyrus fornicatus in still another region.

Dividing the entire cortex after this fashion, on the basis of histological differences, sixteen structural regions have been distinguished, which have been numbered as follows :

Region 1.   The orbital surface of the frontal lobe.

Region 2.   The anterior third of the lateral surface of the first frontal gyrus plus the adjoining portion of the mesial surface.

Region 3.   The entire lateral surface of the second frontal gyrus.

Region 4.   The portion of the lateral surface of the third frontal gyrus anterior to the ascending branch of the Sylvian fissure.

Region 5.   The posterior two-thirds of the lateral surface of the first frontal gyrus.

Region 6.   The portion of the third frontal gyrus posterior to the ascending branch of the Sylvian fissure.

Region 7.   The anterior central gyrus plus the upper sixth of posterior central.

Region 8.   The lower five sixths of the posterior central gyrus.

Region 9.   The superior and inferior parietal gyri.

Region 10. The lateral surface of the occipital lobe.

Region 11. The mesial surface of the occipital lobe.

Region 12. The first temporal gyrus.

Region 13. All the temporal lobe except the first gyrus.

Region 14. The hippocampal gyrus (omitted).[1]

Region 15. The gyrus fornicatus and the portion of the first frontal gyrus bordering immediately upon it.

Region 16. The Island.
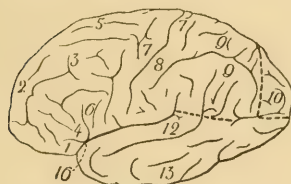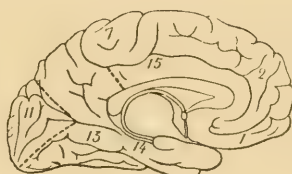
FIG. I.   FIG. II.

EXPLANATION OF FIGS. I AND II.

The accompanying Figures I and II show by the corresponding numerals the regions selected by Hammarberg and enumerated above. By the heavy broken lines the several lobes, frontal, parietal, occipital and temporal, are marked off from one another.

Figure I.—Lateral aspect.   *Figure II.*—Mesal aspect.

D. In all these regions, Hammarberg reduces the cortex to a six layer arrangement which he regards as typical. Any departure from this he represents either as fusion of two layers, or as subdivision of one or more layer or layers. Thus the cortex of region 5 appears to be a four layer cortex, because layers two and three are fused, and layer four is so much reduced that it is scarcely recognizable as a separate layer. Hammarberg's first four layers are identical with Meynert's first four as quoted by Quain.[2] But between Meynert's fourth layer, composed of small irregular shaped cells, and his fifth layer, made up of fusiform cells, Hammarberg finds a layer of pyramidal cells which he calls the ganglion cell layer. The last layer, his

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[1] The data for the hippocampal gyrus were very incomplete, and since the region contains so few cells at any rate, it has been omitted in making the calculations.

[2] Elements of Anatomy. Tenth Edition. Vol. III, Pt. 1, p. 167 ff.

sixth and Meynert's fifth, he calls the layer of spindle cells. His six layers are then as follows:

Layer   I. Nerve fibers with a few small scattered cells.
Layer   II. Small pyramidal cells.
Layer III. Large pyramidal cells.
Layer IV. Small, irregularly shaped cells.
Layer   V. Ganglion cells.
Layer VI. Spindle-shaped cells.

E.   If Hammarberg's records were complete in every detail, they should, then, contain the following data upon each of the sixteen regions into which the cortex is divided: first, the thickness of each of the six layers ; second, two diameters in micra for the average cells of each layer ; and third, the number of cells in each layer contained in a cube measuring 0.1 mm., on a side.   But not all of these data are given for every region. Sometimes the thickness of a layer is omitted ; sometimes the size of the cells is merely indicated by saying that they are larger or smaller than those of a corresponding layer in some adjacent region ; and in some cases the frequency is not given. All these omissions have been supplied as accurately as possible. Frequently the plates of sections accompanying the monograph furnished the required facts ; sometimes the numbers for closely similar regions were adopted ; and in some cases his expressions greater or less, and more or less frequent, were given a definite numerical value.   Wherever such additions to the original data were made, they are indicated in Tables VII and VIII by enclosing the estimated number in parentheses.

II.   Calculation of the Total Number of Functional Nerve Cells in the Cerebral Cortex of Man.

By these preliminary explanations, the ground has now been cleared for the calculations.   The next point to be considered is the method adopted for making use of Hammarberg's data in determining the total number of cells in the cortex.

A.   Hammarberg's record of the frequency of the nerve cells was, as has been stated, kept in terms of the number of

cells in a unit cube o. i mm. on a side.   Now the entire cortex
may be regarded as made up of square columns, whose cross
section is o. i mm. square, and whose height is, in each case,
equal to the thickness of the cortex in the region in which it
belongs.   Each of these unit columns may be considered as
made up of cubes o. i mm. on a side, piled upon one another.
All the columns for any one region must be regarded as ident-
ical in structure, since a single set of measurements serves for
them all.   Since the thickness of each layer is given, the num-
ber of unit cubes which belong in any given layer of a unit
column can be easily determined.   The number of cells in the
unit cube is given immediately.   A simple multiplication of
these two factors, the number of unit cubes in a layer by the
number of cells in the unit cube, gives the total number of cells
in any layer of the unit columns.   To take a concrete instance,
the third layer in region i is o. 5 mm. thick and the frequency of
the cells for the layer is i5. (Vide Table VII.) Since the layer
is o. 5 mm., thick, it must contain 5 of the unit cubes (o. i mm.)[3].
Each unit cube contains i5 cells, therefore the total num-
ber of cells for the third layer of the unit column is 5 × i5, or
75.   By going through with the same operation for each of the
other layers, and then summing the results, the total number
of cells in the unit column of region i is easily obtained.   The
number of cells in the unit columns of each of the fifteen re-
gions considered, was calculated in this way.

    B.   Beside the cells uniform in size included in the fre-
quency number for the layer, the third, fourth and fifth layers
in many places contain scattered large pyramidal cells.   In the
motor regions, these are larger than elsewhere in the cortex.
They appear in the fifth, or ganglion cell layer, and are the so-
called giant cells.   Hammarberg says nothing that would fur-
nish a basis for an estimate of the frequency of these extra
large cells.   The distribution of the giant cells was therefore
adopted as typical of these scattered large pyramidal cells wher-
ever they occur and the average distance between giant cells
determined by measurement of the laboratory sections of motor
cortex.   By this means, it was found that an allowance of io

large pyramids per square mm. of cortex constituted a fair average.[1]   Since there are 100 unit columns in a square mm., the average number of giant cells per unit column is one tenth.   In two of the motor regions, 5 and 6, the giant cells occur only in a small portion of the area bordering upon the anterior central gyrus.   Assuming that they occur in 4% of region 5, and 2% of region 6, the number of giant cells per unit column is reduced to .004 in the former case, and .002 in the latter.   (Vide Table I, regions 5 and 6, also Table VIII.)   In region 7, giant cells are found everywhere, according to Hammarberg, expect in the anterior portion of the gyrus opposite the third frontal gyrus. This statement agrees with the observations of Betz,[2] who states that the giant cells are much less numerous in the lower portion of the anterior central gyrus than elsewhere.   It may seem that considering the giant cells as present throughout all of region 7 is too large a distribution.   But allowing 10 to the square millimeter, is probably a small estimate for the places where the cells are most numerous.   These two factors, therefore, the extension of the area for giant cells and the small estimate of number for the regions where they are thickest, tend to balance one another.

By adding the number of large pyramidal cells per unit column to the former calculation, the final estimate for the total nnmber of cells in the various unit columns is obtained.

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[1] The estimate of 10 giant cells to the square millimeter is confirmed by Betz (Anatomischer Nachweis Zweier Gehirncentra, Centralbl. f. d. Med. Wiss. 1874, Bd. XII, p. 579), where he states that the groups of giant cells are placed from 0.3 to 0.7 mm. apart.   Kölliker (Handbuch der Gewebelehre des Menschen, 6th., Auflage. Bd. 2.   Nervensystem des Menschen und der Thiere. Leipzig, 1896, p. 650.) gives a cut of an enlarged section of motor cortex showing the distribution of the giant cells. Taking the thickness of the section into consideration, an enumeration of the giant cells in the section gives approximately the same result.

[2] l. c. p. 579.

TABLE I.*

Anterior association region		Motor region		Sensory regions		Posterior association region	
Regions	no. of cells per unit column	Regions	no. of cells per unit column	Regions	no. of cells per unit column	Regions	no. of cells per unit column
1	437	5	322.504	8	615.3	9	460.5
2	549.1	6	398.102	10	537	13	498
3	592	7	445.1	11	995.3	15	310
4	470.1			12	498	16	726

*Note.—The small fractions which appear in this table are due to the presence of scattered large pyramidal cells in the regions in which they occur. They might be disregarded without appreciable error, in calculating the number of cells in the cortex but they represent cells of such large size that it is necessary to retain them in calculating the volume of the cells for the various regions.

Table I gives the unit columns for each region, while the details of the process of computing them are recorded in Table VII.

C.   In order that the regions of the cortex which have similar functions might be placed together in the tables for purposes of comparison, Flechsig's[1] division of the cortex into sensory regions, motor regions, and association regions, was adopted.   All the motor regions are grouped together and all the sensory regions, while the two great association regions, anterior and posterior, are placed in separate columns.   Hammarberg's division into structural regions does not coincide in detail with the functional regions marked out by Flechsig.   Region 3, for instance, the lateral surface of the second frontal gyrus (as distinguished from the orbital surface) is, in Hammarberg's subdivision of the cortex, a single region.   According to Flechsig, a portion of the posterior part belongs to the motor region, while the remainder of it belongs to the anterior association region.   The same is true of structural region 4.   Wherever this occurs, the structural region has been placed in the functional region to which the greater part of it belongs.   The discrepancy

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[1] Flechsig: Gehirn und Seele. 2te. Ausgabe. Leipzig, 1896. Flechsig uses the term, association-center, but in English terminology, center has been used to indicate a much more limited cortical area to which a definite function can be assigned. We have, therefore, adopted the word region, instead of center.

in the two classifications is apparent rather than real. There are no hard and fast lines of division corresponding to Hammarberg's structural regions, but each region shades into the next. In region 3, for instance, the posterior portion, Hammarberg says, contains larger pyramids and fewer small irregular cells than the anterior. Where the gyrus passes over into the anterior central, there are even a few groups of giant cells. All of these changes of structure in the posterior part indicate that it would be as appropriate to class this part of the gyrus as motor, as Flechsig does, as to call it part of the association region.

Region 8, the lower five-sixths of the posterior central gyrus, is classed with the sensory regions, primarily because Flechsig considers it the sensory center for the skin senses, while he regards the anterior central gyrus as the motor center.[1] Moreover the anatomical difference reported by Hammarberg coincides with this view. He finds no giant cells in region 8 while the fourth layer is well marked and contains numerous cells. In both these respects the cortex of region 8 differs from the typical motor cortex and approaches the sensory type. Additional evidence for this difference in function between regions 7 and 8 is found in the fact that in Hammarberg's pathological cases, motor disturbances are uniformly correlated with abnormal structure of the cortex of region 7, but not uniformly with defects in region 8. Beevor and Horsely,[2] in their experiments on the motor cortex of the monkey, found that electrical stimulation of the cortex of the anterior central gyrus produced movements much more constantly than stimulation of the lower posterior central. All these lines of evidence point to the fact that the anterior central region is the motor center *par excellence*, and make it seem probable that the posterior central, par-

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[1] l. c. p. 62 ff.   Note 29.

[2] A Minute Analysis (experimental) of the Various Movements Produced by Stimulating, in the Monkey, different regions of the cortical center for the upper limb, as defined by Professor Ferrier, Phil. Trans. Roy. Soc., London, 1887, B.

ticularly the lower portion, is the center for some or all of the skin and muscle senses.   Region 8 has therefore been placed with the sensory centers.

A comparison of the number of cells in the unit columns of the three different functional regions, shows a certain uniformity among the unit columns for each region.   The motor regions have the smallest number of cells on an average, and the sensory the largest, while the association regions range between the two.   The two extreme exceptions to this generalization, regions 15 and 16, the gyrus fornicatus and the island, are distinctly modified portions of the cortex, which are not typical of the great association regions, and perhaps are not fairly to be classed with them.

D.   The plates accompanying the monograph furnish an opportunity for a confirmation of the calculations of the number of cells in the unit columns.   Sections from nine different regions are represented, enlarged 200 diameters. The thickness of each section is given as $20\,\mu$.   By counting the number of in an area 20 mm. wide (0.1 mm. of the original section) and as long as the entire thickness of the cortex, and multiplying this number by five (since the sections shown are $20\,\mu$ thick), the number of cells in the unit column can be found.   The numbers thus obtained by counting the cells in the lithographed plates, tally very closely with those calculated from the data given in the text.

E.   The data upon which the estimates for the unit columns are based, do not apply to the entire cortex of the regions which they represent.   They are in each case, the numbers for the unit columns in the *summits* of the gyri, and do not apply to the cortex covering the sides and bottom of the sulci.   Since the exposed portions of the cortex comprise in all only about one third of the entire area,[1] it is necessary to determine also the unit columns for the other two-thirds, the sunken portions. Hammarberg does not give exact figures for these, but he tells

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[1] Wagner, H.   Maasbestimmungen der Oberfläche des grossen Gehirns. Inaug. Diss. Göttingen, 1864.

in each case how much each layer is reduced in thickness in the sunken portions, and usually mentions whether or not the cells are at the same time increased in frequency. It is possible therefore to obtain for the sunken portions of each region a percentage of reduction of the number of cells which is approximately correct. These percentages are given in Table III.

F. The next step to be taken after determining the unit columns for each region is to find out now many of the unit columns there are in each region. To do this, it was necessary to know, first, the total area of the cortex, and, second, the proportion of the entire area to be assigned to each region. The figure adopted for the total cortical area was that obtained by Donaldson,[1] from a comparison of all the available material. It is 2,352 sq. cm. This total was then divided among the various lobes as follows :[2]

Frontal Lobe	41%.
Parietal Lobe	21%.
Temporal Lobe	27%.
Occipital Lobe	10%.
Island	1%.
Total,	100% = 2,352 sq. cm.

G. At this point it is possible to adopt either of two methods of procedure. The absolute area of each region might be found by portioning out each lobe among its various regions calculated directly ; or an average unit column for each lobe can be obtained—an average in which each region is represented according to its size,— and the total number of cells for each lobe computed by means of its unit column. The lat-

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[1] l.c. p. 202, ff.

[2] The division of the cortex into lobes is taken from Hermann Wagner (l.c. p. 36), with modification. Wagner gives the temporal lobe as 20% and the occipital as 17%. Formerly the ventral aspect of the posterior portion of the brain adjoining the occipital lobe was considered part of the occipital lobe, while now it is included in the temporal lobe. 7% of Wagner's occipital lobe was therefore transferred to the temporal lobe, making the temporal lobe 27% and the occipital lobe 10%.

ter method is the one adopted. Take the frontal lobe for an example. To each of its eight regions is assigned a value which represents its size relatively to the others, and which has been called the value of the region (vide Tables II and III). The unit column, or more accurately, 100 times the unit column (or the number of cells per square mm. of area), is multiplied by the value of its region, giving the weighted numbers of cells per column one square millimeter in section. The sum of the weighted numbers per (square millimeter) column of all of the regions composing the lobe is then divided by the sum of all their values, and this quotient is the average number of cells per (square millimeter) column for the frontal lobe. The calculation of the average number of cells per (square millimeter) column for each lobe is given in Table II.

TABLE II.

THE AVERAGE NUMBER OF CELLS PER SQUARE MILLIMETER IN THE CORTEX OF EACH LOBE.

Regions	no. of cells per sq. mm. cortex	value of region	weighted number of cells per sq. mm.	average no. of cells per sq. mm.	Regions	no. of cells per sq. mm. cortex	value of region	weighted no. of cells per sq. mm.	average no. of cells per sq. mm.
1	43700	6	262200	Frontal	8	61530	1	61530	Parietal
2	54910	15	825150		9	46050	4	184200	
3	59200	4	236800		Totals		5	245730	49146
4	47010	4	188040						Temporal
5	32250.4	6	193502		12	49800			
6	39810.2	2	79620		13	49800			
7	44510	8	356080		Totals				49800
15	31000	5	155000						Occipital
Totals		50	2296392	45927.8	10	53700	1	53700	
				Island	11	99530	1	99530	
16	72600			72600	Totals		2	153230	76615

But the averages in Table II apply to the exposed surfaces of the lobes only. To obtain the average for the sunken surfaces also, an average percentage reduction for each lobe is first found. The method employed in obtaining this average is the same as that described in the preceding paragraph. The percentage for each region is weighted by the value of the region and the sum of the weighted percentage divided by the sum of the values. The quotient is the percentage reduction for the entire lobe (Table III).

TABLE III.

The Percentage Reduction for each Lobe in the Number of Cells in Unit Column for the Sides and Bottom of the Sulci.

Regions	% reduction	value of region	weighted % reduction	average % reduction	Regions	% reduction	value of region	weighted % reduction	average % reduction
1	27	6	162	Frontal	8	30	1	30	Parietal
2	27	15	405		9	28	4	112	
3	27	4	108		Totals		5	142	28.4%
4	26	4	104						Temporal
5	30	6	180		12	40			
6	30	2	60		13	40			
7	30	8	240		Totals				40%
15	27	5	135						Occipital
Totals		50	1394	27.88%	10	30	1	30	
				Island	11	67!	1	67	
16							2	97	48.5%

The average number of cells per (square millimeter) column in the sunken portion of each lobe is then found by reducing the average number of cells in the exposed surface (Table II) by the the average percentage reduction for the lobe (Table III). The averages for the sunken surfaces appear only incidentally in Table IV.

H. Now that the area in square millimeters of the exposed and of the sunken surfaces of each lobe has been found, and also the average number of cells per square millimeter column in the exposed and in the sunken areas of each lobe, a multiplication of these two numbers gives the absolute number of cells for any particular exposed or sunken surface, and the sum of all these products gives the total number of cells in the entire cortex.

TABLE IV.

The Total Number of Functional Nerve Cells in the Cerebral Cortex.

Lobes		area of cortex in sq. mm.	no. of cells per sq. mm. of area	Total no. of cells in cortex
Frontal	exposed	32,144	45,927.8	1,476,303,203
	sunken	64,288	33,123	2,129,411,424
Parietal	exposed	16,464	49,146	809,139,744
	sunken	32,928	35,189	1,158,703,392
Temporal	exposed	21,168	49,800	1,054,166,400
	sunken	42,336	29,880	1,264,999,680
Occipital	exposed	7,840	76,615	600,661,600
	sunken	15,680	39,457	618,685,760
Island	exposed	2,352	72,600	170,755,200
Totals		235,200		9,282,826,403

Table IV, in which this calculation is recorded, shows that the total number of functional nerve cells in the cerebral cortex is 9,282,826,403.

I.   The chief sources of error in the preceeding calculation are two in number ; first, the additions to Hammarberg's data ; and, second, the more or less arbitrary proportion of the total area assigned to each lobe and to the regions within each lobe.   Reference to Tables VII and VIII, where additions are indicated by parentheses, will show that the greater part of them concern the first layer.   The thickness of this layer, where it is given, varies only from 0.1 to 0.3 mm.   In most places it is 0.2 mm.   Wherever the thickness of the layer is not mentioned, therefore, 0.2 mm. has been adopted.   The frequency of the cells in this layer is nowhere mentioned.   Hammarberg says merely that they are very few in number.   A uniform frequency of five per unit cube was assumed.   Now if this entire layer were omitted from the calculation, it would change the result only about 2.5%.   The absolute error involved in assuming values which may not be perfectly accurate, is of course much less than this.   The other additions to the tables are comparatively few in number, and cannot be very inaccurate, since they are based on the values for closely similar regions, or else are indicated by Hammarberg's verbal comments. It seems safe to say, therefore, that the final result cannot be materially affected by this source of error.

The case in which a mistake in the correct proportioning of the lobes would produce a maximum error is that of the occipital lobe.   The averages for the others differ so little, that making one or another of them too large or too small could not affect the final outcome appreciably.   The unit column for the temporal and parietal regions is in round numbers, 500, and that for the occipital region, 750 (Table II).   If the error lay in the direction of making the occipital lobe too small, our result would be a little less than it should be, and the discrepancy between this calculation and others previously published, would only be decreased.   But if the occipital lobe has been made too large the final estimate is somewhat too large.   The occipital

lobe is given 10% of the cortex.   If the entire lobe were reckoned as having a unit column of 300, instead of 700, the mistake would be only 5% of the total result.   The real mistake could not be as much as 2%, an error which would be insignificant in view of the magnitude of the total number.

An inspection of the cortex shows that the mistakes involved in assigning values to the regions within a lobe cannot be very large.   The importance of such mistakes would depend upon the amount of the discrepancy in the unit columns for the regions wrongly estimated.   In the frontal lobe the number of cells in the unit column varies from 310 to 592, in the parietal lobe 460 to 615, in the occipital lobe from 537 to 995 and in the temporal lobe does not vary at all (vide Table II).   Considering the small percentage of the cortex which each region represents, and the comparatively narrow limit of the possible variation in the size of the unit columns for any lobe, any single case of making a region somewhat too large or too small could have but little effect on the total result.   If the calculation does contain a number of small errors due to this source, there is every probability that they tend to balance one another in the final outcome, rather than to sum themselves in either direction. Neither of the chief sources of error, therefore, could cause a mistake which would invalidate or even change appreciably the final outcome.

III.   Calculation of the Percentage of the Total Volume of the Cerebral Cortex of Man Composed of Nerve Cell Bodies.

The next topic to be considered is the method employed for calculating the percentage of the total volume of the cortex made up of functional nerve cells.   Again the unit column, whose cross section is 0.1 mm. square on each side, and whose height is the thickness of the cortex, serves as a basis for calculation.   In general, the method was to find the sum of the volumes of all the cells in the unit column for each region, and then to calculate what proportion of the total volume of the column the cells

occupy. Since each region is made up of unit columns which are regarded as identical in structure, the percentage obtained for the unit column is also the percentage for the entire region[1] (Table V).

TABLE V.

THE AVERAGE PERCENTAGE OF VOLUME COMPOSED OF FUNCTIONAL NERVE CELL BODIES IN EACH REGION.

Anterior assoc. region		Motor region		Sensory region		Posterior assoc. region	
Regions	% of space filled by cells	Regions	% of space filled of cells	Regions	% of space filled by cells	Regions	% of space filled by cells
1	.9%	5	1.5%	8	1.2%	9	1.5%
2	1.2%	6	1.3%	10	1.7%	13	1.4%
3	1.7%	7	1.0%	11	1.3%	15	1.5%
4	.9%			12	1.2%	16	.7%*

* The explanation for the fact that the percentage for the Island (region **16**) is so small, while its number of cells per unit column is large, is that the cells, although numerous, are very small (see Table VIII).

After having found the average percentage for each region, the average percentage for each lobe was estimated by the method of averaging explained above (II, G). The average percentage of the volume of the entire cortex filled by nerve cell bodies was then determined by averaging the percentages for the separate lobes by the same method (Table VI).

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[1] In calculating the percentage of volume occupied by cells, no notice is taken of the reduction of thickness of the cortex in the sulci, because, although the absolute thickness of the cortex is lessened, the number of cells is also lessened. These two factors may not exactly balance one another. In some cases the cells are crowded closer together in the sulci. But there are no data for determining to what extent this is the case. If the greater frequency of the cells were a constant and marked feature of the reduction of thickness in the sulci, it would no doubt have been noted. As it is, Hammarberg occasionally mentions the fact that the cells are somewhat more frequent in the reduced layers. Whatever the error from this source may be, it affects only the last three layers, and is in all probability too slight to change the result more than a small fraction of a per cent.

TABLE VI.

THE AVERAGE PERCENTAGE OF THE TOTAL VOLUME OF THE CEREBRAL CORTEX
COMPOSED OF FUNCTIONAL NERVE CELL BODIES.

Lobe	% for lobe	value of lobe	weighted % for lobe	average % for cortex
Frontal	1.32%	41	54.12	
Parietal	1.48%	21	31.08	
Temporal	1.33%	27	35.91	
Occipital	1.53%	10	15.30	
Island	.69	1	.69	
Total		100	137.10	1.37%

B.   The only portion of this process which needs detailed explanation is the method of obtaining the sum of the volume of all the cells in each unit column.   Hammarberg gives two measurements for the typical cell of each layer, the long and the short diameter, in micra (Table VIII).   Since almost all the cells are pyramidal in shape, the volume of each cell was calculated according to the formula for the cone; one third of the area of the base multiplied by the altitude. The short diameter was of course taken as the diameter of the base of the cone, and the long diameter as its altitude.   The justification for the use of the formula for the cone is perhaps not evident at first sight. If the triangle which represents the projection of a cone is circumscribed about the drawing of a pyramidal cell, using the widest portion of the cell body as the base of the cone, it is at once evident that not all the triangle is filled.   The cell walls, instead of following a straight line from base to apex, sag in and leave part of the space unoccupied.   But on the other hand, the outline of the cell is not all contained within the projection of the cone.   The bottom of the cell is not flat like a cone, but it rounds down from its widest point.   Beside this there are a number of dendritic processes which are to be included with the cell body, but are not contained within the circumscribed cone of the drawing.   Moreover when the cell is thought of, not as projected in a drawing, but as it exists in space, it is evident that the basal outline of the cell would not be a perfect circle like that of the cone, but an irregular figure which would sag away from the circle at some points and pass

beyond it at others. Now the assumption which is made when the formula for the cone is adopted is, that if, when the cone is circumscribed about the cell, the outlying portions of the cell were packed into the spaces between the cell wall and the surface of the cone, the cone would be exactly filled. A study of a large number of cell outlines convinces us that this assumption is approximately correct. The formula for the cone may give a little too large a volume for some cells, and a little too small a volume for others, but it is certainly nearest to correct of any of the geometrical formulæ, and it is probable that its slight inaccuracies balance one another.

The cells of the sixth layer, a very thick layer in most parts of the cortex, are not pyramidal, but spindle-shaped. Conventionalized, they have the form of two cones of the same size set base to base. The volume of two cones of the same size is the same as the volume of a single cone with a base equal to and an altitude twice that of one of the small cones. Since the measurements taken for the spindle cells are the entire length of the cell, which is equal to twice the altitude of one of the component cones, and the breadth of the cell at its widest point, which is the diameter of the base of the component cones, the formula for the cone holds for these cells also.

C. Applying the formula for the cone, then, to the measurements for the average cell in each layer of each region gives the volume of an average cell for each layer.

The number of cells in each layer of each unit column has already been found in calculating the total number of cells in the cortex (Tables I and VII). To find the volume of all the cells in any layer of a given unit column, we multiply the volume of the single cell by the number of the cells in the layer. The sum of the volumes for each layer gives us the total volume of all the cell bodies in any unit column, expressed in cubic micra. Since we know the dimensions of each unit column in millimeters, it is a simple matter to calculate its volume in the cubic micra. The ratio of the total volume of cell bodies in a unit column to the entire volume of that column is the percentage sought for (Tables V and VIII). The way in which the per-

centages for the separate regions are averaged to obtain a percentage for the entire cortex, was explained in III, A. Table VI gives the final outcome of the calculation on volume, which is that only 1.37% of the total volume of the cortex is composed of functional nerve cell bodies.

IV. A CALCULATION OF THE TOTAL NUMBER OF GIANT CELLS IN THE CEREBRAL CORTEX OF MAN, AND A COMPARISON OF THE NUMBER OF GIANT CELLS WITH THE NUMBER OF PYRAMIDAL FIBERS PASSING TO THE SPINAL CORD.

A.   From the time the giant cells of the Rolandic region were described by Betz,[1] they have been regarded as distinctively motor cells, and it has been supposed that they gave rise to some at least of the fibers of the pyramidal tracts. We are now in a position to test the numerical relationship between giant cells and pyramidal fibers, and discover whether we can regard the giant cells as the origin of all the pyramidal fibers, or of only some of them.

The data used in the preceeding calculation furnish a basis for computing the total number of giant cells in the cortex. Only three regions contain giant cells, regions 5, 6 and 7. In each region the cells are given a frequency of 10 to the square mm. But they occur only in 4% of region 5, and in 2% of region 6. The total area of the frontal lobe was given as 96,-432 sq. mm. Region 5 comprises 12% of the entire lobe; region 6, 4%, and region 7, 16%. The cortical area in which giant cells appear, is therefore 462.8 sq. mm. in region 5; 77.1 sq. mm. in region 6, and 15,429.1 sq. mm. in region 7, giving a total cortical area of 15,969 sq. mm., in which giant cells are present. Since the distribution of the giant cells is 10 per square millimeter (II B) there are 159,690 giant cells in the entire cortex.

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[1] Loc. cit. p. 580.

B. The number of pyramidal fibers supplied to the arm, leg and trunk of *one side* of the body, was determined by Blocq and Ozanoff,[1] to be 79,111. The total number of pyramidal fibers for the limbs and trunk, would be twice this number, or 158,222. In addition to this, the pyramidal fibers supplied to the head and neck, for which no data are available, enter into the total number of pyramidal fibers in the body. According to these calculations, the number of giant cells, 159,690, is a little in excess of the number of pyramidal fibers for the limbs and trunk, 158,222. The excess, only 1500, is not sufficient to account for the number of pyramidal fibers which must be assumed for the head and neck.

Since most of the giant cells are located in the upper and mesial portion of the anterior central gyrus (vide II B), which is the center for the limb and trunk muscles, the correspondence in number between giant cells and pyramidal fibers going to the cord, leads to the conclusion that the giant cells give rise to the pyramidal fibers for the limbs and trunk, while the pyramidal fibers supplied to the head and neck have some other source, probably the large pyramidal cells in the fifth layer of the lower portion of the motor region—the centers for the head and neck movements.

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Tables VII and VIII are added to furnish the details of the calculations from Hammarberg's original numbers, the results of which appear in Tables I and V.

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[1] Du nombre comparatif pour Membres superieurs et inferieurs de l'homme des fibres nerveuses d'origine cerebrals destinée aux mouvements. Gaz. des Hôpit. 1892. Sept. 8.

TABLE VII.

CALCULATION OF THE UNIT COLUMN FOR EACH REGION.

REGION 1.

Layers	thickness of layer	cells in (0.1 mm.)³	cells in unit column
1	.2	(5)	10
2	(.2)	40	80
3	.5	15	75
4	.2	60	120
5	.1	12	12
6	.8	17.5	140
Tot.	2.0 mm.		437

REGION 2.

Layers	thickness of layer	cells in (0.1 mm.)³	l. p.*	cells in unit column
1	.25	(5)		12.5
2	.2	40		80
3	.65	13.5		87.75
4	.25	60	(.1)	150.1
5	.35	15		52.5
6	.95	17.5		166.25
Tot.	2.65 mm.			549.1

REGION 3.

Layers	thickness of layer	cells in (0.1 mm.)³	cells in unit column
1	.3	(5)	15
2	.2	60	120
3	1.3	(13)	169
4	.2	45	90
5	.4	12	48
6	1.0	15	150
Tot.	3.4 mm.		592

REGION 4.

Layers	thickness of layer	cells in (0.1 mm.)³	l. p.	cells in unit column
1	.1	(5)		5
2	.1	60		60
3	1.0	(13)	(.1)	130.1
4	.2	40		80
5	.5	(12)		60
6	.9	15		135
Tot.	2.8 mm.			470.1

REGION 5.

Layers	thickness of layer	(0.1 mm.)³	l. p.	cells in unit column
1	.25	(5)		12.5
2	{ †			
3	{ .8	10		80
4	(.3)	5		15
5	.7	15	(.004)	105.004
6	1.1	10		110.
Tot.	3.15 mm.			322.504

REGION 6

Layers	thickness of layer	(0.1 mm.)³	l. p.	cells in unit column
1	.1	(5)		5
2	{			
3	{ .8	15		120
4	(.3)	30		90
5	.4	(12)	(.102)	48.102
6	.9	15		135
Tot.	2.5 mm.			398.102

REGION 7.

Layers	thickness of layer	(0.1 mm.)³	l. p.	cells in unit column
1	.2	(5)		10
2	{			
3	{ 1.0	13.5		135
4	.3	25		75
5	.4	15	(.1)	60.1
6	1.1	15		165
Tot.	3.0 mm.			445.1

REGION 8.

Layers	thickness of layer	(0.1 mm.)³	l. p.	cells in unit column
1	.2	(5)		10
2	{			
3	{ 1.2‡	20	(.2)	240.2
4	.3	60		180
5	.3	(15)	(.1)	45.1
6	.7	20		140
Tot.	2.7 mm.			615.3

REGION 9.

Layers	thickness of layer	cells in (0.1 mm.)³	cells in unit column
1	(.2)	(5)	10
2	.2	35	70
3	.7	15	105
4	.3	(50)	150
5	.65	7	45.5
6	.4	(20)	80
Tot.	2.45 mm.		460.5

REGION 10.

Layers	thickness of layer	cells in (0.1 mm.)³	cells in unit column
1	.1	(5)	5
2	{		
3	{ .6	10	60
4	{		
5	{ .6	(62)	372
6	.5	20	100
Tot.	1.8 mm.		537

REGION 11.

Layers	thickness of layer	cells in (0.1 mm.)³	l. p.	cells in unit column
1	(.2)	(5)		10
2	{			
3	{ .7	40	(.1)	280.1
4	.5	90	(.1)	450.1
5	.5	35	(.1)	175.1
6	.5	15		75
Tot.	2.4 mm.			995.3

REGION 12.

Layers	thickness of layer	cells in (0.1 mm.)³	cells in unit column
1	.2	(5)	10
2	{		
3	{ .7	20	140
4	.2	45	90
5	.4	(12)	48
6	1.2	17.5	210
Tot.	2.7 mm.		498

REGION 13.

Layers	thickness of layer	cells in (0.1 mm.)³	cells in unit column
1	.2	(5)	10
2	{		
3	{ .7	20	140
4	.2	45	90
5	.4	(12)	48
6	1.2	17.5	210
Tot.	2.7 mm.		498

REGION 15.

Layers	thickness of layer	cells in (0.1 mm.)³	cells in unit column
1	(.2)	(5)	10
2	.5	(40)	200
3	{		
4	{ not	present	
5	{ .5	12	60
6	.2 (.7)?	(20)	40
Tot.	1.9 mm.		310

REGION 16.

Layers	thickness of layer	cells in (0.1 mm.)³	cells in unit column
1	(.2)	(5)	10
2	{		
3	{ .7	30	210
4	.18	(40)	72
5	.4	35	140
6	1.05	28	294
Tot.	2.53 mm.		726

*l.p.—Large pyramids.

†Wherever two layers are joined by a bracket, it indicates that the two are not distinguishable as separate layers, but are fused and are represented by a single set of measurements.

‡ Layers 2 and 3 of region 8 are given by Hammarberg as measuring together only 0.2 mm. This number is so unprecedently small for these layers and adopting it reduces the thickness of the cortex in region 8 so much below all the other determinations for the thickness of the parietal cortex, that it has been assumed that 0.2 mm. is a misprint and 1.2 mm. was substituted for it.

⸮ The layer measures 0.7 mm. but only 0.2 mm. of it contains cells.

TABLE VIII.

THE TWO DIAMETERS OF THE AVERAGE CELLS AND THE PERCENTAGE OF THE SPACE OCCUPIED BY THE CELL-BODIES.

REGION 1.

Lay-ers	dimensions of cells in μ	no. of cells	thickness of cortex	% of space filled by cells
1	8×10	10		
2	5×8	80		
3	10×25	75		
4	5×8	120		
5	21×30	12		
6	9×27.5	140	2.0 mm.	.9236%

REGION 5.

Lay-ers	dimensions of cells in μ	no. of cells	thicknesss of cortex	% of space filled by cells
1	8×10	12.5		
2 {	a 11×17.5	40		
3 {	b 17.5×25	40		
4	10×20	15		
5	20×27.5	105		
l.p.	30×65	.004		
6	9×27.5	110	3.15 mm.	1.5306%

REGION 2.

Lay-ers	dimensions of cells in μ	no. of cells	thickness of cortex	% of space filled by cells
1	8×10	12.5		
2	8×10	80		
3	15×22.5	87.75		
4	5×8	150		
l.p.	20×30	.1		
5	21×30	52.5		
6	9×27.5	166.25	2.65 mm.	1.2214%

REGION 6.

Lay-ers	dimensions of cells in μ	no. of cells	thickness of cortex	% of space filled by cells
1	(8×10)	5		
2 {	a 11×17.5	60		
3 {	b 22×30	60		
4	3.5×10	90		
5	12×25	48		
l.p.	30×50	.002		
l.p.	20×30	.1		
6	6×20	135	2.5 mm.	1.3496%

REGION 3.

Lay-ers	dimensions of cells in μ	no. of cells	thickness of cortex	% of space filled by cells
1	8×10	15		
2	8×10	120		
3a	12×20	84.5		
3b	20×30	84.5		
4	3×12.5	90		
5	20×30	48		
6	9×27.5	150	3.4 mm.	1.7412%

REGION 7.

Lay-ers	dimensions of cells in μ	no. of cells	thickness of cortex	% of spaee filled by cells
1	8×10	10		
2 {	a 11×20	75		
3 {	b 17.5×30	60		
4	6×9	75		
5	12.5×25	60		
l.p.	38×65	.1		
6	7.5×22.5	165	3.0 mm.	1.0341%

REGION 4.

Lay-ers	dimensions of cells in μ	no. of cells	thickness of cortex	% of space filled by cells
1	8×10	5		
2	8×10	60		
3	12×20	130		
l.p.	25×30	.1		
4	6×10	80		
5	16.5×27.5	60		
6	6×20	135	2.8 mm.	.9288%

REGION 8.

Lay-ers	dimensions of cells in μ	no. of cells	thickness of cortex	% of space filled by cells
1	(8×10)	10		
2 {				
3 {	(10×20)	240		
l.p.	20×30	.2		
4	6×10	180		
5	19×25	45		
l.p.	21×30	.1		
6	9×25	140	2.7 mm.	1.2068%

REGION 9.

Layers	dimensions of cells in μ	no. of cells	thickness of cortex	% of space filled by cells
I	(8×10)	10		
2	2× 7	70		
3	16×25	105		
4	7.5× 9	150		
5	20×30	45.5		
6	9×20	80	2.45 mm.	1.5421%

REGION 13.*

Layers	dimensions of cells in μ	no. of cells	thickness of cortex	% of space filled by cells
I	(8×10)	10		
2 ∫ a	(10×17)	87.5		
3 ∖ b	(13×24)	52.5		
4	(8×12)	90		
5a	(11×20)	24		
5b	(22×35)	24		
6	(9×30)	210	2.7 mm.	1.3688%

REGION 10.

Layers	dimensions of cells in μ	no. of cells	thickness of cortex	% of space filled by nerve cells
I	(8×10)	5		
2 ∫ a	12×25	30		
3 ∖ b	22.5×30	30		
4				
5	(9×15)	372		
6	9×20	100	1.8 mm.	1.7174%

REGION 15.

Layers	dimensions of cells in μ	no. of cells	thickness of cortex	% of space filled by cells
I	.(8×10)	10		
2	(8×10)	200		
3 ∫				
4 ∖ not present				
5	20×30	60		
6	12×35	40	1.9 mm.	1.455%

REGION 11.

Layers	dimensions of cells in μ	no. of cells	thickness of cortex	% of space filled by cells
I	(8×10)	10		
2 ∫				
3 ∖	10×14	280		
l.p.	20×30	.1		
4	6× 8.5	450		
l.p.	23.5×30	.1		
5	12.5×20	175		
l.p.	21×30	.1		
6	8×20	75	2.4 mm.	1.3323%

REGION 16.

Layers	dimensions of cells in μ	no of cells	thickness of cortex	% of space filled by cells
I	(8×10)	10		
2 ∫				
3 ∖	9×12.5	210		
4	(6×10)	72		
5	10×15	140		
6	6×20	294	2.53 mm.	.69%

REGION 12.

Layers	dimensions of cells in μ	no. of cells	thickness of cortex	% of space filled by cells
I	(8×10)	10		
2 ∫ a	9×15	87.5		
3 ∖ b	12×22	52.5		
4	8×12	90		
5a	10×18	24		
5b	20×30	24		
6	9×30	210	2.7 mm.	1.1534%

* Although Hammarberg gives no exact numbers for the size of the cells in region 13, he makes the general statement that they are the same as for region 12, except in layers 3 and 5, where they are a little larger.

Note to Tables VII and VIII.

Kölliker (l. c., p. 674 ff.) gives a summary of Hammarberg's results in the form of a table which contains a complete record of the thickness of the layers in each region and a partial record of the size of the cells, but gives none of the numbers for frequency. A comparison of Tables VII and VIII with Kölliker's

summary will show a few minor discrepancies between them in the numbers given for the thickness of some layers, and the size of some cells. In defense of the data which appear in these tables, it is only fair to state that where discrepancies occur, they are due to errors in Kölliker's transcription of Hammarberg's numbers. The list of these misprints is as follows:

	Kölliker.	Hammarberg.
Thickness of layers.		
Region 1, layer 4	0.7	0.2
Region 1, layer 6	0.89	0.8
Region 3, layer 4	0.3	0.2
Size of cells.		
Region 7, layer 4,	6-8×10	6×8-10
Region 15, layer 6,	12-30×40	12×30-40

In region 5 layer 3, Kölliker assumes a thickness of 0.1 where Hammarberg does not give the number and Table VII assumes 0.3 as the thickness.

A NOTE ON THE SIGNIFICANCE OF THE SMALL VOLUME OF THE NERVE CELL BODIES IN THE CEREBRAL CORTEX IN MAN.

By Henry H. Donaldson.

Summary.

(1)   The weight of all the nerve cell bodies in the human encephalon is less than 27 grams.

(2) When comparison is made of human encephala grouped according to race, sex, mental power, stature and age, the differences in weight, within each group, are always more than twice that of the nerve cell bodies, and hence these differences depend mainly on variations in the medullary substance.

(3)   Small variations in the mass of the nerve cell bodies (though physiologically highly important) escape detection by the method of weighing, or may be masked by the greater growth of the medullary substance.

The observations of Hammarberg[1] have been utilized by Miss Thompson[2] to show that there are about 9,200,000,000 (nine-thousand two hundred million) nerve cell bodies in the human cerebral cortex, and that they occupy but 1.37% of the volume of the cortex.   Concerning the essential correctness of this unexpected result, there can be no doubt.   It will be urged

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[1] Studien über Klinik und Pathologie der Idiotie nebst Untersuchungen über die Normale Anatomie der Hirnrinde.   Karl Hammarberg, Upsala, 1895.

[2] The total number of functional nerve cells in the cerebral cortex of man and of the percentage of the total volume of the cortex composed of nerve cell bodies calculated from Karl Hammarberg's data ; together with a comparison of the number of giant cells with the number of pyramidal fibers. (Journ. of Comp. Neurol. Vol. IX, No. 2, 1899, pp. 113-140.)

however, that Hammarberg's method of staining the cells (alcohol hardening, followed by methylene blue) did not bring out the dendritic processes, and hence that the volume of the cells determined from his preparations is too small. This is perfectly true, and it is therefore desirable to determine how much of the cell substance has been thus overlooked. In making the correction for the dendrons which were not stained by the methylene blue, some caution must be exercised. To obtain a complete picture of the dendritic branches, we usually refer to a successful Golgi preparation. It must be remembered, however, that the diameters of the dendrons are increased in such preparations beyond their normal size, owing to the incrustation of the silver chromate deposit, and for this reason the true volume of the dendrons is not nearly so great as the silver chromate picture would suggest. From a preliminary survey, I conclude that 2 % will represent the proportional volume of the cortical cell bodies, *including all the dendrons.*[1]

At the moment, an exact statement concerning the volume of the cell bodies in the remaining portions of the encephalon cannot be made. In this remaining portion, including as it does all the white substance beneath the cortex, the proportional volume of the cell bodies[2] is probably much less than the volume of those in the cortex itself. It thus appears that the small volume of the cell bodies is a feature of the entire encephalon.[3]

The volume of the 9,200,000,000 cortical cell bodies being very small, it can be readily shown that their weight is also very small.[4]

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[1] I further assume that this estimate of 2% is large enough to include also the terminals of the axones which end about the dendrons.

[2] By this is meant the cell bodies in the striata, thalami, quadrigemina, cerebellum, pons and central gray substance.

[3] The estimate that the cell bodies of the *entire encephalon* have a volume of 2%, probably errs on the side of excess.

[4] In translating the proportional volume of the nerve cell bodies into proportional weight, no correction is made for the fact that the specific gravity of the cell bodies is slightly less than that of the cortex of which they form a part.

The average male encephalon weighs some 1360 grams.[1] and the cortex in such a case, by estimation, weighs about 658 grams, a little less than half the total weight of the encephalon.[2] At 2%, the cell bodies found in the cortex would weigh 13 grams (exactly 13.16 grams), or a trifle less than 1% of the total weight of the encephalon.

Concerning this small mass of tissue representing the cell bodies of the cortex, several broad statements are justified.

In the paper by Hammarberg to which we have already referred that author reports upon a number of abnormal brains from persons more or less defective in intelligence.

His observations, together with other data from pathology, make it probable that, in the cases examined by him, the defective intelligence depended upon the defective development of the cortical nerve cells. Moreover, Hammarberg shows that a comparatively small deviation from the normal development of these cell bodies was sufficient to reduce the intelligence to moderate imbecility, such that the patient required that care and protection of an asylum.

Finally, we infer from these observations, and from the fact that the dendritic branches of the cortical cells become more numerous as we ascend in the vertebrate series, that the principal means of increasing the *physiologial complexity* of the cortex is represented by the dendrons of the cortical cells, together with the associated terminals surrounding them. As those portions appear to furnish the structural basis necessary to the exhibition of intelligence, variations in their number and

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[1] The Growth of the Brain : by Henry H. Donaldson. Walter Scott, London. Charles Scribner's Sons, New York. 1895. (Volume XXIV, in The Contemporary Science Series), p. 97, Table 13. Averages for males, 20-40 yrs. ; Stature, 167-172 cm. Unless otherwise specified, the subsequent references are all from the book above named. There the original papers are cited.

[2] Page 204, Table 49, Case 2. Cortex given as weighing 55.3% of the weight of the hemispheres. The average weight of the hemispheres is 87.5% of the encephalon. Vide p. 99, Table 14, Males. 20-40 yrs. 87.5% of 1360 (weight of encephalon) gives 1190 grms., as the weight of the hemispheres and 55.3% of this is the weight of the cortex, equal to 658.07 grms.

extent may be fairly correlated with the variations in mental power.

If this value be given to the cell bodies of the cortex, including their dendrons, it is necessary also to find an interpretation for the other portions of the neurones which these bodies represent. For this purpose, the neurone may be resolved into three portions. First, the receiving portion ; second, the conducting; third, the transmitting. These correspond first to the cell body and its dendrons; second, to the axone; and third, to the ends of the branches or the terminals.

By means of the first portion, the neurone is rendered responsive to nerve impulses brought into its neighborhood. By means of the second, inpulses arising in the cell body are conducted to the ends of the axone, and by means of the third, the terminals, these impulses stimulate other neurones.

It is therefore on the dendrons and the terminals, i.e., the receiving and transmitting portions of the neurone, that the complexity of the encephalon is dependent. The axone, acting merely to conduct, may vary widely both in length and circumference (and hence in mass), without modifying in any way the complexity ef the parts which it connects. Hammarberg's observations demonstrate that there is a decided mental deficiency in those cases where the receiving portions[1] of the cortical neurones fail to develop fully. Even when the fully developed cortex is compared with the poorly developed, the difference between the two masses of the cell bodies is comparatively small, for we have seen that the total weight of these cell bodies when normal is only 13 grms. Thus the change in the mass of these elements corresponding to a moderate degree of mental deficiency (say 20 % = 2.6 grm.), would be easily within the limits of error for the brain weight as ordinarily taken.

Furthermore, if differences of the same sort underlie the grades of intelligence exhibited by normal individuals, these dif-

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[1] Probaly there was in these cases corresponding deficiency in the developments of the terminals but on this point his preparations do not give any information.

ferences are probably even less than those occurring between normal and imbecile persons, and would therefore be still more difficult of detection by the method of weighing.

In Table I, have been given the difference in brain weight as determined for race, sex, mental power, stature and age, and we wish now to show how far these differences in weight can be attributed to the several portions of the neurone as enumerated above.

TABLE I.

DIFFERENCES IN THE WEIGHT OF THE ENCEPHALON AMONG DIFFERENT GROUPS OF PERSONS. ALL THE RECORDS ARE AVERAGES GIVEN IN GRAMS.

Grouped according to	Average Weight of Encephalon		Difference	Average Weight of Encephalon	
[1] Race	European Males	1340	150	1190	Australian. Males
[2] Sex	Males	1360	142	1218	Females.
[3] Mental Power	Eminent Men	1494	134	1360	Average Males.
[4] Stature	Males, 173 cm. and above,	1409	78	1331	Males 164 cm. and under.
[5] Age (after maturity)	Males, prime of life. 20-40 yrs.	1360	55	1305	Males (Aged) 41-70 yrs.

[1] p. 115. Table 22. Averages for males—European and Australian.

[2] p. 97. Table 13. Males and females—intermediate stature—age, 20-40 yrs.

[3] p. 128. Table 26. The average of all the brain weights for eminent men between 39-71 yrs., inclusive, equals 1494.

p. 97. Table 13. Males, stature 172-167 cm., and age 20-40 yrs., give the standard for the average male.

[4] p. 97. Table 13. Males. The average for the tallest compared with that for the shortest, both groups 20-40 yrs. of age.

[5] p. 97. Table 13. Intermediate stature group. The average of those 20-40 yrs. of age (prime of life) compared with those 71-90 yrs. (aged).

It is seen that even the smallest difference recorded, namely that between the prime of life and old age, exceeds not only the weight of the nerve cell bodies in the cortex, but in the en-

tire encephalon[1] (27.2 grms.) We assume however, as the records in the Table are from persons having at least normal intelligence, that moderate variations in the number of dendritic branches belonging to the cortical cells and in the associated terminals represent the greatest differences to be expected. We therefore conclude that the largest part of the difference in weight, as exhibited in the Table, is to be referred to the axones, with their medullary sheaths; at the same time recognizing that variations in the mass of the axone are of no value in increasing the complexity of the central system.

Thus far in this argument, it has been tacitly assumed that the encephala compared contained the same number of cortical neurones distributed in the same way. Yet no one would care to maintain the absolute correctness of such an assumption. Probably the fact to which the assumption most nearly corresponds is a comparatively slight variation in the number and distribution of the cortical neurones in the majority of the encephala from ordinary persons. In order to determine the value of the explanation given above, the analysis of the gross results may be carried one step further.

Speaking in a general way, the cortical neurone grows in such a manner that there is a relation between the mass of the cell body (including its dendrons), the axone, and the terminals, and, within certain limits, these mass relations can be inferred one from the other. Nevertheless, the facts warrant us in assuming a rather wide normal variability in the mass of the axone, and, as a consequence, there must follow variations in the mass of the entire encephalon that are very considerable, because the axones form a very large part of it.[2]

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[1] Taking the weight of the average male encephalon as 1360 grms., 2% of it would be 27.2 grms.

[2] If the mass of the nerve cell bodies be taken as 2% of the encephalon, one is at first tempted for the sake of brevity, to speak of the remaining 98% as composed of the axones. This remainder, however, is composed of the blood-vessels and sustentacular tissues as well as the axones, and we have not yet any observations which enable us to give an exact value to these non-nervous constituents. Hence it can only be said that the mass of the axones is very large, forming as it does, the greater part of this 98%.

Accepting this conclusion, the differences in question can be explained in one of three ways. In the larger brain of any group, there is either a greater number of complete neurones, or, second, a more generous development of the axones alone, or, third, a possible combination of both of these conditions.

In making a choice between these several explanations thus suggested, a guide may be found in the observation that, within a rather wide range of absolute weight, there is a remarkable constancy in the proportional weights of the several subdivisions (cerebrum, cerebellum and stem) of the encephalon.[1]

The conditions which cause differences in total weight must therefore act harmoniously among the several subdivisions of the encephalon. It has already been pointed out that the cortex was calculated to weigh 658 grms. in the case of an average male brain. This is somewhat less than one half of the total weight of the encephalon (1360 grms.) If then, the variations in the total weight of the encephalon tend to be harmoniously distributed, only about one half of the difference in the total weight can in any case be attributed to variations in the cortex.

If then, it is granted that slight variations among the dendrons and terminals of the cortex may determine wide physiological differences as indicated by mental power, and further, that the axones may vary widely in their mass, independent of the rest of the neurone, we are left with a strong presumption in favor of explaining the weight differences tabulated above as due mainly to differences in the axones, and therefore as practically insignificant for the *physiological complexity* of the cortex in particular ; and the encephalon in general.

Two special cases still remain to be mentioned. After the age of six years, the encephalon often shows as great a weight as in the prime of life.[2]

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[1] P. 99, Table 14 ; p. 100, Table 15.

[2] P. 104, Table 17.

P. 105, Figure 17.

Intellectually, however, a child of this earlier age, is **very** immature, yet our general theory demands that the growth in intelligence should be accompanied by an increase in cortical complexity, which, if other things were equal, would mean an increase in mass.

In this case, the correlation has not been statistically demonstrated, though in consideration of the small number of records, this is not even presumptive evidence that such a correlation does not exist, and it is here intended to point out merely the reason why the demonstration is difficult.

The psychological changes between the sixth year and maturity are most naturally assumed to depend on changes in the cerebral cortex. But the entire mass of these cell bodies is probably less than 13 grms., and the normal growth of these must be completed by a weight of substance which is but a small fraction of this initial mass ; hence such changes in the cortex must be very small so far as the mass of material involved in enlarging the cell bodies is concerned. There is without doubt an enlargement of axones during this period, as the studies of Kaes[1] and Vulpus[2] on progressive medullation show, but even this is not great enough to counterbalance the other causes of variation ; and for these reasons, the enlargement has escaped demonstration by the method of weighing.

A similar explanation is offered for our failure to find the left hemi-cerebrum heavier than the right, although it is agreed that the left is physiologically the more important, and hence should be structurally more complex, and by inference, heavier.[2]

In this last instance, the independent increase of the axones might mask, on the right side, any deficiency in the mass

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[1] and [2]. P. 241.

[2] The weight relations of the two hemicerebrums are given on pp. 184 and 185. Tables 43 and 44.

of the dendrons, and thus the gross weight differences between the two sides, tend to be obliterated.[1]

This explanation of the last two instances was put forward by me in 1895,[2] and the correctness of it appears to be the more assured as these newer facts lead to a similar conclusion. It is evident, therefore, that where there are differences in encephalic weight determined by the balances, those differences must be further analyzed before they are interpreted, and the absence of a difference as determined by the balances is not evidence that the two parts compared (hemi-cerebrums, for instance) are alike in their complexity.

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[1] Attention is hereby called to the phenomena of variability in the size of axones such as occurs in the encephalon after a part has been removed, the surrounding portions tending to encroach on the cavity by an increase in the mass of the white substance. Also to the change in the diameter of the optic nerve on passing into the sclerotic or the peripheral nerves wherever they are surrounded by a collar of connective tissues and thus contracted. These changes in mass are not correlated with changes in the cell bodies, or with changes in functional activity.

[2] P. 276.

EDITORIAL.

Clearness and Uniformity in Neurological Descriptions.

In the review of Haller's work on the fish-brain in another column of this number Professor Edinger, of the editorial staff of this Journal, makes a number of suggestions which we deem of great practical importance and which we commend to the careful consideration of our readers. The writer takes the more pleasure in calling attention to these incisive criticisms of neurological writings because he himself has fallen under the lash of the same criticism in a recent work of Dr. Edinger. This criticism he thought not wholly deserved, yet, as a sinner in these directions, he may appropriately exhort fellow-sinners to mend their ways.

Every one who has undertaken the study of the brains of any type knows how impossible it is to secure any adequate idea of what has been done by his predecessors in that direction. It is true that American writers usually attempt to go over the literature of German, French and English neurology before publishing, while very few of the German authors betray a knowledge of anything that has been done on this side of the Atlantic. But, as well said by Professor Edinger, to most of us the writings of v. Gudden and much of Meynert's work remain a sealed book. This is due in part to unnecessary involution of descriptions, but chiefly to the use of an unexplained terminology and the lack of detailed figures. The writer gladly seconds the recommendation that all figures be supplied with adequate reference letters fully explained in an accessible part of the paper or, better still, that all plates have full data printed on the plate. It is certainly desirable that there should be as many synthetic diagrams as possible, but we should prefer that there should also be given full illustrations of the actual prepar-

ations used. We confess that we are often in doubt in the case of Edinger's masterly drawings as to how much is interpretation.

It is well that the writer should give his own determinations, but in the unraveling of tortuous tracts which anastomose in the most complicated manner he arrogates a great deal to his own powers who denies that he may have arrived at erroneous conclusions and it is due the student that he should have the opportunity to draw his own deductions. In fact, it often happens that drawings made with the greatest possible faithfulness to nature will supply the subsequent observer with the means of interpreting his own results in the light of his author and thus even errors become of use. It is doubtless true that a writer who has been spending many months in the closest study of an intricate problem finds it impossible to realize how obscure many points, which for him have dropped into the background of assumed fact, will seem to the reader. The present writer remembers the surprise with which he read in Edinger's recent work on the thalamus of reptiles that "the mammillare has perhaps not escaped the notice of Herrick." Is it possible that this and so many other familiar parts recognized by the writer years ago cannot be identified in his writings and must reappear (often under new names) as new discoveries in a work of so carefal a writer as our colleague! This will no doubt prove the source of chagrin to many a student who, in the ardor of his pursuit of the yet unsolved, neglects or postpones the duty of making a complete résumé of his own work and such an analysis as will prevent the ambiguity referred to. For most of us I fancy the labor of composition and revision is so great and seems so unprofitable, so long as there remain sections to study and new facts to garner in, that the necessity for the kind of consideration of the reader for which Professor Edinger pleads does not appear till too late.

In the matter of nomenclature it is plain that everything must be sacrificed to intelligibility. The introduction of new terms does not necessarily introduce obscurity. Professor Edinger has introduced more new terms than any other writer of our acquaintance but they are of a character to explain themselves or

are defined.   Where the two known termini of a tract appear in the name it does not suffer from the reproach of ambiguity. The strongest argument in favor of the reform terminology, or "Wilder nomenclature," as it is sometimes erroneously called, is the fact that every one can determine the meaning of its names.   This cannot be said of the peculiar mixture which is seen in the writings of English and continental authors, upon whom the report of the German Nomenclature Commission seems to have produced no appreciable effect.

One other suggestion and we have done.   No writer who cares for his future peace of mind should permit a technical article to appear without the benefit of his personal revision upon the proof.   In no instance of the writer's experience has this simple precaution been omitted when the results have not proved disasterous, often to the extent that the paper would gladly be relegated to forgetfulness.

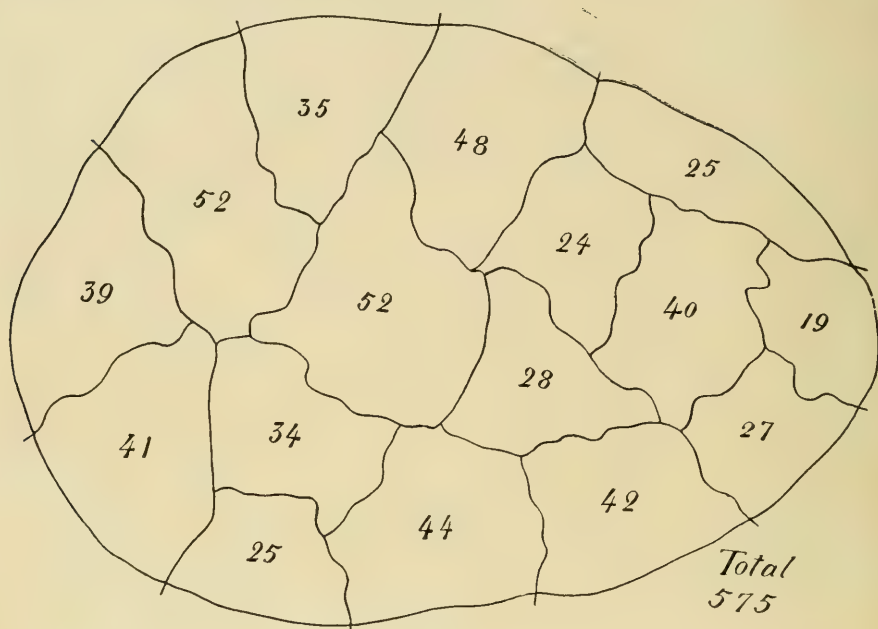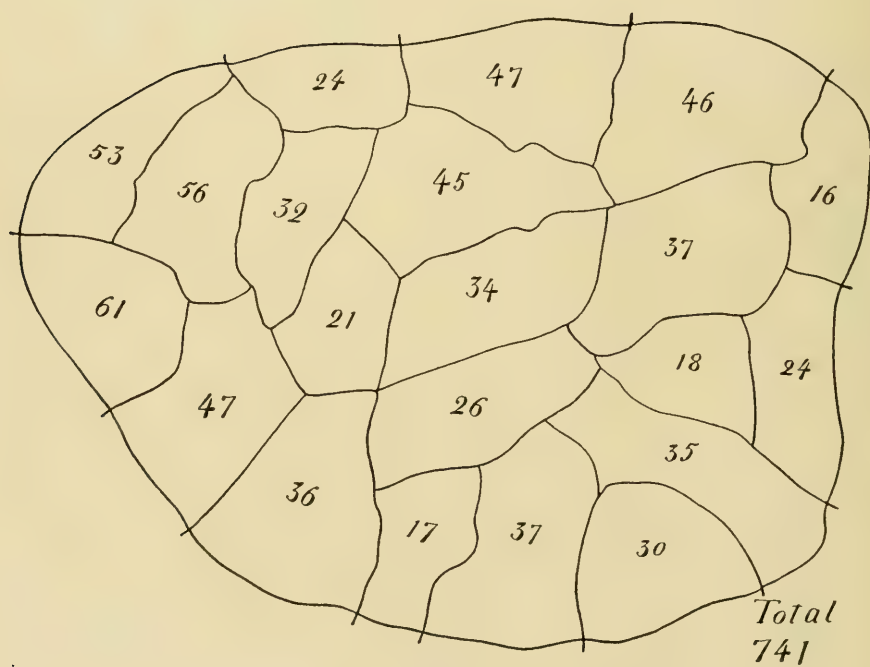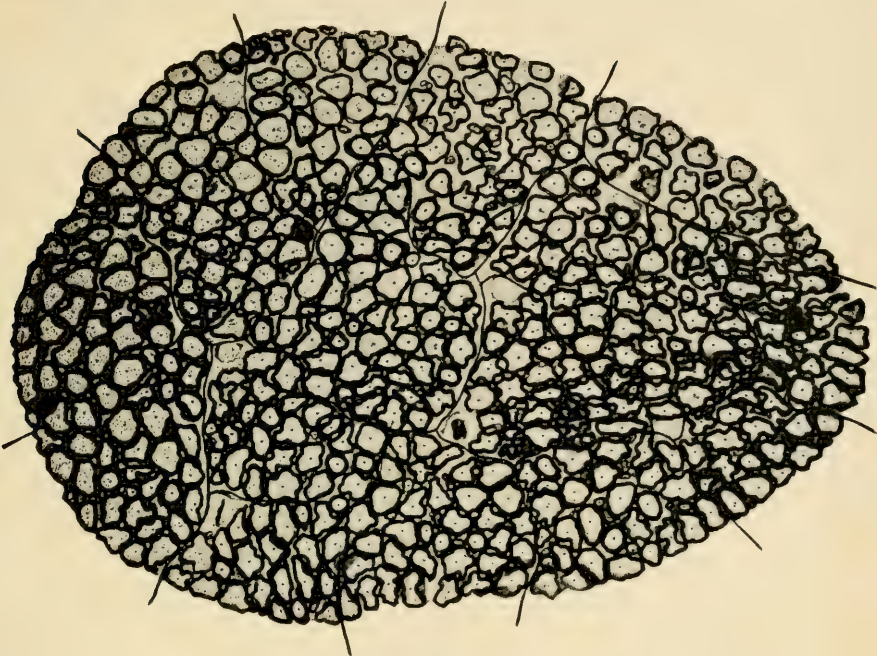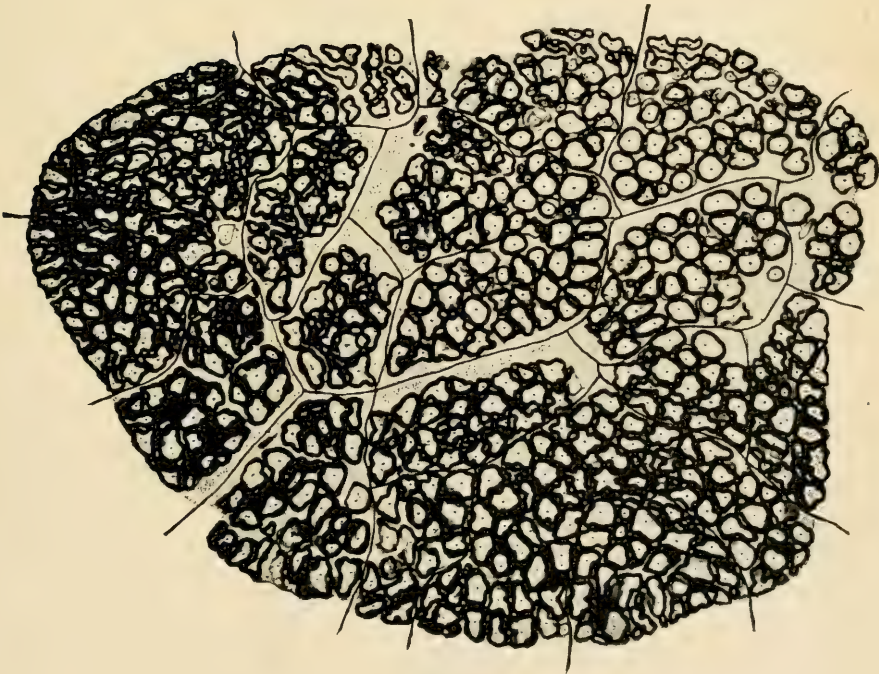<div style="text-align: right">C. L. HERRICK.</div>

PLATE IV.

PLATE VI.
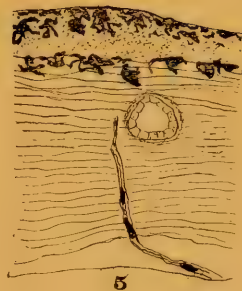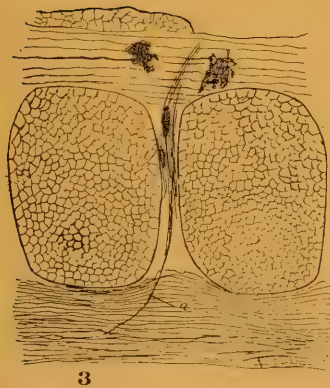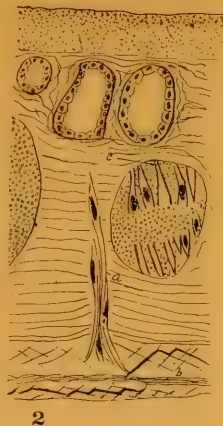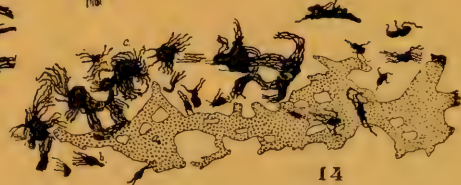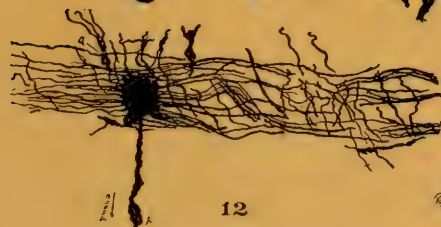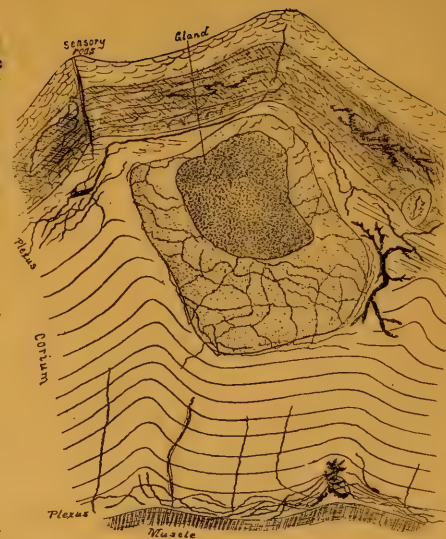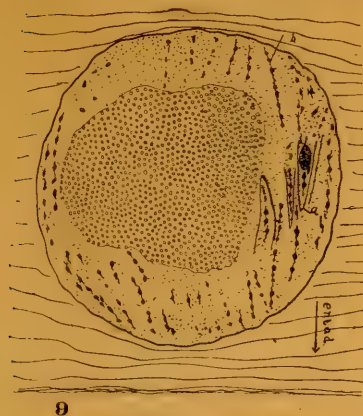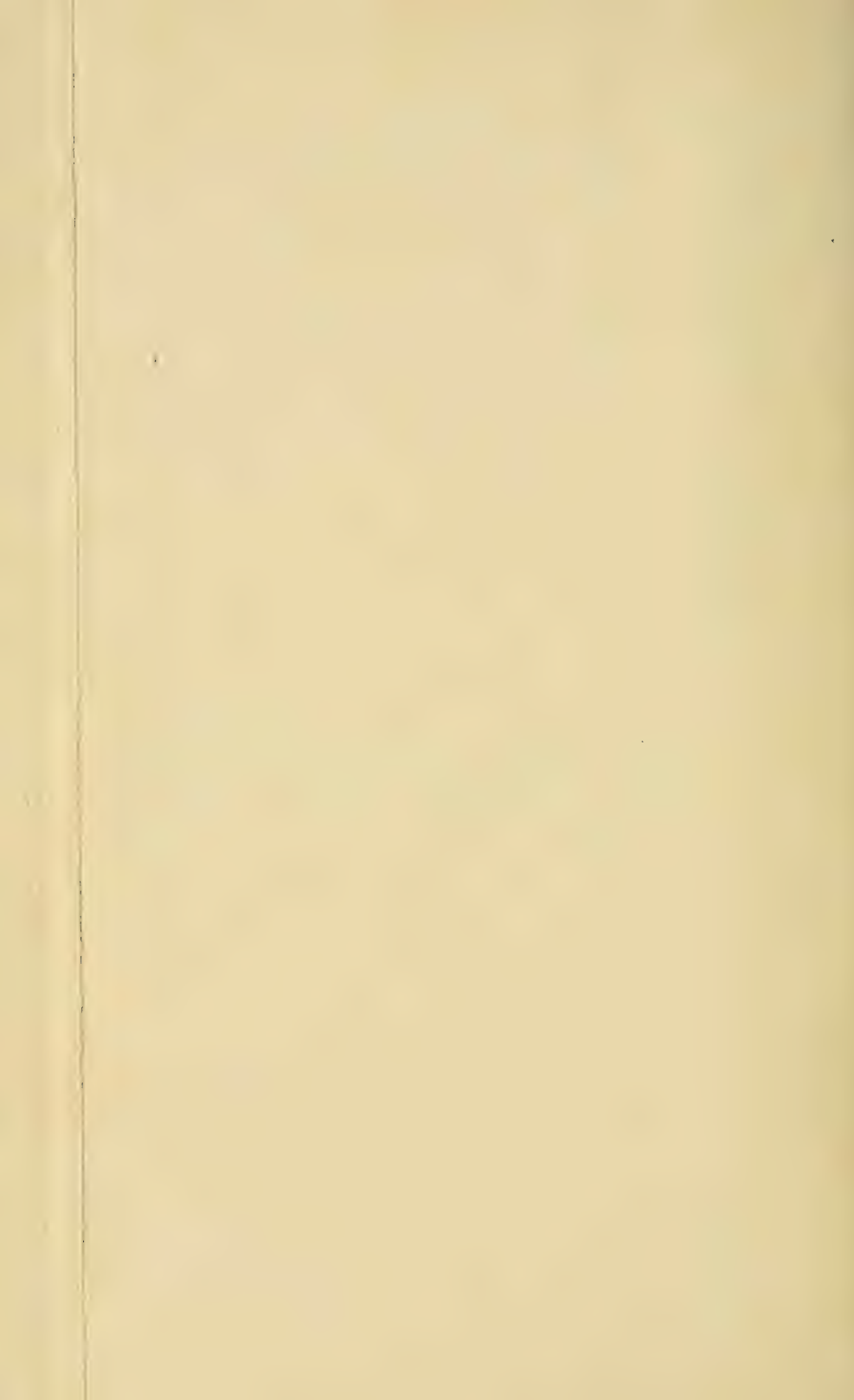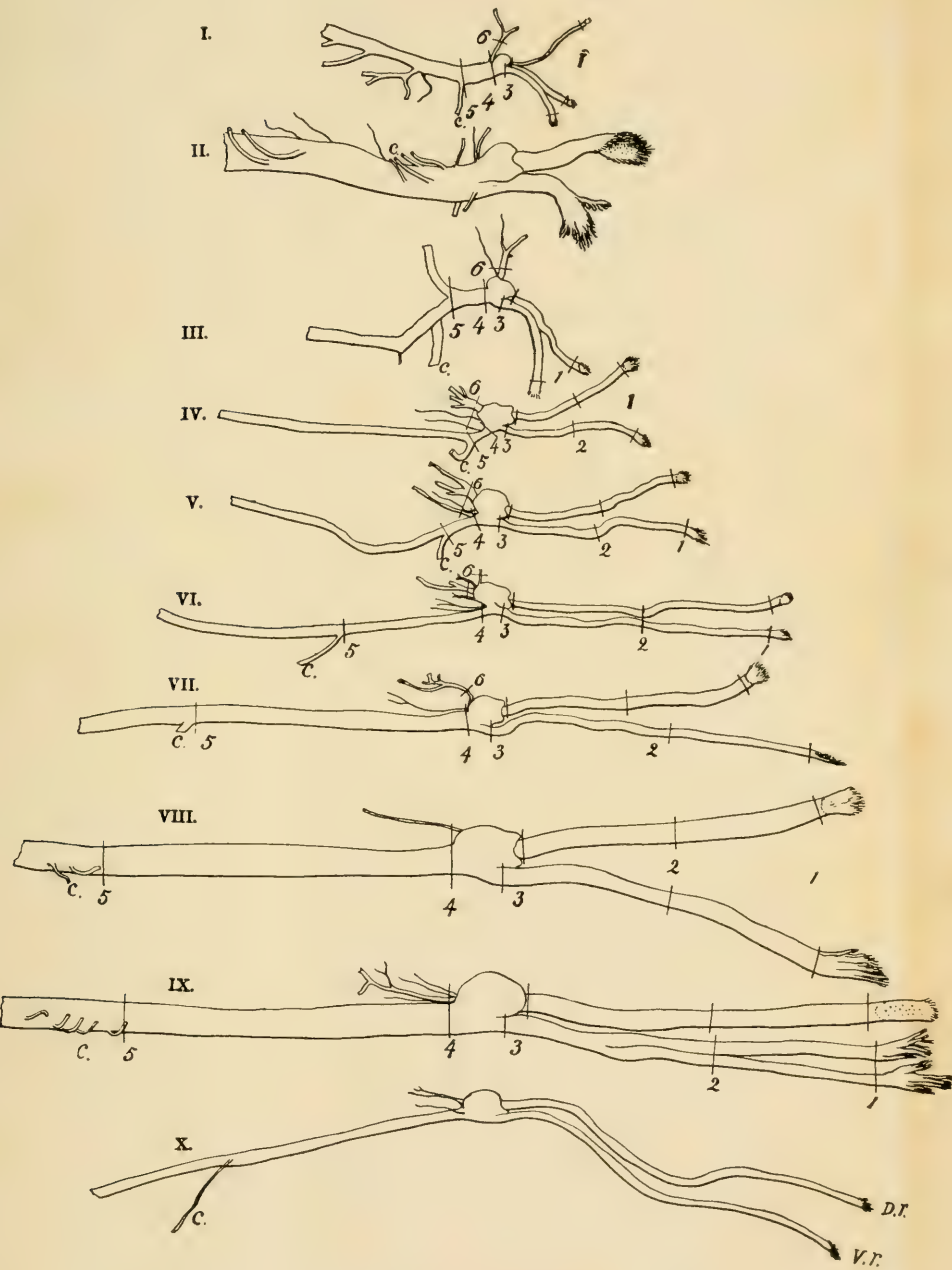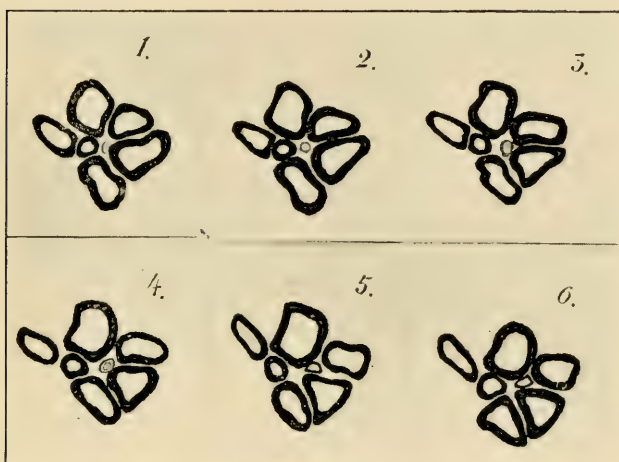
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FIG. 1.

FIG. 2.

FIG. 1.

FIG. 2.

FIG. 1.

FIG. 2.

FIG. 1.

FIG. 2.

PLATE XIII.
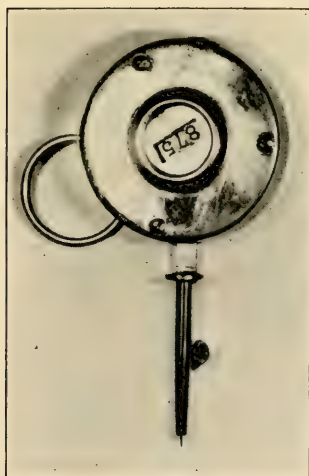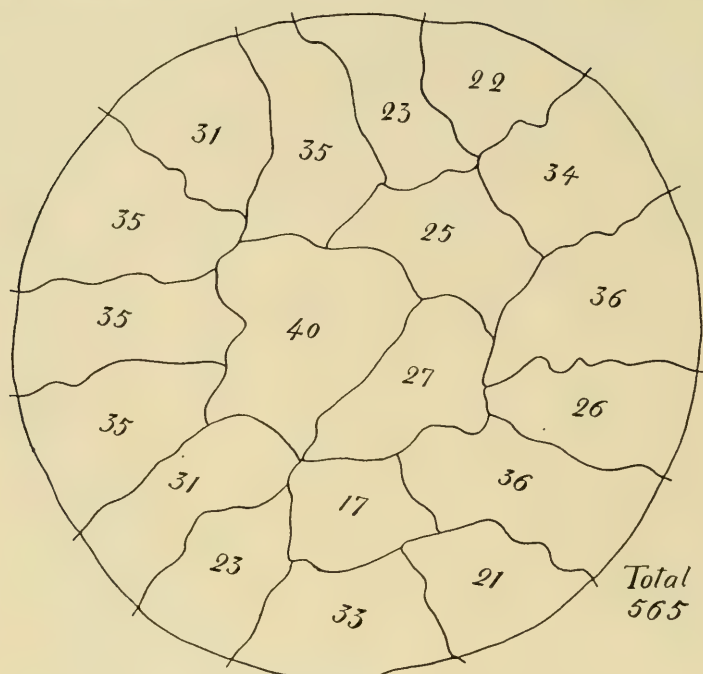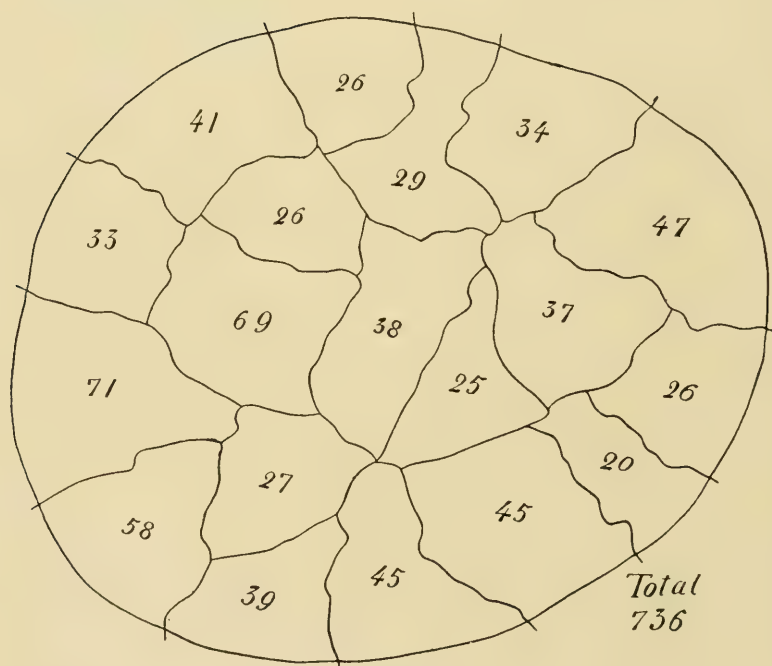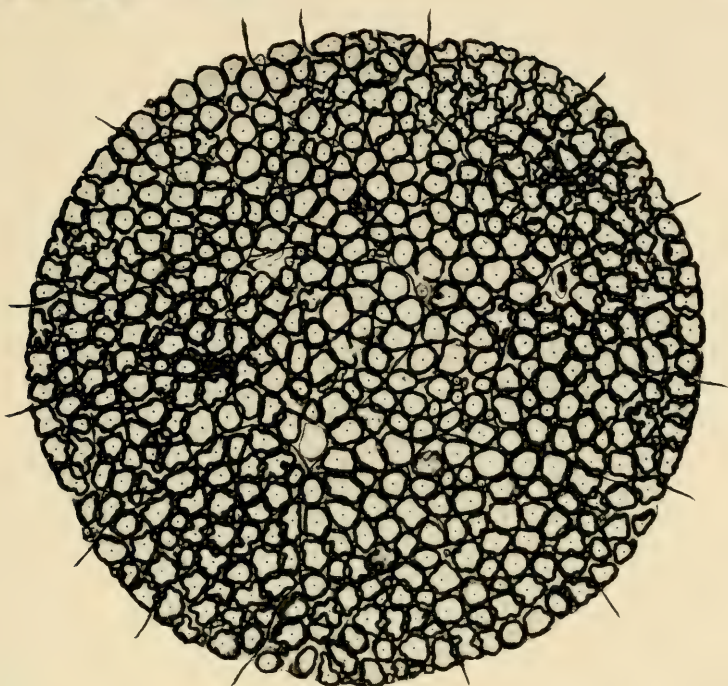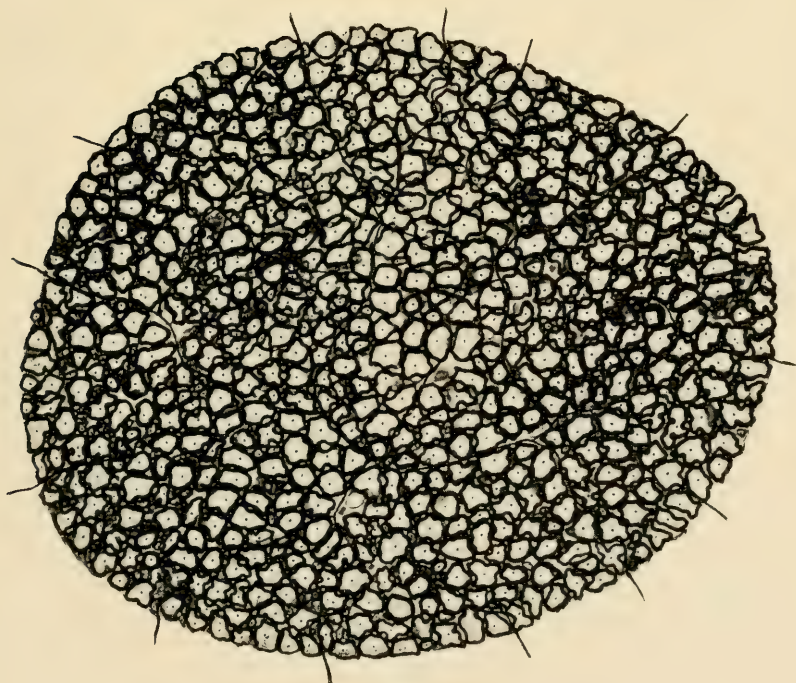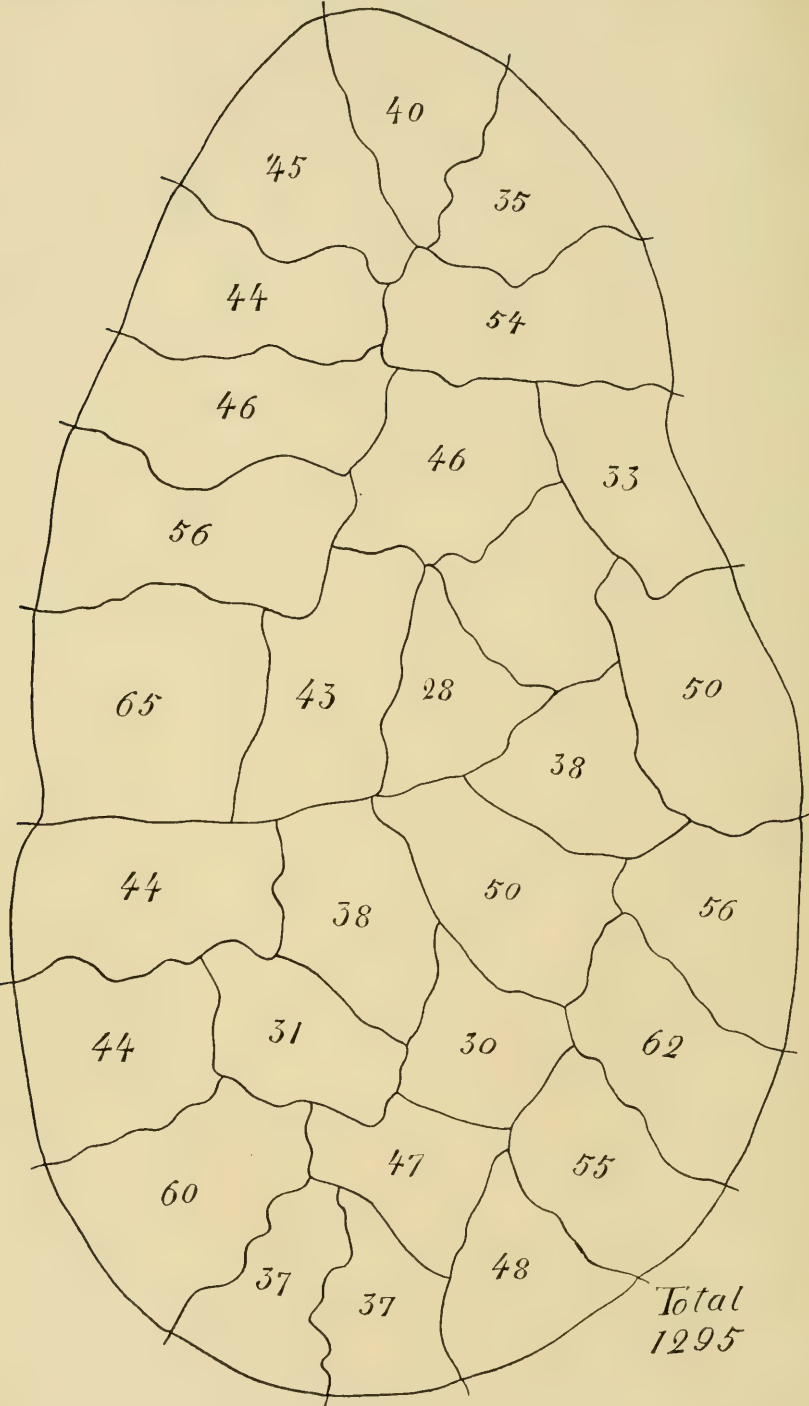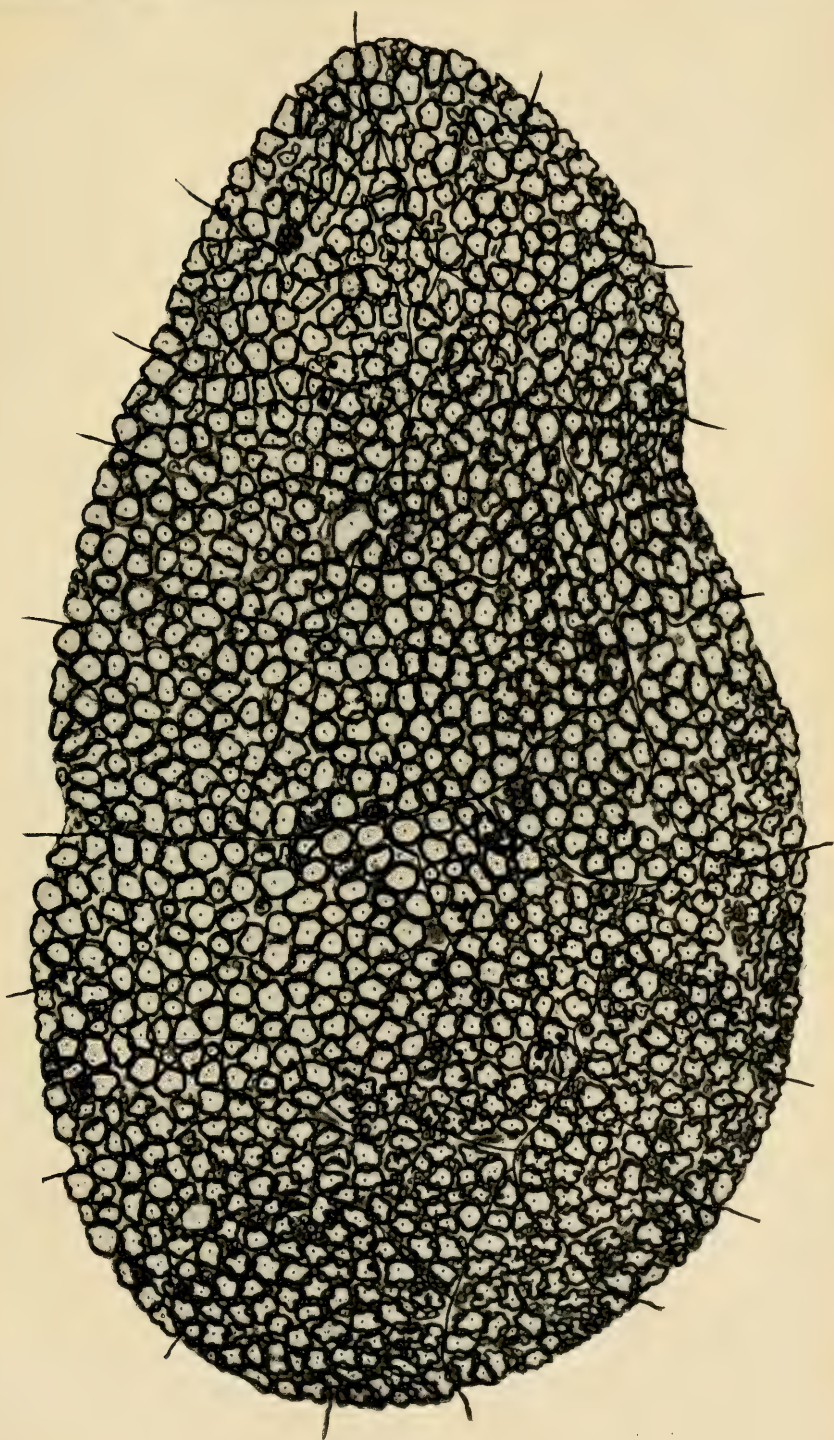
THE CRANIAL AND FIRST SPINAL NERVES OF MENIDIA; A CONTRIBUTION UPON THE NERVE COMPONENTS OF THE BONY FISHES.

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CONTENTS.

Section 1.—Introductory.

I.—General Introduction.

Looked at from the biological standpoint, the primary function of the nervous system is to put the organism into relation with the outer world, the external environment. The health of the body is largely determined, in last analysis, by the perfection of the correspondence between the inner activities and the forces of nature outside.

The immediate mechanism upon which this correspondence directly depends—the sense organs and peripheral nervous system—must not be overlooked by the neurologist who would thoroughly understand the normal or pathological processes of the nervous system as a whole. Even the higher psychic processes in the central nervous system cannot be thoroughly understood without the knowledge of the peripheral nervous system. This is clearly understood by the psychologists who recognize that psychic phenomena cannot be studied without reference to their physiological concomitants, which in turn requires investigation into the morphology of the nervous system both peripheral and central.

It is unnecessary at this late day to urge the importance to normal physiology (and not less to pathology) of a true morphological comprehension of the structure that reacts to stimuli of the external environment. This implies a broad philosophical appreciation of the relations between part and part; of the functional, mechanical and other

factors which determine the forms of the parts; of the modifications induced by the mechanics of growth during the ontogeny; and, finally and most important of all, of the phylogenetic history. It is this latter point which most often gives the clue to structure, and this is a justification for the recognition of comparative anatomy in a scheme of the correlation of sciences for the study of the dynamics and statics of the nervous system.

A generation ago comparative anatomy in this country was chiefly in the hands of the medical profession, and the medical journals contained many memoirs upon the anatomy of the lower animals, memoirs that are standard sources of information to the biologists to-day. With the development of medical specialties and the advance of specialization in other departments of knowledge, all this is changed and it often happens that the pathologist of to-day, for instance, is acquainted with the normal structure of the organs in the human body, the morbid processes of which he is investigating, but knows little of their comparative anatomy, histology and embryology. Of course it is not to be expected that under the present conditions pathologists should conduct special researches in comparative anatomy or embryology; nevertheless an acquaintance with the general principles of these subjects is indispensable for pathology if this science is to gain a broader and more comprehensive basis.

How much would be left of the general laws of the science of embryology if all of the facts acquired by the comparative method were stricken out ? And if physiology had never availed itself of the opportunities afforded by experimentation upon the lower animals, as a science

it would be more than emasculated; indeed it is doubtful if it would ever have been born.

Neurology, not less than these other two sciences, is dependent upon the comparative method for its guiding principles, though the medical profession as a whole has been slow to seize the opportunities thus afforded. Any one who will take the trouble to examine the instruction in the anatomy of the brain in many of our medical colleges (and until very recently in some of the best of them) will find the justification for this latter remark. A glance at the works of Edinger and the other apostles of the comparative method should convince the most skeptical that it is impossible to understand, much less to teach intelligibly, the complexity of the adult human brain without reference to the simpler and more diagrammatic types presented by the lower vertebrates. This is undoubtedly the most valuable advantage to be derived from the study of comparative neurology.

From our standpoint, however, in a system of correlated sciences for the study of abnormal mental and nervous life the most important function of comparative neurology lies in its value as a method of research. Of primary importance in the investigation of the phenomena in this domain, as in all life phenomena, is the method of pathology. By the use of this method the phenomena restricted within the limits of the normal are given a wider range, are magnified. It is obvious that we are thus enabled to get a deeper insight into the nature of the phenomena and have a broader basis to form inductions which are more secure in proportion to the extent of territory from which they are drawn.

The pathological method is one of experiment; indeed pathological conditions are all experiments—nature's experiments—ready at hand for investigation and often more ingenious than we could invent. The great power of the pathological method is that phenomena are often simplified by being split up into their components. A set of greatly complicated phenomena is detached from the others, is dropped out of the intricate series, becomes isolated and thus amenable to control. Having before us isolated and accentuated components of the intricate phenomena forming pathological processes, we can often by means of experiment modify these detached factors and still further analyze them into simpler elements. Finally by studying different phases of a pathological process the component factors of a phenomenon are reduced to simplest terms, analyzed into elementary units. This accomplished, we may undertake a synthesis of the factors, arranging them with relation to cause and effect, and thus arrive at a formula or generalization which will not only explain the single phenomenon, but also all other phenomena of the same kind. The pathological method, then, stands foremost in scientific investigation of organic phenomena, even of the normal manifestations.

Comparative neurology, like all other sciences that deal with life phenomena, must use similar methods, among which the methods of experimental pathology play an important *rôle*. But comparative neurology uses largely the pathological method, in the wider sense of the term; for in the nervous systems of the lower animals we perceive again and again the analogies of pathological conditions with the only difference that they are spread out in time and extended along the phylogenetic pathway

instead of being concentrated and occurring in cataclys-mal fashion as, for instance, in nervous or mental disease in the human subject. Thus, when an animal changes the aquatic for a terrestrial habitat, with the disuse of aquatic sense organs and their substitution by those fit for terrestrial environment, we have practically an example of the pathological method in the atrophic process occurring in the conducting tracts of the sense organs that fall into disuse. Perhaps we might also compare the hypertrophy of the cervical cord in the sea-robin, or that of the vagal lobes in the carp to the hypertrophies occurring as a response to increased function in pathological processes.

The very fact that the natural experiments in the nerv-ous systems of the lower animals are spread out in time gives the method of comparative neurology a particular value, indeed a value not possessed by other methods of investigation in mental and nervous life. For, the terms of the series of the evolutionary process modifying the reactions and structure of the lower forms of the nervous system being extended over great periods of time and taking place exceedingly gradually, the integral phases of the process are obtrusively unfolded. Whereas in disease of the human subject or pathological mani-festations induced in an individual organism the process occurs so rapidly that its serial phases are run together and the progression of the terms of the process eludes one's grasp.

I would emphasize the importance of comparative neurology as a *method of research* in an organization of sciences for the investigation of the phenomena of con-sciousness and their physiological concomitants. This department of science from this standpoint should be turned into account toward the solution of problems of

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the general laws of the dynamics and statics of the nervous system as a whole, rather than towards contributing merely complete knowledge of morphology or even specific physiological data of a particular organism and stopping then and there without probing into the general relations of one particular nervous system to all other nervous systems.

We should study the nervous system of any particular animal or species in a determinate fashion, with the purpose of interpreting structure in dynamic terms and of throwing light upon the nervous system universally and upon the inter-relation of the phylogenetic and onto-genetic progression, bringing comparative neurology into correlation with biology, physiology, pathology and the psychological sciences.   Again, should we find in the neurons of some of the lower animals, peculiarities of reactions to stimuli, or variations in growth or metabolism, evident in function or structure which would throw light upon the life history of *all* neurons, and should we use this knowledge in the form of a generalization, we would then be using comparative neurology in its proper sphere in the co-ordination of sciences for the purpose of determining the nature and laws of the nervous system.

It seems to me that the rôle that comparative neurology plays in the correlation of sciences is primarily in its use as a method, or instrument, keen in investigation of the nature of the nervous system.   Comparative neurology is a means of verification, a control to the deductions gained from the pathological method proper, which in my opinion is the most powerful method in the investigation of *normal* life phenomena.

This brings us to the motive of this paper.   What has it to do with psychiatry ?   The answer to this is very simple.

It has now become a commonplace in science that all parts of the nervous mechanism are so intimately interwoven and interdependent that the study of the functions of the lower parts of the human nervous system is indispensable for a correct comprehension of the higher spheres of the brain.

Our aim in this paper is to lead up to the solution of the functions and structure of the cranial nerves and their intra-axial continuations not only in the lower and higher vertebrates but also in man. With a few notable exceptions, anatomists of the human nervous system have failed to bridge over the gap between their own field and that of the comparative neurologists, especially as to a comprehensive study of cranial nerve morphology and physiology. The same may be said of the comparative neurologists. Hence the subject is full of confusion. Our aim is to bridge over this gap and ultimately not only to contribute to the knowledge of the human nervous system in particular, but also to work out some of the general laws of structure and function of the nervous system in general.

Let us now, although in an introductory manner, consider more specifically the advantages of comparative neurology as a method of research and some of its bearings upon our problem of the phylogenesis of the cranial nerve components.

II.—Introductory Sketch of the Theory of Nerve Components.

One of the most striking of the recent neurological findings has been the discovery of the history of the cerebral cortex. Starting from the fish types, in some of which the pallium is a simple non-nervous membrane, it is interesting to watch the emergence of the cortex and parallel with it the progressive advance in psychomotor

manifestation, as one sense after another effects its secondary connections with the cerebrum. Thus the fluctuations of the relative importance of the organs of higher sense, as the nose and the eye, from type to type are clearly reflected in the size and organization of the corresponding primary and secondary brain centres. We have, it is true, as yet only a few hints in these directions; but yet enough has been gained to illustrate the exceeding fruitfulness of this line of research.

Now, in the domain of the peripheral nerves we have as yet developed but few such illuminating generalizations, and our students still memorize the twelve pairs of cranial nerves, their trunks, rami and ramuli, with the distribution of each, much as one would learn a Greek paradigm. If there is any morphological nexus between the various nerves or any basis for a rational classification, the average text-book gives no hint of it.

In view of the present inchoate condition of the morphology of the cranial nerves and of the fundamental relation of this problem to the proper understanding of the great afferent and efferent systems of the neuraxis itself, it is most fitting that within very recent years there has been a notable increase in the number of researches centering about these questions.

The literature of the cranial nerves is remarkably voluminous, but by far the larger part is either purely descriptive or dominated by crude and false morphological theories. It is only within the present decade that a really practical standpoint has been introduced for the proper morphological treatment of the cranial nerves—at least their sensory portions. This is the doctrine of nerve components, which had been earlier applied to the spinal roots in the very suggestive "four-root theory," and which

now affirms that in a similar way the cranial nerve trunks may contain several varieties of sensory fibres which have different functional and morphological relations and several of which may be present in a single segmental nerve. Since these systems of components are defined by both the peripheral and central relations of their fibres, it is obvious that the ordinary methods of research are inadequate for their study, since these methods have usually examined the proximal termini microscopically and the peripheral courses macroscopically, with but slender basis for an exact correlation of the two sets of findings. The only case thus far published in which both central and peripheral relations of the sensory components have been fully worked out in the same type is Strong's research ('95) upon the cranial nerves of the tadpole of the frog.

Numerous other students, both in this country and in Europe, are now at work upon different phases of the problem, and this activity is expended mainly upon the fishes. The reasons for this are evident, for not only do these primitive types present the problem in its simplest terms and in terms easily assimilable to the paradigm given by Strong, but the extreme diversity among the various groups of fishes in the relative development of the several nerve systems gives us a remarkably beautiful morphological series which sheds much light upon the relationships of the components.

Nature has, as it were, performed for us in the fishes a series of experiments which reveal as clearly what are the primary and secondary anatomical centres for the several systems of sense organs as the experimental method of v. Gudden or even this in combination with the Nissl stain. The working out of the details of this scheme proves more difficult than would at first sight be supposed

and our knowledge of the exact relations in the fishes is as yet very fragmentary. Nevertheless enough has already been done to indicate the broad lines along which these correlations are to be looked for and we may now associate the several lobes of the medulla oblongata which are so characteristic of the fishes with their respective cutaneous or visceral sense organs as definitely as the olfactory nerves are associated with the olfactory lobes or the electric lobes of the torpedo with the electric organs.
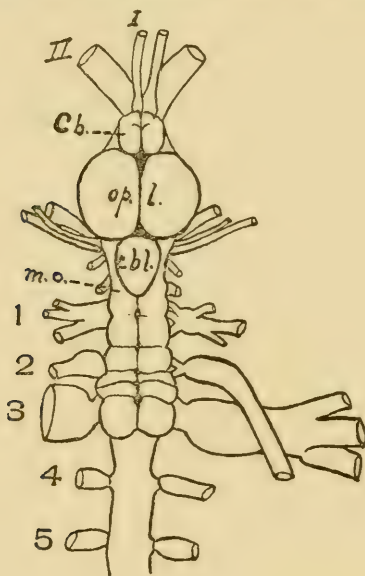
TEXT-FIGURE 1.

TEXT-FIGURE 1.—Brain and part of spinal cord of *Prionotus* seen from above. After Morrill. The spinal nerves are numbered in Arabic numerals. *Cb.*—cerebrum; *cbl.*—cerebellum; *m. o.*—medulla oblongata; *op. l.*—optic lobes.

Moreover the homologies of these lobes among the different groups of fishes and in the higher vertebrates, even up to the human brain, can now be followed with considerable precision, as we shall see beyond.

One of the best illustrations of this central response to peripheral differentiation is found in the sea-robins, in which certain free rays of the pectoral fins have become exceedingly sensitive finger-like tactile organs and their sensory nerves, together with the corresponding dorsal horns of the spinal cord, have been in consequence enormously hypertrophied.

This brain is strictly typical for the bony fishes, but the proximal end of the spinal cord exhibits a series of remarkable lobes which are the terminal centres for the
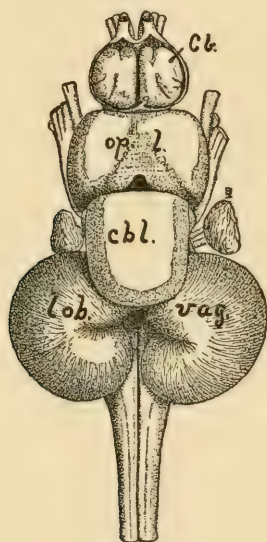
TEXT-FIGURE 2.

TEXT-FIGURE 2.—Brain of *Carpiodes* as seen from above. After C. L. Herrick. *Lob. vag.*—lobi vagi; other letters as in fig. 1.

sensory nerves from the free rays. (Text-figure 1). Here the exaggeration of the general cutaneous component of these first three spinal nerves evokes a perfectly definite and easily recognizable response in the central system.

No new component is introduced; a pre-existing structure is simply enlarged.

Again, one of the most conspicuous features of the brain of certain types of fishes, such as the carp, is the enormous lobi vagi. (Text-figure 2). These constitute the terminal nuclei of the vagus nerves and correspond, at least roughly, to the sensory vagus nuclei of man. They are very small in fishes like the eel, whose gills are
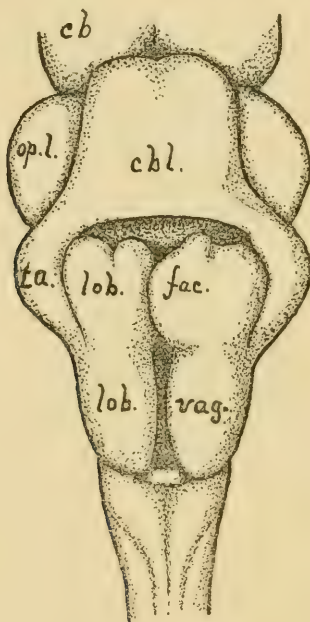
TEXT-FIGURE 3.

TEXT-FIGURE 3.—The brain of *Amiurus* as seen from above. After Kingsbury. *Lob. fac.*—the lobus facialis; *ta.*—the tuberculum acusticum; other letters as before.

reduced, but in the cyprinoid fishes are related not only to the elaborate gill apparatus and the taste buds of the mouth, but especially to the buds of the huge and peculiar palatal organ and also to the widely scattered

sense organs of like nature all over the skin of the head and trunk, the so-called terminal buds. Fishes generally have an elaborate system of taste buds in the mouth, all of which are related to this centre; but they differ widely in the number of terminal buds on the outer skin, and in all known cases the size of the lobi vagi is increased where these latter organs are numerous.

The cat-fishes and some others present an interesting modification of this case. Here the terminal buds which are supplied by the vagus nerve, are reduced in number, but on the head and especially on the barblets, these organs are exceedingly numerous. Accordingly, the branches of the facial nerve which supply these regions are enlarged and a terminal centre in front of the lobus vagi is developed for them, the lobus facialis (the so-called lobus trigemini of the older authors). This lobus is only a pre-auditory derivative of the lobus vagi and all nerves related to these two homodynamous centres can be treated as a morphological unit, the " communis system." (Text-figure 3).

These lobes constitute visceral or special sensory centres and can in no respect be compared with the dorsal horns of the spinal cord. They are new structures developed in the head in correlation with distinctively cranial sense organs. If represented in the trunk at all, it could only be in the feebly developed visceral sensory centres of the spinal cord.

The cat-fish illustrates another one of the medullary centres, whose size is exceedingly variable among the vertebrates. This is the tuberculum acusticum, in man related only to the auditory nerve, but in the fishes serving as the terminal nucleus of the entire lateral line

system of sense organs as well (Text-figure 3, *ta.*). A comparative study reveals the fact that this centre varies in size with the degree of differentiation of the lateral lines.

Thus, in the sturgeon, whose other medullary centres are relatively feebly developed, this system is greatly enlarged and a portion of it has been differentiated in front to form the lobus lineæ lateralis of Johnston (Text-figure 4, *l. l.*), the so-called lobus trigemini of the older authors.
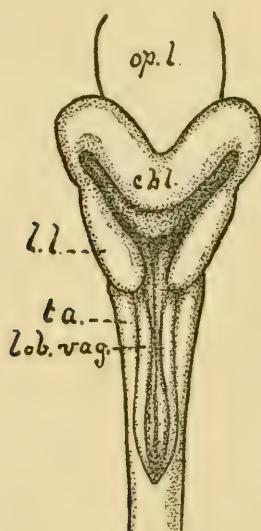
TEXT-FIGURE 4.

TEXT-FIGURE 4.—The brain of the sturgeon, *Acipenser*, as seen from above. After Goronowitsch. *l.l.*—lobus lineæ lateralis; other letters as before.

This acustico-lateral centre, like the vagal lobe, is difficult to correlate with anything found in the spinal cord.

These cases, and many others which might be given, illustrate the way in which comparative anatomy assists

us in the analysis of the sensory components of the cranial nerves by the comparative study of the correlated variation between the sense organ and the centre. It should be remembered, too, that these variations in the primary centres involve corresponding changes in the secondary tracts and centres, and thus contribute to some of the most difficult problems of morphology. Much remains to be done in working out these principles; it is, moreover, the most sound morphology, and the most economical as well, to continue this line of research among the fishes until its most fruitful suggestions have been gathered in before attempting the application in detail to human anatomy, for we find no other group of the vertebrates so diversely specialized in these respects as the fishes, and hence presenting so varied an assortment of stages in the development of the several systems of components.

The research which follows is an attempt to solve some of these problems in the fishes, and it is believed that the results will contribute something toward the development of a true philosophical understanding of the human nervous system. The author feels that at the present time the most important step in this direction is a clear insight into the nature of the several components of the cranial nerves, their relations to each other and to the spinal nerves, and particularly their significance to metamerism and the allied head problems. Until each component can be isolated and treated as a morphological unit and then unraveled in its peripheral courses through the various nerve roots and rami—until this is possible no further great advances in cranial nerve morphology can be looked for even among the lower vertebrates, still less in man. For in the human subject whole systems of nerves have been

dropped out, new ones have been added and primitive re-
lations have been distorted by the usurpation of vast areas
of the head by nerves of distant segments. It is to this
problem that the author has addressed himself primarily
in the following pages.

The doctrine of nerve components dates properly from
the systematic separation of sensory and motor roots and
the formulation of Bell's law. Gaskell's suggestive
"four-root theory" has been a stimulus to further
advances and now it is customary to recognize in the
spinal nerves of the vertebrata four types of fibres:
(1) somatic efferent and (2) somatic afferent (general
cutaneous), making up the major part of the ventral and
dorsal roots respectively, and (3) visceral efferent and (4)
visceral afferent. It is probable that the visceral efferent
fibres go out with both roots and the visceral afferent
enter by the dorsal root.

The proper analysis of the cranial nerves has been
retarded by various uncritical attempts to conform them
rigidly to Bell's law. These attempts resulted only in
confusion so long as qualitative differences other than
sensory and motor in the nerve fibres were not recognized
and all sensory cranial nerves were compared directly
with dorsal spinal roots (general cutaneous), and all motor
cranial nerves were compared with the somatic motor
fibres of the trunk. Our precise knowledge of the sensory
components in the cranial nerves of the lower vertebrates
begins with Strong's paper on the Cranial Nerves of
Amphibia ('95), and the present research was carried out
upon the basis of that work.

Throughout the Ichthyopsida we can at present distin-
guish in the cranial nerves three sensory systems of com-
ponents and two motor, aside from the sympathetic. Each

system may be defined as the sum of all fibres in the body which possess certain physiological and morphological characters in common, so that they may react in a common mode. Morphologically, each system is defined by the terminal relations of its fibres—by the organs to which they are related peripherally and by the centres in which the fibres arise or terminate. The fibres of a single system may appear in a large number of nerves, repeated more or less uniformly in a metameric way (as in the general cutaneous system of the spinal nerves), or they may all be concentrated into a single nerve (as in the optic nerve). The post-optic systems are as follows:

(1). The *general cutaneous system* of the head is clearly the representative of the somatic afferent of the trunk. Its fibres innervate the skin in general, without specialized sense organs and all terminate in the spinal V tract or cells associated with it, these being the continuations into the head of the dorsal horns of the spinal cord.

The term *somatic sensory system* has been used for these components. This usage, however, is ambiguous. Gaskell used this term for all nerves to the outer skin, as distinguished from visceral nerves. Cole would exclude the lateralis nerves, but apparently would include nerves for terminal buds of the skin, which we would exclude as belonging to the communis system. It is better, therefore, to avoid the use of this name altogether.

(2). The *communis system* innervates visceral and mucous surfaces, taste buds and other similar specialized end organs (terminal buds) on the outer skin which do not belong to the lateral line system. These fibres are distinguished by their fine calibre and by the fact that they all end in a single centre, the lobus vagi (which has, however, in some teleosts a specialized pre-auditory portion, the so-called lobus trigemini). They may enter this

centre directly through the vagus roots or indirectly through the fasciculus communis from the IX or VII roots.

I use the term *communis system* in preference to the "fasciculus communis system," proposed by Strong and subsequently employed by Allis, Kingsbury and myself because the system contains many fibres which do not enter the fasciculus communis in the strict sense of that term. Moreover the non-committal character of the shorter term relieves it of the ambiguity which has of late arisen regarding the morphology of the fasciculus communis—see the account in Section 3.
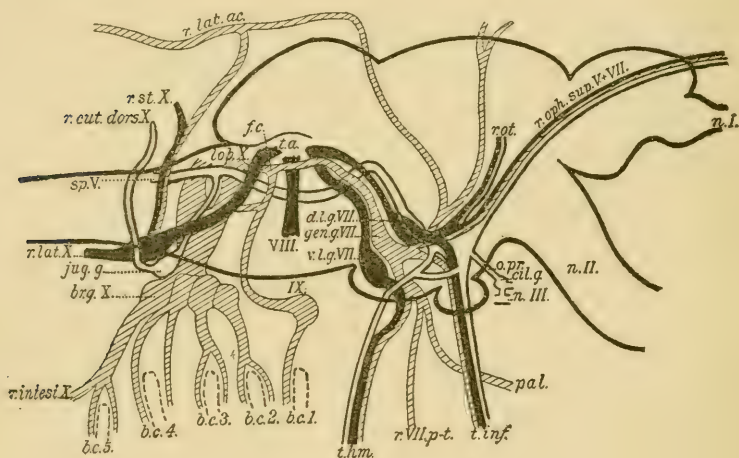
TEXT-FIGURE 5.

TEXT-FIGURE 5.—A diagrammatic view of the sensory components of the cranial nerves of Menidia, as seen from the right side. The diagram is based upon the projection of the cranial nerves upon the sagittal plane which is given in detail on figs. 3 and 4. The general cutaneous component is indicated by the unshaded nerves, the communis component by cross-hatching and the acustico-lateral is drawn in black. For the significance of the reference letters see the table of abbreviations at the end of this article.

(3). The *acustico-lateral system* innervates the lateral line organs and the internal ear. Its fibres are for the most part very large, the coarsest in the body, and they

terminate mainly in the tuberculum acusticum of the medulla oblongata.

(4). The *somatic motor fibres* are commonly regarded as represented by the eye-muscle nerves, the III, IV and VI pairs, and in higher forms by the hypoglossus nerve. In the fishes the latter is a true spinal nerve.

(5). The *viscero-motor fibres* comprise the motor roots of the V, VII, IX and X nerves.

No cranial nerve contains all of these components and it is not necessary to assume that any one ever did contain all of them, for some of these components are evidently neomorphs in the head. Their relations and probable morphological significance are discussed in Sections 3 and 12. This brief outline, together with the accompanying text-figure and figures 3 to 5 and 8 to 12 will perhaps aid in rendering the descriptions which follow more intelligible. Somewhat fuller general accounts have been given in my preliminary papers ('97 and '98a).

III.—Scope and Methods.

This investigation was begun as occupant of the Columbia University Room at the Marine Biological Laboratory at Woods Hole, Mass., in the summer of 1896, was continued during the winter of 1896–7 in the Zoological Laboratory of Columbia University, and subsequently at the Pathological Institute of the New York State Hospitals and at the laboratory of the U. S. Fish Commission at Woods Hole. To all of these institutions I am under obligation, not only for the facilities of research, but for numerous special courtesies; and particularly to Dr. Strong of the Columbia Laboratory for suggestion and advice throughout.

The main object of the study has been, as suggested above, the analysis of each of the cranial nerves, especially the sensory portion, into its components and the tracing of these components continuously from their nuclei in the central nervous system to their ultimate peripheral distributions. As this has necessitated the careful microscopical study of the entire courses of these nerves, it has seemed best to examine and plot the entire peripheral nervous system, even those nerves which, like the pure motor branches, do not bear directly upon this major problem. The following pages, therefore, aim to give a measurably complete account of the cranial and first spinal nerves of the type chosen for the detailed analysis. This mode of treatment receives further justification from the fact that the nervous system of no member of the family represented by this type has ever been described, even topographically, so far as my knowledge goes.

The descriptive details thus accumulated, together with bibliographical and critical comments upon them, so far as they may be of value to special students of comparative anatomy, are given with considerable fulness. A summary at the close of each section and an analytical table of contents will assist the general reader who may not be interested in such details.

The reconstructions plotted upon Figures 3, 4, 5 and 7, all illustrations of cross sections of Menidia, and the diagrammatic cross sections, Figures 8 to 12, are all based upon a single series of sections, and the descriptions in the text have, for the most part, been written from this same series. Thus individual variations do not enter into the descriptions. Other specimens prepared by the same and by different methods have, however, been used

constantly for control and important variations are noted in the text.

The plots are accurately drawn to scale, the magnification being indicated in each case, so that measurements in the text are, as a rule, unnecessary. The figures on the scales in the margins of the plots indicate the serial numbers of the sections plotted, the sections being in all cases fifteen micra thick. To facilitate the location on the plots of objects mentioned and to avoid the introduction in the text of detailed measurements, these serial section numbers are often referred to in the descriptions.

The genus Menidia contains two species, both of which are commonly called "silver-sides." They are very abundant near Woods Hole, Mass., swimming in close schools in shallow water, the larger one, *M. notata*, being found along the open shores, while the smaller one, *M. gracilis*, is more commonly taken in the protected bays and tide pools. They are both small species, the larger one being about 10 cm. long. Their food in captivity seems to be mainly small crustaceans, such as the megalopa larva of the common crab, though they eat smaller fishes of their own or other species.

Regarding the relationships of the family Atherinidæ, to which they belong, I am permitted to make the following quotation from a personal letter received from Dr. Theo. Gill. "The Atherinids, I think, are a primitive type of Acanthopterygian fishes, near the border line between ordinary physostomous and physoclistous fishes. They are genetically related to the ancestors of the pikes, the cyprinodonts and the mullets—related to,

c

but less specialized than the last. I do not look upon them as aberrant." My studies fully confirm the central position given to Menidia, for the nervous system exhibits in many of its most fundamental features the characters of a generalized type; nevertheless it is in many minor respects very highly specialized, these modifications in the nervous system being largely correlated with the exaggerated development of the organs of special sense, notably the eye and the ear.

I have studied both of these species somewhat and, so far as I know, there is no essential difference between them. The figures and descriptions are all based upon sections of Menidia gracilis. Probably they apply to both equally well.

The most essential condition of success in researches on the nerve components is the preparation of perfect serial sections. The series must be unbroken and the medullary sheaths must be perfectly preserved, for it is upon the characters of the latter that we must depend very largely to distinguish the components in the peripheral courses of the nerves. The animal chosen should be small enough to be cut whole or nearly so and should be adult or practically full grown in order that the medullary sheaths may be fully laid down. The latter point is not necessary, but it is certainly a great advantage. I have found, as many before me have done, that the teleostean tissues are refractory to a surprising degree; standard methods which work perfectly with amphibian' or selachian material fail utterly here. Different species of teleosts, moreover, vary somewhat in their reactions to stains.

The necessity for very thorough decalcification of course complicates the problem greatly. In general,

rapid decalcifying solutions, and especially those contain-ing nitric acid, are useless. So also solutions containing picric acid had to be discarded, though several, such as picro-formalin and especially picro-acetic-formalin, prove to be excellent fixers for general tissues; yet none of them preserve the medullary sheaths properly. The attempt was made to blacken the nerve sheaths with osmic acid during the process of decalcification. First Flemming's stronger fluid was tried. If applied for two or three weeks, decalcification is complete and the tissue, though very brittle, is in perfect histological condition; but the nerve fibres usually refuse to precipitate the metal and appear as white cords in the generally blackened tissues.

Hermann's fluid, if applied for several weeks, decalcifies and at the same time blackens the medullary sheaths more or less; but it does not leave the tissue in so favorable histological condition as the Flemming. Indeed, the specimens so prepared were so brittle that it proved im-possible to get sufficiently continuous sections for plotting and this method was finally discarded in favor of a modi-fied Weigert method. Nevertheless, several series which were mounted directly after fixation in Hermann's fluid, without further staining, have proved of the greatest ser-vice in controlling the others, as the sections, if once obtained, give sharper and clearer pictures of the proper-ties of the nerve sheaths than can be secured in any other way. This applies especially to the peripheral courses of the nerves; the penetrating power of the fluid is so slight that it is not of much value centrally.

Upwards of a hundred modifications of the Weigert method were tried, for the most part with unsatisfactory results; nevertheless some of these methods are very

excellent and have given me the preparations upon which most of the work has been done. These experiments I have fully reported upon in a previous paper ('98), and I give here simply the one method which was employed in the preparation of the series upon which the plots and most of the descriptions and other figures are based. The general appearance of these sections is well shown by Figures 1 and 2, drawn for me by Mr. Veenfliet.

After fixation for two or three weeks in Flemming's stronger fluid, frequently renewed, and paraffin embedding, serial sections were cut 15 micra in thickness. Medium-sized adults were chosen, the head severed from the body behind the pectoral fins and mounted entire. To ensure the proper permeation of the paraffin it is well during the embedding to aspirate the specimen under the air pump or with a syringe and thus remove from the cavities of the body the gases evolved in the decalcification.

The sections may be fixed to the slides with Mayer's albumen, first floating them out on warm water, if necessary, to remove all wrinkles. After passing them out of the absolute alcohol one may flow over them a very thin solution of celloidin. Drain quickly, and allow to set before passing down into the lower grades of alcohol. In this way is averted the danger of the sections becoming loosened in the subsequent manipulations. From water the sections pass into a mordant composed of saturated solution of copper acetate, two volumes; water one volume. Here they remain six hours or longer at ordinary summer temperature, after which they are thoroughly rinsed in water and then treated with Weigert's hæmatoxylin for four hours or longer. Decolorize in Weigert's decolorizer, wash thoroughly (one hour or longer, in running water) and mount in the usual manner.

Section 2.—The Lateral Line Canals and their Organs.

The problems of the relations and significance of the sensory nerve components are so intimately bound up with those of the cutaneous sense organs innervated by them that an account of these organs must naturally precede the discussion of the nerves themselves. I have prepared in this section as complete an account as possible with the material at hand of the structure of the special cutaneous sense organs belonging to the lateral line system of the adult Menidia. There is urgent demand for very careful study of the comparative embryology of the various types of lateral line organs and terminal buds. The data thus far furnished by the embryologists are very "suggestive," but what they suggest must for the most part remain a matter of dispute so long as the ultimate fate of their so-called sense organs remains unknown.

I.—The Lateral Lines.

There is probably no teleostean character which is more variable in its details than the lateral line canals. In Menidia we find the system so developed as to conform very nearly to what is usually regarded as the typical form, such as is given by Allis in his diagram ('89, Plate XLII) of Amia one month old or by Cole of the adult cod ('98a, Fig. 2). If we compare with these diagrams my reconstruction of the adult Menidia on Figs. 3 and 5, the resemblance is close, the chief difference being the failure in the case of Menidia of the canals to close over the rows of lateral line organs throughout their entire extent. Thus the rows of organs are present in their typical relations, but the canals are in places interrupted.

The acustico-lateral system as a whole has been isolated from the other nerve systems and plotted upon Fig. 5, the canals being colored to correspond with their nerve supply and the limits of the related bones being indicated. This plot is drawn off from the more detailed plot on Fig. 3 and with the exception of the naked mandibular organ, *man. c.*, and the two opercular organs, *o.1.* and *o.2.*, was all drawn from a single specimen, *i. e.*, it is not a schematic or type sketch, but represents actual conditions, individual variations not being taken into account.   Comparison with many other specimens shows that such variations occur, but that they are of a relatively trivial nature so that this outline may be taken as typical for the species.

In the more detailed plot, Fig. 3, the projection of the canals and their pores is represented by the green outline. The lateral line organs, like their nerves, are colored brown, those organs which are contained in canals being represented by brown rings, naked lateral line organs by brown discs.   Cutaneous organs belonging to the communis system are represented by red discs, their nerves also being colored red.

In naming the lateral lines of the head I have used the following terms: The continuation of the lateral line of the trunk is termed the main line of the head up to the point where it divides behind the eye.   From this point forward the line above the eye is called the supra-orbital, the line below the eye the infra-orbital.   The canal of the operculo-mandibular line is interrupted between the pre-opercular and the articular bones.   The portion caudad of this point is called the opercular line, the portion cephalad the mandibular.   The incomplete cross-commissure in the extra-scapular bone is termed the occipital commissure.

The canals are also named in accordance with the bones containing them. Thus, the main canal has extra-scapular and squamosal portions, the supra-orbital canal has frontal, and nasal portions, the infra-orbital has post-orbital and lachrymal portions, etc.

1.—The Lateral Line of the Trunk.

The family Atherinidæ is characterized in the systematic works as lacking the lateral line. In Menidia the lateral line canal is absent on the trunk, but is represented by a row of very small lateral line organs innervated by the r. lateralis vagi, one for each segment of the body. Whether they extend the whole length of the body I have not ascertained. They can be followed back from the head by surface examination for only a short distance, one on each scale. But the markings on the scales of the lateral line series, *i. e.*, the groove in the centre of the scale in which the organ lies, can be recognized about half-way back to the tail. Probably minute lateral line organs extend still farther caudad.

Merkel ('80) enumerates a number of teleosts which have the lateral line developed in various degrees and there are numerous other accounts in the literature of the absence of the lateral line canals, the lines being represented by rows of naked organs. For example, Leydig ('94, p. 30) states that in Leucaspius delineatus for the caudal sixth of the body the lateral line canal fails, but the lateral line nerve continues and supplies a series of naked organs lying in a groove. The tendency for the canal to fail to appear in the trunk is doubtless to be correlated with the fact that in the ontogeny the trunk canal closes later than the head canals (Allis, '89, Leydig, '94).

2.—*The Lines of the Head.*

The lateral line canal system of the head, like that of the trunk, shows evidence of reduction or arrested development. The primary lines of the head are present in very nearly the typical form, though in part they are represented by lines of naked organs like those of the trunk line. The canals and their organs bear, so far as ascertained, the typical relations to the bones, as described by Allis for Amia ('89) and Cole for Gadus ('98a) and pores are present between each pair of organs, the only exception being the space between the first organ of the trunk canal and the organ of the occipital canal, between which there is no pore. The pores are always short and simple, never showing the dendritic arrangement found in some other fishes. The lateral line organs of the head, whether contained in canals or not, are always supplied by the acustico-lateral system of nerves, and these nerves never supply any other organs.

This is a point which can be determined with certainty in nearly every case by reason of the great size of the lateral line fibres, as compared with those of any other sensory system. These fibres, when bound up in a common sheath with others, usually segregate themselves, so that they occupy a definite portion of the cross-section of the nerve, and this renders their separation still more easy. The most serious difficulties were encountered in distinguishing certain naked organs of the lateral line system, which correspond probably with the pit-lines of Amia, from terminal buds. These organs are sometimes innervated by fibres which are intermediate in character between those of the lateralis and communis systems, being very densely myelinated and hence staining very

dark, like the former fibres, and yet of small size. They are not, however, so small as the ordinary communis fibres.

3.—The Extra-scapular Canal.

i.—The Post-Occipital Main Canal.—Just cephalad of the pectoral fin the canal system of the head appears, as the direct continuation of the lateral line of the body. As we pass cephalad this canal is first a dermal groove which very soon closes to form a narrow canal in the dermis and the latter at once sinks down into a groove in the extra-scapular bone. At the level of the last sense organ of the head (715 on the plots) the bony groove has become a canal. In this osseous canal the membranous canal expands to the normal width, which is maintained with tolerable uniformity throughout the entire canal system of the head.

The sense organ above referred to (*m. 3* of Fig. 5) is the only one of the main line behind the occipital commissure which is enclosed in a canal. It is supplied by the first ramus of the r. lateralis vagi (*r. l. 1.*), excluding the r. supra-temporalis. This organ might be regarded either as the first one of the trunk series or the last one of the head series.

ii.—The Occipital Commissure.—The incomplete occipital commissure branches off from the main canal at an acute angle and extends dorsad and cephalad only about one mm. before it opens out and disappears. A single elongated canal organ is found in this canal (Fig. 1, *m. 4*). It lies very near the origin of the canal and is supplied by a branch of the r. supra-temporalis vagi. No naked buds could be found in the skin along the line continuing the course of the canal, as is the case behind the lateral line canal.

After its separation from the main canal the occipital commissure remains in the extra-scapular bone. The main canal, however, soon leaves this bone, lies close under the skin and immediately opens out for a short dis-

tance (660–675) as a wide shallow pore.   There are no
pores in the main canal caudad of this point, nor in the
occipital commissure.

4.—*The Squamosal Canal.*

Cephalad of this point the main canal sinks down again
and is enclosed in the squamosal (pterotic) bone and in
this portion of the canal is included the single sense organ
of the main line lying between the occipital commissure
and the opercular canal (*m. 2*).   This organ is innervated
from the r. supra-temporalis vagi.   Farther cephalad the
canal comes to lie in a deep narrow groove in the bone up
to the point of union with the opercular canal.   At this
point a rather long narrow pore is found, directed caudad
and ventrad close under the skin.

After giving off the opercular canal, the main canal
(550) sinks again into a deep groove in the squamosal
bone and there is lodged the single canal organ of the
main canal between the opercular and the infra-orbital
canals (*m. 1*).   It lies nearer to the former than to the
latter and is innervated by the r. oticus.   The canal runs
in this groove very nearly to the point where the infra-
orbital canal diverges from the supra-orbital, a tongue of
the squamosal bone running forward to accommodate it.
Here the canal communicates with the surface by means
of a pore.

The operculo-mandibular canal is separated below the
eye into its two portions, opercular and mandibular, which
will be separately described, the canal organs and pores of
each being numbered from before backward.

5.—*The Opercular Canal.*

The opercular canal lies for almost its entire length in
a groove in the caudal and ventral faces of the preoper-
cular bone, which ventrally extends forward to the man-
dible.   The canal has a vertical and a horizontal limb of
nearly equal length and contains seven canal organs, three
in the vertical and four in the horizontal limb, the former

of which are innervated from the truncus hyomandibu-
laris, the latter from the r. mandibularis externus VII.
The groove in the preopercular bone is much deeper in
the vertical than in the horizontal limb and for a small
part of its course the bone entirely encloses the canal,
forming an osseous canal.

There is no pore between the seventh opercular canal
organ and the main canal. The pore between the sixth
and seventh organs (*o. p. 6*, Fig. 5) passes dorso-caudad,
the fifth and fourth pores pass ventro-caudad, and are
rather longer than the sixth. Between the third and
fourth organs the canal again lies close to the surface and
the pore is a mere break in the outer wall of the canal
with no considerable tube. The first and second pores
are similar to the third. For an illustration of a typical
arrangement of these pores see Fig. 27.

The opercular canal extends cephalad to 290, always in
the groove of the preopercular bone except at the ex-
treme cephalic end. After leaving this bone the canal
almost immediately comes to the surface, opens out and
disappears.

6.—*The Mandibular Canal.*

The mandibular canal appears less than one millimetre
in front of the cephalic end of the opercular canal (235)
and its course is a direct continuation of that of the oper-
cular canal. It immediately sinks down into a groove in
the articular bone by which it soon becomes entirely en-
closed. There are five organs in the mandibular canal, of
which the fifth lies in the articular bone, the others in the
dentary. They are all innervated from the r. mandibu-
laris externus VII.

About midway between the fifth and fourth canal
organs is the fourth mandibular pore. The third pore
lies nearer the third organ and the second pore nearer the
second organ, while the first pore arises almost directly
over the first organ. The mandibular canal ends in a
pore at the extreme tip of the mandible without communi-
cating with the canal of the opposite side.

7.—*The Infra-Orbital Canal.*

This canal passes ventrad and slightly caudad and is enclosed at once by the most dorsal of the post-orbital bones. Its course is very short, for as soon as it has passed this bone it opens out and disappears. This bone is rather massive, much more so than any of the other bones of the orbital ring.

There are no pores in this short section of the canal and but one sense organ. The infra-orbital canal is absent from the most caudal edge of the orbit to a point a little beyond its ventral edge, where it resumes. This short portion of the infra-orbital canal we shall call the post-orbital section, the pre-orbital portion, the lachrymal section.

It is interesting to note that the entire orbital ring of bones in Menidia is very much reduced. In view of the fact that the lateral line organs of the head normally lie in bony canals and that, even if the canal is not entirely enclosed in bone, there is a tendency to form bridges of bone over the organs themselves (as, for example, in the supra-orbital canal), it would seem reasonable to conclude that the absence of that portion of the infra-orbital canal which is normally enclosed in the bones of the orbital ring is correlated with the reduction of those bones.

The portion of the infra-orbital line which lacks the canal is represented by a series of naked sense organs which in shape resemble the terminal buds more than they do the canal organs. Those near the open ends of the canals are larger than those in the middle of the naked series. They are all innervated, however, by the coarse fibres of the r. buccalis belonging to the acustico-lateralis system.

There are fifteen sense organs in the infra-orbital series, the first five in the lachrymal section of the canal, nine naked organs in the ventro-caudal quadrant, and one canal organ in the short post-orbital section. The latter and the last two naked organs are innervated by the r. oticus, all of the other organs by the r. buccalis.

Upon the reappearance of the canal in front of the orbit (260), it sinks down into a deep groove in the lachrymal bone and at the level of the fifth infra-orbital sense organ the bone arches up so as to entirely enclose the canal. Between the fifth and fourth canal organs there is no pore. Arising almost directly over the fourth organ is the fourth pore of this series, which is directed cephalad. There is a similar one over the third organ. The second pore lies ventrally of the second organ and the first pore dorsally of the same organ and a little farther removed. Thus the number of pores corresponds to the number of spaces between the organs, though they are somewhat displaced from their normal positions.

The infra-orbital canal terminates, after rising to the top of the head and bending slightly caudad, in a pore which lies near to and laterally of the posterior nasal aperture and separated only by the latter from the supra-orbital canal. It does not communicate with any other canal system.

8.—*The Supra-Orbital Canal.*

After separating from the infra-orbital, this canal sinks at once into a groove in the frontal bone. It contains six canal organs, all supplied by the r. ophthalmicus superficialis VII. This groove at the level of the sixth organ is roofed by a narrow bridge of bone and just cephalad of this point is a narrow pore. The fourth and fifth canal organs are close together and are roofed over by similar narrow bridges of bone. The corresponding pore (fourth) lies over the caudal portion of the fourth organ. The third pore is longer, narrow and directed dorsad and caudad. From this point forward the canal is wholly enclosed by the frontal bone as far forward as the second pore, which lies just behind the second organ. Somewhat cephalad of this point (190) the frontal bone disappears, its place as bearer of the canal being taken by the nasal, in which the first organ of this canal lies. The first pore lies just behind this organ and from this point to the end

of the canal (90) the bone entirely encloses the canal.
The canal ends in a minute pore some distance from the
tip of the snout dorsally of the anterior nasal aperture and
does not communicate with any other canal.

II.—Accessory Lateral Line Organs.

Under the names of accessory lateral lines or pit-lines
other writers have described rows of naked cutaneous
sense organs found in various places on the skin of differ-
ent fishes and innervated from various sources. The
morphological significance of all of these structures is
very obscure and can probably not be definitely settled
until we have more accurate knowledge of their nerve
supply and development. Unfortunately Menidia is not
a favorable type for the solution of these problems, as the
cutaneous sense organs are all developed much less highly
than in many other fishes.

In many fishes and amphibians there have been de-
scribed rows of naked organs on the trunk, the so-called
accessory lateral lines. The most constant of these is the
dorsal accessory lateral line, which runs parallel with the
main lateral line near the mid-dorsal line. Another may
run parallel with and ventrally of the main line, while a
third series of organs may be distributed in various ways
along the course of the main line. In some cyprinoid
fishes such organs are scattered over the whole body, each
scale bearing one or more. Any or all of these organs
may be innervated from branches of the r. lateralis vagi
or the dorsal and ventral lines may be supplied, as in the
gadoids, by branches of the r. lateralis accessorius (r.
lateralis trigemini, or superficial lateral line nerve, of
authors). This latter nerve I have shown to belong to
the communis system. In almost all cases when these

accessory organs on the trunk are supplied by the r. later-alis vagi that nerve is described as receiving anastomosing fibres from either the vagus, glossopharyngeus or facialis which are apparently of communis origin. These organs are commonly considered to belong to the lateral line system and to be similar to the pit-lines described by Allis on the head of Amia; but before such a conclusion can be safely accepted it must be definitely determined that their nerves are of lateralis and not communis origin.

These accessory lateral line organs of the trunk are represented in Menidia by a few naked sense buds along the course of the r. lateralis accessorius (see figures 3 and 4). They are innervated from anastomosing branches from the r. lateralis vagi. The fibres are of small or medium calibre and are, I think, derived from the lobus vagi by way of the anastomosis from the IX root to the lateralis root. A row of similar organs is found farther caudad in very young specimens lying directly over the course of the r. lateralis accessorius. Their nerves could not be traced, though there can be no doubt that they are derived from the nerve last mentioned, especially as such a condition has been described for several other fishes.

I have no sections running through the trunk of the adult, but surface examination with a lens is sufficient to demonstrate that this dorsal series of naked organs persists to adult life. Specimens preserved in ten per cent forma-lin show the organs better than alcoholic material. One or two organs are found above the operculum near the one at 620 on the plots, but never very many. The dorsal body line is represented by an irregular series of organs close to the median line and directly over the position occupied by the accessory lateral nerve. These organs are not numerous and do not occur on each scale as we pass caudad. They are most conspicious in the region of the dorsal fin, which lies rather far caudad, but even here they are not regularly arranged. Between the dorsal fins and the head only a very few scattered organs are found.

From the innervation of these organs I incline to regard them, like the buds on the top of the head, as belonging to the communis system.   Of course it does not necessarily follow that the accessory lateral lines of Fierasfer, Amia, etc., which are innervated by branches of the r. lateralis vagi, are of the same nature.   See the further discussion of the r. lateralis accessorius in Section 12.

Upon the head there are several series of naked cutaneous organs which are clearly innervated by the lateral line nerves and which I homologize with the pit-lines of Amia. See fig. 5.

One row of four large organs (*o.1* to *o.4*) follows the ventral edge of the operculum behind the fourth pore of the opercular canal.   One organ (and I think usually two) lies on the dorsal surface of the operculum behind the sixth pore of the opercular canal (*o.5*).   These five organs are innervated from the r. opercularis superficialis VII and obviously from the coarse-fibred lateralis component. Another similar organ (*o.6*) lies in front of the opercular canal at the level of the fifth pore and is supplied by the first branch of the r. mandibularis VII.

Along the course of the horizontal limb of the opercular canal and just external to the canal are three groups of similar, but smaller, organs innervated respectively by the first, fourth and sixth branches of the r. mandibularis VII.   A group of three similar organs lies along the course of the mandibular canal and is supplied by the eighth branch of the r. mandibularis VII.   A single organ on each side (*man. c.*) lies mesally of the cephalic end of the mandibular canal, the two forming a mandibular commissural line.

There are four organs in the nasal region which are supplied by the r. buccalis (*a. d. e. f.*) which appear also to form a similar pit-line, making, together with a line from the opposite side, a maxillary commissure.   About the anterior nasal aperture there are five organs, two of which (*b. c.*) are supplied by the r. buccalis, and three (*g. h. i.*) are supplied by the r. ophthalmicus superficialis. They are of uncertain nature.   I have provisionally

reckoned them all among the pit-organs. The evidence for this is chiefly comparative, as the nerve supply is ambiguous; see the account of their nerves in Section 7.

The morphology and homologies of all of these pit-organs are further discussed in the pages immediately following and under the head of their nerves in Section 7.

It should be noted that the " pit-organs " of Menidia are not situated in pits, as in ganoids and as in the cod (Cole, '98a). They are strictly naked papillæ projecting above the surface of the skin. Cole (p. 187 ff.) argues with great force that pit-organs, visicles of Savi, ampullæ and lateral line canals, represent a progressively advancing series in the differentiation of these organs. This seems probable, and in that case the pit-organs of Menidia stand nearer the primitive condition than do those of the ganoids.

III.—Comparative.

In all there are thirty-seven organs belonging to the lateral line system proper, exclusive of pit-organs, on each side of the head of Menidia. In Amia Allis' enumeration shows that there are forty-seven (forty, not counting those in the extra-scapular and the other more posterior bones, '89, p. 499), besides the "spiracular organ." To get the former number he enumerates the one organ found in the supra-scapular bone and the two in the supra-clavicular as belonging to the head, thus including three organs behind the extra-scapular bone, while I have included none behind the latter bone, since neither of the other bones comes into relation with the lateral line. In Gadus Cole ('98a) describes thirty-two canal organs in the head. In the distribution and innervation of these organs, Menidia exhibits a striking general similarity to both of these types, though the parallelism is not

D

exact.   Cole gives (pp. 179–185) a brief but very excellent summary of the more interesting variations of the lateral line canals of different kinds of fishes.

The numerous writers who have described the lateral canals of the fishes have, as a rule, until recently, devoted no considerable attention to their nerve supply so that the correlation of their results is in many cases a matter of difficulty.   Pollard first clearly demonstrated in teleosts the independence of the lateral line system of nerves; but both his work and that of Collinge leave much to be desired to complete our knowledge of the innervation of the cutaneous sense organs in the teleosts and especially in the siluroids, which are of special importance in this connection.   Pending further studies here, it will not be necessary to examine their work in detail.   The conditions in Lophius, however, as worked out by Guitel ('91), shed some light upon our findings and will be here reviewed.

The diagram, fig. 6, adapted from Guitel, exhibits the topographical relations of the lateral lines and their innervation.   In spite of the fact that this system is very highly developed in the head, there are no canals in Lophius.   The organs lie in grooves or pits and are overlapped by the peculiar dermal fringes so characteristic of the Pediculati. · The absence of the canals is probably to be correlated with the fact that the skeleton is remarkably loosely aggregated.   Indeed, the older writers classed this among the cartilaginous fishes.   Guitel describes several of the head lines as innervated from the trigeminus.   Of course in the light of present knowledge we must relegate these branches to the facialis, and with this correction the homologies of his lines are clear.

In Lophius there is but one lateral line on the trunk,

which is supplied by the r. lateralis vagi. There are three dorsal branches of the lateral line nerve, of which it is clear from the description that only one contains proper lateralis fibres. The first of these is an opercular nerve which goes to the skin of the operculum, the "superficial opercular," and evidently corresponds to my branches *cut. X. 2* and *cut. X. 3* (see Section 5, VIII). It also sends a branch, the "opercularis profundus," which anastomoses with the r. opercularis profundus VII and supplies the lining of the branchiostegal rays and which evidently corresponds to my branch *n. op. X.* The second dorsal branch is motor and apparently corresponds in part to my branch for the trapezius muscle (*XI*). The third dorsal branch is the proper supra-temporal nerve. It supplies the lines (see fig. 6) *p-o*, *p-b*, *o-b* and *b-l.* These lines evidently represent the supra-temporal commissure and certain of the pit-lines found in Amia.

The lines *b-d*, *d-e*, *d-k*, *e-h*, *e-f*, *f-g* and *f-m* are all innervated by the r. mandibularis externus facialis, and correspond to the operculo-mandibular lines of Menidia. In Lophius there are some anastomoses of these nerves with the r. mandibularis trigemini, but there is no evidence that any of the lateralis fibres come from the latter source. The r. mandibularis externus VII is not, as in Menidia, a single nerve, but is broken up into several independent nerves. Thus, the lines *b-d*, *d-e*, *d-k* and *e-h* are supplied by a single branch which Guitel calls the r. opercularis superficialis VII, and which corresponds to that nerve in Menidia plus a portion of the main r. mandibularis externus VII. The line *b-d-e-f-m* corresponds to the operculo-mandibular line. The other lines of this series I think are to be compared with pit-lines of some other forms. Thus, the line *e-h* corresponds in

position and innervation with the pit-line *o.1* to *o.4* in
Menidia, and the line *d-k* to the organ *o.5* on the dorsal
surface of the operculum of Menidia. In Batrachus
(Clapp, '99) there are lines in these positions like those
of Lophius. These lines also bear some resemblance to
the gular and jugular lines of Chlamydoselachus, and the
organ *o.6* to the angular line of the same fish (Garman,
'88). The line *d-k* apparently also corresponds to the
posterior limb of the hyomandibular canal of selachians
(Ewart, '93) and Chimæra (Cole, '96a), and in the latter
cases there are groups of ampullæ in the same region,
which probably also belong in the same category. In
Amia (Allis, '89) there are pit-lines supplied by similar
branches of the hyomandibular nerve, but these lines lie
cephalad of the opercular canal instead of caudad of it.

The line *f-g* of Lophius lies in the same position as an
area of thickened epidermis in Menidia under the eye
between the infra-orbital and opercular and mandibular
canals, an area containing many pit-organs in Gadus.

The line *q-c-n-g-d* of Lophius would at first sight be com-
pared directly with the infra-orbital line of Menidia. Yet,
in spite of the fact that both lines are innervated by the
r. buccalis, the homology is, I think, only incomplete,
as shown by the peculiar course of the nerve in Lophius
and a comparison with Batrachus (Clapp, '99). In the
latter case there is a small (and obsolescent?) infra-orbital
line and *in addition* a "maxillary line" which runs
caudad from near the cephalic end of the infra-orbital,
laterally of the latter, but does not reach the opercular
line. This latter line is more highly developed in Lophius,
while the caudal portion of the infra-orbital line, which
should connect with the cephalic end of the line *l-b*, has
disappeared. That the line *n-g-d* of Lophius has grown

back from in front of the eye is suggested by the course of its nerve, which first runs forward cephalad of the eye and then sends recurrent twigs to supply the line back to the point where it joins the opercular line. The line *o-c* represents the supra-orbital canal of Menidia. It is probable that the organs belonging to the r. oticus are also included here, for the last organs of this line are innervated by a separate branch of the r. ophthalmicus superficialis VII. Upon comparing the diagram of Lophius with Allis' diagram of the lateral line system of Amia, it is suggested that the line *o-p* is the occipital commissure and its pit-line of Amia, the line *o-b* is the middle pit-line, while the anterior pit-line is represented in the caudal part of the line *o-c*. This last supposition would explain the fact that the supra-orbital line does not join the main line *l-b*, but the others farther dorsad.

Material has been collected and some fragmentary observations have been made upon the development of the lateral lines in Menidia, but these results are as yet too incomplete to yield much of value. In very young specimens about 1 cm. long the cutaneous sense organs were plotted and all of the lateral line organs were found in essentially the same relations as in the adult save that no canals are developed. The number and arrangement of the naked lateral line organs is the same as in the adult. In specimens a few mm. longer the canals have begun to appear and when 2½ cm. long the canals have been completed very nearly as in the adult. The pores are in all cases wider at this age than in the adult and the main canal is interrupted for the entire distance between the point of union of the supra- and infra-orbital canals and the organ lying next caudad. Only four organs are contained in the lachrymal segment of the infra-orbital canal,

instead of five as in the adult, and the mandibular canal has not been closed so as to cover the first organ of that line.

Is the simplicity of the lateral line system in Menidia as compared with many other fishes, especially the lower fishes, to be regarded as primitive simplicity or as the result of degeneration? Cole would say the former, for he argues ('98, p. 245) that the naked condition of the sense organs is always the primitive and that in the decline of the system these organs are lost before the canals. But how about the Amphibia in which the system is fluctuating on the verge of extinction and yet no canals are present, only naked organs? On the whole I incline to regard the condition in Menidia as reduced rather than primitive.

The various recent attempts to show that a part of the lateral line system is innervated by branches of the trigeminus, such as that of Collinge ('95), doubtless rest either upon faulty observation or loose definition. Perhaps the clearest of these cases is that of Chimæra (Cole, '96a) in which two organs of the supra-orbital line are innervated from the profundus; but Cole himself feels confident that a microscopical examination would show that the nerve in question is really a twig of the lateralis system which is detached from the r. ophthalmicus superficialis and secondarily joined to the profundus—a question easily answered by a determination of the central connection of these fibres, whether in the lateralis or the Gasserian ganglion.

Another case difficult of interpretation is given by Miss Platt ('96, p. 530), for Necturus. "I have traced the nerve twigs to each one of the terminal clusters of organs on the infra-orbital line, and find that four of the organs, which I have marked in the reconstruction, are supplied

by nerve twigs composed in equal parts of fibres coming from the buccalis facialis and from the ophthalmicus profundus. These fibres unite in a common twig that goes directly to the heart of the sense organ." This observation is of the highest importance and should be verified if possible upon adult material. Without questioning the accuracy of Miss Platt's observation, a consideration of her description and figures suggest certain cases which I have observed in the case of Menidia, where a general cutaneous twig goes out with the lateralis twig for a sense organ and just before that organ is reached turns abruptly to one side to supply the skin adjacent to or overlying the canal organ. In an undifferentiated embryonic tissue these smaller cutaneous fibres might be overlooked, or they might not at the stage studied have attained their ultimate growth toward the skin.

IV.—Summary of the Lateral Lines.

The lateral line system of Menidia is not highly developed, but presents very nearly the typical arrangement of lines. The canal is wanting in the trunk and in a portion of the infra-orbital line, though these lines are represented by rows of naked lateral line organs. The organs of the lateral lines, whether contained in canals or not, are always innervated by the acustico-lateral system of nerves. The canals are related to the bones of the head in the typical manner, as described by Allis for Amia. A simple pore is normally found between each pair of organs. The lateral lines are accompanied in some cases by rows of naked organs which are also innervated from the acustico-lateral system of nerves and which appear to correspond with the pit-lines of Amia. These pit-lines are in some other fishes represented by true lateral lines.

SECTION 3.—THE CENTRAL RELATIONS OF THE CRANIAL COMPONENTS.

Before proceeding with the description of the nerves it will be profitable to discuss the terminal relations within the brain of some of the components of the cranial nerves and their probable relation to the spinal components. The motor nuclei can best be described in connection with the several cranial nerve roots to which they give origin; they will, therefore, in this section receive only a brief general treatment. The sensory terminal nuclei are, however, grouped into systems each of which is related to several of the cranial nerves as ordinarily enumerated. A preliminary description of each of these systems, taken as a whole, will assist in the ultimate analysis of the cranial roots, ganglia and rami which are related to them.

I.—The General Cutaneous System.

The general cutaneous nerves supply general sensation to the skin without specialized sensory end-organs. Nerves from lateral line organs and from terminal buds are excluded from this system. These nerves correspond in every respect, however, with the cutaneous fibres of the spinal nerves and are serially homologous with them.

In Menidia this system is represented in the V and X cranial nerves only. Such fibres are said to occur in the IX nerve of other forms—Selachians, Ewart ('89 and '92), Chimæra, Cole ('96, p. 664), and Acipenser, Johnston ('98, p. 585).

By far the larger part of these fibres arise from the Gasserian ganglion, and these make up the whole of the sensory trigeminus root. They are so intimately joined to the motor V fibres that within the brain it is not possible to separate the two components perfectly. (Fig. 20).

Most of these fibres turn caudad immediately upon entering the brain and constitute the spinal V tract. A large bundle accompanies the motor root nearly to the median line and constitutes the "deep portion of the descending Vth" of Johnston ('98). Most of these fibres, both sensory and motor, pass at once to the opposite side through the commissura accessoria, but some of the motor fibres terminate in, or more strictly, arise from, the motor V nucleus and the fasciculus longitudinalis dorsalis of the same side. The sensory fibres of this bundle probably also, in part, cross to the opposite side, though they could not be separately followed. Some of them appear to end in a compact nucleus of very small cells lying very near to the motor V nucleus and a little farther caudad. This I take to be the "chief sensory nucleus" of the trigeminus. It should be stated, however, that my knowledge of this nucleus and its connections is not as precise as that of the other roots described. No considerable number of trigeminal fibres turn cephalad from the origin of the nerve. The nucleus lying under the cerebellum to which Johnston traced sensory trigeminal fibres in Acipenser was found, but no fibres were traced to it, nor were the descending cerebellar fibres described by him and by Goronowitsch discovered. No Golgi preparations were made and I cannot deny the presence of such fibres in relatively small numbers, as this region has not been exhaustively studied.

The spinal V tract runs back very close to the lateral wall of the oblongata and ventrally of all of the sensory VII and of the VIII roots, but dorsally of the motor VII (Fig. 19) and motor IX (Fig. 18) roots. The sensory IX fibres emerge dorsally of it, the X fibres both dorsally and ventrally. As the lobus vagi increases in size it crowds

the spinal V tract laterally and dorsally until, at the level of the caudal vagus roots, it occupies the extreme dorso-lateral angle of the oblongata, where it forms a projecting cord or band. This relation is maintained back to the level of the exit of the first spinal nerve, where the spinal V tract merges into the nucleus funiculi and the dorsal cornu.

Between the cephalic and caudal vagus roots the spinal V tracts receives a small bundle of fibres from the jugular ganglion of the vagus.

Haller ('96, p. 64), describes for Salmo, Perca and Anguilla, and figures in the latter case a large tract running from the lobus vagi adjacent to the ventricle to emerge with the trigeminus root. He also figures a smaller root running from the lobus vagi into the VII nerve and says that the chief trigeminus nucleus is directly continuous and serially homologous with the lobus vagi.

Haller's account of the V and VII roots in the eel appeared to me so remarkable that I have myself examined the matter. From a study of both transverse and longitudinal sections of the brain of Anguilla chrysypa Raf. it appears that the V and VII roots of the eel are typical, as compared with Menidia, and that the differences between Haller's account and mine arise from the fact that he has wrongly identified several of the roots.

In Anguilla, the lateralis system is developed about as in Menidia; the general cutaneous system is the same in plan, but enormously developed, the spinal V tract being especially enlarged; the communis system is much reduced. The lobus vagi and its roots are small, doubtless correlated with the reduction of the gills. The communis root of the facial is, however, very large. It runs, as in Menidia, directly to the ventricular wall and turns

caudad, as the fasciculus communis, into an elongated lobus IX + VII. The latter receives the sensory IX root and is continuous caudad with the lobus vagi.

Now, the root which Haller calls trigeminus (Plate IV, fig. 26) obviously contains, besides the sensory and motor V, the communis root of the VII and probably also the dorsal lateralis root of the VII, while his root marked *ac.+fac.* contains the ventral lateralis root of VII, the motor VII and perhaps VIII fibres. The portion of the latter complex which he marks *fac.* is not a sensory facialis root terminating in the cephalic end of the lobus vagi, as Haller supposes, but the motor VII root, which passes out from its nucleus via the fasciculus longitudinalis dorsalis, exactly as in Menidia.

The root which Haller calls the '' obere innere Ramus ascendens n. trigemini (*r. a. tr. sup.*)'' and considers as a root from the cephalic end of the lobus vagi is the communis root of the facialis, *i. e.*, the fasciculus communis. Its terminal nucleus, the lobus VII+IX, is continuous with the lobus vagi, and it is not true that the latter '' is, accordingly, not sharply defined forward, but is continued without interruption into the upper or sensory trigeminus'' (p. 64); for none of the centres in question have anything whatever to do with the trigeminus.

Haller supports the serial homology of the lobes from which the V, IX and X nerves arise by citation of the case of Lota vulgaris, but upon comparing the figure given with a similar figure of the same species by Gorono-witsch in the same Festschrift it is difficult to see any resemblance between the two either in the number and forms of the lobes or of the nerve roots, and little reliance can be placed on any of this evidence until this species is re-examined.

Johnston ('98, p. 594) describes the sensory trigeminus in the sturgeon as arising from the spinal V tract and from the tuberculum acusticum. The latter fibres apparently correspond with those to the chief sensory nucleus of Menidia and other forms. There is no evidence that they terminate in the tuberculum acusticum proper.

The "system y" of Goronowitsch ('88 and '96) in Acipenser corresponds to the spinal V tract and the secondary vago-trigeminus tract of teleosts and the fibres which enter the system y in Acipenser from the lobus vagi ('96, p. 9) and in Lota from the lobi vago-glossophar-yngeo-facialis ('96, p. 21) are obviously the secondary and not the root fibres. In Menidia the secondary vagus bundle (of Mayser) follows the inner and ventral side of the spinal V tract, but can always be clearly distinguished from it (Figs. 17, 18, 19, *Sec. X*). The motor IX and VII roots run between a portion of the secondary vagus bundle and the spinal V. The secondary VIII bundle lies dorsal and somewhat removed from the spinal V (Figs. 18, 19, *Sec. VIII*).

II.—The Acustico-lateral System.

This system includes the nerves which supply the lateral line organs and kindred structures, viz.: the r. lateralis vagi, the VIII nerve and the two lateralis roots of the facialis. Their nerves terminate together in the tuberculum acusticum for the most part, and their fibres are very intimately intermingled.

In the middle portion of the cerebellar peduncles the outer, or molecular, layer disappears laterally, the cerebellum being bounded on these aspects by the fibrous and granular layers only. These layers are continued caudad into the tuberculum acusticum of the oblongata and

receive from the caudal edge of the cerebellum a cap of the molecular layer, the cerebellar crest. Still farther caudad the two cerebellar crests, immediately after their separation from the cerebellum, fuse in the middle line dorsally of the fourth ventricle (Fig. 18). The fusion is substantial, involving the molecular layer, the now rudimentary granular layer and the underlying fibres of the tuberculum acusticum proper. The molecular layer caps the tuberculum for its entire length, *i. e.*, caudad beyond the cephalic end of the lobus vagi and nearly to the caudal tip of the cerebellum. Its extreme caudal tip is shown in Fig. 17.

The cerebellum we know to be related to the secondary tracts of all of the sensory nerves. It is said by several authorities to receive direct root fibres from the trigeminus; but its direct relations to the roots of the acustico-lateral nerves is strikingly characteristic of this system.

Several large bundles of root fibres from the VIII nerve (Fig. 19, *cb. VIII*) can easily be followed in the transections up into the cerebellum near its cephalic end. Probably other similar bundles run into the cerebellum from the three lateral line roots, as described by Johnston ('98).

The VIII nerve and probably also the three lateral line roots send root fibres caudad, thus constituting the spinal VIII tract. These fibres form two close round bundles lying at the periphery of the oblongata. The sensory root of the vagus emerges just dorsally of them (Fig. 17, *sp. VIII*). Immediately caudad of the level here figured (640) they turn ventrad, forming external arcuate fibres to cross in the extreme ventral portion of the raphe. This decussation occupies the extreme ventral surface of the brain for almost the entire extent of the region of the lobus vagi.

Goronowitsch ('96) describes and figures this tract in Lota under the name of "ascending Trigeminus II" and finds it derived from the lateral line VII (his Trig. II, dorsalis) and from the VIII.   It appears to be homologous with the spinal VIII of human anatomy.   It is doubtful whether it is completely homologous, if at all, with the spinal VIII of Acipenser, as described by Johnston ('98). The latter tract appears from the description to be made up largely of secondary fibres from the tuberculum acusticum, and not, as here, and as in human anatomy, of direct root fibres.   Moreover, Johnston's tract runs back closely joined to the spinal V tract and mesally of it, to terminate in a dorsal nucleus lying mesally of the nucleus funiculi.   The tract to which Johnston gives the name spinal VIII is apparently the tract which I term the secondary VIII bundle (Figs. 18 and 19).   In Menidia this tract is apparently composed mainly of ascending fibres, though it may contain descending fibres, such as Johnston describes, also.

The secondary fibres arising in the tuberculum acusticum for the most part cross in the commissura accessoria Mauthneri.   Some, however, enter a secondary VIII bundle on the same side.   The tract to which I have given this name (figs. 18 and 19, *Sec. VIII*) is composed mainly of uncrossed fibres, but partly, I think, of crossed fibres. It passes into the cerebellum.   The other secondary fibres from the tuberculum acusticum, after crossing in the commissura accessoria, enter the tractus bulbo-tectalis (*tr. b. t.*), and most of them, if not all, pass directly up to to the optic tectum.

III.—The Communis System.

Osborn ('88, p. 63) applies the term fasciculus communis to a tract in the amphibian oblongata because of

"its common relations to a number of the cranial nerves."
In the Amphibia the fasciculus communis receives most
of the root fibres belonging to what I have called the com-
munis system. These enter with the VII, IX and X
roots. The fasciculus is a tolerably uniform tract which,
after receiving the root fibres above mentioned, continues
into the spinal cord uninterruptedly as far as the first
spinal nerve, being accompanied for almost its entire
length by a strand of nerve cells which constitute a ter-
minal nucleus for its fibres, the spinal nucleus of the
fasciculus communis. This tract is the "Radix bulbo-
spinalis Vagi et Glossopharyngei" of Edinger ('96, p. 84).

In the fishes, however, the greater part of the fibres of
this system enter the oblongata through the chief vagus
root and pass directly to their terminal nucleus in the
lobus vagi without entering the fasciculus communis in
the original sense of that term. The chief root of the
vagus is in the fishes (and doubtless in the higher forms
also) a complex of at least three kinds of fibres: (1)
Sensory fibres from the general visceral surfaces without
specialized end-organs. (2) Sensory fibres from taste
buds in the mouth and from similar terminal buds vari-
ously scattered over the outer surface of the body. It is
generally assumed that these two classes of buds have a
common origin, as well as a common structure and inner-
vation. They must be sharply distinguished from the
neuromasts, or organs of the lateral line (nerve hillocks of
Merkel), which belong to a distinct system. (3) General
cutaneous fibres from the outer skin. The latter category
and all motor fibres are excluded from the communis
system.

In the communis system, then, there are represented
two types of fibres, the general visceral and the taste bud

(and terminal bud) fibres, which appear to be quite distinct from each other functionally and may be so anatomically, though we cannot as yet effect their analysis. The pre-auditory portion of the fasciculus communis here, as in the Amphibia, is composed mainly, though probably not wholly, of fibres of the second of the classes enumerated above, and it was these fibres which Strong had primarily in mind in proposing the term "fasciculus communis system." In the tract as a whole, however, he recognized both types of fibres and also the motor component ('95, p. 182).

Now the fact that these kinds of fibres are developed in varying degrees in different animals and the fact that more or less of their terminal nuclei have sometimes been included with them under the term fasciculus communis have already occasioned considerable ambiguity as to what is meant by this term and the matter of definition becomes important. I repeat, therefore, that under the term *communis system* I include the sensory cranial nerves supplying the visceral surfaces, taste buds and terminal buds, their ganglia, root fibres, peripheral end-organs and terminal nuclei in the medulla oblongata. The term fasciculus communis I shall use in its original sense as a tract of fibres running from the seventh nerve caudad in the oblongata and receiving in different animals varying proportions of the root fibres of the communis system. Other root fibres of that system may pass to their terminal nuclei directly without entering the fasciculus communis. The fasciculus communis may contain in some part of its course viscero-motor fibres; but, if so, such fibres are not regarded as belonging to the communis system, which is wholly sensory.

In Menidia the pre-vagal portion of the fasciculus com-
munis contains a portion of the root fibres of the VII and
IX nerves, as described in the sections devoted to those
nerves.   I find no indication of a pre-facial fasciculus
communis.   From the communis root of the facialis this
tract passes back to the lobus vagi as a compact round
bundle lying close to the ventricle.   After receiving the
sensory IX nerve (Fig. 18) it begins to be surrounded by
an area of " ground substance " and almost at once enters
the lobus vagi in several strands.

The lobus vagi crowds the other structures of this
region laterally until it occupies nearly the whole of the
dorsal part of the oblongata.   Upon almost the whole of
its lateral face the root fibres of the vagus are received.
The lobi vagi are very moderately developed as compared
with some other teleosts, *e. g.*, cyprinoids, and fuse in the
median line only at their caudal extremities over the tip
of the fourth ventricle.   The small size of the lobus vagi
may be correlated with the reduction of the terminal bud
system in Menidia.

The motor vagus nucleus (nucleus ambiguus) lies ven-
tro-mesally of the lobus, just laterally of the floor of the
ventricle and dorsally of the fasciculus longitudinalis dor-
salis.   (Fig. 17).   Caudad of the exit of the motor vagus
roots the lobus diminishes in size and the other dorsal
structures, *i. e.*, the dorsal cornu, nucleus funiculi and
spinal V tract, appear in their normal relations.   In the
spinal cord of these fishes, it should be noted, the dorsal
horns are crowded mesally as far as possible, so that they
lie up against the dorsal fissure with practically no white
column intervening (Fig. 16).

The following description, though based primarily upon
Weigert sections, has been controlled by the examination
of a series of sections of the brain of Menidia stained by
Nissl's method.   The cells of the lobus vagi are minute
and densely crowded in a narrow zone along the dorsal
and mesal surface of the lobus close under the endyma,
with but few cells in the interior of the lobe.   On the

E

caudal face of the lobus vagi medullated fibres gather and constitute a spinal portion of the fasciculus communis; some of these cross at once to the opposite side dorsally of the fourth ventricle in small irregular bundles. Others continue caudad, where they are joined by additional fibres arising farther laterally, probably from the dorsal cornu, and just caudad of the lobus vagi they participate in the formation of a compact commissure or decussation. All of the transverse fibres above described belong to the commissura infima Halleri, which in Menidia is but feebly developed.

From this place, on each side, a close round bundle of medullated fibres extends caudad to the level of the first spinal root, where it breaks up and disappears in an area of loose reticular tissue which contains few medullated fibres and many rather small pale cells with scattered larger deeply stained multipolar cells and which lies ventrally of the dorsal horn and dorsally and laterally of the canalis centralis. This region is both in Weigert and Nissl preparations very clearly distinguished structurally from the dorsal horns, having a more open reticular structure and larger rather numerous cells. This structure is characteristic of the corresponding region, *i. e.*, the area adjacent to the floor of the fourth ventricle, dorsally of the fasciculus longitudinalis dorsalis, far cephalad under the lobus vagi, and here it contains, besides the medium sized cells mentioned, the very large cells of the nucleus ambiguus. These latter cells extend nearly to the caudal end of the commissura infima (683), where they terminate abruptly.

For this nucleus of the spinal cord laterally of the canalis centralis I shall adopt the name "paracentral nucleus" from Onuf and Collins ('98). The nucleus ambiguus seems to be a specialized cranial portion of the paracentral nucleus.

At the level of the first spinal nerve this reticular area of the paracentral nucleus has spread out laterally and now occupies the region dorsally and laterally of the canalis centralis, the "intermediate zone" of Onuf and Col-

lins, which in higher animals contains the lateral cornu, Clarke's column and other structures now commonly associated with visceral nerves. The cells of the ventral cornu lie farther ventrally. At the level of the paracentral nucleus, but much farther laterally there runs through the spinal cord another ill-defined area of "ground substance" containing few medullated fibres and occasional very small cells (Fig. 16, *l*). This area, like the ventral cornu, is more or less obscurely connected by strands of non-medullated (mainly spongiplasmic) fibres with the other grey matter of the spinal cord. There is no connecting bridge of cells in the case of the lateral area.

In the striped mullet, Mugil cephalus L., which is closely related to Menidia and a young specimen of which (3 cm. long) was cut for comparison, we find the relations of the lobus vagi and its fibre connections very much as above described, with, however, the spinal portion more highly developed and more clearly differentiated. The caudal ends of the lobi vagi contract toward the ventricle and are continued into the spinal cord without an appreciable break. They finally lie closely appressed between the dorsal cornua and the ventricle and now numerous medullated fibres appear in them, a part or all of which cross dorsally of the canalis centralis after the fourth ventricle has closed, thus entering the commissura infima. A small bundle of medullated fibres is continued caudad of the commissure to about the level of the first spinal nerve. Its fibres gradually disappear, leaving the bundle in different directions, chiefly laterally and ventrally.

The motor nucleus of the IX and X (nucleus ambiguus) is very large and its cells are arranged in the characteristic dense rosettes. It extends far caudad beyond the end of the lobus vagi, maintaining the same position, *i. e.*, laterally and dorsally of the canalis centralis, until the level of the first spinal nerve. Here it ends abruptly, as in Menidia. In the mullet the ventral cornu cells extend cephalad considerably farther than the terminus of this

nucleus and the scattered cells which in Menidia lie lat-
erally of the canalis centralis and in the neck of the ventral
cornu (paracentral nucleus) also extend farther cephalad
and form a much more compact nucleus. All of these
structures may be seen in a single transection (Fig. 15),
which passes through the caudal part of the nucleus am-
biguus and the cephalic part of the ventral cornu, while
the paracentral nucleus and the lateral recticular area
extend a considerable distance farther cephalad. At the
level of the first spinal nerve the paracentral nucleus has
come to lie a little farther dorsally than in the figure so
that, instead of lying ventro-laterally of the central canal,
it lies laterally of it; *i. e.*, it occupies the position corre-
sponding to that of the nucleus ambiguus of the medulla
oblongata, and in this position I have followed it as a well-
defined nucleus through nearly the entire length of the
spinal cord. There is no break in the continuity of the
cellular strand, though in parts of the trunk its cells are
more numerous than in other parts. Its cells are through-
out of the same large size as at first, while the cells of the
dorsal cornu are very small. The latter are embedded in
a dense gelatinous stroma, while the cells of the paracen-
tral nucleus lie in a loose reticulum, in this again agreeing
with Menidia.

I have described at length these structures of the spinal
cord in this connection because they seem to me to be
related to the communis system of the oblongata. In the
fishes the communis system, as I have defined the term,
is obviously concerned very largely with visceral sensa-
tions and is very intimately related to the viscero-motor
apparatus.

Morphologically its terminal nuclei are not the most
dorsal structures of the oblongata, as sometimes stated.
Haller, for example ('96, p. 65), agrees with Goronowitsch
in regarding the lobus vagi as the continuation of the dorsal
cornu. It "occupies a position in the oblongata (dorso-

median part) which corresponds to that of the medial part of the dorso-lateral column of the cord."

In judging of the correctness of this assumption we must first determine what is the nature of the movement by which the canalis centralis has expanded to form the fourth ventricle. Remembering that the roof-plate of the nerve tube is membranous in the embryonic condition and is typically so in the adult, any massive structure appearing in it being a secondary ingrowth from the sides, it would appear that the membranous roof of the fourth ventricle represents this roof-plate and is represented in the spinal cord only by the floor of the dorsal fissure. The fourth ventricle is formed, then, by the dorsal and lateral expansion of the canalis centralis so that dorso-median structures of the cord become dorso-lateral structures of the oblongata. This is clearly shown by the course of the spinal V tract, which is unquestionably the cranial continuation of the dorsal horn (or at least of its general cutaneous portion). It is, then, obviously impossible to homologize structures lying in the floor of the fourth ventricle with those lying dorsally of the canalis spinalis, and this is what Goronowitsch and Haller attempt. The lobus vagi is developed in the floor of the fourth ventricle mesially and hence morphologically ventrally of the spinal V tract and the corresponding position in the cord must lie ventrally of the dorsal cornu. The spinal representative of the communis system of the head (visceral sensory), if such a component exists in the trunk, should have its terminal centre in the dorsal part of the intermediate zone, while the viscero-motor centre should occupy the ventral part of that zone.

This intermediate zone in higher animals contains the lateral cornu, Clarke's column and other structures now

commonly regarded as associated with the visceral nerves. Among these structures is the paracentral nucleus. This is regarded by Onuf and Collins ('98) as a motor splanchnic centre. In the cat it resembles very closely the nucleus to which I have given the same name in the fishes. I am willing to hazard the conjecture from the facts already in hand, that this intermediate zone of the fishes is in the broad view a visceral centre and homologous with the visceral centre of the region of the lateral cornu of the mammals. In the fishes the disproportionate size of these nuclei, as compared with the dorsal and ventral cornua, is not surprising, in view of the more important rôle which visceral nerves play in these animals. The paracentral nucleus of these fishes apparently corresponds to the "median nerve cells" of Kölliker ('96, p. 165). Some of the cells described by Van Gehuchten ('95, pp. 118 and 123) in this region of trout embryos probably belong to this nucleus.

Returning now to the oblongata, the homologies can be fixed here with more certainty. The pre- and post-vagal portions of the fasciculus communis in Menidia obviously represent the fasciculus communis of the Amphibia. It is certain that most of the pre-vagal fibres terminate in the lobus vagi. The diffuse terminal nucleus of the Amphibia (the spinal nucleus) has been compacted and enormously hypertrophied in the fishes, being represented in the lobus vagi (which, however, may contain other structures also) and in some fishes the "lobus trigemini" as well. The scattered cells about the lower part of the spinal portion of the fasciculus communis may represent a part of the original spinal nucleus which has not been absorbed into the lobus vagi.

The homologies with the mammals seem to be not less

clear. The fasciculus communis in the restricted (*i. e.*, the original) sense in its typical form as we find it, for example, in the Amphibia, conforms very closely to the fasciculus solitarius of mammals and birds, as has been pointed out by Strong. The same homology will hold in the fishes, with this difference, that all of the communis fibres of the vagus, and in some fishes of the glossopharyngeus as well, enter their terminal nucleus directly, without participating in the formation of the longitudinal tract known as the fasciculus communis. The relations of the terminal nuclei are rather more complicated. In the Amphibia, the spinal nucleus is the more important, the chief IX+X nucleus being relatively small. In the bony fishes the spinal nucleus has been either greatly reduced, or, more probably, fused with the chief nucleus (lobus vagi), which suffers more than a corresponding enlargement. In the mammals both nuclei are present and well developed. We know from Kölliker's work ('96, p. 246) that the fibres of the fasciculus solitarius of mammals give off collaterals into the substantia gelatinosa surrounding this tract and there probably come into relation with the cells of that region, which thus constitute a "spinal sensory nucleus of X," (Van Gehuchten, '97, p. 483). The sensory IX+X nucleus of mammals is represented in the lobus vagi of fishes, though it does not follow, of course, that the two structures are exactly equivalent.

This way of looking upon the sensory IX+X nucleus as merely a specialized portion of the spinal nucleus of the vagus or nucleus of the fasciculus solitarius receives the strongest support from the recent work of Cajal ('96, p. 44) by the Golgi method. In discussing the sensory terminal apparatus of the IX+X nerves of the new-born mouse, he writes: "There are, therefore, in this animal, not two

sensory terminal clusters, nor two separate portions for the two nerves. A single root, common to both nerves, passes over into the fasciculus solitarius without loss of any fibres, in such a way that between the upper, or chief nucleus, and the lower, or descending nucleus, there is no distinction aside from that of position."

The preceding considerations, it seems to me, remove the difficulties raised by Kingsbury, regarding the homology of the fasciculus solitarius of mammals with the fasciculus communis of the Ichthyopsida. He questions this homology ('95, p. 173) because, among other reasons, "by considering the *fasciculus communis* as representing the *fasciculus solitarius* alone, we leave unaccounted for the larger end-nidus of vagal sensory fibres. Strong, apparently, confounds this with the end-nidus of the *fasciculus solitarius*." This position he reiterates in his later paper ('97, p. 31). There is, it is evident, a certain amount of confusion in the recent literature regarding this homology. It is equally evident that this confusion is largely a matter of definition. If we use the terms fasciculus communis and fasciculus solitarius in the narrow sense, as longitudinal fibre tracts, and if we rigidly define the related structures, especially the terminal nuclei, and take into account the various transformations which the latter undergo in different classes of vertebrates (particularly Cajal's results cited above), it appears that in the broad view the fasciculus solitarius and its related structures in the mammals are, taken as a whole, homologous with the fasciculus communis and its related structures in the Ichthyopsida, though if we should attempt to draw up a detailed comparison, the various elements would doubtless not be exactly equivalent in the two groups of animals. Indeed, the fasciculus communis is, as we have

seen, by no means exactly equivalent in the different groups of the Ichthyopsida even.

In the fishes the post-vagal fasciculus communis is feebly developed and of obscure significance. It is chiefly, if not wholly, composed of secondary fibres from the lobus vagi and not of root fibres, so that it cannot be compared with the spinal V and spinal VIII tracts, nor wholly with the corresponding tract in the higher vertebrates (spinal portion of the f. solitarius). Yet its relations to the commissura infima Halleri and the nerve cells therein contained, suggest very strongly Cajal's recent description of the "commissural nucleus" of the mouse ('96, p. 46) which is as follows:

,, Die Fortsetzung der gemeinsamen Wurzel des Vagus und Glossopharyngeus bildet, wie gesagt, den Fasciculus solitarius. Dieses Bündel wird nach innen und hinteren von einer Columne grauer Substanz begleitet, in welche es nach Kölliker eine Unzahl fein verzweigter Collateralen aussendet, die, wenigstens bei wenige Tage alten Mäusen, niemals bis zur Substantia gelatinosa des Trigeminus vordringen. . . . . . Dicht unter dem Ependym nähern sich die Solitärfascikel der Raphe und ihre grauen Terminalmassen vereinigen sich hier in einem Central- oder Mittelganglion, das wir *Commissurenkern* benennen wollen.

,, Drei Viertel der Fasern des Fasciculus solitarius enden, indem, sie sich kreuzen, in diesem Ganglion. Unter demselben besteht ausserdem ein kleines, bis über die Pyramidenkreuzung hinaus verlängertes Bündel, das anfangs in einer, vor dem Kern des Burdach'schen Stranges gelegenen grauen Masse, späterhin, nachdem letzterer verschwunden, im inneren Theil der Basis des Hinterstranges des Cervicalmarks anzutreffen ist. Wäh-

rend dieses intracervicalen Verlaufs sendet genanntes Bündel vereinzelte Collateralen aus, die sich nach innen zu in einen kleinen, ungenau begrenzten, sehr dicht an der hinteren Commisur gelegenen Herd grauer Substanz verzweigen."

A comparison of this description and the accompanying figures with the relations in the fishes which I have examined (including Mugil, Haploidonotus and Fundulus) very strongly suggests that the commissura infima Halleri contains the homologue of the commissure of Cajal's *Commissurenkern.* I am inclined to accept this homology, recognizing, however, that the commissura infima contains other fibres than those pertaining to the fasciculus communis. Whether the cells found in this region in fishes are homologous with the cells of the commissural nucleus of the mouse, I would not venture to guess.

Mayser ('81, p. 296) recognized the intimate relation of the commissura infima in the cyprinoids with the lobus vagi and the vagus nerve. The caudal portion of the commissure he inclines to regard as in part a decussation of the spinal V tract and in part a commissure of the dorsal cornua of the spinal cord. This I can confirm; *i. e.,* I find medullated fibres entering the commissure from the cephalic portion of the nucleus funiculi. They are probably secondary fibres. Niedzvietzky ('97, p. 542) has more recently described in the rabbit a commissure containing medullated fibres between the lower or caudal ends of the two fasciculi solitarii. A similar condition has been previously noted by Koch ('92) in the bird.

The homologies proposed in the preceding section may be summarized as follows:

(1). The fasciculus communis and its related structures (including the lobus vagi and the chief vagus roots)

of the fishes are as a whole homologous with the fasciculus solitarius and its related structures (including the sensory IX + X nucleus and the chief sensory vagus roots), excluding motor and general cutaneous elements in both cases.

(2). In the fishes the pre- and post-vagal fasciculus communis represent the fasciculus solitarius of the mammals, though the parallelism is probably not exact.

(3). The terminal nucleus of the fasciculus solitarius or the "spinal nucleus of the vagus" of the mammals has in the fishes been for the most part absorbed by the lobus vagi. Its caudal portion may persist, however, behind the commissura infima.

(4). The sensory IX + X nucleus of the mammals is merely a specialized portion of the nucleus of the fasciculus solitarius, and, accordingly, is represented with the latter in the lobus vagi of the fishes.

(5). The transverse fibres of the commissural nucleus of Cajal are probably homologous with the fibres of the spinal portion of the fasciculus communis, which appear in the commissura infima Halleri of the fishes.

Since this discussion was written and submitted for publication two papers have appeared which have an important bearing upon the homologies proposed. Both Van Gehuchten's researches upon the real origin of the cranial nerves (*Journal de Neurologie*, 1898) and Bunzl-Federn's paper on the central origin of the vagus (*Monats. f. Psychiatrie u. Neurologie*, V., 1, Jan., 1899) give the results of degeneration experiments by the Nissl method after resection of the vagus. Van Gehuchten shows that section of the vagus roots in the rabbit results in chromatolysis of cells throughout the dorsal or chief vagus nucleus. He concludes that this nucleus is wholly motor and confirms this by Golgi preparations. Marchi preparations showed that the sensory nucleus of the vagus is confined to the cells accompanying the fasciculus solitarius, the "spinal nucleus of the vagus." This would confirm in some degree the results of Forel ('91); but it is significant that Bunzl-Federn, also working upon the rabbit by the same method, and getting essentially the same anatomical results, does not admit that the dorsal nucleus is entirely motor.

If Van Gehuchten's results stand, it would require modification of the homologies proposed above to this extent: The chief, or dorsal, vagal nucleus of mammals would be a viscero-motor centre and the homologue of the sensory portion of the lobus vagi would have to be sought in the "spinal nucleus of the vagus" of mammals only.

Attention may also be called to the fact that the series of transections of the medulla of the rabbit given by Van Gehuchten (pp. 294–295) shows that the dorsal vagus nucleus and the fasciculus solitarius run down into the intermediate zone rather than into the dorsal horn region, thus agreeing with our findings in the fishes.

If we regard the fasciculus communis as the intra-cranial continuation of the visceral system of the "intermediate zone" of the spinal cord, as suggested above, we should expect to find in it or intimately associated with it many kinds of fibres, both afferent and efferent, for the various visceral functions. Such indeed is clearly the case, though we cannot as yet effect their analysis centrally. These being the primitive elements of the communis system, it follows that the fibres from the taste buds and terminal buds of the skin are phylogenetically later acquisitions, developed as a direct result of advancing cephalization. It is a significant fact that fibres from terminal buds are never found in the spinal nerves. Even in an extreme case, like the free tactile rays of the pectoral fins of the Triglidæ, which receive a surprisingly rich innervation from enormously hypertrophied spinal nerves and which by analogy with the barbels of other fishes we should expect to find covered with terminal buds, the most patient and skilful application of modern nerve methods (Morrill, '95) failed to reveal any terminal buds or other similar specialized organs in the areas supplied by these spinal nerves. On the other hand, whenever terminal buds occur on the bodies of fishes, as they often do over the entire surface, they are always innervated by recurrent nerves from the head. The terminal

buds of the trunk, too, we have reason to believe, have grown back into it from the head, as the organs of the lateral line are known to do. We have no evidence that the terminal bud system was primitively present in a metameric way in the trunk, but, as in the lateral line system, all the evidence at hand points to its cephalic origin. The theoretical problems connected with the communis system are further discussed in Section 12.

The secondary connections have not been fully worked out for any of the cranial nerves. In the case of the vagus, as with the acustico-lateral nerves, these connections are of two types, crossed and uncrossed. The uncrossed fibres, or secondary vagus bundle, in the sense of Mayser, gather mesally and ventrally of the spinal V tract and maintain this relation up to the exit of the latter from the brain, when they pass directly up into the cerebellum (Figs. 17, 18, 19, *Sec. X*). The crossed fibres, after reaching the opposite side through the commissura accessoria, enter the tractus bulbo-tectalis (*tr. b. t.*) and a large part, if not all of them, reach the optic tectum.

IV.—The Motor Components.

For the description of the motor nuclei the reader is referred to the accounts of the motor nerves in the following sections. Some points of a more general morphological interest regarding these components have been suggested in the preceding pages of this section. It need only be added here that I confirm, in general, the division of the motor cranial nerves in two series, somatic and visceral. They all belong to the latter type in the fishes save the eye-muscle nerves. The nuclei of the branchio-motor type, viz., nucleus ambiguus, motor VII and motor V, I consider to be cranial differentiations of a

strand of viscero-motor cells of the spinal cord running along the lateral and ventro-lateral side of the canalis centralis, the paracentral nucleus of Onuf and Collins.

Fürbringer ('97, pp. 664 and 680) assigns to these paracentral cells (his ventro-lateral series) and their fibres which emerge with the dorsal roots (his lateral fibres) the viscero-motor function throughout the Vertebrata, including the Cyclostomata and Amphioxus. The visceral component is larger in cyclostomes than in higher vertebrates. These cells he also directly compares with the viscero-motor nuclei of the oblongata.

V.—Summary of Section 3.

The general cutaneous nerves enter the brain by the V and X roots. The trigeminal fibres terminate in part in a chief trigeminal nucleus mesally of the point of entrance of the root, while the larger part pass caudad as the spinal V tract to terminate, after receiving the general cutaneous component of the vagus, in the n. funiculi of the spinal cord. This system is, therefore, the direct cranial representative of the dorsal cornu of the cord.

All nerves of the acustico-lateral system (r. lateralis vagi, VIII, dorsal and ventral lateralis roots of VII) terminate in the tuberculum acusticum, which is intimately related to the cerebellum. This system has also ascending (cerebellar) and descending (spinal VIII) roots.

The communis system is represented in the VII, IX and X nerves. The terminal nucleus for all of its fibres lies in the lobus vagi. This system is very completely isolated and unified in the head, and yet is apparently related to a sensory system of the trunk, closely associated with the spinal viscero-motor centres (intermediate zone). The communis system was primarily a viscero-sensory

(entodermal) mechanism. This is its sole function in the trunk. In its cranial portion it also supplies taste buds and terminal buds (ectodermal organs). The communis system as a whole corresponds with the fasciculus solitarius of mammals, together with its associated structures (sensory vagus nucleus, etc.), though the comparison is not exact. Each of these tracts is related to a dorsal commissure, the commissura infima Halleri in the one case and the fibres crossing in connection with the commissural nucleus of Cajal in the other.

SECTION 4.—THE SPINAL NERVES.

I.—The Fourth Spinal Nerve.

Our examination begins with the fourth spinal, which may be regarded as the first typical trunk nerve. The dorsal and ventral roots, of which the latter is the larger, emerge by distinct but closely approximated foramina through the base of the neural arch of the third free vertebra. The roots, foramina and ganglion all lie in the same transverse plane. The dorsal root (*4 sp. d.*) is composed wholly of fine fibres, the ventral root chiefly or wholly of coarse ones. From the ganglion are given off two minute dorsal rami, a medium-sized medial ramus and a large ventral ramus, besides the r. communicans with the sympathetic trunk.

The *ventral ramus* (*r. v. 4*) pursues the typical course. The *medial ramus* (*r. m. 4*), like the ventral, contains both sensory and motor elements. It passes laterad and caudad, not in the intermuscular septum between the dorsal and the lateral musculature, but through the lateral part of the dorsal musculature, following for part of its course one of the intermuscular bones, which it finally

crosses. Just before reaching the skin it breaks up around the r. lateralis vagi to supply the muscles and skin of that immediate neighborhood.

Baudelot and many others regard the ramus medius as the homologue in the spinal nerves of the r. lateralis vagi. This is undoubtedly an untenable hypothesis; and the r. lateralis cannot be regarded as a collector for the spinal nerves in the sense so commonly assumed. The significance of this anastomosis, where it exists, is discussed at the close of Section 12, I.

The two *dorsal rami* are quite distinct in origin and nature. One (*r. com. 4*), of fine fibres, arises from the ganglion and, directly dorsad on the outer surface of the neural arch of the vertebra, joins the ramus spinosus of the third spinal nerve (*r. sp. 3*), the compound nerve then running dorsally in the intermuscular septum between the general dorsal musculature and the interspinal muscles (the mm. supra-carinales of Owen), where it joins the r. lateralis accessorius. This nerve is the *r. communicans* of Stannius and is apparently exclusively sensory. The other dorsal ramus (*r. sp. 4*) arises from the motor root and is apparently exclusively motor. It effects similar relations with the r. communicans of fifth spinal nerve and then, as before, the mixed nerve thus formed joins the r. lateralis accessorius, previously, however, sending numerous fine branches into the dorsal musculature. This is the *r. spinosus* of Stannius.

This, it appears from the literature, is the typical arrangement of dorsal rami in fishes. (Compare especially, Owen, '66, Vol. I, p. 308.) The fact that the cephalic one of these rami is sensory and the caudal one motor would seem to be correlated with the rhythmical movements of the body in swimming. Thus the sensory

stimuli arising in the contracting segment and transmitted to the spinal cord through the r. communicans might be of use in regulating the motor impulses to be transmitted to the next following segment through the r. spinosus. The anastomosis with the r. lateralis accessorius is in every segment examined a very broad one, the entire sensory component of the dorsal spinal ramus passing bodily into the r. accessorius. See the latter nerve for further mention.

The relations of visceral fibres to the spinal nerves have not been investigated, as my methods are not adapted for that research.

II.—The Third Spinal Nerve.

The origin of the third spinal nerve resembles that of the fourth except that the roots are larger; they emerge in the same way by separate foramina in the second free vertebra, and exhibit the same difference in the calibre of the fibres. The coarse ventral fibres, as before, can be traced through the ganglion. Of the dorsal rami, the *r. spinosus*, *r. sp. 3* (wholly motor), and the *r. communicans*, *r. com. 3* (wholly sensory), are as in the last case; so also the *r. medius*, *r. m. 3*, save that the number of its sensory fibres is smaller.

The *ventral ramus* (*r. v. 3*) is large, the sensory portion being more than three times the size of the motor, which is of about the average size for a spinal nerve. It gives off immediately a minute twig for the dorsal musculature (not shown on the plot), and then runs under the dorsal musculature to the lateral edge of the latter, where it breaks up into three branches. Two of these, which are composed of fine fibres, run caudad and laterad, the first running up over the depressor of the pectoral fin and

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between that muscle and the dorsal musculature, the second behind the insertion of the depressor, and both distributing to the surface of the fin. Their ramuli run out parallel with the fin rays, those of the first branch supplying the skin of the middle portion of the fin, those of the second branch the skin of the ventral portion.

The third branch is the true ventral ramus, containing all of the motor fibres and the remainder of the sensory fibres. Having separated ventrally from the other branches, it receives a small coarse-fibred twig from the brachial plexus, then continues ventrad to supply the ventral musculature (*v. m.*) and the skin lying immediately behind the pectoral girdle. The three branches of the ventral ramus are crossed externally near the point of their separation by the other fibres for the pectoral fin derived from the brachial plexus; but the third spinal has no connection with the brachial plexus save the small motor twig received by the ventral ramus, though on the opposite side of the specimen plotted the relations are somewhat different; see the account of the second spinal.

III.—The Second Spinal Nerve.

The roots of the second spinal nerve are larger than those of any of the succeeding nerves, the dorsal root (*d. 2*) being somewhat larger than the ventral. The two roots pass out through a common foramen in the neural arch of the first free vertebra. The two *dorsal rami* are like those of the third spinal nerve; the *ramus medius* (*r. m. 2*) also has the same relations except that it appears to contain only motor fibres.

The large *ventral ramus* (*r. v. 2*) under the lateral edge of the dorsal musculature is joined by a large bundle of coarse and fine fibres from the mixed ventral ramus of the

first spinal (*r. v. b+c*) and at the point of union there arises from the second spinal the small bundle of motor fibres which has been mentioned as going down to join the ventral ramus of the third spinal. The mixed trunk now gives off about six small branches of coarse fibres for the depressor of the pectoral fin, two of which are drawn upon Fig. 3 (*dep.*) These motor fibres are derived chiefly from the first spinal, though a few seem to come from the second. Those from the first spinal arise certainly mainly and probably exclusively from its caudal motor root, *c*.

The mixed trunk now turns laterally, through the depressor muscle and through a foramen in the scapula just behind the caudal edge of the cleithrum, the fibres meanwhile arranging themselves in three groups, the sensory fibres from the first spinal lying dorsally, the sensory fibres from the second spinal ventrally and the motor fibres between. The latter are derived chiefly from the first spinal, though a small bundle from the second is included. The sensory fibres from the first spinal (*cut 1*) remain distinct from those from the second spinal and pursue a very tortuous course to the skin of the side of the body behind the operculum and overlying the levator muscle of the pectoral fin. The cleithrum here consists of two broad lamellæ with the origin of the levator between them. This nerve runs first cephalad along the outer face of the inner lamella, then laterally through the muscle and then caudad along the inner face of the outer lamella of the cleithrum to the skin behind the latter.

A twig containing motor fibres from the first spinal leaves the trunk at the same point as the last and supplies the dorsal portion of the levator muscle (*lev.*)

The sensory fibres from the second spinal turn dorsad, the remaining motor fibres from the first and second

spinals turn ventrad, along the outer face of the inner lamella of the cleithrum. In the latter nerve the fibres from the two sources cannot be separately followed, but all enter the ventral portion of the levator of the pectoral fin (*lev.*) The sensory fibres last mentioned (*f. d. 2*) pass to the pectoral fin and break up into several ramuli which run out parallel with the fin rays, thus supplying the skin of the dorsal part of the fin, *i. e.*, the portion not inner-vated by the third spinal.

On the right side of the specimen upon which this de-scription is based the composition of the brachial plexus is in one respect different. The middle portion of the pec-toral fin is supplied by a nerve which has the same course over the depressor of the fin as the corresponding nerve on the left side, but which has a double origin. The greater portion of the fibres arise from the mixed ventral rami of the first and second spinals before that nerve has pierced the scapula; they can be traced back to the dorsal root of the second spinal nerve. Shortly after their sepa-ration these fibres are joined by a much smaller twig from the third spinal, which arises at a point corresponding to the origin of the main nerve on the opposite side and then, instead of going caudad to the fin, turns cephalad for a considerable distance to effect the anastomosis. Which of these two cases is to be regarded as typical for this species, it is impossible to state, as comparative data are lacking.

IV.—The First Spinal Nerve.

The first spinal nerve (Fig. 7) differs widely from the others and shows very plainly that it is formed by the in-complete fusion of at least two segmental nerves. There are four roots, two dorsal and two ventral, all well devel-oped and the two pairs widely separated. It is obvious

from the sections that, in the adult, at least one vertebra has been fused with the skull, and through the portion of the cranium thus formed the roots of the first spinal emerge, the caudal pair (dorsal and ventral) through one foramen and the cephalic pair through another.

In conformity with the nomenclature of Fürbringer ('97), the cephalic pair of roots and the nerves issuing therefrom will be designated by the letter *b*, the caudal pair by *c*. The ganglia of the nerves *b* and *c* fuse to a certain extent, so that it is impossible to determine with precision from which sonrce some the sensory fibres of the peripheral rami come. The motor roots of *b* and *c* do not, however, mingle, so that, though the relations of the numerous rami at their origins are very complicated, yet it is possible to trace each with precision to its root.

The ventral roots are much larger than the dorsal, and both roots of *b* are larger than the corresponding roots of *c*, the dorsal root *c* being very minute. As in the case of all of the spinal nerves, the dorsal root arises at the extreme dorsal side of the spinal cord, the ventral leaves at its extreme ventral side, the two roots emerging through the foramen at the same transverse level nearer the ventral than the dorsal side. Some of the fibres of the motor root *c* are clearly seen to arise from the fasciculus longitudinalis dorsalis (Fig. 16). Their ultimate source is unknown. This root has two kinds of fibres, about half of the number being less densely myelinated so that in Weigert preparations they stain a much lighter blue than the others. They are as large as, or even larger than the others which are of the usual character of motor fibres. Their significance is unknown, as they could not be traced far in either direction.

These roots and their rami are indicated in detail in

Fig 7, which is drawn from the same specimen plotted on Fig. 3, but to a larger scale. In this figure the sensory fibres are indicated in yellow, the ganglion being a lighter shade of the same; the motor fibres of *b* are drawn in light blue, the motor fibres of *c* in a darker blue.

Now taking up the rami arising from this complex in order, we have first a *ramus communicans* arising from the cephalic tip of the ganglion *b* (*r. com. b.*) consisting wholly of sensory fibres, and pursuing a typical course cephalad and dorsad over the upper surface of the supra-occipital bone. Leaving this bone, it then runs up in the intermuscular septum laterally of the interspinous muscles to join the r. lateralis accessorius in two strands (Fig. 3), the latter nerve having at this level turned mesally from its former lateral position to run in the same intermuscular septum, which position it maintains from this point caudad.

Close behind the last there arises a minute motor twig (*is. m. b.*), which pursues a course similar to that of a r. spinosus, though the true r. spinosus of this segment lies a little farther caudad. It supplies the interspinal muscles and does not join the r. lateralis accessorius, though it distributes near the latter nerve. The *true r. spinosus of b* (*r. sp. b.*), as it runs back over the supra-occipital bone sends a few fibres into the dorsal musculature and then joins the r. lateralis accessorius in the intermuscular septum in the typical manner, save that it does not anastomose with the r. communicans of the next following segment. It is exclusively motor.

The *r. medius b* (*r. m. b.*) arises between the two nerves last mentioned and contains motor fibres and a smaller number of sensory. Its stem at once divides into two branches, each of which takes some of both motor and sensory fibres and penetrates the dorsal musculature,

within which one runs cephalad and laterad, the other caudad and laterad. The former, having reached almost to the lateral edge of the dorsal musculature, sends a small motor twig farther forward, then turns abruptly caudad until, still within the same muscle, it joins the caudal branch. Here the sensory fibres of both branches unite and, separating from the motor fibres, run up in several bundles to supply the skin about the lateral line near its junction with the supra-occipital commissure. In their course toward the skin these sensory bundles run in an intermuscular septum which is occupied by that limb of the extra-scapular bone which articulates with the cranium, and follow, some the outer, some the inner face of that bone. Both branches of the r. medius *b* give off motor fibres for the dorsal muscle throughout their entire courses, and after their union and the separation of the sensory fibres, their fibres at once distribute to the lateral portion of that musculature.

The large *ventral ramus of b* (*r. v. b.*) takes the remaining motor fibres from that root and also a considerable bundle of sensory fibres. That the latter come from the dorsal root *b* is from every standpoint very probable, nay, almost certain, yet the sections do not afford an absolute demonstration, as the ganglia of the two roots cannot be sharply separated. The mixed ramus runs out under the dorsal musculature, and is there joined by the ventral ramus *c* (*r. v. c.*), with which its further course will be described.

There is no *r. communicans c.* Some fibres from the dorsal root *c* may, however, go out with the r. communicans *b*, the double nature of the anastomosis of that nerve with the r. lateralis accessorius offering a suggestion of such a condition.

The *r. spinosus c* (*r. sp. c.*) is perfectly typical. It runs back over the cranium and first free vertebra and effects the anastomosis with the r. communicans of the second spinal and the r. lateralis accessorius in the septum laterally of the interspinal muscles in the usual manner. It is composed of motor fibres, and just as it leaves the ganglion it gives off a motor branch dorsally for the dorsal musculature.

The *r. medius c* (*r. m. c.*) arises just cephalad of the r. spinosus. It is a small nerve and, like the corresponding nerve of *b*, it contains chiefly motor, with a few sensory fibres. It runs for a considerable distance cephalad in the ganglion, which it leaves close behind the r. medius *b*. It follows the latter nerve, lying ventrally of it, for some distance, though there is no anastomosis between them. It, however, goes much farther caudad than that nerve, running for a time parallel to the first intermuscular bone, and at the level of the third branch of the r. lateralis vagi (765) it crosses the second twig of that nerve (*r. l. 2*) and anastomoses with it. Some of its sensory fibres apparently go out to the skin with that twig, others independently a little farther caudad, the motor fibres having already been given off. Thus it appears that the r. medius of both *b* and *c* conforms to the typical arrangement of the spinal nerves in that the sensory fibres are distributed to the skin about the lateral line.

The ventral ramus of c takes the remaining fibres from the ventral root *c* and a smaller number of sensory fibres. It is smaller than that of *b*. It follows the latter nerve out under the dorsal musculature and soon joins it, the mixed trunk soon thereafter being joined by the r. ventralis of the second spinal nerve. At the point of union with the latter nerve a small motor twig (derived, it is

clear, from the ventral ramus *c*) separates dorsally to enter the depressor of the fin (Fig. 7, *dep.*) and just before this point the so-called hypoglossus nerve (the *r. cervicalis*, Fürbringer, *r. cerv.*) separates from the first spinal. This nerve draws off all of the sensory fibres of the r. ventralis *b* and a smaller number of motor fibres from the same source. It turns directly ventrad from its point of origin, running down in the walls of the abdominal cavity in the manner typical for ventral spinal rami. It descends first along the caudal face of the m. pharyngo-branchialis externus, then lower down in the same relation to the m. pharyngo-branchialis internus. Midway of this course two or three minute twigs of fine fibres are given off which run in a lateral direction along the caudal face of the m. pharyngo-branchialis externus to the skin which covers the cleithrum laterally. Having reached the cleithrum, the remaining fibres of the r. cervicalis turn cephalad along the inner surface of the m. pharyngo-branchialis at its origin from that bone. The origin of the pre-zonal ventral musculature from the cleithrum interdigitates with that of the pharyngo-branchialis, and the r. cervicalis, following the inner border of the latter muscle, comes to lie embedded between two slips of ventral musculature (m. sterno-hyoideus). Here a fine fibred cutaneous twig is given off ventrally to supply the skin of the ventral surface under the united tips of the two cleithra; the coarser motor fibres (Fig. 3, *m. shy.*) ramify through the substance of the sterno-hyoideus, which they innervate. No fibres from this nerve enter either of the pharyngo-branchial muscles, nor is there any anastomosis with the vagus, though the former condition is said to prevail in Amiurus (Wright, '84) and in the lower fishes (Fürbringer, '97) and the latter is figured by

Fürbringer ('97, Plate VIII, Figs. 5 and 6) in Esox and Mullus.

In another specimen from the one just described and figured the composition of the r. cervicalis is somewhat different. In addition to sensory and motor fibres from the first spinal nerve *b*, it receives also a large number of sensory fibres from the ramus ventralis *c*. The latter nerve has a larger proportion of fine fibres than in the specimen figured and it is not improbable that the fibres which it gives to the r. cervicalis are derived from the dorsal root *b*. In this specimen, as in the other, the motor fibres of the r. cervicalis clearly all come from the motor root *b*.

V.—Comparative Review of the First Spinal Nerve.

The cervical nerve corresponds to the cervical, *i. e.*, prezonal, plexus of the Selachii and in part to the n. hypoglossus of the higher vertebrates. Of course in the latter case the sensory element here present will have to be excluded. The results of Harrison ('95) go to show that the sterno-hyoid muscle of the salmon has the same origin ontogenetically as the tongue-muscles of the higher forms, that is, it is a true somatic muscle, derived from the lateral muscle plates. The nerve supply is therefore unquestionably homologous. Nevertheless the r. cervicalis of the bony fish cannot be homologized without reserve with either the cervical plexus of the Selachii or the hypoglossus of higher forms, for in both of these cases the nerves in question supply not only the post-hyal, but also the pre-hyal ventral musculature, while in the bony fish the latter is, as we shall see, absent. These points are again referred to in our account of the m. genio-hyoideus, Section 7, IV, 5, *iv.* For further critical and historical

discussions the reader is referred to Kupffer's excellent digest ('96) and to Fürbringer's great monograph ('97).

It should be noted that neither of these works clears up the problems connected with the pre-hyal ventral musculature of teleostomes and that in regard to another important moot question they are absolutely contradictory, viz., the morphology of the hypoglossus region of the cyclostomes. In the case of Petromyzon Kupffer describes the ventral musculature of the head as innervated from the vagus and not from the "hypoglossus" or first spinals, as in most other vertebrates. He thought that the ventral musculature of Petromyzon is of dermal origin and that it is not derived from the lateral muscle plates, as is the case with the "hypoglossus musculature" of other vertebrates. This would explain the innervation from the vagus instead of the first spinals and there would be no true hypoglossus in Petromyzon, for the corresponding musculature is wanting.

Subsequenty Neal ('97), working under Kupffer's direction, has re-opened the question, and he finds that the ventral musculature of the head is developed in Petromyzon in exactly the same way as in other vertebrates and is homologous throughout the series. He therefore concludes that the r. recurrens vagi of Petromyzon is homologous with the hypoglossus of higher vertebrates, while the so-called hypoglossus of the older writers on Petromyzon is composed of true spinal nerves.

Fürbringer, however, comes to a quite different conclusion. He finds ('97, p. 597), both in Ammocœtes and in adult Petromyzon, that the r. recurrens vagi is improperly named, for it contains no vagus fibres whatever; it is rather a r. recurrens spinalis, only secondarily bound up with vagus fibres and clearly separable from them. Petromyzon, therefore, conforms to all of the other vertebrates, of which Fürbringer has studied types of every class, in that the hypoglossus musculature is innervated by the spinals and the spinals only, the vagus never participating. Alcock ('98, p. 150) fully confirms

Fürbringer's conclusions from a study of serial sections of Ammocœtes.

This is a matter of no small importance, for the innervation of the ventral musculature, including the pharyngo-clavicular muscles, (cleido-branchialis 5) from the spinal nerves in all vertebrates is the key-stone of Fürbringer's argument from comparative anatomy for the distinction of paleocranial and neocranial nerves, a distinction of the most fundamental importance for his scheme of the metamerism of the head. According to that scheme, the primordial cranial nerves, back to and including the IX+X+XI complex, in all forms above the cyclostomes belong to those segments which are comprised in the paleocranium of Gegenbaur and from this point upward are to be sharply separated from the spinal nerves, though secondary anastomoses of various forms may occur. Passing up the taxonomic series a progressively larger number of spinal segments become fused with the head and either wholly or partially degenerate. In no case do their nerves fuse intra-cranially with the paleocranial nerves; on the contrary, they simply atrophy and to their more or less modified vestiges the name "spino-occipital nerves" is given. This group of nerves is further subdivided into "occipital nerves," which have lost their spinal character and have become incorporated into the head so that they emerge through foramina in the cranium, and "occipito-spinal nerves," which, though they emerge behind the cranium, yet have suffered some modification, usually the reduction of the dorsal root. The general rule may be laid down, that among the adults of almost every class of vertebrates, the more primitive forms are characterized by more, the higher forms by fewer, of the spino-occipital nerves. The embryology in most cases where it is known recapitulates more or less completely the steps in this reduction.

In Myxine there are five or six, in Petromyzon two or three spinal nerves which lie cephalad of the first spinal of the lowest selachians (Notidanidæ). With the latter forms the paleocranium is completed and the formation of

the neocranium begins. The higher mammals have lost from five to six of the first spinal metameres as compared with the Notidanidæ, the hypoglossus nerve corresponding probably to the ventral root of the twelfth spinal segment of Myxine.

In the bony fishes there are, as a rule, no occipital nerves, the first occipito-spinal nerve (*a*) of the ganoids, etc., is lost, and the second and third occipital nerves (*b* and *c*) are present, usually more or less intimately united with each other and often with the next following, or first true spinal nerve (4 of Fürbringer's nomenclature, my second spinal). In most of the teleosts examined by Fürbringer the ramus cervicalis is formed chiefly from *b*, with the addition of a variable number of fibres from *c*. In one case it is formed, however, wholly from *b*, as in the specimen of Menidia figured.

It is interesting to note that in Menidia the process of cephalization has gone farther in this respect than in any teleost mentioned by Fürbringer; for the "occipito-spinal" nerves *b* and *c* of those teleosts have here become "occipital" nerves. That is, the corresponding vertebra has been fused with the skull and they therefore emerge through the cranium. This is a phenomenon difficult of explanation in view of the low taxonomic position given to Menidia among the teleosts. It may be a cenogenetic acquisition correlated with the excessive development of the ears and the cranial parts with which they are related. In any case it does not stengthen one's confidence in the spino-occipital nerves as guides to phylogeny.

This latter conclusion I find is confirmed by Allis' latest paper ('98). From dissections of Scomber made under his direction by Dr. J. Dewitz, he finds a condition of the spino-occipital nerves which conforms neither to Fürbringer's account of the teleosts nor to my findings in Menidia, but much more closely to Amia. The spino-occipital nerves *a*, *b* and *c* of Fürbringer are all present, though their roots, as in Menidia, emerge through the occipitale laterale of the skull and fuse into a single ganglionic complex. From this and other cases cited by Allis

it is probable that the teleosts typically possess an occipito-spinal nerve *a* in a reduced condition. Whether that nerve in Menidia has been lost or has fused with *b* I cannot state. I have not made sufficiently extensive comparative studies to speak with authority on these homologies, nor have my methods been adapted for this problem.

In connection with the fact that the spino-occipital nerve *a*, which is lost or reduced in the teleosts, is present both in lower and in higher forms—as a spinal nerve in most Selachii and Amphibia, and as an occipito-spinal nerve in some sharks and ganoids, in Holocephali, Dipnoi and many Amniota (Fürbringer, '97)—it is exceedingly suggestive to notice that it is the teleosts alone of all these forms which lack the true pre-hyal ventral musculature. The so-called genio-glossus of teleosts is supplied by the trigeminus and is quite certainly not derived from the hypoglossus, or ventral spinal musculature (see the discussion in Section 7, IV, 5, *iv*), and with the loss of this musculature the corresponding spino-occipital nerve has naturally also suffered reduction.

Haller ('96, p. 53) says that in Salmo the spino-occipital roots (his post-vagal nerve) do not participate in the innervation of the hypoglossus musculature, but distribute exclusively to the pectoral fin. The ventral musculature is innervated, according to this authority, by a branch from the vagus. It will probably prove that this description is inexact, and that either the vagus branch in question supplies the pharyngo-branchial muscles instead of the sterno-hyoideus or else that the vagus stem is joined by fibres from a spino-occipital nerve which was overlooked by Haller. His generalization (p. 56) that the hypoglossus nerve was primitively included with the vagus and has only secondarily been dissociated from it will certainly not stand in the light of our present knowledge of both higher and lower forms.

VI.—Summary of the Spinal Nerves.

The typical spinal nerve gives off a ventral ramus, a medial ramus and two dorsal rami. The ventral ramus contains motor and sensory fibres for the ventral musculature and skin. The ramus medius contains motor fibres for the dorsal musculature and cutaneous fibres for the skin in the vicinity of the lateral line canal. This nerve is in no sense comparable with the lateral line branches of the cranial nerves, and the term ramus lateralis would better be avoided in the case of the spinal nerves, as suggesting bad morphology. Of the two dorsal rami, the first (r. communicans) is sensory, the second (r. spinosus) is motor. Each r. spinosus anastomoses with the next following r. communicans and supplies the dorsal musculature near the median line, especially the interspinal muscles. The r. communicans joins the r. lateralis accessorius and doubtless innervates the overlying skin of the back.

The brachial plexus receives elements from both portions *b* and *c* of the first spinal nerve and from the second and third spinals. The pre-zonal portion of this plexus— the ramus cervicalis of Fürbringer—receives some of the motor fibres of the r. ventralis *b* and all of the sensory fibres of that ramus. The post-zonal plexus has a single ventral ramus (in the strict sense, *i. e.*, for ventral musculature and skin) which receives some of the sensory fibres from the ventral ramus of the third spinal nerve, all of the motor fibres of that ramus and a small number of motor fibres from the ventral ramus of the second spinal. The sensory ramus for the skin of the side of the body between the pectoral fin and the opercular cleft, contains all of the sensory fibres of the ventral ramus *c* of the first spinal and no others. The depressor muscle of the pectoral fin is innervated chiefly from the ramus ventralis *c*

of the first spinal, though it apparently also receives a few fibres from the r. ventralis of the second spinal. It consumes probably all of the motor fibres of the r. ventralis *c*. The levator muscle of the pectoral fin is supplied chiefly by the r. ventralis *b* of the first spinal, but partly by the r. ventralis of the second spinal. The skin of the pectoral fin is supplied by three branches; the dorsal part by a nerve which comes from the ventral ramus of the second spinal and includes all of the sensory fibres of that ramus; the middle part by a nerve which in one case comes from the ventral ramus of the third spinal, in another case from the ventral rami of both the second and the third spinals; the ventral part by a nerve which comes from the ventral ramus of the third spinal.

The composition of the brachial plexus may be tabulated as follows:

First spinal nerve.
> Ramus ventralis, *b*,
>> Sensory: supplies all of the sensory fibres of the r. cervicalis.
>> Motor: supplies all of the motor fibres of the r. cervicalis (for the m. sterno-hyoideus) and most of those for the levator of the pectoral fin.
> Ramus ventralis, *c*,
>> Sensory: supplies all of the fibres for the nerve for the skin between the pectoral fin and the opercular cleft.
>> Motor: supplies almost all of the fibres for the depressor of the pectoral fin.

Second spinal nerve, r. ventralis,
>> Sensory: supplies dorsal part of pectoral fin and sometimes the middle part.

Motor: supplies some of the motor fibres of the first post-zonal ventral ramus (*sensu stricto*), a few fibres probably for the depressor of the pectoral fin and a small number for the levator of the pectoral fin.

Third spinal nerve, r. ventralis,

Sensory: supplies all of the sensory fibres of the first post-zonal ventral ramus, and sensory fibres for the middle and ventral portions of the pectoral fin.

Motor: supplies most of the motor fibres of the first post-zonal ventral ramus.

The first spinal nerve is a fusion of at least two complete segmental nerves whose motor components can be clearly distinguished from each other. All four of these roots emerge through the cranium, instead of behind it, as in other teleosts. The reduction in the teleosts of the first occipito-spinal nerve *a* is correlated with the absence in the teleosts of the pre-hyal ventral spinal musculature. Both this nerve and the corresponding musculature are found in vertebrates both above and below the teleosts in the taxonomic series.

Section 5.—The Nerves of the Vagus Group.

This section includes the account of the IX, X and XI nerves, including the r. lateralis vagi. The glossopharyngeus and the r. lateralis are anatomically quite distinct from the vagus; nevertheless they can best be described together. These nerves in Menidia conform in general to the usual teleostean arrangement, giving evidence in some features of specialization parallel with an elaborate branchial apparatus as a whole.

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The vagus group, as here defined, contains general cutaneous, acustico-lateralis, communis and viscero-motor components. The general cutaneous component is very small, the acustico-lateralis and viscero-motor are of considerable size, but the communis fibres make up by far the larger portion of the complex. This latter system is, however, far less highly developed here than in some other teleosts, such as the cyprinoids, in which the vagal lobes attain so enormous proportions. The IX nerve receives communis and viscero-motor fibres; the X nerve proper receives communis, viscero-motor and general cutaneous fibres. The n. lineæ lateralis, conventionally associated with the vagus, has no obvious morphological relation to the other components of this complex.

I.—The Roots and Ganglia of the Vagus Group.

The roots of the IX and X nerves are quite widely separated, the former arising under the origin of the r. lateralis vagi. The sensory and motor roots of the IX nerve are distinct at their origins, though close together, and they unite immediately after leaving the brain. The various elements of the vagus (aside from the r. lateralis) are so intimately united that analysis by gross methods would be quite impossible.

1.—The Communis Root of the N. Glossopharyngeus.

The sensory root of the IX nerve emerges from the brain just dorsally of the motor IX and these two roots diverge from each other very rapidly in passing toward their respective centres. The communis root passes dorsally of the spinal V tract, the motor root ventrally of it. This sensory root runs directly inward as a close round bundle of very fine fibres until it reaches the fasciculus

communis, which runs along the lateral wall of the fourth ventricle.   Its fibres turn caudad and enter this fasciculus, which in turn immediately enters the lobus vagi, as already described.

These fibres which enter the lobus vagi by way of the fasciculus communis do not appear to differ in any way from those which enter it directly from the vagus, for their central and peripheral relations are essentially the same.   Indeed in those fishes which have larger lobi vagi the IX nerve enters the lobus directly without participating in the formation of the fasciculus communis, as in the cyprinoids (Mayser, '81) and in the gadoids and Raniceps (Stannius, '49).

The IX nerve emerges close under the origin of the r. lateralis vagi, its origin being covered by the ramus ampullæ posterioris of the VIII nerve.   These latter fibres pursue an intracranial course as a thin flat band, running up until they lie in contact with the r. lateralis vagi.   The IX root runs along the inner side of this acoustic root and finally crosses it ventrally, the two roots lying as close to each other as possible.   There is certainly no extensive anastomosis between these roots and probably there is no exchange of fibres whatever, though from the nature of the conditions it is impossible to be sure of the latter point.

It can, however, be clearly made out that a very small bundle of communis fibres separates from the dorsal surface of the IX root before this nerve has crossed the VIII root.   This bundle goes dorsad between the fibres of the VIII nerve, already mentioned, and the medulla oblongata and enters at once the lateralis root of the vagus.   Its further course will be described with that nerve.

The IX root now continues to run directly outward, penetrates the ear capsule and then turns cephalad along the outer surface of the latter, lying ventrally of the vagus ganglion, but not at any time coming into contact with it. Here it is joined by the sympathetic chain, which accompanies it as far as the IX ganglion and then continues cephalad in the same direction.

The IX ganglion lies at the point where the nerve turns laterally and ventrally into its gill. A small sympathetic ganglion is applied to its proximal portion. The connection with the sympathetic chain and the anastomosing branch to the root of the r. lateralis vagi are the only connections which the glossopharyngeus has with any other nerves.

2.—*The Communis Root of the Vagus.*

The vagus proper arises by one great root (640–660), which contains three components intimately fused. The great majority of these fibres are communis fibres and pass directly into the lobus vagi, forming the outer fibrous layer of that structure. In this intracranial portion of their course these root fibres separate into two ill-defined tracts, a larger caudal root and a smaller cephalic as shown on Fig. 4.

Immediately upon entering the oblongata they cross the spinal V tract. This tract, which caudad of this level forms a cord-like protuberance on the dorso-lateral aspect of the oblongata, here breaks up into several large strands and sinks abruptly down to a more ventral position. The root fibres of the vagus interdigitate with these strands so that the relations here are rather confusing. In Fig. 4 all of the vagus fibres are conventionally drawn as if they crossed the inner and ventral face of the spinal V tract;

in fact the more cephalic of the root fibres run over the outer and dorsal surface of the spinal V tract.

The vagus ganglion seems single macroscopically, like the root, but microscopically it is clearly separable into four ganglia, as shown in Fig. 4, corresponding to the four branchial clefts innervated by this nerve. In each case the ganglion cells are separated from those of the adjacent divisions by the entering and emerging fibres, so that in Weigert preparations especially the discreteness of the ganglia is very conspicuous. This is slightly exaggerated by shrinkage during hardening. Nearly all teleosts, according to Stannius, exhibit such a branchiomeric condition of the vagus ganglia, though there is the widest variation in its amount. We have numerous steps to the condition in Raja (Shore, '89), where the widely separate ganglia lie each in its own branchial ramus. And this is especially interesting in view of Cole's more recent discovery ('96) that in Chimæra the IX nerve and the three branchials and the r. intestinalis vagi have quite independent origins and ganglia, like the IX in teleosts. The distinctness of the vagal ganglia in the present case may therefore be looked upon as vestigeal, and not merely as an adaptation to the existing branchial apparatus.

The fourth ganglion in Menidia (*g. X. 4+5*) is much the largest. It includes, besides the ganglion for the nerves of the fifth gill cleft, which are much smaller than the others of the series, the ganglion for the great visceral and œsophageal rami of the vagus. The ganglia for these various rami are indistinguishably fused. Lying dorsally of this ganglion and only imperfectly separable from it is the jugular ganglion, or ganglion of the rami cutanei dorsales (*g. X. 6*).

Remembering that these communis fibres of the vagus

supply two very different types of sensory structures peripherally (on the one hand the highly specialized taste buds and on the other hand the simplest possible free endings in the general visceral and mucous surfaces), the attempt was made to find some morphological criterion centrally for these two types of fibres. In this I was not very successful, though in the ganglia we get a suggestion which may be of some value. The anterior (cephalic) rami of the communis system undoubtedly contribute most of their fibres to taste buds and a smaller number to the undifferentiated mucosa. On the other hand, as we pass caudad the number of taste buds to be supplied diminishes, while the proportion of undifferentiated viscero-sensory fibres is greatly increased, until in the r. intestinalis and the œsophageal rami the fibres all belong to this latter category. Now, the ganglia of the glossopharyngeus and the first branchial of the vagus are composed of very large cells with medium and very small cells intermingled and occasional little nests of the smallest cells crowded very closely. As we go toward the caudal end of the ganglionic complex, we continue to find cells of the various sizes, but the smaller ones become increasingly numerous. The hypothesis suggests itself that the larger cells are related to the taste buds and the smaller ones to the visceral fibres. A careful cytological study and comparison of the ganglion cells of the several components would doubtless furnish many points of morphological value.

3.—*The Cutaneous Root of the Vagus.*

Peripherally the general cutaneous branches of the vagus are, as we shall see, very clearly separable from all of the other fibres of the vagus complex. On the other hand, the analysis proximally is attended with much

greater difficulty. The ganglion of this component (*jug. g.*, the jugular ganglion of Shore and Strong, not of Gaskell) is not sharply separate from the rest of the vagus ganglionic complex, yet sufficiently so to make plain that here, as in the tadpole (Strong, '95) it is the proximal portion of the ganglion which performs this function. Indeed we shall see below that the mode of origin of the rami cutanei dorsales of the vagus would of itself be sufficient to locate this ganglion quite precisely.

The root fibres of this component are so intimately intermingled with those of the large communis root, which are of nearly the same size, that I found it impossible to follow them into the brain in transverse sections. In longitudinal sections they cannot be separately followed all of the way from the ganglion to the terminal nucleus, but at the superficial origin of the vagus the small bundle of cutaneous fibres separates and, passing in between the cephalic and caudal communis roots, turns abruptly caudad into the spinal V tract.

This root entering the spinal V from the vagus I have found much larger in Haploidonotus than in Menidia and Kingsbury ('97) reports it as well developed in Amiurus, Perca, Roccus, Lepomis and Amia. Strong finds it also in the tadpole and from Kingsbury's description ('95, p. 177) it is clear that the same relation holds for Necturus, though Kingsbury was unwilling to admit the homology. The occurrence of this root is probably general throughout the Ichthyopsida.

4.—*The Motor Roots of the Vagus and Glossopharyngeus.*

i.—*The Nucleus Ambiguus.*—In the spinal cord I have described in Section 3 two nuclei which are presumably both motor, the nucleus of the ventral cornu and the para-

central nucleus at the level of the canalis centralis. The former ceases cephalad of the first spinal nerve and the latter is nearly or quite interrupted for a short distance there also, its place being taken, however, by the motor nucleus of the vagus, the nucleus ambiguus, which lies close to the floor of the fourth ventricle on each side. The rather large multipolar cells which compose this nucleus are arranged in dense rosettes, the cell group terminating very abruptly caudad. In none of the fishes which I have examined does the nucleus ambiguus gradually merge into the ventral cornu, as described by Haller ('96). Its relations are with the paracentral nucleus rather than with the ventral horn.

At the level of the exit of the most caudal fibres of the vagus nerve (663) a small compact bundle of fibres leaves this nucleus, probably deriving some fibres also from the nucleus of the opposite side, and passes to the ventral surface of the chief vagus root. The nucleus, continuing cephalad, is somewhat reduced for a short distance, but at about the level at which the most cephalic vagus fibres leave the oblongata (640) it is again greatly enlarged and at this point gives off a broad band of fibres, which is also probably re-enforced from the opposite side and which enters the vagus root and there joins the other motor root just described. The nucleus continues cephalad to 625, but crowded farther ventrad by the enlarged lobus vagi, so as to lie laterally of the fasciculus longitudinalis dorsalis. Several bands of fibres arise at intervals from the prevagal portion of the nucleus ambiguus and curve back to join the other motor fibres. This nucleus is only diagrammatically indicated in Fig. 4.

Quite separated from the nucleus ambiguus, but a very short distance cephalad is another very small nucleus of

cells of the same character lying close to the median line ventrally of the fasciculus longitudinalis dorsalis. It is partly embedded in, but chiefly dorsally of the commissura accessoria (614–611). Its fibres were not traced.

ii.—The motor vagus derives its fibres mainly from the nucleus ambiguus of the same side. It receives some fibres from the commissura accessoria which probably come in part from the nucleus ambiguus of the opposite side and in part from the fasciculus longitudinalis dorsalis.

The peripheral course of the vagus fibres from the nucleus ambiguus through the ganglionic complex can be followed only with great difficulty on account of the interlacing of the root-fibres. After emerging from the oblongata the two motor roots unite in the cephalic face of the great vagus root; they then descend to the ventral surface of the vagus ganglion and here the common trunk divides into two main branches, one directed cephalad, the other caudad. This is clearly the general course followed by most, if not all, of the fibres. Peripherally from the point of divarication of the motor fibres into the several rami they again appear sharply separated from the finer communis fibres and can thereafter be separately traced to their termini. In the ganglionic complex the motor fibres gather in bundles on the ventral surface of the ganglia. These bundles contain both coarse and deeply staining fibres and fine ones which stain feebly and which resemble communis fibres. The former are unquestionably derived from the nucleus ambiguus and can be followed to the striated musculature of the branchial apparatus, etc.; the latter are probably motor fibres derived from some other source and destined for the unstriated musculature of the œsophagus and viscera.

Kingsbury ('97, p. 5) describes in Amia fibres entering

the caudal motor root of the vagus from the ventral horn,
as well as from the nucleus ambiguus.   Haller ('96)
describes and figures from Golgi preparation similar fibres
from ventral horn cells (his ventral nucleus of the vagus)
in Salmo.   I have not found such fibres in Menidia, but
no Golgi preparations were made and I cannot deny the
possibility of their presence in small numbers.   Compare,
further, the last paragraph of the discussion of the m.
pharyngo-clavicularis externus later in this section.

   iii.—The Motor Glossopharyngeus.—From the nucleus
ambiguus arise also, as in the mammals, the motor fibres
of the IX nerve.   These fibres arise from the most cephalic
part of the nucleus and pass directly cephalad in the same
position as that of their cells of origin, *i. e.*, along the lat-
eral surface of the fasciculus longitudinalis dorsalis.
This course they maintain for a considerable distance
(625–600).   Although closely appressed to the fasciculus
longitudinalis dorsalis, these fibres can always be distin-
guished from it by their smaller size.   There is, more-
over, always a connective tissue septum between them.
In this position the tract from the nucleus ambiguus
divides (Fig. 18) into two distinct round bundles of which
the dorsal (*IX f. l. d.*) is the larger.   The ventral one
alone is the motor IX root (*mot. IX*).   At 600 this bundle
separates to enter its nerve, but the dorsal one continues
cephalad in the original position.   Here the latter is
joined (595) by the motor root of the VII nerve, as
described below, and a little farther forward it indistin-
guishably fuses with that root and with the fasciculus.
The motor IX root after leaving the fasciculus turns
sharply caudad and laterad toward its exit, crossing the
spinal V tract on the ventral side of the latter.   It is
joined just after its exit from the oblongata (620) by the

sensory root of the IX, which passes from the fasciculus communis to its exit dorsally of the spinal V tract.

The entire course of the motor IX fibres can be followed with precision from the nucleus of origin to the peripheral distribution. The general arrangement is essentially as described by Mayser in cyprinoids ('81). In the carp it does not form so sharp a genu and passes out dorsally of most of the fibres of the spinal V tract. Johnston ('98) describes the motor IX as arising wholly from the fasciculus longitudinalis dorsalis, evidently not having traced the fibres back to their nucleus of origin.

iv.—General Considerations.—Two classes of motor fibres emerge with the vagus of fishes, (1) coarse fibres from the nucleus ambiguus for the striated branchial musculature, (2) very fine fibres for the unstriated visceral musculature, such as the constrictor muscles of the lower part of the œsophagus, etc.

The nucleus ambiguus in these cases is the undoubted homologue of the nucleus of the same name in the mammals. The chief nucleus of the vagus in the mammals is commonly regarded as sensory (Van Gehuchten, '97, p. 481; Kölliker, '96, p. 239), yet Forel ('91) brought forth very strong evidence by v. Gudden's method tending to show that it is motor, while the descending, or spinal nucleus, which accompanies the solitary bundle, is sensory. In this he may be too extreme; nevertheless the probability remains very strong that in the mammals the chief vagus nucleus contains some motor cells. (Compare the more recent work of Van Gehuchten cited in Section 3, III).

We get a hint along the same line from the degeneration experiments of Niedzvietzky ('97, p. 534). After resection of the vagus in three adult rabbits he found cells

of the nucleus ambiguus of the same side degenerated and a smaller number of the opposite side. The "sensory nucleus of the vagus" he divides into two parts, an outer, or dorsal part, of small cells which is somewhat affected, and an inner part of larger cells, which is almost completely degenerate. It is probable that the latter is viscero-motor in function, though Niedzvietzky does not consider such a possibility. This probability is strengthened by the researches of Onuf and Collins ('98), in which it is proven experimentally that this nucleus in the cat has a large motor sympathetic element. I may add that they too regard this nucleus with its sensory and motor elements as the continuation of the "intermediate zone," or visceral centre of the spinal cord.

This intimate union of the viscero-motor and communis systems is not confined to the vagal region, but is characteristic of the entire extent of the fasciculus communis. We have a graphic illustration of this in a recent series of experiments by Langley ('98). The vagus and cervical sympathetic were cut and the central end of the vagus joined to the peripheral end of the sympathetic. The result was that "certain of the fibres of the vagus grow along the course of the cervical sympathetic and make functional connection with the cells of the superior cervical ganglion," and there was a restoration of the proper functions of the peripheral sympathetic, including some classes of fibres such as pilo-motor nerves which are not represented in the vagus root. In another experiment the proximal end of the lingual (chorda tympani) was in the same way joined to the peripheral end of the cervical sympathetic, with a similar restoration of the functions of the peripheral cervical sympathetic. These interesting experiments go to show that sympathetic motor (pre-gan-

glionic) fibres go out with all of the roots from the com-
munis system and that these fibres are so similar to the
corresponding fibres which go out with the first spinal
roots that they are capable of functional substitution for
them.

In a preceding section we suggested the theory that in
the oblongata the unspecialized visceral sensory centre
corresponding to that of the spinal cord has had differen-
tiated from it the special sensory system for the terminal
buds, a sensory system which is not represented in the
spinal cord. So also in the head there seems to have been
a special differentiation of the viscero-motor system (nu-
cleus ambiguus, motor VII and motor V) co-ordinate
with the development of the branchial motor apparatus,
which we know to be derived, not from the somites, but
from the splanchnic musculature.

The suggestion made by Cole in a recent paper ('98, p.
233, foot note) is interesting in this connection: "A pos-
sible explanation of the vagus, I think, is that the bran-
chial nerves are secondarily sympathetic, *i. e.*, in function
only, whilst the visceral nerve is primarily sympathetic,
i. e., represents a modified portion of the sympathetic, and
thus both physiologically and morphologically belongs to
that system. Its connection with the vagus is thus a
'blind' and of precisely the same significance as the con-
nection of the sympathetic with the trigeminus and
facialis." The viscero-motor fibres of the trunk belong
to Langley's type of pre-ganglionic fibres, *i. e.*, they ter-
minate in sympathetic ganglia and reach their appropriate
visceral muscles only through the mediation of sympa-
thetic fibres. The same may hold true of the viscero-
motor fibres of small calibre which go out with the vagus,
but it is certainly not true of the motor fibres of large size

which go out from the n. ambiguus to the striated bran-
chial musculature.   If these latter fibres have been
derived from the pre-ganglionic system, they have cer-
tainly suffered a most remarkable metamorphosis.   If, as
implied in Cole's remark above, they have not been thus
derived, we should find it difficult to find any homologue
for them in the trunk and we may be led to assume that
they belong primarily to the branchial region, for several
lines of current research seem to hint at the possibility
that this region may be older than the trunk after all.

5.—*The Root of the R. Lateralis Vagi.*

The root of the lateral line nerve, after separating from
the lateral aspect of the tuberculum acusticum (610)
and emerging from the oblongata immediately dorsally of
the origin of the IX nerve, as it passes caudad, sinks down
until it comes to rest upon the dorsal surface of the ramu-
lus ampullæ posterioris (Fig. 17).   At this level it begins
to be crowded laterally by the emerging vagus root, upon
the ectal surface of which it is closely appressed without,
however, anastomosing with it at all.   It passes through
the same foramen as the vagus.   The auditory ramulus
referred to almost immediately separates and turns laterad
to the proper auditory organ, without any interchange
of fibres with the lateralis root.

The lateral line nerve at its origin is not composed ex-
clusively of the characteristic very large and heavily
myelinated fibres, but there are numerous medium-sized
fibres.   These may be diffusely scattered through the
trunk or they may be gathered into rather compact bundles,
whose positions and relations, however, vary in different
specimens.   They can be followed into the ganglion of
the lateral line nerve.   Their peripheral relations and

central connections are unknown.   The largest root fibres are fully 12 micra in diameter and the average size of all of the fibres is about 8 micra, while the smallest fibres are scarcely 3 micra.

About two-thirds of the distance between the exit of the r. lateralis and its ganglion it receives a small bundle of fibres (about 20 in number) from the IX root.   This little twig is of great interest and has been carefully worked out in a number of specimens.   The fibres are of small or medium size, considerably smaller than the lateralis fibres, but larger than the average communis fibres, the largest ones being 3 or 4 micra in diameter.   After leaving the IX root, they pass dorsad and caudad along the mesal face of the ramulus ampullæ posterioris and close to the medulla oblongata to enter the ventro-lateral surface of the r. lateralis.   On the opposite side of this specimen and in two others they run first up the mesal side of the r. lateralis, then laterally around the dorsal side of this ramus, finally to enter it in the same position as before described.

Neither these nor the other fine fibres of the lateralis root could be separately traced through the ganglion. This ganglion contains medium-sized ganglion cells, much larger than those of the VIII ganglion, but smaller than the largest of the vagus ganglion.   There are a few larger cells among them.   A considerable number of finer fibres leave the lateralis ganglion which are presumably related to those which enter it.   Their further courses will be described below.

II.—The N. Glossopharyngeus.

The organization of the IX nerve is exceptionally simple.   Its peripheral area is limited to one demibranch. It lacks the r. supra-temporalis, which is present in

Chimæra, in most selachians, in ganoids, siluroids and some other fishes, and accordingly it receives neither lateralis nor general cutaneous fibres.   The r. pre-trematicus is also totally wanting.   The ramus post-trematicus is, however, identical with the corresponding branches of the several branchial trunks of the vagus.   The nomenclature employed for the branchial musculature and for the cranial musculature in general is that of Vetter ('78).

The motor IX fibres from the n. ambiguus run along the ventral side of the root and at the ganglion they separate slightly from the latter ventrally, to rejoin the nerve beyond.   The motor component in this region just below the ganglion gives off fibres for the first m. levator arcus branchii internus (*l. l. a. i.*).   Just beyond the ganglion a very minute pharyngeal ramus (*ph. IX*) is given off from the fine-fibred component for the mucosa of the roof of the mouth above the first gill, then a minute motor twig for the first levator arcus branchii externus (*l. l. a. e.*).

All of the remaining fibres enter the first gill, just before entering which they divide into two nearly equal ramuli, a dorsal and a ventral.   The latter contains all of the remaining motor fibres and a somewhat larger number of fine communis fibres, passes down the outer or convex surface of the ceratobranchial bone and supplies the muscles of the gill filaments and their mucous surface.   It lies dorsally of the first demibranch and probably distributes most of its fibres to it.   The dorsal ramulus pursues a course parallel to the last, but on the opposite, or concave side of the ceratobranchial bar, distributing to the large taste buds with which this dorsal surface of the gill is plentifully supplied and to the long gill rakers.   Probably many of its fibres supply the general mucous surface,

though it is certain that most of them go to taste buds.
The sensory fibres of the ventral ramulus, on the other
hand, apparently do not go to taste buds as a rule. After
the first gill has joined the isthmus the dorsal ramulus
continues for a short distance to supply taste buds in the
floor of the mouth; the sensory fibres of the ventral
ramulus, after joining the pre-trematic ramus of the
first branchialis vagi, pass to similar taste buds nearer the
median line than the last, while the remaining motor
fibres separate for the m. obliquus ventralis of this gill.
On Fig. 3 none of the branchial ramuli of the IX and X
nerves are plotted for their full length except the dorsal
one of the IX nerve.

The absence of the r. pre-trematicus IX (r. hyoideus)
is, I think, to be accounted for by the peculiar relations of
the pseudobranch. This structure is very large indeed
and occupies the whole region above and in front of the
first gill cleft. It, however, belongs to the region of the
facial; the peripheral region pertaining to the hyoidean
branch of the IX nerve having been thus crowded out,
the loss of the nerve naturally follows. Stannius reports
the absence of the r. pre-trematicus IX in Esox and Silu-
rus and its great reduction in Belone ('49, p. 76). The
same cause has operated also to reduce the r. pharyngeus.
Cole ('98a, p. 145) has shown that in the fishes, as in the
mammals, this ramus usually joins the visceral portion of
the facialis and thus is a true Jacobson's anastomosis.
The commissure from the IX to the VII in Menidia is,
however, purely sympathetic (see Section 8).

III.—First Truncus Branchialis Vagi.

The origin and course of this nerve from its ganglion
are strictly comparable with those of the glossopharyn-
geus. There is given off first the minute motor twig for

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the second m. levator arcus branchii externus (*2. l. a. e.*) and then the truncus divides into pre-trematic and post-trematic rami. The former is quite small. It gives off immediately a pharyngeal ramus (communis fibres) for the roof of the mouth adjacent, which, though slightly larger than that of the IX nerve, is nevertheless inconsiderable.

The pre-trematic ramus, upon entering the first gill, takes its position on the outer or convex surface of the ceratobranchial bar just above the attachment of the second demibranch to the bar, where it may be followed to the base of the gill. Here it joins the ventral ramulus of the post-trematic IX and can no longer be separately traced. This anastomosis has been found only in the first gill. If it occurs at all in the others, it can involve only the ultimate terminal fibrils of the pre-branchial nerves, as careful examination has failed to demonstrate it. The other pre-trematic branches are smaller and can be traced into their respective gills a much shorter distance than this one.

The post-trematic ramus pursues a course in the second gill which is substantially similar to that of the IX in the first gill. The most important difference (aside from the apparent absence of the anastomosis of the ventral ramulus with the second pre-branchial) is correlated with the fact that the long gill rakers of the first gill are wanting in the second, their place being taken by numerous teeth born on the dorsal side. To these teeth and the large taste buds among them the dorsal ramulus is distributed, as well as to the taste buds of the floor of the pharynx near the base of the gill. The dorsal and ventral ramuli are about equal in size.

The ganglion of the first branchial nerve of the vagus is

more distinct than that of any of the other branchials, and this seems to be the rule among the teleosts. Stannius states that in Clupea and Alosa this ganglion is fused with the IX ganglion. He does not mention the division of the post-trematic nerve into dorsal and ventral ramuli. Baudelot, however, describes ('83) a somewhat similar condition in the carp, though there it is the pre-trematic ramus which is double, the dorsal ramulus being much larger than the ventral.

IV.—Second Truncus Branchialis Vagi.

This division of the vagus gives rise to four branches for the roof of the mouth, two motor and two mixed. First, there are the two purely motor twigs, one, very minute, for the third levator arcus branchii externus (*3. l. a. e.*), the other for the single large m. branchialis obliquus superior (*m. b. o. s.*). The third branch leaves the cephalic face of the post-trematic ramus and passes partly through, partly laterally of the second m. levator arcus branchii internus (*2. l. a. i.*). In its passage through this muscle it forms an intricate plexus and doubtless innervates it, though most of the fibres emerge and anastomose with the more lateral fibres, finally to enter the dentary canal in the upper pharyngeal bones (pharyngo-branchials). The remaining fibres of this pharyngeal nerve distribute to the mucus membrane of the lateral part of the pharynx (sensory buds and glands).

Regarding the levator arcus branchii internus muscles, there seem to be but two muscles in this series. The second one is much larger and longer than the first one. It originates from the skull far cephalad at the level of the exit of the third nerve and passes back almost horizontally to its insertion on the second pharyngo-branchial bone, so that it really serves as a protractor of these bones. The first levator arcus branchii internus arises from the skull much farther caudad

and inserts into the first pharyngo-branchial bone, thus passing more obliquely and serving as a levator as well as a protractor. It is innervated from the IX nerve.

The fourth pharyngeal branch (*ph. X. 2.*) arises directly from the ganglion immediately behind the origin of the truncus. It is mixed, containing both communis and motor fibres. It passes directly ventrad and mesad to the roof of the pharynx near the mid-line, passing along the mesal face of the very strong m. obliquus dorsalis superior and receives an anastomosing branch from the pharyngeal branch of the third branchialis vagi, as described below. In the roof of the mouth it turns cephalad, supplying richly the racemose glands of this region, the taste buds at their mouths and the small striated muscles at their bases.

The pre-trematic and post-trematic rami are as in the preceding case. (Fig. 1).

V.—Third Truncus Branchialis Vagi.

This trunk divides into pre- and post-trematic branches immediately upon leaving the ganglion. Each of these branches gives off a large pharyngeal ramus, the aggregate number of these latter fibres being much greater than in any of the preceding branchial nerves. These pharyngeal rami (*ph. X. 3*) pass ventrad to the superior pharyngeal teeth; they probably also supply taste buds adjacent. They anastomose freely with each other and with the most caudal pharyngeal ramus of the second division, so that the innervation of the roof of the pharynx in this whole region is very intricate. These plexiform anastomoses are not entered upon the plots. There are also two motor rami. One passes directly from the ganglion to the fourth m. levator arcus branchii externus

(*4. l. a. e.*), the other passes from the post-trematic nerve to the m. obliquus dorsalis (*m. o. d.*).

The pre- and post-trematic nerves are as before, save that at the base of their gill (the fourth) the remaining motor fibres of the ventral ramulus supply the m. transversus ventralis (one of the interarcuales ventrales) instead of the m. obliquus ventralis, which does not appear in this gill. The terminal sensory fibres of this ramulus supply the enormous taste buds near the median line of the floor of the mouth, those of the dorsal ramulus similar buds farther laterally, as in the other gills.

VI.—Fourth Truncus Branchialis Vagi.

The fourth branchial (*t. X. 4.*) separates from the general vagus complex farther caudad than any of its other rami. As in the preceding cases, it draws off both coarse and fine fibres. As it arches around dorsally from the mesal to the lateral aspect of the m. obliquus dorsalis posterior (of Vetter) it contributes most and probably all of its coarse fibres for the innervation of this muscle (*m. o. d. p.*).

This muscle, passing from the fourth gill bar to the caudal edge of the lower pharyngeal bone and classed as one of the interarcuales dorsales, is described by Vetter ('78, p. 509) as peculiar to Esox. The relations in Menidia conform in general to his description, though the muscle here seems to be larger and to arise mainly from the fourth epibranchial instead of from the ceratobranchial, as in Esox.

The pre- and post-branchial rami are both very small. The former passes to the fourth gill in the manner typical for the other gills: the latter is very minute and composed exclusively of fine, *i. e.*, sensory fibres. There being no gill behind the fifth gill cleft, it distributes to the general mucosa dorsally of the beginning of the œsophagus and

about the caudal end of the inferior pharyngeal bone. There are no obvious taste buds in this region. If present, they are very small.

VII.—Other Visceral Rami of the Vagus.

Under this head I shall describe motor and sensory rami of the vagus which distribute caudad of those visceral rami which accompany the branchial nerves. The ganglion of this division cannot be separated from that of the fourth branchial and only imperfectly from the jugular, or general cutaneous ganglion (*jug. g.*). There are few, if any, taste buds in the area supplied by it.

1.—*Ramus Intestinalis.*

Most of the fibres of this division are destined for the r. intestinalis or the equally large r. œsophageus. The former (*r. intest. X.*) runs caudad between the kidney and the dorsal wall of the œsophagus, giving off fibres to the latter from time to time and anastomosing at intervals with the main sympathetic chain of the trunk which lies farther dorsad. Its farther course was not traced.

2.—*Œsophageal Rami.*

At the point where the intestinal ramus separates from the branchial complex (730) several very large trunks of apparently the same nature (*r. œs.*) turn directly ventrad to the œsophagus, which is just closing off from the pharynx at this level. These fibres supply the strong œsophageal muscles and probably also the epithelium, which is here very glandular. No taste buds are present. The innervation of this region is surprisingly rich and most of the fibres are apparently motor. Both the circular and longitudinal muscular fibres of the œsophagus

which are supplied by these nerves are all or nearly all striated. In the plots I have not distinguished these fine viscero-motor fibres from the sensory fibres which they accompany because of the impossibility of analyzing them here or of tracing them to their nucleus of origin. In Fig. 4. the œsophageal and infra-pharyngeal rami have been slightly schematized; really they consist of several trunks with an elaborate plexiform anastomosis.

3.—*Ramus Cardiacus.*

As the œsophageal fibres curve ventrally around the œsophagus, a small bundle separates and accompanies the adjacent precaval vein to the heart (*r. car.*) This is the cardiac nerve. Its fibres are partly very fine and partly of medium size and heavily medullated.

4.—*Pharyngeal Rami.*

Of the sensory fibres, a small twig supplies the most caudal superior pharyngeal teeth (*ph. d.*), while several considerably larger nerves enter the caudal edge of the inferior pharyngeal bone for its teeth (*ph. v.*)

5.—*Branchio-Motor Rami.*

Besides the fibres above referred to, I enumerate with this division the following coarse fibred motor nerves for the branchial musculature. They can easily be traced back to the common motor bundle of the vagus and so with tolerable certainty to the nucleus ambiguus. As indicated on Fig. 4, the following motor nerves are given off:

i.—Ramus for m. transversus dorsalis (*m. tr. d.*)— This muscle runs from side to side between the two superior pharyngeal bones.

ii.—Ramus for m. retractor arcus branchii dorsalis (*m. r. d.*), a muscle which runs from the second and third

vertebræ to the superior pharyngeal bone (Vetter, '78, p. 511).

iii.—Ramus for m. pharyngeus transversus (m. ph. t.)— This is a large stout muscle extending between the two inferior pharyngeal bones. It is incompletely divided into two parts, a large ventral part which is supplied by a small number of very coarse and heavily myelinated fibres, like those for the other branchial muscles which can be traced back into the common motor component, and a smaller dorsal part which is dorsally confluent with the general constrictor muscles of the œsophagus and like them is supplied by many very fine fibres whose origin could not be traced. The muscular fibres of the ventral part are very large and thick, those of the dorsal part smaller, but not so small as those of the proper constrictor of the œsophagus.

iv.—Ramus for m. pharyngo-clavicularis internus (m. ph. c. i.)— This large muscle has its origin on the dorsal edge of the cleithrum near its ventral end and passes almost directly dorsad to its insertion along the lower edge of the caudal part of the inferior pharyngeal bone.

v.—Ramus for m. pharyngo-clavicularis externus (m. ph. c. e.).— This is a short thick muscle which has a tendinous origin from the inner face of the cleithrum farther caudad and much farther dorsad than the last. Its fibres are directed mesad, cephalad and slightly ventrad and cross those of the m. pharyngo-clavicularis internus at about a right angle, being closely appressed to the caudal face of the latter muscle near its insertion. Their insertion is tendinous upon the extreme ventro-caudal tip of the inferior pharyngeal bone ventrally of the insertion of the m. pharyngo-clavicularis internus and laterally of the caudal part of that of the m. pharyngeus transversus.

The motor fibres for the last two muscles leave the œsophageal complex near the point where the fourth branchial trunk separates, encircle the œsophagus, then divide and enter their respective muscles from behind and can easily be traced to their ultimate ramifications within these muscles.

This account confirms the general statement of Stannius ('49, p. 90). Wright ('84, p. 371) states that the pharyngo-claviculares are supplied by the first spinal nerve in Amiurus, and Harrison ('95) makes the same statement for Salmo. Vetter ('78, p. 524) states that they are supplied by the vagus in Esox; in Perca he demonstrated the innervation of the internal muscle from the vagus, but in Cyprinus he found that the ventral nerve formed from the first two spinal nerves (XII nerve of authors, r. cervicalis of Fürbringer) runs along the hinder edge of the m. pharyngo-clavicularis internus and he thought that the hinder part of this muscle receives some fibres from that source. In selachians and chimæroids these muscles are supplied by the spinals (Fürbringer, '97). In Amia (Allis, '97, p. 697) they are supplied from the vagus essentially as in Menidia, though in that case their nerve runs out with the ramus post-trematicus n. vagi quarti. Allis corrects McMurrich's statement ('85, p. 138) that the claviculares in Amia are supplied by the first spinal. The nerve (which really is the fourth spino-occipital nerve) merely traverses the muscle.

Fürbringer ('97, p. 469) describes the external and internal pharyngo-claviculares (his cleido-branchialis 5, external and internal) as innervated from the spinal nerves in Esox, Gadus and Caranax, and he considers that Stannius and Vetter are in error when they describe them as supplied by the vagus. In this it would appear as if Fürbringer were unduly influenced by theoretical considerations. Regarding the cleido-branchiales as somatic muscles, it accords ill with his scheme of somatic and visceral nerves to find these muscles innervated from the

paleo-cranial (and hence visceral) motor rami of the vagus (compare the discussion of Fürbringer's theories in topic V of Section 4).

As a matter of fact it is probably quite impossible in some cases to determine by dissection which of these nerves supplies the pharyngo-claviculares or whether both sometimes participate, as Vetter supposed.   For example, in Menidia the r. cervicalis of the first spinal nerve, as we have seen, runs down immediately behind both of these muscles and closely applied to their caudal surfaces along their entire extent.   The relations of this nerve to the internal muscle are especially intimate and while descending along its caudal face several small cutaneous twigs are given off which pass laterally along the surface of the muscle on their way to the skin.   These twigs are very minute and their courses tortuous, and it is doubtful whether even in a large fish they could be dissected out to their terminations, though their whole courses can be easily followed in the sections.   It is probably these fibres which Vetter supposed innervated the hinder part of the muscle and he was mistaken in regarding them as motor, but correct in his further supposition that, aside from these fibres, a branch of the vagus which he had overlooked furnishes the main innervation for these muscles.

In the case of Menidia there is no room for doubt that the relations are as above described.   My sections are perfect and absolutely free from ambiguity.   Of course it does not follow that the same conditions prevail in all teleosts.   If it is true that these muscles are innervated from the first spinals in Amiurus (Wright) and in the lower fishes (Fürbringer), this raises the question whether the muscles so named are homologous in Menidia and Amiurus and whether the pharyngo-claviculares of the teleosts are homologous with the coraco-branchiales of selachians and ganoids, as Fürbringer assumes to be the case.

An embryological examination may be necessary to decide this matter, which is, however, of some theoretical

importance, as mentioned above under the first spinal nerve; for if these are somatic muscles, as Fürbringer maintains, their innervation from the vagus can be explained only upon the assumption that either (1) one or more neo-cranial segments have been secondarily incorporated into the vagus nerve, or (2) that a paleo-cranial nerve may secondarily come into relation with a somatic muscle belonging to a neo-cranial segment.   Both of these assumptions are denied by Fürbringer.   It should be mentioned that there is one further possibility, viz., that these muscles may be innervated by somatic motor fibres from the ventral horn which go out with the vagus roots. Fürbringer does not admit this possibility either, and I have not found such fibres in Menidia, but they are described for Salmo (Haller, '96) and for Amia (Kingsbury, '97).

VIII.—Rami Cutanei Dorsales Vagi.

These comprise those general cutaneous fibres which are included with the vagus.   Three very delicate nerves arise from the jugular ganglion, which lies proximally and just dorsally of the ganglion of the intestinal and fourth branchial rami and only imperfectly separable from it. These nerves pursue devious courses to the skin of the opercular and supra-opercular regions.   Two of these arise from the caudal surface of the ganglion.   One, directed caudad (*cut. X. 3*), is accompanied for a short distance by the motor ramus for the trapezius muscle described below.   It then turns dorsad between the latter muscle and the dorsal musculature, to reach the skin at the caudal edge of the attachment of the operculum. Both the outer and the inner surfaces of the operculum at this point are supplied.

Arising with the last, but abruptly turning cephalad, is a second slender cutaneous twig distributing farther dor-

sally (*cut. X. 2*).   It goes cephalad and dorsad under the mucous lining of the pharynx at the extreme mesal angle of the gill chamber.   Under the caudal edge of the parotic process of the skull (640) it turns laterad and somewhat caudad and dorsad and distributes in numerous small branches to the skin adjacent to the lateral line canal caudad of this point.

From the cephalic face of the jugular ganglion the other cutaneous ramus (r. opercularis vagi) arises by two roots, both directed cephalad, one going ventrally, the other dorsally of the main vagus root, just cephalad of which (660) they unite and, turning dorsad, continue cephalad (*r. op. X.*).   They appear to be composed exclusively of cutaneous fibres, but as these roots are very minute and their courses sinuous, it is impossible to be certain that at their emergence from the general vagus root they do not carry with them some communis fibres also.   Some points in their distribution suggest that they do, though most of the fibres are clearly cutaneous, and as such all have been entered upon the plot (Fig. 4).

From the vagus root this twig goes cephalad and slightly dorsad and laterad under the parotic process, and at the origin of the m. adductor operculi runs laterally between this muscle and the parotic process to a position on the lateral face of the muscle between it and the levator operculi (610).   In this intermuscular space it continues cephalad and ventrad and crosses the deep, or motor, ramus opercularis VII.   It passes externally to the latter nerve and in contact with it, but there is no interchange of fibres, as Baudelot ('83) states is the case in the cyprinoids.

Having passed below the ventral edge of the m. levator operculi, it comes to lie between the m. adductor operculi

and the m. dilator operculi and here it breaks up into several branches which spread out over the inner surface of the latter muscle, (1) one extends cephalad and dorsad, (2) one caudad and dorsad, (3) one caudad and ventrad, and (4) one directly ventrad. Of these, all but the last are undoubtedly cutaneous nerves. The first one (*op. X. 1*) runs between the m. levator operculi and the m. dilator operculi to the skin under the lateral line canal; the second one (*op. X. 2*) can be traced along the inner surface of the m. dilator operculi for almost its entire length (back to 700), from time to time giving off twigs which break through this muscle to the skin of the dorsal part of the operculum. It innervates the cutaneous area lying between those supplied by the two caudal cutaneous branches (*cut. X. 2* and *cut. X. 3*).

The third branch (*op. X. 3*) also runs back along the inner surface of the same muscle, just dorsally of the upper edge of the opercular bone and farther back along the outer side of the dorsal surface of this bone between it and the m. dilator operculi. It can be followed nearly to the caudal end of this muscle (720) and finally passes through it at its insertion on the opercular bone to end in the skin of the dorsal part of the operculum. The area supplied is ventral to that supplied by the *r. cut. X. 3*. This is an exceedingly delicate nerve, containing only about ten fibres in all, and could not be traced with certainty even sections, but for the fact that the fibres are heavily myelinated, being nearly as large as typical motor fibres. Their cutaneous nature is, however, beyond question.

It is probably the intimate relation of the three cutaneous branches just noted to the m. dilator operculi which led Baudelot ('83) to describe branches of the oper-

cular ramus of the vagus as innervating the opercular muscles.

The fourth branch of the the r. opercularis vagi (*op. X. 4*), composed of very fine fibres, passes directly ventrad after separating from the third branch and joins the third branch of the r. opercularis superficialis VII (*op. s. VII. 3*) just above the dorsal edge of the opercular bone. The combined trunk now passes down the inner face of that bone and supplies the mucous membrane of the dorsal part of the lining of the operculum.

Baudelot ('83, p. 132) says of this nerve in the carp: "*Quant à la branche operculaire du pneumogastrique, elle descend jusqu'au bord inférieur de l'opercule en envoyant sur son trajet des filets à la peau : il est possible qu' elle s'anastomose à sa terminaison avec la branche operculaire superficielle*" [VII].

Guitel ('91) finds in Lophius that this nerve anastomoses with both the superficial and the deep opercular rami of the facial, and that the nerve for the mucous lining of the branchiostegal membrane comes from the latter anastomosis, instead of the former, as I find it in Menidia.

These cutaneous vagal fibres are of special interest. Their true relations seem not to have been clearly recognized by any of the older writers. Shore ('89) found in Raja a cutaneous branch in this position which he calls r. auricularis and regards as general cutaneous. Nevertheless it is not quite clear from his description (especially as he describes it as coarse fibred) that this may not be the r. supratemporalis vagi (lateralis fibres), which Ewart and Mitchell ('91) describe as arising in about the same position. It is probable that his cutaneous ramus contains both of these elements, as in Raja there is no r. supratemporalis IX for the canal organs (Stannius, p. 79, Ewart and Mitchell, '91).

Strong was the first to contrast clearly the r. supratemporalis (a lateral line nerve) and the r. cutaneous dorsalis

(= r. auricularis vagi), and indeed has predicted for fishes just the arrangement which we have here ('95, p. 155): "The question arises, then, as to what is the homologue in *lower* forms of the R. auricularis vagi of the tadpole. I may here simply say that I believe that future investigation will bring out more clearly a system of general cutaneous branches in this region coexistent with the lateral line nerves."

Allis' account ('97, p. 689) of these nerves in Amia obviously meets these conditions also, though he does not seem to have interpreted his facts in just this way. His first branch, or r. supratemporalis, of the vagus has two roots. One clearly comes from the nervus lineæ lateralis and was traced to lateral line organs. The other arises from an intra-cranial ganglion which corresponds perfectly to our jugular ganglion. These fibres distribute to the skin of the top of the head and the opercular region. Allis repeatedly emphasizes the fact that this nerve distributes to regions where terminal buds abound, and, though he is not explicit on this point, the inference is that he regards it as wholly composed of communis fibres. That it is largely so composed is probable from his description, but it is equally probable that some of these fibres are of general cutaneous character and comprise the r. cutaneous dorsalis.

It is evident from the descriptions of Stannius and Baudelot that the r. supratemporalis vagi (lateralis fibres) and the proper r. cutaneous dorsalis vagi are in some teleosts fused for the first part of their course, just as in general we find both lateralis and general cutaneous fibres in the analogous r. oticus. In the cyprinoids, for example (Baudelot, '83, p. 133), we have this nerve arising by two roots furnished with separate ganglia and giving rise to opercular rami, anastomosis with r. recurrens V [VII] (=r. lateralis accessorius) and doubtless also lateral line organs, though the latter are not mentioned.

Stannius describes (p. 85) an intra-cranial branch of the vagus in several fishes which doubtless corresponds sometimes to the r. supratemporalis; yet as it contains, in some

of the cases at least, general cutaneous fibres, his account may be introduced here. He finds it to contain both coarse and fine fibres, from the lateralis root and the chief vagus root respectively, but no motor fibres, as shown by the negative results of stimulation. In this latter point he differs from Baudelot, as we saw above. Stannius adds that the intra-cranial branch is absent in Scomber, Pleuronectes, Rhombus, Salmo, Coregonus, Ammodytes, Clupea, Silurus, Spinax and Raja. It is present in Perca, Acerina, Cottus, Trigla, Barbus, Caranax, Zoarces, Cyclopterus, Labrus, Belone, Gadus, Merlangus, Raniceps, Lota, Cyprinus, Abramis, Gobio, Tincta, Esox, Acipenser and Anguilla. Now Perca, Acerina, Cottus, Zoarces, Cyclopterus, Labrus, Belone, Gadus and Anguilla possess a r. recurrens V [VII] and this intra-cranial branch anastomoses with it. Stannius states that all forms which have a r. recurrens V [VII] also possess this intra-cranial branch, with the single exception of Silurus. He describes the intra-cranial branch also in those fishes which have a dorsal intra-cranial or cranial branch of the V [VII] nerve, with which it usually anastomoses, as in most cyprinoids. Or it may pursue an independent course to the skin, as in Barbus and Caranax trachurus, or to the meninges, as in Esox. It occurs, finally, in cases where there is no recurrens V [VII] and distributes mainly within the cranium, as in Trigla and Acipenser.

In the species enumerated by Stannius as lacking the r. cutaneous dorsalis it will probably be found that the nerves are so small and sinuous as to have eluded discovery. The anastomosis with the r. recurrens V [VII], or r. lateralis accessorius, described by Stannius and Baudelot probably pertains to a communis component of the cutaneous nerves. A similar anastomosis occurs in Menidia, though in this case the communis fibres go out with the r. supratemporalis rather than the cutaneous rami. See the account of the r. supratemporalis vagi below for further discussion of the morphology of these nerves, and Section 12 for discussion of the anastomoses with the r. lateralis accessorius.

IX.—Ramus for M. Trapezius (Accessorius).

A small motor twig (XI) which leaves the vagus complex at the ventral edge of the jugular ganglion is worthy of separate treatment. It passes caudad for a short distance in company with the r. *cut. X. 3* and supplies the m. trapezius. It is a very small nerve, containing only from ten to twenty fibres, a much smaller number than the cutaneous nerve which it accompanies. It is very sharply separable from the latter by reason of the greater size of its fibres. The sections are quite unambiguous and leave no doubt that this nerve actually terminates in the m. trapezius and does not merely pass through it. The accompanying cutaneous fibres do not enter the muscle, but pass to the skin mesally of it. The participation of spinal nerves in the innervation of this muscle has been definitely excluded. There are no spinal nerves in its vicinity and the entire course of the muscle has been examined microscopically without revealing any spinal fibres within or near it. As to the central relations of this nerve, we can only say that its fibres arise from the common motor root of the vagus.

The trapezius muscle arises from the ventral surface of the parotic process of the skull (Parker's term) and extends back as a well defined round bundle at the lateral edge of the dorso-lateral musculature to its insertion on the dorsal part of the cleithrum. The dorso-lateral musculature of the corresponding region arises from the dorsal surface of the parotic process and from the skull dorsad and cephalad of it.

Vetter ('78, pp. 526 and 541) states that an independent trapezius muscle from the cranium to any part of the shoulder girdle is absent in the bony fishes and that the

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dorsal musculature running from the skull to the extra-scapular (post-temporal) and supra-clavicular bones and supplied by the first spinal nerves is not homologous with the trapezius of selachians and Chimæra, but is a new structure in the teleosts.   On the latter point he is doubt-less correct, *i. e.*, so far as the proper dorso-lateral muscu-lature is concerned; but in Menidia the trapezius muscle is present in the typical form in addition and receives the typical innervation, so that Vetter's first statement will require modification.   The "trapezius" muscle described by McMurrich ('84) in Amiurus is stated to be innervated from the first spinal, so that it will fall under Vetter's rule.   In Lophius, however, the case is apparently the same as in Menidia, for here the "humero-mastoid" muscle is supplied by the vagus (Guitel, '91).

Vetter regards the m. trapezius of selachians and chimæroids as derived from the superficial "Ringsmuscu-latur," or constrictor system.   Its innervation from the vagus accords with this.

Max Fürbringer ('97, p. 374) verifies the accounts of Rohon, Duméril and Owen that the caudal ascending motor vagus root in Hexanchus is the accessorius Willisii. He has traced its connection in this species with the m. trapezius, which is especially well developed, and thus demonstrates its homology with the accessorius.   He con-troverts the view of Stöhr, Wiedersheim and others that the XI is a descendant of spinal nerves; but regards the vago-accessorius as indigenous to the head, "a primordial cranial nerve which has nothing to do with spinal nerves." This seems probable anatomically but requires embryo-logical confirmation.

X.—The Ramus Lateralis Vagi.

The ramus lateralis at its ganglion turns abruptly out-ward under the dorsal musculature and soon turns caudad. Its branches will be described from before backward.

1.—Ramus Supratemporalis Vagi.

This nerve arises from the dorsal surface of the lateralis ganglion and runs cephalad under the dorsal musculature and external to the auditory capsule. About two-thirds of its fibres are of the coarse lateralis variety, the remainder being finer fibres probably in part derived from the anastomosing communis root from the IX nerve, and representing the vagal root of the r. lateralis accessorius. About .3 mm. from the ganglion it gives off a branch which passes dorsad and caudad to the single canal organ of the occipital commissure, which lies in the same transverse plane as the lateralis ganglion. This branch, though mainly coarse-fibred, draws off a few fine fibres (*a. r. VII. 2* of Fig. 4) which, instead of turning back to the canal organ, go directly dorsad to the skin, under which they pass dorsad and then cephalad to join the r. lateralis accessorius near the median line (600, Fig. 3).

The remainder of the r. supra-temporalis (partly coarse and partly fine fibres) continues cephalad along the dorsal surface of the squamosal bone, being crowded laterally and dorsally by the projecting ear capsule. At 620 the coarse fibres separate and enter the canal organ (Fig. 5, *m. 1.*) of the main canal between the mandibular and infra-orbital canals. The finer fibres continue cephalad for a time along the squamosal bone just dorsally of the bony canal, gradually passing laterally to the skin under which they continue cephalad to 550. Here they divide, the larger portion turning directly laterally to supply a

large naked cutaneous sense organ which lies just above and in front of the pore at the union of the supra- and infra-orbital canals.   The smaller portion turns abruptly dorsad under the skin (*a. r. VII. 1* of Fig. 4) and joins the main trunk of the r. lateralis accessorius near the median line, as shown on Fig. 3.   The branch which supplies the sense organ contains slightly larger fibres than the one which joins the r. accessorius, many of the former being 3 micra in diameter, while the latter rarely exceed 2 micra.   This organ is, I think, a terminal bud, though it may be a free organ of the lateral line series.   Another similar organ was found on the opposite side of the specimen plotted and in a second specimen, lying less than 1 mm. cephalad and somewhat laterally of the upper end of the occipital commissure of the lateral line canal.   Its innervation could not be determined.

The very brief reference to the r. supra-temporalis in my Anzieger preliminary ('97, p. 427) has given rise to a misunderstanding.   Cole (98a, p. 185) interpreted this as implying that the r. supra-temporalis for the canal organs *m. 2* and *m. 4* is a r. supra-temporalis IX.   As a matter of fact the glossopharyngeus has no r. supra-temporalis in Menidia.

<center>2.—The First Lateral Ramulus.</center>

The first nerve given off from the r. lateralis behind its ganglion (*r. l. 1*, Figs. 3 and 5) supplies the first organ of the lateral series behind the occipital commissure, viz., the single organ contained in the post-occipital canal.   It contains a few fine fibres among the coarse ones.   The latter are not as large as some lateralis fibres, being from 5 to 7 micra.   These supply the canal organ, while the fine ones, which are about 3 micra in diameter, separate

from the ramulus in about the middle of its course and turn caudad, anastomosing in the dorsal muscle with the branch of the next ramulus, about to be described, which joins the r. accessorius lateralis (see Fig. 4).

3.—The Second Lateral Ramulus.

This follows close upon the preceding ramulus, and like it contains both coarse and fine fibres. It runs dorsad and in the dorsal muscles divides at once, one portion turning cephalad, the other caudad. At the point of division it effects an anastomosis with the ramus medius *c* of the first spinal nerve, as described in the account of that nerve, some of the latter fibres going out to the skin in the vicinity of the lateral line organ supplied by this ramulus. The fibres of both of these divisions are chiefly of medium size, those for the lateral line organ being from 4 to 6 micra, the others from 1 to 4. The portion running cephalad receives the minute anastomosing twig from the first ramulus, mentioned above, and then, while still within the dorsal musculature, divides. One twig, of fine fibres, turns dorsad and caudad to a naked cutaneous sense organ resembling the one innervated from the r. supratemporalis and situated a short distance dorsad and cephalad of the open caudal end of the post-occipital lateral line canal (735). The other twig (*a. r. VII. 3*, Fig. 4) runs dorsad, and then caudad under the skin and joins the r. lateralis accessorius (830, Fig. 3). These fibres, though slightly coarser than those of the other twig, are still finer than any proper lateralis fibres.

The portion of the second ramulus which is directed caudad, also divides into two twigs. One of these supplies the second post-occipital organ of the lateral line, which is the first free organ of the trunk. The other

twig goes dorsad through the muscle to the skin under which it continues caudad, at the same time turning toward the median line. On account of imperfections in the sections it could not be traced to its termination. It seems strictly analogous with the other twigs which join the r. lateralis accessorius, and I have no doubt that this is its destination.

It is probable that there are other cutaneous sense organs in this region supplied from these anastomosing twigs, which I have overlooked. Indeed in the younger specimens examined these have been found, though their nerve supply has not been traced.

4.—*The Third to Fifth Lateral Ramuli.*

The ramus lateralis was not traced back beyond the fifth ramulus. The last three ramuli observed are very minute, containing only a very few fibres of medium size. They run through the intermuscular septum, then dorsally under the skin to the organ. The first free organ of the trunk line is like the canal organs, large and flat topped. The organs diminish in size caudad and assume more nearly the characters of the smaller terminal buds, the free sensory surface being protected by the upward growth of the edges so as to give the whole organ a globose form with a narrow and shallow pore at the apex. The size of the fibres of the r. lateralis also diminishes as we pass caudad. Near the ganglion both proximally and distally of it, very large fibres predominate, some being as large as 12 micra in diameter, and the average is about 4. The very large fibres soon disappear and as far back as the level of the fifth spinal nerve the average size has diminished to six micra or less. The size of the fibres both here and in the case of the lateralis branches of the

VII nerve, seems to be correlated with the size of the organs to be innervated.

These branches of the lateral line nerve were all carefully traced and verified on the opposite side of the specimen plotted. They agree in detail with the description given above, except for slight variations in the arrangement of the anastomosing fibres. The cephalic and caudal portions of the second ramulus have separate origins from the r. lateralis and the caudal one only effects the anastomosis with the first spinal. There seems to be a subcutaneous anastomosis between the caudad portion and the third ramulus. A less thorough examination of other specimens shows that the general arrangement is the same. There is considerable variation in the details of the anastomoses, but there is always a very rich subcutaneous plexus in this whole region, arising from terminal branches of the r. lateralis, and the medial and dorsal rami of the spinal nerves and converging in the r. lateralis accessorius near the median line between the general dorsal musculature and the inter-spinal muscles.

Cole is certainly in error when he says ('98a, p. 169) that "it is certain that the true lateral nerve never anastomoses with the spinal nerves," if he uses the term anastomosis in the ordinary sense. There are, unquestionably, cases where branches of the lateralis vagi interdigitate with and for a short distance are bound up in the same sheath with branches of the spinals. But this temporary mingling of these dissimilar fibres has neither physiological nor morphological significance, and this is doubtless what Cole means by his statement.

Some further points bearing on the morphology of the ramus lateralis vagi are given in Section 12 under the head of the r. lateralis accessorius.

XI.—Summary of the Vagus Group.

These nerves, including the r. lateralis, receive visceromotor, communis, general cutaneous and acustico-lateralis fibres.

The viscero-motor fibres are of two types, coarse fibres from the nucleus ambiguus for the striated branchial musculature and fine fibres of unknown origin for the musculature (mainly unstriated) of the viscera. The communis fibres all terminate in the lobus vagi. They have three types of peripheral endings, viz.: (1) undifferentiated termini in the general visceral and mucous surfaces and more highly specialized termini in (2) taste buds and (3) terminal buds on the outer skin. The two latter classes of fibres are more numerous in the more cephalic branches of the complex, the former class in the more caudal branches, some of which they compose exclusively (intestinal and œsophageal rami). The general cutaneous fibres terminate in the spinal V tract and are distributed only to the outer skin by means of undifferentiated endings. The acustico-lateral fibres terminate mainly, if not wholly, in the tuberculum acusticum. They enter the brain only through the lateralis root and distribute only to organs of the lateral line.

The general scheme for the branchial nerves in Menidia may be expressed as follows: Each *truncus branchialis* arises from a special lobe of the general vagus ganglion and gives off the following rami.

1.—Pharyngeal rami, motor and sensory, supplying the pharyngeal muscles, taste buds, pharyngeal teeth, glands and mucous surfaces in general. They may arise from the truncus branchialis or from either the pre- or post-trematic ramus, or both, or from the ganglion directly. There is no branchiomeric uniformity as regards either their number or size, though the main sensory pharyngeal ramus is evidently typically associated with the pre-trematic ramus. These sensory fibres increase in number and importance as we pass caudad. They are reduced in the IX nerve.

2.—The pre-trematic ramus.   Always very slender and absent in the case of the IX nerve.   Probably wholly sensory.

3.—The post-trematic ramus.   Divides before entering its gill into two ramuli, the dorsal purely sensory, the ventral mixed.   The last post-trematic ramus, however, is single and sensory.

The internal and external pharyngo-clavicularis muscles are unquestionably innervated from the vagus and not from the first spinals as described for selachians and siluroids.

There are three rami cutanei dorsales of the vagus and these are all distinct from the r. supra-temporalis of the lateral line nerve, and from the associated communis fibres (vagal root of r. lat. acc.).   They supply the skin of the dorsal part of the operculum and the parts adjacent. The most anterior (cephalic) of these rami is the ramus opercularis vagi and it anastomoses with the r. opercularis superficialis facialis.

A true trapezius muscle is present in Menidia, being innervated from the vagus and not from the first spinal, as other authors have described for other species of teleosts.   Its nerve may be homologized with the n. accessorius Willisii.

The ramus lateralis vagi receives lateralis fibres from the tuberculum acusticum and communis fibres from the IX root.   The latter correspond to the vagal root of the r. lateralis accessorius of some other fishes.   Its first branch, the r. supra-temporalis, receives both components. It distributes its lateralis fibres to two canal organs, the one in the supra-temporal commissure and the other in the main canal between that commissure and the opercular canal.   Part of the fibres supply one or two naked sense organs which lie just dorsally of the main

canal.   The communis fibres join, in two branches, the
r. lateralis accessorius.   The succeeding ramuli of the
ramus lateralis supply each one organ of the lateral line,
beginning with the first one behind the occipital com-
missure.   The first and second ramuli each contain com-
munis fibres also, which communicate with the r. lateralis
accessorius.   The naked cutaneous sense organs not in
the lateral lines supplied by these nerves I have regarded
as terminal buds and they are so drawn in the figures; but
subsequent study of Gadus rather favors the idea that they
are pit-organs of the lateral line series.

SECTION 6.—THE AUDITORY NERVE.

The ear of Menidia is highly developed.   The auditory
nerve is, accordingly, large (Fig. 5).   There is an in-
complete division at its origin into caudal and cephalic
rami, the former being intimately associated with the n.
lateralis vagi, the latter with the lateralis roots of the VII
nerve.   The auditory root fibres are so intricately mingled
with those of the roots just mentioned that their intra-
cranial courses could not be analyzed.

There is a considerable bundle of coarse fibres passing
from the dorsal edge of the ramulus acusticus ampullæ
anterioris near its separation from the rest of the cephalic
auditory root dorsally to joint the dorsal lateralis root of
the facialis.   It runs externally to all of the other roots of
the V + VII + VIII complex and crowded in closely be-
tween the communis root of the facial and the recessus
utriculi (Fig. 20, *VIII—d. l.*)   In one of my series I found
what appears to be a similar twig from the VIII running
along the inner side of the ganglionic complex to the ven-
tral lateralis root of the facial (shown in Fig. 20 just dor-
sally of the motor root).   But as this could not be verified

in other series of sections it remains an uncomfirmed observation. Allis ('97, p. 624) describes an anastomosis between the r. ampullæ posterioris of Amia and the lateralis component of the IX root. As in the present case, the farther course of the fibres could not be followed.

The apparent origin of all of the acustico-lateral fibres from the tuberculum acusticum is a single fibre complex, the separation into the roots as we enumerate them taking place just before their emergence from the oblongata. The auditory rami break up to supply the papilla acustica lagenæ, the three cristæ acustici, the macula neglecta, the macula acustica sacculi, and the macula acustica recessus utriculi. The glossopharyngeal nerve runs along the inner face of the caudal ramus and as it emerges from the cranium passes between the ramulus ampullæ posterioris and the ramulus lagenæ just at their point of separation. There is no exchange of fibres between the VIII and the IX nerves. The r. lateralis vagi arises at the same transverse level as the caudal acoustic ramus but farther dorsal. It is crossed externally by the ramulus ampullæ posterioris but, though the two nerves are in contact for a considerable distance, there is no anastomosis. The cephalic ramus arises at the same transverse level as the VII nerve and its ramuli closely follow the outer face of the V + VII ganglionic complex. In this case also I think that there is no interchange of fibres.

Ganglion cells are not found in the auditory roots until they begin to break up into their ramuli, beyond which point they are freely scattered among the fibres reaching in some cases quite to the sensory epithelium. The cells are exceedingly minute, smaller than those of the lateral line ganglia and scarcely larger than the diameter of the medullary sheaths. The calibre of the

fibres of the auditory root varies widely, some fibres being very coarse, as large as those of the lateral line roots, though most are of medium size, while some are quite fine.   The latter are scattered among the coarser ones in rather close bundles at first.   Inasmuch as it was not possible to trace the different kinds of fibres to distinct origins centrally, nor to follow them with precision through their ganglia, the detailed account of the ramuli will hardly be necessary, for the descriptions of Retzius ('81) amply cover the topographical relations. These relations are shown on Figs. 5, 17, 18, 19, 20, 21.

SECTION 7.—THE TRIGEMINO-FACIAL COMPLEX.

The fifth and seventh nerves have been confused in the descriptions of the earlier writers upon the bony fishes and such confusion was inevitable so long as the method of dissection alone was relied upon.   Those who have studied these nerves microscopically have confined their observations to their root portions, and because of their ignorance of the peripheral courses of these roots have often been led into errors of interpretation.   I have succeeded in following all of the facial and trigeminal roots through the ganglionic complex with precision and most of the fibres have been traced to their peripheral endings with equal certainty.   The roots of the fifth and seventh nerves are as distinct in Menidia as in any vertebrate, all of the fifth roots emerging at one transverse level and the seventh at another.   These two root complexes are, however, so close together and so intimately joined immediately after their exit from the brain that their exact analysis would be impossible by dissection.   All of their ganglia fuse into one mass and are indistinguishable

macroscopically, the entire complex being termed by many writers the Gasserian ganglion. The microscope, however, readily analyses this complex and distributes the fibres from each element into their respective rami (Figs. 4, 11 and 12).

The analysis of the rami peripherally is a much more difficult matter. Nevertheless it has been accomplished with results which I think are free from ambiguity except in a very few points. There are very few of the rami which can be assigned to either the fifth or the seventh nerve alone. In a few cases, such as the r. palatinus VII, there is but one component represented; but in the majority of cases fibres from both the fifth and seventh roots are bound up in the same nerve trunk and the question of nomenclature becomes a perplexing one. The time will undoubtedly come, as Strong has pointed out, when the nomenclature of the cranial nerves must receive a thorough revision. The time is certainly not ripe for this now, and I have avoided, so far as possible, the introduction of new names, selecting from the current terms the one which seems the most appropriate in each case, and giving to it a definite and often somewhat arbitrary significance. Thus I have assigned, following the usual custom, the truncus hyomandibularis to the seventh nerve, though it receives general cutaneous fibres from the trigeminus root in addition to its proper facial fibres. Similarly the r. maxillaris trigemini receives communis fibres from the facial root.

As just intimated, the composition of the several rami at their proximal ends can be stated with accuracy. Peripherally the three classes of sensory fibres and the motor fibres can, with few exceptions, again be easily separated before they pass to their terminal organs. In the nerve

trunks the coarse fibres and the fine fibres can be sepa-
rately followed, but it is often not possible to keep the two
classes of fine fibres (communis and general cutaneous)
distinct throughout their courses, nor always the two
classes of coarse fibres (lateralis and motor). Neverthe-
less their terminal relations enable us to infer their courses
in the trunks with sufficient accuracy.

I.—The Roots and Ganglia of the Facialis.

The facial has four roots emerging at the same trans-
verse level, a ventral motor root, widely separated from
the others, ventral and dorsal lateralis roots and the com-
munis root, emerging between the two last. The last
three issue high up towards the dorsal side of the
oblongata.

1.—The Motor Root.

The motor VII nucleus lies near the median line in con-
tact with its fellow of the opposite side and separated
from the fourth ventricle by fibres of the fasciculus longi-
tudinalis dorsalis only. The cells are large and are
grouped on each side in two clusters, from each of which
a strong tract of fibres (secondary tracts or dendrites ?)
runs out laterally and ventrally into the lateral white col-
umns. In connection with the more mesal one of these
tracts are fibres which seem to run from the fasciculus
longitudinalis dorsalis to the VI root. The motor VII
nucleus occupies the position of the commissura accessoria
of Mauthner, which is interrupted in this region.

From both parts of this nucleus facialis fibres run dor-
sad and form a large, close bundle on the lateral aspect of
the fasciculus longitudinalis dorsalis. It lies just ventrally
of the bundle of fibres derived from the nucleus ambiguus,

as described above, and soon fuses with it. Like the latter, these fibres are of finer calibre than those of the fasciculus, which are very large. The fibres of the VII nerve soon withdraw from the fasciculus, but pass forward parallel with it for some distance. Whether the facial root receives additions from the fasciculus or contributes to it could not be determined. Presumably there is some relation by collaterals or otherwise, as the union of the fibres of the root and the fasciculus is here very intimate.

This arrangement of the motor VII root is substantially identical with that described by Goronowitsch in Acipenser ('88, p. 498). Johnston ('98) finds by the Golgi method in Acipenser that part of the motor VII root arises directly from its nucleus and a larger part from the fasciculus longitudinalis dorsalis. The entire course of these latter fibres apparently, was not impregnated, so that it remains uncertain whether they arise from cells of the VII nucleus farther back or whether they belong to the fasciculus proper.

At 577 (Fig. 19) the facialis fibres turn abruptly toward their exit. This motor root immediately after its exit from the oblongata joins the ventral lateralis root proximally of its ganglion and follows the ventral surface of that root, as shown on the plots.

2.—*The Communis Root.*

The communis root of the facialis passes into the fasciculus communis and constitutes the whole of the preauditory portion of that tract (Fig. 4, *f. c.*). It emerges from the oblongata closely wedged in between the dorsal and ventral lateralis roots (Figs. 19, 20, *com. VII*, Fig. 11) and passes, still between those roots, ventrally into the geniculate ganglion. This ganglion is of an elongated

pear shape with the larger end down. It is bounded above by the dorsal lateralis root and ganglion, in front by the Gasserian ganglion, below and behind by the ventral lateralis root and ganglion. The cells of the geniculate ganglion vary greatly in size. The largest ones are fully 50 micra in diameter, while the smaller ones are scarcely more than 10. The large and small cells are irregularly mingled with a tendency for the small cells, which are less numerous than the large ones, to gather in the interior of the ganglion (Fig. 21, *gen. g. VII*).

3.—*The Lateralis Roots.*

The two lateralis roots of the facial immediately upon entering the oblongata fuse and enter the tuberculum acusticum together, the fibres of the dorsal root farther cephalad than those of the ventral one. These root fibres throughout their internal course are so intimately mingled with the most cephalic fibres of the VIII nerve that analysis is impossible.

After emergence from the oblongata the two lateralis roots at once diverge and remain distinct throughout their entire peripheral courses. The fibres from the dorsal lateralis ganglion pass into the r. ophthalmicus superficialis facialis and the r. buccalis; those from the ventral ganglion all pass into the truncus hyomandibularis. The cells of these ganglia are very small, about 20 micra in diameter, and as a rule only two or three times the diameter of their fibres. They are usually not crowded, but, like those of the lateral ganglion of the vagus, they are scattered among the fibres (Figs. 4, 5, 11 and 19–22). The dorsal root, before reaching its ganglion, receives the small bundle of fibres from the VIII root, as described in Section 6 and figured in Fig. 20.

II.—The Roots and Ganglion of the Trigeminus.

The sensory and motor roots of the trigeminus issue high up on the side of the oblongata and so intimately fused that their separation is not easy, even microscopically (Figs. 4, 12, 20–23).

1.—The Motor Root.

The motor nucleus of the trigeminus lies in the floor of the ventricle laterally of the fasciculus longitudinalis dorsalis and somewhat removed from it. Both the motor nucleus and root lie farther dorsally than the spinal V tract and at their exit the motor fibres are dorsal, a relation, however, which is not maintained peripherally. A broad band of fibres arising apparently in the motor nucleus of the opposite side passes through the nucleus and doubtless contributes to the root. It also passes through the fasciculus longitudinalis dorsalis and may derive some fibres from that source.

The motor root passes through and mingles with the general cutaneous root so intimately that it is difficult for a short distance from their exit to distinguish them. Doubtless fibres from other than the motor nucleus, the sensory nucleus and the spinal V tract enter the V nerve, but as they cannot be separately followed peripherally, I have devoted no especial attention to them. Though the general cutaneous and motor fibres cannot be clearly separated for a short distance after their exits, they can be separated both centrally and peripherally of this point, so that their entire courses can be given with all needful accuracy. In the case of none of the other components which participate in the V + VII ganglionic complex is there any difficulty in distinguishing them and following them throughout the complex.

K

2.—*The General Cutaneous Root.*

Immediately upon entering the brain the sensory root of the trigeminus divides. One part joins the motor V to form the deep root (*d. V*, Fig. 20) and goes to the chief sensory trigeminal nucleus. The larger part turns caudad and forms the whole of the pre-vagal spinal V tract. Its internal course has been described in Section 3. It crosses the motor trigeminus root and forms the most dorsal member of the V + VII root complex. It is then crossed externally by the dorsal lateralis root and ganglion. The Gasserian ganglion lies farther cephalad than any of the other members of this complex. Its cells resemble those of the geniculate ganglion, though the largest ones are rather larger.

III.—Comparative Review of the Trigemino-Facial Roots.

Stannius enumerates forms with five and forms with four roots in the trigemino-facial complex and considers the latter as the more characteristic of fishes, counting the two lateralis roots as one. His analysis of these roots is remarkably exact, more so than those of some more recent writers who have had better methods at their disposal. Comparing Menidia with his forms with five roots, it appears that his first root is our general cutaneous plus motor V, *i. e.*, as he states, the trigeminus in the strict sense; his second root is our dorsal lateralis root; his third root, our ventral lateralis root; his fourth root, the communis root; and his fifth root is our motor VII.

Goronowitsch's endeavor in both the earlier ('88) and the later ('96) papers to elaborate a simple serial arrangement of dorsal and ventral roots of which the several pairs should be strictly homodynamous with each other and with spinal roots must be reckoned a total failure, as

he has not taken into account the qualitative differences in the fibres of these roots. The second paper is dominated by this attempt quite as much as the earlier one and Strong's suggestion ('95, p. 168) that the ventral root of Trigeminus II is not motor but sensory (lateralis) is rejected. Nevertheless the papers of Kingsbury ('97) and Johnston ('98) both show that in Acipenser the composition of these nerves is just as in Menidia, viz., Trig. I is the general cutaneous and motor V roots, Trig. II is the two lateral line roots of the facial nerve, and the facial of Goronowitsch is the communis and motor VII roots. See sub-section XII beyond.

IV.—The Truncus Hyomandibularis.

This nerve receives all of the motor VII root, all of the fibres from the ventral lateralis ganglion, a bundle of communis fibres from the geniculate ganglion, and a bundle of general cutaneous fibres from the Gasserian ganglion. Of these the lateralis component is by far the largest, the motor bundle is about one-fifth as large, while the other two components are about as large as the motor. The motor fibres join the lateralis root from the ventral side snd mingle with them. Beyond the lateralis ganglion several small bundles of fine communis fibres are derived from the geniculate ganglion (not shown on any of the plots). Still farther cephalad and just as the truncus is passing through its foramen it is crossed by the large r. palatinus and from the latter receives a large bundle of communis fibres. These constitute a compact bundle on the cephalic face of the truncus and as such can be followed almost the entire length of this nerve, constituting peripherally the r. mandibularis internus VII.

As the truncus hyomandibularis is passing through its

foramen, it crosses a ganglion of the sympathetic chain (Fig. 21, *sy.*) and may derive some fibres from it. After emergence from its foramen it runs outward to the hyomandibular bone and then turns abrubtly ventrad and slightly caudad, entering a canal in that bone.

At this point, *i. e.*, just as the truncus is turning ventrally and some distance outside of the foramen, it receives on its caudal face a considerable bundle of fine fibres which come from the Gasserian ganglion. See Fig. 4. Their course is as follows: The truncus hyomandibularis and the r. palatinus together issue from a foramen which is distinct from that of the V nerve and the remainder of the VII. But a small portion of the Gasserian ganglion extends far caudad nearly to this foramen. Here there is a separate foramen in the cranial wall just cephalad of that of the truncus hyomandibularis through which there passes a large blood vessel and also a narrow tongue of ganglion cells belonging to this caudal tip of the Gasserian ganglion (Fig. 2, *G*). From this little extra-cranial ganglion a considerable bundle of fibres passes out laterally (510) until it reaches the hyomandibular bone (Figs. 2, 4, *t. f. 2*). It then turns caudad and ventrad and is soon joined by another similar bundle of fine fibres (Figs. 2, 4, *t. f. 1*) which is derived from the extreme cephalic end of the Gasserian and which emerges from the cranium with the great infra-orbital trunk, curving back and pursuing a tortuous and rather peculiar course, which will be more fully described in connection with the infra-orbital trunk.

The combined general cutaneous component now passes back and joins the truncus hyomandibularis on its caudal face after it has entered the canal in the hyomandibular bone and begun to turn ventrad (530). Beyond this point it can be separately followed in the truncus with great

ease, for its fibres do not mingle with the other fine fibres, but are separated by the coarse lateralis and motor fibres from the communis bundle.

1.—The Ramus Opercularis Profundus VII.

The motor component of the truncus hyomandibularis can be followed, in spite of its intimate relations with the lateralis fibres, up to the point where the truncus hyomandibularis begins to turn ventrad (515). Here it divides into three parts, one part leaving the main nerve dorsally to turn immediately caudad, another continuing cephalad after the truncus has turned ventrad, while the third follows the truncus in its farther course. The first two parts I include under the term r. opercularis profundus VII.

The dorsal branch, which is the r. opercularis of Stannius, supplies three muscles. It passes directly caudad just dorsally of the apex of the narrow slit-like extension of the pharyngeal cavity which runs up between the pseudobranch and the first gill. It then passes through the dorsal end of the m. adductor hyomandibularis from its mesal to its lateral face, meantime contributing a few fibres for the innervation of this muscle (*m. ad. hy.*, Fig. 4). The nerve continues caudad along the outer face of this muscle to its end, and then farther caudad between the m. adductor operculi and the m. levator operculi, where it divides, the ventral twig supplying the m. adductor operculi (*m. ad. op.*). The remaining fibres continue caudad and almost immediately cross the course of the r. opercularis vagi. The two nerves lie almost in contact for a short distance, but clearly do not anastomose, as is the case in the carp (Baudelot, '83, p. 132, and Stannius, '49, p. 61) and Lophius (Guitel, '91). A little farther

caudad these remaining fibres from the r. opercularis VII enter and innervate the m. levator operculi (*m. lev. op.*).

The motor fibres which continue cephalad from the truncus hyomandibularis soon turn ventrally to reach the dorsal surface of the very large m. adductor arcus palatini (*m. ad. a. p.*), in which position they continue cephalad, giving off twigs for the innervation of this muscle from time to time. This ramus for the adductor arcus palatini is larger than the entire dorsal portion of the r. opercularis profundus.

2.—*The Ramus Opercularis Superficialis VII.*

Immediately after the truncus hyomandibularis has entered the canal in the hyomandibular bone it gives off a ramus directed caudad, the r. opercularis superficialis VII (*op. s. VII*), which at once separates into two, a dorsal and a ventral. The two portions pass through a common foramen in the opercular bone. The ventral one contains only coarse lateralis fibres and supplies the penultimate (6th) canal organ of the opercular canal (*op. s. VII. 1*). In some cases it has a separate origin from the truncus.

The dorsal portion contains coarse and fine fibres. The former, comprising about four-fifths of the area of the cross-section of the nerve, are lateralis fibres; the latter are derived almost exclusively from the general cutaneous component before it has yet fused with the truncus. Upon reaching the preopercular bone about three-fourths of the coarse fibres are drawn off (*op. s. VII. 2*), enter a foramen in that bone and supply the last (7th) canal organ of the opercular canal. The remaining coarse fibres and all of the fine ones continue caudad as a compact round bundle between the preopercular bone and the ventral tip of the hyomandibular.

In this position it begins to give off small branchlets of a few fibres each. One of these (*op. s. VII. 3*) of fine fibres leaves at 580 and turns dorsad, curving around the caudal projection of the hyomandibular bone where it articulates with the opercular, and continues caudad along the dorsal and inner surfaces of the latter bone. Here it joins (600) the fourth branch of the r. opercularis vagi, as described under that nerve, and the combined nerve supplies the adjacent mucous lining of the operculum.

Another branch of the r. opercularis superficialis VII is somewhat larger than the last and is composed of coarse fibres (*op. s. VII. 4*). It originates at the same point as the last mentioned and passes caudad and dorsad by a circuitous path around the base of a scale to a naked sensory papilla (*o.5*) situated a short distance caudad of the seventh opercular canal organ and in a line continuing the direction of the sixth opercular pore.

The fifth branch (coarse and fine fibres, *op. s. VII. 5*) leaves also at the same point. It immediately divides into several branches and supplies the skin of the operculum laterad and ventrad and caudad of the point of origin.

The ramus opercularis continues ventrad and caudad between the opercular bone and the skin and the sixth branch, containing coarse and fine fibres, separates dorsally at 612. This branch can be traced nearly to the caudal edge of the operculum, running dorsally of the main nerve and nearly parallel with it. The finer fibres are given off to the skin early in its course. The termini of the coarser ones, as in the last case, could not be determined by reason of defects in the sections.

The main nerve proceeds to the extreme ventro-caudal edge of the operculum, giving off several small branchlets

similar to the last, and finally terminates in two large naked sensory papillæ (*0.3* and *0.4*). Most of the fine fibres are given off with the earlier branches, but some seem to persist quite to the end of the nerve. The coarse fibres, including those which supply the three sense organs described, as well as those which go out with the other ramuli and were not traced to sense organs, are somewhat smaller than the largest lateral line fibres, but much larger than any communis fibres.

The operculum is covered with large scales; it is, therefore, difficult to get perfectly continuous series of sections of the skin and my sections are imperfect in the middle part of the operculum, so that, while the trunk of this nerve can be followed easily, yet its fine cutaneous branchlets are usually lost before they reach their final distribution.

On the opposite side of the specimen plotted branches of the r. opercularis superficialis VII were traced to four naked cutaneous sense organs. One corresponds to the organ *0.5* of the plots, and another is somewhat behind this and a little ventrally of it. Two organs were found near the ventral edge of the operculum and lying somewhat cephalad of those figured on the plots. The second may correspond to the first of the plots, or both may lie in front of the latter.

Having been led to believe from the appearance of my sections that more perfect preparations would reveal a larger number of cutaneous sense organs on the operculum, I made surface preparations of the operculum of a number of specimens. The operculum of a small specimen which has been preserved in 10 per cent formalin can easily be removed and examined as a transparent object, particularly if the pigment-bearing mucous lining of the inner surface be first stripped off. Fig. **27** is a camera sketch of such a preparation examined in water without staining or clearing and controlled by several similar preparations, as well as others stained in various ways.

The r. opercularis superficialis VII and its principal branches can easily be followed, and it is seen to supply four naked sense organs along the lower margin of the operculum (*o.1* to *o.4*). They are large and flat and lie upon or below the lowest row of opercular scales in a line which is the direct continuation caudad of the horizontal limb of the opercular canal, this line passing through the fourth opercular pore. The number found was uniformly four, except in one case, where the first one seemed to be double. The arrangement varies somewhat in different specimens, but never deviates greatly from that figured. The two organs found in the sections and figured on Fig. 3 are probably numbers 3 and 4 of the series. The naked organs along the outer surface of the opercular canal, to be described presently, could also be distinctly seen. Their number and arrangement vary greatly in different specimens, but they are always smaller than the four organs supplied by the r. opercularis and when examined in the unstained specimens with a low power look like little discs with a brilliant highly refracting centre.

The organ lying behind the sixth opercular pore was seen in a few instances. It may be followed by other organs behind, as suggested above, for the preparations here are opaque and confused by reason of the thick origin of the underlying m. dilator operculi.

Regarding the morphology of these five or six naked opercular organs, I think there is but one conclusion possible. That they belong to the lateral line rather than to the communis system is shown by their innervation. See further, Section 2, III.

Stannius makes no mention whatever of the r. opercularis superficialis. That it is not contained in his r. opercularis VII is shown by the fact that he correctly regards that nerve as exclusively motor; *i. e.*, his r. opercularis is our r. opercularis profundus only.

After giving off the r. opercularis superficialis VII, the truncus hyomandibularis continues directly ventrad in a canal of the hyomandibular bone until the ventral edge of

the bone is reached.   Here it divides into the r. hyoideus
and the larger r. mandibularis.   The latter turns abruptly
cephalad, leaving the canal and running along the outer
surface of the bone to its cephalic tip.

3.—*The Ramus Hyoideus VII.*

The ramus hyoideus (*hy.*) runs ventrad and caudad.
Its first branch (*hy. 1*) separates at once and might be con-
sidered a separate nerve.   It contains only coarse fibres,
enters the lateral line canal of the preoperculum and
supplies the fifth opercular canal organ.

The remaining and larger portion of the r. hyoideus
contains coarse and fine fibres and descends along the
inner face of the preopercular bone, and lower down along
the inner side of the interopercular bone, nearly to the
first (most dorsal) branchiostegal ray.   Here it divides
into two approximately equal divisions, each with both
coarse and fine fibres (560).   Of these one, which may be
regarded as the main ramus, turns slightly cephalad, the
other (*hy. 2*) continues caudad and ventrad and will first
be described.   It follows dorsally a big blood vessel run-
ning along the inner face of the interopercular bone,
giving off at once a small twig which later rejoins the
main trunk, then several smaller branchlets which could
not be traced, and at 610 a slightly larger branch of fine
fibres with a few coarse ones, which passes directly dor-
sally between the subopercular and interopercular bones
to emerge upon the skin dorsad of the latter bone.   It dis-
tributes to the skin covering the cephalic half of the sub-
operculum.   The remainder of this nerve breaks up in
the branchiostegal membrane, which it innervates.

The cephalic or main division of the r. hyoideus passes
ventrad in two branches, each with coarse and fine fibres,

one large one mesally of a big vessel and a minute twig
laterally of it. The latter (*hy. 3*) runs down along the in-
ner face of the interopercular bone and at about the middle
of that bone divides. One ramulus pierces the bone and
supplies the overlying skin cephalad of this point; the
other ramulus continues forward in the original position
along the inner surface of the interopercular and finally
divides again, both parts piercing this bone to end in the
skin covering it. It can be traced forward under the eye
up to 400. The ramuli of this more lateral twig supply
practically the whole cutaneous area over the interoper-
cular bone.

The more mesal branch of the r. hyoideus runs forward
along the dorsal limit of the branchiostegal membrane
under the bones of the hyoid arch. Here it breaks up to
supply the branchiostegal muscles (*hy. 4*, m. hyoideus of
Vetter) and the surfaces of the branchiostegal membrane.
One twig of the latter type (*hy. 5*) can be followed nearly
to the cephalic end of the ceratohyal bone (350).

The coarse fibres of the r. hyoideus are mainly dis-
tributed to the branchiostegal muscles, but some of them
go out to the skin with the general cutaneous branches.
Stannius mentions ('49, p. 62) that movement of the
branchiostegal membrane follows stimulation of the trun-
cus hyomandibularis. No cutaneous sense organs were
found in the areas supplied by any of the branches of the
r. hyoideus. The fine fibres of this nerve are derived ex-
clusively from the general cutaneous nerve bundle, *i. e.*,
the r. communicans from the Gasserian ganglion. They
comprise, moreover, the whole of that component except
the portion already given off to the r. opercularis super-
ficialis. This can be demonstrated with ease, for the
general cutaneous component of the truncus hyomandibu-

laris runs down its caudal and ectal side, while the communis component runs down the cephalic and ental face of the truncus, the two fine-fibred portions being separated through the whole length of the truncus by the coarser lateralis and motor fibres. It is only at the extreme ventral end of the truncus that there is any possibility of any considerable intermingling of their fibres. Here, though the two fine-fibred components lie rather close together, yet the sections show plainly that they do not exchange fibres. We have, therefore, good anatomical evidence that no considerable number of communis fibres enter the r. hyoideus, and that independently of the fact that no terminal buds are found in its course. It is equally clear that no considerable number of general cutaneous fibres enter the r. mandibularis VII, and this is substantiated by the fact, to be noted below, that the areas in which the special cutaneous fibres of the r. mandibularis VII find their terminal organs receive an independent general cutaneous nerve supply from the r. mandibularis V (see Fig. 3).

4.—*The Ramus Mandibularis VII.*

This nerve (*man. VII*) contains lateralis and communis fibres, which though bound up in the same trunk for most of their courses, nevertheless correspond to the r. externus and r. internus of the Amphibia and of some other fishes.

After its separation from the r. hyoideus and immediately upon its emergence from its canal in the hyomandibular bone it sends a very small branch (*m. VII. 1*) around the upper edge of the preoperculum, then ventrally between this bone and the m. adductor mandibulæ. Here it divides, the smaller part (of coarse fibres) running laterally through this muscle to the skin, close under

which it turns dorsad around the base of a scale to a naked sense organ (*o.6*) lying on the outer face of the scale and just overlapped by the free edge of the next dorsal scale. The larger part of this first ramulus continues ventrally along the outer face of the preopercular bone to the opercular canal. It enters the bony canal and just dorsally of the membraneous canal it divides, a minute twig turning cephalad, the larger portion caudad. The latter supplies four naked organs on the outer skin covering the most caudal part of the horizontal limb of the opercular canal and the base of the fourth pore of that canal. The former supplies a single similar but larger organ on the base of the third pore. The fibres of this ventral part stain very intensely, like lateralis fibres, though they are of small size.

On the opposite side of the specimen figured this first branch pursues a course similar to that just described except that all of its fibres pass through from the mesal to the lateral face of the m. adductor mandibulæ before it divides into its dorsal and ventral ramuli. The ventral ramulus then passes down the outer face of the muscle instead of its inner face to reach the opercular canal. Here it supplies four naked organs with its caudal twig, but the cephalic twig, after supplying a naked organ just caudad of the third opercular pore, continues cephalad, receives a considerable addition from the second branch of the r. mandibularis VII just before the latter enters the fourth opercular canal organ and then supplies a large sense organ lying just cephalad of the third opercular pore.

All of the naked organs supplied by this branch, as well as similar ones farther cephalad, to be described immediately, are of the same nature as the similar but larger organs supplied by the r. opercularis superficialis and I homologize them with the pit-lines of ganoids. They correspond, doubtless, to the similar lines mentioned by

Allis ('97, p. 632) in Gadus and Esox, and all of these may represent the gular line of Chlamydoselachus (Garman, '88).

The r. mandibularis VII after giving off its first branch, as just described, runs along the outer face of the hyomandibular bone. In this part of its course it contains chiefly very coarse lateralis fibres, with a small bundle of fine communis fibres along its inner face. At the extreme cephalic tip of the hyomandibular bone (500) the fine fibres separate mesally and dorsally from the coarse ones and a strong fascia in which portions of the m. adductor mandibulæ are inserted, passes between the two divisions, which become widely separated. The fibres of the more lateral bundle are very large with few medium ones and a very few small ones intermingled; those of the mesal bundle are mostly very small with a considerable number of medium-sized and more heavily myelinated fibres intermingled. These bundles represent the r. mandibularis externus and the r. mandibularis internus of the facial nerve.

From the lateral bundle the second branch is given off at 488 (*m. VII. 2*), which descends along the inner face of the preopercular bone, running slightly caudad, to enter the opercular canal and finally to supply its fourth canal organ.

The third branch arises from the fine-fibred communis bundle at 483 (*m. VII. 3*), runs ventrad and caudad and somewhat further mesad than the last. Having reached the mucous lining of the pharyngeal cavity just dorsally of the epihyal bone, it divides into two branches, directed cephalad and caudad respectively. The former runs under and innervates the mucous membrane covering the dorsal surface of the bones of the hyoid arch as

far forward as the cephalic end of that arch (400). The latter distributes in the same way to the mucosa overlying the hyoid bones as far back as their articulation with the hyomandibular. The epithelium in the region supplied by this nerve is thicker than the adjacent pharyngeal lining and is thrown into deep folds, giving the appearance characteristic of a sensory surface, but no taste buds, such as are abundant on the dorsal surfaces of the gill arches at the same levels, were found, though careful search was made for them in several specimens along the whole length of the hyoid arch. This region is, however, more richly supplied with gland cells than usual and these fibres not improbably are distributed in part to them. It is important to note that the corresponding region in Amia is innervated from the fourth branch of the r. mandibularis V (Allis, '97, p. 612).

The two bundles of the r. mandibularis VII continue forward between the m. adductor mandibulæ and the symplectic bone, just above the dorsal edge of the preopercular bone. In this position they again unite (465) and there is more or less confusion of the fibres of the two bundles. After their union they give off the fourth branch (*m. VII. 4*), which is composed chiefly of medium-sized fibres and a few very large ones. It arises apparently wholly from the lateralis component and takes its course ventrad and slightly caudad along the outer face of the preoperculum to the opercular canal. It pierces the bony canal, the fibres running dorsally and laterally of the membraneous canal to supply three naked organs lying in the skin covering the canal, two caudad of and one cephalad of the third opercular canal organ.

On the opposite side of this specimen the fourth branch and the corresponding sense organs caudad of the second

opercular pore are totally wanting, though it should be noted that on that side the first and the sixth branches supply each an additional naked sense organ and that the latter encroaches somewhat upon the area supplied by the fourth branch.

A short distance farther cephalad the fifth branch (*m. VII. 5*) of the r. mandibularis VII, composed wholly of coarse fibres, separates, takes a course nearly parallel to that of the fourth branch and enters the opercular canal to supply its third organ.

At almost the same point as the last the sixth branch (*m. VII. 6*) arises. It is composed of medium or small fibres with very densely staining sheaths of the same type as those of the first and fourth branches. It passes directly ventrad and into the bony opercular canal by a separate foramen in the preopercular bone. It then turns cephalad, running dorsally of the membraneous canal, and supplies three naked sense organs, two lying superficially of and a short distance caudad of the second and first organs of the opercular canal respectively, and one just cephalad of the latter. The origin and course of this branch are strictly analogous with those of the first and fourth branches, which it closely resembles.

On the opposite side this branch supplies four naked sense organs, two cephalad of the second opercular pore and caudad of the second opercular canal organ, one cephalad of the first opercular pore and immediately caudad of the first canal organ, and one cephalad of the first canal organ.

In another specimen we have an arrangement of the first six branches of the r. mandibularis VII which differs from either side of the specimen figured. The two sides of this specimen agree in the following arrangement. The first branch is represented only by its dorsal twig for

the organ *o.6.* The fibres for the other naked organs supplied by this branch in the specimen figured are supplied by a branch arising cephalad of the second branch (the third branch of this specimen). Branches 1 and 2 arise apparently from the coarse-fibred component. Between the second and third branches in this specimen the nerve splits into the fine-fibred and coarse-fibred bundles as in the other case, and the third branch arises from the coarse-fibred bundle. The fourth branch is absent. The fifth arises from the coarse-fibred bundle just as it is rejoined by the fine fibres. The sixth branch supplies two organs caudad of the second canal organ and doubtless some cephalad. Its ultimate course was not traced.

At 430 the seventh and eighth branches of the r. mandibularis VII are given off together. They both arise apparently from the coarse-fibred component and pass ventrad to the dorsal surface of the bony opercular canal. The eighth branch turns cephalad along the dorsal surface of the preopercular bone, while the seventh, which is four or five times as large, passes through a foramen into the bony canal at once, thence cephalad to supply the second and first organs of the opercular canal.

The seventh branch is composed of very coarse fibres; the eighth branch chiefly of medium fibres, with some fine ones intermingled. The latter branch continues cephalad along the dorsal and outer surface of the preopercular bone and under the fleshy origin of the m. adductor mandibulæ. It increases in size cephalad and ultimately joins a branch of the r. mandibularis V (*c. V–VII. 1*). This branch very clearly contains fibres from both the facial and the trigeminus. The former continue forward after the anastomosis with another trigeminal branch and finally supply three naked sense organs along the mandibular canal. They will be further discussed in connec-

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tion with the trigeminal branch with which they are distributed.

After giving off the last two branches the r. mandibularis VII continues forward along the outer surface of the symplectic and almost immediately divides into a ventral bundle composed exclusively of very coarse fibres and a smaller dorsal bundle of very fine fibres with a few of medium size. These bundles become quite widely separated, a few fibres of the m. adductor mandibulæ lying between them. The ventral bundle comes to lie in a deep groove in the symplectic toward the cephalic end of the latter, which finally becomes a closed canal, while the dorsal bundle enters a separate canal lying farther dorsally and bounded by the symplectic, the mesopterygoid and the quadrate. The dorsal bundle almost immediately emerges on the mesal side of the bones and continues cephalad along the inner face of the quadrate; but the ventral division runs much farther cephalad in its canal, a process of the symplectic containing the canal running forward along the inner face of the quadrate to receive it. It also finally emerges on the inner face of the quadrate and here the two bundles re-unite (290). From this point cephalad the two bundles run along the inner face of the quadrate in contact but without mingling of fibres and in this relation several very fine ramuli (not shown on the plots) are given off from the finer bundle to the mucous lining of the mouth immediately adjacent to the nerve trunk. No taste buds can be found in this region, nor is the epithelium so glandular as in the corresponding region overlying the hyoid bones and supplied by the third branch of this nerve.

Farther forward, along the inner side of the articular and dentary bones, the coarse and fine-fibred bundles are

more intimately united, though from time to time they may completely separate for a short distance, as far forward as the cephalic tip of the articular bone. Here the two divisions finally separate (165), the dorsal one, as before, containing fine and medium fibres, while the ventral one contains all of the very coarse fibres with a few of medium size.

Previously to this, however, a coarse-fibred twig has been given off (200) to supply the fifth canal organ of the mandibular canal (*man. VII. 9*).

The fine-fibred dorsal division (*man. VII. 10*) will first be described. It follows, parallel to the other division, the mesal surface of the mandible close under Meckel's cartilage, and at 120 gives a rather strong branch dorsad which supplies numerous taste buds of the mucous lining of the mandible. These fibres were definitely traced in several cases to the buds and not merely to regions where buds abound. This epithelium is also very glandular and doubtless many of the fibres are not destined for the sense organs.

Other similar branches go off cephalad, also branches for the floor of the mouth over the intermandibularis muscle, which is richly supplied with taste buds. The taste buds supplied by this nerve become more numerous as we pass cephalad, being very abundant all over the inner surface of the lower lip. These buds resemble in structure those farther back on the palate and gill arches supplied by the IX and X nerves, being flask-shaped, resting on a high dermal papilla or fold and with the neck of the flask projecting above the epithelium.

The origin of the intermandibularis muscle separates this dorsal division from the remainder of the mandibularis VII, which lies ventrally of this muscle. At the tip

of the mandible a branch of the dorsal division enters the alveolar canal of the dentary bone and apparently supplies its teeth.

Returning now to the coarse-fibred ventral division (165), it follows parallel with the dorsal division the inner face of the mandible and at about 150 gives off ventrally about one-fourth of its fibres, comprising some very coarse ones and some of the medium size (*man. VII. 11*). At 130 these fibres pass through a foramen in the dentary bone into the mandibular canal, where they supply the fourth mandibular canal organ.

At the level of that organ (120) the main nerve is joined by a branch of about the same size which is derived from the r. mandibularis V (*V–VII. 2*) and passes ventrad between the articular bone and Meckel's cartilage to the dorsal surface of the r. mandibularis VII. It is composed of fine, medium and very coarse fibres, the latter occupying about one-third of the area of the cross-section. Though the elements from the VII and V nerves are from this point on intimately united and bound up in the same sheath, yet in good preparations it is possible to follow them independently for a considerable distance, for they are separated by a delicate connective tissue septum. All the coarser and some of the fine fibres from the trigeminus gradually swing around mesally from the dorsal to the ventral side of the mixed trunk, while the remainder of the trigeminal fibres retain the dorsal position. A connective tissue septum appears between these two portions of the trigeminal element and finally (100) the ventral portion separates from the trunk. While it is impossible to be certain that no fibres from the facialis enter this branch, the appearances are against it and it is certain that most of its fibres are derived from the trigeminal element.

It turns toward the median line, enters the m. genio-
hyoideus and then turns caudad in the substance of the
muscle (*m. ghy.*), which it supplies for almost its entire
length. Within the muscle it anastomoses with its fellow
of the opposite side. Some fibres also emerge upon the
surface under the skin of the copula and are, I think, un-
questionably of general cutaneous nature.

Within the m. genio-hyoideus a twig of very coarse
fibres passes to the extreme ventral surface, then cephalad
near the median line (*m. im.*). Having reached the level
of the m. intermandibularis, it goes dorsad and enters the
middle of that muscle spreading out among its fibres in
the manner typical for motor nerves. On the opposite
side of this specimen this twig pursues a similar course
except for the fact that it separates from the motor fibres
destined for the m. genio-hyoideus before they have
entered that muscle. They then run inward along the
dorsal instead of the ventral surface of the genio-hyoideus
and enter the m. intermandibularis at about the same
place as those of the other side.

The relations of this anastomosis from the trigeminus
for the mm. genio-hyoideus and intermandibularis and the
adjacent skin were traced on the opposite side of this
specimen and on both sides of several others and in all
cases they were as above described. Osmic acid prepara-
tions (mounted unstained after fixation in Hermann's
fluid) show with especial distinctness that this nerve arises
from the trigeminus and not from the facialis.

The remaining fibres of this communicating branch
from the trigeminus after the separation of the branch
last described, join the r. mandibularis externus VII and
from the facialis portion of the mixed trunk thus formed,
there arises at once a small twig (*m. VII. 12*) for the third

mandibular canal organ.   Then under the origin of the
m. intermandibularis the trunk divides into two nearly
equal portions of which the dorsal one contains all of the
coarse, *i. e.*, facialis fibres.   These supply the second and
first mandibular canal organs, the remaining or trigeminus
fibres supply the skin of the tip of the mandible and the
middle portion (not the edges) of the lower lip.

5.—*Comparative Review of the Hyomandibularis.*

The truncus hyomandibularis receives fibres belonging
to the viscero-motor and the three sensory components.
The general cutaneous component is very small.   In Lota
and Esox (Goronowitsch, '96) the same relations prevail,
though in Lota (p. 28 and Fig. 12) the general cutaneous
portion is very large and passes off from the Gasserian
ganglion as a broad anastomosing band.   It would be in-
teresting to learn the exact distribution of these trigeminal
fibres in Lota.

i.—The opercular rami.—The muscles supplied by the
r. opercularis profundus are undoubtedly to be compared
with the general constrictor system of the facial region of
selachians.   The lateralis fibres in the r. opercularis
superficialis have been already discussed.   The general
cutaneous portion of this nerve is, I believe, peculiar to
the teleosts.   It is of the same nature as the cutaneous
portion of the r. hyoideus.

ii.—The ramus hyoideus.—This nerve is usually de-
scribed as a pure motor nerve, and such it probably is in
most vertebrates other than the bony fishes.   The mus-
cles supplied in Menidia (hyo-hyoideus) evidently belong
to the constrictor system of the facialis segment and no
other.

All of the general cutaneous fibres which enter the

truncus hyomandibularis are given off to the operculum through the r. opercularis superficialis and the r. hyoideus. Goronowitsch states ('96) that these cutaneous fibres are not present in Ganoids, though from the descriptions and figures of Allis ('97) it is probable that they are present in Amia. Goronowitsch accounts for their presence in tele-osts on the supposition that the suspensory apparatus has been pushed forward into the territory innervated by the trigeminus. This supposition may be correct, and yet the prime motive for the entrance of fibres from the Gas-serian ganglion into the truncus hyomandibularis is to be sought rather in the backward growth from the hyoid arch of the opercular apparatus. The way in which these fibres enter the hyomandibularis, as well as their periph-eral distribution, go to show that they have been ceno-genetically carried back by the growth of the operculum. The cutaneous twigs from the trigeminus which overlie the opercular canal and the preopercular bone (the infra-orbital branch *io. 2*) have apparently also been involved in this backward movement. The skin overlying the cephalic end of the preopercular bone is not, however, innervated from these hyomandibular fibres, but from recurrent twigs from the r. mandibularis V, viz., from the anastomosing branch *V–VII. 1.* We have as yet no definite knowledge of any case where the skin of the facial region is innervated from the facial roots. The general cutaneous fibres which Strong describes as joining the truncus hyomandibularis of the tadpole from the gangli-onic complex of the IX and X nerves and distributing with the r. hyoideus and the r. mandibularis externus are most puzzling, especially in view of the fact that the oper-culum of the tadpole is known to grow back over the gills very much as in the fishes.

iii.—The ramus mandibularis.—The course of the proxi-
mal portion of the r. mandibularis VII after its separation
from the r. hyoideus as above described, differs greatly from
that of the forms described by Stannius, a difference to be
explained, perhaps, by the excessive development of the
preoperculum in Menidia. The temporary separation of
this ramus into two portions (viz., the r. mandibularis ex-
ternus and the r. mandibularis internus) before entering
the mandible, is a common character in the bony fishes,
as appears from the works of Stannius ('49, p. 63) and
Vetter ('78, p. 479). In Cottus alone the two portions do
not re-unite (Stannius).

In my preliminary paper ('97) I described the naked
organs along the opercular canal as innervated from the
communis component. In this I was unduly influenced
by the size of the fibres. These nerve fibres are scarcely
larger than those which supply terminal buds on the top
of the head, yet they are very heavily myelinated so that
they stain very intensely. I have since that time traced
them with great care in a number of specimens and am
convinced that in every case they arise from the lateralis
component (r. mandibularis externus) and not from the
communis (r. man. internus). The organs are, I believe,
to be regarded as more or less degenerate pit-lines. They
are smaller than the similar organs supplied by the r.
opercularis superficialis and this may account for the fact
that the nerve fibres supplying them are of smaller size.

I agree with Ruge ('97, p. 216) that the peripheral rela-
tions of the facial nerve contribute nothing to the hypoth-
esis that a branchiomere was originally intercallated
between the hyoid and the mandible. If such a segment
ever existed, it has left as small trace in the adult periph-
eral nervous system as in the central. Neal ('98) has

shown in Acanthias that a neuromere is found in this position in the brain, but it is early lost, leaving no trace behind. We cannot, then, reasonably look for such a segment in the adult of the more highly specialized teleost.

iv.—The genio-hyoideus and intermandibularis muscles.— Previous investigators have been unable to determine the innervation of these muscles with certainty, as the methods of dissection are obviously inadequate to unravel the anastomoses between the VII and V nerves.

Stannius mentions (p. 23) that the m. genio-hyoideus in some cases contracts when the motor V (his first root) is stimulated; nevertheless he is inclined to regard the proper innervation of the muscle from the facialis. He also found (p. 62) that in Esox stimulation of the truncus hyomandibularis causes movements of the branchiostegal membrane and also weak movements of the lower jaw, and this would favor that view.

Vetter ('78, p. 515) found that in this species the m. genio-hyoideus is supplied largely by extensions of the r. hyoideus which run forward into it after supplying the branchiostegal muscles (m. hyo-hyoideus). This is not mentioned by Stannius and certainly is not true in Menidia, yet I may account for the movements of the jaw observed by Stannius upon stimulation of the truncus hyomandibularis.

Subsequent studies (July, 1899) have shown me that this is, however, true in Gadus. Or at any rate the r. hyoideus runs forward from the branchiostegal membrane in this species to anastomose with the nerve for the genio-hyoideus within the substance of that muscle. The figure and description by Allis ('97, p. 613 and Fig. 43) indicate a similar condition for Amia.

Pending an exact embryological examination, the morphology of the pre-hyal ventral musculature of the teleosts has remained obscure. It is supplied, at least in part, by

the spinal nerves or the spino-occipital nerves (including the hypoglossus) in all other vertebrates. See Für-bringer ('97) for details and literature. The isolation of the teleosts in this respect is striking.

In selachians (Vetter, '78), in Ceratodus (Ruge, '97) and in ganoids (Allis, '97) we have in the pre-hyal region in addition to the longitudinal spinal musculature, a general ventral constrictor system supplied by the V and VII nerves. Now, the mm. intermandibularis, genio-hyoideus and hyo-hyoideus of ganoids and teleosts have unquestionably been derived from this ventral constrictor system of selachians, as has been shown by Vetter ('78), Ruge ('97) and with especial clearness by Allis ('97, p. 582, seq.)

In the teleosts it may safely be asserted that the pre-hyal " hypoglossus musculature," which in other forms is supplied by the first spinal or by the hypoglossus and which is known to grow forward from the post-otic myotomes, is altogether absent. I think that future embryological studies will confirm this and the condition is probably to be explained by the overgrowth of the opercula and the peculiar conformation of the isthmus.

The so-called genio-glossus muscle of teleosts would, then, not be homologous with the muscle of that name in most other vertebrates. It is, however, homologous with that muscle in the ganoids, for both have been derived from the constrictor system and are innervated from the V and VII nerves. The m. branchio-mandibularis of the ganoids is a true pre-hyal ventral muscle and it is accordingly innervated from the spinals, and all authors agree that this muscle is not present in the teleosts. In the bony ganoid Amia, which shows so many other teleostean characters, it is significant that we find the branchio-mandibularis effecting its insertion only in late larval or

adult life and then in so exceedingly variable a manner as to suggest that the muscle is in a process of degenerescence (Allis, '97, p. 700). In this fish the genio-hyoideus and the intermandibularis muscles are clearly supplied from the V, and the trigeminal nerves which supply them (*r. ghs.* and *r. ghi.*) are evidently comparable with my anastomosing branch *V–VII.* 2. Like the latter they contain general cutaneous fibres and Allis thinks ('97, p. 638) also communis fibres for the terminal buds found on the gular plate and the lower end of the gill cover in Amia. In Lota, too, (Goronowitsch, '96, p. 40) the intermandibularis is clearly innervated from the trigeminus (his Trig. I).

In forms like Esox, in which the so-called genio-glossus is innervated from both the VII and V nerves (Vetter '78), we may assume that the muscle represents both facial and trigeminal constrictor systems, comparable with those of Ceratodus, while in Menidia and most other teleosts the VII portion has been lost and the m. "genio-hyoideus," together with the intermandibularis, represents the ventral constrictor muscles of the trigeminus segment, the facialis constrictor muscles being represented only by certain dorsal opercular muscles and by the branchiostegal muscles.

Ruge ('97) is not willing to accept this interpretation; but, being convinced that these muscles must in all forms belong to the facial segment, he makes the entirely gratuitous assumption that the motor fibres for these two muscles, which in Ceratodus and teleosts appear to come from the trigeminus, really come as anastomosing fibres from the facial.

This assumption he makes also for the innervation of the intermandibular muscle of Amphibia, Reptilia and

Mammalia, and since in the two latter cases there are no peripheral anastomoses between the rami of the VII and V nerves, he is obliged to postulate "an intra-cranial fusion of the two nerves," the very existence of such an anastomosis being a pure assumption.

In Menidia, at any rate, it is clear that the exact reverse is true, the apparent innervation from the facial in reality being derived from the motor nucleus of the trigeminus, as there is no possible opportunity for a confusion at any point between motor fibres of the V and VII nerves.

v.—The chorda tympani.—It may be regarded as established that the chorda tympani in man supplies taste buds on the anterior part of the tongue and glands and also perhaps general mucous surfaces at the base of the tongue and between it and the lower jaw. Its nerve fibres arise from the geniculate ganglion of the facial and enter the brain through the portio intermedia of Wrisberg, and internally they are said to pass to the IX nucleus by way of the fasciculus solitarius. Now, the fasciculus solitarius we homologize with the fasciculus communis of the Ichthyopsida and hence it appears that the chorda both centrally and peripherally is a visceral branch of the facialis. That this nerve is a pre-trematic branch is indicated by the peculiar course of the chorda, through the tympanic cavity and above and in front of the Eustachean tube, the latter being regarded as the homologue of the spiracle.

These homologies cannot be regarded as definitely established; nevertheless they are greatly strengthened by the direct embryological evidence brought out by Dixon's work, On the Development of the Branches of the Fifth Cranial Nerve in Man ('96). This author found that the chorda tympani and large superficial petrosal

(Vidian) nerves grow out from the seventh nerve, un-doubtedly from the geniculate ganglion, and that as late as the fifth week the chorda had not effected its connection with the lingual nerve. These results are of themselves quite sufficient to confute such work as that of Penzo ('93), who tries to prove *by dissection* that the chorda tympani and great superficial petrosal nerves contain fibres derived from the trigeminus.

Lenhossék ('94) found that fibres from the cells of the geniculate ganglion enter the portio intermedia, but that the fibres of the large superficial petrosal are not connected with the geniculate ganglion cells. But this negative result cannot stand in the face of the embryological data of Dixon and the degeneration experiments of Amabilino ('98). The latter author got a characteristic Nissl degeneration of the cells of the geniculate ganglion after destruction of the chorda, but no degeneration after resection of the facialis. He demonstrated the degeneration of these fibres peripherally of the lesion and also found that some chorda fibres do not degenerate. It is possibly these ascending fibres which Lenhossék found not to terminate in the ganglion. Amabilino's work has been since confirmed by Van Gehuchten (*Journal de Neurologie, 1898*), with, however, the important difference that Van Gehuchten found that section of the facial nerve of the rabbit immediately after its emergence from the Fallopian canal does cause degeneration of a few cells of the geniculate ganglion, thus showing that the facial nerve receives some communis fibres.

The most important evidence against this conception of the chorda comes from the clinical side. Compare especially the case cited by Adolf Schmidt ('95), which proves conclusively that sensations of taste are transmitted

from the anterior two-thirds of the tongue by means of the lingual nerve (V+VII), rather than by the IX nerve. Clinical evidence is then adduced to show that these gustatory fibres enter the brain through the V nerve rather than the VII, which, however, does not seem to me by any means conclusive.

A pre-facial fasciculus solitarius has been described in man by a few writers (Böttiger, '90, and Roller, '81). Only upon the supposition that such a tract does enter the trigeminus (a condition which has not been demonstrated as yet in any of the lower animals) could the presence of gustatory fibres in the trigeminus roots be explained. In the present state of our knowledge we may most safely consider that Dixon's conclusion in man applies to all of the vertebrates: "The nerve supply of the organs of taste appears to be derived from the facial and glossopharyngeal nerves alone."

In man, then, so far as is definitely known, the pre-auditory communis system is represented by the large superficial petrosal nerve and the chorda tympani, plus a few fibres in the facial proper—see the reference to Van Gehuchten above. Since the days of Stannius the large superficial petrosal is pretty generally regarded as the homologue of the r. palatinus. The homologies of the chorda tympani, however, have given more trouble. In determining this question there are three criteria or lines of evidence which have been very differently estimated by different authors: (1) The character of the fibres, their ganglion and central termination, (2) the peripheral distribution area, (3) the intermediate course of the nerve, especially with reference to the spiracle and its limiting arches.

Froriep's comparison ('87) with a lateral line nerve of

course fails because it contravenes the first criterion. The first and second criteria are perfectly fulfilled by the mandibularis internus VII of the Amphibia (Strong, '95) and by that nerve of the fishes in general, for it supplies the mucosa between the hyoid and mandibular arches and along the inner side of the latter (see also Ruge, '97, p. 209).

Several recent writers in emphasizing the third criterion above have called attention to the fact that the r. mandibularis internus VII of several of the fishes is a post-spiracular nerve and therefore cannot be homologous with the chorda tympani. This point was made by Allis in his preliminary paper in 1895 (p. 488), but his discussion of this nerve in his later paper ('97, p. 638) is not altogether clear. He distinctly homologizes this nerve in Amia with the nerve so named by Ewart, Pollard and Strong in the other Ichthyopsida, for it certainly has the corresponding course for its whole length. Since it appears to take no part in the innervation either of terminal buds externally or of taste buds in the mouth, he seems inclined, however, to conclude that it is not a communis nerve at all, but perhaps general cutaneous. This he bases on the false assumption elsewhere expressed (p. 642), that all, or nearly all, communis fibres are for specialized sense organs. The fact is that they may go to the general mucous surfaces, and I have no doubt that the r. mandibularis internus VII of Amia is structurally, as well as topographically, the same as that nerve in Menidia and the other forms mentioned. As this nerve in Amia and in selachians lies behind the spiracular canal, the corresponding nerve in these other types must also be a real post-trematic ramus and cannot be regarded as a pre-trematic ramus which has coalesced with the post-

trematic nerve (r. hyomandibularis) after the occlusion of the spiracular canal.

The r. mandibularis internus VII of the Ichthyopsida, then, probably does not correspond to the chorda tympani of the higher forms, but it is a primary component of the post-spiracular nerve of vertebrates in general. When absent from that nerve (as sometimes occurs) this fact, rather than its presence, is to be explained as a secondary modification.

The relations of the pre-spiracular communis nerves are exceedingly diverse in different vertebrates. The primary arrangement was doubtless the typical palatine and pre-trematic branches, but even in the selachians there is considerable deviation from the type in various directions. As differentiation progressed, the development of taste buds on the lips (correlated with the absence of communis fibres in the trigeminus) led not only to the extension of the typical facial nerves (palatine, pre-trematic and post-trematic) from their proper arches to supply them, but in some cases to the formation of entirely new nerves, such as the internal rostral nerve of Acipenser, the communis component of the r. maxillaris of other fishes and, as we shall see below, the chorda tympani. The later development of a fleshy tongue has led in higher vertebrates to a similar prolongation of one or more branchial nerves to innervate it.

Now, the known diversity, even in rather closely related fishes, in the nerves which are thus prolonged should incline to the greatest caution in establishing homologies, especially those based upon peripheral relations. Thus, any of four distinct communis nerves may run forward upon the hyoid and mandibular arches:—(1) the r. mandibularis internus VII, (2) the r. pre-trematicus VII,

(3) communis fibres secondarily added to the r. mandibularis V, or (4) a nerve distinct from any of the preceding. Which of these nerves persists in a given case after the obliteration of the spiracle is a matter which it may not be possible to determine from the adult peripheral relations, nor is it safe to assume that it is the same nerve in all cases.

The condition in Raja and Spinax is especially fruitful in suggestions for the interpretation of higher forms. Here Stannius describes ('49, p. 57) three branches of the r. palatinus:

1. A small posterior (caudal) branch, which supplies the pseudobranch of the spiracle. This is manifestly the proper r. pre-trematicus VII, *i. e.*, the nerve for the pre-spiracular demibranch.

2. The first anterior branch. A stronger nerve which sends a twig back for the anterior lining of the spiracle, anastomoses with branches 1 and 3, and then runs forward and inward under the mucous lining of the mouth between the hyoid and the mandible, reaching to the ventral median line. This nerve perfectly fulfils every condition for the chorda tympani, *and is an independent nerve for its entire length.*

3. There is, finally, the second anterior branch, or true r. palatinus.

We have in these fishes, then, a chorda tympani *in addition to* the r. palatinus, the pre-trematic VII and the post-trematic VII.

Chimæra would seem from Cole's description ('96a, p. 652) to present a simple and primitive condition. The r. pre-trematicus VII arises from the base of the palatine and distributes to the ventral portion of the pharynx behind the lower jaw. This he calls (I think correctly) the

M

chorda tympani. The r. pre-trematicus in the strict sense
(number 1 of Stannius' description) may have fused with
this nerve, or more likely has disappeared with its demi-
branch. Midway of its course it receives an anastomosing
branch from the facial proper (post-spiracular) and this is
probably the post-trematic communis element of the facial,
secondarily and incompletely joined to the pre-trematic
ramus—a conclusion suggested to me by Mr. Cole in
private correspondence.

An anastomosis of the type presented in Chimæra is
unusual. More often it is the r. pre-trematicus and
chorda which lose their identity after the closure of the
spiracle, either by fusion with the post-trematic facial
("facial proper" of Ewart and Cole) or by fusion with
the post-trematic trigeminus (r. mandibularis V). The
latter type is the one which would most naturally occur,
since both of the anastomosing nerves run along the same
arch; and, in fact, it is apparently most frequently found
among the fishes. It does *not*, however, appear in
Menidia; for this fish, as we shall see beyond, lacks com-
munis fibres in the r. mandibularis V, though such fibres
occur in the r. maxillaris. But Menidia does possess a
distinct nerve (to be described in the next sub-section)
between the truncus hyomandibularis and the trigeminus
which distributes to the region of the pseudobranch and
which I regard as the r. pre-trematicus VII (in the narrow
sense).

In Amia, Allis finds communis fibres in both the max-
illary and the mandibular rami of the trigeminus. These
fibres come "from the ganglion of the fasciculus com-
munis root," ('95, p. 488), *i. e.*, the geniculate ganglion, as
in Menidia. Since there are no communis (*i. e.*, pre-spi-
racular VII) fibres in the r. mandibularis V in Menidia,

the mucous covering of the upper end of the hyoid arch is supplied from the r. mandibularis internus VII (my branch *m. VII. 3*), *i. e.*, from the post-spiracular VII. Such fibres do occur in the r. mandibularis V of Amia and accordingly we find the taste buds and mucosa of the corresponding region supplied by the fourth branch of the mandibularis V ('97, p. 612). Allis is, doubtless, correct in homologizing these fibres with the chorda tympani, *i. e.*, they correspond to Stannius' branch 2 of selachians. The r. pre-trematicus *sensu stricto* (branch 1) may also be represented in this nerve, but more probably in the " posterior palatine " of Allis (see below).

Goronowitsch ('96) has also described, though without recognizing their significance, similar fibres from the geniculate ganglion to the r. mandibularis V in Lota vulgaris. This I can confirm (July, 1899) in Gadus morrhua, and can add that here, as in Amia, the mucosa of the hyoid region is supplied by these mandibular fibres, and not by the r. mandibularis internus VII.

I would suggest that in Menidia the independence of the r. pre-trematicus VII is to be accounted for by the great size of the pseudobranch, which is innervated by this nerve. Not having fused with the r. mandibularis V, the pre-trematic VII is distributed only to the area about the pseudobranch; and the regions farther cephalad, along the hyoid and mandibular arches, which are supplied by other pre-trematic fibres in some other forms, in Menidia are supplied by the post-trematic branch. Menidia clearly lacks the chorda in the proper sense of that term, the post-trematic communis element replacing it functionally.

I am inclined, therefore, to regard the nerve to be described beyond as the r. pre-trematicus VII of Menidia as the equivalent of Stannius' branch 1 of selachians. It is not properly the homologue of the chorda tympani of mam-

mals, for it does not conform to the third criterion mentioned above. That is, it does not fuse with the r. mandibularis V and hence it does not distribute to the hyoid and mandibular arches in the way characteristic of the mammals.

Cole, in his discussion of the chorda already referred to ('96a, p. 657 ff.), gives a vigorous and I think conclusive argument for the pre-spiracular nature of the chorda, but his homologies in the several groups of fishes and amphibians are open to criticism in several respects.

In the first place, he is misled by a false conception of a typical branchial nerve. The pre-trematic ramus he regards as sensory and the post-trematic as "practically motor." The latter point is incorrect; the post-trematic ramus is typically mixed, and the presence of communis fibres (r. mandibularis internus VII) in the post-trematic VII is strictly typical. (This is true also even in the Mammalia, if Van Gehuchten's most recent work, cited above, is sound.) He homologizes his chorda with Strong's internal mandibular, but considers that the latter is a pre-trematic nerve which has fused secondarily with the post-trematic. He adds: "My reasons for this assertion are two—(1) his man. int. arises *from the base of the palatine*, which is almost invariably the origin of the pre-spiracular nerve; (2) it consists entirely (?) of splanchnic sensory fibres (and thus agrees with the palatine), whereas the post-spiracular division of the VIIth is practically motor."

Now, the first of these reasons loses its force entirely when we remember that nearly all of the communis fibres of the VII nerve diverge into their respective rami immediately upon leaving the ventral edge of the geniculate ganglion, so that both the pre-trematic and the post-

trematic branches must of necessity arise "from the base of the palatine." Compare especially my Fig. 4. His second reason we have criticised just above.

Strong's internal mandibular is, I am confident, the same nerve as the one so named in Menidia, and I believe it to be homologous with the post-spiracular mandibularis internus of Amia (Allis, '97) and of some selachians (Stannius, '49, p. 65, and Jackson and Clarke, '76), and not completely so with the chorda of mammals. I say not completely, for it may well be that the pre-trematic VII in the frog has fused with the post-trematic, or hyo-mandibular nerve, so that the amphibian r. mandibularis internus VII may represent both the pre- and the post-spiracular communis elements.

Cole, in his admirable memoir on the nerves of the cod-fish ('98a), re-states his argument on the chorda (pp. 200– 201). Though no new facts are brought out, yet the "confusion in the terminology of the facial nerve of fishes" is, I fear, rather augmented than diminished, and an examination of his argument in detail is necessary.

In the first place he says: "As I have already pointed out (1896, *46*, p. 657 *et seq.*) *the terms internal mandibular and hyoideus as first used by Stannius are not only synon-ymous but apply to a motor post-spiracular* nerve related to the anterior face of the hyoid arch, just as the pre-spirac-ular nerve should be related to the posterior face of the mandibular arch." This, I think, is hardly fair to Stannius.

In selachians Stannius describes ('49, p. 65) two branches of his (post-spiracular) truncus hyoideo-mandi-bularis, the r. mandibularis externus and the r. mandibu-laris internus s. profundus, which have since that time been very generally regarded as lateralis and visceral nerves respectively, the latter distributing to the mucous lining of the mouth. In his description of the teleostean arrangement both of these components of the r. mandib-

ularis VII are described, though the names external and
internal are not applied to them, and these are *in addition*
to the r. hyoideus.   On pp. 62–63 he describes motor and
general cutaneous elements in the r. hyoideus, exactly as
in Menidia, and in some cases also branches to the lateral
line organs of the operculum.   (In the latter cases it is
obvious that the nerve includes also my r. opercularis
superficialis VII).   He then proceeds to describe the r.
mandibularis, as follows:

,, Dieser Ast, bald schwächer, bald stärker als der vorige,
verläuft bei den Knochenfischen an der Aussenfläche des
Os temporale, bedeckt vom Schläfenmuskel, etwas vor-
wärts, gibt gewöhnlich einen oberflächlichen, zum Os
quatrato-jugale sich erstreckenden Zweig A [r. mandibu-
laris internus VII of Menidia, etc.] ab, tritt dann in einen
Canal des Os tympanicum und gelangt aus demselben an
das Os symplecticum, um längs demselben zum Unter-
kiefergelenke zu treten.   Hier nimt er [*i. e.*, the r. mandi-
bularis externus] gewöhnlich—namentlich bei Cyclopterus,
Belone, Gadus, Pleuronectes, Salmo, Coregonus—den
zuerst abgetretenen grösseren Zweig A, nachdem dieser
das Os quadrato-jugale durchbohrt hat, in seine Bahn
wieder auf; seltener, wie z. B. bei Cottus, bleibt dieser
Zweig A vom Stamme gesondert, und vertheilt sich am
Boden der Mundhöhle unter der Schleimhaut.

,, Der Stamm des Ramus mandibularis erstreckt sich
dann an der Innenfläche des Unterkiefers, unter dem
Meckel'schen Knorpel, in der diesen aufnehmenden
Längsrinne vorwärts bis zur Verbindung beider Unter-
kieferhälften.   Er vertheilt sich, nach eingegangenen
Verbindungen mit dem R. maxillaris inferior N. tri-
gemini,—bei Lophius findet eine doppelte Verbindung
dieser Art Statt [as in Menidia]—in den die beiden Un-
terkieferhälften an einander ziehenden Muskel, in den
Musculus geniohyoideus, an der Schleimhaut des Mundes
und an der den Unterkiefer bekleidenden äusseren Haut.''

My account in Menidia, it will be observed, conforms
exactly to this description; and the branch A (especially
in Cottus where its peripheral course is distinct from the

rest of the nerve) clearly is a visceral nerve for the mucosa of the mouth, the r. mandibularis internus VII of Stannius in the selachians and of Strong for the Amphibia. In Stannius' discussion of the homologue in the selachians of the r. hyoideus of teleosts (p. 65) I find no statement which would identify the "internal mandibular" with a motor nerve in either selachians or teleosts, and there is no reason why that term should not be applied to the communis component of the r. mandibularis VII of the bony fishes as in other vertebrates.

Cole follows (p. 202) with a tabular presentation of his conception of the composition of the facial nerve, a conception which I think inadmissible in several particulars. My own view of the branchiomeric characters of the facial nerve is given under the caption *Metamerism* in Section 12.

As these sheets pass through the press (July, 1899), I am constrained to add a further note. Cole has admitted the misquotation of Stannius, both to me privately, and later publicly in the *Anatomischer Anzeiger* (XVI, 2, 1899, p. 40, ff.) Since the matter is of some morphological importance, I have, however, left the criticism as originally written, in order that Stannius' own words might be before us.

Another matter may be touched upon here. In the course of a microscopical review of the trigemino-facial complex of Gadus morrhua, upon which I am now engaged, I find that the post-spiracular communis element of the facialis is totally wanting (or at most, so reduced as to be unrecognizable), *i. e.*, there is no r. mandibularis internus VII in Gadus (Cole's statement to the contrary, '98a, p. 202, notwithstanding). The nerve which I have called the r. pretrematicus VII is present in exactly the same relations as in Menidia, and there is *in addition* a large communis element in both the r. maxillaris and the r. mandibularis V. The mucosa in the region of the suspensorium and of the mandible which is supplied from the r. mandibularis internus VII in Menidia is supplied from the mandibularis trigemini in Gadus.

In the light of the preceding discussion it would therefore appear probable that in Gadus the r. pre-trematicus VII represents the nerve 1 of Stannius in selachians and that the nerve 2 (*i. e.*, the chorda tympani) has fused with the r. mandibularis V. In any case this emphasizes the difficulty alluded to above of defining the homologies of these nerves by topographical relations alone. It also makes

necessary some qualification of Cole's remark ('98a, p. 200): "There are several cases on record where on the disappearance of the spiracle the pre-spiracular accompanies for a time the post-spiracular nerve and thus becomes a topographical, but not a morphological, post-spiracular nerve. It seems to me that when the early development of the nerves of *Amia* has been investigated it will be found that the 'internal mandibular' nerve is morphologically pre-spiracular, though occupying a post-spiracular position in the adult. This is what we know has happened in *Rana* (cp. Strong's 'internal mandibular'), and what has doubtless also happened in *Chimæra* and *Gadus*." This, it seems to me, simply begs the question. There are no facts, so far as my knowledge goes, which would permit us to say that we "know" of any such secondary changes in the relations of this nerve, though such changes are theoretically possible.

In the case of Amia, Allis has replied (*Anat. Anzeiger*, XV, p. 374), stating specifically that the r. mandibularis internus VII is post-spiracular in the larval Amia. In the case of Chimæra, we concluded above that the post-trematic communis element has fused with the pre-trematic, rather than the post-trematic ramus. And in Gadus the fusion of the pre-trematic communis element with the post-trematic is manifestly impossible, for the simple reason that the post-trematic trunk totally lacks communis fibres.

The r. pre-trematicus VII of my description is unquestionably the same nerve as the posterior palatine nerve of Gadus (Cole, '98a, p. 135). It is not so certain that it is the same as Allis' posterior palatine of Amia ('97, p. 619). It has the same origin and it runs out in front of the pseudobranch, but its distribution seems to be far cephalad and laterally along the border of the maxilla. If it supplies the pseudobranch, then this part would be homologous with the nerve in question. The remainder of the nerve cannot be compared with anything in Menidia.

In Protopterus the r. mandibularis internus VII is evidently from the description of Pinkus ('94) in part, at least, the post-trematic communis element, as in other Ichthyopsida, and not a pure motor nerve, as Cole supposes ('98a, p. 201). Pinkus regards his r. palatinus inferior as the chorda tympani and homologizes it (as Miss Platt does the "external palatine" of Necturus, '96, p. 534) with Strong's r. mandibularis internus VII. The latter of these conclusions is doubtless incorrect, for Strong's nerve is, as we have just seen, also present. Allis may be right in identifying Pinkus' nerve with certain communis branches of the r. mandibularis V of Amia. But these relations must remain hypothetical until we have more exact knowledge of the components in Protopterus.

V.—The Ramus Pre-trematicus Facialis.

A large bundle of communis fibres runs from the ventral surface of the geniculate ganglion, enters the same foramen as the truncus hyomandibularis, crosses the latter nerve and gives to it a considerable communis component, as already described. Immediately after its emergence from the cranium it divides into two approximately equal portions; one, the r. palatinus, passes cephalad along the cranial wall under the origin of the m. adductor arcus palatini, the other (to which I have applied the name r. pre-trematicus VII, *r. VII. p. t.*) turns directly ventrad along the caudal and inner face of that muscle and between it and the large pseudobranch, whose cephalic end is crowded far dorsad (Fig 2). This nerve is chiefly distributed to the mucosa of the roof of the mouth and its contained taste buds cephalad of this point; but several large branches run caudad along the anterior surface of the pseudobranch and between its lobes. Having reached its caudal and ventral surfaces, they spread out and doubtless supply the numerous taste buds of the underlying mucosa and also the pseudobranch itself. Though these fibres on account of their extreme tenuity and delicate myelination could not be traced into the substance of the pseudobranch, yet there can be no doubt that they do innervate this organ, as they spread freely over its surfaces, and besides the pseudobranch receives no nerve supply from any other source.

The morphology of the teleostean pseudobranch, in spite of several recent papers, is in a very unsatisfactory state, and yet it is of great importance for the proper interpretation of all of the branches of the facial nerve.

Stannius states that it is usually in the teleosts innervated from the IX nerve, and cites the following cases:

Cottus, Cyclopterus, Gadus, Tincta, Salmo, Alosa, Clupea ('49, p. 77). In Belone and Esox he gives its innervation from the r. palatinus VII (his r. palatinus V, p. 56).

It is clear that in these two cases either the pseudobranch is not homologous or that a very remarkable secondary shifting of nerve connections has taken place. Now, the teleostean pseudobranch may be conceived of as the vestige of any one of three demibranches of a lower form:

(1)   The hyoid demibranch in the first gill cleft.

(2)   The hyoid demibranch in the spiracular cleft, *i. e.*, the cephalic demibranch of the hyoid arch, or

(3)   The mandibular demibranch of the spiracular cleft.

The first would be supplied by the pre-trematic IX nerve, the second by the post-trematic VII (*i. e.*, the hyomandibular or hyoideus, the third by a pre-trematic VII nerve.

The older writers assumed that the pseudobranch in teleosts is a hyoidean gill, presumably the more caudal demibranch, though the latter point is not usually made plain. See particularly the paper by Maurer ('84). But in a second paper Maurer ('88) traced the embryology of the arterial arches in the salmon and found that it is not the first (mandibular), but the the second (hyoid) arterial arch that atrophies. The pseudobranch therefore develops, we infer, in connection with the mandibular arch and is a mandibular demibranch of the spiracular cleft. This is further supported by the fact that in the forms in which the pseudobranch is said by Stannius to be innervated trom the VII nerve (Belone, Esox) its fibres come from the r. palatinus, which is supposed to be pre-spiracular, rather than from the r. hyomandibularis, supposed to be post-spiracular.

But if this argument from the innervation were followed up, it would lead to the conclusion that in those species which have the pseudobranch supplied by the IX nerve it must be derived from the second hyoid demibranch, while in fact Stannius states that the salmon itself, whose pseudo-branch Maurer decided is spiracular, has that organ inner-vated from the IX instead of the VII nerve. If, then, Stannius is correct regarding the innervation in this species, it follows that either the nerves or the arterial arches have suffered profound secondary modification. And we are not yet in a position to decide between these alternatives—certainly not until Stannius' account of the innervation has been confirmed microscopically.

From the neurological data now in hand it would appear that the pseudobranch of bony fishes is some-times a vestige of a demibranch of the first gill cleft, sometimes of the spiracular cleft. It must be admitted, however, that this mode of procedure may also lead into difficulties, as *e. g.*, in Lepidosteus (Wright, '85), where the spiracular pseudobranch *seems* to be innervated by the IX nerve and the hyoidean gill by the VII. But this case requires further investigation, as all admit.

At all events, pending further study, the case of Menidia can be interpreted on the basis of the nerve supply in only one way. We naturally assume that the pseudobranch represents a mandibular demibranch of a vanished spi-racular cleft, and that the nerve supplying it and the roof of the pharynx adjacent between the areas supplied by the IX and palatine nerves is a true pre-trematic VII nerve, such as is mentioned, *e. g.* by Stannius and by Ruge ('97), in some sharks. This accords with the embry-ological data in the case of the vascular arches of the salmon and Lepidosteus. Müller ('97) has studied the

development of the vascular arches in Lepidosteus and concludes that (in spite of the anomalous innervation) the pseudobranch is a spiracular (mandibular) gill, while the "hyoid gill" is the demibranch of the anterior wall of the first gill cleft.

I am inclined to doubt the participation of the IX nerve in the innervation of the teleostean pseudobranch in any case. In Gadus I am sure that its nerve supply comes from the facialis.

For the morphological discussion of this nerve see the pages immediately preceding.

VI.—The Ramus Palatinus Facialis.

After its separation from the nerve last described, the r. palatinus runs forward along the dorsal surface of the m. adductor arcus palatini and beyond the cephalic edge of that muscle (400) reaches the mucous lining of the roof of the mouth near the median line, which it follows up to the tip of the snout. This epithelium is richly supplied with taste buds and gland cells during almost the whole of this course and both of these are supplied by this nerve.

Stannius states (p. 55) that in fishes which have a well developed sub-cranial canal ("Augenmuskelcanal") the r. palatinus traverses it on the way to the roof of the mouth. This certainly does not apply in the case of Menidia. The sub-cranial canal is well developed, but the r. palatinus does not enter it, but runs along the outer side of the canal, not the inner, as Stannius describes in his types.

VII.—The Truncus Infra-Orbitalis.

This trunk (*t. inf.*) contains the following nerves: the r. mandibularis V, the r. maxillaris V and the r. buccalis VII. It receives the following components: the general

cutaneous, the motor V, the acustico-lateralis, the communis and a large sympathetic element. The communis element also may in some forms, as the sturgeon, go out as a separate nerve.

These components leave the ganglionic complex in a single compact trunk passing laterad, ventrad and slightly caudad from the ganglia. The V + VII ganglionic complex is all intra-cranial except the Gasserian ganglion. At about 500 (Fig. 22) the complex becomes narrower, as all of the VII ganglia lie caudad of this point, while most of the Gasserian ganglion lies cephalad; and here the whole of the complex (with the exception of the truncus hyomandibularis, the palatine and pre-trematic rami and one root of the r. lateralis accessorius, which have been previously given off) turns abruptly outward and emerges from the cranium through a single foramen and continues cephalad along the outer surface of the cranial wall.

The general cutaneous fibres arise from about the middle of the ventral side of the Gasserian ganglion. From the extreme caudal edge of the ganglion a small fascicle of cutaneous fibres emerges through a separate foramen and joins the truncus hyomandibularis, as already described. A similar fascicle arises from the ventral edge of the Gasserian ganglion near its cephalic end (485), curves back along the mesal face of the infra-orbital trunk at its origin, follows for a short distance the r. opercularis V (*t. f. 1*, Fig. 22), then separating from that nerve continues caudad along the dorsal border of the m. adductor arcus palatini, it joins the fascicle from the caudal end of the Gasserian ganglion (Fig. 2, *t. f. 1*) and the two together enter the truncus hyomandibularis.

Of these rami communicantes n. trigemini ad n. facialem, I can find no mention of the more caudal one, while

the cephalic one conforms closely to the typical arrange-
ment as given by Stannius (p. 47).   This latter nerve was
found by Stannius in all of the fishes examined by him,
with the exception of Amiurus and those in which the VII
emerges from the same foramen as the V.   In Belone he
found it to be composed chiefly of coarse fibres, with a
smaller number of fine ones.   I find, however, that both
rami communicantes are composed exclusively of very
fine fibres, though by analogy with other general cutane-
ous nerves I should have expected a few coarse ones to
be mingled with them, and more especially as in some
pure cutaneous ramuli of the r. hyoideus, which must be
derived from these rami communicantes, there are
numerous coarse and medium fibres.   This case is typical
of many others which lead me to believe that the calibre
of individual fibres may vary widely in different parts of
their courses.

The motor V fibres run under the Gasserian ganglion
and after their emergence take a position on the caudal
and inner side of the infra-orbital trunk.   The acustico-
lateralis component arises from the dorsal lateralis gan-
glion and its fibres pass out on the cephalic and lateral face
of the trunk.   The communis fibres from the geniculate
ganglion which have not been given off intra-cranially are
somewhat confused with the general cutaneous from the
Gasserian ganglion.   A part of these fibres go out with
the roots of the r. lateralis accessorius, others go out with
the supra-orbital trunk, but the larger part is clearly seen
to enter the infra-orbital trunk.

The four nerves which are represented in the infra-
orbital trunk are so confused, even in their smaller
branches, that they cannot well be described separately.
I shall, therefore, describe the branches of the trunk in

the order in which they are given off irrespective of the components contained in them. Remembering that the r. buccalis contains all of the lateralis fibres, the r. mandibularis V all of the motor and a part of the general cutaneous, and the r. maxillaris the remainder of the general cutaneous, the peripheral relations of each of these nerves can be easily gathered from the plot (Fig. 3). Before taking up the detailed account, emphasis should again be laid upon the fact that the branches of this trunk are enumerated in this way simply as a matter of convenience in description. The details of the arrangements of these branches and their fusions with each other have no especial morphological significance, but rather seem to be determined by the individual conditions as a matter of mechanical and functional adaptation. The remarkable way in which different nerves have been compacted into the infra-orbital trunk is obviously due to mechanical causes, chiefly to the excessive development of the eyes.

1.—The R. Opercularis V.

The first branch to be given off from the infra-orbital trunk is the motor nerve already referred to, which arises close to the cranium, passes back a short distance in company with the first recurrent twig from the Gasserian ganglion to the truncus hyomandibularis, separates from this twig, turns outward, crossing transversely the cephalic edge of the hyomandibular bone and then divides into ventral and dorsal branches (Fig. 22) for the m. levator arcus palatini (Fig. 4, *m. l. a. p.*) and the m. dilator operculi (*m. d. op.*) respectively. These motor nerves, it appears from Stannius' description of other species in which the truncus divides into its rami before their separation, should be relegated to the r. mandibularis V.

2.—*The Second and Third Branches.*

The trunk runs out under the orbit between the m. rectus externus and the m. adductor arcus palatini and in this position gives off a small branch of coarse and fine fibres which passes laterally and slightly ventrally to the skin overlying the m. adductor mandibulæ (*io. 2*). Here the branch breaks up into several twigs, some of fine fibres for the skin under the eye, a coarse-fibred twig for the 12th organ of the infra-orbital line, which is a naked papilla, and the remainder continues ventrad and caudad under the skin. Having reached the opercular canal, this twig enters the bony canal, having previously penetrated the m. adductor mandibulæ and the pre-opercular bone. In the canal it divides and sends branches to the skin cephalad and caudad of this point. It sends minute twigs to the skin along its entire course.

On the opposite side of the specimen figured the course of this nerve is as described above except that the opercular general cutaneous portion breaks up earlier into a number of very fine ramuli, none of which could be traced into the opercular canal. The fibres of these ramuli join the sub-dermal plexus and lose their sheaths. They evidently supply the same region as on the other side, but by a somewhat different course.

The general cutaneous fibres of this second branch correspond in nature and position rather closely to the most lateral one of the three accessory trigeminal branches which arise from the Gasserian ganglion in the tadpole of the frog (Strong, '95).

After the separation of this second branch, the infra-orbital trunk immediately divides into three divisions, all of which contain both coarse and fine fibres. The ventral

division separates first. It corresponds in part to the r. buccalis, but it contains only a portion of the buccalis fibres and it carries other fibres also not belonging to that nerve, viz., general cutaneous and motor. The middle division contains more fine than coarse fibres and is the proper r. mandibularis V. The dorsal division contains coarse and fine fibres in about equal proportions and corresponds to the r. maxillaris plus a portion of the r. buccalis and a communis element.

After this division has begun, but while the dorsal and middle divisions are still in contact, a small branch (*io. 3*) is given off from the dorsal one. It contains only coarse fibres and goes around the outer (lateral) side of the middle division but around the inner and ventral side of the ventral one. It runs over the dorsal edge of the m. adductor mandibulæ to the skin. It now sends about half of its fibres into the substance of this muscle. These are very coarse and apparently branch freely within the muscle, for the number here is greater than the number which enters the muscle. They are undoubtedly motor fibres. The remaining fibres run a short distance downward between the m. adductor mandibulæ and the skin and in this position cross (apparently without anastomosis) one of the ventrally directed twigs of the second branch of the infra-orbital trunk, the latter twig being outside. They then supply the 11th organ of the infra-orbital line, which is a naked papilla.

3.—The Ventral Division.

This assemblage of fibres turns outward under the eye and over the m. adductor mandibulæ. Here it gives off its first branch of coarse fibres (the fourth infra-orbital branch), which curves laterally around the m. adductor

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mandibulæ to the skin, where it supplies the 10th lateral
line organ, a naked papilla, of the infra-orbital line.
Several smaller branches of fine fibres go off at nearly the
same point and supply the skin adjacent, and particularly
that about the lower border of the eye (fifth infra-orbital
branch).

The ventral division now comes to lie at the dorso-
lateral edge of the m. adductor mandibulæ close under
the skin and the coarse and fine fibres, which hitherto
have been mingled, become segregated, the coarse ones
all lying in the lateral half of the nerve.   This tendency
of lateralis fibres to draw away from the other components
is very characteristic, and is exhibited in nearly all nerves
where they are associated with other fibres.

At 395 another coarse-fibred twig is given off for the
9th (naked) organ of the infra-orbital line (6th infra-
orbital branch).   At 385 the 7th ramulus goes ventrad to
supply the thickened epidermis lying between the oper-
cular canal and the eye.   The 8th ramulus supplies the
8th (naked) organ of the infra-orbital line and also the
similar organ (7th) next cephalad.   Then follow the 9th
ramulus directed ventrad, and the 10th dorsad, both for
the skin.   The latter crosses external to, but apparently
does not anastomose with, the twig from the dorsal
division for the 6th infra-orbital organ (the 18th infra-
orbital branch).   The remaining fibres of this ventral
division (11th infra-orbital branch) are all coarse.   They
enter the ventral part of the m. adductor mandibulæ and
apparently participate in its innervation.

4.—*The Middle Division—R. Mandibularis V.*

The middle division is the r. mandibularis V.   After
its separation from the ventral division this nerve runs
parallel to and almost in contact with the dorsal division

along the ventro-lateral side of the latter for a considerable distance. Its first branch, the 12th of the infraorbital trunk (440), is of coarse fibres, which innervate the mesal portion of the m. adductor mandibulæ cephalad of this point. The main nerve now passes farther laterally in the floor of the orbit, separating somewhat from the dorsal division. Its coarse fibres, which we shall see are all of the motor type, are mingled among the fine ones and do not segregate themselves as lateralis fibres usually do.

The 13th branch leaves the r. mandibularis V at 375. This, too, is of coarse fibres and supplies the lateral portion of the m. adductor mandibulæ. At about 300 the r. mandibularis V turns ventrally, passing between two portions of the adductor mandibulæ and finally running forward along the outer face of the ventral edge of the quadrate near its cephalic end. The r. mandibularis VII lies in a corresponding position on the inner face of the same bone a little farther ventrad.

While in this position the r. mandibularis V gives off another branch (the 14th infra-orbital, *V–VII. 1*) composed of fine and medium fibres. Beyond the cephalic end of the quadrate this branch turns outward and under the skin over the articular bone and between and behind the open ends of the infra-orbital and mandibular canals it divides into numerous ramuli. Several of the smaller ramuli supply the skin adjacent to the end of the infraorbital canal and that about the open space between the mandibular and opercular canals (it will be remembered that the infra-orbital canal disappears for a part of its course and closes in again at this point), and a larger ramulus runs caudad under the skin along the ventral edge of the m. adductor mandibulæ. This is the com-

municating branch with the r. mandibularis VII (*m. VII. 8*)
mentioned in the account of that nerve.   It sends a twig
at once into the muscle, which appears to anastomose with
the motor twig which enters the muscle near the same
point from the ventral division of the infra-orbital trunk.
The fibres of this twig, like the rest of those of the com-
municating branch, are fine or medium and very different
from typical motor fibres.   The rest of this nerve runs, as
before described, along the ventral surface of the m.
adductor mandibulæ, becoming progressively smaller cau-
dad, and finally joins the r. mandibularis VII.   This may
be regarded as a sensory nerve for the muscle or as a
general cutaneous nerve for the overlying skin.

The ramulus last described receives some fibres from
the r. mandibularls VII (*m. VII.* 8) and these enter the
largest ramulus of this group from the 14th infra-orbital
branch, which will next be described.   This nerve runs
forward in several branchlets along the outer face of the
articular and dentary bones to the tip of the mandible (its
distal portion not shown on the plot).   It supplies the
skin adjacent the mandibular canal for its entire length.
Its fibres were also definitely traced to three very minute
naked sense organs (*m. p. l.*, Fig. 5) lying over the man-
dibular canal, one over the fifth canal organ, one at the
fourth pore and one behind the fourth canal organ.   There
may also be other similar organs in the same vicinity, as
they are minute and very slight imperfections in the sec-
tions might obscure them.   The first one mentioned was
found only on the right side of the specimen figured,
though probably present on both sides.

These organs resemble in structure the similar organs
lying over the opercular canal, rather than the terminal
buds on the lips supplied by the r. mandibularis internus

VII. Their nerve fibres, like those of the opercular organs just referred to, are of medium or small size. That these organs are morphologically equivalent to those on the operculum, I think is clear. They therefore probably belong to the lateral line system. Whether they derive their fibres from the r. mandibularis V or from the r. mandibularis VII, I cannot determine with absolute certainty by direct observation. I think undoubtedly from the latter, for, on the one hand, the r. mandibularis V contains no other lateralis fibres, while, on the other hand, all of the similar naked opercular organs are supplied by the facialis. Moreover, it can be definitely determined that the anastomosing branch *8* between the r. mandibularis V and the r. mandibularis VII contains fibres from both the V and VII nerves. Inasmuch as these fibres are all rather fine, those from the VII cannot be separately followed in Weigert preparations. In the osmic acid preparations, however, the analysis of the VII and V fibres in this nerve can easily be made, as the VII fibres, though no larger than the largest cutaneous fibres from V, yet take the metallic impregnation much more intensely. It can here be easily seen that the V fibres all, or nearly all, are given off from the recurrent nerve before it reaches the mandibularis VII, while the fibres from the latter can be separately traced cephalad after the anastomosis with the V into the branch which supplies the three mandibular organs in question. As the skin of this region was not perfectly preserved in these sections, it was impossible to trace these darker fibres into their organs. There is, in my mind, no doubt that the relations expressed in the plots are correct.

Immediately after the separation of the third branch of the r. mandibularis V, a minute twig (the 15th infra-

orbital, not drawn on the plot) separates, which passes back along one of the large tendons of the m. adductor mandibulæ. Its ultimate distribution could not be determined. It may represent a nerve for muscular or tendon sensation.

Having now reached the cephalic end of the quadrate, the r. mandibularis V now turns inward and takes its position on the inner face of the articular bone a short distance dorsad of the r. mandibularis VII. It lies immediately dorsally of Meckel's cartilage, while the mandibularis VII lies ventrally of it, and this position it maintains nearly to the tip of the mandible. Here it gives off a minute coarse-fibred twig (*io. 16*) to a separate slip of the m. adductor mandibulæ which lies mesally of the articular and dentary.

Having reached the cephalic tip of the articular bone (160), there separates from the r. mandibularis V the 17th infra-orbital, which is the second anastomosing branch for the r. mandibularis VII (*V–VII. 2*). This branch contains nearly all of the remaining coarse fibres and some of the fine and medium ones. It descends between Meckel's cartilage and the extreme tip of the articular bone to join the r. mandibularis VII and then distributes to the mm. genio hyoideus and intermandibularis and the skin of the ventral surface of the mandible and lower lip, as already described.

Farther forward the remainder of the r. mandibularis V enters a canal between the dentary bone and Meckel's cartilage and finally emerges through a foramen to the ectal aspect of the dentary bone. As it is passing through its foramen it gives off a small branch (75) and this is followed by numerous similar branches which supply the skin of the side of the mandible both cephalad and caudad

of this point and of the edge of the lower lip, to the extreme tip of the mandible.

Terminal buds are abundant near the mandibular teeth and mesally of them, but not laterally of them in the regions supplied by the fibres of this nerve, and I believe that none of these fibres are destined for these sense organs but that they are all of a general cutaneous nature. One branch, however, enters the alveolar canal of the dentary bone. Here it turns mesad and a part, if not all, of its fibres emerge again to supply the skin of the tip of the mandible near the middle line. It is probable that none of them innervate the tooth pulps, as these have a separate innervation from the r. mandibularis internus VII.

5.—*The M. Adductor Mandibulæ.*

This muscle is innervated in Menidia by several branches of the r. mandibularis V in the way typical for teleosts. The only exceptions to this arrangement known to me are Esox, as described by Vetter ('78, p. 496) and Lota, as described by Goronowitsch ('96, p. 41), who find that this muscle receives in addition to these fibres a small twig from the r. mandibularis VII. This needs confirmation and I may add that an attempt to trace by dissection a cutaneous nerve like my first twig of the r. mandibularis VII for the sense organ *o.6* might easily lead to such a conclusion, for the fibres pursue a tortuous and often branched course through the m. adductor mandibulæ and might easily be lost by the dissector before their emergence upon the skin.

6.—*The Dorsal Division.*

The dorsal division of the infra-orbital trunk contains all of the r. maxillaris V and a portion of the r. buccalis

VII, together with communis fibres from the geniculate ganglion.

After its separation from the middle division it pursues its course parallel to the latter and dorsally of it in the floor of the orbit for a considerable distance without giving off any branches.

The coarse fibres lie on the lateral side of the nerve and comprise about two-thirds of the area of its cross-section. Its first branch (the 18th infra-orbital of my enumeration, *io. 18*) is given off at 325. It contains only coarse fibres and curves around the dorsal and lateral sides of the m. adductor mandibulæ to supply the 6th organ of the infra-orbital line, and under the skin is crossed externally by a general cutaneous twig from the ventral division. The two nerves are in contact, but do not anastomose.

Immediately after giving off this branch, the dorsal division divides into two unequal portions, each containing both coarse and fine fibres. In the larger mesal portion the fine fibres are on the ventral side, though very coarse fibres are mingled among them; in the lateral portion the fine and medium fibres gather on the lateral side and very soon separate from the coarse ones (*io. 19*). These separated fine fibres distribute to the skin under the eye and about the open end of the lachrymal segment of the infra-orbital canal. The coarse fibres of the lateral portion (*io. 20*) supply the second, third, fourth and fifth canal organs of the infra-orbital line and thus belong to the r. buccalis.

The larger mesal portion of the dorsal division while in the floor of the orbit separates into mesal and lateral rami. The latter contains all of the fine fibres with a few very coarse ones scattered among them in the way so characteristic of general cutaneous nerves, and this is the

r. maxillaris (*mx. V*) in the strict sense. The former is composed wholly or nearly so of the very coarse lateralis fibres and is a portion of the r. buccalis.

The r. maxillaris, after separation from these buccalis fibres, contributes to them a general cutaneous bundle and gives off for the remainder of its coarse numerous small twigs for the skin of the side of the head in front of the eye and for the outer surface of the upper jaw. There are also given off large branches (apparently communis fibres) for the mucous lining of the jaw and the edges of the upper lip. These regions abound in taste buds and there is no doubt that these are supplied by this nerve, for there is no other obvious nerve supply. Other branches, doubtless also communis fibres, were traced into the dentary canal of the premaxillary bone and apparently innervate its teeth.

Stannius (p. 42) mentions these fibres for the mucosa of the mouth and also in several cases anastomoses with terminal twigs of the r. palatinus, which seem to be absent here. It is evidently a portion of this communis element in the r. maxillaris which corresponds to the nerve supply for the maxillary barblet of siluroids (Pollard), as suggested by Allis ('97, p. 635).

The remainder of the infra-orbital trunk, comprising lateralis and general cutaneous fibres, runs up along the inner and front walls of the orbit and then passes farther mesad and continues cephalad under the parethmoid bone along the inner side of the lower end of the olfactory fossa and under the posterior nasal aperture. It turns dorsad along the cephalic face of the lateral part of the parethmoid and laterally of the olfactory sac. While still lying close to the mucous membrane of the olfactory sac, which is not in this region sensory, it breaks up into

several branches. It is possible that some fibres pass into the olfactory mucosa, though these could not be demonstrated.

The largest of these branches supplies the first canal organ of the infra-orbital canal. Several branches pass to the skin adjacent. Three of these were definitely traced to naked sense organs lying between the anterior and posterior nasal apertures (*a. b. c.*). Finally a large branch composed mostly of coarser and deeply staining fibres passes mesad under the olfactory fossa and joins the r. ophthalmicus superficialis V. The latter nerve is at this point composed exclusively of fine general cutaneous fibres, the coarse lateralis fibres of the r. ophthalmicus superficialis VII having previously all separated from it. The coarser fibres from the r. maxillaris can, therefore, be separately followed with great ease after they have joined the ophthalmicus superficialis. They soon again withdraw and pass mesad to three large naked sense organs on the top of the snout (*d. e. f.*), one just mesally of the anterior nasal aperture, the others progressively farther cephalad and mesad, so that these three organs, together with the corresponding three of the opposite side, form nearly a perfect semicircle from one anterior nasal aperture to the other over the tip of the maxillary bone. Some of these anastomosing fibres can be traced with certainty to these three organs, but there are others which seem to end free in the skin. This anastomosing branch may carry some general cutaneous fibres.

Five of the six naked organs of the snout supplied by the r. maxillaris were found and their innervation traced on the other side of this specimen. The positions of these organs were also demonstrated in other series of sections and in surface preparations of the skin of this region. It

is not probable that there is any considerable number of superficial sense organs in this region other than those figured, for the surface preparations failed to demonstrate them, while those found were in about the same positions as figured.

The morphology of the three organs which, together with the three of the opposite side, form the supra-maxillary commissure is, I think, quite clear. They and their nerve evidently belong to the lateralis system. In Lophius (Guitel, '91) there is a commissure of the lateral lines in the corresponding position and with the same innervation (see my Fig. 6). In Amiurus and Silurus there is a similar line of pit-organs (Allis, '97, p. 629). The three organs about the nasal apertures (*a. b. c.*) and the three similar ones innervated from the superficial ophthalmic nerve (*g. h. i.*) offer much greater difficulties. The nerves supplying them are smaller than those which supply the commissural organs last mentioned, but larger and more heavily medullated than typical communis fibres so that the nerve supply here is ambiguous, as either communis or lateralis fibres might be drawn off for them. I rank them provisionally with the pit-line and other accessory lateral line organs, and suggest that the buccal group may be related to the inner buccal group of ampullæ of selachians. Comparative or embryological studies might, however, relegate them to the terminal bud system.

Cole ('98a, p. 158, foot note) describes an essentially similar nerve in Gadus from the r. buccalis to supply pit-organs in front of the nasal apertures and near the cephalic end of the supra-orbital canal. He adds: '' This curious nerve is not represented in other fishes, and probably consists of lateral superficial ophthalmic fibres following a buccal course.'' From the quotations given

above it appears that the first supposition is not true; for this nerve seems to be general throughout the teleosts. There is no reason to assume that it is not a proper constituent of the r. buccalis.

Stannius mentions an anastomosis between the r. buccalis, in forms in which it is well isolated from the r. maxillaris (Cottus, Cyclopterus, Gadus) and the r. ophthalmicus superficialis. He has shown, furthermore ('49, p. 41) that among the teleosts there is the widest variation as to the relations of the r. mandibularis V, the r. maxillaris and the r. buccalis, from quite separate origins from the ganglionic complex to the fusion into a common infraorbital trunk, as in the present case. As the other forms which exhibit this infra-orbital trunk belong to widely separated families, it is probable that it is merely an adaptive modification in each case. In Menidia it is clearly produced mechanically by the crowding of the parts due to the enormous size of the eyes. The fusion of the r. buccalis with the r. maxillaris he correlates in Amiurus and other forms ('49, pp. 41 and 43) with the abortion of the bones of the infra-orbital ring and this is confirmed by our relations here. On page 43 he characterizes the r. buccalis as the nerve for the region of the infra-orbital bones and includes both lateralis and general cutaneous fibres. While it is probably true in other fishes, as in Menidia, that the nerves for the organs of the infra-orbital lateral line are usually accompanied by general cutaneous fibres for the adjacent skin, yet it accords better with more recent usage to confine the term r. buccalis to the lateralis fibres and relegate the general cutaneous fibres, no matter how closely related to them, to the r. maxillaris. Thus the independence of the lateralis fibres is recognized and one step is taken toward a more consistent nomenclature.

VIII.—The Ramus Oticus.

This nerve has an independent origin from the extracranial portion of the ganglionic complex. It draws off general cutaneous and lateralis fibres, the former directly

from the Gasserian ganglion, the latter from the dorsal lateral line nerve just at the point where it divides to form the nn. buccalis and ophthalmicus superficialis VII. The r. oticus now runs cephalad and dorsad between the cranium and the m. levator arcus palatini and here divides, one twig continuing cephalad in the original position, the other directly dorsad through a foramen in the base of the post-orbital process of the frontal bone to turn caudad along the roof of the cranium under the main lateral line canal of the head. It contains 15 very coarse fibres and about 20 fine ones. Both components reach the lateral line canal through a foramen in the squamosal bone, the coarse fibres being external. These latter supply the single canal organ of the main lateral line between the opercular and the infra-orbital lines. The fine fibres could not be traced to their termini. They probably break up and lose their sheaths in the loose connective tissue surrounding the membraneous canal and possibly reach the overlying skin.

The twig of the r. oticus which is directed forward also contains both coarse and fine fibres. It turns laterally around the cephalic end of the m. levator arcus palatini and a portion of the coarse fibres enters a foramen in the most dorsal post-orbital bone to supply the single organ of the post-orbital section of the infra-orbital canal. The remaining fibres turn ventrad and anastomose with a fine-fibred nerve from the supra-orbital trunk. Fine fibres from both of these sources supply the skin around the post-orbital section of the infra-orbital canal. The coarse fibres run down under the skin close behind the eye and supply the 13th and 14th infra-orbital lateral line organs, these being the last of the series of naked infra-orbital organs. In my preliminary paper ('97) it was erroneously

stated that the n. oticus innervates two instead of three organs of the infra-orbital line.

The nerve which I have termed the otic evidently corresponds to the r. oticus + the external buccal of Gadus, as described by Cole ('98a).

Wright ('85, p. 491) holds with Van Wijhe that the r. oticus should be defined as the nerve of the neuromasts contained within the squamosal bone. In this case the term should be confined to only one of the twigs here described.

It is, I think, sound morphology to regard the r. oticus as the proper dorsal branch of the facialis segment. The sensory portion of the dorsal rami was primitively of general cutaneous nature without doubt. The morphological character of this nerve is therefore given to it by its general cutaneous rather than by its lateralis fibres and the latter accompany the former to their peripheral distribution secondarily and as a matter of mechanical convenience, just as the lateralis fibres of the r. supratemporalis vagi or glossopharyngei may (or may not) accompany the general cutaneous fibres of the dorsal ramus of the corresponding segment and just as the r. ophthalmicus superficialis VII may accompany the corresponding trigeminal nerve. This conception is justified, further, by the known relations of the r. oticus to the spiracle in forms which possess the latter structure (Wright, '85, Müller, '97, Allis, '97 and others). Pollard, ('91) finds that the r. oticus in Clarias and Auchenaspis also possess both a lateralis branch and a branch to the skin which does not go to any lateral line organ.

The r. oticus, then, was probably originally the dorsal ramus of the facial nerve to which lateralis elements have secondarily been added and whose general cutaneous portion has, like that of the profundus nerve, been cenogetically fused with the Gasserian ganglion. Compare the discussion of metamerism in Section 12.

IX.—The Truncus Supra-Orbitalis.

The supra-orbital trunk contains lateralis fibres from the dorsal lateral line ganglion, general cutaneous fibres from the Gasserian ganglion and a smaller number of communis fibres from the geniculate ganglion. The first comprise the r. ophthalmicus superficialis VII; the second the r. ophthalmicus superficialis V; the third in other fishes are usually relegated to the r. ophthalmicus superficialis V, as in Amia. The two fine-fibred components are so closely united that it is impossible to separate them far beyond the tip of the Gasserian ganglion (compare the cross-sections, Figs. 22 to 25). But the coarse-fibred lateralis component can be easily followed microscopically throughout the entire extent of the trunk. The trunk runs dorsad and cephalad along the outer face of the cranial wall under the post-orbital process and carries with it for a considerable distance an extension of the Gasserian ganglion.

Near the cephalic border of the post-orbital process, but before the tip of the ganglion has been reached, a fine-fibred branch separates dorsally (Fig. 4, *so. 1*). It seems to include both general cutaneous and communis fibres. It passes through a foramen in the sphenotic bone into the cranial cavity and then runs dorsad in the meninges. The subsequent course is closely parallel with that of the most cephalic twig of the third root of the r. lateralis accessorius, with which, however, it does not anastomose. It passes through a foramen in the frontal bone and then divides into two twigs which apparently distribute to the skin overlying the supra-orbital canal.

Slightly farther forward, *i. e.*, just at the tip of the ganglion, another fine-fibered branch separates dorsally (*so. 2*). It sends one twig laterally along the cephalic

face of the m. levator arcus palatini to anastomose with
the r. oticus and supply the adjacent skin, as already
described, and then it breaks up into a number of similar
twigs for the adjacent skin above the eye.   Of these twigs,
however, one joins the r. ciliaris longus (*cil. l.*) for the
dorsal side of the eye-ball and another runs out into the
cornea (*co. 1*).   All of these twigs are colored on the plots
as if they were general cutaneous, though there is doubt-
less a communis element and some are probably directly
derived from the sympathetic ganglion at the base of the
Gasserian ganglion.

The trunk runs forward close under the lateral wing of
the frontal bone and under the supra-orbital canal, the
coarse fibres mostly dorsal and the fine fibres ventral,
though in each case there is some admixture of fibres of
the other type.

At about the level of the last (sixth) canal organ of the
supra-orbital canal (430) three branches are given off—
one of coarse fibres (*so. 3*) for that organ, passing through
a foramen in the frontal bone to reach the canal; the
second one (*so. 4*), passing mesally through a foramen in
the cranial wall to the meninges of the brain at the level
of the cephalic end of the optic lobes, where it turns
dorsad; and the third (*so. 5*) of fine fibres, which goes
cephalad parallel to and slightly dorsally of the main
trunk.

The branch *so. 4* springs from the mixed ventral por-
tion of the trunk and, like that portion, is composed of fine
fibres with a few coarse ones intermingled, probably main-
ly, if not wholly, general cutaneous.   It passes dorsad in
the meninges and divides into numerous very fine branches
which anastomose more or less with each other, but appar-
ently not with any of the other meningeal rami.   Two of

these branches pierce the frontal bone by separate foramina and distribute to the skin of the top of the head over the supra-orbital canal. No sense organs were found in this vicinity. Others pass to the dorsal side of the brain and there in its membranes unite into an intricate plexus which envelops the large pineal vesicle which lies under the skull and over the extreme cephalic tip of the optic lobes and the caudal part of the cerebrum. Some fibres of this plexus pass to the median line cephalad of the epiphysis and there in the meninges unite with a similar fascicle from the other side. The nerve thus formed runs cephalad exactly in the median line between the brain membranes and the exceedingly delicate pallium to the tip of the cerebrum. It then passes dorsad through the cranial cavity to the inner side of the cranial roof in which position it continues forward immediately under the suture of the two frontal bones. Still farther cephalad it lies in the narrow space between the frontal bones and the internasal cartilage, nearly to the tip of the latter. It could be followed beyond the cephalic end of the frontal bones, in the latter part of its course leaving the dorsal surface of the internasal cartilage to run in the subcutaneous connective tissue, where it is finally lost.

This peculiar nerve apparently corresponds to the "intra-cranial ascending dorsal twigs of the N. trigeminus and N. facialis," which in Silurus arise from the ganglionic complex cephalad of the r. lateralis V and run forward intra-cranially and under the skin of the head, one branch ramifying over the nasal bone (Stannius, '49, p. 48). Whether it is of sympathetic, communis or general cutaneous nature, I have no means of deciding positively. As indicated on the plots, I believe that it belongs mainly to the latter component. This, however, needs confirmation.

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The branch *so. 5* runs close to the trunk, but separated from it by a large blood vessel, and gives off numerous branches for the skin between the eye and the supra-orbital canal.   As it approaches the cephalic edge of the eye, it diverges laterally from the trunk and sends several twigs to the cornea (*co. 2*) and eye-ball.   The remaining fibres supply a thickened fold of skin laterally of the nasal openings.   None were traced to special sense organs, the buds in the cephalic part of this region having a different nerve supply.

At the level of the fifth canal organ of the supra-orbital line a coarse-fibred branch (*so. 6*) leaves the trunk to supply this and the fourth organ, these two organs lying very close together, but their nerves passing into the canal through separate foramina in the frontal bone.

Under the pore between the third and the fourth organs of the supra-orbital canal a branch (*so. 7*), comprising fine and medium fibres, passes up through a foramen in the bony floor of the canal to the skin of the top of the head, part of the fibres running forward a long distance within the bony canal, finally to emerge to the overlying skin.

Then follow two coarse-fibred branches (*so. 8* and *so. 9*) for the third and second supra-orbital canal organs, each with its special foramen in the frontal bone.

The trunk meanwhile runs parallel with and close under the canal, being separated from it only by the frontal bone.   This bone consists of two broad wings and a short vertical plate, the canal lying at the point of their intersection.   One of the wings runs inward from the canal, over the brain cavity and internasal cartilage, the other outward over the eye, while the vertical plate runs down from the canal along the lateral face of the supra-orbital and internasal cartilages.   The supra-orbital trunk runs

in the angle between the vertical plate and the lateral wing, parallel with the slender supra-orbital cartilage and the dorso-lateral edge of the massive internasal cartilage. At the point where the branch *so. 9* for the second canal organ is given off the internasal cartilage spreads out laterally under the frontal bone, so that the supra-orbital trunk lies in a canal bounded above by the frontal bone and on all other sides by the cartilage. This lateral projection of the internasal cartilage is covered on its cephalic and lateral aspects by the highly developed par-ethmoid ossification and both the cartilage and its investing bone imperfectly enclose the caudal part of the olfactory sac. From that portion of the par-ethmoid which lies behind the olfactory fossa a V-shaped tongue of bone extends into the substance of the internasal cartilage to form a partial bony wall to the canal which contains the olfactory nerve, and a similar tongue farther dorsad to form the floor of the canal containing the supra-orbital trunk, so that this trunk for some distance before it emerges into the olfactory fossa lies in a deep canal bounded above by the frontal and below by the par-ethmoid.

It emerges at about the same transverse level as the olfactory nerve, but by a separate foramen farther dorsally, previously, however, giving off a very slender nerve (*so. 10*), which turns ventrad and passes into the olfactory fossa by a separate foramen in the par-ethmoid bone and then runs cephalad along the lateral face of the olfactory sac, where it finally joins one of the dorsal twigs of the r. maxillaris V. It probably supplies the caudal (non-sensory) portions of the walls of the olfactory sac.

Immediately upon the emergence of the trunk from its canal a fine-fibred branch (*so. 11*) separates and goes at once to the skin mesally of the post-nasal aperture. The

trunk now continues forward in its former position ventrally of the supra-orbital canal and separated from it by the nasal bone. Mesally of it is the internasal cartilage, laterally the nasal sac and ventrally the olfactory nerve.

Under the caudal end of the nasal bone several twigs are given off, one of fine fibres mesally for the skin (not figured), one laterally of fine and medium fibres (*so. 12*), and two dorsally (*so. 13* and *so. 14*), each of coarse and medium fibres, leaving in the main trunk only very fine fibres with a few coarse ones scattered among them, the typical general cutaneous arrangement. One of the dorsal twigs (*so. 13*) supplies the first canal organ; the other (*so. 14*) and the lateral twig (*so. 12*) turn laterad along the dorsal wall of the nasal sac, anastomose with each other, and terminate in three large naked sense organs (*g*, *h*, *i*) between the dorsal margin of the anterior nasal aperture and the cephalic end of the supra-orbital canal. This arrangement was confirmed on the opposite side of this specimen and the three organs were seen in other sections and in surface preparations of the skin of this region.

From the trunk other cutaneous twigs directed inward go off from time to time and under the first canal organ it receives the anastomosing branch from the infra-orbital trunk. The latter passes between two separated bundles of fibres of the supra-orbital trunk to the naked sense organs *d*, *e*, *f*, above the maxillary bone, as already described. It is possible that some fibres from the infra-orbital trunk remain in the supra-orbital trunk, but certainly no considerable number do so.

After the anastomosis the fibres of the trunk distribute to the skin of the top of the snout to the extreme tip of the upper lip. Near the end of the premaxillary bone a

large branch enters the dentary canal of that bone and turns back in it, probably supplying the teeth. These are, doubtless, communis fibres.

The three sense organs, *g*, *h*, *i*, above the anterior nasal aperture which are supplied by the superficial ophthalmic nerve resemble those of the same neighborhood which are supplied by the infra-orbital trunk and they are, doubtless, of the same nature. The same ambiguity holds here as there; I incline to the belief that they correspond to pit-organs.

Communis fibres can be clearly traced into the supra-orbital trunk. What their distribution may be is not so clear. Apparently they are of a simple visceral nature for the internal organs of the head. Terminal buds are known to be supplied by communis fibres of the r. ophthalmicus superficialis in some fishes (*e. g.*, Amia, Allis, '97). The naked sense organs on the barblets of siluroids are unquestionably supplied by communis fibres. My own preparations of Amiurus substantiate this. The nasal barblet is stated by Wright ('84, p. 367) to be innervated by the r. ophthalmicus profundus in Amiurus; this nerve is, however, the ophthalmicus superficialis, as Allis has suggested ('97, p. 539).

Stannius clearly recognized the lateralis and general cutaneous components of this supra-orbital trunk and the origin and distribution of each. The lateralis component he identified with the r. frontalis, the general cutaneous with the r. nasalis of higher vertebrates (p. 35), the former of course being an impossible homology.

Goronowitsch describes the nerves entering this trunk in Lota vulgaris but erroneously names the ventral, or trigeminal, nerve ('96, p. 27) the r. ophthalmicus profundus. From his brief statement of the peripheral distribution this is clearly impossible. He describes and figures in this nerve (*i. e.*, the r. ophthalmicus superficialis V) a large bundle of communis fibres from the communis root of the facial (his dorsal root of the VII nerve).

X.—The R. Lateralis Accessorius.

This nerve receives communis fibres from the vagus and from the facialis. The latter arise from the geniculate ganglion by several small roots, which will be enumerated from behind forward. The first and largest of these recurrent roots (*rec. 1*) arises from the most caudal portion of the geniculate ganglion in several strands. Their relations are indicated somewhat diagrammatically in Fig. 26, which is a composite of several successive camera outlines of this region. Three of them pass directly dorsad over the emerging spinal V root and mesally of the dorsal lateral line root, while one arises farther forward than the others from the ventral surface of the ganglion and passes dorsad and caudad mesally of the sensory V root just after its emergence from the oblongata and of all the other V + VII roots, but laterally of the IV root. This root it follows back to its origin and then joins the other strands on the dorsal side of the dorsal lateral line root. This strand has a double origin, the two portions separately entering the IV nerve, which they closely follow and from which they separate together. The root as thus composed then continues dorsad into the meninges at the level of the caudal end of the optic lobe, then through a foramen in the cranial roof to turn caudad under the skin. It is composed chiefly of very fine fibres with a few more densely myelinated fibres of medium size scattered among them.

From the cephalic tip of the geniculate ganglion, after the separation of the fibres which go out through the hyo-mandibular foramen, the remaining communis fibres divide into two bundles. The larger one goes out ventrally with the infra-orbital trunk, as already described; the smaller one curves around the outer side of the

sensory V root dorsally. Just caudad of the point where the fibres of the dorsal lateral line root diverge toward their respective trunks this dorsal bundle of communis fibres sends off the second recurrent root (*rec. 2*). This root is then re-enforced by a strand of communis fibres from the ventral bundle. It goes directly dorsad into the meninges covering the optic lobe. Here it breaks up into several small twigs, the largest of which continues caudad to join the first root before it leaves the cranium. Another twig runs in the meninges farther dorsad, where it is joined by a small twig from the third root of the r. lateralis accessorious, and after the anastomosis it at once sends a twig dorsad through a foramen in the cranial roof. The terminus of this twig was lost by imperfections in the sections. I find, however, on the opposite side of the same specimen a naked sense organ in the corresponding position, which is doubtless supplied by this nerve. The remaining fibres of this anastomosing twig run to a foramen in the roof of the cranium farther caudad and probably join the first recurrent root extra-cranially.

The third root of the r. lateralis accessorius (*rec. 3*) arises immediately cephalad of the second and close behind the origin of the r. oticus. It contains very fine fibres and a considerable number of slightly larger and more heavily myelinated fibres. The latter arise from the dorsal communis bundle. Near its origin and embedded among its fibres is a cluster of five or six small ganglion cells. They belong to the finer fibres, and these enter the V + VII ganglionic complex farther cephalad than the other fibres. In several of my series these finest fibres were traced cephalad with tolerable certainty into the most cephalic ganglion (*sy. 1*) of the sympathetic chain, as indicated on Fig. 4. This little ganglion is,

therefore, almost certainly sympathetic.   This root, like
the preceding, runs dorsad in the meninges and then
breaks up into several minute twigs.   The largest of
these runs back and within the cranium joins the most
cephalic branch of the second root.   Of the other twigs
some appear to supply the meninges, but most, and these
containing the coarser fibres, rise to the cranial roof,
which they perforate, each by a minute foramen in the
frontal bone.   Five such branches were followed and of
these three could be traced to naked sense organs on the
dorsal surface of the head.   Probably the others have
similar destinations.

On the opposite side of the specimen plotted the details
of the facial roots of the r. lateralis accessorius are some-
what different.   The first root arises by several strands
essentially as figured for the left side, though the details
of their arrangement are not exactly the same.   The
second root is wanting altogether, and as this is the case
on both sides of another specimen examined, I assume it
to be the more usual arrangement.   The third root is
about as figured, though not exactly.   As before, it con-
sists of some very fine fibres and some a little coarser
with heavier myelination.   The latter come from behind
and clearly from the communis, the former arise a little
farther cephalad and probably from the sympathetic and
are provided with the little ganglion.   The third root
breaks up into numerous branches, some of which were
traced to sense organs, as on the other side.   In the upper
part of the cranial cavity this root sends back a large
branch which joins the main r. lateralis accessorius from
the first root.

As the large scales covering the top of the head make
it difficult to get perfect sections, several surface prepara-
tions of the skin of this region were made to control the
sections.   There are undoubtedly some more organs in
the region overlying the optic lobes than the plots indi-
cate, but that number is not large and is probably not

greater than the number of nerves which penetrate the cranium. The dorsal surface does not present superficial organs in regions other than this one.

The three meningeal nerves just described as roots of the r. lateralis accessorius all have intra-cranial origins and pursue essentially similar courses. They are, moreover, all bound together in an intricate and more or less variable plexus. There are farther cephalad two meningeal nerves which have extra-cranial origins from the supra-orbital trunk and which do not enter this plexus but are destined chiefly, at least, for the skin of the top of the head farther cephalad. I regard them as primarily general cutaneous nerves and as such have described them in the preceding pages. They are, however, doubtless accompanied by sympathetic or other visceral fibres and they may participate somewhat in the general meningeal plexus. Indeed the whole plexus is vastly more complicated than my diagrams indicate, and only the larger nerves could be traced with precision.

These organs overlying the optic lobes, which I have assumed to be terminal buds, are structurally similar to those about the nasal apertures, which I regard as pit-organs. The nerve supply here also is not absolutely free from ambiguity, and I must admit the possibility that these fibres are derived from the lateralis roots by an intra-cranial anastomosis which I have overlooked.

Almost directly dorsad of the origin of the first root of the r. lateralis accessorius and after receiving fibres from the other roots, which vary in number and importance in different individuals, the main r. lateralis accessorius turns abruptly caudad, first, however, receiving the anastomosing fibres from the most cephalic twig of the r. supra-temporalis vagi, as described under that nerve. It runs closely appressed to the outer surface of the cranium not far from the median line and contains very small fibres with a few of slightly larger calibre which are much

more heavily myelinated. It gives off a few fibres from time to time which join the rich sub-cutaneous plexus in which they could not be further traced.

When the dorsal musculature begins to appear the r. lateralis accessorius follows the dorsal surface of this muscle close under the skin and at about this level (600) it receives the second anastomosing branch from the r. supra-temporalis vagi. A short distance farther caudad it receives two anastomosing branches from the dorsal r. communicans *b* of the first spinal nerve, which break through the dorsal musculature in the septum between the general dorsal musculature and the interspinal muscles, nearer the median line. The r. lateralis accessorius now sinks down a short distance into the same intermuscular septum, in which it continues into the trunk. It receives a third anastomosing branch from the first spinal and from this point caudad one such branch for each segment. The first of these is formed by the union of one nerve from the first spinal nerve and one from the second, the second by one from the second spinal and one from the third, and so on. See the account of the spinal nerves, Section 4. Just caudad of the level of the third spinal ganglion the r. lateralis accessorius is joined by the third anastomosing branch from the r. lateralis vagi.

The discussion of the morphology of the r. lateralis accessorius is deferred until Section 12, which see.

XI.—The Ramus Ophthalmicus Profundus.

This nerve is said by most other authors to be absent in the bony fishes, except in the siluroids. I find, however, that a portion of the Gasserian ganglion has been isolated from the rest and fused more or less closely with the most cephalic ganglion of the sympathetic chain and

that from these ganglion cells a nerve is given off which accompanies the radix ciliaris longa to the ciliary ganglion (see Fig. 4). These general cutaneous fibres I tentatively homologize with the r. ophthalmicus profundus. They can best be described in connection with the account of the sympathetic nerves which they accompany; their detailed description and the figures illustrating them will, accordingly, be given in the next section.

The character of these trigeminal fibres in the radix longa of the ciliary ganglion is a matter of great theoretical interest. Van Wijhe, Beard and many others (Marshall and Spencer, '81; Ewart, '89 and '93; Platt, '91; Neal, '98, etc.), as is well known, give in elasmobranchs to the r. ophthalmicus profundus or its embryonic precursor the rank of a separate sensory nerve whose motor part may be represented in the oculomotorius. Or, according to other authors, the motor root of the profundus has disappeared in higher vertebrates, being represented as such in myxinoids.

Its ganglion ("g. mesocephali") often has only a temporary separate existence and fuses with the Gasserian ganglion in the adult. The suggestion (Schwalbe, '79, and others) that the ciliary ganglion is the vestige of the mesocephalic ganglion is apparently discredited by the accumulating evidence that the former ganglion is composed of sympathetic cells only (Retzius, '94 and '94a; Michel, '94; v. Kölliker, '94; Huber, '97).

The profundus nerve of siluroids, as described by Wright ('84) in Amiurus and by Pollard in Clarias and Trichomycterus ('95) requires further study. Allis thinks in the latter case that it is the r. ophthalmicus superficialis V and not the profundus, and the same seems to be the case in Amiurus also.

Trigla is the only one of the teleosts for which anything like the condition in Menidia has been described. Stannius (p. 25) mentions a fine-fibred nerve which separates from the trigeminus root intra-cranially and after emerging by a separate foramen into the orbit enters a small ganglion. From this ganglion, which is, undoubtedly, the profundus ganglion, as Allis ('97, p. 538) has maintained, there are given off a ramus ciliaris longus and a radix longa ad ganglion ciliare, very much as in Menidia.

Allis in the passage last cited has given a very comprehensive review and critique of the literature of the ophthalmicus profundus which need not be again summarized here. The primitive profundus nerve probably contained dorsal and ventral branches. The former is represented by the portio ophthalmici profundi of Amia and in teleosts it is either fused with, or supplanted by, the r. ophthalmicus superficialis trigemini. It cannot be identical with the latter nerve for in several forms both nerves are present. With it may be associated more or less closely the ramus ciliaris longus. The ventral branch comprises the ophthalmicus profundus of selachians and most higher forms and is associated with the radix longa of the ciliary ganglion.

Amia, as usual, exhibits a transitional stage in the evolution of the teleostean specialization. Here the profundus root has fused with the V root, but the ganglion is widely separated. From the dorsal angle of the ganglion is given off the large portio ophthalmici profundi, which joins the r. ophthalmicus superficialis V. The two rami ciliares longi arise in connection with it from the profundus ganglion. From the ventral angle of the ganglion the radix longa is given off, while the very small r. ophthalmicus profundus *sensu stricto* arises from the gan-

glion between the dorsal and ventral angles. This latter nerve is in a very interesting condition, and it would appear from Allis' description to be in a state of degeneration (p. 533)—"When this last nerve was found, it always accompanied the ciliary nerves as they ran forward and outward between the external and superior recti. Beyond that point it was always lost, appearing sometimes to fuse with the ciliary nerves, and at others to disappear in the general tissues."

In Menidia the profundus is still further reduced and more intimately fused with the trigeminus. The portio ophthalmici profundi is lost and the r. ophthalmicus profundus fused for its entire length with the radix longa.

The peculiar and constant relations of the ophthalmicus to the sympathetic are not difficut of explanation. The "head part" of the sympathetic has one or more ganglia associated with the ganglia of all of the cranial nerves, doubtless including the primitive profundus. Now, the sympathetic ganglion lying under the primitive profundus glanglion having become connected with the oculomotor nerve (either secondarily or primarily, if the III nerve should prove to be the motor nerve of the profundus segment, as some maintain), it was retained in this position during the backward migration of the profundus ganglion toward the Gasserian, and now appears as the ciliary ganglion.

Allis remarks that the superficialis trigemini and the profundus seem to vary in relative importance directly as the number of terminal buds found on the top of the head and snout. The primary composition of these nerves is, it seems to me, undoubtedly general cutaneous rather than special cutaneous for terminal buds. The number of the latter fibres is certainly an important factor, never-

theless it must not be forgotten that independently of that the size of these nerves will be determined largely by the relative development of the different parts of the head. Thus in the selachians the development of the rostrum, which is undoubtedly a dorsal region, has necessitated a large increase in the general cutaneous nerve supply. In such teleosts as Menidia, on the other hand, the dorsal surface of the head over and in front of the eyes has been reduced to a minimum, with a corresponding loss in the nerve supply.

XII.—Comparison with Acipenser and Lota.

We have in our discussion of the nerve roots earlier in this section called attention to the failure of Goronowitsch's segmental scheme of the trigemino-facial nerves ('88 and '96, especially the latter). He arranges, it will be recalled, the trigemino-facial roots in three homodynamous series, each with dorsal sensory and ventral motor roots, (1) trigeminus I (my general cutaneous and motor V roots), (2) trigeminus II (my two lateralis roots), (3) facial (my communis and motor VII). In this very attractive scheme there are two fatal defects. The first is that the ventral root of his trigeminus II is sensory, not motor. The second and more radical difficulty arises out of the fact that Goronowitsch considers disparate structures to be serially homologous. Thus, of the three dorsal roots in question which he considers to be homologous with each other and with the spinal dorsal roots, the first is general cutaneous, the second is lateralis and the third is communis. Now, it is of course possible that future researches may show that this root complex represents two or three or more primary metameres; but the origin and distribution of these root fibres in the adult certainly negative any such

direct comparison as that which Goronowitsch attempts to draw.

Goronowitsch's homologies of the rami in the case of Lota are also in some cases confusing. The truncus hyomandibularis is, as we have seen, composed exactly as in Menidia, save that the general cutaneous component is larger. This component he states is absent altogether in Acipenser, *i. e.,* there is no anastomosis from the trigeminus I to the hyomandibularis. The ophthalmicus superficialis VII in Lota is as in Menidia. The ophthalmicus superficialis V, which he incorrectly calls the ophthalmicus profundus, has in addition to general cutaneous fibres from trigeminus I, a large bundle from his facialis, which must be of communis nature, and may supply terminal buds of the top of the head as Allis describes in Amia.

Regarding the maxillary and mandibular nerves there is considerable confusion, which, however, can be cleared up, I think, by comparisons with Menidia. The composition of these nerves in Acipenser is probably as follows: Goronowitsch describes a rostral nerve from each of the three nerves, trigeminus I, trigeminus II and facialis. The first of these is from its origin evidently the proper r. maxillaris (general cutaneous) and it is described as innervating the appropriate cutaneous area. The second is equally clearly the r. buccalis and it accordingly supplies the infra-orbital canal organs. The third arises from the facial (geniculate) ganglion and is accordingly a communis nerve. This is the n. rostri interni of Stannius. It distributes to the upper lip and particularly to the barbels. It is, I think, the homologue of the communis fibres contained in the r. maxillaris of Menidia and distributed to the taste buds of the upper lip. In Acipenser there is anastomosis of these three nerves

peripherally and some confusion of the relations, but I pre-
dict that microscopical examination will reveal essentially
the arrangement which I have given and that the nerves
will not prove to be serially homologous structures as
Goronowitsch assumes. In Acipenser there is also a
r. palatinus which comes from the facial and is doubtless
purely communis, as usual. The r. mandibularis V is
derived wholly from trigeminus I. Goronowitsch regards
it apparently as a pure motor nerve ('88, p. 479), and that,
too, in spite of the fact that he found ganglion cells run-
ning out into its trunk. It doubtless contains general
cutaneous fibres also.

In Lota, Esox and Gobio the first two rostral nerves
were found (viz., my maxillary—the general cutaneous
portion—and my buccal), but the facial (communis) rostral
nerve was not found. Lota has a palatine nerve which is
strictly typical. There is in addition a large bundle of
facial (communis) fibres which joins itself to general cuta-
neous fibres from the trigeminus I and enters the r. man-
dibularis V. Now, Goronowitsch, impressed with the
necessity of finding a homologue in Lota of the rostral
nerve of his third segment in Acipenser, identifies the r.
palatinus of Lota with the r. rostri interni of Acipenser
and then assumes that the facialis fibres which enter the
r. mandibularis V in Lota correspond to the r. palatinus
of Acipenser. These homologies seem impossible, for the
distribution area of the r. palatinus is not at all that of the
r. rostri interni, and how can a lower jaw nerve be homol-
ogous with an upper jaw nerve? Allis ('97) finds com-
munis fibres entering the r. mandibularis V in Amia
and these distribute to terminal buds of the outer skin
and mucous surfaces in the mouth, both of the hyoid
region, and not at all to the palatine region, and it is

probable that these correspond to the facialis fibres in the corresponding nerve of Lota. The palatine nerve of Lota and other teleosts is unquestionably the same as the nerve of that name in ganoids and other forms. The communis fibres for the upper lip which correspond to the r. rostri interni of Acipenser, if present in Lota, doubtless go out with the r. maxillaris as in Menidia, and were overlooked by Goronowitsch. I have personal knowledge that this is the case in Gadus.

XIII.—Summary of the Trigemino-Facial Complex.

The trigemino-facial roots and ganglia can be clearly separated and the peripheral distribution of each has been traced.

The motor VII supplies muscles belonging to the constrictor system of the facialis segment. It does not supply the geniohyoideus and intermandibularis muscles, these being supplied by the motor V. The r. hyoideus is a mixed nerve, motor and general cutaneous; the r. mandibularis VII is purely sensory, though two components are represented, corresponding to the r. mandibularis externus (lateralis) and the r. mandibularis internus (communis) of the Amphibia. It contains no general cutaneous fibres save those derived by peripheral anastomosis from the r. mandibularis V.

There is a pre-trematic branch of the facial nerve, which has an independent course in Menidia and innervates the large (spiracular) pseudobranch and the mucosa adjacent. This is not the chorda tympani of higher forms and I consider it probable that this nerve is absent in Menidia, though present in some other fishes.

The accompanying tables express the relations of the roots, ganglia and rami.

P

A.—Facialis Complex.

Roots.	Central Termini.	Ganglia.	Rami.
I.—Communis ("dorsal geniculate")	fasciculus communis	geniculate	1. truncus hyomandibularis—r. man. int. VII. 2. r. pre-trematicus VII. 3. r. palatinus VII. 4. truncus infra-orbitalis—internal portion of r. maxillaris V. 5. truncus supra-orbitalis—in part. 6. facial root of r. lateralis accessorius.

II.—Motor	motor VII nuc. and fasc. long. dors. ?		truncus hyomandibularis
			   (a) r. opercularis profundus.
			   (b) r. hyoideus—motor component.

III.—Ventral lateralis root	tuberculum acusticum	ventral lateral g.	truncus hyomandibularis
			   (a) r. opercularis superficialis—lateralis component.
			   (b) r. mandibularis externus VII.

IV.—Dorsal lateralis root	tuberculum acusticum	dorsal lateral g.	1. truncus infra-orbitalis—r. buccalis. 2. truncus supra-orbitalis—r. ophth. sup. VII. 3. r. oticus—lateralis component.

B.—TRIGEMINUS COMPLEX.

ROOTS.	CENTRAL TERMINI.	GANGLIA.	RAMI.

I.—General cutaneous	spinal V tract and chief V nucleus	Gasserian	1. truncus hyomandibularis
			  (a) r. operc. superficialis—gen. cut. comp.
			  (b) r. hyoideus—gen. cut. comp.
			2. truncus infra-orbitalis
			  (a) r. mandibularis V—gen. cut. comp.
			  (b) r. maxillaris V—gen. cut. comp.
			3. truncus supra-orbitalis—r. ophth. sup. V.
			4. r. oticus—gen. cut. comp.
			5. r. ophthalmicus profundus.

II.—Motor	motor V nuc. and fasc. long. dors.?		truncus infra-orbitalis—r. mandib. V, motor component.

The infra-orbital trunk is a fusion of four nerves which in some vertebrates are distinct. These are, (1) the r. mandibularis V, with general cutaneous and motor components, (2) the r. maxillaris V, general cutaneous, (3) the r. buccalis, lateralis, and (4) communis fibres to taste buds of the upper lip, which apparently correspond to the n. rostri interni (Stannius) of Acipenser.

The supra-orbital trunk is a fusion of the r. ophthalmicus superficialis VII, for the supra-orbital lateral line, communis fibres of uncertain distribution, and the r. ophthalmicus superficialis V, general cutaneous. The latter nerve must not be confused with the r. ophthalmicus profundus, as several of the most recent writers have done. The profundus nerve is apparently represented by a vestigeal bundle of general cutaneous fibres which run out from the Gasserian ganglion with the radix longa of the ciliary ganglion.

The r. oticus is the dorsal ramus of the facialis segment and was probably originally a general cutaneous nerve to which a lateralis element has been added. Its general cutaneous portion has secondarily fused with the Gasserian ganglion.

The r. lateralis accessorius corresponds to the r. recurrens V, or superficial lateral line nerve, of the older authors. It is composed exclusively of communis fibres and, after receiving other communis roots from the vagus complex, seems to innervate the row of terminal buds under the dorsal fin.

Section 8.—The Sympathetic Nervous System.

The sympathetic system has not been exhaustively studied, as the work of previous investigators has covered the ground quite satisfactorily so far as it can be done

with the methods here employed. The topographical re-
lations of the ganglia and the larger sympathetic nerves
are indicated upon Fig. 4, and will be here briefly re-
viewed, though they deviate but little from Belone and
other well-known examples, for which, compare the de-
scriptions of Stannius.

My examination began on the left side at the level of
the fourth vertebra, where the sympathetic trunk of each
side lies close to the centrum, and the description will
proceed cephalad from this point. The fibres are small
but quite heavily myelinated. They are considerably
larger than the sympathetic fibres which go out with the
cranial nerves. Immediately caudad of the fourth spinal
ganglion, cells appear in the sympathetic cord. This
sympathetic ganglion is very small and ceases before the
spinal ganglion is reached. Now, instead of sending a r.
communicans to the ventral ramus of the spinal nerve in
the usual manner, the whole sympathetic trunk rises up
and becomes embedded in the ventral side of the spinal
ganglion and here additional sympathetic ganglion cells
are found. They can be distinguished from the cells of the
spinal ganglion by their smaller size. Sympathetic fibres
and a portion of the sympathetic ganglion run out into
the ventral ramus. A bundle of fibres passes also from
the sympathetic ganglion across the root of the ventral
ramus and back into the spinal ganglion.

The sympathetic ganglion runs somewhat farther ceph-
alad than the spinal ganglion and from its tip the sympa-
thetic trunk again descends to its former position, laterally
of the centrum of the vertebra, in this case, however,
separated from the latter by the fleshy origin of the m.
retractor arcus branchii dorsalis, so that it lies between
this muscle and the head kidney close to the dorso-mesal
angle of the latter.

Between the fourth and the third spinal ganglia no ganglion cells appear in the sympathetic trunk, which, however, rises up and again becomes embedded in the third spinal ganglion, where it develops a ganglion of its own, as in the previous case. Some of the sympathetic fibres pass through the ganglion without losing their medullary sheaths. This sympathetic ganglion sends fibres from its cephalic end into the ventral ramus and others, as before, back into the spinal ganglion.

The sympathetic trunk now resumes its former position between the m. retractor arcus branchii dorsalis and the head kidney nearly up to the level of the second spinal ganglion. Here a sympathetic ganglion is found, which fuses with the caudal end of the spinal ganglion and the sympathetic trunk runs embedded in the latter to its cephalic tip, where there is another sympathetic ganglion, which effects the usual relations with the ventral ramus (*r. v. 2*). The trunk then again passes down to its former position.

Opposite the second vertebra there is another ganglionic enlargement which extends forward as far as the r. ventralis of the first spinal nerve (*r. v. 1*). The nerve trunk, however, turns ventrad just cephalad of the m. retractor arcus branchii dorsalis and enters a large ganglion (*sy. 7*), within which it divides, one part continuing cephalad, the other passing ventrad and mesad to a small ganglion cœliacum (*g. cœl.*) lying ventrally and laterally of the centrum of the second vertebra. From this ganglion a strong sympathetic commissural nerve runs under the vertebra to a similar ganglion of the opposite (right) side, which in turn is in like manner related to a ganglion of the chain of that side and from which the n. splanchnicus is given off. The latter nerve is confined to the right

side. Of the various modes of origin of this nerve among
the bony fishes enumerated by Stannius (p. 138) the
arrangement here conforms most closely to that of Belone.
The commissural nerve as figured (*sy. c.*) is the left root
of the splanchnic nerve.

The "head part" of the sympathetic trunk may be
regarded as beginning from the same ganglion (*sy. 7*),
which gives rise to the root of the cœliac ganglion (Stan-
nius' usage). It runs cephalad, as before, along the dorsal
surface of the head kidney, and under the ganglion of the
first spinal nerve there is found the last ganglion of the
"head part," the sixth from in front (*sy. 6*), not counting
the ciliary ganglion. This ganglion is much larger than
any of the preceding. It lies close under the ganglion of
the r. lateralis vagi and may send some fibres into it. In
front it fuses broadly with the caudal part of the vagus
ganglion, being particularly intimately united with that
portion which I have termed the jugular ganglion. As in
the preceding cases, some of the fibres pass through the
ganglion without losing their medullary sheaths.

The sympathetic trunk now separates from the vagus
ganglionic complex slightly and runs along its inner and
ventral aspect between it and the lower outer edge of the
vagus foramen. Just cephalad of the closure of that fora-
men ganglionic cells reappear in the trunk. This small
ganglion (*sy. 5*) lies between the vagus ganglion and the
emerging root of the glossopharyngeus, but does not com-
municate with either. The trunk now fuses with the IX
root in which it can be separately followed to the IX gan-
glion. Just before reaching the latter it withdraws from
the IX root, but follows along its dorsal surface as a sepa-
rate round bundle and here there is another minute
sympathetic ganglion (*sy. 4*).

Separating from the IX ganglion, the trunk follows a big blood vessel along the outer wall of the cranium nearly to the foramen of the truncus hyomandibularis, running at the level of the ventral edge of the membranous labyrinth, which lies within the cranium. Throughout this portion of its course ganglion cells are scattered freely along the trunk, which has about the same number and character of fibres as in its post-vagal course through the body. Along with the vessel above referred to, it enters a foramen in the cranial wall which communicates with that of the truncus hyomandibularis, and a sympathetic ganglion which is here formed (*sy. 3*) applies itself closely to the ventral side of the mixed truncus hyomandibularis and r. palatinus within this foramen, and a portion runs out into these nerves. The ganglionic chain continues (*sy. 2*) into a similar foramen cephalad of that of the truncus hyomandibularis, which is occupied by a large blood sinus and by the caudal extension of the Gasserian ganglion from which arises the caudal root of the general cutaneous component of the truncus hyomandibularis, where it applies itself to the ventral side of the extra-cranial part of the Gasserian ganglion (Fig. 2, *sy. 2*) and follows it back into the cranium.

From this point cephalad the sympathetic ganglion is intimately fused with the ventral face of the Gasserian ganglion and sympathetic fibres can be seen to enter that ganglion. Others were traced into the infra-orbital and supra-orbital trunks and, as before stated, into the r. lateralis accessorius.

Sanders ('79, p. 745) describes in Merlangus an extra-cranial connection between the IX ganglion and the Gasserian, which conforms to my sympathetic nerve. He, however, does not regard it as sympathetic, but errone-

ously identifies the latter with the intra-cranial r. recurrens of the carp.

Cole ('98a, p. 145) has shown that in many fishes the r. pharyngeu IX may run forward accompanying this sympathetic nerve to join the r. palatinus VII, thus constituting a true Jacobson's anastomosis like that of the mammals. In Menidia the absense of the r. pre-trematicus IX is correlated with the reduction of the r. pharyngeus IX. The sympathetic ganglion *sy. 4* has, however, a slight fibrous connection with the IX ganglion and among these fibres there may be a few of the proper glossopharyngeal fibres which run forward with the sympathetic as a Jacobson's anastomosis. If such fibres occur, they cannot be distinguished from the sympathetic fibres and in any case their number would be very small. The true nature of this anastomosis, where it occurs, was recognized by Stannius ('49, p. 58, foot-note 1), though he did not make the homology with the Jacobson's anastomosis.

Continuing cephalad from the first sympathetic ganglion on the ventral edge of the Gasserian ganglion are two sympathetic nerves, one the radix longa of the ciliary ganglion, the other farther dorsad, the ramus ciliaris longus, which pursues an independent course to the eyeball. The sympathetic ganglion from which they spring (*sy. 1*) is very intimately related to the Gasserian and in places can be distinguished from it only by the small size of its cells, though farther caudad the two ganglia are quite distinct (Fig. 23). It then becomes bi-lobed (Fig. 24), the median lobe having only the characteristic small sympathetic cells and giving off a branch (*sy. rec. 3*) dorsad through the substance of the Gasserian ganglion for the third root of the r. lateralis accessorius, and farther

cephalad (*sy. oph. sup.*, Fig. 25) running into the sympathetic strand for the supra-orbital trunk, finally to terminate in the ramus ciliaris longus. The more lateral lobe receives a strong bundle of medullated root fibr s from the Gasserian ganglion (*o. pr. r.* Fig. 24) and contains mingled among the sympathetic ganglion cells larger ones which apparently belong to the fibres from the trigeminus root and which become more numerous farther cephalad. The radix longa of the ciliary ganglion arises from this lateral lobe (Fig. 25) and apparently contains both sympathetic and trigeminal fibres. All of the fibres from the lateral lobe enter the radix ciliaris longa.

These fibres from the Gasserian ganglion to the radix longa are presumably of general cutaneous and not sympathetic nature. They could not be separately followed through the ciliary ganglion and hence their peripheral distribution is unknown. Their morphology is discussed in Section 7, XI.

From the lateral lobe of the first sympathetic ganglion a minute sympathetic twig goes off ventrad and joins the ventral ramus of the n. oculomotorius just after the separation of the dorsal ramus and just before its anastomosis (radix brevis) with the ciliary ganglion.

The ramus ciliaris brevis arises from the ciliary ganglion, which is provided with two roots in the typical way, the radix longa from the Gasserian ganglion and the radix brevis from the III nerve. The radix longa is composed mostly of small and medium-sized fibres with a few very large ones. It turns abruptly mesad and ventrad to the ciliary ganglion which lies in contact with the III nerve.

The ciliary ganglion is composed for the most part of the very small cells so characteristic of all of the ganglia

of the sympathetic system, but among them are some of larger size like those of the Gasserian ganglion. The caudal end of the ganglion is composed chiefly of the larger cells, the cephalic end contains a few of them, while the middle of the ganglion is composed wholly of the very small ones. Some of the fibres of the radix longa seem to run through the ganglion without loss of their sheaths, while none of those of the radix brevis appear to do so. The radix brevis arises from the division of the oculomotorius for the internal and inferior recti muscles shortly after its separation from the trunk. The tiny twig from the first sympathetic ganglion joins the same division just before the radix brevis. The ciliary ganglion is drawn on Fig. 4 as if it lay on the dorsal side of the III nerve. It really lies on the lateral side. The ramus ciliaris brevis distally of the ciliary ganglion is drawn as if it contained only sympathetic elements. It may contain general cutaneous, though they could not be separately distinguished.

The mode of origin of the radix longa of the ciliary ganglion is somewhat different on the opposite side of this specimen. The first sympathetic ganglion is, as before, very intimately united to the Gasserian ganglion and the ramus ciliaris longus arises apparently from the sympathetic ganglion only. A small number of medullated fibres, which can be traced back through the Gasserian ganglion and are therefore probably trigeminal root fibres, can be traced from the Gasserian ganglion through the sympathetic ganglion and into the radix longa of the ciliary ganglion. These are accompanied in their course by a small number of large ganglion cells and after the separation of the radix longa from the sympathetic ganglion the number of these large cells is greatly increased.

There is thus formed a long, narrow ganglion made up wholly or nearly so of large cells like those of the Gasserian ganglion, which runs out along the radix longa and reaches from the Gasserian ganglion nearly to the ciliary ganglion. On this side the radix breva is much longer than on the left side and it arises from the undivided trunk of the oculomotor nerve.

Contrary to the statement of Stannius, the fibres of the radix brevis are exclusively of fine calibre, arising from a fascicle of fine fibres on the lateral side of the III nerve.

Distally of the ciliary ganglion the ramus ciliaris brevis lies laterally of all of the branches of the oculomotorius, ventrally of the m. rectus superior and dorsally of the m. rectus inferior and rectus internus. Opposite the optic chiasm it begins to turn ventrad and maintains this course, running under the optic nerve and above the m. rectus inferior until under the insertion of the latter muscle it penetrates the sclerotic and finally enters the iris at its extreme ventral point, almost diametrically opposite the entrance of the ramus ciliaris longus.

The ramus ciliaris longus (*cil. l.*) contains some fine fibres with almost as many very coarse and heavily myelinated ones. It follows the course of a small blood vessel ventrally of and parallel with the supra-orbital trunk and dorsally and somewhat laterally of the m. rectus superior. Dorsally of the eye it receives the anastomosing nerve from the second branch of the supra-orbital trunk. Then, without giving off any obvious branches, it penetrates the sclerotic and enters the iris somewhat caudad and laterad of the insertion of the m. rectus superior.

The arrangements of the ciliary nerves vary exceedingly in different fishes. For the details see Stannius ('49, p. 38) and Baudedot ('83, p. 123). The ramus ciliaris

brevis in most cases enters the eye-ball with or near the optic nerve. To this Menidia is a conspicuous exception.

The fact that fibres of the radix longa can be followed through the ciliary ganglion, while those of the radix brevis cannot, accords with the physiological results of Langley and Anderson ('92) and with the degeneration experiments of Apolant ('96; cf. also Huber, '97, pp. 124, 125).

Summary of Section 8.

The sympathetic nervous system so far as studied conforms in the main to previous descriptions, and most closely to Stannius' account of it in Belone. The " head part " contains six important ganglia, aside from the ciliary. These are related to the roots of the X, IX, VII, V and III nerves. The radix longa of the ciliary ganglion is accompanied by general cutaneous fibres which arise from a special projection of the Gasserian ganglion and were traced into the ciliary ganglion. These fibres I have homologized with the r. ophthalmicus profundus trigemini.

SECTION 9.—THE EYE-MUSCLE NERVES.

I.—The Eye-Muscles.

The eye-muscles themselves merit a brief preliminary description. The sub-cranial canal is greatly developed and within it are the origins of the mm. rectus externus, rectus internus and rectus superior. It originates at the extreme caudal end of the basioccipital (Fig. 1, *s. c*), runs forward as a round canal at first within that bone, progressively expanding until farther cephalad it becomes broadly triangular in cross-section, the base of the triangle being dorsal. (Fig. 2). The floor of the canal is here

formed medianly by the parasphenoid, laterally mainly by the pro-otics, while the dorsal wall is for the most part formed by the pro-otics and by a projection from the basi-occipital bone. In the region of the figure just referred to the dorsal wall is membranous, a condition maintained from this point cephalad except at the extreme cephalic end, where a basisphenoid appears, just behind the optic chiasm. This bone is Y-shaped in cross-section, the lateral wings forming the floor of the brain between the hypophysis and the optic chiasm, and the vertical limb articulating below with the parasphenoid in the median line, thus forming the cephalic boundary of the sub-cranial canal.

Except at its most caudal end the canal is not filled by the eye-muscles, but these are packed densely with fat and connective tissue.

The m. rectus externus originates in the extreme caudal end of the sub-cranial canal, which at first it fills completely (Fig. 1, *r. e*). As the canal enlarges, this muscle rises to its dorsal side, while the m. rectus internus appears below it. With the lateral expansion of the canal still farther forward the externus occupies its dorso-lateral angle and here under the lobi inferiores a separate slip of the muscle takes origin from the fascia on the dorsal surface of the m. rectus internus in the median line, the fibres interdigitating with a similar slip from those of the opposite side (Fig. 22, *r. e*). There is thus formed a broad, thin sheet of muscle which runs dorso-laterally under a mass of fat to join the ventro-lateral side of the main muscular belly near the point where it leaves the sub-cranial canal (Fig. 2), turning abruptly laterad toward its insertion on the eye-ball. The fibres of this separate slip are very much smaller than the other

muscular fibres, a peculiarity which they exhibit from their origin to their insertion. They have, as we shall see, a slightly different innervation.

The m. rectus internus originates, as before indicated, near the caudal end of the sub-cranial canal, in a groove in the dorsal side of the parasphenoid bone. The muscles of the two sides occupy the ventro-median angle of the canal for its entire length (Fig. 2, *r. i. t.*) and still farther cephalad in the same relative position on either side of the parasphenoid along the inner sides of the orbits to their insertions on the cephalic borders of the eye-balls. The fibres which compose the dorsal edge of this muscle are of much smaller diameter than the other fibres.

The m. rectus superior originates in the cephalic end of the sub-cranial canal from the parasphenoid under the m. rectus internus and from the membranous roof of the canal over the same muscle. These two muscles run in close contact (Fig. 2) to the end of the canal, when the m. rectus superior turns dorsad and laterad running over the m. rectus inferior and the optic nerve to its insertion on the eye-ball. The fibres of the dorsal part of the muscle are smaller than the others.

The m. rectus inferior arises from the basisphenoid and runs over the m. rectus internus, under the m. rectus superior and the optic nerve to its insertion on the eye-ball. The ventral edge of this muscle is composed of smaller fibres than the others.

The mm. obliquus superior and obliquus inferior arise together far cephalad from the internasal cartilage running caudad to their insertions. In the centre of this massive cartilage a median unpaired horizontal canal (the anterior eye-muscle canal) is excavated, which runs from it caudal face cephalad for a considerable distance into its

substance and in which are the origins of these four muscles, two on each side, the canal being filled with the muscular fibres.   The two obliqui superiores arise farther cephalad, the obliqui inferiores a little farther back from the dorsal wall of the canal.   The latter lie nearer the median line and pass down between the superiores directly to their insertions on the ventral sides of the eye balls, each receiving a second slip of fibres *in transitu* from the ventral lip of the canal.   The latter fibres are smaller than the others and run down the ventral edge of the muscle.

The obliqui superiores at the lips of the canal diverge and each receives a slip of fibres from the ventral lip which are, as in the former case, smaller, and which run along the dorsal edge of the muscle.

II.—The N. Abducens.

The sixth nerve arises by two fine roots, one .3 mm. caudad of the other.   They arise mainly from a common nucleus of large cells which lies between them some distance from the median line and about two-thirds of the distance between the floor of the fourth ventricle and the ventral surface of the brain.   There is a strong tract running transversely between the sixth nuclei of the two sides, but whether any of the root fibres have a crossed origin was not definitely determined.   Another strong tract runs from each sixth nucleus dorsally through the overlying motor nucleus of the facialis and into the fasciculus longitudinalis dorsalis.   Here again it is impossible to tell whether all or any of these fibres are root fibres, or whether this is a secondary tract.   There are, however, two bundles of fibres, one on each side, which run up, one from each of the VI roots, laterally of the VI nucleus

and through the motor VII nucleus into the fasciculus longitudinalis dorsalis. These appear to be root fibres, thus putting the VI nerve directly into relation with the fasciculus.

Johnston ('98, p. 581) describes all of the VI fibres as arising from the fasciculus in Acipenser.

The sixth nerve at its exit from the brain contains some fine fibres mingled with the coarse ones. It has a short intra-cranial course mesially of the VIII nerve and dorsally of the lateral edge of the sub-cranial canal, which is here very wide. Under the lobi inferiores it passes ventrally through a foramen in the cranial floor into the dorso-lateral angle of the sub-cranial canal. Here it is crowded close against the lateral face of the m. rectus externus, which muscle a part of the fibres soon enter. Other fibres run to the ventral side of the muscle to enter the fine-fibred slip of the muscle which arises in the median line (Fig. 2). Of the latter nerve fibres, some of finer calibre run farther cephalad than any of the coarse fibres to supply these fine muscle fibres near their insertion upon the eye.

III.—The N. Trochlearis.

The nucleus of the fourth nerve is merely a caudal extension of that portion of the third nucleus (*q. v.*) which lies dorsally of the fasciculus longitudinalis dorsalis. The root fibres (mostly very large with a few smaller ones) pass up at once and cross over the mesocœle to emerge in the usual manner behind the optic lobes, after which they form a close round bundle closely applied to the inner face of the sensory V root (this part of their course not being shown on the plots).

Here the trochlearis root receives and carries for a

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short distance a portion of the first root of the r. lateralis accessorius, as already described. After the separation of those communis fibres, it still contains about as many fine as coarse fibres (about 30 of each). The meningeal branches described by several authors as arising from the IV nerve in several types of animals probably are ultimately derived from similar anastomoses with communis roots. After the emergence from the cranium of the V+VII complex the trochlearis continues intra-cranially in the same relation to the brain as before.

At the level of the optic chiasm it pierces the cranial wall, which is here membranous, then, turning dorsad, it follows the outer wall of the cranium under the supra-orbital trunk, the finer fibres gathering on the dorsal side of the nerve. These relations maintain along the outer side of the internasal cartilage until the m. obliquus superior is reached, to the dorsal surface of which the nerve passes and into which it begins to send nerve fibres. The finer fibres, however, separate and run along the dorsal surface of the muscle to supply the smaller muscle fibres which occupy the dorsal edge of the muscle.

IV.—The N. Oculomotorius.

In conformity with the enormous size of the eye, the third nerve is also large. Its nucleus lies far dorsad near the median line, in part mesially of the large fasciculus longitudinalis dorsalis, but also, as it were, squeezed out so that a large part of it lies under the endyma of the floor of the mesocœle dorsally of the fasciculus and some also ventrally of it. Some fibres also plainly come from the fasciculus itself. Its origin being concealed in projection by the V + VII ganglionic complex, is not shown upon the plots.

Leaving the brain along the lateral face of the lobi inferiores, it passes at once through the cranial wall, which is here membranous, under the ventral edge of the sphenotic bone and mesially of the m. rectus externus. The m. rectus superior and the m. rectus internus lie farther ventrally. The III nerve contains at its exit from the brain chiefly the typical very large motor fibres; nevertheless there are mingled with these many of medium or small size, though all are heavily myelinated. The finer fibres tend to gather on the lateral aspect of the trunk and some of them go out with each of the rami. The larger part, however, enters the radix breva of the ciliary ganglion.

Under the cephalic end of the Gasserian ganglion it gives off first the branch for the m. obliquus inferior, then divides into dorsal and ventral portions, the former for the m. rectus superior the latter for the mm. recti internus and inferior.

The branch for the m. obliquus inferior pursues a rather peculiar course. Turning sharply ventrad and a little mesad and caudad, it runs down the cephalic face of the m. rectus externus from its dorsal to its ventral side, then curving around the outer side of the m. rectus superior from the dorsal to the ventral side of this muscle, it turns inward across the caudal face of the m. rectus inferior and around the ventral side of the m. rectus internus, closely wedged in between the latter muscle and the origin of the m. adductor arcus palatini. In this narrow space it crosses dorsally the r. palatinus without anastomosis. Having reached the parasphenoid, it turns dorsad between this bone and the m. rectus internus and then cephalad dorsally of the parasphenoid, mesially of the m. rectus internus and close under the optic chiasm, the

nerves of the two sides lying close together, almost in contact with each other.   At this level the rami palatini of the two sides pursue very similar courses, but on the ventral side of the parasphenoid.   Cephalad of the chiasma it turns dorsad, still in the median line, and continues forward close under the brain and olfactory nerves.   Upon the appearance of the internasal cartilage it begins to diverge from the median line and soon turns ventrad to enter the m. obliquus inferior.   It applies itself to the dorsal surface of the muscle and the coarse fibres enter the belly of the muscle in many strands, while the finer fibres separate and run down among the finer fibres of the muscle nearer their insertion.

The nerve for the m. rectus superior immediately after its separation from the oculomotor trunk divides into a dorsal portion of fine and medium fibres and a ventral coarse-fibred portion, both of which turn dorsad and apply themselves to the ventro-lateral face of the muscle.   The coarse-fibred portion at once enters the belly of the muscle; but the finer fibres follow along the smaller muscle fibres of its dorsal edge, occasionally sending twigs into its substance, to its insertion upon the eye-ball.

The remainder of the III nerve gives the radix breva to the ciliary ganglion and at once divides into rami for the mm. recti internus and inferior.   The former runs directly cephalad under the m. rectus superior and over the mm. recti internus and inferior.   Crowded ventrally by the emerging optic nerve, it crosses the cephalic face of the last mentioned muscle and enters at once the m. rectus internus.   The coarse fibres bury themselves in its substance, but the finer ones run along the dorsal border or embedded in a mass of exceedingly small muscle fibres which occupy the dorsal part of the muscle, in which

relation they can be followed to the insertion of the muscle upon the eye-ball.

The nerve for the m. rectus inferior after separation from the nerve last described descends at once to the dorsal surface of its muscle and here breaks up into numerous branches. Of these those with coarse fibres enter the belly of the muscle, while the fine fibres run to the small fibred ventral edge of the muscle, which they follow to the insertion upon the eye-ball.

V.—Critique of the Eye-Muscle Nerves.

In the case of each of the six eye-muscles of which we have just been treating, the side along which the finer fibres of its nerve run contains much smaller muscle fibres than those which make up the body of the muscle, the diameter of these small muscle fibres often being no greater than that of a large nerve fibre. The smaller muscle fibres are not merely the ends of larger ones which have become attenuated near their insertion, but they run for nearly the whole length of the muscle, maintaining the same diameter and the same relation to the larger ones. They do not appear to differ from the ordinary fibres except in size, in their constant relation to the finer nerve fibres and particularly in the fact that they are in places more closely enveloped by a dense and very rich plexus of these finer nerve fibres and by a nucleated connective tissue interstitial substance. The investigation of the nerve endings here by proper methods might yield interesting results.

That the small muscle fibres and the small nerve fibres are related can scarcely be doubted. The source of the small nerve fibres could not be certainly determined. The most natural supposition is that they come from the

fasciculus longitudinalis dorsalis, though this conjecture could not be verified. We already know that the oculomotor nuclei are placed in relation with each other and several sensory centres through the mediation of this tract. Cf. the diagram of Bonnier, '95. And this would suggest that possibly we have here a sensory mechanism analogous with the muscle spindles. The structure, however, does not conform very well, and we are told, moreover, that spindles do not occur in the eye-muscles (Batten, '97, p. 176). The comparison is rendered more difficult by Sherrington's experimental proof (fide Huber and DeWitt, '98) that the spindle nerves are derived from the dorsal spinal roots, while the small oculomotor fibres quite certainly come out with the other and undoubted motor fibres of the eye-muscle nerves. The whole question demands further study.

In order to facilitate comparison of the eye-muscle nerves of Menidia with Allis' account and the elaborate phylogenetic scheme which he has elaborated ('97), I have prepared the diagram, Fig. 13, which should be compared with Allis' Fig. 12, Plate XXII.

The courses of the trochlearis and abducens are in Menidia essentially as in Amia; but the relations of the oculomotorius are in several respects different. This nerve emerges from the cranium some distance ventrally of the Gasserian ganglion and is crossed externally while still within the foramen by the truncus infra-orbitalis. Its foramen is far caudad of that of the optic nerve and at the level of the latter all of the branches of the third nerve except that for the m. rectus superior lie ventrally of the chiasma. In all of Allis' figures the ophthalmic nerves (superficial and deep) arise from a common stem which lies ventrally of the III nerve, and he states in the text that in Amia the latter nerve "pierces the lining membrane of the cranial cavity opposite and above the

optic chiasma." In Menidia, too, the branches do not
leave the oculomotorius in the same order as in Amia,
or any other form figured by Allis, the nerve for the m.
obliquus inferior being the first instead of the last branch
to be given off. This nerve passes under the inferior and
internal recti, as in Allis' figures, but the main nerve,
viz., the portion for the ciliary ganglion and for the in-
ferior and internal recti, lies above these muscles. Allis'
conjecture that the arrangement in Amia is typical for all
ganoids and teleosts certainly will not hold, so far as the
teleosts are concerned, at any rate.

Allis points out certain errors and ambiguities (due in
part to misplaced reference letters) in my account of the
eye-muscles in Amblystoma ('94). I have re-examined
these nerves and the correct relations in Amblystoma are
as follows (cf. Fig. 14):

The IV and VI nerve require no additional comment
save that they conform to Allis' diagram of the Anura and
not to his diagram of the Urodela.

The foramen of the III nerve is a little caudad and very
slightly dorsad of that of the optic nerve. Immediately
after its exit from the foramen the oculomotorius lies just
laterally of the emerging optic nerve and mesally of the
mm. recti superior, inferior and internus, near their
tendinous origins. Just laterally of these muscles is the
r. ophthalmicus V, all of these structures lying at very
nearly the same dorso-ventral level. Here the III nerve
divides into its dorsal and ventral rami, the former pass-
ing to the m. rectus superior only. This branch and its
muscle lie dorsally of the ophthalmic nerve and the latter
crosses the n. opticus dorsally.

The ventral branch of the III nerve turns down behind
the optic nerve and crosses the latter on its ventral side,
turning laterally and crossing over the m. rectus internus
very near its tendinous origin. Here it lies crowded
closely between the rectus internus and the dorsal edge of
the rectus inferior, the former lying mesally, the latter
laterally of it. In some cases a few fibres seem to enter
the rectus internus at this point. It then enters the

dorsal edge of the rectus inferior and within that muscle divides, some fibres remaining within the muscle and others emerging on the cephalic and ventral side of it. The latter soon separate from the muscle and continue cephalad. A branch is given off which runs dorsad to supply the rectus internus and the remainder runs far forward to supply the obliquus inferior.

The oculomotorius, then, runs under the m. rectus superior, the r. ophthalmicus and the n. opticus. It crosses the m. rectus internus dorsally near its origin, but lies far ventrad of that muscle when the main nerve for it is given off. It pierces the dorsal portion of the m. rectus inferior and enters the obliquus inferior from its dorsal side.

Now, it is obvious that this arrangement in Amblystoma conforms to the scheme which Allis gives for the Anura, rather than the one for the Urodela. The lack of uniformity of my results with his scheme, both in the fishes and the Amphibia, together with the fact that his diagrams do not in all cases correspond with his authorities (*e. g.*, in the diagram of the Cyclostomata, based on Fürbringer, the nerve to the m. rectus superior is drawn over the ophthalmicus profundus, while Fürbringer says that it runs below that nerve) suggest that his entire phylogenetic scheme should be received with some reserve.

Again, to say nothing of the acknowledged incompleteness and possible inaccuracy of the data upon which the table is constructed, it seems rash to construct even a tentative phylogenetic tree upon a single character of this sort. But, aside from this, unless one were to apply the neuro-muscular theory rigidly in the ontogeny (which few morphologists now-a-days are willing to do) it is difficult to see why so exaggerated importance should be given to the relative positions of these nerves and muscles. There is no sufficient evidence that these nerves have been split off from the skin, as Allis assumes that most of the cranial nerves have been (a point to which we shall recur), but on the other hand, the best recent work on this subject (*e. g.* Dixon, '96 and Neal, '98) adds very emphatic testi-

mony to the doctrine that the eye-muscle nerves grow directly out from the brain. If this be true, I see no reason why a given motor nerve should not grow out either above or below some other structure, depending upon the peripheral relations of its end-organ with reference to that structure.

Finally, Allis in his account of the elasmobranchs (p. 522) says: "These different relations of the oculomotorius to the internal and superior recti, in elasmobranchs, are due to and are caused by the gradual shifting from before backward of the origins of all the recti muscles, and also of the place of exit of the oculomotorius from the cranium. As a result of this shifting the internal and superior recti, at their origins, either traverse, or are traversed by, the issuing nerve." That is, he invokes a principle to account for the diverse relations of nerve and muscle in elasmobranchs, which, if applied more broadly, might weaken the phylogenetic value of some of his other cases.

It seems to me, therefore, that Allis' phylogenetic table is based largely upon inconclusive data, and that the various arrangements which he diagrams are of cenogenetic origin rather than phylogenetic significance. In the case of Menidia the deviations from what Allis regards as the typical piscine arrangement can be easily explained mechanically by the great size of the eyes and the consequent crowding of the recti muscles far backward.

VI.—Summary of Section 9.

The sub-cranial, or eye-muscle canal is very highly developed, running back under the cranium for its entire length to the caudal end of the basioccipital bone. Correlated with the large eyes, the eye-muscles are highly developed. The recti, except the rectus inferior, arise in the sub-cranial canal. The obliqui arise in an anterior eye-muscle canal in the internasal cartilage. All of the eye-muscles have some smaller muscle fibres which usually

originate from a different position from the others and are innervated by smaller nerve fibres.   Their significance is unknown.   All of the eye-muscle nerves derive most of their fibres from their nucleus of the same side, but some from the nucleus of the opposite side and doubtless some from the fasciculus longitudinalis dorsalis.   The eye-muscle nerves of Menidia do not conform to the scheme given by Allis for the ganoids and teleosts, and an examination of his whole system leads to the conviction that its phylogenetic value is greatly in need of confirmation.

Section 10.—The Optic Nerve.

This nerve is enormous and is composed of very small fibres.   The chiasm is the simple crossing with the left nerve uppermost which is typical for teleostomes.   The cranial wall at the point of emergence is membranous. The nerve is of the broad, plicated, ribbon-shape so common among the bony fishes, consisting of three laminæ. One septum enters from the dorsal side, the other from the ventral.   The adult structure certainly favors the view of Studnicka ('96) that this form is derived by the folding of a ribbon-shaped nerve, rather than that of Deyl ('95) that it is derived from a cylindrical nerve by the intrusion of connective tissue septa.   This form must be regarded as an adaptation to secure the proper nourishment of the nerve in these large-eyed forms, as Studnicka points out, and Deyl's attempt to deduce phylogenetic conclusions from the forms of the optic nerve can hardly have much value, as the character is too variable and too liable to convergence.   For further morphological considerations see the papers cited above.

SECTION 11.—THE OLFACTORY NERVE AND NASAL ORGAN.

The olfactory bulbs are in part overshadowed by the cerebrum. The bulb gradually tapers into the cylindrical olfactory nerve, which penetrates the membranous wall of the cranium and then continues cephalad along the lateral face of the internasal cartilage. As the latter begins to expand around the nasal sac, the nerve is crowded under the m. obliquus superior near its origin and then penetrates the internasal cartilage through a foramen which is in part lined by a V-shaped projection from the parethmoid bone. Having reached the olfactory fossa, it runs along the inner side of the non-sensory part of the olfactory sac, being separated from it, however, by a great lymph sinus. Here it breaks up into numerous branches which enter the lamellæ of the sensory portion of the sac.

The nasal organs of Menidia are large and well developed, like the other organs of special sense. The anterior (cephalic) opening is a very small pore (*n. a. a.*), lying laterally of and close to the cephalic tip of the supraorbital canal. This pore opens directly into the cephalic end of a wide sac containing three large lamellæ, which are attached to the ventro-mesal wall of the sac and which extend lengthwise for almost the entire length of the latter, and two smaller lamellæ at the cephalic end of the sac. These lamellæ and the walls of the sac adjacent (but not the dorso-lateral wall of the sac) are thickly covered with the bud-like groups of sensory cells so characteristic of the teleosts (Blaue, '84).

These "olfactory buds" are closely packed in the mucous membrane along the whole surfaces of the lamellæ except at their tips, very much like Blaue's figure of Trigla, though not with so great regularity as his drawings would indicate. The "olfactory buds" vary in size,

the largest being half the size of the largest naked cuta-
neous sense organs found on the outer surface of the head.

Passing caudad, shortly before reaching the posterior
nasal opening the lamellæ disappear and with them the
sensory epithelium, the entire sac from this point caudad
being lined by ordinary thin pavement epithelium.   The
sac narrows in its transverse diameter and at the same
time becomes much deeper.   It extends as a rather narrow
cleft so far ventrally that its deepest point lies in the same
horizontal plane as the dorsal ends of the dorsal diverticula
from the lateral edge of the pharyngeal roof, these diver-
ticula lying somewhat laterally of the olfactory sac.   The
outline of the nasal sac is drawn on Fig. 5, the sensory
portion of the wall being shaded.   The posterior nasal
aperture is a long narrow slit four or five times the length
of the anterior.   The nasal sac extends only a very short
distance caudad of it.   For further notes on the conforma-
tion of the olfactory fossa see the account of the terminal
portion of the supra-orbital trunk, Section 7, IX.

The development of the olfactory organ has been
worked out in a series of post-embryonic stages and I
fully confirm Madrid-Moreno ('86) that the ontogeny dis-
proves the elaborate assumptions of Blaue ('84) that the
olfactory epithelium is derived from a bud of the lateral
line system which has wandered into the olfactory fossa,
there multiplied to form the system of "olfactory buds"
of the teleosts and then, in most higher forms, formed
secondarily a continuous sensory surface by the fusion of
the buds.

From the standpoint of theoretical morphology alone
Blaue's results could not stand; but, as it is a question of
no small importance to the fundamental head problems,
and as Blaue's errors reappear in recent editions of several

of our standard text-books (*e. g.*, Minot's and Hertwig-Mark's Embryologies), it seems desirable to emphasize the matter again.

SECTION 12.—GENERAL CONSIDERATIONS.

I.—The Ramus Lateralis Accessorius.

This nerve is the r. recurrens facialis, the r. lateralis trigemini and the superficial lateral line nerve of the literature. It and related nerves have also received many other names. By previous writers it has very generally been regarded as morphologically analogous with the r. lateralis vagi. It is, however, now known that this is not the case and the term lateralis accessorius has hitherto been avoided by me as suggesting bad morphology. The reasons, however, given by Cole ('98a) for the retention of this good old term of Weber's seem to me to be sufficient; it is merely necessary to keep constantly in mind that this nerve has no morphological relationship whatever with the r. lateralis vagi.

This nerve arises by two root complexes, one from the vagus system, the other from the facial. These anastomose above and behind the cranium and the combined nerve runs back into the trunk near the dorso-median line. The most interesting morphological question in this connection is the problem of the relation of this nerve and the organs of the accessory lateral lines supplied by it to the r. lateralis vagi and the main lateral line. As I have before remarked, all of the cutaneous sense organs are somewhat reduced in Menidia and especially the terminal buds, so that this is not a favorable type for the solution of this problem. In effecting the analysis of these nerves we must rely mainly upon the calibre of the nerve fibres and the problem is complicated greatly in this species by

the fact that the reduction in size of some of the organs
of the lateral line has involved the reduction also of the
calibre of the nerve fibres which supply these organs, so
that the normal distinction between lateralis and com-
munis fibres is in a measure obscured. Nevertheless, I
think that the conclusions as expressed on the plots are
correct.

I am convinced that in Menidia the r. lateralis vagi does
not innervate any organs other than those of the lateral
line. The participation in the general innervation of the
skin or muscles can be excluded. The fibres from this
nerve which anastomose with the r. lateralis accessorius
are much finer than any lateralis fibres. In a few cases
fibres from these anastomosing nerves supply naked
cutaneous sense organs. These fibres, too, are finer than
the lateralis fibres and I regard them and the anastomosing
fibres as both belonging to the communis system. They
may be derived from the lobus vagi by either one or both
of two paths: (1) The fine fibres already mentioned as
emerging from the brain in the lateralis root enter that
root on its caudal side and may be derived from the lobus
vagi, though they could not be traced back into it.
(2) The anastomosing fibres from the root of the glosso-
pharyngeus to the lateralis root are almost certainly
communis fibres and I look upon this tract as the probable
source of all of the fibres under consideration. These
fibres, as they separate from the IX root, are rather larger
than the other fibres of that root but not nearly so large
as the proper lateralis fibres, *i. e.*, they are about the same
size as the fibres of the branches of the r. lateralis which I
have designated as belonging to the communis system on
the plots.

The dorsal cutaneous rami of the vagus have been

already partially treated (under Section 5, VIII). These may comprise the general cutaneous rami for the skin, as described by the older writers, and communis fibres for terminal buds, as described by Allis ('97), besides the ramus supra-temporalis proper for the lateral line organs (see Section 5, X, 1). The three classes of fibres may be variously fused. In Menidia we have seen that the general cutaneous fibres arise separately from the jugular ganglion and pursue their devious ways to the skin without at any point coming into relation with the lateral line nerve. It is improbable that any fibres, except lateralis fibres, enter the r. supra-temporalis vagi, save the communis component from the anastomosing ramus from the IX root.

From the rather inharmonious accounts of Stannius and Baudelot it is clear that fusions of other sorts may occur in the bony fishes. In Fierasfer, Emery ('80) describes the r. supra-temporalis vagi (lateralis) and the r. opercularis vagi (general cutaneous) as fused. In Amia (Allis, '89, p. 518), the r. supra-temporalis vagi (lateralis system) and the ramus cutaneous dorsalis are distinct, though closely associated. The latter probably contains both general cutaneous and communis fibres.

The r. supra-temporalis X and the r. supra-temporalis IX, both lateralis nerves, may be present at the same time (Amia, Allis '89 and '97) so that these cannot be regarded as the same nerve, sometimes going out with the X nerve, sometimes with the IX. Both are present also in Læmargus, as we learn from Ewart and Cole ('95, p. 475). It is a most remarkable fact that according to their description the r. supra-temporalis vagi supplies the organs of the occipital commissure and several organs of the main line cephalad of it, while the supra-temporalis IX

supplies the three organs of the main line immediately caudad of the commissure. This is a condition not known for any other vertebrate and indeed Ewart himself had predicted ('93, p. 72) that if the IX nerve should prove to supply any portion of the lateral line of the head it would be the pre-commissural, not the post-commissural portion.

The fibres which I have described running from the IX root to the lateralis root have an exact counterpart on a larger scale in Amia (Allis, '97, p. 625). They are described as coming from the ventral, *i. e.*, communis, portion of the IX root, and not from the dorsal, or lateralis portion. What the fate of these fibres is peripherally in Amia, has not been determined. It is natural to assume that they supply either terminal buds of the trunk or accessory lateral line structures.

Allis ('97) assumes, I think correctly, that the terminal buds scattered over the bodies of many fishes, (*e. g.* gadoids) are innervated by the r. lateralis accessorius, which is distributed to those regions. There are, however, in some fishes extensive regions of the body not reached by this nerve which are known from the researches of Leydig and others to be abundantly supplied with terminal buds, which are said to be innervated by the r. lateralis vagi. Now, if this passage of communis fibres into the r. lateralis, as we find it in Menidia, is of general occurrence, it clears up a serious difficulty in the interpretation of these terminal buds. We have seen that such is the case in Amia and from Allis' account ('89) it would appear that the anastomosis is there much larger than in Menidia.

I predict that in cyprinoids, where the lobus vagi is so large, and the body is known to be covered with terminal buds (Leydig, '94) that these will be found to be supplied

from it via the r. lateralis vagi and other nerves and that in siluroids and gadoids terminal buds of the same regions of the trunk will be supplied from the fasciculus communis via the r. recurrens VII, or r. lateralis accessorius.

The different accounts of the anastomosis between the VII and the IX and X nerves present a very interesting series.

In the cyprinoids and in Gadus merlangus, Baudelot ('83, p. 129) describes an intra-cranial communication from the V (VII?) nerve to the IX. In the former case it is large, runs internal to the ear and VIII nerve and anastomoses with the IX and X nerves and then forms a recurrent branch for the trunk which anastomoses with the first spinal. In Gadus merlangus it is very small and runs internal to the ear, but external to the VIII nerve, with which it anastomoses. He regards the cases as homologous and from a comparative study of a number of cyprinoids concludes "that even in the cyprinoids, the recurrent bundle exhibits a tendency to rise up on the side of the medulla in such a way as to stride over successively, so to speak, each of the nerves which springs from this part of the medullary axis." In Gadus merlangus this process is carried a step farther and we may carry this series even farther than Baudelot has done, to include the extra-cranial anastomoses such as I have described in Menidia.

The intra-cranial communicating branch between the vagus and the "r. lateralis V," which Stannius, Baudelot and others describe in many fishes, is totally wanting in Menidia, as in Silurus, ('49, p. 50), as would be expected if these recurrent nerves all belong to a single system whose position may vary from an intra-cranial anastomosis with the IX and X nerves to a sub-cutaneous anastomosis

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with the same nerves.   The cases all have this in common, that they are related centrally to the communis system of nerves and peripherally supply the meninges and skin of the top of the head and of the trunk.   It appears from the descriptions of Merkel ('80), Leydig ('94), Harrison ('95), Allis ('97) and others that the cutaneous distribution is mainly, if not wholly, to terminal buds.

The relations to the vagus system are most various.   In most, if not all, of these cases it is clear that communis fibres with essentially the same distribution go out with the IX or X nerves or both and the anastomosis of these two sets of fibres is easily explicable.   Since the branches which go into the body supply in some of the cases terminal buds in the same regions as the lateral line organs supplied by the r. lateralis vagi, the more or less intimate anastomosis with the latter nerve is also easy of comprehension.

Phylogenetic speculations are, perhaps, premature, yet from the evidence now in hand I incline to the belief that the peripheral anastomosis is the more primitive.   As terminal buds migrated into the trunk from the head, communis fibres seem to have accompanied them from both the VII and IX roots and probably also the vagus. These nerves effected sub-cutaneous anastomoses with each other and probably with similar fibres accompanying the r. lateralis vagi.   Menidia, then, is probably very near the primitive type.   As the recurrent systems increased in importance, two lines of differentiation were followed.   On the one hand, the facialis portion was exaggerated at the expense of the post-auditory portion and we have forms like the siluroids with enormous r. recurrens VII with no considerable vagal participation.   In

Amia the facialis portion has been reduced almost beyond recognition, being represented only by a delicate anastomosis between the terminal filaments of the first branch of the r. ophthalmicus superficialis V and dorsal cutaneous twigs of the vagus (Allis, '97, p. 600). The post-auditory portion, however, is represented by a large communis element which passes from the IX root to the lateralis root of the vagus and whose distribution is evidently very much like that of the corresponding, but smaller, nerve in Menidia. In forms like the gadoids the superficial recurrent nerve from the VII nerve is of considerable size and it is joined intra-cranially by a small post-auditory portion from the vagus. And finally in some of the cyprinoids the external (superficial) element from the facialis has been altogether lost and the anastomosis from the VII to the IX + X is altogether intra-cranial.

Since the preceding pages were written I have received Cole's paper ('98a) to which reference has already been made, and I am pleased to find that my conclusions confirm in most important respects those of this eminently careful student. In some points regarding the morphology of the r. lateralis accessorius and related structures, however, I cannot follow him. All that could be gained by dissection has been done and well done. The microscopical anatomy, however, was done on sections of very young codfish, which must have been poorly adapted to the purpose, for he did not succeed in his analysis of the trigemino-facial roots.

The conclusions to which he was led, both in his examination of the literature and in his study of the sections, are in some important respects so different from my own that I have been led to examine the condition in Gadus. As this investigation is still unfinished at the time when

these sheets pass through the press (July, 1899), I shall here omit the somewhat extended critique of Cole's work which I had originally prepared, and content myself with the statement that I do not confirm his findings with reference to the geniculate ganglion and the facial root of the r. lateralis accessorius of the cod.

In brief, the relations of the geniculate and sympathetic ganglia are almost exactly as in Menidia, though the whole trigemino-facial complex is much more compact in Gadus. The geniculate ganglion is wholly intra-cranial and so closely joined to the Gasserian ganglion that Cole failed to differentiate them and mistook the extra-cranial sympathetic ganglion for the geniculate. The root of the r. lateralis accessorius arises wholly from the geniculate and not at all from the Gasserian, just as in Menidia. The details of these connections in Gadus with full illustration will be published shortly.

A word further upon the question of "collector" nerves. Of the longitudinal nerve trunks running through the body the sympathetic chain, with its anastomosis with every spinal nerve, is the best illustration of a true collector nerve. The older writers have frequently described the r. lateralis vagi as a similar collector, supposing that it receives accessions from each spinal nerve through the r. medius. This, we now know, is not the case, as there is no anastomosis here such as would justify us in regarding the r. lateralis as a collector. There remains to be considered the r. lateralis accessorius. Stannius lays great stress (p. 151) upon this nerve as a collector of all spinal and spinal-like nerves. In view of its function as the nerve supply for the dorsal row of terminal buds, it is not probable that its primary form was that of a collector; nevertheless its uniform anastomosis with the spinals is to be explained.

It is possible that in the case of both of the lateral line nerves the relation to the spinals is purely accidental and due to the fact that the paths of the nerves in question cross in the inter-muscular septa. This seems especially probable in the case of the n. lateralis vagi from its course in the septum between the dorsal and ventral musculature and from the loose and variable nature of the anastomosis. The relation of the r. lateralis accessorius in the septum between the dorsal musculature and the interspinal muscles is similar. Nevertheless the remarkable constancy of these anastomoses, especially in the latter case, lends credence to the belief that they have a morphological and a physiological basis. Stannius was certainly correct (p. 151) in rejecting the morphological equivalency of the dorsal series of anastomoses related with the r. lateralis accessorius and those of the ventral rami with the sympathetic chain. Nevertheless they may have certain physiological features in common which will justify a comparison.

All of the viscera of the trunk and head seem to be intimately related to each other and to the central nervous system through the mediation of the sympathetic nervous system. Now the communis system, as we have used that term, contains in addition to fibres for terminal buds other sensory fibres which we have termed *visceral.* What may be the relation (if any) between these visceral fibres and those of the sympathetic cannot perhaps be determined at present; but, like the sympathetic, they are known to have a wide distribution to exposed visceral surfaces, and I think also to the internal parts as well. In short, they participate in the general sub-cutaneous and internal plexus which enables the body to react as a physiological unit. The enormous physiological significance of this universal plexus is coming to be better appreciated than

formerly; and it has a morphological value which is not as yet fully recognized. The fibres of this plexus will tend to gather about and distribute with the larger nerve trunks of whatever type simply because these afford the paths of least resistance; and if two nerves cross, even though they be of unlike composition and do not exchange fibres with each other, yet this will form a nodal point in this plexus of visceral fibres. This factor will operate to draw contiguous nerves together, even though they may be of totally dissimilar composition, and may account for the tendency, everywhere noticeable, for nerves of the several components to accompany each other, often coming from widely separated origins and deviating from their natural courses to do so.

The ramus lateralis accessorius originates in Menidia in an elaborate plexus of communis fibres, arising partly from the facial nerve and partly from the vagus complex. This plexus is exceedingly rich and intricate in the meninges and under the skin of the dorsal part of the head and trunk, only the main nerves being indicated on the plots. This nerve was, doubtless, primarily visceral in its proximal portions at least, while in that portion which leaves the head to enter the trunk I incline to the belief that the terminal bud fibres appeared first. But be that as it may, the visceral fibres followed and when the r. lateralis accessorius crossed the dorsal rami of the spinal nerves, connections of their visceral fibres were secondarily effected. In cases where the r. lateralis accessorius sends a ventral branch to the anal fin, as in Gadus, that branch effects similar connections with the ventral rami of the spinal nerves.

The r. lateralis vagi may effect similar quite secondary connections with the r. medius of the spinal nerves; but,

as the latter rami do not bear so constant a relation to the inter-muscular space laterally of the dorsal musculature as the dorsal rami to the space mesially of it, their anastomoses with the r. lateralis are neither so extensive nor so constant as the others.

II.—Metamerism.

Certain questions of metamerism and the relations of the components to each other remain to be considered.

Our conception of the composition of the primitive segmental nerve will depend somewhat upon whether we regard the cranial (branchiomeric) or the spinal type as the more primitive. But in either case we may assume with great probability that the typical segmental nerve in the earliest vertebrate contained somatic sensory, or general cutaneous fibres, also somatic motor for the voluntary musculature and viscero-motor and viscero-sensory components. In the head the form which the segmental nerve takes is dominated by the branchio-merism, and we are justified now in concluding that the original branchiomerism coincided with the metamerism (see especially Neal, '98).

We have suggested in the preceding sections the following comparisons between the components of the head and those of the trunk. The general cutaneous and somatic motor of the cranial nerves are strictly homodynamous with the corresponding components of the spinals. The viscero-motor of the trunk is present in the same form in the head, but has also suffered an extreme differentiation and very profound modification in connection with the branchio-motor apparatus. The rudimentary visceral sensory system of the trunk is represented by the communis system of the head and has also suffered great

specialization and modification, in this case in connection with the sense organs developed in the mouth and secondarily in the outer skin. The acustico-lateral system is evidently a later acquisition developed perhaps from the general cutaneous system, perhaps from the terminal buds.

All of the components which I have enumerated were therefore probably present in the typical primary branchiomeric nerve, except those for the specialized sense organs, lateral line organs, taste buds, terminal buds, and, of course, the organs of higher sense, eye, ear and nose. The fibres for these specialized organs appeared sporadically as evoked by the physiological requirements of each case, and each, for obvious physiological reasons, is related centrally to a single centre. In the case of the cutaneous sense organs especially, these requirements have been exceedingly variable. Thus the lateralis fibres converge toward the tuberculum acusticum from either side of the auditory capsule. The relations of the ganglia and roots of these fibres are quite constant throughout the fishes, as also are the principal nerve trunks, such as the r. lateralis vagi, the r. ophthalmicus superficialis VII, the r. buccalis and the r. mandibularis externus VII. But it is quite different with the smaller lateralis branches, such as the r. oticus, the r. supra-temporalis, etc. The courses which these may take will depend partly upon the arrangements of the corresponding organs and partly upon mechanical convenience growing out of the disposition of adjacent organs, particularly other nerves, for it is a general rule that two nerves which pass near each other, whatever may be their composition, tend to fuse into a common trunk. In the same way communis fibres from terminal buds may accompany any of the cutaneous

nerves, depending upon the arrangement of these organs.

Hence, the arrangement of the components in its main outlines, including the terminal centres of the special sensory systems, is a palingenetic character of great permanence throughout the vertebrata, which is not due to the direct influence of the now present environment. On the other hand, the peripheral courses of these nerves, the number of rami, their individual composition, anastomoses and fusions are to some extent cenogenetic characters to be explained by the pressure of the environment, mechanics of growth, etc.

If, now, we frame a conception of the typical spinal nerve of the existing Ichthyopsida, as illustrated by the bony fishes, we find that it receives all of the four primary components and that each of its rami also receives some fibres of each of these four categories. Thus the ventral ramus of the spinal nerve contains considerable numbers of somatic motor, somatic sensory, viscero-motor and viscero-sensory fibres. The two last components reach their peripheral distribution partially and perhaps wholly through the mediation of the sympathetic nervous system. The medial and dorsal rami contain the two somatic components in large numbers and the two visceral components in very much smaller numbers, chiefly in the form, no doubt, of vaso-motor and excito-glandular fibres with the corresponding return reflex paths.

The central connections of the visceral fibres, and especially of the viscero-sensory fibres in the spinal cord are very obscure. Johnston ('98, p. 597) denies the presence of any viscero-sensory fibres in the spinal nerves. "No sensory fibres of the spinal nerves supply visceral structures. We know of no sensory fibres entering the spinal cord from the sympathetic system." Kölliker ('96, p. 860) makes a similar statement,—"The sensory fibres of the sympathicus all arise from cerebro-spinal fibres and end, like cerebro-spinal sensory elements, in the periphery. The sympathicus possesses no sensory

fibres properly its own." This view is not without opponents. Onuf and Collins ('98) find degenerations after extirpation of sympathetic ganglia which they can explain on no other assumption than that of sensory fibres running from cells of the sympathetic ganglia into the dorsal roots.

But leaving the question of the sympathetic connections to one side, we have the most abundant evidence (see *e. g.*, Thane, '95, p. 350, Kölliker, '96, p. 858, and Huber, '97, p. 131) that sensory cerebro-spinal fibres distribute freely among all of the viscera through the mediation of the sympathetic nerves. The findings of experimental physiology and pathology also necessitate the assumption of such fibres in order to explain the phenomena of the reflexes, etc. Where the spinal centres for these visceral fibres may be has not been accurately determined, but the presumption, it seems to me, is rather in favor of than against the idea that they are distinct from the general cutaneous centres. It is, undoubtedly, true that this spinal viscero-sensory system is very small and that it is not present in all of the spinal segments is very probable; for, as we have seen, the functions of this system have been very largely usurped by the cranial visceral system of the vagus.

Passing now to the head, the presence of the branchial apparatus and the reduction of the somatic musculature have so modified the conditions as to render comparison with the trunk almost impossible. If we exclude the twelfth cranial, which in the fishes is but little modified from the typical spinals, there is no cranial nerve which has a ventral ramus of the typical form. The reason is clear. There is no ventral somatic musculature in the head aside from that which has grown forward from the region of the first spinal. And in the higher fishes the overgrowth of the operculum has eliminated in the branchial region the cutaneous areas which would be innervated from ventral spinal rami. It would be interesting to learn in the sharks the exact details of the innervation of the skin of the venter in the gill region. The branchial trunk is commonly supposed to represent a ventral ramus. Whether this is so can only be determined positively after a more careful examination

of its composition in the lower fishes. If this proves to be the case, it is clear that in the higher fishes it contains, for the reasons already mentioned, only the two visceral components.

The lateral line branches of the cranial nerves have usually been considered equivalent to the lateral or medial rami of the spinal nerves. Thus, the r. lateralis vagi has often been described as a "collector" of these medial rami, and very recently both Fürbringer ('97) and Neal ('98, p. 271 and p. 211) consider that these medial rami have been "supplanted" by the r. lateralis vagi. To this there are at least two very grave objections. In the first place, these medial rami have not been supplanted at all in the bony fishes but they, and they alone, innervate all of the skin and all of the muscles of the dorso-lateral regions of the body. Neither the r. lateralis X nor the r. lateralis accessorius participate in the innervation of these cutaneous areas, but supply only special sense organs which have migrated in the ontogeny back from the head. And from this it follows, in the second place, that these recurrent nerves would be incapable of supplanting the dorsal or medial spinal branches, for they are not of equivalent structure or function. This case is totally different from that of the r. intestinalis, where there has been a supplanting of visceral spinal fibres by visceral cranial fibres.

In the same way we must avoid homologizing such dorsal cranial nerves as the r. supra-temporalis, composed of lateralis fibres, with the general cutaneous fibres of the dorsal rami of the spinal nerves. The rami cutanei dorsales of the vagus and the r. ophthalmicus superficialis V (and possibly the general cutaneous fibres with the r. oticus) are the only nerves in the head of Menidia which can be homologized with dorsal spinal rami, though in

other forms such general cutaneous fibres may be present in other cranial nerves, as in the ninth.

We may now, perhaps, attempt to formulate a scheme to express the typical branchiomeric nerve of higher fishes. This nerve has a dorsal ramus to the skin, which contains general cutaneous fibres and probably a few visceral fibres. Motor somatic fibres are absent on account of the loss of the dorsal musculature. The remainder of the typical nerve is contained in the branchial trunk, which is composed of visceral sensory and visceral motor fibres. From this trunk is given off a palatine branch, which is all sensory, and a pre-trematic branch, which is also sensory, and a post-trematic branch which is mixed.

Now, as the special sense organs are differentiated, fibres from taste buds will come in by way of the palatine and the pre- and post-trematic branches, and other communis fibres from terminal buds on the outer surface of the body may come in with the general cutaneous fibres of the dorsal ramus. With the appearance of the lateral line organs, their fibres may also enter with the dorsal rami, though most of them appear to come in as independent trunks. The latter may represent medial rami in which the general cutaneous fibres have disappeared, or, more likely, they have no representative in the spinal nerves.

This scheme applies in the post-otic branchiomeres, where the growth of the operculum has involved the reduction of the ventral cutaneous areas. In the pre-otic branchiomeres these relations are disturbed by the differentiation of the jaws and of the facial skeleton in general, and also by the exaggeration of the dorsal cutaneous areas, since the whole operculum is morphologically a dorsal or dorso-lateral structure belonging to the facial segment.

In the facial segment the post-trematic ramus has the typical communis and viscero-motor fibres and in addition a large lateralis component and a small general cutaneous bundle which joins it extra-cranially from the Gasserian ganglion and distributes to the skin of the lower part of the operculum. The two last are to be regarded as secondary additions, the former following the differentiation of the operculo-mandibular canal and the latter the backward growth of the operculum. That these general cutaneous fibres of bony fishes have not persisted from a primordial condition in which cutaneous nerves were normally present in branchial nerves is suggested by the fact that they do not emerge with the facial root, but swing back from the trigeminus. If the facialis ever possessed a general cutaneous component properly its own, in all known vertebrate types its ganglion has secondarily fused with the trigeminal general cutaneous (Gasserian) ganglion.

The pre-trematic facial is strictly typical, containing only communis fibres. In some fishes (but not in Menidia) this ramus seems to have secondarily fused after the obliteration of the spiracle, with the r. mandibularis V and to be represented in part by the chorda tympani of higher vertebrates.

The r. palatinus of the facial segment is also typical, save that it is longer than in the other nerves.

There is no general cutaneous lateral branch of the facial segment, though possibly the r. buccalis may represent such a nerve to which lateralis fibres were added and then the original general cutaneous component disappeared. For this no satisfactory evidence can be adduced. The r. oticus, however, may represent a dorsal branch. For we have seen that this nerve contains general cuta-

neous fibres. These now arise from the Gasserian gan-
glion and we should have to assume that their ganglion and
root have secondarily fused with the trigeminal, as the
profundus ganglion is supposed to have done.

The trigeminus segment has suffered still greater modi-
fication. The root contains no communis fibres, for there
is no vertebrate known in which there is a pre-facial fas-
ciculus communis. The post-trematic ramus, *i. e.*, the r.
mandibularis V, has viscero-motor and general cutaneous
fibres, and, as we have just seen, communis fibres belong-
ing to the pre-trematic VII may secondarily be distributed
peripherally with this ramus.

The pre-trematic ramus, or r. maxillaris, has typically
only general cutaneous fibres. In some, perhaps most,
fishes there are joined to these also some communis
fibres from the geniculate ganglion for taste buds about
the upper lip, but these are not proper trigeminal
fibres.

The absence of a pre-facial fasciculus communis and
communis root of the trigeminus involves the lack of a
r. palatinus for this segment. Functionally this is re-
placed by the forward extension of the r. palatinus VII.

The r. ophthalmicus superficialis V may represent a
dorsal branch of typical form, to which communis fibres
are added in some types for terminal buds on the top of
the head and to which the lateralis fibres of the r.
ophthalmicus superficialis VII may also be joined.
The r. ophthalmicus profundus might possibly rep-
resent a lateral ramus of this segment, though more
probably it belonged originally to a segment lying farther
cephalad and is only secondarily joined to the trigeminus
segment.

III.—The Usurpation of Nerves.

From the preceding account it appears that the modifications to which the primitive segmental nerves of the head have been subjected are of two main types: in the first place by the loss of some one or more of the primary components, as the loss of the general cutaneous fibres of the IX and VII, or by the addition of components not primarily present, as in the case of the addition of special cutaneous components to the VII; and in the second place by the prolongation of nerves of one segment so that they encroach upon the area of another. This encroachment may take place either by the terminal organ of the nerve migrating secondarily into the adjacent segment and carrying its nerve with it, or the nerve may effect secondary connection with the terminal organ which belongs primarily in the adjacent segment. The occurrence of the latter case, it is true, is somewhat doubtful and is denied absolutely by some authors. Yet it would seem in the present state of our knowledge to be at least probable in some cases, as, for example, the r. intestinalis vagi, and the innervation of the skin of the head between the vagus and trigeminus by general cutaneous fibres from these nerves.

The way in which a nerve can be carried to the most distant parts of the body by a vagrant terminal organ is best illustrated by the development of the lateral lines and their nerves, as described by Wilson ('91 and '97), Ayers ('92), Mitrophanow ('93), Platt ('96) and others. The development of the so-called hypoglossus musculature from the post-otic myotomes is another illustration and Ruge ('97) suggests the same for the development of the facial musculature of the mammals, viz., that these

muscles of expression are derived from the proper musculature of the facialis segment.

It must be left to future embryological studies to determine which of these modes of encroachment has been followed by the communis nerves which emerge with the VII, IX and X nerves and spread out over the surface of the body. And in the case of the nerves which run forward from the V, VII and IX segments into the jaws and facial regions the problem is much more difficult. If the pre-trigeminal nerves ever did conform to the primitive branchiomeric type, this conformity has been so modified in all existing vertebrates as to be unrecognizable. The embryological evidence of pre-oral branchiomeres certainly needs confirmation and the persistence and metameric constancy of the somatic musculature in these segments would tend to separate them farther from the typical branchiomeres of higher forms, at least. The sensory components of these pre-oral segments, with the probable exception of the profundus, seem to have been wholly consumed in the nerves of special sense or to have degenerated altogether. The general sensory functions of these segments must, then, be supplied from the segments farther back, and we should not say that these general sensory nerves of the first segments have been *supplanted by* those of the following ones, but that the latter have pushed forward *because of* the atrophy of the proper innervation of the first segments.

Mention should be made in this connection of the supposed "vicarious relation" between the V and VII nerves developed by Pinkus ('94) from a study of the relations in the Amphibia. He calls attention to the fact that in the aquatic Amphibia the lateralis branches of the VII are highly developed and that these branches assume

progressively less importance as we ascend to the typically terrestrial Amphibia. He also assumes, though no evidence is given for it, that as the lateralis branches decrease in size the proper trigeminus branches increase and considers this to be a case of substitution of function, the general cutaneous branches compensating for the loss of the lateralis. The lateral line branches, Pinkus thinks, are the older and in higher forms have been supplanted by the general cutaneous.

This, I think, is a direct inversion of the actual relations. The general cutaneous fibres are unquestionably the older and are present throughout the fishes and Amphibians in sufficient numbers to innervate the entire cutaneous surface amply, and that, too, in cases where the lateralis system attains its maximum development. The latter system disappeared as it came, without materially affecting the general cutaneous system, but wholly in relation to the grade of organization of the corresponding sense organs.

IV.—Embryological Problems.

The clearest light upon these questions of metamerism will, I think, ultimately come from the embryological side, though so far, it must be confessed, this light has proved, in many cases, a false beacon. The reason is not far to seek, for, as has been pointed out by Cole ('98) the embryologists have not as a rule been able to follow the fate of the structures which they have discovered up to adult life and in most cases the exact anatomical structure of the adult organs of the types studied is unknown. Thus the brilliant speculations of Kupffer ('94) respecting the relation of the epi-branchial and supra-branchial sense organs to the terminal bud and lateral line systems of

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nerves have thus far remained barren simply because the later development of these so-called sense organs is unknown. Again, the proper comprehension of the neural crest and its significance to metamerism must remain obscure until we learn to which of the components of the adult the cells thus derived are related. The fact that the neural crest is found in the trunk, as well as in the head, and especially Neal's account ('98, p. 238) of its relations to the vagus ganglion, suggest that it is related to the general cutaneous component only, while the special cutaneous nerves are derived from the ectodermal thickenings. But the demand in this connection is not for speculation, but for observations.

Allis, in his later paper ('97) is dominated by the conception that the sensory nerves are "split off" from the skin. This rests largely upon assumption. It is only in the case of the lateral line nerves that there is any considerable evidence for this, and even here it is by no means clear what may be the relation of the cellular strand formed in connection with the skin and the definitive fibrillar nerve. The illustrations given by Neal ('98) indicate that, whether the lateralis nerves are really split off from the skin (and this, I think, needs confirmation), it is quite evident that the general cutaneous nerves are not so derived in Acanthias. I have myself seen Neal's preparations of the r. ophthalmicus superficialis V and VII (the nerves most emphasized by Allis) and believe that such a mode of origin for the ophthalmicus superficialis V is quite out of the question.

The relations of the components as conceived by Johnston ('98) should also be criticised here. As already indicated, this author finds the centres of the acustico-lateral and general cutaneous systems in the oblongata

very intimately related and he considers them but parts of a single system. The communis centre, however, is sharply separated from these, and he regards the latter system as related to entodermal structures, as distinguished from the two former which are related to ectodermal structures. These are undoubtedly related mainly, if not exclusively, to ectodermal sense organs, and it is quite possible that the acustico-lateralis was differentiated from the general cutaneous; but the communis system cannot in the existing Ichthyopsida be regarded as related even chiefly to entodermal structures. The taste buds themselves lie mainly, and probably wholly, in the region of the stomodæum, while the terminal buds of the outer skin, which are undoubtedly innervated from this system, are of course ectodermal.

It is probably true that the communis system is descended from a system of visceral nerves which was primarily related to entodermal mucous surfaces and that it has only secondarily encroached upon the ectoderm of the stomodæum and of the outer skin. These ectodermal surfaces have also retained their proper nerve supply from the trigeminus. This is illustrated by such pathological cases as that of Adolf Schmidt ('95), where the visceral sensation (taste) of the anterior two-thirds of the tongue was totally lost, but tactile sensation not so profoundly affected.

SECTION 13.—CONCLUSIONS.

I.—General.

In addition to this general review, a summary will be found at the close of each of the sections and to these the reader is referred for the chief anatomical and morphological findings.

The general result of the study is to demonstrate that it is possible, even in forms so highly specialized as the teleosts, to trace in serial sections the entire courses of the chief sensory and motor components of the cranial nerves and that the results of such an analysis show a striking fundamental agreement in the plan of the nervous system with the Amphibia, as worked out by Strong. This plan, in its main outlines, seems to be a palingenetic character of great constancy throughout the vertebrates. As in the Amphibia, the sensory components of the cranial nerves, to which attention has been especially directed, fall into three categories, each with its distinct terminal nuclei within the brain, roots, ganglia and peripheral branches. The latter, however, may be secondarily fused and modified in a great variety of ways, so that the peripheral nerves, as commonly named, do not usually bear a simple relation to the roots and ganglia from which they arise; much less can they be regarded as simple metameric units.

On the contrary, each of the sensory cranial systems has been, for physiological reasons, unified and concentrated in the medulla oblongata, and in consequence of this, it has come to be represented in the nerves of but few of the segments, either having been lost or not having been differentiated in the others. Thus it happens that any peripheral ramus may be composed of elements which are not only very diverse functionally, but which may have belonged primitively to different metameres.

Of these systems the general cutaneous is probably the oldest phylogenetically. It has been subjected to very slight modification in the head as compared with its arrangement in the spinal nerves, though it is represented in the V and X nerves only.

The communis system is also probably very ancient in its simple visceral form. It has, however, no pre-facial representative, and in the nerves in which it persists it has been highly modified in connection with the taste bud and terminal bud apparatus.

The acustico-lateral system seems to have been differentiated rather late and in connection primarily with the facialis segment.

The criteria of these components are primarily the central and peripheral relations of the nerves. It happens, however, that each component has certain characteristic and quite constant differences in the character of its nerve fibres which make it possible to separate them, as a rule, throughout their peripheral courses, even when several components are bound up together in a common trunk. Thus, the somatic motor fibres are always large with wide medullary sheaths and large axis cylinders, the visceral motor fibres are usually very small with very feeble myelination, the communis fibres are very minute and with still more delicate medullary sheaths, the general cutaneous fibres are of small or medium size with occasional larger fibres scattered among them, their sheaths being somewhat heavier than those of the communis fibres, and the lateralis fibres are the largest of all, having very large axis cylinders and wide sheaths which usually stain more densely than those of the somatic motor fibres.

These fibre characters, however, are not absolutely constant, but vary with the degree of development of the organs innervated. The clearest illustration of this is in the motor components. The branchial muscles, known to be of visceral origin, have acquired in the fishes the striation and large size of the fibres characteristic

of the voluntary muscles of the somatic series; and in correlation with this modification, we find that their nerve fibres, though quite certainly belonging to the viscero-motor series, are of large size, like the somatic motor nerves. Even among the somatic motor nerves it is a general rule that small muscle fibres are innervated by smaller nerve fibres than are larger muscle fibres. This is illustrated best in the eye-muscle nerves, but frequently also in the general somatic musculature. Among the sensory nerves, too, the size of the fibres seems to depend somewhat upon the state of development of the sense organ to be innervated. Thus, while the canal organs of the lateral lines are always supplied by very large fibres with wide sheaths, when the canals disappear and the organs lie exposed on the skin, as in a portion of the infra-orbital line and in the main line of the trunk, these organs are usually smaller than those in the canals, and are supplied by smaller nerve fibres. And particularly the lateralis fibres which supply the small naked organs of the " pit-lines " are always of medium or even small size, though they have the characteristic very densely stained sheaths, so that they can be easily distinguished from general cutaneous fibres of the same size. And, again, the communis fibres, though very small when distributed to visceral surfaces or taste buds on mucous surfaces, may become somewhat larger and more heavily myelinated when they distribute to large terminal buds of the outer surface of the body, so that it is sometimes impossible to distinguish them from lateralis fibres for the "pit-organs." This, however, is not always the case, for in sections of the siluroids and cyprinoids, where the terminal bud system is much more highly developed than it is in Menidia, I find these organs innervated by the very fine

fibres in the manner typical for organs of the communis system.

II.—Recapitulation of the Nerves.

The review of the components of the several nerves can best be done graphically by means of the diagrams, Figs. 8 to 12. These diagrams are composites constructed from a series of camera outlines of transections of the brain running through the entire extent of the root area of the nerve in question and are drawn with a uniform magnification. They are somewhat schematic, but they are not theoretical, as only the components which I have observed in Menidia are included. They are, of course, far from complete and other components than those figured are doubtless present in many, if not all, of these nerves. In reading the following pages these diagrams giving projections upon the transverse plane should be compared with the projections upon the sagittal plane made from the same series of sections and given in Figs. 3 to 5.

1.—The Spinal Nerves.

The diagram, Fig. 8, exhibits the relations as seen at the level of the fourth spinal. The large ventral root passes through the ganglion into each of the rami in the typical manner. The dorsal root is very small, much smaller, apparently, than the combined sensory components of the rami which leave the ganglion. Fibres are seen to pass from the sympathetic chain into each of the rami. The ventral ramus is the largest and contains more sensory than motor fibres. The ramus medius is rather large and contains rather more motor than sensory fibres. The two dorsal rami are both small. The cephalic one, the r. communicans, is wholly sensory, the caudal one, r. spinosus, is wholly motor. They both run bodily into the

r. lateralis accessorius dorsally, from which they dis-
tribute to the skin and adjacent muscles. The r. later-
alis accessorius appears to serve as a collector for these
nerves, though there is no evidence that any fibres pass
in it very far from the segment in which they are related
to the spinal cord.

Viscero-motor fibres are doubtless present, here as in
other cases, in both the dorsal and ventral roots, though
my methods have not differentiated them. Such fibres
probably originate from the cells of the paracentral nucleus
(*pc.n.*) lying ventro-laterally of the canalis centralis and
in what might be termed the cervix of the ventral cornu.
There are probably also viscero-sensory connections of
some sort in the spinal cord, though what they are in the
fishes remains problematical.

2.—*The Vagus.*

The relations of the components in the vagus nerve are
shown in Fig. 9. The motor fibres all belong to the vis-
cero-motor type and come from the nucleus ambiguus and
the commissura accessoria of Mauthner. The latter prob-
ably come partly from the n. ambiguus of the opposite
side and partly from the fasciculus longitudinalis dorsalis.
They distribute to the pharyngeal muscles and to the m.
trapezius (n. accessorious). There are probably other
motor fibres of smaller calibre which distribute to the
unstriated visceral musculature.

The communis root from taste buds, terminal buds and
general visceral surfaces terminates in the lobus vagi. It
makes up by far the largest part of the vagus.

The general cutaneous root arises from the jugular
ganglion, which gives rise peripherally to the rami
cutanei dorsales vagi. Centrally its fibres terminate in

the spinal V tract. This tract is drawn in Fig. 9 above the communis root, but in Fig. 4 below that root. As a matter of fact, it lies below the cephalic portion of the root, but above the caudal portion. These fibres supply the skin of the occipital region and of the dorsal part of the operculum.

The lateral line root is the most dorsal and cephalic member of the vagus complex. It terminates in the tuberculum acusticum and supplies all of the lateral line organs which are not supplied from the VII nerve.

3.—*The Glossopharyngeus.*

There are but two components present, as shown in Fig. 10. The motor root arises from the cephalic end of the nucleus ambiguus and is the exact counterpart of the motor root of the vagus. It runs out under the spinal V tract and distributes to the muscles of the first gill.

The communis root passes in under the root of the r. lateralis vagi and over the spinal V tract to terminate in the fasciculus communis near its entrance into the lobus vagi. These fibres distribute to the hinder surface of the first gill cleft, *i. e.*, to the first functional gill, exclusively— taste buds and general mucous surfaces—and are extended forward ventrally as a lingual nerve to the tip of the hyo-branchial apparatus. From the sensory root a small anastomosing branch runs up to join the root of the r. lateralis vagi.

4.—*The Auditory Nerve.*

This nerve terminates in the tuberculum acusticum and cerebellum along with the lateralis roots of the X and VII nerves. The details of its central connections were not investigated. So far as known it contains only acustico-lateralis fibres.

5.—*The Facialis*.

There are four roots and three components, as diagramed in Fig. 11.   The motor root arises from the motor VII nucleus and is related in passing out to the fasciculus longitudinalis dorsalis.   It runs out under the spinal V tract and the VIII root, while the other VII roots pass over these structures.   It runs into the truncus hyomandibularis and supplies the mm. levator operculi, adductor operculi, adductor hyomandibularis, adductor arcus palatini and hyo-hyoideus.   These are viscero-motor fibres like those from the nucleus ambiguus.

The communis root enters the brain between the two lateralis roots, arising in the geniculate ganglion and forming the whole of the pre-auditory fasciculus communis.   From the geniculate ganglion fibres go out to form the whole of the r. pre-trematicus VII for the pseudobranch and the mucous lining of the mouth adjacent, and of the r. palatinus for the mucous lining and taste buds of the roof of the mouth and of the r. lateralis accessorius for special cutaneous sense organs.   Other fibres enter the truncus hyomandibularis and supply the mucosa and taste buds of the lining of the mandible and lower lip; others enter the r. maxillaris of the truncus infraorbitalis and supply taste buds of the upper lip; while still others enter the truncus supra-orbitalis.

The two lateralis roots terminate together in the tuberculum acusticum.   The ventral one enters the truncus hyomandibularis and supplies the organs of the operculomandibular line.   The dorsal one distributes its fibres to the supra- and infra-orbital trunks for the organs of the supra-orbital and infra-orbital lateral lines respectively.

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6.—*The Abducens.*

The sixth nerve arises by two roots, each coming in part from the abducens nucleus and in part from the fasciculus longitudinals dorsalis. It is a pure somatic motor nerve and has no connections with any other nerve.

7.—*The Trigeminus.*

In this nerve I have found but two components (Fig. 12). The motor root is like that of the VII nerve. The configuration of the oblongata is such at this point that it emerges really dorsally of the sensory root. It enters the r. mandibularis of the infra-orbital trunk and supplies the mm. depressor operculi, levator arcus palatini, adductor mandibulæ, genio-hyoideus and intermandibularis.

The general cutaneous root, after its entrance into the brain, sends some fibres to the chief sensory trigeminal nucleus and also makes up the whole of the pre-vagal spinal V tract. From its ganglion (the Gasserian g.) fibres enter the supra-orbital trunk (r. ophthalmicus superficialis V), the infra-orbital trunk (r. maxillaris and r. mandibularis V) and two twigs (only the more cephalic one shown on Fig. 12, *t. f. 1*) run back to enter the truncus hyomandibularis for the skin of the lower part of the operculum. In addition to these, a few fibres go out with the radix longa of the ciliary ganglion which are apparently general cutaneous, rather than sympathetic and which I homologize with the r. ophthalmicus profundus trigemini.

8.—*The Trochlearis.*

This is, so far as known, a pure somatic motor nerve, arising from its nucleus in the floor of the mesocœle and doubtless also partly from the fasciculus longitudinalis

dorsalis. In its intra-cranial course it is intimately related to the origin of the r. lateralis accessorius, but no interchange of fibres could be demonstrated.

9.—*The Oculomotorius.*

The third nerve, like the fourth, is a pure somatic motor nerve. The origin is essentially as in the last case and the nerve peripherally has no connections with any other nerve save with the ciliary ganglion.

III.—Review of the Cranial Components.

1.—*The General Cutaneous System.*

Under this head I have included all nerves, exclusive of the sympathetic, which terminate free in the skin without specialized end organs. These are mainly nerves of the tactile sense, but others are also doubtless included and this system will ultimately have to be broken up into several sensory systems. In the head this system includes the two general cutaneous ganglia, the Gasserian and jugular ganglia, the root fibres from these ganglia, including the spinal V tract, and the terminal nuclei of these root fibres, viz., the chief sensory nucleus of the V nerve and the nucleus funiculi. The secondary tracts from these nuclei I have not studied exhaustively. They should also be included in a full account of the system.

The morphology of this system is perfectly simple. It corresponds to the sensory system of the dorsal horns of the spinal cord. It has suffered less modification in the head than any of the other systems, the most important being its suppression in all but the V and X cranial nerves. If it survives in any of the other nerves, it is in so altered form as to be unrecognizable. See Section 3, I; Section 5, I, 3 and VIII; Section 7.

2.—*The Acustico-lateral System.*

These nerves are related exclusively to the organs of the lateral line canals and allied sense organs, and to the similar organs of the internal ear. The system includes the ganglion of the acustic nerve, the ganglion of the r. lateralis vagi and the dorsal and ventral lateralis ganglia of the facialis, together with their root fibres and their common terminal nuclei in the tuberculum acusticum and cerebellum. Most of these root fibres terminate soon after their entrance into the brain in the tuberculum acusticum, but some turn cephalad to terminate in the cerebellum, while others turn as abruptly caudad to form a spinal VIII tract.

This system has no representative in the spinal nerves. The extreme dorso-lateral position of its terminal nucleus and of the ascending and descending root bundles suggests that this system was the last sensory system to be differentiated in the medulla oblongata. It is closely related to the general cutaneous system; nevertheless from a study of Weigert preparations of Menidia I cannot agree with Johnston ('98), who finds from a study of Golgi preparations of Acipenser that the acustico-lateral and the general cutaneous nerves belong to a single system with a common terminal centre in the oblongata. The two systems are very distinct from each other in Menidia both centrally and peripherally. It is possible that the acustico-lateral system has been derived in the phylogeny from the general cutaneous, a view which has been expressed by Cole ('97, p. 234) on embryological grounds.

See Section 2; Section 3, II; Section 5, I, 5 and X; Section 6; and Section 7.

3.—*The Communis System.*

This system was composed primarily of the viscero-sensory nerves, though as we actually find it in the head much has been added upon this foundation; thus, it includes not only nerves to the visceral or mucous surfaces, but to taste buds, to terminal buds of the outer surface and to the teeth. It is represented in the X, IX and VII nerves only, including all of the sensory IX, all but the lateralis portion of the sensory VII and all but the lateralis and general cutaneous portion of the sensory X. Its ganglia are the geniculate ganglion of the VII nerve, the whole of the IX ganglion and the branchio-visceral ganglia of the vagus. All of these fibres terminate in the lobus vagi—the vagus fibres directly, the others through the mediation of the fasciculus communis. There is no "lobus trigemini" or pre-vagal terminal nucleus, as in many other fishes, this being correlated with the reduction of the terminal bud system in Menidia.

The viscero-sensory system of the trunk seems to have been largely supplanted by the r. intestinalis of the vagus, yet the spinal nerves retain a vestige at least of this system. The centre in the spinal cord is uncertain, though in the higher forms Clarke's column seems to be related directly or indirectly to these fibres. In the fishes the corresponding region, the "intermediate zone" probably contains a similar centre. This is suggested by the way in which the descending tract from the lobus vagi after passing the commissura infima Halleri runs back into the intermediate zone.

See Section 3, III; Section 5; Section 7; and Section 12.

4.—*The Motor Components.*

The topographical relations of the motor nerves have been fully worked out. These components were not the

primary objects of study in this research and the teleosts are too highly specialized forms to reveal to the best advantage the fundamental relationships of the motor centres. Nevertheless, accepting the distinction between somatic motor and visceral motor nerves, as now commonly held by the morphologists, it appears that Menidia conforms to the usual schema given for the vertebrates; that is, the eye-muscle nerves belong to the somatic musculature and all of the other cranial motor nerves to the visceral musculature. The latter has been very highly developed in the head to form the branchial musculature. These muscles, to increase their physiological efficiency, have become striated and the nerve fibres which supply them are of large size like the other nerves for the voluntary musculature. Responding to this demand, specialized centres of origin in the oblongata have appeared for these nerves, viz., the nucleus ambiguus and the motor nuclei of the VII and V nerves, and these nuclei are related to the great longitudinal medium of muscular co-ordination, the fasciculus longitudinalis dorsalis, just like the other voluntary nerve centres of the somatic series.

The well-known relations of the motor nuclei of the several cranial nerves to this fasciculus are such as to leave no doubt that it is physiologically a very important medium of correlation of the various cranial and spinal motor centres. The fact that it is related to both the somatic and the visceral (branchio-motor) nuclei of origin makes its morphological interpretation rather perplexing. Its relations to the cranial nerve roots appear to be effected mainly, at least, through the medium of collaterals.

The findings among the motor nerves to which attention is especially directed are, in addition to the preceding points, the following:

1.—The presence in the spinal cord of two motor nuclei, the ventral horn and the paracentral nucleus. The former is a somatic centre and is probably represented in the head by the eye-muscle nerves only; the latter is probably a visceral centre, represented in the head by the viscero-motor nuclei, viz., the motor X, IX, VII and V. See Section 3, III and IV.

2.—The first spinal is a fusion of two segmental nerves. The more cephalic one (occipito-spinal nerve *b* of Für-bringer) contributes a part to the brachial plexus, the remainder supplies the post-hyal hypoglossus musculature. The pre-hyal hypoglossus musculature is wanting in the teleosts and, in correlation with this, the spino-occipital nerve *a* of most other vertebrates is reduced. See Section 4, V.

3.—The post-hyal ventral musculature is innervated by the first spinal nerve, as usual. The pre-hyal hypo-glossus musculature is functionally replaced in the teleosts by a derivative of the constrictor system of the trigeminal segment of the selachians, viz., the so-called m. genio-hyoideus and the intermandibularis. These muscles in Menidia are innervated from the motor V (not motor VII, as commonly described), and can have nothing to do with the true ventral musculature. The first spinal nerve suffers a corresponding reduction. See Section 7, IV, 5, *iv.*

4.—The pharyngo-clavicularis muscles are innervated from the vagus and not from the first spinal. This differs from the accounts of some others, especially Fürbringer, and will necessitate some modifications in that author's scheme of the relations of somatic and visceral muscles in the vagus region of teleosts. See Section 5, VII, 5, *v.*

5.—There is a branch of the vagus for the m. trapezius, *i. e.*, a true spinal accessory nerve, in Menidia. Section 5, IX.

IV.—Special Results.

Among the more specific results to which attention is especially invited are the following:

1.—The fasciculus communis and associated structures of the Ichthyopsida are in a general way homologous with the fasciculus solitarius and its associated structures of the Amniota, though the homology is not exact.

2.—The innervation of the pseudobranch from the facial nerve supports Maurer's later view that the teleostean pseudobranch represents a spiracular demibranch or mandibular gill. This organ is very highly developed in Menidia and has invaded the post-spiracular or hyoidean region of the pharynx so that the pre-trematic ramus of the IX nerve has entirely disappeared.

3.—The nerve to the pseudobranch represents a pre-trematic ramus of the facialis and supplies the adjacent pharyngeal mucosa. This nerve coexists in some fishes with the chorda tympani, or pre-spiracular extension of the communis component for the hyoid and mandibular arches. The chorda is absent in Menidia and the post-trematic r. mandibularis internus VII of fishes cannot be homologized with it, though in higher forms it is possible that the two nerves fuse into a common trunk.

4.—The ophthalmicus profundus is apparently represented by a vestigeal bundle of general cutaneous fibres which run out from the Gasserian ganglion with the radix longa of the ciliary ganglion. Having reached the latter ganglion, they can no longer be traced.

5.—The sensory epithelium of the olfactory organ

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exhibits the "olfactory buds" of Blaue, which are so general among the teleosts. The development, however, shows that these are not survivals of a more primitive condition, but that they are late and secondary acquisitions. Blaue's supposition that they are related to the lateral line organs or terminal buds is impossible for several reasons.

6.—I would reiterate the position taken by most of the recent students of nerves, that the morphological value of a given nerve is to be determined primarily by its terminal relations, *i. e.*, its central nucleus and its peripheral end-organ. These appear to be very constant, while its intermediate course may be modified by so many cenogenetic factors as to be of relatively small value in determining the homologies.

7.—Finally, I would urge that the significance of the sensory components of the cranial nerves for metamerism has been greatly misunderstood. The consequences following the attempt to compare all sensory cranial nerves directly with dorsal spinal roots and to apply Bell's law in its simplest form to the cranial nerves have been so disastrous to sound morphology that the tendency among the most recent writers seems to be to deny the metameric value of the sensory cranial roots altogether and to confine attention to the motor roots. This is also too extreme. The problems of metamerism in the case of the sensory roots are vastly more complicated than in the case of the motor; yet I do not believe that they are insoluble. Some suggestions as to the lines along which I think the solution is to be sought are given in the preceding section.

December 31, 1898.

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DESCRIPTION OF THE FIGURES.

All of the figures of Menidia, viz., all except figs. 6, 14 and 15, are based upon a single series of transections of Menidia gracilis. The findings, however, were controlled by many other series prepared by the same and other methods. The serial numbers of the sections are indicated upon the scales above and below the plotted reconstructions and all drawings of transections are given their appropriate serial number. These serial section numbers are also used frequently throughout the text as a convenient means of referring to positions on the plots. The plots are accurately drawn to scale on the basis of a series of camera lucida outlines of representative sections.

Reference Letters.

a. to *z.*—naked cutaneous sense organs about the nasal apertures.

a. c.—anterior semicircular canal.

a. l.—anastomosing root of the r. lateralis vagi derived from the n. IX.

amp. ex.—external ampulla.

ART.—articular bone.

a. r. VII., a. r. VII. 1. and *a. r. VII. 2.*—anastomosing rami from the vagus to the r. recurrens VII to form the r. lateralis accessorius.

b. c. and *b. c. 1.* to *b. c. 5.*—the five branchial clefts.

br. g. X.—the ganglia of the four branchial rami of the vagus, including the visceral ganglia.

b. v.—blood vessel.

cb.—cerebellum.

cb. cr.—cerebellar crest.

cb. VIII.—cerebellar VIII, root fibres from VIII nerve to cerebellum of same side.

CB3.—the third ceratobranchial bone.

c. d.—dorsal cornu of spinal cord.

cil. b.—ramus ciliaris brevis.

cil. g.—ciliary ganglion.

cil. l.—ramus ciliaris longus.

com. ac. M.—commissura accessoria Mauthneri.

com. inf.—commissura infima Halleri.

com. IX.—communis (sensory) root of the glossopharyngeus.

com. mx.—the communis element for the r. maxillaris V.

com. oph. sup.—the communis element for the r. ophthalmicus superficialis.

com. VII.—communis root of the facialis.

com. X.—communis root of the vagus.

co. 1.—fibres from the second branch of the supra-orbital trunk for the cornea.

co 2.—do. from the fifth supra-orbital branch.

cr.—cranial wall.

cut. V.—the sensory (general cutaneous) component of the trigeminus.

cut. X.—fibres from the spinal V tract to the cutaneous branches of the vagus.

cut. X. 2 and *cut. X. 3.*—rami cutanei dorsales vagi.

cut. 1.—cutaneous fibres from the first spinal to the region behind the cleithrum.

c. v.—ventral cornu of spinal cord.

D.—dentary bone.

d. b.—first dorsal root of first spinal nerve (*b* of Fürbringer).

d. c.—second dorsal root of first spinal nerve (*c* of Fürbringer).

dep.—nerves for the depressor muscle of the pectoral fin.

d. lat. VII.—dorsal lateralis root of the facialis.

d. l. g. VII.—dorsal lateral line ganglion of the facialis.

d. V.—deep root of the V nerve, containing fibres from the motor V nucleus and for the "chief sensory nucleus" of the V nerve.

d. 2. to *d. 4.*—dorsal roots of second to fourth spinal nerves.

EB4.—the fourth epibranchial bone.

e. c.—external semicircular canal.

ESC.—extra-scapular bone.

f. c.—fasciculus communis.

f. d. 2.—nerves from second spinal for skin of dorsal part of pectoral fin.

f. l. d.—fasciculus longitudinalis dorsalis.

f. m. 3.—nerve from third spinal for skin of middle part of pectoral fin.

FR.—frontal bone.

f. v. 3.—nerve from third spinal for skin of ventral part of pectoral fin.

G.—the caudal extra-cranial tip of the Gasserian ganglion, giving rise to the second anastomosing nerve, *t. f. 2.*

Gas. g.—Gasserian ganglion.

g. cœl.—ganglion cœliacum.

gen. g. VII—geniculate ganglion of the facialis.

g. IX.—ganglion of the glossopharyngeus.

g. lat. X.—ganglion of r. lateralis vagi.

g. X. 1. to *g. X. 3.*—the ganglia of the first to third trunci branchiales vagi.

g. X. 4+5.—the common ganglion of the fourth truncus branchialis vagi and the r. intestinalis vagi.

HM.—hyomandibular bone.

hy.—ramus hyoideus facialis.

hy. 1. to *hy. 5.*—branches of the r. hyoideus VII.

IH.—interhyal bone.

III.—the n. oculomotorius.

io. 1. to *io. 20.*—branches of the infra-orbital trunk.

i. p. 1 to *i. p. 4.*—pores of the infra-orbital lateral line.

is.'*m. b.*—dorsal ramus from first spinal nerve *b* to interspinal muscles.

IV.—the n. trochlearis.

IX.—the n. glossopharyngeus.

IX–f. l. d.—fibres from the motor IX root to the fasciculus longitudinalis dorsalis.

IX–l. X.—communicating root IX to r. lateralis vagi.

jug. g.—the general cutaneous ganglion of the vagus, jugular ganglion of Shore and Strong.

k.—common communis root from geniculate ganglion for rr. maxillaris and ophthalmicus superficialis.

ki.—the head kidney.

l.—lateral reticular area of spinal cord.

LA.—lachrymal bone.

lev.—nerves for the levator muscles of the pectoral fin.

l. g. X.—ganglion of the r. lateralis vagi.

lob. inf.—lobi inferiores.

lob. X.—lobus vagi.

m. ad. a. p.—branch of r. opercularis profundus VII for m. adductor arcus palatini.

m. ad. arc. pal.—m. adductor arcus palatini.

m. ad. hy.—branch of r. opercularis profundus for m. adductor hyomandibularis.

m. ad. man.—m. adductor mandibulæ.

m. ad. op.—branch of r. opercularis profundus VII for m. adductor operculi.

m. a. m.—branches of the infra-orbital trunk (r. mandibularis V) for the m. adductor mandibulæ.

man. c.—naked organ, representing a mandibular commissure ("pit-line") on the lower lip.

man. ext. VII.—ramus mandibularis externus facialis.

man. V.—ramus mandibularis V.

man. VII—ramus mandibularis VII.

m. b. o. s.—branch of second branchial trunk for m. branchialis obliquus superior.

m. dil. o.—m. dilator operculi.

m. d. op.—branch of infra-orbital trunk for m. depressor operculi.

men.—meninges.

m. ghy.—branch of the r. mandibularis V, which, after anastomosing with the r. mandibularis VII, supplies the m. geniohyoideus.

m. im.—branch of r. mandibularis V for the m. intermandibularis.

m. l. a. p.—branch of infra-orbital trunk for m. levator arcus palatini.

m. lev. op.—branch of r. opercularis profundus VII for m. levator operculi.

m. lev. p.—m. levator arcus palatini.

m. l. op.—m. levator operculi.

m. n. V.—motor nucleus of the trigeminus.

m. n. VI—motor nucleus of the abducens.

m. n. VII—motor nucleus of the facialis.

mn. 1. to *mn. 5.*—organs of the mandibular canal.

m. o. d.—branch of third branchial n. for m. obliquus dorsalis.

m. o. d. p.—branch of fourth truncus branchialis vagi for m. obliquus dorsalis posterior.

mot. IX.—motor root of the glossopharyngeus.

mot. V.—motor root of the trigeminus.

mot. VII.—motor root of the facialis.

mot. X.—motor root of the vagus.

m. p. c. i.—the m. pharyngo-clavicularis internus.

m. ph. c. e.—branch of vagus for m. pharyngo-clavicularis externus.

m. ph. c. i.—branch of vagus for m. pharyngo-clavicularis internus.

m. ph. t.—branch of vagus for m. pharyngeus transversus.

m. p. l.—mandibular pit-line.

m. p. 1. to *m. p. 4.*—pores of the mandibular canal.

m. r. d.—branch of vagus for m. retractor arcus branchii dorsalis.

m. trap.—trapezius muscle (m. protractor scapulæ).

m. tr. d.—branch of vagus for m. transversus dorsalis.

m. VII. 1. to *m. VII. 12.*—branches of the r. mandibularis VII.

mx. V.—ramus maxillaris V.

m. 1. to *m. 3.*—organs of the main lateral line canal of the head.

m. 4.—organ of the occipital commissure.

NA.—nasal bone.

n. a.—nucleus ambiguus.

n. a. a.—anterior nasal aperture.

n. a. p.—posterior nasal aperture.

n. fn.—nucleus funiculi.

n. I.—the olfactory nerve.

n. II.—the optic nerve.

n. III.—the oculomotor nerve.

oc. c.—occipital commissure of lateral line system.

o. i.—m. obliquus inferior.

o. IX.—apparent (superficial) origin of the IX nerve.

o. i. 1 to *o. i. 15.*—organs of the infra-orbital lateral line.

o. l.—optic lobe.

o. m. VII.—apparent origin of the motor VII nerve.

OP.—opercular bone.

oph.—ramus ophthalmicus trigemini.

op. p. VII.—ramus opercularis profundus facialis.

op. p. 1. to *op. p. 6.*—pores of the opercular canal.

o. pr.—the ramus ophthalmicus profundus.

o. pr. r.—fibres from Gasserian ganglion to lateral lobe of the first sympathetic ganglion, supposed to enter the r. oph. profundus.

op. s. VII.—ramus opercularis superficialis of the truncus hyomandibularis.

op. s. VII. 1. to *op. s. VII. 5.*—first to fifth branches of r. opercularis superficialis VII.

op. X. 1. to *op. X. 4.*—branches of the ramus opercularis vagi.

op. 1. to *op. 7.*—organs of the opercular canal.

o. r. l.—apparent origin of r. lateralis vagi.

o. s.—m. obliquus superior.

o. s. 1. to *o. s. 6.*—organs of the supra-orbital canal.

o. V.—apparent origin of the V nerve.

o. VI.—apparent origin of the VI nerve.

o. X.—apparent origin of the vagus nerve.

o. 1. to *o. 4.*—organs of the ventral opercular pit-line.

o. 5.—similar organ on the dorsal edge of the operculum.

o. 6.—similar organ on the cephalic edge of the operculum.

pal.—the ramus palatinus facialis.

pb.—pseudobranch.

p. c.—posterior semicircular canal.

pc. n.—paracentral nucleus.

ph. d.—branch of the vagus for the most caudal superior pharyngeal teeth.

ph. IX.—ramus pharyngeus IX.

ph. v.—branches of the vagus for the inferior pharyngeal teeth.

ph. X. and *ph. X. 1.* to *ph. X. 3.*—pharyngeal rami of first to third branchial trunks.

PO.—most dorsal post-orbital bone.

POP.—preopercular bone.

post. and *post. 1.* to *post 4.*—post-trematic rami of the first to fourth branchial trunks of the vagus.

post. 2. d. and *post. 2. v.*—dorsal and ventral ramuli of the second post-trematic ramus.

pre. and *pre. 1.* to *pre. 2.*—pre-trematic rami of the first to fourth branchial trunks of the vagus.

PRO.—prootic bone.

PS.—parasphenoid bone.

r. a. a.—ramulus acusticus ampullæ anterioris.

r. a. e.—ramulus acusticus ampullæ externæ.

r. a. p.—ramulus acusticus ampullæ posterioris.

r. b.—m. retractor bulbi.

r. buc.—ramus buccalis facialis.

r. car.—ramus cardiacus vagi.

r. cerv.—ramus cervicalis, Fürbringer; "hypoglossus" of authors.

r. com.—ramus communicans, or sensory portion of dorsal branch of spinal nerves.

U

r. com. b.—ramus communicans between first spinal nerve *b* and the r. lateralis accessorius.

r. com. 2.—do. between second spinal nerve and r. lateralis accessorius.

r. com. 3.—do. do. third spinal nerve do.

r. com. 4.—do. do. fourth spinal nerve do.

r. cut. dors. X.—ramus cutaneous dorsalis vagi.

r. e.—m. rectus externus.

r. é.—fine fibred slip of m. rectus externus.

rec. 1. to *rec. 3.*—roots of the ramus lateralis accessorius (recurrent roots of the facial).

r. if.—m. rectus inferior.

r. intest. X.—ramus intestinalis vagi.

r. it.—m. rectus internus.

r. *IX.*—root of the glossopharyngeus.

r. l.—ramulus acusticus lagenæ.

r. lat. ac.—ramus lateralis accessorius.

r. lat. X.—ramus lateralis vagi.

r. l. 1. to *r. l. 4.*—the first four twigs of the r. lateralis vagi.

r. m.—ramus medius of spinal nerves.

r. m. b.—ramus medius of first spinal nerve *b*.

r. m. c.—ramus medius of first spinal nerve *c*.

r. m. 2. to *r. m. 4.*—ramus medius of second to fourth spinal nerves.

r. n.—ramulus acusticus neglectus.

r. oes.—œsophageal rami of the vagus.

r. oph. sup. V.—ramus ophthalmicus superficialis trigemini.

r. oph. sup. VII.—ramus ophthalmicus superficialis facialis.

r. op. V.—ramus opercularis trigemini.

r. op. X.—ramus opercularis vagi.

r. ot.—ramus oticus.

r. ot. c.—the general cutaneous component of the r. oticus.

r. ot. l.—the lateralis component of the r. oticus.

r. r. u.—ramulus acusticus recessus utriculi.

r. s.—m. rectus superior.

r. sac.—ramulus acusticus sacculi.

r. sp.—ramus spinosus, or motor portion of dorsal branch of spinal nerves.

r. sp. b.—ramus spinosus of first spinal nerve *b*.

r. sp. c.—ramus spinosus of first spinal nerve *c*.

r. sp. 2. to *r. sp. 4*—ramus spinosus of second to fourth spinal nerves.

r. st. X.—ramus supratemporalis vagi.

r. v.—ramus ventralis of spinal nerves.

r. v. b.—ramus ventralis of first spinal nerve *b*.

r. v. c.—ramus ventralis of first spinal nerve *c*.

r. v. b + c.—the combined ventral rami of the first spinal nerves *b* and *c*.

r. VII. p. t.—ramus pre-trematicus facialis.

r. v. 2. to *r. v. 4.*—the ventral rami of the second to fourth spinal nerves.

rx. b.—radix brevis of ciliary ganglion.

rx. l.—radix longa of ciliary ganglion.

s . c.—subcranial canal.

sec. VIII.—secondary acoustic bundle, from tuberculum acusticum to cerebellum of same side.

sec. X.—secondary vagus bundle (Mayser), from lobus vagi to cerebellum of same side.

so. 1. to *so. 14.*—branches of the supra-orbital trunk.

sp. g.—spinal ganglion.

sp. V. t.—spinal V tract.

sp. VIII.—spinal VIII tract.

s. p. 1. to *s. p. 5.*—pores of the supra-orbital canal.

SQ.—squamosal (pterotic) bone.

sy.—the sympathetic nervous system.

sy. c.—the left commissural root of the n. splanchnicus.

sy. oph. sup.—sympathetic fibres for the r. ophthalmicus superficialis.

sy. rec. 3.—sympathetic root for the third root of the r. lateralis accessorius.

sy. 1. to *sy. 7.*—ganglia of the head part of the sympathetic chain.

sy. 1. l.—lateral lobe of the first sympathetic ganglion.

sy. 1. m.—median lobe of the first sympathetic ganglion.

t. a.—tuberculum acusticum.

t. f. 1 and *t. f. 2.*—first and second anastomosing nerves from the trigeminus to the truncus hyomandibularis.

t. hm.—truncus hyomandibularis.

t. inf.—infra-orbital trunk, containing the r. mandibularis V and the r. maxillaris and the r. buccalis, together with communis fibres.

tr. b. t.—tractus bulbo-tectalis, carrying fibres from the lobus vagi and tuberculum acusticum to the optic tectum of the opposite side.

t. so.—truncus supra-orbitalis.

t. X. 1. to *t. X. 4.*—the four trunci branchiales vagi.

u.—utriculus.

V.—the root of the trigeminus.

v. b.—ventral root of the first spinal nerve *b*.

v. c.—ventral root of the first spinal nerve *c*.

VI.—the n. abducens.

VIII—the n. acusticus.

VIII–d. l.—anastomosing root beteen the VIII and dorsal lateralis VII roots.

v. lat. VII.—ventral lateralis root of the facialis.

v. l. g. VII.—the ventral lateral line ganglion of the facialis.

v. m.—post-zonal ventral musculature.

V–VII. 1. and *V–VII. 2.*—anastomoses between the r. mandibu
laris V and the r. mandibularis VII.

XI.—branch of the vagus to the m. trapezius (n. accessorius).

1. l. a. e. to *4. l. a. e.*—branches of the IX nerve and of the first
three branchial trunks of the vagus for the four levator arcus branchii
externus muscles.

1. l. a. i.—branch of IX n. for first m. levator arcus branchii
internus.

2. l. a. i.—branch of second branchial trunk of vagus for second m.
levator arcus branchii internus.

4. l. b. e.—the fourth levator arcus branchii externus muscle.

<div align="center">PLATE XIV.</div>

Figure 1.—Transection through the body of Menidia just in front
of the first spinal nerve (685, cf. fig. 3), ×28. Drawn by Mr. F. W. J.
Veenfliet from a Weigert preparation, after fixation in Flemming's
fluid.

Figure 2.—Transection similar to the last at the origin of the hyo-
mandibular and palatine nerves (514), ×28. The section is slightly
oblique and the skin is defective on the dorsal surface.

<div align="center">PLATE XV.</div>

Figure 3.—The cranial and first spinal nerves of Menidia gracilis,
reconstructed from serial sections and projected upon the sagittal
plane, × 23. The entire plot was constructed from the left side of a
single specimen. No details were introduced from other specimens,
though almost every point was controlled on the opposite side of this
specimen and on other series of sections. The plot is drawn as if
seen from the right side, the drawing having been reversed during
the process of reconstruction. The correct relations would be given
by the mirror-image of the plate as printed.

The outlines of the brain, eye and mouth cavity are given in black
lines, the outlines of the lateral line canals in green lines. The sym-
pathetic nervous system behind the trigeminus is omitted, also the
motor component of the vagus, the general cutaneous component of
the r. oticus and numerous details of the proximal portions of the
cranial nerves. Compare the enlarged plot of this region, fig. 4.

All lateral line organs contained in canals are drawn as brown
rings, all naked lateral line organs, "pit-line" organs, etc., as brown
discs. Taste buds of the mouth cavity and lips are not drawn in.
All sense organs of the outer skin supposed to belong to the commu-
nis system are drawn as red discs. The organs of the lateral lines
are referred to in the text by number, counting in each line from be-
fore backwards. The scales at the top and bottom of the plate indi-
cate the serial numbers of the sections. The latter were 15 micra in

thickness. No measurements are given in the text. These can be easily deduced from the plot.

Compare the enlarged plot on fig. 4, the isolated reconstruction of the acustico-lateral system on fig. 5 and the diagrammatic cross-sections, figs. 8 to 12.

PLATE XVI.

Figure 4.—An enlarged projection of a portion of the same specimen as figured on the preceding plate, showing the proximal courses of the nerves, × 47. The same color scheme as in fig. 3. The transverse parallel lines across the roots of the nerves indicate the points where they leave the medulla oblongata. The ganglia are drawn with lighter shades of the same colors as used for their nerves.

PLATE XVII.

Figure 5. The acustico-lateral system of nerves, sense organs and canals, as seen from the left (apparently right) side, × 23. Based upon fig. 3, q. v. The outlines of the nose, eye and membranous ear are indicated and colored a neutral tint, the outline of the nasal organ being heavier in the sensory portion of the nasal sac. The canals and sense organs are colored in accordance with their innervation; thus, the r. lateralis vagi, green; the r. supra-temporalis vagi, olive green; the auditory nerve, grey; the r. mandibularis externus VII and the r. opercularis superficialis VII, yellow; the r. buccalis, red; the r. oticus, red-brown; the r. ophthalmicus superficialis VII, chocolate brown. In the canals are indicated the limits of the cranial bones to which the canals are related. All details are drawn from a single specimen, except the organs *o. 1, o. 2* and *man. c.*, supplied from other specimens on account of defects in the sections used for the plot.

PLATE XVIII.

Figure 6.—The lateral lines of Lophius piscatorius, 12 cm. long, natural size, seen from above. Adapted from Guitel, '91, p 139. The several lines have been colored in accordance with their innervation, the same colors being used as in the figure of the acustico-lateral system of Menidia (fig. 5), which see. See also the text, Section 2, III. *n. a. p.*, the posterior nasal aperture. The other reference letters refer to the lateral lines; see the text.

Figure 7.—A reconstruction of the first spinal nerve, projected upon the sagittal plane, × 66. This complex includes the occipito-spinal nerves *b* and *c* of Fürbringer. The sensory component is colored yellow, the motor blue—dark blue in the case of nerves arising from the root *c*, and light blue from the root *b*.

Figure 8.—Projection of the fourth spinal nerve upon the transverse plane, × 33. This and the other diagrammatic cross-sections (figs. 9 to 12) are conventionally colored to correspond with the colors of fig. 3. They were constructed by the superposition of a series of camera lucida outlines of transections. They are diagrammatic, but not hypothetical, since no components are entered save those actually observed in the sections.

Figure 9.—Similar projection to exhibit the composition of the vagus nerve.

Figure 10.—Similar projection to exhibit the composition of the glossopharyngeal nerve.

Figure 11.—Similar projection to exhibit the composition of the facial nerve.

Figure 12.—Similar projection to exhibit the composition of the trigeminus nerve.

Figure 13.—Diagram of the relations of the eye-muscle nerves of Menidia. To be compared with fig. 12 of Allis' paper, '97.

Figure 14.—Similar diagram of the eye-muscle nerves of Amblystoma.

Plate XIX.

Figure 15.—Transection of the oblongata of a young specimen of Mugil cephalus L., the striped mullet, taken at the extreme caudal end of the lobus vagi, + 50. Shows the spinal V tract entering the nucleus funiculi, the caudal part of the nucleus ambiguus and lobus vagi and the cephalic ends of the paracentral nucleus and ventral cornu.

Figure 16.—Transection of Menidia at the level of the first spinal nerve *c* (714), × 50. Shows the ventral root arising from both the ventral cornu and the fasciculus longitudinalis dorsalis, also the composition of the brachial plexus.

Figure 17.—Transection of Menidia through the lobus vagi and emerging vagus roots (640), × 50. The section includes the caudal tips of the cerebellum and tuberculum acusticum.

Figure 18.—Transection of Menidia through the tuberculum acusticum and cerebellar crest (605), × 50. The section shows the central courses of the sensory and motor IX and the apparent origins of the r. lateralis vagi and the caudal root of the VIII.

Figure 19.—Transection of Menidia at the apparent origins of the VIII and VII nerves (577), × 50. The cerebellar crest fuses with the lateral lobe of the cerebellum.

Figure 20.—Transection of Menidia at the level of the apparent

origin of the V nerve (555), × 50. The motor V nucleus lies not at the point indicated by the letters *m. n. v.*, but a few sections farther cephalad in the corresponding position.

Figure 21.—Transection of the V + VII ganglionic complex of Menidia through the geniculate ganglion (529), × 50.

<center>PLATE XX.</center>

Figure 22.—Transection of the V + VII roots of Menidia at the level at which the ganglionic complex passes through a foramen to the outer side of the cranial wall (500), × 50.

Figure 23.—Similar transection at the origin of the infra-orbital trunk (485), × 50.

Figure 24.—Similar transection farther cephalad, showing the median and lateral lobes of the first ganglion of the sympathetic chain (481), × 50.

Figure 25.—Similar section farther cephalad, showing the origin of the radix longa of the ciliary ganglion and of the r. ophthalmicus profundus (478), × 50.

Figure 26.—A projection on the transverse plane of the course of the first facial root of the r. lateralis accessorius and the mode of its origin from the geniculate ganglion. A composite constructed by the superposition of a series of camera lucida outlines of transverse sections, × 50. The numbers represent the serial section numbers at the points where they are placed. At the point marked × the second root of the r. lateralis accessorius joins the first root.

Figure 27.—A camera sketch of a preparation of the left operculum of Menidia, × 10. See the text, Section 7, IV, 2.

FIG. 1.

FIG. 2.

Plate XV.

THE GENERAL CUTANEOUS SYSTEM.

THE COMMUNIS SYSTEM.

THE MOTOR SYSTEMS.

THE ACUSTICO-LATERAL SYSTEM.

THE SYMPATHETIC SYSTEM.

THE LATERAL LINE CANALS.

Plate XVI.

Plate XVIII.

FIG. 6.

FIG. 7.

FIG. 8.

FIG. 9.

FIG. 10.

FIG. 11.

FIG. 12.

FIG. 13.

FIG. 14.
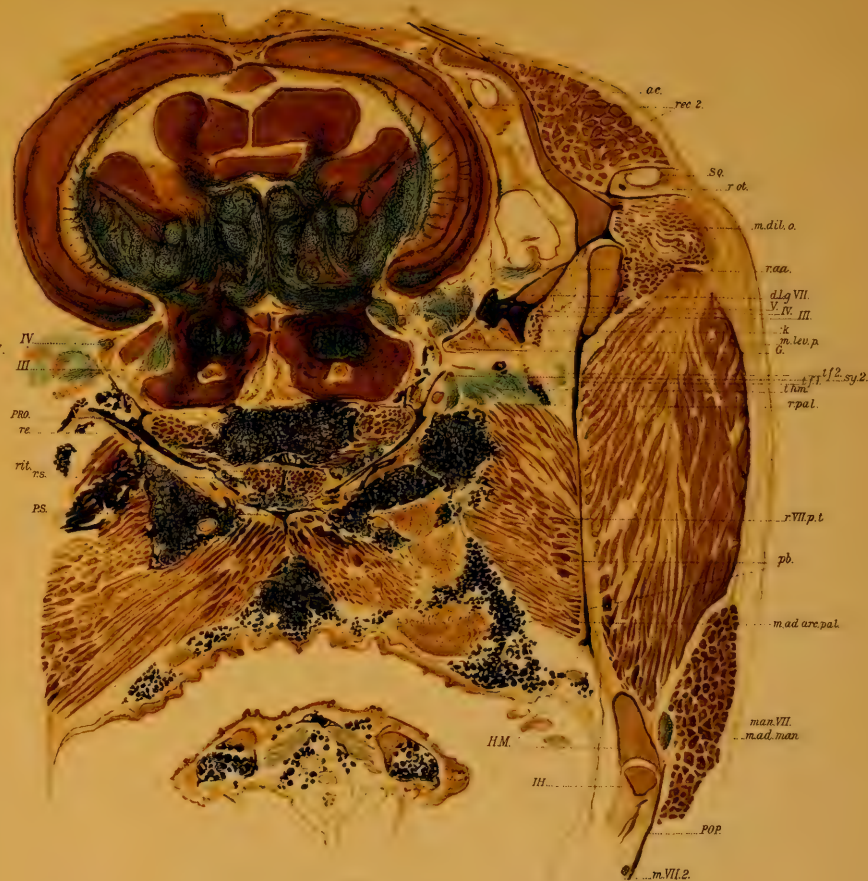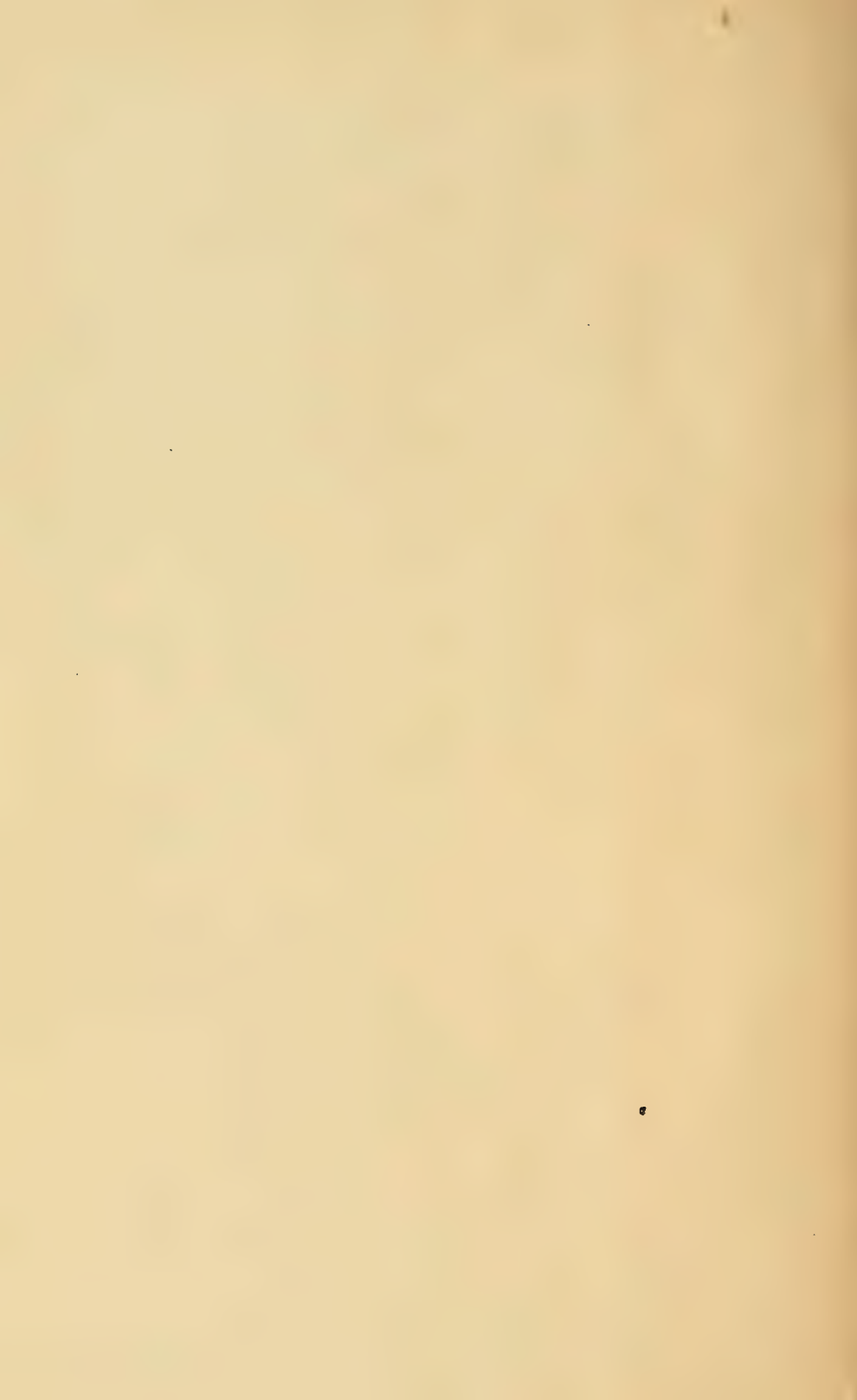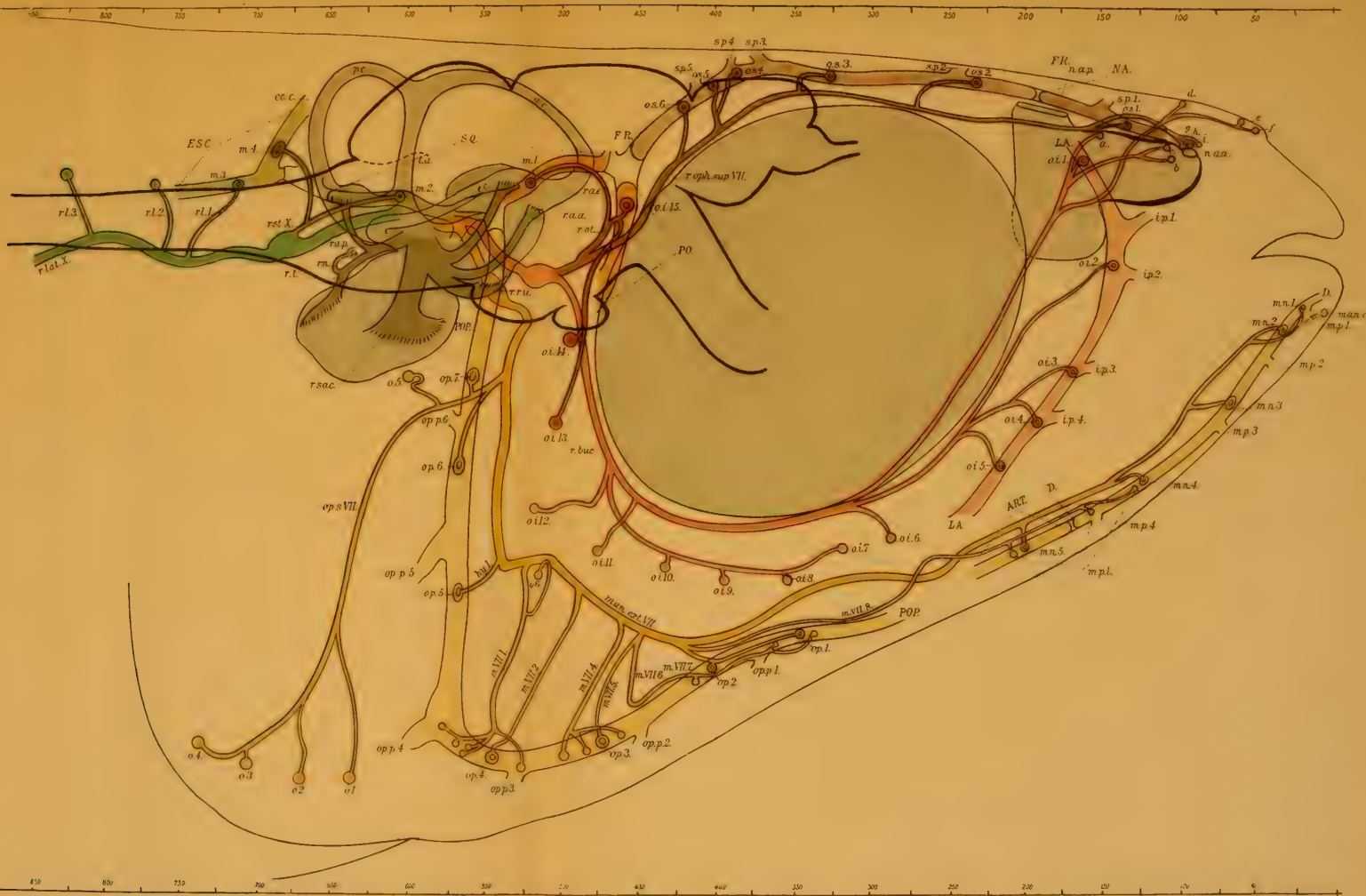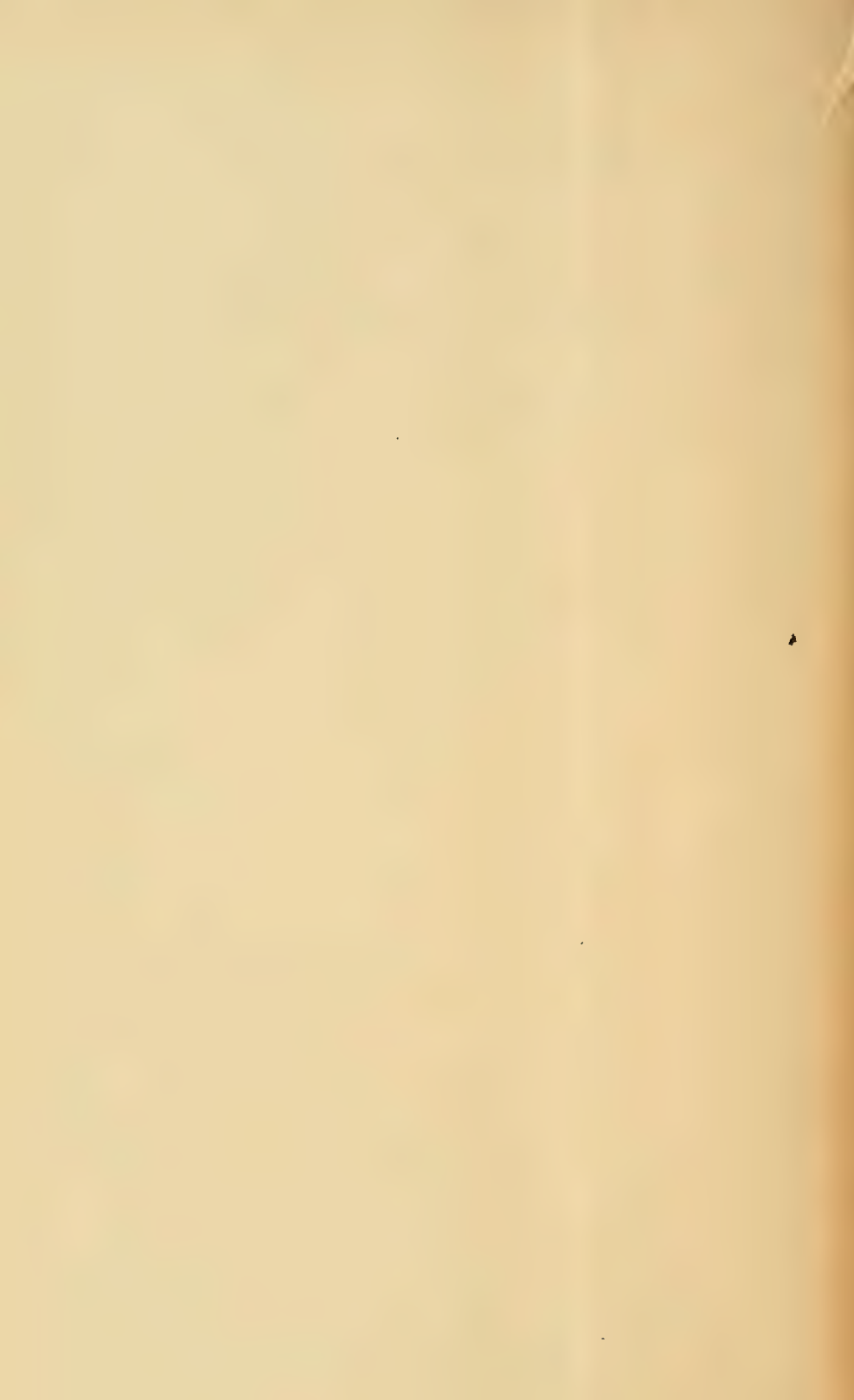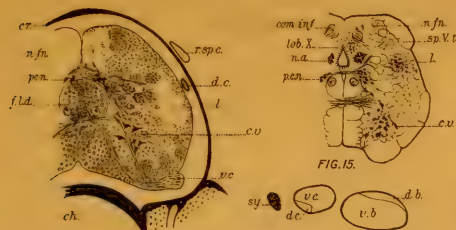
FIG.16.

FIG.15.

FIG.17.

FIG.18.

FIG.19.

FIG.20.

FIG.21.

Plate XX.

FIG.22.

FIG.23.

FIG.24.

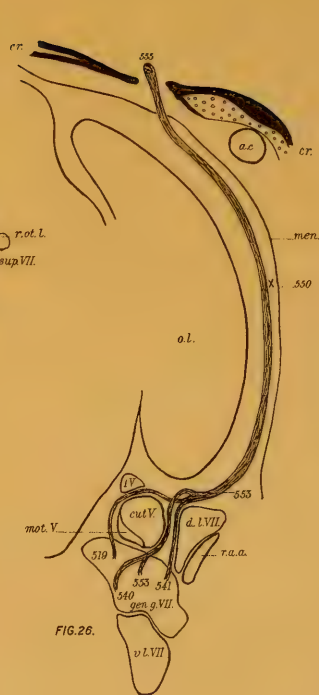FIG. 25.

FIG.26.

FIG.27.

LITERARY NOTICES.

Structure of the Cardiac Ganglia.[1]

The method employed in this research was the methylene blue method as modified by Dogiel. Observations were made on material obtained from new born infants, and from the dog, cat, sheep and rabbit. It may be worth noting in this connection, that in one instance Dogiel was able to stain the heart-nerves in the human heart nine hours after death.

Heart ganglion cells.—In shape, the majority of ganglion cells in the heart are multipolar; some bipolar cells were seen, also a few unipolar cells. The capsules of these ganglion cells extend on to the neuraxes and dendrites.

Three types of ganglion cells are described:

(*a*). *Ganglion cells of type one.* The cell bodies of these cells may be round, oval or angular. They stain less readily in methylene blue than do the cells of the other two types. The number of their dendrites varies from 2 to 16. These are short, thick and sometimes flattened; are beset with varicosities, and divide near the cell, and, after further division, end in a bundle of short, thick, varicose branches, which are often beset with thorn-like branches. These dendrites form a dense network between the cells of the ganglion. The neuraxis begins in a cone, either directly from the cell body or from one of the dendrites, and is of variable size; may be smooth or varicose and is non-medullated. The neuraxes of these cells are thought to end in the musculature of the heart; they may thus be regarded as belonging to the motor sympathetic cells and fibers.

(*b*). *Cells of second type.* In the shape of the cell-body, these do not differ materially from those of the first type. The majority are multipolar; some bi- and unipolar cells belong however to this type. They are usually found in small groups or rows or singly, by the side of, or within nerve-bundles. The number of the dendrites varies from 1

[1] A. S. Dogiel. Zur Frage über den feineren Bau der Herzganglien des Menschen und der Säugethiere. *Archiv f. Mik. Anat.*, Vol. LIII, No. 2, Nov. 1898.

to 10.   These divide near the cell into a number of varicose or smooth branches, which often enter a nerve bundle, in which they may now and then be traced for a long distance.   In the nerve-bundles they resemble varicose neuraxes.   Owing to their length it was difficult to determine their mode of ending.   Dogiel suggests that they end either in a special end-apparatus or in the nerve-trunks.   He favors the former view. The neuraxes of the cells arise by a cone-shaped enlargement.   The majority are non-medullated ; now and then one which had a sheath of myelin was observed.   In a number of instances the neuraxes of the cells of type two could be traced into a neighboring ganglion, where they seemed to terminate.

(c).   *Cells of type three.*   The cells of type three resemble in some respects those of type one, in others those of type two.   The dendrites are longer than found in type one, but do not pass beyond the bounds of the ganglion, forming a network between the ganglion cells.   The neuraxes of the cells of this type are non-medullated and may often be traced for long distances.   Their mode of ending was not determined.

Two kinds of nerves were found to end in the sympathetic ganglia of the heart :

1.   Medullated and non-medullated fibers of various sizes, which divide repeatedly and surround all elements of the ganglion in a dense network, which is, however, always extra-capsular.   As the capsules of the ganglion cells of the heart ganglia extend on to the dendrites for a distance, it may be assumed that the fibrils of this network come into immediate contact with the ganglion cells which they enclose, only at the ends of their dendrites.   As to the origin of the nerves which thus end in the heart ganglia, the following statements are made by Dogiel :

(a).   Many, possibly all, of the non-medullated fibers and a few of the medullated which end in extra-capsular plexuses, are neuraxes of sympathetic nerve-cells, situated in the heart.

(b).   Medullated fibers, probably also some non-medullated fibers, which form extra-capsular plexuses are neuraxes of sympathetic cells situated outside of the heart.

2.   Fibers of the second class are always medullated.   They branch frequently before reaching the ganglia and after entering them, and terminate in intricate plexuses which are intra-capsular, surrounding the cell bodies of the sympathetic cells.   Dogiel believes that only a relatively small number of the heart-ganglion cells are thus surrounded by intra-capsular plexuses, and these are mostly cells of the first type. The nerve-fibers of this second class are neuraxes of cerebro-spinal neurons.   G. C. H.

Distribution of the Cardiac Ganglia.[1]

The method used by Schwartz was to cut the heart of a small mammal in serial sections in three planes—frontal, sagittal and transverse—and to stain the sections in thionin or in tholuidin blue. Every fifth section was stained and mounted and other sections, if thought necessary. Cross-sections were found most suitable for locating the ganglia.

His results may be summarized as follows:

No ganglion cells are found in the ventricle until the sulcus transversus is reached. The ganglion cells, which are arranged in 4 or 5 relatively large groups, between which smaller groups are found, are located on the posterior wall of the auricles, more to the left than to the right of the auricular septum, and under the visceral pericardium. This ganglionic area is bounded laterally by the auricular appendages, and below by the sulcus transversus.

Schwartz finds in the ventricles and auricles, irregular cells, often grouped, which contain granules which stain in the reagents used by him. It is suggested by him that these cells may have been described as ganglion cells by writers who have found ganglion cells in the ventricles. They were looked upon as " Mastzellen."

G. C. H.

Structure of Ganglion Cells of Birds.[2]

The observations were made on material obtained from pigeons and chickens. Of the several fixing and hardening fluids employed, Carnoy's and Zenker's fluids proved most satisfactory. For staining the tigroid substance in the nerve cells, toluidin blau and erythrosin (Lenhossék) were used; for the ground substance, iron-hæmatoxylin (Heidenhain) and erythrosin or Blue de Lyon and saffranin (Mann); for nuclear structure, Ehrlich-Biondi or methyl green-eosin-acid fuchsin.

Spinal and sympathetic ganglia of birds possess a relatively thin capsule and a small amount of interstitial connective tissue. One or several lymph nodules were found in every spinal ganglion.

The size of the spinal ganglion cells varies from $40\,\mu$ to $8\text{-}10\,\mu$, they are surrounded by a capsule which becomes continuous with the

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[1] S. SCHWARTZ. Ueber die Lage der Ganglienzellen im Herzen der Säugethiere. *Arch. f. Mik. Anat.*, Vol. LIII, No. 1.

[2] DR. D. TIMOFEEW. Beobachtungen über den Bau der Nervenzellen der Spinalganglien und des Sympathicus beim Vogel. *Internat. Monatsch. f. Anat. und Physiol.* Vol. XV, No. 9-10.

sheath of the axis-cylinder process.   A single nucleus is found in each cell, situated in its middle.

The cells of the sympathetic ganglia are multipolar, with three to five, or even more processes.   Their size varies from 20-25 μ to 5-6 μ. They are also enclosed in a capsule.   The spinal and sympathetic ganglia of birds are very rich in tigroid substance.   This seems equally distributed through the cell-body with the exception of a narrow peripheral zone, which in the larger spinal ganglion cells seems free from this substance.

A more careful study of the tigroid substance of the spinal ganglia shows the small patches of this substance seen on more superficial examination, to be made up of small, deeply stained granules of variable size.   The tigroid is arranged in the form of a network, of which these fine granules and the larger patches form the greater part.

The tigroid appears early in the embryo.   In a chick of the 4th day, traces are observed; by the 6th day, it is present in appreciable quantity.   It appears in the peripheral nervous system before it does in the central, and seemingly first in the head-ganglia, the jugular ganglion of the vagus being especially mentioned by Timofeew.   In the spinal ganglia, the tigroid makes its appearance as a diffuse, non-granular substance which fills the whole cell.   As the spinal ganglion cells enlarge, this substance is found as a zone in the peripheral portion of the cell, leaving a tigroid-free zone in the center around the nucleus.   This stage seems characteristic for a great part of embryonic life.   The granules appear first in the tigroid-free zone, later in the whole cell, and by the 17th day the cells present the appearance seen in adult life.

The ground substance, both in the spinal ganglion cells and the sympathetic cells is of a fibrillar structure.

The nuclei of both kinds of cells are surrounded by a distinct nuclear membrane, from which fine threads, beset with granules pass into the nucleus, forming a network with narrow meshes.   Network and granules are acidophile; two nucleoli are found, one of which is distinctly acidophile, the other basophile, the latter corresponding to the large nucleolus found in the nerve cells of other vertebrates.   G. C. H.

Ruffini on Nerve Endings in the Skin.[1]

In this monograph Ruffini gives his observations on the nerve endings in the human skin; they were made with Fischer's gold chloride

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[1] ANGELO RUFFINI.   Sulla presenza di nuove forme di terminazioni nervose nello strato papillare e subpapillare della cute dell'uomo con un contributo allo studio della dei corpuscoli del Meissner.

method, which was slightly modified, as the character of the tissues rendered it necessary. The nerves and nerve-endings especially considered are the following :

I. Nerves in the vascular papillæ. The nerve-fibers in the vascular papillæ have a double origin ; generally arising from the superficial dermal plexus, more rarely from the subpapillary non-medullated plexus. The majority of the nerves entering a papilla, of which there may be one or two, rarely more, lose their medullary sheaths before they reach the papilla, in which they divide into a variable number of pale fibers which course toward the apex of the papilla. The nerves in the vascular papillæ form turn about the capillary loops, resembling a vine as it winds around a branch. These nerves end in distinct terminal enlargements, which sometimes are near the capillary loops, at other times at some distance from them. These terminal enlargements vary in shape; sometimes appearing in the form of a terminal plate, similar to a motor plate, or, more rarely, as an arborescent figure. The papillary nerves the author believes to be vaso-motor nerves. [Judging, however, from the author's description, more particularly from his figures, it may be questioned whether the nerves here described may not, more correctly, be regarded as some form of sensory ending. Certainly they have nothing in common with vaso-motor nerves in other organs.]

II. Subpapillary non-medullated plexus. This non-medullated plexus is found in the subpapillary layer, where it forms the superficial vascular plexus. It originates from the superficial medullated plexus. The non-medullated plexus consists of fine pale fibers which present at short intervals varicosities of variable size. Its fibers terminate either in the region of the plexus in fine filaments with terminal enlargements, or enter the vascular papillæ as above stated. From the topographic position, and the anatomic character of the nerves of this plexus the author ascribes to it vaso-motor function.

III. Meissner's corpuscles. Ruffini's observations on Meissner's corpuscles confirm much which has already been known concerning this sensory nerve-ending ; much of what he states need therefore not receive special consideration at this place. One or two medullated nerves go to each corpuscle; these soon after entering it lose their medullary sheath, the naked axis-cylinders forming a series of windings, which the author speaks of as the " spiral turns of the axis-cylinders." The axis-cylinders present in their course in the corpuscles, varicose enlargements of cylindrical or club-shape, of a size equal to or exceeding that of the medullated fibers of which these axis-cylinders are

branches. The club-shaped varicosities are more numerous in the periphery of the corpuscles, while in its central portion the cylindrical ones predominate.

In surface preparations of Meissner's corpuscles, more especially on superficial examination, the observer is led to conclude that the pale spiral fibers give off at the periphery of the corpuscle numerous short processes which end in cylindrical or club-shaped enlargements. That this is not the case Ruffini was able to show in sections and in preparations made by crushing the stained tissue. Such preparations show that the interior of the corpuscles is occupied by an intricate winding of axis-cylinders, in the course of which the cylindrical and club-shaped enlargements are found, these in surface preparations presenting the appearance of short branches. The nerves terminate in a peculiar, granular substance, which stains a pale violet or a rose color in gold-chloride. In this substance nuclei are found, more numerous toward the periphery of the corpuscle; these Ruffini believes to be cells of mesodermic origin, agreeing in this respect with Ranvier. Some of the Meissner's corpuscles present monolobate appendages, one, two or even three having been observed. Meissner's corpuscles, with such lateral or apical extensions are found especially in low papillæ.

IV. Fiocchetti papillari. (Little tassel or tuft of flowers.) Under this name Ruffini describes what he believes to be a new nerve ending in the skin. The nerve-fibers forming this ending may be derived from a nerve-fiber going to a Meissner's corpuscle, or from the superficial plexus of the dermis. It is generally distributed to a vascular papilla, less frequently to a tactile papilla. The fiber as it enters the papilla divides into a variable number of varicose, non-medullated secondary fibers, which intertwine more or less and always end in terminal enlargements. Ruffini believes these nerve endings to have a function similar to that of Meissner's corpuscles.

Accompanying this monograph, there are five double plates containing 62 carefully and artistically executed figures.

<div align="right">DR. DEWITT and G. CARL HUBER.</div>

Researches upon the Real Origins of the Cranial Nerves.

Under this title Professor van Gehuchten during the year 1898 contributed an important series of papers to the *Journal de Neurologie*.

I.   The first study was devoted to the oculomotor nerves and was especially designed to demonstrate by degeneration experiments with the Nissl method the exact number and arrangement of the crossed fibers present in these roots.

That some of the root fibers of the oculomotorius have a crossed origin has long been known. In the rabbit he confirms the findings of Edinger, Perlia, Bach, and others that the dorsal and caudal part of the common oculomotor nucleus gives rise to crossed fibers. The oculomotor nucleus of the rabbit is not obviously segmented in accordance with the muscles supplied from it, yet experimentally it has been possible to analyze it and the details of its composition are given. The nerves for the m. rectus superior (and perhaps for the superior levator palpebrarum) are mainly of crossed origin, while a very few fibers for the mm. obliquus inferior and rectus internus are also crossed. The tract of Duval and Laborde between the VI nucleus and the third nerve of the opposite side could not be demonstrated experimentally in the rabbit; that is, no cells of the sixth nucleus degenerated after section of the branches of the third nerve, while, on the other hand, the section of the sixth nerve was followed by chromatolysis in all of the cells of the sixth nucleus.

Section of the patheticus shows that its fibers almost all have a crossed origin but that a very few cells of the nucleus of the same side are also affected. Whether these fibers cross at their origins from the nucleus and again in the valve of Vieussens was not determined.

The abducens is formed exclusively in the rabbit of uncrossed fibers. In 1893 Van Gehuchten described for the bird in addition to the classical nucleus of the abducens a smaller more ventral nucleus. This has been repeatedly demonstrated since in the mammals, but a controversy has arisen as to whether it belongs to the VI or the VII nerve. Section of the VII nerve in the rabbit was followed by no change in this nucleus, while section of the VI nerve resulted in chromatolysis of these cells.

II. The second contribution is devoted to the facial nerve. The nucleus of origin in the rabbit runs between the superior olive and the n. ambiguus and contains four quite distinct cell clusters, internal, external, middle and dorsal, all characterized by cells of the same type, the motor type of Nissl. Section of the seventh nerve immediately after its exit from the brain and subsequent study of the brain by Nissl's method show that all of the facial fibers arise from the nucleus as above defined, and that all of the cells of this nucleus degenerate and no others. No fibers arise from the opposite side.

The peripheral relations of the several portions of the VII nucleus of the rabbit were determined experimentally. Section of the nerve immediately after its exit from the stylo-mastoid foramen caused degeneration of all cells of the nucleus save the most internal ones of

the internal cluster, thus showing that it is these cells from which the nerves given off in the Fallopian canal arise, viz., the petrous nerve and the nerve for the stapedius muscle. Section of the rami auriculares anterior and posterior causes the degeneration of the remaining cells of this internal cluster. Section of the main branches of the facial nerve, which run out over the masseter muscle and supply the facial muscles (except those supplied by the r. superior and by the auricular rami) caused chromatolysis of all of the cells of the middle and external groups, while section of the r. superior caused the degeneration of the cells of the dorsal cluster. None of these experiments caused any modification in the nuclei of either the III, the VI or the XII nerves.

The geniculate ganglion, it is now well established, is a cerebrospinal ganglion pertaining to the sensory root of the facial nerve (the portio intermedia of Wrisberg). This ganglion, it is known, sends fibers into the chorda tympani. Does it contribute fibers to any other nerve ? This problem was attacked experimentally. In rabbits whose facial nerve was sectioned immediately after its emergence from the Fallopian canal the geniculate ganglion was stained and sectioned. The ganglion cells are clearly of the cerebro-spinal type and most of them were normal, yet a few were clearly degenerate. This last point contradicts the similar experiments of Amabilino on the dog, which were reviewed in the last issue of this JOURNAL. It will be remembered that the latter author found no degenerate cells after section of the facial, but that only four-fifths of the cells degenerate after section of the chorda tympani. Van Gehuchten thinks that the small number of cells which degenerate after section of the facial were overlooked by Amabilino.

III.   The third article is devoted to the IX and X nerves. It is preceded by a long historical review which brings out sharply the great diversity of opinion regarding the nuclei of these nerves. Section of the vagus roots results in chromatolysis of cells throughout the dorsal nucleus and thus permits an accurate determination of its limits. It and the fasiculus solitarius run down into the " intermediate zone " of Onuf and Collins, rather than into the dorsal horn regions, a point of some morphological importance as the latter authors and the present writer have both suggested.

The ventral nucleus (n. ambiguus) is also degenerated throughout its entire length, though there is a small column of normal cells running along its inner side at the cephalic end (the ventral nucleus of the IX root). The ventral nucleus of the vagus, like the dorsal nucleus, is

shown to run much farther caudad than is usually supposed, extending from the VII nucleus to the caudal end of the XII nucleus. No vagus fibers are related to the nuclei (either dorsal or ventral) of the opposite side. The nucleus ambiguus gives rise to no fibers for the XI nerve. After intra-cranial section of the XI nerve no cells of the n. ambiguus were degenerate, while the caudal portion of the dorsal vagus nucleus exhibited many cells in chromatolysis.

As to the physiological character of these nuclei, there can be no question that the ventral nucleus is a nucleus of origin for motor root fibers. Considerable evidence has been accumulating of late that the dorsal nucleus is also motor, at least in part. This van Gehuchten is at last able definitely to demonstrate by Golgi preparations of the nucleus of the cat. The cells are different in form from those of the n. ambiguus and doubtless have a different function, probably visceral, as suggested by the recent work of Onuf and Collins.

Where, then, is the sensory nucleus of the vagus? To test this Marchi's method was applied to the rabbit after section of the vagus roots proximally of their ganglion. The degenerate fibers were found to enter the fasiculus solitarius and to course in it exactly like the glossopharyngeal fibers, ending in the adjacent grey and in the commissural nucleus of Cajal.

Section of the IX nerve results in chromatolysis of a cluster of cells which form the cephalo-mesal part of the nucleus ambiguus. These constitute the motor IX nucleus. None of this motor root is crossed. Marchi's method applied to the IX nerve of the rabbit shows that all of the sensory fibers terminate in the nucleus of the fasiculus solitarius. <div style="text-align:right">C. J. H.</div>

The Central Origin of the Vagus.[1]

It is interesting to compare the last article referred to above with this very similar research, which was also carried out upon rabbits with Nissl's method. The operations reported upon are as follows: 1. resection of the vagus in the neck, (a) above, (b) below the separation of N. laryngeus superior; 2. resection of the vagus below the separation of the N. laryngeus inferior; 3. resection of the N. laryngeus superior; 4. resection of the N. laryngeus inferior.

There is a general agreement with van Gehuchten's results, with, however, important differences. For instance, in the operations of the

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[1] Dr. E. Bunzl-Federn. Der centrale Ursprung des N. Vagus. *Monats. f. Psychiatrie u. Neurologie*, V, 1, Jan. 1899. (This study continues the same author's earlier paper on the spinal accessory nerve. *Ibid.*, II, 6.)

first class mentioned above the present author found a small number of cells of the dorsal nucleus degenerate on the opposite side, while van Gehuchten found no crossed fibers in the vagus, either from the dorsal or ventral nuclei.   Bunzl-Federn agrees that the dorsal vagus nucleus is not in any way related to the IX nerve, but does not admit that the dorsal nucleus is entirely motor.   He verifies his earlier observation and van Gehuchten's that the n. ambiguus is not related to the XI nerve.   The experiments contribute some further data regarding the central connections of the several branches of the vagus.   C. J. H.

Sajous's Annual.

Volume II of the Annual and Analytic Cyclopedia of Practical Medicine, which lies on our table, is in every way a worthy successor of the first volume of this new series of Sajous's Annual.   The present volume includes topics from Bromide of Ethyl to Diphtheria and is fully and well illustraded.   In conformity to the new plan the work serves the double function of a record of recent progress with sufficiently full summaries of cases etc., and that of a cyclopedia with articles by the ablest experts.   Of special interest to neurologists in this volume are the articles on cerebral hemorrhage, chorea, deaf mutism, cerebral abcess, and catalepsy.   In topography and press-work little is left to desire and we may cordially commend the work as adapted to the needs of the progressive and busy practitioner.   C. L. H.

A New Annual.[1]

This annual review of the literature in neurology and psychiatry is planned along lines somewhat similar to those of Schwalbe's Jahresbericht für Anatomie und Physiologie which suspended after its twentieth volume in 1893.   It is, moreover, a worthy successor in its field of that much appreciated work.   The editorial staff is a very strong one, including, in addition to the editors named below, a list of 58 collaborators which contains the names of a large proportion of the leading neurologists of Germany, Austria and Russia.   The work has been well done, its completeness being indicated by the fact that 1447 pages are devoted to the bibliographical lists and abstracts.   These are well classified and the abstracts are short in all cases, so that the total number of books and papers reviewed is very large.   There are moreover excellent idexes of subjects and authors.   On the whole, this is a very useful work, involving an enormous amount of labor, and we hope that it will be well supported.   C. J. H.

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[1] Jahresbericht über die Leistungen und Fortschritte auf dem Gebiet der Neurologie und Psychiatrie. Herausgegeben von DR. E. FLATAU und DR. L. JACOBSON, Redigiert von PROFESSOR DR. E. MENDEL. I. Jahrgang. Bericht über das Jahr 1897.   Berlin, S. Karger, 1898.

LITERARY NOTICES.

Einige Bemerkungen anlaesslich der Arbeit: Bau des Wirbelthiergehirnes von Bela Haller[1]

Es ist bekannt, dass bis gegen Ende der 70er Jahre die Ärzte so gut wie keine Kentniss von den Forschungen über die Anatomie des Gehirnes und Rückenmarkes nahmen, welche durch die Begründer der ganzen Lehre, durch *Stilling* und vor Allem durch *Meynert* veröffentlicht wurden. Ja nicht nur die Ärzte, auch die Anatomen kümmerten sich kaum darum. In den anatomischen Lehrbüchern ist man ja bis in die letzten Jahre hinein noch oft genug geradezu kindlichen Darstellungen begegnet. Die Schuld liegt und lag nicht allein bei den Recipirenden. Aus den umfangreichen Werken von Stilling vermochte nur der sich zu orientiren, der seine ganze Zeit der Frage widmete und aus den kurzen Arbeiten und Darstellungen von Meynert wurde selbst ein solcher Leser oft nicht klug. Als das Lehrbuch von *Hueguenin* seiner Zeit erschienen, wurde es lebhaft als "eine Uebersetzung des 'Meynert' ins Deutsche" begrüsst. Es ermöglichte Vielen die Orientirung. Der schlechte Erfolg hielt Andere leider nicht ab einfache Dinge schwer verständlich vorzutragen. So bildeten z. B. die Schüler *Guddens* eine förmliche, sit venia verbo-Geheimwissenschaft—aus. Den meisten Unbekanntes als bekannt voraussetzend, schilderten sie Details aus einzelnen Gegenden, die Niemand — damals wenigstens — ordentlich unterbringen konnte. *Gudden* galt mit vollem Rechte zeitlebens als ein Hirnanatom ersten Ranges, aber ich zweifle ob ausser den ihm persönlich nahe Stehenden noch Viele da waren, welche einen Ueberblick über seine Leistungen hatten. Anfangs der 80er Jahre war sehr viel mehr vom Bau des Centralnervensystems bekannt als man damals ahnte; es lag nur, gleich den

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[1] Bela Haller: Vom Bau des Wirbelthiergehirnes. 1. Theil, Salmo und Scyllium. Morphologisches Jahrbuch, Band 26, H. 3 und 4. Angezeight von EDINGER, Frankfurt a-Main.

Präparaten im Keller der Museen, unzugänglich für die Mehrzahl der Interessenten aufgestapelt. Noch heute ist aus diesen litterarischen Kellervorräthen manch köstliches Stück zu holen und heute wird es durch unsere bessere Kenntniss des Ganzen auch verständlicher.

Diese Erinnerungen drängen sich auf bei der Lektüre einer sehr ins Detail gehenden Schilderung des Fischgehirnes, welche Herr BELA HALLER eben veröffentlicht hat. Ich selbst bin seit Jahren mit dem gleichen Gegenstand beschäftigt, kenne fast alle die Präparate, welche der Verf. abbildet und darf desshalb wohl den Anspruch erheben Stoff und Bearbeitung beurtheilen zu können. Nun zweifle ich, ob viele sich die grosse Mühe nehmen werden das umfangreiche, mit vielen Tafeln illustrirte Werk so eingehend und mit solcher Mühe zu studiren wie ich es gethan habe. Ich habe mich während dieser Lektüre oft gefragt für welche Leser der Verfasser wohl geschrieben haben möchte, wenn es mir nicht gelang aus der ungeheuren Fülle von Detailschilderungen nun ein Gesamtbild zu construiren.

Gelegentlich giebt der Verfasser ja selbst Zusammenstellungen, aber diese sind so wenig hervorgehoben, dass der gewissenhafte Leser, ehe er sie findet, sich durch eine Unmenge, ihn zunächst verwirrenden, Details durcharbeiten muss. Sehr erschwert wird das Verständniss auch durch die neue Terminologie. Oft genug erkennt man in ausführlich beschriebenen Bahnen alte Bekannte nur schwer, weil sie einen neuen Namen bekommen haben. Ich weiss wohl, dass in der Anwendung einer älteren Nomenclatur auf neuem Felde eine grosse Gefahr liegt, aber wir sind doch heute so weit, dass wir für bestimmte Theile überall wohl die gleichen Namen anwenden dürfen, z. B. für die "absteigenden Nervenwurzeln." Vor Allem scheint es nicht gerechtfertigt heute gerade das Fischgehirn durch eine neue und sehr willkürliche Nomenclatur, die sich nirgendwo an die von den Anatomen angenommene anlehnt, von den übrigen Vertebratengehirnen zu sondern. Im Interesse aller Mitarbeitenden liegt es, wenn zunächst so wenig als möglich an der Nomenklatur geändert wird.

Die Anatomie des *menschlichen* Gehirnes ist wesentlich gefördert worden, als sich für die Praktiker ein dringendes Bedürfniss herausstellte das Gehirn näher kennen zu lernen; da-

mals erst erhielten wir denn auch allmählich Beschreibungen, welche weitesten Kreisen das zu vermitteln geeignet waren, was bis dahin die Geheimlehre eines Kreises von Adepten schien. Die *vergleichende Anatomie* des Nervensystems erweckt keinerlei praktisches Interesse. Sie ist eine noch sehr junge Wissenschaft und sie *bedarf durchaus der Mitarbeit von moeglichst Vielen.* Aber damit sie nicht in den Fehler verfalle, den ihre Vorgänger begangen, damit das Bekannte wirklich Gemeingut der Arbeitenden werde, ist es wohl zweckmässig einmal zu untersuchen welche Anforderungen man an eine hierher gehörige Publication stellen darf, auch zu untersuchen ob wir uns nicht etwa durch Annahme einzelner Grundsätze für solche Veröffentlichungen etwas näher kommen, ob wir uns die Arbeit nicht etwas erleichtern können.

Sind diese Zeilen also auch nach der Lektüre von HALLERS Schrift entstanden, so wird es sich doch nicht etwa nur um Dinge handeln, die in dieser vorkommen, es werden vielmehr auch Punkte zu berühren sein, die dort vortrefflich berücksichtigt sind, anderwärts aber oft verfehlt erscheinen.

Zunächst wenige Worte über das Wesentlichste in einer wissenschaftlichen Untersuchung, über den *Grad der Zuverlaessigkeit* des Erreichten. Der jedesmal höchste Grad der Zuverlässigkeit ist nur zu erreichen wenn für jede Fragestellung resp. jedes untersuchte Object die augenblicklich beste Methodik angewendet wird und wenn uns der Autor keinen Moment im Zweifel über das lässt was die Methodik *nicht* leistet. Es scheint gar nicht genug berücksichtigt, dass es eine Menge von Fragen giebt, an welche man mit der heute vorhandenen Methodik nicht herantreten kann. So lässt sich z. B. der Ursprung der Hirnnerven bei den niederen Vertebraten heute nur in ganz allgemeinen Umrissen zeichnen. Es gehört eine genaue Lösung der da auftauchenden Fragen noch so lange zu den Unmöglichkeiten, als uns nur Färbemethoden und Schnitte zur Verfügung stehen. Der Ueberkreuzungen, der Verflechtungen sind dort auf engem Gebiete so viele, dass nur eine auf das Degenerationsverfahren aufgebaute Technik Klarheit schaffen kann. Auch die eingehendste Beschreibung dessen, was man mit den üblichen Methoden heute da sehen kann, hat desshalb, verglichen mit dem zweifellos erreichbaren Resultate nur geringen Werth. Da wir wissen, dass

nach Durchschneidung eines Nerven sich nur seine Fasern als Degenerationsbild abheben, nur seine Endzellen in Chromatolyse gerathen, so kann das färberisch erreichte Bild vom normalen Nerven nur noch einen relativen Werth beanspruchen. Darüber muss man sich ganz klar werden.

Solange Aufgaben angegriffen werden, für welche die Methodik noch ungenügend ist, werden wir immer wieder mit ausführlichen Schilderungen von Formverhältnissen beschenkt werden, die vielleicht ganz einfach liegen und kurz und bündig darzustellen wären.   Diese ausführlichen Detailbeschreibungen können wir aber nicht synthetisiren.   Ira van Gieson hat sie neulich treffend persiflirt als er das Gleichniss wählte von dem Manne, der die Buchstaben eines Buches Stück für Stück eingehend schildert und nun erwartet, dass aus seiner vielleicht trefflichen Schilderung der Leser den Inhalt des Buches combinire.   Die Schilderung des Details und wäre sie noch so minutiös ist nicht die alleinige Aufgabe einer wissenschaftlichen Arbeit. Eine solche erlangt erst Werth, wenn irgendwo wenigstens ein Stück Synthese möglich ist.

Ein schönes Beispiel für die Richtigkeit des Gesagten hat uns gerade Haller verschafft.   Wir verdanken ihm eine treffliche Arbeit über die Hypophysis, vielleicht das Beste, was überhaupt bisher über die ventralen Hirnanhänge geschrieben ist. Hier hat der Verfasser ein heute gut angreifbares Gebiet gewählt und in mustergültiger Weise bearbeitet.   Die erhaltenen Resultate, vor Allem der Fund, dass die Drüse bei allen Vertebraten mit einem Ausführungsgang in den Schädelraum mündet, können durch allen Fortschritt der Methodik nicht mehr sicherer gestellt werden.   Sie lassen sich zudem in wenig Worten präcis wiedergeben.

Ganz besonders häufig scheint mir in der *Darstellung* des Erreichten gefehlt zu werden.   Viele schreiben nieder bevor sie ein klares Bild von der Sache haben.   Dadurch werden wir mit einem Wust von Detailschilderungen belastet, der völlig überflüssig wird in dem Momente, wo ein Verhältniss klar erkannt ist, weil es sich eben dann präcis schildern lässt.   Oft genug — ich erinnere hier z. B. an Bumms grosses Werk über den Hörnerven — schildert der Verfasser nur die Schnittbilder und wagt nicht einmal eine Synthese zu geben.   Solche Schilderung ist fast

werthlos wenn sie unvollständig ist und von eingeschränktem Werthe, wenn dem Leser eine Synthese zugemuthet wird, vor welcher der Autor zurückwich. Die *Schilderung von Schnittbildern sollte ueberhaupt nur neben dem Texte stattfinden,* wie etwa die Beigabe von Curven zu physiologischen Arbeiten, die Hauptsache bleibt die *Synthese, welche nur der Autor leisten kann.* Und kann er sie noch nicht leisten, so wird er, wenn es sich nicht um ganz wichtige Dinge handelt, immer besser mit der Publication warten bis dahin wo er seine Bilder verstanden hat. Ich will ausdrücklich constatiren, dass HALLER, wo immer es ihm möglich war, Schlüsse zog und dass das Vorstehende viel mehr auf eine grosse Anzahl anderer Arbeiten als auf die seine passt. Als Verfasser des Jahresberichtes der Hirnanatomie seit 1885 weiss ich mit welcher Unsumme unverwerthbarer Detailschilderung wir alljährlich überschüttet werden und desshalb durfte dieser Punkt nicht unerwähnt bleiben.

Vielfach wird auch in darin gefehlt, dass von vorneherein die Aufgabe zu weit gesteckt wird. Was wir brauchen ist die absolut sichere Kenntniss einzelner Verhältnisse. Erst dann, wenn sie da ist, wird man zum Weiteren schreiten können. Namentlich Anfänger sollten das berücksichtigen. Dann würden uns auch die Schilderungen ganzer Gehirne von dem oder jenem Thiere, die oft nichts anderes als fast unbrauchbare Stückwerke sind erspart werden. Es sind viele und grosse Aufgaben noch zu lösen und Meister wird man nur durch Beschränkung.

Wenn ein Forscher schliesslich zu solchem Abschlusse kommt, dass er etwas zu sagen hat, so muss er sich in der Weise wie er es sagt der Grundanschauung fügen, dass er für Solche schreibt, die ihn studiren und verstehen wollen. Je weiter er dabei den Kreis seiner Leser sich denkt, um so klarer und einfacher wird sein Stil ausfallen. Hier kann ich nun in der That dem verehrten Autor den Vorwurf nicht ersparen, dass er wenig gethan hat um seinen Lesern den schwierigen Stoff näher zu bringen. Am schlimmsten geht er mit der Nomenklatur um. Man verfolgt z. B. einen Faserzug unter den verschiedensten Namen hirnwärts, um schliesslich zu erfahren, dass er das ist, was bisher allgemein als descendirende Wurzel irgend eines Nerven bezeichnet wurde. Man findet dann, wenn man etwa über diesen Nerven sich orientiren wollte, die Bruchstücke seiner Be-

schreibung an den mannigfachsten Orten und, was das schlimmste
ist, unter den mannigfachsten Namen. Vielleicht helfen da dem
Lesenden die zahlreichen Abbildungen. Hier aber begegnen wir
bei HALLER, wie heute ziemlich überall, einer neuen Rücksicht-
losigkeit gegen den Leser. Die Tafeln enthalten zahllose Buch-
staben und Abkürzungen. Kaum eine ist direct erkennbar in
ihrer Bedeutung und um einen einzigen Schnitt zu verstehen,
muss man unzählige Mal ein zudem nicht einmal gut geordnetes
Verzeichniss der Abreviaturen einsehen. Es is gar nicht abzu-
sehen warum man auf Tafelbildungen nicht auch wie auf ande-
ren entweder sofort durchsichtige Abkürzungen oder die volle
Namengebung einschreiben sollte. Die Annahme dieses Vor-
schlages würde uns Allen vielfache Erleichterungen bringen.

Schliesslich darf man vielleicht auch dem Autor den Wunsch
aussprechen, dass er am Schlusse seiner Arbeit, wo immer mög-
lich dem Leser eine orientirende Uebersicht über das Erreichte
gebe. Es ist das,, wie ich am eigenen Leibe erfahren habe, oft
ein Prüfstein daraufhin ob überhaupt ein gewisser Abschluss er-
reicht ist. Was man sich selbst noch nicht resumiren kann, ist
zumeist noch unfertig. Geben Sie, sagte einst Waldeyer zu
einem jungen Gelehrten, nie eine Arbeit zum Druck, die nicht
so beschaffen wäre, dass mit den augenblicklichen Mitteln Nie-
mand weiter kommen kann.

Nachdem nun so vielerlei besprochen wurde, das nicht direct
durch HALLERS Darstellung eingegeben ist, das vielmehr nur an-
lässlich dieser sonst so wichtigen Publication zur Erörterung
kam, wird es wichtig sein nun auch auf die Resultate der im
Titel genannten Arbeit einzugehen. Jede Seite zeugt von enor-
mem Fleisse und von grosser Gewissenhaftigkeit in der Schilde-
rung des Gesehenen. HALLERS Buch erinnerte den Lesenden oft
an die berühmte Schilderung des Karpfengehirnes von MAYSER,
welche ganz ebenso reich an Einzelnfacten und originaler Arbeit
und ebenso schwer zu lesen ist.

Wenn ich versuche von dem sachlichen Inhalte eine Ueber-
sicht zu geben so weit das ohne Abbildungen möglich ist, so
werde ich mich thunlichst der Kritik enthalten. Dazu wird sich
später Gelegenheit finden. Bei dieser kurzen Darstellung muss
ich ganz die zahlreichen Angaben über die Nervenzellen und den
Verlauf ihrer einzelnen Fortsätze, die Betrachtungen über die

Ursprungsweise der Nerven aus Axencylindern oder aus Netz-
fortsätzen oder aus einem Nervennetz u. s. w. übergehen, weil
dieses Referat sonst allzu umfangreich würde. Aber gleich Ein-
gangs will ich auf diesen Theil der Abhandlung ausdrücklich hin-
gewiesen haben.

Dicht frontal von dem Abgange des Oculomotorius legt sich
bei den Embryonen schon sehr früh ·eine Querfalte, der Sulcus
interencephalicus KUPPFER's, zuerst beschrieben von *Burkhart*,
an. Er trennt den Hirntheil, welcher metamere Nerven abgiebt,
von dem prächordalen Gehirne, welches solche Nerven nicht be-
sitzt. Der erstere wahrt im Wesentlichen überall seine metamere
Form, der letztere geht schon bei den niederen Vertebraten secun-
däre Veränderungen ein, welche durch die Ausbildung des Ge-
ruchs — oder Gehörorgans, durch die Palliumentwicklung u. s. w.
im Wesentlichen bedingt sind.

Die Untersuchung des metameren Abschnittes geht am Bes-
ten von der des Rückenmarkes aus. Hier unterscheidet H. —
wie übrigens schon früher in einer Arbeit, die ihm ganz entgangen
ist, GASKELL — drei Wurzelarten, dorsale ventrale und mediale.
Die letzteren verlaufen aber schon bei den niedersten Vertebraten
mit den anderen beiden Arten, wenigstens im Rückenmarke.
Den Wurzeln entsprechen im Grau dorsale ventrale und laterale
Kerngruppen und diesen Gruppen wieder entsprechend benannte
Stränge des Markweisses. In diesem verlaufen übrigens auch
lange Bahnen aus der Oblongata, so z. B. der Fasc. med. funiculi
lat., welcher zum System des mittleren Vaguskernes gehört. Die
drei Kerngruppen des Grau setzen sich in die Oblongata fort, wo
sie aus bekannten Gründen dann am Boden und an der Seite des
Ventrikels liegen.

Die Postvagelnerven stammen aus der ventralen und der
mittleren Kerngruppe. Der Vagus selbst ist seinen Ursprungs-
verhältnissen nach schon früher von Verf. geschildert worden.
Hier, wo H. ausser der Forelle auch die Selachier berücksichtigst,
bespricht er ihn noch einmal und wir erfahren, dass dieser Nerv
aus einem dorsalen, einem ventralen und einem mittleren Kerne
entspringt, dass auch aus dem Rückenmarke aufsteigende Fasern
— mit der aufsteigenden Quintuswurzel als "dorsolaterales
Längsbündel" zu gutem Theile zusammengefasst, in ihn eingehen.
Der frontalste Ast, welcher den Ramus lateralis abgiebt, stammt,

wie Strong, Herrick u. A. nachgewiesen haben und wie Verf. bestätigt, nicht aus dem Vaguskerne, sondern aus dem Endgebiet der Acustico-Facialisgruppe und aus demjenigen des Trigenimus. Ein Golgipräparat von der jungen Forelle lehrt, dass in den sensiblen Hautästen des Ramus dorsalis Vagi Fasern verlaufen, welche ihre grossen Ursprungszellen im dorsalen Vaguskerne und nicht wie zu erwarten im Vagusganglion haben, dass also hier, ähnlich wie es von Amphioxus bekannt ist, die betreffenden Zellen sich nicht vom Marke zu Ganglien abgelöst haben. Der dorsale Vaguskern spaltet sich frontal in eine laterale und eine mediale Abtheilung. Aus der ersteren, dem "äusseren sensorischen Oblongatagebeite" entwickeln sich aufsteigende Quintusfasern, aus dem "inneren sens. Obl. geb." stammen ausser Vagusfasern vorn zunächst die "mittlere Facialwurzel" und dann der "obere mittlere (innere)" (sic!) Ramus ascendens N. V.

Auf die schwierige Untersuchung der Nerven des Acustico-Facialis-Trigeminuscomplexes hat der Verfasser ganz besondere Mühe verwendet. Es ist aber kaum möglich aus der Unsumme von beschreibendem Detail und vor Allem aus der ermüdenden Beschreibung der Schnittbilder, zu ermitteln was als gesicherter Besitz anzunehmen ist, was dem Verf. selbst geschlossen darstellbar erscheint. Gerade hier vermisst man auch mit besonderem Bedauern, dass die Degenerationsmethode nicht einmal versucht worden ist, die allein imstande sein dürfte das Gewirr der auf- und absteigenden Bahnen, die mit den verschiedensten Hirnnerven eintreten, zu entwirren.

Aus dem Ganglion Vestibuli — nicht oticum wie Verf. schreibt, der Name oticum ist hier im periph. Ganglion N. V. vergeben — tritt der Acusticus als einheitlicher Stamm in die Oblongata. Hier splittert er auf, wie ein aufgetauchter Pinsel. Es entstehen directe Endäste, sowie auf- und absteigende Züge, welche den Trigeminuszügen oft untrennbar nahe liegen. Ein guter Theil des Nerven endet übrigens nicht in der Oblongata, sondern entspringt da, wesentlich aus dem seitl. Oblongatafeld und aus der Gegend unter der Cerebellarleiste, vielleicht auch aus einem Kerne grosser Ganglienzellen, welcher mitten in den austretenden Fasern des Hirnnerven liegt. Dass die Cerebellarleiste wirklich einen der Kleinhirnrinde ähnlichen Bau und Zellen etwa von dem Type der Purkin'jeschen Zellen hat, das wird hier zum

erstenmale nachgewiesen, ebenso, dass der Axencylinder dieser Zellen zumeist direct in den Acusticus zieht. Der Facialis besitzt eine sensorische Wurzel aus dem inneren Oblongatagebiete und eine motorische aus ventraleren Abschnitten. Bei Scyllium liegen beide übereinander und gehen in einen einheitlichen Stamm, bei Salmo hat sich ein Theil des mot. Facialis abgetrennt um weiter vorn mit dem Trigeminus auszutreten. Das innere Oblongatafeld für den Facialis ist die directe Fortsetzung des caudaler für die Aufnahme van Vagusfasern bestimmten Gebietes. Sein Zellaufbau wird wieder genau geschildert. Zum sensiblen Facialis stossen auch aufsteigende Fasern aus dem "dorsolateralen Längsbündel" — in Bestätigung der Angaben von STRONG. Anlässlich der Besprechung des mot. Facialiskernes im ventralen Oblongataabschnitte erfahren wir auch Näheres über die Zellen der Substantia reticularis und das oft recht complicirte Verhalten ihrer Axencylinder.

Was ich von den sehr ausführlich geschilderten Ursprungsverhältnissen des Trigeminus verstanden habe, ist etwa Folgendes: Der Trigeminus bezieht wie alle anderen sens. Hirnnerven Fasern aus dem Cerebellum, deren längst bekannter Zug hier neu als "dorsale Kleinhirnbahn" benannt wird. Er stammt mit seiner Hauptmasse aus dem lateralen Oblongatafelde und den dort aufsteigenden "dorsolateralen Bündeln" — bisher wurde dieser Antheil allgemein "absteigende Bahn" genannt. Mit einem anderen Antheil entwickelt er sich aus dem medialen Oblongatafelde. Dieses hypertrophirt bei den Cyprinoiden zu dem Lobus impar, welchem nach HALLER auch Facialisfasern entstammen. Nur ein Theil des Quintus entspringt dort, ein anderer endet, indem er aus Zellen des Ganglion Gasseri stammt. Die motorischen Ursprungsverhältnisse lehnen sich direct an diejenigen des Facialis an. Ein guter Theil der Fasern scheint jenem grosszelligen Kerne zu entstammen, welcher mitten in den Austritt seiner und der Acusticusfasern gelagert ist. Es giebt dann noch eine feinfaserige, gekniete mot. Wurzel aus einem eigenen kleinen Kerne in der Höhe der Collossalzellen, welchen die MAUTHNER'schen Fasern entstammen. Diese Zellen selbst sind sehr eingehend untersucht worden, ohne dass man eigentlich über die Auffassung zu der Verf. von ihnen gekommen ist, ins Klare kommt. In der Trigeminusgegend wird auch eine commissurale

Kleinhirnhinterstrangahn beschrieben, deren Verlauf mir leider auch nicht ganz klar geworden ist.

Der Abducens entspringt aus dem ventralen Kerngebiete, wo ein frontaler Kern dem Ursprungbezirk des ersten, ein caudalerer dem des zweiten Trigeminusastes entspringt. Auch der Trochlearis hat zwei Kerne, einen caudalen, welcher direct an das frontale Ende des mot. Trigeminuskerns stösst und einen frontaleren, rundlichen und sehr eigenartig gebauten, welcher in der Tiefe des caudalen Mittelhirnes, lateral von der Valvula cerebelli liegen soll. Die neben der Wurzelkreuzung liegende feinfaserige Decussation bezeichnet H. als "cerebrale Trigeminuscommissur." Die Beziehungen des runden Trochleariskernes zu der Mittelhirnfaserung, ebenso wie diejenigen der verschiedenen Kreuzungen neben der Trochleariskreuzung werden wohl erst durch Degenerationsversuche klar gestellt werden. Des. Verf. Darstellung klärt sie trotz vieler Detailschilderung keineswegs. Ein Theil des Trochlearis soll aus dem Cerebellum stammen. HALLER betrachtet den ganzen Trochlearis als ein abgetrenntes Stück des mot. Trigeminus, dem ein besonders grosser Kleinhirnantheil beigegeben ist. Der Oculomotorius hat einen dorsalen und einen ventralen Kern, ausserdem sollen mit ihm Fasern aus einem peripheren Ganglion eintreten, die erst im Torus semicircularis enden. Er bezieht auch aus dem Kleinhirn einen Zuwachs. Die Endigung des lateralen Längsbündels im Torus, auf deren Bedeutung als secundäre Acusticusbahn WALLENBERG durch schöne Degenerationsversuche hingewiesen hat, wird bestätigt. Dass daselbst auch Fasern aus dem Mittelhirndache enden, wie Verf. annimmt, das lässt sich nach einfachen Schnittbildern unmöglich aussagen.

In der frontalen Verlängerung des ventralen Oculomotoriuskernes liegt ein grosser Kern, welchem die Fasern für das dorsale Längsbündel entstammen. Seine Zellen entsenden öfter zwei Fortsätze, von denen der eine frontal — der andere caudalwärts in dem Bündel einherzieht. REF. glaubt, dass der frontal gerichtete Fortzatz den Kernursprung der Commissura porterior darstellt. S. dessen Unters. über die vergl. Anatomie des Gehirnes. H. IV.

Eine langgestreckte Zellgruppe am medio-ventralen Rande des Tectumgrau wird als Nucleus corticalis bezeichnet und die aus ihr entspringenden Fasern, die wohl identisch sind, mit dem

was man bei den meisten Wirbelthieren längst als "gekreuzte
Bahn aus dem tiefen Mark" bezeichnet wieder einmal neu be-
nannt, diesmal als "gekreuzte und ungekreuzte rostro-ventrale
Associationsbahn des Tectum opticum." Das Bündel liegt be-
kanntlich ventral von dem Dorsalen Längsbündel in der Oblon-
gata. Ventral von ihm findet man von der hinteren Trigeminus-
gegend aufwärts dicht an der Basis ein Längsbündel, welches
aufwärts bis in das gekreuzte Mittelhirndach z. Th. auch in den
ventralen Thalamus verfolgt werden konnte. Es wird als "ven-
trale Associationsbahn" bezeichnet. Beide eben genannten Bün-
del sollen zu Zellen des ventro. mot. Kernes in Beziehung treten.
Zu den Zellen des dors. mot. Kernes lässt Verfasser die gekreuz-
ten und ungekreuzten Theile der lateralen Abtheilung des tiefen
Markes treten. Hier handelt es sich abgesehen von der mir sehr
zweifelhaften Endigung, im Wesentlichen um längst bekannte
Dinge, die man unter den neuen Namen und der complicirten
Darstellung nicht leicht wieder erkennt. Ganz unzureichend
wird die Schnittmethode, auch bei ganz langen Bahnen. Verf.
unterscheidet : Aus dem Torus 2 Bahnen, die rückwärts ziehen,
eine kürzere, welche als Associationsbahn d. Tor. bezeichnet wird
und eine längere, welche wahrscheinlich mit des Ref. seitl.
Längsbündel identisch ist. Verf. nennt sie "innere Lateralbahn."
Sie ist nur bei den Knochenfischen von der "äusseren Lateral-
bahn" gesondert, welchen Namen H., seine eigene Nomenklatur
unberücksichtigend dem Complexe der auf- und absteigenden
Wurzelfasern der metameren Nerven giebt. Auch eine "ventro-
laterale Längsbahn" wird unterschieden, welche Fasern aus dem
Rückenmarke und der Vagusgegend zum Oblongatagrau höherer
Regionen führt, aber auch auf- und absteigende Abducenswurzeln
enthalten soll. Zu all diesen Fasern kommt noch ein nicht einheit-
licher Complex, das "gemischte Längssystem des metameren Ge-
hirnes. Fasern, die zwischen Thalamus, Mittelhern und Oblon-
gata verlaufen, auch Kleinhirnelemente sind darunter.

Von den Kleinhirnarmen dringt der obere vordere, aus dem
caudalen Abschnitt und aus der Valvula mit zum Theil gekreuz-
ten Fäserchen stammend, in die vordere und laterale Rinde des
Tectum opticum und wird desshalb — ohne Rücksicht darauf, dass
gerade von dort so mannigfache Fasersysteme entspringen, auch
ohne Rücksicht auf die Verhältnisse bei anderen Vertebraten als

"Kleinhirn-Opticusverbindung" bezeichnet. Der untere vordere
Bindearm aus dem lateral-ventralen Abschnitt soll die Endgebiete
des basalen Vorderhirnbündels im Zwischenhirn mit dem Klein-
hirn in Verbindung setzen und schliesslich wird, wie auch von
den anderen Autoren der gekreuzte Bindearm beschrieben, der
wesentlich aus der Valvula stammend auch im Zwischenhirn en-
det. Ein diffuses Fasersystem zur Oblongata wird als Vorläufer
des Pons bezeichnet, obgleich dem Verf. nicht unbekannt sein
kann, dass die Ponsfaserung erst durch Auftreten der Rinde, aus
der sie stammt, gebildet wird. Sie ist also bei den höheren Verte-
braten etwas ganz neues. Wenn noch die feine Querfaserung
zwischen den Cerebellarleisten und das bekannte Kleinhirnasso-
ciationssystem genannt wird, ist im Wesentlichen erschöpft, was
von der Kleinhirnfaserung berichtet wird.

Aus dem Mittelhirndache ziehen, abgesehen von den Opti-
cusfasern, thalamuswärts noch eine gekreuzte Opticus-Zwischen-
hirnbahn, wahrscheinlich identisch mit dem, was bisher Decus-
satio transversa hiess, und zwei ungekreuzt bleibende "Associa-
tionssysteme für die Lobi inferiores." Die Beschreibung des
Opticus ist mir nicht klar geworden. Dass sein medianstes Bün-
del nicht mit der von mir beschriebenen Bahn aus dem Mittel-
hirndache zu den Ganglia habenulae identisch ist, wie behauptet
wird, ist mir sicher. Nur sehr kurz wird der trefflichen Unter-
suchungen von Krause über den Opticus gedacht. Merkwür-
diger Weise hat der Verfasser sich nicht veranlasst gesehen an
der Hand dieser auf Degenerationen beruhenden Studien seine
eigenen Angaben noch einmal zu prüfen. Er würde dann min-
destens zu der Klarheit gelangt sein, die wir auf diesem Gebiete
schon seit Belloncis Arbeiten besitzen. Wieder einmal wird
auch die Kreuzung des tiefen Markes in dem Lobusdache als
Theil der Comissura posterior beschrieben. Die seit 10 Jahren
bekannte Trennung der Faserarten ist von allen anderen Autoren
acceptirt.

Ueber das Zwischenhirn der Selachier erfahren wir wenig,
was über das Bekannte hinausginge, doch vermag Verf. mehr-
fach ältere Angaben zu vervollständigen oder zu corrigiren. So
z. B. wird gezeigt, dass die Mantelbündel nach ihrer Kreuzung
im Lobus inferior enden, z. Th. aber dahin auch ungekreuzte
Fasern abgeben.

Auch was vom Epithalamus der Forelle berichtet wird, bestätigt im Wesentlichen ältere Angaben. Nicht ohne einiges Erstaunen wird man, nachdem man sich durch seitenlange Schilderung des "Thalamustheiles des Zwischenhirnes" durchgearbeitet hat, entdecken, dass Verf. das Geniculatum laterale meint, dessen Beziehungen zum Opticus öfter beschrieben sind. Dieser Thalamustheil soll sich übrigens auf das Vorderhirn noch ein Stück fortsetzen. Die weitere Darstellung des "dorsalen Thalamusabschnittes" habe ich leider nicht verstanden. Am fronto-lateralen Infundibulumende liegt eine Kernansammlung, die als "Vereinsganglion" beschrieben wird. Hier sollen die Fasern der FRITSCH'schen Commissur enden. Innerhalb desselben liegt ein Antheil der nur die Nuclei rotundi verbindet. Wie das ohne Degenerationsversuche zu entscheiden ist, weiss ich nicht. In dem "Vereinsganglion" und in seiner Nähe enden alle Fasern, welche in das ventrale Zwischenhirn gelangen. Die lateralen Wände des Infundibulum gehen caudal in das Tuberculum impar inferius über. In ihm verläuft die Commissura infundibularis.

Die Endigung des infundibularen Abschnitte des bas. Vorderhirnbündels in einem eigenen grosszelligen Kerne, dem "ventralen Ganglion der Pars infundibularis" wird beschrieben. Der ventrale Abschnitt des Geniculatum wird neu als "Nucleus opticus lateralis" benannt. Auch sein Stil ist beobachtet —"caudale Verbindungsbahn des Nucleus opticus lateralis."

Die Hirnrinde lässt der Verf. mit STUDNICKA, BURCKARDT u. A. sich entwickeln aus dem Palliumgebiet, welches bei den Selachiern nachweisbar ist. Das epitheliale Pallium der Teleostier kann mit diesem Selachierpallium nicht identificirt werden. Es ist eine späte Bildung, welche nur den ependymalen Theil des Selachierpalliums enthält.

Das Mantelbündel der Selachier will der Verf. bei Salmo in einem medialen Abschnitt des basalen Vorderhirnbündels finden, der mit gleichseitigen und gekreuzten Fasern im Vereinsganglion des Infundibulum enden soll. Nur auf diesen keineswegs sicher zu begründenden Befund hin nimmt der Verf. an, dass im Striatum der Teleostier ein Theil des bei Selachiern in dem Mantel liegenden Gebietes zu finden sei! Dass also bei den Knochenfischen der nervöse Pallialtheil innerhalb des Striatum zurückgehalten worden sei, welches keineswegs dem Striatum der übrigen Verte-

braten homologisirt werden dürfe. Wir erhalten dann eine sehr eingehende Beschreibung der Ganglienzellen in dem massiven Vorderhirn der Teleostier und eine Schilderung der Fasern, die sich im Wesentlichen mit dem Bekannten deckt.

Das Werk endet mit einem Excurse über die muthmassliche Phylogenie des Vertebratengehirnes. Es fällt auf, dass dem Verfasser, welcher im Allgemeinen die Litteratur gut berücksichtigt, die Arbeiten amerikanischer Autoren ganz entgangen sind. Vornehmlich die Arbeiten besonders von STRONG hätte ihm manche Verhältnisse, so die aufsteigenden Wurzeln z. B. klarer erscheinen lassen, auch die Arbeiten der beiden HERRICK hätten durchaus verdient angezogen zu werden.

The Brain of Ornithorhynchus.[1]

This paper, preliminary to a more extensive contribution, was called forth by a memoir of Professor Ziehen.[2] Dr. Smith claims that the differences between his results and those of Prof. Ziehen are due chiefly to faulty preservation of the latter's material. Without entering into the merits of this controversy, we would merely call attention to the three figures of the brain of Ornithorhynchus given in this paper as the clearest and most generally useful of any thus far published. Dr. Smith's paper concludes with the following summary.

It is now possible to state in a concise manner the most 'salient features of the brain in the Monotremata, taking into consideration not only the features discussed in this communication, but in addition those characters which I have previously described.

We may consider these features under two headings :—(A) in comparison with other mammals, and (B) in comparison with reptiles.

A. 1. In comparison with the Marsupialia, Insectivora, Cheiroptera, Edentata, and Rodentia, we must admit that the Monotremata have a large cerebral cortex, the size of which greatly exceeds that of many other mammals.

contrast to that which is common to the whole of the Metatheria and

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[1] Further Observations on the Anatomy of the Brain in the Monotremata. By G. ELLIOT SMITH. *Jour. of Anatomy and Physiology*, XXXIII, 1899, pp. 309–342.

[2] Das Centralnervensystem der Monotremen und Marsupialier. I. Thiel. akr. Anat. *Semon's Zool. Forschungsreisen*, iii. *Jenaische Denkschrift.*, vi, 1897.

2. If we admit that the number of fibers issuing from the pallium affords an index of the quality or degree of histological perfection of this cortical area, it is obvious that in the Monotremata the cortex must be of poor quality in comparison with that of all other mammals, because the large cortex gives rise to a very small internal capsule, *crus cerebri*, and pyramidal tract.

3. These observations point to the conclusion that, in order to meet the demands which its zoological position and mode of life imposes upon it, the Monotreme develops a cortex which rapidly increases in quantity, instead of becoming more highly elaborated.

4. This is especially so in the case of *Echidna*, which, for an animal of its size and lowly status, has an enormous pallium, which exhibits numerous sulci. But it is a very significant fact that the arrangement of these sulci does *not* conform to the plan which, with relatively slight variations, prevails throughout the large group of Meta- and Eutheria.

5. The features of the pyriform lobe, the *tractus olfactorius*, and the *fissura rhinalis* are quite distinctive.

6. The fact that the supra- and precommissural parts of the hippocampal arc (especially in *Ornithorhynchus*) are larger and better developed than the descending part of the arc, is distinctively Prototherian.

7. The absence of a projecting fimbria and the attachment of the choroidal fold at the margin of the fascia dentata are unique features.

8. The round or oval shape of the *commissura dorsalis* (vel *hippocampi*) in sagittal section is characteristic of this order.

9. The attachment of the roof of the fore-brain to the *anterior* lip of the thickened upper extremity of the *lamina terminalis* so as to form a supracommissural diverticulum of the third ventricle (*recessus superior*), is a significant feature which *may* be shared by some marsupials (*Didelphys? Perameles? Notoryctes? Phascolarctos?*), but is certainly not common to all the marsupials.

10. In comparison with the size of the cerebral cortex, the *pons Varolii* is small.

11. The lateral parts of the cerebellum are small, and those regions of the cerebellum which in the Eutheria show a progressive increase in size and complexity are peculiar in the Monotremes, by reason of their diminutive proportions and the paucity of fissures.

12. The plan of the cerebellum in the Monotremes is in marked Eutheria (*vide* "The Brain in Edentata," *Trans. Linn. Society*, London, 1898).

13.   There is the closest agreement between the structure of the cerebellum in *Echidna* and *Ornithorhynchus*.   The fact that in the former the floccular lobe is sessile, and in the latter pedunculated and encapsuled in a special bony case, is of little systematic significance, because such contrasts are not uncommon elsewhere among members of the same family.   [I have recently recorded an example of this in the family of Anteaters, "The Brain in the Edentata," *loc. cit.*]

14.   The absence of a projecting *corpus geniculatum mediale*, the slight prominence of the *testes*, the (possible ?) diminutive proportions of the lateral acoustic tubercule, and the fact that the *corpus trapezoideum* is not a definite and compact bundle, all seem to point to a poorly developed central (or cortical) auditory path in the Monotremata in comparison with other mammals.

15.   It is impossible to say definitely whether the habits of life of the animals, and the resultant diminution of visual acuity, are sufficient to account for the dwindling of the *corpus geniculatum laterale* and the flatness of the *nates*.

We may safely say that every region of the brain in the Montremata shows some peculiarity of structure which enables the observer to distinguish it from the corresponding part of any other mammal, and which indicates the wide gap which separates the Prototheria from the Meta- and Eutheria.

B. 1.   The presence of a definite pallium, which produces an internal capsule, crus cerebri, and pyramidal tract, and the existence of a pons, indicate an advance beyond the Sauropsidan to a distinctly mammalian status.

2.   The features A. 6, 8, and 9, mentioned above, are distinctly Saurian, but the degree of elaboration of the hippocampal formation is characteristically mammalian.

3.   The dwindling of the lateral parts of the cerebellum in the Monotremata is a slight approximation to the Sauropsidian condition, although the cerebellum in Monotremes is very much closer to the mammalian than it is to the Saurian type.

4.   The diminutive size of the geniculate bodies and the smallness of the *testes* in the Monotremata probably indicate that the latter have not yet completely attained to the fully-developed mammalian position, but retain some suggestions of the Saurian status.

5.   The olfactory bulb and nerve in *Ornithorhynchus* afford a peculiar instance of the persistence of the Saurian type.

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