

A PHYLOGENETIC CONSIDERATION OF THE PRIMARY AND SECONDARY CENTERS AND CONNECTIONS OF THE TRIGEMINAL COMPLEX IN A SERIES OF VERTEBRATES

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TWENTY-FOUR FIGURES

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INTRODUCTION

The study reported in the following pages considers the phylogeny of the trigeminal complex in a series of vertebrates including various representatives from cyclostomes through mammals. The chief points of interest in such a study are the excellent illustration it affords of the progressive and correlated development of the centers and tracts involved at various levels of the nervous system, and the fact that they reflect the degree of differentiation of the peripheral receptor and effector systems and, in a general way, indicate the mode of life and the relative position of the animal in question in the phylogenetic scale.

I am deeply indebted to Prof. G. Carl Huber for placing at my disposal the exceedingly rich neurological material available in the Laboratory of Comparative Neurology of the University of Michigan, and for his supervision of the work. The study of the material has been made more productive by the encouragement and the helpful and kindly criticism of Dr. Elizabeth C. Crosby, to whom I wish to extend my most sincere thanks.

GENERAL SURVEY OF LITERATURE

It has been deemed better to discuss the specific results obtained by other investigators of this subject in connection with the detailed description of our own material. However, there are some observers whose contributions are so outstanding as to deserve special consideration. Among those who have worked on the trigeminal complex in cyclostomes should be mentioned Johnston ('02), Tretjakoff ('09), Ariëns Kappers ('20), and Addens ('33) for petromyzonts, and Jansen ('30) for myxinoids. In the study of the selachian brain mention may be made particularly of the work of Ariëns Kappers ('06) and of Wallenberg ('07 a). Numerous observers (Johnston, '01; Droogleever Fortuyn, '12; Theunissen, '14; Hocke Hoogenboom, '29) have studied the relations of the trigeminal in ganoids and even a greater number,

among whom may be mentioned C. J. Herrick ('06, '07, '08), Ariëns Kappers ('06, '20), Tello ('09), and Burr ('28), have considered this complex in teleosts. Noteworthy additions to our knowledge of the trigeminal complex in amphibians have been contributed by C. J. Herrick ('14, '30). Its relations have been studied by Huber and Crosby ('26) and Larsell ('32) in reptiles. The literature concerned with the brain of birds is rich in references to the trigeminal complex. Among those who have contributed data on this form, Brandis (1895), Wallenberg ('03, '04, '04 a, '34), Schroeder ('11), Huber and Crosby ('29), and Sanders ('29) should receive particular mention. Many investigators have considered the trigeminal complex in mammals. Noteworthy contributions have been made by Wallenberg ('05) and Windle ('26 a). A number of phylogenetic studies concerned specifically with, or including discussions of, particular aspects of the trigeminal complex deserve special mention. Among these are the studies of Ariëns Kappers ('10, '12) on the migrations and the phylogenetic development of the motor nuclei, of Black ('17, '20, '22) on the motor nuclei of the cerebral nerves, of van Valkenburg ('11, '11 a) on the descending root of the trigeminal and on the mesencephalic root of the trigeminal, and of Weinberg ('28) on the mesencephalic root of this same nerve.

DESCRIPTION OF THE MATERIAL STUDIED

A. Cyclostomes (Ichthyomyzon concolor and Entosphenus appendix)

I. Nuclear gray associated with the trigeminal roots

1. *The sensory nucleus of the trigeminal root.* There is no trace of a nucleus in *Petromyzon* comparable to the sensory trigeminal nucleus of *Amia* and of the trout. The nucleus of the descending root of the trigeminal nerve forms its only sensory nucleus. The cells are found within the meshes of the root fibers (fig. 2), and the cell column conforms to the configuration of the root in its course through the medulla

oblongata. Cephalically the cells may be found as soon as the root enters the brain and, with the root fibers, extend some distance beyond the calamus scriptorius. The cells of the column are spindle-shaped and are small and medium sized.

Johnston ('02) stated that the nucleus funiculi differentiates anteriorly into the nucleus of the descending root of the trigeminal (his nucleus of the spinal V) and into the nucleus of the tuberculum acusticum. His description of the formation of the two nuclei may be confirmed in our material, but it does not indicate that the cell group lying above the descending root of the trigeminal nerve is the nucleus of that root. The nucleus he described is found in the region of the vagus rootlets, and afferent fibers of the vagus are lost within it. It lies quite dorsal to the root of the trigeminal and is separated therefrom by afferent roots of the vagus nerve. Furthermore, the descending root of the trigeminal extends caudally some distance beyond the calamus scriptorius, whereas the nucleus referred to ends considerably anterior to the caudal limit of the medulla oblongata. His nucleus also falls far short of the cephalic limit of the root and is nowhere mingled with its fibers. The nucleus of the descending root of the trigeminal nerve is, rather, a diffuse cell column contained within the boundaries of the root itself and entirely co-extensive with it. The findings here reported agree with those of Ariëns Kappers ('20) who described the nucleus as a collection of smaller and larger cells which everywhere accompany the descending root and which are similar, in structure and arrangement, to the somatic gray of the spinal cord.

ABBREVIATIONS FOR ALL FIGURES

a, decussation of secondary fibers from the acustico-lateral area	c, dendrites of motor neurones passing into the substantia reticularis ventralis
a.ac.lat., area acustico-lateralis	cell.Holm.et Gold., cells described by Holmgren and Goldstein
aq.S., aqueductus Sylvii	cell.Mull., Müller cell
b, internuclear connection from the nucleus of the descending root of the trigeminal to the dendritic bed of the motor nucleus	cer., cerebellum
	com.cer., commissura cerebelli

- com.horiz., commissura horizontalis
 com.post., commissura posterior
 com.tect., commissura tecti
 com.trans., commissura transversa
 d, decussation of trigemino-mesencephalic fibers
 d.b.n.mo.N.V, dendritic bed of the motor trigeminal nucleus
 dec.fib.lem.ac.lat., decussatio fibrae lemnisci acustico-lateralis
 dec.fib.lem.lat., decussatio fibrae lemnisci lateralis
 dec.N.IV, decussatio nervi trochlearis
 e, nerve to the posterior rectus muscle
 f, decussation of trigemino-mesencephalic fibers
 f.l.m., fasciculus longitudinalis medialis
 fib.arc., fibrae arcuatae
 fib.tect.bulb.et pretect.bulb., fibrae tectobulbares et pretecto-bulbares
 fib.trap., fibrae trapezoides
 g, general cutaneous component of the facial nerve
 gr.perivent., griseum periventriculare
 h, Müller cell lying between the motor trigeminal nucleus and the motor facial nucleus
 lem.ac.lat., lemniscus acustico-lateralis
 lem.bulb., lemniscus bulbaris
 lem.lat., lemniscus lateralis
 lem.trig., lemniscus trigemini
 ling., lingula
 lob.vag., lobus vagi
 m, decussation of secondary fibers of both the acustico-lateral and trigemino-mesencephalic ascending systems
 N.III, nervus oculomotorius
 N.IV, nervus trochlearis
 N.VI, nervus abducens
 N.VII, nervus facialis
 N.VIII, nervus acusticus
 N.XII, nervus hypoglossus
 n, maxillomandibular division of the sensory root
 n.coch.vent., nucleus cochlearis ventralis
 n.gust.sec., nucleus gustatorius secundus
 n.mo.N.V, nucleus motorius nervi trigemini
 n.mo.N.V p.caud., nucleus motorius nervi trigemini pars caudatus
 n.mo.N.V p.cent., nucleus motorius nervi trigemini pars centralis
 n.mo.N.V p.dors., nucleus motorius nervi trigemini pars dorsalis
 n.mo.N.V p.periph., nucleus motorius nervi trigemini pars peripheralis
 n.mo.N.V p.vent., nucleus motorius nervi trigemini pars ventralis
 n.mo.N.VII, nucleus motorius nervi facialis
 n.N.III, nucleus nervi oculomotorii
 n.N.IV, nucleus nervi trochlearis
 n.N.XII, nucleus nervi hypoglossi
 n.r.d.N.V, nucleus radices descendentes nervi trigemini
 n.r.mes.N.V, nucleus radices mesencephalicae nervi trigemini
 n.sen.prin.N.V, nucleus sensitivus principalis nervi trigemini
 o, ophthalmic division of the sensory root
 ol.inf., oliva inferior
 ol.sup., oliva superior
 p, one of the fibers of the mesencephalic root of the trigeminal turning dorso-medially toward the trochlear root
 p.n.sen.prin.N.V, primordial nucleus sensitivus principalis nervi trigemini
 ped.cer.inf., pedunculus cerebelli inferior
 ped.cer.sup., pedunculus cerebelli superior
 r, fibers of the mesencephalic root of the trigeminal passing into the motor root of the trigeminal to make their emergence
 r.d.mo.N.V, radix descendens motoria nervi trigemini
 r.d.mo.N.V p.caud., radix descendens motoria nervi trigemini pars caudata
 r.d.N.V, radix descendens nervi trigemini
 r.d.N.V prof., radix descendens profunda nervi trigemini
 r.d.N.V superf., radix descendens superficialis nervi trigemini

- r.lin.lat.ant.*, ramus nervi lineae lateralis anterioris
r.mes.N.V, radix mesencephalica nervi trigemini
r.mo.N.V, radix motoria nervi trigemini
r.mo.N.V cruc., radix motoria cruciata nervi trigemini
r.mo.N.V maj., radix motoria maior nervi trigemini
r.mo.N.V min., radix motoria minor nervi trigemini
r.mo.N.V p.caud., radix motoria nervi trigemini pars caudata
r.mo.N.VII, radix motoria nervi facialis
r.N.trig.ad cer., radix nervi trigemini ad cerebellum
r.sens.N.V, radix sensitiva nervi trigemini
str.a.cent., stratum album centrale
str.fib.et gr.perivent., stratum fibrosum et griseum periventriculare
str.fib.et gr.superf., stratum fibrosum et griseum superficiale
str.gr.perivent.tect., stratum griseum periventriculare tecti
t, fibers passing from the chief sensory nucleus to the contralateral motor trigeminal nucleus and reticular region
tect., tectum
tor.semicirc., torus semicircularis
tr.bulb.cer., tractus bulbo-cerebellaris
tr.bulb.tect., tractus bulbo-tectalis
tr.cer.mo., tractus cerebello-motorius
tr.cer.mo.cruc., tractus cerebello-motorius cruciatus
tr.cer.mo.et cer.teg.et cer.sp., tractus cerebello-motorius et cerebello-tegmentalis et cerebello-spinalis
tr.gust.sec., tractus gustatorius secundus
tr.lob.bulb., tractus lobo-bulbaris
tr.mes.cer.ant., tractus mesencephalo-cerebellaris anterior
tr.mes.cer.post., tractus mesencephalo-cerebellaris posterior
tr.ol.cer., tractus olivo-cerebellaris et cerebello-olivaris
tr.quint.front., tractus quinto-frontalis
tr.rub.sp., tractus rubro-spinalis
tr.sec.asc.trig.dors., tractus dorsalis secundus ascendens trigemini
tr.sec.asc.trig.vent., tractus ventralis secundus ascendens trigemini
tr.sp.cer., tractus spino-cerebellaris
tr.sp.cer.dors., tractus spino-cerebellaris dorsalis
tr.sp.cer.vent., tractus spino-cerebellaris ventralis
tr.sp.mes., tractus spino-mesencephalicus
tr.sp.thal., tractus spino-thalamicus
tr.tect.bulb., tractus tecto-bulbaris
tr.tect.bulb.et tect.sp., tractus tecto-bulbaris et tecto-spinalis
tr.tect.bulb.et tr.tect.isth.et tr.isth.tect., tractus tecto-bulbaris et tractus tecto-isthmi et tractus isthmo-tectalis
tr.tect.bulb.vent., tractus tecto-bulbaris ventralis
tr.trig.cer., tractus trigemino-cerebellaris
tr.trig.cer.cruc.sup., tractus trigemino-cerebellaris cruciatus superior
tr.trig.cer.dors.rect., tractus trigemino-cerebellaris dorsalis rectus
tr.trig.cer.vent.cruc., tractus trigemino-cerebellaris ventralis cruciatus
tr.trig.cer.vent.rect., tractus trigemino-cerebellaris ventralis rectus
tr.trig.mes., tractus trigemino-mesencephalicus
v.af.r.N.VII, visceral afferent root of the facial nerve
v.af.r.N.IX, visceral afferent root of the glossopharyngeal nerve
v.op., ventriculus opticus
v.IV, ventriculus quartus
val.cer., valvula cerebelli
vel.med.ant., velum medullare anterius

2. *The motor trigeminal nucleus* (figs. 1b, 2, 3). The motor nucleus of the trigeminal nerve consists of a group of very prominent cells occupying the cephalic portion of the lateral motor column of the medulla oblongata, its position being marked by a bulge in the floor of the fourth ventricle. The cells are large and carrot-shaped with a large nucleus and a prominent nucleolus. The cell body tapers ventrally into a robust dendrite, this being a stout single process passing anteriorly and ventrally. The dorsal end of the cell body is more bulbous in form and presents from one to three processes arising separately from the cell body. These dendritic

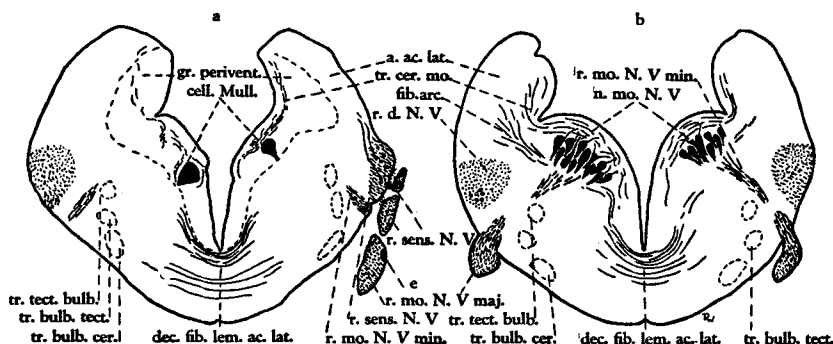


Fig. 1 Two transverse sections of the cyclostome brain at the levels of entrance of the trigeminal roots. a, entrance of the sensory root. b, entrance of the larger motor root. Entosphenus appendix. Chrome silver preparations. $\times 28$.

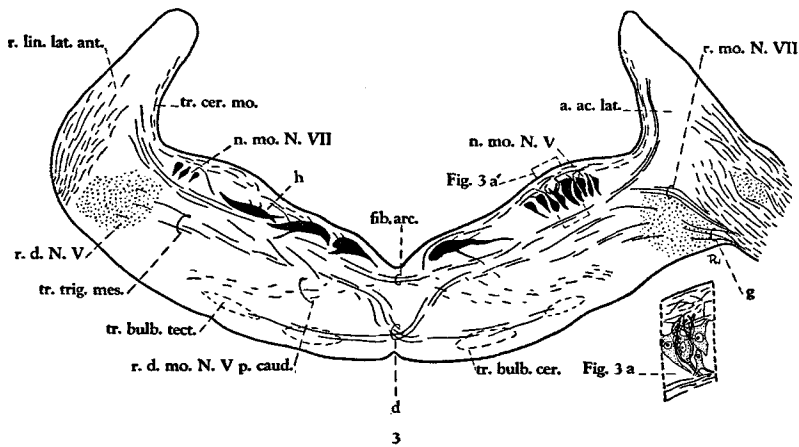
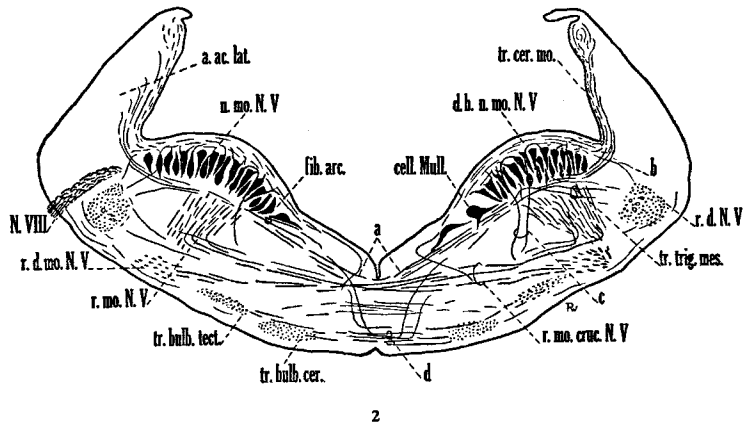
processes also branch in the very thick fiber zone between the motor cells and the ependyme. Anteriorly, the motor trigeminal nucleus is bounded by a group of much smaller cells which continues the column cephalad. Posteriorly, the transition from the trigeminal to the facial nucleus is marked by a small gap in which is found a large Müller cell (fig. 3). Moreover, the motor facial nucleus is composed of relatively very small cells so that it need not be confused with the motor trigeminal nucleus. Figure 3 represents a section at this level. The right side of the section is slightly cephalad to the left side and shows the caudal part of the motor trigeminal

nucleus. On the left side of the section is seen the Müller cell referred to above and the most cephalic cells of the motor facial nucleus. The difference in size between the cells of the motor trigeminal nucleus and those of the motor facial nucleus is apparent in this figure. The distinction between the trigeminal and the facial motor nuclei has not always been made in the literature. Addens ('33) made it as did Tretjakoff ('09), although the latter, working with *Ammocoetes*, found that the motor trigeminal nucleus has small cells and produces no bulge in the ventricle, whereas the cells of the facial nucleus are large, a relationship the reverse of that in the adult. Addens noted that Schilling ('07) and Krause ('23) mistook the hindmost portion of the trigeminal nucleus for the facial nucleus. Ariëns Kappers ('10) stated that no sharply defined limit can be drawn between the cells of these nuclei, 'the continuity being absolute.' The same author later ('29) reported that the distinction could be made between the two nuclei and noted the Müller cell between them. Black ('17) divided the motor trigeminal nucleus of *Bdellostoma dombeyi* into two parts: a large-celled nucleus (nucleus magnocellularis) and a smaller-celled nucleus (nucleus parvocellularis), which are incompletely separated and are continuous caudally with the motor facial nucleus. A similar description was given for *Myxine* by Röthig and Ariëns Kappers ('14) and Jansen ('30). No such large differences are to be noted in the trigeminal nucleus of *Petromyzon*, but there is a slight diminution in the size of the cells in the caudal part of the nucleus.

II. Fiber connections of the trigeminal centers

a. Root fibers

1. *The sensory root fibers* (figs. 1, 2, 3). The descending root of the trigeminal comprises virtually all the afferent fibers from the trigeminal ganglion and enters the brain at the cephalic limit of the medulla oblongata. In the region of the motor column of the trigeminal, the descending root



Figs. 2, 3 Two transverse sections of the cyclostome brain. Figure 2 drawn at the level of the motor trigeminal nucleus showing the decussation of a portion of the motor root of the trigeminal. Figure 3 drawn at the level of entrance of the facial roots. The left side of this section is slightly caudal to the right side and shows the most cephalic cells of the motor facial nucleus, and the Müller cell between the motor facial nucleus and the motor trigeminal nucleus. Figure 3a is a camera-lucida drawing showing the fibers of the tractus cerebello-motorius in synaptic relation with the motor neurones of the trigeminal nerve. *Ichthyomyzon concolor*. Chrome silver preparations. $\times 28$.

has the acustico-lateral area dorsally, the internal arcuate fibers dorsomedially, and is separated from the motor root of the trigeminal nerve ventromedially by a thick and jumbled mass of fine, dark-staining fibers. These are fibers, afferent with respect to the acustico-lateral area and the cerebellum, which are forced into a tortuous course by the simultaneous interposition of the longitudinally running descending root and the transversely running motor root of the trigeminal. Most of these fibers pass external to the root, but some run directly through it and may be confused with fibers of the root, while a very few pass dorsally over the root. The efferent fibers from the motor facial nucleus pass out to their root over the dorsal aspect of the descending root of the trigeminal (fig. 3). Afferent fibers of the facial nerve pass into the root in its ventromedial portion (fig. 3). They cannot be traced through the root and appear to distribute with the descending root of the trigeminal, as also was noted by Addens ('33). This is in accord with the results of Johnston ('09), Ariëns Kappers ('20), and others to the effect that cutaneous fibers are carried in the facial nerve in petromyzonts. Caudal to the region of the facial, the root ascends gradually toward the dorsal horn as the acustico-lateral area diminishes in size. The afferent fibers of the glossopharyngeal and the vagus nerves pass in over the dorsal aspect of the trigeminal root, and their efferent roots pass out ventromedial to it. As the caudal limit of the medulla oblongata is reached it gradually becomes smaller as it extends down into the spinal cord, fading out in the cervical region. The root receives additions from the facial nerve, as noted, and also afferent roots of the glossopharyngeal and vagus nerves enter and are lost within it. Tretjakoff ('09) found the same contributions in *Ammocoetes*, while Johnston ('05) noted them for *Petromyzon dorsatus* and Jansen ('30) for *Myxine glutinosa*. There are no prominent bundles leaving the tract throughout its extent; and, although small fascicles and single fibers continually pass out of it, it suffers no real diminution in cross-sectional size until the

region of the spinal cord is reached. From this it may be affirmed that the main function of this tract in the Lamprey is to provide connections to spinal motor cells in the neck and trunk regions. Fibers pass out of the root, from its medial aspect generally, and course ventrally and medially in the manner typical of all internal arcuate fibers. They make connection with the ventral motor cells of the same and the opposite sides. Ariëns Kappers ('20) verified van Valkenberg's finding, to the effect that in general the sensory fibers of the ophthalmic branch of the descending root descend the farthest and thus these can call forth reflexes of the trunk, while the fibers of the jaw branch of the nerve become lost higher up and, by means of secondary connections, exert much more influence on the motor centers of the medulla oblongata.

Although almost all afferent fibers from the trigeminal ganglion turn caudad in the descending root, a few pass dorsalward immediately after the sensory root enters the brain. They are coursing toward the acustico-lateral area and probably reach the cerebellum. They run with the peripherally situated afferents to the acustico-lateral area and cerebellum from the bulbar centers and cannot be traced apart from them. This is not a bundle but merely a small number of fibers. Some of them appear to be collaterals. Figure 1a is illustrative of this relation. Johnston ('02) noted the presence of these fibers in his material and was also unable to distinguish them from the fibers of the acustico-lateral area.

2. *The motor root fibers* (figs. 1a, 1b, 2). There are two motor roots of the trigeminal nerve in *Petromyzon*, a smaller and a larger. The smaller (figs. 1a, 1b) leaves the brain somewhat more dorsally and anterior to the larger root. At its emergence (fig. 1a), it is more closely related to the sensory root than to the motor. The larger motor root (figs. 1b, 2) emerges ventral to the sensory root. In addition to these two roots, the larger motor root has a descending ramus which joins it just before its emergence. These three structures will now be separately described.

The larger root receives its fibers from approximately nine-tenths of the motor nucleus. The cephalic fibers of this root run obliquely forward and downward while those arising more caudally pass ventralward with less inclination and then swing more sharply forward to make their emergence. The root passes ventrolaterally and rostrally in company with the sensory root and distributes to the thick musculature bordering the oral cavity. It joins the sensory root just outside of the brain.

The smaller root arises from cells of the cephalic one-tenth of the motor nucleus (fig. 1b). This is very definitely shown in the preparations available for study and occurs in both *Entosphenus* and *Ichthyomyzon*. This is the root which Addens ('33) described as the oculomotor-abducens root, postulating that the oculomotor portion of it arises from a caudal part of the oculomotor nucleus located immediately cephalad to the motor trigeminal nucleus. However, this root may be definitely traced to the cephalic portion of the motor trigeminal nucleus in the material available for this study, which portion is definitely and characteristically trigeminal in character. Moreover, the smaller root does not run out to the eye muscles in our material. As stated, it lies closer to the sensory root than to the motor root at its emergence and then passes ventrally to join the motor root just proximal to the trigeminal ganglion. In the preparations used in this study, it may be traced differentially and is seen to course far ventralward and then to turn caudalward in order to terminate in the musculature of the floor of the oral cavity. This is positive evidence that the root is not concerned in the eye muscle mechanism. Johnston ('02) called this root a motor root of the trigeminal as did Tretjakoff ('09), Addens alone having postulated its oculomotor character.

The descending ramus of the main motor root (figs. 2, 3) is to be identified with the structure Addens ('33) called his ventral sensory rami 1 and 2 of the trigeminal. This descending ramus has been noted by Ahlborn (1883) as an

'absteigende Trigeminuswurzel,' which he called motor; by Schilling ('07) as a motor root; by Johnston ('02) as a motor root, possibly of the abducens; and by Tretjakoff ('09) as a sensory root. Addens ('33) found two portions distinguishable; a dorsomedial and a ventrolateral, and considered them both sensory. In this communication he did not discuss their connections but noted that the dorsomedial bundle is made up of coarse, scattered fibers and the ventrolateral of fine, closely-packed fibers. The material available for study sheds some new light on this tract, at least as far as *Ichthyomyzon concolor* and *Entosphenus appendix* are concerned. The preparations show that, at least in part, this tract is a crossed motor bundle of the trigeminal nerve. The fibers are coarse and well impregnated in the material and cross directly transversely and thus can be clearly made out. The crossing axones (fig. 2) run down with the direct motor root about halfway to the ventral surface, then turn sharply and pass medially and cross the raphé among the deep arcuate fibers. They then curve ventrolaterally to reach the descending ramus, and turn forward in it to the emergence of the root; or, if crossing at the level of the emergence, run directly out with the contralateral motor root. Figure 2 illustrates the crossing.

A portion of the descending ramus continues back beyond the caudal limit of the motor trigeminal nucleus; and, of course, all crossing of fibers ends at that point. The portion continuing caudad is also made up of coarse fibers and shows no fiber differences from the crossed component. No fine fibered, closely-packed component was found such as that noted by Addens. The function of this caudally running component of the descending ramus of the motor root of the trigeminal nerve (fig. 3) is not determinable in the material available for study, for its final connections cannot be made out with certainty although the material is strongly suggestive. They might be additional crossed motor fibers of the trigeminal, axones of the abducens nerve, or, as some authors claim, a sensory root of the trigeminal. The explanation

given by Johnston ('02) most clearly corresponds to the indications in the material studied; that is, that these fibers constitute the motor root of the abducens nerve, the cells of origin of which are located in the ventral motor column at the level of the acustico-facial gray. This explanation provides for innervation of the somatic muscle, the posterior rectus muscle of the eye, by cells of the somatic motor column.

Our evidence on this point may be summarized as follows. The axones forming the nerve supply of the posterior rectus muscle may be traced, in the material here used, back to the motor root of the trigeminal nerve in the region of its entrance into the medulla oblongata but cannot be differentiated central to that point. However, the axones are there located ventral and caudal to the rest of the motor root (fig. 1a), a position favorable to their passage into the descending ramus of the motor root of the trigeminal. The fibers of the descending ramus remaining after the root has traversed the extent of the motor trigeminal nucleus pass, throughout the extent of the facial motor nucleus, not directly transversely, but obliquely dorsally, medially and caudally and so are cut in short oblique segments (fig. 3). They course toward the raphé in the region of the crossing of the internal arcuate fibers but become scattered and indistinguishable from other coarse fibers of the longitudinal tracts before they can be traced to their destination. Although their final connections cannot be traced, there is a strong suggestion in the material available for study, that those dorsally located pass to the cells of the homolateral ventral motor column at the level of the acustico-facial gray while those of the ventral portion pass across the raphé to the contralateral nucleus. If such be the case, they form the abducens root as Johnston ('02) has maintained. The ventral motor column at the level of the facial motor nucleus shows a number of large Müller cells, but among them may be found a number of smaller cells which appear to be motor cells and which may conceivably be the cells of origin of the abducens nerve. Johnston ('02) did not discuss the descending ramus of the motor

trigeminal root; but, in his figure 11, he labeled a cross-cut bundle in a position corresponding to that discussed above as 'Vm' and definitely stated in his text that the cephalic end of the ventral motor column in the region of the acustico-facial gray composes the motor nucleus of the abducens nerve. The material studied is confirmatory, as far as it goes, and some detail has been added.

b. Secondary connections

1. *The internuclear connections* (figs. 1b, 2, 3). Internuclear connections associated with both the nucleus of the descending root and the motor trigeminal nucleus are seen in the material studied. Dendrites of the motor nucleus, besides forming connections in the thick dendritic bed lying dorsal to the nucleus, spread widely in the ventral tegmental field, terminating among the cells of the ventrolateral nucleus of the acustico-lateral area and of the nucleus of the descending root of the trigeminal. They also disappear into the substantia reticularis ventralis where they may receive stimulation originating in higher centers. Into the substantia reticularis ventralis also pass fibers arising in the nucleus of the descending root of the trigeminal.

2. *The bulbar lemniscus and its trigemino-mesencephalic and tectal component* (figs. 2, 3). A prominent field of discharge for the nucleus of the descending root of the trigeminal is through ascending paths, and this is represented in Petromyzon by the bulbo-tectal tract, or bulbar lemniscus. This tract is first noted caudally in the cephalic portion of the spinal cord where it appears as a flat, oval band the axis of which is transverse. At this caudal level it lies on each side of the ventral decussation. Tracing the tract anteriorly it is seen to course lateralward in the same ventral field until in the region of the motor trigeminal root it lies just medial to the ventral part of that structure (fig. 2). Its cross-sectional size is increased somewhat as it goes forward by additions from the nucleus of the descending root of the trigeminal. Two other differentially staining areas are now

discernible; one medial and ventral to the tract just described, and one directly dorsal to it. The three tracts turn dorsalward at the level of the cephalic part of the motor trigeminal nucleus, inclining lateralward as they ascend. They are identified as tecto-bulbar dorsally, bulbo-tectal in the middle, and bulbo-cerebellar ventrally. The bulbo-tectal and tecto-bulbar tracts pass close together under the cerebellar decussation to terminate in the tectum. The bulbo-tectal fibers terminate in the tectum and in the midbrain tegmentum, a small portion of them crossing first in the ansulate commissure. Johnston ('02) also noted this. The tecto-bulbar fibers can be seen to arise high on the side of the ventricle from the tectal gray.

The secondary fibers constituting the trigeminal contribution to the bulbo-tectal tract are fibers which arise in the contralateral nucleus and which cross exclusively in the ventral decussation. Typically, they swing out medially from the nucleus of the descending root and pass ventromedially in the curved course of the internal arcuate fibers. When near the midline, they leave the internal arcuate bundles and, turning sharply ventralward, pass at right angles to the main decussating field to reach the ventral decussation. Here they turn medially and make their crossing. This typical course is shown in figure 2. At every level the course from the nucleus of the descending root of the trigeminal to the raphé is quite clear, indicating that the fibers pass directly transversely thus far; after crossing the raphé, they immediately begin to turn forward, the course being obliquely forward and laterally into the ascending bundle, for the fibers are now cut in short oblique segments. This laterocephalic course is much longer in the upper end of the medulla oblongata because the bulbo-tectal tract is there located farther from the midline than it is caudally. At a more caudal level, in the spinal cord region, some fibers conform to the typical pattern noted above; but some, because the smaller number of longitudinal bundles permits it, take a more direct course through the tegmentum with the result that the curves are smoothed

out. The bulbo-tectal and tecto-bulbar tracts were noted by Johnston ('02) for *Petromyzon*, by Tretjakoff ('09) for *Ammocoetes*, and by Jansen ('30) for *Myxine glutinosa*.

3. *The trigemino-cerebellar connection.* The bulbo-cerebellar tract (figs. 1a, 1b) noted in the previous discussion accumulates in the ventral field medial to the bulbo-tectal path. It receives numerous secondary trigeminal fibers which reach it by a path similar to that described for the trigeminal contribution to the bulbo-tectal tract, but which do not, of course, pass as far lateralward after making their crossing. The bulbo-cerebellar tract inclines dorsally and laterally cephalad of the level of the trigeminal nerve and can be traced into the cerebellar decussation.

4. *The cerebello-motorius fibers* (figs. 1a, 1b, 2, 3, 3a). Fine, black fibers from the cerebellum can be traced into the dorsal portion of the acustico-lateral area and thence caudalward and ventralward to the motor trigeminal nucleus. These fibers are cut in relatively short segments and lie close under the ependyme. They are to be distinguished from the internal arcuate fibers from the acustico-lateral area which lie just lateral to them. Reaching the sharp bend of the sulcus limitans, they turn up into the dendritic bed of the motor trigeminal nucleus. Figures 1b, 2 and 3 show these fibers entering the dendritic bed of the motor trigeminal nucleus, and figure 3a is a detail sketch of the pericellular type of termination of the fibers on the cell bodies of the motor neurones. No crossed cerebello-motorius fibers are apparent in the material used in this study.

B. *Ganoids* (*Amia calva*)

I. Nuclear gray associated with the trigeminal roots

1. *The sensory trigeminal nucleus.* No chief sensory nucleus, in the sense in which that term is used for higher forms, occurs in *Amia calva*. There is, however, a small region of differentiated periventricular gray at the level of entrance of the roots forming, at the rostral end of the nucleus of the

descending root of the trigeminal, a larger and more highly differentiated reception center than is afforded by that nucleus. The nucleus is ventral and lateral to the sulcus limitans and immediately adjacent to the motor trigeminal nucleus, from which, however, it is readily distinguished. The cells of the nucleus lie in close association with sensory fibers that penetrate close to the ventricular wall at the level of entrance.

2. *The nucleus of the descending root of the trigeminal nerve.* The nucleus of the descending root of the trigeminal

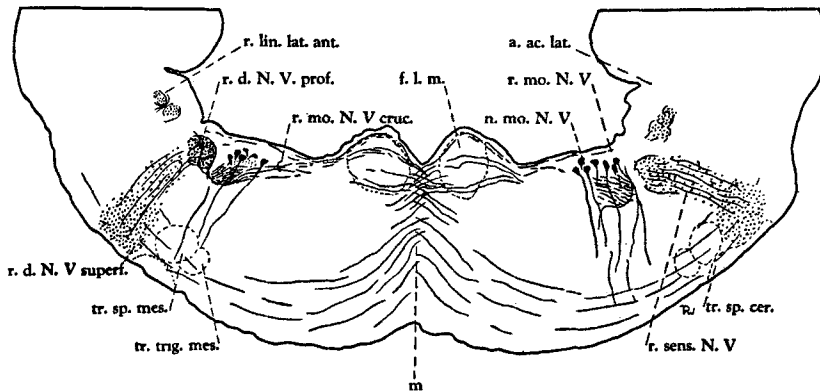


Fig. 4 Transverse section of the brain of a ganoid through the motor trigeminal nucleus caudal to the level of entrance of the nerve roots. *Amia calva*. Chrome silver preparation. $\times 22$.

is very sparse in *Amia*. It consists of small scattered cells distributed between the fibers of the root throughout its length. It is continuous rostrally with the sensory trigeminal nucleus and caudally it passes over into the lateral portion of the funicular nucleus at the junction of the spinal cord and the medulla oblongata. Its configuration throughout its course corresponds completely to that of the descending root of the trigeminal nerve.

3. *The motor trigeminal nucleus* (fig. 4). The motor trigeminal nucleus is composed of a group of relatively prominent cells occupying the cephalic portion of the lateral motor

column of the medulla oblongata. They are large, carrot-shaped cells though smaller than the corresponding cells of *Petromyzon*. Each cell body tapers ventrally into a robust dendrite (fig. 4) which is either single or branched only once and which penetrates ventrally far into the tegmentum. The nucleus is situated in the dorsal, more bulbous portion of the cell, and from the end of this portion several dendritic processes pass dorsally. The nucleus produces a slight bulge in the floor of the ventricle throughout its extent. This cell group is found cephalically at the level of entrance of the trigeminal roots and extends caudalward as far as the level of entrance of the motor root of the facial nerve. The nucleus of the latter root is not found this far cephalad, however, so there is no danger of confusion of these nuclei. The position and extent here noted conform closely with those found by Droogleever Fortuyn ('12) and Ariëns Kappers ('12) for *Amia*, by Theunissen ('14) for *Amia calva*, *Acipenser*, and *Lepidosteus osseus*, and by Hocke Hoogenboom ('29) for *Polyodon*. The motor trigeminal nucleus in *Amia calva*, *Acipenser*, *Lepidosteus osseus*, and *Polyodon* differs from that in teleosts, according to Droogleever Fortuyn, Theunissen, and Hocke Hoogenboom, in having no ventral part. The material studied confirms this for *Amia*, although there are cells which maintain a more ventral position than the rest as if in the process of initiating a ventral migration toward the position of the ventral portion of this nuclear mass in teleosts.

4. *The nucleus of the mesencephalic root of the trigeminal* (fig. 5). In *Amia* the cells of the mesencephalic root of the trigeminal (fig. 5a) are situated in the region of the posterior commissure. They occupy a position medially in the roof of the aqueduct for the most part but are also found in the medial part of the ventral wall of the optic ventricle. The cells disappear at the caudal end of the posterior commissure and extend rostral of this commissure for 0.5 mm. or less. Oftentimes the cells are seen to lie so close under the ependyme as to force a bulge, while the median cells lie among the most dorsal fibers of the posterior commissure. Most of

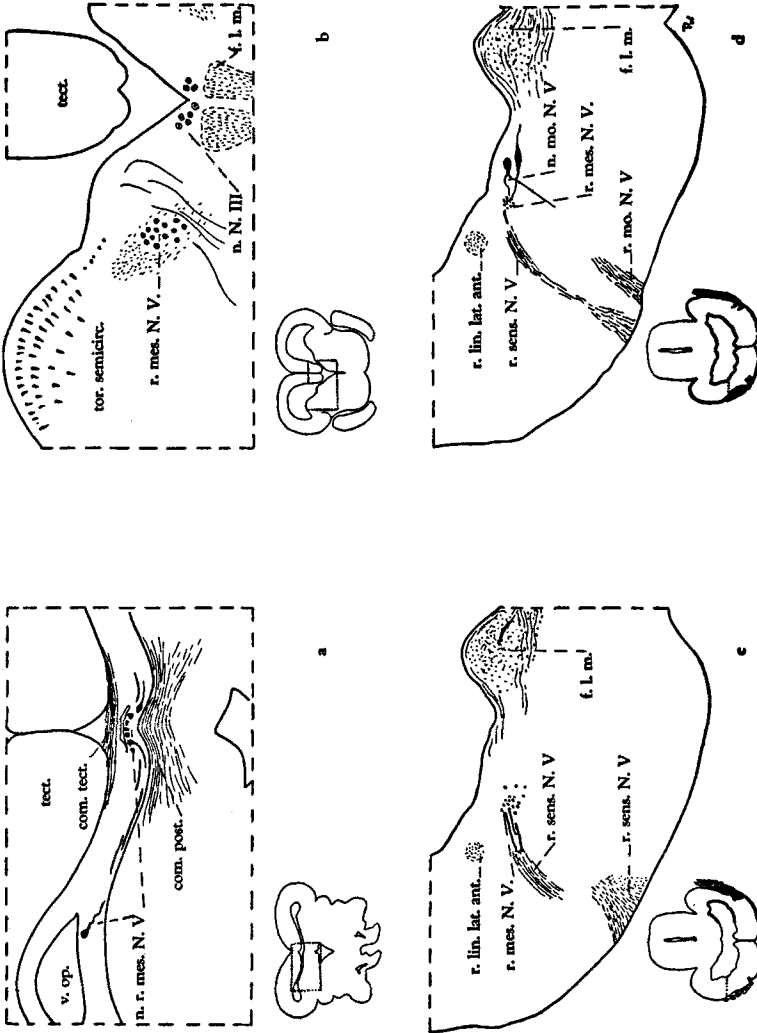


Fig. 5 A series of transverse sections through the midbrain and medulla oblongata of a ganoid to show the course of the mesencephalic root of the trigeminal nerve. *Amia calva*. Chrome silver preparations. X 22.

the cells appear to have but one process, but a number are provided with two or more. These findings are in accord with those of Weinberg ('28). A few representative cells of the nucleus can be seen in figure 5a.

II. Fiber connections of the trigeminal centers

a. Root fibers

1. *The sensory root fibers* (figs. 4, 5). The afferent fibers from the trigeminal ganglion enter the medulla oblongata dorsolateral to the motor root, the majority of them passing backward as the descending root of the trigeminal. This root is composed of a superficial portion lying adjacent to the lateral wall of the medulla oblongata, a deep portion close to the ventricle, and scattered fascicles passing caudalward between these two larger divisions. The deep and superficial divisions of the descending root of *Amia* correspond to similar divisions in *Acipenser* as reported by Johnston ('01).

The fibers enter the medulla oblongata in two bundles, one more cephalic than the other. The more cephalic bundle (figs. 5c, 5d) is the smaller and constitutes the most lateral and dorsal component of the entering nerve. A few of its fibers pass backward in the superficial portion of the descending root but most of them describe a prominent arched course, dorsally and medially, toward the ventricle. This root sends most of its fibers backward in the deep portion of the descending root, while some ascend as the mesencephalic root of the trigeminal, and a number enter into close association with the cells of the periventricular gray constituting the sensory trigeminal nucleus.

The larger, more caudally entering bundle sends most of its fibers into the superficial portion of the descending root but a large bundle of them passes dorsomedially and caudally toward the ventricle to form the bulk of the deep portion of the descending root.

Both portions of the descending root (fig. 4) pass directly caudalward, lying below the subsequent nerve roots as they

enter. Rootlets of the glossopharyngeal and the vagus nerves penetrate the descending root and doubtless contribute to it, but this cannot be established in the material with certainty. Johnston ('01) found contributions from these nerves in *Acipenser*. He also noted a contribution from the acoustic nerve and a large ascending portion of the sensory root. These cannot be confirmed in the *Amia* material studied, the fibers of the mesencephalic root of the trigeminal constituting the only ascending portion of its afferent fibers.

At the level of junction of the spinal cord and the medulla oblongata, the superficial portion of the root forms a cap over the dorsal aspect of the funicular nucleus while the deep portion bounds it ventrally, and both portions terminate in the nucleus. Johnston ('01) found that the deep portion in *Acipenser* ends in the internal part of the acustico-lateral area, a finding which cannot be confirmed in the *Amia* material studied.

The available material gives only incomplete evidence of the presence of direct trigeminal root fibers to the cerebellum; but, near the cephalic end of the entering sensory root, a number of fine fibers appear to turn dorsalward and to course toward the cerebellum. They are perhaps representative of the direct trigeminal root fibers to the cerebellum which have been suggested in various forms, but which are poorly developed in the *Amia* material studied.

2. *The motor root fibers* (figs. 4, 5d). The motor root of the trigeminal in *Amia* passes in to its nucleus of origin with only a slight inclination backward. At its entrance into the medulla oblongata it lies (fig. 5d) ventromedial and caudal to the sensory root. It is composed of two bundles, the cephalic one of which arises from the cells of the cephalic end of the nucleus, while the more caudal bundle turns sharply backward when it reaches the medial position of the nucleus and is seen to arise from those cells in the more caudal portion of the motor column.

No crossed motor fibers are definitely demonstrable in the *Amia* material available, but there is a strong suggestion of

this connection in motor root fibers which pass (fig. 4) through the motor nucleus toward the dorsal midline. The medial longitudinal fasciculus is traversed by numerous fibers which probably contain some of these motor root fibers passing to the contralateral motor trigeminal nucleus, but the connection on the other side cannot be established in the material here used. Figure 4 shows this indication of a possible crossed component.

3. *The mesencephalic root of the trigeminal* (fig. 5). The stout processes arising from the nucleus of the mesencephalic root pass lateralward along the dorsal aspect of the fibers of the posterior commissure and immediately below the ependyme, as may be seen in figure 5a. As the posterior commissure fades out caudally, efferent fibers from the tectal and pretectal nuclei pass to the midline dorsal to the mesencephalic fibers, thus bringing them to a position somewhat deeper with respect to the ependyme. The mesencephalic fibers turn caudad lateral to the aqueduct so that they present a field of diffuse end-cut segments. In this relation they lie on the medial border of the torus semicircularis, those cells of the mesencephalic nucleus on the floor of the ventricle sending their processes directly to this region. The mesencephalic root passes directly caudad in this position as single fibers and small fasciculi. Posterior to the level of the oculomotor nucleus, tecto-bulbar and pretecto-bulbar fibers and other decussating bundles in great quantity pass ventromedially toward the ansulate commissure; and, under this influence, the mesencephalic fibers (fig. 5b) also incline ventrally and slightly medially. The fibers soon straighten caudad again and are seen to have passed around the lateral recess of the ventricle and to lie about halfway between the medial longitudinal fasciculus and the lateral surface of the tegmentum of the medulla oblongata below the lateral recess of the ventricle. They are crossed dorsally by fibers passing medially to the raphé by way of the dorsal and medial aspects of the medial longitudinal fasciculus—probably acustico-lateral lemniscus fibers. In this position they pass directly

caudad and lie just lateral to the motor trigeminal nucleus. As the cephalic tip of the anterior lateral line roots begins to appear in the visceral afferent column, this tract lies lateral to the mesencephalic fibers (fig. 5c). Further, the dorsal arched bundle of the sensory trigeminal root previously described passes in to become a descending root close to the ventricle and also lies lateral to the mesencephalic fibers but medial to the anterior lateral line roots. These relationships may be seen in figure 5d. In the same figure may be seen the manner of connection of the cells of the motor trigeminal nucleus with the fibers of the mesencephalic root. The cells here orient with their ventral extremities toward the root and their ventral dendrites pass laterally to terminate in relation with the mesencephalic fibers.

The afferent fibers of the mesencephalic root appear to pass out with both portions of the sensory root. The dorsal arched sensory root is the more cephalic, and a number of the afferent mesencephalic fibers may be traced (fig. 5c) directly into it. A portion of the mesencephalic fibers remains caudad of this level and some of these appear to pass out with the deep portion of the larger sensory root while others distribute to the cells of the motor trigeminal nucleus. There appear to be no mesencephalic fibers passing out in the motor root. In this connection it is interesting to note that the sensory root is lateral, dorsal, and cephalic to the motor root in *Amia*, whereas the relations are just the reverse in the trout, the motor root being lateral, dorsal, and cephalic here, and the mesencephalic fibers pass to the periphery with the motor root in the trout. No contributions to the oculomotor and trochlear motor roots can be made out in the *Amia* material available for study.

b. Secondary connections

1. *The internuclear connections* (fig. 4). The finer internuclear connections are not readily made out in the silver preparations of *Amia* available, but the coarse dendrites of the motor cells are seen to spread widely and to enter into

important relationships. The most prominent of these dendrites are the stout ventral processes (fig. 4) which pass deeply ventrally, some extending as far as the ventral surface of the medulla oblongata. Disappearing into the substantia reticularis ventralis they may make connection there with fibers of the tecto-bulbar tract and possibly of the reticulo-bulbar tract. Dendrites of the motor cells also pass ventrolaterally and laterally into both the deep and the superficial portions of the descending root of the trigeminal. It is to be noted in these primitive forms that long dendrites pass out from the motor nucleus to the source of stimulation.

2. *The trigemino-mesencephalic and tectal component of the bulbar lemniscus* (fig. 4). Caudally in the medulla oblongata both the deep and superficial roots of the trigeminal are traversed by ventrally running fibers from the acustico-lateral area, and these are joined by fibers emanating (fig. 4) from the nucleus of the descending root. The trigeminal fibers here form the trigemino-mesencephalic and tectal tract, a component of the bulbar lemniscus system. Both groups of fibers pass in a curved course through the middle of the tegmentum toward the raphé. Crossing the raphé, the fibers turn forward and course rostrad in the ventrolateral portion of the reticular area. Passing forward in this region are the contributions from the acustico-lateral area which form the acustico-lateral lemniscus and also the trigemino-mesencephalic and the spino-mesencephalic tracts, with the trigemino-mesencephalic tract lying lateral to the acustico-lateral lemniscus though not separable from it. Dorsolateral to this group lies the spino-mesencephalic tract, not clearly differentiable in the material studied.

3. *The trigemino-cerebellar connections.* The silver preparations here used show such little differential staining that it is not possible to demonstrate secondary fibers from the nucleus of the descending root passing across the raphé to join the contralateral spino-cerebellar tract. However, it is probable that such a trigemino-cerebellar connection is present. The course of the fibers would be similar to that of the

trigemino-mesencephalic and tectal fibers described above and some of the fibers included in that category possibly are actually trigemino-cerebellar fibers.

4. *The cerebello-motorius fibers.* Very fine, black fibers arising in the cerebellum can be seen to pass close under the ependyme of the ventricle caudally and ventrally toward the motor trigeminal nucleus, especially in its caudal portion. They enter the nucleus on its lateral and dorsal aspects. No crossed cerebello-motorius fibers were demonstrable in the material studied.

C. *Teleosts (brook trout, rainbow trout, land-locked salmon trout, and carp)*

I. Nuclear gray associated with the trigeminal roots

1. *The sensory trigeminal nucleus.* There are a few small spindle-shaped cells found in the trout, along and dorsal to the course of the motor root of the trigeminal, linearly arranged dorsal to its fibers and extending up to the periventricular gray. These appear to be similar in nature to the sensory trigeminal nucleus as found in *Amia*. In silver preparations incoming sensory fibers are seen passing dorsal to and close to the motor root toward the periventricular gray and appear to make contact with the cells there. The nucleus is especially well seen in the brook trout preparations.

2. *The nucleus of the descending root of the trigeminal.* The nucleus of the descending root of the trigeminal is composed of small oval cells scattered among the fibers of the root. It is coextensive with the root and conforms to the configuration of that structure throughout its extent. Caudally it extends into the spinal cord with the descending root. Cephalically it is continuous with the sensory trigeminal nucleus whose cells stream toward the ventricle in the course of a small group of sensory fibers lying dorsal to the incoming motor root.

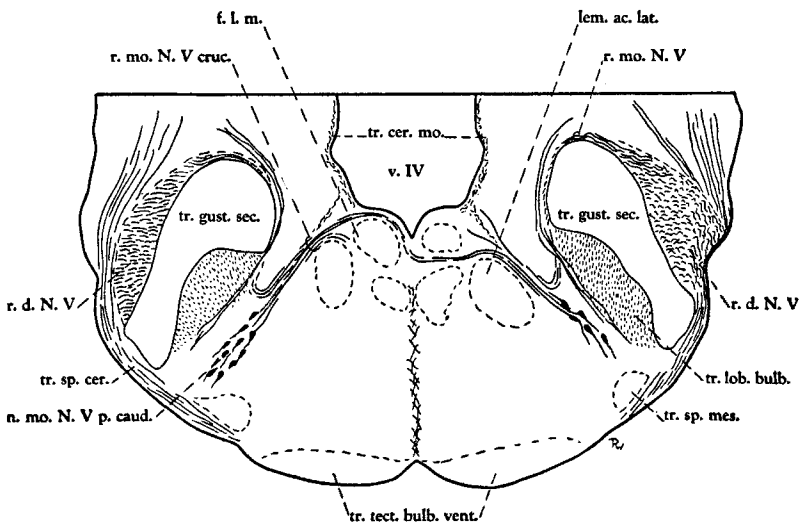
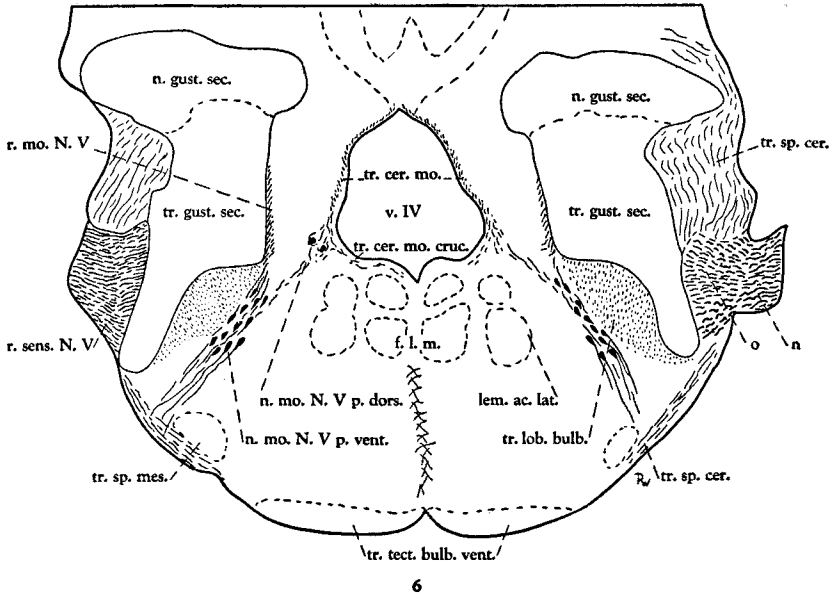
The carp material used in this study comprises only silver preparations and there is no impregnation of either of the

above nuclear masses in the sections. There is doubtless a nucleus of the descending root of the trigeminal maintaining its usual relationship in the carp, but nothing can be said with respect to a sensory trigeminal nucleus.

3. *The motor trigeminal nucleus* (figs. 6, 7, 8f). This nucleus in teleosts shows certain advances in differentiation over that in ganoids. A separation into rostral and caudal portions is apparent in both the trout and the carp material, but the amount of differentiation within these divisions of the nucleus and the amount of ventral migration of cells varies between the trout and the carp. The cell type is much the same as that described for ganoids and the extent of the nucleus is the same in all cases—from the most anterior level of entrance of the sensory trigeminal root caudally to the level of entrance of the facial root.

In all the trout examined, there is a rostral and a caudal portion of the motor trigeminal nucleus, separated only very slightly, but with the caudal portion displaced somewhat medially to the column of the rostral portion. The cells of the rostral portion (fig. 8f) lie in the primitive position close to the ependyme, but those in the caudal portion show a beginning of the ventral migration so prominent in some teleosts.

In the carp there is, in addition to the rostral and caudal separation of the nucleus, a clear separation of the rostral portion into dorsal and ventral parts (fig. 6). The dorsal part extends farther anteriorly and retains the primitive position close to the ependyme. The ventral part appears somewhat caudal to the anterior limit of the dorsal part and extends a like distance farther posteriorly. Its cells lie immediately adjacent to the medial surface of the secondary gustatory tract and the tractus lobo-bulbaris and thus are quite ventral to the cells of the dorsal part. Unlike those of the dorsal part, the cells here are drawn out into a definite spindle shape by reason of the fact that their main dendrites are directed sharply ventrally toward the ventral reticular region, whereas their neuraxes pass directly dorsally.



Figs. 6, 7 Two transverse sections of the brain of the carp. Figure 6 drawn at the level of entrance of the trigeminal roots showing both the dorsal and ventral parts of the rostral portion of the motor trigeminal nucleus. Figure 7 drawn through the caudal portion of the motor trigeminal nucleus showing the decussating motor root fibers. *Cyprinus carpio*. Chrome silver preparations. $\times 18$.

The cells of the caudal portion of the nucleus (fig. 7) are entirely ventral, even more ventrally placed than the ventral part of the rostral portion. The cells are spindle-shaped like the latter but slightly smaller and there is a clear gap between the two groups. They, however, lie in the same sagittal plane whereas the dorsal part of the rostral portion of the nucleus is displaced somewhat medially.

The findings here recorded for the carp exactly correspond to those reported by Tello ('09) for the trout. Since the amount of ventral migration of the trigeminal motor cells is clearly a corollary of the development of the secondary gustatory tract and since this is not marked in our trout material, it is probable that his trout showed a development of this system more nearly like that in the carp. Ariëns Kappers ('10) described the trigeminal motor system in *Tinea*, but apparently failed to note the more medially placed dorsal part of the rostral portion of the nucleus. His rostral portion as shown in his photomicrograph, figure 16, is only the ventral part of this portion, its dorsal part being found in sections cut quite a little nearer the midline.

4. *The nucleus of the mesencephalic root of the trigeminal.* The cells of the mesencephalic nucleus in the trout (fig. 8a) lie in the region of the posterior commissure immediately under the ependyme of the dorsal and dorsolateral surfaces of the torus semicircularis. The cells are large and pear-shaped and are very readily recognized and very characteristic. They are, for the most part, unipolar, the typical ganglion cell form, but some bipolar and some multipolar cells can be seen. The process is heavy and retains its ganglionic glomerular nature especially near the cell body, and so is cut in short, wavy segments. Only rarely is a straight segment of any length found. The processes (fig. 8a) pass backward singly in the region medial and ventral to the tractus mesencephalo-cerebellaris posterior, and it is only at the caudal level of the nucleus that any organization into a mesencephalic root can be determined. Processes of cells lying on the dorsal surface of the torus pass medially and

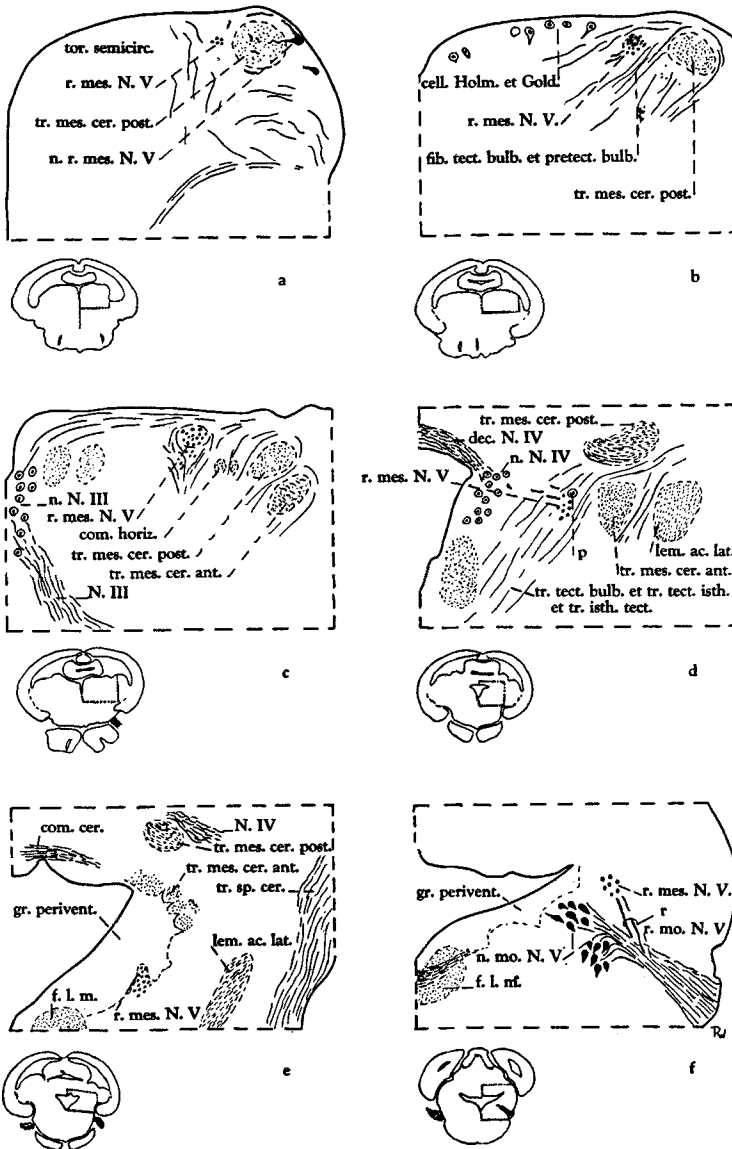


Fig. 8 A series of transverse sections through the midbrain and medulla oblongata of the trout to show the course of the mesencephalic root of the trigeminal. *Salmo salar* sebago. Chrome silver preparations. $\times 22$.

caudally across the dorsal aspect of the tractus mesencephalo-cerebellaris posterior while those lying under the ependyme next to that tract pass medialward through it. Cells lying under the ependyme of the lateral surface of the torus send their processes medialward, ventral to the tractus mesencephalo-cerebellaris posterior. The fibers of these main streams converge to form a bundle medial to the tractus mesencephalo-cerebellaris posterior. The formation of the root is illustrated in figure 8a. The nucleus of the mesencephalic root in the carp is only poorly shown in the material studied. The number of cells impregnated by the silver stain is so small that it is possible that there are present many more which did not take the stain. Those seen indicate a distribution similar to that of the trout.

II. Fiber connections of the trigeminal centers

a. Root fibers

1. *The sensory root fibers* (figs. 6, 7, 11). The sensory portion of the trigeminal nerve of the trout and the carp constitutes the caudoventral portion of the nerve and is almost exclusively descending. In the trout a few sensory root fibers pass in toward the ventricle in a course parallel to but dorsolateral to the motor root to terminate among differentiated cells of the periventricular gray. This cannot be established in the carp and in both forms all other fibers turn caudad as the descending root of the trigeminal.

The general relations of the descending root are essentially the same in both the trout and the carp, and since the carp preparations show these relations much more clearly, although perhaps somewhat exaggeratedly due to the great elaboration of the gustatory complex in this form, the course of the root in the carp will be described. Variations from the pattern seen here will be noted for the trout.

The fibers forming the descending root enter the medulla oblongata while passing caudally, dorsally, and medially and turn caudally along the dorsolateral aspect of the secondary

gustatory tract. At the level of the facial roots, the motor root of that nerve passes along its dorsolateral curvature toward the ventricle in the carp, but penetrates between the descending root of the trigeminal and the secondary gustatory tract in the trout. Contrarily, the motor root of the glossopharyngeal nerve penetrates between the two tracts in the carp but passes toward the ventricle along the dorsolateral aspect of the descending root of the trigeminal in the trout. With the formation of the descending secondary gustatory tract of the facial in the carp, this tract becomes interposed between the secondary gustatory tract and the descending root of the trigeminal and as the large vagal lobes appear there is a shift of the descending root down along the lateral aspect of the secondary gustatory tract. Lateral line vagus fibers pass dorsally between the descending root and the descending secondary gustatory tract of the facial. In the region of the caudal third of the vagal lobe, the sensory root of the vagus sends contributions to the descending root of the trigeminal nerve which traverse the intervening motor root of the vagus. These contributions could not be established with certainty in the trout. As the spinal cord is reached, the descending root of the trigeminal rises rapidly dorsally along the lateral wall of the cord, having sensory vagal roots rising to the dorsal funiculus on its lateral aspect, and the descending secondary gustatory tract of the facial dorsal and medial to it. It terminates in the medial funicular nucleus of the same side directly and in the same nucleus of the opposite side after crossing in the commissura infima Halleri. Through this nucleus correlation of trigeminal tactile impulses with tactile impulses ascending to it from spinal nerves is effected. The nucleus also receives the descending secondary gustatory tract of the facial nerve and thus, as Herrick ('08) pointed out, effects correlation of the tactile and gustatory sensations from that area to which the trigeminal nerve supplies tactile nerve endings.

Fibers from the descending root of the trigeminal join entering rootlets of the vagus and ascend with them into the vagal lobe. In the carp, where the vagal lobe is much elaborated, these fibers appear to run with a motor root while, in the trout, a common rootlet of the vagus passes through the descending root of the trigeminal and receives its contribution. This connection affords another possibility of correlation between tactile and gustatory sensibilities. Herrick ('08) noted that the nucleus intermedius vagi seems to lie in the motor layer of the vagal lobe.

In the carp, there is a clear differentiation of the descending root into an ophthalmic and a maxillomandibular division along the lines suggested by van Valkenburg ('11 a). The more cephalically entering fibers of the sensory root maintain a position medially or ventromedially in the descending root and extend farther caudalward to their termination and so are designated the ophthalmic ramus (fig. 6). The more caudally entering fibers lie either laterally or dorsolaterally in the descending root, and, rising dorsally to the medial funicular nucleus, terminate there more anteriorly than do the fibers of the ophthalmic division. In the silver preparations studied, the ophthalmic division is light staining while the maxillomandibular division exhibits a darker staining reaction and is more dense. These relations of density and staining reaction are the reverse of that reported by van Valkenburg ('11 a) in Weigert preparations of *Lophius*.

In the trout, the ventral portion of the root, the ophthalmic division, extends more caudally to its termination but is clearly composed of the more caudally entering fibers of the sensory root. Sagittal sections show quite distinctly that the cephalically entering fibers turn caudad as the dorsal portion of the descending root, with the caudally entering fibers ventral to them. Since the position in the descending root and the region of termination in the trout accord with the usual classification of divisions of the root, it is assumed, in the absence of verification from whole head sections, that there has been a twist of the nerve before its entrance placing

fibers from the cephalic regions of the head caudal in the nerve. No direct root fibers of the trigeminal nerve to the cerebellum can be demonstrated in either the trout or the carp material studied.

2. *The motor root fibers* (figs. 6, 7, 8f). The motor root in teleosts enters as the dorsal and cephalic portion of the common trigeminal root. The motor fibers pass dorsomedially along the dorsal aspect of the secondary gustatory tract and distribute to the motor nucleus in two bundles corresponding to the two portions of the nucleus.

In the trout the cephalic portion of the motor root (fig. 8f) enters the rostral portion of the nucleus in its caudal portion and its fibers pass forward in the field of the nucleus to find their cells of origin. The caudal bundle distributes to the caudal nucleus, entering its field a little ahead of the middle of its extent, and the fibers pass forward and backward to reach their cells of origin.

In the carp, the cephalic bundle (fig. 6) sends its fibers over the top of the secondary gustatory tract and downward and forward to distribute to both parts of the rostral portion of the nucleus. Turning down the medial side of the secondary gustatory tract, most of the fibers pass straight ventrally into the ventral part of the rostral portion of the nucleus while a small number of fibers, after passing halfway down the side of the secondary gustatory tract turn sharply dorsomedially and pass up to the dorsal part of the rostral portion of the nucleus close under the ependyme. Somewhat caudad of the cephalic bundle, the caudal bundle (fig. 7) of the motor root passes straight down the medial side of the secondary gustatory tract to its cells of origin in the caudal portion of the motor trigeminal nucleus.

Like the cephalic bundle, the caudal bundle also sends its cephalic fibers dorsomedially from a position halfway down the medial side of the secondary gustatory tract. This group of fibers composes the crossed component of the motor trigeminal root and its course is illustrated in figure 7. Having turned sharply dorsomedially without entering the cells of

the caudal portion of the nucleus, these fibers pass directly toward the ependyme lateral to and above the medial longitudinal fasciculus, are traceable under the ependyme dorsal to the medial longitudinal fasciculus to the midline, and then pass ventrally at the raphé. Coursing ventral to the contralateral medial longitudinal fasciculus they continue in a lateroventral direction to enter the cephalic end of the caudal portion of the motor trigeminal nucleus of the opposite side. The entire course may be seen in one section though in broken segments in the midline region, and the preparations leave no reasonable doubt that there is a partial decussation of motor fibers in the trigeminal nerve in the carp. That such a crossed component of the motor root of the trigeminal is present in the trout is indicated by broken segments of root fibers found along the course described for the carp, but the complete course cannot be established with certainty for this form.

3. *The mesencephalic root of the trigeminal* (fig. 8). The mesencephalic root in the trout appears as an organized bundle at the caudal end of the much scattered mesencephalic nucleus (fig. 8a) by virtue of convergence of the cell processes to a position medial to the tractus mesencephalo-cerebellaris posterior. It is separated from that tract by efferent fibers from the tectum, and perhaps from the pretectal nucleus, here running ventrally from the dorsal surface of the torus. The medially converging fibers turn caudalward just ahead of the level of figure 8b. In this figure a few fibers may be seen leaving the bundle, passing from its ventral portion ventrally and then medially and appearing to run with efferent fibers from the tectum destined for the oculomotor nucleus, which lies just caudad of this level. Mesencephalic fibers cannot be traced with complete certainty to the oculomotor nucleus in the material studied, but the fibers mentioned appear to be of that nature.

At this cephalic level, the bundle lies close under the ependyme just lateral and ventral to the most lateral of the large cells noted in this region by Goldstein ('05) and Holmgren

('20) (fig. 6b). In the preparations studied it is bounded medially and laterally by heavy fiber tracts running ventrally from the dorsal surface of the torus semicircularis. The bundle is broken up by pretecto-bulbar fibers passing toward the midline and, increasingly so caudally, by heavy, ventrally running bundles so that the fibers are contained in small cross-cut fascicles. The mesencephalic fibers as seen under high power are characterized as large, round, cross-cut fibers which take the silver stain quite heavily, as do also the cell bodies. Their diameter is equalled by relatively few other fibers in the field. The single fibers often appear in small shrinkage spaces. The bundles pass caudally and somewhat medially so that they diverge somewhat from the tractus mesencephalo-cerebellaris posterior but otherwise keep the same relations, appearing as an oval group close up under the ependyme as shown in figure 8c. In this position they pass directly caudalward though much broken up by heavy bands of fibers traversing the field. They are separated from the tractus mesencephalo-cerebellaris posterior by several cross-cut bundles of the commissura horizontalis (fig. 8c). In the region just cephalad of the trochlear nucleus, there is a very pronounced streaming of fibers from the dorsal surface of the torus semicircularis and the nucleus lateralis valvulae diagonally to the ventral midline; and under the influence of this streaming, the fibers of the mesencephalic root also incline medially and slightly ventrally and are cut in oblique segments but again straighten out before progressing very far. The streaming fibers seem to include tecto-bulbar, tecto-isthmal and isthmo-tectal bundles (fig. 8d) as well as connections to the nucleus lateralis valvulae. Caudad to this streaming, the fascicles of the mesencephalic root seem much reduced, but this is because mesencephalic fibers have been running in company with bundles of other significance which have now passed ventromedially to the tegmental decussations, not because any mesencephalic fibers pass down to the decussations—at least so far as can be seen.

At the level of the cephalic portion of the trochlear nucleus (fig. 8d), the fascicles of the mesencephalic root are in relation ventrolaterally with the tractus mesencephalo-cerebellaris anterior and dorsolaterally with the tractus mesencephalo-cerebellaris posterior, the fibers of which are now beginning to turn medially and dorsally toward the valvula. Lateral to the tractus mesencephalo-cerebellaris anterior lies the acustico-lateral lemniscus. Medial to the mesencephalic fibers a few bundles still stream toward the ventral raphé to enter the tegmental decussations and separate them from the medial longitudinal fasciculus. At the level of entrance of the decussated trochlear root into its nucleus, there are indications in the material studied of mesencephalic fibers passing to that root. In figure 8d, small segments of fibers are to be seen passing dorsomedially and caudally to the region of the root, and a few fibers definitely turn abruptly dorso-medially from the mesencephalic fascicles to join in this ascent to the trochlear root. Though this connection cannot be definitely and obviously established in the material, there are very strong indications of it.

The remaining fibers of the mesencephalic root continue their caudal course, maintaining the same general relationships in the field, although the tractus mesencephalo-cerebellaris posterior continues to turn medially and enters the valvula in close relation to the trochlear root (fig. 8e). Caudal to this level the ventricle widens out, and a thick layer of periventricular gray appears. The acustico-lateral lemniscus now passes more rapidly ventromedially. The widening and flattening of the ventricle, with the replacement of the trochlear nucleus by periventricular gray, results in a lateral displacement of the ventricle wall so that the mesencephalic fibers now are in immediate relation medially with the edge of the periventricular gray, and the tractus mesencephalo-cerebellaris anterior lies above and lateral to them, opposite to the lateral recess of the ventricle. This relationship is clearly seen in figure 8e. The relations remain the same until the level of the trigeminal root is reached. There is

some further widening and flattening of the ventricle with the result that the periventricular gray becomes reduced in width and the tractus mesencephalo-cerebellaris anterior comes to lie against the lateral angle of the ventricle, but the mesencephalic fibers remain close against the periventricular gray. Approaching the level of entrance of the trigeminal root, the fibers tilt slightly laterally in preparation for their emergence; and as the root penetrates through the tegmentum, the mesencephalic fibers are seen to pass into it, the fibers lying in the more dorsal and cephalic part of the motor root. The entrance of the fibers into the motor root is shown in figure 8f.

The above account is based on a study of the landlocked salmon trout, *Salmo salar sebago*, but the behavior and relationships of the tract are the same for the rainbow trout, *Salmo gairdneri iridens*. In neither form were the collaterals from the mesencephalic root to the cells of the motor nucleus of the trigeminal seen. The mesencephalic root of the trigeminal in the carp maintains the same general relationships but its emergence cannot be established clearly in the material studied.

b. Secondary connections

1. *The internuclear connections* (figs. 6, 7, 11). Apart from reflex connections, the main internuclear connections of the motor trigeminal nucleus and the nucleus of the descending root of the trigeminal are established by fibers which pass into the substantia reticularis ventralis associated with the secondary gustatory tract. Into this reticular region the tecto-bulbar tract undoubtedly sends some of its fibers and a portion of the fibers of the lobo-bulbar tract end here. Thus the motor trigeminal nucleus may come under the influence here of gustatory impulses and of impulses from higher centers. The dendrites of the motor cells (fig. 6, 7, 11) end here in great number but it has not been possible to confirm Ariëns Kappers' ('10) statement that the dendrites of the rostral portion of the motor trigeminal nucleus also pass

dorsally to come in contact with the reticular substance of the secondary gustatory nucleus in the carp.

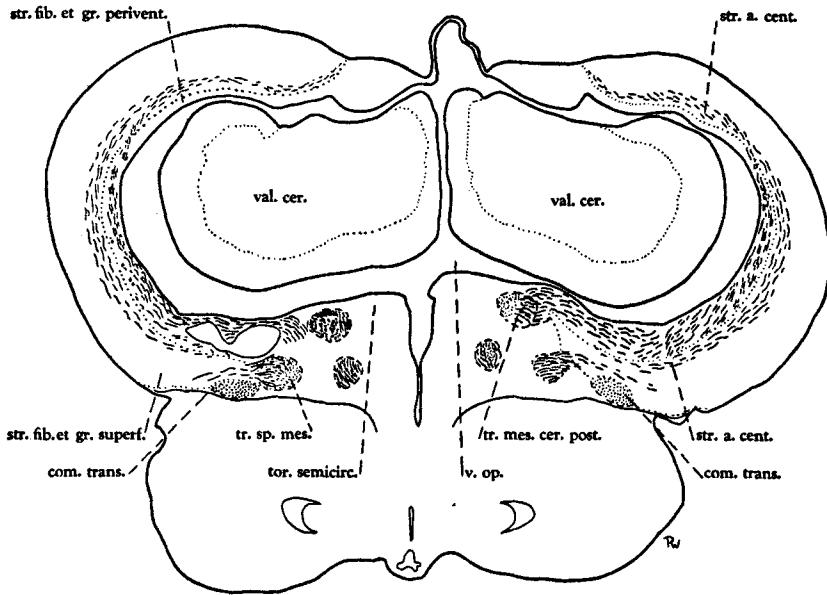
2. *The bulbar lemniscus with special reference to the spino-mesencephalic and trigemino-mesencephalic tracts* (figs. 6, 7, 9, 10, 11). There will be no attempt to give a complete discussion of the bulbar lemniscus in this report, for the course and relations of this system are well known, but the carp material here used is helpful with respect to the question of whether or not spino-tectal or spino-mesencephalic fibers are definitely demonstrable in connection with the rostral end of the tecto-bulbar and tecto-spinal tract. Wallenberg ('07 a) performed degeneration experiments on selachians and teleosts, and the afferent path to the tectum was thereby indicated, but though his figures show the fibers directed toward both the superficial and deep layers of the tectum, they were not traceable quite that far. Burr ('28) noted for *Orthogoriscus mola* that mingled among the coarse fibers of the tecto-bulbar and spinal tract are many fine fibers which he inferred were probably ascending fibers of the spino-tectal tract running from spinal cord to the optic lobes. That such is indeed the case may be demonstrated in the carp material studied. The tilt of sectioning of this material was very favorable for this purpose.

If the tecto-bulbar and spinal tract is examined in the region of the crossing of its ventral tecto-spinal component, it is impossible to obtain any hint of the direction of conduction of the fibers; the complex is a mass of longitudinally and obliquely cut fibers, all of which appear to emanate from the deep layer of the tectum. However, passing forward from this point, a more cross-cut bundle emerges, lying immediately dorsal to the superficial layer of the tectum and to the commissura transversa. This bundle passes forward, cross-cut in transverse section, and as the ventral portion of the tectum rises dorsally and medially to conform to its cephalic curvature, the bundle appears to be engulfed by the superficial layer and its fibers may be definitely traced into that layer. Figure 9 illustrates this. It shows the spino-mesencephalic tract just as the superficial layer of the tectum

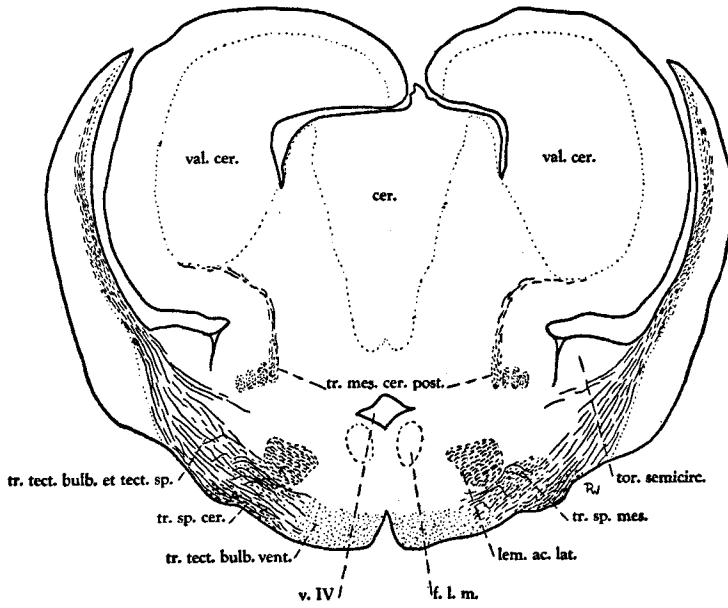
begins to encroach upon it. Cephalically the superficial layer of the tectum continues to extend itself medially and dorsally as far as the tractus mesencephalo-cerebellaris posterior and ultimately almost to the midline. Thus, at its entrance into the superficial layers of the tectum, the spino-mesencephalic tract (fig. 9) lies dorsomedial to the commissura transversa and ventrolateral to the tractus mesencephalo-cerebellaris posterior, the three tracts lying almost in a straight line in our cross-sectional preparations, with the spino-mesencephalic fibers entering the tectum slightly caudal to the entrance of the afferent fibers of the tractus mesencephalo-cerebellaris posterior.

As noted, the spino-mesencephalic fibers are very much intermingled throughout their course caudally with the fibers of the tecto-bulbar and spinal tracts, both crossed and uncrossed, and with those of the spino-cerebellar tract. The descending path is cut quite longitudinally, and its entire extent may be made out in one section although the individual fibers do not, of course, describe the whole course in the section, and it is quite impossible, except very generally, to separate the spino-mesencephalic fibers from the whole complex. Fibers may be seen (fig. 10) passing all the way from the tectum to the ventral tegmental region of the medulla oblongata and into the space occupied by the spino-mesencephalic tract, just lateral and ventral to the bulbar lemniscus. To be sure, only efferent fibers are leaving the tectum this far caudad, but the individual fibers are not cut through their entire length, and only those passing into the ventral tegmental field include spino-mesencephalic fibers (fig. 10), the majority of them being fibers of the uncrossed tecto-spinal tract. Caudally the secondary gustatory tract passes out laterally and ventrally from the 'Rindenknoten' and swings out over and outside of the spino-mesencephalic bundle thus bringing that tract ventromedial to it, with the

Figs. 9, 10 Two transverse sections through the midbrain of the carp. Figure 9 shows the entrance of the spino-mesencephalic tract into the afferent layer of the optic tectum. Figure 10 is drawn through the caudal portion of the torus semicircularis. *Cyprinus carpio*. Chrome silver preparations. $\times 10$.



9



10

spino-cerebellar bundle (fig. 6) passing dorsally to attain the cerebellum external to both of them. As the secondary gustatory tract dips ventrally, the root of the trigeminal nerve enters through the spino-cerebellar fibers and takes its position on the dorsal and dorsolateral aspects of the secondary gustatory tract (fig. 6).

The course of the spino-mesencephalic and tecto-spinal complex has been considered in detail in the preceding account because of its intimate relation with the secondary ascending systems from sensory areas of the brain stem, such as the gustatory and trigeminal centers. These secondary paths from the gustatory and trigeminal regions are sometimes grouped within a bulbar lemniscus, or they may be considered as the more medial bulbo-mesencephalic and bulbo-tectal components of a common spino- et bulbo-mesencephalic system. The present account is concerned primarily with the trigemino-tectal and mesencephalic portion of this system. The fibers constituting this component may be seen in both the trout and the carp material. Due to a better differential staining of the carp than of the trout material, the sections of carp brain were used particularly in following these secondary ascending trigeminal fibers. In this material, due to the elaboration of the secondary gustatory tract, the phylogenetically older descending root of the trigeminal is pushed dorsolaterally, and the arch of the secondary fibers into the spino-mesencephalic tract is more pronounced. These fibers (fig. 11) are seen leaving the nucleus of the descending root of the trigeminal from the dorsal and medial aspects of this root, passing medially to clear the gustatory bundle and then turning sharply ventralward. Reaching the ventral reticular region, the fibers turn medially to cross the raphé in the ventral field. Their course to the spino-mesencephalic tract of the opposite side describes a gentle curve ventrolaterally, and they turn forward on the medial side of that tract. A large part of the course may be seen in one section, as figure 11 indicates, but the path across the raphé and beyond is made out only by the presence of small broken fascicles.

The connection is, further, a small one, and the number of fibers passing from the trigeminal is minimal in any one field, the majority of the crossing fibers being secondary connections to the acustico-lateral lemniscus. That part of the connection visible in the trout material, the proximal portion with respect to the descending root of the trigeminal, describes the same course, but it is smoother because of the fact that the secondary gustatory tract is not so large in this form.

3. *The trigemino-cerebellar connections* (fig. 11). Another group of ascending fibers quite similar in nature to those joining the spino-mesencephalic tract are the secondary fibers from the nucleus of the descending root of the trigeminal which compose the crossed trigemino-cerebellar tract. These secondary fibers (fig. 11) leave the nucleus of the descending root at variable distances caudad of the level of entrance of the nerve, forming small fascicles which arch over the dorsal surface of the gustatory tract, descend ventrally, and then, turning medially, cross the raphé and pass in a gentle curve over the spino-mesencephalic tract of the opposite side to the ventral aspect of the secondary gustatory tract. There they join other fibers (fig. 11) destined for the cerebellum and pass dorsalward and then rostralward with the spino-cerebellar tract to the cerebellum. The course of the trigemino-cerebellar fibers to the contralateral side is quite similar to that of the trigemino-mesencephalic fibers. The former, however, do not swing so far ventralward, and their proximal path is nearer the ventricle. Further, they cross the raphé about midway of its dorsoventral extent, thus somewhat more dorsally than the trigemino-mesencephalic fibers, and cross the ventral reticular region of the opposite side somewhat more dorsally placed. Fibers of this sort do not form any large, well-defined bundle, but may be seen as small fascicles traversing the tegmentum as far back as the entrance of the acustico-lateral complex and somewhat beyond. The course and relations of these fibers may be seen in figure 11.

A connection to the spino-cerebellar tract of the homolateral side may be seen in the preparations studied. The course of the secondary fibers here is, as before, an arch over the dorsal surface of the gustatory tract and a curved path along its medial surface to join the spino-cerebellar tract on its ventral aspect. Figure 11 will illustrate this connection. These connections cannot be made out adequately in the trout material studied, but there are suggestions of their presence.

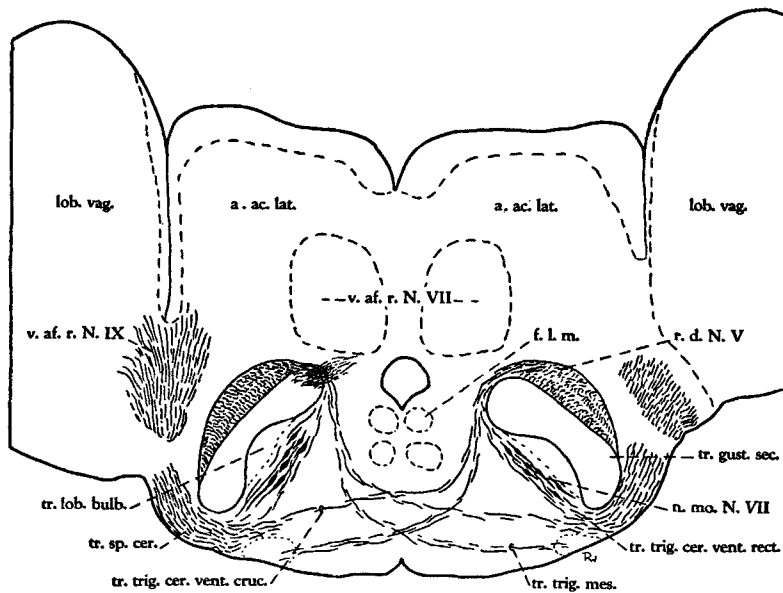


Fig. 11 Transverse section of the medulla oblongata of the carp at the level of the motor facial nucleus showing particularly the crossed and uncrossed trigemino-cerebellar tracts. *Cyprinus carpio*. Chrome silver preparation. $\times 14$.

As noted in connection with the descending root of the trigeminal, the teleost material available does not show any direct trigeminal root fibers passing to the cerebellum.

4. *The cerebello-motorius fibers* (figs. 6, 7). The cerebello-motorius fibers are fine, black fibers which pass caudally from the primordial cerebellar nuclei immediately under the ependyme of the ventricle. The course caudad also inclines ventrally around the ventricle to reach its floor. The fibers can

be seen making connection with motor cells of the dorsal part of the rostral portion of the motor trigeminal nucleus just under the ependyme in figure 6, and other fibers pass ventrolaterally from the lateral recess of the ventricle to make connection with the more ventrally located cells of the nucleus throughout its extent. The termination seems to be pericellular in nature. Burr ('28) found the tractus cerebello-motorius passing caudad in the medial longitudinal fasciculus in *Orthogoriscus mola*, a relationship we cannot confirm in our material.

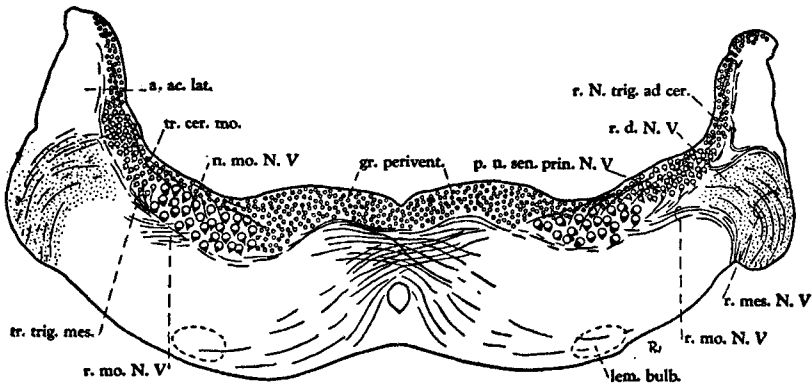
There is a suggestion of a crossed cerebello-motorius connection in the carp material, represented by fine, black fibers, which continue medialward from the region above the motor trigeminal nucleus. They remain close under the ependyme and pass toward the midline over the dorsal surface of the medial longitudinal fasciculus, but their complete course to the contralateral motor nucleus cannot be established in the material available for study. Figure 6 shows the indicated fibers.

D. Amphibians (Necturus, Amblystoma, Siren lacertina, Rana catesbiana)

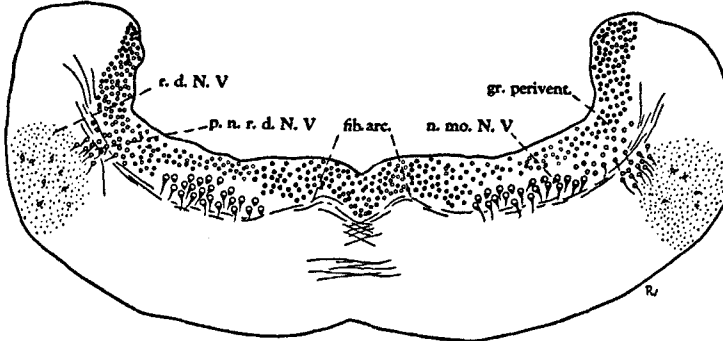
I. Nuclear gray associated with the trigeminal roots in tailed amphibians

1. *The chief sensory nucleus of the trigeminal* (fig. 12). The available material of *Necturus*, *Amblystoma*, and *Siren* shows that there are cells of the dorsal subependymal gray immediately dorsolateral to the sulcus limitans which have undergone differentiation into a chief sensory nucleus of the trigeminal (fig. 12). There is only an indistinct separation of these cells from the nearby gray, but the cells are slightly larger, and their ventrally running processes are somewhat more robust. The cells of the nucleus project a little ventral from the gray zone and lie adjacent to the dorsal aspect of the descending root of the trigeminal. A few sensory trigeminal root fibers (fig. 12) pass into the nucleus, and dendrites of the cells of the nucleus pass ventrally into the

descending root to lie in relation with its fibers. The nucleus in urodeles appears to be quite primitive, there being only slight differentiation of the subependymal gray to form it. It is found at the level of entrance of the trigeminal roots



12



13

Figs. 12, 13 Two transverse sections of the medulla oblongata of tailed Amphibia. Figure 12 drawn through the motor trigeminal nucleus caudal to the entrance of the nerve roots. *Necturus*. Chrome silver preparation. $\times 28$. Figure 13 drawn through the primordial nucleus of the descending root of the trigeminal. *Siren lacertina*. Toluidin blue preparation. $\times 22$.

and slightly caudally and is believed to be the same cell group designated by Herrick ('30) as the superior trigeminal nucleus. Osborn (1888), Kingsbury (1895), and Norris ('13) also noted this association of cells with the sensory root of the trigeminal at the level of entrance of the root.

2. *The nucleus of the descending root of the trigeminal* (fig. 13). The nucleus of the descending root of the trigeminal is extremely sparse in the urodeles studied. It consists of a few small, round, and oval cells (fig. 13) interspersed between the fibers of the descending root, and the configuration of the gray column everywhere conforms to that of the root itself. It appears cephalically at the level of entrance of the trigeminal root and extends caudalward as far as the available material allows tracing of the root; that is, to the upper spinal cord region.

In addition to the differentiation of periventricular gray resulting in the primordium of the chief sensory nucleus, there are here and there throughout the whole caudal extent of the descending root of the trigeminal nerve, occasional ventrally-lying, small and medium sized cells of the periventricular gray (fig. 13) which send their ventrally directed dendrites into the descending root. Herrick ('30) noted these cells especially in the region of the acoustic nerve and referred to them as constituting the incipience of the sensory trigeminal nucleus. He noted a gathering of larger cells in the vagus region and a preponderance of smaller ones at the level of the calamus scriptorius and beyond. This association of cells of the periventricular gray (fig. 13) with the fibers of the descending root of the trigeminal may, in view of the extreme sparseness of the gray contained within that root, foreshadow the more differentiated condition in which the nucleus of the descending root of the trigeminal lies medial to the root, rather than within the meshes of its fibers.

3. *The motor trigeminal nucleus* (figs. 12, 13). The motor trigeminal nucleus of urodeles is a differentiation of the thick layer of periventricular gray of the dorsum of the medulla oblongata. The almost spherical form of the latter is modified into a larger carrot shape through the elaboration of a stout, ventrally running dendrite. The nucleus is large and spherical and almost completely fills the dorsally-directed bulbous end of the cell. The motor trigeminal nucleus (figs. 12, 13) lies in the lower portion of the cell zone of the medulla

oblongata under a slight trigeminal eminence just ventromedial to the rather indefinite sulcus limitans. The column begins cephalically nearly at the level of entrance of the sensory root and anterior to the level of entrance of the motor root, and extends caudally to about the level of entrance of the sensory root of the facial nerve. These anterior and posterior limits are but poorly defined, however, for near these limits the differentiation between the cells of the motor trigeminal nucleus and the undifferentiated periventricular gray is very slight. The motor trigeminal nucleus is entirely dorsal in position but shows a slight separation into a rostral and a caudal portion, the caudal portion lying somewhat more medially. There is not a true separation, for the nucleus is everywhere continuous, but there is a middle region in its extent where the nucleus is represented by only a few cells. Herrick ('30) noted this separation in *Necturus* and ventured the supposition that "it is probably a neurobiotic effect, the upper part serving reflex movements of the jaws excited through the tecto-bulbar tract and the dorsal tegmental fascicles and the lower part serving similar reflexes excited through the fasciculus solitarius and other ascending systems of fibers."

4. *The nucleus of the mesencephalic root of the trigeminal.* The cells constituting the mesencephalic nucleus of the trigeminal are scattered throughout most of the extent of the tectum, though not in the most cephalic levels. They appear anywhere in the dorsal wall of the optic ventricle, more abundantly medially and in the outer cell layer of the stratum griseum, although a few lie against the inner wall of the ventricle. The cells are larger than the other cells of the tectal gray, which are quite uniform in size, but they do not attain the size characteristic of the mesencephalic nucleus in more highly specialized vertebrates. In silver preparations, they show the dense impregnation characteristic of cells of the mesencephalic nucleus everywhere. A certain amount of regional condensation of the cells at the levels of the oculomotor and trochlear nerves and in the caudal end of the

tectum, as noted by Herrick ('30), is apparent in the preparations used in this study, but it is not marked. The main process of the cell passes, for the most part, directly dorsally into the white matter adjacent to the tectal gray, although in the cephalic portion of the nucleus, the processes pass more dorsolaterally. They combine to form fascicles of heavily medullated fibers which pass caudally, ventrally, and laterally to form the mesencephalic root of the trigeminal nerve.

II. Fiber connections of the trigeminal centers in tailed amphibians

a. Root fibers

1. *The sensory root fibers* (figs. 12, 13). The trigeminal nerve of urodeles enters the medulla oblongata as a single structure but immediately upon entering breaks up into sensory, motor, and mesencephalic roots. The sensory root forms the more dorsal portion of the common root. The bulk of it forms the descending root of the trigeminal (figs. 12, 13), which passes directly caudad after its entrance. Mingled with the more cephalically entering fibers are numerous mesencephalic fibers (fig. 12) which pass dorsally and caudally to a position immediately beneath the cells of the sensory trigeminal nucleus and then turn forward. A few caudally entering bundles pass quite dorsally, giving off root fibers (fig. 12) into the acustico-lateral area and then discharging into the chief sensory nucleus. Those fibers entering the acustico-lateral area appear to represent the direct root fibers of the trigeminal to the cerebellum which are better differentiated in higher forms. The material available does not allow a complete tracing of this path but does suggest this conclusion. These fibers are not fine collaterals, as found by Herrick ('30) and designated by him an ascending trigeminal ramus, but are coarse and typical root fibers in appearance. No fine-fibered collateral ascending ramus of the trigeminal is demonstrable in our material.

The descending root (figs. 12, 13) lies superficially in the ventrolateral portion of the medulla oblongata and passes directly caudad in this position. The sensory roots of the facial enter dorsal to it and the motor facial root penetrates through its ventral portion in its course toward the ventricle. A general somatic afferent component of the facial has been described by Norris ('13) entering the dorsal portion of the descending root of the trigeminal. The silver material of Necturus available, sectioned frontally, shows clearly that a few fibers from the caudally directed facial root join the descending root of the trigeminal and run straight caudad in its dorsal peripheral portion. Herrick ('30) noted a general cutaneous component of the glossopharyngeal nerve passing into the descending root of the trigeminal in Necturus. This cannot be demonstrated in the material studied. Such a contribution from the vagus is clearly apparent. Numerous fascicles of this nerve penetrate through the descending root and some turn caudad in the latter.

The descending root rises to the dorsolateral region of the spinal cord and is in association there with a group of cells of the subependymal gray, which shows some separation from the general gray mass and lies ventromedial to the descending root. The roots of the two sides are in association with the commissura infima Halleri and make numerous connections with ventral horn cells as well as giving rise to secondary fibers which cross into contralateral ascending systems.

2. *The motor root fibers* (fig. 12). The motor root constitutes the ventromedial portion of the entering nerve and courses into its cells of origin in a dorsomedial and caudal direction. It is separated into two bundles corresponding to the two divisions of the motor trigeminal nucleus. The cephalic bundle has less caudal inclination in its course than the caudal bundle but passes directly dorsomedially (fig. 12) into the rostral portion of the nucleus, distributing forward and backward to its cells. Caudal to it lies the caudal bundle which, though only slightly separated from the cephalic bundle, inclines more caudally in its dorsomedial course to

the caudal portion of the nucleus. Entering this portion of the nucleus at its anterior end the fibers pass backward within the field of the nucleus to the more caudally lying cells. No crossed motor trigeminal root fibers can be demonstrated in the urodele material available for study.

3. *The mesencephalic root of the trigeminal* (fig. 12). The mesencephalic root of the trigeminal has been described for *Necturus* by Osborn (1888), Kingsbury (1895), and Johnston ('05 a); for *Siren lacertina* by Norris ('13); and for larval *Amblystoma* by Herrick ('14). It is formed by the large processes from the cells of the nucleus of the mesencephalic root, which, having passed through the tectal gray, turn caudally and join to form fascicles of the mesencephalic root. These fascicles course ventrolaterally along the border of the tectal gray in their caudal course and run along the base of the cerebellum where that structure joins the tectum. Mesencephalic fibers from the posterior tectal region pass ventrally, and somewhat anteriorly, to join those from the rest of the tectum where the tectum and the cerebellum unite. The former are seen lateral to the latter in cross-sectional views and constitute the lateral part of the mesencephalic root of Johnston and of others. These fibers are seen to mingle somewhat with fibers of the spinal and bulbar lemnisci systems, and this mingling has caused much confusion in the literature. The material used in this study indicates that there are actually no fibers of other functional significance in the mesencephalic root but simply such a close apposition of the fibers as they enter the tectum that it is difficult to separate them with complete certainty. The preparations show that the fibers of this lateral part of the mesencephalic root arise from the cells of the mesencephalic nucleus of the posterior portion of the tectum. The medial and lateral parts of the root combine and course straight caudad close under the gray zone of the medulla oblongata; and, at the level of entrance of the trigeminal nerve, the mesencephalic root lies dorsomedial to the entering nerve. The fibers (fig. 12) turn sharply laterally as the nerve enters, and pass out in small

fascicles in a somewhat arched course, laterally and ventrally, among the fibers of the sensory root of the trigeminal.

Osborn (1888), Kingsbury (1895), Norris ('13), and Herrick ('14) noted a coarse-fibered tract which passed caudad as far as the roots of the facial nerve and the latter two observers interpreted these fibers as a descending mesencephalic ramus formed as the product of bifurcation of the mesencephalic root of the trigeminal nerve. A careful study of the available material—silver preparations cut in cross, sagittal, and frontal planes—yields little, if any, positive evidence for a descending mesencephalic ramus. Some of the fascicles pass caudad of the point of emergence of the main body of the mesencephalic root to emerge with the caudally placed fibers of the sensory root, just anterior to the point of emergence of the motor root. This is quite clearly seen in sagittal and frontal sections. It is impossible to trace any fibers continuing caudad of this point, and the indication of the available material is that all mesencephalic root fibers pass out with the trigeminal nerve. However, the possibility of a descending ramus represented by the products of bifurcation of the entering mesencephalic root fibers, as suggested by Herrick ('14), cannot be ruled out by the evidence presented from our material.

b. Secondary connections

1. *The internuclear connections.* The internuclear connections noted for the urodele trigeminal complex are briefly as follows. The cells of the motor trigeminal nucleus send their stout, ventrally-directed dendrites into the substantia reticularis ventralis where they may receive impulses from higher centers and where they may also receive stimulation from fibers arising in the nucleus of the descending root and terminating here. The cells of the motor trigeminal nucleus also send dendrites lateralward which terminate among the cells of the primordial chief sensory nucleus at the level of entrance of the trigeminal roots.

Bindewald ('11) noted an intertrigeminal commissure in *Proteus* and *Hypogeophis* which, in the absence of a cerebellum in these forms, appeared to interconnect the trigeminal sensory nuclei. In forms possessing a cerebellum the commissure of the *decussatio veli* is more complex as noted by Norris ('13) and by Herrick ('30). The latter observer found that the myelinated cerebellar commissure of *Necturus* constitutes the intertrigeminal commissure of Bindewald and Röthig. The commissure has been identified in the urodele material studied, but its fibers gradually vanish caudally in the ventrolateral portion of the auricular lobe and cannot be definitely traced to the primordial chief sensory nucleus.

2. *The trigemino-mesencephalic and tectal component of the bulbar lemniscus* (fig. 12). Contributions from the trigeminal complex to the ascending systems of the bulbar lemniscus, the trigeminal lemniscus, are quite clear in the urodele material studied. The fibers arise from both the chief sensory nucleus and the nucleus of the descending root of the trigeminal. Those from the chief sensory nucleus (fig. 12) join the internal arcuates adjacent to the periventricular gray and follow them medially to the dorsal midline. Crossing the raphé they curve ventrolaterally and disappear into the substance of the bulbar lemniscus, the fibers ascending to the tectum and midbrain therewith. Those fibers arising from the nucleus of the descending root of the trigeminal pass to the contralateral bulbar lemniscus by several somewhat divergent courses. Some leave the descending root from its dorsomedial aspect and curve dorsally and medially to pass across the raphé in company with the decussating fibers of the acustico-lateral system. Others leave the medial aspect of the descending root of the trigeminal and pass directly medialward through the tegmentum, intermediate in position until approaching the raphé when they curve dorso-medially to cross in the ventral portion of the dorsal decussation. Their course beyond is, as before, a ventrolaterally directed curve into the bulbar lemniscus. The greater portion of the trigeminal component of the bulbar lemniscus is

formed at the level of the trigeminal nerve and somewhat caudally, although occasional fibers cross to the contralateral bulbar lemniscus throughout the caudal extent of the descending root of the trigeminal. Secondary fibers from the nucleus of the descending root of the trigeminal in its caudal reaches turn forward in the contralateral spinal lemniscus, as was noted by Herrick ('30).

3. *The trigemino-cerebellar connection.* In a form possessing such a slight development of the cerebellum, it would be useless to expect a very well-marked trigemino-cerebellar connection. Indeed, all that the material affords is a suggestion that a few of the crossing trigeminal fibers may turn forward in the spino-cerebellar tract. Arcuate fibers of intermediate position pass through this bundle, and the impression is gained from the preparations that some turn forward here after crossing, but it is an impression to which no feeling of certainty is attached.

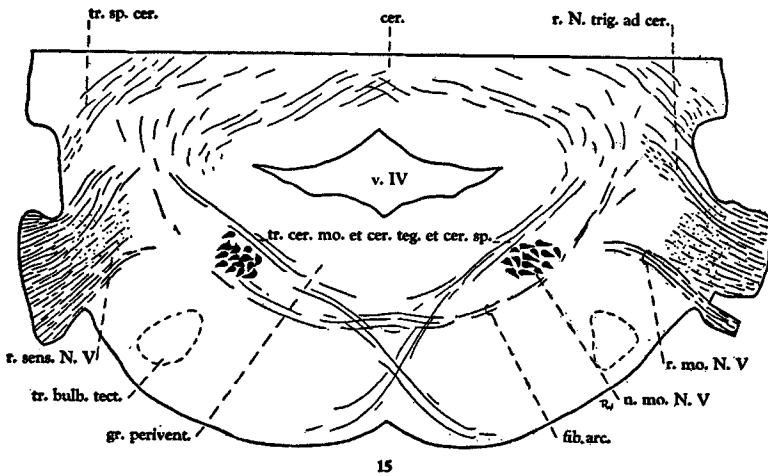
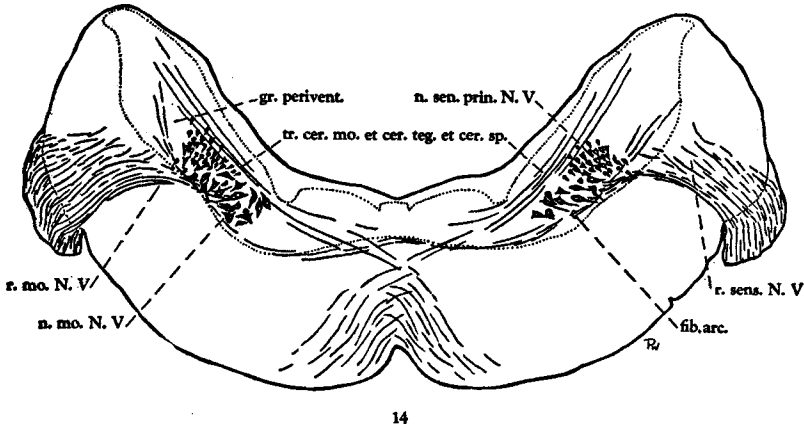
4. *The cerebello-motorius fibers* (fig. 12). Arising from cerebellar gray, fine, black fibers course caudally and medially along the floor of the ventricle. The fibers pass among the cells of the periventricular gray and mingle somewhat with the internal arcuate fibers. They pass among the cells of the motor trigeminal nucleus and appear to end in basket terminations around the dorsally directed, bulbous end of the cell body.

III. Nuclear gray associated with the trigeminal roots in tailless amphibians

1. *The chief sensory nucleus of the trigeminal* (fig. 14). As in the urodele material studied, so in the anuran preparations the periventricular gray adjacent dorsolaterally to the motor trigeminal nucleus and under the sulcus limitans has begun to differentiate into a chief sensory nucleus of the trigeminal. The cells here (fig. 14) are slightly larger, more uniformly arranged dorsoventrally and grouped into an apparent functional unit, and their main dendrites pass ventrally and ventrolaterally toward the incoming sensory root.

The nucleus gradually fades out rostrally and caudally of the root into undifferentiated periventricular gray.

2. *The nucleus of the descending root of the trigeminal* (fig. 17). In the frog, in addition to the small and medium-sized cells scattered between the fibers of the descending root,



Figs. 14, 15 Two transverse sections of the medulla oblongata of the frog at the level of entrance of the trigeminal roots. Figure 14 illustrates particularly the periventricular position of the chief sensory nucleus. Toluidin blue preparation. Figure 15 indicates the passage of direct root fibers to the cerebellum. Weigert preparation. *Rana catesbiana*. $\times 25$.

there is a group of cells (fig. 17) of similar size which maintains a position on the medial aspect of the root throughout most of its extent and on its ventral aspect when the root rises to the dorsal funiculus of the cord. The preparations studied suggest that these cells are, at least in part, contributed from the ventral portion of the periventricular gray. The cells are continuous with, and adjacent to, the nucleus parasolitarius throughout the extent of the fasciculus solitarius, and they pass over into the gray of the dorsal horn of the spinal cord. They lie medial to, and among the medial fascicles of, the descending root of the trigeminal as is typical for the nucleus of the descending root in more specialized forms. The chief sensory nucleus in the frog does not form its cephalic extension but is more definitely periventricular, thus lying medial to the cephalic end of the nucleus of the descending root at the level of entrance of the roots. However, the caudal limit of the chief sensory nucleus does correspond with the cephalic end of this medial portion of the nucleus of the descending root.

3. *The motor trigeminal nucleus* (figs. 14, 15, 16, 17). The motor trigeminal nucleus of the frog, *Rana catesbiana*, consists of a group of large, carrot-shaped cells in the lateral motor column of the medulla oblongata. It lies more deeply than is usual because of the elaboration of a thick layer of periventricular gray dorsal to it. Ariëns Kappers ('10) noted this more ventral position but emphasized the fact that there is no neurobiotactic migration involved, but that all structures that are located entirely dorsally in all animals, are displaced here by this layer of periventricular gray. There is only a very slight trigeminal eminence. The nucleus begins cephalically at the level of entrance of the sensory trigeminal root (fig. 14) and extends caudally somewhat beyond the level of the anterior limit of entrance of the afferent facial root. It is clearly separated from the efferent facial nucleus by a gap of 0.2 mm. The nucleus gives off its root (fig. 16) slightly anterior to the middle of its extent.

The motor trigeminal nucleus of the frog appears to be more differentiated and composed of larger cells than that of the urodeles examined. It consists of a rostral and a caudal portion, separated by a gap of 25 μ . The rostral portion is about twice as long and is also more extensive in width; the caudal portion occupies a slightly more medial position in the motor column. The cell characteristics are the same for both portions: there is a dorsally directed bulbous end containing a large nucleus, and a stout ventrally running dendrite.

4. *The nucleus of the mesencephalic root of the trigeminal.* The preparations available for this study were also used by Weinberg ('28) in his observations on the mesencephalic root and nothing more can be added to the account given by him. The cells of the nucleus of the mesencephalic root are found in the frontal portion of the tectum and are massed principally in its frontal third, there being relatively few cells caudad of the optic ventricle. The cells occupy the dorso-frontal and mediofrontal sectors of the wall of the optic ventricle for the most part, with a few in its lateral wall and a very few in its ventral wall, these last being found extremely frontally. The cells lie in the stratum griseum periventriculare (Huber and Crosby, '34), corresponding to the second, third and fourth layers of Cajal. They send their long straight processes toward the periphery of the tectum, and these can be observed entering the stratum album centrale. In addition, one to three short processes can be observed on many cells.

IV. Fiber connections of the trigeminal centers in tailless amphibians

a. Root fibers

1. *The sensory root fibers* (figs. 14, 15, 16). The sensory root of the trigeminal nerve divides after its entrance into an ascending and a descending ramus, and, in addition, sends a small group of fibers medially which disappear among the cells of the chief sensory nucleus (fig. 14). A short distance

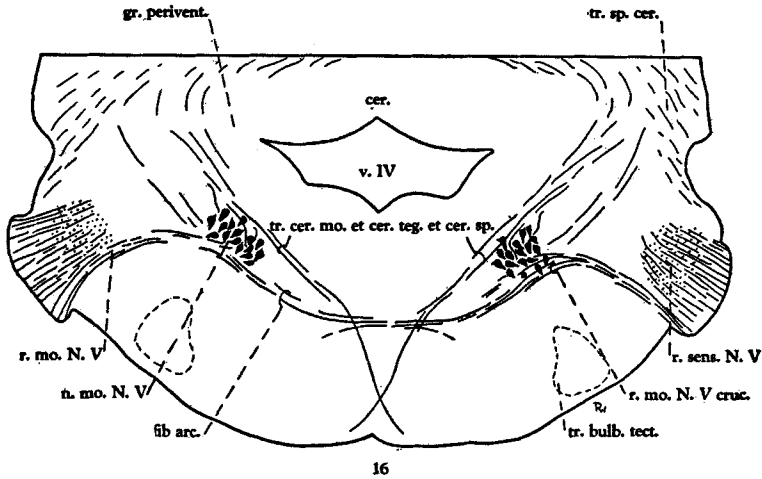
caudad the descending root is penetrated by a few fascicles of the sensory root and by the motor root of the facial nerve but there appear to be no contributions from this nerve to the descending root. The incoming sensory fibers of the glossopharyngeal and the vagus nerves also pass through the descending root to reach the fasciculus solitarius and both contribute general cutaneous fibers to the ventral portion of the descending root. The sensory root of the glossopharyngeal separates a few dorsal fascicles from the rest of the descending root which appeared to van Valkenburg ('11 a) not to rejoin the root caudally, but the material studied shows that they do rejoin the descending root after the glossopharyngeal fascicles have passed through. The caudal limit of the descending root has been found by Wallenberg ('07) to be the lumbar enlargement, part of the root first crossing at the calamus scriptorius.

An ascending ramus of the sensory root has been noted, consisting of direct trigeminal root fibers to the cerebellum (fig. 15). These fibers come out of the cephalic portion of the root and pass forward in the lateral wall of the medulla oblongata to the level of the cerebellum, joining the spinocerebellar tract in its dorsal ascent into that structure. They cannot be followed differentially from that tract.

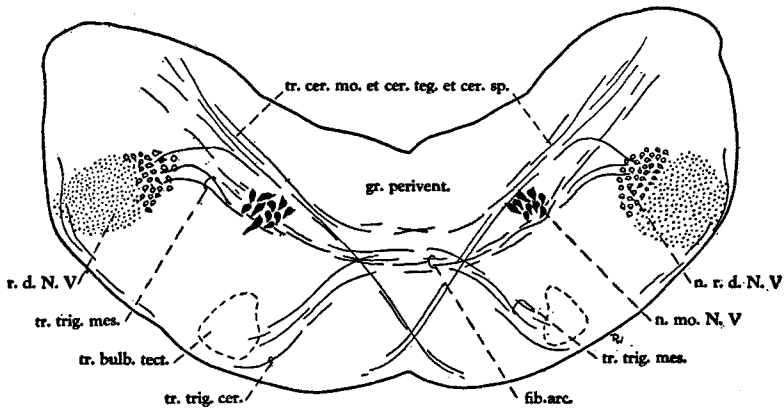
2. *The motor root fibers* (figs. 14, 15, 16). The motor root of the trigeminal nerve enters the medulla oblongata ventrally of the sensory root (fig. 15) and passes into its nucleus of origin in a curved course, dorsally and medially (fig. 16). It is composed of two parts corresponding to the two divisions of the nucleus. The rostral portion enters with only a slight inclination caudalward reaching its nucleus of origin in its caudal half. The caudal portion has a much greater caudal inclination through the tegmentum, straightening medially to distribute to the cells of the caudal part of the nucleus at its level.

There is a suggestion in the material studied of crossed motor trigeminal root fibers. These fibers (fig. 16) leave the motor root in the region of the nucleus and pass among the

decussating fibers from the acustico-lateral area to the mid-line. They cannot be traced to the motor trigeminal nucleus of the opposite side, but it is probable that that is their destination.



16



17

Figs. 16, 17 Two transverse sections of the brain stem of the frog. Figure 16 drawn at the level of the motor trigeminal nucleus just caudal to the plane of figure 15. It illustrates the crossed and uncrossed motor fibers. Figure 17 drawn from the same series but caudal to figure 16. It shows particularly the crossed ascending connections from the nucleus of the descending root of the trigeminal to the midbrain (tractus trigemino-mesencephalicus) and to the cerebellum (tractus trigemino-cerebellaris). *Rana catesbiana*. Weigert preparations. $\times 25$.

3. *The mesencephalic root of the trigeminal.* Renewed study of the material used by Weinberg ('28) allows a little more detail to be added to his account of the mesencephalic root of the trigeminal in the frog. The stout, single processes arising from the cells of the nucleus of the mesencephalic root pass laterally and ventrally around the optic ventricle as they course caudad and appear as coarse fibers lying between the stratum album centrale proper and the stratum fibrosum et griseum periventriculare. They converge caudally to form a compact bundle at the level of the torus semi-circularis, which passes caudally, ventrally, and medially along the inner aspect of the tecto-bulbar and spinal tract, and farther caudally along the inferior aspect of the nucleus isthmi. At the level of the trochlear decussation, there is a suggestion of fibers passing between the decussation and the mesencephalic root, traversing the periventricular gray medial to the nucleus isthmi. This connection cannot be established with certainty, however. Caudal to the nucleus isthmi, the mesencephalic root inclines gradually laterally so that, as the level of the trigeminal is approached, the large cross-cut ends of the fibers are seen just internal to the spinocerebellar tract. The fibers of the mesencephalic root pass into the sensory root of the trigeminal as separate fibers and in small fascicles, turning sharply laterally at the level of the root to enter it. Van Valkenburg ('11) found a distinct mesencephalic root passing out between the sensory and motor roots in the frog. The material here used shows the majority of the mesencephalic fibers entering the sensory root in that portion adjacent to the motor root, but there is no separate mesencephalic bundle, and some of the mesencephalic fibers enter that portion of the sensory root quite removed from the motor root.

b. Secondary connections

1. *The internuclear connections.* Both the stout ventral dendrites of the motor trigeminal nucleus and fibers arising in the nucleus of the descending root enter the substantia

reticularis ventralis where reflex connections may be made and where the former may come under the influence of descending paths from higher centers. The motor trigeminal nucleus also sends dendrites into the field of the chief sensory nucleus and others can be traced dorsally and medially toward the midline above the dorsal decussation. The latter fibers cannot be traced to their termination but may end in the substantia reticularis ventralis and in the chief sensory nucleus of the opposite side.

2. *The trigemino-mesencephalic and tectal tract* (fig. 17). Secondary ascending fibers to the tectum and the midbrain constituting the trigeminal lemniscus arise in the nucleus of the descending root of the trigeminal and pass (fig. 17) dorsally from its dorsomedial aspect. They mingle with the fibers of the decussating acoustic system, and even dorsally with the cerebello-motorius et spinalis fibers, and pass to the midline. Crossing in the dorsal decussation, they pass diagonally across the field in the direction of the tecto-bulbar and spinal tract (fig. 17). They turn forward among the medial fibers of this tract and terminate in the superficial layers of the tectum. These secondary ascending fibers leave the nucleus of the descending root throughout its caudal course, the number of fibers at the level of entrance of the nerve being no greater than farther caudad.

3. *The trigemino-cerebellar fibers* (fig. 17). Secondary ascending fibers from the nucleus of the descending root pass with the trigemino-mesencephalic fibers in their course to the raphé. Diverging somewhat from the course of the latter after crossing, the trigemino-cerebellar fibers pass ventrally (fig. 17) just medial to the tecto-bulbar and spinal tract and course peripheral to that tract. Attaining the ventral aspect of the tecto-bulbar and spinal tract, the fibers turn forward and pass cephalically and dorsally on the inside of the spino-cerebellar tract. Some of the fibers pass through the tecto-bulbar and spinal tract and turn forward ventrolaterally of it. Uncrossed trigemino-cerebellar fibers can also be seen in the material studied. They arise from the nucleus of the

descending root of the trigeminal in the same manner as those that cross and course medially among the decussating secondary acoustic fibers; but, reaching the medial aspect of the homolateral tecto-bulbar tract, they turn ventrally along its medial surface, swinging forward among the inner fibers of the spino-cerebellar tract of the same side peripheral to the tecto-bulbar and spinal tract.

There are a few finer fibers among the somewhat coarser fascicles of the tractus cerebello-motorius et spinalis, lateral to the chief sensory nucleus, that are suggestive of a connection from the cephalic portion of that nucleus forward to the cerebellum. They course slightly obliquely to the cerebello-motorius et spinalis fibers and appear to pass farther lateralward toward the afferent tracts to the cerebellum. Thus, in their cephalic and dorsal course, they lie medial to the direct trigeminal root fibers to the cerebellum, which, in turn, lie medial to the fibers of the spino-cerebellar tract. These are interpreted as early representatives of the group of fibers known as the nucleo-cerebellar tract in higher forms.

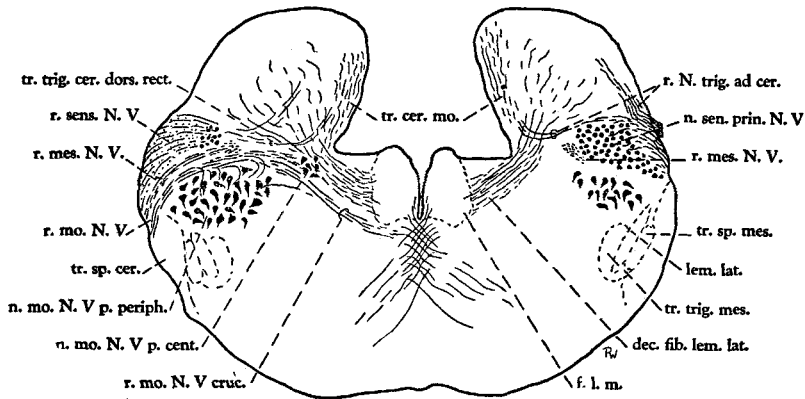
4. *The cerebello-motorius fibers* (figs. 14, 15, 16, 17). The tractus cerebello-motorius et spinalis is a prominent feature of the dorsal part of the tegmentum of the cephalic portion of the medulla oblongata in the frog. Leaving the cerebellum, the fibers course caudally, ventrally, and medially within the thick layer of periventricular gray forming the dorsum of the medulla oblongata. The cerebello-spinal fibers continue ventrally as they near the raphé, crossing it diagonally in the ventral decussation, and turn caudad in the field slightly lateral to the midline. The cerebello-motorius fibers to the motor trigeminal nucleus (fig. 16) leave the common bundle as it passes medially over the dorsal aspect of that nucleus and pass in among its cells, the terminations being pericellular in nature. These fibers appear to be entirely uncrossed. Cerebello-tegmental fibers reach the substantia reticularis of the contralateral side through the dorsal decussation, and the homolateral reticular area through the lateral motor column anterior to the motor trigeminal nucleus.

E. Reptiles (Anolis carolinensis)

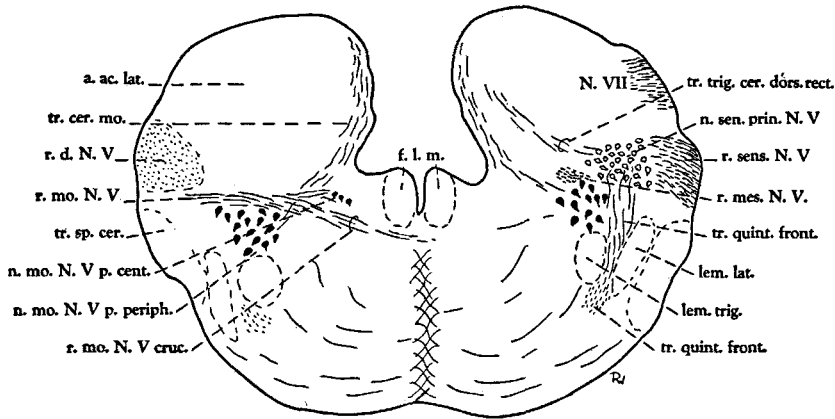
I. Nuclear gray associated with the trigeminal roots

1. The chief sensory nucleus of the trigeminal (figs. 18, 19).

The chief sensory nucleus in the lizard consists of a rostral



18



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Figs. 18, 19 Two transverse sections of the brain of the lizard at the levels of entrance of the trigeminal roots. Figure 18 shows the chief sensory nucleus and the two portions of the motor trigeminal nucleus. Attention is called particularly to the fibers passing from the chief sensory nucleus to the cerebellum, the tractus trigemino-cerebellaris dorsalis rectus, which is accompanied, on the right side of the figure, by direct trigeminal root fibers to the cerebellum. Figure 19 was drawn from a series the plane of which is slightly oblique so that the right side of the section is cephalic to the left side. Of particular interest is the formation of a quinto-frontal tract shown on the right side of the figure. *Anolis carolinensis*. Chrome silver preparations. X 28.

expansion of the gray column associated with the descending root of the trigeminal. It is located at the level of entrance of the trigeminal roots and is composed of small and medium-sized cells, as is characteristic for the entire gray column. In this rostral enlargement of the column, the expansion takes place in a dorsomedial direction, but the cells do not extend far toward the ventricle; indeed, the entire trigeminal nuclear complex lies rather peripheral in this form.

2. *The nucleus of the descending root of the trigeminal.* The nucleus of the descending root is composed of that portion of the trigeminal gray column associated with the descending root. It lies medial to, and among the medial fibers of the root throughout most of its caudal extent, becoming ventromedial to it as the root attains the dorsal funiculus of the cord. It is continuous rostrally with the chief sensory nucleus and caudally with the dorsal horn gray of the spinal cord.

3. *The motor trigeminal nucleus* (figs. 18, 19). The motor trigeminal nucleus consists of a central and a peripheral portion. The central group of cells (fig. 18) lies ventrolateral to the sulcus limitans among the mass of arcuate fibers passing toward the midline and its cells are almost unobservable in fiber preparations. This group is small and is found at the level of emergence of the motor root. The peripheral group (figs. 18, 19) composes the main mass of the nucleus and lies directly ventral to its root. It is incompletely separated into a rostral and a caudal part, there being a rostro-caudal continuity, but the smaller caudal part is displaced somewhat medially. The cells have lost the regular side-by-side arrangement of lower forms, due apparently to the fact that here the axones pass dorsally to enter the motor root. The nucleus extends from the anterior limit of entrance of the trigeminal nerve (fig. 18) caudally somewhat beyond the anterior limit of entrance of the facial nerve.

Black ('20) placed *Varanus* and *Anolis* in a group with *Boa* as exemplifying the dominance of the peripheral position of the nucleus among reptiles, the latter form having no

central portion according to Ariëns Kappers ('12). Others such as *Damonia* (Black, '20) and Alligator (Huber and Crosby, '26) appear to have no peripherally separated portion.

4. *The nucleus of the mesencephalic root of the trigeminal.* The nucleus of the mesencephalic root of the trigeminal in *Anolis carolinensis* lies in the region of the optic tectum and is differentiated into two lateral groups and a median, unpaired group of cells. No cells are located in the frontal wall of the optic ventricle, but the cells of the lateral group begin to appear as soon as the opening of the ventricle is seen in cross sections. This group extends throughout the entire optic ventricle, its cells being located exclusively in the medial wall. The unpaired median group lies in the roof of the aqueduct. Its cells are grouped in the median plane and close to it on both sides, ventral to the tectal commissure. This group begins somewhat anterior to the posterior limit of the posterior commissure and extends caudad almost to the level of the trochlear decussation. It shows the greatest accumulation of cells at its anterior end, and the largest number of cells of the lateral group are found just rostral of this point. The cells of the lateral group are found in that portion of the stratum griseum periventriculare immediately adjacent to the stratum album centrale, while those of the median group lie close against, and ventral to, the tectal commissure. The cells of the lateral group are mostly round and rather small, while those of the median group are larger and oval in shape, with their long axis parallel to the tectal commissure. The total number of cells is not great in *Anolis*; apparently less than reported by Weinberg ('28) in the turtle. The nucleus appears to accord in most particulars with that of the turtle, but not to resemble very closely the homologous cell group in *Alligator mississippiensis* as reported by Weinberg ('28).

II. Fiber connections of the trigeminal centers

a. Root fibers

1. *The sensory root fibers* (figs. 18, 19). The sensory root of the trigeminal nerve (fig. 18) enters the medulla oblongata dorsocephalical to the motor root. At the level of entrance, direct trigeminal root fibers to the cerebellum are given off (fig. 18), and root fibers end in relation with the cells of the chief sensory nucleus; but the major portion of the sensory root passes directly caudad, peripherally, as the descending root of the trigeminal (fig. 19). It receives a contribution from the vagus nerve, and passes over into the dorsal funiculus of the cord at the calamus scriptorius.

Direct trigeminal root fibers to the cerebellum (fig. 18) are clearly observable in the material studied. They are root fibers which, entering among the dorsally placed fascicles of the sensory root, swing immediately dorsally along the periphery into the auricular portion of the cerebellum. A very few of these root fibers (fig. 18) pass medially along the dorsal aspect of the chief sensory nucleus as far as its medial border and then pass dorsomedially in company with the tractus trigemino-cerebellaris dorsalis rectus. This is in accord with the findings of Huber and Crosby ('26) for the Alligator.

2. *The motor root fibers* (figs. 18, 19). The motor root of the trigeminal in *Anolis carolinensis* enters the medulla oblongata caudoventral to the sensory root and ventral to the mesencephalic root. It is composed of two separate fascicles, one entering more rostrally but lying somewhat more ventrally than the other. Both fascicles receive axones from the central portion and from the rostral part of the peripheral portion of the nucleus while the caudal part of the peripheral portion appears to send most of its axones into the dorso-caudal fascicle of the root. In addition axones from the contralateral motor trigeminal nucleus pass dorsomedially toward the midline to contribute to the motor root of the opposite side. It is not possible to trace any one fiber through

the complete crossed course, but axones may be seen passing (figs. 18, 19) from the cells toward the dorsal midline, and root fibers come from the same region so that the preparations leave no reasonable doubt that there is a crossed component in the motor trigeminal root. The crossing appears to take place just ventral to the medial longitudinal fasciculus, and the fibers pass to the midline ventral to (fig. 18) the central portion of the motor trigeminal nucleus.

3. *The mesencephalic root of the trigeminal* (figs. 18, 19). The course and relations of the mesencephalic root of the trigeminal are very clearly portrayed in the *Anolis carolinensis* material available for study. The long medullated processes of the cells pass dorsally, laterally, and then ventrally as the most ventral fibers of the stratum album centrale adjacent to the tectal gray, at the same time passing caudally in small fascicles. Caudad of the optic tectum, they are found lying between the stratum album centrale and the stratum griseum et fibrosum periventriculare of the inferior colliculus along the lateral aspect of the latter stratum, and are here passing caudally and ventrally. In the region of the anterior end of the nucleus of the oculomotor nerve, a few of the fibers are seen to leave the ventral portion of the root and to run medially along the ventral border of the stratum griseum et fibrosum periventriculare to enter the oculomotor nucleus. Passing caudad, the fibers of the mesencephalic root pass ventrolateral to the trochlear root and ventral to the cerebellar commissure. A small group of fibers can be seen joining the trochlear root and passing ventromedially with it toward its decussation. No contributions to the cerebellar decussation are apparent in the material studied. The mesencephalic root is found medial to the nucleus isthmi and, in its course caudally, it passes obliquely along the medial face of that nucleus from its superior to its inferior aspect. The root begins to swing laterally as it passes caudad of the nucleus isthmi, and, continuing its ventrocaudal course, lies adjacent, ventrolaterally, to the periventricular gray of the lateral recess of the fourth ventricle. At the anterior level of entrance of the trigeminal roots (figs. 18, 19), the fibers of the

mesencephalic root lie medial to the chief sensory nucleus of the trigeminal. A few sections caudad, it makes a sharp bend laterally to emerge as a distinct bundle (fig. 18) ventrocaudal to the sensory root and dorsocephalic to the motor root (fig. 18), the fibers appearing to join the motor root in the common nerve trunk outside. A few fine fibers are given off to the cells of the motor trigeminal nucleus as the mesencephalic root turns laterally to its emergence.

b. Secondary connections

1. *The internuclear connections.* The internuclear connections of reptiles correspond to those of lower forms. Dendrites of the motor cells pass ventrally to end in relation with the tecto-bulbar and spinal tract and laterally to come into association with the cells of the chief sensory nucleus and of the nucleus of the descending root. Others, passing medially toward the midline, possibly end contralaterally in relation with the chief sensory nucleus or the substantia reticularis ventralis. Internuclear neurones also appear to enter into these reflex connections.

2. *The trigeminal lemniscus or trigemino-mesencephalic tract* (figs. 18, 19). Secondary trigeminal fibers to the mesencephalon follow the general plan described in lower forms. They arise from the chief sensory nucleus and from the nucleus of the descending root of the trigeminal and pass medially toward the midline. Those from the chief sensory nucleus lie in the dorsal arcuate bundles and cross in the dorsal decussation. Those from the nucleus of the descending root pass dorsally, and then medially, in the above course, but are also directed medially and ventrally, streaming in small fascicles through the tegmentum to the midline. These lower decussating fibers cross the midline in its middle portion. All crossing fibers swing ventrally as they cross the raphé and then pass ventrolaterally through the tegmentum to the lateral periphery of the medulla oblongata. They turn forward just medial to the spino-mesencephalic tract and run cephalically in relation with it. In their ascent to the inferior

colliculus, the lateral lemniscus fibers pass between the trigeminal lemniscus and the spino-mesencephalic tract, as was noted by Huber and Crosby ('26) for the Alligator. The trigeminal lemniscus lies quite medially in the ventral field in the caudal reaches of the medulla oblongata but gradually moves laterally and, at the level of the trigeminal roots, lies (figs. 18, 19) ventral to the peripheral portion of the motor trigeminal nucleus. It rises somewhat with the lateral lemniscus fibers and, in the cephalic portion of the tectum, passes into the superficial layers of that structure. It is altogether probable that some pass forward to the thalamus, but it is not possible to trace them differentially.

3. *The quinto-frontal tract* (fig. 19). The quinto-frontal tract is relatively clear in the lizard material available. Allowing for differences in the size and the position of the chief sensory nucleus, the course and the relations of the tract in the lizard are essentially those found for birds. Because the chief sensory nucleus of the trigeminal is small and quite dorsally placed in the former, and because of the considerable depth of the tegmentum, the ascending secondary trigeminal fibers pass, not straight cephalad as in the dove, but sharply ventralward from the chief sensory nucleus to about the middle of the tegmentum where they turn forward in a position medial to the lateral lemniscus. The bundle inclines medially and ventrally as it goes forward and partially decussates at the level of the trochlear decussation. Farther forward, the bundle joins the lateral forebrain bundle and passes to the striatum therewith. Its relations throughout midbrain and diencephalon appear to be the same as those found in birds. Wallenberg ('03) mentioned a description of the tract in reptiles by Edinger, but gave no reference to it.

4. *The trigemino-cerebellar connections* (figs. 18, 19). The ventral trigemino-cerebellar connections are well developed in *Anolis*. They are both crossed and uncrossed. Fibers arising from cells in the chief sensory nucleus and the nucleus of the descending root cross in the trigeminal decussation in

common with those destined to ascend in the trigeminal lemniscus but, passing farther lateralward in the ventral field, join the fibers of the spino-cerebellar tract. This tract lies peripherally and ascends to the cerebellum just anterior to the level of entrance of the trigeminal roots. Uncrossed fibers arising from the same nucleus pass ventrally around the motor trigeminal nucleus and ventrolaterally through the reticular area of the tegmentum to reach the spino-cerebellar tract, passing forward among its fibers.

A small group of uncrossed nucleo-cerebellar fibers (the tractus trigemino-cerebellaris dorsalis rectus) is also present in *Anolis*. They arise (figs. 18, 19) from the chief sensory nucleus and the nucleus of the descending root and, leaving them medially, turn dorsomedially toward the acoustic area. Some ascend close to the ventricle among the cerebello-motorius fibers; others pass more directly dorsally through the acoustic area. Both groups join the cerebellar peduncle and swing up into the cerebellum therewith. This tractus trigemino-cerebellaris dorsalis was noted by Huber and Crosby ('26) for the Alligator. The fibers are much more prominent here than they were in the frog material studied.

5. *The cerebello-motorius fibers* (figs. 18, 19). These fibers descend from the cerebellum by way of the inferior cerebellar peduncle and swing ventrally and caudally close under the periventricular gray. Passing dorsal to the motor trigeminal nucleus, the tract gives off fibers to the cells of that nucleus. Other fibers pass medially into the medial longitudinal fasciculus, possibly passing through to the contralateral motor trigeminal nucleus, while the accompanying cerebello-tegmental and cerebello-spinal components of the complex pass ventrally, many of the fibers crossing the raphé before turning caudad.

F. Birds (Columba domestica)

I. Nuclear gray associated with the trigeminal roots

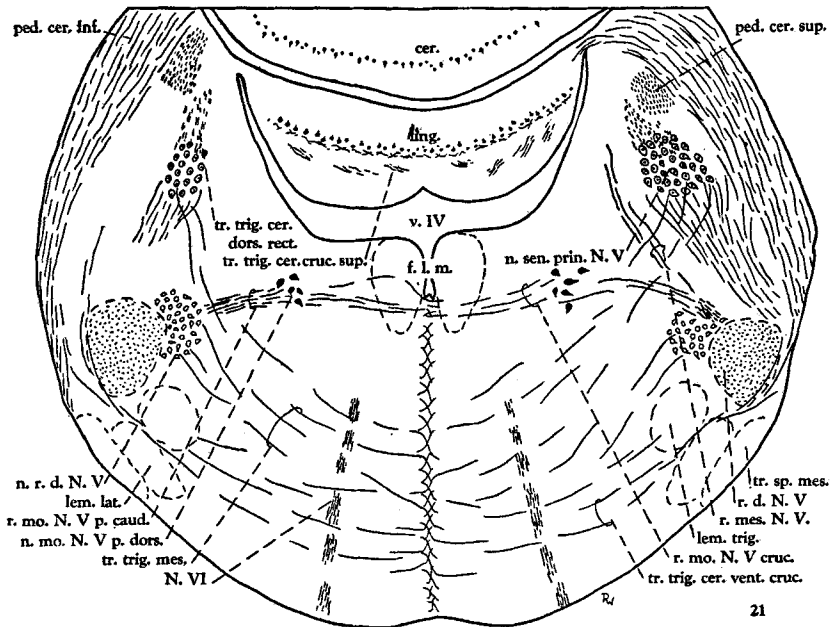
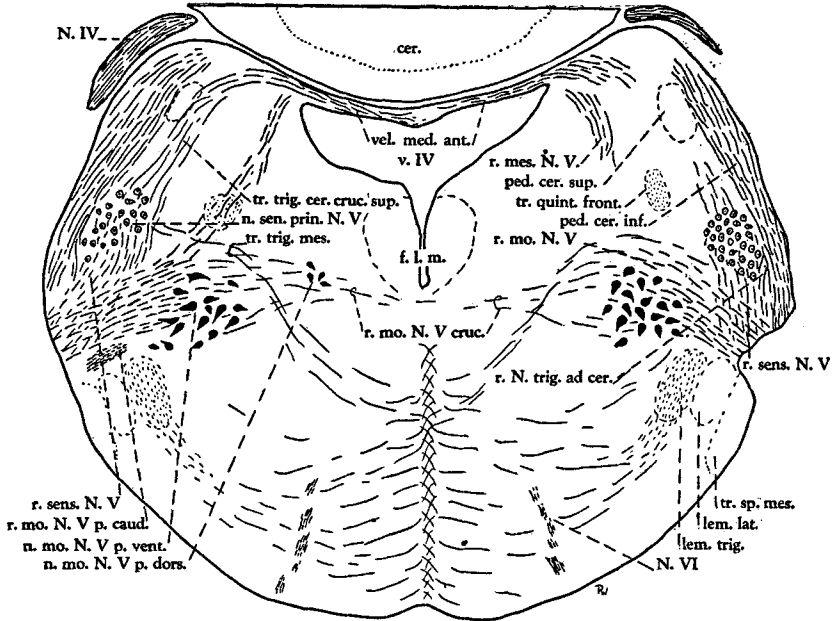
1. *The chief sensory nucleus of the trigeminal* (figs. 20, 21). The chief sensory nucleus of the trigeminal in the dove consists of a group of small and medium-sized, deeply staining cells bounded laterally by the ascending fibers of the inferior cerebellar peduncle. It begins, cephalically, slightly anterior to the rostral limit of the cells of the ventral motor nucleus of the trigeminal, and extends caudally to the level of the anterior limit of the cells of the superior vestibular nucleus. Cephalically, two portions of the complex are apparent: one, lying dorsally, is composed of closely packed cells and is in the path of ascending fibers to the cerebellum; the other appears laterally. Its cells are less closely packed and it soon expands dorsally and ventrally to form a long, slightly curved band of cells along the medial aspect of the inferior cerebellar peduncle. Tracing the complex caudally, the dorsal cell group extends somewhat more ventrally, its dorsal part becomes globular in shape, and it unites with the lateral cell group to form a club-shaped cell mass, the bulbous end of which lies dorsally. A few sections farther caudad, the ventral extension and the lateral cell group are replaced by very small cells presenting a granular appearance among the sensory fibers. There is a band of these lateral to the larger celled, oval trigeminal nucleus and another medial to it. These small cells are intercalated among fibers of passage to the cerebellum, thus forming a capsule for the chief sensory nucleus. Unlike its homologue in reptiles and mammals, the chief sensory nucleus of the trigeminal in birds is entirely independent of the nucleus of the descending root and does not form the cephalic expansion of the latter.

2. *The nucleus of the descending root of the trigeminal* (fig. 21). The cephalic end of the nuclear column accompanying the descending root of the trigeminal can be observed at the level of entrance of the anterior vestibular root fibers. The cells lie in a dorsomedially directed concavity of the

descending root, immediately ventral to the efferent facial root as it enters through the descending root of the trigeminal and dorsolateral to the nucleus of the superior olive. Of two series of transverse sections, one shows a gap of 0.6 mm. between the caudal end of the chief sensory nucleus and the cephalic cells of the nucleus of the descending root, while the other is so cut as to show them both in the same section. Figure 21 is from the latter series and thus shows only their dorsoventral discontinuity. The gap in cephalocaudal plane between the sensory nuclei appears to be quite typical in birds. Caudally the nucleus maintains a position on the medial aspect of the descending root and broadens out in the spinal cord region to become continuous with the dorsal horn gray of the cord.

3. *The motor trigeminal nucleus* (figs. 20, 21). The motor trigeminal nucleus of the dove is clearly divisible into two portions: a dorsal cell group (figs. 20, 21), retaining its primitive position near the ventricle; and a ventral cell group (fig. 20) peripherally placed ventromedial to the motor root. The ventral portion of the nucleus is of much greater extent and contains many more cells than the dorsal. It extends cephalically only slightly less than the chief sensory nucleus, and most of its cells are located in its anterior levels. It disappears caudally at the level of the cephalic tip of the dorsal motor nucleus of the facial. It is round, or oval, in cross section throughout most of its extent and lies in relation laterally and dorsally with the fibers of the motor root (fig. 20). The dorsal portion of the motor nucleus appears along the course of root fibers that are mingling with the decussating fibers of the dorsal field (fig. 21). This group

Figs. 20, 21 Two transverse sections of the brain of the dove. Figure 20 drawn at the level of entrance of the trigeminal roots. Note the positions of the long ascending tracts, the lemnisci systems and the quinto-frontal tract. The connection of the chief sensory nucleus to the cerebellum through the anterior medullary velum (tractus trigemino-cerebellaris cruciatus superior) is illustrated. Figure 21 drawn from a more caudal section of the same series. It shows the crossing motor root fibers of the trigeminal and the course of the dorsal uncrossed and the ventral crossed trigemino-cerebellar tracts. *Columba domestica*. Chrome silver preparations. $\times 14$.



also shows its greatest accumulation of cells in its anterior part and fades out caudally, approximately coincidentally with the ventral group.

There are a few cells scattered along the dorsomedial aspect of the caudal portion of the ventral group which are probably representative of the medial part of the ventral portion of the nucleus that is found to be quite well developed in many birds. It was found in the sparrow and the duck by Sanders ('29). The cells lie cephalad to, but in the position of, the dorsal motor nucleus of the facial and probably represent the combined trigemino-facial complex described by Black ('22) for *Cacatua*.

4. *The nucleus of the mesencephalic root of the trigeminal.* The nucleus of the mesencephalic root of the trigeminal in the dove has been described in detail by Weinberg ('28), using the same material that is available for the present study. As described more completely by him, it consists of a lateral and a medial group of cells. An intermediate group is not distinctly separable from the medial group in the dove.

II. Fiber connections of the trigeminal centers

a. Root fibers

1. *The sensory root fibers* (fig. 20). The sensory root fibers of the trigeminal enter the medulla oblongata dorsal to the motor root fibers. The larger body of fibers passes immediately caudalward as the descending root of the trigeminal (fig. 21), while some pass dorsally and cephalically to enter the caudal part of the chief sensory nucleus of the trigeminal, and others pass directly to the cerebellum (fig. 20).

The fibers of the descending root (fig. 21) accumulate lateral to the caudal end of the ventral portion of the motor trigeminal nucleus, internal to the inferior cerebellar peduncle. The dorsal portion of the root is traversed by entering fascicles of the facial nerve but does not appear to receive any contributions from that nerve. Entering fascicles of the glossopharyngeal and vagus nerves pass over the dorsal

aspect or through the dorsal bundles of the descending root, the vagus contributing cutaneous fibers to the root. The descending root rises dorsally as it goes caudalward and is continuous with the dorsolateral funiculus of the cord.

A clear distinction between ophthalmic and maxillomandibular divisions of the root cannot be made in the material studied, but the ventral part of the root extends caudad into the cord region whereas the dorsal part is lost higher up. Thus there is evidence of a functional division of the root.

Direct trigeminal root fibers to the cerebellum (fig. 20) pass dorsally at the level of entrance with those fibers terminating in the chief sensory nucleus, but pass forward on either side of that nucleus to join the ascending systems to the cerebellum. These direct root fibers have been described by Sanders ('29) for birds and by Larsell, Huber and Crosby, and others for reptiles. They have usually been figured as passing medial to the chief sensory nucleus of the trigeminal, but it has been possible, in both these forms, to identify these fibers passing both medial to and lateral to the nucleus in the preparations available for the present study.

2. *The motor root fibers* (figs. 20, 21). The motor root of the trigeminal enters ventral and cephalic to the sensory root and dorsolateral to its own nuclear mass. It is divisible into two bundles, one lying directly caudad of the other. The frontal bundle (fig. 20), larger but less compact than the caudal bundle, passes, with only a slight caudal inclination, to its cells of origin in the ventral portion of the motor trigeminal nucleus. Its more posterior fibers have a greater caudal inclination than those anteriorly placed and are mainly of contralateral origin (fig. 20), though they also appear to arise from the more cephalic cells of the homolateral dorsal portion of the motor trigeminal nucleus.

The caudal bundle (fig. 21) passes into its cells of origin with quite a noticeable caudal inclination, sending a few of its fibers into the more caudal cells of the ventral portion of the motor trigeminal nucleus. The main body of its fibers (fig. 21) appears to arise from the cells of the dorsal portion of the motor nucleus and from the contralateral nucleus.

The crossed component of the motor root (fig. 21) can be established with a considerable degree of certainty in the dove material available. Numerous motor fibers can be traced to the region of the raphé, some of which appear to emanate from both portions of the motor trigeminal nucleus and some of which are continuous with the motor root bundles, especially the caudal bundle. In the region of the raphé, the crossing fibers are seen to pass both over and under the medial longitudinal fasciculus with the majority passing across below that tract. Those which are dorsal to it appear to turn ventrally on its medial aspect and to complete the crossing ventral to the contralateral tract. The main body of the decussation lies immediately anterior to the genu of the facial nerve.

3. *The mesencephalic root of the trigeminal* (figs. 20, 21). The course and relations of this root in the dove have been reported by Weinberg ('28) from a study of the same material as is available for this paper. His description is confirmed in the present study. In addition, fibers of the mesencephalic root of the trigeminal can be observed in the preparations passing to the oculomotor nucleus and root. These fibers pass from the stratum album centrale of the ventral portion of the optic ventricle, at the level of the oculomotor nucleus, medially and forward along the dorsal aspect of the torus semicircularis. Reaching the medial position of the nucleus, some of the fibers pass into it while others turn ventrally and cephalically to emerge with the oculomotor root. These fibers are seen singly all along the described course and are typical, coarse fibers of the mesencephalic root.

Weinberg ('28) has described possible contributions to the trochlear root. In addition, a small fascicle of fibers of the mesencephalic root can be seen in the dove material passing from that root medially to the trochlear nucleus. It enters the nucleus a few sections caudad of the entrance of the trochlear root into the nucleus. For a complete description of the mesencephalic root of the trigeminal in the dove, the reader is referred to Weinberg's paper.

b. Secondary connections

1. *The internuclear connections.* The internuclear connections are quite rich in the dove. Dendrites of the motor trigeminal nucleus course toward the periphery to terminate in relation with fibers of the tecto-bulbar tract. Others pass laterally to come into relation with short internuclear fibers arising in the chief sensory nucleus and in the nucleus of the descending root. Dendrites passing dorsomedially from the motor nucleus probably provide crossed connections with the substantia reticularis bulbi of the opposite side. Homolateral connections of this latter sort may be provided by short dendrites within the field of the nucleus itself, for its ventral part lies in the reticular region.

The motor facial nucleus is quite rostral in position, its dorsal nucleus lying adjacent to the caudal part of the ventral motor trigeminal nucleus. This rostral position of the facial nucleus is due, according to Ariëns Kappers ('10), to the absence of caudal attraction of large taste centers and to the presence of the frontally-directed neurobiotactic influence of trigeminal stimulation. The dove material indicates that this stimulation comes, at least for the most part, from the nucleus of the descending root. Fibers arising there pass medially and curve dorsally through the ventral aspect of the caudal portion of the motor trigeminal nucleus to terminate among the cells of the dorsal facial motor nucleus.

2. *The trigeminal lemniscus* (figs. 20, 21). Secondary fibers from the chief sensory nucleus and from the nucleus of the descending root of the trigeminal form the ascending system variously known as the trigemino-mesencephalic tract, the trigeminal lemniscus, and the ventral secondary ascending tract of the trigeminal (in mammals). Those from the nucleus of the descending root (fig. 21) pass directly medially and cephalically and cross the raphé in the ventral part of the tegmentum. Fibers from the chief sensory nucleus (fig. 21) appear to leave it from three sides; medial, ventral, and lateral. The fibers emanating from its medial aspect pass medially and cephalically and cross in the dorsal decussation,

inclining then ventrally to join the other components on the contralateral side. Fibers emanating from the lateral aspect of the chief sensory nucleus pass ventrally and turn medially around the ventral aspect of the chief sensory nucleus. Joining there fibers arising from its ventral cells, the combined fascicles pass across the raphé at varying levels of the tegmentum. The fibers turn forward in a field ventral to the motor trigeminal nucleus and in close approximation to the lateral lemniscus, which tract they accompany forward to the midbrain. It has not been possible to trace the trigeminal lemniscus (figs. 20, 21) forward differentially from other ascending systems in this material, but Sanders ('29) noted that it reaches the midbrain region just medial to the nucleus mesencephalicus lateralis pars dorsalis where it terminates, in part, in the area called the nucleus mesencephalicus medialis by Wallenberg and the nucleus mesencephalicus lateralis pars ventralis by Ariëns Kappers.

3. *The quinto-frontal tract* (fig. 20). The quinto-frontal tract has been observed by Wallenberg ('03) in the dove; by Schroeder ('11) in the chicken; and by Huber and Crosby ('29) in the sparrow, the dove, and other avian forms. Normal dove material shows it to have essentially the relations noted by Wallenberg in degeneration preparations. The tract arises from the cephalic end of the chief sensory nucleus, from the 'medialen und ventralen Hilus,' as described by Wallenberg. Passing forward in this position (fig. 20), the fibers incline slightly ventromedially and cross the raphé in scattered fashion through the dorsal decussation, at the level of the trochlear decussation. Inclining ventrally as they cross to the opposite side, they turn forward medial to the tecto-bulbar and spinal tract, joining homolateral fibers in this position. The tract continues forward, inclining gradually ventrolaterally as it proceeds, and cephalically lies ventral to the strio-cerebellar and strio-tegmental components of the lateral forebrain bundle. The relations and termination of this tract in the striatal area have been described in detail by Schroeder ('11) in the chicken and by Huber and

Crosby ('29) in the sparrow. The latter observers also checked the tract in the dove, and nothing can be added, in the present paper, to their description, which can be confirmed in the material here used.

An additional frontal connection of the trigeminal in the bird was noted by Wallenberg ('34) in his occipito-trigeminal component of the occipito-mesencephalic tract. The course of the latter has been carefully studied in the dove material available, but it has not been possible to find any of its fibers passing to the motor trigeminal nucleus in the normal preparations. It does not appear to come into any relation whatsoever with the trigeminal complex.

4. *The trigemino-cerebellar connections* (figs. 20, 21). The trigemino-cerebellar connections are very rich in the bird, which may account, in part, for the size and rostral location of the chief sensory nucleus in this form. Apart from the direct trigeminal root fibers to the cerebellum previously noted, secondary connections with that center, both crossed and uncrossed are present. A large group of fibers (fig. 21) passes dorsally and caudally from the dorsal aspect of the chief sensory nucleus into the cerebellum, the tractus trigemino-cerebellaris dorsalis rectus. This is the tractus trigemino-cerebellaris dorsalis of Sanders ('29). Its fibers accumulate ventral and medial to the superior cerebellar peduncle and enter the cerebellum in relation with it. Crossed trigemino-cerebellar fibers (fig. 21) arise from both the chief sensory nucleus and the nucleus of the descending root of the trigeminal. These are mingled among, and indistinguishable in course from, the decussating fibers destined for the trigeminal lemniscus. However, they pass farther ventrally and laterally than the ascending field of the latter and join the ventral spino-cerebellar fibers ascending to the cerebellum along the periphery of the medulla oblongata.

Another prominent bundle of fibers leaving the dorsal aspect of the chief sensory nucleus of the trigeminal was noted by Sanders ('29) as the tractus trigemino-cerebellaris cruciatus superior (fig. 20). This observer believed that they

enter the anterior medullary velum and decussate and pass to the cerebellum of the opposite side. The path is quite distinct in the dove preparations, the fibers decussating in the anterior medullary velum just caudad to the trochlear decussation. The fibers incline caudally in the anterior medullary velum, entering its caudal extension of cerebellar cortex (fig. 21), the ventral part of the anterior lobe of Ingvar, corresponding to the lingula of mammals. They terminate in the contralateral granular layer and also send collaterals into the homolateral granular layer before decussating. A comparison of the number of terminating fibers with the number of those entering the velum leads one to conclude that a part of this tract is commissural in nature also, a homologue of the commissura intertrigemina of amphibians.

5. *The cerebello-motorius fibers.* Crossed and uncrossed cerebello-motorius fibers come into relation with the motor trigeminal nuclei. They swing from the cerebellum ventromedially under the floor of the ventricle, passing ventrally from their position to reach the cells of the motor trigeminal nuclei. Sanders ('29) noted that they arise from the internal cerebellar nucleus, and possibly from the intermediate and lateral cerebellar nuclei as well. This is confirmed in the material studied here, although it is apparent that her sparrow preparations were more favorable for determining their origin.

G. Mammals (*Mus domesticus*, *Lepus cuniculus*)

I. Nuclear gray associated with the trigeminal roots

1. *The chief sensory nucleus* (figs. 22, 23). The chief sensory nucleus of the trigeminal in the mouse consists of a rostral expansion of the nucleus of the descending root. It appears cephalically (fig. 22) at the rostral level of entrance of the sensory root and rapidly expands along the medial aspect of the root fibers as they turn caudad to form the descending root of the trigeminal. The nucleus (fig. 23) is

roughly crescentic in shape with its concavity directed medially. It lies in relation medially with the motor trigeminal root and nucleus (fig. 22), and dorsally with the dorsal nucleus of the brachium conjunctivum of Winkler and Potter ('11) and, at its most cephalic tip, with the dorsal nucleus of the lateral lemniscus. The cells of the chief sensory nucleus are small and medium-sized with, however, a small group of larger cells in its dorsal portion.

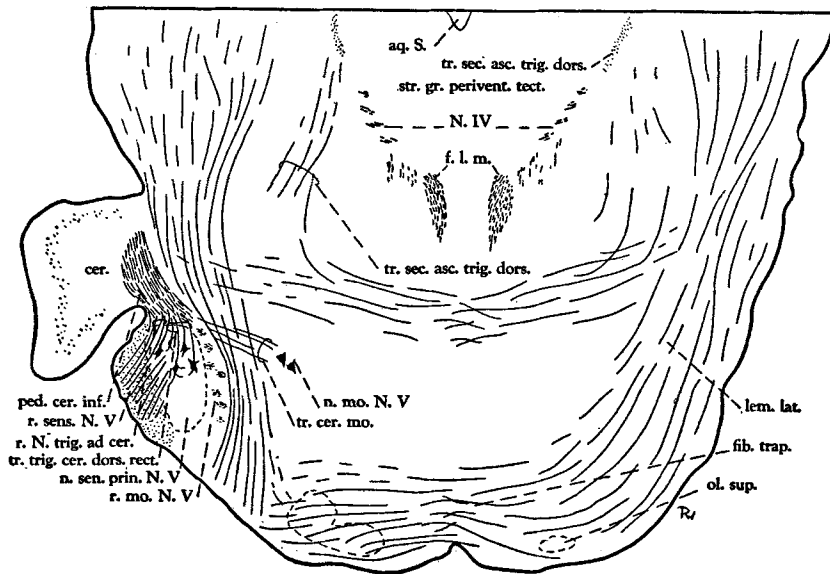


Fig. 22 Transverse section of the rabbit brain at the level of entrance of the trigeminal roots. Emphasis is laid on the connections of the trigeminal complex and on the direct root fibers to the cerebellum. The position of the tractus dorsalis secundus ascendens trigemini which swings forward to the thalamus is shown. *Lepus cuniculus*. Chrome silver preparation. $\times 14$.

2. *The nucleus of the descending root of the trigeminal* (fig. 24). The nucleus of the descending root accompanies that root in its course toward the spinal cord and consists of a large body of cells lying along the medial aspect of the root. It is continuous rostrally with the chief sensory nucleus and caudally with the dorsal horn gray of the spinal cord. Its cell characteristics are similar to those of the chief sensory

nucleus and it has a small number of larger cells in its dorsal part.

3. *The motor trigeminal nucleus* (figs. 22, 23). The motor trigeminal nucleus of the mouse consists of a collection of carrot-shaped cells located medial to the chief sensory nucleus of the trigeminal. It begins anteriorly at the level of entrance of the nerve (fig. 22), coincidentally with the chief sensory nucleus, and extends caudally as far as the level of emergence of the efferent facial root. As noted by Ariëns Kappers ('12), the nucleus is surrounded by fine reticular elements so that it has a somewhat encapsulated appearance. It lies about midway between the dorsal and ventral surfaces of the pons, and thus is somewhat less ventral in position than the ventral portion of the nucleus in birds and fishes. It has no isolated dorsal portion as was noted in some of the lower forms. This portion, small in frogs, reptiles, and birds, is now lost altogether.

There is a small group of cells separated from the caudal part of the main nuclear mass in both the mouse and the rabbit. The root fibers reaching these cells have a peculiar course, as will be described later. In the mouse, this group of cells lies medial to the caudoventral portion of the main nuclear mass but does not extend posterior to the latter. In this form the entire motor trigeminal nucleus lies anterior to the intrapontine course of the efferent facial root. In the rabbit, however, the cell group appears as a small globular collection of cells extending caudad from the main nuclear mass and attached to it by a more slender stalk of cells. This caudal extension also lies medial to the position of the main nucleus and medial to the efferent facial root as that structure passes dorsomedially through the pons.

4. *The nucleus of the mesencephalic root of the trigeminal* (fig. 23). As described more completely by Weinberg ('28), this nucleus in the mouse lies lateral to the aqueduct and to the fourth ventricle, caudal to the posterior commissure, and is divided, by the interposition of the superior cerebellar peduncle, into two groups of cells: a frontal and a caudal.

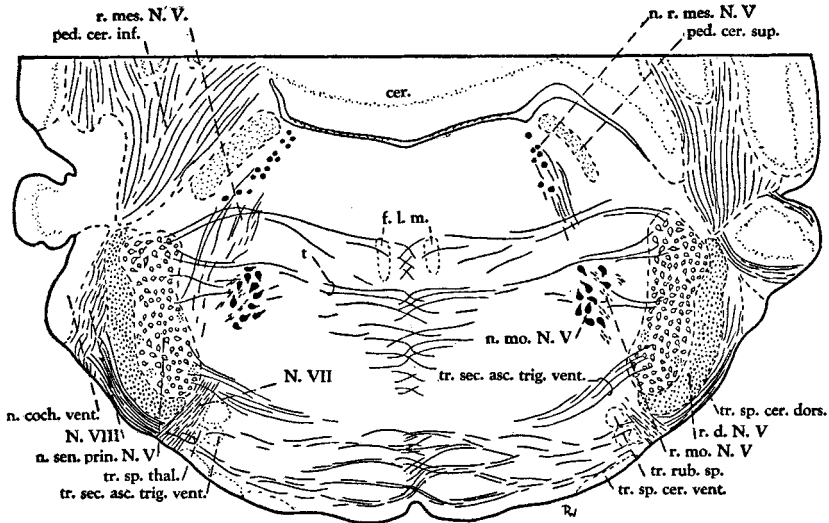
The caudal cell group contains the greater number of cells and extends posteriorly (fig. 23) into the region of the trigeminal nuclei.

II. Fiber connections of the trigeminal centers

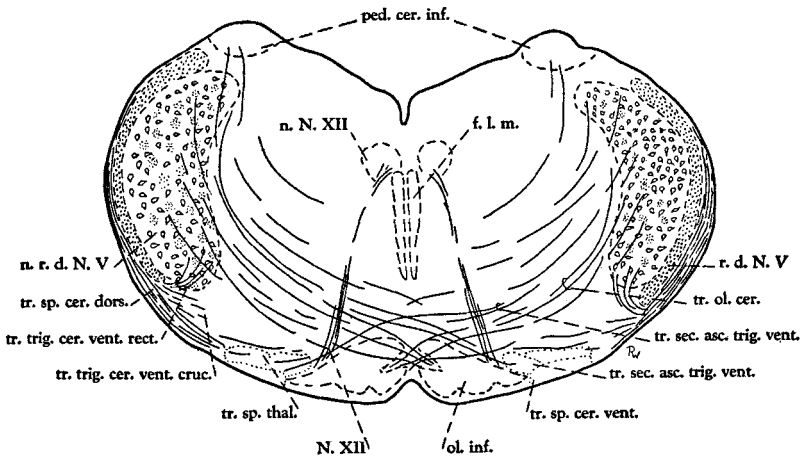
a. Root fibers

1. *The sensory root fibers* (figs. 22, 23, 24). The sensory root of the trigeminal in the mouse enters (fig. 22) the pons at the level of the rostral border of the pons fibers. It penetrates the wall of the pons just ventral to the middle cerebellar peduncle as the latter ascends to the cerebellum and is dorsal and caudal to the emerging motor root. Its more cephalic fibers pass directly caudalward, lying ventrally in the descending root. The fibers of the caudal portion of the entering root pass dorsally, some distributing to the chief sensory nucleus and to the cerebellum (fig. 22), while the bulk of them turn caudalward and form the dorsal part of the descending root. Thus, there is an indication, at the point of entrance, of a division of the root into a maxillomandibular division and an ophthalmic division according to the connections and the position in the root, along the lines worked out by van Valkenburg ('11). Ariëns Kappers ('20) noted that the sensory root fibers entering the chief sensory nucleus are from the maxillomandibular division of the root, and thus this portion of the root is primarily concerned in bulbar connections whereas the fibers of the ophthalmic division pass more caudalward to discharge into the cervical cord. Such a conception, however, must be modified by the results of Windle's ('26 a) study of the functional distribution of the trigeminal root fibers to the trigeminal nuclear gray. For a more complete functional discussion of this distribution the reader is referred to Ariëns Kappers, Huber and Crosby ('36).

As the descending root of the trigeminal turns caudalward, it is separated from its nucleus medially by fibers of the lateral lemniscus and, farther caudally, these fibers continue to pass dorsally along the dorsolateral aspect of the nucleus.



23



24

Figs. 23, 24 Two transverse sections of the brain stem of the mouse. Figure 23 drawn at the level of the motor and sensory nuclei of the trigeminal. The cell bodies of the nucleus of the mesencephalic root of the trigeminal are shown. The origin of a part of the fibers of the ventral secondary ascending tract of the trigeminal from the chief sensory nucleus is seen. Figure 24 drawn at the level of the hypoglossal nerve. The position of the ventral secondary ascending tract of the trigeminal at this level and the origin of its more caudal fascicles from the nucleus of the descending root are shown. *Mus domesticus*. Chrome silver preparations. $\times 18$.

Also, fascicles of the lateral lemniscus penetrate through the descending root from the periphery, coursing cephalad and dorsad to join their more cephalic fellows. Thus, the ascending acoustic fibers are much intermingled with those of the descending root of the trigeminal in the mouse. This condition was not found in a series of rabbit sections studied for comparison, the bundles of the lateral lemniscus all passing medial to the trigeminal complex in the latter form. The vestibular root curves over the dorsal aspect of the descending root to terminate in its own nuclear complex. The descending root (fig. 24) is separated from the lateral periphery of the pons by the dorsal spino-cerebellar tract as the latter rises dorsally to enter the inferior cerebellar peduncle. The sensory roots of the glossopharyngeal and the vagus nerves pass through the dorsal portion of the descending root and there appear to be contributions from these nerves to the root. At the level of the hypoglossal nerve, the descending root is spread out in a thin band along the entire lateral surface of the medulla oblongata. It rises rapidly to the region of the dorsolateral funiculus as the spinal cord is reached, and there presents a mass much more extensive than that of the dorsal funiculus, though very thin.

Direct trigeminal root fibers to the cerebellum are clearly evident in the rabbit material available for study. These consist of fibers of the anterior portion of the entering sensory root (fig. 22) which pass directly dorsally into the anterior part of the inferior cerebellar peduncle and to the cerebellum, therewith.

2. *The motor root fibers* (figs. 22, 23). The motor root of the trigeminal nerve enters immediately anterior to the middle cerebellar peduncle as that structure ascends to the cerebellum and is here cephalic and ventral to the sensory root of the trigeminal. It passes dorsally and caudally, breaking through the anterior fibers of the middle cerebellar peduncle and then turns more medially. Penetrating the lateral lemniscus, the root passes medially across the anterior face of the chief sensory nucleus of the trigeminal. The fibers pass

caudally, medial to the chief sensory nucleus (fig. 22), to reach their cells of origin in the motor trigeminal nucleus. The more ventral fibers pass farther caudalward to their cells of origin. The motor root in the mouse contains the mesencephalic root of the trigeminal. The latter (fig. 23) enters it in its caudal portion.

The crossed component of the motor root is composed of relatively few fibers in the mouse and the rabbit. The fibers lie in the ventral part of the entering root and are among those passing most caudally with reference to the motor nucleus. They swing dorsally along the caudal aspect of the motor trigeminal nucleus and, reaching the plane of the dorsal aspect of the nucleus, turn medially toward the midline. They consist of fibers of several small fascicles. They can be traced, passing directly medially, almost to the midline, but the complete crossed course cannot be seen in the preparations available. The presence of a few fibers of the size and character of root fibers entering the medial aspect of the contralateral nucleus and losing themselves among its cells strengthens the contention that a small, though definite, crossed component of the motor root of the trigeminal is present in these forms.

Another distinct group of fibers in the motor root is seen in the mammalian preparations. These also are among the motor root fibers passing to the caudal end of the motor nucleus. They swing dorsally with, but ventral to, those that cross, reaching the same dorsal plane as the latter though caudal to them. In sections immediately caudal to the decussation of the crossed component of the motor root, these uncrossed fibers turn ventrally and forward, passing obliquely ventrally across the cephalic face of the efferent facial root. They are clearly seen to distribute to the cells of the caudal, separated portion of the motor trigeminal nucleus previously described. These are the only root fibers reaching this portion of the nucleus. The connection is quite clear in an especially well-stained silver series of rabbit material.

3. *The mesencephalic root of the trigeminal* (fig. 23). The mesencephalic root of the trigeminal in the mouse has been described in detail by Weinberg ('28). As noted by this observer, the fibers turn ventrally at the level of the motor trigeminal nucleus and pass in numerous fascicles into the caudal portion of the nucleus where they join the motor root of the trigeminal and pass peripherally therewith.

b. Secondary connections

1. *The internuclear connections* (fig. 23). The internuclear connections of the trigeminal nuclear masses may be summarized as follows. Reflex trigeminal connections (fig. 23) are provided by axones of neurones of the chief sensory nucleus, which pass into the field of the motor trigeminal nucleus, as well as by dendrites of the latter which pass into the chief sensory nucleus. Reflex connections of a crossed nature are provided by fibers which run from the chief sensory nucleus through the dorsal decussation to the motor trigeminal nucleus of the opposite side. These fibers mingle among those destined for the contralateral dorsal secondary ascending tract of the trigeminal, but pass ventrally toward the cells of the motor nucleus after crossing the raphé. Other fibers in the same complex appear to be lost in the reticular region of both sides.

Connections from the nucleus of the descending root of the trigeminal to other motor nuclei of the bulb are also apparent. At the level of the efferent facial nucleus, fibers pass from the ventral portion of the nucleus of the descending root into the former nuclear complex. At the respective levels, other fibers swing medially from the dorsal portion of the nucleus of the descending root to make connection with the cells of the abducens, the glossopharyngeal, the vagus, and the hypoglossal motor nuclei.

The dendrites of the cells of the motor trigeminal nucleus, unlike those in lower forms, are very short, extending only small distances beyond the field of the nucleus. Apart from reflex fibers entering the nucleus, mention may be made in

particular of connections placing the nucleus under the dominance of higher centers. Rubro-bulbar and tecto-bulbar fibers swing dorsally as these longitudinal tracts pass caudalward. The tracts are located (fig. 23) ventral to the motor trigeminal nucleus in relation with the spino-thalamic tract and the ventral secondary ascending tract of the trigeminal, and send their fibers directly dorsalward to end among the cells of the motor trigeminal nucleus.

2. *The ventral secondary ascending tract of the trigeminal* (figs. 23, 24). The ventral secondary ascending tract of the trigeminal, the homologue of the trigeminal lemniscus or of the trigemino-mesencephalic tract of lower forms, arises, as in those forms, from the chief sensory nucleus and from the nucleus of the descending root of the trigeminal. Its ventrolateral position and the course of the fibers as they emanate from the nuclei also correspond to the position and course of its homologues in lower forms. In the mouse and the rabbit material studied, the fibers leave the nucleus of the descending root throughout its extent and pass in a curved course (figs. 23, 24) ventrally and medially to cross the raphé in scattered fascicles. At the level of the inferior olive (fig. 24) these fibers are mingled with those of the olivo-cerebellar and cerebello-olivary systems, the latter passing through the nucleus of the descending root to reach the inferior cerebellar peduncle dorsal to that root. However, at the raphé, the trigeminal fibers (fig. 24) pass over the inferior olive, which is median in position, and curve ventrolaterally along its dorsal surface, turning forward along its ventrolateral aspect. In this position the fibers lie in relation with the ventral spino-cerebellar and the spino-thalamic tracts, dorsomedial to the latter. These tracts pass gradually laterally as they are traced forward and, at the level of the efferent facial nucleus, lie ventral to that structure, the fascicles of the ventral secondary ascending tract of the trigeminal lying in ventral indentations of the gray of the facial nucleus. As the efferent facial root emerges from the brain stem, the above tracts (fig. 23) lie medial to it, the ventral spino-cerebellar tract remaining peripheral while the rubro-spinal

tract begins to swing dorsally along the medial aspect of the root. The ventral secondary ascending tract of the trigeminal and the spino-thalamic tract lie between the other two tracts with the former lying medial to the spino-thalamic tract. They are much broken up at this level by trapezoid fibers. Cephalad the ventral secondary ascending tract of the trigeminal, the spino-thalamic tract and the rubro-spinal tract incline dorsally as they ascend and the lateral lemniscus passes ventral to them and dorsal to the ventral spino-cerebellar tract to attain a more lateral position. It passes dorsally, adjacent laterally to these ascending tracts. Just cephalad of the level of the trigeminal complex, the ventral secondary ascending tract of the trigeminal and the spino-thalamic tract lie adjacent medially to the lateral lemniscus in a position about midway of the dorsoventral extent of the tegmentum, the rubro-spinal tract having been left somewhat ventral. The medial lemniscus now begins to incline dorso-laterally, its dorsolateral fibers coming into relation ventrally with the more medial ventral secondary ascending tract of the trigeminal. At the level of the ventral tegmental decussation the rubro-spinal tract passes medially to the contralateral red nucleus, while the ventral secondary ascending tract of the trigeminal passes forward with the medial lemniscus to enter the diencephalic nuclear complex by way of the external medullary lamina. The fibers of the former appear to distribute with those of the medial lemniscus to the ventral nucleus of the dorsal thalamus.

3. *The dorsal secondary ascending tract of the trigeminal* (fig. 22). The dorsal secondary ascending tract of the trigeminal was described by Wallenberg ('05) in degenerated material. Its fibers are both crossed and uncrossed. As seen in normal preparations, they arise only from the chief sensory nucleus of the trigeminal and from its dorsal and cephalic portion. The uncrossed portion (fig. 22) passes dorsomedially and cephalically through the ventral nucleus of the brachium conjunctivum of Winkler and Potter ('11) and joins crossed fibers immediately lateral to the mesencephalic root of the trigeminal and the associated nucleus.

The crossed portion passes directly medially and cephalically from the rostral end of the chief sensory nucleus, curving over the motor trigeminal nucleus on its way to the raphé. Crossing immediately ventral to the medial longitudinal fasciculus it inclines dorsolaterally (fig. 22) to join the uncrossed fibers in their position lateral to the mesencephalic root of the trigeminal. The tract passes forward in this position and is adjacent laterally to the trochlear root (fig. 22) as the latter passes dorsally around the periventricular gray. Tecto-oculomotor and tecto-spinal fibers pass ventrally through its fascicles. The tract enters the diencephalic nuclei via the internal medullary lamina and disappears into the ventral nucleus and into the internal medullary lamina in the region where the primordial centromedian nucleus of the dorsal thalamus is developing. The tract appears somewhat larger than figured by Wallenberg ('05), and he carried its fibers forward somewhat more medially on the lateral aspect of the medial longitudinal fasciculus. It is assumed that his lesion had not severed all the fibers from their cell bodies and that those degenerated had constituted the more medial portion of the bundle.

4. *The trigemino-cerebellar connections* (figs. 22, 24). The trigemino-cerebellar connections appear somewhat reduced in mammals but are still evident. Fibers of the tractus trigemino-cerebellaris dorsalis rectus (fig. 22) pass dorsally from the anterior portion of the chief sensory nucleus into the cerebellum by way of the inferior cerebellar peduncle. They enter the latter in the same plane as that showing the direct trigeminal root fibers to the cerebellum. Cells of the chief sensory nucleus, which happen to be deeply impregnated by the silver stain of the rabbit series, can be seen sending their long processes among the fibers of the inferior cerebellar peduncle, as indicated in figure 22.

Secondary fibers, both crossed and uncrossed, enter the inferior cerebellar peduncle by way of the dorsal spino-cerebellar tract and thus reach the cerebellum. They form part of the bulbo-cerebellar system. The crossed fibers leave the

chief sensory nucleus and the nucleus of the descending root throughout its extent and take the same course through the tegmentum as do those which turn forward as the ventral secondary ascending tract of the trigeminal. The trigemino-cerebellar fibers, however (fig. 24), pass beyond the latter tract; and, turning forward among the fibers of the ventral spino-cerebellar tract, incline cephalically and laterally to join the dorsal spino-cerebellar tract. With this they pass into the cerebellum by way of the inferior cerebellar peduncle. The uncrossed fibers (fig. 24) pass ventrally from the nucleus of the descending root of the trigeminal and, reaching the ventral periphery of the medulla oblongata, turn laterally around the ventral aspect of the descending root of the trigeminal into the dorsal spino-cerebellar tract.

5. *The cerebello-motorius fibers* (fig. 22). Fibers of the cerebello-motorius and cerebello-tegmental systems pass out of the anterior portion of the inferior cerebellar peduncle at the level of the cephalic limit of the trigeminal nuclear complex. They pass directly medially under the ventral tip of the superior cerebellar peduncle and dorsal to the chief sensory nucleus. Those fibers destined for the motor trigeminal nucleus (fig. 22) pass ventrally and caudally to end around its cells. The majority of fibers, however, pass to the midline and into the reticular region of the pons of the same and of the opposite side. They appear to turn caudad to form connections with tegmental and motor centers caudally in the bulb. Of those crossing the raphé at the level of the trigeminal complex, some appear to terminate in the motor trigeminal nucleus of the opposite side.

DISCUSSION

In concluding this study of the phylogeny of the trigeminal complex, certain features of this system emphasize themselves by their constancy, while others appear only in some of the forms. The interpretation of these broader aspects of the complex will be attempted in the following discussion.

In all forms from cyclostomes to mammals the entering sensory trigeminal fibers end partly at their plane of entrance and in part turn caudalward as a descending root of the trigeminal and become continuous, in most cases, with spinal tracts carrying similar impulses. There is a progressive increase in the number of fibers terminating at the level of entrance in passing from lower to higher forms. Direct root fibers to the cerebellum have been demonstrated in all forms examined except teleosts.

Associated with the descending root of the trigeminal, there are neurones, few in number, intercalated among the fascicles of the root in cyclostomes. These increase slightly in number but show no special organization in ganoids and teleosts. In tailed amphibians, in addition to scattered cells among the fascicles, neurones of the periventricular gray, lying along the dorsomedial border of the descending root of the trigeminal, come under the influence of fibers from this root and form a better organized nucleus. In the frog this differentiation has proceeded even further, for the cells constituting the nucleus of the descending root have separated from the periventricular gray, forming here a discrete nucleus which is partly medial to, and partly among the medial fibers of, the descending root. In reptiles and birds, on the one hand, and in mammals, on the other hand, these fundamental relations of the nucleus of the descending root of the trigeminal, as seen in higher amphibians, are maintained, the size of the nucleus varying somewhat with the form under consideration.

It is clearly evident that in the frog, at the plane of entrance of the sensory root of the trigeminal, certain fascicles of this root swing directly dorsomedialward to end in relation with a differentiated portion of the periventricular gray, forming there a primordial chief sensory nucleus. This nucleus has been foreshadowed in tailed amphibians and in ganoids and teleosts, for in all these forms there are entering sensory root fibers of the trigeminal which end in small number in the periventricular gray lateral or dorsolateral to the motor trigeminal nucleus, although no discrete nuclear group justi-

fyng the name of chief sensory nucleus is formed. In reptiles a chief sensory nucleus has become entirely distinct from the periventricular gray and has formed a cell mass situated at the cephalic tip of the nucleus of the descending root. In birds the chief sensory nucleus has migrated dorsofrontalward, probably under the influence of the cerebellum, and is entirely separated from the nucleus of the descending root. The positional relations in mammals resemble those in reptiles rather than those in birds, for the larger, more bulbous chief sensory nucleus is continuous with the longer, narrower nucleus of the descending root of the trigeminal. The position of these nuclei of termination for cutaneous sensory root fibers of the trigeminal vary, in the different forms, with respect to the ventricle. Their primitive position, phylogenetically and ontogenetically, is in the periventricular gray, but in higher forms they migrate ventrolateralward from this position and, in some forms, lie relatively near the ventrolateral border of the brain stem.

Certain secondary connections of the sensory trigeminal complex are represented in all forms from cyclostomes to (and including) mammals. Among such may be mentioned: a) internuclear connections with the motor trigeminal nucleus, b) crossed trigemino-cerebellar connections from the nucleus of the descending root, and c) crossed secondary ascending fibers to the midbrain region, largely the tectum, which reach their maximum development in reptiles and birds, and are relatively small in cyclostomes and mammals. Other secondary ascending connections appear only in certain forms, generally in correlation with increased nuclear differentiation within the trigeminal complex and at other levels of the nervous system. Such inconstant secondary connections deserve further brief consideration and first among these are certain trigemino-cerebellar bundles.

The crossed trigemino-cerebellar connections mentioned above as found throughout the series are supplemented in most forms by uncrossed fibers from the same area. In addition to these, there appear in higher amphibians, with the

appearance of a primordial chief sensory nucleus, fascicles which constitute the tractus trigemino-cerebellaris dorsalis rectus, which connects this nucleus with the cerebellum. This tract increases progressively through reptiles into birds where it is a conspicuous part of the cerebellar connections. It is small in mammals, although still present.

Of special interest is the gradual elaboration of the systems of fibers which place the brain stem nuclei of the cutaneous trigeminal roots in relation with higher centers. Most primitive of these is the secondary ascending tract which arises from the nucleus of the descending root of the trigeminal in all the forms considered, decussates and passes forward toward midbrain areas. This tract, which has been variously designated—for example, as the trigemino-mesencephalic tract, the bulbo-tectal tract, or the trigeminal lemniscus—is supplemented, with the appearance phylogenetically of a chief sensory nucleus, by crossed fibers arising from that nucleus. In forms below mammals, the major region of termination for this system is the roof of the midbrain, though some fascicles may end subtectally or, possibly, in small numbers, proceed forward to diencephalic areas. This tract remains in mammals, where it is frequently designated the ventral secondary ascending tract of the trigeminal, but the number of fibers which ends in the tectum is relatively small, while its major region of termination is the ventral nucleus of the dorsal thalamus—an indication of the progress of cephalization in these forms, and the rise in importance of forebrain areas, and the relative decline in importance of tectal areas.

The other ascending trigeminal system in mammals, the dorsal secondary ascending tract, is phylogenetically younger than the ventral tract. It is to be emphasized that in mammals this dorsal tract represents a crossed and uncrossed ascending connection from the chief sensory nucleus only. Such a projection of this nuclear group in reptiles and birds is made possible by the quinto-frontal tract which, after a partial decussation, swings forward to diencephalic and

probably telencephalic centers. It seems obvious that this quinto-frontal system serves the reptilian or avian chief sensory nucleus in much the fashion that the dorsal secondary ascending tract of the trigeminal serves the homologous nucleus of mammals.

The nucleus of the mesencephalic root and its associated root fibers have been traced in all the representative forms as far down as the ganoids. In essentials the relations of this nucleus and its root are much alike throughout the series, although the fibers leave the brain in some cases with the sensory root (*Amia*, *Necturus*), in other cases with the motor root (trout, mouse), and in still other cases are in intermediate position between the roots (lizard, dove). Insofar as can be judged, the differences are due to relative shifts in position of the motor and sensory roots, the mesencephalic root tending to emerge with the dorsocephalic root.

The motor trigeminal nucleus shows relatively less cephalocaudal change in position than do many of the efferent nuclei (for instance, the facial nucleus) of the brain stem. Progressive separation of a considerable part of the motor neurones from a position in the periventricular gray to a more ventral or lateral and peripheral position occurs. This is associated with changes in position of the neurones, so that they lose their early regular arrangement, as typified in figures 1, 2 and 3 of cyclostomes. Evidence, as conclusive as possible in the absence of experimental material, indicates the presence of crossed as well as of uncrossed efferent trigeminal fibers in many forms (petromyzonts, carp, frog, lizard, dove, mouse). In all forms studied the correlative influence of cerebellar gray over the efferent trigeminal neurones is evidenced by the occurrence of cerebello-motorius fibers.

It is evident then that the trigeminal complex in its progressive development and differentiation typifies most clearly the progressive evolution of the nervous system and indicates how various levels are developing simultaneously and are correlated in that development.

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