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A Contribution to the Morphology of the Vertebrate Nervous System

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THE CRANIAL NERVES OF AMPHIBIA.

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ANALYSIS OF CONTENTS.

Introduction.

This research may be regarded as, in a manner, a continuation of Professor Osborn's work on the Amphibian brain. In the introduction to his paper, "A Contribution to the Internal Structure of the Amphibian Brain" (Journ. of Morph., Vol.

II, No. 1, July, 1888), occur the following sentences: "Much remains to be done in respect to the *peripheral distribution of the component parts of the several cranial nerves.* Only after this has been thoroughly worked out can we certainly determine the homologies of the cranial nerves and their segmental relations in the Amphibia. The present results go far enough to show that the determination of definite nuclei corresponding to definite peripheral sensory and motor areas is well within the range of possibility. In fact, the provisional character which I have given to some of the conclusions here reached is chiefly due to the close connection between several of the cranial nerves at, or close to, their exit, which makes it necessary to follow each component bundle in continuous sections peripherad to a point where their further distribution can be traced macroscopically. This, I believe, is possible with several of the nerves, but has not as yet been successfully accomplished."

To supply some of these deficiencies was the immediate aim of this investigation, and, I think, some of the obscure points mentioned by Osborn in his paper are satisfactorily cleared up. While very much remains to be done on the forms here investigated, yet a firmer basis has been acquired on which to make comparisons with the cranial nerves in other forms and to draw conclusions as to their nature.

In the opinion of the writer much of the embryological work upon the cranial nerves has been very defective and even misleading, owing to the fact that their adult distribution and function had not first been accurately worked out. I would venture to predict that more light can and will be thrown upon the nature of the cranial nerves in the immediate future by means of anatomical and histological than by purely embryological research.

This paper is by no means a monographical account of the cranial nerves of Amphibia, but will be confined principally to the V, VII, IX, and X nerves. Other nerves will be included in the description as they come into connection with these.

The types upon which the bulk of the work has been done and upon which the description is based are several common species of *Rana* in the late larval stages of development. Other Amphibia, especially the *Amblystoma* larvae, are brought in incidentally as throwing light upon certain points.

This research was begun at Princeton in 1889 at the suggestion and under the direction of Prof. Henry F. Osborn. A summary of the results first obtained appeared in the *Zoologischer Anzeiger*, Nr. 348, 1890 (61). At the Lake Laboratory, established by Mr. Allis at Milwaukee, I was enabled to make some additions to these results, which appeared in the *Anatomischer Anzeiger*, Nr. 15, 1892 (62). The final publication has been delayed, owing partly to other duties and partly to further observations made while Fellow in Biology at Columbia College, and also during the past year.

I wish to express here my deep indebtedness to Professor Osborn for many valuable suggestions and for his assistance in many ways in this research. For the execution of the majority of the drawings I am indebted to Dr. Arnold Graf, to whose skill they bear witness.

I. Technique.

A considerable part of the investigation was upon tadpoles fixed in Perenyi's fluid, stained *in toto* in carmine, imbedded in paraffin and cut in serial sections. These were mounted in order upon large glass slides, strips of thin mica being used as covers. The carmine staining is not to be highly recommended, as carmine solutions do not stain very differentially, and would probably be even more unsuitable with forms where the tissues are more compact than in the tadpole.

The *osmium-bichromate* mixture used for hardening in the Golgi method gives in itself a very good stain for the medullated fibres of the peripheral nerves, and sections prepared by means of this method were thus doubly useful.

The Golgi Method.— For the terminations of the nerves and for demonstrating certain tracts consisting of many non-medullated fibres, the Golgi method proved invaluable. It may be well to describe here in detail the precise procedure which I have found useful and convenient.

Preliminary to hardening, the manner of cutting the tadpole is a matter of some importance. The special region should be opened up to some extent in order to insure a speedy and complete penetration of the osmium-bichromate and the silver nitrate solutions, as neither of them have much penetrating power. On the other hand, by not cutting into too small pieces the precipitate formed by the silver is not deposited so extensively on all the surfaces, and many beautiful pictures can thus be obtained not marred by its presence. In investigating the head region I have found it best to cut the animal transversely into three pieces, one cut being made a short distance caudad of the auditory capsule and Vagus, and the other passing just through the anterior surfaces of the eyeballs. It is, perhaps, best to allow the animal to remain in the fixing fluid half an hour or so first, to acquire a better consistency for this cutting.

With respect to the *osmium-bichromate* mixture, a considerable latitude in the proportions may be taken and good impregnations obtained; the same holds good as to the strength of the *silver nitrate* solution. For example, good preparations were obtained from a tadpole impregnated as follows: Pot. bich. sat. sol. 140 cc. + osmic 1% 10 cc., 21 days, silver nitrate 10%, 3 days. The following, however, are the two solutions chiefly used, the first one (1) being after Berkley (10) and the second (2) very much like that recommended by Ramón y Cajal: (1) Pot. bich. 5% 84 cc. + osmic 2% 16 cc., and (2) Pot. bich. 3½% 4 vols. + osmic 1% 1 vol. I cannot say that I have found much choice between the two.

As seen above, impregnations may be obtained after hardening for 21 days in a solution containing *less* osmic. On the other hand good impregnations of the more superficial parts were obtained in one case as follows: Pot. bich. 3½% 4 vols. + osmic 1% 1 vol., 22 hours, during the first 11 hours in a solution which had been previously used, silver nitrate ¾%, 2½ days. This shows that here again there may be a considerable range within which good results are obtainable. There is a certain hardening period, however, which is much the most favorable; this is 2 to 5 days, and probably about 3 days will usually give the best results throughout the pieces.

Lithium Bichromate Modification for Adult Brains. — I have made a number of attempts to dispense with osmic acid in the fixing fluid, but without success for the tadpole. A modification was discovered, however, which gives some very fine impregnations in the adult mammalian cerebrum and cerebellum, *dispensing with osmic acid and yet requiring only a few days for the process.* It consists simply in the use of *lithium bichromate* instead of potassium bichromate. This salt is very soluble in water and makes a solution somewhat darker than the potassium bichromate, which it resembles. It hardens very much more rapidly than the latter, so that small pieces of brain placed in a 3% solution require only a day or two instead of 20 to 30 days to reach the condition favorable for impregnation. This favorable condition, however, is passed through very quickly. I have not had opportunity, as yet, to test this method thoroughly, but have obtained splendid pictures of the Purkinje and pyramid cells, and also in the fowl's brain of the granule cells, showing the ⊤-shaped division of their axis cylinders in the molecular layer of the cerebellum.

Sodium Sulphate Modification for Increased Penetration. — One of the defects of the Golgi method, especially of the rapid method, seems to lie in the poor penetration of the silver nitrate, resulting in irregular and defective impregnations. It occurred to me that by combining the silver solution with some salt that would be indifferent chemically in the reduction of the silver, but would facilitate its penetration, the results might be improved. Two salts were tried, namely, *sodium sulphate* and zinc sulphate. Both seemed to tend to produce the desired effect, for some of the best and most thorough impregnations were obtained from specimens treated especially by the former. The mixture of silver nitrate and the sodium sulphate was made in varying proportions. In two of the most successful impregnations the following were the solutions into which the objects were brought from the osmium-bichromate mixture: (1) Sodium sulphate 6% 1 vol. + silver nitrate 4% 1 vol.; (2) sodium sulphate 8% 1 vol. + silver nitrate 1% 1 vol. A precipitate is formed in mixing these, and it would be advisable to so adjust the proportions as to prevent this.

Equal volumes of 1% solution of each avoided this, and also gave some good results. *Zinc sulphate* seems to act similarly to the sodium salt and can be mixed with the silver in larger proportions without producing a precipitate.

It must not be understood that this latter modification gives ideal results. In some cases it seems to be an improvement, but further experience is necessary to ascertain its precise value. In the tadpole it has yielded especially good preparations of the nerve terminations in the heart (Pl. IX, Fig. 14). The specimens should be placed in pure silver nitrate a while previous to placing them in alcohol, in order to wash out the sulphate, otherwise the alcohol will precipitate the latter in the tissues. The specimens are left in the dark while in the osmium-bichromate and in the silver bath.

Preservation. — If, for any reason, specimens cannot be cut and mounted immediately after impregnation, they can be best preserved in the silver bath. Specimens will often keep thus for months, but there is considerable risk of deterioration. This latter is probably due, as von Lenhossék suggests (37), to a slow precipitation of the silver in solution, so that in time the specimen is left simply in water which, in turn, bleaches out the stain. Another cause of deterioration appears to be a gradual darkening of the whole tissue. It is obvious from this that if it is necessary to keep the specimens some time before cutting, two precautions should be taken, (*a*) the specimen should be kept in a liberal supply of the silver solution of full strength, and (*b*) it should be kept strictly in the dark in order to prevent, as far as possible, a gradual secondary reduction of the silver.

The double and triple impregnation, as recommended by Cajal (13), was tried with good results. The exact details of procedure in technique are placed in an appendix.

II. DETAILED DESCRIPTION OF THE NERVES AND THEIR COMPONENTS.

The most direct treatment seemed to be, first, to examine each nerve in detail, with a view to ascertaining its components, each section concluding with a table summarizing the results. The term '*component*' is not necessarily synonymous with '*root*,' for often *two or more* components different in fibre structure, internal origin, distribution, and function are given off as *one* root, and *vice versa*, different roots may be composed of similar components. 'Root' has reference to the number of separate bundles by which a nerve issues from the central nervous system — while by 'component' we refer to bundles qualitatively different. In some cases, of course, the two are identical.

A résumé of this part treats the nerves collectively as regards their components.

Second, each of the main components thus determined will be further considered as representing a system, and used as the basis of homologizing the cranial nerves of the Amphibia with those of other orders.

The chart (Pl. XII, *A*) was reconstructed from a series of transverse sections through the tadpole by plotting out the nerves, etc., upon a sheet of paper ruled in squares, the relation between the thickness of the sections and the magnification having been first ascertained. For conciseness and precision the numbers of the sections are used in the text to indicate distances measured along the longitudinal axis. As the sections were 10 μ thick, these numbers divided by 100 will give the actual distances in millimeters and decimals of a millimeter. Each interval in the scale along the sides of the chart equals 10 sections (= 100 μ), and the numbering corresponds to that used in the text. This correspondence, however, is not always exact, owing to slight changes made in the chart in its preparation.

1. *The Trigeminus.*

The *Trigeminus* emerges from the side of the medulla .10 mm. cephalad of the VII + VIII roots (866–848). Its exit takes place principally just anterior to the entrance of the posterior branch of the VIII into the auditory capsule. It proceeds obliquely cephalad occupying, together with the other nerves described below, a position in the cranium immediately inside the ventral portion of the auditory capsule. The bulk of its fibres are rather small, but with a number of medium-sized fibres among them, and a still smaller number of large fibres. The ascending tract of the V contains a few scattered large fibres, and the ventral root of the V (V minor) is coarse fibred.

After proceeding cephalad .7 mm. it becomes ganglionated, .36 mm. further on its Gasserian ganglion begins to divide into a dorsal and a ventral part, the ventral part at the same time passing through the floor of the cranial cavity and consequently lying in the roof of the mouth. Here this ventral portion has lost its ganglion cells and becomes the *Ramus ophthalmicus trigemini.* This partial division of the anterior extremity of the Gasserian ganglion is the only sign of separation between the ganglia of the Rr. ophthalmicus and maxillo-mandibularis trigemini respectively. The R. ophthalmicus continues cephalad and gradually dorsad, thus entering the orbital cavity. .3 mm. cephalad of its separation from the rest of the V, it comes into connection with the III nerve, which divides on its inner side, one part of the III passing up around it, and the other bending forwards beneath it.

During the remainder of its course the R. ophthalmicus gives off several branches to the skin, which need not be described more in detail here. When it breaks up in the anterior extremity of the head one branch is given off (170), which bends down, pierces a layer of fibrous cartilage which separates the skin from the oral subepithelial layers and divides. One division, proceeding caudad, is continuous with a branch of the R. palatinus VII. The significance of this connection will be discussed in the description of the latter. The other division of the R. ophthalmicus, possibly together with some fibres from the R. palatinus VII, proceeds cephalad a short distance, and breaks up into a rich plexus, terminating in the epithelium of the roof of the anterior extremity of the oral cavity. This plexus and its terminations are figured in Pl. VII, Fig. 3, where the plane of the section enables one to obtain a view of its mode of branching and termination.

The fibres of the R. ophthalmicus V are rather small, but of variable size, and with, perhaps, a dozen and a half coarse fibres scattered among them. As the different branches separate from the main trunk they usually draw off several of these larger fibres. The latter have apparently no special significance as far as their peripheral distribution is concerned. They seem to have the same cutaneous terminations as the smaller fibres. Whether a more exhaustive study of them would reveal histological differences in their ultimate terminations, I do not know. The presence of these large fibres in cutaneous branches is readily accounted for by their presence also in the ascending tract of the Trigeminus, in which they can be traced caudad to the posterior columns of the cord.

The other and dorsal division of the V .46 mm. cephalad of its separation from the R. ophthalmicus separates into the *Rr. maxillaris* and *mandibularis*. The last ganglion cells disappear .7 mm. cephalad of the first, thus making .7 mm. the length of the Gasserian ganglion.

Slightly cephalad of the subdivision into the Rr. maxillaris and mandibularis the motor branches of the Trigeminus to Mm. pterygoideus and temporalis are given off. These branches all arise together from the same point on the ventral side of the *R. mandibularis*. Some distance cephalad of this, and in about the same transverse plane as the posterior nares, the R. mandibularis gives off branches innervating the M. masseter. Still further along it bends mesad and gives off the musculocutaneous branch to the M. submaxillaris (mylohyoideus anterior) and the skin beneath it. As it finally breaks up it innervates the Mm. submentalis and mandibulo-labialis of Schulze (54).

The cutaneous branches which compose the bulk of the R. mandibularis need not be described here. The general manner of termination of cutaneous nerves will be touched upon below. The character of the fibres of the R. mandibularis, as well as of the fibres of the R. maxillaris, is similar to that of the fibres of the R. ophthalmicus, and what has been said of the latter applies to them also.

Besides its motor and cutaneous branches, the R. mandibularis innervates a part of the epithelium of the mouth. At 200 a twig is detached which proceeds mesad to the mouth at

150±, about in the same transverse plane as the termination of the R. mandibularis VII, and innervates the epithelium lining the under side of a lateral diverticulum of the oral cavity.

At the terminal portion of the R. mandibularis one branch also proceeds dorsad and then along beneath the epithelium of the labial cartilage (170±). It forms here a dense plexus in the subepithelial connective tissue layer and apparently in close apposition to the cartilage. The appearance of this plexus is difficult to reproduce, but Pl. VII, Figs. 5, 6, and 7, will give some idea of its character. The stain is not so black as that of the other nerve fibres, and the fibres of the plexus certainly appear to fuse with each other, forming a true network. This appearance is not so apparent in sections in which the stain is less complete — or in which the plexus is more diffuse, — and may possibly be due to an excessive precipitation of the silver. I am not inclined, however, in view of the appearances presented to accept this explanation. In this plexus are numerous varicosities and many free endings terminating in small knobs similar to the varicosities.

From this plexus arise at right angles innumerable twigs which break up into arborisations in the epithelium surrounding the cartilage. The fibres of this plexus do not anastomose but simply interlace. A good idea of their appearance is given in Pl. VII, Fig. 5. The thicker fibres from which they arise represent the perichondral plexus mentioned above and which Figs. 6 and 7 represent in horizontal section.

It is noticeable that none of these fibres, or very few, penetrate more than about two-thirds of the thickness of the epithelium. I think it is not unlikely that the explanation of this lies in the character of the epithelium. The outer layers of the latter consist of more flattened cells which are probably partly cornified.

It is difficult to see exactly what the significance of the plexus or network closely enveloping the cartilage is. It corresponds to the basal plexuses lying in, or under, other epidermal and epithelial structures and from which the terminal fibres arise. Here, however, its unusually compact character, its close apposition to the cartilage and the great number of endings it contains would seem to indicate, in addition, some special function.

With one exception the branches of the *R. maxillaris* need not be described further. This one is given off at about 310, passes cephalad and mesad and here subdivides. One subdivision is continuous with a branch of the R. palatinus VII while the other, together, apparently, with a portion of the R. palatinus, proceeds cephalad along the side of the oral cavity supplying its epithelium with fibres and finally breaking up at its extreme anterior end (Pl. VII, Fig. 2).

Besides these branches of the Trigeminus there are a number of others which have been but little noticed and yet, though small, seem to be of some morphological importance. There are usually three of these and all are given off in about the same transverse plane, and about .3 mm. caudad of the division of the V into its maxillary and mandibular branches. Two of these arise from the inner side of the V, — from the inner side of the anterior extremity of the Gasserian ganglion, — and one can be traced caudad along its inner side almost to the point of separation of the R. ophthalmicus. The third and largest branch arises apparently from the outer side of the V but its fibres can be seen passing mesad across the dorsal side of the V, so that they ultimately originate from about the same point as do the other two. These *accessory* branches seem to derive their fibres, in part at least, from the few large ganglion cells in the dorsal and mesal side of the trunk of the V, constituting the apex of the Gasserian ganglion.

These branches, like the other branches of the V, consist principally of small fibres with a few large ones among them. They fuse temporarily with certain branches of the VII, as will be described below.

It will not be necessary to describe the branches of the V further as no departures of importance from, or additions to, the usual descriptions have been noted.

The cutaneous terminations of the fibres of the various branches of the Trigeminus (Pl. VII, Figs. 1 and 4,) present no especial differences among themselves. Their modes of branching and courses differ, however, in different tadpoles, and these differences evidently depend upon differences in the structure of the skin, in the thickness of its different layers and the form and arrangement of the epidermal cells. The branches break up in the deepest layer of the cutis, bend at right angles and form a heavy, coarse plexus of nerve fibres extending parallel to the surface. From this plexus one or several fibres pass vertically through the middle layer of the cutis and in the superficial layer break up into terminal arborisations, the fibrils of which pass into the epidermis, there to ramify still further. The course and configuration of these ramifications is correlated in a general way with the shape of the epidermal cells. In passing through the middle layer of the cutis the vertical fibres give off branches at right angles which course along between the dense parallel strands of connective tissue which constitute this layer. The endings in the different layers appear to be always free and intercellular. The precipitate formed on the surface often interferes with following them to their final terminations.

Immediately beneath the middle layer of the cutis, and still more abundantly in the superficial layer immediately beneath the epidermis, a number of dark bodies are present (Fig. 4, *x*), usually with a smooth oval outline, and are, apparently, a species of pigment cell. While the nerve fibres now and then lie close to these, there is no connection between the two. I have not found any cells, such as those described by Eberth and Bunge (16) in the foot of the frog. While negative evidence, especially with Golgi preparations, is far from conclusive, yet I think, judging even from their own figures, their results are open to the criticisms made upon them by Van Gehuchten (27).

2. *The Facialis and Acusticus* (*Auditory*).

The *Facialis* and *Acusticus* present even greater difficulties in the tadpole than in the Urodela. In the latter the exits of the *Acusticus*, and what is here called the *dorsal VII*, are quite distinct. The latter is considerably reduced in the tadpole and *in proportion as it is reduced the Acusticus is increased*, the exit of the VIII being extended so much dorsad that it and the dorsal VII emerge from the medulla together and only become separated later in their course. An interesting question here arises. Does the Acusticus in its extension dorsad appropriate a portion of the dorsal VII? This could best be determined by a careful study of these nerves and their internal origin through the stages of transformation into the frog. If such a transference takes place it would lead to the remarkable result that the Acusticus of the Urodela is not strictly homologous with that of Anura. It should also then be determined what structures in the ear receive this increased nerve supply. Some further aspects of this question will be dealt with later.

The exit of the VII + VIII (899–876) occupies a large portion of the side of the medulla. In the most caudad part of this exit there may be seen fibres leaving the medulla which, when traced internally, curve ventrad, and evidently have an origin much inferior to that of the bulk of the VIII. This root has been observed by Stieda (59) and others, and is spoken of in Ecker and Wiedersheim's *Anatomy of the Frog.* (17) as derived from the motor trigeminal nucleus. Osborn (45), however, has demonstrated that a similar ventral rootlet in Cryptobranchus is derived directly from the posterior longitudinal fasciculus. My sections, being of smaller brains, are inadequate for the settlement of the derivation of this root in the tadpole. I think it probable that some of the fibres originate from a portion of the trigeminal motor nucleus, and possibly others may come from the posterior longitudinal fasciculus. I have so indicated them in the chart.

These fibres, as they emerge from the medulla, form a bundle close under the large root of the Acusticus. This bundle was termed, in the abstract in the *Zoologischer Anzeiger* (61), the "*ventral root of the ventral VII*" or "*VII ab.*"

Slightly cephalad of this, and between it and the Acusticus, another root can be distinguished, composed of fine fibres, which are derived from a bundle representing the *fasciculus communis* of Osborn (Pl. XI, Fig. 39). This was designated "*VII aa*" in the Anzeiger abstract. It fuses with the first root and these two ventral roots of the VII were, for convenience, together denominated the "*ventral VII*," a name, as seen immediately below, not applicable to some other forms. There is one remarkable peculiarity in connection with this root in the larvae and adults of Anura as contrasted with Urodela. In the latter, as described by Osborn in Cryptobranchus, its exit is just dorsal to the Acusticus, while in the former, as described above, its exit is just ventral to the Acusticus. This transference is probably connected with the change in position of the Acusticus as noted above.

These two roots fuse with the ventral side of the root of the VIII so closely that tracing them in the tadpole is a matter of some difficulty.

The Acusticus shows the division into dorsal and ventral roots described by Köppen (35). In the caudal part of the former the fibres are smaller than those of the latter, which are of varying sizes but contain some very large fibres. The fibres of the dorsal root proceed obliquely ectad and ventrad, and immediately pass within the auditory capsule and enter the posterior portion of the auditory ganglion, which is composed of small ganglion cells. The dorsal part of the ganglion further cephalad, however, becomes composed of large ganglion cells which supply the coarser fibres of the auditory branches. The posterior branch of the VIII consists of both coarse and smaller fibres, as does the anterior, but the latter branch seems to contain a larger proportion of coarse fibres. The larger part of the dorsal root of the VIII seems to supply the posterior auditory branch and the larger part of the ventral root the anterior branch.

The most dorsal fibres, belonging apparently to the cephalic portion of the VIII at its exit, separate from the VIII. They form what was termed in the abstract the "*dorsal VII*" or "*VII b*." This root can be seen to arise in part from fibres running longitudinally in the dorsal part of the medulla at this place. According to Osborn's observations on Cryptobranchus (45) they ultimately arise from nuclei in this part of the medulla. It may be remarked here, however, that the connection between "sensory" nuclei in the central nervous system, such as those mentioned by Osborn, and the roots of ganglionated nerves (as the root in question will be seen below to be), must be considered now to be merely a physiological and not an anatomical one. It is obvious, from more recent investigations, that the only cells with which the fibres of such roots are directly connected are those of the peripheral ganglia belonging to these roots.

This being the case, it will be convenient to denominate such internal nuclei, whose cells are not directly continuous with the root fibres, "terminal nuclei," in distinction to those nuclei whose cells are in direct continuity with root fibres (ganglia of sensory roots and motor nuclei), which may be called "nuclei of origin." This distinction and terminology is that adopted by Kölliker in his *Gewebelehre* (34) ("Endkern" and "Ursprungskern").

In the tadpole it is difficult to determine whether some of the acoustic fibres may not be similar to those of the dorsal VII. From appearances in the tadpole, and from the fact that in the frog the origin of a portion of the VIII is ascribed to similar ganglion cells (Köppen), even from the mere fact of the persistence of these cells after the disappearance of the dorsal VII, this similarity might be inferred.

This root, the dorsal VII, already reduced in the tadpole, disappears in adult Anura. The reasons for this disappearance will become evident when its distribution is considered. It may be well to point out here that this fact has caused some confusion and apparent discrepancy in the accounts of the Facialis by different observers, some of whom assert the origin of the VII to be dorsal to the VIII, while others assert it to be ventral. The latter refer to forms in which the dorsal VII has disappeared; the former overlook the ventral portion of the VII. Köppen (35), however, overlooking the ventral portion in the frog, in which the dorsal root is lost, is obliged to look for the VII in the Trigeminus. He is further misled by expecting to find the Facialis a purely motor nerve.

At 852 ± the ventral roots of the VII separate from the VIII, the coarse-fibred root (VII *ab*) forming the outer and lower portion of the bundle. The description of the dorsal VII will be taken up first.

The Dorsal VII ("*VII b*").—When this separates from the dorsal side of the VIII, a portion of the latter intervenes between it and the ventral VII (VII *aa* + VII *ab*). As the VIII passes into the auditory capsule the V emerges from the medulla, so that there is only a narrow space between the V and the VIII. Into the upper part of this space the dorsal VII is wedged; into the lower part the ventral VII (VII *aa* + VII *ab*) (Pl. X, Fig. 25). The fibres of the ventral half of the dorsal VII soon begin to bend ventrad, and at 842 separate from the dorsal half. Caudad of this a few fibres pass ventrocephalad from this ventral half to unite with some fibres detached from the ventral VII. The ventral half of the dorsal VII, after its separation from the dorsal half, passes ventrad between the V and VIII nerves, and comes to lie (832±) immediately above the ventral VII, with which it unites. It here lies immediately above the bundle of coarse fibres, VII ***ab***, occupying the outer side of the ventral VII (Pl. X, Fig. 25). The union of these two bundles now becomes so close that they can only with some difficulty be distinguished; but the course of their respective fibres can be stated with considerable certainty from three other grounds also, *viz.*, the distribution of the dorsal half of the dorsal VII; the nature of the fibres of certain branches in the distribution of the ventral VII + ½ dorsal VII; and the relations of homologous bundles in Amblystoma. Owing to the close relations of this portion of the dorsal VII to the ventral VII its further course can, however, be most conveniently described in connection with the latter.

The *dorsal half of the dorsal VII* remains close to the V, and as it proceeds cephalad comes gradually to lie immediately above it. At 775 it becomes ganglionated, and at 751 divides into two nearly equal parts.

The lower of these divisions (½ VII b_2) passes ectad just beneath the anterior extremity of the auditory capsule and above the Gasserian ganglion. About here it gives off a twig of a few fibres (½ VII b_{2a}, 732), which can be traced ectad to lateral line sense organs lying in the skin some .15 mm. caudad of the caudal surface of the eyeball.

The main nerve, proceeding further ectad, soon gives off another twig of several fibres (½ VII b_{2b}, 727). This twig immediately fuses with a fine-fibred twig, also very minute, which is given off by the largest and outermost of the accessory trigeminal branches described above (p. 17) as issuing from the anterior extremity of the Gasserian ganglion. These two bundles of fibres thus brought together are distinguishable from each other, owing to their difference in fibre calibre, and soon separate, the trigeminal portion going caudad and dorsad, and coming in contact temporarily with a division of the middle of the accessory trigeminal twigs just above the outer edge of the auditory capsule. The facial portion proceeds ectad and has a distribution near and probably similar to the preceding facial twig, though it could not be so clearly traced.

The main nerve (½ VII b_2) continuing ectad comes in contact (726) with the outer of the accessory trigeminal branches. This contact and temporary fusion is a peculiar one: the facial passes through the trigeminal branch, each, however, seeming to preserve its continuity. At this point of contact each gives off a twig. That from the trigeminal portion is fine-fibred, and fuses — temporarily, apparently — with the facial twig (½ VII b_{2c}). The fibres of these very minute trigeminal twigs are so fine that it is not possible to ascertain in ordinary preparations whether some fibres may not remain with the facial twigs. The main trigeminal branch now breaks up, and supplies the skin of the region just ectad of the posterior surface of the eyeball. The facial twig (½ VII b_{2c}) divides. One part crosses and temporarily fuses with a trigeminal twig (700–687), proceeding cephalad parallel with the principal facial branch. Some of its fibres are traceable to a large lateral line sense-organ in the epidermis, just below the cornea (625). The remaining four fibres proceed further cephalad and innervate a lateral line sense-organ cephalad of the latter and in a similar position (588). The other part of this facial twig could not be completely traced to lateral line sense-organs.

The main branch (½ VII b_2), after giving off these twigs, bends forwards, proceeding cephalad under the eye. At intervals it gives off small twigs of only a few fibres each. Many of these could not be traced into the lateral line sense-organs. When this was the case, the cause must be sought in defects in the preparations, especially where the twigs are so excessively minute. It may be reasonably inferred that all of these twigs end in these organs, whose line the main facial branch follows so closely, especially as an organ is always found in the vicinity of a twig though the complete connection be not present. This branch can be followed, gradually diminishing owing to the separation of twigs, nearly to the very anterior extremity of the head.[1]

Returning to the other subdivision of the dorsal VII (½VII b_1, 751), this proceeds at first directly cephalad just mesad of the lower part of the anterior extremity of the auditory capsule, gradually leaving the Gasserian ganglion. As it separates from the latter it receives a small, fine-fibred twig, which can be traced around the Gasserian ganglion to the sympathetic. Continuing cephalad and dorsad it is joined on its ventral side (694) by the innermost of the three accessory trigeminal branches. It here (687) gives off a twig from its dorsal side which proceeds caudad and ectad (½VII b_{1a}) coming in contact (717) with a division of the middle of the three trigeminal branches, which proceeds to meet it. The subdivisions of the latter pursue courses in part parallel to twigs of the facial, *i.e.*, both proceed ectad and caudad, the facial supplying one (or more) lateral sense-organs lying above the space between the anterior extremity of the auditory capsule and the posterior surface of the eyeball, and also above the latter. Thus a part of the middle of these trigeminal branches is connected with one subdivision of the dorsal VII, and another part with the other subdivision (Pl. XII, *A z*).

The innermost of these three trigeminal branches, after coming in contact with the subdivision of the dorsal VII (½VII b_1, 694), passes dorsad along the inner side of the latter, fusing temporarily with it. From the ventral side of the facial branch a portion of the latter separates. This branch

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[1] These sense organs in the tadpole, as is well known, are noticeable on the exterior as rows of light dots. This appearance is owing to the absence of pigment among their cells. They are not enclosed in canals, and each one is usually slightly depressed.

(½ VII b_{1b}) proceeds cephalad parallel to the main facial branch and finally reunites with it (560), without having, apparently, in the meanwhile, given off any fibres.

The main subdivision of the dorsal VII (½ VII b_1) continues cephalad along the dorsal surface of the head and inside the eye to the extremity of the head. At intervals it gives off twigs similar to those of the other subdivision; like them, evidently supplying the line of lateral sense-organs in this region.

The parallelisms in courses between the trigeminal and facial twigs above described are very striking, and are often observed even in very minute ramifications. The significance of these parallelisms will be discussed below.

Somewhat more light is thrown upon the relations of these trigeminal and facial branches by means of Golgi preparations. The two facial branches, as they separate from the Gasserian ganglion, seem to be composed exclusively of the coarse, heavily medullated fibres so characteristic of them, nor do both, or even one of them, always appear to receive directly a sympathetic twig.

The trigeminal branches, however, contain, besides the medullated fibres of varying sizes as already noted, a number of fibres which do not appear to be medullated and are impregnated. These appear to have rather the character of *nervi nervorum* and some of them, at least, though apparently not all, can be traced to the *sympathetic*. When fusions take place with the facial branches, though the integrity of the two branches is in the main preserved, yet a number of these fine fibres pass from the trigeminal to the facial twig and join the latter.

The ventral VII + ½ *the dorsal VII* (VII *aa* + VII *ab* + ½ VII *b*) consists, as above stated, of three components: one (VII *ab*), the most ventral in derivation, from a motor nucleus (or the posterior longitudinal fasciculus or both), one (VII *aa*) from the fasciculus communis and the third (½ VII *b*) from the ventral half of the dorsal VII which later joins the two former. Where the first two components are fused with the VIII the ventral root (VII *ab*) comes to occupy the outer position and forms a prominence on the ventral side of the Acusticus just mesad of the foramen for the entrance of the posterior branch of the latter into the auditory capsule. The ventral VII finally separates from the Acusticus (852), occupying the position previously described (p. 116), and is joined by the ventral half of the dorsal VII. This and what will be called hereafter the motor root (VII *ab*) occupy the outer side of the nerve, the former (½ VII *b*) lying above the latter (VII *ab*). The whole nerve lies close to the ventral side of the Trigeminus in contact with it but not completely fused with it, *i.e.*, there is always visible a line of demarcation between the two.

At 802± the inner, fasciculus communis bundle (VII *aa*) begins to slip ventrad past the other two so that the greater part of it comes to lie below them instead of on their inner side. It then soon becomes ganglionated (788). This ganglion occupies the extreme ventral part of the V + VII, lying below the other two facial components (½ VII *b* + VII *ab*). It attains its greatest dimensions when the Gasserian ganglion proper is just beginning to appear in the transverse sections, *i.e.*, one half of it lies caudad as well as ventrad of the Gasserian ganglion proper. Its anterior part is fused with the ventral side of the Gasserian ganglion, cephalad of 767, so that it is somewhat difficult to distinguish between them at this point. Finally the fibres of the fasciculus communis bundle are seen emerging (760±) from the ventral part of the ganglion and form the *R. palatinus facialis*. In about the same transverse plane the other two components (½ VII *b* + VII *ab*) begin to pass ectad here from the Gasserian ganglion, a portion of them, presumably that from the dorsal VII, which may now be called the lateral line component, having first come into connection with ganglion cells. They evidently separate, occupying the same relative positions, *i.e.*, the lateral line component uppermost. As they separate from the ganglion these two components receive on their ventral side a bundle from the ganglion of the fasciculus communis component (VII *aa*, Pl. X, Fig. 26). The branch of the Facialis thus constituted is the *R. hyomandibularis*. The R. palatinus VII is thus composed of the bulk of the fasciculus communis component (with possibly the addition of some trigeminal fibres and also of fibres from the sympathetic), while the R. hyomandibularis comprises the ventral half of the dorsal VII, the motor root and a part of the fasciculus communis component (½ VII *b* + VII *ab* + part of VII *aa*). The possibility of its having also received some fibres, not many, from the Trigeminus cannot be excluded, however, and it also receives fibres from the sympathetic.

The course of the *R. palatinus VII* along the roof of the pharynx is sufficiently indicated in the chart. There are some features in its branching, however, which deserve special attention.

At 400± it gives off a branch which proceeds directly mesad and innervates a curious fold which extends transversely across the roof of the pharynx. This fold, which is described also by F. E. Schulze (53), is directed cephalad and is partially continuous laterally with the surrounding pharyngeal epithelium so as to form a shallow pocket opening anteriorly. This is the way it appeared also in another tadpole examined macroscopically. In the two figures of this fold given (Pl. VIII, Figs. 8 and 10) one is taken from a section through its posterior part so as to pass tangentially through its epithelium. The other is from the next section cephalad. In other sections examined this fold appears to be more free and to be directed posteriorly. On and around the fold are a number of end buds (taste bulbs), as are described below, which are innervated by the branch of the R. palatinus just mentioned. This fold, as the figures seem to demonstrate, is especially richly innervated. Nor is this due merely to an inequality in the impregnation as is shown by the presence of the branch from the main trunk, the largest branch given off by the R. palatinus up to this point.

The location of this branch corresponds with that of the vomerine teeth in the adult, possibly being slightly caudad of the latter.

According to Wiedersheim, in the frog the epithelium in the vicinity of these teeth is supplied with taste bulbs (quoted in 17).

At the same place where the branch just described is given off, another larger branch separates from the R. palatinus, proceeds cephalad and, turning ectad, becomes continuous with a branch of the R. maxillaris V as already described (p. 111). The remainder, much diminished, passes on cephalad and becomes continuous with a branch of the R. ophthalmicus V as already described (p. 108).

From the nature of these curious anastomoses, it is difficult to determine exactly where the Facialis ends and the Trigeminus begins. Their significance lies, I believe, in the fact that the R. palatinus VII, on the one hand, and the Rr. ophthalmicus and maxillaris V, on the other, innervate territories morphologically distinct, and that in the region where these fusions occur these two territories meet. In other words, they occur just about on the boundary between the pharynx and the stomodaeum. Of the part becoming continuous with the R. ophthalmicus, it is not improbable that all which continues cephalad beyond this commissure, though indicated as partly composed of each element in the chart (*q.v.*), belongs to the Trigeminus, and that the same is true of a considerable portion of that which is caudad of this point of fusion. Along its course this branch gives off a considerable number of fibres which form a plexus around the openings of the posterior nares into the pharynx. As a line drawn through the anterior part of these openings would indicate the line of demarcation between the stomodaeum and pharynx, it is not impossible that these fibres represent the last fibres from the R. palatinus proper, and that the remainder of the branch consists entirely of fibres coming caudad from the R. ophthalmicus. A still more minute study of this portion, however, would be necessary to determine this point exactly, from observation, and the possibility must also be admitted that the regions innervated by fibres from the R. ophthalmicus V and the R. palatinus VII, respectively, overlap to some extent. This, however, would not impair the general validity of the view here put forward as to the significance of these anastomoses.

What has been said above applies also to the anastomosis between the R. palatinus VII and the R. maxillaris V. Here again the exact delimitation of the R. palatinus cannot be determined.

It may be remarked here that it would be extremely interesting to study, from this point of view, the innervation of the stomodaeum and pharynx of forms in which their relative extents vary. Indeed, this will probably be necessary as supplying one of the guides in reaching accurate knowledge of the homologies of the nerves of this region in different forms, and especially with the higher forms, where the relations are so complicated.

The mode of branching of the R. palatinus VII in the adult frog, and also its terminations in epithelium, glands, and blood vessels, have already been described by Stirling and Macdonald (60). These investigators made use of the gold method, and it will be well to add some results obtained with the Golgi method, especially as the endings in this region have not been so fully described in the tadpole by Retzius (51), von Lenhossék (38), and others, as in other forms.

The structures innervated are blood vessels, general epithelium, glands, and end buds (taste bulbs). In the olfactory region we have the mucous glands, which fall, in part at least, in the trigeminal territory. My impregnations, however, have not demonstrated much respecting the innervation of these glands, merely showing some scattered fibres coursing around their periphery.

Vaso-motor fibres, following the blood vessels and often ending in their walls with little knob-like expansions, are met with here and there. Whether these vaso-motor fibres come merely from sympathetic fibres mixed with those of the R. palatinus proper, or also from the latter, it is hardly possible to determine. Stirling and Macdonald have described nerve cells in this region with spiral fibres. I have also occasionally met with nerve cells, though whether of this type or not I could hardly determine.

Before treating further of the finer terminations of this nerve, and in order to make clearer some points mentioned below respecting the terminations of other nerves, it may be well to indicate briefly the structures found in this region. These have been described so clearly and admirably by F. E. Schulze (53) that I cannot do better than give a brief résumé of a portion of his description. Schulze divides the roof of the stomodaeo-pharyngeal cavity into five regions. These regions are demarcated by certain folds and elevations or papillae. The anterior region or field is that portion lying in front of the transverse fold already mentioned; the middle field, free from any high papillae, is bounded in front by the transverse fold, laterally by a row of high papillae, and posteriorly by a fold. On each side of it are the lateral fields characterized by the presence of high papillae. The fold which forms the posterior boundary of the middle and lateral fields has a scalloped outline and extends transversely across the cavity. Behind it is the posterior field, in which the character of the epithelium changes, being destitute of papillae and studded anteriorly with "multicellular glands," as they are designated by Schulze. Posteriorly this epithelium merges into the oesophageal epithelium. The papillae are elevations of the epithelium, the interior being composed of connective tissue, and they bear one or more "taste bulbs." The latter are found as well between the papillae, and also, according to my observations at least, in the posterior field. The multicellular glands are composed of a number of appressed elongated cells forming a cup-shaped structure whose concavity forms a shallow depression in the epithelial surface, and whose convexity projects slightly into the subepithelial connective tissue.

The floor of the stomodaeo-pharyngeal cavity is divided, according to Schulze, into five similar regions, the rudiment of the tongue marking the boundary between the anterior and middle fields. Here also is a similar transverse scalloped fold marking off the posterior field. In the posterior field the gill cavity opens and is partly covered by the folds formed by the posterior field, *i.e.*, the anterior and posterior velar folds ("Kiemendeckplatten"). On these folds the above mentioned glands are so numerous that they form a continuous layer without intervening indifferent epithelium, a condition which is approached also on the posterior field of the roof in places. It is on the edges and under side of the velar folds that these glands are so numerous, and I may add, from my own observations, that those on the roof of the pharynx are so grouped as to be most numerous always over the opening into the gill cavity. In those parts of the roof not directly above this opening they immediately dwindle away.

The nerve fibres, in my preparations, form beneath the epithelium a dense plexus from which fibres pass upward into the epithelium. In the thinner, indifferent epithelium, which seems usually to be the least richly innervated, they run among the cells irregularly, but do not as a rule seem to penetrate more than about two-thirds through its thickness towards the surface.

A number of nerve fibres approach the base of the *taste bulbs* and there break up, forming a dense structure (Pl. IX, Figs. 15, 16, and 24), often, apparently, more of a granular than fibrous character, and at times staining less black than the nerve fibres. This structure evidently corresponds with that described by von Lenhossék in fishes (38) and termed by him the cupula. From this structure nerve fibres arise which ramify around the bud, often rising nearly to its peripheral surface. Whether they also penetrate between the cells of the bud it is rather difficult to determine.

The nerve fibres passing immediately below the *multicellular glands* send at right angles vertical fibres up into them or close around them. The course of these fibres varies somewhat. In some preparations they rise nearly parallel with each other almost to the very surface of the epithelium where they end in little knobs either among the cells of the bud or immediately around them (Pl. IX, Fig. 17). In other cases the fibres rise more irregularly, and when they have penetrated into the upper third of the epithelium they turn and branch so as to form a dense ring-like plexus apparently encircling or penetrating the gland at this level. From this plexus a number of nearly parallel fibres pass upwards converging towards the central axis of the gland and end in enlargements in or very near the surface of the epithelium (Pl. IX, Figs. 18 and 19). I am inclined to believe that the latter fibres, at any rate, penetrate into the gland near its free surface. Transitional forms are abundant where the fibres from the subepithelial plexus pass upward more as in the first mode of termination, but branch near the surface to a certain extent before terminating (Figs. 20 and 21). These terminations are often not simply rounded knobs but have a more elongated club shape and are somewhat irregular in outline (Figs. 18–21). As a number of fibres press in from all sides towards the centre of the depression in the epithelium formed by the gland, this locality is quite filled with these bodies. The irregularity and size of these enlarged terminations may be due to some irregularity in the staining, but since they occur often in the cleanest impregnations and since expansions of even greater size exist elsewhere, *e.g.*, in terminations in muscles, they may be considered true pictures.

These appearances in the glands seem to me to be not easily reconcilable with Dogiel's (14) denial of free endings and assertion of the prevalence of a closed network as the terminal apparatus. It is, of course, possible that these enlargements which lie immediately below the surface, almost in it, are not the final terminations and that there are always, *e.g.*, unstained transverse fibres connecting them and forming closed meshes. It is also true that the various methods of staining nerve fibres, especially the Golgi method, are irregular and incomplete in their action, yet it is not likely that the latter would always omit certain fibres such as these hypothetical ones. The manner in which these fibres terminate negatives still more strongly their existence. That true anastomoses *may* occur is not to be denied and sometimes the appearances favor their existence (*vide supra*) but they can hardly be of universal occurrence. Neither physiologically nor embryologically would there seem to be any special reason for their existence in such peripheral structures as epithelium, though they might easily occur now and then owing to secondary fusions.

The *R. hyomandibularis facialis*, as described above, leaves the Gasserian ganglion at about the same transverse plane as the R. palatinus (760 ±). As it leaves, it is composed, as has been seen above, of three components, occupying the nerve in the following order: The most dorsal is the dorsal VII component (½ VII *b*); next to this is the motor component (VII *ab*); and most ventral is the fasciculus communis component (VII *aa*) (Pl. X, Fig. 26). The destination of the first and last components can be traced with certainty; that of the second one is not so easily made out, as will be seen below. This is partly owing to the fact that the fibres of VII *b* are remarkable for their uniform coarseness and heavy medullary sheath, and those of VII *aa* for their fineness and very thin sheath. On the other hand, those of VII *ab*, though tolerably coarse and well sheathed, do not possess such well-marked characteristics.

As the R. hyomandibularis proceeds ectad, flattened out under the quadrate, VII *aa* comes to occupy the inner side of the nerve, next to VII *ab*, while outermost is VII *b*, which also overlies VII *ab*. This is about their relation when joined by the communicating branch from the IX + X (690), and is shown in Fig. 27. This latter branch occupies, as is seen in the figure, the outer third of the joint nerve. It is composed of mixed fibres, similar to those of the Trigeminus.

As the R. hyomandibularis emerges from beneath the cartilage it acquires a round outline, as seen in transverse section, but the relations of the components are much the same, except that the portion from the IX + X takes up a somewhat more dorsal position, pushing mesad ½ VII *b*. In Fig. 29 a small twig is seen leaving the ventral side of the nerve and deriving its fibres from VII *ab* (483). This twig passes ectad close under the nerve, and after proceeding cephalad a short distance enters a vertical muscle just outside the nerve, which is identified as the M. orbitohyoideus described by F. E. Schulze (54). A twisting and flattening of the nerve now takes place, so that the positions seen in Fig. 30 are assumed. VII *aa* is now uppermost, ½ VII *b* and VII *ab* next, while the component from the IX + X is ventral. Along in this part of the nerve it is at times difficult, for the reasons mentioned above, to trace VII *ab*. There is little doubt, however, but that its course is as given here.

As indicated in Fig. 30, the nerve divides into two parts. The ventral of these two divisions, the *R. hyoideus*, is composed largely of fibres from the IX + X, with the addition of a bundle from VII *ab*. It proceeds ventrad (433) and caudad through the M. orbitohyoideus, and then turns mesad. It then divides (508), as indicated in the chart, one part supplying the

M. mylohyoideus posterior (= submaxillaris post. = intermaxillaris post. = subhyoideus) and the other supplying the skin below this muscle. There is, thus, quite a marked resemblance to the branch of the R. mandibularis V which innervates the M. mylohyoideus anterior and the skin below it. The R. hyoideus, however, is composed of fibres from *two* nerves, the VII and the IX.

While it is difficult to distinguish the two sets of fibres in the R. hyoideus VII, yet it is probable, from direct observation alone, that the fibres from VII *ab* are those which innervate the muscle.

It is obvious from the preceding that the cutaneous part of the R. hyoideus does not belong to the lateral line system of nerves to the head, and belonging to the VII. As this cutaneous component is derived from the IX + X, it will be further treated below.

The remainder of the R. hyomandibularis proceeds cephalad, and soon divides again (368). Of these two divisions the ventral one comprises the remainder of the communicating branch from the IX + X and ½ VII *b*, while the dorsal one comprises the remainder of VII *ab* and all of VII *aa* (fasciculus communis). The former is the *R. mandibularis externus*. It proceeds ventrad just inside the M. orbitohyoideus. The bulk of the coarse fibres belonging to ½ VII *b* have become aggregated on its outer side. As the nerve emerges on the ventral side of the muscle it becomes divided into two branches, an inner and lower (mand. ex. *a*), composed of the finer fibres of the IX + X component, together with a few coarse fibres, and an outer branch (mand. ex. *b*) comprising the coarse fibres of ½ VII *b*, together with a portion also of the finer fibres of the communicating branch from the IX + X.

The former of these two branches (mand. ex. *a*) sends off a small twig, which is reënforced by fibres from the other branch, and supplies the skin. The remainder, in every way resembling the cutaneous portion of the R. hyoideus, proceeds caudad and ventrad, and is distributed to the skin of the ventro-lateral aspect of the body in this region. No connection was observed between it and lateral sense organs. It is a "*general cutaneous*" branch. This branch is probably the representative of the R. auricularis VII in the frog (17).

The latter of these two branches, *i.e.*, the outer (mand. ex. *b*) soon divides. The upper (dorsal) of these two subdivisions (mand. ex. b_1) gives off twigs, containing the smaller fibres, to the skin. The bulk of the remainder, consisting of coarse fibres, proceeds caudad, supplying a line of lateral sense organs along the side of the head ventrad to those under the eye. The larger ventral subdivision (mand. ex b_2) proceeds caudad, parallel with the other, apparently supplying no lateral sense organs until the dorsal subdivision has terminated. It also appears to gradually lose its finer fibres. It divides at 585. One part, proceeding caudad and dorsad, supplies lateral sense organs with its coarse fibres. The other part proceeds caudad and ventrad to about 800, where it bends mesad, proceeds transversely across the ventral aspect of the body, and probably supplies a line of lateral sense organs present in this region. There is, in addition to these branches of the R. mandibularis externus, a small branch (mand. ex. *c*) which proceeds cephalad, turning ventrad and caudad, as indicated in the chart.

The dorsal of the three principal divisions of the R. hyomandibularis divides. The ventral of these two divisions contains nearly all the remaining fibres of VII *ab*, and soon enters (357–346) the two muscles lying just mesad of the nerve. A few of the coarse fibres of VII *ab* remaining with the dorsal (fasciculus communis) division separate and also enter these muscles. Of these two muscles, one is identified as representing the Mm. suspensorio-angularis and quadrato-angularis described by Schulze (54). It appears to be one muscle here, though there are some evidences of a separation into two. The other muscle is the cerato-hyo-angularis of Schulze. The behavior of these two sharply contrasted bundles of fibres (VII *aa* and VII *ab*) and the manner in which the coarse ones are, as it were, picked out to innervate the muscles, is very interesting and instructive. The remainder of the dorsal division of the R. hyomandibularis consists now of a bundle of fine, lightly-staining fibres, among which are a number of deeply-stained but small fibres. By tracing it out we have seen that this bundle represents the fasciculus communis component. When it separates from the R. hyomandibularis it is the *R. mandibularis internus facialis*. This nerve now proceeds cephalad and bends mesad under the quadrate (310 ±) to the angle of the pharynx. It proceeds cephalad along the pharynx, supplying some fibres to its mucous membrane. Its main distribution is not general, however, but is principally to one locality. This is shown in Pl. VIII, Fig. 11. A great number of the fibres are here seen to supply a large papilla or elevation of the epithelium about at the boundary between the pharynx and mouth. A number of fibres proceed mesad to innervate the floor of the pharyngo-oral cavity. This is in the same transverse plane as the location of the future tongue, as is shown by the N. hypoglossus and R. lingualis glossopharyngaei. I have examined sections of the frog also, with reference to this point, and find that the termination of this nerve, the R. mandibularis internus facialis, is in the region of the anterior part of the attachment of the tongue, and that a part of it, at least, seems to send branches into the anterior part of the tongue itself.

It may be well to point out here that these observations confirm, in most respects, what would be considered *a priori* as the most probable destinations of these components. As the dorsal division of the dorsal VII (VII *b*) was found to supply sense organs of the lateral line system, a similar destination would be the natural supposition respecting the distribution of that ventral portion going over into the R. hyomandibularis. Again, as one portion of the fasciculus communis component (VII *aa*) was found to be distributed, as the R. palatinus VII, to the roof of the pharynx, it is most consistent that the portion entering the R. hyomandibularis should likewise supply a portion of the pharynx. By elimination merely, this would leave the third component, *i.e.*, the *motor root* (VII *ab*), and also the R. communicans IX ad VII to supply the general cutaneous (*i.e.*, cutaneous excluding the specialized lateral line system) and motor branches. VII *ab* has the position and characteristics of a motor root, and is the one which would be considered most likely to enter the motor branches. In this connection an observation of Volkmann (64) may be cited. Volkmann found, by stimulation, that the communicating branch from the IX + X did not contain motor fibres.

These observations are partially checked in another way by a most beautiful extirpation experiment performed by nature. In the frog the lateral line system of sense organs disappears and, as I have verified myself in the common frog, in the toad, and in one of the Hylidae, the dorsal VII (VII *b*) disappears also. Consequently the various rami (see table below) derived from this root are wanting in these forms, but on the other hand, such cutaneous branches as do not belong to this system persist. Accordingly we find in the frog, for example, a cutaneous branch from the R. hyoideus. Furthermore, this affords a firm basis in determining the R. auricularis VII (17) and in excluding, as possible homologues, those cutaneous branches derived from the dorsal VII.

The question of certain homologies is discussed in another portion of this paper. Some, however, are assumed in the table given here, which presents in a convenient form an analytical summary of the N. facialis.

I may add that an examination of serial sections through the brain and proximal portions of the nerves of the frog, stained by Weigert's method, show very clearly the two components of the VII, before joining the V, namely, on the outer side the coarse-fibred motor part and mesad the fine-fibred fasciculus communis component. Although somewhat out of place here, it may be remarked that a bundle of fibres can be traced in the V which preserve their integrity through the Gasserian ganglion entering the R. mandibularis, and which, tracing them proximad, appear to be derived from the motor root of the V.

In *Amblystoma* larvae the relations of these roots are somewhat different. They are shown in the figure occupying the corner of the chart (Pl. XII, *C*). Here the principal difference lies in the fact that the VII is not pushed forward into the V. There are also other differences: in the Amblystoma larva the dorsal VII is considerably larger than in the tadpole, while the Auditory is smaller relatively, not only to the dorsal VII but to the medulla. Furthermore, it is separated from the dorsal VII by an interval; and in that interval, and dorsal to the Auditory, emerges the fasciculus communis root.

"In Amblystoma (Pl. XII, *C*) the fasciculus communis component of the VII, shortly after emerging from the medulla, enters a ganglion lying partly under the anterior extremity of the auditory ganglion and partly anterior to it. From the anterior end of this ganglion emerges the R. palatinus, which then dips downwards piercing the roof of the mouth and proceeding forwards along the latter. Laterally to this and also from the ganglion near its extremity, a small branch is given off which passes directly outwards and forms the most ventral portion of the trunk of the VII. It soon separates, proceeding outwards and downwards to the side of the oral cavity, where it proceeds forwards along it and along the inner side of the lower jaw. It is thus in every respect, except that it is not pushed forwards into the V, identical with the R. mandibularis of Anura, thereby confirming the view that the latter is derived from the fasciculus communis.

"The ventral root, or rootlets, of the VII (VII *ab*) could, in part at least, be traced out, and forms the portion of the trunk of the VII, as it passes outwards, which lies immediately above the fasciculus communis branch just described. Though fused with the latter and with a part of the dorsal VII (VII *b*) mentioned below, it can yet be traced continuously until it likewise separates and is distributed to the Mm. digastricus and mylohyoideus posterior, corresponding to the motor branches of the R. hyomandibularis in Anura, and showing the derivation inferred for them in the latter to be correct.

"The dorsal VII (VII *b*) divides soon after its exit, part passing directly cephalad along the dorsal side of the Gasserian ganglion. It is here this part enters its ganglion, which is fused with the Gasserian ganglion proper. The ventral half of the dorsal VII passes downwards as well as forwards, and then bends outwards directly under the auditory capsule and just anterior to the entrance of the anterior branch of the VII into the capsule. It here fuses with the other components of the VII mentioned, forming the dorsal part of the trunk. In this part of its course and under the outer edge of the auditory

ANALYTICAL SUMMARY OF THE FACIALIS.

ROOTS (COMPONENTS).		BRANCHES.	DISTRIBUTION.
Dorsal VII (VII *b*)	1. Dorsal half (ganglionated)	R. ophthalmicus superficialis VII	Supra-orbital line of sense organs.
		R. buccalis, R. oticus and other small branches	Infra-orbital line of sense organs.
	2. Ventral half (ganglionated)	part of R. hyomandibularis (*q. v.*).	
Fasciculus communis (ganglionated, VII *aa*)		R. palatinus	Roof of pharynx.
		part of R. hyomandibularis (*q. v.*).	
Motor root (VII *ab*)		part of R. hyomandibularis (*q. v.*).	

	COMPONENTS.	BRANCHES.	DISTRIBUTION.
R. hyomandibularis	½ dorsal VII	R. mandibularis externus	Lateral sense organs, mandibular and opercular.
	Fasciculus communis	R. mandibularis internus	Floor of anterior pharynx.
	Motor root	Rr. not named	Mm. orbitohyoideus, suspensorio-angularis, quadrato-ang. and cerato-hyo-angularis.
	Motor root	part of R. hyoideus	M. mylohyoideus posterior.
	Communicating branch from IX + X	part of R. hyoideus	Skin ventrad of M. mylohyoideus posterior.
		R. auricularis +	Skin in vicinity of ear.

capsule it passes into its ganglion, composed of large ganglion cells. It is a cutaneous nerve; and probably, as in the tadpole, supplies the lateral sense-organs. These are here more irregularly arranged.

"Thus the dorsal VII has two ganglia, one on each of its two main divisions, while the fasciculus communis component has one at its point of forking. The motor portion (VII *ab*) is, of course, non-ganglionated."— *Quoted from* (62).

The Abducens. — As this nerve enters into close relations with the VII and V, that part of its course connected with them will be described here. It makes its exit from the ventral side of the medulla in the same transverse plane as the exit of the second root of the IX + X. It proceeds ectad and curves cephalad lying a short distance mesad of the sympathetic nerve. At 912 it crosses the sympathetic, now lying ectad of the latter. At 806 it comes in contact with the ventral side of the VII. It is imbedded in the mesal side of the ganglion of the fasciculus communis component of the VII. Emerging from the anterior end of this it separates from the R. palatinus VII as the latter passes ventrad through the roof of the mouth, lying immediately above the R. palatinus (747±) and below the ganglion of the R. ophthalmicus trigemini. It now unites with the ventral side of the R. ophthalmicus trigemini (734), slipping around to the outer side of the latter. There seem to be ganglion cells in connection with it (703), although these may belong to the oculomotor nerve. The VI leaves the R. ophthalmicus (697), and divides, the larger part proceeding cephalad and ectad to the M. rectus externus, which it innervates.

It may be as well to restate here concisely the relation to the Gasserian ganglion proper of the various nerves and ganglia which are connected with it.

Running along the dorsal side of the Gasserian ganglion proper is the dorsal half of the dorsal VII. Its ganglion is fused with the dorsal side of the Gasserian ganglion. Next, ventrally, are the ganglia of the Rr. maxillo-mandibularis and ophthalmicus trigemini, which compose the great bulk of this ganglionic mass, and constitute the Gasserian ganglion proper. The ophthalmic portion — mostly indistinguishable from the other — seems to occupy more the anterior portion of the ventral side. Occupying the posterior portion of the ventral side we have the ganglion of the fasciculus communis component of the VII, from which come the R. palatinus VII and the smaller branch which goes over into the R. hyomandibularis VII. In the outer side of the whole ganglion, and between the Gasserian ganglion proper and the ganglion of the fasciculus communis component, there are ganglion cells which must be regarded as constituting the ganglion of the ventral half of the dorsal VII, which subsequently forms part of the R. hyomandibularis. Besides these ganglia, we have also non-ganglionated bundles of fibres. There is the bundle of motor fibres of the portio minor of the Trigeminus, passing through the Gasserian ganglion. There is also the motor bundle of the VII which passes, with the ventral half of the dorsal VII, through the outer side of the ganglion. The course of the Abducens has been described. It is in the lower part of the inner side of the whole ganglion. Finally, there are sympathetic twigs which join the various branches emerging from this ganglionic complex (see pp. 118, 119, and 151).

3. *The Glossopharyngeus and Vagus.*

The determination of the composition of these nerves presents considerable difficulty in the tadpole, principally because of the manner in which they are, as it were, pushed together and out of position by the auditory capsule. Following the different roots through the ganglia accurately can hardly be accomplished, yet I believe the general nature of these ganglia is as described below. Some of the peripheral branches also have not been traced as completely as could be desired.

Five roots can usually be distinguished composing the IX + X. They are represented on the chart somewhat spread out, in some particulars, for clearness. The *first root, i.e.*, that one most cephalad, emerges from the medulla at 911. It leaves the medulla at a more dorsal level than the other roots and, as seen in the chart, as it approaches the medulla it curves cephalad. The fibres of this root are exclusively coarse, very uniform in size, and apparently have an internal origin similar to those of the dorsal VII, which they resemble in every way. At 926 it separates from the medulla and proceeds ecto-caudo-ventrad a short distance when it is joined on its ventral side by the second root of the IX + X.

The *second root* emerges from the medulla (936) at some interval from the first and, as mentioned above, at a lower level (Pl. XI, Fig. 37). The bulk of its fibres are derived from the fasciculus communis. It is joined, however, on its ventral side by a slender bundle of fibres which, as they penetrate further into the medulla, curve ventrad and have an origin considerably further inward and ventral to that of the rest of the root. They, apparently, are connected with a group of cells, but no actual continuity with processes of cells was observed. These fibres are coarser than those from the fasciculus communis. This is, undoubtedly, a motor rootlet and seems to be comparable in position and general characteristics with the motor roots of the Trigeminus and Facialis. It is not represented in Fig. 37, which is drawn from a Golgi preparation in which the fibres of this ventral rootlet were not impregnated. As will be observed in the figure, the fibres of this second root break through the ascending Trigeminus tract in order to reach the exterior.

The *third root,* preceded sometimes by a minute intermediate rootlet, often emerges in close juxtaposition with the second root. This root has, at least, a threefold origin. As shown in Fig. 36, the dorsal position of this root is derived from the ascending tract of the Trigeminus. This derivation is, undoubtedly, contrary to the views generally held as to the origin of the IX + X, but is, I believe, shown to be correct not only by a study of the origin of the roots themselves but also by the nature of certain of the branches of the IX + X as described hereafter. As seen in Fig. 36, these fibres come from the lower part of the ascending Trigeminus tract, while those from the fasciculus communis descend on the inner side of this tract in the medulla and, turning outward, emerge below, forming another of the components of this root. This is in contrast to the second root where these fibres passed through the upper part of the ascending Trigeminus. In the Golgi preparation, from which the figure is taken, a considerable number of the fibres from the fasciculus communis are impregnated and appear as straight, delicate fibres proceeding parallel with each other and forming a compact bundle. Carmine preparations show the same characteristic appearances for the fibres from this source, and Weigert preparations of the frog's brain show that here these fibres, proceeding in a similar manner, are fine and delicately sheathed. In the Golgi preparation only a small proportion of the fibres composing the bundle from the ascending Trigeminus is impregnated, and these exhibit a marked contrast to those from the fasciculus communis. They are coarser, more varicose, and have a more irregular, sinuous course. The bulk of this latter bundle issues slightly cephalad of the bundle from the fasciculus communis. In addition to these two components there is a more ventral motor rootlet, similar to that emerging with the second root. It is a possibility that some ascending Trigeminus fibres also pass out with the second root, but this is not certain.

The *fourth root* is indicated in Fig. 35. It is separated by a well-marked interval from the third root. Here, also, the fibres from the fasciculus communis curve down, around, and below the ascending Trigeminus in several compact bundles. No fibres emerge from the ascending Trigeminus, and there is present here, also, a ventral rootlet. As can be seen in the figures, the bundles from the fasciculus communis entering these roots diminish in bulk as we proceed caudad, *i.e.*, those entering the caudal roots are smaller. Emerging with the ventral rootlet of the fourth root, and further caudad than the other bundles, is sometimes to be seen still another very minute bundle from the fasciculus communis.

The *fifth root*, emerging some distance caudad of the fourth root, seems to derive its fibres from one source only. Its fibres can be traced caudad in the medulla some distance until lost among the longitudinal fibres of the lateral region of the medulla. This is the bundle which Osborn has identified, though erroneously as we shall see, with the fasciculus solitarius, and has traced it caudad into the lateral columns of the cord. According to Osborn it contributes, in Cryptobranchus (45), to at least two of the Vagus roots.

This root is very probably motor, but would appear to be quite different in character from the ventral motor rootlets mentioned above.

A further description of the fasciculus communis will be found in another place in this paper.

All these roots now enter the vago-glossopharyngeal ganglionic complex. The general shape of this complex is indicated in the chart. It curves around the posterior end of the auditory capsule, as though pushed back by the extension of the latter, a peculiarity probably due to the very anterior position of the gill clefts and other parts relatively to the auditory capsule. The ganglion attached to its inner portion posteriorly is the sympathetic ganglion. It is drawn too large in the chart.

It is not possible to trace the exact relations of the various roots through this complex; yet, the composition of the latter can, I think, be determined in a general way, and sufficiently to throw considerable light upon its morphology.

In the first place, it appears that this complex falls into three main divisions which are indicated by the shading in the chart. The most proximal ganglionic division is connected with the nerves before they pass around the hinder apex of the auditory capsule. Immediately beyond this lies another ganglion, and still further along, and quite upon the outside of the auditory capsule, the third ganglion. It will be necessary to describe the various branches of the IX + X before discussing the character of these three ganglia.

The *first root*, on account of its large fibres, can be readily followed, and its destination may be finally treated here. Just before entering the vago-glossopharyngeal ganglionic complex it divides. The dorsal division (*1*), remaining in the dorsal part of the ganglion, curves around the auditory capsule and separates. The ventral division (*5*) becomes separated from the dorsal by an intervening bundle of fibres. It remains longer in connection with other fibres of the IX + X, proceeding cephalad for a distance after rounding the auditory capsule, and then finally separates.

These two branches arising thus from the first root are the lateral line nerves supplying the lateral line sense organs of the body; (*1*) soon subdivides.

Besides these principal branches, a small bundle of fibres separates from the ventral division of the first root while still in the vago-glossopharyngeal complex. It proceeds cephalad in the upper inner part of the IX + X trunk, separating as a twig (*8*) at 897. It will be again treated in its proper place below.

The ganglionated portion of this nerve appears to be in the region of its forking, thus forming a part of the inner of the three divisions of the vago-glossopharyngeal ganglionic complex, though sometimes a few scattered ganglion cells are found farther out along its course.

The remaining branches of the IX + X will now be described in the order in which they separate from the ganglia, beginning with those most caudal. The *first branch* is the dorsal division of the bundle from the first root (*1*), as described above.

The *second branch* (*2*) is the bundle interposed between the two divisions of the first root. It consists of rather small or medium fibres with a few large ones intermingled; in other words, it resembles those branches of the Trigeminus and the Hyomandibularis, which we have seen to have a general cutaneous distribution. It proceeds cephalad close to the auditory capsule to 956, where it turns ecto-dorsad, and is distributed to the skin dorsad and mesad of the caudal extremity of the auditory capsule. It has no connection with lateral sense organs. This branch is evidently the same as the one in the frog, known as the *R. cutaneus dorsalis.* Thus the statement made in Ecker's *Anatomy of the Frog* (p. 174), that this branch is the persistent portion of the R. lateralis vagi in the tadpole, is erroneous. The supposition of Stannius and Fürbringer, there referred to, that it is the homologue of the R. auricularis, is evidently correct — if by this it is meant that the Rr. auricularis and cutaneus dorsalis in the frog are similar branches. If it is meant that this branch is the homologue of the R. auricularis vagi of higher forms, this is also correct. But this branch is not a part of the lateral line system.

Along this portion of the main trunk, the ganglion cells, which are nearly or entirely absent from that part of the trunk lying outside the apex of the auditory capsule (*i.e.*, separated by the tip of the capsule from the inner part in transverse sections), increase in number, forming the second ganglion mentioned. This ganglion, however, is confined to the outer part of the trunk, and there is a large bundle of non-ganglionated fibres running along just inside it and close to the auditory capsule.

The *third branch* (*3*) separates from this outer ganglionated part of the trunk (931–949) and proceeds ventrad, sloping mesad and caudad (Pl. XI, Fig. 40). It contains ganglion cells along its course, and finally, on a level with the oesophagus, contains a considerable group of ganglion cells, meriting the name ganglion. The fibres of this branch are principally fine and many of them impregnate in Golgi preparations, as is shown in the figure. Where the branch separates from the main trunk, a small twig is given off from its dorsal side, as shown in the figure, which apparently contains mixed fibres, some of which innervate a blood vessel proceeding dorsad here (cutaneous artery ?) and some of which possibly innervate a muscle just outside the auditory capsule.

Three principal branches proceed usually from the group of ganglion cells. They proceed caudad, some giving off branches to the oesophagus. Others were not traced completely, but they are probably pulmonary or gastric branches. One branch soon curves mesad and, proceeding cephalad, reaches the heart, which it innervates. It is ganglionated on the auriculo-ventricular septum (Bidder's ganglion). From this ganglion the nerve passes down along the ventricle, giving off innumerable branches, which penetrate to every portion. The general appearance of this plexus is indicated in Pl. IX, Fig. 14. As this shows, there are also numerous fibres innervating the walls of the auricles.

The third branch is the *R. visceralis*.

In addition to these branches there are other minute twigs from the clump of ganglion cells mentioned above. One branch, containing coarse and fine fibres, proceeds cephalad and supplies, in part at least, one of the Mm. levatores arcuum branchialium.

The *fourth branch* (*4*+*5*) from the main trunk emerges close to the third, immediately cephalad of it. This really consists of two branches, and immediately divides. The dorsal division (*5*) is the ventral division of the first root, which has been already described, and which separates here (929) to form one of the Rr. laterales. The other division (*4*) consists of rather large and small fibres intermingled. It immediately separates from the R. lateralis, proceeds directly ventrad a short distance and then bends cephalad. It divides at 938; the outer, smaller division (*4 a*), containing most of the coarse fibres, soon enters the M. levator (?) lying just outside. The remainder (*4 b*) proceeds cephalad giving off a minute twig, which appears to enter another M. levator (898). At 888 it divides again, the outer subdivision ($4\ b_1$) apparently containing about all the remaining coarse fibres. The inner subdivision ($4\ b_2$), the *R. laryngeus*, turns mesad (882) and enters the laryngeal muscles (860 ±). The outer subdivision ($4\ b_1$) has a complicated and peculiar course. It proceeds directly cephalad, coming to lie immediately above the heart. It now, still proceeding cephalad, slips ventrad close beside the heart, and at 720 appears to give off a fibre or two to a longitudinal muscle near it and near the heart. It divides at 700, and the outer division at 550 ± enters a longitudinal muscle lying above it here. At 627 some fibres which previously separated from the inner division go over to the outer, which divides and innervates the muscle just mentioned. The remainder of the inner division finally unites with the Hypoglossus, and cannot be followed further as a separate bundle. None but motor branches were observed from the Hypoglossus; and from this fact, as well as from the distribution of the outer division of this branch, that portion uniting with the Hypoglossus may be inferred to have a motor distribution. This muscle, or muscles, innervated, certainly correspond, in part at least, to Schulze's M. diaphragmato-branchialis medialis.

In Ecker's *Anatomy of the Frog*, p. 183, it is said that "Hoffmann describes a communicating branch of the Hypoglossus to the 'pneumogastric nerve,' which the translator has not been able to discover and which no other observer has mentioned." It is quite probable that this is the corresponding branch in the tadpole, thus partly verifying Hoffmann's observation. In a tadpole examined in which the metamorphosis had begun this branch did not unite with the Hypoglossus. It appeared here to innervate possibly the M. interbranchialis also. Whether it was concerned with the innervation of any of the Mm. marginales could not be certainly determined. Branches *3*, *4*, *5*, *6*, and *7* are given off practically together, and from them some coarse fibres separate, forming the *R. accessorius* to a capito-scapular muscle probably representing the M. cucullaris (= *4 a* ?).

At the point of separation at 929 of the branch just described, the trunk of the IX + X consists of two portions. The outer of these is mainly fine-fibred, but with some coarse fibres also. It is still ganglionated, the ganglion cells belonging apparently to the fine fibres. The inner portion is described below. The outer ganglionated portion now bends ventrad, separating from the inner, and divides (910) (*6* and *7*). It here also loses its ganglion cells. The ventral of the two divisions (*6*) gives off two or three fine-fibred twigs, which supply the epithelium of the outer angle of the pharynx in this region and some distance cephalad. One of these twigs (*6 b*) proceeds cephalad and at 759 gives off a twig which contains a few ganglion cells and supplies the mucous membrane of the pharynx ventral to it. At 757 the nerve contains a clump of ganglion cells, and here divides. The inner part ($6\ b_1$) passes mesad to the mucous membrane of the roof of the pharynx. The outer part ($6\ b_2$) supplies the membrane of the roof of the gill cavity, which opens into the pharynx here. The remainder proceeds caudad to 919, around one of the Mm. levatores, and bends cephalad under the latter, giving off a small twig (*6 c*) proceeding ectad, which could not be traced further. This twig takes from the nerve the few coarse fibres it contained. There is reason to believe (see p. 143) that this twig has finally a cutaneous distribution. The main nerve (*6*) now proceeds cephalad under one of the gill bars, a blood-vessel lying below it. At 822 it sends a branch around outside the cartilage to its dorsal side. At 788 the remainder assumes the same position. Its distribution is partly to the gill-raker attached to the dorsal side of the cartilage. Ganglion cells appear in it in places along its course, especially as it nears the point where the gill membrane is merged with the pharyngeal mucous membrane. Here (690 ±) the nerve lies in the floor of the pharynx, near the heart. It breaks up here, part of it turning caudad, and all of it being distributed, as far as could be observed, to the pharyngeal epithelium. It is obviously a *R. branchialis.*

Returning to 910, the dorsal of the two divisions (*7*) receives a short, reënforcing branch from the other, and proceeds cephalad and ectad as far as 840 ±, where it proceeds ventrad along the dorsal and outer side of the blood-vessel and turns caudad, still proceeding ventrad and thus rounding one of the Mm. levatores, where it again turns cephalad. This nerve contains two very large and prominent fibres. As it turns (870 ±) it gives off a twig (*7 a*) containing these two coarse fibres, together with a number of smaller ones. It is evident that this twig resembles the one (*6 c*) given off from the preceding nerve, which could not be traced. This twig is larger, however, and can be traced to its distribution. It divides just subsequently to its separation. One portion ($7\ a_1$), containing one of the coarse fibres, proceeds cephalad around the angle of the branchial cavity, through a thin muscle in the body wall, and thus becomes subcutaneous. It does not appear to give any fibres to the muscle, and is distributed to the skin. This division of the twig is thus probably of the "general cutaneous" type. The other division ($7\ a_2$) rounds the angle of the body cavity at 777, and is in every way similar to $7\ a_1$. After giving off this twig, the main nerve (*7*) passes under one of the gill bars — the one next to the one under which the last-described branch ran. At 807 a fibre or two comes off, which proceeds ventrad, but could be traced only a few sections. At 767 a small branch separates, which could be traced cephalad some distance, running near a blood vessel. At 613 the nerve, having in the meanwhile, like the other, passed around to the dorsal side of the cartilage and lying in the gill-raker attached, bends mesad, nears the place of transition of the gill membrane into pharyngeal epithelium, and rounds the extremity of a small, pouch-like evagination, or pocket, of the pharyngeal cavity, which projects anteriorly. The distribution of this nerve seems to be in every respect similar to the preceding one. It also contains ganglion cells. This branch is also obviously a *R. branchialis.*

At 923, at about the point of separation of the last two branches, the remainder of the trunk of the IX + X becomes ganglionated. A wedge-shaped bundle in the outer central portion of this part of the trunk consists exclusively, or nearly so, of fine fibres, the other portions contain mixed fibres. The ganglion cells are small and seem to be confined especially to the fine-fibred portion.

At 897 a small twig (*8*) separates from the inner side of the trunk. It is coarse-fibred, and proceeds ectad and cephalad from under the edge of the auditory capsule and then turns directly cephalad in the lowest, loose connective tissue, layer of the skin. At 838 it divides. The two divisions proceed cephalad and probably supply lateral sense organs, though only traceable to their vicinity. Its fibres resemble those of the other lateral line branches, and it is the portion which has been described above (p. 139) as separating from the ventral division of the lateral line bundle while in the vago-glossopharyngeal complex. It is this small branch which has been described in fishes by several observers as arising from the IX and innervating a canal organ, and which has been confused with the R. cutaneus dorsalis (auricularis vagi) in the frog (*vide supra*). It may be called the *R. supratemporalis.*

At 854 the main trunk of the IX + X falls into two divisions. The outer of these divisions (*9*) comprises the exclusively fine-fibred bundle and a portion of the mixed fibres, viz., that portion on the outer side of the fine fibres. The inner division (*10*) comprises the remainder of the mixed fibres. The ganglion cells still found in the outer division are in the fine fibred portion.

The outer division (*9*) soon subdivides (852 ±) into a lower or ventral subdivision (*9 a*) composed of a portion of the fine fibres, and an upper, or dorsal, and larger subdivision (*9 b*) composed of the remainder of the fine fibres and the mixed fibres. The lower subdivision (*9 a*) proceeds along the roof of the pharynx a considerable distance, giving fibres to it and to some portions of the filtering apparatus. It finally turns meso-ventrad, runs inward along the floor of the pharynx and supplies the epithelium of the roof of the gill cavity. This branch is obviously similar to those described previously (*6 b*, etc.) as innervating other portions of the pharynx. It is one of the *Rr. pharyngei.*

The upper subdivision (*9 b*) (852) proceeds cephalad and ectad, supplying fibres to the M. levator arcus branchialis in its vicinity, and comes to lie outside the outer angle of the pharynx. At 654 it turns ventrad, passing through a thin muscle lying in the body wall, and divides ($9\,b_1$ and $9\,b_2$).

Before this division occurs, the fibres in the upper subdivision (*9 b*) were so arranged that the mixed fibres occupied the outer and the fine fibres the inner side of the nerve. When the division takes place, however, the anterior, larger branch ($9\,b_1$) receives the fine fibres and also a bundle of coarse fibres (with sheaths deeply stained), and the posterior branch ($9\,b_2$) receives mixed fibres.

The anterior, larger branch ($9\,b_1$) proceeds cephalad and ventrad along near the inner side of the body wall, *i.e.*, around outside the gill cavity. It then bends cephalad, and again mesad, around under the gill cavity. During this part of its course the coarse fibres are very plainly seen occupying its ventral side. The fine fibres constitute the bulk of the nerve. Finally, as the nerve proceeds mesad the majority of the coarse fibres separate out (530 ±). As they separate out ($9\,b_{1a}$) there is a small group of ganglion cells apparently on the coarse-fibred bundle. Some of the fibres of this branch innervate a muscle which appears to correspond with Schulze's M. ceratohyobranchialis. Other fibres seem to merely scatter in the loose connective tissue and could not be traced. This apparent peculiarity was observed in more than one specimen.

A few coarse fibres remaining in the main nerve soon separate and appear to innervate a minute muscle lying near the one previously described, and which might be identified as Schulze's M. basihyobranchialis. The main nerve ($9\,b_1$) then proceeds cephalad in the floor of the pharynx, giving off twigs to its epithelium. It finally terminates at the rudiment of the tongue, taking at this point a sharp little turn mesad. This is, of course, the *R. lingualis glossopharyngei.*

Returning to 654, the posterior division ($9\,b_2$), consisting of mixed fibres, proceeds caudad and ventrad along the inner side of the body wall until at 740 ± it curves, first ventrad and then dorsad and ectad (∿-shaped), around the angle of a fold of the body cavity wall and thus becomes subcutaneous. The bulk of it proceeds cephalad and lies, at 698 ±, near a lateral line branch. It breaks up to supply the skin of this region and ventral to this. It is at once apparent that this posterior branch is similar to the two twigs (*6 c* and *7 a*) given off by the two previously described Vagus branches, one of which could be traced to a cutaneous distribution.

Returning to 854, the other inner division of mixed fibres (*10*) is the *R. communicans ad facialem* to the R. hyomandibularis. Its final distribution is described in connection with the latter, and it has there been found to be a general cutaneous nerve.

Now that the branches have been described, their relations to the ganglia may be made more intelligible. As described above, the most distal ganglion (*C*), from which issues the R. lingualis, belongs to the fine fibred portion of the nerve at this point. The larger mixed fibres which pass off into the R. communicans ad facialem and the cutaneous branches do not appear to be ganglionated here. The majority of them form a bundle on the inner side of the nerve next to the auditory capsule. As we pass further proximad along the nerve trunk, the fine fibres cease to be ganglionated and form the wedge-shaped bundle mentioned, occupying the outer central part of the trunk.

The proximal portion of this ganglion is slightly overlapped externally by the second ganglion (*B*). From the distal apex of this ganglion emerges the Rr. branchiales, to whose fine fibres this part of the ganglion belongs. This is apparently to some extent distinct from the proximal part (B_1) of the second ganglion, being partially separated from the latter by the lateral nerve issuing here. From this proximal part of the second ganglion (B_1) the R. visceralis emerges. Along the inner side of this ganglion also proceed the non-ganglionated fibres mentioned above, together with additional fibres from the cutaneous and motor branches which have in the interval been given off. The fine-fibred R. visceralis must be in part, and perhaps is mostly motor, yet it seems to be ganglionated. Whether it is entirely ganglionated, however, could not be determined.

The innermost or proximal ganglion (*A*) belongs chiefly to the cutaneous branches whose fibres, we have seen, pass by mesad of the two distal ganglia, and also to the N. lateralis. The former are in all probability derived from the ascending Trigeminus. It is very probable, however, that some of the fine fibres, especially, perhaps, those of the R. visceralis, are also ganglionated here.

These ganglia may be designated *A*, *B*, and *C*, as already indicated, *A* being the most proximal one. *B* may be subdivided into *B* 1 and *B* 2.

In the older tadpole above referred to (p. 142), the trunk of the IX + X, after giving off *1* and just as it gives off *2*, divides. From the upper and outer division are given off *3*, *4*, *5*, *6*, and *7*, from the lower and inner division are given off *9* and *10*. As in the other tadpoles, this latter division is ganglionated further distally (ganglion *C*). The Rr. branchiales are reduced and the R. visceralis has apparently increased.

It will be necessary now to describe some points in the finer terminations of certain of these branches. The velar folds mentioned above, a small portion of the filter apparatus, indifferent epithelium, and also some taste bulbs, both on the roof of the pharynx and on its floor in the region of the gill openings, are innervated by the pharyngeal branches described above. The innervation of the taste bulbs is as described above under the R. palatinus VII. That of the glands, which are so plentiful here, requires further notice on account of its remarkable richness. It is not unlikely that the appearances may be exaggerated by inequalities of impregnation, but in Golgi preparations all of this epithelium presents pictures remarkably rich in nerve fibres. We have seen above (p. 124) that the glands in this region are so numerous as to be practically continuous and not separated by indifferent epithelium. In such places the superficial nerve plexus belonging to these glands and described above (pp. 125, 126), naturally is also continuous, and there is consequently a dense plexus extending throughout the superficial part of this epithelium. Its general appearance is indicated in Pl. IX, Fig. 23, and is still more dense in preparations from a larger and probably older specimen.

The greater part of the filtering apparatus, and also the gills, are innervated by the Rr. branchiales. There is a great difference in my preparations between the innervation of these two structures. While in the former are demonstrated a great number of fibres, very few are shown in the gills proper. These latter fibres are very delicate and cannot usually be followed very far into the gills. They proceed along with the blood vessels and seem to be vaso-motor. It is not improbable that the fibres in gills do not impregnate readily, and that the supply is greater than the preparations would indicate.

Into the filtering apparatus bundles of fibres pass upward from the Rr. branchiales. These pass along in the loose connective tissue in the interior of these structures, send fibres into the smaller subdivisions, or side-pockets, and fill these with a snarl or tangle of fibres (Pl. VIII, Fig. 9). Endings are frequently seen on these fibres in the shape of small granules, or sometimes, apparently, several granules. Sometimes the two granular terminations of two fibres seem to meet each other (*x*, Fig. 9). Very often these terminations are in the very outer surface of the filament of the filtering apparatus. The fibres do not usually, at any rate, anastomose.

These gill filters, together with the glandular epithelium described above, evidently form an important apparatus, physiologically. There would seem to be a physiological similarity between these glands and those on the endostyle of Amphioxus.

Analytical Summary of the Glossopharyngeus and Vagus.

Roots.	Source.	Ganglion.	Branches.	Distribution.
1st	Tuberculum acusticum	A	Rr. laterales (*1* and *5*) R. supratemporalis (*8*)	Lateral lines. Lateral line organs near ear.
2d	Fasciculus communis	C	R. lingualis (*9 b*) R. pharyngeus (*9 a*)	Tongue and pharynx. Pharynx.
	Motor nucleus	Non-gang.	R. not named	Mm. levator arcuum branchialium, cerato-hyobranchialis and basihyobranchialis?
3d	Ascending trigeminus	A	R. auricularis (*2*) Rr. cutanei (*6 c*, *7 a*, and $9\,b_2$) R. communicans ad VII (*10*)	Skin near ear. Skin of operculum. Skin at base of operculum.
	Fasciculus communis	B2	Rr. branchiales Rr. pharyngei (*6* and *7*)	Gills and filter apparatus. Pharynx.
		B1 and A?	R. visceralis (*3*) {Rr. gastricus, pulmonalis and cardiacus.}	Oesophagus, heart, lungs, etc.
	Motor nucleus	Non-gang.	Rr. not named	Prob. Mm. levatores arcuum branchialium and (from Rr. branchiales) marginales.
4th	Fasciculus communis	B2, B1 or A?	Rr. branchiales Rr. pharyngei (*6* and *7*)	Gills and filter apparatus. Pharynx.
	Motor nucleus	Non-gang.	R. not named	Prob. Mm. lev. arc. branch. and marginalis.
5th	Ascending lateral	Non-gang.	R. laryngeus + ? (*4*)	Laryngeal muscles + M. diaphragmato-branchialis medialis?

The preceding table of the roots and branches of the IX + X is given for clearness. It is imperfect in some particulars and a number of points are assumed. The motor fibres especially require further investigation, nor can the different roots be followed through separately, if, indeed, they do remain separate, which is not probable. Yet it will give, I believe, some insight into the composition of this complex.

4. *The Sympathetic.*

The general relations of the *sympathetic* to the vago-glossopharyngeal and Gasserian ganglia may be quite briefly expressed. From the ganglion cervicale sympathicum (see chart) one or more branches pass to the vago-glossopharyngeal ganglia. One twig especially can be traced curving around the inner and then the dorsal side of the caudal apex of the inner ganglion. The greater part of this twig unites with the R. auricularis. Other minute twigs may be seen ramifying around the ganglia and appear to pass off, in part, to the various branches. I have not observed any especial supply to the R. visceralis and the latter must be regarded as composed very largely of fibres from the Vagus. The same probably applies to its subdivision, the R. cardiacus.

From the various parts of the IX + X, especially the fine-fibred portions of the trunk and branches, are often seen vaso-motor fibres given off to blood vessels. Along these nerves also, especially the R. visceralis and Rr. pharyngei, particularly among their twigs, are found ganglion cells. These cells usually have a bipolar appearance, but when examined closely one or both of their processes show here and there a splitting indicating a multiple character (Pl. XI, Figs. 41, 42, and 43). The process or processes from one end may supply a blood vessel, as is beautifully shown in Pl. VIII, Fig. 13. At other times it apparently innervates epithelium, though this is not so certain. Whether all these vaso-motor fibres are derived from the sympathetic, cannot be determined, but I regard it highly probable that they are not, and that a proportion of them are from the Vago-glossopharyngeus. This is what would be expected from the innervation of the heart. The ganglia in the latter might be regarded as collections of the ganglion cells just described.

The remainder of the sympathetic passes within the cranium through the vago-glossopharyngeal exit and forwards to the Gasserian ganglion. Its destination here has already been partly described. It supplies the various branches from this ganglion, as already mentioned by De Watteville (66). The lateral line branches appear to be, at times, unsupplied. This deficiency is possibly provided for by the smaller trigeminal branches, as described already (p. 119), from which, apparently, sympathetic fibres pass over into the lateral line branches.

Vaso-motor fibres can be seen at times coming from the trigeminal branches, and they are derived from the fine, probably non-medullated fibres, which are impregnated by Golgi's method, and which are seen in all the trigeminal branches. I have not observed any ganglion cells in connection with these fibres. Whether they are partly or wholly from the sympathetic, I have not determined.

5. *Recapitulation of Nerve Components.*

From the above description it is evident that we have in each nerve the following components, distinguishable by the nature of their fibres, their peripheral distribution and their internal origin:

Trigeminus. — (*a*) What may be termed *general cutaneous* fibres, *i.e.*, those supplying the skin exclusive of the specialized lateral line sense organs. The majority of these fibres are small but there are also among them a number of fibres of medium size as well as some coarse fibres. The bulk of this component is derived from the ascending trigeminal tract which is a continuation of the dorsal columns of the spinal cord. The ganglion (or ganglia) of this component is the ganglion of the maxillo-mandibularis and ophthamicus trigemini, namely, the Gasserian ganglion proper.

(*b*) *Motor Fibres.* — These are mainly coarse, innervate the jaw muscles supplied by the Trigeminus, and are derived from the trigeminal motor nucleus (and descending tract?).

Facialis. — (*a*) What may be termed *special cutaneous* fibres, *i.e.*, those innervating the specialized lateral line sense organs. These fibres are uniformly coarse and enter the dorsal part of the medulla. There are two ganglia belonging to this component. One, the ganglion of the Rr. opthalmicus superficialis and buccalis (and oticus) facialis, has its permanent position above the Gasserian ganglion proper and in contact with it. The other, the ganglion of the R. mandibularis externus VII, is, in the tadpole, imbedded in the outer side of the Gasserian ganglion, or rather between the latter and the ganglion of the next mentioned component. In Amblystoma, however, this ganglion has no relation to the Gasserian ganglion and lies beneath the outer side of the auditory capsule ectad of the ganglion of the next component and of the auditory ganglion.

(*b*) What may be termed the *fasciculus communis* component. This innervates the anterior portion of the pharynx. This component is composed principally of very fine fibres with a number of slightly larger fibres interspersed ; it is derived from Osborn's fasciculus communis. Further remarks upon this tract and its distribution will be made elsewhere. This component possesses one ganglion which is fused in the tadpole with the ventral side of the caudal portion of the Gasserian ganglion proper. In Amblystoma, however, this ganglion has no connection with the Gasserian and lies beneath the cephalic end of the auditory ganglion.

(*c*) *Motor* fibres in part similar to Trigeminus (*b*) and in part derived directly from the posterior longitudinal fasciculus (Osborn).

Glossopharyngeus and Vagus. — (*a*) *General cutaneous* fibres similar to Trigeminus (*a*) and derived from the ascending Trigeminus. The ganglion of this component is a portion of the mass of ganglion cells on the trunk of the IX + X nearest the medulla (ganglion *A*).

(*b*) *Special cutaneous* fibres similar to Facialis (*a*) in every respect and passing into the Rr. laterales. The ganglion of this component lies in the dorsal part of the ganglionic mass just mentioned (*i.e.*, of ganglion *A*).

(*c*) *Fasciculus communis* fibres similar to Facialis (*b*), its distribution being to the alimentary canal and its outgrowths caudad of the area of distribution of Facialis (*b*). There seem to be at least three ganglia belonging to this component, one of these being a portion of the ganglionic mass mentioned (*A*) and the other two the two ganglia lying farther out on the trunk of the IX + X (ganglia *B* and *C*).

(*d*) *Motor* fibres probably similar to Trigeminus (*b*).

Besides the above there are other portions of the IX + X whose nature and position is not clear. One of these is the "*fasciculus solitarius*" mentioned by Osborn, but erroneously so called (*vide infra*, p. 186), and which is also present in the tadpole. It is almost certainly motor.

Rearranging the above, we have at least four components:

I. *General cutaneous*, including V (*a*) and IX + X (*a*).

II. *Special cutaneous*, or *lateral line*, including VII (*a*) and IX + X (*b*).

III. *Fasciculus communis*, including VII (*b*) and IX + X (*c*).

IV. *Motor*, to branchial muscles (including jaw), including V (*b*), VII (*c*), and IX + X (*d*).

It is not to be supposed that this forms an exhaustive analysis of these nerves. Reasons may easily be adduced from this research, as well as from other sources, to show that this analysis is not complete. It is carried as far as can be conveniently done with the means employed, and will form a basis for additional results in the future.

III. COMPARATIVE MORPHOLOGY OF THE COMPONENTS.

1. *General Cutaneous.*

General Cutaneous Component. — V (*a*) and IX + X (*a*). The part of the V belonging to this component is very constant apparently in the vertebrate series. We find that the Trigeminus has an ascending tract from the spinal cord in Petromyzon (Ahlborn), in Acipenser (Goronowitsch), in Selachians (Rohon), and in Teleosts (Mayser, Wright). Furthermore, this tract seems subject to less variation in size than other tracts and the character of its fibres is about the same. As seen

TABLE.

General Cutaneous (ascending Trigeminus).	I. Preauditory. Trigeminus (sensory) proper. (Ganglion Gasseri.)	*a.* Several small branches inside orbit.
		b. Supraorbital, but deep (R. ophthalmicus).
		c. Infraorbital (R. maxillaris).
		d. Side of head and lower jaw (R. mandibularis).
	II. Postauditory. Part of 3d (and 2d?) root of IX + X. (Ganglion in proximal part of IX + X ganglionic complex, namely ganglion A.)	*a.* Branch dorsal around auditory capsule to skin (R. auricularis vagi).
		(*b*) Several cutaneous branches separating from the branchial branches (Rr. cutanei branchiales).
		(*c*) Communicating branch to facialis (R. communicans ad facialem).

hereafter, some portions of the medulla oblongata undergo remarkable variations in size and development in the different types and in this respect the tract under consideration seems to stand in contrast. This is natural when it is considered that it forms the supply to the skin exclusive of the specialized cutaneous sense organs which are peculiar to certain types only, or, at least, in certain types obtain a much greater relative development.

Respecting the nature of this component there can be no question, I think, that it is similar (homodynamous) to the dorsal spinal roots, if internal origin, character of fibres and their distribution are criteria of any weight. Its fibres are a direct continuation of those in the posterior columns of the cord, which they resemble, and are distributed to the skin exclusive of any differentiations in the latter which belong especially to the branchial region. This is also Gaskell's view (23 and 24).

It follows from this that the sensory Trigeminus is largely equivalent to the dorsal spinal roots, minus, possibly, their splanchnic fibres. Besides the Trigeminus, however, the same component is represented in the vago-glossopharyngeal group, and that to a greater extent than is commonly supposed. The homology of what is here denominated the R. auricularis vagi has already been touched upon. The branches, or branch, which Stannius and others have homologized with the R. auricularis vagi in higher forms, appear to be the supratemporal branches to lateral-line organs. There is every reason to suppose, however, that the lateral-line system of nerves completely disappears in the higher forms, especially as the root which supplies them disappears. One of these supratemporal branches in the tadpole is described above. Consequently the homologue of the R. auricularis vagi in higher forms must be the branch in the tadpole which I have described above as the R. auricularis, which has no connection with the lateral-line system and belongs to the general cutaneous system. 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. I have noticed in certain descriptions that dorsal branches are described which the investigator has been unable to trace to lateral sense-organs. Furthermore, Shore (56), in his work on the vagus nerve in Selachians, has described a dorsal cutaneous branch of medium fibres.

Ewart (18) also mentions a dorsal branch from the Glossopharyngeus, immediately beyond its ganglion, which passes upwards through the cranium to reach the skin over the auditory region, and "which apparently does not assist in supplying either mucous canals or sensory tubes." We have, in addition to this, one or two branches which separate from the lateral nerve before its exit from the cranium to supply the aural and part of the occipital mucous-canals, and which are homologous with the minute twig from the lateral-line root in the tadpole (*8*). Ewart and Mitchell further state (19): "The lateralis nerve behind the first branchial cleft consists entirely of special sensory, somatic fibres; in front it seems to be accompanied by a few ordinary, sensory fibres, which reach the skin."

It is possible that the R. meningeus and R. tympanicus in human anatomy are also represented by some of these general cutaneous branches in the tadpole, the R. tympanicus possibly being represented by the R. communicans ad facialem.

A further inference may be made respecting the ganglia. It has been seen above that the ganglionated portion of these general cutaneous nerves lies in the most proximal ganglion (ganglion *A*). It would follow from this and from what has gone before that this ganglion, or ganglia, would represent, in part at least, the two proximal, or jugular, ganglia[1] of the IX + X. This conclusion seems to be similar to Shore's from his study of Selachians (55 and 56).

By a comparison of the tadpole with the higher vertebrates it would seem that there is a considerably larger supply of these general cutaneous fibres, relatively, in the former than in the latter. This is readily accounted for, I believe, by consider-

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[1] There appears to be some confusion in the nomenclature of these ganglia in the text-books of human anatomy. It is not necessary to enter into this here, however, and there need be no confusion if it is understood that the two proximal ganglia on the IX + X are meant.

ing the region thus innervated in the tadpole. It is in general the opercular region; and when, with the loss of gills, *etc.*, it either disappears or is largely reduced, the nerve supply is correspondingly diminished. Thus in the higher forms we have here not only a disappearance of the lateral-line nerves, but a reduction of the general cutaneous nerves of this region.

The homologies of the R. communicans ad facialem present considerable difficulty. In Petromyzon we have a branch, described by Ahlborn and others, which runs around outside the auditory capsule and connects the VII with the IX + X. This branch, however, belongs, according to the observations of Ahlborn, Dohrn (15), and others, to the lateral-line system, and, consequently, cannot be the homologue of the R. communicans ad facialem in the tadpole and frog. This is still further brought out by the fact that while in the tadpole and frog this branch is given off by the IX + X, and passes forwards to reënforce the VII, in Petromyzon the reverse is what occurs, the communicating branch here being given off by the VII and passing backwards around the auditory capsule to reënforce the IX + X, forming a considerable part of the N. lateralis. Kupffer considers this nerve to be a remnant of the "epibranchial" commissure found in Ammocoetes. This view can be best discussed under the consideration of the III component. (See, also, p. 200.)

Goronowitsch (28) describes a communicating branch between the Facialis and the Glossopharyngeus. The nature of this branch can be also best considered later. From his description it would not contain cutaneous fibres.

In Urodela there are described two communicating branches between the IX + X and the VII. One of these, a fine branch, is considered to be the cephalic part of the sympathetic; while the other, stouter branch, does not seem to be always present (Fischer, Hoffmann). Respecting the latter, Fischer (20) remarks that it might pass into either the cutaneous or muscular twigs of the facial branch with which it unites; and, further, according to Volkmann's researches (64), it contains no motor fibres. This agrees with the results above obtained, and this branch is probably the homologue of the R. communicans ad facialem of the tadpole. Its manner of union with the VII is also similar to that in the tadpole. A further study of this nerve in these forms is desirable, especially as it is stated that this branch does not exist in Menobranchus; and yet the R. jugularis has some fine cutaneous twigs. Naturally, Fischer does not distinguish between the cutaneous nerves belonging to this component and those belonging to that next described. From what has been shown, however, there is reason to believe that the cutaneous fibres accompanying the motor branch to the M. mylohyoideus posterior belong to the former, *i.e.*, to the general cutaneous component.

2. *Special Cutaneous or Lateral Line System.*

a. Comparison with other Amphibia.— The second component has been designated, in contradistinction to the preceding, the "*special cutaneous*" component. It includes VII (*a*) and IX + X (*b*). Inasmuch as it is distributed to the lateral sense organs of head and trunk it may also be called the 'lateral component.'

This component is in many respects a remarkable one. Its internal origin or, rather, termination is in certain tracts (and nuclei, Osborn) immediately dorsad to those constituting the origin of the Auditory. These tracts do not seem to be in any way directly continuous with spinal cord tracts as is the case with the ascending Trigeminus. The origin of this component composes, apparently, then, a structure peculiar to the medulla oblongata. The fibres are large and present considerable uniformity in size. This component has evidently a constant and definite distribution, *viz.*, to the lines of sense organs ranged along the head and trunk of the tadpole. The arrangement of these branches and their ganglia has already been described; one point may be here added, namely, that the ganglion cells are not very numerous and do not usually seem to produce any strongly marked ganglionic swelling. There are not, however, very many fibres in these nerves in the tadpole, a fact which accounts for the peculiarity above mentioned. Besides this, its ganglion cells are possibly bipolar (comp. Stannius, 57).

TABLE.

Lateral line system	I. Preauditory. (Dorsal root VII.)	1. Dorsal division proceeding above Trigeminus (ganglion above Gasserian ganglion).	(*a*) Several small twigs inside orbit (R. oticus, etc.).
			(*b*) Supraorbital (R. ophthalmicus superficialis VII).
			(*c*) Infraorbital (R. buccalis VII).
		2. Ventral division joining motor and fasciculus communis roots of VII, and thus forming Truncus hyomandibularis. (Ganglion on this trunk and fused with ventral part of Gasserian ganglion.)	R. mandibularis externus — which divides into several branches (see chart) on lower jaw and side of head.
	[II. Auditory.]		
	III. Postauditory. Most anterior (cephalic) and dorsal root of IX + X.	Lateral nerve ganglion in dorsal and proximal part of IX + X ganglionic complex.	Small temporal twig and Rr. laterales.

The homologies of this system are in the main clear. The *preauditory* portion is represented in Urodela by Osborn's "*7 u* and *l*," which divides after its exit, and a part of which he saw proceed forward to the Gasserian ganglion (45, p. 67, Note). This latter part (*7 u*), passing to the Gasserian ganglion in Cryptobranchus, corresponds to the division in the tadpole, which passes forwards dorsad of the Trigeminus and, after passing through its ganglion above the Gasserian ganglion, divides into the infraorbital R. buccalis VII and the supraorbital R. ophthalmicus superficialis VII, together with smaller branches as already described. These supra- and infraorbital branches have been observed in the tadpole by Fischer (20) and Götte (29), who calls the branch from the VII the radix accessoria. Both investigators correctly surmised their connection with the lateral line system. The ventral division to the R. hyomandibularis, however, seems to have hitherto escaped notice in the tadpole. Fischer describes only four and sometimes only three branches from the Gasserian ganglion in Urodela, and these branches include the usual Rr. ophthalmicus, maxillaris and mandibularis of the Trigeminus proper. The fourth branch, in Siredon, extends directly forwards from the dorsal surface of the Gasserian ganglion, dorsad and mesad of the eye to the nasal region. It is cutaneous. This branch is obviously the R. ophthalmicus superficialis and, indeed, Fischer himself conjectures that it is the homologue of the anterior part of the lateral system found in fishes. For the R. buccalis VII and minor twigs of the lateral system we must look among smaller branches from the Gasserian ganglion not noticed especially in Fischer's description, perhaps because bound up with the Trigeminus branches, — a tendency noticeable, as has been seen, in the tadpole. To properly separate these will require microscopic examination. The cause of this difference between the tadpole and urodele forms is probably found in the different arrangement of the sense organs supplied. In the tadpole they are arranged linearly, in Urodela they appear to be scattered quite irregularly over the head, though exhibiting a tendency to concentration along certain lines. It is possible that the Urodela first pass through the linear arrangement in the course of their development.

That *ventral half* of the lateral line component of the Facialis which apparently unites with the VIII, actually, we have seen, unites with the motor and fasciculus communis portions of the VII, thereby forming the trunk of the Hyomandibularis. It is distributed, we have seen, in the tadpole to lateral line organs lying along the side of the head, and also to a line proceeding around under the ventral side. Here, again, we have in Urodela, as is evident from Osborn's account, a similar division of the lateral component ("VII *l*"), but it is not certain, in all cases, exactly into what branches it finally passes, for the arrangement of the organs is, apparently, different, a fact not surprising when the anatomical differences obtaining between the tadpole and Urodela are considered.

In general, according to Fischer, the arrangement of the Facialis in Urodela is as follows: A reënforcing branch is sent forwards to the Trigeminus, as above discussed. The remainder sends off the R. palatinus and, further along, the R. alveolaris. The discussion of these branches properly comes in another place. Besides these, there are two principal branches, the R. jugularis and the R. mentalis. Either before the separation into these latter two branches or from the R. jugularis, twigs are given off to the M. digastricus. The R. jugularis receives a communicating branch from the IX and supplies the M. mylohyoideus posterior and the subjacent skin. The R. mentalis divides into a branch along the side of the lower jaw, and another branch more mesal. A comparison with the figures of Amblystoma and of the tadpole will, I think, make the homologies perfectly clear. In the tadpole the communicating branch from the IX is received before the VII divides (as is also the case in some of the Urodela) into the R. hyoideus to the M. mylohyoideus and adjacent skin, which = the R. jugularis and the R. mandibularis externus, which = the R. mentalis. Consequently the R. mentalis is the branch belonging to the lateral line system. This homology must be taken with the provision that other fibres, such as general cutaneous fibres from the communicating branch from the IX, may also compose a part of the R. mentalis. A partial mingling of this kind we have found exists in the tadpole. Only a microscopical examination of serial sections, probably, can determine such a point.

It is evident from the above that Osborn was mistaken in his conjecture that the lower of the two most dorsal Facialis bundles, *i.e.*, "VII *l*," is motor. Judging from Amblystoma also, there seems to be no functional difference between the distributions of the two divisions of the dorsal VII. Bürckhardt (12), probably following Osborn, seems to have fallen into the same error of supposing this ventral division to be motor.

The *postauditory* part of the lateral line component, going into the IX + X and emerging as the Rr. laterales is represented by Osborn's most anterior (cephalic) root of the IX (IX 1). Its similar origin to VII *u* and *l* is brought out in his paper. Urodela resemble the tadpole in having several Rr. laterales (Fischer, Ecker). In fishes subdivisions take place further caudad.

A paper by von Plessen and Rabinovicz (48) on the cranial nerves in larvae of *Salamandra maculata* demands some notice, especially as it seems to require correction in several points which are liable to lead to confusion. The authors distinguish two ganglia belonging to the Trigeminus, a "principal ganglion" and, above it, an "accessory ganglion," connected with the Facialis root by their "Radix dorsalis." From the principal ganglion are derived two main branches, (I) the R. mandibularis and (II) the R. nasalis. (I) divides into (*a*) R. communicans cum supramaxillaris, (*b*) R. supramaxillaris inf., (*c*) motor twig to the M. pterygo-temporalis, (*d*) motor twig to the masseter, (*e*) cutaneous twig to jaw angle, and (*f*) R. mentalis. (II) divides into (*a*) twig to rectus superior (?), (*b*) nasal branch, (*c*) R. palatinus, (*d*) cutaneous branch to snout. From the accessory ganglion arise (I) R. communicans c. n. faciali (from the Radix dorsalis) (II) R. frontalis, cutaneous and supraorbital, (III) R. supramax. sup., infraorbital and cutaneous, and giving off a communicating branch to the R. palatinus facialis.

Continuing, they describe the Facialis as arising with the Acusticus. While traversing the auditory capsule it gives off (I) the R. palatinus. After separating from the Acusticus it divides into (II) the R. buccalis and (III) R. hyoideo-mandibularis. (II) after giving off the (*a*) R. alveolaris, termination not stated, divides into (*b*) a branch accompanying the R. hyoideo-mandibularis, cutaneous, and a (*c*) cutaneous branch along the outer side of the lower jaw. (III) receives the communicating branch from the IX and supplies the M. depressor maxillae inferioris, M. intermaxillaris posterior and skin of the lower jaw.

The following criticisms may be offered upon these results: Their "accessory ganglion" evidently corresponds to the lateral ganglion above the Gasserian ganglion, from which proceed the R. ophthalmicus superficialis VII and R. buccalis VII. So R. frontalis = R. ophthalmicus superficialis, and R. supramaxillaris sup. = R. buccalis, excluding any trigeminal elements that may be fused with them. The communicating branch between the latter and the R. palatinus VII, should be between the R. maxillaris V and the R. palatinus. As the R. max. V seems to be reduced or absent (= their R. supramax. inf. ?) and their R. supramax. sup. contains trigeminal elements (from their principal ganglion), this discrepancy may be more apparent than real. In Wiedersheim's *Grundriss* this connection is in one place, by some error, spoken of as between the R. palatinus and R. ophthalmicus profundus.

It is obvious that the branch named R. buccalis by von Plessen and Rabinovicz is misnamed. The branch so named by them corresponds to the R. mandibularis externus (= Fischer's R. mentalis, which they have overlooked in his description, or confused with the V proper), and is derived from the ventral division of the lateral root (= their R. communicans c. n. faciali).

The connection between this system of nerves, *i.e.*, R. ophthalmicus superficialis VII (R. frontalis), R. buccalis (R. supramaxillaris), and R. mandibularis externus (R. buccalis), and the lateral line system, seems to have been entirely overlooked by the above authors, probably for the reason, above mentioned, that these organs do not form definite lines in many Urodela, but are more scattered. Their homology of the R. hyoideo-mandibularis with Fischer's R. jugularis is correct.

These authors have also overlooked the motor and fasciculus communis roots of the VII, owing to their close adhesion to the VIII, and also the ganglion on the fasciculus communis root, which should be at the point where the R. palatinus is given off. The "ganglion buccalis" (= ganglion on ventral half of dorsal VII) of the authors, as shall be seen below, has nothing to do with the ganglion geniculi nor their R. buccalis (R. mandibularis externus) with the chorda tympani.

Another correction of their paper is to be made in connection with the IX + X. According to their text and figures, the anterior (farthest cephalad) and undoubtedly lateral line root emerges from the ganglion, not as the N. lateralis, but as the N. glossopharyngeus. I have traced this coarse-fibred anterior root in Amblystoma larvae through the vago-glossopharyngeal ganglionic complex until it emerges posteriorly as the N. lateralis just dorsal to and parallel with the R. visceralis (R. intestinalis), as figured also by von Plessen and Rabinovicz. This error probably arose from these authors supposing that the most anterior root of the IX + X series must be the Glossopharyngeus.

Arnold (5) has described an interesting condition in *Pipa Americana*, where the VIII, VII, and V are fused at their origin, and the VII and V remain in continuity as far as the Gasserian ganglion. As his work was done upon young specimens, it is possible the lateral line nerves are among those described, and, in fact, the R. ophthalmicus superficialis VII is apparently there identified. What other nerves are to be identified as belonging to this system it is hardly possible to point out, especially as their fusion with the trigeminal branches is here probably carried to an extreme.

I have myself observed in members of the Hylidae, that the separation between the roots of these nerves is quite slight.

Another difference observable between the condition of this component in the tadpole and in Urodela, as seen in Amblystoma and Cryptobranchus, is that it is relatively considerably larger in the latter type. Its final disappearance in the Anura seems to be foreshadowed in the tadpole. (An excellent instance of developing embryonic abbreviation.)

A peculiar circumstance connected with this diminution in the tadpole is the fact, already referred to, that the space relinquished by the dorsal VII is taken up by the VIII. The dorsal VII completely disappears in adult Anura, and the interesting question arises: Does the dorsal VII really atrophy, or does it merely pass over into the VIII? This part of the VII is much more distinct from the VIII in Urodela than in the tadpole. In the former it has a distinctly separate exit; in the latter it and the VIII emerge from the medulla together, the dorsal VII soon separating, apparently as a branch from the VIII. It is certain that when the dorsal VII has disappeared its place is completely occupied by the VIII. The question, however, as to whether there is an extinction or a transference of the dorsal VII can only be answered by following the central terminations of the two nerves on through to the final disappearance of the dorsal VII.

This disappearance of the lateral line component of the VII probably invalidates homologies which have been advanced between its branches in lower forms and its supposed representatives in higher. One of these homologies (R. auricularis) has already been noticed, and another will be discussed below.

In connection with the question here raised arises the interesting problem of the relation of the auditory organ to the lateral line system. The idea that the auditory organ is connected genetically with this system, advanced by Mayser and later by Beard and developed so ably by Ayers, seems likely to find general acceptance. It is not intended to enter into this question in this paper, but it may be remarked that a general survey of the facts of the innervation of these two organs certainly points strongly to a close connection between them.

Incidentally, another point may here be mentioned about which there seems to have been some confusion and which here receives its solution. Osborn says (45, p. 66): "It is seen that, whatever may prove to be the peripheral distribution of the fibres of the fasciculus communis and posterior longitudinal fasciculus, whether to the 7th or 8th, two facts remain: first that the 8th arises ventral to the 7th, although a purely sensory nerve." In a footnote he states that Dr. E. C. Spitzka "questions the determination of the upper bundles, *7 u–l,* in Fig. 15, as parts of the Facial, on the ground that the ventral position of the Auditory reverses the usual order." It is evident that Spitzka meant by the VII the motor portion which actually is ventral to the VIII and present in nearly all vertebrates, possibly in all. Whether the "VII *u* and *l*" which disappears in the higher forms shall be also denominated the VII is largely a question of terminology.

It will now be advisable to compare the condition of these nerves in the tadpole with that in the lower vertebrates. It is not intended, however, to make here a complete analysis of these nerves in fishes especially as I have not made any extended personal investigation upon them.

b. Comparison with the Fishes. — In considering the homologue of this component among lower forms, Goronowitsch's results on *Acipenser* (28) form a convenient starting-point and may be analyzed as follows: Respecting the origin of the N. lineae lateralis, he states that it emerges from the medulla somewhat more dorsally than the Acusticus and between the exits of the Acusticus and Glossopharyngeus. It derives its fibres, which are coarse, from the "dorso-lateral" tract. The fibres form both ascending and descending systems, the latter being notably the larger, of somewhat coarser fibres and traceable to the cerebellum. The Acusticus likewise emerges from the dorso-lateral tract, dorsal to the dorsal root of the VII, "VII" here being used, as we shall see, in a narrower sense. Its principal contingents are from an ascending system in the dorso-lateral tract and a descending system traceable to the lateral part of the cerebellum. The Acusticus also receives fibres from the "durchkreuzten Fasern der hinteren Längsbündel," a part of which are interrupted by the cells of the anterior horn. Some fibres are also received from a group of large cells ventrad of the dorsal root of the VII, which latter root originates from the lobus vagi. Besides these two nerves from the dorso-lateral tract we have the coarse-fibred ventral root of "Trigeminus II" arising from this tract. This root likewise consists of contingents from ascending and descending systems, the former not traceable, the latter, not distinguishable from the other fibres of the dorso-lateral tract, to the cerebellum. A small contingent is derived from the same group of cells that supply a portion of the Acusticus. The exit of this root is somewhat anterior and dorsal to the Facialis and, it may be added from a study of his figures, dorsal also to the Acusticus.

Besides the ventral root of Trigeminus II he describes its dorsal root which has its source in the lobus trigemini. This latter structure reaches distally as far as the exit of the N. lineae lateralis and is separated from the dorso-lateral by the cerebellar "ridge." It consists of a central ganglionic mass which furnishes the principal contingent of fibres to the outer layer consisting of fibres. Relations of fibres to other cell groups which are described need not be dwelt upon here.

Still further cephalad are given off, according to Goronowitsch, the two roots of "Trigeminus I." The dorsal fine-fibred root derived from an ascending system, which he has not traced, and a descending system partly to the lateral portion of the cerebellum and partly to the mid-brain. It is to be observed from the figures given that the immediate source of its fibres is ventral to the dorso-lateral tract. It is this root which we have already identified as the homologue mainly of the Trigeminus major of higher forms. Its ventral coarse-fibred root is derived chiefly from the posterior longitudinal fasciculus, partly also from some cells lying near the curve made by this bundle as it emerges ("Zwischenzellen"). It will be spoken of later.

Goronowitsch, in order to overthrow Balfour's hypothesis as to primitive nerves of a mixed type and to show that Bell's law obtains also for the head, points out that the six roots of the facio-trigeminal complex may be arranged in three pairs, each having a fine-fibred dorsal and a coarse-fibred ventral root, namely:—

FACIALIS	dorsal root from lobus vagi.
	ventral root from posterior longitudinal fasciculus.
TRIGEMINUS II	dorsal root from lobus trigemini.
	ventral root from dorso-lateral tract.
TRIGEMINUS I	dorsal root from ascending and descending systems.
	ventral root from posterior longitudinal fasciculus.

After stating that stimulation had shown some of these roots to be motor and the difficulty of distinguishing them in embryological stages, Goronowitsch lays down the following criteria of a complete spinal nerve: —

(1) The dorsal and ventral roots have different internal origins.

(2) It arises with two roots, a fine-fibred dorsal and a coarse-fibred ventral.

(3) It possesses a ganglion.

It is further remarked by him that the distinction as to thickness of fibre is not very essential.

I may offer the following criticism. These three criteria appear to me hardly sufficient, — the dorsal root should be a ganglionated sensory (afferent) root and the ventral root a non-ganglionated motor (efferent) root. Now in respect to the Facialis and Trigeminus I, the ventral roots spring, consistently, from a bundle (or from ventral cells) which, there is every reason to believe, is efferent. This is not the case, however, with the ventral root of Trigeminus II derived from the dorso-lateral tract. The two other nerves arising from this tract, the Acusticus and Lateralis are *sensory* and the ventral root in question even derives a few of its fibres from the cell group likewise giving origin to a portion of the Acusticus.

My criticism is not especially directed against Goronowitsch's views on the relation between cranial and spinal nerves, but simply to show, from his own observations, that there is no sufficient reason for supposing that the ventral root of Trigeminus II is motor; and thereby to remove, in advance, a possible objection to the homology which I advocate, namely, that Goronowitsch's "ventral root of Trigeminus II" in Acipenser is the same as the one described in the tadpole as the dorsal VII, and that it and the N. lineae lateralis together compose the lateral line system. The character of the fibres and their similar internal origin both point to this homology and, as will be seen below, so probably does their distribution. Moreover, Stannius did not find these roots to be motor.

The above being true, the question naturally arises: what is the homologue in Amphibia of the lobus trigemini? At first sight it would be naturally suggested that the root coming from the lobus trigemini, the dorsal root of Trigeminus II, is represented in Urodela by the upper of Osborn's two Facial roots, *i.e.*, "VII *u*." This, however, I believe is not the case. As has been mentioned, both VII "*u*" and "*l*" together probably correspond to the dorsal VII in the tadpole, as is also shown by Amblystoma. Furthermore, the root from the lobus trigemini is fine-fibred, and though Osborn mentions that the fibres of VII *u* are smaller than those of VII *l*, yet the difference is slight and both are coarse-fibred. From my own observations, and from such investigations as those of Gaskell and others, I am inclined to believe that the size of the fibres is more constant, and consequently of more importance in determining homologies than would at first sight be supposed.

Before looking further for the homologue of the lobus trigemini in Amphibia, a glance will be taken at the condition in the *Teleosts*. In the teleostean medulla oblongata, as is well known, there are three greatly hypertrophied portions known usually as the lobus vagi, the lobus trigemini, and the tuberculum acusticum. Mayser (41) speaks of the common origin of the Acusticus and R. vagi lateralis, and is so much impressed by it that he terms the latter a posterior acoustic root and, further, considers the sense organs supplied by the latter as an accessory auditory organ. He also quotes Leydig, to show the similarity between the semicircular canals and their ampullae and the mucous tubes of the lateral line. Speaking of the same organs on the head he says: "Auch diese Schleimröhren haben nach Stannius nur breite Nervenfasern und zwar aus der II Wurzel des Trigeminus. Die II Quintuswurzel des Stannius entspringt aus dem Tuberculum acusticum und ist bei den Cyprinoiden, wie jener Autor, p. 28, sagt, 'fast ganz verdeckt von der III Wurzel,' d. h. unserer dorsalen geknieten" (= root from lobus trigemini). From this the homology of the tuberculum acusticum with the centre in the medulla of the dorsal VII and N. lateralis of the tadpole, and with the "dorso-lateral Strang" of Goronowitsch in Acipenser is quite evident.

According to Goronowitsch, Trigeminus II gives off the following branches: R. ophthalmicus superficialis, R. buccalis, a small reënforcing branch to the R. oticus, and a stout branch reënforcing the R. hyoideus of the truncus hyoideomandibularis. This agrees with the course of the branches of the dorsal VII in the tadpole, including the stout branch to the R. hyoideus, which obviously represents the ventral half of the dorsal VII which passes ventrad and unites with the Facialis proper in the tadpole. The fact remains, however, that his Trigeminus II includes the dorsal fine-fibred root from the lobus trigemini, obviously the same root as that known as the dorsal geniculated root from the lobus trigemini in Teleosts.

Wright, in his researches on *Amiurus* (72), has traced to a considerable extent, the fibres from these various roots. According to him, the bulk of the fibres of the Rr. buccalis, oticus, and ophthalmicus superficialis come from the broad-fibred tuberculum acusticum root or roots, and the motor VII is also reënforced by the latter fibres, and by others "of narrower diameter from the ganglionic complex." The bulk of the R. lateralis trigemini and ophthalmicus (profundus) are derived from the fine-fibred dorsal geniculate root. Besides these branches two strands are formed: an "infero-medial" derived principally, but not exclusively, from the dorsal geniculate root, and a "supero-lateral" derived principally from the "broad motor" (?) "fibres of the ascending and transverse root." From the former strand, and consequently principally from the dorsal geniculate root, come the Rr. palatinus and cutaneus palatinus to the mucous membrane of the roof of the mouth and gill cover ; from the latter strand, and consequently from the ascending and transverse root, a branch proceeds to the musc. abductor mandibulae. These two strands are then rearranged so that both the R. maxillaris and R. mandibularis receive a portion of each strand. The latter divides into an externus and internus, the internus proceeding along the inner aspect of the jaw and ending in the mandibular barblets, teeth, and mucous membrane, as well as the intermandibular muscle. Wright is probably mistaken in speaking of the ascending and transverse root as motor. The former, ascending part, must be sensory, while the transverse is motor. That the former is not all motor may even be inferred from his own description, inasmuch as while the R. maxillaris receives a portion of this root, yet no motor branches are mentioned in its distribution. This ascending part is the sensory Trigeminus proper.

Wright's account agrees with that of Goronowitsch in some respects, but differs in others. Trigeminus II, or a root from the tuberculum acusticum plus one from the lobus trigemini, gives rise to the Rr. ophthalmicus superficialis, buccalis, and oticus, and reënforces the VII. On the other hand, according to Wright, the ophthalmicus profundus is derived from the lobus trigemini ; according to Goronowitsch, from the non-homologous Trigeminus I. There appears to be no R. lateralis trigemini in Acipenser. Another important difference is that Wright assigns two Rr. palatini to the Trigeminus, derived from the lobus trigemini, while Goronowitsch denies the existence of any such branches from the Trigeminus, and asserts that they belong exclusively to the Facialis. This latter point will be discussed later. There should be three Rr. ophthalmici, one the profundus and the other two Rr. ophthalmici superficiales, of which one belongs to the Trigeminus proper (= Trigeminus I), and the other is derived from the Facialis (ventral root of Trigeminus II = dorsal VII plus, in some cases at least, fibres from a root emerging from the lobus trigemini). Both Goronowitsch and Wright appear, however, to describe only two. This, together with the fact above mentioned, that the ophthalmicus profundus of one does not seem to be strictly homologous with that of the other, is difficult to account for.

It is in Stannius' splendid memoir, *Das peripherische Nervensystem der Fische* (57), that we find the most accurate account, it seems to me, of the peripheral nervous system of fishes. Stannius not merely dissected but also checked his results by stimulating the roots, and, likewise, investigated the character of the fibres composing the roots and branches.

For the N. trigeminus cum nervo faciali in forms where the roots are most separated (*Pleuronectes*), Stannius describes the following roots:

1st root, stout ; mixed fibres, *viz.*, mostly medium, with a number of very large fibres and a smaller number of fine fibres. Contains a motor element to the jaw muscles.

2d and 3d roots, more dorsal ("nach hintere oder obere") and originating from the Lobus medullae oblongatae, s. Lobus posterior (which also gives rise to R. lateralis nervi vagi). Fibres exclusively large, some being as large as motor fibres, *e.g.*, those of the oculomotor, and others, in smaller number, still larger. After their exit these roots exhibit no perceptible ganglionic swelling, but closer investigation shows their fibres to be continuous with bipolar ganglion cells. These roots are non-motor. One goes over into the Trigeminus, the other into the Facialis.

4th root, "entspringt abwärts von den vorigen etwas mehr aufwärts oder hinterwärts als die erste Wurzel, aus der Seite der Medulla oblongata." Fibres fine and ganglionated, but not so apparently connected with ganglion cells, which are seldom bipolar. Non-motor. A part goes over to the Trigeminus, a part to the Facialis, and a part composes the bulk of the R. palatinus.

5th root, smallest, furthest caudad, issuing immediately in front of the first acoustic root. Fibres exclusively large. Motor. Goes over entirely into the Facialis.

In *Raja*, according to Stannius, we have only three roots, which closer examination resolves into four, inasmuch as roots 3 and 4 of bony fishes are in close apposition.

1. Emerges in two strands, is composed of fibres of various size and also of mixed functions, the motor fibres being in the ventral part. This root corresponds to root 1 of bony fishes.

2. Emerging close to VIII, principally from corpus restiforme. Part goes over into V and part into VII. Fibres are partly broad and partly half as broad. Some of the fibres are motor, which belong to the VII exclusively.

3. A large "hintere oder obere" root, arising above the preceding, of broad fibres and non-motor. A part mingles with 2 and part goes over into the V.

Stannius summarizes as follows:

Root I. — Motor and sensory. Fibres mixed. Belongs to the Trigeminus proper. Sometimes divided.

Root II. — Non-motor, "hintere," sometimes single, sometimes divided. From corpus restiforme. Only broad fibres connected with bipolar ganglion cells. Principally distributed to mucous canals.

Root III. — Non-motor, "hintere." Only fine fibres. Large ganglionic masses. Distributed especially to mucous membranes, skin, and touch organs, especially on the barbels.

Root IV. — Exclusively motor, arising close in front of the Acusticus and going over into the VII (coarse-fibred).

The numbers vary owing to subdivisions and fusions.

According to Stannius the Facialis proper (Hyoideo-mandibularis) divides into a posterior, or more caudal branch, the R. hyoideus, and a more anterior one, the R. mandibularis, proceeding along the lower jaw, which either gives off a branch to the mucous membrane of the mouth or subdivides into a R. mandibularis externus to the skin and mucous canals, and a R. mandibularis internus to the mucous membrane of the mouth.

In the first account (Pleuronectes), root 1, evidently, is the Trigeminus proper, 2 and 3 are the lateral line roots, and 5 the motor root. Root 4, probably, is the one described by Stannius elsewhere and by other authors as arising from the lobus trigemini. The question of its homologue in Amphibia will be discussed below. There is, however, some obscurity in Stannius' account of this root. It would appear from his description to lie sometimes ventral and sometimes (*e.g.*, compare his account of Cyprinoids) dorsal to 2 and 3.

Gegenbaur (26) describes, in *Hexanchus*, the Trigeminus as arising from two trunks, an anterior and a posterior one ("vordere" V *a* and "hintere" V *b*). The former is composed of two roots with difficulty distinguishable. The posterior trunk is also composed of two roots, one, the most dorsal (V *α*) arising from a large swelling overhanging the fourth ventricle, and the other more ventral (V *β*) emerging from the medulla close above the Facialis, and somewhat cephalad and dorsad to the Acusticus. V *b* proceeds above V *a* and the two enter the Gasserian ganglion, there being an intermingling of fibres. The R. ophthalmicus is derived principally, but not exclusively, from V *α*.

Jackson and Clarke (32) describe the Trigeminus as arising in *Echinorhinus* from two main trunks. (1) V *a*, furthest cephalad, more ventral, and issuing from the medulla by two roots, and (2) V β further caudad and dorsad, and issuing from the lobus trigemini by two rootlets, one dorsal to the other. V β proceeds above V α and is closely united also to the Facialis root V γ VII, part of whose fibres issue just above the VIII.

Gegenbaur's anterior root, V *a*, is the Trigeminus proper, including both the sensory element from the ascending tract and the motor root. His most dorsal root of V *b*, *i.e.*, V α, is the one derived from the lobus trigemini. V β is, probably, the lateral line root from the tuberculum acusticum. His Facialis is the motor root plus, possibly, a root from the lobus vagi (*vide infra*, p. 193).

In Jackson and Clarke's account, V α = Gegenbaur's V α and V β = Gegenbaur's V *a*. V γ VII is probably compound. That portion of its fibres issuing above the VIII may be derived from the tuberculum acusticum, — in fact must be unless Jackson and Clarke are mistaken in deriving *both* rootlets of V β from the lobus trigemini — and may be also, in part, derived from the lobus vagi (compare Goronowitsch and see below, p. 193). This root must also, of course, contain motor fibres.

Marshall and Spencer (43) describe, in *Scyllium*, a R. ophthalmicus superficialis from the VII having a course closely parallel and superficial to the corresponding trigeminal branch, a buccal branch whose proximal portion forms a connecting branch with the V, and whose distal portion proceeds parallel and superficial to the maxillary branch of the V, and a posterior or hyoidean branch. With respect to the first two, the principal difference between it here and in Amphibia seems to be that the forking into the two branches, Rr. ophthalmicus superficialis and buccalis, takes place more distally in the latter, so that the common trunk of the two forms the connecting branch and contains the ganglion. Respecting the hyoidean branch, they do not seem to be aware that the cutaneous R. mandibularis externus is, in part, a nerve to mucous canals similar to the two preceding branches. They also fall into the error, the existence of which seems to have been first pointed out by Allis in Amia, and later by the writer in the tadpole, of supposing that the Trigeminus takes part in the innervation of the lateral sense organs of the head, an error repeated in most of the text-books.

In treating of the roots, Marshall and Spencer come to the following conclusions: The fifth nerve in the adult arises by two roots: (*a*), an anterior non-ganglionic arising by two rootlets (V γ) = "1st root of Stannius, the anterior root (V *a*) of Gegenbaur, the anterior inferior root (V α) of Jackson and Clarke, and the anterior root (1) of Balfour."

"(*b*) A posterior, larger ganglionic root, the ventral or secondary root (V β)" = "anterior part of the second root of Stannius, the ventral division (β) of the posterior root (*b*) of the the fifth of Gegenbaur; apparently the inferior rootlet of the second root (V β), and possibly part of the third root (V γ and VII) as well, of Jackson and Clarke; the second root (2) of the fifth of Balfour."

"The seventh nerve in the adult arises by two roots: (*a*) A dorsal root arising far up the side of the medulla, at the junction of the thickened sides and thin roof of the fourth ventricle" ("primary" root of VII, VII α). "This root is the third or dorsal root of Stannius; the dorsal rootlet (*a*) of the posterior trunk (*b*) of the fifth of Gegenbaur; the superior rootlet of the second root (V β) of Jackson and Clarke, and the dorsal and posterior root (3) of the fifth of Balfour."

"(*b*) A ventral root arising from the side of the medulla at a rather lower level than the posterior root of the fifth" ("secondary" root of VII, VII β). In the adult it comes to lie in close contact with the secondary root of the fifth. "This root is the posterior part of the second root of Stannius, the root of the seventh of Gegenbaur; part, or possibly the whole of the third root (V γ and VII) of Jackson and Clarke; and the single root of the seventh of Balfour."

These investigators first showed that the R. buccalis belongs to the VII. Their homologies do not appear to me, however, to be entirely correct. Their second posterior ganglionated root (*b*) of the V is plainly the sensory root of the Trigeminus proper. As such, it corresponds, together with the motor rootlets sometimes apparently distinct and sometimes fused with the sensory portion, to Stannius's first root, to Gegenbaur's V *a*, and to Jackson and Clarke's V *a*. Their first dorsal root (*a*) of the VII is the one derived from the lobus trigemini in all probability, and is correctly homologized. Their second ventral root (*b*) of the VII must be regarded as compound, consisting of a lateral line portion, a motor, and possibly a root from the lobus vagi. Compare tadpole (see below) and Goronowitsch's account of Acipenser.

Ewart (18) has described these roots in *Laemargus* as follows: the ophthalmicus profundus arises by a separate root in front of the main Trigeminus. The latter arises by a large root on a line with the ventral roots of the Facialis complex. Its branches are the ophthalmicus superficialis, maxillaris, and mandibularis. The Facialis includes four separate nerves: (1) Ophthalmicus superficialis, arising from the so-called trigeminal nucleus by a root dorsad and caudad of all the others. It communicates with the buccalis as it passes through the cranial walls at a higher level than the Trigeminus and ophthalmicus profundus. (2) Buccalis arises behind and at a slightly higher level than the trigeminal. It is infraorbital. (3) Palatinus and hyomandibularis arise by a large root between the Trigeminus and Auditory, and partly under cover of the buccalis. It receives fibres from (1), and then passes outwards with the Auditory, giving off the R. palatinus, and finally dividing into branches to muscles and to canals and ampullae not supplied by (1), nor (2), nor the R. lateralis.

Here (2) and part of (3) are lateral-line roots. (3) must be regarded as in reality compound, comprising motor and, probably, lobus vagi roots, as well as lateral-line fibres.

Burckhardt (11) has designated the most dorsal root of the Acustico-facialis "VII," and attributed to it a motor character. There can be little doubt that this is in reality the preauditory lateral-line root, and the error noted above (p. 162) has been here repeated. (See, also, page 185.)

The following table shows the probable homologies of the preauditory lateral-line roots in the descriptions of these investigators:

TABLE OF PREAUDITORY LATERAL LINE ROOTS.

TYPE.	AUTHORITY.	ROOTS.	CENTRAL TERMINATION.
Cryptobranchus	Osborn	"VII *u* and *l*."	
Acipenser	Goronowitsch	"Trigeminus II," ventral root	"Dorso-lateral" tract.
Cyprinoids	Mayser		Tuberculum acusticum.
Amiurus	Wright	(Rr. buccalis, oticus and oph. sup.)	Tuberculum acusticum.
Pleuronectes	Stannius	2d and 3d roots	Lobus medullae oblongatae s. lob. post.
Raja	Stannius	2d root (?)	Corpus restiforme.
(Generalized type)	Stannius	2d root	Corpus restiforme.
Hexanchus	Gegenbaur	Vβ.	
Echinorhinus	Jackson and Clarke	part of V γ VII, probably.	
Scyllium	Marshall and Spencer	part of VII *b*.	
Laemargus	Ewart	Buccalis and part of Hyomand. and Pal.	
Protopterus	Burckhardt	VII.	
Larvae of Anura	Strong	"dorsal VII" ("VII *b*").	

Regarding the N. lateralis, we find that it has in Selachii a similar character from Shore's account also of the Vagus in the shark. According to him, the lateral-line portion of the Vagus is coarse-fibred and distinct in origin from the rest of the nerve. It also possesses its own ganglion of rather scattered ganglion cells. Its internal organ is not traced. A peculiar feature, however, is that the lateral-line part of the Vagus arises from a number of fasciculi forming the *most posterior* (*i.e.*, caudal) of the roots of the Vagus, and somewhat *more ventral* than the others. This account differs from the exit of this root in Amphibia, Ganoids, and Teleosts, judging from the writer's observations and the papers of Goronowitsch, Mayser, Wright, and Ewart, as shown above. In all of these the R. lateralis has its exit cephalad and dorsad of the rest of the vago-glossopharyngeal roots.

I may add that in some dissections made at the Marine Biological Laboratory at Woods Holl during the summers of 1892 and 1894, upon *Galeus canis* and *Galeocerdo maculatus*, I found also that the R. lateralis invariably arose by a single root cephalad and dorsad of the other roots of the IX + X. I cannot reconcile Shore's account in this respect with those of other investigators or with my own observations.

The lateral-line nerve, I found, may be reënforced by fibres from one or both of the next two Vagus roots. What the character of these fibres is can only be surmised, and will be discussed below. Ewart and Mitchell (19) have made a similar observation, and judging from what has been quoted (p. 156), some of these at least would be general cutaneous fibres.

(*c*) *Résumé of the Roots in Fishes.* — In general, the arrangement of these roots and principal branches seems to be as follows:

1. The Trigeminus proper, with fibres of varying sizes, which sometimes arises by two roots, in which case the one cephalad is the R. ophthalmicus profundus. Besides this latter it divides into the R. ophthalmicus superficialis, the R. maxillaris, and the R. mandibularis. It is this Trigeminus proper, the central continuation of which is an ascending tract from the cord, which has also a ventral motor root added, and is constant in the main throughout the vertebrate series.

2. One or usually two broad-fibred roots arising from the tuberculum acusticum (=lobus posterior medullae oblongatae, Stannius = corpus restiforme = dorso-lateral tract, Goronowitsch). One of these passes forwards over the Trigeminus proper and Gasserian ganglion and there divides into the supraorbital R. ophthalmicus superficialis and the infraorbital R. buccalis. The other root, nearest the Acusticus, unites with a motor root, and passes into the hyoideo-mandibularis — the Facialis proper.

3. A root, most dorsal of any, from the lobus trigemini (= lobus impar). This root divides in such a way as to send fibres to both divisions of No. 2. While that part of No. 2 joining the Trigeminus does not seem to necessarily form an intimate union with the latter, No. 3 seems to completely mingle with No. 2. Besides mingling with the latter, however, No. 3 in some cases forms a R. palatinus and a R. lateralis, besides other smaller branches. Often the R. ophthalmicus superficialis VII appears to be especially connected with this root.

4. A broad-fibred motor root close to the Acusticus and passing exclusively into the hyoideo-mandibularis.

5. In some cases, at least, a fine-fibred root from the lobus vagi (Goronowitsch).

The N. lateralis vagi always arises by a broad-fibred root from the tuberculum acusticum, dorsad and cephalad of the other roots of the IX + X.

I may add here that this arrangement of the roots is confirmed by my own dissections of Selachians.

It is No. 2 which innervates the lateral canals in all cases, a fact which Stannius seems to have clearly recognized, though he does not always seem to have distinguished clearly between its branches and those of the Trigeminus proper. Marshall and Spencer, and Van Wijhe, I believe, were the first to make this clear. The fact that the Trigeminus proper does not participate in the innervation of the lateral-line system has also been brought out by Allis (Amia), by Ewart (Laemargus and Raja), and by the writer (tadpole).

It is very evident from the above that the lateral-line system of nerves are alike in their main arrangement in all the forms in which they have been studied and carefully distinguished. The agreement between the larval forms of Anura and the fishes is quite remarkable. The same general plan holds for both. It is owing principally to the labors of Allis and Ewart that this general plan has been made clear in fishes. As in the latter forms many variations are found, such, doubtless, will be found the case also in amphibian larvae and in Urodela, both in the arrangement of the organs and the courses and smaller ramifications of their nerve supply; but the roots and principal divisions and their arrangement will probably be found to hold good for all.

One very important difference, apparently, between the conditions in fishes and Amphibia, has emerged however; and this relates to root No. 3. The question of the fate of this root can be most conveniently considered with the next component, though in many respects it falls most properly under the component just discussed.

3. *Fasciculus Communis.*

a. Amphibia.—The third component is, as has been described, derived from the fasciculus communis.

Table.

Fasciculus communis (+ adjoining nucleus?).	Preauditory — one root (gang.)	R. palatinus — roof of pharynx. R. mandibularis — portion of floor of pharynx.
	Postauditory — several roots (gang.)	R. lingualis IX — part of floor of pharynx. Rr. pharyngei — pharynx and part of filtering apparatus. Rr. branchiales — gills, part of filtering apparatus and pharynx. R. visceralis — heart, lungs, oesophagus, etc.

This remarkable tract appears in transverse sections of that part of the medulla of the tadpole just cephalad of the opening of the fourth ventricle, as an oval island, as it were, imbedded in the ganglion cells of the central gray. It is here almost in the extreme dorsal part and quite close to the ventricle. It can be traced caudad into the spinal cord a short distance only, in the adult frog. It lies then in the posterior columns close to the median line. Judging from Weigert preparations it contains in this portion only a very few medullated fibres. According to Golgi preparations in the tadpole there are few fibres in it in this region (Pl. XI, Fig. 31). The remainder is made up apparently, of a "ground substance." The change in position and character of this structure as we advance cephalad is well shown in the Golgi preparations from which Figs. 31–39 inclusive were drawn. The tract gradually comes to lie further ventrad and laterad and also increases in size. The number of fibres in it, all fine and with a thin sheath or none, also increases very greatly as shown both by the Golgi and Weigert preparations. The maximum is reached at the level of the exit of the second root of the IX + X, which, as we have seen, derives a considerable portion of its fibres from the fasciculus. Cephalad of this, it continues as a small bundle, rather difficult to follow in the tadpole, until it passes out in one of the facial roots as described above (p. 113, see also Fig. 39). Whether a portion of it continues on still further cephalad could not be ascertained in the tadpole. According to Osborn (45), it does continue forward in Cryptobranchus. As seen in the figures (31–39) its course is nearly parallel with the ascending Trigeminus tract. Both undergo, on entering the medulla, a downward deflection. Consequently, if the ascending Trigeminus (and this tract?) represent morphologically, in the medulla, the posterior columns of the cord, the tracts and nuclei connected with the lateral line system are superadded structures, inasmuch as they lie dorsal to these. (Compare Ahlborn on Petromyzon.)

As the fasciculus communis retreats from the immediate vicinity of the ventricle or, rather, central, canal and from the mass of cells surrounding the latter in the tadpole, a number of the cells are detached with it and form a group on its inner ventral side. This group of small cells, as shown in ordinary carmine preparations, accompanies the fasciculus throughout its course and, moreover, seems to vary in size *pari passu* with the variations in size of the fasciculus. It nearly or quite disappears cephalad of the second root of the IX+X.

The fibres of the fasciculus communis do not appear to be connected directly with nerve cells in the medulla, though, as indicated in Fig. 12, the surrounding cells frequently send their protoplasmic processes into it. As the nerves originating from it are ganglionated, such ganglia are to be considered as its nuclei of origin ("Ursprungskern," Kölliker 34), while the group of cells above described are to be considered possibly as its terminal nucleus ("Endkern," Kölliker 34). It is possible that some fibres of these roots proceed directly to the nucleus without passing into the fasciculus. From Osborn's description this would seem to be the case in Cryptobranchus, for besides the nuclei corresponding probably to the lateral line nuclei and the motor nuclei we have another nucleus (whose character is considered doubtful by Osborn).

The diminishing size of the fasciculus from the level of the exits of its roots on caudad in the medulla is due to the gradual loss of its fibres as they terminate freely along their route. The peculiar compound character of the fasciculus as described by Osborn is explicable when we consider that the fibres grow into the medulla by means of the various roots and there unite to form the fasciculus.

It is evident that this tract is composed exclusively or almost exclusively of *visceral* (splanchnic) fibres innervating the alimentary canal and its appendages. Whether, however, it is composed of efferent or afferent fibres or both, is not so clear. It would seem quite certain, however, that many, or most, of the fibres terminating in epithelium are to be regarded as afferent. This is true also of many of the fibres innervating the filtering apparatus. The character of the fibres so richly innervating the curious glands found in the vicinity of the opening of the gill clefts into the pharynx is not so clear. If we assume the existence of secretory fibres, it would seem certain that some of them must be of this character. We have also seen that some of the vaso-motor fibres, including those to the heart, appear to belong to this component. The fact that these fibres have peripheral ganglia as their nuclei of origin does not necessarily disprove this, as they may in this respect resemble the sympathetic. Altogether it seems most reasonable to regard this tract together with its nucleus as composed of both afferent and efferent fibres.

This tract has been noticed by several writers, apparently, and I can hardly agree with Osborn when he speaks of it as a bundle not hitherto described if he means this to apply to Amphibia in general. Stieda, in his account of *Axolotl* (59) says: "Die stärkste oder die vorderste Vaguswurzel, welche etwa dem N. glossopharyngeus der Säuger zu vergleichen wäre, verhält sich etwas anders als die hinteren Wurzeln. Bereits ziemlich weit hinten markirt sich im oberen Abschnitt der grauen Substanz und zwar in der Kernzone eine lichte Stelle; hier sammeln sich allmälig feine Nervenfasern zu einem beträchtlichen Längsbundel, welches durch Vermittelung vieler kleiner dicht auf einander folgender Wurzelbündelchen das Mark verlässt. Das ist die Hauptwurzel des Vagus." And again in his description of the central nervous system of the frog: "Bereits in der Gegend der Uebergangstelle des Rückenmarks in die Medulla oblongata macht sich auf Querschnitten dicht zu beiden Seiten des erweiterten Centralcanals ein rundlicher Fleck bemerkbar (Fig. 9 u. 10 *k*), welcher durch einige Kerne und kleine Nervenzellen eingefasst, sich von der übrigen grauen Substanz abgrenzt. Bei Untersuchung einer ganzen Reihe hinter einander liegender Querschnitte erscheinen in dieser runden Gewebsinsel anfangs spärlich, später reichlich querdurchschnittene Nervenfasern in kleinen Bündelchen. Dabei rücken die kleinen Bündelchen immer noch in der Gewebsinsel eingeschlossen allmälig der lateralen Peripherie näher, bis sie endlich derselben ganz nahe gekommen sind. Unterdess ist die scharfe Begrenzung der Bündel durch die sie begleitende Grundsubstanz verloren gegangen und statt des querdurchschnittenen Längsbündels ist auf dem nächsten Querschnitte ein starkes schräg abwärts geneigtes, abtretendes Wurzelbündel des Vagus sichtbar, dem sich ein oder zwei der früher beschriebenen Querbündel anschliessen (Fig. 11 *l*)." Stieda was unable to trace these fibres to any cells. Köppen (35) seems to refer to this tract when he says: "Schon kurz vor der Eröffnung des Centralcanals, bald nachdem die letzte dorsale Wurzel das Rückenmark verlassen hat, tritt dorsal in der grauen Substanz ein Längsbündel feiner Fasern zu Tage, eingelagert in einer dichten grauen Masse, die sich kreisförmig von der übrigen abgrenzt (Substantia gelatinosa Rolando), s. Taf. I, Fig. 3 S. g. R. Diese Substanz ist nur die Fortsetzung der gelatinösen Masse, welche wir im Rückenmark, innen vor den dorsalen Wurzeln, fanden. In ihr zeigen sich nun einige Längsfasern, *ein aufsteigendes Wurzelbündel des Vagus und des Trigeminus.* Es rückt allmälig aus der grauen Substanz immer mehr dem Rande zu und liegt schliesslich median von dem Seitenstrang und den Dorsalsträngen." Köppen seems to have recognized the fact that this tract is continued cephalad of the IX + X but refers it to the Trigeminus instead of the Facialis. As he seems to have overlooked also the motor bundle of the VII which makes its exit with the VIII or, rather, refers it to the VIII, he is compelled to seek for the VII in the V and derives both the VII and the motor portion of the V from the motor nucleus of the V. Osborn remarks: "At this point he (Köppen) fails to distinguish between the Facial and Auditory elements, for his dorsal Auditory root, p. 9, is probably the main portion of the Facial. This error, if error it be, arises from the fact that he expects to find the facial a purely motor nerve, p. 10." Köppen must be acquitted on this point, however, for the "main portion of the Facial" referred to (Osborn's "*7 u* and *l*" = "dorsal VII" to lateral sense organs) has disappeared in the frog. Köppen's real error is in not distinguishing between the V and VII and into this error he may have been led as Osborn suggests.

Osborn gives a correct account of the exit of this bundle, but was unable to determine whether it ultimately went to the VIII or the VII. As shown above, the latter is the case. There exists a remarkable difference, however, between the exit of the fasciculus communis in Urodela, on the one hand, and in Anura and tadpoles on the other. In the former the exit of this fasciculus to the VII takes place just *dorsal* to the

VIII, while in the latter it is just *ventral* to the VIII. This change is perhaps correlated with the change in position of the Auditory, which has already been touched upon.

It may be most conveniently noted here that Burckhardt (11) describes in *Protopterus* a dorsal root belonging to the VII, partly motor, a root beneath it from the fasciculus communis, which he attributes to the VIII ("*VIII* 1") in his nomenclature, a second and largest root to the VIII ("*VIII* 2") below this, then finally and most ventral a root derived partly from the posterior longitudinal fasciculus and partly from a motor nucleus. This latter he also attributes to the VIII ("*VIII* $_{3.4}$"). Burckhardt probably follows Osborn in this assignment of these roots, which are so very similar to those in Cryptobranchus. In this, as we have seen already, he is mistaken. The dorsal root is the lateral line root, and is entirely sensory. The fasciculus communis root and the most ventral root should be assigned to the VII and not to the VIII. The VIII is represented entirely by the largest root ("*VIII* 2") between the two last mentioned.

The most interesting fact to be noticed here is that in the position of its fasciculus communis root, Protopterus agrees with the Urodela and differs from the tadpole, from Anura, from Acipenser, and not improbably, if the views taken on p. 193 be proved correct, from Selachii in this respect.

(*b*) *Higher Vertebrates.* — Before looking further at the lower vertebrates it may be well to take a glance at the higher forms. In the human medulla, as is well known, the principal sources of the IX + X are three, (1) from a motor nucleus, the nucleus ambiguus, (2) from a so-called sensory nucleus, and (3) from the fasciculus solitarius. We have also the motor nuclei of the XI, principally similar or identical with those of the IX + X.

Kölliker, in the latest edition of his *Gewebelehre*, gives a very clear and complete account of the fasciculus solitarius. It is apparent some distance caudad of the calamus scriptorius lying latero-dorsad of the sensory terminal nucleus of the IX + X, and consequently quite near the median line in the dorsal part of the cord. It gradually increases in size as it proceeds cephalad, and also gradually becomes further removed from the median line. It finally passes out into the IX + X by some 8 or 10 rootlets, which break through the ascending trigeminal tract to make their exit. It is here this fasciculus attains its greatest dimensions. A small portion of it, however, continues cephalad, and emerges as the portio intermedia Wrisbergii of the VII. It is accompanied as far as the exits of the IX + X on its inner side by the "sensory" nucleus of the IX + X. The finer structure of this bundle is as follows: it consists of the finest fibres with gray matter intermingled; the fibres both divide and give off collaterals which encircle the nearest ganglion cells.

It is evident, from the above brief résumé of Kölliker's account, that the *fasciculus communis corresponds with the fasciculus solitarius* in every detail, and that the nucleus on the inner side of the former corresponds with the so-called sensory nucleus of the IX + X.

Furthermore, inasmuch as the fasciculus solitarius is continued cephalad into the portio intermedia, it is evident that the *portio intermedia* is represented in the tadpole by the fasciculus communis root of the VII, the *ganglion geniculi* by the ganglion of this root, fused in the tadpole with the ganglion Gasseri, but separate in Amblystoma, and the *chorda tympani* by that portion of the fasciculus communis which, on emerging from its ganglion, unites with the hyomandibularis VII, separates as the R. mandibularis internus, and innervates portions of the floor of the pharynx, especially that part, in the tadpole, near the site of the future tongue. The R. mandibularis internus thus corresponds, point by point, with the chorda tympani, having the same character of fibres, the same internal origin, and the same course and final termination.

That the R. palatinus would correspond, in part at least, to the R. superficialis major, would seem probable. One objection to this view, *i.e.*, that the latter is a motor nerve to the muscles of the palate, has been removed by Turner (63), who has shown that probably the muscles of the soft palate derive their motor supply from the pharyngeal plexus through the pharyngeal branch of the Vagus. Another serious objection, however, arises from von Lenhossék's discovery (39), that the fibres of the superficialis major are not connected with the geniculate ganglion. As we shall see later, the innervation of the mouth (in the broader sense) is a complicated problem.

The homology of the R. mandibularis internus with the chorda tympani was first briefly discussed by me in the articles in the *Zoologischer* and *Anatomischer Anzeigers.* Since then Gaupp (25), reasoning from topographical relations, has come to a similar conclusion.

In Urodela the R. mandibularis internus, or chorda tympani, is represented by the R. alveolaris VII, which usually, for part of its course, proceeds in a canal in the lower jaw. Fischer was not able, apparently, to determine its distribution clearly. He mentions, however, twigs to the skin. This is probably either incorrect, or such twigs leave the proximal part of this branch and are composed of cutaneous fibres not properly belonging to the R. alveolaris. Von Plessen and Rabinovicz do not mention its final distribution.

Although anticipating somewhat, it may be here noted that Ewart describes a bundle of fibres continuous with the root of the R. palatinus and running forwards to end in the "fold of mucous membrane lying between the hyoidean and mandibular cartilages." This he regards as the homologue of the chorda tympani. Pollard (49) also regards the R. mandibularis internus as the chorda, and correctly homologizes it with the R. alveolaris in Urodela. The other view of Froriep (22), that the chorda is represented by a sensory branch to the lower jaw similar to the R. ophthalmicus superficialis and buccalis, *i.e.*, a lateral line branch is certainly not correct. In addition to the criticism made by Wiedersheim (67, p. 286), the chorda in every way corresponds to the R. mandibularis internus, as stated above, and not to the R. mandibularis externus, which innervates lateral line organs.

It is possible, however, if, as Kupffer (36) suggests, Froriep really treats of epibranchial and not lateral ganglia, that he had the correct nerve, but was mistaken in assigning it to the lateral line system.

In the IX + X the two outer ganglia on these nerves

(*B* and *C*), which belong more especially, apparently, to the fasciculus communis component, would correspond to the two outer ganglia on the IX and X in the higher vertebrates, namely, those usually designated the ganglion petrosum IX and ganglion trunci vagi. They would be partially, at least, homodynamous with the ganglion geniculi.

(*c*) *Comparison with the Fishes.* — It is evident that so important a tract as the fasciculus communis must be represented among the forms below Amphibia, and it is tolerably certain that the homologue is the *lobus vagi* of fishes.

In Goronowitsch's article on the brain and cranial nerves of *Acipenser* (28) is the following: "In der Gegend des Calamus scriptorius ist, wie gesagt, die graue Substanz des Hinterhornes breiter entfaltet. Sie hat dieselbe Struktur wie im Rückenmark. Medial vom Hinterhorne erscheint allmählich eine neue Lage von grauer Substanz. Sie besteht aus feinkörnigem Grundgewebe, in welchem viele kleine Nervenzellen eingebettet liegen (Fig. 45 L v.). Zwischen diesen Zellen verlaufen die feinsten Fasern in verschiedenen Richtungen. In proximalen Abschnitten wächst die Querschnittsoberfläche dieser Substanz. Sie verbreitet sich in dorsaler Richtung und verdrängt lateral den Hinterhornkopf. In proximalen Ebenen bildet diese graue Substanzlage einen Vorsprung im ventriculus IV. Es ist das der Lobus vagi." Goronowitsch mentions, as do other writers, the series of swellings visible in the wall of the ventricle, and caused by the lobus vagi, and says they correspond to the bundles making their exit from it. They form the dorsal source of the Vagus and Glossopharyngeus roots, exclusive of the N. lateralis, and are fine-fibred. Goronowitsch also finds that a bundle is given off from the lobus vagi to the Facialis.

In all accounts there is a remarkable agreement, — the situation in which it appears, in the vicinity of the opening of the fourth ventricle, its peculiar appearance and composition there which leads to its description as "eine lichte Stelle," "ein rundlicher Fleck," "eine runde Gewebsinsel," "ein Längsbündel feiner Fasern eingelagert in einer dichten grauen Masse," "eine neue Lage von grauer Substanz," consisting of "feinkörnigem Grundgewebe," the appearance in it of fine fibres which form the chief supply of the IX + X,—all these peculiarities demonstrate the homology here suggested.

This tract is described by other investigators of the medulla of fishes, and there seems to be essential agreement between all their accounts, with variations respecting the number of enlargements presented by it. Rohon (52) gives a more detailed account of it in Selachii, and considers it as representing the summation of a number of nerve nuclei. The nerves originating from these he considers homologous to dorsal spinal roots, — a view which is discussed elsewhere.

Among the *Teleosts*, Mayser (41) gives a detailed account of the structure of the lobus vagi, which is here enormously developed. Mayser distinguishes five parts in the lobus vagi: (1) The outermost layer, comprising the bulk of the fine-fibred roots, of which there are two layers — a thicker outer of medullated fibres, and a thinner inner layer of non-medullated fibres. (2) The gelatinous substance, consisting of a dense ground-substance with numerous nerve cells interspersed. There are also solitary bundles of fine fibres here which join the first layer. (3) The secondary vagus-tract, consisting of fibres from (2) and from the "spongy substance," which is to be considered the central gray. This tract is joined by the secondary tract from the lobus trigemini, and proceeds cephalad to the higher centres. (4) The origin of the thick-fibred motor vagus-roots. (5) Ependyma.

Mayser, it may as well be added here, describes the lobus trigemini as having much the same structure as the lobus vagi, and on this ground and from the fusing of their secondary tracts he regards them as practically identical. He finally says that we have thus in Cyprinoids three great cranial nerve roots arising from a common nucleus, *i.e.*, the continuous substantia gelatinosa of the medulla and spinal cord, these three roots being the ascending and dorsal geniculate (lobus trigemini) Trigeminus, and the sensory Vagus. The ascending and the dorsal geniculate Trigeminus roots together represent the ascending Trigeminus of the higher vertebrates.

Mayser apparently includes more in the lobus vagi than, for example, Goronowitsch, namely, the nuclei of the motor roots. This, of course, does not affect the actual similarities existing. When we compare this description with the condition in the Amphibia we find them, I think, similar. Excluding the motor nuclei, we have in both cases the bundles of fine fibres, the ground substance, and nerve cells, arranged in practically the same manner. The fasciculus communis itself represents the outer layer described by Mayser, the peculiar ground-substance the second layer, and the nerve cells found by Mayser are represented in the tadpole by the group of ganglion cells accompanying the fasciculus; in Cryptobranchus partly, at least, by Osborn's "nucleus of small sensory cells by which the fasciculus communis is apparently reënforced" (45); and in the higher forms by the "sensory nucleus" of the IX + X, and probably by other cells in the vicinity of the fasciculus solitarius.

One great difference is apparent between this tract, or tracts, in fishes, on the one hand, and in Amphibia — especially Anura, — together with the higher vertebrates, on the other, namely, that in the fishes it is much more developed. This is easily intelligible when it is considered that it is essentially the central organ of the branchial nerve supply. Its great development in fishes is correlated with the development of the gills, and where these are in process of reduction or lost it is correspondingly reduced.

The fine-fibred branches of the postauditory portion of this component (see Table, p. 180) correspond, of course, with the similar branches constituting the fine-fibred, visceral portion of the IX + X in fishes, as distinguished by Stannius, Shore, and others. This excludes the larger-fibred branchio-motor portion. The regular arrangement of the roots, ganglia, and branches, as seen in many fishes, is, in the tadpole, mostly obscured, owing to causes noted above (p. 135). This arrangement is partly preserved, however, in the series of roots from the fasciculus communis. The ganglion of the IX (ganglion *C*) is still separate, but the ganglia of the Rr. branchiales are fused with each other and also, partly, with that of the R. visceralis. Owing not only to the forward position of the gills relative to the auditory capsule, but also to the forward position of the heart and part of the viscera, the courses of these branches are likewise altered.

It will now be well to discuss the character of the *lobus trigemini*. It has already been seen that the root from this structure, where best developed, supplies fibres to the various branches of the Facialis, and also independently gives origin to a R. palatinus, R. lateralis, and other recurrent branches. Stannius has already stated (*v. supra*) his belief that this root was concerned largely in the innervation of the terminal buds which are found so abundantly over the surface of the head, gular plate, dorsal part of the body in some cases at least, and in the mouth and gill cavities. Wright has made similar observations as to the innervation of these organs by nerves from this root, especially around and on the barbels where the buds are so concentrated. Whether this root is devoted to the terminal buds as exclusively as those from the tuberculum acusticum are devoted to the canal organs, will require further investigation; that it is largely concerned with the innervation of the buds seems quite certain.

Stannius is not always clear in his description of this root. In some forms — Spinax and Selachians generally — his fine-fibred root emerges quite ventrally, on a level with the motor root of the VII. We have seen, however, that other investigators in Selachians have always described the root from the lobus trigemini as the most dorsal, and that this is its position in Teleosts. From this ventral fine-fibred root of Stannius is derived the R. palatinus. When we consider this, and also that Mayser and Wright do not describe any root of the Facialis derived from the lobus vagi; that Mayser considers the lobus vagi and lobus trigemini to be similar; that the fasciculus communis root of the VII in Amphibia sometimes emerges dorsal and sometimes ventral to the VIII (though always ventral to the lateral-line root); and that there is apparently in Amphibia no lobus trigemini root, it would seem not improbable that we were really dealing here with the same root, which simply shifted its position. On the other hand, as we have just seen, while Stannius describes this fine-fibred root as rather ventral in Selachians, others find in Selachians a dorsal root arising typically from the lobus trigemini. Finally, we have in Acipenser (Goronowitsch, 28), as seen above, *both* roots present, *i.e.*, a fine-fibred most dorsal root from the lobus trigemini, and another fine-fibred root emerging ventrally with the motor root of the VII.

The accounts of the R. palatinus also seem to vary. According to Stannius, it is sometimes given off by the V, sometimes by the VII, and sometimes is independent. It is sometimes reënforced by a branch from the IX (Stannius, Goronowitsch), and by Pollard (49), in Polypterus, is described as composed of united branches from the V, VII, and IX nerves. Goronowitsch denies the existence of any R. palatinus trigemini, and asserts that the R. palatinus belongs to the Facialis. In Amphibia the latter is true. It will not be possible to reconcile these apparent discrepancies until special investigations have been made upon more of the different types. It would seem quite certain that in some cases, at least, a part of the R. palatinus is derived from the lobus trigemini (Stannius, Wright), and that the significance of this lies in the existence in the mouth of numerous end buds to be innervated. It does not seem possible, however, to relegate the supply of all these buds to this source, inasmuch as we have some of them supplied by the R. lingualis IX and even, possibly, by some of the Rr. pharyngei and branchiales X in Amphibia. In this connection, the view of Mayser that the lobus trigemini and lobus vagi are similar structures comes again into consideration. While these two structures obviously, from the final distribution of their nerves, must be considered as largely different, yet the latter may be conceived as containing a number of fibres to end buds in the pharynx, while the lobus trigemini has been specialized off to supply the great bulk of these structures in the mouth and over the head and body.

Respecting these preauditory roots, on a careful examination of the most ventral root of the VII in Selachians I found this root presented the appearance of a double root. Ewart seems to have observed a similar appearance. As far as could be judged from dissections merely, the R. palatinus consists of fibres from both this double root and from the lobus trigemini root. One part of this double root must, of course, be motor and pass into the R. hyomandibularis, the other part will, I believe, be found to arise from the lobus vagi as in Acipenser. I am inclined to believe that this will be found to be the condition in all fishes, namely, the coëxistence of *both* a root from the lobus vagi and one from the lobus trigemini, and, furthermore, always a R. palatinus from the former at least, the variable element in the palatine nerves being the part played by the lobus trigemini root in their formation.

Again, we have the discrepancy, which has been mentioned, with regard to the R. ophthalmicus profundus, which, according to some investigators, belongs to the Trigeminus proper and according to others (*e.g.*, Wright) is derived from the lobus trigemini. It is possible that here again there is not a complete separation or specialization of the fibres to end buds in some forms (see below, however, on this point).

This branch, the ophthalmicus profundus, has been discussed by H. H. Wilder (71), who comes to the conclusion that the ophthalmic branch of the Trigeminus in Amphibia represents the united ophthalmicus profundus and ophthalmicus superficialis trigemini. It seems to me that this is probably correct, but the fusion *has already taken place*, in Salamandra maculata, to which Wilder refers, inasmuch as the R. frontalis of Plessen and Rabinovicz is, as we have seen, the R. ophthalmicus superficialis facialis and not the R. ophthalmicus superficialis trigemini. The latter, then, does not appear to be present as an independent branch, and has already united with the ophthalmicus profundus. The ganglion of the latter has already fused, forming a part of the Gasserian ganglion, for the "Nebenganglion" is a facial ganglion.

Our view as to the fate of the ophthalmicus profundus, however, will partly depend upon whether we find it to belong to the Trigeminus proper or to the lobus trigemini root. If the latter, it very possibly would have either undergone a reduction or aborted, owing to loss of end buds in the nasal region.

The results of the majority of investigators, however, certainly favor the view that the R. ophthalmicus profundus belongs to the general cutaneous system (Ahlborn, Goronowitsch, Ewart).

I may add, in support of Wilder's view, the relation of the R. ophthalmicus trigemini, in the tadpole, to the III and IV nerves. It lies in the fork formed by the division of the III into its inferior and superior branches, and likewise comes into relation with the IV. In Galeus canis the R. ophthalmicus *profundus* bears precisely the same relation to the III while the R. ophthalmicus *superficialis V* bears the same relation with the IV that the single R. ophthalmicus trigemini bears to these two nerves in the tadpole.

As far as I can ascertain, the root from the lobus trigemini is probably coarse-fibred in Selachians. As the roots from the tuberculum acusticum are devoted to the canals, it would seem likely that those fibres in the lateral line nerves of the head derived from the lobus trigemini are devoted to the innervation of the ampullae. If this were true, as further research is necessary to show, the ampullae would represent the end buds of other fishes. The absence of a R. lateralis from the lobus trigemini in Selachians and the concomitant absence of such organs on the trunk is significant in this connection.

The innervation of the pit organs should be studied in this connection. If innervated by fibres from the lobus trigemini, it would appear that they have been secondarily specialized from the end buds and added to the lateral line system.

If it is true, furthermore, that the fine-fibred root from the lobus trigemini in Teleosts and Ganoids is represented by a coarse-fibred root in Selachians, we have a most interesting case bearing upon the significance of fibre-calibre. Here the principal change, apparently, in the structure innervated is a sinking below the surface and a probable increase in size.

As has been seen, there seems to be no lobus trigemini in Amphibia. This is not difficult to understand now when it is considered that the end buds are confined to the mouth in Amphibia, and, consequently, much reduced in number. The Trigeminus, however, as described by Osborn, derives its fibres internally from the following sources: (1) The ascending tract from the cervical region, reinforced by (2) fibres from the deep motor nucleus, representing two tracts. (3) Fibres from the sensory nucleus. (4) The descending tract from the mesencephalic nucleus. (5) The direct encephalic tract. . . . "The sensory nucleus is very large and extends forwards beyond the level of the cerebellum." It is possible this sensory nucleus is representative, partly, of the lobus trigemini.

In any case, the disappearance of this system of nerves as a separate system in Amphibia in correlation with the disappearance of these cutaneous organs is a most interesting phenomenon. In the Amphibia, then, we have a reduction already accomplished in the disappearance of the end bud nerves, and in the Anura another reduction in process of accomplishment in the loss of the lateral line nerves, in several forms at least, as the fully developed anurous condition is attained.

These questions all have an intimate bearing upon the origin of taste and upon the vexed question of the innervation of the taste buds in the higher vertebrates. It is easily seen that the problem is one of extreme complexity. It is not unreasonable to expect, however, that thorough comparative researches upon the exact composition of the cranial nerves will clear up these obscure points.

Stated briefly, we seem to have the following alternatives: (*a*) The taste buds (end buds) are innervated in the lower forms by the root from the lobus trigemini only. As the latter diminishes, owing to the loss of the end buds on the exterior, these fibres fuse with the Trigeminus proper. This view does not seem to harmonize well with the facts in Amphibia, as stated above, namely, the innervation of end buds by the R. mandibularis internus VII, R. lingualis IX, *etc.* The R. palatinus, and even the R. mandibularis internus VII, might indeed receive the fibres in question through the anastomoses with the V. This would tend to show that the V is the nerve of taste in the higher forms.

(*b*) The innervation of these structures can be regarded as shifted from one set of nerves to another, *i.e.*, from those issuing from the lobus trigemini as this diminishes or is lost, to those issuing from the lobus vagi (fasciculus communis).

This involves questions hardly settled, as to change of function of nerves, the innervation of the buds being taken up secondarily in this case by sensory visceral nerves.

(*c*) We may regard, with Mayser, the lobus vagi and trigemini as equivalent structures, in which case there is no difficulty presented by the innervation of the buds by various nerves from these two structures. This ignores, however, the greatly different innervation territory, which the lobus vagi has, in other respects, as compared with the lobus trigemini.

A modification of the latter view seems most probable. The lobus vagi and lobus trigemini cannot be regarded as entirely equivalent structures, but the latter may be considered as devoted to the innervation of the end buds, and the former may be considered to contain similar fibres, in addition, however, to others of a different nature. We have already seen (p. 189) that Mayser distinguishes two sets of fibres, medullated and non-medullated, in the lobus vagi and have also found in the tadpole, in such branches as the R. palatinus VII and R. mandibularis internus VII, two sets of fibres, one somewhat coarser and with a sheath staining much more darkly than the other. This may partly account for the diminishing of the lobus vagi, where the branchial cavities — which are supplied with these buds in fishes — disappear.

One fact is very apparent, both from the investigation of the Amphibia and the comparison with the results of other workers upon the fishes, namely, that there is no direct genetic connection between the lateral line system and its nerves and the sense of taste and its nerve supply. The suggestion of Beard upon this subject has already been criticised in my preliminary communication in the *Anatomischer Anzeiger* (62). Both may have been derived from a more generalized and older form of sense organ, the end bud, present generally on the body and in the mouth. The lateral-line system, whatever its origin, is a specialized system, and its nerves are in every way sharply contrasted with those connected with taste. The auditory organ is the only one whose connection with the lateral-line system is at all probable.

It is also evident that the lateral-line system has no especially segmental character, and that it cannot properly be used in the manner in which it has been attempted to use it, as a general guide in determining the segmentation of the head.

4. *Motor Component.*

The fourth, motor component, shall not be treated here at length. In all the forms above the Cyclostomes we have splanchnic motor roots to the V, VII, IX, and X.

Ahlborn describes no such roots, apparently, except for the V, where it is very large. As Julin (33) and Dohrn (15) assert that the VII has motor elements, it is possible a motor root will yet be found for it. Ransom and Thompson (50) describe large motor fibres, which unite with the Vagus in Petromyzon, but not in Myxine. These fibres, however, are from anterior roots. There are, besides, exceedingly fine fibres to the heart and blood vessels.

It would appear, both judging from this and from the conditions in the tadpole, that a distinction exists between vasomotor and branchio-motor nerves, though both are considered visceral.

The following are these motor roots in the authorities mentioned above:

FORMS.	AUTHORITIES.	NAMES OF ROOTS.
Cryptobranchus . .	Osborn	“ VII–VIII 3 and 4.”
Acipenser	Goronowitsch . . .	ventral root of Facialis.
Amiurus	Wright	transverse root of VII.
Cyprinoids . . .	Mayser	ventral geniculate root of VII.
Pleuronectes . . .	Stannius	root 5.
Raja	Stannius	part of root 2.
Generalized type .	Stannius	root 4.
Hexanchus . . .	Gegenbaur	Facialis.
Echinorhinus . .	Jackson and Clarke .	“ V γ VII.”
Scyllium	Marshall and Spencer	part of “ VII *b* ” ?
Laemargus . . .	Ewart	part of hyomandibular and palatine root of VII.
Protopterus . . .	Burckhardt	“ VIII 3, 4.”

It must be remembered, however, as shown above, that there is reason for believing these roots, except those in Cryptobranchus and Protopterus, are in reality compound, and include a component from the fasciculus communis (lobus vagi).

The motor root and the fasciculus communis root forms, as we have seen, the constant part of the Facialis, including the portio intermedia, which persists in the higher vertebrates. It is, of course, this motor root which becomes so much more important in the highest forms owing to the development of the facial musculature.

5. *Comparison with the Cyclostomes.*

It will be well to take a glance at the conditions among Cyclostomes, which, probably, present very primitive conditions, and which should throw much light upon the origin of the various differentiations existing among the cranial nerves of the higher fishes. There have been many contradictory statements made, however, concerning the Cyclostome peripheral nervous system, and I think it will be evident that our knowledge of it is still far from accurate.

Langerhans (40) describes two kinds of cutaneous sensory organs. One is situated in papillae, which are especially numerous around the mouth and on the dorsal "fin," but are also found scattered over the body and in the mouth and pharynx. The other is situated at the bottom of pits, and these pits are arranged irregularly in lines, there being a line above and a line below the gills, other lines proceeding along the side of the body, above the middle; and still other lines around the mouth and over the head, around the eye. These sunken organs he homologizes with the lateral-line system.

According to Ahlborn (1 and 2), the Trigeminus springs from the medulla by three roots, one above the other. The most dorsal is the ophthalmicus, and arises from the ascending trigeminal tract. It has a separate ganglion. The next is the remainder of the sensory Trigeminus, and has the same origin. The most ventral motor root arises from the motor trigeminal nucleus and a descending tract. The ascending Trigeminus is a direct continuation of the dorsal funiculus of the cord. It consists principally of fine, with a few medium-sized, fibres.

The Vagus roots fall into two divisions. The four roots emerging farthest caudad terminate internally in the "upper lateral ganglion," which is a continuation of the dorsal column of cells in the cord. The four roots emerging most cephalad have the same internal termination as the Acusticus.

The terminal nuclei of the Acustico-facialis, and the four roots just mentioned, lying as they do above the ascending Trigeminus and upper lateral ganglion, which represent continuations of the cord, are thus, according to Ahlborn, something superadded in the medulla oblongata, and are equivalent to the higher brain centres. They are not represented by any portion of the cord, or, at the most, by a very small band mesad of the dorsal funiculus, of which band one can only say that it exists. The nucleus of the Facialis lies well above and separated from that of the Acusticus. The cells in it are small and the fibres of the Facialis issuing from it are fine and of a very uniform size. The Acusticus emerges in two roots, one above the other.

Of the IX + X roots, the four composing the first (cephalic) set unite to form R. branchialis I, which sends a twig to the Hypoglossus. The first two of the second set are joined by a recurrent branch from the Facialis to form the fine-fibred N. lateralis. The last two roots form the Pneumogastricus, which is connected with the N. lateralis through the ganglion of the same.

The first fact that impresses one in this arrangement is that the first set of roots from the Acusticus region do not form the N. lateralis, but the R. branchialis I. Furthermore, the N. lateralis is formed partly by a recurrent branch from the Facialis passing around outside the auditory capsule — a thing which does not occur in the N. lateralis in the higher forms. Again, on comparing the course of the N. lateralis with the arrangement of the pits, it is evident that only a small proportion of them would be innervated by this nerve, which has a position near the mid-dorsal line. When these facts are considered — especially the non-derivation of this nerve from the

Acusticus center, thus differing from the origin so universal for the N. lateralis in all other forms — it must be regarded as very probable that this nerve does not represent the N. lateralis vagi of higher forms. Stannius has also called attention to some of these difficulties and reached a similar conclusion (57, p. 96). What it does represent is probably the R. lateralis trigemini, so-called, of Teleosts — a nerve which is formed principally, as we have seen, by a recurrent branch of the Facialis, derived from the lobus trigemini, and which is reënforced by a branch from the Vagus. It would then much more probably innervate the papillae which are so numerous on the dorsal fin, and which probably correspond to the structures innervated by the so-called R. lateralis trigemini. The R. branchialis I would, apparently, represent the R. lateralis. I am forced to believe that the exact anatomy of these nerves is not yet accurately known, nor have their connections with the cutaneous sense-organs been sufficiently worked out. With respect to the remainder of the Facialis, it has been asserted by Julin (33) and Dohrn (15) to contain motor elements. If this be true, it probably does not arise merely by the one root, as described.

If the character of the so-called N. lateralis be as above supposed, the most dorsal nucleus of the Acustico-facialis center, from which the Facialis emerges, would correspond to the lobus trigemini. Its structure, as described by Ahlborn, would seem to support this view. If this be the case, it is evident that the distinction between the lobus trigemini, on the one hand, and the ascending Trigeminus and lobus vagi, on the other, is already here sharply drawn, and is quite a primitive feature. This would be in opposition to Mayser's views quoted above (p. 189). The course of the Facialis in the head is not decisive on this point, inasmuch as we have seen that in higher forms the lobus trigemini and lateral-line components go together.

In comparison with Kupffer's observations (36), it would seem probable that, in general, Kupffer's medial elements derived from the neural crest and common to both spinal and cranial nerves, would be represented by such ganglionated nerves as emerge from the ascending Trigeminus. It must be remembered, however, that, according to Mayser, not only the ascending Trigeminus, but the lobus vagi and lobus trigemini taken together, represent continuations of the spinal cord; that in the tadpole the lobus vagi (fasciculus communis) can be traced, enormously diminished, into the cord a short distance at least; and that, according to Ahlborn (1), and also according to Ransom and Thompson (50), the Vagus, as well as the Trigeminus, in Cyclostomes, come from centers representing continuations of parts, though different parts, of the cord. Mayser (41) and Ahlborn are in accord, however, in considering the Acusticus-lateralis center as something distinct and superadded. Even in Cyclostomes, however, the Vagus center is a considerably enlarged and developed center in the medulla.

Returning to Kupffer, it would next seem probable that his lateral element, which is derived from the dorsal fusion with the epiblast, is represented by the lateral-line element, plus, perhaps, that to the end buds; and that, finally, his epibranchial ganglia are represented by the ganglia of nerves terminating centrally in the lobus vagi (= fasciculus communis + terminal nucleus = fasciculus solitarius + sensory nucleus IX + X). Whether the ganglia of the nerves supplying the end buds can be considered as belonging to or representing this series rather than the preceding is a question whose answer depends upon the answer to the correlated question, already considered, as to the relation between the lobus trigemini and lobus vagi.

IV. General Considerations.

1. *Relation of Cranial and Spinal Nerves.*

Hatschek (30) has made some interesting and suggestive comparisons between the nerves of Amphioxus and Ammocoetes, which at the same time throw more light upon the origin of such nerves as the lateralis and visceralis, and of the differences obtaining between the cranial and spinal nerves. In brief, this view is as follows: In Amphioxus the dorsal root divides into a dorsal and ventral branch. The dorsal branch subdivides into a N. cutaneus dorsalis and a N. lateralis dorsalis. The ventral branch divides into a N. cutaneus ventralis, a N. lateralis ventralis, and a N. visceralis. Only the latter contains motor as well as sensory fibres (motor to the splanchnic muscles). This primitive relation is retained by the cranial nerves, and the loss of this relation and of certain branches by the spinal nerves is owing to the usurpation of the long trunk-branches of the cranial nerves. The course of the spinal dorsal nerves inside the body muscles he regards as due to the shortening of the dorsal nerve. Kupffer, however, regards the spinal dorsal nerve as a new acquisition. This peculiarity presented by the spinal nerves is very important, and its satisfactory explanation must be a crucial point in any theory of the cranial and spinal nerves.

Two general criticisms that may be made upon Hatschek's views, I think, are that they do not take sufficiently into account qualitative differences in the nerves under discussion, his conclusions being based more upon simply topographical relations, and, secondly, that they consider the nerves too much apart from correlated structures, from those innervated by them especially, and, consequently, offer no explanation why the usurpation in question took place.

We have seen that in the cranial nerves of the higher fishes there are three kinds of cutaneous nerves distinguishable by peculiarities of their fibres, of their distribution, and of their internal origin, *i.e.*, (1) mixed fibres of a general cutaneous character continuous with the posterior columns of the cord, (2) coarse fibres innervating the lateral line organs and terminating centrally in the differentiated tuberculum acusticum, and (3) fine fibres innervating the terminal buds (coarse in Selachians and innervating the ampullae?) and terminating centrally (principally) in the lobus trigemini. The latter, *i.e.*, (3), is possibly not completely differentiated. Among the Cyclostomes, it seems probable, this specialization has not been carried so far, but this is not yet sufficiently known.

It is obvious that it is only similar and specialized structures that are most likely to attain a more unified innervation, and, accordingly, it seems most probable that such a process of usurpation as that mentioned above would take place in connection with the cutaneous sense organs. These latter would concomitantly become more restricted to certain regions and would, not improbably, undergo further specializations. According to this view, the cutaneous sense organs would have had at first a more general innervation, and only later would their nerve supply proceed from only one or two nerves.

Another change which seems to have taken place, similar in character to the above but affecting a different structure, is the assumption by several nerves of the supply to the gills (and other visceral structures?) and concomitantly the creation in the medulla of a special center for this nerve supply (lobus vagi).

Hatschek points out the superficial position of the ganglia in Amphioxus as compared with the spinal ganglia in vertebrates. If the above homologies (p. 200), with Kupffer's results, be correct, it is precisely the branchio-visceral ganglia of the VII–IX–X (epibranchial ganglia), and the special cutaneous ganglia (lateral line ganglia and ganglia of nerves to end buds also, perhaps) which arise from special epiblastic thickenings as opposed to those ganglia derived from the neural crest, and it is precisely these ganglia which belong to the cranial nerves with long trunk branches, in other words, those which have taken the place of certain portions of the spinal nerves. The ganglia, then, of the cranial nerves, arising in connection with epiblastic thickenings, are the ganglia which the spinal nerves do not possess, having probably lost them. This would explain this difference in the mode of origin of cranial and spinal ganglia.

The fusions described, in connection with the Trigeminus, by Beard and Kupffer possibly belong to the lateral line ganglion which lies over the Gasserian ganglion proper, possibly, also, to nerves to end buds.

Of course the presence of the lateral motor roots in cranial nerves constitutes a difference of another character from the above. This and the correlated problem of the sympathetic do not fall within the scope of the present discussion.

There are several anatomical peculiarities which afford further support to Hatschek's comparison, as amended above. These are the remarkable parallelisms existing between these three systems of cutaneous nerves. I have called attention to the existence of this peculiarity in the relations between certain minor branches of the Trigeminus and the lateral line nerves to the head. The parallelism is carried further than this, however. The R. ophthalmicus superficialis VII parallels the R. ophthalmicus V, the R. buccalis VII parallels the R. maxillaris V, the R. communicans IX ad VII parallels the R. mandibularis externus VII, and the postauditory R. supratemporalis parallels the R. auricularis vagi. In fishes this is still more striking where the two pairs first mentioned are in close apposition and can only be separated with difficulty. We have, besides, in fishes the element from the lobus trigemini, whose fibres are not merely in close apposition but, probably, mingle with the lateral-line fibres, forming thereby a still closer union. On the trunk we have the two long branches : the R. lateralis trigemini (facialis) and the N. lateralis.

These parallelisms might be partly explained by the subjection of the nerves in their growth to similar influences by the other parts, but this could hardly explain such close parallelisms. Nor are such parallelisms easily reconcilable with the theory that the lateral-line system of nerves represents a system phylogenetically different from the others. The explanation most naturally suggested is that these three systems were originally one. Of the three, the general cutaneous system to which the Trigeminus proper belongs would represent most nearly the primitive nerves from which the others were differentiated. It is, naturally, only the differentiated cutaneous nerves that we find extending over the trunk from the cranial nerves; or, to put it in another way, the spinal general cutaneous nerves bear the relation to the cranial special cutaneous branches to the trunk that the general cutaneous branches from the ascending Trigeminus bear to such branches in the head. We might even advance a step further and say that the more intimate fusion of the end bud and lateral line nerves indicates the evolution of the latter from the former, a view probable on other grounds and advocated in Wiedersheim's *Grundriss* (67).

Hatschek (30) has called attention to the morphological importance of the dorsal rami as landmarks of former conditions.

The other longer and principal branches have been more influenced and extended by the development and topographical changes in various parts, such as the jaws, sense organs, *etc.* Hatschek, however, as we have seen, does not recognize the fact that there are, even of these dorsal rami, qualitatively three kinds. In determining segmentation, by means of them, it is necessary to decide first, whether each can represent a separate segment, or all must be taken together to represent one segment. The former view would rest upon the supposition that some of the components for any one segmental ramus have been lost. The latter view would, perhaps, seem more probable, and agree better with the views here advanced as to the cause of these differentiations of cutaneous nerves.

It is questionable whether these components belong especially to different levels of the head and body, as Hatschek's comparison with Amphioxus would seem to indicate. Each one of his four sensory branches might consist, actually or potentially, of the three components. From the actual relations in fishes, however, the general cutaneous component is naturally confined to no particular locality in its innervation territory. Its roots are ventral to the other two. Of the other two, in origin, the lateral line component is ventral to the remaining one, and is lateral in its general distribution on the body. On the head there is no difference, topographically, in this particular respect, between the three cutaneous components.

If Hatschek's view, similar in some respects to Balfour's, is correct, and the cranial nerves most closely approach the primitive conditions, the spinal nerves having lost elements, then we would naturally find these tracts, peculiar to the medulla, showing the remnants, at least, of continuations in the cord. Whether this were true or not, however, the validity of this view would hardly be affected.

It is useless to speculate further upon this subject. What it is wished, however, to emphasize here, is the importance of taking into full consideration, as a factor, the cutaneous sense organs, in the attempt to obtain a philosophical understanding of the changes undergone by the peripheral and central nervous systems. The development and specialization of these structures have probably played an important part in the changes leading to the organization of the vertebrate peripheral and central nervous systems. Furthermore, when we come to compare the nervous systems of fishes and Urodela with the higher vertebrates, without the general clue that these structures have disappeared, and the nerves supplying them likewise either disappeared or metamorphosed, only false conclusions are inevitable.

Nor is the question one merely affecting the peripheral nervous system, inasmuch as it affects likewise the central terminations of this nerve supply and indirectly other portions of the central nervous system in physiological connection therewith. A number of changes in the higher centers will probably be found to be connected with these transformations.

As an instance of the effect of these changes upon the central nervous system, aside from the medulla, it is possible, I think, that the reduction of the cerebellum in Amphibia may be correlated, to some extent, with the reduction in these cutaneous organs. Its size in the higher forms would be, perhaps, secondarily reacquired.

As these changes in cutaneous organs are largely affected by habitat, it is obvious that animals widely separated may, by changing their habitat, undergo changes in their nervous system quite similar in character. Here, again, we meet the phenomenon of parallel changes in different forms, due to similar conditions of environment, and, in such cases, of physiological rather than morphological value.

2. *Relations of the Pre- and Postauditory Nerves.*

A peculiarity to which attention may be called here is the position of the Auditory among the nerves.

It is evident, from the description of the nerves of the tadpole, that the pre- and postauditory nerves are not totally different by any means ; yet, in general, there are marked differences in the relative development of the different components corresponding to the differences in the character of the innervation regions. In the preauditory nerves we have a large general cutaneous element for the supply of the extensive surface of that portion of the head, while the preauditory supply for visceral surfaces is naturally comparatively small. We have a large viscero-motor supply, however, for the enlarged branchial (jaw) musculature. In the postauditory region the general cutaneous supply is small, owing to a reduction of the surface supplied, due to the breaking through of the gills, and also possibly to encroachments by trunk nerves. On the other hand, the visceral surfaces supplied are extensive and these nerves correspondingly developed.

The manner in which the auditory organ is interposed, as it were, is evidenced by the many anastomoses around it. In the tadpole, while one half of the lateral-line nerves is related to the V, the other half comes into relation with a general cutaneous nerve from the IX + X (R. com. IX + X ad VII), which unites with it in a manner similar to that in which the first half of the lateral nerves unite with the V, and between their respective branches similar parallelisms seem to exist.

While the trunk nerve to the lateral line issues with the IX + X, the parallel trunk nerve to the end buds of the trunk (R. lateralis trigemini) has a preauditory exit. Furthermore, among the fishes, the palatine nerve would appear to be formed by a union of post- and preauditory nerves (Goronowitsch, Pollard). The development of the auditory organ has probably caused a separation of nerves formerly more closely connected. This is evidenced also by the manner in which the lateral-line nerves converge mesad of the auditory capsule just before entering the medulla. Ayers (6) has brought forward reasons for supposing that the acustico-lateralis system was originally double. We might even go a step further and suggest the possibility that it was once single.

In any case, the general relations of the pre- and postauditory nerves point, I think, to the conclusion that the auditory organ is a neomorph interposed among the nerves and altering their primitive courses.

3. *Bearings upon the Classification and Segmentation of the Nerves.*

The foregoing comparative study of the cranial nerves shows that *the present numerical classification is unphilosophical.*

One principal cause lies in the fact that the classification, with its serial numbering of the nerves, is based upon the conditions existing among the higher vertebrates. Now, as we have seen, the cranial nerves of the higher vertebrates have undergone considerable reduction of primary components.

Much time has been spent in ascertaining whether those preauditory roots, issuing from the tuberculum acusticum and lobus trigemini, belong to the V or VII nerves. For convenience and to emphasize their distinction from the V they have been considered in this paper as belonging to the VII, in accordance with recent researches. If, however, we take the cranial nerves of the higher vertebrata as a basis, which is practically done in the existing nomenclature, these components or roots in question do not belong to either the Trigeminus or Facialis ; they are actually different nerves from either of the above, existing in the lower but not in the higher vertebrates. The principal reason they have been assigned by recent investigators to the VII is because their branches have been shown to originate from these roots lying caudad of the Trigeminus proper, and, consequently, by implication, belonging to the segment of the VII. This, however, is not logical, inasmuch as segmental character is not the basis of existing nomenclature, nor, indeed, would it be possible with our present knowledge to propose a nomenclature for the cranial nerves on this basis. Furthermore, it has not actually been determined to what segment or segments these special cutaneous roots belong.

It will therefore ultimately be necessary to remodel our cranial nerve terminology, but, in my opinion, their exact composition has not yet been sufficiently determined in order to do this successfully.

It may be well to indicate here the weak point in Gaskell's analysis of the nerves (23 and 24), namely, that it does not take account of all the qualitative differences among them.

For example, the lateral-line system is obviously different, whatever may have been its origin, from such cutaneous nerves as the Trigeminus, yet in Gaskell's nomenclature they are both simply classed together as ganglionated afferent somatic nerves. In fact, Gaskell's system also ignores the differences between these nerves and those of the special sense organs, for these latter would also fall under the above category. The chief defects in Gaskell's work appear to arise from the fact that it has been confined to the highest vertebrate types, that it is not comparative. Nevertheless, it is upon lines of work approaching those of Gaskell that, in my opinion, the most fruitful results will be obtained.

It is also evident that an exact determination of the component parts of the nerves is a necessary preliminary step to dealing with questions of segmentation. This fact has already been recognized to a certain extent, as is evidenced by the numerous attempts to find the corresponding ventral roots for dorsal roots, and *vice versa*. In these attempts, however, many other differences in the character of the nerves have been ignored. His, Van Wijhe, Gaskell, and others have demonstrated the presence of two sets of motor nerves, and it is evident that further differences, especially in the sensory nerves, must also be taken into account. For example, in the tadpole, the Trigeminus proper, the "dorsal VII" and the "fasciculus communis" root of the VII, are mainly sensory yet all different; either all three must be included in a complete "segmental nerve" or, if one is omitted, it must be shown why. That some particular component may disappear in certain cases is evident, and the cause is then to be sought in some peripheral change.

In the study of segmentation from the standpoint of the neuromeres, as developed by Béraneck, Orr, McClure, Waters, Platt, and others, these qualitative differences should likewise be taken into account. When the results of these two lines of work shall have been brought into correlation with each other, a better insight will be afforded, on the one hand, into the significance and value of the neuromeres, and, on the other hand, into the transpositions and other changes undergone by the various components.

Finally, without a recognition of these nerve components, embryological research, it appears to me, becomes partly meaningless. The fact that certain ganglia are connected, in course of development, with epiblastic thickenings while others, apparently, are not, is correlated with some difference, structural and physiological, which either exists now or has existed. How can we determine what value to attach to such differences of origin until we know with what differences in the adult structure they are correlated and, as a consequence, what was the original cause of their appearance? A knowledge of the structure itself may be fairly considered a necessary preliminary to ascertaining its embryological origin.

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APPENDIX ON TECHNIQUE.

Although nearly every one who takes up any especial line of work evolves, to a certain extent, his own technique, and although the Golgi method is described in a number of articles and books, yet it may be well to give the details of manipulation, as found convenient in my experience, to benefit those who are not familiar with the subject and literature.

1. *Hardening of Small Pieces in Osmium-bichromate.* — The size of the pieces will naturally depend upon the character of the tissue, but, as a rule, one dimension should not exceed 3 to 4 mm. Perhaps the best mixture for general use is potassium bichromate, 3½%, 4 vols. + osmic acid, 1%, 1 vol. The time of hardening must be largely a matter of experience, depending upon such factors as the character of the tissue, its stage of development, whether embryonic or adult, temperature, and the character of the impregnation aimed at. In general, this time will lie between 2 and 5 days, embryonic tissue requiring less than adult. For the cortex of an 8-months' human embryo, however, I have found from 3 to 5 days — and especially the latter period — gives the best results when using Berkley's mixture. 30 to 50 cc. are required for a medium-sized tadpole. It is best to put the specimen in a smaller quantity first, — a solution that has been used once will answer, — and then change after an hour or so, putting the specimen in the full quantity. The fluid should be changed at any time if it becomes cloudy or ceases to smell quite strongly of the osmic acid.

2. *The Silver Bath.* — 1% may be taken as a standard solution. The pieces of tissue should be washed in several changes of the silver solution (that which has been used once being available), until, after 10 to 15 minutes, the fluid ceases to cloud up with the silver chromate, which is formed when the bichromate and silver solution meet each other. The pieces should be left in a liberal supply of the silver solution — at least double the quantity of osmium bichromate which has been used. Impregnation takes place in 24 to 12 hours, or even less, but it is well to allow the tissue to remain in the silver several days in the dark. Keeping the tissue in the dark in 1. and 2. is not really essential to obtain the reaction, but is preferable, especially if it remains in the silver bath some time (see below).

3. *Cutting and Mounting.* — (*a*) The pieces are transferred immediately, and left ½ to 1 hour in 95% alcohol, this being changed several times in the meanwhile; (*b*) next ½ to 1 hour in absolute alcohol; (*c*) 10 to 15 minutes in alcohol and ether, equal volumes; (*d*) ½ to 1 hour in thin celloidin; (*e*) a few minutes in thick celloidin; (*f*) mounted on a microtome block, and the celloidin hardened in chloroform. This process applies especially to the tadpole, which, when put in the alcohol, is cut transversely into several more pieces to facilitate the washing and, especially, the penetration of the celloidin. For solid tissues, especially the central nervous system, it is better simply to gum them to the block after the washing in alcohol, using celloidin and hardening it by only a short immersion in

chloroform or 80% alcohol. A partial infiltration with celloidin and hardening the latter is apt to crack the tissue inside. With the tadpole and similar tissues it is necessary to fill up the interstices with celloidin in order to obtain complete and coherent sections. When this is done, chloroform is, in my opinion, the best fluid to harden the celloidin. It does this quite rapidly, and does not, for some time at least, seem to affect the impregnation. Specimens may be often left in it over night, apparently without injury.

The sections, 50 to 70 μ thick, usually, are removed from the knife with a camel's-hair brush or piece of tissue paper, and arranged on the slide. 95% alcohol is used in the cutting. The alcohol is then blotted off by gently pressing a piece of filter paper on the slide, and a few drops of absolute alcohol are put on. This is then carefully drained off, — not blotted as before, — and all superfluous alcohol allowed to evaporate, though the sections should not be allowed to dry. The celloidin, softened by the absolute alcohol, will then adhere to the slide during the remaining treatment. The sections are then cleared by means of ol. origanum *cretici*, and the latter is washed off with xylol. They are then mounted in dammar balsam, without a cover slip. The dammar is used in the condition in which it is obtained — a thick fluid. After it is spread over the sections it must be watched for a while, as it tends to run off the sections and accumulate around the edges of the mount, probably owing to diffusion currents. The aim should be, in covering with balsam, to get an even layer of balsam, *as thin as is consistent with covering the sections*. If too thick it does not dry rapidly, even in the oven, and where yellowing takes place subsequently it is most liable to occur where the balsam is thickest. When mounted, the slides are put in an oven, at about 50° C., for a day or two, care being taken that they shall be level. Heat does not seem to affect the preparations, and the sooner the balsam is dried the better. If the balsam should dry off the sections in spots leaving them exposed, the dry places should be first moistened with xylol and then balsam added as required, and the slide dried again in the oven. In my experience, origanum and xylol are much preferable to creosote and turpentine, which are recommended by Golgi. This is especially true with the central nervous system, where turpentine tends to crack the sections. The origanum does not allow the balsam to dry so readily as does xylol and will also, after a while, affect the impregnation, hence the washing with xylol.

The best way to mount loose sections is to transfer them from the xylol into a dish of quite thick balsam instead of immediately to the slide. In this way the above-mentioned diffusion currents upon the slide are avoided.

Note. — Since the above writing, I have found that the period of hardening may be reduced to a day or so and yet good impregnations of adult brains be obtained also by adding *formalin* (*e.g.*, 4%) to a potassium bichromate solution. How this will compare with the lithium bichromate method, I can hardly, as yet, say.

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ABBREVIATIONS USED IN THE PLATES.

Anast.	anastomosis.
aud. cap.	auditory capsule.
aur.	auricle.
Bid. gang.	Bidder's ganglion.
bl. ves.	blood vessel.
cap.	capillaries.
cart.	cartilage.
ch. tymp.	chorda tympani.
con. tis.	connective tissue.
cup.	cupula.
cut.	cutis.
cut.^{1}	outer layer of cutis.
cut.^{2}	middle layer of cutis.
cut.^{3}	inner layer of cutis.
dors. VII.	dorsal VII.
epid.	epidermis.
epith.	epithelium.
epith. plex.	epithelial nerve plexus.
fasc. com.	fasciculus communis.
fib. Mauth.	fibre of Mauthner.
gang.	ganglion.
gang. Gass.	ganglion Gasseri.
gl. n. plex.	glandular nerve plexus.
inf. gl. n. plex.	inferior glandular nerve plexus.
intermed. n. plex.	intermediate nerve plexus.
mot.	motor.
musc.	muscle.
oes.	oesophagus.
perich. plex.	perichondral nerve plexus.
pigm. c.	pigment cell.
post. long. fasc.	posterior longitudinal fasciculus.
prot. proc.	protoplasmic process.

R.	ramus.
Rr.	rami.
r. com. IX ad VII.	ramus communicans glossopharyngei ad facialem.
r. lat.	ramus lateralis.
r. mand. int. VII.	ramus mandibularis internus facialis.
r. pal. VII.	ramus palatinus facialis.
r. visc. X.	ramus visceralis vagi.
silv. prec.	silver precipitate.
subepith. n. plex.	subepithelial nerve plexus.
sup. gl. n. plex.	superficial glandular nerve plexus.
symp.	sympathetic.
term. n. plex.	terminal nerve plexus.
vent.	ventricle.
Z.	in Pl. XII, key, is placed on points of fusion between accessory branches of the Trigeminus and lateral-line nerves.
2 root IX + X.	Second root of Glossopharyngeus and Vagus.
3 root IX + X.	Third root of Glossopharyngeus and Vagus.
4 root IX + X.	Fourth root of Glossopharyngeus and Vagus.
V asc.	Ascending tract of the Trigeminus.

EXPLANATION OF PLATE VII.

FIG. 1. Vertical section through the epidermis of a tadpole, showing terminations of the Trigeminus. × 155.

FIG. 2. Somewhat oblique vertical section through the oral epithelium, showing the terminal plexus of the R. maxillaris V (+ palatinus VII ?). × 192.

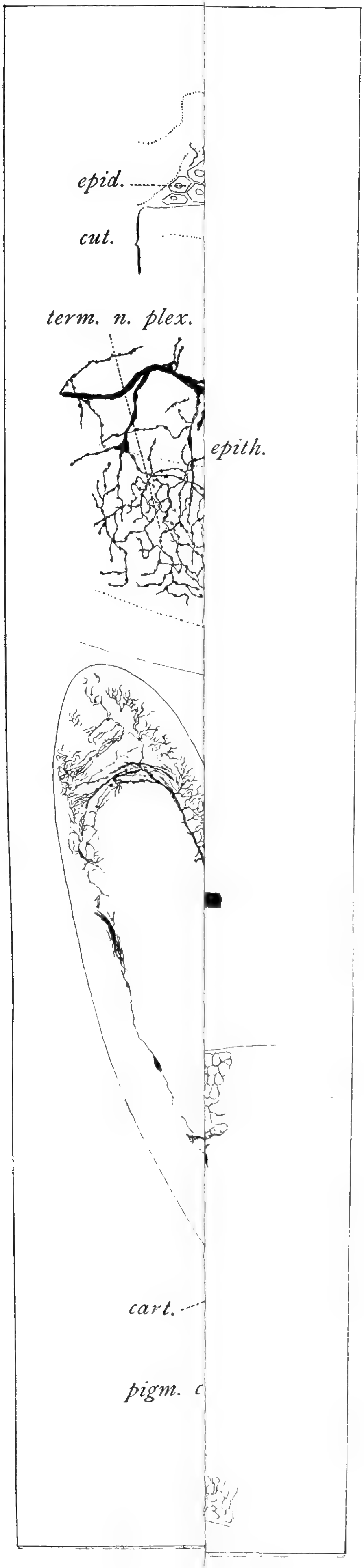
FIG. 3. Section similar to Fig. 2, showing the terminal plexus of the R. ophthalmicus V (+ palatinus VII). × 192.

FIG. 4. Section similar to Fig. 1. × 192.

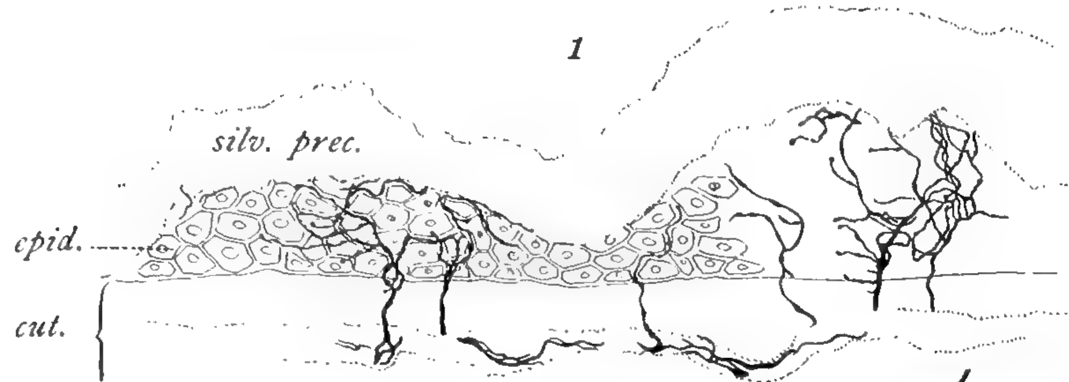
FIG. 5. Section through the lower labial cartilage, showing the perichondral plexus and the intraepithelial plexus arising therefrom of the R. mandibularis V. × 72.

FIG. 6. Horizontal section through the above-mentioned perichondral nerve plexus.

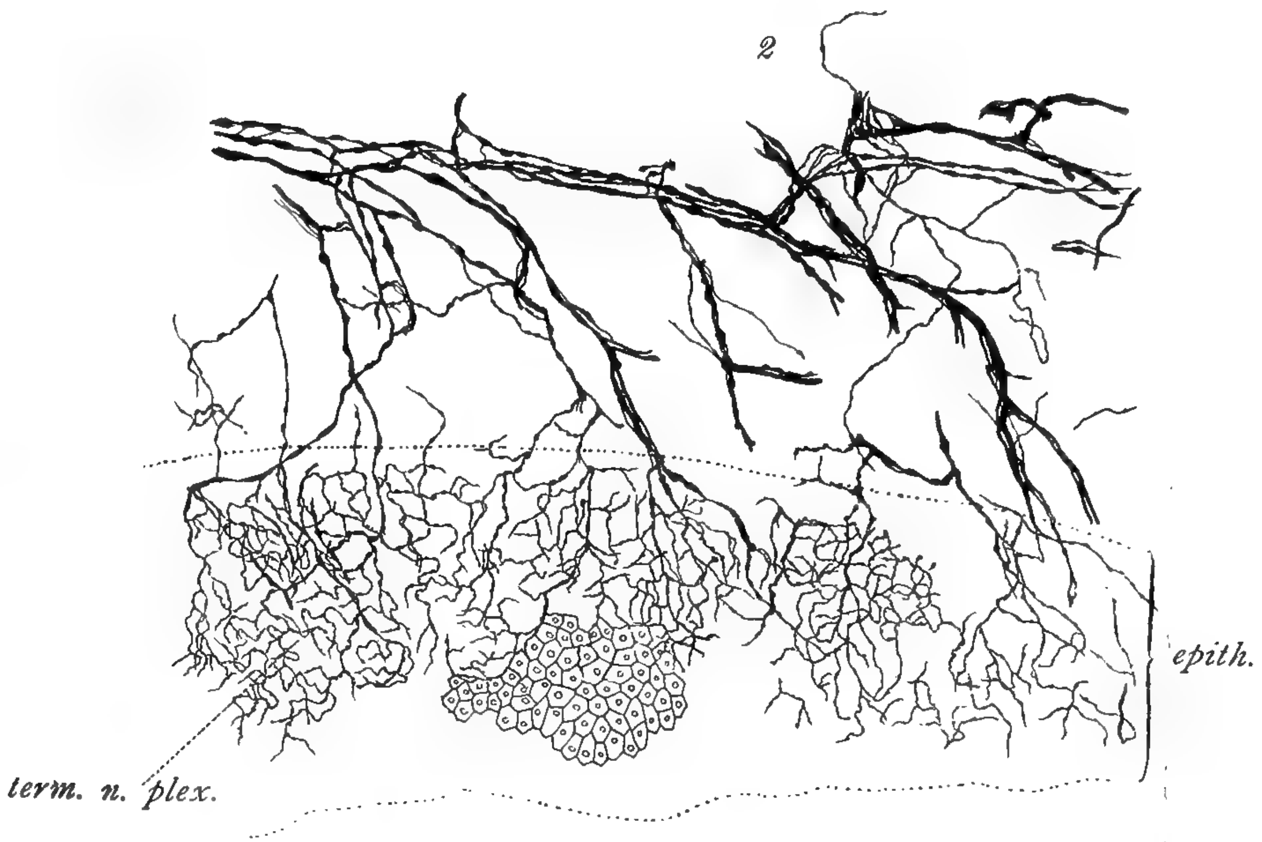
FIG. 7. Similar section through the above, showing also the entire end of the labial cartilage. × 315.


epid.
cut.
term. n. plex.
epith.
cart.
pigm. c

1


silv. prec.
epid.
cut.

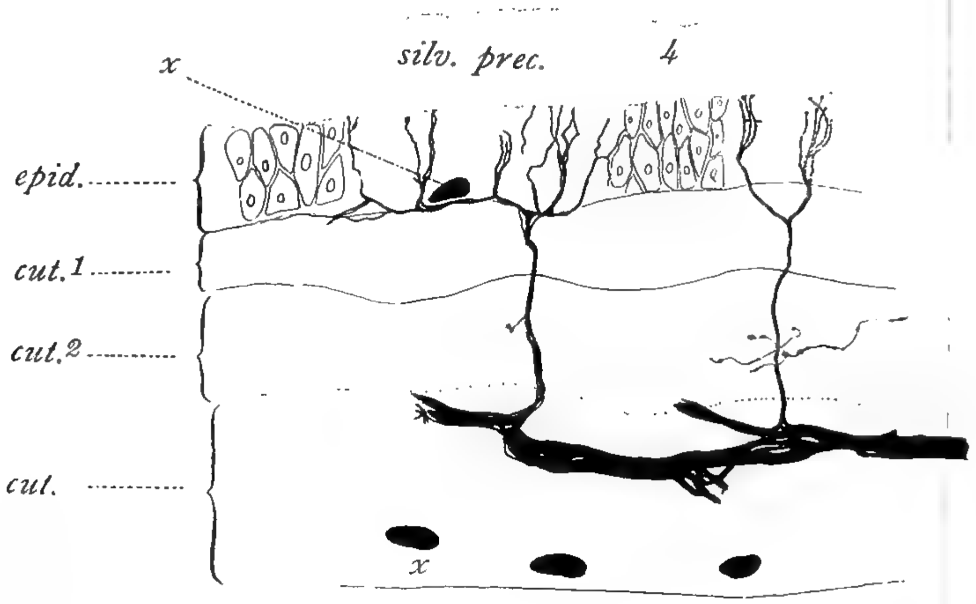
2


term. n. plex.
epith.

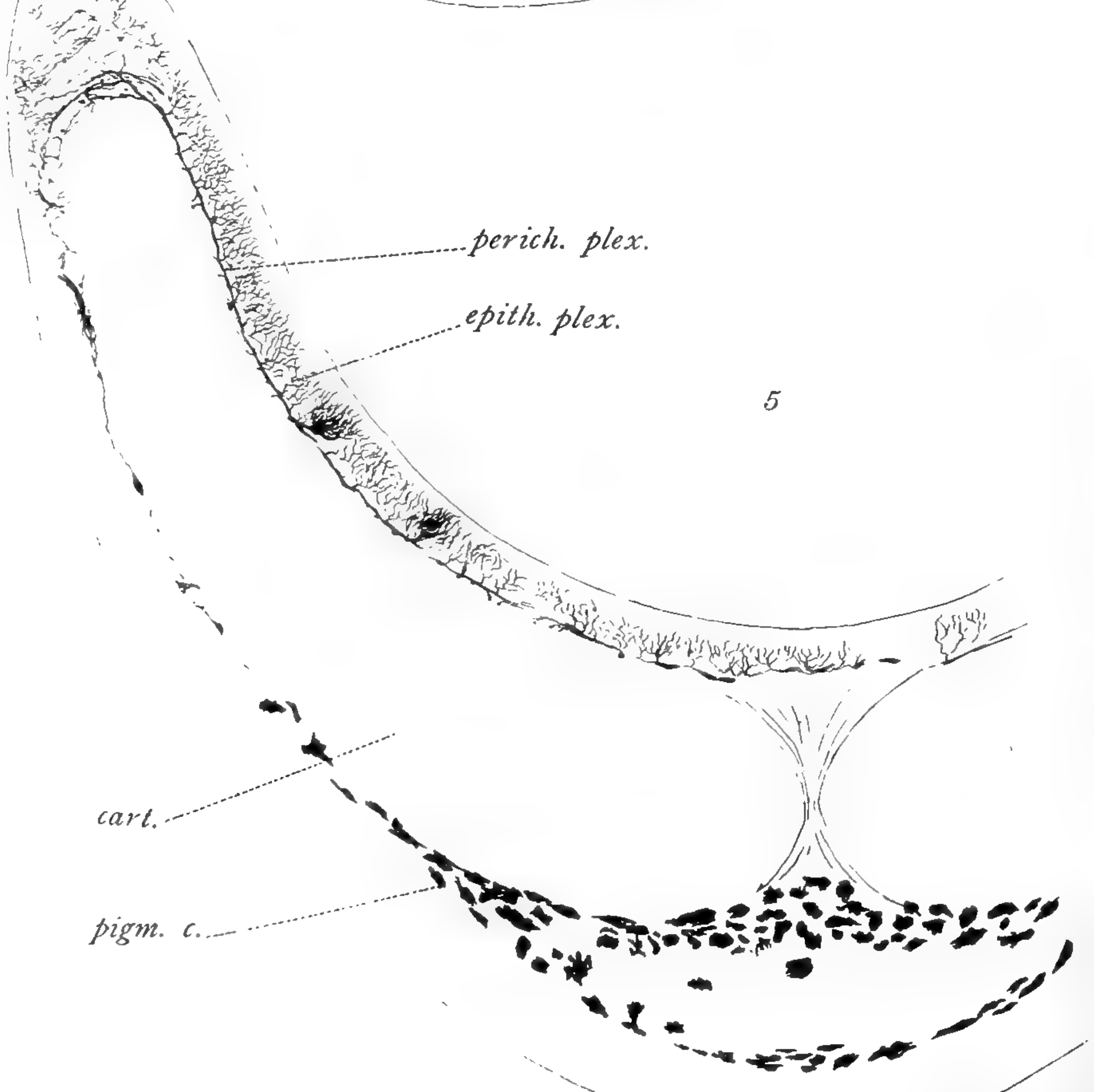
3


term. n. plex.
epith.
epith. cell

4

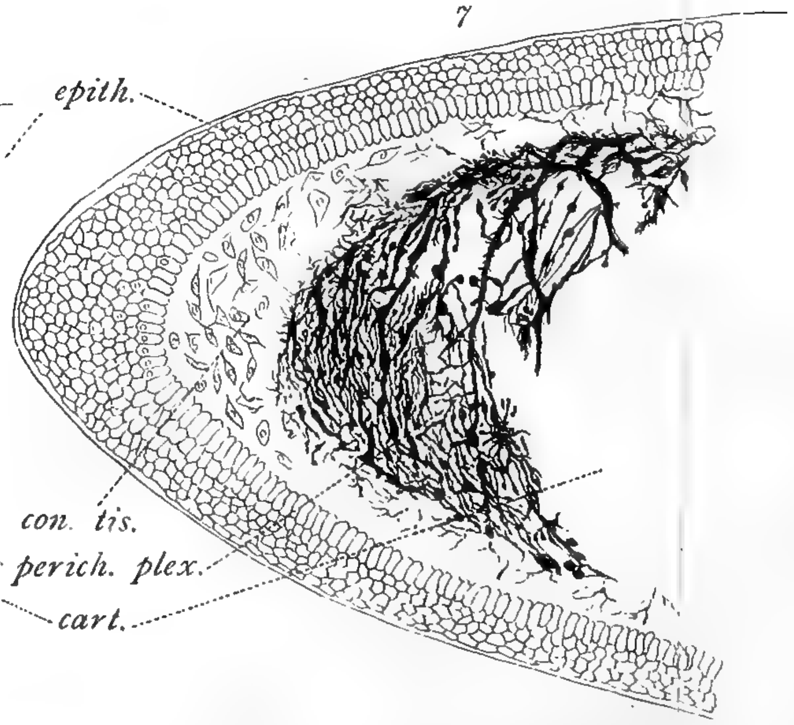

x
silv. prec.
epid.
cut.1
cut.2
cut.
x

5


perich. plex.
epith. plex.
cart.
pigm. c.

6

7


epith.
con. tis.
perich. plex.
cart.

EXPLANATION OF PLATE VIII.

FIG. 8. Vertical transverse section through a part of the roof of the pharynx, passing through the transverse fold of the epithelium and showing the terminations of a branch of the R. palatinus VII in the epithelium and taste bulbs (end buds). × 58.

FIG. 9. Terminations of one of the Rr. branchiales X in the terminal pockets of the filtering apparatus. × 424.

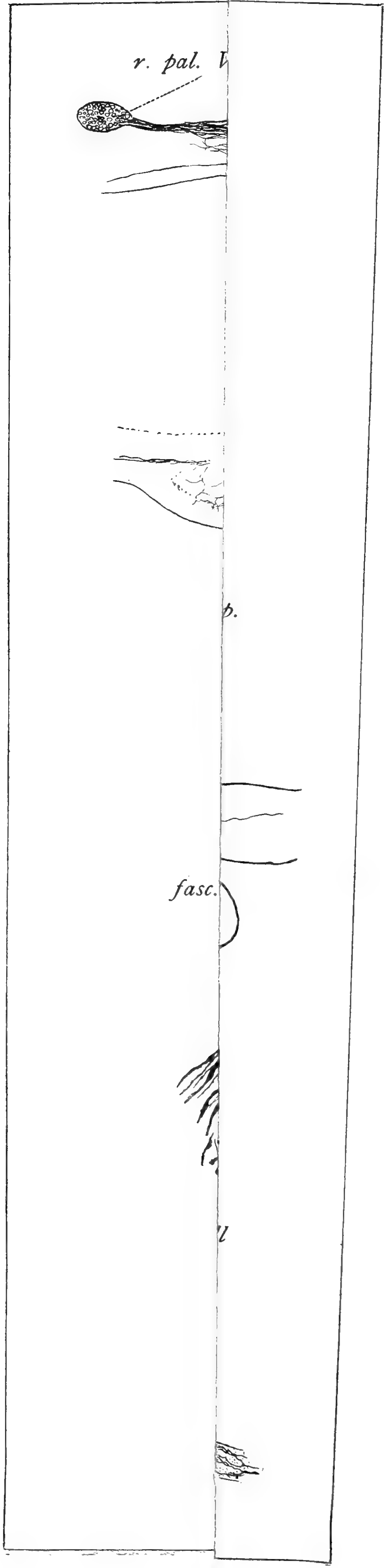
FIG. 10. The next section caudad of the one drawn in Fig. 8. × 58.

FIG. 11. Transverse section through the pharynx, showing the terminal ramifications of the R. mandibularis internus VII (chorda tympani) in a large papilla in the lateral angle of the pharynx. × 41.

FIG. 12. Transverse section through the fasciculus communis. × 315.

FIG. 13. Section showing innervation of a small blood vessel by fibres from one of the ganglion cells found along the course of the visceral nerves. × 111.

Journ. Morp l.VIII



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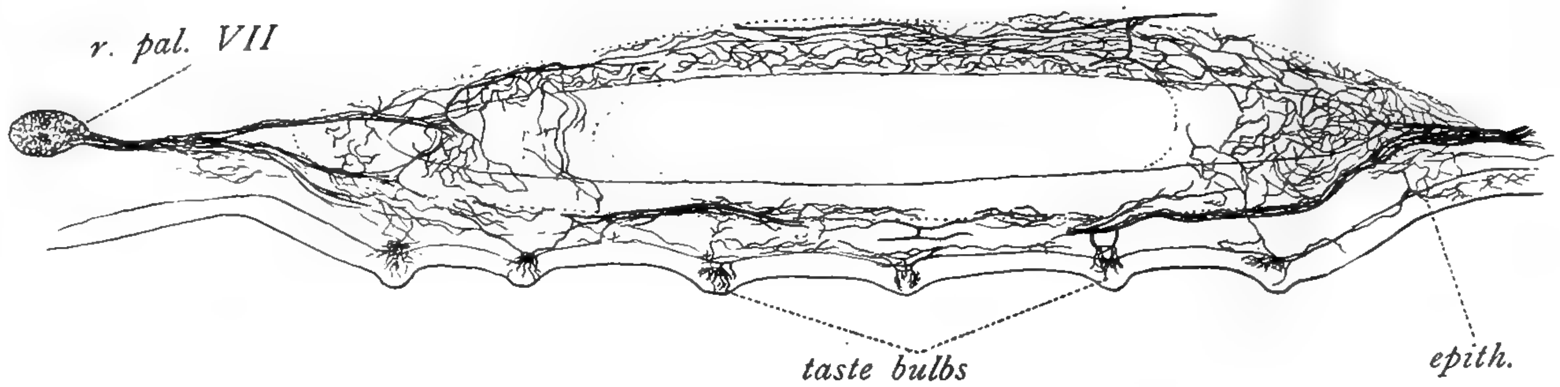
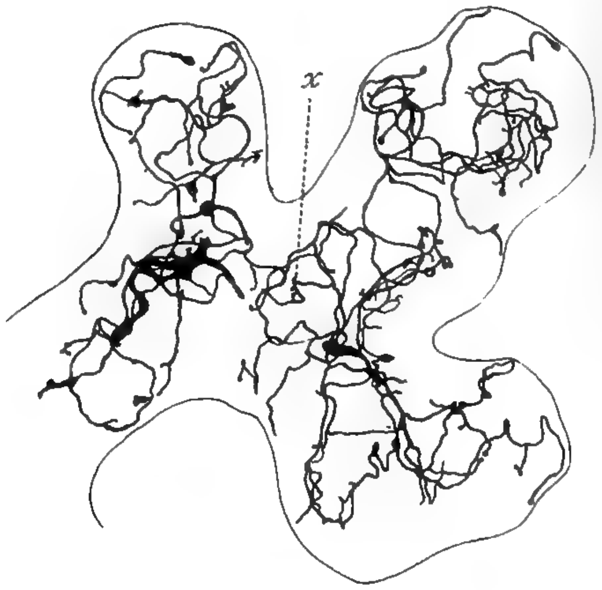
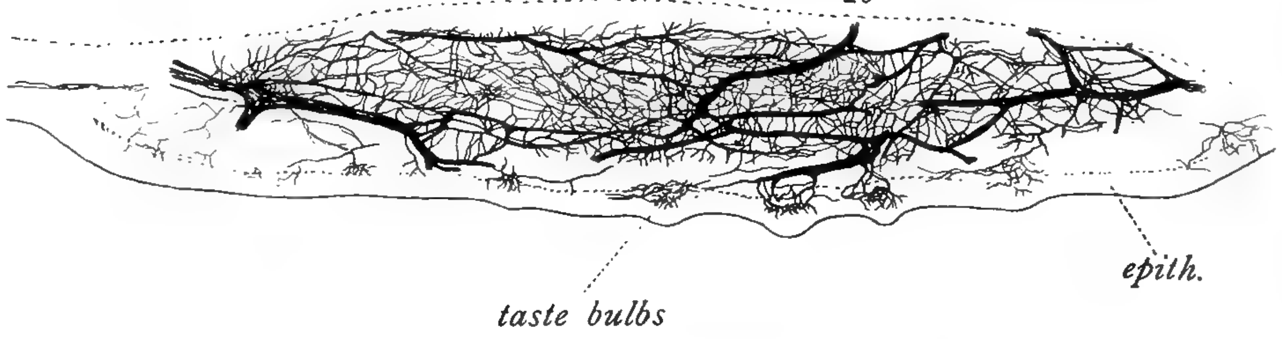

r. pal. VII
taste bulbs
epith.

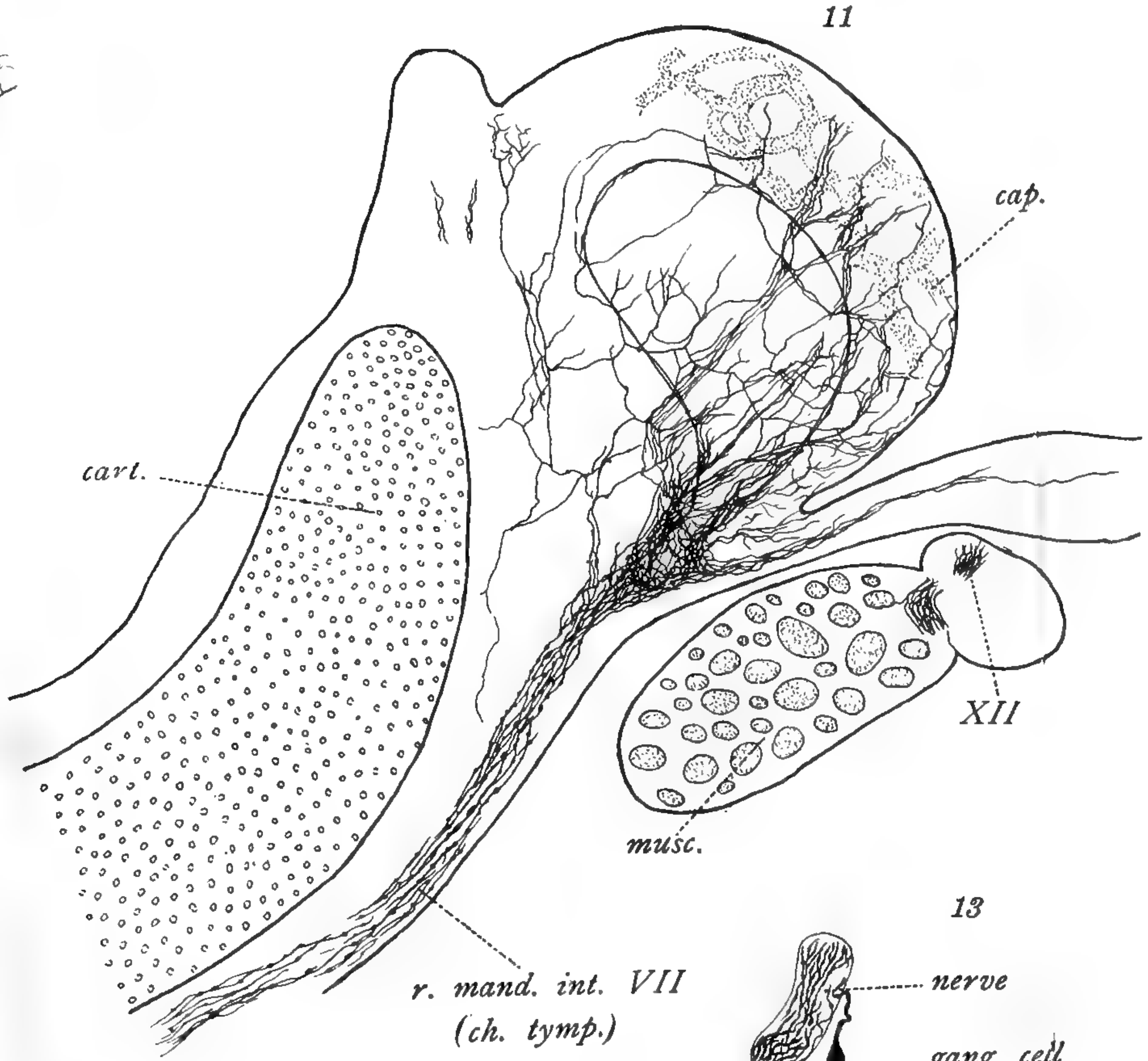
9


x

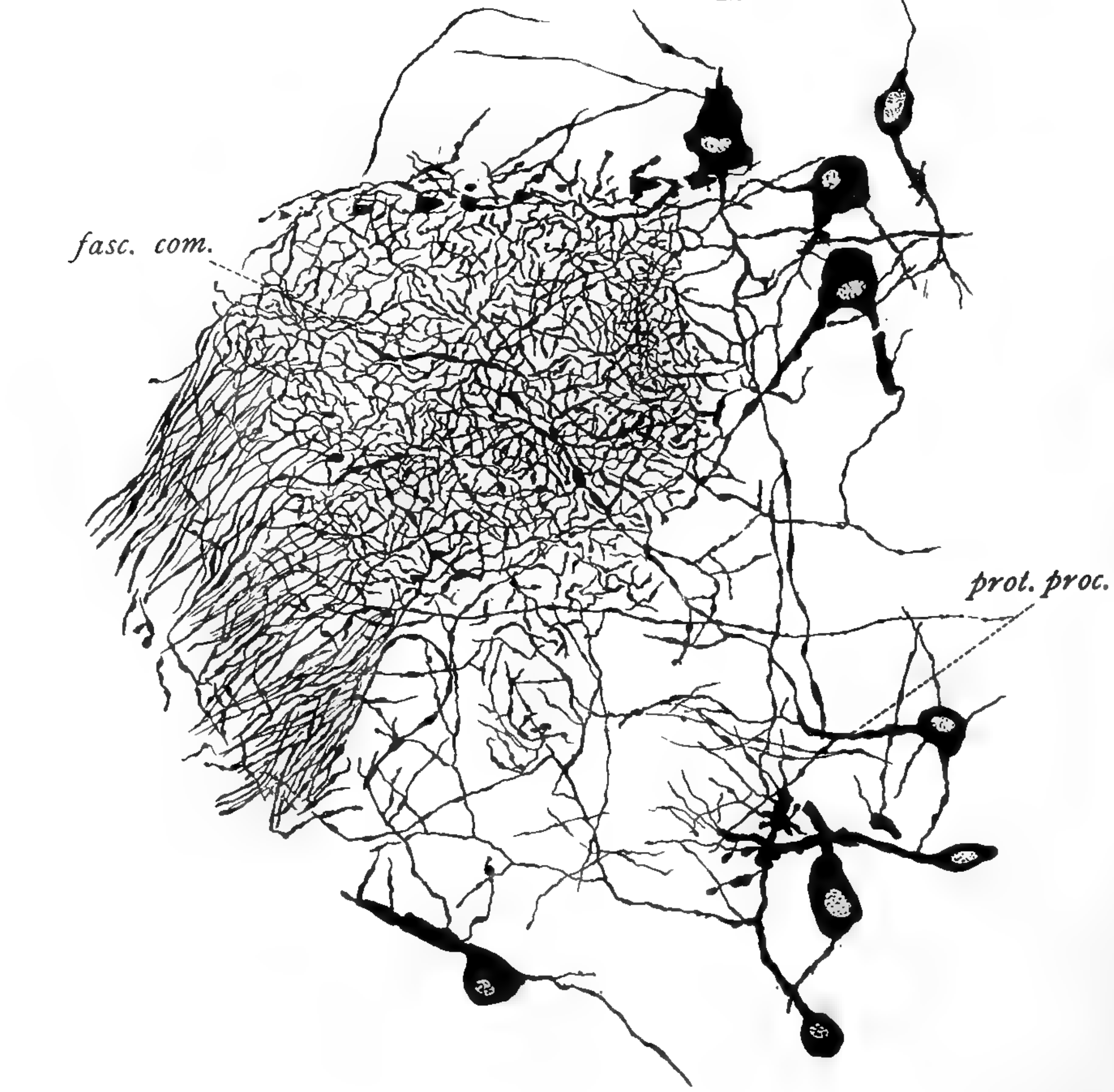
10


taste bulbs
epith.

11


cap.
cart.
XII
musc.
r. mand. int. VII
(ch. tymp.)

12


fasc. com.
prot. proc.

13


nerve
gang. cell
bl. ves.

EXPLANATION OF PLATE IX.

FIG. 14. Longitudinal (frontal) section through the heart, showing the ramifications of the Rr. cardiaci X.

FIG. 15. Vertical section through the pharyngeal epithelium, showing the innervation of a taste bulb (end bud). × 315.

FIG. 16. Similar to Fig. 15.

FIG. 17. Vertical section through the epithelium of the roof of the pharynx, showing the innervation of the multicellular glands of F. E. Schulze. × 155.

FIG. 18. Section similar to Fig. 17, showing the superficial glandular nerve plexus. × 265.

FIG. 19. Similar to Fig. 18. × 315.

FIGS. 20 and 21. Similar to the preceding and showing more precisely the individual nerve endings. × 424.

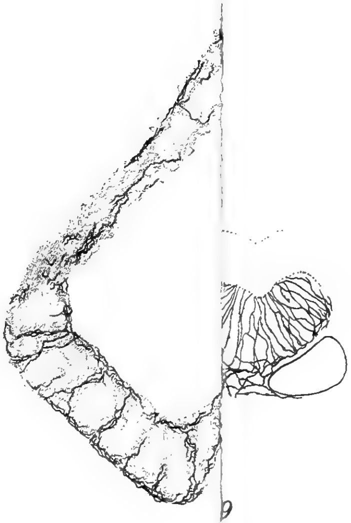
FIG. 22. Horizontal section through superficial glandular nerve plexus. × 192.

FIG. 23. Vertical section through the epithelium of the roof of the pharynx, showing the continuous superficial glandular nerve plexus where the glands are continuous. × 72.

FIG. 24. Horizontal section through pharyngeal epithelium passing through the cupula of a taste bulb. × 315.

Journ. Morph

Pl. IX



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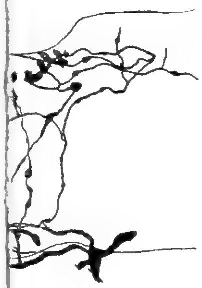
21



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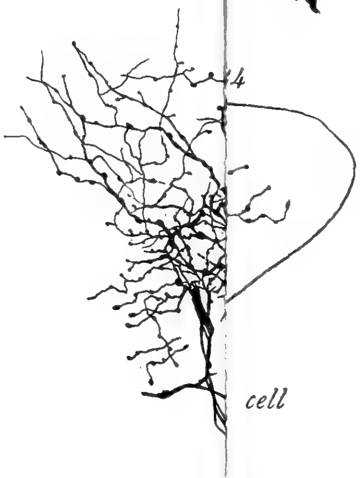

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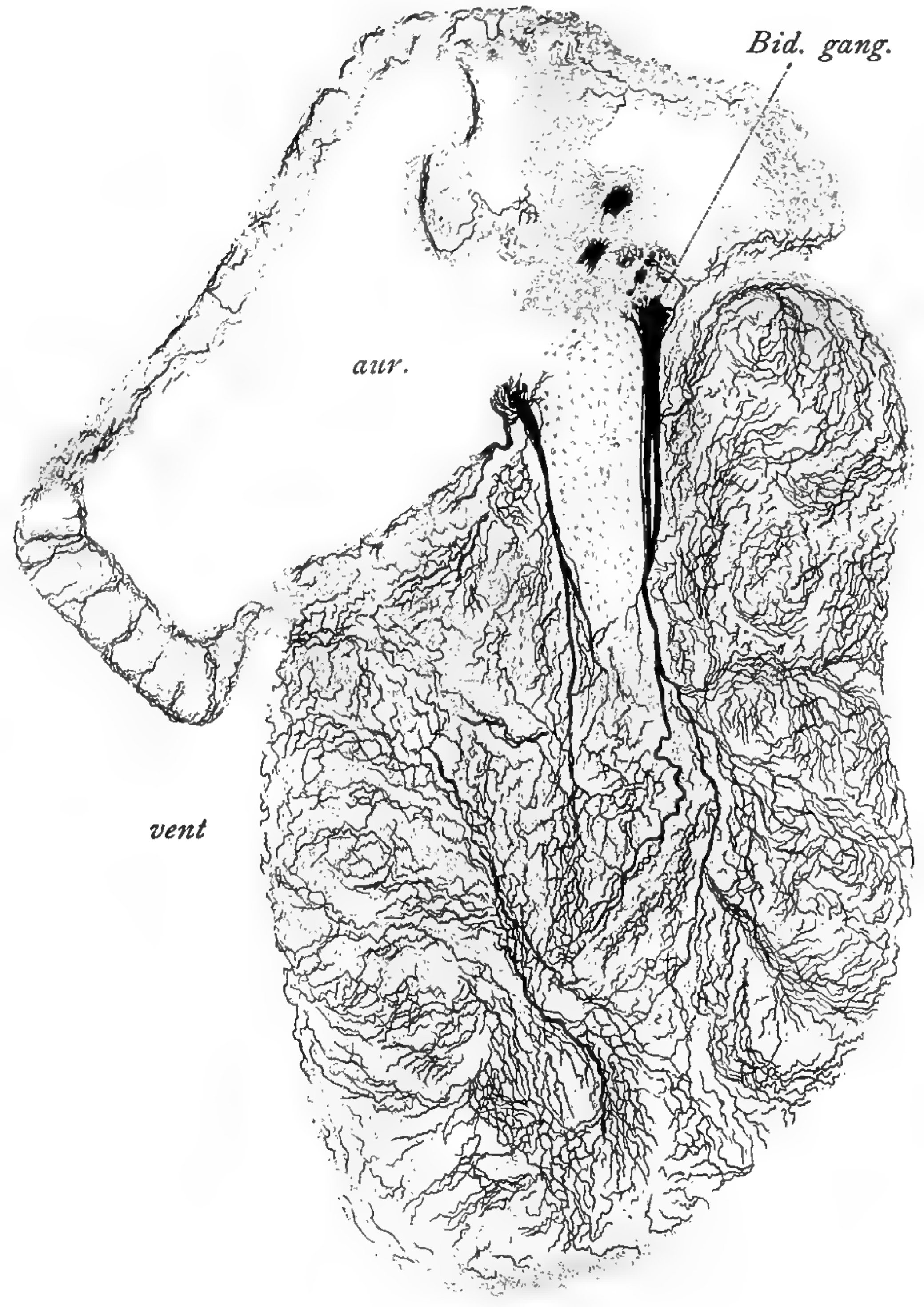

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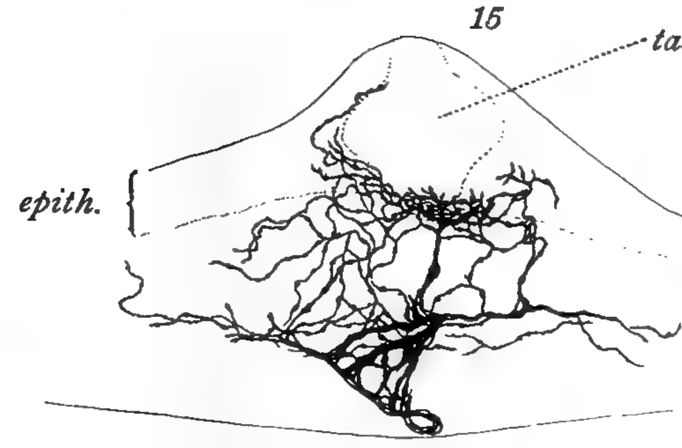

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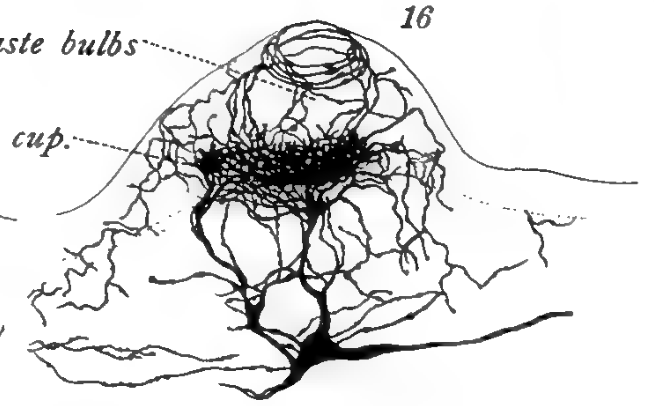

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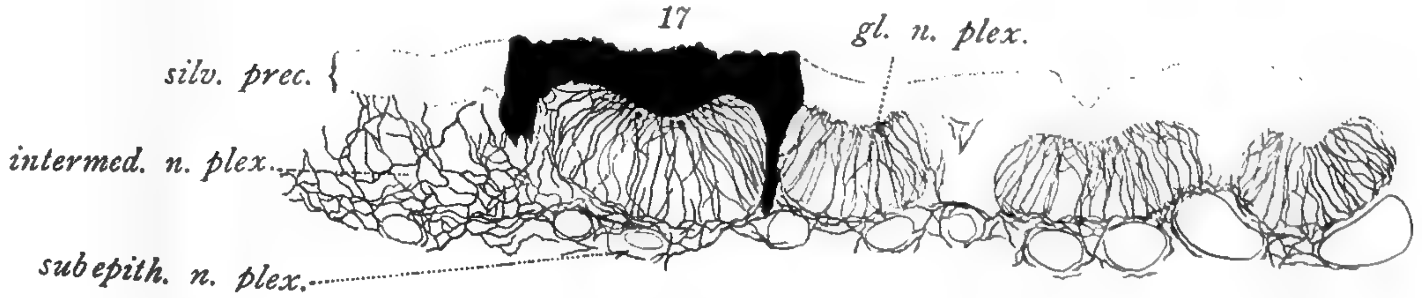

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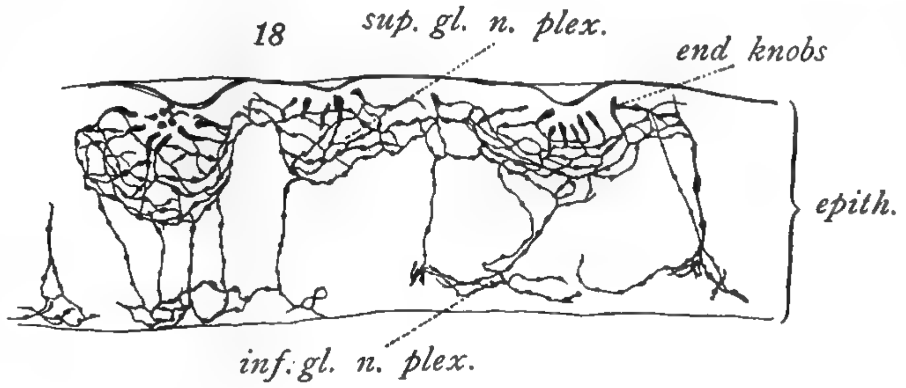

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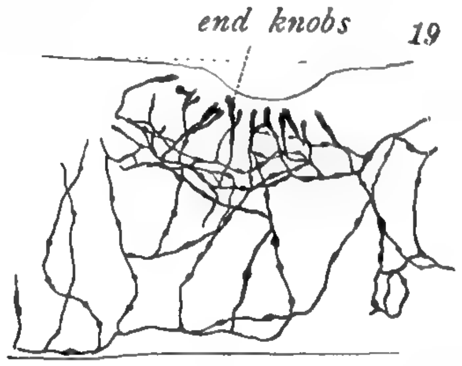

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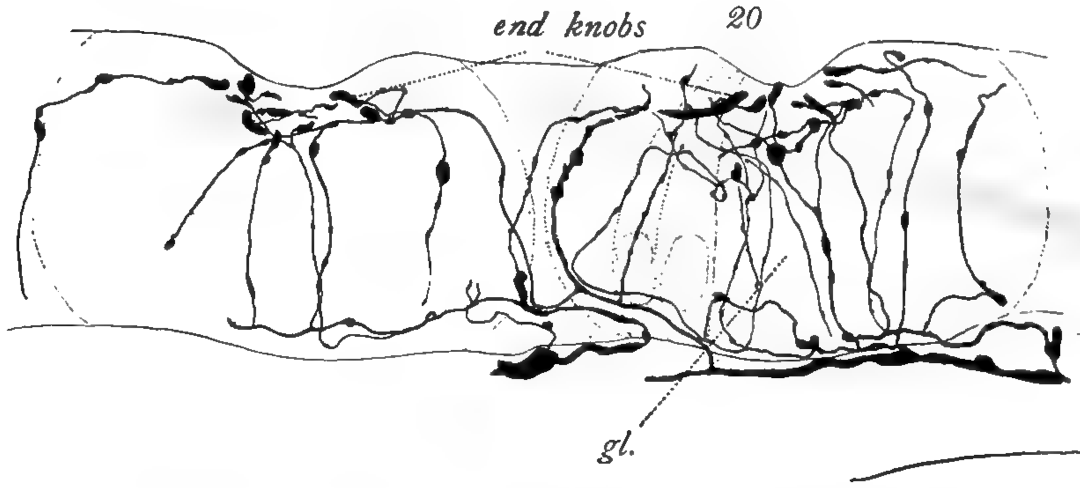

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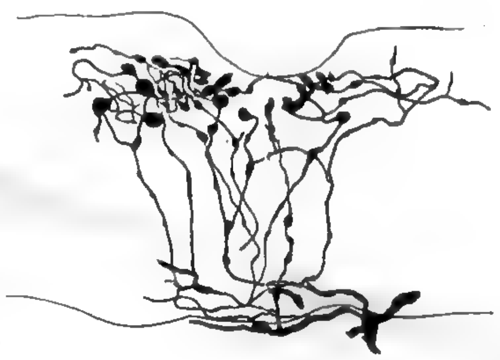

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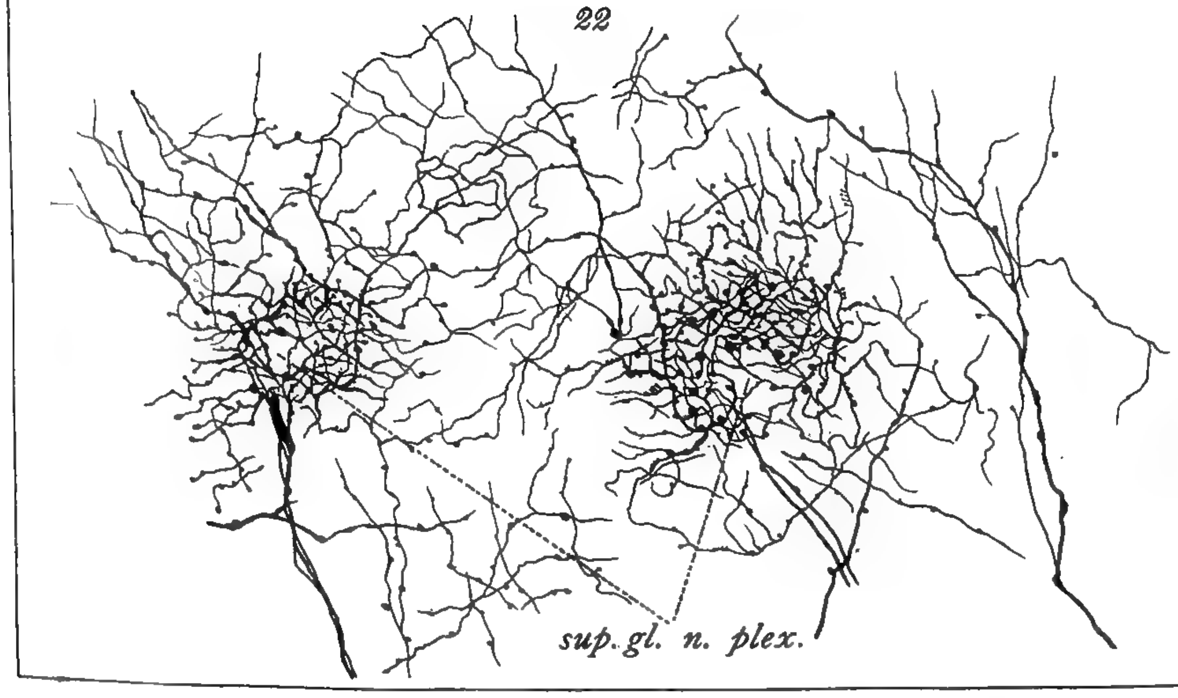

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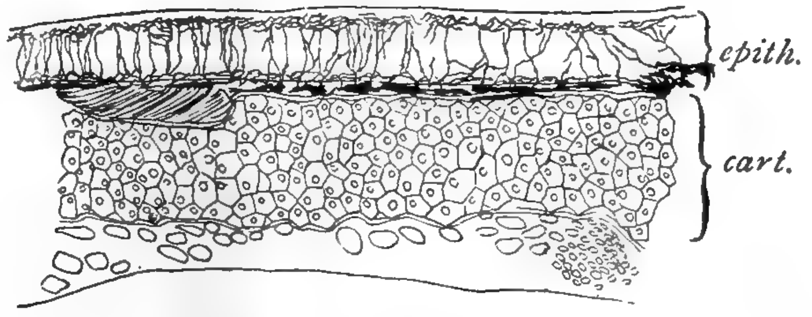

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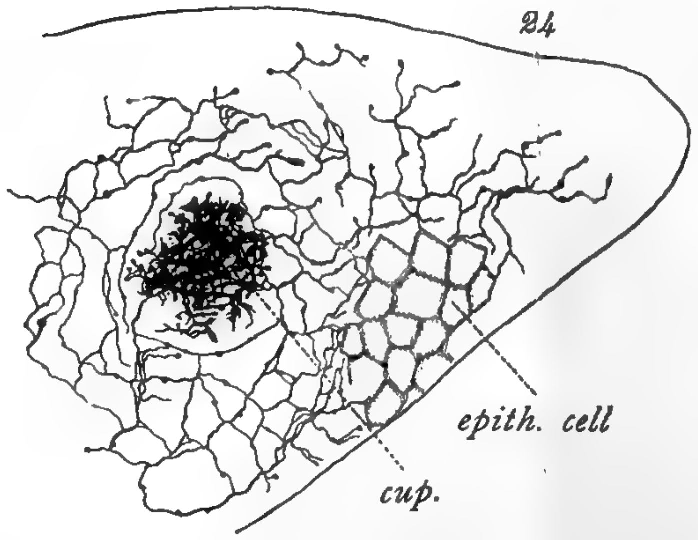
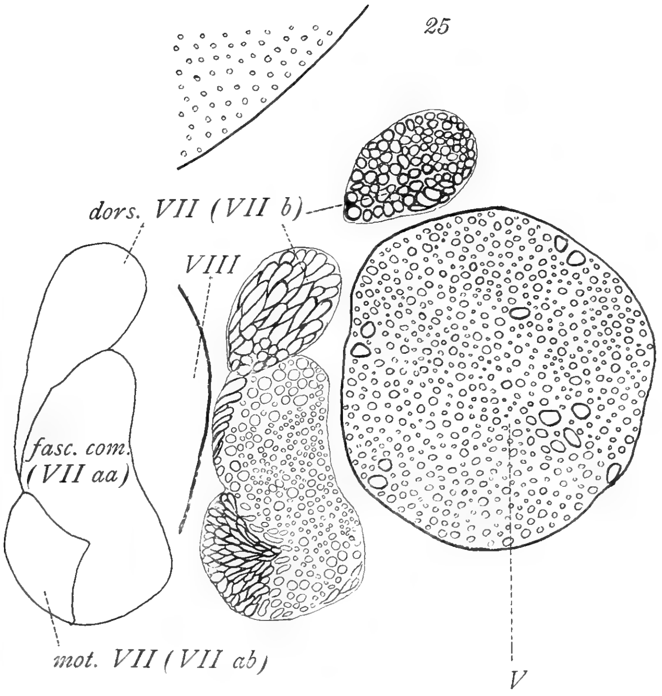


EXPLANATION OF PLATE X.

FIGS. 25–30. Sections through the Hyomandibularis VII at different points along its course, proceeding cephalad (distad), according to the numbering, and showing the components of the nerve. The outlines accompanying each section are to show more clearly the position of the components and to facilitate their designation. Fig. 26 is an oblique section; the others are transverse. × 137.

25



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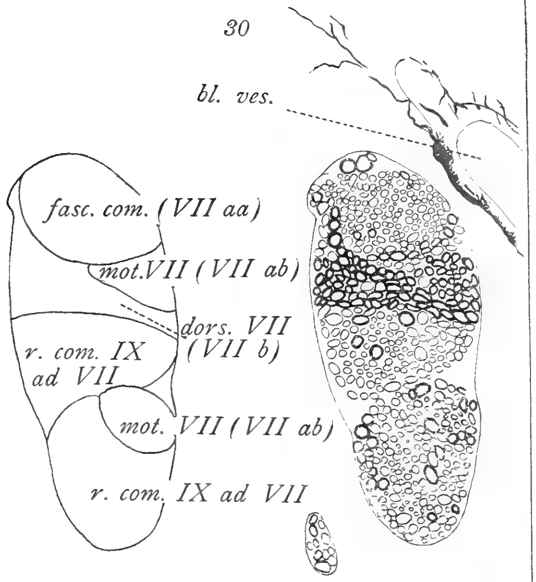

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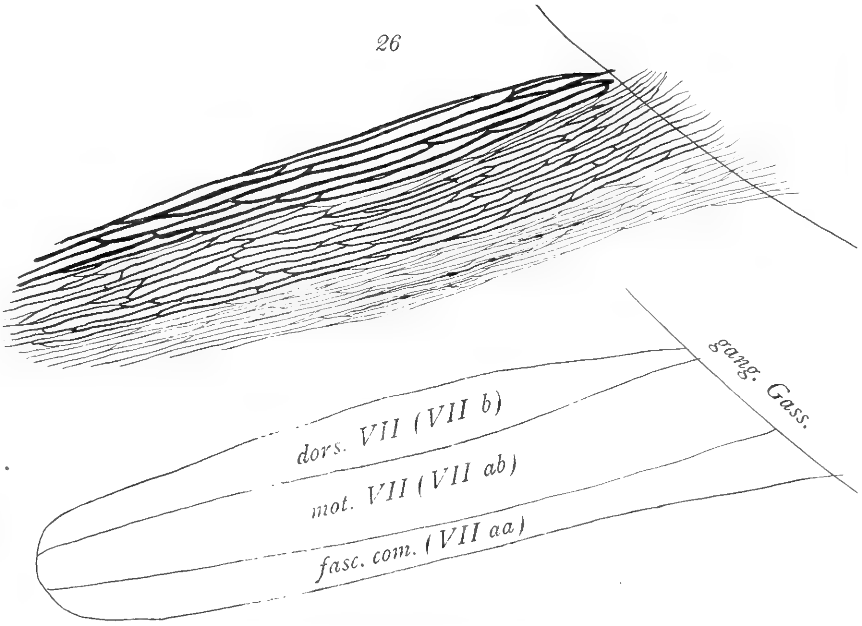

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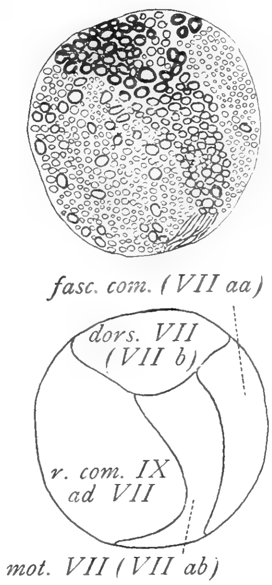

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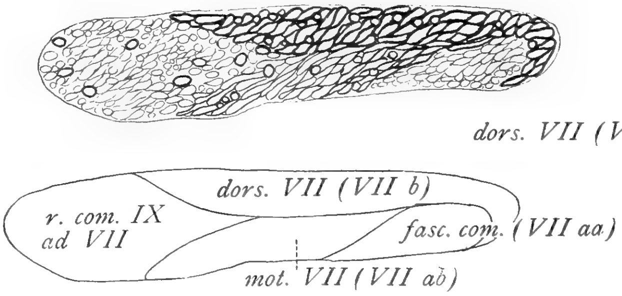

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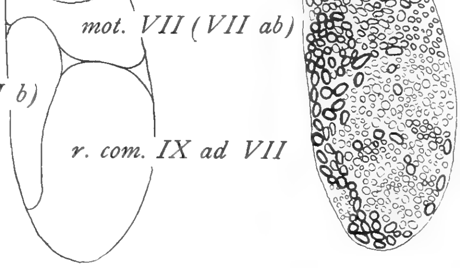


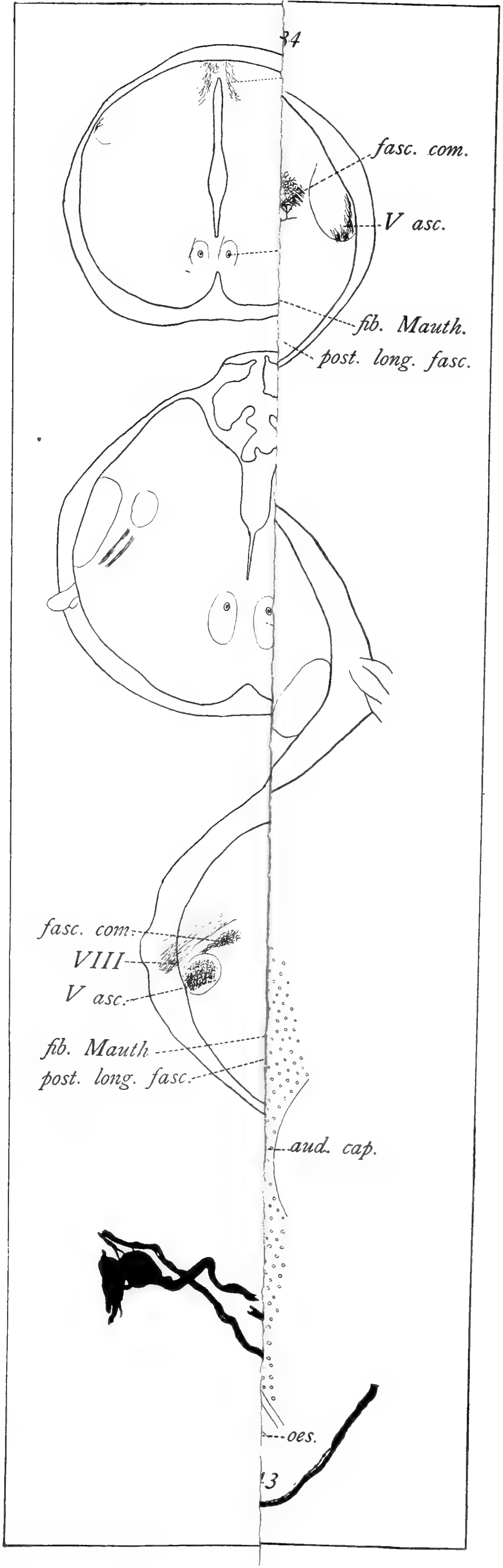
EXPLANATION OF PLATE XI.

FIGS. 31–39. Transverse sections through the medulla proceeding cephalad. They show the position of the fasciculus communis, ascending V and, incidentally, the posterior longitudinal fasciculus and fibres of Mauthner.

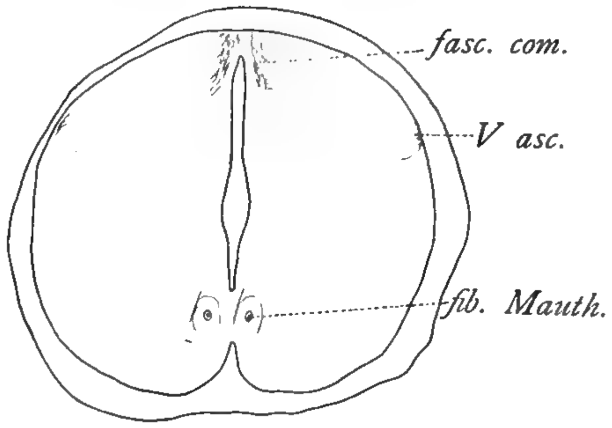
FIG. 40. Transverse section through that portion of the vago-glossopharyngeal complex lying just outside the auditory capsule.

FIGS. 41–43. Some of the nerve cells found along the course of the ramifications of the visceral nerves beneath the epithelium of the pharynx. The dotted line in Fig. 41 indicates the inner boundary of the epithelium.

FIGS. 1, 2, 4, and 17 are from preparations by the ordinary rapid Golgi method, somewhat modified, in some cases, in the proportions in the fluids used. Figs. 5, 6, 7, 18, 19, and 24 are from a series prepared by the triple impregnation modification of Cajal. Figs. 3, 8, 10–16, 31–39, and 40 are from a series prepared by means of the sulphate modification. Figs. 9, 20–23, and 41–43 are from other series prepared by the same modification. Figs. 25–30 are from preparations in which the nerves are stained with osmic acid.


34
fasc. com.
V asc.
fib. Mauth.
post. long. fasc.
fasc. com.
VIII
V asc.
fib. Mauth
post. long. fasc.
aud. cap.
oes.
43

31



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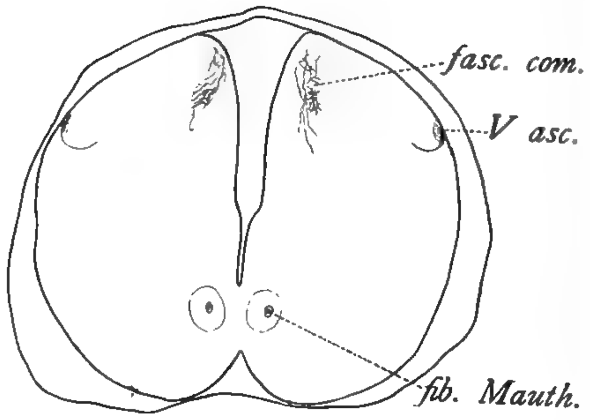

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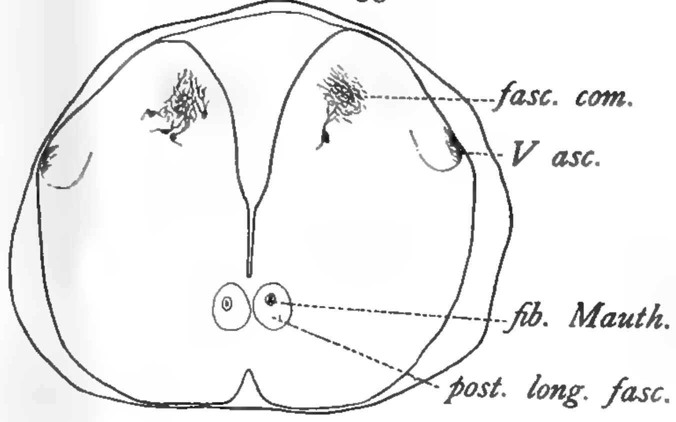

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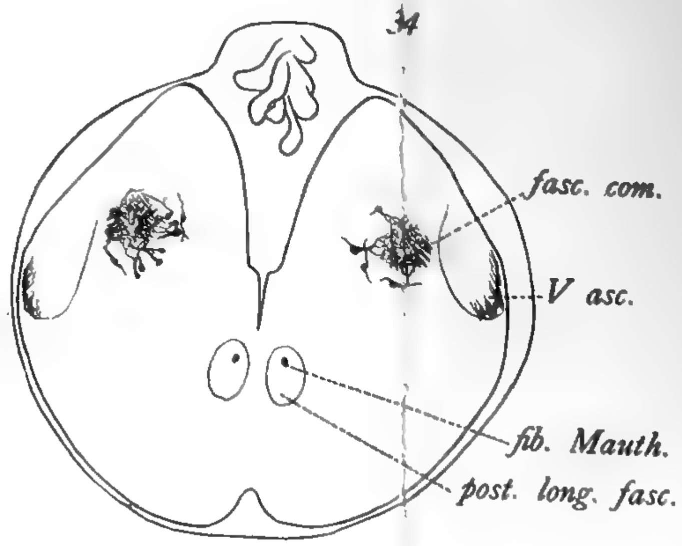

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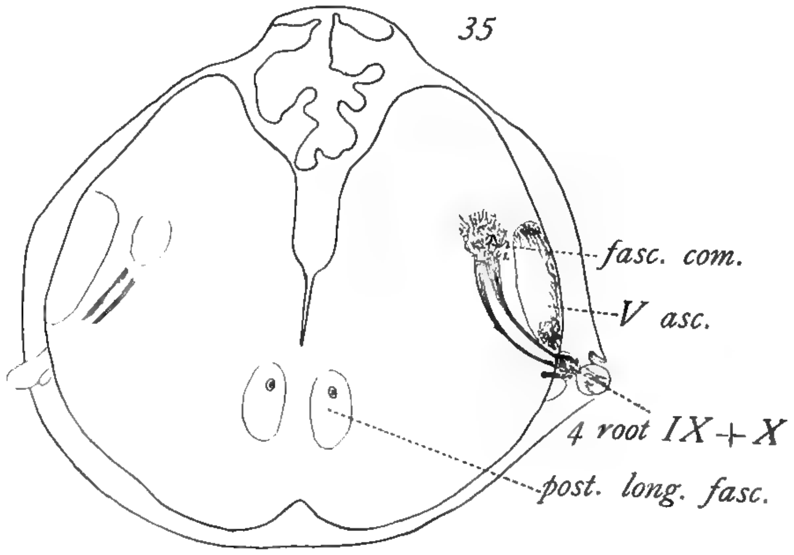

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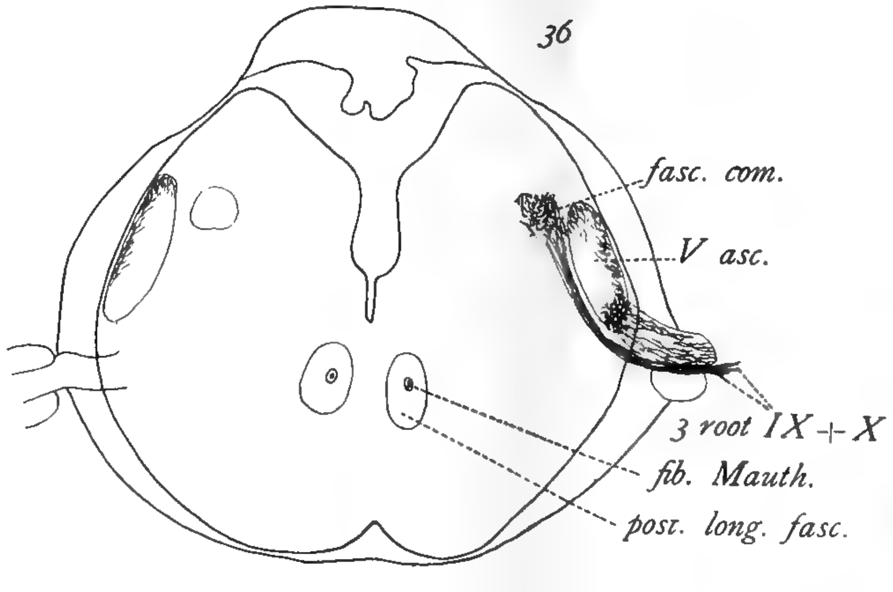

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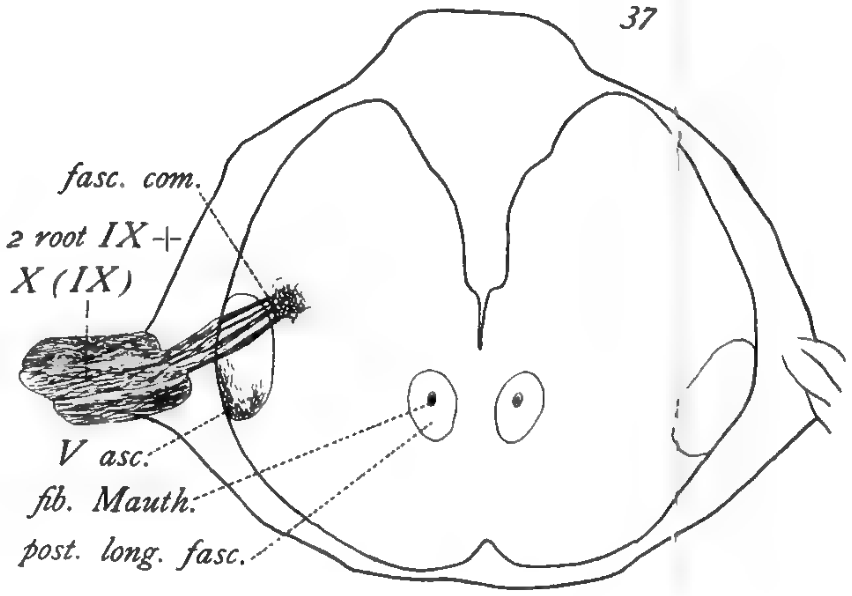

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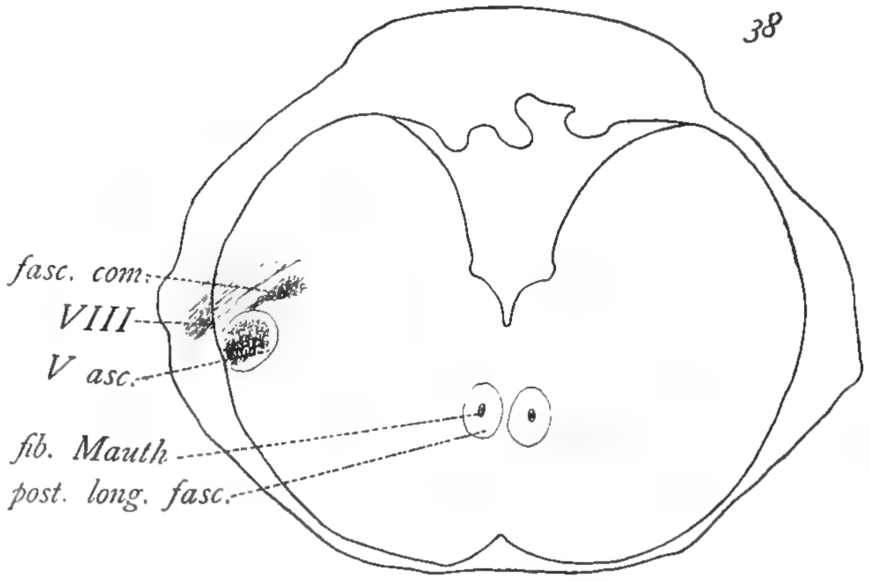

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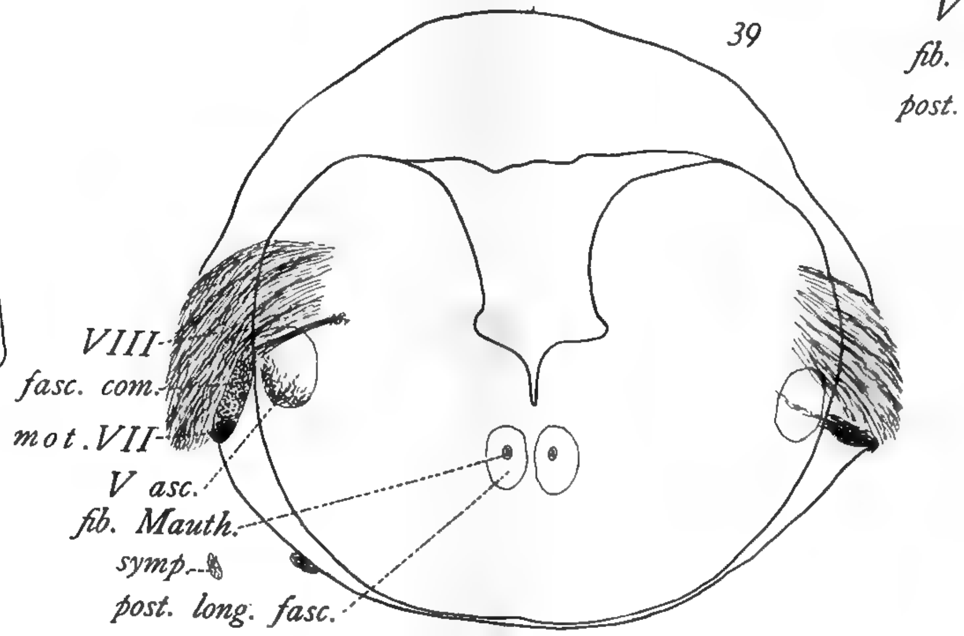

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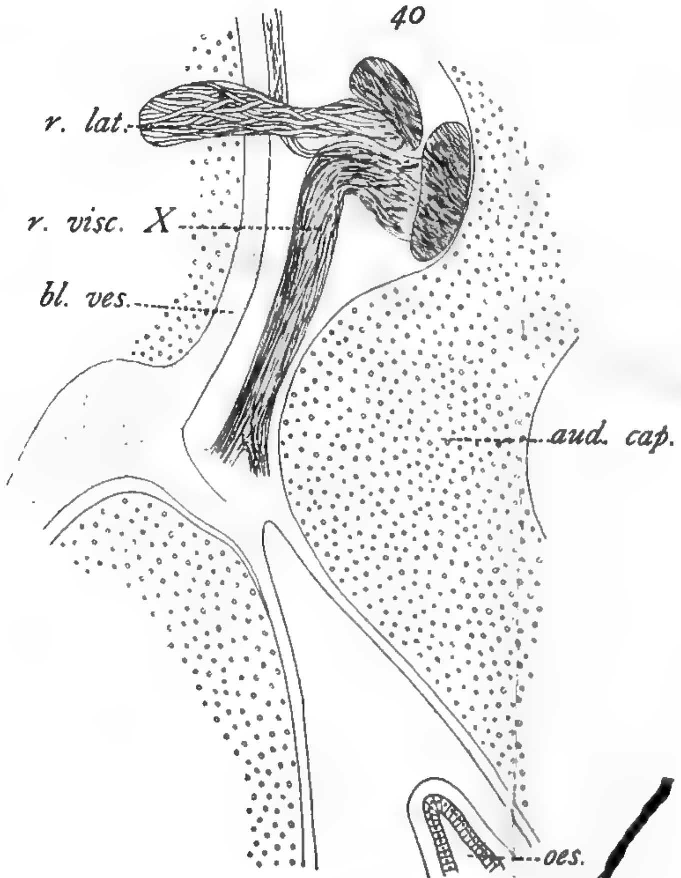

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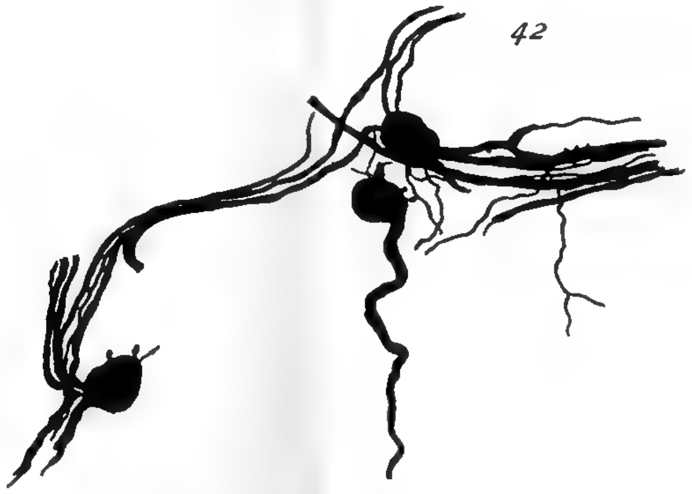

43

EXPLANATION OF PLATE XII.

A. A reconstruction of the V, VII, IX, and X nerves of the tadpole, showing the different components of these nerves in different colors. One half the head is shown in a horizontal plane and dorsal aspect (see also text, p. 107). × 35.

B. A reconstruction showing the roots of the V, VII, and VIII nerves, the first two as far as the Gasserian ganglion. Lateral aspect.

C. A reconstruction showing the roots of the V and VII nerves in the Amblystoma larva. Dorsal aspect.

The eye, ear, and brain are indicated in faint neutral tint, with dotted outlines, portions of the brain being omitted, however, where it overlaps certain of the nerves.

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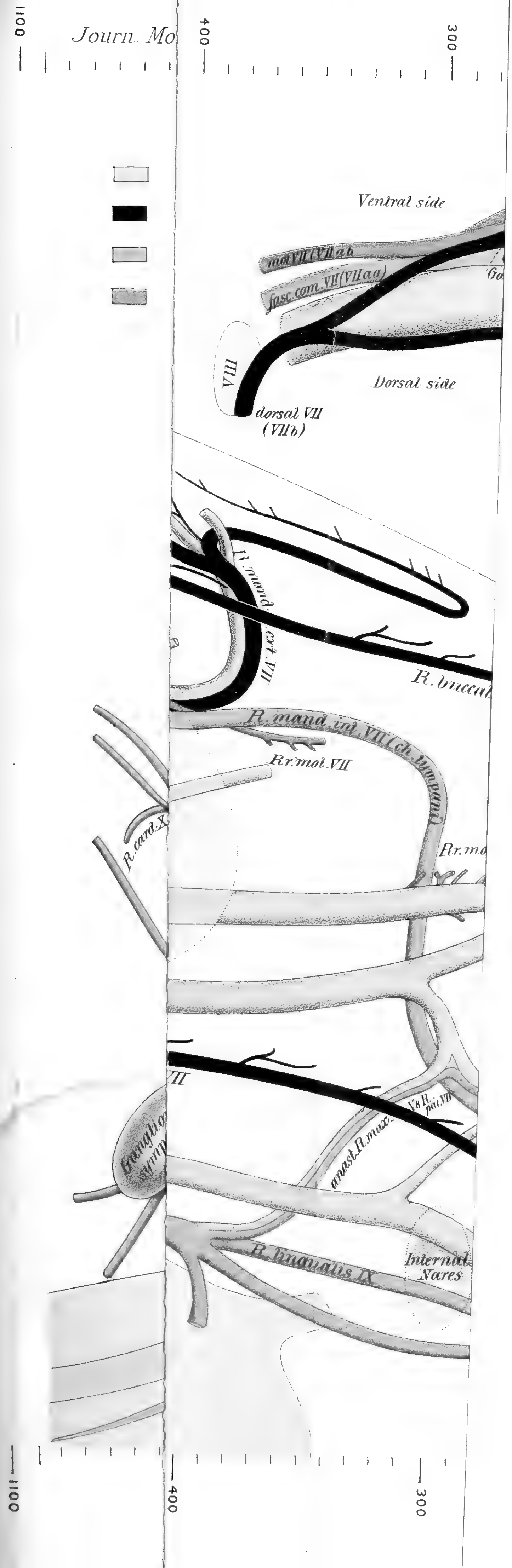
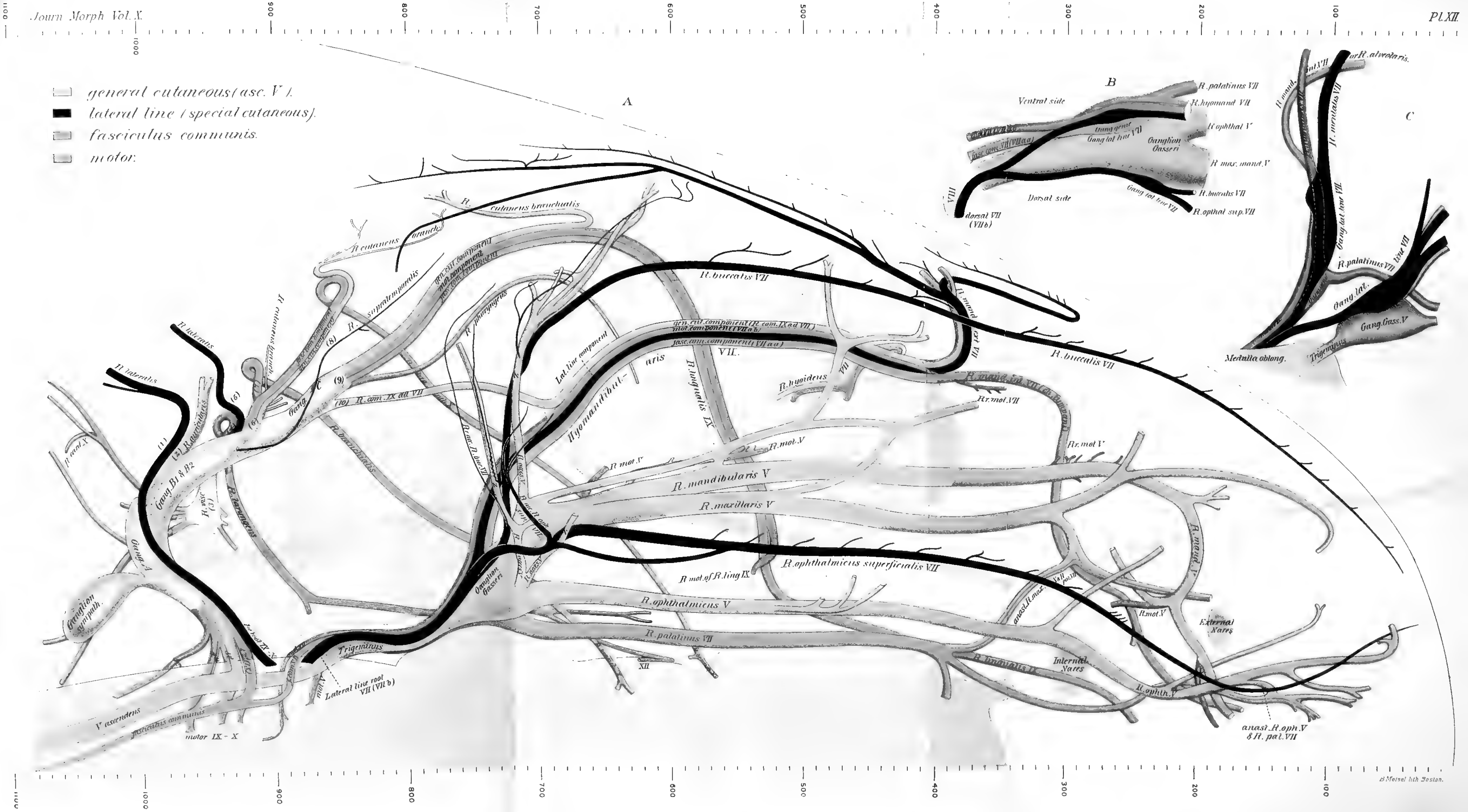

1100
400
300
Ventral side
mot.VII (VII a b
fasc. com. VII (VII a a)
Ga
VIII
Dorsal side
dorsal VII
(VII b)
R. mand. ext. VII
R. buccal
R. mand. int. VII (ch. tympani)
Rr. mot. VII
R. card. X
Rr. ma
VII
Ganglion symp
V & R. pal. VII
anast. R. max.
R. lingualis IX
Internal Nares
1100
400
300



B. Meisel lith. Boston.