MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 94

The Anatomy of the Head of *Ctenosaura pectinata* (Iguanidae)

BY
THOMAS M. OELRICH

ANN ARBOR
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
March 21, 1956

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THE ANATOMY OF THE HEAD OF *CTENOSAURA PECTINATA* (IGUANIDAE)*

INTRODUCTION

PROBLEMS of the origin of mammalian structure have received attention from both biologists and paleontologists. The general outline of descent from reptilian stock is well understood. Accurate interpretation of any form, either fossil or Recent, depends upon an understanding of all body systems. Fossil evidence usually gives direct information concerning only the skeletal system. Knowledge of the structure of other systems of extinct forms must be obtained by interpretation of osseous elements. Analyses of fossil skulls depend upon a knowledge of the basic anatomic plan of the heads of living related forms and the manner in which this plan is related to the osseous structure of the skull. Furthermore, a knowledge of the origin and development of any Recent vertebrate depends upon an understanding of the anatomic plan that can be found only in the more primitive forms now living.

The object of this work is to present an account of the gross anatomy of the head of *Ctenosaura pectinata* in such detail that it may aid in the understanding and interpretation of osseous elements of fossil forms. In addition, the plan is to present the anatomy of a generalized lizard head large enough for profitable use by students of comparative anatomy as a basis for interpretation of the complexities and specializations of higher forms.

The entire absence of such accounts within the Lacertilia is believed to be sufficient justification for the present paper. Moreover, the absence of a description of many details for all reptilian heads further justifies such a presentation.

A review of the literature reveals that among reptiles only *Sphenodon punctatum* (Osawa, 1898) has received anything approximating adequate treatment. The article by Osawa, in addition to numerous other papers on specific systems, makes *Sphenodon* one of the best-known reptiles. The volume of literature is undoubtedly due to the unique evolutionary position of this reptile, which probably parallels that of the Lacertilia. Though it may be desirable to use *Sphenodon* for such a study, its lack of availability limits its usefulness. In the order Lacertilia no study of this sort has been attempted; however, there is an extensive literature covering numerous phases of the morphology of the reptilian head in many

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different species. Most of these are systemic studies. No attempt will be made here to list all of the literature. The most useful references are: skeletal, Bahl (1937), *Varanus*, Siebenrock (1895), *Agama;* muscular, Lakjer (1926), Lubosch (1933); nervous, Willard (1915); circulation, arteries, O'Donoghue (1921), *Sphenodon;* veins, Bruner (1907). A discussion of the major literature pertaining to each system prefaces its description. Since *Ctenosaura pectinata* previously has been only mentioned in morphological literature (Camp, 1923; Edgeworth, 1935; *C.* sp., Negus, 1949), the literature cited here is selected from an extensive bibliography encompassing many facets of reptilian morphology. Those selected are considered to be the most thorough and complete.

Because of the extensiveness of the present study, the plan here employed is not compatible with many functional and comparative problems which arise in relation to various details of the work. It also has deficiencies which cannot be overcome at the present time. Lack of live material and fresh injections necessitate the elimination of the description of the venous system, although relations of its dissectable parts appear throughout the paper. The central nervous system is considered to be within the realm of a microscopic study and is not described here.

The choice of *Ctenosaura pectinata* for such a study was made because of its generalized character, its convenient size for gross dissection, and its availability. For this study the heads of thirteen specimens of *Ctenosaura pectinata* and two specimens of *Ctenosaura similis* were dissected. Eight of these were males and five were females. The heads ranged from 60 mm. to 100 mm. in length. A single specimen (head length of 18 mm.) was serially sectioned at 15 microns and stained by the Bodian silver technique. This allowed accurate correlation of gross relations and tracing of nerves and smaller structures.

Eleven additional skulls of varying sizes were available for study: eight of *C. pectinata* and one each of *C. similis*, *C. acanthura*, and *C. quinquicarinata*. The illustrations were drawn from projections of Kodachrome transparencies.

The singular form is used in the following descriptions to indicate bilateral structures for purposes of simplicity and clarity. Mid-line or azygos structures are so indicated.

Ctenosaura pectinata (Weigmann)

The genus *Ctenosaura* is a group of generalized, terrestrial iguanids composed of thirteen species (Bailey, 1928) or "ten or eleven" species (Smith, 1946), which occurs throughout México and Central America. The lizards of this genus are large, powerful, active, and diurnal and are characterized, in part, by a large spinous tail.

Ctenosaura pectinata (Figs. 1 and 2) ranges along the Pacific coast from southern Sinaloa to the Isthmus of Tehuantepec (Smith and Taylor, 1950). It is found in the rocky hillsides and occasionally in trees. It is a large, herbivorous lizard, reaching a maximum length of approximately 750 mm. The head is elongate and depressed and has a pronounced transverse gular fold. Body scales are small and fine. A dorsal spinous crest extends to the base of the tail (Bailey, 1928). Smith (1935) stated that the sacral crest may be low or absent. Females are proportionally smaller and lack the elongate dorsal spines of the male. The color pattern changes from green in the immature lizard to a varying olive tan or earth color blotched with yellow or orange in the adult (Fig. 1). There is no distinct transverse marking on the body.

The specimens represented in this study were collected in the vicinity of La Playa near Jorullo Volcano and in the vicinity of Coalcomán; both localities are in the state of Michoacán.

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I wish to thank Dr. Claude W. Hibbard for his friendly counseling, suggestions, and criticism. The introduction which he gave me to the subject and to problems of paleontology has been the prime encouragement for the completion of this work. To Dr. Russell T. Woodburne and to other members of the Department of Anatomy I wish to extend my thanks for their patient understanding and support. I am especially indebted to Dr. Alfred H. Stockard for his careful reading of the entire manuscript.

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THE SKULL

Literature on the reptilian skull is extensive, covering hundreds of fossil and Recent species, but it is limited to the comparative aspects of individual elements and their origin and relations to one another within the skull (Siebenrock, 1895; Cope, 1892; Barrows and Smith, 1947). In few studies has the skull been considered in relation to the soft structures which surround it and doubtless influence its shape and characteristics. Bahl (1937) attempted such an analysis with the skull of *Varanus*. Additional papers dealing with the relations of soft structures of specific bones or of limited regions are those of Bellairs (1949), Evans (1939), Säve-Söderbergh (1946), Lakjer (1927), and Versluys (1912, 1936).

The skull of *Ctenosaura pectinata* is characterized by both lightness and strength. It is constructed of cartilage, fibrous membranes, and bones in different degrees of ossification interlocked by a variety of types of sutures which are not obliterated as a result of age. It is low, and the snout, orbits, and temporal fossae are of moderate size and of approximately equal length, reflecting the nonspecialized condition of the ctenosaur.

The skull is streptostylic, possessing a freely movable quadrate bone which is attached dorsally to the paraoccipital process in two places by a syndesmosis and ventrally to the quadrate process of the pterygoid bone by a diarthrosis. This allows considerable freedom of motion at the ventral end of the quadrate. It is also kinetic (metakinetic, Versluys, 1912) in that the maxillary segment can be elevated and depressed, hingelike, on the occipital segment (Bradley, 1903).

Associated with this kineticism are certain modifications within the structure of the skull. The maxillary segment is independent of the occipital segment, except that these two segments articulate by three points of motion. One, the basipterygoid joint, is a diarthrosis, allowing forward and backward motion. The second joint, formed by the paraoccipital process, the parietal, and the supratemporal, is a syndesmosis, allowing only a small amount of motion. The third joint, between the supraoccipital and the parietal, is flexible through the taenia marginalis and the processus ascendens of the synotic tectum, which form it. Since the occipital suture is somewhat restricted, there is a hinge suture between the frontal and parietal elements which adds flexibility to the skull roof. The anterior part of the occipital segment is membranous, favoring flexibility of the skull.

Kineticism, which is characteristic of many but not all lizards, is believed to facilitate chewing (Versluys, 1912). Because of this, the skull is naturally divided into two parts, a fixed axial part, the occipital segment, and the more anterior motile part, the maxillary segment, containing the orbits, nasal capsule, and palate.

The Occipital Segment

The occipital segment consists of the brain case and does not include the ethmoidal region. It is composed of two distinct parts: a posterior, osseous otico-occipital part and an anterior, membranous orbitotemporal part.

Otico-occipital Part

The otico-occipital or osseous part of the brain case (Figs. 8 and 9) forms a median axis around which the remainder of the skull is attached. It is firmly bound to the vertebral column by the flexor and extensor musculature of the neck. It is shaped like a wedge, the apex of which articulates with the pterygoids and the base with the parietals, squamosals, and quadrates by means of two diverging paraoccipital processes. The basisphenoid and basioccipital form its floor, the paired prootic and exoccipitals its walls, and the median supraoccipital its roof. These elements, of endochondral origin, are usually tightly sutured but only occasionally become fused. Centrally the otico-occipital part encloses a median tubular cavity, the brain case, which houses the medulla and cerebellum. Laterally within its walls lies the pair of membranous labyrinths of the ears and the foramina for the last six pairs of cranial nerves (VI, VII, VIII, IX, X, XII). The median foramen magnum (Fig. 6) is enclosed by the basioccipital, exoccipitals, and supraoccipital. The median, tripartite occipital condyle is typically lacertilian in all respects.

The dorsal and posterior surfaces of the otico-occipital part provide attachment for the axial musculature, and the dorsolateral surface serves some of the temporal muscles. The membranous walls of the orbitotemporal region attach to its anterior borders and complete the brain case.

The *basisphenoid, os basisphenoidale* (Figs. 4, 8, 9, and 14) is a median bone forming part of the floor of the cranial cavity and the seat of motion between the brain case (occipital part) and the remainder of the skull. It is situated in front of, and sutured to, the basioccipital, with which it forms the osseous cranial floor. Dorsally it is sutured to the anterior inferior process of the prootic. Ventrally it articulates with the pterygoids by its pair of large expanded basipterygoid processes which terminate in condyles.

The dorsal surface of the basisphenoid (Fig. 9) is concave and is bordered laterally and posteriorly by a continuous suture for the prootic and the basioccipital, respectively. Within a depression on the dorsal surface of the basisphenoid lie the midbrain and part of the hindbrain, separated from the bone by the dura mater. Near the lateral border and at about the mid-point of the dorsal surface of the bone is the abducens canal for the abducens (VI) nerve.

The anterior surface of the basisphenoid (Fig. 14) is a transverse sculptured plate, the dorsum sella. Its lateral angles project dorsad as a pair of small alar processes, the tips of which attach to the pila antotica. Between the alar processes is a concave acute crest, the crista sellaris, to which the ventral part of the metoptic membrane is attached. This membrane is tightly stretched and forms an extension of the cranial floor. At each ventrolateral angle of the anterior surface is a large basipterygoid process. Projecting anteriorly along its median ventral border is a long, thin, parasphenoid process which underlies the paired trabecular cartilages and the interorbital septum (Figs. 5 and 7). On the dorsal surface of this process, near the dorsum sella, the paired trabecular cartilages are ossified in a pair of circular ridges, the cristae trabeculares, each of which gives origin to part of a retractor bulbi muscle.

The dorsum sella is spherically concave and contains a pair of well-defined concavities and three pairs of foramina. At the base of the basipterygoid process, lateral to each crista trabecularis, is the exit of the vidian canal, which transmits the vidian nerve and the palatine artery. Dorsal to each crista trabecularis is a foramen which transmits an internal carotid artery, and between these foramina is a median tubercle to which is attached the pituitary sac. Extending from each alar process to the vidian canal is an elongate excavation, the retractor pit, bounded laterally by the lateral crest and medially by the retractor crest. This pit gives origin to the bursalis muscle and the retractor bulbi muscle. In its center, between the two muscles, is the abducens canal. Between the two retractor pits and dorsal to the carotid foramen is a median smooth triangular area against which the transverse pituitary vein lies. The median space dorsal to the cristae trabeculares and anterior to the dorsum sella is the sella turcica, which houses the pituitary sac.

The lateral surface of the basisphenoid (Fig. 8) is elongate and ventrally expanded as the basipterygoid process, the tip of which bears a condyle approximately seven times as long as it is wide, covered in the flesh by a thick fibrous articular cartilage (see joints). Near the dorsal edge of the condyle is the entrance to the vidian canal. The posterior border of the basipterygoid process, the crista ventrolateralis (Säve-Söderbergh, 1947), forms the anterior border of the floor of the tympanic cavity. The lateral surface of the alar process is flattened for the origin of the superior part of the protractor pterygoideus muscle. Between the alar and the basipterygoid process is a longitudinal concave excavation for the internal jugular vein, and above the condylar part of the basipterygoid process is a triangular depression for the origin of the inferior part of the protractor pterygoideus muscle.

The posteroventral surface of the basisphenoid bone (Fig. 4) is inclined from the suture with the basioccipital to the tips of the basipterygoid processes. The oral membrane of the pyriform recess attaches along the full extent of the ventral surface of the parasphenoid process and the anterior border of the basipterygoid process, and its continuation, the pharyngeal membrane, attaches to the smooth ventral surface of the basisphenoid.

The vidian canal originates on the lateral surface of the bone and emerges on the dorsum sella just lateral to the crista trabecularis. Within the bone it bifurcates, giving rise to the canal for the internal carotid artery, which is just dorsal to the crista trabecularis.

The *basioccipital, os basioccipitale* (Figs. 4, 6, 8, and 13), is an unpaired element which forms the posterior part of the floor of the cranial cavity and the mid-part of the occipital condyle. It is joined anteriorly by a tongue-and-groove suture to the basisphenoid and is sutured dorsally to the inferior process of the prootic and the crista interfenestralis and crista tuberalis of the exoccipital. It provides attachment for the ventral axial musculature.

In the body of the dorsal surface of the basioccipital (Fig. 13) is a concave, smooth excavation, the floor of the cranial cavity, which contains the medulla oblongata. This chamber is partly surrounded by attachments of other cranial bones. At three places, however, a lateral pair and a mid-posterior one, its border is free. The lateral pair, between the suture of the crista interfenestralis and the suture of the exoccipital, is the floor of the foramen rotundum. The mid-posterior one, the margin of the foramen magnum, bears a pair of small nutrient foramina, and just posterior to them is a pair of small excavations for the attachment of the apical ligament of the odontoid process.

Each lateral process of exoccipital bone bears a deeply excavated triangular area (Fig. 13), the occipital recess, which forms the floor of the tympanic cavity and is lined by the membrane of that cavity. The occipital recess is a continuation of a similar cavity of the exoccipital bone and forms with it a large antrum to the foramen rotundum (Fig. 8). The anterior wall of the recess is the ventral margin of the crista interfenestralis (Figs. 8 and 13), and the posterior wall is the inferior part of the crista tuberalis (Figs. 6, 8, and 13), the posterior surface of which provides insertion to part of the rectus capitis anterior muscle. The apex of each lateral process is the spheno-occipital tubercle, covered by an ossified cartilage and giving insertion to the ligament of the longissimus capitis muscle (Fig. 58).

The anterior atlanto-occipital ligament attaches around the periphery of the occipital condyle (Fig. 6). Its ventral surface (Fig. 4) is smooth and excavated and is covered only by the membrane which lines the tympanic (auditory) cavity (Fig. 58).

The *prootic, os prooticum* (otosphenoid bone of Siebenrock, 1895) (Figs. 8, 9, and 11), forms the anterior part of the occipital segment and the anterolateral wall of the brain case, and houses part of the membranous labyrinth. It is sutured to the five other bones of the occipital segment. It is a triradiate bone (Fig. 8). The alar or anterior superior process is short and broad and extends dorsad. Its apex, the marginal process, joins the ventral part of the taenia marginalis, and its posterior border joins the supraoccipital in a suture near the base of which is a small foramen for the anterior semicircular canal (Fig. 11). The anterior border of the alar process forms the thin crista alaris. The ventral end of the crista alaris diverges laterad and terminates at the posterior border of the trigeminal notch (Fig. 8), its dorsal part attaches to the prootic membrane, and its ventral part diverges laterad and attaches to the lateral lamina of the prootic membrane only (see prootic membrane). On the lateral surface of the alar process is an area of origin for the fibers of the pseudotemporalis superficialis muscle, and near its base is an arc-shaped ridge which roofs the anterior semicircular canal.

The inferior process lies ventral to the alar process. It extends anteriorly and terminates as the attachment of the pila antotica. Its dorsal border forms the ventral margin of the trigeminal notch (otosphenoid notch), its ventral border is sutured to the basisphenoid and the basioccipital, and its exoccipital border usually contributes a small part to the rim of the foramen ovale.

The posterior process is long and broad and extends caudad from the body of the prootic to overlap and suture to the anterolateral surface of the paraoccipital process of the exoccipital bone. On its mesial side, near the anterior end of its suture with the exoccipital, is a small foramen for the lateral or horizontal semicircular canal (Fig. 11). The dorsal and lateral surfaces of the posterior process provide for the origin of the adductor mandibularis externus medius muscle. Near the tip of the posterior process is a small notch where the medial crest of the quadrate attaches syndesmotically.

The lateral surface of the prootic (Fig. 8) is smooth and terminates ventrally in the crista prootica, a longitudinal crest which runs from the posterior to the anterior inferior (ventral) process and may extend onto the lateral surface of the basisphenoid. This crest provides attachment for the aponeurosis of origin of the protractor pterygoideus muscle, and, together with this aponeurosis, forms the lateral wall of the tympanic cavity. Extending mesially beneath the crista prootica is a deep recess, the recessus vena jugularis (Fig. 4), along the lateral wall and margin of which lies the internal jugular vein; along its mesial wall is the posteriorly directed facial foramen for the facial nerve. The entire recessus vena jugularis is lined with the epithelium of the tympanic cavity and is the roof and mesial wall of that cavity.

On the medial surface of the prootic, near the base of the alar process, is a recess (Figs. 9 and 11) for the medial cerebral vein. It is continuous with a similar recess on the medial wall of the supraoccipital (Fig. 9). Along its medial border, increasing in size ventrad, is a crest terminating in the anterior supratrigeminal process, which divides the trigeminal notch into a dorsal part for the medial cerebral vein and a ventral part for the trigeminal nerve. The apex of the supratrigeminal process provides attachment for the dorsal (ligamentous) process of the pila antotica, and its crest provides attachment for the medial lamina of the prootic membrane (see prootic membrane).

Posterior to the supratrigeminal process, the medial wall of the prootic bulges as the tympanic bulla (Fig. 9). Ventral to the bulla is the deep acoustic recess, which houses the anterior auditory ganglion and three foramina. Of the three foramina, two are dorsal, lying side by side, and transmit the two branches of the anterior ramus of the acoustic nerve to the anterior ampullar recess; the third foramen, ventral to the others and posteriorly directed, transmits the facial nerve. Posterior to, and to some extent continuous with, the acoustic recess is a fourth foramen (a semiforamen, completed by the exoccipital) which transmits the posterior ramus of the auditory nerve to the cavum capsularis.

The medial surface of the inferior process forms part of the floor of the cranial cavity. The entire medial surface of the prootic, with the exception of the area for the medial cerebral vein, is covered by dura.

Centered between the suture lines of the prootic, exoccipital, and supraoccipital is a recess (Fig. 11) which produces the tympanic bulla of the cranial wall. Dorsally this recess is spheroidal and constitutes the anterior part of the cavum capsularis. Extending anteriorly into the prootic from the cavum is a smaller cavity, the anterior ampullar recess, which houses the anterior and the external ampullae. Ventral to the cavum capsularis and partly separated from it by a ridge, the lagenar crest, is the funnel-shaped lagenar recess which extends into the basioccipital bone and accommodates the lagena.

The *exoccipital, os exoccipitale* (Figs. 6, 8, 9, and 12), is a compound bone formed by the fusion of the exoccipital and the opisthotic, which remain distinct in certain other species. In all specimens of *C. pectinata* examined by me the fusion was complete. Since this is true in many others species of lizards too, the exoccipital will be considered as a single element.

The exoccipital is irregular in shape and serves many functions. It forms a posterolateral wall of the cranium and the lateral element of the occipital condyle, it houses the posterior part of the membranous labyrinth, and it provides a long process for the attachment of the occipital segment to the remainder of the skull. It consists of a central heavy part bearing the occipital condyle and auditory capsule, and a long, posterolaterally directed paraoccipital process.

In lateral view of the exoccipital (Fig. 12) the long paraoccipital process is seen to terminate in a mediolaterally flattened articular tip. The lateral surface of the tip has three facets (Fig. 8) which articulate dorsally, through the mediation of an intercalary cartilage, with the medial surface of the posterior process of the parietal, and ventrally with the medial surface of the posterior process of the supratemporal and the tip of the cephalic condyle of the quadrate. The major part of the lateral surface of the process is rough for suture with the posterior process of the prootic. At the anterior end of this rough surface is a small foramen (Fig. 12) which transmits the external semicircular canal. In the lateral surface of the paraoccipital process, between its articular tip and the posterior process of the prootic, is a slight groove in which the occipital artery courses dorsally to the neck musculature.

Beneath the paraoccipital process is a recess (Figs. 4 and 8) which is continuous anteriorly with the recessus vena jugularis of the prootic. The internal jugular vein crosses the ventral surface of the paraoccipital process proximal to the articular tip and lies for a very short distance in the recessus vena jugularis. Within the jugular recess lies the foramen ovale, the anterior margin of which is formed by the prootic bone. The foot plate of the stapes lies in the foramen ovale. The medial wall of the jugular recess is extended ventrally by a thin sheet of bone, the crista interfenestralis (Säve-Söderbergh, 1947) (Fig. 8), which continues along the anterior margin of the basioccipital and separates the foramen ovale from the foramen rotundum. Lying within the recess are the hyomandibular division of the facial nerve dorsal to the stapes, the internal carotid artery, and the medial cranial sympathetic trunk ventral to it.

Medial to the crista interfenestralis is a deep occipital recess, bounded posteriorly by the crista tuberalis (Säve-Söderbergh, 1945, 1947) and ventrally by a similar recess in the basioccipital. In the occipital recess, near its apex, lies the foramen rotundum, marked by a small crest and covered by the membrana tympani secunda. Beyond this foramen in the cavity of the exoccipital is the small triangular recessus scala tympani, whose medial wall is the foramen perilymphaticus (Fig. 9), which opens into the cranial cavity, and on whose superior wall is the fenestra cochlea (Fig. 12), which opens into the medial surface of the lagenar recess. The recessus houses the terminal end of the saccus perilymphaticus and transmits the glossopharyngeal nerve. This nerve enters the perilymphatic foramen from the cranial cavity and follows the dorsomedial wall of the recessus. It emerges from the foramen rotundum and passes along the dorsomedial surface of the occipital recess.

The posterior surface of the exoccipital bone (Fig. 6) presents the lateral third of the occipital condyle and the medial surface of the paraoccipital process. The exoccipital part of the occipital condyle is triangular and is covered by cartilage. The articular (caudal) surface of the condyle forms a diarthrosis with the lateral plate of the atlas and is surrounded by a recess for the atlas and the attachment of the atlanto-occipital ligament. Extending ventrad from the condyle is the vertical face of the crista tuberalis, onto which the fibers of the rectus capitis anterior muscle insert. Along the superior margin of the crista tuberalis are two small foramina which transmit the two ventral divisions of the hypoglossal nerve. Dorsal to these foramina, in the apex between the condyle and the paraoccipital process, are two others, a ventral one which transmits the dorsal division of the hypoglossal nerve, and a dorsal one which transmits the vagus nerve and, in occasional specimens, a small branch of the posterior cerebral vein. Medial to the latter two foramina is a small recess for the insertion of the tendon of the rectus capitis anterior muscle. A ridge extending from the lateral side of the foramen magnum divides the posterior surface of the paraoccipital process into dorsal and ventral recesses which serve for the insertion of the obliquus capitis and the longissimus cervicis muscle, respectively. The tip of the paraoccipital process receives the insertion of the episternocleidomastoideus muscle. The lateral wall of the foramen magnum is excavated slightly for the major part of the posterior cerebral vein.

The medial, or cranial, surface of the exoccipital bone (Fig. 9) is concave and has a series of foramina. Ventrad can be seen its suture with the basioccipital along the condyle and the cranial floor. Near the anteroventral corner, above the suture line, is the large perilymphatic foramen for the glossopharyngeal nerve and the perilymphatic sac, and posterior to this foramen is a series of three foramina which transmit the three roots of the hypoglossal nerve. A single large vagal foramen lies in the center of the medial wall. Below this foramen is a small pit in which the dentate ligament of the spinal cord is attached. A concave area above the vagal foramen seats the posterior cerebral vein (Figs. 6 and 9). The medial wall of the exoccipital is covered by dura.

The anterior surface of the exoccipital (Fig. 12) presents a concavity, the vestibule, surrounded by a continuous suture line, for the supraoccipital dorsally and the prootic ventrally. In the supraoccipital suture is a small foramen through which the posterior semicircular canal passes. The vestibule consists of a large dorsal part, cavum capsularis, which continues posteriorly into the posterior ampullar recess, and a smaller ventral funnel-shaped lagenar recess. Within the latter can be seen the foramen ovale laterally and the cochlear foramen medially, leading into the recessus scala tympani.

The *supraoccipital, os supraoccipitale* (Figs. 6-10), is a median element roofing the posterior part of the cranial cavity, forming the dorsal rim of the foramen magnum, and housing the dorsal part of the membranous labyrinth. It is hexagonal in appearance, convex dorsally and concave ventrally. It is sutured along its lateral border to the alar process of the prootic anteriorly, and to the exoccipital posteriorly, and joins the parietal anteriorly through a cartilaginous and membranous junction.

The dorsal surface (Fig. 6) is smooth and slopes laterally from a median occipital crest which is the attachment of the ligamentum nuchae. Near the anterior end of the occipital crest are two raised triangular depressions for the insertion of the deep part of the spinalis capitis muscle. The posterior part of the surface lies in a horizontal plane; the anterior ascends to the inferior surface of the parietal bone (Figs. 6 and 10). On each side of the occipital crest is a large depression which receives the insertion of the rectus capitis posterior muscle. The posterior edge (Fig. 6) has a central, smooth, concave rim, the superior border of the foramen magnum to which is attached the dorsal atlanto-occipital ligament.

The anterior border is /\ -shaped. Near its apex (Figs. 7 and 8) is a round, cartilaginous, median process, the remnant of the processus ascendens of the synotic tectum, which extends into the parietal fossa on the ventral surface of the parietal bone (Fig. 7), forming with it a peg-and-socket type of union. Each ventral angle of the anterior border bears a marginal process from which a taenia marginalis arises. The processus ascendens, taenia marginalis, external periosteum, and internal dural linings form a flexible attachment between the occipital and the maxillary segments of the skull.

The ventral surface of the supraoccipital is concave and covers the medulla and the cerebellum. The posterior half is narrowed by a pair of spherical bulges (Fig. 6), each being part of the internal vestibular prominence, the auditory bulla. Completely surrounding each bulla is a suture (Fig. 10) with which the supraoccipital attaches to the exoccipital posteriorly, and to the prootic anteriorly. Each concavity, cavum capsularis, lodges the dorsal part of a membranous labyrinth. Along the medial wall of each cavum capsularis is an elongate recess leading into a narrow tube which houses the common crus of the anterior and posterior semicircular canals. From this recess, leading anteriorly and posteriorly within the supraoccipital, are small tubular canals for parts of the posterior and anterior semicircular canals. Anterior to the aperture of the common crus is a small tunnel, the endolymphatic canal (Fig. 10), which pierces the wall of the cavum capsularis and leads into the cranial cavity (Fig. 9), transmitting the endolymphatic duct. Within the suture line posterior to the cavum capsularis is a minute foramen, the posterior osseous semicircular canal, which continues into the exoccipital bone. Along the posterior end of the prootic suture is a second minute foramen, the continuation of the anterior osseous semicircular canal into the prootic bone.

Along the mid-line of the ventral surface lies the longitudinal cerebral vein. In front of the auditory bulla is a vertical crest (Fig. 9) in which the medial cerebral vein lies. The dura of the parietal bone is continuous onto the ventral surface of the supraoccipital.

Orbitotemporal Part

The orbitotemporal part (Fig. 7) of the brain case continues anteriorly from the otico-occipital part. It houses the hypothalamus, the optic lobes, the cerebral hemispheres, and the olfactory stalks, and from it pass the anterior five cranial nerves (I, II, III, IV, and V). Its cavity, larger than that of the otico-occipital part, is roofed by the frontal and parietal bones. Ventral to it is the cartilaginous interorbital septum, which is considered a part of the obitotemporal region.

The membranous part is formed of cartilaginous plates and processes that produce a framework upon which is stretched a continuous membrane completing its walls. The membrane is double layered, formed externally by a continuation of the periosteum and perichondrium of the adjacent bones and cartilages and internally, in the brain case proper, by a dural lining.

Since this is a tropybasic skull, the trabeculae are fused anteriorly, giving rise to a median cartilaginous and membranous plate, the *interorbital septum*. This septum (Fig. 7) lies on the basitrabecular process of the basisphenoid and continues anteriorly as the trabecula communis of the nasal septum; however, it is not broadly continuous with the nasal septum, being partly separated from it by the expanded olfactory canals. The interorbital septum is attached to the nasal capsule by means of a pair of rodlike sphenethmoidal commissures which extend craniolaterad from its dorsal border (Figs. 43-46). The interorbital septum attaches dorsally to the planum supraseptale and extends caudad as far as the orbitosphenoid bone. The cartilaginous part forms a rounded pyramidal plate anteriorly and sends three posterior projections to attach to the cranium. The first of these processes arises from the apex of the pyramid, extends posteriorly ventral to the olfactory canal, and attaches to the anterior end of the planum supraseptale. The second, a heavier band of cartilage, passes dorsal to the optic nerve and attaches to the floor of the olfactory canal at the posterior end of the planum supraseptale, between the dorsal ends of the orbitosphenoid bones. The third, the *hypochiasmatic cartilage*, passes ventral to the optic nerve and attaches between the lower ends of the orbitosphenoid bones. Between these cartilaginous processes are openings which are filled by the continued membranous perichondrium. Between the first and the second cartilaginous septal processes is the *superior septal membrane;* between the second process and the hypochiasmatic cartilage is the *optic membrane,* which extends as far caudad as the optic chiasma; and between the hypochiasmatic cartilage and the trabecular cartilage is the *supratrabecular membrane* which terminates posteriorly at the anastomotic vein.

The interorbital septum not only separates the orbital cavities but is also the base of origin for the orbital muscles and is the floor of the olfactory canal. The superior oblique and the inferior oblique muscles have their origin along its anterior border, and the tendon of the nictitating membrane attaches near its superior border. The posterior border of the optic membrane serves as origin for the anterior rectus muscle, and the supratrabecular membrane similarly serves the inferior and posterior rectus muscles.

Posterior to the septal region, the *orbital cartilages* remain paired and form the anterior part of the brain case. The embryonic pila metoptica ossifies, producing the orbitosphenoid bone, which lies within the cranial wall. The remainder of the cartilage calcifies to varying degrees, presumably with age. The membranous brain case diverges caudolaterad from the posterior border of the interorbital septum and extends posteriorly to the frontal, parietal, prootic, and basisphenoid bones. The cavity produced is characteristically V-shaped with its floor (apex) formed by the trabecula communis and the posterior border of the interorbital septum. This part of the brain case, unlike the interorbital septum, contains distinct cartilaginous bars which represent the embryonic orbital cartilages described by Gaupp (1900) and de Beer (1937).

Arising from the marginal processes of the supraoccipital and the prootic bones and extending anteriorly along the superior border of the brain case is a cartilaginous bar, the *taenia marginalis*. This bar lies along the ventral surface of the parietal bone near its lateral border and continues along the ventral surface of the frontal bone just medial to the supraorbital ridge. At the anterior end of the frontal it expands ventrally into a broad plate, the *planum supraseptale,* which fuses with its fellow ventrally, and then with the median interorbital septum. The planum supraseptale attaches anteriorly to the dorsal cartilaginous process of the interorbital septum and posteriorly to the supraoptic process of the septum. These plates, together with the frontal bone and its cristae cranii, form the median, closed, olfactory canal which houses the olfactory stalks and bulbs. The posterior part of the floor of the canal is broad and flat and extends ventrad to attach to the pair of orbitosphenoid bones.

The *orbitosphenoid, os orbitosphenoideum* (Figs. 7 and 23), is a crescent-shaped, vertical element surrounding the optic foramen. It represents the embryonic cartilaginous pila metoptica and part of the taenia parietalis (Säve-Söderbergh, 1947). The bone bears three processes, of which the anterodorsal connects to the planum supraseptale, the posterior joins the pila accessoria and the pila antotica, and the inferior is continuous with the cartilaginous part of the pila metoptica. The orbitosphenoid is fused with its fellow in the mid-line and, after being joined by the hypochiasmatic cartilage of the septum, terminates as the *subiculum infundibulum,* a small, median, ventral process which forms the anterior part of the pituitary region and (internally) the attachment of the diaphragm covering that region. The anterior border of the orbitosphenoid forms the posterior margin of the optic foramen; its inferior process, together with the subiculum infundibulum, serves as the origin of the superior rectus muscle. The optic foramen, a median transverse foramen formed by the orbitosphenoid bones, contains the optic chiasma and is divided into two parts by the posterior border of the interorbital septum.

Extending ventrad from the taenia marginalis in the region of the frontoparietal suture is a cartilaginous pillar, the *pila accessoria,* which is attached to the posterior process of the orbitosphenoid bone. This pillar, the taenia marginalis, the planum supraseptale, and the orbitosphenoid bone in the embryo enclose a space, the *epioptic fenestra*. Attached to the anterior inferior process of the prootic bone and the alar process of the basisphenoid bone is a nearly horizontal cartilaginous bar, the *pila antotica,* which also extends to the posterior process of the orbitosphenoid bone. The pila antotica separates a fenestra prootica dorsally from a fenestra metoptica ventrally. In its course the pila antotica arches over the foramen of the trochlear nerve anteriorly and joins the prootic bone posteriorly, giving off here a dorsal and a ventral process. The dorsal process extends posteriorly to the supratrigeminal process of the prootic and attaches to it by a tough tendinous ligament, forming with this bone a complete foramen for the trigeminal ganglion and nerve. The ventral process of the pila serves as the origin of the levator bulbi muscle.

The cartilaginous framework of orbital cartilages and its fenestrae are completely enclosed by continuous *orbital membranes* which carry the names of the embryonic fenestrae closed by them (Säve-Söderbergh, 1947). Of these the *epioptic membrane* is complete and unperforated. The optic fenestra is nearly completely filled by the optic nerve; the *optic membrane* occupies only the periphery of the foramen and is continuous with the optic nerve.

The *prootic membrane* extends between the taenia marginalis, the ala prootica, the pila accessoria, and the pila antotica. Along its posterior border it splits into two laminae, a medial and a lateral. The medial lamina attaches to the supratrigeminal process and continues posteriorly along its crest to the internal cranial wall, where it becomes the dural lining. The lateral lamina attaches to the ala prootica, as far down as the fifth nerve, and is continuous with the periosteum of the prootic bone. Between these laminae, the transverse sinus (medial cerebral vein) passes to the prootic sinus which, in turn, surrounds the trigeminal ganglion and drains into the jugular vein. The lateral surface of the prootic membrane provides attachment for the orbitotemporal membrane and for the origin of part of the levator pterygoideus muscle.

The *metoptic membrane* lies beneath the pila antotica and attaches to the orbitosphenoid bone, the subiculum infundibulum, the parasphenoid process, and the basisphenoid bone. In addition to covering the metoptic fenestra, it forms a sac for the pituitary body, lying between and above the retractor musculature. This sac is separated from the dorsum sella by the pituitary vein and from the interorbital septum by the anastomotic vein. Ventrad it lies on a raphe between the two retractor bulbi muscles. The metoptic membrane is stretched between the alar processes of the basisphenoid and attaches to the crista sellaris, forming a strong membranous floor for the anterior part of the midbrain. Becoming thin it passes around the large pituitary vein to attach to the dorsum sella above the openings for the internal carotid artery. Continuing anteriorly, it passes along the raphe of the retractor bulbi muscle to the anastomotic vein, where it attaches to the subiculum infundibulum. There it diverges and extends dorsally along the orbitosphenoids to the pila antotica. Its lateral walls, enclosing the pituitary body, are extremely thin, but above the pituitary region they are thickened. Within the pituitary sac, between the crista sellaris and the subiculum infundibulum, the dural layer forms a diaphragm which is pierced in the mid-line by the hypophysis. The thickened dorsal part of the metoptic membrane is pierced by the trochlear nerve just beneath the pila antotica and by the oculomotor nerve at approximately its mid-point.

The Maxillary Segment

The maxillary segment comprises the remainder of the skull except the quadrate and epipterygoid bones. The elements, all of intramembranous origin (de Beer, 1937), are firmly sutured and function as a unit, except that the frontoparietal suture is hinged and has slight motion. Its combined elements form the palate, the nasal capsule, the orbits, and the temporal fossae.

Palate

The bony elements of the palate, beginning posteriorly, are the paired pterygoid, ectopterygoid, palatine, vomer, maxilla, and the median premaxilla.

The *pterygoids, os pterygoideum* (Figs. 4, 5, 6, and 18), are paired bones lying alongside the median line. They form the major seat of motion between the occipital and the maxillary segment.

The pterygoid (Fig. 18) is an elongate, slightly curved, dorsoventrally concave bone with a large triangular anterior part and a long slender posterior part. The anterior part has two processes: the palatine process, firmly sutured to the palatine bone dorsally, and the transverse process, sutured to the ectopterygoid (transverse) bone laterally. The slender posterior part, the quadrate process, extends caudolaterad to articulate with the ventromedial surface of the quadrate (Fig. 6) (see joints). By means of facets at its anterior end it articulates movably with the basipterygoid process ventrally and columella cranii dorsally (see joints).

The palatine process, ventrally (Fig. 4), forms the posterior third of the roof of the mouth. On an elevated part of its posterior surface is an arc of 13-16 teeth, which usually lie in a single row but in occasional specimens are in clusters. These teeth are in grooves, as are those of the maxilla and dentary, and are replaceable. Several foramina pierce the palatine process and transmit palatine branches of the infraorbital plexus. This process is covered only by the oral mucosa. The pharyngeal mucosa is attached posterior to the pterygoid teeth and anterior to the ventral border of the transverse process. The dorsal surface of the palatine process (Figs. 3 and 18) forms the ventromedial part of the floor of the orbit. Its dorsomedial surface is covered by part of the pharyngeal membrane, which extends up into this area as the pyriform recess and spreads laterally dorsal to the pterygoid bones. The medial palatine ramus of cranial nerve VII and the palatine artery run along its dorsomedial surface. Its lateral border serves as the area of attachment for the inferior orbital membrane filling the *inferior orbital foramen.*

The transverse process (Figs. 4, 6, and 18) is a perpendicular plate extending anterolaterad. Its posterior surface is excavated (mediolaterad) to accommodate the body of the pseudotemporalis superficialis muscle. Its lateral extremity forms a suture with the ectopterygoid. Its ventral border forms the posterior limit of the oral cavity (Figs. 4 and 5) and gives origin to the pterygomandibularis muscle.

The quadrate process (Fig. 18), the mediolaterally flattened part of the pterygoid, extends posteriorly to articulate with and support the quadrate bone (Fig. 6). On the dorsal border of its proximal end is a deep socket, the fossa columella, in which the ventral end of the epipterygoid articulates. In some specimens, anterior to the columellar fossa there is a small notch or fossa which contains a small cartilaginous plug of unknown significance. On the dorsal ridge, posterior to the columellar fossa, is an elevation, the postcolumellar process (Fig. 5). The levator pterygoideus muscle inserts into this dorsal ridge medial to the columellar fossa and as far posteriorly as the postcolumellar process. On the medial surface of the quadrate process, medial to the columellar fossa, is the pterygoid notch (Fig. 18), a V-shaped shelf into which the basipterygoid process of the basisphenoid is wedged to form a synovial joint with the pterygoid (see joints). Farther caudad on the medial surface of the quadrate process is a long concave excavation (Figs. 6 and 18) which receives the insertion of most of the protractor pterygoideus muscle. (Some of its lateral fibers insert on the dorsal border of the quadrate process, medial to the levator pterygoideus muscle and posteriorly from the columellar fossa.) The lateral side of the quadrate process (Fig. 5) is smooth and convex. The posterior fibers of the pterygomandibularis muscle arise along its ventrolateral border. At the posterior end is a small facet which articulates with the ventromedial surface of the quadrate.

The *ectopterygoid, os transversum* (Figs. 4, 5, and 20), is situated in an anterolateral direction between the lateral border of the transverse process of the pterygoid and the medial surface of the jugal. It serves as a brace between the palate and the external roofing elements. It has a medial vertical process and a lateral horizontal process with a short thick body between. The medial process (Fig. 5) is perpendicularly joined to the transverse process of the pterygoid by a tongue-and-groove suture. Its ventral tip provides origin for the lateral part of the pterygomandibularis muscle. The lateral (horizontal) process (Fig. 4) is sutured to the medial surface of the jugal and bears on its ventral surface a slight excavation which receives the dorsal surface of the posterior process of the maxilla.

Ventrally, laterally, and posteriorly the ectopterygoid is covered by oral membrane. Dorsally it forms the posterolateral part of the floor of the orbit and also the attachment of the orbitotemporal membrane. Its posterior surface (Fig. 20) is excavated and this, together with a small part of the transverse process of the pterygoid, forms a concavity, the coronoid recess, which takes the coronoid process when the mandible is adducted. The anterior border gives attachment to the inferior orbital membrane, filling the inferior orbital fossa.

The *vomer* is a paired bone (Figs. 4, 15, and 16) forming the anterior part of the palate, the medial borders of the fenestra vomeronasalis externus, and the medial borders of the fenestra exochoanalis. The two are sutured in the mid-line of the palate for approximately three-fourths of their length, but posteriorly are separated by the median palatal sinus which passes dorsad between them. The posterior end of each vomer is sutured to the vomerine process of a palatine dorsally; its anterior constricted end is sutured to the medial surface of the premaxillary process of the maxilla, with its pointed tip lying in a V-shaped excavation behind the incisive process of the premaxilla. Between the anterior tips of the pair is a space occupied by the rostral part of the cartilaginous nasal septum.

The ventral surface of the vomer (Fig. 16) is convex. On its lateral border at the constricted anterior end is the lacrimal groove, a crescent-shaped excavation with a perpendicular medial border. In the posterior part lies an extension of the groove, the cartilaginous lamina transversalis anterior. The anterior end of the lacrimal duct occupies the lacrimal groove, the posterior border of which marks the anterior extent of the fenestra exochoanalis. The raised median borders of the pair of lacrimal grooves form a canal in which the unpaired median palatine sinus lies ventrally and the paired ramus medialis of the palatine nerve VII lies dorsally. In each vomer, at the posterior end of this canal, is a foramen through which the nerve enters the canal from the dorsal surface. Branches of the nerve extend both posteriorly and anteriorly on the ventral surface of the vomer; in some specimens those that extend anteriorly are enclosed in an osseous canal (Fig. 16). On the lateral border of the vomer, at the anterior end of the lacrimal groove, is a small notch, the median border of the fenestra vomeronasalis externus.

The dorsal surface of the vomer (Fig. 15) is concave. Posteriorly on it is an excavation for the vomerine process of the palatine bone. Along the mid-line the two bones are raised and support the nasal septum, the paraseptal cartilages, and the cartilages of Jacobson's organ (lamina transversalis anterior). Posterior to the dorsal reflection of the lacrimal groove is a small tubercle for articulation with the septum of the septomaxilla, and medial to this is a foramen for the median palatal nerve. The area posterior to the septomaxillary notch is crossed dorsally by the median palatine nerve and is covered by epithelium of the olfactory chamber. The area anterior to the notch and medial to the lacrimal groove supports the capsule of Jacobson's organ, which fits into irregularities in the surface of the bone. Perforating this area is a single foramen through which a branch of the anterior palatine nerve and the inferior nasal artery enter Jacobson's organ from the ventral surface of the vomer. At the anterior tip of the vomer is a small, triangular, smooth area of suture with the maxilla.

The *palatine, os palatinum* (Figs. 4 and 17), is a bone near the mid-line separated from its fellow by the pyriform space. The pair forms the major part of the palate as well as the floor of the orbits and the floor of the posterior part of the nasal capsules. The palatine has three processes: vomerine anteriorly, pterygoid posteriorly, and maxillary laterally.

The vomerine process is thin and tapers anteriorly. It lies in a horizontal plane and overlies the dorsal surface of the vomer. It is concave dorsally (Fig. 17) and forms the floor of the posterior part of the olfactory capsule. Medially there is a groove in which the paraseptal cartilage lies. The lateral border of the process provides attachment for the paranasal cartilage as far craniad as the vomer and forms with it the fenestra endochoanalis (Fig. 46). The medial palatine nerve lies along the mid-line of the dorsal surface of the process, and the space between its medial borders is filled by a heavy fibrous raphe.

The pterygoid process is robust and quadrangular. It descends posteroventrally at approximately a 30° angle from the projected plane of the vomerine process and is sutured dorsally to the palatine process of the pterygoid. Its medial border forms the lateral margin of the incisura pyriformis (lacuna pterygovomerin of Siebenrock). Its lateral border forms the medial rim of the inferior orbital fossa and gives attachment to the inferior orbital membrane covering this opening. Its dorsal surface is mediolaterally concave and forms the floor of the orbit. At approximately the mid-point of the pterygoid process is an anteroposterior groove which continues forward as far as the vomerine process and contains the principal (medial) branch of the palatine plexus VII. Extending laterally from this groove, in the direction of the infraorbital foramen, there is in most specimens a shallower groove which contains the anterior communicating branch of the palatine plexus. These grooves have numerous foramina which pierce the palatine bone and convey small branches of the plexus to the oral mucosa on the ventral surface of the bone.

The maxillary process is thick and short and extends laterally at the junction of the pterygoid and vomerine processes. It is sutured dorsally to the prefrontal and ventrally to the jugal and the maxillary bones. At its lateral border is the infraorbital foramen, which may be confined to it or may be completed laterally by the jugal or the maxillary bone or both. Through this foramen the superior alveolar nerve and artery pass from the infraorbitals. The posterior border of the maxillary process bears a groove in which lie the lateral palatine ramus of nerve VII and the palatine branch of the infraorbital artery. Just medial and posterior to the suture between this process and the prefrontal bone is the palatine foramen, leading to a transversely placed canal which emerges anterior to the infraorbital foramen within the nasal cavity. This canal carries the intermediate palatine branch of nerve VII, which anastomoses with a medial branch of the superior alveolar nerve, and a lateral twig from the descending branch of the infranasal artery, which anastomoses with the inferior alveolar artery. Dorsal to the canal is a groove in which a communicating sinus from the nasal cavity to the orbit lies. Medial to these foramina in the dorsal surface of the palatine is a notch which lodges the inferior nasal artery and the medial palatine branch of nerve VII. At the junction of the palatine and vomerine processes is a transverse crest, formed partly by the different planes of inclination of the two processes, which provides attachment for the orbitonasal membrane.

The ventral surface of the palatine (Fig. 4) is smooth. The indentation between the vomerine process and the maxillary process is the posterior rim of the fenestra exochoanalis. The palatine is covered ventrally by the oral tissues.

The *premaxilla, os premaxillare* (Figs. 3-5), is the most anterior element of the skull. It is a median, anchor-shaped, bilaterally symmetrical bone, with a pair of lateral processes bounding the external nares and joining the maxillary bones laterally and a nasal process lying between the external nares and terminating in a point between the nasal bones.

The anterior, rostral body is pierced by one or two pairs of foramina (Figs. 3 and 5) for the passage of the medial ethmoidal nerves. On its posterior surface is a pair of foramina through which the medial ethmoidal nerves and the subnarial branches of the maxillary arteries pass. Between these two foramina is a perpendicular, rectangular median excavation in which the rostral part of the cartilaginous nasal septum rests. Lateral to this excavation and ventral to the foramina is a pair of triangular suture scars, each with its apex pointing posteriorly, for attachment with the maxillary bones. The ventral border of each of these processes extends anteroventrally below the roof of the mouth as an incisive process (Fig. 4) which may be either single or bilobed. Its significance is not understood. On the ventral surface of the premaxillary bone is a row of teeth, usually of an odd number with one in the mid-line. Behind the teeth, on each side of the mid-line, is a foramen through which the terminal of the maxillary artery anastomoses.

The nasal process of the premaxilla extends posteriorly in a convex arch and occupies a median excavation of the cartilaginous nasal capsule dorsal to the septum. In cross section it is triangular, the apex directed ventrad. Its posterior end overlies the nasals in the mid-line and sutures with them, leaving two suture scars on its ventral surface. Dorsally this process is smooth and is covered with closely adhering skin.

The *maxilla, os maxillare* (Figs. 4 and 5), is a relatively large, flat, and roughly triangular bone forming the major part of the lateral surface of the snout. It presents two surfaces and three processes: a premaxillary craniad, a nasal, and a posterior. Its ventral margin is almost straight, being slightly upcurved at its anterior end, and bears a single row of pleurodont teeth attached in the angle between its ventral margin and a narrow mesially directed lamina.

The premaxillary process is flattened and overlies the maxillary process of the premaxilla. Its medial part receives the anterior process of the vomer. Dorsally (Fig. 3) it is expanded and forms the inferior rim of the fenestra exonarina. The dorsal surface is grooved for the subnarial artery and has a medial crest for the attachment of the lamina transversalis anterior.

The posterior process (Fig. 5) extends beneath the orbit and is sutured to the jugal and lacrimal bones dorsally and the ectopterygoid medially. It forms the lateral part of the rim of the inferior orbital foramen and an attachment for the inferior orbital membrane (Fig. 4).

Between the premaxillary and the posterior processes is a thin vertical plate, the nasal process (Fig. 5), which extends dorsally to form the lateral wall of the nasal capsule. It forms the posterior rim of the fenestra exonarina anteriorly and is sutured to the nasal and prefrontal bones dorsally. Along its apical part is a series of small foramina for cutaneous branches of the lateral ethmoidal nerve. Along its inferior border is a row of five or six small labial foramina, the most caudal being posteriorly directed and the remainder anteriorly directed, for cutaneous branches of the superior alveolar nerve and maxillary artery. At the base of the anterior border of the nasal process is the anterior inferior alveolar foramen (Fig. 3), either single or double, transmitting the terminal branches of the maxillary artery and superior alveolar nerve to the nasal capsule.

The medial surface is characterized by a palatal shelf which supports the nasal capsule dorsally and the teeth ventrally. Along the palatal surface the shelf (Fig. 4) forms the lateral rim of the fenestra exochoanalis posteriorly and the fenestra vomeronasalis externa anteriorly. It is tunneled for the passage of the maxillary artery and the superior alveolar nerve which enter through the posterior alveolar foramen along its dorsal surface. In the floor of the tunnel are numerous small foramina for dental nerves and arteries. The intermediate palatine nerve lies along its medial border. Dorsal to this shelf lie the lamina transversalis anterior and the lacrimal duct and ridge. Along the medial border of the palatine shelf, posterior to the superior alveolar foramen, is a suture for the attachment of the maxillary process of the palatine bone. The medial surface of the nasal process lies against the cartilaginous nasal capsule.

The teeth, attached along the ventral margin of the maxilla, each tooth in a separate osseous recess, are pleurodont, tricuspid posteriorly; they increase in size and become unicuspid anteriorly. There is an average of 28 teeth in each maxilla.

Nasal Capsule

The anterior elements of the palate, maxillary, and vomer form the floor and part of the walls of the osseous nasal capsule; the nasal, prefrontal, and lacrimal form the roof, and the septomaxilla lies within the cartilaginous part of the nasal capsule. (See also osseous nasal capsule under Snout.)

The *nasal, os nasale* (Figs. 3 and 26), is a paired bone lying along the mid-line of the skull between the premaxilla and the frontal and forming a partial covering for the olfactory capsule. The pair are sutured to each other along approximately the middle one-half of their length. Each nasal has a posterior process which diverges from the mid-line and lies in a triangular excavation of the frontal; the two processes are separated by a median process of the frontal. The two bones are separated anteriorly by the nasal process of the premaxilla which overlies them. Each nasal joins a prefrontal laterally by means of a tongue-and-groove suture. The anterior part of this suture is covered by the ascending process of the maxilla. The anterior border is free and forms the dorsal border of the fenestra exonarina.

The nasal is convex dorsally (Fig. 3), forming a dome over the anterior chamber of the cartilaginous nasal capsule. At the base of the posterior process is a foramen (or two) which transmits both cutaneous branches of the lateral ethmoidal nerve and venous tributaries to the orbital sinus. The nasal may be sculptured or smooth and is covered with closely adhering skin.

The ventral surface of the nasal (Fig. 26) is concave, for the reception of the anterior chamber. On the lateral part of this surface is a conchal ridge running anterolaterad. This ridge lies in the aditus conchae and is the only part of the nasal to which the olfactory capsule is attached. The fused border of the olfactochoanal membrane attaches to this ridge. Posterior to the conchal ridge is an elongate excavation for a tributary of the orbital sinus, and lateral to this are the foramina for the cutaneous branches of the lateral ethmoidal nerve.

The *prefrontal, os prefrontale* (Figs. 3 and 5), is a triangular pyramid whose apex forms the anterior angle of the orbit. Its medial border sutures to the lateral border of the frontal and the nasal by a tongue-and-groove suture. Its ventral border is overlaid by the nasal and the nasal process of the maxilla anteriorly and by the lacrimal posteriorly. Its posterior border, or palatine process, is free and extends between the frontal and the maxillary process of the palatine bone. The medial borders of the palatine process of the prefrontals, together with the palatine and frontal, form an opening, the orbitonasal fenestra, between the nasal and orbital cavities. These borders receive the attachment of the orbitonasal membrane. The posterior surface of the palatine process of the prefrontal is concave, smooth, and medially inflected to form the anterior rim of the orbit; its lateral surface forms the medial border of the lacrimal foramen which houses the lacrimal duct; and its ventrolateral tip sutures with the ventromedial part of the lacrimal bone. The external surface of the prefrontal is smooth and may have slight ornamentation from the closely adhering skin which covers it. The posterior rim serves as an attachment for part of the orbital fascia. The deep surface of the bone is concave and smooth and is lined by the paranasal cartilage and the planum antorbitale, which cover the posterior part of the olfactory chamber.

The *lacrimal, os lacrimale* (Fig. 5), is a small flat bone forming a small part of the anteroventral rim of the orbit. It sutures dorsally to the prefrontal, anteriorly to the nasal process of the maxilla, ventrally to the jugal, and ventromedially to the prefrontal. Its medial surface is separated from the palatine process of the prefrontal by the lacrimal foramen, which transmits the lacrimal duct, and its anteromedial part barely extends into the nasal capsule. It is pierced by a single vein which drains the skin that closely adheres to its lateral surface.

The *septomaxilla, os septomaxillare* (Figs. 5, 25, 27, 44, and 45), is a paired bone lying within the nasal capsule, alongside the nasal septum. It lies in the medial half of the naris, supported in its position by the cartilages of the nasal capsule, but it does not obstruct the nasal passage. It roofs Jacobson's organ and houses the anterior part of the olfactory chamber. It articulates with the dorsal surface of the vomer by means of a ventrally extending septal process, and it may in some individuals also come into contact with the vomerine process of the maxilla. It serves only as a protective element for the cartilages of the capsule lying between the anterior chamber of the nasal capsule and Jacobson's organ.

The septomaxilla is thin, elongate, and convex. The dorsal surface (Fig. 25) is covered by the squamous epithelium of the anterior chamber and forms a part of its floor (Fig. 45). The anterior process rests on the vomerine process of the maxilla (Fig. 5) or the rostral part of the septal cartilage. The medial border lies on a cartilaginous shelf projecting from the nasal septum (Fig. 48). The posterior process extends to the roof of the cartilaginous nasal capsule dorsally, but it does not pierce the dorsal plate cartilage and therefore does not articulate with the nasal. Between the posterior process and the septal cartilage is a notch for the medial ethmoidal nerve (Figs. 27 and 45). The lateral border is uneven, bearing a crescentic depression (Fig. 25) and providing attachment for the medial border of the zona annularis (that part which encircles the anterior chamber ventrally).

The ventral, concave surface (Fig. 27) is divided by a median septum into an anterior and a posterior part. The anterior part forms the roof for the cartilaginous capsule of Jacobson's organ; the posterior part is lined by olfactory epithelium and contains the anterior extension of the olfactory chamber. The medial border of the cartilaginous lamina transversalis anterior (that part posterior to Jacobson's organ) is attached to the ventrolateral border of the posterior part of the septomaxilla. This septum, which extends ventrad to articulate with the lateral border of the vomer, is incomplete, leaving a space between its mesial border and the cartilaginous nasal septum through which the vomeronasal nerves pass to Jacobson's organ.

Orbit

The orbital rim is bounded by the lacrimal and prefrontal anteriorly, the frontal dorsally, the postfrontal and postorbital posteriorly, and the jugal ventrally. Of these, the prefrontal and lacrimal have already been described.

The *frontal, os frontale* (Figs. 3 and 24), is a median bone forming the dorsal border of the orbits and the roof of the anterior part of the brain case. Posteriorly it is joined to the parietal and the postfrontal by a transverse hinge suture. Anteriorly it is sutured to the prefrontals and the nasals.

The frontal (Fig. 3) is dorsoventrally flattened and laterally emarginated. In adults the surface is sculptured, corresponding to the pattern of the scales which closely adhere to the surface. At the anterior end is a pair of triangular depressions which receive the posterior processes of the nasals. At the frontoparietal suture, both frontal and parietal bones are notched by the pineal foramen.

Laterally (Fig. 5) the edges are thickened and rounded, forming supraorbital ridges. There are two suture grooves along each lateral border (Fig. 24), a short posterior one for the postfrontal and a long anterior one for the prefrontal.

The ventral surface (Fig. 24) is smooth. Along each margin is a convex supraorbital ridge, low and rounded posteriorly but higher toward the anterior end, forming the ventral processes or cristae cranii. Between these two ridges is a shallow trough for the olfactory canal which houses the olfactory stalks. Medial to the supraorbital ridges, in the posterior half of the frontal, is a pair of narrow excavations for attachment of the cartilaginous solium supraseptale. Behind these excavations, following the contour of the supraorbital ridge, attach the epioptic membrane and the taeniae marginales, and anteriorly along the cristae cranii of each ventral border the thinner part of the solium supraseptale attaches.

The *postfrontal, os postfrontale* (Figs. 3 and 5), is a very small, but constant, cylindrical bone, forming a small part of the posterodorsal margin of the orbit. Its anterior border is rounded, conforming to the remainder of the orbital rim. Its posterior surface is sutured to the frontal medially, to the postorbital laterally, and to the tip of the anterolateral process of the parietal between them. Functionally, it is an important splint between these bones, forming a strong postorbital arch. Part of it forms an attachment for the skin dorsally.

The *jugal, os jugale* (Figs. 3 and 5), is a long, thin, dorsoventrally convex bone that forms the ventral border of the orbit and a small part of the supratemporal arch. Its anterior or maxillary process is sutured to the maxilla ventrally, to the lacrimal and the maxillary process of the palatine anteriorly, and to the ectopterygoid medially. The dorsal surface of this process is expanded anteriorly and descends ventromesially to form the anteroventral wall of the orbit. The entire rim of the jugal serves as attachment for the orbital fascia. The temporal process extends posterodorsally and is sutured to the inferior border of the postorbital. Anterior to this suture, on the mesial surface of the jugal, is a small foramen through which a branch of the maxillary nerve (1 and 2) passes. A small section of the temporal process gives attachment to the infratemporal fascia. The posteromedial surface of the jugal is concave and forms part of the coronoid recess which takes the coronoid process of the mandible during adduction. The lateral surface of the bone is pierced by numerous suborbital foramina for cutaneous branches of the maxillary nerves and is covered by closely adhering skin.

Temporal Region

The temporal region of the skull possesses two openings, a supratemporal and an infratemporal fossa. Separating the two is an osseous supratemporal arch (postorbital and squamosal). The supratemporal fossa (Fig. 3), surrounded by the parietal, postorbital, and squamosal, is dorsal. The lateral, infratemporal fossa (Fig. 5), enclosed by the jugal, squamosal, and quadrate, is opened ventrally, there being no quadratojugal (infratemporal arch). Posteriorly there is a third opening, the posterior temporal fossa (Fig. 6), surrounded by the parietal and supratemporal dorsally and by the occipital segment mesially and ventrally. The massive temporal muscles occupy these spaces.

The *parietal, os parietale* (Figs. 3 and 22), is an unpaired quadrangular bone expanded at both the anterior and posterior ends and compressed in the middle. The anterior angles extend laterally to form a transverse suture line, whereas the expanded posterior angles, supratemporal processes, extend posterolaterally and enclose an angle of approximately 110°. These posterior angles are expanded proportionately more in the adult than in the immature, corresponding to the hypertrophy of the jaw musculature in adults.

The parietal articulates with the frontal along its transverse anterior border in a manner that permits hinge motion, though it is not a true joint. Within the suture line both bones are indented by the pineal foramen. The tips of the anterolateral processes articulate with the postfrontal anteriorly and with the postorbital posteriorly and ventrally. The posterior end of the parietal overlies the supratemporal (Fig. 6), and its angles in some individuals articulate with the paraoccipital process of the exoccipital. The ventral surface of the parietal articulates with the supraoccipital by a cartilaginous processus ascendens of the tectum synoticum (Gaupp, 1900; de Beer, 1937), which in some specimens is partly ossified and forms the seat of motion between the occipital (posterior brain case) and the maxillary segment (Fig. 7). This process extends from the supraoccipital into a median ventral fossa parietalis.

The dorsal surface of the parietal (Fig. 3) is smooth except for a longitudinal median ridge lateral to which the surface is depressed and convex, providing area for the origin of the jaw muscles. The anterior two-thirds of this area gives origin to the pseudotemporalis superficialis, and the posterior one-third gives origin to the adductor externus medius, the line of separation being marked in some specimens by a slight longitudinal ridge. At the anterior end of the dorsal surface is a flat, triangular, sculptured area to which the skin closely adheres.

The ventral surface (Fig. 22) of the parietal is concave. The supratemporal processes are thinned and are slightly excavated laterally for the articulation of the supratemporal bone. The posterior tip of each gives origin to a small part of the adductor externus profundus muscle. The medial part of each posterior parietal process is flared dorsally, forming a roof for the neck musculature and the adductor externus profundus muscle. In the center of the ventral surface is a deep pit, the parietal fossa, which extends anteriorly and receives the processus ascendens of the synotic tectum. Lateral to the pit and extending anteriorly along each lateral border of the parietal is a groove which contains the taenia marginalis. These grooves extend to the mid-point of the anterior lateral processes where they continue on the ventral surface of the frontal bone. The part of the parietal bone between these marginal grooves is thickened and raised, forming the cranial roof over the cerebral and optic hemispheres.

Lateral to the marginal grooves the edges of the parietal extend ventrally, beyond the taeniae marginales, and give origin to the levator pterygoideus. At the mid-point of these borders is a slight elevation for attachment of the epipterygoid bone.

The posterior border of the parietal gives attachment to the following muscles dorsoventrally: origin of the depressor mandibularis, insertion of spinalis capitis, and insertion of episternocleidomastoideus. It also gives attachment to a dorsal fascia of the neck and the subcutaneous layer of the skin.

The *supratemporal, os supratemporale* (Figs. 6 and 21), is a small, thin, sliver-like bone which forms the major support of the posterolateral angle of the parietal and is the center of motion between the maxillary and occipital segments of the skull. It is divided into an anterior part and a posterior process. The anterior part is dorsoventrally flattened and bears dorsally a groove for the lateral border of the supratemporal process of the parietal. Laterally the anterior part gives partial origin to the adductor externus medius muscle, and medially it gives partial origin to the adductor externus profundus muscle.

The posterior process is thick and mediolaterally flattened, extending ventrally as a wedge between the lateral surface of the paraoccipital process of the exoccipital and the cephalic condyle of the quadrate (Fig. 6). The posterior process of the squamosal lies on the dorsal surface of the posterior process of the supratemporal, the two processes being held in position by an infiltration of fibrous cartilage which may become partly calcified. There are no definite sutures here. This joint is a seat of motion between the quadrate and the occipital and maxillary segment.

The *postorbital, os postorbitale* (Fig. 5), is a flat, triangular bone that forms the major part of the posterior rim of the orbit and the anterior half of the supratemporal arcade. The dorsal apex is inflected medially (Fig. 3) and is sutured anteriorly to the postfrontal and posteriorly to the anterolateral process of the parietal. Its anteroventral border is tongue-and-groove sutured to the jugal, and its posteroventral border is weakly sutured to the squamosal. The concave anterior rim, which forms the posterior border of the orbit, is thick and inflected medially and provides the posterior attachment of the orbital fascia. The free part of the ventral border gives attachment to the infratemporal fascia and the anterior part of origin of the levator angularis oris muscle. The posterior half of the medial surface gives origin to part of the adductor externus superficialis. The lateral surface is smooth and is tightly covered by skin.

The *squamosal, os squamosum* (Figs. 3 and 5), is an elongate paired bone which forms the posterior half of the supratemporal arcade. Its pointed anterior part lies on the ventrolateral surface of the posterior process of the postorbital, and its expanded posterior part lies on the dorsal surface of the supratemporal and the cephalic condyle of the quadrate. Held in place only by a heavy mass of ligaments, the squamosal is relatively mobile. Its lateral surface gives origin to part of the levator angularis oris and the adductor externus superficialis; its medial surface gives origin to part of the adductor externus medialis, and the skin attaches along its dorsal surface.

The *quadrate, os quadratum* (Figs. 3, 4, 5, 6, and 19), is a paired bone situated at the posterolateral angle of the skull and serving as the seat of motion between the cranium and the lower jaw. It and the epipterygoid, both of endochondral origin, form the suspensorium of the skull, the quadrate supporting the lower jaw and the epipterygoid forming a brace between the pterygoid and parietal. The quadrate is united to the other bones of the skull by syndesmotic and synovial joints, which allow for a certain degree of freedom of motion. It forms the housing for the middle ear and provides origin for part of the adductor musculature and attachment for the extracolumella and the tympanum.

The quadrate is auricle-shaped. On its ventral extremity is a large, smooth, convex condyle (Fig. 4), which is divided into medial and lateral parts, separated by a posterolateral sulcus. The medial part is large and rounded and is slightly posterior to the lateral part which is a small tubercle. Surrounding the condyle is a crest, the attachment of the articular capsule.

The dorsal extremity of the quadrate (Figs. 6 and 19) bears a roughly circular, posteromedially directed, cephalic condyle which is the attachment of the paraoccipital process medially, the supratemporal bone dorsally, and the squamosal bone laterally. The attachments are by means of thick pads of fibrocartilage, "intercalary cartilage" (Versluys, 1912). The remainder of the dorsal aspect presents a horizontal surface (Fig. 3), which serves as part of the origin of the adductor mandibularis superficialis and medius muscles.

The anterior surface is concave mediolaterally, broad dorsally, narrower ventrally, and constricted above the condyle. It gives origin to parts of the adductor mandibularis externus superficialis and medius muscles. Above the lateral half of the condyle is the quadrate foramen which carries an anastomotic branch of the anterior tympanic vein and a small anastomotic branch of the posterior condylar artery.

The posterior surface of the quadrate (Fig. 6) is concave and is divided by a vertical ridge, the posterior crest, into medial and lateral halves. The crest originates at the cephalic condyle and diminishes ventrally, flattening out just above the ventral condyle.

The medial half has a medial crest (Fig. 19) which serves as the origin of the adductor posterior muscle. At the dorsal end of the medial crest is a triangular tubercle which attaches by a fibrocartilage ligament to the posterior process of the prootic (Fig. 4), tending to stabilize the quadrate. Beneath this process is the arc-shaped mandibular groove (Figs. 6 and 19), in which the mandibular artery lies. Above the condyle is a slightly enlarged concave excavation, the articular facet for the quadrate process of the pterygoid. Dorsal to this facet is the entrance to the previously mentioned quadrate foramen. Between the pterygoid and the condyle is a small tubercle for the attachment of the medial collateral ligament. On the medial side of the posterior crest is a groove in which the chorda tympani nerve lies. Medial to this groove is a crest for attachment of the processus internus of the extracolumella.

The lateral surface of the quadrate (Fig. 3) has a prominent tympanic crest, and a deep excavation extends laterally from the posterior crest. Along the superior part of the tympanic crest, between it and the cephalic condyle, is a notch, filled by a fibrous membrane over which the lateral border of the tympanic crest continues as a cartilaginous band. The tympanic crest provides attachment for the anterior part of the tympanum, for part of the origin of the adductor mandibularis externus superficialis muscle, and for the skin. Below the termination of the tympanic crest is a constriction toward the condyle. Here is a rough pit for the attachment of the lateral collateral ligament (Fig. 31). The membrane of the tympanic sac covers the entire posterior surface of the quadrate bone and excludes all the previously named structures from the sac.

Extending between the pterygoid and the parietal is an elongate cylindrical bone, the *epipterygoid*, or columella cranii (Figs. 5 and 6). Its ventral end is flattened into a wedge-shaped articular surface which sits in the columellar fossa of the pterygoid (see joints). Its mid-part is flattened and presents a posterior and an anterior crest which serve the origin of muscles. It is slightly bowed laterally as it passes over the origin of the levator pterygoideus muscle and the lateral surface of the cranial cavity. The dorsal tip, which lies against the lateral edge of the parietal, is flattened and held in place by the ligaments of origin of the pseudotemporalis superficialis muscle.

The upper one-third of the epipterygoid serves the origin of the pseudotemporalis superficialis muscle, which arises on its anterolateral and posterior surfaces. The ventral two-thirds serves the origin of the pseudotemporalis profundus muscle.

THE JAWS

The terminology of the bones of the lower jaw follows that of Cuvier (Versluys, 1936). Kingsley (1905) revised the terminology of the articular to conform with its derivation from membrane as well as from endochondral bone. All other elements of the jaws are of intramembranous origin.

The jaws (Figs. 28 and 29) are paired rami united in a syndesmosis anteriorly and articulating with the quadrate bones posteriorly. They bear teeth, serve the insertion of the adductor muscles, transmit the inferior alveolar nerve and internal mandibular artery, and house Meckel's cartilage. Each ramus is composed of six separate bones which form a tubular canal. The five posterior elements form a circular tube; their anterior ends project into, and are encircled by, the dentary bone.

The *articular, os articulare, os dermarticulare* (Kingsley, 1905) (Figs. 28, 29, and 50), is a dagger-shaped element with a posterior condylar part and a small thin anterior process. The condylar part contains a facet which articulates with the condyle of the quadrate. Surrounding this facet is a ridge for the attachment of the articular capsule, and along the posterolateral angle of the facet is a notch from which the lateral collateral ligament arises. Posterior to the condylar facet is a triangular retroarticular process. At the apex of the triangle is a tubercle for the insertion of the depressor mandibularis muscle, and along its lateral border is the tympanic crest to which the skin of the tympanum is attached. A small part of the intermandibularis posterior muscle inserts below the tympanic crest. At the medial angle of the base of the retroarticular process is a foramen which transmits the chorda tympani nerve and the posterior condylar artery. Extending mesially from the condylar part is a second triangle, the angular process. The retroarticular depression receives the insertion of the dorsal fibers of the pterygomandibularis muscle. The remaining dorsal, ventral, and angular surfaces receive the other fibers of the pterygomandibularis muscle.

The anterior process of the articular forms the floor and medial rim of the mandibular foramen. It is rounded dorsally and receives the insertion of the pterygomandibularis muscle posteriorly and the adductor mandibularis externus muscle anteriorly. It continues beneath the coronoid and forms part of the floor of the coronoid recess. Anteriorly its medial border is sutured to the splenial. The lateral surface of the anterior process is concave. Within this concavity lies Meckel's cartilage. On the dorsomedial wall of this concavity, opposite the anterior end of the mandibular foramen, is a small foramen which transmits the chorda tympani nerve and is the exit of a bony canal which traverses the entire length of the articular bone.

The *supra-angular, os supra-angulare* (Fig. 29), forms the lateral wall of the posterior third of the mandible and the lateral rim of the mandibular foramen and with the articular and angular bones completes the posterior part of Meckel's canal. Its dorsal border is rounded and serves the insertion of the adductor mandibularis externus muscle. The lateral surface, smooth and rounded, is the insertion of two muscles, the adductor mandibularis externus dorsally and the intermandibularis posterior ventrally. At its suture with the articular, below the condyle, is a posteriorly directed foramen, the posterior supra-angular foramen, and below the coronoid bone is an anteriorly directed anterior supra-angular foramen. These transmit cutaneous branches of the inferior alveolar nerve. The ventral border is at right angles to the lateral border and is depressed along its surface for the angular bone. The anterior process projects into Meckel's canal of the dentary bone.

The *angular, os angulare* (Fig. 29), is an elongate flattened bone, the posterior part of which forms the ventral surface of the jaw between the articular and supra-angular bones. Its anterior process extends into the dentary for approximately half of its length. At its mid-point is a small foramen, the posterior mylohyoid foramen (Fig. 28), which transmits the posterior mylohyoid nerve. Fibers of the mandibulohyoid I muscle arise from its ventral surface.

The *splenial, os operculare* (Fig. 28), a flat plate of bone on the medial side of the jaw, completes the medial wall of Meckel's canal. It articulates with the angular, articular, supra-angular, dentary, and coronoid bones. Two foramina pierce the splenial. Near its mid-point is the anterior mylohyoid foramen, transmitting the anterior mylohyoid nerve, and near its anterior end is a larger foramen for the lingual branch of the inferior alveolar nerve. It provides for the origin of the intermandibularis anterior profundus muscle.

The *dentary, os dentare* (Figs. 28 and 29), is a tubular bone bearing teeth along its dorsal border. It is rounded anteriorly, and its tip turns mesially to join its fellow in a syndesmosis. It is flattened posteriorly and extends dorsally as a ridge; its medial surface is recessed for the splenial. The dentary surrounds the anterior processes of the other bones of the jaw. Along the posterior border of the lateral surface is a groove for the coronoid bone. Farther anteriorly, five mental foramina pierce the dentary and transmit terminals of the inferior alveolar nerve to the skin which covers its lateral surface. The ventral border, smooth and rounded, provides origin for the anterior fibers of the mandibulohyoids I and III and the genioglossus muscle. At its anterior end is a large foramen, the continuation of Meckel's canal which transmits Meckel's cartilage. The medial surface is excavated dorsally (crista dentalis) to support approximately 32 pleurodont teeth. The internal part of the dentary is hollow (Meckel's canal) and is subdivided anteriorly into a ventral continuation housing Meckel's cartilage and a dorsal chamber housing the inferior alveolar nerve.

The *coronoid, os complementare* (Figs. 28 and 29), is a dorsally extending process which straddles the remaining bones of the jaw by three "feet." The two anterior "feet" straddle the dentary and suture to the dentary and supra-angular laterally and to the dentary, splenial, and articular bones medially. The posterior "foot" extends ventrally on the medial side of the jaw and forms the anterior rim of the mandibular foramen. The posterior, lateral, and apical surfaces of the coronoid receive the insertion of the adductor mandibularis externus and medius muscles and the bodenaponeurosis.

Meckel's cartilage is large and cylindrical; it originates on the articular bone and lies in the floor of Meckel's canal sheathed by dense perichondrium. Posteriorly, it lies on the medial side of the canal in the floor of the mandibular foramen. It decreases in size anteriorly, though it nearly fills the canal. Cephalad it pierces the anterior end of the dentary and terminates in the cutaneous tissue of the chin. The adductor posterior muscle inserts along the dorsal and lateral surfaces of the cartilage as far anterior as the anterior mandibular foramen. The inferior alveolar nerve and internal mandibular artery lie on its dorsal surface throughout most of its length.

THE JOINTS

The bony elements of the skull of *C. pectinata* are held together by a variety of articulations, most of which are sutures. Sutures of various kinds are found at all joints between bony elements except the frontoparietal, the paraoccipital-quadrate complex, the dorsal parieto-epipterygoid, and the occipito-parietal, which are syndesmoses. In addition, this lizard is specialized in having a kinetic skull. It therefore possesses three true diarthritic joints within the cranium in addition to the axial, the atlanto-occipital joint, and the mandibular joint.

The *basipterygoid joint* (Fig. 4), between the basipterygoid process and the pterygoid notch, is the largest and most important of the head, serving as the seat of motion between the occipital and maxillary segments. The basipterygoid condyles are elongate and laterally concave. Each condyle is covered on its ventral and lateral surfaces by a layer of thick fibrous cartilage which is wedge-shaped on the ventral border. The medial surface of the basipterygoid does not enter into the joint. The pterygoid notch is L-shaped, and both surfaces are covered by a thick layer of fibrous cartilage, shaped to receive the wedged cartilage of the basipterygoid process. The capsule, thicker and longer on the medial than on the lateral surface, attaches at the periphery of the articular cartilage. The joint is strengthened by the origin (on capsule) of the pterygomandibularis muscle medially and of the protractor pterygoideus laterally. There is no articular disc.

The osseous condyles are unequal in size, the basipterygoid processes being larger than the pterygoid notches. The wedge-shaped cartilage at the tip of the basipterygoid process facilitates the articulation. The basipterygoid processes diverge from each other at an angle of approximately 90°; the pterygoid notches diverge from each other at a somewhat lesser angle. The motion of the joint is essentially a sliding action, a condition which limits flexion of the maxillary segment on the occipital segment but allows extension. Because of the flexibility of the quadrate processes of the pterygoids, these bones are forced somewhat apart in flexion.

The *columellar joint* (Figs. 5 and 35), just lateral to the basipterygoid joint, is between the wedge-shaped, spheroidal ventral end of the epipterygoid and the elongate columellar fossa of the pterygoid. Both condylar surfaces are covered by a thin layer of fibrous cartilage. The joint capsule, attached to the border of the columellar fossa, forms a diaphragm around the epipterygoid and holds it in the fossa. The joint allows only slight anteroposterior and mediolateral motions. It is supported laterally by the pseudotemporalis profundus muscle.

The *pterygoquadrate joint* (Fig. 6) is a combined synovial and syndesmotic joint and permits only a slight amount of sliding motion. The articular surface, on the medial side of the quadrate, dorsal to the condyle, is concave and medially covered by cartilage; its lateral part is fibrous. The opposing surface of the quadrate process is fibrous posteriorly but it is smooth and covered by a small plaque of cartilage anteriorly. The capsule of the joint is thin and loose anteriorly, but posteriorly it is heavy and bound tightly to the bones. From this arrangement it is to be inferred that the tip of the quadrate process of the pterygoid is firmly attached to the quadrate bone by a fibrous union which serves as a pivot, and that the articular cavity anterior to this allows a small amount of dorsoventral sliding motion.

The *atlanto-occipital articulation* (considered from its osteological components by Gadow, 1933) is a joint of limited motion between the tripartite occipital condyle and the atlas. The occipital condyle is completely covered with articular cartilage and forms a semilunar, convex articular surface (Fig. 6). The articular surface of the atlas is complex, combining the atlas, the odontoid process of the axis, and an articular disc. The atlas is composed of three elements, a median basiventral and two lateral basidorsals, forming, ventral to the neural canal, a U-shaped rim which articulates with the periphery of the occipital condyle. The odontoid process of the axis projects through the recess of this articular rim and attaches to the dorsal recess of the occipital condyle by means of an apical ligament, forming there an uninterrupted floor for the neural canal. The odontoid process is held in place dorsally by a transverse ligament. Between the ventral surface of the odontoid process and the articular rim of the atlas is a space filled by a semilunar, fibrous articular disc which articulates posteriorly with the body of the axis and anteriorly with the posterior surface of the occipital condyle. The thin upper limbs of the disc are attached dorsally to the apical ligament of the odontoid, and its thick, ventral part is attached to the basiventral of the atlas. The disc fits perfectly within the arc of the elements of the atlas. Its thin edges extend onto both the anterior and the posterior surfaces of the atlas, but do not attach to the transverse ligament. These attachments allow continuity between the articular cavities of the occipitoatlantal and atlantoaxial joints.

Since the odontoid process actually lies in the dorsal recess of the occipital condyle, the apical ligament is extremely short. It is fibroelastic, and its fibers converge toward an apical insertion on the basioccipital part of the condyle.

The basidorsals of the atlas are connected by a strong fibrotendinous band, the transverse ligament of the atlas, which divides the canal of the atlas into a dorsal and a ventral part for the spinal cord and the odontoid process, respectively. The ventral surface of the transverse ligament articulates with the dorsal surface of the odontoid. The joint cavity of this space is continuous with the joint cavity of the atlantoaxial joint.

The dura of the spinal column is fused to the dorsal surface of the ligament of the atlas and the apical ligament to the odontoid.

Connecting the arches of the atlas with the margins of the foramen magnum is a continuous articular capsule, the atlanto-occipital ligament. It is essentially a continuous ligament, but it may be divided into anterior and posterior sections by the structures which pass through its lateral surfaces — the vertebral artery (ant. spinal, 1.), the first spinal nerve, and the posterior cerebral vein (Fig. 42).

The *mandibular joint* is formed by the articulation of the head of the quadrate with the articular fossa of the articular bone; it is a spiral type synovial joint allowing great freedom of motion. The condyle of the quadrate bears medially a large convex surface and laterally a small convex surface with a posterolaterally directed concave groove between the two. The reciprocal surface of the articular bone is similar, except that the lateral condyle is generally the larger. The condylar surfaces are covered with a thick layer of white fibrous cartilage which does not appreciably enlarge the area. The axis of the joint is horizontal. In the action of opening the mouth the direction of the intercondylar grooves causes lateral motion of the articular as it glides across the posterior part of the quadrate. As a result, the posterior angles of the mandible are spread.

Surrounding the joint is a loose synovial-lined capsule, the attachment of which follows the immediate periphery of the two articular surfaces of both bones. The capsule, heavier on the medial side, has fibers that extend anteroventrally. This joint is strengthened by medial and lateral collateral ligaments. The lateral collateral ligament (Fig. 31) is a heavy discrete bundle of fibers extending from a notch at the lower border of the auricular ridge, above the condyle of the quadrate, to a notch in the articular bone, just posterolateral to the condylar surface.

The medial collateral ligament is not so heavy nor so distinct as the lateral. It arises as the aponeurotic thickening from the ventral border of the quadrate process of the pterygoid and the medial surface of the pterygomandibularis muscle. From the fan-shaped thickening the fibers converge toward the quadrate to insert just above the center of the medial part of the condyle.

THE MUSCLES

Literature on reptilian musculature is extensive and diverse. Though individual groups of lacertilian head muscles, such as those of the viscera, the jaw, the tongue, and the eye, have been the subjects of many papers, there are few complete accounts of the musculature of any one form; however, Osawa's (1898) account of *Sphenodon* a rhyncocephalian, is very extensive. Lakjer (1926) and Edgeworth (1935) brought the literature up to date, with complete listings of synonyms of muscles. The more recent major contributions to the descriptive, developmental, and phylogenetic studies of the head musculature are those by Brock (1938), Lubosch (1933, 1938), and Säve-Söderbergh (1945). Descriptive aids have been drawn collectively from the selected bibliography.

In accordance with the suggestions of the most recent workers in the field that descriptive terms are more practical than are terms implying homology of muscles with those of other forms, the terminology here employed is based either on function and position or on origin and insertion.

The muscles may be divided, developmentally, into myotome and lateral plate derivatives of specific segments (Brock, 1938), or into functional or regional groups. Since this paper is neither a phylogenetic nor an ontogenetic study, the regional method will be used. The major cranial muscle masses of the head may be divided into the mandibular, the hyoid and branchial, the orbital and the axial. These are primarily also natural ontogenetic divisions.

The mandibular musculature, derived from the mandibular segment and innervated by the trigeminal nerve, has been the subject of a number of recent works, primarily developmental, in an attempt to ascertain phylogenetic homologies: L. A. Adams (1919), Lakjer (1926), Edgeworth (1935), Brock (1938), and Säve-Söderbergh (1945).

Functionally, the mandibular musculature may be divided into three groups: (1) the adductor mandibulae group, a complex muscle mass serving to close the jaw; (2) a constrictor dorsalis group, characteristic of lower forms (e.g. fishes) with a palatoquadrate bar and of reptiles with a kinetic skull, functioning to elevate the maxillary segment; and (3) a ventral intermandibularis group, extending between the mandibular rami. The adductor mandibulae group and the constrictor dorsalis group are found within the temporal fossae, deriving their attachments from the surrounding elements. The first group is superficial to the latter.

Temporal Region

Lying superficial to the musculature of the infratemporal fossa is a thick integument evenly covered by scales and bearing sparsely distributed "tactile organs." Peripherally it is attached to all the bones surrounding the infratemporal fossa, but ventral to them it is free. Beneath the skin is a dense, triangular, aponeurotic temporal fascia, which arises from the condyle of the quadrate bone and from the articular and supra-angular bones of the lower jaw. Its fibers fan out and attach to the inferior border of the postorbital bone. Posteriorly, it is free, but anteriorly it is fused to the skin, and its ventral border forms a thickened condensation, the quadratomaxillary ligament (Lakjer, 1926), which completes the ventral border of the infratemporal fossa.

The ventral border of the skin of the infratemporal area turns under this ligament, is covered by mucous membrane, and forms a recess, the *mundplatt* (Fig. 30), which is the angle of the mouth, and continues anteriorly as the coronoid recess. The medial layer of the *mundplatt* continues ventrally as the skin of the lower jaw. Dorsally, the *mundplatt* receives the insertion of the levator angularis oris muscle. The skin of the infratemporal area and *mundplatt* is innervated by several branches of the maxillary (1) ramus which passes beneath the postorbital bone, by the first anterior branch of the mandibular ramus, and by branches from the posterior inferior labial and posterior supra-angular nerves.

The integument covering the supratemporal fossa is thick, dome-shaped externally, evenly covered with rather large scales, and bears a uniform distribution of "tactile organs." It is firmly attached to the parietal bone anteriorly and to the postorbital and squamosal bones laterally. The skin does not attach to the parietal crest; the right and left supratemporal fossae are separated by only a thin fascial attachment; the skin is loosely attached to the posterior border of the parietal bone. Cutaneous innervation is from a branch of maxillary (1).

Adductor Mandibulae Group

M. adductor mandibulae, or jaw muscle, is divided into three major parts, according to its relations to the three rami of the trigeminal nerve, (Luther, 1914; Säve-Söderbergh, 1945). The adductor mandibularis externus lies lateral to the mandibular and maxillary divisions, the adductor mandibularis internus lies mesial to the maxillary but lateral to the profundus division, and the adductor mandibularis posterior lies posterior or mesial to the mandibular division of the trigeminal nerve.

The *bodenaponeurosis* (Fig. 32) is a multipenniform common tendon of insertion of the adductor mandibularis externus and the pseudotemporalis muscle masses (adductor mandibularis internus). It lies along the posterior border of the coronoid bone and receives a central tendon from the superficial part of the adductor mandibularis, a tendinous lamina from the medial part, and a very long central tendon from the profundus part. Each of these parts may insert by an additional outer aponeurosis. The pseudotemporalis group inserts by means of a tendinous lamina along the medial surface.

Adductor mandibularis externus. — This is a complex muscle mass poorly separated into three parts: superficialis, medius, and profundus. The mass has three distinct heads, but essentially a single body, and inserts by a common tendon, the bodenaponeurosis, onto the posterior and lateral surfaces of the coronoid and the lateral and dorsal surfaces of the articular. The superficialis part, however, is made up of two relatively distinct muscles, the levator angularis oris and the superficialis.

M. levator angularis oris (Fig. 30) covers nearly all of the infratemporal fossa. It arises from the dorsal half of the tympanic crest of the quadrate bone and from the inferior borders of the squamosal and postorbital bones and continues to the point where the postorbital joins the jugal. Some of its fibers also arise from the superficial infratemporal fascia and from the aponeurosis of origin of the muscle deep to it. It extends anteroventrally and inserts into the dorsomedial surface of the *mundplatt,* extending anteriorly to the level of the coronoid process. It lies deep to the superficial infratemporal fascia and lateral to the superficialis proper. Its innervation is by two or three branches of the trigeminal nerve which pierce the superficialis proper and enter the deep surface of the levator angularis oris.

M. adductor mandibularis externus superficialis (Fig. 31) is the most lateral part of the adductor mandibularis externus to insert into the bodenaponeurosis. It lies mesial to the levator angularis oris and the *mundplatt* and lateral to the medius part of the adductor mandibularis externus, but is not well separated from the latter. It arises from the lateral half of the anterior surface, the entire dorsal surface, the tympanic crest of the quadrate, the inferior and mesial surfaces of the squamosal by a tendinous sheet, and from the inferior, medial, and dorsal borders of the postorbital bone, its most anterior fibers coming only from the dorsal border of the postorbital. Its fibers extend anteroventrally. The lateral fibers insert into the mandible on the lateral surface of the coronoid and the entire lateral surface of the supra-angular, covering its anterior supra-angular foramen. The medial fibers insert on the dorsal border of the entire supra-angular, the posterior edge of the coronoid, and the lateral and posterior surfaces of the bodenaponeurosis. The muscle is innervated by several branches of the trigeminal nerve which enter its mesial surface from the medius part. Numerous other nerves enter the superficial part of the externus superficialis. The first branch of the mandibular division passes around the anterior part of its insertion and gives small branches to it. These probably are sensory since the muscle is otherwise well supplied by deep motor branches. It also receives some superficial twigs of the posterior supra-angular nerve and a deep branch of the anterior supra-angular nerve.

M. adductor mandibularis externus medius (Figs. 32 and 40) lies mesial to the superficialis part, dorsal to the parietal bone and profundus part, and posterolateral to the pseudotemporalis muscles. It arises from the mesial side of the posterior half of the squamosal, the posterodorsolateral surface of the parietal, the lateral surface of the posterior half of the supratemporal, and the dorsal surface and mesial half of the anterior surface of the quadrate. The temporal artery pierces the origin of this part and lies on its dorsal surface. The fibers are continuous laterally with the superficialis part and ventrally with the profundus part. They extend anteroventrad and insert into the dorsomesial surface of the supra-angular, the posterior border of the coronoid, and the posterior edge of the bodenaponeurosis. The innervation is by a branch of the trigeminal nerve which is an intramuscular continuation of the nerve entering the profundus head.

M. adductor mandibularis externus profundus (Figs. 33 and 41) is a group of fibers lying lateral to the pseudotemporalis superficialis muscle and the maxillary and mandibular divisions of the trigeminal, the semilunar ganglion, and the cranial cavity proper. In adduction this muscle lies ventral to the parietal and dorsal to the obliquus capitis major muscle and the paraoccipital process of the exoccipital. It arises from the ventral surface of the posterolateral tip of the parietal, the mesial surface of the supratemporal, and the dorsolateral surface of the posterior process of the prootic, presenting two fairly well-defined heads. The fibers of the dorsal head extend anteroventrally and insert by the bodenaponeurosis into the posterior surface of the coronoid process. The more medial fibers, arising from the posterior process of the prootic, insert into the base of the coronoid process. Innervation is by the third branch of the mandibular division of the trigeminal nerve.

Adductor mandibularis internus group. — This group contains two well-defined muscle masses, the pseudotemporalis and the pterygomandibularis. They have divergent insertions; their origins, however, are in the same general area. The pseudotemporalis has two parts, superficialis and profundus, which in other species may be coextensive.

M. pseudotemporalis superficialis (Figs. 33 and 40) is a heavy muscle mass arising from the major part of the dorsal surface of the parietal bone, the lateral border of the anterior half of the parietal, the lateral surface of the dorsal one-third of the epipterygoid, and the lateral surface of the alar process of the prootic bone, dorsal to the trigeminal nerve and foramen. It is medial and anterior to the adductor mandibularis externus muscle, dorsal to the parietal bone, and anterior and lateral to the pseudotemporalis profundus muscle, the dorsal part of the epipterygoid, and the cranial cavity proper. The fibers extend ventrally and insert in the medial surface of the bodenaponeurosis and the posteromedial border of the coronoid bone. At the parietal origin it is crossed dorsally by the temporal artery and laterally by the maxillary division of the trigeminal and the trigeminal branch to the coronoid recess. The innervation is by the first branch of the mandibular division of the trigeminal nerve.

M. pseudotemporalis profundus (Fig. 34) is a triangular muscle lying lateral to the epipterygoid and the levator pterygoideus muscle, lateral and posterior to the pterygoid bone, anterior to the mandibular division of the trigeminal nerve, and posteromedial to the pseudotemporalis superficialis muscle. Arising from the anterior, lateral, and posterior surfaces of the ventral two-thirds of the epipterygoid bone, its fibers fan out ventrally and posteriorly to insert on the posterior surface of the coronoid bone and on the anterior half of the dorsal border of the articular bone, mesial to the mandibular foramen. In some specimens the profundus part is fused to the superficial part near its insertion. It is innervated by the first branch of the mandibular division of the trigeminal nerve.

M. pterygomandibularis (Figs. 32, 35, 37, and 39) is the largest muscle in the head and forms the greater part of the adductor musculature of the jaw. It has been called "pterygoid" by Versluys (1904) in an attempt to homologize it with the mammalian pterygoids. Since more recent investigators have differed as to homologies (Brock, 1938; Luther, 1914; and Lubosch, 1938), descriptive terms follow the usage of Bradley (1903).

The muscle has a small head and tail, but expands into a large body which lies just lateral to the oral membrane, between the mandibular rami. It lies on the ventromesial surface of the mandible, lateral to the pharynx, and is covered ventrally by the mandibulohyoideus 1 and 2 muscles and the intermandibularis posterior. In females and young adults the muscle is small; however, in older males the muscle is greatly enlarged and expands toward the mid-line, where the bodies nearly meet, constricting the pharynx dorsally (Fig. 59). The hypertrophy of this muscle, in adult males, causes a shift in the relations of the posterior structures in the throat.

The pterygomandibularis muscle originates tendinously from the ventral tip of the ectopterygoid and the ventral border of the transverse process of the pterygoid, and fleshily from the tendon along the ventrolateral border of the quadrate process of the pterygoid bone; some fibers also arise from the basipterygoid process of the basisphenoid and from the joint capsule separating the two bones. The fibers arising on the ectopterygoid and the transverse process of the pterygoid and the tendinous sheath expand to cover the ventral surface of the mandible; they insert into the entire ventral surface of the articular bone, including the retroarticular and the inflected angular processes. The more mesial fibers, arising from the ventrolateral surface of the quadrate process of the pterygoid, are smaller; they extend ventrally and insert on the dorsomedial surface of the articular bone, mesial to the mandibular foramen, covering the entire dorsal surface of the articular bone. Some of the anterior fibers of the mesial group insert into a central tendon, which in turn inserts into the tip of the angular process of the articular. The most posterior fibers run from the tip of the quadrate process of the pterygoid bone to the tip of the retroarticular process of the articular, and aid in depressing the mandible. This muscle exerts several forces in adducting the jaw and in closing the mouth. The long lateral fibers lie across the ventral border of the mandible and use the articular bone as a fulcrum; the posterior mesial fibers pull directly on the mandible; and the anterior mesial fibers pull directly on the angular process; all adduct the jaw.

The innervation is by a branch of the trigeminal nerve which descends with, and splits from, the mandibular division. This nerve also gives a small branch to the posterior border of the pseudotemporalis profundus muscle.

Adductor mandibularis posterior (Fig. 34).—This is a single muscle lying lateral to the pterygomandibularis muscle, mesial to the adductor mandibularis externus muscle, and posterior and ventral to the mandibular division of the trigeminal nerve. It arises from the medial crest of the quadrate bone, between the posterior process of the prootic and the quadrate process of the pterygoid, on the mesial and lateral surfaces of a centrally located fan-shaped aponeurosis which extends to Meckel's cartilage. Some of its fibers may originate on the posterior process of the prootic bone.

The fibers of this muscle extend anteroventrally to the mandible. Some of the medial fibers insert with the fibers of the pseudotemporalis profundus muscle on the dorsal surface of the articular bone, mesial to Meckel's fossa; the other fibers extend within Meckel's fossa and insert on the dorsal and lateral surfaces of Meckel's cartilage, as far anteriorly as the anterior mylohyoid foramen. The muscle is innervated by a branch of the posterior supra-angular nerve.

Constrictor Dorsalis Group

The second group of trigeminal musclulature, the constrictor dorsalis group, does not insert into the jaws. It arises from the cranium and inserts into the pterygoid bone or the maxillary segment. Its primary function is elevation and protraction of the maxillary segment. A third muscle of this group has an accessory group of fibers inserting into the lower eyelid.

M. levator pterygoideus (Figs. 34 and 35) is situated mesial to the epipterygoid bone and the pseudotemporalis profundus muscle, lateral to the prootic membrane, the pila antotica, the origin of the levator bulbi muscle, the profundus division of the trigeminal nerve, and the protractor pterygoideus muscle, and anterior to the mandibular division of the trigeminal nerve. It is a flat ribbon-like muscle arising from the ventrolateral border of the parietal bone and the dorsolateral surface of the prootic membrane, mesial to the dorsal end of the epipterygoid bone, by an aponeurosis which extends approximately half the length of the muscle. The muscle fibers extend slightly posteroventrally and insert with the fibers of the protractor pterygoideus into the dorsal border of the pterygoid bone, medial to the columellar fossa and as far posteriorly as the mandibular division of the trigeminal nerve. Some of its fibers may insert on the ventral end of the epipterygoid bone. Its innervation is by an independent motor branch of the trigeminal nerve entering its mesial surface.

M. protractor pterygoideus (Fig. 35) is situated mesial to the levator pterygoideus muscle and the mandibular division of the trigeminal nerve, ventral to the profundus division of the trigeminal nerve, and lateral to the prootic and basisphenoid bones and the internal jugular vein. It forms the lateral wall of the tympanic cavity. It is a large fan-shaped muscle arising from the lateral surface of the anterior inferior process of the prootic, the lateral surface of the alar process of the basisphenoid, and the posterior border of a tendon which extends from the proximal end of the pila antotica to the cartilage covering the anterior tip of the basipterygoid process just above the condyle. The tendinous origin leaves a gap between the muscle and the basipterygoid process through which the internal jugular vein passes to join the communicating vein.

The protractor pterygoideus fibers arising from the prootic bone extend ventrally and insert into the dorsal border of the pterygoid bone, from the level of the columellar fossa to the level of the quadrate bone. Some of the anterior fibers insert with those of the levator pterygoideus muscle, whereas the fibers arising from the tendon and the dorsolateral surface of the basipterygoid process insert along the entire length of the mesial surface of the quadrate process of the pterygoid, giving this muscle a combined action of elevation and protraction.

Innervation is by a separate motor branch of the trigeminal nerve which enters the muscle on its lateral surface and extends for some distance within the muscle before ramifying.

M. levator bulbi (Figs. 35 and 53) is situated lateral to the profundus division of the trigeminal nerve and the distal part of the brain case, ventral to the eye, and anteromesial to the pseudotemporalis muscles. It consists of two parts, a ventralis and a dorsalis. The ventralis part arises from the pila antotica, at its junction with the supratrigeminal ligament, by a ligament which extends anteroventrally to a level posteroventral and mesial to the eye. The muscle fibers arise along the entire ventral side of this ligament and insert into the dorsal surface of the membrane of the pyriform recess.

The dorsalis part of the muscle, *M. depressor palpebrae inferioris*, arises from lateral, dorsal, and mesial surfaces of the distal end of the same ligament which gives origin to the ventralis part. In addition, there is a tendon which arises from the dorsal surface of the trabecular cartilage, in front of the basisphenoid bone, and inserts into the distal end of the common tendinous origin (Fig. 53). The muscle fibers fan out beneath the eye. Continuing laterally, they insert into the orbital fascia of the lower lid. The most mesial fibers extend anteriorly and insert by a tendon into the dorsomesial border of the palatine process of the pterygoid bone. Functionally these fibers serve as an origin, insuring a horizontal rather than a posteromesial pull during contraction.

The innervation of the muscle is by an independent motor branch of the trigeminal. Individual branches enter along the posterior surfaces of each of its two parts.

Throat

The integument covering the throat is of uniform thickness. It is loosely attached to the musculature and to the lateral surface of the lower jaw by a dense fascia, and ligamentously attached to the posterior tip of the supra-angular bone. In the mental region an extensive development of fibrous connective tissue covers the anterior end of the mandibular rami. A raphe formed by the intermandibularis anterior (superficialis and profundus) muscles and by the second mandibulohyoideus muscle attaches to the skin along the anterior one-third of the mid-line. Small quantities of fat and connective tissue are present in the collar region. Near the posterior end of the jaws there is a transverse fold of skin, the throat fan, which is well developed in the males. Its posterior leaf is firmly attached to the fascia of the omohyoideus muscle at the anterior end of the episternum.

The scales of the throat, except the infralabials, are generally small and of uniform size. The scales of the posterior surface of the throat fan are generally smaller than those of the remainder of the throat.

Tactile organs are found extensively on the infralabials, sublabials, gulars, and postmentals. None is present on the mental. Sensory innervation of the skin of the throat is by cutaneous branches of the posterior and anterior mylohyoid and the third cervical nerve. In addition, sensory, labial branches of the inferior alveolar nerve innervate the skin covering the lateral surface of the jaw.

Within the integument the throat is almost entirely muscular, combining the musculature of the hyoid and branchial segments, as well as the third group of the trigeminal musculature (mandibular segment). This division, originally segmental, falls into distinct functional groups, as the constrictors of the neck and the hyoid and tongue musculature.

Constrictors of Neck and Throat

The first descriptive account of throat musculature is on *Iguana tuberculata* (Mivart, 1867). It is by no means a complete account. Other decriptions are found in Bolk and others (1938) and Willard (1915). Kesteven (1944) and Lubosch (1933) have considered them comparatively, and Camp (1923) used the superficial musculature as one basis for his classification of lizards.

M. constrictor colli, sphincter colli (Figs. 30 and 36) is a thin, narrow muscle, the pair encircling the cervical region immediately posterior to the retroarticular process of the mandible. The muscle is superficial, lying immediately beneath the skin of the neck fan. It is covered by extensive fat pads and is overlaid, at its mid-point, by the external jugular vein. The muscle lies posterior to the depressor mandibularis and the intermandibularis muscles. It is superficial to the posterior fibers of the depressor mandibularis and episternocleidomastoideus muscles dorsally, and to the omohyoideus and sternohyoideus muscles ventrally. Its fibers originate from the superficial dorsal fascia at the dorsolateral angle of the neck and run parallel and dorsoventrad to insert into an aponeurosis which is continuous with its partner across the ventral mid-line. This aponeurosis lies dorsal to the posterior ends of the second ceratobranchials, extends dorsal to the posterior border of the intermandibularis muscle, and becomes continuous with the deep fascia of the intermandibularis which is attached along the posterior border of the first ceratobranchial and to the superficial fascia of the omohyoideus muscle. In old animals the anterior border of this aponeurosis may be thickened and forms a narrow tendon which runs anteriorly dorsal to the intermandibularis muscle to insert into the first ceratobranchial.

The constrictor colli is comparatively large in young adults and females, but in large adult males it is small and somewhat constricted at its mid-point, in correlation with the hyperdevelopment of the muscles of the mandible. It is innervated by a small branch of the facial (VII) nerve, which runs beneath the depressor mandibularis muscle and enters the deep surface of the constrictor colli at a point on a line with the inferior border of the angular process. A large sensory branch of the third cervical nerve which perforates the episternocleidomastoideus muscle also enters the deep surface of the constrictor colli near the same point.

M. depressor mandibularis (Figs. 30 and 31) is superficial, though the constrictor colli overlies its posterior part. There is no indication in any specimen that these two muscles are continuous. It lies on the hyomandibular branch of the facial nerve and the episternocleidomastoideus muscle, and ventral to these it overlies the posterior extension of the auditory capsule and the distal ends of the ceratohyal and the first ceratobranchial.

The depressor mandibularis can be divided into three parts. In *Ctenosaura pectinata* these are separable, primarily by their insertions; their bodies connot be separated into three distinct masses as they can be in some amphibians and reptiles.

The muscle originates continuously along the lateral half of the parietal crest, beginning at the squamosal bone and moving mesially along the parietal bone and then to the superficial fascia from the dorsolateral angle of the neck to approximately the posterior edge of the constrictor colli muscle. All of the fibers converge toward the retroarticular process of the lower jaw where they insert. The anterior group of fibers arises from the parietal and the anterior third of the superficial cervical fascia and descends in an almost perpendicular line, forming the thickened posterior border of the external auditory meatus. The next bundle of fibers to originate from the dorsolateral fascia descends to insert on the retroarticular process in a bundle just lateral to the first bundle. The third group of fibers, the cervicomandibularis muscle when separate, originates on the superficial fascia, deep to the origin of the constrictor colli, and descends anterolaterally to insert in the superficial fascia of the intermandibularis muscle and in the skin, the area of insertion covering the posterior one-fourth of the pterygomandibularis.

The depressor mandibularis muscle is innervated by branches of the facial nerve, which leave the skull at the level of the extracolumella and distribute mesially to all parts of the muscle. A sensory branch of the third cervical nerve, which pierces the episternocleidomastoideus muscle, also enters, superficially, the posterior edge of the depressor mandibularis.

M. episternocleidomastoideus (Figs. 31 and 32) is a ribbon-shaped muscle which lies superficial to the longissimus capitis muscle, the internal jugular vein, the tympanic cavity, and the omohyoideus muscle and deep to the depressor mandibularis and constrictor colli muscles and the distal ends of the first ceratobranchial and the ceratohyal bone. It has a superficial origin, from the superficial fascia covering the pectoral muscles, the lateral tip of the transverse process of the interclavicle, and a small part of the lateral surface of the angle of the clavicle. Its fibers run anterodorsally, anterior to the trapezius muscle and deep to the constrictor colli muscle and insert, deep to the origin of the depressor mandibularis, upon the lateral half of the parietal crest and the posterior surface of the paraoccipital process of the exoccipital bone and on the dorsal fascia of the neck. It is innervated by the externus branch of the vagus nerve which passes lateral to the internal jugular vein and then enters the deep surface of the muscle. It also receives several small twigs from the second and third spinal nerves which pierce it to innervate the remainder of the collar region.

Intermandibularis. — The intermandibularis (mylohyoideus, third part of the trigeminal musculature) is a superficial thin sheet lying anterior to the constrictor colli muscle and superficial to the sternohyoideus and omohyoideus and part of the first mandibulohyoid muscles, covered only by the skin and a part of the depressor mandibularis. It extends between the two mandibular rami and covers all of the other throat musculature. Because of its specializations and the divergent pattern of its fibers, it is divided into two parts, an anterior and a posterior.

M. intermandibularis posterior consists of two groups of muscle fibers, an anterior and a posterior. The anterior group, the intermandibularis posterior proper (Figs. 30 and 36) is a broad, thin muscle (one fiber in thickness) covering the posterior half of the ventral surface of the throat. Its origin is on the lateral surface of the mandible, beginning at the midpoint of the retroarticular process and extending anteriorly across the ventral surface of the supra-angular and posterior one-third of the angular. Its fibers extend ventrad parallel to each other and insert into their partners ventral to the second ceratobranchials. The anterior one-fourth of its fibers form a thickened band which, near the mid-line, turns anteriorly and inserts into a mid-line raphe which is continuous with the insertion of the intermandibularis anterior. In older individuals the muscle is attached by its deep fascia to the first ceratobranchial bone. It is innervated by the posterior mylohyoid nerve of the trigeminal which emerges from the jaw through the posterior mylohyoid foramen in the angular bone and passes through the origin of the first and third mandibulohyoids to enter the muscle along its anterior border.

The posterior fiber group of the intermandibularis posterior (Fig. 36) arises in the deep fascia and fibers of the depressor mandibularis and on the superior and posterior surfaces of the retroarticular process of the mandible. It continues ventrad to the mid-line, paralleling the fibers of the constrictor colli as a narrow thickened band of muscle which inserts into its partner and forms with it a continuous transverse band of muscle ventral to the second ceratobranchials. The superficial and deep fasciae of this group are continuous with those of the intermandibularis posterior proper, but are separated from them by an interval of fascia which contains no muscle fibers. This interval is present in immature and female animals and is exaggerated in adult males with extensively developed pterygomandibularis muscles. In old males the muscle may be difficult to distinguish. The posterior group is innervated by a branch of the facial nerve which enters its posterior border. Another branch may enter it along its posterior border near the mid-line. There is no indication that any branch of the trigeminal nerve innervates it. By innervation and origin this group appears to be a continuation of the depressor mandibularis muscle, but positionally and functionally it is part of the intermandibularis posterior.

M. intermandibularis anterior is superficial to all the throat musculature and is deep to the skin. It also is divided into two groups, one deep and the other superficial.

The fibers of the deep group (Figs. 36 and 37) originate on the medial surface of the coronoid and splenial bones on an arc, the dorsal end of which continues anteriorly along a tendon extending with the crista dentalis from the coronoid to the mandibular symphysis. The muscle fibers extend ventrally and then turn transversely on the ventral surface of the throat to join their partners at the mid-line, interdigitating in approximately five intervals with the posteriorly directed fibers of the first mandibulohyoideus muscle. The anterior fibers of the group extend medially and insert in the mid-line raphe. In addition, there is a small bundle of fibers which extends anteriorly from the tendinous origin, paralleling the border of the crista dentalis, takes additional origin from the oral membrane, and inserts into the dorsomesial part of the sublingual gland.

The fibers of the superficial group (Fig. 36), composing a small, narrow muscle, originate on the oral membrane and on those anteriorly directed fibers of the intermandibularis anterior profundus which lie within and mesial to the sublingual gland. From these origins they run posteromedially along the posterior border of the genioglossus muscle and insert into the mid-line raphe, overlying the anterior fibers of the profundus part.

The intermandibularis anterior is innervated by the anterior mylohyoid nerve, a motor branch of the trigeminal, which leaves the anterior mylohyoid foramen and enters the muscle superficially.

Hyoid Musculature

The hyoid musculature functions primarily in respiration, in propulsion and retraction of the tongue, and in swallowing. It is divided into two groups, centered around the hyoid apparatus. The anterior group is composed of the first, second, and third mandibulohyoideus muscles which depress the hyoid, pulling it craniad and ventrad and increasing the size of the oral cavity. The posterior group consists of the omohyoideus and sternohyoideus muscles which retract the hyoid. Their functions in closing the oral cavity or retracting the hyoid apparatus are aided by the ventral constrictors or the intermandibularis muscles. Between the ceratohyal and the first ceratobranchial bone of the hyoid apparatus is a single muscle, the branchiohyoideus, which also aids in both functions. The attachment of the hyoglossus muscle to the anterior border of the hyoid apparatus enables it to aid in the depression of the hyoid apparatus. Correspondingly, the hyoid musculature aids in the propulsion and retraction of the tongue.

M. mandibulohyoideus I (Fig. 37) is broad, thin, and flat; it covers the ventral surface of the pterygomandibularis muscle. It is overlaid by the two parts of the intermandibularis posterior muscle and partly so by the interdigitating muscle fibers of the intermandibularis anterior profundus. The glossopharyngeal and hypoglossal nerves, the hyoglossus artery, and the third mandibulohyoideus and pterygomandibularis muscles lie deep to it, and the posterior mylohyoid nerve pierces it near its origin. The first mandibulohyoideus arises on the ventromesial border of the mandible (dentary), beginning at approximately the level of the inferior alveolar foramen and extending to the posterior end of the dentary or the posterior mylohyoid foramen, where its origin is limited by the mass of the pterygomandibularis. Its fibers interdigitate with the fibers of origin of the intermandibularis anterior profundus and run posteromesially, inserting along the lateral border of the first ceratobranchial bone from its anterior end to the point where the hypoglossal nerve crosses the first ceratobranchial. In old adults the lateral border is especially hard to distinguish because the muscle is thinned into a fascia-like aponeurosis which covers the lateral part of the pterygomandibularis muscle as far laterally as the mandible.

The muscle is supplied from its dorsal or deep surface by one or two branches of the hypoglossal nerve which runs to the tongue musculature deep to the first mandibulohyoideus muscle.

M. mandibulohyoideus II (Fig. 38) is a small paired muscle lying along the mid-line, dorsal to the intermandibularis anterior profundus and ventral to the junction of the medial parts of the genioglossus and the hyoglossus muscles. The pair arise together from the skin of the throat along the anterior mid-line raphe, which may extend to the mandibular symphysis as a small thin ligament between the origins of the genioglossus muscles. The fibers of the muscle run posteriorly, paralleling the hypohyal, and diverge laterally around the body of the hyoid apparatus to insert into the proximal end of the anterior border of the first ceratobranchial bone and the capsule of the first ceratobranchial joint. A small branch of the hypoglossal nerve leaves the anterior edge of the first mandibulohyoideus and enters the posterolateral border of this muscle.

M. mandibulohyoideus III (Fig. 38) is a thick, narrow muscle lying dorsal to the first mandibulohyoideus muscle, ventral to the pterygomandibularis muscle, and lateral to the ceratohyal. It arises from a short origin along the ventromedial border of the mandible, on the dentary and angular bones, between the anterior and the posterior mylohyoid foramina, and dorsal to the origin of the first mandibulohyoideus muscle. The anterior fibers of origin interdigitate with the fibers of the intermandibularis anterior profundus muscle, and the posterior fibers overlie the posterior mylohyoid foramen. Its fibers pass posteriorly between the hyoglossus and the mesial surface of the pterygomandibularis muscles and insert into a short segment of the lateral border of the ceratohyal bone at approximately its mid-point. It is innervated by a branch of the hypoglossal nerve which crosses the ceratohyal bone and enters the mid-ventral surface of the muscle.

M. omohyoideus (Fig. 37) is a thick flat muscle lying along the midline on both sides of the second ceratobranchial. Ventral to it is the intermandibularis posterior group and the constrictor colli muscle and lateral to it, the episternocleidomastoideus. The first spinal nerve and the sternohyoid muscle lie deep to it. It has two points of origin, a mesial and a lateral, separated by the origin of the episternocleidomastoideus muscle. The mesial group of fibers arises from the lateral tip of the transverse process of the interclavicle with the fibers of origin of the episternocleidomastoideus. The lateral group of fibers arises from the lateral half of the anterolateral surface of the clavicle and the anterior border of the suprascapula. The two groups become continuous at their insertion which is along the posterior edge of the first ceratobranchial bone, from the crossing point of the hypoglossal nerve to the proximal end of the second ceratobranchial.

A branch of the first spinal nerve runs dorsal or deep to the lateral border of the muscle and gives off branches to both the omohyoideus and the sternohyoideus muscles. In old adults the muscle may be folded between the two ceratobranchials.

M. sternohyoideus (Fig. 38) is a thick, flat, triangular muscle covered ventrally by the omohyoideus muscle and the first spinal nerve. On its dorsal surface are the thyroid gland, trachea, and pharynx; anterior to it is the pterygomandibularis, and posterior to it is the origin of the pectoral muscles. It arises tendinously from the mid-point of the interclavicle, between the origins of the pectoral muscles, and fans out anterolaterally to insert mostly into the posterior border of the first ceratobranchial bone dorsal to the insertion of the omohyoid muscle. This insertion extends from the proximal end of the first ceratobranchial bone to the point where the hypoglossal nerve crosses that bone. Some of its mesial fibers, which seem to be continuous with the medial fibers of the omohyoid muscle, insert into the distal part of the second ceratobranchial. It is innervated by the first spinal nerve which passes around its lateral border to lie on its ventral surface.

Sectioned specimens demonstrate that the omohyoideus and the sternohyoideus are distinct muscles, with the fibers of one running obliquely to the other. Mesially, however, the fibers of the two muscles appear to be continuous. In young adults the two muscle groups separate readily, but in old adults the fibers along their mesial borders seem to intermingle more completely and become somewhat separable by their thickened mass and direction.

Kesteven (1944), working on other lizards, considered that the muscle fibers here distinguished as omohyoideus and sternohyoideus are all sternohyoid and that no omohyoideus exists. In view of the separate origin of the superficial muscle, it seems probable that the lateral group of fibers, here described as omohyoideus, is not identical with the sternohyoideus.

M. branchiohyoideus (Fig. 39) is a ribbon-like muscle lying on the pharyngeal membrane between the two lateral limbs of the hyoid apparatus. It lies ventral to the pharynx and dorsal to the hyoglossus muscle and the glossopharyngeal nerve and artery. Arising along approximately two-thirds of the length of the posterior border of the ceratohyal, its fibers extend posteriorly, paralleling both of the hyal elements, and insert on the posterior half of the anterior border of the first ceratobranchial bone. The glossopharyngeal nerve, carrying fibers of the vagus and possibly of the hypoglossal, lies on the ventral surface of the muscle and gives off numerous branches to it, some of which pass through it to the pharynx whereas others disseminate within it. Brock (1938) described this muscle as developing from the glossopharyngeal muscle mass and, therefore, as innervated by the glossopharyngeal nerve.

Hyoid Apparatus

The hyoid apparatus (Fig. 39) is essentially a skeletal framework upon which the hyoid and tongue muscles attach. It is formed of seven processes, three of which are paired. It is constructed of cartilage, calcified cartilage, and a fibrotendinous covering of various thicknesses. This covering, composed of longitudinal fibers, completely encircles the cartilaginous and calcified parts and is heavier ventrally than dorsally.

The terminology of Camp (1923) is used in the following description. The central part, or body, of the hyoid, from which the other processes extend, is V-shaped both dorsally and anteriorly and forms a cradle for the larynx. Projecting anteriorly from the base of the body is a long *hypohyal* (lingual process), primarily a cartilaginous structure with only slight calcification. It extends into four-fifths of the length of the tongue, passing between the two hyoglossus muscles and is enmeshed in the intrinsic lingual muscles, the verticalis and the dorsal and ventral transversale. This process is surrounded by a thin, tough membranous sac in which it has some degree of motion. Passing posteriorly from the anterior end of the process to the larynx is the laryngohyoid ligament which follows the dorsal side of the process but is outside of its sheath.

Extending posteriorly from the hyoid body in the mid-line, just ventral to the trachea, is a pair of long adjacent processes, the *second ceratobranchials*. These elements are parallel, but are not attached to each other. They lie dorsal to the intermandibularis posterior muscle, and at its posterior border they pass onto the ventral surface of the constrictor colli. Near their base they are calcified and provide for the insertion of the omohyoideus muscle and of some fibers of the sternohyoideus muscle. Their tips are tapered and flexible and are attached to the subcutaneous connective tissue of the throat.

Laterad to the second ceratobranchial and attached by a true joint to the body of the hyoid apparatus is the *first ceratobranchial*. Curving laterally near its base, this element extends toward the posterolateral angle of the head and then runs dorsally to terminate at the side of the neck, deep to the depressor mandibularis muscle. Proximally this element is well calcified and its *dorsal process* is cartilaginous (Figs. 32 and 33) and remains free of muscle attachments though it is bound in connective tissue. Its major part receives the insertions of the omohyoideus and sternohyoideus along its posterior border and the insertions of the first and second mandibulohyoid muscles, the hyoglossus, and the branchiohyoideus along its anterior border.

The most distinctive characters of the first ceratobranchial are its ossification and its articulation with the body of the hyoid. Its proximal end is dorsoventrally flattened and is rounded at the tip to form a condyle which fits into a semicircular recess in the body of the hyoid. Each surface of this joint is covered by a layer of hyaline cartilage, that of the ceratobranchial being especially thick. A thin articular capsule surrounds the joint, and its fibers fan out dorsally and ventrally from the center of the condyle and form collateral ligaments which span the joint cavity and insert onto the body of the hyoid, restraining vertical movement but allowing horizontal movement of the ceratobranchial.

The most lateral of the paired elements is the *ceratohyal*. It is flattened, cartilaginous, fibrously attached to the anterior projection of the body, and tapers posteriorly. It, too, has a cartilaginous dorsal process which lies on the tympanic membrane deep to the depressor mandibularis muscle. It receives the insertion of the third mandibulohyoideus muscle along its anterior border and gives origin to the branchiohyoideus muscle along its posterior border.

Within the membranous attachments of the first ceratobranchial and the ceratohyal and mesial to their dorsal processes is a small cartilaginous element, the remnant of the dorsal process of the second ceratobranchial.

Tongue

The tongue (Fig. 59) is a V-shaped fleshy organ lying in the floor of the mouth, its apex at the symphysis of the mandible and its posterior limbs lateral to the larynx. All of its ventral surface, except the anterior one-fifth, or tip, is attached to the floor of the mouth. This attachment is by two extrinsic muscles, the genioglossus and the hyoglossus. The root, surrounded by the oral membrane, is narrow and is devoid of papillae. The lateral borders of the tongue are rolled under. In cross section the mucous membrane and papillae give the appearance of a vertically sectioned mushroom. The anterior borders of the genioglossus muscles produce the appearance of a frenulum.

The dorsum of the tongue is rounded and is completely covered with velvety filamentous papillae (Fig. 59) which reach a maximum of 2.5 mm.

in length and 0.2 mm. in width. The papillae continue over the lateral surfaces of the tongue, terminating at the root. At the tip of the tongue, which is slightly grooved, the papillae are low and sickle-shaped, but at the posterior limbs of the tongue they are low and blunt. Between them are crypts of mucous glands which extend approximately two-thirds of the length of the papilla. Each papilla contains one or more muscle fiber and a vascular supply.

The oral membrane covering the root of the tongue is devoid of mucous crypts but contains occasional isolated mucous cells in the epithelium. The membrane bears numerous longitudinal plicae.

The ventral surface of the tip of the tongue bears two somewhat elevated and smooth-surfaced triangular dermal plaques of cornified epithelium. These lie in opposition to the sublingual plicae enclosing the ducts of the sublingual gland and apparently are the receptacles for the secretion of that gland.

Internally the tongue is composed of interlacing, extrinsic and intrinsic muscle fibers. The extrinsic muscles, genioglossus and hyoglossus, control the motions of the tongue; the intrinsic muscles control its shape. The tongue is supported by the lingual process of the hyoid apparatus which occupies approximately four-fifths of its length. The lingual process lies in the ventral mid-line and is ensheathed by the fibers of the verticalis and the interlacing fibers of the dorsal and ventral transverse muscles.

Extending posteriorly from the anterior end of the lingual process is the laryngohyoid ligament. It lies dorsal to, but outside of, the sheath of the lingual process, and inserts into the cartilage of the larynx. Near its posterior end this ligament pierces the superior transverse muscle and inserts into the cricothyroid cartilage. It apparently is a mechanism for opening the glottis when the tongue and hyoid apparatus are protracted.

Extrinsic muscles. — The musculature of the tongue is innervated by three branches of the hypoglossal nerve. In addition, it receives general somatic afferent and special visceral afferent fibers from the mandibular division of the trigeminal nerve, and some special visceral afferent fibers pass from the glossopharyngeal nerve to its posterior part. Its blood supply is by the submandibular artery which lies on the lateral surface of the hyoglossus muscle.

M. hyoglossus (Figs. 38 and 39) is a thick, flat muscle which lies ventral to the glossopharyngeal nerve and artery, the branchiohyoideus muscle, the ceratohyal, the hyoid body, and the pharynx. On its lateral border is the submandibular artery, and ventral to it are the second mandibulohyoideus muscle, the posterior part of the intermandibularis profundus muscle, the hypoglossal nerve, and the genioglossus muscle. It arises from the anterior border of the proximal half of the first ceratobranchial and extends anteriorly ventral to the hyoid body. It turns dorsally to form the major part of the tongue. Ventrally, as it enters the tongue, it receives the insertion of the mesial fibers of the genioglossus muscle. Here it is a ribbon-like muscle, but as the fibers extend anteriorly they form first an oval bundle and then a cylinder. Throughout the entire length of the tongue this muscle is surrounded by the inferior transverse fibers of the tongue proper. The ventromesial fibers of this muscle extend anteriorly and insert into the tip of the tongue, but its dorsolateral fibers swing anteromesially and cross the mid-line to intermingle with the intrinsic musculature and insert into the opposite surface of the tongue.

The hyoglossus is innervated by two branches of the hypoglossal nerve which lie on its ventral surface, posterior to the insertion of the genioglossus muscle. The intermediate branch of the hypoglossal nerve pierces the muscle and courses in its ventral part to the tip of the tongue, and the glossopharyngeal nerve enters its medial border.

M. genioglossus (Figs. 38 and 39) is covered dorsally and laterally by the oral membrane, and ventrally by the third mandibulohyoid and the intermandibularis anterior muscles. It takes origin from the ventromesial surface of the mandibular rami, just lateral to the symphysis. Its fibers can be divided into two groups, a mesial and a lateral, separated by the lingual branch of the inferior alveolar nerve. The mesial fibers extend posteriorly from the symphysis, paralleling the mid-line, and insert into the ventral surface of the hyoglossus muscle. The lateral fibers arise from the ventral surface of the mandible lateral to the symphysis, form the wall of the tongue, and insert into the ventral surface of the tongue lateral to the anterior part of the hyoglossus muscle. The lateral group twists so that at its origin the ventral surface is mesial and the dorsal surface is lateral, the most lateral fibers extending dorsally and inserting anteriorly. The more mesial fibers fan out and insert all along the ventrolateral surface of the tongue to its posterior end, interdigitating with the dorsal transverse fibers of the intrinsic tongue musculature.

The lateral branch of the hypoglossal nerve pierces the mesial fibers near their insertion and continues through them to lie on the ventromesial border of the lateral fibers, giving off several branches to their mesial surface.

Intrinsic muscles. — The intrinsic musculature of the tongue (ringmuskeln, Gandolfi, 1908) is made up of three groups of fibers: superior transverse, inferior transverse, and verticalis. (The terminology follows that of Minot, 1880.) The fibers do not maintain their integrity throughout, but at some levels are intermingled to such an extent that their identity is obscured. In addition to these transversely directed fibers, there is a group of longitudinal fibers that are independently dispersed throughout the tongue. They are found primarily immediately beneath the surface of the tongue which does not have a septum.

The *inferior* (ventral) *transverse* fibers lie on the ventral surface of the hyoglossus muscle. They appear just anterior to the insertion of the mesial fibers of the genioglossus and do not extend to the mid-line but encircle the hyoglossus muscle, forming a sling for its cylindrical part. At the level of the larynx the fibers lateral to the hyoglossus insert into the surface of the tongue; the fibers mesial to the hyoglossus extend dorsally to insert in the surface of the same side. The lateral fibers also cross the mid-line dorsally to encircle the hyoglossus muscles and isolate each into a distinct cylinder. Some of the medial fibers cross the mid-line ventral to the hypohyal and provide attachment for the verticalis fibers. Further anteriorly, however, the medial fibers intermingle with those of the verticalis and cross the mid-line to insert in the surface of the opposite side of the tongue, becoming indistinguishable from verticalis fibers. At the tip of the tongue the fibers return to their respective sides, but maintain their position in respect to the hyoglossus muscle. The medial and lateral rami of the hypoglossal nerve innervate this muscle.

The *superior* (dorsal) *transverse* fibers extend horizontally across the dorsal surface of the tongue, their direction changing at various levels. At the tip of the tongue the fibers maintain their transverse direction, the longer ones extending between the lateral borders of the tongue. With the appearance of major bundles of the hyoglossus muscle as one moves posteriorly, the transverse fibers increase in number. In the middle two-thirds of the tongue some of the fibers turn ventrally, cross the mid-line, and insert in the ventral surface on the opposite side of the tongue, lateral to the hypohyal. Immediately anterior to the larynx, the fibers of the dorsal transverse and the verticalis muscles have similar paths and are indistinguishable from each other. At the posterior end of the tongue, ventral to the larynx and trachea, the fibers again extend transversely across the entire dorsal surface.

The innervation of the majority of the dorsal transverse fibers is by the lateral branch of the hypoglossal nerve, which lies mesial to the lateral fibers of the genioglossus muscle. The fibers that cross the mid-line and insert into the ventral surface of the tongue are supplied by the medial branch of the hypoglossal nerve.

The fibers of *M. verticalis* lie mesially between two hyoglossus muscle masses and extend between the dorsal and ventral surfaces of the tongue, lateral to the hypohyal cartilage. Caudally they are between the two hyoglossus muscles, ventral to the larynx and trachea; they maintain this position beside the hypohyal. With the thickening of the tongue anteriorly, they become longer. In front of the larynx they cross the mid-line dorsal to the hyoglossus muscle, intermingle with the superior transverse muscle, and insert in the dorsal surface on the opposite side of the tongue. They also intermingle with, and become indistinguishable from, the medial fibers of the inferior transverse. Some of the verticalis fibers cross the mid-line ventral to the hypohyal cartilage and encircle it. At the anterior tip of the tongue the verticalis again becomes an independent group of fibers.

The verticalis fibers are innervated by the medial branch of the hypoglossal nerve which lies within the ventral part of the bundle and extends in that position to the anterior end of the tongue.

M. constrictor vena jugularis (Bruner, 1907) (Figs. 33 and 42) is a muscle of striated fibers which encircles the internal jugular vein just as it leaves the head. It is found ventral to the longissimus cervicis muscle, dorsal to the auditory sac, and mesial to the episternocleidomastoideus muscle. Its fibers originate on the intercalary cartilage and extend posteromedially in a cord which expands and encircles the jugular vein distal to the junction of the posterior cerebral vein. Some of the fibers also encircle the base of the posterior cerebral vein. No attachment to the dorsal process of the hyoid cartilages is apparent. The muscle is innervated by a direct branch from the vagus and by a plexus composed of elements from the lateral cranial sympathetic trunk.

M. laxator tympani could not be identified grossly; however, in a few sections some fibers extending from the paraoccipital process to the auditory membrane appear to be a remnant of that muscle.

Neck Musculature

A brief description of the insertions of the cervical extensors and flexors will be given to complete the continuity of cervical and head relations. The most recent works on axial musculature are those of Olson (1936) and Evans (1939), both of whom followed the terminology laid down by Nishi (1916).

In the neck region the fascia beneath the skin is thick and aponeurotic. It covers all the axial musculature of the neck arising from the posterior border of the parietal bone, gives origin to the constrictor colli and the depressor mandibularis muscles, and attaches to the dorsal surface of the spinalis capitis muscle and the ligamentum nuchae.

The ligamentum nuchae (nuchal ligament) is a thick, fibrous median vertical membrane separating the two lateral groups of axial muscles and dorsally continuous with the fascia of the neck. It arises from the angle of the parietal and the crest of the supraoccipital bone, extends posteriorly, and attaches to the posterior atlanto-occipital ligament and the neural spines of the cervical vertebrae.

Extensors

M. spinalis capitis (Figs. 33 and 40) is the cervical part of the dorsal axial musculature. It lies along the mid-line beside the nuchal ligament. Covering the occipital muscles, it inserts into the entire posterior border of the parietal bone just beneath the skin and into the dorsal fascia of the neck. It also attaches laterally to the parietal bone beneath the origins of the episternocleidomastoideus and the constrictor colli. A small medial section of it extends ventrally in the mid-line and inserts on the occipital crest of the supraoccipital bone (Fig. 41). On its ventral surface it receives a mesial and a lateral branch of the first spinal nerve and branches of the hypoglossal. The mesial branch reaches it by passing dorsally between the rectus capitis posterior and the obliquus capitis magnus muscle. The lateral nerve is from the lateral branch of the first spinal and reaches the muscle by extending dorsally, lateral to the obliquus capitis magnus and mesial to the longissimus cervicis muscle.

M. rectus capitis posterior (Fig. 41) represents the fused parts of the rectus capitis superficialis and profundus of other lizards. It lies alongside the mid-line, deep to the spinalis capitis immediately dorsal to the occipitoatlas interval, lateral to the ligamentum nuchae, and medial to the obliquus capitis magnus muscle. The muscle inserts into the dorsal surface of the supraoccipital bone, lateral to the occipital crest. The first spinal nerve extends dorsally, lateral to its belly, and gives off a single branch to it.

M. obliquus capitis magnus (Figs. 34, 35, and 41) lies ventral to the spinalis capitis, lateral to the rectus capitis posterior, dorsomedial to the longissimus cervicis muscle, and dorsal to the interval containing the nerves emerging from the skull. It extends diagonally from the spinal column to insert on the posterior surface of the exoccipital bone (paraoccipital process). It is innervated on its anterior border by a lateral branch of the dorsal ramus of the first spinal nerve.

M. longissimus cervicis (transversalis cervicis) (Fig. 41) lies ventrolateral to the obliquus capitis magnus muscle and dorsal to the longissimus capitis muscle. It inserts on the ventral border of the exoccipital bone, including its paraoccipital process. Its medial side receives the lateral branch of the dorsal ramus of the first spinal nerve.

Flexors

M. rectus capitis anterior extends along the ventral surface of the vertebral column, mesial to the third root of the hypoglossal nerve, the ventral ramus of the first spinal nerve, and the longissimus capitis muscle. It inserts into the entire posterior surface of the exoccipital and basioccipital bones (crista tuberalis), lateral to the occipital condyle. Ventrally it is covered by the epithelium of the auditory sac. A medial branch of the first spinal nerve enters its dorsal surface, and a branch of the third root of the hypoglossal nerve enters its lateral surface.

M. longissimus capitis (transversalis capitis) (Figs. 42 and 58) arises from the transverse processes of the cervical vertebrae and extends anteroventrally, lateral to the insertion of the rectus capitis anterior, to insert upon the spheno-occipital tubercle of the basioccipital. It is innervated by a ventral branch of the first spinal nerve. The third root of the hypoglossal and the ventral root of the first spinal nerve pass between the rectus capitis anterior and the longissimus capitis. Its insertion is crossed laterally by the internal carotid artery, the glossopharyngeal, the first and second roots of the hypoglossal, and the vagus nerve.

THE CRANIAL NERVES

The peripheral nerves of the head of the lizard have been almost completely neglected. Four papers comprise the most important works in the field. Fischer (1852) made a comparative study of eleven lizards and established homologies for the nerves. More recently, Osawa (1898) and Watkinson (1906) added descriptive accounts of *Sphenodon* and *Varanus*. Willard (1915) described the cranial nerve distribution of *Anolis carolinensis* and analyzed their components through fiber-size relation. Willard's study is the most useful and important of the studies on the cranial nerves of lizards.

In the present study the olfactory nerve is considered in the section on the snout; the optic, oculomotor, trochlear, and abducens nerves are treated in the section on the orbit; and the auditory nerve is described with the ear.

Trigeminal Nerve

The trigeminal nerve leaves the brain as three components, two sensory and one motor. Each sensory component has its own independent ganglion. The dorsal or ophthalmic division (nervus ophthalmicus profundus, trigeminal 1) has a small ganglion lying dorsal and mesial to the semilunar ganglion of the maxillary and mandibular divisions, trigeminal 2 and 3, respectively. The motor root lies ventral to the semilunar ganglion and enters it to be distributed with its components. The two ganglia lie within the trigeminal notch of the prootic bone, external to the cranial cavity and ventral to the prootic sinus, the terminus of the medial cerebral vein.

The parts of the adductor musculature are innervated not only by the mandibular division of the trigeminal, which carries both sensory and motor components, but also by independent motor nerves. These independent motor nerves pass mesial to the semilunar ganglion and lie in the angle between the ophthalmic and mandibular divisions. The first motor branch (Fig. 35) is a very short nerve lying mesial to the mandibular division. It pierces the lateral surface of the protractor pterygoideus muscle and extends nearly the full length of the muscle before ramifying. The second branch extends anterolaterally to its termination on the deep surface of the levator pterygoideus muscle. The third and longest branch extends anteriorly, between the levator pterygoideus and the protractor pterygoideus muscles, to the levator bulbi; its terminal part continues along the lateral surface of the levator bulbi and divides into two branches that supply the two parts of that muscle. At the anterior border of the protractor pterygoideus this branch communicates with the palatine ramus of the facial nerve by a bundle which crosses the lateral surface of the connecting vein between the prootic sinus and the internal jugular vein.

Mandibular Division

The mandibular division (ramus mandibularis, trigeminal 3) (Fig. 34) of the trigeminal nerve leaves the ventral side of the semilunar ganglion. It carries both motor and sensory fibers; the motor fibers enter the ventral surface of the semilunar ganglion and become indistinguishable from the sensory fibers within the mandibular division. The division passes ventrally along the posterior border of the pseudotemporalis profundus muscle and then turns anteriorly along the dorsal border of the adductor posterius muscle, coursing along the medial surface of the mandibular artery. Continuing anteriorly and passing ventral to the insertion of the adductor mandibularis externus muscle, it enters the mandibular foramen.

In its path through the head the mandibular division gives off five branches, three motor and two sensory. The first, a short branch (Fig. 34), arises near the origin and enters the pseudotemporalis profundus muscle. The second, a sensory branch (Figs. 32 and 33), parallels the maxillary division and passes with it between the pseudotemporalis superficialis and the adductor mandibularis externus medius. At the anterior border of the adductor mandibularis externus the branch passes laterally between or around the anterior fibers of this muscle, first to lie on the posterior surface of the epithelium of the coronoid recess and then to turn posteriorly along the dorsal surface of the *mundplatt* and enter the skin of the infratemporal fossa. In some specimens the first motor branch runs with this sensory branch. The third branch (Fig. 34), large and probably entirely motor, leaves the posterior border of the mandibular division just below the ganglion, runs ventrad, lateral to the superior border of the protractor pterygoideus muscle, and perforates the adductor mandibularis externus (Figs. 31-33). It then divides into three main bundles to innervate all of the parts of that muscle. The fourth, also a large motor branch (Fig. 35), leaves the anterior border of the mandibular division at the level of the pterygoid bone and runs ventrad to enter the pterygomandibularis muscle. The fifth, a small, posterior, mixed branch, leaves the mandibular division at the superior border of the adductor mandibularis posterior (Fig. 34) and, passing lateral to the mandibular artery, sends twigs to innervate that muscle. This branch continues posteroventrally to join the articular artery and with it enters the posterior supra-angular foramen, within the mandibular foramen. Emerging through the same foramen (Figs. 30 and 31), it is distributed to the skin of the posterior part of the infratemporal fossa and the condylar region.

The mandibular division continues within the mandible as the inferior alveolar nerve, lying on the dorsal surface of Meckel's cartilage, mesial to the insertion of the adductor posterior muscle. After entering the foramen it gives off a large cutaneous branch, the posterior inferior labial, which passes laterally dorsal to the adductor posterior muscle, emerges through the anterior supra-angular foramen (Fig. 32), and extends along the dentary bone, giving branches to the skin, lips, and glands along the posterior two-thirds of the dentary. A second mixed motor and sensory branch, the posterior mylohyoid nerve, leaves the inferior alveolar nerve as the cutaneous branch does and extends ventrally between Meckel's cartilage and the insertion of the adductor posterior muscle. It emerges through the posterior mylohyoid foramen, where it pierces the lateral fibers of the first mandibulohyoid muscle and terminates along the anterior border of the intermandibularis posterior (Figs. 36 and 37). A large cutaneous branch of the posterior mylohyoid nerve extends posteriorly along the pterygomandibularis muscle, and other cutaneous branches from it extend medially to the mid-line; all end in the skin.

At the level of the coronoid process the chorda tympani nerve joins the mesial side of the inferior alveolar nerve. Near this junction is the mandibular ganglion. A small recurrent branch of the inferior alveolar nerve is given off mesially and passes through the suture between the coronoid and splenial bones and appears to terminate in the ventral surface of the pharynx.

The anterior mylohyoid nerve crosses Meckel's cartilage dorsally, encircles it laterally, and emerges on the mesial side of the mandible through the anterior mylohyoid foramen in the splenial bone. This nerve passes dorsal to the fibers of the first mandibulohyoid muscle and enters the ventral surface of the intermandibularis anterior. It also carries some cutaneous fibers which lie along the mesial border of the mandible and on the chin (Fig. 36).

The inferior alveolar nerve continues anteriorly and divides into two rami, the lingual and the alveolar. The lingual ramus, arising mesially, is cutaneous and carries branches of the chorda tympani. It passes mesially across Meckel's cartilage to leave the dentary bone through the anterior inferior alveolar foramen. At its exit it divides into two branches, an anterior or glandular branch (Fig. 37), which extends along the ventral surface of the intermandibularis anterior muscle and terminates along the sublingual gland, and a posterior branch, which pierces the intermandibularis anterior and the genioglossus muscles and joins the lateral lingual ramus of the hypoglossal nerve (Fig. 39). The alveolar ramus continues along the dorsal surface of Meckel's cartilage, passes within an independent dorsal canal in the dentary, supplies four or five anterior inferior labials to the skin, lips, and glands of the anterior one-third and tip of mandible, and terminates over the chin in a large and extensively distributed mental branch.

Maxillary Division

The maxillary division (ramus maxillaris, trigeminal 2) (Figs. 32-34) of the trigeminal nerve leaves the posterodorsal border of the semilunar ganglion, passes anteriorly over the lateral surface of the ganglion, and continues anterolaterally between the muscle masses of the adductor mandibularis, lateral to the internus group and mesial to the externus group. Near the anterior border of these muscle masses several maxillary branches are given off to the temporal and orbital regions. The main part of the nerve passes through the orbit as the inferior orbital nerve and enters the maxilla to supply the tip of the snout, the teeth, and the lips as the superior alveolar nerve.

The first branch, maxillary 1, arises from the dorsal side of the maxillary division in its course between the pseudotemporalis superficialis and the adductor mandibularis externus medius muscles. This branch runs with the maxillary division to the anterior border of the pseudotemporalis superficialis muscle. Here it joins the lateral branch of the lateral cranial sympathetic trunk in a ganglionic swelling which yields plexiform branches in all directions. Two posterior branches extend posterodorsally to the skin covering the supratemporal (Fig. 40) and infratemporal fossae; ventral branches extend to the coronoid artery beneath and to the second maxillary branch. The main trunk of maxillary 1 continues anteriorly, dorsal to the infraorbital artery. It gives off several short dorsal branches to the lacrimal gland and the posteroventral region of the lower lid and then anastomoses with maxillary 2.

The second branch, maxillary 2, arises dorsally from the maxillary division at the anterior border of the pseudotemporalis superficialis muscle; there it receives a communicating branch from the lacrimal plexus. It then continues anteriorly, ventral to the inferior orbital artery, and anastomoses with the continuation of maxillary 1, forming a combined nerve which pierces the orbitotemporal membrane and extends along the entire inferior conjunctival wall, giving off numerous branches to the conjunctiva, the inferior orbital artery, and the orbital sinus. At approximately the level of the posterior orbital rim the nerve gives off a lateral branch which enters the foramen at the posterior end of the jugal bone and passes from that bone beneath the skin as a series of infraorbital cutaneous branches.

The main part of the maxillary division of the trigeminal continues anteriorly as the infraorbital nerve. It pierces the orbital fascia, passes dorsal to the levator bulbi, and lies between this muscle and the bulb, mesial to the inferior orbital artery. In its course it communicates with the infraorbital plexus (lateral palatine ramus) by means of several small branches which pierce the substance of the levator bulbi muscle and the orbital fascia to join the plexus. It also gives off several small branches which extend dorsally over the ventral surface of the inferior orbital artery to the inferior fornix of the eye. After leaving the anterior border of the levator bulbi it turns laterally, receives a large branch from the lateral palatine ramus of the facial nerve, and passes through the infraorbital foramen to become the superior alveolar nerve.

Within the nasal cavity the superior alveolar nerve sends a branch to the intermediate palatine ramus. Laterally, it gives off several long labial branches which pierce the maxilla and supply the superior labial glands and the posterior part of the lip. As the nerve continues into the superior alveolar foramen it gives off other labial branches which pierce the maxilla laterally and dental branches which pierce it ventrally. Emerging from the anterior inferior alveolar foramen, in the fenestra exonarina, it immediately gives a branch to the ventral and posterior surfaces of the naris and turns dorsally to join the lateral ethmoidal nerve.

Ophthalmic Division

The ophthalmic division (trigeminal 1) extends anteriorly from the ophthalmic ganglion. The proximal part is surrounded by the prootic sinus and lies immediately dorsal to the origin of the protractor pterygoideus muscle (Fig. 35). Continuing anteriorly, it lies along the lateral wall of the cranium, passing lateral to the proximal end of the pila antotica (Fig. 53) and mesial to the origin of the levator bulbi muscle (ventralis part). Medial to this muscle it separates into two rami, ramus frontalis dorsally and ramus nasalis ventrally. The division actually occurs just distal to the ganglion, but the rami parallel each other in a connective tissue bundle to the muscle.

Ramus nasalis extends anteriorly into the orbit (Fig. 53), passes around the mesial side of the bulb, enters the nasal capsule, and divides. Within the orbit two cutaneous branches are given off. The first, the long ciliary nerve, detaches ventrally, after the nasal ramus passes the origin of the levator bulbi muscle, and follows the surface of the metoptic membrane lateral to the orbitosphenoid and the dorsal ramus of the oculomotor nerve. Distal to the ciliary ganglion it joins the short ciliary branch of the oculomotor nerve which lies lateral to the origin of the superior rectus muscle. In addition, there are several other long ciliary nerves which extend from the long ciliary root, by-pass the ganglion, and enter the bulb independently. Occasionally, a long ciliary branch leaves the ramus nasalis as it passes beneath the superior rectus and enters the anterior surface of the bulb.

The ramus nasalis continues its course through the orbit, passing lateral to the metoptic membrane, the orbitosphenoid bone, and the origin of the superior rectus muscle; dorsal to the retractor musculature, the optic nerve, and the superior border of the anterior rectus muscle; ventral to the trochlear nerve, the tendon of the nictitating membrane, and the origin of the superior oblique muscle; and mesial to the bulb of the eye and the tail of the Harderian gland. Several small twigs from the junction of the nasal ramus of the ophthalmic nerve and the medial palatine ramus of the facial nerve pass posteriorly along the frontal artery and then laterally on the anterior orbital artery to terminate in the Harderian gland and the glandular strip of the upper lid.

At the anterior end of the orbit the ramus nasalis lies ventrolateral to the body of the superior oblique muscle and mesial to the inferior orbital artery. On the posterior surface of the orbitonasal membrane it is joined by the communicating ramus of the facial nerve (medial palatine ramus), along which is found the sphenethmoidal ganglion. At this junction it gives off a lateral branch which extends to the anterior angle of the eye and supplies the anterior part of the eyelid. The ramus nasalis then passes beneath the sphenethmoidal commissure and turns dorsally, entering the nasal capsule through the lateral olfactory foramen of the planum antorbitale with a lateral branch of the olfactory nerve. Within the nasal capsule it lies between the roof of the paranasal cartilage and the olfactory epithelium, passes dorsal and mesial to the olfactory nerve, and divides into a medial and a lateral ethmoidal nerve.

The *medial ethmoidal nerve* continues to the nasal septum and lies along its lateral wall, dorsomedial to the sakter and the anterior recess. Passing medial to the nasal process of the septomaxilla, it continues along the septum, pierces the apical foramen in the cupola, and divides into lateral and medial branches. The lateral branch extends to the end of the anterior nasal tube, emerges through the fenestra exonarina, and supplies the skin around the anterior rim of the naris. The medial branch pierces the premaxilla and branches extensively over the surface of the snout. Some ventral fibers pass through the ventral foramina of the premaxilla and anastomose with the terminal branches of the medial palatine nerve to supply the area just behind the teeth.

The *lateral ethmoidal nerve* pierces the foramen epiphinale at the superior border of the aditus conchae. At this point it gives off a small dorsal cutaneous branch which pierces the nasal bone to supply the skin around the dorsal surface of the nasal capsule. The main nerve continues anteroventrally in the aditus conchae within the substance of the lateral nasal gland, giving off fine branches to it. A long anterior branch extends along the dorsolateral angle of the zona annularis to supply the dorsal surface of the external naris. The lateral ethmoidal nerve continues ventrally to the lamina transversalis anterior and lies just dorsal to the glandular branch of the postnarial artery. As the nerve reaches the lamina transversalis anterior, it gives off several branches, one piercing the cartilage to supply the lacrimal duct just beneath, and the other perforating the nasal process of the maxilla to supply the skin of that area. The terminal division of the nerve continues to the posterior and inferior surfaces of the naris and then anastomoses with the superior alveolar nerve, forming a plexus around the naris.

The *ramus frontalis* (Fig. 53) extends dorsally from the origin of the levator bulbi muscle and passes along the lateral wall of the cranium medial to the orbitotemporal membrane, just behind the pila accessoria and anterior to the pseudotemporalis superficialis muscle. Here it divides into two main branches, an anterior and a posterior. The posterior branch turns dorsally and receives the medial branch of the lateral cranial sympathetic trunk in a ganglioform swelling just beneath the lateral process of the frontal. Plexiform twigs of this branch extend to the supratemporal fossa, the lacrimal gland, and the posterior part of the glandular line of the superior lid. The anterior branch extends with the frontal artery along the taenia marginalis and planum supraseptale, tightly bound to the undersurface of the frontal bone and giving off branches to the frontal bone and the skin of the orbit. Branches from it also pass laterally to the anterior half of the superior lid.

Tactile organs are present over all of the surface of the head. Grossly they appear as pits within the scales, without covering pigment. There is at least one pit on each scale, and around the lips, chin, snout, and eyes there may be as many as 40 on a single scale (postnarial and loreal). These are concentrations of epidermis which are elevated above the remainder of the epidermis and project into and thin the cornified layer in these areas. On removal (at molts) these scales present circular, transparent areas which reflect the presence of pits. Nerve fibers could not be traced to the pits. Willard (1915) described tactile "hairs" protruding from their centers in *Anolis*. Hairs were not found in *C. pectinata*.

Facial Nerve

The facial nerve emerges from the facial foramen in the prootic bone along the medial surface of the sulcus vena jugularis. The root is small and divides immediately into two rami, an anterior palatine and a posterior hyomandibular. Ventral to the facial foramen is the geniculate ganglion, its major part seeming to lie on the palatine ramus. Along the ventral border of the geniculate ganglion the medial cranial sympathetic trunk joins the palatine ramus and is distributed with it.

Hyomandibular Ramus

The hyomandibular ramus (Fig. 42) extends posterolaterally to the tip of the paraoccipital process where it separates into two divisions, the hyoid ramus posteriorly and the chorda tympani anteriorly. The main hyomandibular ramus is composed of two groups of fibers, a dorsal group which comes directly from the root and a fine-fibered ventral group which passes through the ganglion. This ramus lies within the dorsal surface of the sulcus vena jugularis and ventrally is covered only by the membrane of the tympanic cavity. In its course to the paraoccipital process it crosses dorsal to the columella bone and ventral to the internal jugular vein as the latter enters the head. Farther laterally it crosses dorsal to the stapedial artery just medial to the cephalic condyle of the quadrate, its posterior border receiving one or two branches of the lateral cranial sympathetic trunk (Fig. 42). This trunk gives some fibers to the facial nerve, both medially and laterally, and then leaves the anterior border of the facial nerve to continue into the head. Lateral to the stapedial artery the hyomandibular ramus divides into the chorda tympani and the hyoid nerves.

The *chorda tympani* receives most of the finer fibers of the hyomandibular ramus which are special visceral afferent and parasympathetic. The chorda tympani separates from the hyoid ramus of the hyomandibular nerve just lateral to the stapedial artery and ventral to the cephalic condyle of the quadrate, passes dorsal to what appears in sections to be the laxator tympani muscle, and then turns anteriorly dorsal to the ligament of the extracolumella, maintaining a position just outside of the membrane of the auditory sac. Continuing anteriorly, it lies on the posterior surface of the quadrate (Fig. 34), medial to the posterior crest, and passes lateral to the processus internus of the extracolumella. Turning ventrally, it follows the contour of the medial lamina of the quadrate, crosses the posterior surface of the quadrate process of the pterygoid bone (pterygoquadrate articulation), and is joined by the auricular artery. It also passes over the posterior surface of the mesial half of the condylar capsule of the jaw, lateral to the insertion of the posterior fibers of the pterygomandibularis muscle. Immediately posterior to the condyle it enters the articular bone through a small foramen in the dorsomedial surface of the retroarticular process (Fig. 50).

The chorda tympani runs within the substance of the articular bone to the anterior end of the mandibular foramen. Here it passes on the lateral surface of the articular, medial to Meckel's cartilage and separated from it by the periosteum. As it passes the level of the coronoid process it turns dorsally, pierces the periosteum, and lies on the dorsal surface of the cartilage, still in dorsal relation to the articular. At the level of the anterior process of the coronoid it passes dorsal to Meckel's cartilage and there joins the mandibular division of the trigeminal nerve. Beyond this point the two nerves cannot be separated; however, the fibers of the chorda tympani presumably distribute to the tongue along with the other components of the lingual ramus of the mandibular division of the trigeminal nerve, and the sympathetic fibers probably distribute to the glands with both the lingual and the alveolar ramus of the trigeminal nerve.

The *hyoid ramus* of the facial nerve, primarily motor, arises just lateral to the stapedial artery, where the nerve separates posteriorly from the chorda tympani at the tip of the cephalic condyle of the quadrate and ventral to the origin of the constrictor vena jugularis muscle. It extends laterally, anterior and ventral to the origin of the episternocleidomastoideus muscle, and divides into four branches (Fig. 32). The first three branches are short and immediately enter the anterior part of the depressor mandibularis muscle. The fourth is a long branch which crosses the deep surface of the depressor mandibularis muscle in a posteroventral direction and passes lateral to the distal ends of the ceratohyal and first ceratobranchial cartilage. At the level of the retroarticular process it gives off a branch to that part of the intermandibularis muscle which covers and inserts into the lateral surface of the retroarticular process of the mandible. Continuing to the deep surface of the constrictor colli, it innervates that muscle at approximately the ventrolateral angle of the neck. There also may be a small branch from this constrictor colli nerve to the posterior border of the intermandibularis muscle. The caliber of the nerve is small, and its distal terminations are difficult to dissect macroscopically.

Palatine Ramus

The palatine ramus (vidian) of the facial nerve has an extensive distribution in the palate. Most of the fibers are derived from the medial cranial sympathetic trunk; consequently, the major part of this distribution is sympathetic rather than facial.

The palatine ramus (Fig. 53) extends anteroventrally from the root of the facial nerve and immediately is invested by the geniculate ganglion, at the ventral border of which it is joined by the medial cranial sympathetic trunk. The combined roots extend out of the sulcus vena jugularis to the lateral surface of the basisphenoid bone where they enter the vidian canal, accompanied on the medial side throughout this course by the internal carotid artery. The exit of the nerve from the vidian canal is on the anterior surface of the basisphenoid bone just lateral to the parasphenoid process, medial to the jugular vein, ventral to the origin of the bursalis muscle, and lateral to the pharyngeal membrane (Fig. 35). The nerve is accompanied by the palatine artery.

The palatine ramus continues anterolaterad, passing medial to the articulation of the columella. It gives off small ventral and medial branches to the pharyngeal membrane and receives dorsally the communicating branch of the trigeminal. It extends across the transverse process of the pterygoid to the medial process of the ectopterygoid, passing just beneath the posterior end of the orbital fascia and the depressor palpebra inferioris muscle, where the palatine ganglion lies. This is a sympathetic ganglion (Willard, 1915) which appears only as a slight swelling in the trunk; however, it is located at the proximal end of the inferior orbital plexus.

The inferior orbital plexus lies ventral to the orbital fascia and just dorsal to the pterygoid and palatine bones. It is composed of a medial and a lateral ramus which anastomose several times and give off "gustatory" branches (Willard, 1915) to the palatal glands and the taste buds of the medial and lateral gustatory stripe, and anastomotic branches to the ophthalmic and the maxillary division of the trigeminal.

The *medial palatine ramus,* the continuation of the palatine ramus, is the largest branch in the plexus. It extends anteriorly on the dorsal surface of the palatine process of the pterygoid and palatine bones. At the anterior border of the pterygoid a communicating ramus extends laterally across the inferior orbital membrane to join the lateral palatine ramus. This region of the medial palatine ramus is crossed, dorsally and laterally, by the insertion of the levator bulbi muscle. The medial palatine ramus continues craniad in a groove of the palatine bone. Numerous twigs perforate the bone and terminate in the glands and taste buds of the medial gustatory stripe on the oral side of the palate, and occasional branches extend to the oral membrane of the pyriform recess. Near its anterior end, in the orbit, the medial ramus gives off a second communicating ramus which joins the lateral palatine ramus before the latter joins the maxillary division of the trigeminal nerve.

At the level of the maxillary process of the palatine bone the medial palatine ramus sends a communicating ramus dorsally, along the posterior wall of the orbitonasal membrane, to join the ophthalmic division of the trigeminal nerve. Here is a sympathetic ganglion, the sphenethmoidal, which may be located at any point along the communicating ramus. This communicating ramus is lateral to the origin of the inferior oblique muscle and is on the posterior wall of the nasal capsule and anterior to the Harderian gland. It presumably distributes sympathetic filaments to the nasal distribution of the ophthalmic division of the trigeminal and to the Harderian gland.

As the medial palatine ramus gives off the communicating ramus it also gives off a lateral branch, the *intermediate palatine ramus*. This ramus runs laterad with a branch of the inferior nasal artery along the inferior border of the orbitonasal membrane, passes through the palatine foramen to the medial surface of the maxillary bone, and, as it leaves the dorsal surface of the maxilla, receives a branch from the superior alveolar nerve. Continuing anteriorly along the medial border of the maxillary shelf of the lateral rim of the fenestra exochoanalis, at approximately the mid-point of the maxilla, it receives the medial branch of the lateral palatine ramus and supplies a lateral branch to the ventral surface of the maxilla, two branches which supply the glandular and palatal areas lateral to the choanal apertures, and terminates on the highly glandular area of the premaxilla.

The medial palatine ramus continues anteriorly beneath the orbitonasal membrane, enters the nasal capsule, and lies on the dorsal surface of the vomer just beneath the nasal mucosa and lateral to the paraseptal cartilages. It passes through the middle of the vomer and gives off a posterior branch to the mucosa covering the ventral surface of the vomer. The major part of the ramus follows a groove or osseous canal anteriorly to terminate and distribute in the mucosa of the ventral surface of the vomer and premaxilla. Within the canal a small dorsal branch accompanied by a small artery pierces the vomer and enters Jacobson's organ.

The *lateral palatine ramus* diverges anterolaterally from the palatine ganglion, coursing dorsal to the inferior orbital membrane and giving off numerous branches. Two or three dorsal branches perforate the levator bulbi muscle and communicate with the maxillary division of the trigeminal nerve (infraorbital nerve), and several ventral branches pierce the inferior orbital membrane, extend anteriorly and posteriorly, anastomose with one another, and distribute to the lateral gustatory stripe. The lateral palatine ramus is joined by the communicating branches of the medial palatine ramus, which do not give off any additional branches. The lateral palatine ramus enters the infraorbital foramen and sends a communicating branch to the inferior orbital nerve just as that nerve enters the foramen. At this point are found a sympathetic ganglion and a branch to the oral membrane. The terminal part of the lateral palatine ramus and the lateral palatine artery continue ventrally around the posterior border of the maxillary process of the palatine to reach the ventral surface of that bone. The nerve then continues anteriorly on the ventral surface of the maxilla and divides into two branches, a medial which anastomoses with the intermediate palatine ramus, and a lateral which continues anteriorly on the ventral surface of the maxilla to approximately its mid-point.

Glossopharyngeal Nerve

The glossopharyngeal nerve is a small nerve composed of both sensory and motor components. The ventral root is extremely small; the dorsal is several times larger. The roots leave the medulla ventral to the posterior fibers of the auditory nerve. The nerve emerges through the perilymphatic fossa from the cranial cavity and lies on the medial wall of the recessus scala tympani, covered laterally by the saccus perilymphaticus. It continues posteriorly within this space and emerges at the medial border of the foramen rotundum. After passing through the foramen rotundum it lies within the auditory space, covered laterally by the membrane of this space. It then crosses the dorsolateral border of the crista tuberalis lateral to the first and second roots of the hypoglossal (Fig. 42) and enters the neck where it lies dorsal to the auditory sac loosely bound within the connective tissue around the sac.

In the proximal part of the neck the glossopharyngeal is ventrolateral to the hypoglossal, medial to the medial and lateral cranial trunks of the sympathetic, and dorsomedial to the internal carotid artery. The course of the nerve is posterolateral, lateral to the longissimus capitis muscle. At approximately the level of the tip of the paraoccipital process of the exoccipital, the nerve inseparably joins the cervical sympathetic trunk. At this union a group of the glossopharyngeal fibers joins the medial cranial sympathetic trunk as Jacobson's anastomosis, passes with the sympathetic fibers to the palatine ramus of the facial nerve, and distributes to the palate (Willard, 1915). Immediately following this junction with the sympathetic trunk the group is joined by a small vagal branch which arises distal to the jugular ganglion. The vagus at this point lies immediately dorsal to the glossopharyngo-sympathetic trunk. Posterior to this point the vagus gives off a second and larger branch, the superior laryngeal ramus (Fig. 57), which extends ventrally and joins the glossopharyngeal just anterior to the petrosal ganglion. This, the only ganglion of the glossopharyngeal, is found at the level of the posterior end of the quadrate. Here the glossopharyngeal passes dorsal and lateral to the sympathetic trunk, which separates from the glossopharyngeal and courses posteriorly into the neck.

The pharyngolaryngeal ramus of the glossopharyngeal nerve (superior laryngeal ramus of the vagus plus pharyngeal ramus of the glossopharyngeal) here changes its course ventrad and follows the posterior contour of the auditory sac. Just anterior to the hypoglossal nerve it passes ventrally, medial to the jugular vein and lateral to the thymus gland. At this point two small branches are given off. One, extending posteriorly, passes ventral to the jugular vein and thymus gland and over the lateral surface of the aortic arch to supply the carotid sinus (Fig. 57). The second branch passes anteriorly medial to the dorsal process of the first ceratobranchial and the ceratohyal cartilage, lies on the dorsal surface of the throat musculature, and joins the posterior border of the pharynx. Before this branch turns anteriorly and crosses the posterior cornu of the first ceratobranchial and the ceratohyal, it joins the hypoglossal nerve (Fig. 57) and crosses it dorsally but continues with it across the hyal cornu, contributing a small branch to the hypoglossal.

Immediately after crossing the hyal cornu, most of the glossopharyngeal nerve leaves the hypoglossal (Fig. 38) and extends medially, crosses the hyomandibular artery dorsally, and then takes an anteromedial course between the hyoglossus muscle ventrally and the branchiohyoideus muscle dorsally, giving off numerous (3-5) dorsal branches to the branchiohyoideus (Fig. 39). As it crosses the muscle it lies medial to the hyomandibular artery and accompanies the glossopharyngeal artery to the larynx. Toward the anterior part of the branchiohyoideus muscle several perforating branches pierce the muscle and extend dorsally, fanning out on the floor of the pharynx. On leaving the anterior border of the branchiohyoideus, the nerve lies ventral to the floor of the pharynx and dorsal to the body of the hyoid and gives several (2-3) branches to the pharyngeal membrane. At the level of the eighth tracheal ring it divides into a medial pharyngeal and a lateral lingual ramus (Fig. 39).

The *pharyngeal ramus* extends anteriorly along the lateral side of the trachea to reach the second tracheal ring. At this point it joins its fellow from the opposite side ventral to the trachea in an H-shaped laryngeal anastomosis (Fig. 51), but not in a complete chiasma. The fibers continue anteriorly from the anastomosis, and at the level of the proximal end of the cricothyroid cartilage are joined by the recurrent laryngeal nerve of the vagus, which lies on the dorsolateral side of the trachea. The combined nerves continue anteriorly, between the constrictor and dilator muscles, to innervate them and to carry visceral sensory fibers to the mucous membrane of the larynx.

The *lingual ramus* extends laterally to the dorsomedial surface of the hyoglossus muscle, covered by the superior transverse fibers of the tongue. It can be traced in this position within the tongue, anterior to the laryngeal fossa.

Vagus Nerve

The distribution of the vagus nerve is extensive; it innervates the larynx, pharynx, heart, and other viscera. Branches considered here are those of the head and those which eventually terminate in the head. Fibers of the vagus nerve extend within the glossopharyngeal nerve and the sympathetic trunks, making accurate gross determination of distribution impossible.

The vagus nerve is composed of both sensory and motor fibers emerging from the lateral wall of the medulla by approximately five dorsal and five ventral bundles of fibers. The roots extend dorsally, combine, and emerge through the vagal foramen of the exoccipital bone dorsal to the foramen of the posterior (third) ramus of the hypoglossal nerve (Fig. 42). After emerging from the skull the vagus extends posteroventrally to lie lateral to the insertion of the longissimus capitis muscle, ventral to the obliquus capitis magnus muscle and the posterior cerebral vein, and medial to the auditory sac. Ventral to the vagus are the first and second roots of the hypoglossal nerve, and ventrolateral to it is the glossopharyngeal nerve.

The jugular ganglion (root ganglion) lies at approximately the anterior edge of the axis along the ventral border of the longissimus capitis muscle. A large ganglion, which may be single or in several parts, spreads along the trunk.

Near the division of the jugular vein a single lateral branch is given off which immediately divides into two rami. The posterior one breaks up into a plexus around the constrictor vena jugularis muscle. The anterior ramus may join the plexus, it may give a ventral branch to the lateral cranial sympathetic trunk, or it may extend independently to join the trunk as the latter crosses the hyomandibular ramus of the facial nerve. The constrictor vena jugularis muscle receives innervation from two sources: fibers from the vagus, passing directly to the muscle, and fibers from the lateral cranial sympathetic trunk. These two groups of fibers form a plexus around the muscle. Bruner (1907) described the innervation of the constrictor vena jugularis muscle and demonstrated by stimulation that the source of the innervation was from the vagus. In none of the species which he dissected, however, did he find an independent branch of the vagus to the muscle.

A long, thin external ramus crosses the internal jugular vein to innervate the episternocleidomastoideus muscle. Continuing posteriorly, the vagus gives a single small branch to the combined trunks of the glossopharyngeal-sympathetic complex, and a larger superior laryngeal ramus, containing approximately half of the remaining fibers of the vagus trunk, to the glossopharyngeal nerve anterior to the petrosal ganglion (Fig. 57).

The vagus nerve continues posteroventrally as the ramus visceralis which passes ventral to the hypoglossal nerve and dorsal to the superficial cervical sympathetic trunk. At the anterior end of the thymus, where it lies on the dorsolateral surface of the thymus just medial to the jugular vein, it becomes tortuous and extends to the ventral border of the thymus, where the trunk ganglion (ganglion nodosum) is found.

Three nerves arise from the vagus at the level of the nodose ganglion. The first, ramus pharyngeus, arises medially, passes ventral to the carotid duct, posterior and dorsal to the carotid arch, and then turns anteriorly and divides into two rami which spread out on the dorsal and the ventral sides of the pharynx. Occasionally the pharyngeal ramus may yield a third ramus which extends posteriorly along the pharynx to the esophagus. The second nerve from the level of the nodose ganglion passes anteriorly to the first thymus, and the third, a very small branch, communicates with the sympathetic trunk.

As the main trunk of the vagus turns medially and passes posterior to the systemic arch, it gives off several cardiac branches and one large branch, the inferior laryngeal ramus. This ramus turns anteriorly, dorsal to the systemic and carotid arches and the tracheal vein, to join the trachea at a level just in front of the carotid arch. In joining the trachea it divides into two branches. One of these descends along the trachea and gives off small branches to the trachea. The other is the continuation of the inferior laryngeal ramus; it passes anteriorly along the dorsolateral side of the trachea and medial to the tracheal vein, accompanied by a tracheal artery. In this position it ascends to the larynx and joins the glossopharyngeal (superior laryngeal of X) at the proximal end of the cricothyroid cartilage (Fig. 51), the combined nerves terminating in the constrictor and dilator muscles and the epithelium of the larynx.

Willard (1915) suggested that the recurrent laryngeal ramus is entirely sensory. As it reaches the larynx it combines with the superior laryngeal ramus; the two branches lose their identity as they pass to the larynx. Sectioned material, however, shows that the fibers of the superior laryngeal ramus are coarser than those of the recurrent laryngeal nerve.

Hypoglossal Nerve

The hypoglossal in *C. pectinata* is not exclusively a nerve to the muscles of the tongue. Its fibers are distributed to cervical and hyoid musculature as well as to the intrinsic and extrinsic muscles of the tongue.

As pointed out by Willard (1915) in *Anolis carolinensis,* there are three distinct roots to the hypoglossal, emerging through three separate foramina in the exoccipital bone. The third root carries the cervical component; the three roots do not unite until after the cervical branches are given off. This distinctness of the roots and the cervical component would seem to indicate an origin from three spino-occipital segments.

In *C. pectinata* the hypoglossal nerve is composed of three distinct roots which leave the medulla through three hypoglossal foramina in the exoccipital bone. Each root, leaving the ventral horn, is composed of three fascicles, all in a distinct segmental relation to one another. The two anterior roots are not large, the first being the smaller, and emerge through the two lateral hypoglossal foramina on the dorsolateral border of the crista tuberalis. The third and largest root leaves through the hypoglossal foramen just lateral to the exoccipital condyle and ventral to the vagal foramen.

The first two roots (Fig. 42), after leaving the hypoglossal foramina, extend posterolaterally, lateral to the longissimus capitis muscle, medial to the glossopharyngeal nerve, and ventral to the vagus nerve. At approximately the posterior border of the longissimus capitis muscle the two roots unite, continue posteriorly, and join the third root as they cross the vagus and sympathetic trunks at the level of the anterior end of the third cervical vertebra.

As the third root emerges, a small dorsal branch from it passes ventral to the posterior cerebral vein and then continues dorsally, posterior to the vein and the occipital artery, to join the dorsal ramus of the first spinal nerve. The major part of the nerve root, however, continues ventromedially, passes lateral to the rectus capitis anterior muscle and medial to the longissimus capitis, and sends a large ventral branch to the lateral surface of the rectus capitis anterior. Posterior to this it is joined by the ventral ramus of the first spinal nerve. Emerging from behind the longissimus capitis muscle and carrying the ventral ramus of the first spinal nerve, the third root is joined by the first two roots combined (Fig. 42). The trunk then continues posterolaterally, crossing lateral to the carotid artery and to the cervical sympathetic trunk, from which it receives a contribution. It then passes medial to the vagus and turns ventrally to descend lateral to the above-named structures and the thymus and medial to the internal jugular vein (Fig. 57). The nerve extends over the dorsal and posterior surfaces of the tympanic cavity and descends ventrally behind the dorsal process of the ceratohyal and first ceratobranchial cartilages and medial to the episternocleidomastoideus muscle. It gives off ventrally a large part of the first spinal nerve which takes an independent course to innervate the sternohyoideus and omohyoideus muscles (Fig. 38).

The hypoglossal continues in an anteromedial course, passing ventral to the auditory chamber and crossing the posterior cornu of the ceratohyal and first ceratobranchial to innervate the muscles of the hyoid apparatus and the tongue.

Before the hypoglossal nerve crosses the posterior hyal cornu it is joined by the glossopharyngeal nerve which continues with the hypoglossal nerve for approximately 20 mm. and then takes an independent course to the larynx and tongue. As the hypoglossal nerve enters the throat region (Fig. 38), it lies lateral to the hyomandibular artery at the posterolateral border of the first mandibulohyoid muscle. It courses anteriorly, dorsal to the first mandibulohyoideus and ventral to the hyoglossus muscle. Posterior to the border of these muscles the glossopharyngeal fibers separate from the hypoglossal nerve and take a medial course, dorsal to the hyomandibular artery.

The hypoglossal gives off four small ventral branches to the first mandibulohyoideus muscle, the anterior of the four being long and lying on the dorsal surface of the first mandibulohyoideus, which it perforates to enter the lateral border of the second mandibulohyoideus. A fifth single lateral branch crosses the ceratohyal cartilage to enter the ventral surface of the third mandibulohyoideus muscle. There also may be several dorsal fibers which enter the posterior ventral surface of the hyoglossus muscle.

At approximately the insertion of the genioglossus muscle into the hyoglossus muscle, the hypoglossal nerve divides into three major branches. The lateral branch, *ramus lingualis lateralis,* is the largest and is very tortuous. It extends anterolaterally, pierces the insertion of the medial fibers of the genioglossus, and continues anteriorly between the medial and lateral parts of that muscle, giving off small fibers to both parts. It extends lateral to the medial fibers of the muscle and then lies between the medial surface of the genioglossus (lateral part) and the ventral transverse fibers of the tongue proper (Fig. 39). As it emerges on the lateral surface of the lateral fibers of the genioglossus muscle it is joined by the lingual ramus of the trigeminal nerve, carrying fibers of the chorda tympani of the facial nerve. The major mass of fibers continues forward to the anterior part of the genioglossus muscle (lateral part); other fibers join the lingual branch of the trigeminal nerve and pierce the tongue to supply the superior and inferior transverse muscles and to bring special visceral afferent fibers to the anterior part of the tongue. These fibers could not be traced to taste buds.

The intermediate branch of the hypoglossal nerve (Fig. 38), *ramus lingualis intermedius,* pierces the insertion of the genioglossus muscle at its mid-point and continues dorsally to enter and supply the cylindrical mass of the hyoglossus, within which it extends to the tip of the tongue.

The medial branch, *ramus lingualis medialis,* extends medially, passes through the insertion of the medial fibers of the genioglossus muscle to enter the ventral part of the tongue just to one side of the mid-line, and innervates the vertical fibers. It extends anteriorly, remaining in the vertical fibers, but it may innervate also the medial fibers of the superior and inferior transverse muscles as they cross the mid-line.

First Spinal Nerve

The first spinal nerve is composed entirely of motor elements. Eight to ten fascicles leave the ventral horn and combine into a root which leaves the spinal canal between the occipital bone and the atlas, with, and posterior to, the posterior cerebral vein and the occipital artery (Fig. 42). After emerging, the nerve divides into a dorsal and a ventral ramus.

The *dorsal ramus* divides into three branches, the most dorsal of which is joined by a small branch from the posterior ramus of the hypoglossal nerve. It continues dorsally, passing between the rectus capitis posterior muscle medially and the obliquus capitis magnus laterally, innervating each as it passes. It terminates in the ventral surface of the spinalis capitis muscle (Fig. 41). The ventral branch extends ventrally into the medial surface of the longissimus capitis muscle. The lateral branch extends around the anterior surface of the longissimus capitis and then passes dorsad between that muscle and the obliquus capitis magnus to enter the medial border of the transversalis cervicis. A small branch extends dorsally, medial to the transversalis cervicis, to innervate the lateral part of the spinalis capitis.

The *ventral ramus* extends over the lateral surface of the rectus capitis anterior muscle and divides into two branches. The medial branch turns ventromedially and innervates the rectus capitis anterior and the longus colli muscles. On its dorsal surface it receives the terminal ramus of the deep cervical sympathetic trunk. The lateral branch joins the third ramus of the hypoglossal nerve medial to the longissimus capitis. The nerve resulting from this union continues with the hypoglossal, crosses the internal carotid artery, the sympathetic trunk, and the vagus nerve, and then turns ventrad and passes medial to the internal jugular vein. Before the nerve crosses the hyal cornu, at least part of the ventral ramus leaves the hypoglossal nerve and continues ventrally, lateral to the hyomandibular artery. It then lies between and innervates the omohyoideus ventrally and the sternohyoideus dorsally (Fig. 38).

THE SYMPATHETIC SYSTEM (CERVICAL)

The first treatment of the peripheral branches of the sympathetic nervous system in reptiles is that of Fischer (1852). The most complete work on the reptiles was by Hirt (1921), in a comparative study of several reptiles, mostly Old World species. A detailed comparative study by Terni (1931) laid a basis for a functional understanding of the distribution of the sympathetic nerves. W. E. Adams (1942) showed that the major outflow of the cervical sympathetic system was from the eighth, ninth, and tenth thoracic nerves and that this cervical outflow ran almost exclusively craniad. He suggested that some of these fibers are preganglionic, extending through to the sphenopalatine ganglion, the uppermost ganglion of the head.

The sympathetic system of the head and neck of *Ctenosaura pectinata* begins with the superior cervical ganglion situated at the level of the seventh cervical vertebra immediately ventral to the subclavian artery. The level of the ganglion is variable; it may be anterior to the subclavian artery. It is continuous posteriorly with the abdominal sympathetic chain and gives off to the brachial plexus other branches which are not in the scope of the present study. In the head the thoracic sympathetic and the cranial sympathetic outflows, with the exception of the oculomotor fibers, are combined into a common trunk. There are no ganglia in the neck region above the superior cervical ganglion; however, within the head, groups of ganglion cells may be found along any nerve carrying sympathetic fibers. Four distinct ganglia are constantly present: the mandibular, the palatine, the ethmoidal, and the infraorbital.

The sympathetic system in the neck is composed of two cervical paravertebral trunks: a medial deep and a lateral superficial. The *deep cervical trunk* originates from the medial side of each superior cervical ganglion as one trunk or as two branches, usually passing medially ventral to the prevertebral muscles and dorsal to the systemic aortae, though sometimes penetrating the medial part of the muscle and running among its fibers. If two branches are present, they remain independent throughout their length and extend anteriorly in the interval between the pair of rectus capitis anterior muscles and along the prevertebral artery, generally following its branches. Anterior to the main trunk of the prevertebral artery they lie within the prevertebral muscle mass, entering the muscle mass ventrally at about the level of the sixth vertebra and emerging from it dorsolaterally at the level of the second vertebra.

As the deep cervical trunk passes anteriorly, it gives small branches to the cervical nerves. If it leaves the ganglion as two branches, the more posterior one turns dorsally and runs to the head, passing anterior to the transverse processes of the vertebra along the prevertebral arterial branches and giving branches to cervical nerves. The more anterior one then maintains a superficial distribution and does not give off branches to these nerves, but joins the deeper component as it pierces the rectus capitis anterior muscle.

The largest sympathetic ramus to join any cervical nerve is one that joins the first. The junction occurs on the dorsolateral border of the rectus capitis anterior muscle at the mid-point of the first cervical vertebra and just anterior to the insertion of the longus colli muscle. Stained sections show that the sympathetic trunk joins an anterior primary division of the first cervical nerve and divides, one group of fibers going to the anterior division and the other turning dorsally and probably entering the posterior division. A separate sympathetic ramus to the hypoglossal nerve, as described by Hirt (1921), was not found. Instead, there is a branch, not described by Hirt, from the superficial cervical trunk to the hypoglossal.

The *lateral superficial cervical trunk* (Fig. 57) is a large nerve arising from the anterior end of the superior cervical ganglion. It extends forward into the neck along the ventral surface of the rectus capitis anterior muscle. At its origin it is covered by pleura, but as it continues into the neck the pleura reflects, and the trunk is found dorsally between the carotid artery and the jugular vein.

At a variable point near the carotid arch several branches of the lateral superficial cervical trunk are given off to the "carotid body," the carotid arch, the thymus gland, and the vagus nerve. At the anterior end of the thymus the sympathetic trunk is crossed dorsally by the hypoglossal nerve which receives a small branch from it at this point. In the upper neck region the vagus nerve crosses to the lateral side of the sympathetic trunk and sends a branch to it. The sympathetic trunk joins the ventromedial side of the petrosal ganglion of the glossopharyngeal nerve and continues with the glossopharyngeal nerve for a short distance, eventually separating from it and dividing into two branches, the lateral and the medial cranial trunks (Fig. 42).

The *lateral cranial sympathetic trunk* extends dorsolaterally on the dorsal surface of the stapedial artery. Its main trunk, formed of one or two roots which also supply several branches to the plexus around the constrictor vena jugularis muscle, joins the hyomandibular division of the facial nerve ventromedial to the tip of the paraoccipital process. It then separates a few millimeters laterally from the facial nerve and continues with the temporal artery, over the paraoccipital process posteriorly and over the quadrate bone anteriorly, onto the dorsal surface of the adductor musculature. A lateral ramus from it passes through the superior notch of the quadrate bone and into the lateral space of the tympanic cavity to supply the glands of this area. The trunk then continues anteriorly with the temporal artery and passes between the adductor musculature and the postorbital bone where it divides into a medial and a lateral ramus (Fig. 40). The lateral ramus extends laterally and joins the first maxillary nerve in a plexus, small groups of ganglion cells occurring at each junction. The plexus distributes to the glandular area of the inferior eyelid and possibly also throughout the distribution area of the infraorbital nerve. The medial branch joins the posterior branch of the frontal ramus of the ophthalmic division of the trigeminal, in a plexiform mass, the fibers of which distribute to the lacrimal gland and glandular areas of the upper eyelid.

The *medial cranial sympathetic trunk* (Fig. 42) extends anteriorly on the dorsal surface of the internal carotid artery into the dorsal part of the auditory sac, continues onward without branching to join the facial nerve proximal to the geniculate ganglion, and distributes itself in the palatine ramus of the facial nerve. Its course is ventrolateral to all of the cranial nerves and lies dorsal to the crista tuberalis, across the ventral border of the crista interfenestralis, ventral to the columella auris, and on the medial wall of the sulcus vena jugularis, where it joins the palatine fibers of the facial nerve at the ventral border of the geniculate ganglion. This point is also known as Jacobson's anastomosis, since it is a junction point between the facial nerve and those fibers of the glossopharyngeal which ascend with the medial cranial sympathetic trunk. Further distribution of the fibers of the medial cranial sympathetic trunk is with the palatine ramus of the facial nerve.

THE ARTERIES

Early studies of Corti and Rathke laid a foundation for the present interpretation of the saurian arterial system. Numerous other studies have been made of different species. The most useful and complete studies pertaining to the arteries of the head are those of O'Donoghue (1921), Bhatia and Dayal (1933), Shindo (1914), and Dendy (1909). O'Donoghue's (1921) study on *Sphenodon* is the most complete and forms the basis for the terminology of the present study.

Although the present study does not include the venous system, frequent reference is made to it. Bruner (1907), whose terminology is used here, presented a very complete account of the veins and sinuses of the lacertilian head.

The arterial system of the head and neck is a combination of branches from the three pairs of aortic arches that are common to all lizards.

The Pulmonary Arches

Each pulmonary arch (Fig. 57), the most posterior of the three pairs of aortic arches, gives rise to a single artery, the *laryngotracheal artery*, which extends anteriorly into the neck along the lateral border of the trachea. Equally developed on both sides, it ascends along the ventral border of the tracheal vein to the level of the thyroid gland where the major part of the artery terminates as the *inferior thyroid artery*. This artery is short and extends ventrally to the dorsal surface of the thyroid gland, breaking up into branches to supply the dorsomedial parts of the thyroid. The terminal branch of the laryngotracheal artery, the *tracheal artery*, accompanies the recurrent laryngeal nerve on the lateral surface of the trachea. It extends to the level of the larynx, gives off a branch to the connective tissue of each interannular tracheal space, and terminates on the larynx. Its part in supplying the larynx, however, is practically negligible; the major supply is from the laryngeal branch of the glossopharyngeal artery. The laryngotracheal artery supplies primarily the thyroid gland and trachea. It does not appear to have the pharyngeal branches present in some lizards (Drummond, 1946), nor is it important in the supply of the larynx as in *Sphenodon* (O'Donoghue, 1921).

A variation of this pattern was noted in one specimen in which an unpaired laryngotracheal artery arose from the mid-line bifurcation of the carotid arch. This artery was described as the median thyroid artery by Bhatia and Dayal (1933), who stated that it is unique to *Hemidactylus*.

The Systemic Arches

The systemic arches supply only one artery, the prevertebral, to the cervical region. This artery is ultimately important since its terminal branches may provide a major part of the intracranial supply to the brain.

The *prevertebral (vertebral) artery*, usually unpaired, most often arises from the dorsal surface of the dorsal aorta opposite the seventh cervical vertebra at the level of the subclavian artery, though it may arise from the systemic aorta if the systemic arches unite (posterior to the seventh cervical vertebra) to form the dorsal aorta. This prevertebral extends anteriorly along the ventral surface of the bodies of the seventh and sixth cervical vertebrae, gives off dorsal or vertebral arteries independently to the seventh and sixth interspaces, and then divides into a pair of deep trunks which lie on the ventral surface of the transverse processes of the vertebrae, dorsal to the longus colli muscle. At each interspace except the first a branch arises and divides, which sends a medial ramus through the intervertebral foramen to the spinal cord and a lateral branch to the surrounding musculature. Near its source the prevertebral artery gives off ventrally an anastomotic branch which extends anterolaterally on the dorsal surface of the pharynx. After giving small branches to the pharynx, the branch anastomoses with the medial branch of the musculocervicis artery.

The Carotid Arches

The carotid arches (paired common carotids) (Fig. 57) arise with the right systemic arch from the left ventricle by means of a common trunk (truncus arteriosus). The carotid arches arise from the common trunk separately, not as a carotid prima. Arising dorsal to the anterior end of the interclavicle, the arches diverge laterally, paralleling the systemic arches. Arching forward, each gives rise to an external carotid artery.

External Carotid Artery

The external carotid artery (Fig. 57) arises along the cephalic border of the carotid arch just as it turns dorsally at the lower level of the thyroid gland and lateral to the trachea. The artery is very short and immediately divides into two parts, a superior thyroid medially and a hyomandibular laterally.

The *superior thyroid artery* (Fig. 57) extends ventromedially and divides into two major branches. The posterior of these is large and goes to the ventral mid-line fat body just caudal to the thyroid, where it ramifies extensively and anastomoses with its partner. The anterior branch is small and extends to the lateral pole of the thyroid gland.

The *hyomandibular artery*, the major part of the external carotid, extends anterolaterally along the lateral border of the sternohyoideus muscle, deep to the omohyoideus muscle. At the lateral border of the omohyoideus it turns anteriorly around the dorsal process of the first ceratobranchial bone, where it lies just anterior to the episternocleidomastoideus and deep to the constrictor colli muscle. Its course runs ventral to the jugular vein and the vagus nerve.

Along the lateral border of the sternohyoideus muscle the hyomandibular artery gives off a trunk which immediately divides and sends one branch anteromedially between the omohyoideus and the sternohyoideus muscles, and a second long branch anteriorly to the lateral border of the pharynx. As the hyomandibular emerges from beneath the omohyoideus muscle, it passes dorsomesial to the first spinal nerve. Here it turns anteriorly and mesially and follows the ventral surface of the posterior fibers of the branchiohyoideus muscle (Fig. 38). As it crosses the dorsal process of the first ceratobranchial bone it is ventral to the hypoglossal nerve; on the ventral surface of the branchiohyoideus muscle it is mesial to the hypoglossal.

After crossing the first ceratobranchial bone the hyomandibular gives off laterally the *superficial pterygoid artery* (Fig. 38) which passes ventral to the glossopharyngeal nerve, dorsal to the hypoglossal nerve and ceratohyal cartilage, and around the posterolateral border of the third mandibulohyoid muscle. It then divides into an anterior and a posterior branch. The anterior spreads out on the ventral surface of the pterygomandibularis muscle and perforates it. The posterior extends dorsally to supply the fascia of the dorsal process of the first ceratobranchial bone, the ceratohyal cartilage, the depressor mandibularis muscle, and parts of the auditory sac.

The hyomandibular artery continues anteriorly, between the branchiohyoideus muscle dorsally, and the hyoglossus muscle ventrally and is crossed dorsally by the glossopharyngeal nerve. Here it gives off branches to both the first mandibulohyoid and the branchiohyoideus muscles, and as it reaches the lateral border of the hyoglossus muscle it divides into two terminal arteries, a medial glossopharyngeal and a lateral submandibular.

The *glossopharyngeal artery* (Fig. 39) extends mesiad, between the hyoglossus muscle ventrally, and the branchiohyoideus muscle dorsally. As it crosses the ventral surface of the branchiohyoideus, lateral to the glossopharyngeal nerve, it gives off muscular branches. It then crosses the glossopharyngeal nerve ventrally and lies on the ventral surface of the pharynx just lateral to the trachea. As it reaches the trachea it gives off dorsally a pharyngeal branch and ventrally a muscular one. The pharyngeal branch divides into anterior and posterior rami and supplies the ventral surface of the pharynx in the mid-line. The ventral muscular branch extends to the hyoglossus and the second mandibulohyoideus.

Continuing anteriorly with the glossopharyngeal nerve, the glossopharyngeal artery passes dorsal to the body of the hyoid and gives small branches to the trachea. At the posterior end of the larynx it gives off another pharyngeal branch which divides into an anterior and a posterior branch that distribute to the pharynx.

There are three terminal branches of the glossopharyngeal artery: the medial *laryngeal artery* (Fig. 51) accompanies the glossopharyngeal nerve to the larynx and enters it beneath the medial border of the dilator muscle; the intermediate branch extends ventrally to the medial border of the hyoglossus muscle; the lateral branch extends to the pharynx.

After the glossopharyngeal artery is given off, the hyomandibular artery continues as the *submandibular artery* (Fig. 39) along the lateral border of the hyoglossus muscle. Near the origin of that muscle it is crossed ventrally by the hypoglossal nerve, and anterior to this crossing it sends a ventral muscular branch to the third mandibulohyoid and the lateral border of the hyoglossus. As the submandibular artery crosses the ventral surface of the pharynx, at the anterior border of the pterygomandibularis muscle, it gives off a dorsal branch which spreads out extensively on the lateral part of the ventral surface of the pharynx. This branch gives off a cutaneous branch which pierces the first and third mandibulohyoideus muscles and emerges with the mylohyoid nerve along the anterior border of the intermandibularis posterior muscle to distribute to the musculature and skin of the throat. Continuing anteriorly the submandibular artery pierces the insertion of the genioglossus muscle to lie along the ventrolateral border of the hyoglossus muscle dorsally, the genioglossus muscle ventrally, and the lateral lingual branch of the hypoglossal nerve mesially; it gives off branches to both muscles. At the level of the larynx the submandibular artery divides into a dorsal and a ventral branch.

The ventral branch, the *musculomandibular artery,* extends anteriorly to the symphysis of the jaw, passing between and supplying branches to the genioglossus and the hyoglossus muscles. Laterally, the artery gives off two perforating branches. The first joins with the mandibular artery to pass between the lateral and ventral fibers of the genioglossus and to continue laterally around the posterior border of the anterior superficial intermandibularis muscle. It then divides into two branches. One extends anteriorly between the mandible and the intermandibularis anterior superficialis, supplies that muscle, gives some superficial branches to the skin, and terminates in the musculature around the sublingual gland. The posterior branch sends some superficial branches to the skin around the anterior end of the origin of the first mandibulohyoid muscle, sends an anastomotic branch to the mandibular artery, and perforates the origin of the intermandibularis anterior profundus to supply the lateral part of the oral membrane deep to that muscle at the level of the anterior mandibular foramen. The second (anterior) perforating branch extends laterally into the deep surface of the common origin of the genioglossus muscle.

The dorsal branch, the *genioglossus artery,* extends deeply along the insertion of the genioglossus (lateral fibers) and gives off dorsal branches to supply the tongue (genioglossus lateralis and hyoglossus muscles), all the way to the tip.

After giving off the external carotid, the carotid arch turns caudally. At approximately this point it gives rise to the internal carotid artery (Fig. 57) and then continues posteriorly as the *carotid duct* to join the systemic arch.

"Carotid Body"

Lying on the dorsolateral border of the junction formed by the carotid duct, the internal carotid artery, and the carotid arch there is a small, solid, raised oval body. It appears to be imbedded in the walls of the arch; however, it is partly dissectible from the arch. This is epithelial body III which, according to W. E. Adams (1939), is derived from the ventral part of the third pharyngeal pouch. In general reptilian literature this has been known as the "carotid body" or "carotid gland" (Chowdhary, 1950), without particular emphasis as to its functional relation to the mammalian carotid body. Further studies by W. E. Adams (1952) indicate that it "has no affinity with the mammalian carotid body." Moreover, he described a highly specialized tissue within the walls of the arterial junction in this area as synonymous with the carotid body. This tissue cannot be seen grossly.

If the aortic arch is split open and the entrance to the internal carotid artery examined, seven perpendicular cords can be seen forming a grillwork over this entrance. These cords are fibrous in cross section and apparently function as a mechanism for regulating increases and decreases in pressure, or as a carotid sinus. This area is innervated by fibers from the glossopharyngeal nerve and the sympathetic trunk. From their position and innervation it appears that they do have some regulatory control similar to that of the carotid body and sinus. Physiological proof is not available.

Internal Carotid Artery

The internal carotid artery (Fig. 57) arises at the junction of the carotid arch with the carotid duct. The junction lies along the ventrolateral angle of the dorsal neck musculature, just medial to the vagus nerve, at the level of the thyroid gland. The internal carotid artery extends cephalad through the neck without giving off any branches. It winds around the neck musculature and comes to lie on the lateral surface of the neck. Its course is medial to the thymic glands and jugular vein, ventral to the sympathetic trunk, and ventromedial to the vagus nerve. Maintaining these relations, it comes to lie on the dorsal surface of the tympanic sac at the level of the retroarticular process of the lower jaw. On the dorsal surface of the tympanic membrane and at the level of the posterior border of the longissimus capitis muscle, the internal carotid artery is crossed by the hypoglossal nerve and the glossopharyngeal nerve as they emerge from the head. The vagus and sympathetic trunks also cross from medial to lateral; however, they maintain a continuous relation to the carotid posteriorly. Anterior to these structures the posterior cerebral vein crosses the artery.

At approximately the level of the anterior surface of the third cervical vertebra, the internal carotid bifurcates. One limb is the stapedial; the other is a continuation of the internal carotid. The latter continues anteriorly on the dorsomedial surface of the tympanic cavity, accompanied by the medial cranial sympathetic trunk. It crosses the upper border of the occipital recess in the carotid fold and the crista interfenestralis to lie on the lateral surface of the basioccipital and the basisphenoid until it reaches the entrance of the vidian canal. Within this canal it gives off a single branch, the palatine artery, continues within the basisphenoid, and emerges by the carotid foramen. Here it passes dorsally within the folds of the metoptic membrane and pierces the pituitary diaphragm to supply the brain.

The *palatine artery* (Fig. 53) separates from the internal carotid within the vidian canal of the basisphenoid. It accompanies the palatine ramus of the facial nerve through the basisphenoid and emerges on the anterior surface of that bone. Upon emerging from the canal the artery lies lateral to the pharyngeal membrane, dorsal to the basipterygoid process of the basisphenoid bone, and mesial to the protractor pterygoideus muscle and epipterygoid articulation.

The first branch of the palatine is a small artery which extends ventrally and then posteriorly, ventromedial to the basipterygoid process, to supply the pharyngeal membrane ventral to the basicranium. Just anterior to the first branch a mesial branch, the *medial palatine artery,* turns dorsad on the pharyngeal membrane and proceeds until it reaches the parasphenoid process; it then continues craniad in the mid-line on the dorsal surface of the pharyngeal membrane until it reaches the orbitonasal membrane. Here it sends a lateral anastomotic branch to the palatine artery and is joined by an anastomosing branch from the inferior nasal. In its course it gives small branches to the pharyngeal membrane.

At the level of the epipterygoid condyle a large lateral muscular ramus is given off from the palatine artery to supply the levator and protractor pterygoideus. Additional branches from the palatine artery go to dura and ganglia of the trigeminal nerve.

Continuing anterolaterally, the palatine artery lies ventral to the palatine ramus of the facial nerve on the dorsal surface of the transverse process of the pterygoid. Before passing beneath the orbital fascia, it gives off a lateral artery which goes to the membrane of the coronoid recess. The main ramus continues craniad with the medial palatine nerve beneath the orbital fascia.

Just after passing the transverse process of the pterygoid, it gives off a lateral ramus which pierces the posterior end of the inferior orbital membrane and splits into anterior and posterior branches on the ventral surface of the palate. The posterior of these supplies the palatal area around the pterygoid teeth; the anterior extends along the lateral glandular stripe to supply that area, and anastomoses with the palatine branch of the inferior orbital artery.

The palatine artery continues on the dorsal surface of the palatine bone, accompanying the medial palatine artery and giving off numerous gustatory branches which pierce the palate and supply the medial gustatory stripe. Near the anterior end of the orbital floor a medial branch extends to the mid-line and supplies the pharyngeal membrane. The artery terminates by anastomosing with the inferior nasal branch of the frontal artery.

The *stapedial artery,* a large artery (Fig. 42) which extends laterally toward the paraoccipital process of the opisthotic bone, lies in the dorsal membrane of the tympanic sac and is accompanied on its dorsal surface by the lateral cranial sympathetic trunk. Along its lateral surface are the jugular vein and the constrictor vena jugularis muscle.

Continuing anteriorly, the tympanic artery crosses ventral to the hyomandibular ramus of the facial nerve and the paraoccipital process of the opisthotic bone. As it crosses beneath the hyomandibular ramus it gives off externally a small *auricular artery* which passes around the posterior surface of the cephalic condyle of the quadrate, gives branches to the membrane of the tympanic sac, and divides into three small rami. One ramus continues over the ligament of the extracolumella with the chorda tympani nerve and divides, one twig extending out to the tympanic membrane on the extracolumella and the other supplying the inner surface of the tympanic sac. The second ramus passes with the ligament of the extracolumella to the tympanum on its pars inferior. The third continues with the hyoid ramus of the facial nerve over the surface of the tympanic sac to supply that membrane.

After crossing beneath the paraoccipital process, the stapedial artery turns dorsally to lie in the interval between the lateral surface of the paraoccipital process and the medial surface of the cephalic condyle of the quadrate. At this point the artery divides into two dorsal arteries, the occipital and the temporal, and a ventral one, the mandibular.

The *occipital artery* extends dorsally, medial to the supratemporal bone and the posterior process of the parietal bone, to enter the neck musculature (Fig. 42) where it divides into two rami, a dorsal and a ventral (Fig. 41)

The dorsal ramus extends onto the posterior surface of the adductor mandibularis externus profundus muscle and lies in the interval between the spinalis capitis dorsally and the rectus capitis posterior and obliquus capitis muscles ventrally, forming a freely suspended arc which extends from lateral to medial. Occasionally, this interval is filled with fat, in which case the arc is found deep within the fat mass. The arc gives off branches to the adductor mandibularis and the longissimus cervicis muscles and then divides into an anterior and a posterior branch. The posterior branch gives twigs to the spinalis capitis dorsally and to the obliquus capitis major and the rectus capitis posterior muscles ventrally. The anterior branch extends toward the mid-line and supplies the nuchal ligament; it then extends to the insertion of the rectus capitis posterior, giving off numerous twigs to the fat body surrounding it.

The ventral ramus of the occipital artery passes around the lateral border of the transversalis cervicis and turns medially beneath that muscle to lie on the neurovascular bundle and the tympanic membrane. Here it crosses the posterior cerebral vein and gives off the first spinal artery (Fig. 42), which enters the skull through the lateral part of the atlanto-occipital ligament just posterior to the emerging posterior cerebral vein. Other twigs from the ventral branch supply the muscles of the neck. One twig may enter the skull with the third branch of the hypoglossal nerve.

The *temporal artery* (Figs. 33 and 42) extends dorsad as the second division of the stapedial artery, passing on the lateral surface of the supratemporal process of the parietal bone. As it passes dorsad, it pierces the origin of the adductor mandibularis externus medius and then becomes superficial to that muscle in the supratemporal fossa (Fig. 40), lying just beneath the skin. As it passes craniad through the fossa, over the surface of the adductor mandibularis medius muscle, it is accompanied by the lateral cranial sympathetic trunk. Continuing craniad, it crosses the pseudotemporalis superficialis muscle and then turns ventrad to descend between the postorbital bone and the anterior border of the pseudotemporalis superficialis.

As it passes over the anterior border of the pseudotemporalis superficialis muscle, the temporal artery gives off a mesial ramus, the *frontal artery* (Fig. 40), which extends to the ventral surface of the lateral process of the frontal bone and passes craniad along the lateral border of the taenia marginalis and the planum supraseptale, tightly held in connective tissue and accompanied by the frontal ramus of the ophthalmic division of the trigeminal nerve. The artery continues along the ventral border of the frontal and the olfactory canal to a level just dorsal to the body of the superior oblique muscle, where it gives off a lateral branch, the *anterior orbital artery*. This artery supplies the Harderian gland and then continues laterad to the conjunctival fornix and the glandular areas in the superior eyelid. The frontal artery now lies free in the orbit and continues ventrad beneath the sphenethmoidal commissure. On the posterior surface of the orbitonasal membrane it divides into two branches, a superior and an inferior nasal.

The *superior nasal artery* is a small branch extending anteriorly with the ramus nasalis of the ophthalmic division of the trigeminal nerve. It pierces the planum antorbitale, passing through the lateral olfactory foramen, and terminates in the epithelium of the dorsal and mesial surfaces of the olfactory chamber.

The *inferior nasal artery* extends ventrad in a line perpendicular to the palate. In its ventral course it is lateral (occasionally mesial) to the ophthalmic division of the trigeminal nerve and posterior and lateral to the communicating branch between the ophthalmic division of that nerve and the palatine ramus of the facial nerve. Just beneath the ophthalmic division it gives off a mesial branch which splits and supplies the heads of the superior and inferior oblique muscles. Near its ventral end it becomes first lateral and then anterior to the communicating ramus. As the inferior nasal artery reaches the palate it divides into three branches. The first is an anastomosing branch which extends mesiad, anterior to the communicating ramus of cranial nerves five and seven, and anastomoses with the palatine artery. The second, a lateral branch, passes with the intermediate palatine nerve into the palatine foramen and thence to the nasal cavity, where it anastomoses with a branch of the maxillary artery. It then continues anteriorly along the lateral border of the fenestra exochoanalis, or the mesial border of the maxilla, supplying this lateral palatine area. The third branch, the major part of the inferior nasal artery, continues anteriorly, passing through a foramen formed by the orbitonasal membrane and the palatine bone to lie with the medial palatine nerve on the dorsal surface of the vomerine process of the palatine bone. It gives off short dorsal branches to the epithelium of the olfactory chamber and then continues anteriorly on the dorsal surface of the vomer. It pierces the vomer just posterior to the capsule of Jacobson's organ and passes to the ventral surface where it lies in a canal with the medial palatine ramus of the facial nerve. A small branch of it also pierces the vomer to enter Jacobson's organ. The artery then terminates on the ventral surface of the premaxilla by anastomosis with the terminals of the subnarial artery.

The *temporal artery* continues ventrally beyond the origin of the frontal artery, and on the anterior surface of the pseudotemporalis superficialis muscle. Posterior to the orbital fascia it divides into the superior and the inferior orbital arteries.

The *superior orbital artery* extends from the temporal artery ventromesially across the anterior surface of the pseudotemporalis superficialis muscle and pierces the posterior wall of the orbitotemporal membrane. As it pierces this membrane, it gives off a rather large artery which extends laterally to the posterior angle of the eye and divides, sending one branch to the conjunctival membrane and the other to the lacrimal gland just dorsal to the posterior limb of the orbital sinus. It continues to the dorsal surface of the bursalis muscle just above the tendon of the nictitating membrane. Here, it turns craniad and gives off a ventral branch which extends between the posterior rectus and the bursalis to supply these muscles.

Continuing anteriorly, the superior orbital artery passes between the ventromedial surface of the superior rectus and the tendon of the nictitating membrane, giving a branch to the former. At the posterior border of the optic nerve a ventral and a lateral branch are given off. The ventral branch extends deep, posterior to the optic nerve, and divides into two branches. One passes posteriorly beneath the ciliary nerve and then follows the ventral border of that nerve to the bulb; the other gives a small ramus to the retractor bulbi muscle and a branch to the ventral border of the optic nerve. The lateral branch passes beneath the tendon of the nictitating membrane to the bulb, piercing the posterodorsal surface of the sclera.

As the superior orbital artery passes dorsal to the optic nerve, it gives off mesially the *ophthalmic artery* which passes ventral to the anterior border of the superior rectus muscle, the ophthalmic division of the trigeminal nerve, and the trochlear nerve. It enters the cranial cavity through the optic foramen by piercing the optic membrane dorsal to the optic nerve. Anterior to the optic nerve the superior orbital artery gives off a second lateral bulbar branch which passes ventral to the tendon of the nictitating membrane and pierces the anterodorsal border of the sclera. It also gives off a small branch to the anterior rectus muscle.

The *inferior orbital artery* continues ventrally, accompanied by a branch of the lateral cranial sympathetic trunk. At the level of the tendon of the pseudotemporalis it gives off a branch to that muscle and also a long branch which extends laterally to the anterior border of the adductor mandibularis externus muscle. This branch, the *coronoid artery,* passes dorsally across the inferior orbital branch of the trigeminal nerve and enters the adductor muscle. A branch of this artery extends ventrally to supply the membrane of the coronoid recess.

The inferior orbital artery crosses the lateral side of the inferior orbital branch of the trigeminal nerve, pierces the orbital fascia, and extends anteriorly with the nerve, between the bulb of the orbit and the dorsal surface of the levator bulbi muscle. Its course is craniad; however, near the anterior border of the orbit it turns mesiad, following the contour of the levator bulbi, and as it leaves that muscle it turns laterally to enter the infraorbital foramen of the palatine bone. As it crosses the levator bulbi, it gives off one to three orbital arteries which extend dorsally to the adjacent tissue and the lower lid.

As the inferior orbital artery leaves the levator bulbi muscle, it gives off a ventral branch, the *lateral palatine artery,* which passes around the posterior border of the maxillary process and divides into two branches, a posterior and an anterior. The posterior is small and extends for a few centimeters along the ventral surface of the maxillary bone to the posterior lateral palatal area. The anterior extends along the ventral surface of the maxilla anteriorly, accompanying the lateral palatine ramus of the facial nerve. This anterior branch gives off a small twig which supplies the ventral surface of the maxillary process of the palatine as far as the posterior rim of the fenestra exochoanalis.

Before the inferior orbital artery passes through the infraorbital foramen, it gives off the *anterior orbital artery,* which extends dorsally, mesial to the lacrimal duct, supplies the anterior angle of the eye, and sends a very small branch with the lacrimal duct into the lacrimal canal.

As the inferior orbital artery passes through the infraorbital foramen, it becomes the *maxillary artery.* This is a large artery which continues craniad into the nasal cavity along the dorsal surface of the palatal shelf of the maxilla and then enters the superior alveolar canal, within the maxilla, to emerge in the floor of the external naris. Within the nasal cavity it gives off a mesial anastomosing branch which joins the anastomosing branch of the inferior nasal artery and continues along the lateral border of the fenestra exochoanalis (see inferior nasal artery). The maxillary artery then enters the superior alveolar canal in the maxilla and gives off a large ventral branch which pierces the bone to terminate in an anterior and a posterior labial branch to the skin and lip covering the posterior part of the maxilla. It also gives a dental branch to the posterior part of the maxilla, supplying approximately ten teeth. This branch pierces the bone ventrally and runs in a deeper canal, giving off one or two branches to each tooth.

Within the superior alveolar canal several more labial and dental branches are given off. The most anterior labial branch is long and extends to the tip of the snout, passing beneath the external naris on the lateral surface of the maxilla. A single dorsal branch is given off which pierces the maxillary bone to supply the glandular area of the nasal cavity lying just beneath the lacrimal duct. The dental branches are numerous. Some continue anteriorly within the maxillary bone. Each one supplies approximately five teeth. As the artery reaches the external naris, it pierces the bone and divides into two branches, an ascending postnarial and a subnarial.

The *postnarial artery* turns dorsally on the anterior rim of the maxilla and then posteriorly, within the nasal cavity, to lie on the zona annularis. Passing between that cartilage and the paranasal cartilage into the aditus conchae, it supplies the lateral nasal gland lodged in the conchal cartilage. As the artery turns posteriorly it gives several branches to the plexus around the external nasal tube. Some of these branches emerge through the fenestra exonarina and supply the cutaneous tissue around the snout. A medial branch extends across the dorsal surface of the zona annularis and gives additional branches to the plexus around the anterior external nasal tube. A large medial branch, given off ventrally, extends between the zona annularis and the lamina transversalis anterior in the olfactochoanal membrane. Here it divides into several terminals which extend to the ventromedial border of the zona annularis and then turns dorsally to supply the plexus around the anterior chamber.

The *subnarial artery* extends anteromedially on the vomerine process of the maxilla, ventral to the nasal plexus, to which it gives numerous branches. A single large medial branch crosses the dorsal surface of the lamina transversalis anterior, ventral to the anterior chamber and its plexus and the anterior end of the zona annularis. It pierces the septomaxillary bone and supplies Jacobson's organ in the anterior chamber and the olfactory epithelium in the posterior chamber. The subnarial artery continues to the premaxilla, through which it accompanies the medial ethmoidal nerve to the snout and ramifies broadly there. Before the artery enters the premaxilla, a small branch extends dorsally to supply the anterior and dorsal rims of the plexus around the external naris. At the anteroinferior border of the cupola a ramus turns dorsally within the cupola and along the nasal septum to supply the anteromesial surface of the plexus of the anterior chamber.

The third branch of the stapedial artery, the *mandibular artery* (Fig. 42), extends ventrally on the mesial side of the quadrate. It supplies the lower jaw exclusively and forms an extensive anastomotic network around the mandibular condyle.

The mandibular artery extends anteroventrally between the paraoccipital process of the opisthotic and the mandibular groove of the quadrate bone and continues ventrally along the mesial border of the quadrate and the mesial surface of the adductor posterior muscle until it reaches the quadrate process of the pterygoid bone. Here it gives off the *posterior condylar artery* (Fig. 35), which extends posteroventrally on the posteromesial surface of the quadrate, crosses the pterygoquadrate joint to meet the mandible, into which it passes with the chorda tympani nerve. There it anastomoses with the anastomotic branch of the articular artery. The posterior condylar artery gives off several small branches. The first branch extends laterally into the quadrate foramen, along with the anterior tympanic vein, and emerges on the anterior surface of the quadrate to anastomose with the anterior condylar artery. The second branch extends laterally, giving some branches to the capsule of the pterygoquadrate articulation, and then continues to the chorda tympani nerve where it anastomoses with the chorda tympani branch of the auricular artery. The third, the continuation of the posterior condylar artery, sends some small branches to the capsule of the mandibular joint and gives off another which anastomoses with a medial branch of the articular artery that extends from the floor of the mandibular foramen as it passes over that joint; it then continues into the mandible with the chorda tympani nerve.

The mandibular artery continues ventrally over the lateral border of the quadrate process of the pterygoid and at its lower border gives off a second small branch, the *anterior condylar artery,* which extends laterally, just anterior and dorsal to the condyle of the quadrate, to anastomose with the perforating branch of the posterior condylar artery and to supply the anterior capsule of the mandibular condyle. Its terminal rami supply the adductor mandibularis externus muscles surrounding it and turn dorsally along the auricular border of the quadrate. It also sends a branch to join the lateral perforating branch of the articular artery at the posterior supra-angular foramen on the lateral surface of the mandible.

The mandibular artery continues into the lower jaw, at first mesial to the origin of, and then on the anterior border of, the adductor posterior muscle. It lies between the adductor internus and externus groups and is accompanied by the mandibular division of the trigeminal nerve which lies anterior to it. As it passes between these groups of muscle, it gives off branches to each of them. As the artery enters the mandibular foramen, it gives off a posterior branch, the *articular artery,* which extends between the adductor mandibularis externus laterally and the adductor posterior mesially and is accompanied by a branch of the trigeminal nerve. This artery crosses the lateral side of Meckel's cartilage and splits into two branches, one of which pierces the internal articular foramen in the medial surface of the supra-angular bone and emerges from the posterior supra-angular foramen on the lateral side of the supra-angular, just ventral to the condylar fossa. It then anastomoses with the anterior condylar artery and extends anteriorly and posteriorly, along the origin of the intermandibularis muscle, to the skin. The medial branch extends posteriorly over the angular process of the articular and anastomoses with a branch of the posterior condylar artery at the mandibular condyle.

The mandibular artery continues into the mandibular foramen, where it lies ventral to the mandibular nerve. At the level of the posterior end of the coronoid bone it becomes the *internal mandibular artery* and gives off a branch, the *external mandibular artery,* which extends laterally across Meckel's cartilage to emerge from the anterior supra-angular foramen within the fibers of the adductor mandibularis externus muscle. This artery extends anteriorly on the lateral surface of the coronoid and dentary bones, accompanied by the inferior labial nerve, and supplies the lateral labial glands and the skin of the area. The artery anastomoses with the perforating branches which emerge from the dentary.

The *internal mandibular artery* continues anteriorly within Meckel's canal, on the dorsolateral surface of Meckel's cartilage. It gives several short ventral branches to the adductor posterior muscle and a lateral branch which passes out with the anterior mylohyoid nerve. A large medial branch emerges from the inferior alveolar foramen, ventral to the intermandibularis anterior muscle, to anastomose with the perforating branch of the musculomandibular artery.

The terminal part of the internal mandibular artery lies on the dorsal surface of Meckel's cartilage and gives off three perforating branches which pierce the dentary to supply the lateral labial glands and the skin of the tip of the jaw. The posterior branches of this artery anastomose with the external mandibular.

Musculocervical Artery

The musculocervical artery (Fig. 57) arises from the junction of the carotid arch and the carotid duct, or from the carotid duct alone. It usually arises from the dorsal side of these vessels and almost immediately divides into three branches. One, a large dorsolateral branch, extends dorsad to the neck musculature. It retains the name of the vessel. A small branch extends craniad from this artery along the mesial side of the sympathetic trunk as far as the first interspace and may give rise to the first spinal artery. Sometimes the first spinal is a branch of the occipital artery. The second branch of the musculocervical artery extends anteromesially across the ventral surface of the neck musculature to supply the posterior surface of the esophagus. The mesial branch anastomoses with the esophageal branch of the prevertebral artery, and the lateral branch extends to the junction of the pharyngeal space and the esophagus and supplies this area. The third branch of the musculocervical artery is short; it bifurcates and sends its two rami to the posterior poles of the two thymic bodies.

THE SNOUT

The snout of lizards has been described from various aspects by numerous workers. The development, originally described by Parker (1879) and Gaupp (1900), has been summed up by De Beer (1937). These descriptions of its development form the basis for the terminology of the cartilaginous structure of the nasal region. Jarvik (1942) added to this terminology by defining the entrances and exits. The adult form of the cartilaginous nasal capsule was first described by Born (1879) and more recently by Bellairs (1949a), and by Bellairs and Boyd (1947 and 1950); Pratt (1948) contributed additional interpretations of functions of the snout, and Beecker (1903) distinguished topographic regions of the nasal sac.

The snout is covered by an adherent layer of scaly skin. The scales are flat and uniform, except that rostral, loreal, and labial scales are enlarged. The skin is immovably attached to the deeper skeleton, with the exception of a thickened area on the snout which is slightly motile and is richly supplied with arteries and cutaneous nerves. In the area of the external naris there are highly vascularized and richly innervated thickenings of the skin which support the cartilaginous nasal tube and fill in the interval between that tube and the fenestra exonarina.

Osseous Nasal Capsule

The snout beneath the skin is almost completely invested in bone (Figs. 3 and 5) by the premaxilla, nasals, prefrontals, maxillae, and lacrimals dorsally, the vomers and palatines ventrally (Fig. 4). This strong osseous capsule is perforated by three paired openings: the fenestra exonarina, or external naris, surrounded by the premaxilla, maxilla, and nasal; the fenestra exochoanalis, or internal naris, formed by the vomer, palatine, and maxilla; and the fenestra vomeronasalis externa, an anterior constricted part between the vomer and maxilla, surrounding the duct of Jacobson's organ. In life the latter two fenestrae are separated by the cartilaginous lamina transversalis anterior. The terms applied to these foramina pertain to the osseous apertures only.

The osseous nasal capsule is continuous with the orbital cavity posteriorly through the orbitonasal fenestra which is closed by the orbitonasal membrane. The lacrimal foramina enter the posterolateral angles of the nasal chamber; ventral to these openings are the entrances of the infraorbital foramina. The cavity is smooth inside, with the exception of the nasal ridges in its roof. These ridges are the attachments for the olfactochoanal membranes. Anteriorly the septomaxilla lies on the dorsal surface of the vomer and only slightly constricts the anterior nasal tube. This osseous nasal cavity is completely filled by the paired cartilaginous nasal capsules. Specific bones and their relations are considered in the section on osteology.

Cartilaginous Nasal Capsule

The cartilaginous nasal capsule is an extensive continuous encapsulation of the anterior chamber, olfactory chamber, and Jacobson's organ and contains a continuous epithelial lining, the nasal sac (Figs. 43-49). There are two openings in the nasal capsule: the fenestra endonarina anteriorly (Fig. 43) and the fenestra endochoanalis posteriorly (Fig. 46). Dorsally the tectum is complete, but ventrally the floor has two openings: the ventral part of the anterior nasal tube and the fenestra endochoanalis.

The capsules are separated from each other by a complete *nasal septum* (Fig. 48). The nasal septum forms a small hourglass-shaped projection anteriorly, the rostrum, which is lodged in an excavation on the posterior surface of the premaxilla. The rostrum is constricted laterally by the premaxillary process of the maxilla and forms a median plug between the anterior processes of the vomers. Along its ventral border it is continuous posteriorly with the rounded cartilaginous basitrabecular process which lies between the paraseptal cartilages and becomes separated from the remainder of the septum just anterior to the planum antorbitale. The dorsal part of the septum is a flat sheet, the convex dorsal border of which expands laterally into the tectum nasi composed of the cupola, zona annularis, and paranasal cartilages and terminates posteriorly at the planum antorbitale.

The lateral surfaces are smooth, with the exception of the anterior part, which bears an oblique septomaxillary ridge that supports the septomaxillary bone and divides the septum into two contact surfaces. The area above the ridge is covered by the epithelium of the anterior chamber; that below the ridge, by Jacobson's organ; that posterior to the ridge, by the epithelium of the olfactory chamber.

Extending laterally from the rostral process of the septum is a thickened piece of cartilage, the lateral wing, which continues laterad with the tectum nasi to form the *cupola* (Figs. 43 and 47). This is a convex, tubular roofing cartilage covering the anterior nasal tube. Ventrally it is incomplete. Laterally it extends through the fenestra exonarina and is covered by a thickening of the dermis and skin. Its anterior extent is a free border lying on the premaxillary process of the maxilla, extending laterally through the fenestra exonarina and terminating just anterior to and below the fenestra in the inferior alar process (Figs. 44 and 47). The lateral border of the cupola extends dorsally from the inferior alar process, forming a perpendicular anterior border to the fenestra. It then extends posteriorly to terminate in the superior alar process at the posterior angle of the fenestra. The lateral border of the cupola, with its inferior and superior alar processes, forms the fenestra endonarina.

At the side of the thickened septal cartilage, just above the rostrum, is an opening in the tectum nasi, the apical foramen (Fig. 43), which transmits the terminals of the medial ethmoidal nerve.

Continuous posteriorly with the cupola and dorsomedially with the nasal septum is the *zona annularis* (Figs. 43 and 47). It is a continuous, nearly complete tube of cartilage extending along the nasal septum at right angles to the cupola. It passes laterally from the septum and surrounds the anterior chamber of the nasal sac. Its ventromesial border (Fig. 44) is attached to the annular crescent in the septomaxillary and continues posteriorly to attach along the free lateral border of that bone. The medial border then lies freely along the inferior rim of the foramen between the anterior and olfactory chambers, and at the mid-ventral point of that foramen becomes continuous with the medial border of the lamina transversalis anterior. At its posterior end the tubular zona annularis is closed by a dome-shaped capsule whose apex bears a single large foramen through which passes the duct of the lateral nasal gland. The medial rim of this dome is continuous with the paranasal cartilage and forms the posterior rim of the olfacto-anterior foramen.

The *paranasal cartilage* (Fig. 43) is a nearly complete spherical capsule surrounding a major part of the olfactory chamber of the nasal sac. It continues laterad from the dorsal border of the septum as a dome-shaped roof and appears dorsally as a transversely placed tube. The anterior border of the dorsal surface is thickened. Its lateral surface has a thickened anterior border and continues ventrad to form two processes along its ventrolateral angle, the lacrimal ridge and the posterior maxillary process (Fig. 47). The lacrimal ridge is derived from both the free border of the lamina transversalis anterior and the paranasal cartilage. The ridge extends ventrad, forming a roof for the lacrimal duct. Its ventral surface is incomplete but its posterior end forms, with the maxillary process, a nearly complete ring around the duct.

Extending ventrally and externally from the posterior ventrolateral angle of the paranasal cartilage is the maxillary process (Figs. 43-47). It lies dorsolateral to the structures passing through the superior alveolar canal and medial to the lacrimal duct. Its tip expands to seat itself in a recess formed by the postfrontal and the palatine dorsally and medially and by the maxilla ventrally. It also sends a process ventrally and dorsally around the lateral surface of the lacrimal duct, which nearly joins the lacrimal ridge of the paranasal cartilage, thereby forming an incomplete canal for the duct. It serves as a source of attachment to the osseous nasal capsule.

Ventrally the paranasal cartilage is continuous and forms the lateral, the posterior, and part of the medial rim of the fenestra endochoanalis (Fig. 46). Medially it is attached to the lateral border of the vomerine process of the palatine bone. Its posterior part continues medially and becomes continuous with the paraseptal cartilage. The posterior wall, *planum antorbitale,* of the paranasal cartilage is complete and continuous with the dorsal, lateral, and ventral parts already described. The dorsal part of the planum is continuous with the septum in the mid-line. The ventral part is continuous anteriorly with the paraseptal cartilage and forms a foramen between its medial border and the posterior border of the septum, through which the vomeronasal nerves pass. Its dorsomedial part is perforated by six or seven olfactory foramina which transmit the profundus nerve, the superior orbital artery, and the olfactory "nerves."

The medial wall of the paranasal cartilage is formed dorsally by the septum and ventrally by both the trabecula communis and the superior wall of the paraseptal cartilage. These structures are not adjacent and therefore do not constitute a complete wall. Its anterior wall is complete and forms a conchal invagination into the olfactory chamber (Figs. 44 and 45). The concha is approximately two-thirds the size of the olfactory chamber. In young individuals it is spherical but in older ones its surface may have additional invaginations. The anterior concavity of the conchal cartilage, the aditus conchae, is increased in size by the presence of the posterior wall of the anterior chamber which also constricts its entrance. The anterior nasal gland lies within the aditus. Medially the anterior wall of the paranasal cartilage continues into the zona annularis. At the superior part of this junction is the foramen epiphinale which transmits the lateral ethmoidal nerve. The ventral border of the anterior surface of the paranasal cartilage is continuous anteriorly with the lamina transversalis anterior.

The *paraseptal cartilage* (Figs. 46 and 48) is a distinct element extending anteriorly from the ventral and posterior walls of the paranasal cartilages. Its lateral border is attached in a groove on the posteromedial surface of the vomerine process of the palatine, and its medial border lies in contact with the basitrabecular cartilage. The two borders converge into a narrow process which is firmly attached to the dorsomedial border of the palatine and vomer and continues forward as a raised crest which terminates in the ventral surface of the cartilages of Jacobson's organ and the rostral part of the septum. Between the two paraseptal cartilages lies the ventral border of the nasal septum.

The *lamina transversalis anterior* (Fig. 45) arises from the ventral part of the rostrum of the septum and extends posteriorly along the dorsal surface of the vomer, to which it is attached by small teats. It is separated from the septum by the paraseptal cartilage ventrally and extends as far laterally as the vomerine process of the maxilla, covering the interval between vomer and maxilla. It develops into a spherical hollowed capsule, Jacobson's organ, in the anterior chamber of the septomaxilla. Posteriorly it extends ventral to the zona annularis as a sheet of cartilage forming the roof of the choanal tube and continues posteriorly with the conchal cartilage. At its junction with the conchal cartilage the lamina transversalis anterior forms the anterior rim of the fenestra endochoanalis. Its mesial border extends along the posteroventral surface of the septomaxilla and continues posteriorly to form the inferior rim of the olfacto-anterior foramen. More posteriorly it joins the mesial border of the zona annularis and becomes continuous with the paranasal cartilage. The lateral border continues as the lacrimal ridge along the inferior nasal rim of the maxilla and then along the medial surface of the maxilla. The ridge continues posteriorly with the ventrolateral angle of the paranasal cartilage and with the lateral part of its ventral surface, forming the lateral rim of the fenestra endochoanalis.

The *cartilages of the vomeronasal organ of Jacobson* (Figs. 46 and 49) are derived from the lamina transversalis anterior, the septum, and the paraseptal cartilage. These three cartilages, covered dorsally by the anterior chamber of the septomaxilla and ventrally by the vomer, form a spherical cavity housing a sensory membrane. They are molded into an incomplete chamber with an internally projecting cartilaginous concha and a ventral opening. The septum forms the medial surface of the chamber, and its septomaxillary process extends laterally to form part of the dorsal surface. The lamina transversalis anterior begins at the rostral cartilage and extends posteriorly as a capsule adjoining the septomaxillary shelf to complete the dorsal surface of the chamber. Usually the cartilage is very thin or is fenestrated between the two borders (Fig. 46). The lamina extends laterad to the vomerine process of the maxilla and ventrad to the vomer, forming the lateral wall of the chamber. From this lateral wall a solid cartilage, the concha (Fig. 49), projects posteromedially into the cavity. Ventral to this the cartilage is separated from the vomer by a small interval which forms the fenestra vomeronasalis interna, the opening from the vomeronasal chamber. Posterior to this opening the cartilage of the lamina transversalis anterior, bridging the interval between the maxilla and the vomer, has a groove on its ventral surface which is continuous anteriorly with the lacrimal groove on the ventral surface of the vomer and posteriorly with the lacrimal ridge and which houses the lacrimal duct. Extending posteriorly from the lateral border of this groove is a process, the ectochoanal cartilage, which lies along the palatal shelf of the maxilla and forms part of the choanal fold. The posterior wall of the vomeronasal capsule is formed in part by a medial extension of the lamina transversalis anterior and in part by a lateral extension of the paraseptal cartilage. The wall is perforated medially for the passage of the vomeronasal nerves. Ventrally the floor is incomplete and is formed by the dorsal surface of the vomer, the medial surface of the lamina transversalis anterior, and the lateral ridge of the paraseptal cartilage.

The *sphenethmoidal commissure* (Figs. 43 and 48) is a small rod of cartilage extending from the dorsal anterior border of the interorbital septum laterally to the posterodorsal surface of the planum antorbitale. It surrounds the ventral surface of the olfactory canal and cradles the olfactory nerves. Its lateral tip lies against the frontal process of the prefrontal.

Nasal Sac

The nasal sac is a continuous epithelial tube lining the nasal capsule. It is divided into two chambers according to both its epithelium and the constrictions and dilatations of the capsule.

The nostril is the membranous entrance to the nasal sac. It is surrounded by thick connective tissue covered with a single nasal scale. The general shape is circular; however, its anterior border is vertical. The *anterior nasal tube* (Fig. 44) extends anteromesially toward the septum. Its dorsal and anterior surfaces are covered by the cupola, whereas ventrally and posteriorly it is surrounded by a large, venous sinusoidal mass of tissue which forms a mechanism for closing the nasal passage (Bruner, 1907). This tissue is both structurally and functionally erectile and cavernous (Stebbins, 1948). Ventrally the anterior nasal tube lies on the maxilla, the lamina transversalis anterior, and the septomaxilla. The path of the tube is /\ -shaped. The short limb extends anteromesiad and then turns posterodorsad along the nasal septum and dorsal to the septomaxilla, which projects into it as a high ridge.

The *anterior chamber* (Fig. 44) is a long, J-shaped posterior continuation of the anterior nasal tube. It expands posteriorly and has a large opening for the duct of the lateral nasal gland at its posterior end. The chamber is surrounded by the zona annularis and opens into the olfactory chamber through the olfacto-anterior foramen. This foramen is formed by the zona annularis dorsally, the posterior border of the nasal process of the septomaxilla anteriorly, the medial border of the lamina transversalis anteroventrally, and the paranasal cartilage posteriorly. The anterior chamber is lined by stratified squamous epithelium which is continuous with the epithelium of the nasal scale in the anterior nasal tube and is almost entirely surrounded by a spongy sinusoidal mass continuous with that surrounding the anterior nasal tube.

The *olfactory chamber* is divisible into the anterior space and the posterior conchal zone. The anterior space lies along the nasal septum and extends from the posterior surface of the septomaxilla (Fig. 45); it communicates with the anterior chamber. Ciliated respiratory epithelium lines its surfaces and is continuous ventrad with the choanal tube. The conchal zone lies in the paranasal cartilage and contains the conchal invagination on its anterior wall. Ventrally it opens into the choanal tube through the fenestra endochoanalis. The conchal zone is divided into three parts. Of these, the sakter (Fig. 45) occupies the medial and dorsal walls and the medial wall of the conchal projection. The other two, the lateral recess, lateral to the concha, and the antorbital space, posterior to the concha, are lined with respiratory epithelium. These areas are lined ventrally with mucus-secreting cells and open directly into the choanal tube.

The *olfactory nerve* arises from the olfactory epithelium, which is of relatively small area in relation to the space available. Most of its fibers arise from the medial and dorsal walls of the olfactory chamber, the medial and posterior walls of the concha, and the posterior wall of the antorbital space. These fibers form approximately six bundles which pierce the planum antorbitale and join the olfactory bulb anterolaterally. Other fibers are derived from the medial wall of the conchal zone and run with the nerve of Jacobson's organ.

The *arterial supply* of the snout is derived from three main sources: the superior nasal, the inferior nasal, and the maxillary arteries. The superior and inferior nasal are derived from the frontal and palatine arteries, respectively, and supply the ventral and medial wall of the olfactory chamber, the vomerine part of the palate, Jacobson's organ, and the cutaneous region of the snout. The maxillary is the major artery to the snout and supplies the external naris, the rich plexus surrounding the entire anterior chamber, the anteromedial part of the olfactory chamber, the lateral nasal gland, and the maxillary part of the palate, teeth, and labial glands.

Innervation for other than olfaction is supplied to the snout by branches of the ophthalmic and maxillary divisions of the trigeminal and by the palatine branches of the facial. The cutaneous innervation is by means of medial and lateral ethmoidal nerves supplying the skin over the dorsal and lateral surfaces of the snout and the external naris. The cutaneous branch of the superior alveolar nerve supplies the labial and dental regions. Medial, intermediate, and lateral palatine nerves supply the glandular regions of the palate. They also contain cutaneous branches of the maxillary division. Detailed descriptions of the arterial and nervous supply are given under those systems.

The *lacrimal duct* (canal) arises from two puncta on the rim of the inferior eyelid at its anterior canthus. Each punctum has a posterior conjunctival groove leading into its orifice. The orifices of the puncta are large and remain open. A separate canaliculus leads from each orifice; however, both are bound in a single band of connective tissue, making them appear grossly as a simple tube. They lie immediately beneath the skin of the eye external to the orbital fascia and extend slightly anteroventrad. After traversing the lacrimal foramen, the two canaliculi fuse to form the lacrimal duct, which becomes dilated; they then pass dorsal to the posterior maxillary process and beneath the lacrimal ridge. Throughout most of its extent the duct lies ventral to the lacrimal ridge, lateral and dorsal to the choanal membrane (glandular area), and medial to the maxillary bone.

Near the anterior end of the ventromedial surface of the lacrimal duct there is a long slit, the posterior opening of the lacrimal duct into the choanal groove. The dorsal part of the lacrimal duct continues mediad beneath the cartilages of the lamina transversalis anterior and then passes to the vomer to lie in the lacrimal groove on the ventral surface of that bone. It continues craniad for a short distance and terminates on the anteromedial side of the opening of the duct of Jacobson's organ. On the vomer the ventral surface of the duct is covered by a thin membrane which extends laterally as far as the opening of Jacobson's organ and terminates there in a very small anterior opening.

Jacobson's organ is a paired, spherical, sensory organ lying in the nasal capsule, ventral to the epithelium of the nasal sac and at the junction of the anterior nasal tube and the anterior chamber. Ventrally it opens through the duct of Jacobson's organ into the buccal cavity.

The organ of Jacobson (Fig. 46) lies within an osseous capsule formed by the septomaxilla dorsally and anteriorly and by the vomer ventrally. Posterior to the organ and partly separated from it by the septal process of the septomaxilla lies the anterior space of the olfactory chamber. The osseous capsule is incomplete medially and laterally; however, the resulting openings are closed by a nearly complete cartilaginous capsule of the organ.

The capsule possesses a hollow dome-shaped cavity (Figs. 46 and 49) which is lined by sensory epithelium and has on its anterolateral wall a concha covered with ciliated epithelium. The concha is a projection which nearly obliterates the cavity and divides it into dorsal and ventral parts that are continuous around the medial and posterior section of the concha. The ventral part opens to the mouth by the duct of Jacobson's organ which has a longitudinal slitlike aperture formed by the vomer medially and the lamina transversalis anterior laterally. The lips of this opening are supported by thick fibroelastic connective tissue covered by ciliated epithelium. The epithelium covering the lateral lip is continuous with that covering the concha. The lacrimal duct opens in the medial part of the duct of Jacobson's organ.

Outside the epithelium of Jacobson's organ is a dense layer of fibrous connective tissue containing the numerous vomeronasal nerves. The fibers arise from the epithelium of the dome of the cavity and converge to pass posteriorly. Their course is between the septal process of the septomaxilla and the nasal septum, through the cribriform plate of the paraseptal cartilage, and along the lateral surface of the septum, dorsal to the paraseptal cartilage, where they are covered laterally by the epithelium of the olfactory chamber. As the nerves reach the posterior end of the nasal capsule they combine into a single trunk and pass between the nasal septum and the paraseptal cartilage, through a slitlike space, into the olfactory canal. They terminate in the accessory olfactory bulb on the ventromedial surface of that bulb.

Jacobson's organ receives a small branch from the inferior nasal artery and is innervated by a twig of the medial palatine nerve. These pierce the vomer and enter the organ ventrally.

In the region of the snout there are two layers of connective tissue that are sufficiently discrete to warrant definition. The first, the *olfactochoanal membrane,* is a distinct thickening of the opposing layers of the perichondrium lying between the lamina transversalis anterior and the ventral surface of the zona annularis. It is continuous with the perichondrium of the remainder of the nasal capsule. This membrane begins to thicken on the dorsal surface of the septomaxilla and on the lamina transversalis anterior. Dorsally it is attached to the venous plexus of the anterior nasal tube and the connective tissue of the naris. It continues posteriorly along the lamina transversalis anterior to the region of the aditus conchae, where it splits and surrounds the lateral nasal gland. Along the entrance to the aditus conchae the membrane is attached to the conchal ridge of the nasal and prefrontal. Its lateral border is thickened and loosely attached to the medial wall of the maxilla. This membrane, a specialization of the perichondrium, transports the arteries and veins between the cartilaginous folds of the nasal capsule. In the lateral border of the membrane lies the lateral ethmoidal nerve and also the postnarial artery in its course to the lateral nasal gland. Medial branches from the postnarial artery extend within this membrane to supply the plexus of the anterior chamber.

The *orbitonasal membrane,* a heavy fibroelastic sheet extending across the orbitonasal opening and separating the nasal capsule from the orbital space, appears to be a continuation of the periosteum of the bones to which the membrane is attached. It is attached laterally to the medial rim of the prefrontal, ventrally to the transverse crest of the palatine, and dorsally to the frontal bone and sphenethmoidal commissure. It is continuous across the mid-line beneath the olfactory canal, forming its floor, and attaches to the anterior border of the interorbital septum. Ventrally in the mid-line it surrounds the trabecular cartilages.

Piercing this membrane are four foramina through which pass the ophthalmic division of the trigeminal nerve dorsally, the medial palatine nerve and the inferior nasal artery ventrally, and two venous sinuses. On the anterior surface of the orbitonasal membrane is the planum antorbitale of the olfactory capsule, and posterior to it are the orbital space and the orbital fascia.

The *lateral nasal gland* (Gaupp, 1888; Fahrenholz, 1937) is lodged in the recess of the conchal cartilage and completely fills the aditus conchae. This gland is a compound, tubular, mucus-secreting gland which contains a large common duct, the individual tributary tubules of which are grossly dissectible. Each tubule appears to empty independently into the central common duct. The gland has little parenchymatous tissue and no real capsule; however, the olfactochoanal membrane splits around it to become its functional capsule. Its duct pierces the posterior dome of the zona annularis and empties into the posterior end of the anterior chamber. The gland is innervated by a branch of the lateral ethmoidal nerve, and its blood supply is from the postnarial artery.

Choanal Tube

Lying immediately beneath and continuous with the olfactory chamber is the choanal tube (Fig. 46), an unspecialized longitudinal cavity between the olfactory and the oral space. Dorsally the space is limited by the lamina transversalis anterior, and posterodorsally it is continuous with the antorbital space and lateral recess through the internal choana (fenestra endochoanalis), which is an incomplete foramen. Because of incomplete margins of the foramen, the choanal tube is continuous along its dorsomesial surface with the anterior space and the sakter. Nevertheless, the tubal area is well defined by its epithelial lining. The floor of the choanal tube is formed by the vomer and palatine mesially and the palatine ridge of the maxilla laterally. Between these bones is the external choana (fenestra exochoanalis) which connects the choanal tube with the oral cavity. This opening is formed by the ventral surface of the palatine, the lateral border of the vomer, and the medial border of the palatine ridge of the maxilla. Anteriorly the external choana is constricted by a membranous, choanal fold, extending medially from the maxilla.

The choanal tube is lined by a simple, columnar, ciliated epithelium containing numerous mucous cells. It is continuous ventrally with the stratified squamous epithelium of the oral cavity at the external choana and dorsally with the epithelium of the olfactory space at the internal choana. Lying in its lateral wall just dorsal to the palatal ridge of the maxilla and ventral to the lacrimal duct is a thickened glandular area which contains both serous and mucous cells. Just dorsal to this glandular area is a fold through which the lacrimal duct opens into the anterior part of the choanal tube. At its anterior end the choanal tube is narrow and continues craniad onto the ventral surface of the palate as the choanal groove (Fig. 58). On the ventral surface of the palate it crosses the ventral surface of the bridging part (between the vomer and maxilla) of the lamina transversalis anterior. The choanal groove extends to the opening of the duct of Jacobson's organ.

THE ORBIT

The orbit probably has received the most attention of all of the structures of the reptilian head. As early as 1877 Weber described the orbit of *Lacerta*, and Osawa (1898) described that of *Sphenodon*. These are very complete considerations; however, further studies by Schwartz-Karsten (1937) on the orbital glands, Walls (1942) on the bulb and adnexia, Säve-Söderbergh (1946) on the retractor bulbi muscle group, Bellairs (1949) on the interorbital septum, and Bellairs and Boyd (1947) on the lacrimal duct have corrected many earlier misinterpretations.

The orbits are quadrilateral spaces separated from each other by a cartilaginous interorbital septum. Each orbit is bounded by an incomplete osseous capsule formed of the prefrontal, frontal, postfrontal, postorbital, jugal, and lacrimal bones. Although the bony orbit is exceedingly incomplete, the eye is almost completely housed by the addition of membranes and muscles which bound it on all sides. Anteriorly, the wall of the orbit is formed by the prefrontal bone and the orbitonasal membrane. The muscular mass in the temporal fossa, the orbitotemporal membrane, and the wall of the cranium form the posterior wall. The palatine, pterygoid, ectopterygoid, and jugal bones and the inferior orbital membrane form the floor. The interorbital septum is the medial wall. The dorsal and lateral walls are constructed of the previously listed bones and the integument which covers this area.

The skin covering the dorsal and the lateral walls of the orbit is firmly attached to the rim of the orbit, and between these attachments it is thick and fibrous. The skin covering the dorsum of the orbit is tightly stretched and very thick, reaching a maximum thickness of approximately 1 mm. A fibrous thickening within the dermis of the skin extends along the lateral border of the dorsal surface from a tubercle on the postfrontal bone to one on the prefrontal. It supports the dorsolateral angle and serves to protect the orbit along its dorsolateral margin. The integument extending ventrad from this ligament forms the lateral wall of the orbit. It is divided into the two eyelids, the superior being the smaller and the thicker. At the anterior and posterior palpebral commissures of the palpebral fissure are ligaments. The posterior palpebral ligament is a thickening within the dermis, extending from the postorbital bone to the posterior commissure and fanning out in the posterior part of the inferior eyelid. The anterior palpebral ligament is distinct and separated from the overlying skin. It lies dorsal to the lacrimal canaliculi and extends from the prefrontal to the anterior palpebral commissure.

Conjunctiva and Accessory Structures

Continuing with the free margin of the eyelids, the epithelium turns onto the inner surface of the lids and forms a lining, the palpebral conjunctiva. It then continues over the surface of the bulb as the bulbar conjunctiva to form the conjunctival sac. Superiorly and inferiorly the reflections of the sac form angles, the superior and inferior fornices, which are attached to the orbital fascia.

In several areas the epithelium of the conjunctival sac is differentiated into glandular epithelium or glands. Along the inner surface of the palpebral fissure of both the superior and inferior lids the epithelium is thickened by an area of mucous cells. A second, somewhat thicker area of mucous cells lies at the superior fornix on the palpebral conjunctiva and extends nearly the entire length of the conjunctiva. The largest of these conjunctival glands, the lacrimal, is a thickened circular area of tubuloalveolar mixed-type glands opening into the posterior angle of the palpebral conjunctiva by means of numerous ductules. Walls (1942) stated that some of these tubules are contractile in lizards. The greater part of this gland protrudes into the conjunctival sac.

The blood supply of these areas is by branches from the superior and inferior orbital arteries. Their innervation is by branches of the maxillary and frontal nerves.

Lying in the central part of the lower lid within the lamina propria of the conjunctiva is a circular disc of fibroelastic cartilage, the *tarsal plate*. Its central part is thickened, and laterally its edge is thinned. Ventrally it is attached to the orbital fascia. It serves as a protective covering for the cornea of the eye when the lids are closed.

The *nictitating membrane* is a double layer of conjunctiva, forming a third lid. This fold lies in the anterior angle of the eye, between the palpebral and the bulbar conjunctiva. It arises at the level of the pupil as a small fold in the superior fornix and continues craniad, increasing in depth. It is continuous in the inferior fornix, decreases in size, and terminates at about the level of the posterior rim of the cornea. The free or caudal border of the nictitating membrane is crescent-shaped and is formed by only a double layer of conjunctiva. The border, at rest, lies just anterior to the cornea.

The main part of the membrane is supported by three vertical strips of fibroelastic cartilage which lie anterior to the free margin of the membrane and are not dissectable from it. The inferior tips of two strips join each other and provide attachment for the tendon of the nictitating membrane. The third and largest cartilage is crescent-shaped. It lies in the dorsal part of the membrane and extends anteroventrad. Anteriorly it passes out of the membrane and expands to form a large fibrous plate which covers the lateral surface of the Harderian gland and is attached to it.

The medial surface of the nictitating membrane is smooth and in contact with the bulbar conjunctiva. On this surface, as it becomes continuous with the bulbar conjunctiva, are numerous openings of the ductules of the Harderian gland. The lateral surface of the membrane has three vertical folds; the first two lie along the vertical cartilaginous struts; the third and largest one lies in the anterior angle of the conjunctival sac. These folds serve to catch particles of sand and dirt. The third, the anterior fold, is covered by numerous mucous cells which probably serve to catch the dirt particles in a mucous mass. At the inferior angle of the nictitating membrane, on its lateral surface, is a large, circular, bulging gland of tubuloalveolar mucoserous type. This gland, which opens laterally through numerous small ductules into the inferior fornix, is entirely separate from the Harderian gland.

The function of the nictitating membrane is controlled by a pulley-like mechanism, the tendon of the nictitating membrane, which encircles the bulb and attaches to the inferior border of the membrane. This narrow and fibrous tendon (Fig. 53) arises from the superior border of the interorbital septum, anterior to the planum supraseptale, and extends posteroventrally along the septum, passing dorsal to the ophthalmic division of the trigeminal nerve, the trochlear nerve, and the superior border of the anterior rectus muscle. After crossing these three structures, it continues between the bulb of the eye and the superior rectus muscle, dorsal to the optic nerve, to reach the bursalis muscle. Here it becomes thickened and passes through the substance of this muscle, which functions as a pulley for the tendon. After passing through the bursalis, the tendon passes ventrolateral to the bulb to lie in a fold in the floor of the conjunctival sac and to attach to the inferior process of the two fibrocartilaginous struts of the nictitating membrane.

The *Harderian gland,* the largest of the orbital series, is the major gland of secretion for the eye and, according to Bellairs and Boyd (1947, 1950) and Pratt (1948), is correlated with the function of Jacobson's organ. This gland lies free within the orbit, attached only to the nictitating membrane, which it follows as that structure is brought into motion.

According to Schwartz-Karsten (1937), the gland is a tubuloalveolar mixed-type gland, being both serous and mucous. It lies within the orbital fascia and is covered by a very thin connective-tissue capsule and the wall of the orbital sinus. The ducts of the gland open on the ventromedial side of the nictitating membrane.

The gland consists of three parts: head, body, and tail. The head lies just anterior to the nictitating membrane; however, it is attached to the medial surface of the dorsal fibrocartilage plate of that membrane and is enveloped laterally by the orbital and medially by the bulbar fascia. The body lies completely free on the anterior surface of the bulb between the superior oblique and the inferior oblique muscles. The tail passes around the medial surface of the bulb and follows the anteromedial surface of the anterior rectus muscle along the septum as far caudad as the origin of that muscle. The orbital sinus surrounds the free parts of the gland and, according to Bruner (1907), "lies partly between the tubules of the Harderian gland."

The blood supply of the Harderian gland is through the anterior orbital artery. Its innervation is through a group of fine fibers arising from the junction of the ophthalmic division of the trigeminal nerve and the medial palatine ramus of the facial nerve.

The orbital cavity houses not only the ocular apparatus within the orbital fascia, but in its posteroventral aspect it houses also a large pharyngeal space, the *pyriform recess* (Fig. 58), which extends as far dorsally as the basitrabecular process and as far laterally as the inferior orbital foramen. This recess is of considerable size, in correlation with the posteroventral inclination of the pterygoid bone in the orbit. Also located within the posteroventral part of the orbit is the levator bulbi muscle, closely associated with both the eye and the pharyngeal recess.

Orbital Muscles

The major contents of the orbit, outside of the bulb, are the ocular muscles. These can be divided into two functional types, bulbar rotators (rectus and oblique) and bulbar retractors (retractor and bursalis). The oblique muscles arise from the anterior border of the septum and extend caudad to the bulb; the recti originate caudal to the horizontal axis of the bulb, and all except the posterior rectus surround the optic nerve and extend craniad to the bulb. The bulbar retractors, a specialized group which draws the bulb into the orbit, originate on the basisphenoid. The posterior rectus is closely associated with the retractor group.

M. superior oblique (Fig. 53) lies dorsal to the profundus division of the trigeminal nerve and the tail of the Harderian gland and ventral to the tendon of the nictitating membrane. The ventral border is dorsal to the trochlear nerve and the anterior rectus muscle. It arises from the lateral surface of the anterior end of the interorbital septum as two superimposed fiber bundles. Its fibers extend posterolaterad so that the inferior ones become anterior and the superior ones become posterior. The fibers insert into the dorsal surface of the eyeball in an oblique line ventral to the insertion of the superior rectus muscle. Innervation is by means of the trochlear nerve which enters the muscle on its posteroventral surface.

M. inferior oblique (Fig. 53) arises by a vertical origin from the anterior border of the interorbital septum, just above the trabecular cartilage and just posterior to the nasal cartilages. The origin is anterior to that of the superior oblique, and the fibers pass ventral to the origin of that muscle to insert into the inferior surface of the eyeball, parallel but ventral to the insertion of the inferior rectus muscle. Viewed ventrally as a pair, the two inferior oblique muscles diverge from their origin at an angle of approximately 60°. The muscle is innervated by a branch of the oculomotor nerve which enters its posteromedial border.

M. anterior rectus (Fig. 53) is crossed dorsally by the trochlear nerve, the profundus division of the trigeminal nerve, and the tendon of the nictitating membrane. Lateral to the muscle is the insertion of the retractor bulbi muscle; craniad the origin is covered by the Harderian gland; caudal to the origin is the optic nerve. The muscle arises from the anterior tip of the hypochiasmatic cartilage, the posterior border of that part of the membranous interorbital septum lying anterior to the optic foramen, and the proximal end of the anterior orbital process. Its fibers extend horizontally forward along the interorbital septum and turn laterad at the anterior end of the bulb to insert on its anterior surface, within an apex formed by the origins of the two oblique muscles. The oculomotor nerve crosses the ventral border of the origin of the muscle and enters its medial surface.

M. superior rectus (Fig. 53) is lateral to the trochlear nerve and the cranial wall. Lateral to the muscle are the profundus division of the trigeminal nerve, the ciliary nerve and ganglion, the bursalis muscle, and the eyeball. The muscle arises from a notch on the anteroventral tip of the orbitosphenoid bone and the dorsal part of the subiculum infundibulum. It extends anterodorsolaterad, passing dorsal to the optic nerve, and inserts into the superior surface of the eyeball, overlying the insertion of the superior oblique.

M. inferior rectus (Fig. 53) lies ventral to the retractor bulbi muscle and arises from the lateral surface of the hypochiasmatic cartilage, the supratrabecular membrane just beneath, and the dorsal surface of the trabecular cartilage. Its fibers extend anteroventrolaterad to insert in the inferior border of the eyeball; its insertion is covered ventrally by the insertion of the inferior oblique. Viewed ventrally, the pair of inferior rectus muscles diverge at an angle of approximately 80^0. As the fibers pass to their insertion, the ventral division of the oculomotor nerve passes posterior and ventral to the origin, giving off numerous short branches to the ventral surface of the muscle.

The correct origin of the retractor musculature in reptiles was demonstrated only recently by Säve-Söderbergh (1946). His study of three forms, *Sphenodon, Lacerta,* and *Varanus,* showed definite relationships between the position of the hypophysis and the amount of invasion of the basisphenoid by the retractor musculature.

In *Ctenosaura pectinata* the retractor musculature invades the basisphenoid to a slight extent, extending behind the level of the hypophysis. The presence of a large pituitary vein separates the hypophysis from the dorsum sellae, and the ventral parts of the two retractor bulbi muscles are continuous beneath the hypophysis by a small ventral median raphe. These relations in *Ctenosaura* most closely resemble those in *Varanus;* however, the invasion of the basisphenoid is not as extensive.

The retractor bulbi musculature is contained within a thin membranous sheath which is the posterior part of the orbital fascia. It surrounds the muscles and is attached mesially and laterally to the trabeculae cranii and the crista trabecularis, and posteriorly to the dorsum sellae. Also contained within the sheath are the posterior rectus muscle, the abducens nerve, and the profundus division of the trigeminal. The muscles arise from the anterior surface of the dorsum sellae in an excavation, the retractor pit (Fig. 14).

M. bursalis (Fig. 53) arises from the lateral part of the retractor pit, surrounding the external abducens foramen. The origin continues ventrad, mesial to the vidian canal, and extends onto the lateral border of the crista trabecularis. The fibers extend anterodorsad to the posterior surface of the orbit, where they are pierced by, and form a sheath for, the tendon of the nictitating membrane. This tendon holds the fibers close to the eye. The fibers then turn dorsad along the posterior margin of the eye and insert into the sclera at the posterodorsal angle of the eye. The muscle is innervated by the abducens nerve, which pierces it at its origin, gives off a small branch to the muscle, and then continues through the muscle, emerging on its ventrolateral surface. This muscle lies lateral to the retractor bulbi muscle, the oculomotor nerve, and the profundus division of the trigeminal; it lies dorsal to the posterior rectus muscle and abducens nerve, and medial to the levator bulbi muscle.

M. retractor bulbi (Fig. 53) arises from the medial side of the retractor pit, on an area lateral to the internal carotid artery, from the dorsal surface of the crista trabecularis, and from a mid-line raphe ventral to the pituitary sac. The fibers extend anteriorly, ventromedial to the bursalis muscle, dorsal to the origins of the posterior rectus and the inferior rectus muscles, and ventrolateral to the origin of the superior rectus. It is crossed dorsally by the ciliary root of the oculomotor nerve. The muscle extends ventrad to the optic nerve and inserts into the ventromedial surface of the eyeball as far anteriorly as the insertion of the anterior rectus muscle. It is innervated by a very small branch of the abducens which passes from the bursalis muscle and pierces the retractor bulbi muscle near its origin.

M. posterior rectus (Fig. 53) also is found in the membranous sheath of the retractor muscles. It arises on the dorsal surface of the trabecular cartilage and the most posteroventral part of the subiculum infundibulum. Its fibers extend dorsolaterad and insert into the posterior surface of the eyeball. As the fibers pass to their insertion, they are crossed dorsally and anteriorly by the ventral division of the oculomotor nerve and the other two retractor muscles, the bursalis and the retractor bulbi. The fibers of the muscle are so twisted that at their insertion the posterior border becomes dorsal and the anterior border ventral. Ventral to the insertion the tendon of the nictitating membrane passes to the bursalis muscle. The innervation is by the abducens nerve which emerges from the bursalis muscle and divides into numerous branches that go to the posterior surface of the muscle.

Orbital Nerves

The orbit accommodates the nerves and arteries within it and also those coursing to the nasal capsule. Surrounding the major part of these structures along the ventral and mesial wall of the orbit is the orbital sinus (Bruner, 1907).

Optic nerve.— The optic stalks emerge from the base of the diencephalon, pass around the lateral border of the stalk of the hypophysis, and enter into the chiasma. From the chiasma the optic nerves extend anteriorly and pass out of the cranial cavity through the optic foramen, a common median opening between the orbitosphenoid bones. After emerging, the nerves diverge, one to each side of the interorbital septum. The nerve has only a short orbital course to the posteromedial side of the orbital bulb where it penetrates the sclera. It is covered by a series of sheaths formed by the optic membrane, the dura, and the pia mater.

The external covering of the optic membrane extends from the optic foramen (orbitosphenoid bone and septum) as a very tough sheath of fibers that is continuous with the fascia of the bulb. Within this sheath the dura mater and the pia mater extend to the sclera and terminate.

As the nerve passes into the orbit, it is surrounded by the origins of the muscles of the eye: the anterior rectus anteriorly, the retractor bulbi and inferior rectus ventrally, and the superior rectus posteriorly. It is crossed dorsally by the trochlear nerve and the ophthalmic division of the trigeminal nerve.

Oculomotor nerve.— The oculomotor nerve (Fig. 53) emerges from the ventral side of the mesencephalon by a large root which extends anteroventrally within the cranial cavity, lateral to the internal carotid artery and the stem of the hypophysis. At the anterior end of the hypophysis the root pierces the metoptic membrane near its mid-point and emerges at the superior border of the retractor bulbi muscle. It immediately divides into a small dorsal ramus and a large ventral one.

The *dorsal ramus* extends along the lateral surface of the metoptic membrane, crosses the lateral border of the orbitosphenoid bone, and enters the posterior border of the superior rectus muscle ventral to the trochlear nerve.

The *ventral ramus* extends anteroventrally along the lateral surface of the metoptic membrane. It crosses the lateral surface of the origin of the superior rectus muscle, and at this point gives off the ciliary root. The main ramus extends to the surface of the posterior rectus, crosses the head of this muscle dorsally, and then descends between its anterior border and the inferior rectus muscle. As it passes anteriorly on the ventral surface of the inferior rectus, it gives off ventrally numerous branches to that muscle. Continuing anteriorly, the main ramus divides into a medial and a lateral branch. The medial branch crosses the ventral belly of the retractor bulbi and enters the ventral border of the anterior rectus muscle. The lateral branch extends anteriorly along the ventral border of the retractor bulbi, just lateral to the ventral border of the cartilaginous interorbital septum, and enters the posterior border of the inferior oblique muscle.

The *ciliary root, radix brevis,* is a large root extending craniad to the ciliary ganglion on the lateral surface of the superior rectus muscle. The ganglion is a prominent swelling on the root. Distal to the ganglion the root is joined by the ciliary root of the ophthalmic division of the trigeminal nerve. The root formed from this combination continues anteriorly along the dorsal border of the retractor bulbi muscle to the level of the optic nerve, crosses the dorsal surface of that muscle, enters the posteromedial surface of the cartilaginous sclera of the eye, and runs laterally between the sclera and the choroid coats of the eye to the ciliary muscle where the nerve divides and encircles the muscle. Numerous short ciliary fibers also extend from the ganglion and perforate the sclera of the posterior surface of the bulb, dorsal to the entrance of the optic nerve. These could not be traced within the bulb.

Trochlear nerve. — The trochlear nerve (Fig. 53), a large nerve supplying only the fibers of the superior oblique muscle, runs most of its course in the cranial cavity. It leaves the dorsal surface of the mid-brain, dorsal to the mesocoele and ventromedial to the inferior colliculus, extends anteriorly between the inferior colliculus and the optic tectum, and continues lateral to the base of the optic tectum to pass through the metoptic membrane ventral to the pila antotica.

The nerve continues an anterior course in the orbit, passing across the lateral border of the orbitosphenoid, dorsal to the optic nerve. In the remainder of its course it lies ventral to the epioptic membrane and the planum supraseptale and dorsomedial to the superior rectus muscle. As it continues in a cephalic direction, it lies dorsal to the ramus nasalis of the ophthalmic division of the trigeminal nerve and medial to the tendon of the nictitating membrane. After passing beneath this tendon, the fibers turn laterally to enter the posteroinferior border of the superior oblique muscle.

Abducens nerve.— The abducens nerve (Fig. 53), small and about 15 mm. long in large adults, emerges from the base of the metencephalon and runs anteriorly for a short distance within the cranial cavity. It enters the internal abducens foramen in the dorsal surface of the basipterygoid bone and, after running a ventral course in the bone, emerges from the abducens foramen on the anterior surface of the dorsum sellae, within the origin of the bursalis muscle. The nerve supplies three muscles. Within the origin of the the bursalis muscle it gives off a single small dorsal ramus which divides into two branches, one going laterally to the bursalis and the other medially to enter the head of the retractor bulbi muscle. The main branch continues anteroventrally through the bursalis muscle, emerging on its ventral border, and enters the posteromedial border of the posterior rectus. The main branch of the nerve, going to the posterior rectus, is large; the ramus to the retractor muscles is approximately one-tenth the size of the main one.

Orbital Membranes

The *inferior orbital membrane* (palatine membrane) is a thick fibrous layer of connective tissue, which appears to be a continuation of the periosteum lying within the inferior orbital foramen and attached to the margins of the bones forming that opening. Superiorly it is fused to the periorbital membrane and forms part of the floor of the orbit. Inferiorly it is covered by oral membrane and forms part of the palate. It is pierced by branches of the inferior orbital plexus (lateral palatine ramus of the facial nerve).

The *orbitotemporal membrane* separates the temporal fossa and its muscular mass from the orbital contents. It attaches laterally to the postorbital and frontal bones and ventrally to the ectopterygoid and the transverse process of the pterygoid. It extends obliquely caudad to attach to the membranous cranial wall at the pila accessoria and the basisphenoid bone; then it continues ventrad along the lateral crest of the dorsum sella and the anterior border of the basipterygoid process. It is continuous with the periorbital membrane and is pierced by the branches of the trigeminal nerve and the superior and inferior orbital arteries. Laterally it is independent and thickened. Mesially it becomes thinned and is joined by the orbital fascia.

The *periorbital membrane* is a continuous lining of the inner surface of the orbit. It is loosely attached to the bony surfaces and is continuous with the orbitotemporal and orbitonasal membranes. Attaching to the lower lid, just above the jugal, it passes over the floor of the orbital cavity, dorsal to the inferior orbital plexus, and fuses with the inferior orbital membrane.

It continues dorsally along the interorbital septum, and then extends laterally, over the dorsal surface of the orbit, to attach to the superior eyelid. The lateral parts of the membrane are distinct and thickened; the medial part is fused to the orbital fascia. At its junction with the orbitotemporal membrane it is pierced by the levator bulbi muscle.

The *orbital fascia* is a thin, tough layer of connective tissue lying within the periorbita and investing all the orbital contents. Laterally it is attached to the lids, one-third of the depth of the lid from the palpebral fissure. This attachment corresponds to the first fold of the eyelid. Ventrally it is attached to the tarsal plate and the inferior fornix. On its ventral surface it receives the insertion of the depressor palpebrae part of the levator bulbi. Medial to the insertion of this muscle the fascia becomes continuous with the periorbita which continues dorsally along the interorbital septum to the frontal bone. Continuing laterally, it separates from the periorbita and attaches to the superior fornix and then to the superior lid in the region of the first superior fold. Posteriorly the membrane is attached to the prootic and basisphenoid bones as a circular investment of the retractor musculature. This investment is fused laterally with the orbitotemporal membrane. Anteriorly the orbital fascia is free. Within its cavity it is continuous with the muscular fasciae of the ocular muscles; in its ventral and medial parts the cavity is lined by the epithelium of the orbital sinus.

THE EAR

The reptilian ear has been the subject of only a few extensive works. Retzius (1884) and Versluys (1898) produced the most complete work on the comparative aspect of the membranous labyrinth and the middle ear. More recently (de Burlet, 1929, 1934, 1935; Weston, 1939) the sensory endings and ganglia have been studied.

The ear in reptiles, as in all amniotes, can be divided into three components: the external, the middle, and the inner ear. In *Ctenosaura pectinata* these three components are present; however, as in most lizards, the external ear is confined to the surface of the head.

The External Ear

The external ear is a symmetrical depression at the posterolateral angle of the skull. This recess (Fig. 2) is formed by attachment of the skin to the quadrate bone anteriorly and by a fold in the neck region posteriorly. At its base is a tightly stretched posterolaterally directed membrane, the tympanum, partly covered posteriorly by the fold of neck skin. It is oval, narrower at the top than at the bottom, and protrudes slightly at its mid-point, reflecting the presence of the extracolumella.

The *tympanum* (Figs. 2 and 30) is a thin double-layered membrane separating the external from the middle ear. Its outer layer is formed of a continuation of the cutaneous layer which here is a thin but well-keratinized epithelium. Internally it is covered by a continuation of the tympanic epithelium lining the middle ear, which also is thin but contains no mucous cells. In the posterior half of the tympanum, imbedded between its two layers, lies the pars inferior of the extracolumella covered by its ligament. Along the region of the attachment of the extracolumella is a triangular area of the tympanic epithelium which is thickened and surrounded by additional connective tissue that carries branches of the auricular artery and also contains the pars accessoria anterior and posterior of the extracolumella.

The attachment of the periphery of the tympanum is not as well defined as classical descriptions indicate. Since the tympanum is formed of a continuation of the skin, it is this last definite attachment of the skin around the tympanum which is usually described. The skin is attached to the tympanic crest of the quadrate anteriorly, to the cephalic condyle and cartilaginous extension of the tympanic crest dorsally, and to the lateral border and tip of the retroarticular process of the lower jaw ventrally.

The tympanum is centrally located between these attachments but lies at some distance from most of them, especially ventrally, where it is never attached to the retroarticular process. The membrane does, however, attach dorsally to the cartilaginous extension of the tympanic crest and to the cephalic condyle. Its posterior border is formed by the skin stretched between the retroarticular process and the cephalic condyle. This fold is supported by the depressor mandibularis muscle but is not attached to it.

The Middle Ear

The *tympanic cavity* (Figs. 33-35, 42, and 58), the middle ear, is a large pouch housed within the posterior part of the head. It lies lateral to the otico-occipital segment and extends anteriorly to an apex between the origin of the protractor pterygoideus muscle and the basipterygoid process of the basisphenoid bone. It extends into the neck region, lateral to the axial musculature, as far posteriorly as the third cervical vertebra (Fig. 58). It joins its fellow beneath the otico-occipital segment, and the two tympanic cavities communicate with the pharynx through a median auditory tube or Eustachian canal. The common cavity extends posteriorly to the anterior end of the esophagus. The shape of the cavity fluctuates with that of the muscles and the esophagus. The middle part of each tympanic cavity is held open by the skeletal framework of the occipital region of the skull.

The limits of the tympanic cavity can be defined by the structures which form or pass along them. The lateral wall is formed by the protractor pterygoideus muscle, the quadrate process of the pterygoid, the quadrate, the tympanum, and the depressor mandibularis and episternocleidomastoideus muscles; the dorsal wall is formed by the recessus vena jugularis, the paraoccipital process, and the longissimus cervicis and obliquus capitis magnus muscles; the medial wall is formed by the lateral surface of the otico-occipital segment ventral to the sulcus vena jugularis, the lateral surfaces of the longissimus capitis and the rectus capitis anterior muscles; the floor is formed by the pterygomandibularis muscle, the pharynx, and the esophagus.

In addition to the structures given above, numerous others lie on the periphery of the tympanic cavity. Along the dorsal wall are the internal jugular vein and the internal carotid artery; along the medial wall are the facial nerve, the stapes, the internal carotid artery, the medial cranial sympathetic trunk, and the glossopharyngeal nerve; along the lateral wall are the tympanum and the attached distal part of the extracolumella; the columella and the proximal part of the cartilaginous extracolumella pass through the dorsal part of the cavity. The structures emerging from the skull — vagus and hypoglossal nerves — lie on the dorsomedial surface of the cavity. Passing around the posterior and ventral surfaces of the cavity are the hypoglossal and glossopharyngeal nerves and the dorsal processes of the first ceratobranchial bone and the ceratohyal.

The cavity is lined by the *tympanic membrane,* a mucous epithelium that covers all of the walls and structures, forms the inner layer of the tympanum, and is continuous with the pharynx through the Eustachian tube. It is a simple, low epithelium and contains mucous cells in abundance around the inner margin of the tympanum and in scattered patches elsewhere. It not only invests the structures forming the walls of the tympanic cavity, but also forms several folds by its reflections over the columella and extracolumella.

The *columellar fold* is a reflection of the tympanic epithelium over the columella and extracolumella and is attached along the dorsal wall of the cavity. It surrounds the proximal end of the columella, holding it within the foramen ovale, and then continues laterally along the columella and extracolumella to attach onto the crista interfenestralis and the dorsal wall of the tympanic cavity and onto the ventral surface of the cephalic condyle of the quadrate as far laterad as the processus superior of the extracolumella. A second fold, the *processus internus fold,* extends from the dorsal margin of the processus internus to the anterior surface of the columellar fold and attaches along the inner surface of the quadrate. This fold divides the tympanic cavity above the processus internus into a medial and a lateral part and encapsulates the chorda tympani between its two layers. A third fold, the *carotid fold,* extends over the superior margin of the occipital recess, covering approximately half of the opening and housing the internal carotid artery and the medial cranial sympathetic trunk in its free margin.

The *columella auris, stapes,* ear bone (columella, Fig. 35), is a thin cylindrical bone extending posterolaterally between the foramen ovale of the exoccipital and the cartilaginous extracolumella. Its proximal end is an oval foot plate which nearly fits the opening and, within the inner ear, lies against the wall of the perilymphatic cistern. Distally it is cylindrical, slightly bowed posteriorly, and is expanded where it joins the extracolumella. The columella is completely surrounded by the epithelium of the tympanic cavity and is held in place by the columellar fold.

The *extracolumella* (Figs. 31 and 34) is a cartilaginous extension of the columella to the tympanum. It consists of a tubular body with additional processes of attachment. At the osteocartilaginous junction it is spherical and sends craniad a large perpendicular fan-shaped process, the processus internus (Fig. 34). This process attaches medial to the posterior crest of the quadrate bone and serves to stabilize the columella. At its terminal end the body becomes angular and divides into four radiating processes, the two larger of which constitute the foot plate. The anterior of these two, the pars inferior, extends to the middle of the tympanum, tapering to a point; the posterior one, pars superior, is broad and terminates at the level of the cephalic condyle of the quadrate. Extending dorsad from the border of the pars superior is a pars accessoria posterior (Fig. 31) which terminates in a ligament attached to the cartilaginous border of the cephalic condyle. Extending ventrad is a similar but longer pars accessoria anterior which terminates as a ligament that extends along the posterior border of the tympanic membrane. All of these processes lie within the two layers of the tympanum. Covering the lateral surface of the foot of the extracolumella is a stabilizing ligament, the *extracolumella ligament* (Fig. 34). This ligament arises from the intercalary cartilage and passes laterad along the posterior border of the cephalic condyle of the quadrate to the pars superior of the extracolumella; it then turns anteriad to extend over the foot plate of the extracolumella (pars inferior and pars superior). The chorda tympani nerve crosses the dorsal border of the ligament beneath the cephalic condyle and continues on the posterior surface of the quadrate lateral to the pars internus of the extracolumella.

The Internal Ear

The *osseous labyrinth* (Figs. 54 and 56), an excavation situated within the otico-occipital segment of the skull, houses the membranous labyrinth. It invades the supraoccipital, prootic, and exoccipital bones and is reflected externally by a small crest on the prootic for the anterior semicircular canal (Fig. 8) and by a large projection, the auditory bulla, within the cranium (Figs. 6 and 9). Plastic injections of the osseous labyrinth were made and the resulting internal cast (Figs. 54 and 56) accurately shows its details. Details of the parts housed in specific bones may be found in the section on osteology.

The central hollow cavity, *cavum capsularis,* evident in disarticulated skeletons, is divided into two parts, an upper vestibular and a lower lagenar. The *vestibule* is a large spherical cavity housing the saccule, utricle, and sinuses. Extending craniad from the vestibule is a small cavity, the *anterior ampullar recess,* constricted into an anterior space for the anterior ampulla and a posterior space for the external one. These spaces are continuous with the anterior and the external osseous semicircular canals, respectively. Along the ventromedial wall of the anterior ampullar recess are two foramina which transmit the anterior auditory ramus. Extending from the anterior ampullar recess caudad, along the medial wall of the vestibule, is a tubular recess for the utricle. At the posterior end of the vestibule are two recesses, a small dorsal one which transmits the posterior end of the external semicircular canal and a larger ventral one, the posterior ampullar recess, which houses the posterior ampulla and continues into the posterior osseous semicircular canal. Extending from this recess craniad along the vestibular walls are two grooves, a dorsal one for the posterior sinus and a small ventral one for the nerve of the posterior crista. Extending dorsally on the medial side of the vestibule is the *recessus crus communis,* and just anterior to this is a small canal for the endolymphatic duct. At the base and on the medial wall of the vestibule is a large foramen for the posterior ramus of the auditory nerve.

The ventral part of the cavum capsularis is a funnel-shaped space, the *lagenar recess*, constricted away from the vestibule by the lagenar crest. This houses the lagena and the perilymphatic cistern with its duct. Along its posterolateral wall is the foramen ovale which seats the foot plate of the columella; on its medial wall is a foramen, the fenestra cochlea, which leads to the recessus scala tympani. Extending around its anterior and medial walls is a trough which lodges the perilymphatic duct. This trough continues through the cochlear fenestra into the recessus scala tympani (see exoccipital bone). The tip of the lagenar recess is formed by a wedge of the basioccipital bone.

The osseous semicircular canals, three in number, describe somewhat flattened arcs (anterior, external, and posterior) standing at approximately 90^0 to each other. They house the membranous canals.

The *membranous labyrinth* (Fig. 55) is a tough, transparent, continuous, tubular membrane filled with a fluid, endolymph; it receives the terminals of the auditory nerve. Its shape is similar to that of the osseous labyrinth which molds it.

The membranous semicircular canals are three separate tubes within the osseous canals and are named accordingly. Each canal is approximately half as large as its osseous compartment and is surrounded by perilymphatic space. Each has an expanded ampullar part which receives nerve endings that terminate in an internal crest or ridge, the crista. Externally the crista appears as a groove, the ampullar sulcus, which lodges the nerve bundle. The anterior and the external ampullae are continuous with each other. The anterior semicircular canal extends dorsad from the anterior ampulla to join the posterior semicircular canal in the common crus. The external semicircular canal encircles the sacculus laterally and joins the anterior utricular sinus along the medial surface of the saccule.

Continuing posteriorly from the anterior ampulla is a slightly enlarged tube, the *utricle*. In the floor of the utricle lies the utricular macula which receives nerve terminals. The utricle continues caudad along the medial wall of the saccule as a somewhat reduced tube, the anterior utricular sinus, to join the posterior semicircular canal.

The *posterior ampulla* lies at the caudal end of the membranous labyrinth. The posterior semicircular canal extends dorsad from it to join the common crus, and its ampulla communicates craniad through the posterior sinus which leads along the medial surface of the sacculus to join the anterior utricular sinus. In the floor of the posterior utricular sinus is a small raised area of nerve terminals, the papilla neglecta.

The *sacculus* is a large spherical vesicle filling nearly the whole vestibule and continuing ventrad through an open communication into the lagena. It is many times the size of the utricle, and surrounding the sensory hairs on the surface of its macula is an enormous deposition of calcium carbonate, the otolith, which is loose in preserved specimens and nearly fills the cavity of the saccule. Leaving the dorsal wall of the sacculus is a small tube, the endolymphatic duct, which passes ventrad around the anterior utricular sinus and then dorsad through the endolymphatic foramen of the supraoccipital bone to terminate in an expanded area beneath the dura of the cranial cavity.

At approximately the mid-point of the medial surface of the sacculus the anterior utricular sinus, the posterior utricular sinus, and the external semicircular canal join in a common space. The common crus terminates along the medial surface of this space, completing the continuity between all the semicircular canals. In the floor of this space is a small constricted foramen, the utriculosaccular canal, which joins the sacculus, bringing this cavity into continuity with the others.

The *lagena,* a small funnel-shaped sacculation homologous with the cochlea (cochlear duct) of higher forms, extends ventrad through a somewhat constricted neck from the sacculus to the medial part of the lagenar recess, where it is closely surrounded by the perilymphatic cistern and its duct. Within the lagena are two areas of nerve termination, a large basal papilla along its posterior wall and a small macula lagena at its apex. These areas pick up vibrations which pass through the perilymphatic space and are transmitted to the lagena by the columella of the middle ear. Both of these areas have central connections with the cochlear areas of the brain and therefore are considered auditory (Weston, 1939).

Lining the walls of the osseous labyrinth is a periosteal layer which has extensive trabecular attachments to the membranous labyrinth. Between the periosteal lining and the membranous labyrinth is a *perilymphatic space,* filled with perilymph. Most of this periosteum is thick and without pigmentation; however, that part along the lateral wall of the vestibule and the lagenar recess contains large pigment cells. The latter area is without trabeculae and is separated from the remainder of the perilymphatic space by a cribriform septum which continues across to the membranous labyrinth, becoming very thin on the lateral surface of the saccule and lagena, and completely encircling the perilymphatic space. The large, spacious lateral part lying against the lateral surface of the saccule and the lagena is the perilymphatic cistern. This becomes tubular in the lagenar recess and extends around the anterior and medial parts of the lagena as the perilymphatic duct. It continues through the cochlear foramen and expands into the recessus scala tympani.

Along the lateral surface of the cisterna, in the lagenar recess, is the foramen ovale, and within it is the foot plate of the columella. In the recessus scala tympani, the distal end of the lateral surface of the perilymphatic duct lies against the tympanic epithelium in the foramen rotundum and becomes the membrana tympani secunda. The medial wall of the perilymphatic duct extends through the perilymphatic foramen into the cranial cavity and lies beneath the dura in association with the posterior cerebral vein. This arrangement allows impulses received by the columella to be transmitted through perilymph of the cisterna to the lagena and permits compensation to occur in the foramen rotundum.

The *acoustic nerve* (Fig. 55), an extremely large trunk, leaves the ventrolateral angle of the medulla and runs a very short course within the cranial cavity. As it reaches the wall of the cranium it divides into anterior and posterior rami.

The anterior ramus, in turn, is divided into two branches, an anterior and a posterior, which enter the anterior ampullar recess independently through the two anterior auditory foramina in the prootic bone. The anterior branch receives its fibers from the crista anterior; and the posterior branch receives its from the crista externa and the macula utriculi. The ganglion cells of the anterior ramus lie within the nerve trunk in the cranial cavity.

The posterior ramus is continuous with the anterior ramus and passes into the cavum capsularis through the large posterior auditory foramen of the prootic and exoccipital bones. Within the vestibular space this ramus fans out and receives one major trunk from the macula sacculi and a second major trunk from the papilla basalis on the posteromedial surface of the lagena and the macula lagena. The ganglion cells of this ramus are imbedded in the nerve trunk within the cavum capsularis. The ganglion cells of the papilla basalis are near the endings of the nerve fibers and lie just above the perilymphatic duct. This arrangement is in accord with Weston's (1939) observation that ganglion cells related to perilymphatic or cochlear sensory areas tend to lie nearer to such areas than do those related to endolymphatic areas. Lying just beneath the posterior sinus is a small group of fibers which passes from the posterior ramus of the auditory nerve to the crista posterior and the papilla neglecta. The ganglion cells lie along the fibers, separated from the major posterior auditory ganglion.

THE ORAL CAVITY

The oral cavity (Figs. 58 and 59) is no more highly specialized in *C. pectinata* than in any other vertebrate. It communicates posteriorly with the pharynx and anteriorly, between the lips, with the exterior. The roof is formed by the hard bony palate and its floor by the lower jaws, tongue, glottis, and laryngeal eminence.

The oral fissure is continuous around the entire oral cavity, extending from the level of the coronoid process of one side to that of the other. Posterior to this point it continues as the *mundplatt* (Fig. 30) which is an extension of the superior and inferior lips, lying in apposition to each other, the inferior medial to the lateral, and deep to the skin covering the infratemporal fossa. Since the angle of the oral fissure is anterior to the mandibular condyles and the lips are immovable, the *mundplatt* allows an extremely wide gape of the jaws.

The lips are thin immobile boundaries of the oral fissure. The inferior lips are firmly attached to the paired maxillae. They are bounded externally by supralabial, infralabial, rostral, and mental scales. Internally they are lined along the lower lip by three continuous rows of compound, tubular, labial glands. The glands of the outer row, the openings of which lie along the apex of the lip, are mucoserous. The glands of the two inner rows, the ducts of which are separated by a longitudinal fold of epithelium, open on the medial side of the lips and are mucous. The glands of the upper lip are in two rows, one along the ventral margin of the lip and the other along the medial surface. They appear to be mucoserous.

The teeth, situated just medial to the lips, are pleurodont, heterodont, and polyphyodont. The average numbers are 31 upper and 34 lower teeth, decreasing in size from anterior to posterior. The posterior two-thirds are tricuspid in form. Those on the anterior end of the maxillae are pointed and slightly recurved (caniform); those on the premaxilla and mental areas are short and unicuspid (incisiform). Replacement is continuous; tooth buds are present at all ages.

Palate

The palate forms the roof of the oral cavity. It is composed of a framework of osseous elements: premaxilla, maxilla, and ectopterygoid peripherally; vomer, palatine, and pterygoid centrally. All peripheral elements except the ectopterygoids bear teeth; the central elements are in linear arrangement. The posterior limit of the osseous palate is the transverse process of the pterygoid bones. The surface of the palate is irregularly concave, anteroposteriorly in a long arc and mediolaterally in a shorter arc. The osseous palate is perforated by five openings. Paired anterior openings, surrounded by maxilla, vomers, and palatine, are the exits of the nasal capsule. In cleaned skulls these are large, elongate, semilunar openings and may be divided into an anterior constricted part, the fenestra vomeronasalis externa, and a long posterior section, the fenestra exochoanalis. The name "paleochoanate" (Lakjer, 1927) is applied to a palate in which these fenestrae are continuous. Lying in the posterolateral part of the palate are the inferior orbital foramina, surrounded by the maxilla, palatine, pterygoid, and ectopterygoid. In the flesh these spaces are filled by the inferior orbital membrane and are not patent. The osseous palate is separated in the mid-line, between the palatines and the pterygoid bones, by a space, the "incisura pyriformis" (Bahl, 1937).

The osseous palate is covered by a thin, adherent, oral mucous membrane which, because of varied functions of the palate, reveals some specializations in different areas. At the anterior end, behind the premaxillary teeth and covering the incisive process, is a rather prominent incisive pad containing for the most part connective tissue. Extending posteriorly from the incisive pad in the mid-line is a short vomerine raphe, on each side of which is a triangular, smooth, nonglandular area containing the transverse slit of the duct of Jacobson's organ. These two triangular areas reflect the shape of the dorsal tip of the tongue and probably receive the tongue when the mouth is closed. Extending posteriorly from the medial end of the duct of Jacobson's organ is the choanal groove, a shallow fold of oral epithelium which opens posteriorly into the fenestra exochoanalis. At the posterior end of the vomerine raphe the epithelium is raised, dense, highly vascular, and richly supplied by branches of the medial palatine nerves. Although taste buds could not be found, it may be a gustatory area. At the anterior end of the incisura pyriformis is a second moundlike area of dense connective tissue. In the flesh the ectochoanal cartilage and the lamina transversalis anterior separate the anterior openings into two distinct fenestrae, the fenestra exochoanalis posteriorly, and the fenestra vomeronasalis externa anteriorly.

The posterior part of the palate is covered by a rather thin mucous membrane reflecting the osseous structure beneath. Here also are two longitudinal glandular areas (Gaupp, 1888). One of these, the lateral palatine stripe, lies medial to the teeth and extends from the incisive pad all the way back to the posterior end of the palate (ectopterygoid bones), where it becomes pendulous and hangs into the posterior part of the mouth. The second, the medial palatine stripe, runs from the medial border of the fenestra exochoanalis along the mid-ventral surface of the palatine bones, spreads out, and then terminates at the base of the pterygoid teeth. In these areas simple, tubular, mucous glands occur.

The oral mucosa extends dorsally through the incisura pyriformis and expands laterally to lie on the dorsal surface of the palatine bones, producing a space, the pyriform recess. The roof of this space lies along the ventral border of the parasphenoid bone; its lateral angles lie beneath the orbital bulbs and receive the insertions of the ventralis parts of the levator bulbi muscles which appear to maintain the great extent of this cavity. The lining of the pyriform recess is a thin continuation of oral membrane and contains few mucous cells. Its roof is somewhat fibrous. Posteriorly this recess is continuous between the basipterygoid processes with the auditory space.

The oral mucosa of the palate extends around the lateral and posterior surfaces of the ectopterygoid bone and expands dorsally between the orbitotemporal membrane and the mandibular musculature where it becomes thin and richly supplied with mucous cells. This fold of mucosa forms a space, the coronoid recess, which receives the coronoid process of the mandible in adduction.

Floor

The floor of the oral cavity (Fig. 59) is completely filled by the tongue (described above) and the larynx.

Just medial to the teeth is a fold of epithelium, the sublingual plica, arising at the symphysis of the mandible and extending posteriorly to the coronoid process. At the symphysis the sublingual plica is raised above the level of the teeth and is mediolaterally thickened, extending to the frenulum and base of the tongue. Its dorsomedial surface is transversely ridged for a distance of 10 mm. in large adults. The raised anterior part of the plica overlies the sublingual gland, posterior to which it diminishes in size and is covered by scattered, simple, tubular mucous glands.

The *sublingual gland* (Gaupp, 1888) lies just beneath the oral mucosa behind the symphysis of the mandible and extends 15 mm. posteriorly in large adults. It is covered laterally by the mandible, ventrally by part of the genioglossus muscle, and medially by the intermandibularis anterior superficialis.

Grossly follicular and cylindrical in appearance, the gland is covered by a thin capsule which is attached by ligaments to the symphysis of the mandible at its anterior end and to the ventral surface of the mandible at its posterior end. When sectioned, the gland appears cystic in structure. Fibers of the intermandibularis anterior profundus lie dorsally within the posterior two-thirds of the gland. It appears that these fibers function as a discharge mechanism for the gland; no other function seems plausible. Many small ducts pass dorsally from the gland, especially from its anterior third, and pierce the oral membrane in the thickened sublingual plica.

The blood supply to the gland is by a large artery from the anastomosis of the musculomandibular and internal mandibular arteries. Innervation is by a branch of the lingual ramus of the inferior alveolar nerve.

The oral mucosa of the floor of the mouth is thin, transparent, and longitudinally folded, allowing for great distension. It extends from the sublingual plica to the root of the tongue and forms a frenulum around the anterior border of the genioglossus muscle. There are only a few isolated mucous cells in this area.

THE LARYNX

The larynx (Fig. 59), described in reptiles by Göppert (1889, 1937), is a prominent mid-line structure lying in the floor of the mouth between the posterior limbs of the tongue. It occupies the laryngeal recess, a depression covered by thin oral mucosa, with numerous mucous cells. It is bilobed in general appearance, and its continuation, the trachea, causes an elongate ridge in the floor of the pharynx.

The larynx presents three prominences, the most anterior of which is a thin-edged transverse process, the epiglottis. The presence of an epiglottis in *Ctenosaura pectinata* is distinctive. It has been reported in only two other lizards, *Tupinambis teguexin* and *Ctenosaura acanthura* (Negus, 1949). According to Negus, the presence of the epiglottis is related to the maintenance of olfactory sensation during deglutition. The epiglottis is covered ventrally by a continuation of the epithelium of the laryngeal recess. Its lateral limit is extended by aryepiglottic folds to the arytenoid cartilages. Just posterior to the epiglottis are the arytenoid prominences, a pair of hillocks separated by a short longitudinal slit, the glottis.

The glottis, when opened, is triangular. The apex is pointed and lies between the two arytenoid processes. It is formed by the rim of the epiglottis, the two aryepiglottic folds and the arytenoid prominences. In contraction the glottis is T-shaped; the posterior limb is formed by the two arytenoids in approximation, and the horizontal limb is formed by the epiglottic cartilage which caps these prominences.

The epiglottic cartilage is covered ventrally by a continuation of the epithelium of the laryngeal recess. The arytenoid prominences are covered with the continuation of the loosely adherent pharyngeal membrane, which is longitudinally ridged and composed of thick, stratified, squamous epithelium with straight tubular mucous glands. The interior of the larynx is covered by a continuous pseudostratified, columnar, ciliated epithelium.

The larynx is supported dorsally by the pharyngeal membrane, and ventrally it lies on the lingual process of the hyoid bone and on the lingual musculature.

Cartilages of Larynx

There are three laryngeal cartilages. The largest, the *cricothyroid* (Fig. 52), is a short tubular cylinder of elastic cartilage, complete except for a dorsal aperture. It surrounds and forms the greater part of the laryngeal tube and the epiglottic cartilage. The ventral side of the cricothyroid is the longest and extends anteriorly as the epiglottic cartilage. This cartilage is constricted at the base, slightly expanded at the anterior end, dorsoventrally concave, and flexible. Its base is thickened and in older specimens may be slightly ossified; it provides origin for the constrictor laryngeus muscle and the laryngohyoid ligament (Fig. 51).

The dorsal part of the cricothyroid (Fig. 52) is only a little more than half the length of the ventral and extends caudad as a pointed process which covers the dorsal side of the first four tracheal rings. The central part contains a large lens-shaped foramen which is covered by a thin cricothyroid membrane. The parts of the cartilage just lateral to the foramen are thickened, overhang the tracheal rings, and provide for the origin of the dilator laryngeus muscle. At the anterior end of the dorsal surface the halves are joined by a furcula-shaped cartilage which originates along the thickened border and terminates at the medial process of the arytenoid cartilages. Along the anterior border of the dorsal part is a pair of smooth, convex, transverse condyles which are the articular surfaces for the arytenoid cartilages. The lateral surface is smooth and becomes thin at the posterior end. Here, between the dorsal thickened cartilage and the thinned lateral plate cartilage, is a small slitlike foramen through which the glossopharyngeal-vagus trunk and the laryngeal artery enter the larynx to supply its epithelial lining.

The two *arytenoid cartilages* (Fig. 52), of hyaline composition, are the remaining cartilages of the larynx. They surmount the condyles on the dorsal part of the cricothyroid and bound the posterior longitudinal limb of the glottis. Each cartilage is semilunar in shape, concave dorsally, and convex ventrally (toward the interior of the larynx). The dorsal concavity lodges the body of the constrictor laryngeus muscle and serves it as a pulley. The lateral border of the arytenoid cartilage is straight and provides attachment for the aryepiglottic membrane. The anterior process, or apex of each cartilage, is blunt and directed dorsally. Each posterior process is expanded medially, the two approximating each other and being joined by a heavy connective tissue band which serves as a relatively fixed pivot for movement. The dorsal and lateral borders of the posterior process serve the insertion of the dilator laryngeus muscle. The caudal surface has an oval, concave condyle which articulates with the condyle of the cricothyroid cartilage. The medial border is concave and forms the border of the posterior limb of the glottis. The apices of the arytenoid cartilages are covered by thickened fibrocartilaginous plugs of connective tissue. These plugs, which are not discrete cartilages, perfect the closure of the glottis.

Ligaments of Larynx

The ligaments of the larynx may be divided into intrinsic and extrinsic groups. The intrinsic ligaments are composed of two membranes and an articular capsule. One of these membranes, the aryepiglottic fold, is composed of two layers of epithelium separated by a thin layer of fibroelastic connective tissue. It extends from the lateral border of the arytenoid cartilage to the lateral border of the epiglottic. Its free border forms part of the rim of the glottis. The other, the cricothyroid membrane, is a thin sheet of fibroelastic connective tissue connecting the lateral limbs of the dorsal cricothyroid from the level of the third tracheal ring to the arytenoid cartilage. It completes the dorsal foramen of the cricothyroid cartilage. The third intrinsic ligament, the articular capsule, is a continuous membrane encircling the articulation of the arytenoid with the cricothyroid cartilage. It is thin and loose and is attached to the margins of the articular surfaces.

There is only one extrinsic ligament, the *laryngohyoid ligament.* It is a heavy, round, fibroelastic cord originating on the dorsal side of the lingual process of the hyoid apparatus and extending along the dorsal side of the hypohyal cartilage to the ventral surface of the cricothyroid, posterior and dorsal to the origin of the constrictor laryngeus muscle. It controls the position of the larynx in relation to that of the hyoid apparatus.

Muscles of Larynx

In lizards there are two pairs of muscles that function in the larynx. These open and close the glottis and serve primarily in respiration. One of these, *M. dilator laryngeus,* covered dorsally by the pharyngeal membrane, arises from the dorsal surface of the posterior extension of the cricothyroid cartilage. Its fibers pass anterolaterally, fan out, and insert into the dorsolateral part of the posterior process of the arytenoid cartilage. Some of these fibers traverse the fibers of the constrictor muscle, both dorsally and laterally, to insert into the anterior process of the arytenoid cartilage. The other, *M. constrictor laryngeus,* arises from the ventral surface of the cricothyroid cartilage, at the base of its epiglottic part ventral to the laryngohyoid ligament. Its fibers extend laterally around the cartilage, follow the semilunar groove and the dorsal surface of the arytenoid cartilage, and insert with their fellows into the dorsal mid-line raphe.

THE TRACHEA

The trachea (Figs. 39 and 57) is a tubular structure extending caudad from the larynx through the throat and neck and into the thorax. It lies in the mid-line ventral to the pharynx and in the lower cervical region ventral to the esophagus. Covering it ventrally are the posterior parts of the hypohyal cartilage, the hyoid body, and both second ceratobranchial cartilages with their attached sternohyoideus and omohyoideus muscles. Lying lateral to the trachea, usually on the right, though occasionally on both sides, is the tracheal vein; on the left, at the caudal end of the cervical region, are the ultimobranchial bodies. In the mid-cervical region, the thyroid gland lies across the ventral surface of the trachea; the inferior laryngeal nerve and the laryngotracheal artery lie along its lateral surface.

The course of the trachea is not straight. It extends ventrally from the larynx to the body of the hyoid bone, turns dorsad to the esophagus, and then caudad into the thorax. This ventral deviation of the trachea is slight in young adults.

The trachea is formed of a series of complete cartilaginous rings, linked together by fibroelastic membranes. These rings may bifurcate, each forming several limbs. They are approximately 7 mm. in diameter and 3 mm. long in a head 100 mm. long. There are approximately 45 in the head and cervical region. At the larynx the rings are circular; however, in the cervical region they are dorsoventrally flattened.

The blood supply to the trachea is through the laryngotracheal and glossopharyngeal arteries. Its innervation is through branches of the inferior laryngeal nerve.

THE PHARYNX

The pharynx (Figs. 39, 57, and 59), a funnel-shaped cavity, extends from the posterior end of the oral cavity to the esophagus. It is lined by mucous membrane which is characterized throughout by parallel longitudinal folds. The folds are confined to the epithelium and the lamina propria and cannot be reduced by stretching. The epithelium is ciliated and columnar and contains goblet cells. The pharynx is covered by a thin layer of circularly arranged smooth muscle which increases in thickness toward the esophagus.

The last attachments of the pharynx to the skull are on the coronoid process of the mandible ventrally and on the transverse processes of the pterygoid and ectopterygoid dorsally. Ventrally the pharynx lies on the trachea and hyoid musculature, and dorsally it is continuous in the mid-line with the pyriform recess and the auditory space. It is attached to the surrounding musculature by loose connective tissue.

In adults the hypertrophy of the pterygomandibularis muscle constricts the opening between the pharynx ventrally and the pyriform recess and the auditory space dorsally, leaving only a slitlike communication (Fig. 59). The pharynx becomes constricted at about the middle of the cervical region. The distinction between esophagus and pharynx is difficult to make. The pharynx receives its innervation from the glossopharyngeal and vagus nerves.

THE CERVICAL REGION

Description of the cervical region at this point is essential in order to show the continuity of the structures entering and leaving the head. The cervical region may be designated as that region ventral to the neck musculature and dorsal to the sternohyoideus muscle. Its anteroposterior limits are difficult to establish, since the posterior tip of the mandible and its associated structures overlap the cervical region containing the cervical vertebra. A posterior limit, however, may be designated as the cervical end of the interclavicle.

Besides the structures associated with the mandible, the cervical area (Fig. 57) contains the trachea ventrally, the pharynx and esophagus dorsally, and the auditory sac and neurovascular bundle laterally. Details of these and other associated structures are presented in other sections. The neurovascular bundle contains the internal carotid artery, vagus nerve, sympathetic trunk, and jugular vein. These structures are encased in an extensive mass of connective tissue. The connective tissue elements are more prominent in old adults, but they could not readily be called a sheath. The remainder of the cervical region is a rather large space containing the thyroid and thymus glands and the ultimobranchial body. The absence of connective tissue surrounding these structures is characteristic of this region.

The *thyroid gland* lies anterior to the interclavicle, under cover of the sternohyoideus muscle, and ventral to the trachea and its related structures. It is an elongate organ placed transversely across the trachea. It is composed of two limbs forming an obtuse angle. The junction of the limbs is usually the thicker part of the organ, though occasionally the limbs are large and the isthmus is narrow. The surfaces of the thyroid reflect in variable amount its follicular structure. In adults a well-developed "fat body" is almost inseparably attached to the ventral surface, filling the surrounding space beneath the sternohyoideus muscle.

The vascular supply to the gland is furnished by branches of two aortic arches. The superior thyroid, a branch of the external carotid, joins the thyroid at its lateral pole. When the fat body is extensive, this artery seems primarily to supply it. The inferior thyroid artery, a branch of the laryngotracheal artery, reaches the thyroid along its posterodorsal border and appears to provide its major arterial supply. Thyroid veins, either single or double, drain into the tracheal vein.

A few fine branches of the inferior laryngeal nerve were found passing to the gland along the inferior thyroid artery and veins. No sympathetic fibers could be found.

The *thymic glands,* derivatives of the second and third pharyngeal pouches, almost invariably are present in lacertilians (W. E. Adams, 1939). In *C. pectinata* there are two on each side in the neck, lying ventral to the neurovascular compartment at approximately the level of the retroarticular process. The anterior of the two glands lies on the tympanic cavity, somewhat medial to the posterior one, which is approximately half the size of the anterior gland.

Arterial supply to the thymus glands is from branches of the musculocervical artery. Their veins drain directly into the internal jugular vein. Independent branches of both the vagus and the sympathetic trunk pass to these glands. Ganglion cells can be found within the bodies of the glands.

The *ultimobranchial body* is a small, indistinct, soft mass unilaterally situated on the left side of the trachea at the lower limit of the cervical region. It lies in the angle between the trachea and the pharynx, lateral to the inferior laryngeal nerve and the laryngotracheal artery, from which it receives a large vascular supply. In cross section its appearance is granular. It contains several widely separated follicles of various size which contain particulate matter. These follicles are similar in structure to those of the thyroid gland, being lined by low cuboidal cells.

SUMMARY

The results of this study are embodied in the descriptive part of the work, which presents an account of the macroscopic details of the structure of both the skull and the soft parts of the head of the iguanid lizard *Ctenosaura pectinata.* Emphasis has been placed upon the relations of soft to bony structures in order to facilitate interpretation of fossil forms.

The skull is low and is of light but strong construction. The snout, orbits, and temporal fossae are of equal size. The bony palate is paleochoanate. The cranium is kinetic. The occipital or axial segment (brain case) is divided into two structural parts, a posterior osseous and an anterior membranous. The membranous part is described for the first time in Iguanidae. The maxillary segment, composed of the orbit, palate, snout, and temporal fossae, functions as a unit. The occipital and maxillary segments articulate through two diarthritic and three syndesmotic joints. The basipterygoid joint does not contain an articular disc.

Associated with the kineticism of the skull, there is a constrictor dorsalis group of the trigeminal muscles which moves the two segments of the skull. The throat musculature presents specializations in that M. mandibulohyoideus and M. intermandibularis anterior interdigitate. M. intermandibularis posterior consists of two parts, the posterior of which is innervated by the facial nerve. M. intermandibularis anterior arises along a tendon extending from the coronoid bone to the mandibular symphysis. Fibers of this muscle, arising from the tendon and the oral membrane, insert into the sublingual gland and form a discharge mechanism for it. The superficial fibers of M. intermandibularis anterior arise from the oral membrane. M. branchiohyoideus is innervated by the glossopharyngeal nerve.

The first ceratobranchial bone meets the body of the hyoid apparatus in a diarthritic joint.

The peripheral distribution of the cranial nerves is described. Eleven cranial nerves are present which, in form, are typical of those of other amniote vertebrates. There is no spinal accessory nerve in *C. pectinata;* the elements usually innervated by the spinal accessory are supplied by a branch of the vagus and the second and third spinal nerves.

The sympathetic system consists of superficial and deep cervical cords and medial and lateral cranial cords. There are no true cervical ganglia; however, ganglionic cells and masses occur within the cranium at various points along the entire system.

The head and neck are supplied by arteries from the third, fourth, and sixth aortic arches. The general plan is consistent with that of amniotes. Additional terminals of the arterial system are described.

The snout is described in detail. The osseous nasal capsule is completely covered by dermal bone, which also closely surrounds the anterior nasal tube. The cartilaginous nasal capsule is elongate, unfenestrated, and forms three major chambers: the anterior nasal tube, the anterior chamber, and the olfactory chamber. The floor is perforated by two openings, the fenestra vomeronasalis interna and the fenestra endochoanalis. The olfactory chamber is separated from the oral cavity by a shallow choanal tube. The anterior nasal tube and the anterior chamber comprise more than half of the nasal capsule. These are lined by cornified epithelium. The olfactory chamber is large and has a well-developed conchus. There is a single lacrimal duct which opens into both the choanal tube and the medial side of the duct of Jacobson's organ. Jacobson's organ is well developed. The nasal apparatus is of the generalized type found in terrestrial species of arid regions.

The retractor muscles of the orbit originate in a pit on the surface of the dorsum sellae and slightly invade the dorsum sellae.

A precise description of the extent of the reptilian tympanum is given.

A laryngohyoid ligament extends from the hypohyal to the larynx. It appears to control the position of the larynx in accord with that of the hyoid apparatus.

In the study of the structures of the head no specialization in any region other than adaptations to terrestrial existence was observed.

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FIGURES

Fig. 1. *Ctenosaura pectinata*, adult body.

Fig. 2. *Ctenosaura pectinata*, adult head.

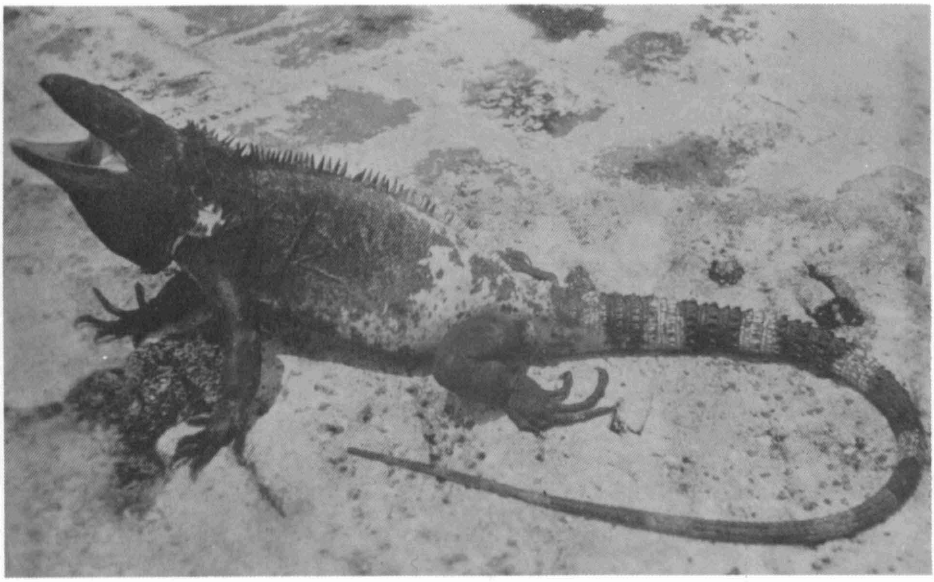


Fig. 1

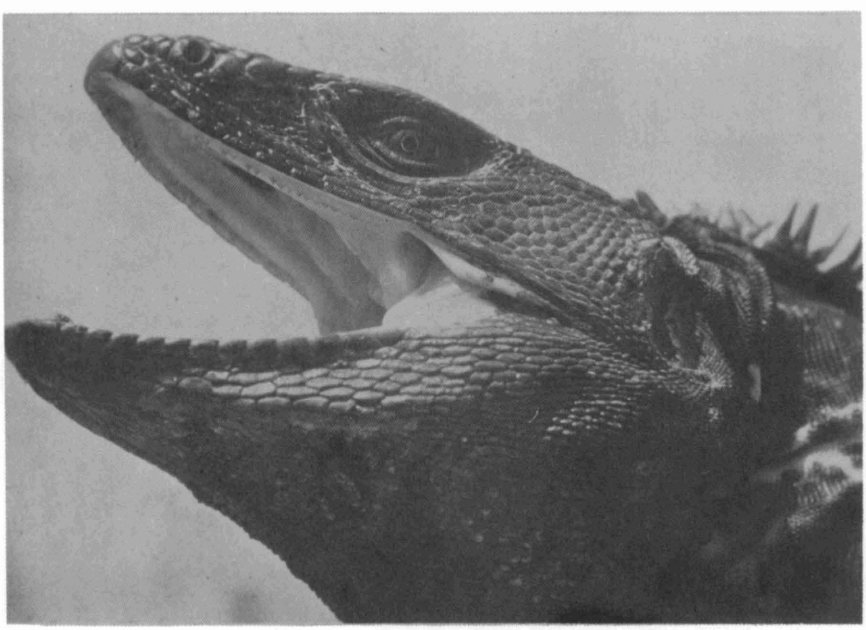
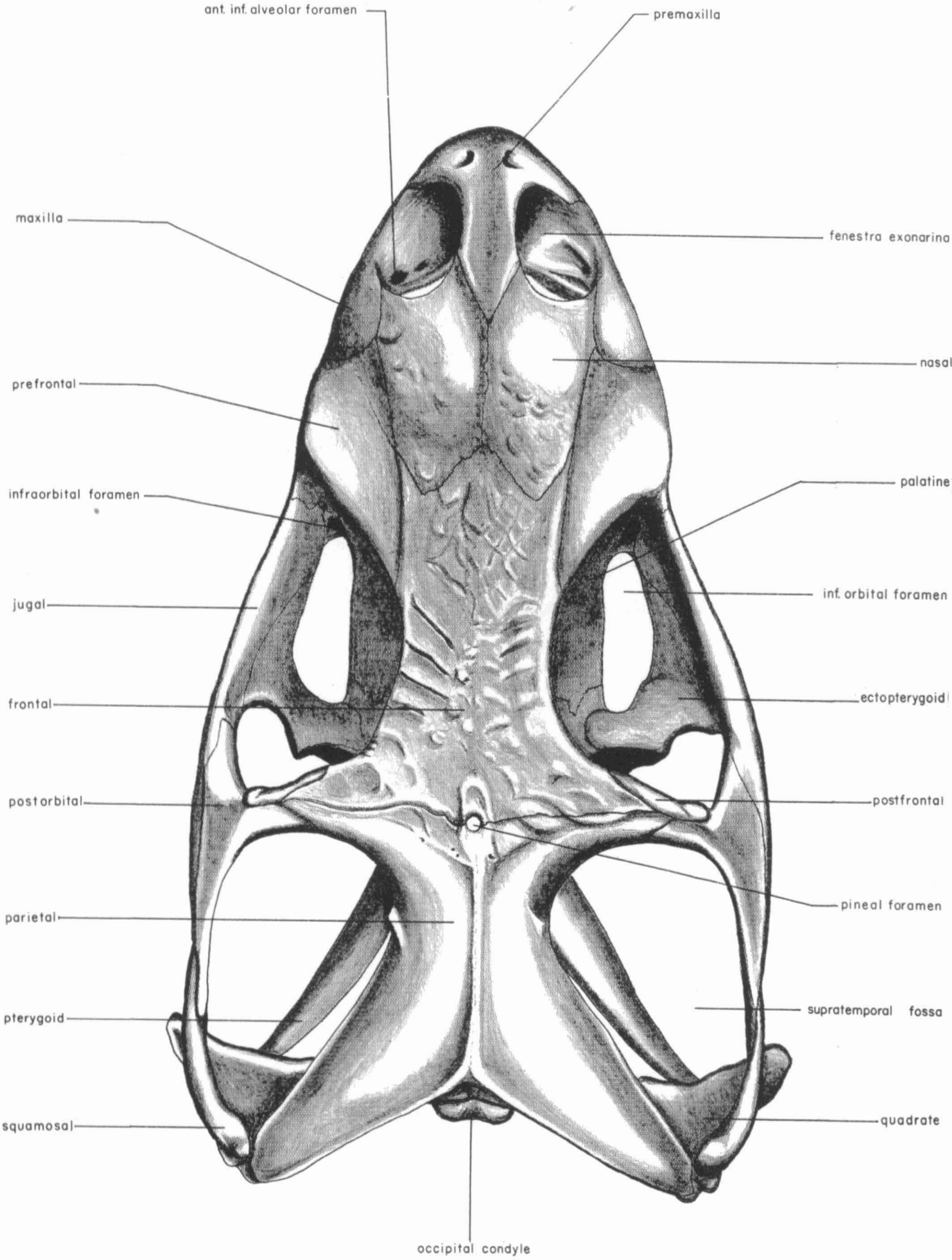


Fig. 2

Fig. 3. Skull of *Ctenosaura pectinata*, dorsal view.



ant. inf. alveolar foramen
premaxilla
maxilla
fenestra exonarina
nasal
prefrontal
palatine
infraorbital foramen
inf. orbital foramen
jugal
ectopterygoid
frontal
postorbital
postfrontal
pineal foramen
parietal
pterygoid
supratemporal fossa
squamosal
quadrate
occipital condyle

Fig. 3

Fig. 4. Skull of *Ctenosaura pectinata,* ventral view.

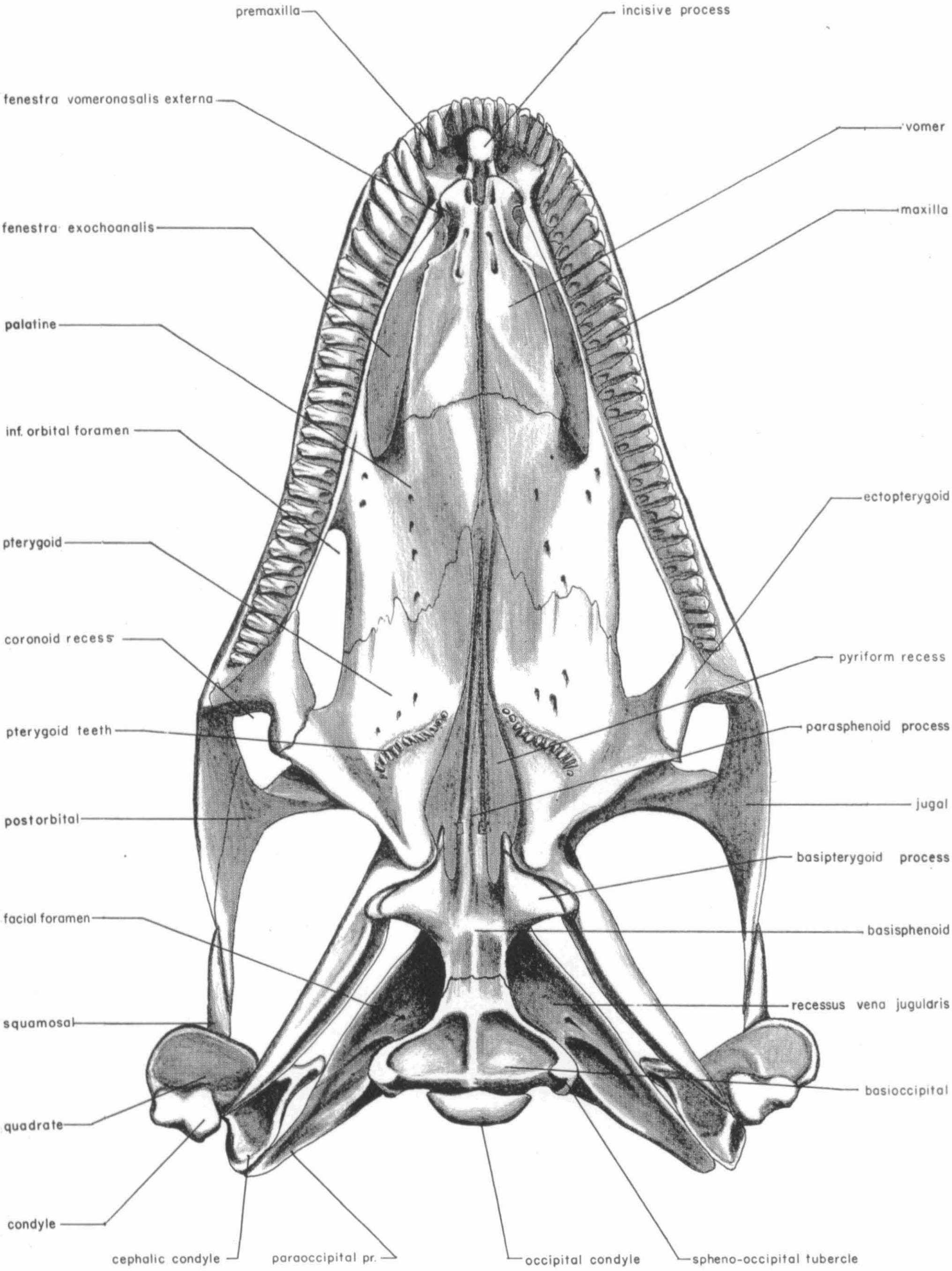

premaxilla
incisive process
fenestra vomeronasalis externa
vomer
fenestra exochoanalis
maxilla
palatine
inf. orbital foramen
ectopterygoid
pterygoid
coronoid recess
pyriform recess
pterygoid teeth
parasphenoid process
postorbital
jugal
basipterygoid process
facial foramen
basisphenoid
recessus vena jugularis
squamosal
basioccipital
quadrate
condyle
cephalic condyle
paraoccipital pr.
occipital condyle
spheno-occipital tubercle

Fig. 4

Fig. 5. Skull of *Ctenosaura pectinata*, lateral view.

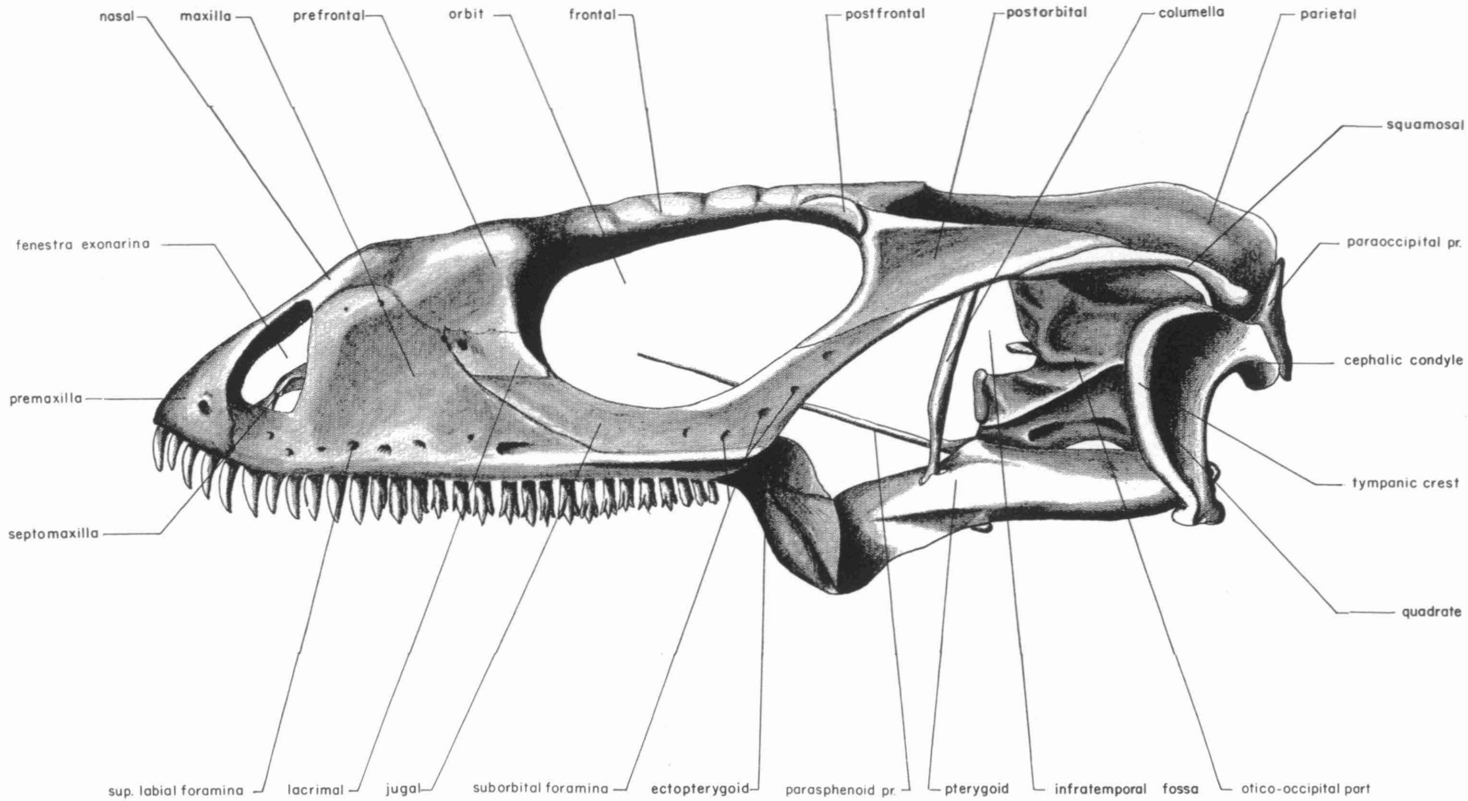

nasal
maxilla
prefrontal
orbit
frontal
postfrontal
postorbital
columella
parietal
squamosal
fenestra exonarina
paraoccipital pr.
premaxilla
cephalic condyle
septomaxilla
tympanic crest
quadrate
sup. labial foramina
lacrimal
jugal
suborbital foramina
ectopterygoid
parasphenoid pr.
pterygoid
infratemporal fossa
otico-occipital part

Fig. 5

Fig. 6. Skull of *Ctenosaura pectinata*, posterior view.

Fig. 7. Orbitotemporal region of *Ctenosaura pectinata*, lateral view.

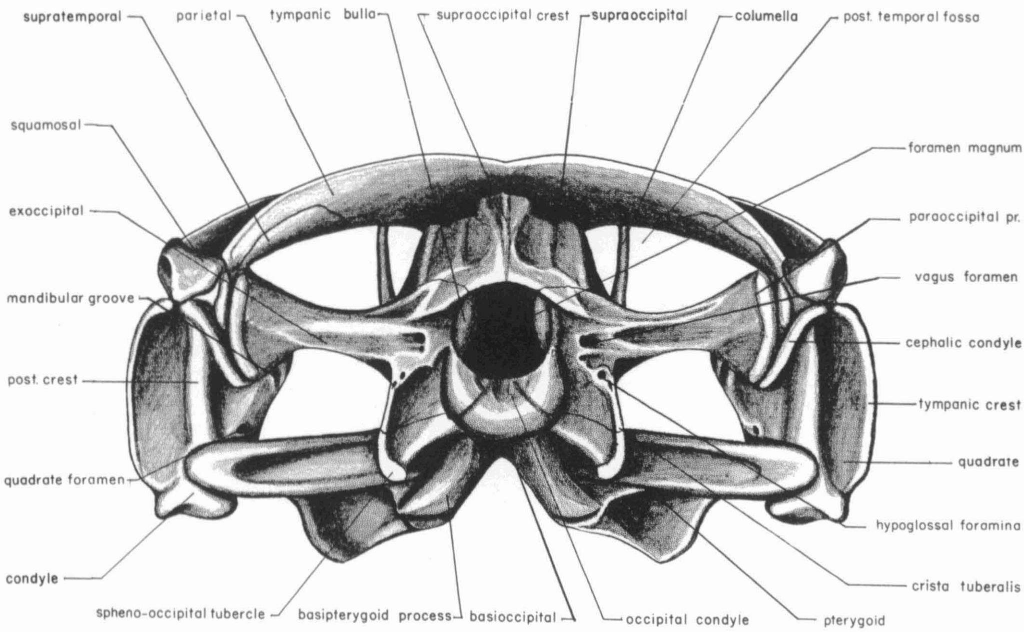

supratemporal
parietal
tympanic bulla
supraoccipital crest
supraoccipital
columella
post. temporal fossa
squamosal
foramen magnum
exoccipital
paraoccipital pr.
vagus foramen
mandibular groove
cephalic condyle
post. crest
tympanic crest
quadrate foramen
quadrate
hypoglossal foramina
condyle
crista tuberalis
spheno-occipital tubercle
basipterygoid process
basioccipital
occipital condyle
pterygoid

Fig.6

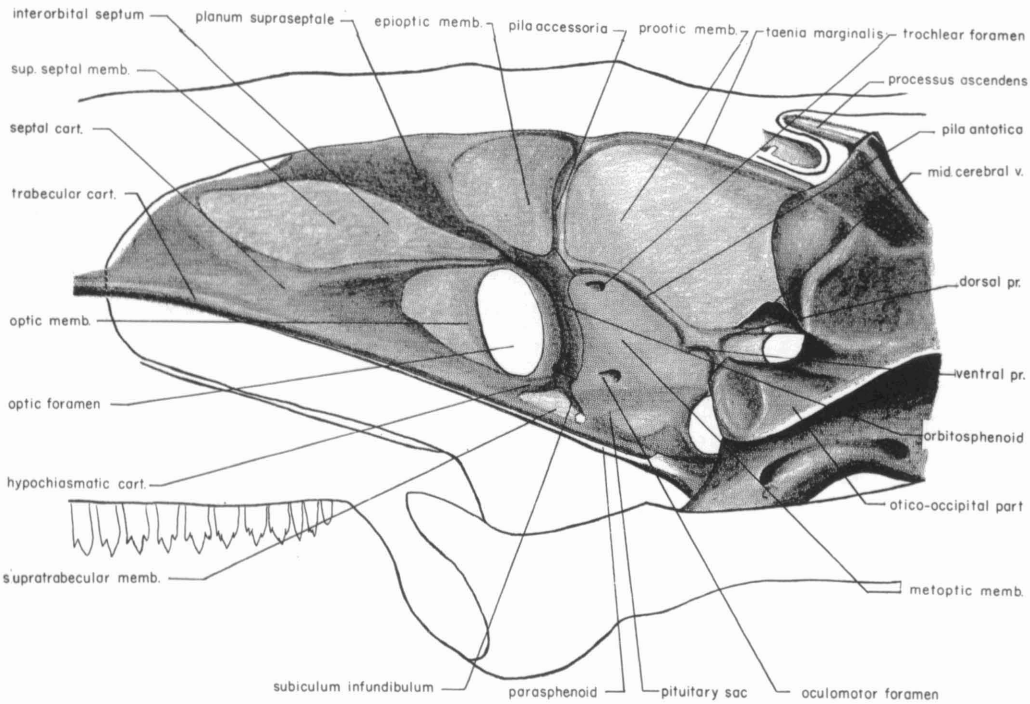

interorbital septum
planum supraseptale
epioptic memb.
pila accessoria
prootic memb.
taenia marginalis
trochlear foramen
sup. septal memb.
processus ascendens
septal cart.
pila antotica
mid. cerebral v.
trabecular cart.
dorsal pr.
optic memb.
ventral pr.
optic foramen
orbitosphenoid
hypochiasmatic cart.
otico-occipital part
supratrabecular memb.
metoptic memb.
subiculum infundibulum
parasphenoid
pituitary sac
oculomotor foramen

Fig.7

Fig. 8. Otico-occipital region of *Ctenosaura pectinata,* lateral view.

Fig. 9. Otico-occipital region, medial view.

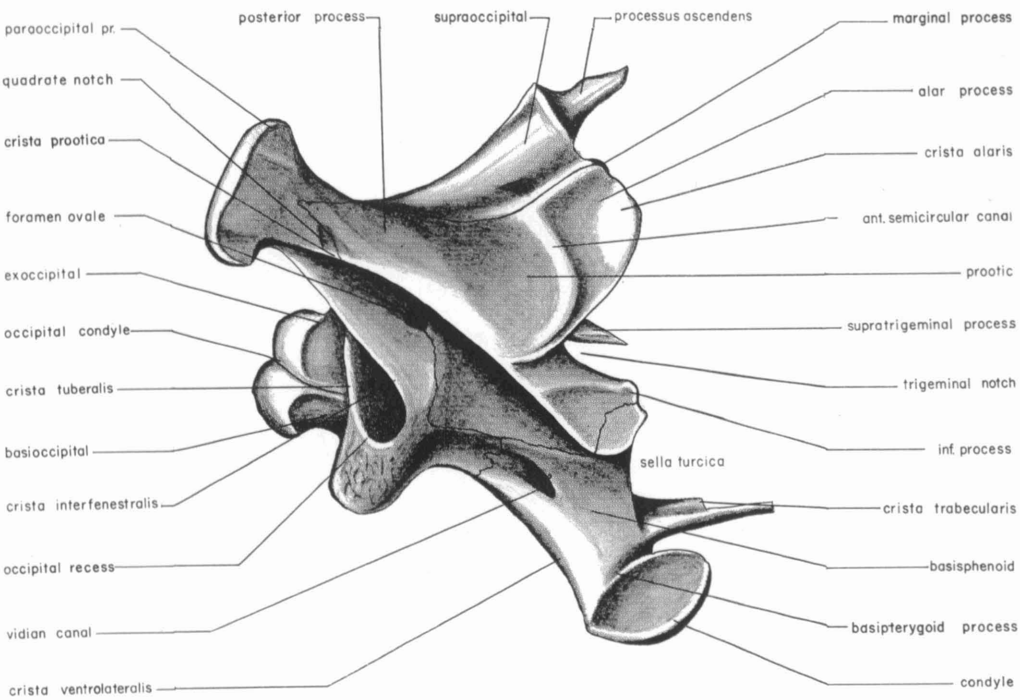

paraoccipital pr.
posterior process
supraoccipital
processus ascendens
marginal process
quadrate notch
alar process
crista prootica
crista alaris
foramen ovale
ant. semicircular canal
exoccipital
prootic
occipital condyle
supratrigeminal process
crista tuberalis
trigeminal notch
basioccipital
inf. process
sella turcica
crista interfenestralis
crista trabecularis
occipital recess
basisphenoid
vidian canal
basipterygoid process
crista ventrolateralis
condyle

Fig.8

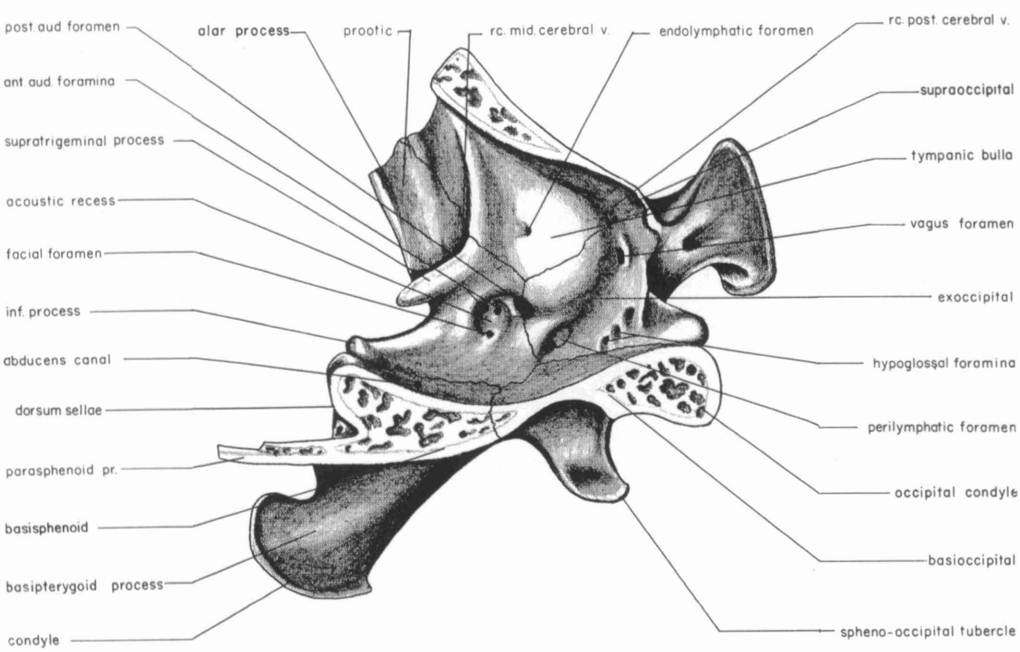

post. aud. foramen
alar process
prootic
rc. mid. cerebral v.
endolymphatic foramen
rc. post. cerebral v.
ant. aud. foramina
supraoccipital
supratrigeminal process
tympanic bulla
acoustic recess
vagus foramen
facial foramen
exoccipital
inf. process
abducens canal
hypoglossal foramina
dorsum sellae
perilymphatic foramen
parasphenoid pr.
occipital condyle
basisphenoid
basioccipital
basipterygoid process
condyle
spheno-occipital tubercle

Fig.9

Fig. 10. Supraoccipital of *Ctenosaura pectinata*, lateral view.

Fig. 11. Right prootic, medial view.

Fig. 12. Right exoccipital, dorsal view.

Fig. 13. Basioccipital, dorsal view.

Fig. 14. Basisphenoid, anterior view.

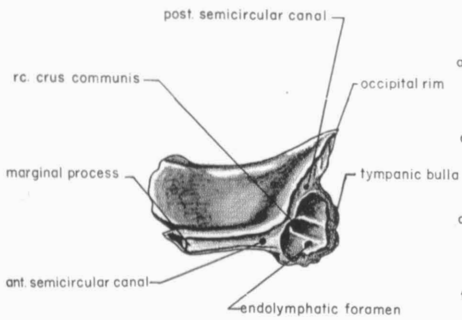
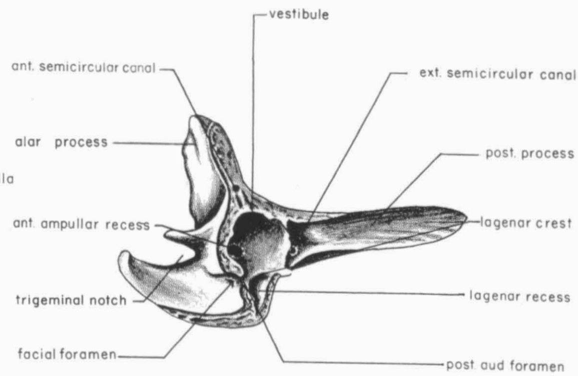


Fig.10



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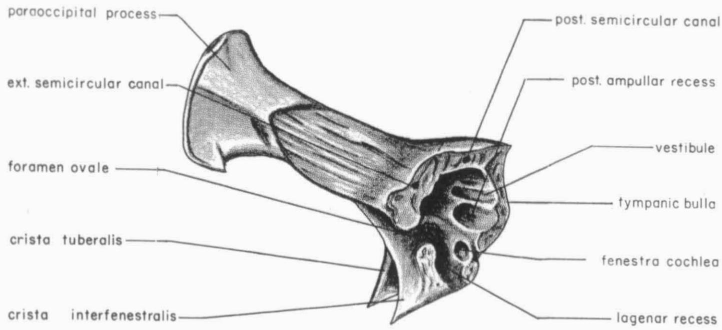


Fig.12

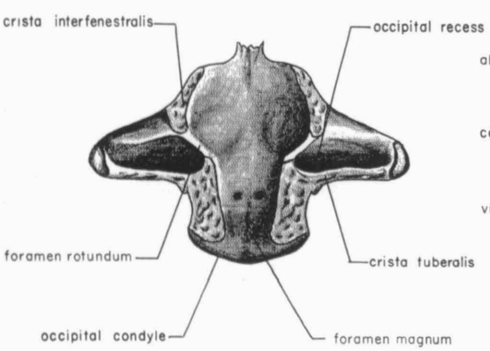


Fig.13

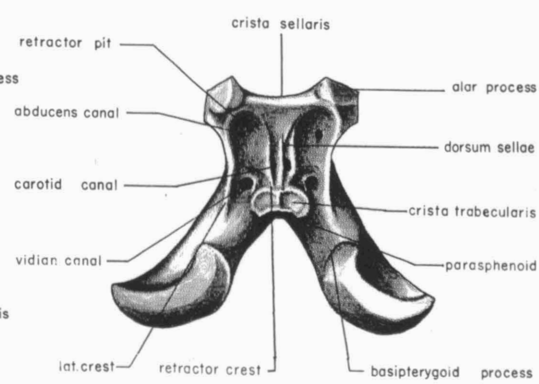


Fig.14

Fig. 15. Left vomer of *Ctenosaura pectinata*, dorsal view.

Fig. 16. Left vomer, ventral view.

Fig. 17. Left palatine, dorsal view.

Fig. 18. Left pterygoid, dorsal view.

Fig. 19. Left quadrate, medial view.

Fig. 20. Left ectopterygoid, posterior view.

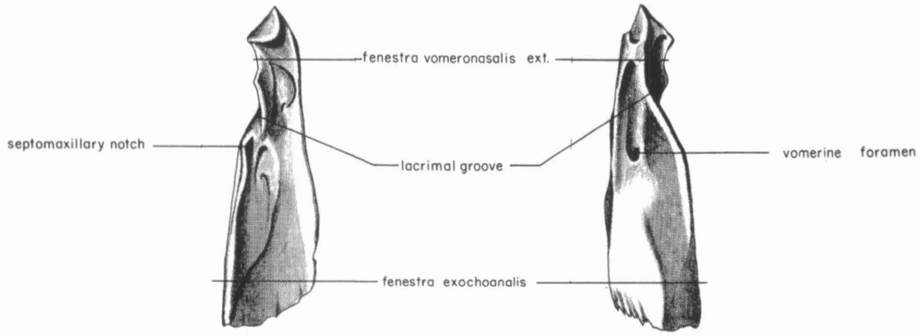


Fig.15

Fig.16

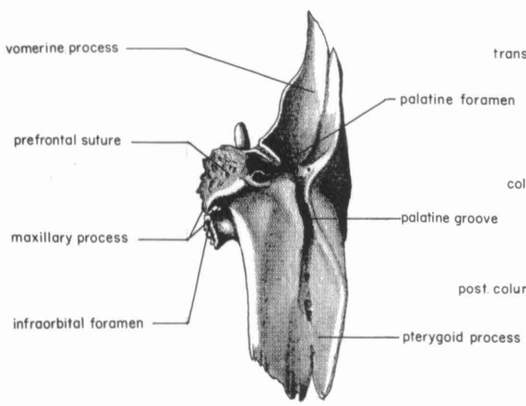


Fig.17

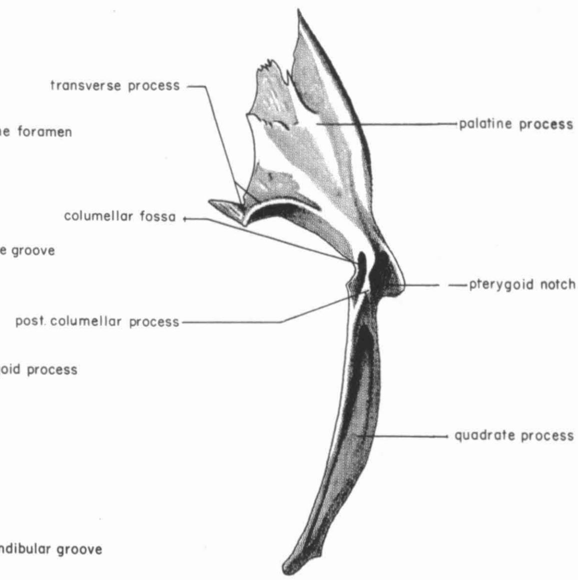


Fig.18

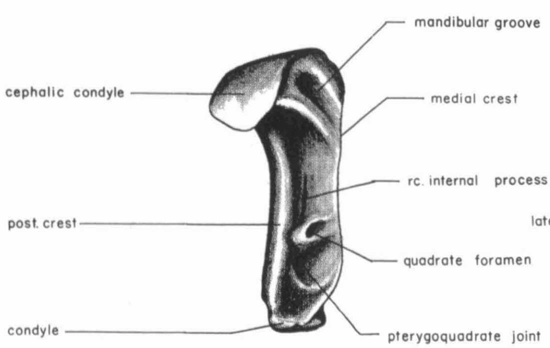


Fig.19

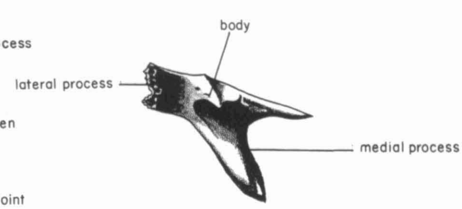


Fig.20

Fig. 21. Left supratemporal of *Ctenosaura pectinata*, dorsal view.

Fig. 22. Parietal, ventral view.

Fig. 23. Left orbitosphenoid, lateral view.

Fig. 24. Frontal, ventral view.

Fig. 25. Right septomaxilla, lateral view.

Fig. 26. Left nasal, ventral view.

Fig. 27. Left septomaxilla, medial view.

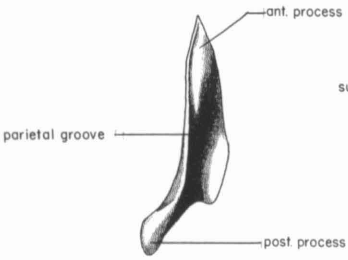


Fig. 21

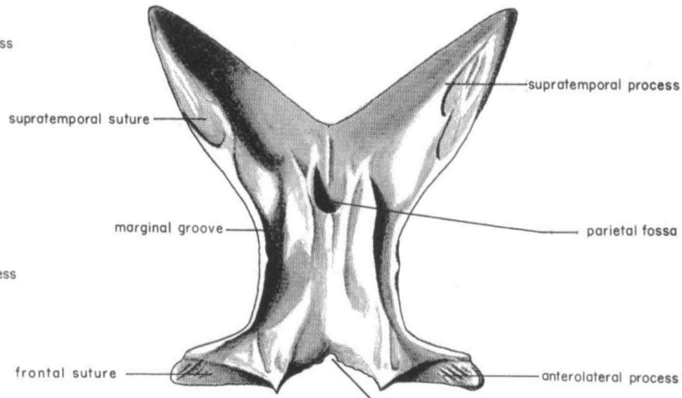
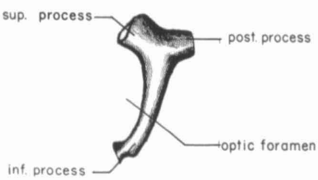


Fig. 22



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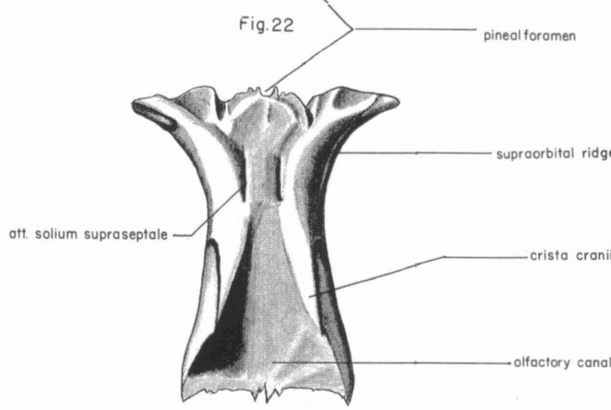

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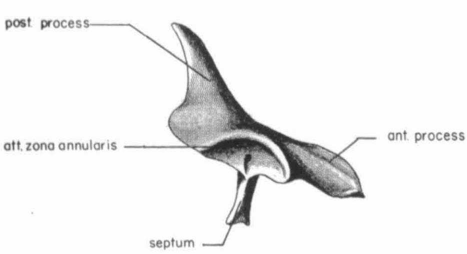


Fig. 25

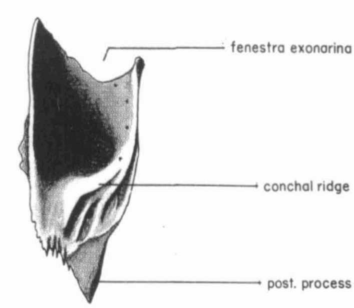


Fig. 26

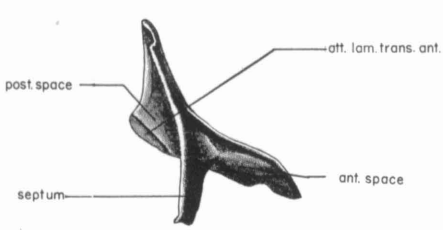


Fig. 27

Fig. 28. Right ramus of *Ctenosaura pectinata*, mesial view.

Fig. 29. Left ramus, lateral view.

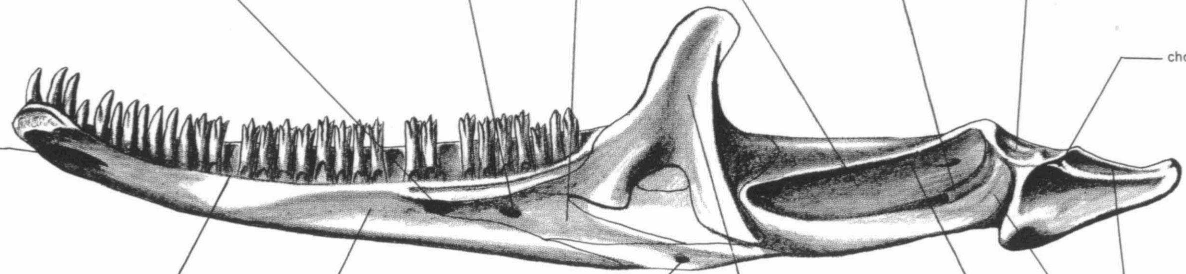

ant. inf. alveolar foramen
ant. mylohyoid foramen
splenial
mandibular foramen
Meckel's cart.
articular condyle
chorda tympani foramen
M'eckel's canal
crista dentalis
dentary
post. mylohyoid foramen
coronoid
angular
supra-angular
articular
retroarticular process

Fig.28

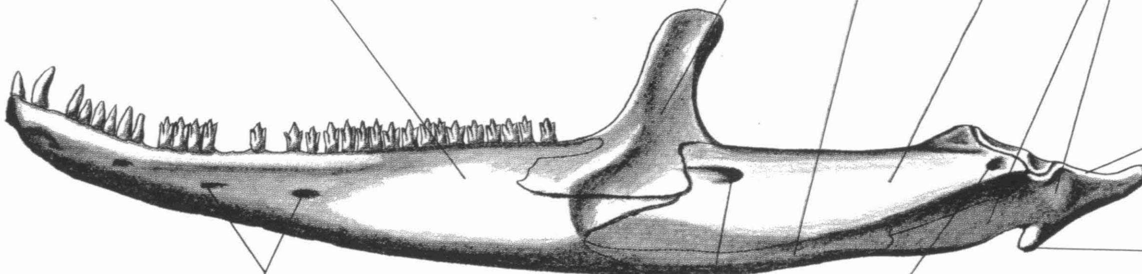

tympanic crest
angular process
mental foramina
ant. supra-angular foramen
post. supra-angular foramen

Fig.29

Fig. 30. Temporal region of *Ctenosaura pectinata*, superficial view.

Fig. 31. Temporal region, first depth.

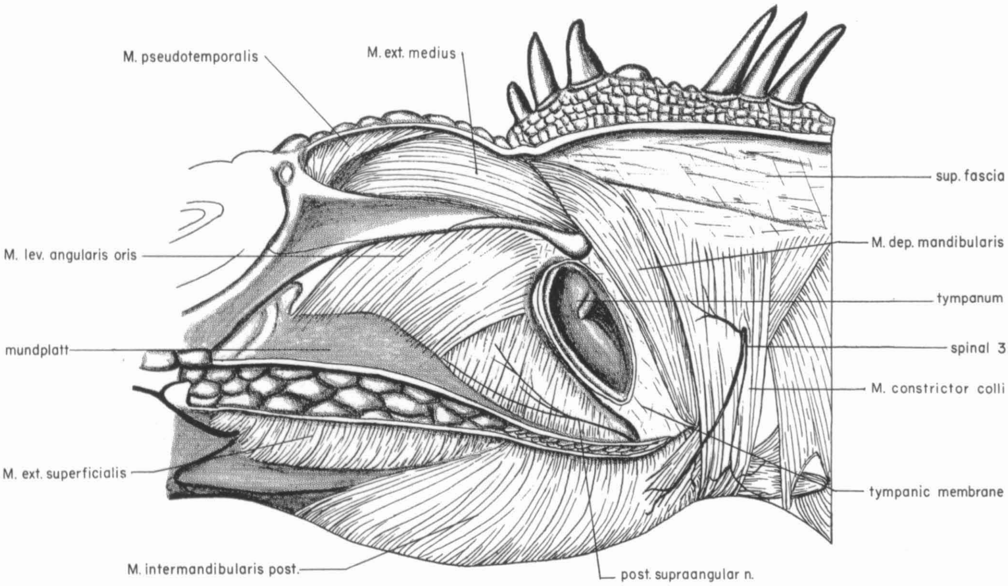

M. pseudotemporalis
M. ext. medius
sup. fascia
M. lev. angularis oris
M. dep. mandibularis
tympanum
mundplatt
spinal 3
M. constrictor colli
M. ext. superficialis
tympanic membrane
M. intermandibularis post.
post. supraangular n.

Fig.30

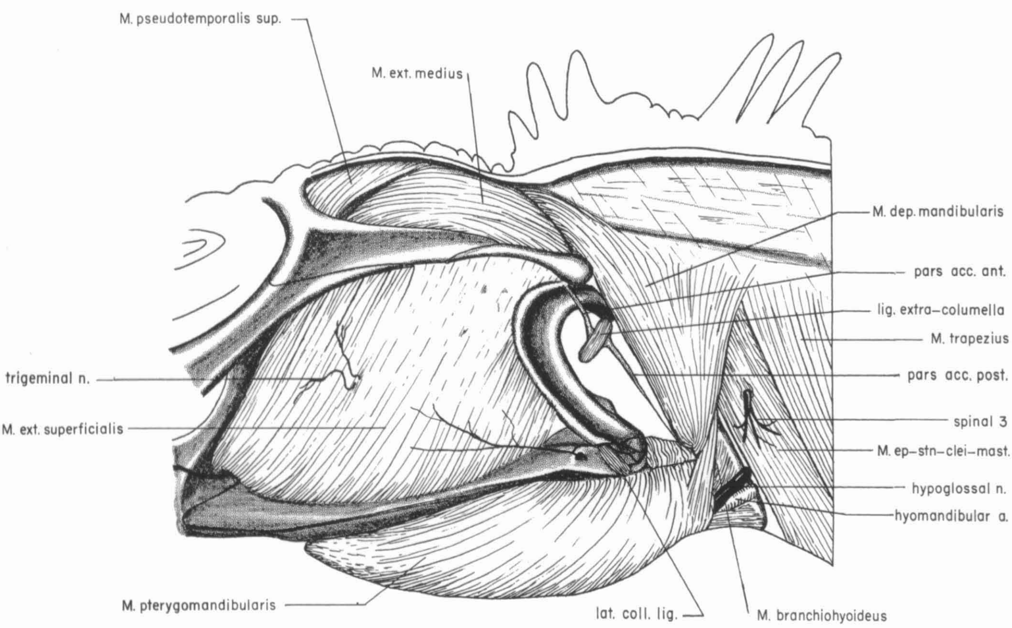

M. pseudotemporalis sup.
M. ext. medius
M. dep. mandibularis
pars acc. ant.
lig. extra-columella
M. trapezius
trigeminal n.
pars acc. post.
spinal 3
M. ext. superficialis
M. ep-stn-clei-mast.
hypoglossal n.
hyomandibular a.
M. pterygomandibularis
lat. coll. lig.
M. branchiohyoideus

Fig 31

Fig. 32. Temporal region of *Ctenosaura pectinata,* second depth.

Fig. 33. Temporal region, third depth.

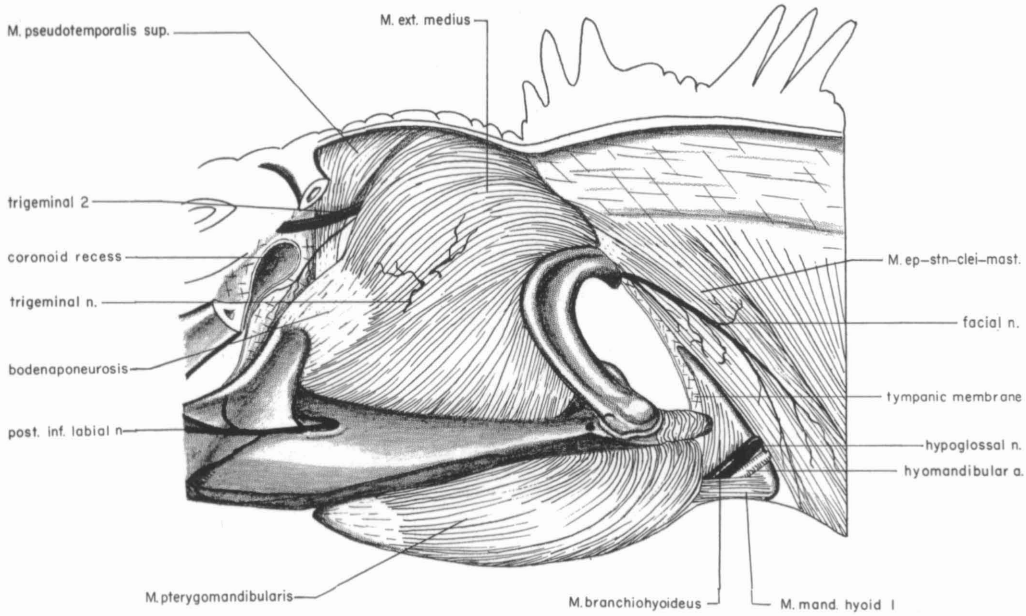

M. pseudotemporalis sup.
M. ext. medius
trigeminal 2
coronoid recess
trigeminal n.
bodenaponeurosis
post. inf. labial n.
M. ep–stn–clei–mast.
facial n.
tympanic membrane
hypoglossal n.
hyomandibular a.
M. pterygomandibularis
M. branchiohyoideus
M. mand. hyoid I

Fig.32

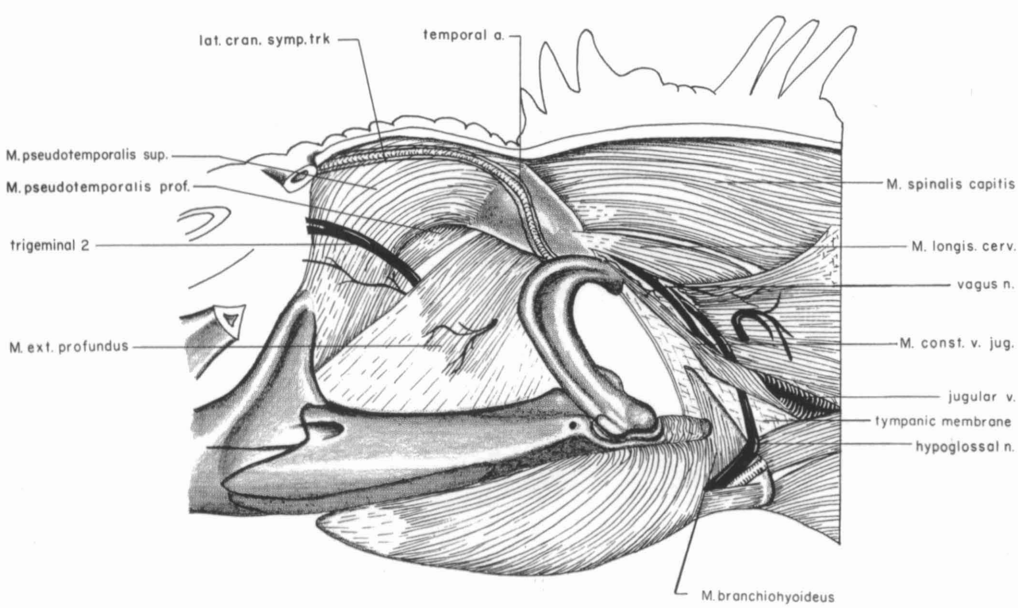

lat. cran. symp. trk
temporal a.
M. pseudotemporalis sup.
M. pseudotemporalis prof.
trigeminal 2
M. ext. profundus
M. spinalis capitis
M. longis. cerv.
vagus n.
M. const. v. jug.
jugular v.
tympanic membrane
hypoglossal n.
M. branchiohyoideus

Fig.33

Fig. 34. Temporal region of *Ctenosaura pectinata*, fourth depth.

Fig. 35. Temporal region, deep view.

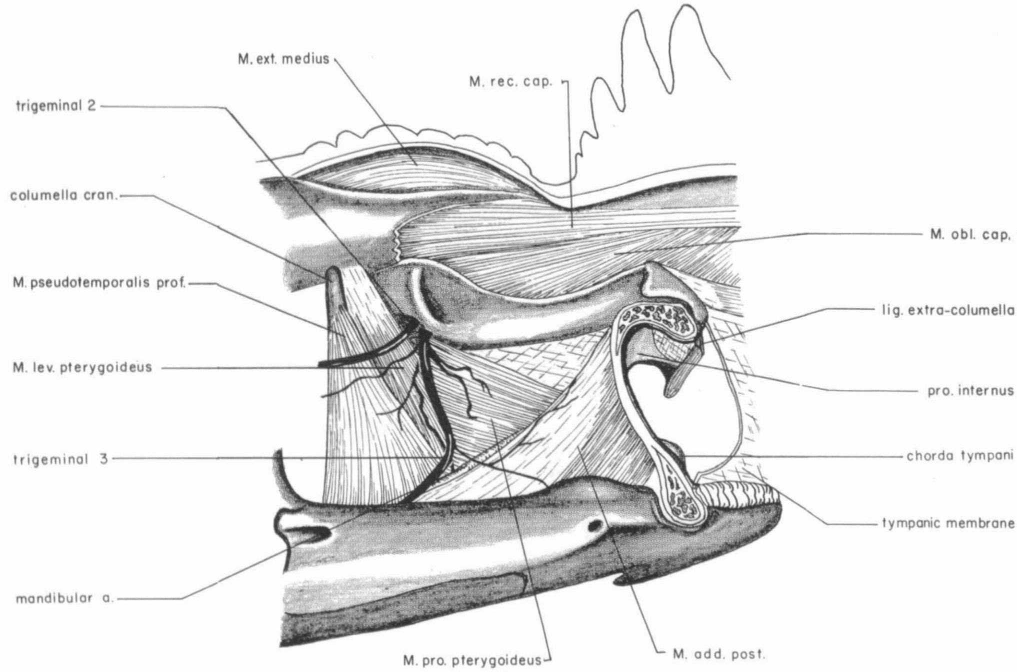

M. ext. medius
M. rec. cap.
trigeminal 2
columella cran.
M. obl. cap.
M. pseudotemporalis prof.
lig. extra-columella
M. lev. pterygoideus
pro. internus
trigeminal 3
chorda tympani
tympanic membrane
mandibular a.
M. pro. pterygoideus
M. add. post.

Fig. 34

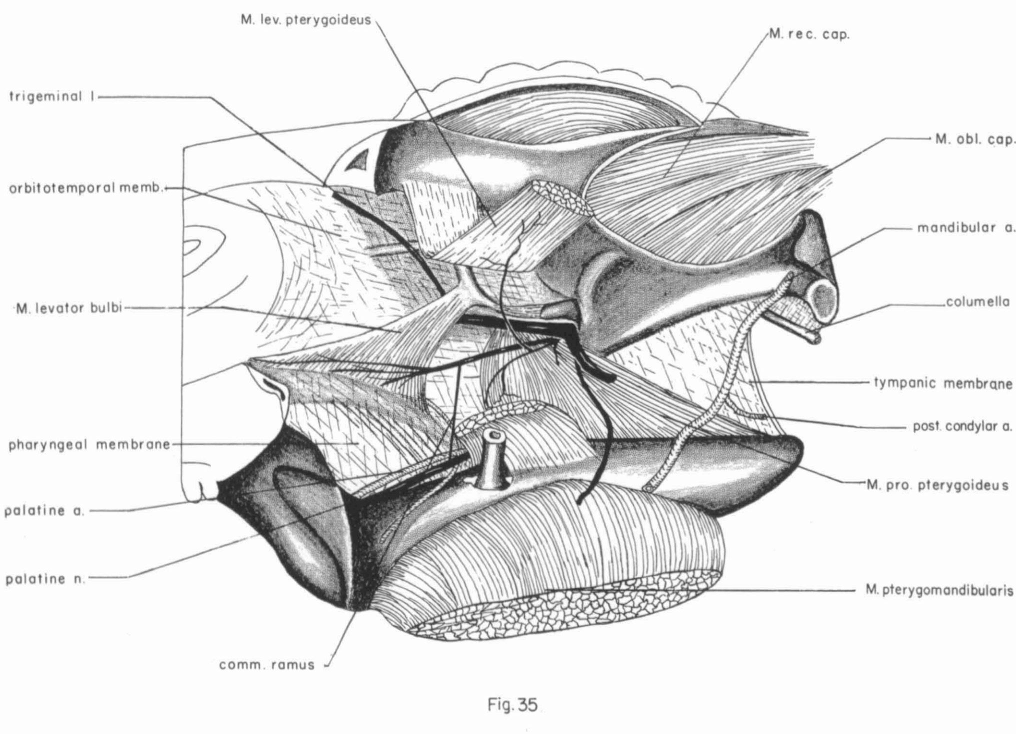

M. lev. pterygoideus
M. rec. cap.
trigeminal I
M. obl. cap.
orbitotemporal memb.
mandibular a.
M. levator bulbi
columella
tympanic membrane
post. condylar a.
pharyngeal membrane
M. pro. pterygoideus
palatine a.
palatine n.
M. pterygomandibularis
comm. ramus

Fig. 35

Fig. 36. Throat region of *Ctenosaura pectinata*, superficial view.

Fig. 37. Throat region, first depth.

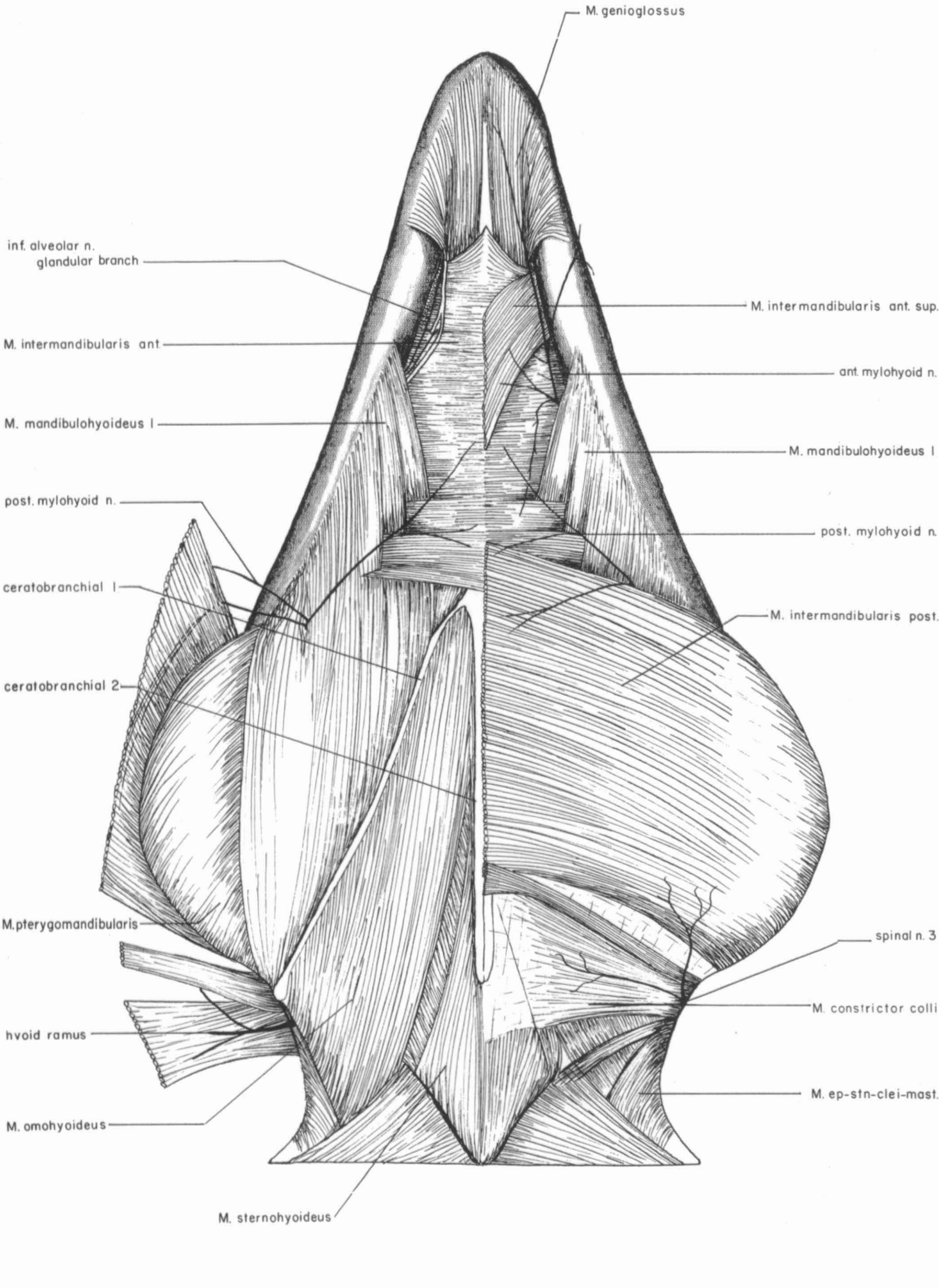

M. genioglossus
inf. alveolar n.
glandular branch
M. intermandibularis ant. sup.
M. intermandibularis ant.
ant. mylohyoid n.
M. mandibulohyoideus I
M. mandibulohyoideus I
post. mylohyoid n.
post. mylohyoid n.
ceratobranchial I
M. intermandibularis post.
ceratobranchial 2
M. pterygomandibularis
spinal n. 3
M. constrictor colli
hvoid ramus
M. ep-stn-clei-mast.
M. omohyoideus
M. sternohyoideus

Fig. 37

Fig. 36

Fig. 38. Throat region of *Ctenosaura pectinata,* second depth.

Fig. 39. Throat region, deep view.

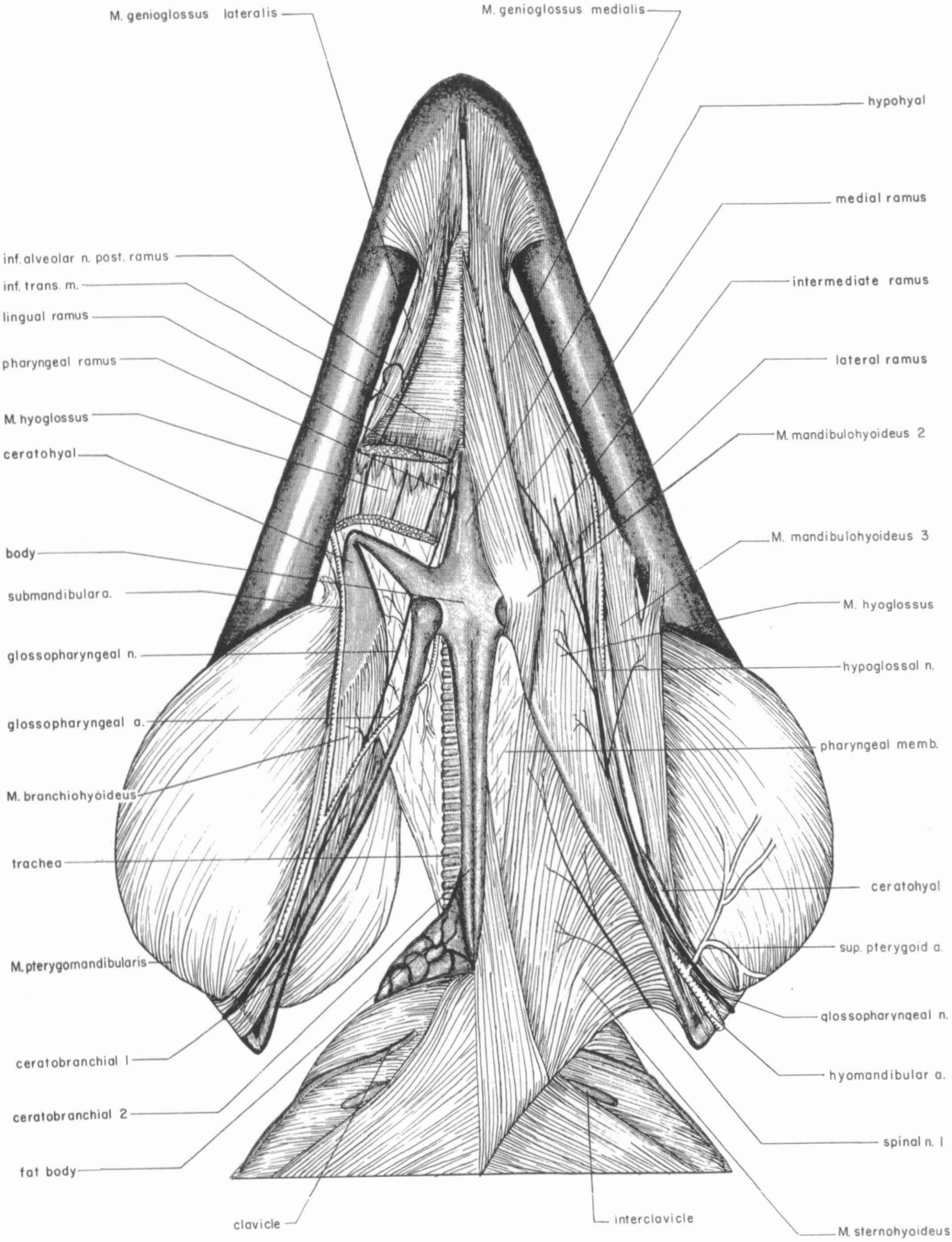

M. genioglossus lateralis
M. genioglossus medialis
hypohyal
medial ramus
intermediate ramus
lateral ramus
M. mandibulohyoideus 2
M. mandibulohyoideus 3
M. hyoglossus
hypoglossal n.
pharyngeal memb.
ceratohyal
sup. pterygoid a.
glossopharyngeal n.
hyomandibular a.
spinal n. I
M. sternohyoideus
interclavicle
clavicle
fat body
ceratobranchial 2
ceratobranchial I
M. pterygomandibularis
trachea
M. branchiohyoideus
glossopharyngeal a.
glossopharyngeal n.
submandibular a.
body
ceratohyal
M. hyoglossus
pharyngeal ramus
lingual ramus
inf. trans. m.
inf. alveolar n. post. ramus

Fig. 39

Fig. 38

Fig. 40. Dorsal neck region of *Ctenosaura pectinata,* superficial view.

Fig. 41. Dorsal neck region, first depth.

Fig. 42. Dorsal neck region, deep view, diagrammatic representation of structures emerging from cranium.

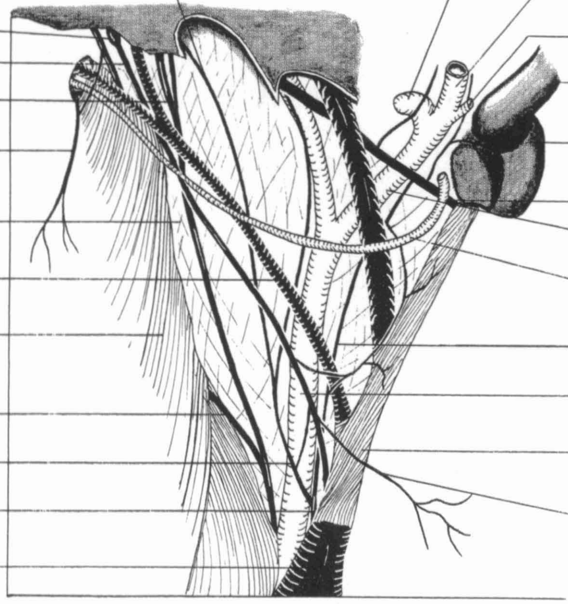


Fig.42

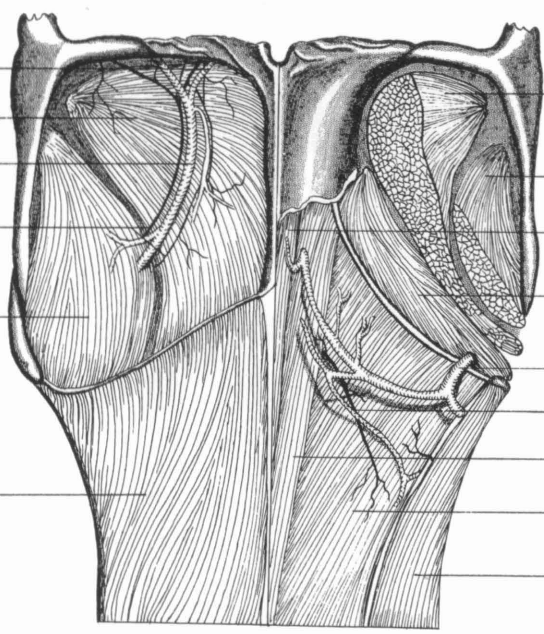


Fig.40 Fig.41

Fig. 43. Cartilaginous nasal capsule of *Ctenosaura pectinata*, dorsal view.

Fig. 44. Cartilaginous nasal capsule, first depth.

Fig. 45. Cartilaginous nasal capsule, second depth.

Fig. 46. Cartilaginous nasal capsule, deep view.

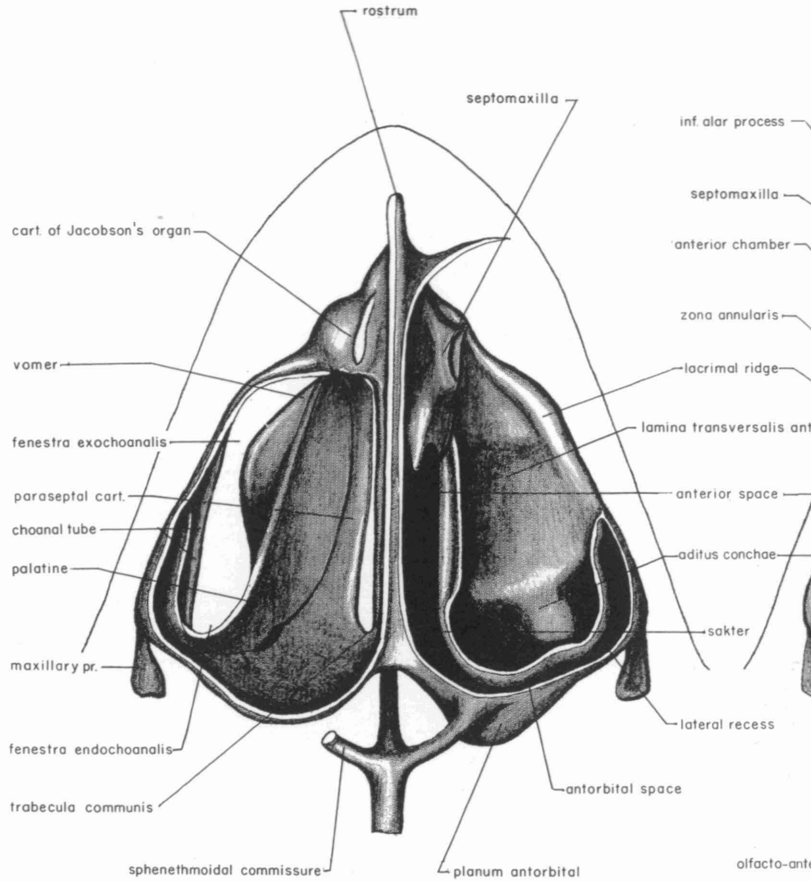


Fig.46 Fig.45

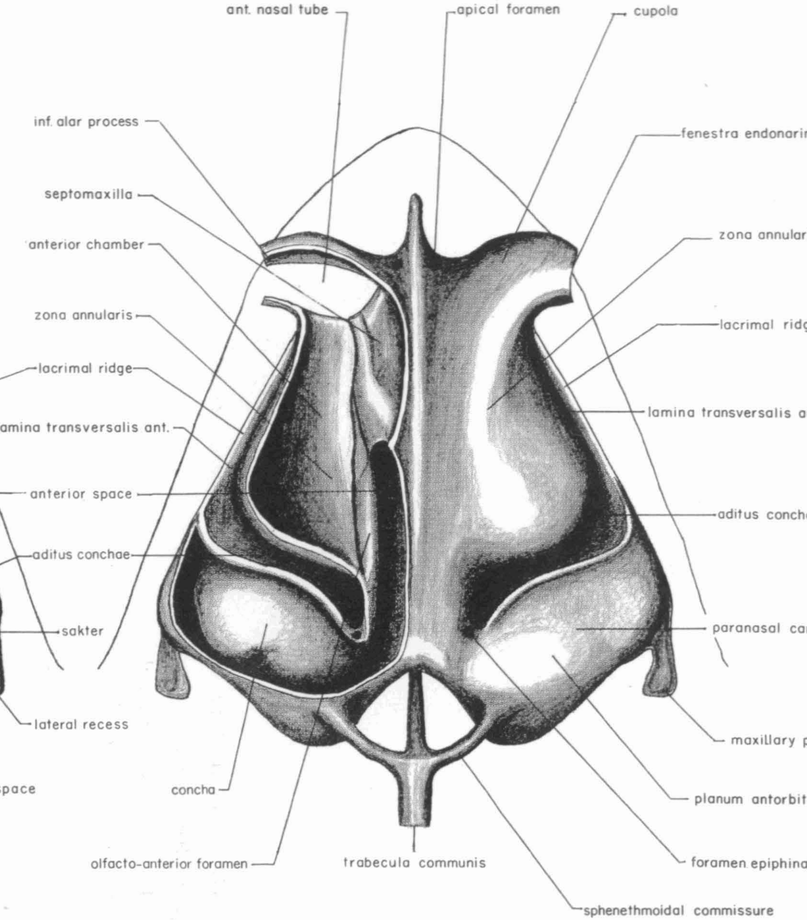


Fig.44 Fig.43

Fig. 47. Cartilaginous nasal capsule of *Ctenosaura pectinata*, lateral view.

Fig. 48. Nasal septum, lateral view.

Fig. 49. Jacobson's organ, dorsal view.

Fig. 50. Articular bone, dorsal view.

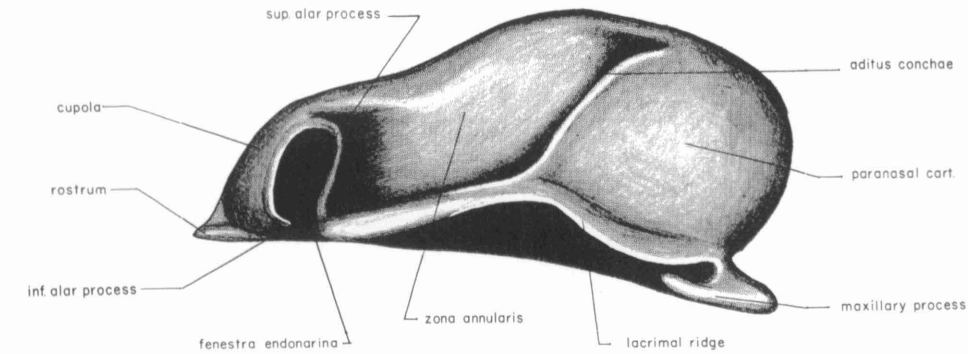


Fig.47

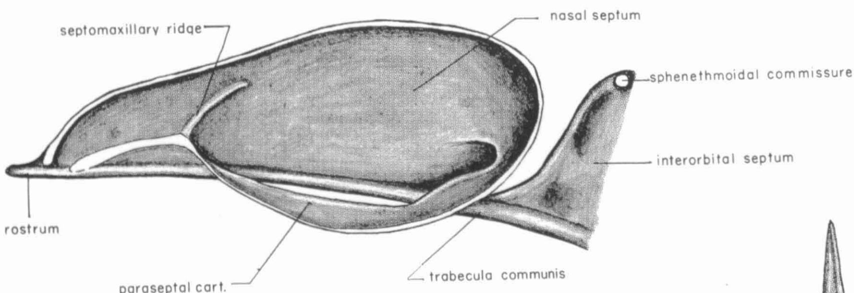


Fig.48

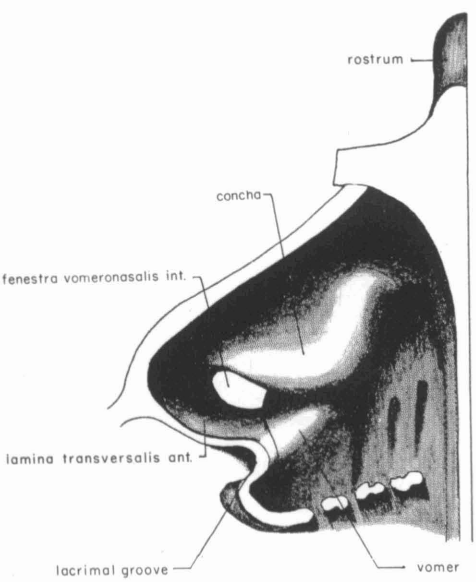


Fig.49

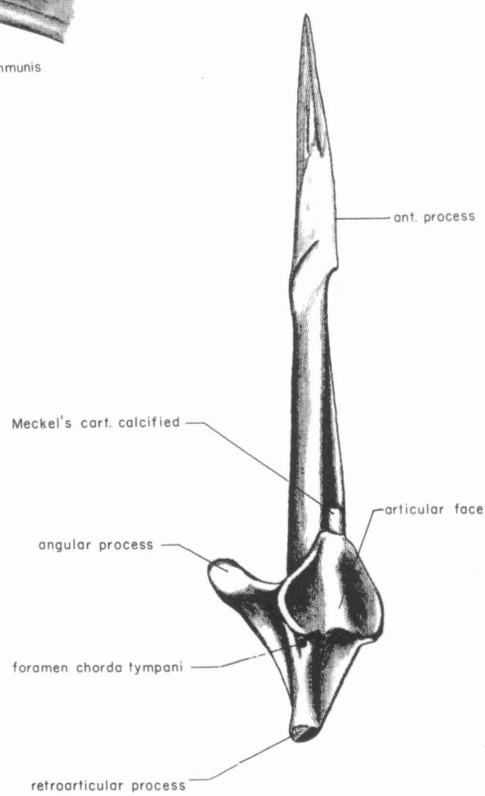


Fig.50

Fig. 51. Larynx of *Ctenosaura pectinata*, ventral view.

Fig. 52. Larynx, dorsal view (cut away to show cartilage).

Fig. 53. Orbital structures, deep view.

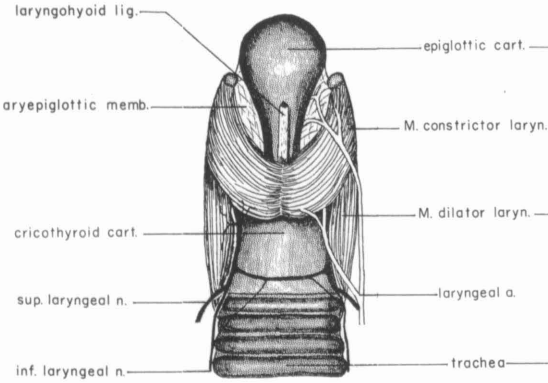


Fig.51

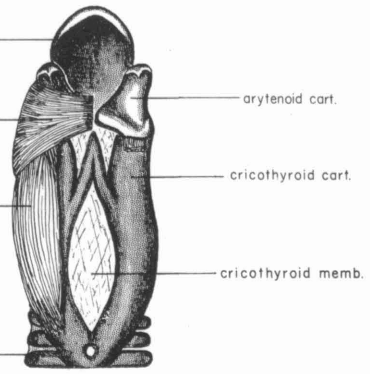


Fig.52

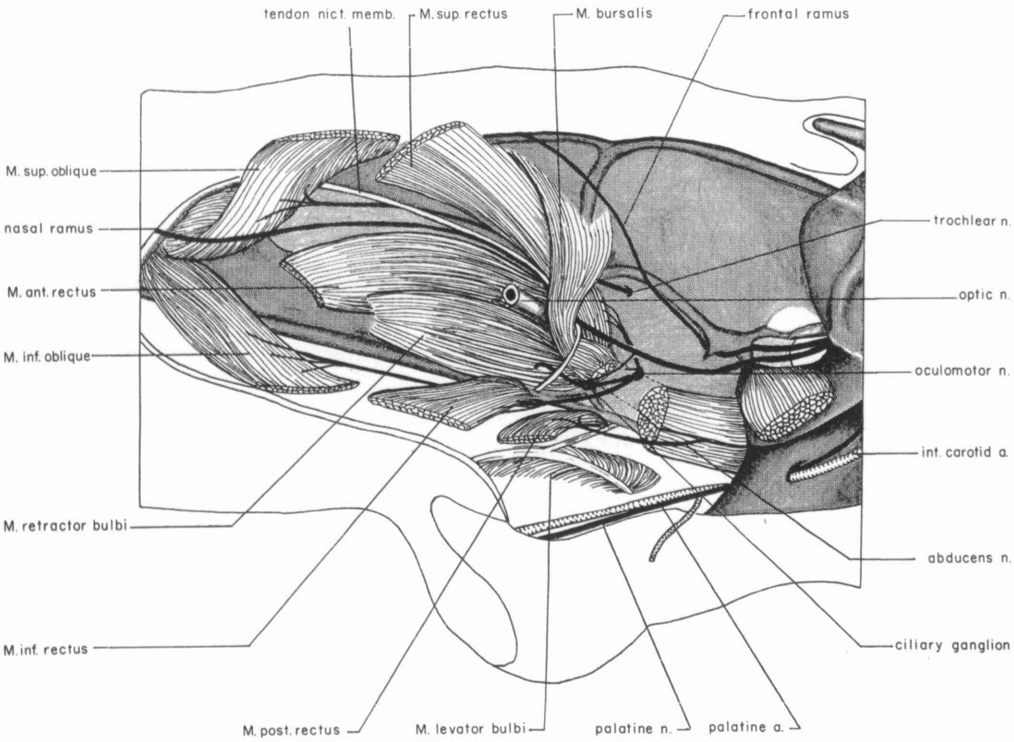


Fig.53

Fig. 54. Osseous labyrinth of *Ctenosaura pectinata*, mesial view.

Fig. 55. Membranous labyrinth, mesial view.

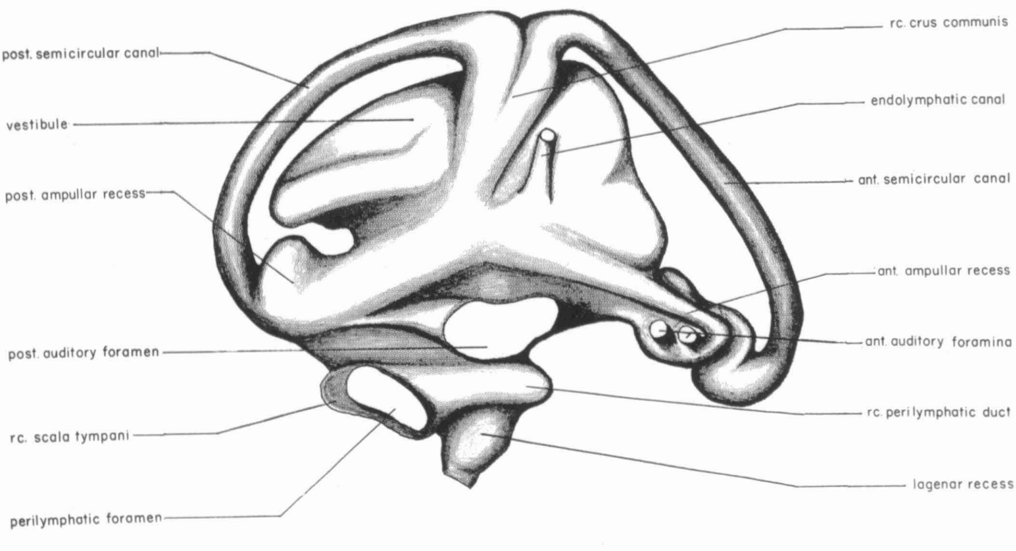

post. semicircular canal
vestibule
post. ampullar recess
post. auditory foramen
rc. scala tympani
perilymphatic foramen
rc. crus communis
endolymphatic canal
ant. semicircular canal
ant. ampullar recess
ant. auditory foramina
rc. perilymphatic duct
lagenar recess

Fig.54

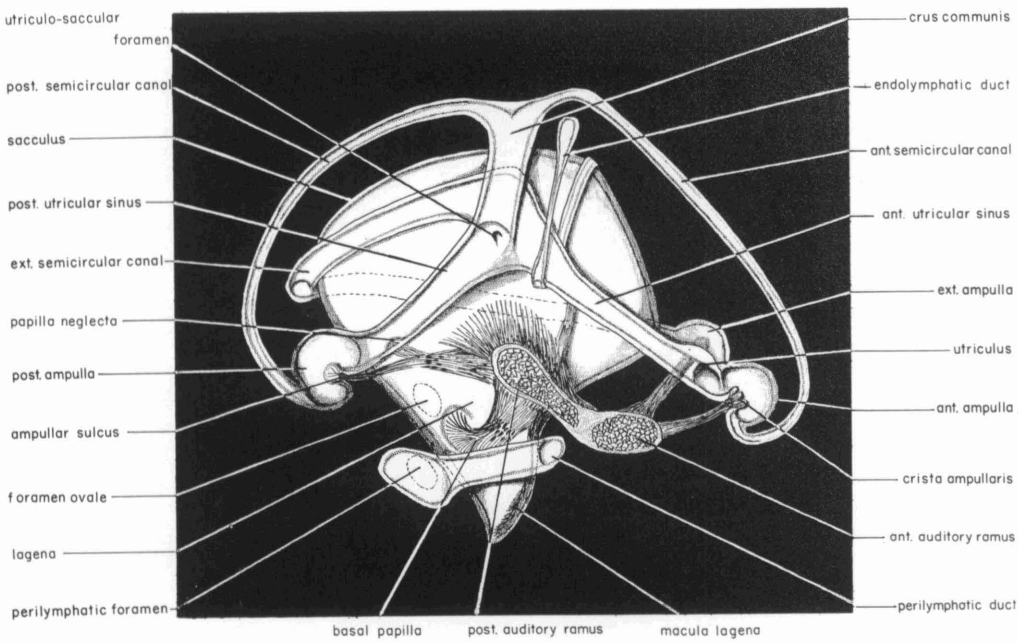

utriculo-saccular foramen
post. semicircular canal
sacculus
post. utricular sinus
ext. semicircular canal
papilla neglecta
post. ampulla
ampullar sulcus
foramen ovale
lagena
perilymphatic foramen
basal papilla
post. auditory ramus
macula lagena
crus communis
endolymphatic duct
ant semicircular canal
ant. utricular sinus
ext. ampulla
utriculus
ant. ampulla
crista ampullaris
ant. auditory ramus
perilymphatic duct

Fig.55

Fig. 56. Osseous labyrinth of *Ctenosaura pectinata*, lateral view.

Fig. 57. Cervical region, ventral view (diagrammatic).

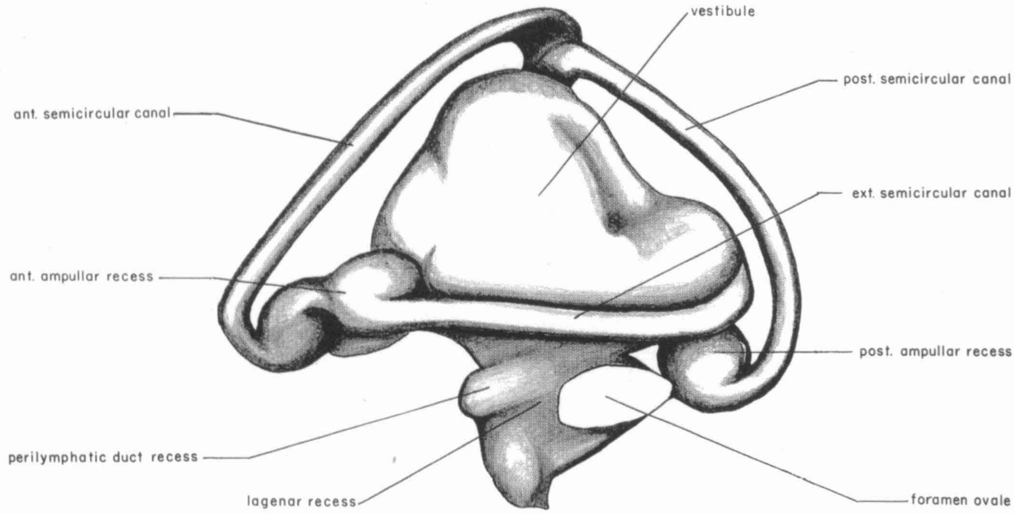

vestibule
post. semicircular canal
ant. semicircular canal
ext. semicircular canal
ant. ampullar recess
post. ampullar recess
perilymphatic duct recess
lagenar recess
foramen ovale

Fig.56

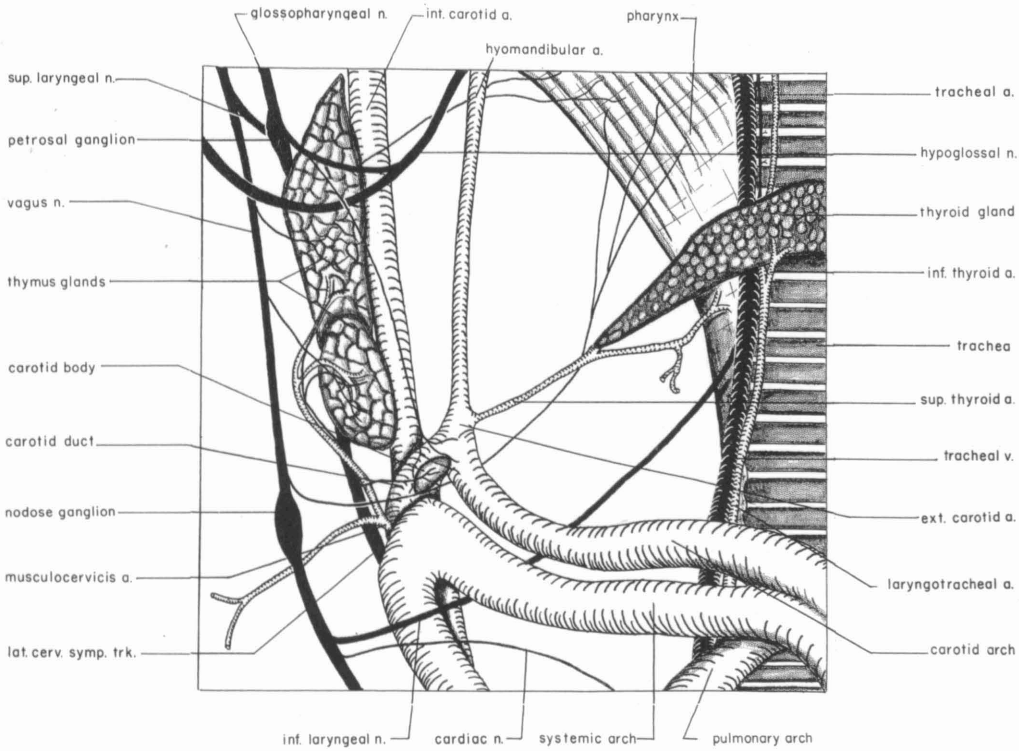
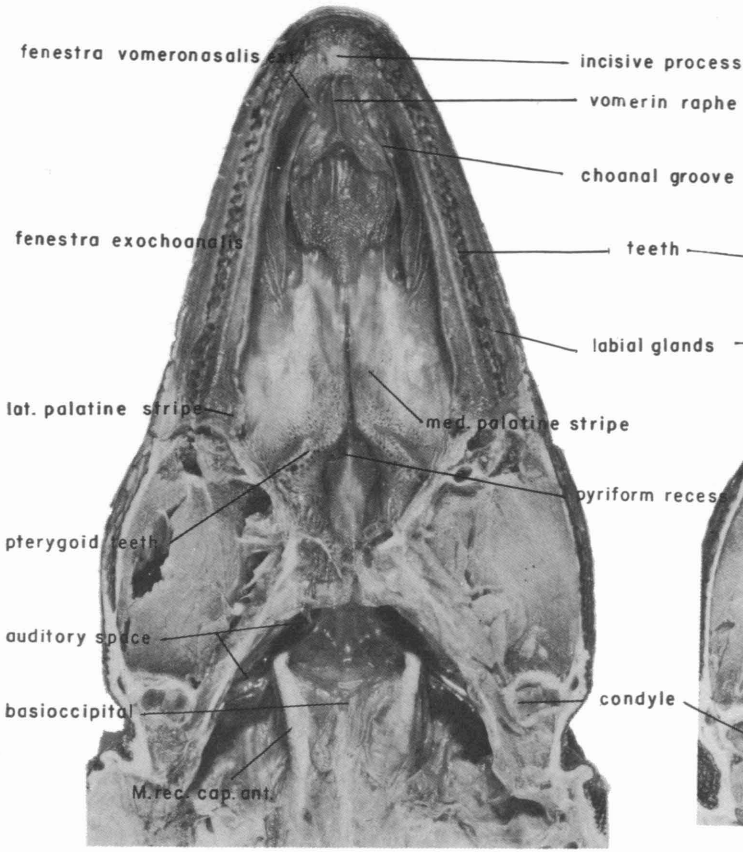

glossopharyngeal n.
int. carotid a.
pharynx
hyomandibular a.
sup. laryngeal n.
tracheal a.
petrosal ganglion
hypoglossal n.
vagus n.
thyroid gland
thymus glands
inf. thyroid a.
trachea
carotid body
sup. thyroid a.
carotid duct
tracheal v.
nodose ganglion
ext. carotid a.
musculocervicis a.
laryngotracheal a.
lat. cerv. symp. trk.
carotid arch
inf. laryngeal n.
cardiac n.
systemic arch
pulmonary arch

Fig.57

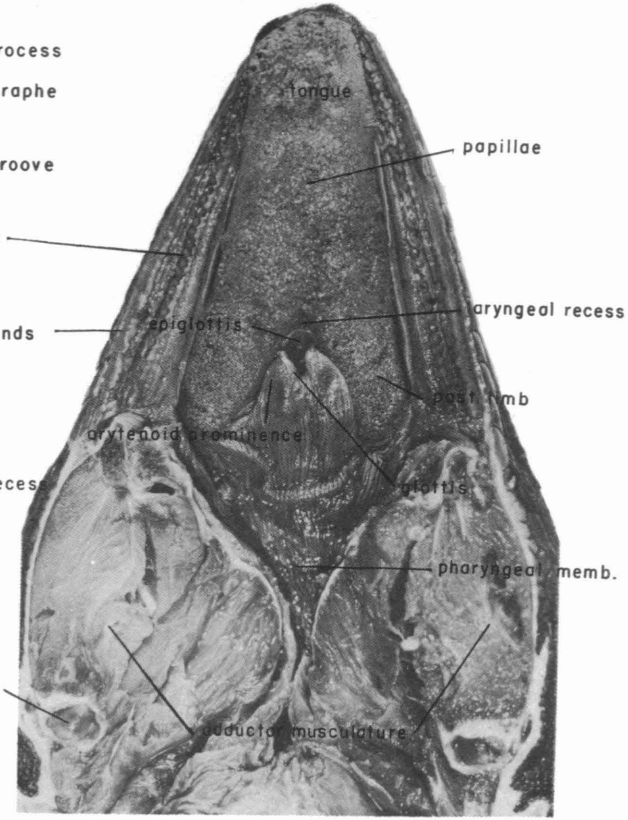
Fig. 58. Oral cavity of *Ctenosaura pectinata*, palatal view.

Fig. 59. Oral cavity, floor.



fenestra vomeronasalis ext.
incisive process
vomerin raphe
choanal groove
fenestra exochoanalis
teeth
labial glands
lat. palatine stripe
med. palatine stripe
pyriform recess
pterygoid teeth
auditory space
condyle
basioccipital
M.rec. cap. ant.

Fig. 58



tongue
papillae
aryngeal recess
epiglottis
post. mb
arytenoid prominence
glottis
pharyngeal memb.
adductor musculature

Fig. 59

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