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The origin of crocodylian locomotion

J. Michael Parrish

Abstract.—The morphology of the tarsi, hindlimbs, and pelves of the earliest crocodylians and their nearest relatives, *Hallopus* and the “sphenosuchians,” indicates that these animals had adaptations for erect posture. The widespread distribution of apparently homologous adaptations for erect gait among the archosaurs with crocodile-normal tarsi suggests that those structures are plesiomorphic for this group, which comprises the Aetosauria, “rauisuchians,” “sphenosuchians,” *Hallopus*, and the Crocodylia. Adaptations for erect posture are seen most clearly in the structure of the proximal tarsus (astragalus and calcaneum).

An important implication of this argument is that the most primitive crocodylomorphs, comprising the “protosuchian” crocodiles, the “sphenosuchians,” and *Hallopus*, had an erect stance and gait. The sprawling stance and associated gait used by modern crocodylians during swimming and upon entering the water can be viewed as secondary adaptations to an aquatic existence. The environments of deposition and faunal associations of “sphenosuchians” and “protosuchian” crocodiles are consistent with primarily terrestrial habits. Living crocodylians have two types of step cycles, sprawling and erect; the sprawling pattern is overprinted onto the inferred ancestral “high-walk,” and onto the gallop sometimes used by juvenile crocodylians.

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Introduction

Living crocodylians use a variety of gaits during locomotion (Schaeffer 1941; Cott 1961; Brinkman 1980). These include one gait requiring sprawling posture, the belly walk, and two gaits requiring an essentially erect stance: the high walk and, in juveniles of some species, a true gallop (Zug 1974; Webb and Gans 1982). Because they assume both sprawling and erect postures, living crocodylians frequently have been regarded as functional intermediates between early, sprawling reptiles and erect dinosaurs and birds (e.g., Charig 1972; Brinkman 1980). Two ideas are implicit in this assumption: a concept of progressivism in locomotor innovations in archosaurs, and the concept that living crocodylians and their sister groups within the paraphyletic archosaurian Order “Thecodontia” (paraphyletic groups are placed in quotation marks throughout this paper to distinguish them from monophyletic lineages) represent an intermediate step in locomotor evolution between primitive reptiles and the later erect groups.

Recent functional studies of the hindlimb and tarsus of the early archosaurs traditionally placed in the “Thecodontia” have shown that erect posture was widespread within the later constituents of that group (Parrish 1983, 1984, 1986a; Bo-

naparte 1984). Erect posture in the Archosauria was apparently derived within two different lineages with functionally similar but structurally distinct ankles: the crocodile-normal and the crocodile-reverse archosaurs (Cruickshank 1979; Chatterjee 1982; Parrish 1983). Study of the tarsi, hindlimbs and pelves of the earliest crocodylians and their nearest relatives, the “sphenosuchians,” indicates that these animals also had adaptations for erect posture. The widespread distribution of apparently homologous adaptations for erect posture within the crocodile-normal archosaurs suggests that those structures are plesiomorphic for the group comprising the Aetosauria, “Rauisuchia,” “Sphenosuchia,” *Hallopus*, and Crocodylia.

Materials and Methods

In a study of the hindlimb and pelvis among the early archosaurs that are usually placed in “Thecodontia” (Parrish 1983, 1986a), paradigms were defined for functional patterns and morphological correlates characteristic of sprawling, erect, and intermediate (“semi-erect”) stances and associated gaits. These paradigms (cf. Rudwick 1964) were based on viewing the mechanical properties of each type of limb as a kinematic chain; insights into the locomotor behavior char-

acteristic of each type were obtained by examining living diapsids that use gaits associated with each of the three stances. In this paper, I summarize the structural and functional characteristics of erect postures in the crocodile-normal archosaurs, and contrast them with the sprawling conditions that are primitive for the archosaurs. The essential feature of the gaits associated with erect stance, as considered here, is that flexion and extension of the major joints of the hind limb (knee and various tarsal and pedal joints) occur within horizontal axes that are perpendicular to the line of march of the animal. Thus the limbs move in or near a vertical plane parallel to the one containing the line of march of the animal during normal erect locomotion. The structural correlates of the erect forms are compared with the pattern that is observed in the primitive proterosuchian and phytosaurian archosaurs and is shared plesiomorphically with other primitive diapsids (Parrish 1986a).

In the course of the earlier study, and in the process of describing a new specimen of the "sphenosuchian" *Hesperosuchus* from the Chinle Formation of Arizona (UCMP 129740), I examined the pelvic and hindlimb material of many specimens of "sphenosuchians" and "protosuchian" crocodiles. I evaluated character states for the hindlimb locomotor complex with respect to the paradigms set forth previously (Parrish 1986a). It was immediately apparent that early members of the Crocodylomorpha (a group comprising the Crocodylia and their close relatives), including "sphenosuchians," *Hallopus*, and "protosuchians" (Walker 1970) fit the paradigm for erect locomotion much more closely than they do the paradigm for a semi-erect posture, which is based to a large extent on the locomotor complex in modern crocodilians. An erect posture (Walker 1970; Brinkman 1980) and terrestrial habits (e.g., Colbert and Mook 1951; Colbert 1952; Lull 1953; Kermack 1956; Walker 1970, 1972; Whetstone and Whybrow 1983; Crush 1984) have been hypothesized before for individual taxa among the primitive crocodylomorphs. But the hypothesis that an erect gait is plesiomorphic to the group has not, to my knowledge, been put forth previously, although Walker (1970, 1972) suggested that some features of the girdles and humerus in modern crocodilians could indicate a more erect, possibly arboreal,

ancestry for the group among the primitive Crocodylomorpha. This study attempts a comprehensive examination of locomotor capabilities throughout the primitive crocodylomorphs. Fossil specimens considered in this paper are listed in the Appendix. Living crocodilians for which hindlimb and pelvic material were examined include specimens of *Alligator mississippiensis*, *A. sinensis*, *Crocodylus acutus*, *C. palustris*, *C. porosus*, *C. rhombifex*, *Caiman sclerops*, *Gavialis gangeticus*, *Osteolemus tetraspis*, *Paleosuchus palpebrosus*, and *Tomistoma schlegelii*. Despite minor differences in limb proportions, the morphology of the hindlimb complex is remarkably conservative among the living forms. Ankle joint axes were measured after the systematic survey of recent crocodilians was taken, and only the following species were available for immediate study: *Alligator mississippiensis*, *Crocodylus niloticus*, and *Caiman sclerops*.

Systematics

Relationships among the primitive crocodilians and among the primitive archosaurs usually referred to as "thecodontians" are not well established. Archosaur taxonomy has been complicated by the erection of many paraphyletic groups, often poorly diagnosed. Several taxonomic groups mentioned here (e.g., "Thecodontia," "Sphenosuchia," "Rauisuchia," "Protosuchia") are paraphyletic assemblages that are in the process of being revised. This study will concentrate on the earliest crocodilians usually referred to the "Protosuchia" and on the non-crocodylian crocodylomorphs usually allied as the "Pedeticosauria" (e.g., Walker 1970) or "Sphenosuchia" (e.g., Bonaparte 1982). Huene (1925) and Broom (1927) first recognized the affinities of the Liassic archosaur *Sphenosuchus* to the protosuchian crocodiles; Walker (1968, 1970) was largely responsible for the establishment of the modern concept of relationships among the crocodilians and their near relatives. He erected an Order Crocodylomorpha, now considered to comprise the Crocodylia, *Hallopus*, and the following "sphenosuchians": *Sphenosuchus*, *Pedeticosaurus*, *Pseudhesperosuchus*, *Hesperosuchus*, *Saltoposuchus*, *Terrestrisuchus*, and possibly the fragmentary type of *Strigosuchus* (e.g., Walker 1970; Bonaparte 1971; Gauthier 1984, although details of classification differ somewhat

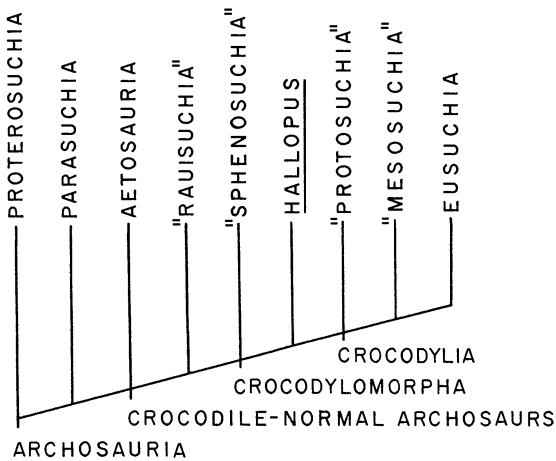


FIGURE 1. Cladogram illustrating relationships among the early archosaurs. Based in part on Gauthier (1984, 1986), Walker (1970), Bonaparte (1982), and Parrish (1983, 1986a). Groups in quotation marks are paraphyletic.

among these studies). *Gracilisuchus*, from the Middle Triassic of Argentina, may be a relative of this group (Brinkman 1981a). However, its systematic position is controversial and it will not be considered here pending further study of the type and referred material.

The so-called crocodile-normal tarsus is an important synapomorphy uniting the Aetosauria, "rauisuchians," and the Crocodylomorpha (Chatterjee 1982; Cruickshank and Benton 1985; Gauthier 1984, 1986; Parrish 1983, 1984, 1986a). Bonaparte (1982, 1984) suggested that *Trialetes* was a crocodylomorph with a mesotarsal ankle, but the single specimen Bonaparte based this conclusion on may well be a composite (J.M. Clark, pers. comm. Gauthier 1984). Gauthier (1984, 1986) united these forms plus the Phytosauria under the established taxon Pseudosuchia. Phytosaurs, which have a number of primitive characters not shared by the more derived groups and lack a true crocodile-normal tarsus (Parrish 1983, 1986b), are the sister group of the crocodile-normal archosaurs.

The presence of two divergent lineages within the early archosaurs has been recognized by several workers (Krebs 1963, 1976; Chatterjee 1978, 1982; Brinkman 1980, 1981a; Gauthier 1986; Parrish 1983, 1984, 1986a), although a few dissenting opinions have been offered (e.g., Paul 1984; Cruickshank and Benton 1985). Here I will accept Gauthier's hypothesis (1984, 1986)

that the crocodile-normal archosaurs and the Ornithosuchia (*Euparkeria*, ornithosuchids, *Lagosuchus*, *Lagerpeton*, pterosaurs, and dinosaurs [including birds]) had their last common ancestor among the most primitive archosaurs (Gauthier 1984, 1986; Parrish 1983, 1984). For this cladogram, the crocodile-normal lineage is listed as the sister group of the phytosaurs. The sister group of these two is the "Proterosuchia," the earliest and most plesiomorphic archosaurs.

The clade comprising the archosaurs with fully developed crocodile-normal ankle joint consists of the Aetosauria, "Rauisuchia," and Crocodylomorpha. Although both Chatterjee (1982) and Gauthier (1986) united these forms as the Pseudosuchia, I have avoided the use of this term because of its long history of divergent usages. In one recent example, Bonaparte (1982) defined the Pseudosuchia as the archosaurs with a crocodile-reversed joint (*Euparkeriidae* plus *Ornithosuchidae*), rather than the crocodile-normal forms. For the purpose of this paper, I have informally united the Aetosauria, "Rauisuchia," and Crocodylomorpha as the crocodile-normal archosaurs, an apparently monophyletic group. Because this paper is concerned with functional analysis rather than systematics, no new phylogenetic terms are proposed. The phylogeny assumed here is shown in Fig. 1.

The crocodile-normal archosaurs share the following derived characters (Krebs 1963, 1976; Gauthier 1986; Parrish 1983):

1. fully developed crocodile-normal tarsus, with a ball-shaped facet on the lateral side of the astragalus articulating with a socket on the medial side of the calcaneum;
2. loss of septomaxilla;
3. osteoderms on ventral surface of tail;
4. loss of postparietal in post-hatchlings (retained at early stages of ontogeny in modern crocodylians; present [secondarily?] in the modern crocodylian *Melanosuchus* [J. M. Clark, written comm. 1986]).
5. modifications of pelvis and hindlimb for erect posture discussed in this paper are also plesiomorphic for this group, although many are lost in some later crocodylians.

The monophyly of the crocodile-normal group is widely accepted (Krebs 1963, 1976; Chatterjee 1978, 1982; Cruickshank 1979; Brinkman

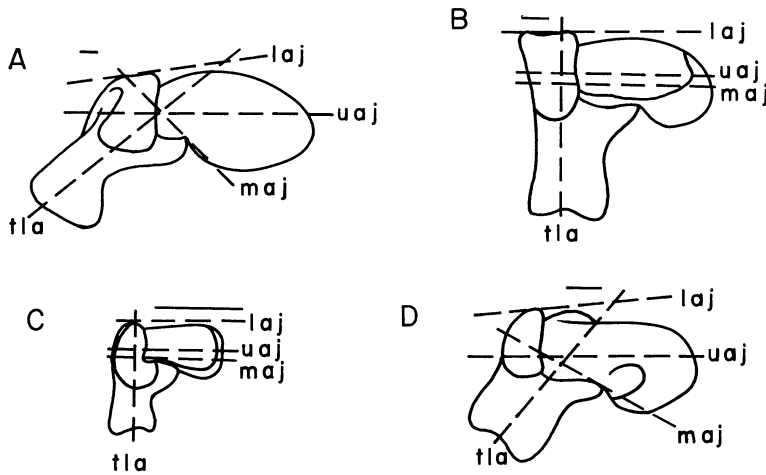


FIGURE 2. Relationship among ankle joint axes in sprawling (A) and Erect (B, C) archosaurs with crocodile-normal tarsi, and in living, "semi-erect" crocodylians. A. The phytosaur *Rutiodon*. B. The rauisuchian *Poposaurus*. C. The "sphenosuchian" *Terrestriisuchus*. D. The crocodylian *Alligator mississippiensis*. All figures in dorsal view with calcaneal tuber in horizontal plane. Scale = 1 cm. tla = long axis of calcaneal tuber; uaj = Upper ankle joint (between crus and tarsus) axis; maj = Middle ankle joint (between astragalus and calcaneum) axis; laj = Lower ankle joint (between proximal and distal tarsals) axis.

1980, 1981a; Thulborn 1980; Parrish 1983, 1984, 1986a; Gauthier 1986; Paul 1984; Cruickshank and Benton 1985), although some authors (e.g., Chatterjee 1982; Thulborn 1980; Paul 1984; Cruickshank and Benton 1985) would place certain dinosaurs as derived members of the clade, and many authors (e.g., Chatterjee 1978; Cruickshank 1979; Gauthier 1986) would place the phytosaurs as the most primitive members of the clade on the basis of Chatterjee's (1978) identification of the phytosaur tarsus as truly crocodile-normal, a position (S. Chatterjee, written comm. 1987) that he apparently no longer supports.

A clade comprising the "Rauisuchia" and Crocodylomorpha can be defined on the basis of the following characters:

1. first (atlantal) intercentrum longer than wide (Gauthier 1986);
2. axial diapophyses reduced or absent (Gauthier 1986);
3. posteriorly elongated basipterygoid processes;
4. paramedial osteoderms longer than wide, subrectangular in shape (armor not known with certainty in poposaurid rauisuchians, and possibly absent in the "sphenosuchian" *Pseudohesperosuchus*);
5. calcaneal tuber terminates in flared expansion, with distinct median, vertically aligned groove

for passage of gastrocnemius tendon to ventral foot;

6. fewer than four phalanges on pedal digit V (Gauthier 1986).

A clade comprising *Postosuchus* and the crocodylomorphs can be defined by the following characters:

1. fewer than three phalanges on pedal digit V, metatarsal V reduced to a splint;
2. posterior margin of lateral temporal fenestra made up entirely of expanded dorsal process of the quadratojugal; ventral process of squamosal reduced.

The monophyletic Crocodylomorpha (Crocodylia plus *Hallopus* plus "Sphenosuchia") can be defined on the basis of the following characters (Walker 1970; Bonaparte 1982; Gauthier 1986 [characters 4, 5 cannot be evaluated in *Hallopus*, as the single specimen lacks a skull]):

1. elongate radiale and ulnare;
2. elongate posteromedial process of coracoid;
3. loss of clavicle;
4. no ventral process of squamosal;
5. partial secondary palate developed by contact between medial processes of the maxillae and premaxillae.

The monophyletic Crocodylia can be defined

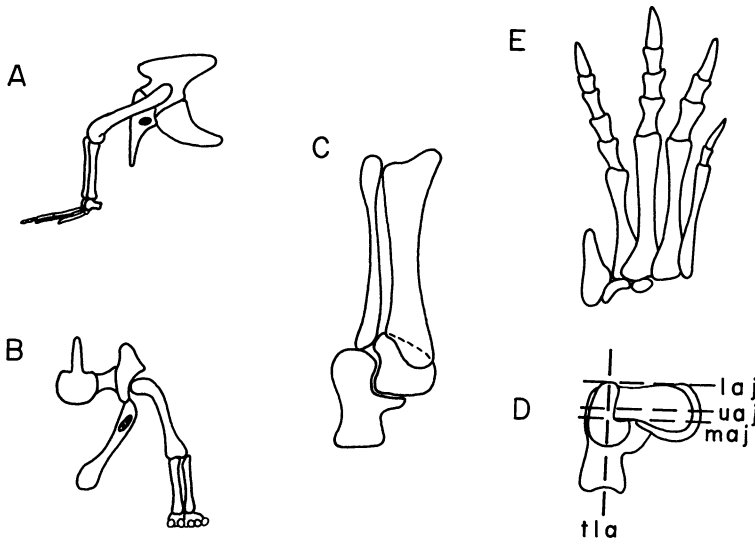


FIGURE 3. Erect gait summary. A. Lateral view of pelvis and hindlimb, showing anterior elongation of the iliac blade, ventral elongation of the pubis and ischium, and anterior direction of the pes. B. Anterior view of left hindlimb, showing columnar limb arrangement, femoral head development, and anterior direction of pes. C. Posterior view of left crus and tarsus (calcaneum fully dorsiflexed), showing vertical relationship between crus and tarsus, and arrangement of astragalo-calcaneal joint. D. Proximal view of left tarsus, showing relationship between various functional axes in ankle. E. Left pes in dorsal view, showing anterior direction and reduction of fifth digit and mediolateral overlapping of metatarsus.

on the following characters (Romer 1956; Steel 1973; Busbey and Gow 1984):

1. extensive suture between quadrate and squamosal;
2. flattened, sculptured skull deck;
3. pubis reduced, nearly excluded from acetabulum;
4. pneumatic quadrate, supraoccipital, and parietal;
5. quadrate and pterygoid strongly sutured;
6. small supraoccipital, excluded from foramen magnum;
7. fused basiptyergoid articulation.

Results

Functional and morphological attributes of erect posture in crocodile-normal archosaurs.—In this section, the morphological features and functional correlates of erect posture in non-crocodylomorph archosaurs with fully developed crocodile-normal tarsi (comprising the “rauisuchians” and Aetosauria) are detailed and contrasted with the condition in the earliest, sprawling archosaurs (Figs. 2, 3). Next, the morphological patterns in “sphenosuchians,” *Hallopus*, and “protosuchi-

ans” are described and contrasted with the structure in the other forms. The hindlimb and pelvis will be discussed element by element. Both an articulated and an exploded *Alligator mississippiensis* hindlimb are illustrated (Fig. 4) to demonstrate how the various limb elements articulate.

Pelvis (Fig. 5).—In the earliest archosaurs (e.g., *Proterosuchus*) and throughout the early diapsids, the pelvis has the following plesiomorphic features:

1. The ilium has a shallow, imperforate acetabulum and lacks any anterior extension of the blade.
2. The ventral pelvic elements are short and form a broad, ventral pelvic trough by extensive midline symphyses between pubes and ischia.

Aetosaurus, “rauisuchians,” and primitive crocodylomorphs differ from the primitive condition as follows:

1. The acetabulum is much deeper, and perforate in some groups (e.g., *Poposaurus*, Colbert 1961; *Postosuchus*, Chatterjee 1985).
2. A prominent anterior flange is developed on the iliac blade, moving the origins of the iliofemoralis muscle group anteriorly, and in-

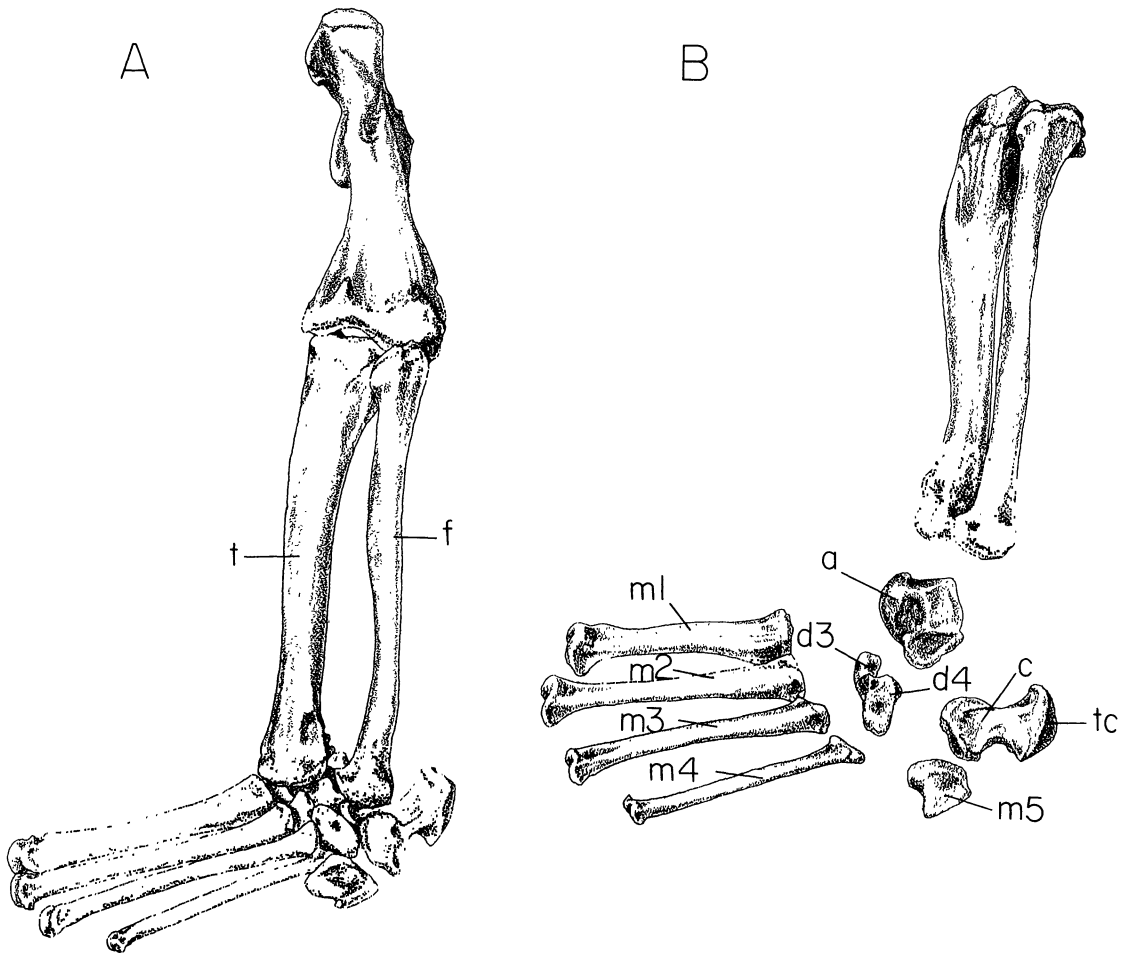


FIGURE 4. Articated and exploded left hindlimb of the recent eusuchian crocodile *Alligator mississippiensis*, showing orientation of bones and positions of facets. A. Lateral view, articulated. B. Lateral view, exploded.

Legend: a = astragalus; c = calcaneum; d3, d4 = distal tarsals three and four; f = fibula; m1–m5 = metatarsals one through five; t = tibia; tc = calcaneal tuber.

creasing their mechanical advantage as femoral protractors.

3. The ventral pelvic elements are expanded ventrally, with subsequent disruption of the pelvic trough and decrease in length of symphyses between pelvic elements. This served to move the origins of the femoral protractors and retractors further from the fulcrum of the femur, increasing their mechanical advantages.

A major point of divergence in pelvic morphology among the crocodile-normal archosaurs involves the angulation of the ilium and the disposition of the acetabulum. In the Aetosauria and some rauisuchid "rauisuchians," the ilium

was angled ventrolaterally, with the result that the acetabulum faced downward more than outward (Parrish 1983, 1986a; Bonaparte 1984). The ventrally oriented acetabulum was probably a graviportal adaptation in these large, often heavily armored animals. In the lighter built and presumably more agile poposaurids (Chatterjee 1985) and primitive crocodylomorphs (e.g., Walker 1970; Crush 1984), the ilium was vertically oriented, the acetabulum faced laterally rather than ventrolaterally, and a prominent supraacetabular shelf is present dorsal to the hip joint (Parrish 1983, 1986a; Chatterjee 1985). Furthermore, the acetabulum was deeper and usually perforate, and the femoral head fitted

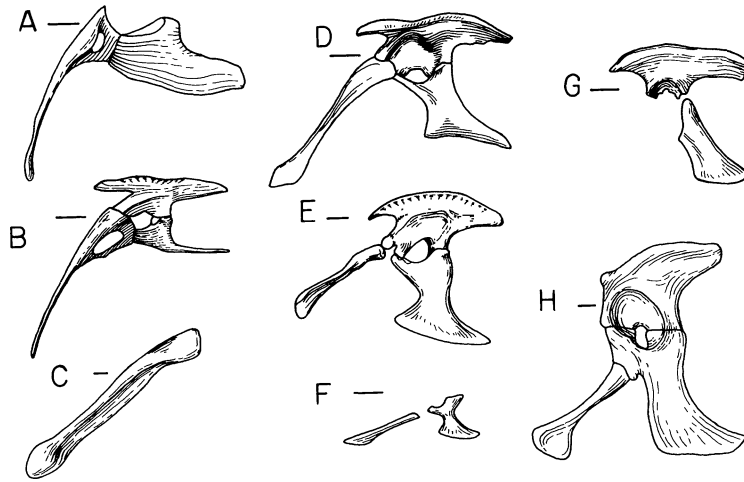


FIGURE 5. Pelves of crocodylomorphs. A. The "sphenosuchian" *Saltoposuchus*, after Huene (1925). B. The "sphenosuchian" *Terrestriisuchus*, after Crush (1984). C. The "sphenosuchian" *Hesperosuchus*, based on new specimen (UCMP 129740). D. The "protosuchian" *Protosuchus*, based in part on Colbert and Mook (1951). E. The "protosuchian" *Orthosuchus*. F. The "protosuchian" *Erythrochampsia*. G. *Hallopus*. H. The recent eusuchian *Alligator mississippiensis*. Scale = 1 cm.

more tightly into the acetabulum. As a result, the hip joint was osteologically constrained to restrict adduction of the femur, which mainly moved in a parasagittal plane.

Pelves of the early crocodylomorphs are all of the same basic pattern, consistent with that of the erect crurotarsal archosaurs. Among the "sphenosuchians," a complete pelvis is known in *Terrestriisuchus*, and ventral pelvic elements are known in *Saltoposuchus* and in the new specimen of *Hesperosuchus* (Parrish, ms.). Complete pelves are known in the "protosuchians" *Protosuchus* and *Orthosuchus*, and ventral elements are known in the type of *Erythrochampsia*. The ilium and all but the proximal end of the ischium are known in *Hallopus*. In *Saltoposuchus* and *Terrestriisuchus*, the pubis is rodlike, downturned ventrally, and has a proximal obturator foramen. In the protosuchians *Protosuchus*, *Orthosuchus*, and *Erythrochampsia*, and in the sphenosuchian *Hesperosuchus*, the pubes are straight or gently sigmoid, expanded slightly at their distal ends, and lack an obturator foramen. In all of these early crocodylomorphs, the pubis is longer than the ischium, and an extensive pubic midline symphysis is present. A single iliac pattern is shared by "sphenosuchians," "protosuchians," and *Hallopus*, with a deep, perforate acetabulum and an iliac blade with a prominent anterior projection. Major points of variation among early crocody-

lomorphs involve the relative length of the pubis (much shorter in *Orthosuchus* than in *Protosuchus* or in the "sphenosuchians") and the absence of the plesiomorphic obturator foramen in *Hesperosuchus* and in the "protosuchians" (Fig. 5).

In living crocodylians, the bony pubis is reduced, and it projects no farther ventrally than the ischium. However, a marked cartilagenous expansion of the pubis occurs, increasing the effective area of muscle attachment. The ischium is similar in development to that of *Protosuchus*, with the exception that the peduncle for articulation with the ilium is expanded anteriorly relative to the primitive condition, excluding the pubis from contact with the ilium. The acetabulum is laterally directed, shallower, and offers fewer osteological constraints to femoral movement than in early crocodylomorphs. The anterior expansion of the iliac blade is reduced to a slight tuberosity.

Femur.—The femora in primitive diapsids (e.g., *Petrolacosaurus*) and in primitive archosaurs (e.g., *Proterosuchus*) have the following characters:

1. proximal end with a simple, terminal head without any medial offset;
2. extensive adductor fossa on the adductor face of the femur (the ventral side in sprawling forms, the medial side in erect forms);

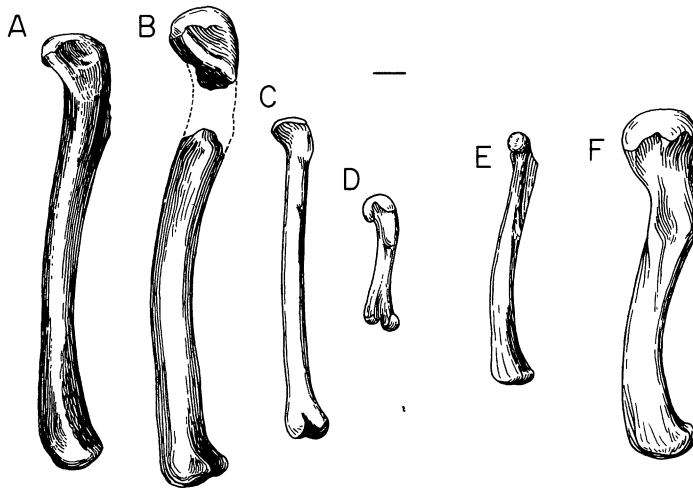


FIGURE 6. Left femora of crocodylomorphs, oriented with long axis through distal condyles perpendicular to page. A. The "sphenosuchian" *Hesperosuchus*. B. The "sphenosuchian" *Pseudhesperosuchus*, after Bonaparte (1971). C. The "sphenosuchian" *Terrestrisuchus*. D. The "protosuchian" *Orthosuchus*, partly after Nash (1975). E. *Hallopus*. F. The recent eusuchian *Alligator mississippiensis*. Scale = 1 cm.

3. broad, poorly defined distal condyles, facing as much distally as posteriorly.

In erect forms, the following modifications are seen:

1. development of a distinct, medially directed head;
2. loss of adductor fossa, development of fourth trochanter on the retractor surface of the femur;
3. development of prominent, posteriorly directed femoral condyles;
4. development of a "fibular condyle" lateral to the femoral condyles for the fibular meniscus to slide across with hingelike flexion of the knee (Parrish 1983, 1986a).

A consistent femoral pattern is seen in "sphenosuchians" and "protosuchians" (Fig. 6):

1. A prominent head deviates medially from the shaft. In the crocodile-normal archosaurs (Parrish, 1983), the head is a rounded bulge that deviates from the proximal shaft, but is not offset by a distinct neck as is the case in dinosaurs (including birds).
2. The condyles are prominent and project posteriorly from the distal end of the femur.
3. In larger animals, such as the new specimen of *Hesperosuchus*, a marked fibular condyle is present lateral to the femoral condyles. *Hal-*

lopus is unique among crocodile-normal archosaurs in having a femoral head offset from the shaft by a prominent, medially projecting neck. In living crocodylians, the morphology of the proximal end of the femur is similar to that in "protosuchians" and "sphenosuchians." The distal condyles are also prominent, although the fibular condyle is more reduced than in the former groups.

Crus.—In sprawling early diapsids (such as *Petrolacosaurus*) and in primitive archosaurs (such as *Proterosuchus*), the tibia and fibula have simple rounded articular surfaces proximally and distally. The tibia and fibula of aetosaurs and "rauisuchians" are distinguished by the following characters:

1. Well defined facets on their distal ends articulate closely with the astragalus and calcaneum. The distal facet on the tibia is saddle shaped, corresponding to the complex tibial facet on the astragalus.
2. Distinct astragalar and calcaneal facets are present on the distal end of the fibula. Sloping facets, separated by a median ridge, are present on the proximal ends of the tibiae. They allow tight articulation with the distal femur, stabilize the knee joint, and permit hingelike flexion of the crus on the femur.

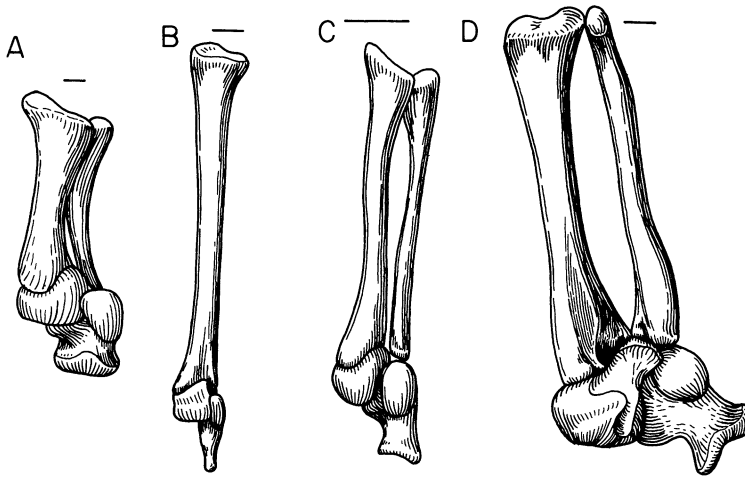


FIGURE 7. Left crura and tarsi of crocodile-normal archosaurs, shown with calcaneum fully dorsiflexed in order to depict relationship between long-axis of tuber and crurotarsal alignment. A. The aetosaur *Desmatosuchus*. B. *Hallopus*. C. The "sphenosuchian" *Terrestriusuchus*. D. The extant eusuchian *Alligator mississippiensis*. Scale = 1 cm.

Crural elements are known in *Pseudhesperosuchus*, *Sphenosuchus*, *Terrestriusuchus*, *Protosuchus*, and *Orthosuchus* (Fig. 7). All conform to the pattern seen elsewhere in erect crocodile-normal archosaurs. In living crocodylians, the proximal end of the tibia is flat, and the distal end of the bone is gently saddle-shaped, in contrast to the sharply contoured astragalus facets in early crocodylomorphs. Both modifications to the primitive pattern serve to simplify the bony knee and ankle joints, permitting the wider range of movement required by the diversity of gaits employed by modern crocodylians.

Tarsus.—For the discussion of tarsal mechanics, three ankle joints are defined, patterned after a terminology set forth by Szalay (e.g., 1984). The upper ankle joint (UAJ) is the joint between the proximal tarsals (astragalus and calcaneum) and the crus (tibia and fibula). The middle ankle joint (MAJ) is between the two proximal tarsals, and the lower ankle joint (LAJ) is between the proximal and distal tarsal rows. Another important axis is the long axis of the calcaneal tuber (TLA), which is related to the line of pull of the gastrocnemius (the main pedal plantarflexor) relative to the tarsus and pes. Axes are illustrated in Figs. 2 and 3.

The UAJ is measured as the line perpendicular to the long axes of the articular facets on the astragalus and calcaneum for the tibia and fibula. Articulation of the crus and tarsus of many recent

and fossil archosaurs has shown that the UAJ can be measured accurately by this method. The MAJ is best measured by manipulation of specimens (i.e., rotating the calcaneum on the astragalus and plotting the subsequent axis of rotation). The axis can also be estimated by examining the conical "socket" on the calcaneum for articulation with the astragalus. Experimentation has shown that the MAJ passes through the apex of the cone, and the central axis of the

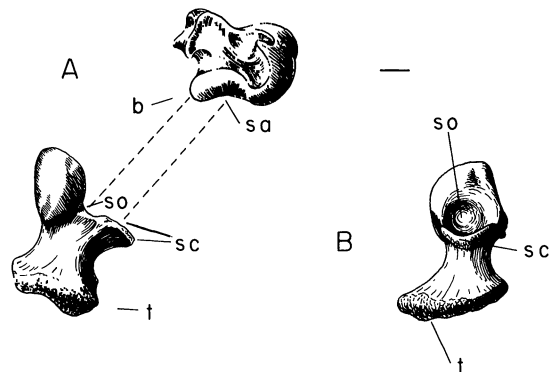


FIGURE 8. Left tarsus of *Alligator mississippiensis*, showing details of articulation between astragalus and calcaneum. A. Astragalus and Calcaneum in posterior view, with calcaneum fully dorsiflexed. B. Medial view of calcaneum. Scale = 1 cm.

Legend: b = "ball" for articulation with calcaneum; sa = astragalus part of sustentaculum; sc = sustentacular groove of calcaneum; so = calcaneal socket for articulation with astragalus; t = calcaneal tuber.

TABLE 1. Angles between functional axes in various archosaur tarsals. See text and Figs. 1, 2 for joint and axis definitions.

Taxon/specimen number	Acute angle between joints or axes (degrees)				
	UAJ/LAJ	UAJ/MAJ	MAJ/LAJ	MAJ/TLA	UAJ/TLA
Primitive Archosaurs					
Proterosuchia					
<i>Proterosuchus</i> MCZ 4301 (cast of NM C 3016)	20	*	*	*	20
Parasuchia (Phytosaurs)					
<i>Rutiodon</i> USNM 18313	20	39	60	83	60
Crocodyle-Normal Archosaurs					
Aetosauria					
<i>Tytophorax</i> MCZ 1488	0	0	0	90	90
Podosauridae ("Rauisuchia")					
<i>Podosaurus</i> UCMP 34477, 34487	0	0	0	90	90
Crocodylomorpha ("Sphenosuchia")					
<i>Terrestriusuchus</i> P 73/1, P110/1	0	0	0	90	90
? "Sphenosuchia" CUP 12/13	**	1	**	90	90
Crocodylia					
"Protosuchia"					
<i>Orthosuchus</i> SAM K 409***	0	0	0	90	90
Modern Eusuchia					
<i>Alligator</i> miss. uncat. UCM #1	9	45	35	85	52
<i>Alligator</i> miss. uncat. UCM #2	11	45	35	85	50
Hatchling <i>Alligator</i> miss. uncat. UCM #3	43	21	23	50	32
<i>Caiman sclerops</i> UCM OR3	18	60	43	85	38
<i>Crocodylus acutus</i> UCM uncat.	8	50	50	72	65

* Immobile middle ankle joint, hence MAJ cannot be measured.

** Anterior part of calcaneum missing.

*** Specimen not examined. Axes taken from figures and photographs.

cone is coincident with the MAJ axis. Furthermore, the sustentacular groove just medial to the socket represents the site of articulation of the calcaneum with the part of the astragalus just medial to the ball-shaped facet for articulation with the calcaneum (Fig. 8). The long axis of the sustentacular facet is parallel to the MAJ.

The LAJ is best determined by direct manipulation of specimens. This is difficult in fossil specimens because few articulated proximal and distal tarsal complexes are known among the fossil crocodylomorphs. It can be estimated by drawing a line connecting the mediolateral long axes of the facets on the astragalus and calcaneum for articulation with the distal tarsals and metatarsals.

In sprawling archosaurs, such as the phytosaur *Rutiodon*, the long axes of the UAJ, MAJ and LAJ are all mutually oblique. In sprawling tetrapods, rotation of both the femur and crus around their long axes is important to the step cycle, hence both rotation and flexion are involved in the various ankle joints (e.g., Rewcastle 1980; Brinkman 1981b). In erect archosaurs, the long axes of the three ankle joints are parallel, favoring simple, hinge-like motion within a plane parallel

to the vertebral column. Ankle joint axis measurements of fossil and recent crocodylomorphs, along with those of some selected primitive archosaurs, are listed in Table 1.

Another feature that reflects gait in archosaurs is the articulation between crus and tarsus. The primitive condition for archosaurs consists of simple, planar or concave-convex joints between tibia and astragalus and between fibula and calcaneum, with a secondary articulation between astragalus and fibula. The astragalus and calcaneum articulated closely, with little, if any, movement possible between the two bones. In the later, crurotarsal archosaurs, a mobile joint developed between astragalus and calcaneum, and this required a mobile joint between fibula and calcaneum. The fibular facet of the calcaneum is a hemicylindrical surface that slides along a simple planar or concave facet on the distal end of the fibula. The astragalus was functionally united with the tibia, and an immobile joint was developed between the two bones. A tight, but slightly more flexible, ligamentous joint was developed between astragalus and fibula. In living crocodylians and in some "thecodontians" such as *Euparkeria*, the joint between tibia and as-

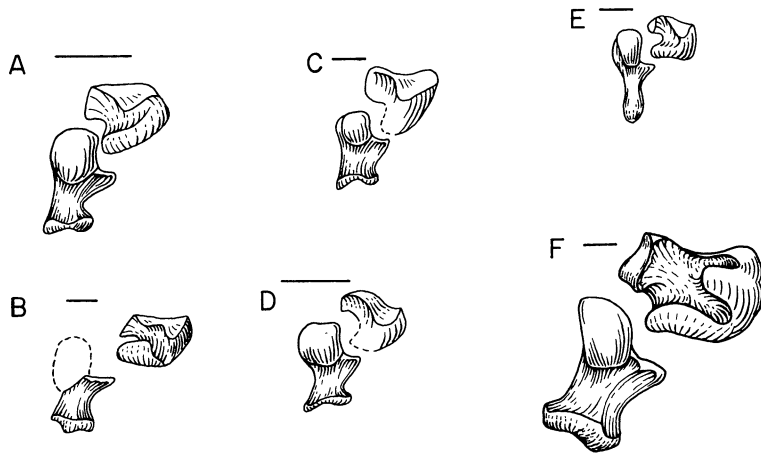


FIGURE 9. Tarsi of crocodylomorphs. A. The "sphenosuchian" *Terrestriisuchus*. B. An isolated "sphenosuchian" tarsus from the Lower Jurassic Lufeng Formation of Yunnan. C. The "protosuchian" *Protosuchus*. D. The "protosuchian" *Orthosuchus*. E. *Hallopus*. F. The crocodylian *Crocodylus niloticus*. Scale = 1 cm. Tarsi in posterior view with calcaneum fully dorsiflexed (i.e., calcaneal tuber in vertical plane). Figure A partially after Crush (1984).

tragalus is tilted when the MAJ axis is horizontal, with the result that the crus is angled somewhat medially (Fig. 7D). In erect crurotarsal archosaurs of both the crocodile-normal and crocodile-reverse types, a vertical joint was developed between tibia and astragalus, by a pair of tightly articulating, saddle-shaped facets. This arrangement served to prevent any movement between the two bones and to stabilize the crurotarsal unit when the foot struck the ground (Fig. 7A–C).

The same basic tarsal pattern is observed in "sphenosuchians" (e.g., *Terrestriisuchus*, *Platyognathus*), "protosuchians" (e.g., *Protosuchus*, *Orthosuchus*), and *Hallopus* (Figs. 2, 9):

1. the three ankle joint axes are parallel, and perpendicular to the line of march for the animal;
2. the calcaneal tuber is directed posteriorly, and is perpendicular to the ankle joint axes and parallel to the line of march;
3. the crus projects vertically from the tarsus and a tightly fitting, saddle shaped joint is present between astragalus and tibia.

In living crocodylians:

1. the three ankle joint axes are oblique to one another;
2. the calcaneal tuber is directed posterolaterally relative to the MAJ axis;
3. the crus is directed somewhat medially when the MAJ axis is horizontal, and the astragalus

and tibia articulate by a curved but near-planar facet. Compared to the "protosuchian" condition, the joint between astragalus and calcaneum in living crocodylians is distinguished by the outturning of the sustentacular groove of the calcaneum. The eversion of the calcaneal part of the sustentaculum and the lateral outturning of the calcaneal tuber relative to the body of the bone are the main modifications to the primitive crocodylomorph tarsal pattern (Figs. 8, 9). These result in the obliquity of ankle joints that characterizes living crocodylians.

Hecht and Tarsitano (1984) studied the pes and tarsus of *Protosuchus* and interpreted it to be more sprawling than modern crocodylians. They based this argument on the presence of an angled distal roller on the astragalus in the holotype of *Protosuchus*. However, the distal roller of the astragalus, which is the facet for articulation with the medial metatarsals, is roughly hemispherical and confluent with a more extensive ventral facet in all crocodile-normal archosaurs. The roller offers no particular restrictions to movement at the joint, and it is not well preserved in the holotype. Thus, assignment of any functional significance to its inclination would be difficult. The preserved features of the hindlimb and pelvis in that specimen are consistent with the morphological patterns for erect posture presented here.

Pes.—The primitive archosaur pes (e.g., *Pro-*

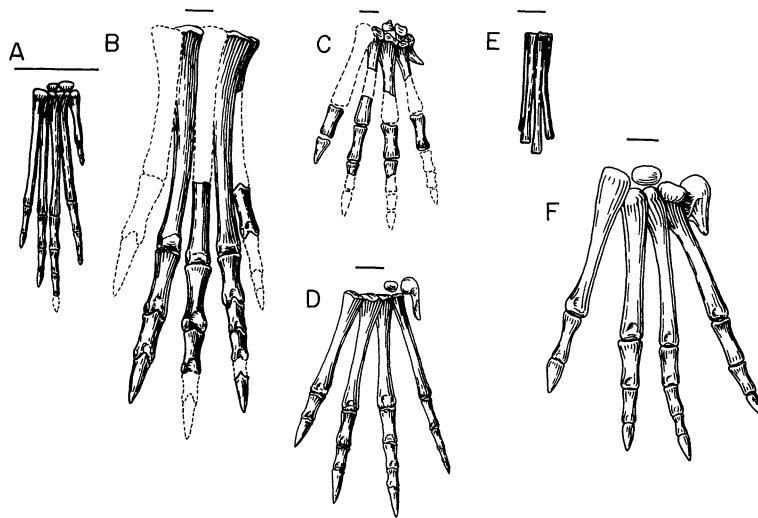


FIGURE 10. Pedes of crocodylomorphs. A. The "sphenosuchian" *Terrestriisuchus*, after Crush (1984). B. The "sphenosuchian" *Hesperosuchus*, after Colbert (1952). C. The "protosuchian" *Orthosuchus*, after Nash (1975). D. The "protosuchian" *Protosuchus*, after Colbert and Mook (1951). E. *Hallopus*, after Walker (1970), in part. F. The extant eusuchian *Alligator mississippiensis*. Scale = 1 cm.

terosuchus, *Erythrosuchus*) is broad, with a divergent fifth digit and minimal overlap between metatarsals. At least in living lizards, the divergent fifth digit serves as a pivot around which the foot rotates during normal locomotion (Brinkman 1981b).

In erect crurotarsal forms, the foot has the following characteristics:

1. the fifth digit is directed anteriorly, and the fifth metatarsal lacks the medially directed process seen primitively;
2. the metatarsals overlap significantly at their proximal ends, forming a strong metatarsal wedge;
3. the foot is symmetrical and mediolaterally compressed, with the external digits often reduced. These modifications of the primitive condition allow the foot to function as a lever for flexion and extension in a single plane.

The pes is well known in *Terrestriisuchus*, *Protosuchus*, *Orthosuchus*, and *Hallopus*. In *Terrestriisuchus*, digit V is reduced, and the remaining digits are symmetrical (Fig. 10; Crush 1984). In *Protosuchus*, *Hallopus*, and *Orthosuchus*, the derived condition retained in living crocodylians is observed, with the fifth digit reduced to a metatarsal splint, and the remaining digits forming a bilaterally symmetrical foot (Fig. 10). In early

crocodylomorphs, the proximal ends of the metatarsals significantly overlap. The condition in extant crocodylians is similar, although the overlap among the proximal ends of the metatarsals is reduced. In the belly walk, living crocodylians may evert the fourth digit to use as a pivot for pedal rotation in much the same way that the fifth digit is employed in lizards (Parrish, pers. obs.).

Discussion

Implications for locomotor capabilities of fossil crocodylians.— A character analysis of the "sphenosuchians," "protosuchians," and *Hallopus* shows that hindlimb morphology in all members of these groups examined is consistent with the pattern seen in erect crocodile-normal archosaurs such as aetosaurs and poposaurids. Because the suite of morphological adaptations for erect posture is shared by primitive outgroups among the crocodile-normal archosaurs, phylogenetic support is offered for the plesiomorphy of these characters in the Crocodylomorpha.

Several of the earliest members of the Crocodylomorpha have been interpreted as terrestrial (e.g., Colbert and Mook 1951; Colbert 1952; Lull 1953; Kermack 1956; Walker 1970; Crush 1984; Whetstone and Whybrow 1983). The other erect crocodile-normal archosaurs have been

widely interpreted as terrestrial (e.g., Walker 1961; Bonaparte 1984; Chatterjee 1985; Parrish 1983, 1984, 1986a). As a rule, an erect stance and associated gaits are largely restricted to terrestrial animals (Charig 1972). Modern aquatic "reptiles," such as turtles (Walker 1973) and marine iguanas, assume a sprawling posture, at least when swimming. Modern *Crocodylus* and *Alligator* assume an erect stance when travelling overland, and the sprawling belly walk when entering or travelling in the water (Cott 1961; Parrish, pers. obs.). Thus, the ubiquity of an erect posture in early crocodylomorphs complements evidence based on paleoecology (this paper) and "protosuchian" armor structure (Ross and Meyer 1984) for terrestriality in these forms.

The mosaic of essentially erect (e.g., high walk, juvenile gallop) and sprawling (belly walk, swimming gait) stances and gaits in living crocodylians can be considered an overprint of a derived type of locomotor behavior on a primitive pattern. That is, the gaits with erect posture are retained morphological and behavioral patterns characteristic of the early crocodylomorphs, whereas those with a more sprawling posture are modifications of the primitive patterns in modern crocodylians and are probably associated with secondarily aquatic habits.

The first clearly aquatic crocodylians are the teleosaurs that appeared in the Liassic, followed by the metriorhynchids in the Middle Jurassic (Buffetaut 1979, 1982). Some other "mesosuchians" have apparently aquatic specializations of limbs and skulls (Buffetaut 1979). A number of later Mesozoic crocodylians have been interpreted as terrestrial on the basis of cranial structure, including the "protosuchian" *Gobiosuchus*, and the notosuchian and sebecosuchian "mesosuchians" (Buffetaut 1979, Busbey 1986).

The earliest members of the living crocodylian suborder Eusuchia appear in the Cretaceous (Buffetaut 1979). Well-preserved postcrania of early eusuchians are rare, and determination of the point at which "modern" crocodylians became secondarily aquatic will have to await further study of later fossil crocodylian material. All living "eusuchians" studied share similar limb specializations permitting sprawling and more erect gaits, so these adaptations either appeared at or near the beginning of eusuchian history or, less prob-

ably, were derived independently in several eusuchian lineages.

Although all primitive crocodylomorphs considered in this paper have adaptations for erect posture, they also show a variety of locomotor specializations within this basic pattern. For example, *Hallopus*, *Terrestriisuchus*, and *Lesothosuchus* all have very elongate limbs relative to their trunk lengths that probably indicate cursorial specializations (Walker 1970; Whetstone and Whybrow 1983; Crush 1984). "Protosuchians" such as *Protosuchus* and *Orthosuchus* have shorter, thicker limb elements and probably were not rapid runners. The Upper Triassic/Lower Jurassic crocodylomorphs were diverse, and probably occupied a variety of small carnivore and omnivore roles.

Paleoecology of fossil crocodylomorphs.— "Sphenosuchians" and "protosuchians" are consistently found in predominant association with terrestrial rather than aquatic faunas (Table 2). The Upper Triassic "sphenosuchians" in America and Europe occur primarily in association with fully terrestrial animals such as aetosaurs (Chinle, Stubensandstein, Los Colorados), rauisuchians (Chinle, Los Colorados, Stubensandstein), saurischians (Chinle, Stubensandstein, and Los Colorados), and ornithischians (Chinle). In the Chinle localities from which *Hesperosuchus* is known, fish associations occur as isolated ganoid scales and lungfish teeth (Colbert 1952; Jacobs and Murry 1980; Parrish, in prep.). Phytosaurs are associated with "sphenosuchians" in the Chinle and Stubensandstein, but they are much less abundant at these crocodylomorph-bearing localities than is the rule in these Late Triassic formations, where they are often the most abundant vertebrate fossils.

Liassic crocodylomorphs occur in fully terrestrial associations with prosauropods, ornithischians, tritylodonts, and early mammals in America, Britain, China, and southern Africa. However, aquatic turtles and fish are associated with a new "sphenosuchian" from the Kayenta Formation of Arizona (Clark and Fastovsky 1986; J. M. Clark, written comm. 1986).

More detailed taphonomic study is required to evaluate the faunal associations of primitive crocodylomorphs in detail. However, the ubiquity of crocodylomorph occurrences with terres-

trial organisms in the Triassic and Early Jurassic and the relative rarity of their associations with aquatic animals support the hypothesis that early crocodylomorphs occurred in more terrestrial environments than do living crocodylians.

Non-locomotor support for the hypothesis of terrestrial habits for the "protosuchians" is provided in Ross and Meyer's (1984) survey of the dorsal armor of crocodylians. They argued that the structure of the armor in protosuchians would limit mobility in their cervical regions and prevent the backward tossing of the head characteristic of modern crocodylians feeding aquatically. Thus, they hypothesized that "protosuchians" were primarily terrestrial and correlated reduction in the completeness of the dorsal armor with attainment of aquatic habits in the "mesosuchians." Frey (1984, 1985) hypothesized that the carapace, vertebral column, and epaxial musculature in living and fossil crocodile-normal archosaurs form a structure analogous to a truss bridge that stabilizes the trunk during locomotion with erect posture.

Implications for the evolution of stance and gait in crocodile-normal archosaurs.—In an influential paper, Charig (1972) debunked the hypothesis that bipedality was the main locomotor adaptation that distinguished archosaurs from primitive amniotes. Charig instead showed that the important transition on the evolution of locomotion in archosaurs was that between sprawling and erect posture. In his scenario, the transition took place in two stages:

1. from a sprawling posture in primitive amniotes to a "semi-improved" stance in crocodylians and most "thecodontians";

2. from the plantigrade, "semi-improved" posture in primitive archosaurs to the erect, digitigrade, "fully improved" stance in dinosaurs and birds. Charig used hindlimb morphology and locomotion in modern crocodylians as the structural and behavioral models for his semi-improved posture.

Several studies have established that an erect posture was widespread among early archosaurs with both crocodile-normal and crocodile-reversed tarsi (Walker 1970; Parrish 1983, 1984, 1986a; Crush 1984; Whetstone and Whybrow 1983; Chatterjee 1985). Morphological evidence for an intermediate gait such as Charig's "semi-

improved" gait is not extensive. "Thecodontians" are either sprawling (e.g., *Proterosuchus*, *Erythrosuchus* [Cruickshank 1972; Parrish 1983, 1984, 1986a]) or erect. The major exceptions are the primitive ornithosuchian *Euparkeria* (Parrish 1983, 1984, 1986a) and the phytosaurs, which apparently had a sprawling to semi-erect posture, but with partial development of a crocodile-normal tarsus and of the femoral head structure seen in crocodile-normal archosaurs (Parrish 1986b). Phytosaurs were clearly amphibious (Parrish 1986b), whereas *Euparkeria* was terrestrial (Ewer 1965). Whether these forms represent good models for transitional forms in the shift from sprawling to erect archosaurs is an open question. Sprawling posture is widespread among the primitive outgroups of the crocodile-normal archosaurs (e.g., Brinkman 1981a; Parrish 1986a). Three possibilities exist for the origin of the erect posture in the crocodile-normal archosaurs:

1. The presence of similar erect gaits in archosaurs with both a crocodile-normal and crocodile-reverse tarsus could suggest that erect gait was primitive for non-proterosuchian archosaurs. If this scenario is correct, *Euparkeria* and the phytosaurs would have attained their more sprawling locomotor adaptations either secondarily or independent of the Ornithosuchidae and crocodile-normal archosaurs. Furthermore, this scenario predicts an ancestral form with an erect posture and an immobile, duplex ankle joint of the type present in proterosuchians and other early diapsids (Cruickshank 1979; Brinkman 1981a; Parrish 1986a), or the derivation of one of the crurotarsal ankle types (crocodile-normal or crocodile-reverse) from the other. The presence of fundamental differences in the locomotor patterns in erect crocodile-normal archosaurs and ornithosuchians (e.g., Chatterjee 1982; Parrish 1983, 1986a) effectively falsifies this hypothesis.

2. If the phytosaurs are the sister group of the crocodile-normal forms and *Euparkeria* is a primitive member of the crocodile-reverse clade, then erect posture would have had to evolve independently in each lineage. If the two different types of functional crurotarsal ankle joints were derived independently from the primitive diapsid condition, allowing a more mobile ankle joint in the erect forms, then independent origins of erect

TABLE 2. Faunal associations of primitive crocodylomorphs.

Taxon	Age/formation	Locality	Associated fauna	Lithology/depositional env.	Reference(s)
Sphenosuchia	Late Triassic				
<i>Hesperosuchus</i>	L. Pet. Forest Mbr., Chinle Fm. L. Pet. Forest Mbr., Chinle Fm.	(1) Ward's Terrace, Az. (2) Placeras Quarry, Az.	phytosaur frags., fish scales <i>Placeras</i> , aetosaurs, cynodonts, rauisuchians, phytosaurs, amph.	mudstone/floodplain dark mudstone/anoxic pond	Colbert 1952 Jacobs and Murry 1980, unpubl. UCMF material
<i>Saltoposuchus</i>	U. Pet. Forest Mbr., Chinle Fm.	(3) Bolt Quarry, Az.	<i>Coelophysis</i> , ?ornithischian, cynodont, phytosaur scrap, metoposaurid, lungfish teeth <i>Procompsognathus</i>	gleyed mudstone/floodplain	Parrish, in prep.
<i>Terrestri-suchus</i>	Upper Stubensandstein Fissure Fills	Pfaffenhofen, W. Germany		ss, mudstone/fluvial, floodplain*	Huene 1921; Tucker and Benton 1982
<i>Pseudhesperosuchus</i>	Los Colorados	Pant-y-ffynon, Wales	trilophosaurid, lepidosaurs	fissure fills, terrestrial	Crush 1984; Kermack 1956; Robinson 1957
<i>Sphenosuchus</i>	Liassic U. Elliot Fm.	La Rioja Prov., Argent.	aetosaur, rauisuchid, theropod, prosauropod, tritylodont*	ss, mudstone/fluvial, floodplain*	Bonaparte 1971
<i>Clarencea</i>	U. Elliot Fm.	Paballong, S. Africa	ictidosaur, ornithischians	mudstone, ss/fluvial, aeolian, floodplain*	Haughton 1924; Kirching and Raath 1984
<i>Pedeticosaurus</i>	Clarens Fm.	Roodrai, Buck Camp, S. Afr.	ictidosaur, prosauropod, ornithischian	mudstone, ss/fluvial, aeolian, floodplain*	Kirching and Raath 1984
<i>Platyognathus</i> , <i>Dibothrosuchus</i>	L. Lufeng Series	Near Rosendal Lufeng, China	prosauropods prosauropods, mammals, tritylodonts, theropods, ornithischian*	ss, siltstone/aeolian, fluvial* mudstone, ss/fluvial floodplain, lacustr.	Kitching and Raath 1984 Simmons 1965
Protosuchia	Upper Triassic				
<i>Hemiprotosuchus</i>	Los Colorados	La Rioja Prov., Argent.	see <i>Pseudhesperosuchus</i> *	fluvial ss, mudst.*	Bonaparte 1971
<i>Protosuchus</i>	Liassic Moenave Fm.	misc. Az. localities		fluvial, floodpl.*	Colbert and Mook 1951
<i>Stegomosuchus</i> "protosuchian"	Portland Fm. Kayenta Fm.	Mass. Ariz.	prosauropod, theropod* tritylodonts, fish scales	fluvial ss* ss, siltstone, floodplain, fluvial	Lull 1953; Olsen 1980 Clark and Fastovsky 1986
"protosuchian" <i>Eopneumatosuchus</i>	Kayenta Fm., Silty Facies	Ariz.	theropods, pterosaurs, turtles, rhychocephalians	siltstone, floodpl.	Clark and Fastovsky 1986
"protosuchian" <i>Orthosuchus</i>	Navajo SS U. Elliot Fm.	Ariz. Sekakes, S. Africa	prosauropod* ornithischian	aeolian ss* mudstone, ss/fluvial, aeolian, floodpl.*	Galton 1971 Nash 1968, 1975; Kirching and Raath 1984

TABLE 2. Continued.

Taxon	Age/formation	Locality	Associated fauna	Lithology/depositional env.	Reference(s)
<i>Notochampsia</i>	L. Clarens Fm.	Funnystone, S. Africa		ss, siltstone/aeolian, lacustr.*	Kirching and Raath 1984
<i>Notochampsia</i> , <i>Baroquesuchus</i>	U. Elliot Fm.	Sunnyside, S. Africa		mudstone, ss/fluviol, aeolian, floodplain*	Kirching and Raath 1984 Busbey and Gow 1984
<i>Erythrochampsia</i>	Elliot Fm.	Noupoortnek, S. Africa	tritylodont, prosauropod	mudstones, ss/fluviol, aeolian, floodplain*	Kirching and Raath 1984
<i>Erythrochampsia</i>	U. Elliot Fm.	Eagles Crag, S. Africa		mudstones, ss/fluviol, aeolian, floodplain*	Kirching and Raath 1984
crocodilian	U. Elliot Fm.	Musong Vall, S. Africa	ornithischian	mudstones, ss/fluviol, aeolian, floodplain*	Kirching and Raath 1984
crocodilian	U. Elliot Fm.	Thabana Morena, S. Afr.	prosauropod	mudstones, ss/fluviol, aeolian, floodplain*	Kirching and Raath 1984
crocodilian	L. Clarens Fm.	Roidrai, S. Africa	tritylodont, prosauropod, "thercodont"	ss, mudstone/aeolian, shallow water*	Kirching and Raath 1984
crocodilian	U. Elliot Fm.	Groot Verwulf, S. Africa	prosauropod	mudstone, ss/aeolian, shallow water*	Kirching and Raath 1984
protosuchian	Forest SS	Zambesi Vall, Zimbabwe	prosauropods, theropod	fluviol ss*	Raath 1981
Hallopodidae	?Upper Jurassic	Colorado		locality unk., ?Fluviol ss	Walker 1970
<i>Hallopus</i>	?Morrison Fm.				

* Information of this category not available for the specific crocodylomorph-producing locality. Information listed is based on stratigraphic interval of entire region.

stances in groups with the two types of ankles are favored. This hypothesis is advocated in most recent archosaur phylogenies (e.g., Cruickshank 1979; Brinkman 1981b; Chatterjee 1982; Gauthier 1984, 1986; Parrish 1984, 1986a).

3. Erect posture could have arisen independently more than once within the crocodile-normal archosaurs. The structural homogeneity in the complex structure of the crocodile-normal ankle seen throughout the members of the group, plus the other characters shared in common by the crocodile-normal forms mentioned above, argue against the hypothesis of a non-monophyletic crocodile-normal group.

All Triassic archosaurs that have fully developed crocodile-normal tarsi (Aetosauria, "Rauisuchia", *Gracilisuchus*, and the primitive Crocodylomorpha) are erect. In any event, the mosaic of gaits in modern crocodylians almost certainly evolved following the transition to erect posture in the crocodile-normal archosaurs. To argue otherwise would require that the eusuchian crocodiles are the primitive sister group of the erect Crocodylomorpha. The evidence for monophyly of the Crocodylia and Crocodylomorpha supports secondary derivation of a semi-erect gait in modern eusuchians.

Another question raised by Charig's (1972) study involves the distribution of plantigrady vs. digitigrady among the primitive archosaurs. Primitive diapsids and the most primitive archosaurs are sprawling and plantigrade, whereas dinosaurs are erect and digitigrade. Thus it was reasonable for Charig to assume a functional link between digitigrady and erect stance. However, most of the erect crocodile-normal archosaurs have feet with mobile, crurotarsal ankles, elongate metatarsals and short phalanges, all indicative of plantigrady (Bonaparte 1984; Parrish 1984, 1986a). In digitigrade dinosaurs, the main ankle joint is mesotarsal (i.e., between proximal and distal tarsals), the metatarsus is often compressed laterally, and the phalanges are elongated. Although the poposaurid *Postosuchus* (Chatterjee 1985) and the crocodylomorph *Hallopus* have elongate, compressed feet that were probably digitigrade, plantigrady was apparently universal among the other crocodylomorphs. In both the ornithosuchian and crocodile-normal archosaurian lineages, the most primitive type of erect posture is plantigrade.

Conclusions

Functional analysis of the tarsus and hindlimb of "sphenosuchians," "protosuchians," and *Hallopus* suggests that these animals were all erect. Erect posture appears to be plesiomorphic for the crocodile-normal archosaurs. Faunal associations support the hypothesis that the Triassic and Liasic crocodylians were terrestrial.

The tarsus and pes of the modern crocodylians must then be viewed as secondary adaptations to an amphibious habit rather than as an adaptive phylogenetic intermediate between those of sprawling and erect archosaurs. The suitability of living crocodylians as a model for an intermediate step between sprawling and erect archosaurs is questioned, as is the functional link between digitigrady and erect gait.

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Appendix. Crocodylomorph material considered in this paper.

Institutional abbreviations: AMNH = American Museum of Natural History; BMNH = British Museum (Natural History); CUP = Catholic University of Peking (housed at Field Museum of Natural History); P = Dept. of Zoology, University College; MCZ = Museum of Comparative Zoology, Harvard University; NM = Nasionale Museum, Bloemfontein; PVL = Universidad Nacional, Laboratorio de Vertebrados Fossiles del Instituto Miguel Lillo, Tucumán; SAM = South African Museum; SMS = Staatliches Museum für Naturkunde, Stuttgart; UCM = University of Colorado Museum; UCMP = University of California Museum of Paleontology; USNM = U.S. National Museum; YPM = Yale Peabody Museum.

Taxon	Location	Age	Reference	Hindlimb and pelvic material preserved	Specimen numbers
"Sphenosuchia"					
<i>Hesperosuchus</i>	Arizona	U Tr	(1) Colbert 1952	(1) femur, partial pes	AMNH 6578
<i>Saltoposuchus</i>	W. Germ.	U Tr	(2) Parrish, in prep.	(2) femur, pubes	UCMP 129740
<i>Pseudhesperosuchus</i>	Argentina	U Tr	Huene 1921	entire hindlimb	SMS 12296, 12297
<i>Terrestri-suchus</i>	Wales	U Tr	Bonaparte 1971	femur, crus	PVL 3830*
<i>Sphenosuchus</i>	S. Afr.	L Jr	Crush 1984	complete hindlimb, pelvis (composite)	Holotype P 47/21,47,22 many other isolated bones
"Sphenosuchia"	China	L Jr	Haughton 1924	tibia	SAM 3014*
			Simmons 1965	tarsus	CUP 12, 13
Protosuchia					
<i>Protosuchus</i>	N. Am.	L Jr	Colbert and Mook 1951	Complete skeleton, other partial skeletons	AMNH 3024, 3025, 3026, 3056 UCMP 36717
<i>Hemiprotosuchus</i>	S. Am.	?U Tr	Bonaparte 1971	partial pes	PVL 3829*
<i>Orthosuchus</i>	S. Afr.	L Jr	Nash 1975	skeleton	SAM K409*
<i>Notochampsia</i>		L Jr	Haughton 1924	partial postcr.	SAM 4013*
<i>Erythrochampsia</i>		L Jr	Haughton 1924	partial postcr.	SAM 455F*
<i>Stegomosuchus</i>		L Jr	Lull 1953	skeleton (mold)	Amherst U. Museum**
<i>Pedeticosaurus</i>		L Jr	Van Hoepen 1915	skeleton (mold)	Orange Free State Museum**
<i>Lesothosuchus</i>		L Jr	Whetstone and Whybrow 1983	femur, crus	BMNH R8503
Hallopoda					
<i>Hallopus</i>	N. Am.	?U Jr	Walker 1970	postcranium	YPM 1914

* Material not seen by author. Studied from photos and figures.

** Material studied from casts.