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

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# The Cranial and First Spinal Nerves of Menidia. A Contribution upon the Nerve Components of the Bony Fishes . .

With Seven Plates

By

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THIS STUDY WAS AWARDED THE CARTWRIGHT PRIZE FOR 1899 BY THE ALUMNI ASSOCIATION OF THE COLLEGE OF PHYSICIANS AND SURGEONS, COLUMBIA UNIVERSITY, NEW YORK.

SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN THE FACULTY OF PURE SCIENCE, COLUMBIA UNIVERSITY, NEW YORK.

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## SECTION I.—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 physi-

ology 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 cataclysmal 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 nervous 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 manifestations 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 consciousness and their physiological concomitants. This department of science from this standpoint should be turned into account toward the solution of problems of

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 ontogenetic 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.

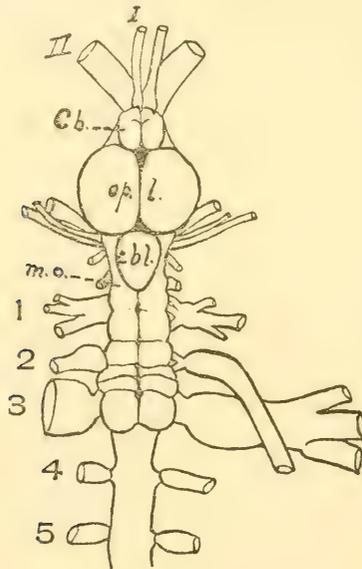
The literature of the cranial nerves is remarkably voluminous, but by far the larger part is either purely descriptive or dominated by crude and false morphological theories. It is only within the present decade that a really practical standpoint has been introduced for the proper morphological treatment 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.



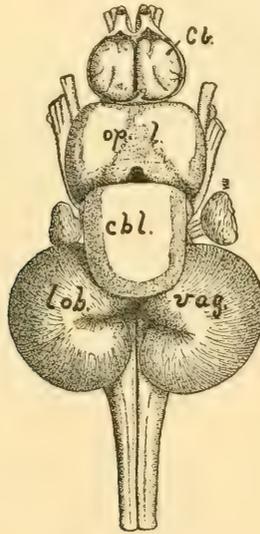
TEXT-FIGURE 1.

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



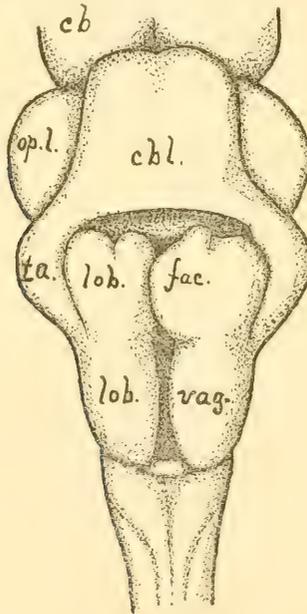
TEXT-FIGURE 2.

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.

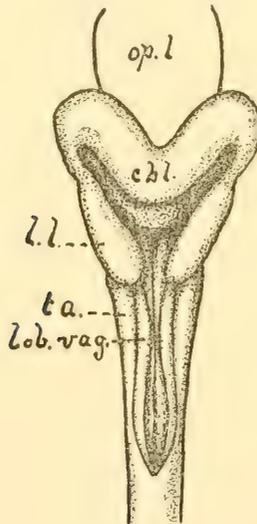
The cat-fishes and some others present an interesting modification of this case. Here the terminal buds which are supplied by the vagus nerve, are reduced in number, but on the head and especially on the barblets, these organs are exceedingly numerous. Accordingly, the branches of the facial nerve which 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 relations 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 distinguish in the cranial nerves three sensory systems of components 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:

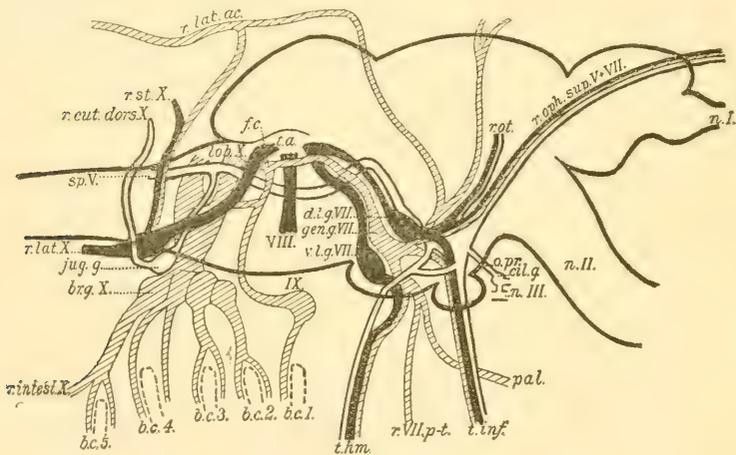
(1). The *general cutaneous system* of the head is clearly the representative of the somatic afferent of the trunk. Its fibres innervate the skin in general, without specialized sense organs and all terminate in the spinal V tract or cells associated with it, these being the continuations into the head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

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 containing 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 impossible to get sufficiently continuous sections for plotting and this method was finally discarded in favor of a modified Weigert method. Nevertheless, several series which were mounted directly after fixation in Hermann's fluid, without further staining, have proved of the greatest service in controlling the others, as the sections, if once obtained, give sharper and clearer pictures of the properties 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, *z. 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 preopercular 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 preopercular bone, which ventrally extends forward to the mandible. 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 hyomandibularis, 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 extreme 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 opercular canal. It immediately sinks down into a groove in the articular bone by which it soon becomes entirely enclosed. 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. mandibularis 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 communicating 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 different 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 described 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. lateralis 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 formalin 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 conspicuous 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 *Pierasfer*, *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

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-k* 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 compared 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  $2\frac{1}{2}$  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 Goronowitsch 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  $\gamma$ " 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  $\gamma$  in *Acipenser* from the lobus vagi ('96, p. 9) and in *Lota* from the lobi vago-glossopharyngeo-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 Trigemini 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 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 communis 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 terminal nucleus for its fibres, the spinal nucleus of the fasciculus communis. This tract is the “Radix bulbo-spynalis 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 variously 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 innervation. 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 visceromotor 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 communis 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 ventro-mesally of the lobus, just laterally of the floor of the ventricle and dorsally of the fasciculus longitudinalis dorsalis. (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

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 spongoplasmic) 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 laterally 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 ambiguus and the cephalic part of the ventral cornu, while the paracentral nucleus and the lateral reticular 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 corresponding 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 throughout 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 paracentral 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 sensations and is very intimately related to the visceromotor 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 visceromotor 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 Solitäräfaszikel 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 vereinzelt Collateralen aus, die sich nach innen zu in einen kleinen, ungenau begrenzten, sehr dicht an der hinteren Commissur 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 visceromotor 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 intracranial 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 *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 visceromotor 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 visceromotor 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 visceromotor 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 visceromotor centres (intermediate zone). The communis system was primarily a viscerosensory

(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 (*r. 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

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 innervated by the third spinal.

On the right side of the specimen upon which this description is based the composition of the brachial plexus is in one respect different. The middle portion of the pectoral 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 separation 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 incomplete fusion of at least two segmental nerves. There are four roots, two dorsal and two ventral, all well developed 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 source 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 interspinous 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 *m. 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 *m. sterno-hyoideus*, which they innervate. No fibres from this nerve enter either of the *m. pharyngo-branchialis* 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.*, pre-zonal, 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.

Subsequently 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 *Ammocoetes*.

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 strengthen 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.

The vagus group, as here defined, contains general cutaneous, acustico-lateralis, communis and visceromotor components. The general cutaneous component is very small, the acustico-lateralis and visceromotor 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 visceromotor fibres; the X nerve proper receives communis, visceromotor 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 branchiomic 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 viscerosensory 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 pre-vagal 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 lateral 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 distinguished from it by their smaller size. There is, moreover, 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 indistinguishably 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 Niedzwietzky ('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 visceromotor in function, though Niedzwietzky 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 visceromotor 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 communis 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 differentiated 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 visceromotor system (nucleus 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 possible explanation of the vagus, I think, is that the branchial 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 connection of the sympathetic with the trigeminus and facialis." The visceromotor fibres of the trunk belong to Langley's type of pre-ganglionic fibres, *i. e.*, they terminate in sympathetic ganglia and reach their appropriate visceral muscles only through the mediation of sympathetic fibres. The same may hold true of the visceromotor 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 branchial musculature. If these latter fibres have been derived from the pre-ganglionic system, they have certainly 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 ramulus 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 exclusively 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. 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. 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 *Silurus* 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 *glossopharyngeus*. There is given off first the minute motor twig for

the second m. levator arcus branchii externus (*z. 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 visceromotor 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

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 doubtless correct, *i. e.*, so far as the proper dorso-lateral musculature 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 "Ringsmuskulatur," 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 controverts the view of Stöhr, Wiedersheim and others that the XI is a descendant of spinal nerves; but regards the vago-accessorius as indigenus to the head, "a primordial cranial nerve which has nothing to do with spinal nerves." This seems probable anatomically but requires embryological confirmation.

## X.—The Ramus Lateralis Vagi.

The ramus lateralis at its ganglion turns abruptly outward 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*.

#### 2.—*The First Lateral Ramulus.*

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. supra-temporalis 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 visceromotor 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 common 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 oesophageal 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 branchiomic 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 commissure. The first and second ramuli each contain communis 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 incomplete 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 intracranial 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 between 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 ventral lateralis root of the facial (shown in Fig. 20 just dorsally of the motor root). But as this could not be verified

in other series of sections it remains an unconfirmed 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 communis* receives 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 separately 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). Nevertheless 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 transverse level, a ventral motor root, widely separated from the others, ventral and dorsal lateralis roots and the communis 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 contact with its fellow of the opposite side and separated from the fourth ventricle by fibres of the fasciculus longitudinalis 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 columns. 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 dorsal 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 pre-auditory 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 Trigeminiis.

The sensory and motor roots of the trigeminiis 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).

### I.—*The Motor Root.*

The motor nucleus of the trigeminiis 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.

*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 Trigemini 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 and 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 abruptly 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 Stan-  
nius, 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 Stan-  
nius, '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 considered 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 running 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 dorsally between the subopercular and interopercular bones to emerge upon the skin dorsad of the latter bone. It distributes to the skin covering the cephalic half of the suboperculum. 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 inner 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 interopercular 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 distributed 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 truncus 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 exclusively 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 superficialis. 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.ó*) 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 mandibulae 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 epiphyal 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 membranous 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 re-joined 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-

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. gly.*), 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, unquestionably 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 preparations (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 visceromotor 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 interesting 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 described as a pure motor nerve, and such it probably is in most vertebrates other than the bony fishes. The muscles 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 teleosts 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 Gasserian 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 peripheral 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 ganglionic 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 operculum 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 proximal 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 externus 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 relations of the facial nerve contribute nothing to the hypothesis that a branchiomere was originally intercalated between the hyoid and the mandible. If such a segment ever existed, it has left as small trace in the adult peripheral 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 Fürbringer ('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 degeneration (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, undoubtedly 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 Fallopiian 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

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 communis 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 maxillary and the mandibular rami of the trigeminus. These fibres come "from the ganglion of the fasciculus communis root" ('95, p. 488), *i. e.*, the geniculate ganglion, as in *Menidia*. Since there are no communis (*i. e.*, pre-spiracular 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 synonymous but apply to a motor post-spiracular nerve related to the anterior face of the hyoid arch, just as the pre-spiracular 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-mandibularis, the r. mandibularis externus and the r. mandibularis 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 vorwärts, gibt gewöhnlich einen oberflächlichen, zum Os quadrato-jugale sich erstreckenden Zweig A [r. mandibularis 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 Unterkiefergelenke zu treten. Hier nimmt er [*i. e.*, the r. mandibularis 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 Unterkieferhälften. Er vertheilt sich, nach eingegangenen Verbindungen mit dem R. maxillaris inferior N. trigemini,—bei *Lophius* findet eine doppelte Verbindung dieser Art Statt [as in *Menidia*]—in den die beiden Unterkieferhälften 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 branchiomic 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. pre-trematicus 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, Tinca, 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 pseudo-branch 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 from 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 pseudobranch Maurer decided is spiracular, has that organ innervated 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 sometimes 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 spiracular 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 embryological 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 arrangement 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 cutaneous 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 lateral ganglion 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.

*I.—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

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 opercular 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 infra-orbital 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 infra-orbital 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 communicating 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 caudad, 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. mandibularis 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 mandibular 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 sections 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  $\delta$  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 infra-orbital 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 extra-cranial 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-fibred 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. r.*). All of these twigs are colored on the plots as if they were general cutaneous, though there is doubtless 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 portion of the trunk and, like that portion, is composed of fine fibres with a few coarse ones intermingled, probably mainly, 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 apparently 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.

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 hyomandibular 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 accessorius, 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 somewhat 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 consists 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 preparations 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 indicate, 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. Stan-  
nius (p. 25) mentions a fine-fibred nerve which separates  
from the trigeminus root intra-cranially and after emerg-  
ing 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 main-  
tained, 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 compre-  
hensive review and critique of the literature of the  
ophthalmicus profundus which need not be again sum-  
marized 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 evo-  
lution of the teleostean specialization. Here the pro-  
fundus root has fused with the V root, but the ganglion  
is widely separated. From the dorsal angle of the gan-  
gion 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 gan-  
gion the radix longa is given off, while the very small r.  
ophthalmicus profundus *sensu stricto* arises from the gan-

gion 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 difficult 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 ganglion 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 predict 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 running 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 cutaneous fibres from the trigeminus I and enters the r. mandibularis 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 homologous with an upper jaw nerve? Allis ('97) finds *communis* 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.

## 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.? tuberculum acusticum	—	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.  truncus infra-orbitalis—r. mandib. V, motor component.
II.—Motor	motor V nuc. and fasc. long. dors.?	—	

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 vestigial 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 relations of the ganglia and the larger sympathetic nerves are indicated upon Fig. 4, and will be here briefly reviewed, though they deviate but little from Belone and other well-known examples, for which, compare the descriptions 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 cephalad than the spinal ganglion and from its tip the sympathetic 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 *coeliacum* (*g. cal.*) 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 coeliac ganglion (Stannius' 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 foramen 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 communicate with either. The trunk now fuses with the IX root in which it can be separately followed to the IX ganglion. Just before reaching the latter it withdraws from the IX root, but follows along its dorsal surface as a separate 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 extracranial 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 extracranial 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 absence 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 fibres 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 its 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

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 brevis 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 inferior 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 passing 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 II.—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 prethmoid 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 supra-orbital 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 cutaneous 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 diverticula 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 conformation 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 disproves 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 *communis* 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 *glossopharyngeus* 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

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 (branchiomic) 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 visceromotor and viscerosensory components. In the head the form which the segmental nerve takes is dominated by the branchiomerism, 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 visceromotor 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 branchiomotor 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 branchiomic 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, visceromotor and viscerosensory 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 viscerosensory fibres in the spinal cord are very obscure. Johnston ('98, p. 597) denies the presence of any viscerosensory 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 viscerosensory 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 branchiomic 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 common 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 branchiomes, where the growth of the operculum has involved the reduction of the ventral cutaneous areas. In the pre-otic branchiomes 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 visceromotor 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 ganglion 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 modification. The root contains no communis fibres, for there is no vertebrate known in which there is a pre-facial fasciculus communis. The post-trematic ramus, *i. e.*, the r. mandibularis V, has visceromotor and general cutaneous fibres, and, as we have just seen, communis fibres belonging 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 replaced 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 represent 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 branchiomic type, this conformity has been so modified in all existing vertebrates as to be unrecognizable. The embryological evidence of pre-oral branchiomes 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 branchiomes 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

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 palingentic 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 visceromotor 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 distribute to the skin and adjacent muscles. The r. lateralis 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 viscero-motor type and come from the nucleus ambiguus and the commissura accessoria of Mauthner. The latter probably 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. accessorius). 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 visceromotor 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 infra-orbitalis 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 operculo-mandibular 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.

*6.—The Abducens.*

The sixth nerve arises by two roots, each coming in part from the abducens nucleus and in part from the fasciculus longitudinalis dorsalis. It is a pure somatic motor nerve and has no connections with any other nerve.

*7.—The Trigemini.*

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 mesocoel 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 viscerosensory 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 viscerosensory 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 visceromotor 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 Fürbringer) 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 hypoglossus 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

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.

## THE LITERATURE CITED.

ALCOCK, R.

- '98. The Peripheral Distribution of the Cranial Nerves of Ammocetes. *Journal of Anatomy and Physiol.*, XXXIII, N. S., XIII, 1.

ALLIS, E. P., JR.

- '89. The Anatomy and Development of the Lateral Line System in *Amia calva*. *Journ. Morph.*, II, 3.
- '95. The Cranial Muscles and Cranial and First Spinal Nerves in *Amia calva*. (Preliminary). *Journ. Morph.*, XI, 2.
- '97. The Cranial Muscles and Cranial and First Spinal Nerves in *Amia calva*. *Journ. Morph.*, XII, 3.
- '98. The Homologies of the Occipital and First Spinal Nerves of *Amia* and Teleosts. *Zoolog. Bulletin*, II, 2.

AMABILINO, R.

- '98. Sui rapporti del ganglio genicolato con la corda del timpano e col facciale. *Ricerche sperimentali. Il Pisani*, XIX, 1-2.

APOLANT, HUGO

- '96. Ueber die Beziehung des Nervus oculomotorius zum Ganglion ciliare. *Arch. mik. Anat.*, XLVII, 4.

AYERS, HOWARD.

- '92. Vertebrate Cephalogenesis. II. A Contribution to the Morphology of the Vertebrate Ear, with a Reconsideration of its Functions. *Journ. Morph.*, VI, 1.

BARKER, LEWELLYS F.

- '97. On Certain Changes in the Cells of the Ventral Horns and of the Nucleus Dorsalis (Clarkii) in Epidemic Cerebro-Spinal Meningitis. *Brit. Med. Jour.*, No. 1930.

BATTEN, F. E.

- '97. The Muscle Spindle under Pathological Conditions. *Brain*, LXXVII-LXXVIII.

BAUDELOT, E.

- '83. *Récherches sur le système nerveux des poissons.* Paris.

BEARD, JOHN.

- '85. The System of Branchial Sense Organs and their Associated Ganglia in Ichthyopsida. A Contribution to the Ancestral History of Vertebrates. *Q. J. M. S.*, XXVI, N. S.

BLAUE, JULIUS.

- '84. Untersuchungen über den Bau der Nasenschleimhaut bei Fischen und Amphibien, namentlich über Endknospen als Endapparate des Nervus olfactorius. *Arch. f. Anat. und Phys., Anat. Abt.*

BONNIER, PIERRE.

- '95. Rapports entre l'appareil ampullaire de l'oreille interne et les centres oculo-moteurs. *Rev. Neurol.*, III, 23.

BÖTTIGER, A.

- '90. Beitrag zur Lehre von den chronischen progressiven Augenmuskellähmungen und zur feineren Hirn-anatomie. *Arch. f. Psychiatrie*, XXI.

BUNKER, F. S.

- '97. On the Structure of the Sense Organs of the Lateral Line of *Ameiurus nebulosus* LeS. *Anat. Anz.*, XIII, 8-9.

CAJAL, S. RAMÓN Y.

- '96. Beitrag zum Studium der Medulla oblongata, des Kleinhirns und des Ursprungs der Gehirnnerven. Trans. by Bresler. *Leipzig, J. A. Barth.*

CLAPP, CORNELIA M.

- '99. The Lateral Line System of *Batrachus tau*. *Journ. of Morphology*, XV, 2. [I am permitted by the kindness of the author to refer to the proof sheets of this work in advance of its publication].

COLE, FRANK J.

- '96. On the Sensory and Ampullary Canals of *Chimæra*. *Anat. Anz.*, XII, p. 172.
- '96 a. On the Cranial Nerves of *Chimæra monstrosa* (Linn.), with a Discussion of the Lateral Line System and of the Morphology of the Chorda Tympani. *Trans. Roy. Soc. Edinburgh*, XXXVIII, Part III (No. 19).
- '98. Reflections on the Cranial Nerves and Sense Organs of Fishes. *Trans. Liverpool Biological Soc.*, XII.
- '98 a. Observations on the Structure and Morphology of the Cranial Nerves and Lateral Sense Organs of Fishes; with Special Reference to the Genus *Gadus*. *Trans. Linn. Soc. London*, 2 Ser., Vol. VII, Part 5.

COLLINGE, WALTER E.

- '94. The Sensory Canal System of Fishes. Part I. Ganoidei. *Q. J. M. S., N. S.*, XXXVI.

- '95. On the Sensory Canal System of Fishes. A. Physostomi. *Proc. Zool. Soc. London*, Apr., 1895.
- '95 a. Some Researches upon the Sensory Canal System of Ganoids. *Proc. Birmingham Nat. Hist. and Philos. Soc.*, Vol. X.
- DEVL.
- '95. Zur vergleichenden Anatomie des Sehnerven. *Prague*.
- DIXON, A. FRANCIS.
- '96. On the Development of the Branches of the Fifth Cranial Nerve in Man. *Trans. Roy. Dublin Soc.*, Ser. 2, VI.
- EDINGER, L.
- '96. Vorlesungen über den Bau der Nervösen Centralorgane des Menschen und der Thiere. 5 Ed., *Leipzig*.
- EMERY, CARLO.
- '80. Le specie del genere *Fierasfer* nel Golfo di Napoli e regioni limitrofe. *Fauna und Flora des Golfes von Neapel. II Monographie*.
- EWART, J. C.
- '89. On the Cranial Nerves of the Elasmobranch Fishes. Prelim. Com. *Proc. Roy. Soc.*, XLV.
- '90. The Cranial Nerves of the Torpedo. Prelim. Note. *Proc. Roy. Soc.*, XLVII.
- '92. Supplementary Note on the Cranial Nerves of Elasmobranchs. *Edinburgh*.
- '93. The Lateral Line Sense Organs of Elasmobranchs. I. The Sensory Canals of *Læmargus*. *Trans. Roy. Soc. Edinburgh*, XXXVII, 1 Pt., Nos. 5-6.
- EWART, J. C. AND COLE, F. J.
- '95. On the Dorsal Branches of the Cranial and Spinal Nerves of Elasmobranchs. *Proc. Roy. Soc. Edinburgh*, XX.
- EWART, J. C. AND MITCHELL, J. C.
- '93. The Lateral Sense Organs of Elasmobranchs. II. The Sensory Canals of the Common Skate (*Raja batis*). *Trans. Roy. Soc. Edinburgh*, XXXVII, Pt. 1, Nos. 5-6.
- FOREL, AUG.
- '91. Ueber das Verhältniss der experimentellen Atrophie und Degenerationsmethode zur Anatomie und Histologie des Centralnervensystems. Ursprung des IX, X und XII Hirnnerven. *Festschr. f. Nägeli und Kölliker, Zurich*.

FRORIEP, A.

- '87. Ueber das Homologon der Chorda tympani bei niederen Wirbelthieren. *Anat. Anz.*, II, p. 486.

FÜRBRINGER, MAX.

- '97. Ueber die spino-occipitalen Nerven der Selachier und Holocephalen und ihre vergleichenden Morphologie. *Festschr. f. Gegenbaur*, Bd. 3.

GARMAN, S.

- '88. On the Lateral Canal System of Selachia and Holocephala. *Bul. Mus. Comp. Zool.*, XVII, 2.

GASKELL, W. H.

- '86. On the Structure, Distribution and Function of the Nerves which Innervate the Visceral and Vascular Systems. *Jour. of Physiol.*, VII.
- '89. On the Relation between the Structure, Function, Distribution and Origin of the Cranial Nerves, together with a Theory of the Origin of the Nervous System of Vertebrata. *Journ. of Physiol.*, X.

GEHUCHTEN, A. VAN.

- '95. La moelle épinière de la truite (*Trutta fario*). *La Cellule*, XI, 1.
- '97. Anatomie du système nerveux de l'homme. 2. Ed., *Louvain*.

GORONOWITSCH, N.

- '88. Das Gehirn und die Cranialnerven von *Acipenser ruthenus*. *Morph. Jahrb.*, XIII.
- '96. Der Trigemino-facialis-Complex von *Lota vulgaris*. *Festschr. f. Gegenbaur*, Bd. III.

GUITEL, F.

- '91. Recherches sur la ligne latérale de la baudroie (*Lophius piscatorius*). *Arch. Zool. Expér.*, 2 Ser., IX.
- '91a. Recherches sur les boutons nerveux bucco-pharyngiens de la baudroie (*Lophius piscatorius*). *Arch. Zool. Expér.*, 2 Ser., IX.

HALLER, B.

- '96. Der Ursprung der Vagusgruppe bei den Teleostiern. *Festschr. f. Gegenbaur*, Bd. III.

HARRISON, R. G.

- '95. Die Entwicklung der unpaaren und paarigen Flossen der Teleostier. *Arch. f. mik. Anat.*, XLVI.

HERRICK, C. JUDSON.

- '94. The Cranial Nerves of *Amblystoma punctatum*. *Journ. Comp. Neurol.*, IV.
- '97. The Cranial Nerve Components of Teleosts. *Anat. Anz.*, XIII, 16.
- '98. Report upon a Series of Experiments with the Weigert Methods with Special Reference for Use in Lower Brain Morphology. *State Hospitals Bull.*, Oct., '97; issued May, '98. Full auto-abstract in *Journ. Comp. Neurol.*, July, '98.
- '98 a. The Cranial Nerves of Bony Fishes. *Jour. Comp. Neurol.*, VIII, 3.

HERRICK, C. L.

- '91. Studies on the Brains of some American Fresh-water Fishes. *Jour. Comp. Neurol.*, I, p. 228-245.

HERTWIG, O.

- '92. Text-book of the Embryology of Man and Mammals. Translated from the third German edition by E. L. Mark. *London*.

HOLM, JOHN F.

- '94. The Development of the Olfactory Organ in the Teleostei. *Morph. Jahrb.*, XXI, 4.

HUBER, G. CARL.

- '97. Lectures on the Sympathetic Nervous System. *Journ. Comp. Neurol.*, VII, 2.

HUBER, G. CARL AND DEWITT, LYDIA M. A.

- '98. A Contribution on the Motor Nerve-Endings and on the Nerve-Endings in the Muscle Spindles. *Journ. Comp. Neurol.*, VII, 3-4.

JACKSON, W. H. AND CLARKE, W. B.

- '76. The Brain and Cranial Nerves of *Echinorhinus spinosus*. *Journ. Anat. and Physiol.*, X.

JENDRÁSSIK, ERNST.

- '96. Allgemeine Betrachtungen über das Wesen und die Function des vegetativen Nervensystems. *Arch. f. path. Anat.*, CXLV, 3.

JOHNSTON, J. B.

- '98. Hind Brain and Cranial Nerves of *Acipenser*. *Anat. Anz.*, XIV, 22-23.

## JULIN, C.

- '87. Recherches sur l'appareil vasculaire et le système nerveux périphérique de l'Ammocètes (*Petromyzon planeri*). *Archives de Biol.*, VII.

## KINGSBURY, B. F.

- '95. On the Brain of *Necturus maculatus*. *Journ. Comp. Neurol.*, V, 3.
- '97. The Structure and Morphology of the Oblongata in Fishes. *Journ. Comp. Neurol.*, VII, 1.

## V. KÖLLIKER, A.

- '94. Ueber die feinere Anatomie und die physiologische Bedeutung des sympathischen Nervensystems. *Ges. Deutscher Naturforscher und Aerzte*, Verh. 1894, Allgemeiner Theil.
- '96. Handbuch der Gewebelehre des Menschen. II Bd., 6. Ed., *Leipzig*.

## V. KUPFFER, C.

- '91. The Development of the Cranial Nerves of Vertebrates. Trans. by O. S. Strong. *Journ. Comp. Neurol.*, I.
- '94. Die Entwicklung des Kopfes von *Ammocètes planeri*. Studien zur vergl. Entw. des Kopfes d. Kranioten. Heft II. *Munich*.
- '96. Entwicklungsgeschichte des Kopfes. *Merkel und Bonnet's Ergebnisse* for 1895, pp. 562-618.

## LANGLEY, J. N.

- '98. On the Union of Cranial Autonomic (Visceral) Fibres with the Nerve Cells of the Superior Cervical Ganglion. *Jour. of Physiol.*, XXIII, 3.

## LANGLEY, J. N. AND ANDERSON.

- '92. The Action of Nicotin on the Ciliary Ganglion and on the Endings of the Third Cranial Nerve. *Jour. of Physiol.*, XIII.

## LEE, F. S.

- '98. The Functions of the Ear and the Lateral Line in Fishes. *Am. Journ. of Physiol.*, I.

## V. LENHOSSÉK, M.

- '94. Das Ganglion geniculi Nervi facialis und seine Verbindungen. In *Beiträge zur Histologie des Nervensystems und der Sinnesorgane*. *Wiesbaden*.

LEYDIG, F.

- '94. Integument und Hautsinnesorgane der Knochenfische. Weitere Beiträge. *Zool. Jhrb. Abt. f. Anat. u. Ontogen.*, VIII, 1.

MADRID-MORENO, J.

- '86. Ueber die morphologische Bedeutung der Endknospen in der Riechschleimhaut der Knochenfische. Bericht von C. Emery. *Biol. Cent.*, VI.

MARSHALL, A. M. AND SPENCER, W. B.

- '81. Observations on the Cranial Nerves of Scyllium. Part I. The Pre-Auditory Nerves. *Q. J. M. S.*, XXI.

MAURER, F.

- '84. Ein Beitrag zur Kenntnis der Pseudobranchien der Knochenfische. *Morph. Jhrb.*, IX.
- '88. Die Kiemen und ihre Gefäße bei anuren und urodelen Amphibien und die Umbildung der beiden ersten Arterienbögen bei Teleostiern. *Morph. Jhrb.*, XIV.

MAYSER, P.

- '81. Vergleichend-anatomische Studien über das Gehirn der Knochenfische mit besonderer Berücksichtigung der Cyprinoiden. *Zeits. f. wiss. Zool.*, XXXVI, 2.

McMURRICH, J. PLAYFAIR.

- '84. The Myology of *Amiurus catus* (L) Gill. *Proc. Canadian Institute*, N. S., II.
- '85. The Cranial Muscles of *Amia calva* L., with a Consideration of the Relations of the Post-occipital and Hypoglossal Nerves in the Various Vertebrate Groups. *Studies from the Biol. Lab., Johns Hopkins Univ.*, III.

MERKEL, FR.

- '80. Ueber die Endigungen der sensiblen Nerven in der Haut der Wirbelthiere. *Rostock*.

MICHEL.

- '94. *Verhandlung des 8. Intern. Ophthalmol. Congr. in Edinburgh.*

MINOT, C. S.

- '92. Human Embryology. *New York*.

MITROPHANOW, P.

- '93. Etude embryogénique sur Sélaciens. *Arch. de Zool. Exp. et Gen.*, 3 Ser., I.

MORRILL, A. D.

- '95. The Pectoral Appendages of *Prionotus* and their Innervation. *Journ. Morphology*, XI.

MÜLLER, FRIEDRICH N.

- '97. Ueber die Entwicklung und morphologische Bedeutung der "Pseudobranchie" und ihre Umgebung bei *Lepidosteus osseus*. *Arch. f. mik. Anat.*, XLIX, 3.

NEAL, H. V.

- '97. The Development of the Hypoglossus Musculature in *Petromyzon* and *Squalus*. *Anat., Anz.*, XIII, 17.
- '98. The Segmentation of the Nervous System in *Squalus acanthias*. A Contribution to the Morphology of the Vertebrate Head. *Bul. Mus. Comp. Zool.*, XXXI, 7.
- '98a. The Problem of the Vertebrate Head. *Journ. Comp. Neurol.*, VIII, 3.

NIEDZVIETZKY, W.

- '97. Zur Frage über Veränderungen im Nervensystem und in inneren Organen nach der Resection des *N. vagus* und des *N. splanchnicus*. *Bull. Soc. Imp. der Nat. de Moscou*, Année, 1896, No. 3.

ONUF, B. AND COLLINS, JOSEPH.

- '98. Experimental Researches on the Localization of the Sympathetic Nerve in the Spinal Cord and Brain, and Contributions to its Physiology. Abstract. *Journ. Nerv. and Ment. Dis.*, XXV, 9.

OSBORN, H. F.

- '88. A Contribution to the Internal Structure of the Amphibian Brain. *Journ. Morph.*, II, 1.

OWEN, R.

- '66. On the Anatomy of Vertebrates. *London*.

PENZO.

- '93. Ueber das Ganglion geniculi und die mit demselben zusammenhängenden Nerven. *Anat. Anz.*, 1893, p. 738.

PINKUS, F.

- '94. Die Hirnnerven des *Protopterus annectens*. *Schwalbe's Morph. Arbeiten*, IV, 2.

PLATT, JULIA B.

- '91. A Contribution to the Morphology of the Vertebrate Head, Based on a Study of *Acanthias vulgaris*. *Journ. Morph.*, V.
- '96. Ontogenetic Differentiation of the Ectoderm in *Necturus*. Study II. On the Development of the Peripheral Nervous System. *Q. J. M. S.*, XXXVIII, 4.

POLLARD, H. B.

- '91. Lateral Line of Siluroids. *Zool. Jhrb.*, V, 2.  
 '95. The Oral Cirri of Siluroids and the Origin of the Head in Vertebrates. *Zool. Jhrb.*, VIII, 3.

RETZIUS, G.

- '81. Das Gehörorgan der Wirbelthiere. *Stockholm.*  
 '94. Ueber das Ganglion ciliare. *Anat. Anz.*, IX.  
 '94a. Ganglion ciliare. *Biol. Unters.*, N. F., VI, 2-3.

ROLLER, C.

- '81. Der centraler Verlauf des N. glossopharyngeus. *Arch. f. mik. Anat.*, XIX.

RUGE, GEORG.

- '97. Ueber das peripherische Gebiet des Nervus facialis bei Wirbelthieren. *Festschr. f. Gegenbaur*, Bd. III.

SANDERS, A.

- '79. Contribution to the Anatomy of the Central Nervous System in Vertebrate Animals. Part I. Ichthyopsida—Teleostei. *Phil. Trans.*, Pt. II, No. 87.

SCHÄFER, E. A.

- '95. The Spinal Cord and Brain. Vol. III, Part I of Quain's Anatomy, tenth edition. *London.*  
 '97. Organs of the Senses. Vol. III, Part III of Quain's Anatomy, tenth edition. *London.*

SCHMIDT, ADOLF.

- '95. Ein Fall vollständiger isolirter Trigemiuslähmung nebst Bemerkungen über den Verlauf der Geschmacksfasern der Chorda tympani und über trophische Störungen. *Dtsch. Z. Nervenhk.*, VI, 5-6.

SCHULZE, F. E.

- '70. Ueber die Sinnesorgane der Seitenlinie bei Fischen und Amphibien. *Arch. f. mik. Anat.*, VI.

SCHWALBE, G.

- '79. Das Ganglion oculomotorii. Ein Beitrag zur vergleichenden Anatomie der Kopfnerven. *Jen. Zeits.*, XIII, 2.

SHORE, THOS. W.

- '88. The Morphology of the Vagus Nerve. *Journ. Anat. and Physiol.*, XXII.  
 '89. On the Minute Anatomy of the Vagus Nerve in Selachians, with Remarks on the Segmental Value of the Cranial Nerves. *Journ. Anat. and Physiol.*, XXIII.

STANNIUS, H.

- '49. Das peripherische Nervensystem der Fische, anatomisch und physiologisch untersucht. *Rostock.*

STRONG, O. S.

- '90. The Structure and Homologies of the Cranial Nerves of the Amphibia as Determined by their Peripheral Distribution and Internal Origin. *Zool. Anz.*, No. 348.
- '92. The Structure and Homologies of the Cranial Nerves of the Amphibia as Determined by their Peripheral Distribution and Internal Origin. *Anat. Anz.* VII, 15.
- '95. The Cranial Nerves of the Amphibia. A Contribution to the Morphology of the Vertebrate Nervous System. *Journ. Morph.*, X, 1.
- '98. Review of Johnston on the Cranial Nerves of the Sturgeon. *Journ. Comp. Neurol.*, VIII, 3.

STUDNICKA, F. K.

- '96. Untersuchungen über den Bau des Sehnerven der Wirbeltiere. *Jen. Zeits.*, XXXI.

THANE, G. D.

- '95. The Nerves. Vol. III, Part II of Quain's Anatomy, tenth edition. *London*.

VETTER, B.

- '74. Untersuchungen zur vergleichenden Anatomie der Kiemen- und Kiefermusculatur der Fische. *Jen. Zeits.*, VII.
- '78. do. Part II. *Jen. Zeits.*, XII.

VOGT AND JUNG.

- '94. *Traité d'anatomie comparée pratique.* *Paris*.

WIEDERSHIEM, R.

- '93. *Grundriss der vergleichenden Anatomie der Wirbeltiere.* 3 Ed. *Jena*.

WILSON, H. V.

- '91. The Embryology of the Sea Bass (*Serranus atrarius*). *Bull. U. S. Fish Com.*, Vol. IX, for 1889, issued 1891. Washington, D. C.

WILSON, H. V. AND MATTOCKS, J. E.

- '97. The Lateral Sensory Anlage in the Salmon. *Anat. Anz.*, XIII, 24.

WRIGHT, R. RAMSAY.

- '84. On the Skin and Cutaneous Sense Organs of *Amiurus*. *Proc. Canadian Institute*, N. S., II.
- '84a. On the Nervous System and Sense Organs of *Amiurus*. *Proc. Canadian Institute*, N. S., II.
- '85. On the Hyomandibular Clefts and Pseudobranchs of *Lepidosteus* and *Amia*. *Journ. Anat. and Physiol.*, XIX.

## 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.  
*CB<sub>3</sub>.*—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 hyoman-dibularis.
- 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.

- 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. íf.*—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. u.*—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.*—utricle.  
*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 between 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. mandibularis 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.

#### PLATE I.

*Figure 1.*—Transection through the body of *Menidia* just in front of the first spinal nerve (685, cf. fig. 3),  $\times 28$ . 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 hyomandibular and palatine nerves (514),  $\times 28$ . The section is slightly oblique and the skin is defective on the dorsal surface.

#### PLATE II.

*Figure 3.*—The cranial and first spinal nerves of *Menidia gracilis*, reconstructed from serial sections and projected upon the sagittal plane,  $\times 23$ . 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 sympathetic 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 communitis 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 before backwards. The scales at the top and bottom of the plate indicate 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 III.

*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,  $\times 47$ . 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 IV.

*Figure 5.* The acustico-lateral system of nerves, sense organs and canals, as seen from the left (apparently right) side,  $\times 23$ . 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 V.

*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,  $\times 66$ . 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,  $\times 33$ . 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 VI.

*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),  $\times 50$ . 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),  $\times 50$ . 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),  $\times 50$ . 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),  $\times 50$ . 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),  $\times 50$ . 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.*—Transsection of the V + VII ganglionic complex of Menidia through the geniculate ganglion (529),  $\times 50$ .

## PLATE VII.

*Figure 22.*—Transsection 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),  $\times 50$ .

*Figure 23.*—Similar transection at the origin of the infra-orbital trunk (485),  $\times 50$ .

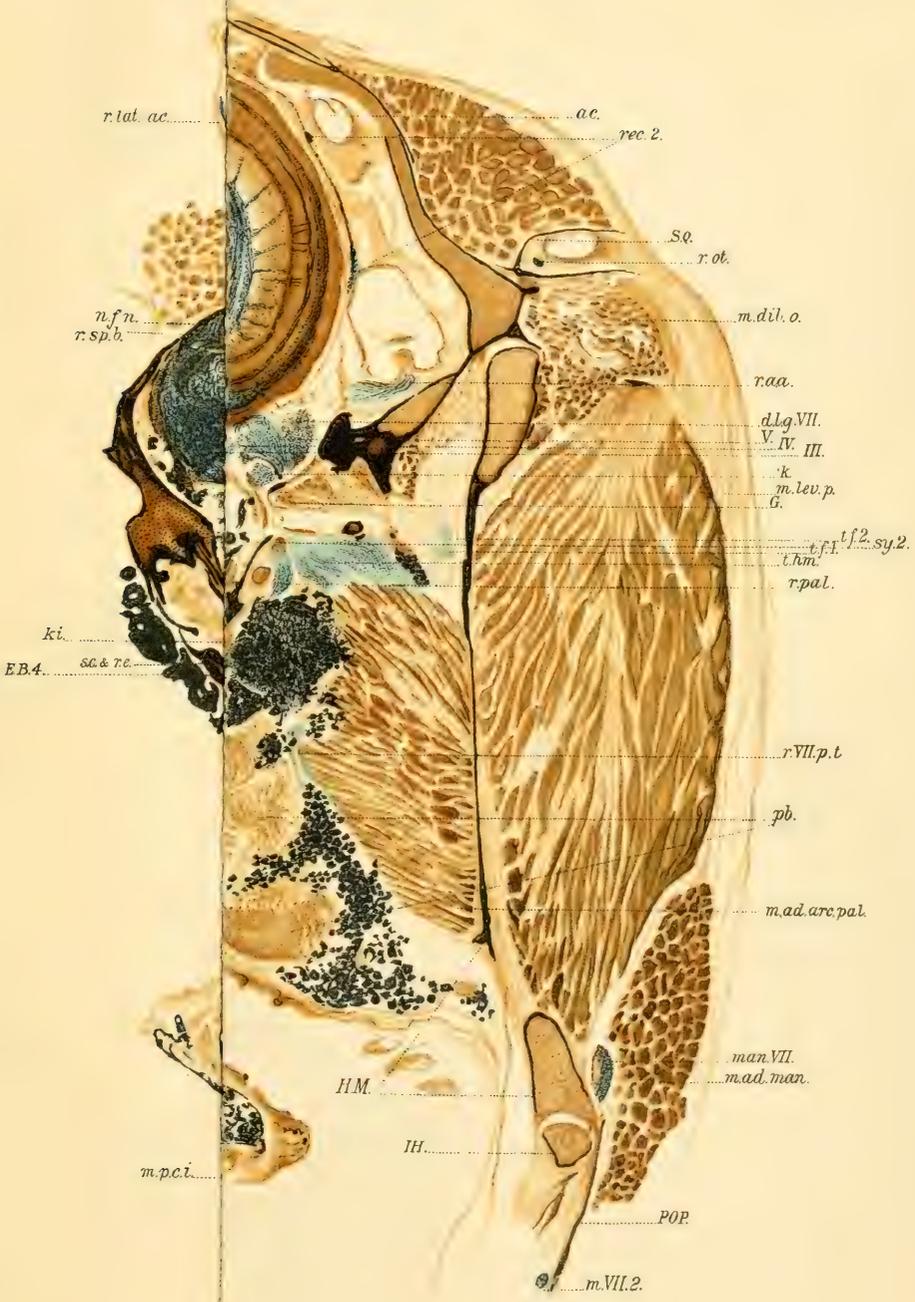
*Figure 24.*—Similar transection farther cephalad, showing the median and lateral lobes of the first ganglion of the sympathetic chain (481),  $\times 50$ .

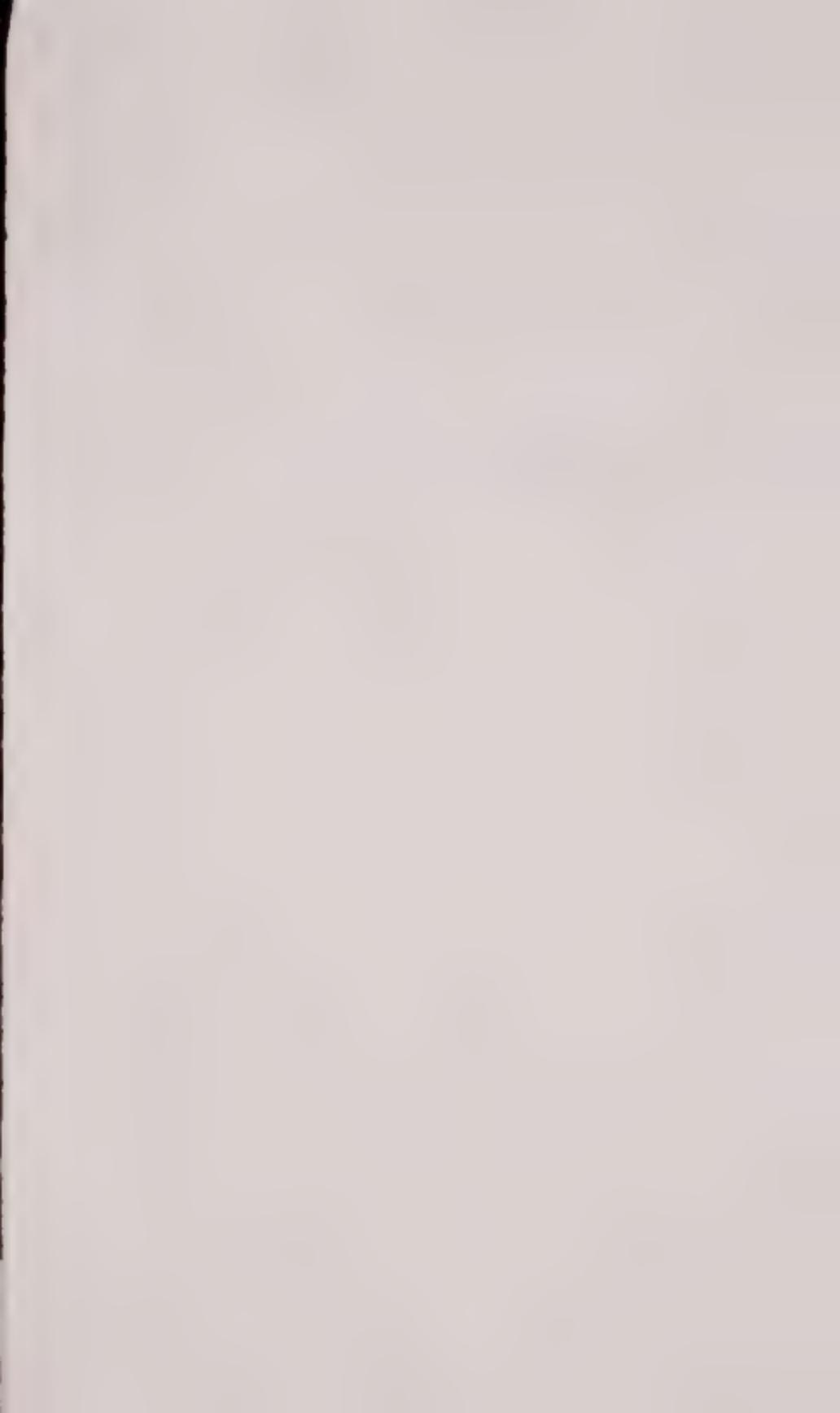
*Figure 25.*—Similar section farther cephalad, showing the origin of the radix longa of the ciliary ganglion and of the r. ophthalmicus profundus (478),  $\times 50$ .

*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,  $\times 50$ . The numbers represent the serial section numbers at the points where they are placed. At the point marked  $\times$  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,  $\times 10$ . See the text, Section 7, IV, 2.

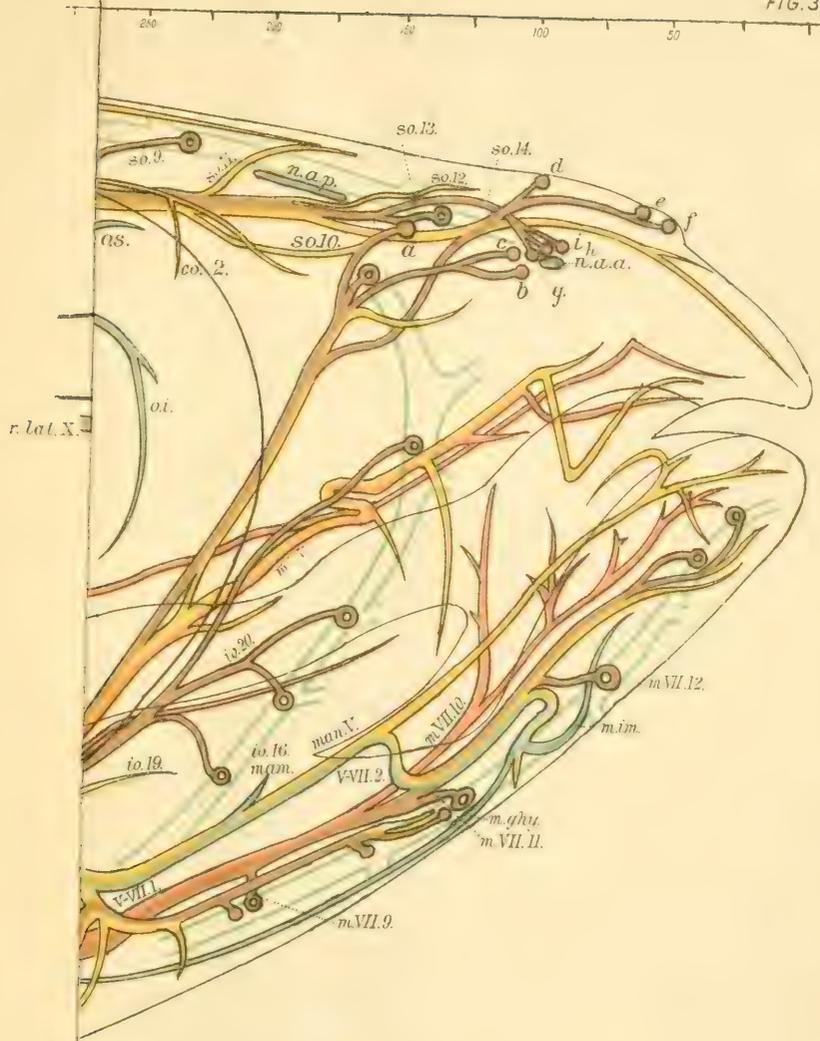












- THE GENERAL CUTANEOUS SYSTEM.
- THE COMMUNIS SYSTEM.
- THE MOTOR SYSTEMS.
- THE ACUSTICO-LATERAL SYSTEM.
- THE SYMPATHETIC SYSTEM.
- THE LATERAL LINE CANALS.

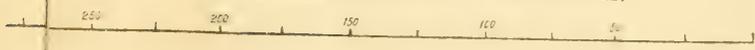
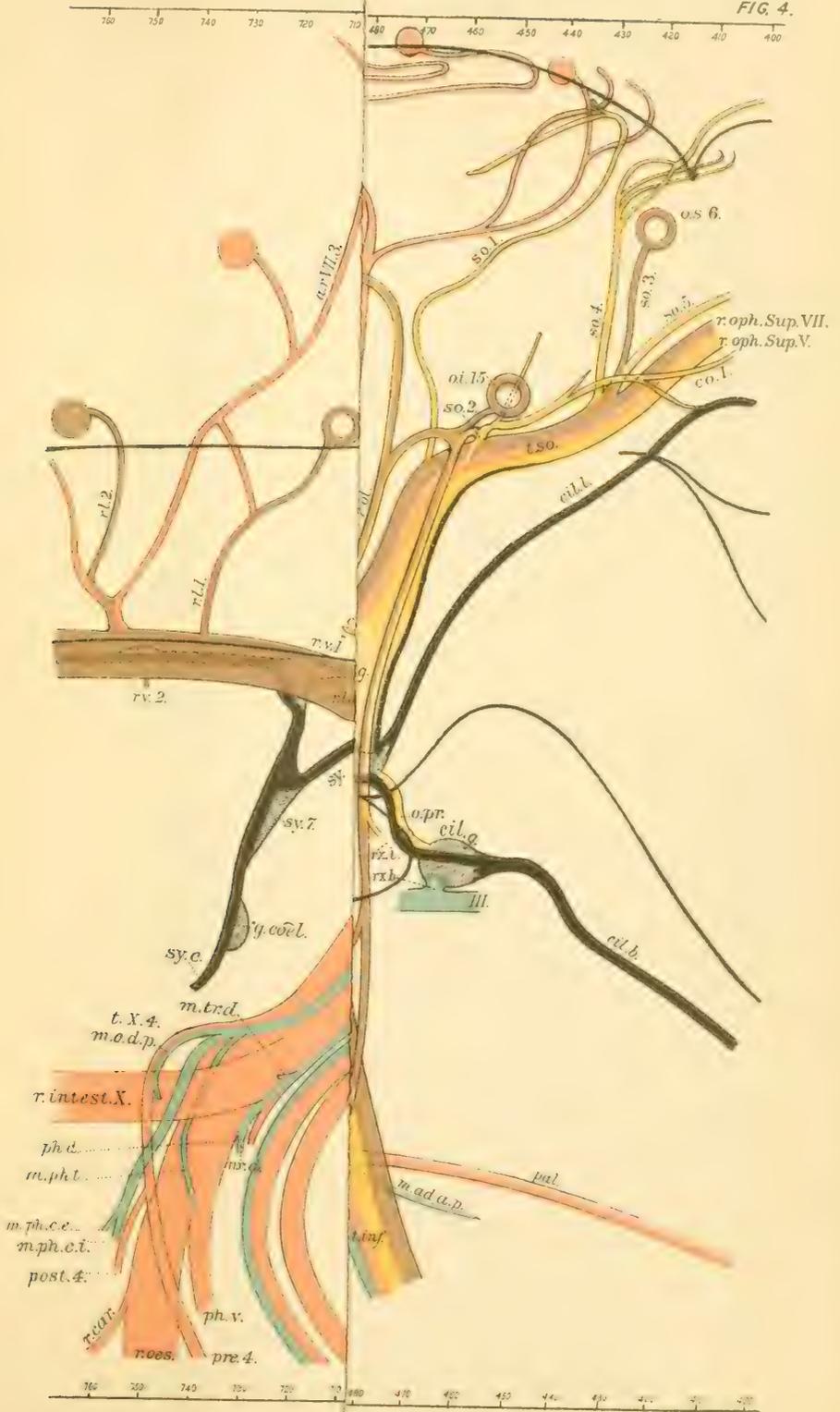








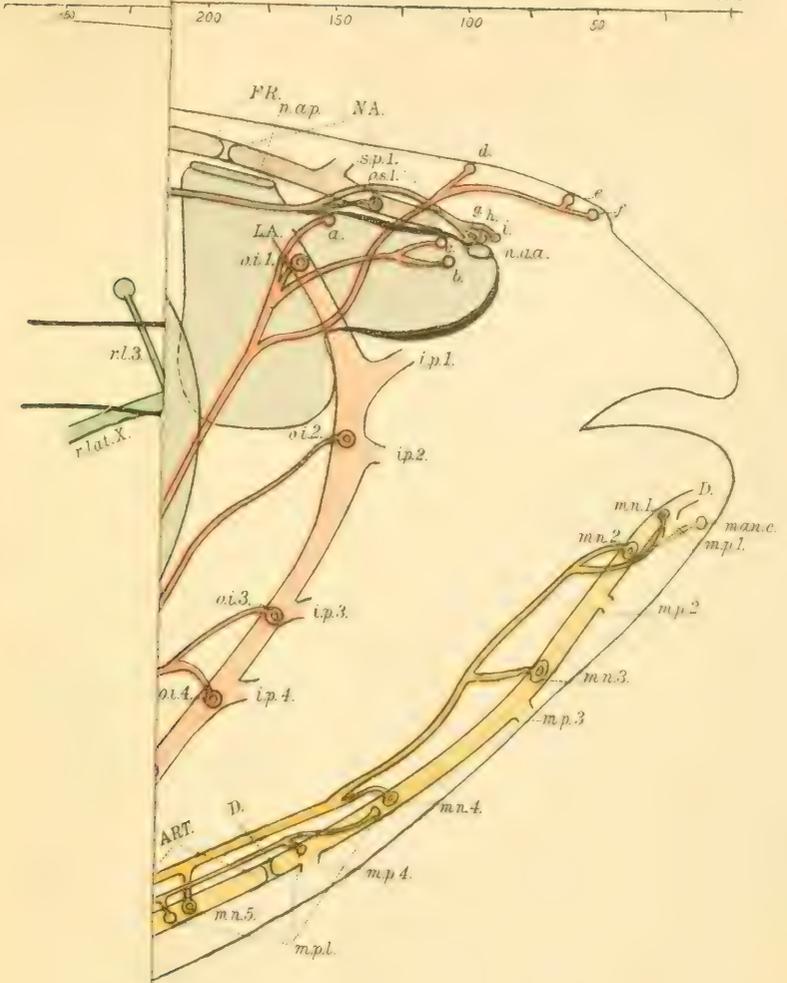
FIG. 4.



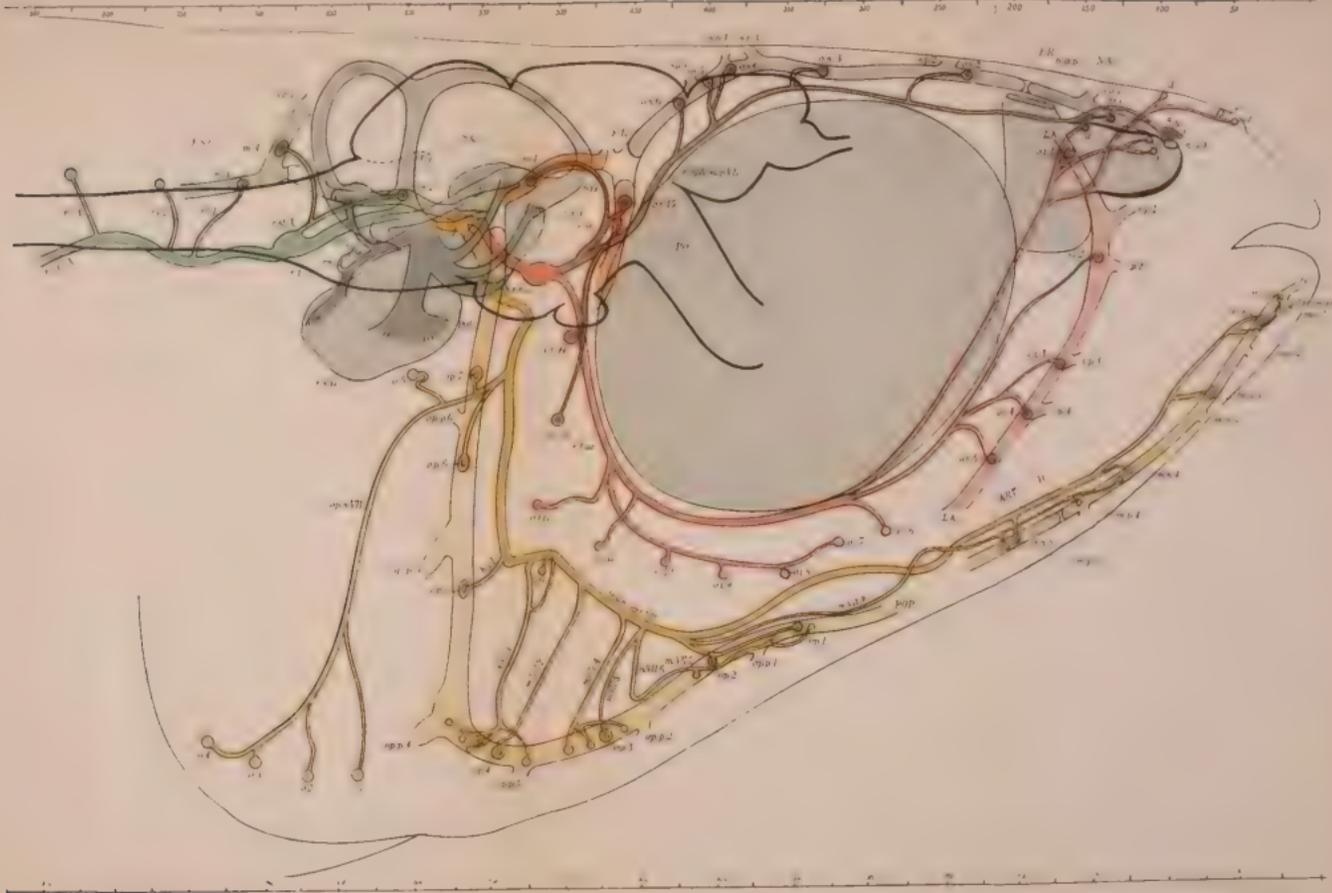














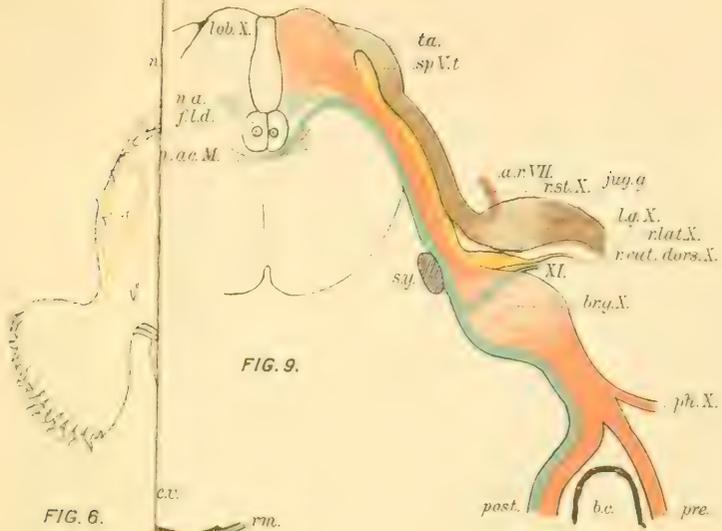


FIG. 6.

FIG. 9.

FIG. 10.

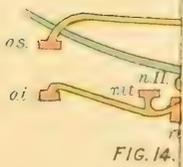
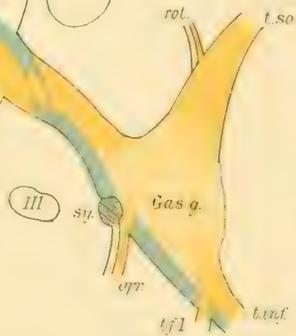


FIG. 12.

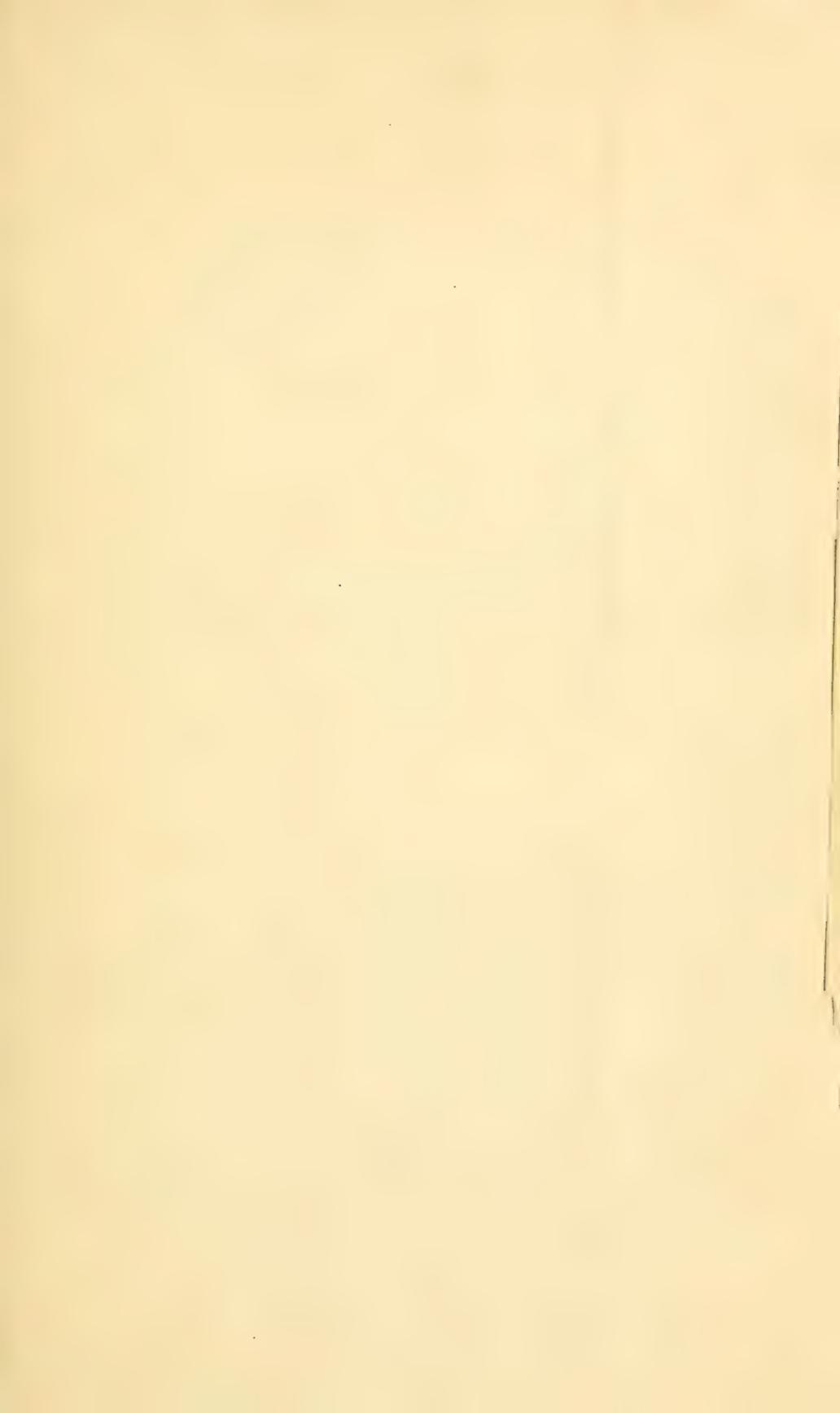
FIG. 14.

















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