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THE SOMATIC MUSCULATURE OF THE CERVICAL AND OCCIPITAL REGIONS OF ALLIGATOR MISSISSIPPIENSIS

by

MICHAEL R. SEIDEL

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

1978

Michael Seidel

This manuscript has been read and accepted for the Executive Committee in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

May 12, 1978
Date

Max K Hecht
Chairman of Examining Committee
Dr. M. Hecht

May 16, 1978
Date

Executive Officer
Dr. L. G. Moriber

Walter Bock
Dr. W. Bock

Columbia University
Institution

Dr. S. MacDowell

Rutgers University
Institution

Dr. G. MacIntyre

Queens College
Institution

Dr. L. Marcus

Queens College
Institution

Institution

Institution

The City University of New York

Abstract

THE SOMATIC MUSCULATURE OF THE CERVICAL AND OCCIPITAL REGIONS OF ALLIGATOR MISSISSIPPIENSIS

by

Michael R. Seidel

Advisor: Professor Max K. Hecht

After new dissections by the author, the cervical and occipital muscles of Alligator mississippiensis are described in detail. The muscles of the cervical and occipital regions are here correlated with the same muscle systems found in the trunk region, and nine muscles are given new names. The bones of the occiput and the cervical vertebrae are re-described since the musculature creates morphological gradients along the axial column. Through anatomical analysis of the bones of the occiput, the cervical vertebrae, the dorsal epaxial musculature, and observations of living alligators, it is inferred that the living alligator cannot bend its neck ventrally, but that it can hyperflex the head upon the neck through a specialization of the atlas and axis vertebrae. Pitch, yaw, and roll movements of the head with respect to the occipital condyle result from specific interactions of occipital musculature with peripherally placed tendinous insertion points. In the light of the functional interpretation of this new description it is shown that it is possible to determine more accurate reconstructions of fossil crocodilians.

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THE SOMATIC MUSCULATURE OF THE CERVICAL AND OCCIPITAL REGIONS OF ALLIGATOR MISSISSIPPIENSIS

INTRODUCTION

The Eusuchian Crocodilia are the surviving reptilian members of a once large and diverse group, the Archosauria. As worldwide habitat destruction grows, the opportunity to study these unique and interesting animals diminishes. Recent classifications of the entire order leave much to be desired (Kälin, 1955, Romer, 1966, Olson, 1971), since phylogenetic relationships between the fossil and living genera are poorly understood. This is the result of much parallel evolution within the group, and of the practice of using time divisions as a convenient basis for classification. Knowledge of the anatomical details of the living animals is not yet complete enough to permit proper interpretation of fossil material. Consequently, this study will focus on those aspects of soft anatomy which, by their relation to preservable bony structure, may eventually aid in the understanding of phylogenetic relationships through accurate reconstruction of related fossil material.

The musculature of the crocodilian cervical and occipital regions is poorly known, although the bones of these regions are often well preserved in fossil material. The most recent description (Vallois, 1922), although an important contribution that is far superior to previous studies, is not entirely accurate. In addition, there is not enough detail in that study to form the basis for a functional analysis, or for phylogenetic comparisons. For that reason, the basic work of this thesis deals primarily with the problem of accurately re-describing the cervical and occipital musculature of Alligator mississippiensis (Daudin) (see ICZN Direction 97, Ruling 1b, 1958 for correct spelling of the scientific name).

An anatomical model based on A. mississippiensis is set forth here, to be used as a basis for comparison with other living Crocodilia. The choice of studying A. mississippiensis was made since this species is now the most readily available crocodilian in the United States. No attempt is made here to homologize the crocodilian musculature with that of other groups of vertebrates.

It was found that the head and neck of A. mississippiensis form a highly specialized functional complex. The specialized nature of the form and the function will be described here, but the functional analysis of the head and neck is still at a primitive level, and experimental physiological work is yet to be done.

This project was originally undertaken as a comparative study of the occipital bones of the crocodilian skull. During his extensive reviews of the crocodilian skull, Mook (1921, for example) often stated that the occipital region had very little to offer for interpretation of fossil and recent material. Unfortunately, Mook did not look very closely at the occipital region, since he consistently mislabeled the exoccipital foramina, and omitted other prominent occipital features in many of his figures (for example, Mook, 1925; p.390). The current, excellent osteological descriptions that include the occiput (Miall, 1878; Romer, 1956; Iordansky, 1973) and the neck (Boschma, 1922; Kälin, 1955; Romer, 1956) omit some of the salient features of these regions because the relevent supporting information for description of these regions was either inadequate, or entirely lacking. As a result of this gap of basic information, the original idea for a comparative study was put aside, and the acquisition of more basic anatomical information was pursued.

Until functionally important osteological landmarks are found, clearly defined, and their significance understood, it is difficult to make judicious decision as to which characters are important to measure and examine closely for a comparative approach. This study will define such landmarks in terms of their functional importance for A. mississippiensis, as well as for other Crocodilia. Occipital measurements which should yield meaningful data for further comparative study are also described here.

In addition to the living and fossil Crocodilia, the Archosauria also includes four more extinct reptilian orders, the Saurischia, Ornithischia, Thecodontia, and Pterosauria. Much attention has been given to the life and habits of these extinct reptiles. Yet, there is no complete reconstruction of the cervical-occipital region of any extinct Archosaur. Colbert, 1946, erroneously interpreted the occiput of Sebecus. His reconstruction of this region is based upon incorrect muscular homologies given by Anderson (1936). This attempt at reconstruction is therefore invalid and will be discussed in a later section. This thesis provides new information for the reconstruction of the head and neck of fossil Archosauria, and although such reconstructions are beyond the scope of this thesis, it is hoped that this thesis can be used for the execution of a future paleontological reconstruction.

It should be noted that references to musculature described in Haughton (1888), Hentz (1825), and Chiasson (1962) are omitted. Since Haughton (1888) had no figures, it is difficult or impossible to determine that author's intended meaning for many of the muscles referred to. In addition, Haughton applied terms of mammalian musculature to describe alligator muscles that are obviously not homologues. Hentz (1825) is basically a description of the heart of A. mississippiensis, even though the title implies something else.

The more recent, "Lab Manual and Dissection Guide for the Alligator" by Chiasson (1962) has been ignored in the present study for the following reasons: 1) Muscle nomenclature was not properly referenced, hence confusing; 2) Descriptions were inaccurate; 3) Drawings that show cervical musculature were not accurate.

To avoid these problems, the present study is abundantly illustrated, and attention is given to accurate correspondence between each drawing and the actual specimen. Muscle synonyms found in the literature are included wherever possible in the text in order to clarify the nomenclature. Synonyms for the trunk musculature are not included since there is clear agreement on the nomenclature of this region in the literature. When it was impossible to determine the identity of a muscle from either text or figures, the synonym has been omitted.

Analysis of the muscular anatomy of the cervical-occipital regions requires that the material be presented in a certain order. In order to describe the musculature accurately, and approximate its function, it was first necessary to ascertain important features of the axial skeleton that are related to the musculature (see Osteology, p. 13). The axial muscle and tendon systems are described in the myology section. Next, the joints are individually described, to present the possible ranges of movement available at each joint. This is followed by a consideration of features that impose restrictions on the range of possible joint movements. The data for joints are then analysed in light of the systems of musculature. Finally, observations made on living animals are presented and related to the previous anatomical analysis.

An important question that arises from this work is "how is the same musculature arranged in other species of Crocodilia?" A comparative project of this nature could only be carried out after the initial description was completed. However, description and comparison of other Crocodilia with *A. mississippiensis* requires dissections for each species that are as equally detailed as those presented here for *Alligator*. For comparative purposes, the range of variation of these muscles in crocodilian populations must be known. Considering the difficulty of obtaining additional material for dissection, and the time element involved in carrying out dissections, data for eight other species is presented, but only with respect to the following question: Is the *pattern* of cervical musculature described for *A. mississippiensis* the same in the eight other species?

In summary, this dissertation addresses three major questions: 1) What is the musculature of the neck and occipital regions of *A. mississippiensis*? 2) How is the musculature orgainzed? 3) What can be inferred about the functioning of the cervical and occipital musculature?

MATERIALS AND METHODS

The descriptive morphology presented here is based upon examination of prepared osteological specimens, and gross dissection of whole, fresh, and preserved material of Alligator mississippiensis. The occipital region of a large number of skulls was examined in order to establish the bony landmarks noted in the section on osteology. In addition, the vertebral column of 7 specimens was closely examined. Below is a list of all osteological material examined.

A. Skulls from the American Museum of Natural History, Herpetology Collection (AMNH numbers are given).

2318
2721
4319
7119
7124
7126
7127
7128
7129
7140
7141
7142
7144
8058
9043
9112
12572
15178
15180
15181
31563
31822
35441*
40578
40579
40580
40581
40583
40584
40585
43314
43315*
43316*
46844
46849
64521
66372
66373
66376
66377
66641
66642
66643
66645
66646
67134
71621
75041
75709

The asterisk (*) refers to skulls that were associated with vertebral columns which were assembled and studied.

B. Skulls from the Field Museum of Natural History, Herpetology Collection (FMNH numbers are given).

8204
25946
31011*
31321
35540
41861
197946

C. Skeletal material from the collection at Queens College, Flushing, New York.

QC R1200 (skull and postcranial skeleton)
R1418 (skull and postcranial skeleton)
4 skulls, no number
1 postcranial skeleton, no number

The fresh material consisted of five specimens obtained from the Rockefeller Wildlife Refuge, Grand Chenier, Louisiana, in November, 1971, through the kindness of Ted Joanen. Four juveniles that had hatched that year (specimens #1,2,3,4) and one adult (specimen #5) of undetermined age were collected.

Juvenile #1 and the adult were dispatched by cooling and freezing. Specimens #2 and #3 died of natural causes after 2 years, and were frozen soon after death. Specimen #4 was dispatched with chloroform. Below is a list of specimens and their snout-tip to occiput length, measured along the dorsal midline.

Specimen	Length (snout-occiput)
#1	6.46 cm
#2	8.58 cm
#3	3.90 cm
#4	8.39 cm
#5	24.98 cm

The large adult specimen was dissected with heavy steel probes, forceps, and hemostat clamps; the use of scalpel and scissors was held to a minimum. Specimen #5 yielded many hours of good dissection by continued freezing and thawing. Desiccation was prevented in frozen specimens by wrapping them in plastic before freezing. It is interesting to note that specimens that were killed by cooling did not rot quickly after thawing, but those that died naturally, and the one that was chloroformed, rotted quickly. This may indicate that during cooling the muscles receive a minimal supply of blood, thus reducing muscle fluid and slowing the rotting process. This was also noted by Hentz (1825, pg. 223) who stated, "In the alligator, the muscles are not very numerous, but extremely large in general, and strong: those of an animal killed as it has just left its winter retreat, are white and flaccid, they stand several days in the open air without any alteration, whilst the muscles of one killed in the summer are red, more firm, and resemble those of any animal with double circulation, except on their great contractile power after apparent death."

After study and dissection on one side, the fresh animals (except for #5) were preserved in alcohol, and more detailed dissections were carried out on the remaining, intact side.

Specimens #1-#4 were small enough to dissect under a dissecting microscope (an American Optical Co. model 570 was used). Most dissection was carried out at a magnification of 7X. Fine needles and forceps were fashioned by grinding and sharpening on carborundum stone. The muscle tissue became brittle in alcohol and for that reason, use of scalpels and other large tools that were destructive, was avoided.

All measurements were made with the same Scherr Tumico 101 vernier caliper. Accurate illustrations were drawn with attention being given to providing correctly measured proportions.

Areas of fleshy muscle insertion on bone were marked by piercing the periosteum with small pins, into the bone and around the muscle. This method was used since the periosteum frequently peeled off the bone, leaving no traces of the former fleshy muscle attachment.

It was frequently useful to articulate various bones for orientation. Specimen QC R1200 was glued together with Duco cement, which was easily removed after the study.

The previous major detailed dissection of the epaxial cervical musculature of A. mississippiensis that was done by Vallois (1922) relied upon a single specimen of unknown condition, age and locality. Here, five specimens were dissected, all were in excellent condition, from early juvenile (specimen #3), three year animals (specimens #1,2, &4), and an adult (specimen #5). It is impossible to obtain a thorough description from one specimen, because in the process of dissecting unknown material, destruction of structures is unavoidable. These five specimens permitted checking and rechecking of many points that had been missed the first time the dissection was performed. This study is based upon more dissected specimens than any previous study.

In addition to the material listed above, a hemi-sected skull and neck was obtained from the Field Museum of Natural History (FM 205888). This specimen was dissected in addition to the fresh material from Queens College. It was preserved in alcohol, and its bones were greenish. This particular specimen vividly shows the relationship between skull, vertebral column, and musculature. It also confirmed the existence of the cervical curvature in a whole specimen. The specimen which had been divided midsagittally measured 22.27cm from snout tip to end of occiput.

Specimens of other species of Crocodilia were obtained from The New York Zoological Park, Bronx, New York, with the help of Mr. P. Brazaitis. These are: 1) Osteolamis tetraspis (54 cm long); 2) Crocodylus johnsoni (66.5 cm long); 3) Crocodylus porosus (50 cm long); 4) Crocodylus novaeguineae (46 cm long); 5) Melanosuchus niger (hatchlings).

An alizarin-stained specimen of Tomistoma schlegeli (snout-occiput length 12.5 cm) was provided by Prof. S. McDowell.

American Museum of Natural History no. 81802 was a whole head of Gavialis gangeticus (snout-occiput length of 26 cm).

Two specimens of Caiman sclerops were dissected when fresh (snout-occiput length of 5.1 cm, and 11.0 cm). These two are frozen specimens at Queens College, and are without numbers.

OSTEOLOGY

INTRODUCTION

It is necessary to present a general view of the skull of *Alligator mississippiensis* in order to place the occipital region in proper perspective.

The Eusuchian skull (fig. 1) is highly adapted for the feeding and capture of prey, since it contains elongated jaws, set with numerous strong thecodont teeth. A secondary palate protects the nasal passage-ways and braincase. The snout is set apart from the braincase by four large oval openings, but is attached to the braincase by four bony bars. The two lateral bars are comprised of the jugals and maxillae. A single, fused, tubular, frontal bar lies above and between the orbits. A single tubular bar made of the paired palatines is also found below the braincase, between the paired palatal fenestrae. This bar is the tube that houses the nasopharyngeal ducts.

The dermal bones of the snout and palate are rigidly sutured to the braincase, as is the quadrate, leading to an akinetic condition for the palate (Langston, 1973). Posterior to the level of the orbits, on the palatal surface, the pterygoid bones flare ventrally and laterally for the attachment and housing of the enlarged pterygoid musculature. The pterygoid bones also surround the internal nares and join with the braincase.

The braincase, including the ear region, is held in place by seven major bony struts: paired post-orbital bars, paired lateral quadratojugal + jugal bars, the frontal bone anteriorly, and the paired, ventral braces of the ecto-pterygoid + pterygoid bones. Posteriorly the braincase is supported by the atlas-axis complex.

The occipital condyle, which articulates the skull with the rest of the axial skeleton, is directly in line with, and at the same dorso-ventral level as, the bony palate of the snout region. Such a low position for the occipital condyle means that the cervical vertebrae are located ventral to the level of the skull roof, and as a consequence, the neural spines of the vertebrae in the neck are not as high as the top of the skull. This results in most of the occipital surface area being located dorsal to the neural spine tips. This is significant since much of the musculature used for head movement also extends between neural spine tips and occipital surface, and the extra height of the occiput above the neural spine tips allows great expansion of those muscles to take place.

The top of the braincase is flattened in the frontal plane, and squared off about the otic region. This flat surface is often referred to as the "cranial table". The perpendicular surface posterior to the cranial table, and vertically oriented in the transverse plane, is the occipital region. This bony area usually faces posteriorly, but sometimes postero-dorsally. It is through muscular tension pulling on the occipital surface that all head movements are controlled. The somatic musculature that acts upon the occipital region includes both epaxial and hypaxial muscle systems. The branchiomeric musculature is not involved in producing head movements, and is not a significant portion of the occipital musculature.

The morphology of the occipital surface is influenced by the functions of the somatic musculature associated it. In another sense, the morphology is a record of ontogenetic events, such as the growth of bone around nerves and blood vessels which have developed in earlier stages. Morphology represents a simultaneous solution to development and function. The necessity for retention of the internal carotid arteries as the major blood supply to the brain is an example of this process. These arteries develop long before the occipital region expands to accomodate the head-neck musculature, and the arteries enter into the braincase in the occipital region. Yet, as the skull changes shape to approach its adult condition, the expanded adult musculature does not interfere at all with the paths and functions of the carotid arteries.

The following description of the occipital region, and its associated axial skeleton, is concerned with certain bony landmarks that were chosen because of their relationship to the muscles that connect the head with the neck. It is essential to understand this choice of landmarks on the bones since the myology occurs in a later section.

THE OCCIPITAL REGION

The occipital region of A. mississippiensis is defined as that part of the skull involved with muscular and bony attachment to the remainder of the axial skeleton. This definition limits the region to four bones: a basi-occipital; two exoccipitals; and a supra-occipital. The quadrate, squamosal, and parietal bones, and others that are visible from the posterior aspect, are concerned primarily with functions that are restricted to parts of the skull (e.g.closing and opening the jaws), and not skull movements as a whole. Since these elements are not occipital bones as defined, they are not included in the following description.

A. Basi-occipital

The basi-occipital (figs. 2a', 2a", 3a,b,c) is a single median endochondral bone of the occiput, which is the floor of the foramen magnum, and bears the major portion of the single occipital condyle. The condyle (figs. 2a', 3a) has a shallow median depression that divides it into two poorly defined lobes. The smooth condylar surface projects posteriorly and is held away from the vertical plane of the occiput by an extended neck (fig. 3b). Sometimes the exoccipitals participate to a minor extent in the dorso-lateral condylar articular surface (a frequency of 3 out of 28 specimens of A. mississippiensis sampled in the Herpetology Collection of the American Museum of Natural History).

Below the condyle there is a prominent median ridge. This ridge divides the shield-shaped surface of the basi-occipital into left and right surfaces for muscle attachment. At the dorsal end of the median ridge there is usually a prominent nutrient foramen. The shield-shaped portion of the basi-occipital is referred to by Iordansky (1973) as the vertical "basioccipital plate" (fig. 2a'). In *A. mississippiensis* this plate is shallowly concave, excluding the median ridge. This plate is flattened, rather than concave, in other genera.

The tendons and fibers of *mm. longissimus capitis profundus* (fig. 5b) and *basi-occipitovertebralis* (fig. 5a) (see Iordansky, 1973) insert on the basi-occipital plate. *M. basi-occipitovertebralis* inserts by a tendon to the dorso-lateral edge of the basi-occipital plate.

M. longissimus capitis profundus inserts by a tendon to the margins of the plate, and by fleshy fibers on the concave surfaces of the plate. The tendon of *m. longissimus capitis profundus* is superficially covered by that of *m. basi-occipitovertebralis* near their points of insertion (fig. 48).

The dorsal surface of the basi-occipital bears the left and right articular surfaces for the exoccipitals (fig. 3c). These two surfaces are longitudinally oriented rectangles with roughened contact areas that face up and out, at about the same angle as the processus post-occipitalis of each side. Between the two wrinkled articular surfaces, in the midline, there is a channel which is transversely concave, but longitudinally convex dorsally. The medulla rests in this channel.

Recessed under the mid-ventral edge of the basi-occipital plate is the entrance for the median Eustachian tube (fig. 5i). The basi-occipital makes up the posterior quarter of this opening in A. mississippiensis. In all 28 specimens examined in the herpetological collection at the American Museum of Natural History, the basi-occipital did not exceed one quarter of the border of the foramen.

A branch of the median Eustachian tube, the "posterior communicating canal" of Miall (1878), enters the basi-occipital and diverges within into two lateral branches (posterior Eustachian passages of Miall, 1878). These branches each meet the posterior lateral canals, the homologues of the paired Eustachian tubes of other vertebrates. At the anterior junction of the basi-occipital and exoccipital, each posterior passage is dilated into the paired rhomboidal sinus (fig. 3e) of Owen (1850).

The ventral half of the rhomboidal sinus is in the anterior lateral portion of the basioccipital. The lower medial corner of the sinus contains the entrance of the posterior lateral canals (fig. 3e).

B. Supra-occipital

The supra-occipital (figs. 2c, 3f) is an unpaired, median bone, between and dorsal to the exoccipitals, and excluded from the border of the foramen magnum. The occipital surface of the supra-occipital resembles a triangular plate, apex down. The upper base of the triangle is usually fused to the parietal bone. There is a large cavity between the epiotics and the anterior surface of the supra-occipital. Anteriorly, the center of this cavity has a double bony pillar that divides the front of the cavity into two large lateral holes, and a smaller median hole. The floor of the cavity, which is also part of the roof of the braincase, is formed by the epiotic ossification of the embryonic otic capsule.

A slight median ridge divides the occipital surface into left and right fossae for the fleshy insertion of m. epistropheo-capitis medialis (fig. 5c). On the upper lateral corners of the supra-occipital (fig. 5d) there are flattened, oval surfaces that look obliquely outwards and upwards (the processus postoccipitales of Kälin, 1933). The tendon of m. transverso-spinalis capitis inserts on the processus postoccipitalis. These structures leave a pair of spaces between the supra-occipital, squamosal, and parietal, that are filled with cartilage in life (Iordansky, 1973). These spaces represent the reduced and obliterated post-temporal fenestrae, and transmit the temporal artery to the tympanic cavity.

C. Exoccipital

These paired bones (figs. 2b, 3g) form most of the boundary of the foramen magnum. They meet at the midline above the foramen magnum, thus excluding the supraoccipital bone from the border of the foramen. In the sagittal plane, the median suture is a broad-based triangle, situated above the posterior portion of the braincase.

The exoccipitals are posterio-ventrally sutured with the basi-occipital bone. The antero-ventral contacts are with the basi-sphenoid and quadrate bones. Dorsally the main sutures are with the squamosal and supra-occipital bones. The opisthotic bones are fused with the exoccipitals.

The anterior sutural surface (fig. 4) is divided by the large cranioquadrate passage into dorsal and ventral areas that each form a broad contact with the quadrate bone. The cranioquadrate passage is formed as a tunnel between the exoccipital and quadrate bones. Its exit (fig. 5e) is strategically located for transmission of a branch of cranial nerve VII, which plunges immediately into the center of m. depressor mandibulae. A branch of the jugular vein, the lateral cephalic vein, and the lateral temporal artery traverse the passage from the middle ear cavity.

Two foramina are found on the internal surface facing the brain (fig. 3g). These internal openings lie behind an inclined slit. The posterior member of the pair transmits the hypoglossal nerve. The smaller anterior foramen carries a vein that joins the vein of the tympanic cavity on its way out of the skull. The inclined slit, a remnant of the metotic fissure, transmits cranial nerves IX, and X + XI. Goodrich (1930) reported (through a figure attributed to Reynolds, 1913) that cranial nerve VIII also entered the slit, but this fact is not confirmed, since that nerve should enter the ear capsule, not the metotic fissure.

The exoccipital surface bounding the posterior tympanic cavity is complicated by fusion with the opisthotic bone. This surface (figs. 4a, b,c) may be considered as three cavities separated by two long horizontal shelves. The ventral longest cavity (fig. 4a) is the top of the rhomboid sinus of Owen (1850). This is open to communicate freely with the lateral tympanic cavity. In this space one can see the thin tubular opening for the carotid artery (fig. 4g) as it enters the tympanic cavity. Lateral to the tube is the horizontal shelf that marks the bottom of the next cavity. The middle cavity (fig. 4b) is openly conical and contains the long columella. This cavity is the place where cranial nerves IX and X + XI begin their exit from the braincase. The two foramina (in fig. 4b) in this cavity unite within the exoccipital and form the jugular foramen (= foramen vagi), seen on the occipital surface (fig. 5g). The opening for cranial nerve IX is the smaller and more anterior of the pair. The uppermost cavity (fig. 4c) is the lateral half of a set of globular air passages that continue into the supra-occipital bone.

The posterior occipital surface is divisible into three distinct regions (fig. 2):

A) A pillar that extends around the foramen magnum, and also rests upon the basi-occipital bone (fig. 2b"). In many Crocodilia this pillar often participates to a small extent in the occipital condyle.

B) A plate of bone (fig. 2b') that extends laterally and horizontally from the midsagittal exoccipital suture, called the paroccipital process by Iordansky (1973). The junction of the two exoccipital bones forms a ledge over the foramen magnum that supports the dorsal part of the proatlas. The surface of the paroccipital plate is in the transverse plane and forms most of the occipital surface area. The paroccipital process is the muscle-bearing portion of the exoccipital bone. The following muscles insert there:

1. M. ilio-costalis capitis. By a tendon on the ventral edge of the paroccipital process, from the extreme lateral border of the paroccipital process, mediad to a point

directly dorsal to the middle of the foramen vagi (fig. 51).

2. M longissimus capitis superficialis. By a tendon on the entire lateral margin of the paroccipital process, as well as the ventral margin that overhangs the cranioquadrate opening (fig. 5m).

3. M. spino-capitis posticus. By a tendon, immediately within the preceeding insertions, on the lateral extremity of the paroccipital process.

4. M. epistropheo-capitis intermedius. Insertion by fleshy fibers on the concave fossa of the limb of the paroccipital process. This insertion is on the lateral half of the paroccipital process.

5. M. atlanto-capitis. A fleshy insertion approximately mid-way along the paroccipital process, ventral and medial to the insertion of m. epistropheo-capitis intermedius.

6. M. transverso-spinalis capitis. The dorsalmost point of the exoccipital carries a small lateral continuation of the processus postoccipitalis of Kälin (1933) (see fig. 2). The dorsal point carries the lateral fibers of the tendon of m. transverso-spinalis capitis.

C) A triangular plate lateral to the occipital condyle, ventral and medial to the preceding two sections (fig.

2b"). This section bears four foramina and is recessed inward (that is, anteriorly) with respect to parts (A) and (B). Three of the four foramina are in an horizontal line, directed towards the base of the condyle, but not extending below the level of the foramen magnum. The hypoglossal nerve exits from the medial foramen (fig. 5h). The next lateral foramen transmits a vein from the tympanic cavity. The hypoglossal foramen and tympanic vein foramen are also to be found in a parasagittal plane (fig. 3g), the hypoglossal foramen being more posterior. The third foramen is lateral to, and much larger than the preceding. Called the foramen vagi by Iordansky (1973), it is actually a fossa that opens through the transverse plane (fig. 5g), and is divided within into two canals. Iordansky (1973) stated, " The medial canal extends to the cerebral cavity and is traversed by the IXth and Xth nerves; the lateral canal extends to the middle ear cavity and contains the Ramus communicans (N. sympathicus) connecting the VIIth and IXth nerves." There is a large ganglion (the jugular ganglion) on the vagus nerve which is housed in the fossa of the foramen vagi.

The fourth foramen on the triangular plate is directly below the foramen vagi, and carries the internal carotid artery (fig. 5k). This foramen is on a small wedge of exoccipital between the basi-occipital and basi-sphenoid bones. The carotid canal leads into the middle ear cavity, through the previously mentioned bony tube. A medial branch of the carotid canal reaches as far as the metotic fissure. A third, interior division of the carotid canal has not been successfully probed.

THE VERTEBRAL COLUMN: CERVICAL AND THORACO-LUMBAR REGIONS

The vertebral column of A. mississippiensis consists of 7 cervical vertebrae, 17 dorso-lumbar (or thoraco-lumbar) vertebrae, 2 sacral vertebrae, and 34 - 40 (or more) caudal vertebrae (Vallois, 1922). These vertebrae are all procoelous, with the exceptions of the axis, the second sacral, and the first caudal vertebrae. The neck is usually considered to include the first nine vertebrae, but since Vallois (1922) and Vialleton (1911) pointed out that the coelom extends as far forward as the 8th vertebra, there are only 7 cervicals. Furthermore, the roots of the brachial plexus of nerves converge and take exit in a position that is ventral and anterior to ribs #8 and #9 before entering the shoulder. Therefore, vertebrae #8 and #9 are not considered true cervicals here, even though their ribs lack the sternal cartilages typical of the thoracic series.

Rib #9 retains its cartilaginous member, which never reaches the sternum. Rib #8 does not articulate with the preceding rib in the manner of ribs #2 through #7 (fig. 6). Furthermore, the lungs extend as far forward as the tip of the 8th rib. Ribs #8 and #9 seem to be in transition from the thoracic segmental type, to the cervical segmental type.

Ventrally, the centra support large diapophyses, from the atlas, through the 7th cervical vertebra (figs. 6, 14). The 8th diapophysis is extremely reduced by comparison with the 7th diapophysis (fig. 6), and rib #8 is functionally distinct from ribs #3 to #7 by being mobile. This additional information limits the cervical region to the anterior 7 vertebrae.

Vertebrae #1 through #7 are termed "cervical #1" through "cervical #7" respectively, and are abbreviated here as C-1 to C-7. Vertebra # 8 is termed "dorsal vertebra #1" (or D-1), and that numbering system continues up to, but not including, the sacral vertebrae. The terminology and abbreviation scheme is modeled after Vallois (1922).

When viewed from the lateral aspect (fig. 7), the cervical neural spines become progressively higher from C-2, the axis, to vertebra C-7. Vertebrae D-1 to D-4 continue this trend into the thoraco-lumbar region. From D-5 to D-12, the neural spines become progressively shorter, but the amount of change is very gradual and just barely noticeable to the eye. A slight increase in neural spine height is noted in the lumbar region. True measurement of the change in height of the neural spines is difficult since there is not a distinct break that marks off the neural spines from the neural arches. Any reference point would be artificial. However, a table of neural arch heights (Table 1) is given to show this gradual change, with the measurements taken from the roof of the neural canal.

The chain of cervical centra forms a curved cylinder that is concave dorsally. The thoraco-lumbar centra also form a curved cylinder, but the concavity is ventral. These two curvatures are known as the "cervical (or nuchal) curvature" and the "dorsal curvature".

The cervical curvature is accentuated in the neck by the neural spines, where the dorsal level of the neural spine tips never exceeds the height of the skull table. The cervical curvature is admirably presented in the hemisected head and neck of Field Museum specimen number 205888. Figure 7 is drawn to show the curvature of the cervical centra, and also the more accentuated curvature created by the neural spine tips. The interesting result of the cervical curvature is that it places the enlarged neural spine tips of the first three thoracic vertebrae at about the level of the cranial table. It is just at that posterior level in the vertebral column that the occipital muscles terminate.

The small increase in height of lumbar neural spines is compensated by the lumbar region being on the posterior, downward side of the dorsal curvature, so that the tips of the neural spines lie on an approximately straight line between D-1 and the sacrum.

The neck vertebrae include the pro-atlas, atlas, axis, and C-3 to C-7 (figs. 6, 7, 8). The pro-atlas, atlas, and axis are described individually; C-3 to C-7 are described collectively.

A. The Pro-atlas

Between the atlas and the occiput there is a small bony element that roofs over the neural canal (figs. 7z, 10). This is the "proatlas" of Albrecht (1880). It has been interpreted as the remnant of a lost vertebra that was once between the atlas and the skull. Boschma's more recent re-interpretation of the significance of the pro-atlas stated: "das dorsale Schlussstück ist ein Teil der oberen Bogen des Atlas" (Boschma, 1922, p. 92). His thorough study of the development, and adult morphology, of the pro-atlas of Crocodilia, led him to that conclusion.

Boschma (1922) showed that the pro-atlas developed from two embryonic cartilagenous anlagen much in the same way that the neural spines develop. Furthermore, the first spinal nerve (N. suboccipitalis) exits beneath the pro-atlas, anterior to the atlas, and does not constitute a nerve representative of an extra anterior segment. This is presented here as evidence in favor of associating the pro-atlas with the atlantal vertebra, possibly as a remnant of its missing neural spine. Regarding the first spinal nerve, it is of interest to note that, as in man, the first spinal nerve of the alligators examined lack a dorsal root and spinal ganglion, and there is a nerve plexus between spinal nerves 1 and 2. This feature may be associated with the formation of a functional atlas-axis in order to allow great mobility between skull and atlas.

The pro-atlas is shaped like an inverted "V", the two limbs held together by ligaments (fig. 10). The two halves are usually separate but may become fused into a single piece. It is attached to the exoccipital bones by ligaments at the prominence overhanging the foramen magnum. Its posterior base is attached on each side to the plate on the anterior dorsal border of the atlantal arch by a ligament (fig. 9d). One of the reasons that Albrecht (1880) placed the pro-atlas between atlantal arches and occiput as an extra vertebra is that he concluded that the pro-atlas articulated with the rudimentary prezygapophysis of the atlantal arch (see Albrecht, 1880, p. 474, figs. 5 and 6). But that is not the case in the specimens examined (see fig. 9).

The periosteum of the atlas forms a covering for the proatlas that is continuous with that of the occiput. The neural surfaces as well as the external surfaces are both covered in this manner, thus sandwiching the pro-atlas between them. The dorsal tip of the pro-atlas is connected to the ligamentum nuchae.

Contrary to Vallois (1922), the specimens of A. mississippiensis that were examined did not show muscle fibers originating or inserting on this element.

B. The Atlas

The atlas consists of four pieces of bone: two arches, a hypocentrum, and the odontoid, or dens.

Atlantal neural arches (fig. 9). Each arch is a reduced, independent element. An attached neural spine is lacking (see pro-atlas, p. 30). The arch element may be described as three parts that are all smoothly connected (fig. 9E).

First, there is a rectangular plate that roofs over the neural canal (figs. 9A,D,E). Medially the plate is attached to its contralateral arch plate by ligaments only. This surface bears the area of origin of m. atlanto-capitis (fig. 9D). The anterior, medial corner of the rectangular plate has a spinous process that resembles a rudimentary prezygapophysis. This spine has a ligament which helps to bind the pro-atlas with the atlas. However, the pro-atlas rests on the entire anterior half of the rectangular plate and is not restricted to the rudimentary prezygapophysis (fig. 9D).

The second portion of the arch is a large, laterally placed basal tetrahedron (fig. 9E). This tetrahedron constitutes most of the arch. The lateral surface is a curved area bearing a part of the multiple origin of m. longissimus capitis profundus. The antero-ventro-medial surface forms part of the capsule for the occipital condyle (figs. 9C, 11E). The posterior surface is convex and makes a gliding joint contact with the sulcus in the odontoid (figs. 9B, 12C,E). The anterior, dorso-medial surface faces the spinal cord and is convex (fig. 9B). The corner formed by the union of the lateral, posterior and antero-ventral surfaces, articulates with the hypocentrum, and is joined to it by ligaments (figs. 9B, 11B, C, D).

The third section is attached to the posterior part of the roof plate, at the apex of the basal tetrahedron (figs. 9A,D,E). This is the atlantal postzygapophysis. Its flattened undersurface faces posterior, medial, and ventral, a condition not seen in any of the other postzygapophyses. The dorsal surface of the postzygapophysis has a longitudinal fossa. The fossa receives muscle fibers from the first interarticular muscle, which originates on the axial neural arch and spine. The ligament of m. interarticularis may prolong the lateral border of the fossa into a small spine in larger specimens (fig. 9A). This spine is a good landmark to look for on fossils and prepared skeletons . The lateral and ventral part of the postzygapophysis has another long fossa, bordered above by a stout spine. Spine and fossa comprise the insertion of the combined tendons of mm. transversospinalis cervicis and longissimus cervicis. This fossa, and the dorsal fossa, play important roles during the movement of the atlantal arch elements, since they are the primary areas of muscle insertion on the arch.

Atlantal hypocentrum (fig. 11). The hypocentrum forms a wedge of bone that can glide across the ventral surface of the odontoid. The anterior concave surface provides the ventral part of the socket that receives the occipital condyle (fig. 11E). The extreme dorso-lateral corner of this element has a facet that contacts the atlantal neural arch halves. The anterior half of the dorsal surface is slightly raised to present a triangular area for a gliding articular contact with the odontoid (fis. 11, 12).

Posteriorly, there are paired semilunar surfaces for articulation with the first pair of ribs. It is best to call these processes atlantal parapophyses, since they correspond to the anterior ventral position on the centrum.

The ventral surface is smooth and convex (fig. 11A). A hypapophysis is lacking, but m. hypocentro-occipitalis and the median Eustachian valve retractor muscle both attach to the hypocentrum (figs. 11A, 48).

The hypocentrum is attached to the neural arches and first ribs by strong ligaments. There is a cartilagenous disc between the atlantal parapophysis and the first pair of ribs.

The odontoid (figs. 12A, C, E). The odontoid, or true centrum of the atlas, is a heavy disc of bone, interposed between the atlantal ring and the axis. Anteriorly it forms a moving joint with the atlantal arches and the hypocentrum of the atlas. Posteriorly the odontoid has a wrinkled surface that forms immovable contacts with both the arches and centrum of the axis.

The dorsal surface is shallowly concave and very smooth. This forms a floor for the spinal cord and juts forward, in between the atlantal arches. This is the tongue of the odontoid (fig. 12A, C, E). On the lateral surface there are two rounded eminences (fig. 12A). The ventral swelling articulates with the capitulum of the second rib. The larger dorsal swelling is an area specialized to hold the ligament from the tuberculum of the second rib, and also ligaments that join the odontoid to the axial neural arches. Between and anterior to these swellings ("di- and para- pophyses") there is a hollowed out fossa that is the origin for m. centro-costalis, which inserts on the second rib (fig. 12B).

The posterior surface complements the anterior surface of the axis (fig. 12D). The sutural area is wrinkled to match the axial neural arches and centrum. The portion facing the centrum is set off from that which meets the arches by a sharp line of bending. The quarter of the surface area for symphysis with the axis neural arches is tilted anteriorly at about a 45° angle.

The anterior surface is complex. It consists of a ventral convex shield (fig. 12C). The shield slopes posteriorly and ventrally to meet the posterior edge of the odontoid. About halfway up the anterior surface, the shield gives way to two deep concave grooves. As these grooves ascend to meet the posterior edge, they encompass the tongue of the odontoid process between them (fig. 12E). Each groove may be called the sulcus of the odontoid.

C. The Axis

The axis (figs 12A, B, D) is a specialized vertebra. The neural spine, although not exceptionally high, is the longest of the vertebral column. The neural spine overhangs the neural canal anteriorly; its anterior border slopes back and up to meet the dorsal border at an obtuse angle; the dorsal border is horizontal; its posterior border slopes sharply ventral and anterior, to a point between the postzygapophyses, overhanging the neural canal.

The neural arches form lateral, vertical laminae, but here they are the shortest (dorso-ventrally) and the most elongated (antero-posteriorly) of the cervical neural arches.

The postaygapophyses resemble those of C-3. The prezygapophyses are held on a thin bony plate, facing dorsally. A line drawn normal to the prezygapophyseal articular surface would point dorsally, laterally, and anteriorly, opposite in direction to all of the other prezygapophyses of the vertebral column.

The base of each arch makes a jagged, horizontal articulation with the centrum, then continues in front of the centrum as a heavy pillar that contacts the odontoid. This pillar is topographically a diapophysis, but it does not carry a rib tuberculum.

The centrum is a cylinder with a flat anterior end. The flattened end is coarsely wrinkled. A condyle is found at the posterior end. There is also a small, rounded mid-ventral hypapophysis at the anterior end.

Note that diapophyses and parapophyses are absent, and there are no axial ribs. The axial rib has apparently shifted anteriorly, onto the odontoid (Baur, 1886).

The anterior border of the neural spine carries two muscles (fig. 12B), m. epistropheo-capitis medialis and m. epistropheo-capitis intermedius. The dorsal border of the neural spine is the origin of m. epistropheo-capitis lateralis and the anterior part of the multiple origin of m. transverso-spinalis capitis. Most of the lateral surface area of the neural spine is occupied by m. epistropheo-capitis lateralis, but the ventral portion also carries the first interarticular muscle (see fig. 12B).

The dorsal surface of the neural arch from the base of the neural spine to the anterior half of the postzygapophysis carries the origin of the first interarticular muscle (which inserts on the atlantal postzygapophysis). Muscle scars from all these muscles can be seen on some osteological material.

Laterally, the plate of the neural arch carries part 2 of the multiple origin of m. longissimus capitis profundus.

The dorsal and ventral limits of this origin are marked by ridges on the bone (fig. 12B) where intermuscular membranes attach.

The posterior surface of the postzygapophysis lodges the insertion of the second interarticular muscle, which is evidenced by a scar on that surface.

The centrum carries the large fleshy insertion of m. centro-costalis, that originates from the third rib (fig. 12B). The hypapophysis is associated with aponeuroses that fix both the second and the first ribs, as well as serving as the tendinous origin for m. basioccipitovertebralis.

D. Vertebrae C-3 to C-7 (figs. 6, 7, 8, 13, 14)

Each vertebra (fig. 13), from C-3 to C-7 possesses a neural spine, a pair of prezygapophyses supported by a pair of bony pillars, a pair of stout postzygapophyses, vertically elongated neural arches, procoelous centra, diapophyses on the neural arch, parapophyses on the centrum, and an hypapophysis midventrally, beneath the centrum. The centra are separated by cartilagenous intervertebral discs. The anterior cup-shaped depression in the centrum is termed the cotyle. The posterior rounded part of the centrum is the condyle. The condyle of one centrum fits into the cotyle of the succeeding centrum.

The neural spine of C-3 is about twice as broad (antero-posteriorly) as those of C-4 to C-7 (fig. 7). The neural spines occupy the posterior half of the vertebrae, leaving a wide space between the spines. Each space is about twice the width of the succeeding neural spine.

The postzygapophyses are found at the posterior base of each neural spine. They are stoutly built and extend at about 45° to the long axis of the column (fig. 13B). This angle varies from C-3 to C-7, being smallest at C-3 and largest at C-7 (fig. 8). A line drawn normal to the articular surface of the postzygapophysis would point ventral, lateral and anterior. The posterior-dorsal surface of each postzygapophysis is roughened by tendons of the transverso-spinalis system, and contains a depression for fibers of the inter-articular muscles. Under each postzygapophysis, and on the neural arch, there is a fossa that receives a band of muscle fibers which take their origin from the prezygapophysis of the preceding vertebra.

The prezygapophyses are supported on the anterior corners of the neural arches by stout pillars of bone (fig. 13A). The articular surfaces face dorsal, medial, and posterior. That of C-3 is nearly vertical and nearly in the parasagittal plane, while that of C-7 is about 45° to the horizontal.

At the base of the neural spines, and in between the prezygapophyses, there is a deep fossa. Another deep fossa is similarly found between the postzygapophyses of each vertebra. These fossae house a massive cylindrical intervertebral ligament.

A curved ridge on the neural arch joins the pre- and post- zygapophyses of a single vertebra (fig. 13). This ridge sets off a dorsal, horizontal plate between itself and the neural spine, referred to here as the dorsal plate of the neural arch. A second, vertical plate comprises the side of the neural arch between the curved ridge and the articulation with the centrum, referred to here as the lateral plate of the neural arch (fig. 13A, B). When viewed from above (fig. 13B), the curved ridges narrow to a waist in the middle, giving each vertebra an hourglass shape. Comparing the sizes of C-3 to C-7, C-3 is the longest (antero-posterior), and also the narrowest, while C-7 is the shortest and widest (fig. 6).

The sides of the neural arches that form a flat vertical plate have borders approximating a trapezoid (figs. 13A, 14). Lateral plate C-3 is almost a rhomboid, and plates C-4 to C-7 become progressively narrow (anterior to posterior). The height of the lateral plates from C-3 to C-7 remains unchanged. The sides of the neural arches terminate at a jagged articulation with the centrum. The diapophyses are found near the termination. The centra of C-3 to C-6 participate to a minor extent in its formation. These diapophyses, which will also be termed cervical transverse processes, are directed ventrad at about a 45° angle (fig. 13C). The transverse processes of C-3 to C-6 form an immobile articulation with the rib tubercula. That of C-7 has a gliding joint, with a rounded articular surface. The diapophysis of C-3 is the smallest of the series, the largest being on C-6. The cross-section changes from round (at diapophysis C-3) to horizontally oval (at diapophysis C-6). C-7 has the longest diapophysis, and its oval cross-section is tilted, with the dorsal border facing anteriorly (fig. 14).

The diapophyses of C-3 to C-6 are on the anterior half of the vertical neural arch plate, but posterior to the level of the prezygapophyses. That of C-7 occupies a position in the middle of the plate, at about 1/3 of the plate surface dorsal to its central suture. All of the cervical diapophyses articulate immovably with their respective rib tubercula.

Almost all of the surface of the vertical plate is occupied by the massive multiple origins of mm. longissimus capitis profundus, and longissimus capitis superficialis (figs. 46, 47).

The centrum-to-neural arch suture is identical with the basi-occipital-to excoccipital suture. The procoelous centrum bears a deep cotyle anteriorly and a rounded condyle posteriorly. The cervical condyles are smaller in diameter than the centrum, in contrast to the condyles of snakes, for example, where the condyles are as wide as the centrum. The smaller condyle size gives the appearance of a hemisphere that is stuck on to a flat surface. The lip or labrum of the cotyle can connect with the centrum shoulder that surrounds the condyle. This arrangement extends the bony-cartilagenous socket strongly and completely around the condyle.

The parapophyses (figs. 6P, 13C, 14). form a series on the ventro-lateral corners of vertebrae C-3 to C-7. Their broad rugose articular surfaces meet the corresponding rib capitula. The parapophyses are attached to the anterior half of each centrum, and increase in size from less than ¼ of the centrum length at C-3, to greater than ½ of the centrum length of C-7 (fig. 6). Note that there is an abrupt change in size and orientation of the parapophysis of the first thoracic vertebral centrum (D-1), and that this indicates C-7 as the most posterior of the cervical series of vertebrae.

The midventral hypapophyses are largest at C-7 and smallest at C-3 (fig. 6). They extend anteriad to a pointed tip, and have a straight, horizontal ventral edge (fig. 14). The hypapophyses greatly increase the surface area for the origins of the hypaxial musculature and their tendons. The hypapophyses are found as far back in the column as D-5.

E. Cervical Ribs

There are seven pairs of cervical ribs. Except for the atlas and the axis, each vertebra has one pair attached. The axis lacks ribs. Instead of joining the axis, the second pair of ribs joins the odontoid, which is derived from the atlas. In addition to the odontoidal ribs, the atlantal ring has its own pair of ribs.

All of the ribs except the first are bicipital, and quite distinct from typical trunk ribs.

Vallois (1922) stated that the atlas is provided with a pair of short oblique ribs. However, all specimens that were examined show the first ribs to be exceedingly elongated by comparison to the other cervical ribs (fig. 15A). Perhaps Vallois (1922) was referring to the condition for Crocodilus which has shorter first ribs than Alligator.

The first rib (fig. 15A) has a single head that probably represents a capitulum. That the tuberculum is probably lost is suggested by the reduced nature of the tuberculum of the second rib. The posterior extremity of the first rib corresponds in life to the position just medial to the end of the pterygoid musculature, i.e., the rib tip is hidden behind the end of the lower jaw musculature. This landmark provides a crude estimate for the bulk of the pterygoid musculature in skeletally prepared specimens, or in fossil alligators.

Depending upon its state of retraction, the tip of the rib can reach to the end of the third vertebra, or the middle of the fourth vertebra. Half way along the rib, the dorso-lateral edge is expanded for the tendinous attachments of mm. ilio-costalis cervicis and ilio-costalis capitis. The tendinous sheet that is the anterior tendinous cover for m. ilio-costalis cervicis extends posteriorly as a direct continuation of the postero-dorsal margin of the first rib. The aponeurosis for m. iliocostalis capitis extends anteriorly from this spine, crossing the former, deeper tendon, at a right angle. The area of overlap corresponds to the expanded postero-dorsal margin of the first rib.

A diamond shaped area on the posterior half of rib-1 carries the fleshy origin of m. ilio-costalis capitis (fig. 15A). The anterior head of the rib has a semi-lunar cross-section, with a ventro-lateral convexity, that is firmly united with the hypocentrum of the atlas. The entire deep surface of the first rib is shallowly concave and fits, as a cover, over the second and third ribs.

Hypaxial muscles to the occiput originate ventrally on the proximal half of the first rib. The rib tip is swollen to receive tendons from: 1) m. sterno-costalis; 2) m. levator scapulae; 3) mm. subvertebro-costales.

The medial border of the first rib is attached to the hypapophyses of the second and third vertebrae by an aponeurotic sheet.

The second rib is elongated, but only two-thirds as long as the first rib (fig. 15B). Therefore, the first rib overlaps the posterior end of the second rib. There is a large capitulum articulating with the odontoid, but the tuberculum is rudimentary and makes no direct articulation (its connection to the odontoid is entirely ligamentous in A. mississippiensis).

The third rib (figs. 16(1), 16(2)) is strongly bicipital. The tuberculum is narrower and longer than the capitulum. The tuberculum and capitulum are immovably sutured to the neural arch and centrum, respectively. Both leave the vertebra in a ventral direction, appearing as transverse, lateral struts. At the point where the capitulum and tuberculum meet, the rib sends one process anteriorly, and another longer process posteriorly. The first and second ribs cover the entire longitudinal portion of the anterior and posterior processes of the third rib. It is important to emphasize that the two rib heads are in the transverse plane, while the longitudinal processes are in the parasagittal and frontal planes, essentially at right angles to both rib heads.

Ribs #4 to #7 are similar to rib #3 except that, in the series, the tuberculum and capitulum reach equal importance at the level of rib #7. The anterior and posterior processse are also of equal size at rib #7. The tuberculum of rib #7 has a synovial joint, a condition not seen in the other cervical rib joints which are symphysially joined.

The tubercula of ribs #6 and #7 exhibit a special process at their posterior, dorsal margins (figs. 16(3), (4), (5)). This process is a short, straight, roughened area for the attachment of a tendinous band. These tendinous bands join the longissimus system and are named here "ilio-costalis cervicis tendon 6b, and 7b". The presence and development of this process on a rib indicates the extent of the longissimus musculature and can be used as a landmark for such a soft structure, for inference from skeletons and fossils.

The posterior edge of all the tubercula, and of the posterior rib processes, support the septae of m. ilio-costalis cervicis.

All of the cervical ribs are imbricated (figs. 6, 8). The anterior process of one rib slides longitudinally within the posterior process of its preceding neighbor.

F. Vertebrae of the Thoraco-lumbar Region

In order to describe the epaxial myology of the neck it is important to examine the simpler epaxial system of trunk muscles, and to show how the basic pattern of musculature is related to the vertebrae that they move.

The seventeen thoraco-lumbar, or dorsal vertebrae are relatively uniform, but show minor gradual changes that progress from anterior to posterior. A typical dorsal region vertebra possesses short neural arches that carry: 1) the neural spine; 2) pre- and post-zygapophyses; 3) the transverse processes. The neural arches articulate with the procoelous centrum. The spool-shaped centrum bears a large condyle and a deeply concave cotyle.

The neural spines of D-1 to D-4 are narrow, high, and intermediate in shape between the typical thoracic and typical cervical neural spines. The neural spines of D-1 are posteriorly directed, and D-2 and D-3 show lateral, knob-like swellings, as well as being antero-posteriorly flattened (fig. 8). D-2 and D-3 have the longest neural spines (Table I) , even though Vallois (1922) stated that the neural spines elongate up to D-4, and then become shorter. The maximum neural spine size of D-2 is an important indication of the placement and functioning of the m. transverso-spinalis capitis.

The neural spines of D-5 to D-17 are plate-like, having a square lateral surface. The dorsal tips are horizontally flattened and laterally expanded. The tips are about twice as broad anteriorly as they are posteriorly.

In cross-section the neural spines resemble the letter "T". In life, the dorsal neural spines are held together by strong ligamentous sheets, the posterior edge of one blade is fastened to the anterior edge of the next succeeding blade by this sheet-like ligament. In older individuals the interspinous ligaments ossify considerably, adding to the blade-like appearance of the neural spine.

The pre- and post- zygapophyses form flat, simple oval surfaces. The prezygapophyseal surfaces face medially and are oriented at a 45° angle to the horizontal. The postzygapophyses have complementary surfaces for the prezygapophyses, and are slightly set off from the neural arch and neural spine on a stout, conical foundation of bone.

The transverse process of D-1 is in the center of the neural arch plate. By the level of D-4 the transverse process occupies a position that is between the pre- and post- zygapophyses, on the dorsal margin of the lateral neural arch plate. From D-1 to D-4 the transverse processes articulate only with the rib tubercula and represent diapophyses. From D-5 to D-13 the parapophyses join the diapophyses.

At D-5 the more anterior parapophysis is found about mid-way along the length of the transverse process. The parapophyses show a gradual migration to D-13, where it becomes nearly terminal. On D-14 the two rib articulations become fused. D-15 to D-17 do not possess bony ribs. The transverse processes jut out laterally and approximately horizontally, but those of D-5 to D-10 form a very shallow "V". From D-5 to D-17 the transverse processes are expanded and blade-like. The dominance of the transverse processes is underlined by the prezygapophyses being carried on the processes.

The parapophysis is on the centrum from D-1 to D-3, but at D-4 both centrum and neural arch join to build the parapophysis. Hypapophyses are found on centra of D-1 to D-5. The condyles are all well rounded, but posteriorly they become slightly dorso-ventrally compressed. The lip around the condyle of D-17 is expanded to articulate with the first pair of sacral ribs, thus greatly enhancing the lumbo-sacral joint.

G. Ribs of the Thoraco-lumbar Region

The two heads of the ribs of D-1 to D-4 are in the transverse plane. All of the rest of the ribs have their two heads in the frontal plane. The ribs of D-12 to D-14 are reduced or rudimentary.

The posterior edge of each rib bears a crest that carries the aponeurotic myoseptum of m. ilio-costalis dorsi. The deep surface bears scars from the hypaxial intercostal muscle series. The tip of the ribs are flattened (sometimes knob-like) for articulation with the cartilagenous ribs.

MYOLOGY

INTRODUCTION

Vertebrate axial musculature has been studied by many workers. Nishi (1919) described and homologized the axial muscles of amphibians, reptiles, and mammals. The Crocodilia were not studied by Nishi. The Crocodilia are not included as part of the "fish-to-man" lineage, and as a consequence, the group did not receive much attention from early twentieth century anatomists. Since the Crocodilia may not have appeared to be very divergent from other reptiles that were studied more intensively, their specialized nature went unnoticed. In other words, it was assumed that the crocodilian muscles were the same as those of reptiles that had been studied in detail. This assumption led to statements of homology of muscles such as those seen in Anderson (1936).

Olson (1936) reconstructed the axial musculature of various extinct forms such as *Eryops*, *Diadectes*, and *Dimetrodon*. Olson (1936) relied upon Nishi's (1919) analysis of *Iguana* to provide a guide for reconstructions. It should be stressed that accurate analysis of the Crocodilia and other archosaurs is absent in these and other studies of axial musculature. Ostrom's (1961) reconstruction of hadrosaurian necks is based almost entirely on Nishi (1919), and included some homologies with lizards that may or may not be true for archosaurs.

Colbert (1946), in reconstructing *Sebecus*, included axial musculature as part of his functional analysis of this fossil crocodilian. As discussed below(pg. 181), Colbert's placement of muscle insertions, and choice of muscle homologies, bear little resemblance to the actual details of the occipital and cervical morphology.

Many of the early students of crocodilian musculature relied upon drawing muscular homology from the mammals, particularly from human musculature, and neglected reptilian patterns of homlogy. As was well illustrated by Vallois (1922), this practice generated a host of confusing terminologies and misrepresentations of the musculature and of their homologies. For example, Hair (1968) tried to fit crocodilian musculature into the mammalian pattern. Muscles such as m. sterno-mastoideus (Hair, 1868) do not have the same meaning for Crocodilia as in mammals since a true crocodilian mastoid is lacking. Furthermore, by using a mammalian model, Hair missed the overall organization of the reptilian axial musculature as exemplified by Alligator mississippiensis, and he misidentified some muscles of the neck.

The axial musculature of reptiles is, in general, far more differentiated than that existing in present day Salientia and Caudata. This greater differentiation is probably due to the greater degree of terrestrial adaptation inferred among early reptiles. Terrestrial adaptations would include muscular and skeletal specializations for locomotion and feeding, as well as for simple support against gravity.

Regional differentiation of the vertebral column is one example of such specialization.

The axial musculature of the crocodilian cervical region must have evolved from a less differentiated condition at some point in its ancestry. The primitive neck region probably possessed the same general plan of organization seen in the less modified trunk. Modifications of the primitive neck region should therefore retain elements resembling the organization of the trunk. Muscles not derived from a generalized trunk muscle system would then be considered as a de novo development. Excluding new musculature, the various epaxial cervical muscles are assignable to one of three general muscle systems.

The three muscle systems are best illustrated in the thoraco-lumbar region. It is presumed that the three muscle systems of the thoraco-lumbar region represent a truly primitive condition for A. mississippiensis (and other Crocodilia) since these three systems are found in all living reptiles, mammals and birds, but not in fish and amphibia. These three systems are (naming from ventral to dorsal): 1) the ilio-costalis system; 2) the longissimus system; and the 3) transverso-spinalis system;(see figs. 17, 18, 19).

This is the nomenclatural framework adopted by Vallois (1922), and it will be carefully followed in this analysis.

Assignment of muscles to any one of these three systems is facilitated by examination of the innervation, and by the relationships of the muscle to the surrounding connective tissues (fig. 18A). The hypaxial cervical musculature is relatively simple and will be considered separately from the epaxial systems.

In the neck mechanical restrictions are place on the capabilities of the musculature by the morphology of the cranial and vertebral bones. These mechanical restrictions (i.e. the physical arrangement of muscle, tendon, bone, joint, etc.) limit the evolutionary potential in terms of feeding behavior. With a given morphology the crocodilian head and neck must adequately perform such varied and mechanically complex functions as capture of prey, manipulation and swallowing of prey, nest building, and care of young. Solution of all of these problems requires a high degree of refined adaptation. Considering the large sizes attained by some Crocodilia, it will become apparent that the crocodilian neck is a highly specialized structure that meets its functional demands. A brief concrete example is that it was found that the neck of _A. mississippiensis_ cannot flex ventrally so the function of ventral flexion is handled entirely by the occipital condyle-atlas-axis joint complex.

The following is first a description of the axial musculature of the trunk in _A. mississippiensis_, and then a description of the axial musculature of the neck and occipital regions. This order of presentation is used to demonstrate that the generalized plan of organization of the musculature in the trunk can be abstracted and applied to the neck region (see Table II). An effort is made to follow the order of presentation of the most recent similar study (Vallois, 1922). Although not explicitly stated by Vallois (1922), in his study he ordered the muscle systems consistently from ventral to dorsal. Under this method the first muscles described are in the ilio-costalis system, and the last muscles to be described belong to the transverso-spinalis system.

Table II is an abstract of the musculature representing the three epaxial systems, considered in three different regions of the body: 1) in the trunk; 2) in the neck (cervical); 3) between head and neck (cervical - occipital). This should greatly facilitate comprehension of the groupings and clarify the system of nomenclature that I have adopted and developed.

A synopsis of the origin, insertion, and action of each epaxial muscle is included in Appendix B.

Terminology and General Introduction to the Epaxial Musculature of the Trunk Region

The somatic musculature of the cervical region is ontogenetically derived from segmented myotomes, as is the musculature of the trunk and tail. The various groups of cervical muscles of the adult show serial homology with trunk muscle segments, since they all develop from similar myotomal segments. Although the cervical muscles are highly differentiated by functional specializations, they can best be studied from the viewpoint of serial homology with the trunk region. Studying the neck muscles by functional groupings does not reveal developmental and phylogenetic relationships between muscles. A description of the basic, simple plan of the trunk musculature is therefore necessary before the cervical muscles can be fully considered.

The epaxial trunk musculature is diagnostically distinguished from the hypaxial muscles by innervation. During embryonic development, a segmental spinal nerve divides into a dorsal ramus serving the epaxial series of muscles, and a ventral ramus for the hypaxially derived muscles. The main trunk of each ventral ramus remains deep to the vertebral transverse processes and ribs, beneath their posterior edge. The dorsal ramus extends between successive transverse processes and lies external to the ribs.

The epaxial musculature of the trunk is divisible into three distinct parts, each being served by its own branch of a dorsal ramus (figs 17, 18, 19, 20). Most ventral and lateral of these parts is the ilio-costalis system, which covers the bony ribs and is limited medially by the costo-transverse articulations and an intermuscular septum. The next of these three divisions is the longissimus system, dorsal and medial to the ilio-costalis system. The longissimus muscles cover the transverse processes of the vertebrae. This series is limited medially by the dorsal intermuscular septum. The third of the divisions, called the transverso-spinalis system, is located dorsal and medial to the longissimus system. The complex transverso-spinalis muscles cover the sides of the neural spines and the dorsal surface of the neural arches (including the postzygapophyses). Its lateral limit is the dorsal intermuscular septum. As will be shown later, these same three epaxial systems are found in the neck region, modified from the simple condition in the trunk by the specialized functioning of the neck and head.

The thoracic and lumbar regions will be referred to together as the "trunk". The ilio-costalis system in the trunk is represented by m. ilio-costalis dorsi (figs. 17A, 18A, 19, 20). Since "trunk" is equivalent of the "dorsal" region, a confusing archaic term by itself, the muscles of the trunk have historically received the appendix "dorsi" to denote placement in the trunk region.

The longissimus system (figs. 17B, 18B, 19, 20) in the trunk consists of two divisions. The part dorsal to the vertebral transverse processes is m. longissimus dorsi. The part between transverse processes, mm. intertransversarii dorsi, seems to be a small ventral division of m. longissimus dorsi.

The transverso-spinalis system of the trunk (figs. 17C, 18C, 19, 20) is more differentiated and complex than the other two epaxial systems. Its more superficial portion is divided into four parts which are limited by the m. longissimus dorsi and the dorsal intermuscular septum laterally, and the nerual spines medially. From lateral to medial these four parts are: 1) m. tendino-articularis dorsi; 2) m. articulo-spinalis dorsi; 3) m. spino-articularis dorsi; and 4) m. neuro-spinalis dorsi.

Two additional deeper series of transverso-spinalis muscles , mm. interarticulares dorsi and interspinales dorsi are best grouped collectively with m. neuro-spinalis dorsi.

Each segment or metamere of the thoraco-lumbar region contains all of these muscles in one form or another.

In the neck, those muscles that attach only to the neck vertebrae are appended with the name "cervicis". Using this terminology, m. ilio-costalis cervicis, m. longissimus cervicis, and m. transverso-spinalis cervicis are restricted to the neck region, i.e., they do not insert upon the head or originate in the trunk. Those muscles originating from the neck and inserting on the head are appended with the term "capitis". The "cervicis and "capitis" musculature will be dealt with in a separate section that follows the description of the simpler trunk musculature (Table II).

Detailed Description of the Epaxial Muscles of the Thoracic and Lumbar Regions

A. Ilio-costalis System

M. ilio-costalis dorsi (figs. 17, 18, 19, 20, 21, 22, 23)

M. ilio-costalis dorsi is a segmented muscular sheet associated with the ribs. The dorsal limit of this muscle is the costo-transverse articulation of ribs with vertebrae (fig. 18A), and the tip of the transverse processes of the vertebrae without ribs. The muscle ends ventrally where the bony ribs articulate with the cartilagenous ribs (fig. 21). The muscle fiber bundles run longitudinally between the 7th rib and the anterior edge of the ilium. The system continues in front of the 7th rib into the cervical region, but is absent posterior and dorsal to the ilium in the sacral and caudal regions.

Each metameric myoseptum is the superficial boundary for the muscle that extends from the posterior edge of a rib, and attaches on the surface of the next posterior septum (figs. 21, 22). The muscle fiber bundles take a direction normal to the rib axis. These bundles originate from a myoseptum and lateral rib surface, oriented normal to these surfaces, and insert on the deep face of the next anterior myoseptum (fig. 21). The dorsal limit of these myosepta is very complex. The costo-transverse joint marks the point where each myoseptum forms a blind-ending wedge which underlies the lateral edge of mm. intertransversarii dorsales between the vertebrae.

The tough fascia which covers all of the surface of the muscle, although mostly superficial, is firmly anchored at the costo-transverse articulation. This same fascia continues superficially in the dorsal direction over all of the other epaxial muscles, forming bands of fascia, but without attachment to the other muscles (fig. 24). These fascial bands end at the most dorsal tip of the neural spines. Along the way to its connection with the neural spines, tendons of m. longissimus dorsi, m. tendino-articularis dorsi, and m. articulo-spinalis dorsi, insert into this fascial band. The band is strongly adherent to the deep surface of the osteoderms and skin. This fascia must be removed to expose all deeper structures. Since it adheres to the skin it is usually removed with the skin during dissection and has previously escaped attention.

The myoseptal junctions slope posteriorly (fig. 18B). The junction of one septum with the next posterior septum occurs over the second intercostal space, posterior to its rib of origin (fig. 22). This puts the bulk of the muscle fibers directly over each rib. Cartilaginous thickenings form bifid uncinate processes in the myosepta a short distance dorsal to the end of the bony rib, but the uncinate processes do not seem to relate directly to any muscular structures. *M. obliquus externus superficialis* originates from the ventral borders of the septae of *m. ilio-costalis dorsi*, as well as from the cartilaginous ribs (fig. 21). The uncinate cartilages may be present to support stresses set up in the iliocostal fascia that results from contraction of *m. obliquus externus superficialis*, even though this muscle has no direct attachment to the processes. The nerve to *m. obliquus externus superficialis* pierces the fascia of *m. ilio-costalis dorsi* at the level of the osseous-cartilaginous rib junction, posterior to the rib (fig. 25). Thus, this junction appears to be an important anatomical landmark. The next group of muscles deep to *m. ilio-costalis dorsi* is the intercostal series, of hypaxial derivation (figs. 19, 20).

Towards the posterior thoracic region the ribs become reduced in size, culminating with the rib-less lumbar vertebrae. As the ribs diminish in size, so do the segments of *m. ilio-costalis dorsi*. When the ribs disappear in the lumbar region, *m. ilio-costalis dorsi* maintains its segmental structure by attaching to the lumbar transverse processes.

Each lumbar segment that is associated with the tip of a lumbar transverse process is maintained as far as the attachment on to the anterior edge of the ilium. Progressing from anterior to posterior in the series, each rib becomes shorter and thus the dorsal and ventral origins of each septum begin their attachments closer together, with each succeeding segment. However, the intersections between successive septa in the fleshy m. ilio-costalis dorsi maintain their length by inclosing the posterior muscle fibers of its segment. This leads to the situation that each segment produces an aponeurosis which is "too large" posteriorly. The production of "too much" aponeurosis is anatomically resolved by the membrane wrapping around the muscle segment. Caudad, rib size diminishes so rapidly that the dorsal and ventral edges of the m. ilio-costalis dorsi aponeurosis approach each other to give the appearance of rolling up around the enclosed muscle segment. This "rolling up" process is completed with the absence of ribs in the lumbar region (fig. 23). The dorsal and ventral origins of a lumbar aponeurosis both meet at the lumbar transverse process, since rib length equals zero at this point. In this respect m. ilio-costalis dorsi of the lumbar region resembles the conical arrangement of m. longissimus dorsi, but with the apex of each cone pointing craniad (fig. 23).

Care must be taken when identifying m. ilio-costalis dorsi in the lumbar region because m. obliquus internus (a similarly disposed hypaxial muscle, with respect to the ribs) strongly resembles m. ilio-costalis dorsi. M. obliquus internus also rolls up and attaches to the transverse processes immediately ventral to m. ilio-costalis dorsi. Because of their proximity and disposition, isolation of two distinct muscles is easily overlooked.

The posterior insertion of m. ilio-costalis dorsi is upon the anterior edge of the ilium by a thick tendon laterally, and by fleshy fibers of the last segment medially. The lumbar segments thin out to a small mass. Vallois (1922) reported only two lumbar segments in his single specimen, but three specimens dissected for this feature (including the one of 2 meters length) showed complete correspondence between number of septa and lumbar transverse processes.

B. Longissimus System

1. M. longissimus dorsi (figs. 17, 18, 19, 20, 26, 27, 28,29, 30)

M. longissimus dorsi consists of a longitudinal series of metameric bundles lying dorsal to the transverse processes of the thoracic and lumbar vertebrae (fig. 18). Superficially, the muscle appears to be a long cylinder interposed between mm. ilio-costalis dorsi and transverso-spinalis dorsi (figs. 17, 18, 19, 20, 26).

M. longissimus dorsi continues posteriorly over the two sacral ribs, without interruption, into the tail. The system is also continued into the cervical region, where it splits to insert on the neck, and the occiput of the skull.

On close examination, the cylinder which forms m. longissimus dorsi is found to be composed of a long series of nested cones (figs. 18, 26), with apices directed posteriorly. Each cone corresponds to a thoracic or lumbar vertebra and consists of an aponeurotic cover that encloses longitudinal muscle fibers.

The aponeurosis is characterised superficially by a band of decussating fibers of connective tissue (fig. 18B). The deeper part of the conical aponeurosis is covered by muscle fibers and looses the criss-crossed appearance to take on the appearance of a smooth, glistening sheet. The nearly parallel fibers in this sheet converge posteriorly to an apex that is closed around the muscle within. Each aponeurotic cone completely encircles the next anterior cone (figs. 26, 27B).

Muscle fiber bundles: The muscle fiber bundles of each segment originate and insert on two adjacent aponeurotic cones (fig. 27C), thus filling the space between. Careful dissection reveals that the fiber bundles are arranged in curved, sagittal sheets (fig. 27C). The sheets originate on the inner surface of one aponeurotic cone and insert on the outer surface of the deeper, enclosed cone (of the next anterior aponeurosis). The bundles continue their origin into the tip of each cone. The ventral-most layer of fibers take origin from the dorsal surface of a transverse process and insert on the deep surface of the next anterior aponeurotic cone. There is a small division of bundles, the intersegmental bundles, that communicate through a fenestra between cones (fig. 28). The intersegmental bundles originate on the dorsal intermuscular septum, traverse the fenestra in the anterior, medial corner of an aponeurotic cone, and insert on the dorsal-medial-outside surface of the next anterior cone.

Fascia: Each superficial criss-cross band (= band of decussating longissimus aponeurosis fibers) is itself covered by the superficial layer of fascia that extends from the ilio-costalis fascia (fig. 24), and in the alligator, each criss-cross band corresponds to the neural arch medial to itself. The anterior origin of each aponeurotic cone is complex. Laterally, superficial fibers of the criss-cross band join the septa and deep fascia of m. ilio-costalis dorsi. Medially, the cone is anchored on the dorsal intermuscular septum (fig. 28). Superficial fibers from each band insert into the skin and osteoderms along with the fascial band of m. iliocostalis dorsi.

The dorso-medial fibers of a criss-cross band join the lateral edges of the superficial tendons of m. tendino-articularis dorsi (fig. 18B) (the most ventrolateral of the four superficial transverso-spinalis dorsi muscles).

The floor of an aponeurotic cone originates from the posterior edge of a transverse process, on a ridge that extends from the lateral extremity of the process to the medial base of the process. Where the ribs are present, the cones are laterally attached at the costo-transverse articulations. In the lumbar region, the cones attach to the lateral ends of the transverse processes. There is a scar on the dorsal, medial surface of the transverse process which marks the medial-most origin of the dorsal intermuscular septum (fig. 30). This scar divides the dorsal surface of the transverse processes into a lateral area for m. longissimus dorsi, and a medial triangular area for fibers of m. tendino-articularis dorsi (fig. 30).

The criss-cross band is continued anteriorly by a thin fascia which encloses the muscle fibers and attaches to the next anterior criss-cross band. The muscle fibers between two successive aponeurotic cones receive a spinal nerve branch, which issues from behind the vertebra associated with the anterior cone. Thus, the segment of muscle is associated with the vertebra just in front.

It should be kept in mind that the aponeurotic cones are not truly round cones, nor are they complete. The cones are anchored at four corners and present a more or less quadrangular base (as opposed to a circular arrangement as shown in fig. 27C) that tapers out to a wedge (fig. 28).

The flat floor comes from the flat surface of a transverse process. The four corners of the base of a cone are the attachments to: 1) lateral tip of a transverse process; 2) medial ridge on a transverse process (area of scar); 3) lateral, dorsal attachment to skin fascia and fascia of m. ilio-costalis dorsi; 4) medial attachment to the tendon of m. tendino-articularis dorsi.

The medial anterior border of each cone has an open fenestra which permits communication of fibers between segments (fig. 28). Because of the conical form of the fascia, this opening is probably reduced to a slit in the living animal, especially since in life the cones would be under tension. Both dorsal and ventral edges of this slit are attached to the dorsal intermuscular septum in line with the posterior edge of the transverse process.

A cone appears to be formed from the fusion of two components (fig. 29B): 1) laterally and ventrally, a broad aponeurosis from the transverse process; and 2) medially, an aponeurosis from the dorsal intermuscular septum. Incomplete joining of these two components results in the open fenestra for intersegmental fibers. The union of the two component aponeuroses joins the two sets of fibers.

Figure 29 shows a cone that is longitudinally slit open, and the muscle fibers cleaned out. The cone is three segments long and is typical for the alligator. Vallois (1922) said that the tip of the cone was open so that muscle fibers from inside of one cone could enter another cone. This is not the case, as shown by the closed tip in figure 29.

2. Mm. intertransversarii dorsales (figs. 26, 27B)

These muscles consist of muscle fibers joining two adjacent transverse processes, from the caudal edge of one, to the cranial edge of the next behind (fig. 27B). The muscle fibers are actually the deepest continuation of m. longissimus dorsi (figs. 26, 27B). These fibers are not always easily distinguished from the ventral cone fibers of m. longissimus dorsi. The lateral extremity of this muscle is underlain by a wedge of m. ilio-costalis dorsi.

C. Transverso-spinalis System (figs. 17, 18)

This muscle system is the most complex of the three epaxial systems. In A. mississippiensis its more superficial portion is composed of four distinct groupings of muscles in the trunk region. The system links together the neural spines and the zygapophyses. From lateral to medial the four muscles are: 1) m. tendino-articularis dorsi; 2) m. articulo-spinalis dorsi; 3) m. spino-articularis dorsi; 4) m. neurospinalis.

The deeper portions of this muscle system includes two intervertebral muscles, mm. interarticulares and interspinales.

1. M. tendino-articularis dorsi (figs. 18, 27, 30, 31, 32, 34, 50)

This muscle, the most lateral of the four subdivisions of the transverso-spinalis system, consists of muscle fibers that are bipinnately arranged about a central tendon. Each muscle-tendon segment spans four vertebrae (figs. 18, 32). The tendon superfically appears as a triangular aponeurosis with its apex anterior (fig. 18B). Laterally, the dorsal intermuscular septum separates m. tendino-articularis dorsi from m. longissimus dorsi. This septum attaches to the prezygapophysis (on its posterior, ventral base) and forms a tendinous arch between the vertebrae (fig. 30). Medially, another septum, anchored to the base of the transverse process, marks off a triangular area on the transverse process (fig. 30). The triangular area on the transverse process between these two septa is the fleshy origin of m. tendino-articularis dorsi. The medial septum separates m tendino-articularis dorsi from the next medial muscle, m. articulo-spinalis dorsi (fig. 34). The two septa form a wedge resting on the transverse process that resembles the bow of an ocean liner.

Each superficial triangular aponeurosis corresponds to a vertebra. The base of this triangle is caudal. The lateral corner of the base is continuous with the medial corner of the base of the aponeurosis of m. longissimus dorsi (fig. 18B). The lateral corner is also attached to the dorsal intermuscular septum. The medial corner of the aponeurotic triangle connects with the tendon of m. articulo-spinalis dorsi, as well as the intermuscular septum between m. tendino-articularis dorsi and m. articulo-spinalis dorsi. The medial and lateral connections of the aponeurotic triangle complete a complex arrangement of superficial tendons linking mm. longissimus dorsi, tendino-articularis dorsi, and articulo-spinalis dorsi (fig. 18B).

Following the superficial triangle anteriorly, the apex of each triangle undergoes a 90° counterclockwise twist on the left side of the animal (clockwise twist on the right side of the animal), as it descends deeply and craniad. It is covered by the next anterior aponeurotic triangle (fig. 31). Each segment consists of muscle fibers inserting on the left and right sides of the tendon and taking origin from the two bounding intermuscular septa (fig. 31). At the tip of a tendon, a bundle of muscle fibers continues anteriorly directly to attach to the vertebral transverse process.

Vallois (1922) described these segments as being imbricated on one-another as shingles on a roof (pg. 229; "ils sont imbriqués les uns sur les autres comme des tuiles de toit et une coupe transversale en recontrera toujours quatre superposés."). Actually, this is the case superficially, but when the tendons dip deeper and twist, the posterior segments take a lateral position with respect to the next anterior one.

Following the segments anteriorly, at the level of D-5, the septum between *m. tendino-articularis dorsi* and *m. articulo-spinalis dorsi* breaks down. Here is where the transition from trunk to neck begins for this muscle. Anterior to D-5 the segments take on the form of vertical triangular sheets, pressed tightly against one another, and joining with the *m. articulo-spinalis dorsi*. These anterior sheets insert on the dorsal intermuscular septum laterally, and end underneath the posterior surface of the prezygapophyses of the cervical vertebrae.

The lumbar segments of this muscle enlarge and the aponeuroses tend to curl under at the edges of their bases. At the level of the sacrum, the curling under process is completed into a conical arrangement, much as in *mm*. *longissimus dorsi* and lumbar *ilio-costalis dorsi*.

2. M. articulo-spinalis dorsi (figs. 18, 27, 33, 36, 50, 56)

Medial to m. tendino-articularis dorsi is m. articulo-spinalis dorsi (fig 18B). Superficially this muscle has the same appearance as m. tendino-articularis dorsi, with the exception that the aponeurotic triangle shows a posterior apex (fig. 18B). The anterior base of the triangle is attached laterally to the medial corner of the superficial tendon of m. tendino-articularis dorsi (figs. 18B, 31, 33). Medially, the corner of the base is drawn into a shining tendon that passes forwards, arching over two muscles (mm. spino-articularis dorsi and neuro-spinalis dorsi), and attaches to the expanded edges of the tip of a neural spine (fig. 18B).

As the apex of the aponeurotic triangle thins out posteriorly into a narrow flat tendon, it twists so that its deep surface comes to face medially. The tendon, with its bipinnate muscle fibers, is 5 vertebrae in length (fig. 33), not 7 as stated by Vallois (1922).

The muscle fibers take origin from an area of the anterior dorso-lateral surface of the postzygapophyses, and its lateral limiting septum. The terminal fibers that eminate from the tip of the tendon are equal in length to the distance between two postzygapophyses. If the muscle originates on the postzygapophysis of D-15, then its anterior insertion is on the neural spine of D-11. The first clearly defined segment of m. articulo-spinalis dorsi inserts on the neural spine of C-7.

Since the tendon twists, the anterior segments of the metameres are medial to the segments that follow behind.

The poorly developed fascial separation of this muscle series from its medial neighbors leaves only weak markings on the postzygapophyses, dividing them into lateral and medial surfaces. The septum limiting this muscle laterally is shared with m. tendino-articularis dorsi.

In frontal section, the lateral limiting membrane forms a zig-zag pattern as it encompasses m. tendino-articularis dorsi (fig. 34). M. articulo-spinalis dorsi fills in the complementary spaces left by the zig-zag septum, and its muscle fibers originate directly from that septum behind the prezygapophyses, as well as on the postzygapophyses.

As the dorsal extremity of the aponeurosis of m. articulo-spinalis dorsi passes over the two medial muscles (to insert on the neural spine), a negligible number of muscle fibers connect the tendon of all three muscles involved (mm. articulo-spinalis dorsi, spino-articularis dorsi, and neuro-spinalis dorsi).

3. M. spino-articularis dorsi (figs. 18, 33, 35, 36, 50, 56)

This muscle possesses a tendon inserted onto the anterior tip of a neural spine (fig. 35). The tendon extends into the muscle, descending ventrally and anteriorly, to disappear after crossing four segments. Muscle fibers continue along the direction of the tendon to take origin on the fifth anterior vertebra, thus, the entire muscle segment spans five vertebrae. The muscle fibers originate from the dorso-medial surface of the postzygapophyses. The tendons stay close to the neural spines so that four tendons are arranged, each dorsal to the succeeding, in a vertical plane(fig. 35). The entire set of the oppositely directed tendons of the next medial muscle (*m. neuro-spinalis dorsi*) is covered by the entire set of spino-articularis dorsi tendons (fig. 35).

4. *M. neuro-spinalis dorsi* (figs. 18, 35, 36, 50, 56)

Tendons from this muscle are medial to those of *m. spino-articularis dorsi*. The tendons insert on the posterior tip of a neural spine, just ventral to the insertion of *m. articulo-spinalis dorsi*. The tendons then extend postero-ventrally, one above the other, resting against the blades of the neural spines (fig. 35). Each tendon is four segments long, and muscle fibers continue for one more segment, bringing the total length to five segments for each individual segment of the muscle. Therefore, a lateral view of one neural spine reveals four tendons and one bundle of muscle fibers against the blade (fig. 35). The fibers take origin from the base of the neural spines. A minor amount of fibers originate on the neural spines and insert into the m. neuro-spinalis dorsi tendons that pass alongside the spines.

The tendons of this muscle pass alongside the neural spines in a nearly horizontal direction (fig 35B), only gradually inclining deeply. The tendons are very closely applied to each other and to the neural spines and form a tensile sheet. The tendons of m. spino-articularis dorsi form a comparable structure, with the direction exactly opposite those of m. neuro-spinalis dorsi (fig. 35B).

5. Mm. interarticulares (fig. 58)

The mm. interarticulares form a longitudinal system of fleshy bundles that hold the vertebrae together between the neural arches and postzygapophyses. They originate from the dorso-lateral surfaces of the neural arches, deep to mm. neurospinalis dorsi and spino-articularis dorsi. The origin also covers the medial, anterior half of the postzygapophyses. The insertion of mm. interarticulares is directly onto the vertical posterior rugose surface of the postzygapophysis of the vertebra immediately anterior. A central tendon strengthens the muscles internally. The dorsal rami of the spinal nerves take exit beneath these muscles, at the waist of the neural arches.

In the large specimen of A. mississippiensis there were two distinct parts of this muscle. The superficial part originated as noted. The deeper part took its origin from the anterior surface of the pillar of the prezygapophyses, immediately beneath the joint, thus, the deeper part actually skips over one vertebra to insert on the next .

6. Mm. interspinales

These muscles join the neural spines alongside their blades. They are particularly prominent towards the base of the neural spines, where they grade into the mm. interarticulares. But they are separable from these muscles by a thin fascial division. In the large specimen of A. mississippiensis they were poorly developed in the trunk, their function apparently replaced by elastic aponeuroses that ran between the neural spines. Vallois (1922) reported that he could not find this muscle in his two specimens, probably because, given their young age, the muscles were fused with m. neuro-spinalis (he looked at one A. mississippiensis and one C. palustris).

Detailed Description of the Epaxial Muscles of the Cervical and Occipital Regions

Introduction

The dorsal axial musculature continues from the trunk region through the neck region and inserts upon the occiput. The ventral axial musculature, although modified, inserts upon the occiput and the tips of cervical ribs. In contrast to these muscles, which are innervated by spinal nerves, the m. depressor mandibulae, a branchiomeric muscle, is innervated by cranial nerve VII; although this muscle superficially appears to be part of the occipital region, it is omitted since it does not fall within the province of the occiput as defined on page 17.

The three epaxial subdivisions of the dorso-lumbar region are represented in the neck by a seemingly complex arrangement of interwoven muscles. The complicated arrangement is simplified by consideration of the relationships of each epaxial division with its bony and connective tissue components as mapped out for the trunk region in the previous sections. For example, the transverso-spinalis system in the neck is concerned with neural spines and pre-and post- zygapophyses, as in the trunk; the cervical longissimus system, as in the trunk, is associated with the cervical transverse processes; the ilio-costalis system of the neck is associated with the cervical ribs. In the case where a skeletal structure is reduced or lost in the neck, such as the loss (or non-development) of epistropheal transverse processes, the musculature, in this case the longissimus system, may be present, although modified. Therefore, attention is given to morphological and topographical relationships, as well as innervation, and should not be overlooked as evidence when a muscle system is identified and characterised.

An example of identification and characterisation of a muscle system from morphological-topographical criteria was illustrated above in identifying the lumbar segments of m. ilio-costalis dorsi. In that case, modification of the muscle system was morphologically consistent with the reduction and loss of ribs (the functional basis of these modifications requires a different type of analysis, and must consider all structures involved, but as yet, the functional reasons behind this particular modification have not been determined).

Using the morphological approach, it is easy to identify those elements which are homologous, in series with the trunk muscles, and which are found in the neck.

Confusion has arisen in the past by inconsistent application of criteria of serial homology (see Vallois, 1922, and Hair, 1868) and also from usage of invalid mammalian homologies. Wherever possible, synonomy with other authors will be included with the description of each muscle. The synonomy also cites where that particular muscle was figured, named, or described; but many authors only partially described the neck muscles and may not be included under each muscle heading.

Dissection of the neck region is made very difficult by the complex fascia of the neck and shoulder. The dorsal intermuscular septum, as in the trunk, divides the transverso-spinalis system from the longissimus system. This fascia expands superficially to enclose all of the cervical and capital parts dorsally, and forms a separate compartment enclosing all of the cervical and capital parts of the longissimus system laterally. The dorsal intermuscular septum also forms the strongest adhesion to the skin and osteoderms of the neck, and must be cut through to reveal the musculature. Laterally and ventrally, the ilio-costalis system is enclosed within its own fascial compartment, but, since some of the ilio-costal myosepta merge with the longissimus system, the distinction between these two systems breaks down and is not readily apparent at the level of C-5 to C-7. However, the ilio-costalis system is distinctly separated from the longissimus system from the occiput back to C-5.

As in the trunk region, the epaxial musculature is described from ventral to dorsal. The last muscle of each series that is described inserts upon the occiput.

A. Ilio-costalis System

1. M. ilio-costalis cervicis (figs. 37, 39, 40, 41, 42, 43, 51, 62, 63, 64)

Meckel (1829) "ascending muscle of the neck"
Cuvier (1835) "enormous intertransversarii cervicalis
as descended from a cervicalis"
Hair (1868) "cervicalis ascendens"
Hoffman (1890) "cervicalis ascendens"
Vallois (1922) " ilio-costalis cervicis"

This muscle, the cervical representative of the ilio-costalis system up to the first rib (fig. 37), is continuous with m. ilio-costalis dorsi. The series is continued from the first rib on to the skull by m. ilio-costalis capitis. The same general relationships to the longissimus system and the ribs are maintained by m. ilio-costalis cervicis as was described for m. ilio-costalis dorsi. However, the cervical rib morphology is so highly modified that the muscular relationships are not readily apparent.

M. ilio-costalis cervicis forms a segmental muscular sheet on the ventro-lateral surface of the neck (figs. 37, 38, 39, 40). The longitudinal muscle fiber bundles are interrupted by six myosepta and terminate anteriorly on an aponeurosis which forms a tendon attached to the first rib. (fig. 38). This anterior aponeurosis may be considered as the first myoseptum in front of the first muscular segment. Thus, each of the seven cervical ribs possesses a septum and muscle segment; septum 1 and segment 1 are from the first rib; septum 2 and segment 2 are from the second rib, etc.

The entire muscle covers all of the cervical ribs. Its dorsal edge is related superficially to mm. longissimus capitis superficialis, and longissimus capitis profundus.

Septum 1 arises as a tendon from the posterior edge of the first rib (figs. 15B, 39), and broadens out posteriorly into a trough-shaped aponeurosis, concave posteriorly, that embraces segment 1 (fig. 42). Most of the fibers of segment 1 insert upon septum 2, but a sheet of the deepest fibers continues medially on the deepest surface of the entire muscle to join the fascia of m. longissimus cervicis (figs. 38, 42). This posterior insertion of the deep muscle sheet is not easily pinpointed since the fibers join up with muscle fibers of m. longissimus cervicis and make dissection of individual muscle fibers very difficult to carry out. In these dissections the sheet seems to arise from the deep surface of longissimus tendon 6 (fig. 42).

Septum 2 arises from the posterior edge of rib 2 and is the shortest of the myosepta. It forms a shallow trough, concave anteriorly, which receives muscle fibers of segment 1. It is pierced by nerves which serve segment 1. In frontal section, septum 2 is oblique, anterior-lateral to posterior-medial. It terminates freely in between segment 1 and 2 (the connective tissue becomes thin and disappears).. Most of the fibers of segment 2 insert upon septum 3. A few of the deepest dorsal fibers accompany those of segment 1 in joining the longissimus system at tendon 6 of that system.

Septa 3, 4, and 5 are similar to septum 2. Segment 3 resembles segment 2. In segment 4 there is a modification which becomes more pronounced as posterior segments are examined. Most of the fibers of segment 4 insert on septum 5, but some of the medial fibers form a sheet which joins a weakly developed tendon of the longissimus system. The weak tendon begins on prezygapophysis 5, arches over the longissimus system muscles and joins the medial margin of septum 5 of m. ilio-costalis cervicis. Those fibers from segments 1, 2, and 3, pass deep to this weak tendon on their way to join longissimus tendon 6 (fig. 42).

Segment 5 has most of its fibers inserting on septum 6. But the deepest fibers originate not from septum 5, but from the weakly developed longissimus tendon just described. These deep fibers form a sheet which disappears into the longissimus system, since it is covered superficially by the tendon and muscle fibers of segment 6 of both the ilio-costalis and the longissimus systems. The sheet inserts on the tendon 7 of the longissimus system, where it joins septum 7 of the ilio-costalis system.

Septum 6 and 7 differ from all of the other septa, and are similar to each other. Both arise from the posterior margins of ribs (ribs 6 and 7 respectively), but they soon divide into two parts (fig. 41B). In septum 6 the lateral part (part A), which forms about 5/6 of the septum, is exactly similar to the preceeding septa. The medial part (part B) forms a thin tendinous band which arches through the longissimus system and attaches to the under surface of the prezygapophysis of vertebra 6. Since septum 6, part B, becomes the tendon of a longissimus segment, and since it is associated with vertebra 6, it is called longissimus tendon 6 (even though it is the first well defined tendon of the longissimus series to appear in the neck).

Just before the split of the septum occurs, a nerve serving the preceeding segment pierces the septum. Muscle fibers which originated on septum 5 pass through the split and insert on septum 7, part B (= 7-B), and in this way become associated with the longissimus system (fig. 42). Segment 6 can be considered in three parts. laterally, most of the fibers form an ordinary segment that originates from 6-A and inserts on septum 7-A. The medial-most fibers from 6-A split off to form a sheet which passes between the split in septum 7, and inserts on septum 8-B. A third sheet arises from the medial tendon (6-B) and passes into the longissimus system, deep to septum 7-B. The muscle fibers of segment 7 are similarly arranged (fig. 42).

In summary, the medial fibers of m. ilio-costalis cervicis are intimately joined to the longissimus system, and the last two tendinous septa split, with the medial part becoming the septa of the longissimus system.

Septa 6-B and 7-B, although joining the longissimus system, originate from the ribs. A tubercle is found on the posterior-dorsal margin of ribs 6 and 7 , indicating the presence of this tendon (fig. 16). This arrangement continues into the trunk up to D-4. After D-4 the "B" tendon is part of the longissimus system and shifts from the ribs to the transverse processes.

There is a tough fascia, here called the investing fascia of the neck, that is superficial to m. ilio-costalis cervicis. This fascia is continuous with that covering m. transverso-spinalis capitis, and it dips down deeply between mm. longissimus cervicis and transverso-spinalis cervicis, to attach to the prezygapophyses. This is the dorsal intermuscular septum of the neck.

In order to delimit this muscle clearly during dissection, the pectoral musculature must be carefully isolated and removed from the investing fascia. Only after this is accomplished can the investing fascia be separated from the muscles within. Omission of this simple step in dissection has led to earlier confusion in the description of this muscle system (see Vallois, 1922).

2. M. Ilio-costalis capitis (figs. 37, 40, 48, 57, 64)

Rathke (1866) "sterno-mastoideus, anterior belly"
Hair (1868) "cervicalis ascendens"
Anderson (1936) "capiti sternalis, pars anterior
(anterior mastoideus)"

This muscle continues the ilio-costalis system from the first rib, up on to the occiput of the skull. The entire distal half of the elongated first rib is covered by this muscle (fig. 15).

The muscle originates from the first rib and fascia of m. ilio-costalis cervicis (septum 1). The origin forms a lozenge-shaped area on the distal half of the first rib. Some tendinous fibers, a continuation of the periosteum of the first rib (that arises from its posterior border) form a deep aponeurosis for this muscle. Some muscle fibers take origin from the superficial surface of the aponeurosis that forms septum 1 of m. ilio-costalis cervicis.

On its way to the occiput the muscle flattens out against the first rib and winds around m. longissimus capitis profundus (fig. 40). The belly is very broad and flat. The insertion is at the ventral margin of the paroccipital process by a broad, transverse tendinous sheet. The sheet is immediately ventral to the insertion of the stout m. spinalis capitis posticus tendon, and the fleshy fibers of m. epistropheo-capitis intermedius. Some of the lateral and superficial fibers insert directly on the insertion tendon of m. longissimus capitis superficialis as it joins the paroccipital process. Most of the fleshy fibers insert as a sheet under the paroccipital process, from the cranio-quadrate passage, mediad towards the foramen magnum (on a direct line). The medial termination of the insertion is directly above the jugular (vagus) foramen.

Since the origin is approximately in the vertical plane (on rib 1), and the insertion is in the horizontal plane (under the paroccipital process), the muscle undergoes a twist from origin to insertion (clockwise on the right side, counterclockwise on the left side). The fibers that originate posteriorly on rib 1 come to insert laterally on the paroccipital process, those originating anteriorly insert medially on the occiput.

A mark on the occiput in the form of a flange can be seen on the exoccipital bone of adult skulls. The flange forms a shelf which overhangs the cranio-quadrate passage and occupies the lateral half of the paroccipital process.

B. *Longissimus System*

The longissimus system continues without interruption from the trunk region through to the cervical region. In the neck, the longissimus system is divided into three parts or divisions. The dorsal-most division is *m. longissimus cervicis*, restricted to the neck vertebrae. The remaining two divisions, *mm. longissimus capitis superficialis* and *longissimus capitis profundus* originate from the neck vertebrae, but insert upon the occiput. *M. longissimus capitis superficialis* is the lateral muscle of the neck and is the only cervical longissimus that can been seen superficially. It is visible where it leaves the neck to insert on the tip of the paroccipital process. *M. longissimus capitis profundus* is the largest and deepest of the cervical longissimus muscles. Anteriorly, it crosses the first rib to insert ventrally around the occipital condyle on the basioccipital bone.

1. M. longissimus cervicis (figs. 38, 39, 41, 44, 45, 50, 51, 52, 57, 64)

Meckel (1829). "splenius colli"
Rathke (1866). "transverso-spinalis cervicis"
Hair (1868). "transversalis cervicis"
Hoffman (1890). "epistropheo vertebralis"
Vallois (1922). "longissimus cervicis"

The longissimus system is continued directly into the neck by m. longissimus cervicis. Of the three longissimus divisions in the neck, m. longissimus cervicis is the least conspicuous. The muscle retains part of the conical arrangement seen in the trunk (figs. 43, 44A, B, 43), but by the level of the fifth vertebra, the cone is reduced to a series of triangular muscular sheets , which are the dorso-medial portions of the former cone (fig. 44A).

M. longissimus cervicis appears to be a single, flat triangular muscle that originates from under the prezygapophyses of vertebrae 5, 6, and 7 (fig. 45). Its insertion is through a strong tendon to the postzygapophyses of the atlas (figs. 9A, 45). The flattened belly is pressed tightly against the dorsal intermuscular septum. The base of the triangular sheet appears wrapped superficially around mm. longissimus capitis superficialis and longissimus capitis profundus (fig. 44A). At its base the muscle fibers are joined by fibers from the ilio-costalis system (fig. 44A), and a clear distinction between the two systems at the point of junction is difficult to demonstrate, even with careful dissection.

A more detailed examination of the muscle reveals the following: Some of the muscle fiber bundles originate on the undersurface of prezygapophyses 5, 6, and 7, but most of the muscle originates as a series of individual segments from a series of tendinous arches. The segments are arranged in the form of sheets. The tendinous arches are formed from thickened bands of connective tissue in the dorsal intermuscular septum (fig. 45). The first band of thickening occurs in the septum below prezygapophysis #4, and forms a weak, incomplete arch over the deep longissimus muscles. That of prezygapophysis 5 also forms a weak arch, but in larger specimens (1 meter or larger) the band may complete its arch by attachment to proximal rib 5 (tendon 5-B of the ilio-costalis system). The tendinous arches from vertebrae 6 and 7 are well developed (fig. 46). Each muscular sheet is as thick as the tendinous band from which it originates. The part of the origin that is beneath the prezygapophyses is merely the continuation of the sheet as it follows along the tendinous arch. The sheets enclose each other, the anterior segments being more medial. The joined segments constitute an independent muscle from the level of the fourth vertebra forward.

The tendon of insertion to the atlas seems to join a corresponding tendon from m. transverso-spinalis cervicis, but both tendons are separated almost up to the common insertion by the dorsal intermuscular septum (fig. 45). The insertion is upon the lateral under-surface of the atlantal post-zygapophysis.

Vallois (1922) defined the muscle as "lying against the roots of the transverse apophysis, which extends the longissimus dorsi to the atlas or the axis". As alreadv shown, this is not the case. In addition, he stated that "the internal part of the deep face of the muscle sends out 6 tendons, which are inserted in the base of the cervical articulary apophyses ... in the alligator, the atlantal fascicle defaults." These 6 tendons are most likely large branches of dorsal rami of cervical spinal nerves (lrst to 6th spinal nerves). Furthermore, in all five of the dissected alligators, this muscle was definately attached to the atlas as described.

2. <u>M. longissimus capitis superficialis</u> (figs. 37, 38, 39, 40, 41, 47, 48, 51, 62, 63, 64)

Buttman (1826). "splenius capitis"
Meckel (1829). "trachelomastoideus"
Cuvier (1835). "either a "descending cervical", or
a small complexus"
Owen (1866). "trachelomastoideus"
Rathke (1866). "trachelomastoideus"
Hair (1868). "trachelomastoideus"
Miall (1878). "trachelomastoideus"
Hoffman (1890). "collo-squamosus"
Vallois (1922). "longissimus capitis superficialis"
Anderson (1936). "occipito transversalis lateralis"
Nishi (1938). "longissimus capitis superficialis"

<u>M. longissimus capitis superficialis</u> is a fusiform muscle immediately dorsal to <u>m. longissimus</u>

capitis profundus (figs. 40, 44B, 47, 48). The muscle fibers originate in four fleshy groups from the lateral plates of the neural arches of vertebrae C-5, C-6, C-7, and D-1 (fig. 47). These fleshy slips converge to insert bipinnately on a tendon. The tendon of insertion approximates a vertical strap that is fixed to the lateral extremity of the paroccipital process. The tendon wraps around the paroccipital process so that the dorsal and ventral margins of the tendon are curled mediad along the lateral-most exoccipital sutures (the paroccipital process).

Fibers of *m. ilio-costalis capitis* may insert superficially on this tendon, near its attachment to the paroccipital process (fig. 40). *M. longissimus capitis superficialis* partially covers the more medial and dorsal *m. spinalis capitis posticus* (fig. 40), and the tendon of insertion of the latter converges with (but does not join) the tendon of insertion of *m. longissimus capitis superficialis*.

Vallois (1922) stated that *m. longissimus capitis superficialis* is a muscle found "from the transverse process of the neck to the squamosal." As shown by the previous description, this statement is in error, since the muscle neither originates on the transverse process, nor does it insert on the squamosal bone. In addition, Vallois (1922) said it originates from the transverse processes of vertebrae C-2 through C-7 in the alligator. In the five specimens dissected for this study, this muscle occured only on vertebrae C-5 through C-7, and also on D-1 (eighth vertebra), in contrast to the observation that Vallois had made on a single specimen. The contribution from the transverse processes of D-2 (fig. 47) is considered as part of *m. longissimus dorsi* in the trunk region.

3. *M. longissimus capitis profundus* (figs. 37, 38, 39, 40, 44, 45, 46, 47, 48, 49, 50, 51, 61, 64)

Meckel (1829). one of the "intertransversarii"
Cuvier (1835). confused with part of the "cervical ascendent"
Rathke (1866). "intertransversarius" that absorbs the "rectus lateralis"
Hair (1868). part of the "cervical ascendent"
Miall (1878). "rectus capitis antici"
Hoffman (1890). "collo-occipitis"
Vallois (1922). "longissimus capitis profundus"
Anderson (1936). "occipitotransversalis profundus"
Nishi (1938). "longissimus capitis profundus"

M. longissimus capitis profundus is the largest of the deep cervical muscles (figs. 40, 44A, 47). It is covered externally by *mm. ilio-costalis cervicis* and *ilio-costalis capitis* (fig. 40). Medially are the vertebrae, and dorsal to this muscle is *m. longissimus capitis superficialis*.

The compound fleshy origins are on the expanded area of the lateral neural arch surfaces of vertebrae C-1 to C-6, and the transverse process of vertebrae C-3 to C-7, plus a small bundle of fascicles from the transverse process of D-1 and a minute fascicle from D-2 (not shown in fig. 47) (fig. 47). Soon after their origins, the large fleshy segments gather together to form a thick longitudinal column of muscle. The muscle fiber bundles insert into a shining aponeurosis that forms a tough envelope for the lateral, anterior portion of the muscle (fig. 48). The aponeurosis inserts on the margins of the basioccipital plate of the basioccipital bone. Medial to the insertion of the shining aponeurosis is the additional fleshy insertion for this muscle. The fleshy bundles are alongside the occipital condyle and its neck. The fibers that participate in the fleshy insertion on the basioccipital originate from the neural arch of the atlas (figs. 9A, 47, 49). The anchorage of the shining aponeurosis is responsible for the striated rugosities that characterize the ventral margins of the basioccipital bone.

Since the muscle originates high up on the sides of the cervical neural arches, and since the insertion is ventral, alongside the occipital condyle, the muscle fibers are slanted in the antero-ventral direction (fig. 48).

M. longissimus capitis profundus wraps around the proximal, bare portion of the first rib, and passes laterally by the atlantal hypocentrum.

The hypaxial m. costo-basioccipitalis has a tendinous insertion on the basioccipital (at the dorso-lateral margins of the basioccipital plate) that superficially covers the insertion of m. longissimus capitis profundus. The connective tissue fibers of both tendinous insertions are at right angles to each other.

Two additional hypaxial muscles, m. hypocentro-occipitalis, and m. centro-occipitalis, have fleshy insertions that are actually on the ventral surface of the shining aponeurosis of m. longissimus capitis profundus.

Figure 49 diagramatically illustrates the arrangement of fleshy segments and their relationship to the vertebrae, insertion tendon, and occiput. This same pattern is seen again in m. spinalis capitis posticus and m. transverso-spinalis capitis.

Contrary to Vallois (1922) this muscle does not originate from ribs of C-3 through D-1. Further, insertion of this muscle is definately alongside and ventral to the occipital condyle, and not the "most lateral flattened tendon on the lateral occipital." as state by Vallois (1922). Vallois also stated that "its cranial insertion is displaced more towards the base and goes to the sides of the foramen magnum." As seen in the osteology section, the only structures lateral to the foramen magnum in the alligator are the pillars of the exoccipital bone, and the various exoccipital foramina (with their associated blood vessels and nerves), but no muscles.

C. Transverso-spinalis System of the Neck

The transverso-spinalis system of the neck includes all muscles found dorsal to the dorsal intermuscular septum. This system in the neck exceeds the complexity of its counterpart in the trunk. There are three major divisions, including a cervicis portion that reaches the atlas (m. transverso-spinalis cervicis), and two capital muscles that insert upon the occiput (mm. transverso-spinalis capitis and spino-capitis posticus). There are additional small interarticular and interspinous muscles. A metameric arrangement is shown by the various divisions of this muscle.

In the trunk this system is concerned primarily with intervertebral articulation and structural support for the entire column, but in the neck there is a shift in dominance to musculature attaching to the neural spines. The four parts of the transverso-spinalis system that are so highly developed in the trunk, are progressively reduced between C-7 and the atlas. The expanded neural spine musculature that dominates over all of the neck musculature is entirely concerned with movements of the head.

M. transverso-spinalis cervicis, immediately dorsal and medial to the dorsal intermuscular septum, is a counterpart of m. longissimus cervicis. Vallois (1922) termed the remaining small, anterior muscles of the transverso-spinalis system "suboccipital" muscles, in reference to the sub-occipital group of muscles in man. These muscles in man are all innervated by the so-called suboccipital nerve, a nerve without a dorsal root that emerges anterior to the atlas as the first spinal nerve. Homology of these muscles in the alligator with the human sub-occipital group of muscles is doubtful and this terminology will be avoided. Those muscles assigned to the suboccipital group by Vallois will be described individually. Vallois (1922) described three sub-occipital muscles; _m. atloido-capitis_, _m. epistropheo-capitis,_ and _m. spino-capitis posticus_. Of these three, I could not find his "atlöido capitis", and his "epistropheo-capitis" is divisible into three distinct parts. Therefore, the following description does not make use of the sub-occipital grouping.

1. _M. transverso-spinalis cervicis_ (figs. 43, 45, 50, 51, 52, 53, 54, 57, 58, 64)

Vallois (1922). "transverso-spinalis cervicis"

The four divisions of the transverso-spinalis system of the trunk continue directly and without interruption into the neck as _m. transverso-spinalis cervicis_. _M. neurospinalis dorsi_ and _m. spino-articularis dorsi_ converge as a distinct group at the level of the neural spines of D-2(fig. 50). _M. articulo-spinalis dorsi_ and _m. tendo-articularis dorsi_ are united from the level of D-4 (12th vertebra) forward, by the disappearance of the intermuscular septum that divides the two in the trunk. In turn, these two compound sets of bundles unite anterior to the neural spine of C-7 to form the _m. transverso-spinalis cervicis_ , which continues anteriorly to insert on the atlantal post-zygapophysis (fig. 52). The muscle diminishes anteriorly and fills in the space between the zygapophyses and the neural spines on the dorsal neural arches of the cervical vertebrae.

The lateral contribution to this muscle by the merged *mm. tendino-articularis dorsi* and *articulo-spinalis dorsi* forms a layer of triangular sheets of muscle fibers that arise segmentally from the medial side of the dorsal intermuscular septum. The tendinous thickenings in the dorsal intermuscular septum that serve as the origin for *m. longissimus cervicis* (laterally), also serve as the lateral origin for *m. transverso-spinalis cervicis*. Thus, each tendon serves as the origin for the base of two sets of vertical triangular sheets of muscle, apex forward.

The dorsal sheets from tendons 7, 6, and 5, insert on the atlas. The lower, ventral sheets from tendons 7, 6, and 5, insert on postzygapophysis #3. Lower sheets from tendon 8 and 9 (from prezygapophyses of D-1 and D-2) insert on the postzygapophysis of the fourth vertebra. The dorsal sheets from tendons 8 and 9 are part of the origin of *m. transverso-spinalis capitis*.

The transition of the tendons of the trunk articulo-spinalis, from trunk to neck, is shown in figure 56. At D-5 and D-4 the lateral limbs are joined to the dorsal intermuscular septum and are merged with the tough fascia of the shoulder region. At D-3 the tendon is beneath the tip of the neural spine and the reduced lateral limb arches over the part of the transverso-spinalis that remains medial (fig. 50), to join the dorsal intermuscular septum under the prezygapophysis of D-3. The dorsal part of this arch serves as an origin for *m. transverso-spinalis capitis*. The lateral part of this arch serves as the common origin for the combined *mm*. *tendino-articularis* and *articulo-spinalis*. Recall that the above description refers to the *medial* side of the dorsal intermuscular septum. On the lateral side of the septum, the same tendinous thickenings serve as origins for the muscle and fascia of the longissimus system (figs. 54, 56, 57). It is of interest to note that the tendinous arches retain their topographical relationship (as from the trunk) by arching over the combined *mm. spino-articularis* and *neurospinalis* in the neck (fig. 50). Anterior to vertebra C-7, the incomplete tendinous arches end in the dorsal intermuscular septum and are not joined with the neural spines.

The deep medial half of *m. transverso-spinalis cervicis* is composed of the complexly merged *mm*. *neurospinalis* and *spino-articularis* muscles that extend from the trunk into the neck (fig. 50). The contribution by spino-articularis muscles is a series of thin muscular slips that arise from tiny tendons mid-way along the anterior edges of the neural spine blades (figs. 58, 59). Those slips originating from neural spines 5, 6, and 7, insert on the posterior medial surface of the postzygapophysis of the third vertebra (fig. 58). The contribution from the neural spines of D-1 and D-2 simply merge and disappear within the mass of the combined m. transverso-spinalis cervicis. There is another set of deep slips from the base of neural spines 7, 8, and 9, that skip over one vertebra and attach anteriorly to vertebrae 5, 6, and 7 (respectively), at the posterior base of those neural spines. A special group of spino-articular fibers converges from the anterior border of neural spines of C-3 and C-4 to insert fleshily on the postzygapophysis of the axis.

M. neurospinalis dorsi was found to contribute to the deep medial surface of m. transverso-spinalis cervicis as the latter arose in the neck. Neuro-spinalis fibers were found as far anterior as the third neural spine (fig. 59). These muscle slips are so thin that it was impossible to determine accurately their length and termination.

Vallois (1922) reported this muscle extended only to the axis. As shown in figures 52 and 57, m. transverso-spinalis cervicis extends up to the atlas. It is most likely that Vallois included the atlantal segments mistakenly with the m. longissimus cervicis, with which it is very closely applied along the dorsal intermuscular septum.

2. Mm. interneurales cervicis (fig. 59)

Vallois (1922). "interneurales cervicis"

This is a series of muscular sheets that run between successive neural spines (fig. 59). The ventral fibers attach to the posterior base of one neural spine, and run posteriorly to attach to the anterior base of the next neural spine. The muscle becomes interarticular at the union of neural spine and neural arch.

Vallois (1922) stated that this system extends up to the axis anteriorly, and as far as D-3 posteriorly. He further pointed out that they end at the termination of the cervical curvature (D-3).

There is a special part of this muscle to be found between the neural spine of the axis and the neural arch of the atlas. It originates on the anterior, ventral margin of the axial neural spine, and inserts on the posterior, dorsal margin of the atlantal neural arch, in a small, dorsal fossa near the postzygapophysis. Since the axial spine overhang the atlas, the fibers of this muscle are transversely arranged, running directly from medial to lateral. This part of the muscle is not so far differentiated that it can receive another name.

A continuation from neck to occiput was not found for this muscle.

3. Mm. interarticulares cervicis

These muscles arise in two series, medial and lateral.

The medial series originates on the dorsum of the neural arches and inserts on the posterior, medial surface of the preceeding postzygapophyses. The second series originates from the anterior surfaces of the postzygapophyses, and from the joint capsules, and inserts on the lateral half of the postzygapophyses of the preceeding vertebra. (i.e. basically from postzygapophysis to postzygapophysis).

That portion between the neural arch of the axis and postzygapophysis of the atlas is merged with a similar special segment of m. interneurales cervicis. Together, they insert into a fossa on the posterior dorsal surface of the atlas. The interneurales portion has more laterally directed fibers (see pg. 102), and the interarticular portion has fibers that are more or less longitudinally oriented, fanning out to the junction of axial neural spine and neural arch.

4. M. spino-capitis posticus (figs. 37, 38, 40, 43, 48, 49, 51, 54, 55, 57, 62, 63, 64)

Buttman (1826). "trachelo-mastoideus"
Meckel (1829). "complexus" or "splenius"
Cuvier (1835). "complexus"
Owen (1866). "complexus"
Rathke (1866). "complexus"
Hair (1868). "splenius secundus"
Miall (1878). "complexus"
Hoffman (1890). "squamoso-cervicalis medialis"
Vallois (1922). "spino-capitis posticus"
Anderson (1936). "squamoso-cervicalis medialis"
Nishi (1938). "obliquus capitis"

This muscle lies immediately deep to m. transverso-spinalis capitis. Although both muscles are tightly bound together in a common fascial compartment, they remain distinct by having different insertions.

M. spino-capitis posticus takes origin from the lateral surfaces of the neural spines of vertebrae C-3 to C-7 and the tips of neural spines of vertebrae D-1 and D-2. In addition, there is a posterior origin from tendons that are attached to the neural spines of D-1 and D-2.

The fiber insertion is obliquely oriented upon a laterally placed tendon that is wrapped around the tip of the paroccipital process, just deep to the tendon of m. longissimus capitis superficialis. Mm. longissimus capitis superficialis and ilio-costalis capitis form a floor deep to m. spino-capitis posticus.

The muscle fiber bundles originate from the neural spines as vertical sheets that are stacked one behind the other. This arrangement gives a dorso-ventral thickness that approximates the height of origin from the neural spines. The dorsal surface is extensive and flat, found at the exact level of the neural spine tips, and at the same vertical level as the dorsal extremity of the paroccipital process.

The slips that arise from tendons are attached to neural spines D-1 and D-2, which demonstrates the relation of this muscle to the m. articulo-spinalis dorsi. Tendons from below the neural spine tips arise from D-1 and D-2, and then run posteriorly into the m. articulo-spinalis dorsi of the trunk region. Figures(50, 55,56)show that by progressive shortening of the dorsal limb of the tendon, the triangular articulo-spinalis tendon serves as the fascial origin for m. spino-capitis posticus.

It is difficult to assign angular values to the muscle fiber insertions as they attach to the lateral tendon of insertion, since the entire continuum from 0° to 45° is expressed from the posterior to the anterior segments with respect to the tendon of insertion (see fig. 56).

5. M. transverso-spinalis capitis (figs. 37, 38, 40, 43, 48, 49, 55, 57, 62, 63, 64)

Buttman (1826). "complexus cervicis"
Owen (1866). "splenius capitis"
Rathke (1866). "M. splenius capitis oder vielleicht M. biventer cervicis" (pg. 271, Tafel IX,5); "splenius capitis" (pg. 272, Tafel X,1); "digastric extensor", attributed to Rathke by Vallois, 1922.
Hair (1868). "digastric extensor"
Miall (1868). "splenius"
Hoffman (1890). "occipito-cervicalis medialis"
Vallois (1922). "transverso-spinalis capitis"
Anderson (1936). "occipitocervicalis medialis"
Nishi (1938). "spinalis capitis"

This large, superficial neck muscle covers the entire dorsal surface of the neck (fig. 63). The dual origin is (a) from the tips of neural spines C-2 to C-7, and D-1 to D-4, and (b) from the deep fascia of the shoulder region. The insertion is by a straplike tendon to the dorsal surface of the processus postoccipitalis (fig.5d). All of this muscle is dorsal to the tips of the neural spines (fig. 49).

Anteriorly, the shiny tendon of insertion is covered superficially by m. depressor mandibulae. For most of its length the muscle is subcutaneous, but protected by the medial rows of nuchal osteoderms. The bulk of this muscle appears to end abruptly at neural spine D-2, but the remaining bundles from D-3 and D-4 are to be found hidden under the dense condensation of shoulder fascia to which m. trapezius is also attached. Vallois (1922) reported two tendinous intersections for his single specimen. Nishi (1938) showed three tendinous intersections in his illustration (Nishi, 1938, pg. 388, fig. 372, labeled "spinalis cap."). The juvenile specimens examined in this study did not show inscriptions, but the large adult specimen had four oblique tendinous inscriptions.

M. transverso-spinalis capitis occupies a position that makes it the most dorsal of the cervical muscles. It is divided mid-sagitally by a nuchal ligament. The nuchal ligament extends from the parietal bone and neighboring fascia, to the neural spines of C-2 thorugh D-2. The very tough but thin nuchal ligament is a doubled membrane that splits after attaching to the neural spine of D-2, to fuse with the fascia of the shoulder region. Dorsally the nuchal ligament is fixed to the under surface of the osteoderms. It is also split anteriorly to enclose the proatlas.

This conspicuous muscle can be divided into lateral and medial portions, based upon its two separate origins. It can be shown that this muscle is basically a cervical continuation of m. articulo-spinalis dorsi (figs. 53, 55, 62, 63). The lateral and medial halves are divided by a very large branch of the first spinal nerve dorsal ramus, that enters its deep face. (In an apparently typographical error, Vallois (1922) had this nerve arriving at the deep face of m. transverso-spinalis cervicis rather than m.transverso-spinalis capitis; Vallois, 1922, p. 241).

The medial portion that arises segmentally from the tips of the neural spines from C-2 to C-7 (figs. 56, 63), runs obliquely anterior, each segment behind the preceeding, and each of a width corresponding to its neural spine of origin. The bundles from neural spines D-1 and D-2 are arranged one above the other vertically (fig 56), since these neural spines are greatly elongated and specialized. This is also accomplished through the cervical curvature.

The bundle from neural spine D-2 is about three times the thickness of the other bundles and forms a long dorsal crest that extends over the entire muscle to insert on the anterior tendon of insertion near the occiput, in a straight line from origin to insertion. The very small bundles from D-3 and D-4 converge immediately and laterally join the bundle from D-2. The neural spine of D-2 is bifid and flattened antero-posteriorly to accomodate the great size of its contributing muscle bundle. The spinous origins of this muscle are mapped out in figure 53.

The lateral half of m. transverso-spinalis capitis adds much bulk to form the superficially conspicuous portion of the muscle. In this case, the origin is difficult to dissect and demonstrate. The origins from fascia appear on tendinous arches that begin behind the seventh vertebral segment (figs. 43, 55, 62). These arches are the cervical continuations of the articulo-spinalis system that connects the neural spines with the dorsal intermuscular septum. The origins of the lateral half of this muscle cover the fascial envelope of the first three segments of m. longissimus dorsi. The possibility exists that this lateral half of the muscle is a part of the longissimus system that split off and joined the transverso-spinalis system to the dorsum of the occiput.

The strap-like tendon of insertion is covered dorsally and laterally by fibers of the lateral half of the muscle, and medially and ventrally by the segmental neural spine portion of the muscle. The tendon joins the periosteum of the processus postoccipitalis that is parallel to the dorsal surface of the process. The tendinous inscriptions were found only in the lateral half of the muscle, not in the segmental medial half (see fig. 64).

Muscles from the axial neural spine to the occiput

These three muscles are distinguished by originating from the neural spine of the epistropheus (axis) and inserting directly upon the occiput. In the alligator these muscles are layered so that superficially there is little or no distinction readily apparent. Careful dissection, from medial to lateral, rather than from superficial to deep, is the necessary approach that clearly reveals this group of muscles.

The axial neural spine is regionally divided into a posterior part, whose dorsal edge is horizontal, and an anterior blade portion, with a ventrally slanting dorsal edge (fig. 12A, B). These two regions correspond to the muscles that insert on the axial neural spine.

6. M. epistropheo-capitis lateralis (figs. 12, 49, 63, 64)

This muscle takes origin from the lateral surfaces of the expanded neural spine of the axis (fig. 12B). The dual insertion is (a) to the medial side of the tendon of insertion of m. spino-capitis posticus, and (b) to a triangular area at the tip of the paroccipital process.

The origin forms as a series of vertical muscle fiber sheets stacked from anterior to posterior as they originate from the axial neural spine; therefore, the dorso-ventral thickness approximates the height of the axial neural spine. The posterior sheets are inserted to the tendon, and the anterior sheets are inserted to the paroccipital process.

The anterior margin is marked by the large branch of the dorsal ramus of the first spinal nerve as it emerges to serve the underside of m. transverso-spinalis capitis. From superficial to deep, m. epistropheo-capitis lateralis is crossed at right angles by this nerve, and presents an oblique planar surface that slants deep medially. The anterior, oblique surface forms a floor for m. epistropheo-capitis intermedius. The posterior margin is closely applied to m. spino-capitis posticus, but careful, blunt dissection around all sides can distinguish m. epistropheo-capitis lateralis from its neighbors.

M. epistropheo-capitis lateralis appears to be a forward extension of the segmental m. spino-capitis posticus, but in view of its capital insertion, it is here given the status of a separate muscle. It is interesting to note that as m. epistropheo-capitis lateralis passes alongside the atlantal neural arch, it is joined by a small bundle of muscle fibers that take origin from the atlas, just posterior to the atlas-pro-atlas contact, but still crossed superficially by spinal nerve no. 1 at its origin. This tiny slip, embedded in a condensation of connective tissues, seems to be a rudimentary atlantal contribution to the forward extension of the segments of m. spino-capitis posticus. It is a very minor slip of muscle, easily overlooked. The name m. atlanto-capitis profundus is suggested to distinguish it from m. atlanto-capitis proper.

7. M. epistropheo-capitis intermedius (figs. 12, 49, 63)

This muscle lies dorsal and medial to m. epistropheo-capitis lateralis. It originates from the anterior part (see p. 37) of the axial neural spine (fig. 12B). It is inserted on the occiput at the exoccipital-squamosal suture. It is divided from m. epistropheo-capitis lateralis by the large branch of the dorsal ramus of the first spinal nerve.

Its muscle fiber bundles cross deeply, under m. epistropheo-capitis medialis, and fan out to a broad insertion that is lateral to the insertion of m. epistropheo-capitis medialis and forms a fossa at the paroccipital-squamosal suture. Mid-way along its medial border, m. epistropheo-capitis intermedius is joined by a well defined, but small bundle of muscle fibers, m. atlanto-capitis, which maintins a ventro-medial position to a common insertion for both muscles.

A feature of this muscle worthy of note is that it crosses over the limbs of the pro-atlas and is capable of imparting pressure upon the pro-atlas.

8. M. epistropheo-capitis medialis (figs. 12, 63)

This muscle arises as a sheet from the anterior part of the axial neural spine, immediately superficial to m. epistropheo-capitis intermedius. It is inserted into the supraoccipital bone, on the occipital surface, under the shelf formed by the processus postoccipitalis. The original anterior, medial fibers become the deepest at the insertion, the more posterior fibers of origin become the most superficial fibers at insertion. This means that there is a twist in the muscle sheet that amounts to about 45°. The insertion forms a small fossa in the occipital surface of the supraoccipital bone, lateral and dorsal to the position occupied by the pro-atlas on the occiput (fig.5).

On both sides of the body, this muscle passes by the dorsal extremity of the pro-atlas and presses against its surface. This tends to limit lateral excursion of the pro-atlas.

A small slip of muscle from the axial neural spine (posterior half), posterior to m. epistropheo-capitis medialis, is the atlantal contribution to m. transverso-spinalis capitis, and it is sandwiched between m. epistropheo-capitis medialis deeply, and m. transverso-spinalis capitis (tendon) superficially. Mention is made of this since it is this slip that can be mistaken for either muscle, with improper dissection.

Dorsal to the atlas, and anterior, there are connective tissue adhesions between this muscle and the nuchal ligament. In addition, there are membraneous adhesions with the pro-atlas. It is suggested that these adhesions may represent the remnant of a former atlantal segment that joined this muscle. m. epistropheo-capitis medialis is the most anterior segment associated with the segmental m. transverso-spinalis capitis, much in the same way that mm. epistropheo-capitis intermedius and epistropheo-capitis lateralis are anterior continuations of the segmental m. spino-capitis posticus.

9. M. atlanto-capitis (fig. 9)

This muscle takes origin as a small, round bundle of fibers from the dorsal surface of the atlantal neural arches and adjacent fascia (nuchal ligament attachment). The bundle flattens out to a sheet that runs along the medial border of m. epistropheo-capitis intermedius to insert with it at the exoccipital-squamosal suture. This is probably the atlantal contribution to the segmental m. spino-capitis posticus.

Vallois (1922) makes mention of m. atlöido-capitis which "has its origin essentially on the tip of the spinous process of the atlas" (Vallois, 1922, pg. 244). In view of the fact that the atlas does not have a spinous process, there can be no m. atlöido-capitis, and this name can not be attached to any muscle described here. Vallois also stated that part of this muscle originates from the pro-atlas. Muscle fibers were not found on the pro-atlas of any specimens of A. mississippiensis dissected here. Further errors in this and the succeeding two paragraphs of Vallois indicate that the various muscles that were described were confused with each other, and there is no way of knowing exactly what he meant in the description. For example, he indicates that m. "epistropheo-capitis" originates from the "wide lateral face of the spinous process of the axis and from the dorsal face of its transverse process...to insert at the superior occipital". This is hard to envision since the axis lacks a transverse process. However, since he places the "proatlantal nerve" anterior to this muscle, it is most likely a combination of, what are named here, mm. epistropheo-capitis intermedius, epistropheo-capitis medialis, and atlanto-capitis. It is impossible to acertain the meaning of the epistropheo-capital muscles of other authors who relegated these muscles to the status of "rectus capitis posterior" as seen in man. Therefore, further synonomy becomes impossible to carry out.

Description of the Hypaxial Musculature

The hypaxial musculature of the trunk (figs. 19, 20) is divisible into three lateral segmental layers, and a ventral rectus muscle (Maurer, 1896, Versluys, 1927). Most external of these layers is the m. obliquus externus of the abdomen, which is segmentally attached to the fascia of m. ilio-costalis dorsi, and also to the dorsal set of cartilagenous ribs (fig. 18). The next internal layer is composed of m. obliquus internus, from which the external and internal intercostal muscles are also derived in the thoracic region. The most internal layer of the abdominal wall is m. transversus abdominis, which provides the transverse layer of the thorax and abdomen.

Either m. obliquus internus, or m. transversus abdominis, or both, become modified into cervical muscles in the neck region. This point of information is not yet fully clear. M. obliquus externus, at the point where it is interrupted by the coracoid bone, becomes associated with the pectoral girdle.

I propose the name "m. sterno-costalis" for that muscle which originates on the cartilagenous sternum, and inserts on the first rib tip (fig. 15A). The scapula has three muscles taking origin from its anterior border and inserting on the first three rib tips, plus two additional similar muscles inserting on the superficial fascia of the neck at positions that correspond to myosepta 4 and 5 of m. ilio-costalis cervicis. This series of muscles is analogous to the mammalian serratus ventralis muscles, and are termed levator scapulae by Rathke (1866).

A series of well developed ventral muscles originate from the vertebral centra of all vertebrae, as far back as, and including D-5 (the 12th vertebra). Tendons from this muscle attach to the hypapophysis. The single, median carotid artery is buried between the muscle bellies of both sides. The insertion of each segment is on the ventral portion of the tips of ribs #1 through #7 inclusive (exclusion of ribs #8 and #9 from this series of muscles is additional reason for limiting the neck region to the first seven vertebrae; see pg. 18). I propose to call these muscles "mm. subvertebro-costales".

Anteriorly, a special division of this muscle connects the axis centrum with the lateral edge of the basioccipital plate, just ventral to the internal carotid artery foramen. This muscle joins the tendon of a muscle here called m. costo-occipitalis (fig. 15A). A third muscle, called here m. hypocentro-occipitalis, joins these two medially and all three together are probably what Iordansky (1973) calls m. basioccipito-vertebralis. The tendinous portion, derived entirely from m. costo-occipitalis, is most lateral and inserts on a pointed eminence under the internal carotid artery foramen. This eminence on the basioccipital plate is strongly developed in young A. mississippiensis, and a regular characteristic of adult A. sinensis.

The Cervical Epaxial Musculature of Other Crocodilia

The neck muscles of other Crocodilia were examined in: Caiman sclerops, Melanosuchus niger, Osteolamis tetraspis, Crocodylus novaeguinea, Crocodylus porosus, Crocodylus johnsoni, Tomistoma schlegeli, and Gavialis gangeticus.

The most striking result of these dissections is the relative uniformity, or regularity of the musculature. All of the same muscles were found in all of the specimens. The differences between the genera, and even species were of proportion and size, and there were apparently no qualitative differences.

Caiman sclerops and Melanosuchus niger resemble A. mississippiensis closely, although the Caiman showed proportionately a greater mass of m. spino-capitis posticus. The muscles in the hatchling Melanosuchus were very easy to separate and distinguish. The short occipital muscles inserted on the rounded juvenile occiput and gave the impression of "eyeball" muscles by their arrangement.

Osteolamus looked exactly similar to Alligator, with the exception that m. transverso-spinalis capitis was not as highly developed as in Alligator. The cervical osteoderms formed a tight fitting tunnel around m. transverso-spinalis capitis. Another interesting fact uncovered by this dissection is that the laterally placed "horns" of protruding osteoderms exactly cover the internal distribution of m. depressor mandibulae which, in Osteolamus, is a very large muscle.

The three specimens of *Crocodylus* had all of the muscles described in this dissertation for *Alligator*, but they were elongated and relatively thin. *M. spino-capitis posticus* is very much reduced since its segments are narrower than even *m. transverso-spinalis capitis* which also has a reduced amount of lateral origin fibers.Figures and illustrate two stages in dissection of neck muscles and can be compared to figures 37 and 40 (of *Alligator*).In *C. novaeguinea*,*m. longissimus capitis superficialis* was found to originate from vertebrae C-6 through D-2, *m. longissimus capitis profundus* from C-1 through D-1. Each of the neural spines of the thoracic region had three neuro-spinalis tendons lying against it. There are some quantitative differences between the genera that would make a worthwhile study.

Tomistoma has a high narrow *m. transverso-spinalis capitis* and, as in the *Crocodylus* the lateral fascial-origin portion was reduced, and *m. spino-capitis posticus* was relatively small. The only thing remarkable about *Tomistoma*'s neck muscles is the great elongation. As a rule of thumb in these dissections I noticed that the long epaxial muscles, both cervical and occipital, are about as long at the snout, measured from a point between the anterior edge of the orbits. Unfortunately, after dissection it was rather difficult to measure the precise length of *m. transverso-spinalis capitis*, for example.

Gavialis had all muscles , but the musculature is notable for the following characters. Part of *m. depressor mandibulae* took origin from the fascia covering m. transverso-spinalis capitis, most from the squamosal, and part from the quadrate. M. transverso-spinalis capitis inserts by a thick, well defined tendon on both sides of the "nuchal spine" that is found in the midline. This insertion is qualitatively different from that seen in the other genera. Also, the lateral fascial origin for the muscles was so extensive that it seem to wrap around the outside of the longissimus system. Another differing feature is the condition of m. longissimus capitis profundus which is extremely flattened and pressed up against m. ilio-costalis cervicis. M. transverso-spinalis capitis was observed to take much of its segmental origin from the nuchal ligament. Skeletons of Gavialis are notable by the absence of a cervical curvature, and the pro-atlas is wrapped aronnd the atlantal arches.

About the only notable feature is that long snouts seem to be correlated with elongated musculature, and that the crocodiles have a reduced spino-capitis posticus and longissimus musculature. In contrast, the flat snouted alligator shows the relative importance of roll and yaw muscles, especially with m. spino-capitis posticus.

The Functioning of the Occipital and Cervical Somatic Musculature

Introduction

This section deals with the analysis of movement of the neck and head. The approach is based upon the anatomy set forth in the previous sections. Once the anatomical frame work for functional analysis is set forth, the next level of functional analysis, based upon detailed physiology then becomes possible.

Anatomical study of the vertebral column of *Alligator mississippiensis* was initiated by Virchow (1914). His anatomical observations were carried out, joint by joint, on a fresh specimen from which all musculature had been removed. His careful observations were then related to data collected on movements of live captive animals.

Virchow (1914) was not able to consider the musculature. His data are confirmed in this study, and will be presented along with additional observations made through dissection of both fresh and preserved material.

Troxell (1925) analysed the problem of mechanical advantage involving the procoelous vertebrae of the Crocodilia, but consideration of the head and neck was not carried out in that study. Apart from Troxell (1925) and Virchow (1914), and speculations made by Vallois (1922), there appears to be no other attempt at analysing the functioning of the crocodilian vertebral column.

The function of the cervical and occipital musculature of A. mississippiensis will be discussed according to the following outline:

1. Freedom of movement.
   a) Degrees of freedom of movement at each joint, from skull to trunk; includes structure of joints.
   b) Restrictions on the freedom of movement of bony elements at each joint; includes the influence of ligaments on the joints.
2. Direction of muscular activity as inferred from the arrangement of musculature, fascia, skeletal, and articular systems. The muscles are not considered in the systematic order presented in the section on myology, but rather in functional groupings, i.e., (a) neck muscles; (b) occipital muscles; (c) multi-segmental muscles.
3. Direction of movement analysis (or the interaction of part (2) upon part (1)).
   a) Definition of head movements
   b) Correlation of movements that are defined, with groups of muscles.
   c) Non-muscular forces acting on the skull; the effect of gravity on the resting position.
4. Observations of living animals, movements associated with observed behavior.
5. Conclusion of analysis of occipital and cervical muscular movements.
   a) The muscle systems
   b) Occipital muscles and cranial morphology
   c) Cervical muscles and cervical bony morphology: gradients in the cervical vertebral column.

Parts (1), (2), and (3) of the above outline were carried out with three basic assumptions about the anatomy. These assumptions are:

1. The possible range of movements can be estimated by inspection of joints and manipulation of fresh material with ligaments intact. It is realized that not all

movements are possible to achieve through manipulation; further, not all manipulative movements may be carried out by the living animals. Anatomical considerations can only lead to a rough approximation, or gross analysis.

2. Muscles can only exert tension at their attachments, i.e., they can only pull, not push. The direction of tension may be inferred from the orientation of the tendon.

3. Bone is thickened in areas undergoing compressive forces; in areas experiencing tensile forces, bone is either reduced or replaced by ligaments (Rockwell, Evans, and Pheasant, 1938, Frazzetta, 1968). This assumption about the bony morphology is used to infer information about the interaction between hard and soft anatomy that can not be directly observed at this time.

Ideally, further data are necessary to provide a more complete picture of function, but the above assumptions make possible a first level approximation of function. Future studies of function would include these data that could not be collected in this study such as: strength of materials; details of nervous organization and integration (i.e., innervation, sequence of nerve firing in multisegmental muscles, reflex activities, etc.); details of blood circulation; center of mass determinations of skull and vertebrae; detailed muscle fiber counts for all muscles involved (including proportions of twitch and tonus fibers).

Although the data presented here make only gross approximations of function, the specializations of the head and neck of Alligator will become apparent, as well as the influence of the occipital musculature on the general architecture of the crocodilian skull.

1. FREEDOM OF MOVEMENT

a) Degrees of freedom of movement at each joint from skull to trunk (see Table III, a synopsis and definition of joints under consideration)

Basi-occipital joint. - The rounded basi-occipital condyle fits into the atlantal cartilagenous cup to form a synovial joint with the neural arches and hypocentrum of the atlas. A ligament joins the basi-occipital condyle with the tip of the odontoid through a mid-sagittal slit (fig. 11E) in the atlantal cotyle. The condylar joint permits movements in three axes; a) lateral flexion; b) sagittal flexion; c) axial rotation. There is no translational movement in this joint since the shape of the condyle and cup, and the capsular ligaments, prevent such movement.

Occipital-pro-atlantal joint. - The pro-atlas is joined to the exoccipital bones above the foramen magnum directly by loose connective tissue fibers. The bone is free to slide upon the occipital surface (full translational movement in the occipital plane), but rotation of the bone is absent, and flexion at the fibrous joint is limited by the fibrous connection (see below under inter-atlantal joint).

Pro-atlas-atlas joint. - The ventro-lateral surfaces of the pro-atlas meet the atlantal neural arches and are loosely joined to the arches by connective tissue fibers. Translational movements upon the surface of the atlas neural arches can occur. Axial rotation of the pro-atlas does not occur at this joint, although the pro-atlas may become passively carried into rotation by other bones. Sagittal tilting of the pro-atlas upon the atlas occurs, but does not result from a specialized joint contact, but rather from postero-ventral sliding of the pro-atlas upon the atlas.

Inter-atlantal joint. - a) Neural arch to hypocentrum: This is a syndesmosis that attaches the atlantal neural arches to the hypocentrum through matching facets (figs. 11B, C, D, E). Movement is restricted and probably involves the separation of elements that results during tension in the fibrocartilage. This type of joint is similar to that between pro-atlas and atlas by being fibrous and by having bony elements that can move away from one another. This is opposite to the functioning of a synovial joint, the key to operation of which rests in the maintainance of firm contact between the elements. There is only one degree of freedom of movement at this joint, where the elements move either together or apart. However, a second type of possible movement, translation in the plane of the bony facets, can occur when the elements are not under tension. The advantage of this joint is that it gives the atlantal cotyle much flexibility in the potential to change shape, through relative independence of each of the three cotylar elements.

b) Neural arch to neural arch. - This "joint" is a loose ligamentous dorsal midline connection of the atlantal neural arches of both sides, a syndesmosis. It permits the two arches to move in any direction with respect to each other, with the connecting ligament serving only a limiting function.

Specialized atlas-axis joint. - The paired, but independent atlantal arches make moveable articular contacts with the axis in two places. First, the base of each arch rests in the parasagittal groove found to either side of the odontoid process; the parasagittal groove serves as a couch for the base of the atlantal neural arch. The other contact is with the neural arch of the axis, the atlantal postzygapophyses meeting the axial prezygapophyses. This is the first, and most specialized, zygapophyseal contact of the axial column, and it is peculiar because: 1) The axial prezygapophyseal surface is the only one that faces outwards; all of the rest face either medial or dorsally. A line drawn normal to the axial prezygapophyseal surface will point laterally and dorsally. 2) It is elongated in the antero-posterior direction; the remaining zygapophyseal contacts are laterally elongated. 3) the axial prezygapophysis is held on a thin, plate-like process, of doubtful value in withstanding heavy stress and strain (compare this with the heavily constructed prezygapophyseal pillars in the rest of the column (fig. 13)). 4) The atlantal postzygapophyseal surface complements the axial prezygapophyseal surface, and is likewise formed on a thin, plate-like bony eminence. (fig. 9).

Consideration of these four points leads to the conclusion that this contact serves as gliding surfaces for anterior-posterior travel of the zygapophyseal elements. Longitudinal and lateral movements in the zygapophyseal plane probably occur with minimal supportive, or weight bearing function at this joint. The thin axial prezygapophysis cannot withstand heavy normal forces, as compared to prezygapophses further posterior in the column, which are structured for support.

Sagittal movement guided by the base of the atlantal neural arches as they fit on the odontoid is one of the prime specializations of the neck vertebrae. The zygapophyses of the cervical vertebrae are so arranged as to prevent ventral flexion of the cervical column, therefore the sagittal movement afforded by this special joint becomes extremely important if the alligator must flex its head against the neck, or to reach objects that are ventrally related.

Hypocentrum-odontoid joint. - The hypocentrum has a great degree of freedom to move about the anterior surface of the odontoid. This is a synovial joint that permits movement in any direction over the surface of the odontoid.

Intervertebral joints. - a) Zygapophyses. The zygapophyses are planar oval surfaces that allow sliding movements in the plane of contact. Virchow (1914) reported the prezygapophyseal surfaces of C-3 to C-7 to be slightly concave, a fact confirmed in this study, but only with osteological material. If this is not an artefact of drying, it indicates strengthening of the turning movements of the vertebrae, and limits movements in the articular plane to either longitudinal, or transverse directions (compare the surface to a part of a tube). It may also indicate articular transfer of compressive forces between neural arches, of importance in weight bearing.

Since an entire vertebra is firmly united around the spinal cord, movement at one zygapophysis of one side is automatically transmitted contralaterally. Therefore, both left and right zygapophyses must be considered together as a single articular contact. This complicates the range of movements possible at the zygapophyses. Movement is restricted by the joint to sagittal flexion. Lateral flexion and rotation of vertebrae can only occur to a slight degree at this joint.

b) Vertebral condyle-cotyle joints. - These joints are similar to the occipital joint. The synovial condylar joints have three degrees of freedom, namely, axial rotation, lateral and sagittal flexion. Translational movements do not occur.

Costo-vertebral joints. - The first pair of ribs are united by fibrocartilage to the hypocentrum. This type of union permits compression and tension at the joint, but the movements of rotation, as well as flexion are restricted.

The joint between the second pair of ribs and the odontoid is peculiar in the alligator. The capitulum can move against the odontoid, but since its surface is elongated dorso-ventrally, there is only flexion (antero-posterior). The tuberculum, although reduced, has a ligamentous connection to the odontoid, so that its movements, although completely free, are dependent upon the capitulum. The remaining cervical ribs are immovably joined to the centra and neural arches through rugose complimentary surfaces, with the exception of the surface of the parapophysis of C-7. The transverse process of C-7 permits dorso-ventral and antero-posterior movement of the tuberculum of rib 7, by acting as a shallow condyle. Since the transverse process articular surface is elongated, axial rotation at this joint is probably only slight (the axis in this case being in the transverse plane). The joint between D-1 and its rib must be considered here, since it is the first freely moving rib joint. Both parts of this joint (transverse process and diapophysis) have surfaces that permit only one type of motion: namely, flexion of rib-8 about an axis that runs between the two contact surfaces. This is lined up so that it is directed from the anterior ventral corner of the vertebra, to the posterior dorsal corner of the postzygapophyses, and, in the transverse plane it is directed in a plane that is parallel to the surface of the ipsilateral postzygapophysis.

Intercostal joints. - The cervical ribs articulate with one another. The first rib overlaps the second and third, and has loose connective tissue fibers to these ribs. The deep posterior surface of the second rib houses the anterior process of the third. The posterior process of the third rib houses the anterior process of the fourth, and this arrangement continues up to the contact between rib-6 and rib-7. Rib-8 does not make articular contact with rib-7. The contacts are maintained through loose fibers of connective tissue, and the shapes of the ribs permit longitudinal sliding of the ribs. Other rib movements between themselves are not restricted, but due to other considerations (see below) only one type of movement is probable. In other words, the potential for complete flexibility of the entire "column" of ribs is present, but not used.

Odontoid-axis joint. - This is an immovable planar joint, with rugose articular surfaces of contact. It is important that this joint maintains a stable configuration since the atlantal arches depend upon the odontoid for their support, as well as the odontoid forming a base for movement of the atlantal hypocentrum. For further details about this joint, see the osteology section (fig. 12).

Neural arch-centrum joints.- The neural arches of the cervical and thoracic vertebrae are immovably joined to the centrum. but complete obliteration of the suture only occurs in old individuals. These joints resemble the basi-occipital-exoccipital joint of the skull.

b) Restrictions on the freedom of movement of the bony elements at each joint. Now that the possibilities for movement have been set forth, some of the restric- on these movements can be examined. These restrictions result not only from ligaments, but from bone-bone interactions, as well as extra-skeletal influences such as muscle. For clarity, these restrictions are considered systematically, for comparisons with the previous information.

Neck vertebrae (excluding the atlas).- Individually, movements between each vertebra and its neighbors are highly restricted, but taken together, the neck can perform flexible, smooth movements (observed by manipulating fresh material). Of most interest is that sagittal ventral flexion cannot occur between vertebrae C-2 and C-7. On the other hand, sagittal dorsi-flexion takes place with great ease. Lateral flexion of a vertebra occurs, but only in conjuction with axial rotation of the same vertebra. That lateral flexion must be accompanied by axial rotation, will be explained below. Although the ribs are firmly fixed to the vertebrae, in no way do they oppose vertebral movements (Virchow, 1914).

The absence of sagittal ventral flexion may be demonstrated in several ways. Virchow (1914, fig. 1), shows a freshly prepared articulated head and neck that is completely suspended beyond the edge of a support. In that photograph the weight of the attached head was not able to ventro-flex the neck. In his preparation, all of the muscles were removed, but one might suppose that intervertebral ligaments joining vertebrae could be responsible for maintain a straight neck. However, the following observation and explanation of this is offered.

If clean, dry vertebrae are on hand, vertebrae C-2 through C-7 can be articulated manually, and it is seen that through intervertebral interlocking, the neck vertebrae are all mutually supporting. It is only necessary to hold the seventh vertebra while the rest stay suspended by themselves. Add to the already stable structure some tension-resisting ligaments at the zygapophyses and between neural spines, and it becomes apparent that the neck vertebrae form an extended girder from the trunk to the axis that becomes stronger as weight is applied to it. In other words, the more weight placed at the end of the neck, the stronger is the interlocking affect, with further restance to ventral flexion.

The reason that this self-supporting structure occurs is that the prezygapophyses form a type of catch mechanism. Recall that the articular facets point slightly posteriorly (fig. 13). The anterior edge of the prezygapophysis poses resistance to movement in the sagittal ventral direction. The axis of flexion resides in the condyles of the centra, and the sagittal arc of movement traced by the postzygapophyses of a vertebra is interrupted by the anterior edge of the next prezygapophyses.

This mechanism is also responsible for giving the typical concave-up curvature of the neck (fig. 7). By interlocking, the vertebrae are forced to maintain the cervical curvature.

There is no opposition to sagittal dorsal flexion of C-2 to C-7, save the knocking together of neural spines, or the dislocation of the condyles. Both of these restrictions never apply since the vertebrae maintain strong ligamentous connections ventrally. Virchow (1914, fig. 2) showed a neck which had been bent dorsally in the sagittal plane through 150°. Virchow (1914) said that "through rigor-mortis the head can be raised to the perpendicular", and that after the muscles are completely removed (without damaging the ligaments), and after the heavy head is removed from the neck, the neck vertebrae bend dorsally by themselves, through the action of the elasticity of the intervertebral ligaments.(whether they have elastic fibers or not is a question not yet answered). Apparently, the weight of the head is in part used to keep the column extended anteriorly, or rather prevents dorsi-flexion of the neck.

Virchow (1914) reported lateral flexion of the neck to either side to be about 90°. Lateral flexion of one neck element upon another cannot result from a lateral component alone. The planes of the zygapophyses form an acute angle when extended ventrally to the midline (Virchow, 1914). because of this angle, orthogonal lateral flexion must be accompanied by a component of axial rotation and dorsi-flexion. The articular planes are more sagittal than frontal, and so lateral flexion movements must also include some sagittal component. A small amount of torsion must also occur during lateral flexion in order to maintain the zygapophyseal contacts. For a cervical vertebra to turn to the left upon its posterior neighbor, its right postzygapophysis rides up and forward on the next prezygapophysis. The left postzygapophysis rides down and medial as well as posterior. This is the only zygapophyseal movement of flexion that is consistent simultaneously with both articular planes. In specimens cleaned by beetles, in which the neck is bent, it was observed that the neck was dorsiflexed. That the axial torsion was also involved is shown by the level of the rib tips. On the side of bending, the tips are much more ventrally placed than on the convex side of the neck. Torsion of the entire neck is thus counterclockwise, looking from trunk to neck, when the neck is turned to the left. The same observation was made on X-ray pictures, where the neck was bent and the ribs were visible. The same affect was also observed on fresh material during bending of the neck.

Virchow (1914) stated that axial rotation is completely absent. It is true that axial rotation of a straight neck is impossible, however as shown, axial rotation can occur, namely that which accompanies flexion. This fact was probably masked to him by his focusing on the concurrent observation of flexion, and his not realizing that both occur together. A large degree of axial rotation of individual elements is obviously limited by the acutely placed articular surfaces, and by the tri-partite nature of the vertebral joints, one condyle plus two zygapophyses. If great pressure is placed at one zygapophyseal contact (as is during axial rotation), further displacement of the two vertebrae is resisted by condyle-cotyle pressure on the opposite side, and the torsional force couple is cancelled by the opposing bony structure of the condyle and cotyle.

Atlas. - The atlantal hypocentrum, as mentioned, can be moved in any direction over the odontoid surface by manipulation. However, its freedom is limited by its attachment to the atlantal neural arches, the occipital condyle, and the first pair of ribs. It becomes retracted when the atlantal ribs are pulled posteriorly, and protracted when the neural arches are pulled posteriorly. Protraction is accompanied by translation of the entire atlas complex in the dorsal direction; retraction moves the hypocentrum ventrally as well as posteriorly. The hypocentrum can be rotated under the odontoid by supplying unilateral tension from a single rib, a single neural arch, or ipsilateral arch and rib together. The most serious limitation on the movements of the hypocentral wedge come from restrictions placed on it by association with the neural arches.

The arches, it appears, move primarily in the sagittal plane. This movement is controlled by the close fit into the groove of the odontoid, and is guided by the tip of the odontoid. Additional constraints are placed on the arch by the zygapophyseal articulation, which is elongated longitudinally and guided by its joint capsule. Movement laterally off of an axial prezygapophysis is limited by both ligaments and the musculature (especially the first *m. interneuralis cervicis*). This same restriction on lateral movements of the arches also means that axial rotation of the atlantal arches about the odontoid is almost non-existent. Therefore, the odontoid is not a true dens used as a center for axial rotation of the atlas, since the arches move in the sagittal plane; a function quite different from that ascribed to the "atlas-axis" of mammals and birds. Protraction of the arches (and subsequent protraction of the hypocentrum) is effected by the common insertion of *mm. transverso-spinalis cervicis* and *longissimus cervicis*, through a stout tendon directly above and alongside of the atlantal postzygapophyses. As can be seen and demonstrated in fresh material, tension on this tendon pulls the arches straight back on the elongated articular surfaces, and sagittally in the grooves of the odontoid.

Lateral movements of the atlas ring can be accomplished in a weak manner by independent retraction of one arch at a time. This type of adjustment (allowing freedom from the hypocentrum) gives the occipital condyle a greater freedom to rotate on the retracted side. The major point here is that movements and adjustments of the atlantal ring are important because this is the mechanism for positioning the occipital joint with respect to the vertebral column. Through retraction of the entire atlantal ring, the occipital joint can be made to face ventrally, while all degrees of freedom are still maintained by the joint.

Protraction of the atlantal ring by <u>m. sterno-costalis</u> and other muscles brings the occipital joint in direct horizontal line with the rest of the column, a position occupied during rest, as discussed later. The individual elements of the atlantal ring, although bound to one another, remain independent of one another throughout protraction and retraction, and this loose arrangement permits the flexibility of movement needed under and around the odontoid.

Protraction of the ring is limited by the sterno-costal muscle that pulls back the first rib. Retraction is limited by the mm. transverso-spinalis cervicis and longissimus cervicis that pull the arches back dorsally. Strong ligaments bind the ring to the lateral edge of the odontoid and prevent lateral dislocations as well as limiting sagittal excursion.

Pro-atlas. - The pro-atlas can occupy a position at right angles to the atlas during extreme posterior tilting of the head. Its further travel on the atlas is limited by connective tissue attachment to the atlas, and in extreme excursion, it may be able to contact the anterior extremity of the axial neural spine. Lateral movements are restricted by inclusion of the pro-atlas within the nuchal ligament, but even more strongly by mm. epistropheo-capitis medialis, epistropheo-capitis intermedius , and atlanto-capitis, all of which cross the surface of the pro-atlas.

Virchow (1914) likened the pro-atlas to the human patella, but since it is covered by muscles, and since it covers the neural canal, it is not transmitting muscular tension around a bend in a manner identical to the patella. This analogy applies in so far as the pro-atlas is constrained on all sides, and when not under tension it shows considerable lateral travel, as does the patella.

The skull. - Movements of the skull must be considered with respect to (a) rotation; (b) lateral flexion; (c) sagittal flexion.

a) Rotation. - Virchow (1914) reported axial rotation of the skull to amount to about 30°, both left and right. This torsion is entirely within the occipital joint, for only at the end of excursion is the atlas moved against the axis (Virchow, 1914). This occurs through pulling of the atlantal arch by the pro-atlas as it is extended to its own limits by axial rotation of the head. Therefore, the strut of the pro-atlas, the nuchal ligament, and their constraining muscles (see pg. 132) place limits on the degree of axial rotation.

Axial rotation with an extended neck is also strongly limited by the occipital musculature. For example, clockwise rotation (looking from posterior to anterior) of the skull is directly opposed on the left by mm. ilio-costalis capitis, longissimus capitis superficialis, spino-capitis posticus, and epistropheo-capitis lateralis, and on the right side by m. longissimus capitis profundus.

It was observed in fresh specimens that great force was required to stretch these muscles at the end of excursion of the head during axial rotation. If the neck is flexed to the side where tension occurs (in this example, flexed to the left), further excursion is facilitated by release of the tension on these muscles. On the right side, m. longissimus capitis profundus is not affected in the same way. However, since m. longissimus capitis profundus is much closer to the center of rotation, it is stretched by only a small amount when compared to the stretching of musculature that is attached to the widely divergent paroccipital processes.

b) Lateral flexion. - Orthogonal lateral flexure of the head is severly restricted by the geometry of the head and by its attached musculature. The posterior limit of the articular bone and the very massive pteryoid musculature ends at the level of the tip of the atlantal ribs. As is demonstrated by superficial dissection, there is almost no room between the neck muscles and the pterygoid muscles. In this way a check is provided upon lateral flexion.

Lateral flexion is also prevented by the pro-atlas and its attachments.

The musculature that opposes lateral flexion to the right side (for example) are: the left mm. ilio-costalis capitis, longissimus capitis superficialis, longissimus capitis profundus, spino-capitis posticus, and epistropheo-capitis lateralis.

c) Sagittal flexion. - Since the neck cannot flex ventrad, all ventral flexion of the head must reside in the occipital and atlas-axis joints. The head can be depressed ventrally "to 90° or at least 70°", (Virchow, 1914). Most of this movement is in the occipital joint, with the atlas-axis joint providing further ventral translation of the entire occipital joint. Virchow (1914) said "this movement probably results for the most part between skull and atlas and only in a narrow sense between atlas and occiput: (Virchow, 1914, p. 108). Substitution of the word epistropheus for the word occiput is needed to correct this statement.

Initially, ventral flexion proceeds without hindrance. But the pro-atlas, through its attachment to the occiput, is pulled to a horizontal position (with further flexion of the head). Continued increase in the angle of flexion causes the atlantal neural arches to be pulled craniad, sagittally, against the odontoid and axis, through the tension developed in the pro-atlas. This series of movements facilitates retraction of the atlantal ring. The only limitations on ventral flexion are the horizontal position of the pro-atlas, and the limit of tension that can develop in the nuchal ligament.

Extreme sagittal dorsal flexion of the skull is limited by the pro-atlas. As the skull is lifted, the pro-atlas is tilted back to the vertical position so that its "ventral surface looks forward" (Virchow, 1914). At the end of its tilting, it pushes the atlantal neural arches posteriorly. Further tilting of the pro-atlas (and occiput) is stopped by the pro-atlas exerting pressure against the atlas, and by the tension that develops in the nuchal ligament between pro-atlas and axial neural spine.

From extreme ventral flexion to extreme dorsal flexion, the pro-atlas travels through an arc of 90°, with a pivot in its ventro-lateral extremity (Virchow, 1914). The check-mechanism involving the pro-atlas protects the occiput from knocking against the large neural spine of the axis. Once the pro-atlas is removed from an otherwise intact specimen, the head may be lifted far enough backwards to contact the axis.

Movement of the head in the dorsal direction at the occipital joint is extremely limited. The head remains more as an extension of the neck column. Since the pro-atlas restricts dorsi-flexion of the head so greatly, the only way that lifting of the head can be accomplished is by dorsal flexion of the neck.

2. DIRECTION OF MUSCULAR ACTIVITY

This section describes the actions of a) the cervical muscles, and b) the occipital muscles, as inferred from their anatomical arrangement. The determination of action also takes into account the restrictions placed upon movements by bones and joints and ligaments involved in a movement (see pp. 119-136).

a) Actions of cervical musculature

M. ilio-costalis cervicis

Although this segmented muscle (figs. 38, 40) spans all of the cervical ribs, only a small portion of its fibers actually attach to bone. Most of the muscle fibers are attached to myoseptae and their superficial fascial sheath. The basic function of the muscle fibers is therefore intersegmental contractions that: laterally turn the neck, provide clockwise and counterclockwise torsion because of the restriction imposed by the zygapophyses; create dorsal, sagittal flexion of the neck; provide support against gravity for the neck.

Considering the muscle of one side first, it is apparent that contraction (unilateral) of the muscle fibers would tend to bring the myoseptae closer together. Since the myoseptae are at an acute angle to the muscle fascicles, some of the muscular tension developed is permitted to pull directly caudad on the entire posterior border of each rib (examine fig. 41B). The myoseptae in the muscle therefore allow the muscle tension to be broken down into two separate components, one that is longitudinal, and the other that is dorsal and posterior. The longitudinal components add together to a pull against the first rib. The myoseptal tension is in turn transmitted directly to each rib, since each one is attached to the posterior edge of the tuberculum and the dorso-lateral edge of the posterior longitudinal process (fig. 41B). Since the ribs are immovably fixed, they impart a lateral turning moment to their vertebra via the dia- and para- pophyses. Note that both diapophysis and parapophysis are anteriorly placed on the vertebra, a position that is as far as is possible from the center of rotation in the condyle. Therefore, unilateral contraction of this muscle can impart lateral bending to the entire neck column, coupled of course with the torsion that results from the zygapophyseal articulations.

Simultaneous bilateral contraction would create dorsal flexion of the neck. In this case the line of pull would be directed dorsally, posteriorly and medially on both sides, towards the trunk. In the case of dorsal flexion, the longitudinal rib members participate by providing lateral, parallel bars to each side, along the length of the neck. Virchow (1914) was puzzled by the function of this feature, since he removed the muscles before collecting his data.

Under tension from m. ilio-costalis cervicis, each overlapping rib segment could push back on its posterior neighbor. This type of activity can reach the extreme in first and second ribs. It can be seen from figures 38 and 40 that the combined muscular tension transmitted to the middle of the first rib by myoseptal tendon #1 would pull the whole first rib dorsally and posteriorly. This is equivalent to dorsal flexion since there is almost no resistance to movements in that direction. The result is further enhanced by the elongated first rib underlying the vertebral column to the level of the third vertebra. When the natural cervical curvature is also taken into account, a posterior pull on the first rib creates dorsal flexion of the first three vertebrae upon the rest of the neck; extreme pulling would carry along the rest of the cervical vertebrae.

Probably the most important function of m. ilio-costalis cervicis is the support of the neck against gravity. The entire weight of the neck (plus the head) is supported between the ribs of the cervical vertebrae (fig.68). Since the cervical vertebrae are mutually supporting, the main problem becomes one of supporting the end of the neck column against the eighth vertebra (where self-support is greatly diminished). The neck is supported from the trunk by m. ilio-costalis cervicis by a special sling that works in the following way:

Firstly, considering the dorsal, caudal pull on the ribs, a dorsal component force is resolved through the tubercula and diapophyses (fig.68). The tension developed in m. ilio-costalis cervicis is converted into a compression between rib diapophysis and neural arch elements, and a tension between parapophysis of the vertebra, and capitulum of the rib.

Secondly, the weight of the cervical vertebrae, plus the head and associated cervical structures, is strongly opposed by the rib capitula + diapophyses, in conjunction with the ventral musculature that is directly beneath the vertebrae. A large magnitude for medial compressive forces from the ventral musculature is suggested by the robustness of the parapophyses (fig. 6). The size of the parapophyses is related to the weight bearing functions through the following reasoning.

From C-3 to C-7 there is the progressive increase in size of the parapophyses, most of the increase taking place longitudinally (figs. 6, 14). Medial compression is transmitted through the rib capitula at right angles to the articular surfaces, causing an even distribution of the compressive forces. By C-7 the parapophses occupy about 3/4 of the centrum length. If there is medial compression, then enough bone has to be interposed between the ribs to resist such force. As can be seen in figure 6, the amount of bone that is physically deposited between a pair of ribs progressively increases up to C-7. If this increasing compressive force is related to weight bearing by the vertebrae, then the relative size of the parapophyses indicates the relative amount of weight borne by a bone within the neck.

Progessing from anterior to posterior, each added segment also adds more weight that is to be supported from the ribs, hence, each segment shows larger and larger parapophyses. At vertebra D-1, where vertebral support is supplied by the tendons of the trunk neural spines, and not its ribs, (and where the cervical curvature is in transition to the dorsal curvature of the trunk), the parapophyses are concordantly reduced (fig. 6).

The medial compressive forces actually do not arise from the weight of the neck itself, but rather from the posterior-medial pull of the ventral neck muscles that originate on the centra and hypophyses, and that balance tension against m. ilio-costalis cervicis. With this in mind it is interesting to note that mm. subvertebro-costales are muscles that originate as far back as the centrum of D-5 (the last hypapophysis), insert only upon the cervical, weight-bearing ribs, rib-1 to rib-7. The posterior-medial pull exerted by these muscles on the ribs is necessary to balance the dorsal component of force on the rib imparted by m. ilio-costalis cervicis.

At rest, all forces on the ribs and vertebrae must be in balance and the vertical and horizontal components must all add to zero. This necessitates two sets of muscle for the cervical ribs, a dorsal set balanced by a ventral set (actually, there is a third set that is purely intercostal and doesn't come to bear on the problem under consideration). The cervical sling created by m. ilio-costalis cervicis and its tough fascia is firmly anchored to the heavy trunk fascia. An additional anchor for this sling is provided by the septal connections on ribs 6 and 7 with the longissimus system.

The fascial anchor for the cervical sling is formed as a very dense condensation of connective tissue in the region of the neural spine of D-2, anterior to the scapulae.

The direction of forces involved with passive support of the neck are exactly the same as those involved in dorsi-flexion. Dorsi-flexion is simply accomplished by increasing the magnitude of the dorsal force component on each rib, to disturb the balanced condition in the dorsal direction. As long as the hypocentro-costal muscles pull the ribs medially, m. ilio-costalis cervicis can operate efficiently. Otherwise, the ribs would tend to dislocate at the parapophyses, in the lack of any other restoring mechanism.

In summary, dorsi-flexion of the neck results from bilateral contraction of m. ilio-costalis cervicis, which must be accompanied by bilateral contraction of the hypapophyseal-costal muscles. Unilateral contraction creates turning of the neck. The muscular morphology and fascia permits passive slinging of the entire neck during rest.

M. longissimus cervicis

Using the longissimus muscles of the trunk, the longissimus tendon system, and the dorsal intermuscular septum, as a strong base for its origin, m. longissimus cervicis exerts a longitudinal, posterior pull on each atlantal neural arch (figs. 52,57,60).

The pull of m. longissimus cervicis is parallel to the zygapophyseal plane between atlas and axis. This action is further guided by the dorsal intermuscular septum, which occupies a dorsal, medial, and longitudinal position with respect to this muscle.

This muscle acts with part of m. transverso-spinalis cervicis on the atlantal postzygapophysis. This action may be transmitted through ligaments and cartilage to the atlantal hypocentrum, thus protracting the atlantal ring and rotating the atlas dorsad relative to the odontoid.

M. transverso-spinalis cervicis

This muscle can have two basic effects. First, it pulls the cervical postzygapophyses directly posterior. That action can be of advantage in three ways: 1) as an aid to dorsiflexion; 2) as an aid to lateral flexion (unilateral contraction); 3) limiting the anterior travel of the postzygapophyses, when the zygapophyses are stressed (isometric contraction).

The second basic effect, in conjuction with m. longissimus cervicis, is that of protraction of the atlantal ring. A special portion of this muscle arises from the dorsal intermuscular septum and inserts with m. longissimus cervicis at the atlantal postzygapophysis.

The size of this muscle diminishes rapidly from posterior to anterior (fig. 50), with the exception of the special atlantal muscular sheet. However, even at its origin from the trunk, this muscle is the smallest of the cervical musculature (with the exception of the deep interspinous and inter-articular muscles, with which m. transverso-spinalis cervicis is complexly intermingled.

Mm. interneurales cervicis

This segmental series of muscles can only pull two successive neural spines (plus adjacent neural arches) of the cervical vertebrae closer together. Being intervertebral muscles placed far away from the center of rotation in the condyles, this muscle system has a high mechanical advantage. These muscles function as an aid to dorsi-flexion and also have a role in the passive support of the neck from the trunk. They are not to be found in the trunk.

The special anterior segment, between axial neural spine and the atlas, is modified to work opposite to all of the remaining segments. It originates from the anterior, ventral edge of the axial neural spine. It then runs directly laterad to the portion of neural arch of the atlas that is overhung by the axial neural spine. Its insertion, primarily on the atlantal postzygapophysis, along with a part of mm. interarticulares cervicis, allows only transverse tension on the atlas.

If permitted, this part of the muscle could spin the atlantal ring about the longitudinal axis, but the odontoid prevents this. It is more likely that this muscle prevents lateral excursion of the atlas against the odontoid during axial rotation of the head, when the arches are laterally displaced by forces from the pro-atlas. This muscle probably also prevents lateral dislocation of the atlas-axis zygapophysis, and keeps these surfaces pressed tightly together.

Mm. interarticulares cervicis

These muscles tie the vertebrae together and can function during dorsi-flexion of the neck as well as lateral flexion. These muscles are very small. They must work in conjunction with m. transverso-spinalis cervicis, since they both share insertions and occasionally the same tendons on the posterior surfaces of the postzygapophyses.

By their small size, and by their position around each zygapophyseal joint, these muscles probably help to stabilize the joint when the neck is extended, while at rest. They act as a muscular addition to the limitation of ventral flexion of the neck.

It is important to note that when the neck is extended at rest, these muscles may become important by preventing small lateral sway of the entire neck. By operating directly on each zygapophyseal joint, any torsion and flexion (ventral) can be directly opposed in the neck.

b) Actions of occipital musculature.

M. ilio-costalis capitis

The joints spanned by m. ilio-costalis capitis include: 1) the joint between rib-1 and the atlantal hypocentrum; 2) the suboccipital joint. The muscle has a firm base for origin from the distal half of the first rib, and the insertion is at the lateral half of the ventral border of the paroccipital process. A secondary insertion upon the tendon of m. longissimus capitis superficialis converts that tendon into a bipennate tendon. the action of this muscle is extremely complex and difficult to analyse very accurately in dead animals. The action involves a combination of ipsilateral flexion (yaw) and axial rotation (roll). There may be a component of dorsi-flexion (pitch) of the skull, dependent upon the joint configuration at the time of muscle contraction.

The joint between rib-1 and the atlantal hypocentrum is here considered non-mobile during the action of this muscle. Assuming that the rib is strongly fixed by mm. sterno-costalis, levator scapulae superficialis, ilio-costalis cervicis, costo-vertebralis (hypaxial), and further that movement at this joint is limited by the tight cover of m. longissimus capitis profundus, it thus follows that the muscle origin of m. ilio-costalis capitis is a strongly fixed and stable one that can closely follow all movements of the neck. Whatever position the neck assumes, this muscle and its origin maintain a constant relationship to the occiput. In addition, if the atlantal ring shifts upon the odontoid-axis, this muscle retains a constant relative position to the occiput.

All movements produced by this muscle then reside in the occipital joint. The muscle fibers are approximately longitudinal and they parallel the long axis of the body. In other words, the lateral (and posterior) origin has a lateral placement upon the occiput and more medial and anterior fibers of origin insert more medially upon the occiput. Therefore, the longitudinal pull exerted by one muscle of one side will cause ipsilateral head flexion, or yaw, to the active side.

Lateral flexion created by this muscle is not nearly as important as the roll movements that can be achieved. The component of roll depends upon the degree of flexion of the head. When the head is maximally flexed ventrally, *m. ilio-costalis capitis* would be pulling directly ventrad in the transverse plane of the skull (which is now the frontal plane of the neck), thus producing nearly pure roll activity. If the neck is flexed dorsally and the head flexed ventrally, at 90° to the neck, *m. ilio-costalis capitis* will then be vertical, at right angles to both the long and transverse axes of the skull. Figure 40 shows this muscle in an intermediate condition, where the neck is partially dorsi-flexed, and the head is partially ventro-flexed.

The posterior lateral-most muscle fibers insert, not on the occiput, but on the tendon of *m. longissimus capitis superficialis*. If there is tension already in the tendon, then contraction of these fibers tends to pull the tendon ventrally, in a parasagittal plane, further increasing the roll produced by the muscle. In this case roll is secondarily imparted to the skull.

The roll activity of one muscle can be exactly counterbalanced by the contralateral muscle. When both muscles contract simultaneously, depending upon the degree of flexion at the occipital joint, varying degrees of dorsal flexion are possible. If the skull is at maximum ventral flexion (90° to the neck) then the line of action passes through the occipital joint and dorsi-flexion does not take place (that is why, in this condition, all activity reverts to roll, yaw being of minor consideration for this muscle). As the skull leaves maximum ventral flexion, the line of action of this muscle passes posterior to the occipital joint and a dorsi-flexion component appears. Since dorsi-flexion at the occipital joint is very limited, this type of activity for this muscle may be considered to play only a minor role in its function.

Through manipulation of fresh material it was observed that: (assuming that a totally non-flexed position of the skull exists before pulling the muscle) pulling the left muscle caused counterclockwise (left) roll& yaw to the left, with a very slight dorsal pitch; If the skull is moved exactly oppositely, then this muscle is greatly stretched.

It could not be determined how translation of the entire occipital joint would affect this operation of this muscle. However, the muscle is such a broad sheet that its activity might be the same for all positions of the hypocentrum.

M. longissimus capitis superficialis.

This muscle has its origin from the tendinous arches of the longissimus system, far posterior to the tip of the first rib, as well as from the lateral part of vertebrae C-5 to C-7 and D-1. The muscle fibers are approximately parasagittal and the entire force generated by this muscle must be directed as tension in its tendon of insertion, parallel to the long axis of the head.

The tendon of insertion is placed at the extreme lateral tips of the paroccipital process.

The joints spanned by this muscle include all of the cervical intervertebral joints and the occipital joint . Exact analysis of this muscle's activity is difficult to impossible to determine. However, approximation of its major activity is less elusive. Assume that for the most part, the entire neck is fixed as a unit, and that lateral flexion of the neck by unilateral contraction of this muscle, are minimal. Starting from the "non-flexed" head, and bilateral contraction, dorsal pitch is achieved. In this manner, the yaw and roll components cancel each other, leaving a line of action that is dorsal to the occipital joint, and equivalent to dorsal pitch activity. As previously mentioned, dorsal flexion of the skull at the occipital joint is severely limited by the pro-atlas, so this cannot be of prime concern as an activity for this muscle.

Unilateral contraction of this muscle causes a pull that is directed longitudinally caudad, parallel to the skull axis, at the tip of the paroccipital process. This creates strong ipsilateral flexion of the skull. Because the insertion is dorsal to the occipital joint and the origin is either ventral to or at the level of, the occipital joint, a small component of roll is introduced to the muscle action.

A tug on this muscle produces activity similar to that of m. ilio-costalis capitis, with the emphasis on the larger degree of yaw, whereas m. ilio-costalis capitis emphasizes the roll component.

M. spino-capitis posticus

This muscle and its tendon span all of the cervical intervertebral joints, and the occipital joint. The multiple origin at the neural spine tips, and the insertion to the tip of the paroccipital process causes the entire muscle to occupy a single, flat frontal plane. The muscle segments add together to create a longitudinal pull on the tendon of insertion (see "analysis of a segmental muscle", p. 156).

The pull of this muscle, directed postero-medially (fig. 63) creates strong lateral flexion of the head with a small dorsi-flexion component. Normally there is not any roll component other than the minor roll that is possible during unilateral contraction. The tiny amount of resulting roll would be towards the side opposite the side of contraction. Minor roll is possible because the line of action is from a point that is dorsal, posteral and lateral to the center of rotation in the occipital condyle.

This muscle is the largest neck muscle, and it is almost entirely concerned with lateral flexion. Bilateral contraction can cause a minor raising of the head through dorsi-flexion at the occipital joint, of use in restoring the head from the extremely ventro-flexed condition, back to the normal position.

Through its pull on the head, it can also aid in lateral flexion of the neck as well as the head.

M. transverso-spinalis capitis

This muscle is entirely dorsal to the level of the neural spines. It spans all of the cervical joints and the occiptal joint. The insertion is the tip of the supraoccipital bone at the processus postoccipitalis. The action is strong dorsi-flexion of the skull and of the neck.

The muscle originates from the neural spines medially and ventrally, and from the trunk fascia laterally, to create a longitudinal posterior pull in the approximate plane of the cranial table.

The insertions at the paired processus postoccipitales are together approximately as wide as the occipital condyle. The tension on this process is at right angles to the occiput. Bilateral contraction would dorsi-flex the head to the end of its excursion, and continue to dorsi-flex the neck. The bilateral muscle is perfectly positioned to cause dorsi-flexion, there being no other muscle capable of such a narrow range of activity.

Unilateral contraction has almost the same affect as bilateral contraction, but weaker, and with the introduction of minor roll and yaw components. The minor roll and yaw cancell out when both left and right muscles work to give a pure dorsi-flexion activity.

The placement of m. transverso-spinalis capitis is such that it has the same basic function throughout the range of possible movements of the skull. This is accomplished by the tendinous insertions that are very near the midline and at right angles to the occipital surface. Through all degrees of lateral flexion of the skull the insertions are directly above the approximate point of rotation in the condyle, in this case also the axis of rotation during lateral flexion.

During all degrees of axial rotation, tension at the insertion is capable of the same function since it is always on the arc of rotation traced by the skull table, and that is at right angles to its line of action.

When the head is depressed, this muscle insertion becomes more acute, and activity in the muscle can be resolved into a ventral force through the occipital condyle, and a posterior force, normal to the occipital plane. During elevation of the head the angle the tendon makes with the occiput is probably maintained at 90° by the investing fascia and dermal armor of the neck. Without fascia and armor acting as retinacula, the tendons of insertion would bowstring away from the neck and allow an angle of insertion greater than 90 ° . An angle of insertion of greater than 90° is also prevented by the anterior segments of the muscle. Muscle fiber bundles from C2 and C-3 insert at the greatest angle to the tendon of insertion and pull that tendon more ventrally than posteriorly to resist the bowstringing (see general function of a segmental muscle, page 157). If bowstringing were allowed to occur, tension generated by this muscle could be resolved into two components; 1) a small one acting at a right angle to the occiput and causing some dorsi-flexion at the occipital joint; 2) a larger component parallel to the occipital surface, through the condyle, pulling the condyle away from its socket. This situation is unlikely to occur.

M. epistropheo-capitis lateralis

Acting between the epistropheal (axial) neural spine and occiput (and tendon of m. spino-capitis posticus), this muscle adds to the action of m. spino-capitis posticus to aid lateral flexion of the head and the neck. Since the origin is almost directly medial, between the paroccipital process tips, the muscle fibers are directed almost laterally, thus minimizing any roll activity for this muscle. The portion that inserts of the tendon of m. spino-capitis posticus also acts to prevent bowstringing.

M. epistropheo-capitis intermedius

This muscle crosses the joints between the epistropheus and occiput, and probably has most of its effect at the occipital joint. This muscle and its medial neighbor cross the pro-atlas and keep it from shifting out of position by pushing against it.

This muscle and its medial neighbor are responsible for the sharp bend in the dorsal margin of the epistropheal neural spine. Since the spine's edge is sharply inclined ventrad for these muscles, the muscle fibers occupy a position that is at right angles to the edge of the spine. The fibers have a thin weak insertion dorsally and laterally at the squamoso-paroccipital suture, suggesting its role in head movements, in terms of power supply, are minor, but that is plays an important part in restraining the pro-atlas.

M. epistropheo-capitis medialis

This muscle, a capital anterior continuation of m. transverso-spinalis capitis, inserts directly anterior, and occupies the supra-occipital bone, directly beneath the tendon of m. transverso-spinalis capitis. Its dorsal edge of origin "looks at" its insertion. It probably functions to a minor extent with m. transverso-spinalis capitis to produce elevation of the head. It can also function with m. epistropheo-capitis intermedius as a restraint on the lateral and dorsal movements of the pro-atlas.

M. atlanto-capitis

This is such a small muscle, with a weak insertion that it is probably of minor importance in creating movement of the atlas, or movement of the skull. Since it crosses the pro-atlas, it probably acts as a restraint along with the previous two muscles.

M. Longissimus capitis profundus

This is a massive muscle that passes alongside the cervical neural arch plates and inserts ventrally on the basi-occipital plate through a strong tendon (laterally) and fleshy fibers (medially). It is segmental and as determined by the direction of muscle fiber bundles, the following joints are crossed by this muscle: 1) the cervical condylar joints; 2) the atlas-odontoid joint; 3) the occipital joint. The action of this muscle is depression of the skull and stabilization of the occipital joint.

Most of the muscle fibers insert into a thickened band or tract of connective tissue that invests the lateral aspect of the multisegmental muscle, and which serves as the tendon of insertion for the muscle. The muscle generates a pull which acts through the insertion tendon on the edges of the basi-occipital bone. The pull is directed dorsally and posteriorly, as inferred from the direction of fibers in the tendon (figs. 44, 45). Since the line of action crosses the occipital joint ventrally and posterior to it, depressioon of the skull results.

Unilateral contraction can cause depression and ipsilateral flexion. Since this muscle is, of all the occipital musculature, the closest to the center of rotation of the skull, and since its tendon is basically longitudinal, it is poorly disposed to create axial rotation of the skull. However, unilateral contraction may be able to cause a minor amount of roll to the opposite side (left contraction, with clockwise roll, to the right, for example). This roll activity is inferred from the placement of dorsal origin and ventral insertion (see fig. 48, position of "shi").

The fleshy part of the insertion on the basi-occipital plate originates primarily from the atlantal neural arches. The occipital condyle, which is extended on a bony neck, is surrounded by this portion of the muscle, as is the occipital joint. This suggests that this most anterior and medial portion of the muscle acts to maintain tight contact between condyle and atlantal ring. Analogy is made here to such joints as the mammalian hip and shoulder joints, characterized by short, joint-stabilizing muscles that maintain tight contacts between joint surfaces during movements in the joint.

c) Multisegmental muscles

Certain muscles that reach the occiput express a peculiar specialization that they all have in common; they are of multi-segmental origin, and insert on a narrow area around the edges of the occiput. The three main occipital muscles that fit this description are mm. longissimus capitis profundus, spino-capitis posticus, and part of transverso-spinalis capitis. They are diagramatically shown in figure 56.

The anterior-most segment of each muscle inserts directly upon the occiput, not on the lateral or superficial thickened tendon. The muscle fibers of the anterior two or three segments that insert on their tendon will create forces that have two important components. One, the longitudinal component, will tend to pull the skull directly posteriorly. The other will be directed toward the central axis of the neck (either medially or ventrally depending upon which muscle is contracting). This action will tend to keep the insertion tendon at a maximal right angle to the occipital surface during all phases of contraction even though the head may move several degrees away from the long axis (see fig. 56D). The distinct advantage of this is that additional power provided by more posterior segment is not dissipated by bow-stringing of the insertion tendon. As can be seen in figure 56, the pull exerted by the most posterior segments is more or less parallel to the insertion tendon, which is normal to the occipital surface, as well as at a maximal distance from the occipital condyle. As soon as the head begins to turn, the normal angle of the insertion tendon exceeds 90°. As the angle of insertion becomes more and more obtuse, less tension is applied at right angles to the occiput, and the moment of force is reduced. But, if the most anterior fibers "pulled in" the insertion tendon near its point of insertion, the tendon will always be pulling at right angles to the occipital surface.

Muscles of multiple origin, but a single insertion can exert a great degree of control over their activity, since not all segments need to be recruited simultaneously.

The true functioning of these muscles is open to many interpretations, but it is clear that multisegmental muscles form a type of muscle specialization that deserves physiological as well as anatomical attention.

My own interpretation is that these muscles provide large amounts of tension to very small areas (or even points) of insertion. The local areas of insertion can then be located to maximize effectual control and application of force, such as moving a large alligator head using a relatively small region of occiput.

3. DIRECTION OF MOVEMENT ANALYSIS

a) Definition of head movements

Introduction

The movements of the head are independent of the neck much as the movements of the human hand are independent of those at the shoulder joint. In the human hand analogy, pronation and supination, and flexion adequately describe the motion at the wrist as opposed to adduction, abduction and rotation that occurs at the shoulder. In the alligator, head movement is conveniently described in terms of pitch, yaw, and roll, with a fixed center of movement in the occipital condyle.

Pitch is defined as sagittal movement of the tip of the snout, with respect to the center of movement. This is rotation about a transverse axis.

Yaw is defined as lateral displacement of the snout tip in the frontal plane, with respect to the center of movement.

Roll is defined as rotation of the skull about a median longitudinal axis that passes through the occipital condyle. There is no displacement of the snout during roll. For reference, the tips of the paroccipital processes are displaced in the transverse plane. Head roll is considered from the point of view of the animal. During right roll, the right side of the head is depressed, left side elevated. Right roll is equivalent to clockwise rotation (looking from posterior to anterior). The opposite movements have the appropriate, opposing terms of left roll and counterclockwise rotation.

The head may also undergo circumduction, here defined as a combination of pitch and yaw during which the entire head describes a cone with its apex at the occipital condyle. During circumduction the snout tip describes a circle.

These terms are used to distinguish movements of the head at the occipital joint, from movements produced by the entire neck. Such movements are termed elevation, depression, and lateral displacement of the head. Translational movements of the entire head are possible through the atlantal ring and are called protraction and retraction with respect to a fixed odontoid.

b) Correlation of movements defined with groups of muscles

Table IV summarizes each type of movement with a group of muscles that produce that movement. Note that for each movement there is one muscle that greatly predominates over the others of its group.

It is also important to note that the epaxial groups maintain specialization of function through the neck to the occiput.

c) Non-muscular forces acting on the skull; gravity.

The pull of gravity acts upon the center of mass of the skull. Moments about the occipital condyle are thus created, and are balanced at rest. For a given skull mass the location of the center of mass will determine the magnitude of the moments about the condyle that must be balanced by the occipital musculature. The nearer that the center of mass can be to the condyle, the smaller will be its rotational moment. Ideally a center of mass that is in the condyle would mean that the head is balanced by itself on the condyle, and head support would center on holding up the condyle rather than balancing rotational forces about the condyle.

A possible mechanism for shifting the center of mass posteriorly is the arrangement of pterygoid musculature. Most of this musculature is wrapped around the retroarticular part of the lower jaws, and extends at least as far back as C-3. Thus, mass is added posterior to the condyle, to balance the weight of the skull that is anterior to the condyle. The marked posterior direction of the quadrates also indicates that the weight of the jaws themselves is being added as a counterbalance to the snout.

The final counterbalance to the mass of the skull is m. transverso-spinalis capitis that inserts on the top, medial part of the occiput, in line with the cranial table. If,.during rest, the weight of the skull is balanced by tension in this muscle, then the head will not rotate, but it will be forced against the atlantal ring. The burden of skull support then falls upon the atlas.

The hypocentral wedge can be locked in place when the atlantal ring is protracted and the atlantal neural arches are resting firmly upon the shoulders of the odontoid.

A simple consideration of force vectors and moments in a suspended head at rest shows how gravitational force is distributed to the vertebral column, and balanced in the neck by the cervical musculature (fig. 69). In the diagram, the force of gravity creates a torque about the fixed occipital condyle. Such a torque is balanced by an equal, opposite torque created by m. transverso-spinalis capitis acting at right angles to the occiput at the edge of the cranial table. In this case, both forces, gravity and muscle tension, are at right angles to each other, this being the situation that actually occurs in the skull and neck. The two forces are added as vectors, and the resultant acts through the occipital condyle to push against the atlantal hypocentrum. The resultant force is also directed along the elongated first rib. This causes ventro-flexion of the vertebral column which is resisted by vertebral interlocking (since the neck has no ventral flexion from C-2 to C-7). Additional support for the first rib is provided by m. ilio-costalis cervicis, which acts like a sling or hammock that supports the entire cervical column against the trunk.

The result given here is that the head can be supported against gravity by 1) m. transverso-spinalis capitis; 2) m. ilio-costalis cervicis; and 3) vertebral interlocking. When m. transverso-spinalis capitis is cut from its insertion in a fresh specimen, the head pitches forwards as would be expected. Also, the resting position of the head, when forces acting on the head about the condyle are all in balance, is achieved when the cranial table is horizontal, in line with m. transverso-spinalis capitis and the neural spine tips of D-1, D-2 and D-3.

If an alligator takes that position and relaxes its jaw musculature, then the gaping posture typical for many crocodilia is seen.

With respect to the gaping pose, Dodson (1975, pg. 342) wrote that, "The much greater mass of the M. Spinalis capitis [what I call m. transverso-spinalis capitis] inserting on the occiput operates at the same or a better mechanical advantage than depressor mandibulae, but with three to four times the force. Thus it is concluded... that the principle force for elevating the skull in gaping is supplied by the cervical epaxial muscles."

Schumacher (1973) envisioned that while using m. depressor mandibulae, "during retraction the skull is lifted like one leaf of a hinge."

The suggestion that the skull is held up by the lower jaw pushing against the ground is not a likely possibility. Usually during gaping the lower jaw doesn't reach the ground so m. depressor mandibulae would have no effect in that case, and in cases where it does reach the ground, the muscle is so tiny that is seems impossible that it can support a skull for any length of time.

It is much more likely that m. depressor mandibulae is relaxed during gaping, and also in those cases where the jaw touches the ground. The gaping pose then is the result of relaxation of the musculature involved, not active energy consuming muscular effort.

A further proof that m. depressor mandibulae cannot easily support the skull is seen when an alligator is held upside-down. The jaw opens while the skull maintains its position, but the jaw cannot be held open for too long since m. depressor mandibulae, which is now holding up the jaw, tires quickly.

Two other sources of potential forces acting on the head are available. One is the addition of the weight of prey that is held in the jaws, especially at the snout tip. When the prey is firmly grasped, it can now be considered as mass added to the head which changes momentarily the weight balance and distribution of the head. The second source stems from hydrodynamic resistance encountered during swimming and submergence.

The effect of holding prey at the snout tip is equivalent to moving the center of mass of the head forward. Since muscle size and insertion point on the occiput are fixed at any given moment, the musculature is called upon for greatly increased forces when prey is held.

During ontogeny, snout length shows positive allometry that is correlated with increased prey size (Dodson, 1975). This means that through ontogeny, manipulation of prey requires : 1) That there is ontogenetic increase in the size of occipital condyle to muscle insertion point distances. This is one way that the mechanical advantage of the occipital musculature can keep step with allometric skull length increase; and 2) Ontogenetic increase of muscle cross-sectional area is another means of dealing with allometric increase in skull length. This solution is what occurs in the multisegmental muscles that move the skull from the edges of the occipital surface.

Both skull height and width (as measured by Dodson, 1975) are correlated with snout-quadrate length increase (Dodson, 1975; R=.99 for both variables); all three of these characters show isometric increase with increased body size. This implies that the moment arms of the occipital musculature are not following the positive allometric increases that are observed for snout-orbit length (Dodson, 1975). A much more accurate measure for comparison of such characters would be the distance between paroccipital process, and the height of the cranial table measured from the center of the occipital condyle, since these relate directly to muscles.

Ontogenetic increase of muscle mass and cross-sectional area must certainly occur, but the magnitude of the increase is not easy to compare and interpret in terms of the effect increased skull length during lifetime. The complex, segmental arrangement of the occipital musculature cannot be converted simply into relative force by adding the cross-sectional area of each segment. The degree of participation of each segment with the tendinous insertion must be taken into account (i.e., what component of each segment is used to create tension in the insertion tendon is the important datum).

The alligators are notable for their broad flat snout. If a flat surface is moved through water, considerable forces arise, normal to the surface, if the plane is tilted away from the long axis of motion. The resistant forces that arise in this manner can be called drag and lift. A swimming alligator must have excellent control over movements of its head in the three axes, in order to avoid erratic, uncontrollable aquatic locomotion. The following examples illustrate this point.

1) Suppose that while swimming forwards, the alligator pitches its snout downwards. This will create drag forces on the animal that, a) reduce longitudinal velocity, and b) increase ventral pitch of the head. If further increase to ventral pitch is resisted by the occipital musculature (using the same "antigravity" muscular arrangement as on land), then the entire body experiences ventral pitch and the animal can initiate a dive. This situation is hypothetical, and not observed.

The reverse circumstance, where the head is pitched up, creating lift, can similarly cause the animal to climb as it swims through the water. To stop climbing, the head can be quickly pitched down independently of the neck. In other words, wherever the head goes, the body follows.

2) Lateral displacement of the flat head in the water creates no special problem. However, since the neck vertebrae undergo a torsion during lateral turning, the head must be

oppositely rolled to maintain its original position with respect to the axis of motion. If the head has no compensatory roll during lateral displacement while swimming, then the animal will initiate a turn, since the water that strikes the exposed ventral snout surface sets up forces normal to that surface that tend to push the head away from the axis of motion.

Similarly, a turn can be initiated by rolling and pitching the head, without even moving the neck. Which method of turning is used in life cannot be determined by casual behavioral observations.

3) During swimming, if the head is rolled around the longitudinal axis, no special additional forces occur that oppose forward motion. This hypothetically allows the predatory alligator a large field of vision while swimming.

The possibility exists that an alligator can see above and below its body, and is not limited to strict lateral vision during hunting. However, roll of the head during swimming has not been observed.

These three hypothetical examples show that the head may be used as an aquatic steering mechanism that can exercise precise control over the powerful propulsion system of the tail. That this mechanism includes specialisation of the skeleto-muscular system was shown in the osteology and myology sections earlier.

4. OBSERVATIONS OF THE LIVING ANIMALS; MOVEMENTS ASSOCIATED WITH OBSERVED BEHAVIOR

Virchow (1914) made the following two observations of movement in captive animals that concern the head and neck:

1) "Ordinarily, the head and neck are not bent sideways, only rarely, for example when pushing the snout with the foreleg."

2) "If an animal snaps up a piece of flesh from the sand, it does so with the side of the snout by twisting its head."

I have made these additional observations involving the head and neck:

3) To swallow food, a type of inertial feeding is used in which the head is elevated, while small anterior and posterior head jerks aid the food in sliding down the gullet.

4) In a 2 meter captive specimen quick, whip-like, powerful lateral motions of the snout were used to tear apart beef kidney that was held together by a central ligament. In that manoever part of the food was inside the closed mouth and a sizable chunk of food (1 to 2 lbs.) was dangling out the right side. The head and neck were first bent to the left, followed by a rapid snap to the right. At the end of the right snap, the head was jerked to the left and the dangling piece went flying across the pen, to hit the wall which was four feet away.

5) During swimming, the head was held in a stiffly extended position without lateral bending.

6) Young alligators were observed in captivity and in the

wild to keep the head at water level and, by bending the head ventrally against the neck, the body was kept submerged (fig. 65).

7) A large A. mississippiensis was observed nest-guarding, and photographed by Watanabe (1976, personal communication). During the observation period the eggs hatched. The nest was opened and some of the young were carried to the water by the alligator. Pushing movements accompanied by right angle ventral flexion and twisting of the head were observed.

8) Bellowing is accompanied by elevation of the head and neck. Photographs of bellowing alligators show bulging of the cervical osteoscutes (Neill, 1971, fig. 10) that indicates activity of m.transverso-spinalis capitis.

10) During threat the head is pitched up and the lower jaw depressed to give increased gape. See Neill (1971, figures 2 and 15) for photographs of this attitude.

11) The resting alligator may have jaws closed and head off the ground, or the lower jaw may sag to the ground.

12) Although not personally observed, it is known that alligators pick objects off the substrate which will become gastroliths. This activity can only be carried out with head movements, since the arms do not reach very far forward.

All movements described are compatable with morphology. The special arrangement of the skull, atlas and axis, that gives independent mobility to the head allows both refined delicate movements (observations 2, 6, and 7), as well as movements requiring great force (observation 4).

The special atlas-axis joint permits extreme flexion of the head in the sagittal plane. This was seen in observations 7 and 8. The advantage of this flexion mechanism is shown during the "aquatic profile" posture (fig. 65). By making a sharp angle with the head, the neck is kept submerged well beneath the water's surface. In this case there is no need for ventral neck flexion, which in any case is impossible. If the neck were ventro-flexed, it would be raised to a position at, or near the water's surface, making it more visible and vulnerable to attack from above. Also, since most of the body is submerged during head flexion, a rapid and quiet retreat is enhanced, especially in juveniles, where predation from large birds is a hazard. Large adults can effectively hide themselve (especially in shallow water) when hunting at the surface, considering that with ventral head flexion, only the exposed head will cause disturbances at the surface, while the rest of the submerged body can provide hidden propulsive machinery.

Since the neck cannot flex ventrally, all ventral manipulations must involve the head and special atlas-axis joint, as seen in observation 7. In Watanabe's photographs, it was seen that ventral pitch was accompanied at times by roll and yaw. It is pointed out here that the exaggerated degree of sagittal flexion observed, most likely is the result of flexion at the occipital joint, coupled with retraction of the atlantal ring against the odontoid. Without the specialized sagittal movement of the atlantal ring, it is doubtful that extreme sagittal flexion would permit the great independence of movements of the head that were observed.

The forceful snapping movements used to tear flesh are probably carried out by mm. spino-capitis posticus and longissimus capitis superficialis. I envision both left and right muscles being used, one side to swing the head in one direction, the other side, upon being stretched, to snap the head reflexly back the other way. During this violent activity, the lateral movements of the atlantal ring are prevented by its being couched in the sagittal odontoid groove, the pro-atlas being held in place, as described above. Otherwise, the effectiveness of a whip-like movement would be dampened by allowing too much joint flexibility.

5. CONCLUSION OF ANALYSIS OF OCCIPITAL AND CERVICAL MUSCULAR MOVEMENTS

After study of the bones, muscles, joints, and some of the behavior concerning the head and neck of A. mississippiensis it was found that the neck cannot flex ventrally, but that the head is specially adapted through the atlas and axis, for marked ventral flexion upon the neck. Furthermore, the independent operation of cervical muscles for moving the neck, and occipital muscles for moving the head was demonstrated.

The Muscle Systems

The ilio-costalis system of the trunk, acting on the ribs, is modified in the neck for elevating, and turning of the neck, and as an anti-gravity sling for neck and head support. At the head, this system is most important for creating roll movement of the head.

The longissimus system in the trunk has longitudinal muscular cones that are arranged to pull on the transverse processes of the vertebrae (elongated levers for turning the vertebrae), thus causing lateral bending of the trunk. In the neck this system is very much reduced, with its most important functions being that of stabilization and protraction of the atlantal ring. At the head the system is represented by a small superficialis portion for turning the head laterally, and the greatly enlarged profundus portion for ventral flexion and stabilizations of the occipital joint.

In the trunk the transverso-spinalis system consists of muscles and tendons that maintain the dorsal curvature. The sagittal orientation of the tendon systems resists lateral bending, as well as torsional movements of the thoraco-lumbar vertebral column. In the neck the sagittal curvature of the column is reversed, and the support function filled behind by the transverso-spinalis system, is taken over by the ilio-costalis system (on the convex side of the bend). Thus the transverso-spinalis system becomes reduced in the neck, with a specialized portion reaching the atlas (as in the cervical longissimus system).

The transverso-spinalis system that reaches the head is perhaps the most greatly expanded and specialized musculature described here . Mm. transverso-spinalis capitis and spinocapitis posticus have differentiated for head elevation, and lateral displacement, to such a degree that they are as massive and important as the hind limb musculature, and exceed by far the forelimb musculature.

Occipital Muscles and Cranial Morphology

The occipital musculature has a profound influence on skull architecture. Previous accounts of the crocodilian skull have concentrated on the importance of adductor jaw musculature in shaping cranial morphology (Iordansky, 1973), and the occiput has never been considered from the viewpoint of axial musculature.

The rounded condyle is held on an extended neck that protrudes beyond the occiput beneath the foramen magnum. This feature permits great freedom of mobility for the head as an independent unit. Analogy is made to the head and neck of the mammalian femur.

A most important result of this study is finding that muscle insertions on the occiput are concentrated on specific bony locations by tendons, permitting increases in musculature without expansions of bony attachment areas. These occipital insertion points are as far as is possible away from the occipital condyle, given the occiput of an alligator. This means that for a given morphology, the maximum length of moment arms from the condyle is achieved. Thus, the occipital surface area is of minimal significance in considering reconstructions of musculature from fossils. Functional conclusions reached by Colbert (1946) about Sebecus were based upon surface area expansion of the occipital surface. Findings in the present study indicate that a different emphasis should be placed on the anatomy for reconstruction of fossils; namely, to examine the edges of the occiput, and to find out how far away from the condyle center each insertion is.

The quadrates and pterygoids are firmly joined to the braincase. The occipital musculature acts directly upon the braincase. The cranial table, frontal bone, prefrontal bones, and prefrontal pillars form an arch that transmits tension from m. transverso-spinalis capitis to the palate and dorsum of the snout, and laterally through the postorbital bars.

Lateral pull generated by m. spino-capitis posticus is probably transmitted through the quadrate-quadratojugal-jugal chain of bones, as well as dorsally through the cranial table-postorbital bar. The postorbital bar is a cylinder of bone that extends vertically from jugal and ectopterygoid up to the anterior corner of the cranial table. It is in a good position as a support or strut between braincase and palate, in addition to being of most importance in transmitting roll movement of the head.

The ventral tube of the pterygoids and palatines resists compression due to gravity and the longitudinal forces that result from dorsal pitch, transmitted through the condyle-basisphenoid axis.

The system of bars that connect the snout and braincase reduce shearing stress on the vertical occipital surface by channeling the stress to more anterior cranial portions. Thus, the supra-occipital and exoccipital bones can be thin-walled (and contain air pasages) since the need for dense compact bone is relieved by the connections between braincase and snout. Furthermore, the opening of the foramen magnum poses no structural weakening since the occipital forces are transmitted through the bar system.

It is interesting to note that the occipital surface is actually a curved one, concave posterior. If lines are drawn normal to the entire occipital surface, they intersect on the neural spine of the axis. In fact the muscle fiber bundles from axial spine to occiput illustrate this point.

During contraction of the short occipital muscles, the direction of pull is about the same for many different positions of the head, since the concave occipital arrangement provides that the maximal numbers of muscle fibers will be oriented normal to the occipital surface at any one time. The same kind of arrangement is shown by the curved retroarticular process, and m. depressor mandibulae. During travel of the lower jaw, m. depressor mandibulae can always be working to its best mechanical advantage.

The cavity formed by the atlantal neural arches and odontoid is as large as the braincase, and exceeds the rest of the spinal canal in its internal dimensions. This feature adds to the freedom of movement of the head, since there is plenty of room for the spinal cord and medulla, should they require it during movements of the head upon the neck. The importance of this space is underlined by the sometimes violent activity that involves the head.

Cervical Muscles, and Cervical Bony Morphology

Because of differentiation of neck musculature into fairly disctinct functional groups, there are several sets of associated morphological changes involving the vertebrae. By considering such characters as: 1) neural spines; 2) zygapophyses; 3) neural arch plates; 4) diapophyseal shape; 5) centra; 6) parapophyseal shape; and 7) hypapophyseal shape; it is noticed that there are gradual changes in these functionally important bony landmarks along the vertebral column.

Each neck vertebra has a distinct set of characters that permit individual identification. This individuality results from the intersection of the various morphological gradients of the above characters at each segment. The gradients are the results of gradually changing functions of parts of vertebrae (with their attached muscles) up and down the vertebral column.

To summarize these anterior-to-posterior gradients that are observed in A. mississippiensis for the cervical vertebrae:

1. Neural spine height increases.
2. The longitudinal dimension of neural spine blades decreases from C-2 to C-7 (and also to D-1); D-3 and D-4 change the orientation of the blade tip to present anterior and posterior tip surfaces, rather than lateral surfaces.
3. Zygapophyseal angle (as defined by Virchow, 1914) steadily increases.
4. Width increases between the prezygapophyses of the individual vertebrae. Likewise, the width between each set of postzygapophyses increases.
5. The anterior-posterior dimension of the lateral neural arch plates decreases.
6. The articular surfaces of rib capitula and parapophyses elongates from C-1 to C-7; it then abruptly changes to a short, movable articulation at D-1; from D-1 to D-4 the parapophyseal articular surface undergoes dorso-ventral elongation, but changes back to a horizontal orientation by D-9.

7. The distance between parapophyses of a vertebra increases from C-1 to C-7; it abruptly decreases at C-8.

8. Hypapophyses steadily increase in size from C-1 to C-7; they then decrease from D-1 to D-5.

9. The dorso-ventral dimension of the neural arch plate diminishes; This is associated with the roots of the diapophyses occupying a more and more dorsal position from anterior to posterior on the neural arches.

10. The posterior surface of the postzygapophyseal pillars changes from horizontal to vertical.

11. The diapophyseal articular surface (and cross-sectional shape) changes from rounded at C-3, to a dorso-ventrally flattened oval at C-6; at C-7 this surface changes to a rounded one, for movable articulation.

12. A line drawn between ipsilateral para- and diapophyses approximately parallels the plane of the ipsilateral prezygapophyses.

The preceding morphological gradients are related to cervical function in the following way (the numbers correspond):

1. With the cervical curvature, increased neural spine height permits the special segmental expansion of the transverso-spinalis system (_mm._ _transverso-spinalis capitis_ and _spino-capitis posticus_) to

occupy a space dorsal to the vertebral column. Thus, the many segments of m. transverso-spinalis capitis are effectively packed along the midline, one segment behind the other, to provide maximum longitudinal tension in the insertion tendon at the occiput. The segment that arises from D-2 is directly dorsal to that of D-1, and both are dorsal to all other anterior segments. By this arrangement the insertion tendons can remain near the midline throughout life and transmit midsagittal posterior tension from the muscular segments most efficiently.

2. The axial neural spine is partly encircled by the occipital surface, and parts of the transverso-spinalis system fan outwards from that surface. The farther away a neural spine is from the occiput, the more longitudinal are the muscle fiber bundles that originate from the vertebral neural spine. Consider m. spino-capitis posticus as an example: Posteriorly there is less and less lateral surface to accomodate fleshy fibers; any increase in musculature must take place on the more laterally placed aponeurosis. The segment from C-3 needs a broad fleshy area on the neural spine since it functions to retain the insertion tendon (through medial tension) at the proper angle to the occiput, while, in contrast, a segment from C-7 is providing longitudinal tension, and functions as a long muscle, rather than as a short fleshy one.

3. Increase in the zygapophyseal angle permits an increasing degree of lateral flexion, and reduces allowable

sagittal dorsi-flexion. This gradient is associated with the change from cervical curvature to dorsal curvature, as well as the functional change from neck function (support of the head) to trunk function (support of body, initiates undulatory locomotion).

4. Increase in this dimension resists torsional effects in the neck column as the vertebrae bear more and more weight posteriorly. This is also associated with the increase in zygapophyseal angle (see above).

5. This dimension is directly related to the segmental origins of m. longissimus capitis profundus. The origin for this muscle diminishes posteriorly, and the superficial longissimus muscle, with its transverse process, becomes more dominant.

6. This increase in articular surface area is directly related to increase in weight bearing of the more posterior cervical vertebrae. The support given by m. ilio-costalis cervicis as it pulls upon the long rib processes, is countered by the medially directed pull of mm. subvertebro-costales (p. 112), and the rib capitula-parapophyseal articular surface is directed at a right angle to the direction of pull of the latter muscle.

7. Increase in this dimension is for the same reason as given in 6, above.

8. Hypapophyses serve as the origin for mm. subvertebro-costales; see 6 and 7 above.

9. The origin for m. longissimus capitis superficialis

are on the diapophyses which must provide a lateral base of origin for this muscle to function efficiently (its insertion is the lateral-most position on the occiput). See 5 above.

10. Related to increased weight bearing of more posterior cervical vertebrae.

11. The flattened oval shape at C-6 of the diapophyses allows fibers of m. longissimus capitis superficialis to pull at right angles with respect to the diapophyseal surface area of origin.

12. Cannot relate this gradient to a function.

Use of cervical and occipital musculature in paleontological reconstruction: Sebecus.

Paleontological reconstruction is difficult and often misleading. Soft anatomy is rarely known for fossils. existing correct information that bears on the problem of reconstruction should be taken into account.

In view of this, the reconstruction of neck muscles for Sebecus by Colbert (1946) cannot be accurate. The occipital morphology of Sebecus is sufficiently similar to Alligator so that it is safe to assume the major muscles inserting there were the same. Colbert (1946) based his analysis and reconstruction on alligator muscles in a report by Anderson (1936). Both Anderson (1936) and Colbert (1946) were not aware that the major muscles for moving the skull insert by tendons on the margins of the occiput since this is information being brought forth in this report. The (erroneous) fleshy insertions given for Sebecus actually emphasizes the less important muscles that act on the occiput. The more important muscles such as m. spino-capitis posticus, could never be preserved, and Colbert (1946) also never suspected the importance of multisegmented muscles. Thus in his evolutionary, functional analysis of the form of the head of Sebecus, Colbert (1946) looked for large occipital area to indicate strong muscle insertions, rather than extensive vertebral areas for large muscle origins.

Colbert's statement that, "there were relatively increased areas for the origins and insertions of the neck muscles in the extinct genus, as compared with modern eusuchia and therefore relatively strong musces in the fossil form." does not follow from the facts now at hand. Further, the actions of the muscles given by Colbert (1946) (1946) are incorrect in light of what is presented here.

It is unfortunate that Colbert (1946) did not have the advantage of a detailed account of Alligator epaxial muscles, since in every other respect, that study provided an important contribution to our knowledge of extinct forms.

First-hand knowledge and close study of specimens of Sebecus are required to reconstruct the occipital and cervical muscles, and to interpret the reconstruction through functional inferrence. However, with the actual specimens, and the anatomy presented in this dissertation, it should be possible to determine the insertions of all of the occipital muscles, and the origins and insertions of most of the cervical musculature.

SUMMARY

This study presents a detailed description of the osteology and myology of the occipital and cervical regions of Alligator mississippiensis. The occiput is defined on a functional basis, and the occipital morphology is related to the attached muscle systems. The bones of the occiput and neck are re-described with attention given to details of related myology. The musculature of the trunk is presented with a new, detailed description of the epaxial muscle systems. A systematic approach to describing cervical and occipital muscles is used to examine the details of those areas. This approach is consistently applied for all muscle groups. Errors of description from earlier studies of epaxial trunk, neck, and occipital musculature are corrected with each description. The naming of cervical and occipital muscles is made clear by a search for synonyms in older literature. Finally, the musculo-skeletal system of the occiput and neck, and the pertinent joints are functionally examined.

It is shown that previous descriptions differed from my own studies on the following major points (minor details are included with individual descriptions):

a. M. ilio-costalis capitis is given a new name since it was considered a sterno-mastoid by Rathke (1866) and Anderson (1936). It is actually part of the ilio-costalis muscle system. Its origin and insertion are here corrected.

b. The origin and insertion of all of the following

muscles have been corrected by this study, either because they were in error, or were not previously described:

1. *m. ilio-costalis cervicis*
2. *m. longissimus cervicis*
3. *m. longissimus capitis superficialis*
4. *m. longissimus capitis profundus*

c. The insertion of *m. transverso-spinalis cervicis* is found to extend to the atlas.

d. The following new epaxial muscles are named and described:

1. *m. epistropheo-capitis lateralis*
2. *m. epistropheo-capitis intermedius*
3. *m. epistropheo-capitis medialis*
4. *m. atlanto-capitis*
5. *m. atlanto-capitis profundus*

e. The following new hypaxial muscles are named:

1. *m. sterno-costalis*
2. *m. subvertebro-costales*
3. *m. hypocentro-occipitalis*
4. *m. costo-occipitalis*

f. The retractor muscle for the Eustachian canal valve was identified, and its origin on the atlantal hypocentrum is illustrated.

g. The muscle "m. atlöido-capitis" of Vallois (1922), supposedly extending from the neural spine of the atlas to the skull, was not found (the atlas lacks a true neural spine). However, the small, deep occipital muscles are here described in great detail.

The re-description of the cervical vertebral column and ribs reveals that there are morphological gradients along the column that can be directly related to the cervical and occipital musculature. The relevent anatomical landmarks are identified.

The descriptions of previous authors are found to be incomplete, and a more detailed description of muscle origins and insertions is presented. The expanded description is presented to enable future work to be carried out on the musculo-skeletal system in a systematic manner.

Absent from previous studies is the statement that all three epaxial muscle systems are represented on the occiput. This bears significantly upon the concept of serial homology, which implies that there is correspondence between the parts of each segment of the body. Serial homology is demonstrated by showing the segmental nature of many of the major neck muscles. Fusion of muscles appears to take place between members of the same epaxial systems and results in development of a "multi-segmental" muscle. As used here, a multi-segmental muscle adds many origins of morphologically similar segmental homologues to a single tendinous insertion. Fusion between muscle systems occurs only rarely.

The morphological observations of Virchow (1914) are corroborated and expanded upon. The musculature and skeleton are considered together to demonstrate the specialization of the atlas and axis of A. mississippiensis for sagittal motion of the atlas upon the axis. It is found that the neck cannot flex ventrally, and manipulations carried out by the jaws and skull involve complex modification of the cervical musculature and skeleton. Major development is best seen in the atlas-axis joint, and in mm. transverso-spinalis capitis, and spino-capitis posticus.

In this study head movements are defined in terms of pitch, yaw, and roll, and the individual muscles providing these components of motion are noted in chart form.

The important relationship of occipital musculature to cranial architecture is pointed out.

Rough analysis of the actions of each muscle and the movements at each joint reveals that the gaping posture of A. mississippiensis could be a means of passive rest while on land. It is also suggested that the head of A. mississippiensis could be used as a steering device in the aquatic medium.

The bearing of results presented here is given on the reconstruction of Sebecus by Colbert (1946), to show that soft anatomy of the living animals can give useful information for paleontological reconstruction. The major muscles that move the head of Alligator, and presumably moved that of Sebecus, insert primarily at peripheral locations on the occiput, such as on the processus postoccipitalis, paroccipital process, and basi-occipital plate margins, and not (as was previously believed) on the occipital surface. Colbert (1946) could not carry out a detailed reconstruction because the basic anatomical work had not been done. I believe it is now possible to reconstruct Sebecus and other fossil crocodilians to a degree of detail not previously attained.

APPENDIX A

TABLES

TABLE I

Neural spine height measured from the neural canal to the tip of the neural spine for presacral vertebrae except the atlas.

Vertebra	AMNH 35441	AMNH 43315	AMNH 43316	QC R1200
C-2	1.87	2.80	1.97	3.02
-3	2.86	3.39	2.49	3.90
-4	3.59	3.77	2.82	3.54
-5	4.07	4.20	3.00	4.78
-6	4.33	4.57	3.18	4.90
-7	4.36	5.20	3.42	5.60
D-1	4.72	5.71	3.80	5.58
-2	4.92	6.69	4.39	6.56
-3	4.92	6.14	4.54	6.77
-4	4.54	6.00	4.09	6.58
-5	4.23	4.62	3.92	5.81
-6	3.91	4.89	3.69	5.45
-7	3.75	4.69	3.79	5.15
-8	3.60	4.50	3.46	5.16
-9	3.36	4.57	3.40	4.95
-10	3.31	4.59	3.40	4.92
-11	3.43	4.37	3.31	4.85
-12	3.43	4.13	3.22	4.83
-13	3.58	4.60	3.29	4.82
-14	3.62	4.70	3.50	4.76
-15	3.62	4.89	3.45	4.76
-16	3.69	4.89	3.41	4.87
-17	3.65	4.89	3.50	5.04

Table II

System	I: Thoraco-lumbar Region	II: Cervical Region	III: Cervico-capital Region (neck-to-occiput)
Ilio-costalis	ilio-costalis dorsi	iliocostalis cervicis	ilio-costalis capitis
Longissimus	longissimus dorsi	longissimus cervicis	longissimus capitis superficialis longissimus capitis profundus
Transverso-spinalis	tendino-articularis dorsi articulo-spinalis dorsi spino-articularis dorsi neuro-spinalis dorsi inter-articulares dorsales interspinales dorsales	transverso-spinalis cervicis inter-articulares cervicis interneurales cervicis	transverso-spinalis capitis epistropheo-capitis-medialis spino-capitis posticus epistropheo-capitis: lateralis intermedius atlanto-capitis

TABLE III

A synopsis of joints considered in this study.

1. Basi-occipital joint. Between basi-occipital condyle of skull and the cartilagenous cotyle of the atlantal ring (=occipital joint).
2. Occipital-pro-atlantal joint. The contact between pro-atlas and exoccipital bones, dorsal to foramen magnum.
3. Pro-atlas-atlas joint. Occurs where the pro-atlas rests upon the dorsal surface of the atlantal arches.
4. Interatlantal joint. The three joints that occur between the three members of the atlantal ring. Including left and right neural arch contact with hypocentrum, plus left and right neural arch contact with each other.
5. Specialized atlas-axis joint. That part of the atlas axis joint which involves the atlantal neural arches as they rest upon the grooves in the odontoid process.
6. Hypocentrum-odontoid joint. An inter-atlantal joint between the hypocentrum of the atlas, and the detached odontoid of the atlas (which is firmly sutured to the axis centrum).
7. Intervertebral joints. Vertebrae usually make contact in three places, once at the centrum, and on both left and right zygapophyses.
8. Costo-vertebral joints. These are present where the ribs join to the vertebrea.
9. Intercostal joints. The cervical ribs are so arranged that the posterior part of one rib meets the anterior part of the next posterior rib.
10. Odontoid-axis joint. A joint between the odontoid (part of the atlas vertebra) that is joined to the anterior surface of the axis centrum.
11. Neural arch-centrum joints. A joint that occurs where the neural arches rest upon the centrum.

TABLE IV

This is a listing of capital muscles ordered by proposed functions for the muscles. Muscles in capital letters are thought to provide the major components of the category. Pitch is broken into dorsal and ventral; For roll and yaw, only the right side need be considered.

A. Dorsal Pitch

TRANSVERSO-SPINALIS CAPITIS
SPINO-CAPITIS POSTICUS (bilaterally)*
ilio-costalis capitis (bilaterally)*
longissimus capitis superficialis (bilaterally)*
epistropheo-capitis lateralis (bilaterally)*
" " intermedius (bilaterally)*
" " medialis (bilaterally)*

B. Ventral Pitch

LONGISSIMUS CAPITIS PROFUNDUS
costo-vertebralis medialis (= splenius colli of Hoffman)
(= scaleni of Rathke)
collo-capitis (= head part of longus colli, = rectus capitis anterior of Rathke)

C. Right Roll

Right ILIO-COSTALIS CAPITIS
Right longissimus capitis superficialis
Left longissimus capitis profundus

D. Right Yaw

Right SPINO-CAPITIS POSTICUS
Right transverso-spinalis capitis
Right epistropheo-capitis lateralis
Right " " intermedius
Right " " medialis
Right longissimus capitis profudus
Right longissimus capitis superficialis

* when these muscles contract bilaterally their respective roll and yaw components cancel, and the result is dorsal pitch.

APPENDIX B

SYNOPSIS OF EPAXIAL MUSCLES

Synopsis of Epaxial Musculature

This synopsis of the epaxial musculature of the back, neck and occiput of A. mississippiensis lists the names of each muscle described within each system, by regions; O=origin of muscle, I= insertion of muscle, A= action of muscle.

A. Ilio-costalis system

1. ilio-costalis dorsi
   O: lateral surface of ribs, and myoseptum of posterior edge of same rib
   I: posterior surface of next anterior myoseptum
   A: compresses ribs together; compresses thorax

2. ilio-costalis cervicis
   O: lateral surfaces of ribs and myoseptum of posterior edge of same rib; medial fibers originate from corresponding longissimus system septa
   I: posterior surface of next anterior myoseptum
   A: support of neck against gravity; dorsi-flexion of neck; lateral movements of neck

3. ilio-costalis capitis
   O: rib-1 and septum-1 of m.ilio-costalis cervicis
   I: ventral margin of paroccipital process; on insertion tendon of m. longissimus capitis superficialis
   A: axial rotation, ipsilateral flexion, and dorsi-flexion of the head

B. Longissimus system

1. longissimus dorsi
   O: vertebral transverse processes and anterior surface of aponeurotic cones; intersegmental fiber bundles from dorsal intermuscular septum
   I: posterior surface of next anterior aponeurotic cone; intersegmental bundles through fenestra of next anterior cone, to the posterior surface of the second anterior cone
   A: move transverse processes as levers for undulation and lateral bending of trunk

2. intertransversarii dorsales
   O: cranial edges of transverse processes
   I: caudal edges of transverse processes
   A: pulls transverse processes together

3. longissimus cervicis
   O: segmental tendinous thickenings in dorsal intermuscular septum (from undersurfaces of prezygapophyses 4,5,6, & 7)

B. Longissimus system (continued)

I: by a tendon to postzygapophysis of atlas
A: pull atlantal ring posterior and dorsad (protraction of atlantal ring); dorsi-flexion of neck

4. longissimus capitis superficialis
O: lateral neural arch plates of C-5, C-6, C-7, D-1
I: by tendon to lateral extremity of paroccipital process
A: axial rotation, ipsilateral flexion, and dorsi-flexion of head

5. longissimus capitis profundus
O: lateral surface of neural arches of C- to C-6, transverse processes of C-3 to C-7; small bundles of muscle fibers from transverse process of D-1 and D-2
I: by tendon to margin of basi-occipital plate; fleshy to surface of basi-occipital plate
A: depression of head, contralateral axial rotation, and stabilization of the occipital joint

C. Transverso-spinalis system

1. tendino-articularis dorsi
O: lateral and medial intermuscular septa
I: segmental aponeurosis; vertebral transverse processes
A: support of dorsal column against gravity

2. articulo-spinalis dorsi
O: postzygapophyses and lateral intermuscular septum
I: by tendons to neural spine tips (5 segments cranial to origin), and to tendons of m. tendino-articularis dorsi
A. support of dorsal column against gravity

3. spino-articularis dorsi
O: dorso-medial surfaces of postzygapophyses
I: by tendon to anterior tips of neural spines (5 segments posterior to its origin)
A: support of dorsal column against gravity

4. neuro-spinalis dorsi
O: base of neural spines; lateral surface of neural spines
I: by tendon to posterior tips of neural spines, ventral to insertion of m. articulo-spinalis dorsi (5 segments caudal to vertebra of origin
A: support of dorsal column against gravity, and resistance to vertebral torsion

5. interarticulares
   O: dorso-lateral surfaces of neural arches of dorsal region vertebrae; anterior medial half of postzygapophysis; a deeper segment originates from pillars of the prezygapophyses ventral to the zygapophyseal joint
   I: posterior surfaces of postzygapophysis of next cranial vertebra; the deep segment skips one vertebra before insertion on postzygapophysis
   A: lateral flexion of neck; stabilizes intervertbral joints

6. interspinales
   O: anterior edge of blade of neural spine
   I: posterior edge of blade of neural spine
   A: dorsi-flexion of neck vertebrae

7. transverso-spinalis cervicis
   O: complex segmental tendon systems that are anchored to a prezygapophysis through the dorsal intermuscular septum, and to neural spines by tendons
   I: posterior portion of postzygapophyses, including the atlas
   A: dorsi-flexion and lateral flextion of neck; protraction of atlas

8. interneurales cervicis
   O: anterior edge of blade of cervical neural spines
   I: posterior edge of blade of cervical neural spines
   A: dorsi-flexion and gravitational support of neck

9. interarticulares cervicis
   O: medial series from dorsum of neural arch base; second series from anterior surface of postzygapophyses and joint capsules
   I: medial series to medial surface of preceding postzygapophysis; second series to lateral half of preceding postzygapophysis

   A: dorsi-flexion and lateral flexion of neck

10. spino-capitis posticus
   O: lateral surfaces of neural spines of C-3 to C-7; tips of neural spines of D-1 & D-2; tendons attached to neural spines of D-1 & D-2
   I: by lateral tendon to lateral tip of paroccipital process
   A: lateral flexion, dorsi-flexion, roll of head; lateral flexion, dorsi-flexion of neck

11. transverso-spinalis capitis
   O: tips of neural spines C-2 to C-7, and D-1 to D-4; deep fascia of shoulder region
   I: by a tendon to dorsal surface of processus postoccipitalis
   A: dorsi-flexion of skull; dorsi-flexion of neck

12. epistropheo-capitis lateralis
    O: lateral surface of neural spine of axis
    I: to medial side of insertion tendon of m. spino-capitis posticus; lateral tip of paroccipital process
    A: prevent bow-stringing of insertion tendon of m. spino-capitis posticus; lateral and dorsi-flexion of head

13. epistropheo-capitis intermedius
    O: anterior edge of neural spine of axis
    I: exoccipital-squamosal suture, lateral to insertion of m. epistropheo-capitis medialis
    A: probably restrains pro-atlas; dorsi-flexion of head

14. epistropheo-capitis medialis
    O: anterior edge of neural spine of axis
    I: supra-occipital bone, ventral to shelf of processus postoccipitalis
    A: probably restraint of pro-atlas; dorsi-flexion of head

15. atlanto-capitis
    O: dorsal surface of neural arch of atlas
    I: exoccipital-squamosal suture
    A: probably restraint of pro-atlas

16. atlanto-capitis profundus
    O: neural arch of atlas, near contact between atlas and pro-atlas
    I: lateral tip of paroccipital process
    A: small muscle blends with epistropheo-capitis lateralis

APPENDIX C

ILLUSTRATIONS

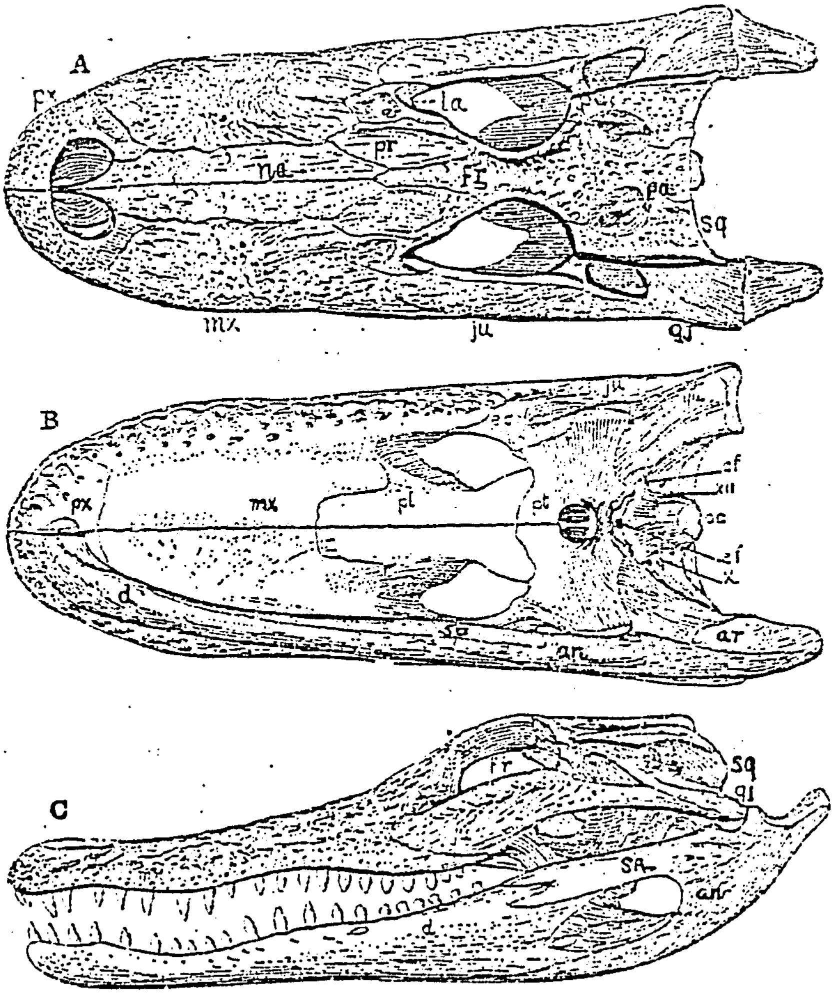

Fig. 1. Typical crocodilian skull as exemplified by Alligator mississippiensis (Daudin). A. Dorsal aspect. B. Ventral aspect. C. Left lateral view. After Williston, 1925.

Fig. 2. Occipital view of the skull of <u>A. mississippiensis</u>. a' = basi-occipital plate; a" = occipital condyle; b' = paroccipital process; b" = exoccipital pillar; b"' = triangular plate of exoccipital; C = supra-occipital; d = squamosal; e = parietal; f = quadrate; g = pterygoid; h = ectopterygoid; i = basisphenoid.

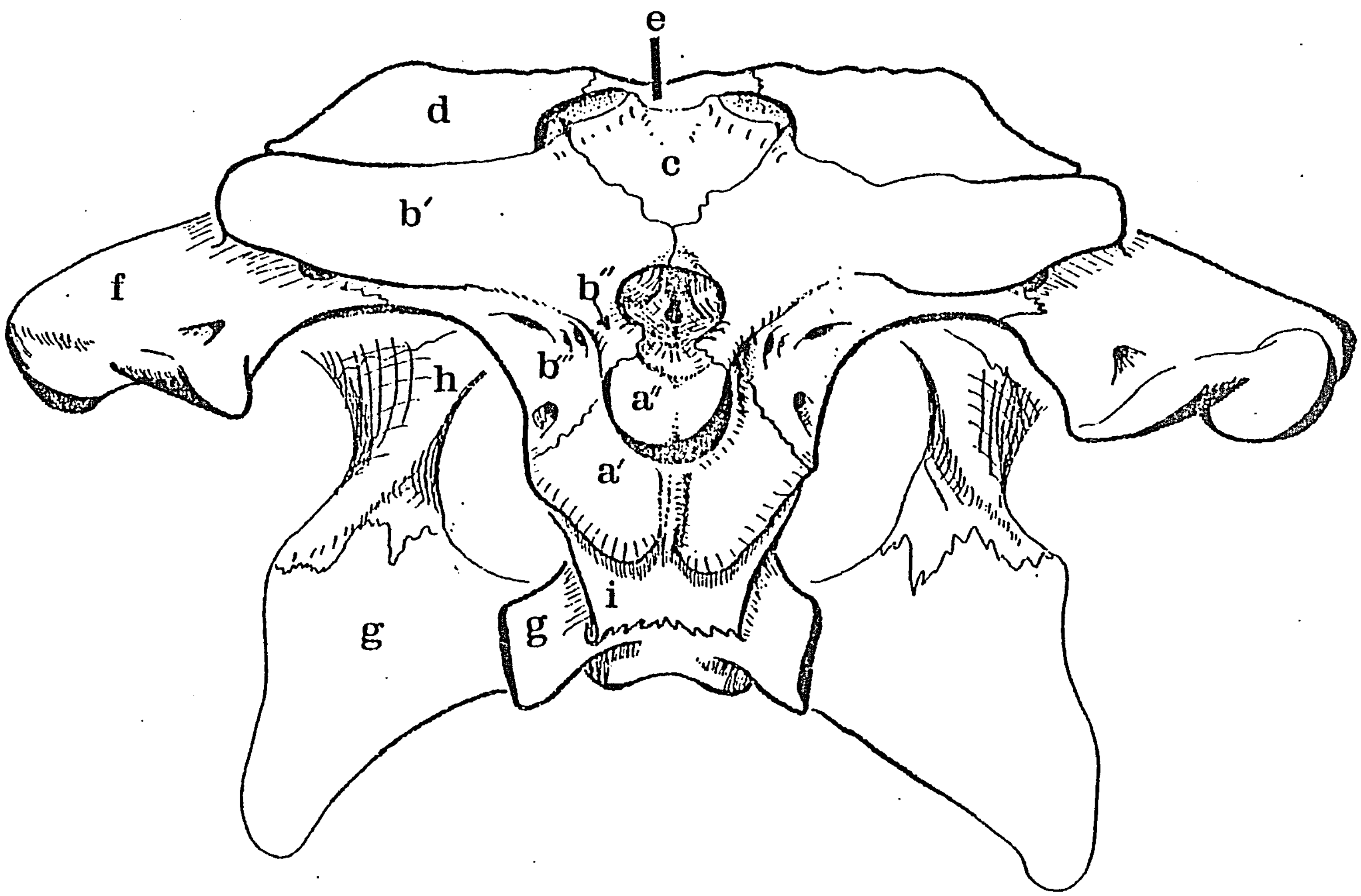

Figure 2

FIG. 3. BRAINCASE OF A. MISSISSIPPIENSIS, LEFT LATERAL VIEW. EXOCCIPITAL, SQUAMOSAL, AND QUADRATE BONES REMOVED FROM THE LEFT SIDE. **a** = OCCIPITAL CONDYLE; **b** = NECK OF OCCIPITAL CONDYLE; **c** = RUGOSE ARTICULAR SURFACE FOR SUTURAL CONTACT WITH EXOCCIPITAL; **d** = LATERAL MARGIN OF BASIOCCIPITAL PLATE; **e** = RHOMBOIDAL SINUS OF OWEN; **f** = SUPRA-OCCIPITAL; **g** = EXOCCIPITAL, WITH HYPOGLOSSAL FORAMEN ON INTERNAL ASPECT; **h** = RIGHT QUADRATE; **i** = SQUAMOSAL; **j** = LATEROSPHENOID; **k** = PTERYGOID; **l** = POSTERIOR WEDGE OF BASISPHENOID; **m** = BODY OF BASISPHENOID; **n** = PRO-OTIC; **o** = FORAMEN OVALE; **p** = AIR PASSAGE THROUGH SUPRAOCCIPITAL THAT CONNECTS WITH THOSE IN EXOCCIPITAL AND THE MIDDLE EAR PASSAGES; **q** = FRONTAL; **r** = PARIETAL. ANT = ANTERIOR, POST = POSTERIOR.

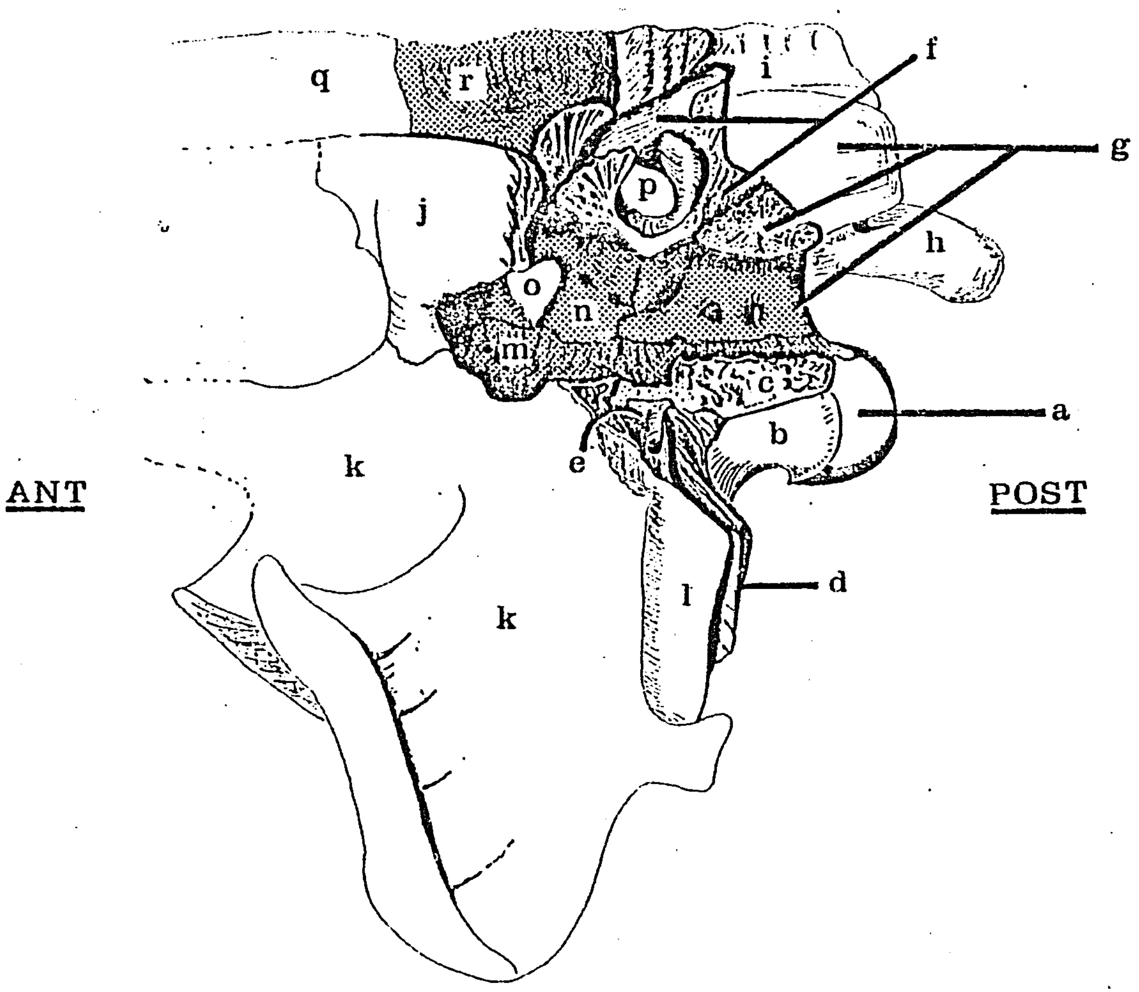

Figure 3

FIG. 4. ANTERIOR SURFACE OF LEFT EXOCCIPITAL BONE. a,b, AND c, POSTERIOR DIVISIONS OF THE TYMPANIC CAVITY, PART c, CONTAINING TWO FORAMINA FOR CRANIAL NERVES #9 AND #10 +11; d = OPISTHOTIC FUSED WITH EXOCCIPITAL; e = SUTURAL CONTACT AREAS FOR QUADRATE; f = CRANIO-QUADRATE PASSAGE; g = TUBULAR OPENING FOR THE INTERNAL CAROTID ARTERY; h = SUTURAL CONTACT FOR THE SUPRA-OCCIPITAL. M = MEDIAL; L = LATERAL; D = DORSAL; V = VENTRAL.

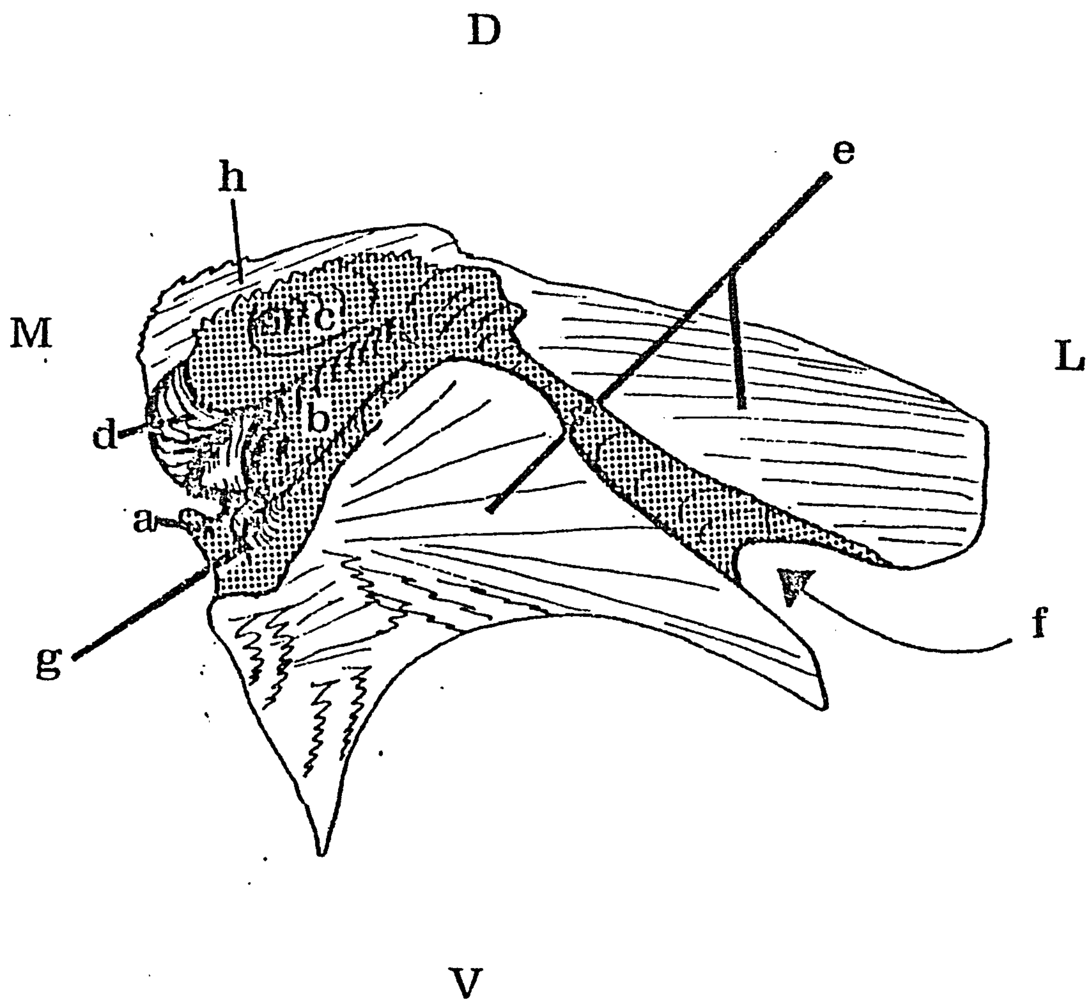

Figure 4

FIG. 5. FORAMINA AND MUSCLE INSERTIONS OF THE OCCIPUT OF *A. MISSISSIPIENSIS*. **a** = INSERTION OF M. *BASIOCCIPITOVERTEBRALIS*; **b** = INSERTION OF M. *LONGISSIMUS CAPITIS PROFUNDUS*; **c** = INSERTION OF M. *EPISTROPHEO-CAPITIS MEDIALIS*; **d** = PROCESSUS POSTOCCIPITALIS; **e** = CRANIO-QUADRATE PASSAGE; **f** = FORAMEN AËRUM; **g** = FORAMEN VAGI; **h** = HYPOGLOSSAL FORAMEN; **i** = MEDIAN EUSTACHIAN PASSAGE; **j** = REDUCED POST-TEMPORAL FENESTRA; **k** = FORAMEN FOR INTERNAL CAROTID ARTERY; **l** = INSERTION OF M. *ILIO-COSTALIS CAPITIS*; **m** = INSERTION OF M. *LONGISSIMUS CAPITIS SUPERFICIALIS*.

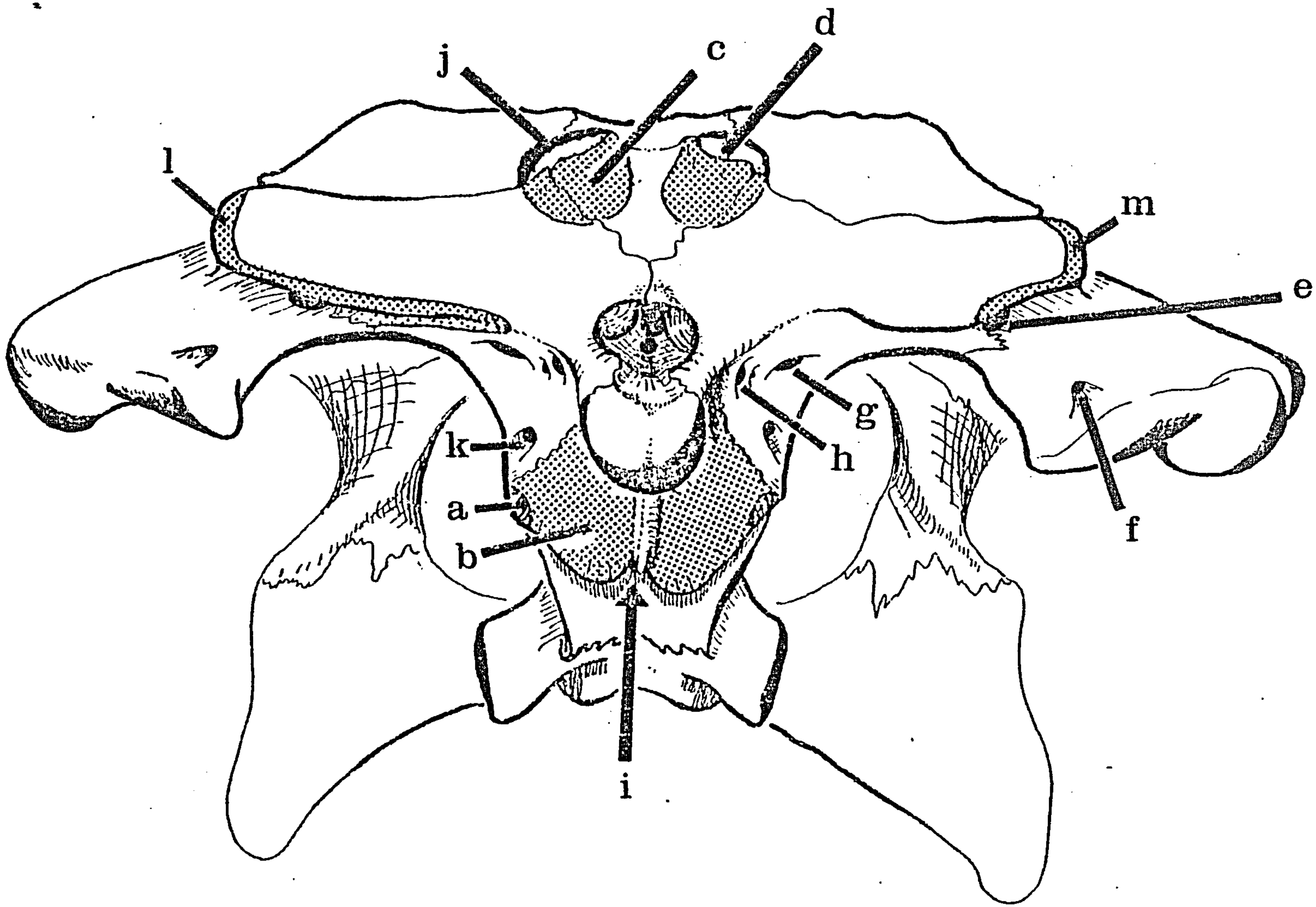

Figure 5

FIG. 6. VERTEBRAL COLUMN OF THE CERVICAL REGION. FOR THE SAKE OF CLARITY, THE ATLANTAL RING AND ITS RIBS, AS WELL AS THE RIBS OF THE LEFT SIDE , HAVE BEEN REMOVED. THIS IS A VENTRAL ASPECT, WITH ANTERIOR TO THE LEFT. OD, ODONTOID PROCESS, AX, CENTRUM OF AXIS, P, PARAPOPHYSIS, D, TWO DIAPOPHYSES, C-3, THIRD CERVICAL VERTEBRA, D-1, FIRST DORSAL (OR THORACIC) VERTEBRA.

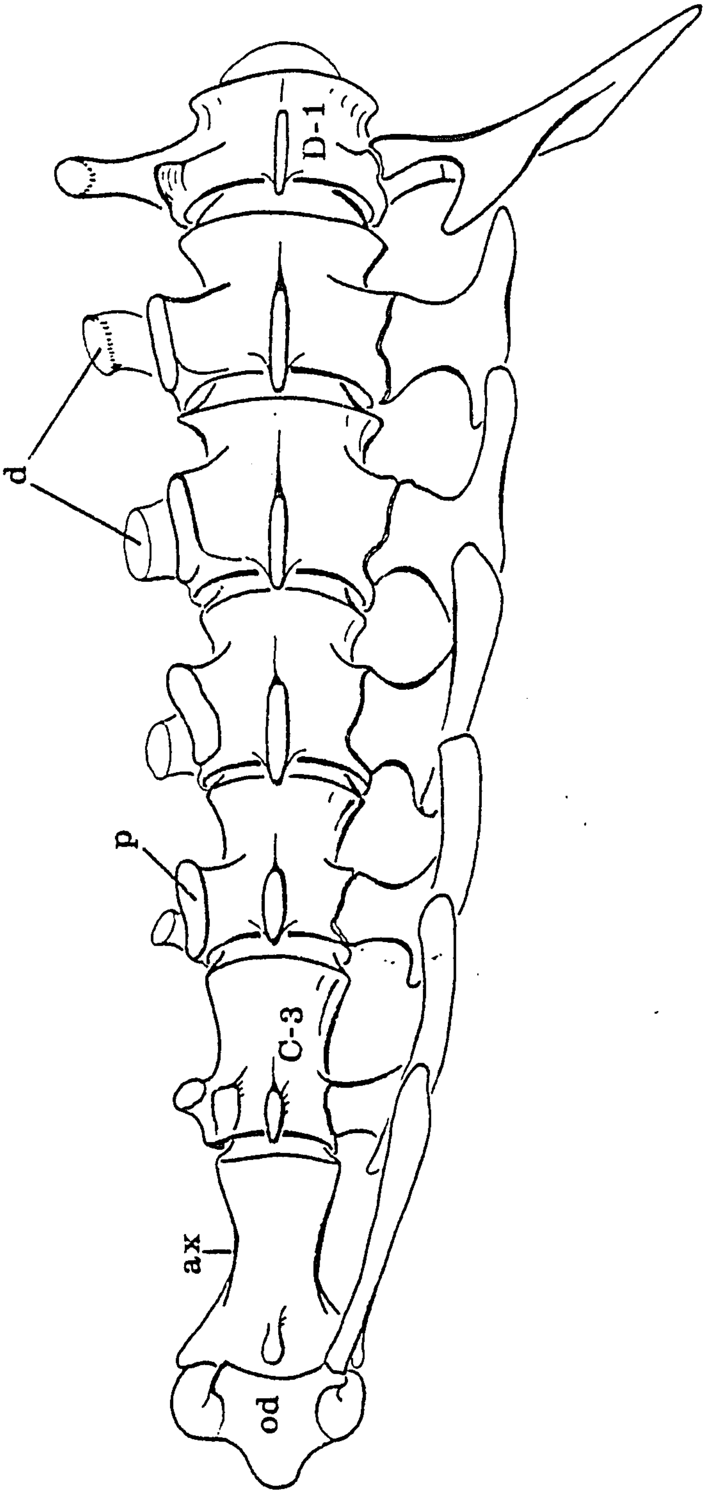

FIG. 6

FIG. 7. THE ANTERIOR 10 VERTEBRAE OF <u>A. MISSISSIPPIENSIS</u>. 2, ATLAS; 3-7, CERVICAL VERTEBRAE C-3 TO C-7; D-1 TO D-3, THE FIRST THREE THORACIC VERTEBRAE; U, POSTZYGAPOPHYSES VISIBLE ON THE LEFT SIDE; W, HYPOCENTRUM OF ATLAS; X, ODONTOID OF ATLAS; Y, RIGHT NEURAL ARCH OF ATLAS; Z, RIGHT HALF OF PROATLAS; ANT, ANTERIOR.

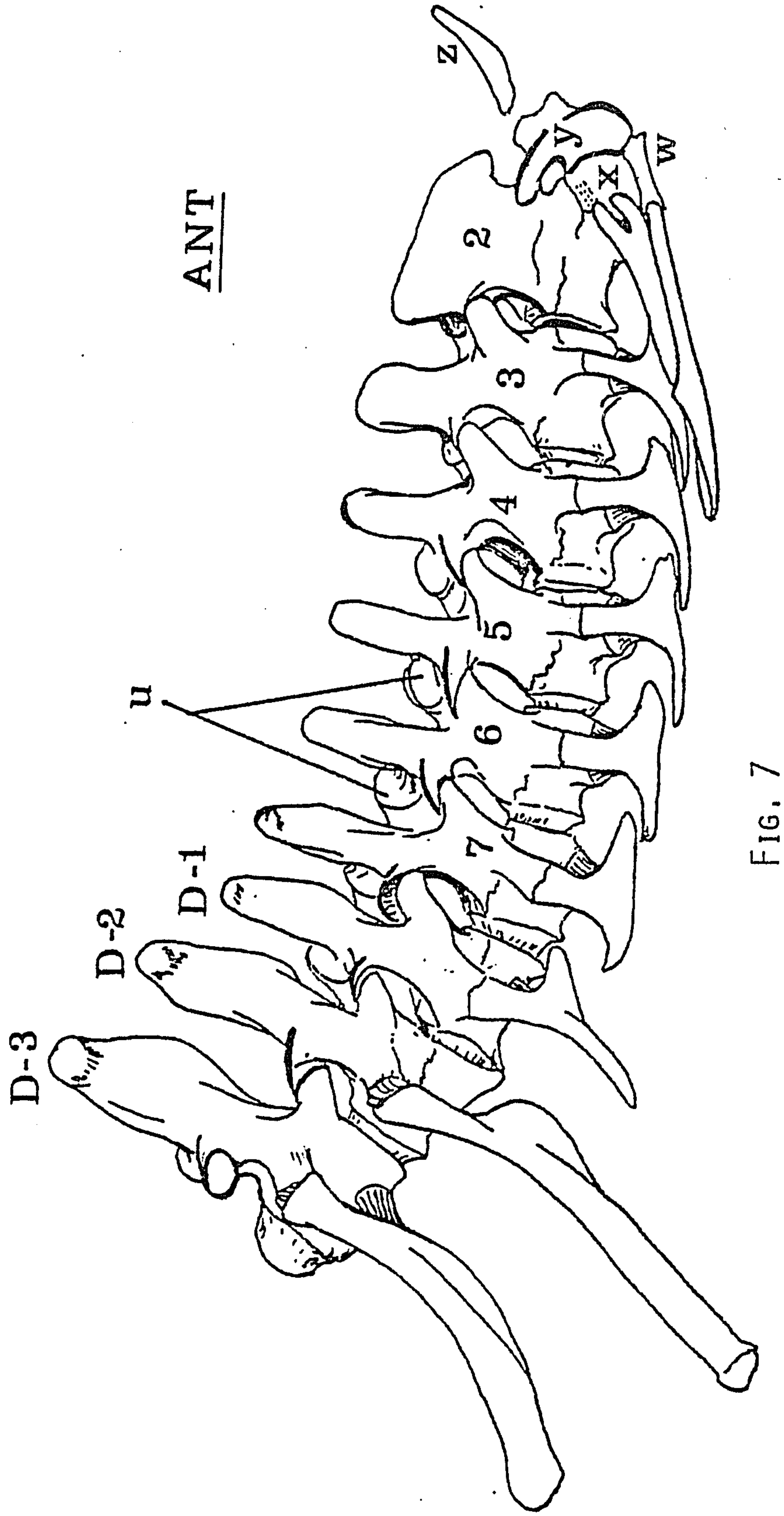

FIG. 7

FIG. 8. DORSAL VIEW OF THE ANTERIOR VERTEBRAL COLUMN OF A. MISSISSIPIENSIS. THE LEFT ATLANTAL NEURAL ARCH AND LEFT RIBS HAVE BEEN REMOVED. AR, RIGHT NEURAL ARCH OF ATLAS, HY, HYPOCENTRUM, OD, ODONTOID, D, DIAPOPHYSES, P, PARAPOPHYSES, D-3, THIRD DORSAL VERTEBRA, R-1, R-2, R-8, RIBS #1, #2, AND #8. NOTE THE DISTINCT, ABRUPT CHANGE IN RIB ORIENTATION BETWEEN THE DIRECTION OF THE FIRST SEVEN RIBS, AND RIBS 8-10 (THE FIRST THREE DORSAL RIBS).

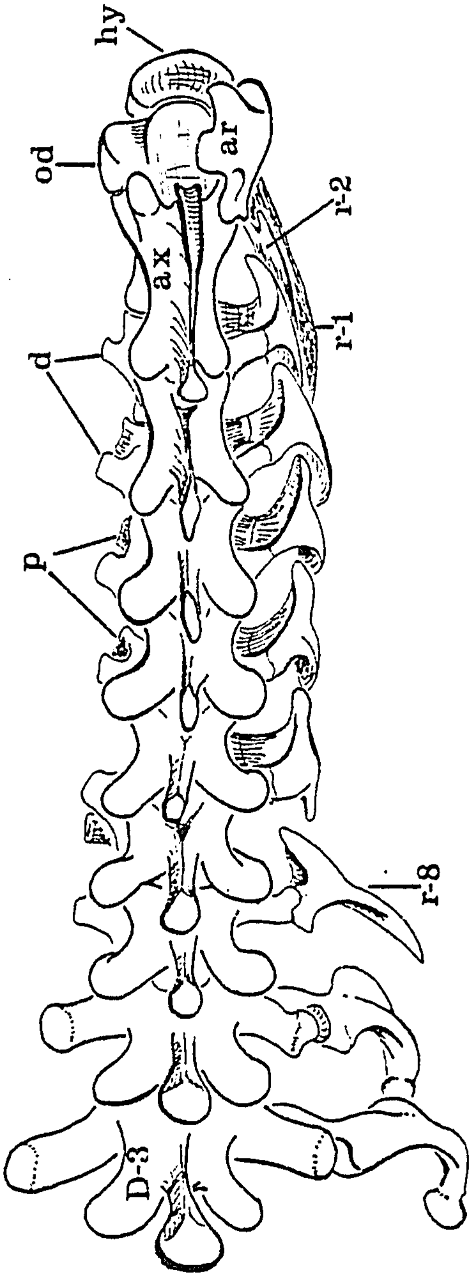

FIG. 8

Fig. 9. The right atlantal neural arch of A. mississippiensis. A) Lateral view, anterior to the right. y, the fossa for the combined ligament of mm. transverso-spinalis cervicis and longissimus cervicis; PO, postzygapophysis; V, fossa for first inter-articular muscle; PL, dorsal plate roofing neural canal; PRE, rudimentary preaygapophysis; W, origin of m. longissimus capitis profundus.

B) Medial view; CO cotylar surface for occipital condyle;

N, neural canal (stippled); POST, postzygapophyseal surface;

K, surface that glides in sulcus of odontoid; M, contact area for the hypocentrum.

C) Anterior view, medial is to the right.

D) Dorsal aspect; T, area of origin of m. atlanto-capitis;

U, area that pro-atlas rests upon; PO, postzygapophyses; PL, roof plate; CO cotylar surface.

E) Diagram representing segments of the atlantal arch (see text).

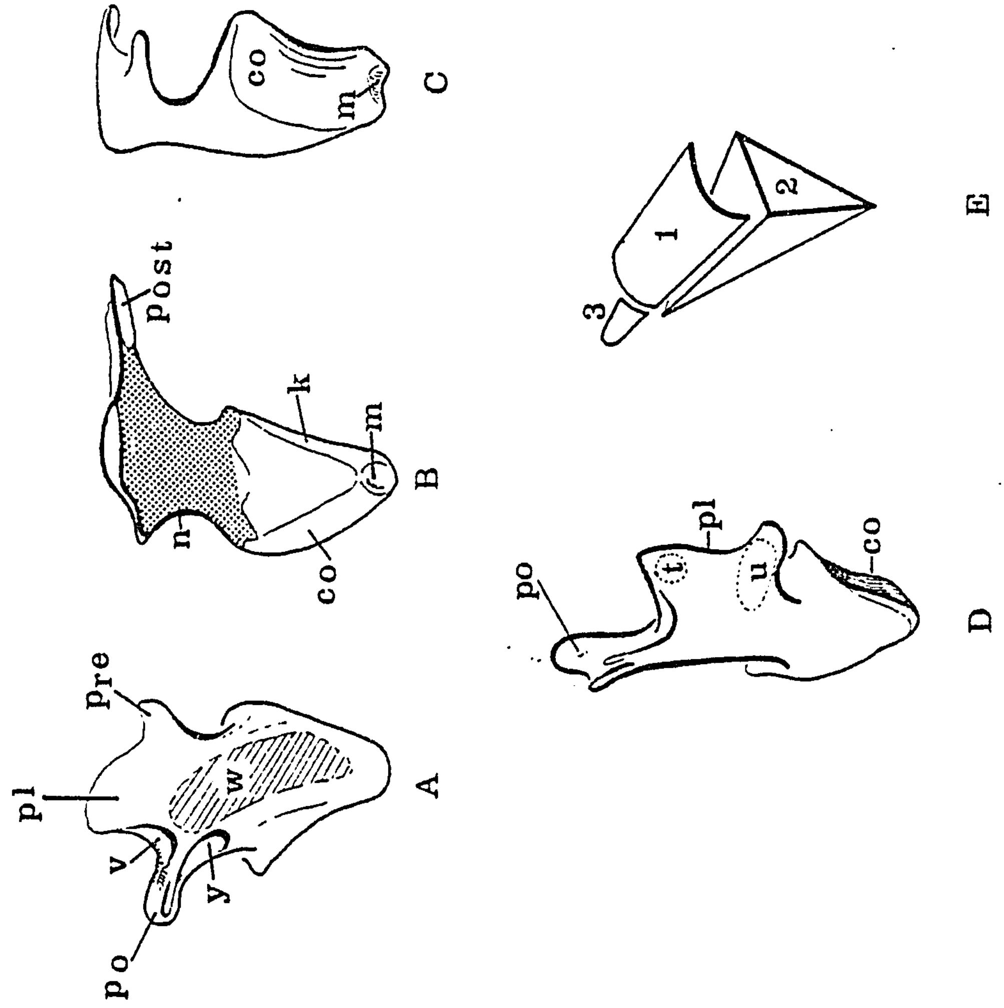

FIG. 9

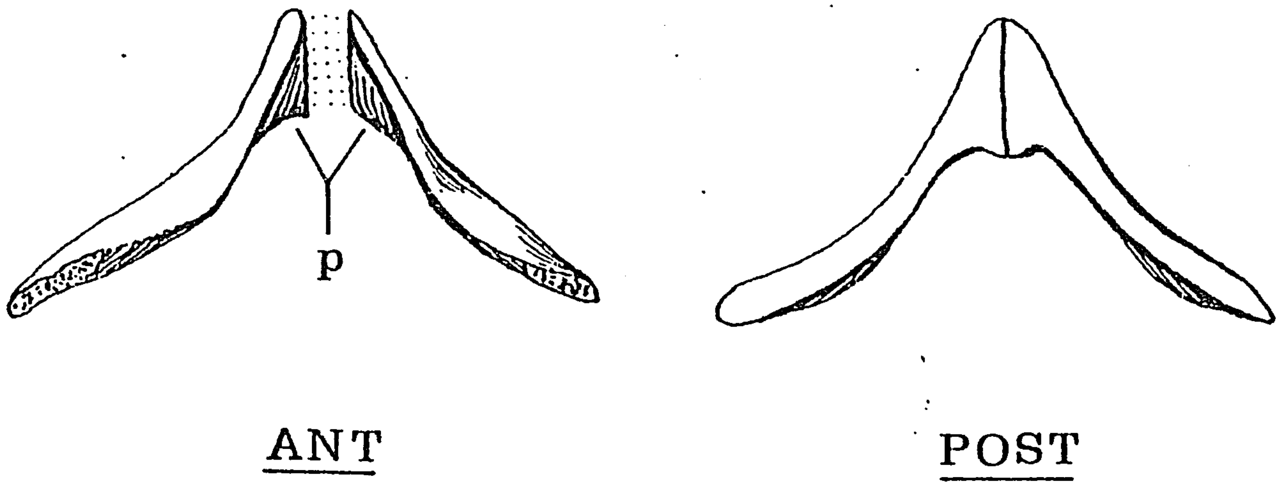

FIG. 10. ANTERIOR (ANT) AND POSTERIOR (POST) VIEWS OF THE PROATLAS OF *A. MISSISSIPPIENSIS*. p, REPRESENTS THE VENTRAL SURFACE THAT RESTS UPON THE EXOCCIPITAL PROMINENCE DORSAL TO THE FORAMEN MAGNUM. THE DOTTED LINES BETWEEN THE TWO PIECES ON THE LEFT IS TO SHOW THAT THE HALVES ARE LOOSELY BOUND BY LIGAMENTS.

FIG. 11. THE HYPOCENTRUM OF THE ATLAS AND THE ATLANTAL RING. A) VENTRAL VIEW OF HYPOCENTRUM; ANT IS ANTERIOR; Z, ORIGIN OF M. HYPOCENTRO-OCCIPITALIS; V, ORIGIN OF MEDIAN EUSTACHIAN VALVE RETRACTOR MUSCLE; B) ANTERIOR VIEW OF COTYLAR SURFACE OF THE ATLANTAL HYPOCENTRUM; C, CAVITY OF THE COTYLE; M, SURFACE FOR ARTICULATION WITH ATLANTAL ARCH (SEE FIG. 9M FOR MATCHING SURFACE). C) DORSAL VIEW OF ATLANTAL HYPOCENTRUM; R, SEMI-LUNAR SURFACE FOR THE FIRST RIB; T, SURFACE THAT GLIDES AGAINST ODONTOID SHIELD; Y, VENTRAL LIP OF COTYLE; M, SURFACE THAT MEETS ATLANTAL ARCH. D) RIGHT LATERAL VIEW OF HYPOCENTRUM OF ATLAS; R, CONTACT AREA FOR FIRST RIB; T, SURFACE THAT GLIDES AGAINST ODONTOID SHIELD; M, SURFACE THAT MEETS ATLANTAL ARCH. E). ANTERIOR VIEW OF INTACT ATLANTAL RING. SMOOTH CARTILAGE FORMS A CUP THAT BINDS TOGETHER THE THREE ATLANTAL ELEMENTS INTO A RING. THE DEEPEST PART OF THE CUP CONTAINS A SLIT, SL, THROUGH WHICH THE TONGUE OF THE ODONTOID (STIPPLES) CAN BE SEEN, AS WELL AS A LIGAMENT THAT CONNECTS ODONTOID WITH OCCIPITAL CONDYLE; N, TRANSVERSELY EXPANDED NEURAL CANAL; R, PART OF HYPOCENTRUM THAT SUPPORTS THE FIRST RIB.

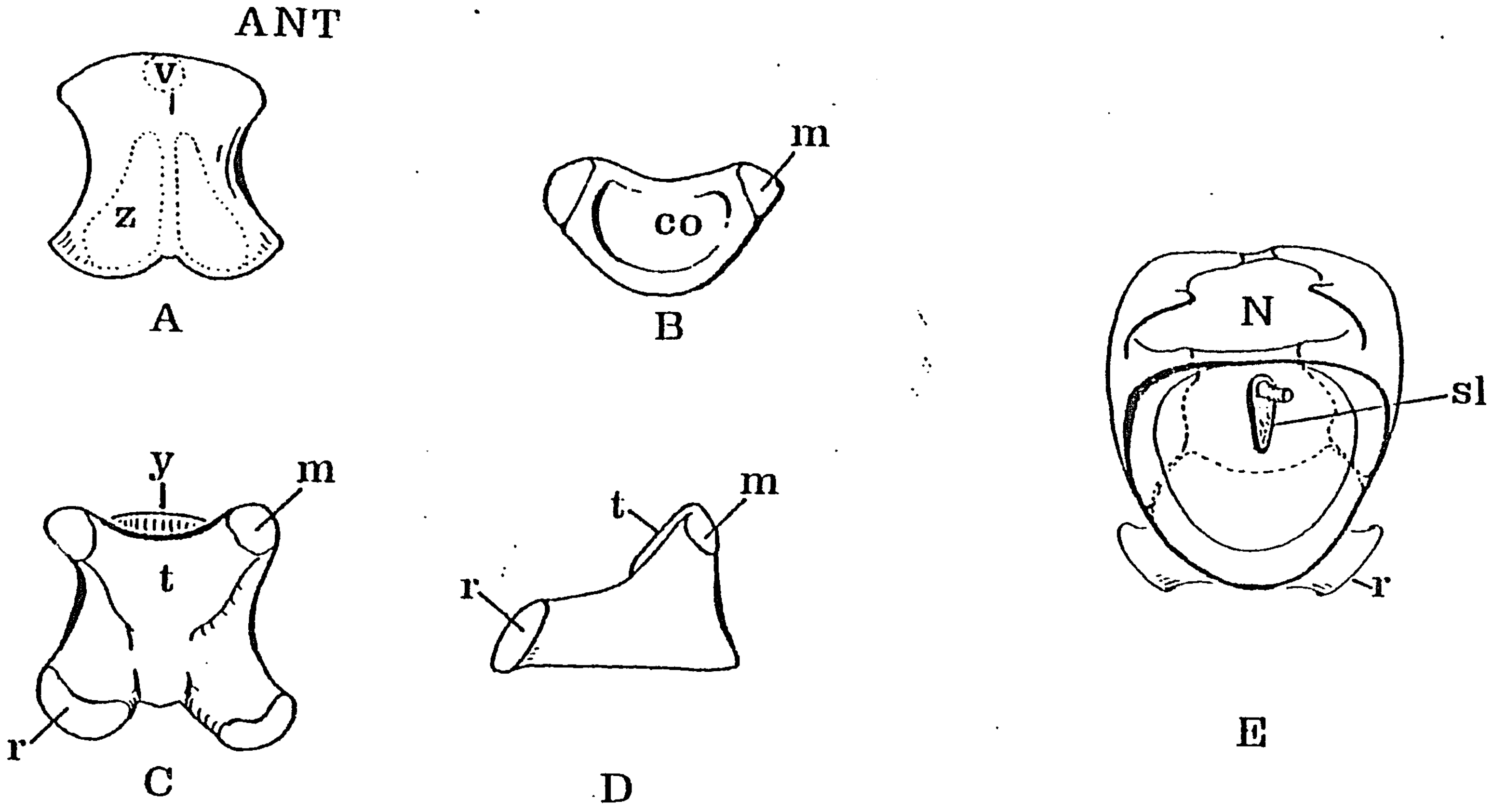

FIG. 11

FIG. 12. THE ODONTOID PROCESS AND AXIS OF A. MISSISSIPPIENSIS. A) RIGHT LATERAL VIEW; NS, NEURAL SPINE; PRE, PREZYGAPOPHYSIS; TNG, TONGUE OF ODONTOID; OD, ODONTOID PROCESS; HP, HYPAPOPHYSIS OF CENTRUM; CENT, CENTRUM OF AXIS; COND, CONDYLE OF CENTRUM; NA, NEURAL ARCH; POST, POSTZYGAPOPHYSIS. B) RIGHT LATERAL VIEW OF AXIS WITH MUSCLE ORIGINS AND INSERTION AREAS. TR-SP-CAP, M. TRANSVERSO-SPINALIS CAPITIS; ECM, M. EPISTROPHEO-CAPITIS MEDIALIS; ECI, M. EPISTROPHEO-CAPITIS INTERMEDIUS; EP-CAP-LAT, M. EPITSROPHEO-CAPITIS LATERALIS; INT, FIRST INTERARTICULAR MUSCLE, LC, M. LONGISSIMUS CAPITIS PROFUNDUS; 2, 3, RESPECTIVE PARTS OF INSERTION OF M. CENTRO-COSTALIS. C) ANTERIOR VIEW OF ODONTOID; SH, SHIELD OF ODONTOID; SUL, SULCUS OF ODONTOID; TNG, TONGUE OF ODONTOID. D) ANTERIOR VIEW OF AXIS WITHOUT ODONTOID; NS, NEURAL SPINE; POST, POSTZYGAPOPHYSIS; NEU, NEURAL ARCH; X', SURFACE THAT MEETS SURFACE X OF FIG. 12 E; CENT, CENTRUM; HP, HYPAPOPHYSIS; PRE, PREZYGAPOPHYSIS. E) DORSAL VIEW OF ODONTOID PROCESS; SUL, SULCUS OF ODONTOID; TNG, TONGUE OF ODONTOID; X, SURFACE THAT ARTICULATES WITH X' OF FIG. 12 D.

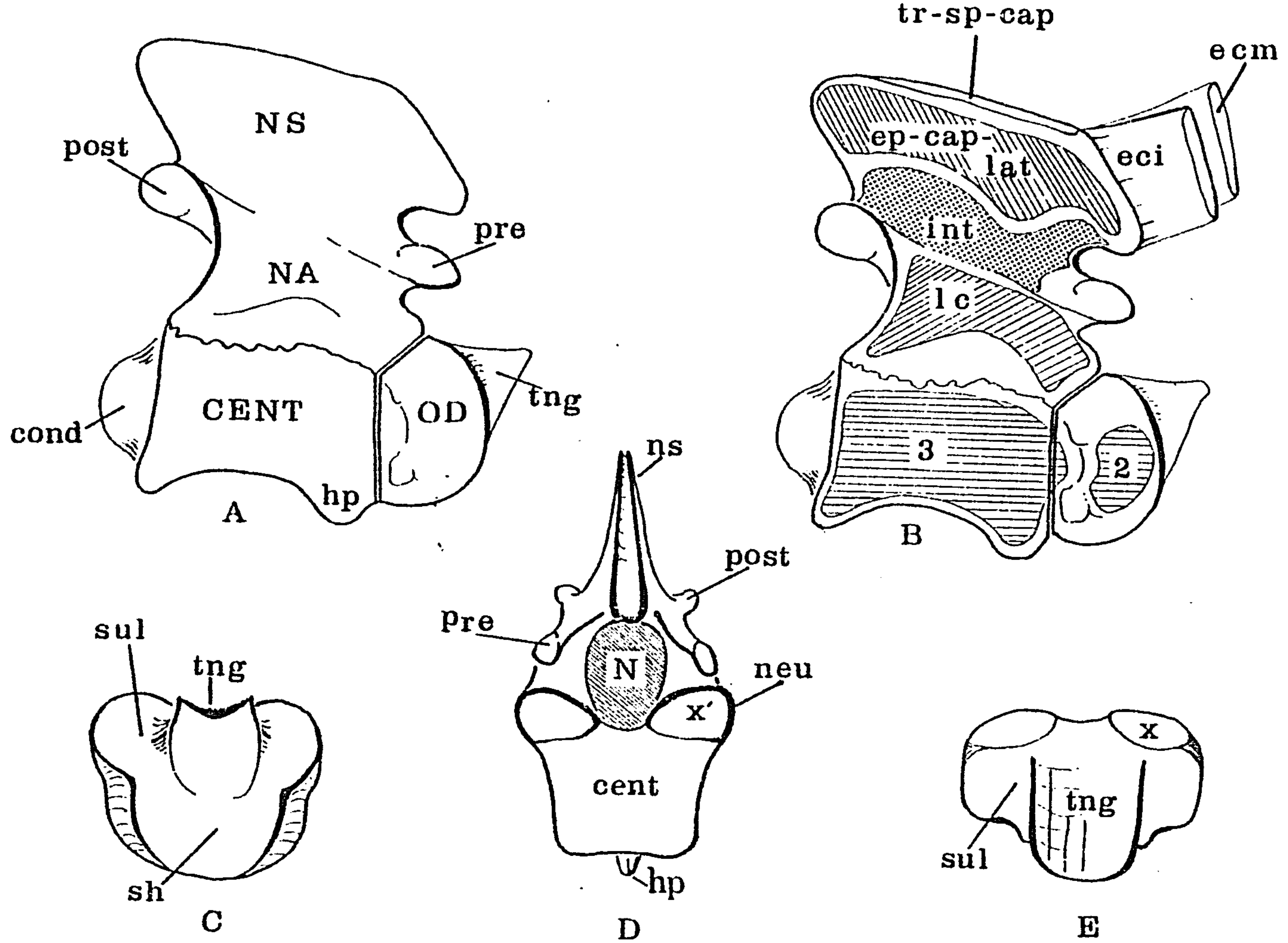
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FIG. 12

FIG. 13. A REPRESENTATIVE CERVICAL VERTEBRA, THE FIFTH VERTEBRA. A) RIGHT LATERAL VIEW. B) DORSAL VIEW. C) ANTERIOR VIEW. THE LEFT RIB HAS BEEN REMOVED TO DEMONSTRATE THE DIRECTION OF THE DI- AND PARA- POPHYSEAL ARTICULAR SURFACES. CENT, CENTRUM; COND, CONDYLE OF CENTRUM; COT, COTYLE OF CENTRUM; DI, DIAPOPHYSIS; HYP, HYPAPOPHYSIS; NEU, NEURAL ARCH; NEU-DP, DORSAL PLATE OF NEURAL ARCH; NEU-LP, LATERAL PLATE OF NEURAL ARCH; N, NEURAL CANAL; NS, NEURAL SPINE; POST, POSTZYGAPOPHYSIS; PRE, PREZYGAPOPHYSIS; RIB 5, FIFTH RIB; SU, GLIDING ARTICULAR SURFACE OF POSTZYGAPOPHYSIS. THE DRAWING IS MADE FROM A 14-FOOT SPECIMEN OF A. MISSISSIPPIENSIS WHO'S SKELETON WAS COLLECTED BY MR. BRIAN MALONE.

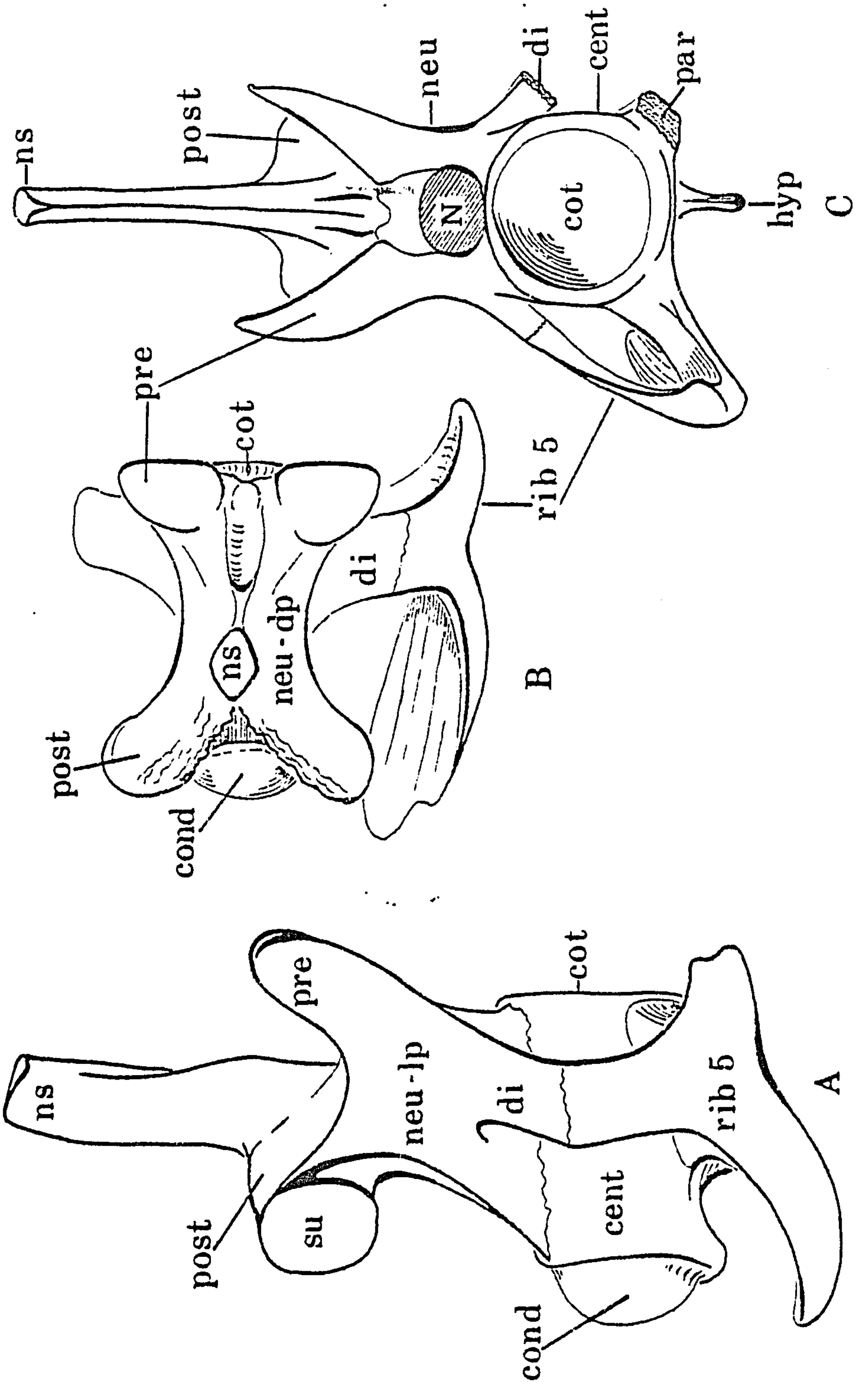
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FIG. 13

FIG. 14. CERVICAL VERTEBRAE C-3 TO C-7 AND DORSAL VERTEBRAE D-1 TO D-3. HYP, HYPAPOPHYSIS. ANTERIOR IS TO THE RIGHT. NOTE THE NUCHAL CURVATURE FORMED BY THE ARTICULATION OF THE CERVICAL VERTEBRAE. THE RIBS OF THE RIGHT SIDE HAVE BEEN REMOVED TO DEMONSTRATE THE DI- AND PARA- POPHYSEAL SUTURAL AND ARTICULAR SURFACES.

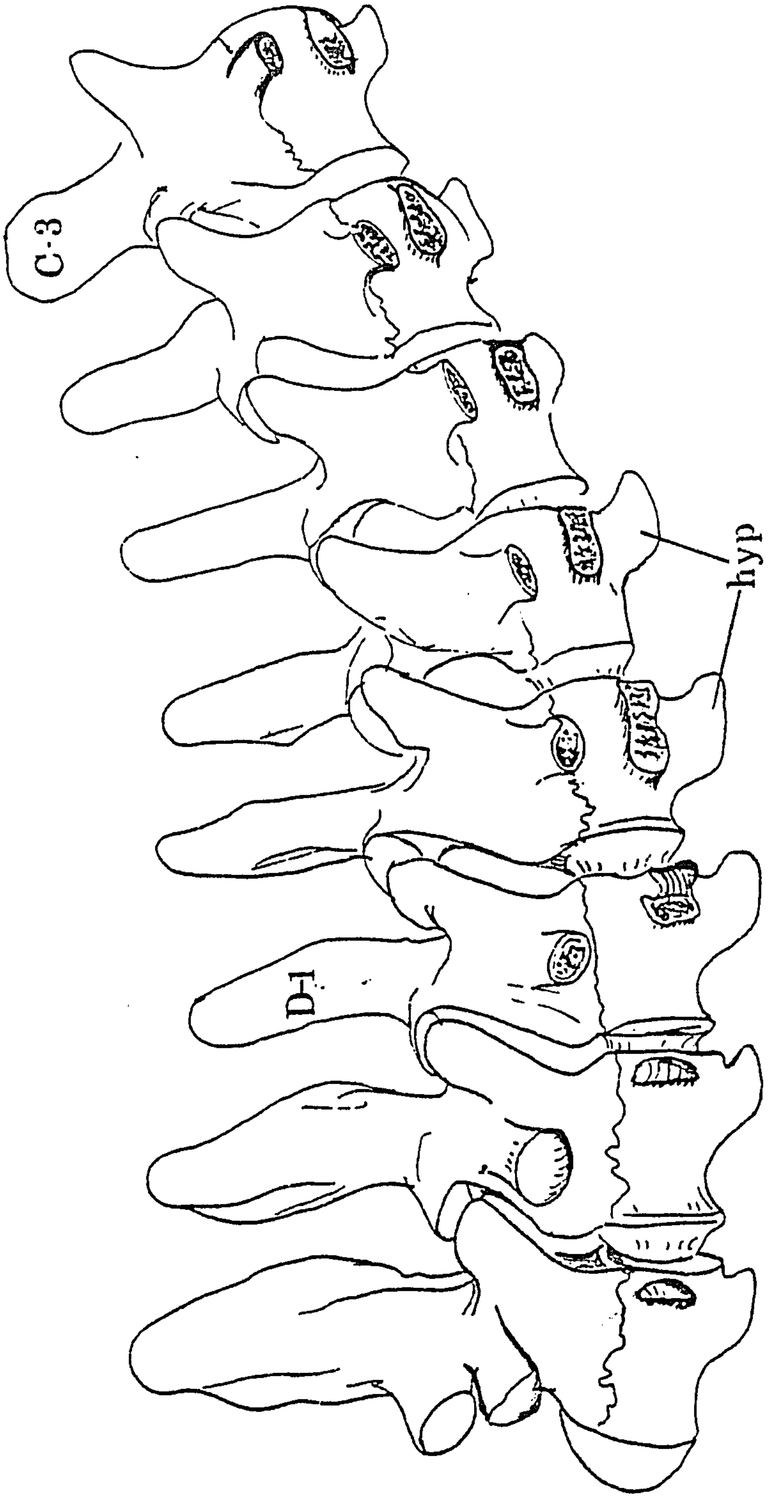

FIG. 14

FIG. 15. A) FIRST RIB, LEFT SIDE, LATERAL VIEW. H, CAPITULAR HEAD FOR ARTICULATION WITH HYPOCENTRUM OF ATLAS; LG, SMOOTH SURFACE THAT M. LONGISSIMUS CAPITIS PROFUNDUS PASSES OVER; ILCA, AREA OF ORIGIN OF M. ILIO-COSTALIS CAPITIS; ILCE, POSTERIOR EDGE OF RIB FOR ORIGIN OF TENDON 1 OF M. ILIO-COSTALIS CERVICIS; LS, INSERTION OF M. LEVATOR SCAPULAE; Z, AREA OF ORIGIN OF M. COSTO-OCCIPITALIS; SC, M. STERNO-COSTALIS.

B) SECOND RIB, LEFT LATERAL VIEW. CA, CAPITULUM THAT JOINS ODONTOID; TU, TUBERCULUM, REDUCED AND SHORTENED ON THIS RIB, AND JOINED TO THE ODONTOID BY A LIGAMENT.

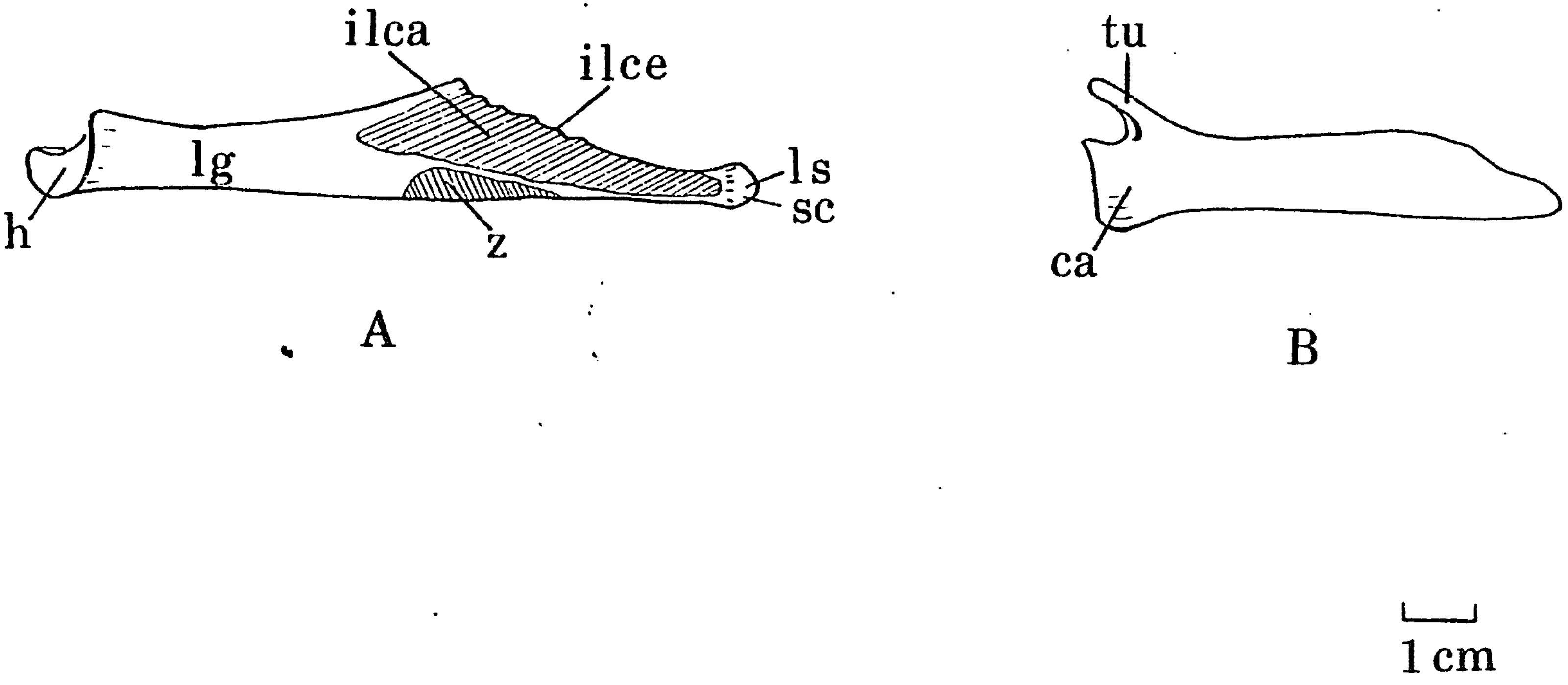

FIG. 15

FIG. 16. (1) THIRD LEFT RIB, LATERAL VIEW. (2) THIRD LEFT RIB, MEDIAL VIEW. (3) SEVENTH LEFT RIB, LATERAL VIEW. (4) SEVENTH LEFT RIB, MEDIAL VIEW. (5) SEVENTH LEFT RIB, ANTERIOR VIEW. A, ANTERIOR; P, POSTERIOR; AL, ANTERIOR LONGITUDINAL PROCESS; CA, CAPITULUM; TUB, TUBERCULUM; X, SPECIAL FACET ON TUBERCULUM FOR TENDON 7B OF ILIO-COSTALIS TENDON SYSTEM.

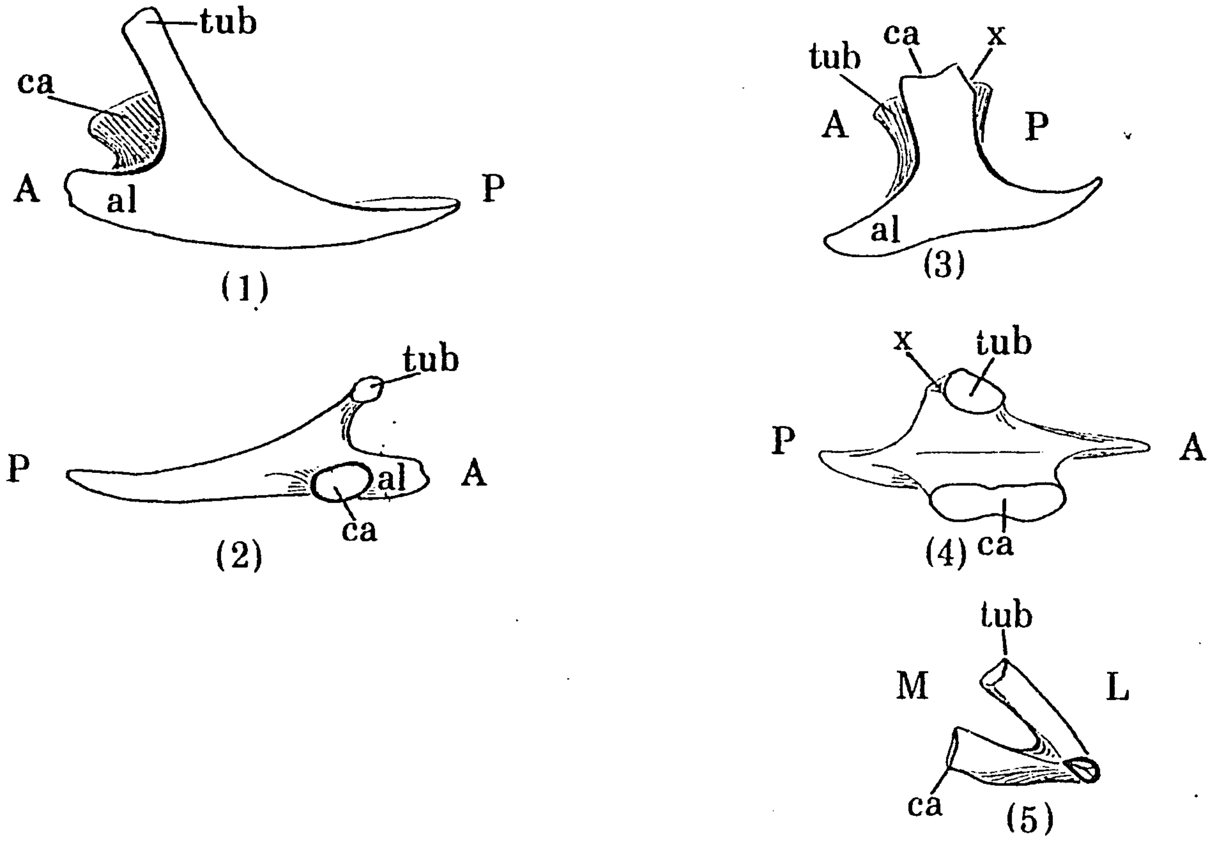

FIG. 16

FIG. 17, A YOUNG ALLIGATOR WITH THE SKIN AND SCALES OF THE BACK OR DORSAL REGION REMOVED. THE PURPOSE IS TO ILLUSTRATE THE RELATIVE POSITIONS AND SIZES OF THE EPAXIAL MUSCLE SYSTEMS OF THE BACK. a, REPRESENTS THE ILIOCOSTALIS SYSTEM THAT COVERS THE RIBS; b, REPRESENTS THE LONGISSIMUS SYSTEM THAT COVERS THE TRANSVERSE PROCESSES OF THE VERTEBRAE; c, REPRESENTS THE TRANSVERSO-SPINALIS SYSTEM, NEAREST TO THE VERTEBRAL SPINES (THE SECTION WITH STIPPLING).

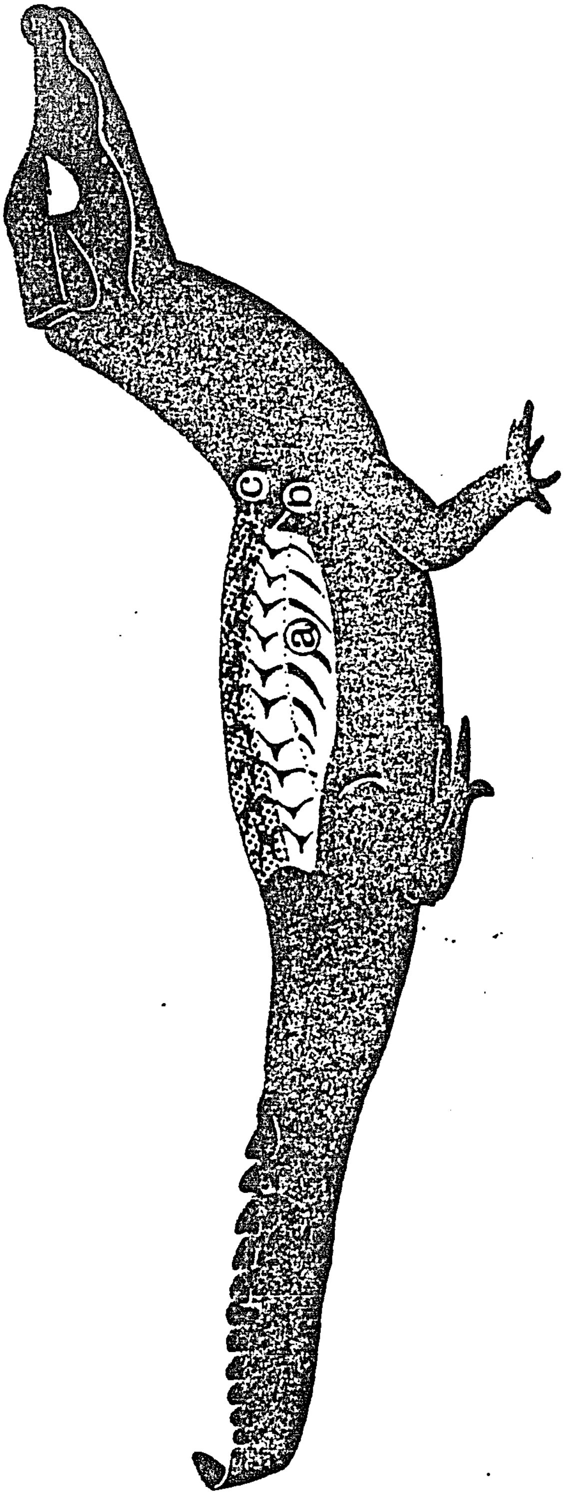

FIG. 17

FIG. 18. A) DIAGRAM OF EPAXIAL MUSCLE SYSTEMS AND THEIR RELATIONSHIP TO A TYPICAL THORACIC VERTEBRA. BR, BONY RIB; COT, COTYLE OF CENTRUM; DS. DORSAL SEPTUM; ILIO, ILIO-COSTALIS SYSTEM; LO, LONGISSIMUS SYSTEM; NS, NEURAL SPINE; PRE, PREZYGAPOPHYSIS; R, CARTILAGINOUS RIB; TP, TRANSVERSE PROCESS; TR, TRANSVERSO-SPINALIS SYSTEM.

B) DIAGRAM TO ILLUSTRATE THE THREE EPAXIAL MUSCLE SYSTEMS, SEEN SUPERFICIALLY FROM THE RIGHT SIDE. THE SUPERFICIAL FASCIA HAS BEEN REMOVED. AS, TENDON OF *M. ARTICULO-SPINALIS DORSI*; AS′, CUT END OF TENDON OF *M. ARTICULO-SPINALIS DORSI*; IL, *M. ILIO-COSTALIS DORSI*; LO, *M. LONGISSIMUS DORSI*; MY, INTERSECTION OF TWO MYOSEPTA OF *M. ILIO-COSTALIS DORSI*, GIVING THE FALSE APPEARANCE OF A TENDINOUS INSCRIPTION; NES, *M. NEURO-SPINALIS DORSI*; NS, NEURAL SPINE; SA, *M. SPINO-ARTICULARIS DORSI*; TA, *M. TENDINO-ARTICULARIS DORSI*; IS, ILIO-COSTALIS SYSTEM; LS, LONGISSIMUS SYSTEM; TS, TRANSVERSO-SPINALIS SYSTEM; 1, NEUROSPINALIS AND SPINO-ARTICULARIS SECTION OF TRANSVERSO-SPINALIS SYSTEM; 2, ARTICULO-SPINALIS SECTION OF TRANSVERSO-SPINALIS SYSTEM; 3, TENDINO-ARTICULARIS PART OF TRANSVERSO-SPINALIS SYSTEM; ANT, ANTERIOR. DOTTED LINE REPRESENTS THE LIMIT OF ONE OF THE INTERNAL, APONEUROTIC CONES OF M. LONGISSIMUS DORSI. MODIFIED AFTER VALLOIS (1922).

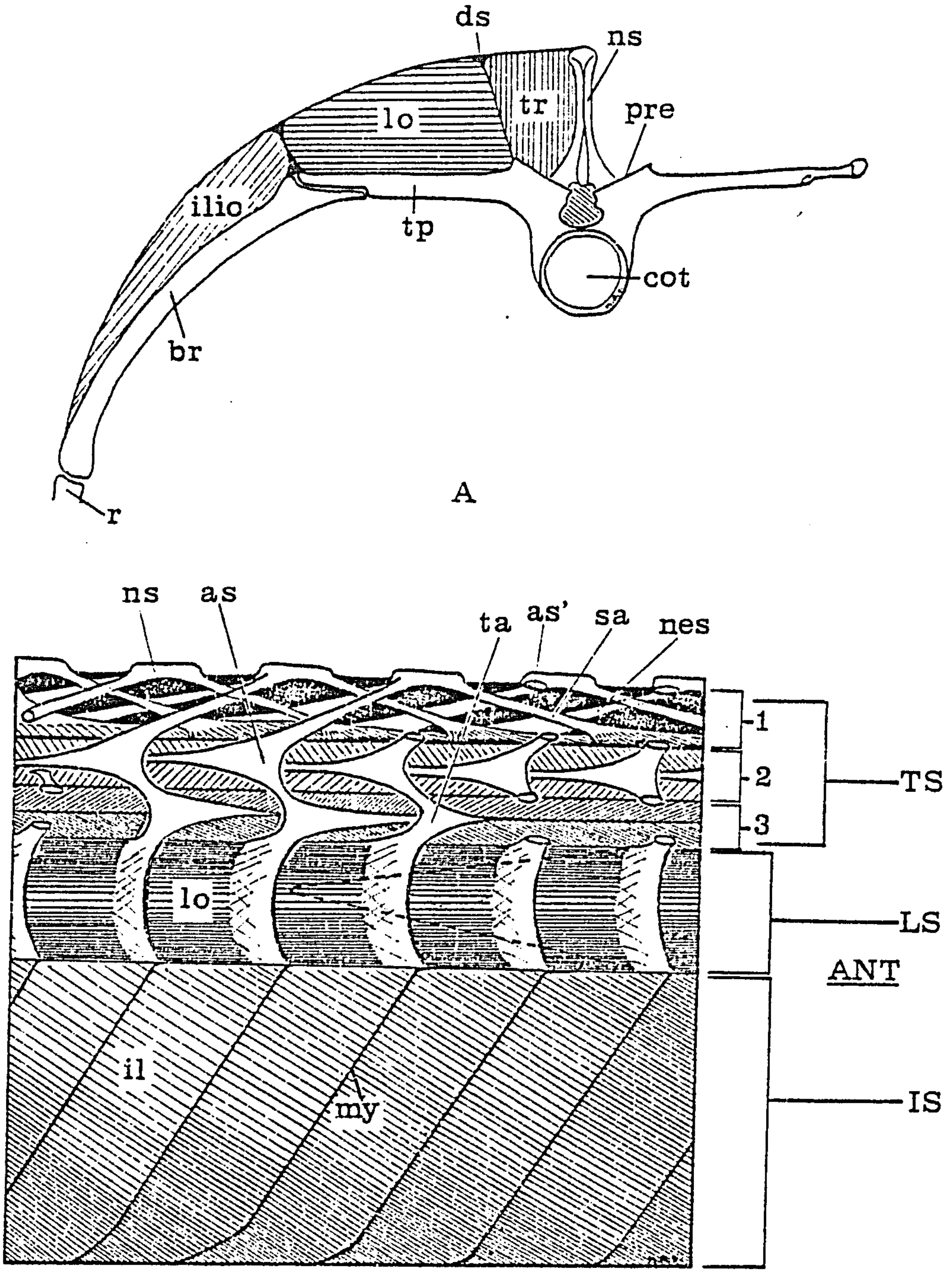
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FIG. 18

FIG. 19. TRUNK MUSCULATURE OF CROCODILUS NILOTICUS. THE LEFT SIDE, SKIN REMOVED. A SEGMENT OF M. OBLIQUUS EXTERNUS SUPERFICIALIS REMOVED TO SHOW M. OBLIQUUS EXTERNUS PROFUNDUS. FL, STUMP OF FORELIMB; HL, STUMP OF HINDLIMB; ILIO, M. ILIO-COSTALIS DORSI; LO, M. LONGISSIMUS DORSI; OEP, M. OBLIQUUS EXTERNUS PROFUNDUS; OES, M. OBLIQUUS EXTERNUS SUPERFICIALIS; P, M. PECTORALIS; R, M. RECTUS ABDOMINIS; TC, M. TRUNCO-CAUDALIS; TR, TRANSVERSO-SPINALIS SYSTEM. ANT, ANTERIOR; POST, POSTERIOR. MODIFIED AFTER MAURER, 1896.

FIG. 20. LEFT SIDE OF CROCODILUS NILOTICUS, DEEP HYPAXIAL MUSCULATURE. SHOULDER GIRDLE AND ITS MUSCLES, M. OBLIQUUS EXTERNUS SUPERFICIALIS, AND M. OBLIQUUS EXTERNUS PROFUNDUS HAVE BEEN REMOVED. SYMBOLS ARE THE SAME AS FOR FIG. 19, WITH THE ADDITION OF: II, M. INTERCOSTALIS INTERNUS; IE, M. INTERCOSTALIS EXTERNUS; MYO, MYOSEPTA; OI, M. OBLIQUUS INTERNUS; R, M. RECTUS ABDOMINIS; RI, RECTUS ABDOMINIS INTERNUS; RIB, CARTILAGE RIBS; ST, STERNUM; T, M. TRANSVERSUS (ABDOMINIS IN THE ABDOMEN). MODIFIED AFTER IHLE-VERSLUYS, VERGL. ANATOMIE, 1927.

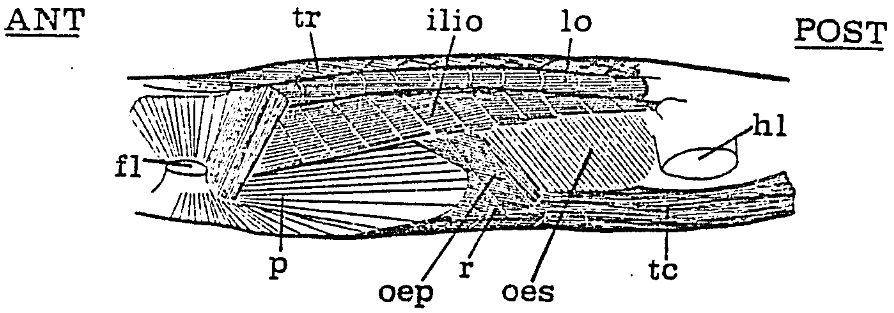
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FIG. 19

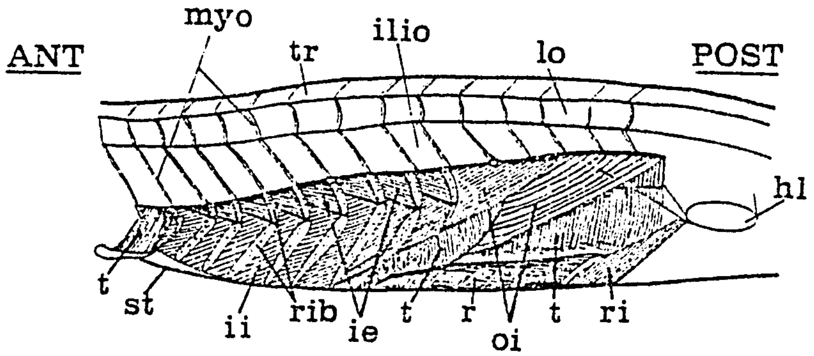
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FIG. 20

FIG. 21. DIAGRAM ILLUSTRATING THE RELATIONSHIP OF M. ILIO-COSTALIS DORSI TO THE THORACIC RIBS. FOR PERSPECTIVE, REFER BACK TO FIGS. 17, 18, 19, AND 20. A, LONGITUIDNAL MUSCLE FIBER BUNDLES THAT ATTACH TO RIBS AND MYOSEPTA; FOR CLARITY, THE MYOSEPTA ARE SOMEWHAT DISTORTED (SEE FIG. 22 FOR A MORE EXACTING REPRESENTATION); B, LIGHT CRISS-CROSSING REPRESENTS TOUGH FASCIA THAT COVERS M. ILIO-COSTALIS DORSI; C, DOTTED LINE SHOWING HIDDEN EDGE OF FASCIA LEAVING POSTERIOR EDGE OF RIB AT THE BONY-CARTILAGENOUS RIB JUNCTION; D, CARTILAGENOUS RIB; E, TWO SEGMENTS OF M. OBLIQUUS EXTERNUS SUPERFICIALIS, ONE ORIGINATING FROM THE ILIO-COSTALIS FASCIA, THE OTHER ORIGINATING FROM THE CARTILAGENOUS RIB; F, LIGHT STIPPLING WHERE MUSCLE FIBERS HAVE BEEN SCRAPED OFF OF MYOSEPTUM; R, BONY THORACIC RIB; V, THORACIC VERTEBRAE. ANT, ANTERIOR.

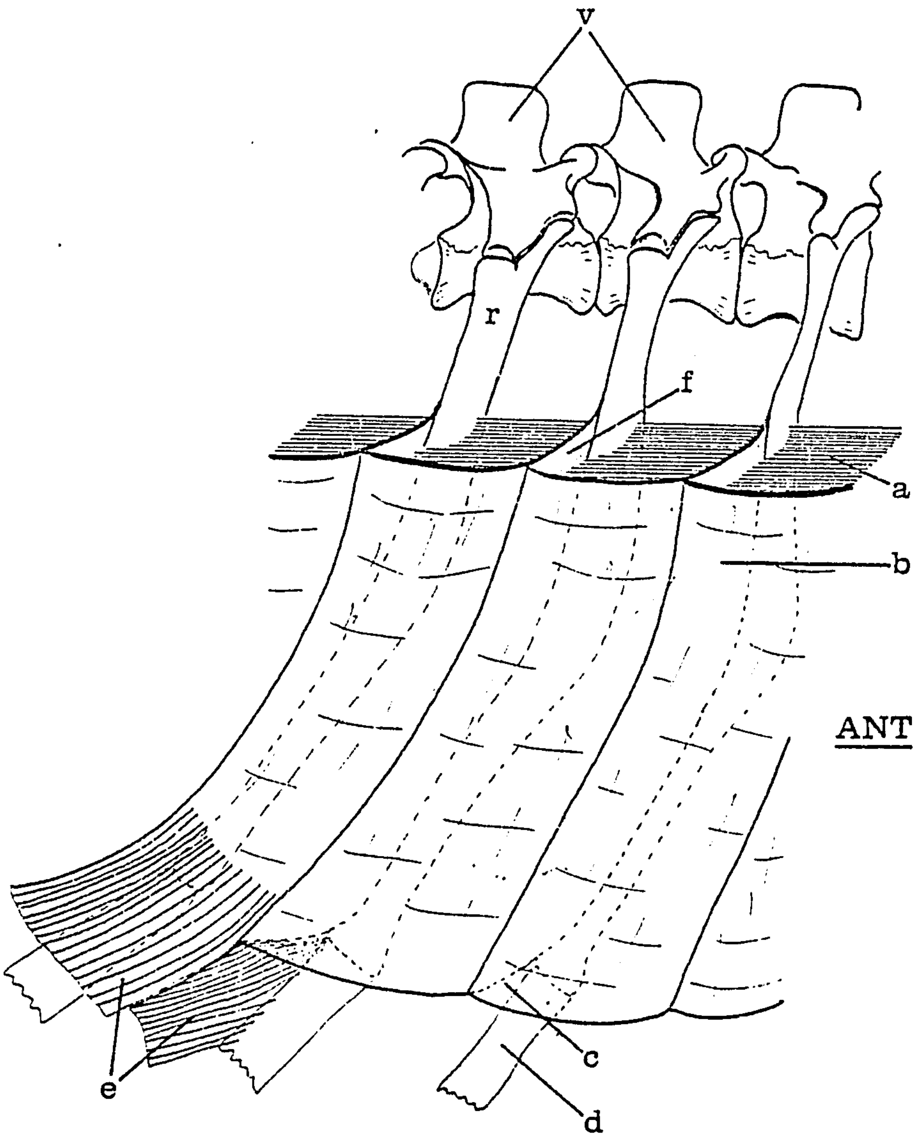

FIG. 21

FIG. 22. DIAGRAMATIC FRONTAL SECTION OF M. ILIO-COSTALIS DORSI OF THE RIGHT SIDE. A, LONGITUDINAL MUSCLE FIBER BUNDLES; B, SECTION THROUGH A THORACIC RIB; C, MYOSEPTA OF M. ILIO-COSTALIS DORSI; D, INTERSECTION OF TWO SUCCESSIVE MYOSEPTA AT A POSITION THAT IS EXTERNAL TO THE INTERCOSTAL SPACE.

FIG. 23. DIAGRAM ILLUSTRATING THE "ROLLING-UP" OF THE LUMBAR SEGMENTS OF M. ILIO-COSTALIS DORSI. 1,2,3,4, ARE IN SEQUENCE TO SHOW THE GRADUAL CHANGE FROM THE THORACIC ARRANGEMENT OF MYOSEPTA TO THE CONICAL LUMBAR MYOSEPTA. I, ILIUM; MF, LUMBAR MYOSEPTUM ORIGINATING FROM THE TRANSVERSE PROCESS OF D-15; PTR, POSTERIOR THORACIC RIBS; TF, THORACIC MYOSEPTA; TR, TRANSVERSE PROCESSES OF LUMBAR VERTEBRAE. ANT, ANTERIOR; D-17, TRASNVERSE PROCESS OF THE 17TH TRUNK VERTEBRA. NOTE THE FASCIA OF THE LAST SEGMENT (LINE 4) ATTACHING DIRECTLY TO ANTERIOR TIP OF ILIUM (ATTACHMENT EXAGERATED). LIGHT CROSS-HATCHING ON SEPTA REPRESENTS APONEUROTIC SURFACE OF SEPTAL SHEET.

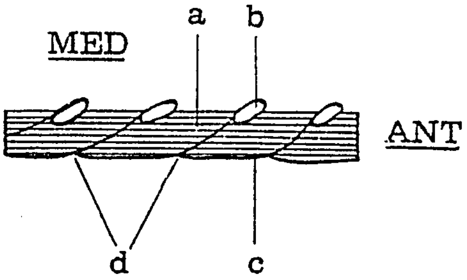

FIG. 22

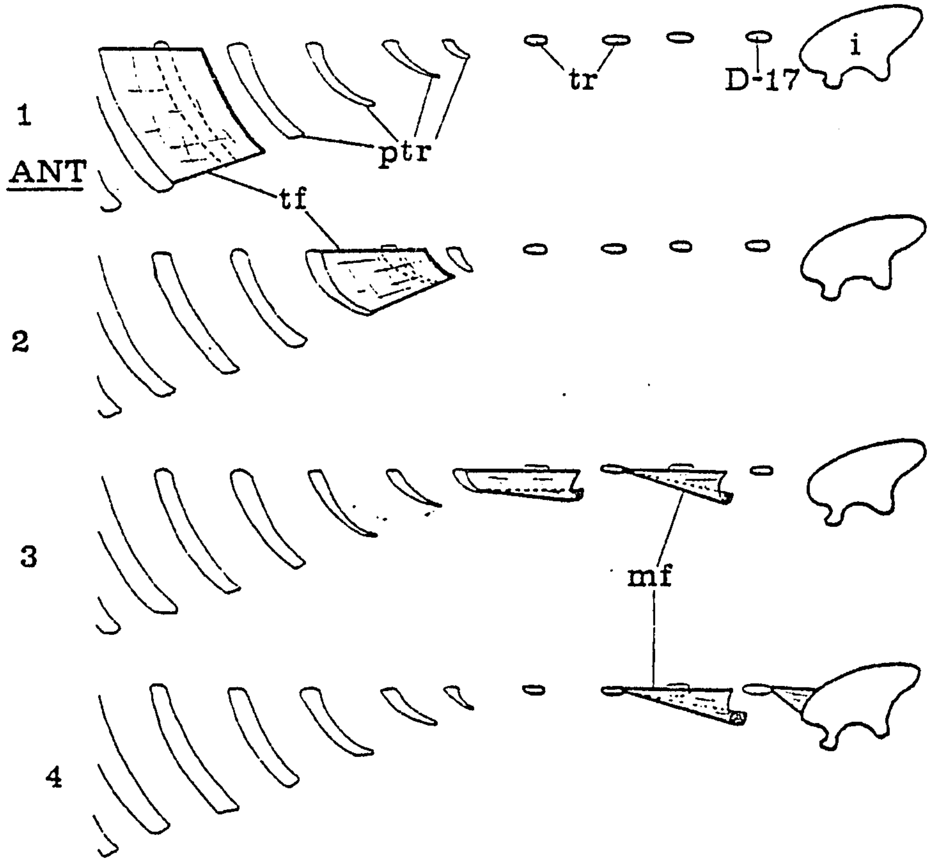

FIG. 23

FIG. 24. DIAGRAM OF EPAXIAL SYSTEMS, LEFT LATERAL VIEW, TO SHOW ATTACHMENT OF ILIO-COSTALIS FASCIAL BANDS TO NEURAL SPINE TIPS. THE BANDS ARE ATTACHED TO THE SKELETAL SYSTEM AT THE DORSAL INTERMUSCULAR SEPTUM AND AT THE COSTO-TRANSVERSE ARTICULATION (COMPARE WITH FIG. 18). FI, SUPERFICIAL FASCIA OF ILIO-COSTALIS FASCIA; K, *M. LONGISSIMUS DORSI*; MS, MYOSEPTAL INTERSECTIONS; NS, TIP OF NEURAL SPINE, TRS, TRANSVERSO-SPINALIS SYSTEM (STIPPLED AREA, AGAINST AND BETWEEN NEURAL SPINES); ANT, ANTERIOR.

FIG. 25. FLOATING RIBS (LEFT SIDE) OF VERTEBRAE D-11 AND D-12. BR, BONY RIB; CR, CARTILAGINOUS RIB; IE, *M. INTERCOSTALIS EXTERNUS*; JCT, JUNCTION BETWEEN BONY AND CARTILAGINOUS RIB; MA, SEPTUM THAT SEPARATES *M. ILIO-COSTALIS DORSI* FROM *M. INTERCOSTALIS EXTERNUS*; MB, SEPTUM DEEP TO *M. INTERCOSTALIS EXTERNUS*, BETWEEN THE RIBS; NOE, NERVE TO *M. OBLIQUUS EXTERNUS SUPERFICIALIS*, TAKING EXIT BENEATH LEVEL OF BONY RIB (VENTRAL LIMIT OF THE ILIO-COSTALIS SYSTEM); OI, *M. OBLIQUUS ABDOMINIS INTERNUS*; VR, VENTRAL RAMUS OF A SPINAL NERVE; ANT, ANTERIOR.

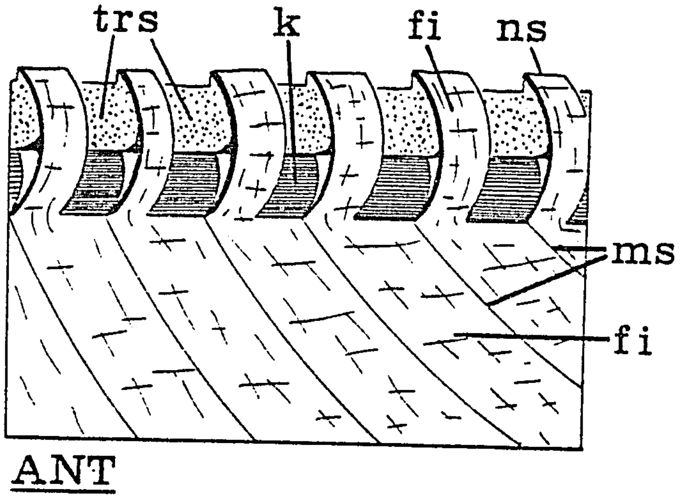

FIG. 24

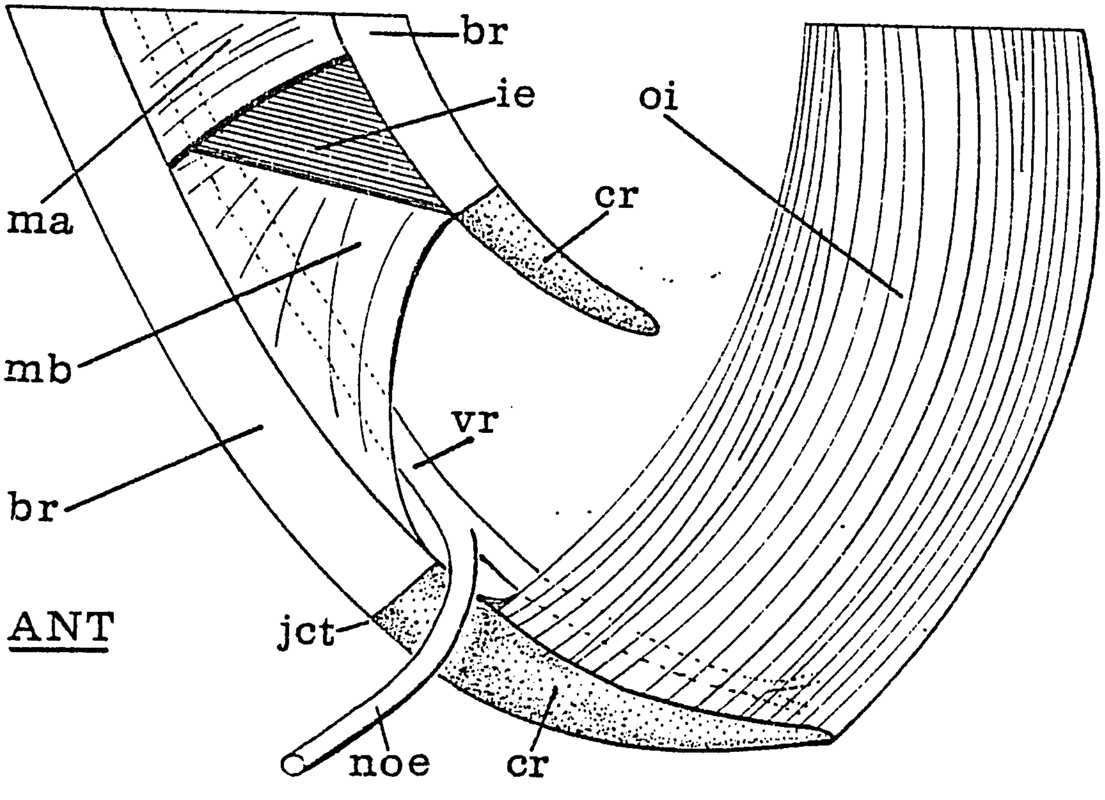

FIG. 25

FIG. 26. SEMI-DIAGRAMATIC REPRESENTATION OF M. LONGISSIMUS DORSI IN A. MISSISSIPPIENSIS. THE MUSCLE FIBER BUNDLES SURROUNDING THE TWO ANTERIOR CONES IN THIS VIEW HAVE BEEN REMOVED TO SHOW HOW THE CONES ARE ARRANGED WITHIN EACH OTHER. AC, APONEUROTIC CONE; DC, DEEP CONE, WITHIN THE NEXT POSTERIOR CONE; DIS, DORSAL INTERMUSCULAR SEPTUM; ILB, FASCIAL CONNECTION TO ILIO-COSTALIS FASCIA BAND (SEE FIG. 24); ILF, FASCIA OF M. ILIO-COSTALIS DORSI; INT, M. INTERTRANSVERSARIUS DORSI; MF, LONGITUDINAL MUSCLE FIBER BUNDLES OF M. LONGISSIMUS DORSI, BETWEEN APONEUROTIC CONES; TA, TENDON OF M. TENDINO-ARTICULARIS DORSI; TRP, TRANSVERSE PROCESS OF A TRUNK VERTEBRA; ANT, ANTERIOR.

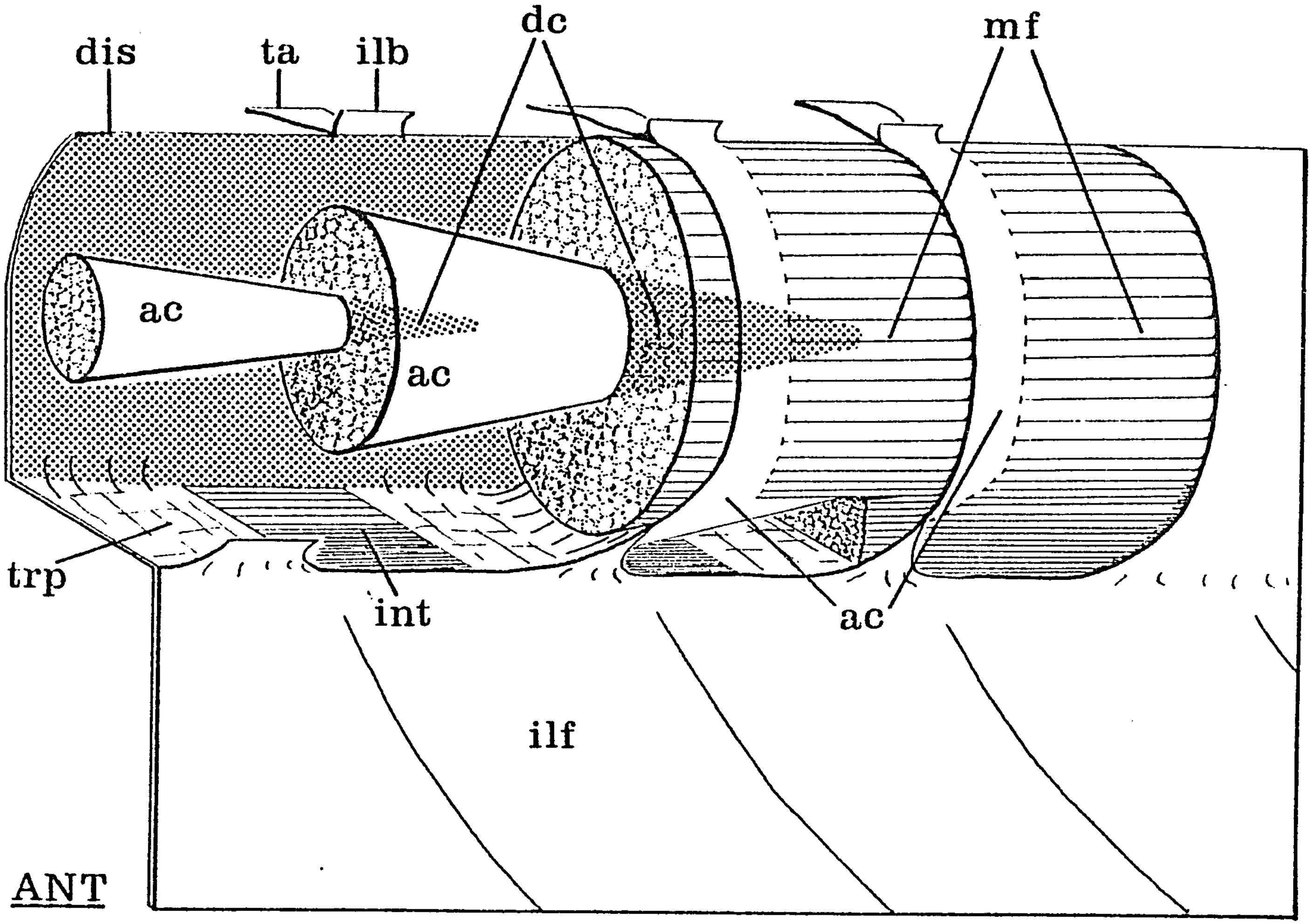

FIG. 26

FIG. 27. THREE DIFFERENT ASPECTS OF M. LONGISSIMUS DORSI. A) DRAWING MADE FROM A JUVENILE SPECIMEN OF A. MISSISSIPPIENSIS (SNOUT TO OCCIPUT LENGTH = 6.48CM), TO SHOW ONE SEGMENT AND ITS RELATION TO SURROUNDING FASCIA. DORSO-LATERAL VIEW OF LEFT SIDE (COMPARE WITH FIG. 18B). AC, APONEUROTIC CONE; AS, TENDON OF M. ARTICULO-SPINALIS DORSI; DF, DEEP FIBERS OF M. LONGISSIMUS DORSI; GL, SUBCUTANEOUS GLAND DESCRIBED BY REESE (1921); ILF, FASCIA OF M. ILIO-COSTALIS DORSI; NS, ARTICULO-SPINALIS TENDON (CUT) AS IT IS DIRECTED TOWARDS THE ATTACHMENT TO ITS NEURAL SPINE; SF, SUPERFICIAL FIBER BUNDLES OF M. LONGISSIMUS DORSI; TA, APONEUROSIS OF M. TENDINO-ARTICULARIS DORSI; ANT, ANTERIOR.

B) SAGITTAL SECTION OF M. LONGISSIMUS DORSI. AC, APONEUROTIC CONES, APEX POSTERIOR; INT, STIPPLING REPRESENTS MM. INTERTRANSVERSARII DORSALES; LF, LONGITUDINAL FIBERS OF M. LONGISSIMUS DORSI; TR, TRANSVERSE PROCESS OF TRUNK VERTEBRAE; X.S., CROSS-SECTION SHOWN IN PAR (C) BELOW.

C) COMPLETE CROSS-SECTION OF M. LONGISSIMUS DORSI, TAKEN AT THE LEVEL SHOWN IN PART (B). AC, APONEUROTIC CONES; MB, MUSCLE FIBER BUNDLES ARRANGED IN VERTICAL SHEETS; N, BRANCH OF DORSAL RAMUS NERVE SUPPLYING MUSCLE FIBER BUNDLES; TR, TRANSVERSE PROCESS OF A TRUNK VERTEBRA. M, MEDIAL; L, LATERAL.

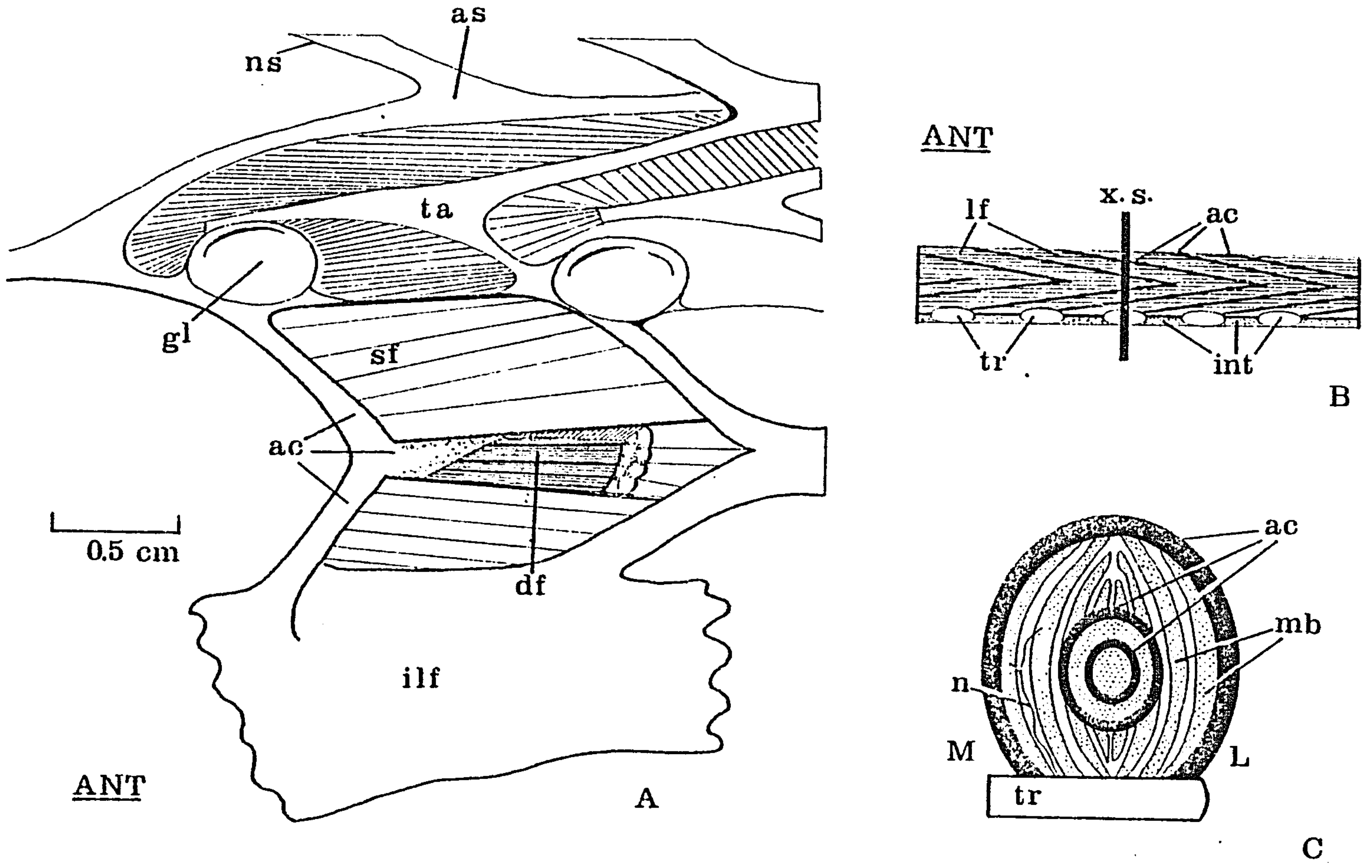
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FIG. 27

FIG. 28. AN APONEUROTIC CONE OF M. LONGISSIMUS DORSI, WITH MOST OF THE MUSCLE FIBERS CLEANED OUT. AC, OUTSIDE SURFACE OF APONEUROTIC CONE; DIS, DORSAL INTERMUSCULAR SEPTUM; F, FENESTRA IN MEDIAL, ANTERIOR WALL OF CONE; IB, INTERSEGMENTAL BUNDLES OF MUSCLE FIBERS THAT TRAVERSE THE FENESTRA FROM THE NEXT POSTERIOR CONE; N, NERVE SUPPLY TO INTERSEGMENTAL BUNDLES; CF, APONEUROTIC FLOOR OF CONE ARISING FROM THE POSTERIOR EDGE OF A TRANSVERSE PROCESS; IS, INTRASEGMENT MUSCLE FIBER BUNDLES THAT ARE LEFT INSIDE THE CONE.

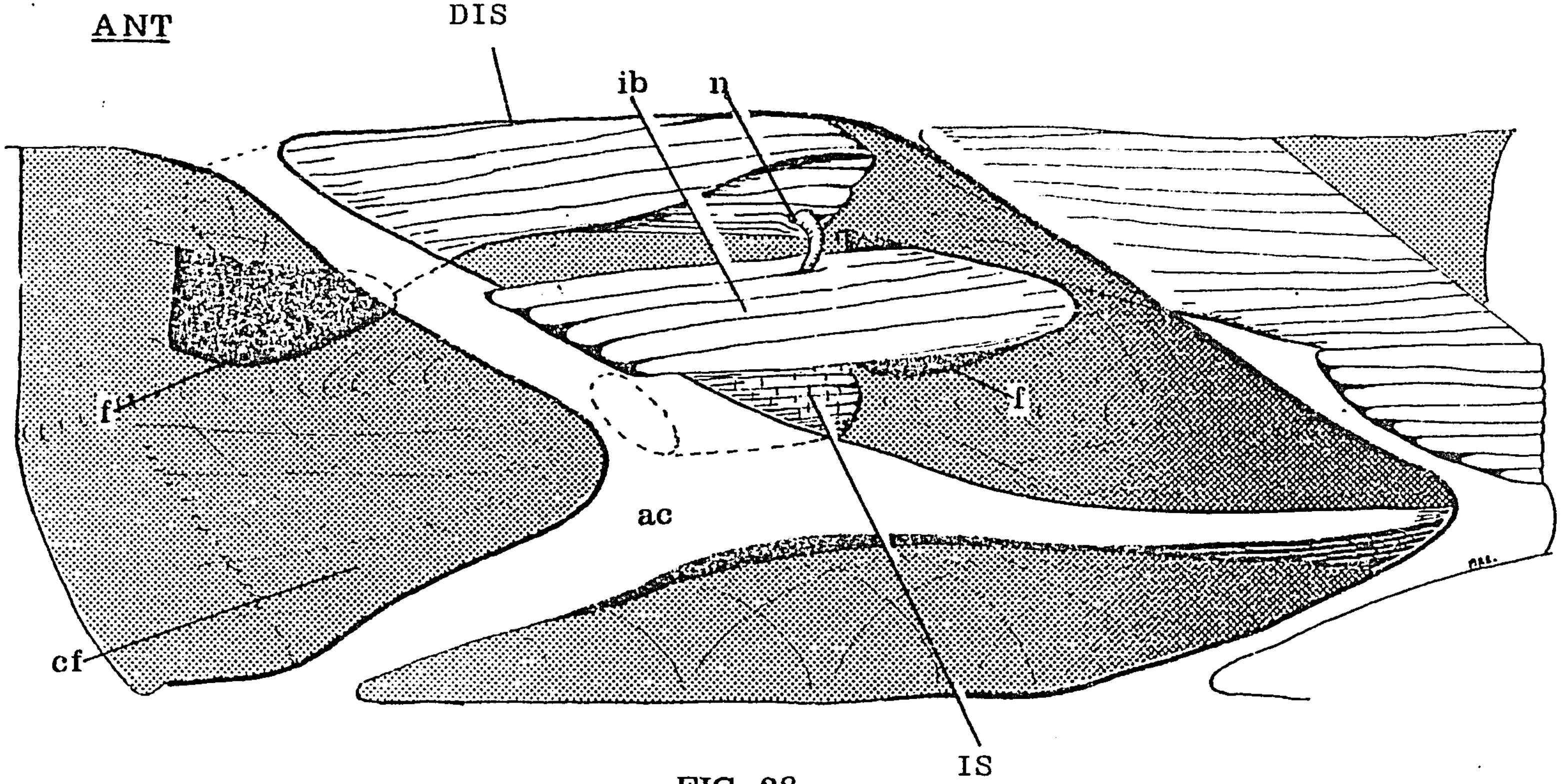

FIG. 28

FIG. 29. A AND B, DORSAL VIEWS OF A SEGMENT OF M. LONGISSIMUS DORSI. A) MOST OF THE MUSCLE FIBERS BENEATH THE CONE-(A) HAVE BEEN REMOVED TO EXPOSE THE FLOOR OF THE SUCCEEDING CONE. A, TENDON OF M. LONGISSIMUS DORSI THAT IS VISIBLE SUPERFICIALLY AND HAS CRISS-CROSSED FIBERS. THE SECOND TENDON HAS BEEN CUT ACROSS TO SHOW THE MUSCLE BENEATH; B, TENDINOUS SHEET THAT FORMS THE MEDIAL WALL OF AN APONEUROTIC CONE, IT ARISES DIRECTLY FROM THE DORSAL INTERMUSCULAR SEPTUM; C, CONNECTIVE TISSUE FIBERS THAT HOLD TOGETHER APONEUROSES A AND B; BA, FLOOR OF AN APONEUROTIC CONE ARISING FROM THE POSTERIOR EDGE OF A TRANSVERSE PROCESS; T, TRANSVERSE PROCESS WITH A SMALL BUNDLE OF MUSCLE FIBERS STILL ATTACHED; I, FASCIAL COVER, CONTINUOUS WITH FASCIA OF ILIO-COSTALIS FASCIA.

B) ONE CONE OF M. LONGISSIMUS DORSI, SLIT OPEN LONGITUDINALLY, WITH MUSCLE FIBERS CLEANED OUT. THE VIEW IS DIRECTLY DORSAL. BA, FLOOR OF CONE ARISING FROM POSTERIOR EDGE OF A TRANSVERSE PROCESS; D, DORSAL INTERMUSCULAR SEPTUM; M, BUNDLE OF MUSCLE TRAVERSING FENESTRA IN MEDIAL WALL OF APONEUROTIC CONE; PRE, PREZYGAPOPHYSIS OF A VERTEBRA; TRP, TRANSVERSE PROCESS OF A VERTEBRA; V, EXPOSED MEDIAL WALL OF APONEUROTIC CONE ATTACHING TO FLOOR OF CONE. LIGHT CROSS-LINES REPRESENT DIRECTIONS OF CONNECTIVE TISSUE FIBERS IN THE APONEUROSES.

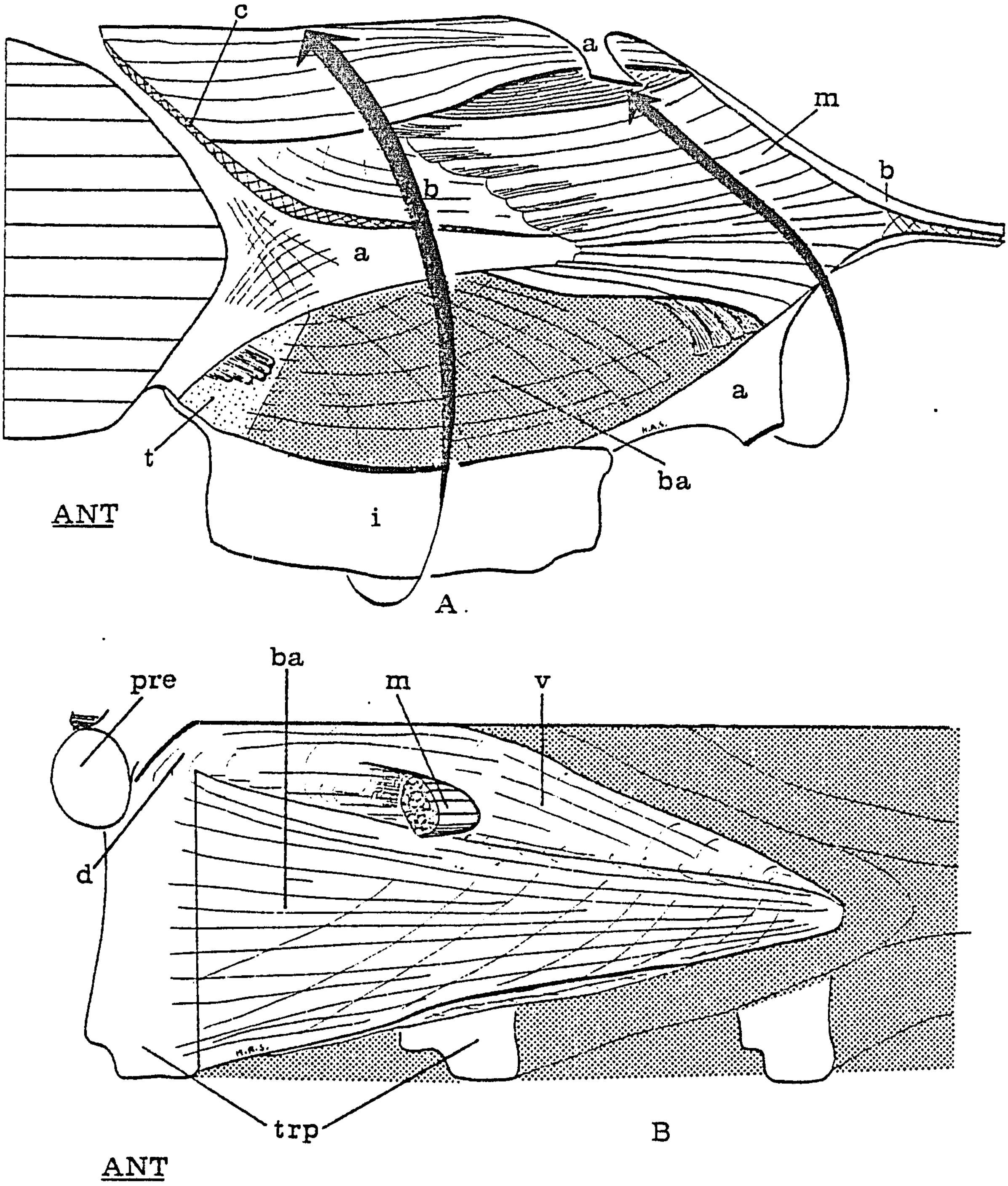

FIG. 29

FIG. 30. DORSAL VIEW OF POSTERIOR THORACIC AND LUMBAR VERTEBRAE. HORIZONTAL LINES REPRESENT AREA COVERED BY M. *LONGISSSIMUS DORSI*, VERTICAL LINES REPRESENT AREA COVERED BY M. *TENDINO-ARTICULARIS DORSI*. DIS, HEAVY LINE REPRESENTS THE DORSAL INTERMUSCULAR SEPTUM; EM, EMINENCE ON TRANSVERSE PROCESS WHERE TWO SEPTA ENCLOSING M. *TENDINO-ARTICULARIS DORSI* MEET; LG, ORIGIN OF M. *LONGISSIMUS DORSI*; LV, LUMBAR VERTEBRAE; NS, NEURAL SPINES; POST, POSTZYGAPOPHYSES; PRE, PREZYGAPOPHYSIS; SC, SCAR ON TRANSVERSE PROCESS THAT REMAINS FROM SEPTUM BETWEEN M. *TENDINO-ARTICULARIS DORSI* AND M. *ARTICULO-SPINALIS DORSI*; TA, AREA OF ORIGIN OF PART OF M. TENDINO-ARTICULARIS DORSI. ANT, ANTERIOR.

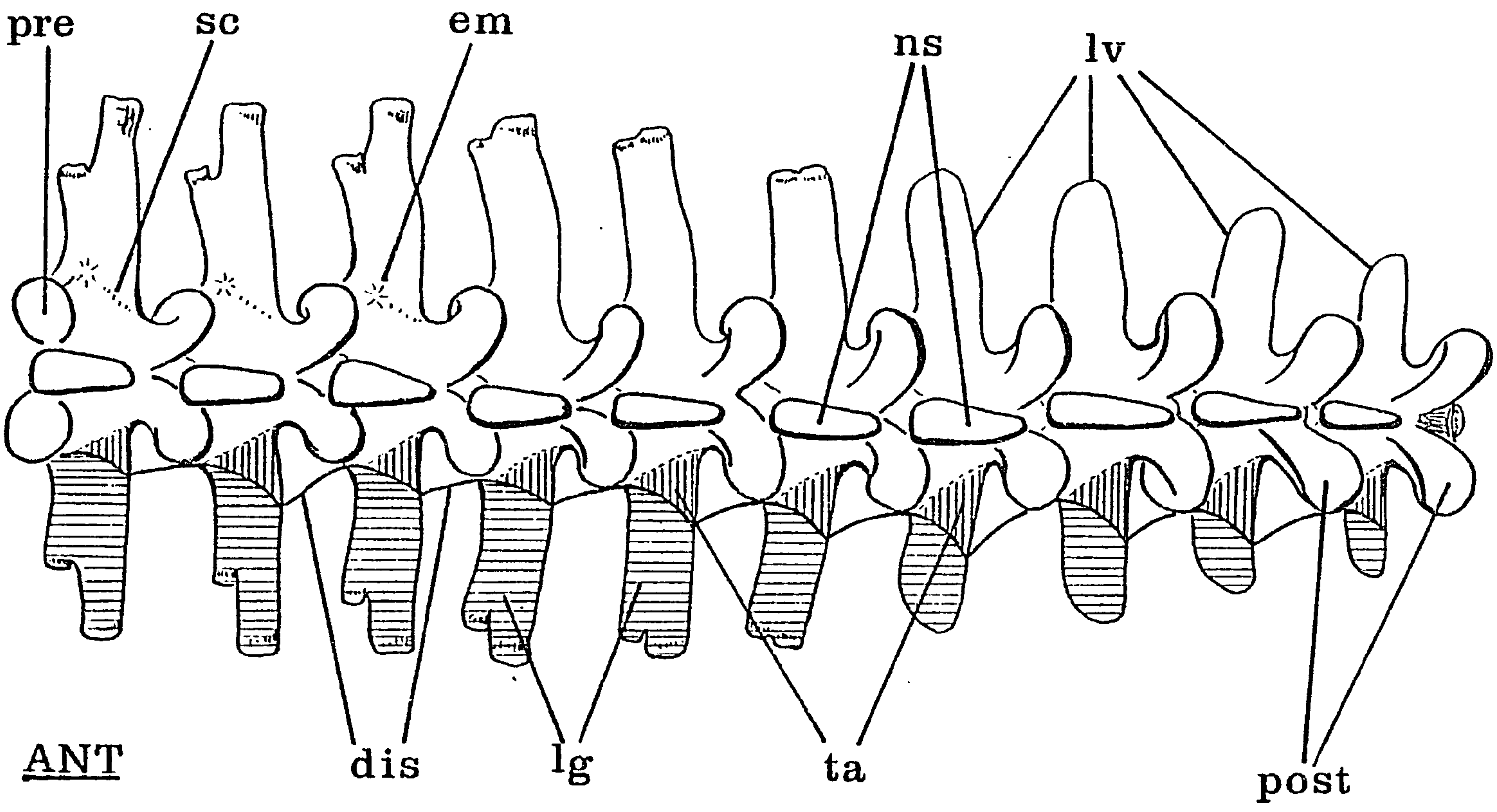

FIG. 30

FIG. 31. M. TENDINO-ARTICULARIS DORSI. COMPARE THE TRIANGULAR ATTACHMENT OF THE DORSAL INTERMUSCULAR SEPTUM (D) WITH MAP OF SAME IN FIG. 30. THIS IS A LEFT LATERAL VIEW. A, TRIANGULAR APONEUROSIS OF M. ARTICULO-SPINALIS DORSI; B, TRANGUALR APONEUROSIS OF M. TENDINO-ARTICULARIS DORSI; C, CENTRAL TENDON OF M. TENDINO-ARTICULARIS DORSI, AFTER IT HAS UNDERGONE A 90° TWIST (SEE TEXT, PG. 68); D, DORSAL INTERMUSCULAR SEPTUM; E, FLOOR OF APONEUROTIC CONE OF M. LONGISSIMUS DORSI; F, TRANSVERSE PROCESS OF A VERTEBRA; G, LONGITUDINAL MUSCLE FIBER BUNDLES THAT ORIGINATE ON A TRASNVERSE PROCESS AND INSERT ON THE END OF THE CENTRAL TENDON; H, AREA WHERE TRIANGULAR APONEUROSIS UNDERGOES A 90° TWIST; I, INTERMUSCULAR SEPTUM BETWEEN MM. TENDINO-ARTICULARIS DORSI AND ARTICULO-SPINALIS DORSI. THE PINNATE MUSCLE FIBERS HAVE BEEN REMOVED FROM THE CENTRAL TENDON (C).

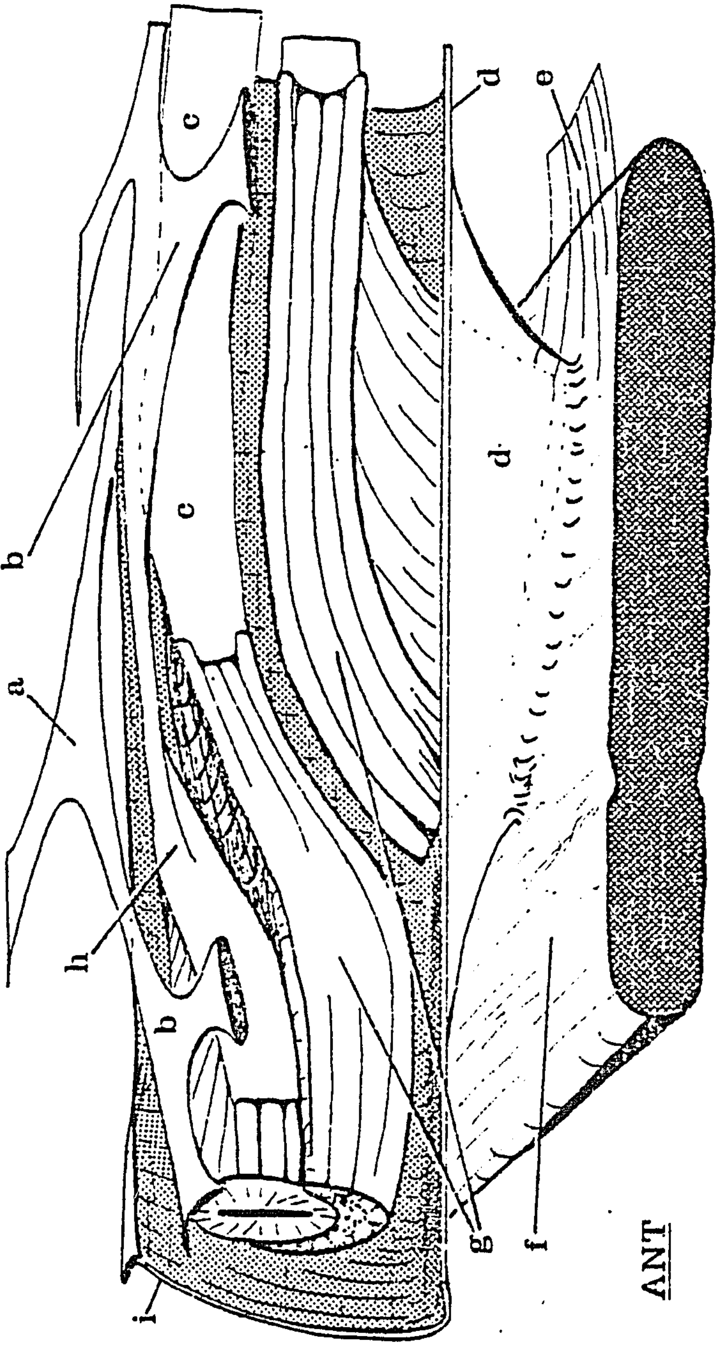

FIG. 31

FIG. 32. DORSAL VIEW OF ARRANGEMENT OF M. TENDINO-ARTICULARIS DORSI TO SHOW RELATION OF ONE SEGMENT TO VERTEBRAE BENEATH. M, TERMINAL MUSCLE FIBER BUNDLES; NS, NEURAL SPINE OF THE VERTEBRAE; PR, PREZYGAPOPHYSES; T, TENDON OF M. TENDINO-ARTICULARIS DORSI; TA, TRIANGULAR SUPERFICIAL APONEUROSIS OF M. TENDINO-ARTICULARIS DORSI. ANT, ANTERIOR. BIPINNATE MUSCLE FIBERS HAVE BEEN REMOVED.

FIG. 33. A) DORSAL VIEW OF TENDONS OF M. ARTICULO-SPINALIS DORSI. ONE TENDON IS SHOWN TO SPAN 4 VERTEBRAE AND ATTACH TO THE FIFTH POSTERIOR ONE BY A SEGMENT OF MUSCLE FIBERS (M). AS, SUPERFICIAL TRIANGULAR APONEUROSES OF M. ARTICULO-SPINALIS DORSI, WITH APEX POSTERIOR; NS, NEURAL SPINE TIPS; PR, PREZYGAPOPHYSIS; PO, POSTZYGAPOPHYSIS; SN, TENDONS OF THE DEEPER MM. SPINO-ARTICULARIS DORSI AND NEUROSPINALIS DORSI; TA, LATERAL ATTACHMENT TO TRIANGULAR APONEUROSIS OF M. TENDINO-ARTICULARIS DORSI; M, FINAL MUSCLE SEGMENT THAT ATTACHES TO ANTERIOR SURFACE OF POSTZYGAPOPHYSIS.

B) LATERAL VIEW OF ONE SEGMENT OF M. ARTICULO-SPINALIS DORSI, SPANNING FIVE VERTEBRAE. AS, TRIANGULAR APONEUROSIS; M, FINAL MUSCLE SEGMENT ATTACHING TO POST-ZYGAPOPHYSIS; NS, NEURAL SPINES; PO, POSTZYGAPOPHYSIS; PR, PREZYGAPOPHYSIS; TA, LATERAL CONNECTION TO SUPERFICIAL TENDON OF M. TENDINO-ARTICULARIS DORSI.

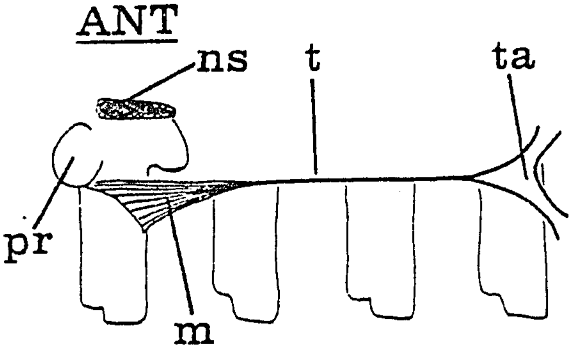

FIG. 32

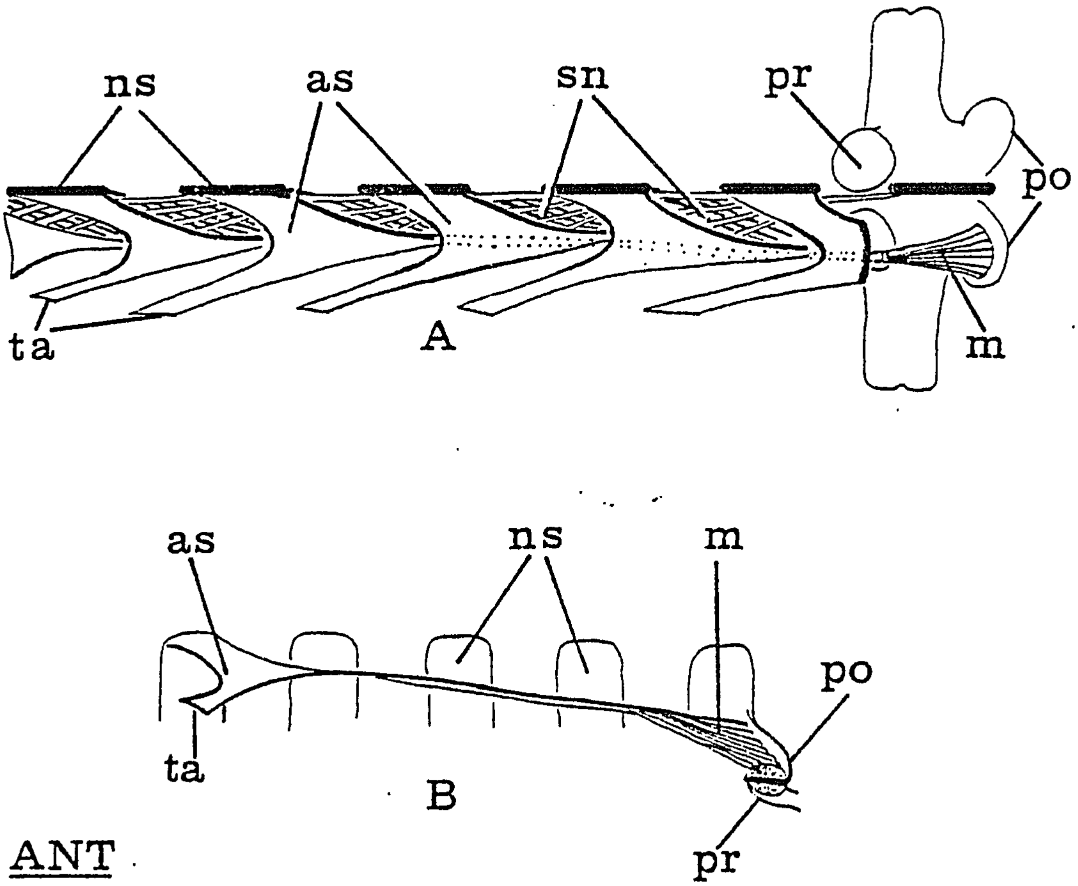

FIG. 33

FIG. 34. DIAGRAM TO REPRESENT THE ARRANGEMENT OF SEPTA BETWEEN *M. TENDINO-ARTICULARIS DORSI* AND *M. ARTICULO-SPINALIS DORSI*. AS, *M. ARTICULO-SPINALIS DORSI*; DIS, DORSAL INTERMUSCULAR SEPTUM; LS, LATERAL LIMITING SEPTUM OF *M. ARTICULO-SPINALIS DORSI*; TA, *M. TENDINO-ARTICULARIS DORSI*.

FIG. 35. M. *SPINO-ARTICULARIS DORSI* AND *M. NEURO-SPINALIS DORSI*. A) SEMI-DIAGRAMATIC TO SHOW HOW *M. SPINO-ARTICULARIS DORSI* OVERLAPS *M. NEURO-SPINALIS DORSI* EXTERNALLY, AND ALSO, THAT BOTH MUSCLES ATTACH TO THE NEURAL SPINES. ANTERIOR IS TO THE LEFT. NS, NEURAL SPINE; NSP, *M. NEURO-SPINALIS DORSI*; SA, *M. SPINO-ARTICULARIS DORSI*.

B) DRAWING OF TENDONS AND MUSCLE OF *M. SPINO-ARTICULARIS DORSI*, AS IT RESTS AGAINST *M. NEURO-SPINALIS DORSI* AND THE NEURAL SPINE. *M. NEURO-SPINALIS DORSI* LOOKS EXACTLY LIKE THIS, EXCEPT THAT THE DIRECTION OF THE TENDONS IS FROM ANTERIOR DORSAL, TO POSTERIOR VENTRAL. CE, CENTRUM; M, MUSCULAR ATTACHMENT AT THE TERMINATION OF THE TENDON; NA, NEURAL ARCH; NS, NEURAL SPINE; PO, POSTZYGAPOPHYSIS; PR, PREZYGAPOPHYSIS; SA, TENDONS OF *M. SPINO-ARTICULARIS DORSI*.

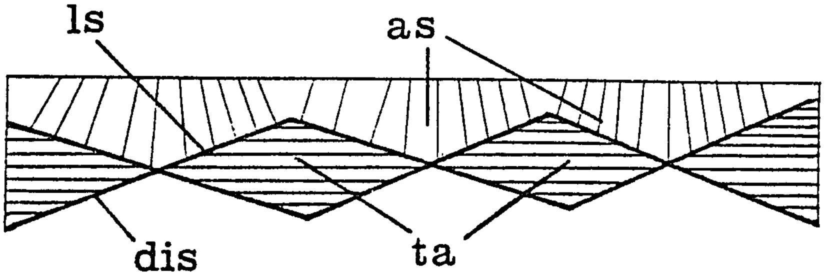

FIG. 34

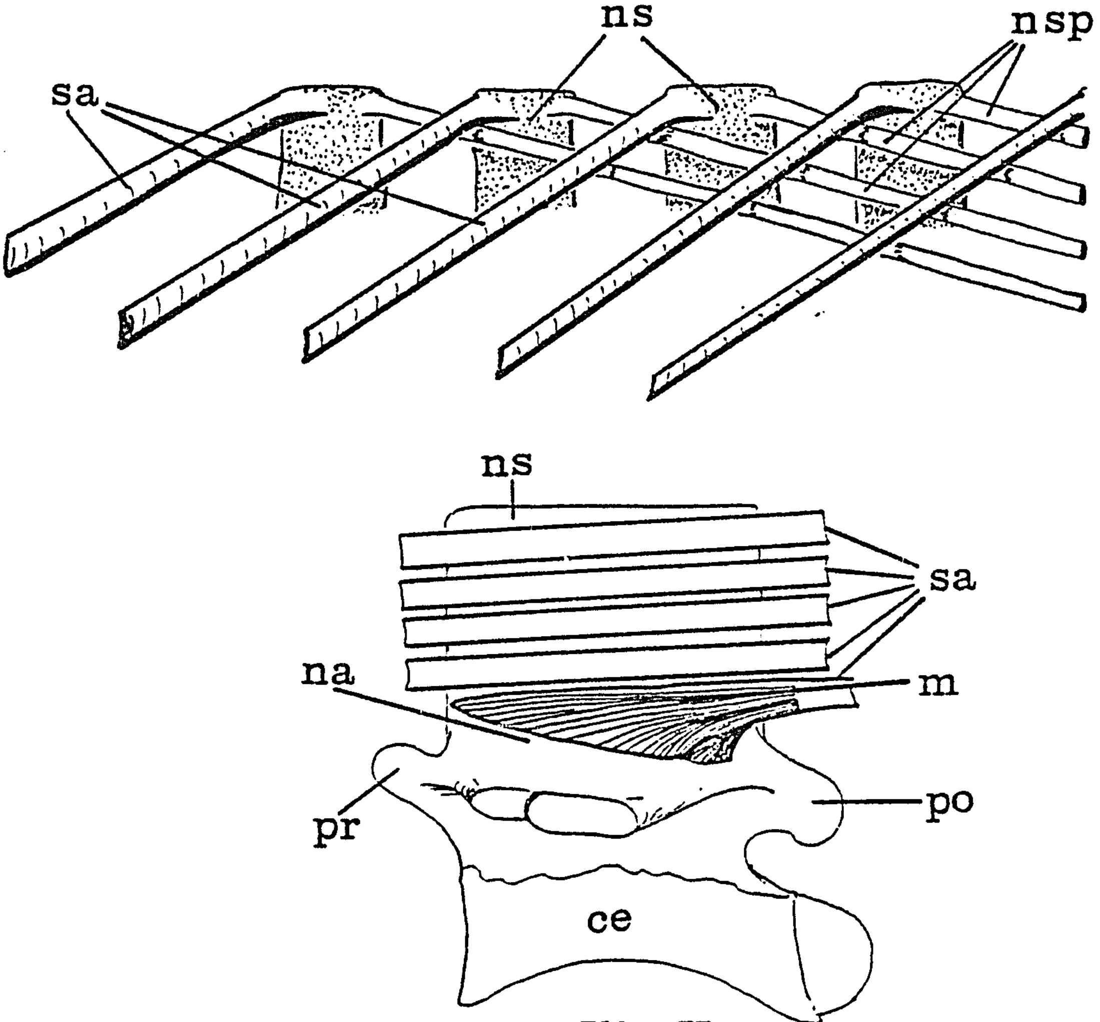

FIG. 35

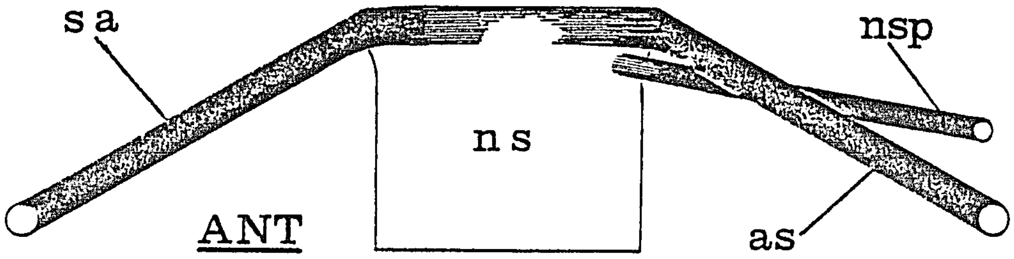

FIG. 36

FIG. 36. LATERAL VIEW OF A TYPICAL NEURAL SPINE OF THE TRUNK REGION. MUSCLE FIBERS HAVE BEEN OMITTED, AS WELL AS THE ILIO-COSTALIS FASICIAL BAND (IT INSERTS ALONG THE ENTIRE NEURAL SPINE TIP, AND ITS INCLUSION HERE WOULD OBSCURE THE VIEW). THE RELATIVE SIZES OF THE TENDONS ARE SHOWN, THE MODEL OF THIS SPECIMEN WAS A JUVENILE. AS, TENDON OF M. ARTICULO-SPINALIS DORSI; NS, NEURAL SPINE; NSP, TENDON OF M. NEURO-SPINALIS DORSI; SA, TENDON OF M. SPINO-ARTICULARIS DORSI. ANT, ANTERIOR.

FIG. 37. RIGHT LATERAL VIEW OF A JUVENILE SPECIMEN OF *A. MISSISSIPPIENSIS*. THE INVESTING FASCIA OF THE NECK HAS BEEN REMOVED AND THE SERRATUS MUSCLES FROM THE RIB TIPS TO THE SCAPULA HAVE BEEN CUT. IL-CA, *M. ILIO-COSTALIS CAPITIS*, PARTLY HIDDEN BEHIND THE *M. PTERYGOIDEUS POSTERIOR* AND THE ARTICULAR BONE; IL-CE, *M. ILIO-COSTALIS CERVICIS*, CONTINUING THE ILIO-COSTALIS SYSTEM UP TO THE FIRST RIB; LG-CD, *M. LONGISSIMUS CAPITIS PROFUNDUS*, DEEPEST OF THE CERVICAL LONGISSIMUS MUSCLES; LG-C-S, *M. LONGISSIMUS CAPITIS SUPERFICIALIS* (THE THIRD LONGISSIMUS OF THE NECK, *M. LONGISSIMUS CERVICIS* IS NOT VISIBLE HERE); R-1, POSTERIOR TIP OF THE FIRST RIB; SP-C-P, *M. SPINALIS CAPITIS POSTICUS*; TR-SP-C, *M. TRANSVERSO-SPINALIS CAPITIS* (ONLY THE ORIGIN FROM THE FASCIA OF THE TRUNK IS VISIBLE IN THIS VIEW, THE ORIGIN FROM THE NEURAL SPINE TIPS IS HIDDEN DEEP, AT ABOUT THE LEVEL OF THE VENTRAL EDGE OF THIS MUSCLE).

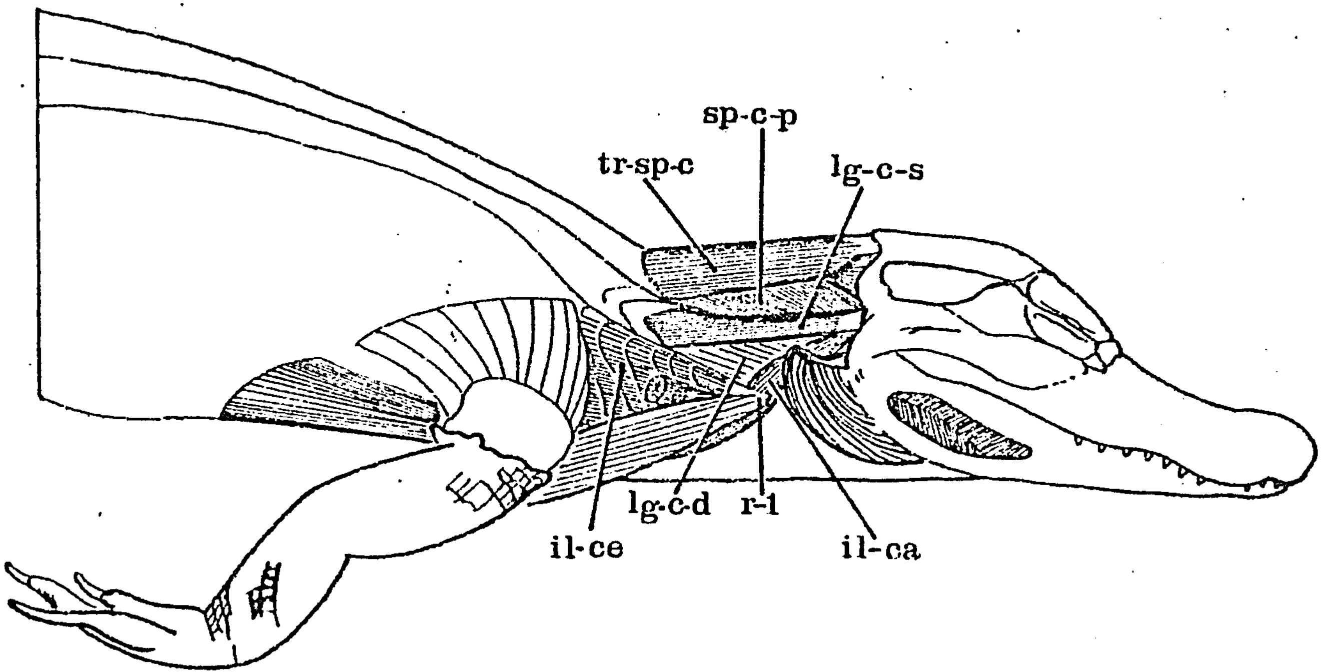

FIG. 37

FIG. 38. RIGHT LATERAL VIEW OF THE CERVICAL MUSCULATURE OF *A. MISSISSIPPIENSIS*. HYP, HYPAXIAL MUSCLES FROM THE RIB TIPS; I-D, FIRST SEGMENT OF *M. ILIO-COSTALIS DORSI*, BEHIND THE 8TH RIB; JCT-LO, MEDIAL SLIPS FROM *M. ILIO-COSTALIS CERVICIS* THAT JOIN UP POSTERIORLY WITH THE LONGISSIMUS SYSTEM; L-D, BENEATH FASCIA IS *M. LONGISSIMUS DORSI*; LG-CAP-PROF, *M. LONGISSIMUS CAPITIS PROFUNDUS* AS IT PASSES OVER THE FIRST RIB; LG-CAP-SUP, *M. LONGISSIMUS CAPITIS SUPERFICIALIS* (CUT); LG-CE, *M. LONGISSIMUS CERVICIS*, DORSAL AND MEDIAL TO *M. LONGISSIMUS CAPITIS SUPERFICIALIS*; MYS-1, INITIAL MYOSEPTUM OF CERVICAL ILIO-COSTALIS SYSTEM, ORIGINATING FROM THE POSTERIOR SURFACE OF RIB-1; R-1, R-4, AND R-8, RIBS # 1, 4, AND 8. NOTE THAT RIBS 2 AND 3 ARE DEEP AND HIDDEN BY THE HYPAXIAL MUSCLES; S-1 AND S-7, FIRST AND SEVENTH MUSCULAR SEGMENTS OF *M. ILIO-COSTALIS CERVICIS*; SP-CAP-POST, *M. SPINALIS CAPITIS POSTICUS* (CUT); ST-C, *M. STERNO-COSTALIS* INSERTING BY A TENDON TO THE TIP OF RIB-1; T-D, *M. TRANSVERSO-SPINALIS DORSI*; TR-SP-C, *M. TRANSVERSO-SPINALIS CAPITIS* (CUT). ANT, ANTERIOR. NOTE ALSO THAT M. *ILIO-COSTALIS CAPITIS* HAS BEEN ENTIRELY REMOVED FROM THE VENTRO-LATERAL SURFACE OF RIB-1 TO PERMIT VIEWING ACCESS TO THE DEEPER MUSCLES. *M. TRANSVERSO-SPINALIS CERVICIS* AND OTHER DEEP MUSCLES CANNOT BE SEEN FROM THIS VIEW.

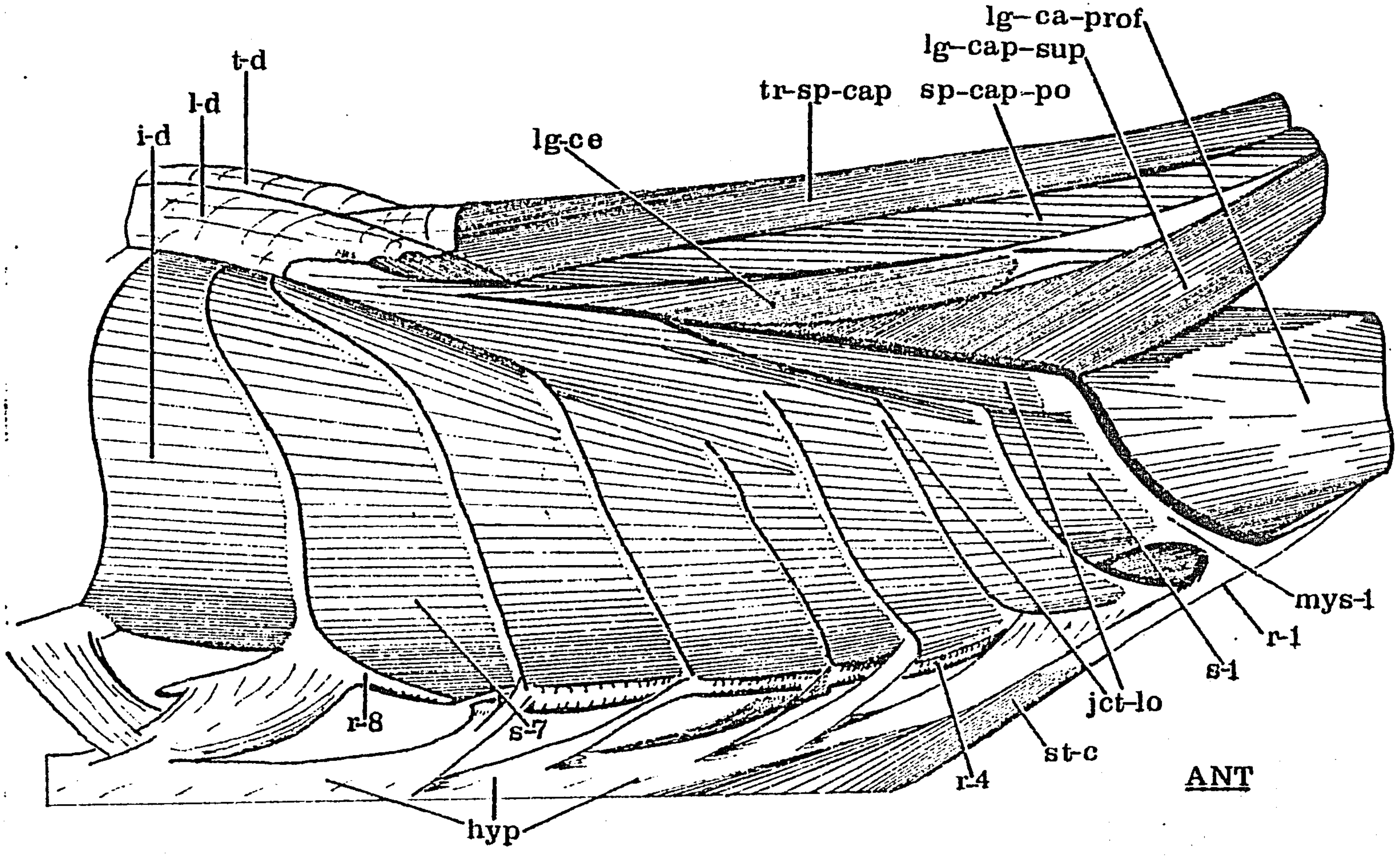
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FIG. 38

FIG. 39. A,B,C, RIGHT LATERAL VIEWS OF M. ILIO-COSTALIS CERVICIS. A) THE MUSCLE, M. ILIO-COSTALIS CERVICIS HAS BEEN REFLECTED VENTRALLY, AWAY FROM THE LONGISSIMUS MUSCLES. TO CARRY THIS OUT, THE CONNECTION BETWEEN THE TWO SYSTEMS HAS BEEN CUT (MATCH UP PARTS "X"). AP-1, FIRST APONEUROSIS OF M. ILIO-COSTALIS CERVICIS THAT ATTACHES TO RIB 1; CAP-PROF, M. LONGISSIMUS CAPITIS PROFUNDUS; CAP-SUP, M. LONGISSIMUS CAPITIS SUPERFICIALIS; CE, M. LONGISSIMUS CERVICIS; R-1, FIRST RIB; REF, REFLECTION LATERALLY AND VENTRALLY OF SHEET-LIKE M. ILIO-COSTALIS CERVICIS; X, MATCHING MUSCLE PARTS THAT HVE BEEN CUT. "X" IS ALSO THE JUNCTION BETWEEN THE ILIO-COSTALIS SYSTEM AND LONGISSIMUS SYSTEM. ANT, ANTERIOR

B) SAME VIEW AS FOR 39A, WITH THE FOLLOWING CHANGES: MUSCLE FIBERS OF SEGMENT 5 HAVE BEEN REMOVED TO SHOW APONEUROSIS 6. PART OF THE NERVE SUPPLY TO M. ILIO-COSTALIS CERVICIS IS SHOWN. T-6A, TENDON 6, PART A; N, NERVE PIERCING M. LONGISSIMUS CAPITIS PROFUNDUS; X, MEDIAL SEGMENTS OF M. ILIO-COSTALIS CERVICIS THAT JOIN THE LONGISSIMUS SYSTEM (SHOWN HERE FROM SEGMENTS 1,2 AND 3 OF THE MUSCLE). ANT, ANTERIOR.

C) THE FIRST FOUR SEGMENTS OF M. ILIO-COSTALIS CERVICIS HAVE BEEN SEPARATED TO DEMONSTRATE THE DORSAL, MEDIAL CONNECTION TO THE LONGISSIMUS SYSTEM. SEGMENT 5 HAS BEEN REMOVED. ABBREVIATIONS THE SAME AS IN 39, A AND B.

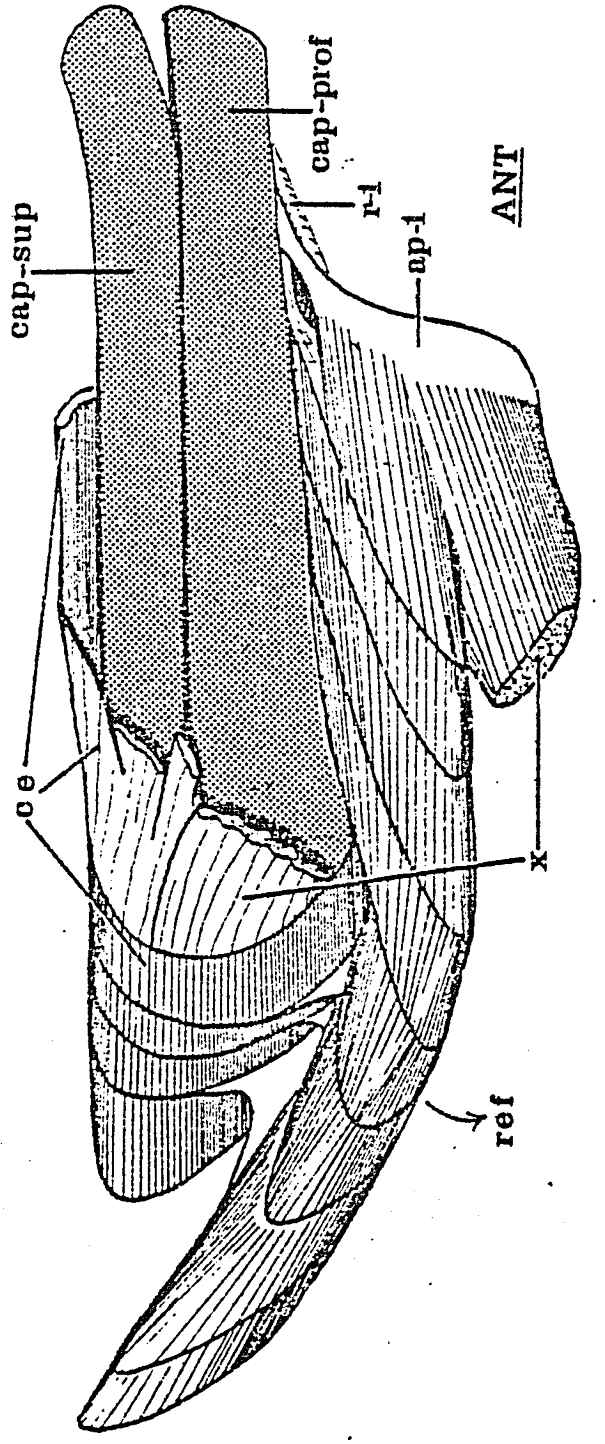


FIG. 39A

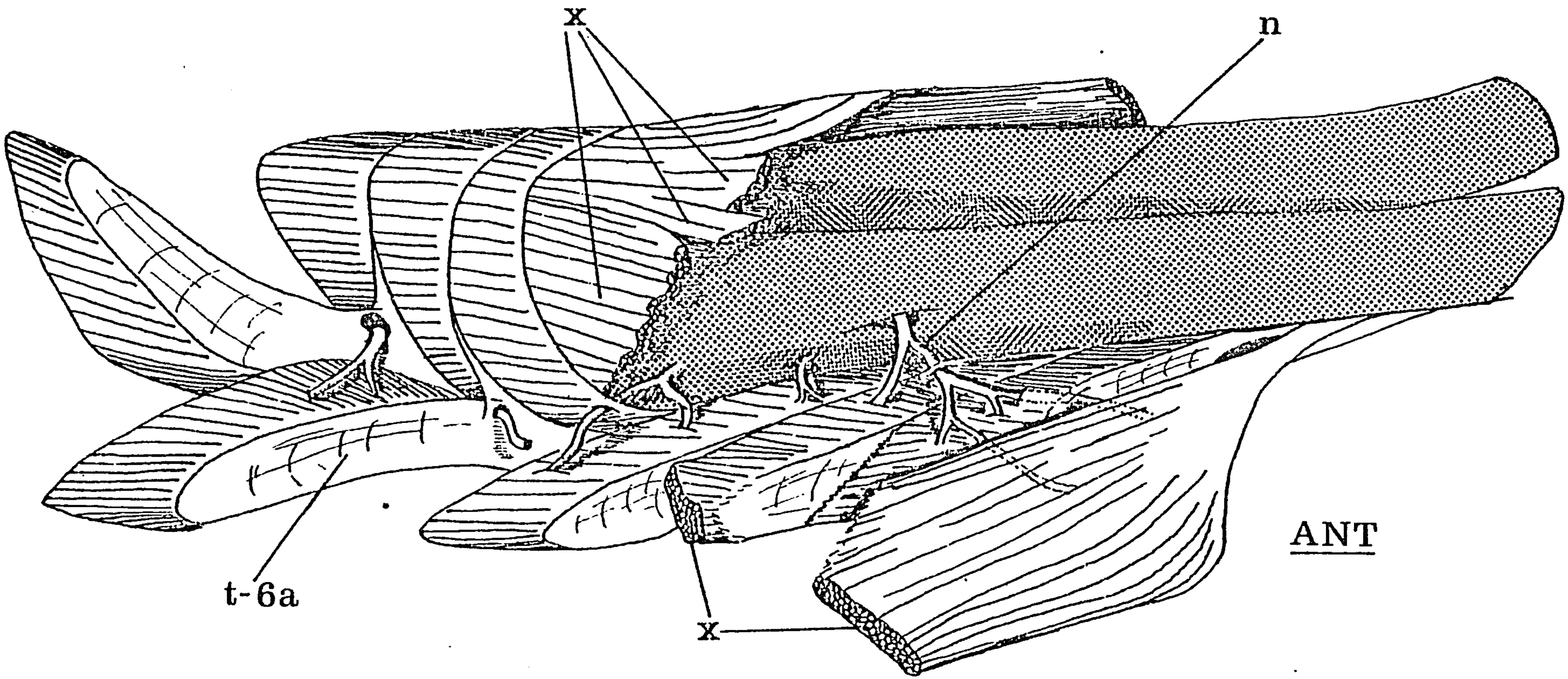


FIG. 39B

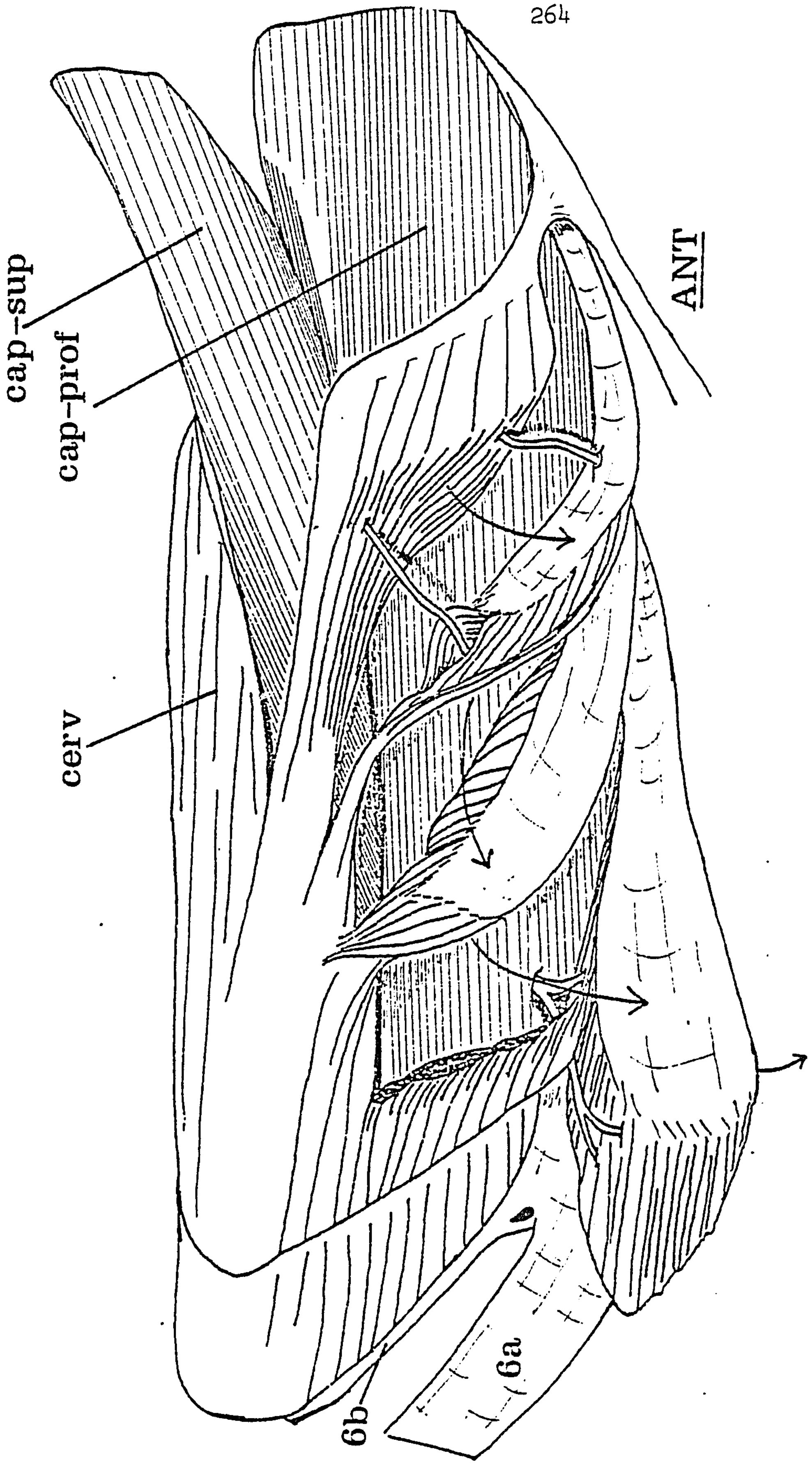


FIG. 39 C

FIG. 40. RIGHT LATERAL VIEW OF THE SUPERFICIAL MUSCLES OF THE NECK. THE LOWER JAW AND DISTAL PORTION OF THE QUADRATE HAVE BEEN REMOVED, AS WELL AS *M. DEPRESSOR MANDIBULAE*. ARM, MUSCLES OF THE UPPER ARM; IL-CA, *M. ILIO-COSTALIS CAPITIS*; IL-CE, *M. ILIO-COSTALIS CERVICIS*; LG-CAP-SUP, *M. LONGISSIMUS CAPITIS SUPERFICIALIS*; SC, SCAPULA; SER; "SERRATUS" MUSCLES; SPIN-CAP-POST, *M. SPINALIS-CAPITIS-POSTICUS*; ST-C, *M. STERNO-COSTALIS*; TR-SP-CAP, *M. TRANSVERSO-SPINALIS CAPITIS*. *M. LONGISSIMUS CAPITIS PROFUNDUS* IS VISIBLE, BUT NOT LABELED, DEEP TO LG-CAP-SUP AND IL-CA.

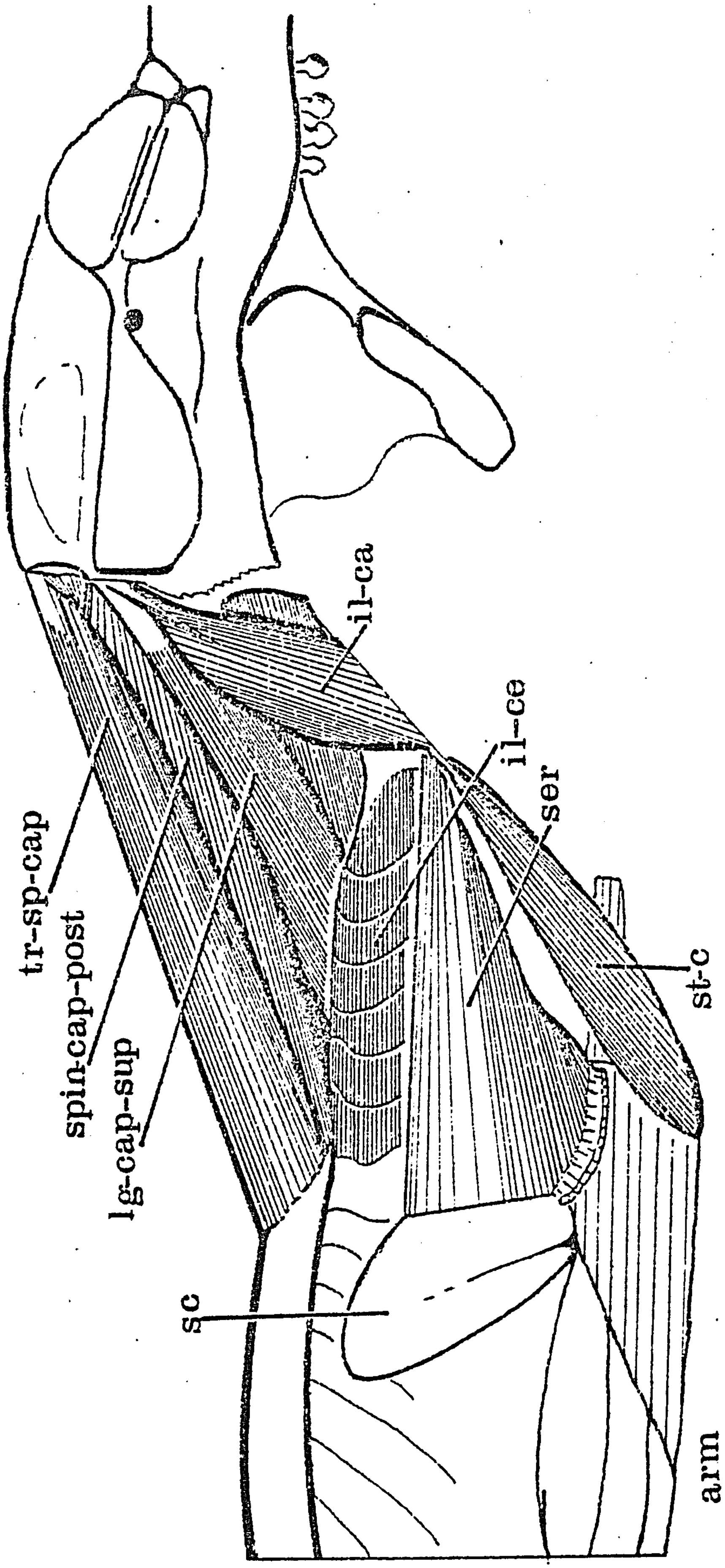


FIG. 40

FIG. 41. RIGHT LATERAL VIEW OF ILIO-COSTALIS SYSTEM, INCLUDING DEEP FIBERS AND MYOSEPTA. A) MUSCLE SEGMENT 5 OF M. ILIO-COSTALIS CERVICIS HAS BEEN REMOVED, SEPTUM 6 IS SLIGHTLY TWISTED AND ITS POSTERIOR FACE IS MOVED TO FACE POSTERO-LATERALLY. CERV, M. LONGISSIMUS CERVICIS; R-6, RIB 6; SEG-6, MUSCLE SEGMENT 6; SEP-5, MYOSEPTUM 5. NOTE: DOTTED LINE INDICATES MYOSEPTUM 5 BEHIND MUSCLE SEGMENT 4; DIAPOPHYSIS 6 IS VISIBLE IN THIS FIGURE.

B) RIB 6 WITH THE MYOSEPTUM OF ILIO-COSTALIS ATTACHED TO IT. DIA-6, DIAPOPHYSIS 6; R-6, SIXTH RIB; 6A, 6B, TENDONS "A" AND "B" OF THE CERVICAL ILIO-COSTALIS SYSTEM OF MYOSEPTAL TENDONS. ANT, ANTERIOR DIRECTION. THE SPECIMEN FOR THESE FIGURES WAS A JUVENILE, WITH A SKULL LENGTH OF 6.5 CM. THE LENGTH OF THE MYOSEPTUM 6 (FROM THE POSTERIOR EDGE OF THE TUBERCULUM) WAS 1.13 CM.

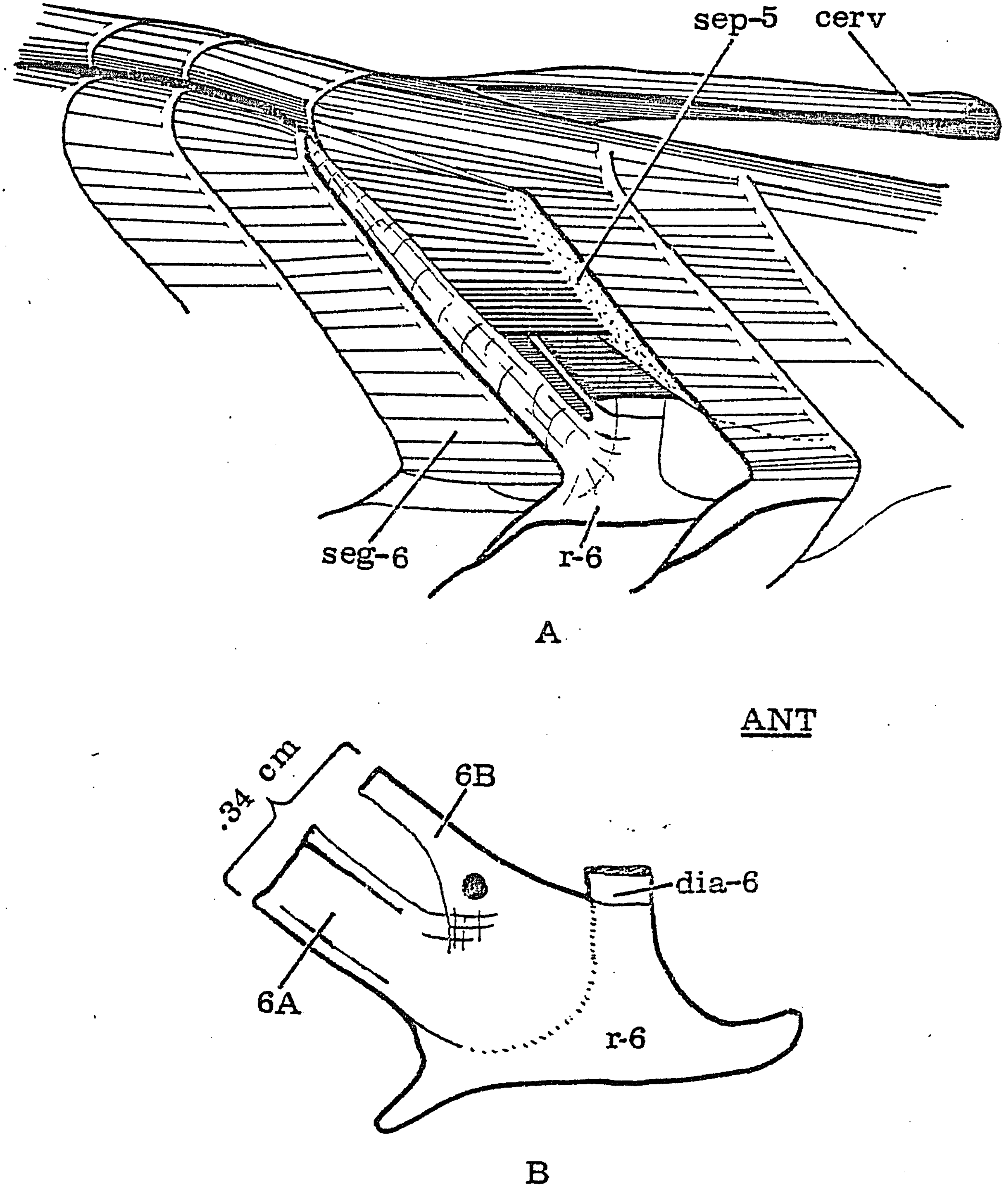


FIG. 41

FIG. 42. DIAGRAMATIC FRONTAL SECTION OF M. ILIO-COSTALIS CERVICIS, TO DEMONSTRATE THE INTERCONNECTION BETWEEN ILIO-COSTALIS AND LONGISSIMUS SYSTEMS. THE HEAVY BLACK BLOCKS REPRESENT THE MUSCLE SEGMENTS THAT JOIN THE TWO SYSTEMS (SECTIONS 1,2, &3 WERE LEFT WITH LINES TO SHOW THAT THEY MERGE AS A DISTINCT GROUP). FA, DENSE SUPERFICIAL FASCIA, CONTINUOUS WITH DORSAL INTERMUSCULAR SEPTUM DORSALLY; L-6, LONGISSIMUS TENDON 6; MY-1, ANTERIOR MYOSEPTUM THAT ATTACHES TO FIRST RIB; S-1, S-7, FIRST AND SEVENTH MUSCLE SEGMENTS OF M. ILIO-COSTALIS CERVICIS; 6-A, 7-B, 8-A, 8-B, TENDONS OF THE ILIO-COSTALIS SYSTEM; 1,2, AND 3, MEDIAL SECTION OF M. ILIOCOSTALIS CERVICIS ARISING FROM SEGMENTS 1,2, AND 3, JOINING EACH OTHER AND INSERTING UPON LONGISSIMUS MYOSEPTUM 6. ANT, ANTERIOR.

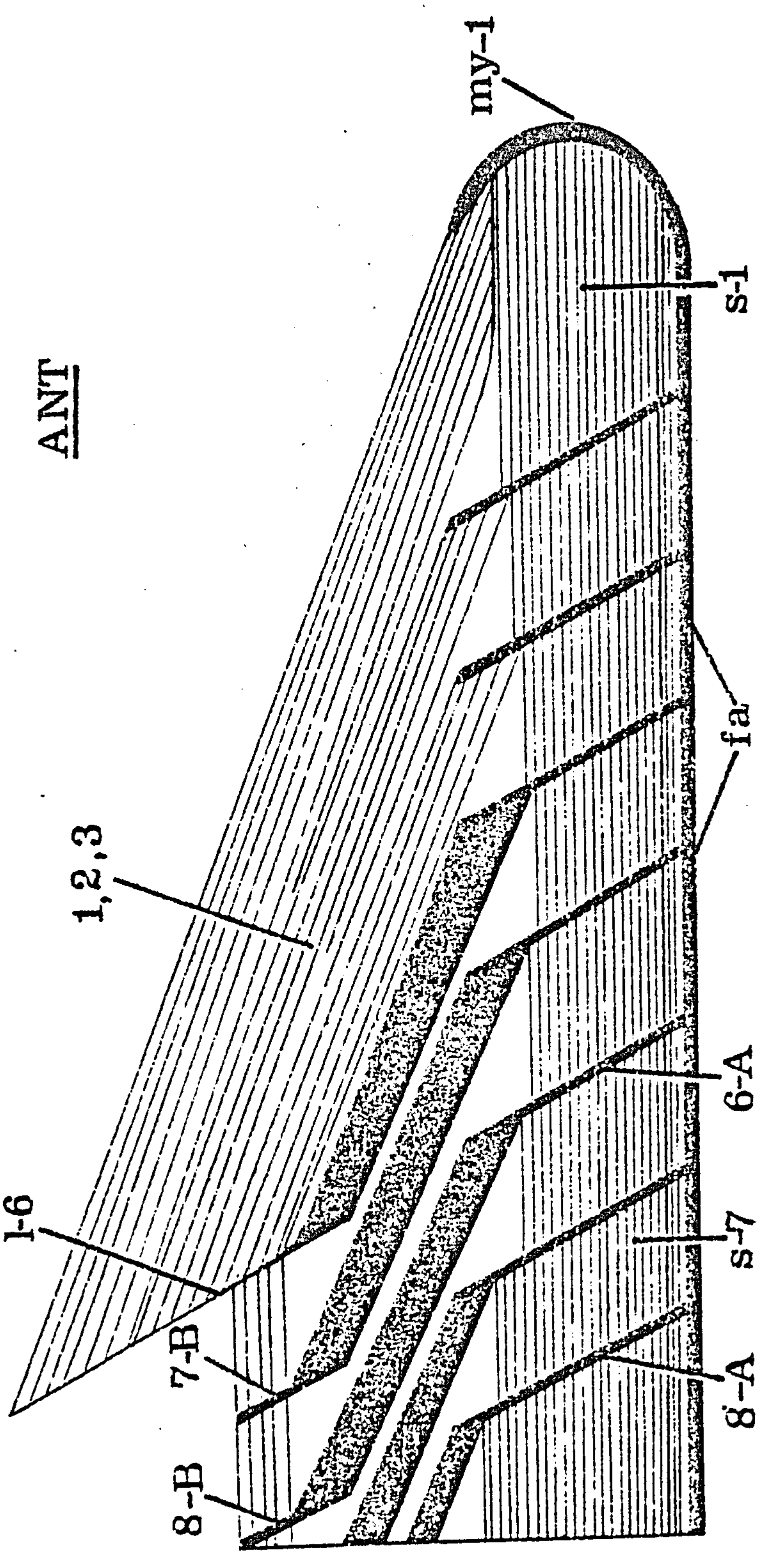


FIG. 42

FIG. 43. TRANSITION OF THE THREE EPAXIAL MUSCLE DIVISIONS BETWEEN TRUNK AND NECK. LEFT LATERAL VIEW. DI, DORSAL INTERMUSCULAR SEPTUM; LD-1, FIRST APONEUROTIC CONE OF *M. LONGISSIMUS DORSI*. NOTE THE ORIGIN FROM A TUBERCLE ON THE POSTERIOR BORDER OF THE EIGHTH RIB; PZ-3, MUSCLE SLIPS INSERTING ON POSTZYGAPOPHYSIS 3. R-7, THE SEVENTH RIB; SP-CAP-POST, *M. SPINALIS CAPITIS POSTICUS*, ARISING FROM THE TIP OF THE SEVENTH NEURAL SPINE AND ADJACENT TENDONS; TR, *M. TRANSVERSO-SPINALIS CAPITIS*, ORIGINATING FROM THE TRUNK FASCIA THAT IS CONTINUOUS WITH THE DORSAL INTERMUSCULAR SEPTUM; VERT-7, THE SEVENTH CERVICAL VERTEBRA; Z-1, Z-2, SECTIONS OF *M. TRANSVERSO-SPINALIS CERVICIS* THAT INSERT (RESPECTIVELY) UPON POSTZYGAPOPHYSES 1 AND 2; A, B, MEDIAL AND LATERAL PARTS OF MYOSEPTUM 7 OF THE ILIO-COSTALIS SYSTEM; ANT, ANTERIOR; 7, SEVENTH AND LAST MUSCULAR SEGMENT OF *M. ILIO-COSTALIS CERVICIS*, REFLECTED ANTERIOR AND VENTRALLY (DOTTED LINE AND ARROW) OFF OF THE ANTERIOR SURFACE OF THE FIRST MYOSEPTUM OF *M. ILIO-COSTALIS DORSI*.

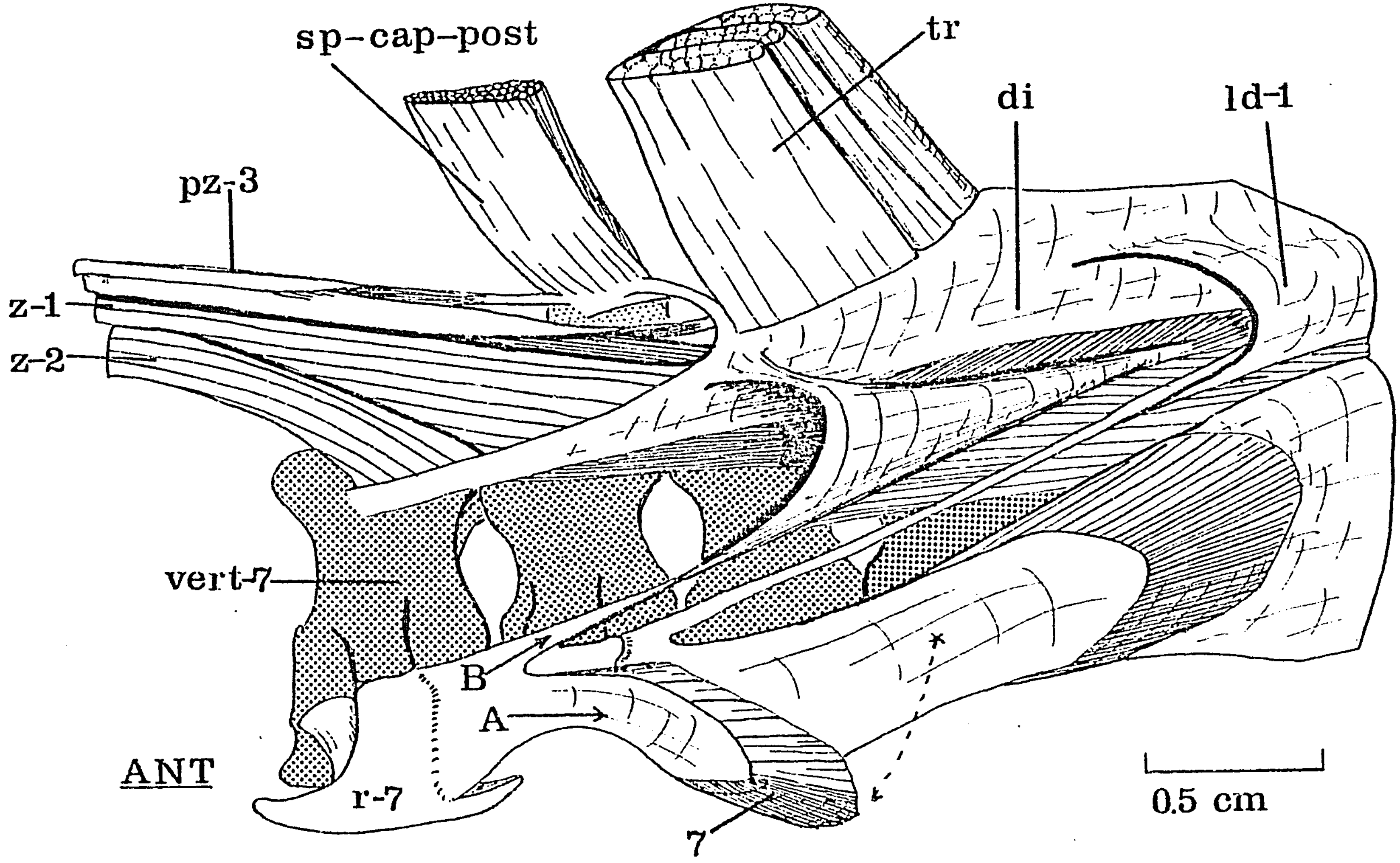


FIG. 43

FIG. 44. RIGHT LATERAL VIEW OF THE CERVICAL LONGISSIMUS SYSTEM. A) DIAGRAM TO SHOW THE ANTERIOR SEGMENT OF *M. LONGISSIMUS CERVICIS* ARISING FROM A TENDINOUS ARCH AND CONVERGING ANTERIORLY (AS IF IT WERE A SECTION CUT OUT OF A CONE, APEX ANTERIOR).

B) CONNECTION OF THE CERVICAL LONGISSIMUS SYSTEM WITH THE CERVICAL ILIO-COSTALIS SYSTEM HAS BEEN SEVERED. *M. ILIO-COSTALIS CERVICIS*, *M. ILIO-COSTALIS CAPITIS* AND THE HYPAXIAL MUSCULATURE HAVE BEEN REMOVED. THE TRASNVERSO-SPINALIS SYSTEM IS NOT SHOWN. A, ANTERIOR SEGMENT OF *M. LONGISSIMUS CERVICIS*(SEE FIG. 45); B, FUSIFORM *M. LONGISSIMUS CAPITIS SUPERFICIALIS*; C, *M. LONGISSIMUS CAPITIS PROFUNDUS*; E, SHINING APONEUROSIS OF *M. LONGISSIMUS CAPITIS PROFUNDUS*; F, HYPAXIAL MUSCLE ATTACHING TO BASIOCCIPITAL; H, HYPOCENTRUM OF ATLAS; I, CUT SEGMENTS THAT CONNECT TO ILIO-COSTALIS SYSTEM; R-1, R-4, R-6, FIRST, FOURTH AND FIFTH RIBS. ANT, ANTERIOR

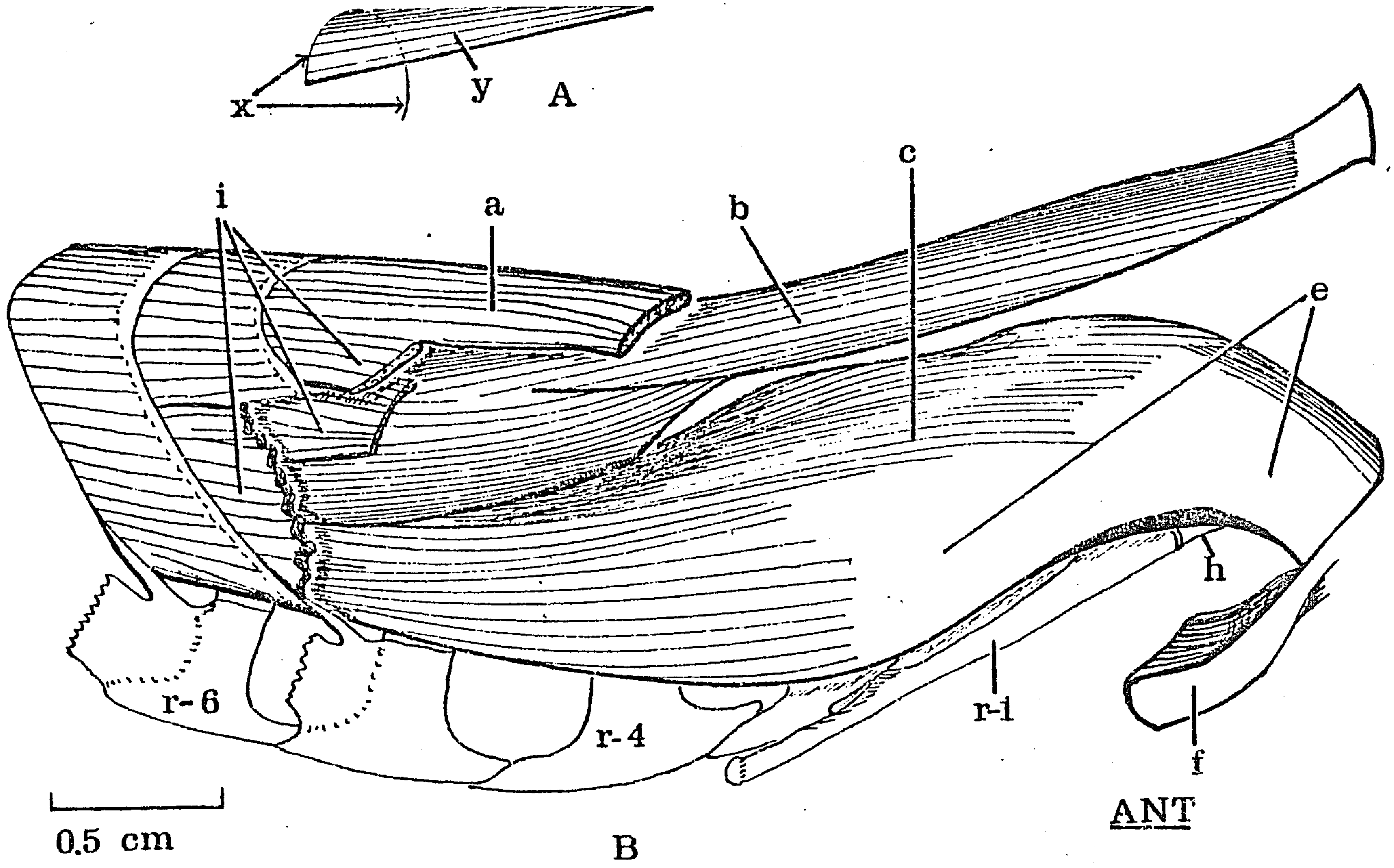


FIG. 44

FIG. 45. RIGHT LATERAL VIEW OF M. LONGISSIMUS CERVICIS. THE DORSAL INTERMUSCULAR SEPTUM THAT SEPARATES THE LONGISSIMUS SYSTEM FROM THE TRANSVERSOSPINALIS SYSTEM IS REFLECTED DORSALLY TO SHOW THE COMPONENTS ASSOCIATED WITH THE FOURTH AND FIFTH VERTEBRAE MORE CLEARLY. AT, NEURAL ARCH OF ATLAS; CERV, M. LONGISSIMUS CERVICIS; DIS, DORSAL INTERMUSCULAR SEPTUM; G-1, FIRST SEGMENT OF M. LONGISSIMUS CAPITIS PROFUNDUS, THAT INSERTS ALONGSIDE THE OCCIPITAL CONDYLE; I-1, TENDON OF THE FIRST SEPTUM OF M. ILIO-COSTALIS CERVICIS, REFLECTED VENTRALLY FROM THE FIRST RIB; ND, DORSAL RAMUS NERVE BRANCH TO M. LONGISSIMUS CAPITIS PROFUNDUS; NS, DORSAL RAMUS BRANCH TO M. LONGISSIMUS CERVICIS; NTR, DORSAL RAMUS BRANCHES TO THE TRANSVERSO-SPINALIS SYSTEM; R-4, R-6, FOURTH AND SIXTH RIBS; TE, TENDON OF M. LONGISSIMUS CERVICIS THAT INSERTS ON ATLANTAL POSTZYGAPOPHYSIS; TR-C, M. TRANSVERSO-SPINALIS CERVICIS, ON THE DORSAL SIDE OF THE DORSAL INTERMUSCULAR SEPTUM; V, SMALL VENTRAL RAMUS FOR INNERVATION OF INTERCOSTAL MUSCLES BETWEEN FIRST AND SECOND RIBS. ANT, ANTERIOR. CROSS-HATCHING REPRESENTS INTERVERTEBRAL NOTCHES AND LOCATION OF DORSAL ROOT GANGLIA.

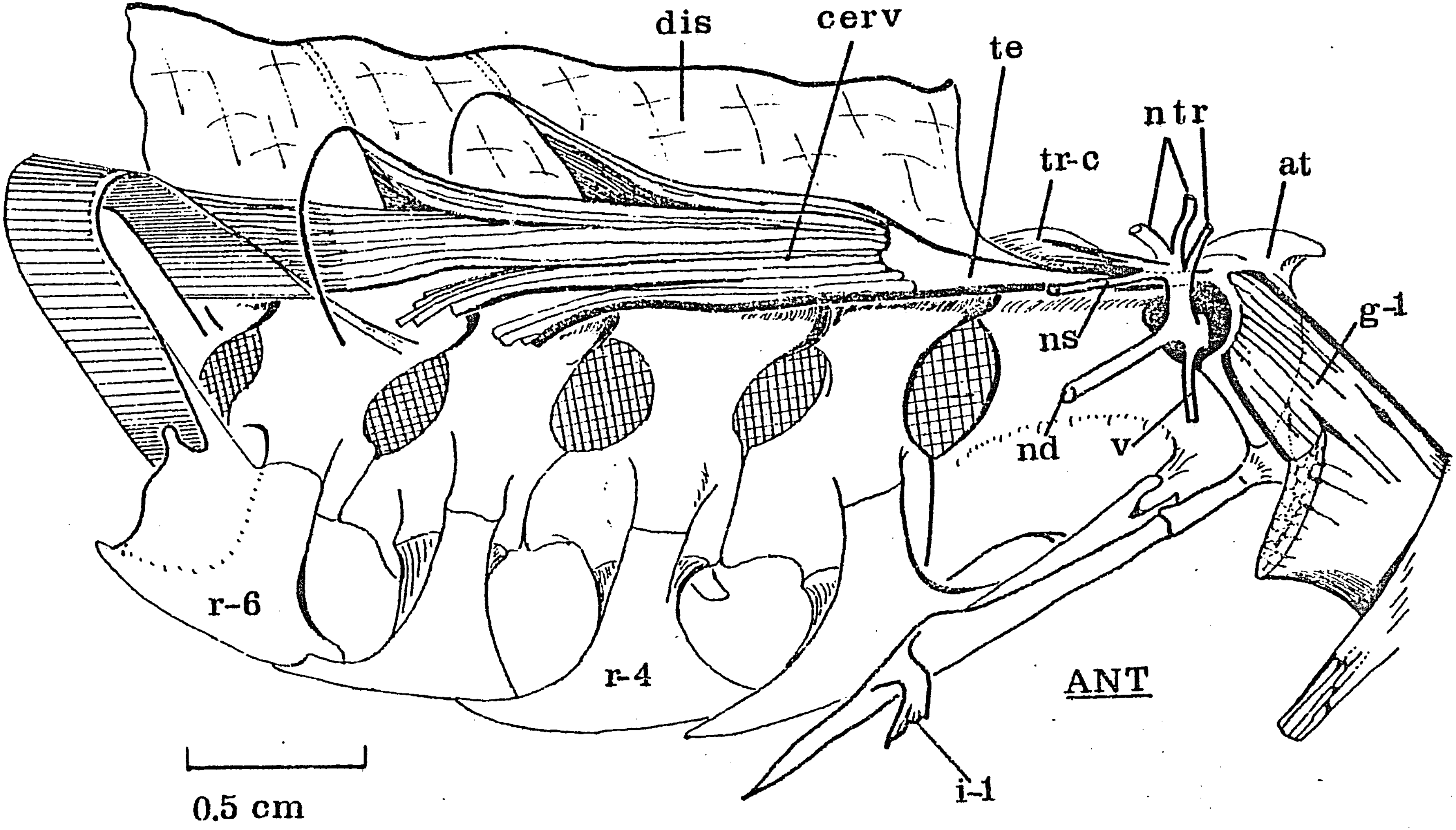


FIG. 45

FIG. 46. ORIGINS OF THE CERVICAL LONGISSIMUS SYSTEM. DIS, DORSAL INTERMUSCULAR SEPTUM; TH, TENDINOUS THICKENING THAT BECOMES THE TENDINOUS ARCH OF THE LONGISSIMUS SYSTEM FOR THE ORIGINS OF *M. LONGISSIMUS CERVICIS*; 6, 7, SIXTH AND SEVENTH RIBS; ANT, ANTERIOR. CROSS-HATCHING ON THE DIAPOPHYSES SHOWS ORIGIN OF *M. LONGISSIMUS CAPITIS PROFUNDUS* ON VERTEBRAE 6 AND 7; HORIZONTAL LINES ON NEURAL ARCHES SHOW AREA OF ORIGIN OF *M. LONGISSIMUS CAPITIS SUPERFICIALIS* ON VERTEBRAE 6 AND 7.

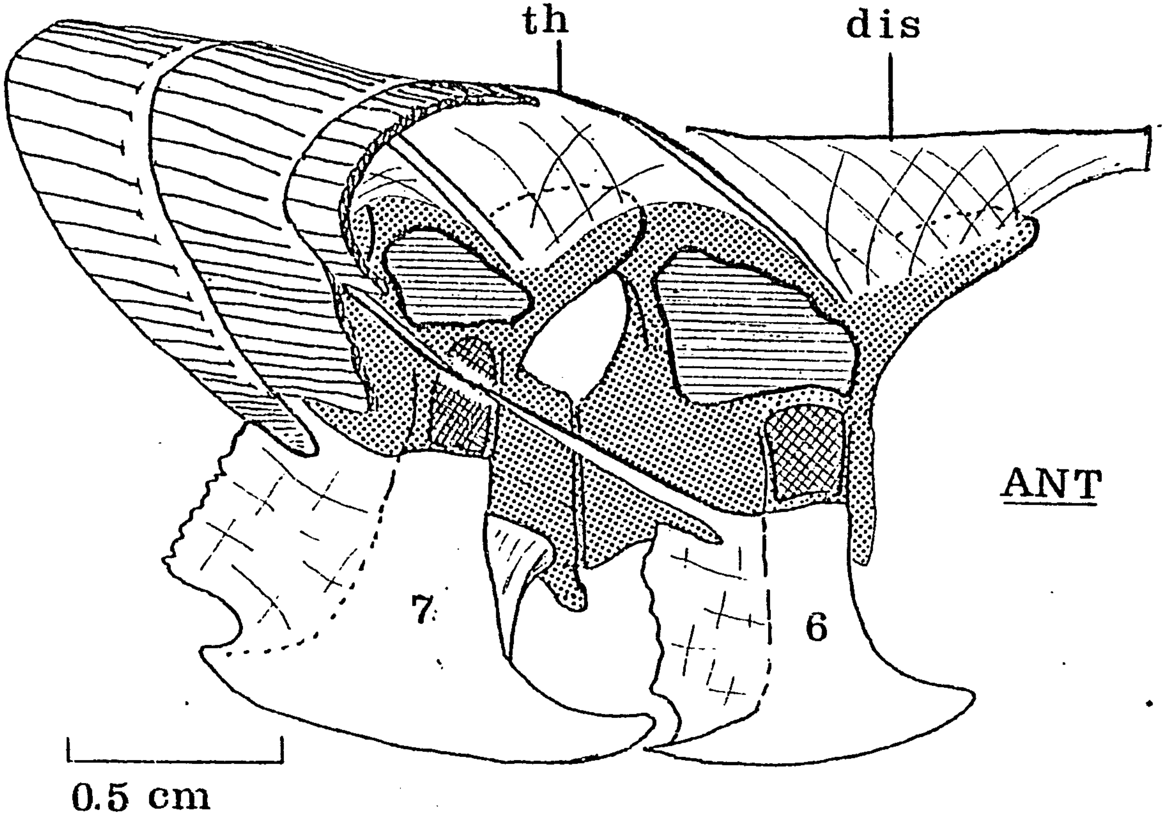


FIG. 46

FIG. 47. ORIGINS OF THE CERVICAL LONGISSIMUS SYSTEM. C-3, C-7, THIRD AND SEVENTH VERTEBRAE; AX, AXIS; D-1, D-2, FIRST AND SECOND DORSAL VERTEBRAE. AREAS WITH HORIZONTAL LINES ARE ORIGINS OF M. LONGISSIMUS CAPITIS PROFUNDUS. AREAS IN BLACK ARE ORIGINS OF M. LONGISSIMUS CAPITIS SUPERFICIALIS. BLACK AREA ON THE TRANSVERSE PROCESS OF D-2 REPRESENTS A VERY SMALL CONTRIBUTION TO M. LONGISSIMUS CAPITIS SUPERFICIALIS BY A BUNDLE OF MUSCLE FIBERS SPLIT FROM M. LONGISSIMUS DORSI.

THIS MAP WAS MADE FROM A JUVENILE SPECIMEN, SKULL LENGTH, 8.58 CM. THE VERTEBRAE WERE DRAWN FROM AN ADULT SPECIMEN.

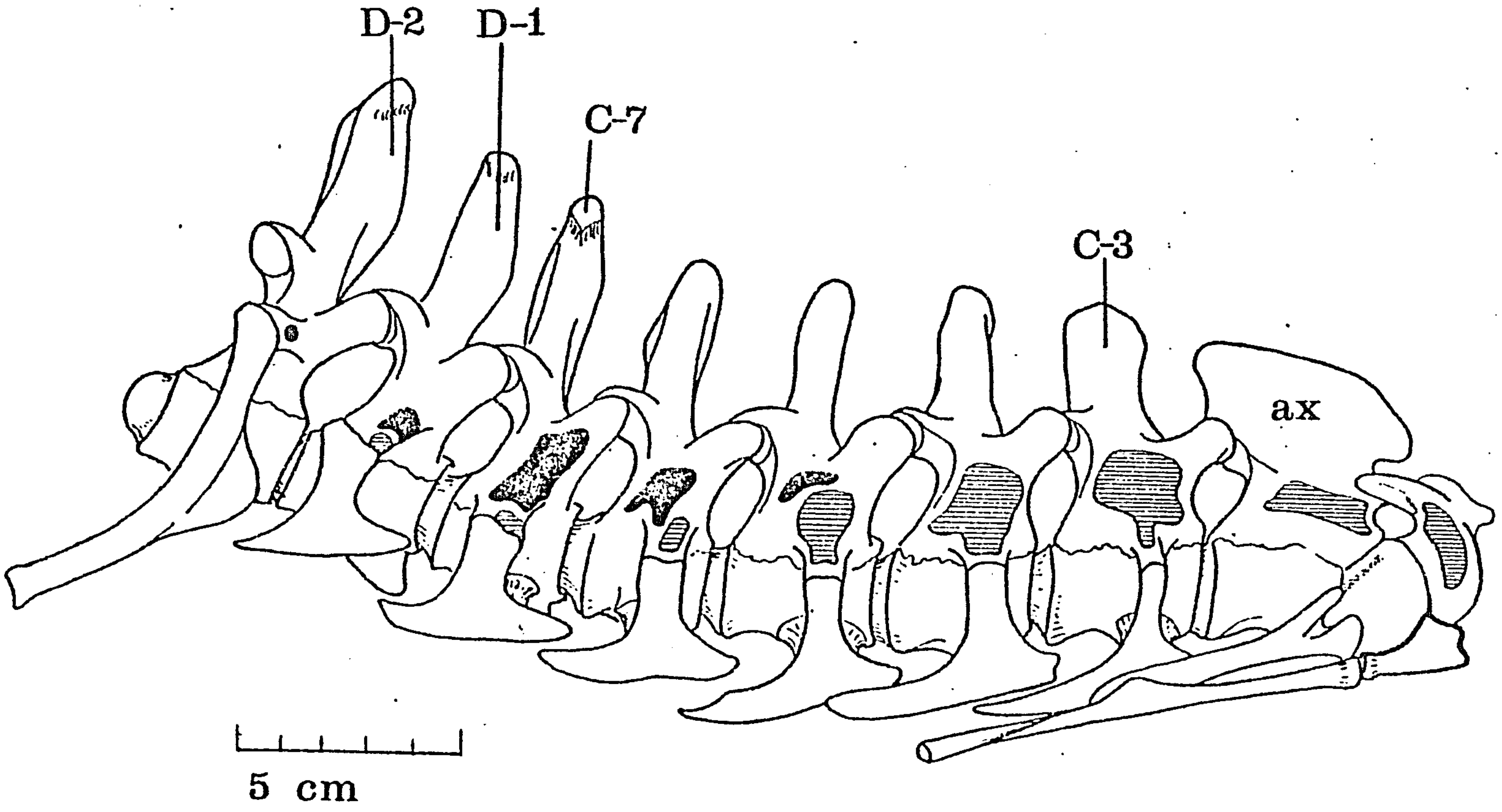


FIG. 47

FIG. 48. NECK MUSCLES, RIGHT LATERAL ASPECT. SKULL HAS BEEN ROTATED AND FLEXED TO BETTER EXPOSE THE OCCIPITAL AREA. THE ROTATION PUTS THE RIGHT QUADRATE (QU) IN A DORSAL POSITION. HEAD FLEXION PLACES THE TIP OF THE SNOUT TO THE LEFT. STIPPLED AREA OF THE SKULL IS FILLED WITH PTERYOID MUSCULATURE. AT, EXPOSED SURFACE OF THE ATLANTAL NEURAL ARCH; IL-C-CAP, M. *ILIO-COSTALIS CAPITIS*, CUT AND REFLECTED VENTRALLY; IL-C-CER-1, TENDON OF THE FIRST SEGMENT OF M. *ILIO-COSTALIS CERVICIS*; INT CAR, INTERNAL CAROTID ARTERY AT POINT OF BIFURCATION; LG-CAP-PROF, M. *LONGISSIMUS CAPITIS PROFUNDUS*; LG-CAP-SUP, M. *LONGISSIMUS CAPITIS SUPERFICIALIS*; L, RIGHT LATERAL EUSTACHIAN TUBE; M-E-M, MEDIAN EUSTACHIAN VALVE; PT, PTERYOID BONE; QU, QUADRATE BONE; R-1, R-4, FIRST AND FOURTH RIBS; SHI, SHINING APONEUROSIS OF M. *LONGISSIMUS CAPITIS PROFUNDUS*; SP-CAP-PO, M. *SPINO-CAPITIS POSTICUS*; TR-SP-CAP, M. *TRANSVERSO-SPINALIS CAPITIS*; U-V-R, EUSTACHIAN VALVE RETRACTOR MUSCLE; XII, TWELFTH CRANIAL NERVE. M. *ILIO-COSTALIS CERVICIS* AND THE ORIGIN OF M. *ILIO-COSTALIS CAPITIS* HAVE BEEN REMOVED. NOT INCLUDED IN THIS FIGURE ARE MM. *LONGISSIMUS CERVICIS* AND *TRANSVERSO-SPINALIS CERVICIS*.

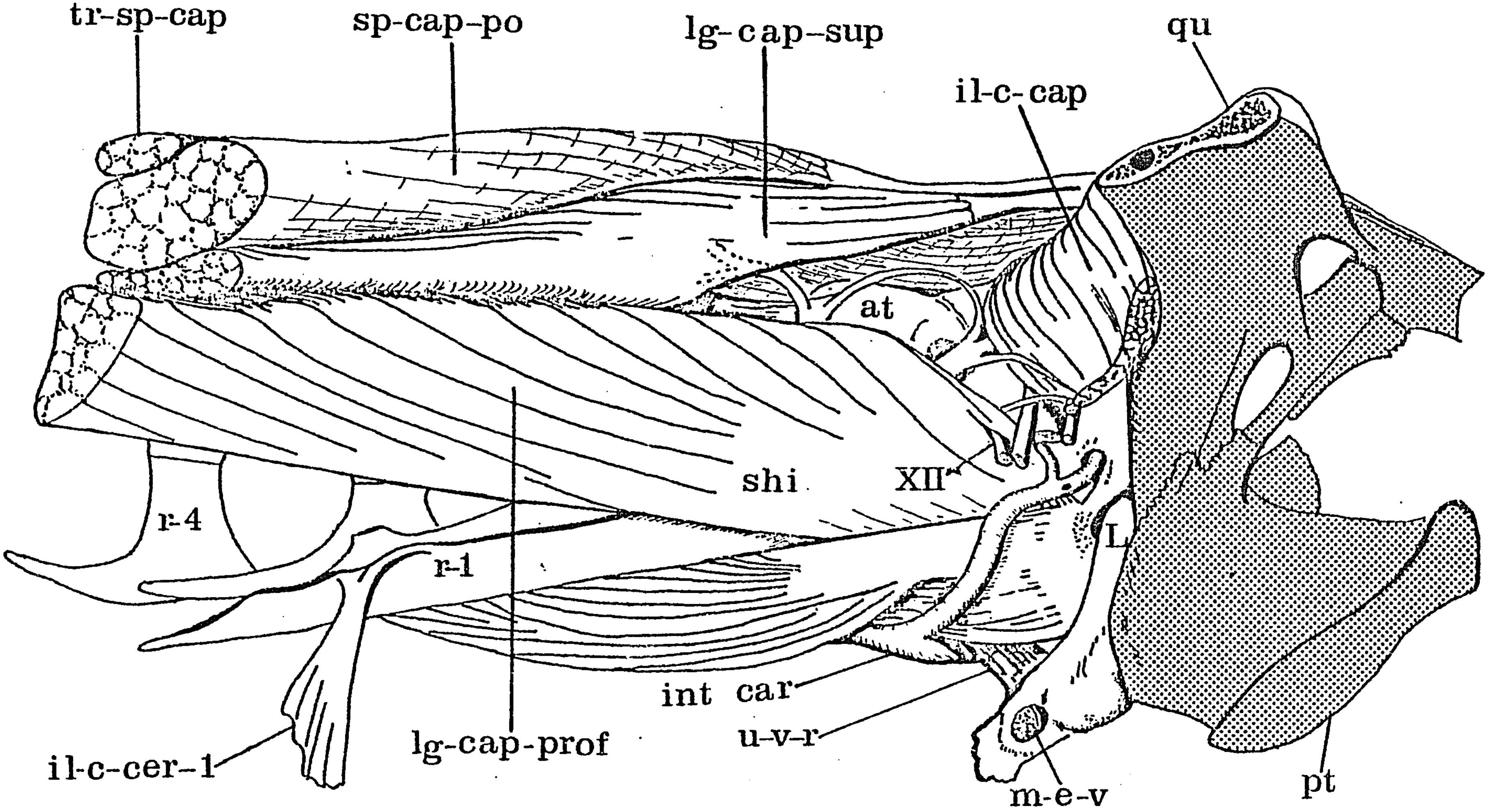
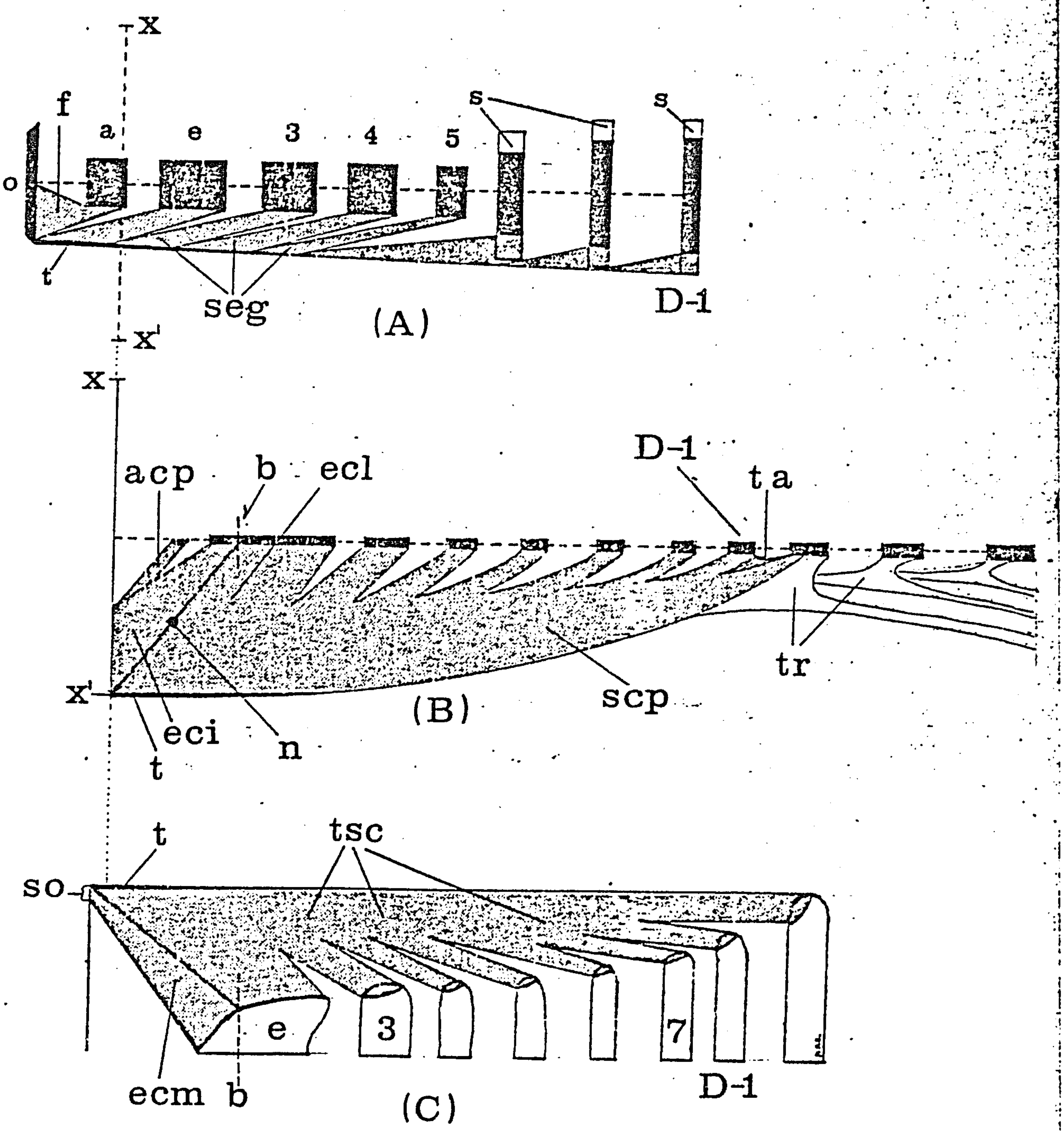

tr-sp-cap
sp-cap-po
lg-cap-sup
qu
il-c-cap
at
XII
shi
L
r-4
r-1
int car
u-v-r
il-c-cer-1
lg-cap-prof
m-e-v
pt

FIG. 48

Fig. 49. (A) Diagram of segmental arrangement of M. longissimus capitis profundus, drawn to proportions taken from an actual specimen (skeleton for fig. 6). Also note that this is anatomically lined up with parts (B) and (C) of this figure. A, neural arch of atlas; D-1, transverse processes of first dorsal vertebra; E, neural arch of epistropheus (axis); F, fleshy portion for insertion on the basioccipital plate; O, occipital surface of basioccipital bone; T, laterally placed tendon of insertion; S, transverse processes; X, X', dotted line represents level of paroccipital processes of exoccipital bones; 3,4,5, neural arches of corresponding cervical vertebrae. Anterior is to the left in this dorsal view.

(B) Diagram similar to (A) for M. spino-capitis posticus. ACP, M. atlanto-capitis profundus; B, bend in axial neural spine; D-1, first dorsal vertebra, neural spine; ECI, M. epistropheo-capitis intermedius; SCP, M. spino-capitis posticus; T, laterally placed tendon of insertion of M. spino-capitis posticus; TA, tendon-arch between neural spines (see figs. 53, 55); TR, tendons of the transverso-spinalis system of the trunk; ECL, M. epistropheo-capitis lateralis; X, X', same as in (A). Anterior is to the left in this dorsal view.

Fig. 49. (C) Diagramatic representation of segmental origin of the neural spine portion of M. transverso-spinalis capitis. Conventions same as for (A) and (B), and it is drawn in alignment with the other diagrams, except this is a lateral view, whereas (A) and (B) are dorsal views. Anterior is to the left. B, bend of axial neural spine; E, axial neural spine; ECM, M. epistropheo-capitis medialis; D-1, first dorsal vertebral neural spine; SO, supra-occipital portion of insertion of muscles shown; T, dorsal tendon of insertion of M. transverso-spinalis capitis; TSC, M. transverso-spinalis capitis; 3,7, third and seventh cervical neural spines.


x
f
a
e
3
4
5
s
s
o
t
seg
(A)
D-1
x'
x
acp
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ecl
D-1
t a
tr
scp
x'
(B)
eci
n
t
t
tsc
so
e
3
7
ecm
b
(C)
D-1

FIG. 49

FIG. 50. SEMI-DIAGRAMATIC REPRESENTATION OF TRANSITION OF TRANSVERSO-SPINALIS OF THE TRUNK TO THAT OF THE CERVICAL REGION. ANTERIOR IS TO THE LEFT. AS, TENDON OF M. ARTICULO-SPINALIS; BR, BREAK IN CONTINUITY OF MUSCLES IN ORDER TO SHOW RELATION OF MORE POSTERIOR MUSCLES TO THE FINAL INSERTION ON THE POSTZYGAPOPHYSIS OF THE ATLAS; LC, M. LONGISSIMUS CAPITIS CERVICIS WHICH IS DEEP AND VENTRAL TO THE CERVICAL TRANSVERSO-SPINALIS MUSCLES; NS, TENDONS OF M. NEURO-SPINALIS; P, POSTZYGAPOPHYSIS OF ATLAS; SA, TENDONS OF M. SPINO-ARTICULARIS DORSI; D-3, THIRD DORSAL NEURAL SPINE; TA, TENDON OF M. TENDINO-ARTICULARIS DORSI; TSC, M. TRANSVERSO-SPINALIS CERVICIS; TA + AS, CONJOINED MM. TENDINO-ARTICULARIS DORSI AND ARTICULO-SPINALIS DORSI; SA + NS, CONJOINED MM. SPINO-ARTICULARIS DORSI AND NEURO-SPINALIS DORSI.

NOTE THAT ULTIMATELY, ALL FOUR OF THE TRANSVERSO-SPINALIS SYSTEM MUSCLES UNITE INTO THE CERVICAL PORTIONS. THE ARCHING (AS) TENDONS SERVE AS EXTRA-VERTEBRAL ORIGINS FOR M. SPINO-CAPITIS POSTICUS.

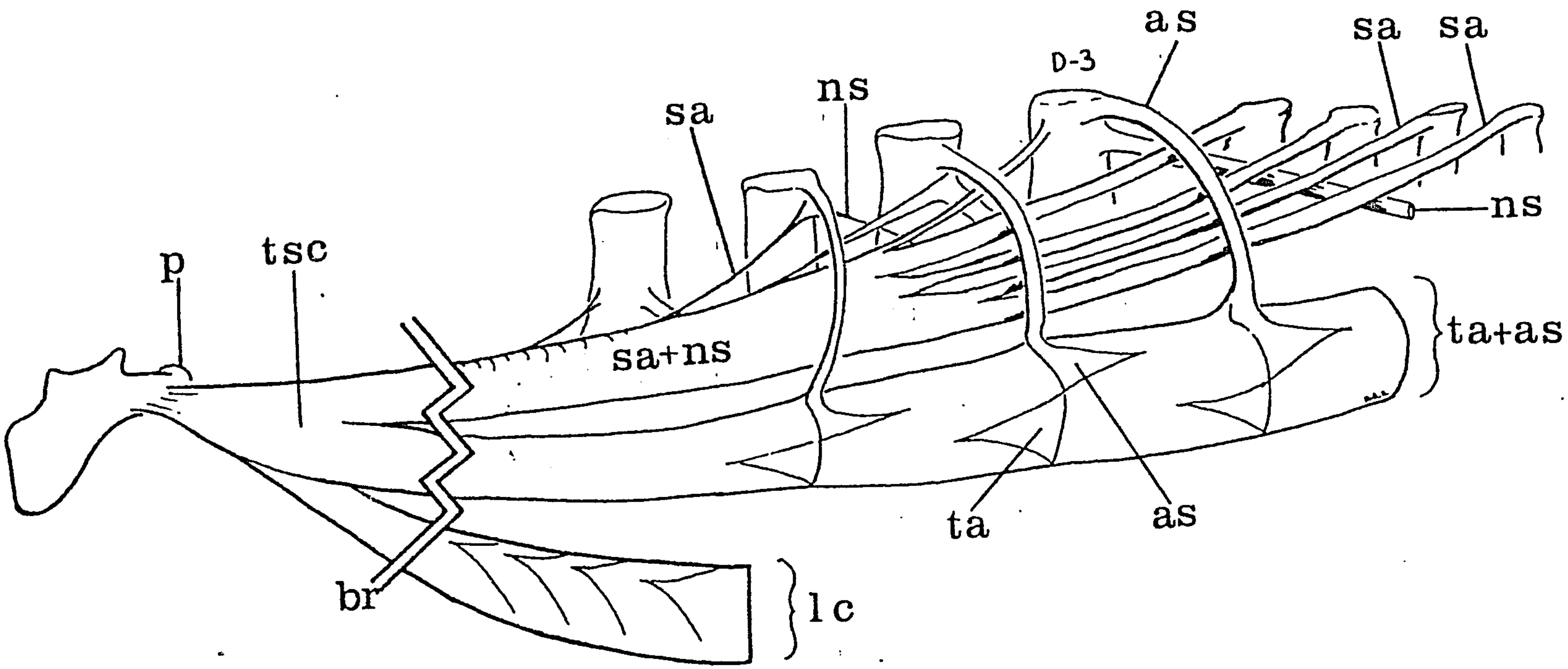

FIG. 50

FIG. 51. LEFT LATERAL VIEW OF CERVICAL EPAXIAL MUSCLES, WITH A DIAGRAMATIC CROSS SECTION AT THE LEVEL OF THE FIFTH CERVICAL VERTEBRA. DIS, DORSAL INTERMUSCULAR SEPTUM. NOTE THAT IT BLENDS LATERALLY WITH THE SUPERFICIAL FASCIAL COVERING OF THE MUSCULATURE; IC, M. ILIO-COSTALIS DORSI; LC, POSTERIOR SECTION OF M. LONGISSIMUS CERVICIS; N, TIP OF FIFTH NEURAL SPINE, WHERE INSERTION OF SPINOUS PART OF M. TRANSVERSO-SPINALIS CAPITIS HAS BEEN REMOVED; P, BELLY OF M. LONGISSIMUS CAPITIS PROFUNDUS; S, M. LONGISSIMUS CAPITIS SUPERFICIALIS; SCP, M. SPINO-CAPITIS POSTICUS; TSC, M. TRANSVERSO-SPINALIS CERVICIS. HOOK WITH ARROW IS LIFTING LATERAL EDGE OF (SCP) FOR A VIEW OF (TSC) AND (LC) THAT ARE USUALLY COVERED.

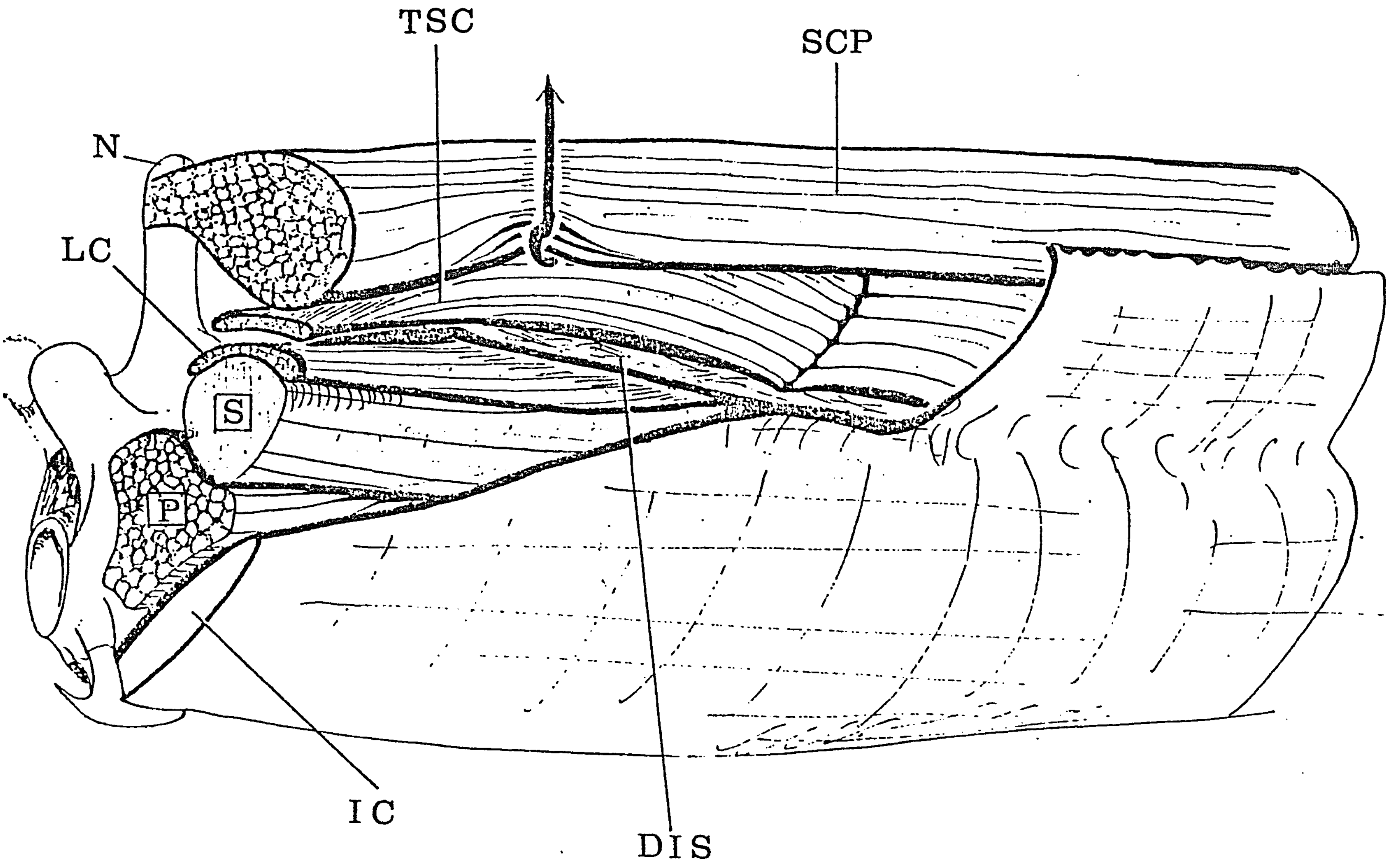

FIG. 51

FIG. 52. RIGHT LATERAL VIEW OF VERTEBRAL COLUMN TO SHOW CONTINUITY OF CERVICAL AND DORSAL TRANSVERSO-SPINALIS SYSTEM MUSCLES, AND RELATION TO CERVICAL LONGISSIMUS MUSCLES. A, NEURAL ARCH OF ATLAS; AX, NEURAL SPINE OF AXIS; C, ANTERIOR SEGMENT OF *M. LONGISSIMUS CERVICIS* (NOTE ORIGIN FROM TENDINOUS ARCH ATTACHED TO 5TH VERTEBRA); O, ATLANTAL HYPOCENTRUM; TSC, *M. TRANSVERSO-SPINALIS CERVICIS*; A, COMBINED *MM. SPINO-ARTICULARIS DORSI* AND *NEUROSPINALIS DORSI*; B, COMBINED *MM. TENDINO-ARTICULARIS DORSI* AND *ARTICULO-SPINALIS DORSI*; D-1, FIRST DORSAL VERTEBRA.

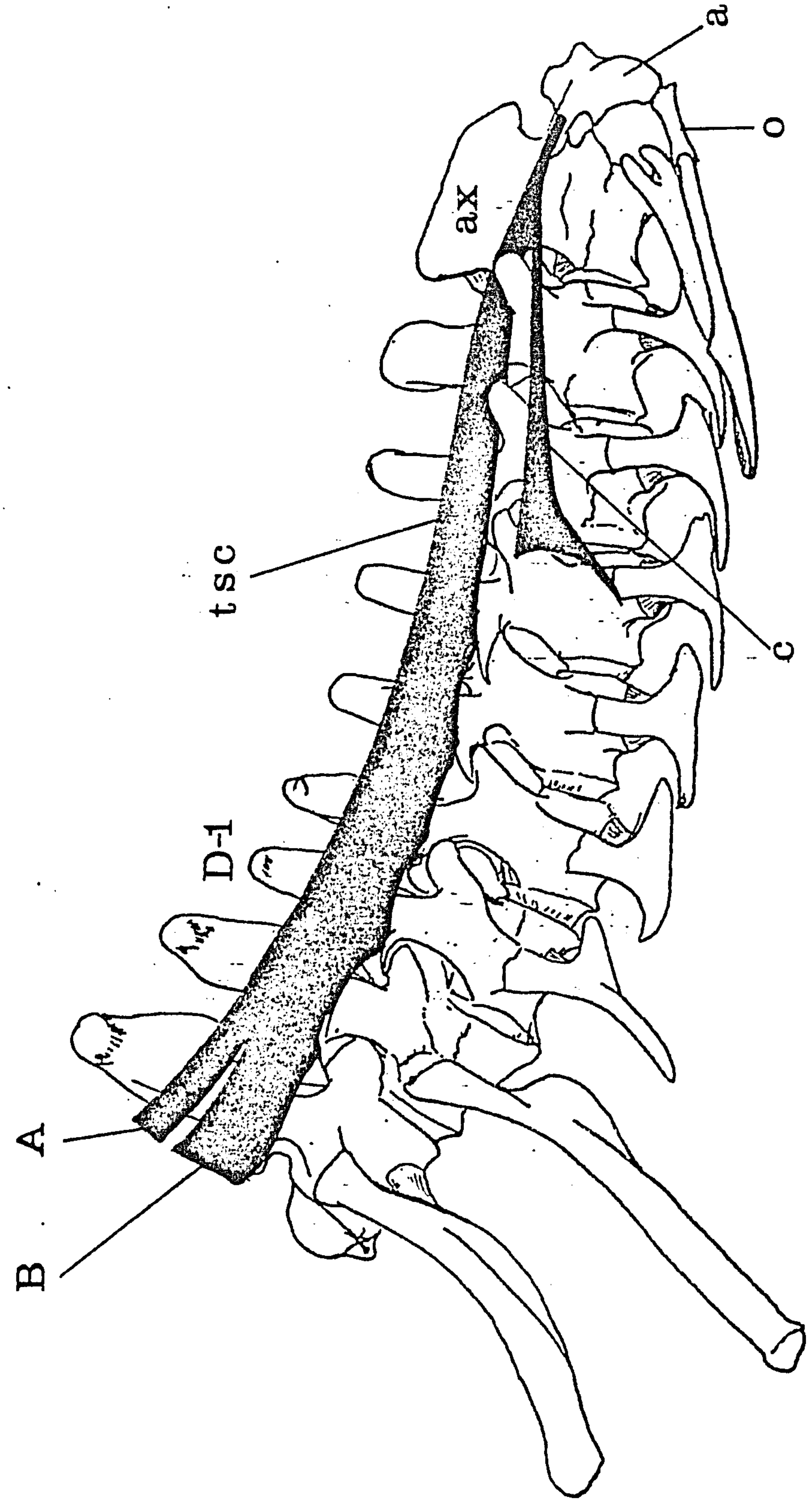

FIG. 52

FIG. 53. LEFT LATERAL VIEW (ANTERIOR TO THE LEFT) OF COMPLEX *M. TRANSVERSO-SPINALIS CERVICIS*. D, LIGAMENTUM NUCHAE; DMA, DORSAL MEDIAN ARTERY; FA, FASCIA THAT ARCHES OVER THIS MUSCLE AND FORMS A LATERAL ORIGIN FOR *MM. TRANSVERSO-SPINALIS CAPITIS* AND *SPINO-CAPITIS POSTICUS*; L, LATERAL PORTIONS OF *M. TRANSVERSO-SPINALIS CERVICIS*; M, MEDIAL SLIPS OF *M. TRANSVERSO-SPINALIS CERVICIS* THAT ARE CONTINUOUS WITH THE TRUNK NEURO-SPINALIS SYSTEM; T, TENDINOUS ARCH BETWEEN VERTEBRAE(SEE FIG. 55).

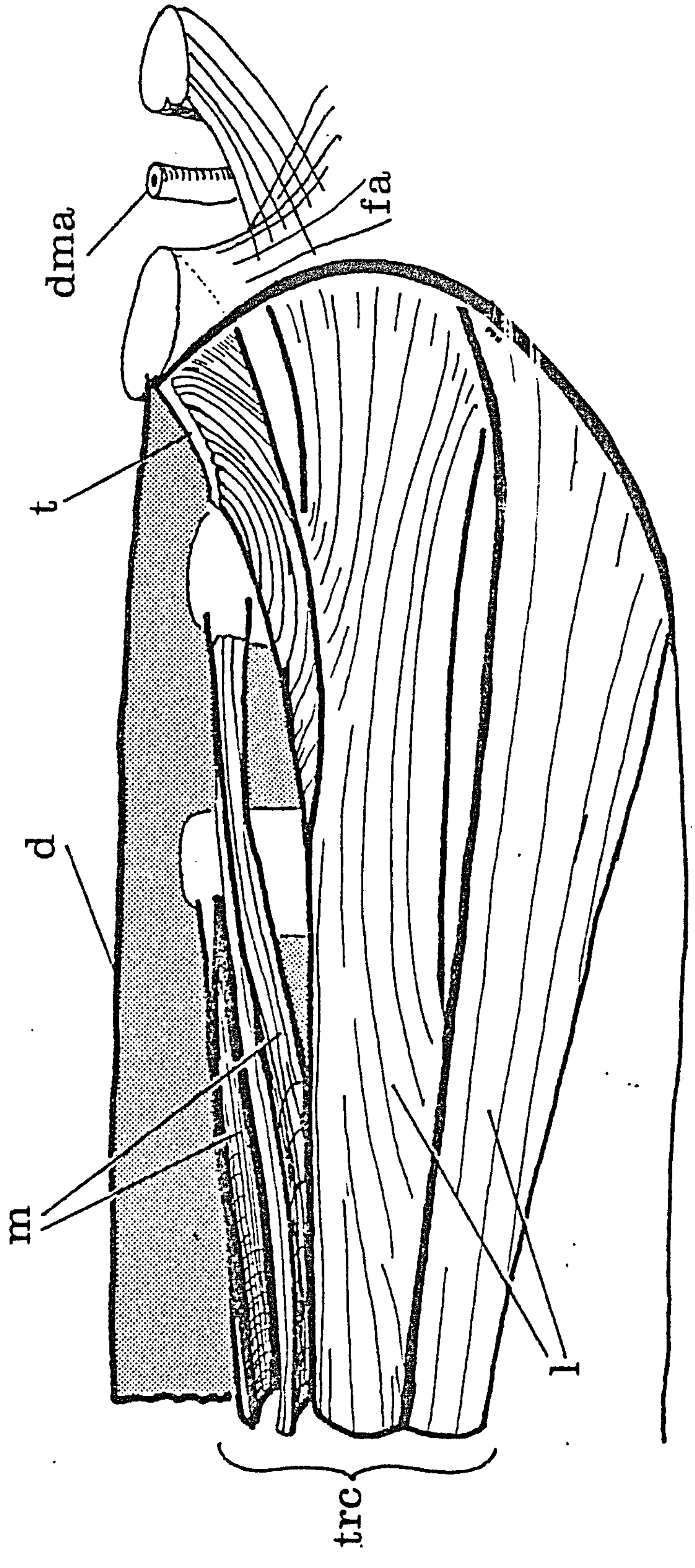

FIG. 53

FIG. 54. RELATION OF THE ORIGIN OF M. TRANSVERSO-SPINALIS CERVICIS TO THE LONGISSIMUS SYSTEM. DRG, DORSAL ROOT GANGLION; LD, MUSCLE FIBERS OF FIRST SEGMENT OF M. LONGISSIMUS DORSI; LF, POSTERIOR-MOST FIBERS LEFT INSIDE "CONE" OF THE FIRST SEGMENT OF M. LONGISSIMUS DORSI; LT, LONGISSIMUS TENDON 7; SCP, M. SPINO-CAPITIS POSTICUS; TR-CERV, VERTICAL SHEETS FORMING POSTERIOR PART OF M. TRANSVERSO-SPINALIS CERVICIS; VR, VENTRAL RAMUS OF SEVENTH CERVICAL SPINAL NERVE EXTENDING DEEP TO TRANSVERSE PROCESS; X, PORTIONS OF LONGISSIMUS TENDONS THAT EXTEND POSTERIORLY AND FORM INCIPIENT CONES. FURTHER POSTERIOR IN THE TRUNK THESE FORM THE MEDIAL PARTS OF COMPLETE CONES (THE PORTION ASSOCIATED WITH THE DORSAL INTERMUSCULAR SEPTUM). ANTERIOR IS TO THE RIGHT.

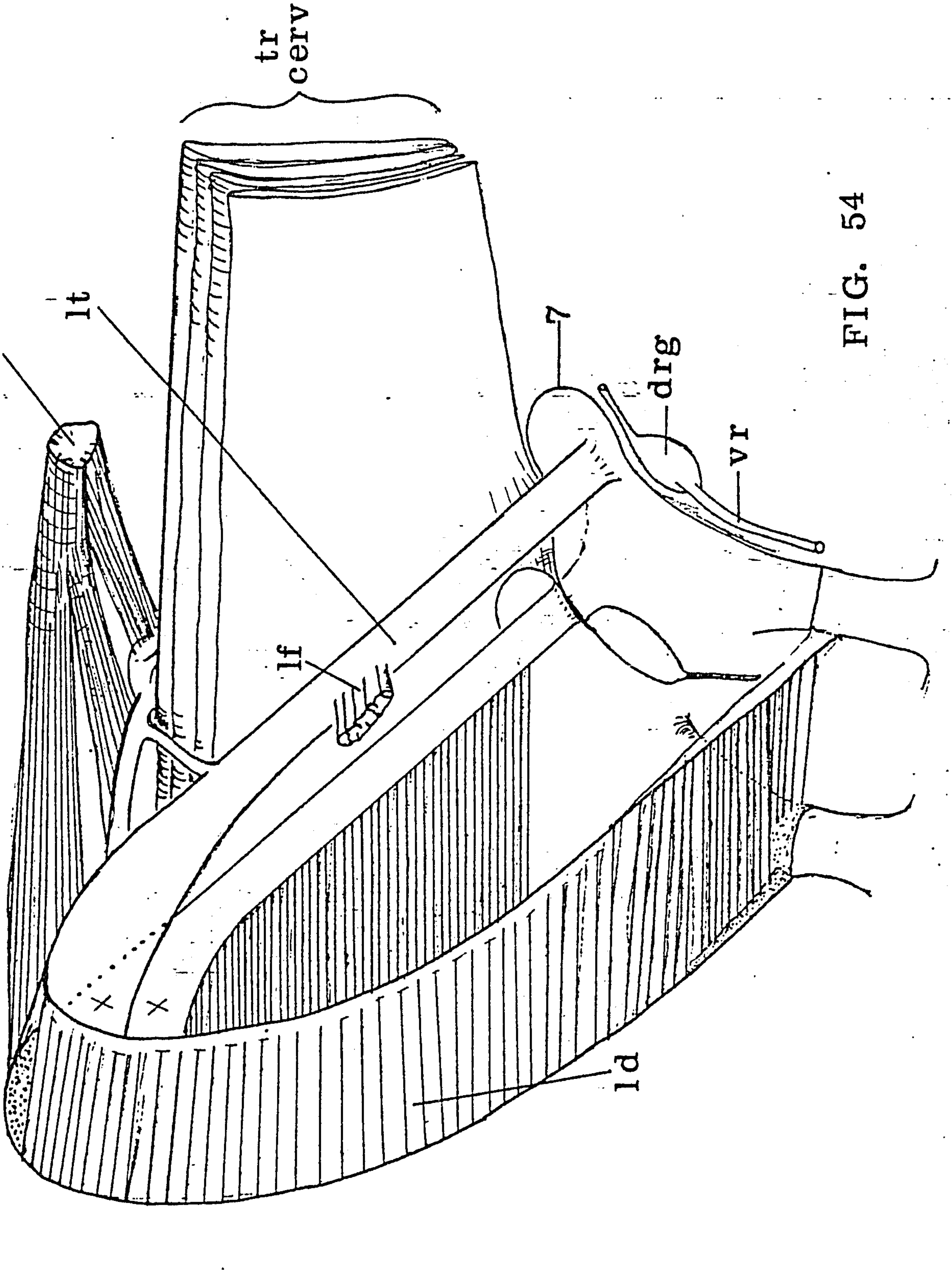

FIG. 54

FIG. 55. ORIGINS OF M. TRANSVERSO-SPINALIS CAPITIS AND M. SPINO-CAPITIS POSTICUS. ANTERIOR IS TO THE LEFT. DIS, CROSS-HATCHING REPRESENTS DORSAL INTERMUSCULAR SEPTUM; SP-CAP-POST, FOUR BUNDLES OF M. SPINO-CAPITIS POSTICUS; TR-SP-CAP, FIVE BUNDLES OF M. TRANSVERSO-SPINALIS CAPITIS. NOTE THE LARGE SIZE OF BUNDLE THAT ORIGINATES FROM (DIS); 8,9,10, TIPS OF VERTEBRAE D-1, D-2, D-3. COARSE STIPPLING IS BONE OF NEURAL SPINES, FINE STIPPLING IS A FASCIAL SHEET CONNECTING SEGMENTAL TENDINOUS ARCHES AND PROVIDING ORIGIN FOR M. SPINO-CAPITIS POSTICUS.

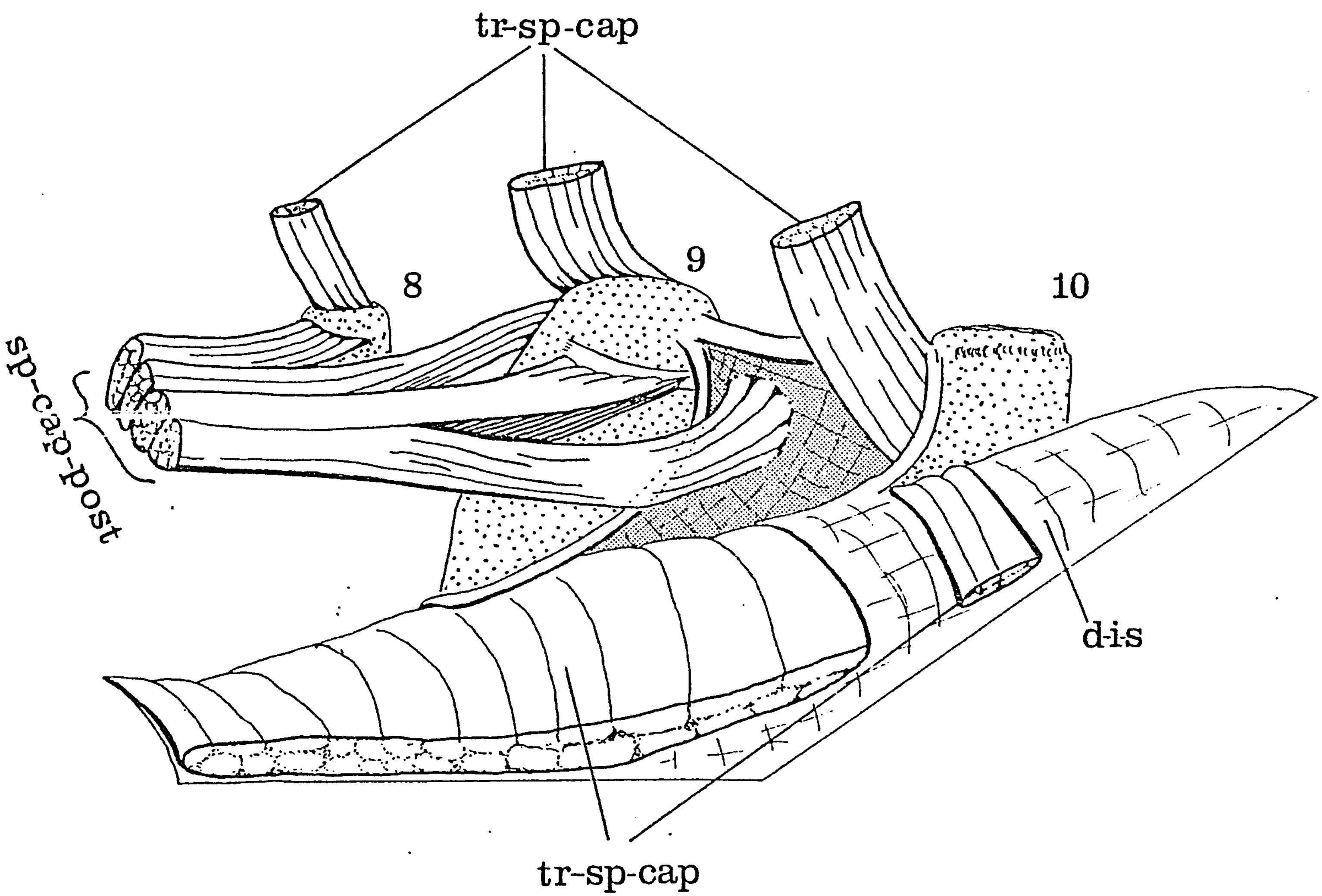

FIG. 55

FIG. 56. DIAGRAM TO SHOW TRANSITION OF TRUNK ARTICULO-SPINALIS TENDONS TO TENDINOUS ORIGIN FOR LATERAL PART OF M. TRANSVERSO-SPINALIS CAPITIS. ANTERIOR IS TO THE RIGHT. AS, ARTICULO-SPINALIS TENDON THAT IS CONNECTED TO NEURAL SPINE TIP MEDIALLY, AND FASCIA (PLUS DORSAL INTERMUSCULAR SEPTUM) LATERALLY; FA, CONNECTION OF ARTICULO-SPINALIS TENDON TO SHOULDER FASCIA; NS, TENDON OF M. NEURO-SPINALIS (IN BLACK); SA, TENDON OF M. ARTICULO-SPINALIS; TR-S-C, PART OF LATERAL ORIGIN OF M. TRANSVERSO-SPINALIS CAPITIS THAT IS IN SERIES WITH (FA); X, ARTICULO-SPINALIS TENDON ATTACHMENT TO NEURAL SPINE TIP; D-4,D-5,D-6, CORRESPONDING TIPS OF NEURAL SPINES OF DORSAL VERTEBRAE 4 TO 6. NOTE THE D-4 TIP IS FLATTENED ANTERO-POSTERIORLY, AND THAT D-6 AND D-5 ARE BIFID.

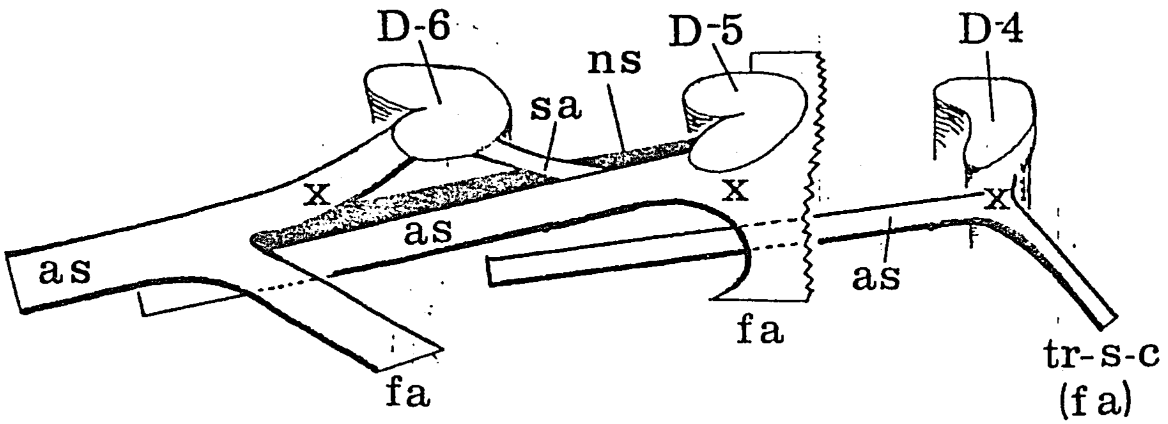

FIG. 56

FIG. 57. ORIGIN OF TRIANGULAR SHEETS OF M. TRANSVERSO-SPINALIS CERVICIS. THE DORSAL INTERMUSCULAR SEPTUM (DIS) HAS BEEN REFLECTED VENTRALLY. ANTERIOR IS TO THE RIGHT IN THIS RIGHT LATERAL VIEW; BONE IS STIPPLED. CAP, CAPSULE OF OCCIPITAL JOINT; DIS, DORSAL INTERMUSCULAR SEPTUM; LC, M. LONGISSIMUS CERVICIS WHICH IS LATERAL AND VENTRAL TO DORSAL INTERMUSCULAR SEPTUM; LCA, M. LONGISSIMUS CAPITIS SHOWN AT ITS INSERTION ON THE PAROCCIPITAL PROCESS; LF, FIBERS OF LONGISSIMUS CERVICIS ATTACHING TO LONGISSIMUS TENDON 7; ILC; INSERTION PART OF M. ILIO-COSTALIS CAPITIS; PA, PRO-ATLAS; PT, LATERAL EDGE OF PTERYGOID BONE; SCP, M. SPINO-CAPITIS POSTICUS; T, TENDON OF (SCP) AT INSERTION ON PAROCCIPITAL PROCESS; TC, TRIANGULAR SEGMENT OF M. TRANSVERSO-SPINALIS CERVICIS ORIGINATING FROM MEDIAL SURFACE OF TENDINOUS THICKENING IN DORSAL INTERMUSCULAR SEPTUM AND INSERTING ON THE THIRD POSTZYGAPOPHYSIS; TSC, TRIANGULAR SHEET OF M. TRANSVERSO-SPINALIS CERVICIS THAT ORIGINATES FROM TENDON 6 OF THE LONGISSIMUS SYSTEM (T-6) AND INSERTS ON THE ATLANTAL POSTZYGAPOPHYSIS; TR, M. TRANSVERSO-SPINALIS CAPITIS. 4,5,6,7, CORRESPONDING PREZYGAPOPHYSES.

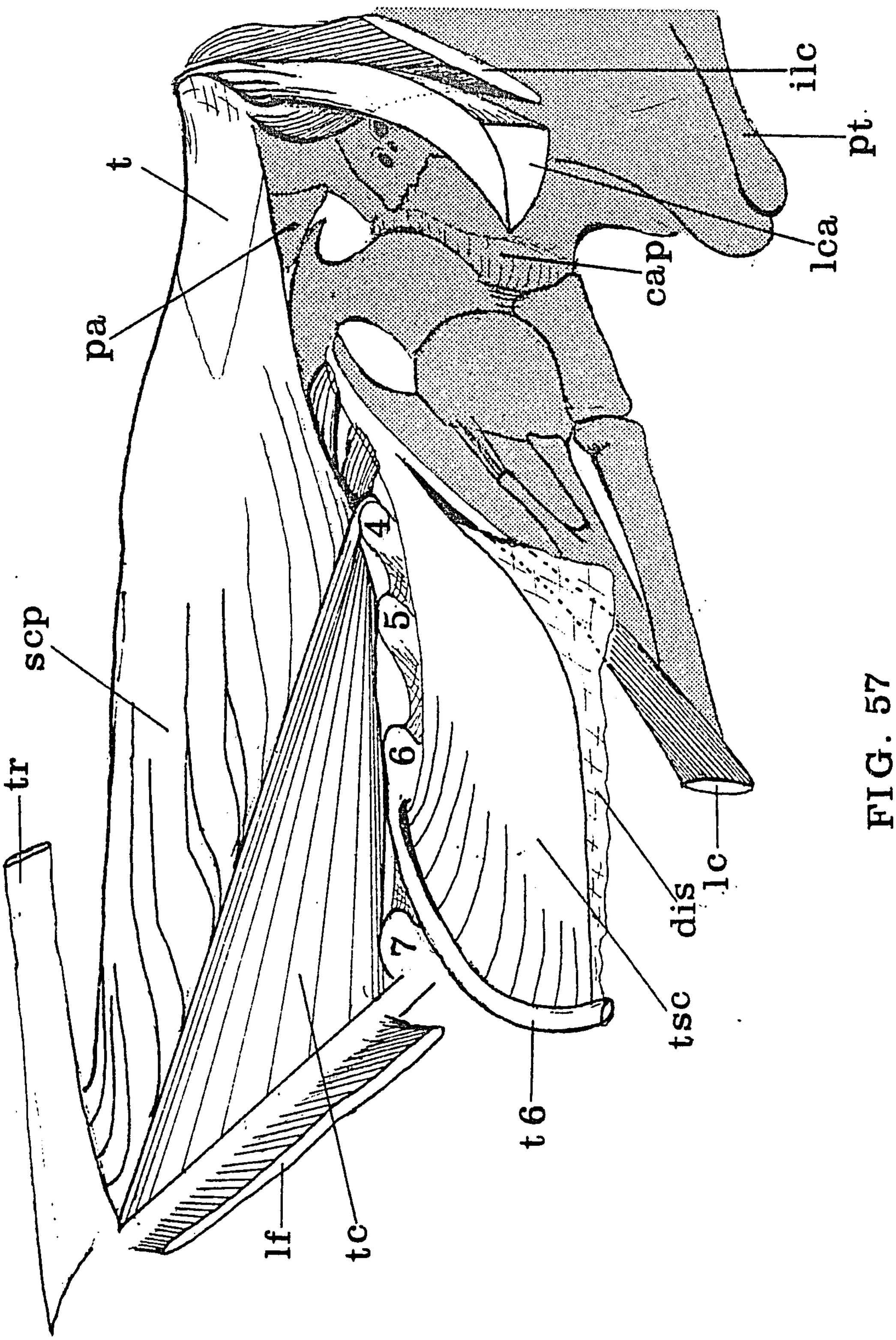

FIG. 57

FIG. 58. ANTERIOR PORTION OF COMPLEX M. TRANSVERSO-SPINALIS CERVICIS. ANTERIOR IS TO THE LEFT. D, DORSAL INTERMUSCULAR SEPTUM; PO3, THIRD POSTZYGAPOPHYSIS; PZ6, SIXTH PREZYGAPOPHYSIS; SA, MINOR SLIPS OF DEEPLY PLACED SPINO-ARTICULAR MUSCLE FIBERS THAT JOIN M. TRANSVERSO-SPINALIS CERVICIS MEDIALLY; NOTE THAT THOSE ORIGINATING FROM NEURAL SPINES 5,6, AND 7 INSERT ON POSTZYGAPOPHYSIS 3; TA, TENDON SIMILAR TO (SA) THAT INSERTS ON THE ATLAS; TC, M. TRANSVERSO-SPINALIS CERVICIS; T-6, SIXTH TENDINOUS THICKENING IN THE DORSAL INTERMUSCULAR SEPTUM THAT SERVE AS ORIGINS FOR LATERAL SHEETS OF M. TRANSVERSO-SPINALIS CERVICIS (Y), AND (X), AND IN POSTERIOR SEGMENTS THIS SAME TENDON ALSO SERVES AS ORIGIN FOR M. SPINO-CAPITIS POSTICUS; X, M. TRANSVERSO-SPINALIS CERVICIS THAT INSERTS ON THE ATLANTAL POSTZYGAPOPHYSIS. THIS PART IS FORMED BY DORSALLY PLACED SHEETS OF THE TENDINOUS THICKENINGS IN DORSAL INTERMUSCULAR SEPTUM. Y, SHEETS SIMILAR TO X, EXCEPT THAT IT ORIGINATES MORE VENTRALLY FROM THE TENDON. 4,5,6, NEURAL SPINES OF CORRESPONDING VERTEBRAE. Z, Z', INTERARTICULAR MUSCLES, FROM POST- TO POST-ZYGAPOPHYSES.

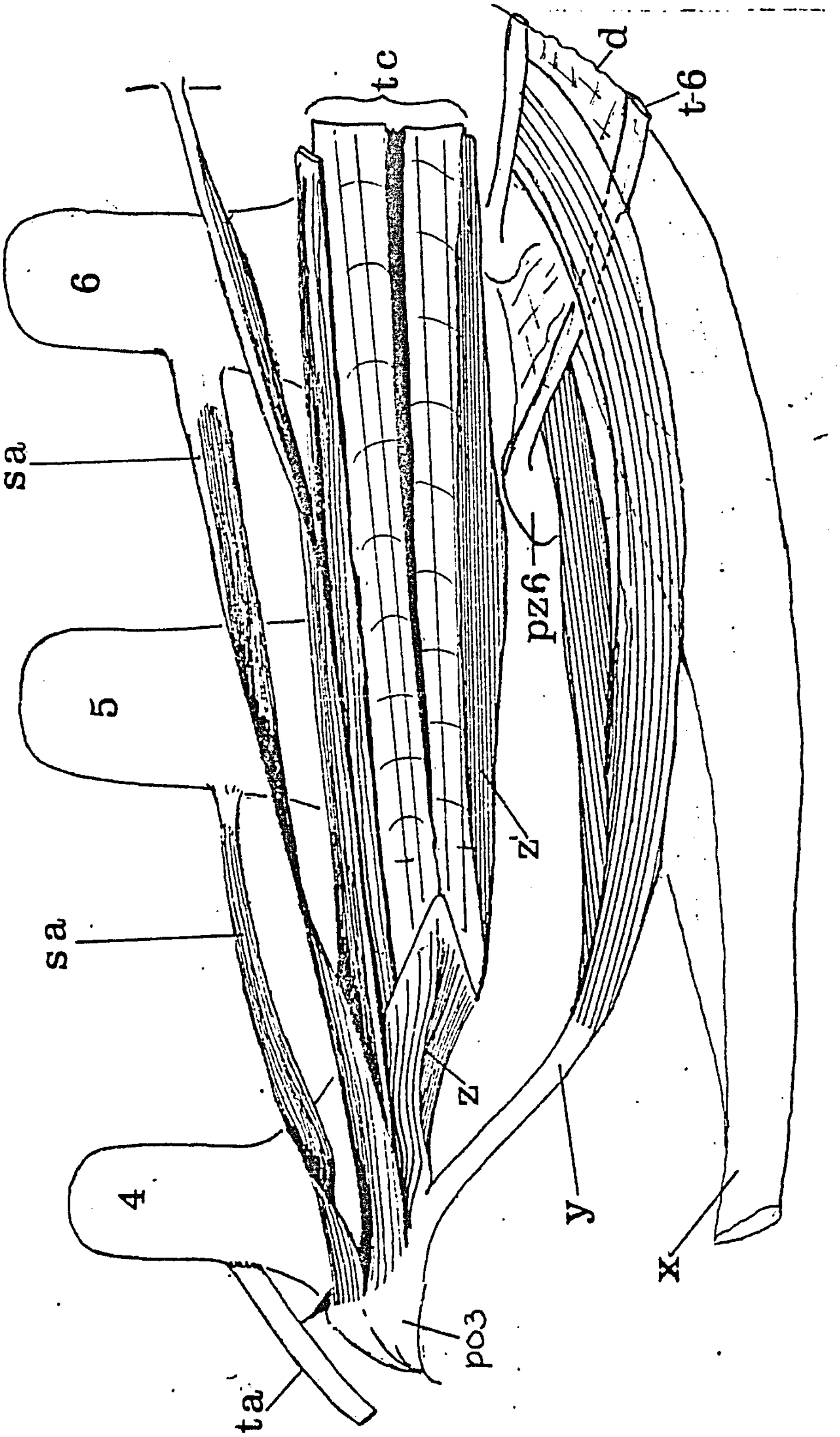

FIG. 58

FIG. 59. MEDIAL MOST PORTION OF CERVICAL TRANSVERSO-SPINALIS SYSTEM. ANTERIOR IS TO THE LEFT, BONE IS STIPPLED. A, SPINO-ARTICULAR MUSCLE SLIPS; I, *M. INTER-NEURALIS CERVICIS*; N, SLIPS OF NEURO-SPINALIS SYSTEM; X, DEEP SLIP THAT INSERTS ON THE BASE OF THE THIRD NEURAL SPINE; C-7, SEVENTH NEURAL SPINE; D-1, FIRST DORSAL NEURAL SPINE.

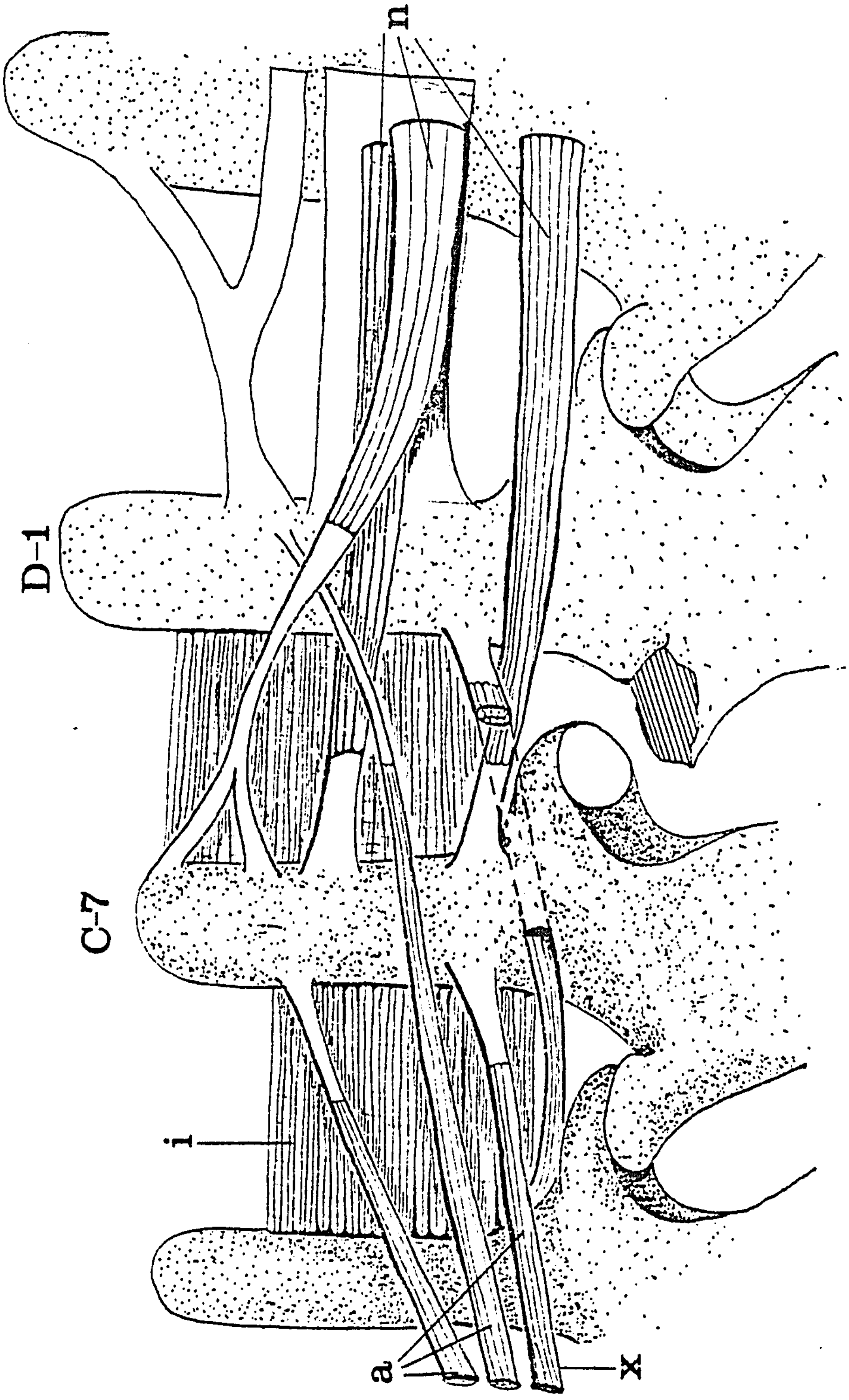

FIG. 59

FIG. 60. DIAGRAM TO ILLUSTRATE PROTRACTION OF ATLANTAL RING. AT, NEURAL ARCH OF ATLAS; AX, NEURAL ARCH OF AXIS; HY, ATLANTAL HYPOCENTRUM; R-1, FIRST RIB; OC, OCCIPITAL CONDYLE; OD, ODONTOID; TEN, TENSION PRODUCED BY MM. TRANSVERSO-SPINALIS CERVICIS AND LONGISSIMUS CERVICIS; ARROWS DENOTE TRAIN OF TENSION THAT PULLS ATLANTAL RING (AT AND HY) UP ON TO SHOULDERS OF THE ODONTOID TO REST IN THE SAGITTAL GROVES.

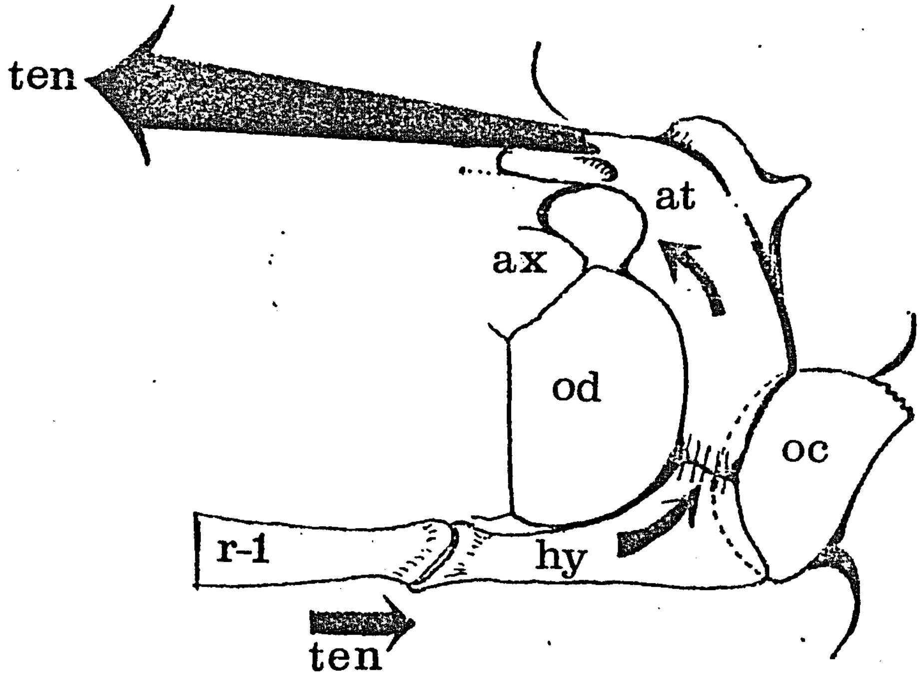

FIG. 60

FIG. 61. RIGHT LATERAL VIEW OF FIRST FIVE CERVICAL VERTEBRAE. STIPPLING SHOWS ORIGIN ON NEURAL ARCHES OF M. LONGISSIMUS CAPITIS PROFUNDUS.

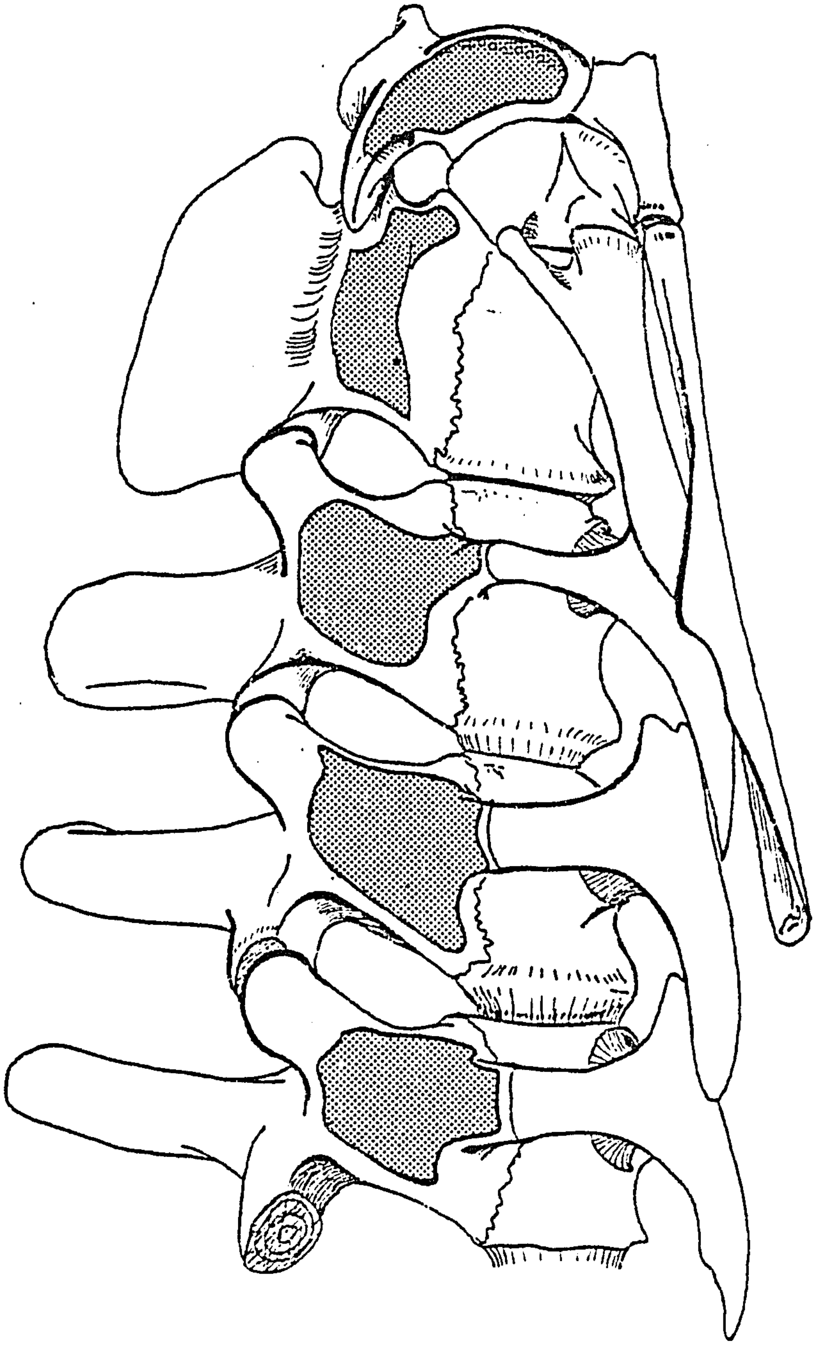

FIG. 61

FIG. 62. SUPERFICIAL DISSECTION OF NECK OF *A. MISSISSIPPIENSIS*, DORSAL VIEW. D-3, TIP OF THIRD DORSAL NEURAL SPINE, COVERED BY SHOULDER FASCIA; ILC, *M. ILIO-COSTALIS CERVICIS*; LCS, *M. LONGISSIMUS CAPITIS SUPERFICIALIS*; SCA, OUTLINE OF SCAPULA THROUGH SHOULDER FASCIA; SCP, *M. SPINO-CAPITIS POSTICUS*; TRA, LATERAL ORIGIN OF *M. TRANSVERSO-SPINALIS CAPITIS* FROM SHOULDER FASCIA (NOTE FASCIAL SEPTA IN MUSCLE); TRB, INSERTION TENDON OF *M. TRANSVERSO-SPINALIS CAPITIS*. MUSCLES AND SKULL WERE DRAWN WITH ATTENTION GIVEN TO MAINTAINING CORRECT PROPORTIONS.

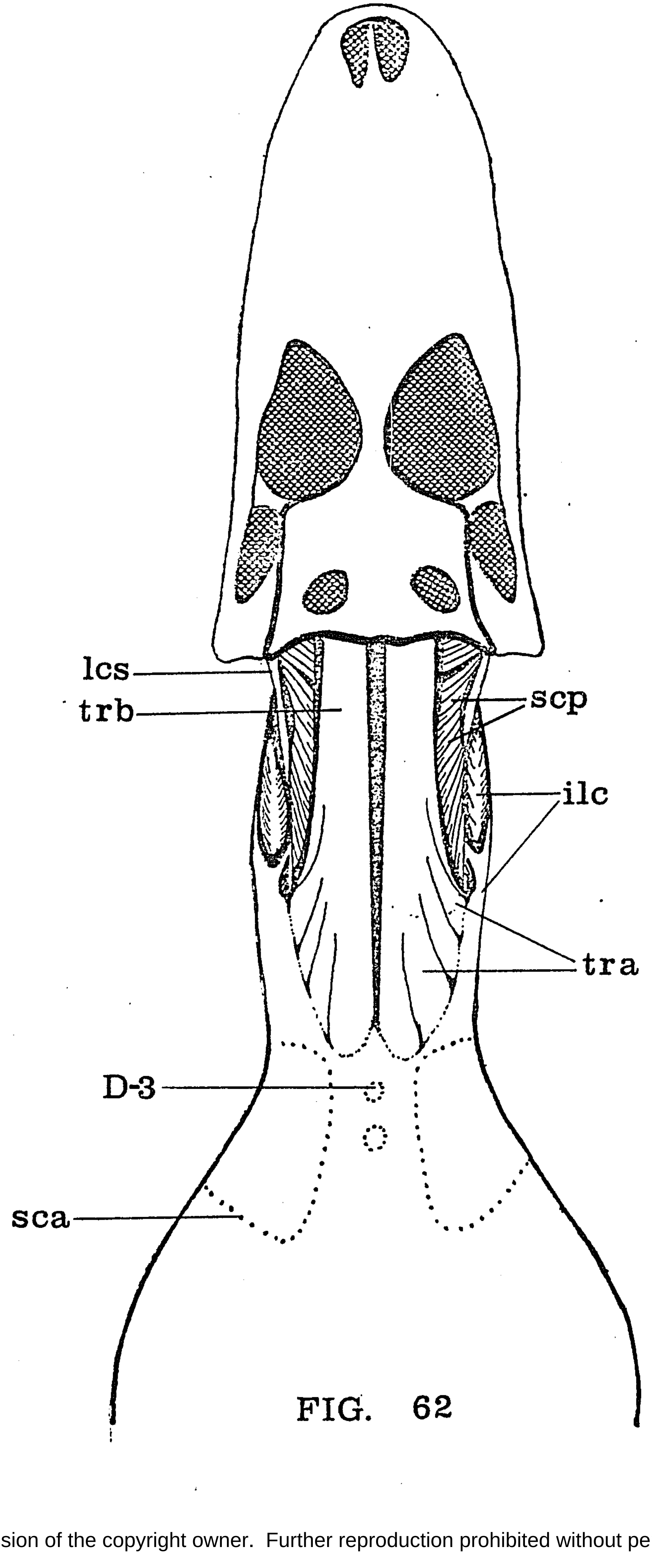

FIG. 62

FIG. 63. SAME AS IN FIGURE 62, EXCEPT THAT IT IS A DEEPER DISSECTION. NOTE THAT M. TRANSVERSO-SPINALIS CAPITIS HAS BEEN COMPLETELY REMOVED FROM THE RIGHT SIDE, AND CUT THROUGH ITS INSERTION TENDON ON THE LEFT SIDE. THE STIPPLING ON THE TRUNK AND BASE OF THE NECK REPRESENTS THE DEEP FASCIA THAT HAS NOT BEEN REMOVED. THE PROPORTIONS OF MUSCLES WITH RESPECT TO THE SKULL HAVE BEEN PRESERVED. C-7, SEVENTH CERVICAL VERTEBRAL NEURAL SPINE TIP; EC, M. EPISTROPHEO-CAPITIS MEDIALIS; ECI, M. EPISTROPHEO-CAPITIS INTERMEDIUS; ECL, M. EPISTROPHEO-CAPITIS LATERALIS; D-1, TIP OF NEURAL SPINE OF FIRST DORSAL VERTEBRA; SCP, M. SPINO-CAPITIS POSTICUS; TRC, M. TRANSVERSO-SPINALIS CAPITIS, REFLECTED TO SHOW ITS MAJOR NERVE SUPPLY.

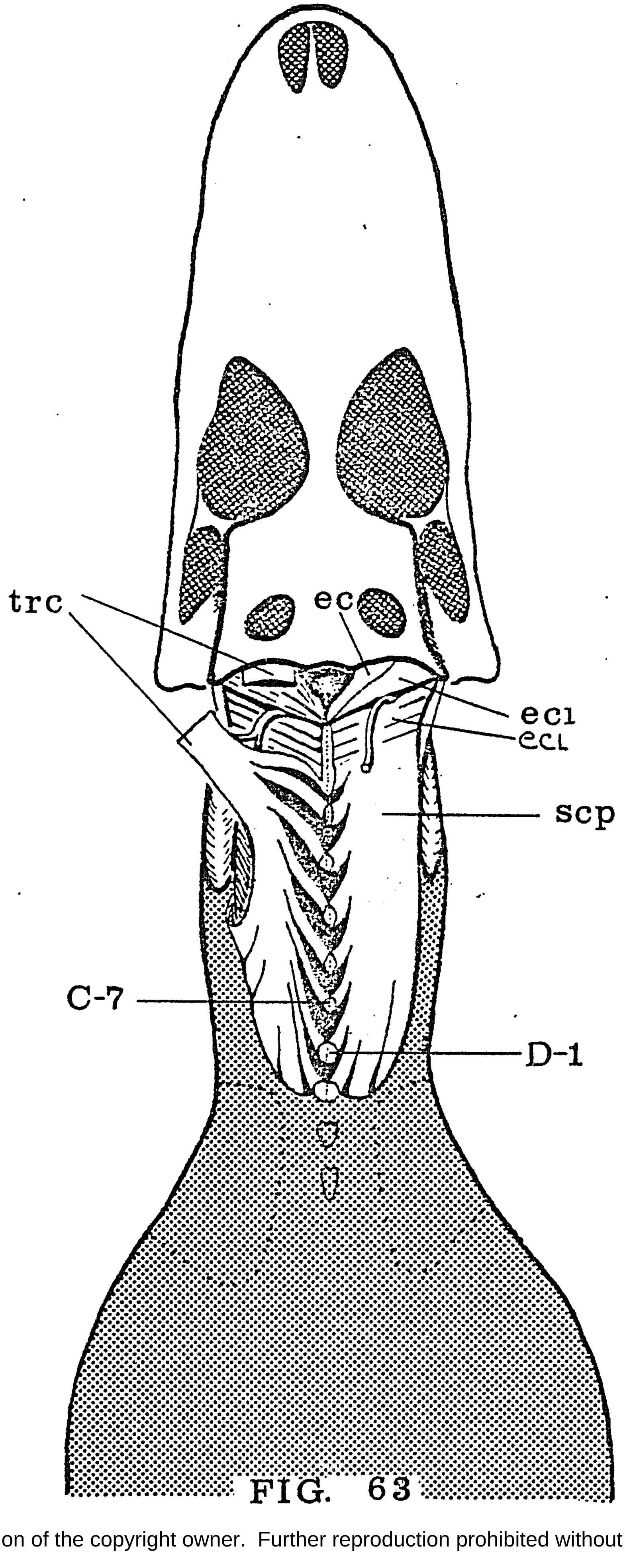

FIG. 63

FIG. 64. LEFT LATERAL VIEW OF A SUPERFICIAL DISSECTION OF *A. MISSISSIPPIENSIS* THAT SHOWS THE TRANSITIONS OF VARIOUS MUSCLE SYSTEMS FROM TRUNK TO NECK. AS, TENDON AND MUSCLE OF *M. ARTICULO-SPINALIS DORSI*; ECL, *M. EPISTROPHEO-CAPITIS LATERALIS*; I-C-CA, *M. ILIO-COSTALIS CAPITIS*; I-C-CE, *M. ILIO-COSTALIS CERVICIS* (SIXTH SEGMENT); I-C-D, FIRST SEGMENT OF *M. ILIO-COSTALIS DORSI*; L-C-P, DEEPLY PLACED *M. LONGISSIMUS CAPITIS PROFUNDUS*; L-C-S, *M. LONGISSIMUS CAPITIS SUPERFICIALIS*; LG-CE, *M. LONGISSIMUS CERVICIS*; LG-D, *M. LONGISSIMUS DORSI*; NS, NEURAL SPINE TIPS; OB-EX, *M. OBLIQUUS ABDOMINIS EXTERNUS*; SC, HYPAXIAL *M. INTERCOSTALIS EXTERNUS*; SCP, *M. SPINO-CAPITIS POSTICUS*; TR-SP-CA, *M. TRANSVERSO-SPINALIS CAPITIS*, SHOWN WITH ITS DUAL ORIGIN (NEURAL SPINES AND TRUNK FASCIA) AND LATERAL TENDINOUS INSCRIPTIONS; TR-SP-CE, *M. TRANSVERSO-SPINALIS CERVICIS*. MODIFIED AFTER NISHI (1938).

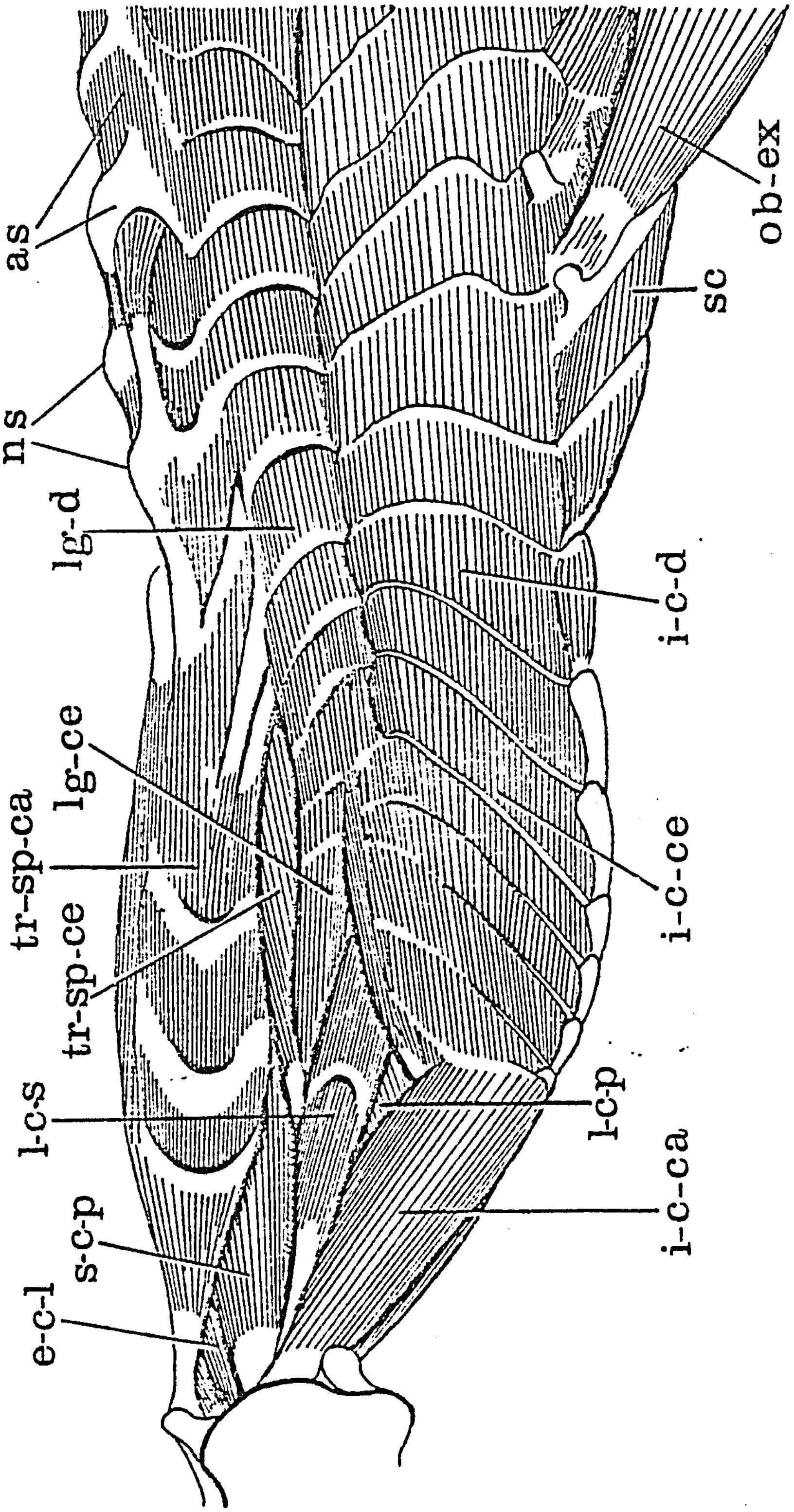
as
ns
lg-d
lg-ce
tr-sp-ca
tr-sp-ce
l-c-s
s-c-p
e-c-l
ob-ex
sc
i-c-d
i-c-ce
l-c-p
i-c-ca

FIG. 64

FIG. 65. AN ILLUSTRATION TAKEN FROM A LIVING SPECIMEN THAT SHOWS THE "AQUATIC PROFILE" OF EXTERNAL NARES, EYES, AND EAR OPENING, THAT ARE ALL MAINTAINED JUST ABOVE WATER LEVEL. NOTE HOW SHARPLY THE HEAD IS BENT UPON THE NECK, BUT THAT THE NECK IS RELATIVELY STRAIGHT, WHILE THE BODY IS SUBMERGED.

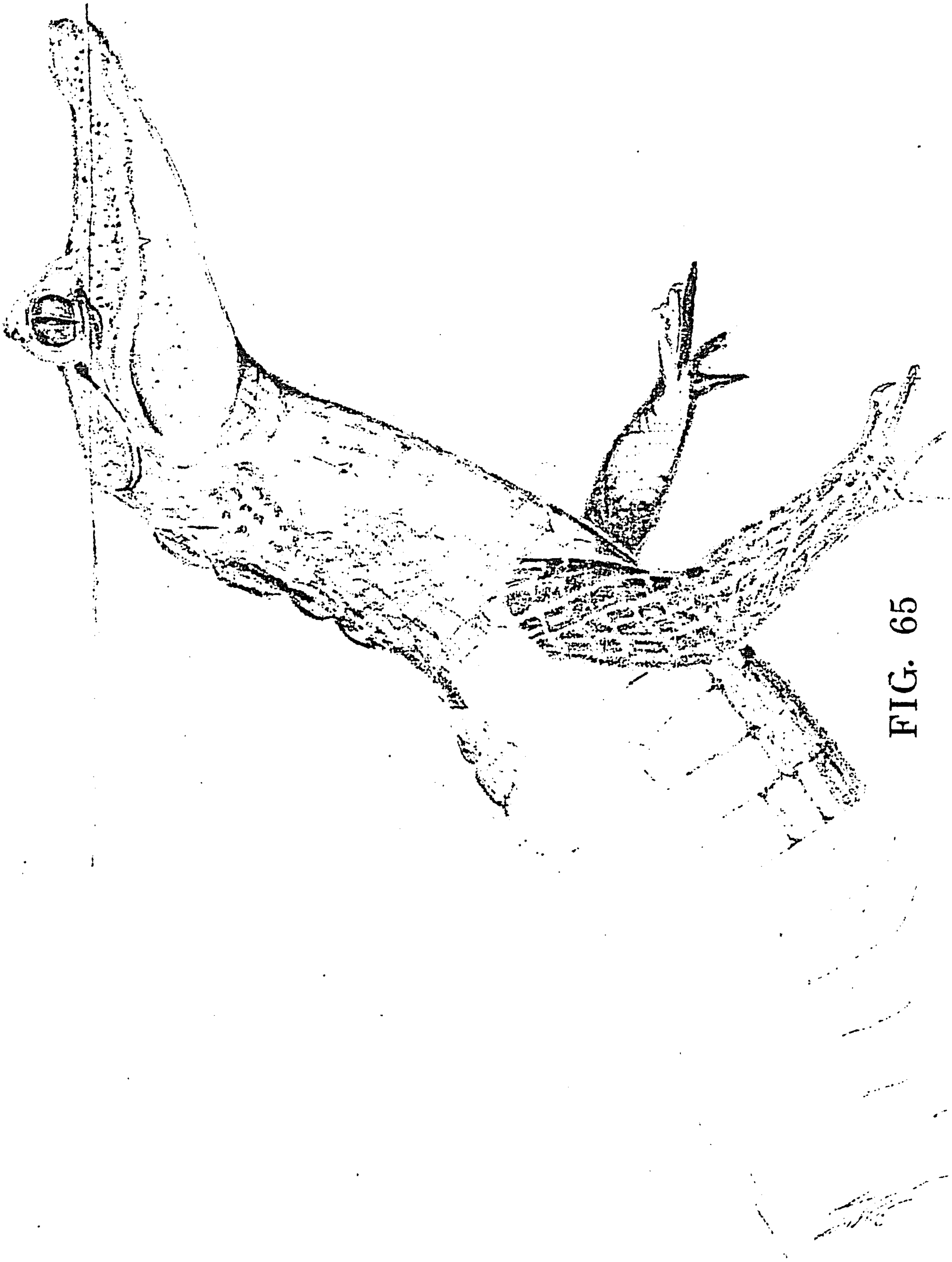

FIG. 65

FIG. 66. A SUPERFICIAL DISSECTION OF *CROCODYLUS NOVAEGUINEAE* FOR COMPARISON WITH *A. MISSISSIPPIENSIS*. ATTENTION WAS GIVEN TO ACCURATELY REPRESENTATION OF MUSCLE PROPORTIONS IN BOTH THIS FIGURE AND IN FIGURE 67.

FIG. 67. A DISSECTION OF THE SAME SPECIMEN AS SHOWN IN FIGURE 66, IN WHICH THE SCAPULAR MUSCLES HAVE BEEN CUT, THE RIGHT *M. DEPRESSOR MANDIBULAE*, AND RETROARTICULAR PROCESS REMOVED, AND THE DEEP FASCIAL COVER OF THE CERVICAL MUSCLES REMOVED. AIR, AIR TUBE FOR PASSAGE CONNECTING ARTICULAR BONE AIR SPACES WITH MIDDLE EAR CAVITY; DM, *M. DEPRESSOR MANDIBULAE*; ECI, *M. EPISTROPHEO-CAPITIS INTERMEDIUS*; IC, *M. ILIO-COSTALIS CERVICIS*; ILC, *M. ILIO-COSTALIS CAPITIS*; SC, *M. STERNO-COSTALIS*; SCP, *M. SPINO-CAPITIS POSTICUS*; TSC, LEFT AND RIGHT PORTIONS OF NARROW *M. TRANSVERSO-SPINALIS CAPITIS*.

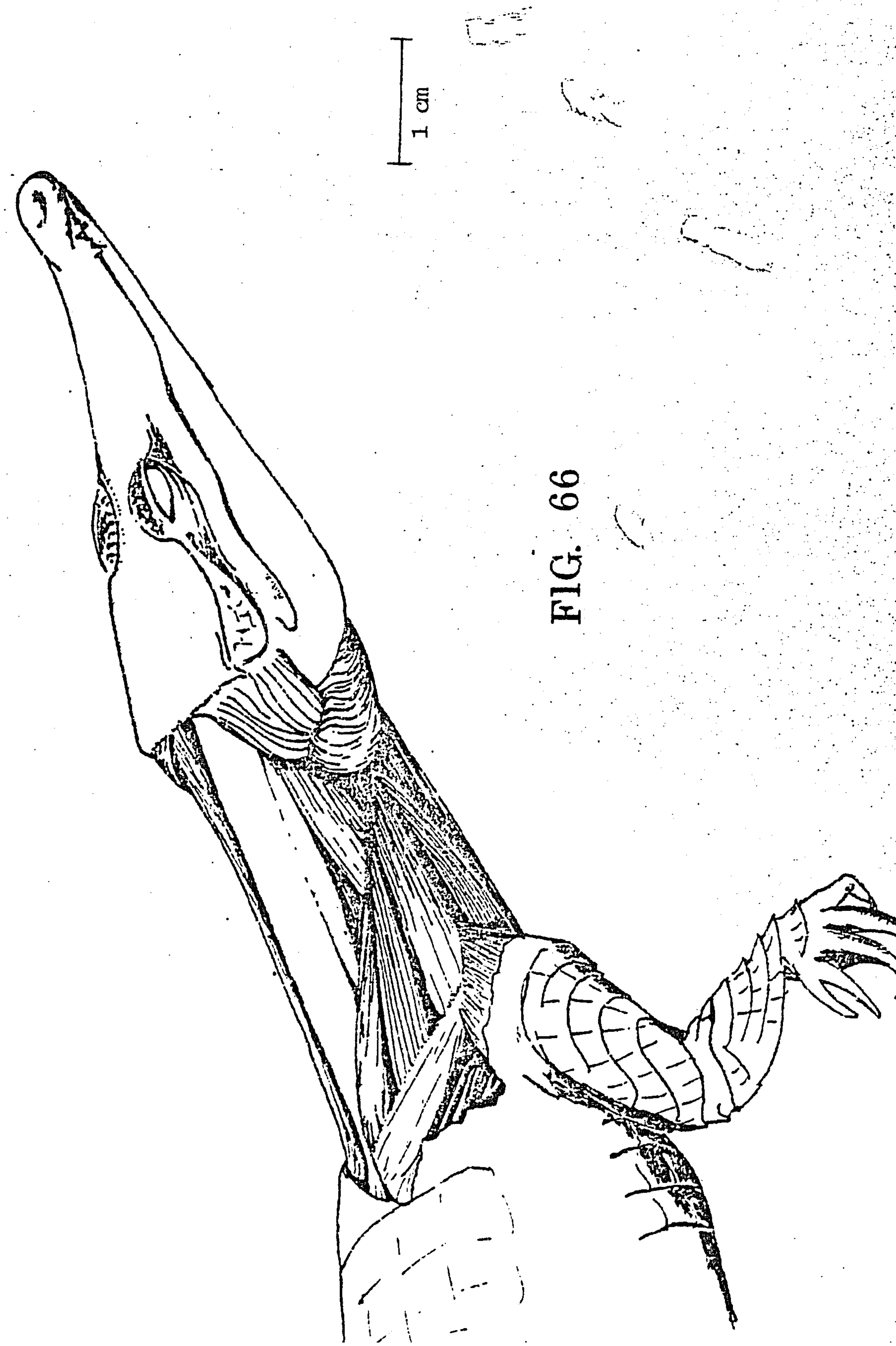

FIG. 66

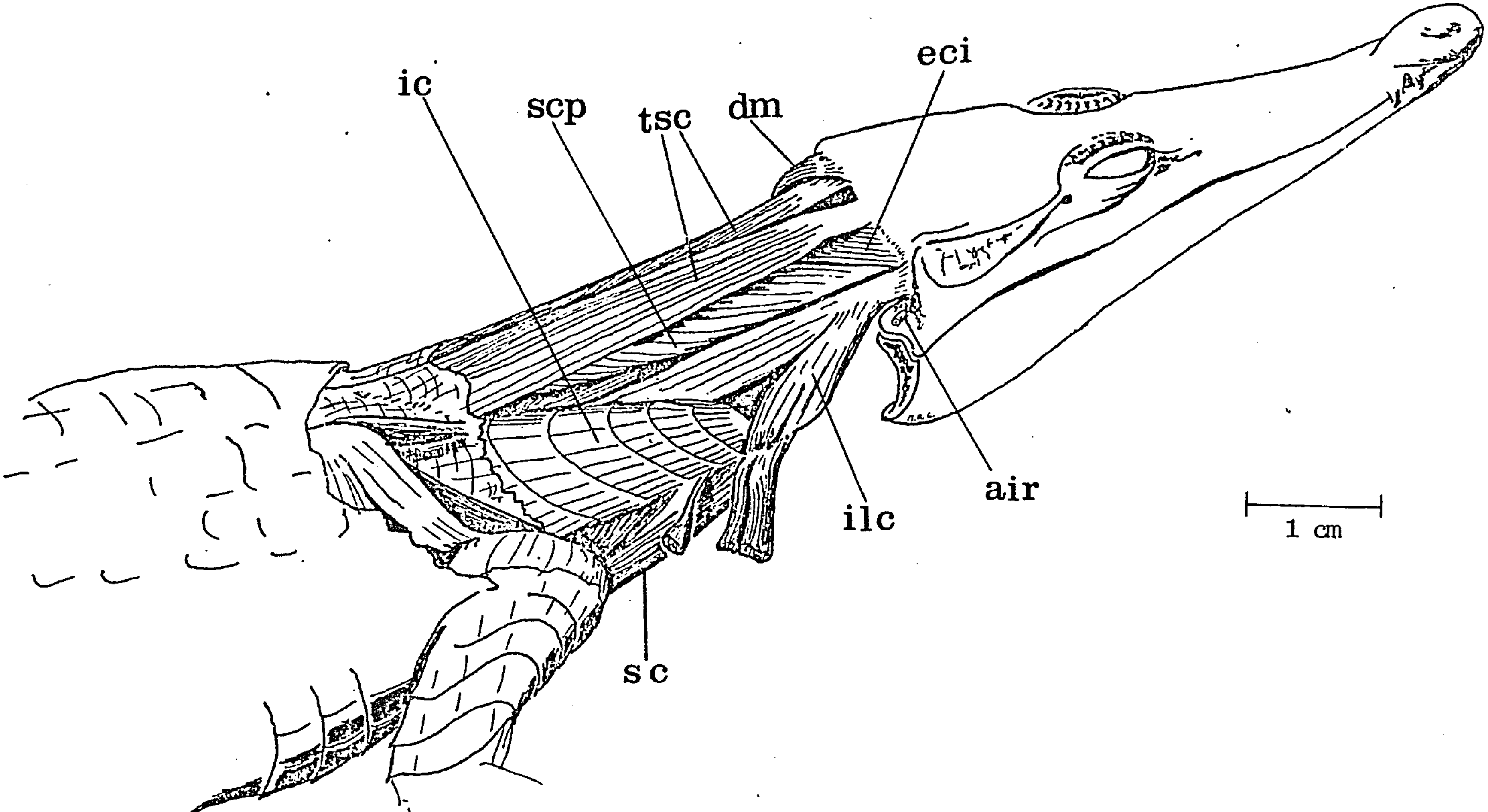

FIG. 67

FIG. 68. THIS DIAGRAM ILLUSTRATES THE SLING EFFECT OF M. ILIO-COSTALIS CERVICIS UPON THE NECK VERTEBRAE. THE FIFTH CERVICAL VERTEBRA AND RIBS WERE CHOSEN AS BEING TYPICAL FOR THIS FIGURE. THE UPWARDS FORCE DUE TO M. ILIO-COSTALIS CERVICIS (IC) IS BALANCED BY GRAVITY (GR), HOWEVER, BECAUSE OF THE ARRANGEMENT OF THE RIB TUBERCULA AND CAPITULA, MEDIALLY DIRECTED FORCES (HY) FROM MM. SUBVERTEBRO-COSTALES ARE NECESSARY TO MAINTAIN THE RIBS IN ARTICULATION.

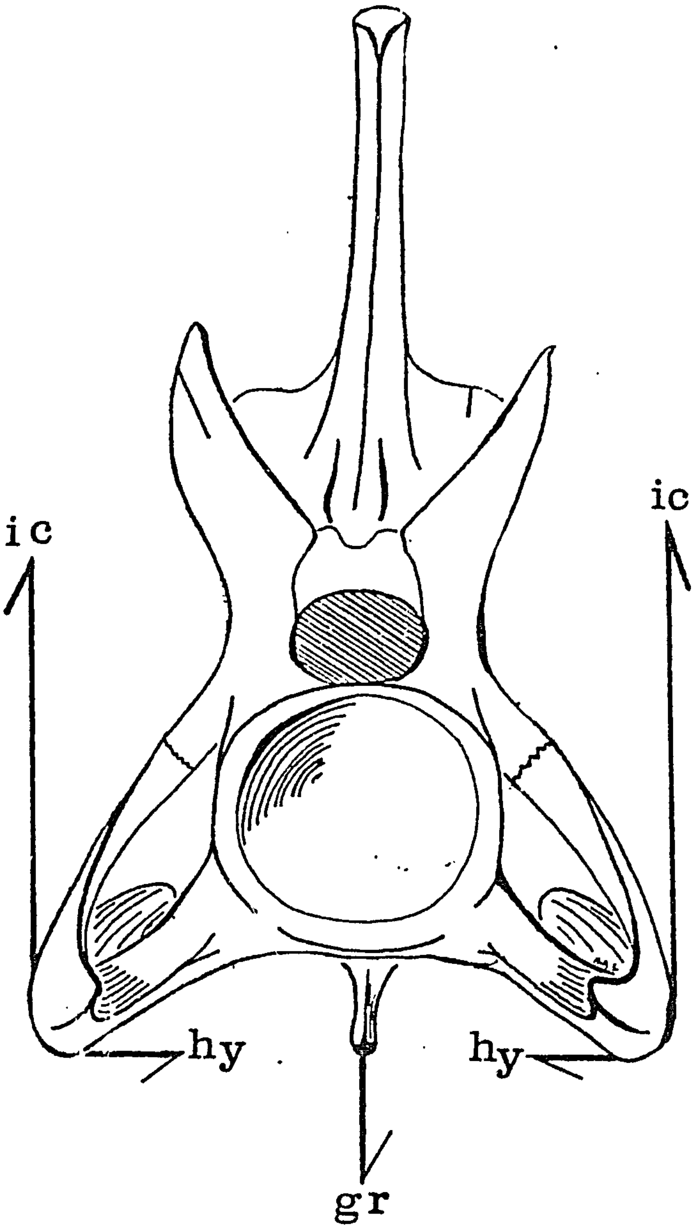

FIG. 68

FIG. 69. THIS DIAGRAM ILLUSTRATES THE BALANCE OF EXTERNAL FORCES ACTING UPON THE SKULL, USING THE OCCIPITAL CONDYLE AS A PIVOT. G, VECTOR FOR FORCE OF GRAVITY (THE COMPONENT THAT IS AT RIGHT ANGLES TO A HORIZONTAL LINE FROM THE OCCIPITAL CONDYLE CENTER OF ROTATION); P, VECTOR SUM OF COMPONENTS OF FORCES (G) AND (TR+SCP) THAT ACTS THROUGH THE OCCIPITAL CONDYLE; R, RESISTIVE FORCE MAINTAINED BY THE ATLANTAL RING THAT BALANCES FORCE (P); TR + SCP, HORIZONTAL, POSTERIORLY DIRECTED FORCE CREATED BY TENSION IN MM. TRANSVERSO-SPINALIS CAPITIS AND SPINOCAPITIS POSTICUS; X, DISTANCE BETWEEN CENTER OF GRAOVITY COMPONENT AND OCCIPITAL CONDYLE IN THE HORIZONTAL DIRECTION; Y, VERTICAL HEIGHT OF THE INSERTIONS OF MUSCLES (TR + SCP) ON THE OCCIPUT. SUM OF FORCES = 0 = Y(TR+SCP) - X(G).

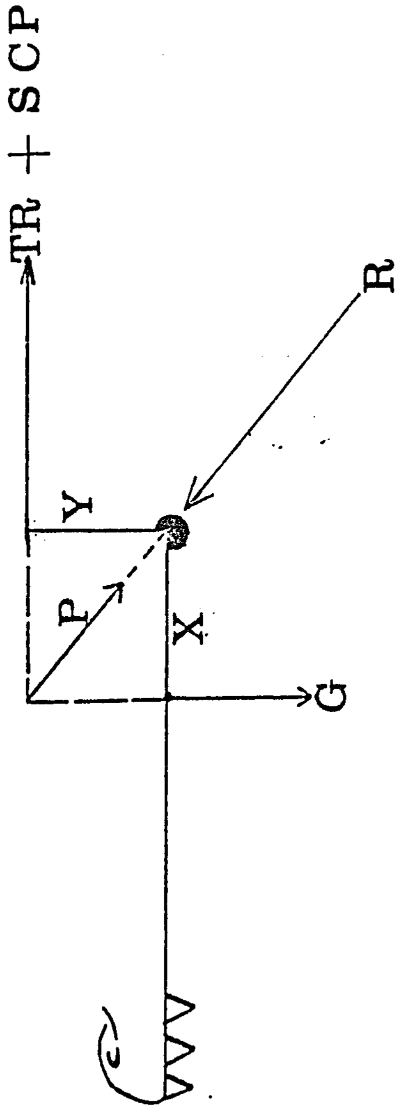

FIG. 69

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