THE SKELETAL AND MUSCULAR SYSTEMS OF LISSEMYS WITH COMPARATIVE NOTES ON THE SAME IN TRIONYX, GEOMYDA AND TESTUDO

A. SKELETAL SYSTEM
B. MUSCUALR SYSTEM

THE SKELETO-MUSCULAR SYSTEM

The most characteristic features of the Chelonia are the possession of the body shell and the skeletal modifications which have acutely affected the other systems of the body, particularly the muscular system. Therefore, the study of the skeleto-muscular system as a single complex seems to be of considerable significance not only to understand the diverse changes that have taken place in the muscles and the skeleton but also to provide reasonable explanations for the modifications in the other systems especially the respiratory system.

With these ends in view, the skeleto-muscular system of the common Indian pond turtle has been studied in detail. The modifications of the important muscles in three other chelonians, Geomyda, Trionyx and Testudo have also been assessed and accounted for.

THE CARAPACE AND PLASTRON

The carapace in Lissemys is formed principally as is typical in Chelonia by three longitudinal rows of dorsal plates. The middle row consists of the anterior-most moveable small plate, the prenuchal, followed by the fixed nuchal and then the eight neurals. Each lateral row consists of eight costal plates. Lateral to the costal plates is a row of marginals which are present only in the posterior half of the carapace. The number of marginals varies not only in the sub-species of Lissemys, but also between the young and old forms of the same species. In younger forms the marginals are more in number, but as the animals get older some of them get fused together and so their number in the older individuals is always less.

The prenuchal(Fig.1) is a small oblong piece and it is followed by the aomparatively large nuchal. The prenuchal is freely mov~~e~~able, since it is attached to the nuchal by a thick ligament and is moved up and down by means of a muscle. The ligamentous joint becomes ossified as the animal grows old making the joint progressively immovable. The movement of the prenuchal is of valvular nature as it can be used to close the aperture of the shell anteriorly. The muscle which brings about the movement of the prenuchal has been named by Hassan (1941) as the *nucho-prenuchalis*. It is probably derived from the *spinalis-semispinalis* system of muscles which is absent at the seventh cervical vertebral region, which is covered by the nuchal and the prenuchal plates (George and Shah, 1955). A fuller description of this muscle is given later while describing the musculature.

The nuchal (Fig.1) articulates laterally with the two costal plates one on either side and posteriorly with the first neural in the median plane. The articulation of the nuchal with the costals and the neural is firm and immovable though the joints show sutures.

The neurals (Fig.1) are fused with the trunk vertebrae. There are seven or sometimes eight neurals arranged one after another in a row along the middle line of the carapace. The neural plates are progressively smaller from the anterior to the posterior end.

The costal plates (Fig.1) are in two rows of eight each on either side of the neurals. They constitute the major portion of the carapace. They and the neurals are firmly joined with one another by sutures and so the intercostal and the costo-neural movements are not possible. This is how the rigid dorsal covering of the carapace is formed.

The marginals (Fig.1) are variable in number and size. They are present only on the posterior half of either border of the carapace. They are articulated with the lateral borders of the costals by thick ligamentous tissue which allows some restricted movement. The variation in the number of the marginals is utilised in the separation of the sub-species of the genus Lissemys. There are three sub-species of the genus *Lissemys punctata*, viz., the *L.p.typica*, the *L.p. granosa* and the *L. p. scutata*. In *L. p. typica* and *L. p. scutata* the number of the marginals in the adult varies from five to eight and in *L. p. granesa* from eight to twelve. The two sub-species *L. p. typica* and *L. p.scutata* are distinguished from one another as the first marginal in the former is the largest of all, while in the other sub-species it is smaller than the second. In all the three sub-species the median pair of the marginals is the smallest in the series and they are loosely attached to the posterior median border of the last pair of costal plates. This pair of marginals is capable of valvular movement caused by the muscle described as the *margino-infracaudal* muscle by Hassan (1941) and which is probably a part of the *flexor-caudae-superficialis* muscle of the tail (George and Shah, 1955). This pair of marginal plates constitutes the so-called supracaudal valve. All the marginals in radial cross sections present -)- shape. Williams and McDowell (1952) have expressed the opinion that the presence of the marginals in Lissemys is a primitive character, since such is not found in any of the other Trionychinae.

As characteristic of Trionychinae, Lissemys is devoid of epidermal scutes and a thin skin covers the plates of the carapace.

The plastron in Lissemys consists of seven plastral plates as found commonly in other soft-shelled turtles and also among the chelonians. The plastral plates of Chelonia are homologised with the clavicles, interclavicle, and the abdominal ribs of the other reptiles (Gadow 1901, Reynolds 1913, Kingsley 1925, Wilson 1925 and Hassan 1941).

The epiplastra (Fig.3) and the entoplastron are homologised with the clavicle and the interclavicle respectively. But recently Williams and McDowell (1952) have suggested that the so-called epiplastra in Trionychenae are not comparable to those of other Testudinates and are really extra elements, the pre-epiplastra, and that the homologue of the entoplastron does not exist in the Trionychenae, and the so-called entoplastron is derived from the fused epiplastra.

The entoplastron (Fig.3) in Lissemys has the shape of a boomerang and has two pointed free ends. Posterolaterally it articulates with the anterior inner cornu of the hyo-hypoplastron of each side. This articulation is not firm, but loose and at this level the plastron moves vertically up and down as the anterior plastral valve, which closes the anterior aperture of the shell.

Generally the hyoplastra are free and separate from the hypoplastra, but in Lissemys they are fused together, Each hyo-hypoplastral plate (Fig.3) possesses five processes consisting of two outer and three inner cornua. Of the two outer ones the posterior one is bifid at its free end, while the anterior one remains undivided and pointed. The anterior inner cornu shows serrations on its free end and articulates loosely with the entoplastron. The middle inner cornu is undivided and remains free, while the posterior inner one is trifid and articulates with the xiphiplastron of its respective side. The articulation with the xiphiplastron is firm and does not show any interplastral movements at this level.

The xiphiplastra (Fig.3) are situated at the posterior end of the plastron. Each one has three processes radiating from a central point. One of them is anteriorly directed towards the outer side which has two large tooth-like projections which articulate with the trifid posterior cornu of the hyo-hypoplastron of its own side. Another is a medially directed short process which articulates with its fellow of the other side, while the third process is posterior with two projections.

In Lissemys, besides these plastral plates there are other bony plates which get superimposed on the plastral plates and are ultimately firmy fused with them. The separate existance of these bony plates other than the plastral plates was noted by Hassan (1941) in the embryos of *L. p. typica*. These superimposed bony plates are called callosities by earlier workers, while Hassan has suggested that they are extra plastral plates.

Among the Trionychinae, Lissemys, Cayclanorbis and Cycloderma possess cutaneous *femoral* flaps at the lateral sides of the xiphiplastra. These flaps are movable and under their cover the hind limbs are retracted. Williams and McDowell (1952) have suggested that the Lisseminae are a primitive sub-family of living Trionychenae as they alone possess the femoral cutaneous flaps and they were probably secondarily lost in other Trionychenae.

Behind the xiphiplastral plates is present a movable flap with an internal core of tough dermis. This was named as the infra-caudal valve by Hassan (1941) which along with the supra-caudal valve of the carapace closes the posterior aperture of the shell after the tail is withdrawn.

THE SKULL

The skull of Lissemys is dorsi-ventrally flattened and is more or less triangular when viewed from either the dorsal or the ventral side. It is well ossified and hardly shows even a trace of cartilage. The sutures separating the various bones are, however, clearly demarcated even in the adult skulls. It differs, however, as do others of the Trionychidae in not having the false roof over the temporal region as is found in many marine forms viz. Chelone mydas.

The cranium forms the axial part of the posterior two-thirds of the skull which is comparatively extensive taking into consideration the skull of lizards, and presents a completely-ossified structure in contrast with the partially-ossified one in the lacertalia. The orbits are large and very well protected by bones and are separated from one another by the thin membranous interorbital septum which extends slightly into the posterior region of the nasal chamber where it forms the internasal septum without dividing the chamber completely into two.

THE CRANIUM

The occipital region of the skull is completely ossified and consists of four bones, (i) the supraoccipital, (ii) the paired exoccipitals, and (iii) the basioccipital, all of which take part in the formation of the foramen magnum. There is a single tripartite occipital condyle as in the lizards, the median ventral part of which is formed by the basioccipital and the two lateral ones by the exoccipitals of the respective sides. In the centre of the condyle there is a slight depression which represents the place of attachment of the ligament connecting the condyle to the odontoid process.

The median basioccipital bone (Fig.3) is more or less triangular in shape with its base in front and the apex behind. By the side of the pointed hind end there are two spiny projections, one on each side. The posterior end of the bone corresponding to the apex of the triangle forms the median part of the occipital condyle and that takes part in the formation of the ventral boundary of the foramen magnum. The dorsal side of the bone presents a wide depression in the anterior region in which lies the *medulla oblongata*. Anteriorly the bone articulates with the posterior border of the basisphenoid and laterally with the exoccipitals. On the lateral border of the ventral surface anteriorly it articulates with the pterygoid. Along the ventero-lateral border of the basioccipital and its two spiny projections, the *intertransversarii colli* and the *rectus capitis ventralis brevis* muscles are respectively inserted.

The paired exoccipitals (Figs 5,6,7.) in the adult are irregularly-shaped bones. Dorsally the bone articulates with the supraoccipital, laterally on the outer side with the opistho-otic bone and ventrally with the basioccipital. The exoccipitals take the major part in the formation of the *foramen magnum*. On the border of the exoccipitals near the basioccipital articulation there are two foramina through which the eleventh and the twelveth cranial nerves emerge out. Dorsal to these two foramina on the outer side where the bone articulates with the opistho-otic there is a large foramen, the jugular foramen or the *foramen lacerum posterius* through which the vagus nerve, the posterior tributary of the internal jugular vein and a very small branch of the carotid supplying blood to the *medulla oblongata*, pass through.

The median supra occipital (Figs 4,5,6,8) forms the roof in the occipital region. Through a small bridging strip, it also takes part in the formation of the *foramen magnum*. Posteriorly it projects backwards to form a very prominent occipital spine. The occipital spine has a conspicuous ridge, the occipital crest, from which the majority of the fibres of the *adductor mandibulae externus* muscle take their origin. At the anterior border of the supraoccipital there is a pair of horn-like projections extending forward, one on each side. With these projections the parietal bone of the respective side articulates. As a result a considerable area of the bone is overlapped by the parietals. The anterior half of each of the lateral borders of the supraoccipital articulates with the pro-otic, while the posterior half articulates with the exoccipital of the same side. The articulation with the pro-otic is not seen on the dorsal side, since it is overlapped by the parietal bone. The ventral surface of the supraoccipital has a deep, broad median groove with thick lateral walls which are hollowed out on each side in a spacious cavity (part of the *cavum capsularis*). The anterior and the posterior semicircular canals of the membranous labyrinth are housed in corresponding concavities which are in communication by tubular passages with the spacious *c. capsularis* lodging the membranous labyrinth. On the inner wall of this cavity mentioned above, is a very narrow canal through which the *ductus endolymphaticus* passes and opens into the cranium.

The opistho-otic (Figs. 4,5,6,9.) is a thick hollow triangular bone, broad anteriorly, and flat and pointed posteriorly. Its inner side articulates with the supraoccipital and the outer lateral side with the quadrate. Antero-laterally this bone joins with the pro-otic, while ventrally it joins with the pterygoid and medially with the ex-and the bsioccipitals. At the anterior part of the opistho-otic there is a large concavity in which the utriculus is lodged and on the upper margin of this concavity are present two small apertures, one through which the posterior semicircular canal enters and the other through which it emerges.

The parietal region of the skull consists of a pair of parietals above and the median basisphenoid below. The parietal (Figs. 4,6,10) extends to the side of the cranium as well and forms the anterior part of lateral wall. The posterior part of the lateral wall is formed by the otic capsule. The pair of parietals is joined together along the median line by a zigzag suture. They cover the greater part of the brain on the lateral sides to The parietal is a more or less triangular bone, the antero-lateral portion of which roofs over the brain. The extreme anterior end of each parietal is drawn out into a small pointed process on which the frontal of the respective side rests. On the lateral side more towards the anterior half is a projection with which the postorbital and the jugal articulate with the parietal. There is a plate-like process of the parietal directed downwards which protects the cerebral hemisphere laterally. It is in this region that the palatine bone articulates with the parietal.

The basisphenoid (Figs.5,11) is a more or less shield-shaped bone when viewed from the ventral side. Anteriorly there is a spacious anteriorly-directed concavity, of the bone, the *sella turcica* in which the hypophysis is lodged. The dorsal plate lying over the hypophysis shows two lateral processes which are called the *alar* processes. The ventral plate of the bone forming the ventral wall of the *sella turcica*, is tapering anteriorly and it is believed to represent the parasphenoid process of the basisphenoid of lizards. On the lateral wall of the basisphenoid runs obliquely a shallow groove which leads into the *sella turcica*. Through this passage the carotid artery enters the cranial cavity.

The dorsal surface of the bone behind the hypophysis is somewhat concave and it forms along with that of the basioccipital a depression to support the brain. The posterior border of the basisphenoid possesses a small process with which it articulates with the basioccipital. Laterally it joins with the pterygoids and anteriorly with the palatines.

The frontal region of the skull consists solely of the paired frontals on the dorsal side, while the lateral wall is partly formed by the extension of the parietal as mentioned before and the membranous wall in front of it.

The frontal (Fig. 4,6,10.) is a somewhat rectangular bone which articulates anteriorly with the prefrontal (nasal), postero-laterally with the postorbital, posteriorly with the parietal, and mesially with its fellow of the other side. It covers the anterior part of the olfactory lobes of the brain and also partly the olfactory nerves. Ventrally at its posterior part there is a deep groove into which as already mentioned the anterior spiny process of the parietal of its side fits.

The prefrontal (Fig. 4,6,13)(nasal), is an elongated bone which articulates as mentioned above with the frontal behind. It is broader at the anterior portion. At its antero-lateral side there is a large downward flap which covers the posterior side of the olfactory capsule, while its main body roofs over the olfactory capsule. This bone articulates with maxilla laterally and the vomer mesially.

THE AUDITORY CAPSULE

The auditory capsule which is formed by the pro-otic, opistho-otic, part of the supraoccipital and that of the exoccipital is fused with the cranium at the occipital region. These bones together contribute to the formation of the *cavum capsularis*, the cavity in which the membranous labyrinth is housed.

The pro-otic (figs.4,6,12) is an irregularly-shaped bone forming the anterior and the antero-ventral wall of the auditory capsule. It is very little seen from the dorsal aspect of the cranium as a considerable part of it is overlapped by the parietal. Antero-medially it articulates with the parietal, posteriorly with the opistho-otic, laterally with the quadrate and ventrally with the basisphenoid. The central part of the bone presents a concavity which is a part of the *cavum capsularis*. Here the semicircular canals meet the utriculus.

The auditory capsule is somewhat spherical in shape and the pro-otic contributes mainly in its formation. The other bones involved are the opistho-otic behind and the supraoccipital to some extent dorsally. The capsule, however, is not completely enclosed by the bony case as medially there is a large gap occupied by the perilymphatic membrane. The cavum capsularis could be divided into the large dorsal vestibular space lodging the utriculus and the sacculus, and the smaller ventral cochlear cavity which obliquely extends to the quadrate and accomodates the cochlea and the lagena. These two cavities are demarcated from one another by the presence of the cochlear crest. At the anterior end of the vestibular cavity there is a small recess, the anterior ampullary recess, where the anterior ampulla and the ampulla of the horizontal semicircular canal are lodged. In the bony frame-work of the dorsal side of the vestibular cavity is lodged the anterior semicircular canal. The posterior ampullary recess formed in the opistho-otic, lodges the posterior ampulla as well as the, in its wall, the posterior vertical semicircular canal. The aperture for the exit of the posterior auditory nerve is actually not a foramen as it leads into the vestibular cavity through a gap in the bony case of the capsule at its medial side. The aperture for the anterior auditory nerve, however, is a well marked foramen in the pro-otic bone on its median face. The fenestra *ovalis* is situated on the outer wall of the pro-otic where the *columella auris* adheres to the perilymphatic membrane of the internal ear.

The *columella auris* is a slender, thin, rod-like bone (Fig. 11) extending from the tympanic membrane to the *fenestra ovalis* and forming a flat cartilaginous oval disc at the external end by which the bone is attached to the tympanic membrane. The medial end of the columella which is concave and cartilaginous fits into the *fenestra ovalis*. The columella is divisible into two parts, the columella or the stapes and the extra-columella or the extra-stapes. The latter which is outer consists of a flat oblong cartilaginous disc with an elongated process directed downwards and backwards, towards the articular end of the quadrate. This is the *processus internus ventralis*. The processus dorsalis of the extra columella is absent. The columella and the extra-columella are also supported by a thin membranous fold running ventrally along them and joining a ventro-lateral ridge situated in the tympanic cavity. This fold is continuous with the lining of the tympanic cavity. The rim of the tympanic cavity to which the tympanic membrane is attached is formed by the squamosal dorsally, quadratojugal anteriorly and by the quadrate ventrally and posteriorly. This rim of the tympanic cavity postero-ventrally is made even by a padding of connective tissue, as the bony element is deficient there. In the case of Varanus, and other lizards, however, the entire posterior margin of the rim of the tympanic cavity is filled up by the *depressor mandibulae* muscle, to the facia of which the tympanic membrane is attached there. The *chorda tympani*, the branch of the seventh nerve comes out through an aparture in the quadratojugal at its posterior end and then passes by the anterior border of the tympanic membrane, runs downwards and finally enters the foramen in the mandible just anterior to its articular surface. In the case of Varanus the *chorda tympani* nerve runs along the posterior border of the quadrate and then enters the foramen of the mandible which is located on the post-articular process.

THE BONES IN RELATION TO THE OPTIC CAPSULE

The optic foramen in Lissemys is bounded only by a few bones when compared to the large number of the bones that take part in that region in the lizards. In the case of Lissemys the antero-dorsal side of the orbital fossa is bounded by the prefrontal. On the dorsal side the frontal takes a small part to form the rim. Postero-dorsally the postfrontal or postorbital of Siebenrock (1894) bounds the border of the orbit. Postero-ventrally the jugal and the entire ventral and partly antero-ventral sides the maxilla take part in the formation of the orbit. There are no supra-orbitals or lacrimals as found in the lizards.

The postfrontal (Figs 4,6,9) or the postorbital consists of a more or less triangular-shaped bone which articulates with the frontal on its medial side and the jugal on its lateral. Posteriorly it articulates with the parietal which forms the partial roof over the deep recess of the orbital fossa, thus protecting the Harderian gland present on the posterior side of the eye ball. There is a single postorbital on each side as found in Varanus.

The jugal (Figs. 4,5,6,14) is a triradiate bone which articulates anteriorly by a small articulating process with the maxilla thus forming the posterior and the lateral borders of the orbit. Dorsally the bone articulates with the lateral border of the parietal. The dorsal process with which it articulates with the parietal merges with the ridge-like elevation of the parietal. The posterior surface of this process of the jugal forms the anterior border of the emarginated temporal fossa, while with a ventral posterior process which appear as a flat plate it articulates with the quadratojugal. This union of the jugal and the quadratojugal forms a transverse bar analogous to the zygomatic arch of mammals. This transverse bar brings about the division of the primitive adductor mandibulae externus muscle into two as is done by the zygomatic arch of mammals. A third process of the jugal occurring ventro-medially articulates with the palatine.

THE OLFACTORY CAPSULE

The olfactory capsule of either side is situated in the anterior region of the skull and is separated from each other by a thin septum which is in continuation of the interorbital septum. The olfactory capsules are pierced by the external nares at their anterior ends. The olfactory capsules communicate with the buccal cavity through the internal nares which are separated from one another by the median rod-like part of the vomer. The olfactory capsule is surrounded by the prefrontal dorsally, the vomer medially and the maxilla and the pre-maxilla ventrally and laterally. The posterior part of the capsule which extends to the base of the optic capsule is roofed over by a thin membranous septum.

THE PALATE AND THE UPPER JAW

The palate and the upper jaw of each side are formed by the pterygoid, vomer, premaxilla and the maxilla.

The pterygoid (Figs. 5,6,15) is an irregular bone more or less flattened on the outer surface; a thick part of this bone slightly concave on the side articulates with the quadrate. Antero-laterally the bone articulates with the maxilla, antero-medially with the palatine and medially at the anterior half with the basisphenoid and at the posterior half with the basioccipital and the exoccipital. Dorsally towards its posterior border it gets articulated with the lower ends of the pro-otic and the opistho-otic bones, while at its antero-lateral border it articulates with the parietal. More or less in the middle it gets drawn out into a process which bends dorsally and articulates with the ventral and the lateral sides of the opistho-otic and exoccipital bones respectively. By this union two foramina are formed, one on the side of the exoccipital and the other on the side of the quadrate. The tenth cranial nerve passes through the first foramen and the jugular vein emerges out of the skull from the second one. Towards the posterior side of the pterygoid bone on the ventral side there is a foramen, the carotid foramen, through which the carotid artery enters the skull. The carotid foramen of the right side is wider than that on the left. The carotid foramen leads into the carotid canal which curves medially and joins with the fellow of the other side. It is here that the two carotid arteries form a loop resulting in an anastomosis. The pterygoid in Lissemys is not movable as it is in Varanus and it does not show any cartilaginous meniscus at the articulation with the basisphenoid. Such a cartilaginous meniscus is present in Varanus and Sphenodon and is said to correspond to the mesopterygoid of the fish (Broom). The pterygoid in Lissemys does not articulate with the vomer as is the case in Varanus, Sphenodon, Uromastix, the Crocodilia and some Chelonia.

The palatine (Figs. 5,6,16.) is 'L' shaped when viewed from the anterior aspect, with the vertical limb smaller. The horizontal limb is plate-like and takes part in the formation of the palate. The vertical limb, the parietal process of the bone, articulates with the parietal. The horizontal plate or the main body shows two slender small projections, one at the medial and the other at the lateral corners. The medial projection is the vomerine process of the palatine and this part of the bone articulates with the vomer medially. The projection at the anterior side on the lateral corner articulates with the maxilla. This projection is the maxillary process of the palatine. The maxilla overlaps the palatine at the lateral border and articulates with it. Its lateral side articulates also with the jugal, while the posterior border articulates with the pterygoid. The posterior border has a broad projection at its medial side, the pterygoid process of the palatine. The bone at its medial border articulates also by a similar border with its fellow of the other side. On the vertical, parietal process of the palatine is present the palatine foramen through which the maxillary branch of the fifth nerve passes. The palatine does not form the floor of the orbit as in Varanus.

The vomer (Figs. 5,17) is a single bone found on the ventral side, on the mid-ventral axis in front of the palatine and behind the premaxilla. This bone has four projections at the anterior end. Of these four processes two project dorso-laterally, and they articulate with the prefrontal. These are the prefrontal processes of the vomer. The other two processes are more or less in the same line as the longitudinal axis of the bone and they project anteriorly articulating with the maxillae. On the ventral side of the bone corresponding to the prefrontal processes there are two small but sharply-pointed projections which are the posterior maxillary processes of the vomer. As already mentioned the vomer separates the two internal nares. On the dorsal side of the bone is situated the interorbital septum.

The paired maxillae (figs. 4,5,6,18) are the largest bones on the ventro-lateral side of the skull which forms the support for the major part of the cheek. The maxilla (Figs. 4,5,6,18) is more or less triangular in shape with a number of articulating projections. It takes part in the formation of the olfactory and the optic capsules. It articulates in front with the premaxilla. On the ventral side at the anterior end it has a vomerine process with which it articulates with the vomer. At the posterior end on the ventral side it articulates with the palatine medially and the pterygoid at its outer side. At the lateral side of the posterior end it articulates with the jugal. At about one-fourth its length from the anterior end is a vertical process directed towards the prefrontal. This process has a septum at its inner aspect which separates the olfactory capsule from the optic one. This vertical process is the prefrontal process of the maxilla. There is a foramen on the body of the maxilla just behind the vertical process, through which the maxillary branch of the fifth nerve enters the bone. On the lateral border of the ventro-lateral surface there is a sharp ridge formed; the ventral as well as the lateral surface of this ridge is covered with the rhamphotheca. The ventral surface of the rhamphotheca possesses small transverse ridges throughout.

The premaxillae (Figs. 5,6,18) of the two sides are fused together to form a conical small bone which fits in the wedge-shaped gap of the maxillae in the front. This bone is covered completely by the horny rhamphotheca.

THE SUSPENSORIUM

The suspensorium in Lissemys is formed by a large quadrate supported by the squamosal posteriorly and the quadratojugal anteriorly.

The quadrate (Figs. 5,6,19.) is a massive irregular bone situated at the postero-lateral end of the skull. On its lateral side there is a wide and deep concavity, the tympanic cavity. In the tympanic cavity of the quadrate there is an aperture through which the *columella auris* attaches itself with the internal ear. As mentioned before, at the postero-ventral part of the inner side of the tympanic cavity is present a bony ridge to which a thin membranous fold supporting the *columella auris* is attached. The quadrate articulates anteriorly with the quadratojugal, dorsally with the squamosal and mesially with the pro-otic, pterygoid, and opistho-otic. Ventrally there is an articular surface, the *condylus mandibularis*, with which the mandible articulates.

The squamosals (Fig. 4,5,6,19.) are also irregular bones each having a deep groove on its ventral side at the anterior two-thirds, while the posterior one-third is a laterally flattened part. The groove part of the bone shows a curved border which forms the upper side of the tympanic cavity. The bone overlaps the dorsal border of the quadrate. Anteriorly it articulates with the quadratojugal, ventrally with the quadrate in front and the opistho-otic behind. Its flattened face, the posterior one-third, is curved like a sickle and provides a large area for muscular attachment.

The quadratojugal (Figs. 4,5,6,15.) is a laterally flattened bone having a broader part at its posterior end. The posterior end shows two processes, a lower pointed one and an upper broad one. The former process articulates with the quadrate, while the latter one with the squamosal. Anteriorly it articulates with the jugal at its lateral side. As already mentioned the quadratojugal in association with the jugal forms the bony bar which is analogous to the zygomatic arch of mammals.

The supratemporal and the epipterygoid bones found in Varanus, are absent in Lissemys.

THE LOWER JAW

The lower jaw (Fig.20) is a massive, laterally flattened structure completely fused with its fellow of the opposite side at its anterior end. Each ramus consists of six bones the dentary, the splenial, the angular, the supra-angular, the coronoid and the articular.

The dentary (Figs. 20,21,) which is the largest bone in the jaw fuses with its fellow of the opposite side forming and acute angle at the point of the union in front. Its inner side is lined partially by the angular, and the splenial. On the outer side it presents a number of foramina towards its anterior half. Of these the ~~post~~ posterior one is the mental foramen through which the mental branch of the inferior alveolar nerve emerges out and the course of this nerve is through a long canal within the body of the bone. On the inner side it presents a groove narrower anteriorly but gradually broadening posteriorly. The narrow parts of the grooves of the either side meet together anteriorly into a medial <u>sulcus cartilaginis Meckelli</u>. The Meckel's cartilage is embedded in this groove. The posterior end of the dentary almost extends as far back as the posterior end of the lower jaw. The upper end of the dentary is flattened at its posterior half and the entire upper border supports the rhamphotheca.

The splenial (Fig.21) is an irregular bone of the inner side at the posterior end of the lower jaw. This bone partially covers the dentary, the supra-angular and the articular. It covers also the foramen through which the mandibular nerve enters the mandible.

The angular (Figs. 20,22) is a wedge-shaped, splint-like bone pointed anteriorly and flattened posteriorly. It covers the dentary and the articular bones. The upper border of the anterior two-thirds of the angular forms the lower posterior boundary of the <u>sulcus cartilaginis Meckelii</u>. The entire lower border of the angular becomes continuous with that of the dentary, to form the lower border of the mandible.

The supra-angular (Figs,10,2) which is situated on the outer side at the posterior end of the mandible, articulates with the dentary at its anterior border, while the posterior end is free and depressed to form an articulating facet for the convex outer tubercle of the quadrate. The bone articulates also with the articular on its inner side. The slight backward projection of the mandible behind its articular surface is compounded by two bones, a projection of the supra-angular outside and an extension of the articular inside. On this projection at its outer side the <u>depressor mandibulae</u> muscle is inserted.

The articular (Figs. 20,22) is a small bone almost covered over on its outer as well as on its inner side. The supra-angular covers it on the outer surface, while the splenial and the angular do so on the inner surface. The bone is most exposed on its dorsal border. At the anterior end of this surface is an articulating facet with which the inner tubercle of the quadrate articulates.

The coronoid (Figs.20,21) is more or less a triangular bone situated on the upper border of the mandible just in front of the supra-angular. It fits in as a wedge in the notch formed on the upper border of the dentary. The upper border of the coronoid on which the <u>temporalis</u> muscle is inserted projects upwards. The coronoid forms the anterior boundary of the mandibular foramen, while its posterior boundary is formed by the supra-angular and the splenial.

THE FORAMINA AND OPENINGS IN THE SKULL

Dorsal side:-

The prefrontal foramina:- There are seven foramina on the prefrontal bone, of which three are prominent. Through these foramina pass minute blood vessels and the branch of the superficial opthalmicus nerve to the region of the snout.

The Postorbital foramen:- On the dorsal side near the outer border of the postorbital bone, the postorbital foramen is situated. Through it passes a minute branch of the maxillary nerve of the trigeminal nerve.

The dorsal pro-otic foramen:- On the dorsal side of the pro-otic bone at its lateral border this foramen is situated. Through this the branch of the seventh nerve comes on the dorsal side of the skull, to innervate the temporal and the masseter muscles.

The anterior narial opening:- In front of the skull there is a single foramen. It leads into incompletely divided nasal chambers, and serves as the external nares.

Ventral side:-

The inter-maxillary foramen:- At the anterior end of the ventral side of the skull, between the two rami of the upper jaw this foramen is situated. It is bounded by the premaxilla anteriorly, maxilla laterally and vomer posteriorly. It connects the roof of the buccal chamber with the nasal chamber, and the Jacobson's organ.

The posterior narial openings:- There are two large openings separated by the slender rod-like part of the vomer.

It is bounded by the vomer antero-medially, maxilla antero-laterally and palatine posteriorly. Through these openings the nasal chambers open into the buccal chamber.

The anterior palatine foramina:- There are two or some times three foramina on the antero-lateral side of the palatine. Of these openings the arteries from the buccal cavity enter the skull to supply blood to the floor of the cerebral hemisheres, and anteriorly to the nasal capsules.

The carotid foramen:- This foramen is situated at the posterior end of the pterygoid bone. Through it the internal carotid artery enters the skull.

The jugular foramen:- On the median posterior side of the quadrate there is a large kidney shaped foramen through which the internal jugular vein emerges out of the skull along with the branch of the seventh and the entire ninth nerve.

The posterior lacernum:- This foramen is bounded by the pterygoid ventrally, opistho-otic laterally and mesially. Through this foramen the tenth, eleventh and the twelvth nerves emerge out of the skull.

The exoccipital foramina:- There is a pair of foramina on the side of the exoccipital bone through one of which the occipital artery enters the skull and through the other the occipital vein emerges out.

The internal palatine foramen:- At the base of the vertical part of the palatine there is a foramen through which the branch of the internal carotid comes out of the skull and enters the optic region.

The foramen ovale:- On the lateral side of the skull there is a large oblong foramen through which the branches of the fifth, the sixth and the seventh nerves emerge out of the skull.

The foramen magnum:- This foramen as is well known is the largest foramen through which the spinal cord emerges out of the skull. It is bounded by the supraoccipital dorsally, the exoccipitals laterally and the basioccipital ventrally.

THE HYOID

The hyoid (fig.23) is well-developed in Lissemys and consists of the hyoid proper and the remnants of the first two branchial arches. A basilingual plate representing the fused part of the ventral ends of the hyoid and branchial arches of the embryo as a composite piece is not formed in Lissemys. On the other hand it consists of six elements articulated to one another as in Cycloderma. These elements are arranged symetrically on either side and can be individually separated from one another. In Chelone and Trionyx a composite basilingual plate is formed. The anterior end of the hyoid is drawn out into a pointed structure which is cartilaginous and to which ~~the~~ ventro-laterally is attached the cartilaginous plate, the hypoglossum. The lateral processes of the hyoid proper are ossified. Those of the first and the second pair of branchial arches are also well-ossified. The dorsal surface of the hyoid is grooved into which the trachea and the glottis are lodged.

The anterior cornu, the process of the first branchial arch is smaller than the posterior one. Both the cornua are well-ossified. The posterior cornua in Testudo and Chelone are flattened and cartilaginous and are much smaller than the anterior ones. In Trionyx, however, though the posterior cornua are smaller than the anterior ones, they are well-ossified.

The anterior cornua articulate by ligaments with the posterior ends of the squamosals of their respective sides. The posterior cornua are not associated with the skull, but are free at their distal ends.

THE VERTEBRAL COLUMN

The vertebral column in Lissemys may be conveniently divided into four regions, the cervical, trunk, sacral and the caudal. The cervical vertebrae distinctly differ from those of the trunk in not having the transverse processes or ribs and in being free from the carapace and thereby affording sufficient scope for the intervertebral movements. The caudal vertebrae too are free from the carapace and they are also capable of intervertebral movements. They, however, differ from the cervical ones in possessing the transverse processes. The trunk vertebrae are fused with the neural plates of the carapace and so are incapable of any intervertebral movements. The ribs joining the trunk vertebrae are fused with the costal plates. The costal plates in turn are fused with the neural plates with which as already mentioned the trunk vertebrae are fused.

The cervical vertebrae:- In Lissemys there are eight cervical vertebrae as found in other chelonians, and several lizards. Sherfeldt (1921) tried to show that there are nine cervical vertebrae in Chelonia instead of eight by considering the loosely articulating odontoid process of the axis as an undeveloped or a modified vertebra.Many other workers namely Owen(1866), Gunther (1886), Boulenger (1889), Reynolds (1897) and most of the modern authors mentioned eight as the number of the cervical vertebrae in Chelonia, while the loosely-articulated odontoid process of the axis is not regarded as a degenerate vertebra. The cervical vertebrae progressively increase in girth from anterior to the posterior region. Boulenger (1889) mentions that there are eight cervical vertebrae in Chelonia generally and that they show four different types of centra, some concavo-convex, some convexo-concave, some biconvex and others biconcave.In *Chelone mydas* the second and the third cervical vertebrae have the opisthocoelous type of centra, the fourth biconvex type, the fifth procoelous, the sixth again procoelous but having the posterior face flat, articulating with a similar flat anterior end of the centrum of the seventh cervical. The posterior face of the seventh vertebra possesses two convexities which fit into two concavities of the anterior end of the eighth centrum (Reynolds, 1897). Almost a similar condition of articulation of the cervical vertebrae is seen in *Emys europea* (Owen, 1866). In Lissemys, however, the centra of all the cervical vertebrae are similar in structure in being opisthocoelous.

In a typical cervical vertebra~~e~~ (Figs. 26,27,28) the body consists of a well-developed opisthocoelous centrum with neural arches. The neural arches present typically two pairs of the zygapophyses of which the anterior possesses the articulating facet on the dorsal side, while the posterior pair has them on the ventral side, thus enabling the posterior zygapophyses of one vertebra to articulate with the anterior zygapophyses of the next vertebra. The posterior zygapophyses are more extensive than the anterior ones. The diapophyses are present as a pair of protruberances of the centrum of the vertebra in front. None of the cervical vertebrae except the axis which has a small spine at the anterior part of the mid-dorsal line, possesses the neural spine.

The atlas, (Fig. 24) however, is much modified and consists of three parts, a pair of neural arches and a single inferior arch. The neural arch of the atlas is divisible into two parts, a dorsal and a ventral. The ventral part is almost a vertical bar called the pedicel and the dorsal one which is flat and curved inwards to meet its fellow of the opposite side, forming the roof of the neural canal is called the lamina. The neural arch is joined with the lateral horn of the inferior arch by the free end of the pedicel. There are three articulating shallow concavities on the anterior side of the atlas, a pair on the pedicel and a median one on the inferior arch. With these concavities the tripartite occipital condyle of the skull gets articulated. The laminae of the atlas have a pair of backwardly directed processes which form the well-developed posterior zygapophyses which articulate with the anterior zygapophyses of the axis. At the region where the lamina is domarcated from the pedicel, a membranous septum runs transversely which serves as the floor of the neural canal. The posterior face of the pedicel and also that of the inferior arch show articulating facets with which the odontoid bone with its corresponding surfaces articulates.

The odontoid process (Fig.25) of the second vertebra is joined with its centrum by means of a loose ligamentous connection. This loosely connected odontoid bone in the Chelonia has been the subject of controversy as to whether it is really the odontoid bone or it is only a modified or reduced axis vertebra. As already pointed out Sherfeldt (1921) had suggested that it is a modified axis vertebra and that there are nine cervical vertebrae in the Chelonia instead of the usal reptilian number, eight.

The seventh cervical vertebra, (~~Fig.~~) though opisthocoelous, the convexity in the front shows a slight depression in the middle line giving the appearance of a double convex anterior end. Moreover, the posterior face of the centrum has two widely separated concavities into which the two corresponding convexties of the anterior face of the centrum of the eighth vertebra fit. All the other parts of the seventh vertebra are typical. With the exception of the first, the eighth, the last cervical vertebrae (fig.29) is the broadest and the shortest of all the cervical vertebrae. This vertebra is much modified being broader and thicker with two convexities anteriorly and truncated posteriorly. The posterior articulation of the centrum of the eighth vertebra with the first trunk vertebra is dispensed with in order to effect a complete bend of the neck in this region in order to facilitate the retraction of the neck under the shell. The anterior pair of zygapophyses of the last cervical vertebra is of a normal type but the posterior is much enlarged and shows deep concave surfaces which lodge the convexities of the anterior pair of zygapophyses of the first trunk vertebra. This joint is evidently quite strong as the whole neck is connected with the trunk at this point. The neural arches of the last cervical vertebra are very well-developed and enclose a larger neural canal which allows free movement of the vertebra without injuring the nerve cord in any way through friction.

Gunther (1886) states that there are twelve dorsal (thoracic) and two sacral vertebrae. Claus (1885) says that generally in all chelonians there are ten thoracic vertebrae, but only eight thoracic and three sacral vertebrae in Cestudo europea. Owen(1866) mentions that there are eight thoracic, one lumbar and two sacral vertebrae in Emys europea. Reynolds (1897) accounts for ten thoracic, two sacral and no lumbar vertebrae in Chelone mydas. On account of the close similarity of the vertebrae, it is perhaps correct to state that there are no lumbar vertebrae in the Chelonia.

In Lissemys there are nine thoracic or trunk vertebrae (Fig. 2) and all are fused with the neural plates as stated before. The centra of these vertebrae are dorsi-ventrally flattened and articulate with each other by flattened surfaces with no possibility of any intervertebral movements. On the flattened and massive centrum there is a pair of neural arches which unite dorsally and form a spaceous neural canal. There are no zygapophyses on any of them except the first trunk vertebrae. The trunk vertebrae have each a pair of ribs attached to them at the level of the intervertebral joint. The ribs are so attached that they are partly associated with the posterior half one centrum and the anterior half of the next. The ribs corresponding to the first trunk vertebra are, however, very slender and rod-like and are attached to the middle of the centrum. These ribs extend obliquely backwards and merge with the anterior border of the second pair of the ribs. The other ribs are fused with the over-lying costal plates of the carapace. The ribs are fused with the carapace, and the intercostal muscles have lost their ~~the~~ usual position. Hence there are no costal movements. The neural plates are not fused with the ribs and as a result a gap is left between them and the ribs. Through this gap passes the reduced Semispinalis ~~Longissimus~~ muscles of the trunk. They are the only remnants of the vertebral muscles of the trunk region. as the others are lost.

The two sacral vertebrae (Fig.2) are more or less firmly joined together. The neural spinal region of these vertebrae does not fuse completely with the carapace. There is a pair of short ribs loosely ankylosed with each of these vertebrae. The distal end of these ribs articulate with the ilia.

The caudal vertebrae in Lissemys(Fig.2) are less in number than in other chelonians Viz., *Emys europea* or *Chelone mydas*, so much so that the tail of Lissemys is much reduced. There are usually eleven caudal vertebrae in this animal but the number may vary from eleven to fourteen. The caudal vertebrae are opisthocoelous. The proximal ones have short stumpy ribs, which are loosely articulated with them, while the distal ones do not bear any ribs, but possess processes which are unossified transverse processes. They have well-developed neural arches and also neural spines. The neural canal extends upto the last but one vertebra. The last caudal vertebra is flattened and ossified without any neural arch or transverse processes. It serves only for the attachment of the caudal muscles.

THE PECTORAL GIRDLE AND THE SKELETON OF THE FORELIMBS

The pectoral girdle in the chelonia occupies a peculiar position in the body in being inside the bony shell under the ribs, while in other tetrapods it is always outside the ribs. Also the two girdles do not meet in a sternum as in most other tetrapods but on the other hand merge with a plastron below.

The girdle in Lissemys (Fig.31) as in other chelonians has a triradiate structure. The scapula (Fig.31) is rod-like and tapers at its distal end to which is attached a small cartilaginous suprascapula that articulates with the carapace at a level between the first and the second thoracic vertebrae. The scapula is attached to the over-lying costal plate and the vertebral column by a thick ligament.

A long process which projects towards the ventral side is regarded by Owen as the acromial process (representing the calvicular process of the scapula), while others regard it as the precoracoid (fig.31) (Reynolds,1897). This process is cylindrical at its proximal end but later flattens out dorsi-ventrally at the distal half which terminates in a small cartilaginous plate which gets attached to the entoplastron by a thick ligament. The size of the precoracoid in relation to that of the scapula also varies greatly among the chelonians. It is shorter than the scapula in Testudo, but longer in Lissemys, Trionyx and Chelys. It serves however, as a very important bone in all chelonians for the attachment of the girdle muscles.

The coracoid (Fig.31) which is also well-developed in this animal, is somewhat cylindrical at its proximal end but flattens out distally. At its distal end a fairly well-developed cartilaginous epicoracoid is present. The coracoid and the scapula join with each other at their proximal end to form the glenoid cavity. The precoracoid is also connected with the coracoid at their free ends by means of a ligamentous sheath, the *acromio-coracoid* ligament. The flattened blades of the coracoid and the precoracoid serve as area for the origin of some of the girdle muscles. The coracoid in *Testudo elegans* is comparatively short, while that in Lissemys, Trionyx, Chelys and Chelone is long.

As a result of the entire girdle being shifted below the ribs, under the carapace, the humerus (fig. 32) is bent. A bend of the humerus has become necessary to project the limb out of the bony box and to allow it to have free play. The proximal end of the humerus bears a hemispherical head which projects upwards and fits into the glenoid cavity. By the side of the head of the humerus there are the lesser and the greater tuberosities. Between these tuberosities and the head, on the ventral side of the bone is present a conspicuous depression in which the *deltoideus muscle* is inserted. The distal end of the humerus which is flattened and broad articulates with the radius medially and the ulna laterally.

The ulna (Figs. 33,34) is shorter than the radius and (figs.33,34) is also broader at both ends. The proximal end of the ulna shows a slight projection at its outer side, the olecranon process. The radius and ulna in Lissemys as in other chelonians are slender, and rod-like, and twisted so much that their natural positions are altered. This shift in position has affected the arrangement of the forearm muscles in this region. The radius and the ulna articulate with the carpal bones (figs. 33,34) which are arranged in two rows with the centrale and intermedium between them. The distal row of the carpal bones are five which articulate with the metacarpals.

The first metacarpal (figs. 33,34) is very short and has a well-developed, broad, articulating surface at its proximal end, while the second, third and fourth are elongated slender bones; the fifth one is slightly longer than the first one. The proximal articulating surfaces of the metacarpals are concave, while the distal ones are convex.

The first digit (Figs. 33,34) has two phalanges of which the distal one is pointed at its free end and bears a large claw. The second and the third digits have three phalanges each and their terminal digits are also pointed with well-developed claws. The fourth and the fifth digits have four phalanges each but their terminal ones are not pointed and are devoid of claws.

THE PELVIC GIRDLE AND THE SKELETON OF THE HINDLIMBS

Like the pectoral girdle, the pelvic girdle (Fig.35) is also triradiate and shifted to the interior of the body shell. Of the three bones, the pubis and the ischium are flattened bones at their distal ends. The two pubic bones (fig.35) are joined with one another at their symphyses and they together contribute to the formation of the cartilaginous plate, the epipubis, anteriorly. Antero-laterally the pubic bone has a wing-like flat process similar to the *processus lateralis* of Uromastix (George, 1956). The flattened out pubic bone with well-expanded *processus lateralis* gives a large area for the attachment of the pelvic muscles.

The ischium (Fig.35) is smaller than the pubis and like the pubis, the ischia join in a symphysis. At the posterior border of the ischial symphysis there is a cartilaginous epi-ischium similar to the epipubis but very much smaller in size. The *spina ischii* are very feebly developed and are much nearer to the ischial symphysis compared to the *spina ischii* of Trionyx and

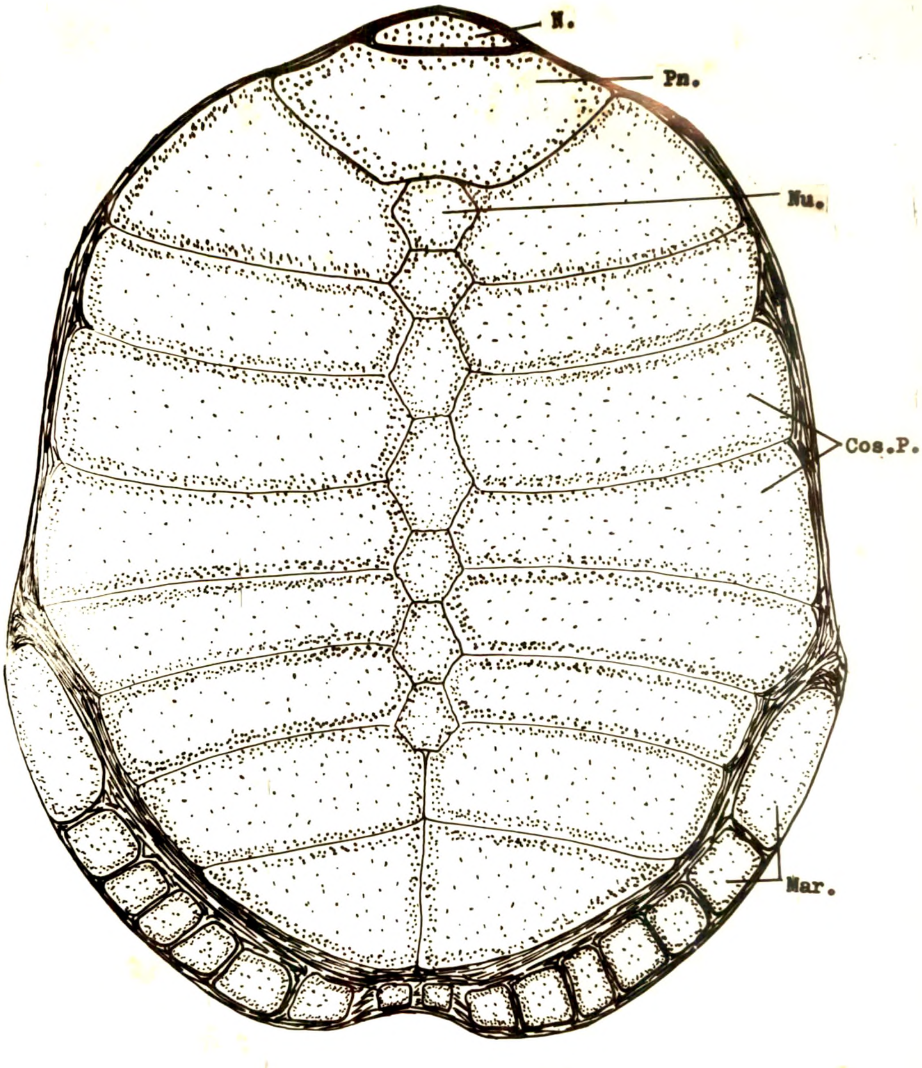
Uromastix which are at the outer side near the acetabulum. The ischium also shows a laterally-directed spiny process on the anterior border. Such a spiny process is not present on the ischium of Testudo or Geomyda or Uromastix. The ischial symphyses does not extend anteriorly to meet the pubic-symphyses so as to form the obturator foramina separate from one another as found in Testudo or Emys, but instead there is a single, confluent obturator foramen. Such a common foramen is also present in Trionyx. There is no epipubic or hypopubic bone as found in Uromastix (George, 1956).

The ilium (Fig. 35) is a curved slender bone, as the scapula. It also tapers down from the proximal to the distal end. It articulates with the carapace dorsally and with the sacral ribs medially. All the three bones of the pelvic girdle take part in the formation of the acetabulum.

The femur (Fig. 36) is longer than humerus and shows a bend as seen in the humerus but to a lesser extent. The head of the femur is rounded and slightly oblong and by its side there are two side processes, the greater and the lesser trochanters as present in the mammals, unlike in Uromastix in which there is only one, the greater trochanter (George, 1956). The shaft of the bone distally becomes gradually flattened and the proximal ends of the tibia and fibula articulate with it. The distal articulating surface of the femur is bicapitate; the larger of the heads articulates with the tibia, while the small outer one articulates with the fibula.

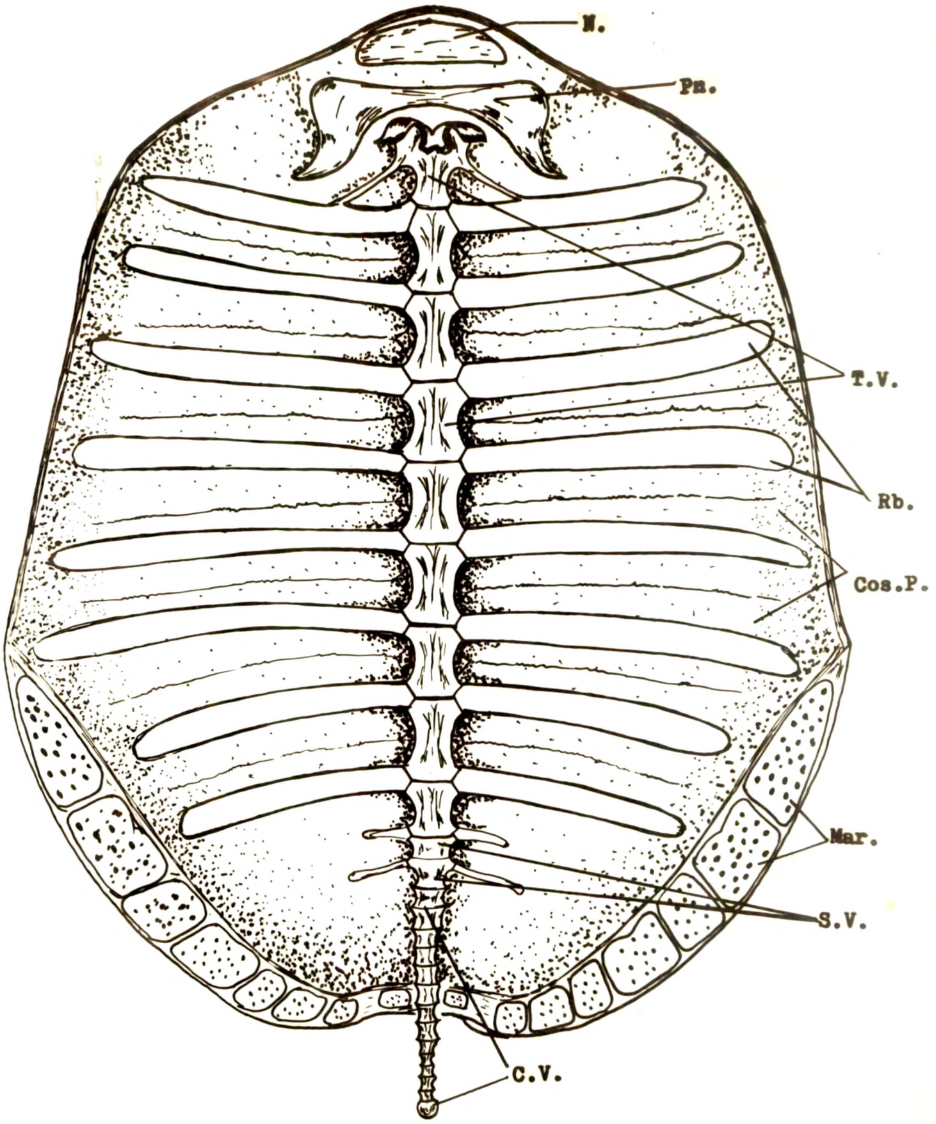
The tibia and fibula (Figs.37,38) are more or less straight slender bones; the tibia is stouter, while the fibula the more flattened and curved of the two. At the middle of the fibula there is a small process to which a thigh muscle gets inserted.

In Lissemys the number of tarsal bones (fig 37,38) is fewer as some having got fused with others. The first row of tarsals which normally consists of the fibulare, tibiale and the intermedium are represented by a single structure which perhaps may include also the centrale. But by the inner and outer sides of the so-called fused tarsus there are two cartilaginous pieces which could be easily separated from it. Perhaps these cartilaginous elements (figs.37,38) represent the tibiale and fibulare, and if this view is correct, the compound tarsus consists of only the centrale and the intermedium. The second row of tarsals consists of five bones of which the fourth and the fifth are larger than the others. In this animal the arrangement of the first row of tarsals differs from that in Chelone mydas in which it consists of a distinct fibulare and a fused piece made up of the tibiale, intermedium and centrale. The second row of tarsals does not show any difference as it consists of five elements in both the animals. There are five digits and each one articulates with its corresponding metatarsal. The fourth metatarsal is the longest. The first digit has two phalanges, the second and the third three, the fourth four, and the fifth two. The terminal phalanges of the first three digits are pointed and they alone provided with claws.



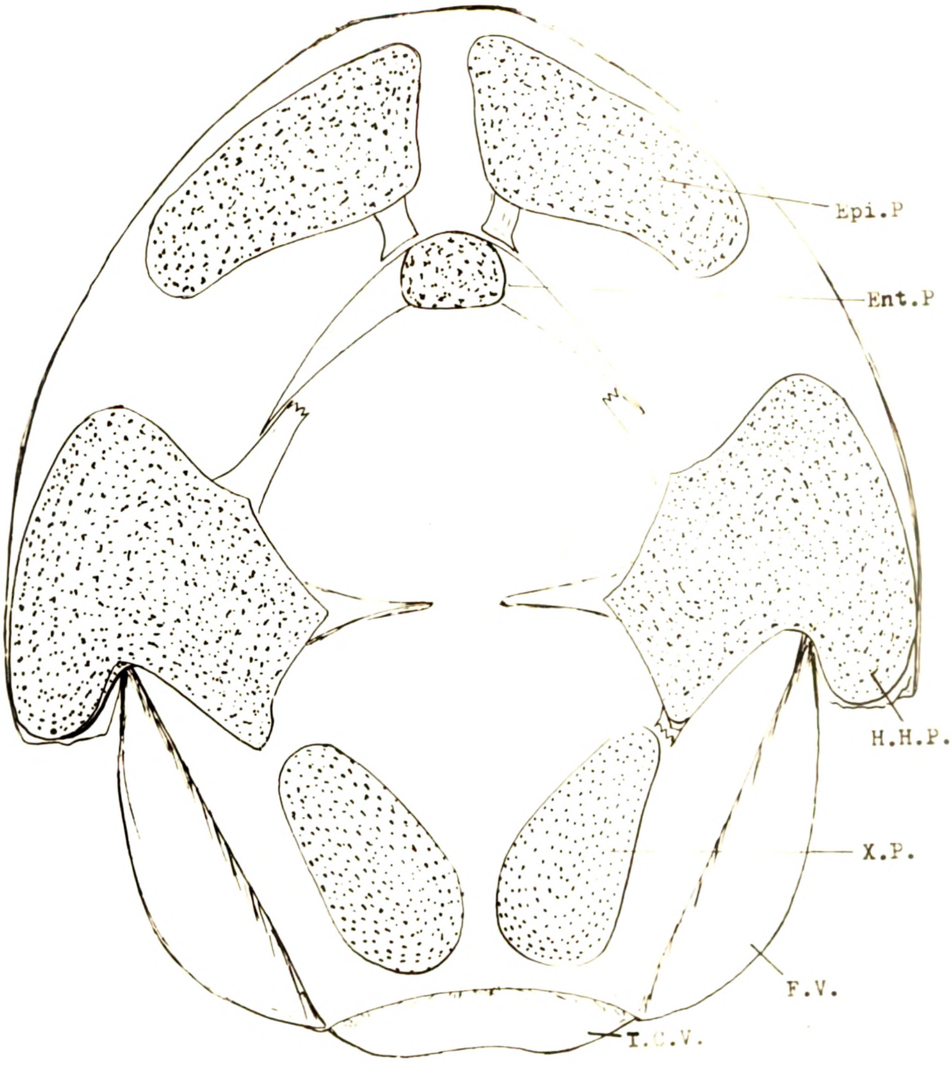
DORSAL VIEW OF THE CARAPACE

FIG. 1



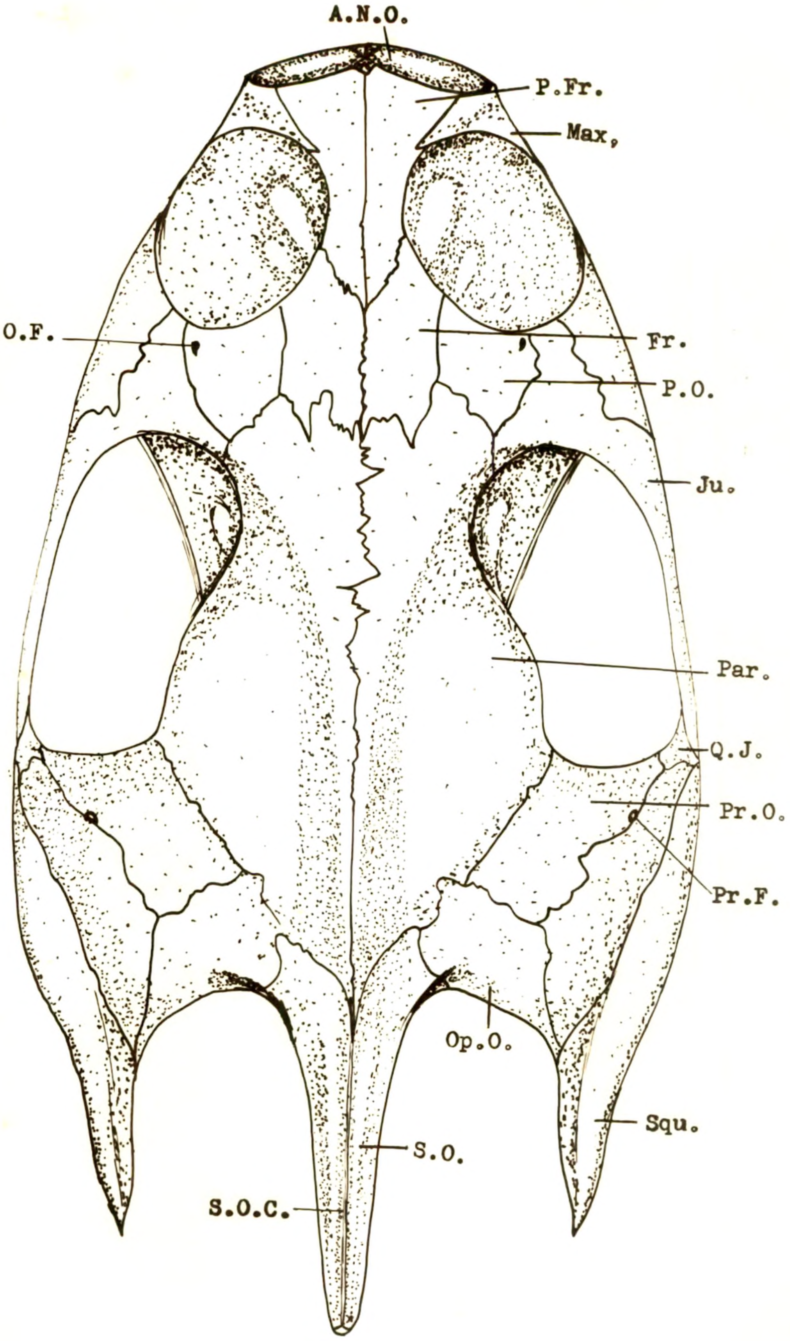
VENTRAL VIEW OF THE CARAPACE

FIG. 2



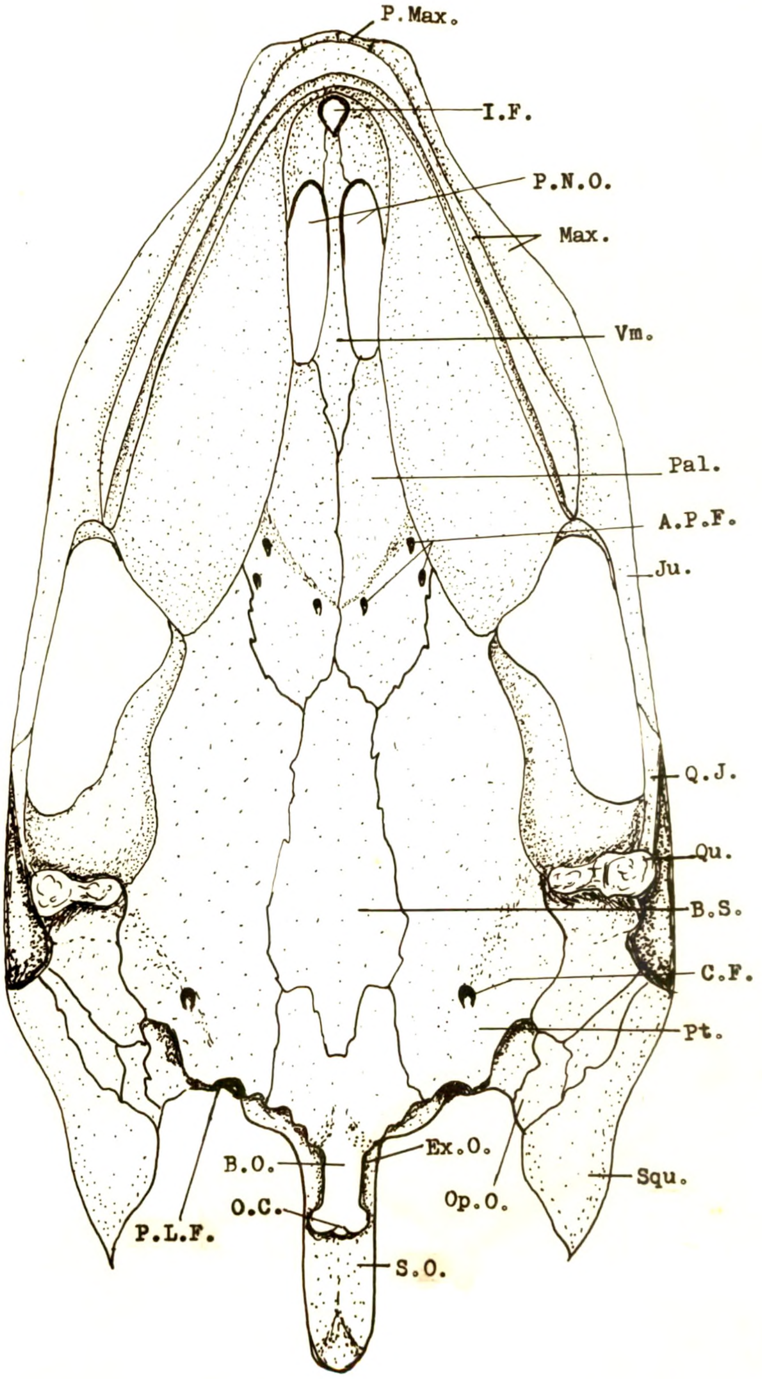
VENTRAL VIEW OF THE PLASTRON

FIG.3



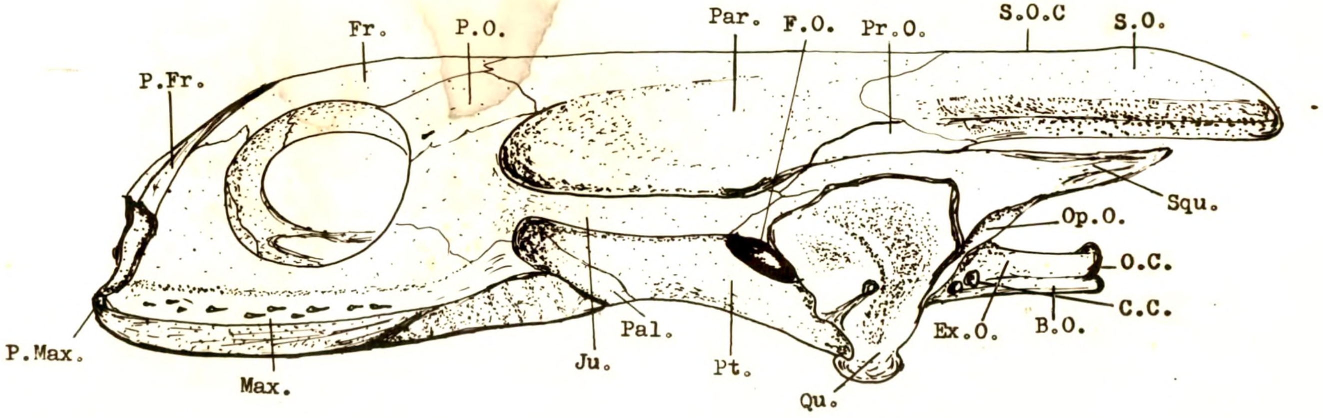
DORSAL VIEW OF THE SKULL

FIG. 4



VENTRAL VIEW OF THE SKULL

FIG. 5



LATERAL VIEW OF THE SKULL

FIG. 6

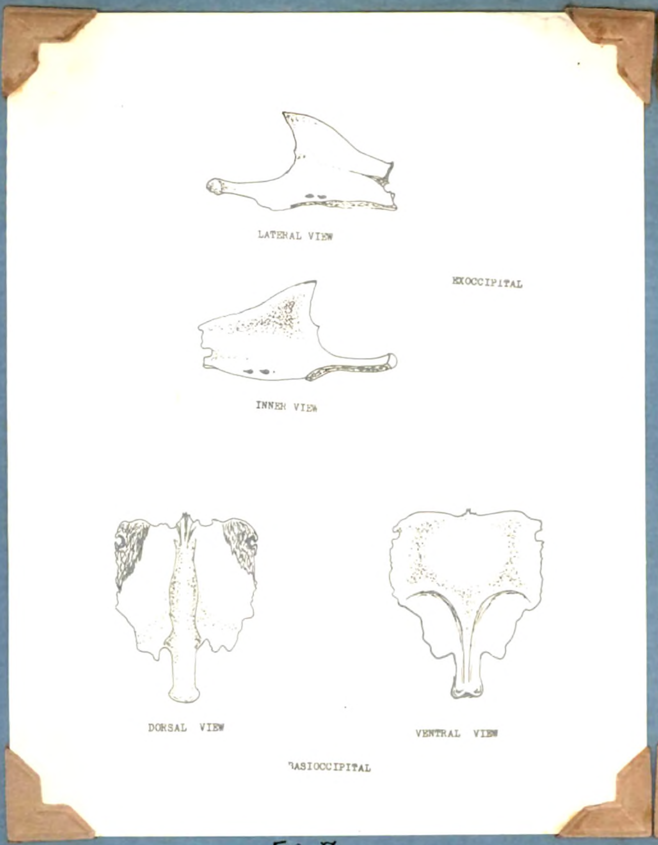


FIG. 7

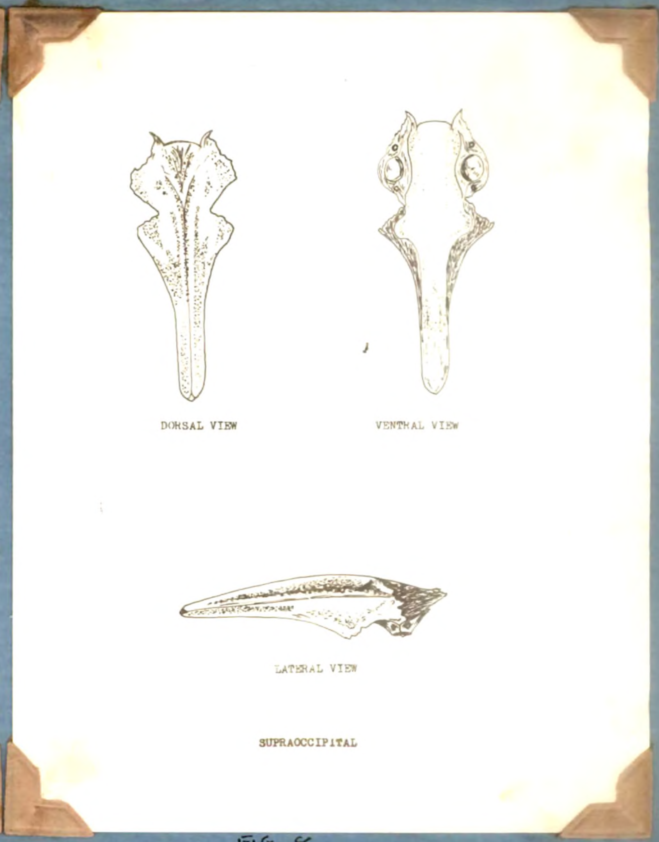


FIG. 8

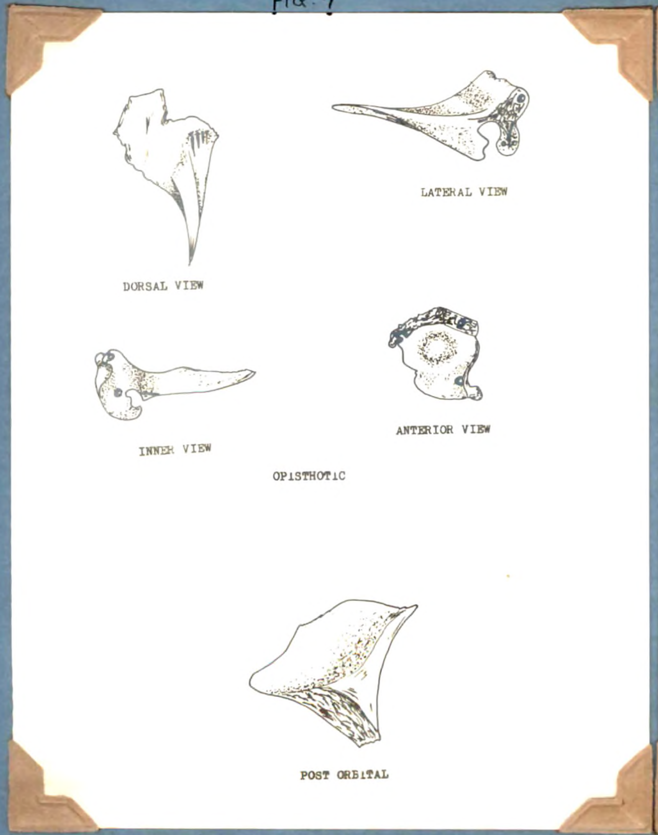


FIG. 9

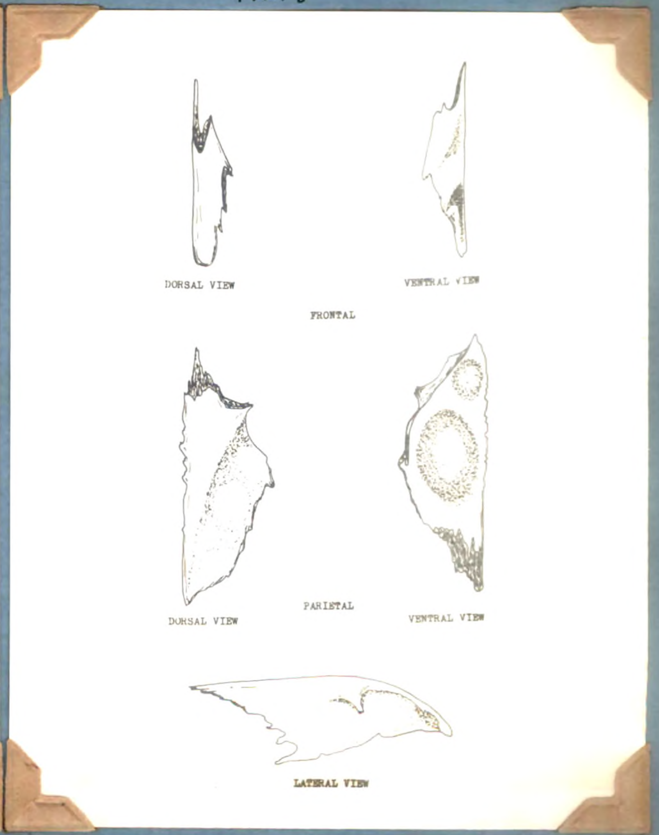


FIG. 10

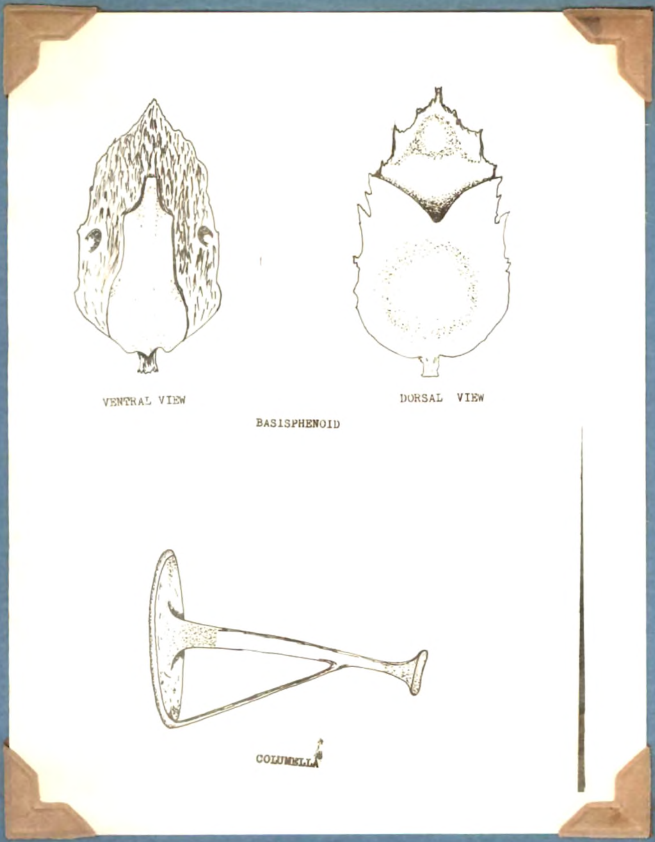


Fig. 11

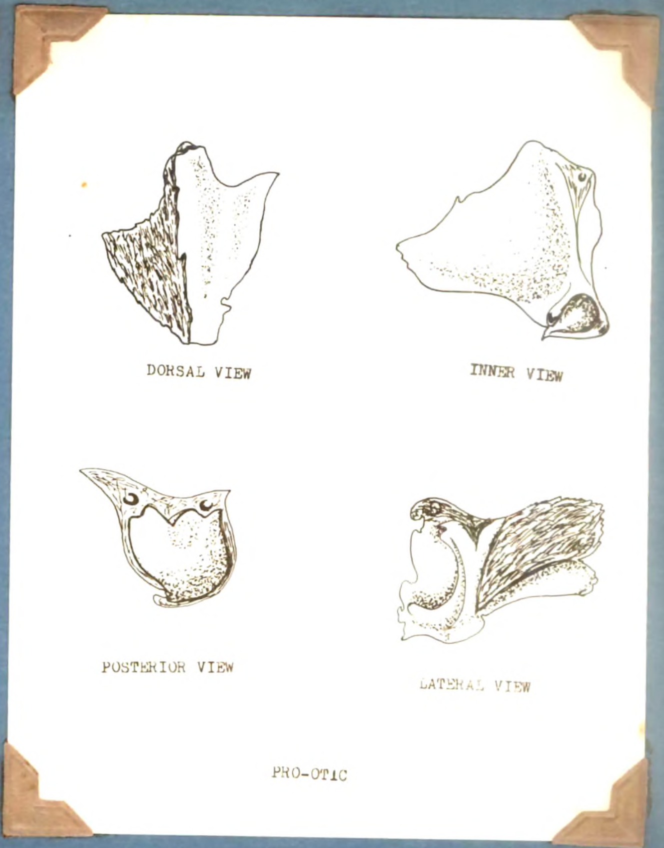


Fig. 12

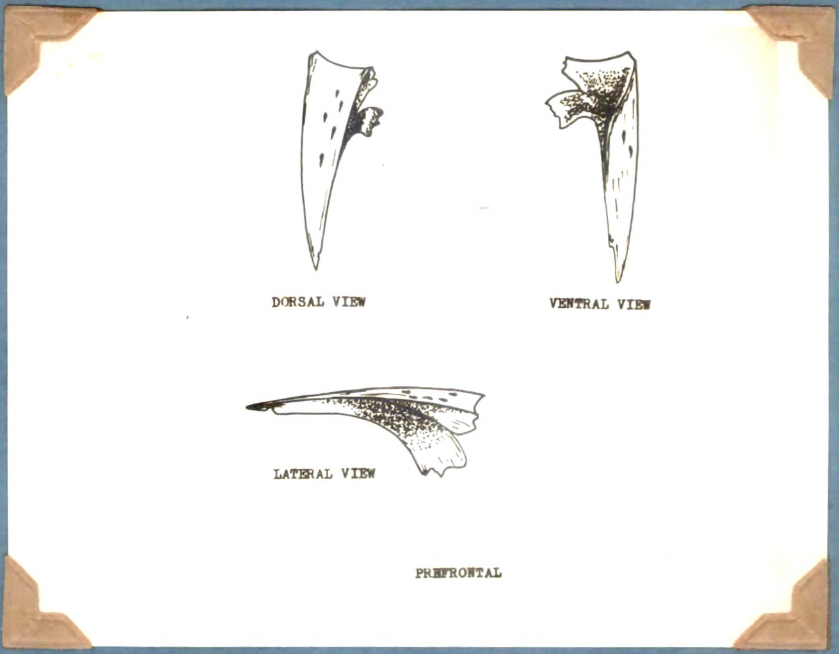


Fig. 13

LATERAL VIEW

JUGAL

INNER VIEW

Fig. 14

VENTRAL VIEW DORSAL VIEW

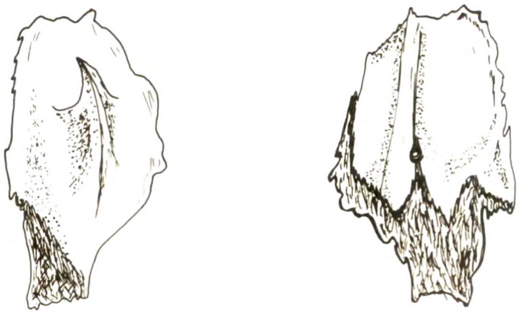
PTERYGOID

LATERAL VIEW

QUADRATO-JUGAL

Fig. 15

LATERAL VIEW



DORSAL VIEW VENTRAL VIEW

PALATINE

Fig. 16

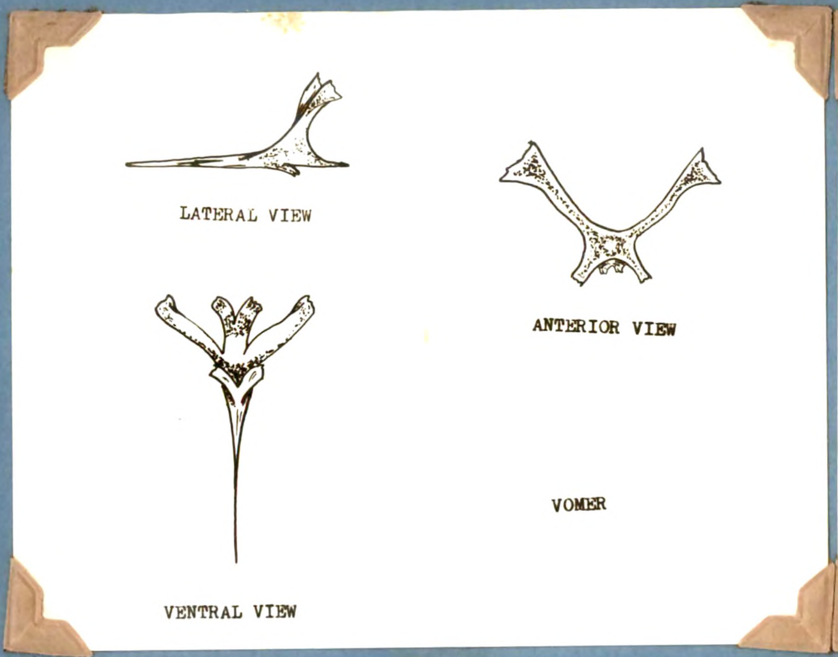


Fig. 17

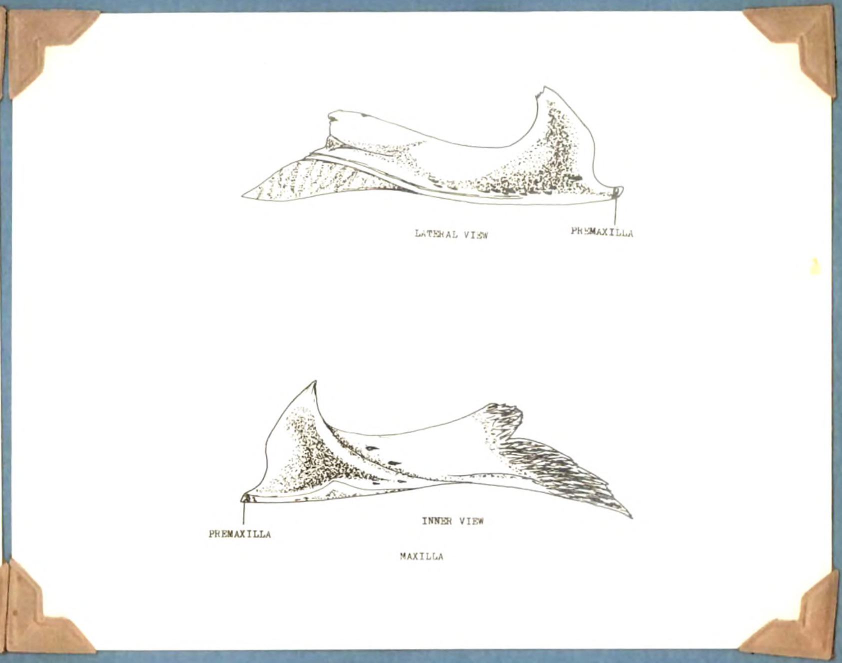


Fig. 18

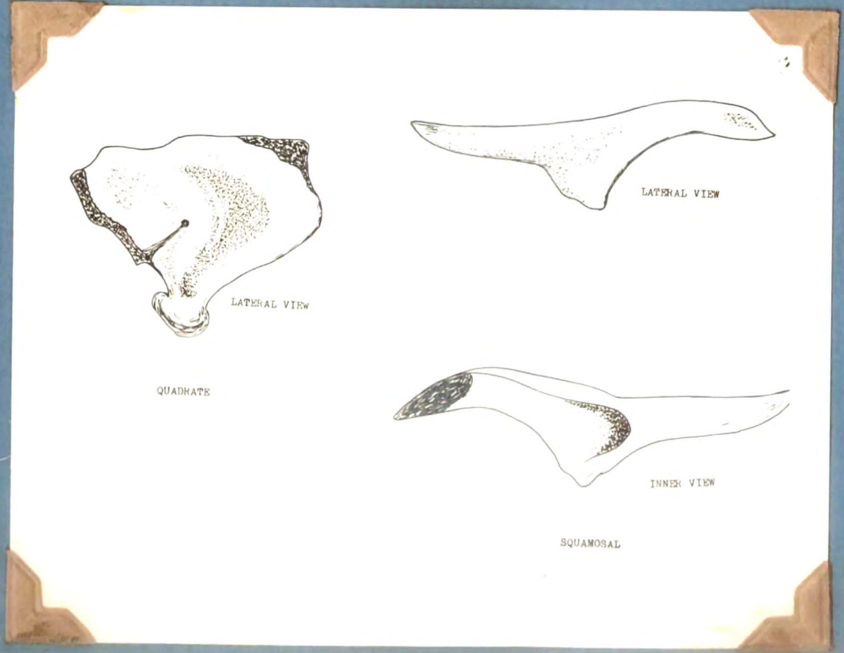
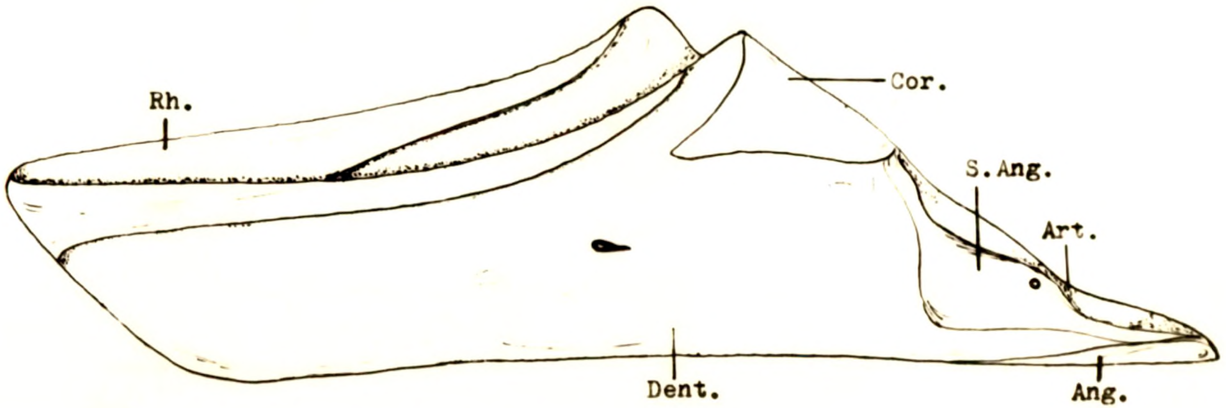


Fig. 19



LATERAL VIEW OF THE LOWER JAW

FIG. 20

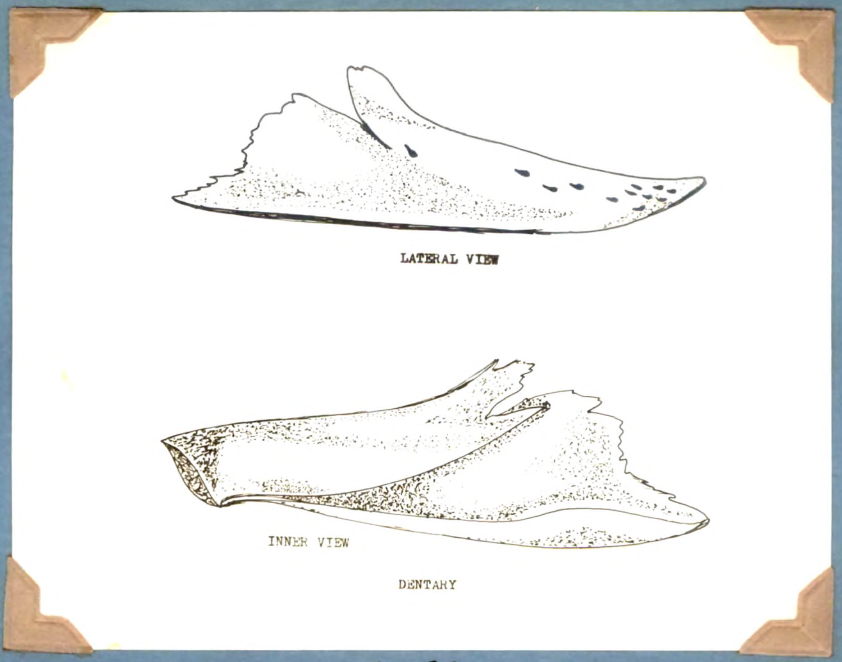

LATERAL VIEW
INNER VIEW
DENTARY

FIG. 21

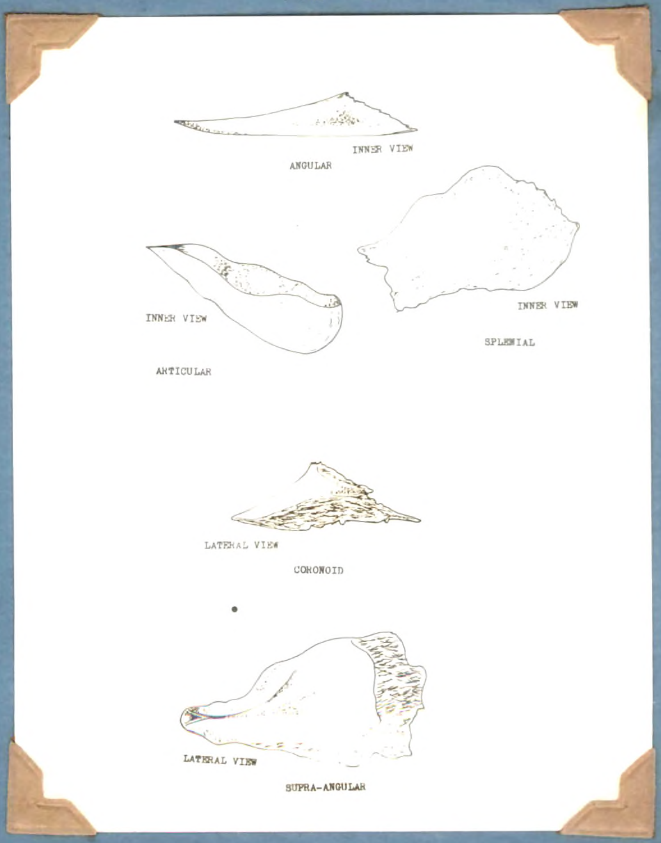
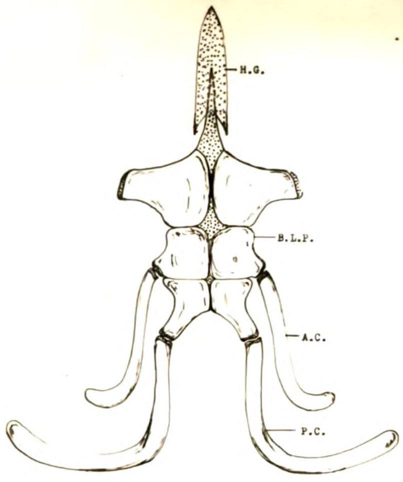
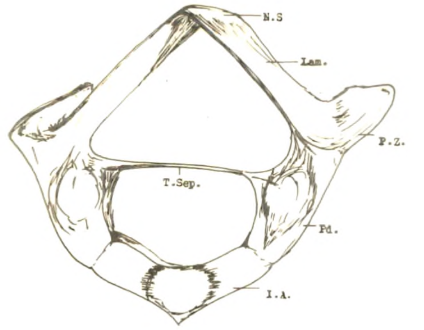

INNER VIEW
ANGULAR
INNER VIEW
ARTICULAR
INNER VIEW
SPLENIAL
LATERAL VIEW
CORONOID
LATERAL VIEW
SUPRA-ANGULAR

FIG. 22



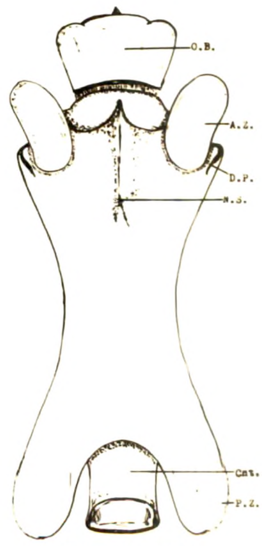
THE HYOID

FIG. 23



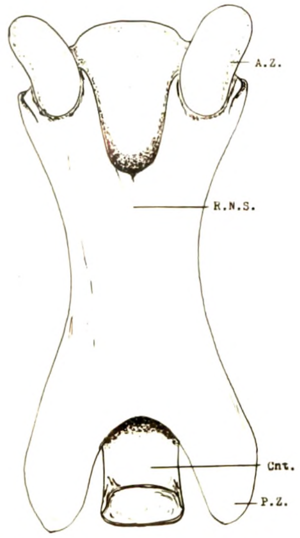
ATLAS

FIG. 24



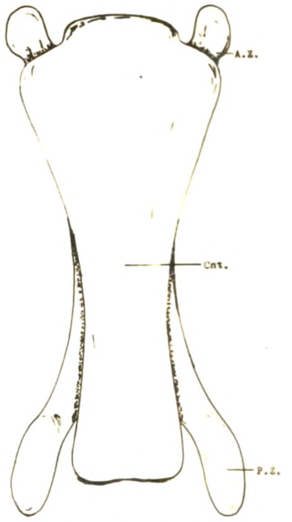
DORSAL VIEW OF THE AXIS

FIG. 25



DORSAL VIEW OF A TYPICAL CERVICAL VERTEBRA

FIG. 26



VENTRAL VIEW OF A TYPICAL CERVICAL VERTEBRA

FIG. 27

LATERAL VIEW OF A TYPICAL CERVICAL VERTEBRA

FIG. 28

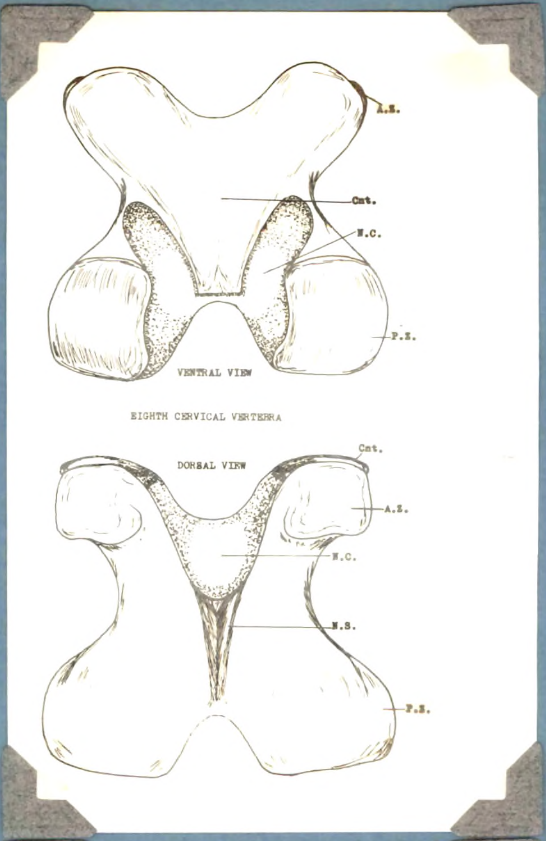

A.Z.
Cnt.
N.C.
P.Z.
VENTRAL VIEW
EIGHTH CERVICAL VERTEBRA
Cnt.
DORSAL VIEW
A.Z.
N.C.
N.S.
P.Z.

FIG. 29

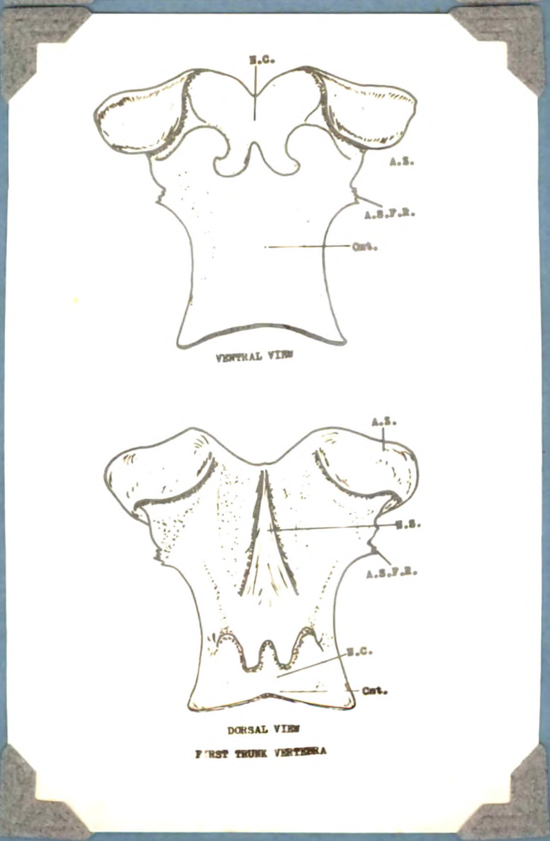
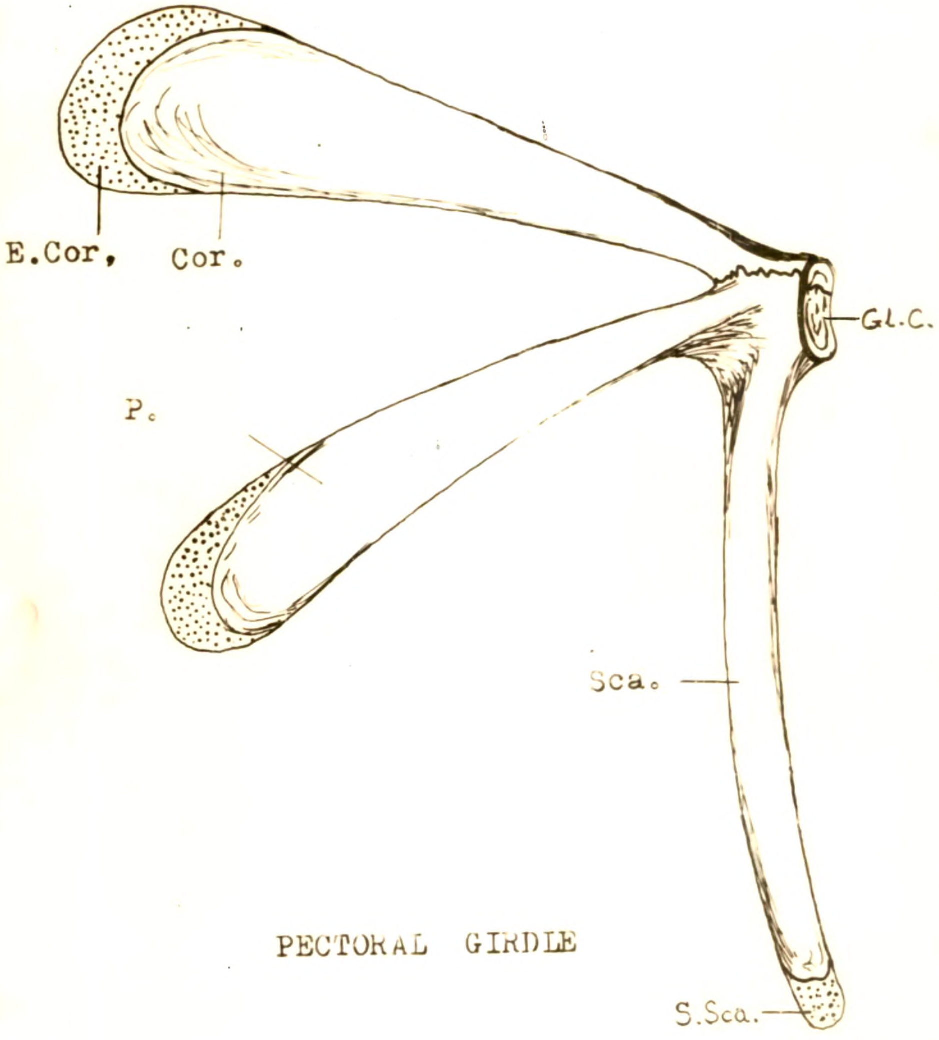
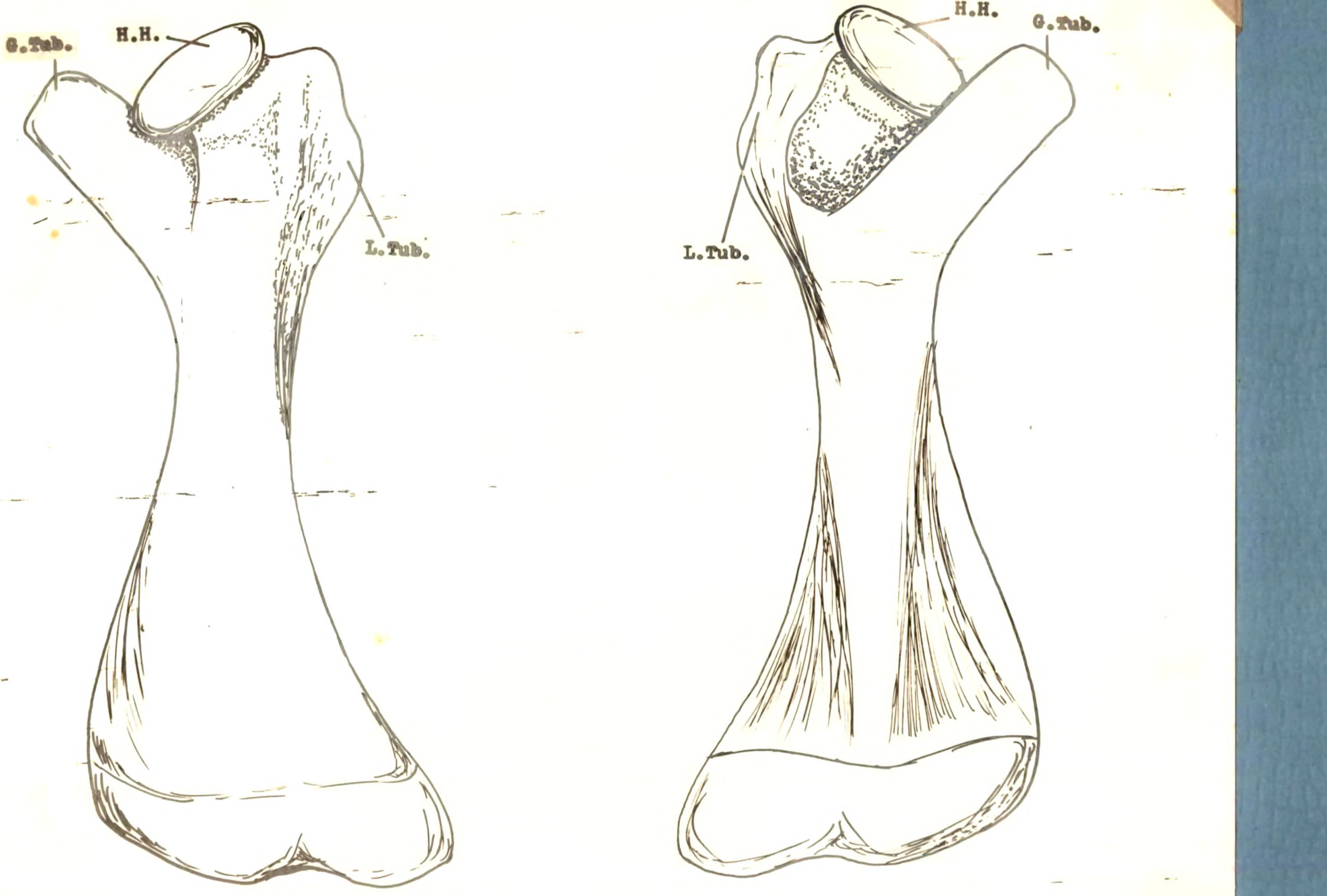

N.C.
A.Z.
A.S.P.R.
Cnt.
VENTRAL VIEW
A.Z.
N.S.
A.S.P.R.
N.C.
Cnt.
DORSAL VIEW
FIRST TRUNK VERTEBRA

FIG. 30



PECTORAL GIRDLE

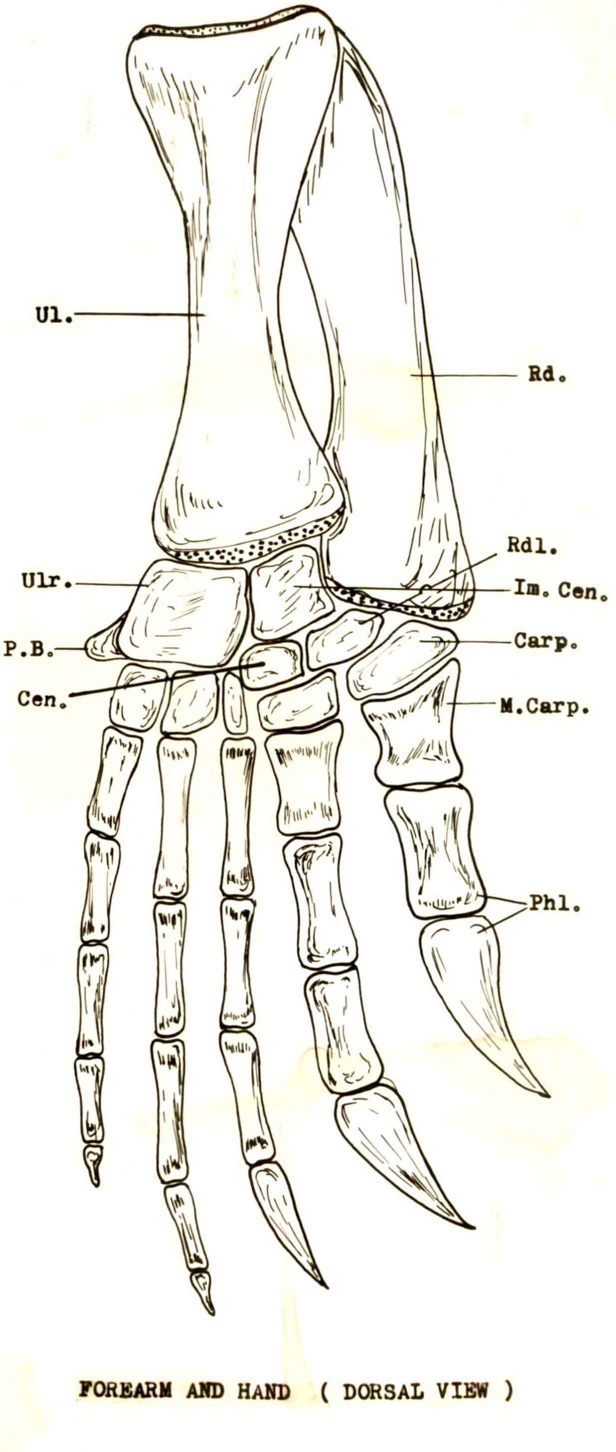
Fig. 31



DORSAL VIEW of HUMERUS

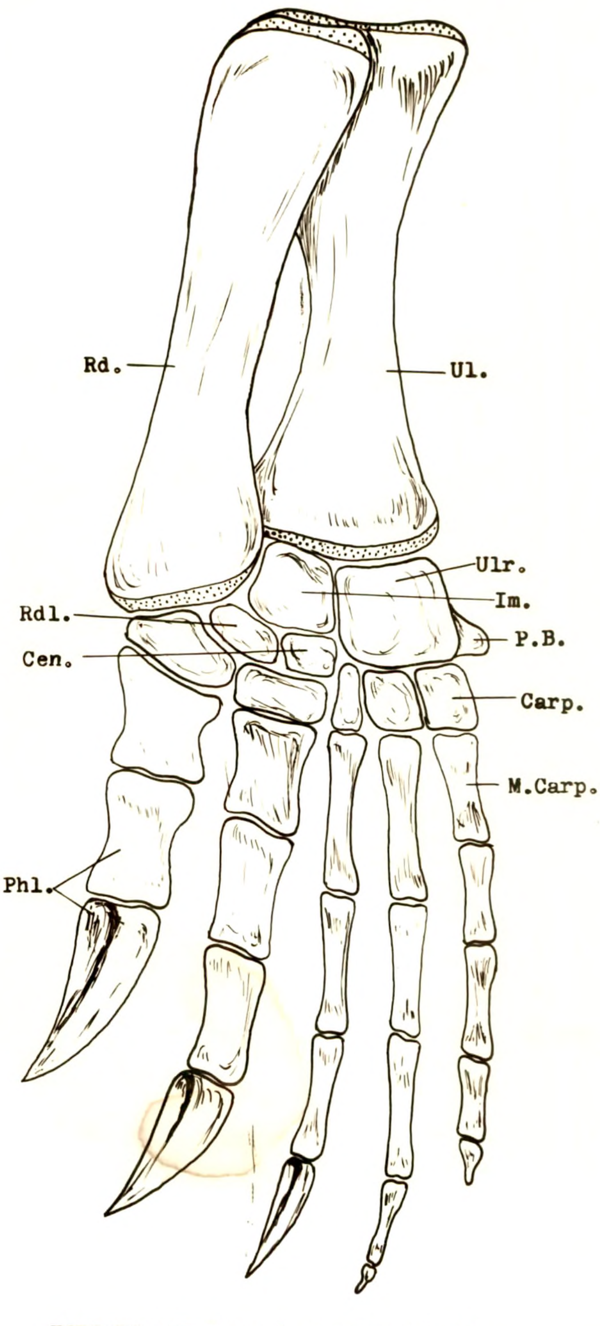
VENTRAL VIEW of HUMERUS

FIG. 32



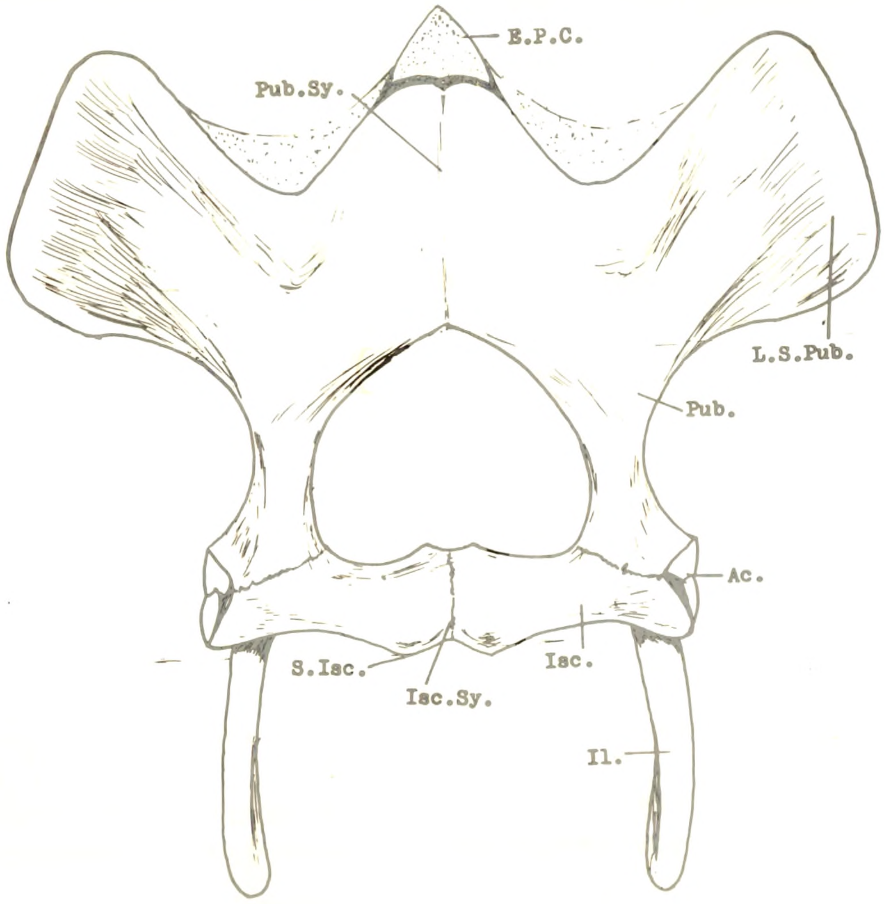
FOREARM AND HAND (DORSAL VIEW)

FIG. 33



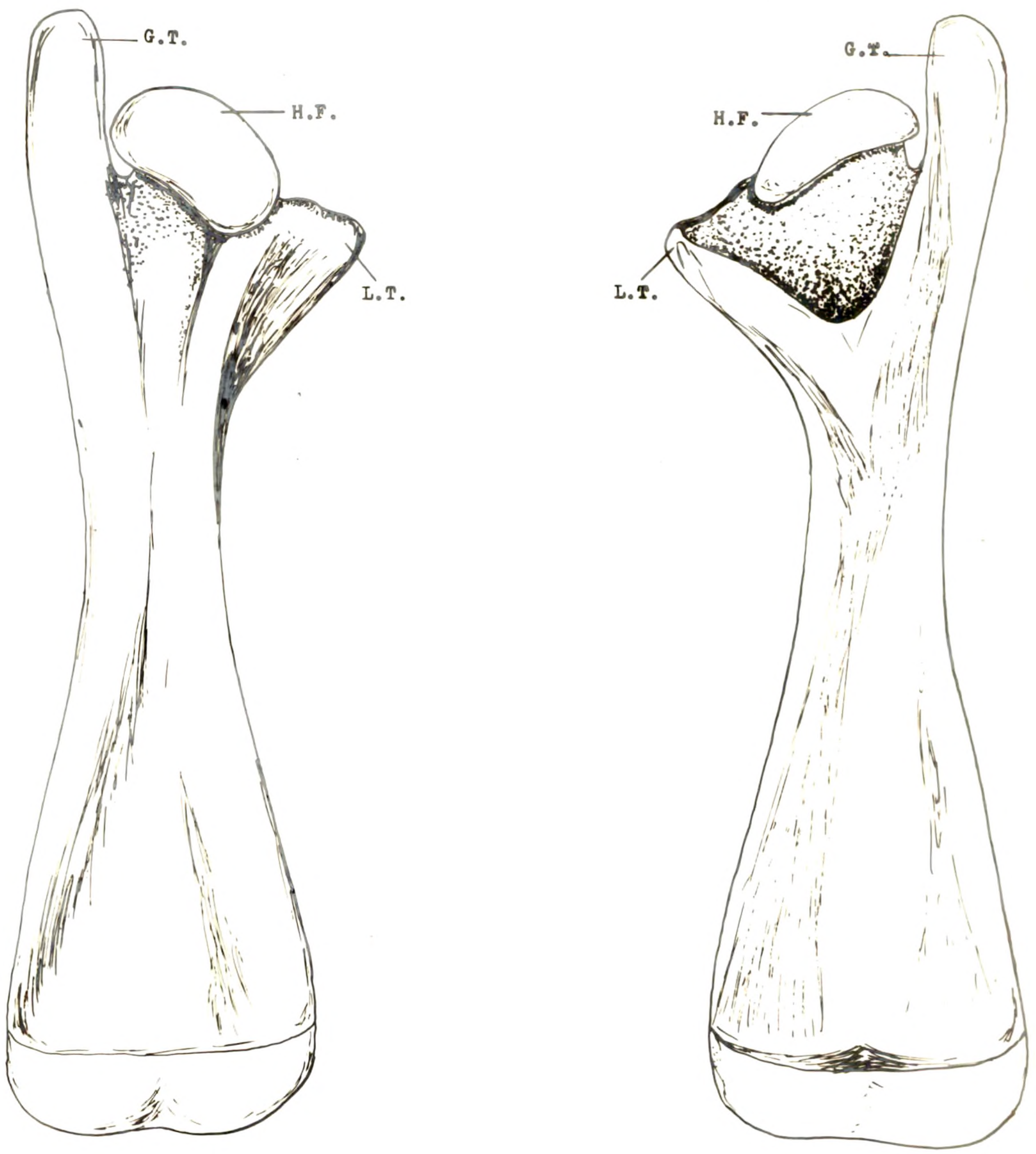
FOREARM AND HAND (VENTRAL VIEW)

FIG. 34



PELVIC GIRDLE (VENTRAL VIEW)

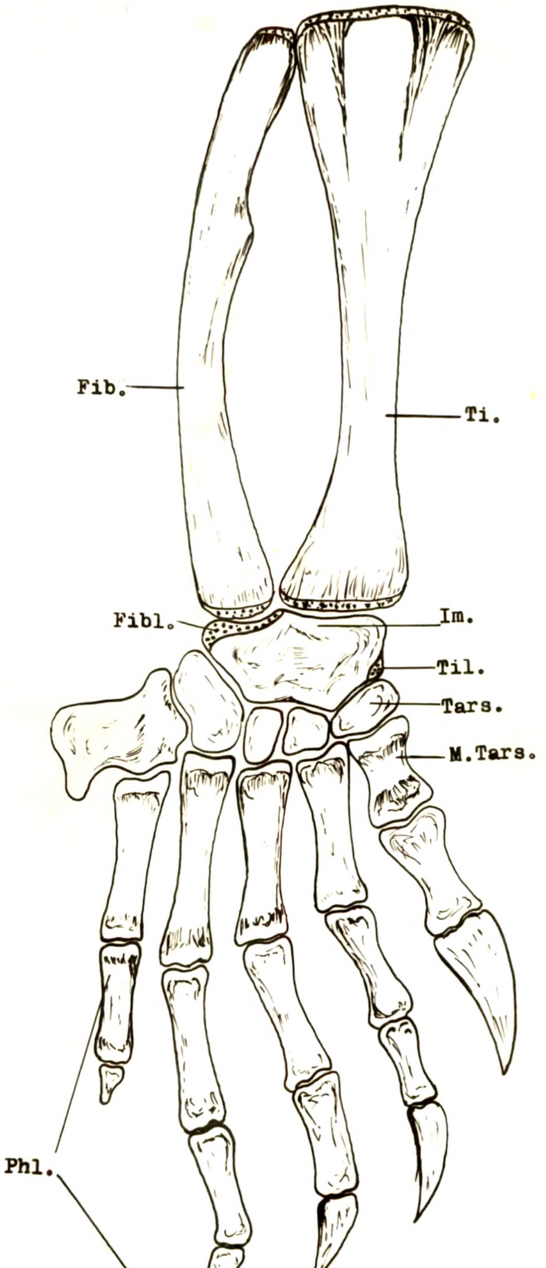
FIG. 35



FEMUR (DORSAL VIEW)

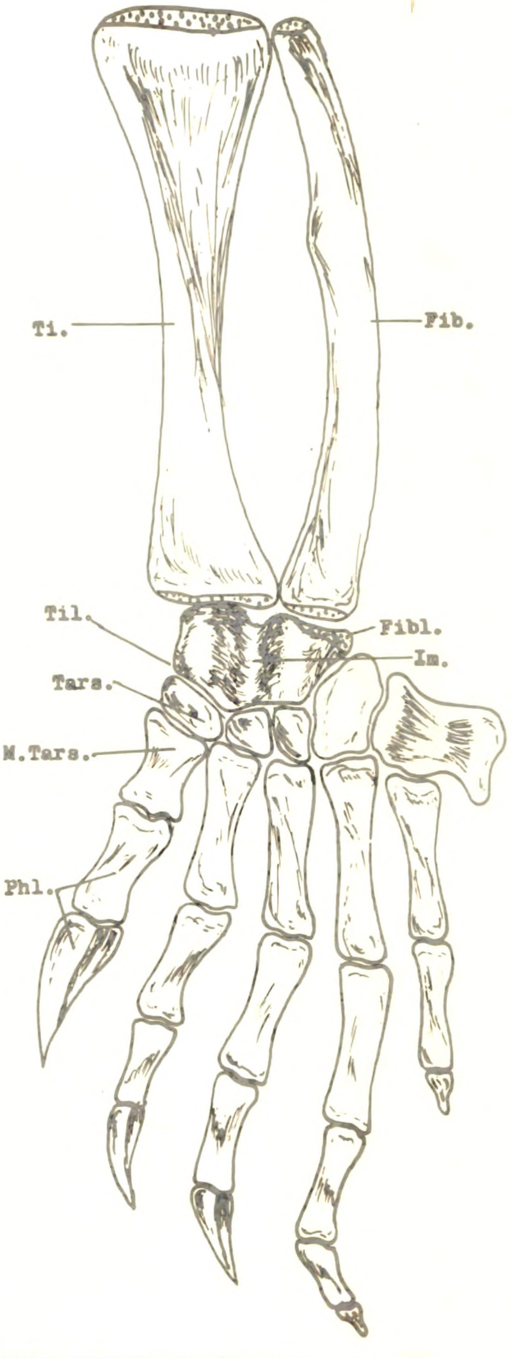
FEMUR (VENTRAL VIEW)

Fig. 36



SHANK AND FOOT (DORSAL VIEW)

FIG. 37



SHANK AND FOOT (VENTRAL VIEW)

FIG. 38

THE MUSCULAR SYSTEM

In the year 1892, Perrin, commented in his paper that, " Si on ouvre un livre d' Anatomie comparée on est immédiatement frappé du peu de developpment donné à la myologie comparée ". This was reiterated by Romer in 1942. Since then many valuable contributions in myology have been made by Howell, Appleton, Romer and Haines and as a result, our picture of the phylogeny of the vertebrate musculature is today much clearer. Nevertheless, compared to the myology of mammals our knowledge of that of reptiles is quite fragmentary indeed. Among the various reptilian groups again, the Chelonia are very highly modified and among the host of changes undergone by them to attain ~~its~~ Their present status, those of the muscular system have not been in any way less remarkable. A detailed comparative study of the musculature of the head, neck and trunk of some of the common Indian chelonians has been carried out, In addition the myology of the limbs of Lissemys was studied and it is envisaged to include the other genera also later on . The task was rendered difficult by the general lack of pertinent literature, and more so on account of the confusion that prevails in the nomenclature of the muscles.

MUSCLES OF THE HEAD AND NECK

The adductor mandibulae in the lower tetrapods consists of three muscle masses, acting as the adductor of the lower jaw, the adductor mandibulae externus, adductor mandibulae medius and the adductor mandibulae internus. In Testudo and Lissemys, the adductor mandibulae externus (Fig. 39,40,42,43,45) is a powerful muscle concerned with the movements of the lower jaw. The muscle has a wide-spread origin from the inner surface of the squamosal, the ventral as well as the lateral surface of the supraoccipital crest and also from the dorso-lateral part of the parietal. The fibres arising from the sqamosal decussate with those from the supraoccipital and parietal and finally become one single muscle mass which turns downwards through the vacuity formed by the emargination of bones, to get inserted on the coronoid process of the mandible. The vacuity in the skull is bounded on the lateral side by a transverse bony bar, the juguloquadrate bar, consisting of the jugal in front, the quadrate behind and the quadratojugal in the middle. This bony bar which is analogous to the zygomatic arch of mammals is also present in Lissemys and Trionyx. The adductor mandibulae externus in Testudo (figs. 40,45) passes behind the jugulo-quadrate bar, while in Lissemys (figs. 39,43) it is split at the level of this bony bar into two muscles, a lower and outer, the *masseter*, arising from the jugulo-quadrate bar and inserted on the lower edge of the mandible, and the upper and the inner part, the *temporalis*, arising from the usual place of origin of the *adductor mandibulae externus* as seen in Testudo, to be inserted on the coronoid process of the mandible. Thus the *temporalis* and the *masseter* muscles in Lissemys are derived from the primitive *adductor mandibulae externus* (George and Shah, 1954). In the mammals too the zygomatic arch effects the formation of the two muscles, the *temporalis* and the *masseter* from the *adductor mandibulae externus* (Quiring, 1950). Inspite of the fact that the jugulo-quadrate bar exists in the Testudo and Emys (Owen, 1866), the primitive nature of the *adductor mandibulae externus* is still retained. The *masseter* and the *temporalis* muscles of Lissemys (which are derived from the primitive *adductor mandibulae externus*) as well as the *adductor mandibulae externus* of Testudo are innervated by a branch of the Trigeminal nerve.

The *adductor mandibulae medius* in Testudo and Lissemys (Figs. 39, 40, 42) arises from the ventro-lateral part of the parietal, posterior part of the pro-otic and also from the inner anterior border of the quadrate. All the fibers converge and form a tendinous part which gets inserted on the coronoid process of the mandible.

The adductor mandibulae internus (Figs. 39,40,42) in Testudo is similar to that of Lissemys. It has a wide range of origin namely from the anterior inner border of the jugal, posterior border of the maxilla, outer border of posterior end of the palatine and the anterior outer border of the pterygoid. It runs backwards and downwards towards the articular bone of the mandible where it gets inserted by a thin tendon.

The depressor mandibulae (Figs. 39,40,43,45) which acts as a depressor of the lower jaw arises from the outer surface of the squamosal and proceeding downwards gets inserted on the lower border of the angular. This muscle in Lissemys unlike in Testudo consists of two parts an anterior and a posterior one. The fibres of both the parts decussate and run downwards to gain their insertion on the mandible.

The intermandibularis (Figs. 40,43,45) of Testudo is also similar to that in Lissemys, is the most superficial muscle on the ventral side of the head and extends from the entire lower border of one side of the mandible to the other. It has a median aponeurotic raphae which is attached posteriorly to the hyoid. On contraction of this muscle the floor of the buccal cavity is lowered, and raised on relaxation.

The constrictor colli (Figs. 39,43,45) which forms the superficial sheath of muscle on the lateral and the ventral sides of the neck arises in two parts in Testudo. An anterior one originates on each side, from a median aponeurotic raphae on the mid-dorsal line of the neck at the level of the atlas and axis. The more extensive posterior part takes it origin from the lateral side of neural arches of the second to the sixth cervical vertebrae. The fibres of both the parts run laterally downwards and form a continuous flat muscular sheath over the lateral and ventral sides of the neck. Thereafter the fibres on one side of the anterior part and those of the anterior half of the posterior part of the same side meet the corresponding ones of the opposite side in the mid-ventral line to form a thin tendinous raphae. The fibres of the rear half of the posterior part with those of the opposite side become continuous with an intermediate aponeurosis. This aponeurosis in the median plane on the ventral side is in continuation with the fibres of the anterior half of the muscle. In Lissemys, however, this muscle consists of only one part which arises from a fairly broad, membranous aponeurosis on the dorsum of the neck with the fibres of the anterior half running laterally downwards and turning to the ventral side of the neck to meet those of the opposite side through a common median raphae, while the fibres of the posterior half converge towards the posterior border of the raphae on the ventral side. A few posterior fibres that fail to reach the raphae become aponeurotic and fuse with the aponeurosis formed by those of the opposite side. So in Testudo as in Emys (Owen,1866) the *constrictor colli* forms a more or less complete muscular envelope of the whole of the neck, whereas in Lissemys it is restricted only to the anterior half of the neck. This difference in Lissemys is evidently due to the longer neck whose versatile movements would otherwise be restricted if this muscle did cover the entire neck as in the other two.

The *branchio-mandibularis* in Testudo is similar to that in Lissemys as it (Figs. 39,40,43,45) arises from the distal end of the anterior cornu and running anteriorly gets inserted on the lower border of the angular and the posterior part of the dentary.

The *geniohyoideus* (Figs 43,45). As in Lissemys this muscle in Testudo arises from the inner border of the mandibular symphyses and after running posteriorly some of the fibres decussate with those of the other side in the mid-ventral line till the level of the basihyal. After this it runs obliquely backwards and out~~to~~wards and finally gets inserted on the ceratohyal and the anterior border of the proximal end of the anterior cornu of its own side. As in Lissemys it brings about the movements of the tongue and the hyoid.

The genioglossus (Figs. 43,45) an elevator and protractor of the hyoid is a single muscle in Testudo arising from the anterior lower border of the dentary and gains insertion on the lateral process of the basihyal. In Lissemys (Fig.43), however, it consists of two distinct muscles, the genioglossus externus and genioglossus internus, the former having a similar origin, course and insertion as that of the single genioglossus of Testudo, but the latter, though has the same origin, has its insertion on the anterior border of the proximal end of the anterior cornu. These two muscles in Lissemys, must have been derived from a composite genioglossus muscle probably to facilitate the greater throat movements seen in this animal.

The hypoglossus (Fig.43) arises from the ventro-lateral and ventro-medial borders of the distal end of the anterior cornu and the fibres get inserted on the lateral process of the ceratohyal in Lissemys, while in Testudo it arises from the entire anterior border of the anterior cornu and gets inserted on the body of the ceratohyal. The muscle acts as a depressor and retractor of the hyoid even though its origin and insertion are different in the two animals.

The hypoglosso-glossus and the hypoglosso-hyoideus are the muscles concerned with the movements of the tongue and they are found only in the Chelonia and not in any other group of reptiles. They arise from a cartilaginous plate, the hypoglossum, situated under the tongue. The hypoglossum is a unique structure found only in the Chelonia, which in Testudo is smaller than the one found in Lissemys. The hypoglosso-glossus arises from the lateral margin of the hypoglossum and is inserted on the hyoid. The hypoglosso-hyoideus arises from the dorsal median surface of the hypoglossum and is inserted on the hyoid. We had ventured to name these two muscles as such (George and Shah, 1954), since we had not come across any mention of such muscles anywhere.

The intercornuatus (Figs31,4) which is responsible for the intercornual movements is a thin membranous muscle connecting the two cornua. Its fibres run somewhat obliquely outwards from the posterior border of the anterior cornu to the anterior border of the posterior cornu. As the posterior cornu in Testudo is very small compared to that of the Lissemys, this muscle in Testudo is very diminutive.

The *constrictor hyoideus* (Fig. 39,40,43) in Testudo compared to that of the Lissemys is a poorly developed muscle and arises on the lateral side, from the region of the neural spine of the seventh cervical vertebra and runs anteriorly downwards towards the hyoid to get inserted on the posterior border of the distal end of the anterior cornu. A few fibres of this muscle are also inserted on the posterior end of the squamosal. In Lissemys, however, it arises as three fleshy fasciculi from the region of the neural spine of the fifth, sixth and the seventh cervical vertebrae. All the three fasciculi run anteriorly and after a short distance join to form a single muscle belly which runs anteriorly towards the hyoid. Again, this belly gets split up into three parts, of which the most lateral part gains its insertion on the posterior border of the distal half of the posterior cornu, the median one is inserted on the posterior border of the proximal half of the posterior cornu, while the middle one proceeding over the posterior cornu gets inserted on anterior border of the distal end of the ceratohyal.

Such an elaborate modification of the muscle in Lissemys should be to bring about a powerful retraction of the head and neck, in addition to its primary function of being a depressor and an elevator of the floor of the buccal cavity and the hyoid. Since the neck in Testudo is comparatively short and the posterior cornu of the hyoid is not developed to the same extent as in Lissemys, the *constrictor hyoideus* remains as a single muscle.

The *tensor nasalis* in Lissemys (Figs. 39,43) arises from the inner surface of the anterior border of the nasals and on the inner side of the maxilla and the fibres run along the dorsal and lateral sides of the nostrils to be inserted on the skin bordering the nostrils. The muscle on contraction acts as the dilator of the external nares. This muscle is absent in Testudo since there is no snout as in Lissemys and Trionyx.

The *rectus capitis cervico-plastralis* in Testudo figs. arises from the sternal plate of the plastron by a fleshy origin and runs anteriorly into the neck on its lateral side as a cylindrical belly which on approaching the base of the skull turns to the dorsal side and finally gets inserted on the posterior end of the dorso-lateral part of the squamosal but in Lissemys (Figs. 39,43) the muscle gets flattened out in the region of the squamosal and gets merged with the skin, which in turn gets closely attached to its place of insertion on the squamosal. When the muscles of both the sides contract simultaneously the head and neck are flexed and retracted, but when the muscle of only one side contracts, a lateral rotation of the head and lateral flexion of the neck are effected.

The spinalis cervico-capitis in Testudo (Figs. 39,40) arises by five muscle bellies each one from the region of the neural spines of the second to the sixth cervical vertebrae respectively. All the parts run anteriorly and unite with one another to form one single muscle mass which goes forwards. Some fibres on the lateral side get inserted on the posterior half of the inner dorsal border of the squamosal, and the medial ones gain their insertion on the posterior end of the supraoccipital crest, while the fibres in the middle which form the major part of the muscle are inserted on the under surface of the skin at the basal region of the skull. The skin is firmly fixed on the parietal and the jugulo-quadrate bar. The parts of this muscle corresponding to the atlas, seventh and eighth cervical vertebrae are absent. This muscle in Lissemys is formed of four parts instead of five as in Testudo. The presence of an additional part in Testudo is perhaps to support the neck which has undergone a severe bend at this position owing to the carapace having become dome-shaped. The muscle in both the animals acts as an elevator and lateral rotator of the head.

The semispinalis in Testudo (Figs. 41,42) shows more or less a typically primitive segmental arrangement. It arises from the posterior zygapophysis of one vertebra and runs anteriorly to get inserted on the posterior border of the region of the neural arch of the next preceding vertebra. This arrangement is seen throughout the neck. In Lissemys the semispinalis muscles (Fig.41) arise from the entire length of the region of the neural spine of each vertebra and also the inner border of the posterior zygapophysis of the same vertebra. In its course it joins with few fibres of the longissimus arising from the succeeding vertebra and also the tendon of the longissimus arising from the second succeeding vertebra, to gain a common insertion which is partly fleshy and partly tendinous, on the posterior zygapophysis of the preceding vertebra. The spinalis and semispinalis muscles of the seventh and eighth cervical vertebrae do not exist separately as spinalis and semispinalis, but are represented as a single muscle mass which has its insertion on the anterior half of the region of the neural spine of the seventh cervical vertebra. The spinalis and the longissimus groups of muscles in the region of the atlas and axis are modified into occipital muscles.

In Lissemys the *longissimus cervicis* (Figs. 39,41) corresponding to the seventh cervical vertebra arises from the anterior zygapophysis of the eighth and in its course forwards it is divided into the medial (A), the lateral (C) and the middle (B) bellies, while the lateral belly of the one corresponding to the sixth vertebra is further divided into two C_1, C_2. The medial one (A) of the seventh is inserted on the posterior zygapophysis of the sixth. The middle one (B) runs forwards as a fleshy belly and later narrows into a tendon and joining with the fibres of the *semispinalis* and the medial belly (A) of the *longissimus* of the sixth gets inserted on the posterior zygapophysis of the fifth. The lateral belly (C) in its course forward joins with C_1 of the sixth and is inserted on the diapophysis of the fifth, while the C_2 of the sixth joins with the C_1 of the fifth to be inserted on the diapophysis of the fourth. The C_2 of the fifth, joins with the C_1 of the fourth and is inserted on the diapophysis of the third, while the C_2 of the fourth proceeds forwards, downwards and laterally to be inserted by a tendinous strip on the lateral border of the atlas and also at the ventral side of the pro-otic. The *longissimus* of the third does not possess the C_1 and C_2 bellies, while the middle belly (B) which is stouter and longer than those of the succeeding vertebrae, joins with the ill-developed middle belly (B) of the second to be inserted on the lateral border of the atlas by a strong tendon. The medial (A) and the lateral C_1 and C_2 bellies of the axis are absent, while the atlas does not possess any of the bellies of the longissimus cervicis.

The longissimus (Fig.41) of the first and second trunk vertebrae are well-developed and arise from the carapace instead of the succeeding vertebrae. The former proceeds forwards and gains its insertion on the posterior half of the region of the neural spine of the sixth cervical vertebra. The latter arises from the dorsal, lateral and the ventral sides of the place of origin of the former so as to envelope it at the base on the three sides. In proceeding forwards, the muscle converges laterally and goes on the ventral side of the former (longissimus of the first trunk vertebra) to be inserted on the anterior half of the region of the neural spine of the eighth cervical vertebra.

The longissimus cervicis in Testudo (Figs. 40,42) ~~this muscle~~ shows basically the primitive segmental arrangement. The part corresponding to the eighth cervical vertebra arises from the lateral border of the neural arch of the same vertebra and the fibres join with a few of those of the longissimus thoracis belonging to the second trunk vertebra, to gain a common insertion on the region of the neural spine of the seventh cervical vertebra. The one corresponding to the seventh cervical vertebra arises from the lateral side of the neural arch of the same vertebra and joins with the fibres of the longissimus thoracis belonging to the first trunk vertebra to gain a common insertion at the region of the neural spine of the sixth cervical vertebra and also the anterior border of the neural arch of the same side of the same vertebra. The part belonging to the sixth vertebra arises from the lateral side of the neural arch of the sixth vertebra and runs anteriorly forwards and inwards to get inserted at the region of the neural spine of the fifth and also on the anterior border of the neural arch of the same side of the same vertebra. This is a typical arrangement of origin, course and insertion of longissimus cervicis in Testudo. The parts corresponding to the fifth and fourth cervical vertebrae also show the above said arrangement in their origin, course and insertion, but those of the third and second cervical vertebrae do not get inserted at the usual place of insertion but join with each other and have a common insertion on the lateral process of the atlas. The longissimus of the first and second thoracic vertebrae are well-developed and they arise partly from the carapace and partly from the first thoracic vertebra which is somewhat free from the carapace. No fibres arise from the second thoracic vertebra because it is completely fused with the carapace. These parts of the muscles which are conspicuously powerful get inserted at the region of the neural spine of the sixth and the seventh cervical vertebrae and at the anterior half of the same region of the eighth cervical vertebra.

The occipital muscles which serve as the lateral rotator of the head comprise a lateral and a medial part. The former consists of the obliquus capitis and the latter of the rectus capitis.

The obliquus capitis in Testudo (Figs. 41,42) arises from the region of the neural spine on the axis and atlas vertebrae. The fibres run obliquely outwards and get inserted on the inner border of the squamosal and the pro-otic bones. In Lissemys this muscle is formed of two bellies, an upper one having the same insertion as the obliquus capitis of Testudo and a lower one (absent in Testudo) gets inserted on the tendinous strip of the longissimus of the third cervical vertebra.

The rectus capitis superficialis in Testudo and Lissemys (Figs. 41,42) arises from the region of the neural spine of the atlas and the fibres run obliquely forwards to be inserted on the pro-otic and the side of the basioccipital.

The *rectus capitis profundus* in both the animals (Figs. 41,42) is a small muscle arising from the lateral process of the atlas and gets inserted on the pro-otic and the opistho-otic bones.

The *rectus cervicis* (Figs. 40,45) in Testudo arises from the dorsal surface of the distal end of the coracoid, proceeds forwards through the trunk and runs ventrally through the entire length of the neck. The muscle in the beginning is somewhat cylindrical but later flattens out and after passing over the posterior cornu of the hyoid gets inserted on the posterior border of the anterior cornu. A few fibres, however, run over the anterior cornu and obtain their insertion on the basihyal and a few others get inserted on the proximal part of the posterior cornu. There is a thin tendinous intersection present on the muscle at a position slightly anterior to its middle. In Lissemys this muscle (Figs. 39,43) is much more modified than in Testudo. Though it arises from the dorsal side of the distal end of the coracoid as in Testudo, the muscles of either side as they enter into the neck region from the trunk converge and the median fibres of both the muscles decussate at a place more or less in the middle of the neck and then proceed anteriorly as a single flat muscle. Shortly after this decussation, is present a thick broad tendinous intersection after which the muscles again separate and run forwards and laterally. After parting company, each one splits up into three parts which lie one over the other. The dorsal part runs forwards along the ventral side of the oesophagus and finally merges with the wall of the oesophagus and the pharynx. The middle part gets inserted on the hyoid where the ceratohyal and the basihyal meet, while the ventral part runs over the posterior cornu and gets inserted on the anterior border of the ceratohyal by a thin tendon. Though the tendinous intersection in the muscle in Testudo is present, the muscle of one side neither meets the fellow of the opposite side nor splits into three different parts having different points of insertion. The three parts together of this muscle in Lissemys correspond to the entire muscle of Testudo. The mammalian sternothyroid and omohyoid are derived from the primitive rectus cervicis of the lower tetrapods. The ventral and middle parts of this muscle in Lissemys could be considered as homologous to the omohyoid and the sternothyroid respectively of the mammals, while the entire rectus cervicis of Testudo to both the above mammalian muscles. The third (dorsal) part of this muscle in Lissemys does not correspond to any other muscle in the vertebrates.

The *retrachens capitis collique* in Testudo and Lissemys is a long, composite muscle (Figs. 39,40,43,45.) which extends from the trunk to the head and it is described along with the muscles of the trunk and tail.

The hypaxial muscles of the neck in Testudo consists of two layers but those in Lissemys of three. The ventralmost layer of muscles in Testudo is the *longus colli*.

The *longus colli* in Testudo (Figs,45), corresponding to the eighth cervical vertebra arises from the mid-ventral line of the body of the same vertebra and the fibres run obliquely forwards and inwards. On its way the muscle splits into two parts, one upper and the other lower. The former gets inserted on the body of the seventh vertebra, while the latter becomes tendinous and gains a common insertion with ~~the muscle~~ the *intertransversarii colli*, on the posterior zygapophysis of the second preceding vertebra. The origin and insertion are the same for the *longus colli* series corresponding to the fourth to the seventh cervical vertebrae. The muscle arising from the third cervical vertebra occurs in two flat bellies. The lower one shows the usual place of origin of the entire *longus colli* but the upper part, the *rectus capitis ventralis longus*, (Fig.46) runs anteriorly and gets inserted on the pro-otic bone by a tendon. The muscles arising from the axis and atlas vertebrae, the *rectus capitis ventralis major* (Fig.46) and the *rectus capitis ventralis minor* (Fig.46) respectively, join with the fleshy fibres of the *rectus capitis ventralis longus*. In Lissemys the *longus colli* (Figs. 43,44) of each side in the posterior part of the neck arises from the mid-ventral line of the bodies of the eighth and seventh cervical vertebrae and running forwards gets inserted on the anterior part of the sixth and posterior part of the fifth cervical vertebrae. The next anterior belly in front, arises from the median line of the body of the sixth cervical and running over the preceding one, gets inserted on the anterior and posterior parts of the bodies of the fifth and fourth cervical vertebrae respectively. Similarly those arising from the first three cervical vertebrae have, however, a different course and insertion. The one arising from the third vertebra, the *rectus capitis ventralis longus* (Fig.44) runs, forwards to gain a tendinous insertion on the pro-otic bone, while the one arising from the atlas and axis, the *rectus capitis ventralis minor* and *major* (Fig. 44) respectively, join with the tendon of the *rectus capitis ventralis longus*.

The *rectus capitis ventralis brevis* (Figs. 44,46). in both Testudo and Lissemys arises from the anterior border of the atlas and the distal end of the basioccipital. It runs anteriorly for a very short distance and gets inserted on the anterior border of the basioccipital.

All these muscles, the *rectus capitis ventralis longus*, the *rctus capitis ventralis major*, and *minor* and the *rectus capitis ventralis brevis* correspond to the *longus capits* of mammals.

The *intertransversarii colli* (Figs. 44,46) muscles lie immediately dorsal to the *longus colli*. In Testudo these muscles are segmental and show the following arrangement of origin and insertion for the muscles of all the cervical segments. The muscle corresponding to the last (eighth) cervical vertebra arises from the mid-ventral line of the body of the vertebra and the fibres run anteriorly and converge to get inserted on the posterior zygapophysis of the seventh cervical vertebra. The muscles of the second to seventh cervical vertebrae show this typical arrangement. The muscle corresponding to the first cervical vertebra arises from the mid-ventral line of the body of the same vertebra and gets inserted on the basioccipital. These muscles in Testudo and Lissemys bring about inter-vertebral movements. The difference between the muscles of Testudo and Lissemys is only in their origin. In Lissemys they arise by two heads, one each from two adjoining vertebrae and in Testudo by only one head. This is necessitated by the presence in Lissemys of a long neck that performs a good deal of inter-vertebral movements unlike in Testudo.

The intertransversarii colli obliqui in Lissemys (Fig.44) forms the third layer of muscles on the ventral side of the neck. The parts corresponding to the second to the sixth cervical vertebrae only are represented. The posteriormost part arises from the diapophysis of the seventh vertebra and running obliquely inwards gets inserted on the entire lateral side of the sixth vertebra. Similarly the muscles arising from the diapophysis of the sixth, fifth, fourth, third and second vertebrae gain their insertion on the lateral sides of the fifth, fourth, third, second and first vertebrae respectively. It must, however, be mentioned that the part corresponding to the atlas which is larger and longer has a different insertion from that of the others in that a few fibres are attached on the antero-lateral border of the atlas, while the rest of the belly gains attachment on the lateral border of the basioccipital. There is a thin long muscle arising from the fascia covering the rib in the region of the scapula. It runs under cover of the scapula and gains its insertion on the lateral side of the eighth cervical vertebra. This muscle probably belongs to the *intertransversarii colli obliqui* group having been shifted from the diapophysis of the first thoracic vertebra to its present attachment, owing to the fusion of this vertebra with the carapace. This layer of muscle, the *intertransversarii colli obliqui* is absent in Testudo, owing again to the restricted movement of the neck.

The *trachelomastoideus* (Fig. 44,46) in Testudo has a broad origin from the mid-ventral line of the body of the first and second cervical vertebrae and from the outer side of the inner muscle belly of the *longus colli* of the third cervical vertebra. All the fibres run obliquely outwards and get inserted on the inner surface of the squamosal and the posterior border of the pterygoid. But in Lissemys this muscle (Fig. 44) arises from the lateral border of the second cervical and the diapophysis of the third cervical vertebrae and the fibres run obliquely outwards and converge into a narrow belly which gets inserted on the medial surface of the posterior end of the squamosal. This muscle in both the animals acts as the lateral rotator of the head.

MOVEMENTS OF THE HEAD AND NECK

The Chelonia among the reptiles possess a singularly long and powerful neck exhibiting a variety of movements. The principal movements of protraction and retraction of the neck together with those of the limbs play the part of the rib~~s~~ movements in other vertebrates of forcing the entry and exit of air into and from the lungs for respiration. In Lissemys and Testudo besides these principal movements there are various movements of the head and neck viz. flexion, flexion and lateral rotation, extension or elevation, extension and lateral rotation and lateral flexion.

The retraction of the head and neck is effected by the simultaneous contraction of the *rectus capitis cervico-plastralis*, the *retrachens capitis collique* and the *rectus cervicis*. In the protraction of the head and neck the retractor muscles relax and it appears as though this act of protraction is a passive one.

The other movements are possible only when the head and neck are in a partly or fully protracted state. Flexion is brought about by the contraction of the hypaxial group of muscles and also a part of the *longissimus* muscle. The hypaxial group also brings about the lateral flexion when only the muscles on one side contract.

Flexion is effected by the contraction of the entire group of hypaxial muscles, with the aid of the *longissimus*, *spinalis cervico-capitis*, *constrictor hyoideus* and the *rectus cervicis*. The *rectus capitis cervico-plastralis* of one side then contracts and brings about the lateral rotation of the head and neck.

Extension of the neck and elevation of the head are brought about by the simultaneous contraction of the epaxial muscles of both the sides. This is an important movement specially when the animal has to raise its head above the water for breathing.

Extension is brought about by the contraction of the *spinalis cervico-capitis*,*semispinalis* and *longissimus* muscles. The lateral rotation is effected then by the *rectus capitis cervico plastralis*, *rectus cervicis* and *constrictor hyoideus* of one side. When these muscles relax medial rotation is effected.

When the *semispinalis*, *longissimus* and the three layers of the hypaxial set of muscles of one side contract a powerful lateral flexion is effected thus aiding the limbs in motion. A change of direction in swimming is also accomplished.

When Lissemys is turned turtle, it rights itself quite elegantly with the help of its head and limbs. It shoots out its head stretching the neck to the utmost and the head turns dorso-ventrally backwards so that the dorsum of the head almost abuts against the carapace. In this position, by pressing the head on the ground, the neck is suddenly straightened by the simultaneous contraction and relaxation of the hypaxial and the epaxial muscles respectively of the neck. In this process, the body with the help of the limbs of the same side is turned over to its normal position. The neck in turtles as already hinted is a strong and powerful organ. The almost interwoven arrangement of muscles, not only adds to its strength and compactness but also to the ability for performing these versatile movements. When Testudo is turned turtle it cannot turn itself right. I had kept several specimens in an upside-down position and watched for days together and found that they could not right themselves to their normal position. This unfortunate condition in Testudo is due to the neck having undergone an abrupt bend which has already been mentioned, as a result of the animal acquiring the massive dome-shaped carapace that is unsuitable for swimming. If such a carapace came up as a mutation, it may be considered as a salient factor in the evolution of completely terrestrial Chelonia (tortoises).

MUSCLES OF TRUNK AND TAIL

The chelonian is popularly called a'reptile in a box' owing to the presence of the rigid shell which has made free movements of the body wall impossible and thereby rendering the body wall useless for the respiratory movements that are so characteristic of all amniotes. These structural modifications in the Chelonia have created a difficult situation for zoologists to explain the mechanism of respiration in these animals. The movements of the neck and limbs are believed to be indirectly serving the purpose of the body wall movements. As a basis for the understanding of the mechanism of respiration in the Chelonia a comparative study of the myology of the trunk and tail of different chelonians is of considerable importance. With this end in view the following common chelonians of this country viz., *Lissemys puncatata*, *Geomyda trijuga*, *Trionyx gangeticus* and *Testudo elegans*, have been studied.

Muscles of the Trunk:

The epaxial and hypaxial muscles of the trunk in Chelonia are obviously much reduced and modified owing to the fusion of the vertebrae with the carapace resulting in the complete cessation of intervertebral movements, and the formation of the plastron.

The <u>spinalis-semispinalis</u> system of muscles in Lissemys (Fig.47) arises by slender slips from the neural plates and the neural arches of the second to the tenth trunk vertebrae and sometimes also from the first sacral vertebra, which follows the tenth trunk vertebra. Those slips arising from the neural arches of the sixth to the tenth trunk vertebrae and their corresponding neural plates are tendinous, but those arising from the second to the fifth trunk vertebrae and their corresponding neural plates are fleshy. The fibres of all the muscle slips from the second to the tenth trunk vertebrae join together and form a single muscle belly. As in other chelonians this muscle system in Lissemys shows no distinction into its component parts, nor the typical criss-cross arrangement of the tendons characteristic of other reptiles, but consists of a linear column of muscle running through a narrow space bounded by the carapace, ribs and the vertebrae. On emerging out of the space at the level of the first trunk vertebra it gets inserted by a thick tendon on the neural arch and the posterior zygapophysis of the last cervical (eighth) vertebra. The muscle acts as an elevator of the neck at the level of the eighth cervical vertebra.

In Trionyx too the *spinalis-semispinalis* system (Fig. 48) has a similar origin, course and insertion, but in Testudo (Fig.50) the muscle slips arise only from the neural plates covering the first and second trunk vertebrae and also from the neural arches of the same vertebrae. The muscle after passing through the space bounded by the ribs and carapace, emerges out at the anterior end of the first trunk vertebra and gets inserted by a tendon on the neural arch and the posterior zygapophysis of the eighth cervical vertebra. The carapace in Testudo and to a lesser extent in Geomyda, having acquired the shape of a dome and the neck having undergone an unextendable bend at about the level of the first trunk vertebra and thereby become unable to be fully extended as in Lissemys and Trionyx, a great reduction in the *spinalis-semispinalis* system of muscles in the trunk, inevitably resulted. The versatile movements of the neck as in Lissemys, Trionyx and other aquatic and amphibious forms are an absolute necessity for their movements in water, and on land for righting themselves when turned turtle. Testudo on the other hand is unable to right itself when turned turtle and this unfortunate condition is primarily due to the neck having undergone the abrupt bend as a result of the animal acquiring the massive dome-shaped carapace that is a hind~~o~~rance in swimming. Geomyda (Fig.49) has only a slightly dome-shaped carapace and has a comparatively small bend at the neck, since only relatively a few vertebrae are involved in the bend and so it is able to right itself only with very great difficulty when turned upside down. This leads us to the inference that in the evolution of the land Chelonia the need to protect themselves from desiccation and other vagaries of an arid environment and to withstand the attack of enemies by taking shelter under cover of a strong armour was a major factor. The trend was naturally towards the acquisition of an extremely hard and heavy shell that could house the whole animal within. Both these ends were achieved in the completely terrestrial forms like Testudo. But all the same they were left behind with a shorter neck with restricted movements and shorter limbs with slower movements as the price for protection. The others on the other hand took to life in water and came to land only occasionally.

In Lissemys there is a small muscle which arises from the anterior border of the nuchal plate and gets inserted on the posterior border and the posterior part of the ventral surface of the prenuchal plate. The muscle when contracts, pulls the prenuchal which is loosely attached to the nuchal, effecting the closure of the shell in front. The muscle (Fig.41) which has been named as nucho-prenuchalis by Hassan (1941) should correspond to the spinalis muscle of the seventh and eighth cervical vertebrae, which have lost their usual attachment and taken a position described above. Such a muscle is not seen in Trionyx, in Testudo or in Geomyda, since there is no prenuchal in their carapace.

The nucho-epiplastralis (Fig. 47) in Lissemys (Hassan, 1941), corresponds to the trapezius which is a well-developed muscle in this animal. It arises from the outer side of the body of the first and second trunk vertebrae and also from the adjoining borders of the nuchal and the first costal plate. The muscle arises as a flat fleshy belly, the fibres of which converge to form a cylindrical mass which in turn curls upon itself and most of the fibres get inserted on the epiplastron, while a few get inserted on the cartilaginous epi-precoracoid. At the level between the last cervical and first trunk vertebrae the cylindrical part of the muscle appears as a pillar at the side of the neck. In Trionyx this muscle (Fig 48) is similar in its attachments to that of Lissemys but differs slightly in having an additional part which arises from the anterior border of the thick fold of skin lining the nuchal plate and blends with the main muscle mass. In the spiny-tailed lizard, Uromastix, this muscle arises from the dorsal fascia and is inserted on the acromio-clavicular joint (George, 1948). The insertion of the muscle in Uromastix is essentially the same as that in Lissemys and Trionyx, when we regard the region of the epiplastron of the plastron as corresponding to the clavicle. So the nucho-epiplastralis of Hassan could be regarded as homologous to the trapezius. This muscle on contraction ensures the closure of the anterior plastral valve after the retraction of the head and neck into the shell. In Lissemys this valve completely closes the anterior part of the shell, but it is not so complete in Trionyx, while in Testudo and Geomyda it is absent as already mentioned.

The rhomboideus (Fig.47) in Lissemys arises as a flat muscle sheath from the lateral border of the first two trunk vertebrae and also from the fascia of the trapezius at its posterior side. The origin of the muscle is fleshy and all the fibres run vertically downwards, where they get inserted on the medial border of the scapula and the dorsal surface of the precoracoid or the acromion process. A few fibres, however, get inserted on the epiplastral cartilage also. The insertion of this muscle on the median border of the scapula is similar to that of the mammalian rhomboideus. The rhomboideus in mammals could be considered as having split off from the well-developed reptilian trapezius and in Lissemys too such a splitting of the primitive reptilian trapezius seems to have taken place. On contraction the rhomboideus pulls the scapula and the precoracoid medially and slightly anteriorly. This retraction of the girdle is needed in order to carry the limbs almost completely under cover of the carapace. No such muscle is present in Trionyx, Testudo or Geomyda.

Regarding the mechanism of respiration in Chelonia, McCutcheon (1943) stressed the role of the flank cavity muscles and showed that throat movements played no significant part in respiration. In my published work (1954a) I have described two flank cavity muscle sheaths, an inner and an outer in Lissemys. The outer muscle sheath consists of the diaphragmaticus anteriorly and *transversus abdominis* (Fig.47) posteriorly, though the boundaries of these two muscles are not clearly demarcated unlike in *Emys europea* (Owen, 1866) or *Malaclemys centrata* (McCutcheon, 1943). In both Lissemys and Trionyx the outer sheath (Fig.47.48) arises from the inner lateral border of the carapace from the first to the seventh ribs, but in the latter it has a wider area of origin. The fibres run laterally downwards and then becoming membranous enclosing the viscera laterally and ventrally, gains insertion at a point in the centre of the plastron. In Testudo the whole of the anterior portion (*diaphragmaticus*) of this muscle sheath is membranous, while the posterior part (*transversus abdominis*) has the same structure as that of Lissemys. In Geomyda, the *diaphragmaticus* consists of two parts, an anterior one which is fleshy and a posterior one which is membranous. The posterior membranous part joins with the fleshy *transversus abdominis* which has a similar disposition as that of the same in Testudo. The nature of the *diaphragmaticus* in Geomyda appears as a transition between that in Lissemys on the one hand and Testudo on the other.

The inner muscle sheath (Fig.47) present in Lissemys and Geomyda arises from a small elliptical tract on the dorsum,dorsal to the bodycavity in the region of the second to the fifth ribs and the fibres run over the lung so as to form not only an envelope around it but even merge with its wall. In Geomyda, however, this muscle consists of fleshy fibres anteriorly and antero-laterally, while in the intervening part it is made up of a thin membrane. On the contraction of this muscle sheath, expiration is brought about and on relaxation inspiration is effected. Thus the two muscle sheaths enable the lungs to fuction as a pair of bellows. I also noted that the inner muscular layer occurring on the wall of the lungs is innervated by the intercostal nerves and suggested (1954a) that it is homologous to the intercostal muscles of other reptiles. The presence of this unique muscle on the lung wall in *Lissemys punctata* and *Geomyda trijuga* (Figs 47,49) encouraged me to look for such a muscle in other Chelonians. Since then I have extended my studies to two more chelonians, *Trionyx gangeticus* and *Testudo elegans* and found that in these the muscle is absent. It must, however, be mentioned that in place of the fleshy muscle bag found in Lissemys a thin membrane is left on the lung wall of these chelonians. It has already been mentioned that in Geomyda the muscle bag is not completely fleshy, but has an intervening portion of membrane. So, the condition of the inner muscle sheath found in Geomyda appears to be an intermediate stage between Lissemys on the one hand and Trionyx and Testudo on the other.

The above mentioned facts lead ~~me~~ us to certain important conclusions regarding the evolution of the Chelonia.

(1) On the fusion of the ribs and the formation of the body shell in the evolution of the early Chelonia resulting in the inability of the body wall to perform the respiratory movements, the inner muscle sheath came to be formed probably from the intercostal muscles. This acquisition of a muscular lung working as a pair of bellows must have given the early Chelonians their survival value.

(2) The study of the flank cavity muscles reveals a general degeneration of some of these muscles in Testudo and Trionyx. In both these forms the inner muscle sheath which is so well preserved in Lissemys is reduced to a mere membrane and

the condition in Geomyda shows a stage of transition. Again, in Geomyda the diaphragmaticus part of the outer muscle sheath, shows a transitional stage between the one in Lissemys and Trionyx on the one hand and Testudo on the other.

(3) In the nature of the flank cavity muscles therefore, Lissemys and Geomyda are to be regarded as more primitive than Trionyx and Testudo with Geomyda as an intermediate form between Lissemys and the other two. Some evidence in support of this is available from the recent work of Williams et al (1952) who on the basis of their studies on the plastron in Testudinata and Trionychidae have suggested that Lissemydinae are a primitive group.

(4) The probable causes for the loss of the inner muscle sheath of the lung of the higher Chelonia and the degeneration of the diaphragmaticus in the terrestrial forms like Testudo could be the evolution in these animals of larger lungs on which the muscle bag was more of a hindrance to their full expansion; and in the mean time the aquisition of a better physiological equipment

for fixing a greater amount of oxygen store in the body for gradual and slow utilization. A physiological study of the lung and blood of these animals is therefore to be undertaken.

The *obliquus externus* (Fig. 47) in Lissemys arises as a flat fleshy belly from the lateral margin of the carapace at the level of the first and the second marginals and the fibres run obliquely, medially and posteriorly and becoming tendinous join with the tendinous part of the outer muscle sheath (*transversus abdominis* part) of the lung and closely enveloping the visceral organs to gain a common insertion on the pubic symphysis and on the hypoplastron. In Trionyx also the *obliquus externus* fig 48 has the same origin, course and insertion as in Lissemys. In Lissemys, on the ventral side of the *obliquus externus* and *obliquus internus* (Fig. 47) there is a ligamentous tissue which arises from the hypoplastron and the first marginal and gets inserted on the fascia of the *gluteal* and the *rectus femoris* muscles. A part also adheres very closely to the skin covering the shank. This ligament perhaps is useful to retract the leg under the femoral valves, of the plastron. In Lissemys and Trionyx at the junction of the tendinous parts of the *obliquus* *externus* and *obliquus internus* a small flat muscle which runs downwards and gets inserted on the outer border of the pubic spine, takes its origin. This is perhaps the continuation of the *obliquus externus* and the *obliquus internus* muscles.

The *obliquus internus* (Fig.47) in Lissemys has its origin, medial to that of the *obliquus externus*, namely on the outer border of the costal plates corresponding to the third to the fifth marginals. The fibres run obliquely forwards and inwards and finally become tendinous and get inserted on the dorsal part of the pubic symphysis. In Trionyx too the *obliquus internus* (Fig 48) has a same disposition.

In Testudo and Geomyda, however, instead of two separate muscles there is a single muscle, the *obliquus externus*, (Fig 49,50) bordering the lateral side of the posterior half of the carapace. This single flat muscle in these chelonians is similar to the one found in *Emys europea* described by Owen (1866). The muscle fibres run obliquely forwards and inwards which finally get inserted on the hypoplastron and xiphiplastron. In Testudo and Geomyda therefore the *obliquus internus* is either absent or is merged with the *obliquus externus*.

The retrachens capitis collique (Fig.51) in testudo arises on the entire side of the vertebral column on the ventral side by four fleshy fasciculi, from the neural plates covering the third to the seventh trunk vertebrae. Of the four, the posterior one is very massive and arises from the neural plate covering the sixth trunk vertebra and also from the anterior half of the neural plate covering the seventh vertebra. The muscle runs anteriorly and enters the neck and after traversing through the entire length of the neck almost all the fibres get inserted by a thick tendon on the basioccipital on the ventral side of the skull, while a few gain separate insertion on the inner posterior border of the squamosal by a thick tendon. The two fasciculi next to the one described above arises from the side of the fifth and fourth trunk vertebrae respectively and both run side by side anteriorly in order to enter the neck region. The one which arises from the side of the fifth trunk vertebra and its corresponding neural plate gets inserted on the diapophysis of the fourth cervical vertebra and the one which arises from the side of the fourth trunk vertebra and its corresponding neural plate gets inserted on the diapophysis of the fifth cervical vertebra. The anterior-most fasciculus arises from the third trunk vertebra and its corresponding neural plate, runs anteriorly and after entering the neck gets inserted on the diapophysis of the sixth cervical vertebra. In describing the *retrachens capitis collique* in *Emys europea*, Owen (1866) states that it arises by six fleshy fasciculi from the neural arches and spines of the dorsals and proceeds forwards blending together and gets detached into four tendinous insertions. But in Testudo there are only four such fasciculi and they remain completely separate without any blending whatsoever. On studying the nerve supply to these four fasciculi it is found that the posterior-most one, the largest and the longest fasciculus, which is inserted on the base of the skull is innervated by a branch from the middle cervical ganglion of the vagus and the sixth thoracic nerve at the region of its origin, whereas the others, the anterior three fasciculi, obtain their nerve supply from the third, fourth and fifth thoracic nerves. The fact that these anterior three fasciculi remain completely separate from the posterior large fasciculus and that they are innervated by a totally different source of nerve supply tends to show that they are different muscles altogether. It is suggested that they correspond to the *longus colli* series of muscle of the trunk and that the posterior large belly is a composite muscle formed anteriorly by the *sterno-cleido-mastoid* as was suggested (George and Shah, 1954a) in the case of Lissemys and posteriorly by the last fasciculus of the *longus colli* series (George and Shah, 1954b).

The *retrachens capitis collique* in Lissemys (Fig.51) is a highly specialized muscle and considerably different from that of the Testudo in its attachments. In Lissemys it arises by three fleshy parts. The lateral one arises from the junction of the first and second marginals and their corresponding costal plates, the middle one arises close to the lateral one from a point posterior to its place of origin, while the medial part arises from the last costal plate at the posterior region near the vertebral column and from the bodies of the five anterior caudal vertebrae. All these parts on each side run anteriorly for a short distance when the lateral and middle ones join with the medial one to form a single massive muscle belly on either side and proceeds towards the head. This linear muscle column on each side runs through the entire length of the region of the trunk and neck to gain a tendinous inertion on the basioccipital and partly on the posterior inner border of the squamosal of the respective sides. These bellies on either side are connected to one another throughout their course from the place of origin to that of their insertion by a thin aponeurosis, which is narrower in the posterior region and gradually becoming broader as the muscle proceeds anteriorly separating the two bellies more and more laterally. On approaching the base of the skull each divides into two, a lateral and a medial part. The former part which is comparatively a minor one gets inserted on the inner posterior border of the squamosal and the latter on the basioccipital and the posterior part of the pterygoid, both the insertions being tendinous. It has been suggested (George and Shah, 1954a) that the retrachens capitis collique muscle in Lissemys is divisible, arbitrarily, into two parts at the level of the episternal plate (epiplastron) of the plastron. These two parts of the muscle have a different nerve supply; the anterior, cervical part being innervated by a branch from the middle cervical ganglion of the vagus, while another branch from the same ganglion innervates the rectus capitis cervico-plastralis. From this I have ventured to homologise, the anterior, cervical part of the retrachens capitis collique with the sterno-cleido-mastoid muscle which is derived from the rectus capitis cervico-plastralis, the primitive cucularis. The posterior trunk part has two sources of nerve supply; anteriorly by the fifth cervical nerve and posteriorly by a nerve from the lumbo-sacral plexus and the twelfth dorsal. it is suggested (George and Shah,1954a) that owing to the skeletal modifications in the formation of the carapace and plastron, the *sterno-cleido-mastoid* muscle did not get its usual attachment but joined with the posterior part which is in turn derived from the *pubo-ischio-femoralis*, from which the *psoas* muscles of mammals were derived. The twelfth dorsal nerve which supplies the posterior-most part of the *retrachens capitis collique* innervates the *pubo-ischio-femoralis* muscle in addition.

(Fig 51)

In Trionyx it consists of six fasciculi of which the anterior first, second and third are very thin and membranous, while the fourth and fifth are massive and well-developed. The last fasciculus which is also a well-developed one, arises from the lateral surfaces of the body of the second, third, fourth and fifth caudal vertebrae. The fourth and fifth fasciculi arise from almost the entire ventral surface of the costal plates covering the ribs between the seventh and eighth, and the eighth and ninth trunk vertebrae. The first, second and third fasciculi arise from the neural plates corresponding to the fourth, fifth and sixth trunk vertebrae respectively. The first two are very thin, while the third one is somewhat fleshy and well-developed.

All these fasciculi of one side blend together to form a single muscle belly which runs anteriorly through the trunk and neck. At the level of the eighth or ninth trunk vertebra the muscle of either side fuse with one another to form a single stout muscle mass. Such a blending of the muscle of either side is completely absent in Testudo and Geomyda, but in Lissemys though they do not fuse with one another directly, there is an indirect connection through an aponeurosis which is very narrow at the posterior end. In Trionyx after the fusion, forming a single muscle, it runs anteriorly forwards into the trunk region, but at the level of the first trunk or the last cervical vertebra, the component parts part company at the same time retaining their connection with each other by a thin aponeurosis which is narrower in this region, and later widens out separating the muscles more laterally, a condition very much similar to the one observed in Lissemys. After reaching the base of the skull the muscle splits up into two, a lateral and a medial part. The latter which is the major part gets inserted on the basioccipital and the posterior part of the pterygoid by a thin tendon, while the former gets inserted on the posterior inner border of the squamosal. In this animal the insertions of this muscle are similar to those of the same muscle in Testudo, Geomyda and Lissemys. Since the muscle in Trionyx consists of six fasciculi of which the last three arise from very much similar places of origin as in Lissemys, this may be regarded as homologous to the same part of the muscle in Lissemys, whereas the anterior part comprising the first three fasciculi in Trionyx are similar to those seen in Testudo and Geomyda, but at the same time it differs in that that all the fasciculi in Testudo do~~s~~ not blend together to form a single muscle as in Trionyx. In this respect of blending, Geomyda differs from Testudo in having the blending of all the fasciculi to form a single muscle belly, almost similar to the one in Trionyx and Lissemys, such a type of blending of the different fasciculi is present in *Emys europea* (Owen,1866). The muscle in Trionyx after the blending remains as a single mass and runs forwards in the trunk and through the neck to gain its insertion similar to the one found in Lissemys. So in Trionyx it is suggested that the first three fasciculi of this muscle are similar to those of Testudo which has been suggested above to be homologous to the *longus colli* series of muscles.

In Geomyda this muscle (Fig 51) arises by five fleshy fasciculi from the body of the fifth, sixth, seventh, eighth and ninth trunk vertebra, and the neural plates covering these vertebrae. All the fasciculi of one side blend together and form a single muscle which runs anteriorly through the trunk and enters the neck. After reaching the third cervical vertebra, some median fibres become tendinous and get inserted on the lateral side of the bodies of the first, second and third cervical vertebrae, while the major part of the muscle runs forwards and gets inserted on the basioccipital by a tendinous insertion and a few lateral fibres also become tendinous to get inserted on the inner posterior border of the squamosal. The retrachens capitis collique of either side, though runs side by side, does not show any fusion or connection with each other by aponeurosis. The posterior part of this muscle consisting of the five fasciculi which have blended together corresponds to the longus colli series, while the anterior part to the sterno-cleido-mastoid muscle. It must, however, be mentioned that the insertion on the bodies of the first three cervical vertebrae of the median fibres of the anterior part which is absent in Testudo, indicates that these fibres are of the longus colli series and that if this inference is true, the anterior part is formed by both sterno-cleido-mastoid (mainly) and the longus colli series.

This composite muscle in its reduction in Trionyx and Geomyda shows a condition somewhat intermediate between that of Lissemys on the one hand and Testudo on the other in which the reduction is maximum. It must be mentioned that of the two, Trionyx is nearer to Lissemys, and Geomyda to Testudo.

Muscles of the Tail:

In the Chelonia the tail has lost its importance as it is neither an organ of locomotion nor of defence and offence, as in the other reptiles and presents no direct muscular link up with the thigh so as to move with the movements of the posterior extremity. This has therefore brought about the great reduction of the muscles in this region of the body.

In Lissemys and Trionyx the tail is extremely small. Compared to this the tail in Geomyda or Testudo is considerably longer and extends beyond the cloacal opening. In all these chelonians as in other reptiles there is a superficial muscle sheath, the flexor caudae superficialis, covering the deep caudal muscles on the ventral and lateral sides of the tail. The deep caudal muscles of Chelonia, in general do not show their normal attachments. The median dorsal muscles comprising the spinalis-semispinalis system of muscles show the typical criss-cross arrangement that is so characteristic of reptiles. This arrangement assuring free intervertebral movements is retained only in the tail region of the chelonian, even though the tail is very much reduced and no longer functions as an active organ. So it becomes evident that the criss-cross type of arrangement in the spinalis-semispinalis system that is so typical of all modern reptiles, must have been present not only in the immediate ancestor of the Chelonia but also in the early reptilian ancestors as well, from which all the modern reptilian forms were evolved.

The flexor caudae superficialis (Figs. 52,53,54,55) muscle is present as a superficial muscle sheath covering the sides of the cloaca and the deeper muscles of the tail. It arises from the neural spines of the caudal vertebrae and also from the medial part of the last costal plate. The fibres run laterally and downwards and join with those of the opposite side forming a thin aponeurosis on the mid-ventral line of the tail. Proximally the aponeurosis gets attached along the dorsal side of the ischial symphysis , while distally the muscle remains fleshy and free from any attachments. The posterior-most part of this muscle is more muscular and becomes the sphincter of the cloaca. The *flexor caudae superficialis* is homologised by Haines (1935) to the *ilio-caudalis* and *ischio-caudalis* of lizards and crocodiles. In Lissemys, Trionyx and Geomyda, however, this muscle seems to correspond to the *ilio-caudalis* only, though has lost its normal attachment to the ilium. The *ischio-caudalis* is a well-developed muscle in these three chelonians. In *Testudo pardalis*, Haines (1935) mentions an unidentified muscle arising from the lateral side of the body and transverse processes of the caudal vertebrae and inserted on the pubis. I too have come across a similar muscle in *Testudo elegans* but not in Lissemys, Trionyx and Geomyda. This leads me to the inference that the unidentified muscle in *Testudo pardalis* and *Testudo elegans* should correspond to the *ischio-caudalis* of Lissemys, Trionyx and Geomyda, since there is no such muscle arising from caudal vertebrae and getting inserted on the pubis in Lissemys, Trionyx and Geomyda, though a few fibres of this muscle in [illegible] Geomyda do get inserted on the pubis. The manner of the insertion of this muscle in Geomyda denotes a condition intermediate between that in Lissemys and Trionyx on the one hand and Testudo on the other. That in Testudo this muscle instead of having its insertion on the ischium, gets itself attached on the dorsal region of the pubic symphysis and that this shift had occurred in this animal could perhaps be visualised if it is realised that the relative positions of the ischium and pubis in Testudo are at a greater angle than that is seen in Lissemys or Trionyx in which they are more or less in the same line or at least at a relatively small angle. The position of these bones in Geomyda is somewhat at a greater angle than that in Lissemys and Trionyx but slightly lesser than that in Testudo. It must also be mentioned that the ischium and pubis in Testudo and Geomyda are placed very close to each other separated by a very small ischial foramen, whereas in Lissemys and Trionyx, they have a considerable distance between them being separated by a large ischial foramen. From this arrangement of the two bones in Testudo and Geomyda, it is possible to visualise a change having taken place in the point of insertion of the unidentified muscle of Haines (1935) in Testudo, from the ischium to the pubis, and I have therefore ventured to call this muscle <u>ischio-caudalis</u> and consequently regard the <u>flexor caudae superficialis</u> as consisting of the <u>ilio-caudalis</u> only and not as a composite muscle formed by the <u>ilio-caudalis</u> and <u>ischio-caudalis</u>.

The sphinctor part of the *flexor caudae superficialis* which aids the opening and closing of the cloacal aperture, is retained in the mammals as the perineal muscles, while the other part is somewhat degenerated (Haines,1935). Laterally on the tail in Lissemys just by the lateral border of the *flexor caudae superficialis* there is a small muscle on both the sides which arises from the anterior border of the last marginals and gets inserted on the caudal valve of the plastron. This muscle is referred to by Hassan (1941) as the *margino-infra-caudalis* . It is very likely that it is only a part of the *flexor caudae superficialis* and the nerve supply to both these is derived from the same source. This muscle brings about the closure of the caudal valves of the carapace and plastron after the retraction of the tail into the shell. Such a muscle is totally absent in Trionyx, Testudo and Geomyda since such caudal valves are absent in these animals.

The *flexor caudae profundus* (Figs.52,53,54),55 of Chelonia is homologised with the *caudo-femoralis* of lizards (Haines,1935). Since the tail has been reduced and has lost its function as an organ of locomotion, the attachment of the muscle on the femur~~e~~ is shifted to the costal plate near the vertebral column at the level of the sacrum. In Lissemys it arises lateral to the origin of the ischio-caudalis from eight caudal vertebrae and runs anteriorly forwards to gain insertion on the last costal plate just near the sacral vertebrae. A few fibres are also inserted on the lateral side of the body of the sacral vertebrae. In Trionyx the origin is almost similar to that in Lissemys but does not cover such an extensive area of origin where it arises from only four caudal vertebrae starting from the eleventh caudal. The muscle runs anteriorly and gains insertion on the costal plates near the first sacral vertebra. A few fibres gain insertion also on the body of the vertebra as seen in Lissemys. In Testudo it is well-developed and arises from the last six caudal vertebrae and gets inserted on a very extensive area on the costal plate corresponding to the eighth and ninth trunk vertebrae. In all these chelonians it acts as the flexor of the tail. The shift of insertion of the muscle from the femur to the costal plate and the muscle becoming the flexor caudae profundus instead of remaining as caudo-femoralis as in lizards and crocodiles are accountable since the tail in the chelonians has lost its function as an active organ of locomotion or defense and offense as in the case of lizards and crocodiles. In lizards and crocodiles the tail bends on one side as the leg of the same side moves forwards. This action of the tail in relation to the leg movements helps in propelling the body ahead. A movement of this kind is possible only if the tail is a massive one and it touches the ground. The tail in Chelonia in general is very much reduced and does not touch the ground or even if it does, it is so ill-developed and is of so little consequence that the propulsion of the body, which has become very bulky, unwieldy and heavy, becomes impossible. In forms which swim, the question of the tail touching the ground and the propulsion of the body by its action does not arise at all and so the tail is musch reduced and ill-developed in them too. Such a change has taken place in the mammals also (Haines, 1935).

The retractor penis (Figs.52,53,54,55) is very well-developed in all male chelonians, while the corresponding one in the female is ill-developed and is attached to the clitoris. It arises from the last costal plate closely adjacent to the sacral vertebrae. The fibres run posteriorly downwards and turn over to the ventral side of the cloaca to be inserted on the wall of the cloaca where the penis or clitoris is situated. The muscle during its course runs over the *ischio-caudalis* and at the point of insertion the fibres of the muscle of either side run side by side and gain their insertion. This muscle acts as its name indicates as the retractor of the penis or clitoris.

Besides these long caudal muscles, there are the short muscles on the dorsal and the ventral sides of the caudal vertebrae. The dorsal group in acting as the extensors and the ventral ones as the flexors of the tail vertebrae bring about intervertebral movements.

On the dorsal side the extensor muscles consist of the *spinalis* and *semi-spinalis* (*extensor caudae*, of Owen, 1866) muscles showing the primitive segmental and the typical reptilian (criss-cross) arrangements. A *spinalis* muscle (Fig.) arises from the posterior border of the transverse process of one vertebra and gets inserted on the region of the neural spine of the next anterior vertebra. A *semi-spinalis* (Fig.) arises from the base of the transverse process and also from the side of the neural arch of one vertebra and running forwards and outwards gains insertion on the posterior border of the transverse process of the next preceding vertebra. In all the Chelonians studied, the *spinalis-semispinalis* system of the first three caudal vertebrae are very well-developed and massive. They are inserted on the posterior border of the last costal plate by the side of the vertebral column. Under cover of the *semi-spinalis* are the short vertebral muscles, the *intertransversarii* which extend between two transverse processes.

On the ventral side of the tail are the flexor muscles called *flexor caudae inferior* (Owen, 1866) arising from the transverse process of one vertebra and inserted on the side of the body of the next preceding vertebra. The muscles arising from the first three caudal vertebrae are well-developed and are inserted on the body of the second sacral vertebra and also on the costal plate covering the sacral vertebrae. This set of caudal flexors present in all the chelonians is called *flexor caudae lumbalis* by Owen (1866).

THE APPENDICULAR MUSCULATURE OF LISSEMYS PUNCTATA

Reptilian musculature exhibits a basic primitive pattern from which the highly advanced and modified musculature of birds and mammals have been derived. The primitiveness is more apparent in the muscles of the limbs owing to the limitation in locomotion. Amongst the reptiles again, the Chelonia are an interesting group which shows several singularities and modifications in practically all the systems of the body primarily as a result of the development of a body shell consisting of the carapace and plastron. With the ability of the animal to tuck itself into the shell as an excellent mode of defense the general orientation of the appendicular skeleton had undergone considerable change with the result that the muscles of the limbs underwent certain pronounced deviations from the typical reptilian pattern as evinced ~~by~~ in the Lacertilia.

MUSCLES OF THE FORELIMB

The pectoralis is a broad, fan shaped muscle having its origin on the plastron and along the margin where the carapace joins the plastron at the postero-lateral boundary. The origin of the pectoralis muscle is the same as in the other reptiles and mammals when it is considered that the plastron of the Chelonia comprises the modified sternum and the clavicles. All the fibres of the muscle run obliquely forward and converge towards the lesser tuberosity on the proximal end of the humerus, where it gets inserted by a thick tendon. It is innervated by the branches of the first and the second dorsal nerves and acts as a powerful adductor of the arm.

The deltoideus (Fig.56) arises by two heads, a clavicular one from the epiplastral region of the plastron and the other, the scapular arising from the outer surface of the acromion process of the scapula (precoracoid).Finally both the heads join together and gain a common insertion on the bony protruberance near the head of the humerus. In the case of the spiny tailed lizard, Uromastix, the scapular part of the deltoideus however, arises from the suprascapula (George,1948).

In lizards the primitive *deltoideus* during the course of its development has given rise to three distinct heads, the clavicular, the scapular and the third one which is the *scapulo-humeralis anterior* muscle (Romer, 1944). The presence of only the first two in Lissemys probably denotes that the third one (*scapulo-humeralis anterior*) has not been separated out as had happened in the lizards. If this supposition is true then the *deltoideus* of this animal is more primitive than that of the lizards. This muscle is a powerful abductor of the arm.

On reflecting the above muscles the second layer of muscles consisting of the *biceps*, the *coraco-brachialis* and the *supra-coracoideus*, is exposed.

The *biceps* (Fig.56) arises by two fleshy heads from the posterior border of the coracoid and proceeds in two bellies one being larger and longer than the other. The larger, the *biceps superficialis* (Fig.56), arises from the posterior margin of the coracoid at its free end, while the smaller one, the *biceps profundus* (Fig.56), arises from the proximal part of the same border of the coracoid. The two bellies run laterally and gain separate insertions. The *biceps* *profundus* becomes thin chord-like and tendinous and gets inserted along with that of *brachialis* on the proximal part of the radius and ulna, where both are closely apposed to one another. The common insertion of the *biceps profundus* and the *brachialis* is the only indication that the posterior part of the *brachialis* was united with the *biceps profundus* during development (Romer, 1947). The *biceps superficialis* shows a slight tendinous constriction on its fleshy belly and finally becomes tendinous as it proceeds outwards. The tendon is partly ensheathed along with the tendon of the *biceps profundus* in a common tendinous covering. The *biceps superficialis* gets inserted on the distal half of the radius and also on the radiale. In Crysemys the *biceps superficialis* consists of two fleshy parts separated by a conspicuous tendinous part but there is no such prominent separation of the two in Lissemys but as already stated only a thin tendinous intersection is present. In Uromastix, however, both the heads of *biceps* have a common insertion on the upper end of the radius (George, 1948). The *biceps* in Lissemys acts as the flexor of the forearm and the adductor of the arm and to a very limited extent the manus also.

The *supracoracoideus* (Fig. 56) (the *subcoracoideus* of Owen) arises from the entire ventral surface of the coracoid and also the posterior border of the precoracoid. The fibres of these two separate heads decussate and finally run outwards and get inserted on the lesser tuberosity of the humerus. The muscle occupies the major part of the fenestra bounded by the precoracoid, coracoid and the acromio-coracoid or precoraco-coracoid ligament. It is an adductor of the arm.

The *coraco-brachialis brevis* (Figs. 56,57) is a small muscle, just under cover of the *supracoracoideus*, in front of the *biceps profundus*. It runs along with the *biceps profundus* in early stages of development but later gets separated. It arises from the posterior border of the coracoid at its proximal end just in front of the origin of the *biceps profundus*, runs outwards and gets inserted on the hollow between the two tuberosities at the proximal end of the humerus. Owen has named this muscle as *teres minor*. It acts as an adductor of the arm.

The dorsal group of muscles that have attachments to the shoulder girdle consists of the *latissimus dorsi*, the *teres major*, the *subscapularis* and the *coracobrachialis magnus* .

The *coracobrachialis magnus* (Fig. 57)(*subcoracoideus* of Owen, 1866, Noble and Noble, 1940) arises from the entire dorsal surface of the coracoid and also some part of the dorsal surface of the acromio-coracoid ligament. It runs outwards and gets inserted on the greater tuberosity of the humerus. It acts as an adductor of the arm and to some extent a lateral rotator of the upper arm. In lizards, too, this muscle is the most prominent muscle on the dorsal side in the coracoid region. In crocodile, however, it is absent (Romer,1944).

The *latissimus dorsi*(Figs.56,57) has a fleshy origin on the carapace at the first costal plate near the vertebral column. After taking a broad origin, the muscle runs outwards and downwards and narrows down into a flat, short tendon which gains insertion on the outer side on the neck of the humerus. This muscle in other reptiles like lizards and crocodiles is flat and fan-shaped arising from the spines of the first few thoracic vertebrae or the fascia covering this region. It acts as a retractor and an adductor of the upper arm.

The *teres major* (Figs.56,57) which is an adductor of the upper arm and forms a large muscle mass on the antero-dorsal side of the scapula arises from the anterior border and the medial surface of the proximal end of the scapula and the suprascapula. It runs laterally towards the humerus and finally gains insertion on the dorsal side of the neck of the humerus. This muscle runs side by side with the *latissimus dorsi* during development and later as the adult stage is reached, gets separated at the point of its origin but still shows a somewhat common insertion, on the neck of the humerus. In Uromastix, (George, 1948) and other lizards the muscle is absent which denotes that it is a special acquisition in the Chelonia among the reptiles and must have remained as a part of the *latissimus dorsi* in the reptiles. In turtles this separation of the *teres major* from the *latissimus dorsi* has been necessitated by the modifications in the skeleton and the limb movements. A separate *teres major* is also present in the birds and mammals and must have made its appearance as a result of the increased scope of the limb movements.

The *subscapularis* (Figs. 56,57) is the most massive muscle on the postero-lateral side of the scapula. It arises from the antero-dorsal and the dorso-posterior border of the suprascapula and also from the entire dorsal and postero-ventral border of the scapula. All the fibres from these different parts run laterally and converge near the dorsal rim of the glenoid cavity, where the muscle becomes tendinous and gets inserted by the side of the insertion of the coracobrachialis magnus, on the outer tuberosity of the proximal end of the humerus. It acts as an adductor and to some extent as a lateral rotator of the arm.

The subclavius (Figs 56,57) arises from the undersurface of the first costal plate and gets inserted on the suprascapula and the adjoing part of the scapula by a thick tendon. It keeps the girdle in position.

The serratus magnus (Figs 56,57) is a flat sheet of of muscle on the dorsal side of the shoulder girdle. It has a long linear origin from the antero-lateral border of the carapace where the carapace gets attached to the plastron. The posterior half of the muscle runs medially and finally gains a fleshy insertion on the entire anterodorsal border of the coracoid, while the anterior half of the muscle gets inserted on the postero-ventral border of the scapula. The muscle acts as a depressor and the lateral rotator of the shoulder therby bringing about a slight abduction of the arm.

The acromio-brachialis (~~Figs.~~) arises from the entire antero-dorsal border of the precoracoid (acromion process of scapula) and gets inserted on the dorsal side of the neck of the humerus and also on the lesser tuberosity of the same bone. Its action is similar to that of the deltoideus but is a less powerful abductor of the arm. The homology of this muscle is doubtful but it could be regarded as the acromial part of the deltoideus.

The triceps (Figs.56,57) muscle completely covers the dorsal side of the humerus. It arises by three separate heads, the dorsal one from the antero-dorsal part of the rim of the glenoid cavity, the second head which is just under cover of the first arises from most of the dorsal surface of the humerus, while the third from most of the ventro-medial surface of the humerus. The first two heads unite together and form a thin flat tendon which gets inserted on the outer surface of the olecranon process of the ulna, while the third one gains its insertion separately by a narrow tendon on the outer condyle of the proximal end of the ulna. The first two heads of the triceps act as an extensor, while the third as the flexor of the forearm.

The brachialis inferior (Figs.56,57) is a fan-shaped muscle having a broad origin and arising from the proximal half of the humerus at the deltoid ridge. The fibres converge to form a thick tendon which finally is inserted on the ulna. The insertion of this muscle is along side with that of the smaller of the two bellies of the biceps, the biceps profundus. The brachialis acts as a flexor and a lateral rotator of the forearm.

MUSCLES OF THE FOREARM AND HAND:

The dorsal muscles of the forearm in Lissemys present an interesting arrangement distinct from the general pattern and disposition of muscles found in other reptilian groups. These changes in the arrangement of the muscles is essentially due to the shifting of the ulna to the dorsal side of the radius. The extensor muscles occur in two layers with the *external radialis longus*; the *external radialis brevis* (*extensor -carpi-radialis brevis*)); the *extensor digitorum communis*; the *external ulnaris* and the *supinator* forming the upper layer and the *extensor digitorum profundus* forming the deeper layer.

The *external radialis longus* (Fig. 58) is a composite muscle formed of the *brachio-radialis*, the *extensor pollicis*, and the *extensor indicis*; all having a common place of origin namely the inner condyle of the humerus at its distal end. More or less at the level of the proximal carpals the muscle is differtiated into three slips. The medial one called the *extensor indicis*, runs towards the lateral side of the index finger and gets inserted on the base of its proximal phalanx along with the slip of the *extensor digitorum communis* to this digit. The middle slip which is the *extensor pollicis* runs on the dorsal side of the thumb and gains a fleshy insertion on the dorsal side of the proximal end of the proximal phalanx of the thumb. The third, the lateral one, which is the most massive of all the three, gets inserted on the inner side of the first phalanx of the thumb and forms the *brachio-radialis*. The *brachio-radialis* in mammals has the same source of nerve supply as the extensor groups of muscles and so it is probable that this muscle is actually derived from the dorsal group of muscles evidently as a result of the shifting of the ulna as already mentioned. Moreover it is not a completely separate muscle but has a common origin with the *extensor pollicis* which is a part of the extensor group of muscles.

The *external radialis brevis* (*extensor-carpi-radialis brevis*) (Fig.58) arises as a very thin tendinous strip from the lateral condyle of the distal end of the humerus and also from the entire outer surface of the radius. It runs towards the thumb and gets inserted on the radiale. It acts as an extensor and a lateral rotator of the first digit.

The *extensor digitorum communis* (Fig.58)arises from the dorso-lateral side of the outer condyle of the humerus at its distal end and also carries fibres arising from the outer side of the shaft of the ulna. Such an origin from the ulna also is rather unusual but has taken place due to the shifting of the ulna dorsalward. As the muscle approaches the manus and comes to the level of the distal end of the ulna it presents a tendinous intersection, from where the muscle proceeds in four fleshy slips each of which gets inserted on the outer side of the second to the fifth metacarpals respectively, and the base of the respective proximal phalanges. The first digit which has an extensor of its own does not receive a slip from this muscle. The insertion of these muscle slips on the lateral side of metacarpals and the base of the phalanges is a specialization for a powerful outward beat of the hand in swimming. It acts as a powerful extensor and a lateral flexor of the manus.

The <u>external</u> <u>ulnaris</u> (Fig. 54) is a well-developed muscle situated on the outer side of the forearm. It consists of two component muscles, which are separate only towards the insertion, an extensor part dorsally and a flexor part ventrally. This common muscle mass arises from the outer condyle of the distal end of the humerus and remains as a single belly upto the distal end of the ulna where it bifurcates. The dorsal of the two gets inserted on the distal end of the ulna and the dorso-lateral side of the ulnare, while the other runs on the ventral side of ulna and gets inserted on the ventral side of the distal end of the ulna and the ventro-lateral side of the ulnare. Such a split composition of the muscle is a specialization for the paddling movement of the forearm in swimming.

The supinator (Fig. 58) which is a powerful muscle does not act as the supinator of the other vertebrates but as a powerful extensor of the forearm. It arises from the dorsal surface of the humerus at its distal end and also from the outer surface of the proximal end of the ulna and gains a tendinous insertion on the fused intermedium and centrale on the palmar side. In the natural course of events the insertion of this muscle should have been on the radius but owing to the ulna having been shifted to a position dorsal to the radius, it has a acquired the present insertion.

The extensor digitorum profundus (Fig. 58) arises from the fused intermedium and centrale. It divides itself into four muscular slips and each one runs forwards, towards the digits, where the first slip which is the longest goes to the thumb and gains insertion on the medial side of the proximal phalanx of the thumb. The second one is inserted on the dorsal side of the middle phalanx of the second digit. The third and the fourth are inserted on the dorsal side of the proximal end of the fourth phalanx of the third and fourth digits respectively. The last digit does not receive any muscular slip from the *extensor digitorum profundus*. The muscle acts as an extensor of the manus as a whole and also of the first four digits in particular through the respective digital slips. It must be mentioned, however, that owing to the insertion of the first slip on the medial side and then on the dorsal side of the proximal phalanx of the thumb, the muscle is more of an adductor of the thumb than an extensor.

On the flexor side of the forearm the superficial layer of muscles consits of the *flexor-carpi-ulnaris*, *flexor-carpi-radialis* and the *palmaris longus*; while in the hand the *flexor digitorum brevis* forms the most superficial muscle.

The *flexor-carpi-radialis* (Fig.57) arises from the inner condyle of the distal end of the humerus. It has a broad origin with the fibres later converging towards the distal end of the radius to be inserted on the distal end of the radius and the radiale.

The *pronator teres* (Fig. 57) is a very well-developed muscle which as the name indicates acts as a pronator of the forearm. It arises by a fleshy origin from the inner condyle of the humerus at its distal end and gets inserted on the distal end of the radius by a thin tendon.

At the distal end of the radius on the flexor side there is a thin tendinous transverse plate the flexor retinaculum covering the distal ends of the *flexor-carpi-radialis*, *pronator teres* and *flexor-carpi-ulnaris*.

The *flexor digitorum brevis* (*flexor brevis superficialis* , Haines, 1950) (Fig.57) arises from the flexor retinaculum and the palmar aponeurosis and soon differntiates itself into four short fleshy slips which go, one each to the second to the fifth digits respectively. The slips corresponding to the second, third and fourth digits are further differentiated into a pair of thin tendinous parts which run on the either side along their respective digits to be inserted on the proximal end of the last but one phalanx. The small thin slip of the fifth digit, however, does not show any such differentiation and its thin tendon gets fused with the main flexor tendon.

The *flexor pollicis brevis* (Fig. 57) arises from the fexor retinaculum and gets inserted on the proximal end of the proximal phalanx of the first digit.

The *abductor pollicis brevis* (Fig. 57) is a small muscle arising from the radiale and gets inserted on the outer lateral border of the first metacarpal and the proximal end of the proximal phalanx of the first digit.

The *abductor digiti minimi* (Fig. 57) arises partly from the outer side of the fascia on the distal end of the *external ulnaris* (the composite muscle formed by *extensor-carpi-ulnaris* and *flexor-carpi-ulnaris*) and partly from the flexor retinaculum. Its fibres then converge and finally get drawn out into a thin long tendon which gets inserted on the outer side of the terminal phalanx of the last digit. It acts as an abductor of the last digit.

The *abductor pollicis brevis*, the *flexor pollicis brevis* and *abductor digiti minimi* belong to the *flexor brevis superficialis* group of muscles (*flexor digitorum brevis*) Haines, 1950.

The deep layer of the flexor muscles consists of the *flexor digitorum longus*, *pronator quadratus* and *pronator profundus*.

The *flexor digitorum longus* (Fig. 57) in Lissemys consists of two heads, unlike in Varanus where it consists of five heads (Haines, 1950) of which the three arising from the humerus, are the , *condylo-radialis*, *condylo-ulnaris*, *centralis* and the other two of which one arises from the shaft of the ulna and the other from the carpal, the ulnare. The one arising from the shaft of the ulna, in Varanus, forms a broad and thick flexor plate to shich the three parts arising from the humerus are attached. In Lissemys, one of the two heads of the muscle arises from the ventral side of the shaft of the ulna and the other arises from the ventral side of the shaft of the radius. The fibres of both the heads decussate and finally run towards the carpus where at the level of the distal ends of the radius and ulna and the carpals these fibres form a well-developed tendinous plate, the flexor plate, which later divides into four thick tendons each of which runs towards its corresponding digit (the first four digits). After traversing through the ligamentous tunnel at the joints of the phalanges each one gets inserted on the proximal end of the terminal phalanx of its respective digit. This muscle is one of the most powerful flexors of the digits. The presence of only a couple of heads for the *flexor digitorum longus* in Lissemys appears to be a degenerate condition, as the animal having considerably lost the prehensile ability of the hand. These muscle heads may therefore be regarded as corresponding to the deep, massive muscle referred to by Haines (1950) as arising from the shaft of the ulna in Varanus.

The *pronator profundus* (Fig.57) is a very powerful pronator of the forearm and manus which arises as a broad massive muscle belly from the proximal end of the ulna and runs obliquely downwards narrowing down to be inserted on the adjacent surface of the distal half of the radius, the palmar surface of the carpals and by a thin tendon which goes further to get inserted on the proximal phalanx of the first digit.

The *pronator quadratus* (Fig.57) is a small pronator muscle situated just under cover of the *pronator profundus*, It arises from the lower half of the medial surface of the ulna and is inserted on the carpal and the distal end of the radius.

The *contrahentes* (Fig. 57) belonging to the first and the last digit arise from the ulnare and the radiale respectively, while those of the second, third and fourth digits arise from the dorsal surface of the flexor plate. All of them proceed towards their respective digits and finally get inserted on proximal end of the second phalanx of their respective digits. These muscles are quite powerful and act as the flexors of the digits.

The *lumbricals* (Fig58,57) arise from the carpals and proceed in four pairs towards the second, third, fourth and fifth digits. The couple on reaching the digit separate and run forwards independently along the sides of the respective digits and gain their insertions on the base of the subterminal phalanx. There is only one *lumbrical* on the medial side of the fifth digit. It is interesting to note that some fibres of the *lumbricals* get inserted on the web also thereby rendering the webbed manus a more efficient organ for swimming.

On the lateral side of the second phalanx of the second, third, fourth and fifth digits the interossei muscles occur as small muscle bundles which arise from the second phalanx and get inserted on the proximal end of the next adjacent phalanx.

MUSCLES OF THE HINDLIMB

The *attrahens pelvium* and the *retrahens pelvium* (Owen, 1866) (Fig. 6°). On removing the plastron these muscles are the first ones to be encountered. They arise from the xiphiplastron and get inserted on the pubic spine and on the ventral side of the distal end of the pubis. The former acts as a medial rotator of the pelvis while the latter acting alternately with the former acts as a lateral rotator of the pelvis. The homology of these two muscles is doubtful. It is suspected that they correspond to the *rectus abdominis*.

The next layer of muscles is exposed when the above muscles are reflected. This layer consists of the following muscles, the *pubo-ischio-tibialis*, *semimembranosus* and *biceps femoris*.

The *pubo-ischio-tibialis* (Fig. 6') is the primitive muscle mass from which the mammalian *gracilis* is derived. The origin of this muscle is from the lateral process of the pubis by a thin, broad and membranous tendon. The tendinous strip of the muscle of either side cross and fuse with one another in the middle of the obturator foramen and then again separate and become fleshy and finally unites with the *semimembranosus* and *biceps femoris* of the same side. All these muscles together form into a single belly which later thins out into a membranous tendon and finally gets inserted on the lateral side of the proximal end of the tibia. It acts as an adductor and also medial flexor of the shank.

The *semimembranosus* (Fig.60) is a massive muscle which arises along the median line on the posterior part of the ischium. This fleshy belly joins the *pubo-ischio-tibialis* to gain a common insertion on the tibia, It is an adductor of the foot and shank.

The *biceps femoris* (Fig.60) arises by two heads, one smaller than the other. The former arises from the vertebrae at the proximal end of the base of the tail, and the latter from the posterior margin, at the junction of the median marginals and the carapace. These two bellies join to form a single massive muscle which finally joins with the *pubo-ischio-tibialis* and *semimembranosus* and have a common insertion on the lateral side of the tibia by a thin flat tendon. It acts as the adductor of the shank and foot.

The third layer of the muscles on the ventral side comprises of the following muscles, the pubo-ischio-femoralis externus, adductor longus, adductor femoris, sartorius and semitendinosus.

The pubo-ischio-femoralis externus (Fig. 60, 61) is a flat triangular muscle which arises from the pubic symphysis and from the ventral surface of the pubic bone. It runs posteriorly outwards and finally gets inserted on the inner trochanter of the femur by a thick tendon. This muscle brings about abduction and medial rotation of the thigh.

The adductor longus (Fig. 66) is a peculiar muscle because its origin is not on the bony part or anywhere else. The bellies of the either side have their median end joined with one another along the mid-ventral line at the level of the ischial symphysis forming the muscle mass which runs from one femur to the other. The bony origin must have been lost as the pubis having moved anteriorly and the ischium posteriorly. The insertion of the muscle is on the inner trochanter along with the pubo-ischio-femoralis externus. As its name suggests the muscle acts as an adductor and a median flexor of the thigh.

The adductor femoris (Fig. 66) is the primitive reptilian muscle which gave rise to the adductor magnus and adductor brevis of the mammals. Here it is found as a single muscle mass, arising from the ischial symphysis on the ventral side of the girdle and runs laterally outwards and finally gets inserted on the inner trochanter along with the pubo-ischio-femoralis externus and the adductor longus. It acts as an adductor of the thigh.

The sartorius (Fig. 60) arises by a thin narrow tendinous strip from the middle of the lateral border of the pubis and runs downwards and outwards towards the leg. During its course it becomes fleshy and finally gains its inertion on the proximal end of the tibia by a flat tendon. This muscle acts as the lateral rotator and to some extent as the extensor also of the thigh.

The semitendinosus (Figs. 60,61) is a large, massive muscle arising from the dorsal surface of the ischial symphysis and runs laterally outwards and gains its intertion on the lateral side of the proximal end of the fibula by a tough tendon, while a thin membranous tendon which separates out from the point of insertion gets inserted on the medial border of the distal end of the femur. The muscle acts as an adductor of the shank.

The following muscles are found on the dorsal side of the pelvic girdle , the *ambiens*, *pubo-ischio-femoralis internus* and *pubo-ischio-femoralis posterior* in the ischio-pubic region while in the region of the ilium the *ilio-femoralis*, *ilio-tibialis*, *ilio-fibularis* and *caudo-tibialis* muscles are present.

The *ambiens* (Figs. 60, 61) is a very long flat muscle which arises from the anterior half of the ischial symphysis on its dorsal side and runs laterally outwards, covering the dorsal side of the thigh, and gets inserted on the proximal end of the tibia by a broad tendon. It acts as an extensor and to a certain extent a lateral rotator and abductor of the shank.

The *ilio-femoralis* (Figs. 60, 61) is formed of four bellies. One is the femoro-coccygeal part which has a wide origin from the lateral side of the centra on the proximal part of the tail and the distal sacral vertebra, is the largest belly and runs over the ilium and then narrows down to be inserted on the outer trochanter of the femur and also on the neck of the femur. The second belly arises from the dorsal side of the middle part of the ilium; runs upwards and gets inserted on the outer trochanter of the femur along with the first. The third part is very small and arises just anterior to the second one on the dorsal side of the proximal end of the ilium. It runs over the neck of the femur and is inerted on the dorsal side of the inner trochanter of the femur. Lastly the fourth one which arises from the last costal plate of the carapace, near the sacral region by the side of the vertebral column, runs laterally upwards and outwards to get inserted on the dorsal side of the outer trochanter. This group of muscle is homologous to the gluteus group of muscles and the tensor fascia lata of the mammals. The action of this muscle group is medial rotation and adduction of the thigh.

The ilio-fibularis (Fig. 60,61) corresponds to the mammalian tenuissimus muscle. It arises from the distal end of the ilium and runs laterally outwards to get~~s~~ inserted on the medial spinous projection of the fibula. This muscle brings about the adduction of the shank.

The ilio-tibialis (Fig. 60,61) which corresponds to the rectus femoris of mammals arises in this animal from the dorsal side of the distal end of the ilium by a very narrow fleshy belly, but as it runs outwards towards the tibia it widens out and later becomes membranous and by a thin tendon gets inserted on the proximal half of the lateral border of the tibia. This is however not a direct insertion on the tibia but on the fascia of the muscles on the tibia. It acts as an adductor of the shank.

The pubo-ischio-femoralis-internus anterior (Fig. 61) arises from the ventral surface of the pubic spine and also from the most of the surface of the pubic bone on the same side. It runs obliquely backwards and outwards and finally gets inserted on the outer trochanter of the femur. There is a posterior part of this muscle which is having its origin from the ventral surface of the pubic spine and gets inserted on the outer trochanter of the femur. This part is the pubo-ischio-femoralis-internus posterior (Fig. 61) Both these muscles act as the abductor of the thigh.

The caudo-tibialis (Fig. 61)is a long muscle which arises by a very narrow origin from the lateral side of the centra of the proximal caudal vertebrae. It runs laterally outwards, widens out into a flat belly and by a thin membranous aponeurosis gets inserted on the muscles on the lateral side of the distal half of the tibia. This muscle acts as an adductor and partly as a medial rotator of the shank.

The femoro-tibialis (Figs 60,61) is a massive muscle lying on the dorsal side of the thigh. It arises from the anterior surface of the ligament which connects the head of femur to the acetabulum and also from the base of the greater trochanter and the medial and lateral surface of the femur anteriorly. The fibres from the medial and the lateral surfaces decussate with each other, giving a pectinate appearance to the muscle. The muscle then becomes tendinous at the level of the distal end of the femur and gets inserted on the proximal end of the tibia. It is an extensor of the shank.

The gastrocnemius (Fig. 63) which is a powerful calf muscle arises by two heads. One arises from the dorso-lateral condyle and the other from the medial condyle of the femur. The former consists of a larger belly than the latter. The two heads remain separate, and their fibres get inserted on the broad aponeurosis which is developed on the anterior surface. The aponeurosis of both the heads unite together and finally gets inserted on the lateral and the dorsal side of the intermedium. It is a powerful flexor of the foot.

The next layer consists of the following muscles, the plantaris, soleus and adductor hallucis.

The soleus (Fig. 6)) is a very well-developed muscle which arises from the lateral condyle of the femur and joins with the tendinous sheath of the plantar aponeurosis, which is partially inserted on the tarsals. This muscle is also a powerful flexor of the foot.

The plantaris (Fig. 6) which in the mammals is not well-developed but is found as a very thin strip in Lissemys consists of two well-developed bellies. Both the bellies have a common origin from the posterior side of the proximal end and also the entire lateral surface of the tibia. They run towards the foot and unite to form a single tendinous membrane which on reaching the foot splits up into two parts a thin a broad one. The thin part gets inserted on the metatarsal of the second digit while the other forms a tendinous sheath over the other muscles in the foot and is known as the plantar aponeurosis. It is a flexor of the foot.

The abductor hallucis (Fig.63) is a very powerful muscle arising from the medial side of the proximal end of the tibia and a few fibres also arise from the ligament which joins the tibia with the femur. This muscle runs on the medial side of the tibia and gains its insertion on the first phalanx of the first digit by a tendon. A long thin strip from this tendon also runs forward and gets inserted on the base of the terminal phalanx of the same digit. The muscle acts as a powerful abductor of the first digit.

The peroneus (Fig.63) consists of a single muscle~~s~~ mass which arises from the proximal end and also the entire lateral border of the fibula and is inserted by a thin tendon on the fibulare. It is also one of the flexors of the foot.

The tibialis posticus (Fig. 62) which is the deepest flexor muscle on the shank is a thin flat muscle which has its origin by two heads. One head arises from the posterior surface of the tibia and the other from the adjacent surface of the fibula. Fibres of both decussate and by a common tendon it gets inserted on the intermedium. It acts as the flexor of the foot.

The popliteus (Fig. 62) is a small triangular muscle arising from the lateral side of the proximal end of the tibia by a very narrow strip. It runs transversely towards the fibula and gains its insertion by a broad tendon on the medial border of the proximal end of the fibulare.

The flexor digitorum longus (Fig. 63) arises from the plantar aponeurosis. It spreads over the metatarsals and gives out tendinous strips one to each digit except the last one. These tendinous strips are inserted on the proximal end of the last phalanx of each digit. The muscle acts as a powerful flexor of the first four digits.

The flexor digitorum brevis (Fig. 63) arises from the tarsals and then splits up into four bellies and each one of them runs towards the digits where they get inserted on the distal end of the respective metatarsals. The last digit does not receive any part of this muscle. The muscle acts as a flexor of the digits.

The *flexor digiti quinti* (Fig.63)arises from the fibulare and gains a fleshy insertion on the proximal end of the first phalanx of the last digit. It acts as a flexor of the last digit.

The muscles of the dorsal side of the leg comprise of the *extensor digitorum communis*, the *extensor hallucis longus*, the *abductor digiti quinti* and the *tibialis anticus*.

The *extensor digitorum communis* (Fig.62) is a very prominent and well-developed muscle which arises by a narrow tendinous strip from the distal end of the femur. The tendinous part later becomes muscular and flattens out and running downwards divides into four small bellies. One has its insertion on the dorsal side of the proximal end of the terminal phalanx of the first digit. The second and the third are inserted on the lateral side of the second phalanx of the second and the third digits respectively. The last one which is inserted on the entire lateral side of the first phalanx of the fourth digit has also a thin tendinous part which runs on the dorsal side of the fourth digit and gets inserted on the third phalanx of the same digit. Owing to this type of insertion the *extensor digitorum communis* is more of an abductor of the hand in action than an extensor. This combined action is of great value in paddling through water.

The *tibialis anticus* (Fig. 61) arises from the anterior side of the proximal end of the tibia, the upper end of the fibula and from the outer side of the distal end of the femur. It runs obliquely downwards and divides into two parts. One gets inserted on the lateral side of the second phalanx of the fourth digit by a tendon while the other also by a tendon gets inserted on the dorsal side of the second phalanx of the fifth digit. The muscle acts as an extensor and slight abductor of the fourth and fifth digits.

The *extensor hallusis longus* (Fig. 61) has a common origin along with the *extensor digitorum communis*, but gets separated from the *extensor digitorum communis* and is inserted on the ventral and the lateral sides of the second phalanx of the first digit. This muscle is situated on the extreme outer side of the *extensor digitorum communis* and acts as the extensor and slight abductor of the first digit.

The *extensor hallucis brevis* (Fig.62) is a small thin muscular strip arising from the lateral side of the distal end of the fibula. It runs obliquely downwards and gets inserted on the inner side of the second phalanx of the first digit. This muscle besides acting as an extensor acts also as an adductor of the first digit.

The *extensor digitorum brevis* (Fig. 62) is a small muscle which arises from the metatarsals at the fibular end and also some fibres from the extreme distal end of the fibula. After its origin the muscle divides into four small strips each of which runs obliquely downwards and gets inserted on the proximal end of the third phalanx of each of the first four digits respectively. The muscle acts as an extenosor of the digits.

The *interossei posterior* (Fig.62) arises from the tarsals and also from the proximal end of the metatarsal corresponding to each digit on the dorsal side. Those of the first two digits get inserted on the terminal phalanx of the respective digit by thin tendons. Those of the third and the fourth digits get inserted by tendinous strips on the third phalanx of the respective digits, and of the fifth digit gets inserted on the proximal end of the first phalanx of the same digit.

The ventral interossei (Fig.63) arise from the tarsals and the medial side of the proximal end of the first phalanx of the second, third, fourth and fifth digits. The insertion of these muscles is on the lateral side of the second phalanx of the first, second, third and fourth digits. These muscles bring about the lateral bending of the digits.

There is one more set of the interossei muscles, the interossei anterior (Fig.62) which is present on either side of the second phalanx of the first, second, third and fourth digits. Each set consists of two muscles, an abductor and an adductor which arise from the medial and the lateral sides of the proximal end of the second phalanx of the first four digits respectively and gain their insertion on the same side on the proximal end of the third phalanx of the respective digits. These muscles act as the lateral abductors of the digits.

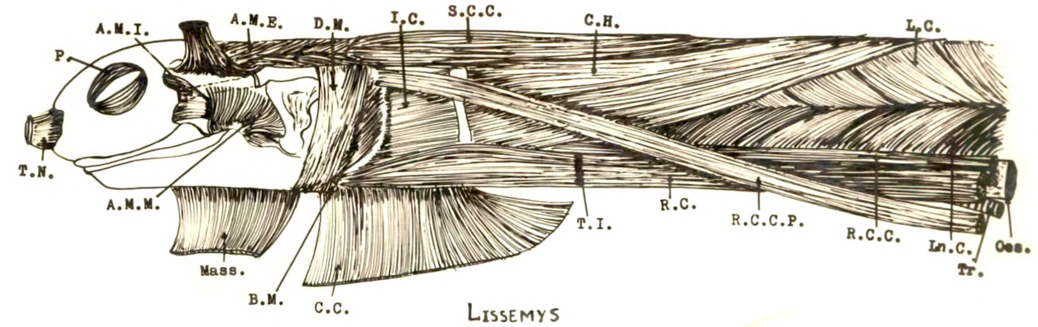

A.M.I.
A.M.E.
D.M.
I.C.
S.C.C.
C.H.
L.C.
P.
T.N.
A.M.M.
Mass.
B.M.
C.C.
T.I.
R.C.
R.C.C.P.
R.C.C.
Ln.C.
Tr.
Oes.
LISSEMYS

FIG. 39

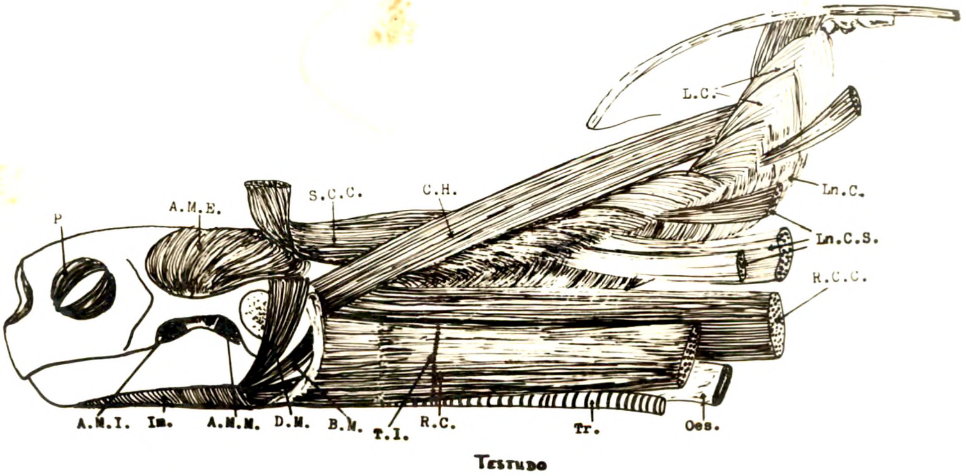

L.C.
P
A.M.E.
S.C.C.
C.H.
Ln.C.
Ln.C.S.
R.C.C.
A.M.I.
Im.
A.M.M.
D.M.
B.M.
T.I.
R.C.
Tr.
Oes.
TESTUDO

FIG. 40

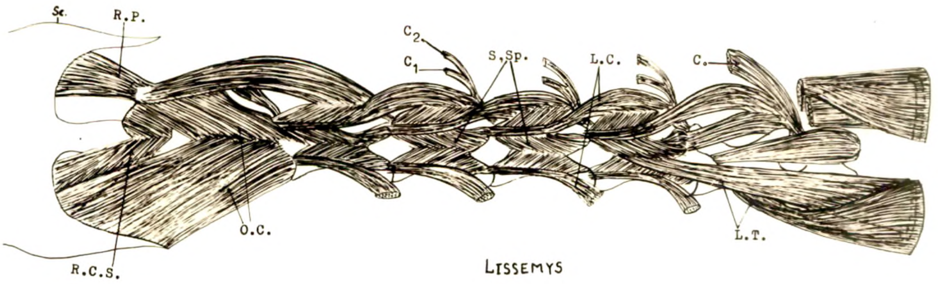

Sc.
R.P.
C2
C1
S.Sp.
L.C.
C.
O.C.
L.T.
R.C.S.
LISSEMYS

FIG. 41

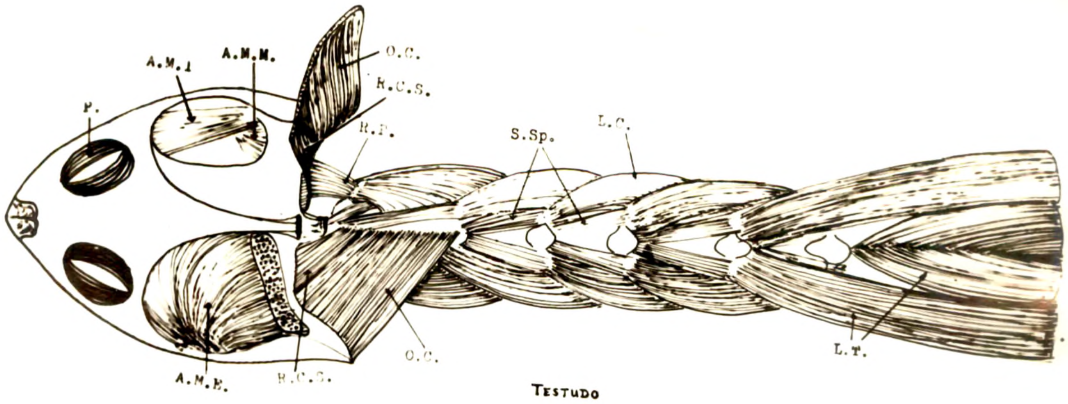

A.M.I
A.M.M.
O.C.
R.C.S.
P.
R.P.
S.Sp.
L.C.
A.M.E.
R.C.S.
O.C.
L.T.
TESTUDO

FIG. 42

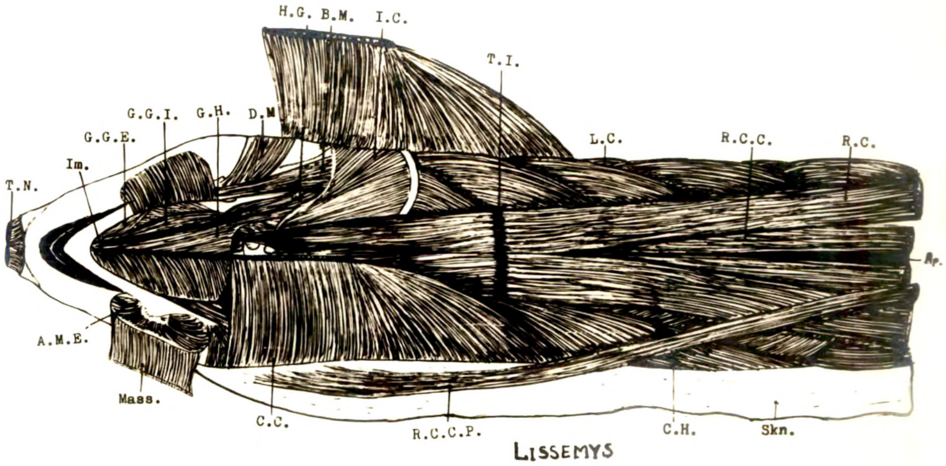

H.G.
B.M.
I.C.
T.I.
G.G.I.
G.H.
D.M.
G.G.E.
L.C.
R.C.C.
R.C.
Im.
T.N.
Ap.
A.M.E.
Mass.
C.C.
R.C.C.P.
C.H.
Skn.
LISSEMYS

FIG. 43

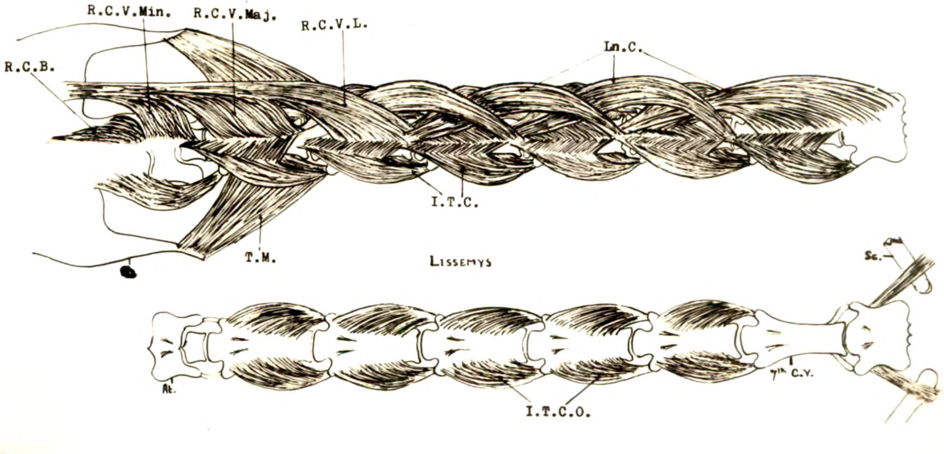

R.C.V.Min.
R.C.V.Maj.
R.C.V.L.
R.C.B.
Ln.C.
I.T.C.
T.M.
LISSEMYS
Sc.
At.
7th C.V.
I.T.C.O.

FIG. 44

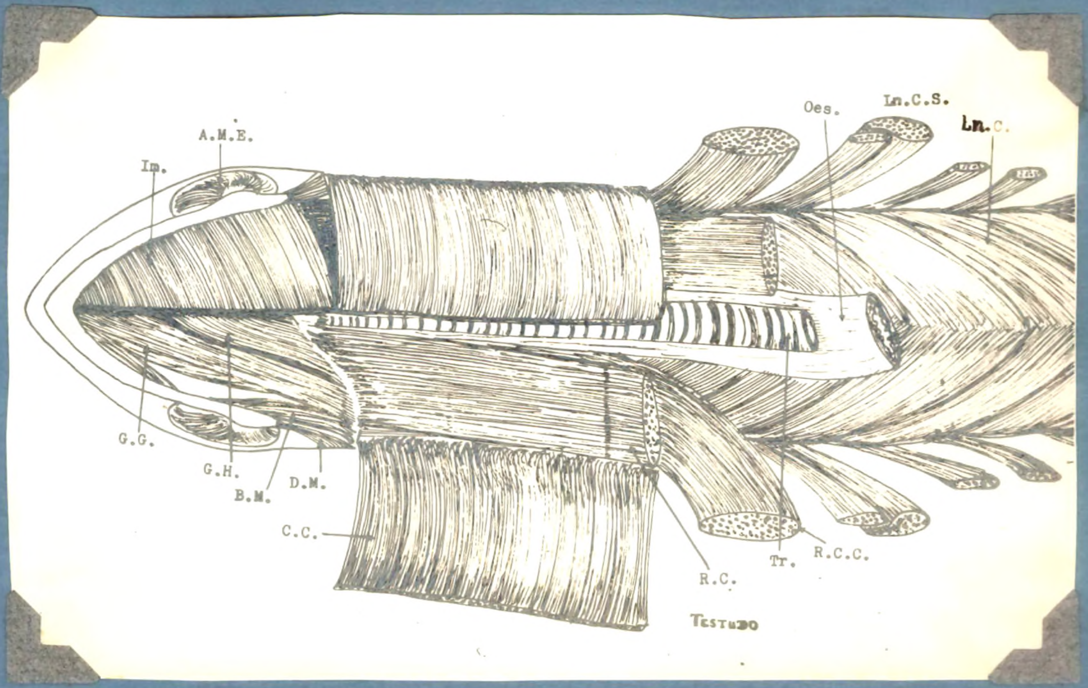

A.M.E.
Im.
Oes.
Ln.C.S.
Ln.C.
G.G.
G.H.
B.M.
D.M.
C.C.
R.C.
Tr.
R.C.C.
TESTUDO

FIG. 45

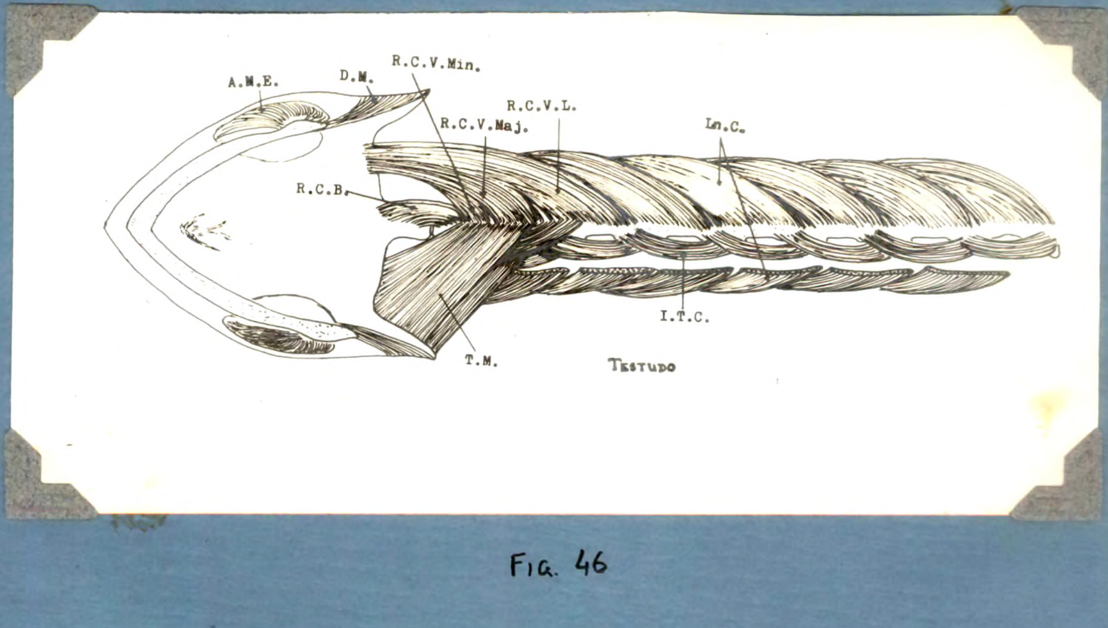

A.M.E.
D.M.
R.C.V.Min.
R.C.V.Maj.
R.C.V.L.
Ln.C.
R.C.B.
I.T.C.
T.M.
TESTUDO

FIG. 46

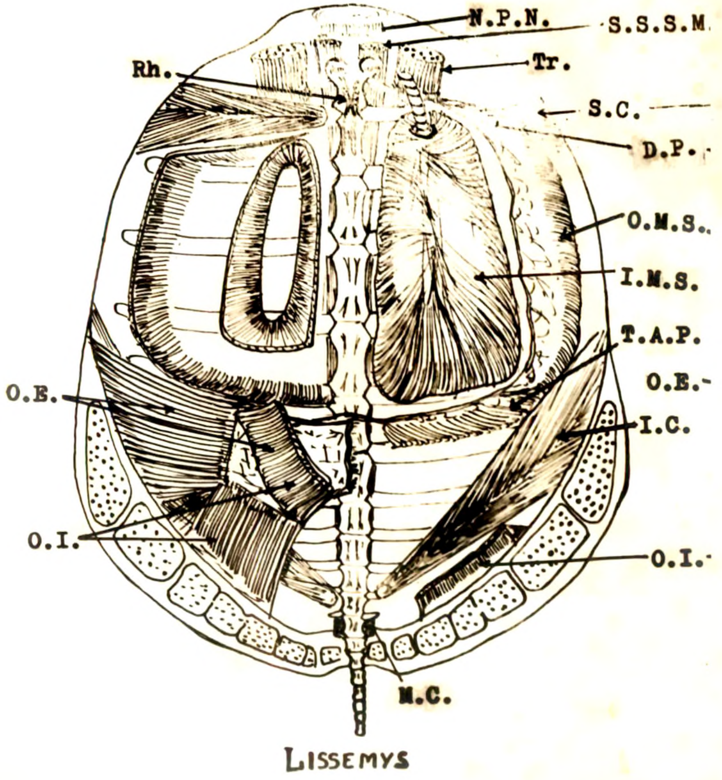

N.P.N.
S.S.S.M.
Rh.
Tr.
S.C.
D.P.
O.M.S.
I.M.S.
T.A.P.
O.E.
O.E.
I.C.
O.I.
O.I.
M.C.
LISSEMYS

Fig 47

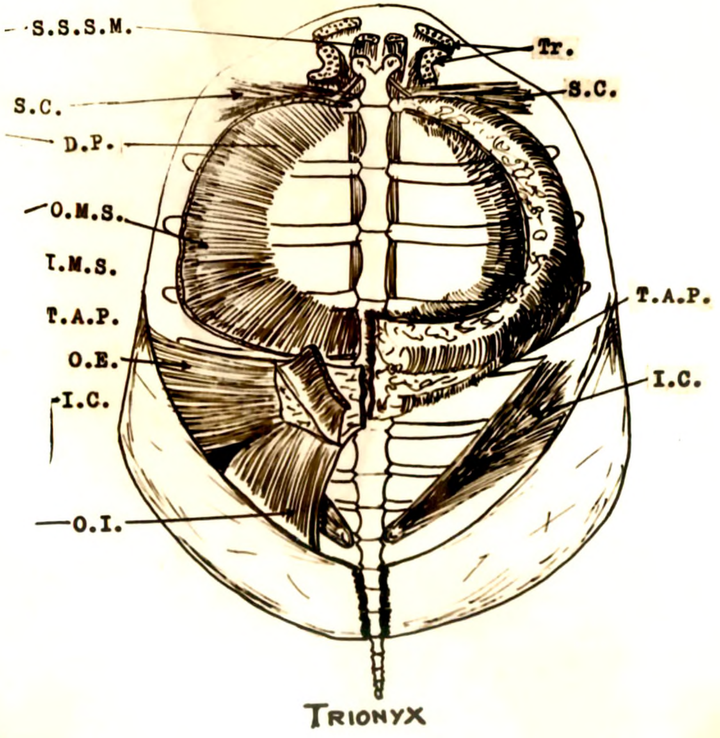
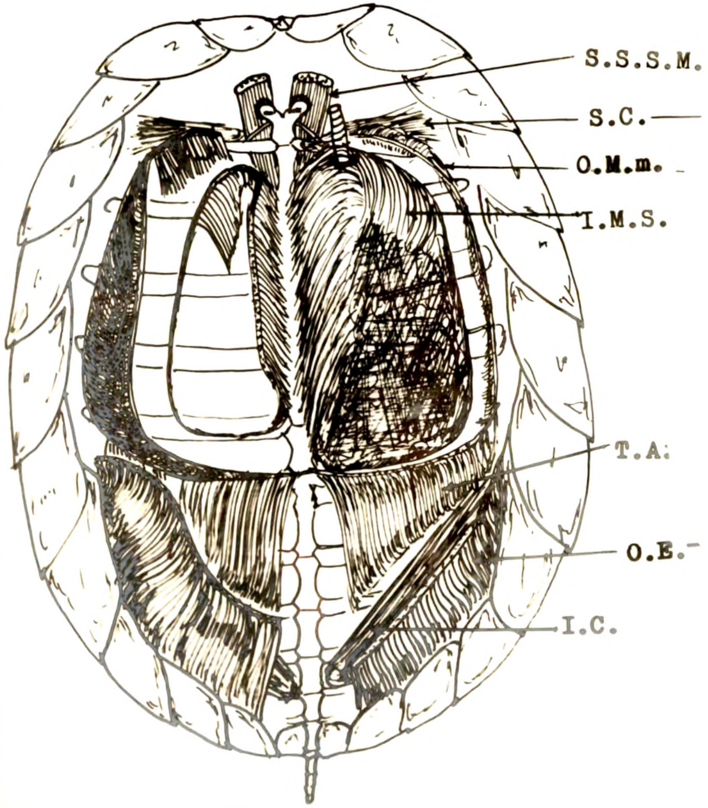
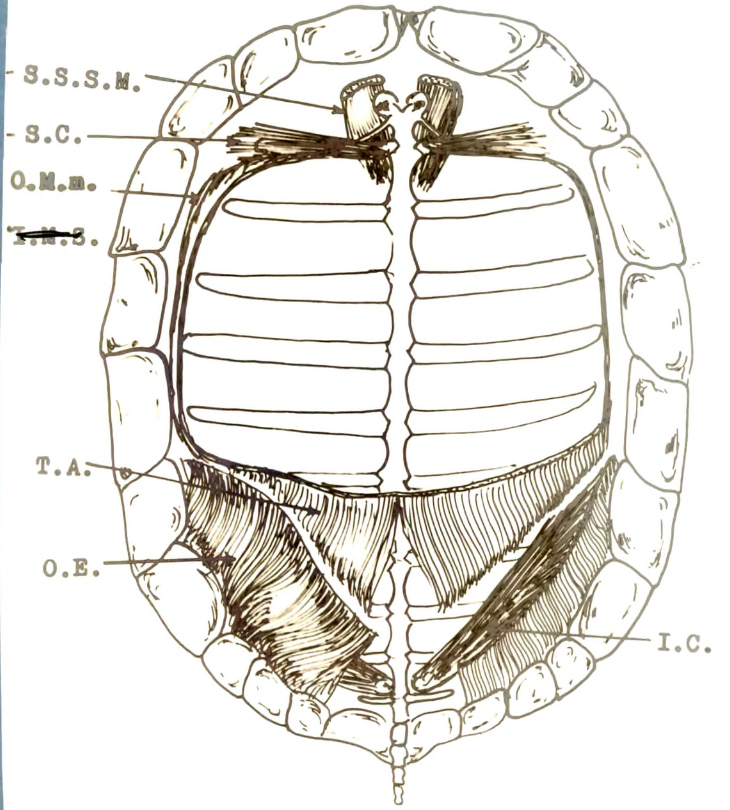

S.S.S.M.
Tr.
S.C.
S.C.
D.P.
O.M.S.
I.M.S.
T.A.P.
T.A.P.
O.E.
I.C.
I.C.
O.I.
TRIONYX

Fig. 48



GEOMYDA

FIG. 49



TESTUDO

FIG. 50

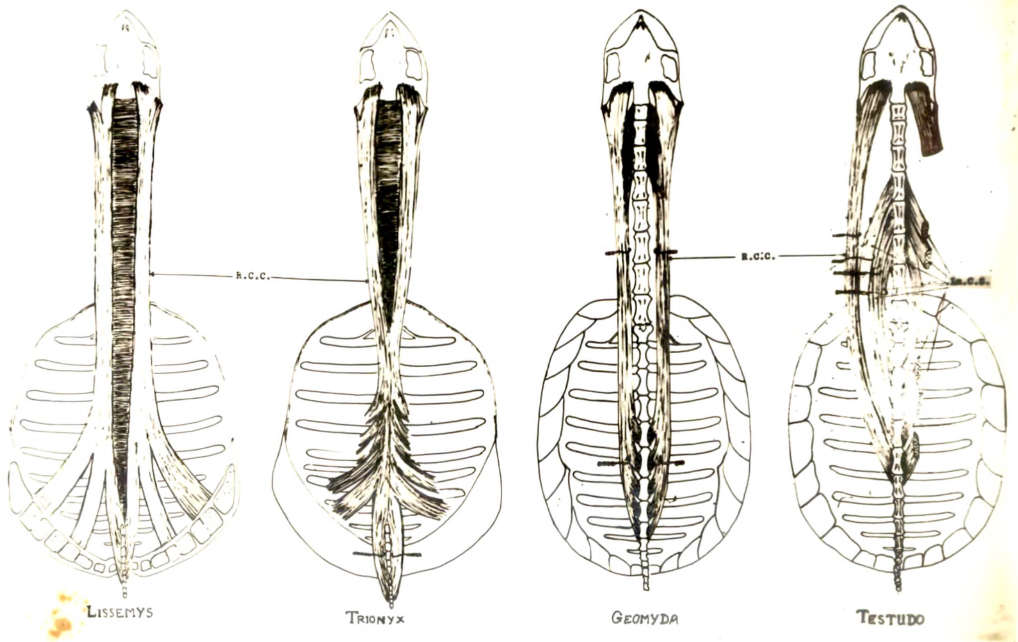
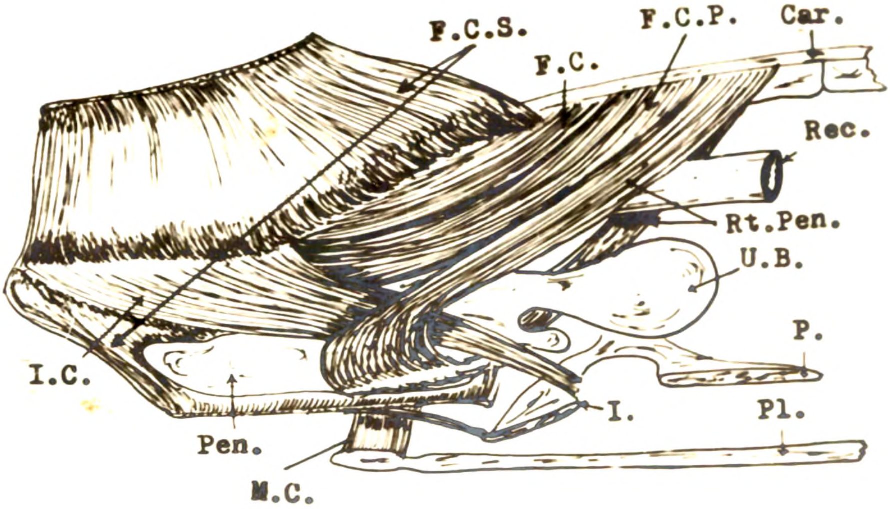
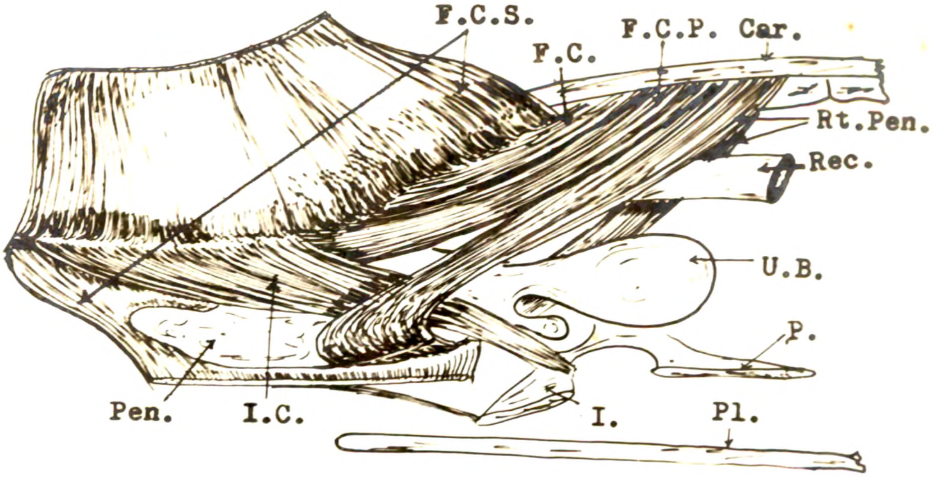


FIG. 51



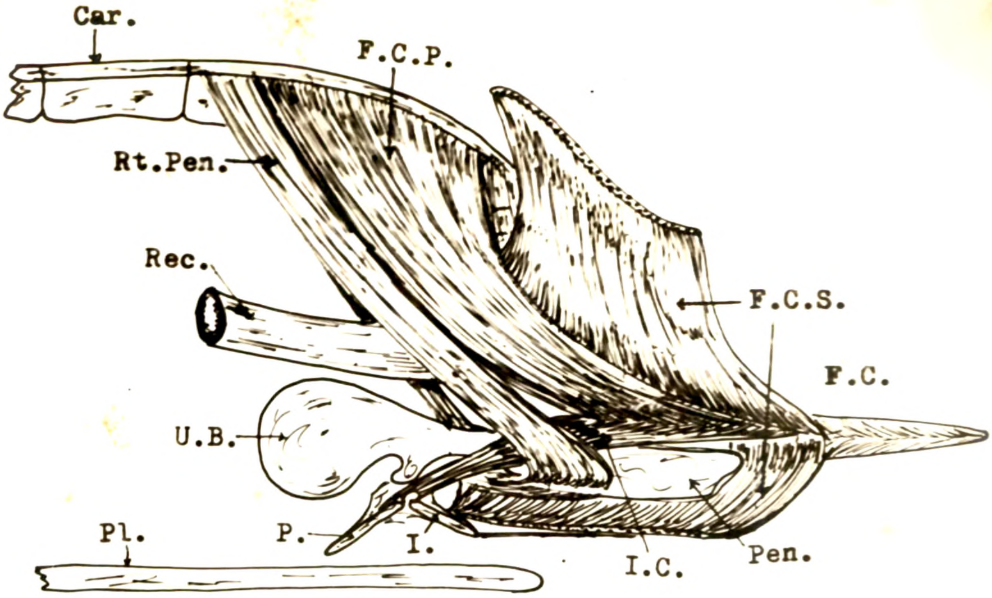
LISSEMYS

FIG. 52



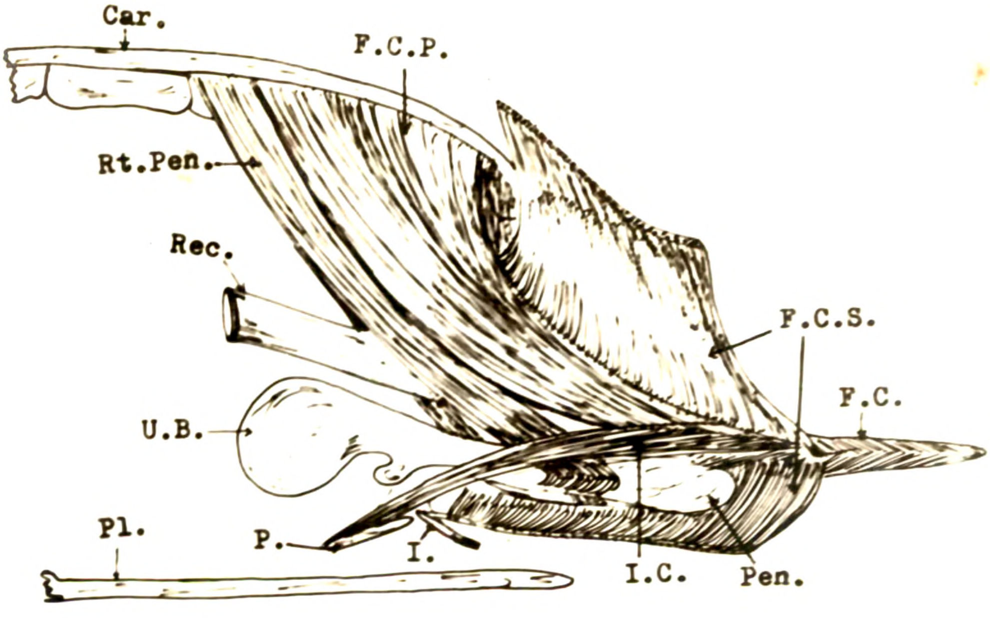
TRIONYX

FIG. 53



GEOMYDA

Fig. 54



TESTUDO

Fig. 55

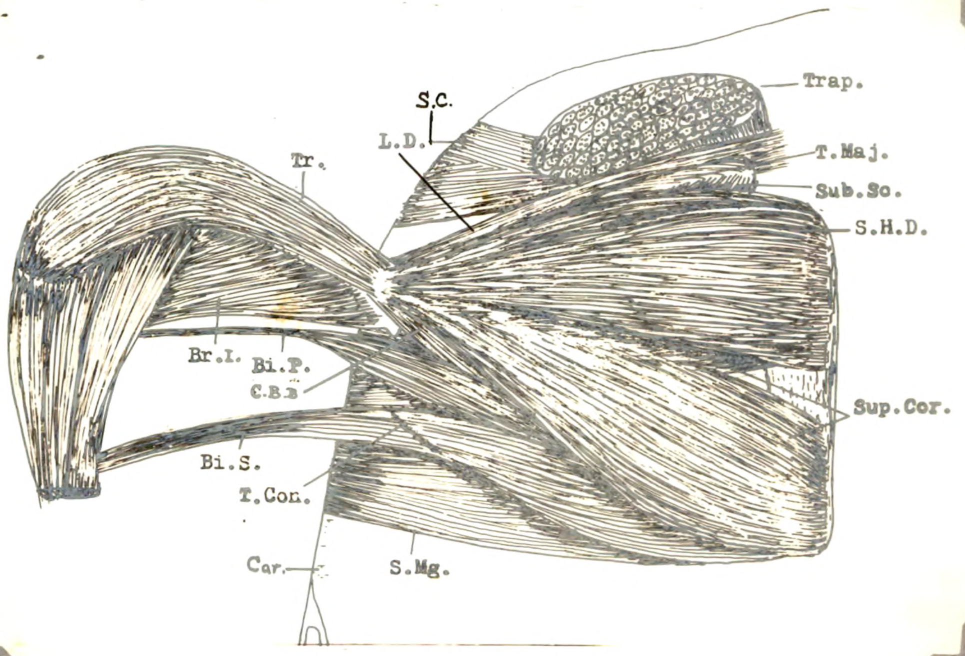

S.C.
Trap.
L.D.
T.Maj.
Tr.
Sub.Sc.
S.H.D.
Br.I.
Bi.P.
C.B.B
Sup.Cor.
Bi.S.
T.Con.
Car.
S.Mg.

Fig. 56

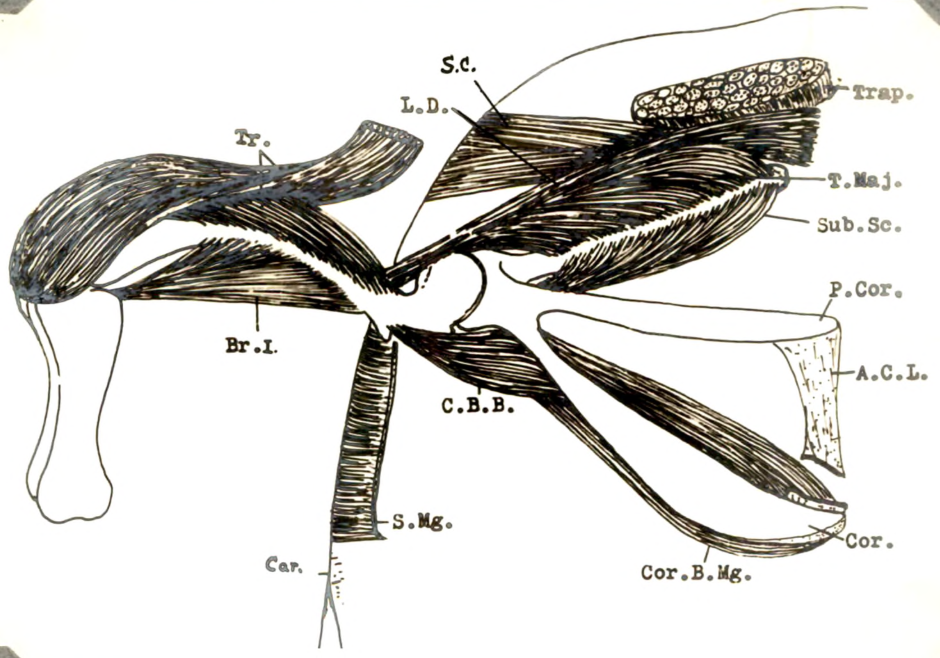

S.C.
Trap.
L.D.
Tr.
T.Maj.
Sub.Sc.
P.Cor.
Br.I.
A.C.L.
C.B.B.
S.Mg.
Cor.
Car.
Cor.B.Mg.

Fig. 57

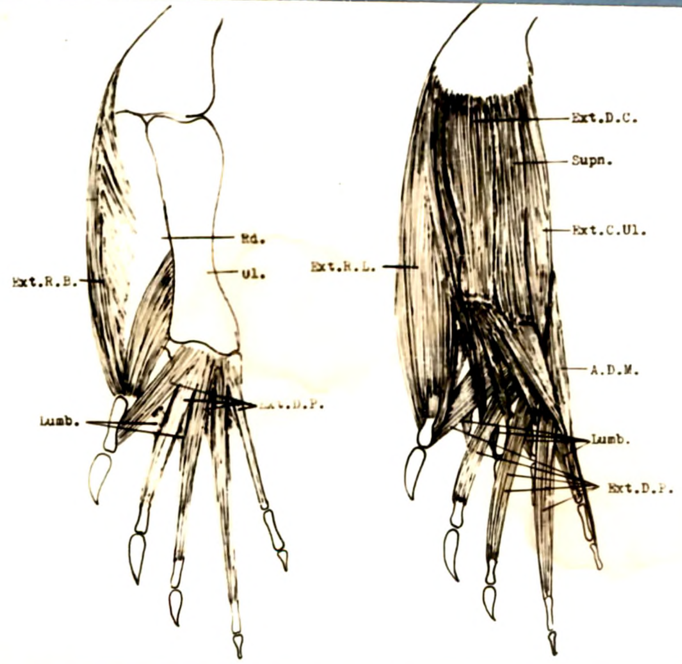

Rd.
Ul.
Ext.R.B.
Lumb.
Ext.D.P.
Ext.D.C.
Supn.
Ext.C.Ul.
Ext.R.L.
A.D.M.
Lumb.
Ext.D.P.

FIG. 58

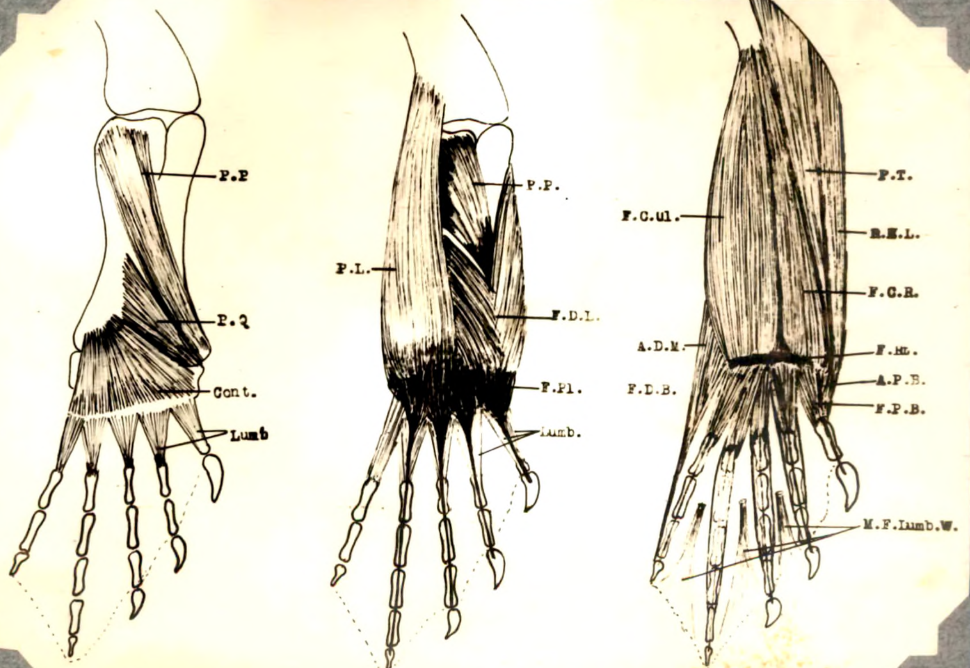

P.P
P.Q
Cont.
Lumb
P.P.
P.L.
F.D.L.
F.Pl.
Lumb.
P.T.
F.C.Ul.
R.E.L.
F.C.R.
A.D.M.
F.Rd.
F.D.B.
A.P.B.
F.P.B.
M.F.Lumb.W.

FIG. 59

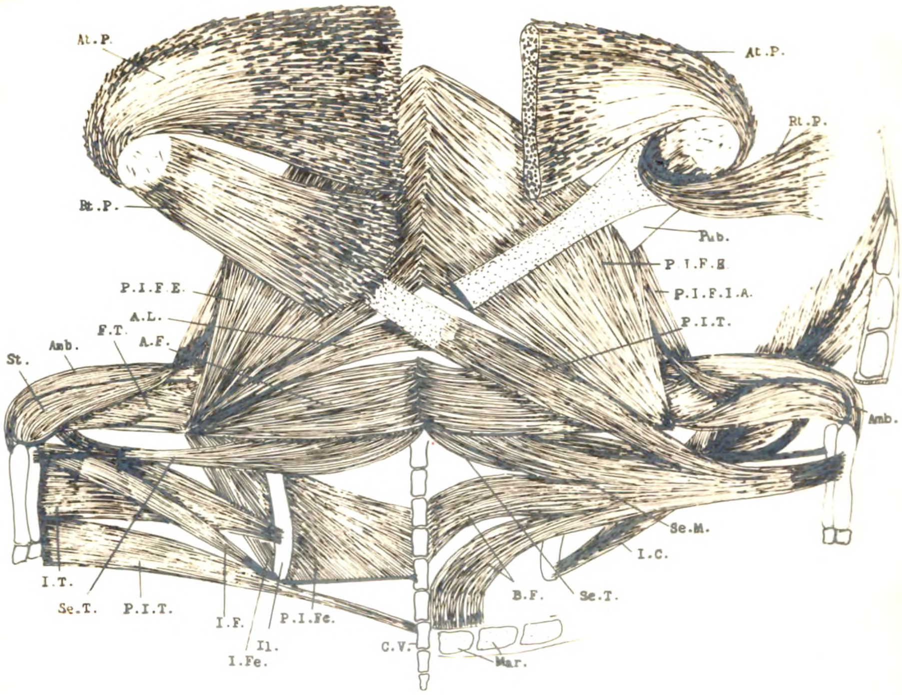

At.P.
At.P.
Rt.P.
Rt.P.
Pub.
P.I.F.E.
P.I.F.E.
P.I.F.I.A.
A.L.
P.I.T.
F.T.
A.F.
Amb.
St.
Amb.
Se.M.
I.C.
I.T.
Se.T.
P.I.T.
I.F.
Il.
I.Fe.
P.I.Fe.
B.F.
Se.T.
C.V.
Mar.

FIG.

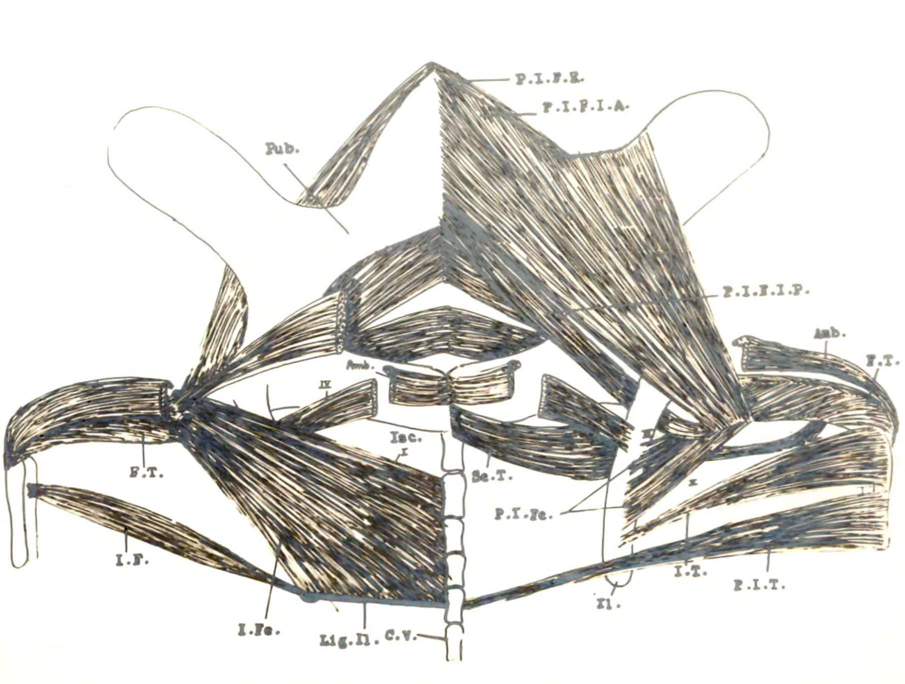

P.I.F.E.
P.I.F.I.A.
Pub.
P.I.F.I.P.
Amb.
F.T.
Amb.
IV
Isc.
I
F.T.
Se.T.
x
P.I.Fe.
I.F.
I.T.
P.I.T.
Il.
I.Fe.
Lig.Il.
C.V.

FIG. 6

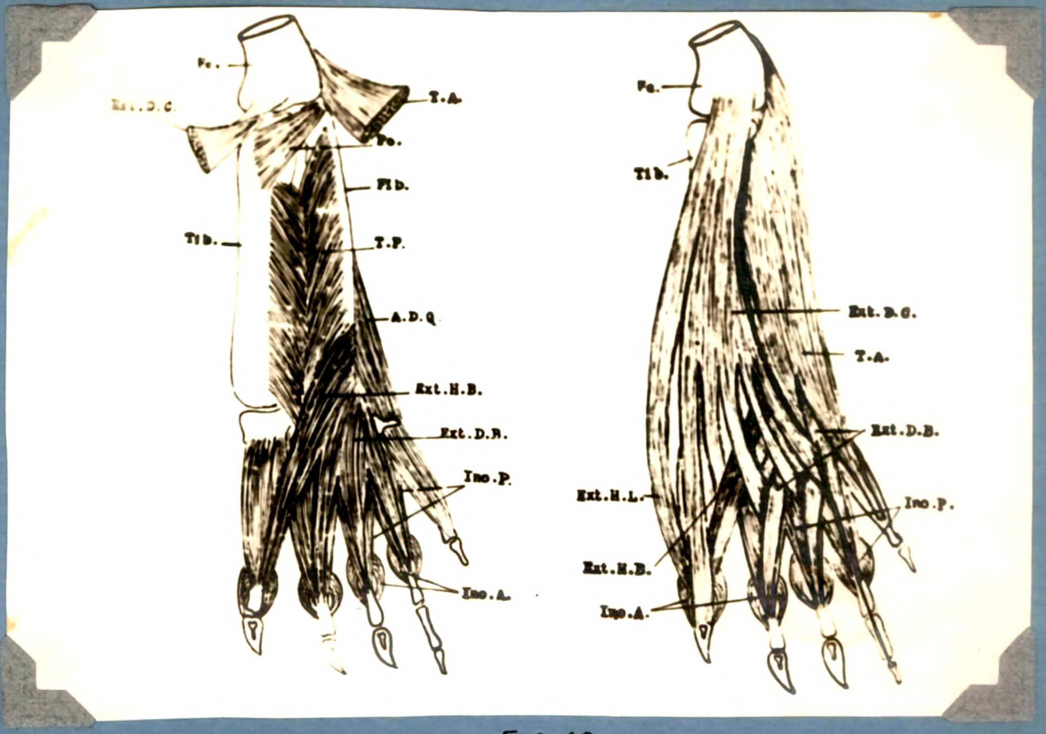

Fe.
Ext.D.C.
T.A.
Pe.
Fib.
Tib.
T.P.
A.D.Q
Ext.H.B.
Ext.D.B.
Ino.P.
Ino.A.
Fe.
Tib.
Ext.D.C.
T.A.
Ext.D.B.
Ino.P.
Ext.H.L.
Ext.H.B.
Ino.A.

FIG. 62

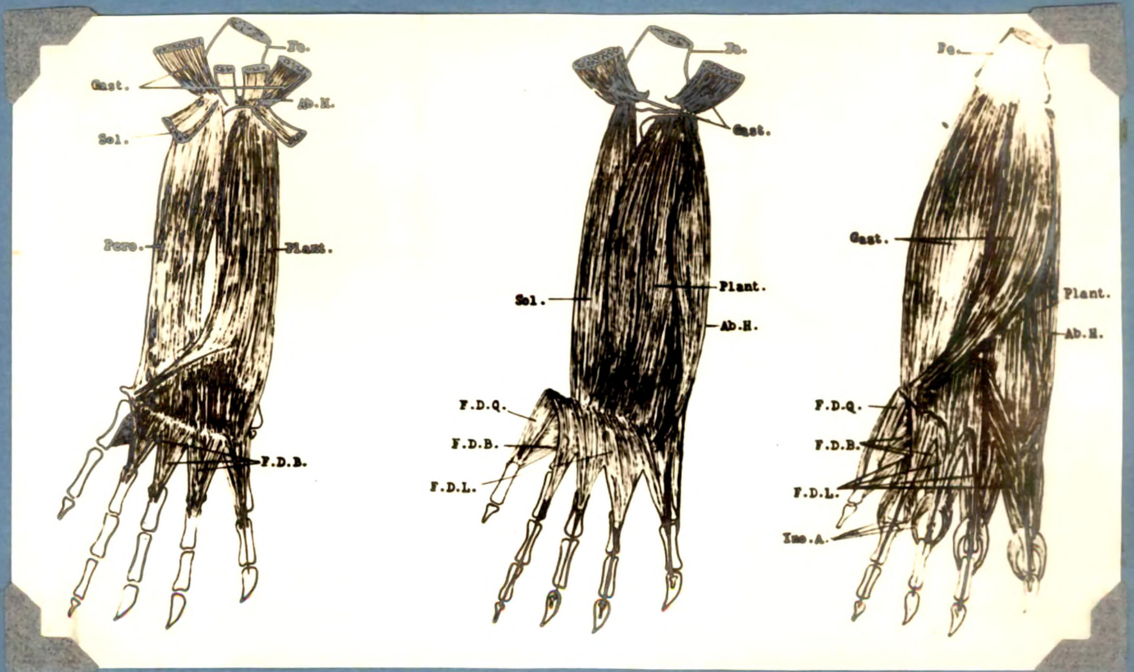

Fe.
Gast.
Ab.H.
Sol.
Pero.
Plant.
F.D.B.
Fe.
Gast.
Sol.
Plant.
Ab.H.
F.D.Q.
F.D.B.
F.D.L.
Fe.
Gast.
Plant.
Ab.H.
F.D.Q.
F.D.B.
F.D.L.
Ino.A.

FIG. 63