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A Protorothyridid Captorhinomorph Reptile from the Lower Permian of Oklahoma

Robert R. Reisz

ROM

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LIFE SCIENCES CONTRIBUTIONS
ROYAL ONTARIO MUSEUM
NUMBER 121

ROBERT R. REISZ

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Contents

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Abstract

A new primitive captorhinomorph reptile has been found near Fort Sill, Oklahoma, in fissure fill deposits believed to be contemporaneous with the lower part of the Arroyo Formation, Clear Fork Group (Leonardian) and possibly the upper part of the Lueders Formation, Wichita Group (Wolfcampian) of northcentral Texas. This find extends the fossil record of the oldest group of reptiles, the family Protorothyrididae, into the upper part of the Lower Permian.

Although many superbly preserved individual limb elements have been recovered, the lack of any specimens in articulation and the absence of diagnostic features below the familial level precludes naming the animal at this time. The proportions of the limb elements and the concentration of the origins and insertions of the muscles important in the power and recovery strokes of the walking motion near the ends of these bones indicate that this reptile was an agile, lightly built animal.

Introduction

The Suborder Captorhinomorpha occupies a unique position in the phylogeny of reptiles. The central captorhinomorph stock, represented by the family Protorothyrididae, includes the oldest known reptiles and the ancestors of three of the four orders of extant reptiles (Reisz, 1977).

Recent studies of Pennsylvanian (Carroll, 1964, 1969; Carroll and Baird, 1972) and Lower Permian (Olson, 1962, 1967, 1970; Fox and Bowman, 1966; Holmes, 1977; Heaton, 1979) captorhinomorphs have shown that two distinct families (Protorothyrididae and Captorhinidae) can be recognized. The Protorothyrididae, are characterized by high narrow skulls; incompletely ossified opisthotics; presence of ectopterygoids and tabulars; unhooked premaxillae; lightly built skeletons; 29 to 32 presacral vertebrae; unswollen neural arches; moderately tall neural spines; presence of cleithra; slender limb elements including humeri with well-developed supinator processes; narrow manus and pedes. They include six Pennsylvanian and two Lower Permian genera. In the Lower Permian only *Protorothyris* and an undescribed species, represented by MCZ 1474, are known to conform to the protorothyridid morphological pattern. The Captorhinidae, known only from the Lower and Upper Permian, are advanced over the Protorothyrididae in many significant features. The Captorhinidae, characterized by low, wide, massive skulls; hooked premaxillae; ectopterygoids and tabulars replaced by the jugals and postparietals respectively; fully ossified paroccipital processes of the opisthotics; heavily built postcranial skeletons; 25 presacral vertebrae with swollen neural arches and low neural spines; absence of cleithra; short massively built limbs; no distinct supinator process on the distal head of the humeri; wide manus and pedes, include 14 Permian genera.

The major osteological differences between the two families of captorhinomorphs recognized by Clark and Carroll (1973) require the placement of *Romeria* within the family Captorhinidae (Heaton, 1979), which unfortunately necessitates, in accordance with the International Code of Zoological Nomenclature, the abandonment of the family designation Romeriidae and its replacement by the familial designation Protorothyrididae (Price, 1937.)

The fissure fill deposits exposed in the Dolese Brothers' Quarry near Fort Sill, Oklahoma have produced thousands of fragmentary specimens of early Permian amphibians and reptiles. Most of the specimens are the remains of the small captorhinids *Captorhinus* and *Eocaptorhinus* (Fox and Bowman, 1966; Heaton, 1979). In his study of the Middle Pennsylvanian captorhinomorph reptile *Paleothyris,* Carroll (1969) noted the similarity between the humerus of this protorothyridid and the distal fragment of an isolated humerus from the much younger fissure fill deposits of the Dolese Brothers' Quarry. Many complete limb elements have since been recovered, including stylopodia (humeri, femora) and zeugopodia (radii, ulnae, tibiae, fibulae) of the fore and hind limb. Although these elements are dissociated, they clearly belong to a small, slenderly built protorothyridid captorhinomorph.

The specimens in the figures in this paper represent the largest, most completely preserved limb elements available to the author, in addition to the hundreds of uncatalogued specimens found in the collections of the American Museum of Natural History, New York, the Field Museum of Natural History, Chicago, and the Museum of Comparative Zoology at Harvard University.

The Fort Sill deposits appear, on the basis of their vertebrate fauna, to be of the same age as the lower part of the Arroyo Formation of the Clear Fork Group and possibly the upper part of the Lueders Formation of the Wichita Group of the Lower Permian of northcentral Texas (Heaton, 1979). This small captorhinomorph is the latest known survivor of the family Protorothyrididae and is a contemporary of the captorhinids *Labidosaurus* and *Captorhinus*. The scarcity of protorothyridid captorhinomorph remains makes the description of these fossils important, especially in view of the superb quality of the known specimens.

Abbreviations Used in the Figures

add cr	adductor crest
anc quart	anconaeus quartus
cap	capitellum
delt	deltoideus
dist art	distal articular surface
ect	ectepicondyle
ect gr	ectepicondylar groove
ent	entepicondyle
ent f	entepicondylar foramen
fib	fibular surface of articulation
int tr	internal trochanter
interc	intercondylar fossa
is tr	ischiotrochantericus
lat d	latissimus dorsi
p	pectoralis
pop	popliteal area
post r	posterior ridge
prox art	proximal articular surface
scor	supracoracoideus
sup	supinator process
t	''trochlea''
tib	tibial surface of articulation
tr 4	fourth trochanter
tric	triceps

Description and Comparison

Humerus

The humeri (ROM 21732 and 21739, Figs. 1 and 2) are remarkably similar to those in the Middle Pennsylvanian protorothyridids *Hylonomus* (Carroll, 1964) and *Paleothyris* (Carroll, 1969), retaining the tetrahedral configuration common to primitive reptiles. The shaft, however, is better developed than in any other known captorhinomorph, with the possible exception of *Anthracodromeus*. The poor preservation and ossification of the latter, however, make direct comparisons difficult.

The width of the proximal end of the humerus is about 25 per cent of the bone's length and the width of the distal end is about 28.5 per cent of the length. The shaft is exceedingly slender, only about 6.5 per cent of the length. These proportions indicate that this humerus is more slenderly built than that of any other captorhinomorph. In *Captorhinus*, for example, the shaft is about 11 per cent of the bone's length, the width of the proximal and distal heads are 40 and 50 per cent of the length respectively (Holmes, 1977).

The twist of the distal upon the proximal plane is 85 degrees. In all other protorothyridids and in most other primitive reptiles this angle can only be estimated

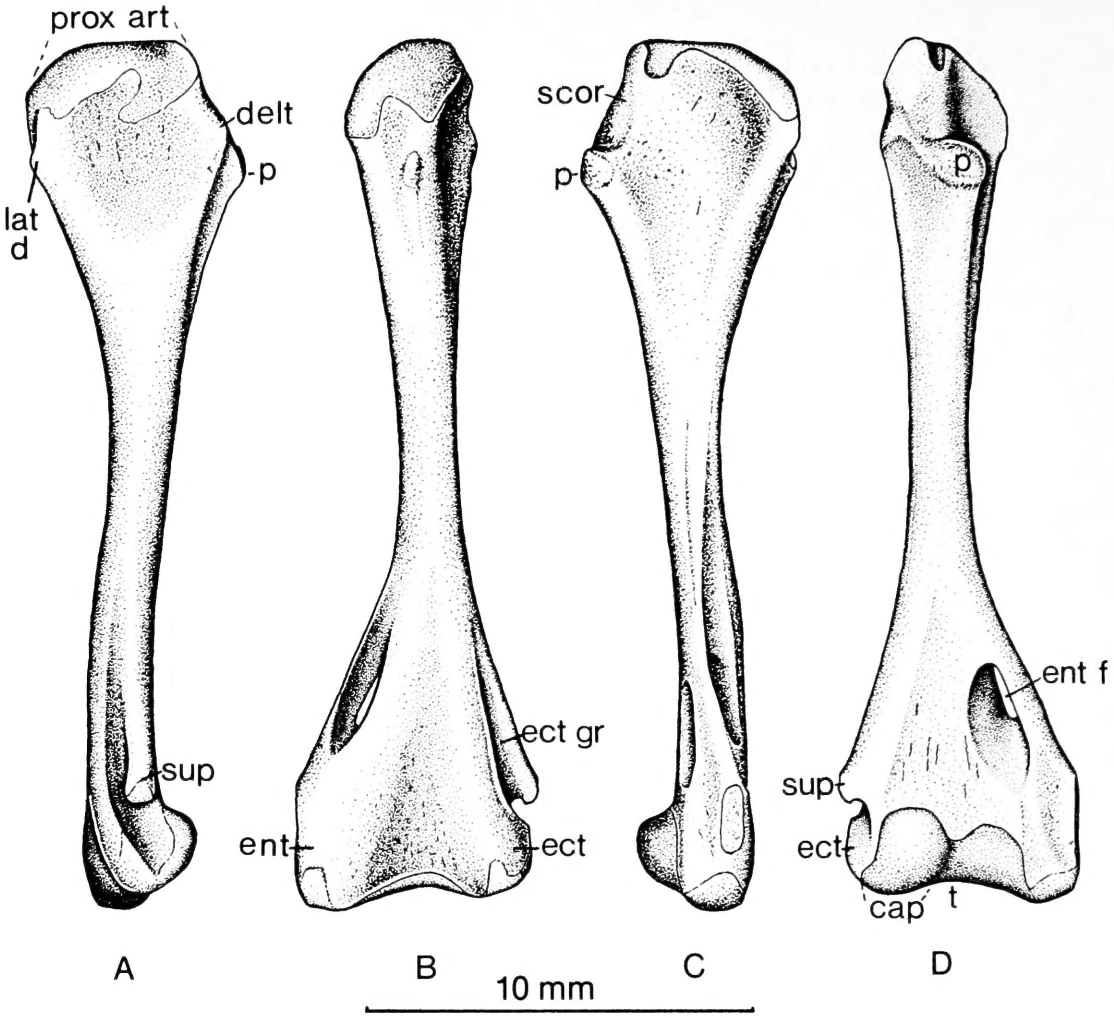

Fig. 1 Humerus (ROM 21732) in (A) proximal dorsal, (B) distal dorsal, (C) proximal ventral, and (D) distal ventral views.

because of crushing. The proximal articulation of the humerus is a long spirally twisting surface composed of an anterior concavity and a large posterior convexity separated by a slight transverse groove. The humeral surfaces are divided into proximal dorsal, proximal ventral, distal dorsal, and distal ventral surfaces (Romer and Price, 1940). Anteriorly, the proximal dorsal surface is separated from the anteroventral deltopectoral crest by a rugose edge. A proximal tubercle on the anterior rugose edge was the region of insertion of the M. deltoideus (Fig. 1). The posterior edge that separates the dorsal surface from the posterodorsal surface also bears a conspicuous ridge and tubercle for the insertion of the M. latissimus dorsi. In ROM 21732 the proximal articulation appears, because of the immaturity of the specimen, to extend onto the dorsal surface beyond its normal confines.

As in most primitive reptiles the deeply concave ventral proximal surface of the humerus was apparently occupied by the insertion of M. coracobrachialis brevis. The anterior proximal area above the deltopectoral crest is rounded and lacks any rugosity (Fig. 1C). In modern reptiles, the M. supracoracoideus inserts in this area. Distally a prominent deltopectoral crest protrudes anteroventrally from the proximal head. At the summit of this crest is a relatively small rugose tubercle for the insertion of the M. pectoralis (Romer, 1922) (Fig. 2B).

Both the deltopectoral crest and the tubercle for the insertion of the M. latissimus dorsi are also visible in *Hylonomus* (Carroll, 1964) and in *Protorothyris* (Clark and Carroll,

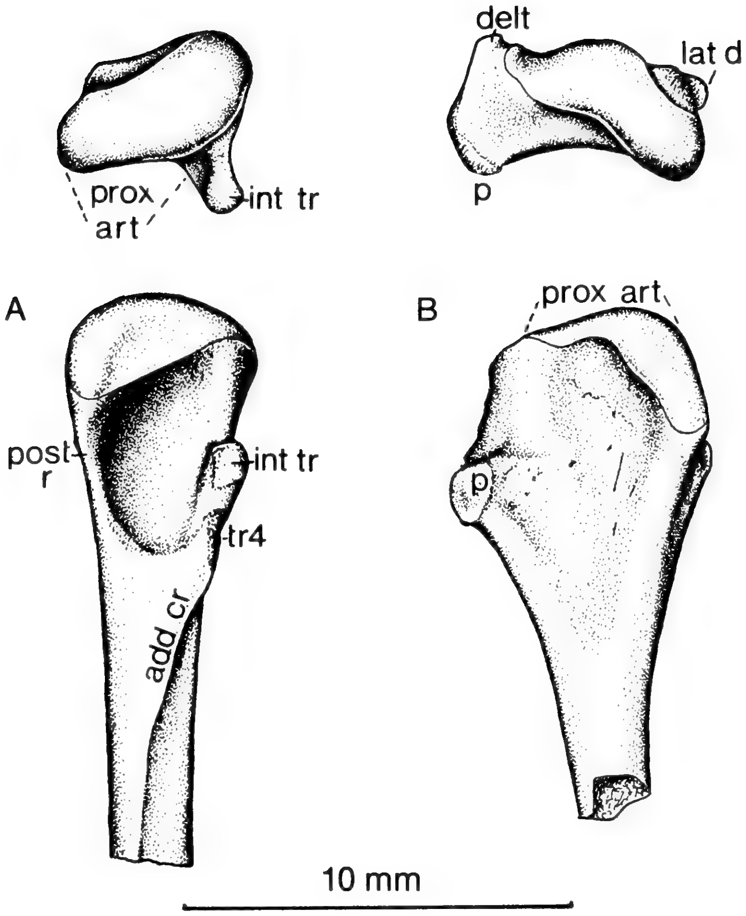

Fig. 2 Proximal ends of mature limb elements. (A) Femur (ROM 21740) in proximal and ventral views; (B) Humerus (ROM 21739) in proximal and proximal ventral views.

1973) but they are located farther distally from the articulating surface than in the Fort Sill protorothyridid. The proximity of these processes to the articulating surface in the new specimens greatly restricts the area available for the insertion of the M. scapulohumeralis and M. subcoracoscapularis on the dorsal and posterior surfaces and the M. supracoracoideus on the anteroventral surface.

A large entepicondylar foramen and a distally oriented supinator process are distinguishing features of the distal head of the humerus. The humeralis inferior nerve probably ran along the deep groove on the dorsal surface of the entepicondyle (Fig. 1B) and passed through the elongate entepicondylar foramen, as in *Sphenodon*. The entepicondyle does not extend far laterally. Its rugose lateral and distal margin, unfinished in ROM 21732, furnished the areas of origin of the flexor musculature of the lower arm and foot. The lateral edge of the entepicondyle at the level of the entepicondylar foramen is formed by a sharp ridge for the probable insertion of the M. coracobrachialis longus. On the distal dorsal surface, the entepicondyle is separated from the ectepicondyle by a shallow concavity that widens distally. The poorly developed entepicondyle, which is much smaller than in pelycosaurs, is a low ridge that turns posteroventrally at its distal end. Anteriorly the ectepicondyle is bounded by the long ectepicondylar groove (Fig. 1A). The ectepicondylar groove is shorter in pelycosaurs than in this protorothyridid and is absent in captorhinids. Anterior to the deep ectepicondylar groove, which carried the radial nerve, the supinator process lies ventral to the level of the ectepicondyle and the general dorsal surface. As in *Paleothyris* the supinator process in the humerus of the Fort Sill protorothyridid extends far distally. The radial nerve was not fully surrounded by bone as it traversed the humerus, but the slight gap between the distal end of the supinator process and the ectepicondyle was probably bridged by cartilage. The supinator and extensor musculature of the lower arm and foot originated from the rugose distal heads of the supinator process and ectepicondyle.

Although the humerus of the best-known protorothyridid *Paleothyris* has a well-developed supinator process, this condition has been considered unusual instead of characteristic of the family. The structure of the humerus of protorothyridids was considered to be similar to that of their captorhinid descendants. All known captorhinids have a single prominent ridge anteriorly on the distal expansion of the humerus, instead of a separated ectepicondyle and supinator process. Examination of a humerus of *Hylonomus,* BM (NH) R. 4168 (Carroll, 1964, fig. 1), reveals, however, the presence of a supinator process similar to that in *Paleothyris* and the Fort Sill protorothyridid. The badly worn humerus of *Protorothyris,* seen in MCZ 1532 (Clark and Carroll, 1973, fig. 7) has a deep groove that runs along the anterior edge of the distal head. This groove corresponds exactly to the ectepicondylar groove of *Paleothyris* and the protorothyridid from Fort Sill; it therefore provides strong evidence for the presence of a supinator process in this species.

The only other protorothyridids that have preserved humeri are the immature specimens of *Cephalerpeton* and *Anthracodromeus*. The region of the supinator process in *Cephalerpeton* is not ossified. Immature specimens of the Fort Sill protorothyridid are also unossified in this region. The only known specimen of *Anthracodromeus* is not only too immature but also is too poorly preserved to show the presence of a supinator process.

The development of a distinct supinator process is a common occurrence in early tetrapods, but its shape and position relative to the rest of the humerus distinguishes protorothyridids from most other tetrapods. In pelycosaurs, diadectids, and limnoscelids, for example, the stout supinator process extends anteriorly, roughly perpendicular to the long axis of the humerus, usually at the level of the entepicondylar foramen (Romer, 1956). The ectepicondylar groove is usually poorly developed. In protorothyridids, by contrast, the supinator process extends far distally, close to the level of the elbow joint and does not project far laterally. The ectepicondylar groove separating the weakly developed ectepicondyle from the supinator process is long. The humerus of the Carboniferous eosuchian *Petrolacosaurus* (Reisz, 1977) has a similar type of supinator process to that seen in protorothyridids, but this eosuchian can be distinguished readily by its much greater size and relative slenderness.

The captorhinids, as already noted, lack a distinct supinator process (Holmes, 1977). The lateral edges of the distal ventral surface are formed by the entepicondyle and the ectepicondyle. Between these margins the ventral surface is relatively flat, but is pierced by the large, oval entepicondylar foramen. This foramen and its related depressions on the dorsal and ventral surfaces are relatively larger than in captorhinids or pelycosaurs.

Most of the distal end of the humerus is occupied by the elongate convex radial, and the slightly concave ulnar, surface of articulation (Fig. 1D). The ventrally facing capitellum is continuous with the ventrodistally oriented ulnar articulation. In contrast to the condition seen in captorhinids and pelycosaurs, the distal expansion of the humerus in the Fort Sill protorothyridid does not extend far beyond the confines of the elbow joint. The slight development of the entepicondyle and of the ectepicondyle, typical of all protorothyridids, greatly restricts the areas of origin and reduces the mechanical advantage of the flexors and extensors, muscles important in the power and recovery strokes of the walking motion in primitive reptiles. Although the shoulder and elbow joints were probably as restricted in the protorothyridids as in all other primitive reptiles, and therefore none of the significant evolutionary changes that freed the movement of the lizard forearm are evident in this or any other protorothyridid, the humeri have become similar in proportions to those of agile extant lizards (Holmes, 1977). The slenderness of the humerus may be a reflection of the light build of the reptile.

Radius

The radius is a long, unusually slender, nearly cylindrical element, with convex dorsal, partially flattened ventral surfaces and slightly expanded ends. In ROM 21733 (Fig. 3) the shaft is about 6 per cent of the bone's length, the breadth of the proximal end measures only about 16 per cent of the length and the distal width only about 13 per cent of the length of the bone. The radii of this captorhinomorph are, therefore, slightly more slender than those of other primitive captorhinomorphs but are much more lightly built than are those of captorhinids and pelycosaurs of small size. In *Captorhinus,* for example, the shaft is about 11 per cent of the bone's length, the width of the proximal and distal heads are 26 per cent of the length (Holmes, 1977).

The proximal head of the radius has a mediolaterally elongated concave articular surface that matches the rounded surface of the capitellum. As in *Paleothyris* (Carroll, 1969) and in *Captorhinus* (Holmes, 1977), the articular surface extends slightly onto the flattened ventral surface (Fig. 3C).

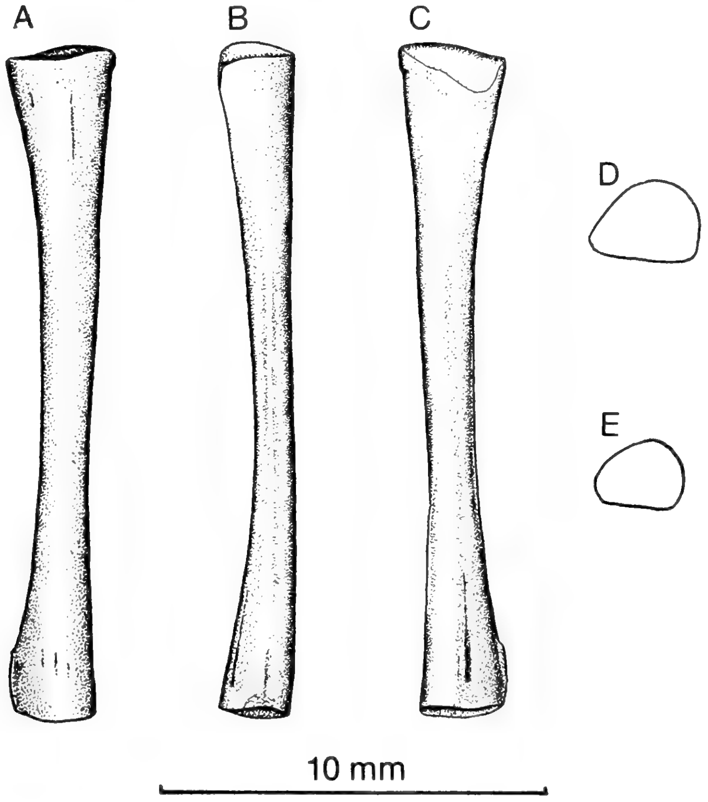

Fig. 3 Radius (ROM 21733) in (A) anterior, (B) medial, (C) posterior views, and outlines of the (D) proximal and (E) distal ends.

A longitudinal ridge that extends on the medial surface (Fig. 3B) along two-thirds the length of the bone is prominent only distally. This radius lacks the prominent tuberosity for the biceps tendon that is commonly found on the medial surface, near the proximal head of the radius, in captorhinids and pelycosaurs. Another longitudinal ridge extends on the lateral surface, as in many pelycosaurs (Romer and Price, 1940: 228), from the distal head onto the posterior surface. This ridge may represent the site of attachment of the M. pronator quadratus, a muscle that originated from the ulna. In contrast to the radius in captorhinids and pelycosaurs, this radius in only slightly arched and the distal articular surface is perpendicular to the long axis of the bone.

Amongst protorothyridids, radii are known only in *Paleothyris* (Carroll, 1969) and *Protorothyris* (Clark and Carroll, 1973). They resemble the radius of the Fort Sill protorothyridid in general proportions, but are too poorly preserved for detailed comparisons.

Ulna

The ulnae (ROM 21734 and 21735, Figs. 4 and 5) of the Fort Sill protorothyridid resemble those of *Paleothyris* and *Protorothyris* in general proportions, in the configuration of the prominent proximal and distal expansions, in the proximal subterminal sigmoid notch for articulation with the humerus, and in the distal articular surface for the carpus. Detailed comparisons with these protorothyridids is not possible because of the poor preservation of this bone.

The olecranon is well ossified in the Forst Sill specimens ROM 21734 and 21735, but less mature specimens have incompletely ossified olecranons. In ROM 21734 (Fig. 4)

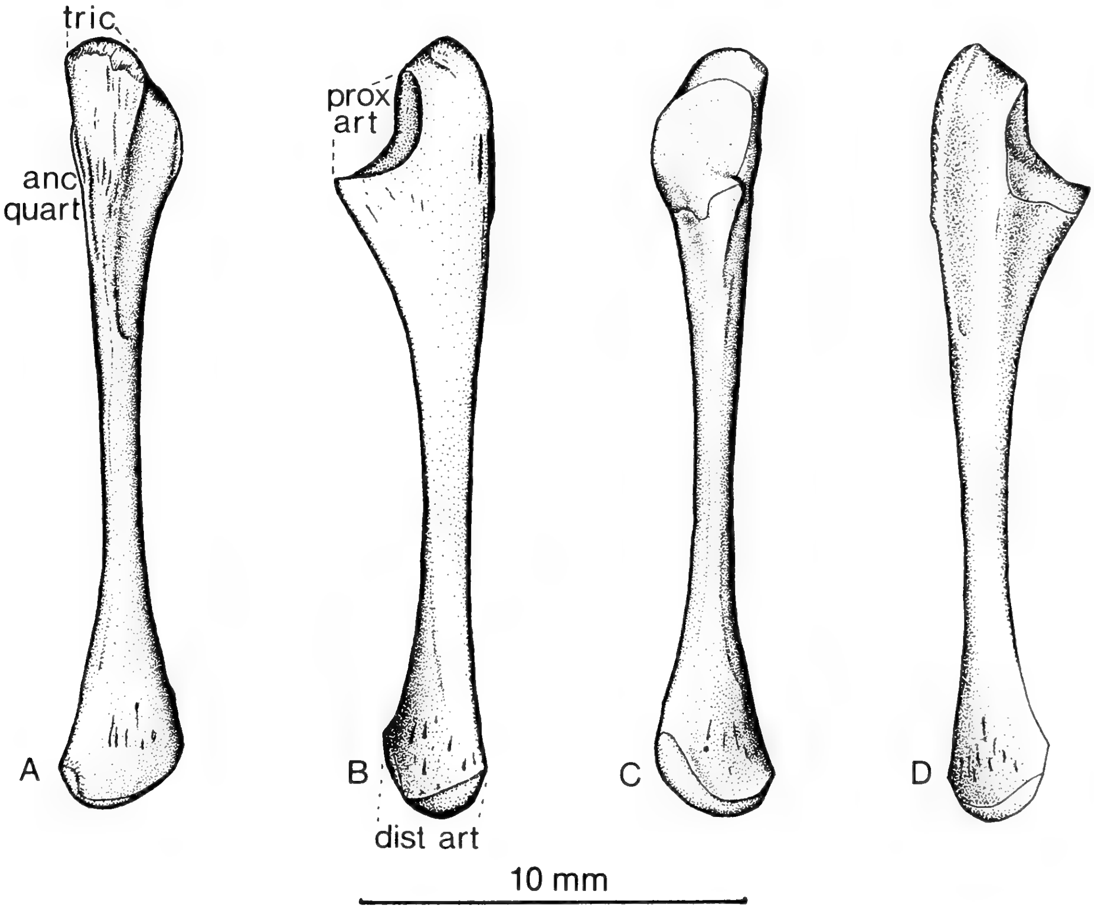

Fig. 4 Ulna (ROM 21734) in (A) lateral, (B) posterior, (C) medial, and (D) anterior views.

the width of the olecranon, measured from the medial end of the sigmoid notch, forms 20 per cent of the length of the ulna. Similar proportions are found in some of the sphenacodontine pelycosaurs (Romer and Price, 1940 : 147) and in protorothyridids (Carroll and Baird, 1972), but it is the small diameter of the shaft, 6 per cent of the length of the bone, which gives the ulna of the Fort Sill protorothyridid its unusually slender appearance. The proximal end of the ulna is capped by a rugose ridge that curves over the apex of the bone. Distally from this ridge, to which the tendon of the M. triceps attached, the rugose lateral surface of the olecranon forms a triangular area for the insertion of the M. anconaeus quartus (Fig. 4A).

The sigmoid notch retains the general pattern seen in most primitive reptiles, a strap-shaped surface composed of a small anteroventral region articulating with the medial surface of the capitellar protuberance of the humerus and a larger posterodorsal surface separated by a curved ridge (Fig. 4C). This ridge fits into a deep groove located medial to the capitellum of the humerus.

The anterior and posterior surfaces of the ulna are separated medially by a gently rounded ridge that carries a rugose protuberance, in *Captorhinus* (Holmes, 1977), for insertion of the M. biceps tendon. The ulna of the Fort Sill protorothyridid lacks this process (Fig. 4C).

Distally the expansion of the ulna ends in an elongate convex surface of articulation with the carpus. The broad, slightly convex surfaces of the distal head face posterolaterally and anteromedially, in accordance with the torsion of the shaft of the bone.

A pathological specimen (Fig. 5) has been found among the dozens of ulnae examined. The highly distorted head of this slightly immature ulna appears to be the result of inadequate repair following a fracture.

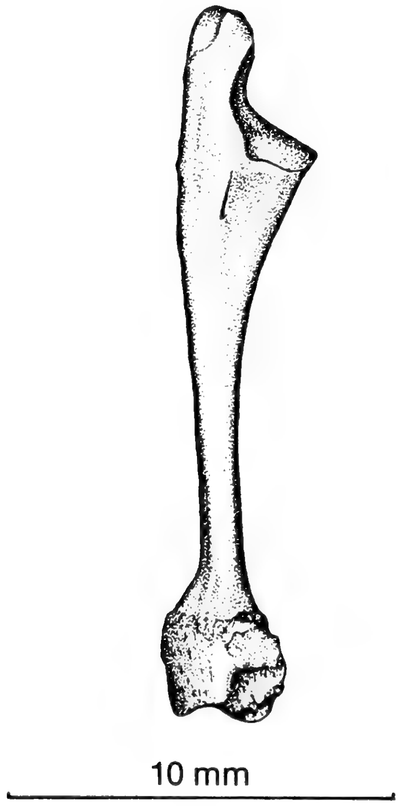

Fig. 5 Pathological ulna (ROM 21735) in anterior view.

Femur

Except for its lighter build and larger size this femur (ROM 21740 and 21736, Figs. 2A and 6) resembles that of *Paleothyris* and *Protorothyris*. The width of the proximal end of the femur forms 17 per cent of the length of the bone. The width of the distal end is about 21 per cent of the length. The shaft is exceedingly slender, only about 6.5 per cent of the length. In all these proportions this femur is much more slenderly built than those of any captorhinid. In *Captorhinus,* for example, the shaft is about 13 per cent of the bone's length, the width of the proximal and distal heads are 30 and 37 per cent of the length respectively (Fox and Bowman, 1966).

There is a definite curvature to the bone (Fig. 6B), the proximal head turned dorsally and the distal head turned slightly ventrally. This curvature, also seen in *Paleothyris* and most extant reptiles, is not found in either captorhinids or pelycosaurs (Romer and Price, 1940). On the ventral surface the deep intertrochanteric fossa is bound posterodistally by a slightly rugose limiting ridge that extends to the prominent internal trochanter. The proximal end of the internal trochanter, set off from the head of the femur by a slight notch as in *Paleothyris,* has a rugose process for the tendinous

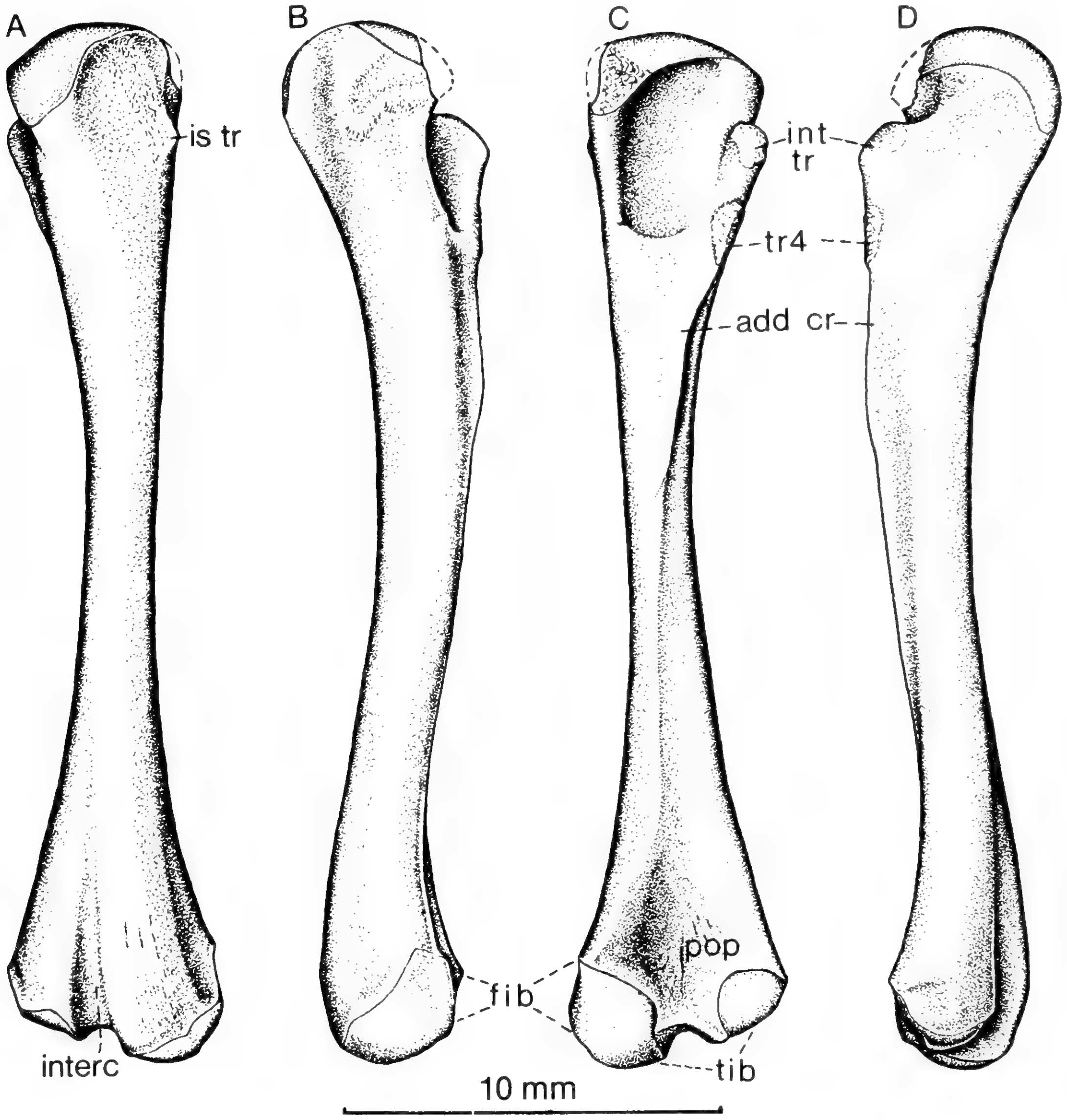

Fig. 6 Femur (ROM 21736) in (A) dorsal, (B) posterior, (C) ventral, and (D) anterior views.

insertion of the M. puboischiofemoralis (Fig. 2B). Distally from this process, the ridge that extends diagonally along the ventral surface of the shaft to the popliteal area has a short slightly rugose surface that probably represents the fourth trochanter for insertion of the M. caudofemoralis, and a long adductor crest that extends nearly to the middle of the bone (Fig. 6C).

On the dorsal surface the areas of attachment of the M. ischiotrochantericus and the M. puboischiofemoralis internus form a conspicuous swelling near the proximal surface of articulation (Fig. 6A, B). On the distal head of the femur the intercondylar fossa is long and quite deep.

Tibia

Except for the smaller size of the cnemial process for the attachment of the M. triceps, the tibia closely resembles that of *Paleothyris*. The bone is strongly arched, much as in other captorhinomorphs and in pelycosaurs; it is deeply concave posterolaterally. The width of the proximal end of the tibia forms 28 per cent of the length of the bone. The width of the distal end is about 16 per cent of the length. The shaft is not unusually slender, about 9.5 per cent of the length.

The much expanded proximal end is occupied by the two femoral articular surfaces, separated by a groove which extends posteromedially from the anterior surface and ends in a deep pocket between the articular surfaces. In ROM 21737 (Fig. 7) a narrow strip of bone extends from the socket to the posterior margin, separating the proximal surface of the bone into distinct medial and lateral articular areas, as in the case of the distal head of the femur. Such a high degree of ossification indicates that this tibia belonged to a mature, adult individual.

The anterior and posterior (extensor and flexor) surfaces are partially separated medially (Fig. 7D) and laterally (Fig. 7B) by a pair of well-developed ridges. The medial ridge commences near the proximal head and extends diagonally across the medial surface onto the posterior surface of the distal head. A well-developed ridge extends along the lateral surface from near the posterior surface of the proximal head diagonally across to the anterior surface of the distal head of the tibia. In the middle of the shaft a pronounced tuberosity is associated with the lateral ridge.

The distal end of the tibia has an oval outline and a small concavity in the center of the articular surface. The long axis of the distal articular surface extends anteroposteriorly, whereas the long axis of the proximal double articular surface is directed mediolaterally. This is in accordance with the general torsion of the tibia, much as in the case of the ulna.

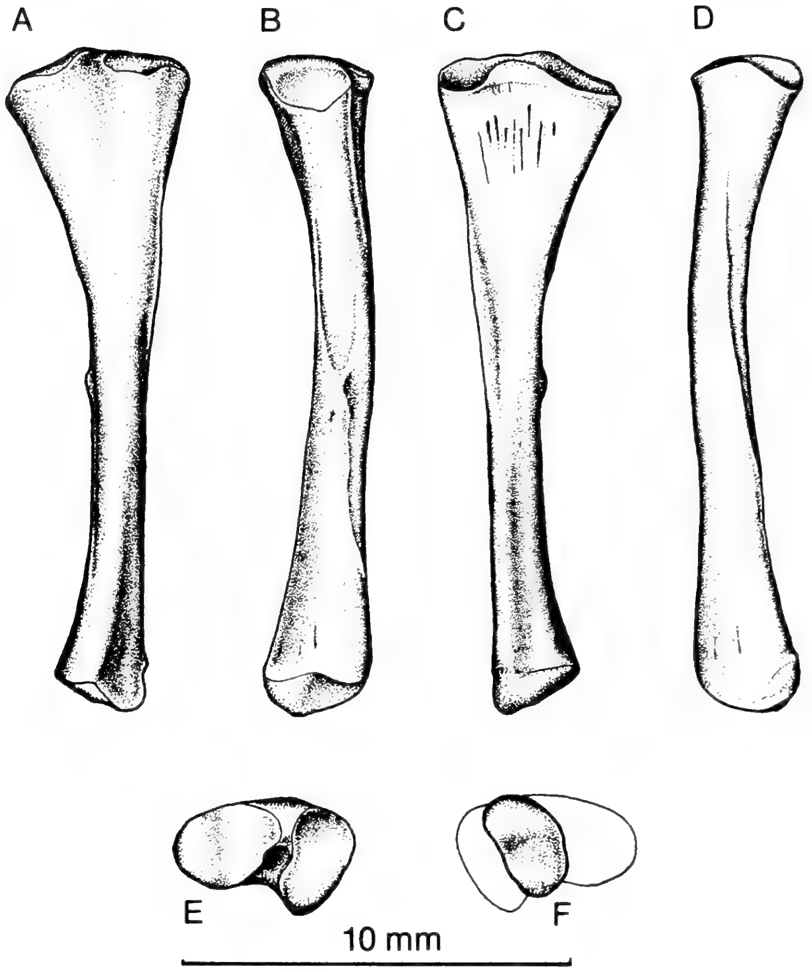

Fig. 7 Tibia (ROM 21737) in (A) anterior, (B) lateral, (C) posterior, (D) medial, (E) proximal, and (F) distal views.

Fibula

The only known fibula (ROM 21738, Fig. 8) is incompletely ossified, without any rugosities or ridges on the finished surfaces of the bone, and with poorly differentiated articular surfaces. The shaft is very narrow, only 6 per cent of the length, but expands proximally and distally to 18.5 per cent of the length. The distal head of the fibula is much expanded mediolaterally to form an elongate surface of articulation with the astragalus and calcaneum. The fibula shows little twisting or arching, in strong contrast to the condition seen in both captorhinids (Holmes, 1977), and pelycosaurs (Romer and Price, 1940), where the medial margin of the bone is strongly concave, and the twist of the distal plane upon the proximal plane is at least 45 degrees.

Amongst other protorothyridids, the fibula is well preserved only in *Paleothyris*. With the exception of a somewhat larger proximal head there is little to differentiate the fibula of the Fort Sill protorothyridid from that of *Paleothyris*.

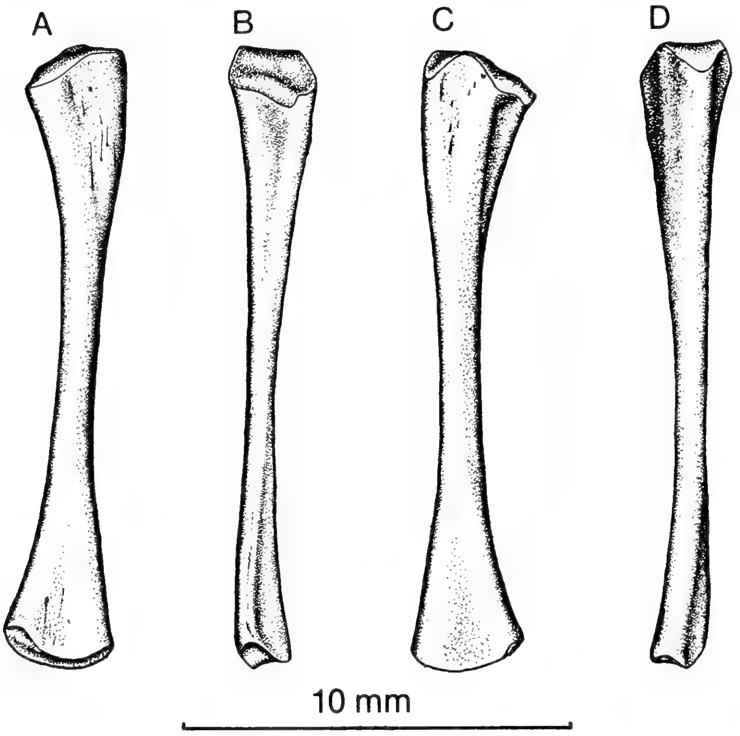

Fig. 8 Fibula (ROM 21738) in (A) posterior, (B) medial, (C) anterior, and (D) lateral views.

Discussion

The limbs of protorothyridids are poorly known, with complete well-ossified stylopodia and zeugopodia preserved only in *Paleothyris*. All other protorothyridids (Carroll and Baird, 1972; Clark and Carroll, 1973) have either incompletely preserved or ossified limb elements. The excellent quality of preservation of the protorothyridid limb elements from Fort Sill, in which all surfaces were exposed when the matrix was completely removed by washing with water, allows a more complete description than in any other protorothyridid.

The specimens show that, as in other protorothyridids, the areas of origin and insertion of the muscles important in the power stroke and recovery are concentrated nearer to the ends of the bones than in either captorhinids or pelycosaurs. These muscles acted in protorothyridids as Class III levers with short moment arms and produced rapid movement of small force at the distal end of the humerus and femur. On the humerus, for example, the areas of insertion of the M. pectoralis, M. deltoideus and M. supracoracoideus were concentrated on the proximal 17 per cent of the bone. In both *Captorhinus* (Holmes, 1977) and *Archeothyris* (Reisz, 1972) power stroke and recovery muscles inserted on the proximal 29 per cent of the humerus. On the femur, the areas of insertion of the M. caudofemoralis, M. puboischiofemoralis externus and internus, and M. ischiotrochantericus were all concentrated on the proximal 24 per cent of the bone. In both pelycosaurs and captorhinids these muscles inserted on the proximal 35 to 50 per cent of the femur (Fox and Bowman, 1966; Romer and Price, 1940). The concentration of the above muscle origins and insertions close to the ends of the bones and the proportions of the stylopodia and zeugopodia indicate that this small reptile from Fort Sill, like the earlier protorothyridids, was a slender, agile, lightly built animal, in strong contrast to the massive, heavily constructed relatives, the captorhinids.

The limb elements described here can be readily assigned to the Protorothyrididae, and can be distinguished from all captorhinids and pelycosaurs on morphological grounds. The humerus and femur of the Upper Pennsylvanian eosuchian *Petrolacosaurus* and its Lower Permian relative *Araeoscelis* are surprisingly similar to those of the Fort Sill protorothyridid (Vaughn, 1955; Reisz, 1977). In only two significant characteristics are the stylopodia and zeugopodia of these two reptiles advanced over the pattern seen in earlier protorothyridids: the first character is limb proportions, the second is zeugopodial to stylopodial ratios.

1) The limb elements of mature individuals of both *Petrolacosaurus* and *Araeoscelis* are at least two and a half times larger than those of protorothyridids. Despite these size differences, the humeri and femora of *Petrolacosaurus* and *Araeoscelis* retain similar proportions (shaft to length ratio, proximal width to length ratio, distal width to length ratio) to those of protorothyridids. Since the shaft diameter of these limb elements is directly proportional to the volume of the animal, the two genera can be considered to be of relatively lighter build, or to have relatively longer limbs than protorothyridids.

2) In all protorothyridids, including that from Fort Sill, the zeugopodia are considerably shorter than the stylopodia. This pattern represents the primitive reptilian condition, where the zeugopodial length is in general equal to about two-thirds of the stylopodial length. In *Petrolacosaurus* the zeugopodia are equal in length to the stylopodia, whereas in *Araeoscelis* the zeugopodia are even slightly longer than the stylopodia, a very specialized condition. In both of these genera the zeugopodia are exceedingly slender, with shaft diameters of 3.5 to 5 per cent of the length.

The limb elements of the Fort Sill protorothyridid are not sufficiently diagnostic below the familial level to warrant the naming of this reptile. Several cranial fragments from Fort Sill have already been named. Of these *Delorhynchus,* based on fragmentary maxillae (Fox, 1962) and *Colobomycter,* based on a partial right cheek and skull table (Vaughn, 1958a) have been placed among the Pelycosauria. Their similarity to primitive captorhinomorphs that were subsequently described (Carroll, 1964; Carroll and Baird, 1972) suggests that these two genera may be protorothyridids, but articulated specimens are needed before their identity can be established.

Relatively small sphenacodont pelycosaurs have also been found at Fort Sill. Both *Thraumosaurus* (Fox, 1962) and *Basicranodon* (Vaughn, 1958b) are based on cranial fragments, but their postcranial skeletons, when found, would be readily distinguishable from the protorothyridid remains, described here, on morphological grounds. In addition, the skull fragments indicate that these sphenacodonts would be considerably larger than the protorothyridid captorhinomorph from these deposits.

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