THE STRUCTURAL AND FUNCTIONAL EVOLUTION OF THE DIAPSID TARSUS

by

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ABSTRACT

During the evolution of diapsids, the tarsus underwent considerable structural change. An analysis of the mechanics of each kind of tarsus based on x-ray studies of locomotion and studies of the structure of the pelvic limb in extant diapsids indicates that the early structural changes are related to the development of an intratarsal joint and consolidation of the metatarsus. Primitively, warping of the distal tarsal row was an integral part of the functioning of the tarsus. Key changes in the origin of the lizard tarsus were changes in the joints that eliminated the need for this movement of the distal tarsals. This was probably followed directly by the hooking of the fifth metatarsal and consolidation of the metatarsus. A distinctive type of tarsus is seen in the earliest rhynchosaurid Noteosuchus, the protorosaurian reptiles, the earliest archosaur Proterosuchus and in Trilophosaurus. This kind of tarsus is a suitable structural ancestor to the tarsus of advanced rhynchosaurids, archosaurs and possible sphenodontids. Three kinds of tarsi are present in advanced archosaurs: the crocodile-normal tarsus, the crocodile-reverse tarsus, and tarsi with mesotarsal ankle joints. The crocodile-normal and crocodile-reverse tarsi probably evolved independently from the primitive archosaur tarsus. The mesotarsal joint in thecodonts and pterosaurs probably originated from the primitive archosaur tarsus, the mesotarsal ankle joint in dinosaurs may have originated from a crocodiloid tarsus.

EXTRAIT

Pendant l'évolution des reptiles diapsides, le tarse s'est changé considérablement. Une analyse des mécaniques de chaque genre de tarse, fondée sur des études radiographiques de la locomotion et des études de la structure du membre postérieur des reptiles diapsides extants indiquent que les changements structuraux initials sont rélatifs à l'évolution d'une articulation intertarsienne et au raffermissement de détatarse. La déformation primitive de la rangée tarsalienne faisait une partie intégrale du fonctionnement du tarse. Les changements importants dans l'origine du tarse du lézard étaient des changements de l'articulation qui ont éliminé la nécessité de ce mouvement des tarsaliens. C'était probablement suivi immédiatement par l'agrippement du cinquième métatarsien et la raffermissent du métatarse. Un type distinctif du tarse est observé dans le rhynchosaurien le plus primitif, Noteosuchus, les reptiles proterosauriens, l'archosaurien les plus primitif, Proterosuchus, et dans Trilophosaurus. Ce genre de tarse est un ancêtre structural convenable au tarse des rhynchosauriens, des archosauriens et peut-être bien des sphenodontiens plus avancés. Trois genres de tarses se trouvent dans les archosauriens plus avancés: le crocodilien-normal, le crocodilien-reverse et des tarses avec des articulations intertarsiennes. Le tarse crocodilien-normal et le tarse crocodilien-reverse ont probablement évolvé indépendamment du tarse des archosauriens primatifs. L'articulation intertarsienne de thecodonts et ptérosauriens a probablement tiré son origine du tarse des archosauriens primitifs, l'articulation intertarsienne des dinosauriens se dérive peut-être d'une tarse des crocodiliens.

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INTRODUCTION

One of the most remarkable examples of the radiation of a structural complex within a distinct phylogenetic assemblage is provided by the evolution of the tarsus during the diversification of diapsid reptiles. From a single ancestral complex, at least six distinct kinds of tarsi evolved. Although some structures assumed entirely new functions during this radiation, the basic roles of the tarsus as a whole were not changed. In diapsids, as in tetrapods generally, the tarsus performs four basic functions: it allows movement of the crus on the pes; it transmits forces between the crus and the pes; it provides a surface over which various muscles pass; and, in some cases, it provides an attachment point for muscles and forms part of a bone-muscle lever system. However, striking differences are seen in the manner in which these functions are performed. For example, in crocodiles, a joint is present between the astragalus and calcaneum that allows movement of the crus on the pes, while in lizards, these two bones are fused and movement occurs distal to them.

The aim of this investigation is to identify the structural changes that occurred during the origin of each of the advanced kinds of diapsid tarsi and determine as far as possible the mechanical and adaptive significance of the structural changes.

HISTORICAL RESUME

The diversity in structure and mechanics of the tarsus in tetrapods has long attracted the attention of comparative morphologists and, as the fossil record became better known, of paleontologists. The structure of the tarsus in the extant diapsid groups was first described by Gegenbaur (1864). He recognized the homologies of the tarsal elements in advanced tetrapods and reconstructed the primitive tetrapod pattern, the ultimate ancestor of the various kinds of diapsid tarsi. Numerous subsequent papers provided additional information on the structure and embryological development of particular kinds of tarsi. Of particular note for their consideration of the tarsus in diapsid reptiles are Born's (1876, 1880) survey of the structure of the tarsus in lizards and description of its embryological development, Howes and Swinnerton's (1901) consideration of Sphenodon, Rabl's (1910) consideration of the tarsus of Sphenodon and in crocodiles, and Steiner's (1934) description of the embryology of the crocodile tarsus.

In the absence of structurally intermediate stages, these workers could not consider the evolution of the tarsus in any particular lineage. Rather, emphasis was placed on determining the homologies of the particular elements. It was recognized that the calcaneum is homologous with the amphibian fibulare and that the astragalus is a composite element. However, the elements involved in the formation of the astragalus were not satisfactorily identified until Peabody (1951), using isolated immature astragali of the early reptile Captorhinus, showed that the astragalus of primitive reptiles was formed by fusion of the amphibian tibiale, intermedium and fourth centrale. Also, apart from casual observations, little attention was given to the mechanics of the tarsi, and no attempt was made to consider mechanical aspects of the evolution of the tarsus by these authors.

The first consideration of functional aspects of the evolution of the tarsus was by Romer and Byrne (1931). They recognized that the tarsus in early reptiles allowed rotation of the crus relative to the pes so that the foot was able to remain stationary as the femur retracted and the crus rotated. However, they were not able to determine how this function was performed in tetrapods without a definitive ankle joint.

Later, the general evolution of the tarsus in tetrapods was reviewed by Schaeffer (1941). As well as using information about the structure and development of the tarsus in extant tetrapods, Schaeffer utilized knowledge of the structure of the tarsus in fossil tetrapods and functional interpretations of particular kinds of tarsi to develop a synthetic picture of its evolution. He recognized that most of the structural changes were related to two major mechanical changes -- the development of a specialized ankle joint and the consolidation of the metatarsus to form a propulsive lever -- and one change in locomotion -- the shift from a primitive sprawling type of locomotion to a more erect pattern. However, as very few tarsi of fossil reptiles were available to him, he had limited success in tracing the structural and mechanical changes in individual lineages. This was particularly so in diapsid reptiles, where the only information about the eosuchian tarsus available to him was the description of the tarsus of Youngina published by Broom

(1921, 1924).

Since Schaeffer published his monograph, much additional material has accumulated, documenting various stages in the history of the evolution of the tarsus in diapsid reptiles. The structure of the tarsus in primitive reptiles has become better known through the work of Carroll (1964, 1969); eosuchian tarsi have been described by Reisz (1975), Gow (1975) and Carroll (1976a); an early lizard tarsus has been described by Carroll (1975, 1977); sphenodontid tarsi have been described by Cocude-Michelle (1963) and Hughes (1968); rhynchosaurid tarsi have been described by Carroll (1976b), Hughes (1968) and Chatterjee (1974); and the tarsus in archosaurs has become better known through the work of Carroll (1976b), Cruickshank (1972), Walker (1961, 1964, 1970) and others.

This new information provides the necessary basis for a further consideration of problems that Schaeffer recognized but was unable to solve, including the mechanics of the tarsus in primitive reptiles, the structural changes associated with the initial development of the intratarsal joint, the mechanical and adaptive significance of the changes that occurred during the origin of the lizard tarsus, and the development of the crocodile tarsus. As well, it has become apparent that the course of evolution of the tarsus in archosaurs and rhynchosaurs is more complex than was previously recognized and presents additional mechanical and phylogenetic problems. A structurally distinct type of tarsus not known to Schaeffer has been shown to be present in early archosaurs, rhynchosaurs and prolacertids (Carroll 1976b; Gow 1975). The mechanics of this tarsus are unknown and the significance of its presence in these three groups is uncertain. Also, the origin of the dinosaur tarsus has been a matter of controversy.

As well, much additional information on locomotion in tetrapods has become available in recent years. Bakker (1971) and Charig (1972) have recognized that three distinct grades of evolution of locomotion are present in tetrapods: a primitive sprawling grade in which the femur moves in a plane close to the horizontal; an intermediate semierect grade in which the femur moves in a plane somewhere between the horizontal and vertical; and an advanced fully erect grade in which the femur moves in a plane close to the parasagittal. At present, detailed descriptions of the movements of the crus relative to the pes are only available for animals in the advanced grade of locomotor evolution, Jenkin's (1971) description of the limb movements of the oppossum and Gambaryan's (1974) consideration of the mechanics of the pelvic limb in advanced mammals being the most notable of these. Some information about the movements of the pelvic limb segments in lizards was provided by Snyder (1949, 1952) and Sukhanov (1974), although these investigations are primarily concerned with the gaits used by those animals and they do not consider the movements of the limb segments in detail.

METHODS

In the consideration of the mechanics of the tarsus, emphasis was placed on the analysis of the joints. This involved answering three separate questions: What movements are possible at particular joints of the tarsus and metatarsus? What is the position of the axis of rotation around which the movement occurs? What is the role of movement at each of the joints in the general functioning of the tarsus?

In the extant diapsids considered in this investigation, an understanding of the movements possible at each of the joints was obtained through manipulation of ligamentous preparations of the tarsus and metatarsus. Comparable manipulations of the limb in a live _Caiman_ and _Iguana_ confirmed that the same movements were possible in an intact animal.

In the fossil diapsids being considered, it was necessary to use the structure of the articular surface to interpret the relative amount of movement at the individual joints. Two aspects of the structure that were used for this are the degree of curvature of the articular surfaces and the congruency of the opposing articular surfaces at a joint. Barnett and Napier (1952) have shown that variation in the curvature of a joint can be correlated with variation in the movements possible at the joint. Thus in comparing different animals, differences in the curvature of homologous joints can be used as an indication of differences in the amount of movement occurring at those joints. To a limited extent, this was also used in estimating the relative amount of movement at different joints within a single tarsus. However, more importance was attached to incongruence of articular surfaces as an indication of significant amounts of movement at the joint. Analysis of the general mechanics of synovial joints (Barnett, Davies and MacConaill 1961) has shown that movement at synovial joints is always some combination of rolling, a movement like a tyre rolling on the ground, in which the points of one articular surface contacts points on a second articular surface that are equidistant from a reference point, and translation, a movement like a tyre spinning on the ground in which all the points of one articular surface contact a single point on a second articular surface. A consequence of this is that the two opposing articular surfaces at a freely moveable joint do not fit each other exactly, and one articular surface is larger than the second. Thus a joint in a fossil that shows these features can be assumed to have been the site of significant amounts of movement.

In the diapsids in which isolated tarsal elements were available, the movements at particular joints could be more certainly identified by manipulation of the elements. Particular attention was given to identification of the positions in which the articular surfaces are maximally congruent, the close packed position as defined by Barnett, Davies and MacConaill (1961), since the habitual movements of a joint — the movement that occurs during the normal functioning of the joint --

are the movements from one close packed position to the second (Barnett, Davies and MacConaill 1961).

The position of the axes of rotation at the joints of the tarsus in extant diapsids was estimated by manipulation of the ligamentous preparation and by consideration of the morphology of the joint. In the fossil material it was necessary to rely on the morphology of the articular surfaces and the configuration of the tarsus for this.

Once the possible movements at the joints were understood, the role of movement at the individual joints in the general functioning of the tarsus could be considered. For this, an understanding of the general pattern of movement of the crus on the pes that occur during locomotion is necessary. In the lizard and the caiman, this information was obtained by observation of live animals in normal unrestrained locomotion. Both cinematography and cineradiography were used for this; the exact techniques used are described below. In the fossil diapsids, it was necessary to reconstruct the pattern of movements of the pelvic limb segments. The pelvic limb movements in Iguana were used as a basis for forming a generalized model of the pelvic limb movements in animals with a primitive step cycle. Information from the anatomy of the pelvic limb and from fossil footprints was used to provide additional details about the pattern of limb movements in the various genera being considered.

Since, as shown by Schaeffer (1941), one of the fundamental mechanical changes that occurred during the evolution of the tarsus was the modification of the metatarsus to form a propulsive lever, attention was also given to the mechanics of the metatarsal lever. The x-rays taken during the cineradiographic study of locomotion in the lizard and the crocodile provide a solid basis for this since the position of the limb elements during various stages of plantarflexion of the pes could be seen directly. In the fossil reptiles, it was necessary to use a model of the pelvic limb movements as a framework to interpret the mechanics of the metatarsus. It was also necessary to consider the position of the major pedal flexors, although a general reconstruction of the pelvic limb musculature was not attempted.

I THE PELVIC STEP CYCLE IN PRIMITIVE TETRAPODS

During the evolution of tetrapods, the pattern of movement of the pelvic limb segments, here called the pelvic step cycle, underwent considerable modification. The primitive pelvic step cycle is usually characterized as one in which the femur projected laterally from the body and moved in a horizontal arc with sigmoidal bends of the vertebral column and a rotation of the femur accompanying femoral retraction (Romer 1956; Charig 1972). While this abstraction has proved useful in interpreting the mechanical and functional significance of some aspects of the pelvic limb in early tetrapods (Romer and Byrne 1932; Schaeffer 1941; Charig 1972), it is deficient in its emphasis on posture rather than movements of the pelvic limb segments and in its neglect of the movements of the crus and pes, and does not provide an adequate basis for interpreting the mechanics of the tarsus in early reptiles. Thus, before considering the structural and mechanical evolution of the tarsus, it is necessary to develop a more accurate model of the "sprawling" type of step cycle. To provide a basis for this, the step cycle of an extant lizard was investigated through the use of cinematography and cineradiography. The green iguana (*Iguana iguana iguana*) was chosen as a subject for this since it is a generalized lizard with limb proportions similar to Permo-Triassic lizards (Carroll 1977) and is large enough to permit accurate analysis. Also, although generally arboreal, it is not uncommonly found on the ground (Swanson 1950), so its step cycle is unlikely to show either arboreal or terrestrial specializations. Comparison with descriptions of the pelvic limb movements in other lizards (Snyder 1949, 1952; Schaeffer 1941; Sukhanov 1974; Russell 1975) provides an understanding of some of the variability present within lizards.

Methods

The subject of the investigation was a moderately active green iguana, at least six years old with a snout-vent length of 57 cm. In order that the animal remain stationary relative to the camera while filming, a treadmill about two times the snout-vent length and one and a half times the width of the trackway was used. These dimensions ensured a linear course but did not interfere with the movements of the pelvic limb.

Cineradiography was in dorsal view under fluoroscopic control with a 100 mm spot film device. The film used was Dupont Coronex SF2 x-ray spot film. Exposures were made at 35-40 kv with 3.0 to 3.2 ma at a rate of six per second. Twenty-eight strides ranging in length from six to fourteen frames were recorded. These were analyzed by making tracings of the image of each frame and superimposing successive tracings to identify the kinds of movement occurring. Rotation of the femur was indicated by the change in the apparent width of its distal end. Rotation of the crus was indicated by change in the overlap of the tibia and fibula. Rotation of the metatarsus was indicated by change in the overlap of the individual metatarsals. Where the limb elements move in a plane close to the horizontal so that no change in the apparent length of the element was seen, the angles between the elements was measured directly from the x-rays. In other cases, the angle between the limb and a horizontal plane was estimated using the formula:

$$\text{secant of angle} = \frac{\text{actual length}}{\text{apparent length}}$$

with the actual length being measured from a frame in the same sequence in which the segment was horizontal. The amount of rotational movement of the elements was estimated by manipulation of the skeletal elements.

High speed cinematographical films were taken to provide a lateral view of the limb, to show the position of the pelvic limb at the extremes of protraction and retraction, and to determine the relative times of occurrence of the movements of each pelvic limb with each other and with the movements of the vertebral column. For this, a treadmill was used with a mirror inclined dorsally over the animal at an angle of 45°, providing simultaneous dorsal and lateral views. A Bolex H 16 camera was used with 16 mm Eastman Double-X negative film 7222 run at 64 frames per second. The camera was above the horizontal at an angle of 15° to ensure that the movements of the toes were clearly visible. Eighteen strides ranging in length from fourty-five frames to seventy frames were suitable for analysis.

The Pelvic Step Cycle of Iguana - A Description

While walking, the body is held well off the substrate and the vertebral column is arched dorsally. Sinusoidal movements of the vertebral column are present at all rates of locomotion. As in Lacerta (Daan and Belterman 1968) these are in the form of standing waves with their nodes at the pelvic and pectoral girdles. They are coordinated with the limb movements so that the vertebral column is straight at the end of the propulsive phase (Fig. 1g) and maximally convex towards the limb being retracted at the end of the restorative phase (Fig. 1j). This rotates the pelvis so the hip of the limb being protracted is moved forwards, lengthening the stride. The pelvis, then, functions as an additional limb segment with its length being equal to the interacetabular width.

At the beginning of the propulsive phase, the femur is directed 15° lateral to a parasagittal plane (Fig. 1j). It usually slopes dorsally when seen in lateral view, although in sequences in which

Figure 1. Dorsal view of the pelvic limbs of *Iguana iguana* showing the position of the limb elements during a single stride. Made by tracing every sixth frame of a 60 frame sequence filmed at 62 frames a second.

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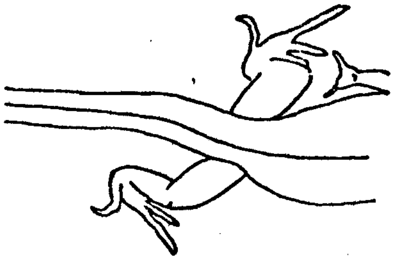

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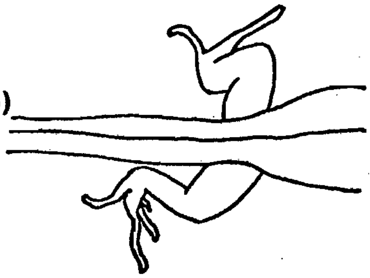

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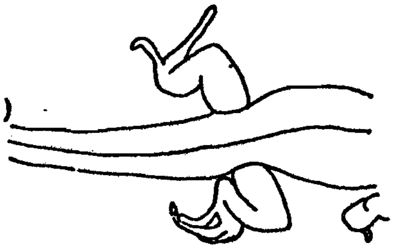

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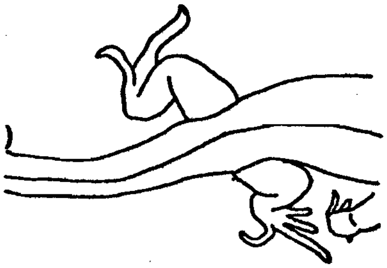

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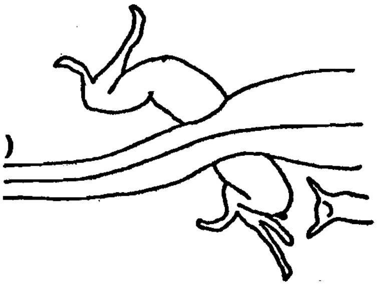

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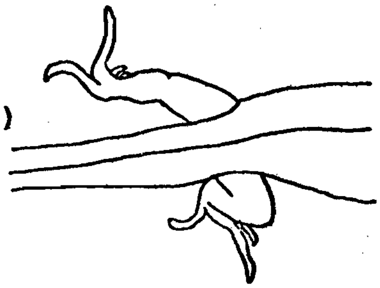

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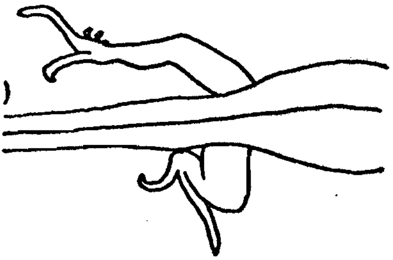

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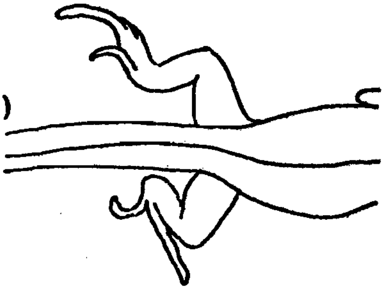

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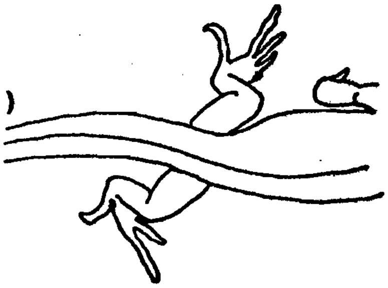

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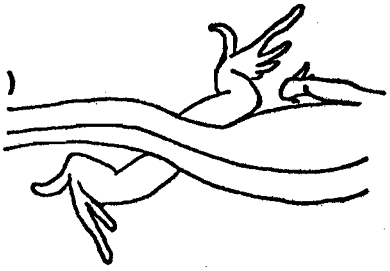

femoral adduction is maximal, its distal end is depressed below the level of the acetabula slightly (Fig. 2i). The crus slopes laterally and slightly posteriorly, and faces anterolaterally, the first four metatarsals extend anteriorly. The hooked construction of the fifth is clearly seen in dorsal view (Fig. 3a); its proximal inturned portion extends laterally from the fourth distal tarsal and its shaft extends anterolaterally at an angle of about 100° to the proximal portion. The first digit points anteromedially. The second to fourth are in line with their metatarsals and extend anteriorly. The position of the fifth is variable, it ususally curves posteriorly with its flexor surface facing posteriorly, although in some cases it is directed anteriorly parallel to the fourth and with the flexor surface facing ventrally.

The initial movements to occur are a flexion of the crus on the metatarsus and an adduction of the femur. These movements continue as the femur retracts through an arc of about 50°, at which time the crus makes an angle of about 30° with the substrate when seen in lateral view (Fig. 2a). Flexion at the ankle is accompanied by a medial rotation of the crus, resulting in its extensor surface facing less strongly laterally (Fig. 3a-b). Also, as the ankle flexes, a medial abduction of the metatarsus occurs. The metatarsus remains in contact, or nearly in contact, with the substrate, but its proximal end is swung medially so the fourth metatarsal becomes laterally directed at an angle of 60° away from a parasagittal plane (Fig. 3a-c). The first three

Figure 2. Lateral view of the right pelvic limb of *Iguana* showing the position of the limb elements during a single stride. Made by tracing a projection of every fourth frame of a forty frame sequence filmed at 62 frames a second.

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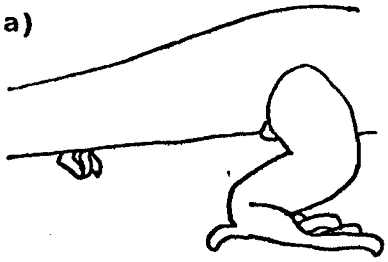

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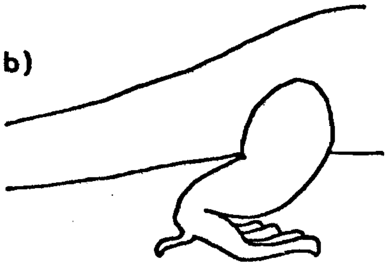

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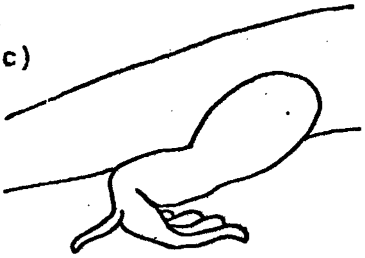

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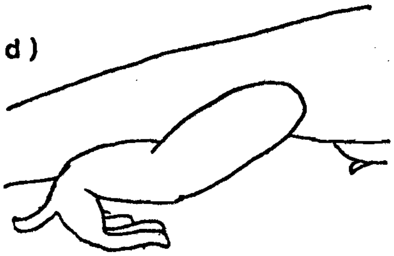

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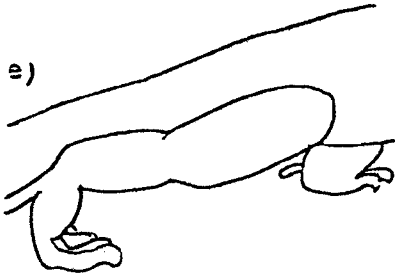

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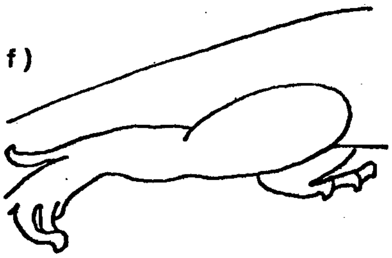

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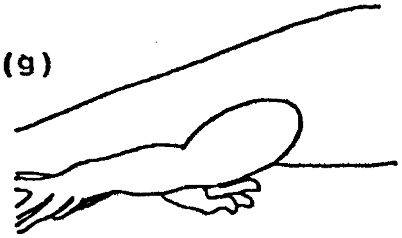

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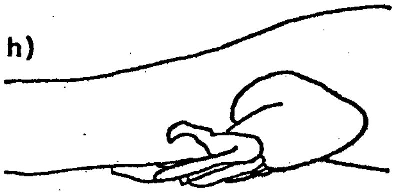

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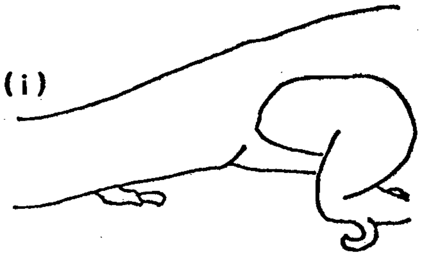

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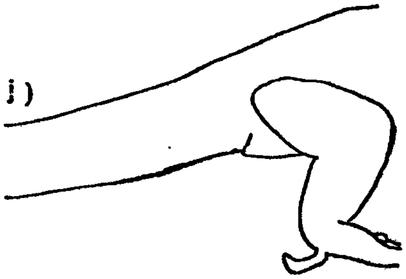
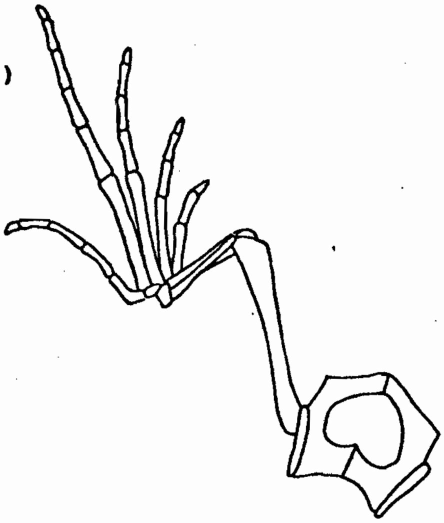


Figure 3. Dorsal view of the left pelvic limb of *Iguana* showing the position of the limb elements during a single stride. Made by tracing x-rays taken at 6 frames a second. Frames a to e are from a single sequence seven frames long. Frames f and g are from a second sequence of equal length. f is a composite of two frames.



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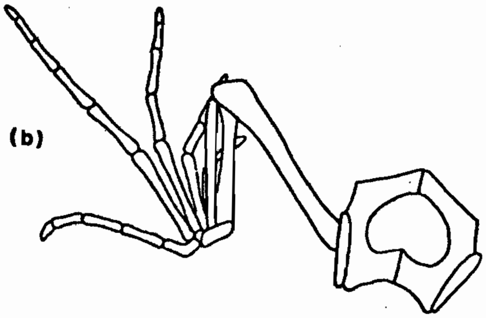

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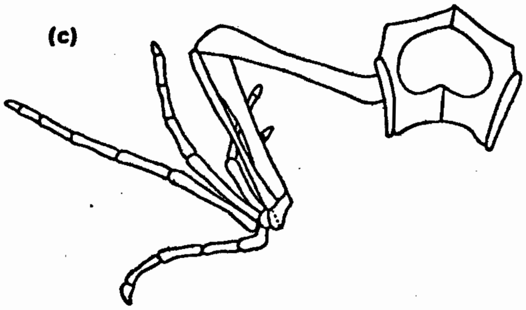

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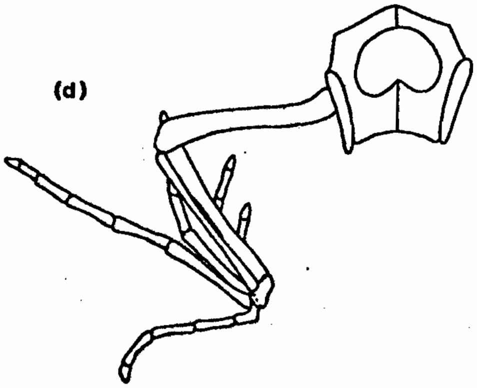

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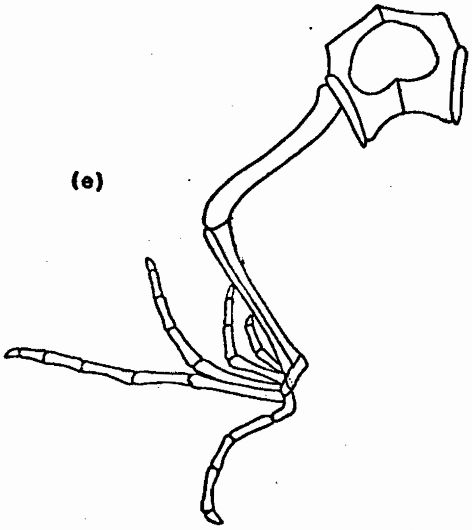
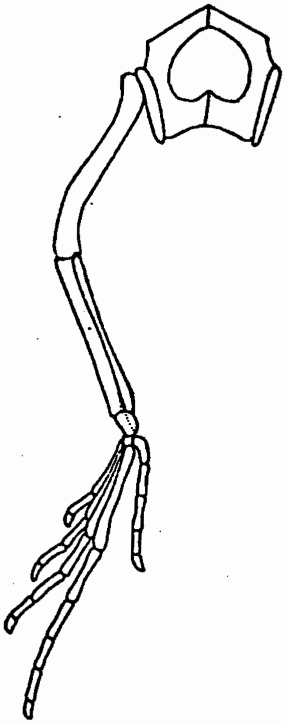
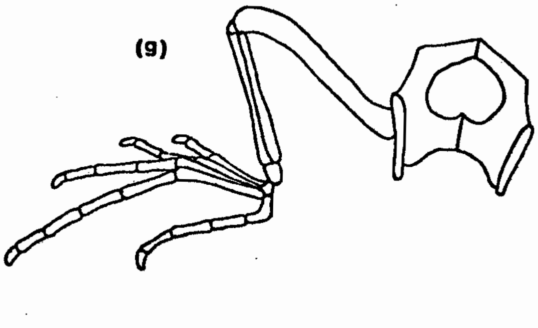


(e)



(f)



(g)

digits remain stationary and point forwards, the fourth usually remains in line with its metatarsal and assumes a lateral orientation.

Retraction of the femur begins after a short initial period when only flexion of the crus and adduction of the femur are occurring and continues through the remainder of the propulsive phase. The arc described by retraction of the femur is consistently large, varying between 140° and 165° in ten sequences showing the femur at the extremes of protraction and retraction. As the femur retracts, it rotates anteriorly approximately 70° around its long axis, bringing the distal articular surface into a vertical position. This rotation begins after the femur has been retracted about 60° (Fig. 1c) and continues through the remainder of the propulsive phase. It moves the crus like the spoke of a wheel, raising the distal end off the substrate. This is evident in lateral view, where the angle between the crus and a horizontal line changes from 35° after flexion of the crus (Fig. 2b) to nearly 0° at the end of the propulsive phase (Fig. 2g).

After the femur was retracted past a line normal to the direction of movement, extension of the crus begins. The crus extends a total of 25° measured relative to a parasagittal plane when seen in dorsal view. This, together with retraction of the femur, results in the knee opening posteriorly so the angle between the tibia and femur changes from a minimum of 55° when the femur is directed laterally (Fig. 3c) to about 155° at the end of the propulsive phase (Fig. 3f). As the crus extends, it rotates laterally so that its extensor surface faces directly laterally at the end of the propulsive phase (Fig. 3f).

Following the earlier medial abduction of the metatarsus, the pes remains stationary until plantarflexion of the metatarsus and pes begins. The initial movement is a rotation of the metatarsus around its long axis (Figs. 1e-f, 3d-e). This lifts the lateral (functionally posterior) border of the metatarsus and moves its proximal end anteriorly. As the metatarsus approaches a vertical orientation, an extension of the ankle joint begins (Figs. 1f-g, 3e-f). This moves the proximal end of the metatarsus anteriorly and laterally, causing the metatarsus to come into line with the crus.

Initially, plantarflexion of the metatarsus involves a flexion of the first three metatarsals on the basal phalanges and the basal on the second phalanx of the fourth digit. Later, the more distal joints of the digits are flexed and the toes roll off the substrate. The fourth toe loses contact with the substrate early and assumes a posterior orientation. The first three digits remain in contact with the substrate until the end of the propulsive phase when they contact the substrate by their distal ends only. Loss of contact with the substrate is nearly simultaneous and is accompanied by a plantarflexion of the digits, bringing them in line with their metatarsals.

The restorative phase can be divided into two portions. During the first (Figs. 1g-h, 3f-g), the femur is adducted and protracted towards a line normal to the body, the crus is flexed on the femur, and the metatarsus is dorsiflexed on the crus and rotated so its extensor surface faces dorsally. The second phase (Figs. 1h-i, 3g, a) involves a continued protraction of the femur, extension of the knee, plantarflexion of the pes, and rotation of the femur, bringing the crus into a vertical oritentation. The restorative phase ends with the contact of the substrate and the beginning of flexion of the crus.

Discussion

During the radiation of lizards, a number of specialized patterns of locomotion developed. The primitive pattern, judging from the presence of well developed limbs in Permo-Triassic eosuchians and lizards, is a quadrupedal gait in which the limbs were of major importance in providing a propulsive thrust. Comparison of the step cycle of _Iguana_ with descriptions of the limb movements in other lizards (_Basiliscus_, Snyder 1949, 1952; _Varanus komodoensis_, _Phynosomus_, _Tetrascincus_, Sukhanov 1974; _Gekko gecko_, Russell 1975) shows that the pelvic step cycle in extant lizards with this pattern varies primarily in the size of the arc described by the movement of the limb segments. The femur generally retracts through a large arc when measured relative to a parasagittal plane, although this is only about 90° in _Gekko gecko_ and _Tetracincus_. Except for _Varanus komodoensis_, the femur is not depressed far below the hip during retraction. In _Varanus komodoensis_, the body is held well off the substrate and the femur is strongly adducted throughout the propulsive phase, although here, as in other lizards, the femur rotates as it retracts so that the extensor surface of the crus and femur face laterally at the end of the propulsive phase. Except for *Gekko gecko* the arc described by movement of the crus is similar: the crus is approximately vertical at the beginning of the propulsive phase and is in line with the femur at the end. In *Gekko gecko*, the crus remains vertical as the femur is retracted towards a line perpendicular to the body and is only extended about 110° at the end of the propulsive phase. Considerable variation is seen in the placement and movement of the pes. The pattern seen in *Iguana* has also been reported for *Basiliscus* (Snyder 1962), *Varanus komodoensis* (Sukhanov 1974) and *Anolis* (Schaeffer 1941). In *Sceloperus*, the metatarsus is directed strongly laterally at the beginning of the propulsive phase and remains stationary until plantarflexion of the metatarsus (Snyder 1962).

Despite these variations, the pelvic step cycle of lizards is surprisingly constant in its general features. Flexion of the knee occurs during the initial portion of the propulsive phase and extension of the knee during the final portion. The femur rotates as it retracts so that its extensor surface faces laterally at the end of the propulsive phase. Plantarflexion of the metatarsus involves an initial rotation, bringing the metatarsus into a vertical position, followed by an extension of the ankle, bringing the metatarsus into line with the crus. The basis for this uniformity can be understood by considering the kinetics of the step cycle.

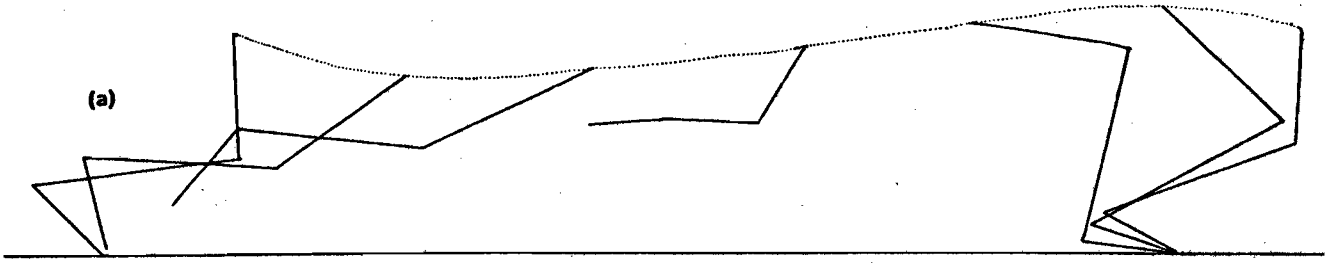
During the propulsive phase, the limbs perform two functions:

they hold the body off the substrate and they provide a propulsive thrust. The energy required for this will be minimized if the centre of gravity is moved forwards without oscillations. In animals in which the path of the centre of gravity is known, it follows a sigmoidal rather than straight path (Alexander and Jayes 1978; Gambaryan 1974). This is also the case in Iguana. An indication of the size of the oscillations is given by the path followed by the hip joint (Fig. 4). In dorsal view (Fig. 4b), the hip is seen to move laterally (towards the pes) throughout the first part of the propulsive phase and medially (away from the pes) as the metatarsus is plantarflexed and through the restorative phase. These oscillations place the hip closer to the pes so the weight of the animal is transmitted to the ground through a strut that is more nearly vertical than would otherwise be the case. In lateral view (Fig. 4a), the hip is seen to be highest at the beginning of the propulsive phase and lowest near the end, at the time the ankle joint begins to extend. These oscillations probably do not accurately reflect the true path followed by the centre of gravity since rotation of the pelvis around its long axis raises and lowers the hip relative to the centre of gravity and thus can dampen vertical oscillations.

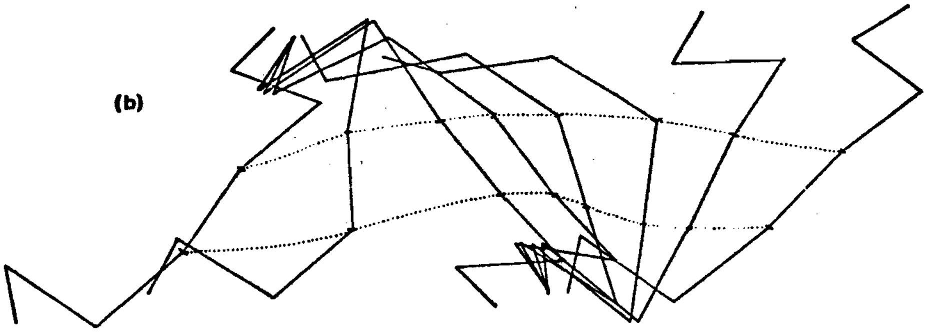
In mammals, the course followed by the centre of gravity is controlled by flexion-extension movements of the limb joints (Gambaryan 1974). Flexion of the joints as the mechanical axis of the limb approaches the vertical controls the dorsal movement of the centre of gravity that would otherwise occur. Extension of the joints as the

Figure 4. Stick figures showing the movements of the pelvic limb segments of Iguana iguana with respect to the substrate. a) lateral view; made by tracing the mechanical axis of the femur, crus and metatarsus of every fourth frame in a sequence forty frames long; b) dorsal view; made by tracing the mechanical axis of the pelvis, femur, crus and metatarsus in every sixth frame of a sequence sixty frames long. The dotted line represents the path of the acetabula.

(a)



(b)



mechanical axis of the limb moves away from the vertical lengthens the mechanical axis of the limb and thereby controls the lowering of the centre of gravity.

In lizards, it is necessary for the movements of the limb segments to be coordinated so that both dorso-ventral and side-to-side movements of the centre of gravity are controlled. The initial flexion at the ankle depresses the knee so that if this movement were occurring in isolation, the centre of gravity would be lowered. This does not occur since the simultaneous "abduction" of the femur lowers its distal end relative to its proximal end maintaining the hip at the same height above the substrate. Retraction of the femur results in lateral movement of the knee relative to the hip as the femur retracts towards a plane normal to the body, and a medial movement of the knee relative to the hip as the femur retracts away from this plane. Also, since the knee is basically a hinge-like joint, femoral retraction rotates the crus and knee laterally. This reorientation of the crus and knee introduces a lateral component into the movement of the crus that results from flexion at the knee. Thus flexion at the knee now moves the proximal end of the crus laterally, anteriorly and ventrally relative to its distal end rather than strictly anteriorly and ventrally as is the case at the beginning of the propulsive phase when the crus faces forwards and the axis of rotation at the knee is about normal to the body. Consequently a continued flexion of the crus on the femur during the time the femur is retracting towards a line normal to the body prevents a lateral movement of the body. Early workers, judging from mounts of articulated specimens, assumed that the crus continued to rotate throughout the propulsive phase so that its extensor surface faced posteriorly at the end of the propulsive phase. However, as recognized by Rewcastle (1978) the amount of crural rotation that actually occurs is reduced from this by rotation of the femur around its long axis. This femoral movement brings the knee into a vertical orientation so that further retraction of the femur simply extends or flexes the knee joint. Once the femur has been rotated, extension of the crus on the femur results in a medial movement of the knee relative to the hip and ankle joints. Thus the simultaneous retraction of the femur and extension of the knee during the final part of the propulsive phase prevents the lateral movement of the hip that would occur if retraction of the femur were an independent movement. Rotation of the femur, as described above, also raises the distal end of the crus relative to the proximal end. This does not lower the body since a simultaneous plantarflexion of the pes raises the ankle off the substrate.

The characteristic combination of rotation of the metatarsus followed by an extension of the ankle joint that occurs during plantarflexion of the metatarsus can be associated with the lateral orientation of the metatarsus. As noted by Snyder (1962) and Rewcastle (1978) the lateral orientation of the metatarsus seen in lizards is not consistent with the production of a significant propulsive force by a simple flexion of the metatarsus since this movement would only move its proximal end laterally. However, the first movement during plantarflexion of the pes is not an extension of the ankle joint as assumed by Snyder and Rewcastle, but is a rotation of the metatarsus around its long axis. This results in the extensor surface of the metatarsus facing anteriorly and causes the metatarsus to lie in a vertical plane at right angles to the vertical plane passing through the crural bones. In this position, extension of the ankle joint does not move the proximal end of the metatarsus dorsally and laterally, but moves it anteriorly and laterally. The lateral movement is compensated for by the extension of the knee so the net result is an anterior movement of the body.

The Generalized Pelvic Step Cycle of Primitive Reptiles

While this consideration of the step cycle in lizards is limited to a few mechanical aspects, it demonstrates that the general pattern of movements of the pelvic limb segments is determined by basic mechanical factors. The restrictions of the movements of the centre of gravity dictated by the need to minimize oscillations of the centre of gravity results in the limb functioning like a closed kinematic chain — a series of links in which movement of one link is accompanied by a predictable movement of the connecting links. The features that determine the general pattern of movements of the limb are the lateral movement of the distal end of the femur that accompanies femoral retraction and the lateral orientation of the metatarsus at the time of pedal plantarflexion. Lateral movements of the distal end of the femur relative to its proximal end results in a lateral rotation of the crus, which in turn is associated with the rotation of the femur around its long axis. The lateral orientation of the metatarsus results in plantarflexion of the pes involving a combination of rotation of the metatarsus followed by extension of the ankle joint. Because of these mechanical interrelationships of the movements of the pelvic limb segments, any tetrapod in which the distal end of the femur moved laterally during femoral retraction can be expected to show a flexion of the knee during the initial portion of the propulsive phase and an extension of the knee during the final portion and a rotation of the femur around its long axis as it retracts. If the metatarsus is directed laterally, plantarflexion of the pes will involved a rotation of the metatarsus followed by an extension of the ankle joint. It follows that this general combination of movements is basic to animals with a sprawling step cycle and can be used as a model for reconstructing the pelvic step cycle in early reptiles. Within this pattern considerable variation related to differences in ecology, in the detailed mechanics of the locomotor apparatus, and the phylogenetic grade of evolution of the animal is possible. Consequently, the inclusion of more detailed aspects of the step cycle of _Iguana_ in a generalized model of the limb movements is not justified in the absence of independent evidence from the morphology of the locomotor apparatus.

II THE STRUCTURE AND MECHANICS OF THE PRIMITIVE REPTILIAN TARSUS

Schaeffer (1941) recognized that the tarsus of diapsid reptiles originated from one like that of the captorhinomorph reptile Labidosaurus, in which only eight elements were present: the astragalus, calcaneum, centrale and five distal tarsals. Peabody (1951), using isolated immature tarsal elements of Captorhinus, showed that the calcaneum is homologous to the amphibian fibulare and that the astragalus was formed by the fusion of the amphibian tibiale, intermedium and fourth centrale. In a series of papers on early reptiles (Carroll 1964, 1969; Clark and Carroll 1973; Carroll and Baird 1972) it was demonstrated that the members of the family Romeriidae are structurally suitable ancestors of all more advanced reptiles and, since an astragalus and calcaeneum are already present here, that the changes in the tarsus occurred during or prior to the origin of reptiles.

While these papers have established the structure of the primitive reptilian tarsus, the mechanics of this functional complex remains unknown. Schaeffer argued that the amphibian tarsus was a flexible structure and the movements of the crus on the pes were a result of a summation of a small amount of movement at a number of joints, with rotation of the crus involving a crossing over of the fibula by the tibia. He recognized that the tarsus of primitive reptiles would not allow this crural movement and, consequently, that its mechanics were different from the situation in amphibians but was unable to interpret the reptilian pattern. Thus, before considering the structure and mechanics of the tarsus in early diapsids, the functioning of the primitive reptilian tarsus must be considered.

Material

The following specimens were examined during the course of this investigation. Those marked with an asterisk were available as casts.

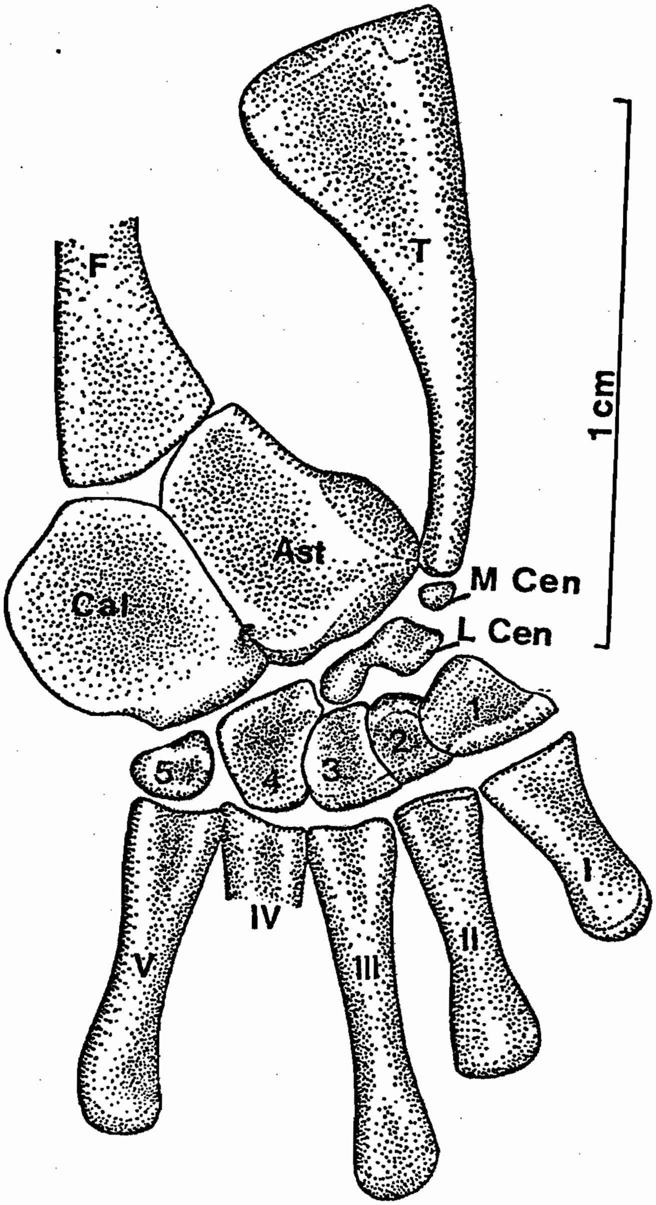
Paleothryis acadiana	Museum of Comparative Zoology 3481. Articulated skeleton showing the right tarsus and metatarsus in dorsal view.
	Museum of Comparative Zoology 3482. Articulated skeleton showing partial right and left tarsus in ventral view.
Hylonomus lyelli	National Museum of Canada 10048. Disarticulated postcranial remains including a left tarsus and metatarsus.
	*British Museum (Natural History) R. 4167. Pelvic girdle, lateral view.

Since *Paleothyris* is the better known of these romeriids, emphasis will be placed on it in the following functional interpretations of the tarsus.

Structure of the Tarsus in *Paleothyris*

The tarsus of *Paleothyris* was described by Carroll (1969), so only a brief description is necessary here. Nine elements are present (Fig. 5). Proximally two large elements, a flat, plate-like calcaneum

Figure 5. Paleothyris acadiana, left tarsus, dorsal view, specimen MCZ 3481. See list of abbreviations for key to abbreviations.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and an L-shaped astragalus support the crural bones. The fibula articulates with both bones along their proximal edge. The tibia articulates with the astragalus at a rounded articular surface located distally on its medial edge. A small opening, the perforating foramen, passes between the astragalus and calcaneum.

Distally, the astragalus articulates with two centralia. The larger of these is the lateral centrale, an hourglass-shaped element contacting most of the distal border of the astragalus. It was extensively covered by cartilage, the finished bone being restricted to a small medial area. The almost complete separation of this element into two parts suggests that it is a composite element formed by fusion of the second and third centrale of amphibians. The medial centrale is a small wedge-shaped element fitting between the astragalus and lateral centrale at the medial edge of their articulation.

The distal edge of the tarsus is formed by five distal tarsals. The largest of these, the fourth, lies distal to the articulation between the astragalus and calcaneum and contacts both these bones and the lateral tip of the centrale. The first three articulate with the distal edge of the centrale, with the concave portion of its distal border receiving the proximal end of the second distal tarsal. The fifth distal tarsal fits between the fourth distal tarsal and the calcaneum.

Each distal tarsal articulates with a single metatarsal. The first four metatarsals increase in length from the first to fourth, the fifth is about equal to the third in length. The phalangeal formula is incompletely known, but was reasonably reconstructed as being 2, 3, 4, 5, 4, as is the case in all adequately known primitive reptiles. The digits increase in length from the first to the fourth with the fifth being about equal to the third in length.

Locomotion in Paleothyris

Carroll (1969) suggested that Paleothyris was an agile terrestrial form. Judging from its entrapment in a hollow tree stump, it was not habitually arboreal. Its femur shows all the features typical of early reptiles, indicating that femoral retraction involved a lateral movement of its distal end relative to its proximal end. Thus the generalized model of the primitive step cycle developed above can be used as a basis for reconstructing the step cycle in Paleothyris.

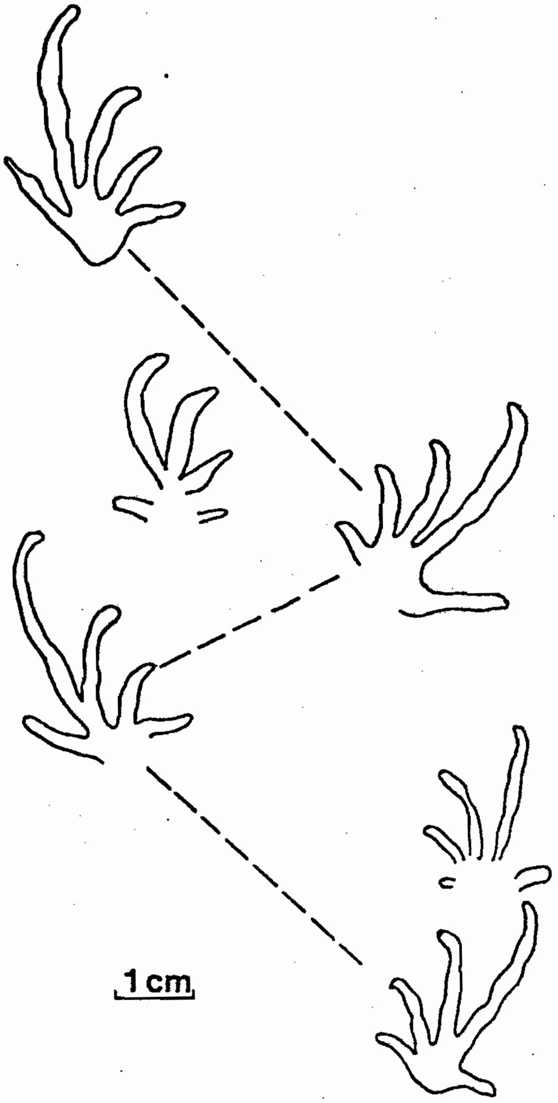
As noted above, considerable variation is possible within this pattern. Of especial interest in view of its possible evolutionary significance are the differences between the pattern seen in salamanders and in lizards. Comparison of the step cycle seen in lizards as described above, and in the salamander as described by Schaeffer (1941) shows that two major differences are present: in salamanders, the crus slopes anteriorly at the beginning of the propulsive phase, while in lizards it is nearly vertical at this time; and in salamanders, the longest metatarsal is directed anteriorly, while in lizards it is directed laterally.

Since the general proportions of the limbs and the body of

Paleothyris are like those in salamanders with well developed limbs, it is reasonable to assume that the arcs described by the movement of the limb elements would have been similar. Indirect support for this comes from the reconstruction of the pectoral limb movements in Captorhinus presented by Holmes (1977), which show that the elements of the forearm moved through large arcs and the distal end of the forearm was set down anterior to the elbow. Since the elements of the pelvic limb are equal in length to the corresponding elements of the pectoral limb, they would have had to move through comparable arcs in order for the hind limb stride length to be equal to the forelimb stride length. Thus the distal end of the crus was probably set down anterior to the knee, as in salamanders.

Direct evidence about the position of the metatarsus and pes in primitive reptiles comes from fossil footprints. Although a number of footprints from the Pennsylvanian and Permian have been attributed to reptiles by Haubold (1974), only those placed in the genus Dromopus agree with the primitive reptile condition in having long slender digits increasing in length from the first to the fourth with the fifth being about equal to the third in length and with a probable phalangeal formula of 2, 3, 4, 5, 4 (Fig. 6). The animals that made these trackways were digitigrade so only the distal end of the metatarsus is generally impressed. However it is clear from the orientation of the toes and this portion of the metatarsus that the fourth metatarsal was oriented about 20°-40° laterally, rather than extending directly anteriorly as in salamanders.

Figure 6. <u>Dromopus</u> <u>lacertoides</u>, from Haubold (1974).


1 cm

The assumption of a lateral orientation of the metatarsus in Iguana is a result of a medial abduction of the metatarsus during the initial portion of the propulsive phase. This movement results in a translation of the digits over the substrate and rotation of the distal end of the metatarsus and consequently blurs the impression of the digits. During rapid locomotion, the footprints consist of shallow depressions scooped out by the turning foot (Sukhanov 1974). In the fossil footprints of Dromopus, the toes are clearly imprinted with the individual phalanges being determinable. Thus there was probably no initial abduction of the metatarsus. The pes would have been set down with a lateral orientation and would have retained this position until plantarflexion of the pes.

The Mechanics of the Tarsus

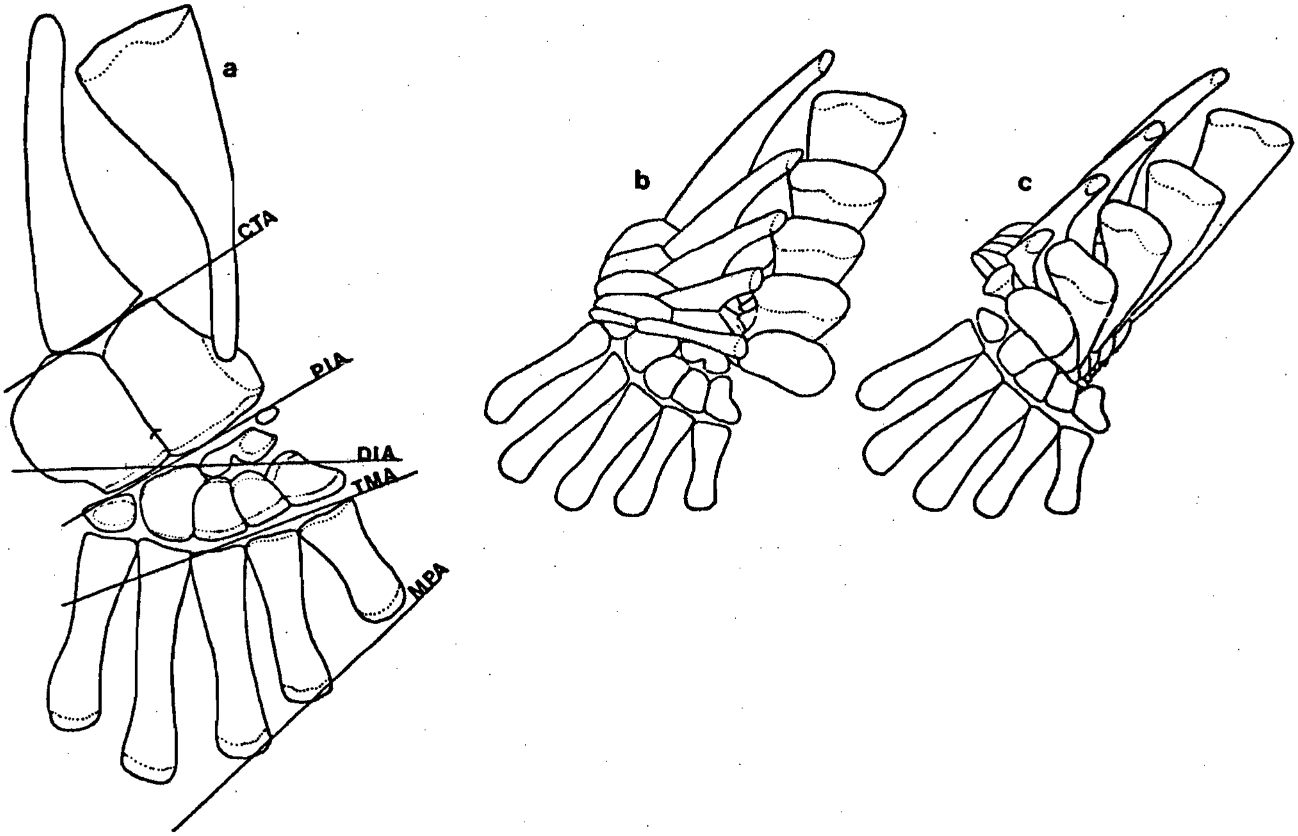
A. The joints

One of the main functions of the tarsus is to allow the pes to remain stationary as the crus was flexed, abducted and rotated. Schaeffer (1941) suggested that in primitive reptiles, the "functional ankle joint" was located between the metatarsals and distal tarsals. There is little doubt that considerable movement was possible here. The articular surfaces between the first, second and third distal tarsals and the corresponding metatarsals indicates that the potential for movement at the tarso-metatarsal joint was greatest here. Hence flexion of the metatarsals on the distal tarsal can be described as a rotation around an axis passing between these metatarsals and distal tarsals (the tarsometatarsal axis, Fig. 7a).

If functionally important movement was restricted to this joint as implied by Schaeffer's use of the term "functional ankle joint", it is difficult to see how a lateral rotation of the metatarsus was prevented. However, the articular surfaces of the remainder of the joints of the tarsus of Paleothyris show that considerable movement was possible elsewhere in the tarsus. Proximally, the broad contact of the fibula and proximal edge of the tarsus would have restricted crurotarsal movement to rotation around an axis passing through the fibular-tarsal articulation (the cruro-tarsal axis, Fig. 7b). Since the tibia articulates with the astragalus distal to the fibula, rotation around this axis would have required a simultaneous dorso-ventral movement of the tibia over the astragalus. The tibial articular surface of the astragalus is strongly convex and is larger than the opposing distal articular surface of the tibia so a large amount of this movement would have been possible.

Within the tarsus, movement would have been possible around two axes. The articulation of the astragalus and the calcaneum with the centrale and fourth and fifth distal tarsals provides a transversely oriented hinge-like axis around which movement could have occurred (the proximal intratarsal axis, Fig. 7a). More distally, movement would have been possible between the lateral centrale and the distal tarsals. Unlike the more proximal joints, the articular surfaces here are highly

Figure 7. The mechanics of the tarsus of Paleothyris: a) articulated tarsus and metatarsus showing the position of the axes of rotation; b) superimposed drawings of the crus, tarsus and metatarsus showing rotation around the proximal intratarsal axis; c) superimposed drawings of the crus, tarsus and metatarsus showing rotation around the distal intratarsal axis. Abbreviations: CTA, cruro-tarsal axis; DIA, distal intratarsal axis; MPA, metatarsal-phalangeal axis; PIA, proximal intratarsal axis; TMA, tarso-metatarsal axis.


a
CTA
PIA
DIA
TMA
MPA
b
c

incongruent. The articular surface of the centrale extends onto the dorsal surface of the bone and the second distal tarsal is thicker than the centrale and has a strongly curved proximal articular surface. Thus the amount of movement possible here would have been greater than at the more proximal joints. This would have included some translation of the centrale over the second distal tarsal as well as flexion around a hinge-like axis passing distal to the centrale (the distal intratarsal axis, Fig. 7a). This axis passes proximal to the calcaneal fourth distal tarsal articulation, so that as rotation occurred around this axis, the calcaneum would be moved away from the fourth distal tarsal. A simultaneous warping of the distal tarsal row and rotation at the calcaneal fourth distal tarsal joint would have served to maintain this articulation.

The heads of the metatarsals do not overlap each other and do not articulate closely with the distal tarsals, so that considerable independent movement of the metatarsals would have been possible. However, since the individual metatarsals would have been held together by interdigital tendons and interosseous muscles as are those of extant reptiles, the metatarsus can be considered to represent a functional unit. The line joining the distal ends of the first three metatarsals would represent the axis of rotation around which flexion of the metatarsus would have occurred (the metatarsal-phalangeal axis, Fig. 7a).

There is no single axis extending the length of the tarsus as there is in amphibians (Schaeffer 1941). Some movement would have been possible between each of the distal tarsals and between the astragalus and calcaneum allowing a warping of the distal tarsal row, but the amount of movement at any single articulation would be slight.

Since each of these axes is predominantly hinge-like in its function, rotation of the crus around its long axis will not be possible as an independent movement. However, none of these axes is perpendicular to the crus, so that as well as flexion, some rotation and abduction or adduction of the crus relative to the metatarsus will result from rotation around these axes. Rotation around those axes that extend from the preaxial edge of the tarsus laterally and distally to the postaxial edge. (the cruro-tarsal axis, the proximal intratarsal axis, the tarsometatarsal axis and the metatarsal-phalangeal axis) will, in addition to flexing the crus on the metatarsus adduct the crus on the metatarsus (decrease the angle between the crus and a vertical plane passing through the metatarsus) as the crus approaches the vertical, abduct the crus on the metatarsus as the crus moves away from the vertical, and will rotate the crus medially (Fig. 7b). If, as was probably the case during locomotion, the pes was stationary and the hip remained in the same horizontal plane, rotation around these axes would be accompanied by a movement of the femur. The exact kind of femoral movement that occurs will depend on the relationship between the axis at the ankle and the axis at the knee. Where the axis at the ankle is approximately parallel to the knee, as is the case with the cruro-tarsal, proximal intratarsal and tarso-metatarsal axes, rotation around these axes at the ankle will be accompanied by a simple flexion of the knee joint. The metatarso-phalangeal axis, however, forms an angle with the axis of rotation at the knee when the limb is extended, so that as rotation occurs around this axis, the postaxial edge of the femur will be raised more than the preaxial edge and the femur will be rotated medially.

The distal intratarsal axis slopes in the opposite direction do the remaining axes of the tarsus. Thus rotation around this axis than will result in the opposite movement of the crus and femur (Fig. 7c). That is, the crus as well as flexing, will rotate laterally and abduct relative to the metatarsus and the femur will rotate laterally.

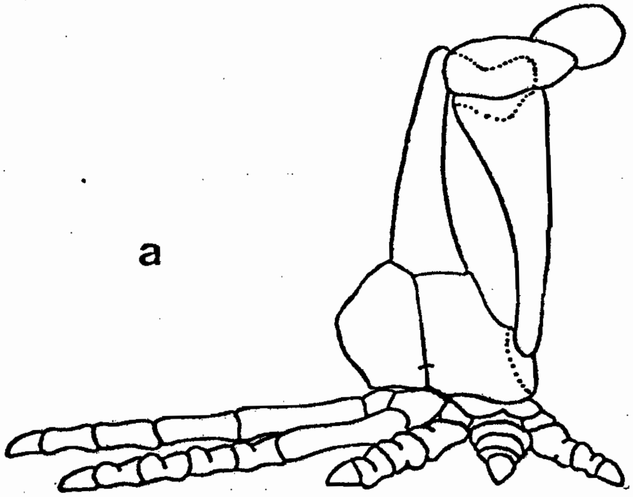
These crural movements are those that would have occurred during propulsion. According to the reconstruction of the step cycle presented above, the initial movement would have been a flexion of the crus on the femur, moving the knee anteriorly and bringing the crus into a vertical plane. These crural movements would have resulted from rotation around the cruro-tarsal, proximal intratarsal and tarso-metatarsal axes. Retraction of the femur would have moved the knee laterally, flexing the crus on the metatarsus and rotating the crus laterally. These are the predominate movements that would have resulted from rotation around the distal intratarsal joint. In addition, there would have been some lateral rotation of the femur, although this could have been compensated for by a ventral movement of the tibia over the tibial articular surface of the astragalus, which would have lowered the preaxial edge of the femur and thereby rotated the femur medially. Rotation of the femur would have abducted the crus relative to the metatarsus, increasing the angle between the crus and a vertical plane passing through the long axis of the metatarsus. Since the metatarsus is directed laterally, this would have moved the knee anteriorly. This movement would have resulted from rotation around the metatarsal-phalangeal axis.

A summation of movement at each of these axes would have allowed the pes to remain stationary as the crus is flexed, abducted and rotated. Rotation around the cruro-tarsal, proximal intratarsal and tarsometatarsal axes would have contributed to flexion of the crus on the femur (Fig. 8a). Rotation around the distal intratarsal axis would have played the important role of allowing the lateral rotation of the crus and flexion of the crus on the metatarsus that occurs as the femur retracts (Fig. 8b). Plantarflexion of the pes would have been associated with rotation of the femur and abduction of the crus (Fig. 8c). The configuration of the tarsus and the proportions of the elements are important in orienting the axes of rotation so that the necessary crural movements results from rotation around these axes and no disruptive movements result. The presence of the centrale is particularly important in this regard, since it is responsible for the orientation of the axis around which crural rotation occurs.

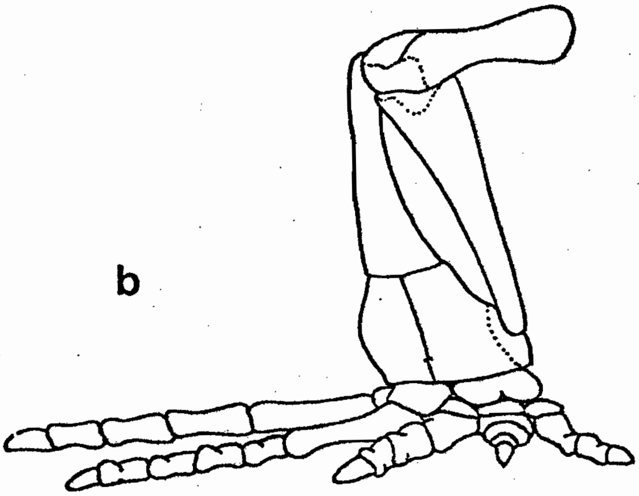
B. Flexion of the metatarsus

Schaeffer (1941) argued that the tarsus of amphibians also functioned like a pulley over which the pedal flexors passed, with these

Figure 8. Reconstruction of the pelvic limb of Paleothyris during locomotion, seen in anterior view: a) the pelvic limb just prior to retraction of the femur; b) the pelvic limb after retraction of the femur and before rotation of the femur; c) the pelvic limb after rotation of the femur and before extension of the knee and ankle joints.



a



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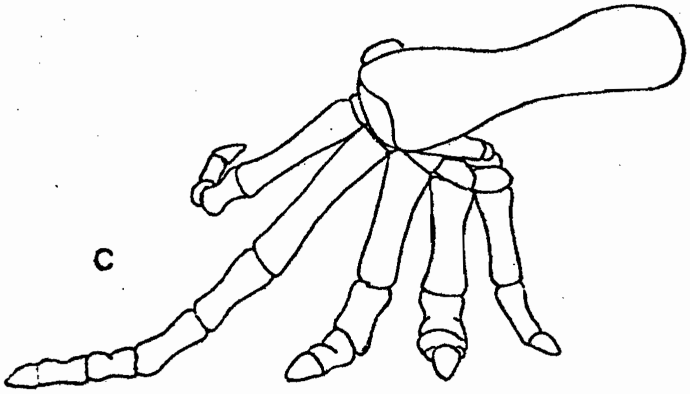


c

muscles producing a compressive force stabilizing the tarsus, and a force pressing against the ventral surface of the tarsus which would have plantarflexed the metatarsals and digits. The proportion of each of these forces would be related to the angle between the crus and the pes; as the angle approached 180°, the compressive component of the force increases. Since the primitive flexible tarsus of amphibians probably formed a shallow curve between the crus and the pes, the force produced by these muscles would have been primarily compressive, and plantarflexion of the metatarsus would not have contributed greatly to propulsion.

Although some consolidation of the tarsus has occurred with the formation of the astragalus, the primitive reptilian tarsus is still basically a flexible mosaic of bones that would have acted as a pulley over which the pedal flexors passed. Since the metatarsus and crus would have been somewhat laterally directed, the flexor tendons extending along the ventral surface of the digits would not be in line with the direction of pull of the muscles. Thus the muscle would have produced a medially directed force tending to pull the plantar aponeurosis across the tarsus. To prevent this, the plantar aponeurosis would have been braced on the lateral edge of the tarsus. From Robinson's (1975) consideration of the arrangement of the flexor muscles in lizards, it is clear that the fifth metatarsal is the major site of this bracing there. An attachment of these muscles to the proximal end of the fifth metatarsal may have been present in primitive reptiles but, where known, the fifth metatarsal does not seem to have been closely integrated with the tarsus so such an attachment would have acted to abduct the fifth metatarsal. Thus, this bone is unlikely to have been the major site at which these muscles were braced. Rather, the expanded lateral edge of the calcaneum probably served this function, with the pedal flexors looping over its lateral edge or having a tie tendon inserting on its anterior face, as is seen in lizards.

C. Force transmission

An additional function of the tarsus is to transmit the propulsive force to the substrate. Schaeffer (1941) argued that the force was passed from the femur to the tibia, across interosseous ligaments to the fibula, and from the fibula to the tarsus. The evidence for this rather indirect method of force transfer is the relationships of the crural bones to the femur and tarsus. Proximally, the tibia articulated with the ventral surface of the femur and therefore is in a position to receive the force from the femur. Distally, the situation is reversed; the fibula articulates with the proximal edge of the tarsus and is in a position to transfer the force from the crus to the tarsus most efficiently.

These relationships are retained by early reptiles, suggesting that a similar method of force transfer from the femur to the tarsus was present there. A more detailed consideration of the forces acting in the limb shows that this method of force transfer minimized the tension that was placed on the ligaments of the joints during locomotion.

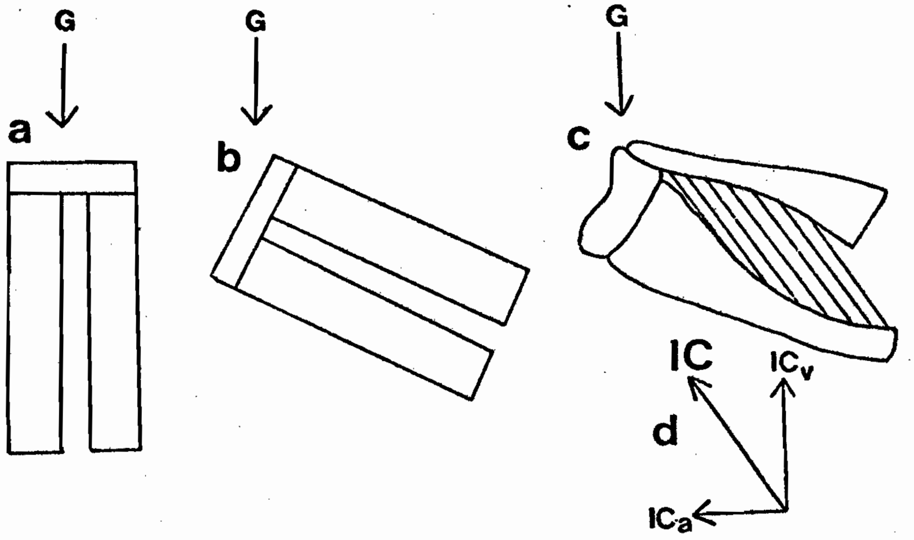
<u>Paleothyris</u> would have been a relatively slow moving animal, so that the force at any one time would have been directed primarily

ventrally as in salamanders (Barclay 1946). That this was the case in the closely related Hylonomus is indicated by the presence in the pelvis of a distinct supraacetabular buttress that would have overlain the head of the femur and resisted the ventrally directed force passing through the acetabula (Fig. 11). The structure of the acetabula is not known in Paleothyris, but in view of the similarity of other features of the locomotor apparatus, this can be assumed to have been comparable.

Using a diagramatic model in which the tibia and fibula both articulate with the distal edge of the femur and the proximal edge of the tarsus, it can be seen that under these conditions, the force transmitted across the joints would be primarily compressive only when the femur was directed anteriorly and the crus was vertical (Fig. 9a). When the femur has retracted and rotated so that the crus extends posteriorly and faces laterally, the force would have been transmitted across the joints at a large angle to the joint surfaces (Fig. 9c), and thus would result in considerable tension being placed on the ligaments of the joints.

The arrangement of the tibia, fibula and femur enables the interosseous cruris muscles to counteract this ventrally directed force. Since the tibia and fibula are relatively short and widely separated, these muscles would have formed a large angle to the crural bones, and when the crus was posteriorly directed and faced laterally, the force produced by these muscles would have involved a large vertical component (Fig. 9d). This component would have pressed the fibula against the

Figure 9. The mechanics of force transfer from the femur to the tarsus. a and b) models of a femur, tibia and fibula in which the crural bones both articulate with the ventral surface of the femur at a; the beginning of the propulsive phase and b; after rotation of the femur. c) The femur, tibia and fibula of Paleothyris after rotation of the femur showing the orientation of the interosseous cruris muscles. d) Analysis of the forces produced by the interosseous cruris muscles. Abbreviations: G, orientation of the force resulting from gravity; IC, the orientation of the force produced by the interosseous cruris muscles; IC_a, the anterior component of the force produced by the interosseous cruris muscles; IC_v, the vertical component of the force produced by the interosseous cruris muscles.


G
G
G
a
b
c
IC
IC_v
d
IC_a

femur and pulled the tibia upwards, counteracting the ventral force resulting from gravity. The antero-posterior component of the force would pull the tibia upwards, pressing it against the femur and would pull the fibula downwards and posteriorly, transmitting the propulsive force to the fibula from the tibia. Thus the major forces being transmitted across the knee and crural-tarsal joints would have been the posteriorly directed propulsive force, the force resulting from the action of the long pedal flexors, and the antero-posterior component of the force produced by the interosseous muscles. All these forces would have been approximately perpendicular to the femoral-tibial articulation at the knee, and the fibular-tarsal articulation at the cruro-tarsal joint, and thus would have placed minimal tension on the ligaments of those joints.

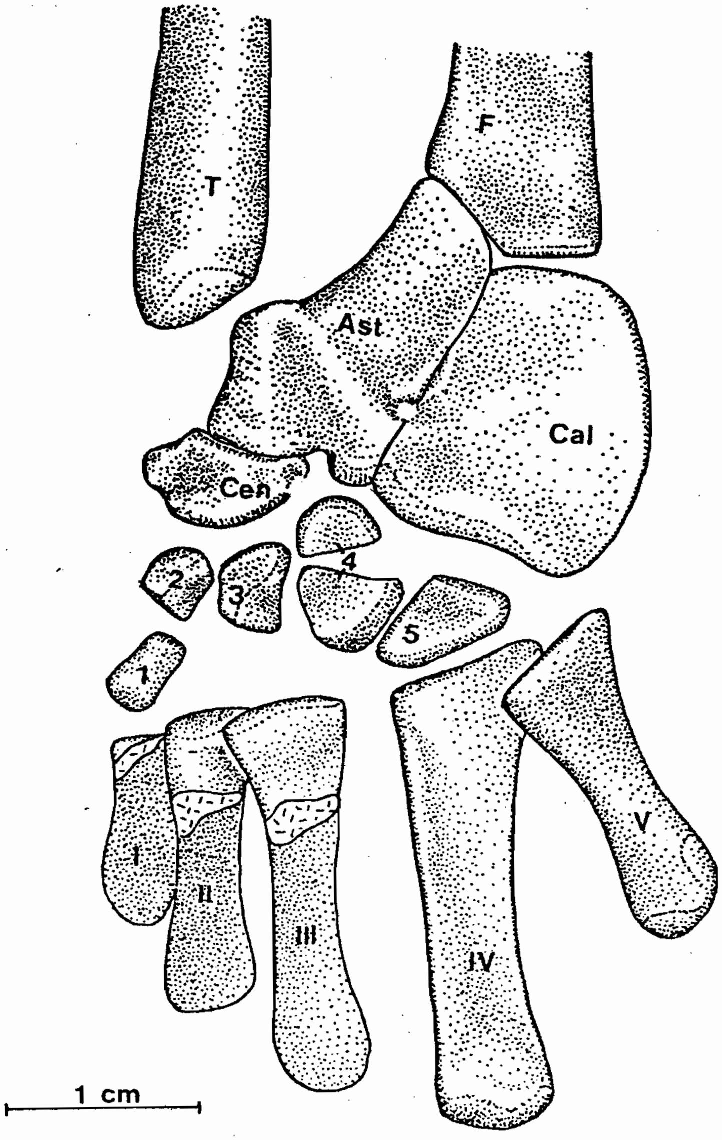
III THE TARSUS OF PETROLACOSAURUS AND THE ORIGIN OF THE DIAPSID TARSUS

The oldest known diapsid reptile is Petrolacosaurus kansensis from the Upper Pennsylvanian of Kansas. A recent description of a large amount of new material has demonstrated the taxonomic affinities of this animal and has provided a detailed understanding of its osteology (Reisz 1975). Reisz concluded that "Petrolacosaurus is closely related to the earliest known eosuchians and that this form presents an ideal combination of primitive and advanced features to make it a plausible ancestor to later diapsids" (Reisz 1975, p. 180). Thus Petrolacosaurus occupies a central position in diapsid evolution and its tarsus provides a basis for identifying the changes in the tarsus that occurred during the origin of diapsids.

Structure

The tarsus of Petrolacosaurus (Fig. 10) is similar to that of Paleothyris in its general configuration, although modifications are seen in the proportions of the elements and in a number of structural details. The major proportional change is a shortening of the tarsus proximodistally relative to the crus -- the contact between the astragalus and calcaneum is one fifth of the length of the tibia in Petrolacosaurus in contrast to Paleothyris where it is one third the length of the tibia (Table 1). A change is also seen in the proportions of the distal tarsals: the second distal tarsal is slightly smaller than

Figure 10. *Petrolacosaurus*, right tarsus, ventral view. Specimen KUMNH 1424. For abbreviations, see list of abbreviations.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Cen
4
2
3
5
1
I
II
III
IV
V
1 cm

Table 1. Measurements of the hind limb in early reptiles.
All measurements are in millimeters.

	Length of tibia	Length of astragalo-calcaneal contact	Length of metatarsals I	II	III	IV	V
Paleothyris							
MCZ 3481	10	3	4	5.5	7	-	6.5
MCZ 3482	10	3	-	4.5	5	8	-
Petrolcaosaurus							
KUMNH 9951	50	11	9	15	18	22	15
tangasaurids							
MPP 1908-21-14a	53	8	10	18	22	24	18
MPP 1925-5-32a	-	8	10	17	21	22	16
MPP 1908-11-56	21	4	-	10	13	13	10
MPP 1925-5-61	-	9	12	21	23	25	20
MPP 1908-21-10a	-	8	10	18	21	23	20
Galesphyrus							
SAM 2758	23	5	5	8	11	13	10
Kenyasaurus							
KNM MA1	34	5	6	14	17	19	13
Claudiosaurus							
MPP 1976-6-1	45	4	12	19	22	23	13
MPP 1911-18	40	4	8	19	21	22	13

the first and third in *Petrolacosaurus* unlike *Paleothyris*, where the second is the largest of the first three distal tarsals.

The calcaneum is unmodified from the primitive condtion. The major structural change in the astragalus is in the configuration of the tibial articular surface. This has become elongate proximodistally and has a central depression that receives the distal end of the tibia. Ventrally, this articular surface is buttressed by a low ridge that extends to the calcaneum just distal to the perforating foramen. This ridge forms the lower border of a shallow groove that extends from the area between the tibial and fibular articular surfaces to the perforating foramen.

Distally, the articular surface for the centrale is notched, resulting in the separation of the ventrolateral corner of the astragalus as a distinct process, called the condyloid process by Reisz. Although there is some indication of a similar notch in *Paleothyris*, a condyloid process cannot be distinguished. In *Captorhinus*, an Early Permian reptile, both the notch and the condyloid process are distinct. From Peabody's (1951) description of the ontogenetic development of the astragalus in this animal, it is clear that the condyloid process is homologous to the fourth centrale of amphibians. The notch serves to allow the hourglass-shaped centrale to fit closely with the astragalus. In *Petrolacosaurus*, the distal border of the centrale has become convex, obscuring the primitive hourglass shape. The proximal articular surface, however, remains similar to that of *Captorhinus*, as does its relationship to the condyloid process and the notch on the distal border of the astragalus. Thus these features are simply the retention of the primitive condition, rather than being specializations associated with the incipient development of an intratarsal joint, as suggested by Reisz.

The medial centrale has been lost. Its fate is uncertain. The single remaining centrale, as well as developing a convex distal articular surface, shows a restriction of the articular surface to its distal and proximal edges with extensive development of the finished bone on its dorsal and ventral surfaces.

The proportions of the metatarsals are similar to those of _Paleothyris_, although their proximal ends have become expanded and overlap each other slightly. Also, the articular surfaces of the fifth metatarsal and fifth distal tarsal correspond closely to each other so that little movement probably occurred between the two bones.

Locomotion in _Petrolacosaurus_

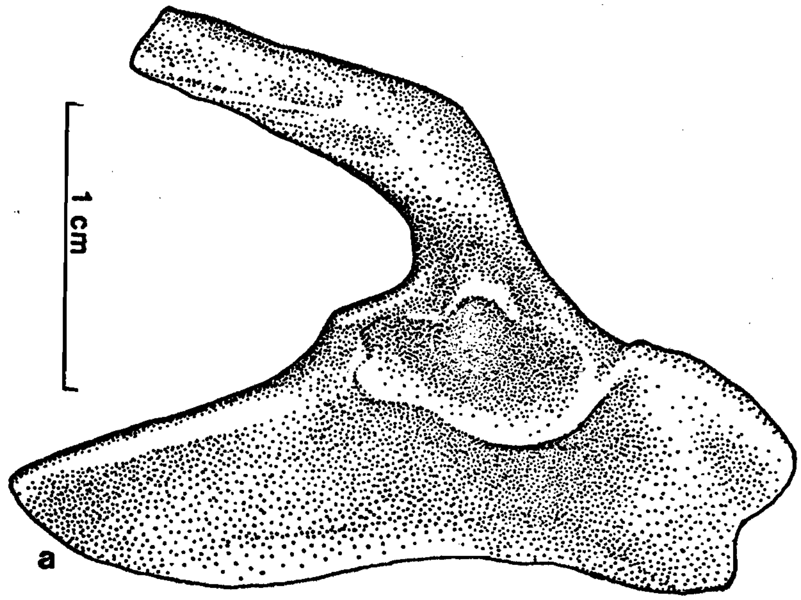
The locomotor apparatus of _Petrolacosaurus_ differs from that of _Paleothyris_ in its proportions. The femur and humerus are longer relative to the length of the presacral vertebral column, the forearm and crus are longer relative to the femur, the tibia has a larger diameter than the fibula, and the limbs have a more slender appearance than in _Paleothyris_ (Reisz 1975). On the basis of these differences, Reisz suggested that _Petrolacosaurus_ was a more agile animal and was capable of more rapid locomotion than were the romeriids. A structural feature that supports this is the buttressing of the acetabulum. As argued above, the presence of a distinct supraacetabular buttress in Hylonomus is indicative of relatively slow movement. In Petrolacosaurus, this has been lost as a distinct structure, with the acetabula being strongly buttressed anteriorly and dorsally (Fig 11b). This indicates that the force transmitted through the hip joint was more anteriorly oriented, as would be the case in a rapidly moving animal.

None of the structural modifications of the limb elements suggests that the improved locomotor abilities of Petrolacosaurus involved modifications of the pattern of movement of the pelvic limb segments. The femur remains primitive, with a well defined adductor ridge, a division of the distal articular surface into two distinct condyles, and a deep groove for the tendon of the triceps femoralis (iliotibialus, femorotibialus and ambiens). Also, the comparable fore and hind limb segments are of equal length as is the case in romeriids. Consequently, the step cycle used in reconstructing the mechanics of the tarsus in Paleothyris can be used as a basis for reconstructing the mechanics of the tarsus in Petrolacosaurus.

Mechanics

In describing the tarsus, Reisz (1975) suggested that an incipient intratarsal joint was present passing distal to the astragalus and calcaneum (the proximal intratarsal axis of this work) with the proximal and distal units being firm, tightly knit structures. There is little

Figure 11. The pelvis in early reptiles: a) Hylonomus lyelli, specimen BM(NH) R.4167; b) Petrolacosaurus, from Reisz (1975, Figure 20), reversed for comparison with Hylonomus.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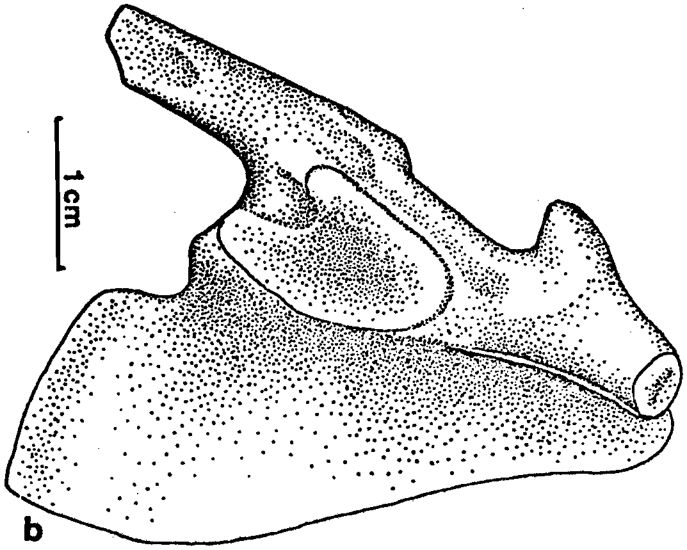
a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b

question that considerable movement was possible around the proximal intratarsal axis. While the cruro-tarsal axis probably still allowed significant amounts of movement, the change in structure of the tibial-astragalar joint indicates that the amount of movement possible here was reduced from that possible in Paleothyris. The tibia would have been restricted to a dorso-ventral movement within the concavity of the opposing articular surface on the astragalus and, since the distal surface of the tibia is almost equal in size to the articular surface on the astragalus, the amount of this movement possible would have been small. The articular surfaces of the distal tarsals and centrale, however, suggest that more movement was possible here than implied by Reisz. The opposing articular surfaces between the centrale and distal tarsals are convex, with that of the centrale being quite strongly so. Thus, as in Paleothyris, an axis of rotation passing distal to the centrale would have been present. Rotation around this axis would have resulted in a lateral rotation of the crus and a flexion of the crus on the metatarsus, the crural movements that occur as the femur retracts towards a line perpendicular to the body. Also, as in Paleothyris, this axis passes through the calcaneum proximal to the calcaneal-distal tarsal articulation, so rotation around this axis would require some warping of the distal tarsal row for the calcaneum to remain on contact with the fourth distal tarsal.

Thus the only change in the movements possible within the tarsus was a reduction in the amount of cruro-tarsal movement. This would not have affected the basic mechanics of the tarsus; the axis of rotation around which movement at this joint occurred is approximately parallel to the axis passing distal to the astragalus and the calcaneum so the crural movements resulting from rotation around these axes would have been identical. The decrease of cruro-tarsal movement could easily be compensated for by an increase in the amount of movement occurring at the proximal intratarsal axis.

The functioning of the tarsus as a pulley is not substantially altered from the condition in Paleothyris. The expansion and slight overlapping of the heads of the metatarsals would reduce the flexibility of the metatarsus. This may have been the initial change in the consolidation of the metatarsus to form a propulsive lever and may reflect a slight increase in the contribution flexion of the metatarsus made to propulsion, but nothing indicates that the arrangement of muscles flexing the metatarsus was modified.

A number of features suggest that the tibia was assuming more significance in the transfer of force from the femur to the tarsus. Chief among these is the increase in the diameter of the tibia relative to the fibula. These bones were loaded axially, and are analogous to columns. Since the strength of a column is proportional to its minimum cross sectional area (Badoux 1974), the relative diameter of the tibia and fibula gives an indication of the proportion of the force transmitted through the two bones. If the entire force was transmitted from the tibia to the fibula, they would be stressed equally, and their diameters would be expected to be equal. This is the case in some amphibians (e.g. Amphibamus, Carroll 1964, his plate 2), but more usually, and consistently in early reptiles, the tibia is slightly larger than the fibula, indicating the propulsive force was not transmitted completely from the tibia to the fibula. In Petrolacosaurus the disparity in size of the tibia and fibula has been increased, with the tibia becoming a robust, cylindrical element and the fibula being slender and blade-like. Thus the portion of the force transmitted from the tibia to the fibula has probably been further decreased with a greater proportion of the force being transmitted across the tibial-astragalar articulation. The changes in the structure of the joint and the buttressing of the tibial-astragalar articulation would increase the strength of this joint, and thus can be directly associated with this.

The increased importance of the tibia in transmitting force from the femur to the tarsus can be associated with the change in orientation of the force produced during propulsion. As argued above, Petrolacosaurus was probably a more agile, faster moving animal than Paleothyris. It follows from this that the posteriorly oriented propulsive force was greater than in Paleothyris, and the force passing through the hip and knee was oriented more strongly anteroposteriorly. Thus the portion of the force that is directed ventrally and with it, the tension placed on the ligaments of the knee, is decreased. The force required from the interosseous muscles to oppose the tension in these ligaments would be less, and these muscles would be reduced. With a reduction in these muscles, there would be a reduction in the proportion of the propulsive force transmitted to the fibula. The proportion that was not transmitted to the fibula across the interosseous ligaments would be passed directly to the astragalus across the tibial-astragalar joint.

Origin of the diapsid tarsus — Mechanical aspects

This description of the mechanics of the tarsus in Petrolacosaurus, suggests that the major change in the tarsus during the origin of diapsids was the solidification of the cruro-tarsal joint. This is of considerable functional importance for the later evolution of the tarsus, since the reduction in the cruro-tarsal movement resulted in the ankle joint developing intratarsally, rather then cruro-tarsally as in synapsids.

IV THE TARSUS IN YOUNGINIFORM EOSUCHIANS

Younginiform eosuchians have long been thought to be the central group in diapsid evolution, with the last common ancestor of lizards, sphenodontids, rhynchosaurids and archosaurs being a member of this group. Youngina itself has been suggested as a suitable structural ancestor of lizards (Robinson 1967), although dissenting views have been expressed (Watson 1957; Gow 1972). When first described, Youngina was considered in relationship to the origin of archosaurs (Broom 1914). This relationship has not been accepted by Reig (1970), although, as shown by Carroll (1976c), the origin of archosaurs from within the Younginiformia is suggested by the presence of a number of archosaur characters in a second eosuchian, Heleosaurus.

Unfortunately, our understanding of the diversity of Younginiformia is at present very incomplete. With the redescription and reassignment of the Paliguanidae to the lizards (Carroll 1975) and of the Prolacertidae to its own order within the Lepidosauria (Gow 1975), only two families, the Tangasauridae and the Younginidae, remain in the Younginiformia. There is little to indicate that these families form a natural association. Rather, the group is more accurately considered to be a grade of evolution including diapsids that are advanced over the primitive grade represented by Petrolacosaurus but are not members of any of the more advanced groups of diapsids. With the exception of some members of the Tangasauridae, the genera of younginiformes are clearly distinct, each genus representing a separate line of evolution stemming from some as yet unknown ancestral group. Also, with the possible exception of a relationship between Heleosaurus and archosaurs, no eosuchian shows characters that can be taken as indicative of a close relationship with any of the more advanced groups. Thus it is not possible to trace in detail the changes in the tarsus that occurred during the origin of the advanced diapsid groups. Despite this, the tarsi of known younginiformes are important in consideration of the functional evolution of the tarsus in diapsids since an intratarsal joint is first seen in members of this group. An understanding of the mechanics of this joint will provide a basis for considering the adaptive significance of the initial development of the intratarsal joint and the kinds of structural and mechanical changes associated with its development.

Material

The following specimens were considered during the course of this investigation. All of these are preserved as natural moulds. Latex peels of the impressions provide a positive image of the bones that could be examined directly. In the case of 1925-8-14 and 1908-32-68, which are part and counterpart of the same specimen, the individual tarsal elements were cast separately and opposing halves joined to give three dimensional replicas of the tarsal elements.

Kenyasaurus mariakaniensis, Kenya National Museum MA 1: Part and counterpart of postcranial skeleton showing the articulated right and left hind limbs in dorsal and ventral view.

Galesphyrus capensis, South African Museum 2758: postcranial skeleton showing the articulated right and left hind limbs in dorsal view.

Tangasauridae, Museum of Paleontology, Paris 1925-8-14: slightly disarticulated pes.

Museum of Paleontology, Paris 1908-32-14: counterpart of specimen 1925-8-14.

Museum of Paleontology, Paris 1908-11-56: postcranial skeleton of an immature individual showing right and left tarsi in ventral view.

Museum of Paleontology, Paris 1908-21-10a: articulated right pes in ventral view.

Museum of Paleontology, Paris 1925-5-32a: articulated right and left hind limbs, pelvis and part of tail, in ventral view.

Museum of Paleontology, Paris 1925-5-61: articulated tarsus and metatarsus in dorsal view.

Museum of Paleontology, Paris 1908-21-14a: articulated tarsus and metatarsus, dorsal view.

The Tangasauridae is currently under review by Philip Currie. At least two genera can be recognized, but assignment of the specimens to particular genera is difficult. Despite this taxonomic confusion, the structure of the postcranial skeleton in general and the tarsus in particular is well known. Thus the structure and mechanics of the tarsus in this family will be considered first.

Structure of the tarsus in the Tangasauridae

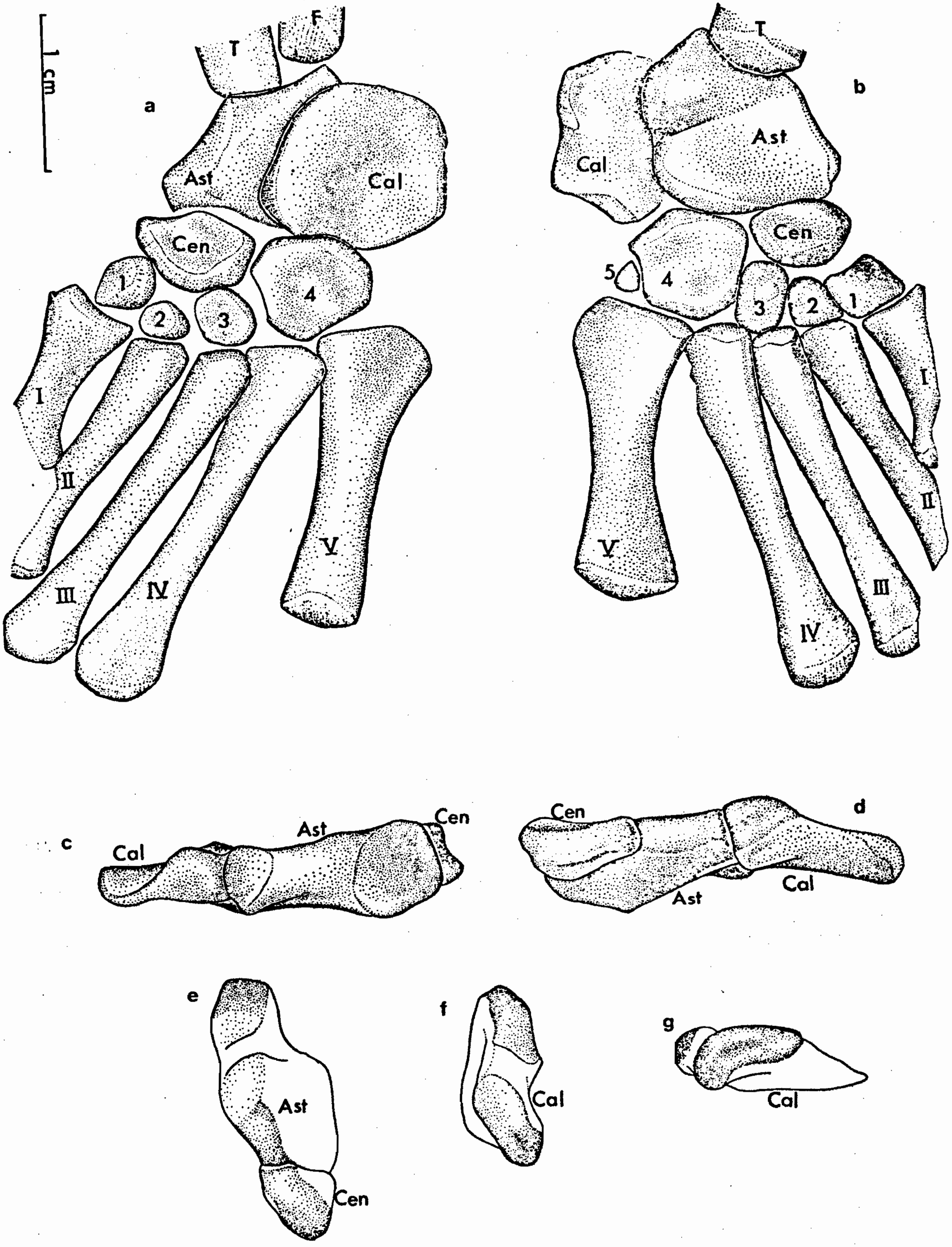
The general arrangement of the tarsal elements (Fig. 12) has been little modified from the primitive diapsid condition. A full compliment of tarsal elements is retained, although the fifth distal tarsal is late to ossify and fuses with the fourth distal tarsal in mature individuals (Harris and Carroll 1977) so only four distal tarsals are generally seen. Within this primitive configuration, a number of proportional and structural changes have occurred. The major proportional changes are a proximo-distal shortening of the astragalus and calcaneum, an increase in the size of the fourth and a decrease in the size of the second distal tarsal relative to the size of the third, and an increase in the length of the metatarsals relative to the tarsus. The change in proportions of the astragalus and calcaneum can be recognized by comparing the length of the contact between the two bones to the length of the tibia: in _Petrolacosaurus_, the tibia is five times the length of the contact between the astragalus and calcaneum in contrast to the tangasaurids, where the tibia is six times the length of this contact (see measurements, Table 1).

The changes in the size of the distal tarsals have accentuated the primitive disparity in proportions. The second distal tarsal, which is only slightly smaller than the third in _Petrolacosaurus_ is about half the proximo-distal length of the third in the tangasaurids, and the fourth has increased in size from about 1.5 times the proximo-distal length of the third in _Petrolacosaurus_ to twice the length of the third in the

Figure 12. The tangasaurid tarsus and metatarsus.

a) slightly disarticulated tarsus in dorsal view. The calcaneum was reversed left for right during preservation so that it appears in ventral view; b) counterpart of a; c) articulated astragalus, calcaneum and centrale in distal view; d) articulated astragalus, calcaneum and centrale in distal view; e) articulated astragalus and centrale showing calcaneal articular surface; f) calcaneum showing astragalar articular surface; g) calcaneum, distal view.

a: specimen P.M. 1925-8-14; b: specimen 1908-32-14. For key to abbreviations see list of abbreviations.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tangasaurids.

The disparity in lengths of the metatarsals in the tangasaurids is similar to the condition in *Petrolacosaurus*. In both, the fourth metatarsal is about 2.3 times the length of the first. However, the metatarsals have been elongated relative to the tarsus. In *Petrolacosaurus*, the fourth metatarsal is twice the length of the contact between the astragalus and calcaneum, while in the tangasaurids it is slightly over three times the length of the contact.

The calcaneum remains essentially unmodified from the plate-like structure seen in more primitive reptiles (Fig. 12). Possibly the lateral edge of the calcaneum extends further lateral to the fibula than it does primitively, although this may be an artifact of the shortening of the calcaneum.

The major structural modifications of the astragalus are the deepening of the groove leading to the perforating foramen, the enlargement of the ridge buttressing the tibial articular surface, and the loss of the notch in the distal edge of the astragalus.

Corresponding to the change in the distal articular surface of the astragalus is a change in the proximal articular surface of the centrale; this has become a trough-like depression that fits over the distal edge of the astragalus. The distal articular surface of the centrale is strongly convex but is differentiated into separate areas for articulation with the distal tarsals.

The structure of the distal tarsals is not greatly modified from the condition seen in Petrolacosaurus, although, as described below, functionally important changes have occurred in the detailed shape of the second and third distal tarsals.

The proximal ends of the metatarsals are expanded and overlap each other, each metatarsal overlapping the next lateral metatarsal slightly. With this expansion, the relations of the metatarsals and distal tarsals has been changed. The second to fifth metatarsals, as well articulating with the immediately proximal distal tarsal, are supported by the next medial distal tarsal. Thus the second metatarsal articulates with the first and second distal tarsals, the third metatarsal articulates with both the second and the third distal tarsals and so on. This is particularly marked in the case of the fifth metatarsal, which is almost completely supported by the fourth distal tarsal.

Locomotion in the Tangasauridae

On the basis of the powerfully developed humerus in the members of this family and a retardation of the ossification of the skeleton, Romer (1956) suggested that these animals were aquatic. Three basic kinds of aquatic locomotion can be recognized: one in which the limbs are used as paddles as is seen in ducks; one in which the limbs are used as wings and the animal flies through the water as is the case in the sea turtle (Walker 1971), and one in which the propulsive force is supplied by lateral bending of the vertebral column and the tail as in the alligator (Manter 1940) and the swimming iguana (Swanson 1959). That the latter mode of propulsion was the one used is indicated by the expanded neural and haemal spines in the tail of one of the tangasaurids (illustrated in Harris and Carroll 1977). In both the alligator and the swimming Iguana, the limbs are held against the side of the animal and used only for braking and steering. Consequently specializations for aquatic locomotion are not seen in the limbs, and both animals are able to utilize an efficient terrestrial pattern of locomotion. The well developed limbs of the tangasaurids and the presence of all the landmarks normally seen in the pelvic limb elements, such as the internal trochanter, the crest on the lateral side of the tibia associated with the insertion of the puboischitibialis, and the perforating foramen between the astragalus and calcaneum, suggests that the tangasaurids were also capable of terrestrial locomotion.

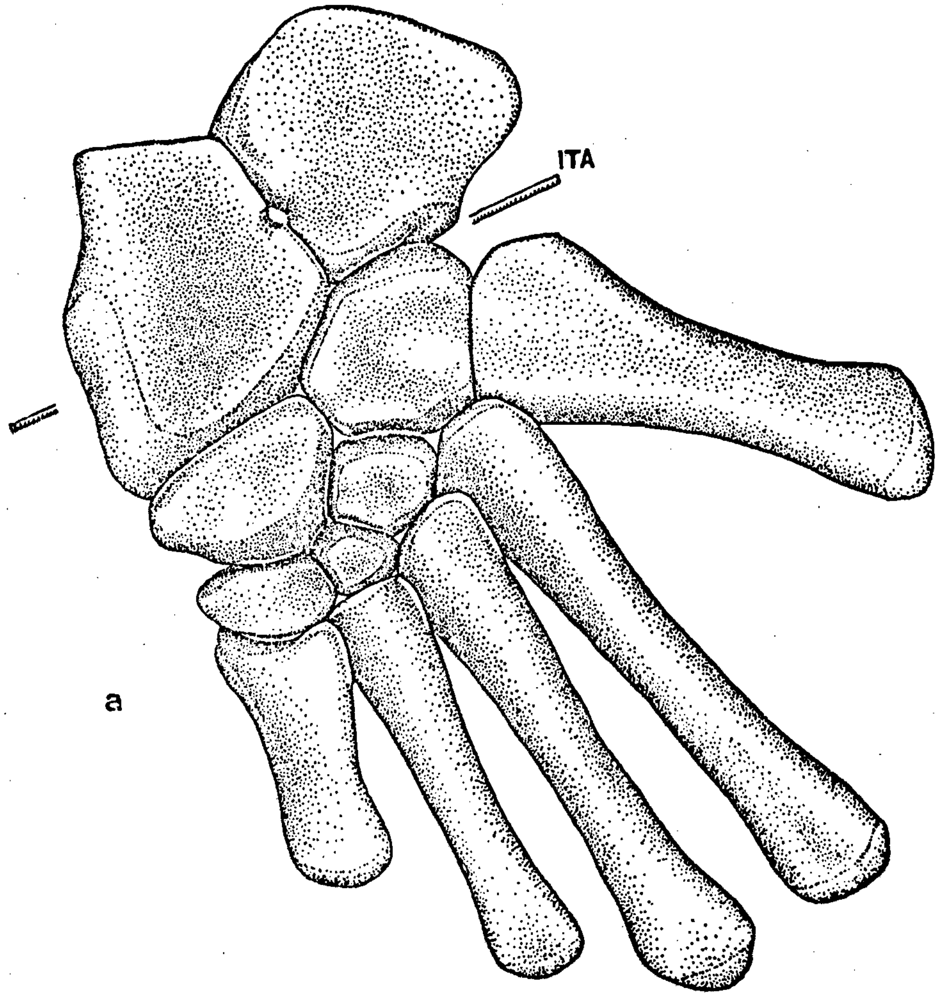
The morphology of the limbs is that typical of animals with a primitive pattern of limb movements so that while walking on land a sprawling step cycle would have been used. However, the structure of the femur and crus and the proportions of the limbs have been modified from the primitive condition, indicating that the step cycle was changed in some details. In primitive reptiles, the fore and hind limb elements, except for the manus and the pes, are of equal length. In tangasaurids, the humerus is shorter than the femur and the forearm is shorter than the crus. Also, the femur has become lizard-like in structure as a result of reduction of the ventral Y-shaped ridge system leaving only the proximal portion of the adductor ridge supporting a prominent internal trochanter, of the decrease in depth of the groove for the tendon of the femoro-tibialis, of the reduction of the division of the distal articular surface into two trochanters leaving a single rectangular surface for the tibia, and of the development of a sigmoidal curvature. The mechanical significance of these changes is uncertain, so it is not possible to identify precisely the associated changes in the pelvic step cycle. However, the development of a lizard-like femur and lizard-like proportions suggest that any changes involved the assumption of a pattern that was similar to lizards. Thus the pelvic step cycle of Iguana described above can be used as a basis for interpreting the mechanics of the tarsus in the tangasaurids.

Mechanics of the tangasaurid tarsus

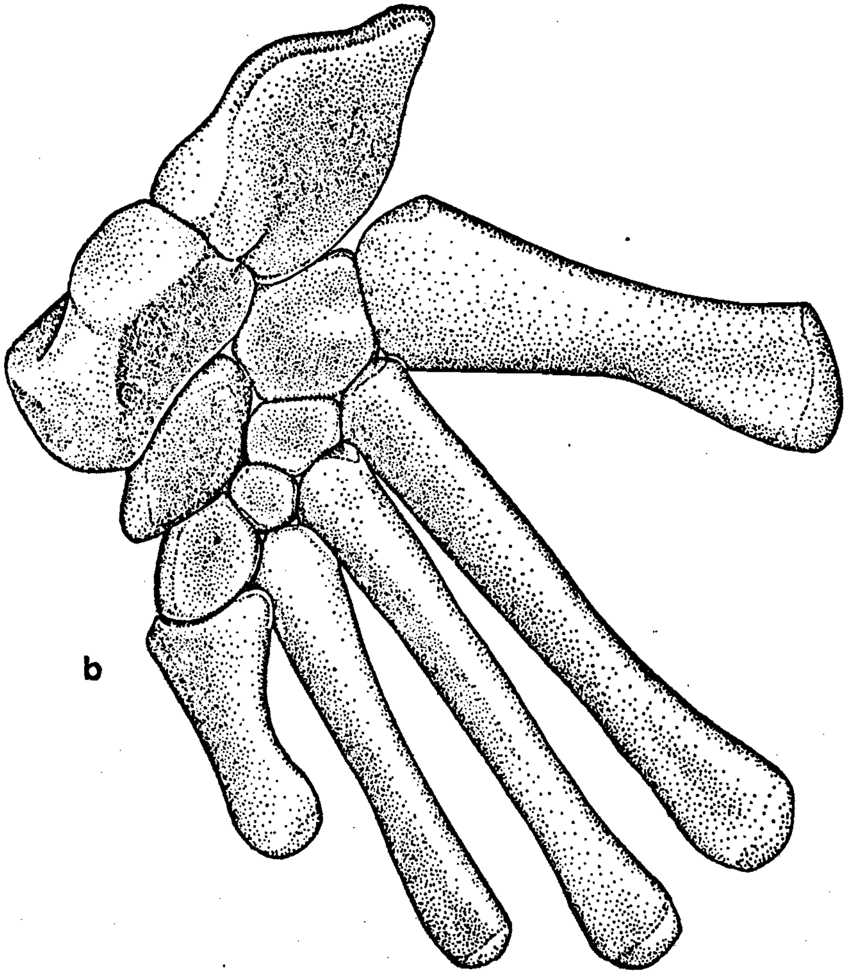
Although the structural changes that occurred during the development of the tangasaurid tarsus are relatively minor, they are of considerable mechanical significance since they are associated with the development of an intratarsal joint. The presence of this joint is indicated by the increase in the curvature and incongruency of the articular surfaces between the proximal and distal tarsal elements over the condition in more primitive reptiles. This is particularly marked medially, where both the distal articular surfaces of the centrale and astragalus and the opposing articular surfaces of the distal tarsals are convex dorsoventrally. Lateral to this portion of the intratarsal joint, a concave-convex articulation is present. The distal articular surface of the calcaneum has a mediolaterally elongate central depression (Fig. 12g) that fits over the convex proximal articular surface of the fourth distal tarsal. This arrangement will restrict movement between the calcaneum and fourth distal tarsal to a hinge-like flexion of the calcaneum on the distal tarsal with the movement occurring around an axis of rotation lying within the depression on the calcaneum (Fig. 13a). In contrast to earlier reptiles, this axis of rotation passes through the body of the astragalus proximal to the astragalus-centrale articulation. Thus if rotation occurred around this axis as an independent movement, the distal edge of the astragalus and centrale would be moved posteriorly away from the distal tarsals. The arrangement of the distal tarsals and metatarsus (Fig. 13a) suggests that significant forces were transmitted from the first and second metatarsals across the distal tarsals to the centrale, so it would be necessary for the astragalus, centrale and distal tarsals to remain in articulation. Flexion of the centrale on the astragalus would have swung the distal end of the centrale anteriorly, but this alone would not be sufficient to maintain contact with the distal tarsals since the entire centrale is moved posteriorly. In addition, some anterior movement of the centrale would have resulted from a warping of the distal tarsal row. The second and third distal tarsals are keystone-shaped when seen in dorsal view, their proximal ends being narrower than their distal edges (Fig. 12a). Since the metatarsus would have been directed laterally, the propulsive force would have been

Figure 13. Reconstruction of the tangasaurid tarsus and metatarsus. a) Joints maximally extended; b) joints maximally flexed.

Abbreviation: ITA, intratarsal axis.



a



b

transmitted across the metatarsus, rather than along the length of the individual metatarsals. This would have compressed the distal tarsal row, pressing the distal tarsals together. The first metatarsal and first distal tarsal would have been stationary so this compression of the distal tarsal row would have rotated the fourth distal tarsal, swinging its proximal end medially and, through its contact with the proximal tarsal bones, moving the centrale distally towards the distal tarsals. This would have rotated the astragalus and calcaneum and with them, the crus, to face laterally. Thus these movements at the ankle result in a flexion of the crus on the metatarsus, moving the knee anteriorly, ventrally and, as the crus is rotated, laterally, and a lateral rotation of the crus. These are the crural movements that occur during the initial part of the propulsive phase as the knee is flexed and the femur begins to retract.

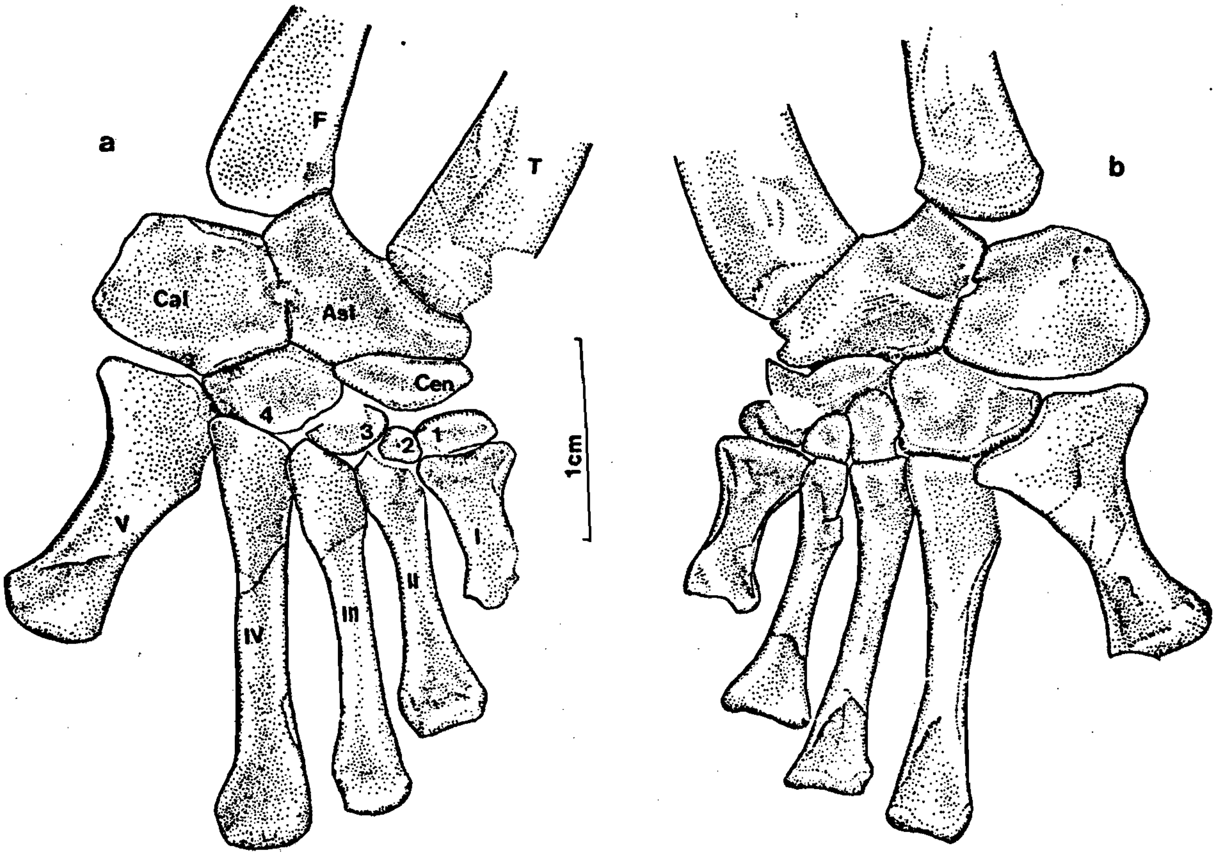
The distal tarsals are also keystone-shaped dorsoventrally with their ventral surfaces larger than their dorsal surfaces. This can be recognized by comparing dorsal and ventral views of the distal tarsals (Fig. 12a, b). Thus as the propulsive force was passed across the distal tarsals, the distal tarsal row would have been bent concave dorsally. Since the first distal tarsal was probably stationary, the fourth distal tarsal would have been lifted and rotated around its proximo-distal axis so that it faced towards the medial side of the tarsus. This would have tilted the astragalus and calcaneum so they assumed a more vertical position. Since the crus would have faced laterally at this time, this would depress the knee and move it anteriorly. Thus the crus would be abducted on the metatarsus (the angle between the long axis of the crus and a vertical plane passing through the metatarsus would be increased), the crural movement that occurs as the femur rotated around its long axis. In the association of this crural movement with movement between the distal tarsals the tangasaurids are different from Paleothyris where, as described above, abduction of the crus was probably associated with plantarflexion of the metatarsus. In tangasaurids, plantarflexion of the metatarsus would have occurred later in the propulsive phase with the joints of the metatarsus extending at the same time. A result of this is that the angle between the crus and metatarsus that was formed prior to the initiation of flexion of the metatarsus would be decreased. This is of considerable functional importance since, as argued by Schaeffer (1941), the proportion of the force produced by the pedal flexors that acts to flex the metatarsus would be increased by decreasing this angle. A morphological feature that suggests that the metatarsus of younginiformes played a more active role in propulsion is the overlapping heads of the metatarsals. This probably reflects a consolidation of the metatarsus associated with an increase in the propulsive force passing through the metatarsus.

The expanded head of the fifth metatarsal may be the initial change leading to the development of the hooked fifth metatarsal in later diapsids. The articular surfaces at the fifth metatarsal-fourth distal tarsal joint are flat and fit closely together so that there would have been little movement between the bones. Consequently the muscles inserting on the metatarsal would act to move the metatarsus rather than the fifth metatarsal alone, and the pedal flexors could flex the metatarsus through an insertion on the fifth metatarsal. However, since the metatarsus and distal tarsal row remains flexible, it is unlikely that any of the long pedal flexors would have had their major insertions on the fifth metatarsal. Rather, they would have used the tarsus as a pulley, with the insertion on the fifth metatarsal acting to change the direction of the pull of the muscels so it was in line with the metatarsals.

The Tarsus of Kenyasaurus

Kenyasaurus, an eosuchian from the Lower Triassic of Kenya recently described by Harris and Carroll (1977), was attributed to the Tangasauridae on the basis of similarities in body proportions and the presence of an ossified sternum. In all features of the tarsus in which the tangasaurids are advanced over the condition seen in Petrolacosaurus, Kenyasaurus is similar to or more advanced than the tangasaurids. The proximo-distal shortening of the astragalus and calcaneum is greater than that seen in the tangasaurids; the tibia is seven times the length of the contact between the astragalus and calcaneum in Kenyasaurus in contrast to the tangasaurids where the tibia is six times the length of this contact. This shortening of the astragalus has obscured the primitive L-shaped configuration, the element being triangular in Kenyasaurus (Fig. 14).

Figure 14. The tarsus and metatarsus of _Kenyasaurus_. a) dorsal view of right tarsus; b) ventral view of right tarsus. Specimen KNM MA 1. For key to abbreviations see list of abbreviations.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With this change, an intimate contact between the astragalus and tibia developed so that a large block of cartilage was not necessary for the two elements to fit closely together.

The calcaneum of *Kenyasaurus* differs from that of the tangasaurids in having a muscle scar on its ventral surface extending from the proximolateral corner to about midpoint on the bone. The only muscle originating from this area in lizards is the adductores digit five (terminology of Schaeffer 1941), a small muscle of uncertain function originating on the ventral surface of the calcaneum and inserting on the lateral edge of the fifth metatarsal. The relationship of the calcaneum and the proximal expanded head of the fifth metatarsal in *Kenyasaurus* suggests that a similar muscle was present here, with the scar marking the proximal extent of its origin.

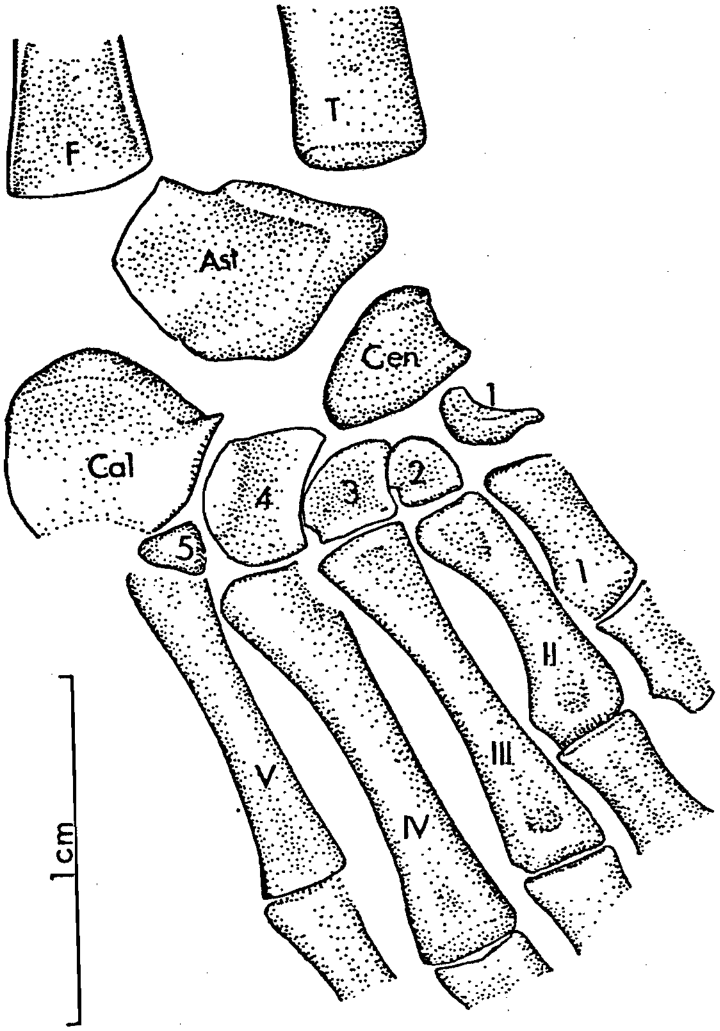
The centrale and distal tarsals are not substantially different from those in tangasaurids. The metatarsus differs only in some details of the structure of the fifth metatarsal. This bone has a strongly developed outer process with a small tubercle on its lateral corner. As noted by Harris and Carroll (1977), the peroneus brevis probably inserted on this tuberosity. The proximal articular surface of the bone is concave mediolaterally with the concavity matching the curved distal end of the fourth metatarsal so the two bones abutt against each other closely.

Despite these differences, the tarsus of *Kenyasaurus* and the tangasaurids would have been similar in their basic mechanics. The articular surface between the proximal and distal tarsal bones and the orientation of the articulation between the calcaneum and fourth distal tarsal are similarly developed in these animals. Also, *Kenyasaurus* shows keystone-shaped second and third distal tarsals with the dorsal surface being smaller than the ventral surface and, at least in the case of the third distal tarsal, the proximal end being narrower mediolaterally than the distal end. Thus a combination of movement at the intratarsal joint and a warping of the distal tarsal row was probably involved in the flexion of the crus on the metatarsus, as was probably also the case in the tangasaurids.

The tarsus of *Galesphyrus*

The earliest known tarsus of a younginiform is that of *Galesphyrus* from the *Cistecephalus* zone of South Africa. In a number of features, it is more primitive than the tarsus in the tangasaurids (Fig. 15). The astragalus and calcaneum have not been shortened proximodistally: the tibia is five times the length of the contact between the astragalus and calcaneum as in *Petrolacosaurus*. The metatarsals are not as greatly elongated as in the tangasaurids: the fourth metatarsal of *Galesphyrus* is 2.75 times the length of the contact between the astragalus and calcaneum in contrast to the tangasaurids where the fourth metatarsal is slightly over three times the length of this contact. Also, the relations of the metatarsals and distal tarsals are primitive. Each metatarsal articulates only with the distal tarsal immediately proximal to it. The fifth metatarsal does not have an expanded head and was not

Figure 15. The tarsus of Galesphyrus, dorsal view of right tarsus. Specimen SAM 2758. For key to abbreviations see list of abbreviations.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permanently divergent, as was probably the case in the tangasaurids and Kenyasaurus.

In a number of features, however, the tarsus is modified from the primitive condition. The astragalus, rather than being L-shaped, is triangular in shape. The tibial articular surface is reoriented to face proximally, and consequently supports the tibia more directly than is the case in tangasaurids. The change in shape of the astragalus has reoriented the articulation between the astragalus and calcaneum so that it extends more transversely across the tarsus. The articulation between the centrale and distal tarsals continues in this fashion so that the joint passes transversely from the proximo-lateral to the disto-medial corner of the tarsus. The curvature of the articular surfaces, especially of the centrale, indicates that considerable movement occurred here. The presence of such a joint is different from the condition in the tangasaurids and Kenyasaurus where the astragalus and calcaneum articulate closely by way of nearly flat articular surfaces. This indicates a fundamental difference in the mechanics of the tarsus. Unfortunately, in the absence of a more detailed knowledge of the structure of the tarsus of Galesphyrus, it is impossible to consider the mechanical significance of this difference.

The Tarsus of Youngina

The tarsus of Youngina was described by Broom (1921) and the fifth metatarsal described and figured by Goodrich (1942). Unfortunately the specimen has been lost, so Gow (1975) in his review of the structure of Youngina, was not able to add to our information on the structure of the tarsus.

The illustrations of the tarsus given by Broom and Goodrich show that the proportions of the elements and the relationship of the fifth metatarsal and fourth distal tarsal is like the condition in tangasaurids. The metatarsals are elongate and the fifth metatarsal has an expanded head like the condition in the tangasaurids but unlike Galesphyrus. Beyond this, however, they do not provide a basis for comparing the structure of the tarsus with other younginiformes or for considering the mechanics of the tarsus.

Discussion - The Origin of the Intratarsal Joint

With this understanding of the structure and mechanics of the tarsus in younginiform eosuchians, the adaptive significance of the origin of the intratarsal joint can be considered. Schaeffer (1941) suggested that the development of the intratarsal joint enabled the pedal flexors to make a greater contribution to propulsion for two reasons: it involved a consolidation of the tarsus which enabled the tarsus to resist a greater compressive force without buckling, and it increased the sharpness of the angle over which the pedal flexors passed, thus increasing the proportion of the force they produce that acts to flex the tarsus.

From the mechanical analysis of the tarsus of the tangasaurids, it is clear that the initial development of the intratarsal joint did not involve the elimination or reduction of movement at any of the joints present in the tarsus. The increase of movement intratarsally was a result of a decrease in the amount of plantarflexion of the metatarsals that occurred during the initial part of the propulsive phase. There is no indication that the amount of movement occurring at the other joints of the tarsus decreased. Thus the initial development of an intratarsal joint does not consolidate the tarsus and, by itself, does not increase the compressive force that could be transmitted through the tarsus. Such a change would have to occur, but, at least initially, this would presumably have been a result of changes in the ligaments and muscles of the pes, rather than a decrease in the amount of movement occurring at the joints.

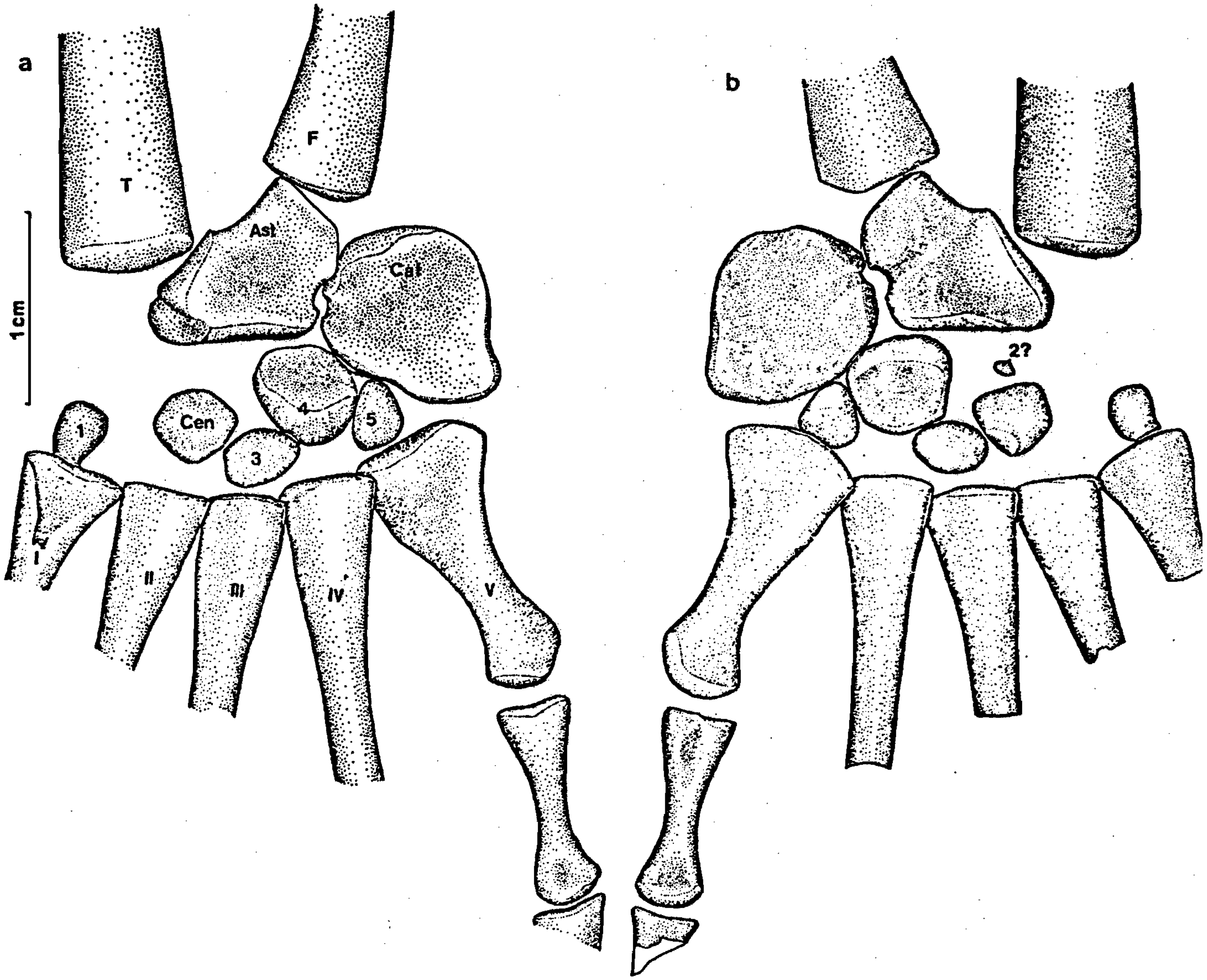
The development of an intratarsal joint does involve an increase in the sharpness of the angle over which the pedal flexors pass. This supports Schaeffer's suggestion that the development of an intratarsal joint was associated with an increase in the propulsive force that was produced by the long pedal flexors. Such an increase would have had considerable adaptive significance, since it would have increased the speed that an animal could attain, thus decreasing the chance that it would have been captured by a predator that had not undergone a comparable change in the locomotor apparatus or increasing the probability that it could capture prey with a primitive locomotor apparatus if it were a predator.

V "*CLAUDIOSAURUS*" AND THE PRIMITIVE SAUROPTERYGIAN TARSUS

"*Claudiosaurus*", an Upper Permian reptile from Madagascar currently being described by Carroll, has been shown to be a member of a lineage that gave rise to sauropterygians (Piveteau 1955). Although there is no trace of a lower temporal bar, the cheek is open laterally and the upper temporal bar is comparable in structure to *Youngina*, so it is probable that the lower temporal bar was lost during the origin of the group to which this animal belongs.

In general, the tarsus of "*Claudiosaurus*" (Fig. 16) is like that of the tangasaurids. The astragalus and calcaneum are primitive in their configuration but are shorter relative to the length of the tibia, so the tibia is seven times the length of the contact between the astragalus and calcaneum (see measurements Table 1). The astragalus has a deep groove on its ventral surface leading to the perforating foramen and a buttress extends from the tibial articular surface to the calcaneal articular surface distal to the groove. The proportions of the distal tarsals are like those in the tangasaurids in that the second distal tarsal is about half the proximodistal length of the third distal tarsal and the fourth is about twice the length of the third. The metatarsals have been elongated so that the fourth metatarsal is four times the length of the contact between the astragalus and calcaneum, slightly greater than the comparable condition in the tangasaurids. Also, the proximal ends of the metatarsals have been expanded and overlap

Figure 16. The tarsus and metatarsus of "Claudiosaurus". a) dorsal view; b) ventral view. Specimen 1910-33-1a. For key to abbreviations, see list of abbreviations.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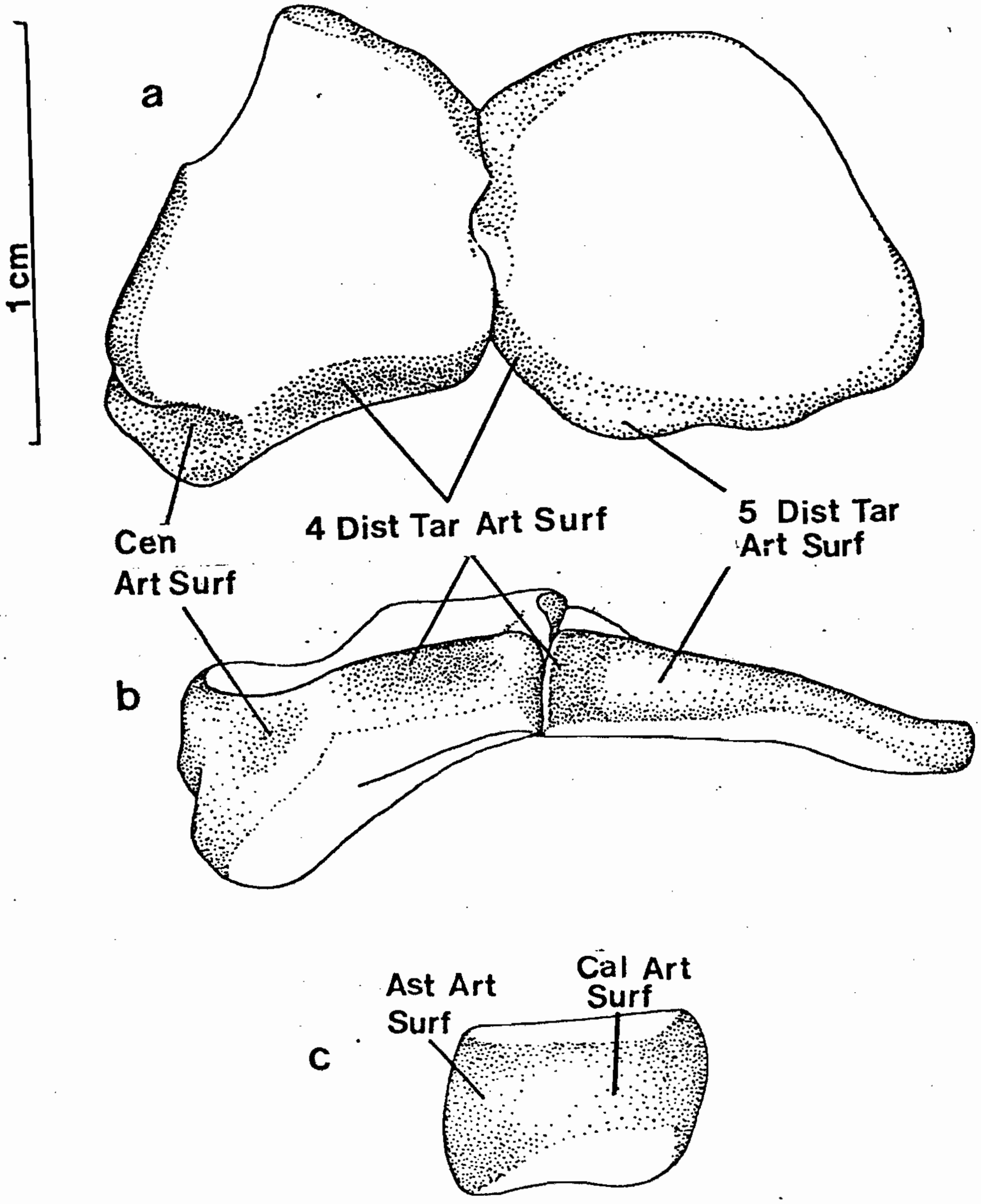
one another. This expansion is particularly strong in the case of the fifth metatarsal, although unlike the tangasaurids, the fifth metatarsal is supported almost entirely by the fifth distal tarsal and the articular surfaces at the joint do not match each other closely.

The arrangement of the distal tarsals and the centrale is somewhat different from the condition in the tangasaurids. The centrale is a cartilage-covered nodule of bone that appears to be incorporated into the distal tarsal row: it fits between the first and third distal tarsals providing a continuous morphological series and, at least in the early stages of development, supports the second metatarsal. The distal tarsals do not have the specialized wedge shape seen in the tangasaurids, but the surfaces of the elements of this row are largely formed by unfinished bone so considerable warping of the distal tarsal row was probably possible.

The articular surfaces show that, as in the tangasaurids, a specialized intratarsal joint was present. However, the structure of the articular surfaces differ in the two groups, indicating that the mechanics of this joint are different. In "Claudiosaurus", the distal articular surface of the calcaneum is convex (Fig. 17b), as is the opposing articular surface of the fourth and fifth distal tarsals. Thus rather than a concave-convex joint as is seen in the tangasaurids, a convex-convex joint is present here. The joint between the astragalus and fourth distal tarsal in "Claudiosaurus" is concave-convex in structure. The distal edge of the astragalus is concave medio-laterally (Fig. 17a, b),

Figure 17. The intratarsal joint in "Claudiosaurus". a) articulated astragalus and calcaneum in anterior view; b) articulated astragalus and calcaneum in distal view; c) fourth distal tarsal in proximal view. Abbreviations: Ast Art Surf, astragalar articular surface; Cal Art Surf, calcaneal articular surface; 4 Dist Tar Art Surf, fourth distal tarsal articular surface; 5 Dist Tar Art Surf, fifth distal tarsal articular surface.


1 cm
a
Cen
Art Surf
4 Dist Tar Art Surf
5 Dist Tar
Art Surf
b
Ast Art
Surf
Cal Art
Surf
c

allowing it to fit over the proximal edge of the fourth distal tarsal. The opposing articular surface of the fourth distal tarsal (Fig. 17c) is taller dorsoventrally than the astragalus, so that as well as flexing, the astragalus would have translated over the fourth distal tarsal, possibly rotating around its long axis as it did so.

Despite these differences in the detailed structure of the intratarsal joint, the general mechanics of the tarsus would have been similar. Movement at the intratarsal joint would have flexed the crus on the metatarsus during flexion of the knee, and warping of the distal tarsal row would have abducted the crus, the movement that occurs during rotation of the femur. Rotation of the crus was probably associated with rotation at the astraglus distal tarsal joint, although warping of the distal tarsal row may also have resulted in this crural movement.

The development of the intratarsal joint probably reduced the amount of plantarflexion of the metatarsus that occurred as the femur rotated. Consequently the sharpness of the angle over which the pedal flexors passed would have been increased and a greater proportion of their force would have acted to flex the metatarsus. Thus the adaptive significance of the development of the joint would have been the same as in the tangasaurids, the differences in structure of the intratarsal joint simply reflecting their independent development of this structure.

Since "Claudiosaurus" is close to the ancestry of nothosaurs and plesiosaurs, its tarsus probably represents the primitive condition for sauropterygians. Piveteau (1955) noted that the tarsus of "Claudiosaurus" and nothosaurs are similar in being excavated medially. To a large extent, this condition results from the presence of an L-shaped astragalus and a tibia with a large distal end, and thus is primitive for diapsids. It is, however, somewhat exaggerated in "Claudiosaurus" by the change in the position and proportions of the centrale, so this similarity in the tarsus of "Claudiosaurus" and nothosaurs may be of phylogenetic significance. Apart from this general similarity, the tarsus of nothosaurs are too imcompletely ossified to permit detailed comparison of the elements with the condition in "Claudiosaurus".

VI STRUCTURE, FUNCTION AND EVOLUTION OF THE LIZARD TARSUS

The lizard tarsus was characterized by Schaeffer (1941) as having a single proximodistally shortened element that is tightly bound to the crus proximally and has a complex tongue and groove articulation for the fourth distal tarsal distally. Additional features that are advanced over the condition in eosuchians include the loss of the first, second and fifth distal tarsals, the hooking of the fifth metatarsal, and the development of a transverse metatarsal arch (Schaeffer 1941; Carroll 1977). Schaeffer considered the lizard tarsus to be directly derived from the eosuchian condition, a conclusion that was supported by the description of Saurosternon, a Permo-Triassic lizard from South Africa, by Carroll (1975, 1977). Although Saurosternon is already a lizard, its tarsus is in many ways intermediate between that of advanced lizards and eosuchians.

Using Saurosternon as an intermediate, Carroll was able to identify the major changes in the tarsus that occurred during the origin of lizards. Our understanding of the mechanical significance of these changes is, however, incomplete. Since, as has been shown by Gans (1963), mechanical analysis of a complex within a distinct phylogenetic radiation frequently most profitably starts with the most specialized members of the group, a solid understanding of the mechanics of the tarsus in extant lizards is desirable before considering the mechanical changes that occurred during the origin of the lizard tarsus. Significant contributions towards an understanding of the mechanics of the lizard tarsus have been made by Robinson (1975) and Rewcastle (1978). Robinson described in detail the structure of the fifth metatarsal and associated muscles and, using this information as a basis, considered the functioning of the bone. Later, in a comprehensive consideration of the crus and pes in lizards, Rewcastle (1978) provided a detailed description of the myology and osteology of the crus and pes. He also considered some aspects of the mechanics of the tarsus, including the intratarsal joint and the cruro-tarsal joint. However, as he did not have available a description of the pelvic limb movements, he was unable to consider the relationships of the structure of the intratarsal joints to the movements of the crus and pes and he did not consider the mechanics of the metatarsal lever. Also, a number of questions concerning the homologies of the elements present in the lizard tarsus and the fate of the missing elements remains unanswered. Thus, before considering the origin of the lizard tarsus, these aspects of the structure and mechanics of the tarsus in extant lizards were examined.

Materials

The following genera were observed during the course of this investigation:

Xantusiidae: _Klauberina_, _Xantusia_; Xenosauridae: _Xenosaurus_; Varanidae: _Varanus_; Teiidae: _Tupinambis_, _Teius_, _Kentropys_, _Cnemidopherus_; Scincidae: _Riopa_, _Sphenomorphus_, _Trophidophorus_, _Emoia_, _Egenia_, _Lumprolepis_, _Mabuya_, _Lobulia_, _Carila_; Lacertidae: _Latasia_, _Lacerta_;

Agamidae: Calotes, Acanthosaura; Gerrhonotidae: Gerrhonotus; Gekkonidae: Gekko, Aristelligar, Hemidactylus, Pachydactylus, Ptychozoon, Lygodactylus; Iguanidae: Iguana, Anolis, Sceloperus; Paliguanidae: Saurosternon. Dissections of the pelvic limbs of Iguana, Varanus, Gekko, Calotes, and Xantusia, together with published descriptions of the myology of the crus and pes in other lizards (Perrin 1892; Snyder 1954; Schaeffer 1941; Kriegler 1961; Russell 1975; Rewcastle 1978) provided an understanding of the soft anatomy of the crus and pes and allowed the relationships of various osteological features to be determined. The terminology used by Rewcastle (1978) was used in naming the muscles here. Iguana iguana was chosen as the subject for the mechanical analysis of the tarsus.

Structure of the Lizard Tarsus

The proximal tarsal element in the lizard tarsus is the large, rectangular astragalocalcaneum. The astragalus and calcaneum are discernable in all lizards examined -- a line extending from the fibular articular surface to the distal edge of the bone separates an astragalar and a calcaneal portion of the astragalocancaneum, referred to below as the astragalus and the calcaneum. Embryological evidence (Mathur and Goel 1976) indicates that the astragalus is composed of a fused astragalus and centrale, a suggestion that is consistent with the intimately articulated astragalus and centrale of Saurosternon. The astragalocalcaneum articulates with the tibia and fibula proximally and with the fourth distal tarsal distally (Fig. 18). In most lizards, the proximal articular surfaces nearly completely cover the proximal edge of the bone, although in gekkos, xantusids and some varanids, the calcaneum has a laterally directed tuber that extends lateral to the fibular articular surface (Fig. 18a, c, e). A distinctive feature of the astragalocalcaneum is the articular surface for the fourth distal tarsal (Fig. 19). This is divided into two separate areas, a flat ventromedially facing surface supported by an anteriorly projecting flange on the calcaneum and a c-shaped ridge on the distal edge of the astragalus located just medial to this. Medially, the c-shaped ridge grades into the bulbous cartilage-covered medial edge of the bone. The only group of lizards, apart from the chameleontids, that departs from this pattern are the varanids (Fig. 18a). There, the c-shaped ridge has become reduced and has shifted medially. Both the astragalus and calcaneum take part in the formation of the more lateral portion of the articular surface, and this surface is convex, rather than being nearly flat. The posterior portion of the cartilage-covered medial edge of the bone has become narrow mediolaterally and extends posteriorly as a prominent wheel-shaped ridge.

In all lizards examined, both the third and fourth distal tarsals are keystone-shaped with their dorsal surfaces larger than their ventral and with finished bone only present on their dorsal surfaces. The fourth distal tarsal is the larger of these elements. As well as articulating with the astragalocalcaneum, it contacts the third, fourth and fifth

Figure 18. The lizard tarsus. a) *Varanus*; b) *Agama*; c) *Xantusia*; d) *Riopa* (Scincidae); e) *Gekko*.

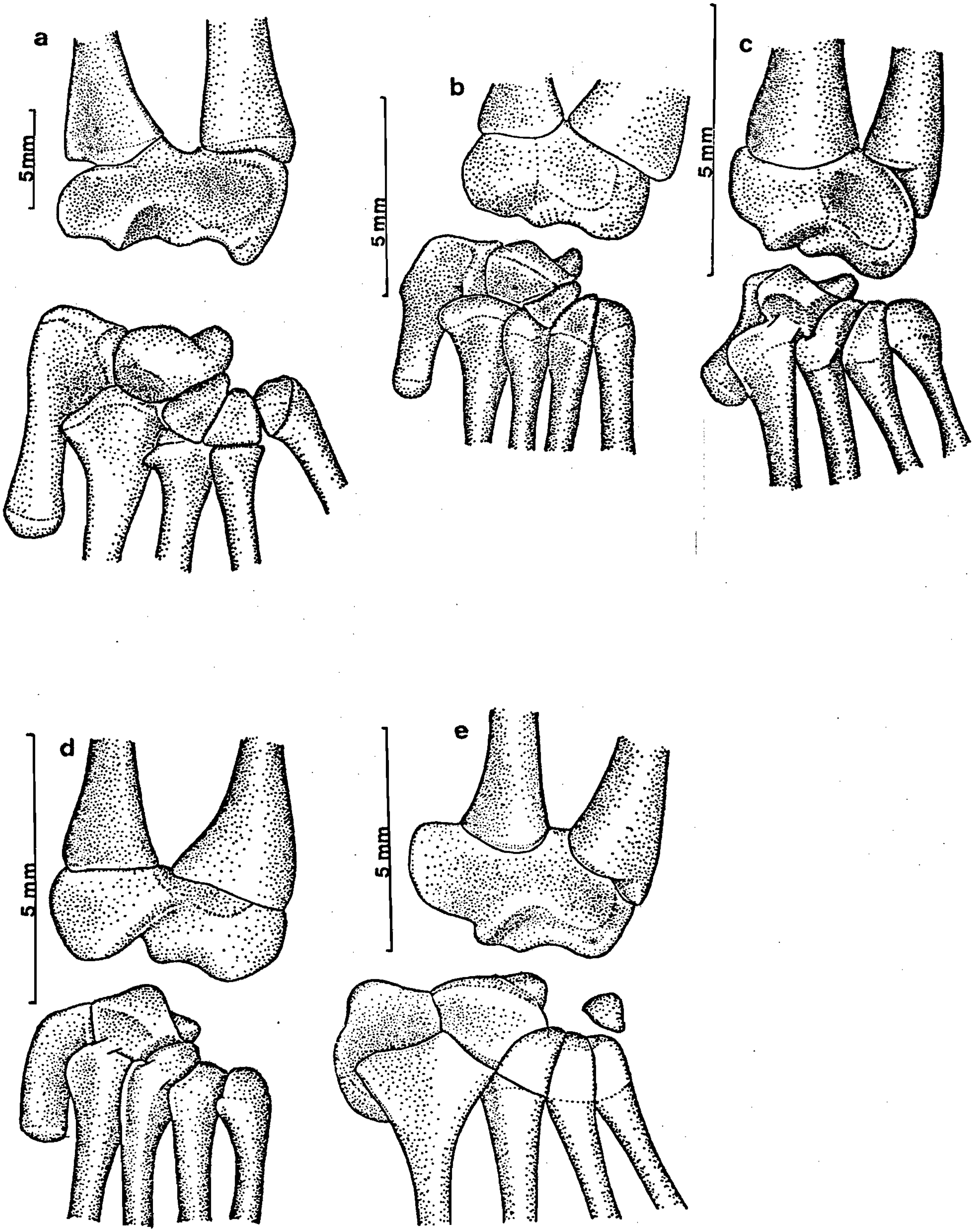
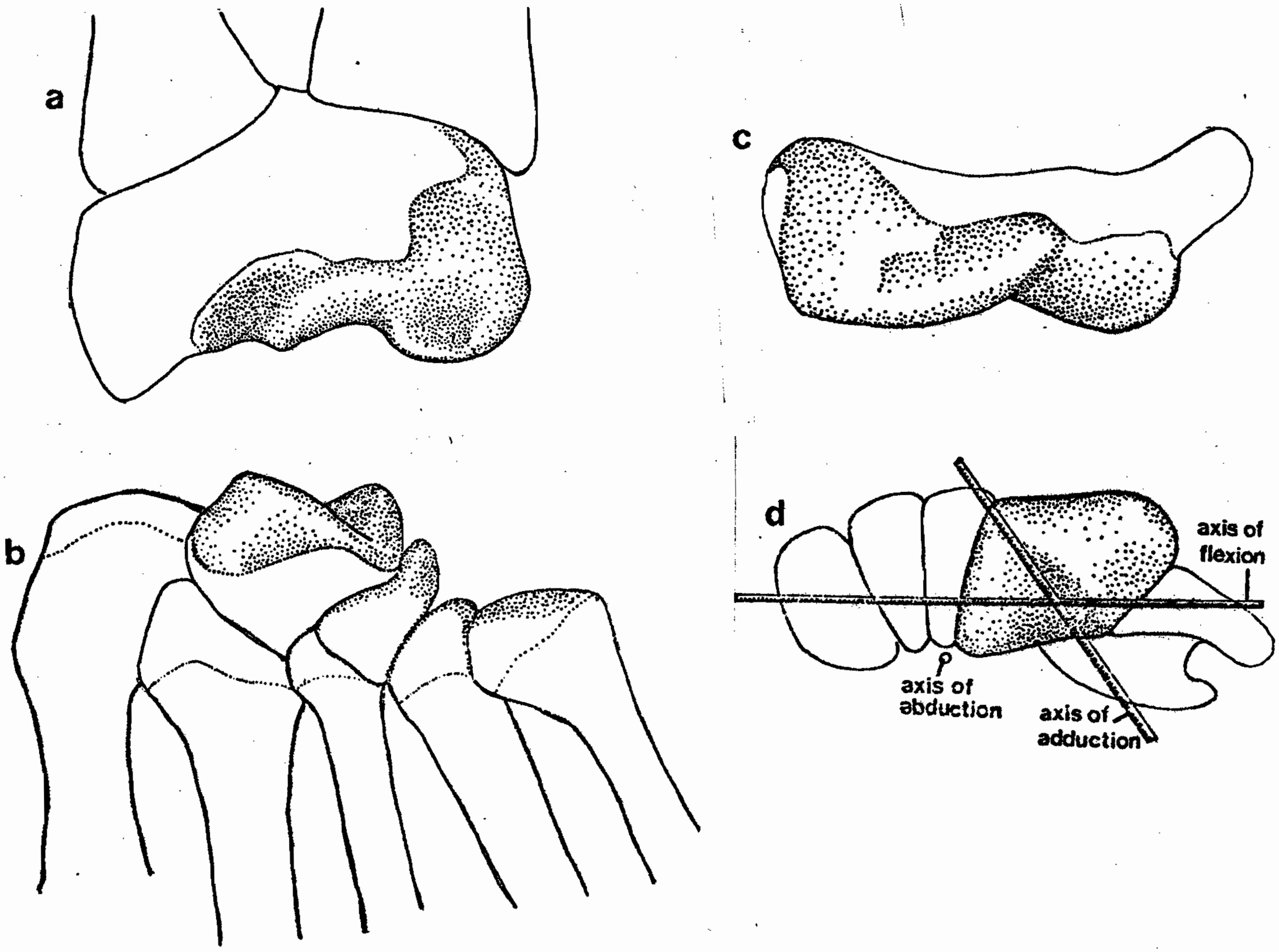

a
5mm
b
5 mm
c
5 mm
d
5 mm
e
5 mm

Figure 19. The intratarsal joint of _Iguana_.

a) astragalocalcaneum, dorsal view; b) distal tarsals, dorsal view; c) astragalocalcaneum, distal view, anterior face lowermost; d) distal tarsals, proximal view, anterior face uppermost.

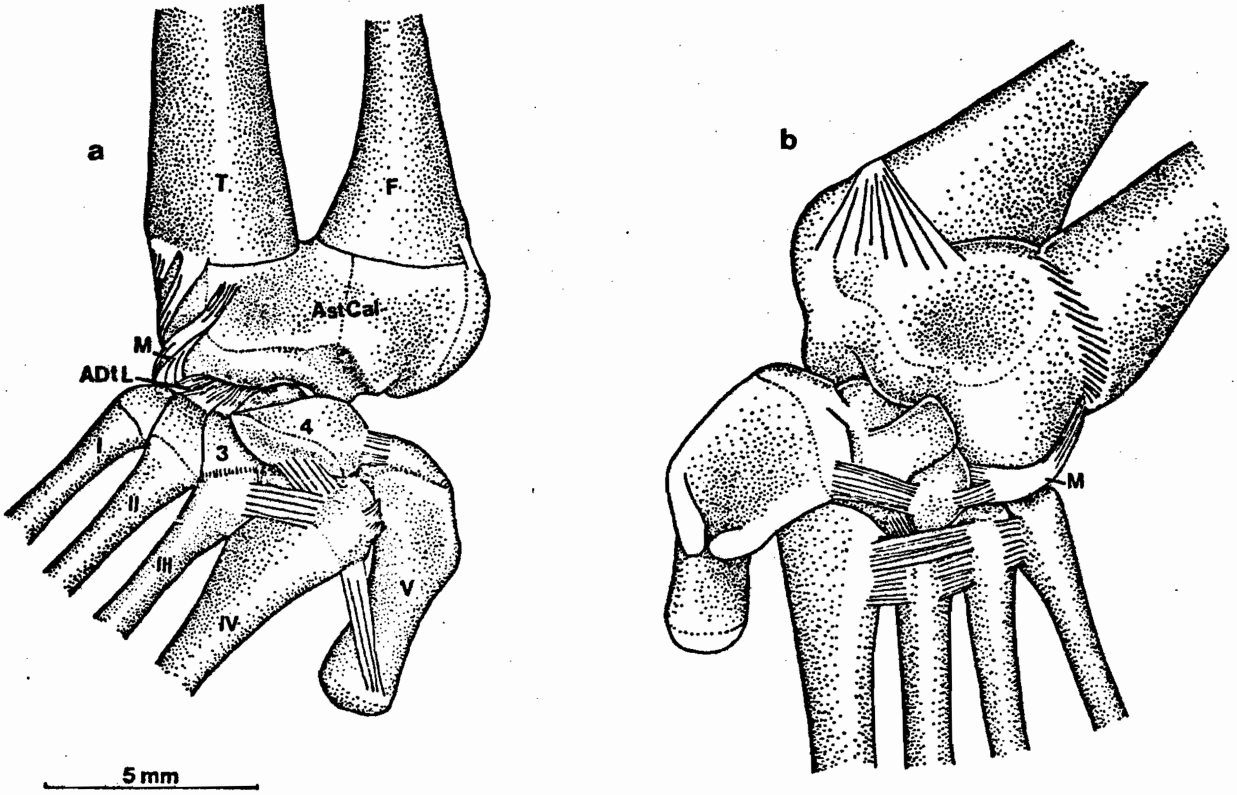

a
b
c
d
axis of flexion
axis of abduction
axis of adduction

metatarsals and the third distal tarsal. Its most prominent morphological feature is the articular surface for the astragalocalcaneum (Fig. 19) which consists of a groove extending across the bone from its ventro-lateral to dorso-medial corner and an articular surface lateral to this that extends from the posterior to the dorsal surface of the bone. The medial wall of the groove is formed by a cone-shaped process that fits under the astragalus, lying within the concavity of the c-shaped ridge.

The distal tarsal row is continued medially by the proximal epiphyses of the first two metatarsals. These are like the distal tarsals in being wedge-shaped and with finished bone on their dorsal surfaces only. Also, their relationship to the ligaments of the intratarsal joint are similar to those of the third distal tarsal: each of these elements has a strong ligament, an astragalar-distal tarsal ligament, originating from their dorsal tip and descending to insert on the distal portion of the anterior face of the astragalus (Fig. 20a). The morphological continuation of the distal tarsal row by these epiphyses suggests that they are homologous with the first two distal tarsals, a suggestion that has been made previously on embryological (Born 1880; Howes and Swinnerton 1900) and morphological grounds (Born 1876), and is supported by the arrangement of the distal tarsals and metatarsals in Saurosternon (Carroll 1977).

An additional ossification is present between the proximal epiphyses of the first two metatarsals and astragalus of some lizards,

Figure 20. The ligaments of the tarsus and metatarsus of *Iguana*. a) dorsal view; b) ventral view. For key to abbreviations see list of abbreviations.


a
T
F
AstCal
M
ADtL
I
II
III
IV
V
3
4
5 mm
b
M

including Gekko gecko (Fig. 16d) and Calotes versicolor (Fig. 21). This element has been identified as a first distal tarsal (Mathur and Goel 1976; Russell 1975; Gegenbaur 1864), a centrale (Born 1876) and an ossified meniscus (Howes and Swinnerton 1900; Sewertzoff 1907-1908). That the latter is the correct identification is indicated by the similar relationship to the ligaments of the pes of this element and a meniscus present in a similar position in other lizards. In Iguana Fig. 20a) an undoubted meniscus is present. This is c-shaped with the metatarsal-astragalar ligaments lying within its concavity. Its dorsal horn is connected to the tibia by two ligaments and the ventral horn is connected to the third distal tarsal by a single ligament. The relationship of the ossification present in Calotes to the astragalar-metatarsal ligaments and the arrangement of the ligaments connecting it to the crus and pes (Fig. 21) are exactly the same as in Iguana. Gekko differs only in that the elements are connected to the tibia by a single ligament that inserts on its lateral surface, rather than by two separate ligaments (Fig. 22). Thus this element is a lunula or ossified meniscus (Haines 1969). Such ossifications develop when menisci are steeply wedged in cross section (Barnett 1954a), which is the case in Calotes and Gekko.

The first four metatarsals are usually elongate and consolidated to form a narrow bar of bone, although in some lizards, such as geckos and xantusids (Fig. 18c, d), they diverge fan-like from the tarsus. The keystone shape of the distal tarsals and proximal epiphyses of the first

Figure 21. The ligaments of the tarsus and metatarsus of the agamid *Calotes versicolor*. a) dorsal view; b) ventral view. For key to abbreviations see list of abbreviations.

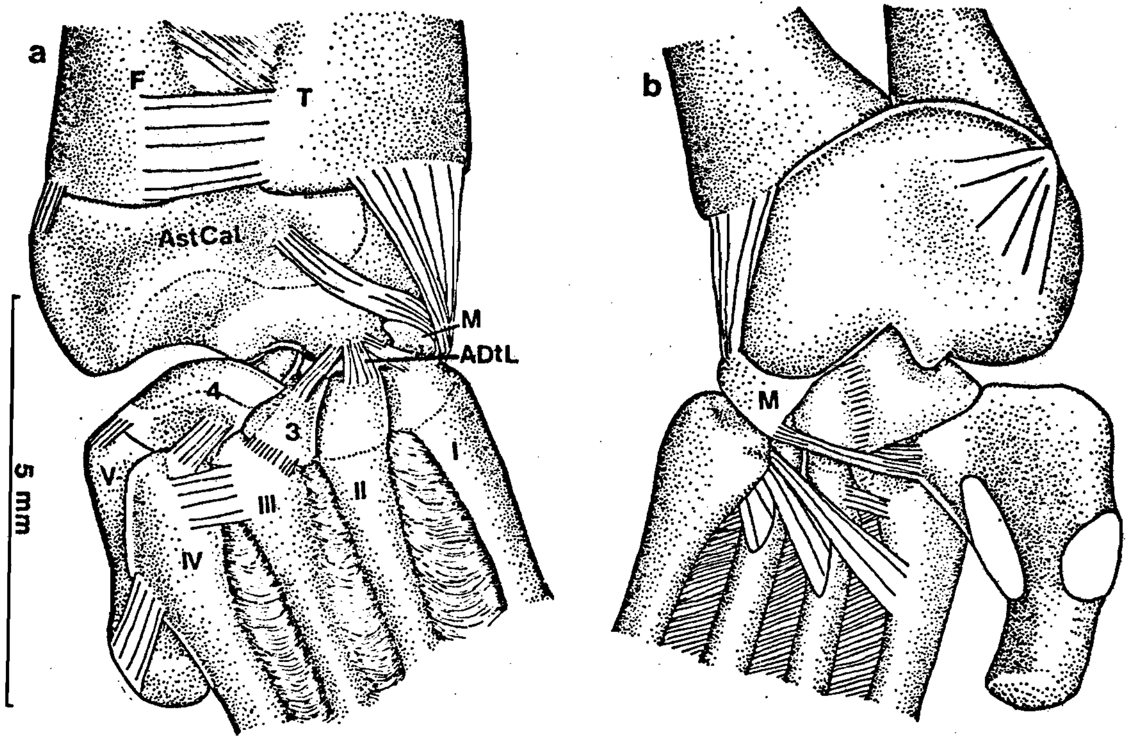
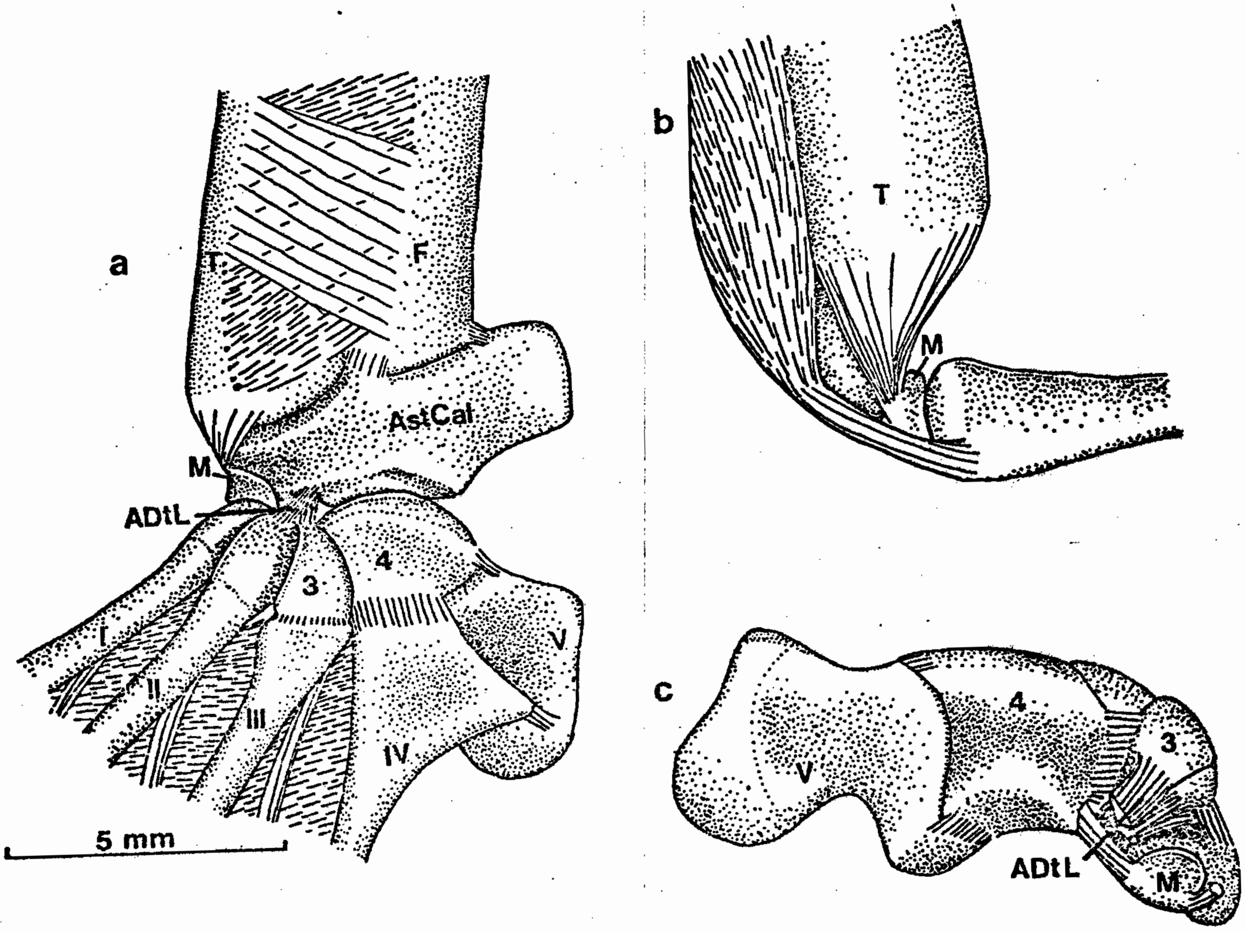

a
F
T
AstCaL
M
ADtL
4
3
V
III
II
I
IV
5 mm
b
M

Figure 22. The ligaments of the tarsus and metatarsus of <u>Gekko</u>. a) dorsal view; b) medial view; c) proximal view of metatarsus. For key to abbreviations see list of abbreviations.


a
T
F
AstCal
M
ADtL
4
3
I
II
III
IV
V
5 mm
b
T
M
c
V
4
3
ADtL
M

two metatarsals arch the metatarsus transversely. The size of the arch is accentuated by the ventral position of the fifth metatarsal.

The detailed description of the fifth metatarsal given by Robinson (1975) applies to most lizards. An important exception is seen in geckos. The fifth metatarsal of Gekko gecko is a short, broad bone with the long axis of the proximal articular surface lying within the plane formed by the body of the bone (Fig. 23a). Three prominent tubercles are present: a medially placed plantar tubercle located at the distal edge of the proximal articular surface, a distally placed plantar tubercle confluent with the distal articular surface, and a laterally extending tuber located on the lateral edge of the bone. A comparison of the relationships of the muscles and ligaments of the pes to the tubercles in Gekko and in Iguana, where the fifth metatarsal has the construction usually present in lizards (Fig. 23b), allows homologous portions of the fifth metatarsal to be identified. In Iguana (Fig. 24), one muscle, the peroneus brevis, inserts on the outer process. The gastrocnemius femoral head inserts on both the medial and lateral plantar tubercles. The flexor brevis superficialis originates in part from the distal edge of the medial plantar tubercle. The flexor tendon of the fifth digit passes around the medial edge of the medial plantar tubercle deep to the gastrocnemius femoral head and flexor brevis superficialus and superficial to the plantar head of the flexor digitorum longus. The plantar head of the flexor digitorum longus originates from the medial plantar tubercle. The calcanean head of the flexor digitorum longus originates by way of

Figure 23. The fifth metatarsal of lizards. a) *Gekko*; b) *Iguana*. Abbreviations: lpt, lateral plantar tubercle; mpt, medial plantar tubercle; op, outer process.

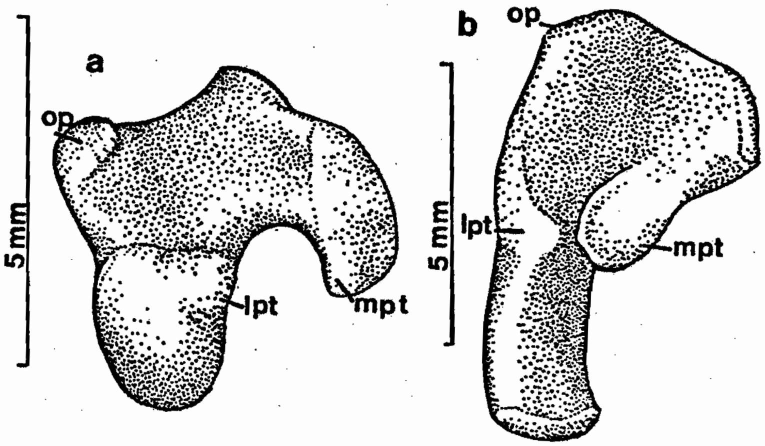

a
op
lpt
mpt
5 mm
b
op
lpt
mpt
5 mm

Figure 24. The relations of the pedal muscle of to the fifth metatarsal of *Iguana*. a) ventral view, gastrocnemius (femoral head), gastrocnemius (tibial head), and flexor brevis superficialus removed; b) lateral view. For key to abbreviations, see list of abbreviations.

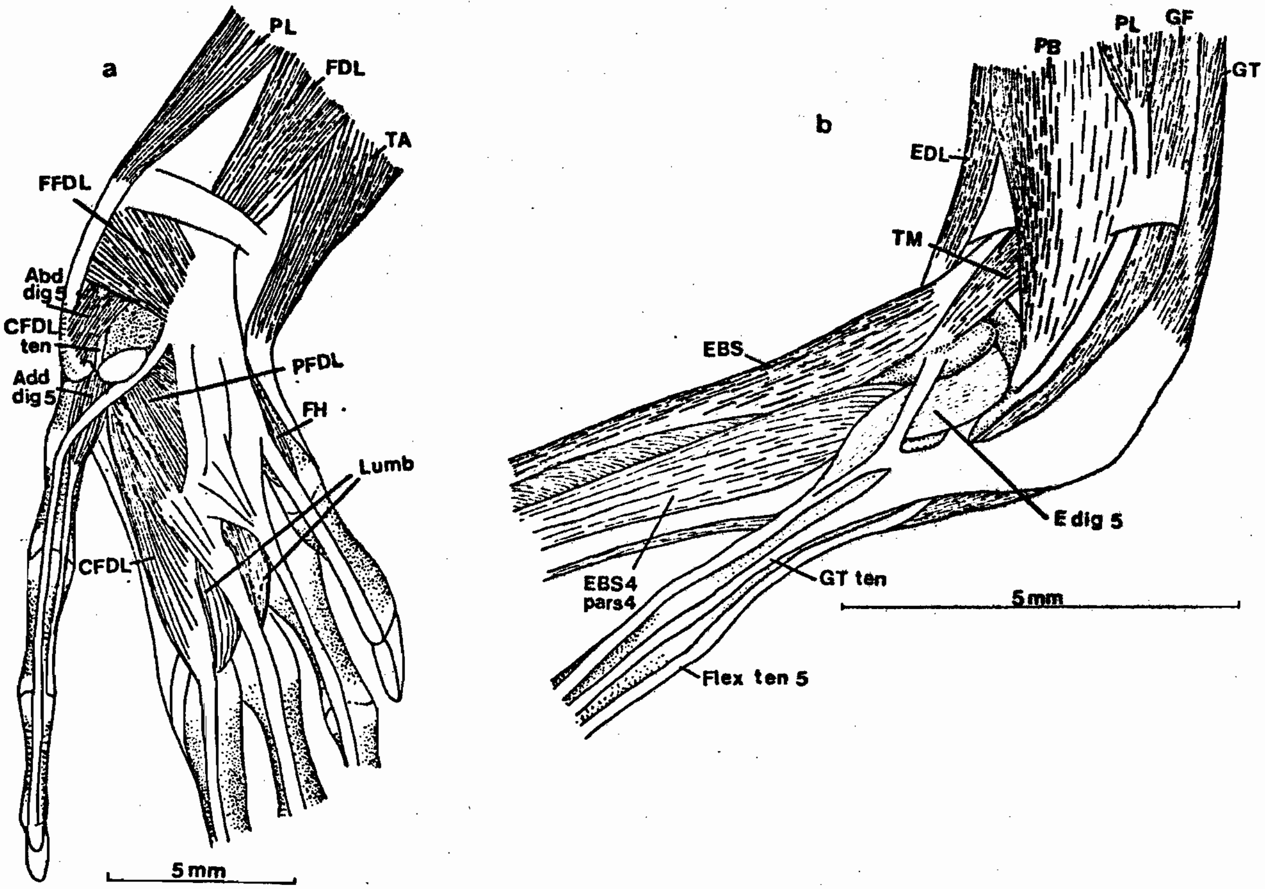
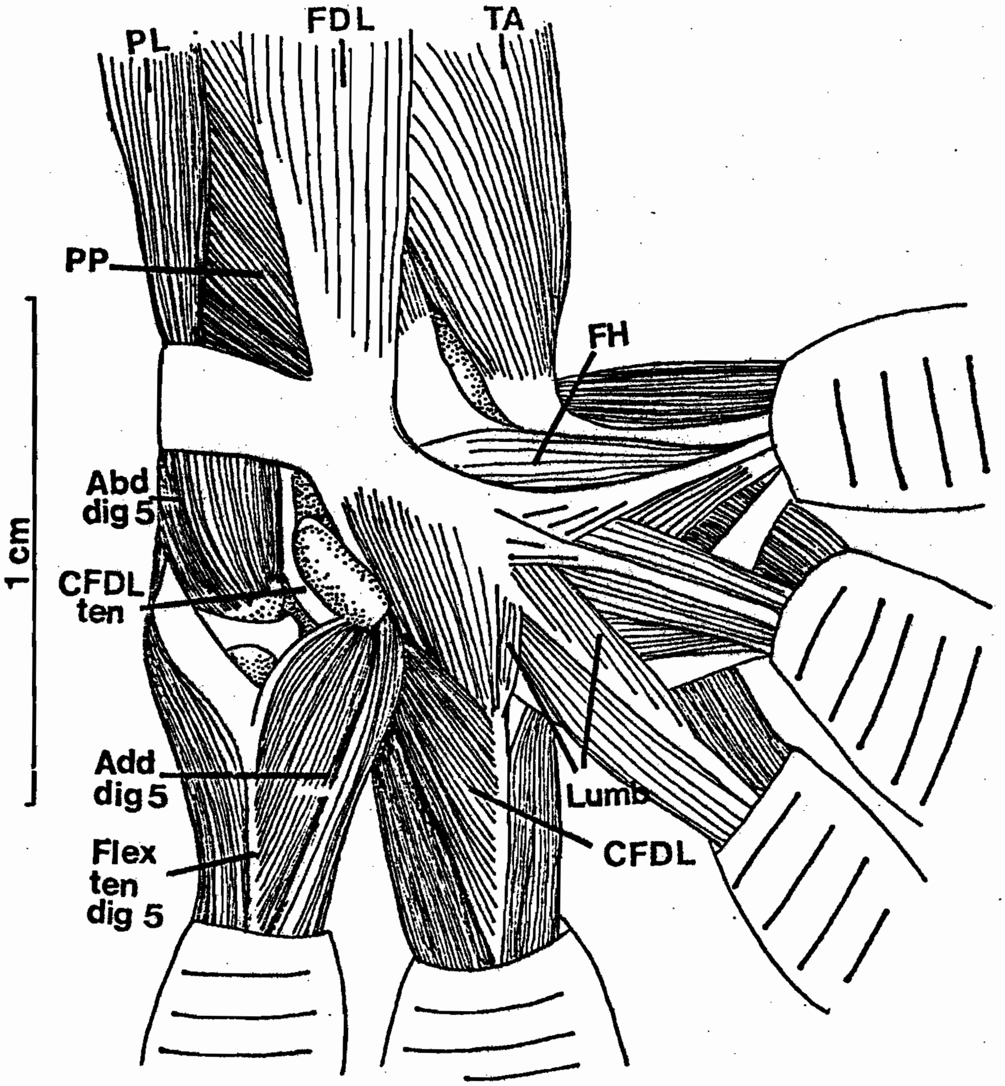

a
PL
FDL
TA
FFDL
Abd dig 5
CFDL ten
Add dig 5
PFDL
FH
Lumb
CFDL
5 mm
b
PB
PL
GF
GT
EDL
TM
EBS
E dig 5
EBS4 pars4
GT ten
Flex ten 5
5 mm

Figure 25. The relations of the pedal muscles to the fifth metatarsal of *Gekko*. Gastrocnemius (femoral head), gastrocnemius (tibial head) and flexor brevis superficialus removed. For key to abbreviations, see list of abbreviations.


PL
FDL
TA
PP
FH
1 cm
Abd dig 5
CFDL ten
Add dig 5
Flex ten dig 5
Lumb
CFDL

a single tendon from the distal edge of the calcaneum with this tendon passing between the medial and lateral plantar tubercles.

In Gekko (Fig. 25), the peroneus brevis inserts on the laterally extending tuber; the gastrocnemius femoral head inserts on both the medial and distal plantar tubercles; the flexor digitorum brevis superficialus originates in part from the distal edge of the medial tubercle; the flexor tendon of the fifth digit passes around the medial edge of the medial tuber deep to the gastrocnemius and flexor digitorum brevis superficialus; and the calcaneal head of the flexor digitorum longus originates by way of a single tendon from the distal edge of the calcaneum, with this tending passing between the medial and distal tubercles. Thus the medial tuber in Gekko is homologous to the medial plantar tubercle in Iguana and other lizards, the distally located tuber is the lateral plantar tuber of other lizards, and the laterally directed tuber is the outer process. With these tubers identified, it can be recognized that the major change that occurred during the origin of the fifth metatarsal of Gekko was a shortening of the shaft of the bone, leaving only the proximal inturned portion of the fifth metatarsal and the distal articular surface. The elimination of the shaft of the bone obscured the inflection of the metatarsal that is present in other lizards, so the element appears to lie within a single plane.

The homologies of the fifth metatarsal of lizards has been a matter of controversy. Perrin (1892) argued that the element was a specialized fifth distal tarsal. This was discredited by Howes and

Swinnerton (1900) who showed that the embryological development of the element is like that of the remaining metatarsals in being ossified ecosteally, rather than endosteally as in the tarsal elements. As quoted by Robinson (1975), Sewertzoff (1907-1908) suggested that the fifth metatarsal was fused to the fifth distal tarsal. This does not appear to be based on any direct evidence. No anlage that could be homologous with the fifth distal tarsal was reported by him or in any other description of the embryology of the tarsus in a lizard (Born 1880; Mathur and Goel 1976). The relationship of the fifth metatarsal to the distal tarsal row was accepted as evidence that the fifth metatarsal and fifth distal tarsal fused to give the hooked fifth metatarsal of lizards by Robinson (1975). Williston (1917) however, has suggested that during the development of the hooked fifth metatarsal, a change in relations of the metatarsal and distal tarsals occurred, with the fifth metatarsal extending proximally to occupy the space primitively occupied by the fifth distal tarsal. This suggestion seems to be supported by the tarsus of Permian eosuchians. There the fifth metatarsal has an expanded proximal end that articulates with both the fifth and fourth distal tarsals and in a number of genera, particularly Kenyasaurus, the tangasaurids and Araeoscelis, the fifth distal tarsal is absent as a distinct structure, while the fifth metatarsal remains unhooked. In all these genera, absence of the fifth distal tarsal is a result of fusion of the fourth and fifth distal tarsals. Saurosternon (Fig. 31) retains a fifth distal tarsal, but this is a small element located on the lateral tip of the fourth distal tarsal. The fifth metatarsal is supported mainly by the fourth distal tarsal. While these relationships do not eliminate the possibility that the fifth metatarsal was fused to the fifth distal tarsal in later lizards, they are more consistent with the loss of the fifth distal tarsal as a result of its reduction or fusion with the fourth distal tarsal.

Thus despite the considerable radiation of lizards and their specialization for a variety of locomotor habits, the tarsus shows little variation in its basic structure. In addition to the features listed by Schaeffer (1941) as characteristic of the lizard tarsus, all lizards examined except for chameleontids, showed the bipartite structure of the intratarsal joint with the fourth distal tarsal having a process that underlies the astragalus and with the calcaneum having an anterior flange that overrides the fourth distal tarsal. Also, the fifth metatarsal is hooked with well developed plantar tubercles. Because of this structural uniformity, it is possible to refer to "a" lizard tarsus as a structural complex characterized by a suite of features and with an underlying mechanical similarity. To gain an understanding of the basic mechanics of this complex, the tarsus of Iguana was examined in detail.

Mechanics of the Tarsus in Iguana

A. The ankle joint

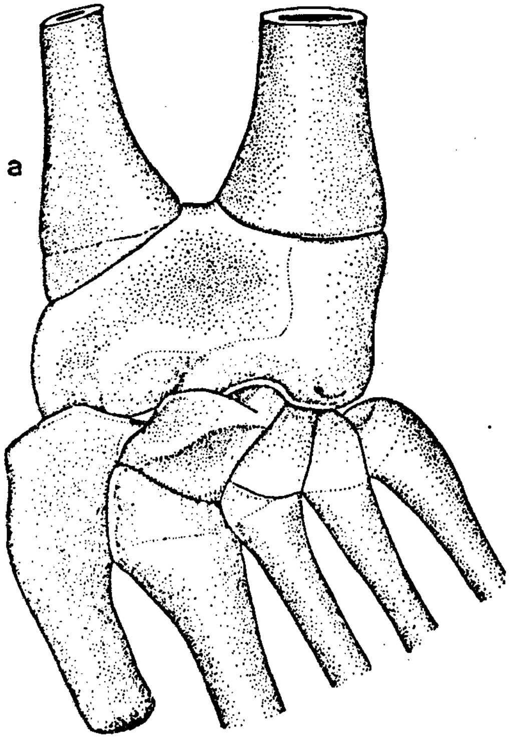
As one of the diagnostic features of the lizard tarsus, the mechanics of the joint between the astragalocalcaneum and fourth distal tarsal are of particular interest. Schaeffer (1941) recognized that this joint is of major importance in allowing the movement of the crus on the metatarsus that occurs during locomotion. In Iguana, the crus can flex on the metatarsus through an arc of 170° with all but 20° occurring at this joint. The articular surfaces here have the characteristic structure described above. The major ligaments of the joint are the three astragalar-distal tarsal ligaments. In addition, two areas of the joint capsule are thickened and act as ligaments. Dorsally, fibres extending from the anterior flange of the calcaneum to the fourth distal tarsal are thickened. Ventrally, the fibres extending from the astragalus to the fourth distal tarsal form a distinct ligament.

The movements possible at this joint and the roles of the articular surfaces and ligaments in controlling these movements are best understood by tracing the path of the centre of articulation as the joint moves from maximal extension to maximal flexion and then considering the rotational and abduction-adduction movements possible.

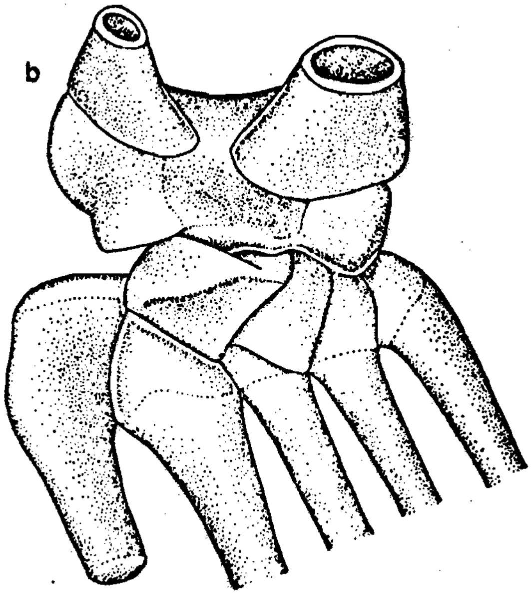
When the joint is maximally extended (Fig. 26a) the crus and metatarsus are in line and their extensor surfaces face dorsally. The astragalar-metatarsal ligaments are tight as are the dorsal fibres of the joint capsule. The c-shaped ridge of the astragalus fits over the ventro-medial cone-shaped process of the fourth distal tarsal with contact being made by the ventral extremes of the articular surfaces. The calcaneal flange does not contact the articular surface of the fourth

Figure 26. The mechanics of the intratarsal joint of _Iguana_. a) crus maximally extended on the metatarsus; b) crus flexed on the metatarsus about 90°; c) crus maximally flexed on the metatarsus.

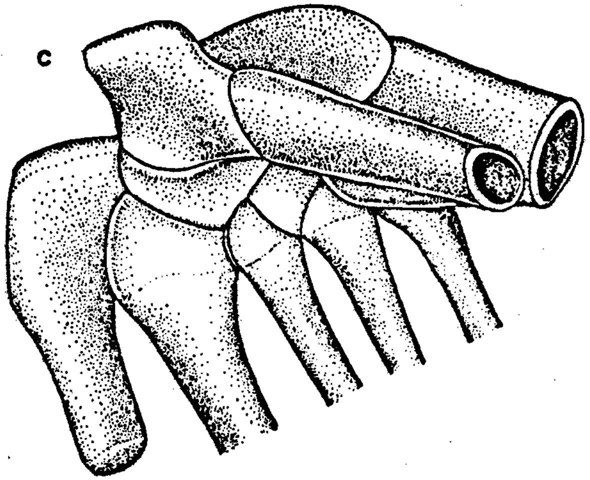
a



b



c



distal tarsal.

The initial flexion of the joint occurs around an axis perpendicular to the crus and passing through the astragalar-metatarsal ligaments and the contact of the astragalus and fourth distal tarsal (axis of flexion, Fig. 19d). It involves a rocking of the c-shaped ridge over the cone-like process of the fourth distal tarsal, bringing the anterior face of the ridge into contact with the lateral wall of the groove on the distal tarsal and the anterior flange of the calcaneum into contact with the opposing articular surface (Fig. 26b). This contact prevents further rotation around the axis of flexion as an independent movement. Instead, the astragalocalcaneum translates over the fourth distal tarsal with the c-shaped ridge following the groove on the distal tarsal and the calcaneal flange passing over the lateral portion of the articular surface on the fourth distal tarsal. This can be described as rotation around an axis that passes through the long axis of the metatarsus and through the astragalar-metatarsal ligament (the axis of abduction, Fig. 19d). Rotation around this axis as an independent movement results in an abduction and medial rotation of the crus. However, the groove shallows as it passes dorsally across the distal tarsal. Consequently rotation around the axis of abduction brings the calcaneal flange away from the distal tarsal. To maintain this contact, rotation around the axis of abduction must be accompanied by rotation around an axis lying within the groove of the fourth distal tarsal and parallel to its lateral wall (the axis of adduction, Fig. 19d).

This will flex and adduct the crus, with the adduction counteracting the abduction that results from rotation around the axis of abduction, so that the net result of these movements is a flexion and rotation of the crus (Fig. 26c).

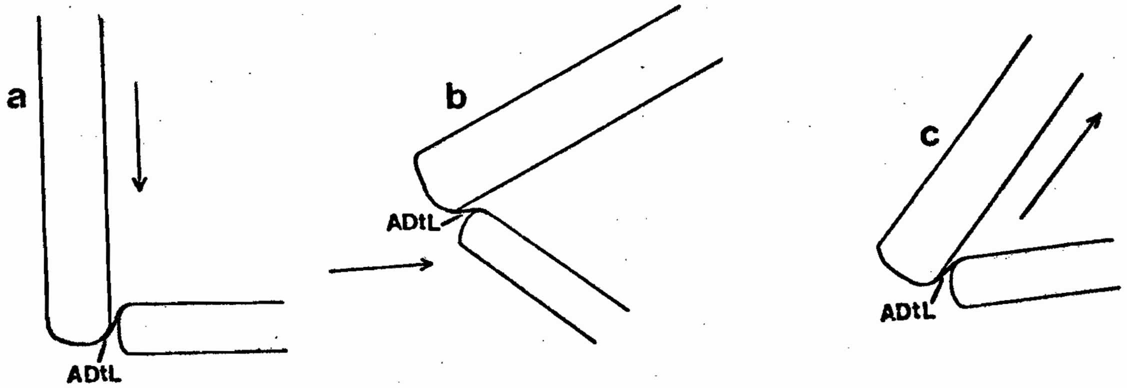
In maximal flexion and maximal extension, both the astragalar-distal tarsal ligaments and the dorsal (in extension) or ventral (in flexion) fibres of the joint capsule are tight. In any other position during flexion of the ankle, only the astragalar-distal tarsal ligaments are tight. In these positions, rotation and abduction of the crus relative to the metatarsus are possible. About 30° rotation of the crus either laterally or medially can occur as an independent movement throughout the full range of flexion of the crus on the metatarsus. Lateral rotation moves the astragalocalcaneum away from the fourth distal tarsal, tightening the fibres of the joint capsule. Medial rotation presses the astragalocalcaneum against the fourth distal tarsal and moves the medial edge of the astragalus away from the metatarsals, tightening the astragalar-distal tarsal ligaments. Some movement between the metatarsals and distal tarsals accompanies this.

Abduction of the crus is a result of rotation around the axis of abduction as an independent movement. The amount of abduction possible is maximal when the crus is at ninety degrees to the metatarsus. Lateral abduction moves the calcaneum ventrally relative to the fourth distal tarsal, tightening the dorsal fibres of the joint capsule. The calcaneal flange translates over the distal tarsal from the dorsal to the posterior aspect of the bone, resulting in a simultaneous lateral rotation of the crus. Medial abduction lifts the astragalocalcaneum away from the fourth distal tarsal with the two bones losing contact completely. The crus can be abducted medially 90°, at which time the ventral fibres of the joint capsule become tight. This is not necessarily accompanied by a rotation of the crus, although some rotation is possible in any position except maximal abduction.

Thus the arrangement of ligaments does not continually hold the articular surfaces together. The resulting mobility of the joint allows the lizard to assume a number of postures not encountered during locomotion, and thus facilitates efficient exploitation of the irregular terrain offered by an arboreal habit. However, as emphasized by Elftman (1966), any joint in addition to allowing the movement necessary for the efficient functioning of the articulating bones, must be stable so that the forces can be transmitted across the joint without disrupting the arrangement of the associated structures and they must guide the movements of the articulating bones so that the muscles produce the exact movement that is required.

In the lizard ankle, the stability is provided by the astragalar-distal tarsal ligaments (Fig. 27). At the beginning of the propulsive phase, the force resulting from gravity will tend to pull the astragalocalcaneum ventrally across the fourth distal tarsal, tensing the astragalar-distal tarsal ligaments (Fig. 27a). Later in the propulsive phase, the dorsally directed force resulting from the flexion of the metatarsals will tense these ligaments (Fig. 27b). During the restorative

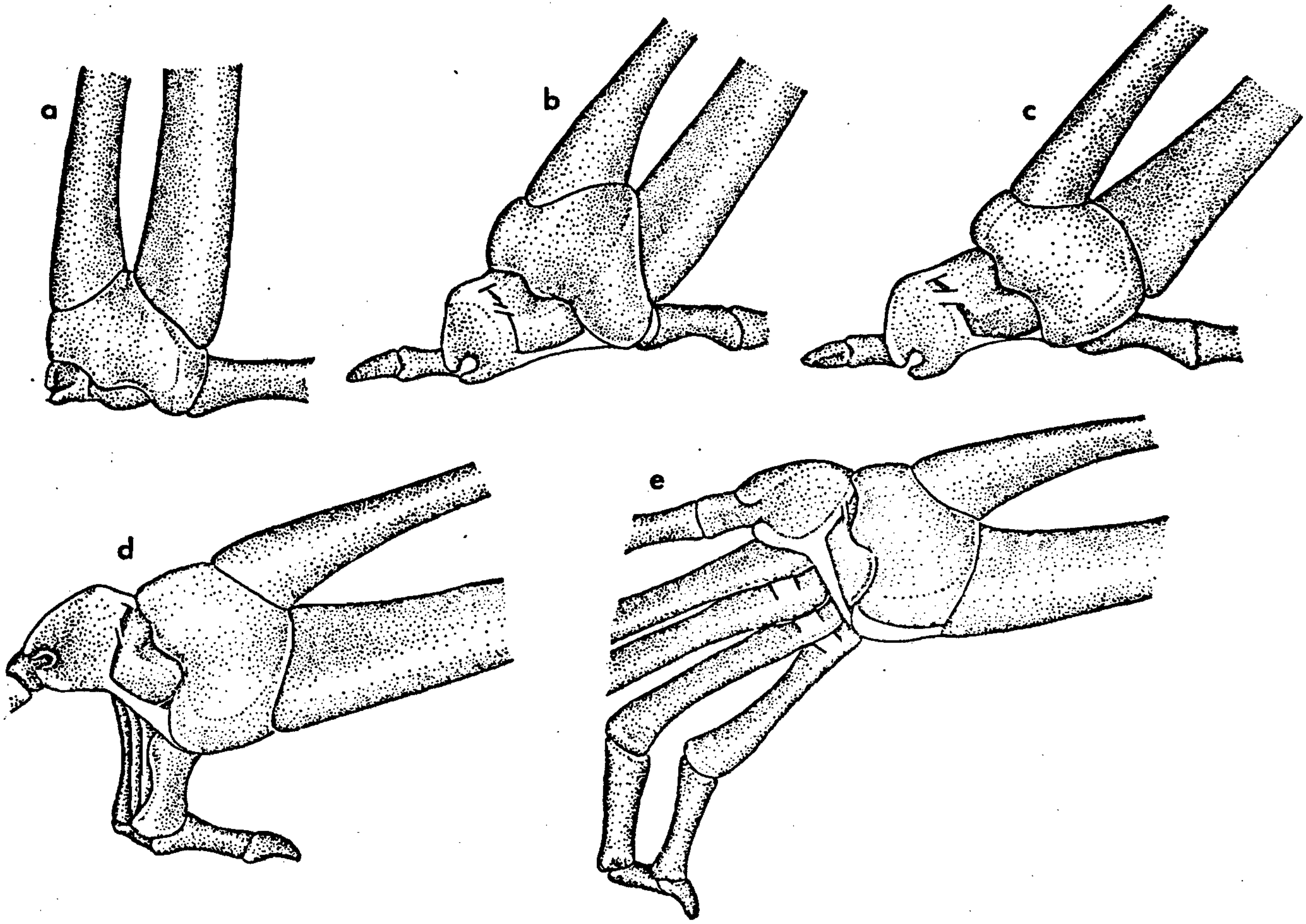
Figure 27. The mechanics of the astragalar-distal tarsal ligaments. a) the crus and metatarsus at the beginning of the propulsive phase, arrow represents the ventrally directed force resulting from gravity; b) the crus and metatarsus during flexion of the metatarsus, the arrow represents the anteriorly directed propulsive force acting on the proximal end of the metatarsus; c) the crus and metatarsus during the restorative phase, the arrow represents the force produced by the extensor digitorum longus.


a
ADtL
b
ADtL
c
ADtL

phase, the muscles dorsiflexing the metatarsus will pull up on the metatarsus and thus will have a dorsal component that will tense the astragalar-distal tarsal ligaments (Fig. 27c).

As shown by Rewcastle (1978), the articular surfaces control the movements of the joints when they are pressed against one another. Thus they play an important role in guiding the movements of the bones. This can be recognized by tracing the movement of the path of centre of articulation across the articular surfaces during propulsion (Fig. 28). At the beginning of the propulsive phase (Fig. 28a), the crus is vertical. The c-shaped ridge of the astragalus lies in the groove on the fourth distal tarsal with its anterior face abutting against the lateral wall of the groove on the distal tarsal, and the anterior flange of the calcaneum contacts the posterior aspect of the lateral portion of the articular surface of the fourth distal tarsal. The initial flexion and rotation of the crus on the metatarsus is a result of rotation around the axis of abduction and the axis of adduction. The astragalocalcaneum translates over the fourth distal tarsal with the c-shaped ridge coming into contact with the dorsal portion of the groove on the fourth distal tarsal and the anterior flange of the calcaneum coming into contact with the dorsal aspect of its opposing articular surface (Fig. 28b). Following this, there is a period when the only movement of the crus to occur is a lateral rotation around its long axis. This lifts the calcaneum away from the articular surface of the fourth distal tarsal, although the astragalar portion of the bone may continue

Figure 28. The intratarsal joint of Iguana during locomotion. Medial view. a) the crus and pes at the beginning of the propulsive phase; b) the crus and pes after flexion of the knee; c) the crus and pes after retraction of the femur and lateral rotation of the crus; d) the crus and pes during rotation of the metatarsus; e) the crus and pes at the end of the propulsive phase. Drawn from ligamentous preparations of the hind limb of Iguana placed in positions indicated by the x-rays (Figure 3).


a
b
c
d
e

to contact the medial edge of the fourth distal tarsal (Fig. 28c). The initial movement of the metatarsus during plantarflexion of the pes is a rotation around its long axis (Fig. 28d). During this time, the c-shaped ridge of the calcaneum rocks over the medial edge of the opposing articular surface of the fourth distal tarsal and the anterior flange of the calcaneum comes into contact with the dorsal aspect of its opposing articular surface. Further rotation of the metatarsus presses the calcaneal flange against the fourth distal tarsal causing a simultaneous plantarflexion of the metatarsus (Fig. 28c). The deepening of the groove on the fourth distal tarsal ventrally results in an increasing amount of extension of the joint as the metatarsus becomes vertical and results in a transition from pure rotation of the metatarsus to pure flexion at the end of the propulsive phase.

The importance of the articular surface in guiding the movements at the ankle is in contrast to most joints, such as the shoulder (Haines 1952) and the knee (Haines 1942; Brantigan _et_ _al_. 1941), where the ligaments play a more direct role in ensuring that the exact rotational and flexion-extension movements occur. In the specialization of the articular surface for this in the lizard ankle, a complex arrangement of ligaments such as is present in the knee and shoulder is avoided and the amount of movement possible is maximized.

B. The metatarsus

The metatarsus of lizards is an important propulsive lever. In _Iguana_ this is consolidated to form a narrow bar of bone. The arrangement of the bones is maintained by a complex system of ligaments and muscles shown in Figure 20. A detailed description of these was given by Rewcastle (1978).

Movements at these joints of this unit of the pes does not contribute greatly to the total amount of movement of the crus on the pes that occurs during locomotion. The small amount of movement possible at the joints is important in preventing stress concentrations. For example, if the joint between the first two metatarsals were not present, any force tending to abduct the bones, that is, increase the angle between the two bones, would result in stress concentration at their point of union. The presence of a joint between the two bones prevents this, since abduction tenses the ligaments of the joint, rather than the bones themselves.

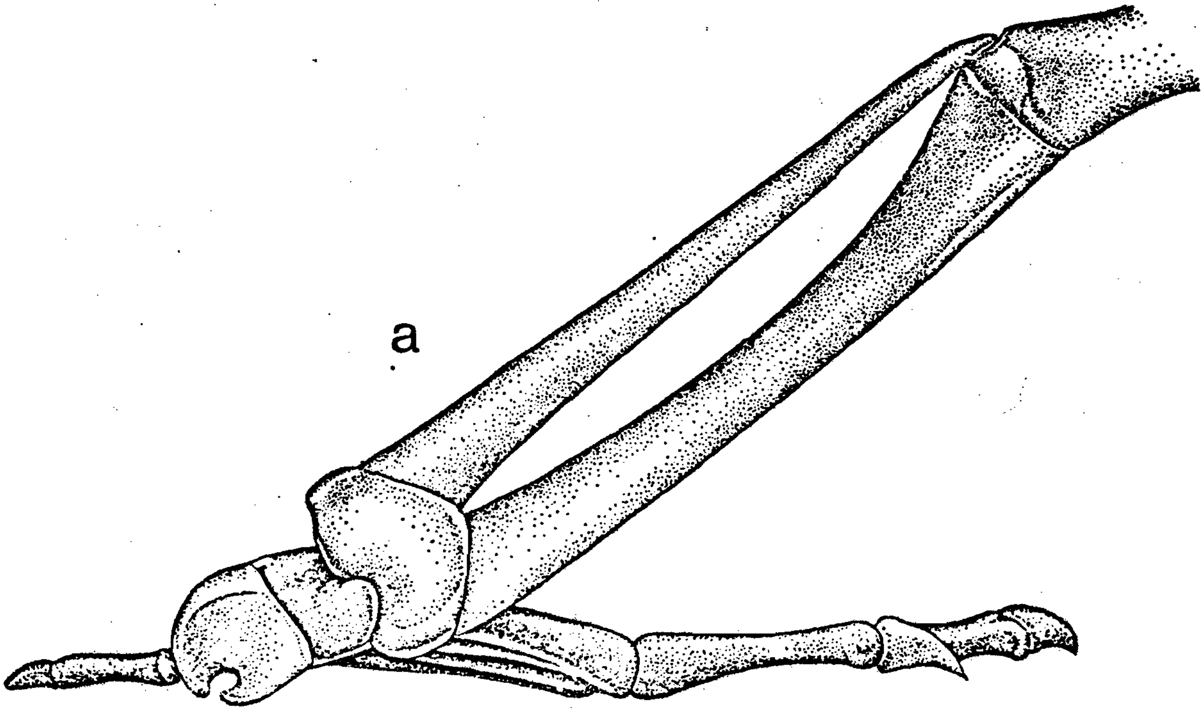
The consolidation of the metatarsals and distal tarsals is clearly an adaptation allowing the metatarsus to be used efficiently as a propulsive lever. As described above, the movement of the metatarsus occurring during pedal plantarflexion involves an initial rotation followed by a flexion of the metatarsus on the crus. Thus, unlike the case in mammals, the mechanics of the metatarsus changes during plantarflexion of the metatarsus. The changes that occur can be recognized by comparing the mechanics of the metatarsus at the beginning of the plantarflexion of the pes to its mechanics near the end of the propulsive phase.

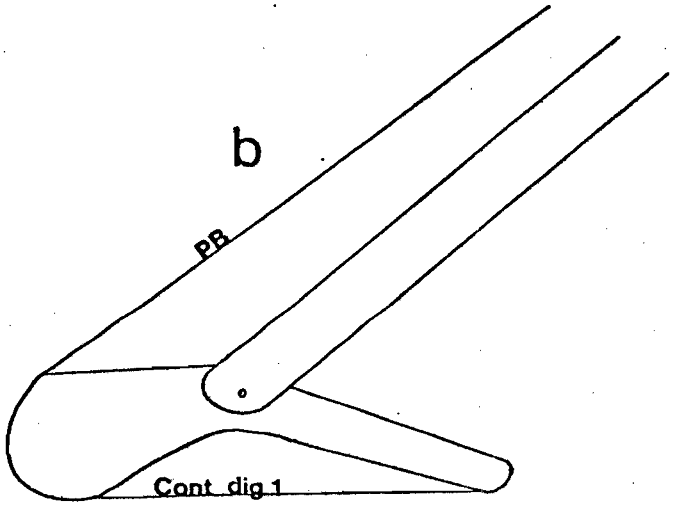
The initial movement of the metatarsus to occur during pedal plantarflexion is a rotation around its long axis, lifting its proximal end and moving this anteriorly. Rotation of the metatarsus occurs around an axis perpendicular to the long axis of the body. The lateral orientation of the metatarsus together with the regular increase in length of the first three metatarsals results in the distal ends of these metatarsals falling on this axis. Thus as the metatarsus is rotated, they will share equally in supporting the body.

The muscle that can rotate the metatarsus most strongly and is probably primarily responsible for this movement is the peroneus brevis. This muscle has a fleshy origin from the anterior and lateral surface of the fibula and inserts on the outer process of the fifth metatarsal. It has been considered to be an extensor of the pes since it passes anterior to the lateral edge of the astragalocalcaneum (Schaeffer 1941). However, since the astragalocalcaneum points somewhat posteriorly rather than being transversely oriented across the metatarsus, its line of action passes slightly posterior to the astragalocalcaneal-fourth distal tarsal joint. Thus as well as rotating the metatarsus, it will tend to flex the metatarsus slightly. Other muscles, such as the peroneus longus and the gastrocnemius femoral head, will also rotate the metatarsus, although they probably act mainly to stabilize the ankle joint at this time. Thus the line of action of the pedal flexors that rotate the metatarsus can be approximated by a line passing along the lateral edge of the crus to the outer process of the fifth metatarsal (Fig. 29b).

The functional length of the metatarsal lever during rotation of

Figure 29. The mechanics of the metatarsal lever during rotation of the metatarsus. a) medial view of the crus and pes of Iguana just prior to rotation of the metatarsus; b) schematic drawing showing the metatarsus as a lever. Abbreviations: Cont dig 1, the line of action of contrahenes digit one; PB, the line of action of the peroneus brevis.


a


b
PB
Cont dig 1

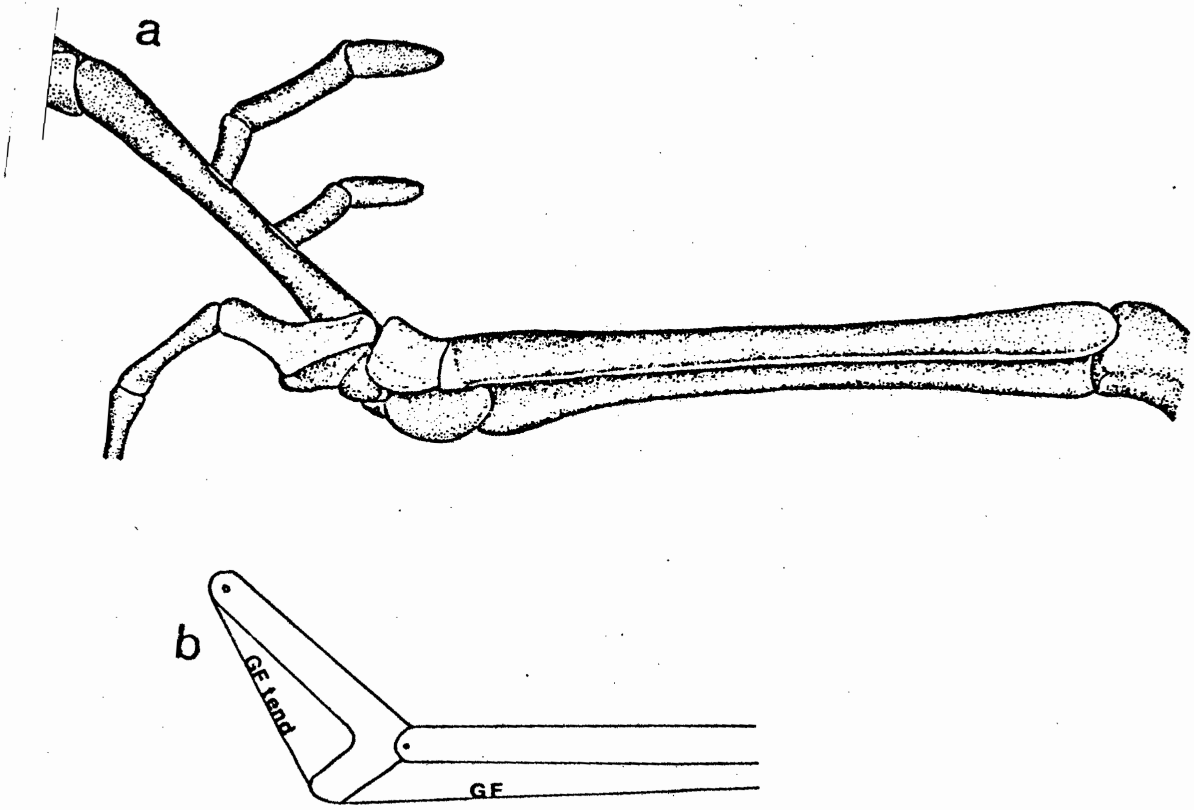
the metatarsus will be the distance between the axis of rotation around which the metatarsus is moving and the outer process of the fifth metatarsal. The point at which the force is transmitted across the joint, the fulcrum when the metatarsus is thought of as a lever, is the astragalar-distal tarsal ligaments. The resistance arm of the lever is the distance along this line between the astragalar-distal tarsal ligaments and the axis of rotation around which movement is occurring. This does not fall along any single skeletal element, although it is approximated by the first metatarsal. The length of the power arm is the distance between the astragalar-distal tarsal ligaments and the line of action of the force flexion of the metatarsus at this time. This line is maximized by the length of the proximal inturned portion of the fifth metatarsal (Fig. 29).

During the final stages of pedal plantarflexion, the ankle is extended. The metatarsus rotates around a vertical axis passing through its distal end, moving the proximal end laterally and anteriorly. The muscles that can flex the metatarsus most strongly at this time, and thus are probably primarily responsible for this movement, are the flexor digitorum longus and the gastrocnemius femoral head. The flexor digitorum longus uses the tarsus as a pulley, flexing the metatarsus by pushing against its proximal end. The medial portion of the gastrocnemius (femoral head) is continuous with the flexor digitorum brevis, and these muscles also use the tarsus as a pulley. The lateral portion of the gastrocnemius (femoral head) inserts on the ventral tips of the plantar tubercles, so in part, the muscle would operate the metatarsus in a manner analogous to a first class lever, with the force being applied at the ventral surface of the plantar tubercles, the fulcrum being the astragalar-metatarsal ligaments, and the resistance being the distal end of the metatarsals (Fig. 30). The power arm of this lever system is the distance between the ventral tip of the plantar tubercles and the astragalar-metatarsal ligaments. This distance is related to the size of the plantar tubercles and the distance they project ventrally from the tarsus. Thus at this time, the plantar tubercles function to increase the leverage of the pedal flexors. This increase is not great in Iguana, but would be in lizards with hypertrophied plantar tubercles (e.g. Basiliscus, Crotaphytus, Snyder 1954).

This mechanical analysis of the metatarsal lever supports Robinson's suggestion that the fifth metatarsal is analagous to the calcaneal tuber of mammals in that it increases the leverage of the pedal flexors. However, the mechanics of the metatarsal lever of lizards and mammals are very different. The fifth metatarsal of lizards, rather than being a simple lever, is a double lever that performs the same function in two different ways at different times during the propulsive phase.

The metatarsus, as any propulsive lever, is subject to considerable forces. Since the metatarsus is directed laterally, the forces in lizards pass transversely across the metatarsals, at least during the

Figure 30. The mechanics of the metatarsal lever during extension of the ankle joint. a) the crus and pes of _Iguana_ during extension of the ankle joint seen in dorsal view; b) schematic drawing showing the metatarsus as a lever. Abbreviations: GF, gastrocnemius (femoral head); GF tend, gastrocnemius (femoral head) tendon.


a
b
GF tend
GF

initial portion of plantarflexion of the pes, and tend to disarticulate the metatarsus and distal tarsals. This is prevented by the reduction in number of elements present and the complex system of ligaments holding the remaining elements together. Disarticulation is also prevented through a morphological arrangement of the bones and muscles that minimizes the tension acting in the metatarsus. Pauwells (1952) has shown that a counterbending-zuggertung arrangement will reduce the tension that would otherwise be present in an element that is used as a lever. A counterbend is a bend in the element opposite in direction to that the force acting on the element tends to bend the bone. A zuggertung is a muscle that lies in the concavity of the bend connecting its ends to one another. Tension is such a muscle will compress the surface of the bone, counteracting the tension that would otherwise be present, with the net force acting in the bone of such a system being compressive. In the metatarsus, the transverse arching of the metatarsus acts as a counterbend during the time the metatarsus is rotating. The lateral orientation of the metatarsus results in the transverse arch being antero-posterior in orientation and in line with the forces that are transmitted across the metatarsus (Fig. 29). Thus it is in a position to act as a counterbend. The short pedal flexors tend to have their origin on the fifth metatarsal and pass across the ventral surface of the metatarsus, so a number of muscles have an arrangement that allows them to be used as a zuggertung. Chief among these is probably the contrahenes digit one, which originates on the ventro-medial portion of the fifth metatarsal and passes across the ventral surface of the metatarsus to insert on the proximal end of the basal phalanx of the first digit.

C. The fifth metatarsal and the functioning of the fifth digit

Robinson (1975) has shown that being able to grasp the substrate is important in tetrapods with a primitive gait. In lizards, this involves opposition of the fifth and (usually) the fourth digits. Robinson suggested that movement between the fifth metatarsal and fourth distal tarsal played in important role in this. However, this joint does not allow the large amount of movement hypothesized by Robinson. The articular surfaces are closely approximated and have four ligaments connecting the bones, one at each tip of the long and short axes of the articular surfaces (Fig. 20). Rotation of one surface relative to the other is prevented by a twisting of these ligaments. Abduction moves the distal end of the fifth metatarsal laterally, tightening the interdigital tendon, a strong tendon extending from the distal end of the fifth to the distal end of the fourth metatarsal. Manipulation of preserved material indicated that the amount of abduction possible is not significantly greater than that seen in the x-rays taken during analysis of the step cycle. Thus the muscles inserting on the fifth metatarsal can not move the fifth digit relative to the remaining digits, but move the metatarsus relative to the crus. Consequently, the movements that Robinson suggested occur at the fifth metatarsal-fourth distal tarsal articulation must be occurring at more distal joints, and the muscles involved in grasping must be different, or acting in a different way, than she suggested. Thus the functions of the joints and muscles involved in opposition of the fifth digit must be reconsidered before the role of the fifth metatarsal in grasping can be understood.

Three movements of the fifth digit occur during grasping -- abduction, rotation and flexion. Abduction is a lateral movement of the fifth digit, increasing the angle between the fifth and fourth digits. As recognized by Robinson, the muscle capable of causing this movement most efficiently is the gastrocnemus (tibial head), which inserts on the lateral digital tendon of the fifth digit (Fig. 24b). The amount of abduction that occurs varies in lizards. In some, such as Anolis, the fifth digit is directed posteriorly with the angle between the fifth and fourth digit being 180° when abduction is maximal. In Iguana and Varanus, the maximal amount of abduction seen was about 120°. Where the abduction is 180°, no rotation of the fifth digit is necessary during grasping, a simple flexion of the fifth and fourth digits will bring the plantar surfaces into opposition. Where the amount of abduction of the digit is less, some rotation of the fifth digit is necessary to bring their plantar surfaces into opposition. The gastrocnemus (tibial head) also has an insertion onto the dorsal surface of the basal phalanx of the fifth digit (Fig. 24b) and can, through this insertion, rotate the entire digit on the fifth metatarsal. In addition, some rotation of each phalange relative to its more proximal phalanx will accompany flexion at the phalangeal joints, and these rotational movements will sum to result in a considerable amount of rotation of the terminal phalanx.

Flexion of the fifth digit following abduction results in the grasping action. The flexor tendon arises from the flexor digitorum longus. The line of action of this muscle can be approximated by a line passing along the posterior of the crus. When the fifth digit is abducted, this line of action is not coincident with the flexor tendon of the fifth digit but forms an angle of generally around 90° to it. Thus, when the muscle contracts, it will tend to pull the tendon laterally across the tarsus. This lateral movement is prevented by the medial plantar tubercle of the fifth metatarsal which acts as a pulley around which the tendon passes, changing the direction of the pull of the muscle.

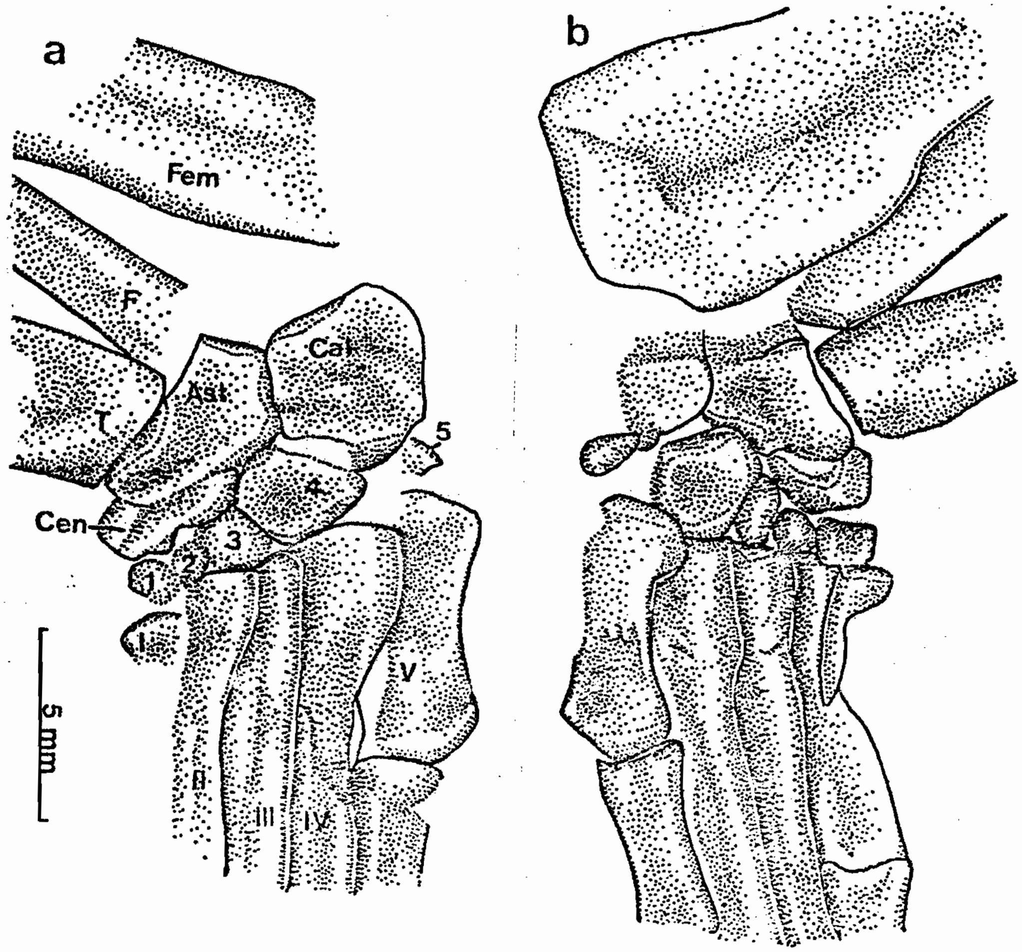
These movements bring the flexor surface of the fifth digit opposite that of the fourth so the only movement of the fourth digit that is necessary is flexion. However, the illustrations given by Robinson (1975, her Figure 12M) show that a lateral abduction frequently occurs as well. Two muscles are present that have the potential to abduct the fourth digit laterally, these being the fourth head of the extensor digitorum brevis of digit four and the calcaneal head of the flexor digitorum longus. The fourth head of the extensor digitorum brevis is a fusiform muscle with a tendinous origin from the dorsal margin of the proximal end of the fifth metatarsal (Fig. 24b). It sends a tendon down the lateral side of the fourth digit, inserting on the proximal end of each phalanx of the digit, and thus will abduct the entire digit by pulling laterally on the proximal end of the basal phalanx of the digit and will abduct each phalanx relative to its more proximal phalanx. The calcaneal head of the flexor digitorum longus originates from the calcaneum by way of a single tendon that passes between the plantar tubercles. The muscle inserts on the lateral portion of the flexor tendon of the fifth digit and will abduct the digit by pulling laterally on that tendon. The medial plantar tubercle acts as a pulley around which the tendon of this muscle pulls and thus serves to maintain the correct relationships of this muscle.

Thus the plantar tubercles, as well as serving to increase the leverage of the pedal flexors, are passively involved in grasping. Of especial significance with respect to this is the large size and comma shape of the medial plantar tubercle that is characteristically seen in lizards.

The Origin of the Lizard Tarsus

Schaeffer (1941) recognized that the major changes that occurred during the origin of the lizard tarsus from that of eosuchians were a fusion of the astragalus, calcaneum and centrale to form a single proximal element, a foreshortening of this element, the development of an intimate contact between the astragalocalcaneum and crural bones, the specialization of the intratarsal joint, the reduction in number of distal tarsals, the transverse arching of the metatarsus, and the hooking of the fifth metatarsal. Carroll (1977) showed that the development of the proximal tarsal bones of Saurosternon (Fig. 31) was intermediate between that of eosuchians and lizards. The astragalus, calcaneum and centrale remain separate and a perforating foramen is present between the astragalus and calcaneum. However, they are closely integrated and probably functioned as a unit. This unit has been foreshortened, giving the proportions characteristic of the astragalocalcaneum of extant lizards. As well, the structure of the distal units of the tarsus are intermediate between the eosuchian and extant lizard condition. Five distal tarsals are present. The first four are wedge shaped, with their dorsal larger than their ventral surfaces. They appear closely articulated in both dorsal and ventral view, and thus impart a slight transverse arch to the metatarsus. The fifth distal tarsal is a small element articulating with the dorsal half of the proximal articular surface of the fourth distal tarsal. As the tarsal elements are closely articulated, it was not possible to observe the articular surfaces of the intratarsal joint directly. However, comparison of dorsal and ventral views of the tarsus shows that the joint between the astragalocalcaneum and fourth distal tarsal already has the basic morphological features seen in later lizards. Dorsally, the astragalus abutts against the fourth distal tarsal. Ventrally, however, the fourth distal tarsal has a process that underlies the astragalus as in living lizards. The fourth distal tarsal articular surface on the calcaneum does not contact the opposing articular surface, as is the case

Figure 31. The tarsus of Saurosternon. a) dorsal view; b) ventral view. Specimen BM(NH) 1234. For abbreviations, see list of abbreviations.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in modern lizards when the joint is maximally extended. In contrast to the advanced condition, however, the calcaneum does not have an anterior flange supporting the articular surface for the distal tarsal, and the opposing articular surface does not extend onto the dorsal aspect of the bone.

The fifth metatarsal has been shortened to become a third of the length of the third metatarsal, in contrast to the condition in eosuchians, where they are subequal in length. The proximal articular surface of the fifth metatarsal is restricted to the medial half of the proximal edge of the bone and faces medially. The lateral half of the proximal edge extends laterally as an outer process. A slight inflection is present, resulting in the proximal articular surface being inclined dorsoventrally slightly. In contrast to the hooked fifth metatarsal of extant lizards, no plantar tubercles are present.

From the mechanical analysis of the pes of Iguana presented above, the adaptive significance of many of the structural changes that occurred during the origin of the lizard tarsus can be readily identified. These include the features associated with the consolidation of the metatarsus, especially the loss of the first, second and fifth distal tarsals and the transverse arching of the metatarsus. The resulting consolidation of the metatarsus would have increased the efficiency with which the metatarsus could resist forces passing across it and thus are a clear improvement over the primitive condition. The hooking of the fifth metatarsal was probably associated with this consolidation since it reflects an increase in the force that the pedal flexors could produce. These modifications could not be developed by an animal with a tarsus at the eosuchian grade of evolution, since movement between the metatarsals and distal tarsals is an integral part of the ankle joint here. Thus a fundamental reorganization of the intratarsal joint must have accompanied the consolidation of the metatarsus. An important aspect of this reorganization was probably a change in the mechanics of weight transmission across the ankle. In the tangasaurids, the weight was probably transmitted by compression between adjacent bones, with the tarsus supported ventrally by the plantar aponeurosis. In such a system, the bones must remain in articulation throughout the propulsive phase. In lizards, however, the weight is transmitted from the crus to the pes through the astragalar-distal tarsal ligaments. The articular surfaces no longer need to remain in contact throughout the propulsive phase. Consequently, the intratarsal joint could become much more flexible, able to allow all the movements of the crus on the pes that occur during locomotion. The importance of the articular surfaces of the joint in modern lizards in guiding the movements at the joint suggest that a loss of stability during this "freeing" of the joint was prevented by a specialization of the articular surfaces. The tarsus of <u>Saurosternon</u> shows the initial steps in this specialization. The peg on the ventromedial corner of the fourth distal tarsal that fits under the astragalus results in the presence of a groove extending across the distal tarsal that will serve to guide the movements of the joint.

Once this stage in the mechanics of the tarsus is reached, the changes associated with the consolidation of the tarsus would follow quickly. The fusion of the astragalus, calcaneum and centrale and the fusion of the first two distal tarsals to their metatarsals would be relatively minor changes with immediate adaptive significance, since this would eliminate the risk of disarticulation of the joints and reduce the amount of material necessary for the construction of the tarsus by eliminating the need for ligaments holding the elements together. Similarly, the loss of the fifth distal tarsal, whether it be by fusion to the fifth metatarsal as suggested by Robinson (1975), fusion to the fourth distal tarsal as suggested by Schaeffer (1941), or complete loss as suggested by Mathur and Goel (1976), would not affect the functioning of the tarsus since the fifth metatarsal already articulated with the fourth distal tarsal. Structurally, the changes in the fifth metatarsal are also minor. From a fifth metatarsal similar to that seen in Kenyasaurus, where an outer process and a medially facing proximal articular surface is already present, the only changes necessary to develop the characteristic hooked fifth metatarsal of lizards are an inflection of the axis, bringing the proximal articular surface into a vertical position, an angulation of the proximal edge of the bone, and the development of two plantar tubercles. Since the relation of the cruro-pedal muscles of Kenyasaurus, in so far as it is possible to reconstruct them, is similar to the condition in lizards, these changes would not be accompanied by a change in the function of the muscles. Rather, there would be an intensification of functions already present, with the result being the production of a greater propulsive force.

The adaptive significance of other changes, particularly the foreshortening of the astragalocalcaneum and the loss of the perforating foramen, is less obvious. It is possible that they are related to a further increase in the proportion of the propulsive force that is transmitted directly from the femur through the tibia to the tarsus, with the foreshortening being associated with a strengthening of the tibia-astragalar articulation. There may, however, be additional reasons for this change.

VII THE RHYNCHOSAURID TARSUS

Rhynchosaurids are moderate (Iguana sized) to large (cow sized), herbivorous diapsids ranging from the Lower to the Upper Triassic (Chatterjee 1969). The structure of the tarsus in advanced members of the family was described in detail by Hughes (1968) who showed that a number of specialized features are present, including: 1) the proximal row consists of three bones, later shown to be the astragalus, calcaneum and centrale by Carroll (1976b); 2) a complex articulation between the astragalus and calcaneum is present with the astragalus having a "peg" that overlies the calcaneum; 3) the calcaneum has a laterally directed tuber; 4) the first four metatarsals increase in length but decrease in width from the first to the fourth; 5) the fifth metatarsal is hooked; and 6) the astragalus has a distinct groove on its ventral surface. Since the early rhynchosaurids Howesia and Mesosuchus were incompletely prepared, Hughes was only able to consider the structural changes that occurred during the origin of the rhynchosaurid tarsus in a general way and was unable to consider the functional aspects of this transition. Recently, the tarsus in these genera was prepared and described and the tarsus of Noteosuchus, the earliest known rhynchosaur, was described by Carroll (1976b), providing a basis for considering these aspects of the evolution of the rhynchosaurid tarsus.

Structure of the Tarsus of Noteosuchus

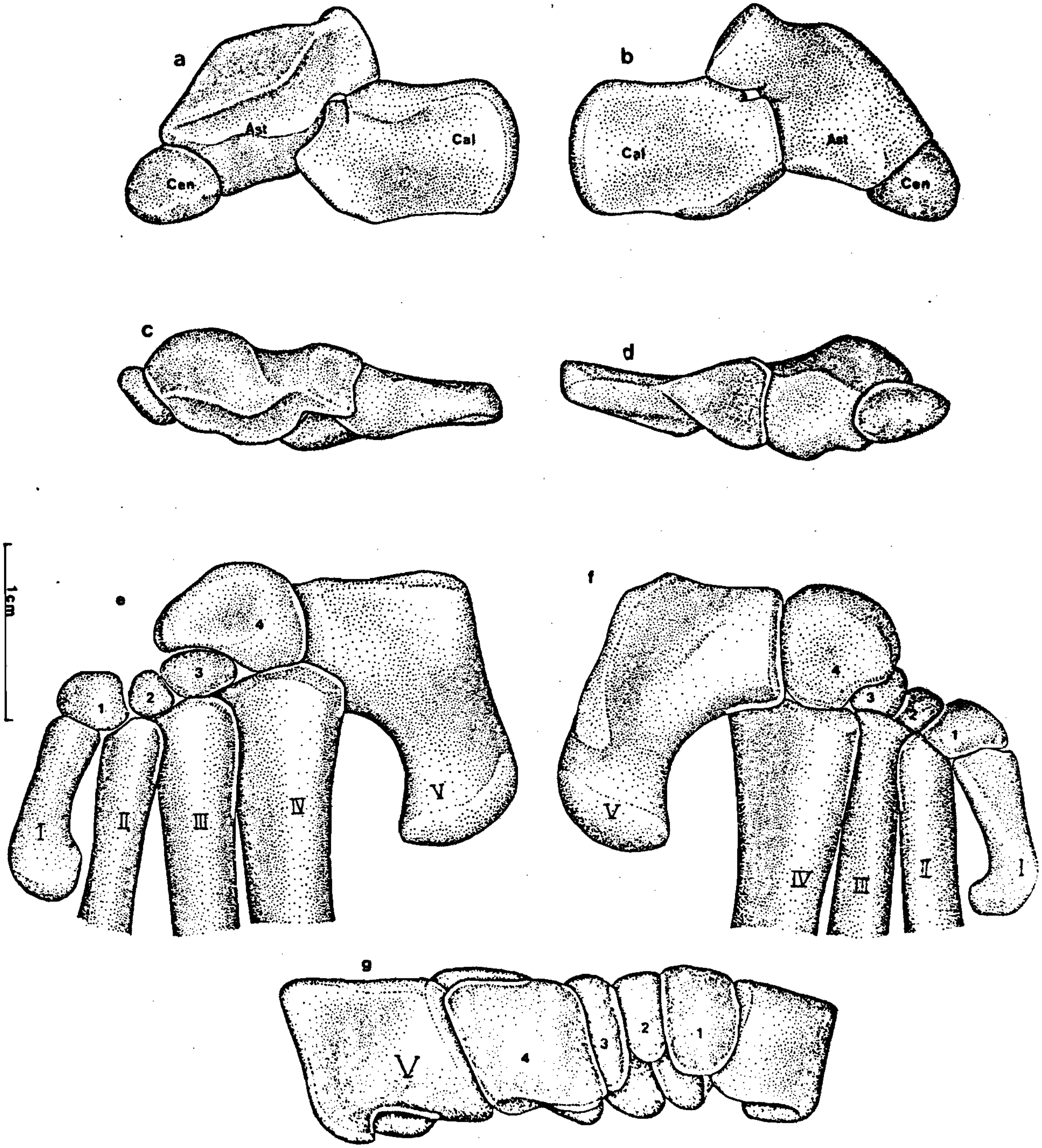
Noteosuchus is represented by a single specimen showing the postcranial skeleton preserved as an impression in fine-grained limestone. Both dorsal and ventral views are present. It was possible to cast the elements of the tarsus and join opposing halves to give three dimensional replicas of the isolated tarsal elements. These give a detailed understanding of the structure of the tarsus and could be manipulated to give an understanding of its mechanics.

The proximal tarsal row, as in advanced rhynchosaurids, is formed by three elements, the astragalus, calcaneum and centrale (Fig. 32). The fibula is supported by both the astragalus and calcaneum, the tibia is supported by the astragalus. The centrale, although closely integrated with the astragalus, does not appear to aid in support of the tibia.

The calcaneum is rectangular in dorsal view. Its lateral edge is modified to form a prominent tuber. This has thin proximal and distal edges but has a thickened medial buttress extending transversely across the body of the bone and an expanded, cartilage-covered lateral edge. When the articulated astragalus and calcaneum are viewed proximally, this tuber is seen to extend almost directly laterally (Fig. 32c).

The astragalus has been foreshortened, obscuring the primitive L-shaped configuration present in younginiformes. A perforating foramen is retained, although the groove on the ventral surface of the astragalus leading to the perforating foramen, and with it, the buttress supporting the tibial articular surface, has been lost. The tibial articular surface is tilted to face anteriorly. It remains ovular and slightly concave, but its posterior edge is rounded and has a strong posterior

Figure 32. The tarsus of Noteosuchus. a-d) articulated astragalus, calcaneum and centrale in a) dorsal; b) ventral; c) proximal; and d) distal views; e-g) articulated distal tarsals in e) dorsal; f) ventral; and g) proximal view. Specimen Albany Museum 3591. For key to abbreviations, see list of abbreviations.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exposure. This forms the dorsal edge of a shallow depression extending transversely across the posterior surface of the astragalus. When the articulated tarsus is seen in posterior view (Fig. 34), this groove is seen to lead from the fibula across the tarsus to the medial side of the metatarsus. Since this is the position of the pronator profundis in modern lizards, it is probable that this muscle lay within the groove.

The articulation between the astragalus and calcaneum has a complex concave-convex structure. The portion of the articular surface distal to the perforating foramen is a ball and socket joint with the socket on the calcaneum. The portion of the articular surface proximal to the perforating foramen is inclined relative to the distal portion with the astragalus overlying the calcaneum. The overlying portion of the astragalus was referred to as a peg by Hughes (1968). Here, the joint is also a concave-convex joint, but the concavity is on the astragalus. The convexity of the calcaneal surface continues laterally on the fibular articular surface, although fibular and astragalar areas can still be differentiated.

The centrale is a small element that articulates with the lateral edge of the astragalus. There is no finished bone on any of its surfaces. The articular surface for the distal tarsals is well defined with a shallow dorsoventrally oriented groove that opposed the proximal edge of the first distal tarsal.

Four distal tarsals are present with the fourth being the largest

(Fig. 32). The first three are wedge-shaped, their dorsal surfaces being slightly larger than their ventral. The first two are somewhat shorter than their metatarsals, leaving a "socket" ventrally that receives the centrale. The third distal tarsal extends the full height of its metatarsal. It fits in an indentation on the disto-medial edge of the fourth distal tarsal. The fourth distal tarsal has extensive areas of finished bone on its dorsal and ventral surfaces.

The first four metatarsals increase in length from first to fourth, as in primitive diapsids. The proximal ends of these metatarsals have become expanded and each metatarsal strongly overlaps the next lateral metatarsal.

The fifth metatarsal is hooked and shows all the features of the hooked fifth metatarsal of lizards, although differences are seen in details of the structure of the bone. In Noteosuchus, the proximal articular surface is wider than in lizards and is slightly concave. The medial plantar tubercle, rather than being a large process, is a low ridge oriented along a line extending from the proximal articular surface to the lateral plantar tubercle. The lateral plantar tubercle is a large comma-shaped structure with its tail extending proximally along the lateral edge of the bone. The distal articular surface is ovular. When viewed dorsally, this surface forms an angle with the shaft of the bone, its medial tip extending furthest distally.

Mechanics of the Noteosuchus Tarsus

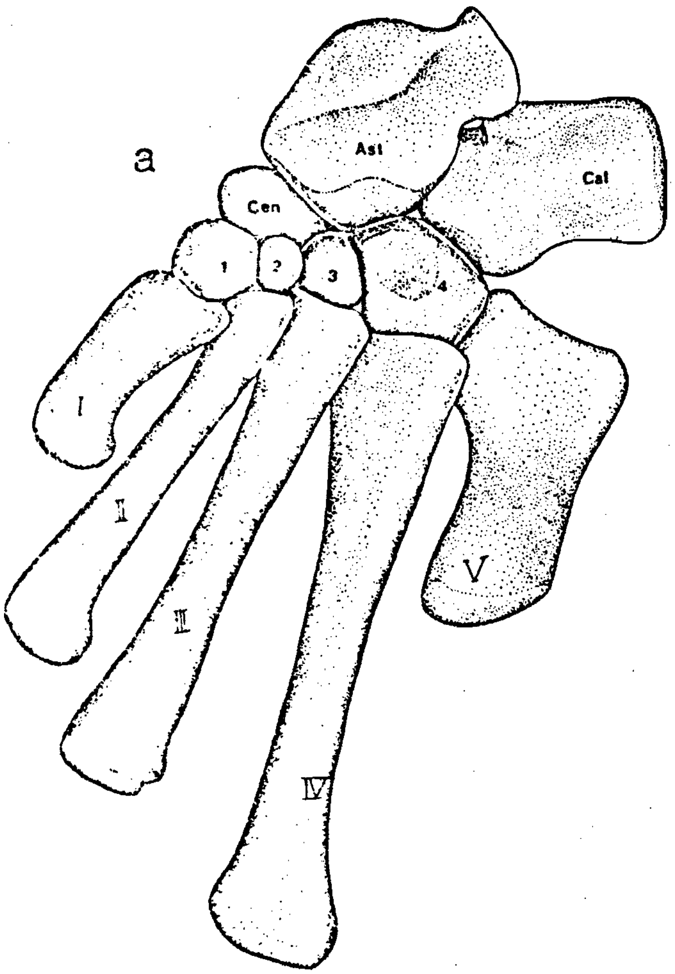
Apart from the tarsus, the pelvic limb of Noteosuchus has been little modified from the pattern seen in younginiform eosuchians, suggesting that the step cycle was not greatly altered during the origin of rhynchosaurids. Thus the pattern of movements of the crus on the pes during locomotion can be reconstructed as being an initial flexion and abduction, moving the knee anteriorly, and a rotation of the crus, resulting in its extensor surface facing laterally, with the reverse movements occurring during the final portion of the propulsive phase as the metatarsus is rotated and flexed on the crus.

As in the tangasaurids, the distal articular surface of the astragalus and centrale are convex and the calcaneum has a concave distal articular surface that fits over the convex proximal articular surface of the fourth distal tarsal. However, the distal articular surface of the calcaneum is circular rather than being narrow and mediolaterally elongate, and the opposing surface on the fourth distal tarsal is taller than in the tangasaurids. Also, the joint between the astragalus and fourth distal tarsal is not a convex-convex joint as in the tangasaurids. The fourth distal tarsal of Noteosuchus has a ventral process that fits under the astragalus and the astragalus has a shallow dorsoventrally oriented groove that fits over the third distal tarsal when the joint is maximally flexed.

The differences in structure of the calcaneal-distal tarsal joint imply that the amount of rotation of the calcaneum relative to the fourth distal tarsal and translation of the calcaneum over the fourth distal tarsal was greater in Noteosuchus than in the tangasaurids. The increase in movement at this joint is compensated for by a restriction in movement at the astragalar-fourth distal tarsal joint. The astragalus would have remained in the depression on the proximal edge of the fourth distal tarsal. Since this depression is formed by a peg that fits under the fourth distal tarsal, two distinct movements are possible: rotation around an axis passing across the surface of the fourth distal tarsal; and rotation around an axis passing through the body of the metatarsus and through the ventral process of the distal tarsal. Rotation around the axis passing across the metatarsus would result in the centre of articulation passing from the ventral to the dorsal aspect of the articular surface on the opposing bones as the joint was flexed (Fig. 33b-c), and would result in a flexion of the crus on the metatarsus. Rotation around the axis passing through the metatarsus would result in the centre of articulation passing from the dorsal to the ventro-medial portion of the articular surface on the fourth distal tarsal as the joint is flexed (Fig. 33a-b). Although some flexion of the crus on the metatarsus results from this, the predominate movement is an abduction of the crus increasing the angle between the crus and a vertical plane passing through the metatarsus.

During propulsion, the first movement would be a flexion of the crus on the femur, moving the knee anteriorly and ventrally. Since the metatarsus would have been directed laterally, this would be an abduction

Figure 33. The mechanics of the joints of the tarsus of *Noteosuchus*. a) reconstruction of the tarsus and metatarsus with the joints maximally extended; b) reconstruction of the tarsus and metatarsus with the intratarsal joint maximally flexed; c) reconstruction of the tarsus and metatarsus with the joint between the astragalus and calcaneum maximally flexed. For abbreviations, see list of abbreviations.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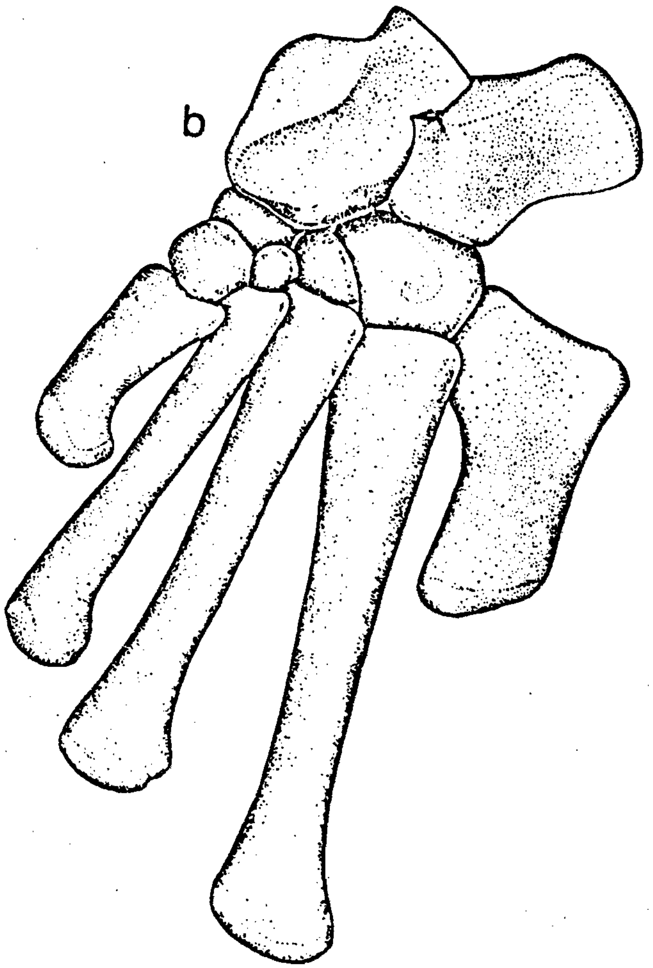
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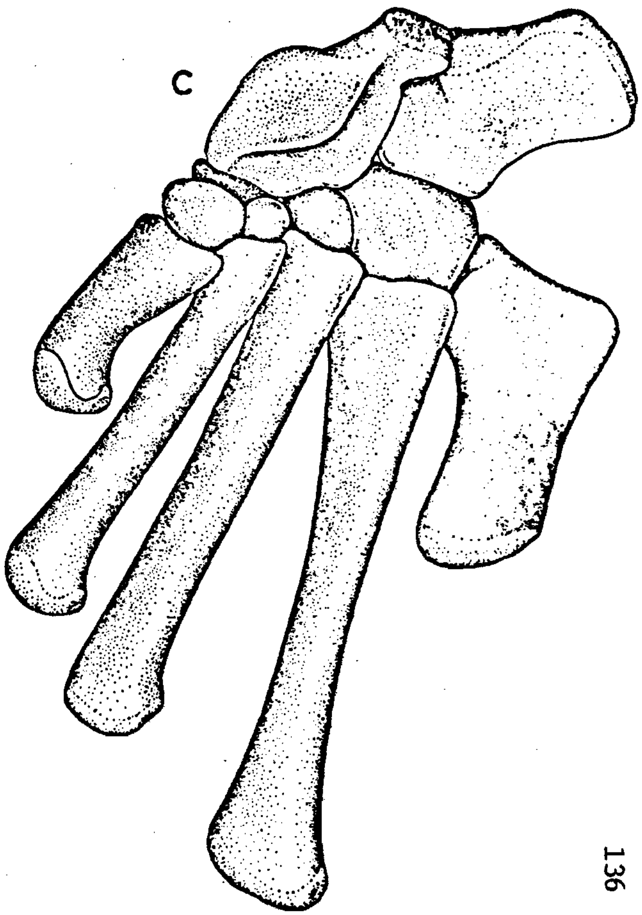
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of the crus relative to the metatarsus. The astragalus would have rotated around an axis passing through the metatarsus and the ventral process of the fourth distal tarsal (Fig. 32a-b). This would have brought the groove on its distal surface into opposition with the first distal tarsal and would have moved the centrale ventrally to fit in the "socket" formed by the proximal articular surface of the first three distal tarsals and the ventral half of the proximal articular surface of the first three metatarsals. The calcaneum would have translated over the fourth distal tarsal from the ventral to the dorsal aspect of the bone and would have rolled over the distal tarsal, bringing the centre of articulation at the joint from the ventral to the dorsal edge of the distal articular surface of the calcaneum.

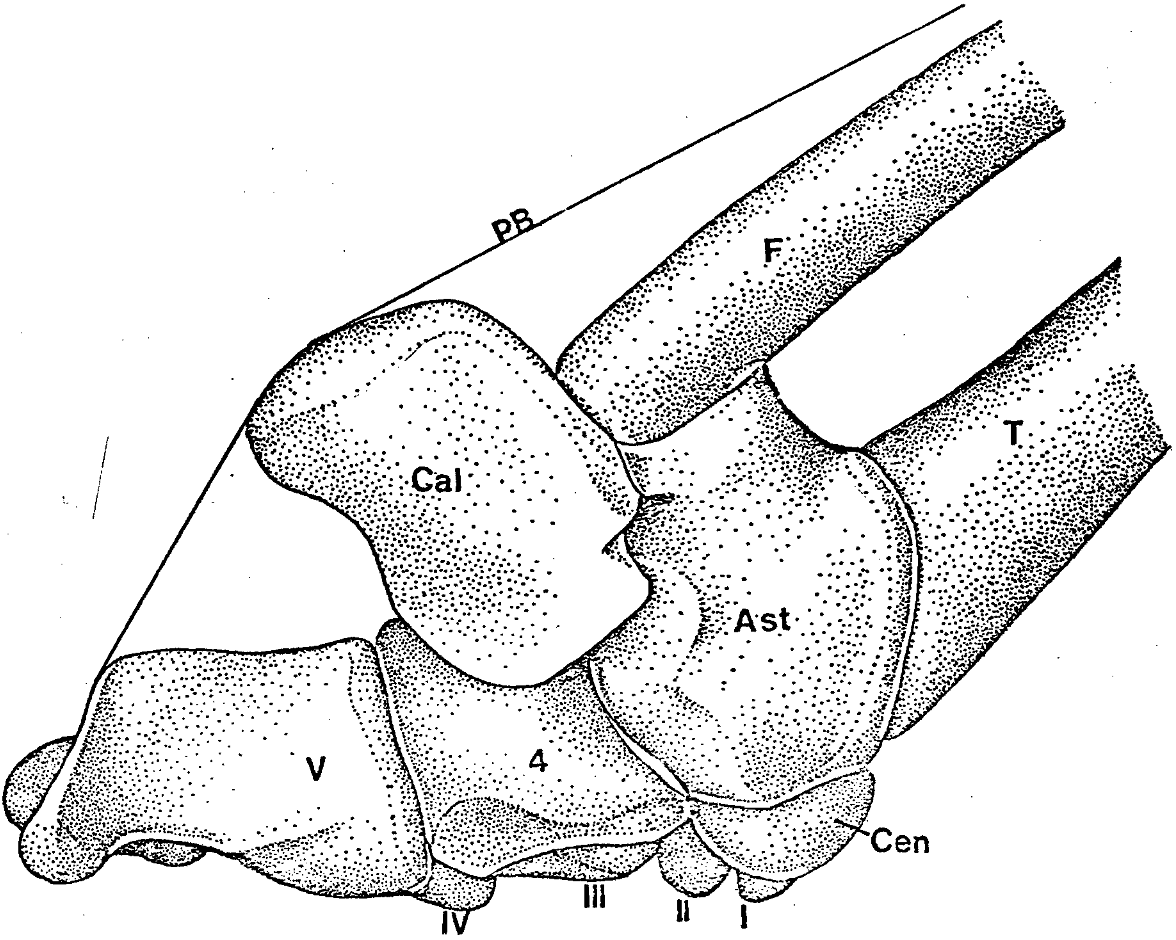
Following these movements there would have been a period when the major movement to occur would have been flexion of the crus on the metatarsus, moving the knee laterally, and a lateral rotation of the crus. The consolidation of the metatarsus and distal tarsals indicates that the part played by warping of the distal tarsal row in allowing these movements was reduced from the condition in the tangasaurids. However, the articular surfaces of the astragalus and centrale are not fully in contact with the distal tarsals, so a rotation around the axis passing between the astragalus and distal tarsals would have been possible (Fig. 32b-c). The resulting movement of the crus would have been a flexion of the crus on the metatarsus and a lateral rotation of the crus. If the astragalus and calcaneum moved as a unit, the calcaneum would be swung posteriorly away from the opposing articular surface of the fourth distal tarsal. This would have been disadvantageous, since the calcaneal-fourth distal tarsal articulation was probably an important site of force transfer across the ankle joint. The disarticulation of this joint would have been prevented by movement between the astragalus and calcaneum (Fig. 33b-c). The concave distal portion of the articular surface on the calcaneum continues the concavity of the fourth distal tarsal, with these bones providing a trough-like depression in which the astragalus could turn. The proximal portion of the astragalar articular surface on the calcaneum does not continue this trough, but it is oriented so that as the astragalus turns in the trough, the "peg" of the astragalus translates over the calcaneum. The fibula would have moved with the astragalus, translating over the convex fibular articular surfaces of the calcaneum.

Origin of the Rhynchosaurid Tarsus

From the description of the mechanics of the ankle joint in Noteosuchus it can be recognized that two major changes occurred in the ankle joint during the origin of the rhynchosaurid tarsus: a change in the mechanics of movement between the proximal and distal tarsal bones, and a specialization of movement between the astragalus and calcaneum. The change in the mechanics of the movement of the proximal on the distal tarsal bones increases the stability of the ankle joint since it replaces a convex-convex joint, that between the astragalus and calcaneum in the tangasaurids, with a concave-convex joint. This would have decreased the probability that forces transmitted across the medial side of the tarsus would have disarticulated the bones.

The specialization of movement between the astragalus and calcaneum enables the crus to flex on the metatarsus without movement of the distal tarsals and without a disarticulation of the calcaneum and fourth distal tarsal. The resulting reduction in the amount of movement of the distal tarsals and metatarsals would have allowed the metatarsus to become consolidated to form an efficient propulsive lever. This in turn would have been associated with the hooking of the fifth metatarsal, which would have increased the leverage of the pedal flexors and thus increased the force that they could produce. The calcaneal tuber was probably functionally associated with the fifth metatarsal since it would have acted as a pulley over which the pedal flexors inserting on the fifth metatarsal would have passed, and would have ensured that the tendons of these muscles were about perpendicular to the fifth metatarsal when the crus was abducted and flexed on the metatarsus (Fig. 34). Without the tuber, the muscles would have formed a more acute angle to the metatarsus, and the metatarsal lever would have had a shorter power arm.

Figure 34. The mechanics of the calcaneal tuber of Noteosuchus. Articulated tarsus in posterior view with the joints maximally flexed, and with the approximate position of the line of action of the peroneus brevis indicated. For abbreviations, see list of abbreviations.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Origin of the advanced rhynchosaurid tarsus

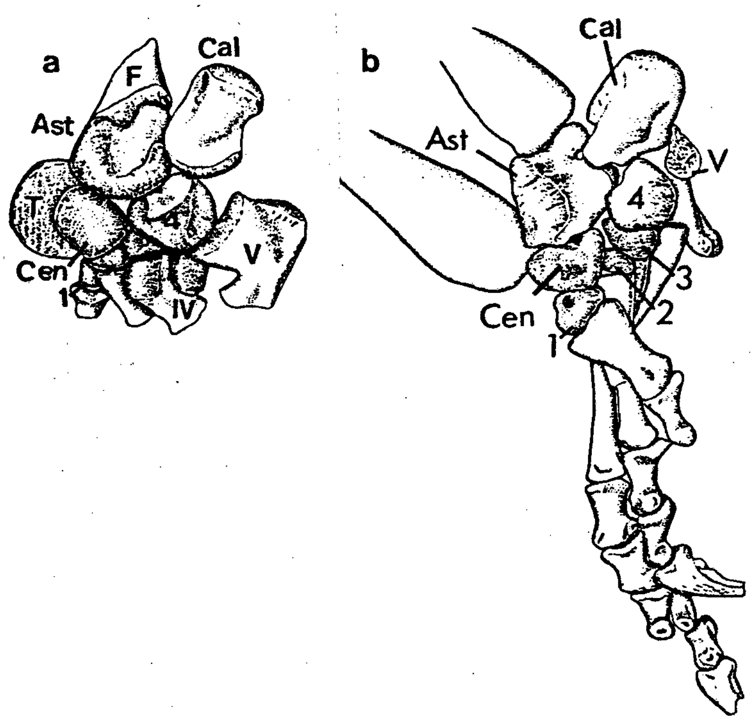
The major structural changes that occurred during the development of the tarsus of advanced rhynchosaurids from one like Noteosuchus are:

1. Enlargement of the centrale and its incorporation into support of the tibia. With this change, the astragalus becomes a more symmetrical element.
2. Loss of the perforating foramen with the articular surfaces proximal and distal to the perforating foramen meeting at a sharp contact.
3. Enlargement of the groove on the posterior surface of the astragalus.

Howesia and Mesosuchus show successive structural stages in the development of these advanced features. In Howesia (Fig. 35a), the centrale is large, although still cartilage covered, and the groove on the posterior surface of the astragalus is deepened, although the dorsal margin of the groove is still recognizable as the rounded posterior edge of the tibial articular surface. It is uncertain whether the perforating foramen is still present. In Mesosuchus (Fig. 35b), the centrale is large and the astragalus is nearly symmetrical. The posterior exposure of the tibial articular surface is strongly differentiated from the proximal articular surface. The perforating foramen has been lost.

The loss of the perforating foramen results in the astragalus and calcaneum becoming closely articulated. That this change reflects a loss of movement between the astragalus and calcaneum is indicated by changes in the fibular articular surface of the calcaneum. In Noteosuchus, this

Figure 35. The tarsus of advanced rhynchosaurids. a) Howesia; b) Mesosuchus. a, specimen SAM 5886; b, specimen, SAM 7416. For key to abbreviations, see list of abbreviations.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is a convex surface, allowing the fibula to translate over the calcaneum as movement occurred between the astragalus and calcaneum. In Howesia, this surface is slightly, and in Mesosuchus markedly, concave. The change in structure of this joint indicates a reduction in the amount of movement occurring between the astragalus and calcaneum. Thus a major mechanical reorganization of the intratarsal joint must have accompanied the origin of the advanced rhynchosaurid tarsus. However, in the absence of detailed information on the structure of the articular surface of the tarsal elements and of the changes, if any, in other aspects of the pelvic limb, it is impossible to determine the mechanics of the advanced pattern.

VIII THE SPHENODONTID TARSUS

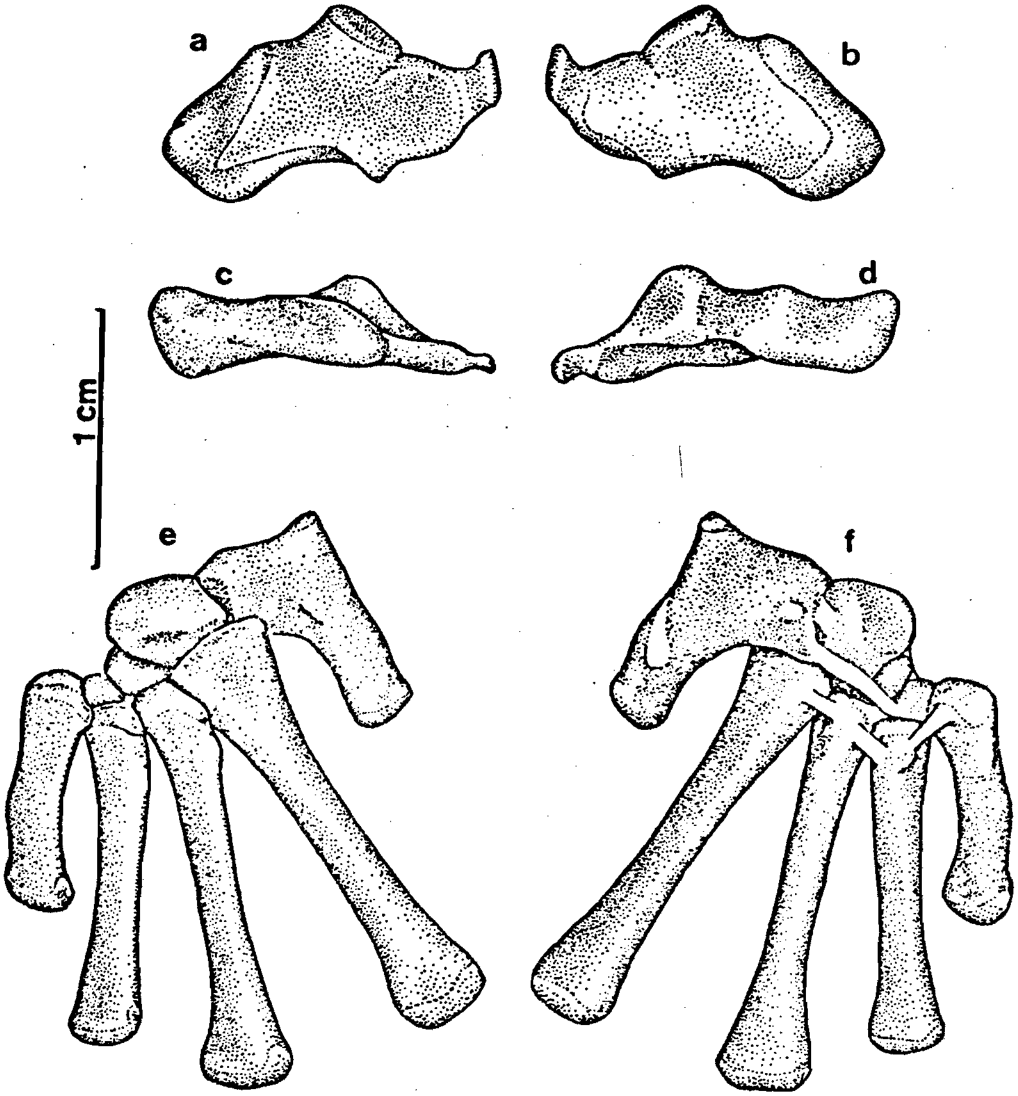
Sphenodontids are a distinct family of diapsid reptiles extending from the Triassic to the Recent. They have long been thought to be related to rhynchosaurids, but this has been brought into question by Carroll (1976b) who pointed out that early rhynchosaurids show little in common with sphenodontids, but are similar to archosaurs in a number of respects, while sphenodontids share many features with lizards. The similarity in structure of the tarsus in sphenodontids and lizards is especially marked, so much so that Schaeffer (1941) used the tarsus of the early sphenodontid *Homeosaurus* as a structural intermediate in considering the origin of the lizard tarsus. Despite this general similarity, the structure of the intratarsal joint and some other aspects of the tarsus of sphenodontids differ from the lizard pattern. Thus the sphenodontid tarsus will be considered in some detail here. Since the tarsus of the extant representative of the group, *Sphenodon*, is known in greatest detail, its structure and mechanics will be considered first.

The Tarsus in *Sphenodon*

A. General osteology

The tarsus of *Sphenodon* consists of four elements, a large proximal astragalocalcaneum and the second to fourth distal tarsals. The astragalocalcaneum (Fig. 36) supports the tibia and fibula

Figure 36. Osteology of the tarsus and metatarsus of Sphenodon. a-d) astragalocalcaneum in a) dorsal; b) ventral; c) distal; and d) proximal views; e-f) distal tarsals and metatarsus in e) dorsal and f) ventral views. For abbreviations, see list of abbreviations.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b
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proximally and articulates with the distal tarsals distally. As in lizards, astragalar and calcaneal areas of the astragalocalcaneum, referred to below as the astragalus and calcaneum, can be differentiated by a faint line marking the contact of the two bones. Embryological evidence (Howes and Swinnerton 1901) indicates that the astragalar portion is formed by fusion of the astragalus and centrale.

When seen in dorsal view, the astragalocalcaneum differs from that in lizards in that the distal edge is incised, allowing it to fit over the fourth distal tarsal. The element narrows medially, giving the astragalus a triangular outline, unlike the rectangular outline of the astragalus in lizards. Also in contrast to the condition in lizards, the tibial and fibular articular surfaces are formed entirely by the astragalus and these are widely separated by finished bone. The fibula has a lateral flange that is connected to the calcaneum by ligaments, but the two bones do not contact each other directly. The calcaneum extends laterally as a rectangular tuber. In mature specimens, grooves are present on the dorsal and ventral surfaces of this process near its lateral end.

The largest distal tarsal is the fourth (Fig. 36). As well as supporting the astragalocalcaneum, it articulates with the third, fourth and fifth metatarsals and the third distal tarsal. Small concave areas covered by finished bone are present on both its dorsal and ventral surfaces. The third distal tarsal has a small area covered by finished bone on its dorsal surface. The second is entirely cartilage-covered.

The distal tarsal row is continued medially by the proximal epiphysis of the first metatarsal, which is probably homologous with the first distal tarsal.

The metatarsus (Fig. 36) is short and broad. The proportions of the individual metatarsals are similar to the condition in lizards with well developed limbs. The fifth metatarsal is hooked and has the two plantar tubercle as in lizards. The lateral plantar tubercle is a comma-shaped structure located distally along the lateral edge of the bone. The medial plantar tubercle is a low rounded prominence located near the proximal articular surface along a line extending from the ventral tip of the proximal articular surface to the lateral plantar tubercle. As noted by Robinson (1975) no inflection of the shaft of the metatarsal is present and the detailed shape of the proximal articular surface differs from that of lizards.

B. Myology

A detailed description of the muscles of the crus and pes of Sphenodon was given by Perrin (1895) and the homologies of the muscles of Sphenodon and lizards was discussed by Kriegler (1961). Dissection of the hind limb of a specimen of Sphenodon during the course of this study agreed with Perrin's description in all details so a further description is not necessary here.

From Perrin's description and comparison, it is clear that the crural and pedal muscles of Sphenodon are little different from the condition in lizards. He considered the presence of an undivided peroneal muscle in Sphenodon to be one such difference, but an undivided peroneus is also seen in Xantsia (pers. obs.) and Lacerta (Rewcastle 1978). The only other difference reported by Perrin is the presence in Sphenodon of small flexor muscles extending from the fourth distal tarsal to the second and (in one specimen) third metatarsals. A comparable muscle layer is not seen in lizards. However, as muscles with similar relationships are seen in crocodiles, these being the flexor brevis profundis muscles, this difference may be a result of the retention in Sphenodon of muscles that were lost in lizards.

C . Structure of the joints

Both the tibia and fibula are supported by the astragalus. The fibular articular surface of the astragalus (Fig. 36d) is circular in end view and is slightly concave. It receives the ball-shaped surface on the medial half of the distal end of the fibula.

The tibial articular surface on the astragalus has two depressions (Fig. 36d), a shallow groove extending from the posterior to the anterior edge of the articular surface becoming broader and deeper anteriorly, and a shallow depression on the medial edge of the articular surface. From the relations of the three anlage that give rise to the astragalus (Howes and Swinnerton 1901), it appears that the elevation separating these two depressions develops from the centrale anlage. The posterior portion of the distal articular surface of the tibia has two low rounded elevations that match the depressions on the astragalus, although contact between the two bones is not intimate.

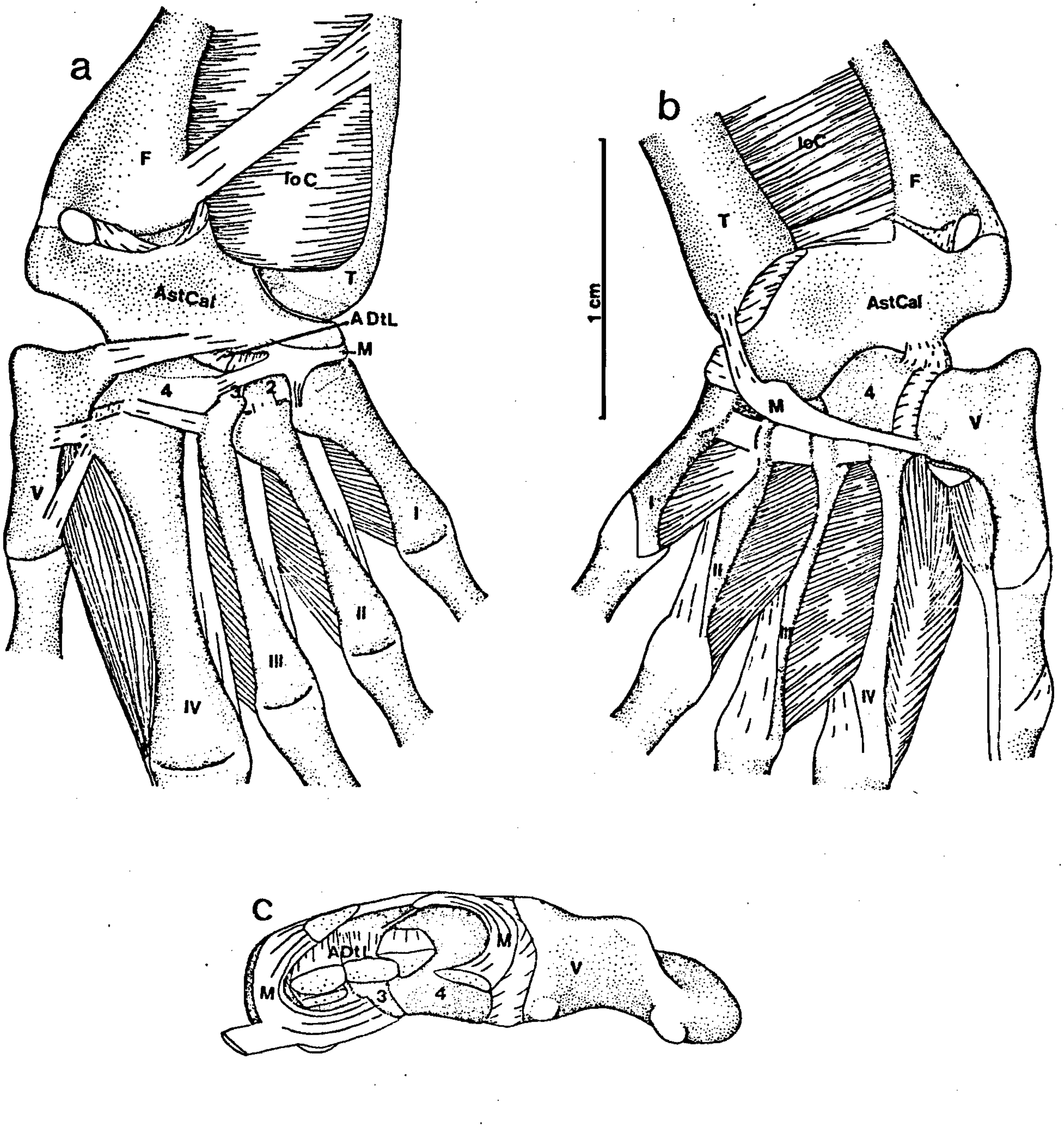
The fibula and astragalocalcaneum are held together by a ligament extending between the lateral tips of these bones and by the joint capsule (Fig. 37). Anteriorly the joint capsule is thin and easily destroyed during dissection. Medially, laterally and posteriorly, the joint capsule is thicker, although it is not differentiated to form distinct ligaments.

The tibia is connected to the astragalocalcaneum only by the fibres of the joint capsule which are generally thickened but are not specialized to form distinct ligaments (Fig. 37a, b). Anteriorly, the fibres extend dorsoventrally between the two bones. Posteriorly, the fibres extend obliquely from the medial edge of the tibia to a more lateral position on the proximal edge of the astragalus.

The tibia and fibula are connected to each other by the inferior anterior and posterior tibio-fibular ligaments. The anterior ligament is the stronger of these. It slopes medially and ventrally from its origin on the fibula to its insertion on the tibia. The posterior ligament is transversely oriented and located more distally, just proximal to the fibula-astragalar articulation.

The intratarsal joint has two distinct portions: the joint between the astragalocalcaneum and fourth distal tarsal laterally, and the more medial articulation between the bulbous medial portion of the astragalocalcaneum and the proximal end of the first metatarsal and second and third distal tarsals. The astragalocalcaneum-fourth distal

Figure 37. The ligaments of the tarsus and metatarsus of *Sphenodon*. a) dorsal view of tarsus and metatarsus; b) ventral view of tarsus and metatarsus; c) proximal view of distal tarsals. For key to abbreviations, see list of abbreviations.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tarsal joint is a concave-convex joint, with the fourth distal tarsal having a ball-shaped surface that fits in the convexity of the astragalocalcaneum. A ligament is present within this joint originating from a concavity on the medial portion of the fourth distal tarsal and inserting on the ventral edge of the astragalocalcaneum. As well, a meniscus is present between the two bones (Fig. 37a, c). This is c-shaped, corresponding in its outline to the edge of the articular surface on the astragalocalcaneum. Ligaments extend from the dorsal surface of the meniscus to the proximal corner of the fifth metatarsal laterally, to the anterior face of the astragalocalcaneum just proximal to the articular surface medially, and to the ventral surface of the astragalocalcaneum ventrally.

Medially, the astragalocalcaneum is connected to the distal tarsals by the astragalocalcaneal-distal tarsal ligaments (Fig. 37a, d), strong ligaments originating on the dorsal tip of the first metatarsal and second and third distal tarsals and inserting on the ventral edge of the astragalocalcaneum. These ligaments are surrounded medially by a c-shaped meniscus. This meniscus is held in place ventrally by three ligaments: one extending from the posterior surface of the tibia to the ventral surface of the meniscus, one extending from the tip of the ventral horn of the meniscus to the fifth metatarsal, and a short ligament extending from the tip of the ventral horn to the tip of the second distal tarsal. The dorsal horn is held in place by three ligaments: one inserting on the anterior face of the astragalus, one inserting on the dorsal tip of the first metatarsal, and one extending medially to the fourth distal tarsal.

In addition to these ligaments connecting the astragalocalcaneum to the fourth distal tarsal, the joint capsule is generally thick both dorsally and ventrally, although it is not specialized to form distinct ligaments.

The metatarsus is a rather broad, flexible structure (Fig. 37). The first four metatarsals are connected to each other ventrally by strong ligaments extending between the heads of the adjacent metatarsals. Dorsally, the heads of the first three metatarsals are not connected to each other directly. The third is connected to the fourth by a transversely oriented ligament. The second metatarsal is connected to the second distal tarsal by a short ligament extending between the dorsal edge of their articular surfaces. The third and fourth metatarsals are connected to the corresponding distal tarsals by the joint capsules, which are thickened but are not specialized to form distinct ligaments. Also, each metatarsal is connected to its distal tarsal by a strong ligament originating on the dorsal portion of the lateral edge of the metatarsal and inserting slightly more ventrally on the lateral edge of the corresponding distal tarsal.

The distal tarsals are connected to each other only by the joint capsules, which are especially strongly developed ventrally.

The fifth metatarsal is connected to the fourth distal tarsal by the joint capsule ventrally. Dorsally, in addition to the joint capsule, two ligaments are present. Both originate from the lateral tip of the proximal end of the fourth metatarsal; one extends to the dorsal face of the fifth metatarsal, the second extends to its distal end.

Mechanics

A. The crurotarsal joint

Two distinct kinds of movement are possible at the crurotarsal joint: flexion of the crural bones on the astragalocalcaneum and rotation of the elements around their long axes. Flexion and extension occurs around an axis lying parallel to the tibial-astragalar joint. The fibular articular surface is nearly perpendicular to this, so that as movement occurs around this axis, the fibula turns in the laterally facing socket on the astragalus. The amount of this movement possible in a ligamentous preparation of a preserved specimen of Sphenodon is approximately 25°. Flexion is limited by the posterior fibres of the joint capsules. Extension is limited by the anterior and medial fibres of the joint capsule between the fibula and astragalus.

It is impossible to evaluate the role of flexion and extension at the crurotarsal joint in the functioning of the tarsus with any degree of certainty. No doubt it contributes to the total amount of flexion and extension of the crus on the metatarsus that is possible in the live animal. Since the axis around which this movement occurs passes obliquely across the crus, flexion of the crus on the astragalocalcaneum is accompanied by some lateral rotation of the crus. Thus this joint may play a special role in allowing rotation of the crus.

Rotation of the fibula around its long axis is limited to a few degrees. Somewhat more rotation of the tibia around its long axis is possible, although the total amount of this movement possible is less than 15°. During this rotation, the medial edge of the astragalus and tibia are held together by the fibres of the joint capsule so that the axis of rotation passes through that area of the joint. Medial rotation is limited by the anterior inferior tibio-fibular ligament. Lateral rotation is limited by the posterior inferior tibio-fibular ligament and the posterior fibres of the joint capsule.

As shown by Haines (1942) an independent rotation of the fibula and tibia occurs during rotation at the knee, with the fibula moving with the femur and passing in front of the tibia. The slight amount of rotation of the tibia and fibula relative to the astragalocalcaneum is significant in that it allows this movement. Since the amount of rotation between the tibia and fibula is greatest, this joint is probably of greatest significance in this regard.

B. The intratarsal joint

The predominate movement to occur at the intratarsal joint is flexion and extension of the crus on the metatarsus. The astragalar-distal tarsal ligaments hold the central portion of the joint stationary. As the joint flexes, the calcaneal portion of the articular surface translates over the fourth distal tarsal from the posterior to the dorsal aspect of the fourth distal tarsal, and the centre of articulation between the bulbous medial edge of the astragalocalcaneum and the distal tarsals moves to a dorsal position on the astragalus. The geometry of the articular surfaces results in some medial rotation of the crus accompanying this flexion. The amount of these movements possible could not be measured accurately, but is considerably less than the movement possible at the comparable joint in lizards. Unlike the case in lizards, the articular surfaces are held in contact with one another continually by the ligaments of the joint, so little rotation or abduction-adduction is possible as an independent movement.

There is little doubt that the intratarsal joint is the major site of flexion and extension of the crus on the pes, although movement between the metatarsals and distal tarsals probably also contributes to this. The joint does not permit significant lateral rotation of the crus, so this movement must be occurring elsewhere in the tarsus, possibly at the cruro-tarsal joint.

C. The metatarsus

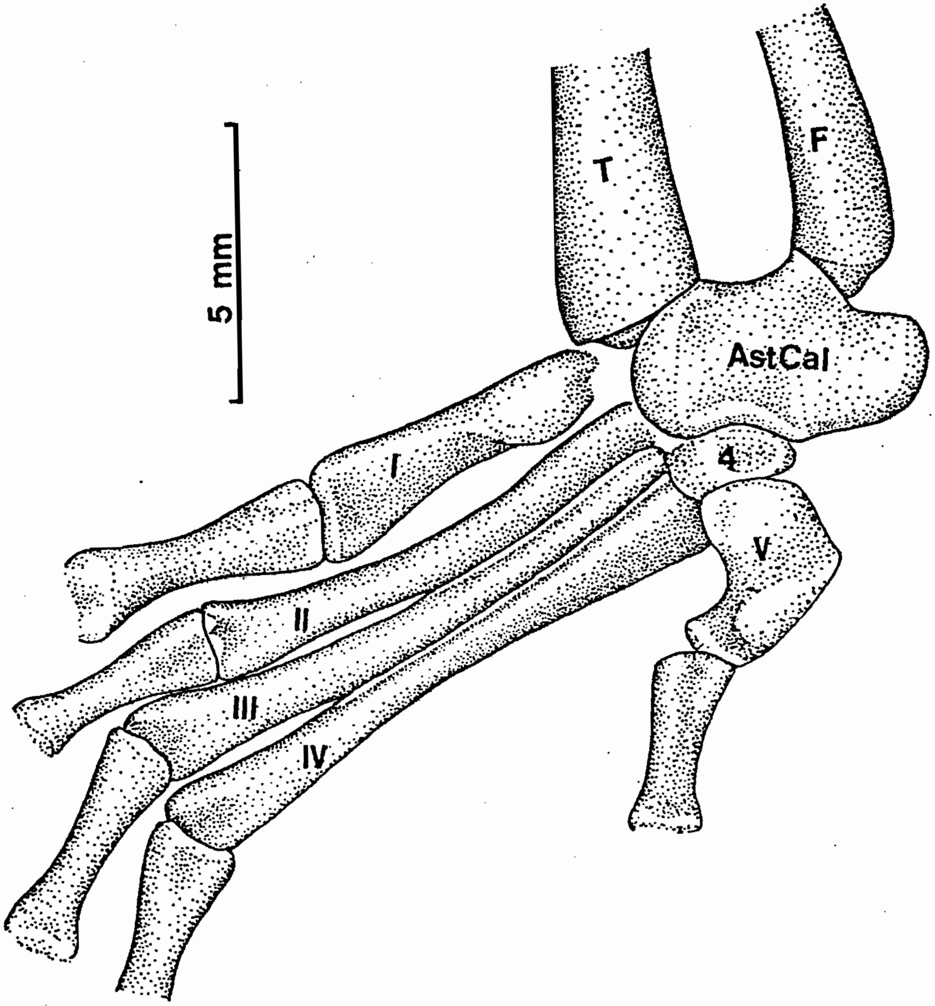
The metatarsus and distal tarsals do not form a solid unit as in Iguana. A small amount of movement in a number of directions is possible at each of these joints. This is combined in the ligamentous preparation to allow a considerable amount of warping and bending of the metatarsus, although no particular movement seem to predominate.

In the absence of detailed information about the movements of the metatarsus during pedal plantarflexion, it is impossible to consider the mechanics of the metatarsal lever in detail. Generally this would have been like lizards, although the different development of the plantar tubercles and the absence of an inflexion of the metatarsus may reflect some differences in the position of the lever arm during the final stages of plantarflexion of the metatarsus, as the joint is flexing.

The Tarsus in Fossil Sphenodontids

Among fossil sphenodontids, the tarsus is adequately known in *Homeosaurus* (Schaeffer 1941), *Sauranodon* (Lortet 1892) and *Kallimodon* (Cocude-Michelle 1963) (Fig. 38). In all features in which *Sphenodon* differs from lizards, the condition in these sphenodontids (where known) is similar to *Sphenodon*. Four elements are present, a proximal astragalocalcaneum and the second to fourth distal tarsals. The astragalocalcaneum has a laterally directed tuber, and its distal edge is incised, allowing it to fit over the fourth distal tarsal. The tibia and fibula are supported entirely by the astragalar portion of the bone, and the tibial and fibular articular surfaces are widely separated. The intratarsal joint is exactly the same as in *Sphenodon*. Differences are seen in the structure of the metatarsus. In the fossil sphenodontids, this is consolidated to a narrow bar of bone unlike the broad, flexible metatarsus of *Sphenodon*. The fifth metatarsal is shorter than the case in *Sphenodon* and has a relatively longer proximal inturned portion, although the development of the plantar tubercles and the shape of the

Figure 38. The tarsus of *Kallimodon*, drawn from a cast of specimen Munich 1887. vi. 1.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articular surfaces are the same in all sphenodontids.

Thus although the differences between the sphenodontid tarsus and the lizard tarsus are not great, they are consistently present. Consequently a sphenodontid tarsus can be recognized as a distinct structural type. The origin of this kind of tarsus will now be considered.

Origin of the Sphenodontid Tarsus

Two distinct modes of origin of the sphenodontid tarsus have been suggested. Schaeffer (1941) impressed by the similarities of the sphenodontid and lizard tarsus, assumed that they followed a similar course of development from an eosuchian tarsus. Hughes (1964), however, suggested that the rhynchosaurid tarsus was ancestral to that of sphenodontids with the three proximal elements of the rhynchosaurid tarsus fusing to give the single astragalocalcaneum of sphenodontids.

Comparison of the lizard and sphenodontid tarsus demonstrates that numerous similarities are present. The general configuration of the tarsus in the two groups is similar: in both, there is a single proximal astragalocalcaneum and a reduced number of distal tarsals with loss of the medial distal tarsals being a result of fusion of those elements to the metatarsals. Also, striking similarities are seen in the details of the ligaments and muscles: astragalo-distal tarsal ligaments and a c-shaped meniscus medial to these are present in both groups, the ligaments joining the metatarsals and distal tarsals are similarly arranged, and the arrangement of the muscles of the crus and the pes is the same in the two groups.

These similarities do not necessarily indicate a close relationship of lizards and sphenodontids. Most of the general features in which the lizard and sphenodontid tarsi are similar are not present in the early lizard Saurosternon, and thus must have been acquired independently by the two groups. The only exception to this is the general proportions of the tarsus. Saurosternon already has a foreshortened proximal unit and the fifth metatarsal is reduced in length. However, the comparable proportions in Noteosuchus are not greatly different from the condition in lizards, so this similarity is of little significance.

As the soft anatomy of a rhynchosaurid pes is not known, the significance of the similarities of the ligaments and muscles of the pes in sphenodontids and lizards is impossible to evaluate. They may be a result of a close relationship of lizards and sphenodontids, but it is also possible that they simply represent a primitive diapsid condition that would have also been present in rhynchosaurids. That the latter is indeed the case is suggested by the presence of the same basic divisions of the pedal muscles in crocodiles.

In contrast to the general similarities in the osteology of the tarsus of lizards and sphenodontids are a number of detailed similarities in the tarsus of sphenodontids and the early rhynchosaurid Noteosuchus. The astragalocalcaneum of sphenodontids is similar in outline to the proximal three bones of *Noteosuchus*. In both, the distal edge is incised allowing it to fit over the fourth distal tarsal, a lateral tuber is present on the calcaneum, the astragalus-centrale portion of the unit is triangular in outline, and the tibial and fibular articular surfaces are widely separated. A contact between the fibula and calcaneum is present in *Noteosuchus*, but this is reduced and, according to the mechanical interpretation offered above, mobile, and thus could easily give rise to the condition in sphenodontids. The details of the intratarsal joint is the same in sphenodontids and *Noteosuchus*. Also, in all features in which the fifth metatarsal of sphenodontids and lizards differ, sphenodontids are like *Noteosuchus*.

These similarities support the suggestion made by Hughes (1968) that the sphenodontid tarsus originated from that of rhynchosaurids through fusion of the three proximal elements and loss of the perforating foramen. However, none of these are fundamental enough to eliminate as a reasonable alternative the independent acquisition of these features by the two groups. Thus the mode of origin of the sphenodontid tarsus must remain uncertain until the relationships of sphenodontids are better understood.

Without an understanding of the structural changes that occurred during the origin of sphenodontids, nothing can be said of the mechanical aspects of the transition. Clearly, the mechanical factors involved would be quite different in these two alternative courses of evolution. Whatever the case was, the ultimate result was a tarsus basically similar to lizards in its mechanics.

IX THE TARSUS IN PROLACERTA, PROTOROSAURUS AND THEIR DERIVATIVES

Prolacerta and the aquatic reptiles from the Middle Triassic, *Macrocnemus* and *Tanystropheus* have long been recognized to form a natural group. These reptiles have usually been aligned with lizards because of the presence of an incomplete bar bordering the lower temporal opening ventrally. However, Gow (1975) has shown that *Prolacerta* has little else in common with lizards but may be more closely related to archosaurs than to other diapsids and on the basis of this, placed it in its own order. In the original description of *Prolacerta* (Camp 1945) and the later description given by Watson (1957), comparison was made to *Protorosaurus*. A relationship between these genera was not accepted by Romer (1956) because it was generally believed that *Protorosaurus* had a solid cheek. However, the original description by Seeley (1888) shows that the lower temporal opening is present bordered ventrally by an incomplete lower temporal bar, exactly as in *Prolacerta*. Also the cervical vertebrae, limb proportions and structure of the pelvic limb are similar in the two genera but unlike the condition in lizards.

An additional genus that may belong to this group is *Trilophosaurus*. This genus was suggested to be related to *Protorosaurus* by Gregory (1945) on the basis of similarities in the structure of the postcranial skeleton. A solid cheek is present in the skull of *Trilophosaurus*, but the entire skull is highly specialized, so this may be a derived condition.

Among the primitive members of this group, the best known tarsus is that of *Prolacerta*, recently described and illustrated by Gow (1975). This tarsus is like that of *Noteosuchus* in almost all details of its construction: the calcaneum is rectangular and has a laterally directed tuber, a complex concave-convex articulation is present between the astragalus and calcaneum exactly as in *Noteosuchus*, the centrale has become closely integrated with the astragalus, the articular surface on the fourth distal tarsal shows a convex surface for the calcaneum and a concave surface for the astragalus as in *Noteosuchus*, and the fifth metatarsal shows a similar development of the plantar tubercles in the two genera. The only difference that is apparent is the larger size of the perforating foramen in *Prolacerta*.

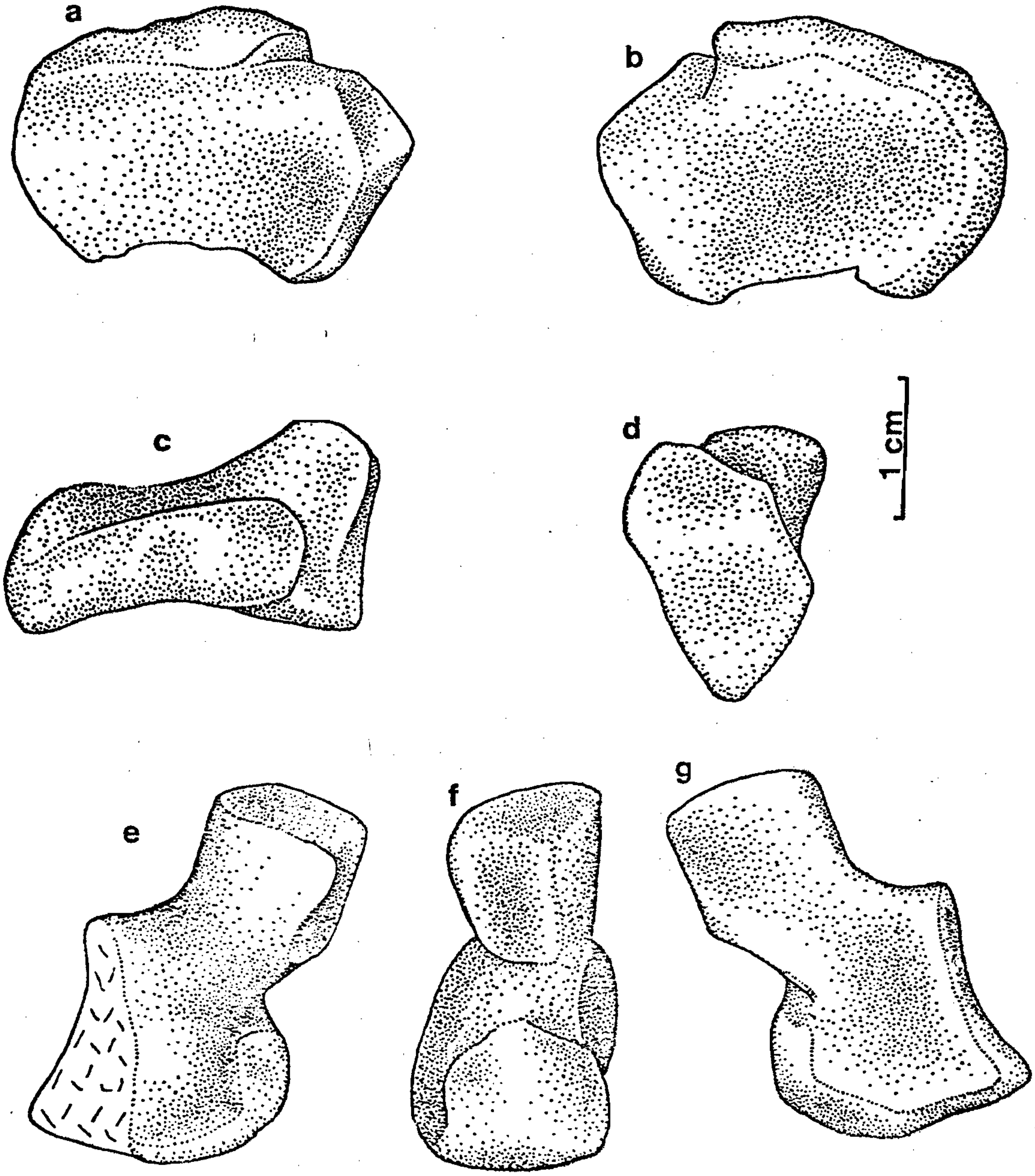
The tarsus in *Protorosaurus* was illustrated in dorsal view by von Meyer (1856). A number of differences between this tarsus and that of *Prolacerta* are evident. Many of these may simply be a result of poor preservation. Of more significance are the similarities in the basic structure of the elements: a complex articulation between the astragalus and calcaneum is present with the proximal portion of the astragalus overlying the calcaneum, the calcaneum has a laterally directed tuber and the fifth metatarsal is hooked.

The tarsus of the advanced aquatic members of the group, *Tanystropheus* and *Macrocnemus* are poorly ossified, a common specialization of aquatic reptiles. However, the complex concave-convex articulation between the astragalus and calcaneum and the lateral tuber of the calcaneum are present (Peyer 1937; Wild 1974), so the terrestrial ancestor of these animals probably had a tarsus like that of *Prolacerta*.

The tarsus of *Trilophosaurus* is well known from isolated and articulated specimens. An articulate pes was illustrated by Gregory (1945). An isolated astragalus and calcaneum are illustrated here (Fig. 39). In most features, particularly the development of the articular surface between the astragalus and calcaneum and the structure of the joint between the astragalus and calcaneum, this tarsus is like *Prolacerta*. Differences are seen in the outline of the calcaneum, this being taller and with a rounded ventral edge in *Trilophosaurus*. Also, the development of the tubers on the fifth metatarsal has been modified from the primitive condition.

The structural similarity of the tarsus of these reptiles and *Noteosuchus* indicates that they were functionally very similar and must have followed a similar course of development during their early evolution. Indeed, it is possible that rhynchosaurids, prolacertids, and archosaurs are more closely related to each other than any of these were to other diapsid groups (the relationship is indicated in Figure 57), and that the common ancestor of these groups already had developed this peculiar structural complex.

Figure 39. The astragalus and calcaneum of Trilophosaurus. a-d) cancaneum in a) dorsal; b) ventral; c) proximal; d) medial views; e-g) the astragalus in e) ventral; f) lateral; and g) dorsal views. Astragalus: Texas Memorial Museum 110-3-Q1-102. Calcaneum: Texas Memorial Museum 31025-192.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X THE ARCHOSAUR TARSUS

The final group of diapsids to be considered is the archosaurs. Unlike most diapsid groups where a peculiar structural and mechanical complex originated early in the development of the group and was retained with little modification in later members, a number of fundamentally different kinds of tarsi are present.

The mechanically simplest of these are tarsi in which the astragalus and calcaneum are associated with the crus and the distal tarsals are associated with the metatarsus and the ankle joint passes between the two units (the mesotarsal position). This type of tarsus is seen in pterosaurs, both orders of dinosaurs, and in a few thecodonts.

In crocodiles and a number of pseudosuchians, the ankle joint passes between the astragalus and calcaneum with the astragalus being functionally integrated with the crus and the calcaneum moving with the metatarsus. The calcaneum has a prominent posteriorly directed tuber that increases the leverage of the pedal flexors. Movement between the astragalus and calcaneum is allowed by a complex peg and socket joint between the two bones. Two types of crocodiloid tarsi have been recognized on the basis of the structure of this joint: the crocodile-normal tarsus, seen in crocodiles, rauisuchids, and probably pedeticosaurids, in which a peg on the astragalus fits in a socket on the calcaneum; and the crocodile-reverse tarsus, seen in advanced ornithosuchids and Euparkeria, in which a peg on the calcaneum fits in a socket on the astragalus.

The earliest known type of tarsus seen in archosaurs is that present in *Proterosuchus* (Fig. 40). This tarsus is almost identical to the tarsus of the early rhynchosaur *Noteosuchus* (Carroll 1976b), and presumably the tarsi of the two genera would have been similar in their functioning.

The evolution of the tarsus in archosaurs poses a series of related questions:

1. What is the primitive archosaur pattern, and what structural and functional changes occurred during the origin of this kind of tarsus?
2. What structural and mechanical changes occurred during the origin of the crocodile tarsus, and what is the relationship of the crocodile-normal and the crocodile-reverse tarsi?
3. Did the tarsi with a mesotarsal joint originate directly from the primitive archosaur pattern or from the crocodiloid tarsus?

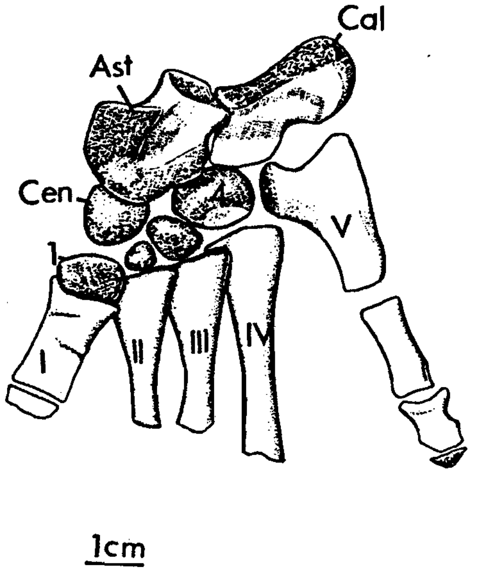
   What structural and mechanical changes occurred during the origin of the mesotarsal joint?

These questions will be considered in turn.

1. THE PRIMITIVE ARCHOSAUR TARSUS

The earliest known archosaur tarsus is that of *Proterosuchus* (Fig. 40). As shown by Carroll (1976b) this tarsus is similar to that of *Noteosuchus* in almost all details of its construction. The only difference apart from size that Carroll recognized is the presence of a

Figure 40. The tarsus of <u>Proterosuchus</u>. a) dorsal view; b) ventral view. From Carroll 1976b.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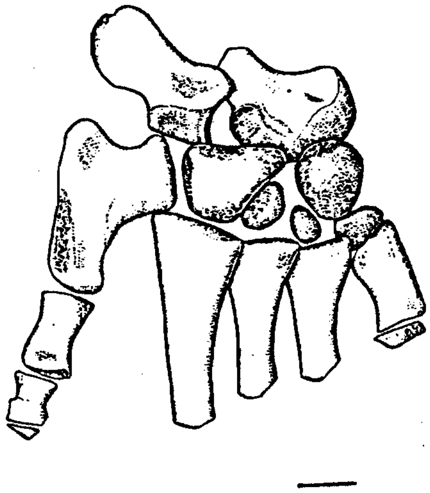


convex tibial articular surface on the astragalus of Noteosuchus, as opposed to a concave surface in Proterosuchus. The convex appearance of this articular surface in Noteosuchus is a result of the posterior expansion of the edge of the articular surface. As shown above, this is associated with the development of a characteristic groove on the posterior surface of the astragalus in rhynchosaurids. The portion of the articular surface that supports the tibia is concave so, functionally, this joint would have been the same in the two genera.

Since Proterosuchus is in many respects the most primitive known archosaur, its tarsus has been assumed to represent the primitive archosaurian pattern (Hughes 1963). This assumption has been brought into question by Cruickshank (1972), who suggested that Proterosuchus is a carnivorous rhynchocephalian. Cruickshank's suggestion implies that Proterosuchus is not an archosaur but is a specialized rhynchosaur and, consequently, that its tarsus is not the primitive archosaurian pattern. Recent work on archosaurs has provided a number of lines of evidence that show that this is not the case. One of these is the similarity in structure of the tarsus of Proterosuchus and Erythrosuchus, a second archosaur from the Lower Triassic. The tarsus of Erythrosuchus, recently described and illustrated in detail by Cruickshank (1978) retains only four poorly ossified elements. Although a number of structural details are obscured by the poor ossification of the elements, the structure of the tuber on the calcaneum and the structure of the joint between the astragalus and calcaneum are similar in the two genera. In both, the calcaneal tuber is a rectangular laterally-directed structure with thin proximal and distal edges and with a thickened buttress extending transversely across the body of the bone, and with an expanded, cartilage covered edge. Also, in both genera the structure of the joint between the astragalus and calcaneum is a concave-convex structure with the concavity on the astragalus proximal to the perforating foramen and on the calcaneum distal to the perforating foramen. This structural similarity indicates that a tarsus similar to that seen in *Proterosuchus* was present in the ancestor of *Erythrosuchus*, and thus that the proterosuchian tarsus is not a peculiarity of *Proterosuchus*.

A second line of evidence that the proterosuchian tarsus is primitive for archosaurs is provided by the wide distribution of this kind of tarsus in diapsids. As shown above, the tarsus of *Noteosuchus*, *Prolacerta* and *Trilophosaurus* are all strikingly similar in their basic construction. The suggestion of a relationship between rhynchosaurids and *Proterosuchus* was based entirely on the similarities of the tarsus. However, these similarities are no more fundamental than the similarity between the tarsus of *Proterosuchus* and *Prolacerta* or *Proterosuchus* and *Trilophosaurus*. Thus the tarsus does not indicate that *Proterosuchus* is related to rhynchosaurs more closely than to any other diapsid group. If the similarities in the structure of the tarsus have phylogenetic significance, it is that archosaurs, trilophosaurids, proterosuchians and rhynchosaurids form a natural group the ancestral member of which had already developed the characteristic tarsus. This being the case, any primitive archosaurs would have had a proterosuchian tarsus.

The tarsus of Proterosuchus was not available for study but, in view of the structural similarity of the tarsus of Proterosuchus and Noteosuchus, it must have been similar to Noteosuchus in its mechanics. If these groups had evolved their tarsi separately, the course of evolution of the tarsus must have been identical.

2. STRUCTURE, MECHANICS AND ORIGIN OF THE CROCODILOID TARSUS

The crocodiloid tarsus has long been recognized to be peculiar among extant reptiles. Despite this, its evolutionary history is, at present, poorly understood. Schaeffer (1941) assumed that it was present only in crocodiles. He interpreted the tarsus of the early crocodile Protosuchus and the pseudosuchian Aetosaurus, then only poorly known, as having mesotarsal ankle joints. Krebs (1963) later demonstrated that the crocodiloid tarsus was widespread in pseudosuchians. He suggested that the crocodiloid tarsus developed early in the history of pseudosuchians and was retained without much modification in crocodiles. This suggestion was later supported by Walker (1970) who showed that a group of pseudosuchians that are closely related to crocodiles, the Pedeticosauridae (= the Sphenosuchidae of Romer 1972a),has a crocodiloid tarsus. A further complicating factor in the history of the crocodiloid tarsus was introduced by Bonaparte (1971) who showed that two distinct types of crocodiloid tarsi can be recognized. In crocodiles and most pseudosuchians, a peg on the astragalus fits in a socket on the calcaneum (the crocodile-normal condition). In some ornithosuchids and in Euparkeria, the calcaneum has a peg that fits in a socket on the astragalus (the crocodile-reverse condition).

While a number of suggestions about the locomotor adaptations associated with the development of the crocodiloid tarsus have been made (Charig 1972; Welles and Long 1974), the structural changes that occurred during the origin of the crocodiloid tarsus and the mechanical and adaptive significance of these changes are not known. This is not surprising since, at present, a number of aspects concerning the functioning of the tarsus in extant crocodiles remain unknown. The basic mechanics of the ankle joint is well understood through the work of Rable (1910) and Schaeffer (1941), but the functioning of the remaining joints of the pes are not known. Rotation of the pes relative to the crus has been assumed to be an important aspect of the step cycle in crocodiles (Welles and Long 1974), but no study of locomotion has been undertaken to determine the kinds, amounts or relative time of occurrence of these movements or the joints at which these movements occur. In addition, the mechanical significance of some aspects of the structure of the calcaneal tuber and the relationships of the muscles to the tuber remain unexplained. Thus, before considering the evolution of the crocodiloid tarsus, the mechanics of this kind of tarsus as seen in Caiman sclerops were examined in detail. The structure of the tarsus in Caiman is similar to that of the alligator as described by Schaeffer (1941), so the functioning of the tarsus in the caiman can be considered general for crocodilians.

Materials and Methods

As in any functional analysis of a structural complex, both behavioural and structural information are necessary for the analysis of the crocodile tarsus. The behavioural information necessary in this case is the pattern of movements of the pelvic limb segments occurring during locomotion, that is, the pelvic step cycle, and the postures assumed by the pelvic limb during various non-locomotory activities. The information about the movements was obtained through cineradiography and high speed cinematography. The methods of filming and analysis of the films were the same as those used in studying locomotion in the lizard described previously.

The structural information was obtained through dissection of caimans preserved in formaldehyde. Manipulation of ligament preparations indicated the amount of movement possible at the various joints and the roles of the ligaments in limiting these movements. Manipulation of the foot in a live caiman confirmed that the total amount of movement of the pes relative to the crus possible was not significantly different in the ligament preparation.

The Pelvic Step Cycle of the *Caiman*

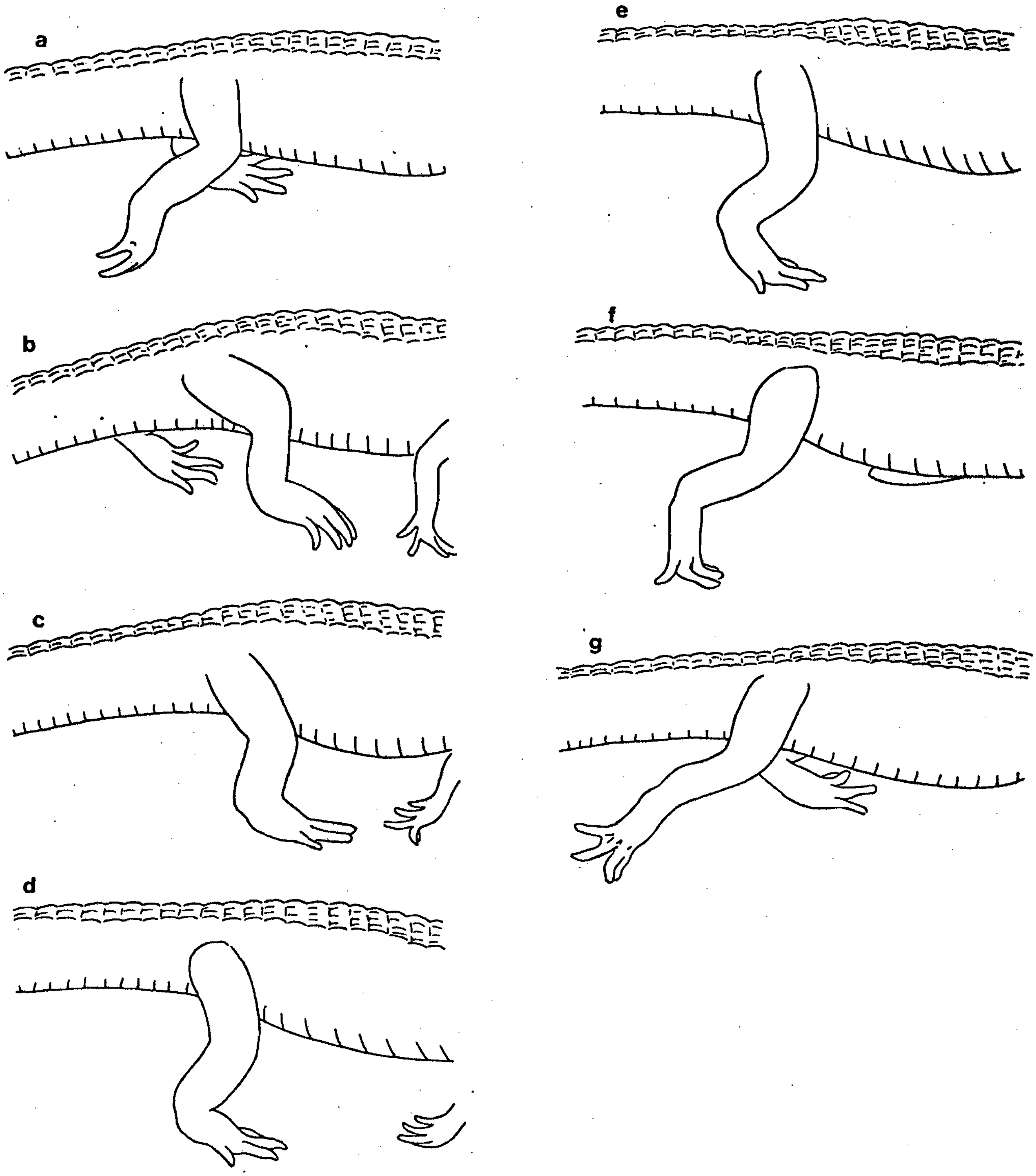
Crocodiles are unusual for tetrapods in that they are able to employ two fundamentally different step cycles. As has long been recognized, crocodiles are able to use a pattern of limb movements similar to that of mammals. This is seen in its extreme form in the high walk, a pattern of locomotion characterized by Cott as one in which "the animal moves like a leopard, the legs swinging beneath the body and so carrying the belly high off the ground. The sacrum is held higher than the shoulder and the back is arched, only the lower surface of the tail tip is trailing" (Cott 1962, p. 230). In addition, they are able to use a more sprawling pattern in which the body is held closer to the ground and the distal end of the femur moves in a plane closer to the horizontal. This step cycle was not reported by Cott (1962) but in the captive caimans used in this study, it was seen when the animals are moving only a few strides, when walking along the bottom of the tank with the belly supported by water, and occasionally a few steps of this step cycle were used at the end of a series in which the high walk was used. Also, Zug's (1974) illustrations of galloping in a *Crocodylus porosus* shows that the sprawling step cycle is used in this gait. Both the high walk and the more sprawling step cycle were filmed during the course of this investigation, giving a detailed understanding of these step cycles.

A. The high walk

In the step cycle used in the high walk, the most prominent movements of the pelvic limb segments are flexion and extension of one segment relative to another. At the beginning of the propulsive phase (Fig. 41c), the femur is directed anteroventrally with the knee depressed about 20°-30° below the horizontal; the crus slopes anteriorly with the angle of the knee measured posteriorly being about 135°; the pes is digitigrade with the heel raised off the substrate about 10°. The initial movements are a retraction of the femur, flexion of the ankle joint, and extension of the metatarsal-phalangeal joints (Fig. 41c-d). Extension of the metatarsal-phalangeal joints usually results in the heel being lowered to touch the substrate, although when moving rapidly, the animal remains digitigrade. Initially, no movement occurs at the knee, although a slight flexion of this joint occurs as the hip approaches the level of the heel. Plantarflexion of the metatarsus is begun when the hip passes over the ankle. During the initial portion of this plantarflexion as the hip moves from the level of the ankle towards the metatarsal-phalangeal joints, the angle of the ankle remains at about 75°, the femur, crus and metatarsus moving as a unit (Fig. 41d-e). Further retraction of the femur is accompanied by an extension of both the knee and ankle joints so that at the end of the propulsive phase, the angle at the knee is about 145° and the angle of the ankle is about 127° (Fig. 41g).

In addition to these flexion-extension movements, rotation and

Figure 41. The high walk of *Caiman sclerops*, lateral view. Made by tracing projections of every fifth frame of a sequence 35 frames long filmed at 62 frames a second.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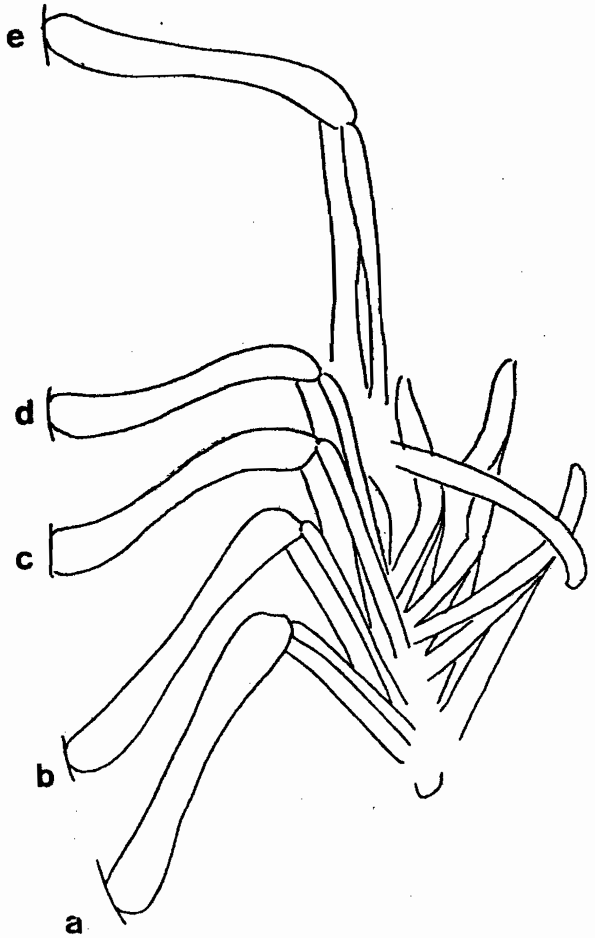
and abduction-adduction movements of the limb segments are important in the step cycle. During the initial portion of the propulsive phase, as the hip moves towards the heel, retraction of the femur is accompanied by an abduction, increasing the angle between the femur and a parasagittal plane passing through the hip from about 10° at the beginning of the propulsive phase to about 30° when the femur is normal to the body (Fig. 42a-c). A simultaneous lateral bending of the vertebral column results in the hip moving away from the pes that is in contact with the ground, rather than the knee moving laterally relative to the heel. As the femur retracts posterior to the vertical plane normal to the body, the hip is moved towards the pes, and the crus is abducted, the knee moving slightly laterally so that the crus comes to lie in a parasagittal plane (Fig. 42c-e). At the end of the propulsive phase, the crus and metatarsus rotate laterally through an arc of about 15° (Fig. 41f-g), although they continue to face ventrally (Fig. 42d), rather than directly laterally as in Iguana. The weight is shifted to the medial digits and the toes roll off the substrate with the last portion of the foot to contact the substrate being the terminal phalanx of the first and second toes.

The restorative phase, as described by Schaeffer (1941) is like that of mammals in being divided into an initial portion of flexion of the joints, lifting the pes and moving it forwards, followed by a period of extension of the joints, lowering the foot and bringing the toes into contact with the substrate.

Figure 42. The high walk of Caiman sclerops, dorsal view. Made by tracing and superimposing successive x-rays in a squence filmed at six frames a second.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B. The sprawling step cycle

In the sprawling step cycle, the pes is initially digitigrade with the crus sloping laterally slightly (Figs. 43b, 44b). The initial movements are a retraction of the femur, flexion of the knee, flexion of the ankle, and extension of the metatarsal-phalangeal joints (Fig. 44b-c). Once the heel contacts the substrate, the pes remains stationary until the hip moves over the ankle (Figs. 43b-d, 44b-d). During this time, the femur retracts, the knee flexes, and the ankle flexes. As the hip passes over the ankle, plantarflexion of the metatarsus is begun. The ankle remains stationary until the hip passes over the toes, at which time extension of both the ankle and the knee is begun (Figs. 43d-g, 44d-g).

Thus, with the exception of the greater amount of flexion and extension occurring at the knee, the pattern of flexion-extension movements is similar to that of the high walk. However, differences are seen in the associated rotational and abduction-adduction movements. A major difference is the increased amount of abduction of the femur that occurs as it retracts in the sprawling step cycle. When the femur is normal to the body, the angle between it and a parasagittal plane is about 60° (Figs. 54e, 44e). This abducts the crus, moving the knee laterally relative to the pes. Usually an associated lateral rotation of the crus does not occur, the extensor surface of the crus continues to face ventrally and the pes remains anteriorly directed as the femur retracts towards a vertical plane

Figure 43. The sprawling step cycle of Caiman sclerops, dorsal view. Made by tracing projections of every sixth frame in a sequence of 48 frames long.

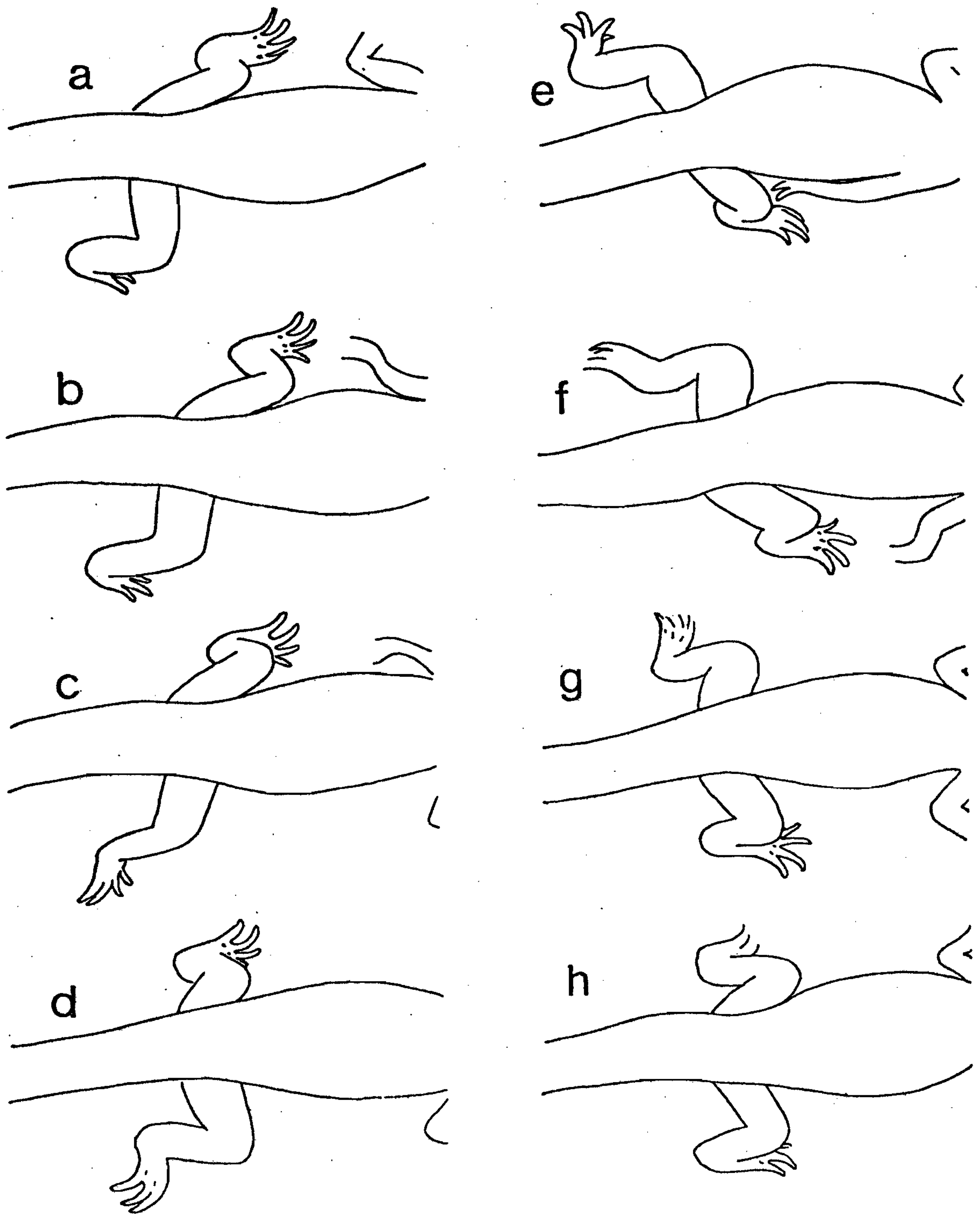
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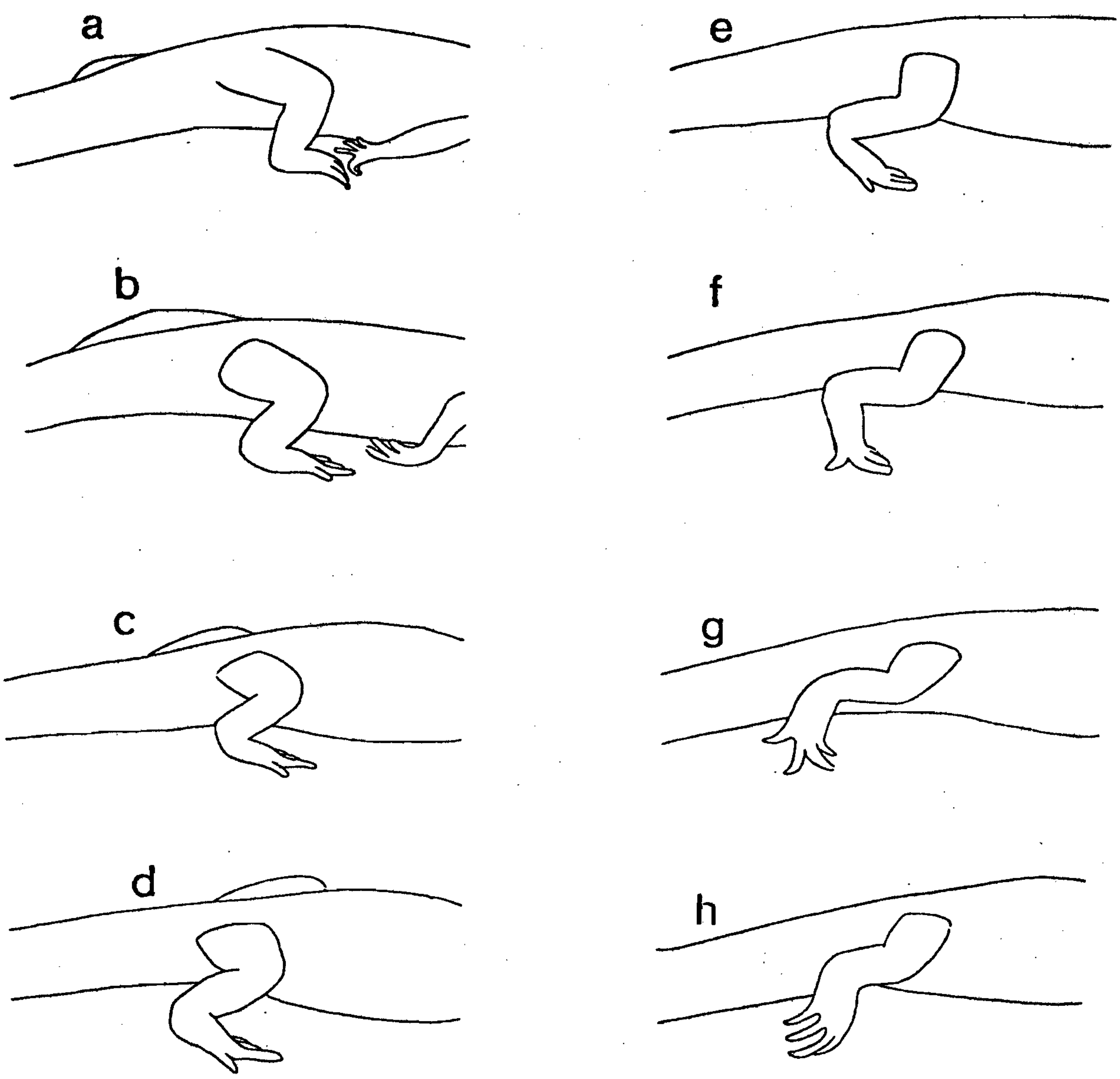
Figure 44. The sprawling step cycle of Caiman sclerops, lateral view. Made by tracing projections of every sixth frame in a sequence 48 frames long.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normal to the body and passing through the hip (Fig. 44c-f). When this is the case, the initial plantarflexion of the metatarsus occurs around an axis passing through the distal ends of the first three metatarsals and perpendicular to the body and is not accompanied by a rotation of the metatarsus around its long axis. These movements result in the limb assuming the characteristic posture seen in Figures 44f and 45, in which the femur is directed laterally with its extensor surface facing anteriorly, the crus is directed posteriorly with its extensor surface facing ventrolaterally, and the metatarsus is about vertical with its extensor surface facing anteriorly. Further retraction of the femur is accompanied by a lateral rotation of the crus and an abduction of the metatarsus so that the extensor surfaces of the femur, crus and metatarsus face laterally (Figs. 43F-h, 44f-h).

In some step cycles, as in the sequence illustrated by Schaeffer (1941), retraction of the femur is accompanied by a rotation of the crus so that it faces somewhat laterally when the crus is about perpendicular to the body (Schaeffer 1941, Fig. 17, I). In these sequences, the metatarsus abducts as the crus rotates so that the long axis is directed 20°-30° laterally at the end of the propulsive phase. When this is the case, plantarflexion of the metatarsus is accompanied by a medial rotation so that its extensor surface continues to face anteriorly.

The restorative phase in the sprawling step cycle is similar to that in the high walk in being divided into a period of flexion of the knee and ankle followed by a period of extension of these joints. However, the amount of abduction of the femur that accompanies retraction is greater. Also, in some sequences, the metatarsus undergoes a large amount of lateral rotation so that midway through the restorative phase, its extensor surface faces dorsally and the metatarsus lies in the same plane as the femur and crus (Fig. 43b-d, left foot). A lateral rotation of the femur at the end of the restorative phase brings the crus into a vertical position.

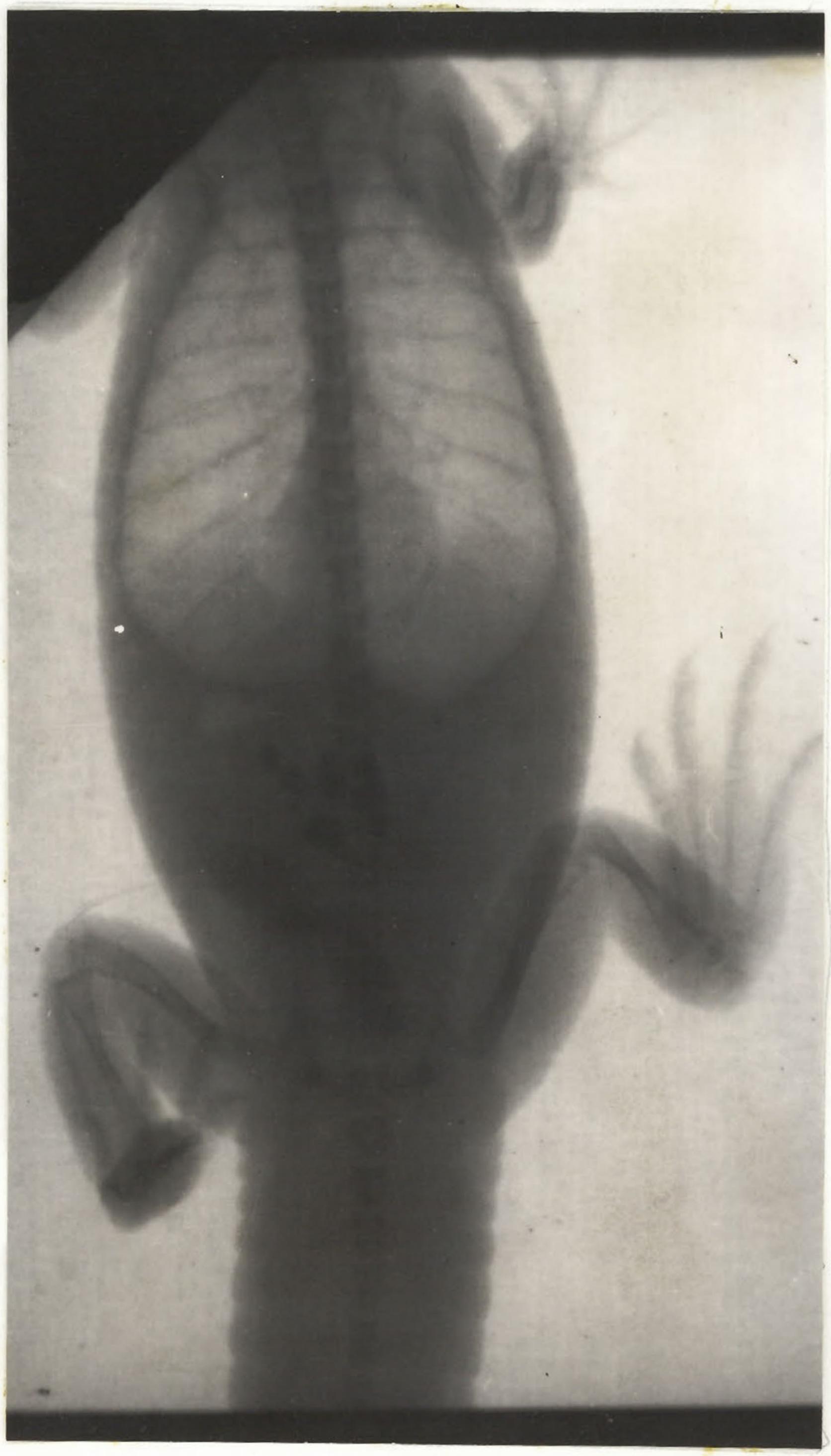
Comparison

The two step cycles described above as the high walk and the sprawling step cycle are two extremes in what is probably a continuous range of variation. The step cycle described by Schaeffer (1941) is in many ways an intermediate pattern. In the posture of the body and the predominance of flexion-extension movements, the step cycle is like the high walk described above. However, in the relatively large amount of abduction of the femur seen during retraction (Schaeffer 1941, Fig. 17, G-I), in the lateral rotation of the crus and the abduction of the metatarsus accompanying retraction of the femur, and in the lateral orientation of the crus and metatarsus at the end of the propulsive phase, this sequence approaches the sprawling step cycle.

The extremes of the high walk and the sprawling step cycle differ primarily in the amount of rotation of the metatarsus relative to the crus (the same movement as abduction of the crus relative to a stationary metatarsus), and the amount of rotation of the crus relative to the femur (the same movement as abduction of the femur relative to a stationary crus when the two limb segments are at right angles to one another), that occurs during the two step cycles. In the high walk, only a small amount of abduction of the crus relative to the metatarsus occurs. Some crural abduction is seen at the end of the propulsive phase, but the pes is digitigrade at this time so the crus and metatarsus are probably abducting as a unit. In the sprawing step cycle, the crus abducts about 20° as the femur retracts towards a vertical plane normal to the body (Fig. 43b-c). The metatarsus is stationary during this time, so the crus and metatarsus are not moving as a unit. Up to about 70° rotation of the crus relative to the metatarsus is occasionally seen in the restorative phase of this step cycle.

In the high walk, the amount of abduction of the femur that occurs as the femur retracts is about 20°; in the sprawling step cycle, this is increased to about 50°. This increased abduction does not necessarily result in a rotation of the crus as would be expected if the knee were a simple hinge-like joint. X-rays of a caiman in which the crus and metatarsus have assumed the characteristic posture seen in Fig. 44f, confirm that the abduction and retraction of the femur leading to the assumption of this posture is not associated with a lateral rotation of the crus (Fig. 45). Thus in the step cycles in which the crus does not rotate laterally as the femur retracts, abduction of the

Figure 45. X-ray of *Caiman sclerops*. Note the posture of the left pelvic limb.



femur is a result of rotation at the knee. In those sequences in which the crus rotates laterally as the femur retracts, a simultaneous abduction of the metatarsus and pes is seen, so that the crus and metatarsus are moving as a unit.

Thus the ability to use both a sprawling and erect step cycle is allowed by the large amount of rotation of the crus relative to the femur and rotation of the metatarsus relative to the crus that are possible as independent movements potentially accompanying retraction of the femur but not obligatorily doing so. Rotation of the crus relative to the metatarsus does not accompany retraction of the femur in the sprawling step cycle as has been assumed previously (e.g. Welles and Long 1976). In the absence of this movement and especially in the utilization of rotation at the knee to prevent rotation of the crus, the sprawling step cycle of the caiman is unlike that of the lizard These differences indicate that the sprawling step cycle of crocodiles was not retained unchanged from the primitive reptilian condition. It may be that the ability to use a sprawling step cycle is a specialization of crocodiles associated with their aquatic mode of life, and this was not widespread in Triassic thecodonts.

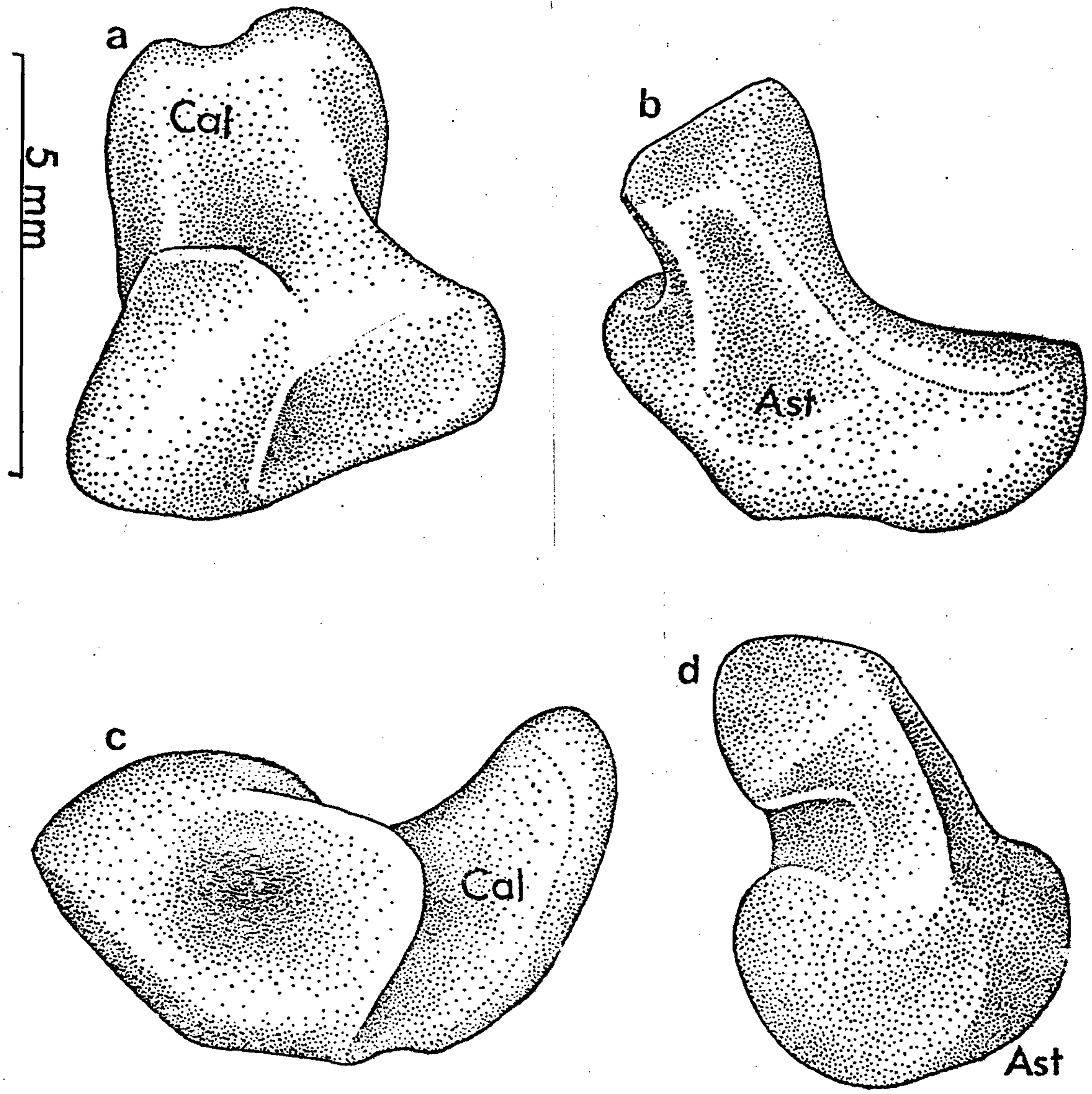
With this understanding of the step cycle in the caiman and the variation possible in the step cycle, the structure and mechanics of the tarsus and metatarsus will now be considered.

Structure of the Tarsus in Caiman sclerops

Five elements are present in the tarsus: the astragalus, calcaneum, and second to fourth distal tarsals.

The astragalus (Figs. 46b, d; 47b-d), probably includes both the astragalus and centrale of primitive diapsids (Rabl 1910; Steiner 1934). It supports the tibia and fibula proximally by articular surfaces that nearly completely cover the proximal edge of the bone. The tibia articular surface is a strap-shaped area located along the anterior margin of the proximal end of the bone. A nonarticular area is present posterior to this with a number of ligaments connecting the tibia and astragalus lying in this space (the posterior tibial-astragalar ligaments A-D, described below). The fibular articular surface is a slightly concave medially facing surface that receives the convex medial portion of the distal articular surface of the fibula. Anteriorly, the astragalus has a strongly convex surface that articulates with the proximal edge of the first two metatarsals and the medial edge of the second and third distal tarsals. Above this, the anterior face of the astragalus is formed by a concave area covered by finished bone. Posteriorly, a proximo-distally oriented groove is present in which lies the tendon of the flexor digitorium longus. Medially, the characteristic articular surface for the calcaneum is present. This is divisible into two separate areas. The ventral area has the shape of a portion of a cone, its apex being at the tip of the lateral peg. Dorsal to this, a notch in the lateral edge of the astragalus supports a

Figure 46. Astragalus and calcaneum of Caiman sclerops. a) calcaneum in dorsal view; b) astragalus in anterior view; c) calcaneum in medial view, showing astragalar articular surface; d) astragalus in lateral view, showing calcaneal articular surface.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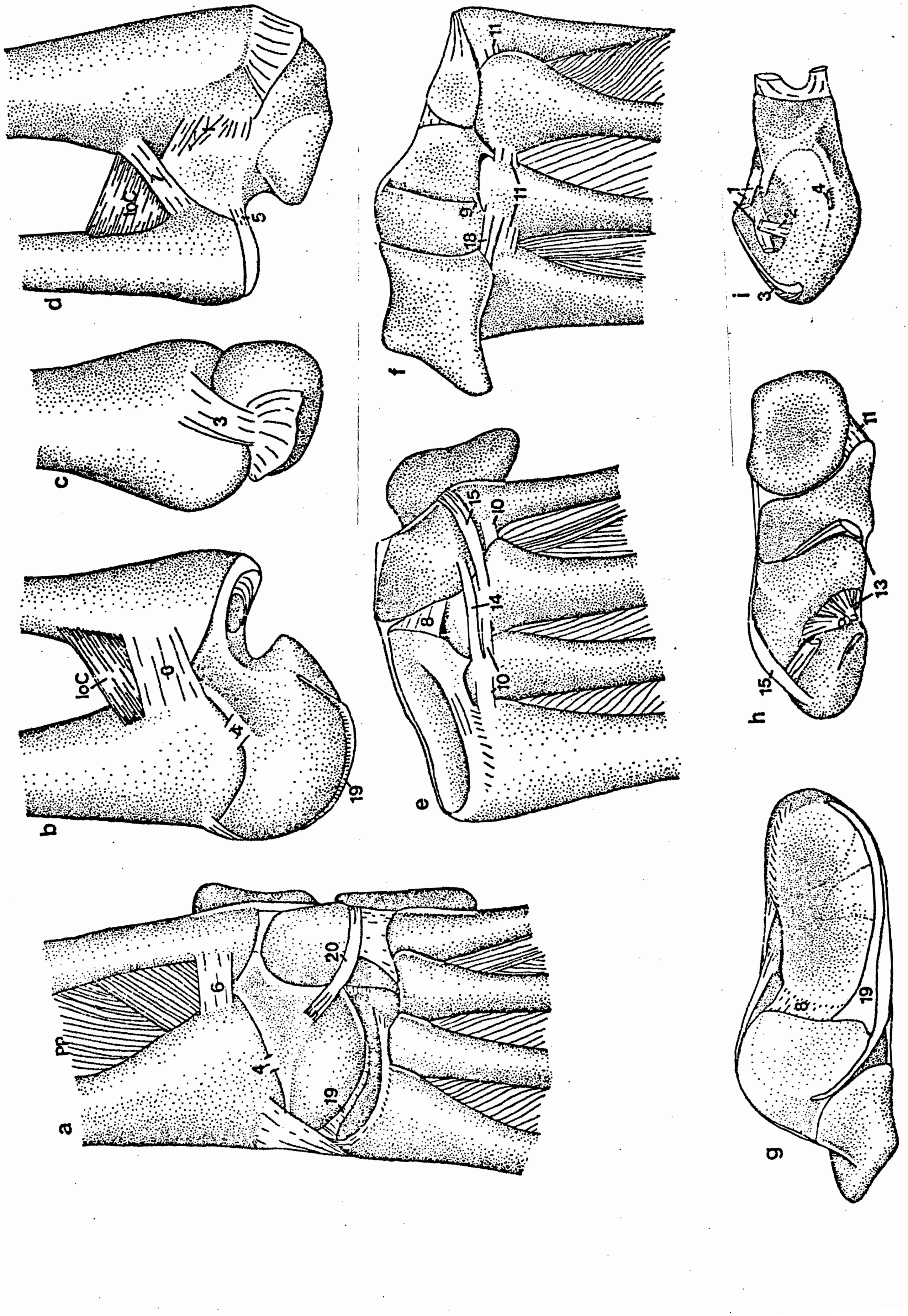
band-shaped articular surface.

The calcaneum (Fig. 46a-c) articulates with the fibula proximally, the astragalus medially, and the fourth distal tarsal distally. The astragalar articular surface consists of two portions, a dorsal surface that has the shape of a portion of a wheel, and a posteroventral surface that is supported by a medial flange from the calcaneum. The medial edge of the wheel-shaped articular surface fits in the notch on the lateral edge of the astragalus. The lateral portion of this articular surface supports the fibula. The fibular and astragalar surfaces are differentiated by a slight change in the curvature of the surface. The medial flange of the calcaneum underlies the astragalus and articulates with the cone-shaped articular surface. Posteriorly, the calcaneum forms a strong tuber. The distal end of this tuber is expanded and has a dorsoventrally oriented groove on its posterior surface. The tendon of the gastrocnemus (femoral head), which passes over the calcaneal tuber to insert on the fifth metatarsal, lies in this groove.

The distal tarsals (Fig. 47f-g) are wedge-shaped, with their ventral surfaces being slightly larger than their dorsal surfaces. They increase in size from the second, a cartilaginous element only half the height of the second metatarsal, to the fourth. The second distal tarsal is supported entirely by the second metatarsal. The third articulates with both the second and third metatarsals, and the fourth articulates with the third, fourth and fifth metatarsals.

The first four metatarsals are elongate, slender elements

Figure 47. The ligaments of the tarsus and metatarsus of *Caiman sclerops*. a) articulated tarsus in dorsal view; b-d) articulated crus and astragalus in b) dorsal; c) medial; and d) ventral views; e-g) articulated distal tarsals and metatarsus in e) dorsal; f) ventral; and g) proximal views; h) metatarsus in proximal view, distal tarsals removed; i) astragalus in proximal view. Numbers refer to ligaments described in the text.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(Figs. 47e, f, h; 53). The first and fourth are subequal in length, as are the second and third. Their proximal articular surfaces are ovular and are tilted so that each metatarsal overlies the next lateral metatarsal. This is particularly strong in the case of the first two metatarsals, where the first is almost completely supported ventrally by the second.

The fifth metatarsal (Fig. 47e-g) is a splint-like bone articulating with the lateroventral side of the fourth distal tarsal. Although it does not show the plantar tubercles characteristic of the hooked fifth metatarsal of earlier archosaurs, its articulation with the lateral side of the fourth distal tarsal and the medial, rather than proximal, position of the proximal articular surface suggests that it developed from a hooked fifth metatarsal.

Only four digits are present, the fifth having been lost. The phalangeal formula of these is that characteristic of primitive reptiles, 2, 3, 4, 5, but the phalanges of the fourth digit have been reduced so this digit is shorter than the third.

A complex system of ligaments is present connecting the elements of the tarsus. To facilitate description of these, each will be given a name derived from its position and insertions, and the attachments and form of each ligament will be described separately. The numbers in the following list are used to identify the ligaments in Figures 47 and 48.

1. Posterior tibial astragalar ligaments A-C (Fig. 41, D, I): three ligaments lying between the distal end of the tibia and the

proximal end of the astragalus that extend laterally from the tibia to the astragalus.

2. Posterior tibial astragalar ligament D (Fig. 47i): a ligament lying between the tibia and astragalus that extends anteriorly from its origin on the tibia to its insertion on the astragalus.
3. Lateral tibial astragalar ligament (Fig. 47c): a fan-shaped ligament extending from the medial and anterior surface of the tibia to its insertion on the medial tip of the astragalus.
4. Anterior tibial astragalar ligament (Fig. 47, B, I): a narrow ligament sloping laterally from the tibia to insert on the proximal edge of the astragalus just lateral to the metatarsal articular surface.
5. Fibular astragalar ligament (Fig. 47, D): a small ligament extending between the fibula and astragalus at the posterior end of their articulation.
6. Inferior anterior tibio-fibular ligament (Fig. 47a, b): a broad ligament extending nearly directly transversely between the anterior face of the tibia and fibula.
7. Inferior posterior tibio-fibular ligament (Fig. 47d): a narrow ligament originating on the fibula and sloping proximally and anteriorly to insert on the tibia.
8. Anterior distal tarsal ligament (Fig. 47, E, G): a broad short ligament, probably simply a thickened area of the joint capsule, extending transversely between the anterior face of the third

and fourth distal tarsals.

9. Posterior distal tarsal ligament (Fig. 47, F): a short transversely oriented ligament extending between the disto-inferior corner of the third and fourth distal tarsals.

10. Proximal dorsal intermetatarsal ligaments I-IV (Fig. 47, E): a series of transversely oriented ligaments extending between the heads of adjacent metatarsals.

11. Proximal ventral intermetatarsal ligaments I-IV (Fig. 47, F, H): a series of ligaments consisting of short fibres extending from the ventral surface of each of the first three metatarsals to the dorsal surface of the underlying portion of the next lateral metatarsal.

12. Interdigital tendons I-III (Fig. 49, F): long tendons originating on the lateral side of each of the first three metatarsals and extending distally and ventrally to insert on the ventral side of the next lateral metatarsal.

13. Internal metatarsal-distal tarsal ligaments (Fig. 47h): a series of ligaments originating on the medial side of each of the second and third metatarsals and sloping distally to insert on the ventral extreme of the proximal end of the third and fourth metatarsals.

14. Second metatarsal-fourth distal tarsal ligament (Fig. 47e): a narrow ligament extending from the proximo-lateral tip of the second metatarsal to the fourth distal tarsal.

15. Fifth metatarsal-third metatarsal ligament (Fig. 47e): a narrow ligament extending from the dorsal edge of the fifth metatarsal over the dorsal edge of the fourth metatarsal to the proximolateral corner of the third metatarsal.

16. Fifth metatarsal-third distal tarsal ligament (Fig. 48b): a ventral ligament that extends medially from the fifth metatarsal to the ventral surface of the third distal tarsal.

17. Fifth metatarsal-fourth metatarsal ligament, not illustrated: a ligament extending from the anterior tip of the fifth metatarsal to the fourth metatarsal.

18. Fifth metatarsal-third metatarsal ligament (Fig. 47f): a ventral ligament extending from the distal tip of the articular surface of the fifth metatarsal to the ventral surface of the head of the third metatarsal.

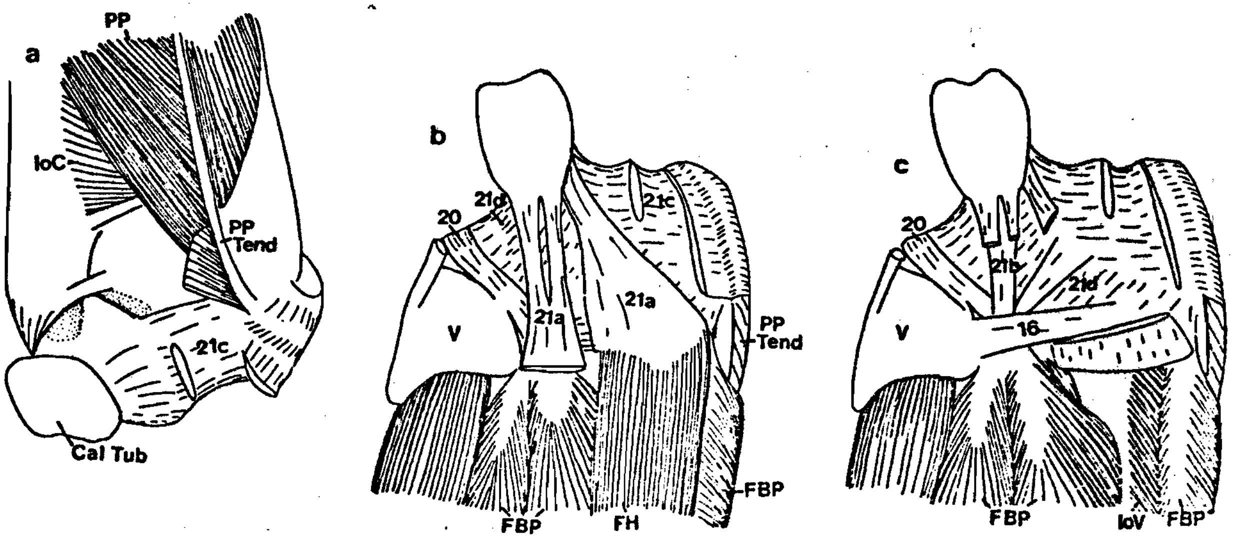
19. Astragalar-metatarsal ligament (Fig. 47a, b): a short thick ligament originating on the entire distal edge of the metatarsus just distal to the metatarsal articular surface and from the medial and distal tip of the calcaneum and inserting on the ventral edge of the distal tarsals and first metatarsal.

20. Fifth metatarsal-astragalar ligament (Fig 47a; 48b, d): a strong ligament originating from the ventral surface of the fourth distal tarsal and the proximal edge of the fifth metatarsal, and passing dorsally over the articulation between the calcaneum and fourth distal tarsal to insert on the anterior face of the

astragalus. It is braced on its internal side by a thin layer of cartilage that fits between the calcaneum and fourth distal tarsal when their opposing articular surfaces are appressed against one another. A small tie tendon connects this ligament to the tip of the calcaneum so when the calcaneum moves away from the fourth distal tarsal, this ligament moves with the calcaneum.

21. Tarsal aponeurosis (Figs. 48a-c; 49c-f): a complex ligamentous sheath that covers the ventral surface of the tarsus, connecting the various elements and serving as a site of origin of certain of the short pedal flexors of the pes. This tendinous sheath is divided into a number of layers as follows: a, a superficial layer connecting the calcaneum to the distal tarsals. The fibres of this layer originate on the distal edge of the calcaneal tuber and extend distally and medially to the distal edge of the tarsus where they insert on the proximal edge of the first two metatarsals and the ventral surface of the distal tarsals. Medially, the flexor hallucis and laterally, the plantar head of the flexor digitorum longus originates from this layer. b, a deep layer connecting the calcaneum to the fourth distal tarsal. The fibres of this layer are organized into a narrow band that originates from the distal edge of the calcaneum and inserts on the ventral surface of the fourth distal tarsal. The flexor digitorum brevis profundis of metatarsals

Figure 48. The tarsal aponeurosis of Caiman sclerops. Articulated crus and pes with ankle joints flexed in a) posterior; b, c) ventral views. Numbers refer to ligaments described in the text. For other abbreviations, see list of abbreviations.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21c
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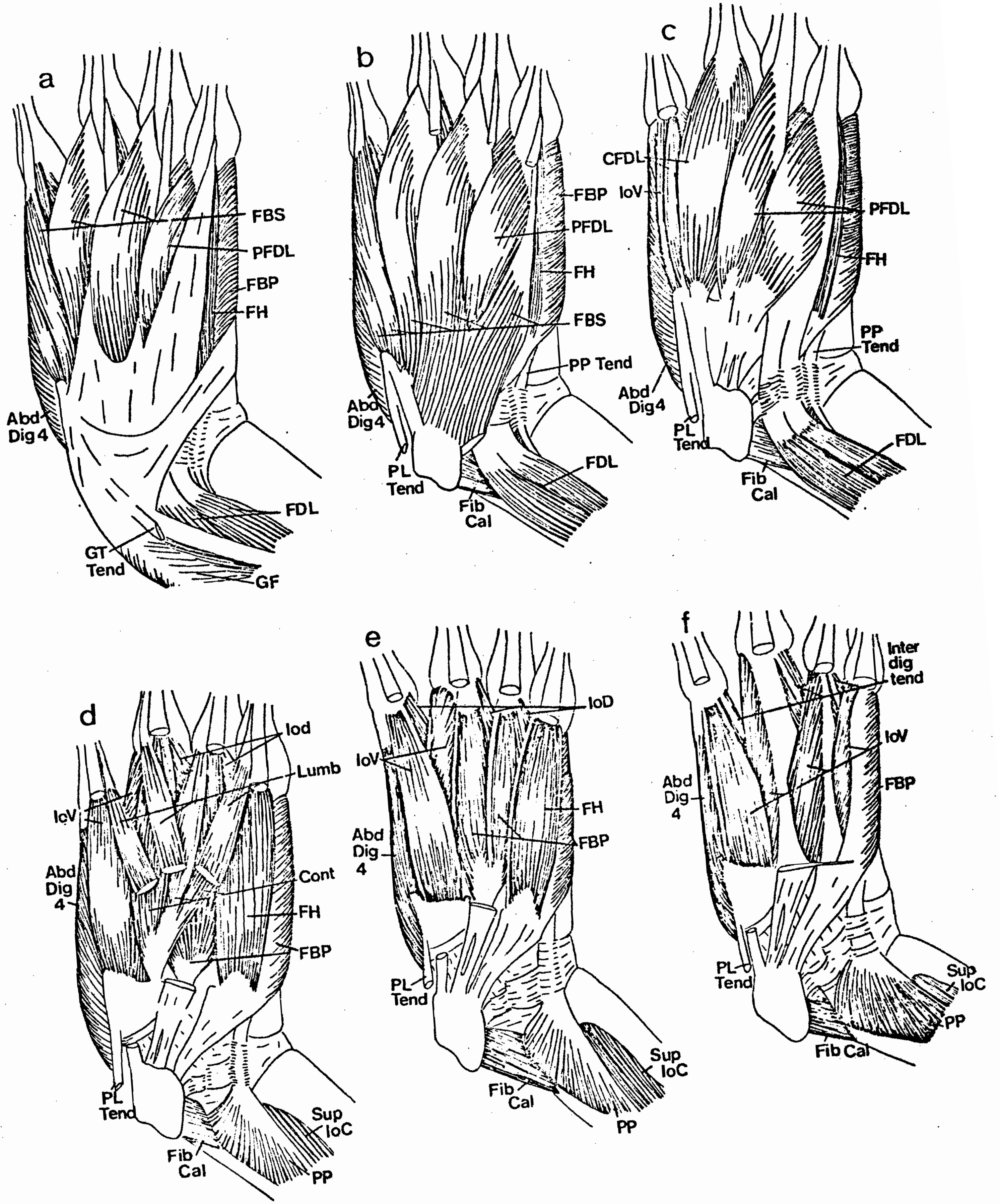
FBP
FH
c
20
21b
21d
V
16
FBP
IoV
FBP

Figure 49. The short pedal flexors of *Caiman sclerops*. a) the superficial muscles of the pes, gastrocnemius (tibial head) and tibialus anterior removed; b) gastrocnemius (femoral head), associated tendons and peroneus longus removed; c) flexor brevis superficialus removed; d) flexor digitorum longus, plantar head of flexor digitorum longus, and calcaneal head of flexor digitorum longus removed; e) lumbricales and contrahenes removed; f) flexor brevis profundus of second and third metatarsals and flexor haluxis removed. For abbreviations, see list of abbreviations.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PL Tend
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two and three originates from this layer. c, a proximal area of transversely oriented fibres extending between the astragalus and calcaneum; and d, a distal area of obliquely oriented fibres extending from the proximal area to the distal tarsals.

In addition to these ligaments, some areas of the joint capsules are thickened and play a role in limiting the movements at the joints, but are not differentiated to form distinct ligaments. These include the lateral portion of the joint capsule connecting the fibula to the calcaneum (Fig. 47a), and the joint capsule connecting the calcaneum to the fourth distal tarsal (Fig. 47a).

Also a number of muscles are present which contribute to the stability of the joints. The inferior interosseous cruris muscle (Fig. 47a, b, d) is a small triangular muscle originating on the medial face of the fibula and sloping distally to insert on the opposing face of the tibia. The interosseous muscles between the four metatarsals are separated into a dorsal and a ventral layer (Fig. 49f). The muscles of the dorsal layer originate on the lateral side of each of the first three metatarsals and slope distally and medially to insert on the medial side of the next lateral metatarsal. The origin of the first interosseous muscle extends along the entire length of the shaft of the first metatarsal. The origin of the second interosseous muscle is restricted to the proximal third of the second metatarsal, although its insertion extends to the distal end of the third metatarsal. The third interosseous muscle is a narrow band-shaped muscle that originates from a small area on the head of the third metatarsal and inserts on the distal end of the fourth metatarsal. The slope of the interosseous muscles of the ventral layer is opposite that of the dorsal interosseous muscles, but, as in the dorsal layer, a progressive increase in the distance between the origin and insertion of the muscles laterally is seen. Only one interosseous muscle is present between the fourth and fifth metatarsals, this being a strong muscle originating on the anterior surface of the fifth metatarsal and inserting on the lateral surface of the fourth metatarsal.

The origins and insertions of the remaining muscles of the pes were described by Ribbling (1909), so a general description is not necessary here. However, as Ribbling did not illustrate the relations of the muscles to the calcaneal tuber and to the fifth metatarsal, illustrations of the flexor muscles of the pes are included here (Fig. 49). With two exceptions, the divisions of the muscles are the same as in lizards and there is little question about the correct homologies. One of the exceptions is a small muscle extending from the posterior surface of the fibula near its distal end to the dorsal surface of the calcaneal tuber. As a muscle with a similar relationships is not present in lizards, this muscle will simply be termed the fibulocalcaneal muscle. The second muscle of uncertain homology is a large muscle originating on the lateral side of the fifth metatarsal and inserting on a tendon extending down the lateral side of the fourth toe. The development of this muscle was probably associated with loss of the fifth toe. It could have developed from one or more of the small muscles associated with the fifth metatarsal in lizards or from a muscle extending between the fifth metatarsal and fourth metatarsal or digit. As this muscle probably acts to abduct the fourth digit, it will be termed abductor of digit four here.

Mechanics and Function of the Tarsus of *Caiman*

A. The cruro-tarsal joint

The ligaments connecting the tibia and astragalus allow little movement between the two bones. Medial rotation of the tibia is prevented by the medial tibial astragalar ligament and the posterior tibial-astragalar ligaments A-C (Fig. 50a). Lateral rotation is prevented by the anterior astragalar-tibial ligament and the posterior tibial-astragalar ligament D (Fig. 50b).

Since the fibula is connected to the astragalus only by the fibular-astragalar ligament, more movement is possible between the fibula and the astragalus. Rotational movements of the fibula are limited by the inferior tibio-fibular ligaments with medial rotation tightening the anterior and lateral rotation tightening the posterior inferior tibio-fibular ligament. The total amount of rotation possible is about 20°. Flexion of the fibula on the astragalus moves its proximal end anteriorly, tightening the ligaments of the knee. The amount of this movement possible is about 5°.

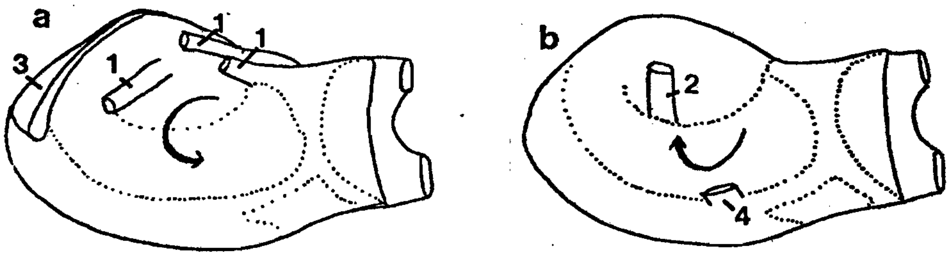
Although the movement between the fibula and astragalus is not

Figure 50. The mechanics of the tibial-astragalar joint.

a) ligaments tightened during lateral rotation of the tibia;

b) ligaments tightened during medial rotation of the tibia.

Numbers refer to ligaments described in the text.


a
1
1
3
1
b
2
4

great, it is of considerable functional importance since, as shown by Haines (1942), rotation at the knee involves an independent movement of the tibia and fibula, the fibula moving with the femur and passing in front of the tibia. Clearly the fibular-astragalar joint serves the function of allowing the independent movement of the tibia and fibula that this requires.

B. The ankle joint

As has long been recognized, the joint passing between the astragalus and calcaneum functions as the ankle joint during locomotion. Movement at this joint is primarily a flexion and extension with, as the joint flexes, the astragalar notch and fibula moving anteriorly over the wheel-shaped articular surface of the calcaneum, the cone-shaped articular surface of the astragalus turning in the socket of the medial edge of the calcaneum and the centre of articulation between the astragalus and distal tarsals moving to the dorsal edge of the articular surface on the astragalus. The maximal amount of this movement that is possible is about 90°, with the joint being maximally extended when the crus forms an angle of about 155° to the metatarsal-calcaneal unit, and maximally flexed when the crus is about 65° to the metatarsus. No rotation is possible at this joint in maximal flexion. Extension of the joint loosens the ligaments so that rotation becomes possible, the amount increasing to about 25° when the joint is maximally extended. The function of this rotational component is not clear -- it cannot be responsible for the rotation of the metatarsus relative to the crus that is seen in the sprawling step cycle since the crus is approximately perpendicular to the metatarsus when these movements occur.

C. The mesotarsal joint

Schaeffer (1941) reported that movement was possible between the calcaneum and fourth distal tarsal. The presence of movement here was confirmed in the ligament preparations and by manipulation of the pes in a live caiman. The calcaneum is strongly attached to the distal tarsals ventrally by the tarsal aponeurosis, but is only connected to the distal tarsals dorsally by the thin joint capsule. This arrangement allows flexion of the calcaneum away from the fourth distal tarsal with the movement occurring around an axis of rotation passing through the ventral corner of their articulation. As this flexion occurs, the astragalus moves with the calcaneum away from its opposing articular surface. This contributes significantly to the total amount of extension of the crus on the metatarsus that is possible, allowing the metatarsus to come into line with the crus. Since the caimans frequently assume postures in which the crus and metatarsus are in line, it is clear that movement at the metatarsal joint is of considerable functional importance.

D. The joints of the metatarsus

No single joint within the distal tarsal-metatarsal unit appears specialized to allow movement in a particular direction. Rather, a small amount of movement in each direction is possible at these joints.

This results in a general flexibility of the metatarsus allowing modifications of its shape to conform to irregularities in the substrate and allowing the toes to be spread apart, increasing the surface area of the foot so the animal is less likely to sink into soft substrate. In addition, movement between the distal tarsals and metatarsals contributes about 30° to the amount of flexion of the crus on the metatarsus, so that in maximal flexion, the angle between the crus and metatarsus is about 35°. Also of major importance is a combination of plantarflexion of each metatarsal relative to its next medial metatarsal. Plantarflexion of the second relative to the first metatarsal is limited to about 10° by the well developed interosseous muscles between the two bones. The successive increase in distance between the origin and insertion of the interosseous muscles laterally allows an increased plantarflexion of the metatarsals laterally. A combination of these movements will rotate the metatarsus laterally nearly 90°, and thus is of major importance in allowing the utilization of the sprawling step cycle. A comparable medial rotation of the metatarsus is not possible.

E. The mechanics of the metatarsus

In general, the mechanics of the metatarsus are like those of mammals (Schaeffer 1941). However, a number of structural details of the pes, including the relationship of the pedal flexors to the calcaneal tuber, the form of the fifth metatarsal, and absence of a longitudinal arch are different from the condition in mammals, suggesting that some aspects of the mechanics of this bone-muscle system are peculiar to crocodiles. The mechanics of the crocodile metatarsus will now be considered to determine the nature of these differences.

The muscles that flex the metatarsus most strongly are the gastrocnemius (femoral head), gastrocnemius (tibial head), peroneus longus, and flexor digitorum longus. The largest of these is the gastrocnemius (femoral head) (Fig. 49a). It originates from the ventral surface of the femur and from a tendon that extends from the ambiens to the proximal end of the calcaneal tuber. Most of its fibres insert on a thick tendon that passes over the calcaneal tuber, lying within the groove on the proximal end of the tuber, and extends across the ventral surface of the pes as a thin aponeurosis that divides to form three tendons, one extending down the ventral surface of each of the first three digits deep to the flexor tendons of those toes. This aponeurosis is braced laterally on the lateral edge of the fifth metatarsal. In addition, the most superficial fibres of the muscle insert on a tendinous sheath that covers the calcaneal tuber and inserts on the lateral edge of the fifth metatarsal and the medial edge of the first metatarsal.

The peroneus longus originates from the lateral side of the fibula along the distal three quarters of its length. It inserts on the superficial tendinous sheath of the gastrocnemius (femoral head) just lateral to the calcaneal tuber (Fig. 49b).

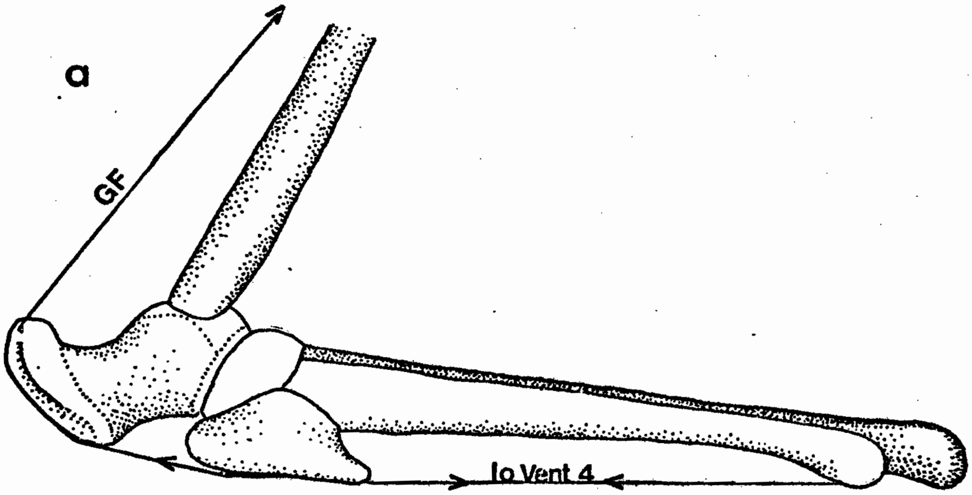
The gastrocnemius (tibial head) originates on the medial edge of the femur. It inserts on the superficial tendinous sheath just medial to the proximal end of the calcaneal tuber. The fibres of the sheath are oriented from this insertion across the tuber to the fifth metatarsal (Fig. 49a).

The flexor digitorum longus lies deep to the gastrocnemeal muscles (Fig. 49c). It is divided into a superficial portion that originates from the ventral surface of the femur, and a deeper portion that has a fleshy origin from the tibia and fibula. At the level of the tarsus, these muscles insert on broad tendons that pass over the tarsus medial to the calcaneal tuber. Just distal to the tarsus, these tendons unite to form a broad plantar aponeurisis which later divides to form the flexor tendons of the three medial toes.

Thus the muscles that use the calcaneal tuber to increase their leverage are the gastrocnemal muscles and the peroneus longus. These do not flex the metatarsus by pulling upwards on the tuber as is the case in mammals. Rather, they use the tuber as a pulley (Fig. 51a). While this does not affect the leverage of the muscles, the power arm of the metatarsal lever is approximated by the length of the tuber in both cases, it does result in differences in the forces acting on the tarsus. The flexor muscles of the crocodile, rather than pulling upwards on the distal end of the tuber, pulls back on the fifth metatarsal and presses against the posterior surface of the calcaneal tuber (Fig. 51a). Thus these muscles do not produce bending movements in the tuber, as is the case in mammals. However, the metatarsus would be subject to such movements if the pedal flexors were acting in isolation. The ventral position of the fifth metatarsal results in the

Figure 51. The mechanics of the crocodile metatarsus.

a) lateral view of the crus and metatarsus of Caiman showing the mechanics of the calcaneal tuber; b) dorsal view of the metatarsus showing the significance of the lateral orientation of the metatarsus. For key to abbreviations, see list of abbreviations.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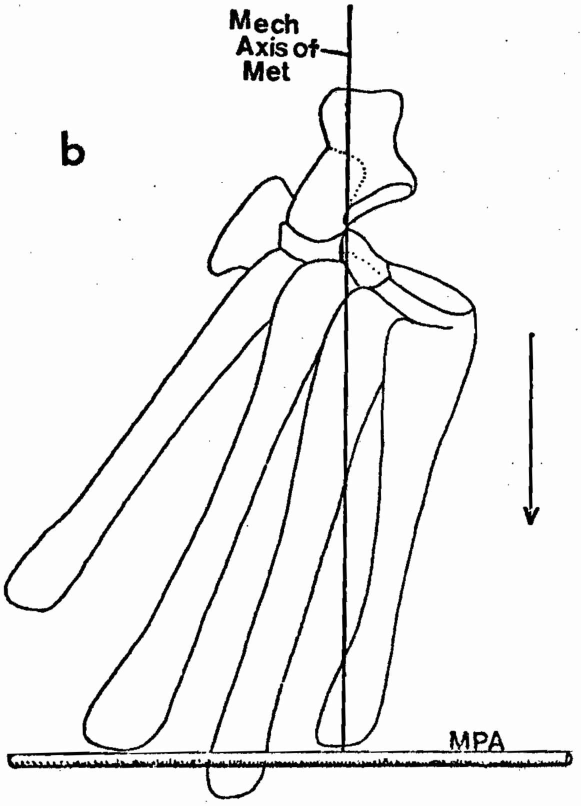
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metatarsus being concave ventrally. Although this is not a longitudinal arch of the kind seen in mammals, it does act as a counterbend that, together with the short pedal flexors such as the interosseous ventralus 4, will minimize the bending movements to which the metatarsus is subjected (Fig. 51a).

The lateral orientation of the calcaneal tuber can be associated with the orientation of the metatarsus during plantarflexion of the pes (Fig. 51b). The metatarsus is rarely oriented with its longest metatarsal (the second) directed anteriorly, and was never seen to be so oriented during pedal plantarflexion. Usually, the first metatarsal is directed most strongly anteriorly, with the second directed about 20° laterally. This slight lateral orientation of the metatarsus results in the calcaneal tuber being posteriorly oriented and about perpendicular to the axis of rotation around which the initial flexion of the metatarsus occurs.

Structure and Mechanics of the Crocodile-normal Tarsus in Pseudosuchians

The crocodile-normal tarsus is present in the pseudosuchian families Rauisuchidae (Krebs 1965, 1973; Sill 1974), Aetosauridae (Sawin 1947; Walker 1961; Bonaparte 1971; Sill 1974), in Gracilosuchus (Bonaparte 1975a), and in Saltoposuchus (von Heune 1921), which may be a member of the Pedeticosauridae (Walker 1970). A crocodile-normal calcaneum from the uppermost Lower or lowermost Middle Triassic was figured by Young (1964, Fig. 60) and attributed to Wangisuchus.

The astragalus in these pseudosuchians, where known, differs from that of crocodiles in having more extensive development of finished bone on its anterior face and in the proportions of the articular surfaces, the metatarsal articular surface being narrower mediolaterally in most genera, as in Gracilosuchus (Fig. 52b). The proportions of the calcaneum also shows some variation; the calcaneal tuber of some genera, especially the aetosaurs, being considerably broader than in crocodiles. However, these differences are relatively minor. In all important details, the astragalus and calcaneum are like those of crocodiles and would have been similar in their basic mechanics.

The major difference of the metatarsus is the presence of a normally developed hooked fifth metatarsal and fifth digit in the pseudosuchians. The presence of a similar condition in Proterosuchus indicates that this is a primitive condition. In aetosaurs, the metatarsus is short and broad and the individual metatarsals do not overlap strongly, so that movement between individual metatarsals could probably occur, resulting in a rotation of the metatarsus as in Caiman. In the rauisuchid Saurosuchus, the metatarsals are more strongly integrated and form a single functional unit. Their proximal ends are tall dorsoventrally and wedge-shaped with their dorsal surface wider than their ventral surface (Sill 1974, his plate 3 B), giving a slight transverse arch to the metatarsus. This construction is similar to Iguana and, as in Iguana, the amount of independent movement of the metatarsals would have been small. Since the rotation of the metatarsus resulting from this movement is an integral part of the sprawling stance, this difference in structure of the metatarsus suggests that rauisuchids were not able to use a crocodile-like sprawling stance.

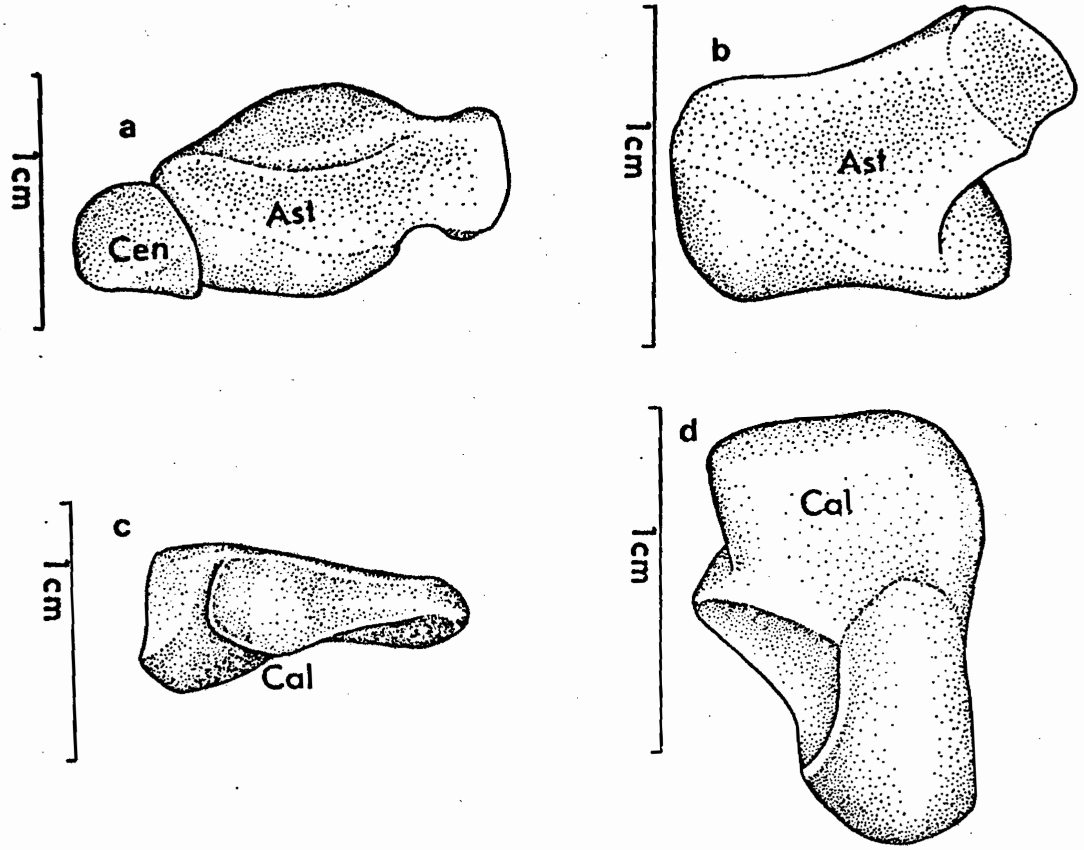
The Origin of the Crocodile-normal Tarsus

A. Structural aspects

If, as argued above, the proterosuchian tarsus is the primitive archosaur condition, then the ultimate ancestor of the crocodile-normal tarsus would be a proterosuchian tarsus. Comparison of these two kinds of tarsi (Fig. 52) allows the major structural changes that occurred during the transition from the proterosuchian to the crocodiloid tarsus to be identified.

The astragalus and centrale of Noteosuchus are comparable to the astragalus of the crocodile-normal tarsus in all features. The major differences are in the structure of the calcaneal articular surface. The condition in Noteosuchus could easily give rise to that of the crocodile-normal tarsus by extension of the proximal portion of the calcaneal articular surface distally along the anterior edge of the perforating foramen to meet the distal portion of the calcaneal articular surface, and an increase in the size and convexity of the distal portion of the calcaneal articular surface. Apart from these changes and the fusion of the astragalus and centrale, the only other changes that would have occurred during the transition from the proterosuchian to crocodiloid astragalus would be in the proportions of

Figure 52. Comparison of the astragalus and calcaneum of *Noteosuchus* and *Gracilosuchus*. a) astragalus and centrale of *Noteosuchus* in anterior view; b) astragalus of *Gracilosuchus* in anterior view; c) calcaneum of *Noteosuchus*, proximal view; c) calcaneum of *Gracilosuchus*, dorsal view.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of the element.

The calcaneum underwent greater structural change. The fundamental modification would be the reorientation of the tuber so that it was directed posteriorly. Given this orientation, the articular surface for the fibula and astragalus would be oriented along the long axis of the bone, rather than transversely across it, and a simple enlargement, together with the extension of the proximal portion of the astragalar articular surface onto the medial edge of the perforating foramen, would give the wheel-shaped articular surface of the calcaneum present in the crocodile-normal tarsus.

The major change in the metatarsus would have been a reorientation so that the long axis was directed anteriorly, rather than anterolaterally. Also, the disparity in lengths of the metatarsals was reduced giving a more rectangular metatarsus, and the entire metatarsus was lengthened.

B. Mechanical aspects

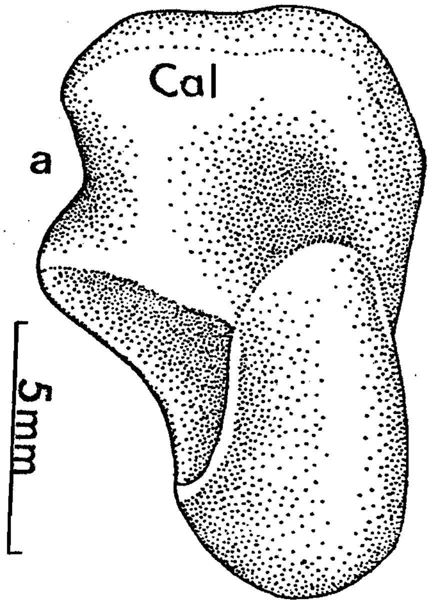
The structural changes in the astragalus and calcaneum that occurred during the origin of the crocodile-normal tarsus reflect an exploitation of movement between the astragalus and calcaneum and a reduction in the amount of movement occurring between the calcaneum and fourth distal tarsal. This represents a shift in the function of the joints. As argued above, movement was possible at both the mesotarsal joint and the joint between the astragalus and calcaneum in the proterosuchian tarsus. Movement between the astragalus and calcaneum allowed the lateral movement of the knee and lateral rotation of the crus that occurs as the femur retracts. In the crocodile-normal tarsus, the joint between the astragalus and calcaneum is the functional ankle joint during locomotion, and it allows the anterior and ventral movement of the knee that occurs as the femur retracts.

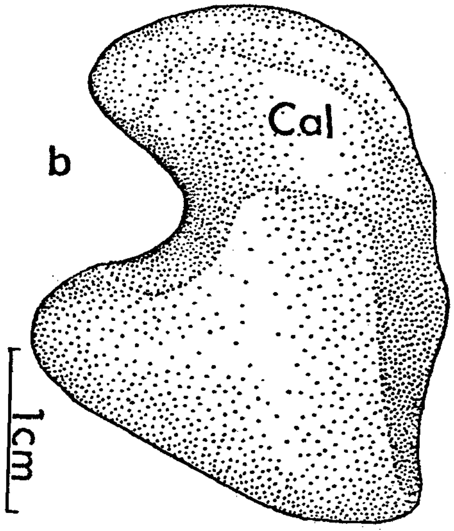
This shift in the function of the joints can be attributed to a fundamental change in the step cycle. Proterosuchus has a primitive plate-like pelvis and a lizard-like femur (Cruickshank 1972) and so probably has a primitive pattern of limb movements in which flexion, extension, rotation and abduction of the crus relative to the metatarsus all occurred during locomotion. Later pseudosuchians have a femur that is like that of crocodiles in having a stronger sigmoidal curvature and a reduced internal trochanter and thus probably utilized a step cycle like that seen in the high walk of crocodiles. One of the major differences between the sprawling step cycle of lizards and the erect step cycle of crocodiles is a reduction in the amount of abduction and rotation of the crus relative to the metatarsus that occurs during locomotion. This change would eliminate the need for the double ankle joint of the proterosuchian tarsus; movement would now occur around a single axis of rotation that was oriented transversely across the tarsus. Clearly the joint between the astragalus and calcaneum was specialized for this. This was probably the case since it enabled the animal to maintain the leverage function of the calcaneal tuber. The rotation of the tuber posteriorly probably mirrored the change in orientation of the metatarsus with the tuber serving as a pulley to increase the leverage of the pedal flexors throughout this transition.

Structure and Origin of the Crocodile-reverse Tarsus

The existence of a tarsus like that of crocodiles in having a moveable peg and socket joint between the astragalus and calcaneum and in having a calcaneal tuber but unlike that of crocodiles in that a "peg" on the calcaneum fits into a "socket" on the astragalus was first recognized in the ornithischid Riojasuchus by Bonaparte (1971). Comparison of the calcaneum of this animal with the corresponding element in Gracilisuchus, where the joint has the crocodile-normal arrangement (Fig. 53) shows that the medial peg of the calcaneum is homologous to the medial edge of the wheel-shaped articular surface of the crocodile-normal tarsus and that the absence of a socket on the medial surface of the calcaneum is a result of the absence of the ventral flange that underlayed the astragalus in the crocodile-normal tarsus. In addition, differences are seen in the shape of the calcaneal tuber. In the tarsus of Riojasuchus, the tuber is narrow medio-laterally and its distal end curves medially. No groove for the tendon of the gastrocnemius (femoral head) is present. The differences in the astragalus of the crocodile-normal and crocodile-reverse tarsus mirror the differences in the calcaneum. With the hypertrophy of the medial edge of the wheel-shaped articular surface, the portion of the astragalus that overlies the calcaneum is elongated and the "notch" that fits over the edge of the wheel-shaped articular surface of the calcaneum in the crocodile-normal

Figure 53. Comparison of the crocodile-normal and the crocodile-reverse calcaneum. a) the crocodile-normal calcaneum, *Gracilisuchus*; b) the crocodile-reverse calcaneum, *Riojasuchus*.


a
Cal
5mm


b
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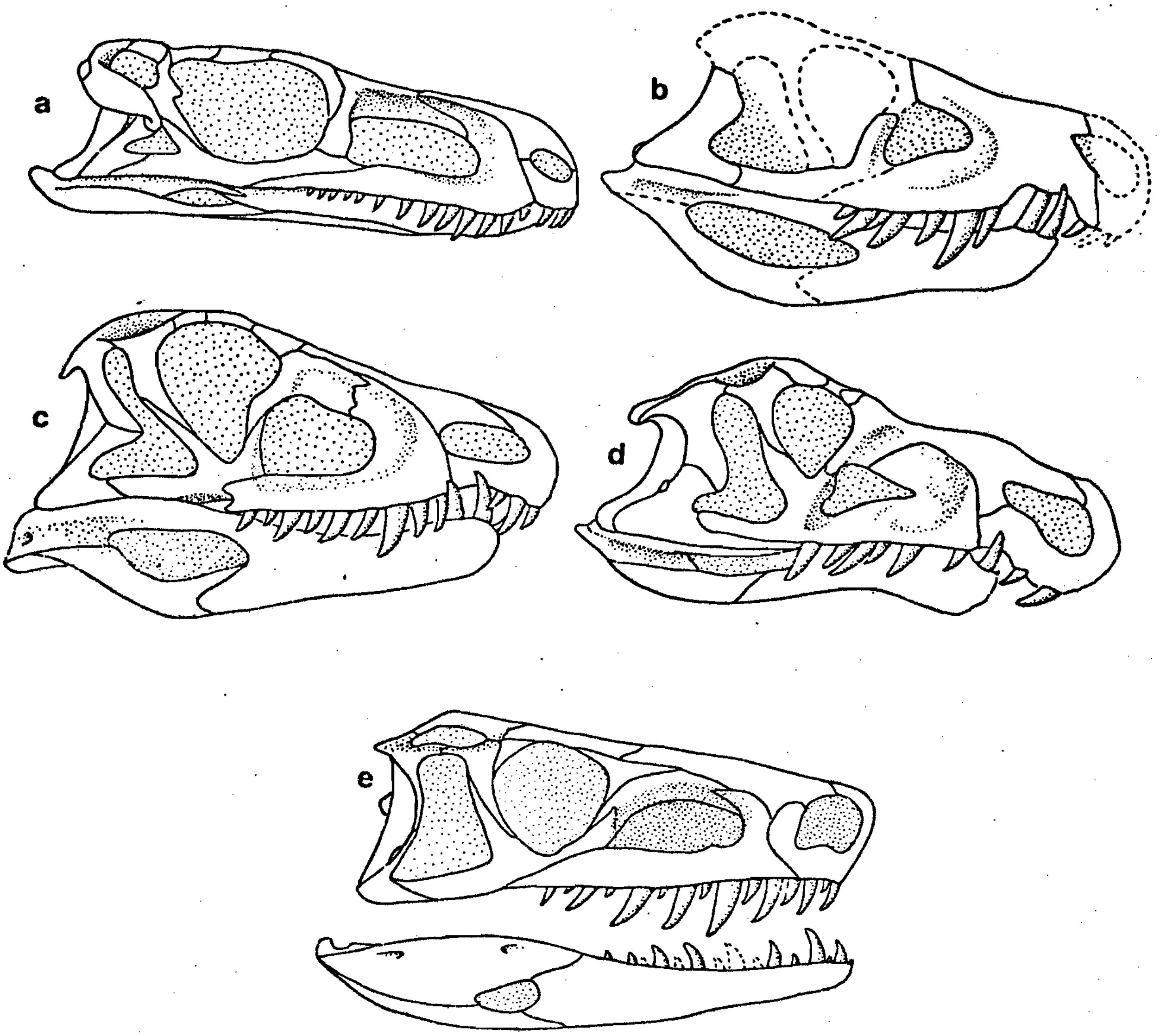
tarsus has the form of a socket. Corresponding to the absence of the ventral flange of the calcaneum that underlies the astragalus is the absence of a ventral cone-shaped articular surface and the resulting absence of a "peg" on the astragalus of the crocodile-reverse tarsus.

Bonaparte (1975a) recognized that in a second ornithosuchid, Ornithosuchus, the calcaneum (and presumably also the astragalus, which is unknown) is like that of Riojasuchus, but in Gracilisuchus, which he, following Romer (1972b) placed in the Ornithosuchidae (Bonaparte 1975a), the tarsus is of the crocodile-normal construction. If Gracilisuchus is an ornithosuchid, then the crocodile-normal tarsus must have given rise to the crocodile-reverse pattern. The structural changes involved in such a transition are easily visualized. The differences in the shape of the wheel-shaped articular surface of the calcaneum would reflect a hyptertrophy of this area during the origin of the crocodile-reverse tarsus, the absence of the medial socket on the calcaneum would be a result of the loss of the ventral flange that underlies the astragalus, and the difference in the structure of the calcaneal tuber would be a result of change from the crocodile-normal condition, presumably in association with changes in the organization of the long pedal flexors. However, a comparison of the skulls of the ornithosuchids (Fig. 54) shows that the position of Gracilisuchus within this family is far from certain. In many features, Gracilisuchus is unlike the remaining ornithisuchids, Riojasuchus, Venaticosuchus and Ornithosuchus. These include:

Figure 54. The skulls of pseudosuchians. a) Gracilisuchus; b) Venaticosuchus; c) Ornithosuchus; d) Riojasuchus; e) Euparkeria. a-d, from Bonaparte (1975a); e, from Ewer (1965). Not drawn to scale.


a
b
c
d
e

1. The antorbital fenestrae is rectangular in Gracilisuchus and is triangular in the remaining genera.
2. The lower temporal fenestrae is triangular in Gracilisuchus and L-shaped in the remaining ornithosuchids.
3. The ventral border of the orbit is round in Gracilisuchus. In the remaining genera this is pointed as a result of the close approximation or fusion of the preorbital and postorbital rami of the jugal.
4. The tooth margin on the skull is complete in Gracilisuchus, with all the teeth of the lower jaw fitting inside the upper tooth row. In the remaining ornithosuchids, a gap is present between the anterior tooth of the maxilla and the posterior tooth of the premaxilla, with the anterior one or two teeth of the dentary passing lateral to the premaxilla.
5. In Gracilisuchus, the dorsal process of the premaxilla anterior to the external narial opening is shorter than the posterior process. Where known in the remaining ornithosuchids (Ornithosuchus and Riojasuchus), the anterior dorsal process of the premaxilla is the longer and this process extends to the dorsal margin of the skull, rather than being restricted to its anterior edge.
6. In Gracilisuchus, the mandible is slender with its ventral edge being nearly straight. In the later ornithosuchids, the posterior portion of the mandible is deep and its ventral edge is strongly curved.

7. In Gracilisuchus, the posterior end of the dentary extends dorsal to the mandibular fenestrae. In the remaining ornithosuchids, the posterior end of the dentary is forked with one branch extending dorsal to and one branch extending ventral to the mandibular fenestrae.
8. In Gracilisuchus, the splenial forms the ventral margin of the jaw along the posterior half of the dentary and is visible laterally. In the remaining ornithosuchids, the splenial is restricted to the inner surface of the jaw.
9. In Gracilisuchus, the cervical vertebrae are not keeled. In the remaining ornithosuchids where known (Riojasuchus and Ornithosuchus), the cervical vertebrae are keeled.

Some of these differences are almost certainly the retention of the primitive archosaur condition by Gracilisuchus. These include the size and shape of the antorbital fenestrae and the presence of a complete tooth row with all dentary teeth fitting inside the upper tooth row. Comparison with the earliest known pseudosuchian, Euparkeria (Fig. 54e), which was described in detail by Ewer (1965) and can be tentatively considered to show the primitive condition, demonstrates that Gracilisuchus does not retain the primitive condition for the other features listed above. In Euparkeria, the lower temporal opening is subrectangular with the posterior edge of the opening being a smooth curve convex anteriorly. This condition could easily give rise to the L-shaped temporal opening of the typical ornithosuchids by an enlargement of the ventral portion of the squamosal and the dorsal portion of the quadratojugal. Romer (1972a) suggested that the small triangular lower temporal opening of Gracilisuchus developed by extension of the anterior projection of the quadratojugal and squamosal anteriorly to meet the anterior border of the temporal opening, leaving only the ventral portion of the temporal opening. In addition to this, there would have to be a shortening of the resulting broad arch and a shortening of the ventral process of the squamosal. Clearly this is a derived condition and could not give rise to that of later ornithosuchids without a reversal of evolutionary trends.

The arrangement of the ant-orbital and post-orbital rami of the jugal in Euparkeria is like that of the advanced ornithosuchids in that both of these rami are well developed and nearly coalesced at their base and is unlike the condition in Gracilisuchus where the two rami are widely separated and the pre-orbital ramus is short. While the condition in Euparkeria could give rise to the condition in both Gracilisuchus and the advanced ornithosuchids without difficulty, the origin of the advanced ornithosuchid condition from that of Gracilisuchus would involve the redevelopment of the primitive condition.

In all features of the lower jaw in which Gracilisuchus and the typical ornothosuchids differ, Euparkeria is like that of the typical ornithosuchids. It is deep posteriorly with a curved ventral border, rather than being nearly straight as in Gracilisuchus. The splenial is developed on the internal surface of the jaw only, it does not form a part of the lower margin and is not exposed laterally as it is in *Gracilisuchus*. Also, the posterior end of the dentary in *Euparkeria* is forked with one branch going dorsal to and one branch going ventral to the lateral mandibular fenestrae. Thus, here as well, derivation of the advanced ornithosuchid condition from that of *Gracilisuchus* would necessitate the redevelopment of the primitive condition.

The cervical vertebrae are keeled in *Euparkeria*, as in *Ornithosuchus* and *Riojasuchus*, but unlike the condition in *Gracilisuchus*.

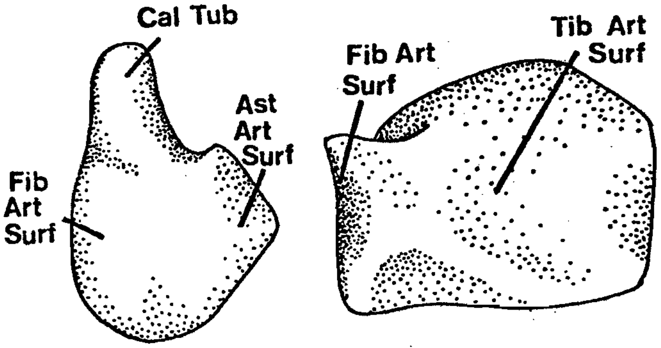
In evaluating the evolutionary implications of these similarities and differences of *Euparkeria*, *Gracilisuchus* and the typical ornithosuchids, three possible relationships need to be considered:

1. That *Euparkeria* represents a primitive condition that was ancestral to most later pseudosuchians (the relationship implied in the above discussion).
2. That *Euparkeria* is more closely related to advanced ornithosuchids than to any other pseudosuchians (that is, that it or a closely related genus was ancestral to ornithosuchids but to no other family of pseudosuchians as indicated in the phylogenetic chart given by Bonaparte (1975a).
3. That *Euparkeria* is not involved in the ancestry of ornithosuchids. The primitive ornithosuchid condition in this case would be similar to *Gracilisuchus*, and the similarities between *Euparkeria* and advanced ornithosuchids would be the result of parallel evolution.

Of these three possibilities, the third requires the assumption of a large amount of parallel evolution without any direct evidence that this occurred. In the absence of such evidence, this possibility can disregarded.

If the first possible relationship is true, the distribution of the features discussed above indicates that Gracilisuchus is specialized and not on the lineage that gives rise to later ornithosuchids, although they do not eliminate the possibility that the ancestor of Gracilisuchus, if known, would be a typical ornithosuchid. If the second relationship is the correct one, then Gracilisuchus has nothing to do with ornithosuchids and should be removed from the family. That the second relationship is most probably the case is indicated by the structure of the tarsus. As noted above, the tarsus of Gracilisuchus has the crocodile-normal contruction, while advanced ornithosuchids have the crocodile-reverse pattern. While the crocodile-normal condition could conceivably give rise to the crocodile-reverse condition, the opposite relationship is extremely unlikely. From the illustration of the tarsus of Euparkeria given by Bonaparte (1975a) (Fig. 55, this paper), it can be recognized that although primitive in some respects, such as the small size of the calcaneum relative to the astragalus and the short tuber, it already has a structure typical of the crocodile-reverse pattern. The dorsal portion of the articular surface of the calcaneum is divisible into two portions, a narrow portion along the lateral edge of the bone that would have articulated with the fibula, and a medial portion that

Figure 55. The astragalus and calcaneum of *Euparkeria*. From Bonaparte (1975b). For key to abbreviations see list of abbreviations.


Cal Tub
Ast Art Surf
Fib Art Surf
Fib Art Surf
Tib Art Surf

would have been overridden by the astragalus. The astragalar portion of the articular surface is in the shape of a portion of a cone with its apex directed medially. No ventral flange that would have underlain the astragalus is present in the calcaneum of Euparkeria. In all these features, the tarsus of Euparkeria is similar to the crocodile-reverse tarsus. It is impossible to tell if the tarsus of Euparkeria functioned like that of advanced ornithosuchids in that most movement occurred between the astragalus and calcaneum or was primitive in retaining movement at the mesotarsal joint. However, structurally, the tarsus of Euparkeria has already attained the crocodile-reverse pattern and is an excellent ancestor for the tarsus of advanced ornithosuchids, but could not reasonably be considered ancestral to the crocodile-normal tarsus. On this basis, then, Gracilisuchus can be removed from the Ornithosuchidae, leaving the three genera, Ornithosuchus, Riojasuchus and Venaticosuchus in the family with Euparkeria being close to the ancestry of the family.

With the Ornithosuchidae thus redefined, the evidence that the crocodile-reverse tarsus was derived from the crocodile-normal tarsus is removed. The primitive condition of the tarsus in Euparkeria suggests that the crocodile-reverse tarsus originated independently from the primitive archosaurian tarsus, with the differences in structure of the crocodile-normal and crocodile-reverse tarsi reflecting their independent exploitation of movement between the astragalus and calcaneum. This implies that the pseudosuchians can be divided into two major groups on the basis of the structure of the tarsus, those with crocodile-normal tarsi and those with crocodile-reverse tarsi (Fig. 59).

3. ORIGIN OF THE MESOTARSAL ANKLE JOINT OF ARCHOSAURS

The third type of tarsus seen in archosaurs is characterized by a mesotarsal ankle joint; that is, an ankle joint passing distal to the astragalus and calcaneum with these bones functionally integrated with the crus and the distal tarsals integrated with the metatarsus. This type of ankle joint is seen in birds, ornithischians, saurischians, pterosaurs and a few thecodonts. Barnett (1954b) has shown that in birds, this joint is mechanically similar to the human knee, the major difference being that the knee points forward while the ankle points posteriorly. The absence of a well developed intercondylar groove on the astragalocalcaneum of most archosaurs (pterosaurs are an exception, Williston 1903), indicates that differences would have been present in the detailed mechanics of the joint. In general, however, they are similar in being medio-laterally elongate ovoid joints with the convex surface on the proximal elements and the concave surface being formed by the distal tarsals and metatarsals.

Two major modes of origin of the mesotarsal ankle joint have been suggested: (1) origin from the tarsus of a primitive archosaur before the development of a specialized crocodiloid joint (Krebs 1963), and (2) origin from the tarsus with a fully developed crocodiloid joint (Walker 1964; Charig _et al_. 1965). These can be considered in turn.

Origin from the Proterosuchian Tarsus

The tarsus of Lagosuchus, recently described and illustrated by Bonaparte (1975b), offers a number of features that suggest that it evolved directly from a tarsus of a proterosuchian type. Of prime importance is the presence of a small tuber on the calcaneum. This was compared with the tuber of crocodiles by Romer (1972c), implying that this tarsus originated from a crocodiloid tarsus. However, the illustration of the astragalus and calcaneum of Lagosuchus given by Bonaparte (1975b) shows that the tuber is directed laterally, rather than posteriorly as in crocodiles, and thus is more directly comparable to the tuber of Proterosuchus. Also, a complex articulation is present between the astragalus and calcaneum. While this was also implied to be indicative of origin from the crocodiloid tarsus, it would be expected to be present at least primitively in a tarsus derived from the proterosuchian condition.

Thus at least some thecodonts with a mesotarsal joint probably evolved directly from an animal with a proterosuchian tarsus. Such structural change offers no major structural or mechanical problems. The structural changes involved would simply be the reduction in complexity of the elements, the incorporation of the astragalus, calcaneum and central into the crural unit, and solidification of the distal tarsal-metatarsal unit. These changes would be a reflection of loss of movement between the astragalus and calcaneum, loss of the leverage function of the calcaneal tuber and exploitation of movement at the mesotarsal joint. Their development can be associated with the assumption of an erect stance -- the reduced amount of crural rotation and abduction resulting from this change in the step cycle would eliminate the need for the double joint present in the proterosuchian tarsus and would allow the astragalus and calcaneum to be consolidated.

Charig (1972) has suggested that the development of the mesotarsal joint was somehow related to the presence of a digitigrade stance in the ancestral proterosuchian. A mechanical basis for this rests in the dual nature of the mechanics of the pedal flexors. Since the metatarsus would have been laterally directed, a combination of rotation followed by flexion of the metatarsus, as is seen in lizards, would have been necessary for the metatarsus to contributed to propulsion. If the animal was digitigrade during rapid locomotion, as is Basiliscus (Snyder 1949), those muscles that passed over the tarsus and used it as a pulley during flexion of the metatarsus would have made the greatest contribution to flexion of the metatarsus. The leverage of these muscles is not increased by the calcaneal tuber, and consequently there would be no selection for the maintenance of this structure during the assumption of an erect stance. In contrast, an animal that is plantigrade during the transition from a sprawling to an erect step cycle would use the tuber as a pulley during the initial stage of plantarflexion of the metatarsus and selection would act to maintain this function.

Origin of the Mesotarsal Ankle from the Crocodiloid Ankle Joint

Two lines of evidence have been used to support the derivation of the dinosaur tarsus, which has a mesotarsal joint, from the crocodiloid tarsus. One of these is the presence of similarities in the postcranial skeleton of rauisuchids and prosauropods, an early group of dinosaurs, that have been taken to indicate that rauisuchids are ancestral to dinosaurs (Charig _et_ _al_. 1965). Since rauisuchids have a fully developed crocodile-normal tarsus, this implies that the crocodile-normal tarsus is ancestral to the dinosaur tarsus. Unfortunately, the possible relationship between dinosaurs and rauisuchids has never been analyzed in detail so it is impossible to evaluate the significance of the similarities against the differences in structure of the tarsus in the two groups.

The second line of evidence used to support derivation of the dinosaur tarsus from the crocodiloid tarsus is the presence of a calcaneal tuber and a complex joint between the astragalus and calcaneum in the tarsus of the early ornithischian _Pisanosaurus_, recently described by Bonaparte (1976). As noted previously, these features do not necessarily indicate derivation from a crocodiloid tarsus. They are also present in the proterosuchian tarsus and would be expected in tarsi derived from the proterosuchian tarsus. However, in _Pisanosaurus_, the calcaneal tuber is directed posteriorly as it is in crocodiles. Also, according to Bonaparte (1976), an effective articulation is present between the calcaneum and fibula. While this evidence is not conclusive, it is suggestive that the mesotarsal joint of at least ornithischians originated from the crocodile tarsus.

Two functional problems are involved in the origin of the mesotarsal joint from the crocodiloid tarsus: (1) a change in the relationships of the calcaneum from being integrated with the metatarsus to being integrated with the crus; and (2) loss of the calcaneal tuber.

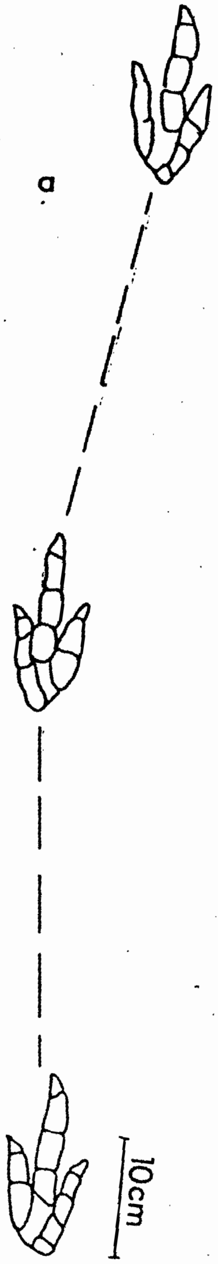
The first of these changes is less fundamental than first appears. In crocodiles, the calcaneum, although functionally integrated with the metatarsus during plantarflexion, is not firmly attached to it as is the astragalus to the tibia. Considerable movement is possible between the calcaneum and distal tarsals with movement at this joint contributing to extension of the metatarsus. Thus a functional mesotarsal joint is retained in crocodiles, and the specialization of the mesotarsal joint for use during locomotion poses no major mechanical problems. Such a change would likely follow a decrease in size of the calcaneum and an increase in size of the astragalus. It is significant with respect to this that the calcaneum in early dinosaurs was consistently small, the main joint surface being supplied by the astragalus. However, reduction of the calcaneum relative to the astragalus is inconsistent with the maintenance of the calcaneal tuber as an important lever. Thus the main functional problem is an identification of the factors that would lead to loss of the calcaneal tuber.

Before considering the loss of the calcaneal tuber, it is necessary to consider the differences in the pelvic step cycles of pseudosuchians and dinosaurs. Both dinosaurs and at least some of the pseudosuchians, such as Hallopus (a specialized digitigrade crocodile or pseudosuchian closely related to the group that gave rise to crocodiles (Walker 1970)) and, judging from the reconstruction of Krebs (1965), Tictinosuchus, probably had an advanced erect step cycle in which the limbs were held and moved in a parasagittal plane. As in mammals, this description of the limb movements is an approximation of the actual condition. Small but important abduction-adduction and rotational movements would have accompanied flexion and extension of the limb segments. An indication of the direction of the abduction of the femur is given by the knee joint. In pseudosuchians, the articular surfaces at the knee are like those of the crocodile. The distal end of the femur is divided into two distinct condyles with the lateral condyle being slightly larger than the medial condyle. In dinosaurs, however, including Staurikosaurus, the earliest known saurischian (Colbert 1970) and the slightly later Herrerasaurus (Reig 1963), the medial condyle of the femur is larger than the lateral condyle. Assuming that the axis of rotation at the knee was approximately horizontal as it is in man (Steindler 1955), this difference in the relative sizes of the condyles of the femur indicates that the orientation of the femur was different in the two groups. In pseudosuchians, as in crocodiles, the femur would have been directed somewhat laterally so that the knee was lateral to the hip, while in dinosaurs, the femur would have been directed medially so that the knee was below or even medial to the hip. Thus, during retraction of the femur, the femur would have been abducted laterally in pseudosuchians and abducted medially in dinosaurs.

Also, the orientation and movements of the metatarsus would have been different in the two groups. In most pseudosuchians, the metatarsus is slightly asymmetrical with the lateral metatarsals being the longest. As in crocodiles, this would have been associated with a slight out-turning of the foot. That this was so is indicated by footprints attributed to pseudosuchians, such as Apatopus (Fig. 56a). In this orientation, a slight medial rotation of the tarsus would have occurred as the metatarsus plantarflexed. An exception to this is Hallopus, where the metatarsus is consolidated to form a long narrow bar of bone with the metatarsals rather symmetrically arranged around the third metatarsal. There, the metatarsus would have been directed anteriorly. In dinosaurs, as in Hallopus, the pes is generally rather symmetrically arranged around the central toe and, as indicated by footprints (e.g. Anchisauropus, Fig. 56b), the feet were set down very close to the midline and with the longest toe directed anteriorly. Possibly, the difference in movement of the femur was associated with a difference in the direction of rotation of the pes so that pseudosuchians, including Hallopus, rotated their metatarsus medially

Figure 56. Trackways of Triassic archosaurs.

a) <u>Anchisauropus</u>; b) <u>Apatopus</u>. a, from Haubold (1974); b, from Baird (1957).


a
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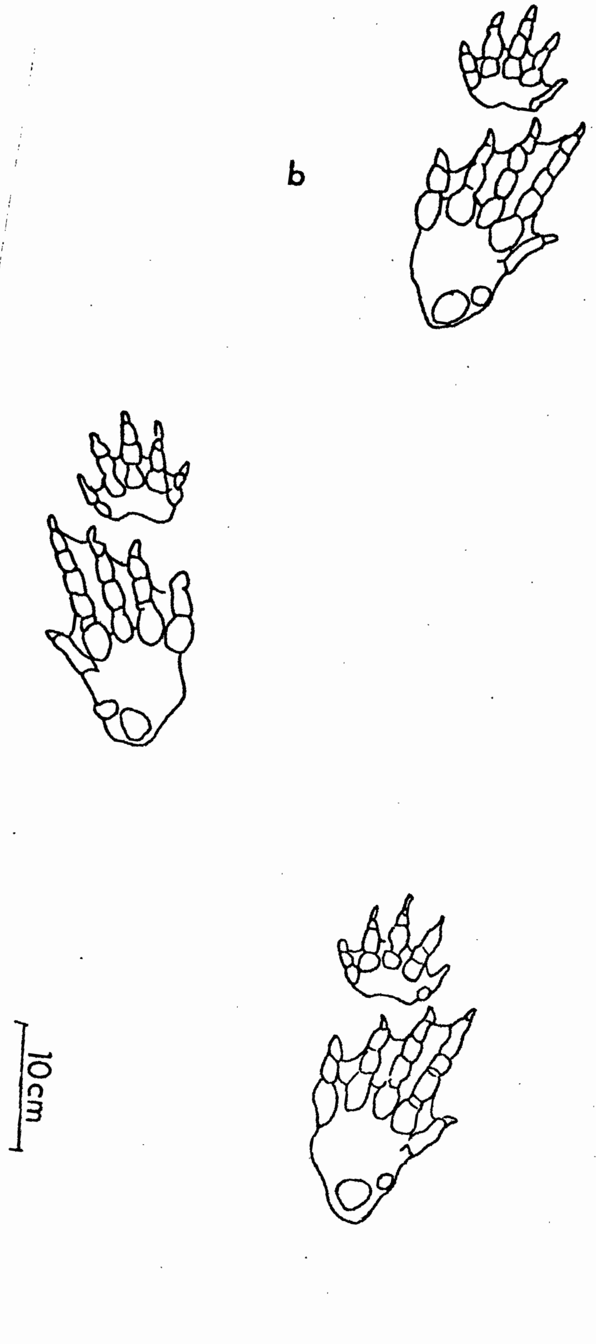
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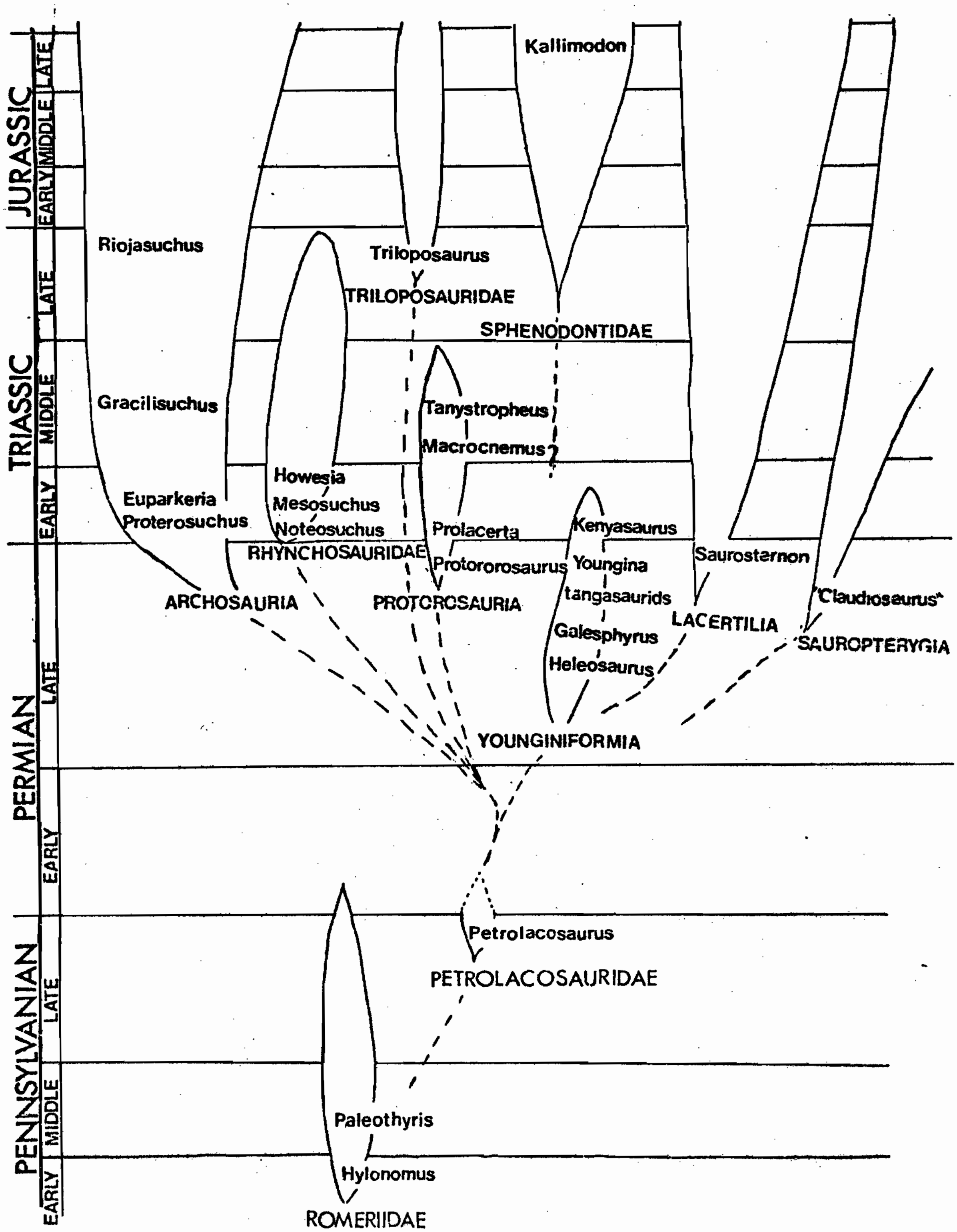
during the later part of the propulsive phase while dinosaurs rotated their metatarsus slightly laterally. In any case, the large amount of medial rotation seen in crocodiles would not have been present in dinosaurs.

These changes in the step cycle may have provided a selection regime that promoted the loss of the calcaneal tuber. Since the tuber is formed entirely by the calcaneum and the calcaneum is lateral to the astragalus, the calcaneal tuber has a morphologically lateral position. As shown above, in crocodiles the morphologically lateral position of the tuber is compensated for by the slight lateral orientation of the metatarsus so that functionally, the tuber extends directly posteriorly. If, as happened during the origin of the dinosaurs, the metatarsus was reoriented to point more directly forwards, a corresponding modification in the position of the tuber would have to occur so that it continued to extend posteriorly. That such a change does occur is indicated by Hallopus, where the calcaneal tuber is directly in line with the metatarsus and would have pointed posteriorly. Here, the extreme compression of the tarsus results in the calcaneal tuber being nearly the full width of the metatarsus. In a tarsus that is wider, this would not be so. There the calcaneal tuber would have been restricted to the lateral side of the tarsus. Thus the force produced by the pedal flexors would be concentrated on the lateral side of the metatarsal lever, and would result in a rotational force tending to rotate the metatarsus medially. The size of this force would be related to the width of the metatarsus.

If the metatarsus is narrow, as in Hallopus, this force would be relatively small and could easily be opposed by ligaments or by the action of muscles, such as the pronator profundus, that rotate the metatarsus in the opposite direction. The magnitude of the rotational force will increase with an increase in the width of the metatarsus. At a certain point, use of muscular force or ligaments to oppose the rotational force would become inefficient, and a mechanical arrangement in which the pedal flexors do not produce a disruptive rotational force would be selected for. Loss of the calcaneal tuber and the medial shift of the tendons of the pedal flexors is one such arrangement that would have this effect. In addition, if the change in movements of the femur was associated with a change in the direction of rotation of the metatarsus, loss of the calcaneal tuber would be promoted by the need to develop an arrangement of the pedal flexors that tended to rotate the metatarsus medially, rather than laterally.

Thus while the mode of origin of the dinosaur tarsus is still uncertain, an origin from a crocodiloid tarsus is mechanically feasible. Any pseudosuchian that developed a step cycle like that of dinosaurs would be subject to selection pressures that would lead to a change in the arrangement of the pedal flexors. The loss of the calcaneal tuber is not the only change that would have the required results. Superposition of the astragalus on the calcaneum could conceivably have the same effect and possibly the change in the relations of the astragalus and calcaneum in mammals was a response to similar selection pressures. Consideration of the factors that lead to loss of the calcaneal tuber rather than superpositioning of the astragalus on the calcaneum, if indeed the dinosaur tarsus evolved from the crocodiloid tarsus, must await a more detailed understanding of the structural and locomotor changes that occurred during the origin of the dinosaurs.

Figure 57. Phylogenetic chart showing the interrelationships of the major groups of diapsids. The archosaurs are shown in more detail in Figure 58.


JURASSIC
EARLY
MIDDLE
LATE
TRIASSIC
EARLY
MIDDLE
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PERMIAN
EARLY
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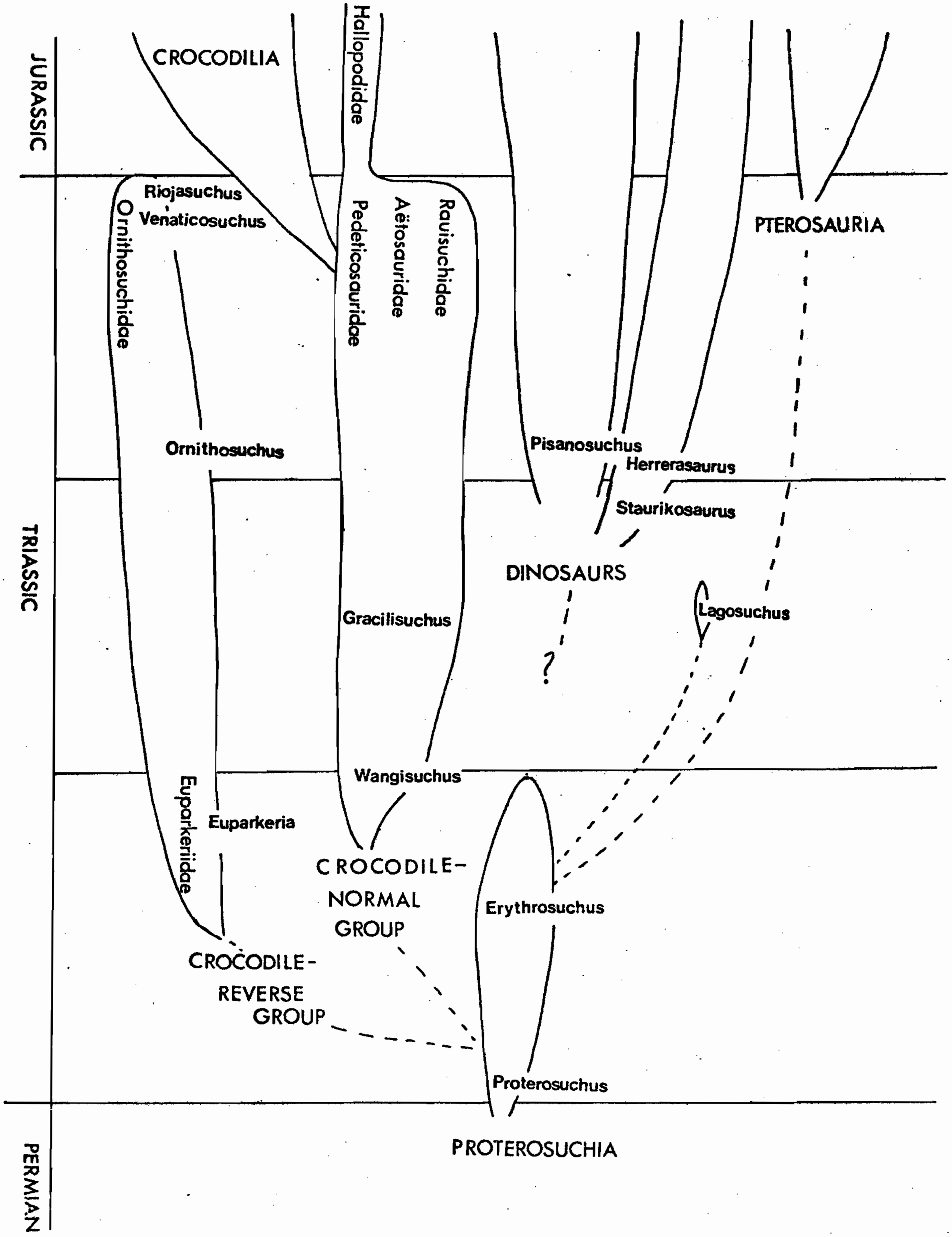
PENNSYLVANIAN
EARLY
MIDDLE
LATE
Kallimodon
Riojasuchus
Triloposaurus
TRILOPOSAURIDAE
SPHENODONTIDAE
Gracilisuchus
Tanystropheus
Macrocnemus
?
Howesia
Mesosuchus
Noteosuchus
Euparkeria
Proterosuchus
Prolacerta
Kenyasaurus
RHYNCHOSAURIDAE
Protororosaurus
Youngina
Saurosternon
ARCHOSAURIA
PROTOROSAURIA
tangasaurids
LACERTILIA
"Claudiosaurus"
Galesphyrus
SAUROPTERYGIA
Heleosaurus
YOUNGINIFORMIA
Petrolacosaurus
PETROLACOSAURIDAE
Paleothyris
Hylonomus
ROMERIIDAE

Figure 58. Phylogenetic chart showing the interrelationships of the archosaur groups considered in this paper.


JURASSIC
TRIASSIC
PERMIAN
CROCODILIA
Hallopodidae
Riojasuchus
Venaticosuchus
Ornithosuchidae
Pedeticosauridae
Aëtosauridae
Rauisuchidae
PTEROSAURIA
Ornithosuchus
Pisanosuchus
Herrerasaurus
Staurikosaurus
DINOSAURS
?
Lagosuchus
Gracilisuchus
Wangisuchus
Euparkeriidae
Euparkeria
CROCODILE-NORMAL GROUP
Erythrosuchus
CROCODILE-REVERSE GROUP
Proterosuchus
PROTEROSUCHIA

CONCLUSIONS

1. The pelvic step cycle of Iguana is described and compared with descriptions of the limb movements in other lizards. The pelvic step cycle in lizards conforms to a single general pattern. This pattern is a result of mechanical limits placed on the possible movements of the pelvic limb segments by the need to move forward without unnecessary oscillations of the centre of gravity. It can be used to reconstruct a model of the primitive pelvic step cycle.

2. The tarsus of the romeriid reptile Paleothyris is used as a basis for considering the mechanics of the tarsus in early reptiles. The pelvic limb movements would have been generally similar to lizards, but the crus was probably directed further anteriorly at the beginning of the propulsive phase. The metatarsus would have been directed laterally. The movement of the crus on the pes would have involved a combination of movement at a number of basically hinge-like axes. The greatest force acting on the animal at any one time was probably the ventrally-directed force resulting from gravity. This would have been passed from the femur to the tibia, across interosseous ligaments or muscles to the fibula and from the fibula to the tarsus, as was probably the case in early amphibians. The forces acting in this system are considered in some detail, and it is shown that this seemingly indirect mode of force transfer enables the interosseous cruris muscles to minimize

tension in the knee.

3. The major changes in the tarsus during the origin of the diapsids was a change in the structure of the tibio-astragalar joint. This can be associated with an increase in the proportion of the force that is passed from the femur to the tarsus directly through the tibia.

4. A definitive intratarsal joint is first seen in younginiform eosuchians. Movement at this joint involved a combination of flexion of the astragalus and calcaneum on the distal tarsals around an axis lying between the calcaneum and the fourth distal tarsal and a warping of the distal tarsal row. The development of an intratarsal joint increases the sharpness of the angle between the crus and metatarsus that is attained prior to flexion of the metatarsus and thus increased the proportion of the force produced by the pedal flexors that acts to flex the metatarsus. It does not involve a solidification of the tarsus. The fifth metatarsal was probably the major site of bracing of the long pedal flexors.

5. "Claudiosaurus" has a tarsus superficially like that of younginiform eosuchians but the detailed structure and mechanics of the intratarsal joint are different; the joint between the astragalus and fourth distal tarsal is a concave-convex joint unlike the condition in the younginiform tarsus and more rotation would have been possible at the intratarsal joint than in younginiform

eosuchians.

6. The structure of the tarsus in lizards is surveyed and the homologies of the elements are discussed. The astragalocalcaneum is composed of the astragalus, calcaneum and centrale of eosuchians, the proximal epiphyses of the first two metatarsals are homologous with the first two distal tarsals, the ossification between the astragalus and the first two metatarsals is a lunula , and the fifth metatarsal probably does not include the fifth distal tarsal. Little variation is seen in the basic structure of the tarsus. In Iguana, the intratarsal joint is exceptionally mobile. The articular surfaces guide the movements at the joint when they are pressed against each other, but they are not held together permanently by the ligaments of the joint. The metatarsal-distal tarsal ligaments are important in transmitting the forces across the joint. The fifth metatarsal acts as a lever in two separate ways. During the initial part of the propulsive phase as the metatarsus is rotated, the proximal inturned portion of the fifth metatarsal increases the leverage of the pedal flexors and during the final part of the propulsive phase as the ankle joint is extended, the plantar tubercles increase the leverage of the pedal flexors. The fifth metatarsal plays a passive role in grasping, its main function during this action of the digit being to act as a pulley around which various tendons of the foot pass. The tarsus of Saurosternon is primitive in a number of respects but already show proportions similar to lizards

and an incipient development of the characteristic intratarsal joint of lizards. It is suggested that the key change in the origin of the lizard tarsus was a change in the mechanics of the intratarsal joint that reduced the amount of warping of the distal tarsal row that occurred during locomotion. With a reduction in the flexibility of the distal tarsal row required for the functioning of the tarsus, the metatarsus could be consolidated and the fifth metatarsal could be hooked.

7. Two grades of evolution of the tarsus are seen in rhynchosaurids: a primitive grade which has a tarsus like that of <u>Noteosuchus</u> in which the centrale is small and a perforating foramen is present, and the tarsus of advanced rhynchosaurids in which the centrale is large and is involved in support of the tibia and no perforating foramen is present. The tarsus of <u>Noteosuchus</u> had both a movable articulation between the astragalus and calcaneum and a well defined intratarsal joint. Movement at these two joints would have combined to allow the total range of movement of the crus on the metatarsus that would have occurred during locomotion. Thus the development of this joint would have reduced the amount of warping of the distal tarsal row that was necessary and would have allowed the metatarsus to become consolidated to form an efficient propulsive lever. The calcaneal tuber probably plays a passive role in the mechanics of the metatarsal lever by acting as a pulley over which the pedal flexors pass and maintaining a large angle between the

line of action of these muscles and the metatarsal lever. Advanced rhynchosaurids show features that indicate that movement between the astragalus and calcaneum was greatly reduced. The mechanics of the tarsus of advanced rhynchosaurids are not completely understood.

8. Sphenodontids have a tarsus that is distinct for the group, although in many ways it is similar to lizards. The cruro-tarsal and intratarsal joints are both distinct from lizards. The intratarsal joint does not allow as much movement of the crus on the metatarsus as the comparable joint in lizards. Possibly crural rotation was a result of movement at the cruro-tarsal joint. In a number of details of its construction, the sphenodontid tarsus is like that of Noteosuchus and it may have originated from an animal with a tarsus like that of Noteosuchus through fusion of the proximal elements to give the single astragalocalcaneum.

9. Prolacerta, Tanystropheus, Macrocnemus, Proterosaurus and Trilophosaurus probably form a natural group. In all these genera, the tarsus is similar to that of Noteosuchus in the structure of the joint between the astragalus and calcaneum, the arrangement of the three proximal elements, the presence of the calcaneal tuber, where known, the details of the intratarsal joint, and the details of the fifth metatarsus. The mechanics and origin of their tarsi would have been identical to Noteosuchus.

10. The tarsus of the early archosaur Proterosuchus is identical to that of Noteosuchus in all functionally important details of its structure. The difference in the structure of the tibial-astragalar joint is a result of the posterior expansion of the lip of the tibial articular surface of the astragalus in Noteosuchus. Mechanically, the tibial-astragalar joint would have been the same in the two genera. Three lines of evidence show that the proterosuchian tarsus is primitive for archosaurs: the generally primitive construction of Proterosuchus, the presence of a structurally similar tarsus in another early archosaur Erythrosuchus, and the presence of identical tarsi in other groups of diapsids that are not archosaurs but are probably closely related to archosaurs.

11. The pelvic step cycle in crocodiles is described in detail. The cineradiographic analysis of locomotion confirms that two distinct kinds of pelvic step cycles are present, the erect step cycle seen in the high walk and a more sprawling step cycle. The movement of the crus on the pes in these two kinds of step cycles differ primarily in the amount of rotation of the metatarsus relative to the crus that occurs: almost none of this movement occurring in the erect step cycle, and up to 70° in the sprawling step cycle. The sprawling step cycle is not retained unchanged from the primitive reptile condition, but probably represents a specialization of crocodiles.

12. The mechanics of the tarsus in crocodiles is described. The tibia is firmly held to the astragalus. Some movement is possible between the fibula and astragalus, this movement serving to allow the independent movement of the tibia and fibula that occurs during rotation at the knee. The ankle joint is the main site of flexion and extension of the crus on the metatarsus during locomotion. A considerable amount of flexion and extension of the crus on the metatarsus is possible at the intratarsal joint. Movement at this joint allows the pelvic limb to assume a number of postures that would otherwise not be possible. It does not function during locomotion. Rotation of the metatarsus is a result of a successively greater flexion of the metatarsals laterally. The lateral orientation of the metatarsus compensates for the laterally directed calcaneal tuber so that functionally, it is directed posteriorly.

13. The crocodile-normal tarsus in pseudosuchians is similar to that of crocodiles in the basic mechanics of the ankle joint, but the metatarsus is more consolidated in some genera and a fifth digit is retained. Comparison of the crocodile-normal tarsus and the tarsus of Noteosuchus shows that the crocodile-normal tarsus probably evolved directly from a proterosuchian-like tarsus. The changes involved in this transition are in the structure of the astragalocalcaneal joint, changes in proportions of the elements, and a reorientation of the calcaneal tuber. These changes are probably

associated with the assumption of an erect step cycle.

14. The crocodile-reverse tarsus is found in the ornithischids Riojasuchus and Ornithosuchus and in Euparkeria. It probably originated independently from the primitive archosaur tarsus. The relationships of Gracilisuchus are discussed. It is concluded that Gracilisuchus is not an ornithischid.

15. The mesotarsal ankle joint in archosaurs probably originated more than once, at least once from the proterosuchian tarsus and possibly once from the crocodiloid tarsus. The changes in structure during the transition from the proterosuchian tarsus to a tarsus with a mesotarsal ankle joint were probably associated with the assumption of an erect stance. The major change involved in the origin of a mesotarsal ankle joint from a crocodiloid tarsus is the loss of the calcaneal tuber. This may have been a result of the assumption of a forward orientation by the metatarsus and a step cycle that does not involve medial rotation of the metatarsus.

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LIST OF ABBREVIATIONS

ADtL	astragalar-distal tarsal ligaments
Abd Dig 4	abductor digit four
Abd Dig 5	abductor digit five
Ast	astragalus
Ast Art Surf	astragalar articular surface
AstCal	astragalocalcaneum
Cal	calcaneum
Cal Tub	calcaneal tuber
Cen	centrale
CFDL	calcaneal head of the flexor digitorum longus
CFDL Tend	tendon of the calcaneal head of the flexor digitorum longus
Cont	contrahentes
EBS	extensor brevis superficialus
EBS 4 pars 4	fourth head of the extensor brevis superficialus of digit four
EDL	extensor digitorum longus
E Dig 5	extensor of digit five
F	fibula
FBP	flexor brevis profundus
FDL	flexor digitorum longus
FFDL	fibular head of the flexor digitorum longus
FH	flexor hallucis

Fib Art Surf	fibular articular surface
Fib Cal	fibulocalcanealus
Flex Ten 5	flexor tendon of digit five
GF	gastrocnemius (femoral head)
GT	gastrocnemius (tibial head)
GT Ten	tendon of the gastrocnemius (tibial head)
Inter Dig Ten	interdigital tendon
IoC	interosseous cruris
IoD	interosseous dorsalis
IoV	interosseous ventralis
L Cen	lateral centrale
Lumb	lumbricales
M	meniscus
M Cen	medial centrale
Mech Axis of Met	mechanical axis of the metatarsus
PB	peroneus brevis
PFDL	plantar head of the flexor digitorum longus
PL	peroneus longus
PL Tend	tendon of the peroneus longus
Sup IoC	superior interosseous cruris
T	tibia
TA	tibialis anterior
TM	tarsometatarsalis
Tib Art Surf	tibial articular surface

1-5	distal tarsals one to five
I-V	metatarsals one to five