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THE MYOLOGY OF SPHENODON PUNCTATUM

by

THEODORE C. BYERLY

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INTRODUCTION

Due to the generosity of Prof. C. C. Nutting, the writer was allowed to dissect the muscles of two specimens of *Sphenodon punctatum* which were brought back by the Fiji-New Zealand Expedition of the summer of 1922. These specimens are of special interest since they belong to the only living species of Rhyncocephalia, the lowest of all the existing orders of the class Reptilia. The species is rapidly becoming extinct and careful myological studies should be made while it is still existant. Further emphasis is placed on such studies since, according to Cope's law of the unspecialized: "The perfection produced by each successive age has not been the source or parent of future perfection. The types which have displayed the most specialized mechanism have either passed away, or, undergoing no change, have witnessed the progress and ultimate supremacy of those which were once their inferiors."[1]

Sphenodon is, of all living reptiles, probably the most closely allied to the amphibians on the one hand and the higher vertebrates on the other. Since this is true, one should expect *Sphenodon* to show more or less transitional stages between the unspecialized urodele condition found in the salamanders and the specialized form of creatures higher in rank than itself. Cope's law of the unspecialized seems pretty well substantiated by paleontological evidence, and it is generally accepted, so *Sphenodon* should possess characters very like those possessed by the progenitors of birds and mammals. According with this hypothesis, *Sphenodon* is very primitive in all its characters and no less so in its musculature.

Among the most interesting fields in myology is that of serial and special homology. *Necturus* has been used as the base form, by many workers, for determining serial and special homologies in limbed vertebrates and it is *Necturus* which has been used as a basis for such conclusions drawn in this paper. As a matter of fact, there is

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1 Cope, E.D., Origin of the Fittest, p. 234.

no one absolute basis for determining either serial or special homologies, unless it would be through a series of models prepared from serial sections of successive embryonic stages. Even these, were they available, would present very grave difficulties. However, since nerve supply for each muscle comes from the somite from which that muscle was derived, the nerve supply probably furnishes the most reliable criterion for the determination of homology. When the nerve supply is obscured by complex branching and anastomosis, as in the brachial plexus, muscle insertion must aid in the determination of homology. Arterial blood supply, origin and position must sometimes be considered but can by no means be regarded as reliable bases for judgment.

Homology of the muscles of the proximal portions of the limbs has long been a controversial subject among students of myology. It is hoped that a critical examination of the muscles of *Sphenodon* may contribute something to the solution of this difficult problem. Some investigators have homologized the great extensors of brachium and thigh (Quain); while others (Owen) homologize the extensors of the brachium with flexors of the thigh and vice versa. The difference of opinion is due to the opposite direction of flexion of the two limbs. The condition in *Sphenodon* is somewhat transitional between the unspecialized condition in the limbs of *Necturus* and the stereotyped stele-zeugopodial articulation in the higher reptiles and the mammals.

While the present attempt to homologize the muscles of *Sphenodon* serially in the limbs and especially with the muscles of *Necturus* will doubtless leave much to be desired, it is hoped that the dissections have been so carefully described and illustrated by diagrams that they will furnish a reliable basis for further work. This is especially true because, apparently, very few men have availed themselves of the opportunity actually to dissect a well-preserved specimen, and undoubtedly the opportunity will become rarer as the material becomes more difficult to obtain.

The most complete description of the muscles of *Sphenodon* is that of Osawa. This paper was published in 1899 and may be found in the "Archiv für Mikroskopische Anatomie," Bd. 51. It contains a complete description of the muscles and their nerve supply together with a partial list of serial and special homologies. His illustrations leave much to be desired and a few of his descriptions are incorrect.

The earliest account in the available literature is that of Gunther,

published in 1867. His account is accurate but covers only a few of the limb muscles and a partial dissection of the intercostal musculature. He took his nomenclature from anthropotomy and some of his special homologies will hardly stand. Gadow, 1887 and 1890, published very thorough accounts of the caudal musculature, including both drawings and discussion. Furbringer's paper, 1892, has been available through extracts made from it by Gregory and Camp in a paper published in the "Bulletin of the American Museum of Natural History," vol. 38. Gegenbaur (Leipzig, 1896) gives an account of the integumental musculature of the head and neck (after Ruge). For *Necturus*, Wilder's excellent account has been the chief reference.

Both specimens dissected for this account died of a bone and muscle necrosis diagnosed, with some doubt, as osteo-myelitis. The first specimen had a large necrotic mass on the dorsum of the left manus and the carpals of that member were nearly destroyed; the symphysis menti was also destroyed. After death it was skinned and preserved in five percent formalin. Dissection brought to light other necrotic masses in the m. pectoralis, in the liver and at the juncture of a regenerated caudal portion with the original body segments. The caudal region of both specimens was regenerated for the last fourteen or fifteen segments.

The second specimen became very ill in May 1923, was killed and the entire body was fixed in chrom-aceto-formaldehyde in order to preserve the tissues for histological work. The symphysis menti was destroyed by necrosis in this specimen.

The dissection of these members of an ancient race, occupying so important a position in any schema of the sequence of forms in the course of organic evolution, and so nearly extinct, has been of great interest. Perplexing differences between the specimens dissected and the work of other men, and some few differences between other workers, have come up from time to time and the suggestions of Dr. F. A. Stromsten, under whom this work was undertaken, have been very helpful in arriving at conclusions.

THE VISCERAL MUSCLES

The visceral muscles are located in the head and neck. They arise, embryologically, from the hypomeres rather than the epimeres. Phylogenetically, they are the survivals of the musculature of the gill arches of lower forms. In *Sphenodon*, they include the integu-

mental and facial musculature, the intrinsic muscles of the hyoid and larynx, and the muscles of mastication.

"Following[2] the lines laid down by Gegenbaur in his 'Lehrbuch der Anatomie der Menschen', on the origin of the facial muscles, G. Ruge has made detailed researches on the facial musculature of lemurs, from which he arrives at the following results:

The fact that all the muscles supplied by the facial nerve belong to the same series indicates that those related to the visceral skeleton, and having originally nothing to do with the face, which are supplied by the same nerve, must have shifted upwards from the region of the lower jaw and neck, so as to come into close relation with the soft parts surrounding the apertures of the ear and mouth, that is, to the secondarily formed lips and to the external ear. From these points, they extended further, taking on new relations to the eye, nasal aperture and to the frontal and temporal regions, those behind it from the occipital region. The upward change of the position of the musculature thus took place along two lines,—in front of, and behind the ear, as is proved by its innervation, ...

. . . . The platysma myoides thus forms the matrix for the facial muscles, and it represents the remnants of a musculature continued forward to the head, which has retained (e.g. in man) an undifferentiated form in the neck (Gegenbaur).

Besides the platysma myoides there is a second deeper dermal system of muscles in the neck, the sphincter colli. This, like the platysma, also takes on secondary relations to the head, and gives origin to the levator labii-superioris proprius, levator anguli oris, sphincter oris, buccinatorius and the proper muscles of the nose. The facial muscles not named here arise from the platysma."

Gegenbaur[3] mentions the facial musculature in *Sphenodon* in connection with Ruge's work and gives one text figure.

"Einen sehr primitiven Zustand bietet der Facialismuskulatur bei *Sphenodon*, wo alle Theile noch im Zusammenhang stehen. An den noch weit oben entspringenden Abductor mandibulæ schlieben sich Zuga (Sphincter dorsalis) die ventral in den Intermandibularis sich fortsetzen, und daran reihen sich weiter abwarts entspringende Bundel, welche in den schwachen Sphincter colli fortgesetzt sind."

Sphenodon presents, in the adult, a very primitive condition of the facial musculature. Except for a few fibers in the eyelids, constituting an orbicularis oculi, there is little differentiation of the primitive muscle sheet. This sheet is continuous ventrally from the shoulder region to the symphysis menti. The posterior portion may be termed the sphincter colli and that between the rami of the mandible, the intermandibularis. The antero-dorsal portion is contigu-

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2 Wiedersheim, R., Comparative Anatomy of Vertebrates, p. 121.

3 Gegenbaur, C., Vergleichende Anatomie der Wirbelthiere, p. 631.

ous with the depressor mandibulæ (abductor mandibulæ of Gegenbaur) and passes anterior to the membrana tympani; Gegenbaur terms this the sphincter dorsalis.

VISCERAL MUSCLES OF THE HYOID REGION

This group includes: m.mylohyoideus, m.stylohyoideus, m.ceratohyoideus and the proper muscles of the larynx.

Mylohyoideus

This muscle lies dorsal to the anterior portion of the intermandibularis and is pretty well differentiated from it. It forms a thin but strong sheet of muscle fibers which stretches between the anterior third of the rami of the mandibles. With the intermandibularis, it serves to raise the floor of the mouth.

Innervation: N. trigeminus.

Stylohyoideus

This is a very small muscle that stretches from the styloid process to the lateral border of the posterior portion of the cerato-hyal; levator of the hyoid.

Innervation: N. facialis.

Ceratohyoideus

This muscle lies between the lateral border of the geniohyoideus and the mesial surface of the pterygoideus internus. It extends from the anterior border of the postero-lateral portion of the hyohyoid to the mesial part of the antero-lateral portion of the ceratohyoid.

Innervation: N. facialis.

MUSCLES OF THE LARYNX

These muscles present no specialization in *Sphenodon*; they consist of a single constrictor and a pair of dilators.

Dilatores laryngei

These consist of a pair of muscles, one on either side of the larynx. Each extends from its origin on the cricoid to its insertion on the antero-lateral surface of the arytenoid. By abduction of the arytenoids, they serve as dilators of the larynx in inspiration.

Constrictor laryngeus

Except for a very short distance on the mid-dorsal surface, this muscle completely surrounds the larynx. It covers almost the entire

surface of the arytenoid cartilages from which its fibers are exserted and into which they are inserted.

Innervation: N. vagus.

MUSCLES OF MASTICATION

Sphenodon is largely predaceous in its food habits. It eats lizards, bones and all, so one might expect to find rather heavy muscles of mastication. The jaws are very strongly muscled, the pterygoideus internus being exceptionally heavy. The group consists of three adductors, m. temporo-massetericus, m. pterygoideus externus, m. pterygoideus internus and a single abductor, m. depressor mandibulæ.

Temporo-massetericus

This muscle is homologous with both the temporalis and the massetericus of more specialized animals. It forms a heavy muscle mass which lies beneath the superficial fascia and the temporal arcade on the postero-lateral surface of the head.

Origin: From the fascia which covers the lateral temporal fossa and from the inner surfaces of the squamosal, jugal and postorbital bones, its fibers extend ventrally to their

Insertion: As muscle fibers, on the coronoid process and the subjacent dorso-lateral surfaces of the dentary and supra-angular bones. There is some indication of division into external and internal masses at the point of insertion.

Action: Closes the mouth; it is most efficient when the mouth is almost closed.

Innervation: N. trigeminus.

Pterygoideus externus

This muscle is not sharply defined from the preceding but its fibers run at a somewhat different angle. It lies just beneath the temporo-massetericus.

Origin: From the inner surface of the postorbital, the lateral surface of the epipterygoid, and from the fascia which covers the supratemporal fossa, its fibers extend postero-laterally to their

Insertion: On the dorso-mesial surface of the supra-angular.

Action: Aids in closing the mouth and in the grinding action when the mouth is almost closed.

Innervation: N. trigeminus.

Pterygoideus internus

This is the heaviest and most powerful of the muscles of mastica-

tion. It is the innermost of the group and forms a large rounded protuberance into the mouth cavity.

Origin: From the basi-sphenoid, the parietal, the pterygoid and from the fascia covering the supra-temporal fossa.

Insertion: On the ventral and lateral surfaces of the dentary.

Action: Abductor of the mandible, most efficient when the mouth is widely gaping.

Innervation: N. trigeminus.

Depressor mandibulæ

This muscle follows the posterior contour of the squamosal and lies just beneath the sphincter colli, except in the region near the dorsal mid-line where it is covered by the aponeurosis of the cranial portion of the trapezius.

Origin: From the dorsal portion of the posterior surface of the squamosal and the lateral portion of the posterior surface of the parietal.

Insertion: On the posterior and ventral surfaces of the articulare.

Action: Abductor of the mandible.

Innervation: N. facialis.

THE AXIAL MUSCULATURE

The axial musculature of *Sphenodon* is perhaps more significant than the appendicular. The intercostal system is almost as complex as that of the Ophidia, due to the presence of movable and perhaps functional ribs or gastralea on the abdominal surface. The muscles that function in respiration show many characters transitional between the simple Urodele type and the condition found in the more specialized reptiles. A m. triangularis sterni is differentiated from the[4] transversalis sheet; this fact is one of many which may serve to indicate that *Sphenodon* is very close to both bird and mammal forms in its myology.

The usual differentiation into dorsal and ventral groups is quite marked. The following muscles have been considered as belonging to the ventral axial group but there are a few others, discussed under the trunco-zonal muscles of the appendicular group, which might be considered here: m. geniohyoideus, m. genioglossus, m. hyoglossus, m. cleido-episterno-hyoideus, m. omohyoideus, m. sterno-coracoideus

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[4] In discussing the myology of birds, Wiedersheim says; "External and internal intercostals are well developed, and a triangularis sterni appears for the first time on the inner surface of the sternal ends of the ribs." Wiedersheim, R., Comparative Anatomy of Vertebrates, p. 140.

superficialis, m. sterno-coracoideus profundus, m. costo-sterno-scapularis, m. costo-coracoideus, m. serratus posterior, m. serratus anterior, m. rectus abdominis externus, m. rectus abdominis internus, m. obliquus externus, m. obliquus internus, m. transversalis abdominis, m. triangularis sterni, mm. intercostales externi longi, mm. uncini-costales longi, mm. uncini-costales breves, mm. intercostales externi breves, mm. intercostales interni breves, mm. intercostales interni longi, mm. intercostales ventrales, mm. abdomino-costales, m. longus colli, m. ilio-sacro-costo-costalis, m. ilio-ischio-caudalis.

Geniohyoideus

Origin: From the inner surface of the mandible, from a space a quarter inch in width just laterad of the symphysis. Its fibers extend caudad beneath the intermandibularis to their

Insertion: On the anterior border of the medial half of the hyoid.

Action: Draws the hyoid forward; perhaps aids in protrusion of the tongue.

Genioglossus

Origin: From the inner surface of the mandible, just dorsal to the origin of the geniohyoideus.

Insertion: On the ventral surface of the tongue; its fibers mingle with those of the lingualis.

Action: Aids in manipulation and protrusion of the tongue.

Hyoglossus

Origin: From the anterior border of the hyoid, beneath the middle portion of the geniohyoid. Its fibers extend anteriorly to their

Insertion: On the ventral surface of the tongue, about an inch from the tip.

Action: It serves as a retractor of the tongue, opposing the action of the geniohyoideus.

These three muscles have been discussed with the ventral axial muscles in spite of the fact that they are frequently considered with the visceral muscles. Wilder[5] makes the following statement: "The musculature of the tongue, especially its extrinsic muscles, such as hyoglossus, genioglossus, styloglossus, etc., is probably derived from the visceral muscles, . . ." On the other hand, Ecker,[6] in describing the course of the hypoglossal nerve in the frog, states: "N. hypoglossus or n. spinalis I. (A)—(B)—(C) When near the glosso-

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[5] Wilder, H.H., History of the Human Body, p. 216.

[6] Ecker, A., Anatomy of the Frog, p. 182.

pharyngeal it supplies twigs to the geniohyoideus, sternohyoideus and omohyoideus. (D) One of the branches passes inward to supply the hyoglossus.'' Sobotta,[7] in his work on human anatomy, says: ''The geniohyoid is supplied by fibers from the first and second spinal nerves which accompany the hypoglossal nerve.'' In *Sphenodon*, the hypoglossal furnishes the nerve supply for the geniohyoideus, genioglossus and hyoglossus. Since the n. hypoglossus is not yet established as one of the cranial nerves in the Anura, and since it does not supply a branchial arch at any time, it seems logical to assume that in *Sphenodon* those muscles which it supplies should be considered with the ventral axial muscles.

If this postulate be accepted, there is in *Sphenodon*, as one might expect in a primitive form so close to the Urodeles, an almost unbroken, ventral, longitudinal muscle sheet extending from the posterior border of the ischiadic plate to the symphysis menti. It includes the following muscles which are probably serially homologous: m. geniohyoideus, m. hyoglossus, m. genioglossus, m. cleido-episterno-hyoideus, m. sterno-coracoideus superficialis, m. sterno-coracoideus profundus, m. rectus abdominis externus, m. rectus abdominis internus.

Cleido-episterno-hyoideus

This is a thin muscle which covers most of the ventral surface of the œsophagus and trachea. Its fibers run postero-anteriorly just beneath omohyoideus and the sphincter colli.

Origin: From the anterior border of the mesial half of the clavicle and from the whole anterior border of the episternum.

Insertion: On the posterior border of the lateral half of the hyoid cartilage, beneath and lateral to the insertion of the omohyoideus.

Action: Retractor of the hyoid.

Omohyoideus

This muscle and the preceding one act as depressors and retractors of the hyoid, thus serving to oppose the action of the geniohyoideus and ceratohyoideus and to maintain a stable point of origin for the hyoglossus.

Origin: It takes origin from the antero-medial portion of the mesial surface of the scapula, just dorsal to the articulation of that bone with the clavicle, and from the scapulo-coracoid ligament. It

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[7] Sobotta, J., Atlas and Textbook of Anatomy, p. 212.

curves ventro-anteriorly passing dermad of the cleido-episterno-hyoideus to its

Insertion: On the medial surface of the hyoid.

Sterno-coracoideus superficialis

The various elements of the pectoral girdle are not fused to form a solid, inflexible unit in *Sphenodon* as they are in the Anura and the more highly specialized reptiles. The sternum and coracoid are quite free from each other as far as bony or cartilaginous connections are concerned. The T-shaped episternum (interclavicularis) anchors the clavicles, coracoids and sternum rather loosely in place but permits a considerable amount of interplay. This interaction is controlled in part by the sterno-coracoideus superficialis.

Origin: It takes origin from the medial half of the extreme posterior portion of the inner surface of the sternum. Its fibers extend in a thin sheet about a half inch in width, antero-laterally to their

Insertion: On the coracoid, along the medial border of the epicoraco-humeralis.

Sterno-coracoideus profundus

This muscle lies just ventral to the sterno-coracoideus superficialis but is somewhat wider, extending laterally to fuse with the costo-coracoideus. Together with the muscle just described, it aids in retraction of the coracoid and unification of the pectoral girdle.

Origin: From the anterior border of the sternum, beneath the sterno-coracoideus superficialis. Its fibers extend cephalad to their

Insertion: Ventral and mesiad to those of the sterno-coracoideus superficialis, along the medial border of the epicoraco-humeralis.

Costo-sterno-scapularis

This muscle is probably serially homologous with the intercostales ventrales.

Origin: From the anterior border of the first complete rib, just ventral to the ventro-mesial curvature of that rib; it extends cephalad to its

Insertion: On the dorsal third of the sterno-scapular ligament and thence on the mesial surface of the ventral portion of the scapula.

Action: Retractor of the scapula, compressor of the ribs.

Costo-coracoideus

This muscle lies mesial to the costo-sterno-scapularis beneath the

sterno-coracoideus superficialis, and lateral to the sterno-coracoideus profundus.

Origin: It takes origin from the anterior border of the first complete rib, just mesial to the origin of the costo-sterno-scapularis. It extends cephalad to its

Insertion: On the mesial face of the coracoid, between the junction of the subscapular and the coracoid heads of the subscapulo-coraco-humeralis.

Action: Retractor of the scapula, compressor of the ribs.

Rectus abdominis externus

This muscle is divided into segments by the abdominal ribs and is further indistinctly divided into a superficial and a deeper layer. The external layer has many fibers which insert into the integument.

Origin: This muscle takes origin from the whole posterior border of the ischium. It is a little difficult to say certainly which end of this muscle is its origin and which its insertion but since the pelvic girdle is more or less firmly fixed and the pectoral girdle is flexible, the origin as stated is the more probable. It extends anteriorly over the origin of the pubo-ischio-tibialis and continues to its

Insertion: On the entire posterior border of the sternum.

Rectus abdominis internus

Origin: It takes origin from the lateral tuberosity of the pubis and from an accessory ligament which extends between the rectus abdominis externus and the pubo-ischio-tibialis to the pubic symphysis. It extends antero-mesially to its

Insertion: On the internal midline of the abdominal ribs and on the inner surface of the rectus abdominis externus.

Obliquus externus

The obliquus externus forms a continuous sheet from the pelvic girdle anterior to the first or second rib, where it becomes modified to form a part of the serratus group. It is indistinctly divided into a superficial and a deep layer, the fibers of both running in the same direction and having almost the same origin and insertion.

Origin: By digitations from each of the complete ribs, after the second, and from the lumbar fascia; the fibers of both sheets pass ventro-laterally to their

Insertion: By muscle fibers on each of the abdominal ribs and by a strong ligament on the lateral tuberosity of the pubis laterad to the rectus internus.

Obliquus internus

The obliquus internus shows very clearly that it has only recently, phylogenetically speaking, been broken into transversalis and obliquus. It does not form a complete sheet over the entire inner abdominal wall, but covers only the dorso-mesial portion of it. It lies just retro-peritoneal and the peritoneum adheres very closely to it.

Origin: By tendinous digitations from the centra of each of the vertebræ from the tenth to the twenty-fifth. It extends antero-laterally to its

Insertion: By muscle fibers on each of the complete ribs, for a space about a quarter inch in length on the posterior border, about an inch laterad from the centrum and two intercostal spaces anterior to the vertebra of origin.

Transversalis abdominis

The transversalis abdominis sheet lies lateral to the obliquus internus and just beneath the peritoneum, except at the anterior end where it passes behind the triangularis sterni. The peritoneum adheres to it very tightly.

Origin: From each of the complete ribs by digitations which take origin just lateral to the insertions of the obliquus internus and from the lumbar fascia in the lateral line region. The fibers extend ventrally to their

Insertion: On the peritoneum along a very even line just at the ventro-internal terminations of the costæ and on the sternum, just laterad to the insertion of the triangularis sterni.

Triangularis sterni

This muscle forms a sheet about a half inch in width just mesiad from the transversalis sheet. Its presence has not been recorded by others who have worked on *Sphenodon* but it forms a very distinct muscle whose fibers cross those of the transversalis abdominis in a markedly distinct direction.

Origin: It takes origin from the last incomplete rib, that of the eighth vertebra, and from the first complete rib, from the postero-medial border between the insertion of the obliquus internus and the origin of the transversalis abdominis.

Insertion: On the inner surface of the sternum, along the lateral border of the sterno-coracoideus profundus.

MUSCLES OF THE RIBS AND SCUTES

There is some difference of opinion among men who have worked on *Sphenodon* as to the use or non-use of the ventral scutes in locomotion. From observation of the movements of the creatures it would seem that they may use these scutes as auxiliary means of movement. This observation is much strengthened by dissection of the musculature. The abdomino-costales tilt the scutes so that they form an efficient friction surface. Contraction of the external oblique series of muscles would slowly project the body forward, using the scutes as fixed points by their contact with the ground. Since Sphenodons inhabit burrows, this action would be of considerable service to them in progress through narrow places where use of the limbs would be impeded.

Intercostales externi longi

Just beneath the obliquus externus lie two sets of semisegmental muscles whose fibers run in the same direction as those of the obliquus externus. The more ventral series, which consists of the intercostales longi, is rather irregular in occurrence but fairly regular in form.

Origin: It is formed by a number of slips, each of which rises from the posterior border of the lower medial portion of a rib, extends backward and downward over the rib next posterior to its origin to its

Insertion: On the anterior border of the second rib posterior from the origin, just dorsal to the antero-ventral curvature of that rib. Such slips do not rise regularly from every rib but do so fairly regularly from the more anterior ribs, after the first, and less regularly from the more posterior.

Uncino-costales longi

This muscle sheet forms the dorsal series of the second layer of the oblique musculature.

Origin: Each slip rises from the posterior border of the proximal half of an uncinate process and a small area of the rib adjacent. Each slip extends postero-ventrally over the rib next posterior, to its

Insertion: On the rib second posterior to the origin, just dorsal to the insertion of the intercostales externi longi.

Uncino-costales breves

This series is rather more regular in form and occurrence than the two preceding but, belonging to the same muscle layer, forms a

third series of semisegmental muscles, each slip of which extends from its

Origin: On the ventral border of an uncinate process to its

Insertion: On the lateral border of the rib next posterior to its origin, on a space about a fourth inch in length just ventral to the uncinate process.

Intercostales externi breves

These muscles form the usual thin sheet with fibers running diagonally dorso-ventral from the posterior border of one rib to the anterior border of the one next posterior.

Abdomino-costales

Slips from the inner surface of the rectus abdominis and from the gastralea attach to the posterior border of the external surface of the ventral portion of each rib.

Intercostales ventrales

The ventral portions of the intercostal spaces are without fibers of the intercostales externi breves. Ventral to the sharp antero-ventral curvature of the ribs, many loosely bound fascicles of muscle fibers extend from one rib to the next. These fascicles run from a higher posterior origin to a slightly lower anterior insertion on the next rib. Some of these fibers traverse the outer surface of the rib of their insertion to insert on its anterior border.

Intercostales interni breves

This muscle sheet might be construed to include the intercostales ventrales. Its fibers traverse the intercostal spaces in the same direction but dorsal to the preceding. They lie just internal to the intercostales externi breves.

Intercostales interni longi

This series consists of a slip for each rib after the second. A stout tendinous sheet from the ilium serves as origin for the slips to the last two ribs.

Origin: The muscle slips comprising this muscle take origin from the anterior border of each rib for a space about a half inch long just below the point of origin of the ilio-sacro-costo-costalis slip and the insertion of the obliquus internus slip and then run antero-ventrally to their

Insertion: On the posterior border of the rib second anterior from the rib of origin, just dorsal to the antero-ventral curvature of that rib.

Respiration in Sphenodon

The change from aquatic to terrestrial habits required, of course, considerable readjustment of the trunk musculature to make lung breathing possible. The Urodeles, living a sluggish semi-aquatic life, are never more than partially dependent on their lungs for oxygen supply, and as a consequence need very little specialization for lung breathing. Even in the more active Anura, which characteristically spend a major portion of their adult existence on land, most of the oxygen supply is obtained through the skin and œsophago-pharyngeal surfaces. Not until the dry skinned, terrestrial dwelling reptiles are reached in the phylogenetic scale, do the lungs assume a rôle of major importance in respiration.

Sphenodon is the most primitive of the existing Reptilia; so one might postulate that in *Sphenodon* might be found a situation almost exactly transitional between the Amphibia and the higher terrestrial vertebrates. This is exactly the condition they present in dissection. Instead of a simple segmented muscle sheet forming the body wall, there appears quite an intricate, but not wholly regular group of series of muscle slips which act as levators and depressors of the ribs.

The following muscles act as levators of the ribs: m. obliquus externus, mm. uncini-costales breves, mm. uncini-costales longi, mm. intercostales externi longi, mm. intercostales externi breves.

They are opposed by the following depressors and compressors of the ribs: depressors; mm. intercostales interni breves, mm. intercostales interni longi, m. obliquus internus, mm. intercostales ventrales; compressors; m. triangularis sterni, m. transversalis abdominis. The rectus abdominis internus may aid in respiration as a compressor of the body cavity.

Since both specimens had already been used in the preparation of a paper on the digestive system, a careful study of the diaphragm was impossible. As far as could be ascertained, it was incomplete and not muscular.

Longus colli

Origin: From the ventral surfaces of vertebræ two to twelve inclusive and from their transverse processes, a slip from the rib of

the seventh vertebra; it extends cephalad, just lateral to the median line, to its

Insertion: On the ventral surfaces of the axis and the occipital condyle.

Action: Aids in lateral movements of the head and in holding it erect.

Ilio-sacro-costo-costalis

Origin: From the ilium, the sacrum, the ribs, and by fibers from the longus colli.

Insertion: On the transverse processes and centra of all the vertebræ anterior to the sacrum.

Action: Flexor and tensor of the trunk.

Remarks: This muscle seems to be unique in its continuation anteriorly beneath the ribs. Its posterior portion is probably homologous with the quadratus lumborum of higher forms.

Ilio-ischio-caudalis

Origin: From the ilium, the ischium and from the ventral surfaces of the transverse processes of the caudal vertebræ.

Insertion: On the transverse and hæmal processes of the caudal vertebræ.

Action: Abductor-adductor of the tail.

DORSAL AXIAL MUSCLES

This group includes all the axial muscles dorsal to the lateral line and above the ribs. These muscles are not in all cases clearly separated from one another and their description is somewhat problematical, their designation more or less arbitrary. The group is customarily divided into a median and a lateral portion; this plan has been followed as far as practicable. The medial group includes the m. semispinalis capitis, m. transverso-spino-spinalis, mm. interspinales. The lateral group includes the m. cervico-capitis, m. sacro-transverso-transversalis, m. caudæ dorsalis, m. obliquus capitis, m. rectus capitis posticus.

Medial

Semispinalis capitis

Origin: From the antero-lateral surfaces of the spinous processes of the fourth to eighth cervical vertebræ inclusive, it runs cephalad to its

Insertion: On the dorsal portion of the posterior surface of the parietal.

Action: Aids in lateral and dorsal movements of the head.

Transverso-spino-spinalis

Origin: This muscle receives many fibers from the sacro-transverso-transversalis from which it is not sharply defined. Most of its fibers take origin from the spinous processes of vertebræ three to twenty-six and from the proximal portions of their transverse processes.

Insertion: The deepest layer of fibers inserts on the spinous process of the vertebra second anterior to their origin; the fibers of the middle layer skip two vertebræ to insert on the spinous process of the vertebra third anterior from their point of origin; the fibers of the superficial layer unite with fibers of the sacro-transverso-transversalis and insert on the vertebra sixth anterior to their origin.

Action: Serves as a flexor of the body.

Interspinales

Origin: From the anterior surfaces of the spinous processes of all the vertebræ.

Insertion: On the posterior border of the spinous process of the vertebra next anterior to the point of origin.

Caudæ dorsalis

Origin: There is no break between this muscle and the sacro-transverso-transversalis but its position makes separate consideration necessary. It takes origin from the sacrum, the ilium, and the spinous and transverse processes of the caudal vertebræ and extends caudad to its

Insertion: On the spinous and transverse processes of the caudal vertebræ.

Action: Flexor of the tail.

Lateral

Cervico-capitis

Origin: From the lateral surface of the neck at the level of the sixth vertebra and from the transverse process of that vertebra; by fibers from the sacro-transverso-transversalis. It extends superficially to its

Insertion: On the posterior border of the squamosal.

Action: Aids in lateral and dorsal movement of the head.

Sacro-transverso-transversalis

Origin: From the sacrum, from the anterior border of the ilium, from the transverse processes of vertebræ three to twenty-six, from the anterior surfaces of the dorsal portions of all the ribs and from the dorsal surfaces of the uncini.

Insertion: For the most part, on the transverse processes and ribs from the axis to the sacrum. From the level of the fourth, fifth, sixth and seventh vertebræ, four more or less distinct slips arise which insert on the occipital condyle, the axis, the atlas and the tip of the transverse process of the third cervical vertebra.

Action: Flexor of the body.

Obliquus capitis

Origin: This muscle is differentiated from the sacro-transverso-transversalis at about the level of the fourth vertebra. It takes origin from the transverse processes of vertebræ three, four and five.

Insertion: On the ventral portion of the posterior border of the squamosal and on the posterior border of the exoccipital.

Action: Aids in lateral movements of the head.

Rectus capitis posticus

Origin: From the spinous processes and dorsal surfaces of the axis and atlas.

Insertion: On the posterior surfaces of the squamosal and occipital.

Action: Aids in lateral movement of the head.

Innervation: All the dorsal axial muscles are supplied by the rami dorsales of the spinal nerves.

THE APPENDICULAR MUSCLES

Sphenodon is a very sluggish creature and since it is phylogenetically so close to the Amphibia, its limb muscles present few specializations. In the forelimb, the olecranon process is present making the direction of flexion fixed; in the posterior limb, however, there is no osseous differentiation to fix the direction of flexion of the crus on the shank. The direction of flexion in the hind limb is fixed only by the position of muscle insertions, as is the case in the Urodeles. *Sphenodon* thus presents a perfect transitional stage between the Urodeles and the more highly specialized reptiles, birds and mammals which have the direction of flexion between the first and second segments of both limbs fixed by osseous differentiations.

This is a very important fact from the viewpoint of serial homology for, since the forelimb has attained the form characteristically presented in the higher, limbed vertebrates, and the hind limb still remains in a rather generalized condition, it should be possible to determine certainly whether the extensor groups of the two limbs are or are not serially homologous. This probability is further strengthened by the fact the hind limb is just sufficiently fixed in its action to make possible an irrefutable numbering of the digits.

The sluggish habits of the creatures have not made the development of a powerful extensor of the digits necessary. As a result, the muscle of the antibrachium homologous to the dorsalis antibrachialis of *Necturus,* m. extensor communis digitorum, is in no way specialized. The extensor communis of the hind limb has progressed a little way and sends a tendon along the lateral surfaces of the third and fourth digits. The flexors of both limbs are well developed, as one might expect since *Sphenodon* is a burrowing animal. The rotators of the femur are very well developed to oppose the action of the powerful caudal muscles. Throughout the appendicular musculature of *Sphenodon,* there occur many accessory tendons, perhaps make-shift adaptations to a changing environment.

Both the specimens dissected had lost and regenerated the last twelve or fourteen caudal segments.[8] This regenerated portion was very interesting because the regeneration was far from perfect. The regenerated portion showed no segmentation whatever. Instead of vertebræ, a hollow cartilaginous rod was formed into which the spinal cord did not penetrate. Between the last vertebra and the regenerated portion of the first specimen studied, there was a necrotic mass about the size of a pea. The muscle fibers in the regenerated portion were arranged in fasciculi which ran its entire length. The interstices were filled with firm fatty connective tissue.

CLASSIFICATION OF THE LIMB MUSCLES

In classifying the limb muscles, the method devised by Bolk will be used.

Anterior Limb

Truncozonal: dorsal; m. serratus anticus, m. levator scapulæ dorsalis superficialis, m. levator scapulæ ventralis superficialis, m. trapezius, m. cephalo-clavicularis; ventral; m. costo-coracoideus, m.

[8] Byerly, T.C., Note on the Partial Regeneration of the Caudal Region of *Sphenodon punctatum.* Anat. Record, Jan. '25.

costo-sterno-coracoideus, m. serratus posterior, m. rectus abdominis externus, m. rectus abdominis internus.

Trunco-stelepodial: dorsal; m. latissimus dorsi; ventral; m. pectoralis.

Zono-stelepodial: dorsal; m. dorsalis scapulæ, m. epicoraco-humeralis, m. scapulo-humeralis anterior, m. scapulo-humeralis posterior, m. subscapulo-coraco-brachialis, m. cleido-humeralis; ventral; m. coraco-brachialis brevis, m. coraco-brachialis medius, m. coraco-brachialis longus, m. supracoraco-humeralis.

Zono-zeugopodial: dorsal; m. anconeus medialis; ventral; m. coraco-antibrachialis.

Stele-zeugopodial: dorsal; m. humero-radialis, m. anconeus lateralis, m. anconeus brevis, m. supinator longus, m. anconeus quartus; ventral; m. humero-antibrachialis, m. pronator teres.

Stele-actinopodial: dorsal; m. extensor carpi radialis, m. extensor carpi ulnaris; ventral; m. flexor carpi radialis, m. flexor carpi ulnaris.

Zeugo-phalangopodial: dorsal; m. supinator brevis; ventral; none.

Interzeugopodial: dorsal; none; ventral; m. pronator quadratus.

Stele-phalangopodial: dorsal; m. extensor communis digitorum; ventral; m. flexor communis digitorum.

Basi-phalangopodial: dorsal; mm. extensor communis digitorum breves, m. extensor pollicis brevis; ventral; mm. flexores communis digitorum breves, mm. lumbricales, mm. adductores communis, m. flexor pollicis, m. abductor pollicis, m. abductor digiti minimi, opponens digiti minimi.

Actino-phalangopodial: dorsal; mm. interossei dorsales; ventral; mm. interossei dorsales.

Posterior Limb

Trunco-zonal: dorsal; m. ilio-sacro-transverso-transversalis and m. caudæ dorsalis might be placed under this head but fall more properly under the head of dorsal axial musculature because they are innervated by the dorsal rami of the spinal nerves and the dorsal rami never supply limb muscles in higher forms; ventral; m. ilio-sacro-costo-costalis and m. ilio-ischio-caudalis have already been discussed under the ventral axial musculature, m. caudi-femoralis, m. caudi-ischio-tibialis, m. ischio-caudalis.

Zono-stelepodial: dorsal; m. ilio-femoralis, m. ischio-trochan-

tericus, m. pubo-ischio-femoralis internus; ventral; m. pubo-ischio-trochantericus, m. pubo-femoralis, m. ischio-femoralis.

Zono-zeugopodial: dorsal; m. extensor ilio-tibialis, m. ambiens, m. ilio-fibularis; ventral; m. pubo-ischio-tibialis, m. pubo-tibialis, m. ischio-tibialis posticus.

Stele-zeugopodial: dorsal; m. femoro-tibialis; ventral; m. gastrocnemius.

Stele-phalangopodial: dorsal; m. extensor communis digitorum; ventral; m. flexor communis longus digitorum.

Zeugo-basipodial: dorsal; m. tibialis anticus, m. peroneus, m. fibulo-tarsale 4; ventral; m. tibialis posticus.

Zeugo-phalangopodial: dorsal; m. abductor et extensor hallucis longus.

Interzeugopodial: m. pronator quadratus.

Basi-phalangopodial: dorsal; mm. extensores breves digitorum, m. abductor et extensor minimi digiti; ventral; mm. lumbricales, mm. adductores communis, mm. flexores breves digitorum, mm. abductores hallucis et secundi.

INNERVATION OF THE LIMB MUSCLES

Designation of the source of nerve supply for each muscle is made by indicating the number or numbers of the spinal nerves contributing. All the foregoing muscles designated as dorsal are supplied by dorsal branches of the ventral rami of the spinal nerves indicated while those designated as ventral are supplied by ventral branches of the ventral rami. The nerves are numbered consecutively from anterior to posterior in preference to the application of names taken from human anatomy.

Anterior Limb

Trunco-zonal—Dorsal

SERRATUS ANTICUS

This muscle consists of four slips from the level of vertebræ six, seven, eight, and nine. Its slips take their

Origin: From the fascia overlying the ilio-sacro-transverso-transversalis at the lateral line level. They extend dorsad, overlapping somewhat, to their

Insertion: On the dorsal border of the suprascapula.

Action: Adductor and levator of the scapula.

Innervation: Nn. spinales 6, 7, 8, and 9.

Colli-scapularis

This muscle occupies a similar position in the fifth body segment. It is a levator of the scapula.

Levator scapulæ dorsalis superficialis

Origin: From the anterior two-thirds of the lateral surface it runs cephalad beneath the trapezius to converge with the levator scapulæ ventralis superficialis and to its

Insertion: On the transverse process of the axis.

Action: Levator of the scapula; aids in lateral movement of head.

Innervation: Nn. spinales 2 and 3.

Levator scapulæ ventralis superficialis

Origin: From the anterior portion of the mesial surface of the scapula above the origin of the trapezius, it runs cephalad to its

Insertion: By a slip to the transverse process of the axis and by a second slip on the transverse process of the third vertebra.

Action: Levator of the scapula and abductor-adductor of the head.

Innervation: Nn. spinales 2 and 3.

Trapezius

This muscle forms a broad, superficial sheet which covers the dorsal two-thirds of the side of the neck, extending caudad as far as the seventh vertebra.

Origin: From the temporal arch, dermad of the depressor mandibulæ, and from the fascia of the dorsal midline, its fibers converge to their

Insertion: On the dorsal third of the anterior border of the scapula.

Action: It is a protractor of the scapula and aids somewhat in holding it in place.

Innervation: Nn. spinales 2, 3, and 4.

Cephalo-clavicularis

This muscle is analogous and probably homologous with the cleidomastoid of higher forms.

Origin: From the posterior border of the dorsal portion of the squamosal beneath the depressor mandibulæ. Its fibers extend ventro-caudally to their

Insertion: On the anterior border of the clavicle, ventral to the insertion of the trapezius.

Action: Levator of the scapula, abductor-adductor of the head.
Innervation: Nn. spinales 2, 3, and 4.

Trunco-stelepodial—Dorsal

LATISSIMUS DORSI

This muscle consists of a large, superficial fanshaped sheet. It opposes the action of the trapezius, cephalo-clavicularis and cleido-humeralis.

Origin: From the fascia of the dorsal midline from the level of the eighth to the level of the fifteenth vertebræ its fibers extend ventro-anteriorly, its fibers converging toward their

Insertion: It passes between the scapular and coracoid heads of the anconeus medius to insert on the postero-dorsal surface of the head of the humerus.

Action: Abductor and retractor of the femur.
Innervation: Nn. spinales 8 to 15.

Trunco-stelepodial—Ventral

PECTORALIS

This muscle is a very powerful adductor of the humerus. Its anterior portion draws the humerus forward, acting independently, while the posterior fibers draw the humerus backward.

Origin: From the posterior border of the episternum and the medial portion of the clavicle, from the medial border of the coracoid, and by digitations from the anterior fifteen gastralea.

Insertion: On the ventral portion of the head and adjacent proximal portion of the humerus.

Innervation: Nn. spinales 7 to 10.

Zono-stelepodial—Dorsal

DORSALIS SCAPULÆ

Origin: From the lateral surface of the dorsal third of the scapula its fibers converge ventrally to their

Insertion: On the anterior surface of the head of the humerus, dorsal to the insertion of the cleido-humeralis.

Action: Abductor of the humerus.
Innervation: N. spinalis 6.

EPICORACO-HUMERALIS

Origin: From the dorsal (inner) surface of the coracoid, it curves posteriorly around that bone to its

Insertion: On the posterior surface of the proximal end of the humerus.

Action: Retractor of the humerus.

Innervation: Nn. spinales 6 and 7.

SCAPULO-HUMERALIS ANTERIOR

Origin: From the lateral surface of the scapula, beneath the dorsalis scapulæ.

Insertion: On the posterior border of the head of the humerus just lateral to the insertion of the scapulo-humeralis posterior.

Action: Rotator of the humerus.

Innervation: Nn. spinales 7 and 8.

SCAPULO-HUMERALIS POSTERIOR

Origin: From the posterior border of the scapula, its fibers extend ventrally to their

Insertion: On the posterior border of the head of the humerus.

Action: Rotator of the humerus.

Innervation: Nn. spinales 7 and 8.

SUBSCAPULO-CORACO-BRACHIALIS

Origin: From the posterior two-thirds of the mesial surface of the scapula, it passes laterally between the scapula and the first complete rib to its

Insertion: On the posterior border of the proximal portion of the humerus, ventral to the insertions of the scapulo-humeralis anterior and posterior.

Action: Rotator of the humerus.

Innervation: N. spinalis 8.

CLEIDO-HUMERALIS

Origin: From the posterior border of the lateral four-fifths of the clavicle, it extends posteriorly to its

Insertion: On the anterior border of the head of the humerus and a slip which gives rise to the humero-radialis.

Action: Protractor of the humerus.

Innervation: N. spinalis 7.

Zono-stelepodial—Ventral

CORACO-BRACHIALIS BREVIS

This is a very small but distinct slip of the coraco-brachialis which lies between the anterior portion of the pectoralis and the coraco-brachialis medius. It aids in adduction of the brachium.

Origin: From the anterior portion of the medial border of the coracoid, it passes laterally to its

Insertion: On the ventral surface of the head of the humerus mesiad from the insertion of the pectoralis.

Innervation: Nn. spinales 6 and 7.

Coraco-brachialis medius

This muscle comprises the anterior portion of the coraco-brachialis mass; it is separated from the coraco-brachialis longus by the ventral nerve trunk to the antibrachium.

Origin: From the anterior half of the ventral surface of the coracoid it extends laterally to its

Insertion: On the ventral surface of the head of the humerus and the proximal portion of its posterior surface.

Action: Adductor and retractor of the humerus.

Innervation: Nn. spinales 6 and 7.

Coraco-brachialis longus

This muscle comprises the posterior moiety of the coraco-brachialis mass. Together with muscle just described, the coraco-brachialis longus and the pectoralis are the chief mechanical agencies used in raising the anterior portion of the body from the ground. Because of the poor adjustment of the limbs for walking—they are still truly 'lateral' appendages and sprawl badly—this group of muscles is necessarily very heavy.

Origin: From the posterior half of the ventral surface of the coracoid, it extends laterally to its

Insertion: Along the distal two-thirds of the posterior border of the humerus.

Innervation: Nn. spinales 7 to 10.

Supracoraco-humeralis

This muscle is continuous at its origin with the coraco-brachialis medius but separates from that muscle to pass dorsad to the head of the humerus.

Origin: From the dorsal portion of the anterior border of the coracoid, it passes beneath the cleido-humeralis and dorsal to the head of the humerus to its

Insertion: On the posterior border of the proximal portion of the humerus, just lateral to the insertion of the scapulo-humeralis anterior.

Action: Rotator of the humerus.
Innervation: N. spinalis 8.

Zono-zeugopodial—Dorsal

ANCONEUS MEDIALIS

Origin: By a tendon from the ventro-caudal portion of the lateral surface of the scapula and by a second tendon from the posterior border of the coracoid. These tendons unite and become muscular just lateral to the latissimus dorsi, which passes between them, and become muscular. The tendon from the scapula receives an accessory tendon which passes to it from the humerus beside the anterior border of the latissimus dorsi. Its fibers extend laterally to their

Insertion: In common with the other two portions of the anconeus group, on the olecranon process of the ulna.

Zono-zeugopodial—Ventral

CORACO-ANTIBRACHIALIS

Origin: From the third fourth posterior of the coracoid, it passes laterally, narrowing to a thin flat ligament as it passes the head of the humerus, and finally passes between the coraco-brachialis longus and the humero-antibrachialis to its

Insertion: On the proximal portion of the medial border of the radius.

Action: Flexor of the antibrachium.
Innervation: Nn. spinales 6, 7, and 8.

Stele-zeugopodial—Dorsal

HUMERO-RADIALIS

Origin: From the lateral portion of the cleido-humeralis, whence it extends laterally to its

Insertion: On the proximal portion of the medial surface of the radius.

Action: It is a flexor of the antibrachium.
Innervation: N. spinalis 7.

ANCONEUS LATERALIS

Origin: From the lateral surface of the head of the humerus, just caudal to the insertions of the cleido-humeralis and of the dorsalis scapulæ, it extends laterally between the humero-radialis and the anconeus medialis, unites with the latter and passes to its

Insertion: On the olecranon process by the aponeurosis common to the group.

Action: Extensor of the antibrachium.
Innervation: Nn. spinales 7 and 8.

Anconeus brevis

Origin: From the posterior border of the humerus, beneath the anconeus medialis. It is a small muscle lying just dorsal to the coraco-brachialis longus and passes laterally from its origin to its
Insertion: In common with the anconeus medialis and the anconeus lateralis, on the olecranon process.
Innervation: Nn. spinales 7 and 8.

Zono-zeugopodial—Ventral

Humero-antibrachialis

Origin: From the proximal portion of the antero-ventral surface of the humerus just distal to the insertion of the pectoralis.
Insertion: On the proximal portion of the ventro-mesial surface of the radius.
Action: Flexor of the antibrachium.
Innervation: Nn. spinales 6, 7, and 8.

Pronator teres

Origin: From the anterior surface of the medial condyle of the humerus it extends laterally and anteriorly beneath the flexor carpi radialis to its
Insertion: On the ventro-mesial surface of the distal half of the radius.
Action: Pronator of the antibrachium.
Innervation: N. spinalis 6.

Stele-actinopodial—Dorsal

Extensor carpi radialis

Origin: From the anterior surface of the outer condyle of the humerus it extends along the outer surface of the radius to its
Insertion: For the most part, by muscle fibers on the outer surface of the distal portion of the radius; a slip inserts by tendinous fibers on carpale 1.
Action: Extensor of the carpus and adductor of the antibrachium.
Innervation: N. spinalis 7.

Extensor carpi ulnaris

Origin: From the outer condyle of the humerus, just distal to the origin of the extensor communis digitorum.

Insertion: Outer surface of carpale 5.
Action: Extensor of the carpus, abductor of the antibrachium.
Innervation: Nn. spinales 6, 7, and 8.

Zeugo-phalangopodial—Dorsal

SUPINATOR BREVIS

Origin: From the medial surface of the middle third of the ulna, its fibers run antero-distad to their
Insertion: On the base of the inner surface of the first metacarpal.
Action: Supinator of the manus.
Innervation: N. spinalis 7.

Interzeugopodial

PRONATOR QUADRATUS

Origin: From the inner surface of the distal two-thirds of the ulna its fibers traverse the space between the radius and the ulna to their
Insertion: On the inner surface of the distal head of the radius.
Action: Pronator of the antibrachium.
Innervation: Nn. spinales 6, 7 and 8, ventral.

Stele-actinopodial—Ventral

FLEXOR CARPI RADIALIS

Origin: From the medial condyle of the humerus, its fibers extend distad and diagonally across the antibrachium to their
Insertion: On the lateral surface of the base of the first metacarpal
Action: Flexor of the manus.
Innervation: Nn. spinales 6 and 7.

FLEXOR CARPI ULNARIS

Origin: From the inner surface of the medial condyle of the humerus, it extends along the outer border of the ulna to its
Insertion: On the outer surface of carpale 5.
Action: Flexor of the carpus and abductor of the manus.

Stele phalangopodial—Dorsal

EXTENSOR COMMUNIS DIGITORUM

Origin: From the lateral condyle of the humerus, it extends superficially to its
Insertion: Into the aponeurosis covering the dorsum of the manus and on the dorsal surfaces of the distal series of carpals.

Action: Levator of the manus and extensor of the antibrachium.
Innervation: Nn. spinales 7 and 8.

FLEXOR COMMUNIS DIGITORUM

Origin: 1) By one head from the medial condyle of the humerus; 2) a second head from the proximal half of the ulna; 3) a small lateral head from the distal portion of the ventral surface of the ulna.

Insertion: This muscle broadens into a flat tendinous sheet which divides into five tendons which are inserted into the bases of the ultimate phalanges of each of the digits.

Action: Flexor of the phalanges.
Innervation: Nn. spinales 7 and 8.

Basi-phalangopodial—Dorsal

EXTENSORES COMMUNIS DIGITORUM BREVES

a) Adductor pollicis brevis

Origin: The muscles comprising the group have a common origin on the distal portion of the dorsal surface of the ulna. The adductor pollicis brevis is the first slip of the group.

Insertion: On the inner surface of the first phalanx of the first digit.

b) Extensor pollicis brevis

This is the second slip of the group.

Insertion: On the ultimate phalanx of the first digit.

c) Extensores communis digitorum breves

The slips to the four remaining digits have been grouped under this head as no abductor minimi digiti has been differentiated.

Insertion: On the ultimate phalanges of digits two to five.

Action: This group of muscle slips furnishes the chief means for extension of the digits.

Innervation: N. spinalis 7.

Basi-phalangopodial—Ventral

FLEXORES COMMUNIS DIGITORUM

Origin: By a head from the distal portion of the ventral surface of the ulna and by a head from the flexor communis digitorum.

Insertion: This sheet is perforated near the points of insertion by the tendons of the flexor communis digitorum and thus has a point of insertion on both sides of each of the phalanges of the proximal series.

Action: Flexor of the digits.
Innervation: Nn. spinales 6, 7, and 8.

Lumbricales

Origin: These muscles, six in number, take origin from the ventral surface of the tendinous distal portion of the flexor communis digitorum.
Insertion: On the lateral surfaces of the proximal phalanges of digits two, three, and four.

Adductores communis

Origin: From the ventral surface of the ulnare, this sheet extends antero-dorsad to its
Insertion: On the ventral surface of the proximal phalanges of digits one, two, and three.
Action: Adductor and pronator of the manus.
Innervation: Nn. spinales 6, 7, and 8.

Flexor pollicis

Origin: From the ventral surface of carpale 1.
Insertion: On the base of the proximal phalanx of the first digit.

Abductor pollicis

Origin: From the ventral surface of the intermediale.
Insertion: On the medial surface of the proximal phalanx of the first digit.
Action: Abductor of the pollex.

Abductor digiti minimi

Origin: From the ventral surface of carpale 4.
Insertion: On the inner surface of the proximal phalanx of the fifth digit.

Opponens digiti minimi

Origin: From the lateral surface of the ulnar sesamoid.
Insertion: On the ventral surface of the proximal phalanx of the fifth digit.

Actino-phalangopodial—Dorsal

Interossei dorsales

Origin: From the bases of all the metacarpals.
Insertion: On the dorsal and lateral surfaces of the bases of the proximal series of phalanges.

Actino-phalangopodial—Ventral

INTEROSSEI VOLARES

Origin: From the ventral surfaces of the bases of the metacarpals.

Insertion: On the ventral and inner surfaces of the bases of the proximal series of phalanges.

Action: Both series of interossei act as abductors and adductors of the digits.

Innervation: All the deep muscles of the hand are innervated by nn. spinales 7 and 8.

Posterior Limb

Trunco-zonal—Ventral

CAUDI-FEMORALIS

Origin: From the lateral surfaces of the hæmal spines of the caudal vertebræ, its fibers extend antero-laterally to their

Insertion: The fibers of this muscle converge and pass between the ilium, the ischium, and the tendinous portion of the caudi-ischio-tibialis to insert on the proximal portion of the ventral surface of the femur. An accessory tendon arises on the lateral surface of the muscle near the point of insertion and runs laterally, parallel to the femur, to insert on the proximal portion of the medial surface of the tibia.

Action: This muscle serves a three-fold function; it is a rotator of the femur, adductor of the femur and an abductor-adductor of the tail. By means of its accessory ligament to the tibia, it also aids in tensing the leg.

Innervation: Nn. spinales 27 and caudal.

CAUDI-ISCHIO-TIBIALIS

Origin: From the ventral surfaces of the transverse processes of the six anterior caudal vertebræ and from the tuber ischium.

Insertion: On the proximal portion of the medial surface of the tibia.

Action: Flexor of the crus on the shank.

Innervation: Nn. spinales 26, 27, and caudal.

ISCHIO-CAUDALIS

Origin: From the lateral surfaces of the hæmal spines of the caudal vertebræ.

Insertion: On the tuber ischium.

Action: Depressor and abductor-adductor of the caudal region.

Innervation: N. spinalis 27 and the succeeding caudal nerves.

Zono-stelepodial—Dorsal

ILIO-FEMORALIS

Origin: From the dorsal portion of the lateral surface of the ílium.

Insertion: On the middle third of the caudal surface of the femur.

Action: Abductor and rotator of the femur.

Innervation: N. spinalis 24.

ISCHIO-TROCHANTERICUS

Origin: From the caudal portion of the inner surface of the ischium, it curves around the posterior border of the ischium and then runs anteriorly to its

Insertion: On the posterior surface of the inner trochanter.

Action: Rotator of the thigh.

Innervation: Nn. spinales 25 and 26.

PUBO-ISCHIO-FEMORALIS INTERNUS

Origin: From the inner surface of the pubis and from the anterior portion of the inner surface of the ischium, this muscle curves antero-dorsally around the anterior side of the pubis just lateral to the pubic tuberosity, to its

Insertion: On the second proximal fourth of the dorso-anterior surface of the femur, along the anterior border of the origin of the femoro-tibialis.

Action: Extensor and rotator of the femur.

Innervation: N. spinalis 23.

Zono-stelepodial—Ventral

PUBO-ISCHIO-TROCHANTERICUS

Origin: From the entire ventral surface of the pubo-ischiadic plate its fibers extend laterally to converge at their

Insertion: On the ventral surface of the inner trochanter of the femur.

Action: Adductor of the thigh.

Innervation: N. spinalis 24.

PUBO-FEMORALIS

Origin: From the inner surface of the pubis and the lateral pubic tuberosity, this muscle extends laterally between the femoro-tibialis which lies dorsal to it and the pubo-tibialis which lies ventral to it, to its

Insertion: On the middle portion of the ventro-caudal surface of the femur.

Action: Abductor and rotator of the femur.

Innervation: N. spinalis 24.

Ischio-femoralis

Origin: From the middle proximal portion of the dorsal surface of the pubo-ischio-tibialis and it extends into the thigh parallel to that muscle.

Insertion: On the ventral surface of the femur, lateral to the insertion of the pubo-femoralis.

Action: Adductor of the thigh.

Innervation: Nn. spinales 26 and 25.

Zono-zeugopodial—Dorsal

Extensor ilio-tibialis

Origin: From the dorsal half of the anterior border of the ilium.

Insertion: On the proximal portion of the anterior surface of the tibia.

Action: Extensor of the crus.

Innervation: N. spinalis 24.

Ambiens

Origin: By tendinous fibers from the lateral tuberosity of the pubis.

Insertion: On the proximal portion of the anterior surface of the tibia.

Action: Extensor of the crus.

Innervation: N. spinalis 24.

Remarks: The two preceding muscles have a common insertion and have been termed the extensor triceps femoris.

Ilio-fibularis

Origin: From the posterior border of the ilium, just above the level of the acetabulum.

Insertion: On the lateral surface of the proximal end of the fibula.

Action: Flexor of the crus.

Innervation: N. spinalis 25.

Remarks: This muscle has been termed the biceps femoralis by Furbringer and since it is quite certainly supplied by the nerve which is homologous with the peroneus communis of higher forms,

this homology may certainly be accepted. If this be true, however, the ilio-fibularis can in no case be serially homologous with the coraco-antibrachialis of the forelimb which has been termed the biceps brachii by Furbringer.

Zono-zeugopodial—Ventral

PUBO-ISCHIO-TIBIALIS

Origin: From the ventral surface of the lateral pubic tuberosity, from the ischiadic and pubic symphyses by a thin, tough, tendinous sheet; the separate elements of this sheet converge and thicken into a heavy, flat muscle which covers almost the entire ventral surface of the thigh.

Insertion: On the proximal portion of the ventral surface of the tibia.

Action: Flexor of the tibia; adductor of the entire leg.

Innervation: Nn. spinales 25 and 26.

PUBO-TIBIALIS

Origin: From the lateral surface of the lateral pubic tuberosity.

Insertion: On the proximal portion of the inner aspect of the tibia.

Action: Adductor and flexor of the crus.

Innervation: N. spinalis 24.

ISCHIO-TIBIALIS POSTICUS

Origin: From the lateral tuberosity of the ischium.

Insertion: On the medial aspect of the tibia, just distal to the insertion of the caudo-ischio-tibialis.

Action: Flexor of the crus.

Innervation: N. spinalis 24.

ISCHIO-TIBIALIS POSTICUS

Origin: From the lateral tuberosity of the ischium.

Insertion: On the medial aspect of the tibia, just distal to the insertion of the caudo-ischio-tibialis.

Action: Flexor of the crus.

Innervation: Nn. spinales 26 and 27.

Remarks: A slip arises from the distal end of this muscle and forms a part of the origin of the flexor communis digitorum.

FEMORO-TIBIALIS

Origin: From the middle third of the dorso-anterior surface of the femur.

Insertion: On the proximal portion of the antero-lateral surface of the tibia, in common with the ambiens and the extensor ilio-tibialis.

Action: Extensor of the crus.

Innervation: By the second nerve of the lumbar plexus.

Stele-phalangopodial—Dorsal

EXTENSOR COMMUNIS DIGITORUM

Origin: From the dorsal surface of the distal end of the femur, it extends superficially along the middle of the dorsal side of the crus to its

Insertion: On the inner surfaces of the bases of the third and fourth metatarsals; each of the two slips is continued as a tendon which runs along the inner surface of the third and fourth digits to insert on their penultimate phalanges.

Action: Levator of the pes and adductor of the third and fourth digits.

Innervation: N. spinalis 25.

Stele-phalangopodial—Ventral

FLEXOR COMMUNIS LONGUS DIGITORUM

Origin: From the medio-caudal surface of the femur, from the medial surface of the fibula, a head from the gastrocnemius and a head from the ischio-tibialis posticus.

Insertion: On the ultimate phalanges of each of the digits.

Action: Flexor of the digits.

Innervation: N. spinalis 26.

Stele-zeugopodial—Ventral

GASTROCNEMIUS

Origin: From the ventral surface of the distal end of the femur, from the fibula and a head from the ischio-tibialis posticus.

Insertion: Into the plantar aponeurosis.

Innervation: N. spinalis 26.

Zeugo-basipodial—Dorsal

TIBIALIS ANTICUS

Origin: From the proximal portion of the anterior surface of the tibia.

Insertion: On the lateral surface of the tibiale, continued forward as a tendon to the lateral surface of the first digit, terminating on the penultimate phalanx.

Action: Adductor of the pes and of the first digit.
Innervation: Nn. spinales 25 and 26.

PERONEUS

Origin: From the proximal portion of the lateral surface of the fibula.
Insertion: On the lateral surface of the fibulare and on the lateral surface of the penultimate phalanx of the fifth digit.
Action: Abductor of the pes and of the fifth digit.
Innervation: N. spinalis 25.

FIBULO-TARSALE 4

Found in one specimen.
Origin: Dorsal surface of the distal head of the fibula.
Insertion: Tarsale 4.
Action: Levator of the foot.
Innervation: N. spinalis 25.

Zeugo-basipodial—Ventral

TIBIALIS POSTICUS

Origin: From the head of the tibia and the ventral surface of the fibula.
Insertion: Latero-ventral surface of the first phalanx of the hallux, and on the tibiale.
Action: Abductor of the hallux and flexor of the pes.
Innervation: Nn. spinales 25 and 26.

Zeugo-phalangopodial—Dorsal

ABDUCTOR ET EXTENSOR HALLUCIS LONGUS

Origin: From the lateral surface of the third distal fourth of the fibula.
Insertion: 1) Extensor portion: On the extensor tendon of the hallux; 2) Abductor of the hallux: On the dorso-lateral surface of the base of the first phalanx of the hallux.
Innervation: N. spinalis 25.

Interzeugopodial

PRONATOR QUADRATUS

Origin: From the medial surface of the distal half of the tibia.
Insertion: Slightly distal to the point of origin, on the medial surface of the fibula.
Action: Rotator of the crus.
Innervation: Nn. spinales 25 and 26.

Basi-phalangopodial—Dorsal

EXTENSORES BREVES DIGITORUM

Origin: The first from the dorsal surface of the tibiale, the remaining three from the dorsal surface of the fibulare.

Insertion: On the extensor tendons of the first four digits.

Action: Extensors of the digits.

Innervation: N. spinalis 25.

ABDUCTOR ET EXTENSOR DIGITI MINIMI

Origin: From the dorsal surface of the fibulare.

Insertion: On the extensor tendon of the fifth digit and the dorsal interossei.

Action: Abductor and extensor of the fifth digit.

Innervation: N. spinalis 25.

Basi-phalangopodial—Ventral

FLEXORES BREVES DIGITORUM

Origin: From the dorsal surface of the plantar aponeurosis.

Insertion: On the bases of the proximal phalanges.

Action: Flexor of the pes.

Innervation: N. spinalis 26.

LUMBRICALES

Origin: From the ventral surface of the distal portion of the flexor communis digitorum.

Insertion: On the inner surfaces of the proximal phalanges of the second, third and fourth digits.

Action: Adductor of the second, third and fourth digits.

Innervation: Nn. spinales 25 and 26.

ADDUCTORES HALLUCIS ET SECUNDI

Origin: From the ventral surface of the fibulare, beneath mm. adductores communis.

Insertion: On the dorsal and lateral surfaces of the penultimate phalanges of the first and second digits.

Action: Abductors of the first and second digits.

Innervation: Third nerve of the lumbar plexus.

Actino-phalangopodial—Dorsal

INTEROSSEI DORSALES

Origin: From the inner surfaces of the bases of all the metatarsales.

Insertion: On the dorsal and lateral surfaces of the bases of the proximal row of phalanges.

Action: Abductor-adductors of the digits.

Innervation: N. spinalis 25.

Actino-phalangopodial—Ventral

INTEROSSEI PLANTARES

Origin: From the inner surfaces of the bases of the second, third, fourth, and fifth metatarsales.

Insertion: On the outer surfaces of the penultimate phalanges of the first, second, third, and fourth digits.

OPPONENS DIGITI MINIMI

Arises from the inner surface of the base of the fifth metatarsal and inserts on the inner surface of the penultimate phalanx of the fifth digit.

Innervation: N. spinalis 26.

ANAL AND COPULATORY MUSCLES

Dne to the fact that one of the specimens dissected had a necrotic mass in the wall of cloaca, and that the alimentary canal of the second had been removed for another study, previous to the dissections for this paper, a thorough dissection of these muscles was impossible. Consequently, no figures were attempted. The following account by Gadow, taken from his "Remarks on the cloaca and on the copulatary organs of the Amniota,"[9] is, as far as could be determined, correct. Unfortunately, he made no figures to show the arrangement of the muscles.

"*Hatteria* possesses a m. perinei s. transverso-analis like the Lizards; also a m. transversus medianus almost exactly like that described in the Crocodilia; its most superficial fibers are transformed into a distinct outermost sphincter, which, according to the shape of the anal opening, lies transversely and not longitudinally as in the Crocodilia.

"From the outside of the m. transversus medianus, and covered by the m. sphincter, starts on each side a broad but thin muscle, which runs back and attaches itself aponeurotically on the skin and on the fascia of the ischio-caudalis, behind the anus. It resembles a very similar pair of muscles in the Lizards.

"The odoriferous glands get a coating of striped muscle fibers from the m. transversus medianus."

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[9] Gadow, H., Phil. Trans. of the Roy. Soc., B 178, p. 12.

SERIAL HOMOLOGIES

Serial homologies are based in this paper, whenever it is possible, on nerve supply. In cases in which the nerve supply was doubtful or seemed unconvincing, an attempt was made to correlate them with the more primitive condition found in *Necturus* and through such a correlation to arrive at a definite conclusion regarding their serial homology.

Before any homology can be attempted, the musculature must be divided into visceral and parietal groups according to its embryonic derivation. The visceral musculature includes all the muscles developed from the hypomeres and is confined to the anterior region of the body; this includes the integumental musculature of *Sphenodon*. The parietal musculature includes all the axial and appendicular musculature. Most of the homologies correspond to those described in previous work on this and other forms and in such cases no discussion was considered necessary.

VISCERAL MUSCULATURE

This group consists of the highly modified remnants of the gill arch musculature of lower forms. In *Sphenodon* it consists of the m. intermandibularis, m. sphincter colli, m. sphincter dorsalis, m. cerato-hyoideus, m. stylohyoideus, m. mylohyoideus, m. temporo-massetericus, m. pterygoideus externus, m. pterygoideus internus, m. depressor mandibulæ, m. constrictor laryngeus and m. dilator laryngeus.

SERIAL HOMOLOGUES IN THE VISCERAL MUSCULATURE

Derivatives from the mm. Levatores arcuum

Innervation by

N. trigeminus	N. facialis
temporo-masseterícus	depressor mandibulæ
pterygoideus externus	stapedius (Osawa)
pterygoideus internus	

Derivatives from the Depressors

Innervation by

N. trigeminus	N. facialis	N. vagus
mylohyoideus	intermandibularis	constrictor laryngeus
	sphincter colli	dilator laryngeus
	sphincter dorsalis	
cerato-hyoideus	stylohyoideus	

Judging from its position and relations, and by the process of elimination, the cerato-hyoideus must represent the anterior belly of the digastric of higher forms. Stretched as it is between two elements of the hyoid, and lying between the pterygoideus internus and the hyoglossus, its position is almost exactly that of the anterior belly of the digastric. Then, too, the remaining muscles of the hyoid of *Sphenodon* are constant or fairly so, through the higher forms while this muscle disappears entirely. Its innervation is that of the mylohyoid and the anterior intermandibularis of lower forms, the hypothetical phylogenetic precursor of the anterior belly of the digastric.

SERIAL HOMOLOGUES IN THE PARIETAL MUSCULATURE

Axial Musculature

Innervation by

Rami dorsales of nn. spinales

semispinalis capitis

cervicis capitis
obliquus capitis
rectus capitis posticus

sacro-transverso-transversalis
interspinales
caudæ dorsalis
sacro-transverso-transversalis

Rami ventrales of nn. spinales

Geniohyoideus, cleido-episterno-hyoideus, sterno-coracoideus profundus, rectus abdominis externus, ischio-caudalis (*partim*).

This, the most ventral series of axial muscles, is practically continuous from the symphysis menti to the caudal extremity. The geniohyoid is innervated by the hypoglossal nerve but that nerve is essentially a spinal nerve in function and phylogeny. The inclusion of the sterno-coracoideus profundus in this series might be questioned but since the coracoid and clavicle are movable, are moved, by this muscle, its internal position should not exclude it from the series.

Genioglossus, hyoglossus, sterno-coracoideus superficialis, rectus abdominis internus.

This second and deeper ventral series is not so complete as the more primitive superficial layer; it is broken in both the cervical and pelvic regions.

longus colli (*partim*)
longus colli (*partim*)
triangularis sterni

ilio-sacro-costo-costalis
obliquus internus
transversalis abdominis

ilio-ischio-caudalis
ischio-caudi-tibialis

omohyoideus
costo-coracoideus
costo-sterno-coracoideus

abdomino-costales
intercostales interni breves
intercostales externi breves

trapezius
latissimus dorsi (*partim*)
levator scapulæ superficialis dorsalis
cephalo-clavicularis
serratus posterior (superficial layer)

colli scapularis
serratus anterior
levator scapulæ ventralis superficialis
serratus posterior (deeper portion)
intercostales ventrales

intercostales interni longi

obliquus externus

obliquus externus

uncini-costales breves
uncini--costales longi

intercostales externi longi
costo-sterno-scapularis

The coccygeal portion of the caudi-ischio-femoralis and the ischio-caudalis (*partim*) are probably posteriorly the serial homologues of the above series, beginning with the omohyoideus.

SERIAL HOMOLOGY OF THE INTRINSIC MUSCLES OF LIMBS

Innervation by nn. spinales

6 and 7

Dorsal

cleido-humeralis

latissimus dorsi (*partim*)
dorsalis scapulæ
scapulo-humeralis anterior
scapulo-humeralis posterior

humero-radialis
supinator longus

Ventral

supracoraco-humeralis

coraco-brachialis brevis
coraco-brachialis medius

subscapulo-coraco-humeralis
epicoraco-humeralis

6, 7, 8

anconeus lateralis

24 and 25

Dorsal

pubo-ischio-femoralis internus

ilio-femoralis

ambiens

Ventral

pubo-femoralis

ischio-femoralis
pubo-ischio-trochantericus

ischio-trochantericus.

25

ilio-fibularis

The finding of satisfactory evidence for or against declaring the extensors and flexors of the forelimbs to be homologues of the extensors and flexors of the hind limbs has been difficult and has led to more or less disagreement among anatomists. Thane gives the following provisional homologies in the flexors of the proximal portions of the limbs in man; biceps flexor cubiti (innervation by the musculo-cutaneous nerve, C. 5 and 6) with the ischiadic head of the biceps cruris, the semitendinosus and the semimembranosus (innervation by the nerve to the hamstrings, L. 4 & 5, S. 1, 2, 3.); the humeral head of the biceps and the brachialis internus (innervation by the musculo-cutaneous) with the femoral head of the biceps cruris (innervation by the peroneal nerve, L. 5, S. 1, 2). Now Cunningham has propounded the following laws which he says are applicable to both fore and hind limbs: "The dorsal and ventral strata of muscles are always supplied by the corresponding dorsal and ventral branches of the nerves concerned—of two muscles, that nearer the head end of the body tends to be supplied by the higher nerve and that nearer the tail end of the body by the lower nerve." (Herringham)[10]

According to these laws, Thane's provisional homologies are impossible; but Thane makes exception to them as follows: "Nervous supply is undoubtedly the best and most valuable guide to muscular homology, but is however not infallible, since variations in the nerve supply occur sometimes in man, and muscles which undoubtedly correspond are occasionally supplied by different nerves in allied animals."[11] The innervation of these flexors and extensors, so far as can be ascertained, is constant throughout the limbed vertebrates from *Sphenodon* upwards, at least so far as the dorsal or ventral nature of their nerve supply is concerned, so Thane's exception would hardly seem to hold for them. His first homology, that of the biceps flexor cubiti with the three muscles of the hamstring group, may be correct though there would seem to be room for doubt because of the comparatively anterior innervation of the biceps flexor cubiti. But since it and its proposed homologues are all innervated by ventral branches, the homology may be correct, the discrepancy due to an elimination of the more posterior nerve fibers in an anterior shifting of the muscle.

As for the second homology, that of the humeral head of the biceps

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[10] Cunningham, D.J., Textbook of Anatomy, p. 671.

[11] Quain's Elements of Anatomy, Tenth ed., vol. 2, part 2, p. 277.

cubiti and the brachialis internus with the femoral head of the biceps cruris, that cannot hold. Even in man, as in the other limbed vertebrates possessing these muscles, the femoral head of the biceps is almost unique in its customary innervation by the common peroneal nerve, being the only muscle in the proximal portion of the hind limb to be regularly so supplied. In the anterior limb, the anconeus, (triceps) holds the same unique position as regards the musculospiral nerve, with the exception of a portion of the brachialis internus (and this far the proposed homology may be correct). Now the humeral head of the biceps cubiti is innervated by the musculocutaneous nerve, which is clearly a ventral nerve, and the femoral head of the biceps by n. peroneus communis, clearly a dorsal nerve. This dorsal character of the peroneus communis is exceptionally clear in *Sphenodon*. The peroneus communis is the sole source of nerve supply for the m. ilio-fibularis, which is certainly analogous in position, insertion and function with the femoral head of the biceps cruris of higher forms and, since its nerve supply is homologous with that of the femoral head of the biceps cruris of those higher forms, must be homologous with that muscle. Such a special homology has been proposed by Osawa and accepted by Gregory and Camp in their papers on osteology and myology.

The n. peroneus communis of *Sphenodon* is quite certainly serially homologous with the nerve of the anterior limb which supplies the m. anconeus since both are dorsal branches and the sole source of nerve supply for the superficial muscles of the distal portions of the limbs. For the same reasons, this anterior nerve must be accepted as the special homologue of the musculo-spiral of higher forms. Would it not then be reasonable to assume that, instead of the homology proposed by Thane, the m. anconeus lateralis and the m. ilio-fibularis should be serially homologous?

anconeus medius	extensor ilio-tibialis
anconeus brevis	femoro-tibialis

Innervation by nn. spinales

6, 7, 8 — 25, 26, 27

Ventral

pectoralis	caudi-femoralis
coraco-antibrachialis	pubo-ischio-tibialis
humero-antibrachialis	pubo-tibialis

	ischio-tibialis posticus
coraco brachialis longus	caudi-ischio-tibialis
flexor communis digitorum	flexor communis dig. longus.
flexor carpi radialis	gastrocnemius
flexor carpi ulnaris	tibialis posticus (*partim*)
pronator teres	tibialis posticus (*partim*)
pronator quadratus	pronator quadratus
flexores breves digitorum	flexores breves digitorum
adductores communis	adductores communis
abductor pollicis	abductores communis
interossei volares	interossei plantares
flexor pollicis	tibialis posticus (distal portion)
apponens digiti minimi adductor pollicis	flexores breves dig. (*partim*)

Dorsal

extensor carpi radialis	tibialis anticus
extensor carpi ulnaris	peroneus
supinator brevis	abductor et extensor hal. long.
extensor communis digitorum	extensor communis digitorum longus
extensor communis dig. breves	extensor pollicis brevis
abductor et ex. dig. min.	ex. com. dig. breves.
fibulo-tarsale 4	
interossei dorsales	interossei dorsales

DISCUSSION AND COMPARISON

While the musculature of *Sphenodon* is still very primitive in its nature, it shows some marked advances from the condition in the more primitive Urodeles. In discussing the advances found in the musculature of *Sphenodon,* the very excellent work of H. H. Wilder on the muscles of *Necturus* is used as a basis. *Necturus* presents the most primitive condition found in any of our living and familiar limbed vertebrates.

A brief survey would show a few major changes. Functional gills do not appear in *Sphenodon* and this fact with the elongation of the cervical region (it is longer by three segments) make a marked change in the musculature of that region. The greatest specialization in the muscular system of *Sphenodon* is shown in the axial

musculature and that of the distal portions of the limbs with the caudal musculature shows the least.

In making the special homologies necessary to such a comparison, the following points brought out by previous workers have been carefully heeded: that vertebrate parietal muscles are primarily divided into a group above the lateral line and a group or mass below the lateral line; that the limb muscles come from this ventral mass and that they too, are divided into a dorsal and a ventral mass; that the nerve supply is constant and split in the same way as the primary muscle masses; that these primary muscle masses may split longitudinally, transversely or horizontally to meet the needs of the stresses of varying habitat conditions that are important enough to make such splitting a survival character; that the units so produced may later fuse or disappear or shift their origins or insertions or both but that they seldom or never shift their nerve supply.

In the visceral musculature, there has been a considerable amount of shifting and restriction, due to the loss of the functional gills. The loss of the levatores arcuum and a corresponding spread of the posterior intermandibular, present the most striking superficial changes. The depressors of the most posterior gill arch have shifted to form the intrinsic muscles of the larynx and the anterior intermandibularis has given rise to the mylohyoideus and the coracohyoideus.

The disappearance of the gills has also led to a readjustment of the superficial axial muscles of the neck. The omohyoideus has shifted its insertion ventrally with the development of the hyoid apparatus. The trapezius has spread dorsally to the midline and anteriorly to the head; the cephalo-clavicularis is probably a product of the splitting of the trapezius. There have also been marked changes in the remainder of the axial musculature. The dorsal portion, which is without differentiation in *Necturus*, is split, except in the caudal region, into rather definite medial and lateral portions. Each of these longitudinal divisions has undergone a considerable amount of specialization which has been described in the body of this paper. The ventral axial musculature, which is also very simple in *Necturus*, has broken into a complex system of muscles for respiration and perhaps for crawling.

Proximal Portions of the Limbs

Anterior

Very few significant changes from the primitive condition have

taken place in this region. The procoraco-humeralis has disappeared or is present as the supracoraco-humeralis. An epicoraco-humeralis has developed from the ventral muscle mass and the brachio-radialis has split to form the humero-radialis and the supinator longus of *Sphenodon*. The coraco-brachialii have spread their origin to cover the entire ventral surface of the coracoid plate.

Posterior

The changes from the urodele condition shown in this region are not extensive. The pubo-ischio-tibialis has spread over the more anterior pubo-ischio-femoralis externus which in turn has split into the ischio-femoralis and the pubo-ischio-trochantericus. The pubo-tibialis has given rise to a m. pubo-femoralis and the pubo-ischio-femoralis to an ambiens. The rectus abdominis externus has extended posteriorly to the caudal border of the ischiadic plate. There has been a great increase in the extent but not in the number of the caudal muscles. The caudali-pubo-ischio-tibialis has split to form an ischio-tibialis posticus and the caudo-ischio-tibialis.

Distal Portions of the Limbs

Anterior

The dorsum of the antibrachium is quite like that of *Necturus*. There is, of course, an additional interosseous muscle and an additional short extensor for the first digit that which is not present in *Necturus*. The only other changes are a shift of the origin of the supinator to the medial surface of the ulna and the formation of an aponeurotic insertion for the extensor communis digitorum. The ventral surfaces show a single long flexor which inserts by tendons on the ultimate phalanges instead of into a palmar aponeurosis. A pronator teres appears, probably split from the flexor carpi radialis. The four layers of so-called flexors intrinsic to the foot[12] are still present. The only important changes they have made is that the flexor medius layer takes origin from the ventral surface of the long flexor tendon as the lumbricales, six in number, and the flexor profundus group is limited in its action to the three inner digits. Besides the typical fourth layer of interossei volares, there have split from the superficial flexor group an opponens digiti minimi, an abductor digiti minimi, an abductor pollicis and a flexor pollicis.

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12 McMurrich, J.P., Am. Journ. of Anat., vol. 6, p. 471.

Posterior

In the dorsum of the distal portion of the hind limb, the only noteworthy advances are the restriction of the insertion of the extensor communis digitorum to the third and fourth digits and the development of the abductor et extensor hallucis longus. Of the muscles in the ventral surface in this region, there is little to say. The long flexors have increased somewhat in extent and number of points of origin. The layers in the foot are quite like those in the hand except that there are only three lumbricales and that the third layer has split to form the adductores communis and abductores communis. Then, too, the opponens minimi digiti, abductor minimi digiti and abductor pollicis have no homologues, as separate entities in the foot. The flexor hallucis[13] is a direct continuation of the tibialis posticus.

SUMMARY

1. Description of muscles: origin, insertion, action, and innervation have been given in tabular form for the sake of brevity; the figures are sufficient to illustrate the relations.

2. A distinct m. triangularis sterni was found; such a muscle has not previously been described in any animal lower than the class Aves.

3. The ventral axial musculature which has not previously been completely described or fully figured, has been completely discussed and illustrated.

4. Serial homologies have been made on a basis of innervation. An argument from facts brought to light by dissection and based on the most widely accepted laws for serial homology has been presented to prove the homology of the femoral head of the biceps cruris with the anconeus lateralis.

5. Diagrams of the complete innervation of both limbs have been included for greater clearness in the comparisons.

6. Special homologies of the muscles of *Necturus* with those of *Sphenodon*, with comparisons, have been made.

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[13] Osawa, G., Archiv. fur Mikros. Anat., Bd. 51.

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EXPLANATION OF FIGURES

1. Superficial muscles of the lateral aspect
2. Integumental muscles
3. Musculature of the dorsal aspect of the posterior limb
4. Ventral aspect of the anterior half of the body
5. Middle layer of the ventral muscles of the forelimb
6. Lateral aspect of the intercostal musculature
7. Medial aspect of the intercostal musculature
8. Ventro-internal aspect of the ventral axial muscles
9. Lateral aspect of the deeper muscles of the anterior region
10. Ventral aspect of the deeper muscles of the hyoid
11. Ventral aspect of the deep palmar muscles
12. Laryngeal muscles
13. Ventral aspect of the caudal half of the body
14. Ventral aspect of the deep muscles of the posterior limb
15. Fifth layer of muscles of the plantar aspect of the foot
16. Sixth layer of muscles of the plantar aspect of the foot
17. Seventh layer of muscles of the plantar aspect

NOMENCLATURE

A. m. ambiens. A.C. m. adductores communis. ACo. mm. abdomino-costales. ADM. m. abductor pollicis. AEDM. m. abductor et extensor digiti minimi. AL. m. anconeus lateralis. AM. m. anconeus medius. AP. m. adductor digiti minimi. APB. m. adductor pollicis brevis. CA. m. coraco-antibrachialis. CBBr. m. coraco-brachialis brevis. CBL. m. coraco-brachialis longus. CBM. m. coraco-brachialis medius. CC. m. costo-coracoideus. CD. m. caudæ dorsalis. CEH. m. cleido-episterno-hyoideus. CF. m. caudi-femoralis. CH. m. cleido-humeralis. CHy. m. cerato-hyoideus. CL. m. constrictor laryngeus. CS. m. colli-scapularis. CSC. m. costo-sterno-coracoideus. DL. m. dilator laryngeus. DM. m. depressor mandibulæ. DS. m. dorsalis scapulæ. ECD. m. extensor communis digitorum. ECDB. m. extensor communis digitorum brevis. ECDL. m. extensor communis digitorum longus. ECR. m. extensor carpi radialis. ECU. m. extensor carpi ulnaris. EH. m. epicoraco-humeralis. EIT. m. extensor ilio-tibialis. FCDB. m. flexor communis digitorum brevis. FCDL. m. flexor communis digitorum longus (pedis). FCDS. m. flexor communis digitorum. FCR. m. flexor carpi radialis. FCU. m. flexor carpi ulnaris. FM. m. fibulo-tarsale 4. FP. m. opponens digiti minimi. FT. m. femoro-tibialis. G. m. gastrocnemius. GG. m. genioglossus. GH. m. geniohyoideus. HA. m. humero-antibrachialis. HG. m. hyoglossus. HR. m. humero-radialis. IC. m. ischio-caudalis. ICT. m. ischio-caudi-tibialis. IEB. mm. intercostales externi breves. IEL. mm. intercostales externi longi. IF. m. ilio-femoralis. IFi. m. ilio-fibularis. II. mm. intercostales interni breves. IIL. mm. intercostales interni longi. INT. m. intermandibularis. IPL. mm. interossei plantares. ISCC. m. ilio-sacro-costo-costalis. IST. m. ilio-ischio-caudalis. ITP. m. ischio-tibialis posticus. IV. mm. intercostales ventrales. IVo. mm. interossei volares. L. mm. lumbricales. LC. m. longus colli. LSDS. M. levator scapulæ dorsalis superficialis. LSVS. m. levator scapulæ ventralis superficialis. M. m. mylohyoideus. OC. m. obliquus capitis. ODM. m. flexor pollicis. OE. m. obliquus externus. OH. m. omohyoideus. OI. m. obliquus internus. P. m. pectoralis. Pe. m. peroneus. PF. m. pubo-femoralis. PI. m. pterygoideus internus. PIT. m. pubo-ischio-tibialis. PT. m. pubo-tibialis. PITr. m. pubo-ischio-trochantericus. PT. m. pronator teres. RAI. m. rectus abdominis internus. RAE. m. rectus abdominis externus. RCP. m. rectus capitis posticus. S. m. supinator longus. SB. m. supinator brevis. SC. m. spinalis capitis. SeC. m. semispinalis capitis. SCP. m. sterno-coracoideus profundus. SCS. m. sterno-coracoideus superficialis. SH. m. stylohyoideus. SHa. m. scapulo-humeralis anterior. SP. m. scapulo-humeralis posterior. STT. m. sacro-transverso-transversalis. TA. m. tibialis anticus. TM. m. temporo-massetericus. TP. m. tibialis posticus. TrA. m. transversalis abdominis. TS. m. triangularis sterni. UCB. mm. uncino-costales breves. UCL. mm. uncino-costales longi.

PLATES

PLATE I

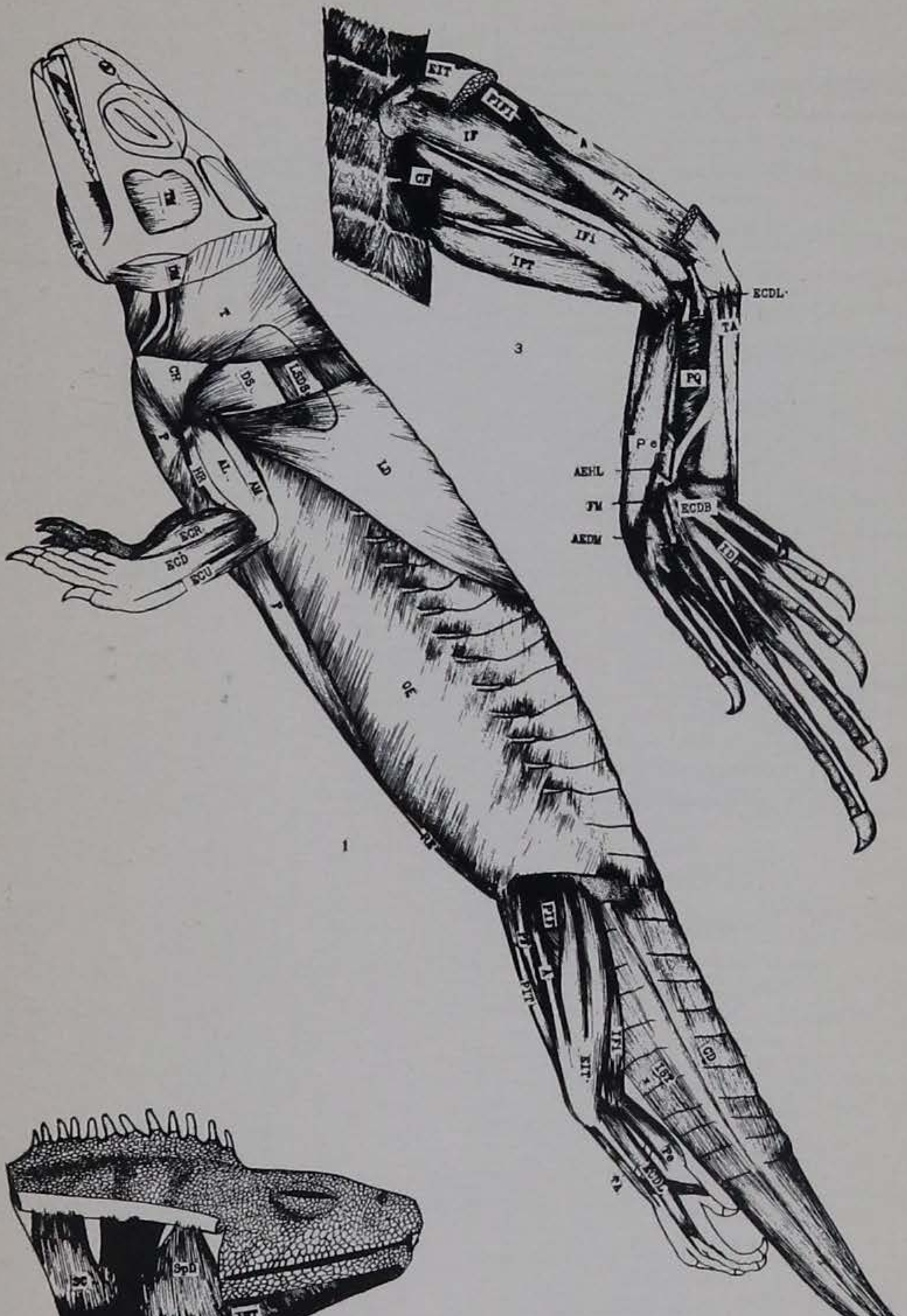

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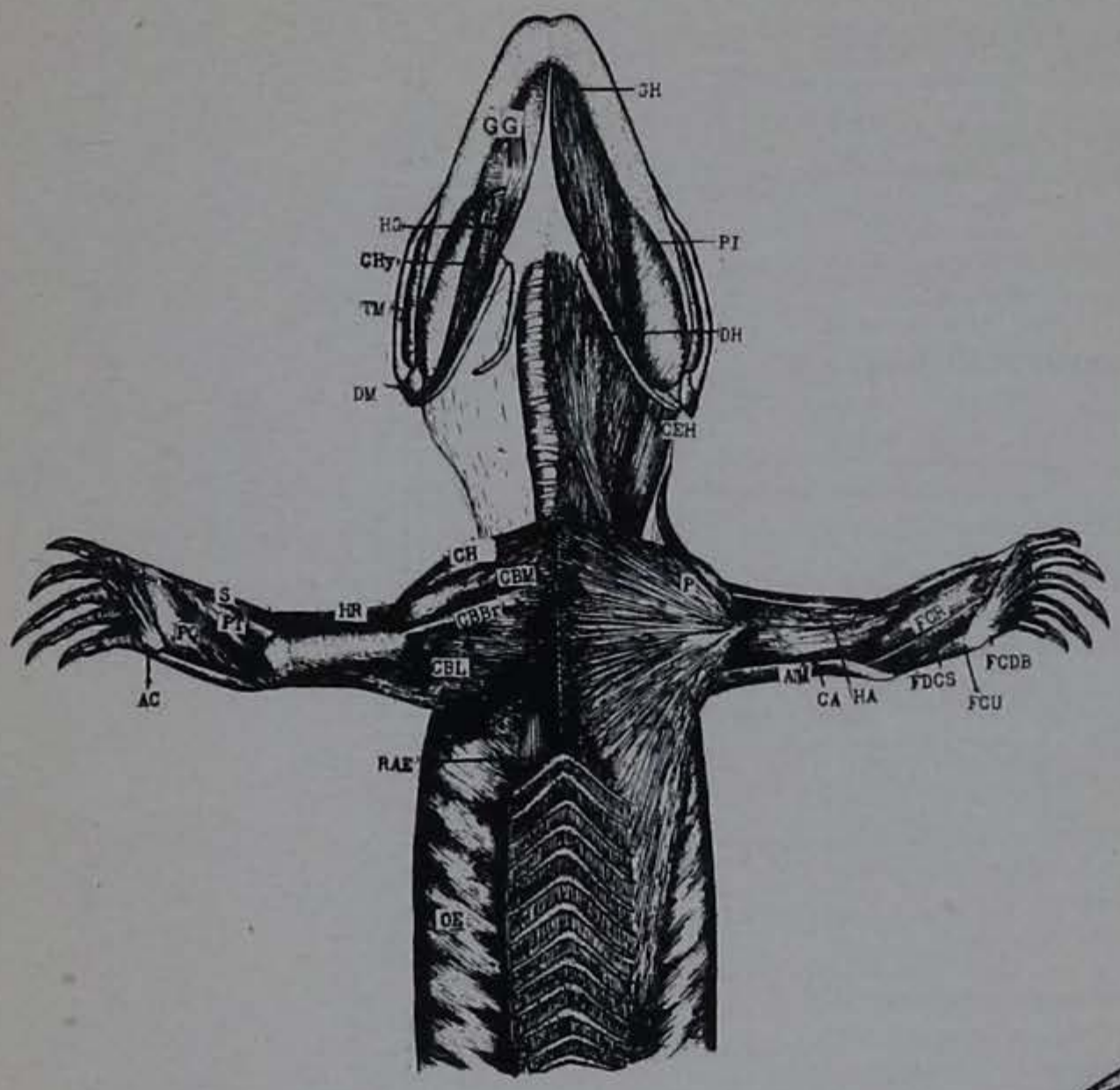
PLATE II



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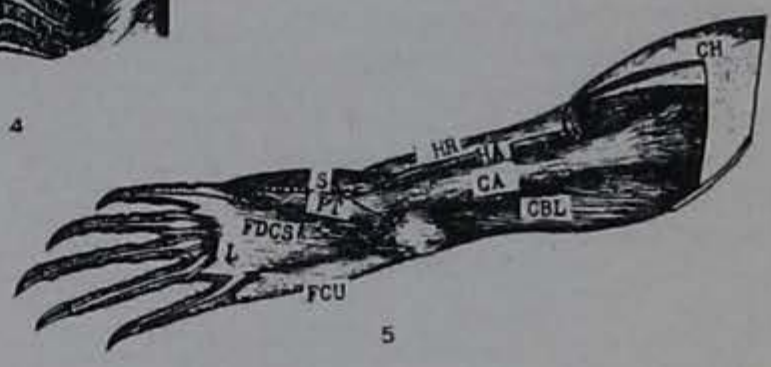

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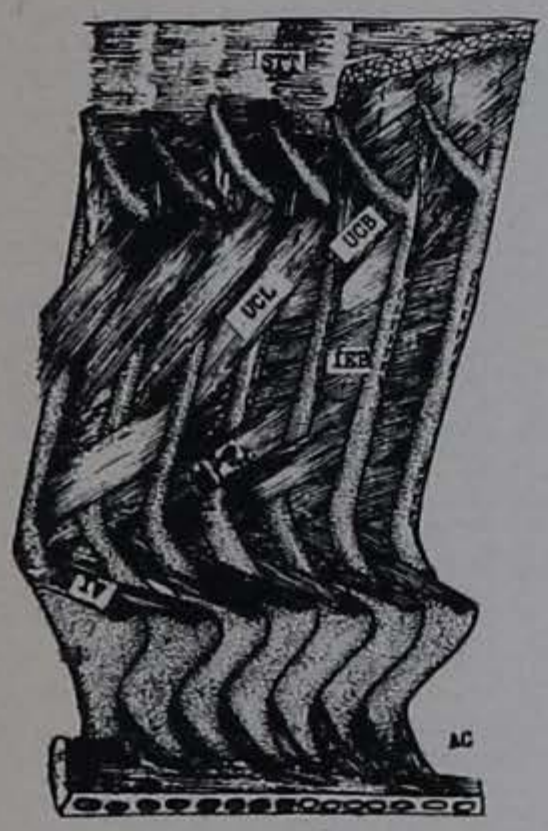

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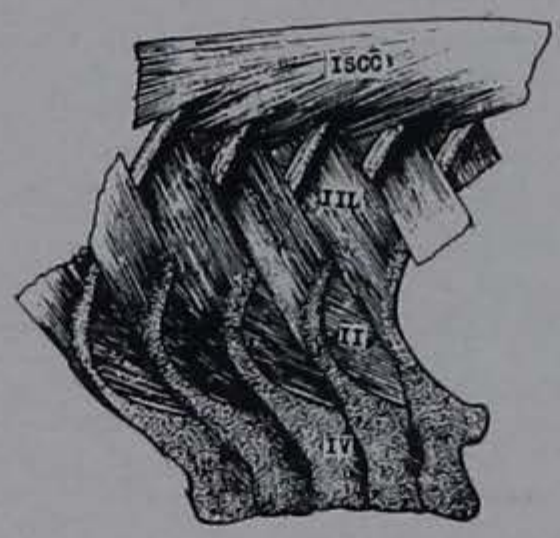

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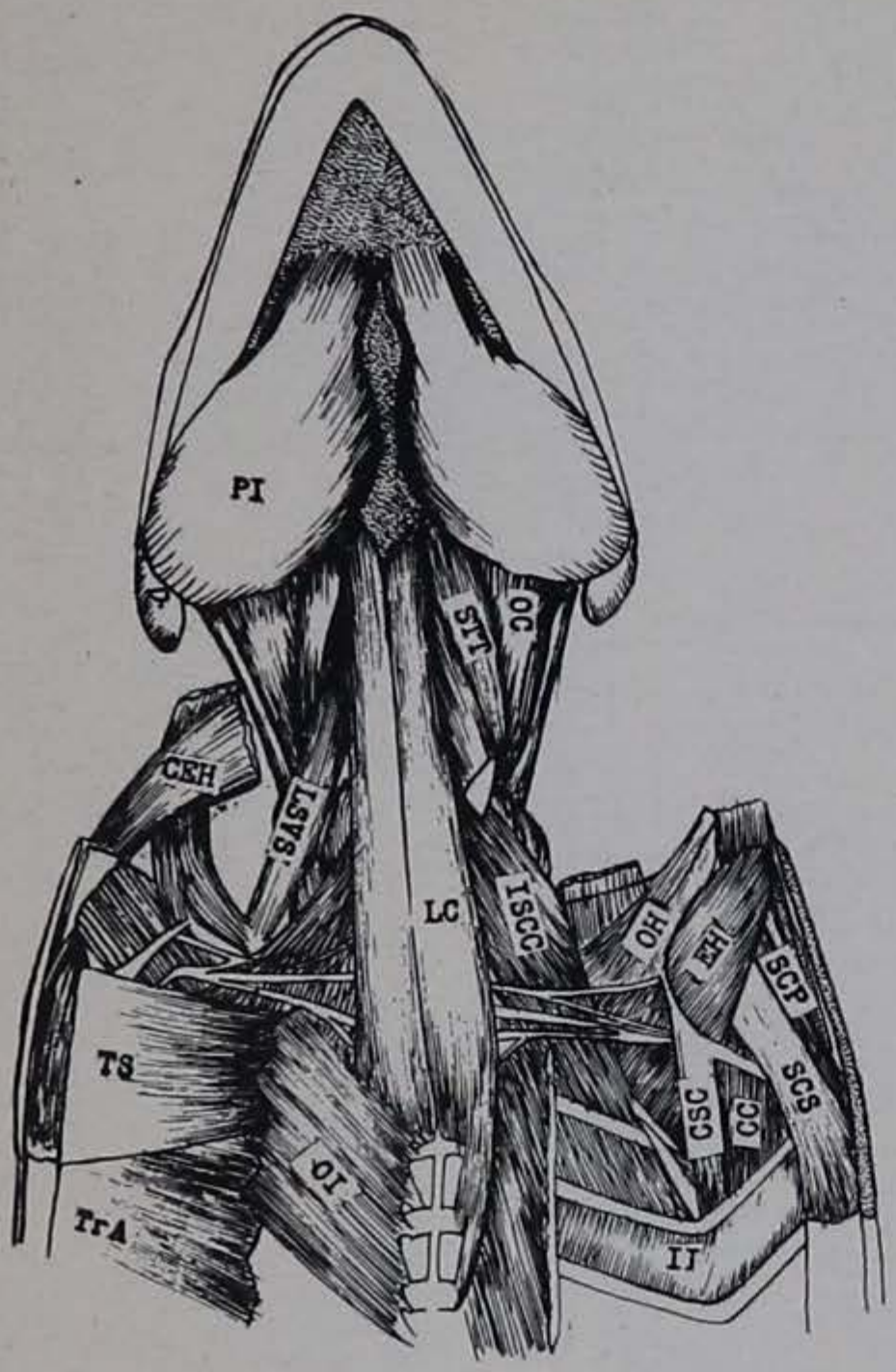

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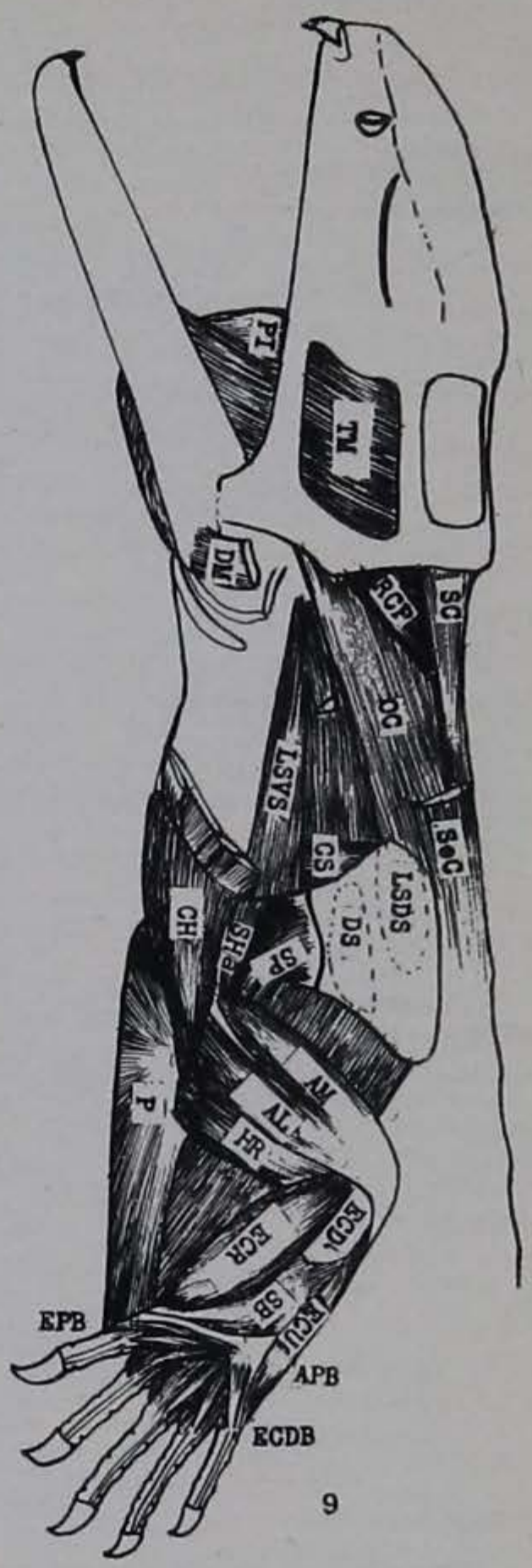

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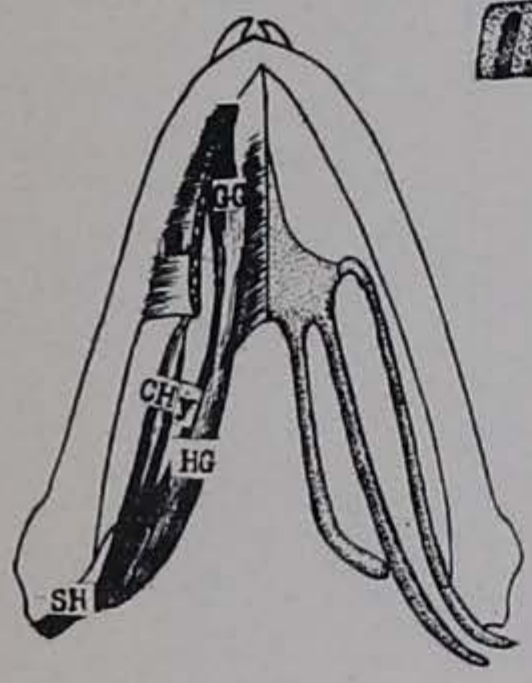

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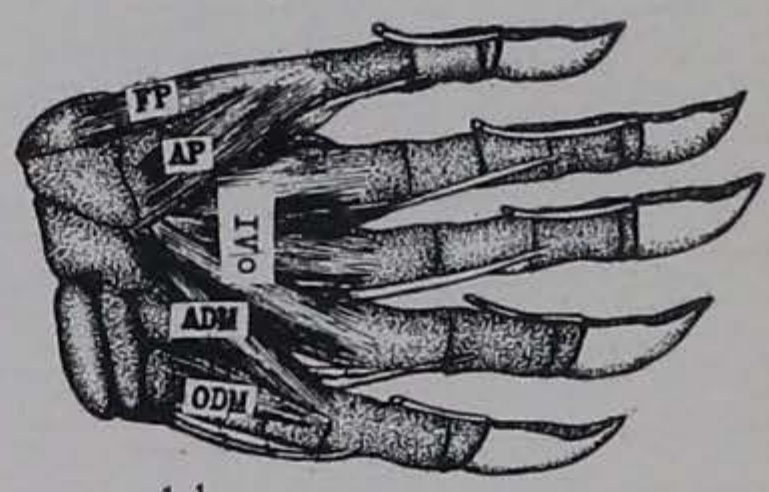

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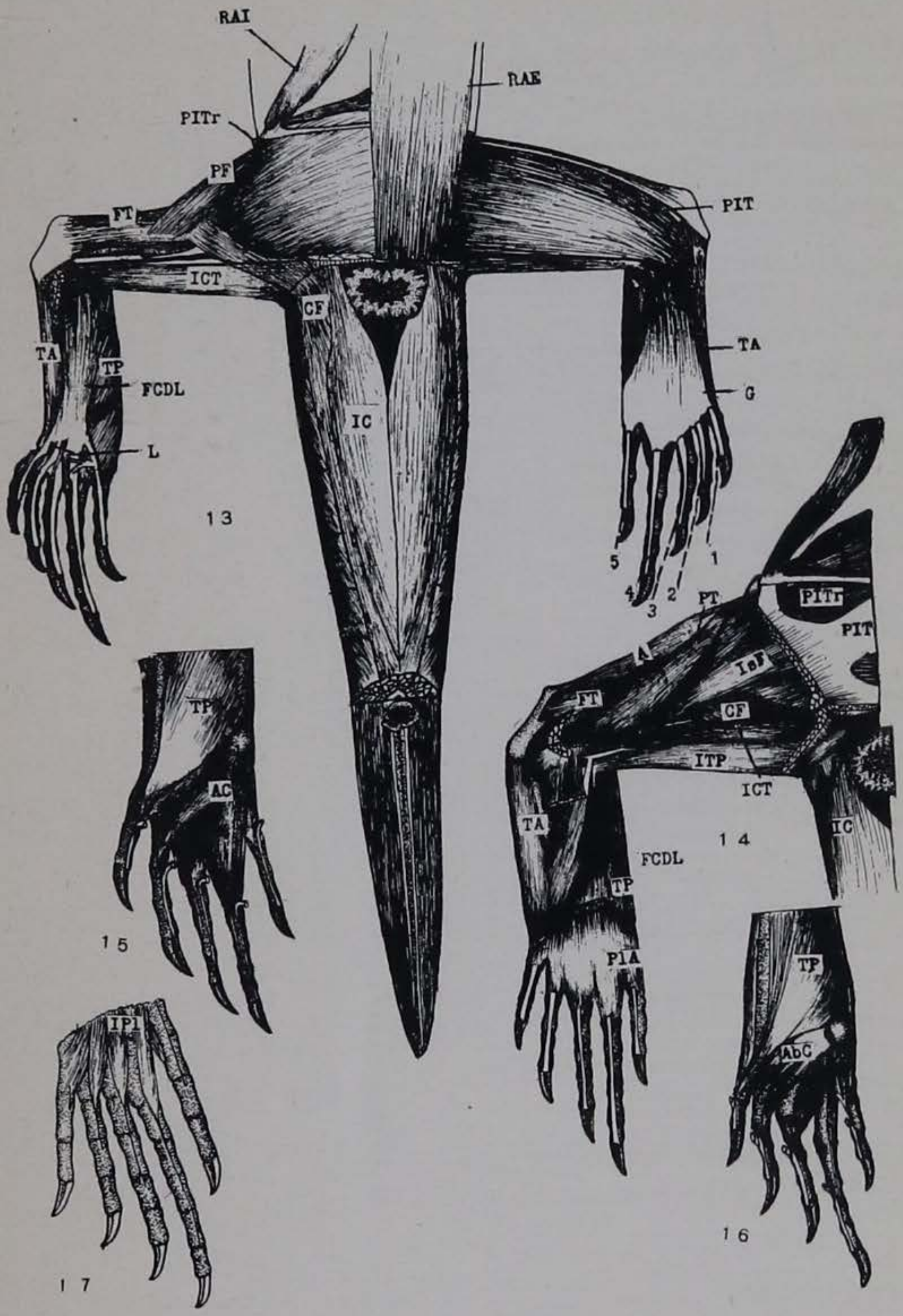
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