59.14.98,1:81

Article X.—THE LOCOMOTOR APPARATUS OF CERTAIN PRIMITIVE AND MAMMAL-LIKE REPTILES[1]

By Alfred S. Romer

Plates XXVII to XLVI

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[1]Studies in Comparative Myology and Osteology from the Laboratory of Comparative Anatomy, No. VI.

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INTRODUCTION

The locomotor apparatus of the primitive Permo-Carboniferous reptiles of the Texas deposits, and of the mammal-like forms of the South African Permian, has been of interest since the first discovery of these groups in the middle of the last century. The accumulation of evidence shows that the cotylosaurs and pelycosaurs are in their limb structure close to the typical Stegocephalia and through them not far removed from the primitive tetrapod type; while, on the other hand, the ancestors of all the amniotes are to be sought among them. Hence their limbs, although radically different from those of any existing forms, are close to the common type from which those of higher sauropsids and mammals have arisen. The mammal-like forms, or therapsids, bridge much of the gap between primitive reptiles and mammals. These two groups thus have an important bearing on the study of the tetrapod limb.

Unfortunately, most workers on these forms have been intent on skull structure and few comparative studies have been made of the limbs. Recently, however, Watson (1917*a*) has discussed many of the questions involving the fore limb and Gregory and Camp (1918) have discussed the general homologies of tetrapod limb muscles and restored the musculature of some South African forms. The present paper is an attempt at a further analysis of the locomotor apparatus of certain cotylosaurs, pelycosaurs, and therapsids, with reference to the musculature, bony structure, and movements of the girdles and limbs. Comparisons have been made with the Stegocephalia, some of which are exceedingly close in their structure, and certain points which seem of interest in connection with the first stages in the evolution of the tetrapod limb have been considered.

In the restoration of the musculature, the immature state of comparative myology has been a great handicap. This is reflected in the texts on comparative anatomy, which under musculature usually speak briefly of a few general topics, as flexors and extensors, and then pass quickly on to firmer ground. Numerous excellent papers on special forms or muscle groups have appeared, those of Fürbringer (1873, 1874, 1876, 1900) on the shoulder and Gadow (1882) and Perrin (1892, 1895) on the posterior extremity being especially noteworthy; but few have attempted any broad comparisons between groups. Consequently, I have found it necessary in great measure to make anew an analysis of the relations of the muscle groups of the living types in order to interpret the indications of muscular origins and insertions found on the fossil skeletons. A discussion of the various groups of limb muscles has been in-

cluded in the hope that this would be of benefit to comparative myology, especially so because here it is unnecessary to appeal to imaginary "Archetypes" since the forms under discussion are exceedingly close to the actual connecting links.

An attempt at a complete restoration of these extinct types allows much opportunity for error. Even if sure of the origin and insertion of a muscle, its exact size may be uncertain. The definite boundaries of a fleshy origin are difficult to delimit. Often, as in the case of the latissimus dorsi, one end of a muscle may be determined with much certainty but the other extremity may be beyond our power to locate exactly. The poor character of the surface of the fossil bones, especially of those types the material of which is scant, leaves doubt as to the details of the muscles connected with them. This is especially true of the South African forms, where the matrix is usually very difficult. But in spite of this, it has been thought best to present a completed picture in order to provide a basis for further work.

Under both fore and hind limb, the probable musculature of *Diadectes* (a primitive cotylosaur), *Dimetrodon* (an advanced pelycosaur), and *Moschops* (one of the lowest therapsids) has been restored, with a discussion of the distribution of the muscles involved in various modern and extinct forms. For comparison, views are given of the muscles of *Iguana* and *Didelphys*, as fairly representative of living reptiles and mammals. Then follows a general dicussion of the bones in relation to locomotion in the fossil groups as a whole. Brief summaries are given of the various types of locomotion discussed and some of the points on the relationships of the various groups, as suggested by the limbs, are noted. Finally, a table of homologies of limb muscles in urodeles, reptiles, and mammals is presented.

For uniformity, all views are of limbs and bones of the right side. Because of breaks, crushing, erosion, and immaturity of the specimens at death, it is seldom that any one fossil bone will give a complete picture. Consequently, the illustrations are almost without exception composites, based upon a study of most of the American material and of the Broom collection from South Africa in The American Museum of Natural History.

It is impossible to give in a brief space the complete synonymy of muscle terminology. In each instance the most commonly used names of the muscle or muscles involved are given; if the mammalian terms differ from the reptilian, the latter are given first, the former added in parentheses.

The criteria for muscular homologies have been often discussed. Function, it is agreed, is of little value. Homology of origin and insertion are of great value. The relative position of adjacent muscles is of importance.

The question of innervations is most often debated. That there is a relation of some sort between muscle masses and nerves, a thesis especially

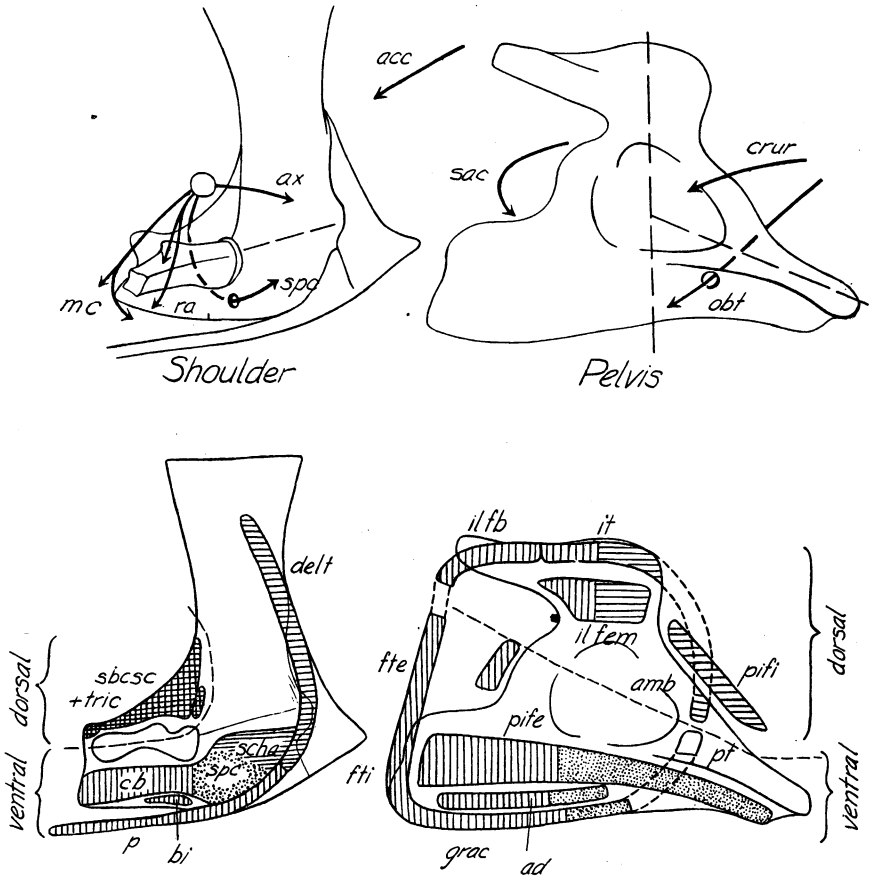

Figure 1. Diagrams to show the primitive areas of innervation of pectoral and pelvic girdles (above) and the distribution of the proximal portions of the primitive dorsal and ventral muscle masses (below). In the pectoral girdle the dorsal muscle mass is innervated by short branches from the plexus and radial nerves (*Ra*) (cross-hatching). The ventral mass is innervated by the "axillary" nerves (*Ax*) (horizontal ruling), the supracoracoid or suprascapular (*Spc*) (stippled), and by them usculo-cutaneous (*Mc*), median and ulnar nerves (vertical hatching). The accessory (*Acc*) nerve innervates all or part of the primitive trapezius group. In the pelvis the posterior portion of both dorsal and ventral masses is innervated through the sacral plexus (*Sac*) (vertical ruling). The anterior end of the dorsal mass is innervated by the femoral or other nerves of the lumbar plexus (*Crur*) (horizontal ruling); the anterior end of the ventral mass by the obturator nerve (*Obt*) (stippled).

upheld by the Heidelburg school, cannot be doubted; many peculiarities in innervations are explained by reference to their phylogenetic history; the peculiar distribution of the saphenous nerve in the monotremes, as discussed by Ruge (1878, p. 599), Westling (1889, p. 54), and Frets (1910, pp. 20, 21), is the only flat contradiction to this assumption and even this may prove to have an explanation, while some of the recent experimental work (as Detweiler, 1920) seems to show that similar relations exist in ontogeny.

Great difficulty is caused by our inability to be sure of the homology of the nerves themselves in two different animals. A homology of the finer branches, such as that attempted by De Man (1873) in the Amphibia, has proved valueless. Many general topographic divisions, such as Fürbringer's into dorsal and ventral rami, are also of little value in this connection. It is obvious that, if a muscle is ventral in position, the nerve innervating it will of necessity be a "ventral ramus," and vice versa; and he himself (1876, p. 719) admits that the distinction breaks down in the case of the suprascapular (supracoracoid) nerve, where the muscular homologies are fairly obvious. Neither will the course of a nerve in relation to the adjacent muscles prove its identity, as is witnessed by the tibial nerve of salamanders, which Siegelbaur (1904, p. 390) has shown may pass to either side of the femoro-tibialis or through it. It is usually impracticable to trace the fibers through the plexus and ascertain their segmental origins; and, with our present lack of knowledge of segmental values, the usefulness of this would be questionable.

On the other hand, the relation of the nerves to the bones of the limbs and girdles seems fairly constant and gives us at least some major topographical divisions upon which we may rely with fair certainty. (Fig. 1.) In the fore limb (Fürbringer, 1873, etc.), the distribution of the supracoracoid (suprascapular) nerve (*Spc*) seems to be distinct from that of the nerves which pass from the axillary region either antero-dorsally (axillary or radial nerve or equivalents, *Ax, Ra*) or postero-ventrally (musculo-cutaneous or equivalents, *M–C*); while the distinctive vagal innervation of the trapezius and its derivatives offers another point of attack. In the hind limb, three regions, recognized by Gadow (1882), may be distinguished: (1) that of the lumbar plexus and femoral nerve, anterior to the ilium (*Crur*); (2) that of the obturator nerve (*Obt*); and (3) that of the nerves of the sacral plexus emerging posterior to the ilium (*Sac*).

The question of double innervations is of great importance in the study of musculature. Cases of this occur in most of the muscle groups

of the upper leg and in the muscles running to the humerus. Some have tended to look upon these cases as examples of a secondary fusion of primitively separate muscles, but their constant reappearance in similar muscles in widely separated forms tends to discredit this view. Even on *a priori* grounds there is no reason to believe in the "purity" of innervations, since unquestionably the limb musculature is derived from a primitively segmental musculature. Frets (1910, p. 91) suggested that this might be the case in those instances which occur in the Monotreme; these double innervations will be discussed further on in connection with the muscular groups concerned.

The following is an outline of the general systematic position of the fossil forms discussed. Fuller classifications of these groups have been made recently by Watson (1917) and Williston (1916 and 1917).

Class AMPHIBIA

Subclass STEGOCEPHALIA.—Including all primitive forms of the class; all extinct

Order Temnospondyli

Suborder Embolomeri.—Considered (especially by Watson, 1919, etc.) as the most primitive tetrapod group. *Cricotus*

Suborder Rachitomi.—More "advanced" forms. *Eryops, Cacops, Achelomma, Cochleosaurus*

Order Lepospondyli.—"Microsaurs," etc. Possibly a composite group; although most of its members are very specialized, their relationship to primitive reptiles has been suggested. *Diplocaulus, Ichthyacanthus, Batrachiderpeton, Keraterpeton*

Class REPTILIA

Series ANAPSIDA

Order Cotylosauria.—"Stem reptiles," with roofed skulls. As to limb structure they may be divided as follows

(*a*) Forms with primitive limbs. (American) *Seymouria, Diadectes, Diasparactus, Limnoscelis.* Although these forms differ greatly in other respects, the limbs are essentially the same

(*b*) More advanced American types. Captorhinomorpha of Watson in part, *Captorhinus, Labidosaurus, Pariotichus, Pleuristion*

(*c*) Of uncertain position. *Archeria*, known only from the humerus

(*d*) Pareiasauria. Old world Permian forms with a combination of primitive, specialized, and mammal-like characters, the latter usually considered as specializations. *Pareiasaurus, Propappus*

Series SYNAPSIDA

Order Pelycosauria or Theromorpha.—An assemblage of great diversity, possessing a lateral temporal opening and usually other advanced characters over the last-named order.

Family Caseidæ. *Casea*
Family Poliosauridæ. *Varanosaurus, Varanoops, Pœcilospondylus*
Family Ophiacodontidæ. *Ophiacodon, Theropleura*
Family Clepsydropidæ. *Dimetrodon, Clepsydrops*
Family Edaphosauridæ. *Naosaurus, Edaphosaurus*
Forms of uncertain position. *Aræoscelis* and *Kadaliosaurus*. Considered by Williston to be ancestral to lizards

Order Therapsida.—Mammal-like reptiles, chiefly South African.

Suborder Dinocephalia.—The most primitive therapsid group adequately known. *Moschops*

Suborder Dicynodontia.—Advanced therapsids, but specialized in dentition, etc. *Dicynodon*

Suborders Gorgonopsia, Therocephalia, Bauriamorpha, Cynodontia (Theriodontia) —A series of groups more generalized in character and with stages leading toward the mammalian type of organization. *Cynognathus, Ictidosuchus*

I wish to acknowledge my debt of gratitude to Dr. W. K. Gregory, of Columbia University and The American Museum of Natural History, at whose suggestion and under whose direction this work was undertaken. I have benefited greatly from discussion with my fellow students in myology, C. L. Camp, J. P. Chapin, and G. K. Noble.

I am greatly indebted to the authorities of The American Museum of Natural History, and especially to Dr. W. D. Matthew, Curator of Vertebrate Palæontology, for allowing me free use of their abundant material, as well as giving me every working facility. To the New York Academy of Sciences I am indebted for a grant which has enabled me to visit the other principal American Permian collections. I owe my thanks to Dr. E. C. Case of the University of Michigan, Dr. T. C. Chamberlin and Mr. Paul C. Miller of the University of Chicago, Dr. R. S. Lull of Yale University, and Dr. C. W. Gilmore of the National Museum of Washington, for allowing me the opportunity of studying the many interesting forms to be found in the collections in their charge.

After the completion of this paper, I had the pleasure of discussing the shoulder musculature with Mr. R. W. Miner, who is engaged in the restoration of that region in *Eryops*, and found that we were in substantial agreement as to many of the determinations involved.

FORE LIMB, MUSCULATURE

1.—Trapezius (and Sterno-cleido-mastoideus)

Plates XXVII, dotted outlines; XXXIII, insertions

Superficial; usually the only muscle of the shoulder belonging to the visceral arch series, as shown by its whole or partial innervation by the vago-accessorius nerve. Its history is obscured by the fact that its in-

sertion leaves little impression on the bone. Further, its history is bound up with that of the dermal girdle and we have no living tetrapod in which this is complete. In the elasmobranchs, the muscle originates from the back fascia and runs diagonally down and back to the anterior border of the scapulo-coracoid. In higher forms its anterior portion attains the skull, a connection retained by at least some part of the mass in most tetrapods. The more ventral and anterior part tends to be split off in higher forms as a sterno-cleido-mastoideus or its equivalent.

The presence of the dermal girdle has affected the muscle in three ways: (1) the connection between girdle and skull has resulted in a reduction of the muscle in some forms, as the sturgeon, and its absence in teleosts (the "trapezius" of that group belonging to another system, Vetter, 1876, p. 526); (2) the series of bones from the head to the girdle may result in the separation of localized slips, as the one running from supracleithrum to the scapula in *Acipenser* (Meissner, 1908, p. 466); and (3) the insertion may be taken over by the dermal girdle. The latter is partly the case in the sturgeon (Meissner, 1908, p. 466) and *Polypterus* (Shann, 1920, fig. 24), and the conditions in Stegocephalia and cotylosaurs force us to the conclusion that this has also happened in the tetrapod stem.

The ventral portion (sterno-cleido-mastoid) usually inserts on the dermal girdle when clavicles (and interclavicle) are present. The trapezius proper either inserts into the "acromial region" (urodeles, lizards, *Sphenodon*, crocodiles) or the mammalian scapular spine, thus extending farther dorsally. This suggests that, with the loss of connection between dermal girdle and head, a backward extension of the muscle took place; that it then inserted along the whole length of the subsequent "capping" cleithrum of *Eryops*, *Diadectes*, etc; and that with the reduction of this element the muscle insertion either followed the dwindling bone down to the "acromial" region in reptiles or was transferred *in situ* to the scapula in the mammalian line (to the spine or its earlier homologue, the anterior edge of the primitive scapula).

2.—Axial Muscles Acting on the Girdle

Plates XXVII, XXVIII; XXXIII, XXXIV, insertions

a.—Dorsal: *Levator Scapulæ* (and *Atlanto-scapularis*, *Atlanto-acromialis* or *Omo-trachelius* and *Rhomboideus*), *Serratus Anterior*. These variously named muscles are apparently antero-posterior differentiations out of a series arising from the lateral axial muscles. Their origins take a general course from the skull back and down along the tips of the ribs (or

transverse processes if cervical ribs are absent) to a termination posterior to the scapula. They insert mainly on the dorsal portion of the inner surface of the scapular blade. The most anterior and posterior members of the series are usually better differentiated.

The former, as a levator scapulæ, is found in many reptiles inserting on the anterior edge or the outer surface of scapula and clavicle. This suggests that it attached to the cleithrum in primitive forms and that the history of its insertion has been similar to that of the trapezius. (Miner makes the interesting suggestion that it may be related to that muscle.) The monotreme omo-trachelius is similar. The development of the supraspinous fossa in higher mammals has apparently caused a break in the muscle, part (as in *Didelphys*) moving dorsally with the supraspinatus as an atlanto-scapularis or omo-trachelius dorsalis, part often remaining ventrally as a levator scapulæ ventralis, atlanto-acromialis, or omo-trachelius ventralis, as suggested by Gregory and Camp (1918, p. 466).

The posterior muscle, serratus anterior superficialis, has a well-marked point of attachment to the upper part of the posterior edge of the scapula in most Permian forms, comparable to that in modern reptiles. This condition is also indicated in *Cynognathus* by Gregory and Camp (in the figures, Pl. XL, teres major and serratus superficialis are accidentally reversed). It was probably later than this, and connected with the development of teres major, that the muscle disappeared in the mammalian line.

The median group (deep levators, serratus anterior) is remarkably uniform throughout, their insertions occupying a small area near the top of the scapula. The origins (marked in a number of extinct forms by uncinate processes much as in some lizards) are from the transverse processes and ends of the ribs. The number of slips increases greatly in mammals.

b.—VENTRAL: *Sterno-(episterno) hyoideus* and *omo-hyoideus*; *Sterno-costo-coracoidei* (*Subclavius*, *?Pectoralis minor*). Above urodeles, the rectus in living forms is separated from the hyoid muscles at the girdle. The continuity of the two in the urodeles is probably secondary, due to a loss of the dermal girdle; but in some reptiles the omo-hyoid is connected with the sterno-"clavicular" ligament (a rectus derivative).

The reptiles show in general a thin sheet of muscle running from clavicles and interclavicle, when present, and the acromial region forward to the hyoid. There is no palæontological evidence for these slender muscles, but the similar build of the girdle indicates the same position,

the acromial portion arising from the cleithrum originally. In the mammals part has been transferred to the sternum, part has migrated dorsally, apparently in connection with the growth of the supraspinatus, as the omo-hyoid.

In all living reptiles and monotremes there is a ventral group of muscles running from the ribs and sternum and inserting into the coracoid. The hollowed-out ventral portion of the inside of the girdle in *Diadectes* and *Dimetrodon* suggests that they occupied a similar position here, more probably being part of the rectus in the probable absence of an intervening sternum. The monotreme condition is similar. It is recognized (Fürbringer, 1876, p. 711) that the subclavius is a remnant of this set (costo-coracoideus) which has survived the reduction of the coracoid plate.

The lizards and *Sphenodon* (Fürbringer, 1876, etc.) are unique in the possession of a ligament and muscle running to the scapula from this group, often connected with the coracoid head of the triceps, and passing over the ventral portion of the subcoraco-scapularis or subcoracoideus. I shall show later that the diadectids and *Dimetrodon* probably did not have a true subcoracoideus. Running across a space corresponding to the course of the modern reptilian tendon is a strong ridge of bone, pointing backward in the direction of the sterno-costo-coracoid group and probably affording an insertion for the sterno-costo-scapularis muscle. With the reduction of the posterior upper portion of the coracoid, the muscle would have been left "in the air"; apparently this has resulted in the formation of the ligament, into which the muscle now attaches instead of the bone. In *Sphenodon*, where the reduction of the coracoid has not been so extreme, the coracoid head of the triceps has kept its position; in many lizards, where the upper edge of the coracoid is too far ventrally for a coracoid head to operate from, its origin is from this ligament. Hence, it would seem that this ligament is in the main equivalent to the original upper edge of the coracoid.

No such differentiation seems to have taken place in the mammalian line; the coracoid head of the triceps has been lost, and the musculature has followed the bone in its retreat, to give the sterno- and costo-coracoidei of monotremes and their placental derivatives.

3.—Latissimus Dorsi and Teres major

Plates XXVII; XXXIII, origins; XXXV, XXXVII, insertions

The latissimus, with an origin posteriorly on the dorsal fascia and converging to an insertion which is usually near the head of the humerus, is a constant tetrapod feature. The points of interest in connection with

the muscle are: (1) the origin of the teres major; (2) the humeral insertion, in relation to the triceps heads; and (3) the dorso-epitrochlearis.

At several times the latissimus, whose anterior edge runs close to the scapular blade, seems to have acquired an insertion upon it. An equivalent of the mammalian teres major is seen in the Crocodilia and a number of lizards. There is no evidence of such an origin in the known Permian forms; considering the proximity of the latissimus to the scapula, the attachment might easily have taken place in any series. The reptilian teres major seems unquestionably a derivative of the latissimus, as shown by their common insertion, which is well distal of the subscapulo-coracoideus (the only muscle from which it might otherwise have been derived). The only therapsid indication of the muscle is that suggested in *Cynognathus* by Gregory and Camp (1918, p. 471). The placental teres, as shown by its insertion, is apparently also a latissimus derivative.

At first sight, the contrast in the insertion of the latissimus in reptiles and mammals is puzzling. In *Sphenodon* and lizards, the insertion is between the median and lateral heads of the triceps; in mammals, it is posterior to the whole triceps. But the history of the triceps heads clears up this. In *Diadectes*, the insertion of the latissimus was probably on a roughened area just external to that of the subcoraco-scapularis, between the proximal ends of medial and lateral triceps heads. In *Dimetrodon*, the insertion is shown (in six of thirty-six humeri of this type in Dr. Case's collection, for example) as a slightly roughened area farther out along the ridge separating the heads, this leading to the usual reptilian condition. But in the mammalian line, the loss of the medial mass of the triceps, to be discussed later, has left it posterior to the whole triceps.

Primitively, some of the fibers of the latissimus inserted into the medial head of the triceps; this is the usual urodele and reptilian condition. But, with the loss of the medial head of the triceps, some of this connection seems to have often been retained as a dorso-epitrochlearis, which seems to act much as a compound of latissimus and median triceps; in the monotremes, the whole latissimus seems to have adopted this course.

4.—Pectoralis

Plates XXVII; XXXIII, origins; XXXVI, insertions

The origin, primitively, seems to have been from the length of the interclavicle, the sternum when present, and the surface of the rectus. Traces of the interclavicular origin are preserved in some American Permian specimens in the grooving of the edge of the interclavicle.

Watson apparently observed the same in *Broomia* (1914, p. 998), but suggested that these grooves were shelves to receive the internal borders of the coracoids. He himself remarks that such a position of the interclavicle would be unusual.

The insertion in the fossil forms under consideration is never in doubt, a stout process ventrally from the anterior proximal portion of the humerus, the most prominent mark on the bone. This process runs proximally into a ridge at the edge of the bone into which the supracoracoideus inserts. The ridge is extremely long in the therapsids, usually about half the length of the bone.

5.—Deltoid

Plates XXVII; XXXIII, origins; XXXV, XXXVII, insertions

The deltoid group is unmistakable throughout as a series of superficial muscles running from the dorsal and anterior portions of the girdle to the proximal external (anterior) portion of the humerus. The insertion is practically stationary, being dorsal to the pectoralis, proximal to the brachialis, distal to the supracoracoideus, and external (anterior) to the scapulo-humeralis anterior.

As was the case with the trapezius, the lack of a functional cleithrum in recent forms makes its exact history somewhat less certain. But it seems probable, as Watson (1917*a*, p. 4) has suggested, that its history is closely connected with that of the dermal girdle. In primitive forms, where the clavicle and cleithrum stretched far toward the glenoid over the scapula, its dorsal reach must have been small; its dorsal expansion followed the shrinking of the cleithrum. This serves to explain the position of the deltoid throughout the series, and I have plotted the muscle on that basis. The dorsal portion still probably had a cleithral origin for the most part in diadectids, but had probably lost most or all of it in all higher forms, with the diminution or loss of the cleithrum. The same transfer to the scapula took place in the therapsids, in which a vestigial cleithrum is retained in the lower forms. It will be noted in this connection that the scapular spine is the functional representative not only of the primitive anterior border of the scapula, but of its predecessor, the cleithrum, as well.

Connections between the deltoid and trapezius and sterno-cleido-mastoideus, as into a cephalo-humeralis, are frequent. This, however, cannot have been a primitive character, as there was then a wide stretch of dermal girdle between the trapezius insertion and the deltoid origin.

6.—Subcoraco-scapularis and Scapulo-humeralis posterior (Subscapularis)

Plates XXIX, XXX; XXXIII, XXXIV, origins; XXXV-XXXVII, insertions

This group may be defined in general by its origin from the inner surface of the girdle, or posterior to the scapular head of the triceps if on the outer surface; its course between scapular and coracoid heads of the triceps when the latter is present; and its insertion on the proximal internal (posterior) angle of the humerus. This will serve to prevent confusion with the scapulo-humeralis anterior and (except in mammal-like forms) with the coraco-brachialis group below.

In *Salamandra*, the muscle originates internally, anterior to the glenoid, and takes a course to a pronounced process at the head of the humerus.

The situation in *Diadectes* and *Dimetrodon* is at first sight confusing (the cotylosaurs and pelycosaurs are similar in this region). The smooth scapular blade is bounded posteriorly by a sharp ridge, which extends upwards as the posterior border of the scapula. Behind this is found a triangular surface, perforated in many forms, by the supraglenoid foramen. Above, this surface grooves internally into the inner surface of the scapula; posteriorly, it dwindles into a narrow shelf which terminated at the coracoid triceps origin. The relative positions indicate that the scapular head of the triceps inserted on or near the anterior ridge bounding the triangular surface, and hence the subcoraco-scapularis must have inserted back of this, evidently in this triangular area. The transition to the inner surface of the scapula above leads to the inference (Watson, 1917*a*, p. 12) that the origin extended upwards here; but it is doubtful if this portion of the muscle was of much strength.

Watson (1917*a*, p. 12) suggested that there was also a subcoracoid, but any muscle running from the internal surface of the coracoid to the humerus would have to turn an angle of about 270° (Figure 2). The build of the glenoid with the ridge above it and the fact that the point of insertion cannot look down into the cavity from which the muscle arises (as it does in most reptiles) speak strongly against this view. This also agrees with the salamander condition, where the origin is anterior, and not ventral to the glenoid. The crocodile, too, has the same character of subcoraco-scapularis; there is no ventral portion.

From such a condition, peculiar as it seems at first sight, the muscle of higher forms may be easily derived. The most posterior part of the origin probably lay on the shelf above the glenoid; with the reduction of the coracoid region in lizards and *Sphenodon*, the muscle would have an

opportunity to extend down on to the coracoid, probably at first at the posterior angle. I have already discussed the possible relation of the sterno-scapular ligament to this movement.

While we have no transition from the Permian forms to the modern Reptilia, it seems probable that the triangular area, at the anterior edge of which is the scapular triceps origin, has become part of the external surface of the scapula of lizards and *Sphenodon* (where the scapular head

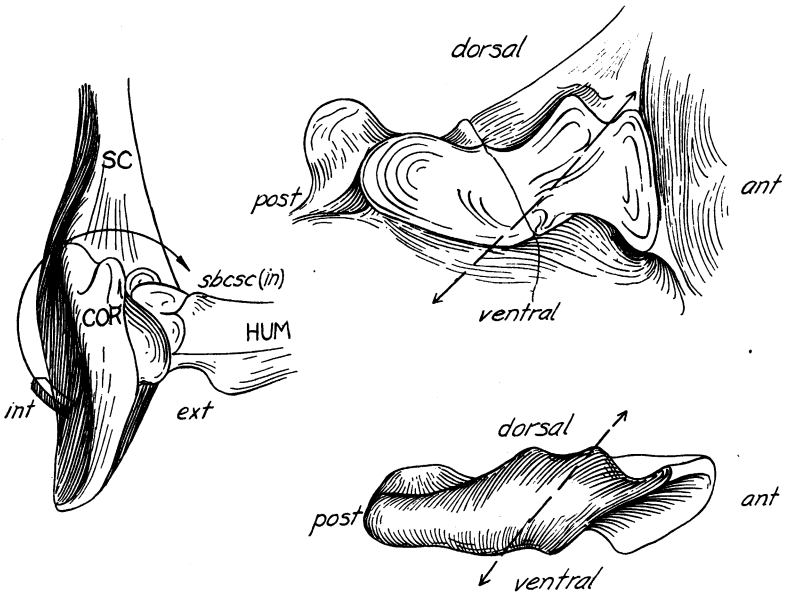

Figure 2 (left). To show the improbability of the presence of a true subcoracoideus muscle in primitive forms. The arrow indicates the course such a muscle would necessarily have taken in *Dimetrodon*.

Figure 3 (right). The right glenoid and head of the left femur of *Dimetrodon*. The broken arrows show the suggested point of division of the articular surfaces into two portions.

of the triceps is on this surface, and not at its posterior edge), and the scapulo-humeralis posterior is merely a portion of the subcoraco-scapularis mass carried outward in this process. Its course to the humerus always lies behind the scapular head of the triceps.

The evidence seems to show that the therapsids did not have a subcoracoideus homologous with that of lizards and *Sphenodon*. The monotremes have a muscle, which is similar at first sight, in the epicoraco-brachialis, the insertion of which seems to refer it to this group rather than to the coraco-brachialis (with which it is sometimes homologized, as by Westling, p. 16). But there is no formation of a sterno-scapular ligament; the entire costo-sterno-coracoideus is internal to it instead of

separating it from the subscapularis as in reptiles; and it runs more in an anterior direction than a ventral one. This all tends to show that it is formed by an antero-internal widening of the shelf primitively internal to the glenoid and thus belongs to the subscapularis rather than to the true reptilian subcoracoideus, as suggested by Gregory and Camp (1918, p. 472). In *Cynognathus* there is no evidence of a separation of the subcoraco-scapularis into two parts. The placental subscapularis is of course dorsal to the subclavius (representing the old sterno-costo-scapularis).

7.—Scapulo-humeralis anterior (Teres minor), Supracoracoideus (Supra- and Infraspinatus), and Coraco-brachialis

Plates XXX, XXXI; XXXIII, origins; XXXV, XXXVII, insertions

a.—Scapulo-humeralis anterior and Supracoracoideus. This set of muscles is of great interest because of its relations to the supra- and infraspinatus of mammals, which, as is well known, have pushed their way up on to the scapula from below.

If we look for the homologues of the supra- and infraspinatus in reptiles, the assumption from position would be that they represent the scapulo-humeralis anterior of such a form as *Sphenodon*, as has been assumed by Watson (1917*a*, p. 55). But that muscle, as noted by Fürbringer (1876, p. 735), is innervated by a nerve partly homologous with the axillary, while the spinatus muscles of placentals are innervated by the suprascapular, clearly the homologue of the supracoracoid nerve of reptiles. Hence it appears that the supra- and infraspinatus represent part or all of the reptilian supracoracoideus, as Fürbringer believed (1876, p. 718).

But *Echidna* renders the problem more complicated, for the infraspinatus (Westling, 1889, p. 46) is innervated to a slight extent by the axillary nerve as well as by the suprascapular; the former also innervates the teres minor, the homology of which has proved a puzzle to many workers (Watson, 1917*a*, p. 56). This suggests (1) that the teres minor is a remnant of the old scapulo-humeralis anterior, (2) that the monotreme infraspinatus also contains elements of that muscle, lost in the placentals, and from this (3) that the scapulo-humeralis anterior and supracoracoideus had a common history throughout. A comparison of the various groups tends to confirm this.

These two muscles, scapulo-humeralis anterior and supracoracoideus, or their representatives, may always be identified by their position. They arise from the external surface of the girdle, bounded dorsoposteriorly by the scapular head of the triceps (which thus sets them off

clearly from the scapulo-humeralis posterior), externally by the deltoid and pectoralis, and ventro-posteriorly by the coraco-brachialis. The innervation is a double one; the upper portion, by a nerve running anteriorly over the humerus or girdle ("axillary"); the lower portion, by the supracoracoid nerve. This appears to be a primitive condition. (The separation from the coraco-brachialis is in some cases an entirely artificial one, but the two ends of the series have a different history and may be considered separately for that reason.) The primitive insertions seem to have been a fleshy one on the antero-lateral corner of the dorsal humeral surface, followed by a tendinous insertion into the proximal end of the pectoral ridge at the proximo-lateral border of the bone, from which it merges below into the coraco-brachialis region of insertion.

In urodeles are found (1) the precoraco-humeralis, which possesses a similar double innervation, below which is (2) a supracoracoideus with its proper innervation. In turtles there is a supracoracoideus and, at least in *Trionyx* (Ogushi, 1913, p. 389), just anterior to it an "infraclavicularis," which is indistinguishable except for its "axillary" innervation. In lizards and *Sphenodon*, on the other hand, the differentiation into a scapulo-humeralis anterior and supracoracoideus has taken place by a split through the division of the two innervation areas. In the crocodile, the scapulo-humeralis anterior has disappeared entirely, while the supracoracoideus is well developed and runs farther dorsally than primitively. This is interesting as a parallel to the mammalian condition, and in a way has even gone beyond it through the entire loss of the dorsal mass. The placental differs from the monotreme by the loss of the dorsally innervated part of the infraspinatus and of the supracoracoideus proper. (In *Didelphys* there is no separate teres minor.)

It will be seen that in practically no case is there an exact homology of any two muscles; but the homology of the group as a whole seems quite clear.

The chief interest of the fossils in this connection is the question of the rotation of the more anterior and dorsal portions onto the scapular surface to form the infraspinous fossa and the creation of the supraspinous fossa in front of the original anterior edge. In the primitive stage, as illustrated by *Diadectes*, the posterior portion of the group, with the coraco-brachialis, covered the whole of the coracoid plate below. We are unable to distinguish between the three elements involved to any great degree, as the distinction, as we have seen, often rests on the innervation. But we may conclude from the fact that the supracoracoid foramen is more posteriorly placed than in any living animal that the

supracoracoid elements of the muscle group also extended more posteriorly. In the mammalian series, the foramen can be traced forward nearly to the edge of the girdle, which, the mammals show, it eventually reached, freeing the nerve as the supra-scapular.

In *Diadectes*, the most dorsal part of the muscle cannot have extended upward on the scapula beyond the point where the clavicle leaves the edge of that bone. Above this, there would be no room for another muscle under the deltoid; below, the girdle is "set in" to some extent, leaving plenty of space under the clavicular deltoid. The insertions seem to have been on the dorsal surface of the girdle, proximal to the line limiting the lateral head of the triceps, tendinously at the angle of the humerus, and below, on the coraco-brachial surface. The situation in *Dimetrodon* seems to have been essentially similar. This represents practically the position of the three muscles concerned in lizards and *Sphenodon*, except that the foramen has moved anteriorly and the supracoracoid innervation does not extend so far into the ventral mass as the more posterior position of the foramen in the fossils would indicate for the Permian forms.

No pareiasaur girdle is available, but the situation seems to have been similar, except that the elevation of an acromion may have given an opportunity for a somewhat greater dorsal expansion.

In *Moschops*, the acromial region is placed rather high up, and the upper limit of the hollow containing these muscles is a line running diagonally up and forwards from the glenoid, showing a considerable advance. The insertion on the dorsal surface of the humerus appears to be restricted by the developing head and the apparent usurpation by the triceps and brachialis anticus of the entire dorsal surface of the bone; the position of tendinous insertion of the supracoracoideus seems to have been about the same.

The therocephalian and gorgonopsian girdles seem to have been similar in this region, as far as they can be made out from descriptions. In *Cynognathus*, as has been pointed out, the infraspinatus is able to reach the dorsal part of the scapular surface for the first time (Watson, 1917*a*, p. 27; Gregory and Camp, 1918, p. 511) by the eversion of the spine; but, as has been shown by both Watson (1917*a*, p. 28) and Gregory and Camp (1918, p. 511), this girdle is specialized by the stoppage of the groove leading from the lower anterior portion of the scapula up under the clavicle, which undoubtedly was the place whence the supraspinatus developed. On the other hand, the girdle of the dicynodonts, while not permitting the dorsal extension of the infraspinatus, has a small anterior shelf (Watson, 1917*a*, p. 35).

From such a condition, the monotreme or ordinary mammalian condition of the supraspinatus may be readily derived. As regards the monotreme, the extension of the supraspinatus up through the opening between clavicle and scapula to the inner surface of the latter would render the original (proximal) area of origin useless, as the covering clavicular deltoid would not allow room for the reception of additional fibers from this region. Further, the retention of this surface would be a hindrance, because of friction and the necessity of the muscle turning a greater angle from its internal origin than would otherwise be necessary. With the loss of this surface (the lower part of the anterior edge of the scapula and the upper part of the anterior coracoid) a therapsid girdle would be essentially similar to that of the monotremes. We have, unfortunately, nothing which bridges the gap between therapsids and higher mammals to show the formation of the supraspinous fossa.

Watson (1917*a*, p. 55) has homologized the supra- and infraspinatus with the scapulo-humeralis anterior, which we have shown to be impossible because of the innervation. Gregory and Camp (1918, p. 475) doubtfully homologize the infraspinatus with the anterior and posterior scapulo-humeralis; as before, the innervation stands in the way, and the posterior scapulo-humeralis muscle lies behind the scapular head of the triceps while the present group is always anterior to it. The same relation to the triceps renders out of the question any homology of the teres minor with either teres major, scapulo-humeralis posterior, or subscapularis. Fürbringer (1900, p. 430) and Gregory and Camp (1918, p. 470) have homologized the teres minor with part of the deltoid; but it is widely removed from that muscle in origin and insertion, and no evidence for this conclusion is presented.

b.—Coraco-brachialis, brevis and *longus.* The anterior relations of the origin of this muscle with the preceding group has already been discussed. The origin in modern reptiles and probably in primitive forms is from the posterior part of the coracoid plate.

The coraco-brachialis in existing tetrapods usually fills the space on the ventral surface of the humerus between the pectoral insertion anteriorly and the medial head of the triceps posteriorly. A long portion may be distinguished, whose fibers usually rise more posteriorly; this may be absent, as in turtles, the crocodile, and many mammals (*Didelphys*, for example). The area of insertion in all the fossil forms is practically the same; it occupies the proximal ventral one of the four primitive surfaces of the humerus, to be described later. The long portion seems to have a distinct area of origin (reduced in *Moschops* and *Cynognathus*) from a region at the back corner of the coracoid.

8.—Biceps and Brachialis

Plates XXXI; XXXIII, XXXV-XXXVII, origins

These two flexors of the lower limb are closely associated throughout by their common function, innervation, and insertion, the insertion being primitively a common one at the adjoining portions of the proximal ends of the radius and ulna, which are usually marked by rugosities in the fossils. It will be noted that the two muscles have a common action in the primitive forms, in which they converge at an angle, presenting an interesting analogy to the triceps on the opposite surface.

We may discuss the two muscles separately.

a.—Biceps. Present in all reptiles and mammals, and absent in existing Amphibia. In its primitive form it arises from the coracoid plate, passing over the coraco-brachialis to a union with the brachialis. In turtles two heads (as in the brachialis) are often present. In the monotremes there are two heads, both ulnar; in placentals the insertion is radial. The primitive condition is repeated in *Didelphys*, with both insertions. The coracoid origin is retained, in part, at least. The fossils give no evidence of separation of the surface of origin of this muscle from that of the adjacent coraco-brachialis mass.

While the homologies of the muscle are clear, its historical origin is confused by its absence in Amphibia. Authors (as Fürbringer, 1876) have thrown out of court the coraco-radialis proprius of these forms because of its supracoracoid innervation. However, the biceps seems to be intimately related as a superficial portion to the deeper coraco-brachialis, which is in turn related to the adjacent supracoracoideus muscle. The biceps might be considered as a posterior part of a primitively continuous flexor whose anterior part is preserved as the coraco-radialis or, as the frequent presence of proximal and distal bellies suggests, it may have arisen from the same group but in a slightly different way, by fusion of elements of coraco-brachialis and brachialis.

b.—Brachialis. The structure of the primitive humerus will be discussed in another section, tending to show that it originally consisted of four triangular surfaces. It is with one of these that the brachialis is associated, filling the distal ventral surface with its origin (as explained in the next section, a more dorsal origin is impossible) and at the extremity meeting the biceps to run to their usual common insertion. This typical condition is traceable in all the fossil forms considered. With the tendency to place the two ends of the humerus parallel, the distal portion of this surface tends to be more directly ventral; but proximally the area of origin curves up dorsally over the surface of the humerus. This con-

dition is closely approximated in all living forms. Variations in insertion are found; in the turtle, there are two parts to correspond with the biceps split. The monotremes possess the double insertion, but in many mammals it is merely ulnar (it will be noted that here the biceps is radial only). The origin in therapsids is large, occupying nearly one-half the (apparent) dorsal surface, above the delto-pectoral ridge; and thus separating the deltoid widely from the triceps.

9.—Triceps

Plates XXXII; XXXIII, XXXV, XXXVII, origins

The general reptilian and amphibian condition of the triceps is that of a great extensor consisting of two main masses: (1) a median portion, with a long head from the coracoid (or its dorsal replacing ligament), passing posterior to the subcoraco-scapularis and latissimus, and a short head from the medial side of the humerus; (2) a lateral portion, with a long head from the scapula near the joint capsule and a short head from the lateral surface of the humerus. These conditions are found duplicated in a very striking fashion in the fossil forms under consideration. The dorsal surface of the humerus consists of two approximately triangular surfaces, at a sharp angle to one another in primitive forms. The posterior (distal dorsal) one, with a distal base, is unquestionably the point of origin for the medial humeral head. The coracoid origin is best seen in *Dimetrodon*, where it is a large tuberosity, to which the proximal apex of this surface is directed. This may be traced back through some of the lower pelycosaurs to a roughened surface in the cotylosaurs, just above the posterior end of the glenoid. Of the lateral portion, the scapular head in primitive forms must have arisen from the lower part of the ridge bounding the scapular blade posteriorly or a rugosity posterior to that ridge. The lateral humeral head arose from the proximal dorsal surface. In a large number of forms, good material shows a line running from the latissimus insertion anteriorly across this surface toward the delto-pectoral crest. I believe that this was the proximal end of the area of origin and separated the muscle from the scapulo-humeralis anterior insertion. This area cannot belong to the brachialis; it is at a sharp angle to the general area of origin of that muscle, almost 180 degrees in *Cricotus* and *Archeria*. Further, an *Eryops* humerus shows a distinct concavity distal to this line, as if for the reception of the head of a muscle. In the therapsids and mammals this area has apparently crowded out the scapulo-humeralis anterior and reduced the origin of the latter to a small area near the head; this is in contrast, however, to the reptilian condition.

I have mentioned the way in which the two portions meet at an angle for their insertion on the olecranon, or the universally roughened head of the ulna representing this. This condition is retained in living reptiles, except that the coracoid head is lost in turtles. But in the pareiasaurs, therapsids, and mammals, there is reduction and loss of much of the medial mass, apparently correlated with the changed pose of the limbs. No known therapsid or pareiasaur could have possessed a coracoid head (unless the lizard ligament system had been separately evolved), because of the reduced condition of that bone. Similarly, the medial humeral head is reduced proximally with the reduction of the proximal portion of the posterior dorsal triangular surface of the humerus. This is partially true of *Propappus;* in *Moschops* it is practically absent as is the case with all higher forms. Hence it follows (and this clears up the latissimus position as well) that the mammalian medial head is the distal part only of its reptilian predecessor.

10.—Brachio- (humero-) radialis (Supinator longus) and Supinator

Plates XXXII; XXXV, XXXVII, origins

In mammals, *Sphenodon,* some lizards, and the crocodile is found a muscle not elsewhere present, the brachio-radialis or humero-radialis (in *Uromastix* represented only by a ligament from triceps to supinator). It runs from the humerus (superior to the brachialis) to the inner edge of the radius or, as in *Sphenodon,* connecting with the supinator. *Sphenodon* and the stegoceph-cotylosaur-pelycosaur series give the probable explanation, and show the relation of these two apparently unrelated muscles and the part they have played in the formation of the ectepicondylar foramen.

It must be first noted that these muscles, although placed close to the brachialis (including the "supinator longus" of *Echidna*), are sharply differentiated from that muscle; they are innervated dorsally, by the nerves to triceps and extensors, (*Ra,* Fig. 1) while the brachialis is innervated from the lower side of the humerus (*M-C,* Fig. 1).

The process which we see in *Dimetrodon* just proximal to the extensor origin is unquestionably that which fuses with the ectepicondyle to form the ectepicondylar foramen (found in many fossil forms and in all living reptile groups except Crocodilia). In *Sphenodon,* the supinator arises from a similar position, and it probably did the same in *Dimetrodon* (Watson, 1917*a,* p. 5, etc.; but he suggests brachialis anticus as well). If we follow this process back through some such series as *Ophiacodon,*

Diadectes, *Seymouria*, and the typical stegocephs (it is sometimes suppressed as in *Diasparactus*, Case and Williston, 1913, p. 21), we find that it has progressed downwards from a position near the proximal portion of the boundary between the anterior dorsal and ventral anterior humeral surfaces (anterior dorso-ventral line, Plates XXXV, XXXVII), a position from which we would expect the brachio-radialis origin. The probability of a common origin of brachio-radialis and supinator is strengthened by their fusion and common innervation in *Sphenodon*, their close relation in placentals and crocodiles, and the possession by some primitive humeri (*Cricotus*, etc.) of a well-marked ridge in the position of the anterior dorso-ventral line. Apparently, as the shaft of the humerus develops, the brachio-radialis and supinator tend to go to the distal end and associate themselves with the extensors. In the process, a part of the radial nerve is enclosed, with the resulting formation of the ectepicondylar foramen.

There is no homologue of these muscles in urodeles. Possible explanations of them are that they were a radial homologue of the triceps in some primitive condition of the limb before the elbow "got its crook," or that they were primitively, as they later appear again to be, a part of the forearm extensors.

11.—Forearm: Extensors

The urodeles show a generalized condition of these muscles, as a group running from the ectepicondyle and divided into three portions: (1) radial extensor, to the outer surface of the radius and radial edge of the carpus; (2) the extensor digitorum communis longus, to the digits; and (3) ulnar extensor, to the external border of the ulna and the carpus.

The lower cotylosaurs and stegocephalians show a sharp contrast to later types in the presence of a huge extensor crest nearly at right angles to the distal expansion of the humerus, giving the extensors as large an angle as possible to the lower limb (Watson, 1917*a*). This is found in the process of reduction to the general level and fusion with the supinator crest in *Propappus*, the higher cotylosaurs, pelycosaurs, and therapsids. Two ulnar areas may often be discerned, the more lateral for the origin of the abductor and extensor pollicis, the medial for the origin of the pronator profundus. A dorsal radial surface probably was for the radial extensor insertion.

During the change to the mammalian condition, these lower arm insertions have been lost except the anconæus (possibly the remains of the ulnar inserting part), while the ulnar extensor has acquired a new

ulnar head (the crowding in of the supinator has apparently prevented the radial extensor from doing the same). I have found no clear indication of this in the therapsid series.

12.—Forearm: Flexors, Including Pronators

The urodele condition is that of a series of muscles running from the entepicondyle to the flexor side of the limb: (1) radial flexor, to the radius and a short distance on to the carpus; (2) pronators, from condyle and ulna to radius; (3) flexor digitorum communis, to the digits, with accessory heads from the ulna, the detailed homologies of which will not be considered here; and (4) ulnar flexor, to the ulna and ulnar side of the hand.

The reptilian condition shows little change. In the fossils under consideration, the huge entepicondyle for the origin of the flexors (Watson, 1917*a*, p. 15) is one of the most striking features of the primitive types and its reduction can be traced through a number of forms. At the tip of the condyle is a pit in *Diadectes, Propappus, Dimetrodon,* perhaps for the origin of a tendon in the ulnar flexors such as is seen in *Echidna.*

The insertions of the ulnar flexor, the ulnar head origin of the flexor digitorum communis, and the course of the pronator quadratus may be seen in fossil ulnæ. In reptiles the ulnar insertion may be reduced. In the mammalian line several changes, not apparent in the fossils, have taken place; radial and ulnar insertions are lost (except pronator teres); the flexor communis acquires a radial as well as an ulnar head (not yet present in monotremes) and becomes highly differentiated; the ulnar flexor acquires an ulnar head (the radial extensor cannot do the same without "jumping" other muscles). There seem to be the same tendency for motion down the limb noticed in the extensors.

13.—Grouping of Fore Limb Muscles

We have noted in several places suggestions of relationships between a number of the muscles considered. In the first place, we have shown the relations of scapulo-humeralis anterior, supracoracoideus and coracobrachialis. Again, the deltoid and pectoralis, with adjacent insertions, similar character, and continuous origins, seem related; and this would be even more evident in a primitive form where a large dermal girdle would restrict the deltoid to a more ventral origin. These seem to be primitively in position an anterior superficial portion of the same mass as the first group mentioned. These also seem to be related to the biceps and brachialis, which in turn lead to the flexors of the lower leg.

On the other hand, the subcoraco-scapularis and scapulo-humeralis posterior seem to have the latissimus (with teres major) as a more superficial portion, with a usually closely related insertion; this group is in turn embraced primitively between the two great heads of the triceps; this leads again to the supinators and extensors.

This conception leads to the idea that the primitive tetrapod arm musculature consists of two great groups, one of which originated on the coracoid plate and the ventral portion of the dermal girdle as the primitive ventral group, the other reaching the arm dorso-posteriorly, above the glenoid, from within as the primitive dorsal group (Fig. 1). If we turn to the bony fish (Pychlau, 1908), we find two similar groups; the abductors arising from the ventral plate and the ventral portion of the cleithrum, and the adductors from the "mesocoracoid" region, dorso-posteriorly (Fig. 4). This suggests the possibility, which will be considered further under the bony elements, that we might homologize these two great masses of the fish and the tetrapod, although the subdivisions would not of course be distinguishable.

(1) Primitive dorsal (fish "adductor") group.—Subcoraco-scapularis, scapulo-humeralis posterior, latissimus dorsi (including teres major), triceps, supinators, extensors.

(2) Primitive ventral (fish "abductor") group.—Deltoid, pectoralis, scapulo-humeralis anterior (teres minor), supracoracoideus (supra- and infraspinatus), coraco-brachialis, biceps, brachialis, pronators, and flexors.

FORE LIMB, BONY ELEMENTS

1.—Dermal Shoulder Girdle

Plates XXXIII and XXXIV

The fact that we have no living tetrapod with a full set of dermal elements has already been commented on. But without question, as the crossopterygian evidence shows, the ancestors of the tetrapods were furnished with a well-developed dermal girdle, and, as seems probable from *Eusthenopteron* and dipnoans, with but a small cartilage bone girdle (Bryant, 1919, p. 19, etc.). The evidence of the living ganoids is that the dermal girdle possessed, on its anterior side, the insertions (wholly or partly) of the trapezius, superficial levator and hyoid muscles and, as is shown by ganoids and teleosts, it gives origin, on its postero-ventral edge, to part of the superficial abductor of the fin, comparable with the deltoid (Fig. 4).

As a supporting structure, it bound the fin bases to the head through the attachment to its inner sides of the primary girdles, and ventrally connected the two girdles. A change to land locomotion would of necessity profoundly alter these relations. A girdle firmly attached to the head would be a handicap on land, since movements of the head and of the girdles would mutually interfere. Furthermore, the great strain upon the girdles caused by raising the body from the ground would put a connection between limb and body by way of the dermal girdle at a disadvantage; the weight of the body would have to be transferred first to the dermal girdle, from that to the primary girdle, and then to the limb. As explained below, this function was taken over by the primary girdle.

With this loss of function, we expect, and find, a dwindling of the dorsal part of the dermal girdle, and the connection with the head only found or suggested, so far as I know, in *Bratrachiderpeton*, and *Keraterpeton* (Watson, 1913, p. 955). Ventrally, however, the clavicular bridge between the two sides of the girdle would still be of use in a slow moving animal; and the connection is strengthened by a new element, not present in fish, the interclavicle.

In respect to musculature, the dorsal portion, the cleithrum, would seem to have preserved its original relations to the trapezius on one side and to the deltoid on the other. The primitive type appears to have had a T-shaped bone, the anterior "prong" connecting with the head (through the post-temporal); the posterior "prong" remains, giving, in *Diadectes*, as in many Rachitomi, the capping type of cleithrum, embracing the front and upper edges of the scapula. This suggests that the trapezius followed this bone in its backward extension following the loss of the head connection. The deltoid seems to have followed the ventroposterior edge of the bone in its retreat dorsally and anteriorly. Ventrally, the clavicle retains part of the deltoid origin. The interclavicle gains prominence with the development of the pectoralis and extends backward in both typical Rachitomi and primitive reptiles to give this muscle its anterior region of origin. While there is nothing new to add to the question of the origin of the sternum, this posterior prolongation would be extremely weak if it were not backed by some sort of sternal structure.

The typical dermal girdle, then, of the primitive reptile is of the type seen in *Diadectes;* a cleithrum which has lost its supporting function and which has not yet transferred its muscular relations to the scapular blade, curving over the upper end of the scapula; clavicles curved in a quadrant shape, reduced above at the cleithral articulation, still ex-

panded ventrally to lay over the head of the interclavicle, and offering an origin to the deltoid posteriorly and hyoid muscles anteriorly; interclavicle expanded anteriorly for the clavicular articulations, and with a moderate backward process for the pectoralis origin. This description would apply nearly as well to any of the generalized Rachitomi, as *Eryops*, or *Cacops*.

The further history of these elements is for the most part one of reduction, in which they are paralleled in the Amphibia (except for the secondary formation of huge ventral plates in later aquatic Stegocephalia). The function of the cleithrum here is merely for the muscular insertions and origins mentioned. These were later transferred to the scapula. The capping cleithrum is not found beyond the near relatives of *Diadectes;* even *Limnoscelis*, which is similar in other parts of the skeleton, has a small cleithrum, while the clavicle reaches far up the front of the scapula; while in *Seymouria*, also close in most of the appendicular skeleton, the cleithrum had disappeared. It has apparently vanished in many or all Captorhinomorpha, in *Procolophon*, and, as far as known, in all pelycosaurs except some clepsydropids, and in *Edaphosaurus*. Most pareiasaurs still retained one, as do members of the Dinocephalia, Gorgonopsia, ? Therocephalia, and Dicynodontia (Watson, 1917*a*, pp. 20, 31, etc.). The trapezius seems to have followed the bone during its reduction to the condition of a small splint on the anterior edge of the scapula before transferring its origin to the latter. It will be noted that the anterior border of the reptilian scapula and the spine of the mammalian scapula are the functional homologues of the primitive cleithrum.

The ventral elements have undergone little further reduction; they are of practically the same pattern in all Permian forms and are but little changed in lizards, *Sphenodon*, and monotremes, and still present, although much modified, in the Chelonia. There is no sign of reduction in any of the mammal-like reptiles. Their presence seems indicative of slow and regular terrestrial locomotion; it is only when the animal attains speed, accompanied by sudden impact, or agility in arboreal life (both requiring a loose shoulder girdle capable of free motion and the transference of strain to the body independently of the other half of the girdle) that the strength afforded by the clavicular arch becomes a hindrance and is given up. This has apparently been done independently in a number of lines, such as the chameleons, dinosaurs, crocodiles, and mammals; but in many of the last, the loosened clavicles have been retained.

2.—Primary Shoulder Girdle

Plates XXXIII and XXXIV

The shoulder girdle of the typical bony fish (Pychlau, 1908) consists of: (*a*) a scapular portion of small extent lying underneath, and firmly bound to, the dermal girdle; (*b*) the mesocoracoid arch, above the fin articulation, and bracing it, part of the adductor muscles originating on the arch, the others running through it from the inner surface of the girdle; (*c*) the fin articulation; (*d*) below this and the scapular portion, a coracoid plate, placed inward at an angle from the scapula, and free from the dermal girdle, giving origin to most of the adductors.

The type from which the tetrapod girdle has been derived was in all probability not far from this, and the two may be directly compared (Fig. 4). In the stage of the typical Rachitomi and primitive cotylosaurs, the girdle consists of: (*a*) the scapular blade, now nearly free externally from the dermal girdle, and extending far dorsally; (*b*) a supraglenoid buttress, sharply marked off from the scapular blade; (*c*) the glenoid below this; (*d*) a coracoid plate lying below the glenoid and the scapular blade, set off at an angle from the scapular blade, and everywhere free from the dermal girdle. We may follow the history of these parts separately.

a.—The Scapular Blade. In *Eusthenopteron* (Bryant, 1919, p. 19), as in most of the bony fish, there is practically no extension dorsally of the blade of the scapula; in the terrestrial stegocephs and in the primitive Reptilia, the scapular blade is very well developed. The probable explanation for this development has been suggested above, namely, support for the body. The hind limb has gained this support by the union of ilium and vertebral column. The problem in the fore limb, however, is more complicated; a union directly with the axial skeleton would entail the same disadvantages (in connection with the head) that the old dermal support had (at least in primitive forms with short necks); and, besides a mere support for the weight of the body, the shoulder must adjust itself to the effects of the propelling force of the hind legs. This difficulty has apparently been overcome by the differentiation of the serratus series, thus affording a muscular rather than a bony connection in the trunk. A dorsal growth of the scapula would give a longer distance for the play of the muscles and would give the "underslung" condition of the thorax.

It will be noted that this explanation of the growth of the scapular blade is concerned with the inner surface of the bone alone; and that this is the true explanation finds confirmation in the fact that there is no

known muscle, apart from the upper part of the deltoid (which was confined to the cleithrum or a position close to it), which could have originated from the outer surface of the blade at this stage; externally it was otherwise a bare expanse of bone.

In connection with this, we have noted that stout bodied forms, such as *Diadectes*, and *Eryops* among the Stegocephalia, possess "uncinate processes" on the ribs in the region of the shoulder, which Williston (1912, p. 463) suggested articulated with the scapula. As previously mentioned, they probably served as points of origin for the serratus anterior.

Further changes have occurred to the scapula apparently for three reasons: (1) dermal girdle reduction, affecting the dorsal portion and anterior edge; (2) loss of the supraglenoid buttress, affecting the posterior and internal portions; and (3) invasion of the blade by the coracoid plate musculature in the mammalian series.

Changes Due to Dermal Girdle Reduction.—As mentioned in a previous section, the cleithrum has been reduced or lost in all reptiles except the diadectids. This has resulted in a transfer to the blade of the muscles originating or inserting on that bone. Dorsally and externally, the deltoid origin is now on the scapula; the trapezius inserts on the anterior border; and if, as seems possible, the superficial levator had a cleithral insertion, that also has transferred to the scapula, while the other levators and serratus anterior have retained their original position.

Loss of the capping cleithrum seems to be usually accompanied with the shortening of the ossified portion of the scapula and the probable appearance, for the first time in this series, of a cartilagenous suprascapula which of course takes over part of the deltoid, and the levators and serratus anterior. The retention of a cleithrum on the anterior edge is usually associated with a better ossification of the scapula in the forms which possess it; in almost every case of a Permian form with a long scapular blade, the cleithrum is present in that, or a related form. The scapulæ of therapsids are usually of good length, and the late retention of the cleithral splint in this series may be noted.

The invasion from the supraglenoid buttress will be discussed in connection with that portion of the girdle.

Invasion by the Muscles of the Coracoid Plate.—In the living Reptilia, whose mode of locomotion has remained much the same, there has been no such invasion or only a slight one; the deltoid remains in possession of the dorsal portion of the scapula. But in the mammalian line, the changed position of the humerus has entailed a profound alteration

in the position and function of the muscles in the region under consideration; a change which may be compared with the development of the gluteals in the hind leg.

In the primitive type with the humerus straight out from the body, the main support of the humerus was through the coraco-brachialis, which prevented the shoulder joint from "buckling." But in the change to the mammalian type, where the humerus is turned in and parallel to the long axis of the body, a situation arises where this support is not practicable. However, the advantageous position of the insertion of the more dorsal and anterior portions of this muscle mass, on the proximal anterior border of the humerus, enables it to act as a lever of the second class (while aiding in the advance of the body by depressing the humerus distally) since its humeral insertion is anterior to the glenoid. But this advantage will only be retained if the area of origin moves upward in proportion as the humerus shifts to a vertical plane. Further, while the supporting function has been partly shifted to the bone by the more vertical position of the glenoid, it will be noted that this same set of muscles also has the old supporting function of the coraco-brachialis. Again, the most dorsal portion of the mass, the scapulo-humeralis anterior, has a more distal insertion which prevents it from being effective as an extensor; and we have already noted that it is practically lost in mammals, only existing as the teres minor.

As has already been mentioned, the invasion proceeded along two courses: (1) directly up the blade, as teres minor and infraspinatus, limiting the trapezius and deltoid to the anterior edge (spine); and (2) by working up anteriorly, beneath the clavicle to the internal surface of the blade, or by building up a new surface anterior to the old anterior edge of the scapula as the supraspinous fossa (Watson, 1917*a*; Wilson and McKay, 1893). The formation of the infraspinous fossa seems to have been accomplished, to start with, by the more dorsal position of the line marking the upper limit of the coracoid plate (this is seen in *Moschops*), and, secondly, by the eversion of the acromion and spine. The acromion is seen in pareiasaurs (this is probably an independent evolution) but in the therapsids is seen only in the anomodonts and cynodonts; and it is only in the latter that the spine is everted, thus allowing the infraspinatus to reach fully up the blade. As would be expected from the monotremes, the evolution of the supraspinatus took place at a later period; there is no therapsid with a supraspinous fossa. But, as Watson has pointed out, the anomodonts are interesting as showing a small ledge extending up under the acromion from the coracoid plate which was undoubtedly the beginning of this surface.

The main steps in the evolution of the scapular blade are, therefore, seen to be: (1) taking over of supporting function from the cleithrum; (2) taking over of the cleithrum's further muscular connections; (3) invasion from the supraglenoid buttress in reptiles; and (4) invasion by the muscles of the coracoid plate in therapsids and mammals.

b.—THE SUPRAGLENOID BUTTRESS. This is marked off sharply from the scapular blade. Externally it presents a triangular surface slanting upward from the anterior half of the glenoid, pierced by a foramen (primitively large), the supraglenoid of Williston (1909, p. 648), and with its internal side extending backward above the posterior portion of the glenoid. Internally, the buttress extends down and anteriorly, with a large cavity (subscapular fossa) anterior to it, from which the supraglenoid and supracoracoid foramina arise, while posteriorly it merges into the internal surface of the coracoid plate.

It is, of course, impossible to escape the close comparison with the mesocoracoid bridge, despite the fact that the centers of ossification in the teleosts are differently distributed. But, whereas in fish the deeper adductors arise within and extend out through the homologue of the supraglenoid foramen, it is highly improbable that in the primitive tetrapod this was the case, because of the difference in the direction of movement of the limb; in an antero-posterior movement the muscle could have very little play. Watson (1917*a*, p. 2) suggested that the joint tissue may have extended through it; Williston has demonstrated its presence as a foramen for a blood vessel in some lizards (1911, p. 389). At all events, it had become rather small by the time we first see it in the reptiles, and the only remains of the primitive short dorsal muscles is the subcoraco-scapularis which arose from its outer surface, the supraglenoid buttress under consideration.

The supraglenoid foramen becomes further reduced in size, in captorhinomorphs, in *Ophiacodon*, and in *Edaphosaurus;* in the poliosaurs and clepsydropsids it has its external opening shifted to the outer surface of the scapula; in *Casea* it has vanished, although the glenoid region is of the same type. One fragmentary girdle, assigned to *Theromus* by Seeley (1895*a*, p. 152), is the only described South African form with a supraglenoid foramen. (?Amphibian?)

We have no certain transitional type to that of modern reptiles. The finished product shows that dorsally the buttress has been inherited partly by the inner surface, partly by the posterior edge of the outer surface of the scapular blade; for the original subcoraco-scapularis is now represented internally by the subcoraco-scapularis proper, while the

posterior outer surface is occupied by the scapulo-humeralis posterior, a part of the same mass. The scapular head of the triceps is still farther anterior in most cases, instead of occupying a position on the modern posterior border. We have discussed in a previous section the probable falling away of the back border of the buttress towards the inside, with the formation of the sterno-scapular ligament, and the invasion of the internal surface by the postero-ventral portion of the subcoraco-scapularis.

In no mammal-like reptile is there any indication of this surface; even in *Moschops*, there is only a short round transition above the glenoid between inner and outer surfaces. The position of the triceps head and the subscapularis of mammals show that the surface has turned inwards, and that the old posterior edge of the scapular blade has been retained (the dorsal external expansion of the subscapularis in monotremes is probably secondary).

c.—THE SHOULDER JOINT. The peculiar nature of the glenoid of the characteristic American Permo-Carboniferous tetrapods has long been recognized. Its function may perhaps be better understood through a general consideration of the origin of the tetrapod limb.

While the hind limb is principally concerned with advancing the body and not so much with support, the latter function is very important in the fore limb. It must bear the weight of the very heavy head and thorax. Manifestly, the simplest type of limb would be that of one segment, with some sort of supporting structure, or hand, at the end. But it is obvious that such a crutch-like arrangement would cause a great loss of energy through the upward swing and sag at every step. This has been overcome by the use of two segments, of which the proximal one, the humerus, is mainly concerned with the fore and aft motion, the distal, radius and ulna, is more concerned with support. But the motion of the humerus cannot be a purely fore and aft one, for the action of the radius and ulna still demand that the humerus be raised and lowered somewhat; and, further, a rotation of that element is required in order to preserve the articulations of the humerus with the forearm, and is further caused by the action of the forearm muscles on the condyles of the humerus.

As noted by Watson (1917*a*, p. 13), the main motion of the fore limb for the advance of the body is one from a position in which the humerus is advanced and the forearm extended to one in which the humerus is in its most posterior position and the forearm flexed.

Watson has assumed that the glenoid is a single screw-shaped surface, but this seems rather improbable, because of its great length. The

opposing surfaces, on this view, are segments of rather large circles, and any considerable movement of the distal end of the humerus would be out of the question, as he notes. Any motion of more than about 20 degrees would cause the humerus to cut the muscular surfaces at the anterior and posterior edges of the joint. The joint capsule and ligaments would be greatly strained; for example, in *Diadectes* a twenty-degree movement would displace a point on the articular surface of the humerus from a corresponding point on the girdle about an inch and a half sideways. Further, motion over the whole surface would entail a great deal of friction.

Although it is hard to be certain, due to the amount of cartilage which probably covered the joint in life, it seems probable that there were two partially separated articular surfaces, and not one, in the shoulder joint. A well-preserved humerus, such as that of *Dimetrodon* (Fig. 3), sometimes shows on its articular surface a ridge running posteriorly and ventrally and separating two surfaces. One commences broadly at the anterior dorsal edge and dwindles as it curves underneath to terminate at a distinct notch on the under side of the bone. The other commences behind the first and continues dorsal to it to the posterior end of the articular surface. No such ridge can be found on the glenoid, but it will be noted that anteriorly there is a broad beginning of the glenoid, followed by contraction of the surface, and then by a sudden expansion. This change in the width of the articular surface, found in all types, is difficult to explain on the theory of the unity of the surface, but fits perfectly with the idea of two distinct surfaces. The second expanded surface is the anterior termination of the second surface of the joint.

The screw type is present with remarkable uniformity throughout the American cotylosaur and pelycosaur series, most of the apparent discrepancies probably being due to the presence of greater or lesser quantities of cartilage on its surface. We have no transition to the modern reptilian condition; here, as otherwise, the *Araeoscelis* girdle does not shed any sure light.

The African reptiles, as well described by Watson (1917*a*, fig. 26, etc.), show a sharp contrast, although somewhat of an intermediate type is found in the pareiasaurs. Here the "screw" is still present, although in a much shortened form. The therapsids show a progressive series of forms in which the screw is almost obliterated; the vertical plane of motion of the humerus tends to bring the two primitive glenoid surfaces into parallel positions as the posterior and anterior portions of a single surface running from the dorsal side of the humerus to the ventral,

extending only slightly posteriorly below, and with a corresponding surface on the glenoid. This would apparently lead to a disappearance of any distinction between the surfaces, functionally alike.

d.—THE CORACOID PLATE. This extends antero-posteriorly below the scapular blade and glenoid, is turned in at a sharp angle from the former, and gives origin, in the main, to the great ventral group of short humeral muscles (scapulo-humeralis anterior, supracoracoideus, and coraco brachialis) as well as the biceps. In position and function this surface may be compared to the pubo-ischiadic plate in the pelvis.

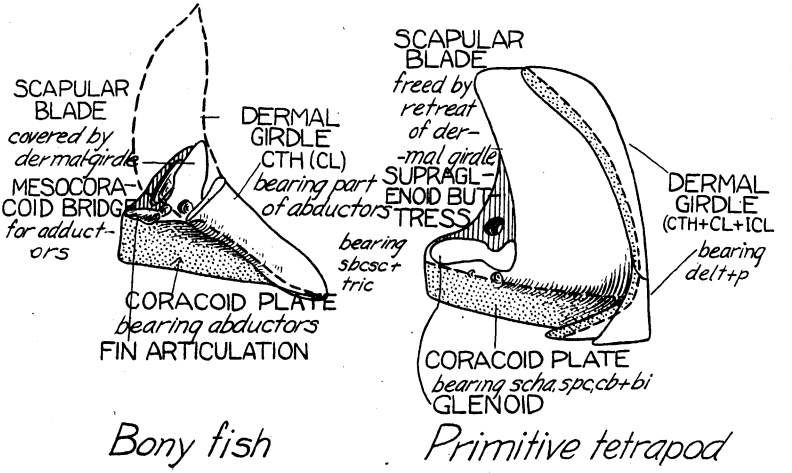

Figure 4. Diagram to show comparison of fish and tetrapod shoulder girdles. In the fish (left) the upper part of the dermal girdle has been cut away to show the scapular blade beneath. The primitive dorsal and ventral masses of the limb musculature are indicated. The dorsal mass in fish arises from the mesocoracoid bridge and the region internal to it; in tetrapods from the region of the supraglenoid buttress. The ventral mass in either case arises from the coracoid plate and the dermal girdle.

This region, which gives rise to the abductors, is even more clearly defined in the bony fish, since the small scapular blade is mainly covered by the dermal girdle (Fig. 4). In the primitive reptilian and rachitomous types, however, the reduction of this secondary girdle had progressed so far that it is only the anterior border of the scapular blade which is covered by dermal elements. The upper boundary is marked by a change in surface which frees the anterior border from the clavicle (this is the acromial equivalent) and at the same time allows room for musculature beneath the deltoid. This line usually runs across the scapula forward from the anterior edge of the glenoid; and it will be noted that the boundaries of the plate are thus not exactly those of the coraco-scapular suture.

The anterior and ventral borders often show surfaces which indicate cartilagenous extensions, the exact extent of which it is difficult to determine. Ventrally, it is probable that in most if not all cases they continued the plate to the mid-line or nearly to it; Williston (1916*a*, p. 182; 1917*a*, fig. 6; etc.) has found well-articulated specimens, the coracoids touching. Anteriorly, it will be noted that in no forms which may be considered at all primitive is there ever shown to be any contact between the coracoid and the clavicles or interclavicle; the anterior extent of the plate and its cartilage is limited only by the extent of development of the muscles which it bears, and may extend forward internal to and beyond the clavicles. This is also the usual lacertilian condition.

The supracoracoid (coracoid) foramen, for the nerve of the same name, is found in the same primitive position as in Stegocephalia, opening widely below the anterior end of the glenoid; posterior to it in both groups is sometimes found a third foramen, the glenoid of Williston (1909, p. 648), the character of which is unknown, but which probably carried a blood vessel. In connection with the supracoracoid foramen may be noted a similarly placed foramen in teleosts (Pychlau, 1908, p. 713) which carries a nerve supplying the abductors.

We have earlier noted the fact that there are few indications of separate portions of this plate for the muscles originating from it, except for the usual presence of a small distinct surface posteriorly for a coracobrachialis longus.

Internally, the plate region presents at its posterior end a concave surface, running down and then in from the ridge above the glenoid. It is pierced by the small internal opening of the glenoid foramen and offers insertion for the axial musculature. Opposite the anterior edge of the glenoid, the surface falls away sharply for the subscapular fossa which gives origin to the supraglenoid and supracoracoid foramina. In front, the plate is much thinner and corresponds in curvature to the outer surface, and probably had no musculature.

In modern reptiles, where the mechanics of locomotion are similar, the coracoid plate has remained much the same except for the dorsal posterior loss of surface mentioned in connection with changes in the glenoid region. It gives origin to the scapulo-humeralis-supracoracoideus-coraco-brachialis mass and the biceps. An item of interest is the fenestration of the lizard coracoid, which seems to correspond to the areas of origin of these muscles and forms an analogy to the fenestration of the skull which is associated with the distribution of the jaw muscles.

We have already discussed the changes in supporting function which have rendered the muscles of the coracoid plate of little value *in situ* in the mammalian type of locomotion and have led to their invasion of the scapular blade. This has been accompanied by a reduction of the coracoid plate, progressive stages in which may be observed in the therapsids from *Moschops* to *Cynognathus*. In monotremes, the plate is of approximately the same extent, except for a loss of the anterior dorsal portion. In higher mammals, we have only a "nubbin" remaining, as the coracoid process (for the origin of the biceps and reduced coracobrachialis). The glenoid foramen disappears above the cotylosaurs.

The suture between scapula and coracoid has already been described in every group of cotylosaurs except the diadectids (Watson, 1917*a*, p. 5); and one of the *Diadectes* shoulder girdles in the American Museum indicates this suture. In this, the cotylosaurs present a contrast to the known Rachitomi, in which there is no indication of any division of the shoulder girdle. The question of the number of coracoids is more complicated. Pareiasaurs, captorhinomorphs, and *Procolophon* have two elements, as does *Limnoscelis*, the girdle of which is otherwise similar to that of *Diadectes*. Only in this latter form and in *Seymouria* is there a single element. This is, as Watson (1917*a*, p. 49) has pointed out, a primitive character.

The evolution of a posterior coracoid in addition to the primitive anterior one has thus taken place within the Cotylosauria. The two elements are found in almost all pelycosaurs, as well as all therapsids. Modern reptiles, however, have but one. We may either assume, with Watson (1917*a*, p. 59), that these groups sprang from a form which had never developed a posterior coracoid, or, with Williston (1911, p. 99), that they have secondarily lost the posterior coracoid. Watson's argument would necessitate splitting off all living and most fossil reptiles at the very base of the cotylosaurs.

Williston finds no ossification in the posterior coracoid region of *Varanoops* (1911, p. 99) (the related *Varanosaurus* has a well-developed bone (Watson, 1914*a*, p. 305)), and Case and Williston demonstrate (1913, p. 50) its late ossification in *Ophiacodon*, suggesting loss of a separate center of ossification. In either case, it will be noted that it is the anterior coracoid which is retained by the reptiles.

The monotreme has two elements similar in appearance to those of the therapsids, and hence it would appear that the anterior coracoid (the "coracoid" of living reptiles) is the anterior element (epicoracoid or precoracoid) of monotremes (Broom, 1912; Watson, 1917*a*, pp. 49–52).

The posterior element of the monotreme girdle is generally recognized as the true marsupial and placental coracoid.

But it will be noted that this destroys the homology of the mammalian coracoid with that of living reptiles; and attempts have been made to preserve the older conception. The evidence for this point of view has been well presented by Gregory (1918, pp. 545–552), restated by Hanson (1920), the main lines of argument being: (1) the anterior reptilian coracoid is similar in position to the posterior one of monotremes, (2) the epicoracoid of monotremes is the "epicoracoid" of lizards and *Sphenodon*, and (3) the muscular origins prove these two homologies. No one of these arguments will hold.

(1) The argument for position is summed up in Hanson's statement (1920, p. 399) that "it is hard to imagine any rotation or migration of this element (the posterior coracoid of reptiles) which would bring it from a position distinctly posterior of the glenoid to its present distinctly anterior one." This statement can only be made in a comparison of living reptiles and higher mammals, with a disregard of phylogeny. The posterior coracoid of reptiles when present is never posterior to the glenoid. In primitive reptiles it occupies the posterior portion of it; in the therapsids, it almost or entirely excludes the anterior element from the glenoid, as Broom (1912) and Watson (1917, p. 50) have demonstrated. Neither is the acknowledged coracoid anterior to the glenoid in the monotreme; it occupies it. The relation of the two monotreme elements coincides almost exactly with those of higher therapsids, except that the antero-dorsal portion of the coracoid plate is missing in the monotremes. I have in a previous section suggested the reason for its absence.

(2) The presence of the epicoracoid in monotremes must be explained away. Gregory (1918, pp. 545, 547) maintains that this bone is the homologue of a cartilage known to exist anterior to the bony girdle in some extinct forms and a similarly placed cartilage or calcified cartilage in lizards and *Sphenodon*. It is admitted by Hanson (1920, p. 335) that we have nowhere else except in monotremes any ossification to fit in with this theory. Such a cartilage was certainly not always present in extinct reptiles; I have seen some clepsydropsids with a finished outline to the bone in this region. In lizards and in extinct forms where it is believed to be present, this cartilage seems to be merely an unossified peripheral portion of the coracoid, of which it is functionally a part. This contrasts sharply with the monotreme epicoracoid, a bony element quite distinct from the coracoid.

In this connection, this theory ignores the fate of the posterior coracoid, as Gregory notes (1918, p. 547). Between therapsids and monotremes, it necessitates a sort of March Hare's tea party, in which every element shifts one place: (a) an *ossified* epicoracoid suddenly appears and takes the place of the anterior coracoid; (b) the anterior coracoid shifts into the position of the posterior coracoid; (c) the old posterior coracoid is forced out of the glenoid (after having taken it over completely) and disappears.

(3) Argument for homology of bones from muscular origins is extremely dangerous; in this very region we have shown that a radical change in the musculature has taken place. It is stated that the same muscular elements arise from the coracoids of monotremes and *Sphenodon* (Gregory, 1918, p. 546). This is only partially true. The musculature found on the modern reptilian coracoid (the primitive supracoracoideus and coracobrachialis) is distributed between the scapula (supra- and infraspinatus), epicoracoid (supracoracoideus), and coracoid (coracobrachialis) in monotremes. It is stated (Gregory, 1918, p. 546) that the same muscles originate from the monotreme epicoracoid as from its supposed homologue in *Sphenodon* (supracoracoideus in part). But a portion of them are found on the scapula in monotremes, as supra- and infraspinatus.

All in all, I fail to see any evidence for this theory which will stand examination, while the therapsid-monotreme resemblances are extremely obvious. As Broom and Watson conclude, the mammalian coracoid seems unquestionably the posterior primitive element, which is hence a true coracoid; the modern reptilian "coracoid" is certainly the anterior primitive element, hence, the epicoracoid or precoracoid of monotremes; and the coracoids of the two modern groups are not homologous.

The history of the primary girdle may be summarized as: (1) the taking over by the scapula of the functions of the cleithrum; (2) evolution of the glenoid and supraglenoid buttress; (3) loss of the latter of these, with invasion of scapula and inside of the coracoid plate by the musculature of the buttress; and (4) reduction of the coracoid plate in the mammals and invasion of the scapular blade by its musculature.

3.—Humerus

Plates XXXV, XXXVI, XXXVII; Figure 5

The primitive humerus, characteristic of both Reptilia and Amphibia of the American Permian is at first sight hard to understand. Proximally, it is terminated by the long curve of the glenoid articulation; distally,

the bone is expanded between the two epicondyles and including the radial and ulnar articulations at an angle which, in such a form as *Diadectes*, is nearly a right angle. This type of humerus is often spoken of as "twisted" and later types as "less twisted." Its universal primitive occurrence, and the presence of transitional types to modern humeri, necessarily leads to the acceptance of this type as the primitive one. Reduced to its simplest form, as perhaps seen best in *Achelomma* (Fig. 5), the primitive humerus was built as a tetrahedron, composed of four roughly triangular surfaces, two having their bases proximally, and two distally, with the planes of these bases at right angles to one another. The four surfaces may be described separately.

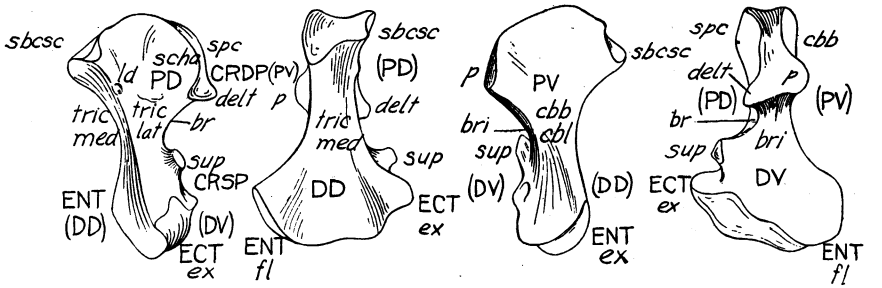

Figure 5. Humerus of *Achelomma*, showing the four surfaces of the primitive tetrahedral humerus (proximal and distal dorsal, proximal and distal ventral, PD, DD, PV, DV) and their relations to the musculature.

(*a*) A proximal dorsal surface, with its base at the curved head, its plane facing antero-dorsally in natural articulation, and its apex at the ectepicondyle. Its anterior border is marked proximally by the supracoracoideus insertion and delto-pectoral crest, then by a ridge (anterior dorso-ventral line) for brachio-radialis origin, separating this surface from the brachialis surface anteriorly and termination at the supinator crest. The posterior border begins proximally with the insertion of the subcoraco-scapularis, followed by the latissimus; then there is a sharp ridge (medio-lateral line), terminating at the extensor crest, separating this surface from the distal dorsal one. There usually runs transversely across it a line (transverse humeral line) from the deltoid to the latissimus insertions (not seen in *Achelomma*); the lateral head of the triceps originated distal to the transverse line; the scapulo-humeralis anterior inserted proximally to it.

(*b*) A distal dorsal surface, having its base between the distal condyles, its apex at the posterior end of the head, and the plane of its surface looking dorso-posteriorly. Its anterior dorsal border adjoins the

last described surface. Its posterior border distally is the huge entepicondyle; beyond this, the border curves in to the ventral posterior corner of the head of the humerus. This surface gave rise to the median head of the triceps. On it is the upper opening of the entepicondylar foramen when this is present.

(*c*) A proximal ventral surface, having its base at the head and tapering out to an end at the proximal end of the entepicondyle. The posterior edge is co-terminous with the last described. The anterior edge is bounded by the supracoracoid insertion, which continues into the pectoralis crest, then down across the gap through which the biceps passes, and on to the proximal border of the entepicondyle. The greater part of the surface was occupied by the coraco-brachialis, the longus occupying the narrow descending distal end.

(*d*) A distal ventral surface. Its base at the distal end, between the condyles, and its lateral boundaries coinciding with those of (*a*) and (*c*). From a beginning proximally at the delto-pectoral crest, it spreads out posteriorly to form the under side of the entepicondyle, and distally is occupied by the radial and the ulnar articulations, while the entepicondylar foramen when present opens posteriorly and proximally to them. This surface, where occupied by muscles, is for the brachialis.

It will be seen that the only major difference between this type and that found in the most primitive reptiles, as *Seymouria*, *Diadectes*, and *Limnoscelis*, is the absence of an entepicondylar foramen, and it is natural to conclude that the one type is directly ancestral to the other.

A complication, however, is caused by the occurrence of flattened types, in which the distal and proximal surfaces, above and below, are in nearly the same plane. This is found in a form, *Archeria* of Case (1915, p. 170), known only from the humerus, which possesses an entepicondylar foramen and is inferred to be reptilian, and also in the humerus assigned to *Cricotus* (Case, 1915, p. 162). This latter is the only embolomerous type of which the humerus is accurately known, and deserves consideration because of the primitive position of the Embolomeri as a whole. But in other features *Cricotus* is usually considered to be secondarily aquatic, and it seems probable that this flattened humerus is also secondary. The similar *Archeria* humerus also seems to belong to an aquatic type.

From our present evidence, then, it seems justifiable to regard the tetrahedral type of the typical Stegocephalia, without an entepicondylar foramen, as the most primitive, and to derive the reptilian humerus from this by the addition of the entepicondylar foramen. This foramen seems

to be caused by a greater development of the flexor musculature, and a proximal extension of their humeral area of origin, which has surrounded the median nerve and blood vessel. Even in *Cricotus*, there is a notch at the proximal end of the condyle which suggests that only a slight growth of the condyle would cause their inclosure. The foramen is found in the Amphibia only in *Diplocaulus* and questionably in *Cochleosaurus*.

The history of the humerus beyond the primitive reptilian condition is concerned mainly with: (1) development of a shaft; (2) development of the ectepicondylar foramen; (3) secondary "untwisting" of the humerus by placing the proximal and distal surfaces in more of the same plane; and (4) reduction of the condyles and their foramina.

There is no shaft, properly, in *Seymouria*, the diadectids, nor *Limnoscelis*, nor in the pareiasaurs, although the humeri of the latter are advanced in other characters. Most of the captorhinomorphs, on the other hand, have well developed shafts, the extreme of which is seen in *Pleuristion* (Williston, 1910, p. 589); they have better developed shafts than many pelycosarus, especially *Ophiacodon*. There is a gradual increase in length in the therapsids, the Dinocephalia having rather short humeri. *Aræoscelis* (Williston, 1910, p. 588) is remarkable for the extreme length of its humerus.

The causes of the formation of the ectepicondylar foramen were discussed in a preceding section. The foramen is primitively absent in all cotylosaurs, except perhaps the pareiasaurs, all pelycosaurs except *Edaphosaurus*, and probably in the "Archosauria" and many other extinct reptiles. It is present in Chelonia, Nothosauria (Seeley, 1895*b*, p. 1017), lizards, "Proterosauria" (*Aræoscelis* and *Kadaliosaurus*, Williston, 1914, p. 126), *Edaphosaurus* (Case, 1913, p. 81) and therapsids (Seeley, 1889, p. 264, and 1895*c*, pp. 30, 45; Watson, 1914, p. 773, etc.) It is lost in mammals and is not often described in therapsids. It is certainly secondarily absent in the latter group in many cases, as in *Moschops*, where the radial nerve clearly ran proximal to the fused supinator crest and ectepicondyle; but I am inclined to believe that its apparent absence is often due to its small size, which has caused it to be left unexcavated. The foramen is not described in pareiasaurs, but I am convinced that some of the group, at least, will be found to possess it; there is no separate supinator crest, and the configuration of the humerus distally resembles that of forms which primitively possessed the foramen.

The placing of the distal plane at nearly right angles to the proximal is correlated with the position of the forearm, which works in a plane which is more nearly parallel to the ground in the more primitive types,

as noted by Watson (1917*a*, p. 13, etc.). When the forearm works in a more nearly vertical position, and one more nearly in the same plane as the long axis of the humerus, the distal plane shifts to preserve its relations, rotating up posteriorly and down anteriorly, hence being more nearly in a horizontal position and more nearly parallel to the plane of the proximal part of the humerus. An early and striking example of this is seen in the pareiasaurs, some of which early acquired a more upright gait (Watson, 1917*a*, pp. 8, 9); in *Propappus*, for example, the difference between the planes is only about 30°. The higher cotylosaurs and theromorphs still retain very distinct surfaces, but the angle is not great, usually varying from about 30° to 60°. This condition is essentially the same in the modern lizards and *Sphenodon*, in most of which a fair degree of "twist" and fairly distinct surfaces are retained. In the therapsids the "untwisting" process is very early and very marked, and leads to an approximation of the two planes, a loss of the proximal part of the distal dorsal surface, and a blending of the other surfaces, so that they are not readily distinguishable in modern forms unless we attempt to determine them from the muscle areas concerned. The proximal part of the distal ventral plane appears as the anterior half of the dorsal side of the humerus (the brachialis origin).

The primitively large epicondyles gave strength to the extensors and flexors by creating an open angle of insertion which was especially necessary in the flexors because of the strain upon them caused by the inclined position of the forearm and the necessity of their exerting a great lifting force (Watson, 1917*a*, p. 15, etc.). In all higher types, the condyles are reduced (except for a probably secondary expansion in digging forms), correlated with a more vertical position of the forearm, putting the supporting function more on the radius and less on the forearm muscles, and smaller angles of insertion, correlated with greater speed and less strength, rendering large condyles unnecessary.

Propappus shows an early example of this reduction, for the first reason; although the humerus is extremely short, the condyles do not extend far beyond the articular surfaces (Watson, 1917*a*, p. 9). Both foramina are probably present, although reduced. In the Captorhinomorpha the epicondyles of the slender humerus are much reduced; even more so than in any pelycosaur, the lower types of this order, such as *Ophiacodon* being only a slight refinement of the lower cotylosaurian type. *Aræoscelis*, with a slender pair of epicondyles, still retains both foramina. In all modern groups of reptiles, with the exception of *Sphenodon*, the old entepicondylar foramen, strangely enough, has disappeared in this

process of reduction, while the new ectepicondylar foramen has persisted in all except the "Archosauria," in which line it is quite possible that it was never evolved. The *Moschops* epicondyles are reduced, although the upper end of the humerus is still well expanded; little more reduction is needed to reach the mammalian condition. The entepicondylar foramen is retained right through to the mammals; the ectepicondylar is lost, apparently independently in different phyla.

The modifications of the humerus from the primitive type may be interpreted thus functionally as for (1) upright pose without inturning of the limbs in pareiasaurs; (2) slenderness for speed without upright posture or inturning of the limbs in higher cotylosaurs, pelycosaurs (slight), *Araeoscelis*, and most modern reptiles; and (3) upright pose with inturning of the limbs in therapsids.

4.—Radius and Ulna

Few points of interest are connected with these bones so far as I have been able to discover in the fossil material. The evidence from modern forms shows that there is little variation in their muscular insertions apart from the mammalian line; and here the evidence is too fragmentary to give us much help.

HIND LIMB, MUSCULATURE

1.—Axial Muscles Acting on the Pelvis

Plates XXXVIII; XLIV, XLV, insertions

As the pelvis is little movable, we are interested here mainly in the pelvic origins or insertions of this group.

The axial muscles of the pelvic region may be divided into (*a*) a dorsal group, above ribs and transverse processes, and (*b*) and (*c*) a ventral group, below. The former group is partially interrupted by the pelvis, the latter completely so.

a.—Dorsal Musculature. The most medial muscles of the back (spinales and semispinales) are never interrupted by the ilium. The more lateral muscles, coming from the trunk as longissimus dorsi and iliocostalis and extending down on to the tail as an extensor caudæ lateralis or abductor caudæ externus, have had an interesting history. In urodeles the ilium is mainly a supporting structure, appendicular muscles arising only near its base. The situation was probably similar in *Eryops*. The dorsal boundary of the appendicular muscles seems to have been a transverse line, sometimes not well defined, running diagonally down across the ilium from a tubercle on the posterior border. Since this line is

about opposite the lower end of the sacral articulation internally, we may conclude that the origins and insertions above this point for axial muscles were those of the dorsal system, that is, the longissimus and ilio-costalis anteriorly and the extensor caudæ lateralis posteriorly, the more medial muscles passing freely above the top of the iliac blade.

The situation in modern reptiles, such as the lizards, is radically different. The limb muscles occupy the whole outer surface; the dorsal axial muscles are restricted to the posterior tip (extensor caudæ lateralis) and an internal shelf above the sacral ribs (longissimus and ilio-costalis). It would seem from a direct comparison with the amphibian condition that, with the growth of the appendicular muscles, the dorsal axial system had simply been pushed off the blade of the ilium. The fossil forms, however, give an entirely unexpected answer. With the growth of the limb muscles, the ilium has folded over; the old outer portion above the transverse line is the internal surface above the sacral ribs, which now offers insertion to the dorsal axial muscles formerly found on the outer surface; the transverse line, originally far down the blade, becomes the definitive dorsal termination of the ilium.

The intermediate stages are well illustrated by the fossils. In *Diadectes*, *Diadectoides*, *?Seymouria*, and *Limnoscelis*, the transverse line is the outer limit of a dorsal shelf, set in some distance from the surface below. In *Pœcilospondylus* and *Ophiacodon* or *Theropleura* this shelf is a trough, with the inner and outer surfaces of about equal height, but tending to have the outer surface higher in *Ophiacodon;* in *Dimetrodon* the shelf has now definitely become a part of the inner surface and the ilium is similar to the lizard ilium.

In mammals, the ilium has not changed greatly from the reptilian condition. The lateral caudal extensor is still found above the sacral ribs on the posterior edge or inner surface, and the longissimus group anterior to this.

b.—Anterior Ventral Musculature. This system terminates in lizards and *Sphenodon* in great measure on a ligament, described by Perrin (1895, p. 78), running from the anterior dorsal extremity of the ilium to the pubic tubercle (the most anterior external point of the pubis). This ilio-pubic ligament is continuous ventrally with the pubo-ischiadic ligament running from the external edge of the pubis over the pubo-ischiadic plate to the posterior border of the ischium. Along this first ligament and its dorsal and ventral insertions are found the posterior terminations of the obliques, pyramidalis, and transversalis, while ventrally the rectus continues back over the pubo-ischiadic ligament to

an insertion on the ischiadic symphysis. It will be noted that the ligament affords space for the emergence of the pubo-ischio-femoralis internus (iliacus and psoas) from the inner side of the pubis. The points of insertion of the ligament (probably variable in development) may be easily inferred in the fossils, as, dorsally, the anterior termination of the upper edge of the reptilian ilium (or its amphibian predecessor, the transverse iliac line) and ventrally the antero-external corner of the pubis, often not exactly determinable because of the presence of cartilage. It is of course impossible to state whether or not the rectus extended back over the ventral symphysis to any great degree.

In the mammals the ligament is retained, as Poupart's ligament. At the ventral end, it will be noted that the marsupial bones have developed medial to the pubic tubercle, and the insertion of the ligament is found, in forms possessing these bones, at the external point of union of pubis and marsupial bone.

In living groups the quadratus lumborum, as an internal dorsal member of this group, originates internally from the ilium below and anterior to the sacral ribs or the ribs themselves. Its origin has thus not been concerned with the changes undergone by the external musculature of the ilium. Gadow (1882, p. 418) refers to this group a large muscle running to the femur in the Crocodilia. This is found nowhere else and its relations to a true quadratus lumborum are questionable.

c.—Posterior Ventral Musculature. From the posterior end of the ilium to the tuber ischii in lizards and other groups is a ligament, ilio-ischiadic, probably the mammalian sacro-ischiadic, beneath which the ischio-trochantericus (obturator internus) and coccygeo-femoral muscles emerge on to the leg and from which part of the tibial flexors arise. This ligament is not as intimately connected with the pelvic attachments of the axial muscles as the anterior ligament. These muscles are divided into several groups, interrupted by the coccygeo-femoral muscles. An external mass (reptilian ischio-caudalis) arises from the tuber ischii and proceeds backward ventrally, being met by a dorsal external group (ilio-caudalis) arising from the transverse processes and, through a connection with the upper end of the ilio-ischiadic ligament, from the ilium. There are (apparently as derivatives of this group) a number of variable cloacal muscles, with which we are not concerned. The tuber ischii may be inferred as the general point of origin of this ischio-caudal muscle in the Permian forms.

In the typical mammalia no caudal muscle originates from this region, which, it will be noted, is posterior to the point where the ob-

turator internus passes out of the girdle, while the flexors of the tail (levator ani) originate from the pubis, ilium, and ischium, anterior to the obturator internus. Nothing of this sort is described in the reptiles, as far as I have found, except in the turtles and for a small slip passing down alongside the rectum in lizards. But in *Cryptobranchus* I find a muscle, similar in its relations to this group in mammals, arising from the ischium anterior to the ischio-trochantericus (obturator internus) and running back internal to the coccygeo-femoral muscles (ilio-caudalis, deep part). In most fossil forms there is a ridge running diagonally upwards anterior to the ischio-trochanteric surface which probably served as an origin for this caudal flexor. Its loss, in lizards, etc., is probably due to the great development of the coccygeo-femoral muscles. It is possible that the small cloacal muscle of lizards already mentioned may be a remnant of this. With the enlargement of the ischio-trochantericus as the mammalian obturator internus, the area of origin has been pushed anteriorly on to pubis and ilium and the upper border of the ischium, always preserving the primitive relations to the obturator internus.

2.—Long Dorsal Muscles to Lower Leg

Plates XXXIX; XLIV, XLVI, origins

These two sets are essentially similar in their primitive relations, the triceps or quadriceps laying anteriorly and running to the tibia, the biceps or ilio-fibularis posteriorly and running to the fibula. In the triceps (quadriceps) is found one case of the double innervations found in all the antero-posterior series in the hind leg.

a.—Triceps (Quadriceps and Sartorius). The general reptilian arrangement consists of: (1) extensor ilio-tibialis (rectus femoris) originating from the ilium; (2) ambiens (sartorius) arising from the pubis; and (3) femoro-tibialis (vasti) from the femur, the three heads uniting to insert into the head of the tibia (or through the medium of a patella in most mammals).

(1) The ilio-tibialis generally originates from a tendon covering the top of the ilium, sometimes fleshily near the anterior edge, and sometimes extending on to the ilio-pubic ligament. The origin may be double, as in many lizards, Chelonia, and crocodiles. In all cases there is a double innervation, from crural and sacral branches. The close resemblance of the pelycosaur ilium to that of the lizards renders a similar origin probable, and from this it may be traced back to the already mentioned transverse line of the ilium of lower forms. Whether or not there was a slight fleshy origin anteriorly cannot be said with certainty.

In the mammals the rectus femoris is a derivative of this muscle. The upgrowth of the gluteals in the therapsid series has apparently restricted the muscle to the anterior edge of the blade. It will be noted that it is the anterior portion of the muscle which has been preserved and, as might be expected from this, the mammalian rectus has a purely crural innervation.

Gadow (1882, p. 381), followed by Gregory and Camp (1918, p. 488), says the ilio-tibialis becomes the gluteus maximus. This might possibly be true in part, but (apart from the peculiar monotreme "gluteus maximus," which is radically different from that found in most placental mammals) the gluteus maximus is clearly related to the deeper glutei in origin, course, and insertion, and has no relation to the triceps. Gregory and Camp (1918, p. 486) would derive the rectus femoris from the ambiens; but, as noted below, ambiens seems to be the homologue of the monotreme sartorius, which is clearly that of higher mammals.

(2) The reptilian ambiens, with an innervation which is always crural, originates from the pubis in front of the acetabulum and below the course of the pubo-ischio-femoralis internus out over the edge of the pelvis (it often receives a slip from this muscle), while the ilio-tibialis is always above the pubo-ischio-femoralis internus. No such muscle is found in urodeles. But the origin of this muscle is not far from the lower insertion of the ilio-pubic ligament, and it is conceivable that it may have traveled down this ligament to its present position from an original dorsal one (Noble, 1922); or the contrary may have been the case and the urodele condition resulted from the muscle shifting upward to give two "ilio-tibial" muscles.

The origin of this muscle (and the pubo-tibialis) in Permian fossils may be always recognized as a roughened area on the pubis anterior to and below the acetabulum. This may be recognized also in therapsids. In the monotremes, the homologue of the sartorius of higher mammals arises from this same position, and hence the homology of the two muscles seems unquestionable. In the higher mammals it originates from the anterior superior spine of the ilium and is not closely associated with the quadriceps. This change of position may be easily accounted for by the assumption that, with the changed position of the leg, it has migrated upward over Poupart's ligament, which here inserts close to the origin of the muscle; it is on the ligament in some marsupials. The sartorius is not a derivative of the true pubo-tibialis (ventralis) (Gregory and Camp, 1918, p. 487), for this is by contrast a ventral muscle with usually an obturator innervation (Frets, 1910, p. 83, Gadow, 1882, p.

351) and a ventral tibial insertion between the gastrocnemius heads. The confusion is apparently due to Gadow's indiscriminate use of the term pubo-tibialis.

(3) Femoro-tibialis (Vasti), in reptiles and mammals a great mass from the shaft of the femur of unquestioned homology. Its absence in both urodeles and Anura suggests that it is truly a secondary acquisition. A clue to its origin is given by *Eryops* and *Ichthyacanthus*, which possess a ridge on the femur some distance above the intercondylar sulcus, manifestly too far up the shaft for any sort of capsular arrangement and probably representing the origin of a small femoro-tibialis. While it is impossible to say that this is the actual beginning of the femoro-tibialis, it would seem probable that it is at least a close parallel. The absence of the muscle in the Stegocephalia is rendered more probable by the general slender build of the femoral shaft, with large posterior and anterior surfaces (for ilio-femoralis and adductor) but little dorsal surface, except proximally for pubo-ischio-femoralis internus. On the contrary, the primitive reptiles have a broad shaft, with probably a wide-spreading femoro-tibialis. Its actual boundaries are not very definite in the fossils; it probably covered most of the dorsal surface of the shaft between the adductors antero-ventrally, ilio-femoralis postero-ventrally, and the pubo-ischio-femoralis internus proximally. Its relations have not changed during the evolution of the mammalia except that the iliacus, psoas and pectineus (old pubo-ischio-femoralis internus) are now anterior rather than proximal.

The principal points in the history of the triceps are, thus, (1) development of femoro-tibialis; (2) displacement of ilio-tibialis in the mammalian line; and (3) shifting of sartorius in the higher mammals.

b.—Ilio-fibularis (Biceps). Its general reptilian and urodele condition is that of a muscle of sacral innervation paralleling the ilio-tibialis posteriorly and running from the posterior corner of that part of the ilium concerned with leg muscles to the fibula, external to the course of the triceps. A similar location may be confidently made in the Permian fossils. There is a roughened area of insertion near the head of the fibula.

In mammals there is at first sight no homologue of this muscle, but, by a process of elimination, the biceps, running from the tuber ischii (with a secondary short head in some forms) to the outer, fibular, side of the leg must be a derivative of this muscle (Gadow, 1882, p. 385, Gregory and Camp, 1918, p. 489). Although reckoned as a ventral muscle and connected with the flexor series, the reptilian flexors cannot

give a homologue for this muscle and never insert on the lower leg on the outer side, the most internal of them inserting between the two heads of gastrocnemius (Plate XLI). The marked change in the origin is easily explained by the existence of the ilio-ischiadic (sacro-ischiadic) ligament, running from the old origin directly to the new one on the tuber ischii. We may assume this change in origin to have been associated with the change in position of the limb. From the nature of the case, we have no therapsid evidence as to when this transfer down the ligament took place.

3.—Dorsal Muscles to the Femur

Plates XXXIX, XL; XLIV, XLV, origins; XLVI, Figure 6, insertions

A series, well differentiated in all known forms, probably representing the deeper layer of the primitive dorsal muscle mass, running from the dorsal side of the girdle to the limb; but with the middle portion now originating from the ilium, the upgrowth of which bone has broken the probable original continuity of the group. This same middle portion presents another case of double innervation.

a.—Pubo-ischio-femoralis Internus (Iliacus, Psoas, and Pectineus). The most anterior of the series, with a crural innervation, running from the interior of the girdle out over its anterior border beneath the ilio-pubic ligament to the dorsal surface of the femur. Its original area of origin would seem to have been a strongly built shelf on the anterior internal surface of the pubis, containing the upper opening of the obturator foramen near its posterior border. This shelf, with the muscle in position, is found in *Cryptobranchus*. A similar shelf is found in *Eryops, Cricotus* (inferred from the shape of the ilium), and in the lower cotylosaurs, as *Diadectes*. The shelf is progressively less well defined in the pelycosaurs (it is not as sharply marked in *Dimetrodon* as in modern lizards and *Sphenodon*) but the narrowness of the pelvic outlet renders it improbable that in these Permian forms the muscle had spread backward over the inner surface of the girdle as it has done in the living reptiles mentioned.

The insertion would seem to have spread out over the whole dorsal surface of the femur in the Stegocephalia as in modern urodeles, with a prominent rugosity near the proximal posterior border of this area for a tendon, such as may be found in existing lizards. In the American Permian forms the tendon is retained, but the growth of the femorotibialis has restricted the dorsal insertion. In *Diadectes* a limiting line may be seen to extend transversely across from the tendon rugosity. In

Dimetrodon the line is pushed further proximally at the anterior edge, and the muscle would thus seem to be cut into two parts at its insertion, a posterior tendon and an anterior portion crowded down the anterior edge of the femur outside of the "internal trochanter." This is similar to the lizard condition.

The original function of the muscle seems to have been to raise and advance the femur. Obviously this cannot be done in mammals by a muscle placed so far ventrally. The area of origin has shifted to a dorsal position, the ilium and the lumbar vertebræ. There is no evidence of this change in any therapsid. The old internal area of origin is still fairly well defined in the highest members of the group; nor is there any trace of a trihedral type of ilium which the monotremes and marsupials suggest as the ancestral mammalian condition. Apparently this change of origin is a late step. The pectineus apparently represents a few fibers left behind in this migration.

The psoas minor inserts on the pelvis. Its point of insertion in the monotremes is that of the origin of sartorius and suggests that it is the same set of fibers of the pubo-ischio-femoralis internus which connected with the ambiens at this same point.

A further change in the area of insertion has also taken place. We have seen that the reptilian condition tended to two proximal areas, one posterior or external, and one on the anterior or internal border. The first area is lost in mammals, the second retained. It will thus be seen that the reptilian internal trochanter is partially a homologue of the mammalian minor trochanter (Fig. 6), both having the insertion of the muscle in question on its outer side but with the difference that the summit is not occupied in mammals, as it was in reptiles, by a portion of the insertion of the obturator externus (pubo-ischio-femoralis externus). The trochanter, and the ridge leading to it, may be seen in some therapsid humeri, often remarkably far over on the ventral surface.

b.—Ilio-femoralis (Glutei and Tensor Fasciæ Femoris). The middle portion of the series, with a double sacral and crural innervation from urodeles to monotremes, but sacral only in higher mammals, except for a partial femoral innervation of gluteus maximus in some cases. The general primitive area of origin in living lower tetrapods and hence in the Permian fossil forms under consideration consists of most of the iliac surface below the transverse line or the definitive dorsal boundary, except for the posterior dorsal corner occupied by the ilio-fibularis. The original area of insertion, comparable to that in existing lizards, urodeles, etc., seems to have been an area bounded postero-ventrally by the great ridge

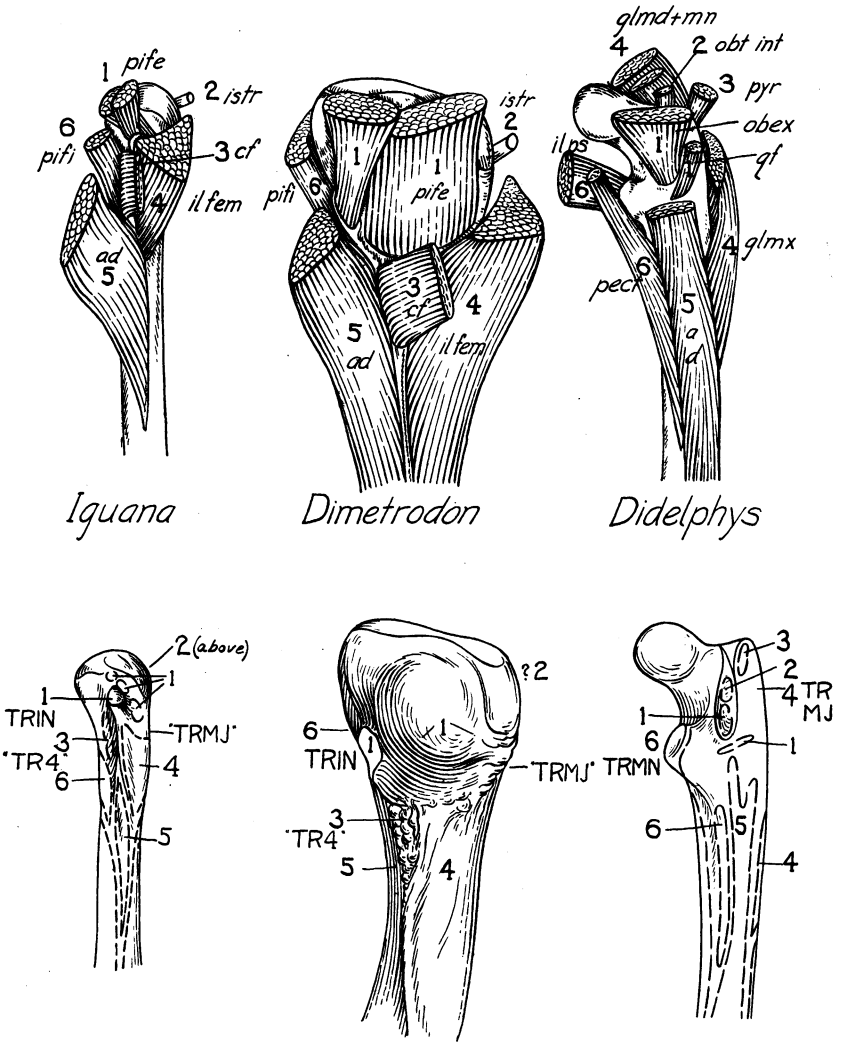

Figure 6. To show the relation of the femoral trochanters (below) and related musculature (above). *Dimetrodon* shows the primitive Y-system, and may be compared with *Iguana* and *Didelphys*. It will be seen that there has been little change in the relative position of the muscles involved, except the mammalian pyriformis. The anterior branch of the Y is the reptilian inner trochanter and, by a change of function, the mammalian minor trochanter. The posterior branch, with the development of the gluteals, becomes the mammalian greater trochanter. The fossa between the two trochanters always contains part of the insertion of pubo-ischio-femoralis in ternus. The junction of the branches is occupied by the insertion of the coccygeo-femoral muscles (fourth trochanter). On either side of the Y-system lie the adductors anteriorly and the ilio-femoralis posteriorly.

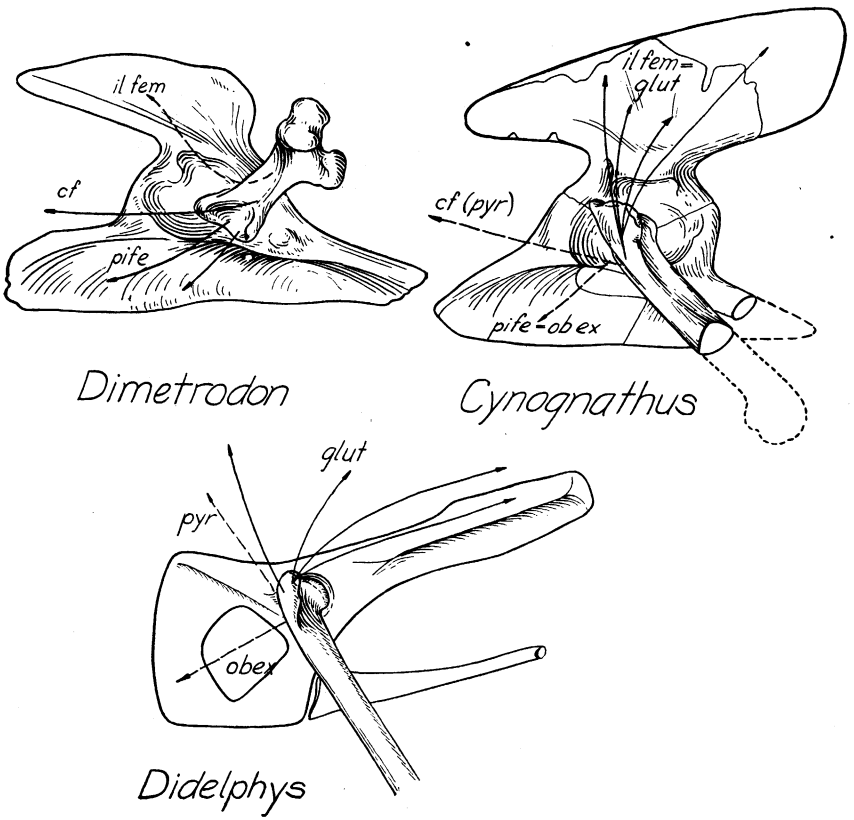

Figure 7. To show the change in the method of supporting the body and extending the femur in mammals as compared with reptiles. In the former the ilio-femoralis has only a small function as an extensor, and support and extension are carried on to a great degree by the ventral musculature. In the mammals the changed position of the femur and development of the greater trochanter transfers these functions to the glutei, enabling them to act as levers of the second class, since the greater trochanter is now posterior to the hip joint.

on the under side of the femur and its posterior proximal branch. Above, there is no clear line of demarcation from the primitive insertion of the pubo-ischio-femoralis internus, and later from the femoro-tibialis (which then occupies this same area). Proximally it abutted on the insertion of the tendon of the pubo-ischio-femoralis internus.

This muscle is of great interest in the mammalian series because of its expansion and differentiation connected with the changes in the position of the limb, analogous to the development of supra- and infra-spinatus in the fore limb (Gregory and Camp, 1918, p. 520). In the primitive type the work of support was performed by the ventral

muscles (Fig. 7). An antero-posterior position of the femur has caused a great loss of this function ventrally. But with the development of the head from the antero-internal angle of the femur the proximal portion of the insertion of the ilio-femoralis, at the posterior corner, was in an advantageous position to exert a leverage and attain a supporting function. This also pulls the femur back, aids much in locomotion, and enables the muscle to retain its old function as well. With this change has come a great expansion in the area of origin. The iliac blade has grown up and forward, giving a greater leverage and pushing the rectus femoris before it. In the Mammalia, a portion of the origin has been transferred to the fascia of the back or tail vertebræ with a secondary reduction of the extent of the ilium. The beginning of such a process may be seen in *Lystrosaurus*, where the posterior portion of the upper edge of the blade is scalloped and apparently in the process of being lost.

The longer portions of the muscle have retained the old position between adductors and vasti on the posterior side of the femur. The proximal portion of the area of insertion, representing the outside of the proximal termination of the posterior branch of the ventral ridge, is developed into the greater trochanter, which is thus seen to be partly homologous with the old posterior ridge. (Fig. 6.)

c.—ISCHIO-TROCHANTERICUS, "ISCHIO-FEMORALIS" OR PUBO-ISCHIO-FEMORALIS POSTERIOR (OBTURATOR INTERNUS AND GEMELLI). A short muscle originating from the posterior dorsal surface of the pelvis and running out under the ilio-ischiadic (sacro-ischiadic) ligament to insert by a tendon into the proximal end of the femur. In primitive fossil pelves (as also in *Cryptobranchus*) there is a small fan-shaped area of origin inside the ischium, converging to the representative of the "lesser sciatic notch." This, with possibly the area just external to this and representing the gemelli, constituted its area of origin. In the mammalian series this area is still well marked in *Moschops;* in some mammals, however, the muscle has spread widely over the inner surface of the pelvis. The small tendon of insertion cannot be recognized with certainty on fossil femora.

4.—LONG FLEXORS

Plates XLI; XLIV, origins

PUBO-TIBIALIS, PUBO-ISCHIO-TIBIALIS, FLEXORES TIBIALES INTERNUS ET EXTERNUS OR ISCHIO FLEXORIUS (GRACILIS, SEMITENDINOSUS, SEMIMEMBRANOSUS). A complicated series of ventral muscles running from the lower side of the pelvis and generally inserting on the internal

and ventral aspects of the tibia or into the lower leg musculature. While the homologies as a group are always apparent, the various portions are hard to compare. There is a general double innervation, as usual in antero-posterior series, almost altogether sacral in urodeles, with more of the obturator innervation in higher groups.

Primitively the origin is entirely from the pubo-ischiadic ligament, if developed, from the pubic tubercle along the symphysis to the tuber ischii and thence up along the ilio-ischiadic ligament. This type of origin was undoubtedly that of the primitive forms, as it is of urodeles, lizards, and *Sphenodon* today. The typical differentiations are: (1) pubo-tibialis, from the pubic tubercle; (2) pubo-ischio-tibialis (including probably the pubo-tibialis of urodeles) from the pubo-ischiadic ligament; and (3) deeper and more posterior portions, centering in origin around the tuber ischii and the adjacent ligaments, making up the flexores tibiales internus et externus (ischio-flexorius of urodeles). Into this last group, in urodeles, the coccygeo-femoralis longus, as caudi-pubo-ischio-tibialis, inserts.

The insertions are mainly tibial, extending ventrally from the internal to the external border of the bone. In lizards and *Sphenodon* the most internal is the gracilis or pubo-ischio-tibialis extending down the inner side of the tibia, together with a part of the flexor tibialis internus. Next, somewhat shorter and slightly more external, is another portion of the flexor internus, which may bridge the internal head of the gastrocnemius or insert partially at the end of the femur. At the outer ventral portion of the tibia between the two femoral heads of the lower leg flexors when both are developed are found insertions for pubo-tibialis and portions the of flexor tibialis internus and flexor externus, parts of which may also connect with the lower leg musculature. A strong ridge on the inner surface of most American Permian tibiæ indicates the insertion of pubo-ischio-tibialis and the associated part of the flexor internus. There is a tuber on the fibular side of the tibia for the portions inserting in the region.

In mammals, most of which possess the inner femoral head of the gastrocnemius, the gracilis, semitendinosus, and semimembranosus are found to insert on the inner side of the tibia or the shaft of the femur immediately above, and hence we may reasonably homologize them with the gracilis and the internally inserting portions of the flexor internus, (Gadow, 1882, pp. 402, 404; Gregory and Camp, 1918, pp. 489–491) and conclude that those portions (pubo-tibialis and part of the two flexors) which inserted outside of the internal gastrocnemius head have been

lost, no mammalian muscles inserting in this region. These homologies agree well with the origins and innervations of the muscles. The mammalian gracilis has an obturator innervation, as does most of the usual reptilian pubo-ischio-tibialis; the reptilian flexors have a double innervation, as do the semimembranosus and semitendinosus of monotremes (sacral purely in higher forms). The gracilis has the same general area of origin as its reptilian equivalent; the reptilian flexors originate near the tuber ischii, as do their mammalian equivalents.

It is of course impossible to determine the exact distribution of the various portions of the group in the fossil forms; the reconstructions given are based on a comparison of the various reptilian conditions. It will be noted that the insertions never pass external to the external femoral head of the lower leg flexors, as would be necessary were biceps a part of this group.

5.—Adductors, "Ischio-femoralis" or Pubo-ischio-femoralis

Plates XLII; XLIV, origins; XLVI, Figure 6,insertions

Apparently representing a middle layer of the primitive ventral musculature, running in modern reptiles and urodeles from the pubo-ischiadic ligament, internal to the long flexors, to the antero-ventral side of the shaft of the femur. The innervation, as with all these series, is generally a double one, obturator and sacral, this being preserved in the adductor magnus of mammals.

The history of the area of origin has been the same as that of the flexors; with the loss of the pubo-ischiadic ligament in mammals, the adductors are found, as expected, along the ventral surface internal to the flexors.

The insertion in primitive fossil types may be laid out as the surface antero-dorsal to the ventral femoral ridge and coccygeo-femoralis tendon, bounded proximally by the pubo-ischio-femoralis internus, and by that muscle antero-dorsally until replaced in reptiles by the femoro-tibialis. On the opposite side of the ridge is found the ilio-femoralis. These relations are preserved through into the Mammalia, where the adductors are found located between pectineus and iliacus proximally and internally, vastus interno-dorsally, and the ridge running down from the gluteal insertion posteriorly.

6.—Pubo-ischio-femoralis Externus (Obturator Externus and Quadratus Femoris)

Plates XLIII; XLIV, origins; XLVI, Figure 6, insertions

Gregory and Camp (1918, pp. 491–493) do not differentiate this muscle from the adductor. It is a stout, short muscle from most of the

pubo-ischiadic plate, or the replacing fenestra, to the proximal ventral surface of the femur. The innervation, as expected, is almost always double, sacral and obturator. The insertion in all the Permian fossil forms (essentially similar to the more generalized reptiles and urodeles) is into the fossa between the two proximal branches of the ventral femoral ridge and on to the internal trochanter which terminates the inner branch. In the mammalian series the insertion on the inner (minor) trochanter has been lost, but the fossa is retained as the intertrochanteric fossa, into which the obturator externus inserts. The quadratus femoris inserts into the distal boundary of the fossa. This latter muscle, from this much more distal insertion, appears not to be a part of the ischio-trochantericus or obturator internus, as has sometimes been stated (Gregory and Camp, 1918, p. 493). It will be noted that this split into obturator externus and quadratus femoris has been along the division between the two innervations, the obturator externus being purely obturator, the quadratus femoris purely sacral.

7.—Caudal Muscles to the Limb

Plates XLI, XLII; XLVI, Figure 6, femoral insertions

Coccygeo-femoralis Brevis or Caudi-ilio-femoralis (Pyriformis), and Coccygeo-femoralis longus, Caudi-femoralis or Caudi-pubo-ischio-tibialis. Originally two muscles, both arising ventrally from the anterior caudal vertebræ and running out under the ilio-ischiadic ligament to the limb. The more dorsal of the two (brevis) inserts by a tendon into the femur part way down the shaft, reaching the bone between ilio-femoralis and adductors. The longer, ventral to this, either inserts into the flexor mass, as in urodeles, or has a tendon of its own in reptiles, this inserting with the short muscle into the femur and sending a branch out to accompany the flexors to the lower leg or the end of the femur. That this separation from the flexors is a secondary one is rendered more probable from the discovery by Noble (1922) of a typical caudi-pubo-ischio-tibialis in primitive frogs.

The insertion of the coccygeo-femoral tendon is one of the landmarks of the primitive femur, being a roughened and often much elevated area at the point where the two proximal branches of the adductor ridge separate. It is usually less prominent in short-tailed forms, as would be expected. This point is comparable with the crocodile fourth trochanter.

The fate of these muscles in the mammalian series is doubtful. I have never seen a therapsid humerus that clearly indicated the femoral insertion. Their reduction is, of course, expected with the functional

reduction of the tail in the mammalian line. The coccygeo-femoralis brevis is probably represented by the mammalian pyriformis (Gregory and Camp, 1918, p. 497), which has been carried up to the greater trochanter in the rearrangement of the gluteals; the longus by slips from the tail to join or accompany the semitendinosus or biceps in various mammals (such as the cruro-coccygeus of the opossum).

8.—Lower Leg: Extensors

The reptilian condition is that of three groups as follows. (*a*) Fibular, usually a peronæus longus from the external margin of the femur and the head of the fibula, and a peronæus brevis from the shaft of the fibula, and both running down to metatarsal 5 and the lower surface of the foot. Both are dorsal (external) to the ilio-fibular insertion. (*b*) An extensor digitorum communis longus, from the end of the external condyle, and sending tendons to the toes. (*c*) Tibialis anticus, from the outer surface of the tibia, dorsal and external to the pubo-ischio-tibial insertion, to metatarsal 1. In addition, there is an extensor hallucis running diagonally across from the lower end of the fibula. As far as can be determined, the relations were similar in the American Permian forms. There are roughened surfaces for the common extensor and peroneus longus on the external condyle of the femur. The outer surface of the fibula was undoubtedly for the peronaeal origins, except for a roughened area near the head for the ilio-fibularis. There is no indication of an origin of tibial extensors from the internal condyle; a small tuberosity always found here was undoubtedly for the medial ligament to the tibia. The tibialis anticus occupied a somewhat uncertain area bounded externally by the roughened line for the interosseous ligament, internally by the ridge for the pubo-ischio-tibialis and part of the flexor tibialis internus, and by the ridge for the triceps (quadriceps) insertion.

It will be noted that the urodele extensors differ in several particulars from the conditions in higher forms. The tibial mass originates from the femur, internal to the course of the triceps; part of tibial and fibular masses insert on those bones; there are no origins there. The triceps, although breaking through the tibial mass to reach the tibia, is mostly continuous with the fascia covering these muscles, the break leaving variable slips external to it. The fossils give, as far as I have seen, no suggestion as to the relations of this urodele type to that of higher forms.

Between the reptilian and mammalian conditions, there is little change. Many forms tend to lose the femoral heads; the peronaeal group becomes differentiated.

9.—Lower Leg: Flexors

For our purposes, the varied development of the end tendons of this group do not come into consideration.

The general reptilian condition is that of three superimposed layers. (*a*) Gastrocnemius, in two parts, one from the external condyle of the femur, the other from the internal condyle, the head of the tibia (ventrally) or both; the two uniting to form the superficial layer of the sole. (*b*) Flexor digitorum communis longus, from the external condyle of the femur, and from most of the length of the fibula, usually with several heads. This lies beneath the gastrocnemius; both may be united with flexor tibialis externus. (*c*) A deeper layer, lying close to the interosseous ligament, with typically three parts: (1) tibialis posticus, of *Sphenodon* and turtles, from the fibula diagonally down towards the first toe; (2) a popliteal muscle from the head of the fibula to the back of the tibia; and (3) an interosseous cruris lower down between fibula and tibia.

In urodeles *a* and *b* are apparently fused. The last group is similar but there is no popliteal, except possibly a small muscle from femur to tibia mentioned by Wilder. In urodeles there are no origins from the tibia or tibial condyle of the femur, nor from this condyle of the femur in *Sphenodon* or the crocodile.

There is little fossil evidence as to the detailed structure of these muscles.

There are few important changes in mammals, except in connection with the end tendons.

10.—Groupng of Hind Limb Musculature

The grouping of the hind limb musculature in primitive dorsal and ventral masses (abductor and adductor groups of the fish) is a more simple problem than that presented in the fore limb as, with few exceptions, the muscles may be arranged in two groups, dorsal and ventral (each subdivided into more superficial and deeper layers on the proximal segment) and distally the extensors and flexors of the lower leg and foot, each group having double innervations suggesting its primitive metameric condition (Fig. 1).

a.—Primitive Dorsal Group: ambiens, ilio-tibialis, femoro-tibialis, ilio-fibularis, pubo-ischio-femoralis internus, ilio-femoralis, ischio-trochantericus, and lower leg extensors (in mammals, sartorius, rectus femoris, vasti, biceps, psoas, iliacus, glutei, gemelli, obturator internus, and lower leg extensors).

b.—PRIMITIVE VENTRAL GROUP: pubo-tibialis, pubo-ischio-tibialis, flexor tibialis internus, and externus or ischio-flexorius, adductor, pubo-ischio-femoralis externus (in mammals, gracilis, semitendinosus, semimembranosus, adductors, obturator externus, quadratus femoris and lower leg flexors). With these the two coccygeo-femoral muscles (pyriformis, cruro-coccygeus, etc.) may possibly be associated.

HIND LIMB, BONY ELEMENTS

1.—PELVIS

Plates XLIV, XLV

This uniformly consists of three bones of unquestioned homology, the dorsal ilium, the anterior ventral pubis, and the posterior ventral ischium, the three usually meeting at the acetabulum.

Little is known concerning the evolution of the girdle from the fish condition. The fish girdle is usually a simple plate from which muscles arise on both sides, and which seems to correspond with the continuous pubo-ischiadic plate of primitive tetrapods. Except in dipnoans, there is no development of an iliac process.

We shall consider (*a*) the iliac blade, (*b*) the dorsal or inner surface of the pubo-ischium, (*c*) the pubo-ischiadic plate, and (*d*) the acetabulum.

a.—ILIUM. Need for support in terrestrial life has modified the pelvis even more than the shoulder. We have previously called attention to the fact that in the posterior extremity a fixed relation to the body does not entail the disadvantages that it had in the fore limb; and it is the fixed position that has been attained by the growth of the ilium upward, interrupting the lateral musculature.

It will thus be seen that the ilium is primarily for support, connecting the pelvis and limb with modified sacral ribs (or rib) and that the appendicular muscular relation, so prominent in later forms, has been a secondary development. Existing urodeles and fossil stegocephs bear this out. In urodeles, as in *Eryops*, the limb musculature has little to do with the ilium, being confined to a small area just above the acetabulum. The muscles (ilio-tibialis, ilio-fibularis, ilio-femoralis) which originate from it are of small extent in primitive forms; all three show some tendency to slip around to the inside of the bone; the ilio-femoralis is hard to delimit from the pubo-ischio-femoralis internus in some urodeles. It seems probable that all three are really muscles from the inside of the girdle which the ilium has "picked up" in its development. The rest of the stegocephalian blade is concerned with axial muscles and is usually rather long and narrow.

As we have mentioned in the discussion of the axial muscles, the outer surface of the amphibian ilium is homologous not only with the outer side of the higher forms but also with the inner dorsal part above the sacral ribs. This is undoubtedly due to the great growth in size of the part of the pelvis connected with appendicular muscles, and especially due to the increase of the muscles used to extend the limb and draw back the femur. We have shown that this upward growth has folded over the upper end of the ilium, and have mentioned a series of forms showing this.

The posterior dorsal portion of the ilium is often expanded more or less into a posteriorly directed process, which seems to be correlated with the length of the tail and the consequent development of the tail extensors. Thus in *Eryops*, where the tail was short, there is practically no backward extension; in *Diadectes* it is slight; while the longer tailed *Limnoscelis* has a longer backward expansion. In the pelycosaurs, *Dimetrodon* has only a short backward extension as compared with the longer tailed *Ophiacodon*.

Cricotus has a very long posterior process, which at first seems remarkable in the fact that this does not spring from the upper end of the bone but from near the acetabulum. This is easily explained; in *Cricotus* this position is at the posterior end of the transverse iliac line previously referred to: hence this posterior process is really the homologue of that seen in reptiles, which comes off from the posterior end of this same line, which becomes the dorsal end of the ilium. *Cricotus*, it will be noted, has a well-developed tail.

In reptiles, the whole outer surface is for appendicular muscles, the axial muscles being confined to the borders and the new dorsal internal surface; the primitive pelycosaurian and captorhinomorph ilium is not unlike that of the Lacertilia.

In the change to the mammals, the main factors are as follows. (1) Transfer of ilio-fibularis, which travels back down the ilio- (sacro-) ischiadic ligament to become the biceps. (2) Great growth of the ilio-femoralis, which has conditioned a great upward and forward growth of the ilium, and changed the relations of the ilio-tibialis. This is seen under way in the therapsids. There has been a secondary reduction of the iliac surface at some point below the monotremes, probably by such an emargination as is seen in *Lystrosaurus*. (3) The pubo-ischio-femoralis internus has invaded the ilium, coming up forward to form the lower external surface of the trihedral type and then subsiding into the external part of the gluteal surface; and a possible incipient stage may be seen in some dicynodonts, with the lower anterior margin of the ilium somewhat broadened.

There has been an increasingly close association of the ilium with the backbone through the sacral ribs, of which there was probably but one originally. This union in *Eryops* was probably not close, the single sacral being but slightly modified and expanded for its articulation with the pelvis, which covers most of the inside of the iliac blade. The *Cricotus* ilium seems to indicate a similar relation.

The change to the Reptilia usually makes the number of ribs two instead of one, although Williston (1916, pp. 202, 216, etc.) has noted exceptional Amphibia with two and exceptional reptiles with but one. The number and closeness of articulation increases in mammals. This relationship seems highly adaptive.

The principal evolutionary changes in the ilium are thus seen to be (1) development of primitive supporting function by increase of sacral connections; (2) development of dorsal limb musculature and crowding out of axial elements externally; (3) anterior expansion in mammalian ancestry correlated with gluteal growth; and (4) invasion in this line by the iliacus from the original pubo-ischio-femoralis below.

b.—Dorsal (Internal) Surface of the Pubo-ischium. As suggested above, we may believe this to have been the primitive place of origin of all the dorsal muscles. The ilium by its development has broken the dorsal series so that, with the partial transfer of muscles to that element, we find merely (1) pubo-ischio-femoralis internus from the anterior part and (2) ischio-trochantericus (ischio-femoralis posterior) from the posterior part of this surface.

We have noted the well-marked shelf for the pubo-ischio-femoralis internus in the primitive Amphibia and the gradual inturning of this in reptiles. Near the posterior border of this shelf is found the internal opening of the probably primitive obturator foramen. Then, posteriorly, there is a smooth surface, probably without muscular relations, between the two ilia, and, still more posteriorly, behind a ridge for the caudal flexors, a fan-shaped surface on the upper side of the ischium for the ischio-trochantericus, running back to the tuber ischii and the posterior end of the symphysis. Anteriorly and posteriorly there are means of escape for these muscles on to the limb underneath the ilio-pubic and ilio-ischiadic ligaments. There has been little variation in the ischio-trochanteric surface; even in most mammals, the muscle is of only small extent. In reptiles, the pubo-ischio-femoralis internus has spread widely over the inner surface of the pelvis, in a further development of the old type of locomotion, while in the mammal the muscle has abandoned this area and migrated up (except for pectineus) on to the ilium in response to a different type of movement.

The symphysis seems to have been inversely proportionate in its strength to that of the sacral articulations. For example, in *Eryops*, with a weak sacrum, the symphysis is extremely thick; in the higher forms, with a better sacrum, the thickness is reduced, although the old pattern of *Eryops*, which has the thickness reach a maximum at the posterior edge of the pubis, is still seen especially in *Diadectes* and *Limnoscelis*. In later forms, the symphysis is shorter and may be reduced to two connections, anterior and posterior, as in lizards and *Sphenodon*, or be greatly reduced in length, as in mammals. (The foramina will be discussed under the next head.)

c.—PUBO-ISCHIADIC PLATE. This is highly comparable in primitive position and function to the coracoid plate. In the primitive forms it is a broad expanse on the outer, lower side of the pubis and ischium, beneath the acetabulum. Most of its surface gives origin to the pubo-ischio-femoralis externus. From the dorsal border, behind the acetabulum, is a ridge separating the plate from the internal surface and often giving origin to fibers probably homologous with the mammalian quadratus and gemelli. This terminates at a corner marking the tuber ischii, from which the edge of the bone turns inward to the symphysis. Anteriorly, from the rugosity just anterior to the acetabulum whence the ambiens and pubo-tibialis originate, there is a ridge, usually turned strongly outward which separates the plate from the anterior part of the dorsal surface. This ridge terminates anteriorly at the most anterior and external corner of the pubis, representing the pubic tubercle (especially well developed in *Ophiacodon*, Case and Williston, 1913, p. 53) and the ventral insertion of the ilio-pubic ligament. The surface running in from the tubercle to the symphysis usually has indications of a cartilagenous extension. Medially, the symphysis is primitively continuous throughout the whole length of the plate; from the symphysis, the posterior border of the ischium to the tuber, and the pubic tubercle, originate the adductors and the flexors, directly or, probably generally, by means of the pubo-ischiadic ligament. The dorsally running ligaments attach anteriorly and posteriorly, to the pubic tubercle and tuber ischii. On the edge of the ischium behind the tuber are the attachments of the ischio-caudalis and cloacal muscles; anteriorly the axial musculature is attached to the end of the pubis, often running down over the symphysis. The opening for the obturator foramen is found in the pubis, beneath the anterior end of the acetabulum.

This primitive type of plate is well represented in *Eryops*, and is not markedly changed in the Permian cotylosaurs and pelycosaurs. The

two halves of the pelvis are more widely separated, and the plates are more nearly horizontal in position.

The modifications in the plate which lead to the characteristic "archosaurian" type do not concern us here but may easily be derived from this, such forms as *Euparkeria* showing transitional stages. In the more typical reptiles, lizards and *Sphenodon*, a large foramen is developed, as has also been done in mammals, into the origin of which we might inquire.

In the reptilian cordiforme or thyroid fenestra, the opening is a circular one in the middle of the plate, separating the pubis and ischium, except in the acetabular region; below, the two bones are usually connected by a ligament; the foramen is covered by a membrane. In the lizard, as contrasted with mammals, the obturator nerve is not included in the opening, but has its own passage through the pubis.

Williston (1911, p. 105, etc.) has suggested, because of the incomplete ossification of the ventral connection between pubis and ischium in certain pelycosaurs, that the formation of the reptilian fenestra may have taken place by the formation of an opening here between the four bones of the two sides; that the opening then extended dorsally on either side to its modern position; and that later there was a secondary cartilagenous union across the ventral gap. Both shape and function of the fenestra argue against this.

The function of both reptilian and mammalian fenestræ (Gregory and Camp, 1918, p. 524), besides lightening the girdle, is to give an open area instead of bone for the great muscular origin of the pubo-ischio-femoralis externus (obturator externus), analogous to the temporal and coracoid fenestræ. No such function would be subserved by an incipient opening of the character suggested by Williston. Such an opening as is seen in these pelycosaurs is a notch in shape and would have to undergo radical changes in order to assume a closed circular form, changes for which we have no evidence nor find apparent reason. The "fenestra" seems to be merely a case of incomplete or delayed ossification, as is found in other parts of the skeleton of the same animals (as in the late ossification of the *Ophiacodon* posterior coracoid). A similar notch is found in some dicynodonts (Broili, 1908, p. 8), which is certainly not an incipient fenestra, as this is already formed in a more dorsal position. It seems more probable that the reptilian fenestra is a parallel to that of the mammals, a fenestration for the obturator externus.

The lower therapsids have no fenestra; in the dicynodonts it is merely an enlargement of the obturator foramen; in *Cynognathus*, it is a

somewhat larger opening, but still mostly confined to the pubis; considerable further growth has been necessary for it to reach its full mammalian development. Here it will be noted that the obturator has been included from the beginning and apparently forms the basis for the opening.

Apart from the fenestra, the typical reptilian plate is much like the primitive one. The mammalian type can be readily derived from this, the other major change having to do with a great elongation anteriorly, followed by a secondary reduction. The pubis is uniformly reduced in antero-posterior extent; but "marsupial bones," still present in monotremes and marsupials, have been formed in advance of the pubis, mostly in relation to the axial musculature. At first these were probably merely undifferentiated cartilagenous extensions of the pubis, as suggested by the fact that in monotremes the gracilis continues indifferently on to them from that element. The anterior contour of the pubis in *Cynognathus*, from "pectineal process" to symphysis, suggests the presence of cartilages. With this development, the old pubo-ischiadic ligament has apparently been lost.

Although short, the pubis is still strongly turned out dorsally in *Moschops* and *Cynognathus;* posteriorly there is a suggestion of a slight differentiation of a posterior region of the plate for a quadratus femoris. The gemellus surface is distinct.

Changes in the plate from the primitive condition are thus seen to be (1) a more horizontal position of the plate, (2) opening of a fenestra in at least two parallel lines, and (3) changes in shape of pubis, with addition and subsequent loss of marsupial bones in the evolution of the mammals.

d.—ACETABULUM. The history of this is comparatively simple as compared with the glenoid. There is never any "screw"; it is a cup from the first. This is undoubtedly correlated with the facts that (1) there is little need for support, the whole action of the limb being for propulsion, and (2) the comparatively fixed condition of the lower limb, with little power of pronation or supination, has rendered it necessary that the femur rotate to preserve its relations to these bones.

The acetabulum is relatively constant throughout the series, as a cup formed from the three bones of the pelvis. Primitively the pubis and ischiadic borders are raised considerably above the surface, indicating that the femur was normally elevated distally. In *Eryops*, the pubic process is very prominent, indicating that here the femur was probably turned somewhat back in its middle position; in pelycosaurs, the pubis

is reduced here, the femur probably looking out and somewhat forward. In the mammalian line, where the head was turned towards the side of the femur, the acetabulum is large and looks directly outward.

A constant feature is the presence of a prominent wedge above the acetabulum, merging gradually into the general surface of the bone anteriorly, but posteriorly dropping back sharply as a distinct supra-acetabular notch. This is found practically the same in almost every form examined, from *Eryops* to the highest therapsids. As suggested by Broili, who first noticed it in dicynodonts (1908, p. 3), it indicates the position of a ligament similar to that found in the cotyloid notch of the ischium of mammals; the changed position of the mammalian femur would account for a shifting ventrally of the notch.

2.—Femur

Plate XLVI; Figure 6

The femur may be considered in its two aspects of a supporting structure and of an object for muscular origin and insertion.

As has been mentioned, the primitive femur did not have to contend with the complicating necessity for support that the primitive humerus had; its function was merely that of giving a forward push to the body, and in its simplest form was a straight rod running from a terminal head in the acetabulum to distal ventral condyles for the lower leg bones. As Williston has noted, it is usually a longer although more slender element than the humerus. Its main movement is one down and back from an anterior and dorsal position, coupled with rotation (clockwise as seen in the right leg from the side view). This movement, as far as the femur is concerned, is principally accomplished by: (1) the depression caused by the pubo-ischio-femoralis externus; (2) a backward pull, by the posterior part of that muscle and the coccygeo-femoralis muscles; and (3) rotation, caused somewhat by these two and partly by the opposed ilio-femoralis and pubo-ischio-femoralis (adductor). It is these muscles that primitively give the main characters to the bone; they are concerned with the ventral and lateral surfaces.

We may best understand the construction of the primitive femur by a description of such a form as *Eryops*. Seen ventrally, the main characters are as follows. (1) A ridge, sometimes termed the "adductor ridge," running distally down the shaft, usually terminating near the external condyle. Proximally to the middle of the shaft, the ridge divides like the letter Y into (2) a posterior and (3) an anterior branch, between which is (4) a large ventral fossa. Near the point of union of the two

branches is (5) a large roughened area. The insertion of the adductors (pubo-ischio-femoralis) probably lay on the anterior side of the "adductor ridge"; that of the ilio-femoralis adjoined on the posterior side. The area at the fork of the ridges was for the insertion of the coccygeo-femoralis tendon. Between the branches of the ridge was part of the insertion of the pubo-ischio-femoralis externus, and the remainder of the muscle inserted on the end of the anterior limiting ridge, or internal trochanter, which drops suddenly to the level of the bone. Above the posterior limiting ridge, the ilio-femoralis insertion probably continued nearly to the head; above the anterior limiting ridge, the pubo-ischio-femoralis internus insertion ran down to meet the adductor, from which it is not clearly separable. This agrees well with the lacertilian condition.

The dorsal side of the femur of such a form as *Eryops* presents few landmarks; as a point of insertion, it functions only for pubo-ischio-femoralis internus. I have previously suggested that the slenderness of the amphibian shaft is due to the absence, or presence merely below a limiting ridge, of the femoro-tibialis, and that the pubo-ischio-femoralis internus covered the dorsal surface rather loosely, being only apparent at a posterior rugosity near the head.

Distally, there is a double condyle for the two articular portions of the head of the tibia; an accessory condyle on the outer side for the fibula; a small internal eminence, probably for the medial ligament; a roughened surface and pit on the outer condyle for the extensor digitorum communis and peroneus; below, an area for the external head of the lower leg flexors.

There is some variation in the Stegocephalia; the posterior limiting ridge is frequently reduced, leaving one continuous ridge from the internal trochanter diagonally down the limb to the external condyle. In one form (whether amphibian or reptile is uncertain) found by Case (1915, Pl. XXIII, figs. 5 and 6) the area for the coccygeo-femoralis is an enormous development projecting out backwardly for a distance equal to half the length of the femur.

In the most primitive cotylosaurs (*Seymouria, Diadectes, Limnoscelis*) there is essentially the same plan on the under side; dorsally, the only change is that the median portion is expanded, apparently because of the intrusion of the femoro-tibialis, giving the bone a more rounded form, in general, than in the Amphibia and thus reducing the apparent size of the ventral ridge system, which is still prominent.

There is in the higher cotylosaurs and pareiasaurs a parallel to the Amphibia in the reduction of the posterior limiting ridge ventrally, and

the height of the ridge is somewhat reduced. The poliosaurs are similar. On the other hand, the femora of *Edaphosaurus* (and *Ophiacodon*) are still rather primitive and the ridges are well developed. In *Dimetrodon*, the ridges are much reduced, there being little elevation at the pronounced rugosity for the coccygeo-femoralis insertion.

Such a form as the femur of the lizard can be easily derived from the Permian type (Fig. 6). The anterior limiting ridge is the well-developed inner trochanter (for most of the pubo-ischio-femoralis externus); some of this muscle still inserts into the neighboring fossa, less pronounced; the relations of adductors and ilio-femoralis to the adductor ridge is represented by their relations to the so-called "linea aspera." The coccygeo-femoralis still inserts in a similar position. This, it will be noted, is the same as the "fourth trochanter" of crocodiles, etc., and this name might well be applied to this whole series of coccygeo-femoralis insertions in all primitive forms. Von Huene (1911, pp. 55–56) has claimed that the internal and fourth trochanters have the same origin; this is, of course, incorrect but explicable, because of the once continuous ridge between these two points noted by Gregory and Camp (1918, p. 534).

The transition to the mammalian type has been a puzzle. The monotreme femur and those of the therapsids help to clear up the matter, but it is impossible to speak with too great certainty because of the usually poor condition of the surface of African fossils.

The evolution of the head is simple. As seen in therapsids, there is merely a flexure of the old head upon the shaft, so as to allow the femur to be directed forward and have an up and down movement; this has been paralleled in some reptilia. The primitive therapsid head was large, and flattened antero-posteriorly, thus necessitating the large acetabulum to which reference has been made.

But the muscular insertions at first appear strangely different. The therapsids give a clue to this change. There has been a flattening of the femur in the horizontal plane, which is preserved in the monotremes; the ventral ridge and posterior proximal ridge have become the posterior edge of the therapsid and monotreme femur. This is no great change, as the position of the ridge in the natural primitive pose was rather to the back as well as the ventral side, and a similar tendency is shown in *Propappus* and *Ophiacodon*, etc. The old insertion of the ilio-femoralis was at the posterior dorsal side of this ridge; it now inserts, as the glutei, in this posterior edge of the femur, sometimes extending well down the shaft as the lateral lip of the linea aspera. The more proximal insertion was outside the posterior limiting ridge; it is from this surface that the

greater trochanter has arisen and thus occupies the position of the old ridge, although not its exact function. Primitively it was for the most part merely a boundary for the fossa beneath.

With the loss of any extensive area of insertion of the gluteals well down the shaft, the adductors have come to meet the vastus on the posterior border of the femur; it is the boundary between these two muscles, the lateral lip of the linea aspera, extending proximally up to the greater trochanter, which is the modern representative of the old adductor ridge. The vasti still occupy the dorsal surface and now meet the adductors on the anterior (internal) side of the femur as well. It is here that the median lip of the linea aspera is found;. it is thus a new formation, and has no reptilian predecessor. The pubo-ischio-femoralis internus (iliacus, psoas, pectineus) has lost its old dorsal insertion and has merely retained the anterior portion of the old insertion, which it will be noted was just above the anterior limiting ridge or internal trochanter. It is in this position, anterior (internal) to and above the ventral fossa, that we find the lesser trochanter, which gives insertion to iliacus and psoas major (the pectineus insertion continuing down the shaft). This trochanter is in the position of the old internal trochanter (anterior limiting ridge) of the primitive forms, but it is entirely different in function; the former offered an insertion for the pubo-ischio-femoralis externus; the new lesser trochanter carries the representatives of the pubo-ischio-femoralis internus. But the ridge on the under side of many therapsid humeri (Gregory and Camp, 1918, p. 530) seems homologous in position with both mammalian pectineal line and lesser trochanter on the one hand and on the other with the old internal proximal ridge (or internal trochanter). These are now not connected with the posterior proximal ridge and stem of the Y-system, which have become, respectively, the greater trochanter and lateral lip of the linea aspera.

The fossa, for pubo-ischio-femoralis externus, is still present and functional; its boundary, the inter-trochanteric ridge, gives insertion to a portion of this muscle's representatives, the quadratus femoris.

The growth of the greater trochanter has pushed the internal obturator down into the fossa. It is on the greater trochanter in monotremes.

The coccygeo-femoralis insertion is not recognizable, as expected, in any of the mammalian series and, as indicated from the position of the pyriformis, has been carried up on to the greater trochanter.

Thus we see in the mammals the retention of the old ventral fossa, a partial homology of the trochanters with the old limiting ridges and

internal trochanter, and reduction of the adductor ridge and "fourth trochanter." It will be noted that in this process, apparently of flattening and secondary rounding of the femur, there has resulted a general rotation of points of insertion, downward anteriorly and backward ventrally.

3.—Tibia and Fibula

There are few points of interest obtainable in regard to the history of the tibia and fibula from the fossil forms. It is probable that the two were subequal primitively or, as has been advanced, that the fibula was the main axis of the primitive limb. It is comparatively well-developed in Amphibia. But the position of the limb has caused the tibia to be the main bearer of the weight and the main point of insertion of muscles coming from the more proximal part of the leg. The fibula is reduced in higher forms, and functions mainly as a point of origin for muscles running down the leg.

As far back as the history can be followed, the tibia has two points of articulation for the two condyles of the femur, the two partially separated; on its anterior surface is a ridge proximally for the insertion of the triceps tendon. Internally and externally are found longitudinal markings and ridges separating flexor and extensor surfaces. The fibula, usually attached at the side of the external condyle, is usually a flattened bone, with the anterior or internal edge concave; the two opposing surfaces are universally filled by the areas of origin of the flexor and extensor muscles of the lower leg. In Permian forms a proximal rugosity for ilio-fibularis is found near the head.

LOCOMOTOR ADAPTATIONS AND COMPARISON OF TYPES

1.—Diadectes

We may best start with a consideration of this form as representative of the most primitive reptilian condition of which we have knowledge. While specialized in other respects, *Diadectes* is close to *Seymouria* and *Limnoscelis* in girdle and limb structure.

The general impression given by *Diadectes* is that of an animal with short but stout limbs, capable of slow but rather powerful movement.

In the fore limb, the principal motions for the advance of the body consisted of a backward and downward movement of the humerus, combined with rotation, and flexion of the forearm. The coraco-brachialis maintained the level of the humerus and pulled backward. The back-

ward pull was assisted by the latissimus and sub-coraco-scapularis above. Rotation was accomplished by the coraco-brachialis longus. The flexion of the fore arm was accomplished by the biceps and brachialis, assisted by the pronator and ulnar flexor. The opposite motion of the arm, up and foward and an opposite rotation, was accomplished by the deltoid, scapulo-humeralis anterior and supracoracoideus, triceps, extensors of the fore arm, and supinator. The body was carried sling-wise by a strong series of levator and serratus muscles.

In the hind limb, the principal motion was a down and backward pull of the femur, accompanied by rotation of the femur (clockwise in the right limb) and extension of the lower leg. The pubo-ischio-femoralis externus and adductor draw the femur down; the caudi-femoral muscles, assisted by the posterior part of the first named muscle, pull the femur back; rotation is accomplished by the ilio-femoralis and adductor; extension of the lower limb by the triceps and short extensors of the lower leg, if present. The opposite motion is caused by the pubo-ischio-femoralis internus, ischio-trochantericus, long flexors, and lower leg flexors.

In this connection, we may note the following features of the skeleton. A fairly tall scapular blade, and large uncinate processes on the under-lying ribs, denoting a strong serratus anterior-levator series. A capping cleithrum (not true of other primitive reptiles). Large supra-glenoid buttress with foramen. Well-developed clavicles and inter-clavicle (the stem of the latter moderately long). A large coracoid plate (apparently one element, two in *Limnoscelis*). Glenoid foramen. Primitive type of glenoid. Humerus short, no shaft, of tetrahedral type, with large muscular processes. Entepicondylar foramen. Very large entepicondyle. Large supinator crest, not approaching the ectepicondyle. The latter large and overhanging.

Iliac surface fairly large, axial muscles restricted to upper borders and shelf at top. A sharply marked anterior surface on the pubis for the pubo-ischio-femoralis internus, containing the internal opening of the obturator foramen. A thick pubic symphysis. A small surface dorsally on the ischium for the ischio-trochantericus. A large pubo-ischiadic plate, with the obturator foramen, but no fenestra. A strong, short femur. The Y-shaped system of ridges well developed, especially the caudi-femoralis insertion, the anterior (internal) branch of the Y being continuous with the stem. A large dorsal surface for the femoro-tibialis.

2.—Comparison with Amphibian Types

The type of motion and the structural plan of *Diadectes* are remarkably similar to the general stegocephalian type, such as the well-known *Eryops*. The only differences of note are as follows. *Eryops* has a taller scapula, but this is probably related to its extremely large head; many other Rachitomi have shorter scapulæ. The coracoid plate is smaller, probably denoting a smaller backward movement of the humerus. There is no trace of division of the primary girdle into elements. The interclavicle is shorter, indicating a weaker pectoralis. There is no entepicondylar foramen, and a smaller entepicondyle, indicating weaker flexors. The sacral connections are looser. There is a smaller appendicular and larger axial surface on the ilium, without formation of a shelf. The pubo-ischio-femoralis internus origin is very strongly developed. There is a very thick pubic symphysis, probably related to the weaker sacrum. A small femoro-tibialis, indicating little extension of the lower leg.

Thus *Eryops* and other Rachitomi are seen to be an essentially similar type, but more primitive in certain respects. There is no bar to considering an animal with such a type of locomotor apparatus as almost directly ancestral to the primitive reptiles, as far as we know them.

The microsaurs are a poorly understood group which probably contains several distinct lines. The presence of the entepicondylar foramen in *Diplocaulus* has been noted, as has the *Eryops*-like femur of *Ichthyacanthus* and the T-shaped cleithrum of some forms. But, as a whole, the microsaurs are too specialized, too degenerate in limb structure, and too poorly known to make comparison profitable.

Back of the primitive Stegocephalia, and in the province of the embolomerous forms whose primitive characters have been so much emphasized by Watson, the path is none too clear; there is not one type of which the limb structure is known in any detail. Primitive features, leading back toward the fish, can, however, be identified here and there. The widely opened supraglenoid foramen of lower forms, as the girdle assigned to *Cricotus* by Case (1915, p. 163), suggests the mesocoracoid region of the fish. The posterior prolongation of the ilium, correlated with the long tail, cannot be safely set down as a primitive character. The problem as to whether the flattened trihedral type of humerus of *Cricotus* is primitive has been discussed.

3.—Higher Cotylosaurs, Captorhinomorpha

Limnoscelis cannot be grouped here (as Watson would do on the basis of the skull) in regard to limb structure. The type is generally

primitive, but with more of a shaft to the limb bones. The general type of motion is that of the lower cotylosaurs. The cleithrum is absent or very small. There are two coracoids (also true of *Limnoscelis*). There is no ectepicondylar foramen, but the supinator crest is close to the ectepicondyle. There is a fairly well distinguishable pubo-ischio-femoralis internus surface on the pubis. The posterior branch and main body of the Y ridges of the femur are reduced, the anterior branch still being a continuation of the rugosity marking the main body. The caudi-femoral insertion is reduced.

The in-turning of the axial portion of the ilium has been accomplished, in marked contrast to some of the supposedly higher pelycosaurs.

There do not seem any obstacles to a derivation of these forms from the lower types of cotylosaur, very possibly through some such a form as *Limnoscelis*.

4.—Pareiasauria

In a great number of respects this Old World group differs radically from both the lower cotylosaurs, with which the latest classifications would include them (Watson, 1917), and from the higher Captorhinomorpha as well. In almost every case the differences are characters which are found in therapsids. The cleithrum is present. There are two coracoids, as true of many American cotylosaurs, but the anterior one does not enter the glenoid. An acromion is present (found elsewhere only in the higher therapsids). No supraglenoid buttress or foramen has been described. The primitive type of glenoid is partially or entirely lost. The coracoid plate is not developed posteriorly. No glenoid foramen has been described (also absent in Captorhinomorpha). The humerus, while short and massive, is strikingly different from the primitive tetrahedral type. Some forms very probably possessed an ectepicondylar foramen. The proximal part of the median humeral surface for the triceps is greatly reduced. The entepicondylar foramen is small and is turned down on the back surface. There is a long delto-pectoral crest and a large brachialis surface. The iliac blade has completed the turning in of its axial surface (also true of Captorhinomorpha). The separate surface for the pubo-ischio-femoralis internus is not well developed. The ilium is extended anteriorly. The Y-system of femoral ridges is reduced, except for the anterior branch, and the coccygeo-femoral insertion is also reduced (much as in Captorhinomorpha); the posterior edge of the femur, leading distally from the posterior branch of the Y, is emphasized.

Almost all of the characters are highly characteristic of therapsids and are in sharp contrast with the typical cotylosaurs and with the pelycosaurs. The anterior coracoid enters the glenoid in the latter groups. The supraglenoid buttress is characteristic of all pelycosaurs, even, and the supraglenoid foramen is absent only in *Casea*. The primitive glenoid is otherwise universal. The humerus is quite unlike that of any other cotylosaur or pelycosaur. The ectepicondylar foramen (if present) is not found in other cotylosaurs or pelycosaurs, except for *Edaphosaurus*. The median tricipital surface is well developed in the American cotylosaurs and pelycosaurs. The form of the entepicondylar foramen is in marked contrast. The iliac blade is never developed anteriorly (except in *Casea*) in the groups mentioned and is still incompletely evolved in some pelycosaurs. The short pubis contrasts with the usual long pubis of the American groups. The femoral ridges are usually better developed and the posterior edge of the femur is never pronounced in American forms, a somewhat similar appearance in *Ophiacodon* being merely the stem of the Y-system.

It has been said that the therapsid-like characters of this group are only the results of parallelism or convergence; but, even with our present knowledge of these phenomena, it seems impossible that the pareiasaurs could have made this amount of positive advance over the primitive cotylosaurs and not be at all connected with the therapsids. Considering the few faunas of Carboniferous and early Permian age of which we have knowledge, it would seem not improbable that the pareiasaurs may be a specialized offshoot of a cotylosaurian group from which the therapsids have sprung, and that these resemblances are due to a real, although distant, relationship.

5.—Pelycosauria

The general conception of the pelycosaurs, in a broad sense, is that of a group of reptiles of a somewhat higher grade of organization than the cotylosaurs and with the one common feature of a lateral temporal opening. Other than this, there seems to be little to bind the group together; common features are mostly inheritances from a cotylosaurian ancestry. In general, the limbs are of cotylosaurian type, and functionally about on a level with those of the Captorhinomorpha. We may distinguish at least five groups, each with characteristic limb features.

a.—Caseidæ. The cleithrum is lost. There is no supraglenoid foramen. Probably two coracoids. No ectepicondylar foramen. The iliac blade completely developed, and extended somewhat forward.

Posterior branch of femoral Y and caudi-femoralis insertion reduced, anterior branch leading to reduced stem.

b.—OPHIACODONTIDÆ. Possibly a cleithrum. Supraglenoid foramen in primitive position. Two coracoids. No ectepicondylar foramen. A trough dorsally above iliac blade. Posterior branch of Y leads down into prominent stem.

c.—POLIOSAURIDÆ. No cleithrum. Supraglenoid foramen far forward. One or two coracoids (the posterior may be unossified). A trough dorsally above iliac blade. The posterior branch of the femoral Y reduced, anterior branch leading to the stem.

d.—CLEPSYDROPIDÆ. Cleithrum only in *Clepsydrops*. Supraglenoid foramen anterior to supraglenoid buttress. Two coracoids. No ectepicondylar foramen. Formation of iliac blade completed. Stem of femoral Y reduced, anterior branch leading into the rough line marking its position.

e.—EDAPHOSAURIDÆ. Cleithrum present. Supraglenoid foramen in primitive position. Probably two coracoids. An ectepicondylar foramen present. The ilium is somewhat uncertain. The femoral Y system is much like that of lower cotylosaurs.

The only advanced American form from the Permian not included in the Pelycosauria is *Araeoscelis*. The slim humerus has an ectepicondylar foramen. I am unable to interpret the shoulder girdle. The ilium is of the ophiacodont or poliosaurid type.

The pelycosaurs, as summarized above, are seen to have in their various groups various combinations of primitive and advanced characters. The derivation of the limb structure from that of cotylosaurs is evident, but there is an apparent lack of genealogical sequence between the known pelycosaurian groups themselves, and between certain of them and the typical captorhinomorphs. The latter group cannot be considered as directly ancestral to the Poliosauridæ and Ophiacodontidæ, because of the primitive character of the ilium of these two families, and because of the peculiar femur, with an emphasis of the posterior ridge not found elsewhere, of the latter. *Casea* cannot be derived from any other known pelycosaurian family. The peculiar position of the poliosaurian supraglenoid foramen puts them out of the line of ancestry of the other groups, except possibly the Clepsydropidæ, although their skull is of a generalized nature. The femur of *Ophiacodon* is a debarring specialization. *Edaphosaurus* presents the interesting combination of a limb-structure of extremely primitive character in most respects and recalling only the primitive cotylosaurs, with one startling advance, not found

elsewhere in American cotylosaurs or pelycosaurs—the presence of the ectepicondylar foramen. This structure offers some interesting possibilities as to the possible relationships of the main groups of reptiles. It was certainly developed, at least once, in the cotylosaurian grade of organization, as shown by its presence in the Chelonia as well as possibly in the pareiasaurs; and it is possible that *Edaphosaurus*, with otherwise cotylosaurian limbs, may have been derived from a cotylosaur having this foramen. The foramen is found in lizards and their supposed ancestor, *Aræoscelis;* in *Sphenodon*, but not in other "Diapsids"; in Nothosauria; and in therapsids.

It is, of course, quite probable that the structure has been separately evolved in two or more lines; but it seems extremely improbable that it has been evolved four or five times, as our usual conceptions of the relationships of the groups concerned would involve. It is unwise to base any scheme of classification upon a single character; but, on the other hand, this and other points of girdle and limb structure, which tend to reverse our usual opinions of the relationship of pareisaurs and pelycosaurs other than *Edaphosaurus* to the therapsids, should make us less hasty in coming to a final decision as to therapsid ancestry. It will be noted that even the homology of the lateral temporal fenestra is at stake.

6.—Therapsida

Even in *Moschops*, one of the lowest members of this series, we encounter a new type of structure and function, markedly different from that characterizing the American Permo-Carboniferous fauna and without connecting stages, unless a relationship of therapsids and pareiasaurs be admitted.

Functionally, the changes are those which culminate in the mammals and consist principally in an inturning and more vertical position of the proximal segments of the limbs, with which is associated a partial change in the means of support of these segments from ventral bracing by the muscles of coracoid and pubo-ischiadic plates to a leverage system, with the force exerted by dorsal muscles, from scapular and iliac blades (supra- and infraspinatus in the fore limb, glutei in the hind).

Significant structural characteristics include the following. Cleithrum primitively present. Clavicle and interclavicle present, the latter usually somewhat expanded. Rather tall and well-ossified scapula of primitive type with a single flat surface for the deltoid. No supraglenoid buttress or supraglenoid foramen described. Glenoid not of primitive type. A fairly large coracoid plate of two elements, the anterior entering little if

at all into the glenoid, and the plate not well developed posteriorly. No glenoid foramen. Apparently no point of origin for a coracoid head of the triceps. Humerus with a long and laterally expanded delto-pectoral crest, causing a broad dorsal surface of origin for the brachialis. Median surface for the triceps greatly reduced. The ectepicondylar foramen is present primitively, although absent in *Moschops*, etc. The humerus is comparatively little "twisted." The entepicondylar foramen is turned down to appear on the ventral surface. The ilium is entirely for appendicular muscles externally and is produced forward. The pubis is short and turned out, and its symphysis greatly reduced. The femur is flattened dorso-ventrally, the posterior margin running proximally into the "greater trochanter," left isolated by the loss of connection of its homologue, the posterior branch of the Y ridge system, with the stem and anterior branch. These two latter are reduced in *Moschops*, but somewhat better developed in other and more typical therapsids.

Apart from a few dicynodonts and cynognathids, the limb and girdle material of sure association at my disposal is too scanty and ill-preserved to justify any broad comparisons between the different therapsid groups. Watson has recently reviewed the fore-limb material (1917*a*), and Broom (1913, etc.) had summarized many of the chief points of interest in the history of the group. A number of the factors of advance have been discussed in previous sections. Within the known therapsids, several decided advances have taken place, including the loss of the cleithrum (very late), eversion of the scapular spine and formation of the acromion, the beginning of the formation of a supraspinous fossa, considerable reduction of the coracoid plate, loss (at a number of times, apparently) of the ectepicondylar foramen, further extension forward of the ilium and shortening of the pubis, and development of the greater trochanter of the femur.

It is probably only within the limits of the mammalia, as partially indicated by the monotremes, that a number of other advances have taken place, including the following: the formation of the supraspinous fossa; entire loss of the coracoid plate; loss of the interclavicle; narrowing of the humerus; a secondary narrowing of the ilium and probably acquisition of a trihedral form with the addition to this element of the iliacus origin; and a secondary rounding up of the shape of the femur.

MUSCULAR HOMOLOGIES

The following is a table of the muscular homologies of the limbs of urodeles, reptiles and mammals. In so far as it covers the same territory, it may be considered as a revision of that given by Gregory and

Camp (1918). The innervations (italics) are given, as shown in Figure 1, when of importance. The arrangement followed in the appendicular muscles is that of the proposed division into dorsal and ventral masses. I am indebted to Mr. G. K. Noble for information concerning a number of urodele innervations.

Fore Limb

Body Muscles Acting on the Shoulder Girdle

Urodeles	General Reptilian Condition	General Mammalian Condition
Trapezius (Cucullaris)	Trapezius (Cucullaris) (+Episterno-cleido-mastoideus)	Trapezius +Sterno-cleido-mastoideus
Levator scapulæ	Levator scapulæ (superficialis)	Levator scapulæ (+"Omotrachelius") +Romboideus
Serratus anterior	Serratus anterior Serratus anterior superficialis	Serratus anterior
(Part of Rectus abdomnis)	Sterno-costo-scapularis + Sterno-costo-coracoidei	Subclavius (+Sternoclavicularis)
Omo-hyoid + Sterno-hyoid	Omo-hyoid + Episterno-hyoid	Omo-hyoid + Sterno-hyoid and-thyreoid

Primitive Dorsal Group

Latissimus dorsi	Latissimus dorsi (+Teres major)	Latissimus dorsi (+ Teres major)
Subcoraco-scapularis	Subcoraco-scapularis + Scapulo-humeralis posterior	Subscapularis
Triceps: Scapular head Lateral humeral head Coracoid head Medial humeral head	Triceps: Scapular head Lateral humeral head Coracoid head Medial humeral head	Triceps: Long (scapular) head Lateral humeral head Dorso-epitrochlearis and distal part of old medial head

Primitive Dorsal Group (continued)

Urodeles	General Reptilian Condition	General Mammalian Condition
(Absent or part of extensors)	Brachio (humero)-radialis, *Rad* + Supinator, *Rad*	Brachio-radialis, *Rad* + Supinator, *Rad*
Short radial extensor (part of following) Humero-radialis dorsalis or Extensor carpi radialis + "Supinator"	Short radial extensor + Extensor carpi radialis	Extensor carpi radialis longus + brevis
Extensor digitorum communis	Extensor digitorum communis longus	Extensor digitorum communis + Extensor digiti quinti proprius
Short ulnar extensor (part of following) Extensor carpi ulnaris or Humero-ulnaris dorsalis	Short ulnar extensor + Extensor carpi ulnaris	?Anconæus? + Extensor carpi ulnaris

Primitive Ventral Group

Pectoralis	Pectoralis	Pectoralis
Deltoid (?scapular portion only)	Deltoides scapularis or Dorsalis scapulæ + Deltoides clavicularis	Deltoid, in two or three parts
Precoraco-humeralis, *Ax* + *Spc* Supracoracoideus, *Spc*	Scapulo-humeralis anterior, *Ax* Supracoracoideus, *Spc*	Teres minor, *Ax* Infraspinatus, *Spc* (+ *Ax*) Supraspinatus, *Spc* (+ Supracoracoideus)
Coraco-brachialis brevis + longus, *M-C*	Coraco-brachialis brevis + longus, *M-C*	Coraco-brachialis, *M-C*
Coraco-radialis proprius, *Spc* Brachialis, *M-C*	Biceps, *M-C* Brachialis, *M-C*	Biceps, *M-C* Brachialis, *M-C*
Flexor carpi radialis	Flexor carpi radialis	Flexor carpi radialis + Flexor pollicis longus
(?part of above) Radio-ulnaris	Pronator teres + Pronator profundus or quadratus	Pronator teres + Pronator quadratus

Primitive Ventral Group (continued)

Urodeles	General Reptilian Condition	General Mammalian Condition
Flexor digitorum communis + Flexor digitorum profundus (or ulnari-phalangei II-V)	Flexor digitorum profundus or longus	Palmaris longus + Flexor digitorum sublimis + Flexor digitorum profundus
Short ulnar flexor (part of following) Flexor carpi ulnaris	"Epitrochleo-anconeus" short ulnar flexor Flexor carpi ulnaris	Epitrochileo-anconæus? Flexor carpi ulnaris

Hind Limb
Body Muscles acting on the Pelvis

	Dorsal	
Dorsalis trunci = Caudæ dorsalis	Spinales + Semispinales = Caudæ dorsalis, part Sacrospinalis: Ilio-costalis + Longissimus dorsi = Extensor caudæ lateralis or Caudæ dorsalis, part	Multifidus + Semispinales = Extensor caudæ medialis Sacrospinalis: Ilio-costalis + Longissimus dorsi = Extensor caudæ lateralis or Abductor caudæ externus
	Ventral anterior	
Obliquus externus Obliquus internus Transversus Rectus abdominis	Quadratus lumborum Obliquus externus Obliquus internus Transversus Rectis abdominus	Quadratus lumborum Obliquus externus Obliquus internus Transversus Rectus abdominis + pyramidalis
	Ventral posterior	
Ilio-caudalis + Sacro-caudalis Ilio-caudalis, deep ventral portion Ischio-caudalis, superficial portion	Ilio-caudalis Vestigal except probably in Chelonia	(Ilio-sacro-coccygeus = Levator ani in part) (Pubo-ischio-coccygeus = Levator ani in part) Abductor caudæ inferior or internus, or Flexor lateralis)

Primitive Dorsal Group

Urodeles	General Reptilian Condition	General Mammalian Condition
Ilio-extensorius, *Sac*	Extensor ilio-tibialis, *Crur* + *Sac*	Rectus femoris, *Crur*
Ilio-tibialis, *Crur*	Ambiens, *Crur*	Sartorius, *Crur*
	Femoro-tibialis, *Crur*	Vasti, *Crur*
Ilio-fibularis, *Sac*	Ilio-fibularis, *Sac*	Biceps, *Sac*
Pubo-ischio-femoralis internus (or Ilio-femoralis, in part), *Crur*	Pubo-ischio-femoralis internus, *Crur*	Ilio-psoas, *Crur* + Pectineus, *Crur*
Ilio-femoralis, *Sac* (+*Crur*)	Ilio-femoralis, *Sac* + *Crur*	Glutei (+?tensor fasciæ latæ), *Sac* (+ *Crur*)
"Ischio-femoralis," *Sac*	Ischio-trochantericus, (brevis) (=Pubo-ischio-femoralis posterior), *Sac*	Obturator internus + Gemellii, *Sac*
Femoro-tibialis (2 parts, including "Extensor primitif du tibia," Perrin) Fibulæ metatarsus II	Tibialis anticus=Tibio-metatarsalis longus	Tibialis anticus
Extensor longus digitorum = Femoro-digiti I–V	Extensor longus digitorum = Epicondylo-metatarsalis dorsalis medius	Extensor longus digitorum + Peronæus tertius + ?Extensor hallucis longus
Femoro-fibularis Femoro-tarsali-fibularis	Peronæus anterior + posterior = Fibulo-metatarsalis dorsalis + Femoro-metatarsalis dorsalis	Peronæus longus Peronæus brevis

Primitive Ventral Group

Pubo-ischio-tibialis, *Sac* (+ *Obt*)	Pubo-ischio-tibialis, *Obt* + *Sac*	Gracilis, *Obt*
Pubo-tibialis, *Sac*	Pubo-tibialis, *Obt* + ?*Sac*	
Ischio-flexorius, *Sac*	Flexor tibialis internus, *Obt* + *Sac*	Semimembranosus, + Semitendinosus, *Sac* (+ *Obt*)
	Flexor tibialis externus, *Sac*	

Primitive Ventral Group (continued)

Urodeles	General Reptilian Condition	General Mammalian Condition
"Adducteur du femur," Perrin, *Sac*	Adductor = "Ischio-femoralis," *Obt* + *Sac*	Adductors, *Obt* + *Sac*
Pubo-ischio-femoralis externus, *Obt* + *Sac*	Pubo-ischio-femoralis externus, *Obt* + *Sac*	Obturator externus, *Obt* + Quadratus femoris, *Sac*
Fibulæ metatarsi et digiti I-V + Femoro-fibulæ digiti I-V + Femoro-fibulæ metatarsi I, II, III	Gastrocnemius c. femorale s. externus + Gastrocnemis c. tibiale s. internus + Flexor longus digitorum	 "Triceps suræ" + Plantaris Flexor digitorum longus + ?Flexor hallucis longus
"Rotateur direct du pied," Perrin	Tibialis posticus = Tibio-metatarsalis ventralis	Tibialis posterior
	Fibulo-tibialis superior s. Popliteus	Popliteus
Fibulæ tibialis	Interosseus cruris = Fibulo-tibialis inferior	Interosseus cruris
Caudali-femoralis	Coccygeo-femoralis brevis = Caudi-ilio-femoralis	?Pyriformis
Caudali-pubo-ischio-tibialis	Coccygeo-femoralis longus = Caudi-femoralis	?Cruro-coccygeus

SUMMARY

The following are the chief points presented for the first time or for which additional evidence is presented.

1.—The musculature of tetrapod limbs may be resolved into primitive dorsal and ventral groups, comparable with the two opposing muscle masses of the fish fin.

2.—In the pelvic region especially, these groups are divisible into deeper and more superficial layers, which have primitively double anteroposterior innervations.

3.—The tetrapod shoulder girdle and its muscular relations are comparable to those of the bony fish.

4.—Reduction of the dermal girdle and growth of the scapular blade in tetrapods, as compared with fish, are related to a change in the method of transfer of strain between body and limb.

5.—The trapezius, levator scapulæ, hyoid muscles, deltoid and pectoralis (part) are primitively attached to the dermal girdle. With the loss of the cleithrum the dorsal portions of these insertions and origins were taken over by the scapula.

6.—The muscles of the coracoid plate have invaded the scapular blade in therapsids and mammals, limiting the older musculature (derived from the cleithrum) to spine and acromion.

7.—The great development of the scapular blade and ilium in mammals is due to the changed position of the proximal segments of the limbs, which has enabled muscles advantageously placed to take on a supporting function as levers of the second class.

8.—The coracoid plate muscles concerned in this rotation are the scapulo-humeralis anterior, supracoracoideus, and coraco-brachialis, which are parts of a primitive single deep ventral muscle mass.

9.—The teres minor is the reptilian scapulo-humeralis anterior; the supra- and infraspinatus are derived from the supracoracoideus.

10.—Of the two coracoid elements of primitive and mammal-like reptiles, the modern reptilian "coracoid" is the anterior, and the mammalian coracoid is the posterior. The coracoids of these two groups are not homologous.

11.—The triangular supraglenoid buttress of primitive tetrapods with its musculature (subcoraco-scapularis and long heads of triceps) is comparable to the mesocoracoid bridge of bony fishes. The invasion of the internal surface of the reptilian coracoid by the subcoracoid is related to the disappearance of this buttress and of the postero-dorsal corner of the coracoid and their replacement by the sterno-scapular ligament.

12.—The primitive tetrapod shoulder-joint was composed of two separate although adjacent surfaces.

13.—The primitive humerus was a tetrahedron composed of four roughly triangular surfaces.

14.—The proximal ventral surface was occupied by the coraco-brachialis, the distal ventral by the brachialis. The proximal and distal dorsal surfaces were occupied mainly by lateral and medial heads of the triceps; the proximal surface also by scapulo-humeralis anterior (teres minor).

15.—At the anterior proximal corner were the insertions of the supracoracoideus (supra- and infraspinatus) and, more distally, deltoid and pectoralis. At the posterior proximal corner were the subcoraco-scapularis and, more distally, latissimus dorsi.

16.—At the distal corners were the ect- and ent-epicondyles for origins of flexors and extensors.

17.—The amniote entepicondylar foramen is due to an increase in the area of origin of the flexor muscles and the consequent enclosure of the artery and median nerve.

18.—Anteriorly, a ridge and crest for brachio-radialis and supinator separated dorsal and ventral surfaces. The ectepicondylar foramen is caused by fusion of this crest with the entepicondyle, surrounding part of the radial nerve.

19.—The primitive triceps consisted of four heads, of which the mammals retain only the scapular, lateral humeral, and distal portion of the median humeral heads. The dorso-epitrochlearis is a fusion of part of the primitive median mass with the latissimus.

20.—The tetrapod pelvic girdle consists essentially of (1) a pubo-ischiadic plate, comparable to the fish girdle and bearing comparable dorsal and ventral muscle masses, and (2) an iliac blade, essentially for support, which has interrupted the dorsal muscle mass and taken over the origins of a portion of it.

21.—Pubo-ischio-femoralis internus (ilio-psoas) and ischio-trochantericus (obturator internus) are portions of a primitive deep dorsal mass of which the middle portion (ilio-femoralis) has been taken up by the ilium. These muscles (and the coccygeo-femorales) escape to the external surface beneath the ilio-pubic and ilio- (sacro-) ischiadic ligaments.

22.—The upper portion of the iliac blade was primitively associated with the axial muscles, as in existing urodeles. In the transition to reptiles this portion has folded over on to the inner surface, leaving the external surface free for appendicular muscles.

23.—The increasing importance of the ilio femoralis (gluteals) in the mammalian line, correlated with the changed position of the femur and their supporting function as levers of the second class, has caused the anterior expansion of the ilium and has pushed the ilio-tibialis anteriorly and ventrally as the rectus femoris.

24.—The mammalian sartorius is the ambiens, the origin of which has travelled upwards along the ilio-pubic ligament.

25.—The biceps is the reptilian ilio-fibularis, the origin of which has travelled downwards along the ilio- (sacro-) ischiadic ligament.

26.—The femoro-tibialis (vasti) is an amniote muscle which took over the dorsal surface previously occupied by pubo-ischio-femoralis internus.

27.—Only the internally inserting portions of the long ventral muscles to the lower leg are retained as the mammalian gracilis, semimembranosus, and semitendinosus.

28.—A supra-acetabular (cotyloid) notch is a primitive feature of the hip joint.

29.—A ventral Y-shaped system of ridges is characteristic of the primitive femur. The anterior branch of the Y is the reptilian internal trochanter and, by a change of function, the mammalian minor trochanter. The posterior branch, with the development of the gluteals, becomes the mammalian greater trochanter. The fossa between the two branches always contains the insertion of part of the pubo-ischio-femoralis internus. The junction of the branches is occupied by the insertion of the coccygeo-femoral muscles (fourth trochanter). On either side of the Y-system lie the adductors anteriorly and ilio-femoralis (gluteals) posteriorly.

30.—The limbs of *Diadectes*, a primitive cotylosaur, are essentially of the basic amniote type.

31.—The rachitomous Amphibia differ from the primitive reptiles only in the presence of a small number of probably more primitive characters.

32.—The pareiasaur limb agrees with the therapsid, rather than with the cotylosaurian type.

33.—In limb structure the "pelycosaurs" have no common features other than those attributable to a common cotylosaurian ancestry.

34.—The peculiar distribution of the ectepicondylar foramen suggests that our conceptions of the relationships of many amniote groups may be subject to future revision.

35.—The therapsid type of limb is in sharp contrast to that of primitive groups (except the pareiasaurs) and shows many mammalian tendencies. The changed position of the proximal segments of the limbs is the key to the therapsid and mammalian type of locomotor apparatus.

36.—The detailed characters of the girdles and limbs of therapsids lend strong support to the conclusion that the mammals have been derived from or are closely related to the therapsids, especially the cynodonts.

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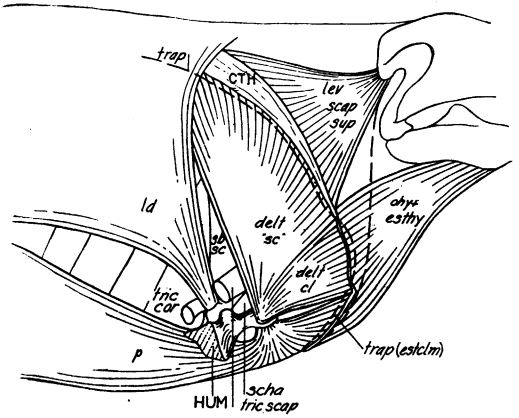
TABLE OF ABBREVIATIONS

ACET.	acetabulum
AC.N	acetabular notch
ACR.	acromion
ad.	M. adductor (s)
ad. br.	M. adductor brevis
ad. l.	M. adductor longus
ad. mg.	M. adductor magnus
ADVL.	anterior dorso-ventral line of humerus
amb.	M. ambiens
anc.	M. anconeus
at. ac.	M. atlanto-acromialis
at. sc.	M. atlanto-scapularis
bi	M. biceps
br.	M. brachio-radialis
bri.	M. brachialis (inferior)
cb.	M. coraco-brachialis
cbb.	M. coraco-brachialis brevis
cbl.	M. coraco-brachialis longus
cd.	M. caudæ dorsalis
cf.	MM. coccygeo-femorales
cfb.	M. coccygeo-femoralis brevis (caudi-ilio-femoralis)
cfl.	M. coccygeo-femoralis longus (caudi-femoralis)
CL.	clavicle
clm.	M. cleido-mastoideus
COR.	coracoid, posterior coracoid
cost. cor.	M. costo-coracoideus
COT.N.	cotyloid notch
cr. cx.	M. cruro-coccygeus
CR. DP.	delto-pectoral crest
CR. SUP.	supinator crest
CTH.	cleithrum
delt.	M. deltoideus
delt. sc.	M. deltoides scapularis
delt. cl.	M. deltoides clavicularis
dep.	M. dorso-epitrochlearis
ecl.	M. extensor caudæ lateralis
ecm.	M. extensor caudæ medialis
ECT.	ectepicondyle
ENT.	entepicondyle
estclm.	M. episterno-cleido-mastoideus
est. hy.	M. episterno-hyoideus
ex.	MM. extensores
excd.	M. extensor communis digitorum
excr.	M. extensor carpi radialis
excu.	M. extensor carpi ulnaris
FE.	femur
FECT.	ectepicondylar foramen
"FECT."	spiral groove, replacing the foramen
FENT.	entepicondylar foramen
FGL.	glenoid foramen
fl.	MM. flexores
flcu.	M. flexor carpi ulnaris
fld.	M. flexor longus digitorum
F. OBT.	obturator foramen
FOR. TH.	thyroid foramen
FOS. SBSC.	subscapular fossa
F. SGL.	supraglenoid foramen
F. SPC.	coracoid, or supracoracoid, foramen
ft.	M. femoro-tibialis
fte.	M. flexor tibialis externus
fti.	M. flexor tibialis internus
gast.	M. gastrocnemius
gem.	MM. gemelli
GLEN.	glenoid
gl. md.	M. gluteus medius
gl. mn.	M. gluteus minimus
gl. mx.	M. gluteus maximus
glut.	MM. glutei
grac.	M. gracilis
HUM.	humerus
ICL.	interclavicle ("episternum")

IL.	ilium
ilc.	M. iliacus
il. caud.	M. ilio-caudalis
"il caud"	deep ventral portion of M. ilio-caudalis (=? levator ani)
il. coc.	M. ilio-coccygeus (levator ani, part)
il. cost.	M. ilio-costalis
il. fb.	M. ilio-fibularis
il. fem.	M. ilio-femoralis
il. ps.	M. ilio-psoas
in.	insertion
is. caud.	M. ischio-caudalis
is. coc.	M. ischio-coccygeus (levator ani, part)
isp.	M. infraspinatus
is. tr.	M. ischio-trochantericus
it.	M. (extensor) ilio-tibialis
ld.	M. latissimus dorsi
lev. scap.	M. levator scapulæ
lev. scap. prof.	M. levator scapulæ profundus
lev. scap. sup.	M. levator scapulæ superficialis
lig.	ligament
lig. il.-isch.	ilio-ischiadic ligament
lig. il.-pub.	ilio-pubic ligament
lig. med.	internal lateral ligament of knee
lig. poup.	Poupart's ligament
lig. pub.-isch.	pubo-ischiadic ligament
lig. sch.	scapulo-humeral ligament
lig. stsc.	sterno-scapular ligament
LML.	latero-medial line—separating proximal and distal dorsal surfaces of humerus
long. d.	M. longissimus dorsi
MAR.	marsupial bone
ob. ex.	M. obturator externus
obl.	MM. obliquus internus and externus
obt. int.	M. obturator internus
ohy.	M. omo-hyoideus
or.	origin
p.	M. pectoralis
PCOR.	precoracoid, anterior coracoid of reptiles
pect.	M. pectineus
per.	M. peronæus
per. b.	M. peronæus brevis
per. l.	M. peronæus longus
pife.	M. pubo-ischio-femoralis externus
pifi.	M. pubo-ischio-femoralis internus
pit.	M. pubo-ischio-tibialis
pop.	M. popliteus
prt.	M. pronator teres
ps.	M. psoas
ps. mj.	M. psoas major
ps. mn.	M. psoas minor
pt.	M. pubo-tibialis
(*pt.*)	part of
PU.	pubis
pub. coc.	M. pubo-coccygeus (levator ani, part)
pyr.	M. pyriformis
qf.	M. quadratus femoris
ql.	M. quadratus lumborum
RA.	radius
r. abd.	M. rectus abdominis
rf.	M. rectus femoris
rh.	M. rhomboideus
sac. coc.	M. sacro-coccygeus (levator ani, part)
SAN.	supra-acetabular notch
sart.	M. sartorius
sbc.	M. subcoracoideus
sbcsc.	M. subcoraco-scapularis
sbsc.	M. subscapularis
SC.	scapula
SCCOR.	scapulo-coracoid
scha.	M. scapulo-humeralis anterior
schp.	M. scapulo-humeralis posterior
ser. ant.	M. serratus anterior

ser. ant. sup.	M. serratus anterior superficialis	*trans.*	M. transversus abdominis
sm.	M. semimembranosus	*trap.*	M. trapezius
smsp.	MM. semispinales	*tric.*	M. triceps
sp.	MM. spinales	*tric. cor.*	M. triceps caput coracoideus
SP.	spine of scapula		
spc.	M. supracoracoideus	*tric. hum.*	M. triceps c. humeralis
SR.	articulation with sacral ribs	*tric. hum. lat.*	M. triceps c. humeralis lateralis
ssp.	M. supraspinatus	*tric. hum. med.*	M. triceps c. humeralis medialis
ST.	sternum		
st.	M. semitendinosus	*tric. scap.*	M. triceps c. scapularis
st. cl. m.	M. sterno-cleido-mastoideus	TR. IN.	internal trochanter
		TRL.	transverse line (humerus, ilium)
st. cor.	MM. sterno-coracoidei		
st. hy.	M. sterno-hyoideus	TR. MJ.	greater trochanter of femur
st. m.	M. sterno-mastoideus		
subcl.	M. subclavius	TR. MN.	minor trochanter of femur
sup.	M. supinator		
ta.	M. tibialis anticus	TR. 4	fourth trochanter
t. maj.	M. teres major	TB. IS.	tuberosity of ischium
t. min.	M. teres minor	TUB. PUB.	tuberculum pubis
		UL.	ulna.

PLATES XXVII TO XLVI



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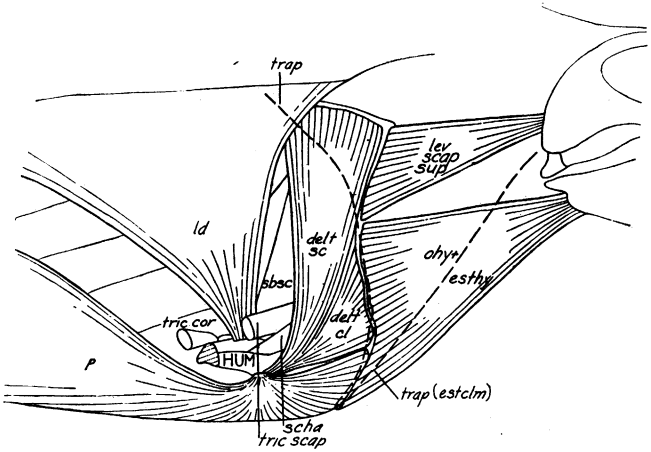

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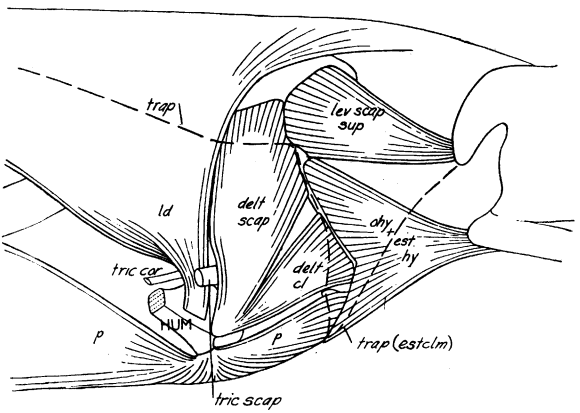
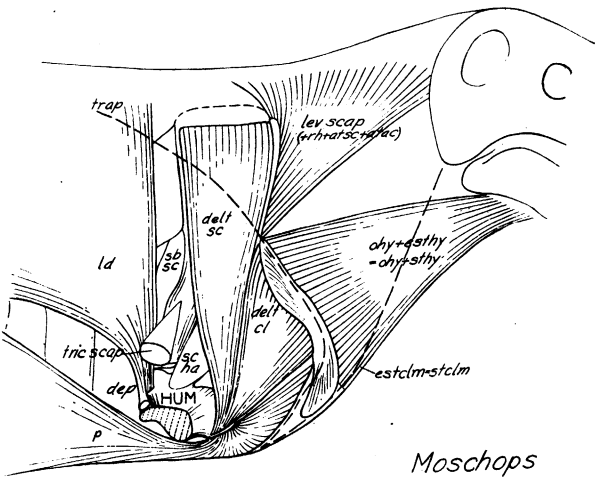


Iguana



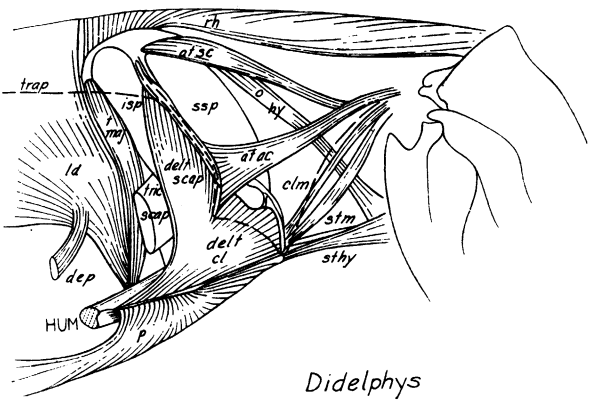
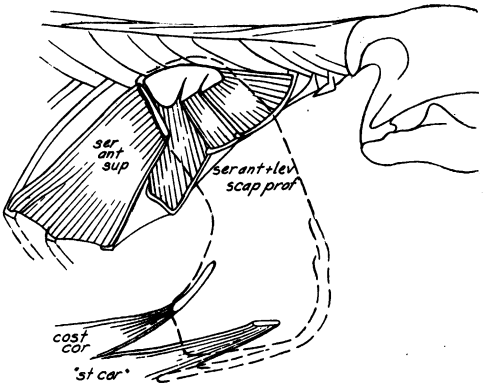


PLATE XXVII

Superficial lateral views of the shoulder musculature of type forms. The trapezius is represented in dotted outline. The relations of this muscle, the levator scapulæ, the hyoid muscles, the deltoid and pectoralis to the dermal girdle will be noted. The superficial portion of the serratus anterior is absent in mammals. The atlanto-acromialis and atlanto-scapularis of *Didelphys* are portions of the levator scapulæ separated by the upgrowth of the supraspinatus. (In this and following figures muscles shown but not treated are given in outline only. A table of abbreviations will be found at the end of the paper.)



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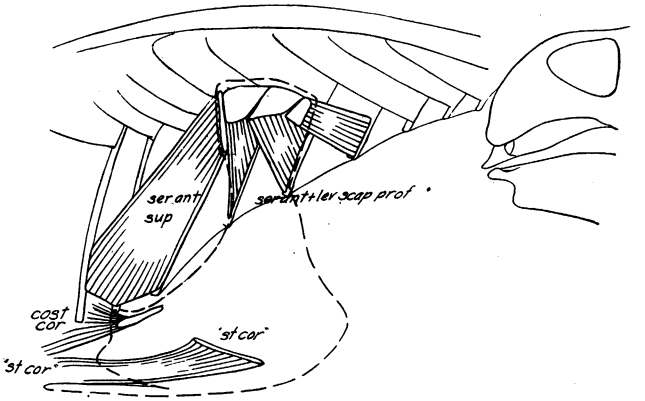

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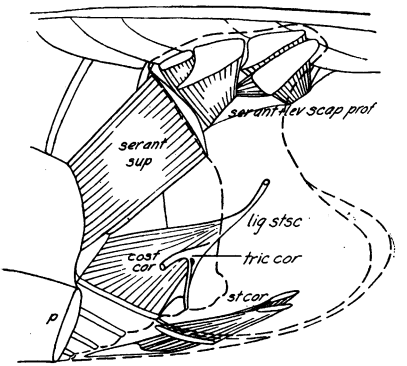
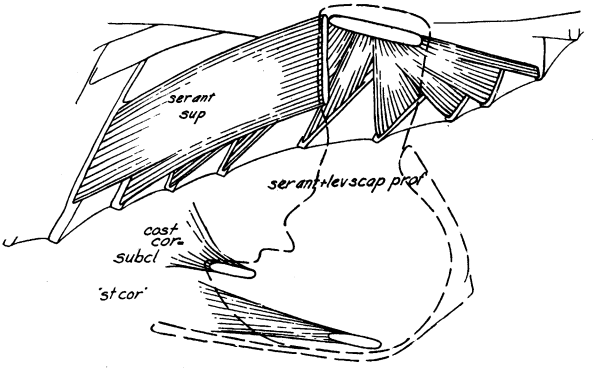
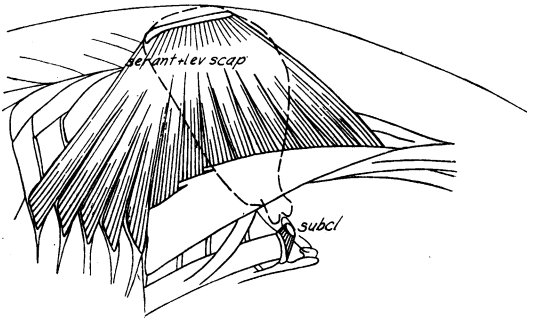


Iguana



Moschops



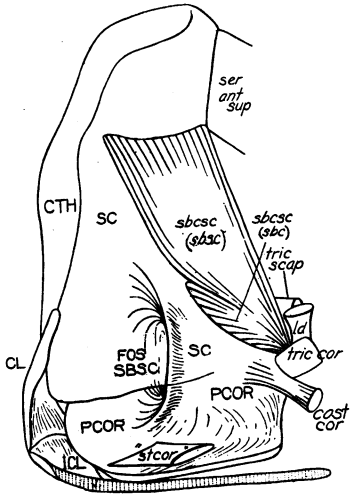
Didelphys

PLATE XXVIII

Deep lateral views of the shoulder musculature of types, the shoulder girdle being removed and represented in dotted outline. With the reduction of the reptilian coracoid the costo-coracoideus is seen to insert on the sterno-scapular ligament in *Iguana*. In mammals the posterior ventral muscles are reduced to the subclavius.

Plate XXIX

Internal views of the shoulder region of types, showing the subcoraco-scapularis and posterior ventral body musculature of the girdle. The primitive subcoraco-scapularis probably arose from the shelf above the glenoid (and the inner surface of the scapula) and extends into the inner surface in *Iguana* through loss of the postero-dorsal corner of the coracoid and the evolution of the sterno-scapular (coracoid) ligament.



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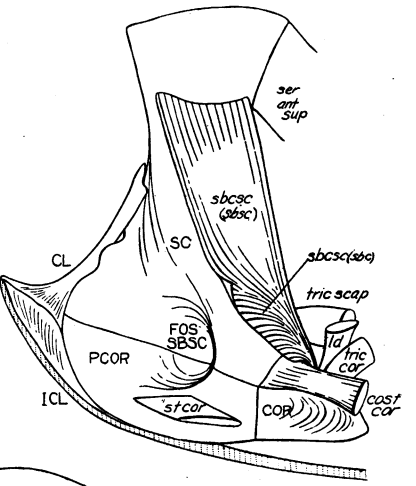

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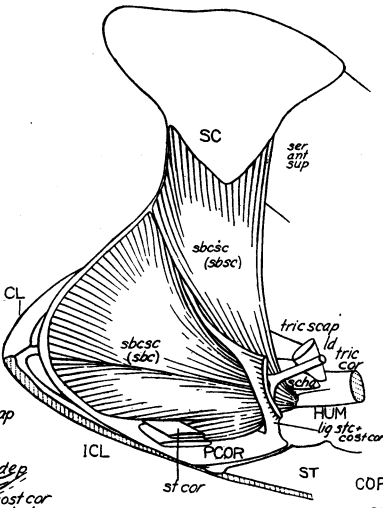
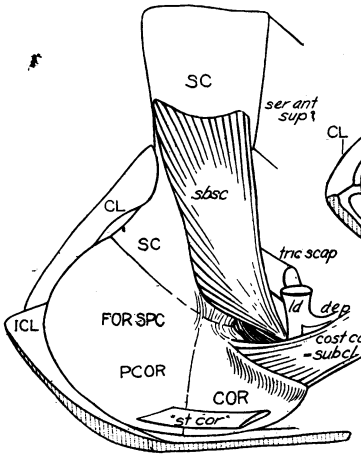
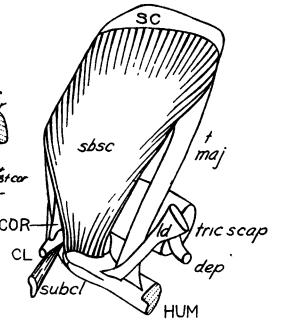


Iguana



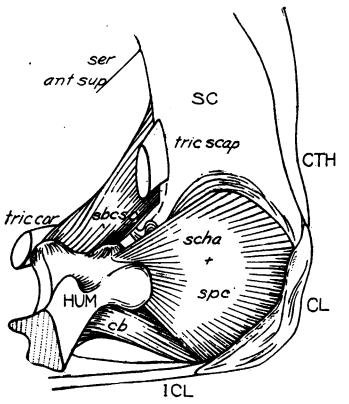
Moschops



Didelphys

Plate XXX

External views of the deep muscles of the shoulder. The original area of origin of the scapulo-humeralis anterior, supracoracoideus and coraco-brachialis is seen as ventral and anterior to the glenoid; it is seen extending dorsally in *Moschops* and *Didelphys*. This group is always anterior to the scapular head of the triceps, as compared with the subcoraco-scapularis group (including scapulo-humeralis posterior) which inserts primitively between coracoid and scapular heads of the triceps.



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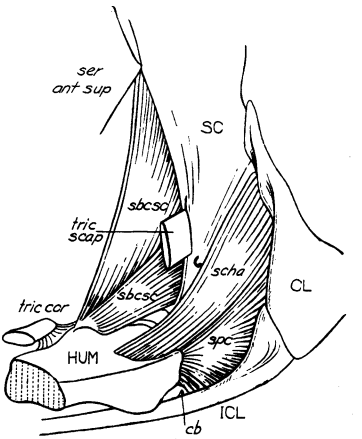

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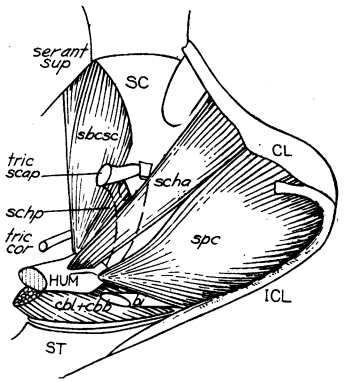
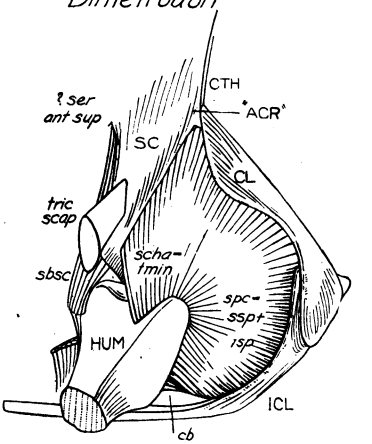
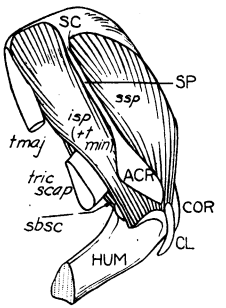


Iguana



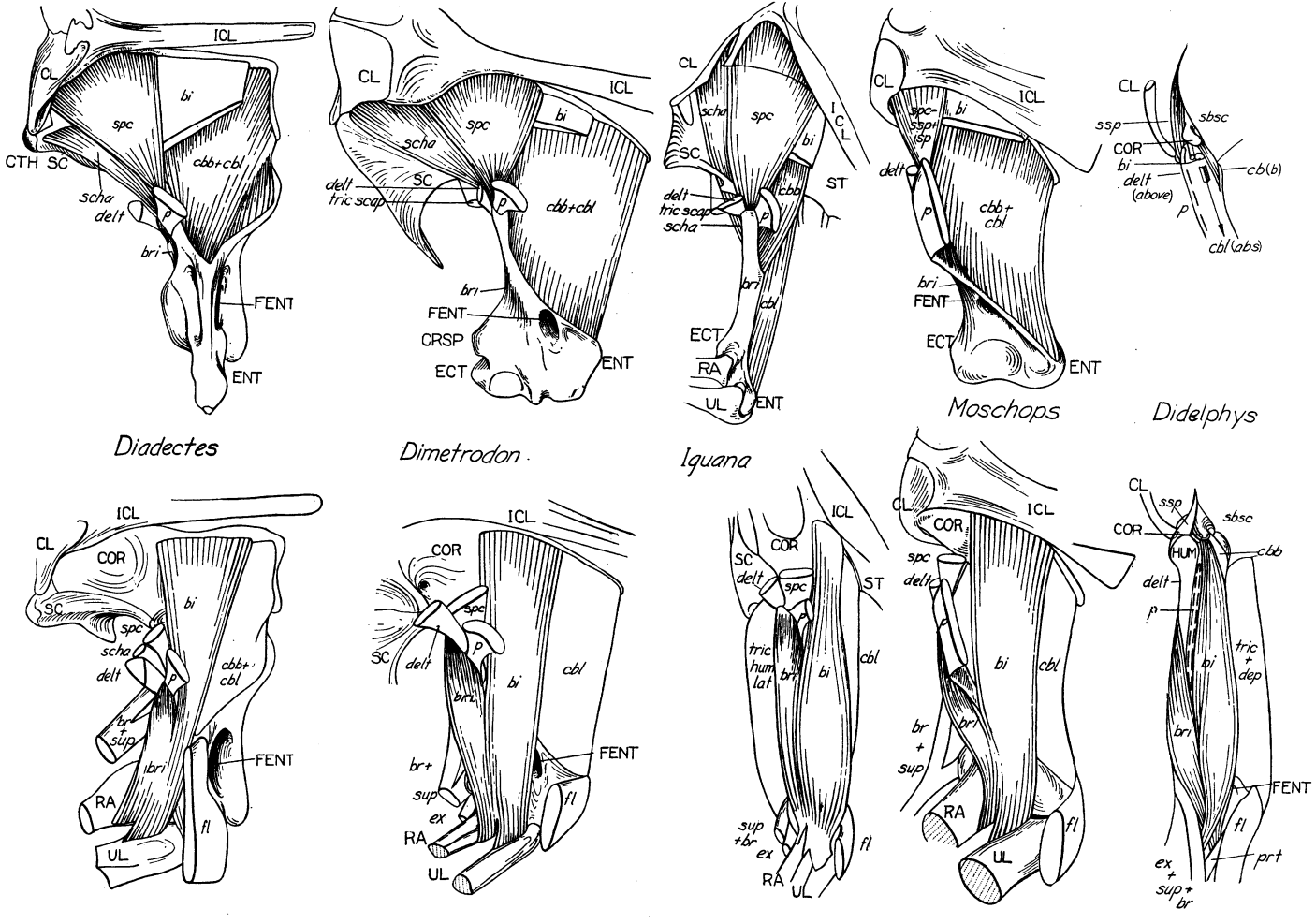
Moschops



Didelphys

Plate XXXI

Ventral views of shoulder region of types. Above, the relations of the group scapulo-humeralis anterior, supracoracoideus and coraco-brachialis. The dorsal rotation of the group removes all of them from the ventral surface except the coraco-brachialis. The long portion of this muscle is absent in *Didelphys;* its course in other mammals is indicated by an arrow. Below, the biceps, originating from the coracoid plate, and joining with the brachialis to unite in a common primitive insertion on both radius and ulna.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cbl
bri
FENT
ECT
ENT
Moschops
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ssp
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Didelphys
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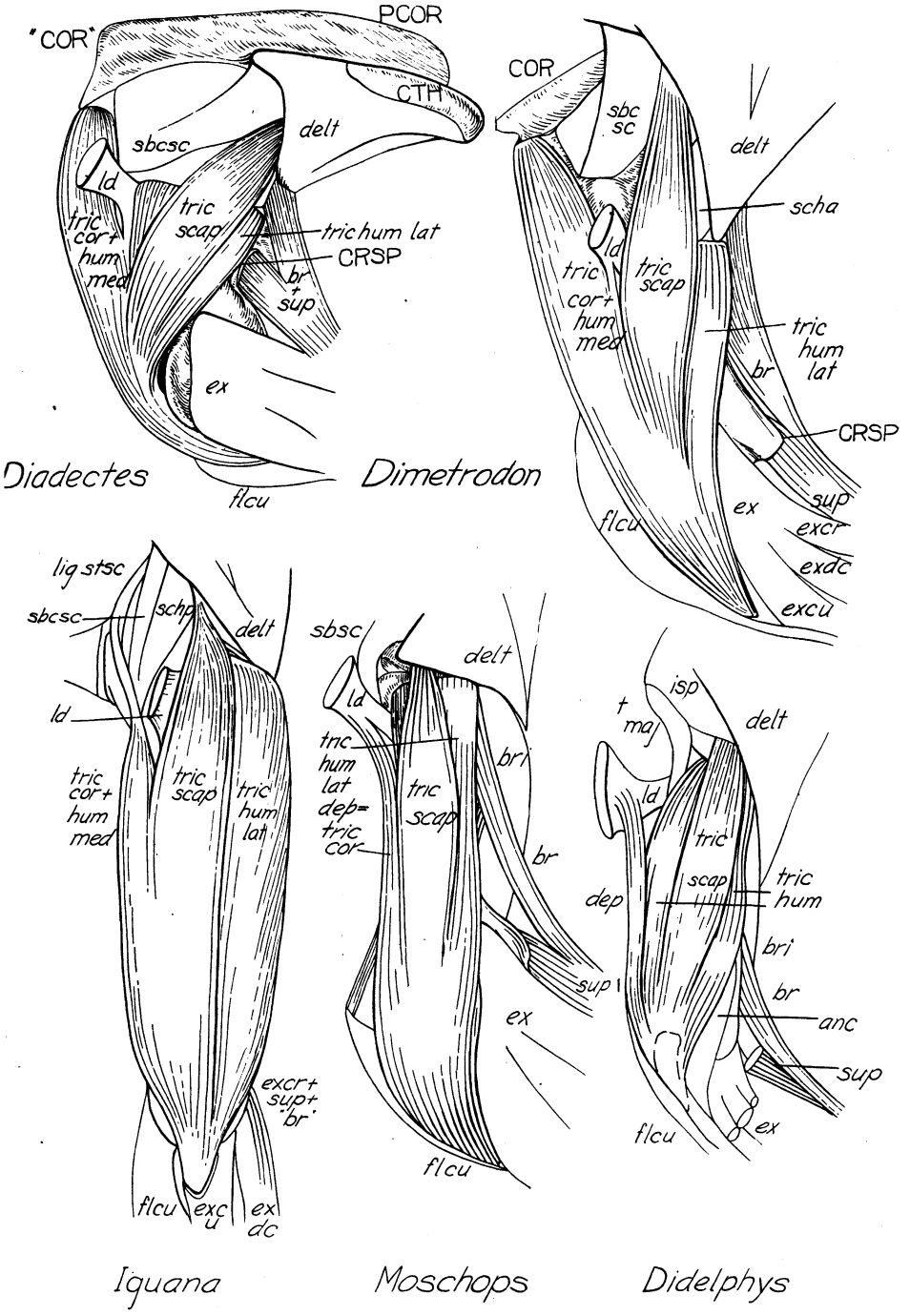
Plate XXXII

Triceps, brachio-radialis and supinator of types. The triceps is divided primitively into (*a*) a lateral (anterior) mass, with a scapular head at the posterior edge of the scapula under cover of the deltoid, and a lateral humeral head (*b*), a medial (posterior) mass, with coracoid and medial humeral heads (the latter not shown, being covered by the former). In mammals, the medial humeral head is reduced to a distal posterior part often (as in *Didelphys*) blended with the lateral head. The dorso-epitrochlearis is a portion of the medial mass primitively connected with latissimus. This latter muscle inserts between the two heads in reptiles, posterior to the triceps in mammals, with loss of the coracoid and part of the medial heads. The supinator and brachio-radialis are shown originating primitively from the supinator crest and anterior dorso-ventral line, and blending with the extensors by fusion of crest and ectepicondyle (this mass is not well developed in *Iguana*).


"COR"
PCOR
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tric cor+ hum med
tric scap
tric hum lat
CRSP
br + sup
ex
flcu
Diadectes
COR
sbc sc
delt
scha
ld
tric cor+ hum med
tric scap
tric hum lat
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tric scap
tric hum lat
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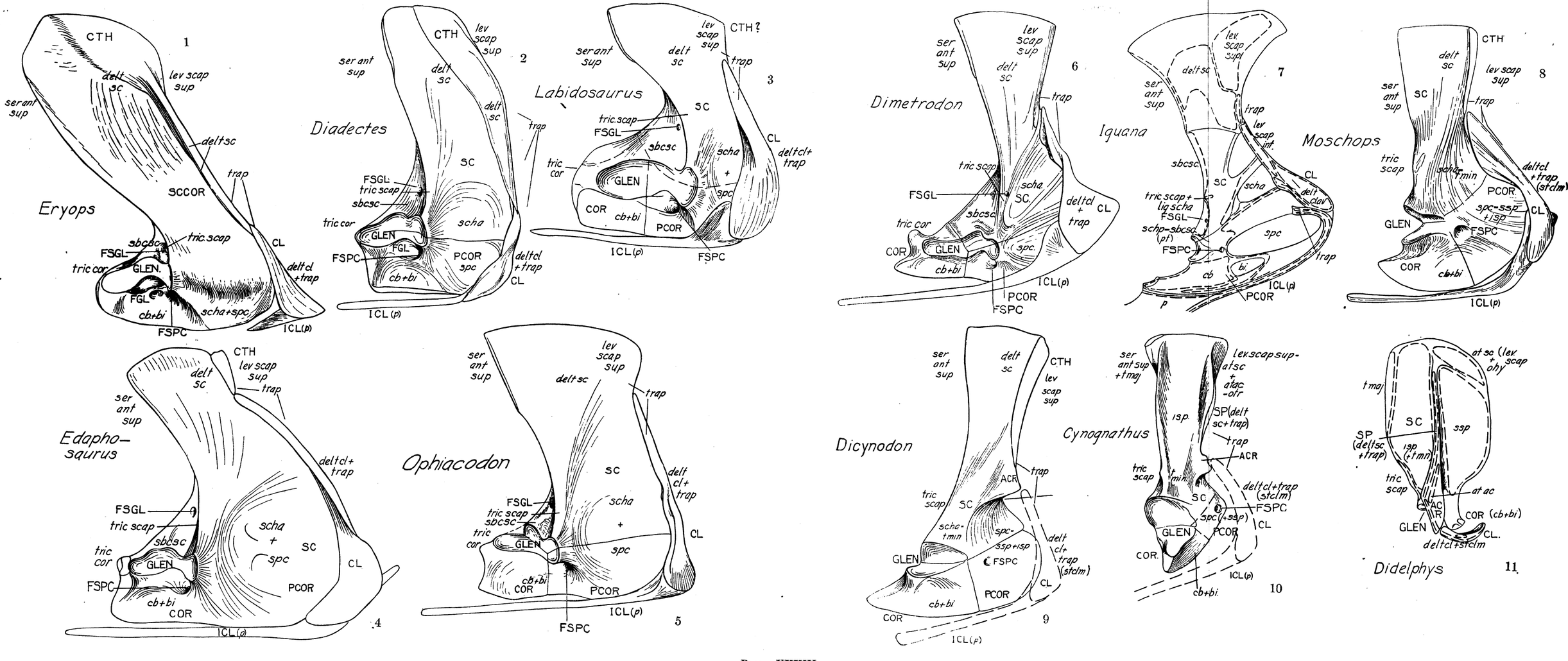
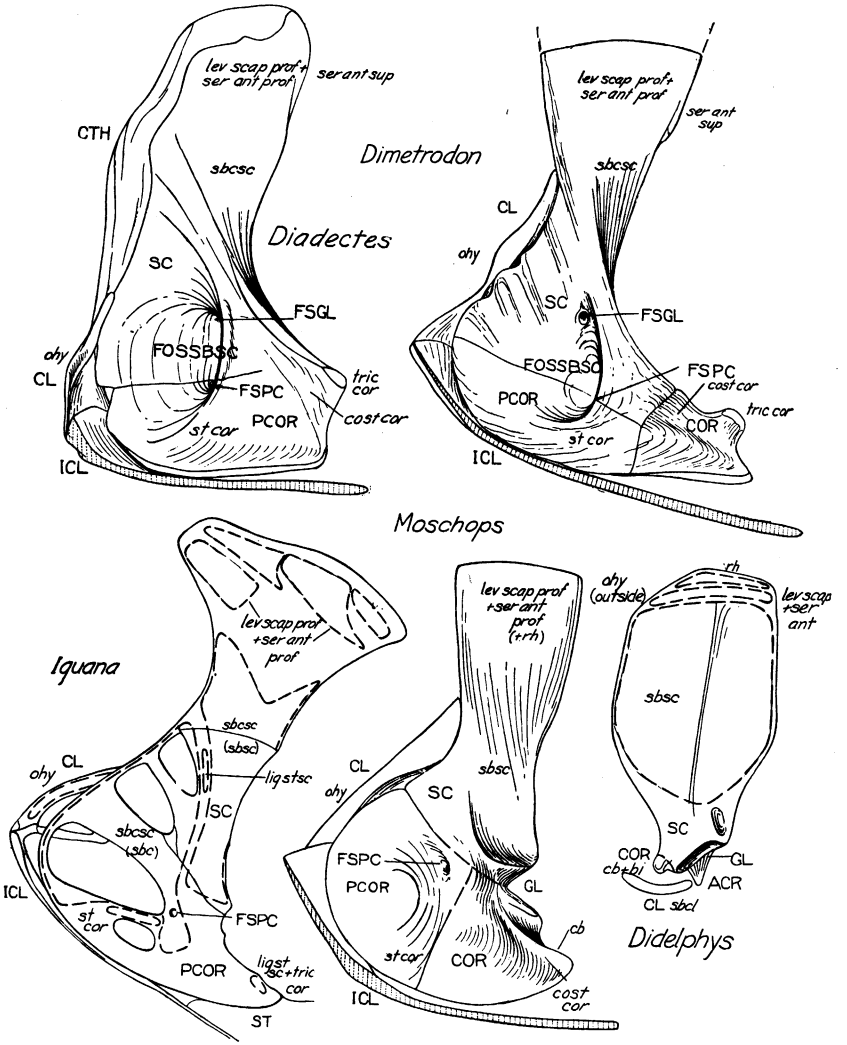


PLATE XXXIII

External view of shoulder girdles of various tetrapods. The reduction of the primitive dermal girdle and the transfer of its musculature to the scapula, and the later spine and acromion is shown. The primitive ventral and anterior position of the deep ventral musculature and its upward movement in the mammalian line is indicated. The relations of the coracoid (except in *Edaphosaurus*), the supraglenoid buttress, the primitive foramina, and the scapular and coracoid heads of the triceps, are shown.



Internal views of the shoulder girdles of types, showing the muscular insertions.

Plate XXXV

Proximal and distal dorsal surfaces of humeri of types. The latero-medial line separates the two dorsal surfaces; in *Moschops* and *Didelphys* the proximal portion of the distal dorsal surface is reduced. The anterior line separating dorsal and ventral surfaces appears far dorsally in *Moschops* and *Didelphys*. The ectepicondylar foramen is present in *Iguana*, but absent in *Moschops*, where the spiral groove represents its old position (see also Plate XXXVII).

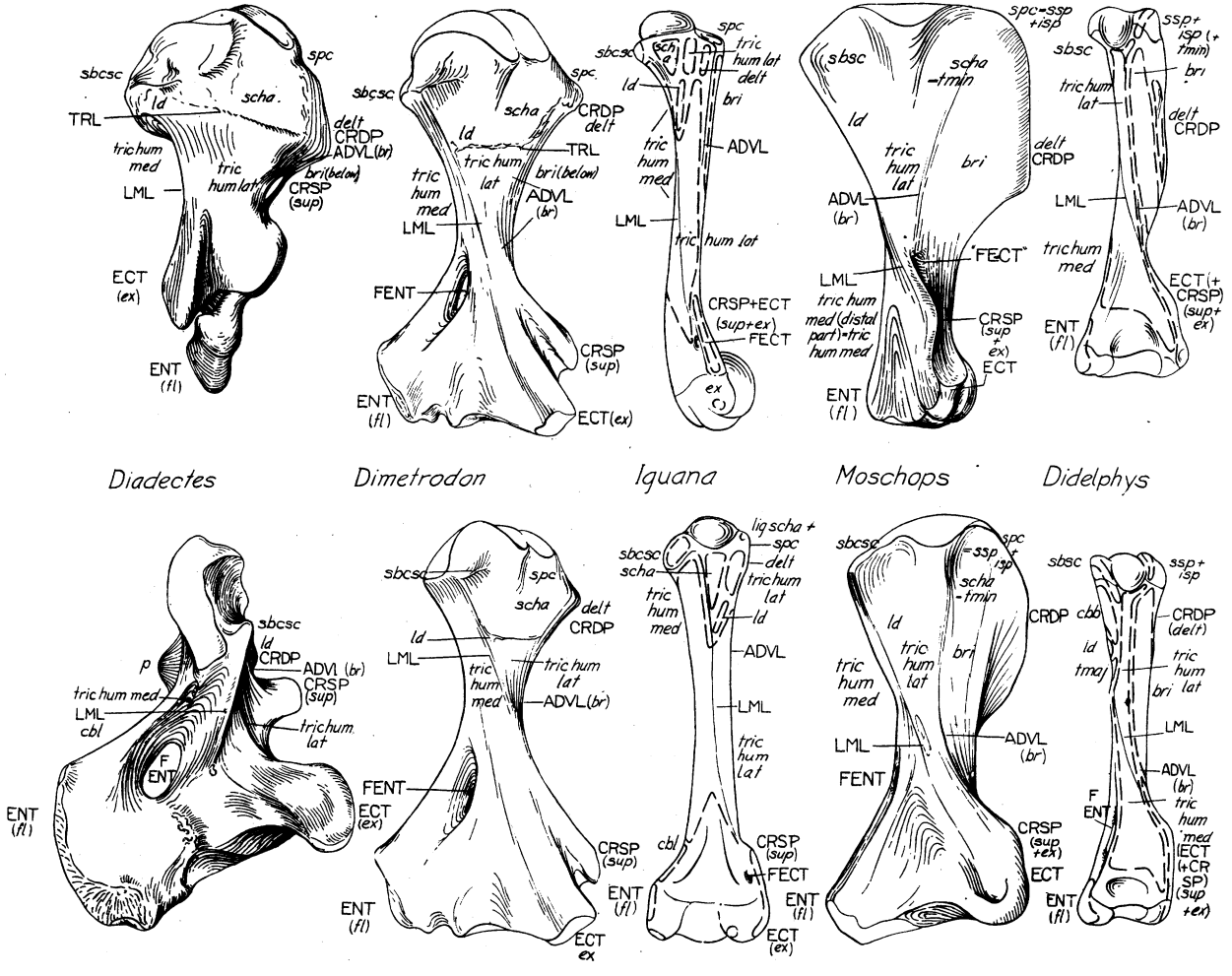

sbcsc
spc
ld
scha
TRL
delt
CRDP
ADVL(br)
tric hum med
tric hum lat
bri(below)
LML
CRSP (sup)
ECT (ex)
ENT (fl)
sbcsc
spc
scha
CRDP delt
ld
TRL
tric hum lat
bri(below)
tric hum med
ADVL (br)
LML
FENT
CRSP (sup)
ENT (fl)
ECT(ex)
sbcsc
sch a
spc
tric hum lat
delt
ld
bri
tric hum med
ADVL
LML
tric hum lat
CRSP+ECT (sup+ex)
FECT
ex
sbsc
scha -tmin
ld
tric hum lat
bri
delt CRDP
ADVL (br)
"FECT"
LML
tric hum med (distal part)=tric hum med
CRSP (sup + ex)
ECT
ENT (fl)
spc-ssp +isp
sbsc
ssp+ isp (+ tmin)
bri
tric hum lat
delt CRDP
LML
ADVL (br)
tric hum med
ECT(+ CRSP) (sup+ ex)
ENT (fl)
Diadectes
Dimetrodon
Iguana
Moschops
Didelphys
sbcsc
ld
CRDP
ADVL (br)
p
CRSP (sup)
tric hum med
LML
cbl
tric hum lat
F
ENT
ENT (fl)
sbcsc
spc
scha
delt CRDP
ld
LML
tric hum med
tric hum lat
ADVL(br)
FENT
ECT (ex)
CRSP (sup)
ENT (fl)
ECT ex
lig scha +
sbcsc
spc
scha
delt
tric hum lat
tric hum med
ld
ADVL
LML
tric hum lat
cbl
CRSP (sup)
FECT
ENT (fl)
ENT (fl)
ECT (ex)
sbcsc
spc + ssp + isp
scha -tmin
ld
tric hum lat
bri
CRDP
tric hum med
LML
FENT
ADVL (br)
CRSP (sup +ex)
ECT
ENT (fl)
sbsc
ssp+ isp
cbb
CRDP (delt)
ld
tmaj
tric hum bri lat
LML
ADVL (br)
F
ENT
tric hum med
ECT (+CR SP) (sup +ex)
ENT (fl)

Plate XXXVI

Proximal and distal ventral surfaces of humeri of types. The coraco-brachialis occupies the proximal surface, the longer portion inserting on the narrow distal ridge as in *Iguana* and many mammals (absent in *Didelphys*). The distal ventral surface is occupied by the brachialis which in the mammalian line (last two figures) extends proximally above the delto-pectoral crest to appear as part of the dorsal surface (compare Plates XXXV and XXXVII).

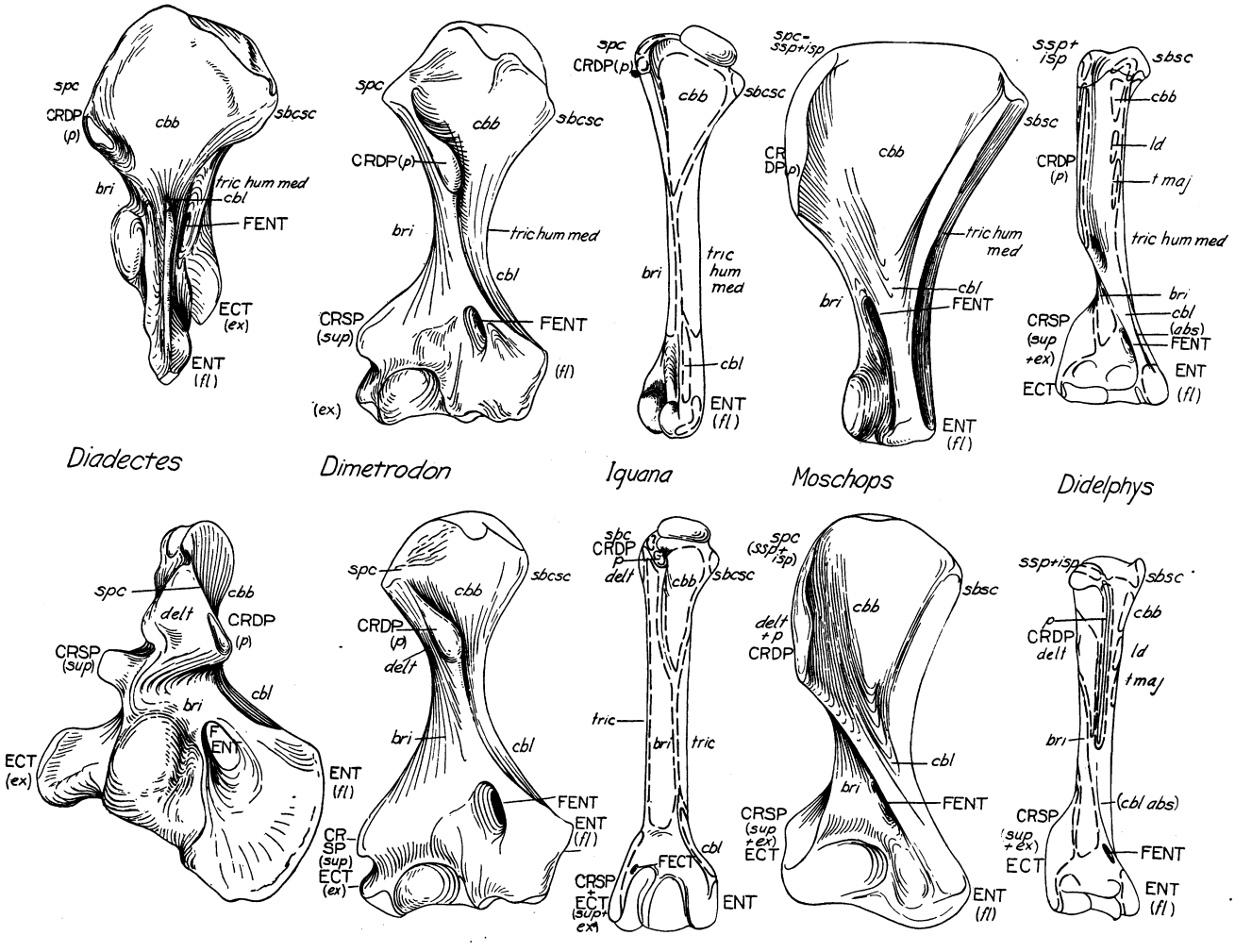
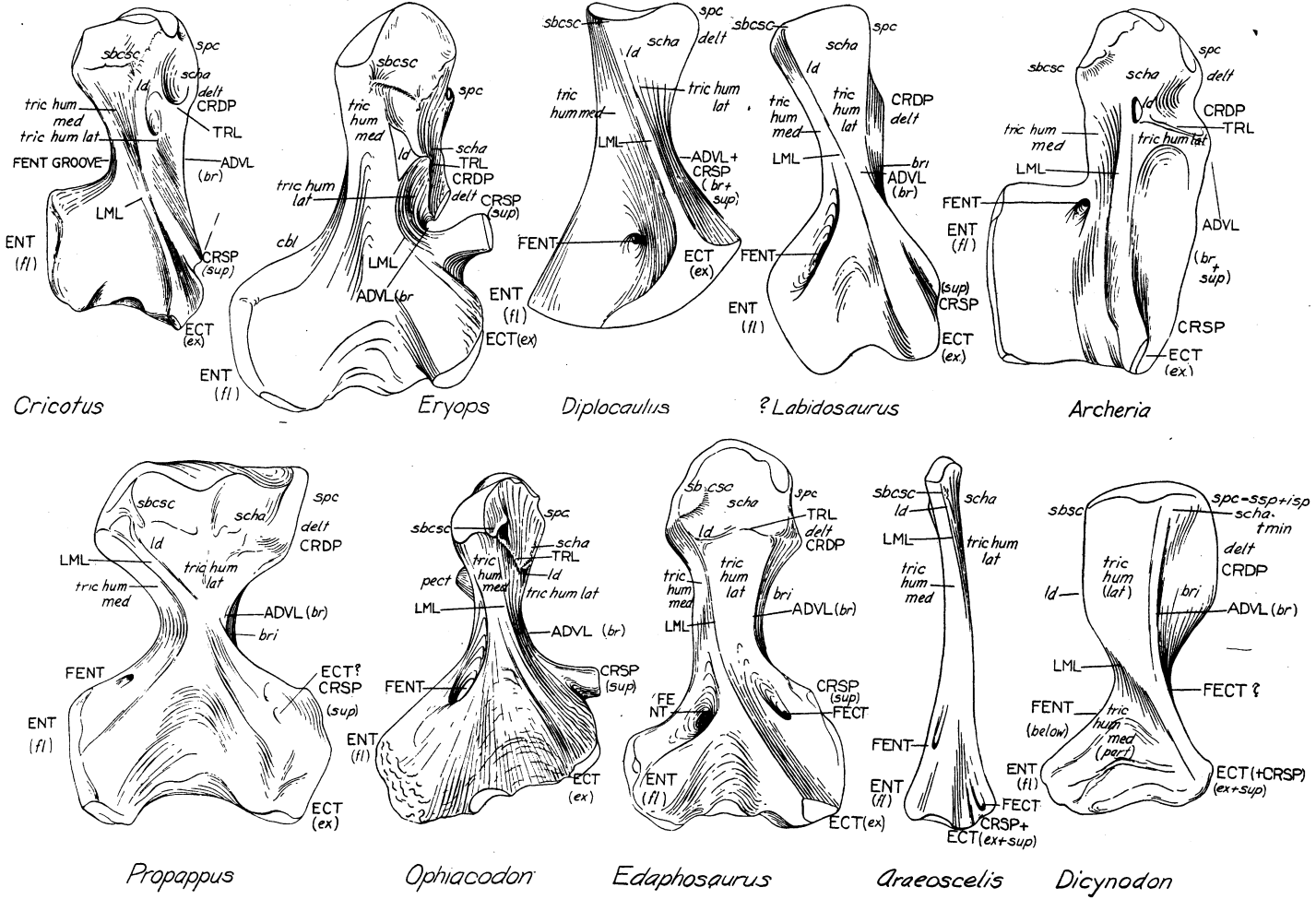
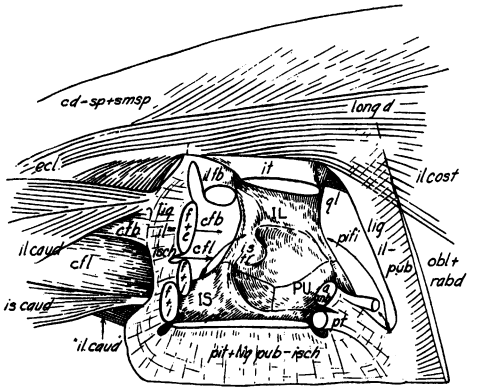

spc
CRDP (p)
cbb
sbcsc
bri
tric hum med
cbl
FENT
ECT (ex)
ENT (fl)
Diadectes
spc
cbb
sbcsc
CRDP(p)
bri
tric hum med
cbl
FENT
CRSP (sup)
(fl)
(ex)
Dimetrodon
spc
CRDP(p)
cbb
sbcsc
bri
tric hum med
cbl
ENT (fl)
Iguana
spc-ssp+isp
sbcsc
CR DP(p)
cbb
bri
tric hum med
cbl
FENT
ENT (fl)
Moschops
ssp+ isp
sbsc
cbb
ld
CRDP (p)
t maj
tric hum med
bri
cbl (abs)
FENT
CRSP (sup +ex)
ENT (fl)
ECT
Didelphys
spc
cbb
delt
CRDP (p)
CRSP (sup)
bri
cbl
ECT (ex)
ENT
ENT (fl)
spc
cbb
sbcsc
CRDP (p)
delt
bri
cbl
FENT
ENT (fl)
CR SP (sup)
ECT (ex)
spc
CRDP p
delt
(cbb)
sbcsc
tric
bri
tric
cbl
FECT
CRSP + ECT (sup+ ex)
ENT
spc (ssp+ isp)
sbsc
cbb
delt + p CRDP
cbl
bri
FENT
CRSP (sup + ex) ECT
ENT (fl)
ssp+isp
sbsc
p
cbb
CRDP delt
ld
t maj
bri
(cbl abs)
CRSP (sup + ex)
FENT
ECT
ENT (fl)

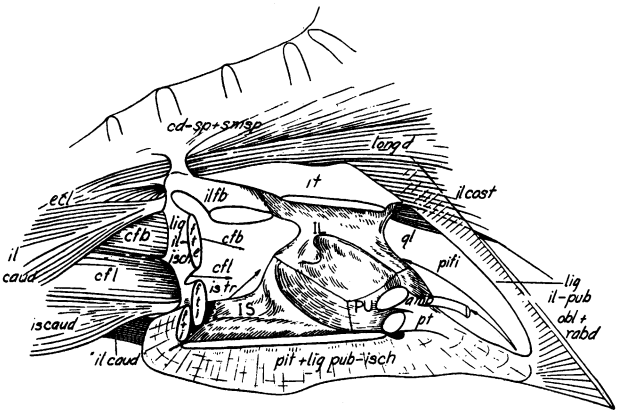
Plate XXXVII

Humeri of various Amphibia and Reptilia, drawn on the plane of the distal dorsal surface (compare with Plate XXXV). The entepicondylar foramen is not present in *Cricotus* and *Eryops*, except as a groove in the former, in the position indicated. It is found in all the other forms shown, although turned ventrally in *Dicynodon*. The shape of the *Propappus* humerus leads to the suggestion that the ectepicondylar foramen was present, although not described. This foramen is formed by the fusion of the supinator crest seen in earlier forms, with the ectepicondyle, and is shown in the last three humeri.

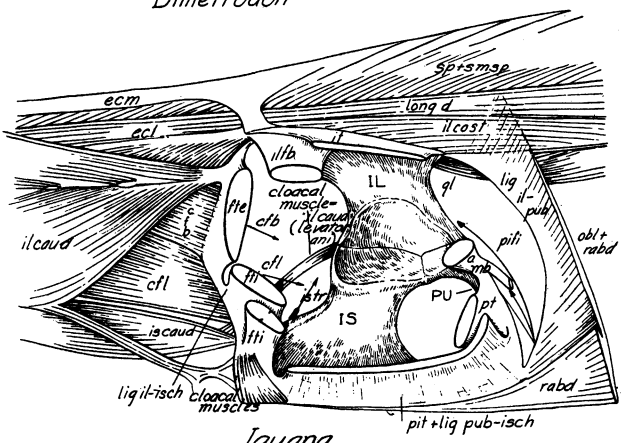

sbcsc
spc
scha
ld
delt
CRDP
TRL
tric hum med
tric hum lat
FENT GROOVE
ADVL (br)
LML
ENT (fl)
CRSP (sup)
ECT (ex)
Cricotus
sbcsc
spc
tric hum med
scha
ld
TRL
CRDP
delt
CRSP (sup)
tric hum lat
cbl
LML
ADVL (br
ENT (fl)
ECT (ex)
Eryops
sbcsc
spc
scha
delt
ld
tric hum med
tric hum lat
LML
ADVL + CRSP (br + sup)
FENT
ECT (ex)
ENT (fl)
Diplocaulus
sbcsc
spc
scha
ld
tric hum lat
CRDP
delt
tric hum med
LML
bri
ADVL (br)
FENT
(sup) CRSP
ENT (fl)
ECT (ex)
? Labidosaurus
sbcsc
spc
scha
delt
ld
CRDP
TRL
tric hum med
tric hum lat
LML
FENT
ENT (fl)
ADVL
(br + sup)
CRSP
ECT (ex)
Archeria
sbcsc
spc
scha
ld
delt
CRDP
LML
tric hum lat
tric hum med
ADVL (br)
bri
FENT
ECT? CRSP (sup)
ENT (fl)
ECT (ex)
Propappus
sbcsc
spc
scha
TRL
ld
tric hum med
pect
tric hum lat
LML
ADVL (br)
CRSP (sup)
FENT
ENT (fl)
ECT (ex)
Ophiacodon
sbcsc
spc
scha
TRL
delt
CRDP
ld
tric hum lat
tric hum med
bri
ADVL (br)
LML
CRSP (sup)
FENT
FECT
ENT (fl)
ECT (ex)
Edaphosaurus
sbcsc
scha
ld
LML
tric hum lat
tric hum med
FENT
ENT (fl)
FECT
CRSP+
ECT (ex+sup)
Araeoscelis
sbsc
spc-ssp+isp
scha-tmin
delt
CRDP
tric hum (lat)
ld
bri
ADVL (br)
LML
FECT ?
FENT (below)
tric hum med (part)
ENT (fl)
ECT (+CRSP) (ex+sup)
Dicynodon



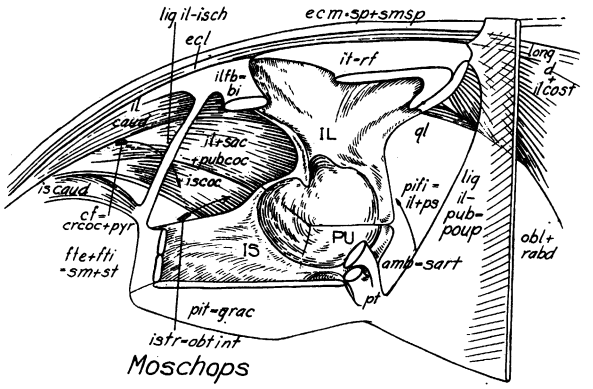
Diadectes



Dimetrodon



Iguana



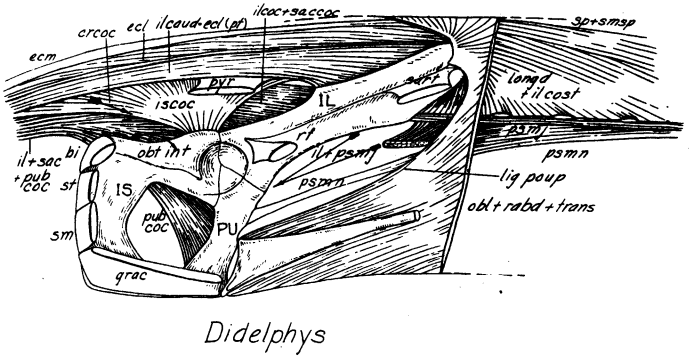


PLATE XXXVIII

Lateral views of the pelvic region of type forms, with the axial musculature and cut ends of the longer appendicular muscles. The system of ligaments from which and under which many of the limb muscles arise are shown (except the sacro-ischiadic ligament of *Didelphys*). The inner system of ventral caudal muscles, the "levator ani" (ilio-, sacro-, pubo- and ischio-coccygeus) is absent in *Iguana*, except for a small slip. This system is restored, similar to the amphibian deep portion of "ilio-caudalis" in *Moschops, Diadectes* and *Dimetrodon*. The ischio-caudalis of reptiles is absent in *Didelphys*.

Plate XXXIX

Superficial dorsal views of the pelvic musculature of types. The triceps (quadriceps and sartorius), ilio-fibularis (biceps) and ilio-femoralis (glutei). The ilio-tibialis (rectus) is cut in the first four figures, and the gluteus maximus and medius in *Didelphys*. The growth of the glutei has pushed the ilio-tibialis forward and ventrally to become the rectus. The ilio-fibularis has migrated down the ilio- (sacro-) ischiadic ligament to become the biceps; the ambiens has migrated up the ilio-pubic ligament to become the sartorius.

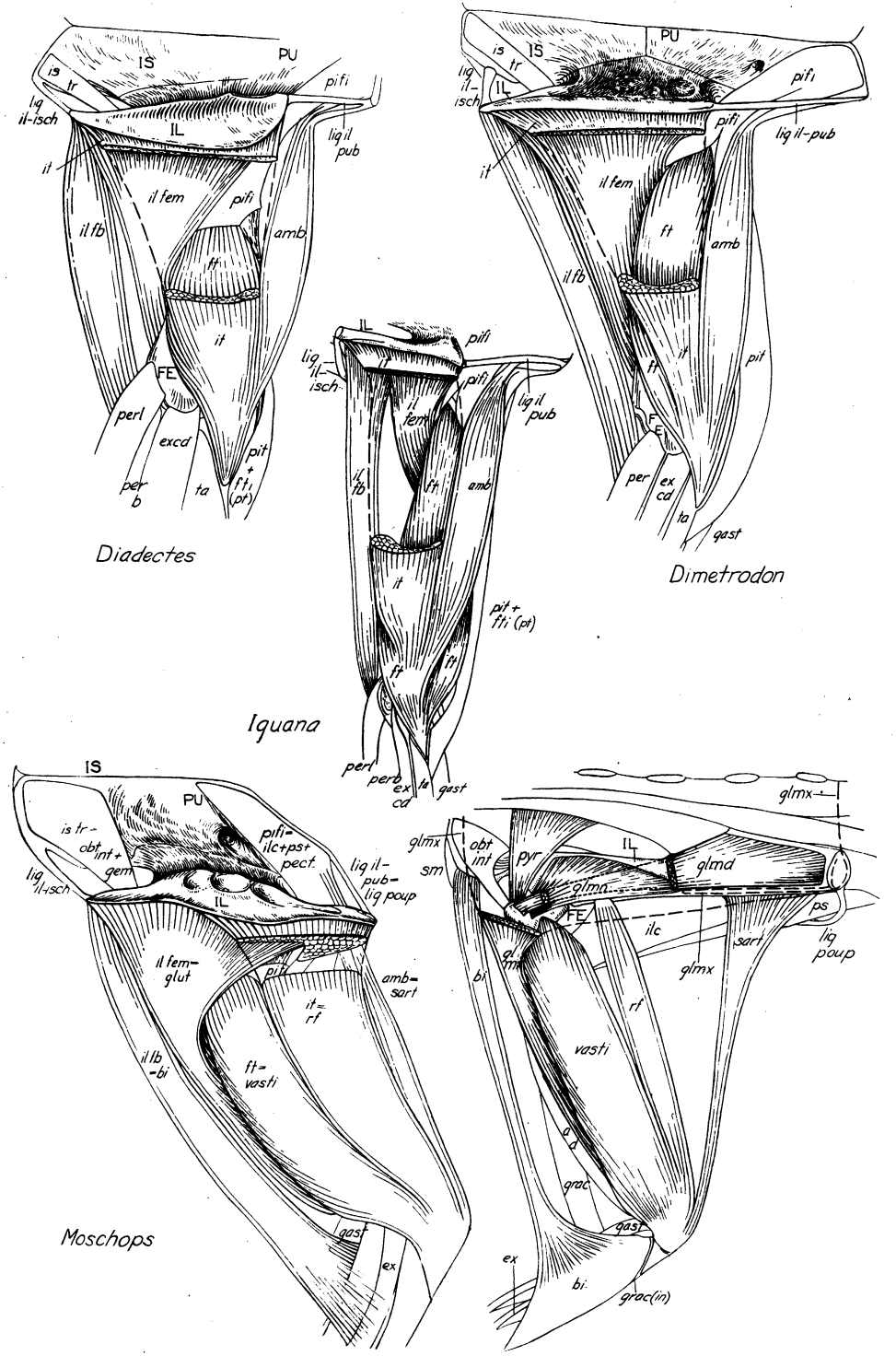
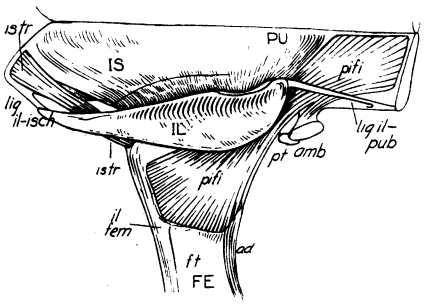
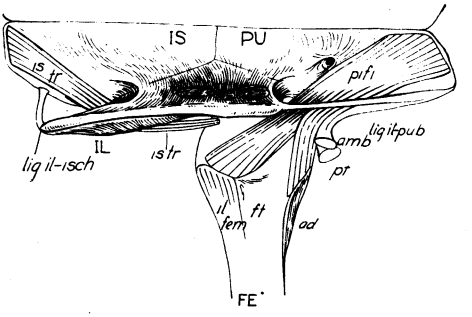

IS
PU
is
tr
pifi
lig il-isch
IL
lig il pub
it
il fem
pifi
il fb
amb
ft
it
FE
perl
excd
pit + ft1 (pt)
per b
ta
Diadectes
IL
pifi
lig il-isch
pifi
il fem
lig il pub
il fb
ft
amb
it
pit + fti (pt)
ft
ft
perl
perb
ex cd
ta
gast
Iguana
PU
IS
is
tr
lig il-isch
IL
pifi
pifi
lig il-pub
it
il fem
ft
amb
il fb
ft
it
pit
FE
per
ex cd
ta
gast
Dimetrodon
IS
PU
is tr
obt int + gem
pifi= ilc+ps+ pect.
lig il-isch
IL
lig il-pub= lig poup
il fem= glut
pit
amb= sart
it= rf
il fb =bi
ft= vasti
gast
ex
Moschops
glmx
glmx
obt int
sm
pyr
IL
glmd
glmn
FE
ps
ilc
sart
lig poup
glmx
bi
rf
vasti
grac
gast
ex
bi
grac(in)

Plate XL

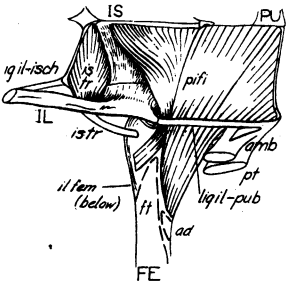
Deep dorsal views of the pelvic musculature of types. The pubo-ischio-femoralis internus and ischio-trochantericus are seen emerging beneath the ligaments. The reduction of the insertion and change of origin in mammals of the pubo-ischio-femoralis internus (ilio-psoas) are shown. (The pectineus, part of the latter, is shown in a ventral view.)



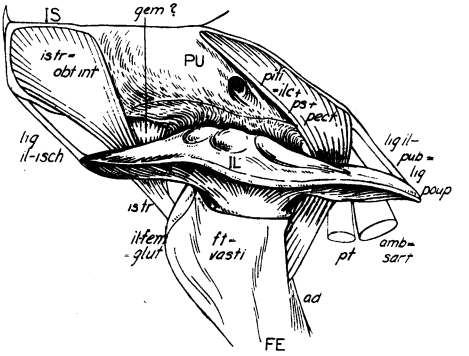
Diadectes



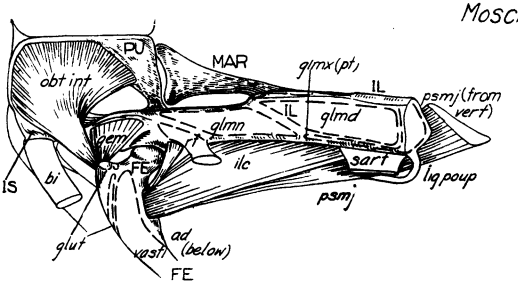
Dimetrodon



Iguana



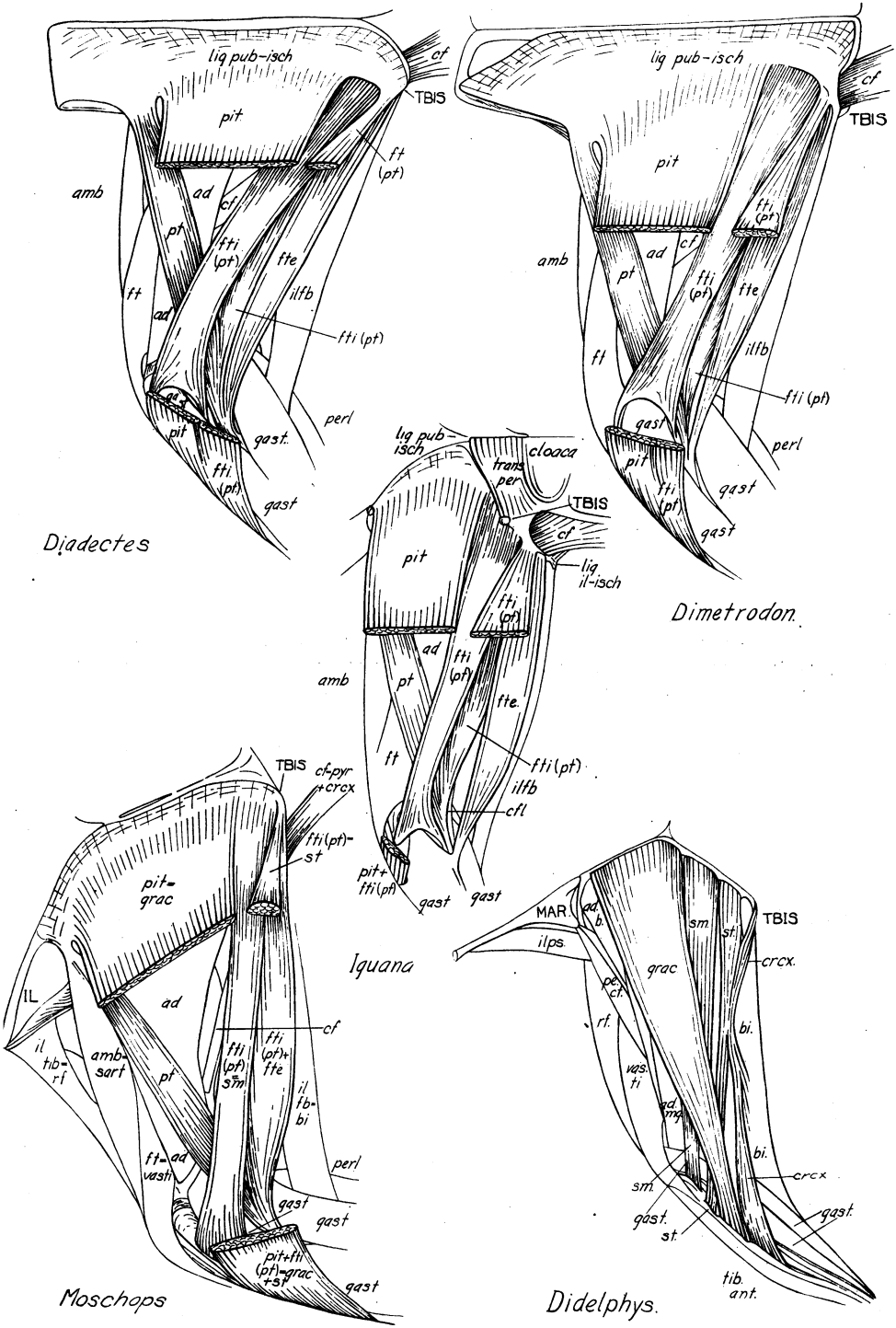
Moschops



Didelphys

PLATE XLI

Superficial ventral views of the pelvic musculature of types. The long ventral muscles are shown (a portion of them is cut to expose the deeper layers). It is impossible to determine the number of slips in the extinct forms; they have been restored by comparison with lizards and *Sphenodon*. Note that the mammalian representatives of this group are merely those portions which insert internally on the tibia, as contrasted with the large reptilian mass inserting between the two heads of the gastrocnemius.


lig pub-isch
cf
TBIS
pit
ft (pt)
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fti (pt)
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fti (pt)
perl
gast
Diadectes
lig pub-isch
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TBIS
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pt
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ilfb
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Dimetrodon
lig pub-isch
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TBIS
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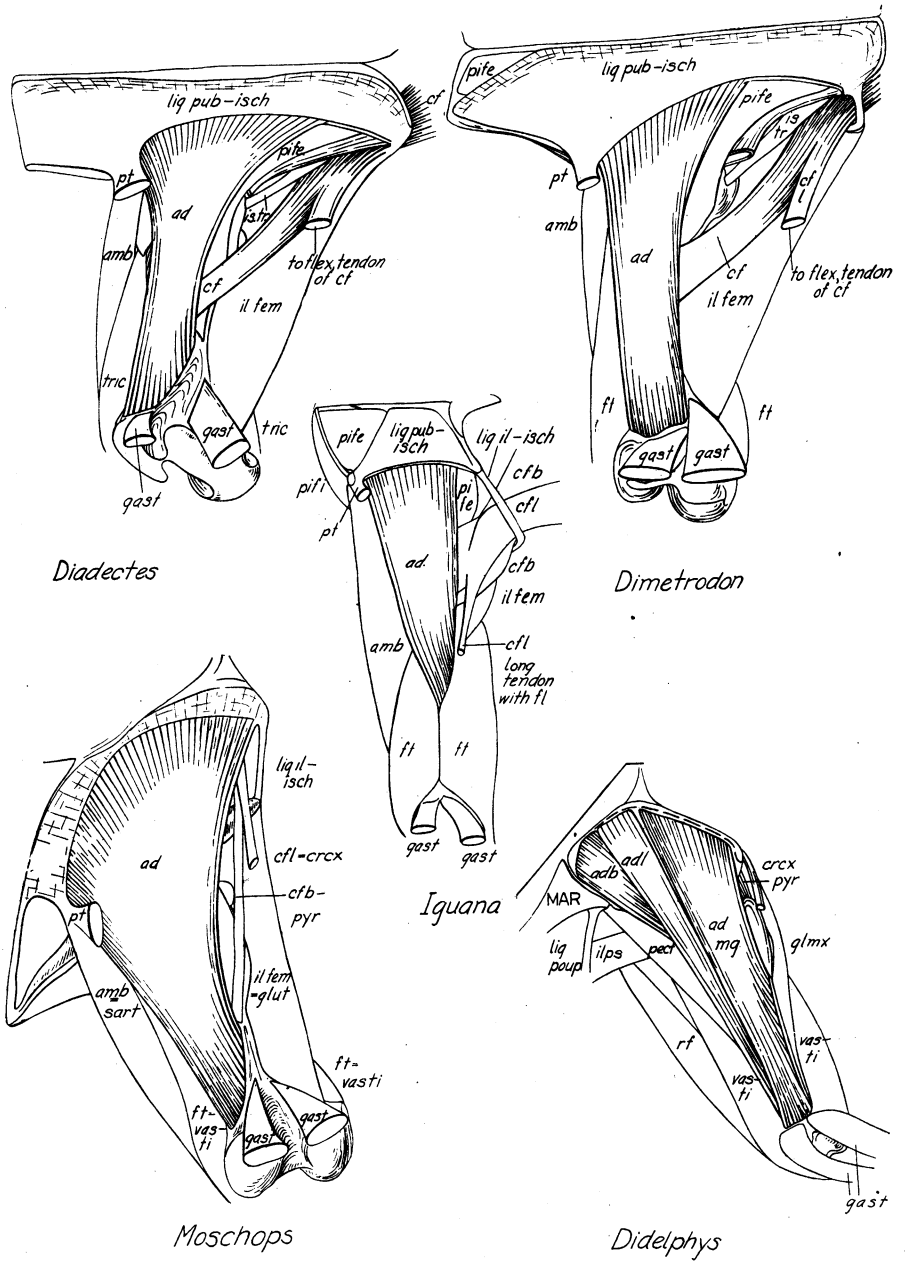
lig il-isch
pit
fti (pt)
amb
ad
fti (pf)
pt
fte
ft
fti (pt)
ilfb
cfl
pit+ fti (pf)
gast
gast
Iguana
TBIS
cf-pyr +crcx
fti (pt)- st
pit- grac
IL
ad
cf
il tib- rf
amb- sart
pt
fti (pf) sm
fti (pt)+ fte
il fb- bi
ft- ad vast
perl
gast
gast
pit+fti (pf)-grac +st
gast
Moschops
MAR
ad b
ilps
sm
st
TBIS
crcx
grac
pe cf
rf
bi
vas ti
ad mp
bi
crcx
sm
gast
st
gast
tib ant
Didelphys

Plate XLII

Ventral views (long flexors removed) of the pelvic musculature of types. The primitive adductor mass and its relations with neighboring muscles. In both this and the preceding plate the coccygeo-femorales are seen in part.



Diadectes

Dimetrodon

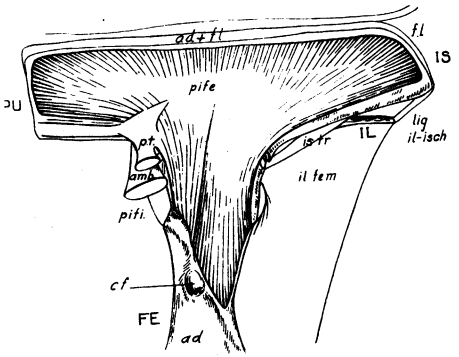
Iguana

Moschops

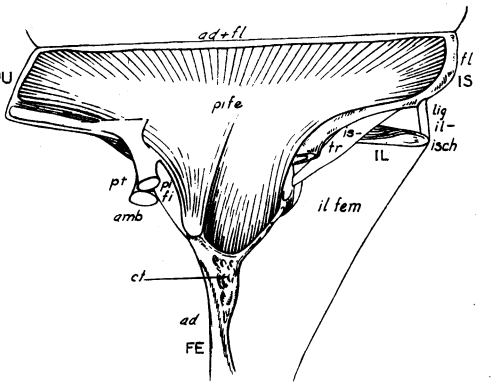
Didelphys

Plate XLIII

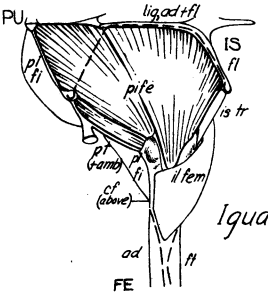
Deep ventral views of the pelvic musculature of types. The pubo-ischio-femoralis externus and its derivatives, the obturator externus and quadratus femoris. (The pectineus of *Didelphys* belongs to the dorsal series, with pubo-ischio-femoralis internus.)



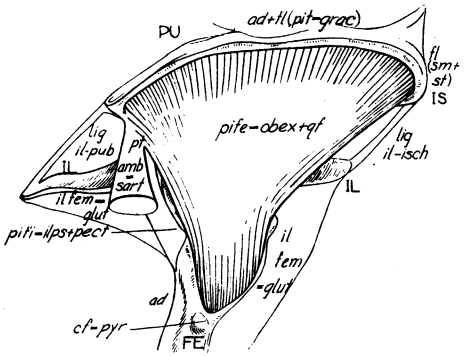
Diadectes



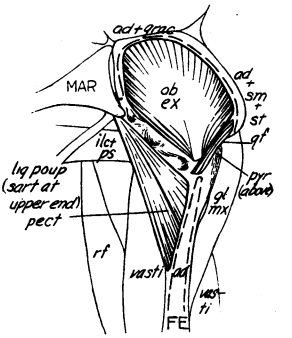
Dimetrodon



Iguana



Moschops



Didelphys

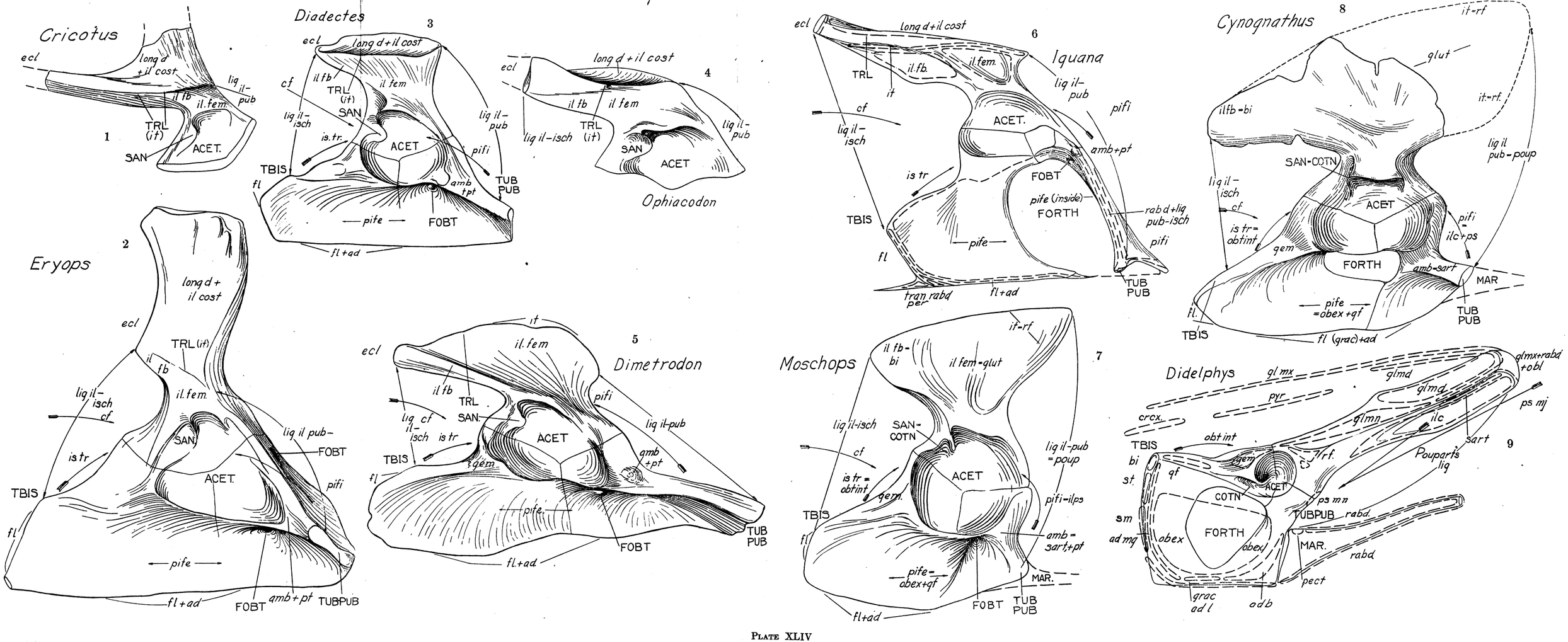


PLATE XLIV

External views of the pelves of various tetrapods. The ligaments, except the sacro-ischiadic of mammals, are indicated by arrows. Short arrows show the emergence of internal and caudal muscles beneath the ligaments. The transverse line of *Cricotus* and *Eryops* is seen to become the dorsal edge of the ilium of *Dimetrodon* and later forms. The anterior expansion of the ilium in the therapsid-mammal series is indicated (the dotted lines above the *Didelphys* ilium indicate muscles which have transferred their origin to the back fascia and vertebræ).

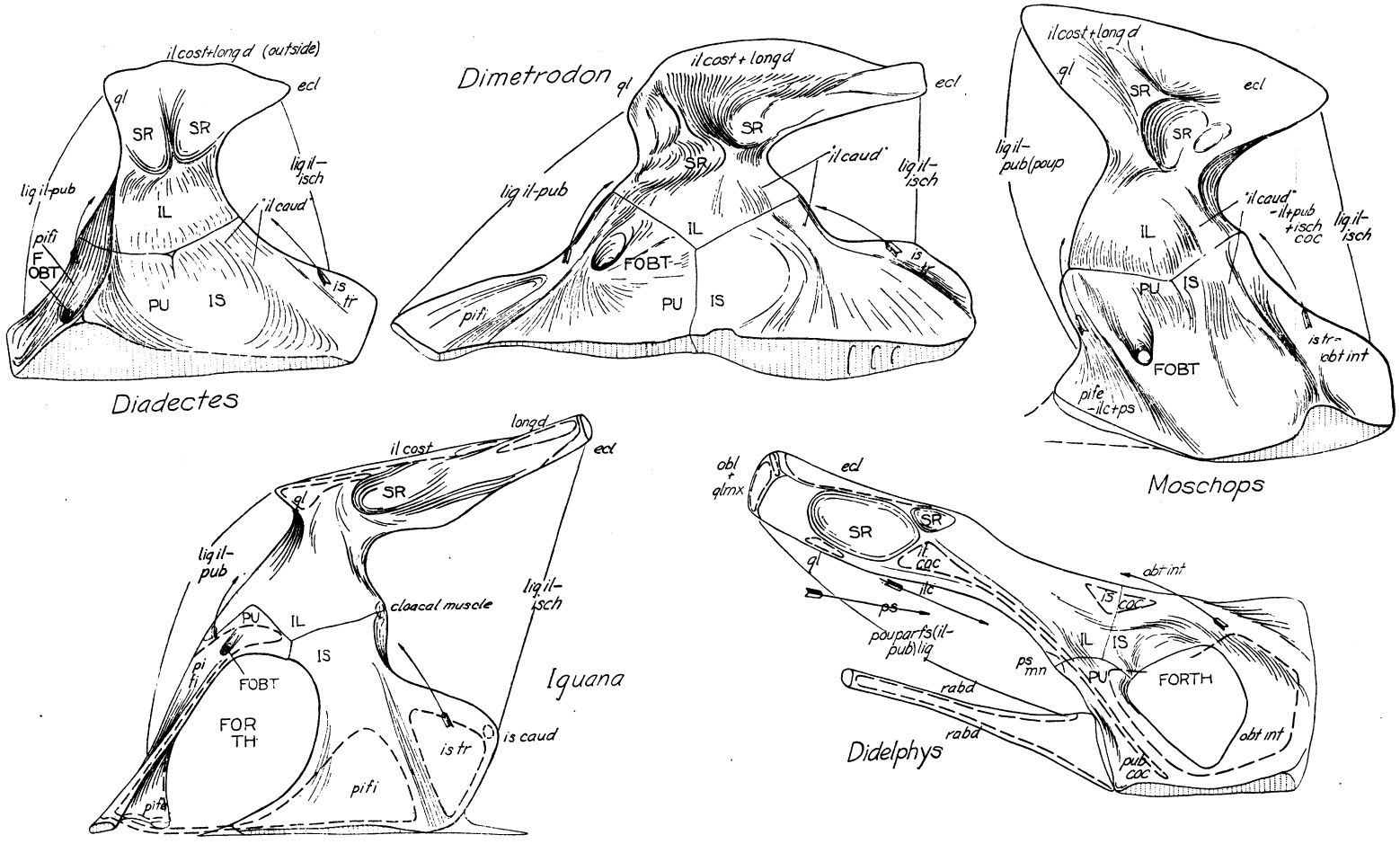


PLATE XLV

Internal views of the pelvic girdles of types. The surfaces for pubo-ischio-femoralis internus anteriorly and ischio-trochantericus posteriorly are primitively well-marked, and their courses out beneath the ilio-pubic and ilio- (sacro-) ischiadic ligaments are represented by short arrows. The former muscle has spread inside the girdle in *Iguana*, the latter (obturator internus) in *Didelphys*. The ilio-psoas (pubo-ischio-femoralis internus) has abandoned its original area of origin in mammals. The ridge anterior to the ischio-trochantericus probably represents the insertion of the deep portion of the ilio-caudalis, lost except as a cloacal muscle in reptiles and represented by the ilio-sacro-pubo-ischio-coccygeus of mammals (levator ani).

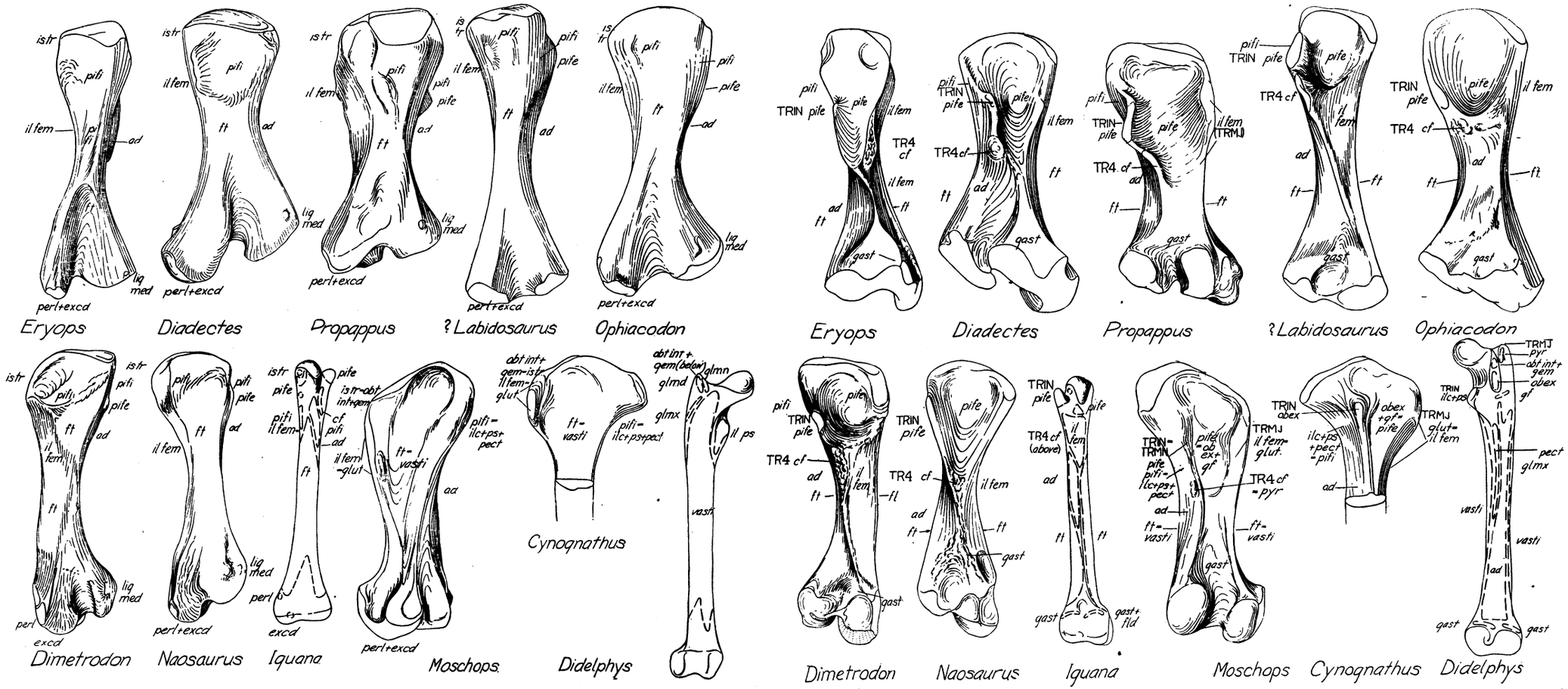


PLATE XLVI

Femora of various tetrapods, dorsal views at left, ventral views at right. The dorsal surface is primitively occupied by the pubo-ischio-femoralis internus, this being limited to the proximal portion by the growth of the femoro-tibialis, seen distally in *Eryops*. The ilio-femoralis is found posteriorly, the adductors anteriorly. The growth of the greater trochanter, associated with the former muscle (=the gluteals) is seen in the last three femora. Ventrally the primitive system of ridges is especially well seen in *Eryops* and *Edaphosaurus*. The transformation to the reptilian and mammalian trochanters is illustrated (compare figure 6).