

MISCELLANEOUS PUBLICATIONS  
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 80

**A Comparative Study of the Osteology and  
Myology of the Cranial and Cervical Regions  
of the Shrew, *Blarina Brevicauda*, and the  
Mole, *Scalopus Aquaticus***

BY  
GEORGE R. L. GAUGHRAN

ANN ARBOR  
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A COMPARATIVE STUDY OF THE OSTEOLOGY AND  
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AND THE MOLE, *SCALOPUS AQUATICUS*\*

INTRODUCTION

THE short-tailed shrew *Blarina* and the North American mole *Scalopus* are members of the superfamily Soricoidae, mammalian order Insectivora. The former is a representative of the family Soricidae; the latter, of the Talpidae. The moles and shrews have probably evolved from a common nonfossorial ancestor. The Recent talpids and soricids, however, have evolved along separate courses over a long period of time and present many morphological specializations, although retaining certain primitive characters.

The present investigation was initiated for the purpose of making a small contribution to the meager knowledge of the anatomy of North American insectivores. This paper is not a taxonomic study, but it contains a certain amount of morphological data which will prove useful after subsequent analyses of a greater number of species. Although the cranial and cervical regions are axial structures, which generally demonstrate more conservatism in their modifications than is shown by appendicular parts, they were chosen for this study because of their greater appeal to me and because no similar study of any of the North American insectivores has ever been reported. Whenever possible, an attempt has been made to interpret the functional significance of anatomical modifications. As was anticipated, however, the functional importance of many structural differences could not be ascertained. My decision to use the prairie mole (*Scalopus aquaticus*) and the short-tailed shrew (*Blarina brevicauda*) as comparative forms was based on their membership in the two lipotyphlan families of insectivores represented in this country, their differences in habits, and their regional availability. *Blarina*, despite its fossorial tendencies, was chosen in preference to *Sorex* because the small size of *Sorex* makes it an extremely difficult subject for dissection.

Skeletal material examined consists of five skulls and three skeletons of *Talpa europaea*, 30 skulls and six skeletons of *Scalopus aquaticus machrinus*, and 30 skulls and eight skeletons of *Blarina brevicauda kirtlandi*. One adult prairie mole, one adult short-tailed shrew, two nest young of *Blarina*, and two nest young of *Scalopus* were cleared and stained following the Spalteholz technique. In the course of this work I was impressed with the value of specimens prepared by this method, for they present a more reliable picture of the relationships of hard parts than can

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be obtained from a study of osteological preparations. Eight specimens of the short-tailed shrew and 12 specimens of the prairie mole, which were used for dissection, were preserved in embalming fluid composed of 3 per cent phenol, 2 per cent formalin, 20 per cent glycerin, and 75 per cent water. All dissections were done under a stereobinocular microscope, and measurements were made with vernier calipers calibrated to 0.1 mm.

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## OSTEOLOGY

Despite the wealth of information on mammalian osteology, gleaned through many years of research by competent men, apparently no one has investigated the development of the skull in North American insectivores. W. K. Parker's monograph on the development of the mammalian skull (1885) remains a classic and has been extremely valuable in this work. Other investigations include: G. R. de Beer's study of *Sorex araneus* (1929), P. N. van Kampen's work on the tympanic region in insectivores (1905), E. Fischer's study of *Talpa* (1901), G. H. Roux's paper on certain Ethiopian insectivores (1947), G. E. Dobson's monograph (1882-90), St. G. Mivart's work on the osteology of the insectivores (1867), C. Giebel's note on *Scalopus* (1858), and P. M. Butler's study of the Erinaceidae (1948). Though of greater scope, but not to be neglected, are H. G. Bronn's erudite tome on mammalian anatomy (1874-1900), M. G. Saint-Hilaire's lessons (1834), G. Cuvier's volumes (1800-37), M. H. M. de Blainville's osteology (1839-64), and M. Weber's text on mammals (1927-28). Additional, less pertinent, references are: on *Talpa*, Bertelli (1909), Brandt (1836), Camerano (1886), Fitzinger (1869), Göppert (1894), Gregory (1910, 1920), Jacobs (1816), Kober (1885), Muller (1935), van der Klaauw (1924), Wilkie (1925), and Winge (1941); on *Scalopus*, Baird (1859), Cope (1880), de Beer (1937), Eckhard (1847), Jackson (1915), and True (1897); on *Condylura*, Jackson (1915) and True (1897); on *Blarina*, Allen (1894), Baird (1859), and Merriam (1895); on *Sorex*, Brandt (1836), de Beer (1929, 1937), Jackson (1928), Keen (1942), and Keen and Grobelaar (1941).

The present investigation is not concerned with embryology; hence, only the bony elements that could be identified in immature specimens,

without embryological techniques, are considered. In addition, foramina are identified, but only the nervous structures which they transmit are given, since the blood vascular system was not investigated. A characterization of the general form and proportions of the cranium of *Blarina* introduces more detailed descriptions of the cranium in dorsal, ventral, lateral, frontal, and occipital views. The auditory ossicles are considered under a separate heading, followed by a study of the dentary. The next section describes the hyoid and laryngeal cartilages. A consideration of the cervical region of the vertebral column includes a description of the cervical segment as a unit and a detailed study of certain vertebrae. The scapula, clavicle, and sternum are considered only insofar as they are related to cervical and cranial musculature. The discussion of *Scalopus* follows the same pattern. All references in this paper to the mole or to the shrew refer to the particular forms under investigation, unless it is otherwise specifically stated.

### *Blarina brevicauda kirtlandi*

#### Cranium

**General Form.**—The cranium of an adult *Blarina* is a fused, rugose, osseous structure, sagittate in dorsal view, with only a few prominent sutures suggestive of certain of its component elements. In comparing it with that of the long-tailed shrew, one is impressed with the angularity of the posterior region. Its greatest breadth is at the zygomatic processes of the squamosal; this measurement is almost twice the breadth at the zygomatic processes of the maxillary bones. The mean height of the cranium, at the intersection of the sagittal and lambdoidal sutures, approximates one-third the greatest length, measured from the tip of the rostrum to the most posterior region of the occipital condyles. The height of the cranium increases gradually from the roof of the rostrum to the posterior edge of the parietals from which the supraoccipital bone descends sharply, describing a small arc, to the dorsal rim of the foramen magnum. The height of the posterior region of the cranium is more than twice that of the postnasal rostral region. The roof of the cranium is well rounded; the lateral walls of the rostrum descend more abruptly than those of the parietal region, producing a conoid outline rostrally and a cycloid outline in the parietal region. The osseous wall, anterior to the zygomatic processes of the maxillary, is considerably thicker than the wall of the expanded posterior region of the skull. The zygomatic arch is incomplete; the malar (jugal) is absent. There are no auditory bullae; the tympanic forms only a ring of bone. Two articular facets for the articulation with a double facet on the condylar process of the mandible are visible. To aid in the interpretation of the bony elements of the cranium, two nest young of *Blarina* were cleared and stained for bone (Fig. 66).

**Norma Verticalis (Fig. 1).**—The occipital and parietal regions are broad and thin walled, occupying a little less than one-half the length of the skull; in outline they form a rounded contour from the zygomatic

process of the squamosal of one side to the same process of the opposite side, then turn sharply mesiad to join the frontal region. Here the walls parallel each other for about 2 mm., then flare out slightly to the zygomatic process of the maxillary and taper gradually to the tip of the snout. A median sagittal crest visibly separates the parietals but disappears in the frontal region of the cranium. A transverse lambdoidal crest distinguishes the parietals from the supraoccipital, and a sharp transverse ridge, just caudal to this suture, suggests the presence of a small interparietal. On the lateral surface of the rostrum can be seen the very large infraorbital foramina for branches of the maxillary division of the fifth cranial nerve. At the junction of the rostrum and frontals a pair of small variable foramina is situated beside the most anterior tip of the median sagittal ridge. Of eight specimens, one was without foramina, one had a foramen on the right side only, four had a foramen on the left only, and in two there was a foramen on each side. At the lateral edge of the frontal region, dorsal to the thickened supraglenoid articular surface (not visible in this view), there may be a tiny bilateral foramen. This and the preceding foramina transmit vascular structures. The lateral edge of the parietal continues anteriorly from the lambdoidal crest as a prominent ridge separating the squamosal from the parietal and terminating in a small triangular process immediately caudal to the glenoid cavity. Visible on the parietal is a low longitudinal ridge paralleling the sagittal crest for about 4.5 mm. The nares are represented by a single rectangular opening. A small protuberance, probably the supraorbital process (zygomatic process of the frontal), projects laterad in the frontal region. The coronal, sagittal, and lambdoidal sutures can be seen.

Norma Basalis (Fig. 2).—The dentition has been figured by S. F. Baird (1859), F. W. True (1897), and C. H. Merriam (1895). The cleared and stained nest young of *Blarina* confirmed the dental formula:  $\underline{3}, \underline{1}, \underline{3}, \underline{3}$ . A nomenclature of the molar cusps of *Sorex* is given by Jackson (1928). The palate is narrow anteriorly and becomes wider in the premolar and molar region, terminating in a median palatine lip overhanging the mesopterygoid fossa. No indication of sutures between the premaxillary, maxillary, and palatines could be discerned. A pair of foramina lies mesial to the second incisor, followed immediately caudad by a pair of smaller foramina. The anterior foramina are probably incisive, but I could not trace a palatine branch (nasopalatine nerve) from the maxillary division of the trigeminal to this opening. The posterior foramina transmit a definite structure, but it was impossible to trace this structure to any main vascular or nervous trunk. Except for several small suture lines, the remainder of the cranium is a fused osseous unit. The only elements to be distinguished with certainty are the periotics, which are attached loosely to the rest of the cranium. There is a short but prominent pair of hamuli of the pterygoids projecting divergently caudad. About 1.5 mm. lateral to the hamuli and immediately ventral to the inferior glenoid articular surface can be seen a pair of large foramina lying in the alisphenoid region, which transmit the mandibular ramus of the trigeminal nerve. In the posterior part of the orbitotemporal fossa is the superior glenoid articular facet, and at its anterior border is a small



foramen for a blood vessel. This foramen is situated immediately caudal to the cribriform plate and is continued craniad by a longitudinal sulcus along the lateral edge of the roof of the orbitotemporal region. On the mesial vertical wall of the orbitotemporal fossa is a thin-walled alisphenoid canal, the lips of which open into the fossa and carry the ophthalmic and maxillary branches of the trigeminal nerve and the optic nerve. In the basisphenoidal region, mesial to the anterior tip of the annulus tympanicus, a pair of foramina transmits two small vessels obliquely through the cranial wall. The caudal edge of the squamosal can be seen abutting the annulus tympanicus and the tympanohyal. Here the squamosal forms a thin lamina of bone roofing the pocket in which rests the capitulum mallei. The lateral lip of the squamosal is a thickened bony crest continuing craniad as the short zygomatic process. The annulus tympanicus is an almost free incomplete ring of bone attached laterally to the processus anterior Folii (processus gracilis) and mesially to the tympanohyal. The periotic lies between the squamosal laterally and the basioccipital and exoccipital mesially; it is free from the latter two bones with exception of a narrow exoccipital strut which forms the caudal margin of the jugular foramen (foramen lacerum posterius) for nerves IX, X, and XI. The bony arches of the posterior and horizontal semicircular canals can be seen in this view. Immediately mesial to this foramen is the condylar (hypoglossal) foramen for the twelfth cranial nerve. The condyles form the most caudal part and extend for about 2.5 mm. on the ventral surface of the cranium. The ossicula auditus and cochlear regions will be discussed later in more detail.

Norma Lateralis (Fig. 3).—In this view the cranium is wedge-shaped in general outline, with a perceptible depression in the dorsal surface several millimeters caudal to the frontopremaxillary suture. All the teeth are visible with the exception of the fifth unicuspid ( $P^2$ ). The sagittal and lambdoidal ridges become increasingly prominent with age. The large infraorbital foramen opens anteriorly, dorsal to  $M^1$ . Immediately caudal to this foramen is a small opening into a bony canal which passes craniodorsad along the lip of the infraorbital foramen before communicating with the nasal cavity. This canal carries the lachrymal duct. The orbitotemporal fossa is triangular, the apex directed ventrad. The convolutions of the ethmoturbinals can be seen through the thin wall of the fossa. Within the orbitotemporal fossa is the sphenopalatine foramen which transmits the palatine twigs of the maxillary branch of the trigeminal nerve. Slightly anterior to the middle of the fossa is a foramen representing the combined inferior orbital fissure (foramen lacerum anterius) and foramen rotundum which transmits the optic nerve and the ophthalmic and maxillary divisions of the fifth cranial nerve. The mandibular (glenoid) articular facets can be seen in the posterior half of the fossa. The superior articular surface is directed cephalomesiad and presents a convex facet; the inferior articular surface lies transversely and has a concave articular facet. The squamosal, forming the most caudal region of the orbitotemporal fossa, is not distinctly limited anteriorly but is separated dorsally from the parietal by a ridge of bone. There is no evidence of the boundaries of the lachrymal bone. The "prootic" (Parker, 1885) extends

anteriad as a bony tongue between the parietal and the squamosal. The dorsal region of the posterior wall of the cranium is formed by a supraoccipital bone, limited anteriorly by the lambdoidal crest; its ventral part contains the exoccipitals and is separated from the periotics by a narrow cleft.

**Norma Occipitalis.**—In this view the cranium presents an elliptical outline, approximately twice as broad as high. Its central part is formed by the supraoccipital and exoccipitals, enclosing an almost circular foramen magnum, without visible suture. The occipital condyles border the ventral three-fourths of the foramen and are coracoidal in outline. The arched roof of the cranium presents a median sagittal ridge and a parasagittal ridge on each parietal. The supraoccipital is convex centrally and concave lateral to the center, sweeping outward to a prominent lambdoidal crest which terminates lateroventrally at the posterior end of the ridge formed by the lateral edge of the parietal. The periotic is distinct from the parietal and exoccipital, and the "prootic" extends laterad to terminate sharply between the parietal and the squamosal. A heavy strut of the exoccipital bone extends laterad and abuts the region of the posterior canal of the osseous labyrinth. A small foramen for the facial nerve lies at the posterior border of the tympanohyal. The cochlea appears as a swollen region anterior to the aforementioned strut.

**Norma Frontalis.**—The nares form a heart-shaped opening at the apex of the rostrum. Within the nasal cavity can be seen the median perpendicular plate of the ethmoid, extending from the roof to the V-shaped vomer in the floor. Lateral to the plate is a tonguelike bone, the nasoturbinal, extending ventrad from each nasal but not reaching the floor. Adjacent to the lateral walls of the nasal cavity are the small maxilloturbinals.

#### Ossicula Auditus

(Figs. 4, 5, 6)

The works of Doran (1878), Keen and Grobbelaar (1941), Stroganov (1945), Wilkie (1925; 1929), and Wassif (1948) deal with the auditory ossicles of insectivores. The periotic and the tympanic ring lie in a horizontal plane in the floor of the cranium at about a 30° angle to the sagittal plane. The osseous labyrinth is the most posterior element of this complex and consists of the orbiculate cochlea, semicircular canals, and the vestibule. The cochlea is adjacent to the basioccipitals and exoccipitals. A scooplike plate of bone extends cephalad from its anterior end, and the posterior semicircular canal passes caudad from its posterior tip. From the posterolateral surface of the cochlea a bony plate passes laterad to become contiguous with the mesial edge of the tympanohyal. The most caudomesial part of the squamosal, the tympanohyal, and the plate from the cochlea form a tentorium over the stapes, the incus, and the head of the malleus. The tympanic ring is an incomplete oval of bone, with the opening caudad. The mesial arm expands at its posterior extremity, covering the ventral aspect of the orbicular apophysis of the malleus, and is weakly united to the tympanohyal. The lateral arm, falciform at its

terminus, is fused solidly with the processus anterior Folii. The manubrium projects cephalad toward the center of the tympanic ring.

**Malleus (Fig. 4).**—The malleus is the largest of the three ear bones. It may be resolved into two prominent anteriorly directed processes, communicating caudally by a mesiolateral plate. The delicate, anteriorly directed manubrium broadens posteriorly at its base, from the inferior surface of which the short stout processus lateralis (brevis), wedge-shaped in cross section, passes craniolaterad. A thin lamina from the anterior tip of this process follows the manubrium almost to its tip, then disappears into the dorsoventrally compressed, spoonlike terminus of the manubrium. The dorsal edge of the manubrium is also bounded by a very narrow lamina, visible upon examination of the mesial surface. A prominent globular projection, the orbicular apophysis, arises imperceptibly from the base of the manubrium and extends mesiad at an angle of about  $65^\circ$  from its base. The bases of the orbicular apophysis and the manubrium join each other and on the ventral surface of the malleus send a tongue of dense bone into the lamina, whereas on the dorsal surface this tongued projection forms a thin arch connected with the lamina only at its edges. Arising from the posterodorsal aspect of the junction of the neck and the base of the orbicular apophysis and directed slightly posteromesiad, is a short protuberance, the processus muscularis. From the posterobasal part of the orbicular apophysis arises a thin ledge of bone which extends caudolaterad, describes a smooth arc ventrally, and, flaring out on its ventral surface, dips gently craniolaterad to join the mesial edge of the posteriorly directed articular surface of the head of the malleus. On the posteroventral surface of the malleus is a cup-shaped structure, the capitulum mallei, which has a somewhat narrow connection with the orbicular apophysis. A long plate passes anteriad from the base of the head, describes a shallow sigmoid curve, and fuses with the dorsal surface of the tympanic ring. This plate, the processus gracilis, has a dorsomesial and a ventrolateral edge; it has about the same width as the head of the malleus and the same length as the manubrium. A thin bony lamina connects the neck, the orbicular apophysis, and the posterior region of the processus gracilis. This lamina joins the mesial surface of the processus gracilis longitudinally along the mid-line of the caudal arc of the sigmoid curve. Immediately below this point of union is a small foramen for the passage of the chorda tympani nerve.

**Incus (Fig. 5).**—The incus consists of a prominent V-shaped body with the apex directed caudad. The inside of each arm forms a surface for articulation with the head of the malleus, the shorter arm for the dorsal surface and the longer arm for the ventral surface. The dorsomesial surface of the body constricts into the tapering, cylindrical crus longum (processus longus), which, after passing mesiad, bends sharply dorso-caudad at about a  $90^\circ$  angle and terminates by a mesiolaterally constricted, narrow, terminal peduncle which ends in the center of, and perpendicular to, the flat, circular processus lenticularis (os orbiculare).

**Stapes (Fig. 6).**—The stapes is in the form of a signet ring, the capitulum stapedis and the basis stapedis being rather delicate structures. The former is an almost circular plate, somewhat larger in diameter than the

os orbiculare of the incus, and has a roughened, somewhat concave, ventral articular surface inclined slightly caudad. From the posterior base of the capitulum stapedis arises a heavy bar, the posterior crus, which passes dorsad in a small, posteriorly convex arc and unites dorsally with the posterior edge of a thin oval plate, the basis stapedis. The base is contained within the fenestra vestibulae and is thinner at its center than around its margin but is not arched dorsally. The entire stapes lies at a slight angle to the longitudinal axis of the skull; the posterior crus is directed caudolaterad; the anterior crus, anteromesiad. Just dorsal to the capitulum stapedis the posterior crus bears a slight elevation, the stapedia process. The thinner, more highly arched anterior crus arises from the anterior base of the head and passes dorsad to join the footplate.

### Dentary

Lateral View (Fig. 7).—The dentary consists of a horizontal body which is joined caudally at an angle of about  $150^{\circ}$  by a triradiate ramus. The body is relatively heavy, being about twice as long as high, and its dorsal and ventral edges are parallel posteriorly but converge anteriorly toward the apex. A mental foramen, surrounded by a slight depression, is visible ventral to the first molar. The margin of the ramus, which forms the anterior edge of the coronoid process, slopes sharply dorso-caudad, whereas its posterior edge makes an obtuse angle with the ventral border of the body, the angle being tipped by a small tuberosity. From the short stem of the ramus arise a broad coronoid process directed dorsad, a weaker cusplike condyloid process directed dorsocaudad, and a thin angular process directed horizontally caudad. A supracondylar (mandibular, sigmoid) notch lies between the coronoid process and the condyle, and an infracondylar notch lies between the condyle and the angular process. Each notch is about 1.5 mm. deep. A small tubercle projects caudad from the dorsocaudal edge of the coronoid process. Originating from the mid-line of the coronoid process is a spicular process which sweeps caudad just ventral to the tubercle. Six mandibular teeth—one incisor, one canine, one premolar, and three molars—are visible, capping the alveolar border of the body. The first incisor is pronate and extends about 3 mm. anterior to the canine, concealing the cephalic extent of the body of the dentary.

Medial View (Fig. 8).—This view reveals the anterior extent of the body of the dentary, which forms a tongue of bone terminating just anterior to the border of the canine. The symphysis is about 2.5 mm. long and lies along the ventral border of the body. The angular process has an incurved spatulate tip. A heavy bony ridge arises just below the apex of the coronoid process and, becoming broader as it descends ventrocaudad, merges into the superior edge of the condyle. Originating on the body of the condyle and connected by a lamina of bone with the main mass of the condyle caudal to it, is a well-formed process which projects mesiad. Running transversely along the posterior surface of the condylar lamina and continuing across the main body of the condyle is a concave, bipartite, articular facet. The dorsal part of the facet articulates with the

supraglenoid articular surface of the cranium, and the ventral part articulates with the infraglenoid articular surface.

At the base of the coronoid process can be seen the rim of the cavernous posterointernal ramal fossa which extends vertically for 2 mm. into the ramus of the dentary and accommodates the insertion of some fibers of the massive temporal muscle. The fossa through which these temporal fibers enter the dentary has been noted by earlier investigators. It has been termed the pterygoid fossa by C. W. Hibbard (1943; 1944) and the internal temporal fossa by Stirton (1930) and Macdonald (1947). The former name is misleading since the pterygoid muscle bears no relation to this fossa, and the latter is confusing because a similar term is used to define a region on the skull. Because of this ambiguity, Jackson proposed the term "posterointernal ramal fossa" (Hibbard, 1953). Dorsal to this fossa lies a shallow fossette, and ventral to the mouth of the fossa are two small foramina, a dorsal one opening into the fossa, and a ventral one opening into the mandibular canal. Both foramina carry twigs of the inferior alveolar branch of the mandibular ramus of the fifth cranial nerve. These two foramina may be represented by one opening, the greater part opening into the posterointernal ramal fossa and only the most anterior region, separated by a thin vertical plate of bone from the fossa, opening into the mandibular canal.

#### Hyoid and Laryngeal Cartilages

Parker (1885), van Kampen (1905), van der Klaauw (1931), and Sprague (1944) have considered the hyoid region in placental mammals.

Hyoid (Figs. 16-19).—The hyoid apparatus consists of eleven ossified elements. A thin, median, transverse bar, the basihyal, articulates posterolaterally with the pair of thyrohyals and anterolaterally with the pair of hypohyals. The thyrohyal, arcuate and flattened, articulates by a short cartilaginous stem with the anterior cornu of the thyroid cartilage. The hypohyal is a short flattened element passing anterolaterad and bending sharply upon itself near its end to meet a slender cylindrical ceratohyal, which in turn articulates with the caudally directed stylohyal element. The tympanohyal is fused to the cranium anterior to the stylomastoid foramen and is joined with the stylohyal by a tympano-styloid synchondrosis.

Thyroid (Figs. 16, 17).—The thyroid, the largest of the laryngeal cartilages, is a semilunar calcified arch, open dorsally. The anteroventral border of the arch has a prominent anterior thyroid notch, and the ventral surface is slightly keeled posteriorly. At the open side of the arch each edge has an anterior and a posterior cornu. The posterior cornu articulates with the lateral surface of the cricoid cartilage, and the anterior cornu joins the thyrohyal by a small bar of cartilage.

Cricoid (Figs. 16, 17, 18).—The calcified cricoid cartilage consists of a dorsal lamina and a ventral arch. The lamina, concave dorsally, is rectangular in outline; the narrow ventral arch joins the lamina at an angle of between 30° and 40°.

Arytenoid (Fig. 18).—The arytenoids are small triangular calcified cartilages capping the anterolateral surfaces of the cricoid lamina.

## Cervical Vertebrae

**General Form.**—The cervical series of vertebrae as a unit describes a very shallow arc, concave dorsally. Sagittal lengths of centra three to seven are almost equal to one another. The centrum of the axis, however, is about 2.8 times longer than that of the other cervicals, mainly because of its large prezygapophyses and odontoid process. The atlas, possessing no centrum, is the smallest cervical vertebra in this dimension. The width of the pedicels and the span of the neural arches increase very slightly and gradually from the axis to the seventh cervical vertebra. The laminae are well developed, but the neural arches, except those of the first two vertebrae, are depressed. The vertebral canal is ovoid in transverse section in the atlas and axis, but it is somewhat depressed in the remaining cervicals. The neural spines are poorly developed, being represented by very small tuberosities capping the anteriorly inclined arches on the third and fourth cervical vertebrae, but becoming progressively more distinct on the fifth to seventh vertebrae. The dorsal edges of the atlas and axis extend several millimeters above the spines of the remainder of the cervical series, owing in the atlas to the greatly enlarged vertebral canal and in the axis to the well-developed spine. A foramen transversarium perforates each cervical vertebra except the seventh. The wings of the atlas and the transverse processes of the axis are poorly developed, but those on the remaining cervical vertebrae are prominent bony struts projecting laterad from the centra. The transverse processes of the more anterior vertebrae are directed caudolaterad, forming an acute angle posteriorly with the lateral edges of the centra. This angle increases gradually in successive vertebrae until the transverse process of the seventh cervical is at right angles to the centrum. The apices of the transverse processes are the extreme lateral points of the cervical series. Costal processes, present on the fourth to sixth cervical vertebrae, project cephalomesiad. The costal process of the sixth cervical vertebra has a bifid terminus; the posterior tine is more than twice as large as the anterior tine and extends caudad to the anterior border of the first thoracic vertebra. In a ventral view the reniform centra are concave anteriorly and convex posteriorly. In end view they are three times as broad as high and are about half as wide as the vertebral canal. Medially situated hypapophyses project caudoventrad from the second to fourth vertebrae of the series. Prezygapophyses and postzygapophyses are well developed with articulation surfaces becoming more oblique in the posterior region.

**Atlas (Figs. 9, 14).**—The width of the atlas is only slightly greater than its height. The dorsal tubercle (spinal or neural process) is not distinct from the neural arch, being only a small projection cranial from the anterior mid-sagittal line of the arch. The ventral tubercle is a prominent hastate process directed caudoventrad. The dorsal arch is gently convex; the ventral arch is deeply convex, leaving a somewhat oval vertebral canal. The transverse process is deltoid in shape and projects ventrocaudad. A foramen transversarium pierces the lateral mass between the transverse process laterally and the posterior articular facet mesially and passes obliquely cephalodorsad through the bone to emerge

immediately ventral to the anterior edge of the base of the transverse process. A large atlantal foramen pierces the dorsolateral surface of the neural arch and is connected by a shallow channel with the foramen transversarium. The posterior articular facets, mesially directed reniform concavities on the lateral mass of the atlas, form the ventral border of the vertebral foramen. The anterior articular facets, which occupy the interval between the dorsal and ventral neural arches and articulate with the occipital condyles, are 3 mm. in height and are dorsoventrally oblique.

Axis (Figs. 9, 14).—The length of the centrum is equal to the total height of the vertebra, but the width is considerably less. The floor of the vertebral canal is formed by the flat roof of the centrum, its ventrolateral walls are formed by the short pedicels, and its well-arched roof is formed by the strongly curved laminae which bear a well-developed spinous process. The convex prezygapophyses lie horizontally, their medial edges merge imperceptibly into the walls of the peglike odontoid process, and the ventral edges of their facets are recurved caudally below the base of the centrum, forming a small fossette between their surface and the ventral surface of the centrum. A conspicuous dichotomous plate of bone, the hypapophysis, arises from a median longitudinal line of the ventral surface of the body; the anterior part of the plate is a small blunt spur, the posterior part terminates in a ventrocaudally directed falciform blade. The postzygapophyseal facets are oval in outline and lie almost horizontally, the articular surfaces facing ventrad.

Cervical Vertebrae Three to Seven (Figs. 9, 14).—These vertebrae, very similar to one another, have delicate, compressed, neural arches, vertebral canals of modest dimensions, stunted spinous processes, prominent intervertebral foramina, and cephalocaudally compressed and transversely broadened centra. The transverse processes on cervicals three to seven are well developed. Cervical vertebrae four and five bear sickle-shaped costal processes directed craniodorsad, whereas the costal process on the sixth cervical is dichotomous and has a large posterior falciform part which extends caudad to the anterior border of the first thoracic vertebra. Projecting ventrocaudad from the mid-ventral line of the centra of the third and fourth cervical vertebrae are prominent, scythelike, terminally bifid blades of bone, the hypapophyses.

#### Scapula (Figs. 10, 11)

The scapulae of insectivores have been considered in the works of de Blainville (1839-64), Bronn (1874-1900), Edwards (1937), Slonaker (1920), Campbell (1939), and Reed (1951). The first two authors gave excellent illustrations of the scapulae of *Talpa* and *Sorex*; Edwards and Slonaker illustrated the scapula of *Scalopus*, Campbell compared the scapula of *Blarina* with the scapulae found in various talpids, and Reed considered the scapulae of *Scapanus*, *Nellrotrichus*, and *Sorex*.

The scapula of *Blarina* is triangular in outline, elongate dorsoventrally, but narrow anteroposteriorly. The axillary and superior borders gradually approach each other ventrally to form a constricted neck region

before expanding to form the lips of the glenoid cavity. The vertebral border of the infraspinatus area of the scapular blade is capped by a smoothly convex tuberosity. A prominent suture lies between this cap and the scapular blade. The spine, 2 mm. at its greatest height, extending from the mid-point of the vertebral border to the anterior edge of the neck of the scapula, forms a thin, triangular, anterodorsally situated supra-spinatus fossa and a thicker, rectangular infraspinatus fossa. The latter reaches from the vertebral border to the glenoid cavity; the former occupies only the dorsal third of the blade. A small tubercle is visible at the apex of the lateral edge of the spine. A Y-shaped osseous process continues ventrally from the spine; the anterior horn is the spiculate acromion process which articulates with the clavicle, and the posterior horn, the metacromion process, is the longer of the two and bears an expanded terminus. A prominent ridge which follows the long axis of the medial surface of the neck of the scapula may represent the coracoid process. Reed (1951) stated that the coracoid process is prominent in *Sorex*, but he did not label it in his figure.

#### Clavicle (Fig. 12)

The clavicle has an orthodox mammalian form. It articulates mesially with the manubrium and laterally with the acromion process of the scapula, and a ligament connects its body to the superior lip of the glenoid cavity.

#### Manubrium (Fig. 13)

The manubrium (presternum), the first segment of the sternum, represents almost one-fourth of the total length of the sternum. The body is narrow and bears a median ridge along its ventral surface. Its posterior half is about as wide as the succeeding sternebrae, but it expands anteriorly to form a trefoil. The tip of the manubrium lies ventral to the articulation plane between the centra of cervical vertebrae five and six.

#### *Scalopus aquaticus machrinus*

#### Cranium

Literature dealing with the cranial osteology of insectivores contains only a few direct references to *Scalopus*. The most valuable aids to my interpretations have been Parker's monograph (1885), van Kampen's studies of the tympanic region of the European mole (1905), and the work of Giebel (1858) and of Dobson (1882-90).

In my effort to analyze the cranium I have studied thirty crania from adults and two from young specimens, cleared and stained after the Spalteholz method (Williams, 1941). The most immature specimen was a nestling with the following measurements (in mm.): total length, 60;



head length, 30; hind foot, 11; tail, 10 (Fig. 67). Even at this early stage some synosteosis had already taken place.

**General Form.**—The cranium of the mole, like that of the shrew, is a fused osseous complex in which only a few of the component elements can be delineated with certainty. It is smoother and more streamlined than the angular skull of the shrew. At first glance, its proportions appear to differ from those of *Blarina*, but when actual measurements are made the two skulls are found to be very similar. In the cranium of *Scalopus* the mean length is three and four-tenths times the greatest height. As in *Blarina*, the greatest width is at the base of the zygomatic processes of the squamosal. The greatest height of the cranium, which is more anterior than in the shrew, is at the point where the temporal lines limiting the posterior edge of the temporal fossa meet at the suture between the parietal bones. The height of the cranium increases gradually from the rostrum to this point. There is, however, no lambdoidal ridge, so that the rear of the brain case is smoothly rounded and does not present the angularity seen in *Blarina*. In *Scalopus* the postnarial rostral height is less in relation to the greatest height at the posterior region of the cranium than it is in *Blarina*. Here, as in *Blarina*, the rostral part is of a denser bony construction than are the frontal and parietal regions. The roofing bones, though thin, are by no means fragile, a considerable amount of pressure being required to fracture them. In contrast to the condition in the shrew, a rather thin, bony zygomatic arch is present, stronger in fact than in appearance. The auditory ossicles are covered ventrally by tympanic bullae, and only one articular facet appears on the cranium for articulation with the condyle of the dentary.

**Norma Verticalis** (Fig. 20).—The occipital and parietal regions are broad, but not so thin walled as they are in the shrew. Posterior to the base of the zygomatic arches the cranium forms a gently curving convex arc; anterior to this point its walls converge rapidly to form a narrow constriction, flare out slightly over the turbinals, which are visible through the overlying frontals, and then at the level of the infraorbital foramen its walls blend into the still broader maxillary area. From this area forward the walls parallel each other and end abruptly at the bifurcated narial apex. The zygomatic arches, connecting the base of the squamosal region with the more anterior maxillary, fill out the orbito-temporal constriction and complete the general fusiform shape. Visible in this aspect are a median sagittal and two transverse sutures. The sagittal suture marks the denticulate medial margins of the two very large parietal bones, and its anterior half is raised to form a slight crest continuous anteriorly with the more prominent crest between the frontals. Of the transverse sutures, the anterior, which resembles an inverted W, is the frontoparietal articulation. The posterior suture lies between the parietal and a large platelike supraoccipital, forming the dorsal border of the foramen magnum.

Parker (1885) has indicated the presence of an interparietal in *Talpa*, as well as in the other insectivores included in his monograph. The presence of an interparietal in *Talpa* is confirmed by de Beer (1937), though it is not clear whether his statement represents a personal

observation or a repetition of Parker's findings. I examined several crania of *Talpa europaea*, all of which showed a very extensive interparietal. Concerning the Talpidae, Winge (1941: 169) stated, as translated by Deichmann and Allen: "*Supraoccipitale*, together with *Interparietale*, expands in the roof of the braincase." Giebel (1858), in one of the two reports I have been able to find in which the North American mole is specifically considered, did not mention an interparietal bone. Likewise, Dobson (1882-90), in his section "*Condylura*, *Scapanus*, *Scalopus*, *Talpa*, etc." made no statement concerning an interparietal. Jackson (1915), however, under the heading "*Scalopus*," said: "Interparietal short and narrow, somewhat irregular in outline, but usually narrower anteriorly." In the adult cranium I find absolutely no evidence to substantiate Jackson's statement. Moreover, in the nestling *Scalopus* which I examined, if an interparietal was present, it had already fused with the supraoccipital or the parietals.

In the immature specimen studied the nasals are paired, distinct elements, the anterolateral borders being overlapped slightly by the dorsal edges of the premaxillaries and maxillaries. Their anterior apices reach as far forward as the anterior tips of the premaxillaries, so that it is impossible to be sure that the premaxillaries form the tip of the most anterodorsal part of the bony rostrum as reported by Giebel (1858) and Jackson (1915). One skull, however, which I obtained from the casting of a barn owl does show the suture between the premaxillaries and nasals and definitely confirms the observations of these men. The posterior tips of the nasals are intercalated between the medial margins of the frontals. No distinct lachrymal was visible, but there was evidence in the nestling that this element had already fused with the maxillary.

The large paired parietals of the mature cranium have already been mentioned. Along their posterolateral borders is a weak indication of the parietosquamosal suture and, farther posterior, of the suture between the parietal and Parker's "prootic" element. The thinnest bone exists in the lateral wall of the maxillaries where it covers the molar roots. The infraorbital foramen transmitting the homonymous branch of the trigeminal nerve can be seen at the base of the zygomatic process of the maxillary. The base of the zygomatic process of the squamosal forms a broad, triangular, horizontal ledge, from which fibers of the temporal muscle originate. The squamosal projects laterad at the lateral surface of the base of the arch, forming a prominent crest. Medial to the crest, at the parietosquamosal suture, is a large venous foramen. The nasal openings are vertical and are not visible in dorsal view as they are in the cranium of *Blarina*.

Norma Basalis (Fig. 21).—The dentition of *Scalopus* has been figured by de Blainville (1839-64), Baird (1859), and True (1897) and has been described by numerous other authors. The nestling mole which I examined showed both lacteal and permanent dentition, in addition to the premaxillary-maxillary suture, and confirmed the correctness of the dental formula:  $\underline{3}, \underline{1}, \underline{3}, \underline{3}$ .

The palate is narrow anteriorly between the canines and premolars but widens at the level of the third premolar, forming laterally a convex

arc which terminates several millimeters caudal to the third molar in a transverse plate, the posterior edge of which is similar in shape to a brace (}). In the narrow part of the palate mesial to I<sup>2</sup> and I<sup>3</sup> is a pair of perforations which appear to be the incisive foramina, but I could not identify the structures which they transmit. About 2.3 mm. caudal to these openings, in the mid-line between the canines, is a minute foramen through which a structure passes caudad to emerge on the floor of the nasal cavity by paired foramina on the lateral surface of the mesethmoid. It was impossible to identify this structure in gross dissection. A pair of prominent foramina is seen in the palate at the region of M<sup>2</sup>, the dorsal walls of which are continued forward on the palate by a pair of furrows. These are the posterior palatine foramina which transmit the palatine branches of the maxillary division of the trigeminal nerve. At the posterolateral edges of the palate, caudal to M<sup>3</sup>, is a pair of foramina, the lesser palatine foramina, which transmit palatal twigs from the maxillary division of the trigeminal nerves. Butler (1948), in his paper on the Erinaceidae, figured a similar pair of openings which he identified as the posterior palatine foramina. This term, however, is more properly reserved for the foramina situated at the maxillopalatine suture. Between the anterior palatine foramina (incisive foramina) and the posterior palatine foramina are several inconstant perforations for palatal twigs of the trigeminal nerve, which I leave unnamed. In the immature cranium the foramina caudal to M<sup>3</sup> are merely notches at the posterolateral margins of the palate.

The premaxillaries are small elements bearing a median tongue-like process which passes caudad and intercalates between the extensive maxillary bones. A very long zygomatic process of the maxillary projects caudad from a point near the base of M<sup>3</sup>. This suggests an early fusion of the malar bone with the zygomatic process of the maxillary. The premaxillaries surround the palatal part of the palatine bones anteriorly and laterally. The floor of the cranium, posterior to the palate, is rather thin-walled, inflated, and without visible sutures. The boundaries of the pterygoid, palatine, sphenoid, tympanic, and periotic bones cannot be determined. A well-developed mesopterygoid fossa is present.

In the nestling the palatines continue caudally from the posterior border of the hard palate as paired plates bounding the mesopterygoid fossa. The sphenoid elements have already started to fuse, forming a median mass with a pair of lateral alae. The pterygoid has fused with the sphenoid complex, and a pair of pterygoid hamuli projects caudoventrad from this region. The basioccipital, a small hexagonal bone notched posteriorly, lies posterior to the sphenoid, its posterolateral edges being flanked by the reniform exoccipitals. A large squamosal, having a very short zygomatic process, forms the lateral wall of the brain case, followed by a platelike part of the periotic which appears to be homologous to Parker's "prootic." The remainder of the periotic lies between these elements.

Several perforations are seen in the posterior region of the mature cranium. In the groove between the diploic alisphenoid region and the tympanic bones, about 2 mm. from the mid-line, is the foramen for the

Eustachian tube. A very small opening lies at the anterolateral edge of the tympanic bone, and through it the chorda tympani nerve, a branch of the facial nerve, emerges after its passage through the tympanic chamber to continue anteroventrad and join the lingual nerve. Posterolateral to this foramen, at the lateral edge of the tympanic, is the flattened, oval, external auditory meatus. At the caudal edge of the tympanic is the large carotid foramen through which the internal carotid artery enters the cranium. In the anterior rim of the carotid foramen is a small perforation for the passage of a branch of the superior cervical ganglion of the sympathetic nervous system. Several millimeters posterolateral to the carotid foramen is the stylomastoid foramen for the exit of the facial nerve. At the posterior rim of the tympanic, about 2 mm. lateral to the carotid foramen, is a small perforation for the tiny chorda tympani twig of the facialis. This twig passes forward into the tympanic cavity to enter a canal in the lamina of the malleus, emerges from it by a small hole in the processus gracilis, and continues its passage through the tympanic chamber. At the anterolateral edge of the condyle are two perforations. The smaller, more posterior of the two, perforating the edge of the condyle, is the hypoglossal (condylar) foramen for the exit of the homonymous nerve; the larger, more anterior perforation, lying between the condyle and the periotic, is the posterior lacerate or jugular foramen for the exit of the glossopharyngeal, vagus, and spinal accessory nerves. A bony canal, running posterolaterad from the opening for the facial nerve to the posterior lacerate foramen, contains a twig from the facial nerve, which passes to the base of the vagus nerve.

*Norma Lateralis* (Fig. 22).—In this aspect the cranium presents the same general proportions as does that of the shrew, but is less angular in the occipital region, more swollen in the sphenoidal and basioccipital regions, and possesses a complete zygomatic arch. The superior alveolar shelf presents a sinuous border. The basal part of the zygomatic process of the maxillary bone, at the level of  $M^2$ , is bifurcated by the triangular infraorbital foramen. The dorsal arm of the yolk is a thin spiculum, whereas the ventral bar is of heavier proportions. At the base of the zygomatic process of the squamosal is a prominent ledge directed obliquely dorsocaudad and terminating dorsally in an anteriorly projecting process. This ledge provides the surface for origin of the snout muscles.

Numerous perforations can be seen in the side of the cranium in the region between the maxillary and squamosal bones. Immediately dorso-caudal to  $M^3$  is the very large sphenopalatine foramen for the palatine branches of the maxillary division of the trigeminal nerve. About 3 mm. caudal to this opening is a small bony shelf projecting dorsally and concealing a very small foramen which transmits the Vidian nerve, of which only the deep petrosal branch from the superior cervical ganglion of the sympathetic nervous system could be traced. Several millimeters dorsal to the bony ledge are one or more tiny ethmoidal perforations for homonymous twigs of the ophthalmic division of the fifth cranial nerve. Posterodorsal to the bony ledge is the optic foramen for the optic nerve, and following this is a very large aperture, the combined foramen rotundum and inferior orbital fissure, transmitting the ophthalmic and maxillary

divisions of the trigeminal nerve and the internal maxillary artery (pterygopalatine artery). Usually a vertical bony strut divides the opening into a median foramen for the division of the fifth cranial nerve and a lateral foramen for the artery. About 1.5 mm. farther caudad is an opening through which the internal maxillary artery passes. The bony lateral wall, connecting the last two foramina, caps the dorsal edge of the inflated part of the alisphenoid bone and forms the alisphenoid canal.

Farther caudad, ventral to the base of the zygomatic arch, is the large foramen ovale for the passage of the third division of the trigeminal nerve. Immediately lateral to this opening, seen only in an anterolateral view, is the perforation for the exit of the internal maxillary artery from a furrow in the floor of the cranial case. Posterolateral to this opening, not visible in a direct lateral view, at the medial edge of the infraglenoid lip is a foramen through which a vein emerges from the interior of the brain case. Approximately midway between the extremities of the zygomatic arch and several millimeters dorsal to the level of the arch is a foramen which pierces the frontal bone. From it a very thin-walled canal passes within the frontal bone of the skull to a similar perforation on the opposite side. This canal contains a vein which communicates with the median sagittal sinus within the brain case. Visible in this view are the external auditory meatus, the stylomastoid, the jugular, and the hypoglossal foramina which have already been discussed. At the base of the zygomatic arch is the transverse, cup-shaped mandibular fossa which receives the head of the condylar process of the dentary. The flattened, platelike base of the zygomatic process of the squamosal extends several millimeters anterior to the base of the articular surface and allows for some anteroposterior movement of the mandible.

*Norma Occipitalis.*—The rear of the cranium is roughly ovate in outline. The roof is less convex than the floor and presents two ventrolateral hillocks produced by the cancellous basisphenoids and the inflated tympanic bullae. The median sagittal crest does not extend far enough caudad to be visible in this view. The most lateral margin of the brain case is formed by the heavy flanges of the squamosal, which has been described. In the ventral surface of the cranium is the very large, oval foramen magnum. Its lateral margins are formed by the rather heavy occipital condyles, and its dorsal margin is formed by the supraoccipital bone. The supraoccipital has a median convexity and a pair of lateral convexities and is capped by the large parietals. The posterior wall of the cranium is more delicate than the roof.

*Norma Frontalis.*—The nares are pentagonal in outline; their periphery is limited by the premaxillaries except at their most dorsal point, where the two arms of the premaxillaries do not meet, leaving a gap of about .5 mm. to be filled by the interjected tips of the nasals. In the midline of the nasal cavity the perpendicular ethmoid plate can be seen about 2 mm. caudal to the apex of the snout, and the V-shaped vomer is visible at the anterior tip of the floor of the snout. Flanking either side of the ethmoid are simple platelike nasoturbinals attached at their dorsal edges to the nasal bones, and lateral to these nasoturbinals a part of the scroll-like maxilloturbinals can be seen. In this view the flattened, streamlined

contour of the cranium can again be appreciated. Also seen in this view are the median sagittal crest on the frontal, the ridges delimiting the fossa anteriorly, and the large triangular infraorbital foramina at the base of the zygomatic processes of the maxillaries.

Ossicula Auditus  
(Figs. 23, 24, 25)

With the removal of the tympanic bulla only the processus gracilis, the manubrium mallei, the lamina, and the collum mallei are visible. The caput mallei and the corpus incudis rest in a cavity, the epitympanic recess, roofed over by the squamosal and hidden by a vertical bony septum. The crista tympanica forms a complete ring, the posterior rim of which is barely visible. The malleus is tilted obliquely dorsolaterally; the manubrium and the processus gracilis parallel each other as they pass anteriorly almost at right angles to the neck. The caput mallei is lateral in position and articulates with the head of the incus. The processus longus of the incus passes posteromesially to articulate with the head of the stapes. The anterior end of the footplate of the stapes is more medial than its posterior end, and the head of the stapes is more lateral than the footplate. The malleus of the prairie mole lacks a processus lateralis (brevis) and a processus muscularis, both of which are found in the malleus of the shrew. The orbicular apophysis is rudimentary, and the lamina is not so extensive as in the shrew. The incus possesses a short crus, and the stapedia crura enclose a circular space through which passes a bony tube. The ossicles of *Scalopus* have been figured by Stroganov (1945).

Malleus (Fig. 23).—When viewed from the ventral surface, the caput mallei is a flattened, knob-shaped cap bearing a shallow, sigmoid, convex articular surface for the head of the incus. A narrow collum mallei passes anteromesially from the head at about 90°, then turns sharply medially to form an obtuse angle. Also, from the head two bony plates pass forward, one originating from the anterodorsal and the other from the anteroventral part of its base. At about 8 mm. mesially to its origin the dorsal plate turns sharply ventrad to meet the ventral plate, thus enclosing a deep fossa which opens anteriorly. A delicate lamina, triangular in outline, extends from the point of fusion of these two plates to the base of the manubrium mallei. On the basis of Wassif's studies (1948) this lamina is the processus gracilis. The manubrium is a thin falcate process, flattened laterally and directed anteriorly. At the medioventral edge of its base is a small rounded prominence which probably represents a much reduced orbicular apophysis. I found no suggestion of a processus cephalicus. The posterior edge of the neck immediately medial to the head bears a deep furrow at the base of which a small foramen can be seen. From this opening a canal passes laterally through the neck to emerge as a minute hole in the fossa enclosed on the lateral side of the base of the processus gracilis. This bony canal carries the chorda tympani twig from the facial nerve. To my knowledge, the passage of this twig through the malleus has not been reported in any previous study of talpid anatomy. Wassif (1948), however, described this condition in *Crocidura religiosa* (Geoffroy),

*Hemiechinus auritus* (Gmelin), and *Paraechinus dorsalis* Anderson and De Winton. This perforation of the processus gracilis of the malleus by the chorda tympani is in harmony with the ontogenetic origin of these bony elements. Concerning the anterior process of the malleus de Beer (1937) stated:

The *processus anterior* (Folli, gracilis) of the malleus may with reasonable certainty be regarded as in part formed of the homologue of the *prearticular* (*postopercular* of Gaupp, 1905b, or *goniale* of Gaupp, 1908) of reptiles, and birds (Voit, 1924). As Gaupp (1911b) has shown, it is a *membrane-bone* situated on the medial side of Meckel's cartilage, and the chorda tympani nerve runs forward between the two, which is a characteristic relation. Later, the prearticular fuses with the articular in birds (Cords, 1904; Voit, 1924), or with its homologue the malleus in mammals. It is to be noted that some authors regard the terms "processus anterior (gracilis or Folli)" and "prearticular" as equivalent. However, it should be noted that the processus anterior is primarily a part of the malleus representing all that is left of its connexion with Meckel's cartilage and ossifying as cartilage-bone, to which the prearticular membrane-bone subsequently becomes fused.

**Incus** (Fig. 24).—The second ossicle in *Scalopus*, the incus, is mushroom-like in outline; its head and the processus brevis represent the pileus, and its processus longus represents the stipe. The articular surface is convex and projects posterolaterad beyond the medial edge of the processus longus to form a short spur. The processus brevis is a short conical prominence anchored securely at its apex to the wall of the epi-tympanic chamber by a ligament. The long process is a thin triangular plate of bone folded to form a conical gutter, the concavity opening posteroventrad. The process passes posteromedial for about 1.5 mm., then turns dorsad and terminates almost immediately in a very delicate ligamentous thread capped by the disclike lenticular process (Sylvian apophysis). Invariably, this ligament breaks when the ossicles are removed, leaving the cartilaginous apophysis attached to the capitulum stapedis. In fact, Stroganov's illustrations of the ossicles of *Scalopus* figure this unnatural condition. Wilkie noted this unusual condition in *Talpa*, but did not mention the existence of the delicate ligament between the tip of the long crus and the apophysis.

**Stapes** (Fig. 25).—The capitulum stapedis in *Scalopus* is also discoidal, but is slightly greater in diameter than the apophysis and is scarcely separated from the crura. The anterior crus is generally heavier than the posterior crus and circumscribes a wider arc than the latter. A small but readily recognizable stapedial process projects caudad from the posterior leg of the stapes. This process is not shown in Stroganov's plates. The two crura widen as they approach the footplate, their lateral edges end sharply at the plate, but their medial edges pass centrifugally, gradually to disappear in the substance of the plate, leaving an almost circular intercrural canal for the stapedial artery. The footplate is an elongate oval and may be flat, or its inner surface may be concave. The part caudal to the posterior crus is more extensive than that forward of the anterior crus. The stapes was well ossified in the seven specimens which I examined, a condition unlike that cited by Wilkie for the European mole.

### Dentary

**Lateral View (Fig. 29).**—The length of the body of the dentary is over three and one-half times its greatest width; its ventral margin is markedly convex in the molar region. Almost 2 mm. posterior to the base of  $M_3$  the thickened anterior edge of the coronoid process passes dorsocaudad from the body of the dentary to a level several millimeters dorsal of the zygomatic arch. Here it forms a small posterior spur which meets the sinuous posterior edge of the coronoid to form a dorsomesially sloping triangular plate. Ventrally, separated from the body by a marked ventral concavity and passing caudoventromesial, is a large, shovel-like, thin-walled, angular process. A ridge, concave dorsally, extends from the inferior edge of the infracondylar notch to the base of the angular process. A triangular condylar process passes dorsocaudad from the ramus, forming an obtuse angle with the posterior border of the coronoid process and an acute angle with the superior edge of the angular process. The inferior edge of the condylar process is thickened, forming a ridge which reaches to the base of the thickened anterior lip of the coronoid process, thus causing the greater part of the condyle and coronoid to appear depressed. The mental foramen is about 1 mm. ventral to the alveolar border of  $P_4$ . The dental formula is:  $\bar{2}, \bar{0}, \bar{3}, \bar{3}$ .

**Medial View (Fig. 30).**—This surface of the body has a greater dorsoventral dimension than the lateral surface, but appears conspicuously narrower near the trifold posterior ramus. The symphysis menti, at the anteroventral region of the body, is about 3 mm. in length. A ridge passes from the base of the supracondylar (mandibular) notch to the dorsal edge of the body. The mandibular foramen is approximately 3 mm. anterior to the base of the infracondylar notch, and its canal enters the dentary through the ridge. The articular surface capping the condylar process can be seen in this view; its surface is convex, and its plane extends lateromesioventrad. At the base of its medial edge is a small concavity into which fibers of the external pterygoid muscle are inserted. The angle and the coronoid processes are more extensive, and the dentary as a whole is less angular in the prairie mole than in the shrew.

### Hyoid and Laryngeal Cartilages

**Hyoid (Figs. 37, 38).**—The hyoid apparatus consists of nine recognizable elements. A median unpaired element, the basihyal, lies transversely between the greater and lesser cornua. It articulates anterolaterally with the arcuate hypohyals and posterolaterally with the thyrohyal cartilages. The hypohyal cartilages pass cephalad, and at their mid-point they bend ventrolaterally to meet the proximal ends of the ceratohyals. The thyrohyals, directed posterolaterally, expand at their terminals and articulate with the anterior cornua of the thyroid cartilage. The ceratohyal, a flattened rodlike element, passes posterolaterally to articulate with the anterior extremity of the stylohyal, a thin cylindrical element directed caudolaterad. All of these elements are ossified. The caudal tip of the stylohyal does not articulate directly with the cranium, but an arcuate rod of cartilage, showing regional calcification, passes farther



caudolaterad from it to attach to the posterolateral margin of the carotid foramen. There is no recognizable tympanohyal element present in the adult; however, in the cranium of the nestling a small, lunate element, which I consider to be the tympanohyal, can be seen between the tympanic annulus and the "prootic."

**Thyroid (Figs. 36, 37, 38).**—This element is calcified and C-shaped. Its laminae are narrow and are fused in the ventral mid-line. The thyroid lies in an oblique plane, its leading edge anteroventral and its termini posterodorsal. The termini articulate by a pair of posterior cornua with the posterodorsal surface of the lamina of the cricoid cartilage.

**Cricoid (Figs. 36, 37, 38).**—The cricoid is in the form of a hollow calcified cylinder with its long axis in the sagittal plane and its dorsal wall flattened. The anterior and posterior rims of the tube are tangential to the dorsal wall, thus producing a quadrangular outline when viewed laterally. Its dorsal surface is saddle-shaped, its anterior and posterior edges are acuminate, and its ventral wall is notched both anteriorly and posteriorly.

**Arytenoid (Fig. 36).**—The arytenoid cartilages are two small triangular calcified elements which cap the anterior edge of the cricoid cartilage. The base of the triangle is directed cephalad.

#### Cervical Vertebrae

**General Form (Figs. 28, 31).**—The cervical segment describes a shallow arc, convex ventrally, and forms an obtuse angle with the thoracic segment. The sagittal length of the centra decreases from the second to the fifth cervical vertebra, inclusive; the length of the sixth cervical centrum is approximately the same as that of the third. The seventh cervical centrum is the shortest of the series. The centrum of the axis is, as in *Blarina*, the largest of the series. The interlaminar span of the neural arches increases gradually from the second to the sixth cervical vertebra, and at the same time the arches become somewhat less convex dorsally. The pedicels, which are tangential in the anterior cervicals, become progressively more nearly horizontal in a caudad direction. The very prominent spines (hypapophyses), which project caudoventrad from the mid-line of the ventral surfaces of cervical centra two to four in *Blarina*, are represented in *Scalopus* by very aborted spurs. The spinous processes are well developed only on the atlas and axis and reach farther dorsad than do those of the remaining cervical vertebrae. The spine of the atlas is better developed in the mole than in the shrew, but the spine of the axis is relatively larger in the shrew. A rudimentary spine is present on the seventh cervical vertebra. The transverse foramina are similar to those in the shrew.

The transverse processes are very small on the atlas and axis, but are recognizable on all of the cervical vertebrae. They are shorter and heavier than those in *Blarina* and, except on the seventh vertebra, do not project beyond the lateral edges of the articular processes, in sharp contrast to the situation in the shrew where there is a lateral flare of the transverse processes. These processes on the first six cervical vertebrae

pass directly caudad and their terminals are cleft. Costal processes are present on cervicals three, four, five, and six. Those on the third, fourth, and fifth vertebrae pass cephalad from the anteroventral surfaces of the centra, whereas the costal process of the sixth cervical vertebra forms a T-shaped lamina with one spur projecting craniad and the other caudad and slightly laterad for about 1 mm. beyond the posterior edge of the centrum. The dorsal surface of each cervical centrum has a pair of lateral semicircular concavities; the median elevated part of the centrum appears biconcave in outline and has two lateral foramina for intraspinal veins. In general, the breadth to height ratio of the centra in *Scalopus* is similar to that in *Blarina*, and their prezygapophyses and postzygapophyses are similar in character.

Atlas (Figs. 28, 31).—The atlas of the prairie mole is more nearly circular in outline than that of the shrew, owing primarily to the greatly increased surface of the inferior arch. Its anterior articular facets are club-shaped concavities occupying approximately three-fourths of the dorsoventral dimension of the atlas. The facets narrow ventrally and occupy almost the entire anterior surface of the ventral arch. The dorsal arch is wider than the ventral arch and a well-developed dorsal tubercle projects anterodorsad from its surface. The ventral arch, unlike the chevron-shaped arch in the shrew, is a heavy rectangular plate connecting the ventral terminals of the articular facets. Laterally, the atlas of the mole forms a shallow arc, concave anteriorly. A minute transverse prominence projects caudad from the lateral lip of the foramen transversarium and continues anteriorly as a slight ridge which disappears into the substance of the lateral mass of the atlas. Inferior to the foramen transversarium is a fossette for the insertion of the longus atlantis muscle. Ventral to the atlantal foramen is a diminutive opening which transmits the small ventral ramus of the first cervical nerve. Posteriorly, the right and left articular facets for the atlantoaxial joint are continuous ventral to the vertebral canal, forming a U-shaped figure. Immediately dorsolateral to each head of this bicipital facet is the circular opening of the transverse foramen through which the vertebral artery enters the atlas. About 1 mm. dorsolateral to the vertebral foramen is a fossa. A large atlantal foramen for the passage of the first cervical nerve lies at the dorsomesial region of the fossa, and a pair of foramina lies at the ventrolateral region of the fossa. The larger, more medial, of the latter two foramina is for the exit of the vertebral artery from the substance of the atlas; the smaller, more lateral foramen is for the entrance of the ventral ramus of the first spinal nerve which passes ventrolaterad, emerging through the opening already mentioned. The ventral spine is not distinct from the arch, and together they form a transverse plate projecting caudoventrad and serving for the insertion of the more anterior fibers of the longus colli muscle.

Axis (Figs. 28, 31).—The axis of the mole is similar in general form and proportions to that of the shrew. Differences to be noted in the mole include the absence of an anterior process of the neural spine, the heavier construction of the neural arch, the less oblique course of the transverse canal, and the absence of a hypocentral plate.

Cervical Vertebrae Three to Seven (Figs. 28, 31).—These vertebrae are similar in character to the corresponding vertebrae in the shrew. The centra, however, have a smaller width-to-length ratio, and the laminae are better developed in the prairie mole than in the short-tailed shrew. The transverse processes are poorly represented and are directed caudad rather than laterad. A neural spine is recognizable only on the seventh cervical vertebra. In a ventral view the anterior and posterior edges of the centra form parallel transverse plates.

#### Scapula (Fig. 33)

The scapula is an extremely elongate bone very unlike the scapula in other mammalian groups. Its length exceeds four times the greatest width of the blade. It is so oriented that the vertebral border is directed posterodorsad, its dorsal border anterodorsomesiad, and its axillary border posteroventrolaterad. The glenoid fossa for articulation with the humerus is an oval concavity surrounded by a raised lip with no distinct supraglenoid or infraglenoid tubercle. At the base of the glenoid border is a prominent acromion process to which a strong and fibrous acromioclavicular ligament is attached. A small foramen for the passage of the suprascapular nerve pierces its base (Campbell, 1939). There is no suggestion of a coracoid process. The proximal part of the scapula is cylindrical; the distal part is spatulate and bears on its mesial surface a median longitudinal infraspinous fossa enclosed by a horseshoe-shaped ridge which serves to separate it from the more lateral extensions of the blade. The tuber is represented by a small spur overhanging the distal extremity of the infraspinous fossa. The supraspinous fossa is not well represented, but is better developed than Campbell's figure would suggest. The dorsal surface of the vertebral border is flattened and serves for the insertion of the rhomboideus capitis and rhomboideus cervicis muscles. At the distal region of the dorsal border of the blade is a prominent crest several millimeters in length, not mentioned by Campbell, Edwards, or Reed, to which are attached the fibers of insertion of the levator scapulae et serratus anterior cervicis muscle.

#### Clavicle (Fig. 35)

This element is a small, compact, cubical bone very unlike its homologue in the shrew. Its anterior and posterior surfaces are rectangular, with the greater dimension directed dorsoventrad; its body is pierced by a canal passing anteroventrad for the passage of a blood vessel. It bears two articular facets. The lateral facet is saddle-shaped in conformation and ovate in outline, its dorsoventral measurement being about twice as great as its anteroposterior measurement; it articulates with the more expansive clavicular facet of the humerus. The medial facet is an elongated concavity, conspicuously narrower than the lateral facet; it articulates with the anterolateral surface of the manubrium. In the nestling

mole examined the clavicles were of the same general proportion, ossified centrally, but surrounded by a peripheral region of unossified cartilage. Fibers of the cleidomastoid muscle and the cleido-occipital muscle originate from its anteromedial surface.

#### Manubrium (Fig. 34)

This anterior element of the sternum is an elongate falciform bone which extends from the level of the second thoracic vertebra to the region of the centrum of the axis. It carries the limbs far forward to a position immediately caudal to the skull, producing an illusion of the absence of a neck segment. It is compressed laterally, forming a large keel. The anterior three-fourths of its dorsal surface is flattened and hollowed in the mid-line, with alar plates extending lateral to the carina. The anterior edge is T-shaped; the stem of the T lies in the mid-sagittal plane and the crossbar is directed transversely at the ventral edge. Its anterolateral edges bear facets for articulation with the reciprocal surfaces of the clavicles. The costal cartilages of the first and second ribs articulate with the manubrium and the manubriosternal joint, respectively, as is common in other mammals. The superficial and deep layers of the sternomastoid muscle originate from its anterior edge; the sternohyoid and sternothyroid muscles originate from its dorsal surface between the sternocostal articulations of the first rib.

#### MYOLOGY

The following descriptions of muscles have been based on the dissection of nine adult *Blarina brevicauda kirtlandi*, the short-tailed shrew, and twelve adult specimens of *Scalopus aquaticus machrinus*, the prairie mole. Certain regional dissections were made of related forms for comparison and confirmation of observations by earlier workers. These forms included: one adult *Talpa europaea*, the common European mole, one adult *Condylura cristata*, the star-nosed mole, one adult *Neurotrichus gibbsi*, the shrew mole, and two adult *Sorex*, the long-tailed shrew. All dissections were made with the aid of a stereobinocular microscope of 21X magnification.

Since innervation is still the best criterion for determining the homology of muscles, I have traced the nerve supply of muscles in the prairie mole wherever possible (Figs. 64A, B, C, and 65). The small size of the animal, however, placed serious restrictions on the accuracy and completeness with which this could be accomplished. Considerable difficulty was experienced in locating and tracing nerve twigs in the mole, and therefore no attempt was made to determine muscle innervations in the short-tailed shrew, a much smaller animal.

Despite the phylogenetic significance of the insectivores, a careful survey of the rather extensive literature on mammalian anatomy reveals a paucity of useful published research on any member of the order. Among the works treating specifically the Soricidae, Talpinae, Scalopinae,

or Condylurinae are: Camerano's paper (1886), which contains one unlabeled plate of the head muscles of *Talpa*; Boas and Paulli's monograph on the elephant's head (1908), which contains a colored plate of the head of *Talpa* showing the masseter, temporal, and snout muscles; Chaine's article (1914), which considers the digastric and stylohyoid muscles in *Talpa* and *Crocidura*; Campbell's work (1939), which deals with the shoulder anatomy of numerous members of the order; Ackert's paper (1912), which has one plate showing some superficial cranial and cervical muscles of *Scalopus*; Bijvoet's paper (1908), which describes the digastric muscle in *Talpa*; Dobson's work (1882-90), which is prodigious, but which has a very superficial treatment of the regions here under consideration in the North American forms; Dubecq's paper (1925), which considers the temporal and masseter muscles of *Talpa europaea* and *Crocidura aranea*; Edwards' paper (1937), concerning the forelimb of *Scalopus aquaticus*; Fiedler's fine study (1953) on the masticatory muscles of insectivores; Graber's book (1886), which contains illustrations showing some of the musculature of the mole; Jacobs' dissertation (1816), dealing with several muscles in *Talpa europaea*; Møller's work (1901), which discusses the laryngeal muscles in *Sorex vulgaris* and *Talpa europaea*, with supplementary figures; volume four of Owen's work on the anatomy of vertebrates (1868), in which some of the musculature of *Talpa* is described and illustrated; Petit's paper (1927), which considers the temporal and masseter muscles of *Talpa europaea* and *Sorex minutus*; Reed's very excellent and recent anatomical study (1951), which deals with the appendicular osteology and myology of *Scapanus*, *Neotrichus*, and *Sorex*; Rouvière's (1906) study of the digastric, mylohyoid, and geniohyoid muscles of *Talpa*; Slijper's work (1946), which has some data on the epaxial musculature of *Talpa europaea*; Slonaker's paper (1920), dealing with the eye muscles of *Scalopus aquaticus*; Sprague's paper (1944), containing a brief discussion of the hyoid muscles of Talpidae and Soricidae; volume two of Todd's work (1836-39), in which the superficial muscles of *Talpa* are illustrated; Wilkie's article (1925), which considers the stapedius and tensor tympani muscles in *Talpa*; Winge's study (1941), which discusses some of the cranial musculature of moles and shrews; and Žlábek's very detailed analysis (1938) of the masseter muscle in *Talpa europaea* and *Crocidura russulus*.

Whenever possible I have used the terminology of *Basle Nomina Anatomica*. (Barker, 1907).

### *Blarina brevicauda kirtlandi*

## I. Myomeric Musculature

### A. Dorsal Division (Epaxial)

1. Ocular.—No ocular muscles were found in gross dissection, though rudimentary slips of them may be present as reported by Cei (1946). Evidence of their presence in *Blarina* is the following statement by Ärnäck-Christie-Linde (1900): "Ein anderer Unterschied besteht darin, dass, wenn die Untersuchungen Gansers richtig sind, die Nn. oculomotorius, trochlearis und abducens bei *Talpa* fehlen. Bei *Sorex* sind sie vorhanden."

2. *Transversocostalis*.—The epaxial musculature in mammals is a complex system of fascicles of varying length connecting elements of the vertebrae and extending from the ilium to the cranium. Originating ontogenetically from myomeres dorsal to the horizontal skeletogenous septum, it is supplied by dorsal rami of spinal nerves.

*M. splenius* (Figs. 1, 40, 41, 42).—This muscle, lying deep to the pars capitis of the anterior trapezius and rhomboideus capitis muscles, originates along an extensive mid-sagittal raphe in common with its antimere and reaches from the level of the third thoracic vertebra to within 3.5 mm. of the lambdoidal ridge. It is strap-shaped, narrowing as it passes antero-laterad; it splits to insert onto the lateral half of the lambdoidal ridge and on the ridge between the parietal and the periotic bones immediately caudal to the insertion of the semispinalis capitis. The mesial insertion is very weak. This muscle covers the deeper rhomboideus cervicis.

*M. iliocostalis, pars cervicis* (Fig. 43).—Narrower but thicker than the pars dorsi, this muscle has fibrous origins mesial to its insertion on ribs four to eight. Its anterior fibers of origin are hidden by the rhomboideus thoracis. It passes anterolaterad to insert on the heads of ribs one and two and on the tips of the transverse processes of cervical vertebrae six and seven. Its insertion is intimately fused with that of the longissimus cervicis.

*M. longissimus, pars dorsi et cervicis* (Figs. 9, 41, 43).—This muscle band originates aponeurotically on the anterior tip of the ilium, the anterior third of the sacral spine, and the spines of the last thoracic and all the lumbar vertebrae, by tough tendons on the transverse processes of thoracic vertebrae three to seven and by fleshy fibers on the bases of the neural arches of the first and second thoracic and the seventh cervical vertebrae. Its fibers pass anterolaterad to insert by fleshy slips laterally on ribs five to thirteen, by deeper slips mesially on the transverse processes of thoracic vertebrae three to ten, and on the tips of the transverse processes of cervical vertebrae three to six. In the cervical region the insertion is closely blended with the origin of the levator scapulae et serratus anterior cervicis and is lateral to that of the longus atlantis muscle.

(*M. longus atlantis*) (Figs. 9, 43).—A heavy fusiform muscle originates on the zygapophyseal articulation of cervical vertebrae four and five and passes anterodorsad to insert on the caudal tip of the atlantal transverse process. If the splenius capitis is bisected and reflected, this muscle can be seen lying in the triangle bounded by the lateral edge of the semispinalis capitis, the mesial edge of the longissimus capitis, and the insertion of the splenius capitis. Its mesial edge is covered snugly by the lateral edge of the semispinalis capitis and is very easily transected in error.

*M. longissimus capitis* (Figs. 1, 9, 41, 43).—This element, also known as the trachelomastoid, is a narrow muscle, elliptical in cross section; its mesial edge is covered by the splenius capitis to which it is united by a loose fascia. It originates on the neural arches of the last four cervical vertebrae and the first two thoracic vertebrae, and from the transverse

processes of thoracic vertebrae three and four. Its fibers pass antero-dorsad to insert on the skull along the suture between the squamosal and the "prootic" bones dorsal to the maxillary process of the squamosal. Its attachment lies anterolateral to the insertion of the splenius and covers the insertion of the sternomastoid and cleidomastoid muscles.

*M. spinalis*.—I was not able to identify fibers which I felt certain belonged to this element.

### 3. Transversospinalis

*M. semispinalis, pars capitis* (Figs. 1, 9, 42, 44).—The pars capitis is a heavy, well-developed muscle originating on the arches of the last five cervical vertebrae and the first two thoracic vertebrae, and on the transverse processes of thoracic vertebrae three to five. It passes antero-dorsad to insert on the supraoccipital region of the skull about .5 mm. posterior to the lambdoidal suture. Its fibers of origin are fused with those of the longissimus capitis laterally and the semispinalis cervicis mesially; it is almost completely covered by the more superficial splenius capitis muscle.

*M. semispinalis, pars dorsi et cervicis* (Fig. 9).—The semispinalis, multifidus, and rotatores muscles are not distinct units; accordingly, all three elements are described in this section. The origin is on the mesial edge of the ilium, on the zygapophyseal articulations of the last thoracic and all of the lumbar vertebrae, on the transverse processes of thoracic vertebrae three to twelve, and on the arches of cervical vertebrae three to seven. These fibers pass cephalomesiad, spanning an interval of one, two, three, or more vertebrae, the longest fibers being more cephalad. The fibers insert on the spines and dorsal part of the arches of the last six cervical, all thoracic, and all lumbar vertebrae.

*Mm. intertransversarii*.—These fibers form distinct fusiform muscles connecting adjacent transverse processes.

*Mm. interspinali*.—No cervical interspinous elements were observed.

*M. rectus capitis posterior (dorsalis) major* (Figs. 1, 9, 44).—This muscle is a thin triangular element having an acuminate origin on the dorsal edge and the anterior tip of the axial spine. It widens as it passes anteriorly to insert on the back of the skull immediately deep to the insertion of the semispinalis capitis.

*M. rectus capitis posterior (dorsalis) minor* (Figs. 1, 9).—The rectus capitis posterior minor is a smaller muscle than the major. It lies deep to the major and can not easily be separated from it. The minor originates on the superior edge of the dorsal arch of the atlas and passes cephalad to insert with the major.

*M. obliquus capitis superior (anterior)* (Figs. 1, 9, 43).—The obliquus capitis superior originates on the posterior tip of the transverse process of the atlas and widens as it passes anteromesiad to insert on the posterior shelf of the lateral part of the lambdoidal crest.

*M. obliquus capitis inferior (posterior)* (Figs. 9, 44).—The obliquus capitis posterior is a heavy muscle having an extensive origin on the lateral surface of the spine of the axis. It passes anterolaterad to insert on the superior surface of the transverse process of the atlas under cover of the origin of the obliquus capitis superior.

## B. Lateroventral Division (Hypaxial)

### 1. Axial

#### a. Hyposkeletal

*M. rectus capitis anterior (ventralis)* (Figs. 2, 9, 47).—The rectus capitis anterior is a well-developed muscle band originating on the entire inferior surface of the transverse process of the atlas and passing anteroventrad to insert on the basisphenoidal region of the base of the skull mesial to the periotic.

*M. longus capitis* (Figs. 2, 9, 47).—This straplike muscle originates on the costal process of the sixth cervical vertebra and passes craniad to insert on the floor of the cranium anterior to the insertion of the rectus capitis anterior.

*M. longus colli* (Figs. 14, 47).—This muscle, the mass of which lies dorsal to the longus capitis muscle, is similar to the epaxial musculature in that it is composed of a number of fiber groups of various lengths and passing in different directions, which span a variable number of vertebrae. Nevertheless, it acts as a functional unit in the flexion of the vertebral column and is treated as one muscle. Its origin is on the tip of the transverse process of the axis, the costal processes of cervical vertebrae three, four, five, and six, and the ventral surface of the seventh cervical centrum. Its fibers pass craniad and insert on the tip and lateral edge of the ventral spine of the atlas, on the transverse process, centrum, and ventral spine of the axis, on the ventral spine and centrum of the third cervical vertebra, on the costal process, ventral spine and centrum of the fourth cervical vertebra, on the ventral surface of the centrum of the fifth cervical vertebra, and on the costal process and ventral surface of the centrum of the sixth cervical vertebra.

#### b. Lateral Group

*M. scalenus* (Figs. 9, 42).—The scalene is composed of three distinct elements—ventral, mesial, and dorsal—all of which are dorsal to the brachial plexus. The most ventral element originates on the first rib and inserts on the transverse processes of the axis and the five posterior cervical vertebrae. The mesial element originates by several slips on ribs three, four, and five. It passes anterodorsad, becoming more constricted in its passage to insert by tendons on the tip of the transverse processes of the third and fourth cervical vertebrae and onto the tendon of the dorsal element. The dorsal element originates on the third and fourth ribs under cover of the serratus anterior thoracis, and, emerging between the serratus anterior thoracis and the levator scapulae et serratus anterior



cervicis, it passes anterodorsad superficial to the latter. It narrows as it passes cephalad to be joined by the tendon of the mesial element. These two then join the ventral element of the scalene to insert with it on the transverse process of the axis. The tendon of the mesial and dorsal elements lies deep to the superior border of the muscle mass of the ventral element.

### c. Ventral Group

*M. sternohyoideus* (Figs. 13, 19, 45A).—The sternohyoideus is a wide, well-developed muscle completely concealing the trachea. Its origin is not separable in *Blarina* from that of the sternothyroid, though Årnäck-Christie-Linde (1907) apparently considered this origin distinct in *Crocidura*. The common origin is on the ventrolateral surfaces of the posterior two-thirds of the second and third sternebrae, whence it passes cephalad on the ventral surface of the trachea to insert on the posterior edge of the basihyal and thyrohyal cartilages. It is attached by fasciae to its antimere and to the surface of the trachea.

*M. sternothyroideus* (Figs. 16, 45B).—This muscle forms a narrow band running along the ventrolateral surface of the trachea. Anterior to the manubrium, at the level of tracheal ring four or five, it becomes recognizable as a muscle distinct from the sternohyoid. It inserts on the posterolateral edge of the thyroid cartilage under cover of the omohyoid.

*M. omohyoideus* (Figs. 11, 41, 42, 45A and B).—Årnäck-Christie-Linde (1907) stated that the omohyoid is not present in *Crocidura murina* or *Sorex vulgaris*. Sprague (1944) also listed the omohyoid as absent in *Sorex*. It is, however, represented in *Blarina* by a thin straplike muscle without a tendinous intersection. It originates on the anterior border of the neck of the scapula for a vertical distance of about 1.5 mm. from the anterior glenoid tubercle. Its fibers pass anteriorly, lateral to the sternohyoid muscle, and near the insertion of the latter muscle they turn mesiad to pass between the sternohyoid and sternothyroid muscles and insert on the lateral region of the basihyal bar.

*M. geniohyoideus* (Figs. 8, 19, 45A, 47).—The geniohyoid is a thin muscle band which is fused with its antimere along the mid-line. It originates aponeurotically on about 1 mm. of the ventromesial edge of the dentary, immediately caudal to the symphysis, and widens as it passes caudad to insert on the basihyal element. This muscle covers the mesial part of the hyoglossus and the genioglossus muscles and is in turn concealed by the more ventral mylohyoid.

*M. hyoglossus* (Figs. 19, 45B).—This element is the heaviest of the three tongue muscles. It originates on the basihyal, the thyrohyal, and the joint between them. Its fibers pass cephalodorsad into the tongue.

*M. genioglossus* (Figs. 8, 45A and B).—Covered by the more ventral geniohyoid muscle, this muscle forms with its antimere a triangular mass whose apex is directed caudad. It originates on the ventral edge of the dentary for 3.5 mm. anterior to the tubercle of attachment of the anterior belly of the digastric. Its fibers pass posterodorsad into the tongue.

*M. styloglossus* (Figs. 16, 45A and B).—This muscle is the smallest of the three tongue muscles and originates on the lateral surface of the anterior half of the stylohyal. Its fibers pass anteromesiad, covering part of the hyoglossus, with the fibers of which it intermingles as it enters the tongue.

*M. thyrohyoideus* (Figs. 17, 45B, 47).—The thyrohyoid is a triangular muscle whose fibers have a narrow origin on the anterior and posterior cornua of the thyroid cartilage and fan out as they pass cephalad to insert on the thyrohyal cartilage. It conceals the origin of the superior part of the thyropharyngeus muscle and is itself partly covered by the sternohyoid muscle.

(*M. transversus hyoideus*).—Sprague (1944) stated that this muscle is present in *Echinorex* and *Erinaceus*, its fibers passing between the proximal elements of the anterior cornua. It was not found in *Blarina*.

## 2. Appendicular

*M. levator scapulae et serratus anterior cervicis* (Figs. 9, 10, 42, 43).—This muscle is well developed and originates on the transverse processes of the last four cervical vertebrae and from the first and second ribs. It narrows as it passes dorsocaudal to insert on the mesial edge of the vertebral border of the scapula.

*M. rhomboideus (capitis)* (Figs. 1, 10, 11, 41).—The rhomboideus capitis is a large muscle originating deep to the cervical rhomboid on the anterior region of the tubercle capping the vertebral border of the scapula. It passes cephalad, widening considerably, to insert along the posterior border of the lambdoidal ridge, reaching laterad for 3.5 mm. from the mid-sagittal crest. It covers the deeper splenius muscle and is bound laterally and slightly overlapped cephalically by the cleido-occipital muscle.

*M. rhomboideus (cervicis)* (Figs. 11, 40, 41).—The cervical rhomboid is a triangular muscle originating from the posterior region of a roughened tubercle capping the vertebral border of the scapula. Its fibers pass anteromesiad to insert in common with its antimere in the mid-line along a tendinous raphe terminating anteriorly about 2 mm. caudal to the anterior tip of the cervical part of the anterior trapezius. It covers the posterior part of the rhomboideus capitis.

(*M. atlantoscapularis anterior*)(*ventralis*)(Figs. 9, 11, 40, 41, 47).—The atlantoscapularis anterior is a cylindrical muscle whose insertion is found on the posteroventral edge of the metacromion process of the scapula, immediately ventral to the insertion of the posterior trapezius and the origins of the pars capitis and pars cervicis of the anterior trapezius. Its fibers may be traced mesiad, lying against the side of the neck, to their origin on the ventral arch of the atlas, covering the insertion of the atlantoscapularis posterior.

(*M. atlantoscapularis posterior*) (*dorsalis*) (Figs. 9, 11, 40, 41, 47).—This muscle, also, is cylindrical in outline, but is of smaller diameter than the

preceding. Its insertion is found on the edge of the scapular spine dorsal to the tuber. From here it may be traced anteroventromesial along the mesial surface of the preceding muscle to its origin on the ventral arch of the atlas. Årnäck-Christie-Linde (1907) did not mention this element in *Crocidura*.

## II. Branchiomic Musculature

### A. Trigeminal Field

*M. temporalis* (Figs. 3, 7, 8, 39, 40, 41, 43, 45A and B).—The temporal is a massive muscle with an extensive origin covering most of the parietal and frontal regions of the skull. The coronoid process of the dentary produces a prominent elevation immediately caudal to the muscle's anterolateral edge. According to Årnäck-Christie-Linde (1907), the temporal muscle is split into three parts in *Crocidura* and *Sorex*. In *Blarina* separate parts cannot be delineated with sufficient clarity to warrant subdivision. Superficial fibers originate on the parietosquamosal ridge, the lambdoidal crest, the sagittal crest, and the temporal fascia and converge toward the coronoid prominence, producing two tendinous inscriptions. Deeper fibers originate from the surface of the parietal, the larger part of the frontal, and that part of the squamosal lateral to the tympanic ring. The fibers originating on the parietal and frontal bones insert on the mesial surface of the coronoid, and the fibers which originate along the supraorbital ridge form a cylindrical mass which enters the substance of the ramus to insert within the posterointernal ramal fossa. The part originating on the squamosal passes anteriorly, forming a ventrally convex arc, to insert on the lateral surface of the coronoid process and on a prominent spicule projecting caudolaterad from the lateral surface of this process. The dorso-mesial edge of the masseter is contiguous with, but separable from, the ventrolateral edge of the temporal.

*M. masseter* (Figs. 3, 7, 39, 40, 41, 42, 45A and B).—This muscle is a heavy mass originating on the lateral surface and apex of the zygomatic process of the maxillary bone. Its more dorsal fibers pass caudad, and its more ventral fibers pass caudoventrad, but the two groups converge toward the posterior region of the mandibular ramus and insert by tough connective tissue on the very narrow angular process.

*M. pterygoideus externus* (Figs. 3, 7, 8, 44).—The external pterygoid is a bicipital muscle. One of its heads originates along a line reaching from the anterior edge of the superior articular facet of the mandibular fossa of the skull to a point within the rim of the sphenopalatine foramen, and the other head originates on the ventral lip of the sphenopalatine foramen. The optic nerve emerges between them, and these two heads fuse lateral to the large infraorbital branch of the maxillary division of the trigeminal nerve. The fibers then pass caudad to insert on the anterior edge of the superior articular facet of the dentary, on the anterior edge of the inferior articular facet of the dentary, and in the fossa between these facets.

*M. pterygoideus internus* (Figs. 3, 8, 44).—This muscle has its origin from the base of the skull, extending from a point just anterior to the

tympenic ring to the posterior border of the palate, with some fibers originating from the floor of the infraorbital foramen dorsal to the last superior molar. The fibers pass posterolaterally to insert on the mesial surface of the reduced angular process of the dentary.

*M. digastricus* (Figs. 3, 7, 40, 41, 45A and B).—This bicapital muscle exhibits a weak tendinous intersection about 2 mm. caudal to the region where the stylohyoid muscle crosses the digastric. The intersection passes obliquely anteromesiad paralleling the slope of the stylohyoid. A superficial head originates on the lateral surface of the periotic region of the skull immediately ventral to the ventral tip of the lambdoidal crest, and a deep head composed of a narrow, flat sheet of fibers originates on the lateral surface of the tympanostyloid synchondrosis. The common muscle mass passes cephalad between the angle of the dentary and the larynx to insert on the prominent tubercle formed at the intersection of the ventral borders of the body and the ramus of the dentary. The anterior part of the muscle is connected with its antimere by a fascial sheet which is closely attached to the mylohyoid muscle.

*M. mylohyoideus* (Figs. 7, 8, 45A and B).—The mylohyoid is a thin sheet of fibers running transversely between the two dentaries. On the basis of attachment of its fibers, the muscle can be divided into two parts, one deep and the other superficial, the posterior fibers of the superficial part and the anterior fibers of the deep part being connected by fasciae.

*pars superficialis*.—This element is a transverse muscle sheet extending between the ventral borders of the bodies of the dentaries from a point approximately 1 mm. posterior to the symphysis to a prominent tubercle on which the digastric inserts. The mylohyoid branch of the trigeminal nerve runs cephalad along its deep surface and innervates it. There is no suggestion of a median sagittal tendinous intersection. Its deep surface can be separated without difficulty from the superficial surface of the geniohyoid muscle.

*pars profundus*.—This part is approximately twice as large as the superficial sheet and shows a median sagittal fibrous intersection. It originates on the mesial surface of the dentary along an oblique line passing posteroventrad from the base of the last molar to the base of the angular process. It runs mesiad to form a median sagittal tendinous intersection with its antimere and inserts on the median part of the basihyal element. The mylohyoid branch of the trigeminal nerve runs along the mesial side of the dentary on the ventral surface of this muscle.

*M. tensor veli palatini* (Fig. 47).—The tensor is a fusiform muscle which appears to originate from the mesial rim of the squamosal. The tendon passes anteromesiad along the lateral border of the tympanic ring and becomes fleshy as it passes cephalad between the internal pterygoid and the levator palati muscles to become aponeurotic at the level of the pterygoid hamulus. The aponeurosis bends mesiad and passes over the ventral surface of the hamulus to insert into the soft palate.

*M. tensor tympani* (Figs. 4, 47).—The tensor is a terete muscle originating on the posterior edge of the squamosal and passing posteromesiad deep

to the malleus. As it reaches the anterior wall of the cochlea, it forms a 90° genu and passes ventrad to become tendinous and insert on the processus muscularis of the malleus. At its genu this muscle passes under a plate of fasciae which run mesiad from the mesial wall of the promontorium to the adjacent floor of the periotic.

## B. Facial Field

*M. zygomaticus major* (Figs. 3, 30, 39, 41).—The major is an elongate fusiform muscle, the tendon of which is equal in length to its belly. It originates on the crista of the squamosal and passes anteriorly, superficial to the small zygomatic and the levator alae nasi inferioris and superioris, to insert into the fasciae at the base of the snout, immediately anterior to the incisors. Its origin is concealed by the insertions of the splenius, sternomastoideus, and cleidomastoideus muscles. The anterior part of its belly is covered by the dorsal border of the masseter muscle. The ventral edge of the belly rests on the masseter and the dorsal rim of the auditory tube. Near the base of its deep surface it receives a twig from the facial nerve.

*(M. zygomaticus minor)* (Figs. 3, 39, 40, 41).—The belly of the small zygomatic is completely hidden by the large zygomatic muscle. The muscle has its origin on the more ventral part of the crest of the squamosal and passes anteriorly in a valley formed by the masseter. Its ventral edge rests on the superior surface of the auditory tube, and its superior edge is contiguous with the levator alae nasi inferioris. The long delicate tendon inserts into the fascia of the side of the snout 1 to 2 mm. caudal to the insertion of the great zygomatic muscle. It also receives a twig near its base from the large branch of the seventh cranial nerve which courses forward along its deep surface.

*(M. levator alae nasi inferioris)* (Figs. 3, 39-41).—The belly and origin of this muscle are completely hidden by the inferior margin of the temporal muscle and by the great zygomatic. It is heavier than the small zygomatic. Its origin, fused with the inferior surface of the great zygomatic, is from the dorsal part of the crista. Its tendon is heavy and passes anteriorly and slightly dorsad to insert in the laterobasal edge of the rhinarium. The large branch of the facial nerve continues along its inferior edge.

*(M. levator alae nasi superioris)* (Figs. 3, 39-41).—This muscle is of approximately the same size as the small zygomatic. The larger part of its belly is hidden by the levator alae nasi inferioris and the inferior border of the zygomatic muscles. It originates on the dorsal part of the crista, its origin being fused with that of the preceding muscle. Just posterior to the eye, the belly is visible and becomes tendinous as it passes ventral to the eye. This tendon passes anterodorsad, crossing over the infraorbital branch of the trigeminal nerve and inserting into the dorso-lateral edge of the base of the rhinarium. About 4 mm. from its origin it receives a twig of the facial nerve.

*(M. levator labii superioris proprius)* (Figs. 3, 39-41).—This is a well-

developed bicipital muscle. Its dorsal head is the smaller of the two and originates on the median sagittal crest immediately caudal to the fronto-nasal suture, whence it passes anteroventrad to blend with the superficial fibers of the ventral head. The ventral head originates from the maxillary bone directly anterior to the infraorbital foramen and passes antero-dorsad to join the dorsal head. A common tendon runs forward from the region where the two heads unite and inserts into the base of the cartilaginous snout.

*M. digastricus, venter posterior*.—This muscle has been described above as a single unit of the trigeminal field.

*M. stylohyoideus* (Figs. 2, 19, 45A, 47).—The flattened origin of the stylohyoid is on the base of the skull posterior to the stylo-mastoid foramen and lateral to the origin of the jugulohyoid; it is intimately related at its origin with the fascia of this muscle, and its fibers pass cephalad contiguous with the mesial surface of the facial nerve. At the level of the base of the auditory tube this muscle turns mesiad, looping around the lateral edge of the digastric and, continuing its mesiad course, passes over the ventral surface of the digastric muscle to insert by an aponeurosis at the side of the larynx in the region of the proximal part of the thyrohyal.

(*M. jugulohyoideus*) (Figs. 2, 16, 45A, 47).—The jugulohyoid is represented by a distinct muscle clearly separable from the digastric. It is triangular in shape with its apex directed cephalad; it originates along the ridge produced by the horizontal semicircular canal and along the lateral border of the posterior lacerate foramen. Its fibers converge as they pass anteromesiad and insert on the tympanostyloid synchondrosis. Fiedler (1953) called this muscle the *M. mastostyloideus*.

*M. stapedius* (Figs. 6, 47).—This is a triangular muscle lying deep to the jugulohyoid, with which it could be confused on superficial observation. It originates along the posterior rim of a fossette formed between the posterior semicircular canal, the lateral semicircular canal, and the basal turn of the cochlea. The muscle passes anteromesiad, becomes more constricted, and enters the tympanic chamber through a fissure between the tympanohyal and the periotic. It inserts by a narrow tendon onto the stapedial process of the stapes. The tendon of this muscle gives no evidence of a skeletal element of Paauw, the os quartum of de Beer (1937).

### C. Glossopharyngeal Field

*M. stylopharyngeus* (Figs. 16, 45B, 47).—Fibers of this muscle originate along the distal half of the mesial surface of the stylohyal cartilage and pass anteromesiad to insert on the ceratohyal lateral to the insertion of the ceratohyoid muscle. Deeper fibers also pass into the pharyngeal wall.

(*M. ceratohyoides*) (Figs. 17, 19, 47).—The ceratohyoid is a fan-shaped muscle hidden by the origin of the hyoglossus. It originates about 1 mm. from the base of the thyrohyal cartilage for a distance of about .9 mm. along the lateral surface of this cartilage. Its fibers pass cephalad to

insert on the hypohyal and the proximal part of the ceratohyal cartilages. The stylopharyngeus muscle lies immediately lateral to it, and some of its fibers pass deep to the ceratohyoid.

#### D. Vagus Field

(*M. pterygopharyngeus*) (Fig. 47).—This muscle is a small terete structure originating on the tip of the hamular process and passing caudad. It turns mesiad in its posterior third to meet its antimere in a middorsal raphe anterior to the chondropharyngeus. The levator veli palatini muscle enters the palate at its posteromesial border.

(*M. chondropharyngeus*) (Figs. 17, 47).—The chondropharyngeus is a well-developed muscle originating from the posterior and anterior edges of the more dorsal half of the thyrohyal cartilage. It passes anterodorsad around the pharynx to meet its antimere in a median dorsal raphe anterior to the thyropharyngeus.

(*M. thyropharyngeus*) (Figs. 17, 47).—This element is represented by two distinct muscle sheets. The more posterior sheet, which is very thin, originates on the dorsal edge of the posterior cornu and passes dorsad around the pharynx partly under cover of the other sheet. This second, more anterior sheet is terete at its origin, which is on the lateral surface of the thyroid arch where it joins the cornua and on the base of the anterior cornua. This element also passes anterodorsad around the pharynx to meet its antimere in a middorsal raphe.

(*M. cricopharyngeus*).—This element was not seen in the short-tailed shrew.

*M. thyroarytenoideus* (Figs. 17, 18, 47).—This flattened muscle originates on the deep (dorsal) surface of the ventral arch of the thyroid cartilage and narrows as it passes laterad to insert on the arytenoid cartilage. It can best be observed after part of the ventral arch of the thyroid cartilage is removed.

*M. cricoarytenoideus posterior (dorsalis)* (Figs. 17, 18).—The posterior cricoarytenoid is a well-developed muscle covering the entire dorsal surface of the cricoid cartilage. It originates on the posterior edge of this surface of the cricoid and passes cephalad, narrowing as it approaches its insertion on the arytenoid cartilage.

*M. cricoarytenoideus anterior (ventralis)* (Figs. 18, 47).—This muscle, covered ventrally by the thyroarytenoideus, originates on the anterior edge of the ventral arch of the cricoid cartilage and passes anterolaterad to insert on the arytenoid cartilage.

*M. cricothyroideus* (Figs. 16, 17, 45B, 47).—The cricothyroid is a thin platelike muscle, the fibers of which originate on the posteroventral edge of the cricoid cartilage and pass cephalad to insert on the posterior edge of the body of the thyroid cartilage and on the entire ventral edge of the posterior cornu.

*M. arytenoideus*.—The arytenoid is composed of a meager group of fibers

passing anteroventromesial from the arytenoid cartilage to meet its antimere in a median ventral line.

*M. thyroepiglotticus*.—This muscle was not observed in the short-tailed shrew.

*M. aryepiglotticus*.—This muscle was not observed in the short-tailed shrew.

#### E. Accessory Field

*M. levator veli palatini* (Fig. 47).—This small, fusiform muscle lies immediately mesial to the tensor palati muscle, and its origin appears to be fused with that of the tensor, the two muscles becoming distinct at the anterior border of the tympanic ring. The levator diverges from the tensor as it passes cephalomesial to insert into the soft palate mesial to the pterygopharyngeus.

*M. sternomastoideus* (Figs. 1, 13, 39-41).—The sternomastoid is larger than the cleido-occipital or the cleidomastoid. It originates on the anterolateral edge of the manubrium and along a mid-line raphe which extends 4 mm. anterior to the tip of the manubrium. It passes anterodorsad and fuses with the cleidomastoid, the two having a common aponeurotic insertion on the dorsal rim of the "prootic" immediately caudal to the squamosal-"prootic" suture. The sternomastoid does not show a dichotomy as is given by Årnäck-Christie-Linde (1907) for *Crocidura*.

*M. cleidomastoideus* (Figs. 1, 12, 39-41, 45A).—The cleidomastoid, a heavier muscle than the cleido-occipital, originates along 2 mm. of the anteroventral surface of the clavicle immediately lateral to the cleido-occipital and passes anterodorsad to fuse with the sternomastoid and enter into a common insertion with it, as stated above.

*(M. cleido-occipitalis)* (Figs. 1, 12, 39-41, 45A).—This element is a narrow straplike muscle originating along the anterior and ventral surfaces of the clavicle immediately lateral to the sternoclavicular articulation. It passes anterodorsad, crossing the splenius and covering the contiguous surfaces of the sternomastoid and cleidomastoid muscles, to insert by a narrow tendon on the rear of the skull about 4 mm. lateral to the midline between the insertions of the temporal and the rhomboideus capitis muscles.

*M. trapezius (anticus, pars capitis)* (Figs. 1, 11, 39-41).—This element originates on the club-shaped terminus of the metacromion process of the scapula and passes anteromesial to attach along the lambdoidal crest lateral to the mid-line. It covers part of the rhomboideus capitis.

*M. trapezius (anticus, pars cervicis)* (Figs. 11, 39-41).—The pars cervicis is considerably wider than the pars capitis. It also originates on the terminus of the metacromion process, but lies superficial to the origin of the capitis and conceals part of this element. As it passes dorsad it widens and becomes conspicuously separated from the pars capitis to insert with its antimere along a median cervical raphe about 7.5 mm. in



length, covering the rhomboideus capitis and cervicis muscles. The origins of this and the preceding muscle are fused in *Crociodura*, according to Årnäck-Christie-Linde (1907).

*Scalopus aquaticus machrimus*

I. Myomeric Musculature

A. Dorsal Division (Epaxial)

1. Ocular.—No ocular muscles were found in gross dissection, nor was there any indication of cranial nerves III, IV, or VI.

2. Transversocostalis

*M. splenius* (Figs. 22, 32, 48, 52, 53).—The splenius is a well-developed, fleshy, straplike muscle lying on the surface of the semispinalis capitis and deep to the rhomboideus capitis muscle. It originates along the entire length of the calcified nuchal ligament, on the median raphe immediately anterior and posterior to that ligament, and on the anterior surface of the very heavy, fibrous, interscapular ligament. Passing anterolaterad, the muscle inserts by an aponeurosis along the oblique ridge at the squamoso-occipital suture deep to the aponeurosis of the cleido-occipital muscle. This muscle lacks the more medial fibers of insertion seen in *Blarina*.

It is supplied by dorsal rami of cervical nerves two and three.

*M. iliocostalis, pars cervicis*.—This element was not seen in the prairie mole.

*M. longissimus, pars cervicis* (Figs. 28, 56).—This element of the longissimus system, thin and falcate in outline, lies along the ventral border of the semispinalis capitis muscle, deep to the levator scapulae et serratus anterior cervicis. It has fleshy origins on the transverse processes of thoracic vertebrae three to six and on the zygapophyseal articulation of thoracic vertebrae one to two and two to three. Each slip is superficial to and conceals the one next anterior. Its insertions are fibrous on the zygapophyseal articulation of cervical vertebrae four to five, five to six, and six to seven.

The innervation of this muscle could not be found.

(*M. longus atlantis*) (Figs. 28, 63).—The longus atlantis is a small but well-developed wedge of muscle completely hidden by the longissimus capitis. It originates from the ventral surface of the prezygapophysis of the fourth cervical vertebra and inserts on the lateral mass of the atlas, concealing the origin of the rectus capitis anterior.

This muscle is supplied by the dorsal rami of the second and third cervical nerves.

*M. longissimus, pars capitis* (Figs. 22, 28, 52, 54, 58, 60).—The pars capitis is a muscle having a narrow tendinous origin, more restricted than in the shrew, on the zygapophyseal articulation of cervical vertebrae three to four. From its origin the muscle widens to insert aponeurotically

on the posterior surface of the skull along the squamosal suture deep to the insertion of the splenius, by a fibrous sheet common to it, the deep part of the sternomastoid, and the cleidomastoid. This muscle covers the posterior region of the digastric and is in turn partly hidden ventrally by the levator scapulae et serratus anterior cervicis and the semispinalis capitis, and dorsally by the splenius, the cleido-occipitalis, and the superficial part of the sternomastoideus.

The dorsal rami of cervical nerves two and three were seen to supply this muscle.

*M. spinalis*.—No definite spinalis fibers were observed. Winckler (1931) stated that a spinalis dorsi is present in *Talpa europaea* and that it is composed of three segments, the composite mass passing from the mammillary processes of the thoracodorsal vertebrae thirteen, fourteen, and fifteen to the spinous processes of the thoracodorsal vertebrae three to thirteen inclusive. Slijper (1946), however, identified in *Talpa europaea* an element which passes from the spines of lumbar vertebrae one and two to the spines of thoracic vertebrae one to eleven as the spinalis muscle and considered that Winckler's element represents part of the semispinalis.

### 3. Transversospinalis

*M. semispinalis, pars capitis* (Figs. 20, 28, 54, 56, 58, 60).—Dobson (1882-90) did not consider any of the epaxial musculature under his heading, "*Condylura, Scapanus, Scalops, Talpa, etc.*" He repeatedly called attention, however, to the similarity between the musculature of this group and that of *Myogale*. In *Myogale*, Dobson listed both a biventer cervicis and a complexus. In the specimens of *Scalopus* and the single specimen of *Condylura* which I dissected, an undifferentiated semispinalis capitis element was present without visible separation into these two muscles. A single specimen of *Talpa* studied showed a distinct division of the semispinalis capitis into a narrow mesial band and a broad lateral band. This agrees with the observation made by Winckler (1947) for *Talpa europaea*. In the prairie mole this muscle originates on the base of the neural arch of each vertebra from cervical three to thoracic three, inclusive. It lies immediately deep to the longissimus cervicis, and extends anterodorsad to insert by a tough aponeurosis on the dorsal part of the occipital bone, the lateral half of its area of insertion being covered by the rhomboideus capitis. The mesial edge is contiguous with that of its antimere. The origin of this muscle is more extensive in *Blarina*.

The dorsal rami of cervical nerves one, two, and three supply this muscle mass.

*M. semispinalis, pars dorsi et cervicis* (Figs. 28, 56).—The multifidus and the rotatores muscles are included with the description of the semispinalis. This element, though distinct from the capitis part of the semispinalis system, is not clearly separable from the more posterior transversospinalis system. Its origin is on the apex and mesial edge of the ilium, the metapophyses of each of the lumbar vertebrae and the last thoracic vertebra, the transverse processes of each of thoracic vertebrae three to

twelve, the base of the neural arch of each vertebra from the fifth cervical to the second thoracic, and from the tendons of the longissimus muscle. Its fibers are directed anteromesiad, spanning from one to seven vertebrae or connecting adjacent vertebrae, and inserting on the spinous processes of each of the first five lumbar vertebrae (the sixth lumbar lacks a spine), on the spine of each thoracic vertebra, on the caudal edge of the arch of each of the last five cervical vertebrae, and on the caudal tip of the spine of the axis.

A tiny twig, the dorsal ramus, of cervical nerve four was the only nervous element found innervating the semispinalis dorsi et cervicis muscle.

*Mm. intertransversarii.*—These muscles consist of very short fibers connecting adjacent transverse processes in the cervical region. They are not clearly separable from the fibers of the longus colli and are covered superficially by strong intertransverse ligaments. The fibers of this muscle are shorter and form a smaller mass in *Scalopus* than in *Blarina*.

The innervation of these elements was not seen.

*Mm. interspinosi.*—Cervical elements of this component were not seen.

*M. rectus capitis posterior (dorsalis) major* (Figs. 20, 28, 57).—This is a well-developed muscle deep to the semispinalis capitis with a narrow fleshy origin from the entire dorsal edge of the spine of the axis. It becomes wider as it passes anteriorly, and its fibers insert by a wide aponeurosis onto the occipital bone deep to the obliquus capitis superior and the semispinalis capitis.

This element is supplied by a twig from the dorsal ramus of the first cervical nerve.

*M. rectus capitis posterior (dorsalis) minor* (Figs. 20, 28, 58).—The rectus capitis posterior minor is a smaller muscle than the preceding and is so closely bound to it by intervening fasciae that it is not easily observed. Its fibers originate from the dorsal spine and arch of the atlas and insert on the skull deep to the rectus capitis posterior major.

A twig from the dorsal ramus of the first cervical nerve supplies this muscle.

*M. obliquus capitis superior (anterior)* (Figs. 20, 28, 57).—The straplike superior oblique is partly concealed by the longissimus capitis and the semispinalis capitis. It originates from the lateral mass and arch of the atlas immediately ventral and anterior to the atlantal foramen for the dorsal ramus of the first cervical nerve and runs anteromesiad to insert on the posterior part of the occipital bone of the skull between the semispinalis capitis and the rectus capitis posterior major.

This muscle is innervated by the dorsal ramus of the first cervical nerve.

*M. obliquus capitis inferior (posterior)* (Figs. 28, 57).—This muscle originates on the spine of the axis ventral to the origin of the rectus capitis posterior major and passes anterolaterad to insert on the dorsal arch of the atlas anterior to the atlantal foramen. It lies ventral to the rectus

capitis posterior major, the edge of which slightly overlaps its superior edge. The origin of this muscle is more extensive in *Blarina*.

The inferior oblique receives a twig from the dorsal ramus of the first cervical nerve.

## B. Lateroventral Division

### 1. Axial

#### a. Hyposkeletal

*M. rectus capitis anterior (ventralis)* (Figs. 21, 28, 57, 63).—The rectus capitis anterior is a narrow muscle partly hidden ventrally by the longus capitis. Its fibers originate on the lateral mass of the atlas, beneath the insertion of the longus atlantis and immediately caudal to the origin of the obliquus capitis superior, and pass anteromesiad to a fleshy insertion on the base of the skull along the mid-line between the two tympanic bullae.

This muscle is supplied by a twig from the ventral ramus of the first cervical nerve.

*M. longus capitis* (Figs. 21, 28, 63).—The longus capitis is a long muscle band originating directly from the anterior tip of the costal process of the sixth cervical vertebra and indirectly from that of the fifth by attachment to fibers of the longus colli which originate on the latter. As the muscle passes cephalad it extends toward the median sagittal plane, covering the lateral edge of the rectus capitis anterior. It inserts on the base of the skull in the mid-line at the region of insertion of the rectus capitis anterior.

Twigs from the ventral rami of cervical nerves two and three enter the longus capitis muscle.

*M. longus colli* (Figs. 31, 54, 63).—This muscle, smaller in *Scalopus* than in *Blarina*, covers the ventral surfaces of the cervical and anterior thoracic centra, its antimeres forming between themselves a trough for the esophagus. On the basis of fiber direction the muscle is composed of an anterior and a posterior part. The anterior part originates on the costal processes of cervical vertebrae three to six and inserts on the ventral arch of the atlas, the ventral surface and crest of the axis, and the median ventral crests of cervical vertebrae three to five. The posterior element has its origin on the ventral surfaces of the centra of the seventh cervical and the first three thoracic vertebrae and the costovertebral articulations of the first three ribs. Its fibers from the seventh cervical pass craniad to insert on the centra of cervicals five and six, and those from the three thoracic vertebrae insert on the entire mesial surface of the posterior tip of the costal process of the sixth cervical vertebra.

Branches from the ventral rami of the second, third, and fourth cervical nerves were found to supply this complex element.

#### b. Lateral Group

*M. scalenus* (Figs. 28, 55).—The scalene is a well-developed falcate muscle, the fibers of which originate on the first, second, third, fourth, and fifth ribs. A heavy superficial bundle of its fibers takes origin on

ribs three, four, and five ventral to the levator scapulae et serratus anterior cervicis and passes anteriorly into a strong tendon which inserts on the transverse processes of cervical vertebrae five and six. Another bundle of fibers also takes origin on the third rib, dorsal to the superficial bundle, and passes anteroventrad to join it. A distinct bundle originates lateral to the costovertebral articulation of the first rib and splits into two parts. The mesial part lies deep to the plate of fibers of the superficial bundle, which originates from rib five, and joins with this part. The lateral bundle, lying ventrolateral to the mesial part, passes cephalad and unites with fibers originating at the costovertebral articulation of the first rib and inserts with them on the transverse processes of cervical vertebrae two, three, and four. Separate deep plates of fibers pass anteriorly from the second and third ribs to join the main mass at the level of the first rib.

The scalene muscle is innervated by branches of the ventral rami of cervical nerves six, seven, and eight, and thoracic nerve one.

### c. Ventral Group

*M. sternohyoideus* (Figs. 34, 37, 53-55, 60).—This is a long muscle, narrower than in *Blarina*, covering the ventral surface of the trachea, its mesial edge adjacent to that of its antimere. It originates from the dorsal edge of the manubrium immediately caudal to the articulation area of the first rib and inserts onto the cartilages of the basihyal and the mesial part of the thyrohyal.

The sternohyoid is innervated by the ansa hypoglossi.

*M. sternothyroideus* (Figs. 34, 37, 60).—The sternothyroid is a paired muscle similar to but narrower than the preceding muscle which completely or partly covers it ventrally. The muscle originates immediately caudal to the sternohyoid and inserts by a thin aponeurosis on the posterolateral edge of the thyroid cartilage under cover of the thyrohyoid.

This muscle is supplied by the ansa hypoglossi.

*M. omohyoideus*.—The omohyoid, which is represented in the shrew, is absent in the prairie mole.

*M. geniohyoideus* (Figs. 30, 37, 60, 61).—The geniohyoid is a strong muscle closely knit to its antimere in the mid-line and taking origin on the mesial surface of the dentary for a distance of several millimeters caudal to the symphysis. Only its most anterior fibers are visible anterior to the superficial mylohyoid muscle. Posteriorly, its fibers are intimately bound to the deep surface of the deep mylohyoid muscle by a dense tough fascia. They insert on the basihyal and mesial part of the thyrohyal cartilages.

A branch of the hypoglossal nerve supplies the geniohyoid.

*M. hyoglossus* (Figs. 37, 61, 62).—This plate of muscle has a broad fleshy origin, deep to the geniohyoid muscle, on the entire anterior surface of the thyrohyal cartilage and the anterior edge of the basihyal, including the basihyal-thyrohyal articulation. The fibers pass laterally to enter the tongue.

The hypoglossal nerve innervates the hyoglossus muscle.

*M. genioglossus* (Figs. 30, 61, 62).—The fibers of the genioglossus originate on the anteromesial surface of the dentary and are directed posteromesiad to insert into the base of the tongue. This muscle extends deep to the basihyal cartilage as far caudad as the epiglottis.

A twig from the hypoglossal nerve innervates the genioglossus muscle.

*M. styloglossus* (Figs. 37, 60-62).—The styloglossus is a narrow muscle originating by fleshy fibers on the posterolateral three-fourths of the stylohyal cartilage. Passing anteromesiad, its fibers blend with those of the hyoglossus. Its ventral part is covered by the geniohyoid muscle.

This element is supplied by cranial nerve XII.

*M. thyrohyoideus* (Figs. 33, 37, 60).—The thyrohyoid is a triangular muscle originating on the lateral side of the larynx from the superior cornu of the thyroid cartilage. Its fibers fan out anteriorly and insert on the basihyal and thyrohyal elements of the hyoid apparatus. The origin is covered ventrally by the thyropharyngeus muscle. The thyrohyoid in the shrew has a more extensive origin with deeper fibers arising on the anterior cornu of the thyroid cartilage.

The thyrohyoid muscle is supplied by the ansa hypoglossi.

(*M. transversus hyoideus*) (*interhyoideus*) (Figs. 37, 62).—This muscle is a very thin transverse band of fibers interconnecting the hypohyal cartilages immediately anterior to the basihyal. It is absent in *Blarina*.

I could not locate the nerve supplying this element. Sprague (1944) stated that it probably receives a twig from the hypoglossal nerve.

## 2. Appendicular

*M. levator scapulae et serratus anterior cervicis* (Figs. 28, 33, 51).—This is a large, fan-shaped muscle with a broad origin from the transverse processes of cervical vertebrae three to seven, the costovertebral articulation of the first rib, and the intertransverse ligaments. Its fibers pass obliquely dorsocaudad to insert by a narrow tendon on a prominent ridge at the dorsovertebral border of the scapula. Reed (1951) identified this element as the serratus anterior cervicis.

The muscle is innervated by branches of the ventral rami of cervical nerves four to seven.

*M. rhomboideus (capitis)* (Figs. 20, 33, 50).—The pars capitis is a strong superficial muscle covering the neck dorsally and cupped around the lateral side of the splenius, which lies beneath it. Its origin, closely bound with that of the rhomboideus cervicis, is on the posterior edge of the scapula between the tuber of the scapula and the prominent ridge serving for the insertion of the levator scapulae et serratus anterior cervicis. It fans out as it passes cephalad and inserts by a broad aponeurosis on the dorsal surface of the skull, a slight gap of several millimeters remaining between the antimeres. The origin of the pars capitis in the mole is in the region of the fifth or sixth rib, whereas its origin in the shrew is in the region of the first or second rib.

Twigs from the ventral rami of the second and third cervical nerves supply this muscle.

*M. rhomboideus (cervicis)* (Figs. 32, 33, 48, 55).—With its antimere this muscle forms a conspicuous median triangle covering the posterior origin of the rhomboideus capitis. Its origin is on the posterior edge of the scapula between the tuber and the levator scapulae ridge, in common with that of the capitis part. Its fibers, however, pass anteromesiad to insert along the full length of the nuchal ligament.

The rhomboideus cervicis receives twigs from the ventral rami of cervical nerves two, three, and four.

*(M. atlantoscapularis anterior)(ventralis)*.—This muscle is not present in the prairie mole.

*(M. atlantoscapularis posterior)(dorsalis)*.—This muscle is not present in the prairie mole.

## II. Branchiomic Musculature

### A. Trigeminal Field

The musculature of this field is supplied by the fifth cranial nerve, though this was not observed for all muscles described. For those elements whose innervation was not observed, a specific statement to that effect will be found under the muscle concerned.

*M. temporalis* (Figs. 20, 29, 30, 48).—The temporal is a massive muscle with fibers of origin from the temporal fossa of the skull and from the strong temporal fascia. A temporal line on the bone delimits the temporal fossa. The temporal fascia is attached to the median sagittal crest and along a line extending laterad to the zygomatic arch. The optic nerve and cutaneous branches of the trigeminal nerve emerge between the anterolateral edge of the temporal and the adjacent anteromesial edge of the zygomaticus major muscles. A superficial sheet of fibers from the anterior half of the temporal muscle passes ventrad mesial to the zygomatic arch; the fibers converge to insert on the anterior margin of the coronoid process of the dentary. Superficial fibers arising from the inner surface of the base of the zygomatic arch, from the fossa immediately mesial to the base of the arch, and from the posterior 3 mm. of the mesial surface of the zygomatic arch pass cephalad to insert deep to the superficial sheet on the entire lateral surface of the coronoid process. Deeper fibers attach to the mesial surface of the platelike coronoid process. These deep fibers are not distinct from the deeper part of the masseter muscle. The temporal muscle in the mole has a more restricted origin than in *Blarina* and lacks the more complicated oblique fascicular arrangement seen in the latter.

*M. masseter* (Figs. 22, 29, 49, 50).—This is a well-developed muscle, roughly triangular in outline, and lying ventral to the zygomaticus major. Its posterior half is separated superficially into a dorsal and a ventral mass by a longitudinal groove in which the fascia is thickened. The muscle also is divisible into a superficial layer and a deep layer. The superficial layer, clearly distinct from the deep layer posteriorly but blending

anteriorly with its fibers, originates from the broad basal bridge on the maxillary bone which forms the ventral margin of the infraorbital foramen and from the anterior fourth of the zygomatic arch. Its fibers pass obliquely posterolaterad to insert on the lateral surface of the angular process ventral and anterior to a prominent semilunar groove. The deep layer arises from the inferior surface of the zygomatic arch, from the region below the infraorbital foramen to within 1 or 2 mm. of the base of the arch. These fibers converge ventrally to insert on the ascending ramus of the dentary along a dorsally concave arc, extending from the condyloid process to the base of the anterior edge of the coronoid process. The deep layer of the masseter is absent in *Blarina*. Fiedler (1953) recognized what I have termed the deep layer of the masseter as a distinct muscle which he called the *M. zygomaticomandibularis*.

*M. pterygoideus externus* (Figs. 22, 30, 57).—The external pterygoid is a triangular, bicipital muscle lying deep to the temporal muscle. Its dorsal head originates from the lateral wall of the frontal bone anterior to the frontoparietal suture. Its ventral head arises from the ventral region of the orbitotemporal fossa along a line extending from the sphenopalatine foramen to the alisphenoid canal. The fibers of the two heads converge as they pass posteriorly and insert on the mesial surface of the condyle of the dentary. A branch of the trigeminal nerve, innervating the masseter and the temporal, emerges between the two heads. According to Toldt (1905), this muscle is single-headed. The fibers of this muscle are relatively longer in *Blarina* than in *Scalopus*.

*M. pterygoideus internus* (Figs. 21, 30, 57).—The internal pterygoid is a fleshy, massive muscle between the angle of the dentary and the lateral wall of the skull, visible ventrally after removal of the digastric. It originates from the entire ventral surface of the basisphenoid bone. The fibers are directed caudad to insert on the medial surface of the angle of the dentary. The internal pterygoid is better developed and has a greater area of insertion in the mole than in the shrew.

*M. digastricus, venter anterior* (Figs. 30, 49, 51, 54).—Since the anterior belly of this muscle is innervated by the trigeminal nerve, and the posterior belly is innervated by the facial nerve, the two bellies are described separately under the trigeminal and facial fields. There has been considerable discussion concerning the condition of the digastric in *Talpa*. Dobson (1882-90), in his description of the digastric, based on the star-nosed mole, did not mention a venter anterior. In the single specimen of the star-nosed mole which I dissected the digastric showed an anterior belly and a posterior belly of essentially the same form as those seen in the prairie mole. Dobson's work contains the only description of this muscle in the North American talpids. In *Talpa*, Rouvière (1906) and Chaine (1914) observed only one belly to the digastric. The single specimen of *Talpa europaea* which I dissected showed a double-bellied digastric, which agrees with the description and figure given by Bijvoet (1908). Neither "inscriptio tendinea" nor a narrow "transverse mylohyoideus" was observed as shown in Bijvoet's illustration. Toldt (1905) described



two parts to the digastric muscle of *Talpa*. In *Talpa* the oblique fibers of the anterior belly do not decussate; instead, the fibers originating from the left tendon pass deep to and cross those of the antimere. A tendinous intersection or inscription was not observed in any of the forms which I dissected. The anterior belly is a superficial plate of fibers intimately bound by fibrous connective tissue to the deeper mylohyoid. It originates along the ventral surface of the dentary for a distance of 2 or 3 mm. caudal to the superficial mylohyoid. It passes posteromesiad, its fibers interlacing along the median sagittal line with those of its antimere. Its origin is fibrous and is continuous with the tendon of the posterior belly. A tough aponeurotic sheet, concave posteriorly, connects the posterior belly with the anterior belly. The digastric in *Scalopus* is more primitive than in *Blarina*.

*M. mylohyoideus, pars superficialis* (Figs. 30, 49, 60).—The superficial mylohyoid is a very thin muscle layer, the fibers of which run transversely, connecting the dentaries for a distance of about 4 mm. caudal of the symphysis menti. It lies ventral to the geniohyoid and is connected by a fascia with the anterior belly of the digastric.

It is innervated by the mylohyoid branch of the fifth cranial nerve, which runs along its dorsal surface.

*M. mylohyoideus, pars profundus* (Figs. 30, 37, 60).—The deep layer of the mylohyoid is a wide hexagonal band of muscle between the digastric, to which its superficial fibers are intimately united, and the geniohyoid, to which its deep surface is fused; its origin is on the mesial surface of the ramus of the dentary along the ridge of the bone limiting the inferior alveolar canal. Passing ventromesiad and increasing in width, this muscle terminates with its antimere in a median sagittal raphe. Its most posterior fibers insert on the ventral surface of the basihyal cartilage.

This element also is innervated by the mylohyoid nerve.

*M. tensor veli palatini* (Fig. 21).—The tensor is a small cuneiform muscle originating from the ventral surface of the skull along the transverse furrow between the basisphenoid and the auditory bulla. It lies ventral to the Eustachian tube. The muscle narrows as it passes cephalad, becomes aponeurotic lateral to the pterygoid hamulus, and turns sharply mesiad, passing over the ventral surface of the hamulus to insert into the fleshy soft palate.

A branch from the trigeminal nerve, passing mesiad in a bony trough immediately anterior to the orifice of the Eustachian tube, supplies the tensor veli palatini muscle.

*M. tensor tympani*.—No trace of a tensor tympani muscle was discovered in gross dissection. The tensor is present and is well developed in the shrew.

## B. Facial Field

The musculature of this field is supplied by the facial nerve.

*M. zygomaticus major* (Figs. 22, 48, 50, 53).—The zygomaticus major is a well-developed fusiform muscle lying between the temporal and masseter

muscles. Its fibers originate from a lateral crest which is directed obliquely dorsoventrad. The muscle passes anteriorly, forming at the region of the infraorbital foramen a strong round tendon which continues cephalad through a fascia and inserts into the ventral surface of the tip of the snout. The branch of the facial nerve which innervates all of the snout muscles runs along the ventrolateral edge of the zygomaticus major; the infraorbital branch of the trigeminal nerve emerges between the tendons of the zygomaticus major and minor. The tendon is attached to the premaxillary bone by two sheaths, the first immediately posterior to the first incisor and the second immediately lateral to the mid-line at the base of the first incisor.

*M. zygomaticus minor* (Figs. 22, 53).—This is a narrow fusiform muscle originating from the dorsal half of the aforementioned lateral crest at the base of the zygomatic arch. The muscle narrows as it passes anteriorly, and at about the level of the infraorbital foramen it forms a small round tendon which is superior to the levator labii superioris proprius. The tendon runs through the snout fascia and inserts into the ala. This muscle is completely hidden by the zygomaticus major and in turn covers the greater part of the levator alae nasi superioris and levator alae nasi inferioris.

*(M. levator alae nasi inferioris)* (Figs. 22, 53).—This narrow muscle, with its origin fused to that of the zygomaticus minor, is about half as wide as the latter. Its tendon is longer than its belly and runs dorsal to the zygomaticus minor and the levator alae nasi superioris, inserting into the base of the nasal septum.

*(M. levator alae nasi superioris)* (Figs. 22, 53).—The levator alae nasi superioris is a narrow fusiform muscle superficial to the inferioris. Its origin is fused with those of the zygomaticus major and the levator alae nasi inferioris. The small rounded tendon passes anteriorly, ventral to the tendon of the levator inferioris, and inserts into the rhinarium dorsal to the nares.

*(M. levator labii superioris proprius)* (Figs. 22, 48, 53).—This large, well-developed muscle is covered superficially by the zygomaticus major; it lies ventral to the three preceding muscles and is not bicipital as in the shrew. Its origin is from the dorsal surface of the posterior three-fourths of the zygomatic arch. The fibers of origin from the base of the arch are fused with those of the levator alae nasi superioris, the levator alae nasi inferioris, and the zygomaticus minor. Its tendon is heavy and passes cephalad, dorsal to the infraorbital branch of the trigeminal nerve, joining with its antimere by a tough fibrous sheet which passes over the dorsal surface of the bony rostrum. The united pair of tendons inserts into the dorsal part of the snout near its tip.

The branch of the facial nerve which innervates these muscles runs along the ventral border of the levator labii superioris proprius.

*M. digastricus, venter posterior* (Figs. 21, 22, 54).—The posterior belly is a large muscle lying deep to the trachelomastoid muscle and covering the posteroventral part of the masseter muscle. Originating from the

base of the skull, lateral to the occipital condyle, and from the aponeurotic sheet of the jugulothyroid, its fibers pass anteroventrad and form a strong tendon which attaches to the inferior edge of the dentary and connects aponeurotically with the venter anterior. The submaxillary duct passes deep to its superior edge.

*M. stylothyroideus* (Figs. 21, 22, 37, 60, 61).—This narrow muscle lies on the ventromesial surface of the posterior digastric and originates by a narrow tendinous plate from the base of the skull, lateral to the occipital condyle. As it passes anteriorly it becomes more clearly separated from the posterior digastric and attaches on the apex of the thyrohyal cartilage.

(*M. jugulothyroideus*) (Figs. 37, 61).—The jugulothyroid originates from the base of the skull posterior to the stylomastoid foramen. Its fibers pass cephalad to insert on a ventral aponeurosis, which attaches on the tympanostyloid synchondrosis and on the terminus of the stylohyal cartilage. This muscle represents Fiedler's (1953) *M. mastostyloideus*.

No special twig of the facial nerve could be found innervating this element in the mole.

*M. stapedius* (Fig. 21).—The stapedius is a poorly developed muscle, actually and relatively smaller than in *Blarina*, difficult to locate because of its small size and very light color. Deltoid in outline, it originates on the base of the skull immediately mesial to the stylomastoid foramen. It narrows rapidly as its fibers pass cephalad to enter the auditory chamber through a small fissure. Upon removal of the bulla a thin, glistening, cylindrical tendon can be seen extending from the muscle to insert on the stapedial process of the posterior crus of the stapes. Though Wilkie (1929) reported that an extension of this tendon inserts on the head of the stapes in the European mole, this condition was not observed in *Scalopus*. Nor did I observe an anterior ligament as illustrated and described for *Talpa* by Wilkie. In fact, from his illustration it appears that this anterior ligament may actually be the chorda tympani twig of the facial nerve. This twig is not described in his article. An os quartum was not observed.

The branch innervating the stapedius muscle could not be found.

### C. Glossopharyngeal Field

The musculature of this field is supplied by cranial nerve IX.

*M. stylopharyngeus* (Figs. 37, 63).—The stylopharyngeus, a well-developed muscle, originates from the mesial surface of the stylohyal cartilage and passes anteromesiad; its lateral fibers insert on the posterior edge of the ceratohyal cartilage, and its mesial fibers insert into the pharyngeal roof between the superior and medial pharyngeal constrictors. Hidden ventrally by the digastric, it is tucked between the pharynx and the dentary.

(*M. ceratohyoideus*) (Figs. 37, 62).—This muscle has its origin on the anterior edge of the thyrohyal cartilage, deep to the hyoglossus. Its fibers pass cephalad to insert on the posteromesial edge of the ceratohyal cartilage, the ceratohyal-hypohyal junction, and the caudal edge of the entire hypohyal cartilage.

## D. Vagus Field

The musculature of this group receives branches from the tenth cranial nerve through the pharyngeal plexus.

(*M. pterygopharyngeus*) (Figs. 21, 63).—This terete muscle originates from the summit of the pterygoid hamulus and passes posteroventrad, meeting its antimere in the roof of the pharynx in a median sagittal raphe.

(*M. chondropharyngeus*) (Figs. 37, 61).—The chondropharyngeus is a platelike muscle with its origin from the lateral surface and apex of the thyrohyal cartilage. Its fibers course dorsad around the pharynx to form a median dorsal raphe with its antimere.

(*M. thyropharyngeus*) (Figs. 37, 61).—The thyropharyngeus is a heavy band of fibers originating from the dorsolateral surface of the thyroid cartilage and passing cephalodorsad to insert into a median dorsal raphe on the roof of the pharynx.

(*M. cricopharyngeus*) (Figs. 37, 61).—This constrictor is a narrow band of fibers taking origin from the posterior region of the cricoid cartilage and inserting in a manner similar to that in which the preceding muscle inserts. The cricopharyngeus was not seen in *Blarina*.

*M. thyroarytenoideus* (Figs. 38, 62).—The thyroarytenoid is a narrow but heavy-bodied muscle. It originates from the posterior surface of the thyroid cartilage and from a mid-line raphe deep to the cricothyroid muscle. Its fibers pass laterad and insert by a broad flat tendon on the base of the arytenoid cartilage.

*M. cricoarytenoideus posterior (dorsalis)* (Figs. 36, 38).—The posterior cricoarytenoid, a broad muscle, originates from most of the dorsal surface of the cricoid cartilage. The fibers pass anteriorly, converge slightly, and insert on the base and mesial edge of the arytenoid cartilage. This muscle and its antimere cover almost completely the dorsal surface of the cricoid cartilage.

*M. cricoarytenoideus anterior (ventralis)* (Figs. 36, 38, 62).—This muscle is hidden ventrally by the cricothyroid. Its fibers originate from the lateral oblique edge of the cricoid cartilage and also from the posterior cornu of the thyroid cartilage. The muscle courses anterodorsad, inserting on the ventral surface of the arytenoid cartilage.

*M. cricothyroideus* (Figs. 37, 62).—Fibers of the cricothyroid pass cephalad from the posterior surface of the cricoid cartilage to attach on the caudal border of the thyroid cartilage. The muscle covers the entire ventral surface of the cricoid cartilage and is concealed by the more ventral sternothyroid and sternohyoid.

*M. arytenoideus* (Fig. 36).—The arytenoid forms a very thin band of fibers, originating from the lateral border of the arytenoid cartilage and passing mesiad to insert with its antimere along a median raphe. It covers part of the epiglottis, cricoid, and arytenoid cartilages.

*M. thyroepiglotticus*.—This muscle was not found.

*M. aryepiglotticus*.—This muscle was not found.

#### E. Accessory Field

This musculature is supplied by branches of the spinal accessory nerve and the ventral rami of cervical nerves two and three.

*M. levator veli palatini* (Fig. 21).—The levator is a small terete muscle with fibers arising from the base of the skull mesial to the foramen for the Eustachian tube and, after a ventromesial course, inserting in the roof of the soft palate.

I was not able to discover the innervation of this element.

*M. sternomastoideus* (Figs. 35, 51, 53, 54).—Dobson (1882-90) described this muscle for *Condylura cristata*, the star-nosed mole, and assumed that the condition of the musculature in this form and in *Scalopus*, *Scapanus*, and *Talpa* was sufficiently uniform to merit a single description. My observations do not confirm this assumption. I checked his information on the sternomastoid by dissecting a specimen of *Condylura* and found that his description of the sternomastoid as a single unit without division into several layers was accurate. In *Scalopus*, however, this is not the case, since the sternomastoid is composed of readily recognizable superficial and deep layers.

*pars superficialis*.—This part is a well-developed mass with a tough fibrous origin from the extremely heavy sternoclavicular capsule and from the deep surface of the pectoralis superficialis. It widens as its fibers run dorsad to insert deep to the rectus capitis, on a prominent oblique ridge on the posterolateral surface of the skull between the squamosal and the parietal bones, by an aponeurosis common to it and the cleido-occipital muscle.

*pars profundus*.—This deep part is somewhat heavier than the superficial sheet and has a similar origin from the median sagittal plane. The profundus joins the cleidomastoid as it passes dorsolaterad and narrows to a heavy tendon of insertion on the crest at the base of the zygomatic arch. The sternomastoid is a smaller, unilaminar muscle in *Blarina*.

*M. cleidomastoideus* (Figs. 35, 51, 53).—The origin of the cleidomastoid is very narrow and tendinous from the anterior surface of the clavicle between the mesial edge of the bone and a large more lateral foramen. This muscle is heavier than the deep sternomastoid which it joins to insert as has been stated. This element is smaller in the shrew.

(*M. cleido-occipitalis*) (Fig. 54).—This element is wider than the preceding muscle with an origin several times greater, reaching from the level of the above-mentioned foramen to the dorsal edge of the clavicle. This muscle joins the superficial sternomastoid, the insertion of which has already been given.

*M. trapezius (anticus)*.—There is a group of very weak fibers arising from the mid-line of the cervical region, which I could not trace as they pass anterolaterad around the side of the neck. Campbell (1939) called this element the anterior trapezius.

## DISCUSSION

## Osteology

## Cranium

**General Form.**—The greatest disparity between the crania of *Blarina* and *Scalopus* is in size, the maximum length of the cranium of the former being slightly less than two-thirds that of the latter. The occipital and parietal regions in *Blarina* are more angular than in *Scalopus*, and the posterior wall of the brain case in the shrew slopes anterodorsad, forming an acute angle with the horizontal plane of the floor of the brain case, whereas the posterior wall of the cranium in *Scalopus* lies in a vertical plane. The general fusiform contour of the cranium in the shrew is interrupted by the absence of a malar bone.

A flattening of the brain case of the mole has been claimed by many earlier workers to be a fossorial adaptation. Reed (1951) made comparative measurements of the length, height, and width of the crania of *Sorex*, *Neotrichus*, and *Scapanus* and from the resulting data concluded that the cranium of *Scapanus* is no flatter than that of *Sorex*. I have measured these dimensions in thirty specimens of the prairie mole and thirty specimens of the short-tailed shrew with the following results: *Scalopus*—mean length  $36.9 \pm .18$ , standard deviation 1; mean height  $10.8 \pm .06$ , standard deviation .31; *Blarina*—mean length  $22.3 \pm .18$ , standard deviation 1; mean height  $7.1 \pm .01$ , standard deviation .05. The ratio of length to height is 3.4 in the mole and 3.1 in the shrew. These proportions agree with Reed's conclusions and indicate that the cranium of *Scalopus* is no flatter than that of *Blarina*.

Differences between various cranial bones of the shrew and the mole were noted in immature animals (Figs. 66, 67). In the adult mole only the coronal, sagittal, and lambdoidal sutures are visible; in the adult shrew the nasofrontal, sagittal, and lambdoidal sutures, and those surrounding the temporal complex can be distinguished.

**Premaxillary.**—This element in the mole lacks a well-developed nasal process, which is present in the shrew; in the mole the premaxillaries extend anterior to the tip of the nasals.

**Maxillary.**—The zygomatic process is poorly represented in *Blarina*. The lachrymal canal courses cephalad through the maxillary bone in the shrew, but a lachrymal canal could not be located in the mole.

**Palatine.**—The pterygoid processes of the palatines form wider plate-like structures in *Scalopus* than in the shrew. The vertical part of this bone in both forms assumes a minor role in forming the floor of the orbito-temporal fossa.

**Pterygoid.**—The boundaries of the pterygoid bones were not distinct in either form, and it was impossible to determine with certainty the extent to which this element may participate in the pneumaticity of the floor of the skull in *Scalopus*.

**Basisphenoid.**—In the mole this element is cancellous and bears a tympanic process which forms the anteromesial part of the roof of the

tympanic cavity; in the shrew it is not cancellous and lacks a tympanic process.

Presphenoid.—This element could not be identified in either form.

Alisphenoid.—The alisphenoid in the mole is extremely cancellous and inflated to form all or part of the large thin-walled prominences lateral to the pterygoid hamuli and probably also a small part of the roof of the tympanic cavity. This pneumatic process adds strength to the skull with little increase in density. The alisphenoid in the shrew lacks a tympanic process and is not diploic.

Orbitosphenoid.—In the nestlings of both forms this element is penetrated by the optic foramen, but in the cranium of the mature shrew the persistence of this foramen is variable.

Basioccipital.—This is a chevron-shaped bone which is partly cancellous in *Scalopus*; in *Blarina* it is Y-shaped and is not diploic.

Temporal.—The osseous labyrinth is similar in both genera. The tympanic element is an incomplete ring in the shrew, but forms a plate-like auditory bulla in the mole. The squamosal in the shrew bears two articular facets for the reception of the dentary, as compared with the usual mammalian single facet which occurs in the mole. The zygomatic process of the squamosal is well developed in *Scalopus* but is vestigial in the shrew. A number of investigators have reported the absence of this process in the shrew.

Exoccipital.—This bone lies in the ventral surface of the cranium in the mole, but it is in the posteroventral wall of the cranium in the shrew.

Nasal.—The nasals in the shrew are rectangular in outline and do not extend so far cranial as the apex of the premaxillaries; in the mole the nasals are triangular and extend cranial almost to the apex of the premaxillaries. Thus, the nares face forward in the mole and dorsocephalad in the shrew.

Lachrymal.—The lachrymal was not located with certainty in the mole. In the shrew it forms the lateral wall of the infraorbital canal and is pierced by a lachrymal foramen. Muller (1935) stated that the lachrymal is absent in the Soricidae.

Frontal.—The frontal is a smaller bone in the shrew than in the mole and at its anterior border is pierced by a venous foramen which is probably homologous to that seen near the lateral border of the frontal in the mole. Muller (1935) stated that the frontal is inflated in the Talpidae, but I did not find this condition in *Scalopus*.

Parietal.—The parietals are similar in both forms, but the mole lacks a sagittal crest.

Interparietal.—This element could not be identified in either *Blarina* or *Scalopus*.

Supraoccipital.—The supraoccipital lies in an oblique plane in the shrew and in a vertical plane in the mole. The latter lacks a lambdoidal crest.

Malar.—The malar is absent in the short-tailed shrew, and, though the zygomatic arcade is complete in the mole, no positive evidence was found of a malar bone in the skull of the nestling. The zygomatic process of the maxillary was very long, however, and probably represents a fused malar.

The loss of the zygomatic arch in *Blarina* and in other soricids has never been satisfactorily explained. Winge proposed the following interpretation for the loss of the zygomatic arch, as translated by Deichmann and Allen (1941:166):

In those genera in which the conditions are most nearly normal these "lower snout muscles" (as they may briefly be termed without asserting too much in regard to their homologies) have their origin upon the outer side of the zygomatic arch approximately beneath the orbit; the anterior part of the zygomatic arch becomes strong through their origin but is rather weakened and thin posteriorly; the jugal is indeed present but much reduced (*Gymnura*, *Hylomys*). From this condition development may proceed in two directions: Either the origins of the muscles may retain their position below the orbit, becoming thereby more powerful and producing the *Prc. zygomaticus* of the maxillary, which they chiefly influence, to become stronger and more tubercularly projecting, while the larger posterior part of the zygomatic arch is reduced and disappears (most centetids); — or the muscles may extend their point of origin backward along the zygomatic arch or probably along the ligament which takes its place until they reach the base of the *Squama* or *Tegmen tympani*, where they may give rise to crests and tubercles. In the latter case the zygomatic arch is also weakened and at last completely disappears, probably because it is made to atrophy by being squeezed and displaced by the long snout muscles which slide along it (*Erinaceus* as a transitional form; *Talpidae*, *Soricidae*, *Hemicentetes* and in some respects *Chrysochloris*).

This explanation for the loss of the zygomatic arch does not seem probable. It appears more likely that this pressure would cause a remodeling, but hardly a loss, of the arcade. The direct cause of the loss of the arch may not have been pressure, but rather the loss of the deep layer of the masseter. The arcade still persists in the *Talpidae*, in which it serves for the origin of part of the masseter and part of the snout muscles. In these forms the snout muscles are very well developed. Other investigators have hypothesized that the loss of the zygomatic arch is related to a change in the masticatory muscles. In her study of the structure of the *Soricidae*, Årnäck-Christie-Linde (1907) stated that as a result of the altered origin of the masseter muscle, the zygomatic arch lost its most important reason for existence and therefore has undergone atrophy. Cuvier (1800-37) stated that the composition, force, form, and expanse of the zygomatic arcade has an essential relationship with the movements of the mandible. Giebel, in Bronn's anatomical tomes (1874-1900), considered the development of the malar and the form of the zygomatic arch to be related to the function of the lower jaw. These relationships given by Årnäck-Christie-Linde, Cuvier, and Giebel appear to be more nearly correct.

In *Blarina* the origins of the snout muscles have migrated caudad to the base of the arch so that none of their elements arises on the arcade. This movement serves to lengthen the fibers and increase the speed of contraction of these muscles, thereby increasing the mobility of the snout. The deep layer of the masseter, which utilized almost the entire length of the zygomatic arcade as its base of origin, has also disappeared in *Blarina*. The cause for its loss has not been explained, but most likely is related to dietary habits; yet I can discern no functional reason for its loss. In forms retaining this deep layer of the masseter the resultant force on contraction is primarily dorsad and, as will be discussed later,



in *Blarina* compensation for its loss has been achieved by an increase in the mechanical efficiency of the temporal muscle. Whatever the cause for the loss, its absence leaves the arch without muscular attachments. Slade (1895) considered the structure of the zygomatic arch in numerous mammalian orders in relation to the muscles of mastication, though he did not discuss the significance of its absence in certain forms. He did point out, however, that the development of the arch in mammals is related to the energy and character of the masticatory muscles.

**Telethmoid.**—A cartilaginous snout of considerable size projects cranially from the bony rostrum in both the shrew and the mole, and a firm, mid-sagittal, cartilaginous nasal septum continues forward into this cartilaginous structure. There are regional areas of calcification in this structure in the mole, which are shown in Figures 26 and 27. Reed (1951), in his very fine analysis of insectivore anatomy, wrote:

The role of the mole's nose in burrowing has been variously, and wrongly interpreted. Cuvier (1817:137) wrote that there is a special bone in the nose of the mole, *Talpa europaea*, which the animals [*sic*] uses for digging. Mansion (1902) mentioned the same bone in the nose of *Talpa*, but Shimer (1903) and Winge (1941:169) stated this as if general for all moles; . . . . I can only say that there is no special "digging" bone in the nose of *Scapanus latimanus* or *Neurotrichus gibbsii*, and I doubt if any other mole has one.

My observations on the prairie mole agree with Reed's rejection of the idea that the mole's snout is used as a digging structure. The many references however, to a prenasal or telethmoid bone in the mole's nose have caused me considerable concern, for I do not think these references are entirely false. Statements similar to those cited by Reed appear in Flower and Lydekker (1891), Flower (1885), Boas and Paulli (1908), Bolk, *et al.* (1934), Brandt (1836), and Weber (1927-28). It is impossible to ascertain how many of these reports are based on primary observation. A dissection of the snout of the European mole disclosed that the nasal septum, which runs forward in a mid-sagittal plane of the alinasal, is of a cartilaginous nature. This median septum has undergone some degree of calcification as is shown by its sound and resistance in sectioning. The same structure in the prairie mole, however, has the appearance and consistency of hyaline cartilage. Concerning *Talpa europaea* Parker (1885) stated:

This latter part [the snout] has been effected by the generally intense ossification of the skull, and not only the proper septum nasi (s.n.) has been well ossified on from the perpendicular ethmoid, but that foregrowth of the septum (s.n'.) which divides the long alinasal region (al.n.), in front of the premaxillaries, has acquired an endosteal tract, almost to its front end . . . .

It seems probable that this ossification in the nasal septum, which may be better developed in old individuals, has induced earlier investigators to identify a telethmoid bone in the snout of *Talpa* and that this interpretation has been followed in publications by subsequent authors. The stiffening of the cartilaginous snout serves not so much to make the snout rigid for digging or for hammering, as Böker (1935) thought, but to provide the nose with a degree of firmness for movement by the snout muscles, the long tendons of which attach to its terminus.

### Auditory Ossicles

**Malleus.**—The malleus of the shrew has a well-developed orbicular apophysis, a long processus gracilis and manubrium, an extensive lamina, a processus lateralis, and a processus muscularis. The malleus of the mole has a reduced orbicular apophysis, a shorter processus gracilis and manubrium, a smaller lamina, and lacks a processus lateralis and a processus muscularis.

**Incus.**—This bone in the short-tailed shrew does not have a processus brevis, but the connection between the lenticular process and the processus longus is heavier in the shrew than in the mole.

**Stapes.**—The stapes is similar in both forms.

### Dentary

This bone in the shrew has a narrow, spicular, angular process, a short, stout, condylar process with two articular facets, a heavy, rather tuberos coronoid process, and a posterointernal ramal fossa. In the mole the angular process forms a well-developed scooplake plate; the condylar process is longer and heavier and bears one articular facet; the coronoid process is thin, without tuberosities; and a posterointernal ramal fossa is absent.

### Hyoid and Laryngeal Cartilages

All of these elements are much the same in *Blarina* and *Scalopus*. In *Blarina*, however, the basihyal is longer, and the ventral arch of the cricoid is more delicate than in *Scalopus*. The tympanohyal is fused to the cranium in both forms.

### Vertebrae

**Atlas.**—The transverse process of the atlas, though weak in both forms, is more pronounced in *Blarina* than in *Scalopus*; the dorsal spine is weaker, but the ventral spine is stronger in the shrew than in the mole.

**Axis.**—The vertebral spine and hypapophysis are better developed in the short-tailed shrew than they are in the mole.

**Cervicals Three to Seven.**—In the shrew, in contrast to the mole, hypapophyses are present on cervicals two, three, and four; there is a very noticeable transverse concavity of the anterior articular surfaces of the centra, and there is an equally pronounced transverse convexity of the posterior articular surfaces. In *Scalopus* the anterior and posterior surfaces of the centra are almost plane transversely. The pedicels and laminae are similar in both genera. In *Blarina* the transverse processes are more delicate and exhibit a more prominent lateral flare than in *Scalopus*. The vertebral spines are very feeble in both forms; they are better developed in the shrew.

One might anticipate finding a distinct shortening in the cervical segment of the vertebral column in a form so well adapted to fossorial habits as the mole. The writings of earlier scholars would also suggest a

shortening of the cervical region. Hisaw (1923) wrote: "The neck is sufficiently shortened to give the fore legs the appearance of articulating with the body alongside of the head." Nelson and Fuertes (1918) discussed the short neck in *Scapanus townsendi*, and Cahalane (1947) spoke of the very short neck of the common and western moles. Superficially, this false neckless appearance is effected by the forward extension of the manubrium and an anterior migration of the forelimbs. To determine whether or not the cervical series is relatively shorter in *Scalopus* than in *Blarina*, both this segment and the thoracic central series from thoracic vertebrae two to eleven were measured in six columns in *Scalopus* and six columns in *Blarina*, and the mean lengths of the two segments were determined. By comparison of the mean lengths of the two segments, it was found that the thoracic series of *Scalopus* is 1.6 times this series in *Blarina*, whereas the cervical series in the former is 1.96 times the cervical series in the latter. This data would indicate that the neck of *Scalopus* is relatively longer than that of *Blarina*.

Synostosis has been associated with the fossorial habit and often has been described in moles. Shimer (1903) regarded fusion of the cervical vertebrae as a fossorial adaptation. Weber (1927-28) reported that in *Talpa* the second, third, and fourth cervical vertebrae are fused; Bolk, *et al.* (1934) mentioned the coalescence of the cervical vertebrae in the mole; Böker (1935) and van der Klaauw (1948) also noted this bony fusion, and most recently Young (1950) stated that the cervical vertebrae in *Talpa* are fused. I found no indication of fusion among the cervical vertebrae of the prairie mole either in osteological preparations or in dissected specimens. The obvious conflict between my observations and the statements given above led me to check the condition in *Talpa europaea*. An examination of three osteological specimens of this species showed no suggestion of fusion between any of the cervical elements, the character of the vertebrae being very much like that of *Scalopus*.

Hatt (1932), in his study of the vertebral column in ricochetal rodents, noted that ankylosis of the cervical vertebrae occurred in those forms in which the cervical segment was less than 15 per cent of the thoracolumbar series. In *Scalopus* this ratio is 29.4, almost twice that critical for fusion.

#### Ligamentum Nuchae

This structure is a fibrous mid-line raphe in the shrew, but is heavier and formed of calcified cartilage in the prairie mole.

#### Scapula

The scapula of the shrew differs from that of the mole in that it has a coracoid process, a metacromion process, a better developed acromion process, and is not attenuated in its long axis.

#### Manubrium

This element in the shrew is very much smaller than that in the mole and occupies a more posterior position in the body.

## Clavicle

The clavicle of the shrew is rodlike, but that of the mole is cubical and possesses a facet for articulation with the humerus.

## Myology

The musculature of both the short-tailed shrew and the prairie mole presents a mosaic pattern with regional individualities in the two species. Volumetric analyses of the muscles were not made because of the difficulty in determining an accurate standard by which the volume of a particular muscle in the one form can be related with that of its homologue in the other form. Another problem was the difficulty of obtaining accurate data because of the small size and manner of attachment of many of the muscles. I have attempted a functional analysis of certain muscles, but it is to be borne in mind that these conclusions are largely tentative. The effectiveness of muscle action is dependent on many factors, such as the number, length, and disposition of muscle fibers, the mechanics of the leverage system, and the tonus of muscle fibers. My theoretical considerations are based on observations of the living animal, the study of cleared and stained animals, preserved specimens, and cleaned osteological preparations.

### Myomeric Musculature

The splenius muscle has a wider area of insertion but is a thinner and relatively shorter element in the shrew than in the mole. Correlated with the development of the splenius, the nuchal ligament in the mole, which serves as a surface of origin for the fibers of the splenius and rhomboid-eus cervicis muscles, is calcified and offers a greater and more stable surface for muscle origin. The iliocostalis band is relatively and actually wider in the shrew and has a cervical part which is not present in *Scalopus*. The longissimus cervicis muscle is also more extensive in the shrew. These muscles, members of the transversocostal and transversospinal groups, function in extending the vertebral column when acting synergetically, but with unilateral antagonistic action they bend the column laterally. This muscular development in respect to lateral flexion is related to the structure of the transverse processes and of the articular surfaces of the centra.

The transverse processes are directed laterad in the shrew, but in the mole they are directed caudad, limiting lateral flexion. In fact, these processes in the mole dovetail on the third and fourth cervical vertebrae with those of the vertebrae next posterior, allowing little lateral flexion in this region. In *Blarina* there is a very noticeable transverse concavity on the anterior and an equally pronounced transverse convexity on the posterior surfaces of the centra, whereas in the prairie mole these surfaces are almost plane.

The significance of the better developed cervicis elements in the shrew is probably related to the shrew's more characteristic cursorial locomotion which involves considerable extension and flexion of the

column. In contrast, if the mole is placed on a firm substrate, one can observe in its locomotion a rapid movement of the limbs with no visible flexion or extension of the column, much as a metal toy animal with hinged limbs and a rigid axis would move across the floor. The longissimus capitis has an extensive origin on the cervical vertebrae in the shrew which functions largely in retracting the head, whereas the very restricted origin of this muscle in the mole largely limits the action of the muscle to rotating the head and elevating the snout. The semispinalis dorsi et cervicis is a heavier muscle and is composed of longer fibers in *Blarina*. The semispinalis capitis has a greater surface of origin in the shrew. The intertransverse musculature is better developed in *Blarina* in accord with the larger transverse processes in this form. In the mole the intertransverse musculature extending between cervicals three to seven is not well developed and is covered superficially by a strong intertransverse ligament. The rectus capitis posterior muscles are similar in *Blarina* and *Scalopus*, but, as a result of the different planes occupied by the occipital condyles in the two species and the correlated differences in the angle between the base of the skull and the anterior cervical vertebrae, these muscles have a greater angle of pull in the shrew and hence a greater force vector caudad, whereas the greater force vector in the mole is ventrad. The longissimus capitis and semispinalis capitis muscles operate on a similar muscle function correlation. The obliquus capitis inferior muscle has a larger surface of origin in the shrew.

The longus colli muscle is heavier in the shrew and is related to the strong development of the hypapophyses in this form. By means of these larger processes its fibers are afforded a greater angle of pull and an increased power arm with a resultant increase in effective force. The sternohyoid and sternothyroid muscles are fused at their origins in *Blarina*, the former element being heavier in *Blarina* and the latter element being heavier in *Scalopus*. There is an omohyoid muscle present in the short-tailed shrew.

The more vertical direction of the fibers of the levator scapulae et serratus anterior cervicis muscle in *Blarina*, as compared with their oblique direction in *Scalopus*, is correlated with the position of the long axes of the scapulae in the two genera. In the short-tailed shrew the rhomboideus capitis is a shorter, and probably a thinner, muscle than in *Scalopus*. The part of the scapula on which it originates is in the region of the second and third ribs in the former and at the level of the fifth or sixth rib in the latter. The structure of the rhomboideus capitis and the splenius in *Scalopus* may be related to the characteristic method by which this animal eats worms. When the mole traps a worm under one of its massive hands, it nips various regions of the body a number of times. The worm is then held between the claws of both hands, which are placed in front of the snout, palms forward. The free end of the worm is grasped with the side of the mouth, and the head of the mole is pulled back sharply with considerable cervical extension, thereby drawing a part of the worm through the claws. That part of the worm thus prepared is masticated and swallowed, and the operation is repeated. The part of the worm being chewed remains protruding from the side of the mouth. This rapid

retraction of the head, accompanied by cervical extension, is probably accomplished by the contraction of fibers of the splenius and rhomboideus capitis muscles, their long fibers accommodating movement of greater amplitude. The atlantoscaphularis anterior and posterior muscles are present in the shrew.

#### Branchiomic Musculature

In the shrew the sternomastoid, cleidomastoid, and cleido-occipitalis complex appears weaker than in *Scalopus*, and the cleidomastoid is bilaminar in the mole. These three elements in the mole provide a powerful lateral rotator and depressor of the head. The anterior trapezius is well developed in *Blarina*, but is barely represented in *Scalopus*. The presence of the anterior trapezius and atlantoscaphularis anterior and posterior muscles in the shrew is related to the greater mobility of the scapula in this form. The stylohyoid is smaller and probably weaker in the shrew. The stapedius muscle is less developed, and the tensor tympani muscle is absent in *Scalopus*. The digastric in the two forms is distinctly different, its structure being more primitive in the prairie mole than in the short-tailed shrew.

The fibers of the external pterygoid muscle have a greater surface of insertion and a more anterior point of origin in *Blarina*. This element not only protracts the jaw but also opens the mouth, and in this latter action a greater moment of force is effected by the situation of the fulcrum at the ventral articular facet of the dentary and not at the terminus of the condylar process (Fig. 46). The internal pterygoid muscle is not well developed in the short-tailed shrew and has a smaller origin and insertion because of the limited amount of bone in these regions. Though it still functions in closing the jaw, the application of force is very close to the new mechanical axis resulting in a low effort arm and moment of effort (Fig. 46).

The masseter in the short-tailed shrew has its fibers directed obliquely and is not distinctly separated into more than one layer. It lacks a deeper part and hence a vertical force component, but the penniform structure of this muscle increases its power. Petit (1927) briefly discussed the masseter of *Sorex minutus* and mentioned that it also is an indivisible mass. Ärnback-Christie-Linde (1907), in her analysis of the masseter of the shrew *Crocidura murina*, stated that the masseter originates on the zygomatic process of the maxillary and the lower border of the upper jaw and inserts on the angular process of the mandible. Žlábek (1938), for *Crocidura russulus*, and Dubecq (1925), for *Crocidura aranea*, described a similar origin and insertion. Fiedler (1953) described a M. zygomaticomandibularis in *Sorex indicus*. I found a group of fibers in *Blarina* having a similar origin, insertion, and course, but I consider these to be a part of the temporalis muscle.

Figure 59 represents the fibers and fasciae of the masseter of the prairie mole. Žlábek (1938) gave an excellent detailed analysis of this muscle in *Talpa europaea* and in eight other insectivores. He reported that the external masseter in *Talpa* is so twisted that the fibers inserting

most anteriorly originate most posteriorly and ventrally, and those inserting most posteriorly originate most anteriorly and dorsally, a structure which can be visualized by bending a rectangular card into a semi-circle with the base of the curve along the diagonal of the card. This condition, which I was able to observe in *Talpa* also, Žlábek attributed to the forward migration of the masseter fibers onto the maxillary bone. In both *Talpa* and *Scalopus* the anterior fibers of the external masseter have migrated as far forward on the maxillary bone as the first molar tooth, but in *Scalopus* the torsion is not as easily discerned, and the attachment to the zygomatic arch is more extensive. This origin on the zygomatic arch is 4.5 mm. caudal to the posterior border of the infraorbital foramen in the prairie mole and only 2.5 mm. in the European mole. The masseteric zygomatic fibers which I saw in *Talpa* were fleshy, an observation which is in contrast to Žlábek's statement. The fascicles of the masseter are for the most part short and numerous and form a multipennate structure which adds considerably to the power of contraction.

Žlábek analyzed the masseter as follows: (A) superficial layer, (1) maxillary part composed of anterior, preangular, angular, and supraangular fascicles, (2) zygomatic part; (B) middle layer; (C) deep layer; and (D) internal layer. Allen (1880), in a general article on the masseter of mammals, also divided this muscle into four layers. I can see no reason for applying terms to the various fascicular elements of the superficial layer of this muscle in the prairie mole since they are not separable, but constitute a unit. This objection, however, does not detract from the value of Žlábek's detailed analysis, and the basic structure in *Scalopus* corresponds to that which he described in *Talpa*. Žlábek's "couche superficielle" represents Allen's (1880) first layer and Toldt's (1905) superficial part. Žlábek stated that the fleshy fascicles of this layer originate on the anterior part of the zygomatic arch by a large aponeurosis, which he termed the "tendon superior superficiel," and insert by fleshy fibers on the mandible. Žlábek's "couche moyenne" is Allen's second layer and part of Toldt's deep layer of the masseter. It originates on the zygomatic arcade, on the internal surface of the superficial superior tendon, and on the lateral surface of the superior deep tendon, and is bipennate. Its intramuscular tendon, Žlábek's "inferior tendon of the masseter," serves to attach the fibers onto the angular process. Žlábek's "couche profonde" is Allen's third layer and a part of Toldt's deep part of the masseter. Its fibers originate on the mesial surface of the superior deep tendon and on the zygomatic arch and insert on the angle of the mandible. Žlábek's "couche interne" is Allen's fourth layer, probably Toldt's zygomaticomandibularis muscle, and Fiedler's (1953) *M. zygomaticomandibularis*. It originates on almost the entire length of the zygomatic arcade and inserts on the lower rim of the fossa occupying the lateral surface of the coronoid and condylar processes. The first three layers can be seen in Figure 59, illustrating the condition of the masseter in the prairie mole; the fourth layer is illustrated in Figure 54. Because each layer is not a separate sheet divided by clear fascial planes but is an integrated unit, I have not grouped the various fascicles under specific names. In the masseter muscle of *Talpa europaea*, Petit (1927) described an oral and a deep

part which correspond to my superficial and deep parts. His oral or my superficial part includes Žlábek's external, middle, and deep layers. Dubecq (1925) described an anterior and a superficial fascicle and a posterior fascicle for *Talpa europaea*. The anterior and superficial fascicles correspond to my superficial, and the posterior fascicle corresponds to my deep layer. In the prairie mole there is not a clear separation between the posterior part of the deep layer of the masseter and the posterior superficial fibers of the temporal, nor is there any evidence of a change in the course of their fibers. This agrees with Leche's (Bronn, 1874-1900) observations, and according to Žlábek a similar condition exists in *Talpa*. In the absence of developmental stages, the plane of cleavage between these two muscles must be arbitrarily designated.

Žlábek made a very interesting functional analysis of the masseter muscle, as applied particularly to Centetoidea, in which the fibers of the superficial layer have attained an almost horizontal orientation. This tendency is seen in *Talpa*, *Scalopus*, and *Blarina*, in which the fibers assume an oblique direction. Žlábek hypothesizes that the appearance of a tuberculosectorial dentition is associated with this orientation. The resultant force of contraction is anterodorsad, protracting the mandible and insuring the shearing action of the anterior blades of the inferior molars against the posterior blades of the superior molars, an action which would be efficient in cutting the chitinous shells of insects.

The functional mechanism of mastication has been studied in various forms and presents different modifications to effect various movements for the attrition of diverse kinds of food. Carnivores, herbivores, and rodents have received considerable attention, yet in no other forms, to my knowledge, is such an interesting modification in the mandibular articulation found as in certain of the insectivores. This unique articulation has been noted and described by Weber (1927-28), Winge (1941), and others. The two articular facets on the dentary of *Blarina* are shown in Figure 8. The interesting point concerning the articulation, and apparently one that has been previously overlooked, is its effect upon the mechanics of movement of the lower jaw and, concomitant with this, on the masticatory musculature. The net result of this double articulation is that the original hinge joint has become a gliding articulation; the new, more ventral, articulation represents a hinge joint and the mechanical fulcrum of the dentary. Figures 7 and 8 show very well the displacement cephalad of the fulcrum.

The masseter in *Blarina* lacks a deep layer. Its fibers are vertical, whereas those of the superficial stratum are oblique, resulting in a greater vertical vector and a smaller horizontal vector in the deeper layer than in the superficial layer. The mechanism of masseter action involves a lever of the third order, i.e., the force is applied between the resistance and the fulcrum, the force and resistance operating in opposite directions (Fig. 46). If the fulcrum is moved closer to the effort, the power arm is reduced. This is exactly what has happened by the forward migration of the mandibular articular surface. As a result of these two factors, the masseter acts largely in the rapid protraction of the mandible and, hence, in the speedy operation of the nipping action of the incisors.



This action is supplemented by the internal pterygoid muscle. From this analysis one would conclude that the short-tailed shrew has little power in its bite. Further observation, however, reveals a very interesting compensatory mechanism. The temporal muscle is well developed in the short-tailed shrew and in the prairie mole but cannot be separated into distinct layers in either form. It has a more extensive origin in the shrew than in the mole, covering about 60 per cent of the length of the cranium in the shrew and only about 50 per cent in the mole. The temporal muscle in the shrew originates from the temporal fascia and the parietal, frontal, and squamosal bones; it inserts on the coronoid process of the dentary. In the mole it originates on the temporal fascia and the surface of the parietal, frontal, and squamosal bones, and inserts on the coronoid process of the dentary, a very low but perceptible temporal ridge demarcating its origin.

According to Allen's (1880) study of the temporal muscle in mammals, there is a deep and a superficial set of fibers. The deep set originates from the floor of the temporal fossa, and the superficial set originates from the temporal aponeurosis; both insert on the coronoid process. Årnäck-Christie-Linde (1907) considered the temporal muscle of *Crocidura murina* to be split into three parts, but its origin and insertion are essentially as in *Blarina*. Dubecq (1925) did not divide the temporal muscle in *Sorex*. Petit (1927), in his work on the temporomasseter muscles of insectivores, described a supramasseteric muscle which originates on the anterior extremity of the temporal crest and inserts on the anterior slope of the coronoid process. This element he observed in *Sorex minutus*, but reported it absent in *Talpa europaea*. In *Blarina* a group of fascicles comprising what I have interpreted as a part of the temporal muscle may represent the muscle. There is a similar set of fibers in the prairie mole. This muscle is identified by Allen as the suprazygomatic part of the masseter. Årnäck-Christie-Linde considered it the third head of the temporal, and Leche described it as the second part of the temporal. Žlábek gave an illustration of a suprazygomatic part of the temporal in *Potamo-gale velox*, which appears to be the same element. Most recently, Fiedler (1953) described a suprazygomatic part of the temporal muscle. The consensus of investigators relates these fibers with the temporal muscle, an interpretation which agrees with mine.

The operation of the temporal muscle also involves a lever of the third order (Fig. 46). With the establishment of the fulcrum of the dentary more anteroventral, the power arm is increased because of the very oblique direction of the fibers of the temporal muscle, and the resistance arm is decreased. Thus, as a result of the new fulcrum, with any standard effort and resistance the torque is increased and contributes measurably to the power of contraction of the temporal muscle. This condition applies to the bulk of the temporal. Some of the deeper fibers of this muscle, however, are inserted on the mesial surface of the dentary close to the fulcrum and have lost power with the development of the new hinge articulation. These fibers have burrowed forward into the substance of the dentary to insert cephalad of the point, thereby operating on the principle of a third order lever. Actually, their insertion appears to remain too near to the joint for any considerable increase in the moment of the

force, though there is the compensating factor of speed.

It is significant that the two articular facets on the dentary are not well separated in *Sorex* (Fig. 15) and that the more ventral surface has moved farther anteriorly in *Blarina* and still farther forward in *Crocidura russula*. Barrett-Hamilton's (1910-21) illustrations of the mandibles of *Sorex araneus* and *Neomys fodiens* show the double facets. Winge (1941) considered the evolutionary development of the two mandibular articular facets and pointed out that a European tertiary soricid *Plesiosorex* has a single primitive articular surface. M. de Blainville's (1839-64) plates support this statement. There is some doubt, however, concerning the taxonomic position of *Plesiosorex*. Butler (1948) placed it in the Erinaceidae, others consider it a soricid, and Simpson (1945) apparently has omitted it in his classification of the mammals. Whatever the position of *Plesiosorex*, this modification probably has developed as a mechanism to compensate for the loss of the deep masseter, and one should expect to find various intermediate stages between the single and the double facet.

## Special Senses

### Middle Ear

The malleus of the prairie mole does not possess a muscular process, nor was I able to discover in the mole the tensor tympani muscle which in other forms inserts on this process. Six careful but fruitless dissections, using various approaches, were made. To my knowledge, the absence of this muscle has been reported only in the pangolin (Weber, 1927-28). The insertion of the tensor tympani muscle in mammals is on the dorsal surface of the malleus near the base of the manubrium, and upon contraction it pulls the manubrium and tympanic membrane dorsad. Supposedly, it functions to prevent excessive displacement of the membrane and ossicles particularly in response to low tones, and thus protects the internal ear from injury. Concerning the stapedius and tensor tympani muscles in dogs and rabbits, Beatty (1932) stated: "The animal's hearing is less acute when there is contraction of either or both of these muscles, and is more acute if the muscles are put out of action by cutting off their nerve supply." The absence of the tensor tympani muscle in the prairie mole would suggest an increased acuteness in auditory reception. The stapedius muscle is present in the prairie mole but is poorly developed and composed of very lightly colored fibers.

One encounters frequent statements and suggestions in respect to the acute auditory sense in moles. Cuvier (1800-37) stated that there is a large tympanum in the mole. Slonaker (1920) expressed the following view concerning *Scalopus*: "Even though no external aural appendage is present (Huxley, '90; Herrick, '92), the sense of hearing is apparently rather acute." Cahalane (1947) considered hearing fairly acute in *Scapanus* and *Scalopus*. My observations on the tensor tympani muscle suggest that these statements on hearing are valid, but there are other factors to be considered.

Many investigators have called attention to the large diameter of the tympanum in various mammals, with an implication that acute hearing is concomitant with a large tympanic membrane. Howell (1932), in his study of *Dipodomys*, stated that the tympanic membrane in a certain species of this genus is 6 mm. in diameter. The measurements of the tympanic membrane of *Talpa europaea*, as given by Wilkie (1925), are 4 mm. by 3 mm. To appreciate this data on so small a form, Wilkie (1925, 1936) cited the following tympanic drum measurements (in mm.): ox, 12.5 by 11; horse, 11 in length; domestic sheep, 9 by 7. My measurements for the eardrum in the prairie mole are approximately 4 by 3.5, which agree with Wilkie's data on the size of the membrane in *Talpa*. In man the tympanic membrane measures only 9 by 8 (Grant, 1948). Despite such impressive data on the size of the membrane, these authors have neglected a factor which plays a most important part in auditory acuity, namely, that the intensification of vibrations at the oval window is proportional to the excess in area of the tympanic membrane over that of the oval window. As will be shown later, one can obtain a completely erroneous idea of auditory acuity from a consideration of membrane size alone. In the prairie mole the area of the tympanic membrane is approximately 19 times the area of the oval window. In man the area of the drum membrane is about 20 times that of the oval window (Best and Taylor, 1943). Thus, it appears that if the mole does possess an acute auditory sense, it is not the result of any great disparity in relative area between the eardrum and the oval window.

Another factor which could be responsible for an intensification of vibrations at the oval window is the leverage action of the auditory ossicles. No attempt has been made, however, to determine either the axis of rotation or the relative lengths of the lever arms in the forms considered in this study.

Concerning the hearing of the short-tailed shrew, Seton (1909) quoted Kennicott as saying: "I observed no indication that an acute sense of smell enabled it to recognize objects at any considerable distance; but its hearing was remarkable." Nelson (1918) wrote about the short-tailed shrew: "While equally active by day and by night, the eyes of these shrews seem to be of little use except to distinguish between light and dark, but their senses of hearing and smell are highly developed, . . ." Approximate measurements of the tympanic membrane and the footplate of the stapes in the short-tailed shrew were made with the following results (in mm.): tympanic membrane, 2.7 by 2; footplate, .4 by .2. By calculating the approximate areas of each from these data, the amazingly high tympanic membrane/oval window ratio of 68 to one was obtained. This lends support to observations concerning the auditory acuity of the short-tailed shrew.

In relation to the auditory mechanism of mammals, Keen and Grobelaar (1941) proposed a different interpretation of sound conduction through the middle ear. According to them, the auditory ossicles in most small mammals are not mechanically constructed to transmit sound waves, since the ossicles of many mammals are vestigial structures, and sound reaches the cochlea directly through the air in the middle ear. To quote from their paper:

In very small mammals (e.g. Bats, Shrews, Mice) the ossicles are such minute structures that it is difficult to find them. However carefully one breaks away the floor of the bulla and the walls of the epitympanic recess, the ossicles, if they have not dropped out before, get detached and often become lost among the chips of bone . . . . The minute ossicles in Rodents and Insectivores are clearly useless for a complicated sound conduction process, and may be looked upon as vestigial structures.

These workers have utilized a very poor method of studying the auditory ossicles and the mechanics of their operation. I encountered no difficulty in locating the auditory ossicles in specimens of *Blarina*, *Sorex*, *Scalopus*, and *Talpa*. In *Blarina* and *Scalopus* with careful dissection one can move the handle of the malleus and observe the resultant lever action of this bony chain system, clearly demonstrating a mechanical method of ossicular function which supports the older idea that the ossicles function in sound conduction.

### Eye

The eyeball of the short-tailed shrew is minute though it is relatively and actually of a greater diameter than the eyeball of the mole. In gross dissection the eyeball and attenuated optic nerve are recognizable, but the ocular muscles and oculomotor nerves could not be discerned. Clark (1932) did not mention the presence or absence of nerves II, III, IV, and VI in *Blarina brevicauda*, but Cei (1946) illustrated a longitudinal section of the eye of *Blarina brevicauda* and labeled an optic nerve and ocular muscles. The small size of the eye, the elongated optic nerve, and the microscopic size of the ocular muscles support the conclusion of other workers that the vision of the short-tailed shrew is very poor.

The eye of the prairie mole is not visible externally, but one can locate a small, circular, naked area of skin which covers it and which is pierced by a very tiny aperture visible under the dissecting microscope. The eye is a small black sphere capping a very attenuated optic nerve which emerges between the temporal and snout muscles. The sphere does not occupy an orbit, but lies far forward on the maxillary region of the skull. In gross dissection the optic nerve was visible, but neither oculomotor muscles nor nerves could be identified. Clark (1932) reported that he did not detect optic nerves in *Scalopus aquaticus* or in *Talpa europaea*, but he did not mention cranial nerves III, IV, and VI. Ganser (1858), in an earlier but very excellent study of the brain of *Talpa europaea*, recorded the absence of the oculomotor nerves and identified an optic nerve. Cei (1946) illustrated an optic nerve and oculomotor muscles in *Scalopus aquaticus*, agreeing with the earlier finding of Slonaker (1899, 1902). Winckler (1931-32) was unable through gross dissection to find the oculomotor muscles and nerves in *Talpa europaea*, a fact which agrees with my observations. The researches of Ganser, Slonaker, and Cei, founded on histological examination, can be considered the most reliable. It may be reasonably concluded, therefore, that the ocular muscles are present but attenuated and that the oculomotor nerves are lacking. All of these data are in agreement with the conclusion of earlier workers that the eye of the prairie mole is of little or no use in vision. Shimer (1903) attributed

atrophy of the visual apparatus to the assumption of a fossorial life. I am inclined, however, to favor the view of Winge (1941:171) as translated by Deichmann and Allen: "The eye, which is not used, yields to the pressure of the surrounding parts. From behind it becomes compressed by the enormous temporal muscle; from above and below it is squeezed by the snout muscles; it is reduced in size and forced out of the primary eye-socket in such a manner that it becomes placed beyond the foremost edge of the outer wall of the *Canalis infraorbitalis*; . . ." This condition is also true of the soricids, despite the fact that they are only slightly or not at all fossorial in habit.

### SUMMARY

A comparison of the osteology and myology of *Blarina brevicauda kirtlandi* and *Scalopus aquaticus machrinus* discloses the following significant features:

#### A. Cranium

1. The crania of *Blarina* and *Scalopus* have similar general proportions, and most of the bones are fused; thus many of the sutures are obliterated.

2. The cranium of *Blarina* has no cancellous bone and has lost the zygomatic arcade, a loss believed to be related to modifications in the mechanism for mastication.

3. The auditory ossicles and tympanic annulus of *Blarina* are primitive. The auditory ossicles of *Scalopus* are similar to those of *Blarina*, but the mole has a tympanic bulla rather than an annulus.

4. The validity of the dental formula  $\underline{3}, \underline{1}, \underline{3}, \underline{3}$  for *Blarina* and *Scalopus* was confirmed.

5. The cartilaginous median septum of the snout is not calcified in either *Blarina* or *Scalopus*.

#### B. Visceral Skeleton

1. The dentary of *Blarina* possesses a double articular condyle and a posterointernal ramal fossa, modifications related to mastication.

2. In both *Blarina* and *Scalopus* the hyoid elements are primitive in form, and the tympanohyal is fused to the base of the cranium.

#### C. Cervical Segment

1. In *Blarina* the transverse processes are better developed and are more flared laterally than in *Scalopus*; prominent hypapophyses occur on certain vertebrae in *Blarina*, but not in *Scalopus*. The central articular surfaces are almost plane in *Scalopus*, but very markedly concave anteriorly and convex posteriorly in *Blarina*.

2. Contrary to expectations in a fossorial form, neither significant shortening nor synostosis of the cervical vertebrae occurs in *Scalopus*.

3. Correlated with the more prominent skeletal features in *Blarina*,

the cervical elements of the longitudinal back muscles are better developed, the longus colli is wider, and the intertransverse musculature is heavier in it than in *Scalopus*.

4. The stronger cervical musculature, the more effective leverage, and the greater freedom of movement provided by the cervical vertebrae in *Blarina* agree with the greater agility and strength of axial movement which it possesses over *Scalopus*.

5. The calcification of the nuchal ligament in *Scalopus* offers a more stable surface for muscle attachment.

6. The rectus capitis posterior, the longissimus capitis, and the semi-spinalis capitis muscles operate with more power in *Scalopus* than in *Blarina* because of the greater angle between the anterior part of the cervical vertebrae and the base of the skull in *Scalopus*. These muscles in *Scalopus* retract the head in eating, and raise the head to push the soil upward in making subsurface galleries.

#### D. Myomeric Musculature

1. The atlantoscapularis anterior and posterior muscles are present in *Blarina* but not in *Scalopus*. The presence or absence of these elements is related to scapular mobility.

#### E. Branchiomic Musculature

1. The digastric muscle is more primitive in form and relationships in *Scalopus* than in *Blarina*.

2. The tensor tympani muscle is present in *Blarina* but not in *Scalopus*.

3. The sternomastoid, cleidomastoid, and cleido-occipital muscles are heavier in *Scalopus* than in *Blarina*, providing a power for depressing and rotating the head.

4. The anterior trapezius is well developed in *Blarina*, but is poorly represented in *Scalopus*.

5. The external pterygoid is strong in *Blarina*. It produces a greater torque, effected by the new fulcrum for the dentary, and increased speed, resulting from the greater length of its fibers.

6. The internal pterygoid in *Blarina* is small, in agreement with the reduction of bone at its origin and insertion, and its effectiveness as a jaw levator is diminished because of a reduction in its torque.

7. In *Blarina* the deep layer of the masseter muscle is lost, and the superficial layer is reduced in size. The mechanical advantage gained by the temporal muscle through the development of a new articular surface on the dentary and skull compensates for these reductions.

8. The effective speed of action of the temporal muscle in *Blarina* is enhanced both by an increase in length and by the insertion of some of its fibers closer to the fulcrum and their extension into the substance of the dentary.

#### F. Sense Organs

1. The tympanum and middle ear appear to be more effective transmitters of sound in *Blarina* than in *Scalopus*.

2. In both forms the relationship of the auditory ossicles supports the theory of the mechanical conduction of sound.

3. The eyes in both *Blarina* and *Scalopus* are very poorly developed; little of their anatomy is discernible in gross dissection in *Blarina* and even less in *Scalopus*. The eyeball and optic nerve are recognizable, but neither any ocular muscles nor their nerves were found. Because of the degree of atrophy of the eyes, vision probably is poor in the shrew and absent in the mole.

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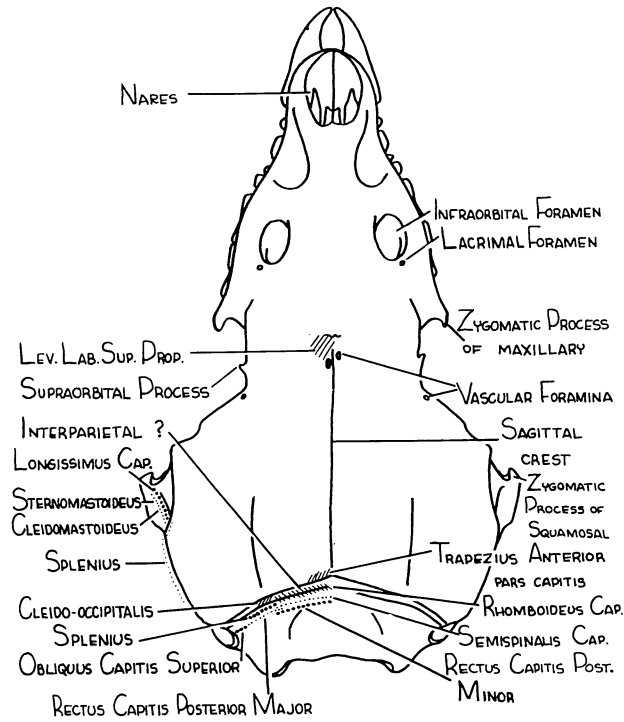
PLATES

PLATE I

- Fig. 1. Skull of *Blarina brevicauda kirtlandi*, dorsal view. In this and subsequent skeletal figures muscle origin is crosshatched and muscle insertion is stippled.
- Fig. 2. Skull of *Blarina brevicauda kirtlandi*, ventral view.

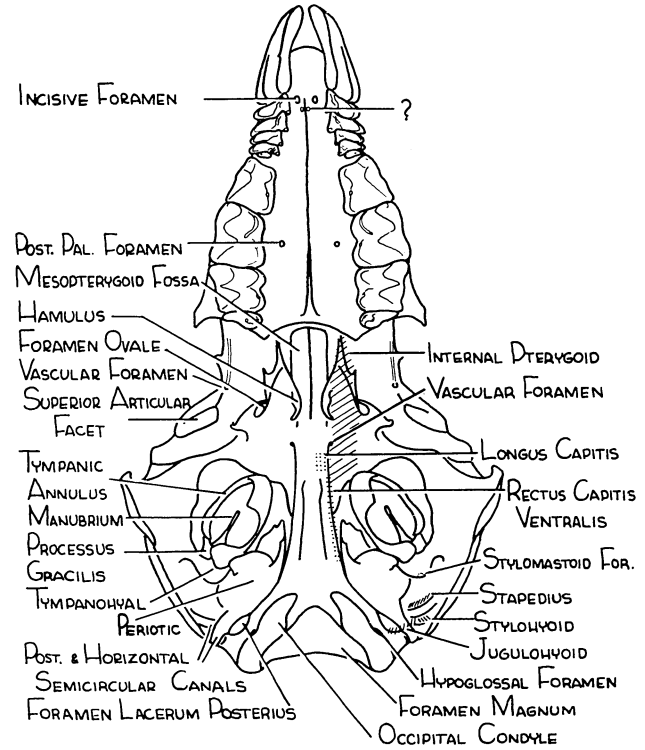


PLATE I



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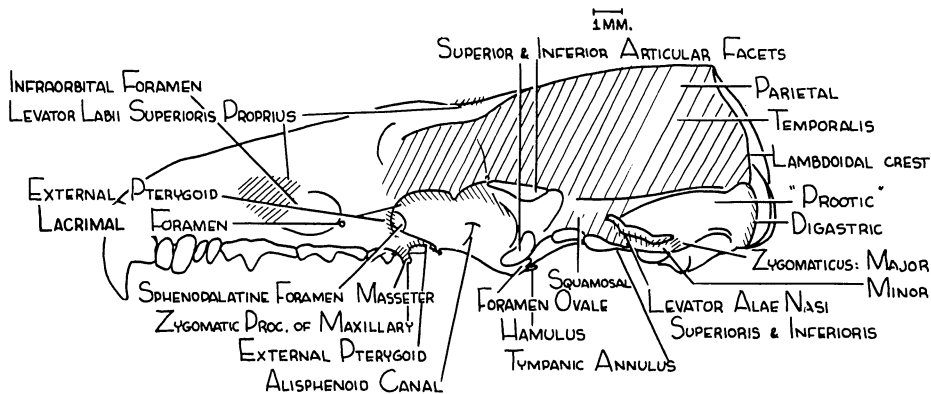
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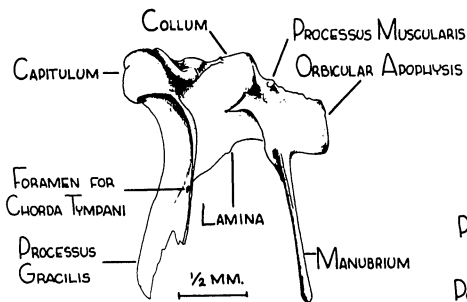
PLATE II

- Fig. 3. Skull of *Blarina brevicauda kirtlandi*, lateral view.  
Fig. 4. Right malleus of *Blarina brevicauda kirtlandi*, dorsal view.  
Fig. 5. Right incus of *Blarina brevicauda kirtlandi*, dorsal view.  
Fig. 6. Right stapes of *Blarina brevicauda kirtlandi*, lateral view.  
Fig. 7. Right dentary of *Blarina brevicauda kirtlandi*, lateral view.  
Fig. 8. Right dentary of *Blarina brevicauda kirtlandi*, medial view.

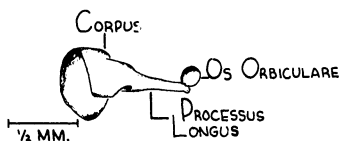
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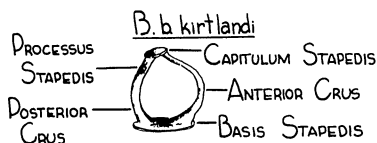
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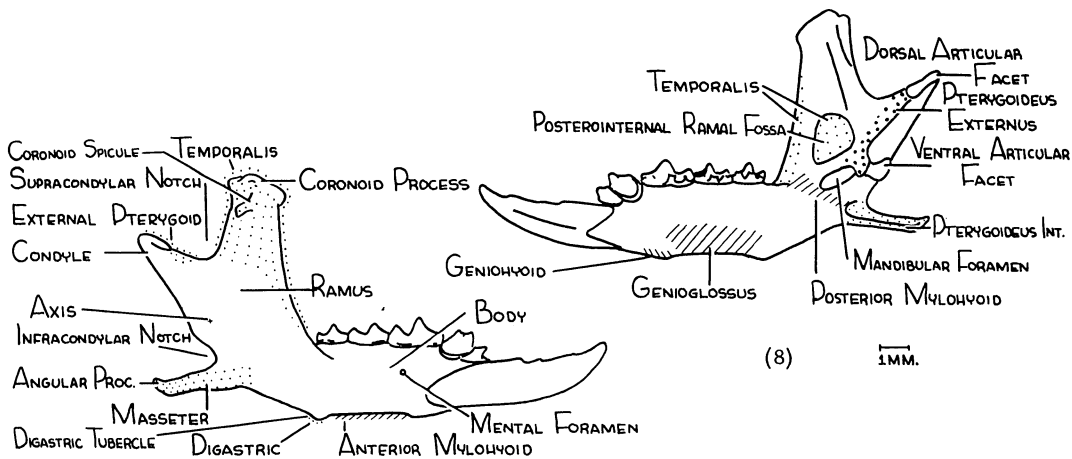
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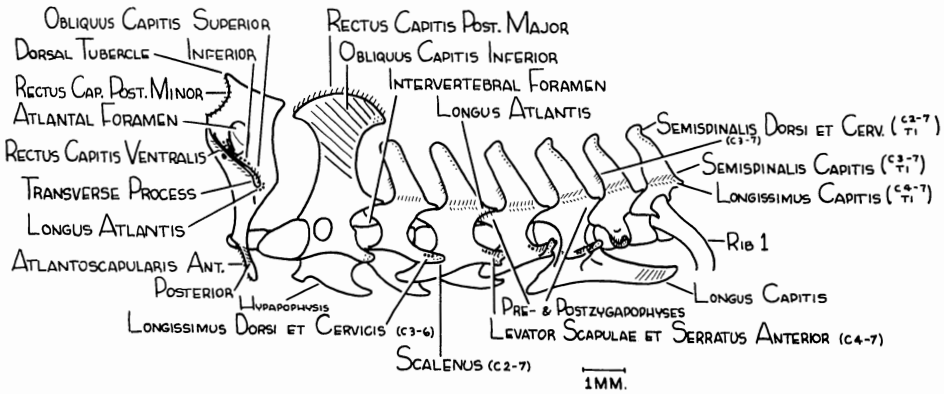
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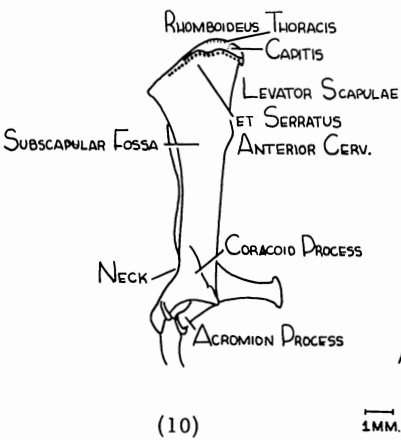
PLATE III

- Fig. 9. Cervical vertebrae of *Blarina brevicauda kirtlandi*, lateral view.  
Fig. 10. Right scapula of *Blarina brevicauda kirtlandi*, medial view.  
Fig. 11. Right scapula of *Blarina brevicauda kirtlandi*, lateral view.  
Fig. 12. Left clavicle of *Blarina brevicauda kirtlandi*, anterior view.  
Fig. 13. Manubrium of *Blarina brevicauda kirtlandi*, ventral view.

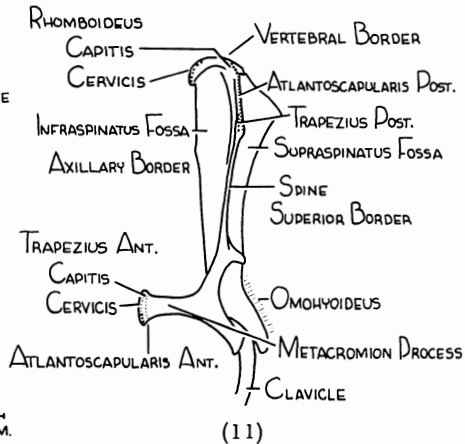
PLATE III



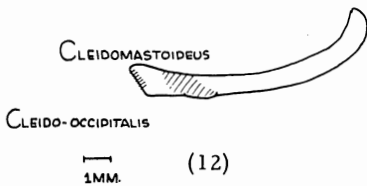
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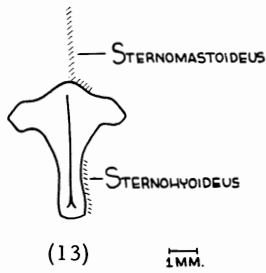
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PLATE IV

- Fig. 14. Cervical vertebrae of *Blarina brevicauda kirtlandi*, ventral view.  
Fig. 15. Medial view of rami showing forward migration of ventral articular facet compared with *Sorex*.  
Fig. 16. Hyoid and laryngeal cartilages of *Blarina brevicauda kirtlandi*, ventral view.  
Fig. 17. Hyoid and laryngeal cartilages of *Blarina brevicauda kirtlandi*, lateral view.  
Fig. 18. Dorsal aspect of arytenoid cartilages of *Blarina brevicauda kirtlandi*.  
Fig. 19. Hyoid of *Blarina brevicauda kirtlandi*, ventral view.

PLATE IV

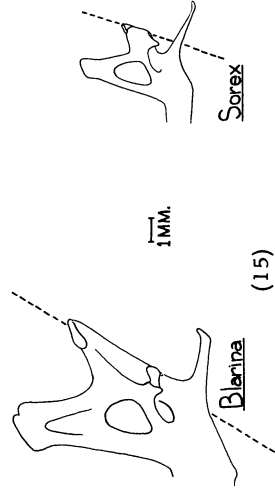
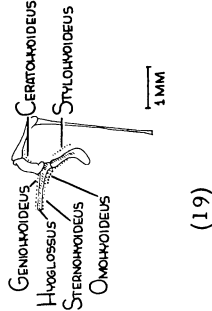
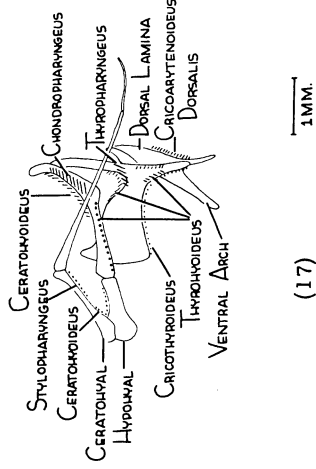
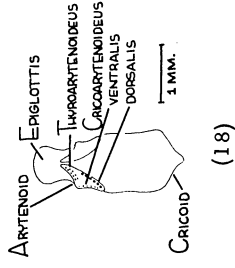
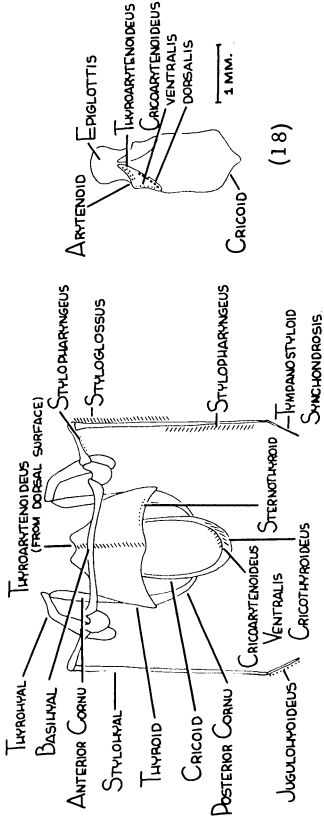
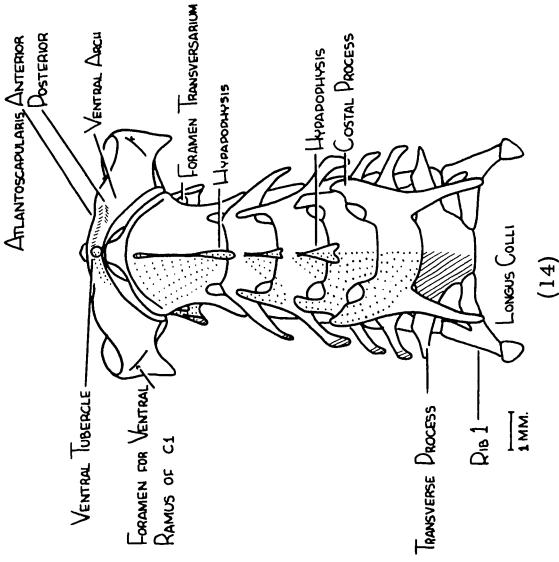


PLATE V

- Fig. 20. Skull of *Scalopus aquaticus machrimus*, dorsal view.  
Fig. 21. Skull of *Scalopus aquaticus machrimus*, ventral view.



PLATE V

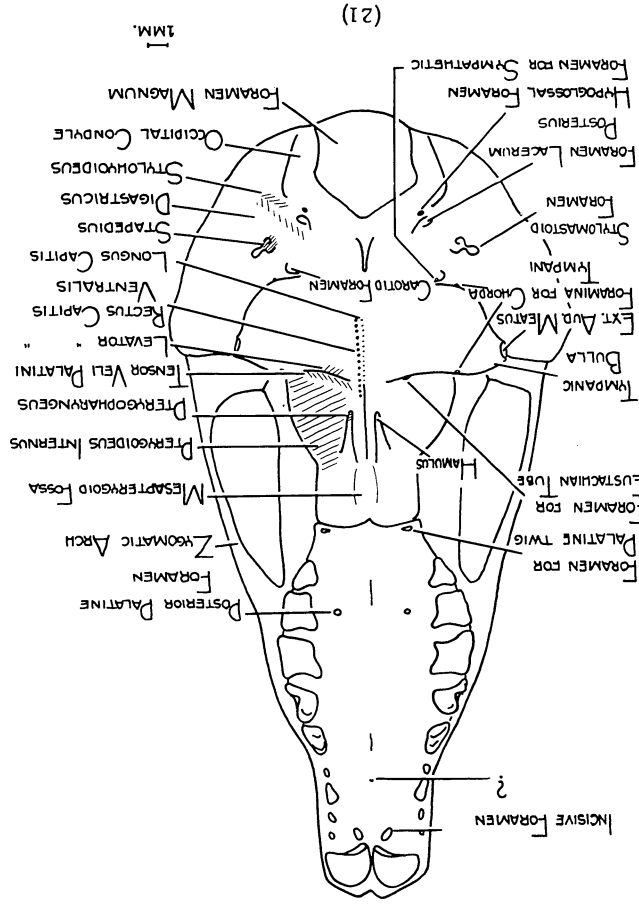
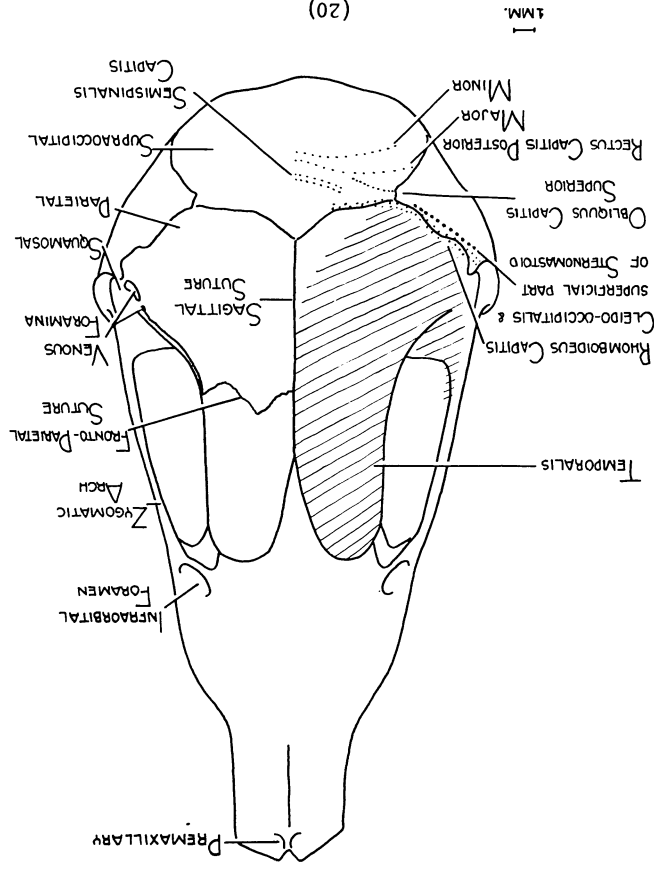
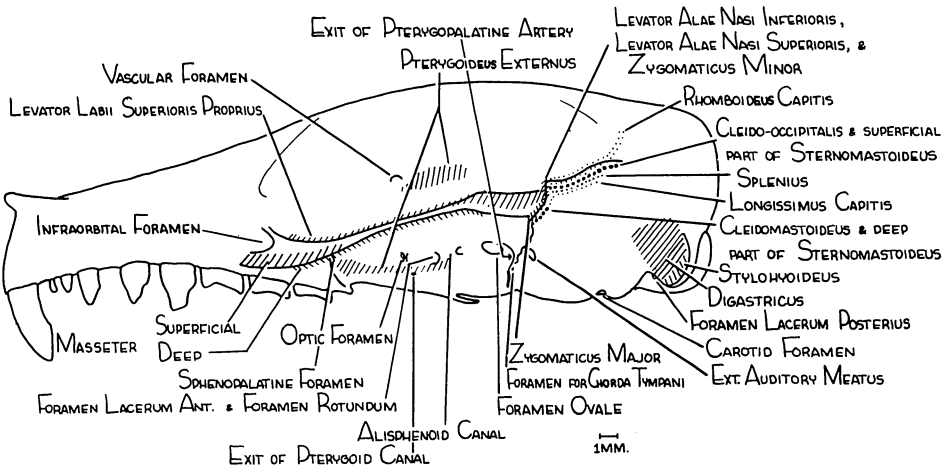


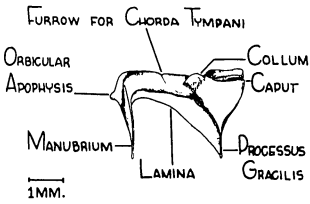
PLATE VI

- Fig. 22. Skull of *Scalopus aquaticus machrimus*, lateral view.  
Fig. 23. Left malleus of *Scalopus aquaticus machrimus*, dorsal view.  
Fig. 24. Left incus of *Scalopus aquaticus machrimus*, dorsal view.  
Fig. 25. Left stapes of *Scalopus aquaticus machrimus*, lateral view.  
Fig. 26. Anterior aspect of snout of *Scalopus aquaticus machrimus* showing cartilaginous plates.  
Fig. 27. Ventral aspect of snout of *Scalopus aquaticus machrimus*, showing cartilaginous plates.

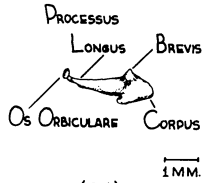
PLATE VI



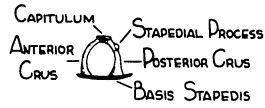
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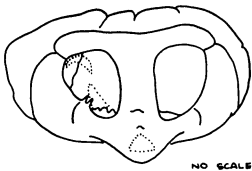
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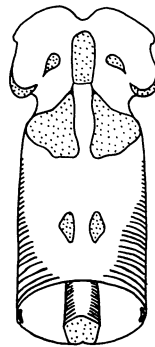
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(25)



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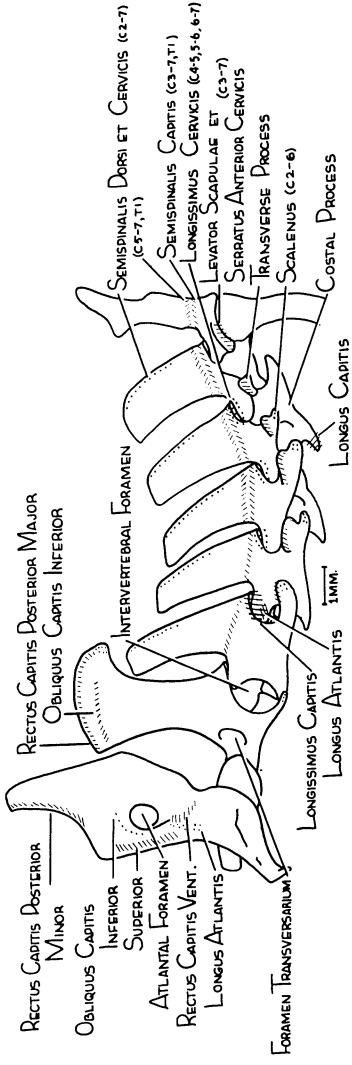


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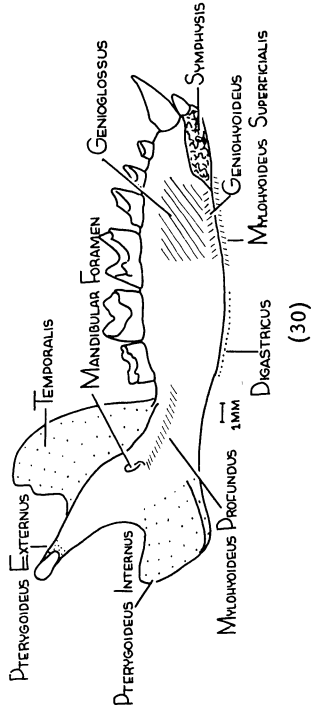
PLATE VII

- Fig. 28. Cervical vertebrae of *Scalopus aquaticus machrimus*, lateral view.  
Fig. 29. Left dentary of *Scalopus aquaticus machrimus*, lateral view.  
Fig. 30. Left dentary of *Scalopus aquaticus machrimus*, medial view.

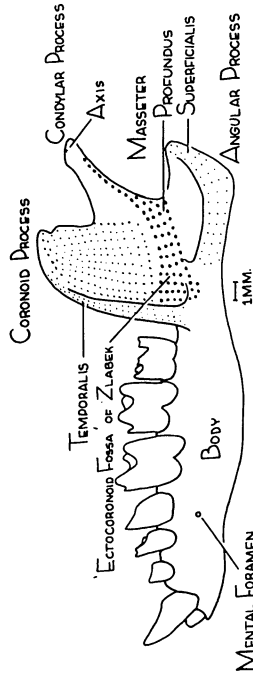
PLATE VII



(28)



(30)



(29)

PLATE VIII

- Fig. 31. Cervical vertebrae of *Scalopus aquaticus machrinus*, ventral view.  
Fig. 32. Ligamentum nuchae of *Scalopus aquaticus machrinus*.  
Fig. 33. Left scapula of *Scalopus aquaticus machrinus*, lateral and vertebral surfaces.  
Fig. 34. Manubrium of *Scalopus aquaticus machrinus*, right side.

PLATE VIII

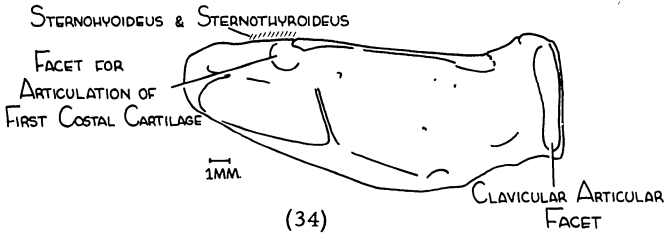
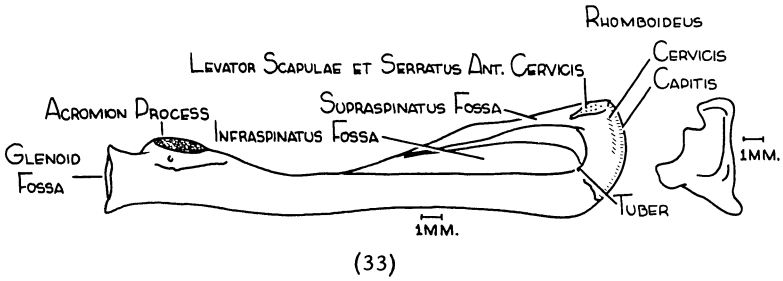
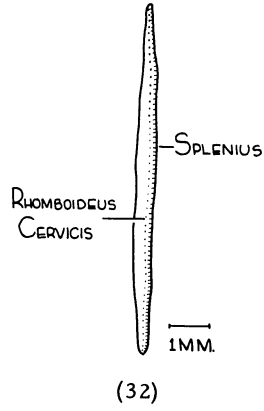
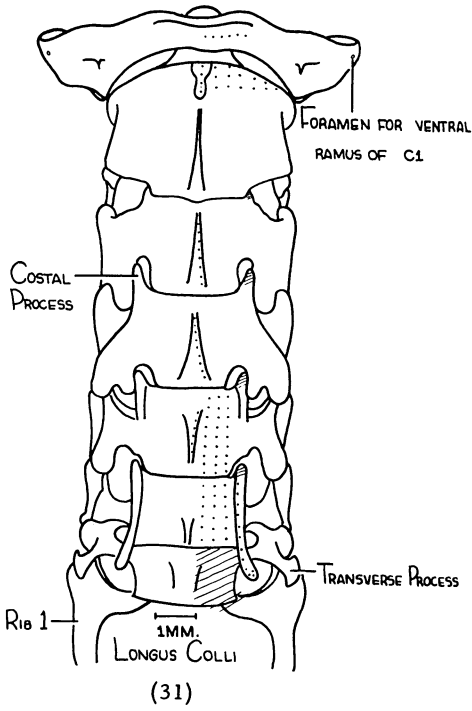


PLATE IX

Fig. 35. Clavicles of *Scalopus aquaticus machrimus*, anterior view.

Fig. 36. Cricoid, arytenoid, and epiglottis of *Scalopus aquaticus machrimus*, dorsal view.

Fig. 37. Hyoid and laryngeal cartilages of *Scalopus aquaticus machrimus*, ventral view.

Fig. 38. Hyoid and laryngeal cartilages of *Scalopus aquaticus machrimus*, right side.



PLATE IX

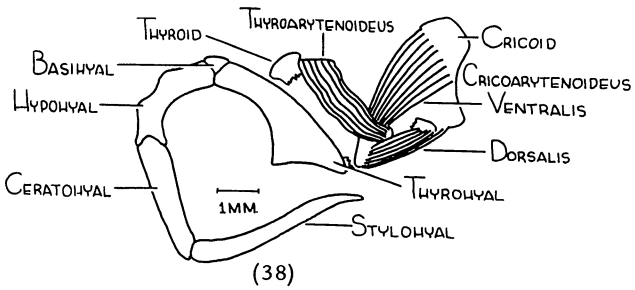
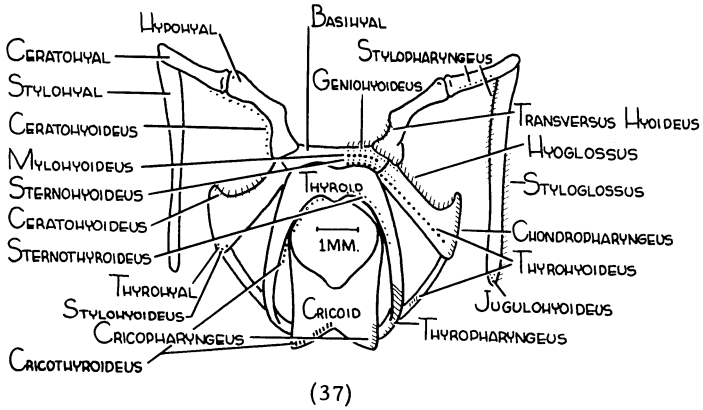
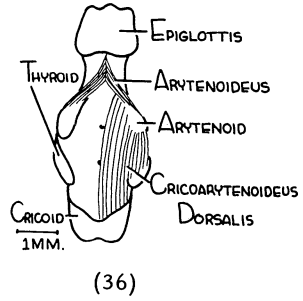
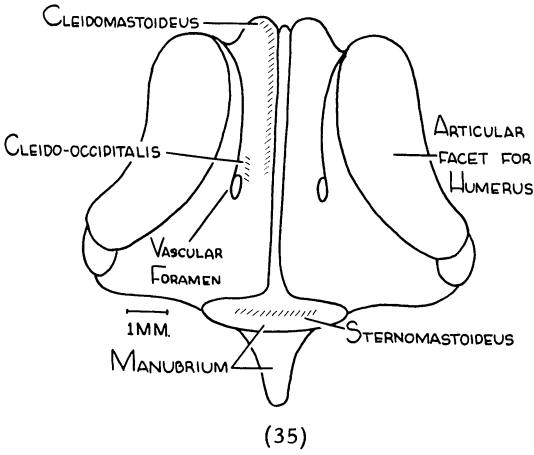


PLATE X

Fig. 39. Superficial musculature of *Blarina brevicauda kirtlandi*, lateral view.

Fig. 40. First depth of musculature of *Blarina brevicauda kirtlandi*, lateral view.

Fig. 41. Second depth of musculature of *Blarina brevicauda kirtlandi*, lateral view.

PLATE X

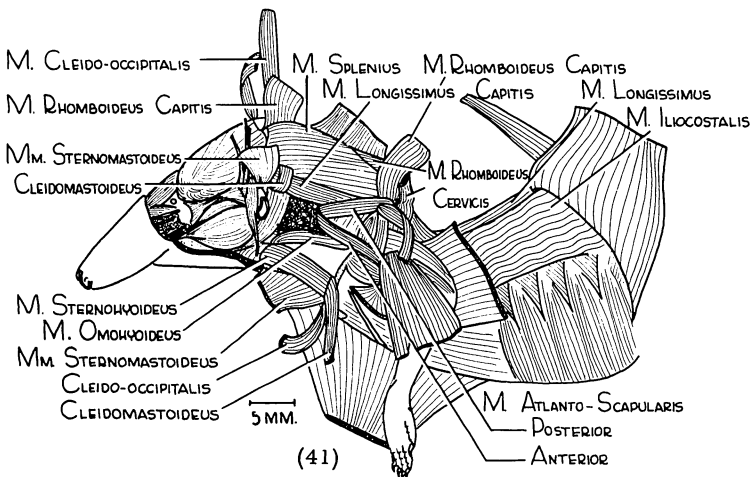
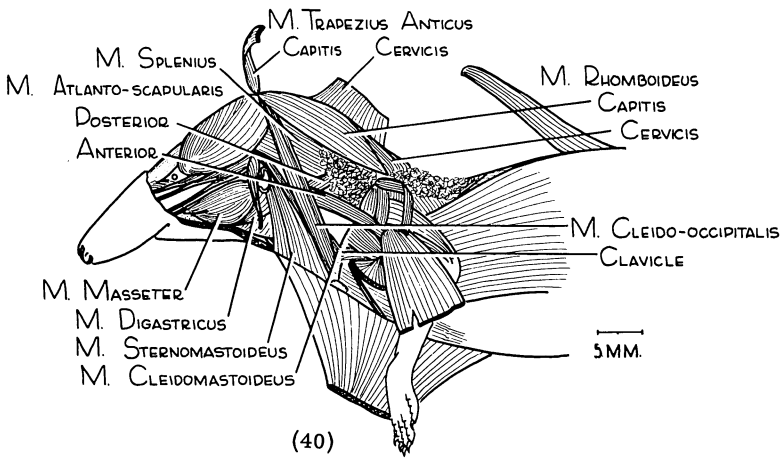
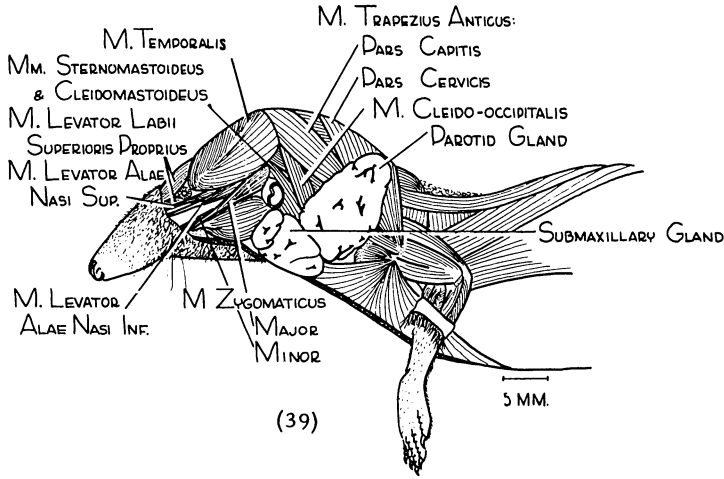
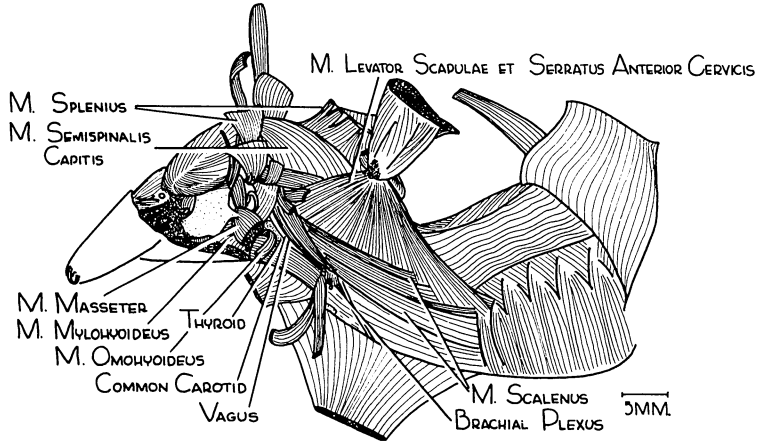


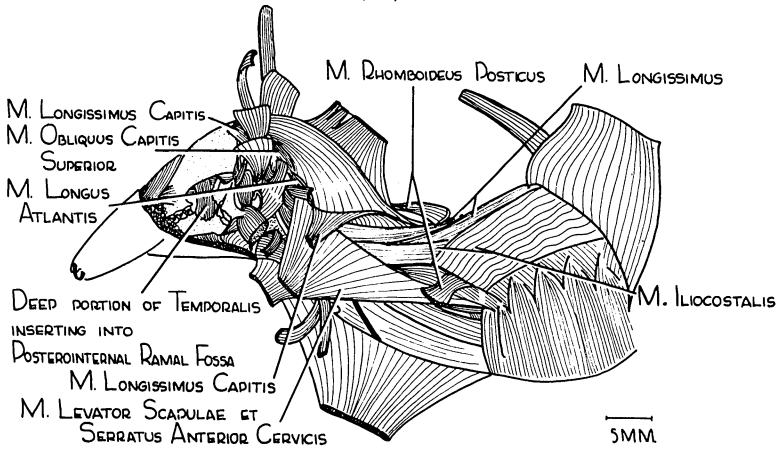
PLATE XI

- Fig. 42. Third depth of musculature of *Blarina brevicauda kirtlandi*, lateral view.  
Fig. 43. Fourth depth of musculature of *Blarina brevicauda kirtlandi*, lateral view.  
Fig. 44. Fifth depth of musculature of *Blarina brevicauda kirtlandi*, lateral view.

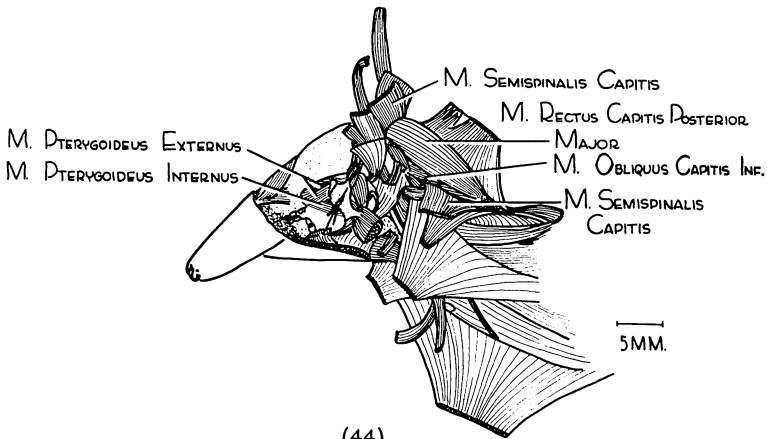
PLATE XI



(42)



(43)

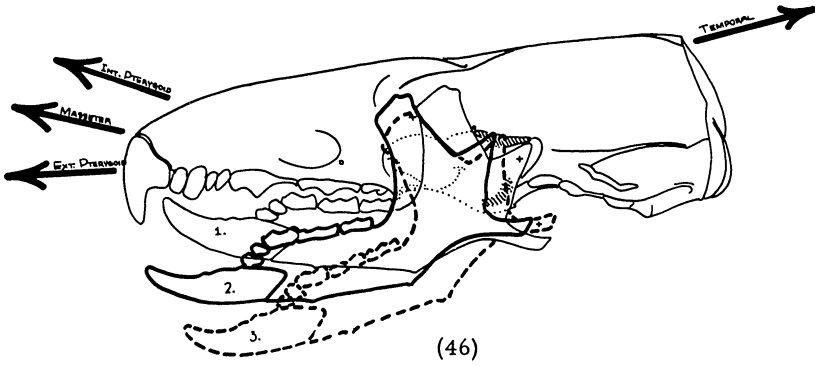
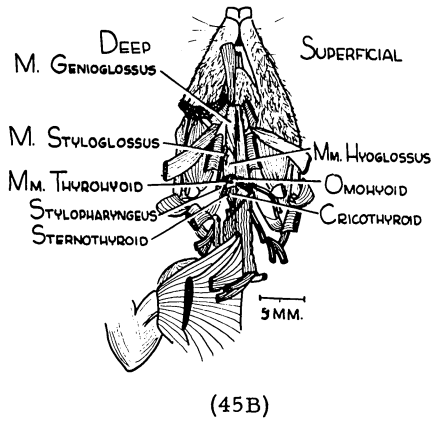
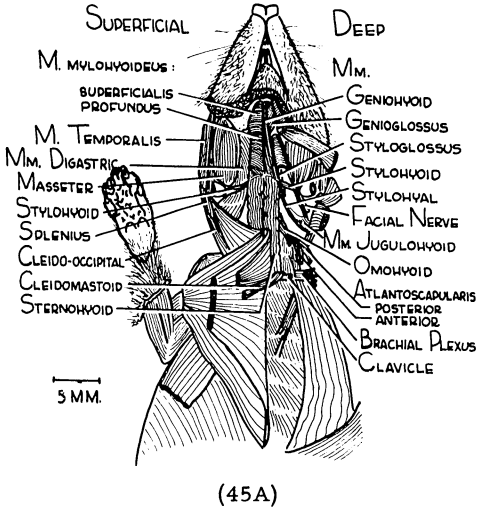


(44)

PLATE XII

- Fig. 45A. Superficial layer and first depth of musculature of *Blarina brevicauda kirtlandi*, ventral view.
- Fig. 45B. Second and third depths of musculature of *Blarina brevicauda kirtlandi*, ventral view.
- Fig. 46. Schema of force vectors of masticatory muscles of *Blarina brevicauda kirtlandi*: (1) mandible closed, (2) mandible protracted, (3) mandible open.

PLATE XII



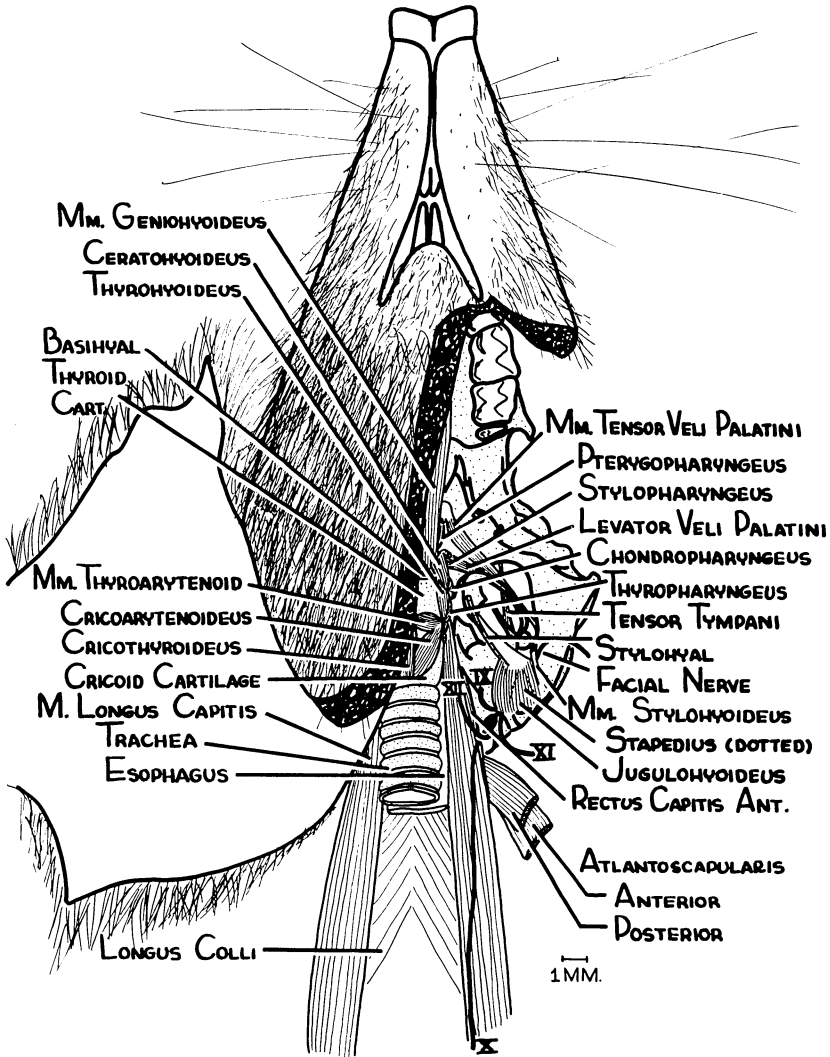
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PLATE XIII

Fig. 47. Fourth depth of musculature of *Blarina brevicauda kirtlandi*, ventral view.



PLATE XIII

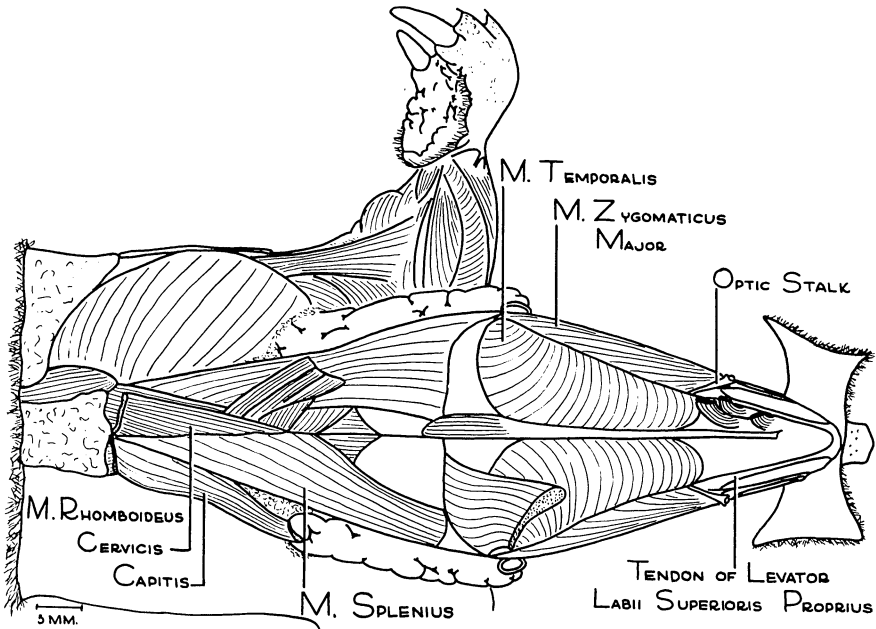


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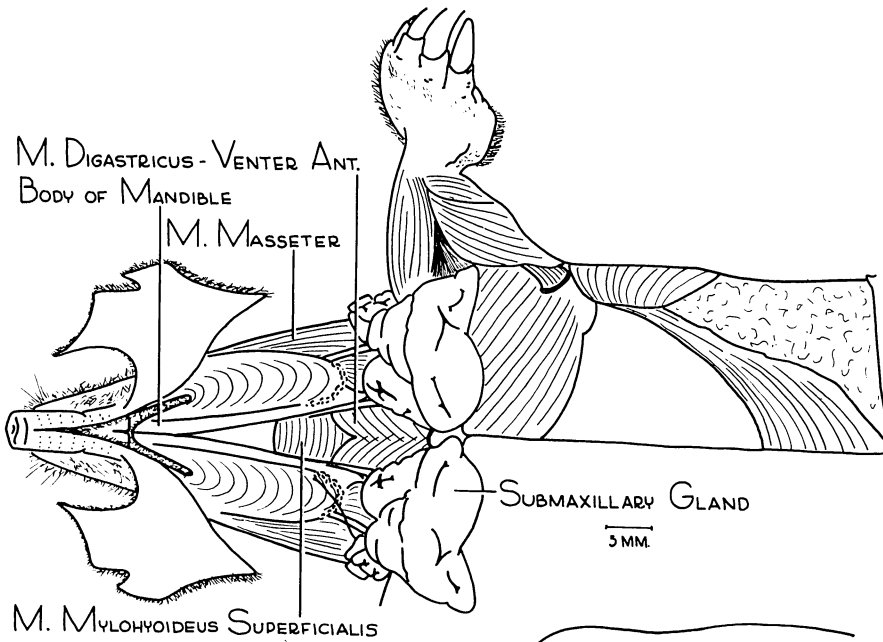
PLATE XIV

Fig. 48. Superficial layer of musculature of *Scalopus aquaticus machrimus*, dorsal view.  
Fig. 49. Superficial layer of musculature of *Scalopus aquaticus machrimus*, ventral view.

PLATE XIV



(48)



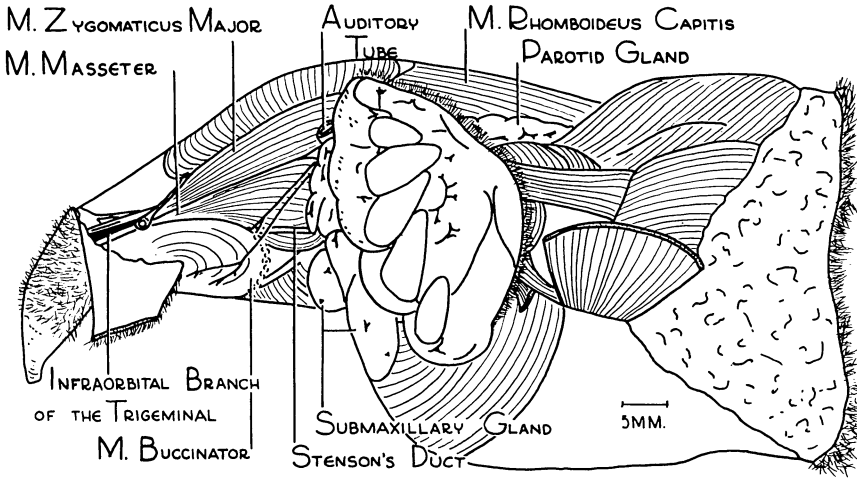
(49)

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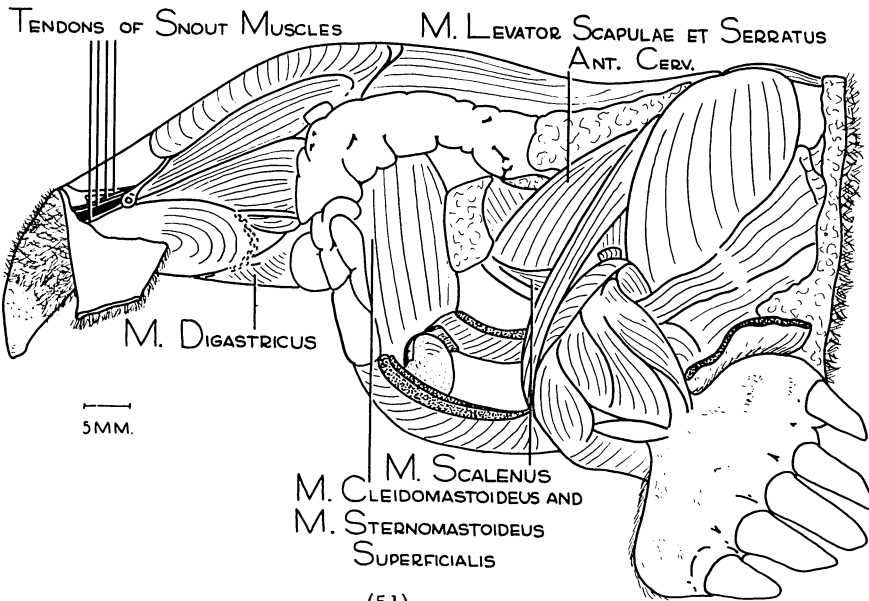
PLATE XV

Fig. 50. Superficial layer of musculature of *Scalopus aquaticus machrinus*, lateral view.  
Fig. 51. First depth of musculature of *Scalopus aquaticus machrinus*, lateral view.

PLATE XV



(50)

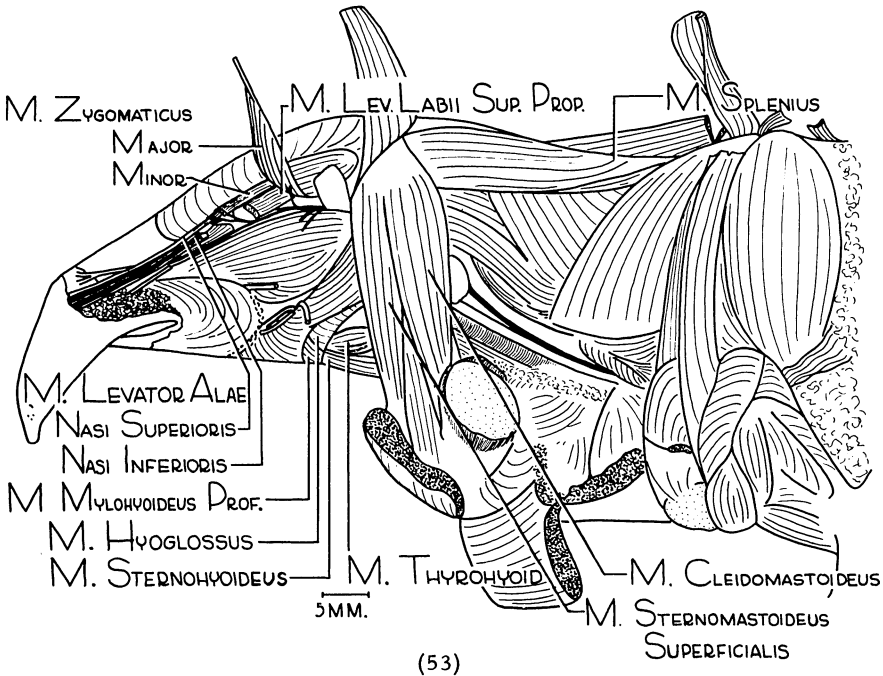
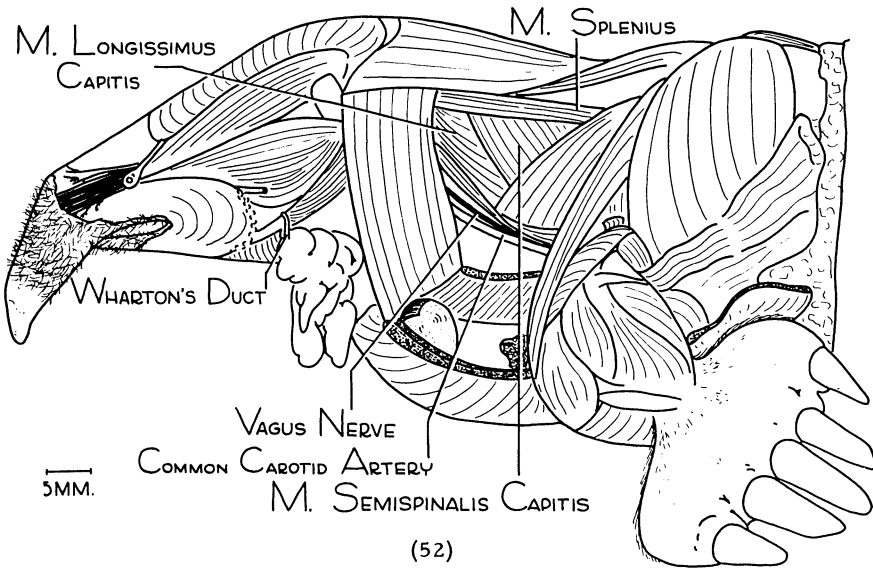


(51)

PLATE XVI

- Fig. 52. Second depth of musculature of *Scalopus aquaticus machrimus*, lateral view.  
Fig. 53. Third depth of musculature of *Scalopus aquaticus machrimus*, lateral view.

PLATE XVI



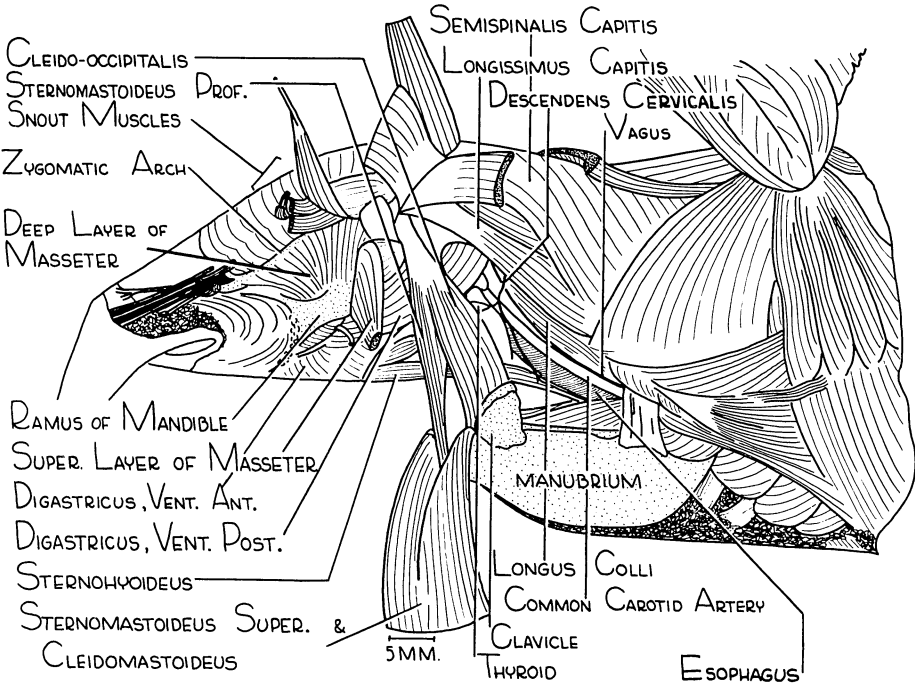
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PLATE XVII

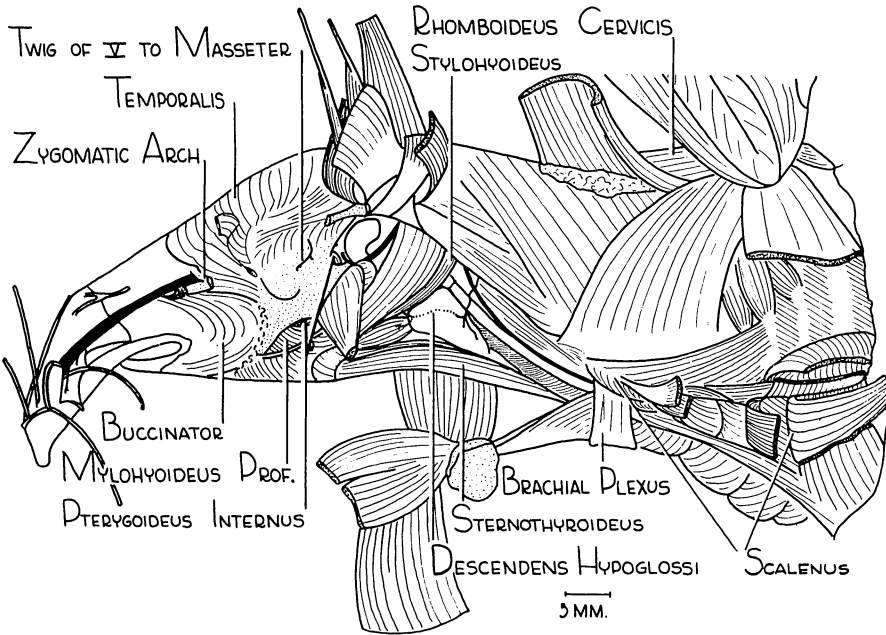
- Fig. 54. Fourth depth of musculature of *Scalopus aquaticus machrimus*, lateral view.  
Fig. 55. Fifth depth of musculature of *Scalopus aquaticus machrimus*, lateral view.



PLATE XVII



(54)



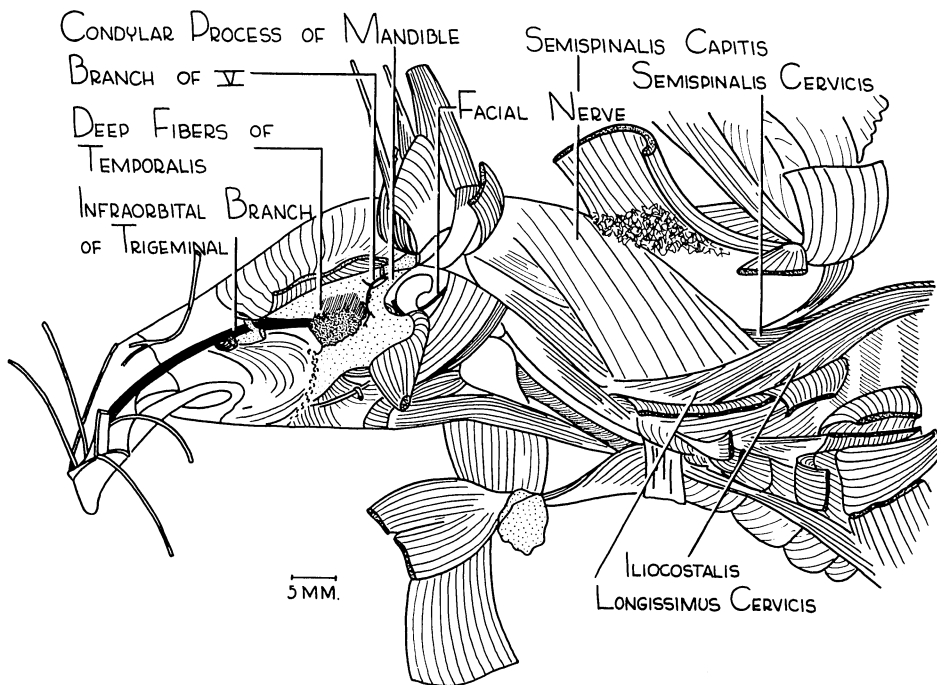
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PLATE XVIII

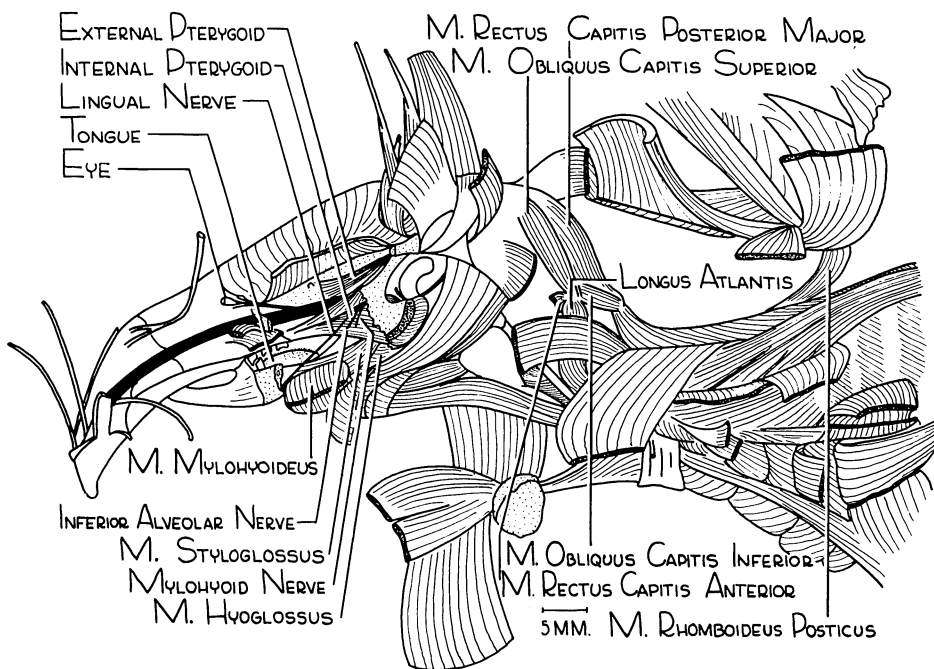
Fig. 56. Sixth depth of musculature of *Scalopus aquaticus machrimus*, lateral view.

Fig. 57. Seventh depth of musculature of *Scalopus aquaticus machrimus*, lateral view.

PLATE XVIII



(56)



(57)

PLATE XIX

- Fig. 58. Eighth depth of musculature of *Scalopus aquaticus machrimus*, lateral view.  
Fig. 59. Medial, dorsal, and lateral views of the superficial masseter of *Scalopus aquaticus machrimus*.

PLATE XIX

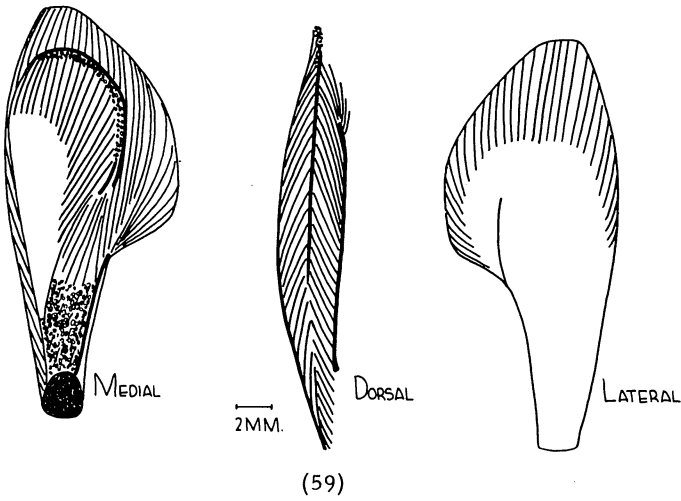
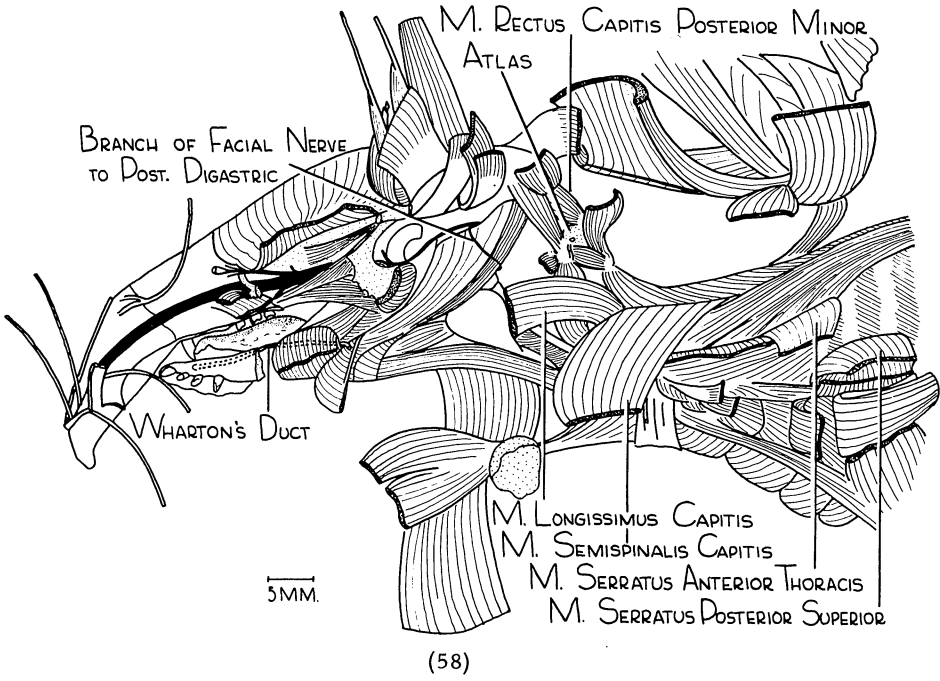
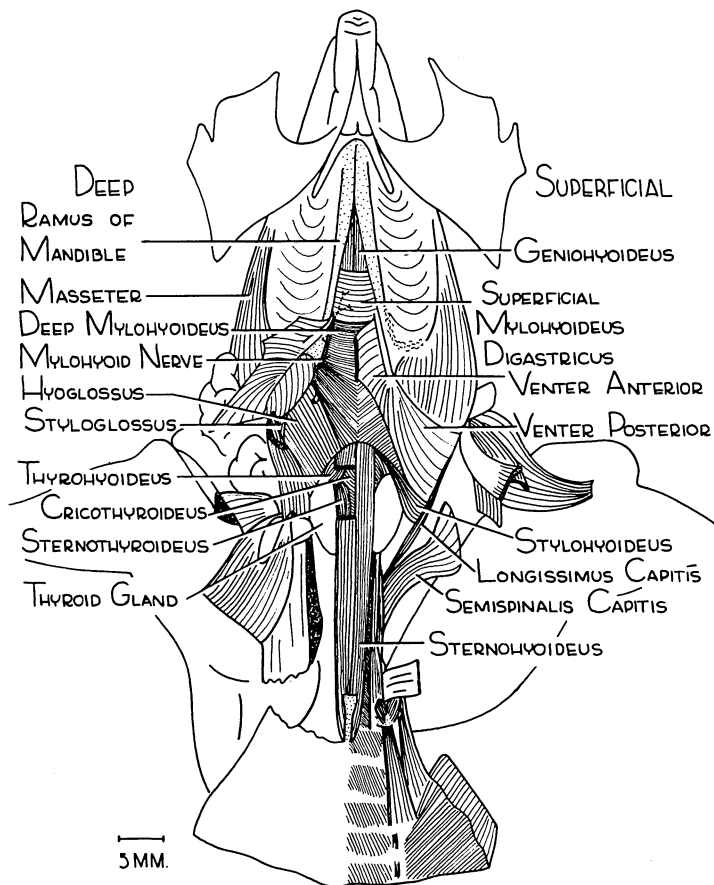


PLATE XX

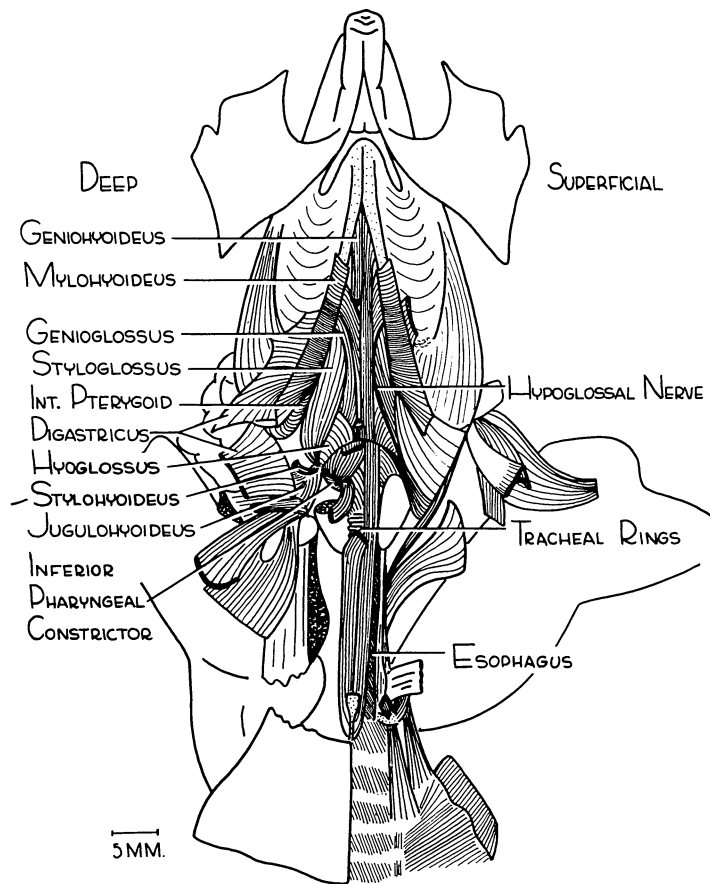
Fig. 60. Superficial layer and first depth of musculature of *Scalopus aquaticus machrimus*, ventral view.

Fig. 61. Second and third depths of musculature of *Scalopus aquaticus machrimus*, ventral view.

PLATE XX



(60)



(61)

PLATE XXI

Fig. 62. Fourth and fifth depths of musculature of *Scalopus aquaticus machrimus*, ventral view.

Fig. 63. Sixth and seventh depths of musculature of *Scalopus aquaticus machrimus*, ventral view.



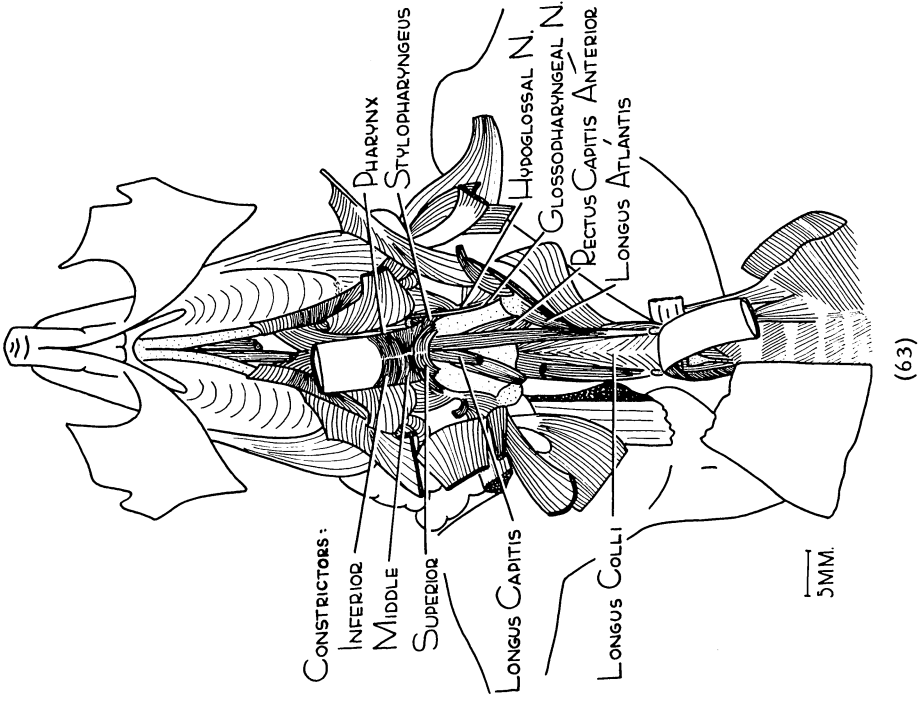
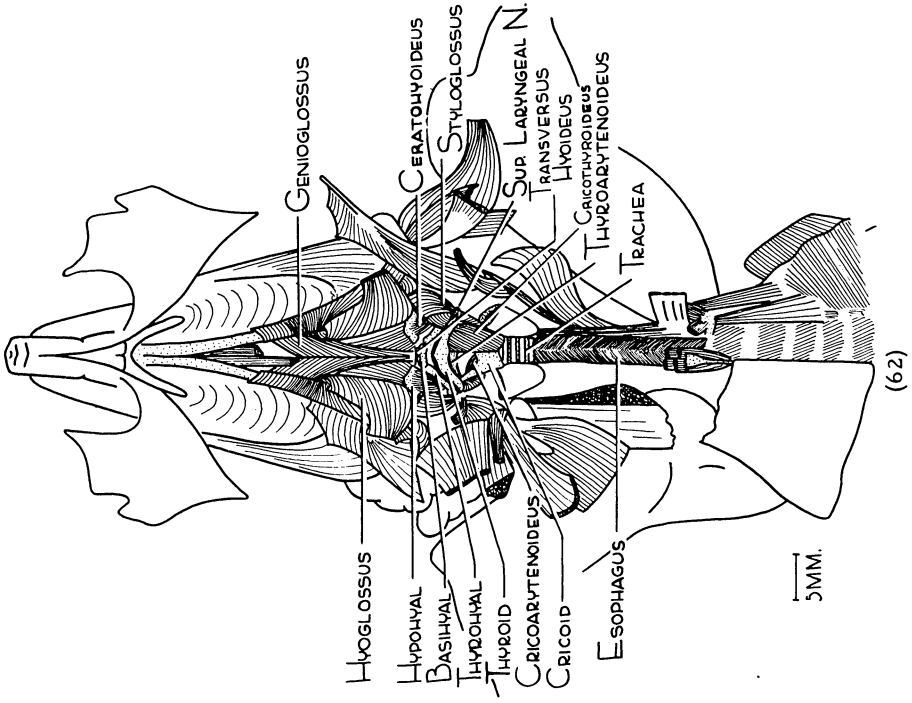


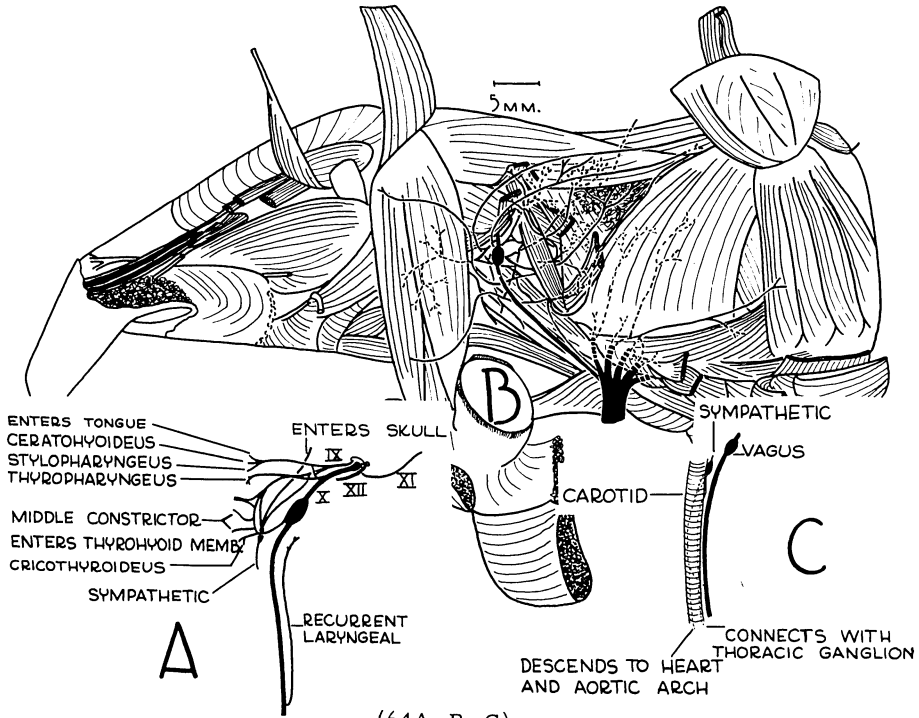
PLATE XXII

Fig. 64A and C. Pattern of distribution of nerves IX, X, XI, and XII in *Scalopus aquaticus machrimus*.

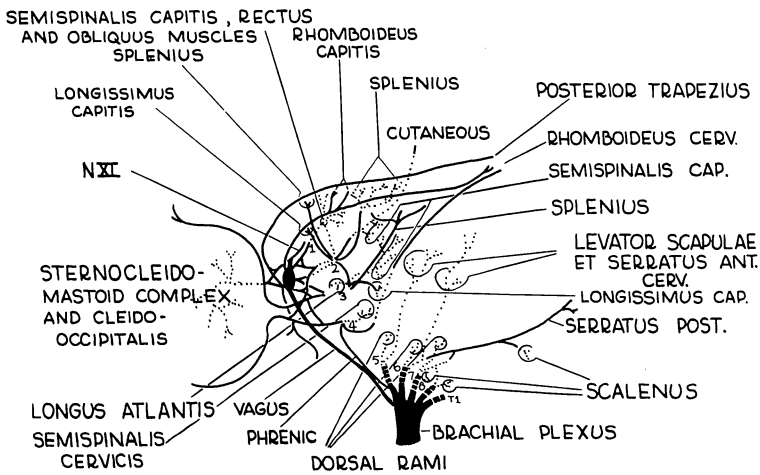
Fig. 64B. Pattern of distribution of cervical nerves in *Scalopus aquaticus machrimus*.

Fig. 65. Key to Figure 64B.

PLATE XXII



(64A, B, C)



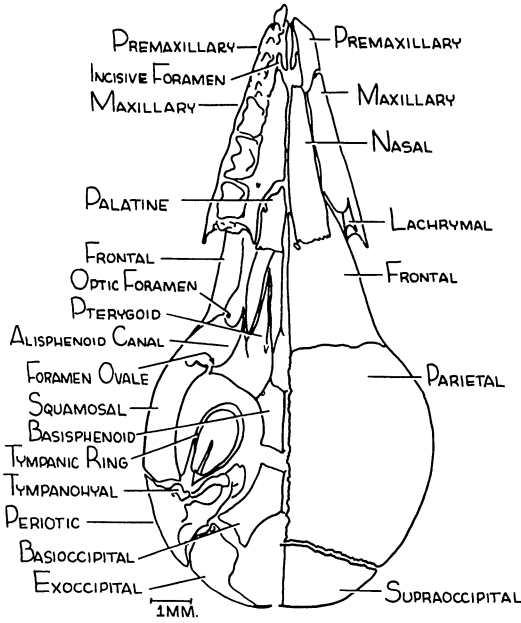
(65)

PLATE XXIII

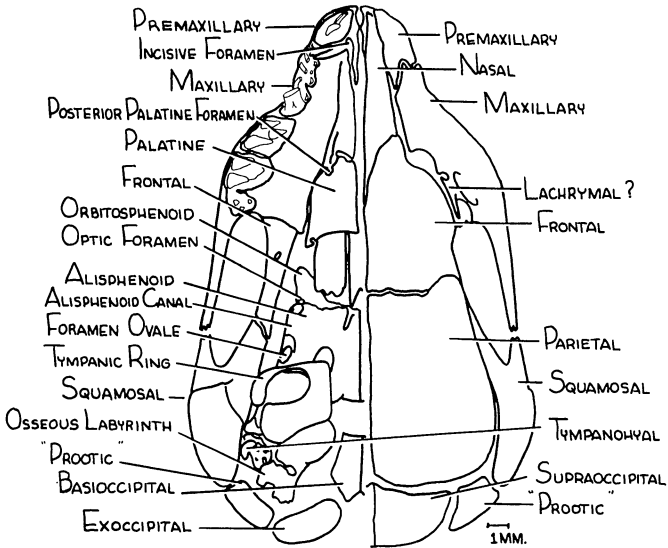
Fig. 66. Reconstruction of skull of nestling *Blarina brevicauda kirtlandi*: ventral (left side), dorsal (right side).

Fig. 67. Reconstruction of skull of nestling *Scalopus aquaticus machrinus*: ventral (left side), dorsal (right side).

PLATE XXIII



(66)



(67)



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