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THE CRANIAL NERVES OF AMPHIUMA MEANS.

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I. INTRODUCTORY.

The only descriptions of the cranial nerves of *Amphiuma*, with the exception of more or less incidental mention, are to be found in the papers of FISCHER (1864), WILDER (1892), KINGSLEY (1902a), and DRÜNER (1904), but none of these attempts a systematic account from the standpoint of nerve components.

The present paper is an outline of the more salient features of the origin and peripheral distribution of the cranial nerves of *Amphiuma* means with reference to their components. Inasmuch as the nervous systems of but two of the urodele amphibians have been analyzed into their components (see BOWERS 1900, and COGHILL 1902), it seems to the writer that the time is not ripe for making detailed comparisons. For that reason the present account deals chiefly with facts of description.

The material studied consisted of individuals varying from 55 to 300 millimeters in length, sectioned through the head transversely and sagittally. Fixation was for the most part in VOM RATH'S picric-acetic-osmic-platinic mixture. Plate IV is from plottings of a series of cross-sections, ten micra in thickness, prepared by the paraffin method, supplemented and checked up by a number of series sectioned in celloidin. Plates V to VII are chiefly from material sectioned in celloidin, sections fifteen and twenty micra in thickness. Counter-stains, when used, were either gold-orange or acid fuchsin. As individuals small enough to make sectioning of the entire body feasible are seldom obtained, there is still lacking detailed information regarding some of the cranial nerve branches that pass back into the trunk of the body. The nervous system of *Amphiuma* is favorable for study because of the differential staining that results from fixation in VOM RATH'S fluid. The lateralis components become intensely black; motor fibers are a dark gray; general cutaneous fibers are brown-black; and the communis system with slight development of myelin is but lightly colored. As the methods employed do not differentiate the sympathetic fibers, no description of the sympathetic system is attempted here.

There is evidently a need for a thorough revision of the nomenclature of the sub-divisions of the cranial nerves of *Amphibia*, but more facts are needed upon which to base comparisons. In this paper the older names are employed as far as consistent with the existing state of information upon the subject.

2. THE OLFACTORY NERVE.

Little need be added to the account given by KINGSLEY. A little anterior to the level of the posterior border of the eyeball fibers begin to arise from the olfactory glomeruli on the dorso-

lateral border of the brain (figs. 13 and 20). From this point to the anterior end of the brain the emerging fibers constitute a dorsal part of the olfactory trunk. A ventral smaller part is formed by fibers that leave the more ventral glomeruli. Anteriorly, before the nerve leaves the brain, the two portions have become indistinguishably united; in fact there appears to occur an interlacing of fibers. Other smaller roots join these two main portions. As the nerve passes into the nasal capsule (fig. 3) it is seen to consist of about eight branches, arranged in two or three bundles. The ventral branch in the more ventral of the three bundles passes to JACOBSON'S organ (figs. 2 and 20) giving off also some branches to the ventral olfactory epithelium. The nerve to JACOBSON'S organ passes to the anterior lateral ventral border of that structure, thence dorsally and posteriorly along its dorsal wall. The other branches in the ventral group innervate the ventral olfactory epithelium; the fibers of the middle bundle supply the median wall of the olfactory epithelium; and the dorsal bundle goes to the dorsal wall, except that immediately on entering the nasal capsule one of the dorsal branches sends a large twig to the ventral wall (fig. 20). It may be true that the branch innervating JACOBSON'S organ comes from the ventral portion (or root) of the nerve, but it is certainly too small to contain all the fibers that arise by that root. It will thus be seen that the condition in *Amphiuma* contributes little in answer to the query whether or not there are two morphologically distinct elements in the olfactory nerve.

3. THE OPTIC NERVE.

The account given by KINGSLEY is confirmed throughout. Myelinic sheaths are not in evidence. Sagittal sections show that as the nerve leaves the brain a small ventricular diverticulum reaches out to the point of emergence of the nerve, but apparently the cavity has no peripheral extension.

4. THE EYE-MUSCLE NERVES.

Of these KINGSLEY was able to find but one, the oculomotorius. I find that the oculomotorius, the trochlearis and the abducens nerves arise in the typical manner, but are much reduced in size. The oculomotor nerve leaves the lateral wall of the anterior

part of the medulla oblongata, although its deep origin is ventral (fig. 13). Soon after its emergence it comes into intimate relation with the gasserian ganglion and more anteriorly with the ramus ophthalmicus profundus V, for some distance being embedded in the median border of these structures (figs. 13 and 6). Passing through its own foramen in the skull (fig. 5) it runs a short distance to the vicinity of the origins of the eye-muscles and there divides into two branches, the dorsal of which supplies the superior rectus muscle, and the ventral the inferior and internal rectus and the inferior oblique muscles (fig. 22). It will be seen (fig. 13) that the dorsal branch passes dorsal to the main trunk of the r. ophthalmicus profundus while the ventral branch runs ventral to this nerve. The trochlear nerve, consisting of two or three fibers, arises at the extreme posterior border of the dorsal part of the mid-brain (figs. 13, 7 and 9) and passes anteriorly to its foramen of exit closely pressed against the inner wall of the skull (figs. 5 and 6). It ends in the superior oblique muscle (fig. 22). The abducens is extremely attenuated. It takes its exit from the ventral surface of the brain a little posterior to the level of the origin of the seventh nerve as a few fibers, usually two in number (figs. 7 and 13). These I have been able to follow but a short distance. But anteriorly at the point where the r. mandibularis of the fifth nerve leaves the gasserian ganglion (figs. 6 and 13) there may be found leaving the ganglion or the r. mandibularis a nerve of two fibers that passes out of the skull along with the r. ophthalmicus profundus and ends in the external rectus muscle (fig. 22). Before reaching the muscle the abducens nerve is sometimes in very intimate relation with a small nerve that innervates two small muscles which have their insertions upon the antorbital cartilage. But there seems to be no exchange of fibers between the two nerves. The incomplete development of the eye-muscle nerves precludes any more extended account of their relationships. Of ciliary nerves or ganglia I have found no traces.

5. THE TRIGEMINAL NERVE.

a. The roots of the trigeminal nerve.—The fifth nerve derives its fibers from four sources: (1) From the spinal V tract whose fibers may be traced as far posteriorly as the level of the second spinal nerve. (2) From fibers just dorsal to the spinal V tract.

It is doubtful whether this should be considered as a source distinct from the preceding. (3) According to KINGSBURY (1895a) and to OSBORN (1888) there occurs in *Necturus* a tract of fibers from the so-called trigeminal nidus in the roof of the mid-brain that passes in part into the spinal V tract near the exit of the fifth nerve. I find in *Amphiuma* a similar tract of large fibers from the mid-brain passing into close proximity to the spinal V tract and apparently giving off fibers to the latter near the motor root of the fifth nerve, but the fibers so given off are few in number, the greater number passing apparently posteriorly mesal to the spinal V tract, as many do in *Necturus*. (4) From motor fibers in one or two rootlets that come from a nidus of cells lying in the floor of the medulla.

KINGSLEY speaks of the fact that the fifth nerve leaves the brain as three roots: dorsal and ventral small roots and a median large one. The small dorsal root is made up of fibers that compose (2) above. In this region the spinal V tract is reinforced by numerous fibers from the adjoining cinerea. This small dorsal root appears to be merely some of these fibers that delay the union until after emergence from the brain. The small ventral root is the motor component. As it leaves the brain the fifth nerve contains only motor and general cutaneous fibers.

b. The ramus mandibularis V.—The fibers of the fifth nerve leave the gasserian ganglion in three groups. There is first given off the r. mandibularis, composed of motor and general cutaneous fibers, innervating the temporal, masseter, pterygoid, intermandibular (mylohyoid anterior), retractor bulbi and levator bulbi muscles, and supplying the skin of the lower jaw and the side of the head (in part). The r. mandibularis passes out of the cranium through a foramen common to it and the "dorsal VII." It emerges at the posterior dorsal border of the pterygoid muscle, at first enters the masseter muscle, then passes anteriorly, ventrally and laterally between the pterygoid and masseter muscles, finally out through the masseter. On emerging from the skull it gives off a number of small twigs to the pterygoid and masseter muscles. As the main trunk of the nerve is passing through the foramen there is given off a large branch which rising rapidly between the pterygoid muscle and the internal portion of the masseter and giving off branches to the anterior part of the pterygoid muscle passes around to the dorsal side of the cranium and runs pos-

teriorly to supply the temporal muscle on the top of the head. While this branch to the temporal muscle is passing anteriorly there is given off from it a short distance from its origin from the main trunk a small branch which running mesally into the pterygoid muscle gives off twigs to the latter and descending applies itself so closely to the outer border of the r. ophthalmicus profundus as to be with difficulty distinguished from it. Leaving the r. oph. prof. nerve at the ventral border of the latter, it runs anteriorly to innervate the two small muscles, previously mentioned, which have their insertion upon the antorbital cartilage (figs. 5, 13 and 22, *mb.*).

These two muscles appear to have escaped the notice of previous writers. One of these (figs. 4 and 22, *rtb.*) has its origin on the posterior part of the maxillary bone and the anterior part of the pterygoid cartilage. As seen in the illustrations, its action is to depress the antorbital cartilage. From the position of the tip of the latter ventral to the eyeball the contraction of the muscle will bring about a retraction of the eye, or it acts as a retractor bulbi muscle. Its position and origin make such an homologizing not improbable. The other muscle (*lvb.*) has its origin on the orbito-sphenoid and parietal bones. Its contraction opposes that of the retractor muscle, or elevates the antorbital cartilage. It is here designated as levator bulbi muscle. As previously noted, the nerve supplying these two muscles sometimes comes into intimate relations with the abducens nerve. But that there is no fundamental anastomosis between them is shown by the fact that this small branch to the retractor and levator bulbi muscles sometimes arises directly from the gasserian ganglion and passes out of the cranium through the foramen of the oph. prof. nerve and lateral to the latter, thence anteriorly through the pterygoid muscle dorsal and mesal to the oph. prof. without coming in contact with the latter, and nowhere approaching closely to the abducens nerve (fig. 22).

As the r. mandibularis passes out through the masseter muscle it gives off twigs to the latter. One large branch, composed of motor and general cutaneous fibers, runs for some distance nearly parallel with the main nerve. Its motor fibers finally pass to the anterior part of the masseter muscle; its general cutaneous fibers run as a large branch nearly to the level of the mandible, and a little anterior to the angle of the jaw break up into twigs that run

in all directions to supply the skin on the side of the head. The main mandibular nerve on reaching the mandible enters a groove on the dorsal side of the latter (fig. 5) and soon divides into two branches. The ventral of these passes directly down through the jaw between the dentary bone and Meckel's cartilage and on emerging between the angulo-splenic and the dentary bones divides anteriorly and posteriorly into branches that supply the mm. intermandibularis (mylohyoideus anterior) anterior and posterior and the skin of the ventral surface covering these muscles. The dorsal division runs along in the groove above Meckel's cartilage between the dentary and the angulo-splenic bones, and soon divides into two branches. The larger of these, of darker staining fibers (*md (3a)*), occupies a canal in the dentary bone (fig. 4) and in turn divides into two divisions. Small branches to the skin pass out from the canal, but the two chief divisions (represented as one nerve in fig. 1) do not emerge from the dentary until well near the tip of the jaw where they supply the skin. The smaller lighter stained division of the ramus in the mandibular groove (*md (3b)*) shifts mesally and ventrally from the larger division and runs along dorsal to Meckel's cartilage in a groove between the dentary and angulo-splenic bones (fig. 4). There unites with it a branch of the r. alveolaris VII (*alv. (4)*), the combined nerve passing anteriorly just ventral to the teeth and apparently supplying the latter and possibly the lateral floor of the mouth. It may be traced as far as the extreme anterior teeth and always in close relation to the latter. An anastomosis between that part of the mandibularis supplying the intermandibular muscles and the portion of the r. jugularis VII innervating the interhyoideus muscle, such as COGHILL describes in *Amblystoma*, I do not find in *Amphiuma*, but it is certain that the two nerves in question approach very close to each other. KINGSLEY was inclined to believe that branches of the ramus mandibularis in *Amphiuma* supply lateral line sense-organs. I can state with certainty that no such relationship exists.

c. The ramus ophthalmicus profundus V.—The ramus ophthalmicus profundus leaves the extreme anterior portion of the gas-serian ganglion and after passing anteriorly and somewhat dorsally into the region of the eye divides into a number of branches, of which there may be said to be five that are fairly constant in their occurrence and relationships. Of these the first given off, the

nasalis internus (*op.* (1)), arises as a group of nerves, or as a single nerve, that soon divides into branches. The larger of these branches (*op.* (1a)), that goes up through the edge of the cranium in a passage-way between the frontal and the prefrontal bones and then runs along in a canal in the edge of the frontal as far as the nasal capsule, was called by KINGSLEY "ethmoideus caudalis." Anteriorly this can be traced along the upper surface of the frontal bone to a point halfway between the eye and the tip of the snout. As it passes along its canal and on the surface of the frontal it gives off numerous twigs to the overlying skin. Arising from the posterior part of the nasalis internus, or directly from the trunk of the oph. prof., are one or two branches (*op.* (1b)) that pass to the skin of the dorsum dorsal and a little posterior to the eye. The main portion of the nasalis internus passes anteriorly and enters the dorsal portion of the nasal capsule near its mesal border. A little before its entrance to the nasal capsule it gives off a branch (not figured) that passes forward in the capsule and emerging dorsally from the skull is distributed to the skin near the tip of the snout. After entering the nasal capsule the nasalis internus anastomoses with the r. ophthalmicus superficialis VII, when passing nearly to the ventral side of the nasal capsule divides, one branch ascending and uniting with the r. ophthalmicus superficialis in a second anastomosis, and the other passing out of the anterior end of the capsule to be distributed, like the dorsal division anastomosing with the oph. spf., to the skin of the tip of the snout. It will thus be seen that the distribution of the nasalis internus and its branches is to the skin of the dorsal side of the head from the extreme anterior end to a point some distance posterior to the eye. In its distribution it seems to answer approximately to the ophthalmicus superficialis V of fishes. It probably gives off fibers to structures in the nasal capsule, but I have detected none such. It evidently does not supply the nasal epithelium.

A second branch of the ophthalmicus profundus (*op.* (2)) is one that arises usually in part from the nasalis internus and in part from the main trunk. It was designated by WILDER as r. glandularis II, on the supposition that it innervates the lateral nasal gland. It and its branches, of which there are commonly two divisions, anastomose with each other and with the nasalis internus, enter the lateral dorsal portion of the nasal capsule, run anteriorly and emerging from the capsule are distributed to the skin of the side

of the snout from near the anterior end of the latter posteriorly about halfway to the eye. The fibers, if any, given off to the lateral gland are certainly few in number, for I have been unable to detect them. The ramus is characteristically cutaneous and the name, r. glandularis II, is a misnomer.

The next branch given off from the oph. prof. ((*op. 3*)) is the one that anastomoses with the r. palatinus VII. The union occurs at the posterior border of the nasal capsule. The palatine rapidly ascends from its ventral position and the trigeminal ramus descends to meet it. As the two nerves approach each other each divides into two parts, and the union occurs between the branches in pairs, so that there result two nerves, each containing general cutaneous and communis fibers (fig. 26). The dorsal of the two nerves thus formed ascends slightly and divides into three branches. The dorsal one of these three branches (*op.-pal.d.*) from its mode of formation and from the appearance of its fibers consists of general cutaneous fibers only. It may divide and its two divisions on entering the nasal capsule run along the lateral wall of the nasal epithelium on the dorsal border of JACOBSON'S organ to the extreme anterior end of the latter. The posterior wall of the nasal epithelium is supplied by branches (*op.-pal.pn.*) derived from this same source, of general cutaneous fibers only. The ventral posterior nasal epithelium is supplied by a branch from a division with mixed components (*op.-pal.mn.*), and its exact composition has not been determined. The other two branches of the dorsal of the two nerves resulting from the palatine-trigeminal anastomosis (*op.-pal.l.*) pass to the lateral portions of the roof of the mouth innervating the lateral teeth, etc. The ventral branch of the anastomosis (*op.-pal.m.*) passes ventrally into the inner ventral angle of the nasal capsule and running forwards supplies the median series of teeth, etc. From it branches are also given off to the posterior ventral nasal epithelium (*op.-pal.mn.*). According to the figure given by WILDER this ramus of the trigeminus that anastomoses with the palatine comes from the nasalis internus. The origin of the two from the main trunk of the ophthalmicus profundus is such that it is not improbable that in some cases they may arise by a common branch. The mode of anastomosis, it will be seen, is like that described by COGHILL in *Amblystoma*.

The remaining portion of the ophthalmicus profundus divides

into two large branches. Of these the larger lateral one (*op.* (4)) fuses with one (*buc.* (1)) of the two main divisions of the buccalis VII. Sometimes the fusion occurs between the two undivided trunks, but more often each divides into three or four branches which then fuse in pairs or approximately so (fig. 25). The resulting mixed nerves (*r. nasalis externus* of WILDER) supply the neuromasts of the infraorbital series and the skin of the side of the snout. The other profundus branch (*cp.* (5)) comes into close relation with the second division of the buccalis VII (*buc.* (2)), but I can find little evidence of actual anastomosis. The combined nerves (*r. glandularis I* of WILDER) supply the skin and the infra-orbital series of neuromasts at the side and tip of the snout.

KINGSLEY refers to this union of branches of the ophthalmicus profundus with the buccalis (maxillaris according to him) as a condition reported only in *Amphiuma*. A casual examination of the figures which WILDER gives of *Cryptobranchus* (*Menopoma*) and of *Siren* will show that similar (if not identical) anastomoses occur in these forms. The prediction may be safely made that careful study of these forms will reveal the fact that as in *Amphiuma* it is a union between lateral line (buccalis) and general cutaneous (ophthalmicus profundus) components.

d. Trigeminal fibers entering the dorsal VII.—A third group of fibers leaving the gasserian ganglion is made up of general cutaneous fibers that at once associate themselves with *rr. ophthalmicus superficialis VII* and *buccalis VII*. Their subsequent course will be considered in connection with the facial nerve.

6. THE FACIAL AND AUDITORY NERVES.

a. Roots of the facial and auditory nerves.—The fibers of this complex arise by two groups of rootlets. The more dorsal group comprises the lateral line fibers of the seventh nerve and is formed by three rootlets. Of these the dorsal rootlet (*VIIb* (1)) enters that portion of the medulla oblongata which in *Necturus* is designated by KINGSBURY as the "dorsal island," a mass of alba occupying the extreme dorsal part of the medulla (figs. 7-10, *ll.*) This "dorsal island" suggests an homology to the lateral line lobe (*lobus lineæ lateralis*) of cyclostomes, selachians and ganoids, although JOHNSTON (1906) asserts that the lateral line lobe and the dorsal root of the "dorsal VII" are absent in aquatic amphi-

bians. The other two rootlets (*VIIb* (2) and *VIIb* (3)) enter the sensory column ventral to the dorsal island.

In the second and more ventral group of rootlets we find true facialis and acusticus fibers. There may be recognized five rootlets, three belonging to the auditory and two to the facial nerve (figs. 1, 7 and 8). Of the auditory fibers there are four groups: (1) medium and large fibers that pass posteriorly into the spinal VIII tract (*VIII* (1)); (2) medium fibers that pass anteriorly in the so-called (incorrectly) "descending VIII" tract (*VIII* (2)); (3) medium and small fibers that pass into "tract b" (Necturus, KINGSBURY) (*VIII* (3)); (4) large fibers forming a tract at first distinct from (1) but posteriorly passing into the spinal VIII tract or into very close proximity to it (*VIII* (4)). (1) forms an anterior rootlet; (2) and (3) form a larger posterior rootlet; (4) forms a rootlet dorsal and intermediate to the other two (figs. 1 and 23a). Of these rootlets (1), (2) and (3) supply the sacculus, lagena, macula neglecta and the posterior canal; (4) supplies the utriculus and the anterior and horizontal canals. The peripheral divisions of the auditory branches will not be considered here.

The two facial rootlets consist of a dorsal one of communis fibers (*VIIaa*) entering the brain at the anterior dorsal border of (4) above mentioned, and passing into the fasciculus communis, and a ventral motor rootlet (*VIIab*). The relative positions of these rootlets of the facial and auditory nerves are subject to some variation.

b. Lateral line components of the facial nerve.—From the points of entrance of its fibers into the brain the root of the lateral line portion of the seventh nerve passes anteriorly as a flattened band closely compressed between the brain and the ear capsule. Most if not all of the fibers of its dorsal rootlet, together with part of the fibers of the ventral rootlet, pass ventrally into the acustico-facial ganglion and thence out in the main trunk of the ventral portion of the seventh nerve. The fibers of the middle rootlet and part of those of the ventral rootlet pass anteriorly as the "dorsal VII" into the lateral line ganglion lying dorsal to and confluent with the gasserian ganglion. Passing anteriorly from this dorsal lateralis ganglion the lateral line fibers are joined by general cutaneous fibers from the gasserian ganglion (the third group of fibers mentioned under the head of the trigeminal nerve). These general cutaneous fibers are in two distinct bands, one of which is applied to the ventral

and the other to the mesal surface of the lateralis trunk. As the combined nerves pass anteriorly the general cutaneous components shift their positions, the median one becoming dorsal and the ventral one shifting to a lateral position. The main combined trunk soon divides into a dorsal and a ventral division, each consisting of lateralis and general cutaneous fibers. Each division then divides into two rami.

c. Ramus buccalis VII, and ramus maxillaris V.—The ventral, or infra-orbital division, forms a ventrally situated ramus consisting solely of lateralis fibers, the buccalis VII, and a more dorsal one of general cutaneous fibers with a few lateralis fibers, the maxillaris V. The few lateral line fibers mixed with the maxillaris are soon given off to certain neuromasts of the infra-orbital series posterior to the eye. The r. buccalis innervates the neuromasts of the infra-orbital series anterior to the eye. Its two main divisions that anastomose with the r. ophthalmicus profundus V have been described. The maxillaris of *Amphiuma* seems to be distributed chiefly to the skin of the side of the head posterior and a little anterior to the eye, but it does not run as far anteriorly as in most Urodela that have been figured, in the more anterior parts of the head being replaced by branches of the ophthalmicus profundus.

The term, ramus maxillaris V, is here used with the limitations that COGHILL gave it. STRONG (1895) called attention to the striking parallelism between trigeminal and lateral line branches in the tadpole of the frog. This is especially noticeable between certain so-called accessory lateral line branches of the ophthalmicus superficialis and the buccalis and so-called accessory trigeminal twigs. Of these the most striking is the close relationship between the buccalis and the larger of the accessory trigeminal branches. COGHILL's contention that the so-called maxillaris in Urodela is the homologue of this larger accessory trigeminal twig of the tadpole seems to me valid. The distribution of the maxillaris in *Amphiuma* agrees very closely with the distribution of this accessory twig in the tadpole. The intimate union of maxillaris and buccalis in *Amphiuma* suggests the parallelism in the tadpole between the buccalis and the accessory trigeminal branch. The distribution of the terminal branches of the ophthalmicus profundus V, palatinus VII and maxillaris V in *Amphiuma* agrees almost to details with that in *Amblystoma*. COGHILL's conclusions that "there is no distinct maxillaris branch of the trigeminus

in *Amblystoma*” can be as truly applied to *Amphiuma*. The smaller accessory general cutaneous and lateralis twigs given off from the combined lateral line and gasserian ganglia in *Rana* seem to represent possibly a ramus oticus. A determination of their exact terminations would be necessary before coming to any conclusions in the matter. But it must be noticed that in both *Amphiuma* and *Amblystoma* there occur some minute rudimentary nerves given off from the gasserian ganglion. These possibly correspond to the smaller accessory twigs in *Rana*.

d. Ramus ophthalmicus superficialis VII and ramus oticus.—The supra-orbital division of the “dorsal VII” forms a ventral lateralis ramus and a dorsal portion consisting of both lateralis and general cutaneous fibers. The ventral ramus is the r. ophthalmicus superficialis VII, that supplies all the neuromasts of the supra-orbital series except some at the posterior end of the series. Anteriorly in the nasal region it anastomoses with the nasalis internus, as already noted. The dorsal portion of the supra-orbital division, consisting of general cutaneous and lateralis fibers, divides into a number of small branches supplying the skin of the dorsal part of the head posterior to the eye, and the neuromasts that form the posterior end of the supra-orbital series and four or five neuromasts at the posterior dorsal end of the infra-orbital series (fig. 24). In its distribution to neuromasts this dorsal division seems to represent the ramus oticus of fishes. In the latter it supplies the neuromasts of the posterior end of the supra-orbital series and the first few neuromasts of the infra-orbital series. In the r. oticus of fishes are found general cutaneous fibers from the gasserian ganglion associated with the lateralis fibers. In *Amphiuma* these general cutaneous fibers are distributed to a region which in some other Urodela, as *Amblystoma*, is innervated by branches of the ophthalmicus profundus. In some specimens of *Amphiuma* there occurs an anastomosis between the maxillaris and this dorsal general cutaneous division just before the latter breaks up into its smaller branches. We have here the suggestion that these dorsal general cutaneous fibers represent in part the posterior portion of the ophthalmicus superficialis trigemini. Both WILDER and STRONG are of the opinion that the ophthalmicus profundus in Amphibia “represents the united ophthalmicus profundus and ophthalmicus superficialis trigemini” of fishes. It is certainly true that the distribution of these dorsal

general cutaneous branches and of the nasalis internus collectively corresponds to that of the piscine ramus ophthalmicus superficialis V.

e. The ventral trunk of the facial nerve.—As the ventral division of the facial nerve leaves the acustico-facialis ganglion complex it consists of lateralis, communis and motor fibers. As above noted, the lateral line fibers are derived from the dorsal and ventral rootlets of the dorsal division of the facial nerve. In this acustico-facial ganglion are three distinct groups of cells: (1) the large lateralis ganglion cells of the lateral line component. These are situated mostly on the anterior and dorsal borders of the complex. (2) Small cells of the geniculate ganglion, situated on the anterior mesal border of the complex. (3) Medium sized acoustic cells, situated at the posterior and along the dorsal border of the ganglionic mass. Of these the cells of the vestibular branch of the VIII nerve are larger and situated anterior to the others.

f. Ramus palatinus VII.—There is first given off from the ventral facial trunk the r. palatinus of communis fibers from the geniculate ganglion. The palatine runs anteriorly and shortly after its emergence from the cranium receives an anastomosing branch from the r. pretrematicus IX. This anastomosing branch is JACOBSON'S commissure, of communis fibers. The anastomosis of the r. palatinus with the r. ophthalmicus profundus V has been already noticed. In *Amblystoma* according to COGILL there occurs a ganglion on the r. palatinus at the junction of its lateral division with the lateral division of the trigeminal branch. In *Amphiuma* there seems to be a ganglion on the palatine nerve shortly before the anastomosis with the trigeminus is reached. From this region (fig. 26) are given off a number of small nerves some of which pass to the roof of the mouth and the median series of teeth. Some of these small nerves contain general cutaneous as well as communis fibers, but the exact composition of all of them was not determined.

g. The ramus alveolaris VII.—The second branch given off from the ventral facial trunk is the r. alveolaris of communis fibers. From the r. pretrematicus IX it receives two anastomosing branches (*alv.* (1) and (2)). Near the angle of the jaw it gives off a small branch (*alv.* (3)) that passes mesally, ventral to the quadrate cartilage, to the roof of the mouth. There seem to be no peculiarities about the distribution of the alveolaris in *Amphiuma*. It divides

into a number of terminal branches, one of which anastomoses with the mandibularis V as already noted. The other branches supply the ventral lateral wall of the anterior floor of the mouth. In this account the alveolaris is assumed to be a pretrematic nerve.

h. The rami mentalis externus and internus VII.—From the hyomandibular trunk of the facial nerve there are given off two large lateral line rami, of which the anterior dorsal one supplies the angular and the oral series of neuromasts, and the posterior ventral one the gular series of neuromasts. KINGSLEY designated the first as r. mandibularis externus, and the second as r. hyomandibularis accessorius. Each contains lateral line fibers only, and the two evidently correspond to the two nerves which in other Urodela hitherto figured arise by a common trunk from the hyomandibularis, and which in *Amblystoma* are termed by COGHILL r. mentalis externus and r. mentalis internus. FISCHER seems to have overlooked the internal division in *Amphiuma*. At a point about opposite the articulation of the lower jaw the r. mentalis internus divides into two branches that pass anteriorly parallel to each other. I find no anastomoses between the r. mentalis internus and the r. mandibularis V, such as KINGSLEY reports, much less can I substantiate the statements of DRUNER that numerous anastomoses occur between these nerves.

At the point where the r. mentalis externus leaves the hyomandibular trunk there are given off a few small nerves (figured as two in number in the illustrations), partly from the main nerve and partly from the mentalis externus, which supply the post-orbital and jugular series of neuromasts. These small lateralis branches have a very wide distribution for their size. Some of their smaller divisions may be traced through hundreds of sections, yet consist of but two or three fibers each. In their origin and distribution these small lateralis nerves seem to represent opercular branches of fishes. DRUNER reports a small cutaneous branch given off from the mentalis externus and passing to the skin overlying the depressor mandibulæ muscle. I fail to find such a nerve. Moreover the occurrence of general cutaneous fibers in a branch of the seventh nerve before the anastomosis X ad VII is received is improbable. I do find a small branch of lateralis fibers leaving the r. mentalis internus and supplying the posterior neuromasts of the gular series overlying the depressor mandibulæ muscle.

i. The ramus jugularis VII.—At about the level of the origin of the r. mentalis internus there is given off from the hyomandibular trunk a small motor branch to the anterior division of the depressor mandibulæ muscle. Another motor branch to the same division of the muscle runs along and in the anastomosis X ad VII. At about the place where the hyomandibularis finally breaks up into the larger divisions of the r. jugularis it is joined by the anastomosis from the glossopharyngeal-vagal complex carrying general cutaneous fibers. The origin and composition of this commissure will be considered under the subject of the glossopharyngeus and vagus nerves. The r. jugularis is distributed to the interhyoideus (mylohyoideus posterior), depressor mandibulæ (digastricus) and sphincter colli (levator maxillæ inferioris ascendens of FISCHER, quadrato-pectoralis of DRÜNER) muscles, and in addition carries general cutaneous fibers to the skin overlying these muscles. Lateral line fibers also occur in the r. jugularis.

k. The ramus lateralis VII.—There is one branch of the r. jugularis, if indeed it may be considered as a branch of the latter, that requires especial mention. It was first described by FISCHER as a structure peculiar to Amphiuma, and said to be traced to the hyotrachealis (interbranchialis 4) muscle. KINGSLEY states that it supplies the dorso-trachealis muscle. The writer (1904) gave a brief description of this nerve, showing that it does not end in the dorso-trachealis muscle, but passes posteriorly into the trunk region as far as the pelvis. There was suggested a possible relation to the neuromasts of the trunk, and the nerve was provisionally designated as r. lateralis VII. In the same year (1904) appeared the paper of DRÜNER in which he described the nerve, calling it nervus lateralis VII and asserting that it supplied in part the median series of neuromasts of the trunk, that is, he considered it a lateral line nerve. In the following year the writer in a second paper withheld the name, r. lateralis VII, believing that the evidence of the presence in the nerve of lateral line fibers was not convincing. The statements of DRÜNER as to the composition of the nerve may now be confirmed. It is composed largely, if not entirely, of lateralis fibers; I have not, however, as yet detected any connection between it and the neuromasts of the trunk. Such connection doubtless exists. Most of its fibers come from those branches of the r. jugularis that supply the posterior division (cerato-mandibularis) of the depressor mandibulæ muscle. In

addition it is reinforced by fibers from the jugularis branch that supplies the sphincter colli muscle. If the nerve contains any general cutaneous fibers they must come from the latter source. The exact mode of origin of this nerve is subject to a great deal of individual variation, and as it leaves the posterior border of the depressor mandibulæ muscle it may consist of two or more parallel twigs that run for some distance before uniting (as in fig. 1). In passing the thymus gland the nerve is always in two or more divisions. Sometimes a small branch runs back into the trunk along with the main nerve (fig. 1). In some individuals a small branch is seen to leave the main nerve in the neighborhood of the thymus gland, and to pass antero-dorsally anastomosing with the r. supratemporalis X. In one instance the anastomosis was also with one of the twigs of the r. lateralis medius X. The r. lateralis VII seems to be peculiar to *Amphiuma* among the amphibians. Its origin and distribution suggest a possible homology with the r. lateralis recurrens VII of fishes, but in these latter, as shown by HERRICK (1899, 1900, 1901) and CLAPP (1898) the ramus recurrens, or lateralis accessorius, is primarily a communis nerve, with which a few lateralis or general cutaneous fibers may be associated. As shown above, there may occur an anastomosis between the lateralis VII and the r. supratemporalis X, suggesting a similar relation in fishes. In the trunk region there occur some peculiar relations between the lateralis VII and the spinal nerves, but further study of this region will be necessary before it will be safe to attempt exact comparisons. KINGSLEY (1902b) in comparing the Cæcilians and *Amphiuma* gives as one of the supposed points of resemblance: "The occurrence in both of a ramus lateralis recurrens branch of the facial nerve," but he gives no further explanation.

All of the branches of the r. jugularis, except those supplying the anterior portion of the depressor mandibulæ muscle, may contain lateralis fibers. From the branches of the jugularis that pass back into the posterior division of the depressor mandibulæ muscle there are given off two or three small lateralis twigs which after emerging superficially from the muscle run posteriorly just beneath the skin to supply a few of the more posterior of the jugular series of neuromasts. These commonly anastomose more or less with the twigs of the lateralis branches that supply most of the neuromasts of this series. The fore-going small lateralis

twigs are possibly the "rr. cutanei jugulares" mentioned by DRUNER. From the descriptions of FISCHER, KINGSLEY and DRUNER, we are led to infer that the two jugularis branches that pass back through the depressor mandibulæ muscle are distinct from each other, but in fact they anastomose. In the dorsal one, the r. lateralis VII which may be double, there are motor fibers associated with the lateralis fibers. The ventral one, primarily motor, may be exclusively motor or it may contain lateral line fibers also. I have not been able to demonstrate general cutaneous fibers in these; in fact in the r. lateralis VII I have been able to demonstrate beyond question that in some individuals no general cutaneous fibers can possibly be present until it receives the branch from the nerve that supplies the sphincter colli muscle. As noted above, it is not impossible that the r. lateralis VII after it has emerged from the muscle may contain general cutaneous fibers. Cross-sections of the main nerve show scattered among the intensely black-stained lateralis fibers that compose the bulk of the nerve some lighter colored ones. It may also contain communis fibers, but I have detected no evidence of this.

7. THE GLOSSOPHARYNGEAL AND VAGUS NERVES.

a. *The roots of the IX-X complex.*—The IX-X complex in Amphibia is generally described as arising by five roots, but careful comparison by determination of components shows that the roots described in one species by one writer do not always correspond to the roots of a second species described by another writer. Hence a statement that in general the IX-X complex in Amphibia arises by five roots requires some qualifications. In *Amphiuma* the IX-X nerves arise from the brain by five roots, or rather groups of rootlets (fig. 1); but these roots do not correspond in detail to those described in *Necturus* by KINGSBURY, nor to those in *Amblystoma* as described by COGHILL. The five roots are those mentioned by KINGSLEY. The first group of rootlets (figs. 1, 10 and 23) is composed of lateralis (*X* (1)), communis (*IX* (1)) and motor (*IX* (2)) fibers. The communis and motor fibers after passing through the ganglion form the glossopharyngeal or first branchial nerve, with the exception of the general cutaneous component in the latter. The lateralis component supplies all the lateral line fibers of the vagus group. This lateralis component

enters the brain by two rootlets which seem to correspond in origin to the median and ventral rootlets of the lateral line component of the facial nerve. The second group of rootlets consists of general cutaneous ($X(2a)$), communis ($X(2b)$) and motor ($X(2c)$) rootlets. The communis rootlet carries all the communis fibers of the second ($X.1.$) and third ($X.2.$) branchial nerves and of the r. intestino-accessorius. The general cutaneous component supplies fibers to the glossopharyngeus nerve, to the ramus communicans cum faciali, to the r. auricularis X, and to the second and third branchial nerves. The motor rootlets supply the second and third branchial nerves and contribute fibers to the r. intestino-accessorius. The third ($X(3)$), fourth ($X(4)$), and fifth ($X(5)$), groups of rootlets are exclusively motor. They may be considered as constituting one root. With some fibers from the second group of rootlets they form the motor component of the r. intestino-accessorius. In some individuals the fifth root is lacking or extremely attenuated on one side (fig. 23). In one specimen there was found a posterior vagal rootlet emerging with the first spinal nerve. A comparison of the IX-X roots in *Amphiuma* with those in *Necturus* and *Amblystoma* is shown in the following table:

AMPHIUMA.	NECTURUS. (KINGSBURY)	AMBLYSTOMA (COGHILL).
IX (1 + 2)	IX ^{3 + 4}	IX
X (1a + 1b)	IX ^{1 + 2}	X.1
X (2a + 2b + 2c)	X ^{1 + 2 + 3 + 4} (approximately)	X.2 + 3
X (3), X (4), X (5)	X ^{5 + 6 + 7}	X.4

The IX-X ganglion is elongate in shape, somewhat oval posteriorly, and anteriorly flattened wedge-shaped where it passes under the ear capsule. The nerves leaving the ganglion are eight in number.

b. The ramus communicans cum faciali.—Of these the ramus communicans cum faciali, or anastomosis X ad VII, will be considered first. It would appear from the different accounts given that this trunk in origin and composition is subject to considerable variation in the amphibians. It is usually described as leaving the ganglion in a common trunk with the glossopharyngeus proper. KINGSLEY and DRUNER both so describe it in *Amphiuma*, but I

have yet to find an instance in *Amphiuma* where the two do not emerge from the ganglion separate from each other. In *Amblystoma* (COGHILL) the r. communicans is composed of general cutaneous and communis fibers; in *Spelerpes* (BOWERS) of general cutaneous fibers only, apparently. DRÜNER assumes that in the Urodela in general the anastomosis contains motor fibers. For example, in *Amblystoma* and *Triton* he describes (1901 and 1904) a motor component in the anastomosis X ad VII, but COGHILL (1906) can find no evidence of motor fibers in the anastomosis in these forms. In *Amphiuma* DRÜNER believes the anastomosis to consist solely of motor fibers, but I can find nothing to support such an opinion. Beyond question DRÜNER is correct in figuring the r. communicans as giving off fibers to branches of the jugularis VII, but it is not necessary to draw his conclusion that these are motor fibers. In *Amphiuma* the r. communicans consists chiefly, if not wholly, of general cutaneous fibers. In serial cross-sections these can be followed with precision from the second IX-X root into the ganglion, thence out into the anastomosis. I have not been able to demonstrate with certainty that no communis fibers pass from the first IX-X root into the r. communicans. Such fibers pass very close to the beginning of the latter, and possibly some enter. That none of the coarse deeply staining motor fibers of the first IX-X root enter the anastomosis seems certain. As the anastomosis approaches the VII nerve it is seen to divide into a dorsal and a ventral branch (figs. 9, 9a, 14-16, 18 and 21). These two branches unite with branches of the r. jugularis that innervate the sphincter colli and interhyoideus muscles. The variability in the mode of union is shown in figs. 14-18. In some cases (fig. 17) the r. communicans does not divide on approaching the r. jugularis. FISCHER noticed the double nature of the anterior end of the r. communicans and designated the dorsal portion as "Kopftheil des Sympathicus." DRÜNER also describes a dorsal smaller portion that passes ventrally into the r. jugularis. In *Amblystoma* (Siraon) he recognizes a sensory component in the r. communicans, and suggests the possibility of some of the fibers being sympathetic.

In *Amphiuma* motor branches from the facial nerve commonly run posteriorly into the anterior portion of the depressor mandibulæ muscle closely joined with the dorsal branch of the anastomosis. When these branches are finally distributed to the muscle there

is an appearance of fibers being given off from the r. communicans but careful search shows that all of the fibers so given off come from the VII nerve. I can find no indication of motor fibers associated with the posterior part of the anastomosis. DRÜNER figures the anastomosis as giving off fibers to the anterior portion of the depressor mandibulæ muscle the direction of the fibers being such that the only interpretation that can be given to the figure is that these fibers come from the IX-X complex. I have sought carefully in all my series of sections, the material being so sharply differentially stained that nerves such as figured by DRÜNER could not escape detection, and I find not a suggestion of the presence of such fibers. In one series of sections, sagittally cut, with most excellent differentiation of components, the motor fibers from the VII nerve that usually run posteriorly along the smaller dorsal portion of the r. communicans are everywhere distinct from it, and not a single twig is given off from the r. communicans until the r. jugularis is reached (figs. 15 and 21).

In a preliminary communication (1908) I stated that the r. communicans contains communis fibers. While I am not yet ready completely to retract that statement, I now regard the presence in the r. communicans of such fibers as highly improbable.

We may summarize the foregoing statements regarding the ramus communicans in *Amphiuma* as follows: (1) DRÜNER's contention that the r. communicans is exclusively motor will not stand. A large general cutaneous component enters the ramus from the second IX-X root. The general cutaneous fibers in the VII nerve can come from no other source. (2) That the r. communicans contributes fibers to the r. jugularis does not indicate that these fibers are motor. The branches that receive fibers from the r. communicans are those that contain general cutaneous fibers; they must receive them from that source. (3) DRÜNER's statement and figure showing branches given off from the r. communicans to the anterior division of the depressor mandibulæ muscle are incorrect. It has been seen in some instances that this cannot possibly be true; in other cases the fibers so given off do not originate from the IX-X ganglion, but come from the r. hyomandibularis, that is, are not to be considered a part of the r. communicans. (4) That motor fibers enter the r. communicans from the IX-X ganglion has not been demonstrated, and is highly improbable. (5) The r. communicans is composed of

general cutaneous fibers from the second IX-X root; it may possibly contain other sensory fibers, communis or sympathetic.

c. The rami supratemporalis and auricularis X.—Passing out from the ganglion with the r. communicans is a small nerve that evidently answers to the r. supratemporalis as described by various writers. Its course out through the cranial wall is correctly described by KINGSLEY. It is exclusively lateralis, and, as KINGSLEY suggests, supplies neuromasts in the occipital region. Anastomosing with the terminal divisions of the r. supratemporalis are branches of a second nerve springing dorsally from the IX-X ganglion. It is composed of lateralis and general cutaneous fibers. The general cutaneous component evidently corresponds to the r. auricularis vagi of the tadpole (STRONG 1895), and to the general cutaneous component of the nerve in *Amblystoma* termed r. auricularis vagi by COGHILL.

d. The glossopharyngeal nerve.—General cutaneous, communis and motor fibers are contained in the glossopharyngeus, or first branchial nerve, which divides just before or soon after it leaves the ganglion into a r. pretrematicus and a r. posttrematicus. According to DRUNER the r. pretrematicus is larger than the r. posttrematicus and the r. communicans larger than either. Cross sections of the three as they leave the ganglion show that the r. posttrematicus is the largest of the three, and the r. communicans the smallest. The manner of branching of the r. pretrematicus is so variable that it is difficult to make statements regarding it at all accurate. Shortly after leaving the ganglion the r. pretrematicus gives off its principal branches. One small branch goes ventrally to supply the dorsal wall of the pharynx ventral and posterior to the ear capsule. Another branch which may be called the pharyngeal proper (*ph. IX.*) is given off dorsally. From it there passes a slender nerve anastomosing with the r. palatinus VII, forming JACOBSON'S commissure. The fibers of this anastomosis on entering the r. palatinus are seen to pass some centrally and some peripherally. From the anterior portion of JACOBSON'S commissure near where the latter joins the r. palatinus there is given off a branch to the roof of the mouth. The pharyngeal branch sends an anastomosis to the r. alveolaris VII. The main portion or ramus pretrematicus proper, passes antero-ventrally and mesally until the hyoid arch is reached. Thence, after dividing sooner or later into two branches, it passes anteriorly a little dorsal

to the hyoid arch as far as the tip of the latter, supplying the floor of the mouth at the sides. From the pretrematic proper there passes an anastomosis with the r. alveolaris VII. The fibers of the anastomosis on entering the alveolaris pass some centrally and some peripherally. Between the pretrematic proper and the pharyngeal branch there may occur anastomoses (fig. 21). Sometimes the pharyngeal anastomosis with the r. alveolaris comes from the main pretrematicus (fig. 1). From the pharyngeal branch there may pass a branch into the main hyomandibular trunk (fig. 21). Thus there may be formed in the hyoid and mandibular region a plexus between the IX and VII nerves, consisting of communis and possibly sympathetic fibers, all the fibers of which are destined presumably to supply blood vessels and the mucous membrane of the mouth and pharynx. Some of the smaller twigs of this plexus can be traced into the close vicinity of blood vessels of this region. Of isolated ganglia or ganglion cells in this region I find none.

It is the pretrematic division of the IX nerve that KINGSLEY considered the glossopharyngeus proper. He was thereby led into the error of supposing that the IX nerve contains no motor fibers. He failed to discover the actual anastomoses with the seventh nerve. The branch that anastomoses with the palatine he correctly termed the pharyngeal. The main pretrematic branch he designated provisionally the hyoid branch. According to him the r. supratemporalis X is a branch of the glossopharyngeus. I find the former more intimately associated with the r. communicans at its exit from the ganglion.

As the posttrematic division of the glossopharyngeus ascends to the level of the dorsal border of the branchial arches it gives off from its ventral border several small pharyngeal twigs, as described by DRUNER. As the trunk turns to pass laterally between the dorsal ends of the hyoid and first branchial arches it gives off a small motor branch (*lab. 1*) to m. levator arcus branchialis 1. A little more laterally a small general cutaneous branch runs obliquely postero-laterally over the first branchial arch to the skin of that region. This general cutaneous component of the glossopharyngeus is so small that I have as yet detected it in but one individual. Mention of it was omitted in my preliminary paper. DRUNER says that the first branchial nerve sends two branches to the m. lev. arc. br. 1. As he does not mention this general

cutaneous branch he possibly mistook it for a motor branch. KINGSLEY describes and figures a branch of the first branchial nerve as innervating the posterior portion of the depressor mandibulæ muscle. Such a relation would certainly be anomalous. I do not find such a nerve, but in one specimen I find that the ramus posttrematicus just as it begins to descend along the outer anterior border of the first branchial arch divides into a posterior portion that runs nearly in the usual course, and an anterior portion that becomes almost lost among the fibers of the depressor mandibulæ muscle, rejoining the other division more ventrally. This anterior portion, or possibly a still more aberrant but corresponding branch, may be the one mistaken by KINGSLEY for a division to the muscle. Ventrally the posttrematicus divides into motor branches to the ceratohyoideus internus muscle and communis branches to the lateral pharyngeal wall between the hyoid and first branchial arches, the extreme anterior portion being the ramus lingualis of communis fibers to the tongue.

e. The second and third branchial nerves.—The second and third branchial nerves (*X.1.* and *X.2.*) sometimes leave the ganglion as a common trunk that soon divides; sometimes they originate separately, but close together. They have the same general arrangement of parts. They send branches to mm. levatores arcuum branchialium 2 et 3 respectively. Each divides into a ramus posttrematicus and a ramus pharyngeus. From the latter ramus in each there runs anteriorly a small branch just dorsal to the extreme dorso-lateral angle of the pharynx as far as the preceding branchial arch and thence along the inner border of the latter, supplying the ventro-lateral wall of the pharynx. This answers to a pretrematic ramus in its distribution. DRUNER's failure to find a distinct pretrematic branch on either of these two nerves is probably due to the fact that in adults, such as he examined, it has become much attenuated. The main portion of the r. pharyngeus is distributed to the dorsal wall of the pharynx. The r. posttrematicus after giving off a branch or branches to its corresponding m. levator arcus branchialis turns ventrally and sending off one or two small general cutaneous branches to the skin, passes antero-ventrally along the outer border of its respective branchial arch.

The second branchial posttrematic sends branches to mm. subarcuales recti 1, 2 et 3 (m. constrictor arcuum branchiarum

inferior), and to m. subarcualis obliquus (m. constrictor arcuum branchiarum superior), and continues anteriorly to innervate the m. ceratohyoideus internus. It also sends communis branches to the ventral wall of the pharynx. The third branchial posttrematic according to DRÜNER has no motor fibers in its ventral portion, although in describing the mm. subarcuales he says they receive branches from the second and third branchial nerves. I find that the greater part of the ventral portion of the third branchial posttrematic is of communis fibers distributed, as DRÜNER says, to the ventral pharynx wall at the sides of the larynx; but I also find a small motor branch given off to m. subarcualis rectus 3, and in one instance I have traced fibers to the m. subarcualis obliquus. Between the posttrematic divisions of the second and third branchial nerves and the ramus intestinalis recurrens X there occur anastomoses such that it is difficult to distinguish the source of some of the fibers innervating the subarcual muscles.

f. The rami laterales X.—From the posterior end of the IX-X ganglion there pass out two large nerve trunks. The dorsal of these is composed solely of lateralis fibers, and soon divides forming a smaller dorsal r. lateralis dorsalis supplying the neuromasts of the dorsal series of the trunk of the body, and a larger ventral r. lateralis medius supplying the median series of neuromasts of the trunk. The remaining lateralis component of the vagal group will be described in the following section.

g. The ramus intestino-accessorius X.—The second great trunk passing posteriorly from the IX-X ganglion is the r. intestino-accessorius, composed of lateralis, communis and motor fibers. The communis and motor fibers have a very diverse distribution. A short distance posterior to the ganglion there leaves the main trunk a small nerve of communis and motor fibers, that in part represents fourth and fifth branchial nerves. It sends motor fibers to mm. levator arcus branchialis 4, trapezius and dorso-laryngeus. The branches to the trapezius and dorso-laryngeus muscles may arise separately from the main int.-acc. trunk. After giving off fibers to the m. lev. arc. br. 4, the nerve, now of communis fibers only, passes near the dorsal ends of the third and fourth branchial arches and there divides, one branch running along the anterior median border of the third branchial arch, and evidently forming a fourth ramus pretrematicus (*prt. X. 3*),

and a second branch running similarly along the fourth branchial arch and constituting a fifth ramus pretrematicus (*prt. X. 4*). The main intestino-accessorius trunk finally divides (figs. 1 and 12) into a r. lateralis ventralis supplying the ventral series of neuro-masts of the trunk; three rr. intestinales that pass posteriorly, one dorsal to the œsophagus and the other two latero-ventral to the same; and a r. intestinalis recurrens that turns anteriorly to supply m. interbranchialis 4 (m. hyotrachealis) and mm. subarcuales. From one of the intestinal branches there turns anteriorly a r. laryngeus recurrens that innervates muscles of the larynx, mm. dorso-laryngeus, constrictor laryngei, etc., and also supplies communis fibers to the pharyngeal wall in the same region. Communis fibers are also given off to the pharyngeal wall from the r. intestinalis recurrens in the laryngeal region. The rr. intestinales were traced posteriorly as far as the heart only and nothing can be stated precisely of their destination.

8. THE FIRST AND SECOND SPINAL NERVES.

The first spinal nerve in its early stages, as described by KINGSLEY, arises by four roots, two dorsal and two ventral, and is thus in origin clearly double (fig. 19). The common trunk formed by these roots passes out through a foramen in the first vertebra. In individuals of 120 mm. length I have found the first spinal nerve to possess two very rudimentary dorsal roots, two large ventral roots, and a small ganglion (fig. 19). In individuals of 140 mm. length the dorsal roots have disappeared, but the ganglion remains. In individuals of 175 mm. length the ganglion has disappeared. In older individuals the nerve appears to arise by four ventral roots in two groups. According to DRÜNER the hypobranchialis (hypoglossus) nerve is derived from the first and second spinal nerves. Careful search through my preparations fails to show any anastomosing between these two nerves. I have found no instance where they come into contact even. The nearest approach to contact is between a general cutaneous division of the second spinal nerve and the main hypoglossal trunk of the first spinal nerve. The hypoglossus nerve is formed solely from the first spinal nerve, and contains only motor fibers. The main ventral portion of the first spinal nerve soon after it emerges from the spinal canal passes posteriorly and after giving off a few small

branches runs back to the region where the r. int.-acc. divides into its several branches (figs. 1 and 12). Here the hypoglossus comes into intimate relations with the r. lateralis ventralis and the r. intestinalis recurrens X, but there is no fusing between them such as KINGSLEY describes and figures. In some cases there may be a temporary mingling of fibers, but in other instances the distinction between hypoglossal and other nerves is absolutely clear throughout, so that we may confidently deny the occurrence of any anastomosing between the hypoglossal and vagal nerves. From the point of the branching of the r. int. acc. trunk the hypoglossal nerve runs antero-ventrally, giving off no branches until it reaches the anterior section of the sternohyoid muscle. This it innervates and then runs along in the geniohyoid muscle supplying it, to end anteriorly in the genioglossal muscle. The main ventral branch of the second spinal nerve passes posteriorly in a direction nearly parallel with that of the hypoglossal trunk. A short distance posterior to the place of branching of the r. int.-acc. it turns sharply about and running antero-ventrally comes into close relations with the r. intestinalis recurrens X. It receives a general cutaneous branch from the third spinal nerve and then divides into a general cutaneous and a motor division. The general cutaneous branch supplies the latero-ventral skin in the anterior post-branchial region; the motor branch divides into a nerve that runs anteriorly to innervate the anterior segment of the sternohyoid muscle, and a second branch that runs ventrally to supply other sections of the same muscle, after anastomosing with a motor branch of the third spinal nerve. The brachial plexus is formed from branches of the third and fourth spinal nerves. The ramus lateralis ventralis X becomes very intimately associated with portions of the brachial plexus, but it is very clearly seen that no anastomosing occurs, such as BOWERS describes (doubtless incorrectly) in *Spelerpes*.

9. CONCLUDING STATEMENTS.

It is evident that the arrangement of the cranial nerves of *Amphiuma* gives support to the view that this species represents in many respects a primitive amphibian type. The group of nerves here designated as ramus oticus; the nasalis internus V; the clear differentiation of pretrematic, posttrematic and pharyn-

geal rami in the branchial nerves; possibly also the ramus lateralis VII; the lateral line lobe; all these have distinctly fish-like characteristics. Although the nerves connected with the eyes are degenerate, this cannot be said of the other cranial nerves. As compared with other Urodela, *Amphiuma* shows in the arrangement of its cranial nerves a tendency towards great diffuseness and individual variability. A nerve trunk in one individual may break up into a number of divisions later to become consolidated into a main trunk again. In another specimen the same nerve may show no such tendency to diffuse subdivision. General conclusions based upon one or two specimens, in *Amphiuma* at least, are likely to be much in error.

The resemblances between the cranial nerves of *Amphiuma* and those of *Amblystoma* are very striking. When the components of the cranial nerves of *Cryptobranchus*, *Necturus*, *Siren*, and one or two more of the *Salamandridæ* have been carefully worked out, we shall be in a position to define the urodele type of cranial nerves, and in the opinion of the writer, not until then.

The distribution of the lateral line organs of *Amphiuma* has been carefully mapped out and described by KINGSBURY (1895b). The innervation of these organs on the head has been worked out by the writer with precision, corroborating the description of KINGSBURY, except in some details. A detailed account of the innervation of these organs in *Amphiuma* is withheld from this paper because of the uncertainty as to the exact distribution of the ramus lateralis VII on the trunk of the body.

Iowa College,
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EXPLANATION OF THE PLATES.

REFERENCE LETTERS.

- acc.* branch of the X nerve supplying the anterior part of the trapezius muscle.
ags. angulo-splénial bone.
alv. r. alveolaris VII.
alv.(1). first anastomosing branch between r. alveolaris VII and r. pretrematicus IX.
alv.(2). second anastomosing branch between r. alveolaris VII and r. pretrematicus IX.
alv.(3). branch of r. alveolaris VII that supplies roof of mouth.
alv.(4). branch of r. alveolaris VII that anastomoses with r. mandibularis V.
am. muscles of the arm.
ao. antorbital cartilage.
auc. cartilage of the ear capsule.
auo. ossifications of the ear capsule.
aur. r. auricularis X.
bhy. basihyal cartilage.
bplx. branches of the brachial plexus.
ibr.,zbr.,3br. first, second and third branchial arches.
buc. r. buccalis VII.
buc.(1),buc.(2). branches of the r. buccalis VII that anastomose with the r. oph. prof. V.
ch. cerebral hemisphere.
chi. m. ceratohyoideus internus and branches of IX nerve innervating it.
chi.X.1. branch of the second branchial nerve innervating m. ceratohyoideus internus.
chy. ceratohyal.
cor. coracoid cartilage.
dent. dentary bone.
dien. diencephalon.
dl. m. dorsolaryngeus.
dlm. branches of the X nerve innervating the dorsolaryngeus muscle.
dm. m. depressor mandibulæ.
dma. anterior division of m. depressor mandibulæ and the nerve innervating it.
dmp. posterior division of m. depressor mandibulæ and nerve innervating it.
fc. fasciculus communis.
flm. fasciculus longitudinalis medius.
fr. frontal bone.
gac. ganglion acusticum.
gen. ganglion geniculatum.
gg. ganglion Gasseri.
gh. m. geniohyoideus.
g.I.sp. first spinal ganglion.
g.VIIba. ganglion on "dorsal VII."
g.VIIbb. lateral line ganglion fused with ganglion acusticum.
g.VII-VIII. acustico-facial ganglion.
g.IX-X. ganglion common to IX and X nerves.
h. humerus.
hgl. n. hypoglossus.
hhy. hypohyal cartilage.
hm. tr. hyomandibularis VII.
hy. hyoid arch.
ib.4. m. interbranchialis 4 = m. hyotrachealis.
ih. m. interhyoideus and branches of r. jugularis VII innervating it = m. mylohyoideus posterior.
im. m. intermandibularis = m. mylohyoideus anterior.
int. rr. intestinales X.
int.-acc. r. intestino-accessorius X.
int.rec. r. intestinalis recurrens X.
io. m. obliquus inferior.
jc. JACOBSON'S commissure.
jc.(a). branch of JACOBSON'S commissure innervating the roof of the mouth.

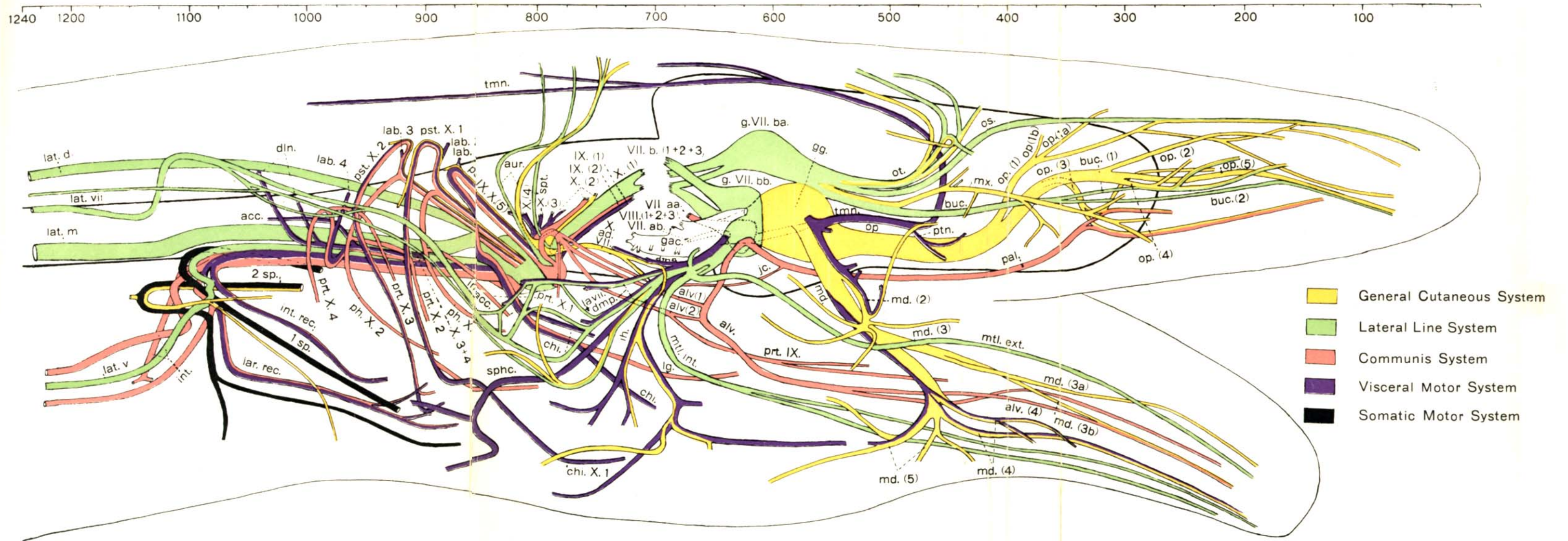
- jgl.* r. jugularis VII.
jo. JACOBSON'S organ.
lab.1,2,3, and 4. mm. levatores arcuum branchialium and the nerves innervating them.
lag. lagena and branch of the VIII nerve innervating it.
lar. rec. r. laryngeus recurrens X.
lat.d. r. lateralis dorsalis X.
lat.m. r. lateralis medius X.
lat.v. r. lateralis ventralis X.
lat.VII. r. lateralis VII.
lg. communis branch of r. posttrematicus IX to the tongue.
ll. lobus lineæ lateralis.
lbb. m. levator bulbi.
mas. m. masseter.
max. r. maxillaris V.
mb. branch of r. mandibularis V innervating the retractor and levator bulbi muscles.
mck. MECKEL'S cartilage.
md. r. mandibularis V.
md.(2). branch of r. mand. V innervating skin of side of head.
md.(3). branch of r. mand. V running just above and in the mandible.
md.(3a). branch of preceding innervating skin near tip of lower jaw at the side.
md.(3b). mandibular branch anastomosing with r. alveolaris VII.
md.(4),md.(5). branches of r. mand. V innervating m. intermandibularis and overlying skin.
mes. mesencephalon.
mplx. metaplexus.
mtl.ext. r. mentalis externus VII.
mtl.int. r. mentalis internus VII.
mx. maxilla.
na. neuromasts of the angular series.
nas. nasal bone.
nas.int. rm. nasalis internus, first terminal division of r. profundus V.
nc. nasal cartilage.
ngm. median nasal gland = JACOBSON'S gland (?).
nio. neuromasts of the infra-orbital series.
nio.(a). neuromasts of the infra-orbital series innervated by the r. oticus.
nso. neuromasts of the supra-orbital series.
nso.(a). neuromasts of the supra-orbital series innervated by the r. oticus.
op. r. ophthalmicus profundus V.
op.(1). first terminal division of the r. oph. prof. V. = rm. nasalis internus.
op.(1a). branch of the preceding that passes into a canal in the edge of the frontal bone = ethmoideus caudalis of KINGSLEY.
op.(1b). branch of op. (1) innervating the skin of dorsum posterior and dorsal to eyeball.
op.(2). second terminal division of r. oph. prof. V = r. glandularis II of WILDER.
op.(3). third terminal division of r. oph. prof. V, anastomosing with r. palatinus VII.
op.(4) and (5). Fourth and fifth terminal divisions of r. oph. prof. V, anastomosing with the two main divisions of r. buccalis VII.
op-pal. anastomosis of the third terminal division of r. oph. prof. V with r. palatinus VII.
op-pal.d. branch or branches from the oph-pal. anastomosis passing antero-dorsally innervating the dorsal lateral nasal epithelium and JACOBSON'S organ.
op-pal.l. branches from the oph-pal. anastomosis supplying the lateral (maxillary), series of teeth and roof of mouth.
op-pal.m. branch from the oph-pal. anastomosis supplying the median (vomero-palatine) series of teeth and the roof of the mouth.
op-pal.mn. branch from the oph-pal. anastomosis supplying the median nasal epithelium.
op-pal.ph. small branches from the oph-pal. anastomosis passing chiefly to the roof of the mouth at the posterior border of the nasal capsule.
op-pal.pn. branch from oph-pal. anastomosis supplying the posterior nasal epithelium.
os. r. ophthalmicus superficialis VII.
osph. orbitosphenoid bone and cartilage.
ot. r. oticus.
pa. parietal bone.

- pal.* r. palatinus VII.
pf. prefrontal bone.
ph.IX. r. pharyngeus IX.
ph.X.1. r. pharyngeus of the second branchial nerve.
ph.X.2. r. pharyngeus of the third branchial nerve.
pmx. premaxilla.
pn. postnares (edge of wall).
pplx. prosoplexus.
pri.IX. r. pretrematicus IX.
pri.X.1. r. pretrematicus of the second branchial nerve.
pri.X.2. r. pretrematicus of the third branchial nerve.
pri.X.3. branch of the r. intestino-accessorius X, representing a pretrematic ramus of a fourth branchial nerve.
pri.X.4. a nerve associated with the preceding and representing a pretrematic ramus of a fifth branchial nerve.
psph. parasphenoid bone.
pst.IX. r. post-trematicus IX.
pst.X.1. r. post-trematicus of the second branchial nerve.
pst.X.2. r. post-trematicus of the third branchial nerve.
pt. m. pterygoideus.
ptc. pterygoid cartilage.
ptn. nerve innervating m. pterygoideus.
pto. pterygoid bone.
rext. m. rectus externus.
rinf. m. rectus inferior.
rint. m. rectus internus.
rs. m. rectus superior.
rtb. m. retractor bulbi.
sar.1,2,3. mm. subarcuales recti 1, 2 and 3, = constrictor arcuum branchiarum inferior.
sc. scapula.
so. m. obliquus superior.
se. saccus endolymphaticus.
Isp. first spinal nerve.
Isp.d. dorsal branch of first spinal nerve.
Isp.r.d. dorsal roots of first spinal nerve.
Isp.r.v. ventral roots of first spinal nerve.
Isp.v. ventral branch of first spinal nerve.
2sp. second spinal nerve.
3sp. third spinal nerve.
sp.V. tractus spinalis trigemini.
sp.VIII. tractus spinalis acusticus.
sphc. m. sphincter colli and the nerve innervating it.
spt. r. supratemporalis X.
sq. squamosal bone.
ssc. suprascapula.
sthy. m. sternohyoideus.
stp. stapes.
th. thymus gland.
thr. thyroid gland.
tm. m. temporalis.
tma. anterior division of m. temporalis.
tmn. branch of the r. mandibularis V innervating m. temporalis.
tmp. posterior division of m. temporalis.
tmpt. tendon of the posterior division of m. temporalis.
tr. trachea.
tra. "tractus a" of KINGSBURY.
trap. m. trapezius, posterior division.
trapa. m. trapezius, anterior division.
trb. "tractus b" of KINGSBURY.
trc. tracheal cartilages.

- trm.* muscles of the trunk.
vp. vomero-palatine bone.
I. n. olfactorius.
Ijo. branch of n. olfactorius innervating JACOBSON'S organ.
Irrt. roots of n. olfactorius.
II. n. opticus.
III. n. oculomotorius.
IV. n. trochlearis.
V(2). motor root of the V nerve.
VI. n. abducens.
VIIa. the ventral roots of the facial nerve, communis and motor components.
VIIaa. the communis portion of the preceding.
VIIab. the motor root of the facial nerve.
VIIa+VIIbb. the ventral or main trunk of the facial nerve.
VIIb. the lateral line portion of the facial nerve.
VIIb(1+2+3). the three rootlets of the preceding.
VIIba. the "dorsal VII."
VIIbb. that portion of the lateral line component of the facial nerve that passes ventrally and joins VIIa.
VIIba+V. the trunk formed by the union of general cutaneous fibers from the gasserian ganglion with the "dorsal VII."
VIII. n. acusticus.
VIIIap. branch of VIII nerve to the posterior ampulla.
VIIIag. branch of VIII nerve to the lagena.
VIIImn. branch of the VIII nerve to the macula neglecta.
VIIIpb. branch of the VIII nerve to the pars basilaris.
VIIIs. branches of the VIII nerve to the sacculus.
VIIIv. vestibular branch of the VIII nerve.
VIII(1). fibers of the VIII nerve that pass into the tractus spinalis VIII.
VIII(2). fibers of the VIII nerve that pass anteriorly into the acusticum.
VIII(3). fibers of the VIII nerve that enter "tract b."
VIII(4). coarse fibers that enter the sp. VIII tract distinct from VIII (1).
IX(1). communis root of the IX nerve.
IX(2). motor root of the IX nerve.
X.1. second branchial nerve.
X.2. third branchial nerve.
X.3+4. branch of r. int.-acc. representing the fourth and fifth branchial nerves.
X(1). first or lateral line root of the X nerve.
X(2). second root (group of rootlets) of the X nerve.
X(3),X(4),X(5). third, fourth and fifth roots of the X nerve.
X.adVII. r. communicans between the X and VII nerves.
X.adVII.d. dorsal division of r. communicans.
X.adVII.v. ventral division of r. communicans.

EXPLANATION OF PLATE IV.

FIG. 1. A projection upon the sagittal plane of the V, VII, VIII, IX and X cranial nerves, together with portions of the first and second spinal nerves, of *Amphiuma means*. The roots and ganglia are slightly schematic for the sake of clearness. In only a few cases have the positions of nerve trunks been slightly changed. The scale above the figure indicates the serial numbers of the transverse sections employed in the reconstruction, the sections being 10 micra thick X 32.



EXPLANATION OF PLATE V.

FIGS. 2 TO 10. Cross-sections of the left half of the head at different levels. The outlines were drawn with a camera lucida; the details are schematic. These were made from a different series of sections than that from which fig. 1 was plotted. After the description of each figure is given the number of the section in fig. 1 which corresponds approximately to the section described.

FIG. 2. Cross-section through the nasal capsule at the level where the branch of the olfactory nerve that innervates JACOBSON'S organ is passing around to the dorsal side of the latter structure. Section 200. \times 30.

FIG. 3. Cross-section through the nasal capsule at the point where the olfactory nerve trunk breaks up into its terminal divisions and enters the capsule. Section 260. \times 30.

FIG. 4. Cross-section cutting through the posterior portion of the eyeball. To show the retractor and levator bulbi muscles and their insertion on the antorbital cartilage. Section 350. \times 20.

FIG. 5. Cross-section at the level where the r. mandibularis V enters the lower jaw. Section 460. \times 20.

FIG. 6. Cross-section through the origin of the r. mandibularis V. The abducens nerve is seen separating from the gasserian ganglion. Section 560. \times 30.

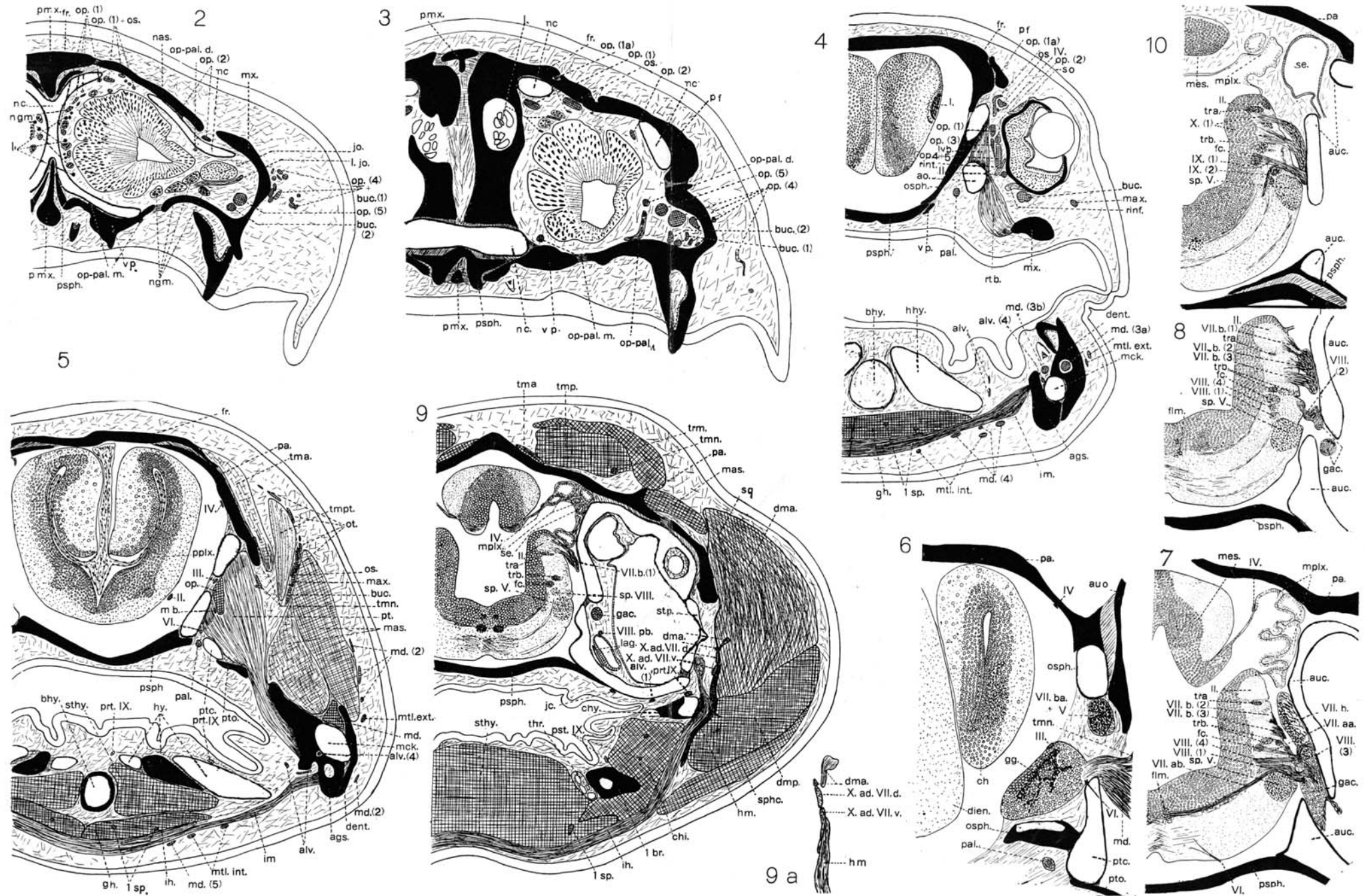
FIG. 7. Composite cross-section through the roots of the VII and VIII nerves. Sections 675-680. \times 30.

FIG. 8. Cross-section through the roots of the lateral line component of the VII nerve. Section 685. \times 30.

FIG. 9. Cross-section slightly posterior to that of fig. 8. \times 20.

FIG. 9a. An enlargement of a part of the preceding, showing the r_1 communicans.

FIG. 10. Cross-section at the level where the roots of the lateral line components of the X nerve enter the brain. Section 710. \times 30.



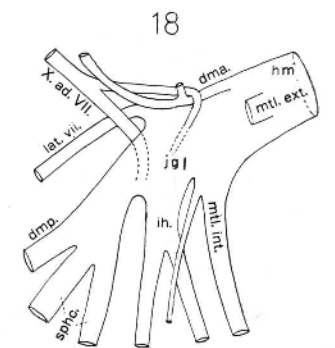
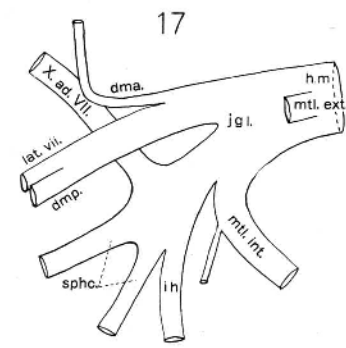
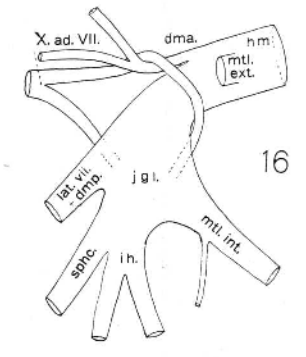
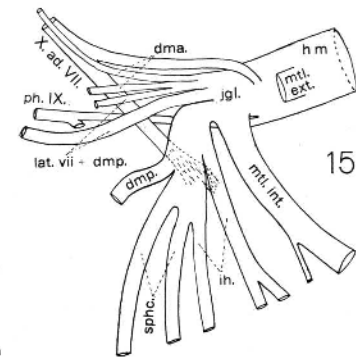
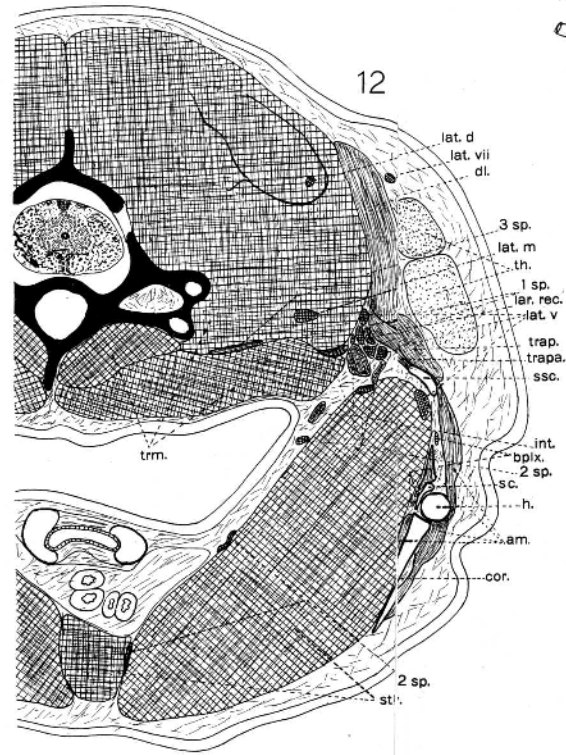
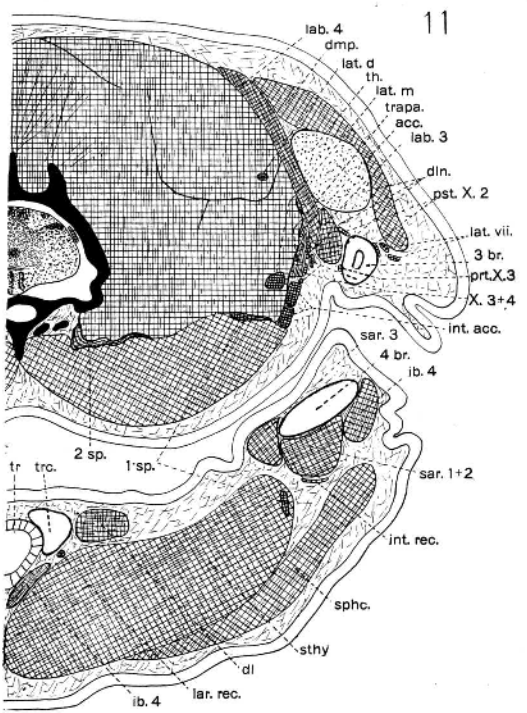
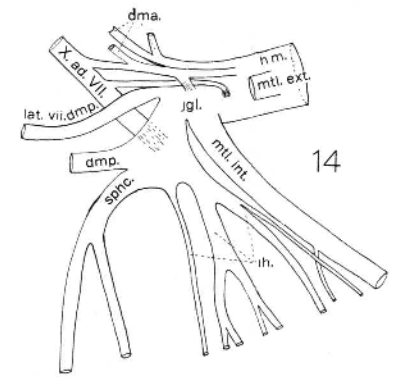
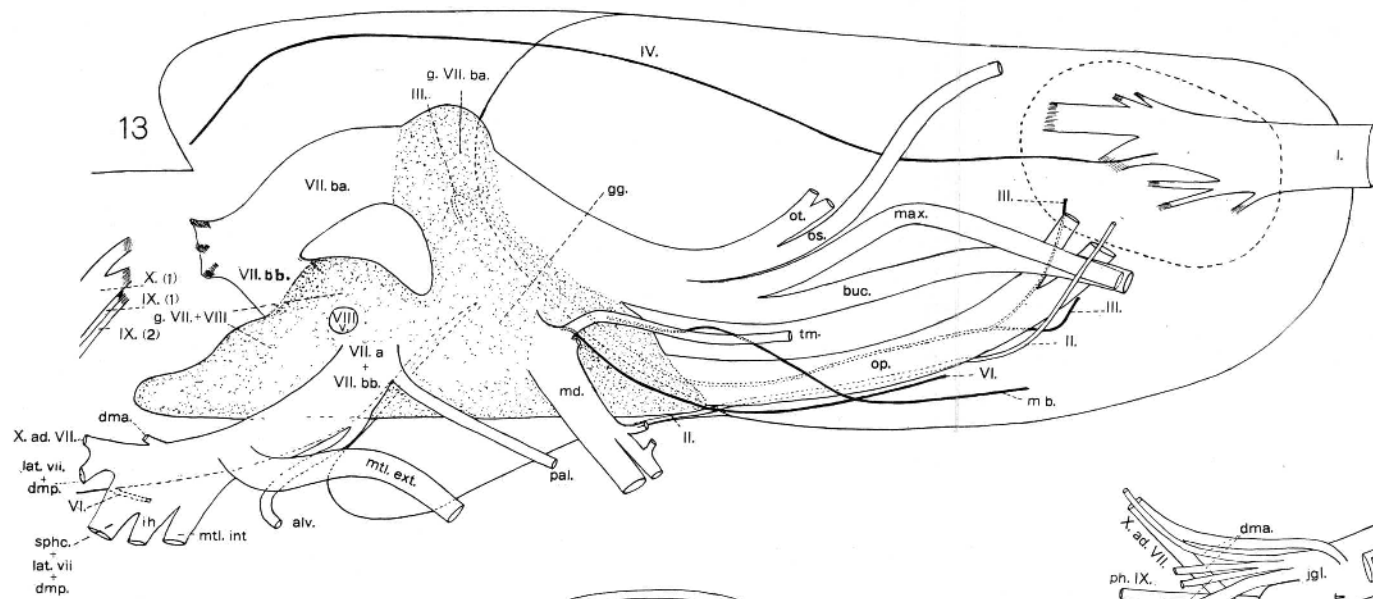
EXPLANATION OF PLATE VI.

FIG. 11. Cross-section through the gill-cleft. Section 960. $\times 19$.

FIG. 12. Cross-section at the level where the r. intestino-accessorius breaks up into its branches. Section 1090. $\times 19$.

FIG. 13. A projection upon the sagittal plane to show chiefly the olfactory, optic and eye-muscle nerves. The outlines of the acustico-facial, gasserian and dorsal lateral line ganglia are drawn in their correct relations.

FIGS. 14 to 18. Projections upon the sagittal plane of the r. hyomandibularis VII in the region where it divides into its chief branches. These are from four different individuals. Figs. 14 and 15 are from the same individual. All are represented as seen from the right side. These sections are to show primarily the variable mode of fusion between the anastomosis X ad VII and the r. jugularis VII.



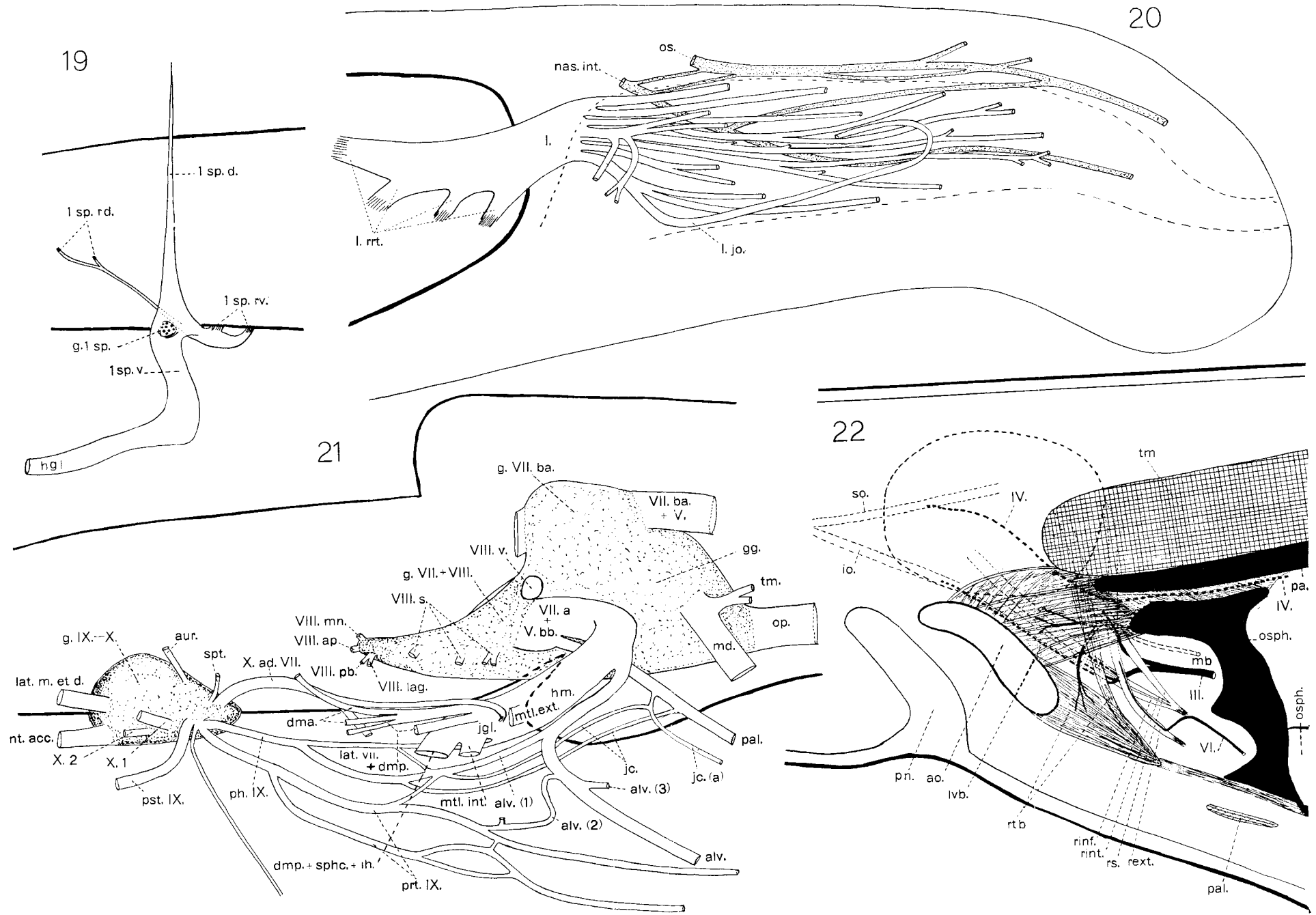
EXPLANATION OF PLATE VII.

FIG. 19. A projection upon the sagittal plane of the origin of the first spinal nerve, in an individual of 120 mm. length, seen from the right side.

FIG. 20. A projection upon the sagittal plane of the olfactory nerve, its roots and principal branches.

FIG. 21. A projection upon the sagittal plane of the IX-X, and V-VII-VIII ganglionic complexes, and the plexus developed between the IX-X, and VII nerves. The roots of the ganglia are omitted. In the individual from which the plotting was made JACOBSON'S commissure is double; from the r. pharyngeus IX there passes an anastomosis to the tr. hyomandibularis VII. The V-VII-VIII ganglionic mass is much more compact than in younger individuals, such as shown in figs. 1, 13 and 24.

FIG. 22. Composite sagittal section through the insertion of the retractor and levator bulbi muscles upon the antorbital cartilage, as seen from the left side. The eyeball and the greater portion of the eye-muscles are situated lateral to the section and are represented in dotted outlines. For the sake of clearness the branches of the r. ophthalmicus profundus V and of r. ophthalmicus superficialis VII are omitted. The outlines of the section were drawn with a camera lucida.



EXPLANATION OF PLATE VIII.

FIG. 23. A projection upon the horizontal plane of the roots, ganglia and principal trunks of the V, VII, VIII, IX and X nerves.

FIG. 23a. The roots of the VIII nerve.

FIG. 24. A projection upon the sagittal plane of the ramus oticus and its branches, together with the neuromasts which it innervates.

FIG. 25. A projection upon the sagittal plane of the anastomoses between the r. oph. prof. V and the r. buc. VII. The condition here is more complicated than in fig. 1.

FIG. 26. A projection upon the sagittal plane of the anastomosis between the r. oph. prof. V and the r. pal. VII. The exact composition of a few of the smaller branches is uncertain; hence they are only partly colored.

