THE CRANIAL NERVE COMPONENTS OF THE TOADFISH

(OPSANUS TAU)

by

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I. INTRODUCTION

Our knowledge of the structure and function of the nervous system, based upon experimental analysis, dates back to the work of Galen (130-200 A.D. ?). He recognized and described seven pairs of cranial nerves. Magnus ('03) in his "Die Anfänge der Anatomie" says, "Er kennt ferner 7 paar Gehirnnerven, unterscheidet weiche Gehirnnerven, harte Rückenmarksnerven und mittelharte des verlängerten Markes". Galen distinguished between sensory and motor nerves, and apparently recognized the existence of mixed nerves, although anatomically he was in error since he derived the sensory nerves from the brain and the motor nerves from the spinal cord.

From that time to Charles Bell (1810-1844) no further contributions were made to our conception of the functional significance of the peripheral nerves. Sir Charles Bell opened up a new epoch in the physiology of the nervous system when he showed that the dorsal roots are sensory in function and the ventral roots motor. He also recognized that sensory and motor fibers are distributed to the viscera as well as to the rest of the body. Then followed the classical work of Stannius (1849) "Das Peripherische Nervensystem des Fische," who studied the cranial nerves from a morphological and physiological viewpoint. The next important work was that of Gegenbaur (1871) who demonstrated the compound nature of the vagus in Notidanus griseus. Gaskell (1886) was the first to make a detailed study of the nerve fibers supply-

ing the visceral and vascular systems; he subdivided the somatic and visceral systems according to the physiological and histological characters and thus initiated the modern conception of the functional components of the nerves.

At the close of the century we have the extensive works of Strong (1895) on the Amphibia, Cole (1898) on Gadus, and Herrick (1899) on Menidia. These investigators made a much more complete analysis of the nerve structures by the use of serial sections, special stains and graphic plotting of the nerve components. Later investigators, Cole and Johnstone ('01), Coghill ('02 and '06), Norris ('13), Norris and Hughes ('20), and Norris ('25) extended our knowledge further by comprehensive studies on other lower vertebrates.

No complete analysis of the cranial nerves of any bird or mammal has been made in any single contribution. There is, however, an extensive literature on the structure of individual nerves in these groups, especially in numerous species of mammals. It will be impossible here to refer to all these papers; the following are among the more important. A contribution on the development of the cranial nerves in the chick was made by Marshall (1878). Barratt ('99 and '01) has studied the branchial and motor cranial nerves in human. Rhinehart ('18) investigated in detail the VII nerve in the mouse. Freeman ('27) gives the most recent comprehensive discussion of the literature on the afferent cranial system in man. Fenton and Larsell ('28) studied the sphenopalatine ganglion and its connections in human. The numerous investiga-

tions on the nervus terminalis and eye-muscle nerves are discussed later in this paper.

The present author has made a general analysis of the cranial nerves of the toadfish (Opsanus tau) upon the suggestion of Dr. H. C. Tracy. Aside from the work of Cole and Johnstone on Pleuronectes, no study of the cranial nerves has been made on any of the aberrant teleosts, and that group is, of course, of special interest in quite different directions from the Batrachidae or any related forms. It was also considered desirable to have a detailed knowledge of the structure of a teleost species which is so accessible and admirably adapted to physiological work as the toadfish, particularly a species which belongs to a segment of the order of fishes which is so incompletely known.

The author here wishes to express his deep appreciation for the continued kind suggestions and helpful criticisms given by Dr. H. C. Tracy, Dr. H. B. Latimer, and Dr. G. E. Coghill.

Further, the writer is greatly indebted to Margaret Schumann, departmental technician, and to the Wistar Institute of Anatomy and Biology for special aid given during the progress of this work.

II. MATERIAL AND METHODS

The material* used was toadfish larvae varying from 6 mm. (recently hatched) to 20 mm. (free-swimming), a number of young adults (5-10 cm. body length), and full grown adults. Fixation was in Bouin's fluid, formalin, corrosive sublimate-acetic for the 6-20 mm. stages, and Flemming's stronger solution for the young adults. The embryos were embedded in paraffin and sectioned transversely, horizontally and sagittally. This material was then stained by various methods. Best results were obtained with Haidenhain's iron alum haematoxylin counterstained with eosin, Delafield's haematoxylin and eosin, and toluidine blue and erythrosin. Cytological studies on the various nerves were made from these preparations.

The heads of the 5-10 cm. specimens were left in Flemming's stronger solution until decalcified, and then imbedded in celloidin according to the general method of procedure. Sections 50 micra thick were cut in transverse and horizontal planes. These sections were stained in Pal-Weigert's haematoxylin after mordanting with one-half saturate solution of copper acetate following Coghill's technique (Coghill '06) in his work on Triton. From these stained sections, projections were made and the nerves plotted according to the method used by Herrick, Coghill and Norris.

*These specimens were collected at the Marine Biological Laboratory, Woods Hole, Mass., by Dr. H. C. Tracy and the writer during a number of summers.

III. DESCRIPTION OF THE BRAIN AND CRANIAL NERVES

1. External Anatomy of the Brain.

In order to show the origin of the cranial nerves and the relations of their roots to the different parts of the brain, three views are given. The brain presents the usual teleostean form and characteristics. It is relatively small and fills only part of the large cranial cavity.

The olfactory lobes (Ol. L. fig. 3) are fairly distinct and give rise to the large, long, round olfactory nerves. A conspicuous feature is the deeply lobated fore-brain.

The optic lobes are large, correlated with the size of the eye-ball. The epiphysis is small and attached by a thin, very short stalk.

The cerebellum and valvula cerebelli are both relatively smaller than in typical teleosts. The slight development of these structures is apparently correlated with an under-developed lateral line system and with the sluggish habits and clumsy swimming movements of this species.

The tuberculum acusticum (Tub. Ac. 1, 2, and 3) and the vagal lobe produce a definite protuberance on each side of the rhomboid fossa on the dorsal surface of the medulla oblongata. On the ventral surface can be seen a very prominent saccus vasculosus and highly developed inferior lobes (Sac. Vas., L. Inf., figs. 2 and 3).

The thalamus and hypothalamus are well developed. A

somewhat bilobed hypophysis protrudes ventro-cephalad (Hy., figs. 2 and 3).

A conspicuous feature is the large optic chiasma in which the optic tracts cross at a very narrow acute angle. The optic tracts form very wide bands as they pass dorso-cephalad toward the optic lobes (fig. 2).

2. The Olfactory Nerve.

The long olfactory nerve originates from a large number of filaments under the nasal epithelium (figs. 7 and 8). These filaments almost immediately unite into bundles which soon converge to form a solid round nerve (fig. 6). It passes backward into a short bony canal in the ethmoid, then lies free in the orbit, passing between the two oblique muscles which usually cause a flattening of the nerve. It leaves the caudal part of the orbit to enter the cranium and ends in the ventro-lateral portion of the olfactory lobe (figs. 1, 2, and 3).

Kudo ('28) describes an apparently hitherto unobserved nucleus in the fore-brain of bony fishes. He makes no mention of a nervus terminalis but he describes cells migrating out from this nucleus toward the placode to a position associated with the blood vessels which would suggest the cells described by the various authors as ganglion cells of the nervus terminalis. In the toadfish, I have noted a similar group of cells, but I am led to believe with Stewart ('20) and Brookover and Jackson ('11) that the cells found along the olfactory nerve and under the nasal

epithelium are migrating in from the olfactory placode.

In larval toadfish, the author has observed small nerve cells under the nasal epithelium and along the olfactory nerve (fig. 16). These ganglion cells were observed from the time that the olfactory placode first became connected with the fore-brain (20 somite stages or earlier)* up to the free-swimming stage (20 mm.). At first these cells form a continuous mass at the base of the olfactory placode and extending along the olfactory nerve. These cells are apparently elements of the nervus terminalis as Sheldon ('09), Brookover and Jackson ('11), McKibben ('11) and others have figured and described them. Since the nervus terminalis has been described in related forms, one would expect to find it in the toadfish. But so far, all methods (Pal-Weigert, Cajal, and Haidenhain's iron haematoxylin) have failed to demonstrate it in the free-swimming or adult stages (fig. 6). Apparently the nervus terminalis is only a transitory nerve in the toadfish. Brookover ('10) says that the ganglion of the nervus terminalis in Amia originates in common with the olfactory nerve, from an ectodermal placode, and that in early stages the cells of the ganglion cannot be distinguished from the undifferentiated mass of cells which produce sheath cells of the fila olfactoria. In the case of the toadfish, these ganglion cells are not so numerous as in many forms previously described. During the process of development all of them form sheath cells. Different stages (6, 8, 11 and 13 mm.) of this process were observed. At first the

*These stages were obtained through the kindness of Mr. Lucas of the Anatomy Department.

cells look like ganglionic cells, but with the elongation of the olfactory nerve these cells later are "drawn in" among and between fiber bundles proceeding from the olfactory sac. In this process the ganglion cells become elongated and scattered along the long nerve, between the nerve fibers. Thus at the free-swimming stage (20 mm.) no ganglion cells remain.

In the stages in which the cells can be distinguished, they lie in intimate relation to blood spaces, ventro-medial to the olfactory nerve, a fact which other observers have noted in many instances and which has led them to infer that these cells might be sympathetic in function. The relations of the cells in Opsanus are not inconsistant with these views; but it is evident that whatever their primitive nature may have been, in this species they become transformed into sheath cells.

Cells of the same type in essentially the same relations to the olfactory placode and nerve were found in larvae of Lophius piscatorius* (1-2 mm.) and in the hatching, 2, and 4-day old stages of Cyclopterus lumpus*. The cells were apparently migrating as in Opsanus tau, but late stages of these species were not available for determining their fate.

3. The Optic Nerve.

The optic nerve is large, corresponding to the well-developed eyeball. Its chiasma is not constant, for in about 30 specimens examined, the left nerve is dorsal in about half, and in

*These specimens were available to the author by the courtesy of Mr. William Procter, from collections made by the Biological Survey of Mt. Desert Island.

the others the reverse is true. In this respect, the toadfish conforms to what appears to be the typical teleost type as described by Allis ('03) in Scomber, and by Parker ('03) who investigated the chiasmata in ten species. Parker says, "In each of ten species of symmetrical teleosts the optic chiasmata were dimorphic, in that in some instances the right optic nerve was dorsal, in others left."

One exceptional specimen was found in which the major part of the left optic nerve passed dorsally, but a small strand of its fibers passed ventrally to the right optic nerve (figs. 13 and 14). The decussation is complete and forms a very small acute angle (figs. 1 and 2); and from it each nerve passes to its foramen. Extra-cranially, it courses cephalo-lateral, dorsal to the superior rectus muscle; in the greater part of its extent it is dorso-lateral to the inferior rectus muscle.

4. The Oculomotor Nerve.

The oculomotor nerve emerges from the ventral surface of the brain stem, dorsal to the inferior lobes at the level of the geniculate ganglion (figs. 7 and 8). It passes laterally to a position ventral to the Vth-VIIth complex, coursing just inside the cranium for some distance. At this part of its course, it comes in very close relation with the palatinus VIIth, which runs just ventral to it (fig. 7); it is not probable that any exchange of nerve fibers takes place.

The oculomotor nerve consists of coarse and fine fibers,

like this nerve in Ganoids (Schneider '82) and in Menidia (Herrick '99). I have not been able to determine whether the fine fibers connect with the ganglion cells found along the oculomotor nerve. According to Freeman ('27), Weinberg ('28) and others, the proprioceptive fibers for the eye-muscle nerves may have their cell bodies in the mesencephalic root of the fifth.

While still in the cranium, a small twig to the superior rectus muscle is given off (figs. 7 and 8). After the exit of the main trunk from the cranium it enters the eye-muscle canal where it gives off a ramus to the medial rectus muscle which courses somewhat ventro-medially, piercing the superior rectus muscle. A little more distal, a second extracranial ramus (r.s.r.) soon ends in the superior rectus muscle at the proximal portion (figs. 7 and 8). The main trunk of the oculomotor nerve then passes between the superior and lateral recti muscles to dip ventrally and gives off the long ramus to the inferior oblique muscle (r.i.r. figs. 7 and 8). The remainder soon terminates in the inferior rectus muscle (r.i.r. figs. 7 and 8). On the other side of the specimen plotted, somewhat different conditions were found; the rami to the inferior rectus, medial rectus, and inferior oblique all originate at the same level.

The ciliary ganglion is connected with the ramus that divides to innervate the inferior rectus and inferior oblique muscles. It is a small (5 mm. long) oblong ganglion lying over the lateral rectus muscle (figs. 7 and 8). From it arises the short ciliary nerve passing over the lateral rectus to anastomose

with the ciliaris longus around the ophthalmic artery. The long ciliary root comes from the first sympathetic ganglion on the ventral surface of the gasserian ganglion (figs. 7 and 9). Kuntz ('14) has described these relations in the young toadfish.

5. The Oculomotor Nerve Cells.

In the free-swimming stage (20 mm.), the author has observed scattered groups of nerve cells along the oculomotor nerve (figs. 19 and 20). In one specimen such nerve cell groups were found on the extracranial ramus to the superior rectus, below and above the superior rectus muscle, and a large ganglion on the inferior ramus at the point where it divides into branches to the medial and inferior recti muscles. A definite mass of cells in another specimen of the same stage was observed between the third and fourth nerves; these intracranial cell groups were connected by a protoplasmic process to the third and fourth nerves on the right side (figs. 18, 20 and 21). On the other side of the same specimen the nerve cells were located on the nerve trunks (fig. 20).

Miss Tozer ('12) speaking of the third nerve in Gadus, says, "There the cells are mostly found not in the roots themselves but in the connective tissue between or near the roots, in other cases the majority of the cells are embedded in the roots. The position of these nerve cells outside the main bundles of the nerves is of interest since it does not quite correspond with the position of Thomsen's patches or Gaskill's degenerated ganglion. The cells in Gadus are possibly sufficiently numerous to represent

the source of the afferent fibers since the III contains roughly only about 800 fibers." In one case she observed 80 cells on the IIIrd root.

Miss Bowers ('00) describes a cluster of ganglionic cells associated with the oculomotor nerve in Spelerpes bilineates. She states that in the 23 mm. stage these ganglionic cells are grouped into a compact mass but in older stages (40 mm.) they are somewhat scattered along the nerve.

Such cell groups were found in each specimen examined at the free-swimming stage. In the adult a very definite mass of cells was observed which was identified as the ciliary ganglion (figs. 7 and 8), and a group of cells (9-10) was also found on the intracranial part of the oculomotor nerve root. Schneider ('82) says that the oculomotor nerve in the ganoids is composed of two elements, nerve fibers and ganglion cells. In Amia he found ganglion cells at two places. He did not determine the origin of these cells, but he thinks that they may be either sympathetic or derived from the fifth nerve. In Selachians, according to Schwalbe ('79), the third nerve has: (1) a ciliary nerve, a branch of the third; (2) an anastomosing branch from the fifth; (3) a number of nerve fibers coming from the ganglion cells on the third. The first are motor, the second sensory, and the third vasomotor to the eye. Norris and Hughes ('20) figure and describe scattered groups of nerve cells along the oculomotor nerve of Squalus acanthias. Coghill ('06) describes groups of nerve cells along the oculomotor of Triton in essentially the same relation

as the author has found in the toadfish, and he suggested that they may be muscle-sensory or sympathetic in nature. Clark ('26) says that the cells along the oculomotor nerve in the dog resembled the second and third types described for the ciliary ganglion more than the types related to muscle spindles. In Menidia, Herrick ('99) describes a definite ciliary ganglion, while Coghill ('02) says that the ciliary ganglion is transitory and probably at no time functional in Amblystoma.

The works of Sherrington and Tozer ('10), Tozer ('12), Sherrington ('18), Nicholson ('24), Clark ('26), and Freeman ('25 and '27) give strong evidence that there are proprioceptive elements in the oculomotor nerve. For a discussion on the origin, development and significance of the oculomotor nerve and cells related to it, the reader is referred to Neal's ('94) excellent article on the morphology of the eye-muscle nerves.

The oculomotor nerve is developed at about the 6 mm. stage (Kuntz '14) while the fourth and sixth develop somewhat later (7-8 mm.). This correlates with the observations made by Tracy ('26) who found the eye movements appearing in larvae somewhat earlier than 9.5 mm. long.

6. The Trochlear Nerve.

The trochlear nerve emerges from the dorsal surface of the brain, in the angle between the optic lobes and the cerebellum (figs. 1, 2 and 3). It passes latero-cephalad toward the Vth-VIIth ganglion complex and for some distance is in direct

relation to the gasserian ganglion on its median side. In some specimens it was even embedded in the capsule of the gasserian ganglion, but no exchange of fibers was ever observed.

It leaves the cranium through its own foramen and passes cephalad as a very slender nerve, ventral to the ophthalmic superficial nerves, and dorso-mesial to all the muscles and nerves of the eyeball as in Scomber scomber. It terminates in the superior oblique by two small twigs (figs. 7 and 8), one of them near the insertion of the muscle.

The trochlear nerve is first seen in 6 to 7 mm. larvae. In the free-swimming stage of the toadfish, a mass of nerve cells (10-15 in number) was observed intracranially on the trochlear nerve just cephalad to its relation with the gasserion ganglion (figs. 18 and 20). In some specimens these nerve cells apparently are related to the ones found on the oculomotor root as described above (page II)(fig. 18). In the adult no such cells have been observed on the trochlear nerve, but coarse and fine fibers are present as Herrick ('99) describes in Menidia. It may be that these nerve cells are sympathetic and transient in the fourth nerve as Neal ('14) suggests. What the fate of the nerve cells found on the developing trochlear nerve is, has not been determined. Neal ('14) has discussed this matter very thoroughly. The works of such investigators as Golgi ('93), Harrison ('09), Tozer ('12), Sherrington ('18), Freeman ('27) and others indicate that there is a sensory, possibly proprioceptive component in the fourth nerve. Although Schneider ('82) did not find ganglion cells on the fourth nerve, he surmised the same to be present.

7. The Abducens Nerve.

The sixth nerve arises by two fine roots, one 4 mm. caudal to the other (figs. 7 and 8) in the specimen plotted (adult). The two roots soon unite to form one trunk which passes ventro-laterally, having a long course along the cranial wall. During its passage it comes into very close relation with the ramus palatinus of the seventh nerve. It lies just ventral to this ramus for some distance, but no exchange of fibers could be found. Here the third, sixth, and palatine nerve course in a common canal (fig. 7), formed by a slight groove in the cranial wall covered over with connective tissue. Near the orbit the abducens issues from the cranium by turning laterally and separating itself from the other nerves in the canal. Then it terminates, usually by two rami, in the proximal third of the lateral rectus muscle (figs. 7 and 8).

As in Menidia (Herrick '99), the author observed fine and coarse fibers in the abducens, but nerve cells have not been observed either in the young or in the adult stages. These findings agree with those of Herrick ('99), Allis ('03), and Neal ('14), but are quite different from those found in Spelerpes bilineatus (Bowers ('00), in Amblystoma and Triton (Coghill '02 and '06), in Gadus (Tozer '12), and in man (Nicholson '24).

8. The Sensory Elements in the Eye-muscle Nerves.

Concerning the location of the proprioceptive nerve cells in the eye-muscle nerves, investigators may be divided into two groups. Such investigators as Golgi ('93), Johnstone ('09), Valkenburg ('11), Kosaka ('12), Winkler ('21), Freeman ('25 and '27), Clark ('26), and Weinberg ('28) point toward evidence that there are proprioceptive fibers in the eye-muscle nerves and their cell bodies lie in the mesencephalic root of the fifth nerve. In his summary, Weinberg ('28) says, "The relation of the mesencephalic root of the Vth to the masticatory muscles is established; its relation to the eye-muscles in very probable."

On the other hand, the works of Schneider ('82), Bowers ('00), Coghill ('06), Tozer ('12), Sherrington ('18), Nicholson ('24), and others suggest that the cells along the roots of the eye-muscle nerves are proprioceptive in nature. Some suggest that possibly they are sympathetic in character. From observations on different stages of the toadfish the author is inclined to interpret them as sympathetic cells. Careful study has shown these scattered cells to have the same size and structure as the cells of the ciliary ganglion.

9. The Fifth-Seventh Ganglion Complex.

The fifth-seventh ganglion complex in the toadfish is less intimately fused than in any of the fishes previously described. It lies intracranially, close upon the inner wall of the cranium. The gasserian ganglion is located in a bony pocket from

which its various rami leave the skull. The geniculate ganglion lies flat on the inner surface of the cranium just caudal to the gasserian ganglion. From the geniculate ganglion exit a large number of communis fibers, forming a heavy trunk which passes, in a bony canal, into the ventral portion of the gasserian ganglion. Bony processes and heavy connective tissue firmly anchor the fifth-seventh complex and its rami in the cranial wall.

10. The Trigeminal Nerve.

Although the relations of the Vth-VIIth complex are less intimate than in other fishes described, the discussion of the different rami and their components necessitates considerable overlapping and repetition of material.

The fifth root emerges from the mid-lateral surface of the medulla, ventral and just caudal to the lateral line root of the seventh (figs. 1, 2, 3, and 10). The motor portion could be seen coming from under the fasciculus longitudinalis medialis and the sensory from the spinal Vth tract. The two form one large root (figs. 11 and 12). At the level of the geniculate ganglion a heavier myelination makes the motor root more conspicuous and it can readily be followed to the masticator muscles and the m. dilator operculariș. This root courses through the gasserian ganglion (fig. 10).

10a. The Superficial Ophthalmic Ramus of the Fifth Nerve.

The superficial ophthalmic ramus arises from the dorsal surface of the gasserian ganglion near the superficial ophthalmic of the seventh and courses cephalad in close relation to it, and somewhat ventral. Its first branches are small twigs (somatic sensory) which pass to the dorsal region of the head and small branches supplying the skin of the supraorbital region (fig. 10). At the level of the eye the superficial ophthalmic Vth comes to lie lateral to that of the VIIth, and then dorsally. Near their termination (as Miss Clapp ('98) describes) the two practically fuse, but no real evidence of fiber exchange could be found. It terminates in the tip of the snout, sending small twigs around the lateral line canal and the nasal sac (fig. 10). These terminal twigs come into the same region which is supplied by the internal maxillary ramus. Norris ('25) p. 361, describes a somewhat similar relation except that in the toadfish no ramus profundus exists.

Neither the superficial ophthalmic Vth nor any other part of the fifth nerve contains lateralis elements. This corroborates Norris ('29) who showed the error of Hyman ('22) and Cahn ('26) who state that the ampullae were supplied by some fibers of the Vth. The superficial ophthalmic Vth is like Polyodon and Scaphirynchus in that respect, since it has only general somatic sensory fibers. Like Menidia and Scomber, the toadfish has no profundus nerve.

The author observed a small fine fibered twig leaving the ventral part of the gasserian ganglion which passed to the walls of the cranium. It could not be traced any further. This might possibly be a sympathetic branch to the meninges, probably derived from the sympathetic chain (Sy. 1 of Kuntz '14).

10b. The Infraorbital Trunk.

The Maxillary nerve emerges from the anterior end of the gasserian ganglion, ventral to the lateral line trunk of the seventh (buccalis facialis of Miss Clapp ('98)), with which it courses cephalad in a common sheath.

A similar relation exists in the other lower vertebrates. This combined trunk is frequently referred to in the literature as the infraorbital trunk. In the caudal part of the floor of the orbit, the combined trunk (maxillary Vth and buccalis facialis VIIth) divide, forming two rami (externus and internus, fig. 10). The two rami, which may be designated as infraorbital externus and infraorbital internus, are thus each composed of elements from the maxillary nerve (cutaneous) and from the facial (lateral line and communis). The externus passes latero-caphalad in the floor of the orbit to the edge of the maxilla and supplies the suborbital portion of the infraorbital lateral line (Clapp '98) with lateralis fibers, and the suborbital and pre-opercular skin with cutaneous fibers. It also has some communis fibers from the seventh, which supply some taste buds in the upper lateral region of the buccal cavity (fig. 10).

Concerning the occurrence of the communis fibers, the author wishes to quote Herrick ('99): "The communis fibers from the geniculate ganglion which have not been given off intracranially are somewhat confused with the general cutaneous from the gasserian ganglion. A part of these fibers go out with the roots of the ramus lateralis accessorius, others go out with the supraorbital trunk, but the larger part is clearly seen to enter the infraorbital trunk." These statements hold true, in general, for the toadfish, as in Menidia, except that the communis fibers are relatively less numerous in the infraorbital trunk.

The infraorbital internus courses cephalad in the floor of the orbit to terminate in the snout. Its fibers supply the skin and the lateral line organs in the medial region of the upper jaw, in close relation with the superficial ophthalmic ramus of the fifth (fig. 10).

10c. The Ramus Oticus.

Between the infraorbital externus and internus is a small ramus which Miss Clapp ('98) discusses with the medial buccal nerve. This nerve has both lateral line and cutaneous fibers (fig. 10).

The author has called this the otic ramus, since it corresponds very closely to the nerve thus named and discussed in Menidia by Herrick ('99). In respect to the maxillary and buccal nerves, Herrick ('99) makes this statement: "While it is probably true in other fishes, as in Menidia, that the nerves for the organs

of the infraorbital lateral line are usually accompanied by general cutaneous for the adjacent skin, yet it accords better with more recent usage to confine the term buccalis to the lateralis fibers and relegate the general cutaneous fibers no matter how closely related to them, to the ramus maxillaris." In accordance with this principle, the author uses the terms buccalis and maxillaris, discussing them together, although the buccalis fibers are entirely derived from the VIIth nerve.

In the floor of the orbit are found a large number of nerves crowded together and even flattened, due to the large eyeball (fig. 10). Herrick ('99) states that in Menidia the remarkable way in which different nerves have been compacted into the infra-orbital trunk is obviously due to mechanical causes, chiefly to the excessive development of the eyes.

10d. The Ramus Mandibularis Fifth.

The ramus mandibularis leaves the gasserian ganglion from the latero-cephalic border and emerges from the cranium by a separate foramen (figs. 10, 11, and 13). As it courses latero-cephalad, it first gives off a small ramus to the levator premaxillaris muscle. The second group of rami, usually two or three, supply the pterygoid muscles (R. pt., fig. 10). The third and largest motor portion is distributed to the large adductor mandibularis muscle. Sensory twigs pass out from the surface of these muscles to supply the overlying cutaneous areas as described in Menidia. A large sensory ramus is given off at the articular

region which supplies the skin over the dorso-lateral edge of the lower jaw, (fig. 10). Miss Bowers ('00) describes a similar cutaneous branch which comes into very close connection with the more anterior branch of the ramus mandibularis externus VII.

The mandibular nerve under the substance of the adductor mandibularis muscle, and medial to the mandible, divides into the ramus mandibularis internus fifth and the ramus mandibularis externus fifth. The latter makes a unique curve around Meckel's cartilage, nearly a circle, to pass ventro-cephalad to innervate the geniohyoid muscle (R. Gh., fig. 10). As it makes this turn it sharply curves over the ramus mandibularis internus seventh. A small part of the mandibularis externus fifth continues cephalad as a visceral sensory nerve. This component was added to the mandibular from the seventh nerve as described under that nerve (figs. 11 and 13). The ramus mandibularis internus fifth continues to course cephalad, dorsal to the cartilage and mandible, later coming to lie close to the ramus mandibularis internus seventh (fig. 10).

As far as the author could determine from Pal-Weigert preparations, the teeth receive small twigs from the ramus mandibularis internus fifth. The relations are very difficult to follow with certainty in this region. This ramus also appears to carry a communis element which was added to it at the Vth-VIIth ganglion complex. These fibers join the communis fibers of the ramus mandibularis internus facialis (fig. 10).

11. The Facial Nerve.

The facial nerve originates closely associated with the trigeminal and the acoustic. It has three somewhat distinct roots; the lateralis, sensory, and motor. The lateralis root, which is relatively conspicuous in the toadfish, lies most dorsally (figs. 10, 11, and 12); it emerges from the tuberculum acousticum in very close relation with the acoustic nerve, as discussed in connection with the latter.

A short distance from its origin the lateralis root divides into two parts, a dorsal and a ventral. The dorsal division passes dorsal to the fifth root and possesses a ganglion just caudal to the gasserian ganglion (d.l.g. VII, figs. 11 and 12). This is the dorsal lateralis ganglion of Herrick ('99) in Menidia, and has been previously described by Miss Clapp ('98). From this ganglion are given off the lateral line nerves, buccalis internus and buccalis externus, superficial ophthalmic VII, and otic ramus (fig. 10). Miss Clapp ('98) has similarly figured them, except for the otic ramus. The ventral lateralis trunk passes laterally and somewhat ventrally to the ventral lateralis ganglion (v.l.g. VII) in a similar manner as described in Menidia. This ganglion (figs. 11 and 12) lies caudal to the geniculate ganglion and from it arise the lateralis fibers that pass out in the hyomandibular trunk (fig. 10).

The sensory portion of the seventh nerve emerges immediately ventral to the lateral line root and passes latero-cephalad

with the motor portion of the seventh to end in the geniculate ganglion (figs. 11 and 12). Beyond the ganglion it continues as a large trunk which passes to the ventral surface of the gasserian ganglion (figs. 11 and 12). From the geniculate ganglion emerge the communis fibers found in the hyomandibular trunk. Components from this trunk pass out with the mandibular nerve as described above; the external maxillary nerve, and the remaining part forms the palatine seventh.

Thus far, the writer has not been able to demonstrate any cutaneous sensory element in the facial nerve proper, as has been described in the albino mouse by Rhinehart ('18) and in man by Fenton and Larsell ('28). The hyomandibular trunk, however, does carry along with it a cutaneous sensory element but this comes from the gasserian ganglion.

The motor components of the seventh nerve emerge by two small roots which soon unite to form one trunk. This motor trunk takes a lateral position and passes through the pear-shaped geniculate ganglion, a short distance beyond which it divides to contribute visceral motor fibers to the hyomandibular trunk and to form the ramus to the muscles of the palatine arch (R. m. p., fig. 10).

In the toadfish, the relations of the hyomandibularis are so nearly like those in Scomber that Allis's description applies equally well to both species (Allis '03): "Having issued from the facial canal, onto the external surface of the hyomandibula, the truncus hyoideo-mandibularis runs downward and back-

ward in the groove on the hind edge of that bone, lying in a canal formed by the hind edge of the hyomandibula and the anterior edge of the operculum. Near the ventral end of the hyomandibula the truncus separates into two main parts, the ramus hyoideus and the truncus mandibularis."

Proximal to this division, in fact, a short distance from its exit from the facial canal, the hyomandibular trunk gives off a ventral muscular branch which supplies the adductor hyomandibularis and the adductor arcus palatini muscles (R.m.p., fig. 10); it passes cephalad on the ventral surface of the cranium and lateral to the ramus palatinus VIIth; and gives off small twigs to this layer of muscles in the palatine arch. These relations are similar to the conditions found in Menidia.

Further on, near the edge of the operculum and proximal to the division into the hyoid and mandibular trunk, two rami arise a short distance from each other. The more proximal branch, the ramus dilator opercularis (R. lop., fig. 10), supplies the levator and adductor opercularis muscles and probably supplies the skin over the operculum. This branch seems to anastomose with the vagus as Norris ('25) reports in Polyodon and Scaphirhynchus, and Stannius ('49) in Acipenser.

The second ramus is the lateral line branch, ramus dorsalis opercularis lateralis (R. dol., fig. 10) described by Miss Clapp ('98).

11a. Ramus Hyoideus.

More distally the large hyoid ramus passes ventro-laterally to supply the skin in the region caudad to the mandible and gives off motor branches (Tr. Hy., fig. 10) to the mm. levator branchiostegorum and the mm. depressores branchiostegorum (Pankratz '28). A twig from this ramus also innervates the caudal portion of the large genio-hyoideus muscle (fig. 10). This ramus to the genio-hyoideus muscle anastomoses with the ramus mandibularis Vth as Norris ('25) describes in Amia and Lepidosteus, Vetter ('78, p. 515) and Herrick ('98, p. 313) in Menidia. Likewise, this ramus supplies sensory fibers to the whole branchial basket.

The hyoid ramus in Opsanus tau is very similar to the ramus hyoideus VIIth in Menidia (Herrick '99, pp. 298-300, 333). It contains visceral motor, visceral sensory and cutaneous fibers. The last group of fibers is added to this ramus from the gasserian ganglion (figs. 10, 13 and 14). Regarding this relation, Herrick says, "From the extreme caudal edge of the ganglion (Vth) a small fascicle of cutaneous fibers emerges through a separate foramen and joins the truncus hyo-mandibularis."

11b. Ramus Mandibularis VIIth.

The truncus mandibularis, from the point where the hyoid ramus is given off, courses cephalad and in the articular region divides into three rami: (1) mandibularis externus facialis, (2) mandibularis internus facialis, and (3) a ramus which passes

medial to the mandible to the lateral buccal floor where it supplies a large number of taste buds. This ramus (visceral sensory) probably is the mandibularis of Norris ('25, p. 375) and the chorda tympani of Herrick ('98, pp. 316-328). For a comparative discussion of the chorda tympani, the reader is referred to Herrick's ('99) work on Menidia, and Sheldon's ('09) paper on the phylogeny of the chorda tympani.

11c. Ramus Mandibularis Externus Facialis.

The ramus mandibularis externus facialis is almost fused with the ramus mandibularis externus Vth. The two continue cephalad lateral to the mandible (R. m. ext. V., R. m. ext. f., fig. 10). The ramus mandibularis externus VIIth, innervates numerous end-organs and lateral line organs of this region along its course to the tip of the lower jaw. The lateral line organs occur throughout this whole region, but are more numerous in the articular region. The end-organs here are probably taste buds (fig. 17).

These end-organs develop later than the lateral line organs, and are about one-third smaller (fig. 17). They appear at the 10 mm. stage and can be found in all the older stages (5 cm.-20 cm. body length). The relative time of their development agrees with the description of the taste buds in Ameiurus by Landacre ('07). Such end-organs were found scattered over the whole head, most numerous around the lip regions, fins, and operculi, and some over most of the trunk. According to the present analysis, they receive their nerve supply from the facial and the

vagus nerves. Further investigations as to their actual structure, innervation, and function are now in progress.

11d. Ramus Mandibularis Internus Facialis.

The ramus mandibularis internus VII passes cephalad medial and ventral to the externus VIIth, through the unique curve made by the ramus mandibularis externus Vth. It comes to lie in close relation with the mandible and the cartilage, ventral and in close relation with the ramus mandibularis internus Vth (fig. 10). These two rami continue cephalad in the mandible; the ramus mandibularis internus VIIth carries lateralis and communis fibers, and the ramus mandibularis internus Vth sensory fibers to the teeth (fig. 10). Before the entrance into the mandibular canal, the ramus mandibularis internus VIIth gives off a ventral lateralis branch (r. l.) which passes latero-cephalad to supply a number of lateral line organs (fig. 10) on the lower edge of the jaw.

The ramus palatinus VIIth emerges from the ventral surface of the geniculate ganglion and passes to the ventral surface of the gasserian ganglion. It forms the most median portion of the visceral trunk which passes between these ganglia; the lateral part of this trunk is made up of the visceral elements which pass to the mandibular and infraorbital trunks. Close to its emergence from the cephalic end of the gasserian ganglion, the palatinus VIIth passes ventral to the other Vth and VIIth nerves, and bends slightly medial to course forward (figs. 7, 8 and 10) in close relation to the IIIrd and VIth nerves in the common canal, as pre-

viously described (p. 15).

11e. Ramus Palatinus VII.

After its exit from the cranium, the palatinus courses cephalad, dorsal to the muscle layer in the palatine arch through the roof of the mouth. As in Menidia, beyond the cephalic edge of these muscles it reaches the mucous lining of the roof of the mouth near the median line, which it follows to the tip of the snout. In the toadfish it may pierce the cephalic portion of the m. adductor arcus palatini. This nerve appears to be the homologue of the great superficial petrosal in the higher forms (Fenton and Larsell '28).

A short distance from its origin, the ramus palatinus VIIth is joined by small fibers which appear to be sympathetic in nature. These fibers come from the sympathetic chain ventral to the gasserian ganglion (probably from the Sy. 1. ganglion of Kuntz '14). One of its twigs passes laterally to the region of the m. adductor arcus palatini. These fibers probably correspond to the great deep petrosal nerve.

11f. Recurrens Facialis.

The recurrens facialis arises from the ventral surface of the geniculate ganglion. As Miss Clapp ('98) states, it turns directly backward within the cranial cavity, and passes obliquely through the cranial wall. The author was unable to find a loop in the IXth nerve through which the recurrens facialis passes.

according to Miss Clapp ('98). In her description of the further course of this nerve she says, "Beyond which (the loop of the IXth nerve) it forms an anastomosis with an ascending branch from the posterior root of the vagus, at a point just behind the auditory capsule." The author found the course of this nerve as described. Miss Clapp (p. 235) says, "The dorsal and ventral lines of the body are innervated, in part at least, by the ramus facialis." The examinations of Pal-Weigert serial sections failed to reveal any exchange of fibers at the apparent anastomosis, and the present author has been unable to trace the recurrens facialis to the lateral line organs. It appears to contain communis fibers, which corresponds to Herrick's findings in Menidia. As a whole, the recurrens facialis lies dorsal to the sympathetic trunk (fig. 9).

11g. Jacobson's Anastomosis.

In Opsanus tau, the ramus which Herrick ('99) calls the ramus pre-trematic VIIth (VII pt., page 329) anastomoses with the pharyngeal ramus of the IXth to form Jacobson's anastomosis. Goronowitsch ('96) describes a connection between the VII and IXth in Lota vulgaris, much like the one found in the toadfish. Associated with the ramus from the seventh, forming the anastomosis, passes a small motor twig to the m. adductor arcus palatini (J.A., figs. 9 and 10). The ramus formed by this anastomosis supplies communis fibers to the pharynx in the region caudal to the area supplied by the palatinus VIIth. The homologies of these connections have been extensively discussed by numerous authors.

11h. Superficial Ophthalmic Ramus of the Seventh Nerve.

The superficial ophthalmic VIIth (fig. 10) arises from the dorsal lateral line ganglion (D. lat. G., figs 10 and 11) which lies dorso-caudad to the gasserian ganglion. Somewhat ventral and lateral to it arises the superficial ophthalmic Vth already described with the trigeminal nerve. These two branches course cephalad in close relation as described by Miss Clapp ('98). The first branch of the superficial ophthalmic VIIth may be given further consideration. It passes dorsally, caudal to the eye, to a free lateral line organ and is accompanied by a small sensory twig from the superficial ophthalmic Vth (fig. 10).

The orbital group of lateral line organs are supplied by the buccalis internus and buccalis externus rami of the VIIth which arise from the dorsal lateralis ganglion (D. lat. G., figs. 10 and 11). These rami are accompanied by sensory portions from the Vth as already described under the maxillary nerve.

11i. Lateralis Portion of the Hyomandibular Trunk.

The lateralis fibers passing out with the hyomandibular trunk originate in the ventral lateralis ganglion of the seventh (as stated on page 23). The first lateralis branch is the dorsal opercular lateralis (R. dol., fig. 10) which supplies a number of lateral line organs over the operculum. The operculo-mandibular line receives its nerve supply, as Miss Clapp ('98) describes, from the hyoideo-mandibularis facialis nerve (see page 234). The ventral

opercular line is supplied by the ramus ventralis opercularis lateralis (v. o. l., fig. 10). Numerous small rami of the mandibularis externus and internus supply the end-organs located along the mandible (fig. 10).

12. The Auditory Nerve.

As in Menidia, the ear and its nerve are highly developed in the toadfish. The nerve differs, however, in the fact that it arises by two separate roots, a caudal and a cephalic root figs. 4, 5 and 9). Dr. Coghill, in a personal communication, informed me that he had observed a distinct caudal and cephalic root in Amblystoma. The caudal root is much smaller than the cephalic and is quite distinct. Within the cranium the glossopharyngeal nerve, as in Menidia, passes between the two rami of the caudal root (figs. 4, 5, and 9). This root divides into two rami, one of which supplies to the crista acustica of the posterior ampullae and the other, a shorter one, runs to the papilla acoustica lagenae.

The cephalic root arises from the tuberculum acusticum in very close relation with the lateral line component of the seventh nerve, but no actual exchange of fibers was observed as has been described by some earlier writers. This root breaks up into typical rami, the ramus sacculus being especially large. As in Scomber scomber (Allis '03) a large lenticular otolith is found in the sacculus. Small ganglion cells are found at the terminations of the different rami, near the sensory epithelium.

For a more detailed discussion of the auditory nerve, the reader is referred to Herrick's work on Menidia ('99), and to Burlet ('29) who has discussed the development and comparative anatomy of the innervation of the labyrinth.

13. The Glossopharyngeal Nerve.

The ninth nerve is rather simple in its structure. As in Menidia, it arises from the lateral surface of the medulla, ventral to the lateralis tenth. It has a single root and passes laterally between the two posterior rami of the acoustic nerve (figs. 4, 5 and 9). It courses to the wall of the cranium through the auditory capsule just caudal to the sacculus. After its exit from the cranium it turns sharply cephalad into its ganglion which lies immediately at the foramen. Here the recurrent facial nerve lies dorso-medially and the tenth-seventh communicating trunk (Miss Clapp '98) is directly ventral. From all studies it appears that the communicans VII-X figured and mentioned by Miss Clapp ('98) is the sympathetic trunk (fig. 9) and is described and shown by Kuntz ('14). From the latter trunk, as it appears from Pal-Weigert preparations, the ninth nerve receives some sympathetic fibers. The author does not wish to stress this point since no special methods were used to trace any sympathetic fibers. As a whole, the findings agree with those of Kuntz ('14) on the sympathetic of the toadfish.

From its ganglion, two branches emerge cephalad. The first twig supplies the small anterior internal levator arcus

branchialis muscle (R. lbai., fig. 9). The main trunk continues cephalad for a short distance when it divides into two rami. The more caudal ramus (post-trematic) passes to the first gill arch by curving caudally (fig. 9). This ramus contains motor and communis fibers and with the small pre-trematic Xth provides the nerve supply of the first gill arch (fig. 9). The second (dorsal) ramus soon turns ventro-laterally and from it arises a small twig to the anterior levator arcus branchialis externus (R. lbae, fig. 9). A detailed description of the muscles supplied by the cranial nerves has been previously given by the present author (Pankratz '28).

The major part of the second ramus continues as the pharyngeal nerve, which communicates with the seventh by Jacobson's anastomosis (fig. 9). From this, communication fibers pass ventrally to supply the mucous lining and taste buds of the roof of the pharynx. The communicating branch of the VIIth (Jacobson's anastomosis) sends a small branch caudally to the mucosa of the roof of the mouth in the area of the first gill arch.

No connections with the Xth were ever demonstrated; neither were any lateral line nor cutaneous components observed as described in most other fishes, except Menidia. For a comparative discussion of the glossopharyngeal nerve, the reader is referred to Norris' ('25) paper on the cranial nerves of the ganoids.

14. The Ramus Lateralis Vagi.

The lateralis tenth arises as a distinct root from the dorso-lateral portion of the tuberculum acusticum, dorsal and somewhat cephalad to the origin of the glossopharyngeal nerve (figs. 3 and 9). It passes caudally to exit from the skull just dorsal to the vagus proper but through the same foramen. It does not receive any fibers from the ninth as described in Menidia by Herrick ('99). It is more like the lateralis tenth in Scomber scomber (Allis '03).

Its ganglion, which forms merely a slight enlargement on the nerve, is close to the origin of the nerve in the free-swimming stage (20 mm.) and hence is intracranial. Apparently it shifts its relative position later, for in the adult the only ganglion present on this nerve was extracranial just distal to the exit of the nerve from the skull. Material was not available to investigate intermediate stages in this process. An analogous distal migration of ganglion cells of the IX and X nerves in human has been described by Fahmy ('27).

Distal to the lateralis ganglion, the main portion divides into the dorsal and ventral rami which pass caudally to innervate the two series of lateral line organs of the body, as described by Miss Clapp ('98).

From the ganglion of the lateralis tenth, a dorsal ramus is given off which passes to the supra-temporal region (fig. 9). It corresponds to the supratemporal ramus described by Allis ('03, p. 279) who stated that it was composed of lateral line fibers of the lateralis tenth and fibers (not traced to their termination)

of the tenth proper. This branch in the toadfish has been found by the present author to be composed of lateral line fibers of the lateralis tenth and a small ramus of cutaneous sensory fibers from the tenth proper (V_2, fig. 9).

15. The Vagus Nerve.

The vagus nerve proper arises from the medulla ventro-lateral to the lateralis tenth and caudad to the ninth nerve (figs. 3 and 9). It emerges from the caudal end of the prominent vagal lobe by several rootlets, which are more or less fused; the visceral motor portion, however, emerges most ventrally by two separate small rootlets. The remainder of the nerve comes from the dorsal part of the vagal lobe. All the rootlets, including the two motor parts, combine immediately into the root of the vagus which courses latero-caudally to leave the cranium ventrally to, and in common with, the lateralis tenth; it then bends ventrally and laterally to terminate in the ganglionic mass described below.

From the vagus root between its exit from the cranium and the ganglionic mass two branches arise, the first supratemporal ramus (intracranial) and the second supratemporal ramus (extracranial). The first supratemporal ramus is a small fine-fibered twig which passes dorsally from the intracranial portion of the root of the vagus. The ganglion cells of this ramus could not be located definitely in the available Pal-Weigert preparations. It courses dorso-cephalad, caudal to the cerebellum, to leave the cranium by a foramen in the supra-occipital bone near the mid-dorsal

line (fig. 9). This is the supratemporal ramus (S. t. $v^{\prime}$.) described by Miss Clapp ('98) leaving the cranium through the foramen o.c.f. in her figure. It supplies a group of temporal lateral line organs.

Just distal to the exit of the root of the vagus, a small sensory twig joins the lateralis (V_2, fig. 9) as discussed above under the lateralis tenth. This component could be distinctly followed to the skin around the supra-opercular region. The general sensory fibers in this second supra-temporal branch come from a small ganglion located on the dorsal surface of the tenth root (jugular ganglion, fig. 9) probably homologous to the separate cutaneous (cut. $X_2$2) described by Herrick ('99). Norris ('25) describes an intra-cranial ganglion on the tenth from which dorsal rami are given off (p. 398). He calls this the supra-temporal ganglion of the tenth nerve. The lateral line portion is distinctly seen coming off from the dorsal part of the lateralis tenth and goes to a row of lateral line organs (dl. Clapp, '98).

At the termination of the root of the vagus, which is located near the dorsal end of the gill arches, the vagus trunk bears a large ganglionic mass and breaks up into the branches described below. This ganglionic mass lies just cephalad to the anterior end of the kidney and on the ventral surface of the caudal portion of the otic capsule. It is subdivided into two parts, of which the oval shaped caudal ganglion is the largest and corresponds to the fourth vagus ganglion in Menidia (Herrick '99); the other ganglionic mass is irregular in form and lies dorsal and cephalad to the

caudal mass. This cephalic portion of the tenth ganglion is made up of two more or less completely distinct ganglia with a dorsal protuberance from which the supra-occipital ramus arises.

From the caudal ganglionic mass arises the branch to the retractor branchialum arcuum dorsalis muscle, the oesophageal ramus and the large intestinal ramus (R. oes. and R. Int., fig. 9).

From the cephalic ganglionic mass arise the branches (fig. 9) to the three gill arches, and to the dorsal branchial muscles described in the author's previous paper (Pankratz '28). The following chart shows the different muscles supplied by the vagus nerve.

Table of Muscles supplied by the Vagus Nerve.

Muscle Group	Name of the Muscle	Number	Nerve Supply.
Branchial (dorsal)	Levator arcuum branchialis	3	X
	Oblique Dorsalis	2	IX-X
	Transversus dorsalis (anterior and posterior)	1	X
	Retractor arcuum branchialis	1	X
Branchial (ventral)	Transversus ventralis (anterior and posterior)	1	X
Hyoid	Pharyngo-clavicularis ext.	1	X
Pharyngeal	Pharyngo-clavicularis int.	1	X

The pre-trematic element of the first gill arch is small and supplies the first gill arch in common with the post-trematic branch of the IXth (page 34). From the cephalic ganglionic mass also arise the communis fibers to the gills and a large pharyngeal ramus to the mucosa of the pharynx (Ph. X, fig. 9). The course of the rami to the gill arches has not been completely plotted since they are typical and would only confuse the figure.

From the cephalic ganglionic mass arises also the opercularis Xth ramus (R. Sup. t., fig. 9) which passes dorso-laterally, and pierces the levator operculâris muscle, and courses mostly between the levator and dilator opercularis muscle and terminates along the operculum, up to the area supplied by the second supratemporal ramus. Fibers in this ramus were traced to lateral line organs. It apparently corresponds to the ramus opercularis vagi in Menidia. As stated above (page 30), the author feels confident that there is no interchange of fibers between the recurrent seventh and the opercular tenth. The fibers of this latter ramus appear dark like the lateral line fibers. Though the possibility of the presence of some cutaneous fibers could not be excluded, on the other hand, the fibers of the recurrent seventh are only slightly medullated and are probably communis. Hence, the author doubts the exchange of fibers at this point.

The vagus, in most respects, is similar to that nerve in Menidia. The greater part of its fibers are communis, visceral motor, and a few cutaneous and lateralis fibers.

16. Table of the Cranial Nerve Components of the Toadfish.

NERVES	COMPONENTS
Olfactory nerve. (Nervus terminalis in larval stages only)	Special visceral and somatic sensory. Sympathetic. (?)
Optic nerve.	Special somatic sensory.
Oculomotor nerve.	Special somatic motor. General visceral motor. Proprioceptive ?.
Trochlear nerve.	Special somatic motor. General visceral motor. Proprioceptive ?.
Abducens nerve.	Special somatic motor. Proprioceptive ?.
The Trigeminal nerve. a. The superficial ophthalmic	General somatic sensory.
b. The infraorbital trunk	General somatic sensory (V). Lateralis and *Communis VII.
c. The ramus oticus.	General somatic sensory (V). Lateralis (VII).
d. The ramus mandibularis.	General somatic sensory (V). Special visceral motor (V). Communis (VII).

NERVES	COMPONENTS
The Facial Nerve. 1. Ramus hyomandibularis.	General somatic sensory (V), lateralis, communis, and special visceral motor (VII).
a. Ramus hyoideus.	Special visceral motor (VII). Communis fibers (VII). General somatic sensory (V).
b. Ramus mandibularis internus VIIth.	Lateralis fibers. Communis fibers.
c. Ramus mandibularis externus VIIth.	Lateralis fibers. Communis fibers. General somatic sensory (V).
d. Ramus palatinus.	Communis fibers. Sympathetic fibers ?
e. Ramus recurrens facialis.	Communis fibers.
f. The superficialis ophthalmic	Lateralis fibers.
Auditory nerve.	Special somatic sensory
Glossopharyngeal nerve. a. Muscular rami	Special visceral motor.
b. Trematic and Pharyngeal rami	Communis fibers. Sympathetic fibers ?
The lateralis vagi.	Lateralis fibers.

NERVES	COMPONENTS
The vagus nerve. a. Supratemporal (1)	Lateralis fibers.
b. Supraoccipital	Lateralis fibers.
c. Supratemporal (2)	General somatic sensory.
d. Trematic and pharyngeal rami	Communis fibers.
e. Muscular rami	Special visceral motor.
f. Visceral rami	General visceral motor.

* The term "communis" is used as defined by Herrick ('98).

IV. SUMMARY

1. The brain conforms, in general, to the teleostean type. The fore-brain is deeply lobated, the optic lobes are large, while the cerebellum and valvula cerebelli are small.

2. The olfactory nerve is long and solid, and ganglion cells of the nervus terminalis are present in the embryo from about the 20 somite stage; during the early larval stages they are gradually "drawn in" between the nerve fibers to form sheath cells. In the free-swimming stage (20 mm.) and in the adult no trace of nervus terminalis ganglion cells or fibers could be found.

3. The optic nerve is large, correlated with the well-developed eye-ball, and the chiasma is dimorphic.

4. The eye-muscle nerves are typical for teleosts. Two types of fibers, fine and coarse were observed in the III, IV and VI nerves. In addition to the ciliary ganglion, nerve cells were found associated with, and in the trunk of, the III and IV nerves. These probably are sympathetic in nature.

5. The fifth and seventh ganglia are less intimately related anatomically than in fishes previously described. The fifth nerve supplies the somatic sensory components to most of the head, and its motor components are large, due to the highly developed muscles of mastication. Its branches contain no lateralis or communis elements.

6. The facial nerve supplies all the lateralis fibers of the head with the exception of the supra-temporal region above the operculum, which is supplied by the two supra-temporal rami of the vagus. It also provides communis fibers to the mouth and lip.

7. The auditory nerve arises by two roots, a caudal and a cephalic, the latter, which is the largest, being very closely associated with the lateralis of the VIIth.

8. The glossopharyngeal nerve is rather simple in its structure. it has only communis, visceral motor, and possibly some sympathetic fibers. It supplies pre- and post-trematic branches to the first branchial cleft.

9. The lateralis tenth arises as a distinct nerve, which divides extra-cranially into the dorsal and ventral lateral line nerves of the body. Its ganglion is intra-cranial up to the free-swimming stage (20 mm.), but in the young adult, it is extra-cranial.

10. The vagus nerve arises by a number of rootlets which fuse immediately into a single trunk. It leaves the cranium in common with the R. lateralis tenth. A small jugular ganglion is present at the cranial exit from which the second supra-temporal ramus arises. Three other closely associated ganglia are present, which give rise to the trematic, muscular, and visceral rami. The vagus supplies the pharyngeal and branchial muscles of the branchial arches.

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Abbreviations for all Figures.

B. V. blood vessel.

Br. r. branchial rami.

Buc. f^1 medial buccalis branch of the seventh.

Buc. f^2 lateral buccalis branch of the seventh.

C. cerebrum.

CB. cerebellum.

C. G. ciliary ganglion.

c. l. ciliaris longus.

Ch. Ty. chorda tympani.

D. lat. G. dorsal lateralis ganglion.

Ep. epiphysis.

F. B. forebrain.

G. C. ganglionic cells.

G. G. gasserian ganglion.

V. G. gasserian ganglion.

Gen. G. geniculate ganglion.

VII. G. geniculate ganglion.

Hy. hypophysis.

J. A. Jacobson's anastomosis.

J. G. jugular ganglion.

L. G. X. lateralis tenth ganglion.

L. Inf. inferior lobe.

Lob. Inf. inferior lobe.

L. Op. optic lobe.

Lat. G. lateralis ganglion.

Lat. VII. lateralis seventh.

Lat. X. lateralis tenth.

M. V. maxillary nerve (V).

Max. V maxillary nerve (V).

M. int. maxillaris internus.

M. ext. maxillaris externus.

Md. medulla oblongata.

N. N. nuclei of sheath cells.

N. Op. optic nerve.

N. Ol. olfactory nerve.

N. Sp. spinal nerve (1st.).

Ol. L. olfactory lobe.

Ol. sac. olfactory sac.

Op. C. optic chiasma.

Op. L. optic lobe.

Pal. VII palatinus seventh.

Ph. IX pharyngeal rami of the ninth nerve.

Ph. X pharyngeal rami of the tenth nerve.

R. adm. rami to the adductor mandibularis muscle.

r. a. p. ramus to the posterior acoustic ampullae.

R. Ao. ramus to the adductor opercularis muscle.

r. cad. caudal root of the acoustic nerve.

R. Ca. caudal root of the acoustic nerve.

r. cep. cephalic root of the acoustic nerve.

R. Cep. cephalic root of the acoustic nerve.

R. c. b. communis branch to buccal floor.

R. D. dentary ramus.

R. d. br. ramus to the depressor muscles of the branchiostegals.

R. dol. ramus to the dorsal opercular line.

R. G. h. rami to the geniohyoideus muscle.

R. Hy. ramus hyoideus.

R. Int. ramus to the stomach, intestine, etc.

r. i. ob. ramus to the inferior oblique muscle.

r. i. r. ramus to the inferior rectus muscle.

r. l. lateralis twig of the internal mandibular seventh.

R. lap. ramus to the levator arcus palatinus muscle.

R. lbai. ramus to levator branchialis anterioris internus muscle.

R. lbae. ramus to levator branchialis anterioris externus muscle.

R. lop. ramus to the levator operoularis muscle.

R. M. muscular rami (Xth.).

R. m. VII ramus mandibularis seventh.

R. m. ext. V ramus mandibularis externus Vth.

R. m. ext. f. ramus mandibularis externus facialis.

R. m. int. V ramus mandibularis internus Vth.

R. m. int. f. ramus mandibularis internus facialis.

R. m. p. ramus to the muscles of the pharyngeal roof.

r. m. r. ramus to medial rectus muscle.

R. Oes. oesophageal ramus.

R. Op. ramus to the dilator operoularis muscle.

R. Ot. ramus oticus.

r. p. VII ramus palatinus VII.

R. Ph. Cl. ramus pharyngoclavicularis.

R. Ph. Hy. ramus pharyngohyoideus.

R. pr. ramus to the premaxillaris muscle.

R. pt. ramus to the pterygoid muscles.

R. rbad. ramus to the retractor branchialis arcuum dorsalis muscle.

r. s. r. ramus to the superior rectus muscle.

R. Sup. t. ramus opercularis Xth.

R. t. m. ramus to the transverse muscles.

Rec. f. recurrent facial ramus.

Rec. t recurrent facial ramus.

Sac. Vas. saccus vasculosus.

Sup. op. V. superficial ophthalmic branch of the fifth nerve.

Sup. op. VII superficial ophthalmic branch of the seventh nerve.

Stv'. supratemporal branch of the vagus (Clapp).

Sy. 5 fifth sympathetic ganglion (Kuntz).

Sy. 6 sixth sympathetic ganglion (Kuntz).

Sy. t. sympathetic trunk.

Tr. IX ninth trunk.

Tr. Hyo. Mand. hyomandibular trunk.

Tr. Mand. mandibular trunk.

Tub. Ac. tuberculum acusticum.

Tub. C. tuber cinereum.

v^2. second branch of the vagus (Clapp).

v. o. l. ventral opercular lateralis branch.

V. Lat. G. ventral lateralis ganglion of the seventh.

VII. Lat. R. lateralis-seventh root.

IX. G. ninth ganglion (petrosal).

X. G. tenth ganglia.

Description of figures.

Fig. 1 Dorsal view of the adult brain of Opsanus tau.

Fig. 2 Ventral view of the adult brain.

Fig. 3 Lateral view of the adult brain.

Fig. 4 Lateral view of the acoustic nerve plotted from Pal-Weigert preparations. The numbers indicate the number of the (50 μ) celloidin sections.

Fig. 5 Dorsal view of the plotted acoustic nerve.

Fig. 6 Cross section through the olfactory nerve of the free-swimming stage.

Fig. 7 Lateral view of the eye-muscle nerves and ciliary ganglion.

Fig. 8 Dorsal view of the eye-muscle nerves. The numbers on the sides indicate the number of the sections.

Fig. 9 A lateral view of the ninth and tenth nerves, showing the components according to the system used by Norris ('25). The numbers indicate the sections (50 μ) plotted.

Fig. 10 Lateral view of the fifth and seventh nerves, showing their respective components.

Fig. 11 Dorsal view of the fifth-seventh ganglion complex with its roots and rami.

Fig. 12 and 14 Cross sections through an aberrant type of optic chiasma of a small adult toadfish (p.).

Fig. 13 A ventral view of the fifth-seventh ganglion complex showing the roots and rami.

Fig. 15 Low power projection of the head region, showing the olfactory nerve, nasal sac and part of the forebrain (from a 6 mm. embryo).

Fig. 16 Olfactory nerve and ganglionic cells of the same section shown in Fig. 15 under higher magnification (camera lucida drawing).

Fig. 17 Camera ludica drawing of an end-organ in the skin of the posterior region of the mandible.

Fig. 18 Camera lucida drawing of the IVth nerve and associated cells on the left side, in a free-swimming stage (20 mm.).

Fig. 19 Camera lucida drawing of the IIIrd nerve on the same side and in the same section shown in Fig. 18.

Fig. 20 Camera lucida drawings of the IIIrd and IVth nerves on the right side of the same specimen (20 mm.) from which Figures 18, 19 and 21 were made.

Fig. 21 Camera lucida drawings of the IIIrd and IVth nerves a few sections caudad to the section shown in Fig. 20, showing a group of ganglionic cells associated with the oculomotor nerve.

Drawings in Figures 16, 17, 18, 19, 20 and 21 were made with a Leitz binocular microscope using 4b eye-pieces and 1/12a oil-immersion lens.

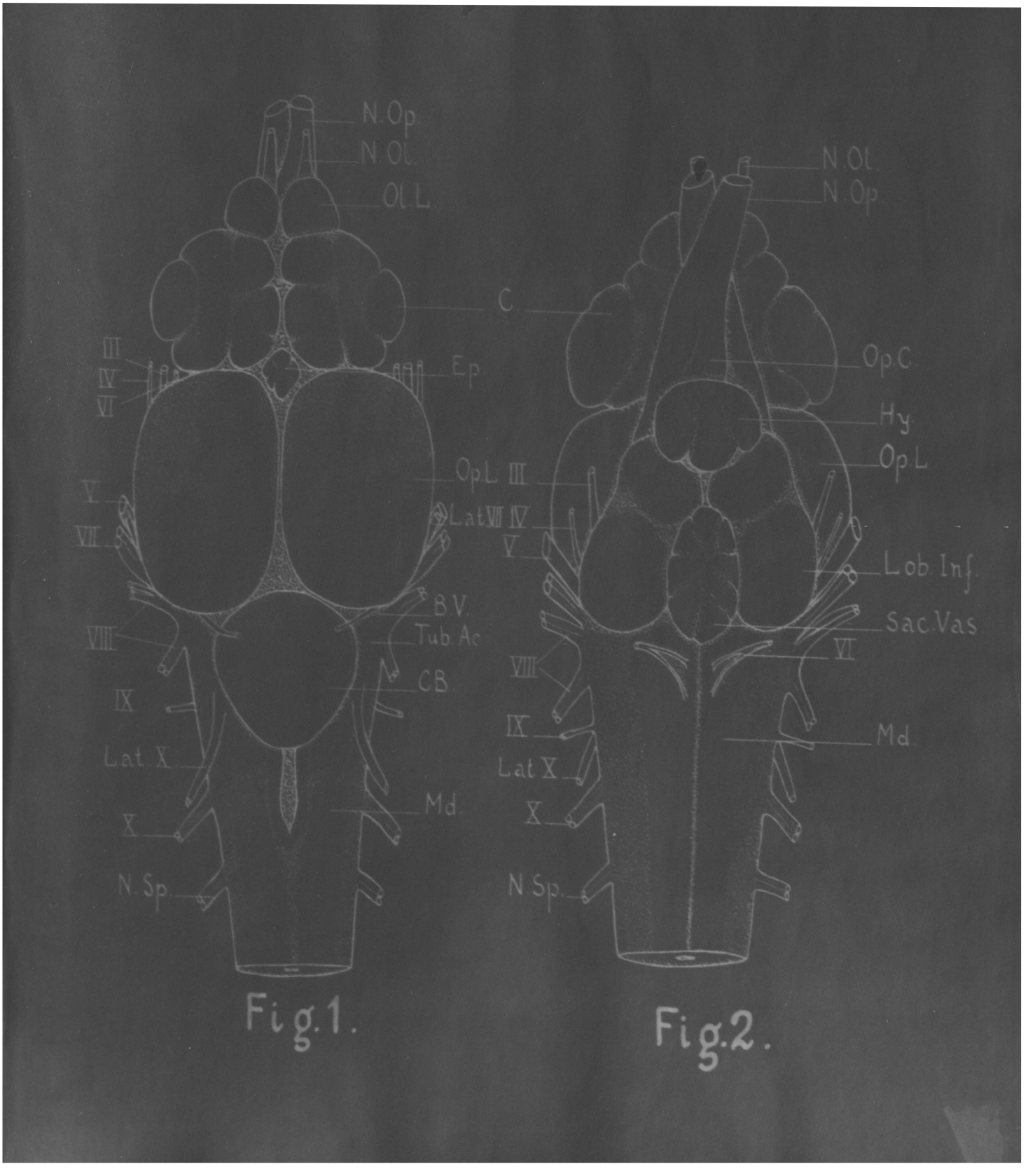
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Fig.1.

Fig.2.

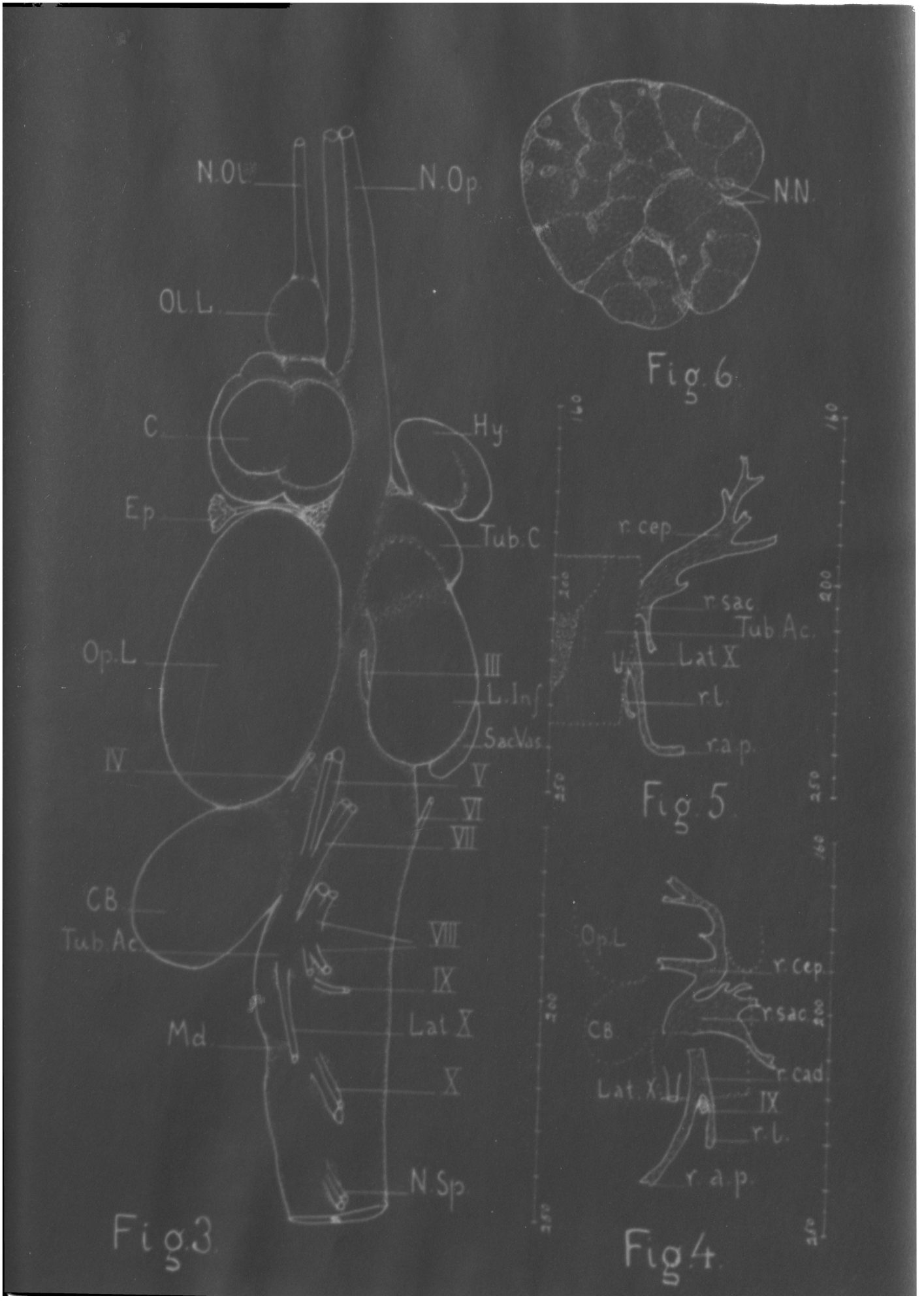

Fig. 3

Fig. 6

Fig. 5

Fig. 4

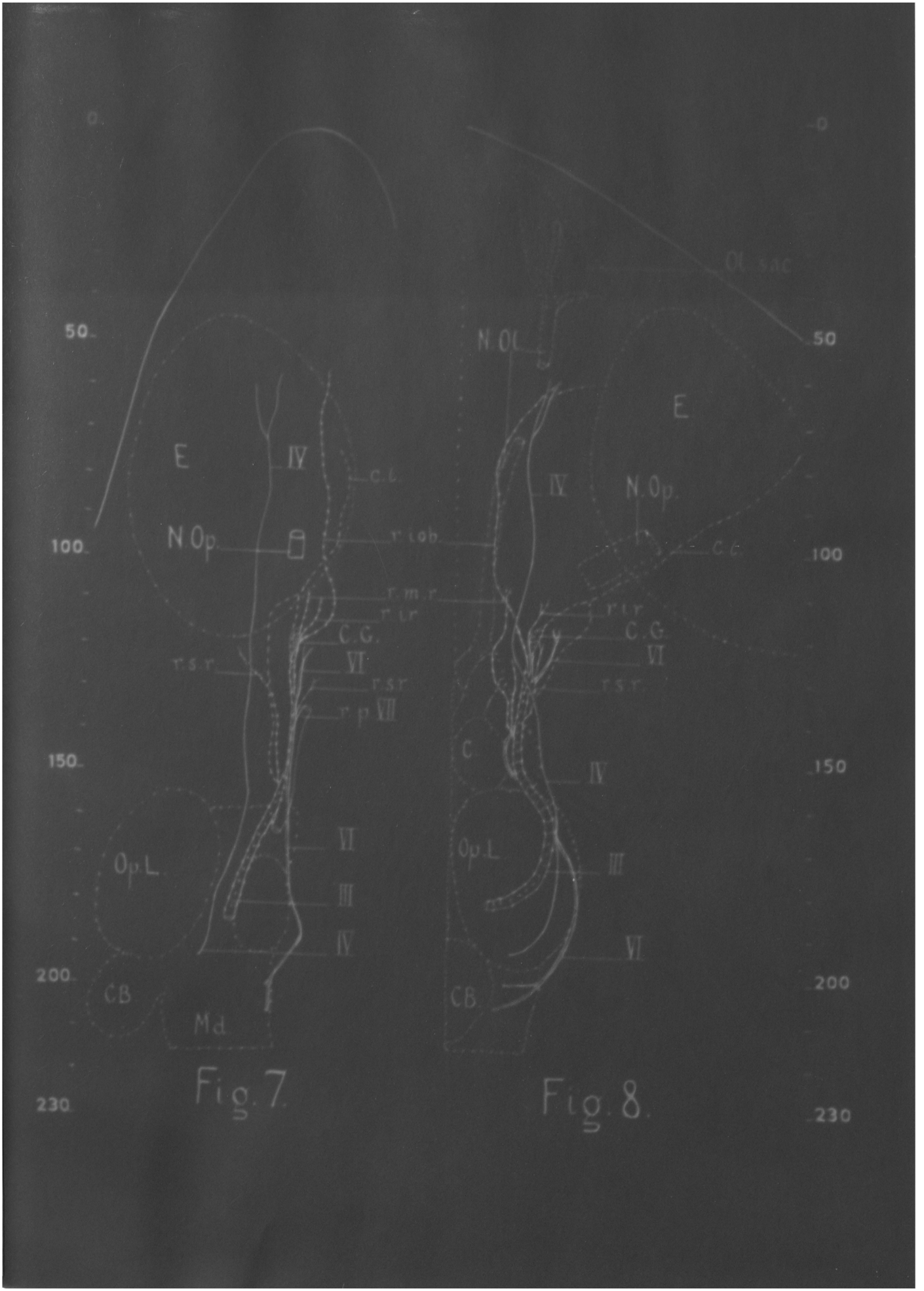
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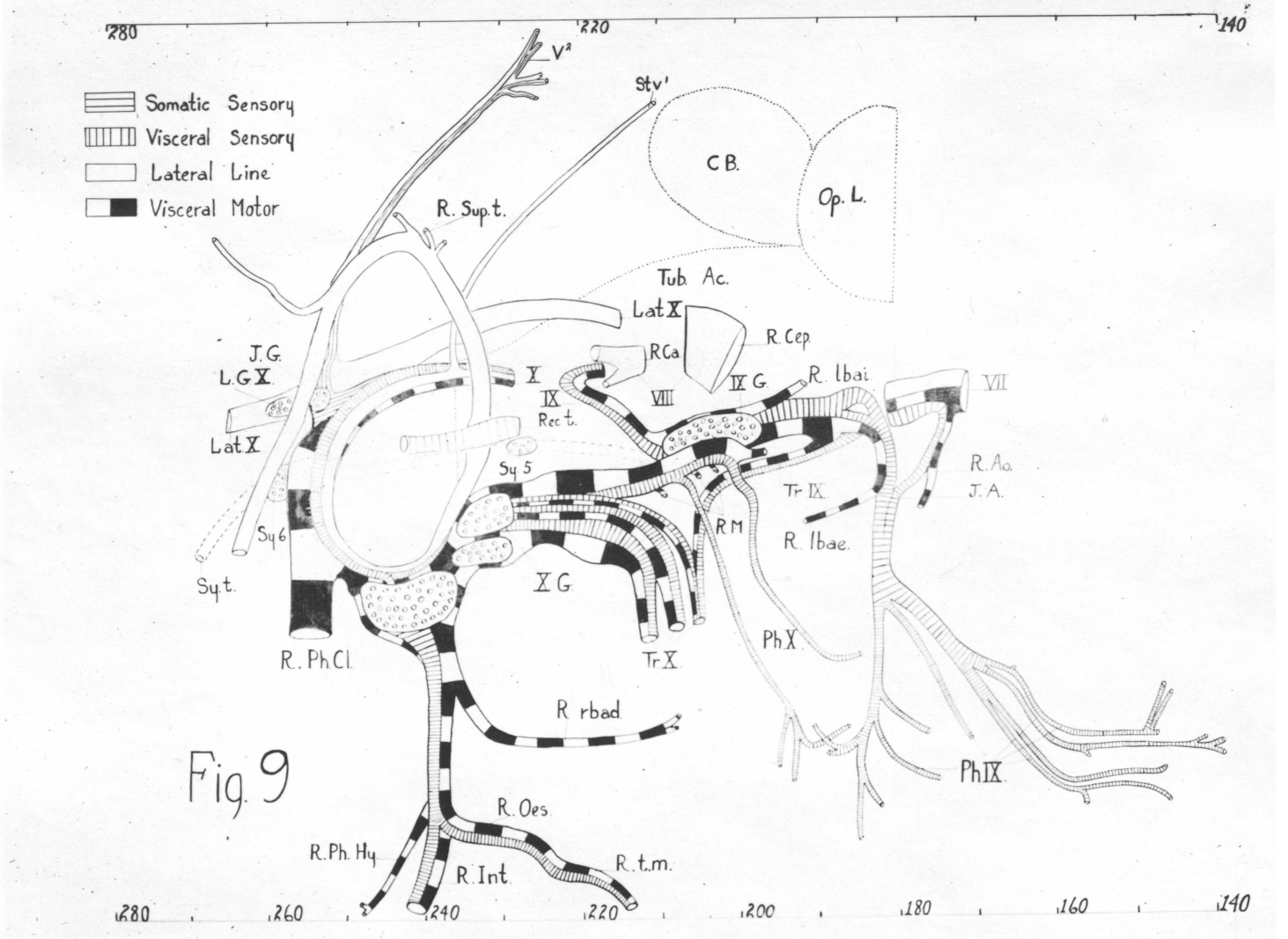
Fig. 7

Fig. 8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Somatic Sensory
Visceral Sensory
Lateral Line
Visceral Motor
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Lat X
R. Cep
RCa
J. G.
L. G X.
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R. Ibai
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R. Ao.
J. A.
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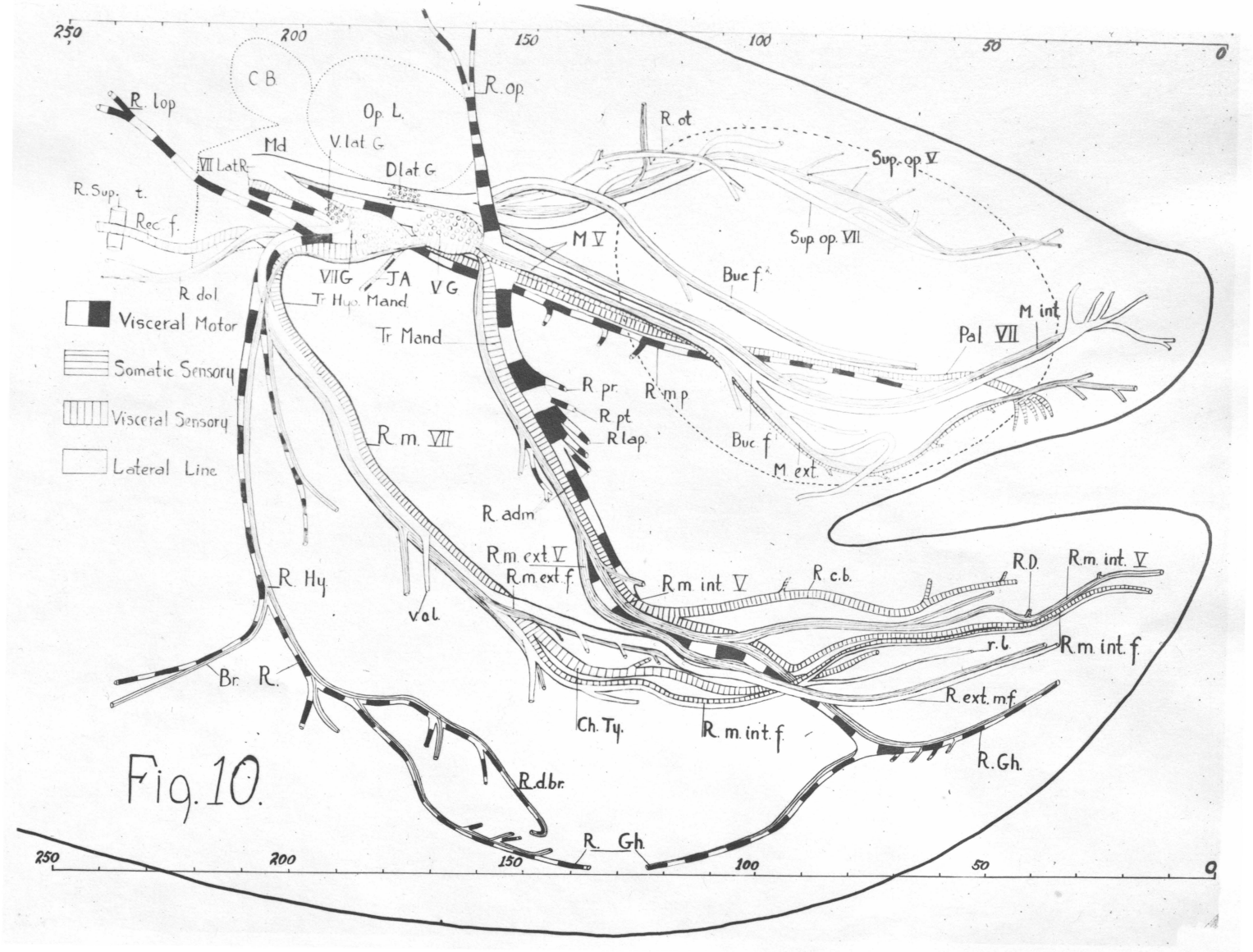
140

Fig. 9


250
200
150
100
50
0
C B
Op. L.
R. lop
R. op
Md
V. lat G.
VII LatR.
D lat G.
R. Sup. t.
Rec. f.
R. dol
R. ot
Sup. op. V
Sup. op. VII
M V
Buc f.
VIIG
JA
V G
Tr Hyo. Mand
Tr Mand
Visceral Motor
Somatic Sensory
Visceral Sensory
Lateral Line
M. int.
Pal VII
R pr.
R mp
R pt
R lap.
Buc f
M. ext.
R. m. VII
R adm
Rm. ext V
R.m ext f.
R. Hy
Val.
Rm. int. V
R c.b.
R.D.
Rm. int. V
r.l.
Rm. int. f
Br. R.
R. ext. mf.
Ch. Ty.
R. m. int. f
R. Gh.
R.d.br.
R. Gh.
Fig. 10.

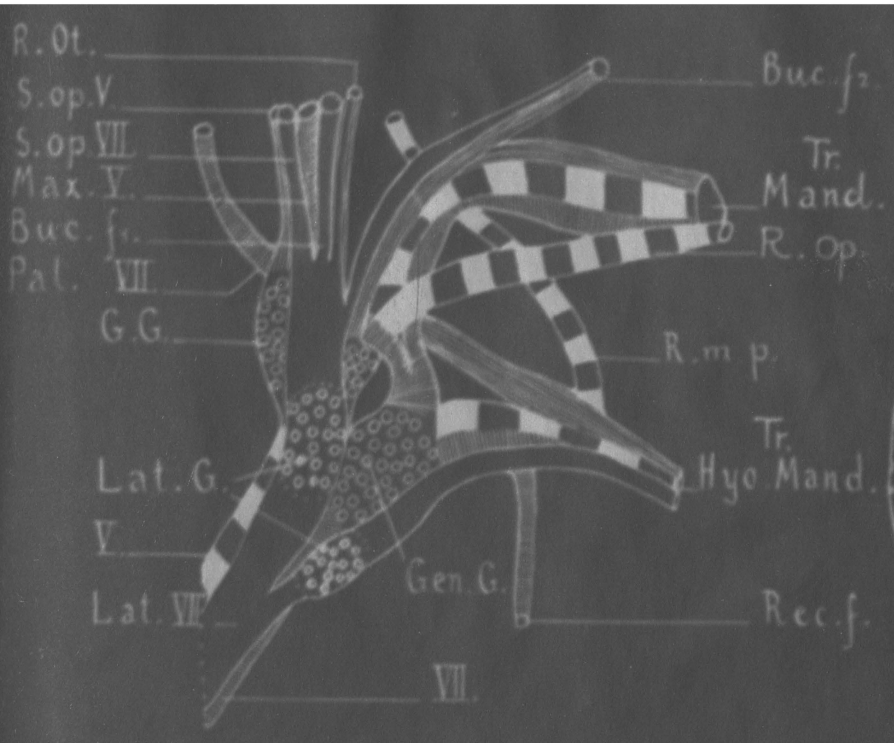


Fig. 11.

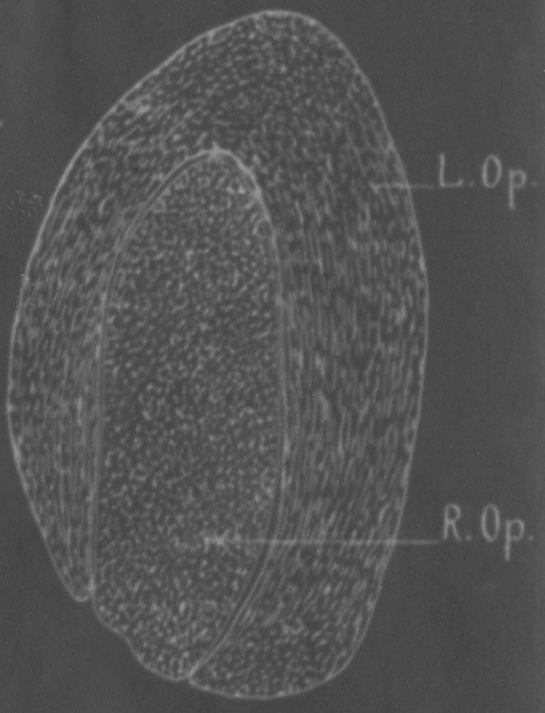


Fig. 12.

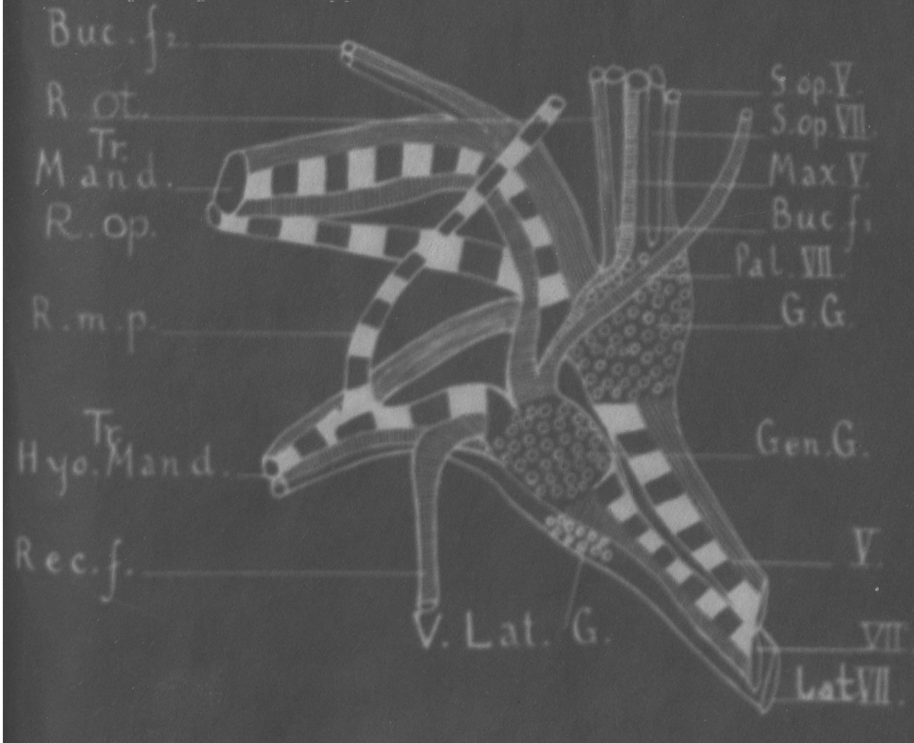


Fig. 13.

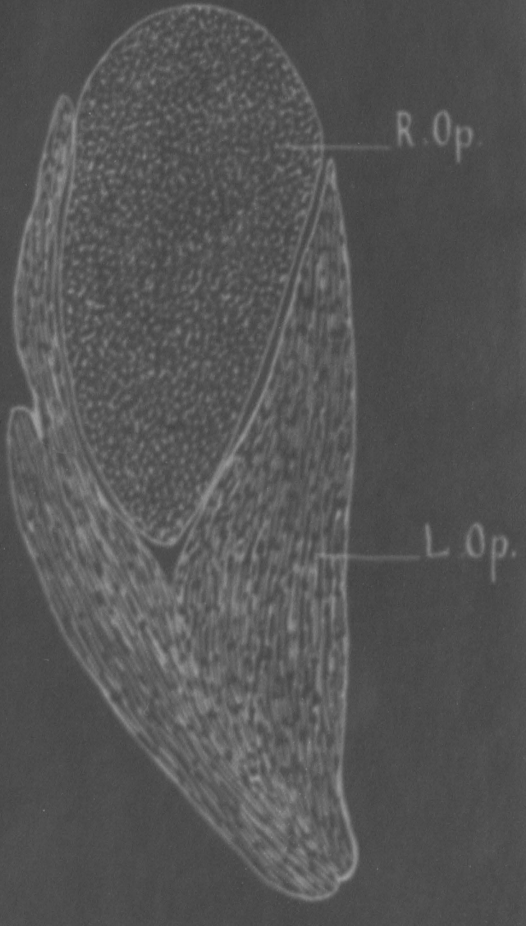


Fig. 14.

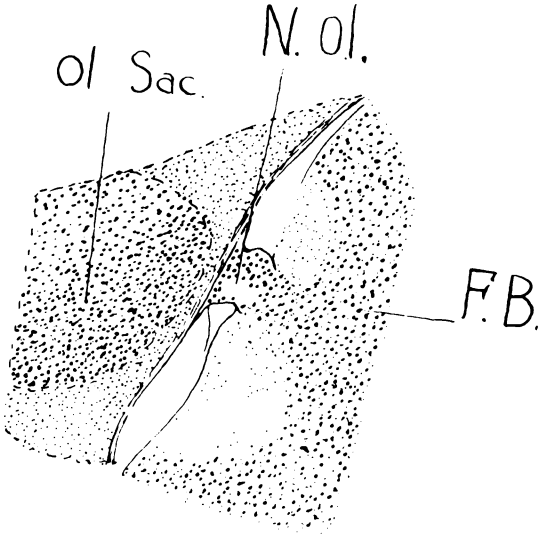


Fig. 15

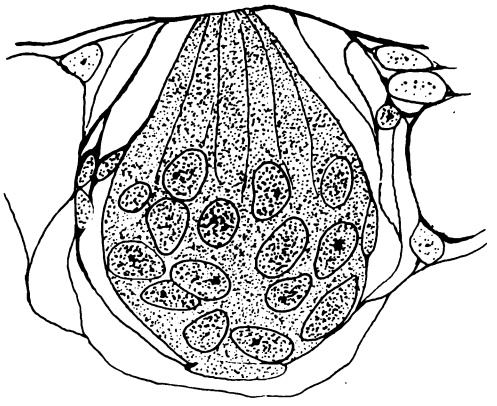


Fig. 17

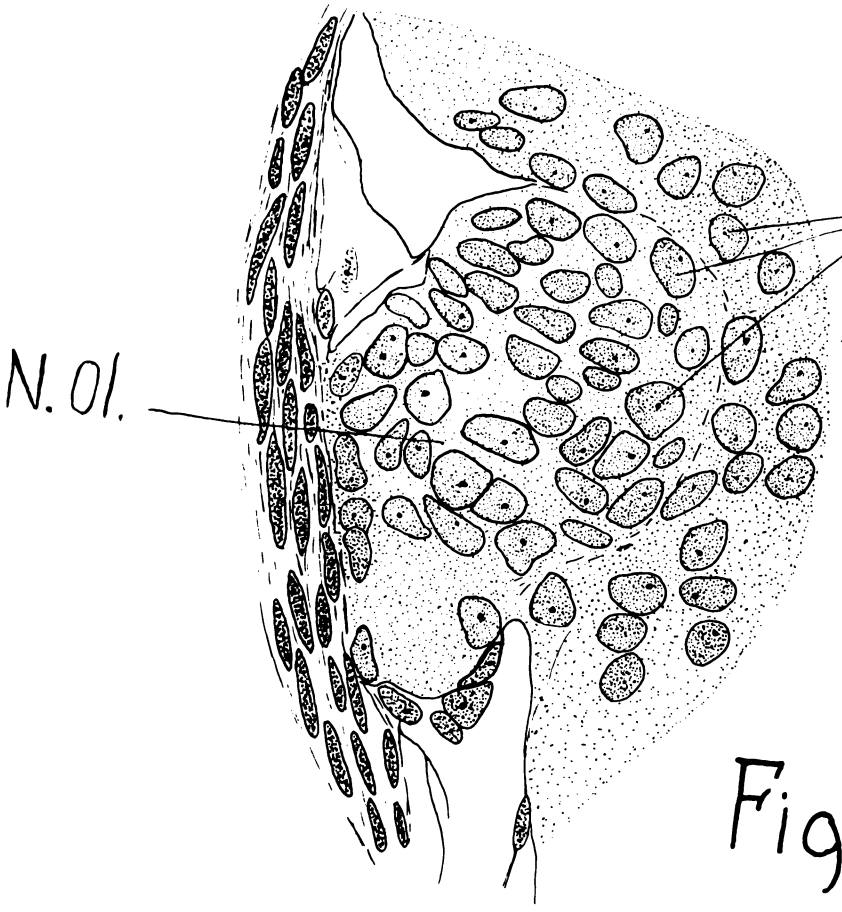


Fig. 16