THE PECTORAL LIMB OF SMALL CAPTORHINIDS

THE OSTEOLOGY AND MUSCULATURE OF THE PECTORAL LIMB OF SMALL CAPTORHINIDS

by

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TO THE READER

This thesis has been written and organized according to the style and format of the Journal of Paleontology.

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ABSTRACT

The osteology of the pectoral limb of small captorhinids is described and figured in detail. A cartilaginous sternum was present. The function of the glenoid is analyzed. It is not a simple, sliding or rocking joint, as was previously supposed, but considerable rotation was also an integral part of humeral movement. The structure of the elbow joint is such that when the lower arm is extended, its distal end swung forward and extended the anterior reach of the hand. When the lower arm was flexed, the posterior reach of the hand was extended. Articulated specimens allow a recontruction of the manus. There is no well developed wrist joint, but rather the manus, as a whole, was a flexible structure. A pisiform is present. Sesamoid bones were developed in the tendons of the palmaris communis profundis muscle.

A comparative study of forelimb musculature of living reptiles based on dissections and on a survey of the literature indicates that the evolution of this musculature has been very conservative. The forelimb musculature of small captorhinids is very similar to that of all living reptiles except turtles.

L'OSTEOLOGIE ET LA MUSCULATURE DU MEMBRE ANTERIEUR DE PETIT CAPTORHINIDES

EXTRAIT

L'osteologie du membre anterieur des petits captorhinidés est decrite et representée en detail. Un sternum de cartilage était present. La fonction de l'articulation glénoïde est analysée. La surface articulante de l'humerus ne coulisse ou n'oscille pas seulement comme l'avait été supposé auparavant mais une grande proportion de la rotation faisait partie intégrale du mouvement de l'humerus. La construction de l'articulation de l'épaule est telle que l'extension de l'avant bras produit aussi une rotation vers l'avant de la main. Quand l'avant bras est tendu, la main est poussée vers l'arrière. Le produit combiné de ces deux facteurs permet un plus grand pas. Les specimens articulés permettent une reconstruction de la main. L'articulation du poignet n'est pas bien developpée, mais dans l'ensemble la main est une structure flexible. Une pisiforme est presente. Des os sesamoïdes sont presents dans les tendons du muscle palmaris communis profundis.

Une étude comparée de la musculature de l'avant bras des reptiles modernes basée sur des dissections et des recherches littéraires permet de conclure que l'évolution de cette musculature a été très restreinte. La musculature de l'avant bras des petits captorhinidés est très similaire à celle de tous les reptiles vivants à l'exception des tortues

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INTRODUCTION

Although numerous papers have been written on the comparative myology of lower tetrapods, few have dealt with the reconstruction of the musculature of extinct forms. Watson (1917) was among the first to discuss the shoulder muscles of Permian reptiles. Of particular significance was Romer's detailed, systematic attempt to reconstruct the appendicular musculature of primitive and mammal-like reptiles (1922). Diadectes, a large and rather specialized anapsid reptile was used by Romer as a basis for this reconstruction, presumably because it was one of the few primitive reptiles of which good postcranial material was available. The taxonomic position of Diadectes is presently in dispute, but it seems quite certain that the animal is far from primitive in many regards.

Compared with the great volume of material written on the pelvic limb of extinct, lower tetrapods, relatively few papers have considered the pectoral limb in these forms, presumably because the pectoral limb does not display the radical evolutionary changes between primitive and advanced forms which characterize the pelvic limb. Miner (1925) made a comparative study of the anterior limb of the urodele Megalobatrachus and Sphenodon, and used this information to reconstruct the musculature of the extinct temnospondyl Eryops.

Howell (1936) made a comparative study of reptile musculature and its bearing on the musculature of primitive, extinct reptiles. Haines (1939) reviewed the extensor musculature of the forearm of tetrapods, and attempted a reconstruction of these muscles of the pelycosaur Ophiacodon. Romer (1942, 1944) studied the embryological development of the limbs of Lacerta as a means of clarifying some of the problems related to the evolution of reptilian appendicular muscles.

Since those papers were written, our knowledge of primitive reptiles has increased immensely. The Family Romeriidae is now recognized as having included the ancestors of all later reptiles (Carroll 1964, Carroll and Baird 1972, Clark and Carroll 1973), and a detailed study of their appendicular musculature would contribute much to an understanding of the primitive pattern of locomotion in reptiles. Unfortunately, preservation of the postcranial elements is generally not good enough nor is ossification sufficiently complete in these small reptiles to allow such a study. The Family Captorhinidae evolved directly from the romeriid stock. Captorhinids are not directly ancestral to either diapsids or synapsids, but may be close to the ancestry of turtles. The earliest members of this group are only slightly larger than their romeriid ancestors, and their appendicular skeleton is very similar. Because of the unusually good preservation of skeletal elements of captorhinids, especially of specimens from the Lower Permian locality at Fort Sill, Oklahoma, muscle scars are easily visible. Muscles with restricted attachment areas or that attach by tendons can be readily reconstructed on this basis. Some muscles, however, have broad, fleshy attachments,

and leave little evidence of their former attachment on the bone surface. Reconstruction of these muscles is facilitated by knowledge of the positions of those for which there is direct evidence. The excellent state of preservation of this material, as well as its phylogenetic significance, indicates the value of an attempt to reconstruct the appendicular musculature in its entirety.

Study of the musculature of living reptiles of such divergent types as Sphenodon (Miner 1925), Iguana (Romer 1944), Pseudemys (Walker 1973), and crocodiles (Fürbringer 1876) shows many common features, suggesting a similar pattern for primitive reptiles as well. On the basis of this literature and dissections of preserved material, the musculature of the pectoral girdle and limb of small captorhinids has been reconstructed. Work is continuing on the musculature of the pelvic girdle and rear limb. This will be considered in a subsequent publication.

Reconstruction of the musculature of primitive reptiles requires that their osteology be very well known. Captorhinus has been discussed by many authors, most recently by Fox and Bowman (1966). They considered probable attachment areas of the major muscle masses of this animal, but unfortunately no relevant diagrams of detailed comparisons with living forms were provided. Published figures are not generally sufficiently detailed to be used for anything but the most generalized reconstruction of the musculature. Consequently, most skeletal elements have been redrawn for this study, using specimens that show most clearly the evidence for muscle attachment.

In this study of the appendicular musculature of captorhinids, I have confined myself to the smaller members of the group. The smaller genera are generally more primitive than the larger, later members of the family, and therefore should show a muscular architecture closer to the romeriid pattern. The smaller forms are also much better preserved and easier to prepare than the larger animals. Much of the material is from Fort Sill, where the matrix may be removed by washing with water, allowing complete exposure of the bone surface so that even very small muscle scars are readily visible.

Although the state of preservation of isolated elements at Fort Sill is excellent, the disarticulated condition of most of the remains makes the reconstruction of structural units such as the carpus or shoulder girdle difficult due to the presence of a large number of individuals of various sizes. These reconstructions have been aided by the use of several specimens of a second captorhinid genus, discussed below, that is slightly older and probably directly ancestral to Captorhinus, from the Lower Permian McCann Quarry of Oklahoma. This material is well articulated and generally in an excellent state of preservation. The nature of these specimens allows a more accurate determination of the relative size and proportions of the elements of the appendicular skeleton than has been possible in the past.

Seltin (1959) and Fox and Bowman (1966), who have previously described members of the Family Captorhinidae, were of the opinion that most specimens from the Upper Wichita (Clyde Formation) and

and Lower Clear Fork (Arroyo Formation) belonged to a single species, Captorhinus aguti, characterized by multiple tooth rows. The majority of the specimens from the Clyde Formation in Texas or beds of equivalent age in Oklahoma belong to an antecedent form possessing only a single tooth row. These forms were mentioned briefly by Clark and Carroll (1972). A detailed study of the genus is now being completed by Heaton (personal communication). Despite the significant differences in dentition, the skulls of the two forms are otherwise almost indistinguishable, and no differences in the postcranial skeleton have been detected. A common pattern of musculature can therefore be assumed, and so there is no reason to differentiate them in this study.

The following abbreviations will be used to denote the location of each specimen:

AMNH	American Museum of Natural History
FMNH	Field Museum of Natural History (Chicago)
KU	Museum of Natural History of the University of Kansas
MCZ	Museum of Comparative Zoology of Harvard University
OUSM	Oklahoma University Stovall Museum

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THE OSTEOLOGY OF THE PECTORAL LIMB OF SMALL CAPTORHINIDS

The pectoral girdle in small captorhinids, as in all primitive reptiles, consists of both dermal and endochondral elements. In the dermal girdle, the interclavicle (fig. 1 and 2) is a delicate structure, and has almost always been broken either during preservation or preparation. The head is roughly diamond shaped, with a thickened central portion. The edges are thin and fragile, especially in the anterior region. Recesses on the ventral surface of this border indicate the area of articulation with the clavicles. The central part of the ventral surface is sculptured with a pattern of fine, radiating grooves. The dorsal surface of the interclavicle is marked with a series of irregular, interconnecting channels suggesting the impressions of blood vessels, adhering close to the bone surface.

On the dorsal surface of the posterior one-third of the stem are two prominant, slot-like grooves. These give evidence for the presence of a cartilagenous sternum. The stem of the interclavicle apparently passed ventral to the sternum, with the sternum fitting into these slots, much as it does in the modern lizard genus, Iguana. The ventral plate of the clavicle (fig. 3 and 4) articulates with the broad, thin expanse of bone lying anterior to the central, thickened portion of the head of the interclavicle, and its irregular medial border interdigitates with the medial border of the opposite clavicle at the midline. A prominant posterior process of the

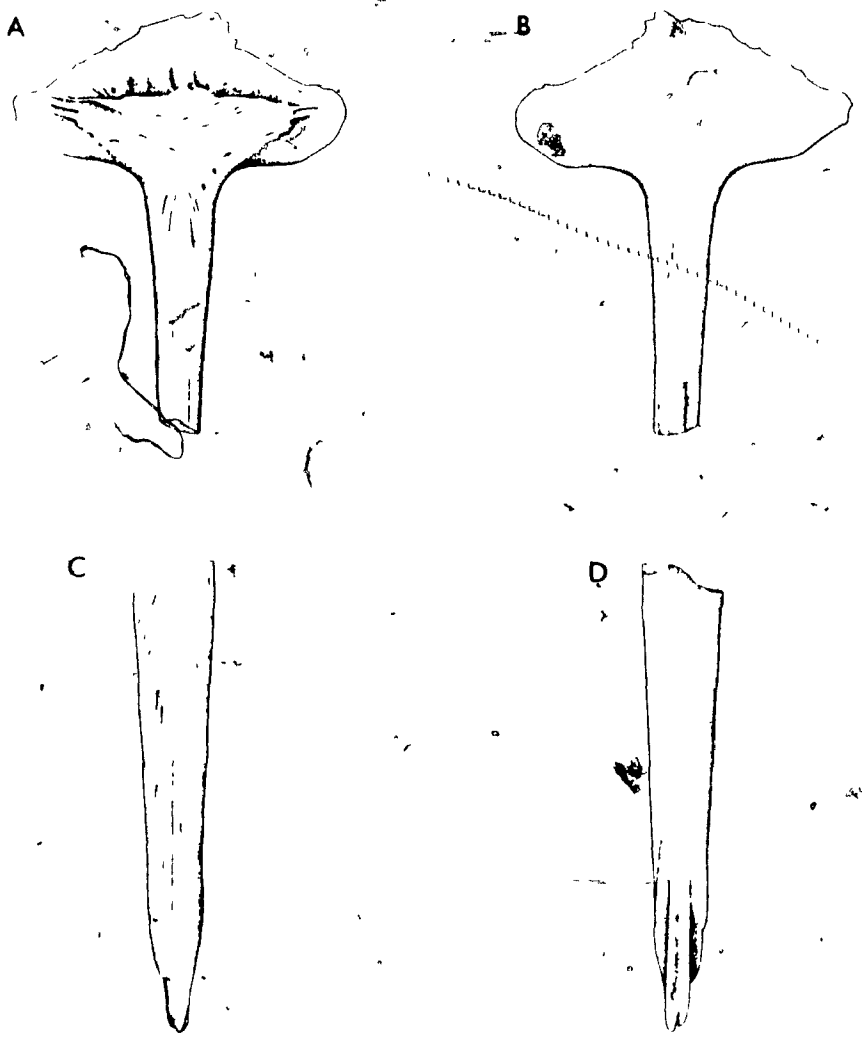


Fig. 1 Interclavicle of Captorhinus aguti (Cope). A, Ventral view of anterior portion, KU FEP 60c. B, Dorsal view of A. C, Ventral view of stem, KU FEP 60c. D, Dorsal view of C. Both specimens X3.

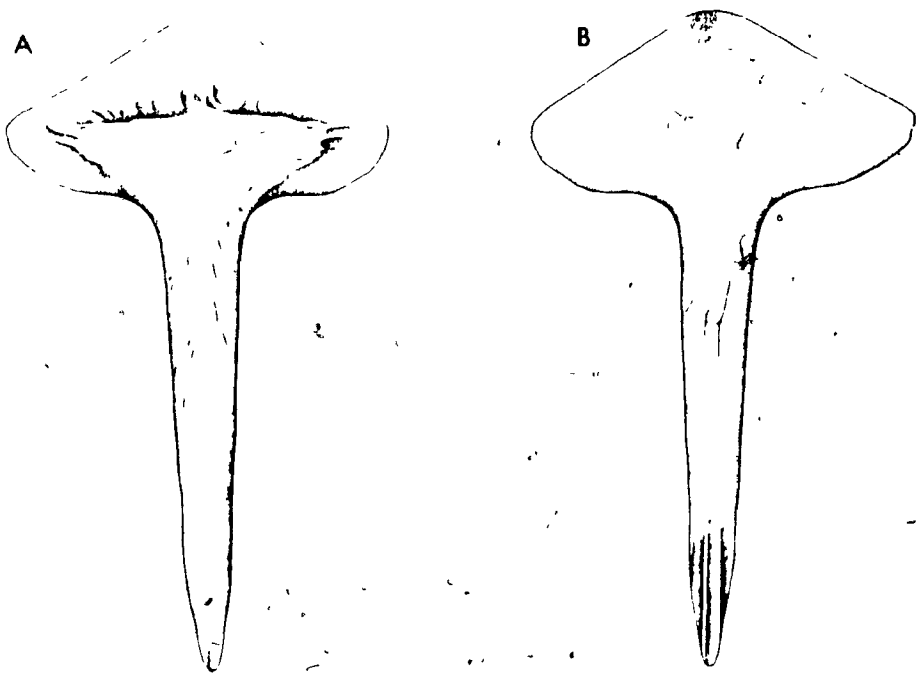


Fig. 2 Reconstruction of the interclavicle of Captorhinus aguti (Cope). A, Ventral view. B, Dorsal view. X3.

Fig. 3 Shoulder girdle of single tooth rowed captorhinid, OUSM 15020 B, ventral view. X2.

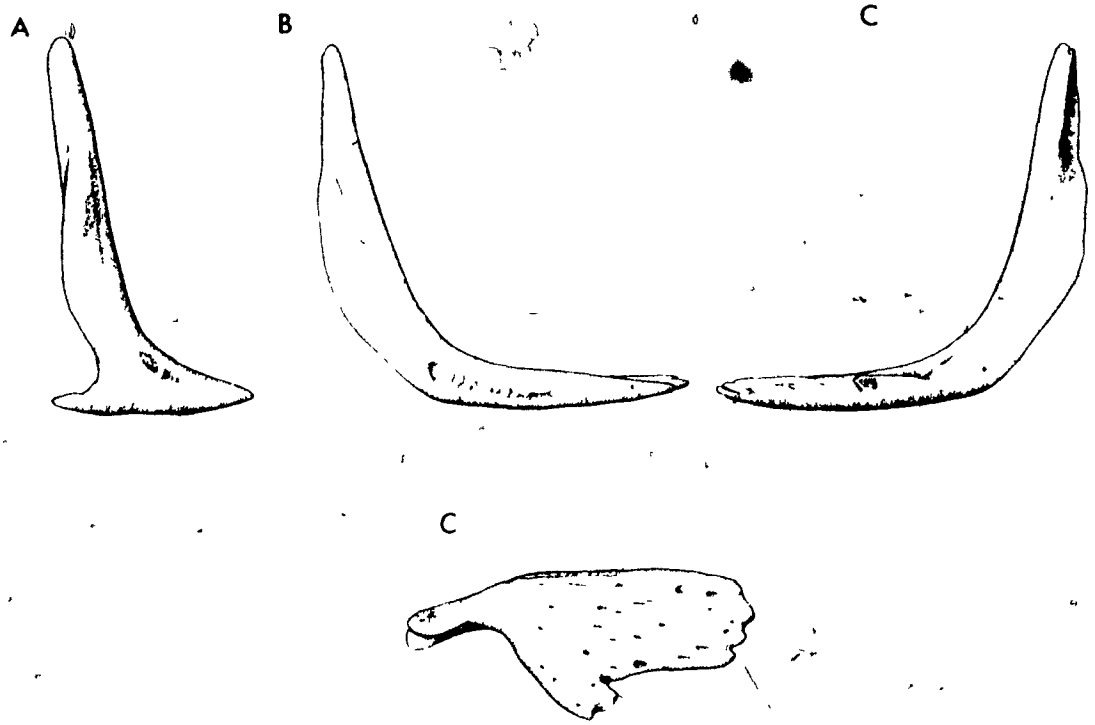


Fig. 4 Right clavicle of Captorhinus aguti (Cope) AMNH 2463. A, Lateral view. B, Anterior view. C, Posterior view. D, Ventral view. X3.

ventral plate diverges from the main part of the structure and articulates with an accessory articular surface located in the postero-lateral part of the diamond shaped head of the interclavicle, much the same as figured for Labidosaurus (Williston 1917, fig. 6). A small, round depression of the anterior surface of the clavicle in the region of the angle between the stem and ventral plate is present in all specimens examined, but its function could not be determined.

A cleithrum could not be indentified in any of the captorhinids examined. However, this element has been recognized among the remains of most Paleozoic reptiles, and its presence in captorhinids is likely, since they are direct derivatives of the primitive romeriid stock. As pointed out by Romer and Price (1940) the cleithrum was probably present in all pelycosaurs, but the bone was small, and lost in the majority of specimens. Its apparent absence in captorhinids indicates that it was probably reduced to a small splint of bone, loosely attached to the anterior border of the scapula above the dorsal stem of the clavicle.

Many fragmentary scapulocoracoids of captorhinids have been discovered at the Fort Sill locality, but complete specimens are rare. An essentially complete specimen, MCZ 4345 from Fort Sill is figured here (fig. 5). It has been compressed laterally during preservation, and consequently the angle made by the scapular blade on the coracoid plate is considerably greater than it would have been on an undistorted specimen. The region anterior to the glenoid

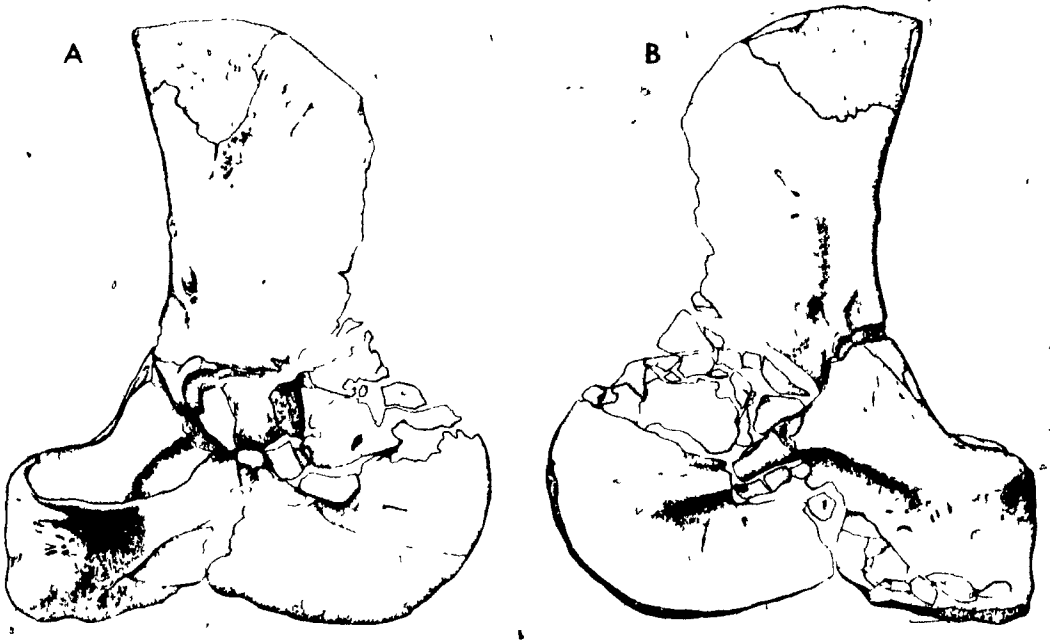


Fig. 5 Right scapulocoracoid of Captorhinus aguti (Cope), MCZ 4345. A, Lateral view. B, Medial view. X3.

is crushed and fragmented, and a large crack runs from above the glenoid ventrally through the coracoid plate at the level of the supracoracoid foramen. Sutures dividing the three elements of the scapulocoracoid are not visible on this specimen, although they are often apparent in immature specimens (fig. 6).

A partial scapulocoracoid, KU FEP 60c (fig. 7) with most of the scapular blade missing provides many details that were obliterated in MCZ 4345. The information provided by these two specimens allows a complete reconstruction of the scapulocoracoid (fig. 8).

A description of the major topographical features of both the lateral and medial surfaces of the scapulocoracoid was furnished by Fox and Bowman (1966).

In its natural position, the plane of the coracoid plate was close to horizontal, forming a gently curving floor of the cradle into which the trunk was slung. The scapular blade meets the coracoid plate at an angle of about 125 degrees in undistorted specimens. The scapula, therefore, was not vertically oriented in life, but must have extended laterally away from the trunk at an angle of at least 15-25 degrees from the median plane. Estimation of the radius of curvature of the ribs of an articulated specimen of a primitive captorhinid OUSM 15020 B reveals that the ossified portion of the scapula was too short to have reached the level of the rib articulation in the living animal.

Consideration of the probable musculature of this region suggests the presence of a cartilaginous suprascapula. In living reptiles,

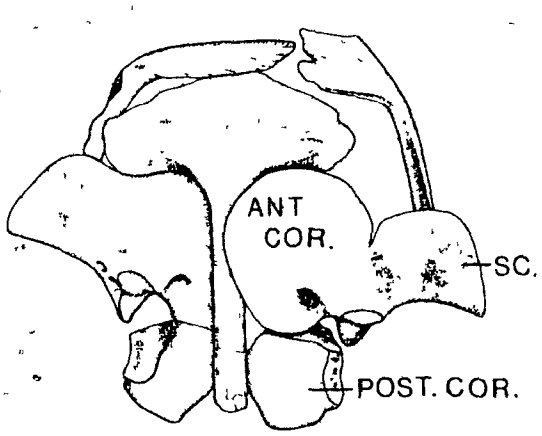


Fig. 6 Shoulder girdle of immature specimen of Captorhinus aguti (Cope), Ventral view, OUSM 15003 showing the three separate elements making up the scapulocoracoid. The scapula has partially fused to the anterior coracoid. X3. For abbreviations, see " Explanation of Abbreviations " at end of text.

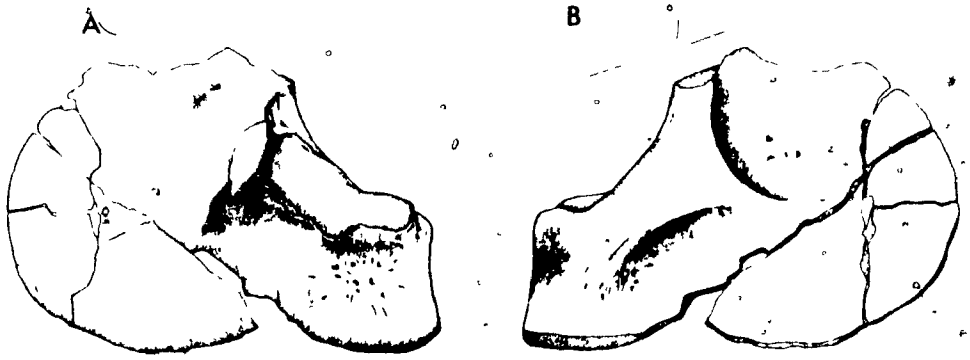


Fig. 7 Left scapulocoracoid of Captorhinus aguti (Cope), KU FEP 60c. A, Lateral view. B, Medial view. Both specimens X3.

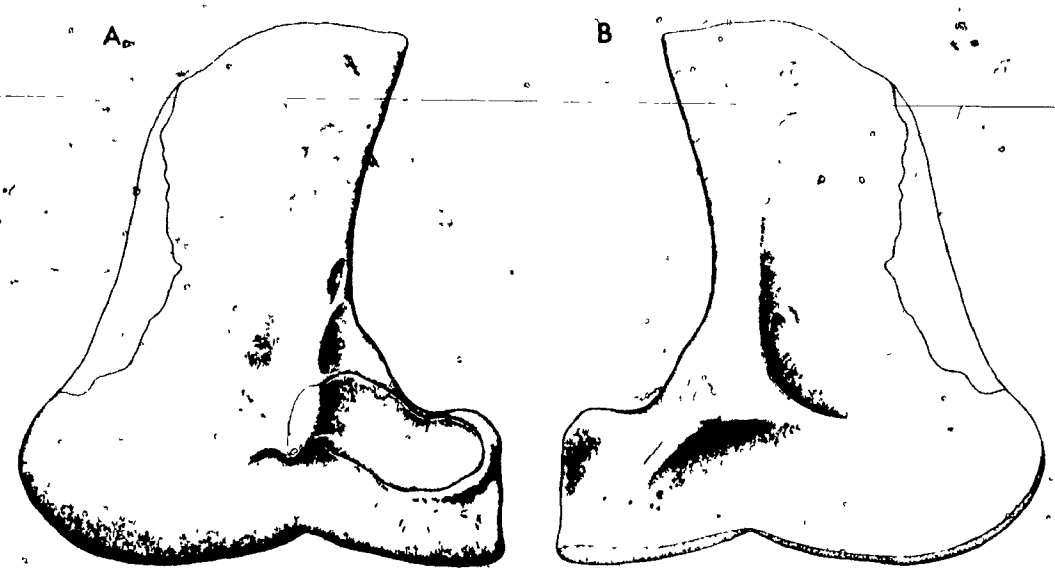


Fig. 8 Reconstruction of the scapulocoracoid of Captorhinus aguti (Cope); based on MCZ 4345 and KU FEP 60c. A, Lateral view. B, Medial view. X3

the serratus musculature is largely responsible for suspending the body from the pectoral girdle. It can work to the best mechanical advantage if the muscles are oriented in a vertical position, passing from the medial surface of the top of the girdle ventrally to the ribs. If there were only a small suprascapula in captorhinids, the serratus musculature would have had to be directed laterally from the ribs to the suprascapula. This would have been quite awkward from a mechanical standpoint. The limited dorsal extent of the scapular blade of captorhinids suggests the existance of a large suprascapula continuing dorsally from the top of the ossified scapula above the angle of the ribs and then spreading medially over the dorsal surface of the rib cage to provide sufficient area of insertion for the serratus musculature, much as it does in modern lizards and Sphenodon.

The Function of the Glenoid

The articular surfaces of the glenoid of primitive tetrapods were originally covered by cartilage, although this cartilage was very thin, allowing confident restoration of the actual articulating surface on the basis of the fossilized remains (Haines 1969, P.72).

Several workers have attempted to analyze the mechanics of the shoulder joint in primitive tetrapods. Watson (1917) noted the peculiar, strap-shape of the glenoid articular surface. He correctly observed that the nature of the joint prevented any rotation of the humerus about its long axis while it retained a fixed orientation

relative to the trunk, and also strictly limited the extent of fore and aft movement of the humerus. He also realized that the distal head of the humerus faced anteroventrally when the humerus was held full forward, and that it rotated to a horizontal position as the humerus was drawn back through the glenoid.

Romer (1922) was the first worker to recognize that the proximal articular surface of the primitive tetrapod humerus was actually composed of two distinct surfaces separated by a groove passing diagonally across the surface. " One commences broadly at the anterior dorsal edge (of the humerus) and dwindles as it curves underneath to terminate at a distinct notch on the underside of the bone. The other commences behind the first and continues dorsal to it to the posterior end of the articular surface " (Romer 1922).

Romer could find no corresponding ridge on the glenoid, but pointed out that " anteriorly there is a broad beginning of the glenoid, followed by contraction of the surface, and thereby a sudden expansion ". Romer felt that this contraction of the surface of the glenoid divides the structure into two surfaces, corresponding to the two surfaces on the humerus. He also argued that the humerus could not have swung more than 20 degrees in the glenoid, because any additional movement would have caused the humerus to cut the muscular surfaces at the anterior and posterior edges of the joint, and strain the joint capsule.

Fox and Bowman (1966) attempted a functional analysis of the glenoid articulation of Captorhinus. They correctly pointed out

that the articular surface of the proximal head of the humerus of Captorhinus is longer than the glenoid, and no matter how the humerus was oriented, some of its articular surface would have been outside of the glenoid. Movement back and forth would only have magnified this effect at one end of the joint. Romer's reason for limiting the range of movement of the humerus in primitive tetrapods to 20 degrees apparently does not hold for Captorhinus, nor, I suspect for any other primitive tetrapod. Fox and Bowman (1966) also reported a ridge on the glenoid surface which corresponded to the groove on the proximal articular head of the humerus described above. They maintained that this ridge on the glenoid fits into the groove on the humerus, and that these were the main surfaces of articulation of the shoulder joint, forming a pivot point for the movement of the humerus in the glenoid. According to them the surfaces on either side of the ridge and groove only acted to guide the humerus by sliding on each other.

Further study of the shoulder girdle of Captorhinus indicates that the ridge identified by Fox and Bowman could not have functioned in the manner proposed by them. A re-evaluation of shoulder joint movement in captorhinids is therefore necessary.

When the humerus was drawn forward to its fullest extent, the dorsal lappet of the anterior articular surface of the humerus was in contact with the posterior facing, anterior surface of the glenoid (fig. 9A). The ridge of the glenoid fits firmly into the transverse groove on the humeral articular surface. The ventrolateral process

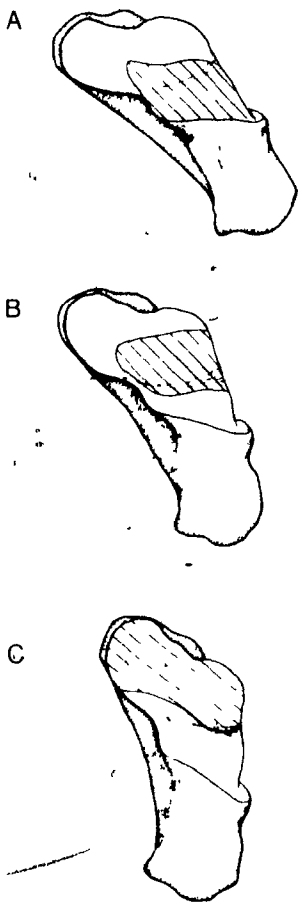


Fig. 9 Proximal end of humerus of Captorhinus aguti (Cope). A, At the beginning of the power stroke. B, Half way through the power stroke. C, At the end of the power stroke. Cross-hatch indicates the area of contact with the glenoid.

of the anterior part of the glenoid abutts against a depressed area on the anterodorsal surface of the humerus, immediately distal to the dorsal lappet of the anterior articular surface. This functionally locked the humerus in the glenoid, preventing any excessive forward movement. Although the entire anterior articular surface of the humerus and the articular surface around the groove are in contact with the glenoid, most of the posterior articular surface was free. The proximal and distal heads were oriented at about 45 degrees to the horizontal, and the long axis of the forward directed humerus made an angle of about 60 degrees to the median plane of the animal.

Since the major direction of force applied to the deltopectoral crest by the pectoralis and coracobrachialis muscles was ventral and posterior, the humerus was not only drawn back and down, but it was also rotated on its long axis, causing the proximal head to approach a vertical attitude and the distal head a horizontal attitude. But if the ridge on the glenoid had remained in the groove on the articular head of the humerus as Fox and Bowman suggested, this rotation would have been inhibited. Rather than the ridge retaining a parallel orientation with respect to the groove and sliding through it as Fox and Bowman (1966) proposed, the torsional forces set up by the depressor musculature on the humerus caused the groove on the articular surface to move ventrally and rotate with respect to the ridge on the glenoid as the humerus was pulled back and rotated (fig. 9B). The anterior articular surface of the

humerus that had previously been in contact with the posteriorly directed, anterior surface of the glenoid moved diagonally across the latter surface and left the anteroventral end of the glenoid. As the humerus rotated, the anterodorsal part of the posterior articular surface came into contact with the area of the glenoid previously occupied by the anterior articular surface of the humerus. Simultaneously, more of the posterior articular surface of the humerus gained contact with the posterior part of the glenoid (fig. 9C). The anterior articular surface of the humerus left the glenoid completely as the transfer of surfaces took place. The posterior articular surface of the humerus is slightly longer than the glenoid surface, and slid a short distance through the glenoid until the posterior limits of the articular surfaces of humerus and glenoid met, at which point the backward directed humerus made an angle of about 60 degrees to the median plane of the animal. At the termination of the power stroke, the plane of the distal expansion of the humerus was horizontal to the ground, with the ulna and radius held approximately vertically, rather than directed downward and posteriorly, as suggested by Fox and Bowman.

Since the deltoid and scapulohumeralis muscles pulled the humerus forward and dorsally during the recovery stroke, the posterior articular surface of the humerus would have slid backward in the glenoid until the anterodorsal end of the former surface met the anterior edge of the glenoid. To prevent the glenoid from " running off " of the anterior end of the posterior articular surface and

thus disarticulating, the humeral articular surface then slid diagonally upward, its groove sliding onto the ridge of the glenoid. This action caused the humerus to rotate about its long axis so as to raise the anterior edge of the distal head and direct the lower limb forward. As the anterior articular surface of the glenoid once more made contact with the glenoid, the posterior articular surface left the glenoid, and the humerus was in position for the beginning of another power stroke.

The Humerus

A very well preserved humerus of the captorhinid from Fort Sill (KU FEP 60-439), is shown in figure 10. Fox and Bowman (1966) provided a detailed description of this bone in the text of their paper, and only a few additional comments will be made here.

The humerus of most primitive reptiles is composed of two widely expanded heads set at 90 degrees to one another, and connected by a short shaft. Except for the longer shaft, slightly lighter build, and the presence of an ectepicondylar foramen, the humerus of Sphenodon is very similar to that of captorhinids. The proximal and distal heads are expanded in a similar manner, but the long spiral articular surface of the proximal head of captorhinids has been replaced by a shorter, raised surface that articulates with an abbreviated glenoid and forms what is essentially a ball and socket joint.

The distal expansion is composed of a prominant lateral (or anterior)

Fig. 10 Left humerus of Captorhinus aguti (Cope), KU FEP 60c 549. A, Posteroventral view. B, Anterodorsal view. C, Posterodorsal view. D, Anteroventral view. E, Proximal view. F, Distal view. X3.

ectepicondyle for the origin of the extensor musculature of the lower arm and hand, and a larger medial (or posterior) entepicondyle for the origin of the flexor musculature of the lower arm and hand. At the beginning of the power stroke, the lower arm would have been very close to horizontal. In this position, considerable demand would have been placed on the flexor musculature in sustaining the power stroke and preventing the animal from collapsing onto its elbows. In order to prevent this, the entepicondyle, or flexor condyle, of captorhinids and most other primitive tetrapods extends far beyond the confines of the elbow joint (Watson 1917). This effectively moves the origin of the flexor musculature as far from the joint as possible, increasing their mechanical advantage. The ectepicondyle, or extensor crest, is not as prominant as the entepicondyle since the associated muscles are not involved in the power stroke, during which time maximum muscular force is required. It is significant, however, that both entepicondyle and ectepicondyle of captorhinids are much better developed than in modern lizards, reflecting a more critical role of their associated musculature in the power and recovery strokes of the walking motion.

In captorhinids, posterior rotation of the humerus is strictly limited by the screw shaped glenoid, most of which is located on the well developed posterior coracoid. These animals were therefore obligatory sprawlers. Because of the reduction of the posterior coracoid and consequent alteration of the structure of the glenoid in modern reptiles, it is possible for these animals to rotate the

humerus posteriorly to a new position parallel to the long axis of the trunk and draw the anterior limb under the body. In this position, the biceps and triceps muscles became the main flexor and extensor muscle masses of the lower limb involved in forward progression.

Because of the limited potential for anteroposterior movement of the humerus in captorhinids, the main component of force of the biceps and triceps was directed at right angles to the progression of the animal, possibly causing some lateral movement of the body during the power stroke, with a smaller component of force working parallel to the progression of the animal. The latter component will be discussed more fully below. Under these conditions, the extensor and flexor muscles originating from the distal condyles of the humerus were much more important in accomplishing forward progression in captorhinids than in living lizards. It is for this reason that the condyles are so well developed in these forms.

In order for these extensor and flexor muscles originating from the distal condyles to be used to their full advantage, there must be the potential for considerable movement between the humerus and lower limb in a plane at right angles to the long axis of the humerus. However, as Jenkins (1973) pointed out, the elbow joint of pelycosaurs (which is functionally the same as that of captorhinids) tends to resist precisely this type of movement by providing maximum engagement of the bones under torque. To understand how the extensor and flexor muscles of the forelimb operates in the walking motion of captorhinids, the structure and function of the elbow joint must

be considered.

The Elbow Joint

The articular surfaces on the distal end of the captorhinid humerus (fig. 10) are similar to those of pelycosaurs, consisting of a bulbous capitulum and a humero-ulnar articulation that is quite distinct from the mammalian trochlea (Jenkins 1973). The capitulum is in the form of an eliptical dome when viewed ventrally. The long axis of the elipse is set off at an angle of about 22 degrees from the long axis of the humerus. The proximal articular surface of the radius (fig. 11) of captorhinids is concave in shape and elongated mediolaterally to match the rounded surface of the capitulum. The " trochlea " is composed of two surfaces as in pelycosaurs; a concave area that includes the medial surface of the capitular protuberance and all of the ventral articular surface medial to this. A groove passing proximodistally at the base of the capitular protruberance divides this surface and gives it a concave shape. A large flat surface faces dorsally. The proximal articular surface of the ulna (fig. 12) is composed of a smaller anteroventral surface articulating with the capitular protruberance, and a larger, posterodorsal surface articulating with the posterior part of the " trochlear " surface, separated by a prominent, curved ridge passing diagonally in a posteroventral direction through the articular surface, describing a small part of a spiral. This ridge fits into the deep groove on the ventral " trochlear " surface of the humerus, located directly

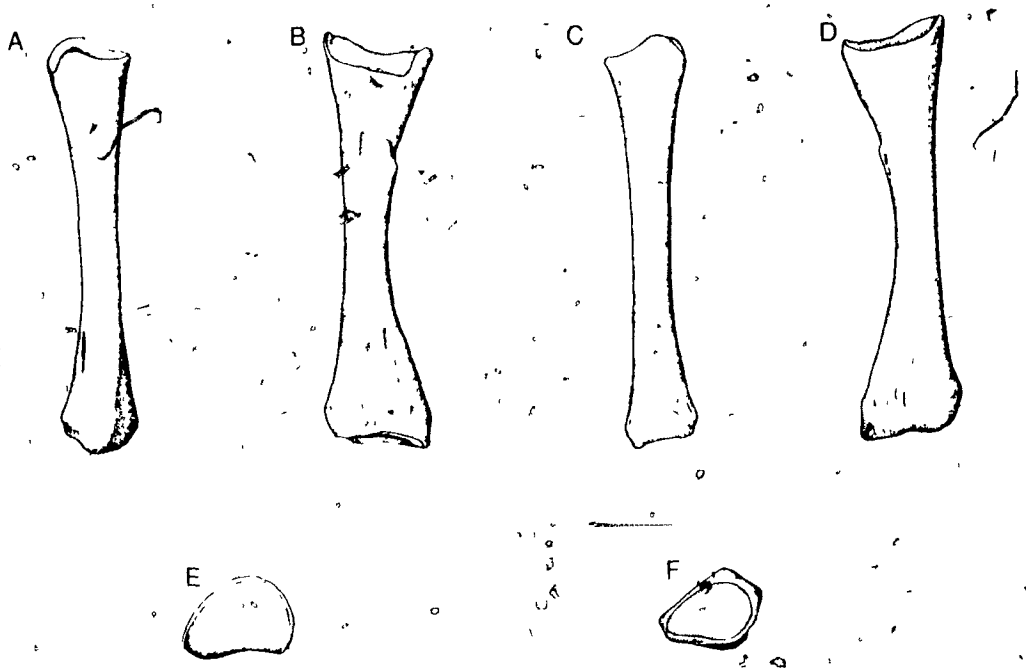


Fig. 11 Left radius of Captorhinus aguti (Cope), KU FEP 60c. A, Medial view. B, Posterior view. C, Lateral view. D, Anterior view. E, Proximal view. F, Distal. X3.

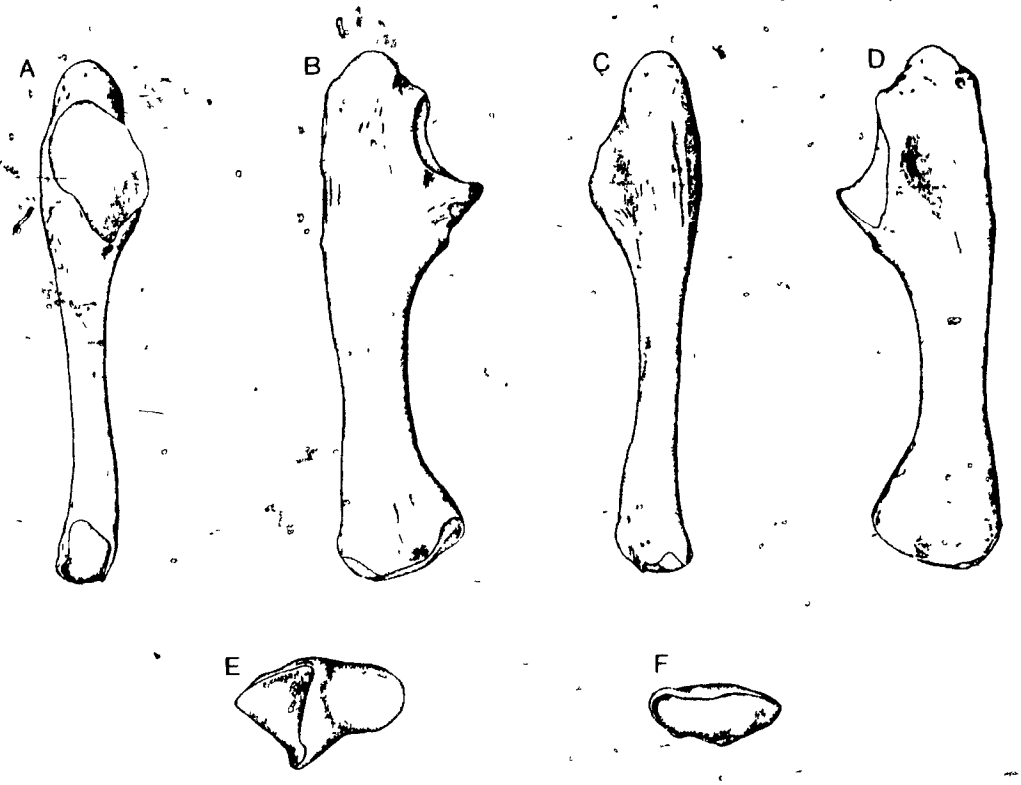
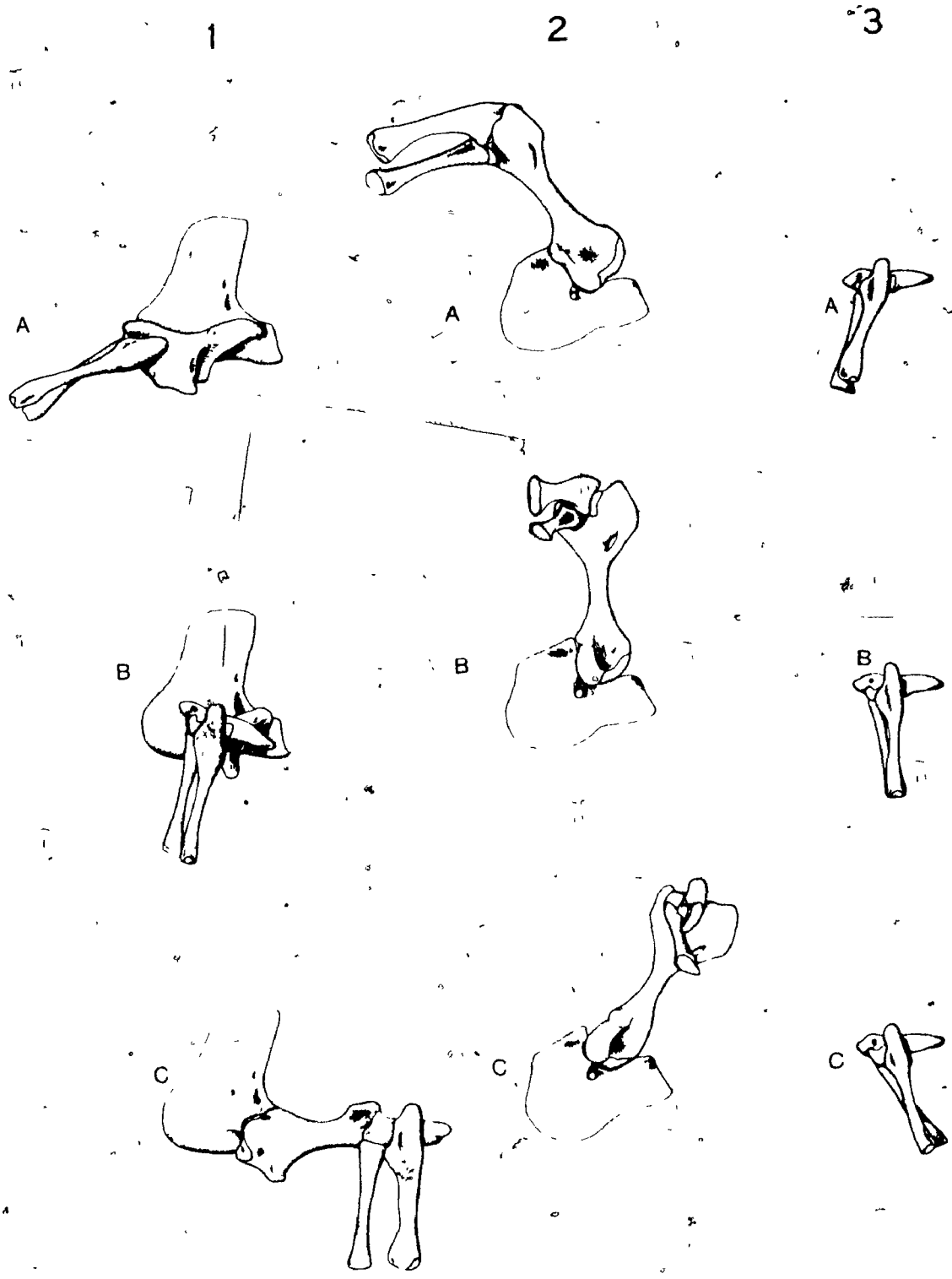


Fig. 12 Left ulna of Captorhinus aguti (Cope), AMNH 2464. A, Medial view. B, Posterior view. C, Lateral view. D, Anterior view. E, Proximal view. F, Distal view. X3.

medial to the capitulum. The close articulation between the ridge of the ulna and groove of the humerus provides considerable resistance to the torsional forces set up during the walking motion, as Jenkins noted for pelycosaurs.

When the ulna was flexed by the biceps or extended by the triceps muscles, however, the spiral shape of the ridge on the proximal articular surface of the ulna caused the distal end of the ulna to describe a small arc lying in a plane at right angles to the long axis of the humerus (see fig. 13 IIIA, B, C), and at the same time causing a slight rotation of the ulna about its long axis as this ridge passed through the groove of the humeral articular surface. When the ulna was flexed to its fullest extent, the entire posterodorsal articular surface of the ulna was in contact with the " trochlear " surface, but the anteroventral surface was not in contact with its corresponding capitular surface. In this position the distal end of the ulna was at the most posterior point of its arc, (fig. 13 IIIC) making an angle of about 70 degrees with the plane of the flexor crest. As the triceps muscles extended the ulna and the ridge of the ulna slipped through the groove of the humerus, its spiral shape forced the distal end of the ulna to swing anteriorly, relative to the humerus, causing the anteroventral articular surface of the proximal end of the bone to engage the medial surface of the capitular protuberance. Simultaneously, there was a slight rotation of the ulna about its long axis, causing the extensor surface of the bone, and hence the manus, to turn

Fig. 13 A, scapulocoracoid, humerus, ulna, and radius of Captorhinus aguti (Cope) in articulation, illustrating the spatial relationships of these elements at different points in the power stroke. Column 1, Lateral view: A, Beginning of power stroke. B, Middle of power stroke. C, End of power stroke. Column 2, Ventral view: A, Beginning of power stroke. B, Middle of power stroke. C, End of power stroke. Column 3, View of distal end of humerus: A, Beginning of power stroke (lower arm fully extended). B, Middle of power stroke (lower arm partially flexed). C, End of power stroke (lower arm fully flexed).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laterally. When the ulna was fully extended, the distal end was at the most anterior point of its arc, making an angle of about 70 degrees with the plane of the ectepicondyle (fig. 13 IIIA).

Flexion and extension at the elbow of captorhinids, therefore, did not only produce side-to-side movements of the distal end of the lower limb, but also considerable anteroposterior movement, acting to augment the fore and aft reach of the manus produced by the anteroposterior movement and rotation of the humerus.

The extensors originating from the condyles reinforced this anterior rotation of the ulna on the humerus, as well as extended the manus, as the triceps extended the lower arm. The antagonistic flexor muscles similarly assisted the posterior rotation as the biceps flexed the lower arm during the power stroke.

The Manus

Fox and Bowman apparently relied on disarticulated material for their description of the manus of Captorhinus, as the only figure was a composite. The pisiform was not shown and, although not explicitly stated, the identification of some of the other elements appears to have been only tentative. Consequently, a consideration of the function of the hand must be based on other material. Since the publication of the above work, several specimens of a captorhinid from the McCann quarry of Oklahoma equivalent in age to those of the Clyde Formation of Texas became available. There are several skulls with associated postcranial material

including one complete manus, OUSM 15024 (fig. 14 A,B). The description of the ulnare, radiale, and intermedium of Captorhinus given by Fox and Bowman is correct in its essentials. Because they were working from disarticulated material, however, their reconstruction of the manus showed the intermedium as being much larger in relation to the other two proximal elements than is actually the case.

The proximal articular surface of the radiale is flat, precluding all but a minor amount of flexion between this bone and the radius. The radiale was probably functionally an extension of the radius. The distal articular surface of the radiale is more rounded in outline, especially when viewed from the extensor surface. The convex distal surface facilitates mediolateral sliding of the distal surface of the radiale on the proximal surface of the lateral centrale during the power stroke. This movement must have been considerable, as the articular surface of the distal end of the radiale extends almost to the medial border of that bone, whereas the medial centrale does not extend medially enough to cover more than two-thirds of the above articular surface, leaving one-third of this free when the limb is held in the normal position (fig. 15).

The ulnare and intermedium appear to form a single structural unit. The articulation between them is long and straight. The articular surfaces are flat, and their planes are oriented in such a way that the two bones articulate to form a dorsally directed wedge rather than a flat plate.

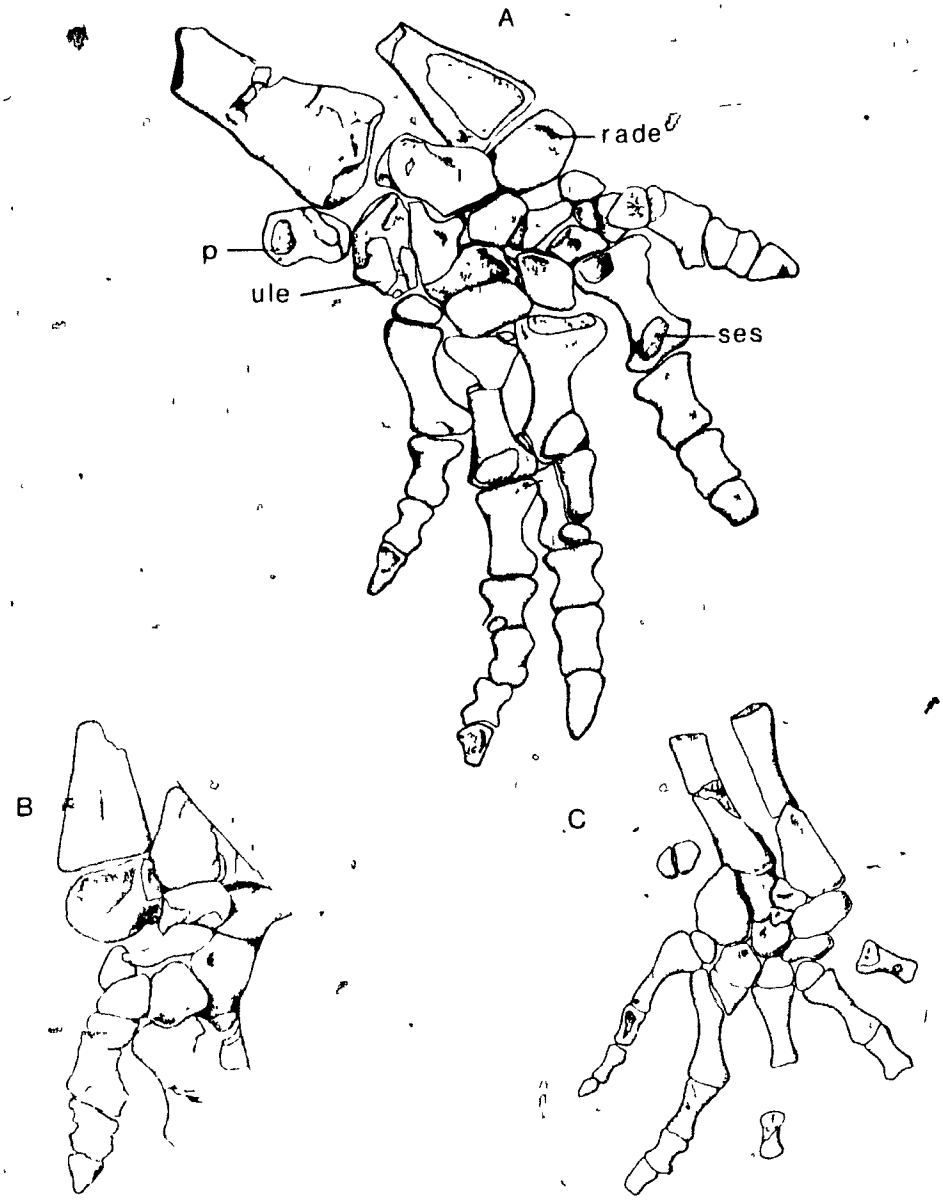


Fig. 14 Single tooth rowed captorhinid. A, Right manus from McCann Quarry OUSM 15024, Ventral view. B, Same specimen as in A, Dorsal view. C, Left manus from FMNH UC 642, dorsal view. Both specimens X2. For abbreviations, see " Explanation of Abbreviations ".

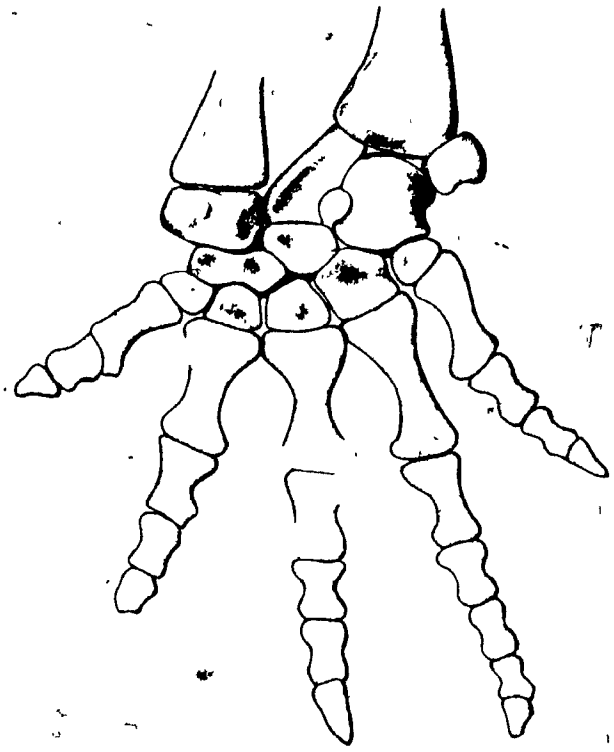


Fig. 15 Reconstruction of the manus of a captorhinid, based primarily on OUSM 15024. Dorsal view. X2.

The articular surfaces between the ulnare-intermedium and ulna proximally, and centrale and distal carpals distally, are quite flat, and there was probably only a relatively small amount of movement possible at these joints.

The presence of a pisiform in captorhinids is shown by OUSM 15024 (fig. 14A) and UC 642 (fig. 14C). By referring to the shape of the bone in these specimens, it was possible to identify several of these elements in the material from the Fort Sill locality (fig. 16D). It is generally rectangular in outline, with a concave ventral border, and a slightly convex dorsal border. The antero-posterior dimension is twice as great as the dorsoventral dimension. The bone has two adjoining articular surfaces medially, a dorsal one for the ulna, and a ventral one for the ulnare. In articulation, the pisiform projected posteriorly and slightly laterally.

The lateral centrale occupies the center of the carpus (fig. 15) and articulates with every bone in the carpus except the first and second metacarpals. The fourth distal carpal is pentagonal in shape and is the largest of the distals. The third distal carpal is the second largest. It possesses a peculiar wedge-shaped process distally, which projects ventral to the third metacarpal (fig. 14A,B). The position of this process suggests that it may have functioned to prevent excessive flexion of the third digit. A similar process of the third distal carpal is also present in the early diapsid Petrolacosaurus (Reisz, personal communication). The remaining

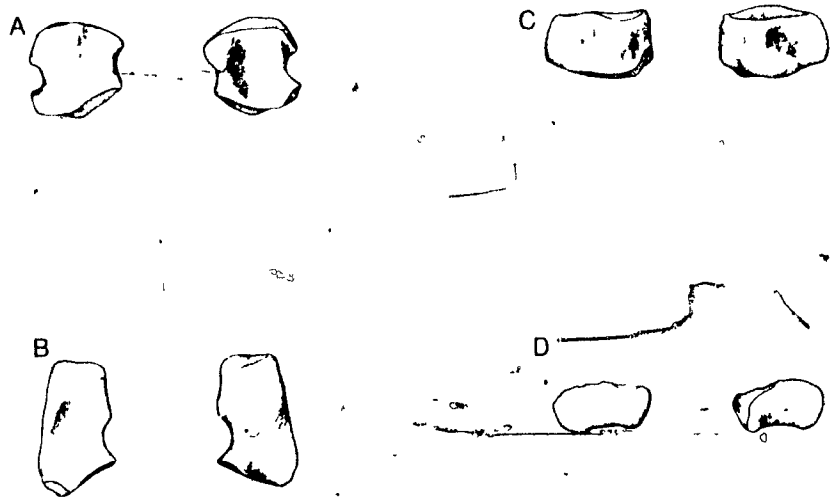


Fig. 16 Carpal elements of Captorhinus aguti (Cope). A, Ulnare, KU FEP 60c, dorsal and ventral views. B, Intermedium, KU FEP 60c, dorsal and ventral views. C, Radiale, AMNH 2465, dorsal and ventral views. D, Pisiform, AMNH 2466, lateral and medial views. All specimens X3.

distal carpals are of approximately equal size and of similar configuration.

The carpus of captorhinids is an interlocking mosaic of bones. The articulating surfaces of the bones are essentially flat allowing only limited movement between each carpal and its neighbour. In addition, these bones are arranged in such a way as to prevent the formation of any distinct transverse joint between the carpus and lower arm, or within the carpus itself. Some movement was possible between the ulna and ulnare-intermedium, but because the articulation between the radius and radiale is more distally located in the carpus, the potential joint between the ulna and ulnare-intermedium, was blocked by the shaft of the radius (fig. 15). Similarly, a joint between the radiale, intermedium and ulnare, and the more distal carpals is blocked by the position of the lateral centrale (fig. 15). The functional wrist joint in captorhinids was probably between the distal carpals and metacarpals, with only limited movement possible between the distal carpals and more proximal elements of the carpus. Although the distal carpal-metacarpal joint appears to have been the major wrist joint in captorhinids, the flat articular surfaces of these elements in comparison with the very rounded articular surfaces found in the carpus of lizards emphasizes the relative inflexibility of these joints. Although each individual joint in the carpus of captorhinids is not capable of much independent movement, the carpus as a whole was probably quite flexible, not only in terms of flexion and extension, but the capabilities for moderate movement

between each carpal probably allowed some twisting and arching of the manus as well.

The digits of captorhinids are quite short and the metacarpals and phalanges are heavily built (fig. 15). On the ventral surface of the digits, in close association with the joints between the phalanges, is a series of irregularly shaped ossifications. In OUSM 15024 (fig. 14A), a few of these ossifications can be seen adhering to the ventral surface of the metacarpals and phalanges of digits II, III, and IV. Some appear to be missing, but in the living animal, there was probably one such ossification for each joint. Similar accessory bones have been reported in some living lizards (Romer 1956). They are sesamoid bones, developed in the tendons of the palmaris communis superficialis muscle. Their purpose appears to be to increase the distance between the tendon and the joint, and thereby increasing the mechanical efficiency or flexing power of the palmaris communis superficialis.

A RECONSTRUCTION OF THE MUSCULATURE OF THE PECTORAL LIMB BASED ON DIRECT EVIDENCE AND COMPARATIVE STUDIES ON LIVING REPTILES

The musculature associated with the anterior limb of tetrapods can be classified broadly into three categories according to their embryological origin. The sternocleidomastoideus, or trapezius of lower tetrapods is distinct from all other shoulder muscles in being derived from the visceral arch musculature. The trapezius muscle of higher tetrapods, costocoracoideus, sternocoracoideus, serratus, and levator scapulae muscles differentiate from the axial muscle mass (Romer, 1944). The omohyoideus and episternohyoideus also appear to be part of this group (Miner 1925). The true limb musculature is derived by differentiation from the limb bud of the embryo.

Romer (1922, 1944) attempted to classify the last assemblage of muscles into a dorsal group and a ventral group, derived from the levator and depressor muscle masses, respectively, of fish. The dorsal group includes the latissimus dorsi, subcoracoscapularis, scapular and clavicular deltoid, scapulohumeralis, triceps, and more distal extensor muscles. The ventral group includes the pectoralis, supracoracoideus, coracobrachialis brevis and longus, biceps, brachialis and more distal flexors.

Although a standard nomenclature of the pectoral limb muscles of lower tetrapods has never been adopted by all workers, each

muscle normally has one name that is accepted by the majority of authors. I have used these names in this work. In cases where more than one name is in common usage, the most convenient term has been used, followed by alternate names in parentheses.

Trapezius and Sternocleidomastoideus

The trapezius of living anamiotes, derived from the branchial musculature, is innervated by visceral branches of the vagus nerve. Some lizards (Gecko and Lacerta among others - see Furbringer 1900) exhibit what is probably the primitive amniote condition, in which there is still a single muscle in this region, but with its innervation from two distinct sources. The anterior portion of the muscle, comparable to the sternocleidomastoideus of other amniotes and originating from the back of the skull, possesses visceral innervation comparable to the trapezius of living anamniotes. The innervation of the posterior portion of the muscle, the trapezius proper, is by somatic branches arising segmentally from the spinal column.

This was interpreted by Miner (1925) as indicating that it was the sternocleidomastoideus and not the trapezius proper of amniotes that was homologous to the anamniote trapezius, and that the trapezius of amniotes was developed as a posterior extension of the anamniote trapezius by inclusion of myotomal fibres concurrent with the development of a neck region in more completely terrestrial forms.

It is now generally accepted that the most primitive reptiles, the romeriids, and the gephyrostegid anthracosaurs which gave rise

to them were essentially terrestrial (Carroll 1964, 1970) rather than semi-aquatic as originally postulated by Romer (1946). Although the necks of these tetrapods were not long (approximately 5 cervical vertebrae in most cases) the head and shoulder girdle were well separated and moved quite independently of each other. A trapezius muscle running from the back of the skull could not have supported the girdle as well as it could have in forms in which the girdle was immediately behind and below the skull. Recruitment of myotomal musculature to form an amniote trapezius behind the anamniote trapezius probably occurred in the gephyrostegid line leading to reptiles in order to maintain at least part of the origin of the muscle above its insertion.

The trapezius and sternocleidomastoideus muscles probably formed a continuous, unbroken sheet of muscle in primitive reptiles, taking their origin from the back of the skull and dorsal fascia of the thoracic region. This condition can be observed in Lacerta and other living lizards (Furbringer 1900) and is approximated in Sphenodon, where the two muscles are very incompletely separated (Miner 1925). This was almost certainly the condition of these muscles in captorhinids.

As is the case with other fossil reptiles, specific osteological evidence for the origin and insertion of the trapezius-sternocleidomastoideus muscle mass is lacking. The sternocleidomastoideus portion presumably had a fleshy origin on the postparietals and on the unsculptured portion of the squamosals that curves medially

onto the occipital surface. The somatic trapezius surely originated from the dorsal fascia of the back, as is the case with the vast majority of vertebrates.

The sternocleidomastoideus of lizards inserts on the lateral tip of the interclavicle. In Sphenodon, this muscle inserts on the clavicular stem (Miner 1925). Dorsally, the insertion of the trapezius of lizards wedges between the origin of the scapular deltoid and the insertion of the levator scapulae, and continues ventrally along the stem of the clavicle. The trapezius of Sphenodon is limited to a small insertion on the " acromion " of the scapula. The trapezius-sternocleidomastoideus muscle sheet of captorhinids probably had a long curved insertion running ventrally from the anterior part of the scapular blade and possibly from the suprascapula between the areas of attachment of the scapular deltoid and levetor scapulae, onto the posterior part of the cleithrum and well down onto the lateral surface of the clavicular stem (fig. 17A, 18B).

Levator Scapulae

In Sphenodon and lizards this muscle is divided into two slips; the levator scapulae superior (superficialis), and the levator scapulae inferior (profundus). The two slips originate together from the first few cervical ribs or transverse processes of the corresponding cervical vertebrae. They separate almost immediately and the superior slip inserts on the anterior part of the lateral surface of the suprascapula. The inferior slip inserts on the

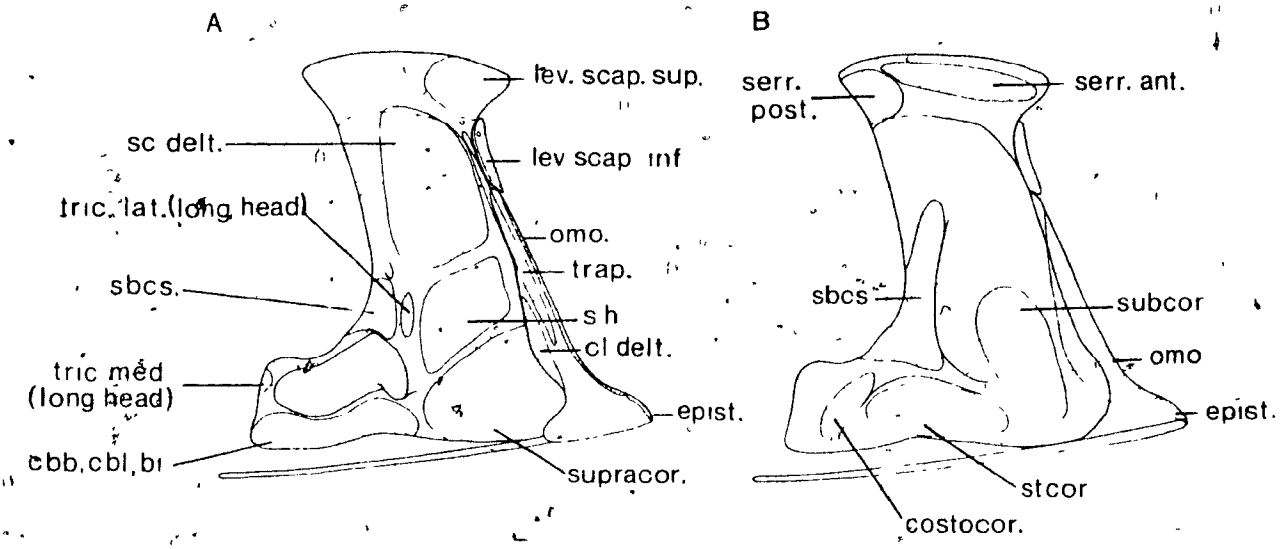


Fig. 17 Areas of shoulder muscle attachment of a captorhinid. A, Lateral surface. B, Medial surface. For abbreviations, see " Explanations of Abbreviations ".

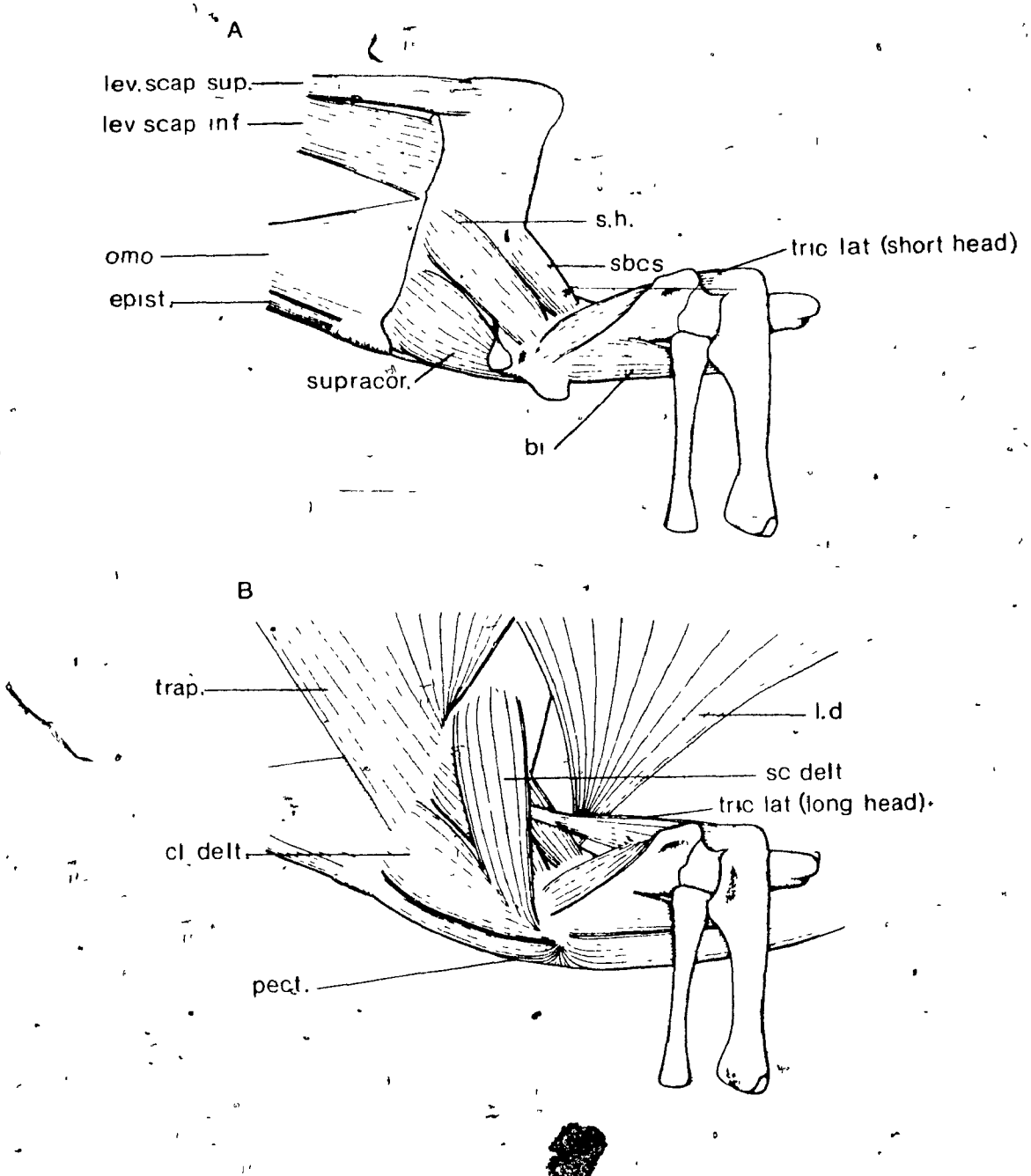


Fig. 18 Shoulder musculature of a captorhinid, lateral view. A, Deep. B, Superficial. For abbreviations, see " Explanation of Abbreviations ".

anterior border of the bony scapula and dorsal part of the clavicular stem.

Miner (1925) supposed that the splitting of the muscle into two was related to the development of a large cartilagous suprascapula in Sphenodon and lizards. It may be significant that in crocodiles, in which the suprascapula is very small, the levator scapula is a single muscle. (The " levator scapulae profundus " portion of the collothoraciscapularis profundus muscle of Furbringer (1876) appears to be part of the serratus musculature).

The captorhinids probably possessed a suprascapula of substantial size. It would be expected therefore, that the levator scapulae existed in two parts as it does in both lizards and Sphenodon. The superior slip would have inserted on the anterior portion of the external surface of the suprascapula (fig. 17A, 18B). The inferior slip must have inserted onto the top of the clavicular stem, and anterior edge of the cleithrum, or on the anterior edge of the bony scapula if the cleithrum was absent (fig. 17A, 18B).

Serratus Superficialis

The serratus superficialis muscle of Iguana and Sphenodon is remarkably similar in regards to origin and insertion. In both cases the muscle arises as two slips from the last cervical and first thoracic ribs. These slips unite and insert on the posterior and medial surfaces of the suprascapula. Unlike Iguana, the serratus superficialis also gains limited attachment to the posterodorsal

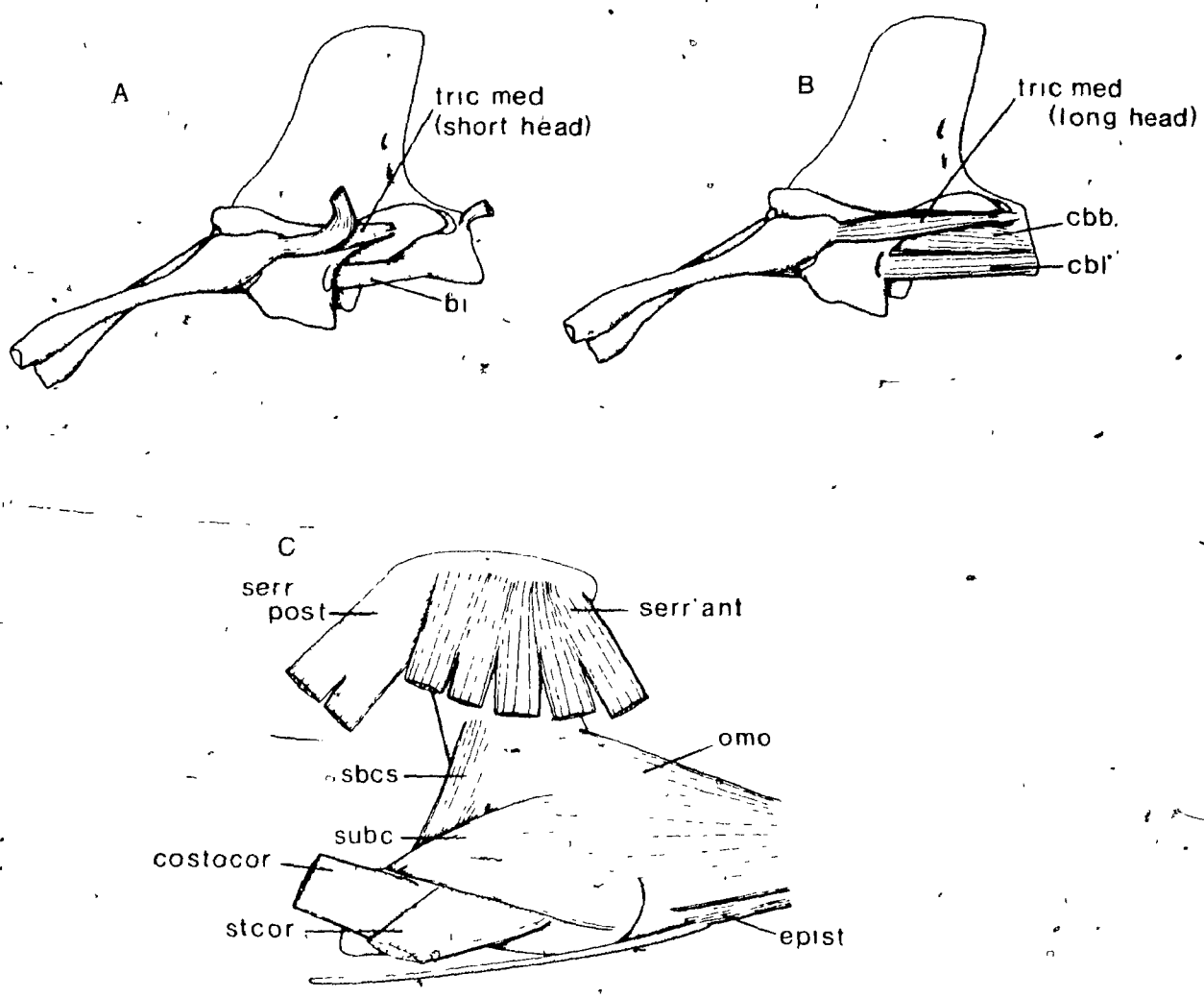


Fig. 19 Shoulder musculature of a captorhinid. A, Lateral view, with long head of triceps " cut " and deflected. B, Lateral view. C, Medial view. For abbreviations, see " Explanation of Abbreviations ".

corner of the bony scapula in Sphenodon (Miner 1925).

In the alligator, the serratus superficialis originates from the first through fourth thoracic ribs (Chiasson 1962). The expansion of this muscle is probably due to the increased stress imposed upon it by a much greater body size and does not reflect a primitive condition. The suprascapula is very small, and consequently the serratus superficialis attaches to the posterior border of the bony scapula.

It is probable that the serratus superficialis of captorhinids resembled Iguana and Sphenodon in its general relations to the skeletal elements (fig. 19C). Since these animals are all about the same size (ie. similar weight imposed upon the serratus superficialis), it is likely that the muscle in small captorhinids took its origin from the last cervical and first thoracic rib only, as in Iguana and Sphenodon. The insertion was a fleshy one on the posterior edge and posterior part of the medial surface of the suprascapula (fig. 17B). It is quite possible that the insertion spread ventrally onto the dorsal part of the medial surface of the bony scapula as it does in Sphenodon, but there is no indication of this on the bone surface.

Serratus Profundus (Serratus Anterior)

As is the case with the previous muscle, the serratus profundus of Sphenodon and Iguana are very similar. Both animals possess a deep and superficial layer. In Iguana, the superficial layer

consists of three slips originating from the first three cervical ribs. In Sphenodon, the deep layer originates as five slips, one from each of the five cervical vertebrae (Miner 1925). In both animals, these individual slips unite and pass dorsally and slightly anteriorly, inserting along the dorsal part of the inner surface of the suprascapula. The superficial layer in Iguana is a single muscle originating on the third cervical rib. The corresponding muscle sheet in Sphenodon consists of two slips (Miner 1925). In both cases, these slips pass diagonally anterodorsally between the deep slips of the same muscle and the scapula to insert on the medial surface of the suprascapula anterior to the insertion of the deep layer in the case of Iguana and ventral to that of the deep layer in Sphenodon.

The serratus profundus of the alligator originates from the last few cervicals and first thoracic ribs, and because of the reduced nature of the suprascapula in these forms, inserts on the medial surface of the bony scapula (Chiasson 1962). Although this muscle is somewhat different from its condition shown by Iguana and Sphenodon, the resemblances are surprising for an animal that is so distantly related to the above forms. Apparently there has been very little deviation from a common pattern in the divergent living reptiles.

The serratus profundus muscle of captorhinids can be reasonably conceived as originating from most if not all of the cervical ribs, and inserting of the dorsal margin of the medial surface of the suprascapula (fig. 17B, 19C).

Omohyoideus and Episternohyoideus

The omohyoideus of Sphenodon originates from the anterior and medial surfaces of the scapula, and from the ligamentum sternoscapulare internum (Miner 1925), which is equivalent to the supporting ridge of the posterior coracoid of captorhinids (Romer 1922). The omohyoideus of Iguana originates as in Sphenodon, from the anterior edge of the scapula, and also from the clavicular stem in front of the insertion of the trapezius. In both animals, the episternohyoideus originates from the anterior edge of the ventral part of the clavicles and interclavicle. Both muscles insert on the hyoid apparatus.

Since the clavicles are absent in the alligator, the origin of the omohyoideus is necessarily from the dorsal part of the coracoid. The episternohoideus originates below the origin of the omohyoideus from the episternum (Chiasson 1962). As is the case with the above animals, these muscles insert on the hyoid apparatus.

There is no osteological evidence for the presence of either an omohyoideus or episternohoideus in small captorhinids. It seems most reasonable, however, to assume that the two muscles took essentially the same form as those in Iguana and Sphenodon, originating from the entire length of the anterior margins of the clavicle and from the interclavicle (fig. 17A, B, 18A). Attachment to the adjacent scapular and coracoid surfaces on the medial side was also possible.

Sternocoracoideus and Costosternocoracoideus (Costoscapularis)

All living reptiles possess a set of ventral shoulder girdle muscles running from the sternum and ribs, and inserting on the coracoid (Romer 1922), derived from the rectus abdominis musculature of lower vertebrates (Miner 1925).

The sternocoracoideus and costosternocoracoideus muscles are essentially the same in Sphenodon and Iguana. The sternocoracoideus consists of two slips. A profundus layer originates from the inner surface of the posterior part of the sternum and inserts on the junction between the coracoid and scapula. The superficial layer originates along a ridge on the anterior margin of the sternum, and inserts on the coracoid, medial to the insertion of the profundus slip. There are no equivalent muscles in crocodiles (Furbringer 1876), or in turtles (Walker 1973).

The costosternocoracoideus originated from the sternocostale of the first thoracic rib, and inserts on the ligamentum sterno-scapulare internum in living lepidosaurs. The origin of this muscle in crocodiles is the same. The insertion is on the posterior part of the internal surface of the coracoid (Furbringer 1876). This muscle does not exist in turtles (Walker 1973).

Since the sternum and sternocostale did not ossify in primitive reptiles, evidence for the origins of the sternocoracoideus and costosternocoracoideus muscles is lacking. The depression on the medial surface of the coracoid plate beneath the horizontal supporting ridge of the scapulacoracoid (fig. 8B) is the probable insertion

of the sternocoracoideus muscle mass (Romer 1922) (fig. 19C). The posteroventrally directed supporting ridge of the posterior coracoid exhibits a roughened, grooved surface (fig. 8B), indicating the insertion of the costosternocoracoideus muscle along its length (fig. 19C).

Pectoralis

The pectoralis muscle in living reptiles is massive and its origin extends anteroposteriorly over most of the ventral surface of the pectoral girdle just to one side of the midline. In both Sphenodon and Iguana, the muscle has a long origin from the clavicle, interclavicle, sternum, and sternocostale. The clavicles are absent in the crocodile, and the pectoralis muscle originates on the extensive sternum, and sternocostale (Furbringer 1876). The muscle originates from the dorsal surface of the anterior part of the plastron in turtles (Walker 1973).

The insertion in all living reptiles is on the deltopectoral crest of the humerus.

An examination of the girdle and humerus of captorhinids reveals that the pectoralis muscles was probably similar to that of living forms. However, sculpturing on the ventral surfaces of the clavicles and anterior portion of the interclavicles precludes the possibility that the muscle originated from these surfaces, since this sculpturing indicates a very close proximity of the bone to the dermis. It is probable that the origin of the pectoralis muscle from the dermal girdle was confined to the posterior edge of the clavicles, and

the edge of the interclavicular head and stem. The heavy construction of the head and shoulder girdle probably necessitated an extensive area of attachment on the ventral surface of the sternum and ventral ribs, and possibly on the surface of the rectus abdominis muscle posterior to the sternum (fig. 20).

A flattened tuberosity of the tip of the deltopectoral crest of the humerus in captorhinids, ventral to the insertion of the deltoid muscles, indicates the insertional area of the pectoralis muscle (fig. 18A, 21A, D).

Coracobrachialis, Biceps Brachii (Coracoantibrachialis), and Brachialis

That these muscles share a common evolutionary origin is evidenced by a very close proximity to one another (their attachments to the coracoid of Sphenodon are difficult to separate) and by similar innervation. On the basis of the innervation, Miner (1925) has regarded them as a deeper layer of the pectoralis system.

The coracobrachialis muscle of Sphenodon and lizards can be divided into a longus and brevis head. In lizards, the fleshy origin of the brevis muscle occupies most of the lateral surface of the coracoid posterior to the origin of the supracoracoideus. The origin of the longus muscle is limited to a small area on the posterolateral corner of the coracoid, posterior to the origin of the brevis muscle. Some fibres reach around the posterior edge of the coracoid and attach to the medial surface of that bone. Essentially the same condition exists in Sphenodon, except that the

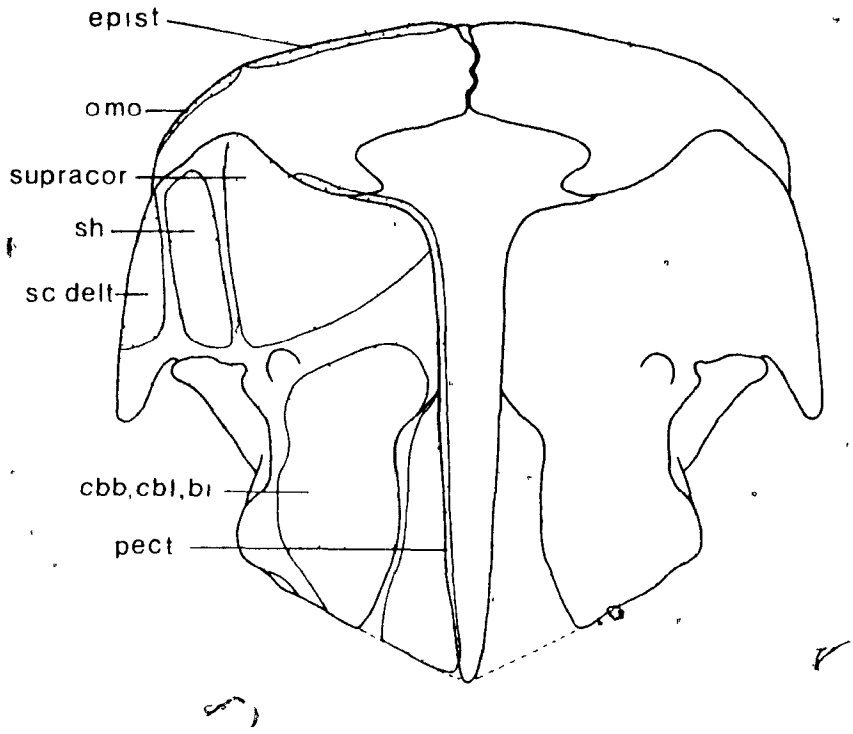


Fig. 20 Areas of muscle attachment in the shoulder girdle of a captorhinid, ventral view. For abbreviations, see " Explanation of Abbreviations ".

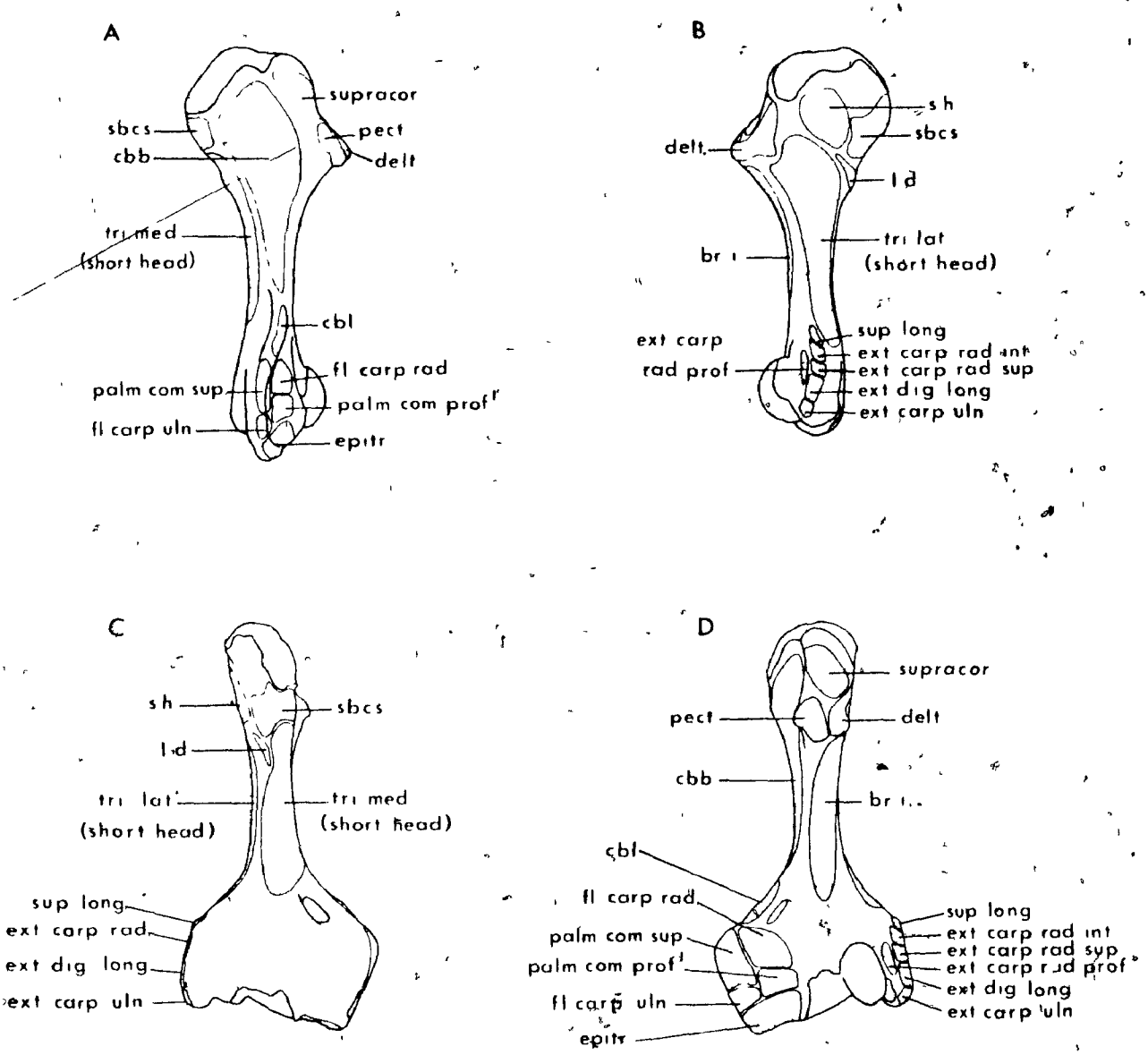


Fig. 21 Areas of muscle attachment on the humerus of captorhinids. A, Posteroventral view. B, Anteroventral view. C, Posterodorsal view. D, Anteroventral view. For abbreviations see " Explanation of Abbreviations ".

origin of the longus muscle is limited to the lateral surface of the coracoid (Miner 1925). The longus muscle is absent in crocodiles (Furbringer 1876).

The insertions of these muscles are adjacent to one another, but distinct in Sphenodon and lizards. The brevis muscle has an extensive insertion on the proximal half of the flexor surface of the humerus. The longus muscle also inserts on the flexor surface, but more distally than the brevis head.

The external surface of the posterior coracoid of Captorhinus shows no evidence of more than one coracobrachialis muscle having originated from the bone. In lizards and Sphenodon, the origins of the two muscles are hardly separable. It is probable that the coracobrachialis brevis and longus msucles originated as a single muscle from the posterior coracoid in captorhinids (fig. 17A).

The insertion of the brevis muscle in captorhinids undoubtedly occupied the concave, proximal flexor surface of the humerus, and probably extended onto the adjacent surface of the shaft (fig. 21A, D). A prominent ridge on the edge of the entepicondyle at the level of the foramen indicates the insertion of the coracobrachialis longus (fig. 21D).

The biceps brachii of Sphenodon takes a fleshy origin from the coracoid posterior to the origin of the supracoracoideus and medial to the origin of the coracobrachialis brevis (Miner 1925). It runs into a tendon which passes over the joint capsule. This tendon is continuous in turn with a more distal belly of the same

muscle which merges with the brachialis inferior before inserting by two tendons on the radius and ulna.

The proximal belly of the biceps in Iguana is reduced, and the tendon has expanded medially to take over the posterior part of the origin of the biceps along the medial border of the coracoid. The proximal belly is represented by a small triangular muscle sheet running from the tendon to the coracoid anterior to the tendinous origin. The development of a largely tendinous origin in Iguana appears to be secondary, and can possibly be correlated to the extreme reduction of the coracoid as compared to the primitive reptilian condition. In Sphenodon, the reduction of coracoid surface available for muscle attachment is not as severe, and there is room for a fleshy origin. However, in the crocodile, where space on the coracoid does not seem to be limited, the proximal belly is entirely tendinous (Furbringer 1876).

The brachialis inferior of living reptiles generally originates from the lateral and ventrolateral surface of the proximal part of the humerus. In Sphenodon and lizards, it fuses distally to the biceps, and the resulting muscle inserts by a double tendon to the radius and ulna. The crocodile shows a similar condition (Furbringer 1876). Although some specialized turtles have a double biceps (Walker 1973), the primitive pattern for turtles is probably the same as for other reptilian groups.

There is no specific evidence for the origin of the biceps muscle in captorhinids. Since the posterior coracoid was large

enough to have provided plenty of space for a fleshy attachment, a tendinous attachment (which would have likely left a scar) as occurs in Iguana would have been unnecessary. The muscle surely originated in common with the coracobrachialis mass from the ventral surface of the posterior coracoid in captorhinids (fig. 17A).

The limits of the origin of the brachialis inferior in captorhinids is also difficult to define precisely on the basis of fossil remains, but it is reasonable to assume that it originated from much of the lateral and ventrolateral surface of the humerus, as it does in living reptiles (fig. 17A).

The distal union of the biceps and brachialis inferior seems to be a primitive characteristic of reptiles, and probably occurred in captorhinids. Raised scars on the proximal ends of the medial surfaces of both the radius and ulna indicate (fig. 11B, D, 12A, B, D, 22A, B) the tendinous insertions of this flexor muscle mass.

Supracoracoideus

The innervation of the supracoracoideus (from the supracoracoid nerve) clearly sets this muscle apart from the muscles of the pectoralis system. In Sphenodon, this muscle originates on the anterior portion of the outer surface of the coracoid, in front of the origins of the coracobrachialis and biceps muscles. Much the same condition is found in lizards. The crocodile has a similar arrangement, except that with the disappearance of the scapulohumeralis anterior, the supracoracoid muscle has spread dorsally and gained an attachment to

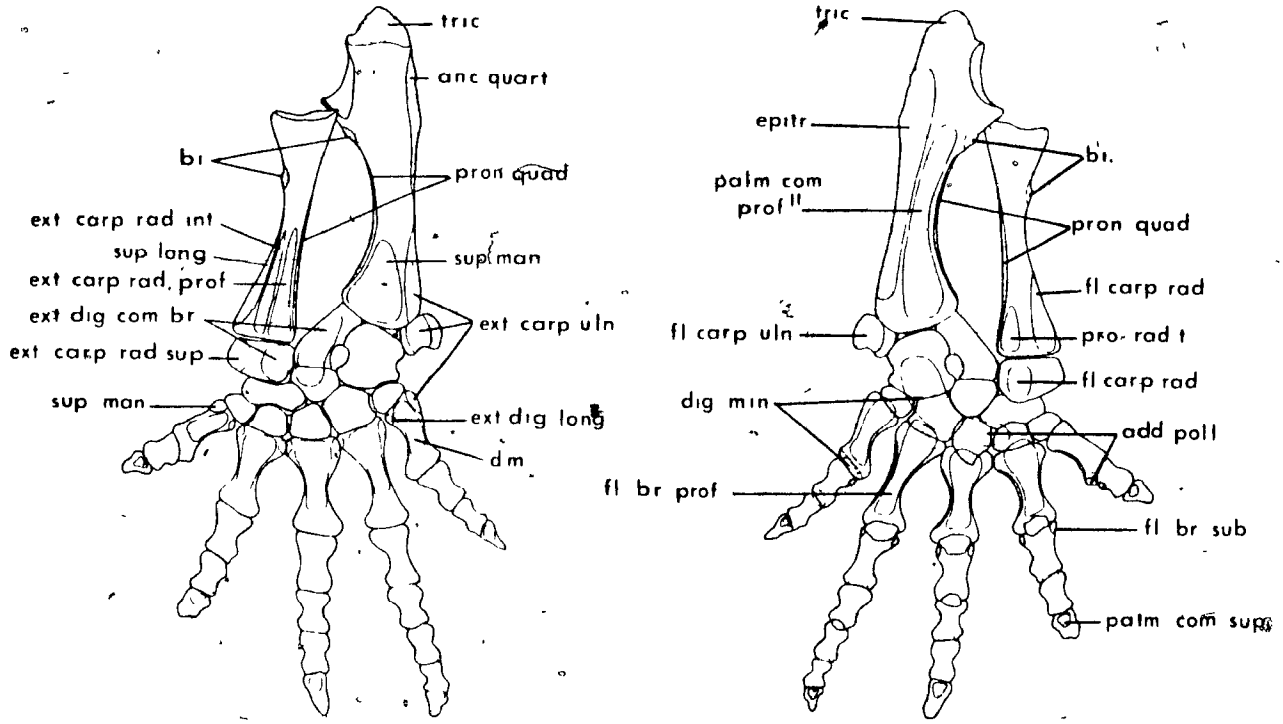


Fig. 22 Areas of muscle attachment in the forelimb of a captorhinid. A, Extensor surface. B, Flexor surface. For abbreviations see " Explanation of Abbreviations ".

the scapular surface as well (Romer 1922). There is no doubt that the supracoracoideus of captorhinids originated from most, if not all, of the external surface of the anterior coracoid.

The insertion of the supracoracoideus muscle in living reptiles is invariably located on the long, curving surface of the deltopectoral crest between the insertions of the pectoralis and deltoid muscles and the proximal articulating surface of the humerus. Rough bone surface of this area of the humerus of captorhinids indicates a similar insertion for the muscle in these forms (fig. 18A, 21A, D).

Clavicular and Scapular Deltoids (Deltoides Clavicularis and Scapularis)

The clavicular deltoid originates from the clavicle in all reptiles in which this element remains (Miner 1925). The scapular deltoid originates from the suprascapula and anterodorsal part of the lateral surface of the scapula in Sphenodon and lizards. It has been suggested by Miner (1925) and Romer (1944) that these two deltoid muscles primitively formed a continuous sheet taking its origin from the clavicle and cleithrum. As the cleithrum became reduced in more advanced forms, the dorsal part of the muscle sheet separated from the clavicular portion and spread its origin over the scapular surface adjacent to the disappearing cleithrum, becoming the scapular deltoid.

As has already been pointed out, no cleithrum has been found in association with captorhinid remains. Although it is quite possible that one existed in captorhinids, it certainly was not a large,

primitive, " capping " cleithrum such as the one present in Diadectes, and probably could not have provided a satisfactory anchor for the scapular deltoid. It seems, therefore, that the deltoids of captorhinids were in the form of two distinct muscles. The scapular deltoid of captorhinids may have taken part of its origin from a cleithrum, but the major attachment was undoubtedly on the anterior part of the scapula and suprascapula. A very shallow depression on the dorsal part of the scapula of captorhinids indicates the area of origin of this muscle (fig. 17A).

The clavicle of captorhinids possesses a posteriorly directed flange on the ventral half of the stem which served as a site for the origin of the clavicular deltoid muscle (fig. 17A).

A conspicuous rugose ridge runs along the upper, proximal part of the deltopectoral ridge from the insertion of the pectoralis to the proximal articulatory surface of the humerus of captorhinids (fig. 21B,D). The position of this ridge corresponds to the area of insertion of the deltoid muscles in living reptiles. It is not possible to identify two separate insertional areas on the ridge, but it is probable that the clavicular and scapular deltoids inserted, perhaps by a partially tendinous attachment, next to each other on this ridge.

Scapulohumeralis

Romer (1922, 1944) considered that the scapulohumeralis posterior could not have been derived from the scapulohumeralis anterior

because the two muscles are separated by the tendinous origin of the triceps scapularis muscle in living reptiles that possess both scapulohumeralis muscles. He postulated that the scapulohumeralis posterior had been derived from the subcoracoscapularis muscle. However, as Miner (1925) pointed out, the innervation of the scapulohumeralis posterior is closely associated with that of the scapulohumeralis anterior, but quite distinct from that of the subcoracoscapularis. He also cited Furbringer (1900), who demonstrated the extreme variability of the origin of the scapular triceps among different lizard genera. Miner argued that similarities in innervation are more valid for the establishment of muscle homologies than the physical relationships between the muscles themselves, especially when these relationships are as variable as those between the scapulohumeralis muscles and scapular triceps. I believe that Miner was probably correct in emphasizing the similar innervation of the scapulohumeralis anterior and posterior in establishing a close relationship between the two muscles, and rejecting the hypothesis that the scapulohumeralis posterior was derived from the subcoracoscapularis.

Only Sphenodon amongst living reptiles possess both a scapulohumeralis anterior and posterior. The crocodiles possess only the posterior muscle (Romer 1944 homologized the deeper fibres of the clavicular deltoid originating from the lateral surface of the scapula with the scapulohumeralis anterior of other tetrapods), and in lizards, only the anterior muscle is present. This suggested

to Miner (1925) that the primitive scapulohumeralis mass was a single muscle, but divided early to produce the condition seen in Sphenodon. Reduction of the posterior muscle gave rise to the lizard condition, and reduction (or fusion with the clavicular deltoid) of the anterior muscle to the crocodilian condition.

There is no osteological evidence for the existance of a separate scapulohumeralis anterior and posterior in captorhinids. It is probable that the separation of the scapulohumeralis into an anterior and posterior slip took place in the progressive, presumably agile, diapsid reptiles to improve the efficiency of their locomotor apparatus. Evolution in various directions has yielded the results seen in living forms. Captorhinids were not closely related to this progressive diapsid group, and although specialized in some features of the skull, constituted a conservative lineage. If it is correct to assume that a single scapulohumeralis muscle is primitive in reptiles, it is probable that captorhinids showed this characteristic.

On the ventral part of the lateral surface of the scapula of captorhinids is a shallow depression, separated by low ridges from the areas of origin of the scapular deltoid muscle dorsally and supracoracoideus muscle ventrally (fig. 16A). This is, no doubt, the location of the origin of the scapulohumeralis muscle. The insertion of this muscle was a fleshy one on the top of the proximal head of the humerus between the insertion of the deltoid and subcoracoscapularis muscles, and proximal to the lateral head of the triceps. An irregular ridge marks this area (fig. 21B).

Latissimus Dorsi

The latissimus dorsi has essentially the same configuration in all living reptiles. It originates as a wide sheet from the fascia of the back, and narrows to insert on the lateral surface of the medial (posterior) process of the proximal head of the humerus, distal to the insertion of the subcoracoscapularis muscle.

The nature of the origin of the latissimus dorsi renders the detection of this area of attachment impossible in fossil forms. The insertion is discernable as a conspicuous ridge running in an anteroposterior direction on the medial surface of the proximal head of the humerus (fig. 21B, C).

Subcoracoscapularis

This muscle in reptiles characteristically originates from the posterior and medial surfaces of the girdle and passes posteriorly behind the base of the scapula to insert on the edge of the medial (posterior) process of the proximal head of the humerus. In lizards, as exemplified by Lacerta (Romer 1944) and in Sphenodon, the subcoracoscapularis can be separated into two slips. The subcoracoscapularis proper originates along most of the posterior border of the bony scapula, and from much of the upper medial surface of that bone as well. A more ventral slip, often called the subcoracoideus, originates from most of the medial surface of the coracoid. Romer (1922) identified the triangular area on the posterior edge of the scapula immediately above the glenoid as the area of origin of the

subcoracoscapularis muscle in primitive reptiles. He, however, doubted the existence of a subcoracoid muscle in these forms. Because of the ridge above the glenoid and the presence of the posterior coracoid in primitive forms, Romer argued, any muscle running from the internal surface of the coracoid to the humerus would have had to turn an angle of about 270 degrees (fig. 23A). However, an examination of his figure 2 (compare with fig. 23A in this paper) suggests that the illustration of the girdle of Dimetrodon was drawn without sufficient compensation for the post-mortem flattening of the scapulocoracoid. Consequently, the scapulocoracoid figured was unnaturally flattened, and the coracoid plate was reconstructed as facing laterally rather than primarily ventrally as would have been the case in an undistorted girdle. If this is taken into account, and the humerus is placed at its proper angle in the glenoid, the largest arc that the fibres of the muscle would have had to describe, from origin to insertion, would have been a semi-circle, a turn of 180 degrees (fig. 23B). This is assuming that the muscle fibres attached at right angles to the plane of the bone surface. In reality, muscles tend to attach to bone surface so that the major force component is directed tangientially to the bone surface (Frazzetta 1968). This means that the angle of attachment was probably much less than 90 degrees for both origin and insertion, considerably reducing the size of the arc through which the muscle fibres must have passed. Furthermore, the insertional area on the humerus is much higher relative to the ridge behind the glenoid,

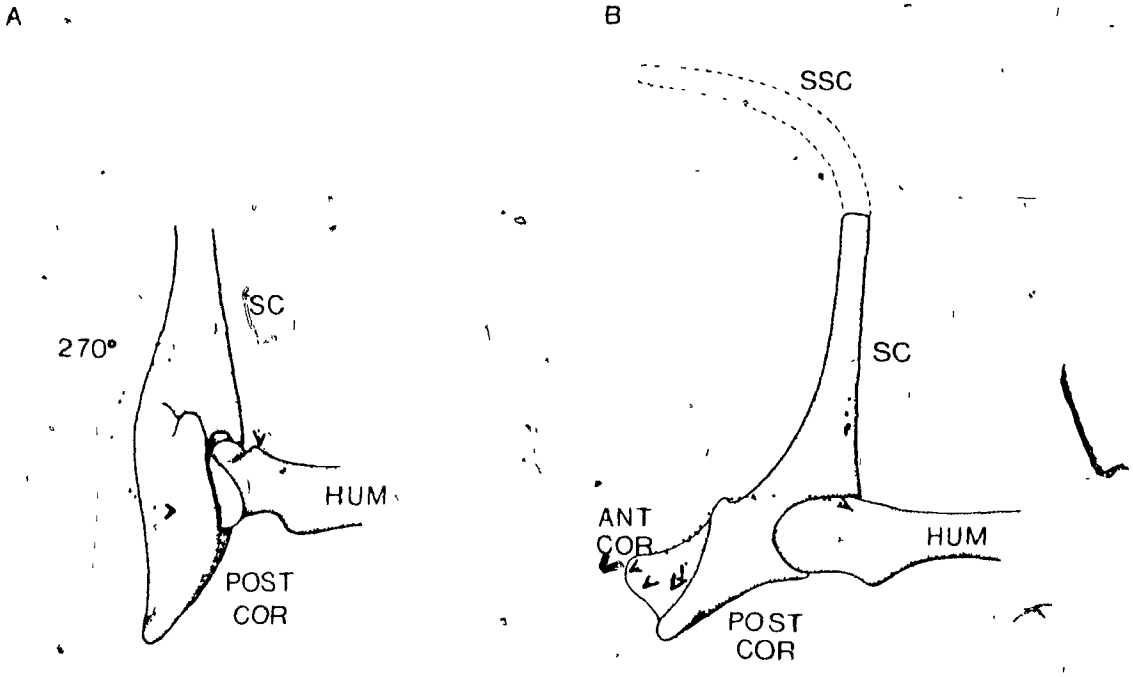


Fig. 23 An illustration of the argument for the possible existence of a subcoracoid muscle. A, Reproduction of figure used by Romer (1922) to establish the improbability of the existence of a subcoracoid muscle in the pelycosaur Dimetrodon. B, Drawing of captorhinid shoulder region corresponding to " A ". For abbreviations, see " Explanation of Abbreviations ".

and although the insertion " cannot look down into the cavity from which (the muscle) arises " (Romer 1922), the existance of a subcoracoid portion of the subcoracoscapularis muscle is conceivable.

The subcoracoscapularis of captorhinids originated from the triangular area on the scapula above the glenoid, as it does in other primitive tetrapods. It also attached to the medial surface of the posterior part of the scapular blade, following the supporting brace of that bone dorsally (fig. 17B). There was probably also a subcoracoid slip of the above muscle that gained some contact on the medial surface of the coracoid as well (fig. 17B). The insertion of this muscle is indicated by a raised area of bone on the proximal part of the process medialis of the humerus of captorhinids (fig. 21B, C).

Triceps (Anconaeus)

The triceps muscles of lower tetrapods can be divided into a medial and a lateral muscle mass. Each can be further subdivided into a long muscle originating, often by a tendon, from the shoulder girdle, and a short muscle originating fleshily from the shaft of the humerus. The long muscle of the medial mass originates from the posterior coracoid (in lizards and Sphenodon from the tendon which functionally replaces the latter), and the short mass originates from the dorsomedial surface of the humerus. The long muscle of the lateral mass originates from the base of the scapula between the subcoracoscapularis and scapulohumeralis anterior muscles, and the

short muscle originates from the dorsolateral surface of the humerus. The long and short heads of each muscle mass fuse together, and the resulting muscles converge on the olecranon process of the ulna. This pattern is quite consistant for all living reptiles except the turtle, where the coracoid head has been lost (Romer 1922). The configuration of the triceps muscles in captorhinids was probably essentially the same as in Sphenodon or lizards. The origin of the long head of the medial (coracoid) muscle mass can be seen as a slight swelling on the posterodorsal corner of the posterior coracoid (fig. 17A). A depression on the edge of the processus medialis of the humerus distal to the insertion of the subcoracoscapularis and ventral to the insertion of the latissimus gives evidence for the proximal extent of the short head of the medial mass (fig. 21C).

The long head of the lateral (scapular) mass must have originated from the vertical ridge of the supraglenoid buttress immediately anterior to the origin of the subcoracoscapularis muscle (fig. 17A), but there are no scars to identify the exact location of the attachment. The same is true for the humeral head of the lateral mass, but it presumably took its origin from most of the dorsolateral surface of the humerus distal to the insertion of the deltoid, scapulohumeralis, and subcoracoscapularis muscles and dorsal to the insertion of the brachialis inferior (fig. 21B,C). A faint ridge, visible on some humeri, running from the processus medialis to the ectepicondyle (fig. 10B) indicates the boundry between the short heads of the medial and lateral muscles. Prominent ridges and grooves covering

the olecranon process of the ulna (fig. 12) suggest that these muscles converged on a tendinous sheet that inserted widely over the surface of this process (fig. 22).

The Musculature of the Forearm

An excellent description of the forearm musculature of Sphenodon and Megalobatrachus was given by Miner (1925). Despite the wide phylogenetic gap between these two animals, this musculature is quite similar. Furthermore, dissection of Iguana and turtles reveal that these animals also share this basic pattern of forearm musculature, especially the lizard. This suggests that the evolution of the forearm musculature has been quite conservative in these tetrapods, and that the arrangement of these muscles reflects a primitive condition similar to that which would be expected in captorhinids.

The formation of the extensor musculature of tetrapods was no doubt a result of differentiation of a primitive extensor mass present in ancestral rhipidistian crossopterygians. That these muscles share a common evolutionary origin is demonstrated by the close proximity of their muscular origins (they form an essentially continous origin from the ectepicondyle) and their common innervation by the brachialis longus superior nerve (see Miner 1925).

The supinator longus (tractor radii) of reptiles originates from the proximal part of the ectepicondyle, and inserts on the medial surface of the radius. Pelycosaurs developed a supinator process on the ectepicondyle, presumably to increase the mechanical

advantage of the supinator longus muscle. Although there is no true supinator process in captorhinids, there is a small knob on the proximal portion of the ectepicondyle that indicates the point of origin of the supinator longus (fig. 21D). The ectepicondyle does not reveal specific evidence of any other muscular origins, but judging from the pattern shown in living reptiles, it seems reasonable to reconstruct these origins as shown in fig. 21B,D.

A ridge running distally from the area of the insertion of the biceps muscle on the radial side of the radius in captorhinids indicates the insertion of the supinator longus (fig. 22A).

The extensor carpi radialis muscle mass primitively appears to have been composed of three muscles. Turtles and Sphenodon show this condition, both possessing an extensor carpi radialis superficialis, profundus, and intermedius head originating adjacent to one another on the ectepicondyle (Haines 1939). In lizards, the superficialis muscle is secondarily missing (Haines 1939). In all living reptiles, these muscles insert adjacent to one another on the extensor surface of the distal end of the radius and on the radial side of the carpus. Haines, in his reconstruction of the extensor musculature of Ophiacodon followed a pattern common to Sphenodon and turtles, in which the profundus and intermedius heads insert on the extensor surface of the radius and the superficialis head inserts on the radiale. Captorhinids show no specific evidence for the insertions of the profundus and intermedius heads, but it is most likely that these muscles attached to the radius as proposed

by Haines for Ophiacodon (fig. 22A). A strong proximodistal ridge and a prominent depression radial to this ridge on the extensor surface of the radiale (fig. 22A) of captorhinids suggests the area of insertion of the extensor carpi radialis superficialis.

The extensor carpi ulnaris of Sphenodon (Miner 1925) and Iguana inserts on the lateral surface of the distal end of the ulna, pisiform, and on the metacarpus V. In crocodiles, the muscle inserts on the entire extensor surface of the ulna and ulnare. In the turtle, the muscle inserts only on the ulna. Although there is no direct evidence of this muscle in captorhinids, the similarities in structure of the carpus between these animals and Sphenodon indicate that its insertion in captorhinids would have been on the distal end of the lateral surface of the ulna, extensor surface of the pisiform, and metacarpal V, (fig. 22A). The anconaeus quartus, a closely related muscle, originates in living reptiles with the extensor carpi ulnaris and inserts along the lateral border of the ulna, proximal to the insertion of the latter muscle. A ridge on the proximal end of the lateral surface of the ulna in captorhinids may indicate the division between the anconaeus quartus and the epitrochleoanconaeus, the latter inserting on the adjacent flexor surface of the ulna (fig. 22A,B).

The extensor digitorum longus (humerodorsalis) presumably arose in captorhinids (fig. 21B,D) from the ectepicondyle between the extensor carpi radialis and extensor carpi ulnaris muscles, as it does in all living reptiles. In Sphenodon and Iguana this

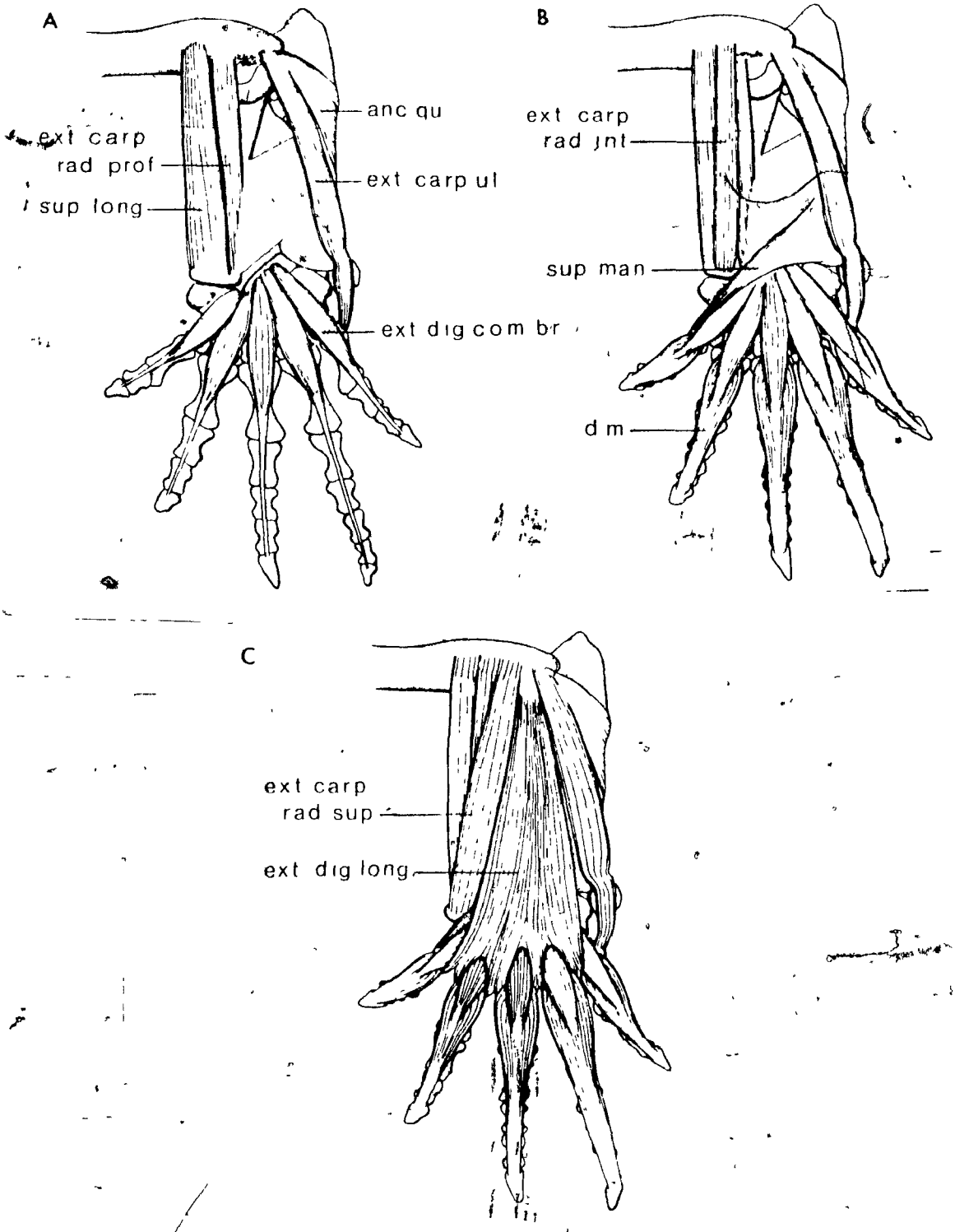
separates at its distal end into several small slips, each slip attaching to a tendon inserting on the ulnar side of the proximal end of a metacarpal (fig. 22A). In the turtle (Walker 1973) the muscle separates, as in other living forms into a series of slips, each with a tendon inserting on the proximal end of a metacarpal. It is significant, however, that tendons from this muscle insert not only on the ulnar side of the metacarpals, as in lizards and Sphenodon, but on the radial side as well. The condition seen in turtles, I believe, is primitive. In most modern reptiles, the carpus has been reduced in relative size as compared with that of captorhinids. The distal end of the carpus is not wide enough to accommodate the proximal expansions of the metacarpals of most living reptiles unless the metacarpals are twisted and oriented so that the ulnar side of the proximal expansion of each of metacarpals I-IV overlaps the radial side of the metacarpal situated laterally to it. This means that the radial sides of metacarpals II-V are covered by the adjacent metacarpal and it would be impossible for a tendon from the extensor digitorum longus muscle to insert on this side of the proximal expansion of these metacarpals. In the turtle, on the other hand, the carpus is very wide, and consequently it is unnecessary for the metacarpals to be stacked as in other living reptiles. This leaves both sides of the proximal expansions exposed. It seems likely that tendons of the extensor digitorum longus inserted on both sides of each metacarpal in captorhinids, much as they do in turtles. Haines (1939) assumed a similar arrangement of the insertions

of the tendons in his reconstruction of the extensor muscles of Ophiacodon. The origin of the extensor digitorum communis brevis muscle in living reptiles is from the proximal, ulnar side of the carpus, usually from the ulnare and intermedium. Depressions on the dorsal surfaces of the intermedium, lateral centrale, and ulnar side of the radiale of captorhinids indicate the probable origin of the extensor digitorum communis brevis (fig. 15, 22A).. These muscles presumably radiated out from this common origin to insert on the dorsal surface of the distal phalanges by tendons, as in lizards and Sphenodon, but there is no osteological evidence for these insertions.

The supinator manus originates from the distal end of the ulna in all living reptiles. The muscle passes diagonally across the lower leg to a more distal insertion of the radial side of the wrist. In Sphenodon, crocodiles and turtles, this muscle inserts on the radial side of the carpus and proximo-radial corner of metacarpus I (Haines 1939). In lizards, the insertion has shifted up onto the distal end of the radius. This transfer of attachment from the carpus to the radius is most likely a result of a general reduction in the size of the carpus in these animals and is therefore a specialized feature of lizards. The insertion of the supinator manus of captorhinids was probably in the more typical reptilian position, located on the radial side of the proximal end of the first metacarpal and surrounding connective tissue.

Dorsometacarpales were presumably present on the dorsal surface

Fig. 24 Extensor musculature of the distal part of the anterior limb of a daptorhinid. A, Deep, B, More Superficial, C, Superficial. For abbreviations, see " Explanation of Abbreviations ".


A
anc qu
ext carp
rad prof
ext carp ul
sup long
ext dig com br
B
ext carp
rad jnt
sup man
d m
C
ext carp
rad sup
ext dig long

of the digits, but there is no osteological evidence for them in captorhinids The origin of each of the dorsometacarpales of many lower tetrapods spreads over several metacarpals. This multiple origin of the dorsometacarpales, although widespread among lower tetrapods, appears to be a specialization (Haines 1939). Haines suggests that primitively, each dorsometacarpale originates from one metacarpal only, as in turtles, and he reconstructed these muscles in this manner in Ophiacodon. It is probable that the dorsometacarpales of captorhinids originated in a similar manner (fig. 22A).

The entepicondyle forms a broad plate which provides ample room for the origin of the flexor muscles of the lower arm and hand (fig. 21D). The pitted and roughened ventral surface of the condyle indicates the general location of the origin of the flexor muscle mass, but it is impossible to distinguish the attachment areas of individual muscles. Only a comparative study of living reptiles has made it possible to reconstruct the origins of the flexor muscles shown in fig. 21D.

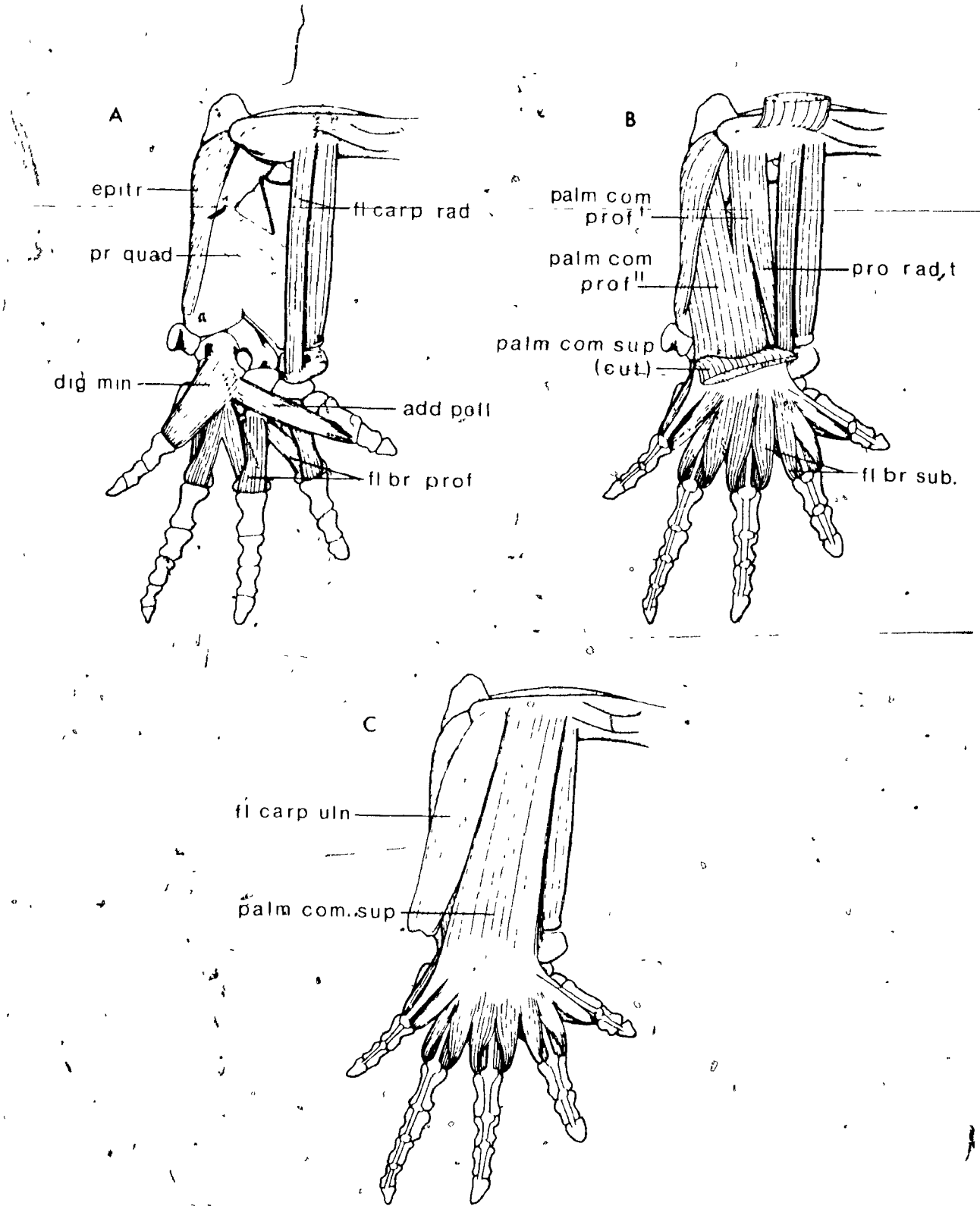
The palmaris communis muscle of lower tetrapods appears to have been generally composed of three heads, a superficial head originating from the ventral surface of the flexor crest (fig. 21D) and two profundus heads, one originating from the flexor crest internal to the superficial head, (fig. 21D) and the other from most of the radial flexor surface of the ulna (fig. 22B). These three heads converge on an aponeurosis. This aponeurosis wraps around the ventral surface of the hand and then breaks up into narrow tendons, each

inserting on a terminal phalanx. This pattern is duplicated in lizards, Sphenodon, and crocodiles. In turtles, there is no profundus head, as such originating from the humerus as it does in the other forms. This exception will be considered more fully in the discussion of the pronator radii teres below. Although there is no direct osteological evidence for this muscle in captorhinids, it seems quite certain that lizards, crocodiles, and Sphenodon demonstrate the primitive condition of the palmaris communis muscle, and it should be restored as such in captorhinids (fig. 25B,C).

The pronator radii teres originates with the humeral head of the palmaris communis profundus in Sphenodon and lizards (McMurrich 1903), from which the former muscle was obviously derived (Miner 1925). It separates from the latter distally and inserts on the distal end of the flexor surface of the radius. In turtles, the pronator radii teres is very large, and appears to have incorporated the humeral head of the palmaris communis profundus, which has lost its attachment to the plantar aponeurosis, and fused with the pronator. The pronator radii teres is present in one form or another in all living groups of reptiles, and must have existed in captorhinids, originating with the humeral head of the palmaris communis profundus (fig. 21D) and inserting as a separate muscle of the distal end of the flexor surface of the radius (fig. 22B, 25B).

The ulnar flexors of reptiles consist of two closely related muscles, the epitrochleoanconaeus, and the flexor carpi ulnaris. The epitrochleoanconaeus takes its origin from the most distal part

Fig. 25 Flexor musculature of the distal part of the anterior limb of a captorhinid. A, Deep, B, More Superficial. C, Superficial. For abbreviations see " Explanation of Abbreviations ".


A
epitr
fl carp rad
pr quad
dig min
add poll
fl br prof
B
palm com prof I
palm com prof II
pro rad, t
palm com sup (cut)
fl br sub.
C
fl carp uln
palm com. sup

of the entepicondyle, and the flexor carpi ulnaris originates immediately proximal to the origin of the former. The epitrochleoanconaeus inserts along the distal portion of the ulnar side of the flexor surface of the ulna in Sphenodon and lizards. Walker (1973) does not recognize a separate epitrochleoanconaeus in Pseudemys, but a specimen that I dissected definitely shows this muscle. It inserts along nearly the whole lateral portion of the flexor surface of the ulna. Roughened bone surface in this region of the ulna of captorhinids (fig. 11C) suggests a similar condition in these forms. In lizards and Sphenodon, the flexor carpi ulnaris muscle originates on the humerus, and passes diagonally across the lower arm from the preaxial to postaxial borders and inserts on the pisiform. In captorhinids, this muscle appears to have taken the same form. The action of the flexor carpi ulnaris muscle in captorhinids, lizards and Sphenodon, judging by its origin, insertion and direction of pull is to supinate the hand as well as flex the ulnar side of the carpus (fig. 25C). The posteriorly projecting pisiform increased the supinating power of the muscle. In crocodiles, the muscle inserts on the ulnare, and in turtles, on the ulnare and pisiform. This shift of insertion away from the pisiform reflects the reduced condition of the pisiform in turtles and especially crocodiles. The pisiform is large in captorhinids, and it seems likely that the muscle inserted on this bone exclusively in this group, as it does in lizards and Sphenodon (fig. 22B, 25C).

The flexor carpi radialis mass of lower tetrapods originates

from the proximal part of the entepicondyle. In all living reptiles except turtles, it splits into two heads. In lizards and Sphenodon, one head inserts on the radial border of the radius, while the other inserts on the flexor surface of the radiale. In crocodiles, both heads insert on the radius. The lone head of the flexor carpi radialis of turtles inserts on the proximal end of the flexor surface of the first metacarpal. The condition shown by Sphenodon and lizards is probably closest to the primitive one, and consequently captorhinids have been restored with two flexor carpi radialis muscles, one inserting on the radius, and the other on the flexor surface of the radiale (fig. 22B, 25A).

Lower tetrapods typically possess a pronator quadratus, normally taking the form of a broad sheet of muscle origination from the radial border of the ulna and inserting on the ulnar border of the radius. This is the condition of the muscle in lizards and Sphenodon. The pronator quadratus (profundus) muscle is absent in some turtles. Where present, it normally originates from the medial border of the ulna, but unlike the condition in other reptiles, inserts on the radial side of the carpus (Walker 1973). No ridges exist on the bone surface of the radius or ulna of captorhinids in the regions where one would expect such a muscle to attach. However, the general condition of the pronator quadratus in lower tetrapods indicates that it originated from most of the radial border of the ulna, and inserted on most of the ulnar border of the radius, and possibly also on the radiale (fig. 22B, 25A).

Living reptiles possess short digital flexors, the flexores breves sublimes. They consist of three muscle sheets, two superficial to the palmar aponeurosis and originating from its ventral surface, and one deep to the aponeurosis, originating from its dorsal surface. The most superficial sheet splits up and the slips of muscle loop around each long tendon of the plantar aponeurosis and converge to form a tendon dorsally. These tendons run distally, dorsal to the tendon of the plantar aponeurosis and insert, each on the base of a phalanx of a digit. The more dorsal superficial muscle sheet of the short digital flexors also breaks up into several slips which loop around the long tendons of the plantar aponeurosis but insert fleshily on either side of one phalanx of each digit. The deep muscle sheet inserts fleshily with the above.

Miner (1925) was able to recognize all three layers of this muscle in urodeles, although they are very small and underdeveloped, and unlike the condition in reptiles, all layers take their origin from the dorsal surface of the plantar aponeurosis, leaving the latter completely exposed ventrally. He suggested that a reptilian condition could have been derived from the urodele condition by an expansion of muscle of two of the three primitive slips of short digital flexors around the long tendon of the palmar aponeurosis, gaining a new attachment on its ventral surface. This, Miner claimed, occurred in response to a need for increased power to flex the digits of reptiles, which were as a group, more terrestrial in habit than amphibians. Since it now appears that the immediate ancestors

of reptiles and the most primitive reptiles were quite terrestrial, it seems most likely that this expansion of the flexores breves sublimes to the ventral surface of the palmar aponeurosis occurred before or during the amphibian-reptilian transition. For this reason it seems most likely that captorhinids possess a short digital flexor system much like that present in modern reptiles (fig. 25B,C).

The contrahendes digitorum of urodeles and amphibians in general is composed of several slips originating from the carpus and inserting on the digits. Because of the development of a powerful short digital flexor system, the contrahendes digitorum mass became reduced in reptiles, and is only represented by two slips in Sphenodon, the adductores pollices and digiti minimi. These muscles originate together from the distal carpals 2, 3, 4, and the ulnare. The adductores pollices inserts on the ulnar side of the joint of the metacarpal and phalanx of digit V. Since the short digital flexors of captorhinids were probably well developed, the contrahendes digitorum musculature would most likely have been no more extensive than that of Sphenodon (fig. 22B, 25A).

Captorhinids also presumably had flexor brevis profundus muscles similar to those found in living reptiles. These muscles typically originate from the distal carpals II-V and metacarpals II-V. Each muscle divides into two, with one slip inserting onto the same metacarpal from which it originates, and the other slip inserting on the metacarpal situated radial to the metacarpal from which the muscle originates (Miner 1925), (fig. 22B, 25A).

SUMMARY AND DISCUSSION

Although separated by a span of at least 230 million years, living reptiles and captorhinids possess a pectoral limb of remarkably similar structure. This similarity, particularly in musculature, not only between captorhinids and living forms, but also among living forms as well testifies to the conservative nature of its evolution in reptiles. There are, however, a few differences in the osteology of the pectoral limb that are important in terms of limb function.

There is a tendency in modern forms towards reduction of the dermal girdle. The cleithrum has disappeared in all living reptiles, the clavicles are absent in crocodiles, and the remaining dermal bones are much lighter and thinner than in captorhinids. The scapulocoracoids of lizards are perforated by a series of fenestrae, each fenestra associated with the origin of a shoulder muscle. The surface of the scapulocoracoid of captorhinids is unfenestrated, but the bone is substantially thinner in the areas corresponding to the locations of the openings in recent forms.

The modifications of the glenoid and associated reduction of the posterior coracoid in modern forms as compared with the condition seen in captorhinids is probably the single most important difference in terms of limb function. The screw shaped glenoid of captorhinids appears to have been a strong joint, strictly regulating the degree of twisting of the humerus as it was drawn back and down through the power stroke. This regulation, however, severely reduced the mobility

of the humerus, and forced the captorhinids to move their forelimb through a stiff, sprawling gait, with little variation in the pattern possible.

The reduction of the posterior coracoid of living reptiles extends the posterior range of the movement of the humerus, and in conjunction with the abbreviation of the glenoid to a ball and socket joint, gave a greater potential range of movement in a vertical as well as horizontal plane. These changes allowed modern forms to abandon the sprawling stance of primitive reptiles, and move the humerus into a position parallel with the trunk.

Since rapid locomotion of modern reptiles is accomplished with the humerus parallel to the trunk and the pectoral limbs under the body, the triceps and biceps carry most of the burden of extension and flexion of the lower limbs. The distal condyles of the humerus of living forms are consequently reduced from the condition seen in captorhinids, where the flexors and extensors played much more important roles in the power and recovery strokes. During the power stroke, the elbow joint of primitive reptiles is placed under severe torsional stress due to their sprawling posture. Because of the major reorientation of the humerus in living reptiles, torsion does not play a major role in the design of the joint. The elbow joint is much more loosely constructed, with none of the modifications for resisting torsion that are present in captorhinids.

There is also a tendency in living reptiles to reduce the relative size of the carpus. In lizards particularly, one or more

of the carpal bones are often reduced or absent, and a simple hinge joint between the radius and ulna and the carpus often develops to replace the complex interlocking of the captorhinid-type carpal structure. In Sphenodon, this interlocking structure is retained, but the carpus is relatively smaller than that seen in captorhinids. In crocodiles, the carpus is relatively narrow, but the ulnare and radiale are greatly elongated, causing the carpus to be longer than in other reptiles. Only turtles possess a carpus of a size comparable to that of captorhinids. Associated with the reduction in width of the carpus among most living reptiles is the tendency for the proximal heads of the metacarpals to overlap in all modern forms except turtles.

Some of the muscles that must have been present in the pectoral limb of captorhinids left no direct evidence in the form of muscle scars, so that their nature and position was determined primarily on the basis of living forms. In the absence of more specific evidence of these muscles, it is inadvisable to discuss the evolutionary changes in their configuration that presumably occurred between primitive and recent reptiles, since such discussion would involve circular reasoning. However, there is direct evidence of the areas of origin and insertion of many of the muscles in captorhinids, and so, a more secure basis for comparison with those of living forms. Of the latter muscles many have not changed appreciably in their origins, insertions, or functions in any of the surviving lineages. Other muscles have become modified in one or two of the living groups, but remained primitive in form in the other orders. The most radical changes in musculature

occur in the Chelonia, where the presence of a shell profoundly altered the architecture of the proximal portion of the pectoral limb.

It is valuable to summarize our knowledge of the muscles that have gone through the most marked evolutionary change from the primitive captorhinid condition to the configuration seen in the various living groups.

In primitive reptiles, the pectoralis muscle originated from the edges of the ventral portion of the clavicle, interclavicle ventral surface of the sternum, and sternocostale. This remains unchanged in Sphenodon and lizards. Since the dermal girdle is reduced in crocodiles, the origin of the pectoralis is limited to the ventral surfaces of an expanded sternum and sternocostale. With the development of a shell and consequent modification of the girdle in turtles, the pectoralis has shifted its origin to the dorsal surface of the plastron. The insertion of this muscle, on the deltopectoral crest of the humerus, is evident in captorhinids and remains constant in most living reptiles. In sea turtles, the deltopectoral crest is shifted distally, increasing the mechanical advantage of the muscle. In the Cheloniidae, the insertion bifurcates. One part of the muscle inserts on the deltopectoral crest of the humerus, and the other part extends as a tendon that inserts on the radius (Walker 1973).

The evolution of the latissimus dorsi is conservative. Primitively, its origin is from the fascia of the back, and inserts on the posterior part of the dorsal surface of the proximal head of the humerus, between the origins of the lateral and medial humeral heads of the triceps

muscle. This general pattern is followed by all living reptiles except turtles. In this group, the muscle originates from the ventral surface of the carapace. The latissimus dorsi and teres major of turtles develop embryologically from the same muscle mass (Walker 1973), and it appears that the teres major of tetrapods evolved from a slip of the latissimus dorsi that gained attachment to the lateral surface of the scapula (Romer 1922). The teres major developed separately in turtles and crocodiles. In turtles, it originates from the anterior surface of the top half of the scapula and fuses distally with the latissimus dorsi. In crocodiles, the teres major originates from the posterior half of the lateral surface of the scapula, and also inserts distally with the latissimus dorsi.

The coracobrachialis musculature of captorhinids had a broad origin from the external surface of the posterior coracoid. Distally, this muscle mass separated into a brevis and a longus head. The brevis head had a large insertion of the proximal half of the flexor surface of the humerus. The longus head inserted distal to the brevis head, on the entepicondyle at the level of the entepicondylar foramen. This pattern has not altered appreciably in lizards and Sphenodon, except that the loss of the posterior coracoid in these forms has limited the area of origin of these muscles. In crocodiles, the longus head has been lost, and the area of the humerus normally occupied by the insertion of that muscle has been taken over by the origin of the triceps humeralis medialis. The coracobrachialis brevis of turtles is very small, but otherwise similar to the condition exhibited by

other reptiles. The coracobrachialis longus has shifted its insertion from the entepicondyle to a much more proximal position on the medial (posterior) surface of the proximal head of the humerus. Since this muscle is very strong, and since it is shorter than the brevis head, Walker (1973) prefers to call it the coracobrachialis magnus.

The proximal head of the biceps brachii of captorhinids originated with the coracobrachialis mass from the posterior coracoid, and inserted on a tendon that passed over the joint capsule. This tendon served as the origin of a more distal head that merged with another muscle, the brachialis inferior. The brachialis inferior took its origin from the ventrolateral surface of the proximal head of the humerus. The muscle formed by the fusion of the distal head of the biceps and the brachialis inferior gave rise, at its distal end, to two tendons tha inserted on the ulna and radius. The biceps and brachialis inferior of Sphenodon are essentially the same. In lizards, the muscular part of the proximal belly of the biceps is reduced, and is represented for the most part by tendinous material. In crocodiles, the proximal belly is completely tendinous. Many turtles have a double biceps, consisting of a superficialis and a profundus mass. The profundus mass usually unites distally with the brachialis inferior. Testudinines and sea turtles have only one biceps, similar to that of other reptiles. It is probable that the double biceps of turtles originated from a splitting of the original single biceps.

In captorhinids, the supracoracoideus muscle originated from most of the lateral surface of the anterior coracoid. The area of

insertion, unchanged in living reptiles, was on the deltopectoral crest of the humerus, proximal to and between the insertions of the pectoralis and deltoid muscles. In Sphenodon, and lizards, the muscle remains unchanged. In crocodiles, the muscle is divided into a coracoid and a scapular head. The development of a separate scapular head of the supracoracoideus can be correlated with the loss of the scapulohumeralis anterior muscle in crocodiles (Romer 1922). The surface of the scapula that normally serves as the origin for the scapulohumeralis anterior of other reptiles is occupied by the scapular head of the supracoracoideus muscle. In turtles, the ventral part of the shoulder girdle is composed of a slender anteromedial projection termed the acromion and a posteromedial projection termed the coracoid. These two elements are connected at their medial tips by a ligament. The supracoracoideus, as a result, consists of two stout heads. The anterior portion takes its origin from the ventral surface and adjacent ligament, and the posterior portion takes its origin from the ventral surface of the coracoid and adjacent ligament.

In primitive tetrapods, the deltoid muscle mass probably originated as an unbroken sheet from the lateral surfaces of the cleithrum and clavicle. With the reduction in the size of the cleithrum in all but the most primitive reptiles, the upper portion of the deltoid mass shifted its origin from the cleithrum to the adjacent lateral surface of the scapula. This process was probably quite advanced in captorhinids, and a separation of the deltoid mass into a scapular and clavicular deltoid muscle seems almost certain. The insertion

of the deltoid muscles was on the dorsal surface of the deltopectoral ridge, as is the case in all living reptiles. The cleithrum is absent in lizards and Sphenodon, and the transfer of the origin of the scapular deltoid onto the scapula is complete. In crocodiles, the clavicles are absent, and the clavicular deltoid originates from the anterior edge of the lower part of the scapula. (Furbringer (1876) claimed that the deltoides scapularis inferior was also partially homologous to the deltoides scapularis of lizards). The deltoid muscle mass of turtles often forms a continuous sheet, originating from the anterior edge of the scapula below the origin of the teres major, from the anterior surface of the acromion, and from the plastron. The ventral (clavicular) half of the muscle is much better developed than the dorsal (scapular) half.

The scapulohumeralis muscle mass of captorhinids probably consisted of a single muscle originating from the lateral surface of the scapula below the origin of the scapular deltoid, and inserting on the dorsal surface of the proximal head of the humerus posterior to the insertion of the scapular deltoid. This muscle appears to have split into two heads in primitive diapsid reptiles. The scapulohumeralis anterior originated from the lower part of the scapula and inserted on the dorsal surface of the humerus. The scapulohumeralis posterior originated more posteriorly and dorsally from the scapula than did scapulohumeralis posterior, and inserted on the dorsal surface of the proximal head of the humerus posterior to the scapulohumeralis anterior. This is the condition seen in Sphenodon. In crocodiles, the anterior head

is lost, functionally replaced by the scapular head of the supracoracoideus. In lizards, the posterior head is usually reduced (Furbringer 1900). Turtles have no muscle corresponding to the scapulohumeralis mass of other reptiles which appears to be functionally replaced by the deltoid musculature.

The subcoracoscapularis muscle of captorhinids originated from the triangular area at the base of the scapula above the glenoid, and from the posterior edge and medial surface of the supporting brace of the scapula. There was probably also a subcoracoid head of this muscle, originating from much of the medial surface of the anterior coracoid. The insertion of the subcoracoscapularis muscle was on the process medialis of the humerus, as it is in all living reptiles. In Sphenodon and lizards the muscle retains two heads. The subcoracoideus portion is probably better developed than it was in captorhinids. In crocodiles, the muscle originates by a single head from most of the medial surface of the scapula. The scapulohumeralis posterior originates from the posterior part of the scapula, preventing the subcoracoscapularis muscle from attaching there. The subcoracoscapularis (subscapularis) of turtles is a very large muscle. It originates from most of the lateral, posterior, and medial surfaces of the scapular prong.

The triceps of captorhinids consisted of a medial and a lateral mass. The long head of the medial mass (coracoid head) originated from the posterior part of the lateral surface of the posterior coracoid, and was joined distally by a short (humeral) head that originated

from the dorsomedial surface of the humerus. The long head of the lateral mass (scapular head) originated from the base of the scapula just anterior to the origin of the subcoracoscapularis muscle, and was also joined distally by a short (humeral) head originating from the dorsolateral surface of the humerus. The medial and lateral muscle masses then united and attached to the olecranon process of the ulna. This is essentially the arrangement in Sphenodon, lizards, and crocodiles. With the loss of the posterior coracoid in Sphenodon and lizards, the long head of the medial mass originates from the sternoscapular ligament, which is the functional replacement of the supporting ridge of the posterior coracoid of primitive reptiles. In crocodiles, the coracoid area is more extensive, and the long head of the medial mass (anconaeus coracoscapularis (Furbringer 1876)) takes its origin from the dorsoposterior corner of the coracoid. Turtles have departed markedly from the primitive pattern. The entire medial mass is gone. The lateral mass is similar in origin and insertion to that of other reptiles, but the long head is very weakly developed.

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EXPLANATION OF ABBREVIATIONS

add. poll.	adductor pollicis
anc. qu.	anconaeus quartus
ANT. COR.	anterior coracoid
bi.	biceps
br. i.	brachialis inferior
cbb.	coracobrachialis brevis
cbl.	coracobrachialis longus
cl. delt.	clavicular deltoid
delt.	common insertion on scapular and clavicular deltoids.
dig. min.	digiti minimi
d.m.	dorsometacarpalis
epist.	episternohyoideus
epitr.	epitrochleoanchonaeus
ext. carp. rad. int.	extensor carpi radialis intermedius
ext. carp. rad. sup.	extensor carpi radialis superficialis
ext. carp. ul.	extensor carpi ulnaris
ext. dig. com. br.	extensor digitorum communis brevis
ext. dig. long.	extensor digitorum longus
fl. br. prof.	flexores breves profundus
fl. br. sub.	flexores breves sublimes
fl. carp. rad.	flexor carpi radialis
fl. carp. uln.	flexor carpi ulnaris
HUM.	humerus

i.	intermedium
l.d.	latissimus dorsi
lev. scap. inf.	levator scapulae inferioris
lev. scap. sup.	levator scapulae superioris
omo.	omohyoideus
p.	pisiform
palm. com. prof.'	palmaris communis profundus, originating from entepicondyle of humerus
palm. com. prof."	palmaris communis profundus originating from flexor surface of ulna
palm. com. sup.	palmaris communis superficialis
pect.	pectoralis
POST. COR.	posterior coracoid
pr. quad.	pronator quadratus
pro. rad. t.	pronator radii teres
rade.	radiale
sbcs.	subcoracoscapularis
SC.	scapula
sc. delt.	scapular deltoid
serr. ant.	serratus anterior
serr. post.	serratus posterior
ses.	sesamoid bone
s.h.	scapulohumeralis
SSC.	suprascapula
stcor.	sternocoracoideus

subc.	subcoracoideus
sup. long.	supinator longus
sup. man.	supinator manus
supracor.	supracoracoideus
trap.	trapezius
tric. lat.	triceps lateralis
tric. med.	triceps medialis
ule.	ulnare